

Revision of *Tropopterus* Solier: A disjunct South American component of the Australo-Pacific Moriormorphini (Coleoptera, Carabidae)

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Abstract

Tropopterus Solier, 1849, precinctive to southern South America, is taxonomically revised. Six new species are described: *T. peckorum* sp. nov., *T. robustus* sp. nov., *T. canaliculus* sp. nov., *T. trisinuatus* sp. nov., *T. minimicro* sp. nov., and *T. fieldianus* sp. nov. *Merizodus catapileanus* Jeannel, 1962, is synonymized with *T. montagnei* Solier, 1849. Lectotypes are designated for *T. montagnei*, *T. giraudyi* Solier, *T. duponchelii* Solier, and *T. nitidus* Solier (= *T. duponchelii*). *Tropopterus peruvianus* Straneo is noted as a *nomen dubium*, with its identity and taxonomic placement to be substantiated via neotype designation. Phylogenetic relationships among *Tropopterus* spp. are hypothesized based on 37 morphological characters, the distributions of which are analyzed under the parsimony criterion, with the cladogram root established between *Tropopterus* and its adelphotaxon from New South Wales, Australia. Speciation in the group has occurred predominantly at a limited geographical scale relative to the overall generic distribution, with three pairs of sister species sympatric. However phylogenetic divergence between taxa in the more northern, sclerophyllous forest characterized by *Nothofagus obliqua* (Brisseau de Mirbel) and those occupying the Valdivian and North Patagonian Rain Forest dominated by *N. dombeyi* (Brisseau de Mirbel) is observed in two instances of phylogenetic history. Using specific collecting locality records, it is shown that *Tropopterus* beetles have been collected syntopically and synchronically with species of *Glypholoma* Jeannel (Coleoptera, Staphylinidae), *Anaballetus* Newton, Švec & Fikáček (Coleoptera, Leiodidae), *Andotypus* Spangler (Coleoptera, Hydrophilidae), and *Novonothrus* Balogh (Acari, Oribatida). These concordant ecological occurrences document a cohesive *Nothofagus* forest leaf-litter community. These genera plus other Valdivian Rain Forest invertebrate taxa all exhibit an Austral disjunct biogeographical pattern that corroborates trans-Antarctic vicariance between the *Nothofagus* forests of southern South America and Australia. Male genitalic antisymmetry is shown to be a synapomorphy of *Tropopterus*, though the female reproductive tract retains the plesiomorphic orientation observed in all other moriomorphine taxa.

Key Words

Austral biogeography, dispersal, genitalic antisymmetry, vicariance, Western Antarctica

Introduction

The carabid beetle tribe Moriormorphini exhibits an aggregate geographical distribution that includes Australia, New Zealand, New Caledonia, the Sunda Islands, the Society and Hawaiian Islands in Polynesia, and Chile. The greatest generic diversity in the tribe is centered in Australia with representatives of 21 genera (Liebherr 2020) and New Zealand with six genera represented (Larochelle and Larivière 2013, Liebherr 2018a, 2020). Conversely,

the bulk of species-level diversity in the tribe is represented by species of the genus *Mecyclothorax* Sharp, with that genus represented by 239 species in Hawaii (Liebherr 2015) and 108 species in Tahiti and Moorea (Liebherr 2012, 2013). These two Polynesian radiations commenced on the islands of Maui and Tahiti Nui, respectively, indicating very rapid speciation in the radiations of both archipelagoes. Thus the total diversity of the tribe has been built both by relatively slower, generic-level evolution on geologically old Australia and New Zealand, but explo-

sive speciation on the younger, geologically more ephemeral islands of Polynesia. An adjunct to this disparate mix is *Tropopterus* Solier, which is geographically restricted to South America and isolated across the Pacific Ocean from the rest of the members of its tribe.

