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High alpine sorcerers: revision of the cave wētā genus *Pharmacus* Pictet & de Saussure (Orthoptera: Rhaphidophoridae: Macropathinae), with the description of six new species and three new subspecies

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Abstract. The New Zealand alpine cave wētā genus *Pharmacus* was first described by Pictet & de Saussure (1893) as a monotypic taxon. Three species were added to the genus by Richards in 1972. Here we clarify the status and appearance of all known species of *Pharmacus*. Based on morphology and mtDNA sequences we determine that the species *Pharmacus brewsterensis* Richards, 1972 is better placed within the genus *Notoplectron* Richards, 1964. We also resolve the species *Isoplectron cochleatum* Karny, 1935 and show that it belongs to the genus *Pharmacus*. Additionally, we describe six new species and three new subspecies from the southern regions of South Island, New Zealand. We provide key traits and known distributions for all known species and subspecies in this alpine genus. New combinations: *Pharmacus brewsterensis* Richards, 1972 becomes *Notoplectron brewsterense* (Richards, 1972) comb. nov.; *Isoplectron cochleatum* Karny, 1935 becomes *Pharmacus cochleatus* (Karny, 1935) comb. nov. New species and subspecies: *Pharmacus cochleatus rawhiti* subsp. nov., *Pharmacus cochleatus fiordensis* subsp. nov., *Pharmacus cochleatus nauclerus* subsp. nov., *Pharmacus concinnus* sp. nov., *Pharmacus cristatus* sp. nov., *Pharmacus notabilis* sp. nov., *Pharmacus perfidus* sp. nov., *Pharmacus senex* sp. nov. and *Pharmacus vallestris* sp. nov. New synonyms: *Pharmacus dumbletoni* Richards, 1972 = *Pharmacus montanus* Pictet & de Saussure, 1893 syn. nov.; *Pharmacus chapmanae* Richards, 1972 = *Pharmacus cochleatus* (Karny, 1935) syn. nov.

Keywords. Cave wētā, *Pharmacus,* Rhaphidophoridae, systematics, Mount Cook flea, New Zealand.

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Introduction

Cave wētā (Family Rhaphidophoridae Walker, 1869) are common and widespread in the alpine regions of New Zealand, where they hide in rock crevices and in holes under boulders, in landscapes that are covered by snow for more than six months a year, and survive at elevations as high as 2800 m a.s.l. (Pictet & de Saussure 1893; Dumbleton 1935; Richards 1972; Walker 1977; Sweney 1980). Sampling in the alpine regions is made difficult by the rugged terrain and the short summer seasons, which is probably why studies of alpine Rhaphidophoridae in New Zealand have been few and far between. Not only is the list of publications limited to the few titles listed above, but most species were described based on a very small number of individuals.

The alpine cave wētā genus *Pharmacus* was established by Pictet & de Saussure (1893) as a monotypic genus, with *Pharmacus montanus* as type species, based on the examination of one adult male specimen. For nearly 80 years, this remained the only New Zealand alpine rhaphidophorid known to science, with the common name 'Mount Cook flea'. A re-description of the genus *Pharmacus* by Hutton (1896) did not add anything, since Hutton did not acquire any new material, nor did he examine any specimens, but relied on verbal information supplied by Pictet. A revision of the genus *Pharmacus* was completed by Richards (1972), who re-described *Pharmacus montanus* after examination of additional material, and designated three new species: *Pharmacus brewsterensis*, *P. chapmanae* and *P. dumbletoni*. Richards (1972) was able to secure a good number of male and female specimens of *Pharmacus montanus* and of her new species *P. chapmanae*. However, she described *P. dumbletoni* and *P. brewsterensis* based on one male and two females respectively.

The possible existence of additional species of *Pharmacus* was hinted at by a number of authors but has never been formally resolved. In her revision of *Pharmacus*, Richards (1972) wrote "A possible fifth species occurs in the Diorite Range, northern Fiordland. It is closely related to *P. chapmanae*, but is known only from one damaged adult female. More specimens are required before its true affinities can be determined". A Diorite Range does not exist in Fiordland, nor anywhere in New Zealand. Based on alliteration and geographical placement, we can only assume that Richards was referring to Fiordland's Darran Mountains. A new species of *Pharmacus* is also listed as having been collected on Way Spur (Symmetry Peaks, Eyre Mountains) during an ecological survey of the Eyre Ecological District (Mark *et al*. 1989). The whereabouts of the materials collected during the survey is unknown. Two putative new species of alpine cave wētā from the Remarkables (Wakatipu) and Gertrude Saddle (Darran Mountains) are pictured in the popular book "*Which New Zealand Insect?*" (Crowe 2002); both clearly belong to the genus *Pharmacus*.

Richards (1972) assigned the two female type specimens of *Pharmacus brewsterensis* to the genus *Pharmacus* based on these having been collected in a high alpine environment, on them being armed with one retro-lateral apical spine at the apex of the mid femur, and on the smooth upper valve of their ovipositors. Female rhaphidophorids are more difficult to classify since they do not show the same level of variation in the terminalia as males do (Hegg *et al.* 2019). It does not help that Richards did not collect any of her alpine specimens and had to rely for her descriptions on material collected by others, often poorly preserved. Considering these limitations, it does not surprise that she could have made mistakes in her taxonomy.

The taxonomy of New Zealand Rhaphidophoridae is further complicated by the fact that several species were described in German or French, and that translations of the original descriptions have never been published. The original description of *Pharmacus montanus* for instance is in French. Richards (1972) assumed the description provided by Hutton (1896) to be a faithful translation of the original. However, this is not the case, and important detail was lost in Hutton's rendition. Likewise, the original description of *Isoplectron cochleatum* Karny, 1935 is a wordy and poorly illustrated three pages written in German.

As a result, the species *Isoplectron cochleatum* has remained obscure to most and has been ignored by entomologists until present, as shown by its complete absence in the literature on New Zealand Rhaphidophoridae. To remedy this, faithful translations of the original descriptions of *Pharmacus montanus* and of *Isoplectron cochleatum* are published in this paper's Supp. file 1: Appendix A and B.

Here, we review the status of the alpine cave wētā genus *Pharmacus* using morphological and genetic data from a large sample. We identify male *Pharmacus brewsterensis* for the first time, since no males were included in the original description. We compare *Pharmacus brewsterensis* with other species in the genus *Pharmacus* and in other genera of New Zealand Rhaphidophoridae, to test its placement in *Pharmacus*. After examination of the type material, we resolve the species *Isoplectron cochleatum* and we revise its taxonomic status. We use a combination of dense sampling throughout the South Island of New Zealand's alpine regions, morphological traits and DNA sequence data to test the status of putative *Pharmacus* taxa. We use morphological traits to identify six hitherto undescribed species and three new subspecies within this genus. We also provide new descriptions for previously described species, to account for new synonymies and for the variability of traits in specimens we have collected over a much wider geographical range compared to previous studies.

Material and methods

Collection and morphological methods

Cave wētā were collected opportunistically around New Zealand, including at the holotype location of all known species, using day and night searching of cliffs, mountain ridges, rock tors, forests and caves, and occasional pitfall trapping. More than 5200 specimens have been catalogued; many have been examined in detail and sampled for DNA sequence comparison, among these 373 specimens of *Pharmacus* (including *Isoplectron cochleatum* and excluding *Pharmacus brewsterensis*). Specimens are held in the Phoenix Lab collection at Massey University (MPN), except for type material, which is lodged at Museum of New Zealand Te Papa Tongarewa (NMNZ). *Pharmacus* specimens were identified based on the descriptions by Pictet & de Saussure (1893), Hutton (1896), Karny (1935) and Richards (1972).

Specimens were examined and photographed using a DSLR camera (Nikon D800, Nikon D850 or Sony α7RII) attached to a Nikon Plan 4/0.13 microscope tip and Nikon PB-6 bellows, mounted on a Cognisys Stackshot 3× automated rail. Focus stacks were generated using the software Helicon Focus ver. 6.8.0 Pro (Helicon Soft Ltd 2000). Adults were distinguished from immature individuals by darker, sclerotised bodies and fully formed external genital structures. In particular, the pigmentation, shape and sharpness of ovipositors, subgenital plates and cerci were informative about developmental stage. We looked for the presence/absence of each of 22 apical leg spines (Fitness *et al*. 2015) (Supp. file 1: Fig. S1), as well as the combinations and numbers of linear spines on the legs, and the shape of the subgenital and suranal plates.

Measurements of key body parts were obtained using digital callipers (Table 1). All linear measurements and count data were tested for sexual dimorphism using Linear Mixed Models in JASP ver. 0.14.1 (JASP Team 2020), with measurement as the response variable, sex and species as fixed factors and geographical location as random factor. Where sexual dimorphism is detected and is statistically significant, measurements are reported separately for males and females; otherwise the measurements for both sexes are pooled. Some traits included in Table 1 are invariable in *Pharmacus* (e.g., teeth on dorsal valve of ovipositor; pairs of longer spines on hind tibia) – they are included nonetheless since they are useful for comparison with other genera of NZ Rhaphidophoridae (see for example Fitness *et al.* 2018: table 1 and Hegg *et al.* 2019: table 1).

Collection acronyms

CMNZ = Canterbury Museum, Christchurch, New Zealand
iNaturalist = Available from iNaturalist.org [accessed 30 August 2021]
MNHN = Muséum national d'histoire naturelle, Paris, France
MHNG = Muséum d'histoire naturelle de la Ville de Genève, Switzerland
MPN = Phoenix Lab, Massey University, Palmerston North, New Zealand
NMNZ = Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand
NZAC = New Zealand Arthropod Collection, Auckland, New Zealand
OMNZ = Otago Museum, Dunedin, New Zealand

Two-letter codes in the 'Material examined' sections below refer to the New Zealand entomological regions (Crosby *et al.* 1998) (Fig. 1B).

Molecular methods

Genomic DNA was extracted from leg tissue of specimens representing each morphotype, using a salting-out protocol (Trewick & Morgan-Richards 2005). For most samples, a ~1500 base pair (bp) fragment spanning most of the mitochondrial cytochrome *c* oxidase I (COI) gene of the mitochondrial genome was amplified using polymerase chain reaction (PCR) with the invertebrate primers: LCO1490 (Folmer *et al*. 1994) and L2-N-3014 (Simon *et al.* 1994). Where DNA was of lower quality a shorter fragment (~800 bp) was amplified using primers C1-J-2195 and L2-N-3014 (Simon *et al.* 1994).

Successful PCR products were sequenced with Bigdye chemistry on an ABI 3730 genetic analyser (Applied Biosystems Inc., Carlsbad, CA) using primer L2-N-3014 at the 3' end of COI. A subset of 14 specimens were sequenced with LCO1490 (Folmer *et al*. 1994) and L2-N-3014 (Simon *et al*. 1994) to provide sequences spanning COI. Nucleotide sequences were assembled and aligned using Geneious Prime ver. 2020.2.2 (https://www.geneious.com; Kearse *et al.* 2012). No insertions/deletions were detected and sequences were translated to confirm that there were no stop codons or frame shifts that would indicate the presence of nuclear paralogs. A selection of 60 sequences was submitted to GenBank; accession numbers (OM293676–OM293737) are listed in the Material examined section.

We examined the relationships of putative *Pharmacus* taxa by phylogenetic reconstruction using Maximum Likelihood criteria applying a GTR evolutionary model with a gamma-distributed rate variation across DNA sites and a proportion of invariable sites. This was implemented with the PhyML plugin (Guindon *et al*. 2010) in Geneious Prime. Representative, homologous mtDNA COI sequences from other New Zealand cave wētā: *Talitropsis sedilloti* Bolívar, 1882 (MPN CW1830), *Setascutum pallidum* Richards, 1972 (CW3158) and *Notoplectron campbellense* Richards, 1964 (CW2152) were used for comparison; *Macropathus filifer* Walker, 1869 (CW226B) was included as an outgroup based on available phylogenetic information (Allegrucci *et al.* 2010; Fitness *et al.* 2018; Hegg *et al.* 2019) and unpublished analyses. A reduced taxon dataset with just 14 putative *Pharmacus* specimens (including *P. brewsterensis*) allowed Maximum Likelihood inference with 1000 bootstrap replicates to assess monophyly of the genus. We identified adult specimens using morphology and used mitochondrial DNA sequences to test these species hypotheses, to confirm association of males and females within each taxon, and to identify nymphs, which are often too difficult to identify to species level based on morphology alone. Maximum Likelihood was then used with mtDNA sequence from 60 putative *Pharmacus* specimens to infer evolution relationships of the haplotypes to illustrate the concordance between morphologically distinct taxa and unique haplotypes.

Mitochondrial DNA sequence variation allowed us to verify prior hypotheses of distinct taxa based on morphological traits and to seek concordance with the newly morphologically identified taxa in this genus. The correlation of morphological and genetic clusters is expected from distinct evolutionary

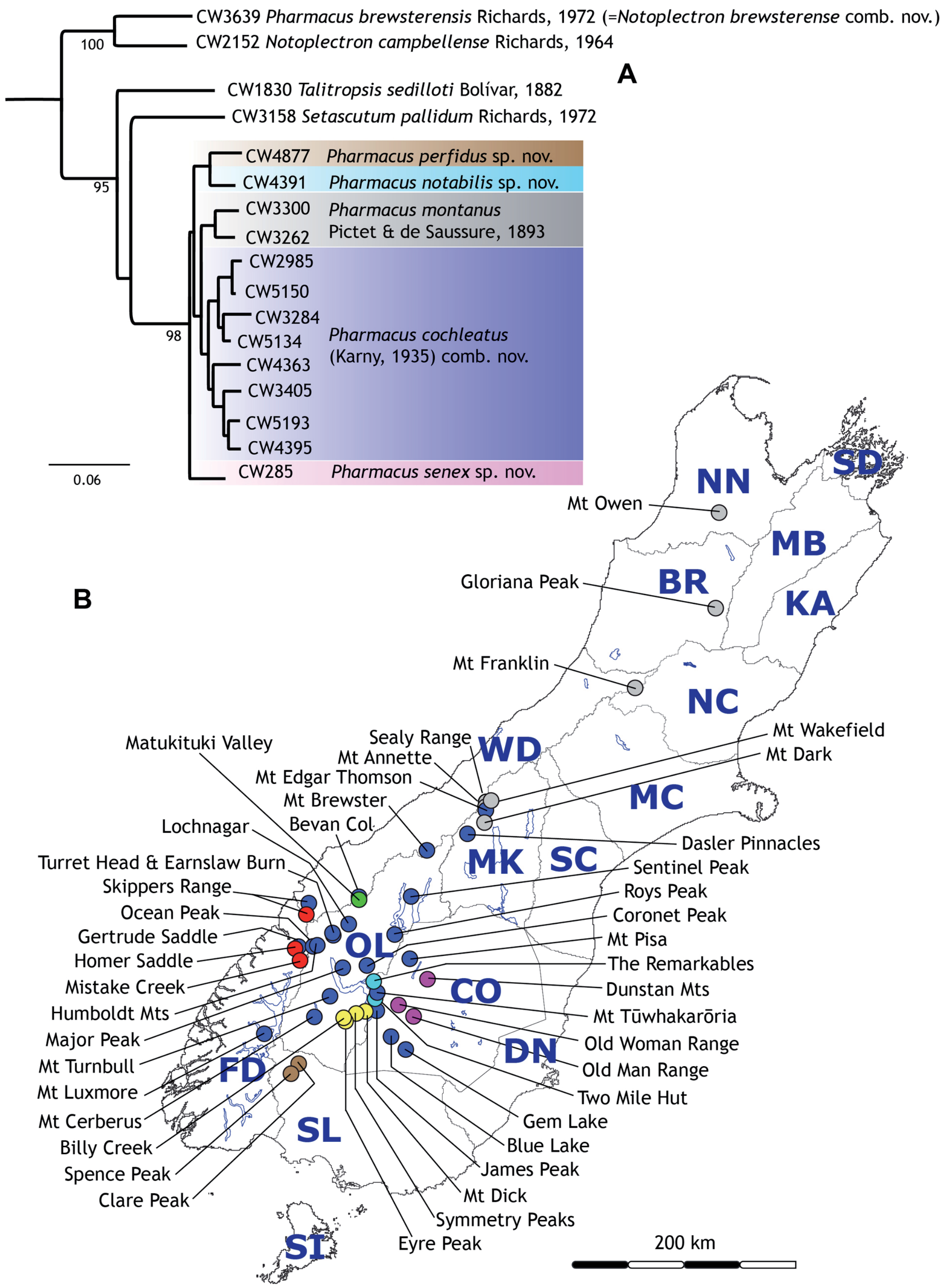

Fig. 1. A. Genetic relationships of cave wētā support monophyly of the genus *Pharmacus* Pictet & de Saussure, 1893. Gene tree from mtDNA sequences (~1500 bp of COI) using Maximum Likelihood with 1000 bootstraps and *Macropathus filifer* Walker, 1869 to root the tree. **B**. Map of South Island of New Zealand, showing locations of *Pharmacus* specimens used in phylogenetic analyses (Figs 1A, 2). Colours correspond to different species. Two letter codes indicate the New Zealand entomological regions (Crosby *et al.* 1998). These codes are reported in the Material examined section for each species.

lineages that are consistent with their treatment as distinct taxonomic units (Mallet 1995, 2013b). We note that large stable populations observed in New Zealand insect species tend to yield distributions of pairwise mtDNA differences that deviate from the expected exponential distribution owing to their common history (Slatkin & Hudson 1991; Morgan-Richards *et al*. 2017), which can mislead species delimitation tools that rely on this single non-recombining locus (Dellicour & Flot 2015). In addition, lack of lineage sorting, selection on morphology and hybridisation can all result in gene trees differing from species trees. Therefore, we were not attempting to resolve a fully supported phylogenetic hypothesis, simply illustrating the concordance between haplotypes and phenotype.

Results

Identity of previously described species

Using the morphology of terminalia in adult specimens and the key provided by Richards (1972), we identified cave wētā that could be assigned to all known species of *Pharmacus*, and six other related and as yet undescribed species. Our phylogenetic analysis of mtDNA sequences places *Pharmacus brewsterensis* outside the *Pharmacus* clade, sister to *Notoplectron campbellense* from the subantarctic Campbell Islands (Fig. 1A). This result was supported in 1000 out of 1000 bootstrap resamples of our data. Five of the six new species identified by morphology were each found to correspond to a distinct mtDNA lineage within the monophyletic *Pharmacus* clade (Fig. 2). Specimens of a morphologically distinct taxon from Fiordland (*P. cristatus* sp. nov.) had mtDNA haplotypes that nested within the diversity of widespread *P. cochleatus* (Karny, 1935) comb. nov. Due to the wide distribution and colour and spine variation detected within *P. cochleatus* we analysed COI sequence variation using an unrooted network approach (not shown); however, we could not resolve two of the four new subspecies of *P. cochleatus* using just mtDNA.

We found Pictet & de Saussure's (1893) and Richard's (1972) descriptions of *Pharmacus montanus* to be accurate. The species is readily identified based on the shape of the male terminalia (Fig. 3A–E) and the lack of dorsal spines on the first hind tarsus segment. One interesting piece of information present in Pictet & de Saussure's (1893) original description in French is the statement "The apex of the hind tibiae is armed below with three small spines, two of which are on the inner edge" (see the translation in Supp. file 1: Appendix A). This detail was omitted in Hutton's (1896) translation and subsequently by Richards (1972). We have found this trait in two of five males we examined from the Sealy Range near Aoraki/Mount Cook Village (Fig. 3F–G), but not in any specimens collected elsewhere. We know that the *Pharmacus montanus* holotype location is somewhere near Aoraki/Mt Cook at 7000 ft of elevation (Pictet & de Saussure 1893). It is possible that the holotype of *P. montanus* may have originated from Mt Annette, a readily accessible mountain that is popular with climbers, at an elevation of 7000 ft in the Sealy Range. Given our small sample size however this remains little more than an educated guess.

After collecting several specimens of *Pharmacus dumbletoni* near the holotype location on Gloriana Peak, Spenser Mountains, we found that we could not tell these apart from *Pharmacus montanus* morphologically or genetically (see red frame in Fig. 2). The colour pattern of the tergites and the shape of the male genitalia are the same. Richards (1972) judged one male specimen from the Spenser Mountains to belong to a new species (*P. dumbletoni*) based on the lack of ventral linear spines on the hind femora. While *P. montanus* mostly has armed hind femora in the Mount Cook Region and unarmed hind femora in the Spenser Mountains, we did collect specimens with unarmed hind femora in the Mt Cook Region, and specimens with armed hind femora in the Spenser Mountains. We conclude that the number of ventral linear spines on the hind femora in *P. montanus* is subject to both regional and individual variation and is not characteristic of the species. This is consistent with what had already been observed in other taxa of New Zealand Rhaphidophoridae (Fitness *et al*. 2015; Hegg *et al*. 2019). *P. dumbletoni* Richards, 1972 is thus a junior synonym of *P. montanus* Pictet & de Saussure, 1893.

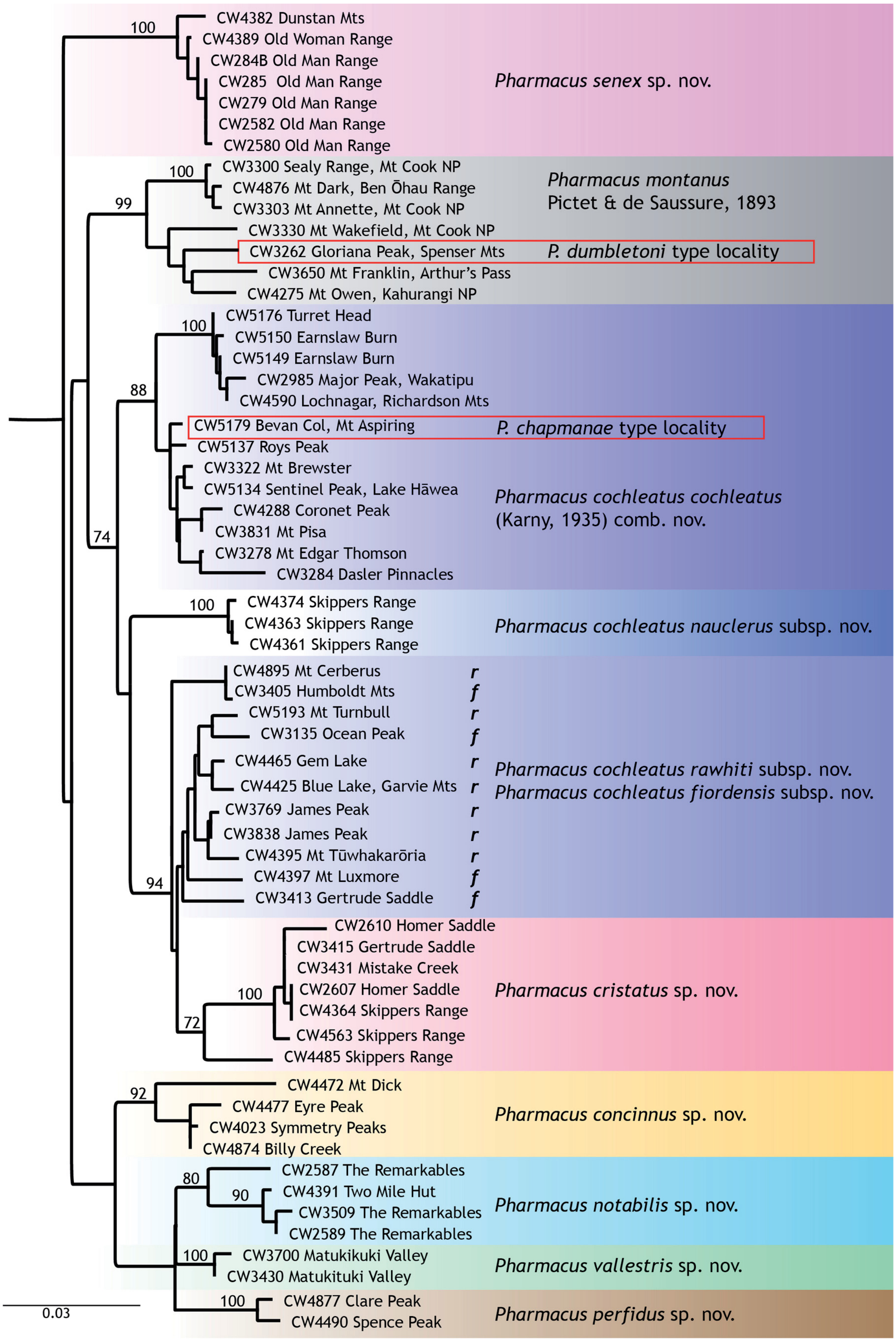

Fig. 2. Gene tree for the eight morphologically identified species of *Pharmacus* Pictet & de Saussure, 1893 using Maximum Likelihood analysis of ~850 bp of mtDNA (COI) from 60 specimens of *Pharmacus*.

