Taxonomic revision of the Australian stick insect genus Candovia (Phasmida: Necrosciinae): insight from molecular systematics and species-delimitation approaches

Taxonomic revision of the Australian stick insect genus *Candovia* (Phasmida: Necrosciinae): insight from molecular systematics and species-delimitation approaches

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The Phasmida genus *Candovia* comprises nine traditionally recognized species, all endemic to Australia. In this study, *Candovia* diversity is explored through molecular species-delimitation analyses using the COI_{Fol} gene fragment and phylogenetic inferences leveraging seven additional mitochondrial and nuclear loci. Molecular results were integrated with morphological observations, leading us to confirm the already described species and to the delineation of several new taxa and of the new genus *Paracandovia*. New *Candovia* species from various parts of Queensland and New South Wales are described and illustrated (*C. alata* **sp. nov.**, *C. byfieldensis* **sp. nov.**, *C. dalgleishae* **sp. nov.**, *C. eungellensis* **sp. nov.**, *C. karasi* **sp. nov.**, *C. koensi* **sp. nov.** and *C. wollumbinensis* **sp. nov.**). New combinations are proposed and species removed from synonymy with the erection of the new genus *Paracandovia* (*P. cercata* **stat. rev.**, **comb. nov.**, *P. longipes* **stat. rev.**, **comb. nov.**, *P. pallida* **comb. nov.**, *P. peridromes* **comb. nov.**, *P. tenera* **stat. rev., comb. nov.**). Phylogenetic analyses suggest that the egg capitulum may have independently evolved multiple times throughout the evolutionary history of these insects. Furthermore, two newly described species represent the first taxa with fully developed wings in this previously considered apterous clade.

ADDITIONAL KEYWORDS: Australian fauna – capitulum – molecular phylogenetics – *Paracandovia* – phasmids – wings.

INTRODUCTION

The order Phasmida Leach, 1815 (Hexapoda: Insecta) consists of *c.* 3400 valid species (Brock *et al.*, 2022), mostly with a tropical or subtropical distribution. It contains insects that are well known for their remarkable mimicry, from crypsis and background matching to disruptive coloration and masquerade (Merilaita & Lind, 2005; Skelhorn, 2015). Their morphology presents instances of interspecific convergent evolution, possibly combined with intraspecific phenotypic plasticity (Gutiérrez-Valencia *et al.*, 2017). Therefore, it is important to rely on the integration of different approaches to unravel their diversity, such as the integration of molecular data and morphological observations. Despite several shortcomings about the usage of a single mitochondrial gene locus for this purpose having been highlighted (Moritz & Cicero 2004), this approach is widespread as a quick and efficient exploratory strategy for the delimitation and validation of species boundaries. Yet, many empirical studies have shown that some species-delimitation methods can lead to under- or over-splitting of species, therefore the outcomes of molecular species-delimitation should be better interpreted along with complementary information of species morphology and/or ecology (Dellicour & Flot, 2018; Jacobs *et al.*, 2018; Luo *et al.*, 2018).

Molecular species delimitation has been successfully used in phasmids in several instances (Glaw *et al.*, 2019; Bank *et al.*, 2021; Cumming *et al.*, 2021). Velonà *et al.* (2015) first applied DNA barcoding on 16 Australian stick insect taxa, and retrieved a high differentiation among three putative morphospecies of the genus *Candovia* Stål, 1875: *Candovia* spp. A, B and C, and found their divergence from *C. annulata* (Brunner, 1907). Traditionally, the genus *Candovia* (Lonchodidae: Necrosciinae: Necrosciini) consisted of nine recognized species, all endemic to Australia, feeding on a wide range of trees, shrubs and ferns. The species *C. evoneobertii* Zompro & Adis, 2001, usually listed as the tenth taxon, is endemic to South America, sharing only a superficial similarity to *Candovia* (Brock & Hasenpush, 2009)*; it has recently been synonymized with Arumatia dubia (Caudell, 1904) (Ghirotto et al., 2022).* *Candovia* are small to medium-sized, stick-like, Australian phasmids known from few records, with the apparent scarcity of specimens relating to limited interest in phasmids and to their nocturnal lifestyle. Thus their species richness and true distribution may be much more extensive than recorded. Although enthusiasts rear them from time to time, there is no published information on the biology of *Candovia* species, with the exception of the publication by Brock & Hasenpusch (2009). Furthermore, older phasmid descriptions are often listed from just a single location and rely on damaged material of one sex only: the type species of *Candovia*, originally described as *Phasma* (*Bacteria*) *coenosum* Gray, 1833, is a fitting example, consisting of a damaged holotype female.

A recent sampling effort revealed morphologically diverse *Candovia* specimens, not recognizable as known species. Therefore, this study aims to unravel the *Candovia* species

richness, to support and validate formal descriptions of putative new taxa and to understand their phylogenetic relationships. As a result, the new genus *Paracandovia* (described below) is erected alongside the traditional *Candovia*, while we also validate already known species and describe several new ones.

Taxonomic history of *Candovia*

Since *Candovia* was described (Stål, 1875) to accommodate *Phasma* (*Bacteria*) *coenosum* Gray, 1833, the genus has been little mentioned and was often confused by subsequent authors. Stål believed Gray's holotype to be a male, but Westwood (1859) clarified this, and also described and figured the supposed male and synonymized *Phasma* (*Bacteria*) *fragilis* Gray, 1833. In a checklist of phasmids (Kirby, 1904), *Candovia* was synonymized with *Hyrtacus* Stål, 1875. Brock & Hasenpusch (2007) redescribed *Candovia* and removed the genus from synonymy with *Hyrtacus* (the latter is also in need of revision, as the type species has spine-like tubercles on the head, thorax and abdomen, which are lacking in other taxa, including undescribed species; in females, the end of abdomen is beak-shaped and pointed at tip). They also transferred several species to *Candovia* that had been originally listed as *Parasipyloidea* Redtenbacher, 1908 in checklists of Australian phasmids by Vickery (1983) and Balderson *et al.* (1998). Vickery (1983) was the first to place several wingless Australian species in *Parasipyloidea* (an Asian genus of several small, wingless species), presumably thinking they were allied to *C. strumosa* (Redtenbacher, 1908), originally described in *Parasipyloidea. Candovia* species were otherwise originally described as belonging to *Bacillus* Berthold, 1827, *Bacunculus* Burmeister, 1838, *Dyme* Stål, 1875, *Hyrtacus*, *Marcenia* Sjöstedt, 1918 or *Menexenus* Stål, 1875, due to vague similarity; that is, in most cases elongate, wingless taxa, originating from different geographical regions, with various distinguishing morphological characters. To add to confusion, later Zompro & Adis (2001) incorrectly linked a South American species as 'Australian' and placed it in the Australian genus *Echetlus* Stål, 1875 (which have short antennae, not reaching the end of fore femora), instead of the more appropriate *Candovia* (with long antennae), if it had really been an Australian species [transferred to *Candovia* in Brock & Hasenpusch (2007)]. As with many phasmids, the several genera mentioned above have not been studied in any detail by researchers and are in need of revision.

MATERIAL AND METHODS

Taxon sampling

Adult specimens were collected between 2009 and 2017 across 21 locations in southern and eastern Australia (Fig. 1; Table 1) by Paul Brock (PDB), Braxton Jones (BRJ) and Noelene Tweed, or were examined in museums. All type material of existing species was examined by visits to various collections, with photographs and type data included on the Phasmida Species File (Brock *et al.*, 2021). Specimens of new taxa collected in Queensland by BRJ were obtained under the permit #WITK18701717; others associated with PDB via Australian Biological Resources Study permits over several years. In a few cases, Jack Hasenpusch (JH) reared specimens on PDB's behalf. Sampling sites were visualized geographically using the R package ozmaps (https://cran.r-project.org/package=ozmaps). Eggs from live insects were collected where possible (with females kept in suitable plastic containers with ventilation and a supply of foodplant leaves) and specimens were mounted, with the right midleg stored in 100% ethanol for molecular analysis. Voucher specimens were deposited at the Queensland Museum, Brisbane (QM), Australian National Insect Museum, Canberra (ANIC) and the Natural History Museum, London (NHMUK). We referred to new specimens which could not be reliably assigned to any known species as morphospecies D to L, therefore adding to the three putative morphospecies A–C previously proposed (Supporting Information, Table S1; Velonà *et al.*, 2015). Sixty-seven individuals (Table 1) were selected for molecular analyses; their leg tissues were preserved in ethanol and stored at 4 °C until use. For phylogenetic analyses, 18 publicly available sequences of Necrosciinae species were drawn from GenBank and *Extatosoma tiaratum* (Macleay, 1826) (Phasmatidae, Extatosomatinae) was used as outgroup (Supporting Information, Table S1a).

Map ID	Sampling site	Initial species / morphospecies	*N*	Latitude	Longitude	Sample ID
APP	Springbrook, Apple Tree Park (QLD)	*C. annulata*	5	-28.166	153.259	PB-(0207-0211)
APP	Springbrook Apple Tree Park (QLD)	*C. strumosa*	5	-28.166	153.259	PB-(0214-0218)
BAR	Baralaba, Duaninga Road (QLD)	morphospecies G	1	-24.136	149.830	PB-0295
MTV	Montville, Narrows Road (QLD)	*C. annulata*	9	-26.698	152.866	JH-00(37,39-42); PB-00(66,67,77,98)
MTV	Montville, Narrows Road (QLD)	morphospecies A	9	-26.698	152.866	JH-00(26-31,43,44); PB-0060
MTV	Montville, Baroon Pocket Dam (QLD)	morphospecies C	5	-26.698	152.866	JH-00(66-70)
MTV	Montville, Baroon Pocket Dam (QLD)	morphospecies A	1	-26.698	152.866	PB-0058
BTL	Blackdown Tableland (QLD)	morphospecies D	4	-23.582	149.063	PB-0(188-191)
BTL	Blackdown Tableland (QLD)	morphospecies E	4	-23.582	149.063	PB-0(184-187)
BUL	Bulli (NSW)	*C. robinsoni*	7	-34.330	150.901	PB-0(107,108,112,115, 118,119,121)
BYF	Byfield (QLD)	morphospecies F	3	-22.847	150.650	PB-0(325, 327, 328)
CAV	Rossmoya Road, The Caves (QLD)	morphospecies F	4	-23.159	150.457	PB-0(258,261,271,272)
COH	Colo Heights (NSW)	*C. coenosa*	1	-33.369	150.722	PB-0164
DAR	D`Aguilar Range, Boombana (QLD)	morphospecies A	1	-27.404	152.794	PB-0058
DIN	Charlevue Road, 18km West of Dingo (QLD)	morphospecies I	4	-23.638	149.110	BJ-00(91-94)
ECB	Ellery Creek Big Hole, West Macdonnell National Park (NT)	*C. pallida*	4	-23.778	133.073	BJ-00(30,31,32,34)
ENP	Eungella National Park, Broken River (QLD)	morphospecies B	4	-21.162	148.512	PB-00(18 -21)
EVH	Evans Head (NSW)	*C. aberrata*	5	-29.108	153.431	PB-0(157-161)
FSR	Fountain Springs Rest Area, 60km East of Mount Isa (QLD)	morphospecies L	1	-20.800	139.996	BJ-00(95)
KOS	Kosciuszko National Park, Guthega Road (NSW)	*C. spurcata*	2	-36.500	148.266	PB-00(155, 156)
LIB	Little bay, Harvey Street (NSW)	*C. coenosa*	2	-33.983	151.244	BJ-00(41-42)
MTG	Mount Gambier (SA)	*C. peridromes*	3	-37.843	140.765	PB-0(178-180)
MTW	Mt Warning, Wollumbin (NSW)	*Candovia* sp. H	2	-28.400	153.282	PB-0(173, 174)
PIL	Pilliga (NSW)	*C. robinsoni*	1	-30.350	148.890	PB-0162
RST	Springbrook, Repeater Station Rd (QLD)	*C. granulosa*	4	-28.234	153.267	PB-0(220-223)
WIL	Wilmington, Park road (SA)	*C. peridromes*	5	-32.840	138.036	BJ-0(12-16)

Table 1. Sampling information about analysed *Candovia* samples. Map IDs refer to Figure 1. Sampling site abbreviations are: QLD = Queensland, NSW = New South Wales, NT = Northern Territory, SA = South Australia. Sample IDs refer to Figure 2.

