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RESEARCH ARTICLE

Deconstructing the Australian *Tetrix* (Orthoptera: Tetrigidae): three new genera and a new species, *Cyphotettix ellurae*

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Abstract. Until now, the Australian fauna of Tetriginae has been represented predominantly by the genera *Paratettix* Bolívar, 1887 and *Tetrix* Latreille, 1802, with the latter mostly consisting of apterous species. The Australian members of these genera show remarkable morphological diversity, which prompted us to reexamine the relationships between them using cladistic analysis based on morphological characters of head and thorax. We have found that the Australian *Tetrix* spp. are easily separable into three distinct genera: *Captivus* gen. nov., *Custodia* gen. nov., and *Enattor* gen. nov. Additionally, we describe a new species of the Tetriginae genus *Cyphotettix* Rehn, 1952, *C. ellurae* sp. nov. We provide an identification key to the Australian Tetriginae genera and hypothesize that the apterous species are related to *Tetrix collina* Rehn, 1952.

Key words. Orthoptera, Tetrigidae, *Custodia*, *Captivus*, *Enattor*, new genus, new species pygmy grasshopper, taxonomic revision, wingless, Australia

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Introduction

The Tetrigidae family, commonly known as pygmy grasshoppers, comprises approximately 2000 described species (Cigliano et al. 2025). This family thrives in diverse habitats across the globe and is characterized by its members' small size. Tetrigidae are cosmopolitan but are predominantly distributed in tropical regions, including those of Australia (Cigliano et al. 2025, Kasalo & Skejo 2024). The Australian Tetrigidae represent a taxonomically neglected group as evidenced by the limited scholarly attention they have received (Sjöstedt 1932, 1936; Rehn 1952; Kasalo et al. 2023a; Kasalo & Skejo 2024). While 48 species are currently recognized, the existing literature is sparse (Cigliano et al. 2025). This lack of investigation implies a high probability of undiscovered species and necessitates comprehensive taxonomic revisions to accurately delineate the diversity within this family on the Australian continent (Kasalo & Skejo 2024).

Rehn's (1952) extensive descriptions of new Tetriginae species, all initially categorized within the genus *Tetrix* Latreille, 1802, have presented enduring taxonomic challenges. The cosmopolitan nature of *Tetrix*, coupled with its poorly defined boundaries, has resulted in the inclusion of numerous species that are likely misclassified (Devriese et al. 2023). This issue extends to related genera, notably *Paratettix* Bolívar, 1887, further complicating the accurate delineation of species boundaries (Devriese et al. 2023). Apterous forms within Tetrigidae, exemplified by the tribes Metrodorini, Echopraxiini, and Quasimodini (Kasalo et al. 2023b, Kasalo & Skejo 2024), are particularly problematic as convergent evolution obscures phylogenetic relationships and hinders the estimation of divergence times from winged ancestors (Skejo et al. 2024). Namely, winglessness is often correlated with a robust body, pronotal projections, and tuberculated legs, all of which could arise independently as adaptations to a corticolous and largely immobile lifestyle (Rebrina et al. 2025). This underscores the necessity of using less variable characters for taxonomic classification, like head characters and the morpho-

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logy of the pronotal carinae (Devriese et al. 2023, Kasalo & Skejo 2024).

Interestingly, the genus *Cyphotettix* Rehn, 1952 was initially placed within Metrodorinae (Rehn 1952) and currently lacks subfamilial classification. According to Rehn (1952), it comprises two species, *Cyphotettix camelus* Rehn, 1952 and *Cyphotettix tindalei* Rehn, 1952. However, a significant number of morphologically similar taxa within the Australian Tetriginae, presently assigned to *Tetrix* and the globally distributed *Paratettix*, suggest the possibility of substantial underestimation of diversity. The latter genus likely represents a conglomeration of multiple distinct genera, as evidenced by recent revisions such as the work by Devriese et al. (2023) on the African *Paratettix*. Consequently, a critical reevaluation of the Australian *Tetrix* complex is urgently required to establish a robust and workable taxonomic framework, particularly prior to the integration of molecular phylogenetic data, the quality of which depends on the selection of a taxonomically representative sample.

This research endeavors to address the taxonomic complexities within the Australian Tetriginae, specifically focusing on the genus *Tetrix* and the enigmatic *Cyphotettix*. The primary objective is to undertake a comprehensive revision of Australian *Tetrix* utilizing a cladistic analytical framework. Furthermore, this paper will contribute to the understanding of *Cyphotettix* by describing a previously unrecognized species. The combined objectives of revising *Tetrix* and describing a new *Cyphotettix* species underscore the study's commitment to advancing the systematic knowledge of Australian pygmy grasshoppers, laying a foundation for future molecular phylogenetic investigations.

Materials and methods

Measurements were made in ImageJ 1.53t (Bourne 2010) following Tumbrinck (2014) and Skejo & Kasalo (2024). Taxonomy and type locality data follow the Orthoptera Species File (Cigliano et al. 2025). Type specimens of *Cyphotettix ellurae* sp. nov. were collected by Brett and Marie Smith in Ellura Sanctuary and deposited at the Australian National Insect Collection (ANIC), where they were photographed. The distribution map (Fig. 1) was created using QGIS 3.34.8 (QGIS Development Team 2024). Type specimens of other species are deposited at the Swedish Museum of Natural History, Stockholm (NHRS), Naturhistorisches Museum Wien (NMW), Natural History Museum, London (NHMUK), Museum für Naturkunde Berlin (MfN), Australian Museum, Sydney (AM), and Museum of Comparative Zoology, Cambridge (MCZ).

A cladistic matrix consisting of 19 species and 11 morphological characters was prepared (Tables 1 and 2). The selected species were assigned to the genera *Tetrix* and *Paratettix* until now. The characters were selected based on their previously identified taxonomic importance (Devriese et al. 2023, Kasalo & Skejo 2024). Character states are described in Tables 1 and 2, and illustrated in Figs 2 and 3. Some characters were omitted because they were uninformative (with identical states in all considered species) or because they could not be reliably observed in the old photographs, which are the only available material for some species. The characters used in this study were previously determined not to be significantly variable among specimens of the same species (Kasalo & Skejo 2024). To code the character states of each species, type specimens were examined (Table 3). *Paratettix nigrescens* Sjöstedt, 1921 was selected as an outgroup because the rectagular, narrow, and low vertex, the placement of frontal costa bifurcation, low median carina, and pauropronotal form all suggest that it is more closely related to other *Paratettix* species than to *Tetrix* and its relatives (Devriese et al. 2023). The relationships between the Australian *Paratettix* species are well beyond the scope of this study as *Paratettix* requires a comprehensive revision (Devriese et al. 2023).

The cladistic analysis was performed using the „implicit enumeration“ option in TNT (Goloboff & Morales 2023). All multistate characters were treated as additive, i.e. we hypothesize an order in which the character states can transition from one to another. Namely, the rounded vertex is intermediate between the straight vertex and the triangular vertex, which is just an extension of an already rounded one. The width of the pronotal apex is unlikely to freely change from narrow to wide without first assuming the „moderate width“ state. Similarly, the elevation of the median carina has been observed to be a stable character that is unlikely to rapidly shift between the extremes (Kasalo & Skejo 2024). Finally, the shape of the anterior margin of the pronotum can assume three states: straight, rounded, and triangular. We labeled the margin as triangular both if it bears a sharp spine and if its middle part is shaped like a small blunt triangle (e.g. *Tetrix collina* Rehn, 1952). We labeled the margin as rounded only in cases where it is strongly uniformly rounded. The cladogram was visualized using iTOL (Letunic & Bork 2024).

Results

Cladistic analysis

The cladistic analysis produced a single most parsimonious tree (length = 29 steps, consistency index = 0.55, retention index = 0.84), which is depicted in Fig. 4. *Tetrix collina* is reconstructed as sister to all other Australian wingless Tetriginae. Within the wingless clade, three monophyletic groups were recovered in the analysis, which we treat here as the genera *Enattor* gen. nov., *Cyphotettix* gen. nov., and *Captivus* gen. nov. The three together constitute a monophyletic group, which is sister to *Custodia* gen. nov. Notably, the relationships between the three aforementioned genera, and *Custodia accola* (Rehn, 1952) comb. nov. and *Custodia montivaga* (Rehn, 1952) comb. nov. were left unresolved in the analysis. Nevertheless, we group these two species in a new genus because they share a high placement of the frontal costa bifurcation in relation to the position of the paired ocelli (see the *Custodia* section below). This character was not included in the cladistic analysis as it cannot be reliably observed in many of Rehn's (1952) depictions, but its state in *Custodia* seems to be unique and apomorphic.