Tropopterus was described by Solier (1849), who placed it immediately after species now assigned to the genus *Incagonum* Liebherr (tribe Platynini) because he considered the two taxa to be closely related due to shared tarsal configuration (Solier 1849: 212). Reed (1874), Chaudoir (1876), and Germain (1911) followed suit with this tribal placement. Bates (1874) and Broun (1880, 1882) expanded the generic concept by describing New Zealand taxa in combination with *Tropopterus*. Sloane (1898) then proposed *Tropopterus* as a member of an Australian assemblage of genera assignable to today's Moriomorphini, while considering three Australian species to represent *Tropopterus*. This trans-Pacific interpretation of *Tropopterus* unravelled over time, with Broun proposing several precinctive New Zealand genera to hold species he previously described under *Tropopterus* (summarized in Larochelle and Larivière 2013), and Moore (1963) removing the Australian species from *Tropopterus* and placing them in the precinctive Australian genus *Theprisa* Moore. Most recently, Liebherr (2020) conducted a cladistic analysis of the tribe Moriomorphini, finding that *Tropopterus* exhibits a sister-taxon relationship with a monotypic Australian genus. This contribution revises *Tropopterus* based on substantial new material collected by field surveys conducted from the 1980s to the present. Phylogenetic relationships among *Tropopterus* species are hypothesized based on parsimony analysis of morphological characters. It is shown that the *Nothofagus*-dominant Valdivian Rain Forest supports a cohesive assemblage of leaf-litter inhabiting taxa, with *Tropopterus* beetles living alongside beetle and mite taxa also exhibiting the Austral disjunct biogeographical pattern involving Chile and Australia. Thus, we can now recognize an Austral disjunct ground litter fauna of the Valdivian Rain Forest, the members of which take part in trans-Antarctic biogeographical relationships. Finally, male genitalic antisymmetry, rarely observed among carabid beetles (Liebherr and Will 2015), is shown to be a synapomorphy for *Tropopterus*.

Nomenclatural disclaimer. *Pharetis* Liebherr and *Pharetis thayerae* Liebherr are disclaimed for nomenclatural purposes (ICZN 1999, Article 8.3) and are unavailable until published (Liebherr 2020).

Material and methods

Taxonomic material

This revision is based on 162 specimens borrowed from the following institutions (institutional acronym and responsible curators in parentheses): California Academy of Sciences (CAS, David H. Kavanaugh); Carnegie Mu-

seum of Natural History, Pittsburgh, PA (CMNH, Robert Davidson); Essig Museum of Entomology, University of California, Berkeley, CA (EMEC, Kipling W. Will); Field Museum of Natural History, Chicago, IL (FMNH, Al Newton and Margaret Thayer); Florida State Collection of Arthropods, Gainesville, FL (FSCA, Paul Skelley); Museum of Comparative Zoology, Harvard University, Cambridge, MA (MCZ, Philip D. Perkins and Crystal Maier); Museum national d'Histoire naturelle, Paris (MNHN, Thierry Deuve); Department of Geosciences, North Dakota State University, Fargo, ND (NDSU, Allan C. Ashworth); and Oregon State Arthropod Collection, Oregon State University, Corvallis, OR (OSAC, David R. Maddison). Specimens stored as whole bodies in 100% ethanol for DNA sequencing are noted by "etoh" following the institutional coden. Specimens were requested from the Museo Nacional de Historia Natural, Santiago, but none were available.

Laboratory methodology

Specimens were relaxed for dissection in nearly boiling distilled water held in shell vials placed in a double boiler, the water containing a drop of Kodak Photo-Flo® detergent. For males, the aedeagal median lobe, associated parameres and 9th laterotergite and antecostal apodeme, and 8th ventral apodeme when possible, were disassociated from the abdomen using minuten pins mounted on wooden dowels. The genitalic apparatus was removed, cleared overnight in cold 10% KOH, deacidified in 10% acetic acid, and then placed in glycerin. The male internal sac, or endophallus, was everted in KOH using modified minuten nadeln. Female dissections involved removal of the entire abdomen, and clearing in cold 10% KOH overnight. After removal from the abdominal ventrites and dorsal membranous tergites, the reproductive tract assembly was deacidified briefly in dilute 10% acetic acid, cleared and stained in a mixture of Kodak Chlorazol Black stain suspended in methyl cellosolve for as long as it took for the associated fat tissue to dissipate. The cleared dissection was viewed in glycerin on a microslide. Macrophotography was accomplished using a Microoptics (now Visionary Digital) photographic apparatus employing a Nikon D1 camera, the K2 lens system, and a three-wand photographic strobe fiber-optic light source. Female dissections were photographed in ventral view, with the gonocoxites additionally presented as line drawings.