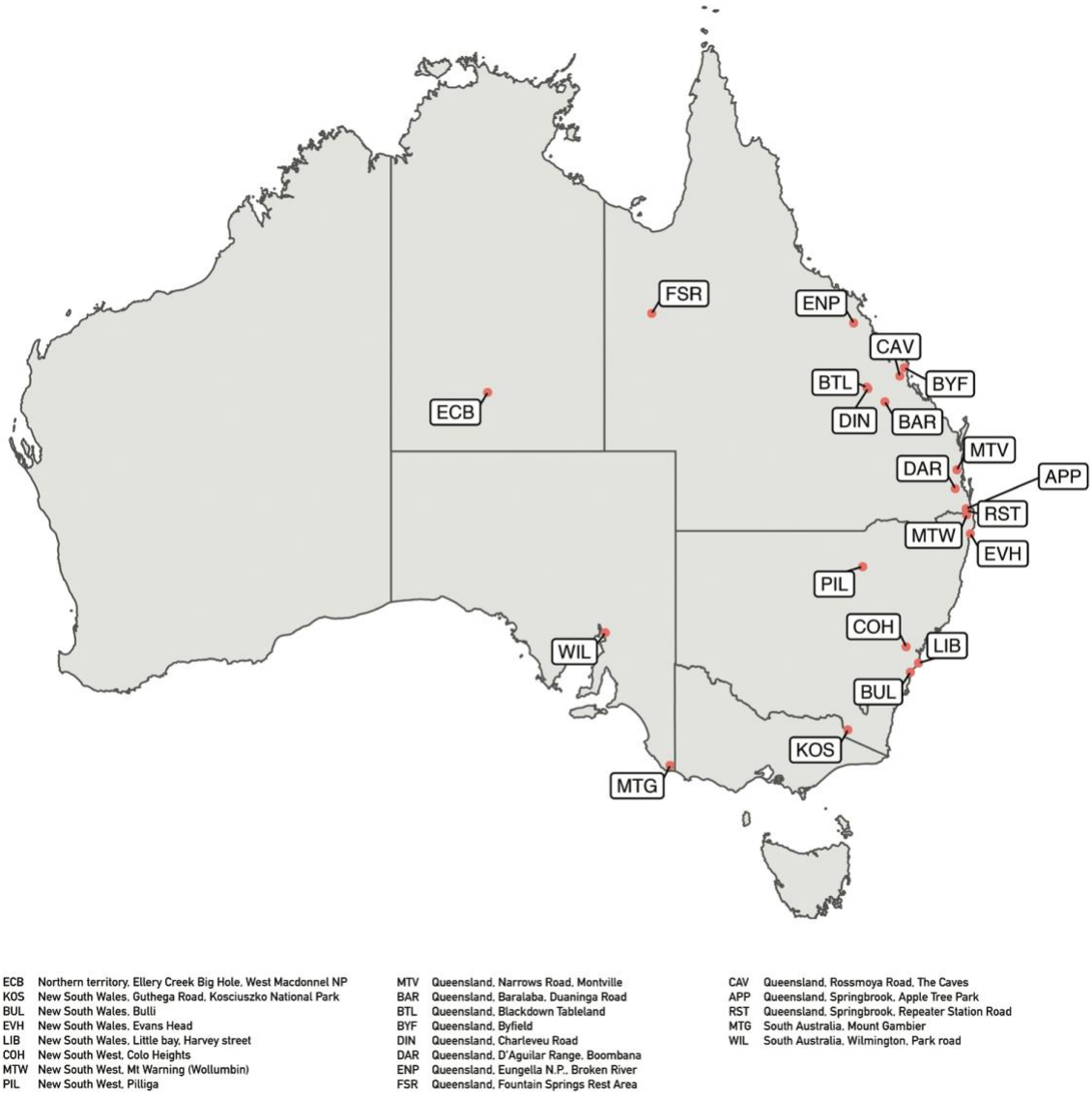

Figure 1. Geographical distribution of the 21 Australian sampling sites.

DNA extraction, amplification and sequencing

Genomic DNA was isolated for the 67 newly collected specimens using the kit Smarter Nucleic Acid Preparation (Stratec) following the manufacturer's standard protocol. The Folmer region of cytochrome *c* oxidase subunit I (*COI*) for DNA barcoding (Folmer *et al.*, 1994; henceforth referred to as *COIFol*) was polymerase chain reaction (PCR) amplified from all samples using primers and the condition is given in the Supporting Information, Table S2. On the basis of the species delimitation results, we selected 39 specimens for which, in addition to the *COIFol*, we amplified seven further loci: four mitochondrial [a *COI* fragment downstream of the *COIFol* region, and indicated as *COI*; cytochrome oxidase *c* subunit II

(*COII*); 12S and 16S rDNAs] and three nuclear markers [histone subunit 3 (*H3*); 18S and 28S rDNAs]. Amplified fragment length, primers and thermal cycling conditions can be found in the Supporting Information, Table S2. All PCR products were visualized by 1% agarose gel electrophoresis, subsequently purified using ExoSAP-IT PCR Product Cleanup Reagent (Thermofisher) and sequenced by Macrogen Inc. Chromatograms were inspected using SEQTRACE v.0.9.0 (Stucky, 2012) and the resulting sequences were manually checked using ALIVIEW v.1.26 (Larsson, 2014). We then compared the obtained sequences with the NCBI GenBank database using BLAST (with *blastn* algorithm: Altschul *et al.*, 1990) to identify potential contaminants. New sequences were submitted to GenBank under the accession numbers MT077516–MT077845 (Supporting Information, Table S1b for the *COIFol* sequences used for species delimitation and the Supporting Information, Table S1c for the seven additional gene fragments used for phylogenetic analyses).

Molecular species delimitation

COIFol fragments have been aligned as amino acids using MAFFT v.7 with *--auto* parameter setting (Katoh & Standley, 2013) and then retrotranslated to nucleotides. The dataset was partitioned in the three-codon positions and analysed by both maximum likelihood (ML) and Bayesian inference (BI) methods. All phylogenetic analyses were carried out with XSEDE (eXtreme Science and Engineering Discovery Environment, https://www.xsede.org) through CIPRES Science Gateway (www.phylo.org; Miller, Pfeiffer & Schwartz, 2012). ML tree was obtained with IQ-TREE v.1.6.12 (Nguyen *et al.*, 2014). The best-fit models of nucleotide substitution were identified using ModelFinder (Kalyaanamoorthy *et al.*, 2017; Supporting Information, Table S3a); then, ten ML searches were run with 1000 ultrafast bootstrap replicates and the run with the best likelihood was selected as the most reliable. For the BI, we determined the best-fit nucleotide substitution model using PARTITIONFINDER2, based on the corrected Bayesian Information Criterion using the edge-linked parameter and the greedy strategy (Lanfear *et al.*, 2016; Supporting Information, Table S3a). But the partition scheme and the substitution model selected by PARTITIONFINDER led to poor mixing, most likely due to over-parametrization. We thus modified the partition scheme to use the less parametrized model HKY.

The *COIFol* dataset was analysed using several species-delimitation approaches to explore the species diversity of the genus and to explore the species hypotheses. For this purpose, we used both distance and evolutionary model-based methods, without a priori species

hypothesis: (1) automatic barcode gap discovery (ABGD; Puillandre *et al.*, 2012) analysis was performed using Jukes–Cantor distances, a relative gap width of 1 and 10 bins; (2) the different Poisson tree processes approaches (PTP and mPTP; Zhang *et al.*, 2013; Kapli *et al.*, 2017) were carried out using the IQ-TREE best ML tree as input: two runs of 1 000 000 generations with sampling every 100 and a burn-in of 20% as parameters were carried out and compared for convergence; (3) the general mixed Yule coalescent (GMYC; Pons *et al.*, 2006) was run on ultrametric trees, using the single threshold parameter. The concatenated sequence alignment (see below) was analysed with BEAST v.2.5 (Bouckaert *et al.*, 2019) to generate ultrametric trees for the GMYC species-delimitation method. We used four combinations of different clock and speciation model priors: strict or relaxed clock model and Yule or coalescent process. Each analysis was run with trees and parameter values sampled every 5000 steps over a total of 60 million generations. A burn-in of 20% steps was discarded and adequate sample sizes (ESS > 200) were checked using TRACER v.1.6 (Rambaut *et al.*, 2018). Trees were summarized in the maximum clade credibility tree from the posterior distribution in TREEANNOTATOR v.1.4.7 (Drummond *et al.*, 2012). GMYC and ABGD were used with their online implementation (available at https://species.h-its.org/gmyc/ and https://bioinfo.mnhn.fr/abi/public/abgd/abgdweb.html, respectively).

Molecular phylogenetic analyses

Each gene was aligned separately using MAFFT v.7 with the option *--auto* for protein-coding genes (PCGs) and with the option *--X-INS-i* for the rDNA genes (Katoh & Standley, 2013). We then manually inspected alignments using AliView (Larsson, 2014) to select the correct reading frame and to check for stop codons. Ambiguously aligned regions were removed from the single-gene alignments with GBlocks (Talavera & Castresana, 2007) with options for a less stringent selection. We then concatenated gene sequences to form a single-character matrix using PHYUTILITY (Smith & Dunn, 2008).

Model selection, ML and BI analyses were carried out with XSEDE (eXtreme Science and Engineering Discovery Environment, https://www.xsede.org) through the CIPRES Science Gateway (www.phylo.org; Miller *et al.*, 2012). For the ML approach, the best-fit partitioning scheme and models of nucleotide substitution were identified using IQ-TREE v.1.6.12 ModelFinder (Kalyaanamoorthy *et al.*, 2017) (Supporting Information, Table S3b) using the edge-proportional parameter. We then inferred ten trees using IQ-TREE v.1.6.12 (Nguyen *et al.*, 2014) with 1000 ultrafast bootstraps, and the run with the best likelihood was selected.