The other genera have clearly identifiable synapo-

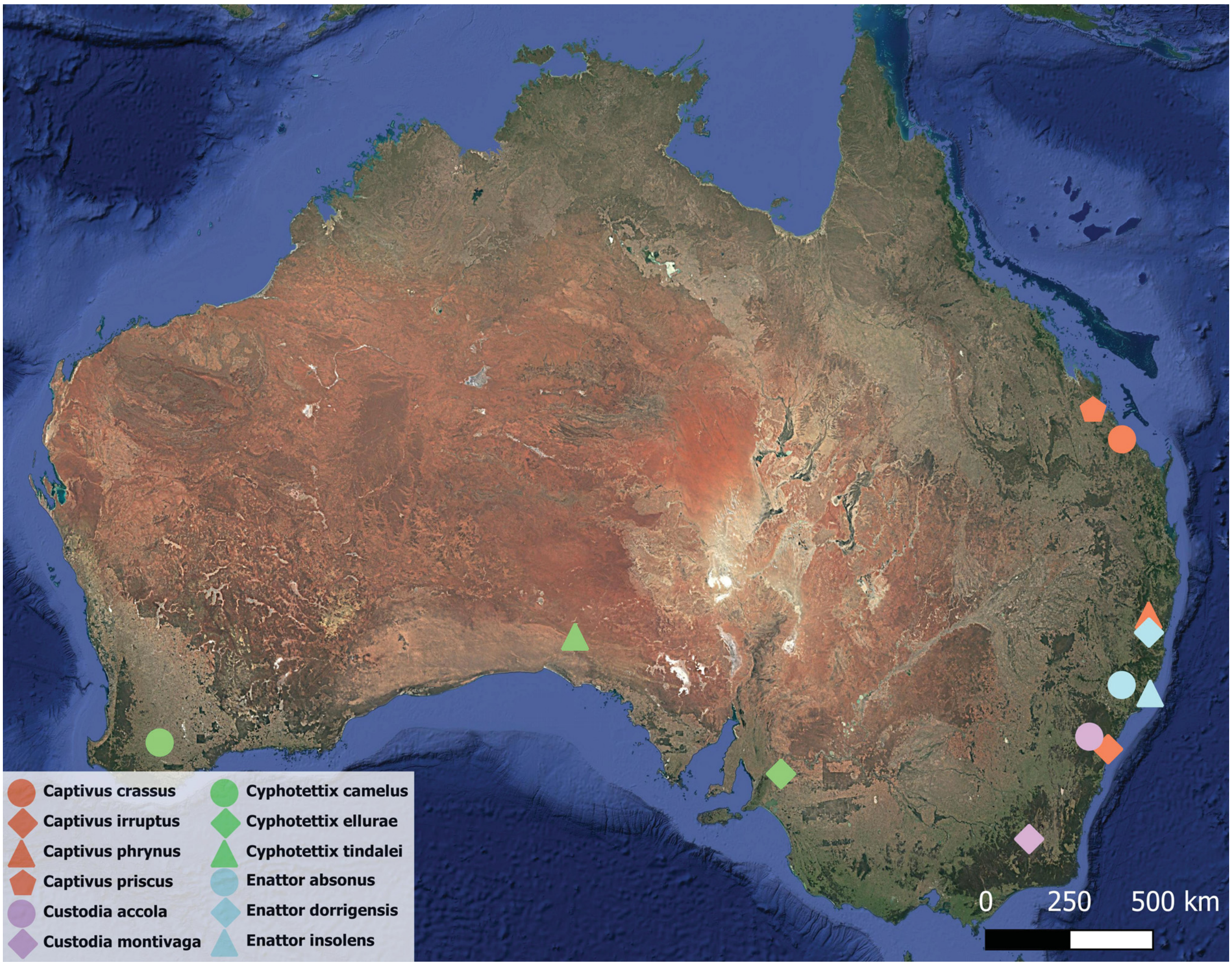

Fig. 1. Type localities of *Captivus* gen. nov., *Custodia* gen. nov., *Cyphotettix* Rehn, 1952, and *Enattor* gen. nov. species.

Table 1. Characters used in the cladistic analysis and description of their states.

Character	States
Head	
1. Frontal costa length	0 – short (quarter of the eye height or shorter); 1 – elongated (around half of eye height or longer)
2. Vertex elevation	0 – base of vertex not elevated above eyes in frontal view; 1 – elevated
3. Vertex width	0 – approximately equal to eye width; 1 – wider than eye
4. Vertex protrusion	0 – not protruding past eyes; 1 – protruding past eyes
5. Anterior margin of vertex shape	0 – straight; 1 – rounded; 2 – triangular
Pronotum	
6. Prozona length	0 – shorter than eye in dorsal view; 1 – longer than eye
7. Median carina shape	0 – low; 1 – anterior part moderately to strongly elevated; 2 – elevated throughout
8. Pronotal apex shape	0 – narrow (narrower than half of prozona width); 1 – moderately wide (about as wide as prozona); 2 – wide (distinctly wider than prozona width)
9. Anterior margin of pronotum shape	0 – straight; 1 – rounded; 2 – triangular
Wings	
10. Hind wings	0 – absent; 1 – reduced (shorter than pronotum); 2 – full length (as long as pronotum or longer)
11. Tegmina	0 – absent; 1 – present

morphies and reverse homoplasies. *Enattor* gen. nov. is defined by straight anterior margin of the pronotum, which is triangular in other considered species and which represents a reversal to the state of this character present in the outgroup. *Cyphotettix* is defined by strongly protruding triangular vertex (shared only with *C. montivaga* in which the vertex is much lower in anterior view than in *Cyphotettix*) and highly elevated median carina. *Captivus* gen. nov. is defined by the base of the vertex not being visibly elevated above the eyes in anterior view, which is the case for all other species except for *T. collina* and the outgroup, marking another reverse homoplasy. Further, *C. irruptus* (Bolívar, 1887) comb. nov. is shown as sister to the other *Captivus* species, which share short frontal costa and short prozona. Representatives of all newly described genera are depicted in Fig. 5.

Regarding the intergeneric relationships, *Captivus* gen. nov. is reconstructed as sister to *Cyphotettix*, which are together sister to *Enattor* gen. nov. The species of *Custodia* gen. nov. are basal in the wingless Tetriginae clade. As discussed later, we do not treat the suprageneric groupings as phylogenetically informative.

Taxonomy

Family Tetrigidae Rambur, 1838
Subfamily Tetriginae Rambur, 1838
Genus *Captivus* gen. nov.

Type species. *Tettix priscus* Bolívar, 1887, here designated.

Diagnosis. Apterous and brachypronotal. Anterior margin of pronotum triangular. Prozona relatively short, approximately as long as eye in dorsal view. Pronotal apex moderately wide to narrow, weakly bilobate. Median carina forming a moderately tall hump in the anterior half of its length. Vertex wider than eye in dorsal view, slightly protruding past the eyes, rounded. Midline of antennal grooves in line with ventral margin of eyes. Frontal costa very short, nearly non-existent. Vertex flat in anterior view.
Composition. *Captivus priscus* (Bolívar, 1887), comb. nov. (from *Tettix*), *Captivus phrynus* (Rehn, 1952) comb. nov. (from *Tetrix*), *Captivus irruptus* (Bolívar, 1887) comb. nov. (from *Tettix*), *Captivus crassus* (Sjöstedt, 1936) comb. nov. (from *Paratettix*).
Distribution. Eastern Australia (Fig. 1).
Etymology. Latin second declension noun *captivus*, *captivi* (prisoner) of masculine gender. This genus name refers to the long imprisonment of these species in the Australian *Tetrix*.
Note. *Captivus irruptus* comb. nov. is at first glance highly similar to the other species in this genus, but it differs from them in having a visibly longer frontal costa (meaning that all the facial features are shifted ventrad when compared to its congeners), and a slightly crown-like vertex. This placement is tentative until more data is gathered.

Genus *Custodia* gen. nov.

Type species. *Tetrix montivaga* Rehn, 1952, here designated.