While Richards (1972) had examined several specimens of *Pharmacus montanus* collected in Canterbury between Aoraki/Mount Cook Village and the Craigieburn Range, we found the species as far north as Mount Owen in Kahurangi National Park (see Fig. 18A). The variability of the species over such a wide geographical range and the synonymy of *Pharmacus dumbletoni* warrant a re-description of *P. montanus*.

We collected several specimens of *Pharmacus brewsterensis* on Mt Brewster (holotype location) and elsewhere and identified males for the first time, since the species was described based only on two females. In her species description Richards (1972) noted several differences compared to other species of *Pharmacus*, namely the lighter overall coloration, the presence of fewer teeth on the ovipositor, the greater number of linear spines on the hind femur, and the shape of the female subgenital plate. The latter has two acute, pointed lobes, as opposed to the rounded lobes found in all other species of *Pharmacus* (Fig. 4D–G). Richards described the hind tibiae of *P. brewsterensis* as being “armed above with 11 to 13 prolateral and 12 to 13 retrolateral linear spines”, but did not comment on how these numbers are only one half to two thirds of the number of dorsal linear spines on the hind tibiae in all other species of *Pharmacus* (see Table 1, Fig. 4H–I). Neither did she note that the dorsal linear spines on the hind tibiae of *P. brewsterensis* are visibly socketed at the base, whereas they are fused to the shaft of the tibia in all other species of *Pharmacus* (Fig. 4J–K). Most importantly, Richards did not have a chance to examine the structure of the male terminalia in *P. brewsterensis*, which is entirely different from all other *Pharmacus*, without a subgenital plate, the paraprocts very prominent at the apex of the body (Fig. 4A–C). Our mtDNA sequence analysis (Fig. 1A) shows that *Pharmacus brewsterensis* is more closely related to *Notoplectron campbellense* Richards, 1964 than to any of the *Pharmacus* species. We suggest that this species be transferred to the genus *Notoplectron* Richards, 1964 as *Notoplectron brewsterense* (Richards, 1972) comb. nov. Further discussion of this species awaits a revision of the genus *Notoplectron*.

We identified *Pharmacus chapmanae* based on the original description and the shape of the male and female terminalia (Fig. 5C–F). We also examined the type material held at the Otago Museum in Dunedin, New Zealand (Supp. file 1: Fig. S4). The holotype’s (male) sub-genital plate was removed by Richards and was not preserved with the specimen. This makes the holotype of limited use for identification to species level. Richard’s drawings remain our best diagnostic tool (Fig. 5C, E), and are in good agreement with the terminalia of an alpine species that is both common and widespread in the Southern Alps south of Aoraki/Mount Cook (Fig. 5D, F). An examination of the holotype of *Isoplectron cochleatum* reveals that this is the same species (see Fig. 5A–B). Having identified all known species of New Zealand Rhaphidophoridae, we can confidently state that there is no other species of cave wētā this could be confused with. Since *Isoplectron cochleatum* was described first, the name takes precedence. At the same time, the species belongs to the genus *Pharmacus* Pictet & de Saussure, 1893, not to *Isoplectron* Hutton, 1896 (see Fig. 2). We thus designate the new combination *Pharmacus cochleatus* (Karny, 1935) comb. nov., with *Pharmacus chapmanae* Richards, 1972 as a junior synonym.

It is worth noting that the allotype (MNHN EO-ENSIF4927) and the female paratype (MNHN EO-ENSIF4929) of *Isoplectron cochleatum* belong to a different species. The allotype is a female nymph, and the only one of four type specimens to have retained its hind legs. The dorsal spines on the hind tibiae suggest this specimen belongs to the species *Talitropsis sedilloti*. Identification of the female paratype is more difficult, but the shape of the sub-genital plate suggests this is likely to also be *Talitropsis sedilloti*. The insect in Karny’s (1935) original description (see the translation in Supp. file 1: Appendix B) is thus a chimera since it has the body of *Pharmacus cochleatus* and the hind legs of *Talitropsis sedilloti*.

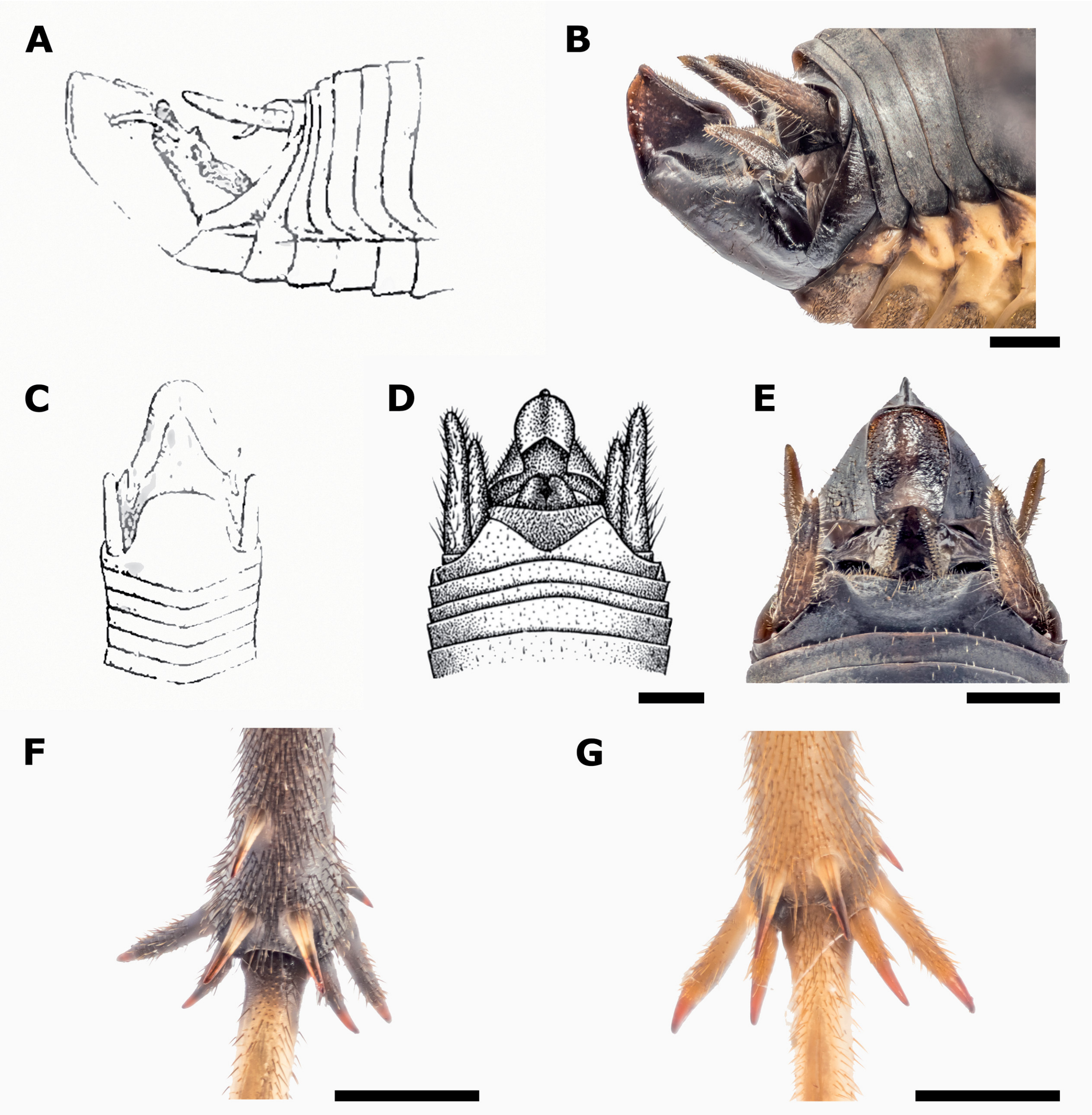

Fig. 3. *Pharmacus montanus* Pictet & de Saussure, 1893. Adult ♂. **A–B**. Lateral view of terminalia. **A**. Original drawing by Pictet & de Saussure (1893): Holotype, Mt Cook (MHNG ARTO-24289). **B**. Mt Annette, Sealy Range, Mt Cook (MPN CW3302). **C–E**. Dorsal view of terminalia. **C**. Original drawing by Pictet & de Saussure (1893): holotype, Mt Cook (MHNG ARTO-24289). **D**. Original drawing by Richards (1972), from unspecified material. **E**. Mt Annette, Sealy Range, Mt Cook (MPN CW3302). **F–G**. Detail of ventral spines at apex of left hind tibia. **F**. Mt Annette, Sealy Range, Mt Cook (MPN CW3302), with two sub-apical spines on inner edge and one on the outer edge as per the species' original description. **G**. Lake Anna, Mt Franklin, Arthur's Pass (MPN CW3989), with one sub-apical spine on both inner and outer edges, a configuration typical of all *Pharmacus* Pictet & de Saussure, 1893. Scale bars = 1 mm.

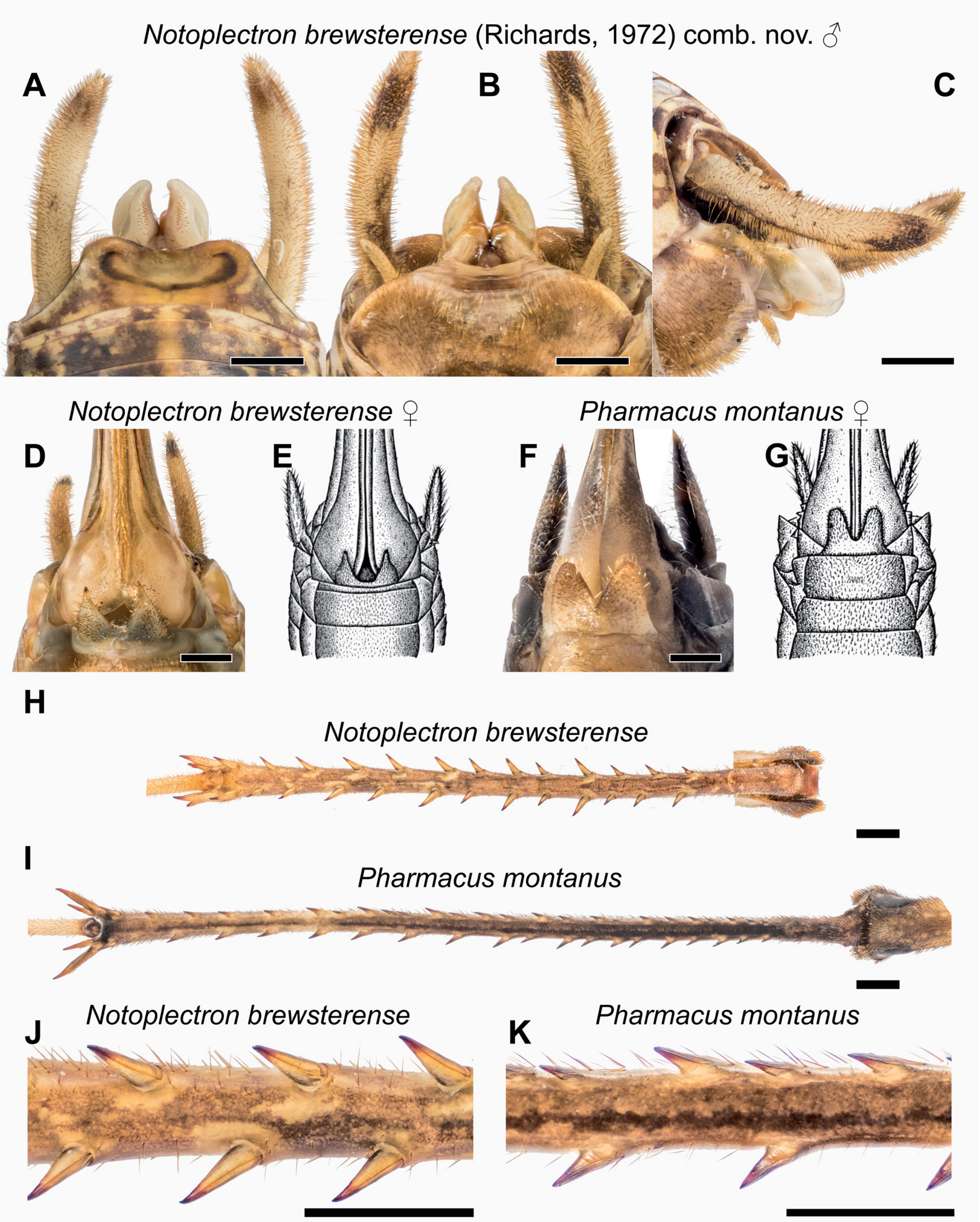

Fig. 4. Side by side comparison of *Notoplectron brewsterense* (Richards, 1972) comb. nov. and of *Pharmacus montanus* Pictet & de Saussure, 1893. **A–E, H, J**. *Notoplectron brewsterense* (Richards, 1972) comb. nov., Mt Brewster, Haast Pass. **A–C**. Dorsal, ventral and lateral view of terminalia. Adult ♂ (MPN CW3307). **D–E**. Subgenital plate. Adult ♀. **D**. MPN CW3391. **E**. Original drawing by Aola Richards (1972): holotype (CMNZ 000267). **H, J**. Dorsal view of hind tibia with enlarged detail. Adult ♀ (MPN CW3391). **F–G, I, K**. *Pharmacus montanus* Pictet & de Saussure, 1893. **F–G**. Subgenital plate. Adult ♀. **F**. Mt Annette, Sealy Range (MPN CW3303). **G**. Original drawing by Aola Richards (1972), from unspecified material. **I, K**. Dorsal view of hind tibia with enlarged detail. Adult ♂. Lake Anna, Mt Franklin, Arthur's Pass (MPN CW3989). Scale bars = 1 mm.

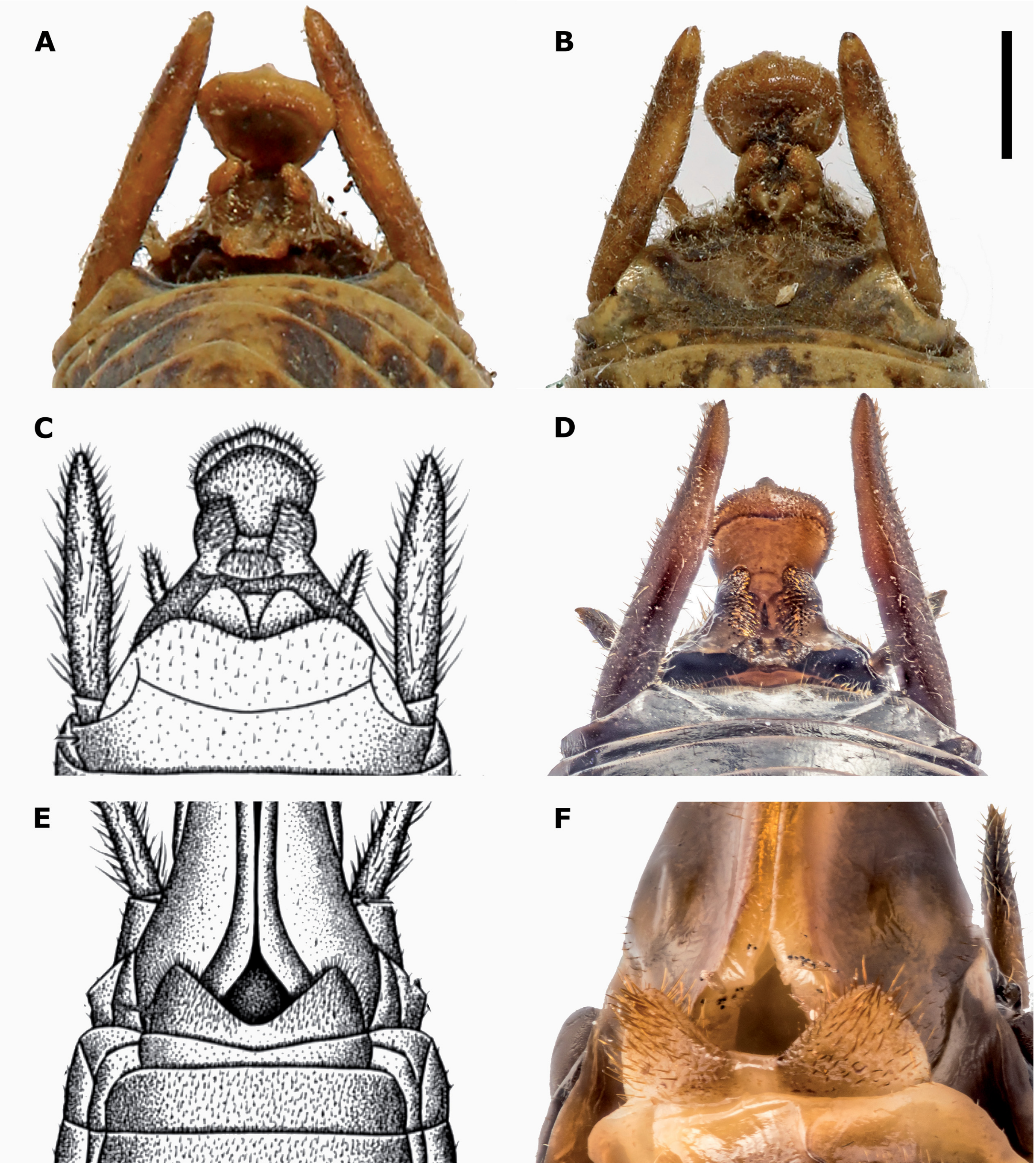

Fig. 5. *Pharmacus cochleatus* (Karny, 1935) comb. nov. **A**–**D**. Adult ♂. Dorsal view of terminalia. **A**. Holotype, from unknown location (MNHN EO-ENSIF4926). **B**. Paratype, from unknown location (MNHN EO-ENSIF4928). **C**. Original drawing by Aola Richards (1972): *Pharmacus chapmanae* Richards, 1972 holotype. Bevan Col, Matukituki Valley (OMNZ IV7927; prev. OMNZ A70:6). **D**. Mt Edgar Thomson, Ben Ohau Range (MPN CW3278). **E**–**F**. Adult ♀. Ventral view of terminalia (subgenital plate). **E**. Original drawing by Aola Richards (1972): *Pharmacus chapmanae* Richards, 1972 allotype. Bevan Col, Matukituki Valley (OMNZ IV7924; prev. OMNZ A70:8). **F**. Mt Brewster, Haast Pass (MPN CW3325). Scale bar = 2 mm. Images A and B courtesy of Marion Depraetere, MNHN, reproduced under CC BY-NC-ND 4.0 licence.

The labels for the holotype (MNHN EO-ENSIF4926) and the male paratype (MNHN EO-ENSIF4928) of *Pharmacus cochleatus* comb. nov. state that these specimens were collected in Nelson, New Zealand, in 1876, sixty years before the species was described. We are confident that the collection locality was recorded incorrectly, and that the specimens originate from the alpine regions in the south of New Zealand's South Island. This is not surprising, as other studies have highlighted how the location of origin of specimens in museum collections is often recorded incorrectly (Boessenkool *et al.* 2010; Verry *et al.* 2019).

While the exact origin of Karny's type specimens remains unknown, Richards (1972) obtained several specimens from the Otago Alps for her description of *Pharmacus chapmanae*. We have extended the known distribution range of *Pharmacus cochleatus* comb. nov. significantly, having examined specimens from a much wider spread of locations including northern Fiordland, Central Otago and the Southern Alps south of Aoraki/Mt Cook (see Fig. 18B).

Specimens of *Pharmacus cochleatus* comb. nov. from the Southern Alps and Fiordland are morphologically identical, yet genetically they fall into three clusters (Fig. 2). Nested within the mtDNA diversity of *Pharmacus cochleatus* is the clade of the morphologically distinct *Pharmacus cristatus* sp. nov. found sympatric with *P. cochleatus* but with unique male terminalia (Figs 2, 10). The central-northern clade of *P. cochleatus* is separated from the southern (Fiordland) clade by the northern arm of Lake Wakatipu and the valley of the Dart River (Figs 6, 18B). The third clade is endemic to the Skippers Range in South Westland, an isolated mountain range that reaches an elevation of 1650 m a.s.l. and is surrounded by valleys and passes that are entirely below 50 m a.s.l. (Fig. 6). We suggest that that the concordance of geographical separation and clustering of mtDNA haplotypes warrants these three populations being assigned to different subspecies (Cronin *et al.* 1996; Miller *et al.* 2011). A difficulty arises in that we do not know where the holotype of *Pharmacus cochleatus* was collected in 1876. Morphologically, it could belong to any of the three groups. Extracting DNA from a 145 year old, dry holotype specimen does not seem like a realistic proposition, either. The best we can do is to infer from the history of exploration of New Zealand's southern regions. While the exploration of coastal Fiordland started in the 18th century, the first expedition into the interior where any mountain tops were climbed was by surveyors James McKerrow and Goldie in 1862/63 (Hall-Jones 1976). This was a two-man expedition with no scientists on board; no scientific samples were collected. The mountain ranges between Lake Te Anau and Milford Sound were not crossed until 1888, and the exploration of Fiordland's alpine regions did not start in earnest until the turn of the 20th century (Hall-Jones 1976). The Skippers Range had to wait even longer, until the late 1950s. In contrast, scientists James Hector and John Buchanan started collecting botanical and zoological samples on mountain tops in the Matukituki Valley in 1862 (McClymont 1959). Given that the holotype of *Pharmacus cochleatus* was collected in 1876, we consider it highly likely that it would have originated from the central region of the Southern Alps. We thus assign the name *Pharmacus cochleatus cochleatus* to the central-northern clade and designate two new subspecies, *Pharmacus cochleatus fiordensis* subsp. nov. from Fiordland, and *Pharmacus cochleatus nauclerus* subsp. nov. from the Skippers Range in South Westland.

A further complication arises in a population of *Pharmacus cochleatus* comb. nov. from the mountain ranges either side of Lake Wakatipu and south of the Greenstone and Kawarau Rivers (see Fig. 6), inhabiting two alpine islands that are geographically disconnected from the species' main distribution range. Males and females from this population have the same terminalia as all other *Pharmacus cochleatus* examined and are not genetically partitioned from *Pharmacus cochleatus fiordensis* subsp. nov. Nevertheless this eastern population is readily distinguished by body- and eye-colour, different spines at the apex of fore and mid femur, and longer legs in proportion to the rest of the body (see Table 1). We suggest that this population also fits the definition of a subspecies in that it inhabits

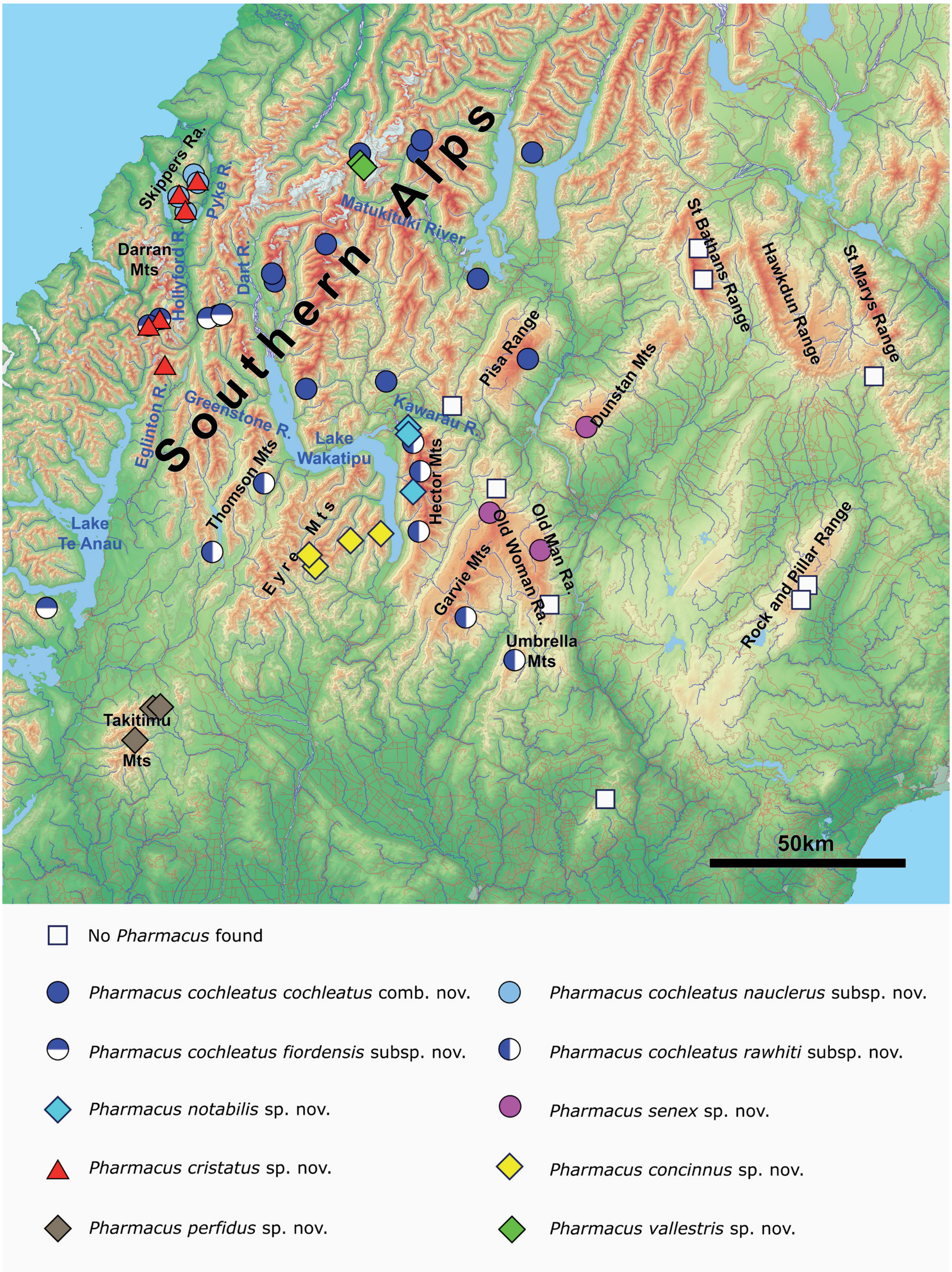

Fig. 6. Known distribution of cave wētā in the genus *Pharmacus* Pictet & de Saussure, 1893 in the south of the South Island, New Zealand.

a clearly distinct and separated part of the species' range and is morphologically notably different (Monroe 1982; Mallet 2013a); we propose the name *Pharmacus cochleatus rawhiti* subsp. nov.