For the BI, we determined the best-fit nucleotide substitution model and the optimal partitioning scheme using PARTITIONFINDER2, based on the corrected Bayesian information criterion, using the edge-linked parameter and the greedy strategy (Lanfear *et al.*, 2016), with each rDNA and each codon position of the four PCGs as separate initial partition (Supporting Information, Table S3b). The MCMC analysis was run with the tree and parameter values sampled every 5000 steps over a total of 50 million generations. A burn-in of 10% steps was discarded, and adequate sample sizes (ESS > 200) were checked using TRACER v.1.7.7 (Rambaut *et al.*, 2018).

Morphological examination

Many specimens were examined as part of this study, including the type and molecular material detailed in this paper. Images were taken with a Nikon D5500 with a Nikon 105 mm macro lens and macro flash, often in nature at night. Images were processed in ADOBE PHOTOSHOP with slight changes, if any. When measuring specimens, the body length of examined specimens was measured to the nearest 0.5 mm and eggs to the nearest 0.1 mm. Microscopes used included available equipment during visits to ANIC and QM, also a specially made GX research microscope (GT Vision, UK), with a flat base suitable for phasmids by PDB.

RESULTS

Molecular species delimitation

The *COIFol* alignment was 666 bp long, and correctly translated for 222 amino acids sequences without any stop codon. BLAST searches against NCBI GenBank database consistently resulted in congeneric species best-hits. The final dataset consisted in 67 newly generated sequences and 29 previously published sequences, bringing the total number of operational taxonomic units (OTUs) to 96. The obtained ML and BI trees showed fully compatible topologies (Fig. 2; Supporting Information, Fig. S1). Using the different species-delimitation approaches, the number of hypothetical species ranged from 19 to 24 for PTP, which proved to be the most conservative approach, while GMYC was the method identifying the highest number of hypothetical species (24 spp.; Fig. 2).

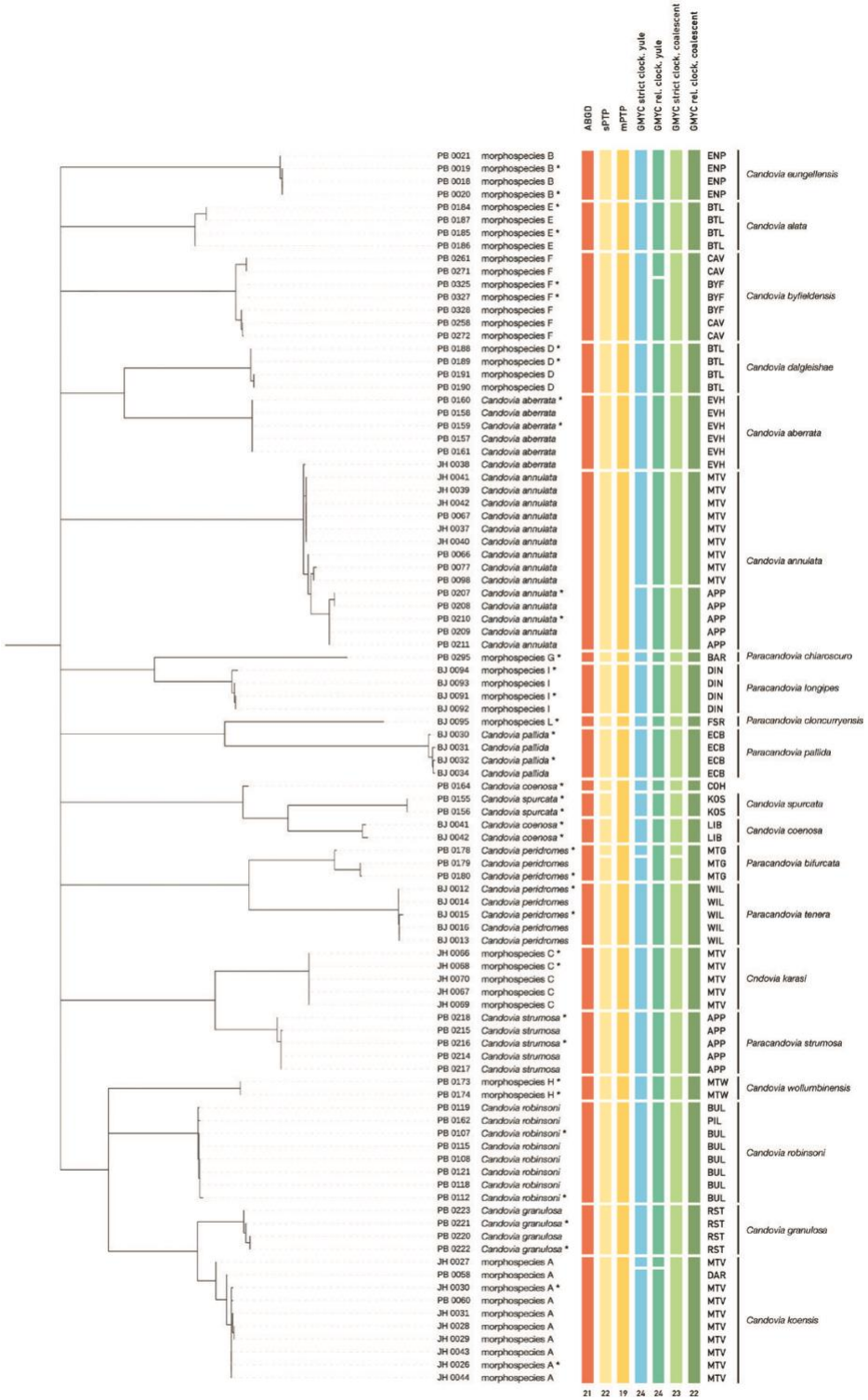

Figure 2. Species delimitations summarised on the maximum likelihood tree with a bootstrap cut off of 80%. The names at the tips of the COI_{FOI} phylogenetic tree represent the initial species identifications and hypotheses; coloured bars represent hypothetical species identified by the different approaches; the names on the right represent the final species identified. Acronyms on the right are relative to geographic collection points, as reported in Figure 1.

A full agreement of molecular-delimitation approaches with most known taxa can be observed, such as for *C. aberrata* (Brunner, 1907), *C. granulosa* (Brunner, 1907), *C. pallida* (Sjöstedt, 1918), *C. robinsoni* Brock & Hasenpusch, 2007 and *C. strumosa.* This holds also for the previously recognized putative morphospecies B and C. In other instances, morphospecies are split in different taxa or merged in a single entity. *Candovia peridromes* (Westwood, 1859) splits in all approaches in two groups, according to a geographical pattern, while this occurs for *C. annulata* in the GMYC analyses only. The specimen PB-0178, identified as *C. peridromes*, is further found as a separate taxon by sPTP and the two GMYC approaches using the strict molecular clock, therefore calling for particular attention on this entity. *Candovia coenosa* (Gray, 1833) is consistently recognized as composed by two putative species, separating the PB-0164 specimen from the other two congeneric samples. On the other hand, the mPTP method merges all *C. coenosa* specimens with those of *C. spurcata* (Brunner, 1907) in a single hypothetical species. Finally, the specimen JH-0027 of morphospecies A is recognized as divergent by two GMYC analyses (Fig. 2). Regarding the newly collected specimens, in both ML and BI trees they have been partitioned into well-defined clusters identified by the species-delimitation analysis as new putative taxonomic entities (henceforth named spp. D to L; Fig. 2). Although, for sp. F, two specimens were recognized as a separate taxon by two GMYC analyses (Fig. 2).

Molecular phylogenetic analyses

The final dataset used for phylogenetic analyses, a concatenation of the eight analysed mitochondrial and nuclear markers, consisted of 4540 sites and 58 specimens representing 30 species. The ML and BI analyses provided identical tree topologies, with most nodes more strongly supported in the BI tree than in the ML tree. Both phylogenetic analyses identify *Candovia* as monophyletic with respect to the other Necrosciinae taxa included in the present analysis (Fig. 3; Supporting Information, Fig. S2). Within the clade, the observed clustering pattern appeared more resolved, in terms of phyletic relationships and nodal supports, than in the analysis of *COIFol* dataset alone.

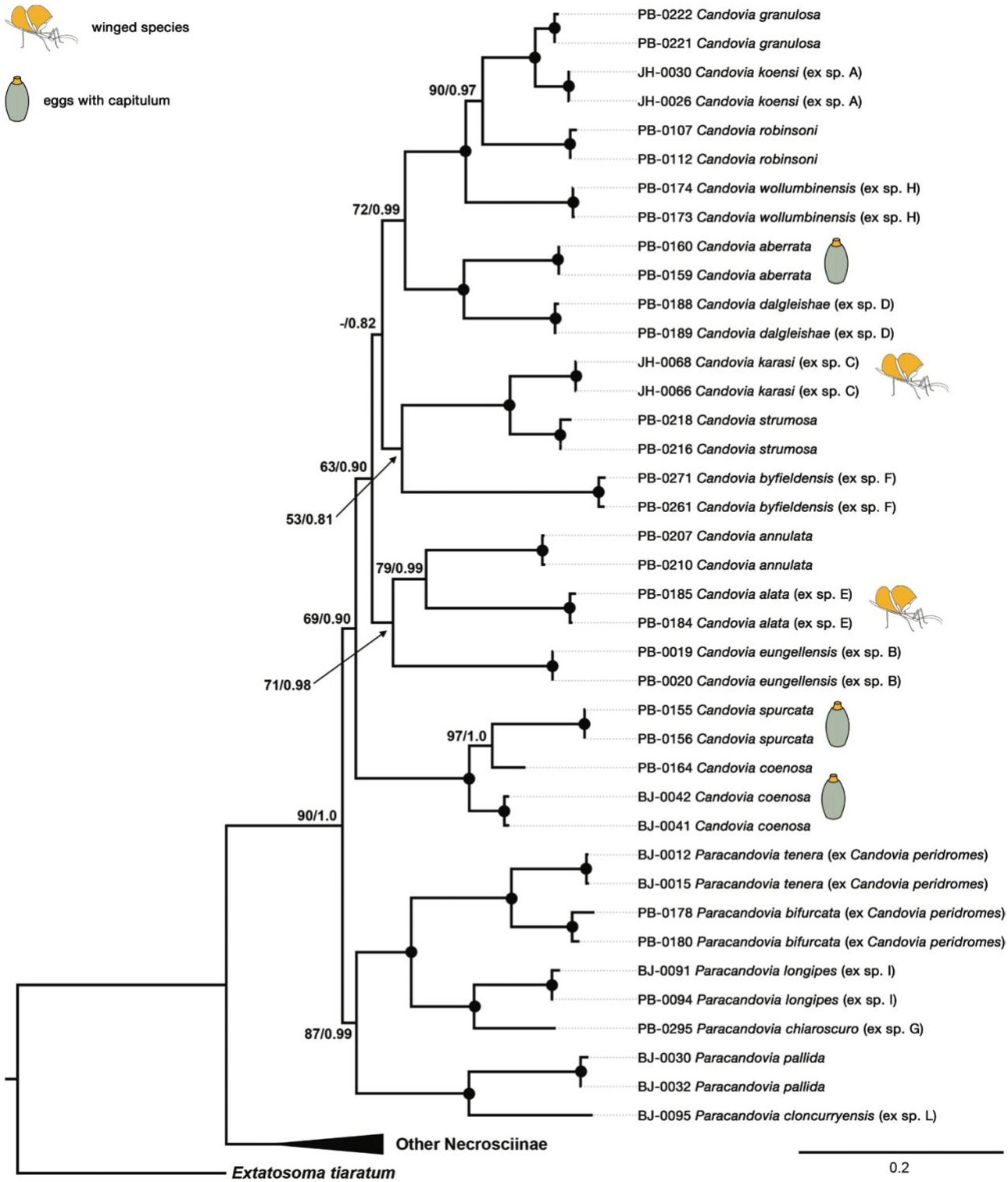

Figure 3. Combined maximum likelihood and Bayesian inference trees. Maximum nodal support (bootstrap = 100%; posterior probability = 1.0) are indicated with a black dot on the node; when support values are lower than the maximum, actual values are shown (dashes indicate no support at all). Species presenting eggs with capitulum or wings are highlighted on the right of the corresponding species.