Diagnosis. Apterous and brachypronotal. Anterior margin of pronotum rounded. Prozona extremely long with prominent prozonal carinae. Pronotal apex narrow, rounded. Median carina forming a small hump above prozona. Vertex wider than eye in dorsal view, moderately protruding past the eyes, rounded or slightly triangular. Midline of antennal grooves in line with ventral margin of eyes. Frontal costa very short, nearly non-existent. Frontal costa bifurcation dorsad of paired ocelli by about two ocellus radiuses. Vertex slightly elevated in anterior view, rounded, with the medial carina protruding above the base of vertex.
Composition. *Custodia montivaga* (Rehn, 1952) comb. nov. (from *Tetrix*), *Custodia accola* (Rehn, 1952) stat. & comb. nov. (from *Tetrix irrupta accola* Rehn, 1952).
Distribution. Southeastern Australia (Fig. 1).
Etymology. Latin first declension noun *custodia*, *custodiae* (prisoner) of feminine gender. This genus name refers to the long imprisonment of these species in the Australian *Tetrix*.
Note. Although the analysis does not group the two species of this genus into a clade with a clear synapomorphy, they are highly similar to each other except for the exact shape of the anterior margin of the pronotum (rounded but wavy in *C. accola* gen. & comb. nov., bluntly rounded in *C. montivaga* gen. & comb. nov.) and the shape of the vertex (rounded in the former, triangular in the latter). Future research might show them to be more distantly related and separable according to these characters, but until more data is gathered, we group them in a single genus since both of them strongly differ from the other wingless Australian species. The most notable similarity that groups these two species together is the high placement of the frontal costa bifurcation in relation to the paired ocelli (see the diagnosis), which might suggest shared ancestry even if these species are separated at the generic level in the future. This is due to the fact that head morphology in Tetrigidae has been shown to carry phylogenetic signal (Devriese et al. 2023).

Genus *Cyphotettix* Rehn, 1952

Type species. *Cyphotettix camelus* Rehn, 1952 by original designation.

Diagnosis. Apterous and brachypronotal. Anterior margin of pronotum triangular (strongly in *C. ellurae* sp. nov., weakly in *C. tindalei*) or straight (in *C. camelus*). Prozona relatively short, a little longer than eye in dorsal view. Pronotal apex very wide, weakly bilobate. Median carina elevated throughout its length, either uniformly elevated or forming a rounded hump above humeral angles (in *C. camelus*). Vertex wider than eye in dorsal view, strongly protruding past the eyes, distinctly triangular. Midline of antennal grooves in line with ventral margin of eyes. Frontal costa long, extended above the eyes due to the elevation of the vertex. Vertex strongly elevated in anterior view, dome-like.
Measurements (mm) (see Table 4).
Composition. *Cyphotettix camelus* Rehn, 1952 (Fig 6A–C), *Cyphotettix tindalei* Rehn, 1952 (Fig 6D–E), *Cyphotettix ellurae* sp. nov. (Figs 7–9).
Distribution. Southern and southwestern Australia (Fig. 1).

Note. *Cyphotettix camelus* is morphologically quite distinct from the other two *Cyphotettix* species. Although all three are obviously related to each other, the fact that they are known from only a few localities across almost the entire southern Australia could imply that *Cyphotettix* is a much larger and more diverse group than is currently known.

Cyphotettix ellurae sp. nov.

(Figs 7–9)

Type material. Holotype: ♀, Australia, Ellura Sanctuary, 25 km East of Cambrai, SA; -34.591256, 139.497462; 29.V.2023; B. and M. Smith leg. (ANIC). Paratypes: 2 ♂♂ 1 ♀, the same data as holotype (Figs 7–8).

Differential diagnosis. Differs from *C. camelus* in uniformly elevated median carina (bulging in anterior half in *C. camelus*), more prominent teeth on ventral margin of anterior femur, vertex protruding farther in front of eyes, and in transverse carinae not reaching the medial carina of vertex (joining the medial carina in *C. camelus*). Differs from *C. tindalei* in more prominent teeth on ventral margin of anterior femur, transverse carinae of vertex straight (slightly concave in *C. tindalei*), and in transverse carinae not reaching the medial carina of vertex (joining the medial carina in *C. tindalei*).

Description. Frontal costa bifurcation at dorsal margin of eyes. Facial carinae mostly parallel, a little indrawn in middle part of scutellum. Paired ocelli at dorsal quarter of eye height. Antennal grooves at level of ventral margin of eyes. Antennae filiform, made up of 13 visible antenommeres. Vertex approximately 3 times wider than eye. In anterior view, base of vertex above dorsal margin of eyes; middle part bulging upwards. In dorsal view, anterior margin of vertex protruding in front of anterior margin of eyes by approximately eye's length. Anterior margin of vertex triangular, with roundly widened base. Medial carina visible from anterior margin of vertex to level of anterior margin of eyes. Lateral carinae and transverse carinae following outline of vertex. Transverse carinae not reaching medial carina. Anterior margin of pronotum triangular, slightly projected. Prozonal carinae little longer than eye in dorsal view, slightly converging caudally, incurved caudally. In lateral view, median carina distinct, elevated and curved throughout its length, highest part above middle leg insertion. Lateral lobes moderately to strongly projecting outwards. Ventral sinus blunt. Tegminal sinus absent. Infrascapular area wide above middle femur, narrowing towards pronotal apex and terminating at apex. Humeral angles blunt. Pronotal apex wide, slightly rounded, with shallow and narrow triangular incision. Tegmina and wings absent. Anterior femur serrated; dorsal margin curved; ventral margin with three teeth. Anterior tibia with slight spines throughout its length. First segment of anterior tarsus long, with three pulvilli. Middle femur serrated; dorsal margin wavy; ventral margin with three teeth. Middle tibia expanded throughout its length. Hind femur robust, with slightly serrated margins, genicular and antegenicular teeth barely visible. Hind tibia straight and smooth with small teeth throughout its length. First tarsal segment longer than third. Pulvilli triangular with rounded apices, proximal pulvillus smaller than distal two. Ovipositor valves elongated, bearing multiple sharp teeth. Ventral valve uniformly narrowing towards tip; dorsal valve distinctly widened in its middle part. Female subgenital plate apically rounded, with triangular groove in its distal third. Male subgenital plate strongly upturned, with low median carina along its ventral surface.

Table 2. Cladistic matrix. Characters are numbered and coded as in Table 1.

Species	1	2	3	4	5	6	7	8	9	10	11
Cyphotettix camelus	1	1	1	1	2	1	2	2	0	0	0
Cyphotettix tindalei	1	1	1	1	2	1	2	2	2	0	0
Cyphotettix ellurae	1	1	1	1	2	1	2	2	2	0	0
Captivus irruptus	1	0	1	1	1	1	1	2	2	0	0
Captivus priscus	0	0	1	1	1	0	1	1	2	0	0
Captivus phrynus	0	0	1	1	1	0	1	2	2	0	0
Captivus crassus	0	0	1	1	1	0	1	1	2	0	0
Custodia accola	0	1	1	1	1	1	0	0	1	0	0
Custodia montivaga	0	1	1	1	2	1	0	0	1	0	0
Enattor insolens	?	?	1	1	1	1	0	1	0	0	0
Enattor absonus	?	?	1	1	1	1	0	1	0	0	0
Enattor dorrigensis	1	1	1	1	1	1	0	1	0	0	0
Tetrix collina	0	0	0	1	1	1	0	0	2	2	1
Paratettix spathulatus	0	0	0	0	0	0	0	1	0	1	1
Paratettix nigrescens	0	0	0	0	0	0	0	0	0	2	1
Paratettix femoralis	0	0	0	0	0	0	0	0	0	2	1
Paratettix australis	0	0	1	0	1	0	0	0	0	2	1
Paratettix argillaceus	0	0	1	1	1	0	0	0	0	1	1
Paratettix amplus	0	0	0	0	0	0	0	0	0	2	1