Mountain ranges where we did not find Pharmacus

While cave wētā in the genus *Pharmacus* are widespread in the mountain regions of New Zealand's South Island, there are several mountain ranges we have searched, where we have not been able to find them. These include the Blue Mountains, Rock and Pillar Range, St Bathans Range and St Marys Range in Otago; Mt Somers, Mt Peel, Taylor Range, Craigieburn Range and Torlesse Range in Canterbury, the Paparoa Range in Westland, the Organ Range in North Canterbury, the Kaikōura and the Richmond Ranges in Marlborough, Mt Arthur in Kahurangi National Park and Mt Taranaki in the North Island. We found other genera of Rhaphidophoridae at all locations searched, except for the Paparoa Range and Mount Taranaki. A complete list of alpine locations searched and of Rhaphidophoridae found (other than *Pharmacus*) is in Supp. file 1: Table S12.

Richards (1972) did examine *Pharmacus montanus* from Hamilton Peak in the Craigieburn Range, which means the species is most likely to be present there even though we did not find it. Meads & Notman (1992) listed *Pharmacus montanus* among their 'incidental invertebrates observed during surveys' for giant wētā (*Deinacrida* sp.) in the Inland and Seaward Kaikōura Ranges. Meads & Notman did not give locations, nor did they state whether they collected any specimens. While their identification appears dubious, the Kaikōura Ranges could be a worthy target of more intensive searches in the future.

Measurements and spine counts

The measurements and spine counts for 239 adult *Pharmacus* are reported in Table 1. A linear mixed model with sex and species as fixed factors and location as random factor indicates that the body length of female *Pharmacus* (mean 15 mm) is significantly larger than the body length of male *Pharmacus* (mean 13 mm) by an average 14% (df = 1211.80; F = 167.69; p < 0.001). The hind tibiae are significantly longer in female *Pharmacus* (mean 14 mm) compared to male *Pharmacus* (mean 13 mm) by an average 5% (df = 1196.69; F = 31.163; p < 0.001). The ratio of hind tibiae over body length however is larger in males (mean 1.05) than in females (mean 0.98) by 8.8% (df = 1201.93; F = 42.451; p < 0.001). This means that while females are consistently larger, they are stockier, whereas males have longer legs in relation to overall body size. There is no significant sexual dimorphism in the number of dorsal linear spines on the hind tibiae (23 prolateral and 21 retrolateral spines) (df = 1200.87; F = 0.27; p = 0.602). The density of dorsal linear spines on the hind tibiae in males (1.75 spines/mm prolateral, 1.59 spines/mm retrolateral) is significantly higher than in females (1.68 spines/mm prolateral, 1.52 spines/mm retrolateral) (df = 1207.07; F = 7.53; p = 0.007).

Table 1 (continued on next three pages). Dimensions and spine count of species of *Pharmacus* Pictet & de Saussure, 1893.

		Pharmacus montanus	***Pharmacus cochleatus cochleatus***	***Pharmacus cochleatus nauclerus* subsp. nov.**
Sample size		27 (12 ♀♀, 15 ♂♂)	56 (24 ♀♀, 32 ♂♂)	10 (6 ♀♀, 4 ♂♂)
Apical spines fore, mid and hind femora [1]		0 0 , 0 1 , 0 0	0 0 , 0 1 , 0 0	0 0 , 0 1 , 0 0
Apical spines fore, mid and hind tibiae		4-4-8 2 ♂♂: 4-4-9	4-4-8	4-4-8
Body length (mm) [2]		♀ 15.0 (13.1–18.5) ♂ 14.4 (13.1–20.0)	♀ 14.4 (12.1–17.4) ♂ 12.6 (11.1–14.9)	♀ 15.3 (14.1–15.5) ♂ 12.3 (11.9–13.2)
Pronotum length (mm)		♀ 4.3 (3.8–4.9) ♂ 4.2 (3.5–4.6)	♀ 3.8 (2.8–4.8) ♂ 3.4 (2.5–4.2)	♀ 3.6 (3.3–4.2) ♂ 3.3 (2.5–3.5)
Eye colour		brown / black	brown / black	brown / black
Ovipositor length (mm)		10.2 (9.4–11.3)	10.3 (8.0–12.1)	10.1 (9.5–11.3)
Ratio ovipositor to body length		0.70 (0.52–0.78)	0.69 (0.60–0.87)	0.69 (0.63–0.75)
Teeth: ventral valve of ovipositor		7 (5–8)	7 (5–9)	7.5 (7–9)
Teeth: dorsal valve of ovipositor		0	0	0
Length of hind tibia (mm)		♀ 15.5 (12.3–18.1) ♂ 17.8 (14.6–18.5)	♀ 12.6 (10.4–16.3) ♂ 12.0 (10.0–15.4)	♀ 12.8 (11.1–14.5) ♂ 11.7 (11.0–11.9)
Ratio hind tibia to body length		♀ 1.04 (0.83–1.30) ♂ 1.18 (0.90–1.35)	♀ 0.86 (0.77–1.09) ♂ 0.94 (0.78–1.17)	♀ 0.88 (0.73–0.94) ♂ 0.93 (0.90–0.97)
Superior spines hind tibia	prolateral retrolateral	23 (17–32) 22 (16–28)	23 (14–29) 20 (14–29)	19.5 (18–22) 18 (16–21)
Spine density on hind tibia (count/ mm)	prolateral	♀ 1.42 (1.22–1.62) ♂ 1.36 (1.09–1.78)	♀ 1.75 (1.16–2.31) ♂ 1.95 (1.09–2.55)	♀ 1.50 (1.31–1.89) ♂ 1.79 (1.51–1.91)
	retrolateral	♀ 1.44 (1.15–1.55) ♂ 1.24 (0.96–1.45)	♀ 1.54 (1.13–2.31) ♂ 1.73 (1.09–2.36)	♀ 1.31 (1.24–1.71) ♂ 1.64 (1.43–1.76)
Pairs of longer spines on hind tibia		0	0	0
Superior spines on 1st tarsus segment		0	5 (1–9)	5 (4–7)
Superior spines on 2nd tarsus segment		0	0 (0–2)	0
Fore tibia, inferior spines	prolateral retrolateral	2 (1–3) 2 (1–2)	2 (1–2) 2 (1–2)	2 (2–2) 2 (2–2)
Fore tibia, superior spines		0	0	0
Mid tibia, inferior spines	prolateral retrolateral	2 (2–3) 2 (1–2)	2 (2–3) 2 (1–3)	2 (2–2) 2 (2–2)
Mid tibia, superior spines	prolateral retrolateral	0	0 0 (0–2)	0 0 (0–1)
Fore femur, Inferior spines	prolateral retrolateral	0	0	0
Mid femur, inferior spines	prolateral retrolateral	0	0	0
Hind femur, inferior spines	prolateral retrolateral	0 (0–1) 1 (0–2)	2 (0–3) 4 (0–5)	2 (1–2) 3.5 (2–4)

Table 1 (continued). Dimensions and spine count of species of *Pharmacus* Pictet & de Saussure, 1893.

		Pharmacus cochleatus fiordensis **subsp. nov.**	***Pharmacus cochleatus rawhiti*** **subsp. nov.**	***Pharmacus cristatus*** **sp. nov.**
Sample size		8 (4 ♀♀, 4 ♂♂)	44 (16 ♀♀, 28 ♂♂)	11 (4 ♀♀, 7 ♂♂)
Apical spines fore, mid and hind femora [1]		0 0 , 0 1 , 0 0	4 ♀♀, 2 ♂♂: 0 0 , 0 1 , 0 0 12 ♀♀, 20 ♂♂: 1 0 , 0 1 , 0 0 6 ♂♂: 1 0 , 1 1 , 0 0	1 0 , 1 1 , 0 0
Apical spines fore, mid and hind tibiae		4-4-8	4-4-8	4-4-8
Body length (mm) [2]		♀ 15.4 (15.0–18.0) ♂ 14.6 (12.5–15.4)	♀ 14.7 (11.1–16.4) ♂ 12.8 (10.4–13.9)	♀ 14.2 (11.9–15.4) ♂ 12.2 (10.4–13.5)
Pronotum length (mm)		♀ 4.0 (3.7–4.8) ♂ 4.1 (3.7–4.3)	♀ 3.8 (3.2–4.6) ♂ 3.4 (2.6–4.1)	♀ 4.4 (3.7–4.6) ♂ 3.4 (2.9–4.0)
Eye colour		brown / black	grey	grey / brown
Ovipositor length (mm)		12.3 (12.0–13.1)	9.9 (8.7–10.7)	10.2 (9.6–10.5)
Ratio ovipositor to body length		0.81 (0.67–0.85)	0.66 (0.60–0.84)	0.73 (0.66–0.81)
Teeth: ventral valve of ovipositor		7.5 (6–8)	7 (5–8)	8 (7–8)
Teeth: dorsal valve of ovipositor		0	0	0
Length of hind tibia (mm)		♀ 15.4 (12.2–17.3) ♂ 13.1 (11.7–15.7)	♀ 16.0 (13.7–18.7) ♂ 14.9 (11.8–16.9)	♀ 16.8 (16.5–17.6) ♂ 15.1 (12.6–17.9)
Ratio hind tibia to body length		♀ 1.01 (0.68–1.12) ♂ 0.94 (0.82–1.05)	♀ 1.07 (0.96–1.43) ♂ 1.19 (1.03–1.37)	♀ 1.17 (1.14–1.42) ♂ 1.21 (1.14–1.45)
Superior spines hind tibia	prolateral retrolateral	20.5 (16–26) 19 (15–24)	25 (21–28) 23 (18–28)	24 (22–26) 22 (20–27)
Spine density on hind tibia (count/mm)	prolateral	♀ 1.32 (1.30–1.43) ♂ 1.57 (1.42–1.71)	♀ 1.55 (1.27–1.97) ♂ 1.66 (1.45–1.95)	♀ 1.37 (1.30–1.46) ♂ 1.59 (1.45–1.91)
	retrolateral	♀ 1.37 (1.27–1.44) ♂ 1.31 (1.24–1.54)	♀ 1.41 (1.28–2.04) ♂ 1.48 (1.20–1.90)	♀ 1.25 (1.21–1.30) ♂ 1.51 (1.34–1.79)
Pairs of longer spines on hind tibia		0	0	0
Superior spines on 1st tarsus segment		4 (1–6)	3 (1–6)	4 (4–6)
Superior spines on 2nd tarsus segment		0	0 (0–1)	0
Fore tibia, inferior spines	prolateral retrolateral	2 (2–3) 2 (2–3)	2 (2–3) 2 (1–2)	2 (2–2) 2 (1–3)
Fore tibia, superior spines		0	0	0
Mid tibia, inferior spines	prolateral retrolateral	2 (2–2) 2 (2–2)	2 (2–3) 2 (1–2)	2 (2–2) 2 (1–2)
Mid tibia, superior spines	prolateral retrolateral	0	0 0 (0–1)	0
Fore femur, Inferior spines	prolateral retrolateral	0	0	0
Mid femur, inferior spines	prolateral retrolateral	0	0	0
Hind femur, inferior spines	prolateral retrolateral	2 (0–3) 4 (2–5)	0 (0–2) 2 (0–5)	2 (1–2) 2 (1–3)

Table 1 (continued). Dimensions and spine count of species of *Pharmacus* Pictet & de Saussure, 1893.

		***Pharmacus notabilis* sp. nov.**	***Pharmacus senex* sp. nov.**	***Pharmacus concinnus* sp. nov.**
Sample size		12 (5 ♀♀, 7 ♂♂)	29 (12 ♀♀, 17 ♂♂)	22 (12 ♀♀, 10 ♂♂)
Apical spines fore, mid and hind femora [1]		4 ♀♀: 0 0 , 0 1 , 0 0 1 ♀, 7 ♂♂: 1 0 , 0 1 , 0 0	0 0 , 0 1 , 0 0 1 ♀: 1 0 , 0 1 , 0 0	8 ♀♀, 9 ♂♂: 0 0 , 0 1 , 0 0 4 ♀♀, 1 ♂: 1 0 , 0 1 , 0 0
Apical spines fore, mid and hind tibiae		4-4-8	4-4-8	4-4-8
Body length (mm) [2]		♀ 16.5 (15.7–17.1) ♂ 14.1 (12.7–14.9)	♀ 15.8 (13.4–17.3) ♂ 13.9 (12.3–15.6)	♀ 17.1 (15.0–20.7) ♂ 16.0 (13.3–16.9)
Pronotum length (mm)		♀ 4.2 (3.6–4.6) ♂ 3.7 (3.2–4.1)	♀ 3.7 (3.2–4.4) ♂ 3.4 (2.7–4.1)	♀ 4.0 (3.5–4.7) ♂ 3.7 (3.2–4.3)
Eye colour		grey / green	grey / brown	grey / brown
Ovipositor length (mm)		10.3 (9.0–10.7)	11.0 (10.2–12.2)	12.9 (10.3–14.0)
Ratio ovipositor to body length		0.63 (0.57–0.64)	0.70 (0.62–0.87)	0.72 (0.63–0.82)
Teeth: ventral valve of ovipositor		6 (5–7)	6 (5–7)	7 (6–8)
Teeth: dorsal valve of ovipositor		0	0	0
Length of hind tibia (mm)		♀ 14.7 (14.3–15.9) ♂ 14.3 (12.7–15.1)	♀ 12.2 (10.8–12.7) ♂ 11.3 (9.3–12.2)	♀ 16.3 (12.7–17.7) ♂ 14.4 (12.1–17.4)
Ratio hind tibia to body length		♀ 0.90 (0.89–1.00) ♂ 1.05 (0.90–1.15)	♀ 0.77 (0.67–0.94) ♂ 0.82 (0.65–0.91)	♀ 0.94 (0.75–1.02) ♂ 0.92 (0.80–1.11)
Superior spines hind tibia	prolateral	25 (21–28)	22 (15–28)	23.5 (18–33)
	retrolateral	22 (20–29)	19 (15–26)	20 (17–26)
Spine density on hind tibia (count/ mm)	prolateral	♀ 1.63 (1.47–1.70) ♂ 1.85 (1.43–2.04)	♀ 1.89 (1.68–2.28) ♂ 1.83 (1.47–2.43)	♀ 1.56 (1.36–2.12) ♂ 1.71 (1.20–2.09)
	retrolateral	♀ 1.43 (1.32–1.54) ♂ 1.73 (1.36–2.12)	♀ 1.70 (1.34–2.11) ♂ 1.61 (1.32–2.23)	♀ 1.37 (1.12–1.82) ♂ 1.50 (1.14–1.70)
Pairs of longer spines on hind tibia		0	0	0
Superior spines on 1st tarsus segment		5 (0–8)	5 (2–7)	5 (1–10)
Superior spines on 2nd tarsus segment		0 (0–1)	0 (0–1)	0 (0–2)
Fore tibia, inferior spines	prolateral	2 (2–2)	2 (2–2)	2 (2–3)
	retrolateral	2 (2–2)	2 (2–3)	2 (2–2)
Fore tibia, superior spines		0	0	0
Mid tibia, inferior spines	prolateral	2 (2–2)	2 (1–3)	2 (2–2)
	retrolateral	2 (2–2)	2 (1–3)	2 (2–2)
Mid tibia, superior spines	prolateral	0	0	0
	retrolateral		0 (0–1)	0 (0–2)
Fore femur, Inferior spines	prolateral retrolateral	0	0	0
Mid femur, inferior spines	prolateral retrolateral	0	0	0
Hind femur, inferior spines	prolateral	2 (2–3)	1 (0–3)	2 (1–3)
	retrolateral	4.5 (3–5)	2 (1–6)	5 (3–7)

Table 1 (continued). Dimensions and spine count of species of *Pharmacus* Pictet & de Saussure, 1893.

		Pharmacus perfidus **sp. nov.**	***Pharmacus vallestris*** **sp. nov.**
Sample size		14 (5 ♀♀, 9 ♂♂)	6 (3 ♀♀, 3 ♂♂)
Apical spines fore, mid and hind femora [1]		1 ♀, 2 ♂♂: 0 0 , 0 1 , 0 0 4 ♀♀, 7 ♂♂: 1 0 , 0 1 , 0 0	1 0 , 0 1 , 0 0
Apical spines fore, mid and hind tibiae		4-4-8	4-4-8
Body length (mm) [2]		♀ 13.5 (12.4–14.6) ♂ 11.5 (10.9–12.6)	♀ 13.3 (11.9–14.0) ♂ 11.1 (10.1–11.3)
Pronotum length (mm)		♀ 3.5 (3.4–4.3) ♂ 3.2 (2.9–3.7)	♀ 3.9 (3.7–4.0) ♂ 3.4 (3.3–3.7)
Eye colour		grey / brown	brown / black
Ovipositor length (mm)		10.9 (9.9–11.4)	8.7 (8.1–9.0)
Ratio ovipositor to body length		0.82 (0.71–0.86)	0.65 (0.58–0.76)
Teeth: ventral valve of ovipositor		7 (6–8)	6 (6–6)
Teeth: dorsal valve of ovipositor		0	0
Length of hind tibia (mm)		♀ 11.6 (11.2–12.6) ♂ 11.6 (11.2–12.6)	♀ 13.3 (12.7–13.6) ♂ 11.5 (11.4–12.2)
Ratio hind tibia to body length		♀ 0.89 (0.77–0.94) ♂ 1.00 (0.96–1.12)	♀ 0.97 (0.96–1.12) ♂ 1.04 (1.01–1.21)
Superior spines hind tibia	prolateral	23 (16–28)	23.5 (21–28)
	retrolateral	21 (15–27)	22 (16–25)
Spine density on hind tibia (count/mm)	prolateral	♀ 1.88 (1.38–2.26) ♂ 1.98 (1.75–2.48)	♀ 1.96 (1.54–2.21) ♂ 1.97 (1.93–2.00)
	retrolateral	♀ 1.67 (1.29–1.83) ♂ 1.81 (1.58–2.39)	♀ 1.81 (1.18–1.88) ♂ 1.91 (1.80–1.93)
Pairs of longer spines on hind tibia		0	0
Superior spines on 1st tarsus segment		5 (4–7)	5 (3–7)
Superior spines on 2nd tarsus segment		0	0
Fore tibia, inferior spines	prolateral	2 (2–2)	2 (2–2)
	retrolateral	2 (2–2)	2 (2–2)
Fore tibia, superior spines		0	0
Mid tibia, inferior spines	prolateral	2 (2–2)	2 (2–2)
	retrolateral	2 (1–2)	2 (2–2)
Mid tibia, superior spines	prolateral retrolateral	0	0
Fore femur, Inferior spines	prolateral retrolateral	0	0
Mid femur, inferior spines	prolateral retrolateral	0	0
Hind femur, inferior spines	prolateral	0.5 (0–2)	1 (0–2)
	retrolateral	2.5 (0–3)	2 (1–2)

Footnotes:

[1] The six numbers are, in order from left to right: fore femur prolateral and retrolateral, mid femur prolateral and retrolateral, hind femur prolateral and retrolateral. ‘1’ means that an apical spine is present, ‘0’ means that an apical spine is absent.

[2] Body length is measured from the apex of the fastigium to the posterior margin of the suranal plate.

Taxonomy

Order Orthoptera Latreille, 1793
Superfamily Rhaphidophoroidea Walker, 1869
Family Rhaphidophoridae Walker, 1869
Subfamily Macropathinae Karny, 1930
Tribe Macropathini Karny, 1930

Genus ***Pharmacus*** Pictet & de Saussure, 1893

Pharmacus Pictet & de Saussure, 1893: 301–302.

Pharmacus – Hutton 1896: 238. — Richards 1972: 154–156.

Type species

Pharmacus montanus Pictet & de Saussure, 1893.

Etymology

‘*Pharmăcus*’ is Latin for ‘sorcerer’. The noun’s gender is masculine.

Description

A genus of small to mid-sized cave wētā (adult body length 10 to 18 mm, typically around 15 mm) with a distribution limited to the high alpine regions of the South Island of New Zealand. Only found above tree-line, often above snow-line, at elevations as high as 2800 m a.s.l.

All species in the genus look similar to each other. While this makes it easy to characterise the genus, an examination of the adult male terminalia is often required for a reliable identification to the species level. A detailed description of the genus follows below; individual species descriptions focus on those traits that vary between species or that differ from the generic description.

HEAD. Oval in shape; glabrous except for maxillary palps and antennae. Frons with a pale median line and two dark stripes converging to the fastigium on either side (Fig. 7A, C). Eyes rounded, but with a straight inner edge facing the fastigium. Face generally mottled with dark and pale patches. Fastigium pointed and ending abruptly below; dark with pale patches on either side; divided by a deep median groove. Scapes of antennae approximately three times as long as pedicel. All parts of the antennae pale or reddish-brown and covered with fine setae, except for the rotating joints. No visible sexual dimorphism in scapes of antennae or any other head-part (Fig. 7). Maxillary palps pale, of varying length, with moderately dense covering of hair.

THORAX. Colour and tomentum on pronotum variable both between and within species. A pale, thin median line is generally present, although it may be inconspicuous (see Fig. 8). Lateral edges of pronotum with a pronounced rim and bent upwards in all species.

LEGS. Moderately long. Hind femora generally shorter than body; hind tibiae between 30% shorter and 10% longer than body in females, between 20% shorter and 20% longer than body in males. Coxae and trochanters mottled light and dark brown. Fore and mid femora and tibiae may be uniform pale or brown, or variegated; hind legs variegated. Fore coxae with a pronounced lateral anterior spine. Fore femora without linear spines above or below, but may be armed with one prolateral spine at the apex in some species. Fore tibiae armed below, generally with two linear spines on both anterior and posterior edge in all species. Fore tibiae armed with two long spines below (one prolateral and one retrolateral) and two short spines above (one prolateral and one retrolateral) at apex. Mid femora without linear spines above or below, but always armed with one retrolateral spine at apex. A prolateral spine at the apex of the mid femur may be present in some species. Mid tibiae armed below, generally with two linear spines on both anterior and posterior edge in all species. Dorsal linear spines on the mid tibiae are rare but possible. Mid tibiae armed with two long spines below (one prolateral and one retrolateral) and two short spines above (one prolateral and one retrolateral) at apex. Hind femora may be armed with linear spines below, but never with apical spines. Hind tibiae armed with an average of 22 linear spines above, of varying length, on both anterior and posterior edges (Fig. 9). The spines are fused to the shaft of the tibia and are not socketed or articulated (Fig. 4K). Hind tibiae with two superior subapical spines (one prolateral and one retrolateral), two superior apical spines (one prolateral and one retrolateral), two inferior apical spines (one prolateral and one retrolateral) and two inferior subapical spines (one prolateral and one retrolateral). Superior apical spines approx. 50% longer than inferior apical spines; inferior apical spines approx. 50% longer than superior subapical spines; superior subapical spines approx. 50% longer than inferior subapical spines. Hind tarsi with four segments; first and second segments with a pair of spines on distal end. First segment and occasionally second segment armed above with small, alternate dorsal spines, in all species except *Pharmacus montanus*. The length of the tarsus segments (ordered from first to fourth) is in a ratio of 9 : 3 : 1 : 5.

ABDOMEN. Colour of tergites typically chequered, alternating pale and dark patches (Fig. 8). A uniform brown colour is common in adult *Pharmacus montanus* and in the nymphs of several species; a uniform black colour is common in both *P. montanus* and *P. cochleatus* populations above the permanent snowline. Dorsal median line generally visible but may be thin and inconspicuous. Tomentum variable both between and within species.