The first split within the clade identified a cluster including *C. peridromes*, *C. pallida* and five putative species (*Candovia* spp. G, I and L) in a sister-relationship to all remaining *Candovia* species (consisting in the newly erected *Paracandovia* genus). Samples of *C. spurcata* and *C. coenosa* (the type species of *Candovia*) form a monophyletic clade, with the latter taxon being paraphyletic. Further well-defined clusters are given by: *C. annulate* + spp. B and E; *C. strumose* + spp. C and F; *C. aberrate* + sp. D; *C. robinsoni* and *C. granulosa* + spp. A and H (Fig. 3). The pattern observed in the species-delimitation analysis for *C. coenosa* appears also here, with the sample PB-164 more related to the *C. spurcata* clade than to the putatively conspecific specimens.

Morphological analyses

Thanks to a detailed taxonomic analysis supported by molecular data, we present the description and illustration of seven new *Candovia* species from various parts of Queensland and New South Wales, including eggs, where available (named below as *C. alata* Brock & Jones sp. nov, *C. byfieldensis* Brock & Jones sp. nov., *C. dalgleishae* Brock & Jones sp. nov, *C. eungellensis* Brock & Jones sp. nov., *C. karasi* Brock & Jones sp. nov., *C. koensi* Brock & Jones sp. nov. and *C. wollumbinensis* Brock & Jones sp. nov.). These are placed in species groups also in agreement with molecular phylogenetic evidence. Finally, several new *Candovia* species combinations are proposed and removed from synonymy. To partially account for molecular suggestions, but also given clear-cut morphological characters, a new genus *Paracandovia* is erected: *P. cercata* (Redtenbacher, 1908) stat. rev., comb. nov., *P. longipes* (Brunner, 1907) stat. rev., comb. nov., *P. pallida* (Sjöstedt, 1918) comb. nov., *P. peridromes* (Westwood, 1859) comb. nov. and *P. tenera* (Brunner, 1907) stat. rev., comb. nov. Three taxa were removed from synonymy with *C. peridromes* (Westwood, 1859). Detailed images of type specimens will be available upon publication of this paper via the Phasmida Species File on-line http://phasmida.speciesfile.org (see Taxonomic account for details). A key to *Candovia* groups and a guide to *Candovia* and *Paracandovia* species are given in Supporting Information, File S1.

TAXONOMIC ACCOUNT

***Candovia* Stål, 1875: 12, 70.**

Type species:

Phasma (*Bacteria*) *coenosum* Gray, 1833: 28, pl. 2: 2 [= *Candovia coenosa*], by original monotypy.

Remarks:

Brock & Hasenpusch, 2007: 7, 70 (removed from synonymy with *Hyrtacus* Stål, 1875, in which it had been placed by Kirby, 1904: 331). Brunner, 1907: 301 [listed the type species as a synonym of *Hyrtacus eutrachelia* (Westwood, 1859)], Vickery, 1983: 7 (reinstated the type species as valid, as *Hyrtacus coenosa*). For other references, see Brock *et al.* (2021), but it is notable that Westwood (1859: 33) regarded the figure in Gray (1833) as being 'too large and robust' but he rightly points out that the female body has 'shrunk in various parts' and this is an accurate assessment. He illustrated a potential male on pl. 27: 2. To further add to confusion, several species currently in *Candovia* were regarded as belonging to *Parasipyloidea* Redtenbacher, 1908 by Vickery (1983) and Balderson *et al.* (1998); hence Brock & Hasenpusch, 2007 placed all Australian *Parasipyloidea* species and *Candovia coenosa* in *Candovia*, as a temporary step, in the knowledge that this needed splitting and that several other undescribed wingless, and even winged, species appeared to belong to this genus.

Description:

Small to medium-sized (40–89 mm), plain or mottled, in nature brown or green, sometimes (as in type species and some others) with central black marks at end of most body segments, usually wingless (if winged, can be short-winged in female), elongate (one species group with plumper females), moderately long to long-legged phasmids, with the body smooth, granulated or with sparse tubercles, the latter particularly conspicuous in females. Cerci short in both sexes.

Head at least as long as, or slightly longer than, wide. Head, pronotum and mesonotum smooth, sparsely or extensively granulose with some tubercles possibly present on mesonotum and metanotum, including laterally. Antennae exceeding length of forelegs, with numerous segments (up to 132); two basal segments broadened. Pronotum slightly shorter or equal in length to head, mesonotum long, 4.9–6.4 × length of pronotum; mesonotum 1.5–2.4 × combined length of metanotum and the shorter median segment. Wingless, except wings known in two species so far, which are short in the female of one species (forewings short, hindwings tiny) and hindwings in male reach up to just beyond the end of the fifth abdominal

segment. Anal segment in female rounded at tip, may be slightly incised in centre, with supra-anal plate just visible beneath. Operculum not broad, rounded at tip, almost reaching end of ninth abdominal segment to beyond it. Anal segment tip in male slightly triangular emarginated, poculum a modest size with rounded tip, reaching just over half length of ninth abdominal segment. Cerci short, slender but sometimes stout and hairy. Legs long, smooth; hindlegs reaching in excess of elongate abdomen (midlegs longer than many phasmids, only slightly shorter than hindlegs, except for some species in *C. strumosa* group, which have midlegs short, only just reaching beyond end of hind femora when set near body). Egg: oval or nearly so, or almost rectangular, some species with low raised, broad mound-like structure on operculum (Supporting Information, Fig. S3). Micropylar plate elliptical or spear-shaped. Capsule rugged appearance, with various sculpturing and sometimes pitted.

Distribution: Australia.

Species included:

***C. aberrata* group**

Candovia aberrata (Brunner, 1907) [aberrant stick insect]: New South Wales, Queensland.

Candovia dalgleishae [Dalgleish's stick insect] [= *Candovia* sp. D]: Queensland.

***C. annulata* group**

Candovia alata [winged candovia] [= *Candovia* sp. E]: Queensland.

Candovia annulata (Brunner, 1907) [banded-legged stick insect]: New South Wales, Queensland.

Candovia eungellensis [Eungella stick insect] [= *Candovia* sp. B]: Queensland.

***C. coenosa* group**

Candovia coenosa (Gray, 1833) [muddy stick insect]: New South Wales.

Candovia spurcata (Brunner, 1907) [Blue Mountain stick insect]: New South Wales

***C. robinsoni* group**

Candovia granulosa (Brunner, 1907) [granulated stick insect]: New South Wales, Queensland.

Candovia koensi [Koens's stick insect] [= *Candovia* sp. A]: Queensland.

Candovia robinsoni [Robinson's stick insect] (Brock & Hasenpusch, 2007): New South Wales, Queensland.

Candovia wollumbinensis [Wollumbin stick insect] [= *Candovia* sp. H]: New South Wales.

***C. strumosa* group**

Candovia byfieldensis [Byfield stick insect] [= *Candovia* sp. F]: Queensland.

Candovia karasi [Karas's stick insect] [= *Candovia* sp. C]: Queensland.

Candovia strumosa (Redtenbacher, 1908) [Richmond River stick insect]: New South Wales, Queensland.

Removed from the Australian list:

Candovia evoneobertii (Zompro & Adis, 2001) [Evoneoberti's stick insect], a species with long cerci thought to be 'introduced' to Brazil and Paraguay but misidentified as *Candovia*. Brock & Hasenpusch (2009) stated that this species belongs near *Paracalynda*Zompro, 2001. The species is now a synonym of Arumatia dubia (Caudell, 1904) (Ghirotto et al., 2022).

***Candovia alata* Brock & Jones sp. nov.**
(Supporting Information, Fig. S4A for female and S4B for male)

[winged candovia]

Zoobank registration: urn:lsid:zoobank.org:act:099FF0EA-9365-4786-94E6-8B5519ADB4EA.

Type material:

Holotype: ♀, QUEENSLAND, Blackdown Tableland National Park, 23.582˚S, 149.063˚E, 14.iii.2016, N. Tweed, DNA project PB-0184 (QM). *Paratypes:* QUEENSLAND: 1 ♂, same data, DNA project PB-0185 (QM); 2 ♂♂, same data, DNA project PB-0186 to PB-0187 (NHMUK). (Note, all DNA project data was provisionally labelled *Candovia* sp. E). Eggs also deposited in NHMUK (not paratypes).

Overview of both sexes:

Elongate body brown in both sexes, with lateral tubercles on thorax. Black line on head between eyes and also black, longitudinal line running length of body. Hindwings dusky brown, modest length. Legs indistinctly mottled.

Female

(Supporting Information, Fig. S4A*):* Damaged. Head: longer than wide. Antennae long, with numerous indistinct segments; basal segment and shorter segment 2 broader than remaining segments. Thorax: mesonotum with granules and several tubercles laterally. Pronotum slightly shorter than head, with central impression. Mesonotum 4.3 × length of pronotum. Mesonotum 1.5 × combined length of metanotum and median segment, the latter about same length as metanotum. Winged, hindwings of modest length. Abdomen: eighth to tenth segment similar in length. Operculum tapered to pointed tip, reaching end of anal segment; the anal segment has tapered sides towards tip, which is incised in centre. Cerci shorter than anal segment. Legs: long.

Male

(Supporting Information, Fig. S4B*):* Much slenderer, but similar in general appearance, with more black marks than female. Wings reach up to just beyond up of fifth abdominal segment. Anal segment tip slightly incised in centre; cerci shorter than segment. Poculum not reaching end of ninth abdominal segment.

Egg

(Supporting Information, Fig. S3A*):* Brown, dark and heavily sculptured in paler brown; broad, almost oval capsule. Micropylar plate pear-shaped, dark brown, surrounded by paler mottled area; whilst central, higher up than eggs of related species. Operculum dome-like and heavily sculptured.

Measurements (mm). Length of body:

Female 84, male 61–64. *Head:* female 4, male 2. *Antennae:* female 50 (tip broken), male 57–64. *Pronotum:* female 3.5, male 2. *Mesonotum:* female 15, male 10–11. *Metanotum:* female 5, male 3.5–4.0. *Median segment:* female 5, male 3.5–4.0. *Forewings:* female 5, male 3. *Hindwings:* female 36, male 28–30. *Femora, fore, mid, hind:* female 25, 19, 22, male 21–22, 16, 21–22. *Tibiae, fore, mid, hind:* female 24, 20, 27, male 25, 17–18, 25–26. *Cerci:* female 2.3, male 1.2–1.3. *Eggs:* capsule length 2, width 1.6, height 1.6.