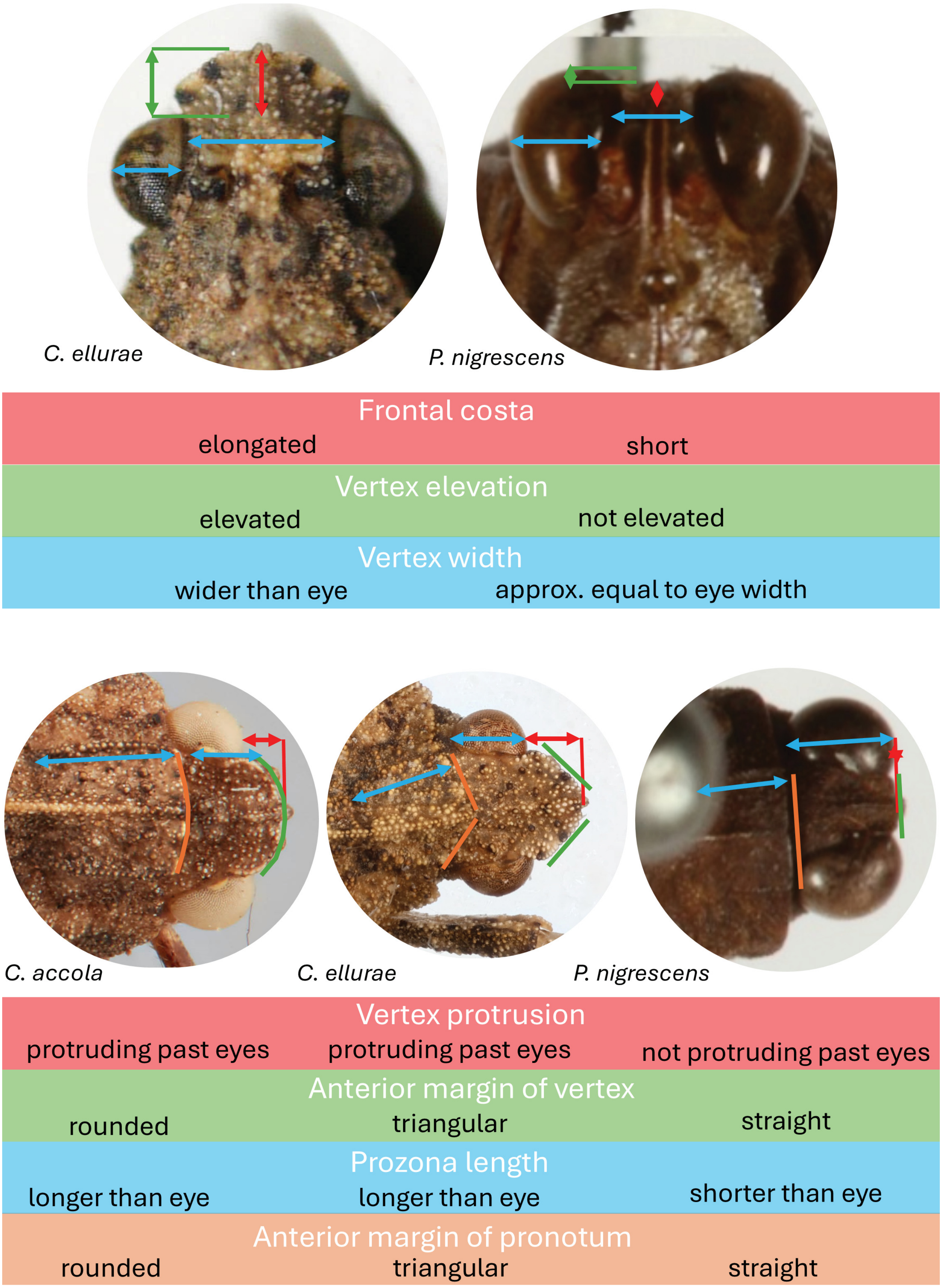

Fig. 2. Illustration of head and pronotum characters used to code the cladistic matrix. Photos: Brett Smith (*C. ellurae* sp. nov. frontal view), Commonwealth Scientific and Industrial Research Organisation, 2024 (*C. ellurae* dorsal view, *C. accola* (Rehn, 1952)), Josef Tumbrinck (*P. nigrescens* Sjöstedt, 1921).

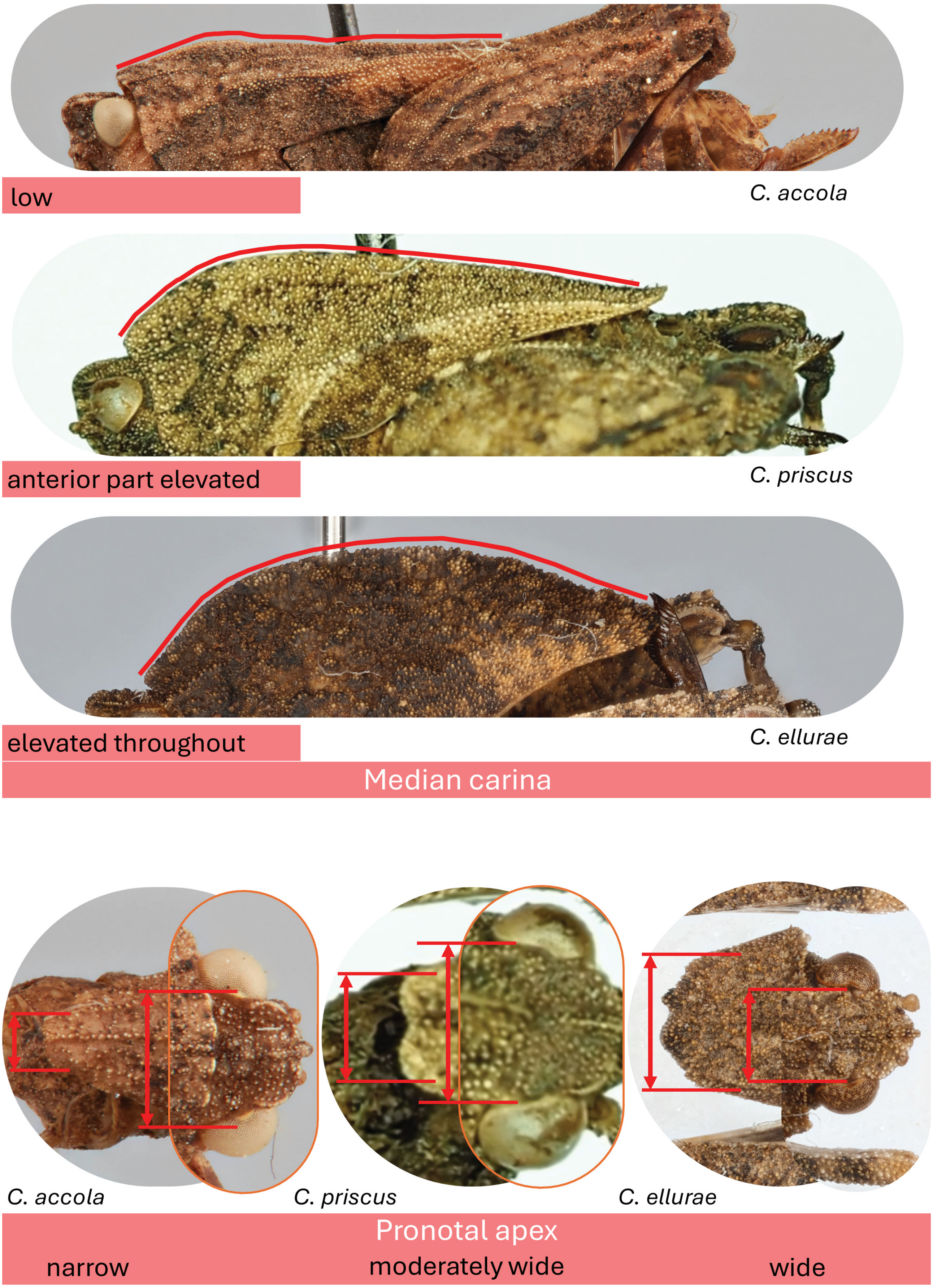

Fig. 3. Illustration of pronotum characters used to code the cladistic matrix. Photos: Commonwealth Scientific and Industrial Research Organisation, 2024 (*C. ellurae* sp. nov., *C. accola* (Rehn, 1952)), Josef Tumbrinck (*C. priscus* (Bolívar, 1887)).

Etymology. Named after Ellura Sanctuary, a private sanctuary in the Murray Mallee, South Australia, near Swan Reach Conservation Park, bought and maintained by Brett and Marie Smith. The specific epithet is a feminine noun in genitive.
Habitat. The specimens of this species are commonly found on rocky surfaces without any permanent water sources nearby (Fig. 9A). The type locality is dry, getting an average of 280 mm of rainfall in a year, with a 23 mm monthly average. The species could potentially be associated with the dryland tea tree (*Melaleuca lanceolata*) which is found near the type locality. So far, specimens have been observed between May and October and in January, which might suggest that this species predominantly feeds on lichens as they are available throughout the year, unlike other fungi and mosses that are usually observed around June and July.
Distribution. Known from the type locality, Ellura Sanctuary, and from Brookfield Conservation Park just north of the type locality.
Note. The males designated as paratypes appear to be adults but this cannot be confirmed due to the fact that the antegenicular tooth is nearly invisible in this species, especially in males. The specimen from Brookfield Conservation Park Figs 9B–D appears to be a nymph. It appears identical to the type specimens of *C. ellurae* sp. nov. but the anterior margin of its pronotum seems less triangular. Whether this is the result of the angle of photography and the potential nymphal state of this character, or whether it represents a new closely related species should be examined using more material from Brookfield Conservation Park.

Genus *Enattor* gen. nov.

Type species. *Tetrix dorrigensis* Rehn, 1952, here designated.