MALE TERMINALIA. Cerci between 15% and 20% of body length, pointed at apex, variable in colour, clothed in setae. The distal half is often visibly thicker than the proximal half (see Figs 5A–B, 10E, K, 11E, G–H). Styli short and stumpy, covered in sparse setae. The subgenital plate looks fairly similar in all species, broadly triangular, but enlarged in a spoon-like structure at the apex. The difference between species however is pronounced enough to provide the strongest character for species level identification (see Figs 10–11).

FEMALE TERMINALIA. Subgenital plate bilobed and rounded in all species. Ovipositor reddish-brown, straight or gently curved upwards at apex, terminating in a sharp point; relatively short (approximately two thirds of body length). Upper valve always smooth above; lower valve with 5 to 9 strong teeth at apex on ventral edge (Figs 12–13).

Nymphs generally look the same as adults, only smaller, which makes them readily identifiable as *Pharmacus*.

Pharmacus montanus Pictet & de Saussure, 1893

Figs 1–3, 4F–G, I, K, 7, 8A–B, 9A, 10A–C, 12A–C, 14A–B, 16A, 18A

Pharmacus montanus Pictet & de Saussure, 1893: 302–303, pl. I fig. 5–5c.
Pharmacus dumbletoni Richards, 1972: 161–162, fig. 4. **Syn. nov.**

Pharmacus montanus – Hutton 1896: 239. — Richards 1972: 156–158, fig. 1.

Diagnosis

A mid-sized cave wētā found in the Southern Alps from the Ben Ōhau Range northwards, at elevations greater than 1200 m. Body colour varies from marbled brown to black, generally with a thin but well visible median dorsal line along the whole length of the animal, and pale first tarsal segments. The pronotum and tergites are always covered in fine tomentum, giving the animal a matt appearance.

At the southern end of its distribution range, *Pharmacus montanus* overlaps with *P. cochleatus* comb. nov. and could be easily confused with the latter, especially at the higher elevations, where both insects are black. *P. cochleatus* is often glabrous and shiny in appearance and has first segment of the hind tarsi armed with dorsal linear spines, which are absent in *P. montanus*.

On the higher mountain tops east of the Main Divide of the Southern Alps, *P. montanus* shares the habitat with *Petrotettix serratus* Richards, 1972. The latter species is often dark with pale tarsi like *P. montanus* but has dorsal linear spines on the first two segments of the hind tarsi, and a serrated upper valve of the ovipositor.

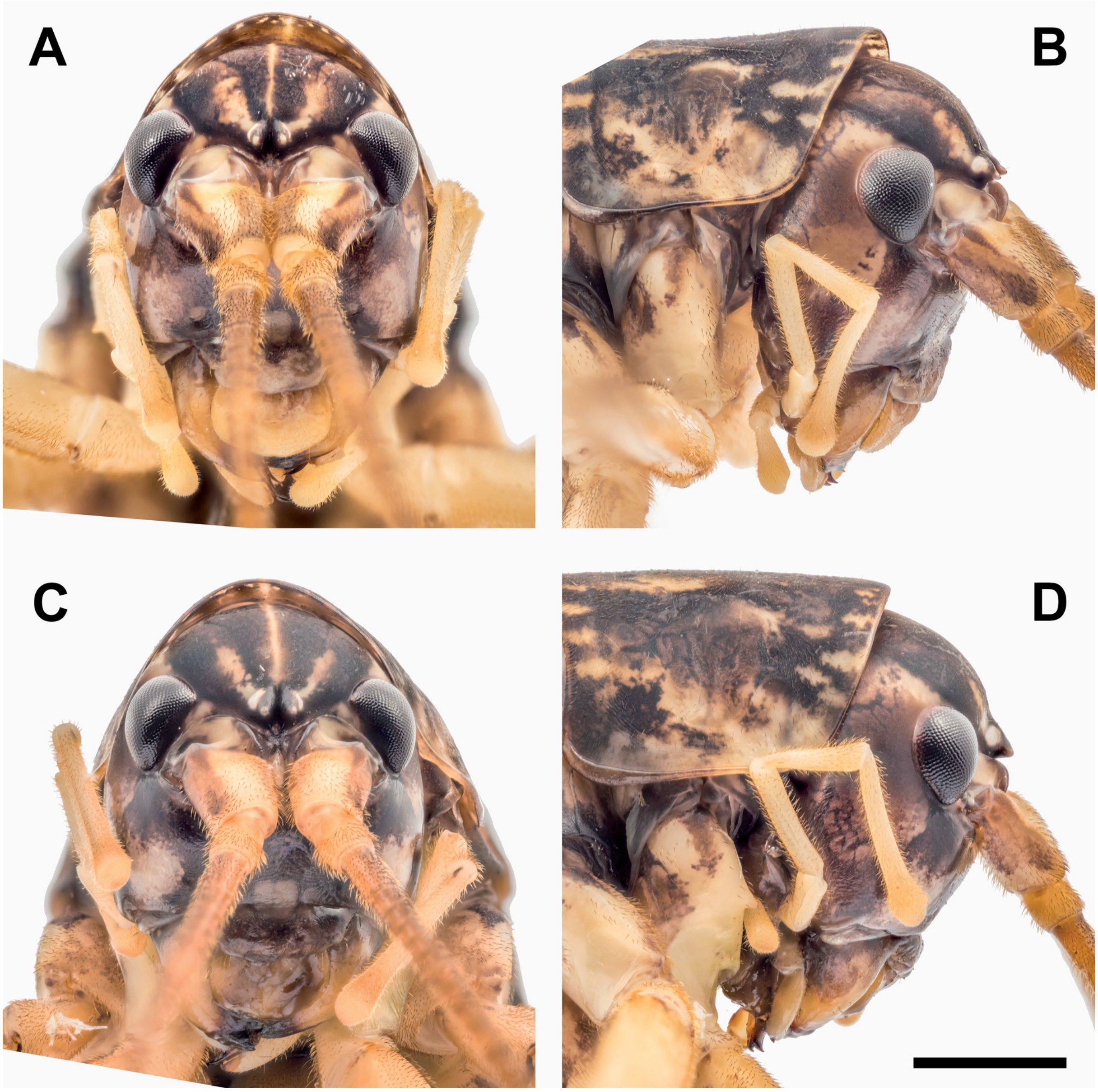

Fig. 7. Head of *Pharmacus montanus* Pictet & de Saussure, 1893, Lake Anna, Mt Franklin, Arthur's Pass. **A–B**. Adult ♂ (MPN CW3989) **C–D**. Adult ♀ (MPN CW3988). Scale bar = 2 mm.

In the alpine regions around Mt Cook, *P. montanus* forms mixed populations with *Notoplectron brewsterense* comb. nov. The latter is yellow-orange in colour, has a stocky appearance due to its shorter legs, and has fewer, larger dorsal linear spines on the hind tibiae. See also Fig. 4 for a comparison between the two species.

At the northern end of its distribution range in Kahurangi National Park, *P. montanus* is uniform brown and shares the habitat with *Macropathus filifer*, which is also brown. The latter species however has much longer legs, which give it a very slender appearance.

Etymology

'*Pharmăcus montānus*' is Latin for 'mountain sorcerer' – an inspired name for Pictet's and de Saussure's (1893) "entirely black insect".

In common English, *P. montanus* is also known as 'Mount Cook flea'. The name is explained by the insect's "reprehensible habit of leaping in showers out of a crevice in the rock upon the unsuspecting climber" (Dumbleton 1935), and is still in common use today.

Material examined (see also Supp. file 1: Table S1 and Figs S2–3)

Holotype

NEW ZEALAND • ♂, adult; Mackenzie (MK), Mt Cook region; 43.75° S, 170.06° E; 2100 m a.s.l.; date unknown; G. Mannering leg.; MHNG ARTO-24289.

Other material

NEW ZEALAND – **Mackenzie (MK)** • 1 ♀; Mt Annette, Sealy Range; 43.75129° S, 170.06210° E; 2200 m a.s.l.; 25 Feb. 2017; D. Hegg leg.; summit rocks, above glacier; night search; GenBank: OM293693; MPN CW3303 • 1 ♂, 1 ♀; same collection data as for preceding; MPN CW3302, CW3323 • 1 ♂; Mueller Hut Track, Sealy Range; 43.71504° S, 170.06982° E; 1500 m a.s.l.; 24 Feb. 2017; D. Hegg leg.; under large boulder; night search + insect net; GenBank: OM293692; MPN CW3300 • 3 ♂♂, 2 nymphs; same collection data as for preceding; MPN CW3299, CW3532 to CW3535 • 1 nymph; Mt Wakefield, Mount Cook Range; 43.70707° S, 170.12170° E; 1660 m a.s.l.; 18 Mar. 2017; D. Hegg leg.; on rock bluffs; night search + insect net; GenBank: OM293695; MPN CW3330 • 4 ♀♀, 1 nymph; same collection data as for preceding; MPN CW3331, CW3406, CW3660 to CW3662 • 1 ♀, 1 nymph; Mt Wakefield, Mt Cook Range; 43.71989° S, 170.12771° E; 1750 m a.s.l.; 13 May 2017; D. Hegg leg.; on rocky ridge; night search + insect net; MPN CW3516, CW3699 • 1 nymph; Mt Dark, Ben Ōhau Range; 43.87117° S, 170.04536° E; 1800 m a.s.l.; 17 May 2020; D. Hegg leg.; under boulder on scree slope; casual find while climbing; GenBank: OM293728; MPN CW4876 • 1 nymph; same collection data as for preceding; MPN CW4875. – **North Canterbury/Westland (NC/WD)** • 1 nymph; Lake Anna, Mt Franklin, Arthur's Pass; 42.87567° S, 171.65048° E; 1720 m a.s.l.; 23 Dec. 2017; D. Hegg leg.; on rock bluffs; night search; GenBank: OM293702; MPN CW3650 • 1 ♂, 1 ♀; same collection data as for preceding; MPN CW3988, CW3989. – **Buller (BR)** • 1 ♂, holotype of *P. dumbletoni*; Mount Mahanga, Spenser Mountains; 42.102° S, 172.635° E; 2100 m a.s.l.; Oct. 1950; L.J. Dumbleton leg.; NZAC 03015679 • 1 ♂; Gloriana Peak, Spenser Mountains; 42.27437° S, 172.48992° E; 1750 m a.s.l.; 5 Feb. 2017; D. Hegg leg.; on rock bluffs; night search + insect net; GenBank: OM293689; MPN CW3262 • 1 ♂, 1 ♀, 2 nymphs; same collection data as for preceding; MPN CW3263 to 3266 • 4 ♂♂, 2 ♀♀; same collection data as for preceding; 25 Apr. 2017; MPN CW3656 to CW3659, CW3665, CW3666 • 1 ♀; Between Sunset Saddle and Mt Hopeless, Travers Range; 41.91926° S, 172.73519° E; 1900 m a.s.l.; 31 Dec. 2020; D. Hegg leg.; in rocky chasm; visual search in daylight; MPN CW5183. – **Nelson (NN)** • 1 ♀; Poverty Basin, Mt Owen; 41.54712° S, 172.52864° E; 1640 m a.s.l.; 8 Jan. 2019; D. Hegg leg.; on limestone bluffs; night search + insect net; GenBank: OM293708; MPN CW4275 •

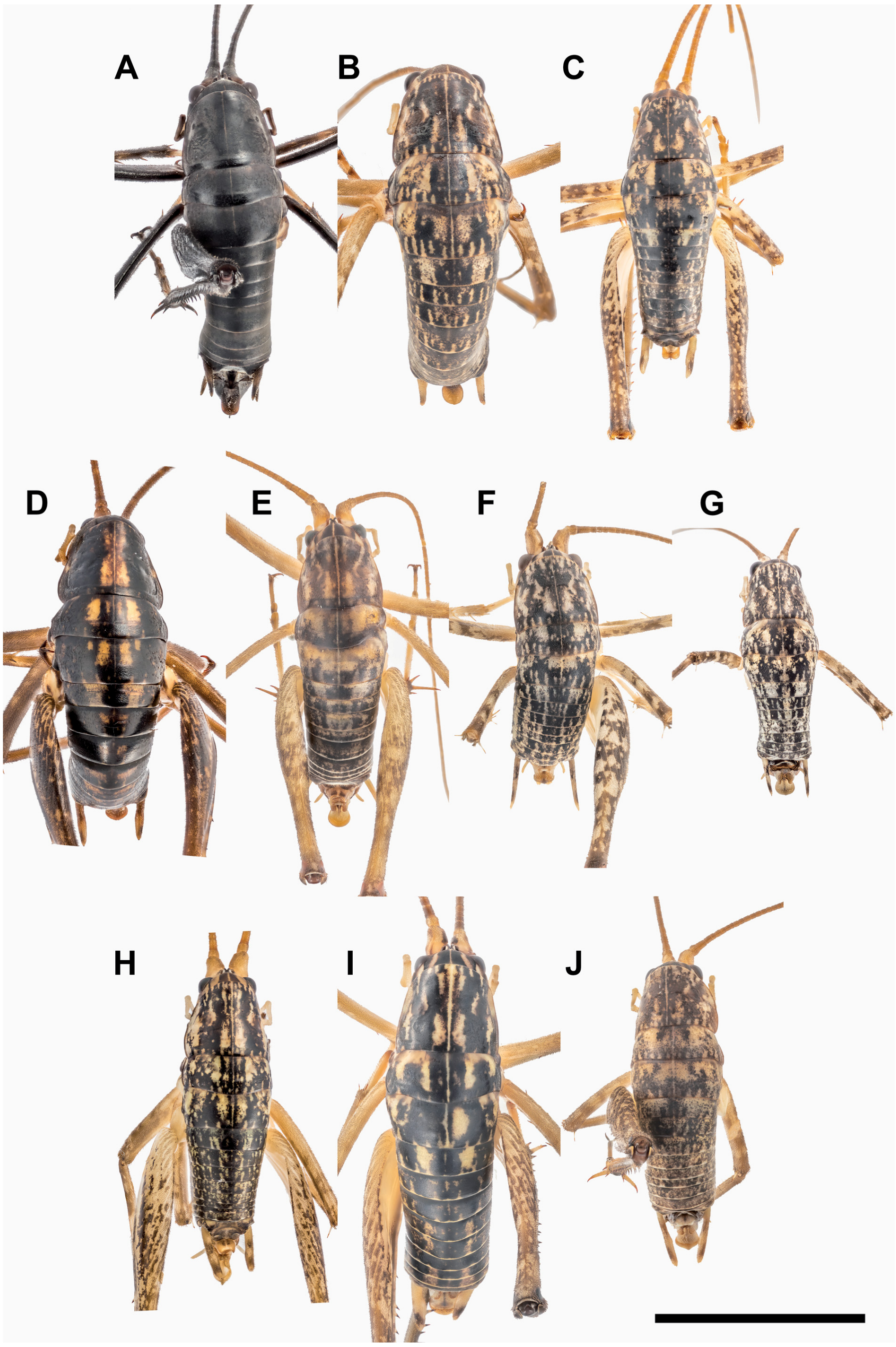

Fig. 8. Dorsal views of adult ♂ cave wētā in the genus *Pharmacus* Pictet & de Saussure, 1893. Notice loss of natural pigmentation of pale body parts due to preservation in ethanol. **A–B**. *Pharmacus montanus* Pictet & de Saussure, 1893 **A**. Mt Annette, Sealy Range, Mt Cook (MPN CW3302). **B**. Lake Anna, Mt Franklin, Arthur's Pass (MPN CW3989). **C**. *Pharmacus senex* sp. nov., Old Woman Range, Central Otago (MPN CW4387). **D**. *Pharmacus cochleatus cochleatus* (Karny, 1935) comb. nov., Topheavy, Mt Brewster, Haast Pass (MPN CW3324). **E**. *Pharmacus cochleatus rawhiti* subsp. nov., Mt Tūwhakarōria, Hector Mountains (NMNZ AI.052290). **F**. *Pharmacus cristatus* sp. nov., Skippers Range, South Westland (MPN CW4562). **G**. *Pharmacus vallestris* sp. nov., Matukituki River West Branch (MPN CW3700). **H**. *Pharmacus notabilis* sp. nov., Remarkables ski-field access road (NMNZ AI.052296). **I**. *Pharmacus concinnus* sp. nov., Eyre Peak, Eyre Mountains (MPN CW4482). **J**. *Pharmacus perfidus* sp. nov., Spence Peak, Takitimu Mountains (MPN CW4494). Scale bar = 10 mm.

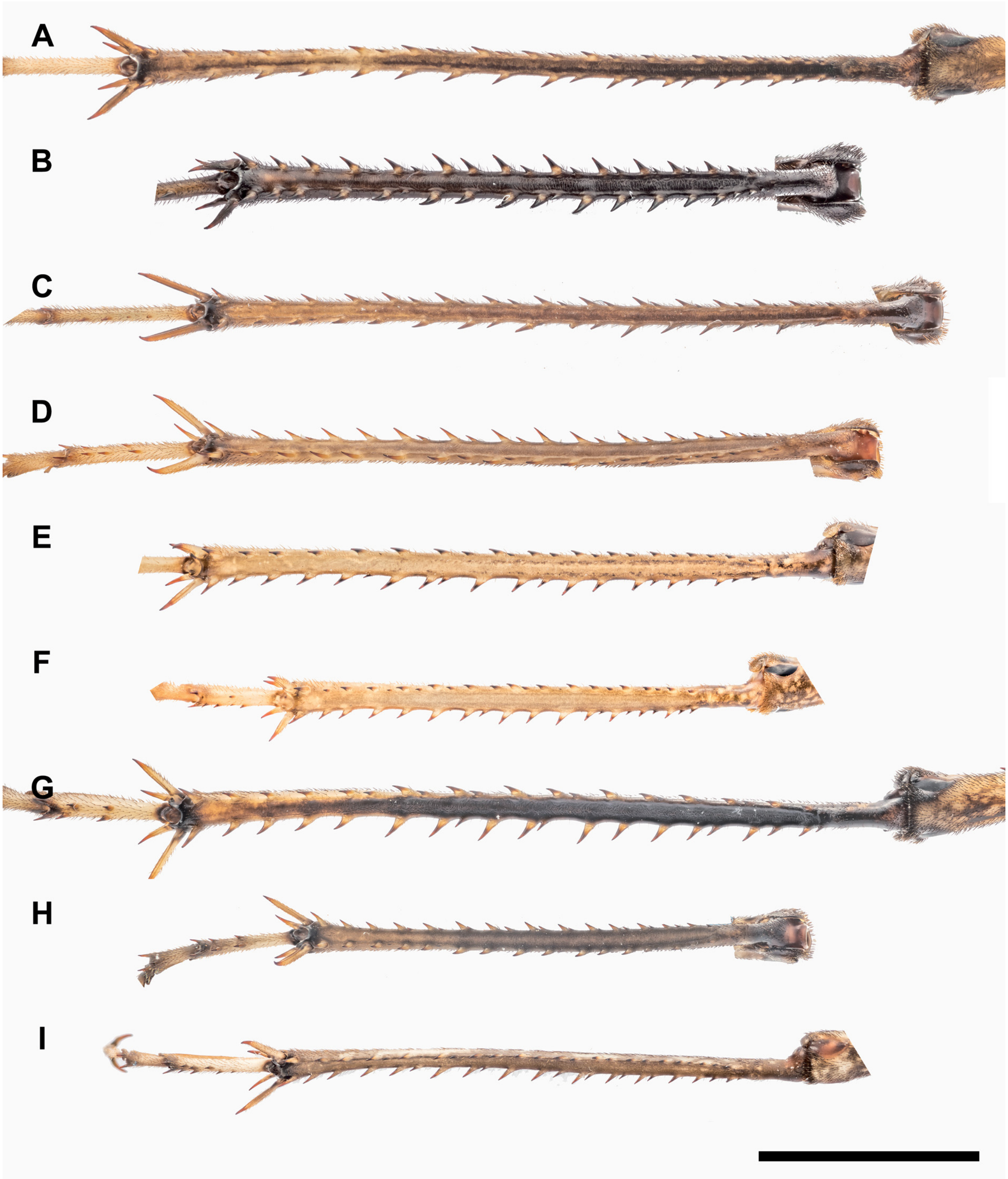

Fig. 9. Left hind tibia of adult ♂ cave wētā in the genus *Pharmacus* Pictet & de Saussure, 1893, dorsal view. **A**. *Pharmacus montanus* Pictet & de Saussure, 1893, Lake Anna, Mt Franklin, Arthur's Pass (MPN CW3989). **B**. *Pharmacus cochleatus cochleatus* (Karny, 1935) comb. nov., Gertrude Saddle, Darran Mountains (MPN CW3413). **C**. *Pharmacus cochleatus rawhiti* subsp. nov., Mt Tūwhakarōria, Hector Mountains (MPN CW4431). **D**. *Pharmacus cristatus* sp. nov., Skippers Range, South Westland (NMNZ AI.052292). **E**. *Pharmacus notabilis* sp. nov., Remarkables ski-field access road (NMNZ AI.052296). **F**. *Pharmacus senex* sp. nov., Obelisk, Old Man Range (NMNZ AI.052294). **G**. *Pharmacus concinnus* sp. nov., Eyre Peak, Eyre Mountains (MPN CW4480). **H**. *Pharmacus perfidus* sp. nov., Spence Peak, Takitimu Mountains (NMNZ AI.052300). **I**. *Pharmacus vallestris* sp. nov., Matukituki River West Branch (MPN CW3700). Scale bar = 5 mm.

4 ♂♂, 1 ♀, 4 nymphs; same collection data as for preceding; MPN CW4272, CW4273, CW4446 to CW4450, CW4456, CW4457.

Description

Measurements. See Table 1.

Head. As per generic description. Specimens living above the permanent snowline are entirely black. This includes all head parts that are usually pale otherwise, e.g., maxillary palps and antennae.

Thorax. As per generic description; always covered in fine hair, which gives the animal a matt look.

Legs. Longer than in most *Pharmacus* species. The hind tibiae are 5% longer than the body in females, 20% longer than the body in males. Fore femora always unarmed at the apex. Mid femora armed with one retrolateral spine at the apex; prolateral apical spine absent. Hind femora occasionally armed with up to two linear spines below, on either or both inner and outer edge. Hind tibiae armed with two superior subapical spines (one prolateral and one retrolateral), two superior apical spines (one prolateral and one retrolateral), two inferior apical spines (one prolateral and one retrolateral) and two inferior subapical spines (one prolateral and one retrolateral), as in all other *Pharmacus* species. However, in some specimens in the Mt Cook region, a third inferior subapical spine may be present on the inner edge of the tibia (see Fig. 3F–G). First and second tarsal segments without any linear spines above – a trait that differentiates *P. montanus* from all other *Pharmacus* species. The first tarsal segment is generally pale on all six legs, even in specimens that are entirely black otherwise – the contrast is in fact especially noticeable in the darker specimens and gives the insect a characteristic look (Fig. 14A).

Abdomen. Tergites always covered in fine hair, which gives the animal a matt look. A thin, pale median line along the whole length of the insect is generally visible, even in the darker specimens. The colour of the tergites is most commonly brown at the lower elevations (Fig. 14B), transitioning to black at the higher elevations, especially above the permanent snow-line (Figs 8A, 14A). Specimens in the Arthur's Pass region are chequered, unlike other *P. montanus* but like other *Pharmacus* species further south (Fig. 8B).

Male terminalia. Subgenital plate triangular when seen from below; deeper than in all other *Pharmacus* species when seen from the side (Fig. 10A–C). In a dorsal view, a thin plate or membrane covered in tomentum is attached to the vertex of the triangle. The plate varies in shape from oval (Figs 3D, 8B) to rectangular with rounded corners (Figs 3E, 10A).

Female terminalia. Subgenital plate strongly bilobed, the two rounded lobes long and narrow, separated by a deep V-shaped depression; hairy (Figs 4F–G, 12A). Ovipositor on average 70% of body length, relatively straight, tapering gently at first then more strongly near the apex; lower valve with 5 to 8 strong teeth below at the apex (Fig. 12B–C).

Pharmacus cochleatus (Karny, 1935) comb. nov.

The species, originally described by Karny (1935) as *Isoplectron cochleatum* based on two male specimens of unknown origin, was described a second time as *Pharmacus chapmanae* based on seven specimens from a relatively small geographical region in Otago and northern Fiordland. We have expanded the known range for the species considerably to the north, south and east (Fig. 18B). While specimens collected along the length of the Southern Alps and Fiordland are morphologically indistinguishable, they fall into three genetically and geographically distinct clades. Specimens collected in the mountains either side of Lake Wakatipu and south of the Greenstone and Kawarau River show some noticeable morphological differences compared to the populations further west. We thus propose to recognise four separate subspecies.

Pharmacus cochleatus cochleatus (Karny, 1935) comb. nov.

Figs 1–2, 5–6, 8D, 9B, 10D–E, 12D–F, 14C–D, 16A–C, 18B

Isoplectron cochleatum Karny, 1935: 383–385, fig. 44.
Pharmacus chapmanae Richards, 1972: 158–160, fig. 2. **Syn. nov.**

Pharmacus chapmanae – Chinn & Chinn 2020: 361–389.
Pharmacus brewsterensis – Chinn & Chinn 2020: fig. 4d.