Descriptive conventions and characters

Previously described species are provided an extensive diagnosis sufficient for identification, whereas new species are also provided with a description that complements the diagnosis. Male genitalic terminology follows that of Liebherr (2018b, 2020), with abbreviations used in the figures presented in Table 1. Terminology of the female

Table 1. Key to abbreviations for morphological structures labelled in illustrations of male genitalia (Figs 3–5), female reproductive tracts (Fig. 7), and female gonocoxae (Fig. 8).

Abbreviation	Structure
acIX	antecostal apodeme of abdominal IX, male
afs	apical fringe setae, basal gonocoxite
ans	apical nematiform setae, apical gonocoxite
bc	female bursa copulatrix
co	female common oviduct
des	dorsal ensiform seta, apical gonocoxite
fl	flagellum, male aedeagal internal sac
fs	flagellar sheath, male aedeagal internal sac
gc1	basal gonocoxite, female
gc2	apical gonocoxite, female
hg	hindgut
les	lateral ensiform setae, apical gonocoxite
mu	micro on aedeagal median lobe apex
popb	pleated ostial border, male
r	ramus, basal gonocoxite
sd	spermathecal duct, female
sg	spermathecal gland, female
sp	spermatheca, female
vss	ventrobasal spiracular sclerite, male

reproductive tract characters (Table 1) follows Liebherr and Will (1998). The numbers of individuals used as the basis for describing male and female genitalia are indicated at the start of descriptive sections for those structures. Several ratios are used to describe body conformation (Table 2). To describe eye configuration three ratios are used: (1) ocular ratio (MHW/mFW), or the maximal head width across the eyes divided by the minimal frons width between the eyes; (2) ocular lobe ratio (EyL/OLL), or eye length measured in dorsal view, divided by the distance from the anterior margin of the eye to the inflection at the juncture of the ocular lobe and the gena, also measured in dorsal view; and (3) eye convexity (EyL/EyD), or the eye length measured as above, divided by the depth of the convex eye, with the eye's dorsal margin uppermost in the field of view. Eye development was also quantified by counting the number of ommatidia crossed by a diametric line passing across the maximal horizontal dimension of the eye, that number assessed in lateral view. Pronotal shape was described using two ratios: (1) maximal pronotal width divided by the basal pronotal width, measured between the hind angles (MPW/BPW); and (2) maximal pronotal width divided by pronotal median length (MPW/PL). The relative shape of the elytra was described using the ratio of maximal elytral width measured where that occurs, divided by elytral length, defined as the distance from the base of the raised scutellar surface to the elytral apex, measured along the suture (MEW/EL). The range of specimens chosen for measurement included both the largest and smallest individuals, males and females, and representatives from multiple localities where available. Standardized body length is defined as the sum of three linear measurements: (1) the distance from the anterior labral margin to the cervical ridge, a transverse carina posterad the vertex; (2) the medial length of the pronotum; and (3) elytral length as defined above.

Holotype label data are presented verbatim, including typeface. Individual labels are indicated by a double slash “//”, and lines within labels by a single slash “/”. Nomenclatural actions conform to the International Code of Zoological Nomenclature (ICZN 1999). Institutional repositories for holotypes were assigned based on the earliest collections of the newly described species, thereby recognizing those collectors who first discovered them.

Cladistic analysis. An hypothesis of phylogenetic relationships among the species was generated using parsimony analysis implemented by the Winclada data platform (Nixon 2002) running NONA (Goloboff 1999) and the parsimony ratchet (Nixon 1999). The complete data matrix, character states, and single most parsimonious tree (Fig. 10) are presented in Suppl. material 1.

Characters. The analysis was based on 37 morphological characters; 22 binary two-state characters, and 15 ordered multistate characters of 3 or 4 states.