Diagnosis. Apterous and brachypronotal. Anterior margin of pronotum straight. Prozona long. Pronotal apex moderately wide, rounded. Median carina not significantly elevated or forming a low hump above prozona. Vertex wider than an eye in dorsal view, moderately protruding past the eyes, rectangular with rounded edges. Midline of antennal grooves in line with ventral margin of eyes. Frontal costa elongated, about as long as two ocellus radiuses, bifurcation at dorsal quarter of eye height, paired ocelli at middle of eye height. Vertex elevated in anterior view, quadratic.
Composition. *Enattor insolens* (Rehn, 1952) stat. & comb. nov. (from *Tetrix irrupta insolens* Rehn, 1952), *Enattor dorrigensis* (Rehn, 1952) comb. nov. (from *Tetrix*), *Enattor absonus* (Rehn, 1952) stat. & comb. nov. (from *Tetrix irrupta absona* Rehn, 1952).
Etymology. Coined from the Latin verb *ēnatō*, *ēnatāre* (swim away, escape by swimming) and the suffix *-tor* to form an agent noun of masculine gender, *enattor* (one who swims away). This genus name combines the general affinity of tetrigids for water with the nomenclatural theme of this paper, i.e. the long imprisonment of these species in the Australian *Tetrix*.
Distribution. Eastern Australia (Fig. 1).
Note. The length of the frontal costa in *E. insolens* stat. & comb. nov. and *E. absonus* stat. & comb. nov. could not be confirmed with certainty so we did not code it in the character matrix. The *Enattor* gen. nov. species are highly similar according to other examined characters, but their facial morphologies should be reexamined when more

Table 3. List of specimens examined for each species. For each species, the type locality, its coordinates (EPSG:4326 - WGS 84 coordinate system), and the depository are listed.

Species	Depository	Type locality	Coordinates	Specimens examined
Cyphotettix camelus	ANIC	Western Australia, Katanning	-33.678,117.550	Holotype
Cyphotettix tindalei	ANIC	South Australia, Immarna	-30.516,132.223	Holotype
Cyphotettix ellurae	ANIC	South Australia, Ellura Sanctuary	-34.591, 139.497	Holotype, paratype
Captivus irruptus	NHRS	New South Wales, Sidney	-33.870,151.053	Holotype
Captivus priscus	NMW	Queensland, Port Curtis	-23.431,150.519	Holotype
Captivus phrynus	ANIC	New South Wales, W of Dalmorton	-29.863,152.484	Holotype
Captivus crassus	NHRS	Queensland, Colosseum	-24.369,151.543	Holotype
Custodia accola	ANIC	New South Wales, Blue Mountains, Mt. Wilson	-33.504,150.387	Holotype
Custodia montivaga	AM	New South Wales, Mount Kosciusko	-36.457,148.263	Holotype
Enattor insolens	ANIC	New South Wales, Forster	-32.217,152.538	Holotype
Enattor absonus	MCZ	New South Wales, Macleay Range, Barrington Tops	-31.975,151.533	Holotype
Enattor dorrigensis	MCZ	New South Wales, The Dorrigo	-30.396,152.497	Holotype
Tetrix collina	ANIC	New South Wales, near Walcha	-31.06177,151.696379	Holotype
Paratettix spathulatus	NHRS	New South Wales, Sydney	-33.880,151.207	Holotype
Paratettix nigrescens	NHRS	Queensland, Malanda	-17.357, 145.589	Lectotype
Paratettix femoralis	NHRS	New South Wales, Sidney	-33.870, 151.053	Holotype
Paratettix australis	NHMUK	South Australia		Lectotype
Paratettix argillaceus	MfN	Tasmania, Woolnorth	-40.757, 144.765	Holotype
Paratettix amplus	NHRS	Queensland, Bellenden Ker	-17.278, 145.945	Lectotype

data become available. We chose *Enattor dorrigensis* comb. nov. as the type species because we could confirm its distinctness from the other genera.

Identification key to Australian genera of Tetriginae

1 Alae and tegmina present, even if reduced. 2
– Wings completely absent. 3
2 Anterior margin of pronotum straight; anterior margin of vertex straight or only slightly rounded on edges. ... . ***Paratettix*** Bolívar, 1887
– Anterior margin of pronotum weakly triangular; anterior margin of vertex strongly rounded. .... ***Tetrix*** Latreille, 1802
3 Median carina of pronotum elevated throughout its length; vertex strongly extended in front of and above eyes, triangular; pronotal apex very wide. .... ***Cyphotettix*** Rehn, 1952
– Median carina not elevated or elevated only anteriorly; vertex not significantly extended in front of eyes or only moderately so, not strongly extended above eyes in frontal view; pronotal apex narrow to moderately wide. 4
4 Prozona about as long as eye in dorsal view. .... ***Captivus* gen. nov.**
– Prozona visibly longer than eye in dorsal view. 5
5 Anterior margin of pronotum rounded; pronotal apex narrow, frontal costa very short, nearly non-existent. .. .. ***Custodia* gen. nov.**
– Anterior margin of pronotum straight; pronotal apex moderately wide, frontal costa elongated (about as long as two ocellus radiuses). .... ***Enattor* gen. nov.**

Discussion

Rehn (1952) described many new *Tetrix* species in Australia without trying to further develop the taxonomy of Australian Tetriginae. He recognized the weak definition of *Tetrix* and noted that changes to its scope are expected in the future. He noted *Tetrix collina* as morphologically closest to the European *Tetrix* representatives, especially *T. subulata* (Linnaeus, 1758) with which it shares the roundly triangular shape of the vertex and anterior pronotum margin, as well as the general facial morphology (Rehn 1952). The other Australian *Tetrix* species are not discussed beyond the fact that they appear neotenic.

The amount of morphological differences among the wingless species is best illustrated by Rehn's *Tetrix irrupta* (now *Captivus irruptus* gen. & comb. nov.) which he split into four subspecies. In an extreme disruption of the status quo, our analysis showed those four subspecies to be easily separable into three different morphologically distinct genera. Further, the specimen of the nominotypical subspecies photographed by Rehn does not appear identical to Bolívar's holotype. Rehn's (1952) text on *Tetrix irrupta irrupta* is unclear on how familiar Rehn was with the holotype. Since his and Bolívar's specimens are similar, it seems likely that Rehn saw it but did not keep a detailed reference because they differ in the size of the pronotal crest and the position of facial features (placed lower in the holotype). Rehn usually made photographs in frontal view, but neglected to do so for the *T. irrupta* subspecies. His descriptions did not focus on the facial features, which led to him missing the fact that there are several distinct facial morphologies among his species, which we have here addressed through descriptions of new genera.

Table 4. Measurements of the holotype and the paratypes of *Cyphotettix ellurae* sp. nov

	HT ♀ (mm)	PT ♀ (mm)	PT ♂ a (mm)	PT ♂ b (mm)
body length	8.61	7.78	4.27	5.03
pronotum length	6.04	5.88	3.64	4.31
pronotum width (between shoulders)	2.89	2.73	1.86	1.73
pronotum width (maximal) (PWM)	3.18	3.29	2.32	2.35
infrascapular area length	4.04	3.93	2.67	2.92
infrascapular area width	0.81	0.85	0.50	0.55
pronotum height (maximal)	3.12	3.24	1.99	1.79
vertex width	0.93	0.89	0.64	0.65
compound eye width	0.32	0.32	0.26	0.26
antennal groove width	-	0.21	0.15	0.15
scutellum width	-	0.18	0.14	0.17
fore femur length	1.34	1.35	1.04	1.09
fore femur width	0.68	0.53	0.42	0.37
mid femur length	1.73	1.66	1.24	1.41
mid femur width	0.54	0.67	0.68	0.51
hind femur length	4.12	4.22	3.00	3.05
hind femur width	1.62	1.49	1.32	1.40

The morphology of species within the newly described genera is in most cases highly uniform and putatively monophyletic groups can be defined based on morphological characters of the head and thorax. *Tetrix collina* is reconstructed as sister to the group containing *Cyphotettix* and the new genera, implying that its winged and slender morphology common to many tetrigids is ancestral to this group. This is expected as the loss of dispersal ability seems to have happened countless times in the evolution of Tetrigidae, which led to definitions of many polyphyletic groups (Kasalo & Skejo 2024). The Australian wingless Tetriginae are obviously related but it remains unclear when and how they diverged. While the general morphology places all of the genera described here in the subfamily Tetriginae, the dissimilarity of some important characters (including the shape of the median carina and facial morphology) between genera implies that they could have diverged early in the evolution of Australian Tetriginae. This leads to the other question: were the wings lost only once, as shown in our analysis, or did some of the genera arise from a winged ancestor that left no winged descendants and therefore could not be included in the analysis? Different branches of this group could have arisen in different ways and molecular studies will be needed to shed more light on this issue.

Australia is known for its high endemism of flightless invertebrates (Yeates & Monteith 2008) and recent work (Kasalo & Skejo 2024) described many new genera and species of flightless tetrigids in eastern Australia. In that study, species of the same genus were found to inhabit the same general area, each with a relatively narrow distribution range separated from others by clear biogeographical barriers (Bryant & Krosch 2016). The only exception is the genus *Peraxelpa* Sjöstedt, 1932, which has many representatives in northeastern Australia and a single widespread species in central-eastern Australia (Kasalo & Skejo 2024). The latter pattern seems to apply to the Australian flightless Tetriginae as well.