Diagnosis

A mid-sized cave wētā found in the Southern Alps from Aoraki/Mt Cook south to the Dart River and east into Central Otago, at elevations greater than 1200 m. Body colour varies from chequered yellow/black to all black. Dorsal surfaces may be covered in fine tomentum, giving the insect a matt appearance, or glabrous, giving the insect a shiny appearance. The latter trait is more common at the northern end of the species' distribution range.

At the northern end of its distribution range, *P. cochleatus cochleatus* overlaps with *P. montanus* and can easily be confused with the latter, especially at the higher elevations, where both insects are entirely black. The most reliable trait to differentiate the two species is the presence of dorsal spines on the first hind tarsus segment in *P. cochleatus*.

Across much of its range, *P. cochleatus cochleatus* overlaps with either *Notoplectron brewsterense* comb. nov. or with *Talitropsis chopardi* (Karny, 1937) east of the Main Divide of the Southern Alps. Both of the latter two species have lighter colour, shorter legs with fewer spines on the hind tibiae and no dorsal spines on the first hind tarsus segment.

Etymology

'*Cŏchlĕăr*' is Latin for 'spoon'. '*Cochleatus*' means 'equipped with a spoon' – after the shape of the male subgenital plate.

Material examined (see also Supp. file 1: Table S2 and Fig. S4)

Holotype

NEW ZEALAND • ♂, adult; locality unknown; 1876; H. Filhol leg.; MNHN EO-ENSIF4926.

Paratype

NEW ZEALAND • 1 ♂, adult; same collection data as for holotype; MNHN EO-ENSIF4928.

Other material

NEW ZEALAND – **Otago Lakes/Westland (OL/WD)** • 1 ♂, holotype of *Pharmacus chapmanae*; Bevan Col, Matukituki Valley; 44.393° S, 168.689° E; 1850 m a.s.l.; Dec. 1958; M.A. Chapman leg.; OMNZ IV7927 (prev. OMNZ A70:6) • 1 ♀, allotype of *Pharmacus chapmanae*; same collection data as for preceding; OMNZ IV7924 (prev. OMNZ A70:8) • 1 ♂; Bevan Col, Matukituki Valley; 44.39424° S, 168.68760° E; 1850 m a.s.l.; 29 Jan. 2021; D. Hegg leg.; rock bluffs; night search + insect net; GenBank: OM293736; MPN CW5179 • 1 ♂, 1 ♀; same collection data as for preceding; MPN CW5178, CW5180. – **Westland (WD)** • 1 ♀; Topheavy, Mt Brewster, Haast Pass; 44.06548° S, 169.42843° E; 2000 m a.s.l.; 18 Feb. 2017; D. Hegg leg.; on rocky ridge above glacier; night search; GenBank: OM293694; MPN CW3322 • 2 ♂♂, 5 ♀♀; same collection data as for preceding; MPN

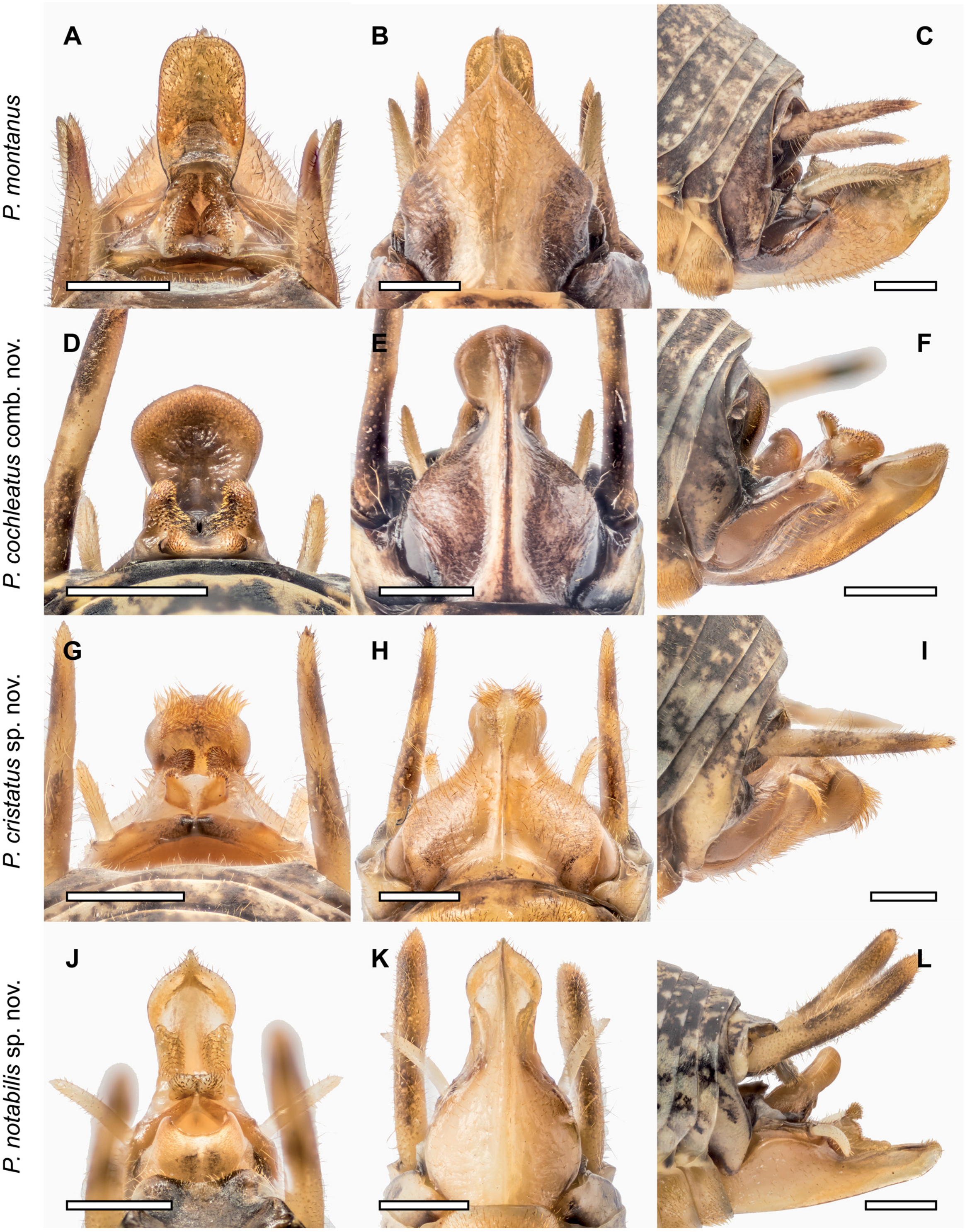

Fig. 10. Adult male terminalia of cave wētā in the genus *Pharmacus* Pictet & de Saussure, 1893. Left column: dorsal view; central column: ventral view (subgenital plate); right column: lateral view. **A–C**. *Pharmacus montanus* Pictet & de Saussure, 1893, Mueller Hut Track, Sealy Range, Mt Cook (MPN CW3532). **D–F**. *Pharmacus cochleatus* (Karny, 1935) comb. nov. **D–E**. Humboldt Mountains (MPN CW3698). **F**. Blue Lake Creek, Garvie Mountains (MPN CW4462). **G–I**. *Pharmacus cristatus* sp. nov., Skippers Range High Point, South Westland (NMNZ AI.052292). **J–L**. *Pharmacus notabilis* sp. nov., Remarkables Ski-field access road (NMNZ AI.052296). Scale bars = 1 mm.

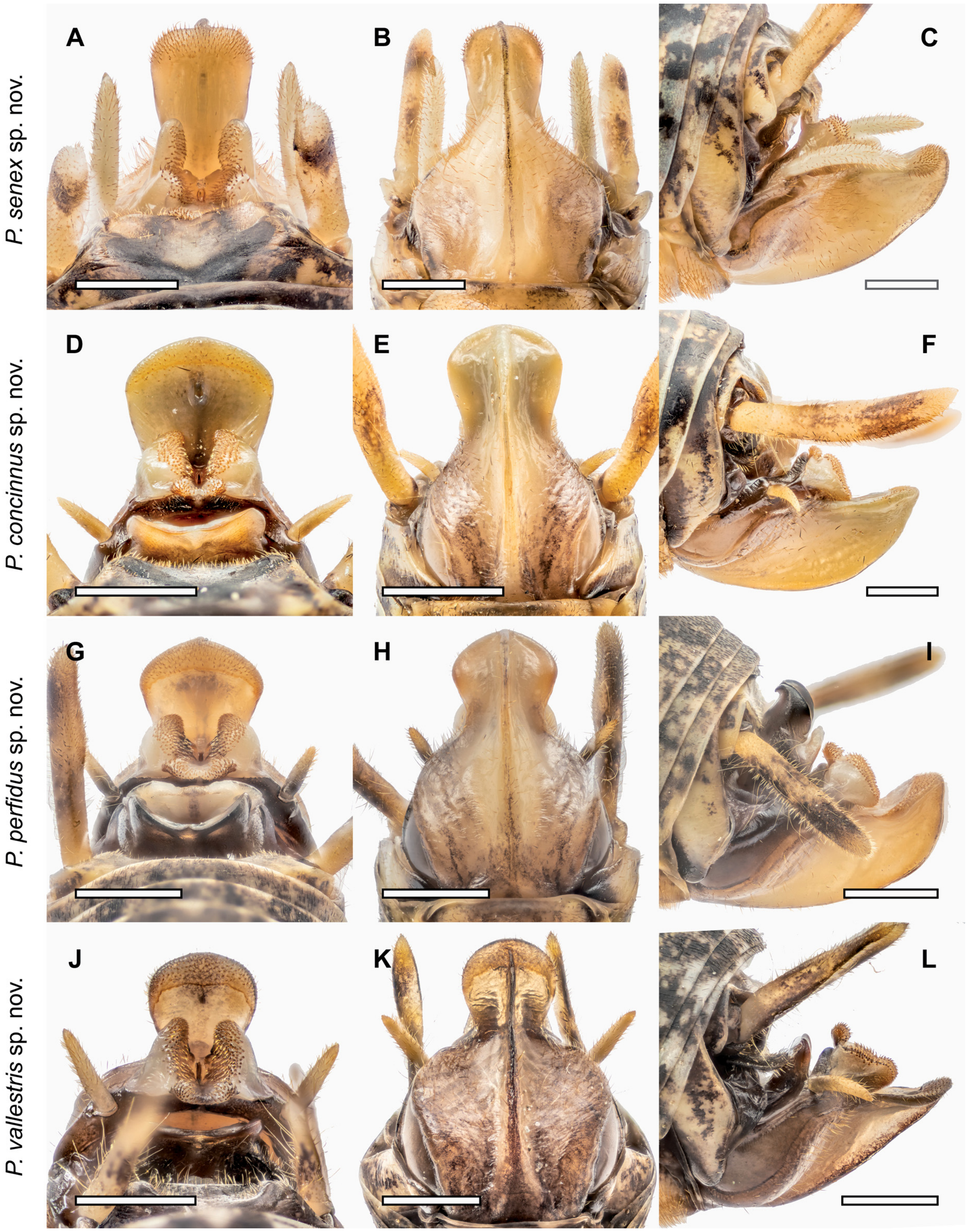

Fig. 11. Adult male terminalia of cave wētā in the genus *Pharmacus* Pictet & de Saussure, 1893. Left column: dorsal view; central column: ventral view (subgenital plate); right column: lateral view. **A**–**C**. *Pharmacus senex* sp. nov., The Obelisk, Old Man Range (NMNZ AI.052294). **D**–**F**. *Pharmacus concinnus* sp. nov., Symmetry Peaks, Eyre Mountains (NMNZ AI.052298). **G**–**I**. *Pharmacus perfidus* sp. nov., Spence Peak, Takitimu Mountains (NMNZ AI.052300). **J**–**L**. *Pharmacus vallestris* sp. nov., Matukituki River West Branch (NMNZ AI.052302). Scale bars = 1 mm.

CW3277, CW3279 to CW3282, CW3324, CW3325. – **Otago Lakes (OL)** • 1 ♀; Luna Basin, Major Peak, Wakatipu; 44.92490° S, 168.47476° E; 1470 m a.s.l.; 9 Apr. 2016; D. Hegg leg.; on large rocks in alpine basin; night search; GenBank: OM293686; MPN CW2985 • 3 ♂♂, 1 ♀; same collection data as for preceding; MPN CW2979, CW2981, CW2999, CW3000 • 1 nymph; Coronet Peak, Queenstown; 44.91774° S, 168.73423° E; 1540 m a.s.l.; 18 Jan. 2019; D. Hegg leg.; on rock formations; night search + insect net; GenBank: OM293709; MPN CW4288 • 5 ♂♂, 3 ♀♀; same collection data as for preceding; MPN CW4414 to CW4418, CW4432 to CW4434 • 1 ♀; Lochnagar, Richardson Mountains; 44.59627° S, 168.56400° E; 2080 m a.s.l.; 21 Sep. 2019; D. Hegg leg.; on rocks on side of snow couloir; casual find while climbing; GenBank: OM293726; MPN CW4590 • 1 ♂; Sentinel Peak, Lake Hāwea; 44.41029° S, 169.24003° E; 1580 m a.s.l.; 5 Dec. 2020; D. Hegg leg.; on rocky ridge; night search + insect net; GenBank: OM293731; MPN CW5134 • 2 ♂♂, 2 nymphs; same collection data as for preceding; MPN CW5132, CW5133, CW5135, CW5136 • 2 ♂♂; Earnslaw Burn; 44.67482° S, 168.39371° E; 1280 m a.s.l.; 13 Nov. 2020; D. Hegg leg.; on rocky ridge and cliffs; night search + insect net; GenBank: OM293733, OM293734; MPN CW5149, CW5150 • 1 ♂, 1 ♀, 2 nymphs; same collection data as for preceding; MPN CW5151 to CW5154 • 1 ♀; Roys Peak, Wānaka; 44.69477° S, 169.04644° E; 1500 m a.s.l.; 19 Nov. 2020; D. Hegg leg.; rock bluffs; night search + insect net; GenBank: OM293732; MPN CW5137 • 5 ♂♂, 2 ♀♀, 2 nymphs; same collection data as for preceding; MPN CW5138 to CW5144, CW5147, CW5148 • 1 ♀, 1 nymph; below Bevan Col, Matukituki Valley; 44.39546° S, 168.68503° E; 1750 m a.s.l.; 29 Jan. 2021; D. Hegg leg.; rock slabs; casual find while climbing; MPN CW5181, CW5182 • 1 nymph; Turret Head, Earnslaw Burn; 44.65757° S, 168.37977° E; 2300 m a.s.l.; 2 Feb. 2021; D. Hegg leg.; rocky ridge; casual find while climbing; GenBank: OM293735; MPN CW5176 • 1 nymph; same collection data as for preceding; MPN CW5175 • 3 ♂♂, 1 ♀, 1 nymph; Turret Head, Earnslaw Burn; 44.65681° S, 168.38646° E; 2100 m a.s.l.; 2 Feb. 2020; D. Hegg leg.; rock bluffs; night search + insect net; MPN CW5244 to CW5247, CW5177 • 1 ♂, 2 ♀♀, 5 nymphs; Albertburn Saddle, East Matukituki; 44.39752° S, 168.87310° E; 1600 m a.s.l.; 5 Feb. 2021; D. Hegg leg.; rock bluffs; night search + insect net; MPN CW5170 to CW5174, CW5238 to CW5240 • 2 ♂♂, 1 ♀; East Matukituki/Albertburn divide; 44.36994° S, 168.8887° E; 1830 m a.s.l.; 6 Feb. 2021; D. Hegg leg.; rock bluffs; night search + insect net; MPN CW5241 to CW5243 • 2 ♀♀; French Ridge, West Matukituki; 44.42520° S, 168.69874° E; 1800 m a.s.l.; 20 Feb. 2021; D. Hegg leg.; rocky ridge; night search + insect net; MPN CW5207, CW5208. – **Central Otago (CO)** • 1 ♂; Mt Pisa, Pisa Range; 44.88278° S, 169.19500° E; 1650 m a.s.l.; 27 Feb. 2018; D. Hegg leg.; on tor; night search + insect net; GenBank: OM293705; MPN CW3831 • 4 ♂♂, 5 ♀♀, 2 nymphs; same collection data as for preceding; MPN CW3795 to CW3797, CW3828 to CW3830, CW3847 to CW3851. – **Mackenzie (MK)** • 1 ♀; Dasler Pinnacles, Naumann Range; 43.95237° S, 169.86241° E; 1800 m a.s.l.; 14 Jan. 2017; D. Hegg leg.; on rock bluffs; night search; GenBank: OM293691; MPN CW3284 • 3 ♂♂; same collection data as for preceding; MPN CW3283, CW3285, CW3296 • 1 ♂; Mt Edgar Thomson, Ben Ōhau Range; 43.78252° S, 170.05561° E; 2350 m a.s.l.; 28 Jan. 2017; D. Hegg leg.; on mixed rock and snow ridge; casual find while climbing; GenBank: OM293690; MPN CW3278.

Description

MEASUREMENTS. See Table 1.

HEAD. As per generic description. Eyes dark. Specimens living above the permanent snowline are entirely black. This includes all head parts that are usually pale otherwise, e.g., maxillary palps and antennae.

THORAX. As per generic description.

LEGS. Notably shorter than in *P. montanus*. The hind tibiae are approx. 10% shorter than the body in both males and females. Fore femora always unarmed at the apex. Mid femora armed with one retrolateral spine at the apex; prolateral apical spine absent. The first hind tarsus segment is armed with a variable number of linear spines above (up to nine); the second hind tarsus segment is only rarely armed with dorsal linear spines. The first tarsal segment on all six legs is pale at times, but not always; the insect can be entirely black (Fig. 14D).

Abdomen. Tergites tomentose or glabrous; the latter trait appears to be more common in the northern half of the range. A thin, pale median line along the whole length of the insect may or may not be present. The colour of the tergites is mostly chequered yellow/black or light grey-brown/black at the lower elevations (Fig. 14C), transitioning to mostly black (Fig. 8D) or all black (Fig. 14D) at the higher elevations, especially above the permanent snow-line.

Male terminalia. Subgenital plate an isosceles triangle with very rounded corners and a spoon on the vertex; keeled and mostly glabrous, with some sparse hair near the edges; shallow when seen from the side. In a dorsal view, only the spoon is visible, protruding beyond the paraprocts; these are covered in short, dense bristles (Fig. 10D–F).

Female terminalia. Subgenital plate bilobed, the two rounded lobes short, broad, and asymmetrical, with a wide gap in between; very hairy (Fig. 12D). Ovipositor on average 70% of body length, only very gently curving upwards; lower valve with 5 to 9 strong teeth below at the apex (Fig. 12E–F).

Pharmacus cochleatus nauclerus subsp. nov.

urn:lsid:zoobank.org:act:D540A190-8DEE-4CDD-AA28-EA92A31550BF

Figs 1–2, 6, 17D, 18B

Diagnosis

A mid-sized cave wētā endemic to the Skippers Range in South Westland. Morphologically indistinguishable from *Pharmacus cochleatus cochleatus* comb. nov., but geographically separated and genetically distinct.

Pharmacus cochleatus nauclerus is sympatric with *Pharmacus cristatus* sp. nov. and with *Notoplectron brewsterense* comb. nov. It is easily differentiated from the former by its darker coloration and lack of prolateral apical spines on the fore and mid femora and from the latter by its darker colour, longer legs with more numerous spines on the hind tibiae and the presence of dorsal spines on the first hind tarsus segment.

Etymology

'*Nauclērus*' is Latin for 'skipper', after the Skippers Range in South Westland.

Material examined (see also Supp. file 1: Table S3)

Holotype

NEW ZEALAND • ♂, adult; Westland (WD), Skippers Range; 44.50459° S, 168.12086° E; 1400 m a.s.l.; 7 Feb. 2019; D. Hegg leg.; on rock bluffs; night search; NMNZ AI.052288 (prev. MPN CW4412).

Paratype

NEW ZEALAND • 1 ♀, adult; Westland (WD), Skippers Range High Point; 44.43914° S, 168.16515° E; 1600 m a.s.l.; 3 Feb. 2019; D. Hegg leg.; on scree and rock bluffs; night search; NMNZ AI.052289 (prev. MPN CW4376).

Other material

NEW ZEALAND – **Westland (WD)** • 1 ♂, 1 ♀, 1 nymph; Skippers Range; 44.42005° S, 168.15399° E; 1360 m a.s.l; 2 Feb. 2019; D. Hegg leg.; on rock bluffs; night search; MPN CW4366, CW4378, CW4413

• 1 nymph; same collection data as for paratype; GenBank: OM293711; MPN CW4363 • 1 ♀; Skippers Range; 44.46821° S, 168.10095° E; 1200 m a.s.l.; 6 Feb. 2019; D. Hegg leg.; on rock bluffs; night search; GenBank: OM293713; MPN CW4374 • 2 ♂♂, 1 ♀; same collection data as for preceding; MPN CW4377, CW4410, CW4411 • 1 nymph; same collection data as for holotype; GenBank: OM293710; MPN CW4361 • 2 ♀♀; same collection data as for holotype; CW4379, CW4380.

Description

Measurements. See Table 1.

Pharmacus cochleatus nauclerus subsp. nov. is morphologically identical to *Pharmacus cochleatus cochleatus* comb. nov. See the description for the latter.

Pharmacus cochleatus fiordensis subsp. nov.

urn:lsid:zoobank.org:act:91533C5F-726A-4A6E-A6C8-AC56E1DC7BF3

Figs 1–2, 6, 18B

Diagnosis

A mid-sized cave wētā found in the alpine regions of Fiordland and of Mt Aspiring National Park south of the Dart River, at elevations greater than 1200 m. Morphologically indistinguishable from *Pharmacus cochleatus cochleatus* comb. nov., but geographically separated and genetically distinct.

In Fiordland, *Pharmacus cochleatus fiordensis* subsp. nov. is sympatric with *Pharmacus cristatus* sp. nov. It is easily differentiated from the latter by its darker coloration and lack of prolateral apical spines on the fore and mid femora.

Across much of its range, *P. cochleatus fiordensis* overlaps with *Notoplectron brewsterense* comb. nov. The latter species has lighter colour, shorter legs with fewer spines on the hind tibiae and no dorsal spines on the first hind tarsus segment.

Etymology

'*Fiordensis*', inhabits Fiordland, the geographical region in the south-west corner of New Zealand.

Crowe (2002) refers to this insect as 'black tumbling cave wētā' in light of his observations of how "to escape danger, it leaps, then rolls down the scree to tumble into a gap between the stones".

Material examined (see also Supp. file 1: Table S4)

Holotype

NEW ZEALAND • ♂, adult; Fiordland (FD), Gertrude Saddle, Darran Mountains; 44.74521° S, 168.01649° E; 1300 m a.s.l.; 25 Mar. 2017; D. Hegg leg.; on rock bluffs; night search; GenBank: OM293697; NMNZ AI.052286 (prev. MPN CW3413).

Paratype

NEW ZEALAND • 1 ♀, adult; Fiordland (FD), Mt Luxmore, Kepler Mountains; 45.38929° S, 167.59154° E; 1350 m a.s.l.; 22 Mar. 2019; D. Hegg leg.; on rock bluffs; night search + insect net; NMNZ AI.052287 (prev. MPN CW4398).