- Character 0 Antennomere 9 length/width ratio: $1.42 < x < 1.98$, Figs 7, 8 (0; Fig. 1D); $2.0 < x < 2.8$ mm (1; Fig. 1F).
- Character 1 Number of ommatidia-horizontal diameter: 12–17 (0); 18–21 (1; Fig. 1C); 23–26 (2; Fig. 2C).
- Character 2 Paraglossae relative to ligula: adjacent (0); set off laterally from basal portion of glosal sclerite (1).
- Character 3 Mentum paramedial depression: broad, shallowly depressed (0); deep but without abrupt pit (1); deep with narrow, distinct pit at depth (2).
- Character 4 Labral apical margin: straight (0); moderately concave (1); deeply concave (2).
- Character 5 Ocular ratio: < 1.30 (0); $1.30–1.40$ (1; Fig. 1C); $1.41–1.50$ (2; Fig. 1B).
- Character 6 Ocular lobe ratio: < 0.70 (0); $0.76–0.83$ (1; Fig. 1C); $0.85–0.90$ (2; Fig. 2C); $0.91–0.94$ (3; Fig. 1F).
- Character 7 Anterior pronotal margin: smooth medially, margined laterally (0; Fig. 1F); with marginal bead medially and laterally (1; Fig. 1E).
- Character 8 Pronotal median base: coplanar with disc medially (0); depressed relative to disc medially (1).
- Character 9 Pronotal basal margin: straight (0; Fig. 2B); trisinate (1; Fig. 2A).
- Character 10 Lateral setal position: 1 setal diameter from lateral marginal depression (0); 2 setal diameters from lateral marginal depression (1).
- Character 11 Pronotal breadth ratio MPW/PL: $1.20–1.32$ (0; Fig. 1D); $1.33–1.40$ (1; Fig. 2C).
- Character 12 Prosternum and prosternal process: broadly depressed medially in basal half of prothorax (0); deeply and narrowly depressed medially in basal half (1).

- Character 13 Apex of scutellum: extended onto elytral disc between elytral bases (0); not or only slightly extended onto disc, mostly in basal groove (1).
- Character 14 Elytral shape MEW/EL: 0.66–0.68 (0; Fig. 1C); 0.69–0.74 (1; Fig. 1E); 0.75–0.81 (2; Fig. 1D).
- Character 15 Elytral humeral angle: broadly rounded (0); narrowly rounded to obtuse-angulate (1).
- Character 16 Elytral basal groove: present from scutellum to humeral angle (0; Fig. 1); absent medially, at most present just mesad humeral angle (1; Fig. 2).
- Character 17 Elytral striae on disc: 1–4 shallow, punctate, and 5–7 progressively obsolete (0; Fig. 1D); 1–2 shallow, punctate, and 3–7 progressively obsolete (1; Fig. 1F); only sutural stria 1 present, and 2–7 obsolete (2; Fig. 2); all discal striae obsolete (3; Fig. 1A, B).
- Character 18 Elytral striae on apex: 1–3 to 1–5 traceable on apex, 7 evident mesad subapical sinuation (0; Fig. 1D); only striae 1–2 and 7 visible near apex 3–6 obsolete (1; Fig. 2); only sutural stria or no striae traceable near apex (2; Fig. 1B).
- Character 19 Sutural stria at apex (when present): uniformly punctate (0); with antepical punctate section and apical canalicula (1); absent antepically, smooth apically (2).
- Character 20 Elytral stria 8: smooth throughout length, deep at midlength (0); smooth throughout, shallow at midlength (1); deep fore and aft, isolated punctures at midlength (2); present fore and aft, absent at midlength (3).
- Character 21 Mesepisternum: smooth to 3 small punctures (0); with ~4–7 punctures in 1 row (1); with 8–18 punctures in 2–3 rows (2).
- Character 22 Metepisternum width/length: < 0.75 (0); 0.78–0.83 (1); 0.85–0.88 (2); 1.0 (3).
- Character 23 Metathoracic flight wing: foreshortened, stenopterus (0); vestigial, apex not extended past metanotum (1).
- Character 24 Lateral abdominal suture between ventrites 1 and 2: straight or slightly sinuate (0); sinuate with ventrite 2 depressed within sinuosity (1).
- Character 25 Base of ventrites 4–6: smooth, small punctures may be present along basal margin (0); sulcate, the sulcus lined with distinct punctures (1).
- Character 26 Apical abdominal ventrite 6 (male): with 1 seta each side (total of 2) (0); with 2 setae each side (total of 4) (1).
- Character 27 Metatarsomere 4 apex: truncate apically (0); emarginate, outer lobe longer than inner lobe (1).
- Character 28 Male aedeagal orientation: plesiomorphic, right side ventral (0); inverted left side ventral (1) (Figs 3–6).
- Character 29 Abdominal IX antecostal apodeme: distinctly angulate distally, extension may be present (0; Figs 3B, F, H, 4B, D); rounded or obtusely rounded distally (1; Fig. 4G).
- Character 30 Aedeagal median lobe apex: smoothly rounded or acuminate (0); with small mucro on ventral margin (1; Fig. 5A, C, E); with large mucro on ventral margin (2; Figs 3A, E, 4E, F).
- Character 31 Male aedeagal median lobe ostial opening: surrounded by smooth membrane (0); surrounded by pleated membrane (1; Fig. 4A).
- Character 32 Female basal gonocoxite 1: with one apical fringe seta each side (0; Fig. 8E); with two apical fringe setae each side (one may be smaller) (1; Fig. 8A–C).
- Character 33 Microsculpture of vertex between eyes: evident isodiametric mesh (0); shallow isodiametric mesh (1); indistinct, surface glossy (2).
- Character 34 Microsculpture of pronotum: dense transverse mesh (0); transverse lines (1).
- Character 35 Microsculpture of elytra: transverse mesh, up to 3–4 × (0); elongate transverse mesh to transverse lines causing spectral iridescence (1).
- Character 36 Standardized body length: < 5.0 mm (0); 5.0–6.1 mm (1); 6.7–8.4 mm (2).