By mapping type localities, we showed that the genera addressed in this study occupy large geographical areas but their ranges do not seem to overlap. The only exception is the presence of *Captivus irruptus* gen. & comb. nov. in southeastern Australia between the distribution ranges of *Custodia* gen. nov. and *Enattor* gen. nov. As noted earlier in the text, this species is not morphologically fully congruent with the other *Captivus* gen. nov. species and

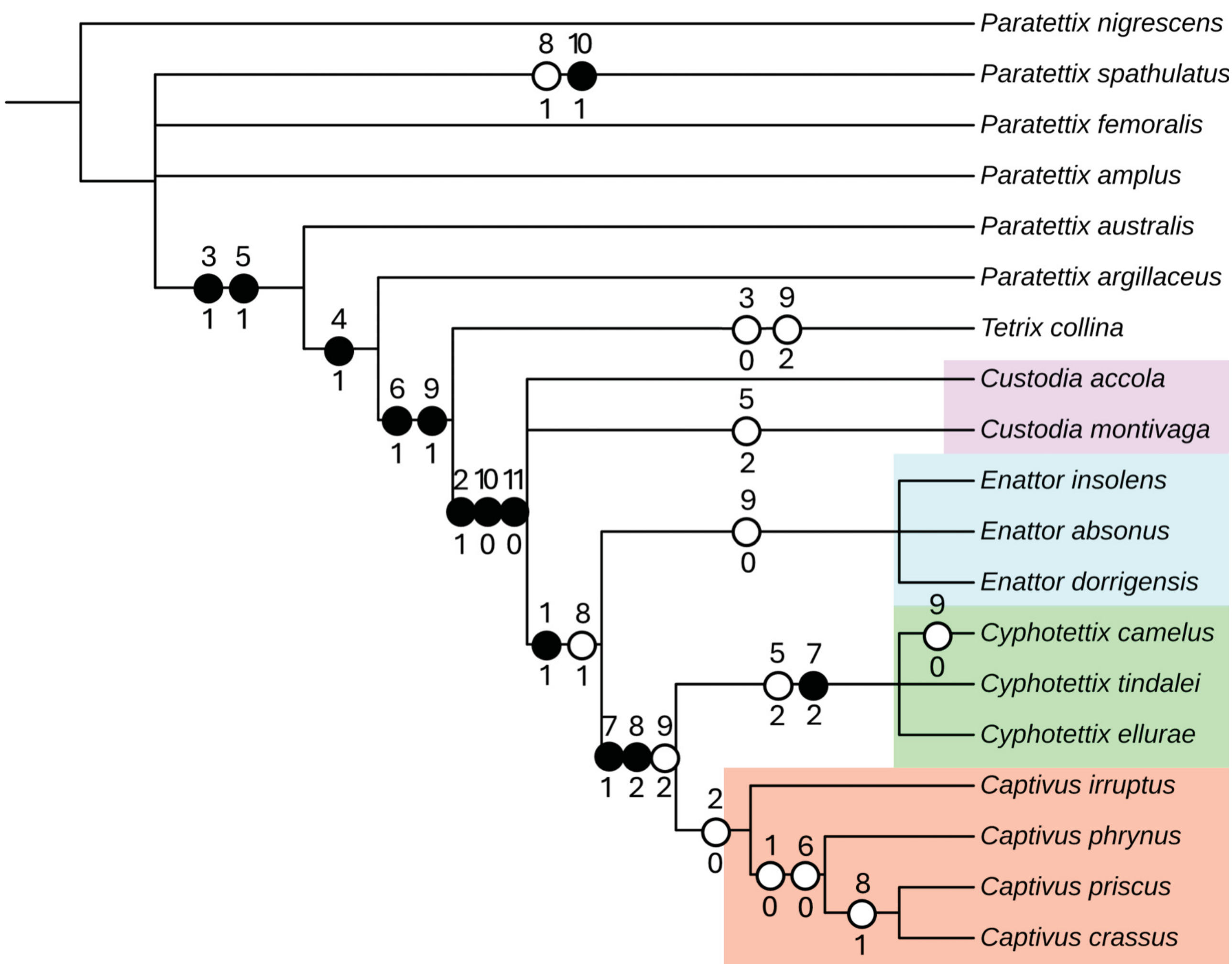

Fig. 4. Cladogram of the Australian Tetriginae. The tree was generated based on 11 phylogenetically informative characters using implicit enumeration in TNT. Synapomorphies are represented by black circles, while homoplasies are represented by light circles. Numbers above the circles refer to the character numbers, while the numbers below the circles refer to the character states (Table 2).

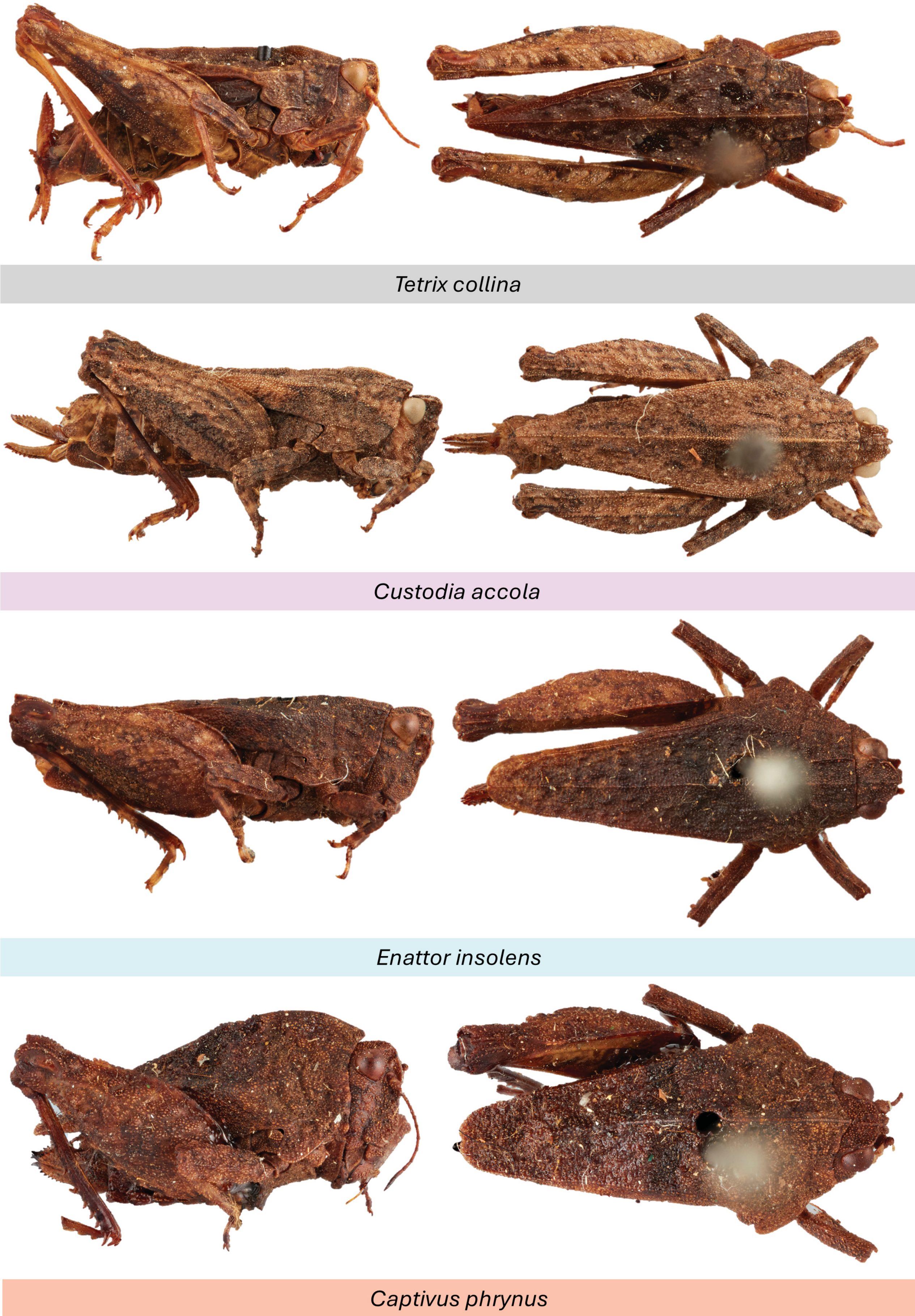

Fig. 5. Representatives of the newly described Tetriginae genera and *Tetrix collina* Rehn, 1952. Photos: Commonwealth Scientific and Industrial Research Organisation, 2024.