Other material

NEW ZEALAND – **Fiordland (FD)** • 1 ♀; Homer Saddle, Darran Mountains; 44.760° S, 167.983° E; 1200 m a.s.l.; Jan. 2014; T. Jewell leg.; in dry cracks in rock bluff; hand collected in daylight; MPN CW2611 • 1 nymph; same collection data as for holotype; MPN CW3412 • 1 ♂; same collection data as for paratype; GenBank: OM293718; MPN CW4397 • 3 nymphs; same collection data as for paratype; MPN CW4547 to CW4549. – **Otago Lakes (OL)** • 1 ♀; Emily Peak, Ailsa Mountains; 44.74594° S, 168.20446° E; 1800 m a.s.l.; 14 Feb. 2015; D. Hegg leg.; on snowgrass; photograph; iNaturalist 2421936 • 1 ♂; Ocean Peak, Ailsa Mountains; 44.75041° S, 168.17270° E; 1300 m a.s.l.; 29 Oct. 2016; D. Hegg leg.; on large rocks in alpine basin; night search; GenBank: OM293687; MPN CW3135 • 1 ♂, 3 ♀♀, 1 nymph; same collection data as for preceding; MPN CW3133, CW3134, CW3136, CW3137,

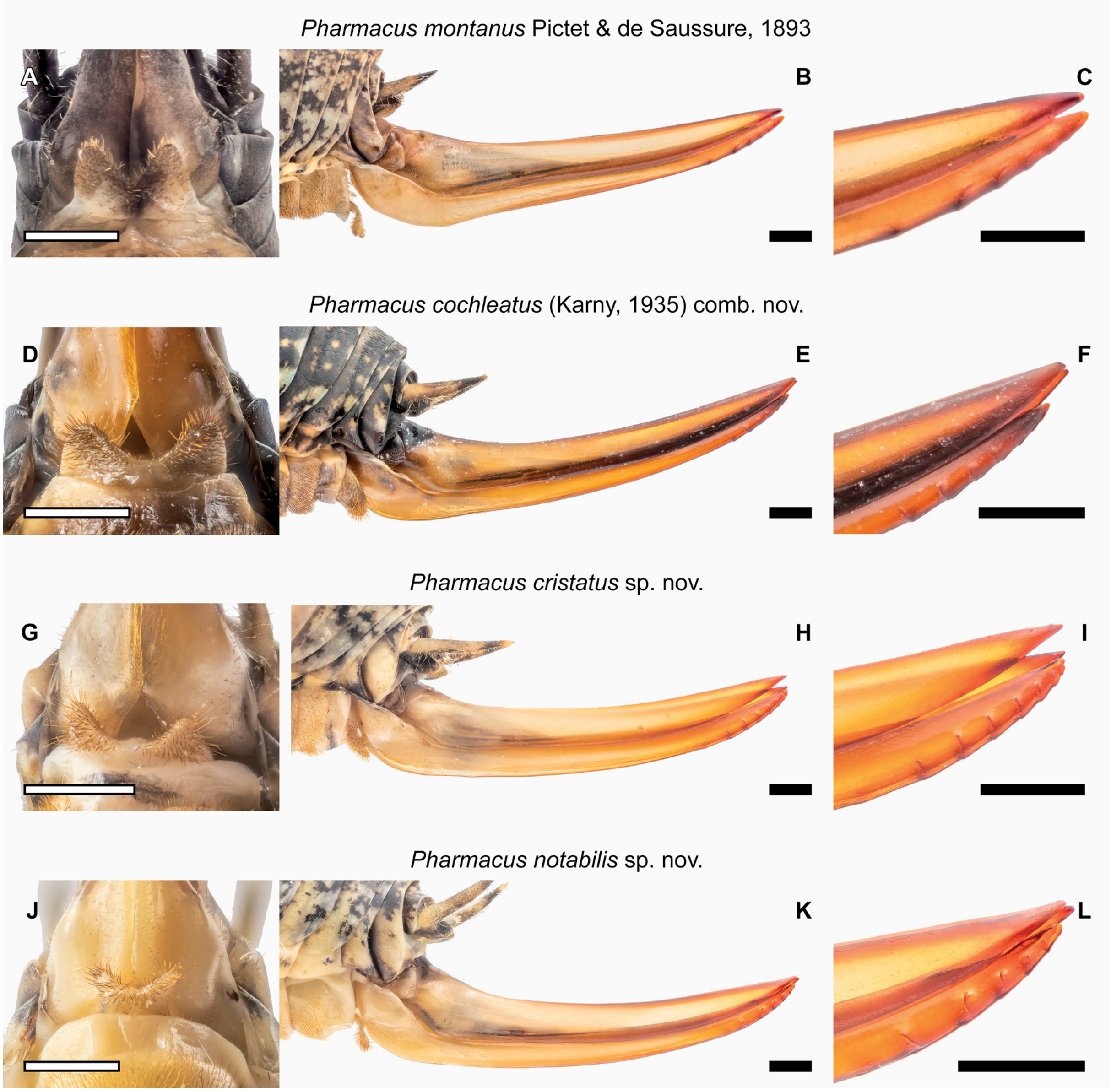

Fig. 12. Adult female terminalia of cave wētā in the genus *Pharmacus* Pictet & de Saussure, 1893. Left column: subgenital plate; central and right columns: ovipositor. **A**–**C**. *Pharmacus montanus* Pictet & de Saussure, 1893. **A**. Mt Annette, Sealy Range, Mt Cook (MPN CW3303). **B**–**C**. Mt Wakefield, Mount Cook Range (MPN CW3362). **D**–**F**. *Pharmacus cochleatus* (Karny, 1935) comb. nov., Lochnagar, Richardson Mountains (MPN CW4590). **G**–**I**. *Pharmacus cristatus* sp. nov., Skippers Range High Point, South Westland (NMNZ AI.052293). **J**–**L**. *Pharmacus notabilis* sp. nov., Two Mile Hut, Hector Mountains (NMNZ AI.052297). Scale bars = 1 mm.

CW4127 • 1 ♀; Humboldt Mountains; 44.74356° S, 168.21742° E; 1800 m a.s.l.; 8 Apr. 2017; D. Hegg leg.; on rock bluffs; night search; GenBank: OM293696; MPN CW3405 • 1 ♂; same collection data as for preceding; MPN CW3411.

Description

MEASUREMENTS. See Table 1.

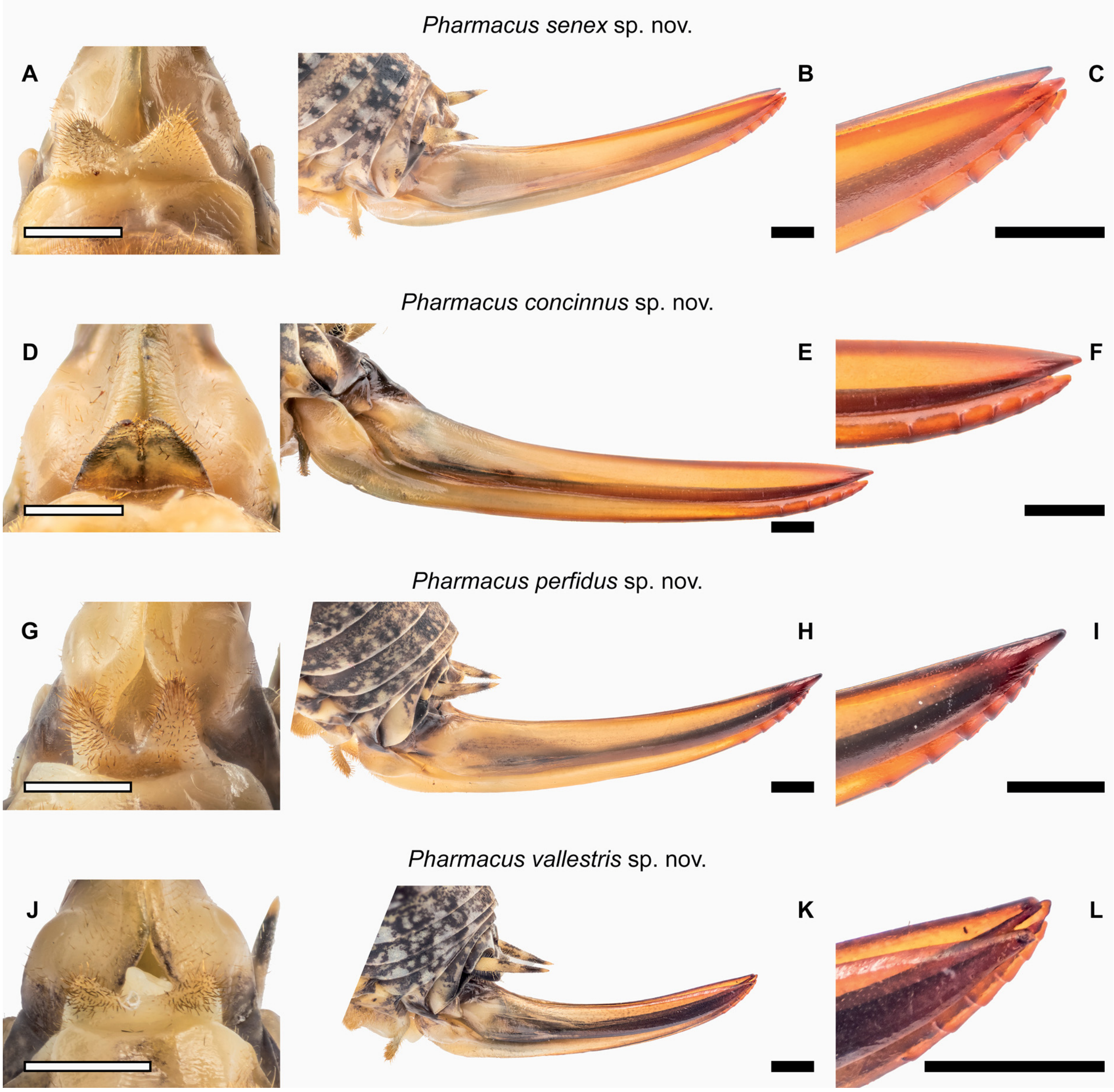

Fig. 13. Adult female terminalia of cave wētā in the genus *Pharmacus* Pictet & de Saussure, 1893. Left column: subgenital plate; central and right columns: ovipositor. **A–C**. *Pharmacus senex* sp. nov., Old Woman Range (NMNZ AI.052295). **D–F**. *Pharmacus concinnus* sp. nov., Symmetry Peaks, Eyre Mountains (NMNZ AI.052299). **G–I**. *Pharmacus perfidus* sp. nov., Spence Peak, Takitimu Mountains (NMNZ AI.052301). **J–L**. *Pharmacus vallestris* sp. nov., Matukituki River West Branch (NMNZ AI.052303). Scale bars = 1 mm.

Pharmacus cochleatus fiordensis subsp. nov. is morphologically almost identical to *Pharmacus cochleatus cochleatus* comb. nov. See the description for the latter. While *Pharmacus cochleatus fiordensis* subsp. nov. is a larger insect on average and tends to have a longer ovipositor in relation to body length, the overlap between the two subspecies' physical dimensions is such that measurements cannot be used to discriminate between them.

Pharmacus cochleatus rawhiti subsp. nov.

urn:lsid:zoobank.org:act:BE259438-D4DD-467F-BE72-27526E2D6B53

Figs 1–2, 6, 8E, 9C, 10F, 14E, 16D, 18B

Diagnosis

A mid-sized cave wētā found in the mountains either side of Lake Wakatipu and south of the Greenstone and Kawarau Rivers, at elevations greater than 1300 m. Body colour is chequered light brown/dark brown, with reddish legs and antennae. A prolateral apical spine is often present on the fore femur, and occasionally on the mid femur also. Hind legs longer than in *P. cochleatus cochleatus*.

The sympatric *Pharmacus notabilis* sp. nov. is mainly found at lower elevations and is easily identified by its turquoise/grey tergites, as well as its unique male terminalia. Two other species of Rhaphidophoridae share the habitat with *P. cochleatus rawhiti* subsp. nov., these are *Talitropsis chopardi* and *Macropathus* sp. . The former has shorter legs and fewer, larger spines on the hind tibiae, and unarmed hind tarsi; the latter has uniform brown colour and much longer legs, which give the insect a very slender appearance.

Etymology

'*Rāwhiti*' is Te Reo for 'eastern' – this subspecies inhabits mountain ranges east of the Southern Alps.

Unaware of the fact that it belongs to the same species as his 'black tumbling cave wētā', Crowe (2002) refers to this insect as 'Remarkables cave wētā'. We discourage the use of this common name, since there are at least four species of cave wētā found in The Remarkables, including two species of *Pharmacus*. The range of *Pharmacus cochleatus rawhiti* subsp. nov. extends well beyond The Remarkables, as far south as the Garvie and Umbrella Mountains, and west to the Livingstone Mountains.

Material examined (see also Supp. file 1: Table S5)

Holotype

NEW ZEALAND • ♂, adult; Central Otago (CO), Mt Tūwhakarōria, Hector Mountains; 45.12771° S, 168.82939° E; 2000 m a.s.l.; 25 Apr. 2019; D. Hegg leg.; on large boulder; night search + insect net; NMNZ AI.052290 (prev. MPN CW4429).

Paratype

NEW ZEALAND • 1 ♀, adult; Central Otago (CO), James Peak, Hector Mountains; 45.26417° S, 168.81555° E; 1600 m a.s.l.; 17 Feb. 2018; D. Hegg leg.; in cracks in rock tor; night search + insect net; NMNZ AI.052291 (prev. MPN CW3833).

Other material

NEW ZEALAND – **Central Otago (CO)** • 2 ♂♂; same collection data as for paratype; GenBank: OM293704, OM293706; MPN CW3769, CW3838 • 2 ♂♂, 3 ♀♀, 1 nymph; same collection data as for paratype; MPN CW3770, CW3832, CW3834 to CW3837 • 1 ♀; Gem Lake, Umbrella Mountains; 45.57097° S, 169.10525° E; 1300 m a.s.l.; 13 Apr. 2019; D. Hegg leg.; in boulder field; night search + insect net; GenBank OM293720; MPN CW4465 • 5 ♂♂, 1 ♀; same collection data as for preceding; MPN CW4466 to CW4471 • 1 ♀; Blue Lake Creek, Garvie Mountains; 45.46778° S, 168.95290° E ; 1280 m a.s.l.; 21 Apr. 2019; D. Hegg leg.; on rock tors; night search + insect net; GenBank: OM293719;

MPN CW4425 • 6 ♂♂, 3 ♀♀, 3 nymphs; same collection data as for preceding; MPN CW4424, CW4426, CW4427, CW4458 to CW4464, CW4510, CW4511 • 1 ♀; same collection data as for holotype; GenBank: OM293717; MPN CW4395 • 3 ♂♂, 1 ♀; same collection data as for holotype; MPN CW4396, CW4428, CW4430, CW4431 • 2 ♂♂, 1 ♀; Lake Alta, The Remarkables; 45.06176° S, 168.81096° E; 1820 m a.s.l.; 26 Mar. 2021; D. Hegg leg.; on large boulder; night search + insect net; MPN CW5219 to CW5221. – **Otago Lakes (OL)** • 1 nymph; Cerberus, Livingstone Mountains; 45.28570° S, 168.14069° E; 1460 m a.s.l.; 26 Jun. 2020; D. Hegg leg.; on rocky outcrop; night search; GenBank: OM293730; MPN CW4895 • 1 ♀; Mt Turnbull, Thomson Mountains; 45.13566° S, 168.32134° E; 1600 m a.s.l.; 15 Jan. 2021; D. Hegg leg.; on rock bluffs; night search + insect net; GenBank: OM293737; MPN CW5193 • 8 ♂♂, 2 ♀♀; same collection data as for preceding; MPN CW5184 to CW5192, CW5194.

Description

MEASUREMENTS. See Table 1.

HEAD. As per generic description. Eyes grey/green. Antennae red-brown.

THORAX. As per generic description.

LEGS. Longer than in *P. cochleatus cochleatus*; approx. same length as in *P. montanus*. The hind tibiae are on average 5% longer than body in females and 20% longer than body in males. Fore femora often armed with one prolateral spine at the apex. Mid femora always armed with one retrolateral spine and occasionally with one prolateral spine at the apex. The first hind tarsus segment is armed with a variable number of dorsal linear spines above.

ABDOMEN. Tergites sparsely tomentose. A thin, pale median line along the whole length of the insect may or may not be present. The colour of the tergites is mostly chequered light/dark red-brown or brown (Fig. 8E). Nymphs may be uniform brown.

MALE TERMINALIA. Same as in *P. cochleatus cochleatus*.

FEMALE TERMINALIA. Same as in *P. cochleatus cochleatus*. Ovipositor only marginally shorter.

Pharmacus cristatus sp. nov.

urn:lsid:zoobank.org:act:B9EEEC40-AB6E-4184-89BF-B78E086B4F6B
Figs 1–2, 6, 8F, 9D, 10G–I, 12G–I, 14F, 17D, 18C

Diagnosis

A mid-sized cave wētā found in the alpine regions of northern Fiordland and South Westland, at elevations greater than 1000 m. Body colour is chequered pale/brown, with variegated legs and brown antennae. A prolateral apical spine is always present on both fore and mid femora.

The species is sympatric with *P. cochleatus nauclerus* subsp. nov. in the Skippers Range (South Westland) and with *P. cochleatus fiordensis* subsp. nov. in Fiordland. Across its whole distribution range, it is also sympatric with *Notoplectron brewsterense* comb. nov. It is differentiated from all of these taxa by the presence of prolateral apical spines on fore and mid femora.

Etymology

'*Cristātus*' is Latin for 'tufted'. Named after the prominent hair tufts on the vertex of the male subgenital plate (Fig. 10G–H).

Fig. 14. Live *Pharmacus* Pictet & de Saussure, 1893 in their natural environments. **A–B**. *Pharmacus montanus* Pictet & de Saussure, 1893. **A**. Adult ♂, with dark coloration typical of high elevation specimens. Mt Annette, Sealy Range, Mt Cook, 2200 m a.s.l. (MPN CW3302). **B**. Adult ♂, with coloration typical of low elevation specimens. Mueller Hut Track, Sealy Range, Mt Cook, 1500 m a.s.l. **C–D**. *Pharmacus cochleatus cochleatus* (Karny, 1935) comb. nov. **C**. Adult ♀, with yellow / black chequered coloration that is most typical for the species, parasitized by red mites (Order Trombidiformes). Luna Basin, Major Peak, Wakatipu, 1470 m a.s.l. **D**. Adult ♂, with dark coloration typical of high elevation specimens. Mt Edgar Thomson, Ben Ōhau Range, 2350 m a.s.l. (MPN CW3278). **E**. *Pharmacus cochleatus rawhiti* subsp. nov. Adult ♂, Blue Lake Creek, Garvie Mountains, 1280 m a.s.l. **F**. *Pharmacus cristatus* sp. nov. Adult ♀, Skippers Range High Point, South Westland, 1520 m a.s.l.

Fig. 15. Live *Pharmacus* Pictet & de Saussure, 1893 in their natural environments. **A–B**. *Pharmacus senex* sp. nov. **A**. Adult ♂, Dunstan, Dunstan Mountains, 1670 m a.s.l. **B**. Adult ♂ and ♀. The Obelisk, Old Man Range, 1680 m a.s.l. **C**. *Pharmacus notabilis* sp. nov. Adult ♂, Remarkables Ski-field Access Road, Wakatipu, 1200 m a.s.l. **D**. *Pharmacus concinnus* sp. nov. Adult ♂, Symmetry Peaks, Eyre Mountains, 1500 m a.s.l. **E**. *Pharmacus perfidus* sp. nov. Adult ♀ and ♂, Spence Peak, Takitimu Mountains, 1450 m a.s.l. **F**. *Pharmacus vallestris* sp. nov. Adult ♀, French Ridge, Matukituki River West Branch, 1700 m a.s.l. (MPN CW5145).

Material examined (see also Supp. file 1: Table S6)

Holotype

NEW ZEALAND • ♂, adult; Westland (WD), Skippers Range High Point; 44.43914° S, 168.16515° E; 1520 m a.s.l.; 3 Feb. 2019; D. Hegg leg.; on rock bluffs; night search; NMNZ AI.052292 (prev. MPN CW4561).

Paratype

NEW ZEALAND • 1 ♀, adult; same collection data as for holotype; NMNZ AI.052293 (prev. MPN CW4486).

Other material

NEW ZEALAND – **Fiordland (FD)** • 2 ♂♂; Homer Saddle, Darran Mountains; 44.760° S, 167.983° E; 1200 m a.s.l.; Jan. 2014; T. Jewell leg.; in dry cracks in rock bluff; hand collected, in daylight; GenBank: OM293684, OM293685; MPN CW2607, CW2610 • 1 ♀, 1 nymph; same collection data as for preceding; MPN CW2608, CW2609 • 1 nymph; Gertrude Saddle, Darran Mountains; 44.74521° S, 168.01649° E; 1300 m a.s.l.; 25 Mar. 2017; D. Hegg leg.; on rock bluffs; night search; GenBank: OM293698; MPN CW3415A • 2 ♂♂, 2 nymphs; same collection data as for preceding; MPN CW3398, CW3399, CW3414, CW3415B • 1 ♂; Mistake Creek, Earl Mountains; 44.85123° S, 168.02471° E; 1000 m a.s.l.; 21 Apr. 2017; D. Hegg leg.; under boulder; night search; GenBank: OM293700; MPN CW3431. – **Westland (WD)** • 1 ♀; same collection data as for holotype; GenBank: OM293723; MPN CW4485 • 1 ♂, 1 ♀, 2 nymphs; same collection data as for holotype; MPN CW4365, CW4376, CW4484, CW4562 • 1 ♂; Skippers Range; 44.46821° S, 168.10095° E; 1200 m a.s.l.; 6 Feb. 2019; D. Hegg leg.; on rock bluffs; night search; GenBank: OM293725; MPN CW4563 • 1 nymph; Skippers Range; 44.50459° S, 168.12086° E; 1400 m a.s.l.; 7 Feb. 2019; D. Hegg leg.; on rock bluffs; night search; GenBank: OM293712; MPN CW4364.

Description

MEASUREMENTS. See Table 1.

HEAD. As per generic description. Eyes grey/brown. Antennae brown.

THORAX. As per generic description.

LEGS. Relative to the body, longer than in any other *Pharmacus* species. The hind tibiae are on average 15% to 20% (max. 45%) longer than the body in both males and females. Fore and mid femora always armed at the apex with a prolateral spine, in addition to the retrolateral apical spine on the mid femur. The first hind tarsus segment is armed with a variable number of dorsal linear spines.

ABDOMEN. Tergites sparsely tomentose. A thin, pale median line along the whole length of the insect may or may not be present. The colour of the tergites is mostly chequered pale/brown (Fig. 8F).

MALE TERMINALIA. Subgenital plate similar to *P. cochleatus*, but shorter and bent upwards. Moderately hairy underneath, with two characteristic hair tufts on the spoon's vertex, both dorsal and ventral (Fig. 10G–I).

FEMALE TERMINALIA. Very similar to *P. cochleatus*. Subgenital plate bilobed, the two rounded lobes short, broad, and asymmetrical, with a wide gap in between; very hairy (Fig. 12G). Ovipositor on average 70% of body length, only very gently curving upwards; lower valve with 5 to 9 strong teeth below at the apex (Fig. 12H–I).

Pharmacus notabilis sp. nov.

urn:lsid:zoobank.org:act:C181B24B-F2EC-4E23-87C8-C795AA133604
Figs 1–2, 6, 8H, 9E, 10J–L, 12J–L, 15C, 16D, 18D

Diagnosis

A mid-sized cave wētā found in the low alpine regions of The Remarkables and Hector Mountains, east of Lake Wakatipu, at elevations between 1200 m and 1600 m. Body colour is chequered turquois/grey and eye colour is blue/grey. A prolateral apical spine on the fore femur is always present in males, occasionally in females.

The sympatric *Pharmacus cochleatus rawhiti* subsp. nov. is mainly found at higher elevations and is easily differentiated by its brown tergites and reddish legs and antennae. Two other species of Rhaphidophoridae share the habitat with *P. notabilis* sp. nov., these are *Talitropsis chopardi* and *Macropathus* sp. . The former has shorter legs and fewer, larger spines on the hind tibiae, and unarmed hind tarsi; the latter has uniform brown colour and much longer legs, which give the insect a very slender appearance.

Etymology

'*Nŏtābĭlis*' is Latin for 'remarkable', after the location where the species was first discovered, The Remarkables near Queenstown. *Pharmacus notabilis* means 'remarkable sorcerer'.

Material examined (see also Supp. file 1: Table S7)

Holotype

NEW ZEALAND • ♂, adult; Central Otago (CO), Remarkables Ski-field Access Road; 45.02651° S, 168.79748° E; 1220 m a.s.l.; 12 May 2017; D. Hegg leg.; under boulders in road escarpment; night search + insect net; NMNZ AI.052296 (prev. MPN CW3528).

Paratype

NEW ZEALAND • 1 ♀, adult; Central Otago (CO), Two Mile Hut, Hector Mountains; 45.17392° S, 168.80270° E; 1460 m a.s.l.; 26 Apr. 2019; D. Hegg leg.; on large boulders; night search + insect net; NMNZ AI.052297 (prev. MPN CW4394).

Other material

NEW ZEALAND – **Central Otago (CO)** • 2 ♂♂; Remarkables North ridge; 45.0413° S, 168.7977° E; 1600 m a.s.l.; Jan. 2013; T. Jewell leg.; in cracks in rock bluffs; GenBank: OM293682, OM293683; MPN CW2587, CW2589 • 1 ♂, 5 ♀♀; same collection data as for preceding; MPN CW2588, CW2590 to CW2594 • 1 ♀; same collection data as for holotype; GenBank: OM293701; MPN CW3509 • 3 ♂♂, 3 ♀♀, 5 nymphs; same collection data as for holotype; MPN CW3510 to CW3513, CW3524 to CW3527, CW3529 to CW3531 • 1 ♂; same collection data as for paratype; GenBank: OM293716; MPN CW4391 • 2 ♂♂, 1 nymph; same collection data as for paratype; MPN CW4392, CW4393, CW4500.

Description

Measurements. See Table 1.

Head. As per generic description. Eyes grey/blue. Antennae brown.

Thorax. As per generic description.