Table 2. Ratios of dimensions of the head, pronotum, and elytra for *Tropopterus* spp., along with number of ommatidia intersecting a line crossing horizontal diameter of eye. Abbreviations described in Material and Methods. Number of specimens denotes those measured to establish ranges of ratios.

Species	No. specimens	MHW/mFW	EyL/OLL	EyL/EyD	No. ommatidia	MPW/BPW	MPW/PL	MEW/EL
<i>T. montagnei</i>	4	1.32–1.36	0.83–0.90	3.0–3.3	18	1.21–1.26	1.21–1.27	0.70–0.72
<i>T. giraudyi</i>	5	1.41–1.47	0.83–0.89	2.6–3.0	23	1.25–1.31	1.21–1.25	0.69–0.74
<i>T. peckorum</i>	3	1.30–1.33	0.82–0.83	3.1–3.2	18–20	1.23–1.25	1.21–1.31	0.66–0.68
<i>T. robustus</i>	5	1.35–1.48	0.90–0.92	3.1–3.3	20	1.18–1.21	1.36–1.41	0.74–0.81
<i>T. canaliculus</i>	5	1.40–1.50	0.85–0.93	2.9–3.3	25	1.21–1.33	1.20–1.25	0.70–0.74
<i>T. duponchelii</i>	5	1.37–1.46	0.91–0.94	2.5–3.1	20–25	1.20–1.24	1.25–1.32	0.70–0.75
<i>T. trisinuatus</i>	2	1.36	0.76–0.81	2.7–2.8	25–26	1.22–1.24	1.30–1.36	0.72–0.74
<i>T. minimucro</i>	5	1.41–1.45	0.85–0.89	3.0–3.3	25	1.24–1.33	1.27–1.37	0.70–0.73
<i>T. fieldianus</i>	2	1.42–1.44	0.87–0.88	2.4	26	1.18–1.25	1.37–1.39	0.74–0.75

Results

Taxonomic treatment

Genus *Tropopterus* Solier, 1849

Tropopterus Solier 1849: 211; Reed 1874: 58; Chaudoir 1876: 124; Sloane 1898: 471; Sloane 1903: 585.

Tropidopterus Gemminger and Harold 1868: 385 (unjustified emendation).

Type species. *Tropopterus giraudyi* Solier by subsequent designation (Enderlein 1909).