Distribution

(Fig. 2*):* This species is so far only known from the Blackdown Tableland National Park.

Habitat and foodplants:

The species is found in forest edge, foodplants not recorded.

Etymology:

Named after the presence of wings in this species.

***Candovia byfieldensis* Brock & Jones sp. nov.**
(Supporting Information, Fig. S5A, B)

[Byfield stick insect]

Zoobank registration: urn:lsid:zoobank.org:act:C7C16BF6-C376-4D18-AB0B-B3770398D2CE.

Type material:

Holotype: ♀, QUEENSLAND, Byfield, 22.847˚S, 150.650˚E, 13.i.2013, N. Tweed, DNA project PB-0327 (QM). *Paratypes:* QUEENSLAND: 1 ♂, same data, except 09.i.2013, DNA project PB-0324 (QM); 1 ♂, same data, 09.i.2013, DNA project PB-0325 (NHMUK); 1 ♂, 1 ♀, same data, 18.i.2013, DNA project PB-0330 to PB-0331 (NHMUK); 1 ♀, same data, 15.i.2013, DNA project PB-0328; (NHMUK); 1 ♂, 1 ♀, Rossmoya Road, The Caves, 23.159˚S, 150.457˚E, 15.i.2012, DNA project PB-0271 to PB-0272 (NHMUK); 1 ♀, same data, 22.i.2012, DNA project PB-0258 (NHMUK); 1 ♀, same data, 04.ii.2012, DNA project PB-0261 (NHMUK); 1 ♀, Pistol Gap, 10 km SSE of Byfield, 10.i.1970, Britton, Holloway & Misco (ANIC). (Note, all DNA project data was provisionally labelled *Candovia* sp. F.) Eggs also deposited in NHMUK (not paratypes).

Overview of both sexes:

Female body fairly elongate, plain brownish green, head yellowish, mesonotum with sparse whitish tubercles, mainly laterally. Head with suffused blackish band from eyes to back of head. Antennae dark brown. The male has a dark greenish mesonotum and metanotum with pale yellowish brown head, pronotum and abdomen, both with black lines and streaks, including broad, black, median line on whole body, which may be broken in places. Antennae black. Both sexes have eyes with two horizontal, dark mauve to black lines.

Female

(Supporting Information, Fig. S5A*):* Head: longer than wide. Antennae longer than forelegs, with numerous indistinct segments; basal segment broad and much longer than segment 2. Thorax: pronotum slightly shorter than head, with central impression. Mesonotum about 6 × length of pronotum. Mesonotum 1.7 to 2.0 × combined length of metanotum and short median segment. Wingless. Abdomen: elongate eighth segment longer than ninth; the latter and tenth (anal) segment are of similar size. Operculum tapered to pointed tip, reaching up to half

length of segment, which has rounded tip. Cerci short. Legs: moderately long, hindlegs sometimes exceeding tip of abdomen.

Male

(Supporting Information, Fig. S5B*):* Apart from being much slenderer, similar in general appearance, except distinctive dark colour. Anal segment subtruncate at tip, cerci short, curved. Poculum reaching about half length of ninth abdominal segment.

Egg

(Supporting Information, Fig. S3C*):* Dark brown, with a modest amount of pale brown sculpturing, almost oval capsule. Micropylar plate central, broad and pointed at tip, slightly lighter shade of brown than capsule ground colour, surrounded by broad pale whitish brown area, as on opercular rim. Operculum with sculptured paler inner circle.

Measurements (mm). Length of body:

74–88 (holotype 76), male 59–68. *Head:* female 4–4.5, male 2.5–2.7. *Antennae:* female 60–70, male 55–65. *Pronotum:* female 3, male 2.3. *Mesonotum:* female 18–20, male 14–16. *Metanotum:* female 5.5–6.0, male 4–5. *Median segment:* female 3.5–4.0, male 2.7–3.0. *Femora, fore, mid, hind:* female 21–23, 16–18, 20–24, male 18–22, 18–20, 20–22. *Tibiae, fore, mid, hind:* female 24–26, 16–18, 24–27, male 20–28, 15–21, 22–29. *Cerci:* female 0.5, male 0.5. *Eggs:* capsule length 1.8, width 1.2, height 1.4.

Distribution

(Fig. 2*):* This species is fairly widespread in the Byfield area and also recorded 84 km away at The Caves.

Habitat and foodplants:

The species is found in rainforest edge and more open areas with saplings, foodplants include *Acacia* Mill. and *Eucalyptus* L'Hér. species.

Etymology:

Named after the main type locality, Byfield, which has some superb rainforest habitat, in gardens as well as national parks.

***Candovia dalgleishae* Brock & Jones sp. nov.**
(Supporting Information, Fig. S6A, B)

[Dalgleish's stick insect]

Zoobank registration: urn:lsid:zoobank.org:act:93A1D5CA-92ED-43A1-947D-503BD20B6009.

Type material:

Holotype: ♀, QUEENSLAND, Blackdown Tableland National Park, 23.582˚S, 149.063˚E, ii.2017, reared by B. Jones, DNA project PB-0168 (QM). *Paratypes:* QUEENSLAND: 3 ♂♂, same data, DNA project PB-0165 to PB-0167 (QM); 1 ♀, 3 ♂♂, same data, i.2017, N. Tweed, DNA project PB-0188 to PB-0191 (NHMUK). (Note, this DNA project data was provisionally labelled *Candovia* sp. D.)

Overview of both sexes:

Elongate, pale greenish female, each side of head with a narrow, part blackish longitudinal band, running from eyes to back of head. Upper part of pronotum with two black lines well separated from narrow black median line, which runs length of body. The male has a dark green thorax (except black pronotum, hind part of mesonotum and metanotum) with pale yellowish brown head and abdomen, both with black streaks. Antennae black. Both sexes have hind part of thoracic and abdominal segments with broad orange band (preceded by indistinct darkish marks and more distinct marks beneath), also brown legs. Eyes paler than head with horizontal black line.

Female

(Supporting Information, Fig. S6A*):* Head: longer than wide. Antennae long and pale, not as long as forelegs, with numerous indistinct segments, darkened at tip; basal segment and much shorter segment 2 broader than remaining segments. Thorax: smooth, pronotum slightly shorter than head, with central impression. Mesonotum just under 6 × length of pronotum. Mesonotum 1.5 × combined length of metanotum and short median segment. Wingless. Abdomen: elongate. Eighth segment much longer than ninth and tenth (anal), which are of similar size. Operculum tapered to tip, not reaching end of anal segment, which has rounded tip. Cerci short. Legs: elongate.

Male

(Supporting Information, Fig. S6B*):* Apart from being much slenderer, similar in general appearance, except distinctive dark colour. Anal segment rounded at tip; cerci short. Poculum reaching about half length of ninth abdominal segment.

Egg

(Supporting Information, Fig. S3E*):* Brown, dark with pale brown sculpturing, almost oval capsule. Micropylar plate central, broad and pointed at tip, lighter shade of brown than capsule ground colour, surrounded by broad pale whitish brown area.

Measurements (mm). Length of body:

female 89, male 60–66. *Head:* female 4, male 2.5. *Antennae:* female 25, male 53 (tips broken off in both sexes). *Pronotum:* female 3.5, male 2.5. *Mesonotum:* female 20, male 14. *Metanotum:* female 9, male 6.5. *Median segment:* female 4, male 3. *Femora, fore, mid, hind:* female 27, 21, 26, male 22, 22, 24. *Tibiae, fore, mid, hind:* female 30, 24, 31, male 30, 25, 33. *Cerci:* female 0.4, male -. *Eggs:* Capsule length 2.2, width 1.1, height 1.2.

Distribution

(Fig. 2*):* This species is widespread, at least in the Blackdown Tableland National Park (Beth Ripper, Noelene Tweed, pers. comm.).

Habitat and foodplants:

The species is found in forest and often seen paired, where they feed on *Acacia* and *Eucalyptus* spp., also accepted in captivity.

Etymology:

Named after Kirsten Dalgleish, a keen phasmid rearer who travelled a considerable distance to hand PDB samples of live *Candovia* spp. for molecular work.

***Candovia eungellensis* Brock & Jones sp. nov.**
(Supporting Information, Fig. S7A, B)

[Eungella stick insect]

Zoobank registration: urn:lsid:zoobank.org:act:27778BA0-C336-440F-82D1-C0978110A3F1.

Type material:

Holotype: ♂, QUEENSLAND, Broken River, Eungella National Park, 21.1681˚S, 148.5044˚E, 19.xi.2009, P.D. Brock, DNA project PB-0018 (QM). *Paratypes:* QUEENSLAND: 1 ♂, 2 ♀♀, same data, DNA project PB-0019 to PB-0021 (QM). (Note, this DNA project data was provisionally labelled *Candovia* sp. B), 2 ♂♂, 1 ♀, QUEENSLAND, Eungella National Park, late xii.1992 (the ♀ labels state 'laid eggs' the ♂♂ state reared from eggs laid in laboratory xii.1992). Hatched 15.ii.1993 and 15.xii.1993 respectively (ANIC).

Overview of both sexes:

Elongate green or brown female, possibly with darker marks and indistinctly banded legs. Male slenderer, brown with black marks laterally on pronotum, hind part of mesonotum, metanotum (more indistinct or absent in female), including specks on abdomen, apices of femora and tibiae. Whitish marks may also be present laterally. Head and pronotum with sometimes indistinct darker marks. Both sexes with black lines from eyes to back of head, orange mouthparts and eyes brown or orange with two horizontal black lines. Thorax granules and tubercles sometimes whitish. Dull-orange bands may be present on hind part of all thoracic and abdominal segments, with small black central mark, but this seems occasional and mainly in some females.

Female

(Supporting Information, Fig. S7A*):* Head: slightly longer than wide. Antennae long, with numerous indistinct segments; basal segment and shorter segment 2 broader than remaining segments. Thorax: with granules and tubercles, the latter more on mesonotum. Pronotum about same length as head, with central impression. Mesonotum up to 4.4 × length of pronotum. Mesonotum 2.4 × combined length of metanotum and median segment, the latter slightly longer than metanotum. Wingless. Abdomen: ridged, with granules. Eighth segment longer than ninth which is longer than tenth (anal) segment. Operculum tapered to tip, just exceeding end of segment 9; the anal segment has tapered sides towards tip. Cerci short. Legs: moderately long.

Male

(Supporting Information, Fig. S7B*):* Slenderer, but similar in general appearance, except for distinctive body patterning. Anal segment rounded at tip; cerci short. Poculum about reaching end of ninth abdominal segment.

Egg

(Supporting Information, Fig. S3F*):* Brown, dark with paler brown mottled sculpturing, broad almost oval capsule. Micropylar plate central, broad and pointed at tip, lighter shade of brown than capsule, surrounded by paler mottled area. Operculum dome-like and heavily sculptured.