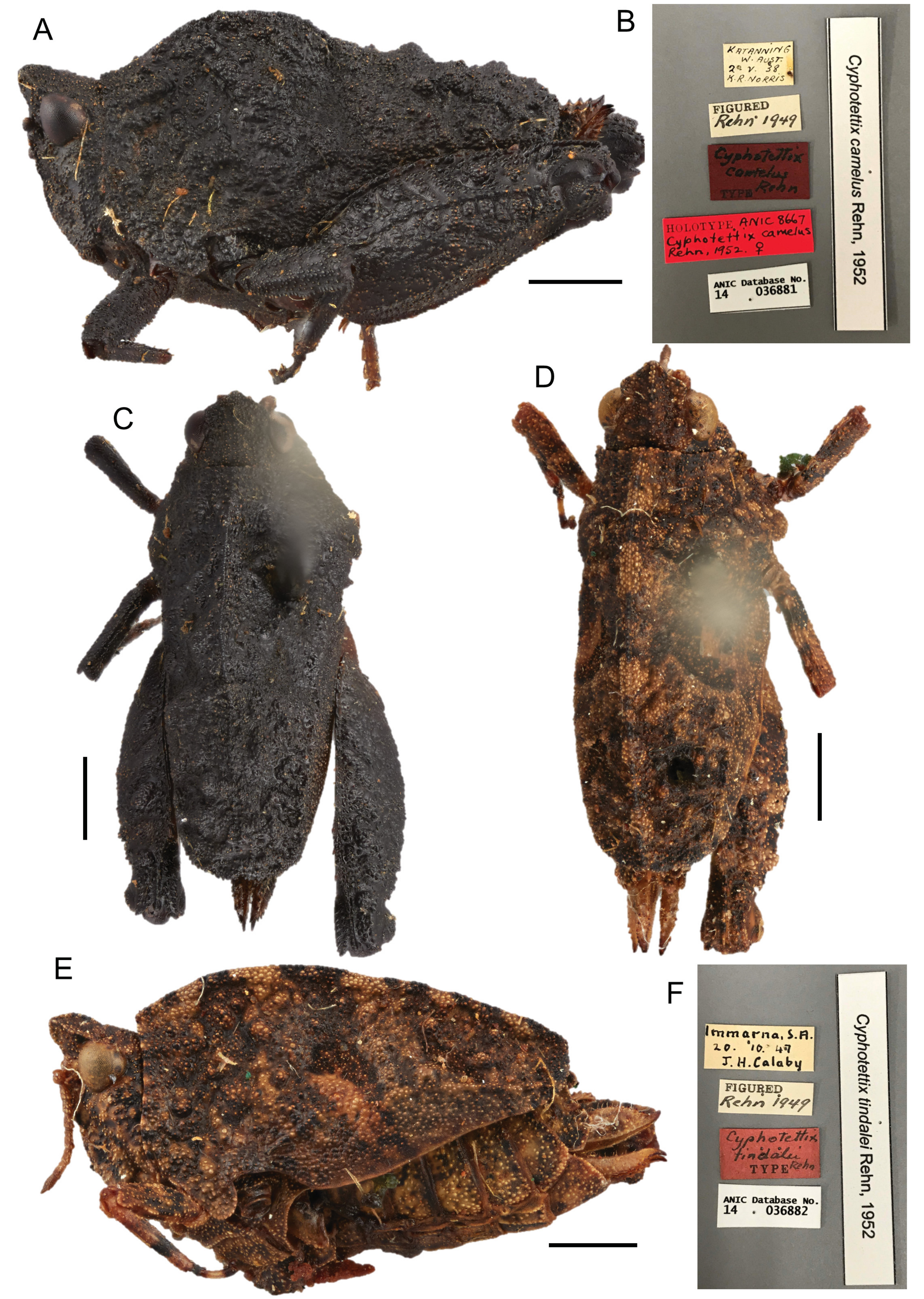

Fig. 6. Type specimens of *Cyphotettix camelus* Rehn, 1952 and *C. tindalei* Rehn, 1952. A – *C. camelus* in lateral view, B – label data of *C. camelus*, C – *C. camelus* in dorsal view, D – *C. tindalei* in dorsal view, E – *C. tindalei* in lateral view, F – label data of *C. tindalei.* Scale bars: 1mm. Photos: Commonwealth Scientific and Industrial Research Organisation, 2024.

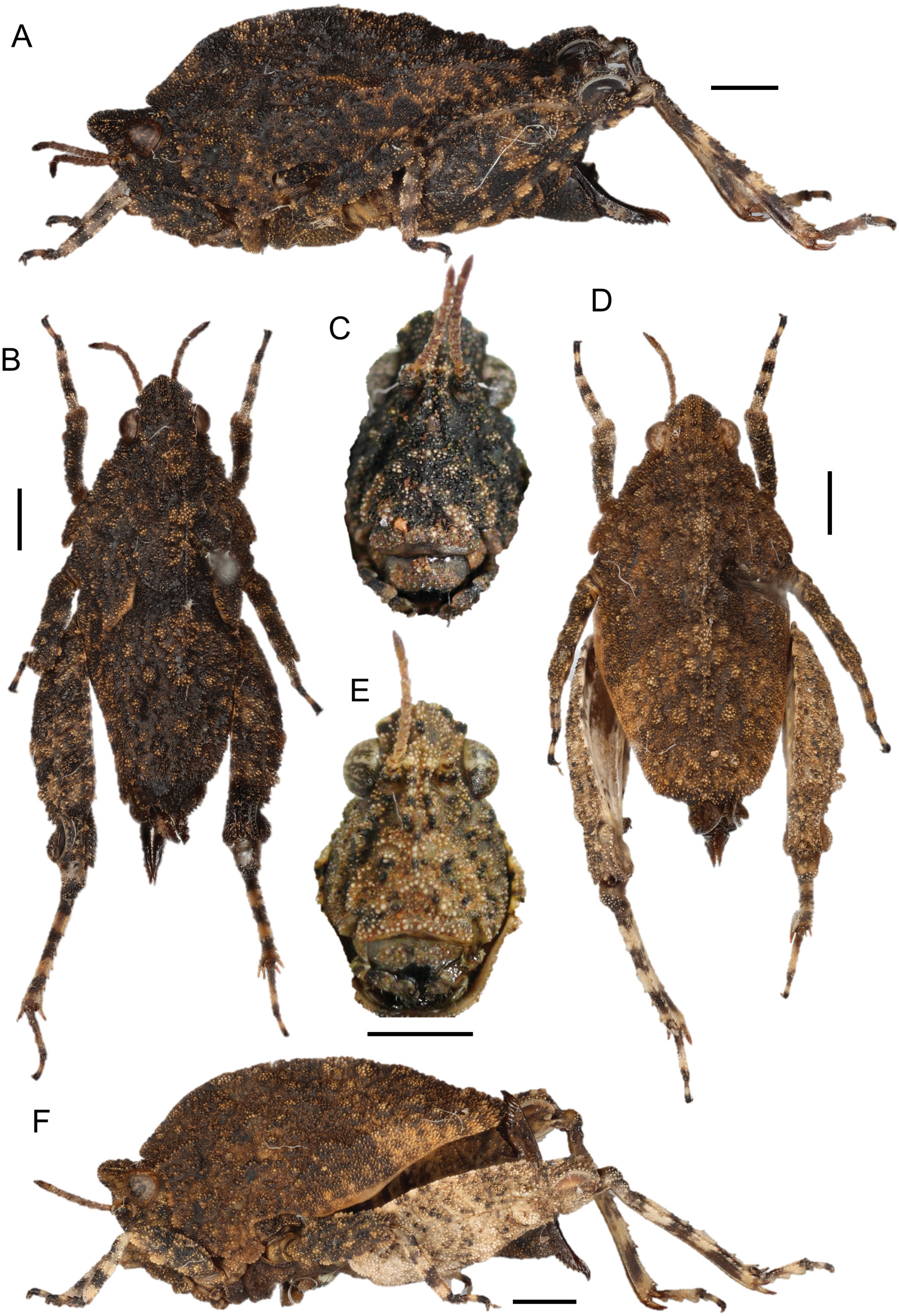

Fig. 7. Female holotype and female paratype of *Cyphotettix ellurae* sp. nov. A–C – holotype (A – lateral view, B – dorsal view, C – frontal view); D–F – female paratype (D – dorsal view, E – frontal view, F – lateral view). Scale bars: 1mm. Photos: Commonwealth Scientific and Industrial Research Organisation, 2024.