Legs. The hind tibiae are approx. 10% Shorter than the body in females, equally long as body in males. Fore femora always armed at the apex with one prolateral spine in males, occasionally also in females. Mid femora armed with one retrolateral spine at the apex; prolateral apical spine absent. The first hind tarsus segment is armed with a variable number of linear spines above (up to eight); the second hind tarsus segment is only rarely armed with dorsal linear spines.

ABDOMEN. Tergites glabrous or sparsely tomentose (Fig. 8H), coloured chequered brown in nymphs, chequered turquois/grey in adults (Fig. 15C). A thin, pale median line along the whole length of the insect is generally present.

MALE TERMINALIA. Subgenital plate unmistakeable, elongated, the vertex of the spoon acuminate, shallow when seen from the side (Fig. 10J–L).

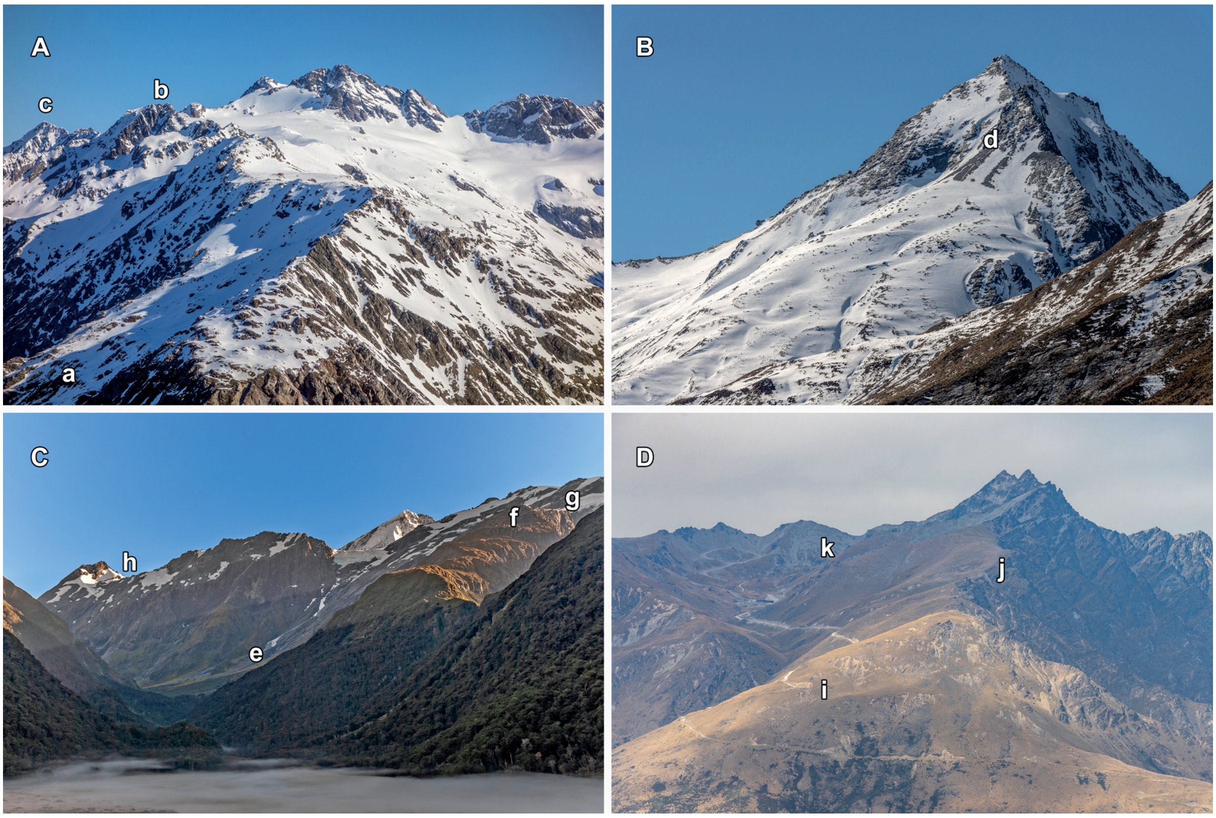

Fig. 16. Habitat of *Pharmacus* Pictet & de Saussure, 1893. **A**. Sealy Range, Mount Cook. **a–b**. Collection localities of *Pharmacus montanus* Pictet & de Saussure, 1893. **a**. Mueller Hut Track, 1500 m a.s.l. (MPN CW3299, CW3300, CW3532–3535). **b**. Mount Annette, 2200 m a.s.l. (MPN CW3302, CW3303, CW3323). **c**. Mount Edgar Thomson, Ben Ohau Range, 2350 m a.s.l., collection locality of *P. cochleatus cochleatus* (Karny, 1935) comb. nov. (MPN CW3278). **B**. Lochnagar, Richardson Mountains. **d**. Rock bluffs at 2080 m a.s.l., collection locality of *P. cochleatus cochleatus* (Karny, 1935) comb. nov. (MPN CW4590). **C**. Matukituki River West Branch. **e–f**. Collection localities of *P. vallestris* sp. nov. **e**. Valley floor, dry creek bed at 1000 m a.s.l. (MPN CW3430, CW3700). **f**. French Ridge, 1650 m a.s.l. (MPN CW5145, CW5146, CW5213–5215). **g–h**. Collection localities of *P. cochleatus cochleatus* (Karny, 1935) comb. nov. **g**. French Ridge, 1800 m a.s.l. (MPN CW5207, CW5208). **h**. Bevan Col, 1850 m a.s.l. (OMNZ IV7927 and MPN CW5178 to 5180). **D**. The Remarkables, Queenstown. **i–j**. Collection localities of *Pharmacus notabilis* sp. nov. **i**. Remarkables Ski-field Access Road, 1220 m a.s.l. (NMNZ AI.052296). **j**. The Remarkables North ridge, 1600 m a.s.l. (MPN CW2588 – 2594). **k**. Lake Alta, 1820 m a.s.l., collection locality of *Pharmacus cochleatus rawhiti* subsp. nov. (MPN CW5219 – 5221).

Female terminalia. Subgenital plate small, narrow at the base and widening at the vertex, bilobed, the two rounded, narrow lobes very hairy (Fig. 12J). Ovipositor relatively short, on average 60% of body length, gently curving upwards; lower valve with 5 to 7 teeth below at the apex (Fig. 12K–L).

Pharmacus senex sp. nov.

urn:lsid:zoobank.org:act:0F63FF1F-2CC1-4920-816F-1AA57AB7B907
Figs 1–2, 6, 8C, 9F, 11A–C, 13A–C, 15A–B, 17B, 18E

Diagnosis

A mid-sized cave wētā known only from the rock tors on the wind-swept tops of the Old Man, Old Woman and Dunstan Ranges in Central Otago. Typical of *Pharmacus* in its habitus, it is differentiated from all other species by its short hind legs. It does not share the habitat with any other Rhaphidophoridae that we are aware of.

Fig. 17. Habitat of *Pharmacus* Pictet & de Saussure, 1893. **A**. Mount Dick, Eyre Mountains. **a**. Rock bluffs at 1550 m a.s.l., collection locality of *Pharmacus concinnus* sp. nov. (MPN CW4472–4475, CW4501–4504, CW4592, CW4593). **B**. Dunstan, Dunstan Mountains. **b**. Rock tors at 1670 m a.s.l. collection locality of *P. senex* sp. nov. (MPN CW4381–4385, CW4402–4405, CW4506–4509). **C**. Spence Peak, Takitimu Mountains. **c**. North ridge, 1450 m a.s.l., collection locality of *P. perfidus* sp. nov. (NMNZ AI.052300, AI.052301; MPN CW4487, CW4489, CW4490, CW4494–4496, CW4498, CW4499, CW4553–4555). **D**. Skippers Range High Point, South Westland. **d–e**. Scree and rock bluffs around lake, 1600 m a.s.l., collection locality of *P. cochleatus nauclerus* subsp. nov. (NMNZ AI.052289, MPN CW4363) and of *P. cristatus* sp. nov. (NMNZ AI.052292, AI.052293; MPN CW4365, CW4376, CW4484, CW4485, CW4562).

Etymology

'*Senex*' is Latin for 'old' (of a person), after the Old Man and Old Woman Ranges in Central Otago. *Pharmacus senex* means 'old sorcerer'.

Material examined (see also Supp. file 1: Table S8)

Holotype

NEW ZEALAND • ♂, adult; Central Otago (CO), Near Obelisk, Old Man Range; 45.32567° S, 169.20826° E; 1680 m a.s.l.; 1 Dec. 2017; D. Hegg leg.; cracks in rock tors; night search + insect net; NMNZ AI.052294 (prev. MPN CW3867).

Paratype

NEW ZEALAND • 1 ♀, adult; Central Otago (CO), Old Woman Range; 45.23048° S, 169.05058° E; 1630 m a.s.l.; 3 May 2019; D. Hegg leg.; cracks in rock tors; night search + insect net; NMNZ AI.052295 (prev. MPN CW4408).

Other material

NEW ZEALAND – **Central Otago (CO)** • 1 ♀; Near Obelisk, Old Man Range; 45.334° S, 169.210° E; 1650 m a.s.l.; Jan. 2013; T. Jewell leg.; in cracks in rock bluffs; GenBank: OM293680; MPN CW2580 • 1 ♂; same collection data as for preceding; GenBank: OM293681; MPN CW2582 • 1 ♂, 1 ♀; same collection data as for preceding; MPN CW2581, CW2583 • 1 ♀; The Obelisk, Old Man Range; 45.323° S, 169.207° E; 1680 m a.s.l.; 21 Jan. 2014; S. Trewick leg.; in cracks in rock bluffs; GenBank: OM293676; MPN CW279 • 1 ♂; same collection data as for preceding; GenBank: OM293677; MPN CW284B • 1 ♀; same collection data as for preceding; GenBank: OM293678; MPN CW285 • 1 ♂, 2 ♀♀, 1 nymph; same collection data as for preceding; MPN CW278A, CW278B, CW280, CW284A • 8 ♂♂, 7 ♀♀, 4 nymphs; same collection data as for holotype; MPN CW3860 to CW3866, CW3868 to CW3879 • 1 ♂; same collection data as for paratype; GenBank: OM293715; MPN CW4389 • 4 ♂♂, 3 ♀♀, 3 nymphs; same collection data as for paratype; MPN CW4386 to CW4388, CW4390, CW4406, CW4407, CW4409, CW4491 to CW4493 • 1 ♂; Dunstan, Dunstan Mountains; 45.04471° S, 169.37418° E; 1670 m a.s.l.; 10 May 2019; D. Hegg leg.; in cracks in rock bluffs; night search + insect net; GenBank: OM293714; MPN CW4382 • 4 ♂♂, 4 ♀♀, 4 nymphs; same collection data as for preceding; MPN CW4381, CW4383 to CW4385, CW4402 to CW4405, CW4506 to CW4509.

Description

Measurements. See Table 1.

Head. As per generic description. Eyes grey or brown. Antennae brown.

Thorax. As per generic description.

Legs. All legs coloured a variegated reddish brown in adults, dull in nymphs. Hind tibiae approx. three quarters of body length in females; just over 80% of body length in males. This makes the hind legs of *P. senex* the shortest (proportionally to body size) in all *Pharmacus* species (Fig. 9F). Fore femora generally unarmed at the apex. One specimen (female) out of 29 examined had a prolateral spine at the apex of the fore femur. Mid femora armed with one retrolateral spine at the apex; prolateral apical spine absent. The first hind tarsus segment is armed with a variable number of linear spines above (up to seven); the second hind tarsus segment is only rarely armed with dorsal linear spines.

Abdomen. Tergites glabrous or sparsely tomentose, coloured chequered a vibrant yellow/brown in adults (Fig. 15A–B), dull brown in nymphs. A thin, pale median line along the whole length of the insect is generally present.

Male terminalia. Subgenital plate deep like in *P. montanus* when seen from the side, but not covered by a membrane in the distal half; square-ended and hairy at the vertex. Styli long, reaching almost to the end of the subgenital plate (Fig. 11A–C).

Female terminalia. Subgenital plate bilobed and wide, similar to the one in *P. cochleatus* comb. nov. (Fig. 13A). Ovipositor on average 70% of body length, nearly straight; lower valve with 5 to 7 teeth below at the apex (Fig. 13B–C).

Pharmacus concinnus sp. nov.

urn:lsid:zoobank.org:act:2582DF14-FB0D-4F8B-A393-6F731907EB8B
Figs 1–2, 6, 8I, 9G, 11D–F, 13D–F, 15D, 17A, 18F

Diagnosis

A mid-sized cave wētā known only from the alpine regions of the Eyre Mountains south of Lake Wakatipu; it is the largest of all *Pharmacus* species. Body colour is dark, nearly black.

It shares the habitat with *Talitropsis chopardi* and *Macropathus* sp. The former has lighter colour, shorter legs and fewer, larger spines on the hind tibiae, and unarmed hind tarsi; the latter has uniform brown colour and much longer legs, which give the insect a very slender appearance.

The species cannot be reliably differentiated from *Pharmacus cochleatus* comb. nov. without an examination of the terminalia. The two species however are not sympatric.

Etymology

'*Concīnnus*' is Latin for 'pleasing', 'elegant', also 'symmetrical', after the Symmetry Peaks in the Eyre Mountains where it was first discovered. *Pharmacus concinnus* means 'elegant sorcerer'.

Material examined (see also Supp. file 1: Table S9)

Holotype

NEW ZEALAND • ♂, adult; Otago Lakes (OL), Symmetry Peaks, Eyre Mountains; 45.27797° S, 168.59113° E; 1500 m a.s.l.; 12 May 2018; D. Hegg leg.; on rock tor; night search + insect net; NMNZ AI.052298 (prev. MPN CW3853).

Paratype

NEW ZEALAND • 1 ♀, adult; same collection data as for holotype; NMNZ AI.052299 (prev. MPN CW3843).

Other material

NEW ZEALAND – **Otago Lakes (OL)** • 1 nymph; same collection data as for holotype; GenBank: OM293707; MPN CW4023A • 1 ♂, 1 ♀, 4 nymphs; same collection data as for holotype; MPN CW3842, CW3852, CW4023B to CW4023E • 1 ♀; Eyre Peak, Eyre Mountains; 45.33260° S, 168.47225° E; 1500 m a.s.l.; 16 Feb. 2019; D. Hegg leg.; on rock bluffs; night search + insect net; GenBank: OM293722; MPN CW4477 • 4 ♂♂, 3 ♀♀, 1 nymph; same collection data as for preceding; MPN CW4367, CW4476, CW4478 to CW4483 • 1 ♀; Mt Dick, Eyre Mountains; 45.26572° S, 168.69083° E; 1550 m a.s.l.; 16 Mar. 2019; D. Hegg leg.; on rock bluffs; night search + insect net; GenBank: OM293721; MPN CW4472 • 4 ♂♂, 3 ♀♀, 2 nymphs; same collection data as for preceding; MPN CW4473 to CW4475, CW4501 to CW4504, CW4592, CW4593 • 1 ♀; Billy Creek, Eyre Mountains; 45.30540° S, 168.45460° E; 1400 m a.s.l.; 23 Feb. 2020; M. Thorsen leg.; on rock bluffs; casual find; GenBank: OM293727; MPN CW4874 • 1 ♀; same collection data as for preceding; MPN CW4873.

Description

Measurements. See Table 1.

Head. As per generic description. Eyes grey or brown. Antennae brown or black.

Thorax. As per generic description.

Legs. Variegated colour, occasionally dark or almost black; hind tibiae black above. Hind tibiae approximately as long as body, or just under, in both males and females. Fore femora armed with one prolateral spine at the apex in four out of twelve females and one out of ten males examined. Mid femora armed with one retrolateral spine at the apex; prolateral apical spine absent. The first hind tarsus segment is armed with a variable number of linear spines above (up to ten); the second hind tarsus segment is only rarely armed with dorsal linear spines.

Abdomen. Tergites glabrous or sparsely tomentose; colour chequered yellow/black in adults (Fig. 15D), the black being predominant and giving the insect a dark look. A thin, pale median line along the whole length of the insect is generally present.

Male terminalia. Subgenital plate deep when seen from the side; shaped like a spoon when seen from above, broader at the vertex and less constricted at the neck compared to the subgenital plate of *Pharmacus cochleatus* comb. nov. Paraprocts large and swollen, bristled on the inside, glabrous on the outside (Fig. 11D–F).

Female terminalia. Subgenital plate bilobed, the incision between the two lobes sutured (Fig. 13D), a trait not found in any other *Pharmacus* species. Ovipositor long and straight, just under three quarters of body length; lower valve with 6 to 8 teeth below at the apex (Fig. 13E–F).

Pharmacus perfidus sp. nov.

urn:lsid:zoobank.org:act:9AB3A946-049F-42B6-8EBE-D57ED33CB3E0
Figs 1–2, 6, 8J, 9H, 11G–I, 13G–I, 15E, 17C, 18G

Diagnosis

A mid-sized cave wētā known only from the alpine regions of the Takitimu Mountains in Southland. It is among the smallest of all *Pharmacus* species. Body colour is brown, with a distinctive dark brown or black frons.

The species shares the habitat with *Talitropsis chopardi*. The latter is larger, has fewer, larger spines on the hind tibiae, has unarmed hind tarsi, and generally shows a prominent dorsal yellow stripe or diamond on the abdomen in the Takitimu Mountains population.

Etymology

'*Perfidus*' (noun) is Latin for 'criminal', 'crook'. *Pharmacus perfidus* means 'criminal sorcerer'. Try scrambling on the jagged, crumbly ridgelines of the Takitimu Mountains at night and you will know why. It is also banished to an isolated mountain range, a great distance away from all other *Pharmacus* species (see Fig. 6).

Material examined (see also Supp. file 1: Table S10)

Holotype

NEW ZEALAND • ♂, adult; Southland (SL), Spence Peak, Takitimu Mountains; 45.70540° S, 167.85058° E; 1450 m a.s.l.; 30 Mar. 2019; D. Hegg leg.; on rocky ridge; night search + insect net; NMNZ AI.052300 (prev. MPN CW4497).

Paratype

NEW ZEALAND • 1 ♀, adult; same collection data as for holotype; NMNZ AI.052301 (prev. MPN CW4488).

Other material

NEW ZEALAND – **Southland (SL)** • 1 ♀; same collection data as for holotype; GenBank: OM293724; MPN CW4490 • 5 ♂♂, 2 ♀♀, 3 nymphs; same collection data as for holotype; MPN CW4487, CW4489, CW4494 to CW4496, CW4498, CW4499, CW4553 to CW4555 • 1 ♀; Clare Peak, Takitimu Mountains; 45.63303° S, 167.94057° E; 1300 m a.s.l.; 23 May 2020; D. Hegg leg.; on rock bluffs; night search + insect net; GenBank: OM293729; MPN CW4877 • 3 ♂♂, 1 nymph; same collection data as for preceding; MPN CW4878 to CW4881 • 1 ♂ [dead]; Clare Peak, Takitimu Mountains; 45.63516° S, 167.91564° E; 1340 m a.s.l.; 6 Jun. 2021; D. Hegg leg.; on snow slope; casual find while climbing; MPN CW5257.

Description

MEASUREMENTS. See Table 1.

HEAD. As per generic description. Eyes grey/brown. Antennae brown. Frons dark brown or black; darker than body.

THORAX. As per generic description.

LEGS. Variegated colour, mostly brown; hind tibiae dark above. Hind tibiae approximately as long as body in males, 10% shorter than body in females. Fore femora armed with one prolateral spine at the apex in four out of five females and seven out of nine males examined. Mid femora armed with one retrolateral spine at the apex; prolateral apical spine absent. The first hind tarsus segment is armed with a variable number of linear spines above (up to seven); the second hind tarsus segment is only rarely armed with dorsal linear spines.

ABDOMEN. Tergites tomentose; colour chequered light/dark brown (Figs 8J, 15E). A thin, pale median line along the whole length of the insect is generally present.

MALE TERMINALIA. Nearly identical to the male terminalia of *Pharmacus concinnus* sp. nov. Subgenital plate deep when seen from the side; shaped like a spoon when seen from above, broader at the vertex and less constricted at the neck compared to the subgenital plate of *Pharmacus cochleatus* comb. nov. Paraprocts large and swollen, bristled on the inside, glabrous on the outside (Fig. 11G–I).

FEMALE TERMINALIA. Subgenital plate bilobed, the two lobes narrow and elongated (Fig. 13G), very similar to the subgenital plate of *Pharmacus montanus*. Ovipositor longer in proportion to body size than in any other *Pharmacus* species; approximately 80% of body length; lower valve with 6 to 8 teeth below at the apex (Fig. 13H–I).

Pharmacus vallestris sp. nov.

urn:lsid:zoobank.org:act:FDF85976-EE24-4948-B4F1-FFCC3A7E6D89

Figs 1–2, 6, 8G, 9I, 11J–L, 13J–L, 15F, 16C, 18H

Diagnosis

A mid-sized cave wētā known only from the low to mid alpine regions at the foot of Mount Aspiring in the Southern Alps. It is one of the smaller *Pharmacus* species. Body colour is chequered brown. The fore femur is always armed with a prolateral apical spine.

The species is sympatric with *Notoplectron brewsterense* comb. nov. and with *Pharmacus cochleatus cochleatus* comb. nov., although it occupies lower elevations compared to the latter. *Notoplectron* *brewsterense* has fewer, larger spines on the hind tibiae and has unarmed hind tarsi. *Pharmacus cochleatus cochleatus* is larger, has darker colour, and lacks the prolateral apical spine on the fore femur.

Etymology

'*Vallestris*' is Latin for 'of the valley'. In contrast to sympatric species that inhabit the mountain tops.

Material examined (see also Supp. file 1: Table S11)

Holotype

NEW ZEALAND • ♂, adult; Otago Lakes (OL), French Ridge, Matukituki Valley; 44.42560° S, 168.69784° E; 1650 m a.s.l.; 20 Feb. 2021; D. Hegg leg.; on rocky ridge; night search + insect net; NMNZ AI.052302 (prev. MPN CW5214).

Paratype

NEW ZEALAND • 1 ♀, adult; Otago Lakes (OL), Matukituki River West Branch; 44.41637° S, 168.69130° E; 1100 m a.s.l.; 6 May 2017; D Hegg leg.; under boulder; night search; GenBank: OM293699; NMNZ AI.052303 (prev. MPN CW3430).

Other material

NEW ZEALAND – **Otago Lakes (OL)** • 1 ♂; same collection data as for paratype; GenBank: OM293703; MPN CW3700 • 1 ♀, 1 nymph; French Ridge, Matukituki Valley; 44.42520° S, 168.69871° E; 1700 m a.s.l.; 22 Nov. 2020; D. Hegg leg.; on rocky ridge; night search + insect net; MPN CW5145, CW5146 • 1 ♂, 1 ♀; same collection data as for holotype; MPN CW5213, CW5215.

Description

MEASUREMENTS. See Table 1.

HEAD. As per generic description. Eyes brown/black. Antennae brown.

THORAX. As per generic description.

LEGS. Variegated colour, mostly brown. Hind tibiae of equal length as body or longer in both males and females. Fore femora armed with one prolateral spine at the apex. Mid femora armed with one retrolateral spine at the apex; prolateral apical spine absent. The first hind tarsus segment is armed with a variable number of linear spines above (up to seven); the second hind tarsus segment is only rarely armed with dorsal linear spines.

ABDOMEN. Tergites tomentose; colour chequered light/dark brown (Figs 8G, 15F). A thin, pale median line along the whole length of the insect is generally present.

MALE TERMINALIA. Subgenital plate roughly in the shape of a French wine cask, similar to but shorter than in *Pharmacus cochleatus* comb. nov.; very thin and translucent; the paraprocts visible through the subgenital plate from underneath (Fig. 11J–L).

FEMALE TERMINALIA. Subgenital plate bilobed, the two rounded lobes short, broad, and asymmetrical, with a wide gap in between (Fig. 13J); very similar to the subgenital plate of *Pharmacus cochleatus* comb. nov. Ovipositor relatively short and curved upwards; on average 65% of body length; lower valve with 6 teeth below at the apex (Fig. 13K–L).