Measurements (mm). Length of body:

female 71–75, male 53–55. *Head:* female 4–5, male 2.5. *Antennae:* female 54–60, male 60. *Pronotum:* female 4–5, male 2.3. *Mesonotum:* female 17–18, male 10. *Metanotum:* female 3.3–4.0, male 3.5. *Median segment:* female 3.7, male 3.5–4.8. *Femora, fore, mid, hind:*

female 22, 16, 20, male 18, 12, 17. *Tibiae, fore, mid, hind:* female 22, 14, 21, male 18, 11, 17. *Cerci:* female 1, male 0.8. *Eggs:* Capsule length 2.2, width 1.6, height 1.8.

Distribution

(Fig. 2*):* This species is so far only known from Eungella National Park.

Habitat and foodplants:

The species is found in forest edge, feeding on *Eucalyptus* spp. and others.

Etymology:

Named after the type locality, Eungella National Park, a superb area of subtropical rainforest, well known for its platypuses.

***Candovia karasi* Brock & Jones sp. nov.**
(Supporting Information, Fig. S8A, B)

[Karas's stick insect]

Zoobank registration: urn:lsid:zoobank.org:act:EB26E337-EC01-401E-8F84-E01AE5B878DB.

Type material:

Holotype: ♂, QUEENSLAND, Narrows Road, nr Baroon Pocket Dam, Montville, 26.6983˚S, 152.8656˚E, 10.xii.2009, A. Karas, DNA project JH-0070 (QM). *Paratypes:* QUEENSLAND: 1 ♀, same data, DNA project, JH-0068 (QM); 1 ♂, 2 ♀♀, same data, DNA project JH-0069, JH-0066, JH-0067 (NHMUK). (Note, this DNA project data was provisionally labelled *Candovia* sp. C.)

Overview of both sexes:

Female body greenish brown, with black marks on head and pronotum, also remainder of thorax and abdomen. Male more colourful, greenish brown with green mesonotum and black marks on head, pronotum and abdomen. Mesonotum and metanotum with sparse granules/occasional tubercles. Hind part of female abdominal segment 6 slightly swollen. Forewings and pre-anal part of hindwings dark brown, net-like with pale veins, hindwings dusky. Female short-winged with tiny hindwings, male long-winged, hindwings reaching beyond end of abdominal segment 5. In both sexes eyes are green and bases of antennal segments indistinctly pale banded.

Female

(Supporting Information, Fig. S8A*):* Head: slightly longer than wide. Antennae longer than forelegs, with numerous indistinct paler bands at base of segments; basal segment and much shorter segment 2 broader than remaining segments. Thorax: pronotum slightly shorter than head, with central impression. Mesonotum almost 5 × length of pronotum. Mesonotum 1.6 × combined length of metanotum and short median segment. Mesonotum and metanotum with sparse granules and few well-spaced tubercles on mesonotum. Forewings short, hindwings tiny. Abdomen: elongate. Eighth segment much longer than ninth and tenth (anal), which are of similar size. Operculum rounded at tip, reaching about half length of anal segment, which has almost truncate tip. Cerci short. Legs: all of modest length, hindlegs not reaching end of abdomen.

Male

(Supporting Information, Fig. S8B*):* Apart from being much slenderer, similar in general appearance, except wings. The forewings are truncate, hindwings reaching beyond end of abdominal segment 5. Anal segment rounded at tip; cerci short. Poculum reaching about end of ninth abdominal segment.

Eggs:

Unknown.

Measurements (mm). Length of body:

female 70–75, male 54–55. *Head:* female 3.5–3.6, male 2.4. *Antennae:* female 34–36, male 45. *Pronotum:* female 3.2, male 2. *Mesonotum:* female 15.0–15.5, male 9.8. *Metanotum:* female 4.2, male 2.8. *Median segment:* female 5.0–5.2, male 3.3. *Forewings:* female 2.0–2.3, male 2.8 *Hindwings:* female 1.8–2.0, male 27. *Femora, fore, mid, hind:* female 13–14, 9–10, 14, male 13, 8, 14. *Tibiae, fore, mid, hind:* female 12–13, 8–9, 15, male 14–15, 8, 16. *Cerci:* female 0.5, male 0.7.

Distribution

(Fig. 2*):* This species is so far only recorded from Montville.

Habitat and foodplants:

The species is found in forest, foodplants include *Eucalyptus* spp.

Etymology:

Named after Alexander Karas who supplied the research stock, via Jack Hasenpusch who kindly processed it before a visit by PDB.

***Candovia koensi* Brock & Jones sp. nov.**
(Supporting Information, Fig. S9A, B)

[Koens's stick insect]

Zoobank registration: urn:lsid:zoobank.org:act:5BCC0EB0-6241-4B45-A400-6133BBDE78F3.

Type material:

Holotype: ♀, QUEENSLAND, Narrows Road, nr Baroon Pocket Dam, Montville, 26.6983˚S, 152.8656˚E, 15.xi.2011, A. Karas, P.D. Brock & J. Koens, DNA project PB-0060 (QM). *Paratypes:* QUEENSLAND: 4 ♀♀, 2 ♂♂, same data, 04.ix.2009, J. Koens, DNA project, JH-0026 to JH-0031 (QM); 2 ♀♀, same data, xi.2009, A. Karus, DNA project, JH-0043 to JH-0044 (QM); 1 ♀, D'Aguilar Range, Boombana, 27.4045˚S, 152.794˚E, 13.xi.2011, P.D. Brock & N. Tweed, DNA project PB-0058 (QM). (Note, this DNA project data was provisionally labelled *Candovia* sp. A.)

Overview of both sexes:

Stout, brown female, with darker marks and indistinctly mottled legs, but can vary and include light and dark areas and whitish marks. Thorax heavily granulated and abdomen ridged. Small, orange marks may be present on thorax and thorax, also part of mouthparts. Male slenderer, brown with broad, black line laterally on body from back of eyes (orange line above this on mesonotum and metanotum). Darker on head, pronotum and towards hind part of thoracic and abdominal segments. Thorax with less distinct granules. Both sexes with eyes whitish with two horizontal black lines.

Female

(Supporting Information, Fig. S9A*):* Head: longer than wide, sparse granules present. Antennae long, with numerous indistinct segments; basal segment broader than remaining segments. Thorax: heavily granulated dorsally and ventrally. Pronotum slightly shorter than head, with central impression. Mesonotum up to 4.3 × length of pronotum. Mesonotum 1.7. × combined length of metanotum and median segment, the latter shorter than metanotum. Wingless. Abdomen: heavily ridged dorsally and ventrally, with granules, less numerous than on thorax. Eighth segment longer than ninth, which is about the same length as tenth (anal)

segment. Operculum reaching end of segment 9; anal segment tip tapered, with tip incised in centre. Cerci broad but short. Legs: long.

Male

(Supporting Information, Fig. S9B*):* Much slenderer, but similar in general appearance. Anal segment subtruncate at tip, cerci short. Poculum not reaching half length of ninth abdominal segment.

Eggs:

Unknown.

Measurements (mm). Length of body:

female 71.6–82.0, male 59–60. *Head:* female 4.2–5.0, male 3.2. *Antennae:* female 48–62, male 48. *Pronotum:* female 3.4–4.4, male 2.9. *Mesonotum:* female 14–19, male 13. *Metanotum:* female 5–6, male 4.4. *Median segment:* female 4–5, male 3.2. *Femora, fore, mid, hind:* female 17–20, 13–16, 15–20, male 21, 15, 20. *Tibiae, fore, mid, hind:* female 16–23, 11–16, 17–25, male 25, 16, 23.5. *Cerci:* female 0.6, male 0.5.

Distribution

(Fig. 2*):* This species is so far only known from Montville and Boombana.

Habitat and foodplants:

The species seen by forest tracks, feeding on various rainforest plants; often observed resting on ferns.

Etymology:

Named after John Koens who helped PDB research this species in the wild.

***Candovia wollumbinensis* Brock & Jones sp. nov.**
(Supporting Information, Fig. 10A, B)

[Wollumbin stick insect]

Zoobank registration: urn:lsid:zoobank.org:act:91D10862-1E32-4A7A-8ADF-91E5FF99AC34.

Type material:

Holotype: ♀, NEW SOUTH WALES, Mt. Warning (Wollumbin), 28.4˚S, 153.270278˚E, 14.ii.2017, B. Jones, DNA project PB-0174 (QM). *Paratypes:* NEW SOUTH WALES: 1 ♂, same data, DNA project, PB-0173 (QM). [Note, this DNA project data was provisionally labelled *Candovia* sp. H (initially thought to be *C. robinsoni*).]

Overview of both sexes:

Stout female, slenderer male, green with cream lateral stripe (in male running length of body, narrower stripe in female and mainly from thorax, low down); eyes whitish with two horizontal black lines. Narrow, black stripe running from eyes to back of head, but indistinct or partial in female. Mouthparts orange, also trochanters. Cerci pink.

Female

(Supporting Information, Fig. S10A*):* Head: longer than wide. Antennae long and hairy, with numerous indistinct segments; basal segment broader than remaining segments. Thorax: sparsely granulated and ridged. Pronotum shorter than head, with central impression. Mesonotum about 3.5 × length of pronotum. Mesonotum 1.8 × combined length of metanotum and median segment, the latter shorter than metanotum. Wingless. Abdomen: heavily ridged, with sparse granules. Eighth segment longer than ninth, which is longer than tenth (anal) segment. Operculum reaching end of anal segment, of which tip tapered at sides and incised in centre. Cerci short and slender. Legs: long, tibiae and tarsi hairy.

Male

(Supporting Information, Fig. S10B*):* Much slenderer, but similar in general appearance. Anal segment slightly triangular incised at tip, cerci short and slender, slightly incurved. Poculum reaching end of ninth abdominal segment.

Egg

(Supporting Information, Fig. S3K*):* Almost rectangular, heavily sculptured and rugged capsule, with keel; micropylar plate with surrounding area pale.

Measurements (mm):

Length of body: female 52.8, male 47.5. *Head:* female 3.6, male 2.8. *Antennae:* female 37, male 38. *Pronotum:* female 3.1, male 2.5. *Mesonotum:* female 10.7, male 10.8. *Metanotum:* female 3.6, male 3.3. *Median segment:* female 2.4, male 2.6. *Femora, fore, mid, hind:* female

13, 9.5, 13, male 15, 12, 16. *Tibiae, fore, mid, hind:* female 17, 11, 14, male 18, 10, 19. *Cerci:* female 1.4, male 1. *Eggs:* Capsule length 2.54, width 1.71, height 1.94.

Distribution

(Fig. 2*):* This species is so far only known from high altitude ~900–1000m in Mt. Warning (Wollumbin).

Habitat and foodplants:

The species occurs at the top of a mountain, foodplant(s) uncertain, but accepts *Eucalyptus* spp. in captivity.

Etymology:

Named after Mt. Warning (Wollumbin), given its English name by Captain Cook in 1770.

***Paracandovia* Forni *et al.*gen. nov.**

Zoobank registration: urn:lsid:zoobank.org:act:59B2EB61-EF82-4457-8421-B4CC58BF99B2.

Type species:

Paracandovia chiaroscuro, here designated.