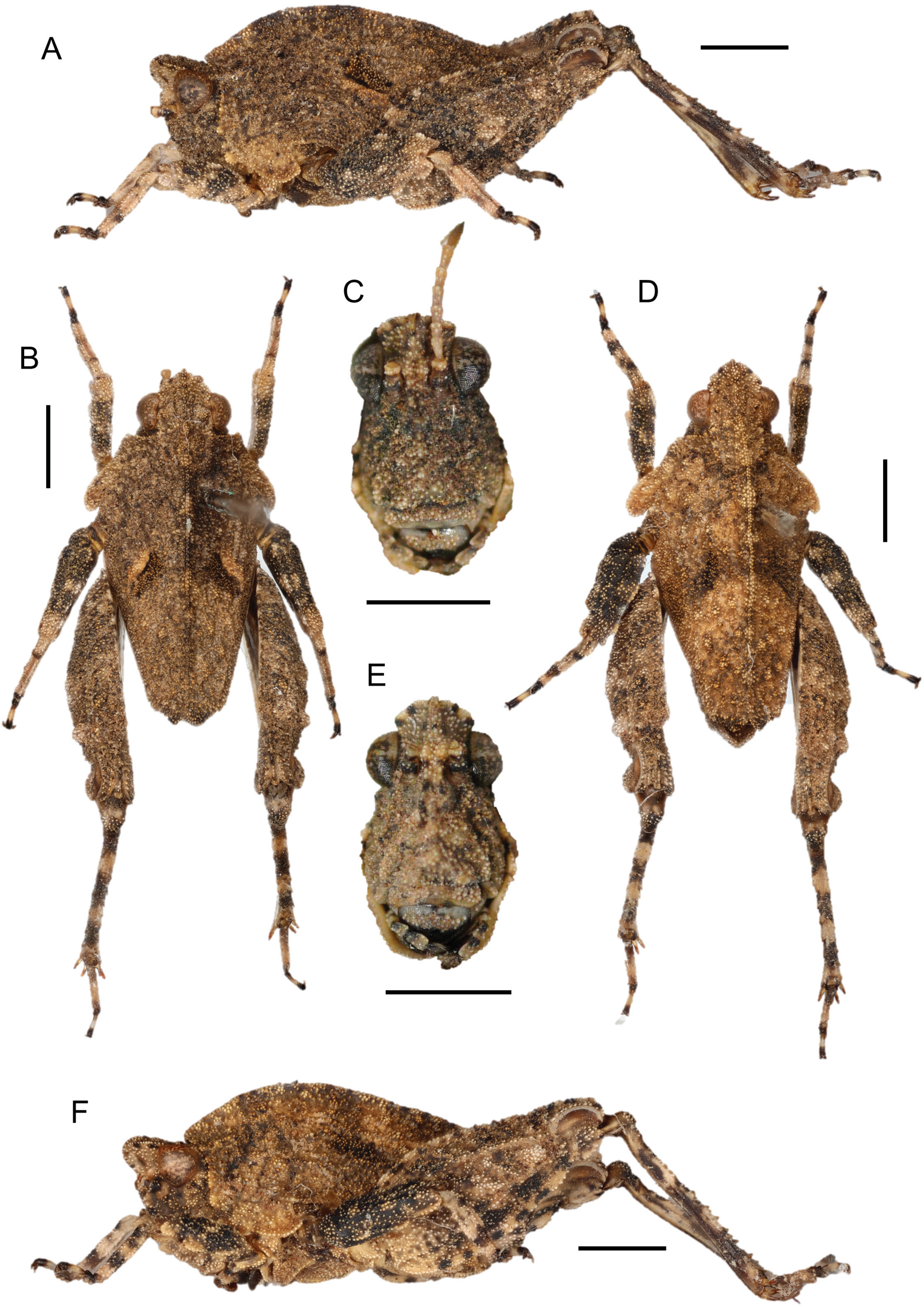

Fig. 8. Male paratypes of *Cyphotettix ellurae* sp. nov. A–C – male paratype a (A – lateral view, B –dorsal view, C – frontal view), D–F – male paratype b (D – dorsal view, E – frontal view, F – lateral view). Scale bars: 1mm. Photos: Commonwealth Scientific and Industrial Research Organisation, 2024.

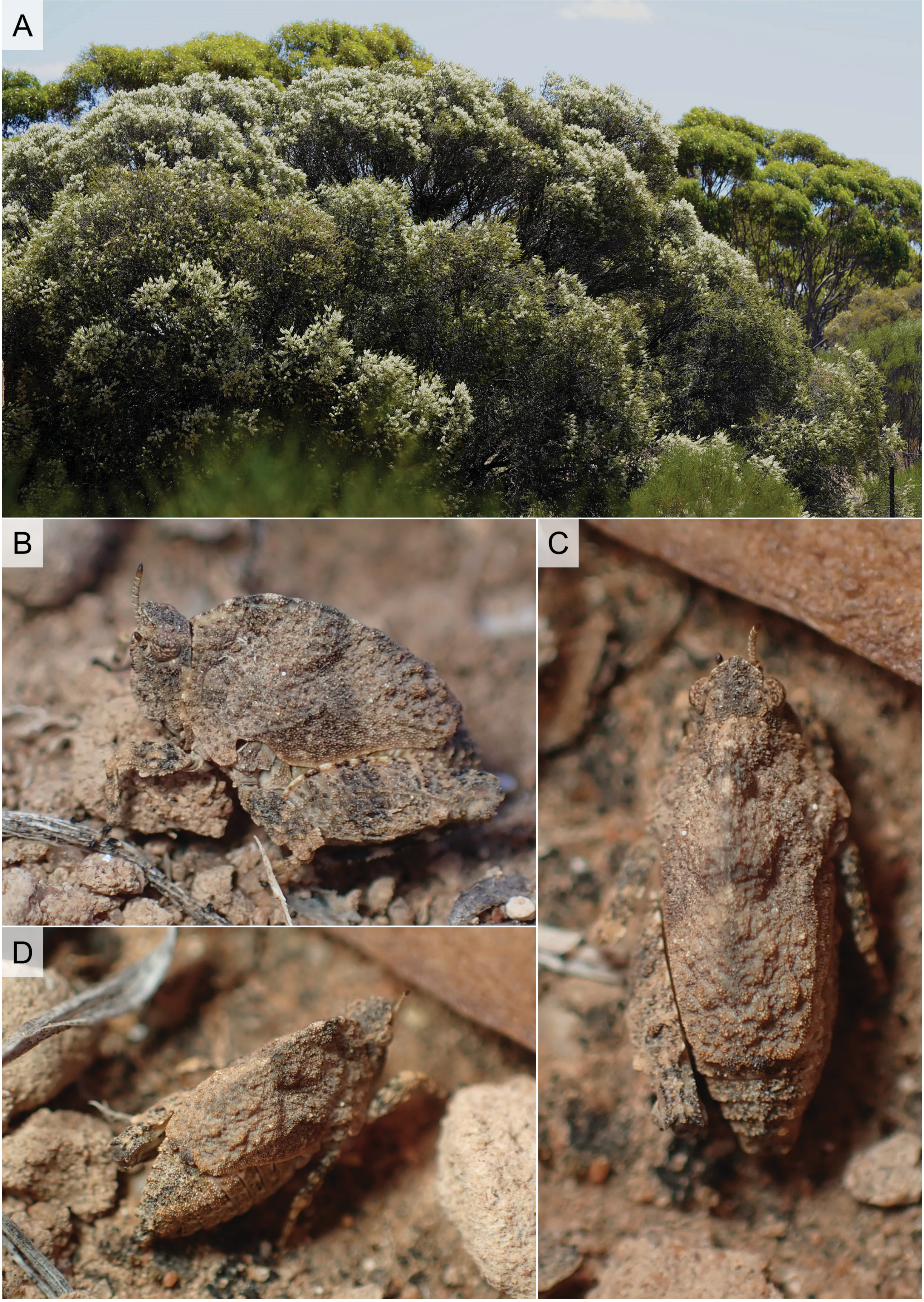

Fig. 9. Habitat and a living specimen of *Cyphotettix ellurae* sp. nov. A – The dryland tea tree (*Melaleuca lanceolata*) found near the type locality. Photo: Brett and Marie Smith. B–D – living specimen of *C. ellurae* sp. nov. Photo: Joshua S. Martin.

may represent an early-diverging member of this group, if not an entirely new genus. We lack true distribution data for all these species, but Rehn (1952) noted that they are confined to relatively small geographical areas. This allows us to broadly conclude that the distribution of type localities supports the idea that the herein-defined genera are largely monophyletic. Another interesting biogeographical observation to note is the extremely wide distribution of *Cyphotettix* across southern Australia. The three known *Cyphotettix* species were described from geographically very distant localities, which leaves the possibility of identifying many more species of this group in the future.

Morphology allowed us to define distinct groups, although the placement of *C. irruptus* gen. & comb. nov. remains doubtful, as does whether the two *Custodia* gen. nov. species actually represent two different genera. For now, keeping all of the species under the same genus would not only complicate the already strained definition of *Tetrix*, but would also understate the incredible diversity of wingless Tetriginae in Australia. The final step to resolving the issues discussed in this study will have to be made with molecular data since we are nearing the limits of information provided by morphology alone.

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