Discussion

Habitat and distribution

Rhaphidophorids in the genus *Pharmacus* are true alpine specialists. They are only found above the tree line, at elevations of 1300 m a.s.l. or higher and well into the nival zone. Our lowest record of *Pharmacus* is a male *P. cristatus* sp. nov. collected at 1000 m a.s.l. at the head of Mistake Creek, Earl Mountains (44.851° S, 168.025° E). This is a south facing valley where snow persists well into summer, in perennial shade at the toe of the imposing face of Pyramid Peak. Tree line is 3 km down the valley at 750 m of elevation. Our highest record of *Pharmacus* is a male *P. cochleatus* comb. nov. collected at 2350 m a.s.l. near the summit of Mt Edgar Thomson, Ben Ōhau Range (43.782° S, 170.056° E). Sweney (1980) however recorded a population of *Pharmacus montanus* at an elevation between 2700 m and 2800 m a.s.l. on the north face of Mt Annan above the Tasman Glacier (43.527° S, 170.348° E),

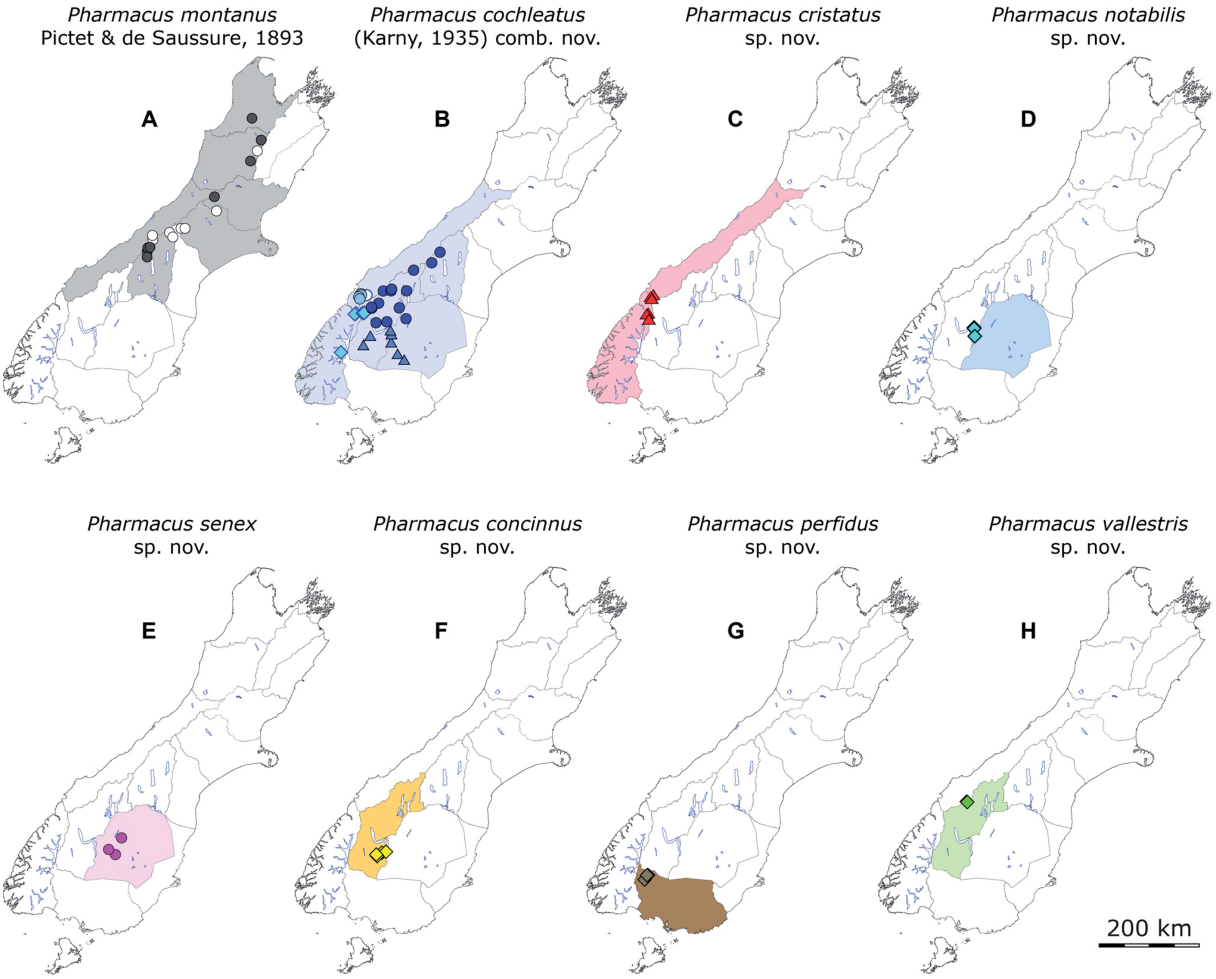

Fig. 18. Map of South Island, New Zealand, showing the known distribution of cave wētā in the genus *Pharmacus* Pictet & de Saussure, 1893. **A–B**. Solid shapes indicate material collected as part of this study; empty circles indicate additional locations of material examined by Richards (1972). **B**. Shapes represent different subspecies: dark blue circle = *Pharmacus cochleatus cochleatus*; light blue circle = *Pharmacus cochleatus nauclerus* subsp. nov.; diamond = *Pharmacus cochleatus fiordensis* subsp. nov.; triangle = *Pharmacus cochleatus rawhiti* subsp. nov.

and a nymph of *P. montanus* at 3400 m a.s.l. on the west ridge of the Low Peak of Aoraki/Mt Cook (43.608° S, 170.136° E).

The genus *Pharmacus* is endemic to the South Island of New Zealand. *Pharmacus montanus* and *P. cochleatus* are the two most widespread species, occupying the length of the Southern Alps from Fiordland to Kahurangi National Park between them. *Pharmacus cochleatus* is found in the south from Fiordland to Aoraki/Mt Cook, while *P. montanus* is found in the northern half of the Southern Alps from Aoraki/Mt Cook to Mt Owen in Kahurangi National Park. Our southern-most specimen of *P. montanus* was collected on Mt Dark in the Ben Ōhau Range (43.871° S, 170.045° E), whereas our northern-most specimen of *P. cochleatus* is from Mt Edgar Thomson (43.778° S, 170.064° E), also in the Ben Ōhau Range, 12 km north of Mt Dark. These locations pin-point a narrow region just south of Aoraki/Mt Cook where the two species overlap (Fig. 1B). A similar geographical and phylogenetic divide either side of the Mt Cook region had been previously documented for numerous alpine birds and insects (Weston & Robertson 2015; Wallis *et al*. 2016) and is attributed to extensive glacial ice during the Early Pleistocene glaciation 1.8 million years ago (Wallis *et al*. 2016). This barrier might also have separated *Pharmacus montanus* and *Pharmacus cochleatus* 2 Ma ago.

Additional genetic and morphological differentiation has occurred within *Pharmacus cochleatus* in the southern regions, justifying the recognition of four subspecies. The divide between *Pharmacus cochleatus cochleatus* and *Pharmacus cochleatus fiordensis* subsp. nov. follows a line along the major glacial axis of the Dart River and Lake Wakatipu. *Pharmacus cochleatus rawhiti* subsp. nov. spans Lake Wakatipu and is delimited by the low-lying Greenstone and Eglinton Rivers to the north and west, and by the Kawarau River to the north and east. *Pharmacus cochleatus nauclerus* subsp. nov. appears to be endemic to the Skippers Range in South Westland, a true alpine island surrounded by land entirely below 50 m a.s.l. The lack of mtDNA COI sequence differentiation between *Pharmacus cochleatus fiordensis* and *Pharmacus cochleatus rawhiti* may be explained by recent connectivity of the populations on either side of the Greenstone River. However, it is not uncommon for mtDNA (DNA barcoding) to be unable to discriminate recently divergent lineages due to incomplete lineage sorting or hybridisation (e.g., polar bears – Liu *et al*. 2014; bison – Wang *et al*. 2018; *Drosophila* – Yassin *et al*. 2010).

Pharmacus cristatus sp. nov. is currently known from the Skippers Range in South Westland and from the Darran and Earl Mountains in Fiordland, west of the major depression in the landscape aligned with the Eglinton, Hollyford and Pyke Rivers (Hollyford Fault System). *Pharmacus cristatus* sp. nov. is sympatric with *P. cochleatus* throughout its range; the two species share the same habitat and form mixed populations. However, not only are they different enough morphologically to be easily identified in the field, they also differ in their patterns of activity. While primarily nocturnal, *Pharmacus cochleatus* is often seen out and about during daylight and jumps readily when disturbed by the light of a torch. *P. cristatus* on the other hand appears to be exclusively nocturnal and freezes when exposed to a source of light.

While west of the Eglinton River we have two sympatric species, *Pharmacus cochleatus fiordensis* subsp. nov. and *P. cristatus* sp. nov., east of the Eglinton and south of the Greenstone River there is only one species, *P. cochleatus rawhiti* subsp. nov. The latter has the terminalia and mitochondrial DNA of *P. cochleatus fiordensis*, but its brown body colour, apical spine combination and the longer legs are more similar to *P. cristatus* sp. nov. Whether this is due to gene flow or convergent evolution would require information from additional genetic markers.

The remaining five species of *Pharmacus* appear to be restricted to much smaller geographical regions. *Pharmacus perfidus* sp. nov. and *Pharmacus concinnus* sp. nov. are endemic to the Takitimu and the Eyre Mountains respectively, two well defined alpine islands. *Pharmacus senex* sp. nov. is currently only known from the Old Man and Old Woman Ranges and from the Dunstan Mountains in Central Otago. None of these mountain ranges are geographically isolated. *Pharmacus senex* sp. nov. appears to be defined by habitat rather than geographical isolation. It is only found on the rock tors that dot the desolated high plateaus of Central Otago. The extreme winds that constantly buffet these high plateaus are a plausible explanation for the species' short legs, since opportunities to jump are limited and long legs could in fact be detrimental, increasing the chance of the insect being caught and swept away by the wind.

Pharmacus notabilis sp. nov. appears to be confined to The Remarkables and Hector Mountains south of Queenstown, where it is sympatric with *P. cochleatus rawhiti* subsp. nov. The two species seem to occupy different elevation bands, *P. notabilis* sp. nov. at elevations lower than approx. 1500 m a.s.l., *P. cochleatus rawhiti* subsp. nov. at the higher elevations. So far, we have not found any populations where the two species mix.

Pharmacus vallestris sp. nov. is currently only known from the Matukituki River West Branch, where it is sympatric with *Pharmacus cochleatus cochleatus*, but inhabits lower elevations compared to the latter. The two species seem to utilize different habitats, too, as *P. vallestris* sp. nov. was found in screes and small boulders, whereas the habitat where *P. cochleatus cochleatus* was found mostly consists of fissures in solid rock. However, our number of *P. vallestris* sp. nov. observations is small. The seemingly limited range of *P. vallestris* sp. nov. is somewhat puzzling. We searched the adjacent Matukituki River East Branch and the nearby Earnslaw Burn at different elevations and in different habitats, but only found *Pharmacus cochleatus cochleatus*. We consider it most likely that *P. vallestris* sp. nov. may exist cryptically in neighbouring valleys and expect future searches to extend the species' known distribution range.

We note that *Pharmacus notabilis* sp. nov. and *P. vallestris* sp. nov. share a recent common ancestor (see Fig. 2) and are both 'low elevation' species. We speculate that separation between the species groups may have occurred during a glacial maximum, *Pharmacus cochleatus* surviving at high elevation on nunataks, *P. notabilis* sp. nov. and *P. vallestris* sp. nov. below the glaciers. All species would have expanded their range in warmer times, top-down in the case of *Pharmacus cochleatus*, bottom-up in the case of *P. notabilis* sp. nov. and *P. vallestris* sp. nov. In the current interglacial, *Pharmacus cochleatus*, *P. montanus* and *Notoplectron brewsterense* comb. nov. are the only rhaphidophorids found on nunataks in the glaciated regions of the Southern Alps today.

New Zealand glaciers are currently in a phase of rapid recession (Willsman *et al.* 2015) as a result of anthropogenic climate change (Vargo *et al*. 2020), and alpine invertebrates are responding to the shifting snow-line by moving to higher elevations (Chinn & Chinn 2020). *Pharmacus montanus* and *Pharmacus cochleatus cochleatus* occupy elevation bands that are at least 1000 m wide and have plenty of room to move upwards. *Pharmacus perfidus* sp. nov., *P. senex* sp. nov. and *P. cochleatus nauclerus* subsp. nov. on the other hand are confined to elevation bands less than 300 m wide on mountain ranges with a maximum elevation of 1650 m a.s.l. These species and subspecies are at risk of extinction as their alpine islands are 'submerged' as a consequence of global warming.

Notes on the biology of *Pharmacus*

Pharmacus take shelter in fissures in rock cliffs and ridges and in holes under boulder fields. While they are predominantly nocturnal, in the nival zone of the Southern Alps they are often active during the day and are seen by climbers on hot, sunny days as they jump from rock onto snow (hence the common name 'Mount Cook flea'). We propose two possible explanations for diurnal activity in the high alpine regions. Firstly, night-time temperatures at high elevation frequently drop well below 0°C even in summer, making foraging difficult, especially when lichens become coated in ice. Milder day-time temperatures may thus present better conditions for foraging. Secondly, on hot, sunny days *Pharmacus* may seek snow to cool down and avoid desiccation, as solar radiation can warm up the rock to temperatures that feel uncomfortable on climbers' fingers, conditions that are probably unbearable for insects.

Pharmacus are mainly herbivore, although they probably also scavenge on other invertebrates when available. Dumbleton (1952) noted that "examination of faecal pellets from a specimen from Mt Mahanga suggested that insect flotsam and jetsam on the snow may form at least part of their diet". Sweney (1980) also examined faeces of *Pharmacus montanus* in Aoraki Mt Cook National Park and found that they only contained plant fragments. Sweney (1980) observed *P. montanus* being associated with *Veronica haastii* Hook.f., *Veronica birleyi* N.E.Br., *Chionochloa* spp., *Dolichoglottis scorzoneroides* (Hook.f.) B.Nord., *Ranunculus grahamii* Petrie and rock lichens. The vast majority of *Pharmacus* we have observed in the wild were feeding on rock lichen, only occasionally on *Chionochloa* spp. We have never observed *Pharmacus* actively scavenging on other invertebrates. We also consider it likely that when on snow, *Pharmacus* may feed on the rich red algal growth that coats snow-fields during the summer season (Novis 2002), a condition commonly known as 'watermelon snow' or 'red snow'.

The life span and the number of instar stages in *Pharmacus* are unknown. Richards (1961) found nine pre-adult instars in male and seven in female *Pachyrhamma edwardsii* (Scudder, 1869) and a duration of two years for the complete life cycle of *Pachyrhamma cavernae* (Hutton, 1900); both species are larger than *Pharmacus*. Eight male and nine female pre-adult instars occur in *Insulanoplectron spinosum* Richards, 1970 (Butts 1983), while there are seven in both males and females of the Australian rhaphidophorid *Pallidotettix nullarborensis* Richards, 1968 (Richards 1970). Studies on cave dwelling Rhaphidophoridae overseas have shown a lifespan of one year in *Ceuthophilus stygius* (Scudder, 1861) (Lavoie *et al*. 2007), two and a half years in *Dolichopoda geniculata* (Costa, 1860) (Carchini *et al.* 1994). Similar studies on high alpine Rhaphidophoridae are lacking.

Given the short duration of the snow-free season on New Zealand mountains (November to April), it is unlikely that *Pharmacus* could complete their life cycle within one season. *Pharmacus* adults and nymphs are active in spring as soon as temperatures become warm enough (pers. obs.), indicating that these insects can survive winter in a dormant state at all life stages. This life history trait is also typical of New Zealand's alpine grasshoppers (family Acrididae MacLeay, 1821) (Ramsay 1978; Koot *et al.* 2020). Unpredictable seasonal conditions in the New Zealand alpine zone may result in uneven development rates and growth whenever the environment permits (Sutherland 1964), which is consistent with the prevalence of freeze tolerance in southern hemisphere insects (Sinclair *et al.* 2003; Sinclair & Chown 2005). Freeze tolerance is known in other New Zealand Orthoptera, including species of *Deinacrida* White, 1842 and *Hemideina* Walker, 1869 in the family Anostostomatidae de Saussure, 1859 (Sinclair *et al.* 1999, 2003; Wharton 2011). *Pharmacus* however shelter deep inside rock crevices, where temperature fluctuations are reduced by the rocks' thermal inertia and in winter by the additional presence of snow cover. Once the ground freezes over for winter, we consider it unlikely that they would resume any activity before spring. From this point of view, *Pharmacus* are subject to environmental conditions more typical of the northern hemisphere. We have observed *Pharmacus* actively forage at air temperatures as low as –5°C, although they move slowly and are unable to jump. The ability of *Pharmacus* to remain active at air temperatures below 0°C, combined with the fact that they live at elevations much higher than any New Zealand invertebrates known to be freeze-tolerant, suggests that in *Pharmacus* freeze avoidance may play a greater role than freeze tolerance (Sinclair & Chown 2005).

Melanism in *Pharmacus* is apparent where they occur at the higher elevations. On the Sealy Range in Aoraki/Mt Cook National Park, *Pharmacus montanus* is brown at 1500 m a.s.l. (Fig. 14B), mottled brown/black at 1700 m to 1800 m a.s.l. (pers. obs.) and entirely black at 2200 m a.s.l. (Fig. 14A). Throughout the bottom half of the Southern Alps, *Pharmacus cochleatus* is chequered yellow/black at

1500 m a.s.l. (Fig. 14C), transitioning to pitch black at higher elevation (Fig. 14D). Melanism is likely to provide a two-fold advantage in the high alpine regions where air temperature is low but solar radiation is high. Firstly, darker individuals are expected to warm up faster when exposed to sun-light, resulting in increased ability to jump and escape predation. This would be especially important for *Pharmacus* in the nival zone where they are commonly diurnal. The thermal melanism hypothesis has been tested in alpine grasshoppers in the European Alps (Köhler *et al.* 2017) and in Australia (Harris *et al.* 2013), and in several species of winged insects (Roland 1982; Guppy 1986; Wittkopp *et al.* 2011). Secondly, cuticular melanism is associated with increased resistance to desiccation in several invertebrate taxa (Parkash 2010) including the mountain stone wētā *Hemideina maori* (Pictet & de Saussure, 1893) (King & Sinclair 2015).

In the Southern Alps, *Pharmacus* and *Notoplectron brewsterense* comb. nov. are sympatric and are often found in mixed populations on the same cliffs. At medium elevations (1500 m to 1800 m) *Pharmacus* are outnumbered by *Notoplectron* at a ratio of 10:1 or higher. Indeed, *Notoplectron brewsterense* comb. nov. at times form dense colonies, emerging onto alpine cliffs after dark in their hundreds. It is not only a very widespread but also a very common species. At the higher elevations (above 2000 m) *Pharmacus* seems to be more common, but we lack enough data to support our sparse anecdotal evidence. East of the Southern Alps, in the mountains of Southland and Otago, *Notoplectron brewsterense* comb. nov. is replaced by *Talitropsis chopardi*. While *Pharmacus* and *Talitropsis chopardi* are also sympatric and found in mixed populations, here the ratios are inverted, as *Pharmacus* are by far the most numerous and form dense colonies. It would seem that, while *Pharmacus* are highly adapted to life in the most inhospitable alpine habitats, the more sheltered ranges of Southland and Otago are where conditions are optimum for these cave wētā to thrive. In the rain-parched ranges of East Canterbury and Marlborough however, *Pharmacus* are entirely absent and are replaced by Rhaphidophoridae in the genus *Petrotettix* Richards, 1972.

Morphology of *Pharmacus* and differentiation from other New Zealand Rhaphidophoridae

Pharmacus is a well-defined, compact genus of Rhaphidophoridae. The exclusively alpine habitat, ovipositor with smooth upper valve, triangular male subgenital plate with a 'spoon' at the apex, body length between 10 mm and 18 mm and the slender legs with two rows of 20 to 30 dorsal linear spines on the hind tibiae differentiate it from all other New Zealand Rhaphidophoridae.

Some interesting considerations arise from an examination of the apical spines on the fore and mid femora of *Pharmacus* (Table 1). In his synopsis of the genera of New Zealand Rhaphidophoridae, Hutton (1896) assumed the presence of prolateral and retrolateral spines at the apex of each femur to be characteristic of a genus. The presence of a retrolateral spine at the apex of the fore femur in *Pleioplectron diversum* Hutton, 1896 for instance was enough for Hutton (1898) to justify moving the species to a new genus, *Miotopus* Hutton, 1898. His view on the importance of the spines at the apex of each femur remained unchallenged for decades. Hutton (1896) described *Pharmacus* as having "all femora without apical spines".

Based on Hutton's previous work, Karny assigned his new species *Isoplectron cochleatum* to the genus *Isoplectron* Hutton, writing that "in light of its body build and spines on the legs this species belongs without doubt to the genus *Isoplectron*". In more recent times, the only two published keys to the genera of New Zealand Rhaphidophoridae still assume the configuration of spines at the apex of each femur to be a key characteristic of a genus (Ward 1997; Johns & Cook 2013). Richards (1959) was first to challenge the idea when dealing with the species *Miotopus diversus* (Hutton, 1896), writing that "Admittedly the presence of two apical spines on the fore femora is a different character to that found in *Pleioplectron*; but variation is so common that too much weight cannot be placed on it when only one specimen is available for examination". And yet Richards defined a number of new species based on the configuration of apical spines of the material she examined; in her generic description of *Pharmacus* (1972) she wrote "Apical spines on legs constant in number. Fore femur unarmed; fore tibia bears four apical spines, one above and one beneath both prolaterally and retrolaterally; fore tarsus unarmed. Middle femur bears one prolateral apical spine beneath; middle tibia bears four apical spines, one above and one beneath both prolaterally and retrolaterally; middle tarsus unarmed. Hind femur unarmed".

In their work on the genus *Pachyrhamma* Brunner von Wattenwyl, 1888, Cook *et al.* (2010) found that the configuration of spines at the apex of the hind femora varies not only within the genus, but also within a species. The same applies to the genus *Pleioplectron* Hudson, 1896 (Hegg *et al.* 2019). The presence of a spine at the apex of the hind femur can thus not be used as a trait to characterise a species. Hegg *et al.* (2019) also found that a retrolateral spine at the apex of the fore femur is present in four out of ten species in the genus *Pleioplectron*. The configuration of apical spines on the fore and mid femur however is constant within each species.

In the genus *Pharmacus*, only three out of eight species have a constant configuration of apical spines on the fore and mid femora (see Table 1). These are *Pharmacus montanus* (27 specimens examined), *P. cristatus* sp. nov. (11 specimens examined) and *P. vallestris* sp. nov. (6 specimens examined). Larger sample sizes could introduce variation in some of these species also. In *Pharmacus cochleatus* comb. nov., three out of four subspecies also have a constant configuration of apical spines on the fore and mid femora: *P. cochleatus cochleatus* (56 specimens examined), *P. c. nauclerus* subsp. nov. (10 specimens examined) and *P. c. fiordensis* subsp. nov. (8 specimens examined). In all other species or subspecies, the only constants are the presence of a retrolateral spine at the apex of the mid femur, and the absence of a retrolateral spine at the apex of the fore femur. A prolateral spine at the apex of the fore and/or mid femur may or may not be present. In *Pharmacus cochleatus rawhiti* subsp. nov., we have found three different configurations of apical spines on the fore and mid femora of ten specimens collected on the same rock.

In general, the configuration of apical spines on the fore and mid femora of New Zealand Rhaphidophoridae is a useful trait when disambiguating between species and even genera. However, there are exceptions; the genus *Pharmacus* is one of these exceptions. We do not know if apical spines on the fore and mid femora of Rhaphidophoridae are functional, or what their function might be. We highlight the fact that the configuration of spines at the apex of the femora in Rhaphidophoridae cannot be taken as sole evidence to define a species, let alone a genus. This is consistent with the findings from previous studies on the European genus *Dolichopoda* Bolívar, 1880, which showed that spinulation in Rhaphidophoridae is not a valid trait for resolving systematic issues (Allegrucci *et al*. 2005).

A note on nomenclature

In reassigning the species *Pharmacus brewsterensis* to the genus *Notoplectron* we have assumed *Notoplectron* to be gender neuter. This is in spite of Richards (1964) having named the only existing species in the genus *Notoplectron campbellensis*.

Several genera of New Zealand Rhaphidophoridae have names that end in *–plectron*: *Isoplectron* Hutton, 1896; *Pleioplectron* Hutton, 1896, *Ischyroplectron* Hutton, 1896; *Pallidoplectron* Richards, 1958; *Novoplectron* Richards, 1958; *Notoplectron* Richards, 1964; *Dendroplectron* Richards, 1964; *Insulanoplectron* Richards, 1970. All of these names are gender neuter, *Notoplectron* being no exception.

Richards made several grammatical mistakes when naming species. While she did consistently use first- and second-declension adjectives correctly (e.g., *Pallidoplectron peniculosum* Richards, 1960; *Pallidoplectron subterraneum* Richards, 1965; *Insulanoplectron spinosum* Richards, 1970), she never used the correct neuter form in third-declension adjectives. As a result of this, she made incorrect use of Latin declensions when naming *Notoplectron campbellensis* Richards, 1964 and *Dendroplectron aucklandensis* Richards, 1964.

In compliance with article 31.2 of the ICZN Code (ICZN 1999), the correct declension for the Auckland Islands cave wētā is *Dendroplectron aucklandense* Richards, 1964 and the correct declension for the Campbell Island cave wētā is *Notoplectron campbellense* Richards, 1964. Likewise, the correct declension for the new combination of *Pharmacus brewsterensis* is *Notoplectron brewsterense* (Richards, 1972) comb. nov.

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