This group has confused entomologists, with five described species (including three with revised status) being initially linked to five different mainly non-related genera, then later often transferred to other genera. Notably *Echetlus* Stål, 1875 was used by Zompro & Adis (2001), which is similar in general appearance, but has short, not long antennae, in addition to tiny forewings in known females, also long cerci in both sexes (only females in *Paracandovia*). *Candovia evoneobertii* (Zompro & Adis, 2001) was erroneously described in *Echetlus*, and this South American species is removed from the Australian phasmid fauna in this paper. As no existing generic name is appropriate for this particular group, it is necessary to erect a new genus. It became apparent when studying adults and eggs in detail, also considering molecular analyses, that samples originally identified as *P*. *peridromes* (PB178–PB180 and BJ13–BJ16) were not a single species, hence three other synonymized species (*cercata*, *longipes* and *tenera*) are reinstated as valid. The only one with distribution not known with certainty, nor egg, is *P. peridromes*. Other species from Western Australia and Three Hummock Island (near Tasmania) await formal description once further research has been undertaken. Molecular work indicates that this genus has a sister relationship to all *Candovia* species.

Description:

Small to medium-sized (45–118 mm), plain, in nature brown or green (sometimes with lines by head), wingless, elongate, long-legged, fragile-looking phasmids, with the body smooth, granulated or with tubercles, the latter particularly conspicuous in females. Abdomen with carina or ridges distinct or indistinct. Cerci long in females, short in male. Head much longer than wide (typically about 1.8 × longer). Head, pronotum and mesonotum often smooth, or sparsely granulose in some species. Mesonotum more heavily granulose in one species and tubercles noted in one species. Antennae exceeding length of forelegs, with numerous segments (up to 89); two basal segments slightly broadened. Pronotum equal in length or shorter than head, mesonotum long, 4.3–6.0 × length of pronotum; mesonotum 1.6–1.9 × longer than combined length of metanotum and the shorter median segment. Wingless. Anal segment in female rounded at tip, usually tapered at sides and may be triangular incised in centre, with supra-anal plate visible in some species. Operculum not broad, rounded at tip, reaching beyond end of ninth abdominal segment, up to half length of anal segment. Anal segment tip in male (where known) with rounded tip, poculum a modest size with rounded tip, not reaching end of ninth abdominal segment. Anal segment tips are splayed. Cerci long in female, 2.0–2.4 × length of anal segment; much shorter in male, no more than same length as anal segment. Legs long, smooth; hindlegs reaching in excess of elongate abdomen. Egg: more elongate, almost rectangular, possibly with indented micropylar plate. Micropylar oval or round. Capsule rugged appearance, with various sculpturing. Distribution: Australia.

Etymology:

Named after the close resemblance and affinity to *Candovia*.

Species included: The first five here transferred from *Candovia* Stål, 1875:

Paracandovia cercata

(Redtenbacher, 1908) [Sydney stick insect] stat. rev., comb. nov.: New South Wales (known from culture stock), Victoria [removed from synonymy with *Candovia peridromes* (Westwood, 1859), which was originally described in the genus *Bacillus*]. No molecular data were available for this taxon, but is supported by its different-shaped egg.

Paracandovia longipes

(Brunner, 1907) [Bowen Stick insect] stat. rev., comb. nov.: Queensland [lectotype locality Bowen = *sample Candovia* sp. I *from Dingo*]. The paralectotype from Western Australia is a misidentified female of *Echetlus peristhenes* (Westwood, 1859) [removed from synonymy with *Candovia peridromes* (Westwood, 1859)].

Paracandovia pallida

(Sjöstedt, 1918) [pale stick insect] comb. nov.: Northern Territory, Western Australia.

Paracandovia peridromes

(Westwood, 1859) [peridrome stick insect] comb. nov.: 'Australia' localities as yet uncertain, possibly Western Australia. No morphological nor molecular data were available for this species.

Paracandovia tenera

(Brunner, 1907) [Adelaide stick insect] stat. rev., comb. nov.: South Australia [type locality Adelaide, = *sample of 'peridromes' from Wilmington, SA*] [removed from synonymy with *Candovia peridromes* (Westwood, 1859)].

Paracandovia bifurcata sp. nov. [bilobed stick insect] [= 'peridromes']: South Australia.

Paracandovia chiaroscuro sp. nov. [Chiaroscuro stick insect] [= *Candovia* sp. G]: Queensland.

Paracandovia cloncurriensis sp. nov. [Cloncurry stick insect] [= *Candovia* sp. L]: Queensland.

***Paracandovia bifurcata* Brock & Jones sp. nov.**
(Supporting Information, Fig. S11A, B)

[bilobed stick insect]

Zoobank registration: urn:lsid:zoobank.org:act:CC72FDC8-078B-4808-A538-90569087852F.

Type material:

Holotype: ♀, SOUTH AUSTRALIA, Mount Gambier, 37.842931˚S, 140.764820˚E, ii.2017, B. Jones, DNA project PB-0180 (QM). *Paratypes:* 1 ♂, same data, DNA project PB-0178 (QM), 1 ♂, same data, DNA project PB-0179 (NHMUK). (Note, this DNA project data was provisionally labelled *Candovia peridromes*).

Description:

The female specimen is based on the only one found so far. Elongate, greenish brown, each side of head with a narrow, brown longitudinal band, running from eyes to back of head. The male is brown with reddish beneath mesothorax and metathorax.

Female

(Supporting Information, Fig. S11B*):* Head: twice as long than wide. Antennae long and pale, not as long as forelegs, with numerous indistinct segments; basal segment broader than remaining segments. Thorax: pronotum slightly shorter than head, with central impression. Mesonotum 4.6 × length of pronotum, with 18 tubercles laterally up to final third. Mesonotum 1.7 × combined length of metanotum and short median segment. Wingless. Abdomen: elongate, with two indistinct ridges each side. Length of eighth, ninth and tenth (anal) segments similar, although anal segment is a little shorter. End of anal segment with bilobed tip with supra-anal plate visible beneath. Operculum tapered to tip, reaching half length of anal segment. Cerci elongate, 2 × length of anal segment, tapered to tip. Legs: elongate.

Male

(Supporting Information, Fig. S11B*):* Apart from being much slenderer, similar in general appearance, except colour. Mesonotum 1.9 × combined length of metanotum and short median segment. Cerci appear short, less than length of anal segment, which is slightly triangular incised at tip. Poculum tapered towards rounded tip, not reaching end of ninth abdominal segment.

Egg

(Supporting Information, Fig. S3L*):* Brown, rough, heavily sculptured, almost oval capsule with darker markings. Micropylar plate darker brown, central and almost oval.

Measurements

(mm): Two males and 1 female. *Length of body:* female 62, male 45–51. *Head:* female 3.5, male 2.5–3.0. *Antennae:* female 33, male 29. *Pronotum:* female 3, male 2.0–2.4. *Mesonotum:* female 13.6, male 9–12. *Metanotum:* female 5.8, male 7.5. *Median segment:* female 2.4, male 1.4–1.5. *Femora, fore, mid, hind:* female 21, 16, 24, male 17, 14, 18. *Tibiae, fore, mid, hind:* female 22, 17, 25, male 17, 15, 19. *Cerci:* female 6, male 1. *Eggs:* Capsule length 1.8, width 1.3, height 1.4.

Distribution

(Fig. 2*):* The type series is from Mount Gambier and is expected to be found elsewhere in at least South Australia.

Habitat and foodplants:

The species was taken in forest.

Etymology:

Named after the bilobed anal segment.

***Paracandovia chiaroscuro* Brock & Jones sp. nov.**
(Supporting Information, Fig. S12A, B)

[Chiaroscuro stick insect]

Zoobank registration: urn:lsid:zoobank.org:act:26AC230F-4E1B-4D21-B279-4ADF9983A59A.

Type material:

Holotype: ♀, QUEENSLAND, Baralaba, Duaninga Road, 24.136˚S, 149.830˚E, 09.i.2013, N. Tweed, DNA project PB-0295 (QM). *Paratypes:* QUEENSLAND: 1 ♂, same data, except on 19.i.2013, DNA project PB-0305 (QM); 7 ♀♀, same data, except for dates as shown, DNA project PB-0290 on 20.xii.2012, PB-0293 and PB-0294 both on 31.xi.2012, PB-0310, PB-0311, PB-0312, PB-0313 all on 22.ii.2012 (NHMUK). (Note, all DNA project data was provisionally labelled *Candovia* sp. G). Eggs also deposited in NHMUK (not paratypes).

Overview of both sexes:

Elongate, green female with whitish sides, tip of abdomen, cerci and antennae (underside paler) basal area of legs brownish. Sometimes brown and may have a black, central line running length of the body, which can have black flecks; they can change shade in captivity. The male is invariably brown, darker on the dorsal surface, with a broad brown longitudinal band from eye to back of head and a black longitudinal lateral line running length of much of the body (second black sublateral line on mesonotum), also a broader whitish lateral stripe, reaching to about end of second abdominal segment. There is also an orange patch of the underside of the thorax. Eyes in both sexes with narrow brown stripe in centre.

Female

(Supporting Information, Fig. S12A*):* Head: twice as long than wide. Antennae long and slightly hairy, with numerous segments (*c*. 45, but indistinctly segmented and difficult to determine under a microscope), basal segment broader than remaining segments. Thorax: smooth, pronotum slightly shorter than head, with central impression. Mesonotum 4.8 × length of pronotum. Mesonotum also 1.6 × combined length of metanotum and short median segment. Wingless. Abdomen: elongate, with two indistinct ridges each side. Length of eighth, ninth and tenth (anal) segments similar, although anal segment is a little shorter. End of anal segment with rounded tip, supra-anal plate visible. Operculum tapered to tip, reaching

half the length of anal segment. Cerci elongate, 2 × length of anal segment, slightly hairy and tapered to tip. Legs: elongate.

Male

(Supporting Information, Fig. S12B*):* Apart from being much slenderer, similar in general appearance, except colour. Mesonotum 5.8 × length of pronotum, mesonotum 1.5 × combined length of metanotum and short median segment. Cerci appear short, but are the same length as anal segment, which is triangular incised at tip. Poculum tapered towards rounded tip, not reaching end of ninth abdominal segment.

Egg

(Supporting Information, Fig. S3N*):* Small, brown, rough, uneven and pitted but almost rectangular capsule with wide indentations, also raised ridge before operculum. Micropylar plate indented, surrounded by darker brown area.

Measurements

(mm): One male and 8 females. *Length of body:* female 66–76, male 56. *Head:* female 4–5, male 2.5. *Antennae:* female 37–44, male 54. *Pronotum:* female 3.6–4.5, male 2.3. *Mesonotum:* female 14–18, male 13. *Metanotum:* female 7.5–9.0, male 7.5. *Median segment:* female 2.5–3.2, male 1.5. *Femora, fore, mid, hind:* female 20–22, 18–20, 24–26, male 23, 20, 23. *Tibiae, fore, mid, hind:* female 19–21, 18–20, 24–28, male 22, 18, 25. *Cerci:* female 3–5, male 1. *Eggs:* Capsule length 1.9, width 1.2, height 1.3.

Note:

As is usual in phasmids, there can be variation in colour within a species. Detailed photographs will be uploaded to http://phasmida.speciesfile.org.

Distribution

(Fig. 2*):* The type series is from Baralaba (95 km NW of Biloela) but is likely to be found elsewhere in Queensland.

Habitat and foodplants:

The species was taken in forest with a dense understorey of grasses and low-growing plants feeding on a mixture of the latter. Grasses are sometimes dead, which may influence female body colour. In captivity they also accept *Eucalyptus* spp. and *Acacia* spp. It has been noted as adults so far at least between December and February.

Etymology:

Named after *chiaroscuro* (from the Italian chiaro, ‘light,’ and scuro, ‘dark’) due to the contrast of green dorsal and whitish lateral and ventral surface, similar to strong contrasts of light and dark (a technique used in the visual arts).

***Paracandovia cloncurriensis* Brock & Jones sp. nov.**

(Supporting Information, Fig. S13A, B)

[Cloncurry stick insect]

Zoobank registration: urn:lsid:zoobank.org:act:535570ED-0C5E-4AE6-AFBE-26F3519719E0.

Holotype:

♀, QUEENSLAND, Fountain Springs Rest Area, Cloncurry, 60 km E of Mount Isa, 20.800˚S, 139.996˚E, 30.i.2018, B. Jones, DNA project BJ-0095 (QM). (Note, this DNA project data was provisionally labelled *Candovia* sp. L.)

Overview of female:

A single female only found so far (in poor condition, with only three legs intact). Elongate, greenish brown, each side of head with a broad, dark-brown longitudinal band, running from eyes to back of head, followed by broad lateral whitish band. Lower part of pronotum dark brown, narrow longitudinal sublateral dark line either side of thorax.

Female

(Supporting Information, Fig. S13A*):* Head: twice as long than wide. Antennae long and pale, tips broken, but presumed longer than forelegs, with numerous indistinct segments, basal segment broader than remaining segments. Thorax: smooth, pronotum slightly shorter than head, with central impression. Mesonotum 6 × length of pronotum. Mesonotum 1.9 × combined length of metanotum and short median segment. Wingless. Abdomen: elongate. Length of eighth, ninth and tenth (anal) segments similar, although ninth segment is a little shorter. End of anal segment with tapered tip. Operculum tapered to tip, reaching almost end of anal segment. Cerci elongate, 2 × length of anal segment, tapered to tip. Legs: elongate.

Male:

Unknown.

Egg

(Supporting Information, Fig. S3O*):* Greyish, rough, almost oval capsule with large black spots and markings. Micropylar plate black, low down, surrounded by lighter area.

Measurements (mm): One female. *Length of body:* 84. *Head:* 4.3 *Antennae:* 50 + but tips broken off. *Pronotum:* 3.7. *Mesonotum:* 22. *Metanotum:* 8. *Median segment:* 2. *Femora, fore, mid, hind:* 22, 20, 25. *Tibiae, fore, mid, hind:* 22, ? damaged, 29. *Cerci:* 6. *Eggs:* mislaid, not available for measurement.

Distribution

(Fig. 2*):* The type series is from Cloncurry and is likely to be found elsewhere in the vicinity, in Queensland.

Habitat and foodplants:

The species was taken in forest with understorey near the permanent waterhole of Fountain Springs, on spinifex.

Etymology:

Named after the type locality, Cloncurry.

DISCUSSION

A consensus on which is the more robust method for molecular species delimitation is lacking, and different methods can outperform, depending on the specific characteristics of a dataset (Luo *et al.*, 2018). Therefore, the combination of different species-delimitation approaches and phylogenetic reconstruction methods (Tang *et al.*, 2014) gave us more confidence in exploring the diversity of this phasmid clade. Although all methods, whether distance (ABGD) or tree-based (PTP and GMYC), were able to detect most interspecific boundaries, the use of a single approach could have been misleading in some instances. Generally, the different species-delimitation analyses consistently recognized previously described species and identified new putative species (spp. A–L; Fig. 2). For some lineages, the GMYC method highlighted some degree of intraspecific divergence, for example specimen JH-0027 of sp. A, specimens PB-0261 and PB-0271 of sp. F and five specimens of *C. annulata*. This could be due to either general properties of our dataset, including unbalanced geographical range sampling, skewed species abundances and the availability for analyses of a single specimen (Talavera *et al.*, 2013; Ahrens *et al.*, 2016), or because of paraphyly/polyphyly of some clades (Hendrich *et al.*, 2010; Scicchitano *et al.*, 2018).

Interestingly, the intraspecific differentiation observed in *C. annulate* corresponds to samplings at different geographic areas (Montville and Apple Tree Park – Springbrook). Therefore, the geographical ground of the observed pattern suggests the presence of structured populations that may represent different subspecific entities. A peculiar situation is seen with specimen PB-164 of the *C. coenosa* species, recognized as a different entity by all species-delimitation methods except the mPTP method. Although this could be due to the paraphyly of *C. coenosa*, which is also confirmed by phylogenetic analyses with high nodal support (see below), it is possible that specimen PB-164 may represent a more differentiated taxon. Despite a substantial proportion of species-level diversity being represented by species described on a single specimen (Lim *et al.*, 2012), in our opinion, only a wider sampling of specimens from different geographical locations will allow to properly describe the aforementioned lineage. Overall, data observed here do not seem to suggest significant deviations from known or provisional taxonomy, especially considering that inferences drawn from species-delimitation approaches should rely on a conservative consensus (Carstens *et al.*, 2013). The results of the detailed analyses on body and egg morphology well match molecular species delimitation; formal descriptions of novel taxa are presented in the Taxonomic account in the Results with keys to *Candovia* groups/species, also including egg morphology, which in some lineages appear to be a more reliable character than traditional body morphology (Scali *et al.*, 1987; Sellick, 1988; Cubillos & Vera, 2020 and references therein).

The phyletic relationships in the clade appear well defined, despite a general decrease of nodal support at the deeper nodes (Fig. 3), and agree with morphological characters (such as leg length and egg morphology) allowing species identification of the *Candovia* groups (see Taxonomic account and Supporting Information, File S1 for details).

While in the present analysis the nodal support of the clade monophyly is high (BS:90; PP:1.0), it is to be noted that the dataset for comparison is fairly limited, as no other Australian Necrosciinae species were available for comparison. Moreover, two recent studies considering all Phasmida provided contrasting evidence, showing this clade either monophyletic (Forni *et al.*, 2022) or paraphyletic (Bank & Bradler, 2022). Therefore, the possible monophyly of the clade should be reconsidered after a more extensive taxon sampling. On the other hand, body and egg morphological characters are clear-cut in defining an intraclade divergence of generic level, so that a split of the genus *Candovia* into two genera (*Candovia* and *Paracandovia*) is below reported (see Taxonomic account for details), which coincides with differences in morphological characters, although this genus has up to now been largely neglected by researchers and poorly understood, hence previous errors in synonymy. At variance with some intraspecific divergences retrieved in the species-delimitation analysis, no clear geographical pattern emerges from the phylogenetic analysis. Most *Candovia* taxa are distributed along the eastern Australian coasts, with overlapping ranges. Yet, the newly erected *Paracandovia* genus appears to have a broader geographic

distribution, with *P. pallida* found in central-western Australia, *P. cloncurriensis* collected from central Australia and *P. longipes* and *P. chiaroscuro* from the east coast.

As for *Candovia coenosa–spurcata* relationships, also the sample morphologically identified as *Candovia peridromes*, they have revealed a situation that will require a more extensive sampling to be clarified. When considering morphological and molecular analyses, the samples initially identified as *C*. *peridromes* (PB178-PB180 and BJ13-BJ16) were retrieved as multiple species, and morphologically differentiated from *C. peridromes*, thus reinstating as valid its synonyms *P. cercata*, *P. longipes*, *P. tenera* (all now placed in the new genus *Paracandovia*). Further analyses are required for *P. peridromes* itself, along with: (1) *P. cercata*, which is reinstated as valid on the basis of eggs morphology observations (Supporting Information, Fig. S3); (2) *P. tenera*, which is reinstated as valid in molecular analyses (Figs 2, 3); and (3) *P. longipes*, which is also reinstated as valid on molecular ground. For the two latter species, a formal description is in preparation, but additional samples are necessary.

The phylogenetic analysis presented here provides a framework to correctly identify the morphological characters that can be used for clade taxonomy, but also allows a better understanding of taxa evolution. Phasmida taxonomy often relies on egg morphological character, like the capitulum (Clark, 1976; O'Hanlon *et al.*, 2020): the function of this lipid-rich extension of the operculum was not understood until recently, when it was shown to serve as a reward to promote ant-mediated dispersal of the egg (myrmecochory; Compton & Ware, 1991). This adaptation represents one of the most extraordinary examples of convergent evolution across different kingdoms of life, where the capitulum in phasmid eggs is analogous to elaiosomes of angiosperm seeds (Stanton *et al.*, 2015). Both structures are used to exploit ant behaviour: this mutualistic relationship allows for both plant seeds and phasmid eggs to be buried in the soil, protected from environmental changes, predators and parasites, also greatly enhancing the dispersal abilities of the species (Hughes & Westoby, 1992). A study on an African phasmid species also suggests the possibility to escape recurrent bushfire when ants drag the egg into their nest (Compton & Ware, 1991). *Candovia aberrata*, *C. coenosa* and *C. spurcata* lay eggs with a capitulum, (Supporting Information, Fig. S3) and mapping this character on to our phylogenetic tree (Fig. 3) suggests the non-monophyly of this feature. At the order level, it has been shown that capitula probably evolved independently in several lineages across the phasmid tree of life (Robertson *et al.*, 2018 and references therein), but to our knowledge this has never been proposed among congeneric species. It is interesting to note that, although belonging to different phylogenetic clusters, the three *Candovia* species that present the capitulum, have strictly overlapping distribution in the southern part of the Australian east coast. Further efforts should investigate whether the presence of a capitulum can be linked to local adaptations, such as the presence of a particular ant species performing myrmecochory. Recently, a strong interest has been renewed towards the patterns of wing evolution in Phasmida (Bank & Bradler, 2022; Forni *et al.*, 2022). Among the

newly described species, two species (*C. alata* and *C. karasi*) present males with fully developed hindwings and females with reduced hindwings. The latter represents the first winged species in this previously considered apterous clade. As such, the observed pattern may support the phenomenon initially proposed by Whiting *et al.* (2003): wings were absent in extant phasmid ancestors, to which they subsequently reverted back independently in several instances throughout their evolutionary history.

CONCLUSIONS

Molecular analyses represent a reliable framework to refine taxonomy and systematics, and to reconsider diagnostic characters for species description and identification in this Australian phasmid clade. While this work represents a substantial step forward, further species collection and rearing is needed – including similar specimens from different geographical areas, which may prove to be valid, cryptic species. Museum collections could also represent useful resources, with a large amount of material available in Australia clearly suggesting the presence of additional undescribed taxa, not considered in this study. Furthermore, molecular data for *P. peridromes* and *P. cercata* are still lacking, as their distribution remains uncertain, and no samples were available for molecular analyses. Nonetheless, our effort represents a way forward to better understand the phenomena underlying the evolution and diversification of this overlooked, yet remarkable, clade.

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