Diagnosis. *Tropopterus* may be placed in the Moriormorphini based on: presence of a seta in the mandibular scrobe; frontal grooves present mesad eyes and traversing the frons anteromedially to the frontoclypeal suture; clypeus narrower than distance between antennal insertions; penultimate maxillary palpomeres glabrous, not setose over the entire surface; apical palpomeres fusiform and as long and broad as penultimate palpomere; head with two pairs of supraorbital setae; procoxal cavities closed posteriorly; mesocoxal cavities conjunct; prothoracic leg bearing an antennal cleaner with a distal zone of short, separated setae, and a basal arc of confluent setae that performs the cleaning function (Grade C of Hlavac 1971). The first eight characters will place *Tropopterus* within Psydrini in the system of Roig-Juñent and Domínguez (2001). The last antennal cleaner character differentiates the Psydrini from Moriormorphini (Baehr 1998; Liebherr 2020), as Psydrini exhibit a shorter, less well-developed antennal cleaner (Grade B of Hlavac 1971) versus that observed in Moriormorphini. The morphological results conform to phylogenetic hypotheses based on molecular sequence data (Maddison et al. 1999, 2019).

Within Moriormorphini *Tropopterus* may be diagnosed by the inversion of the male aedeagus, a character observed in several other Moriormorphini: *Mecyclothorax storeyi* Moore (1963) of Queensland; and polymorphically within Western Australian populations of *Mecyclothorax punctipennis* (MacLeay) (Liebherr and Will 2015). Nowhere else in Moriormorphini does this character define a monophyletic grouping of species. Other characters supporting monophyly of *Tropopterus* include deep, pit-like paramedial depressions of the mentum, also observed in *Meonis* spp. of Australia (Moore 1963; Liebherr 2020). The metathoracic scutellum projects little onto the disc of the elytra, whereas it is more narrowly triangular and elongate in the sister group *Pharetis* (Liebherr 2020). The elytral basal groove (when present) meets the lateral marginal depression at a distinct angle, whereas this juncture is more rounded in *Pharetis thayerae*. Both *Pharetis* and *Tropopterus* are characterized by a tooth along the dorsal margin of the humerus. Though the elytral striae vary in configuration among *Tropopterus* spp., their reduction is derived, and the presence of only the first, or sutural stria in a fully developed condition on the elytral apex is a synapomorphy. All species of *Tropopterus* are characterized by vestigial flight wings, and the metepisternum

is correspondingly foreshortened. That sclerite's dimensions range from length 1.2× breadth to length and breadth subequal; length measured along lateral margin and maximal breadth measured perpendicular to that line. Relative to *Pharetis*, the fourth metatarsomere is more emarginate, with the outer, lateral lobe longer than the inner, mesal lobe. Finally, the setal configuration across the dorsal body is diagnostic, though not synapomorphic, with: presence of both anterior and posterior supraorbital setae; presence of both lateral and basal pronotal setae; presence of the parascutellar setae; absence of any dorsal elytral setae; and presence of both subapical and apical setae near the elytral apex. Consistent with most other moriomorphines there are seven (rarely eight) anterior lateral elytral setae bordering the eighth stria, and six posterior setae: though the posterior two setae of the anterior series, or the anterior two setae of the posterior series may be isolated from their respective series' partners in *T. robustus*, sp. nov. Also, males, where known for the various species, have two setae each side of the apical abdominal ventrite, representing a potential synapomorphy for the genus relative to its Australian adelphotaxon, *Pharetis thayerae* Liebherr (2020). The male aedeagal median lobe is robust, i.e. broad dorsoventrally, with the internal sac flagellar apparatus also large (e.g. Fig. 4A). The aedeagal median lobe of males, for all species so far examined, bears dense longitudinal pleating across the sclerotized surface surrounding the ostium (Fig. 4A, C), with this pleating allowing broad extension of the aedeagal surface during eversion of the internal sac. Females also have two setae each side along the apical margin of ventrite 6 accompanied by four median setae of length subequal to the more lateral setae, these variously arranged in an apically broad trapezoid or in a straight line. The female reproductive tract is characterized by absence of a helminthoid sclerite; a sclerotized projection at the junction of the bursa copulatrix wall, common oviduct, and spermathecal duct (Liebherr and Will 1998). The derived loss of the helminthoid sclerite, observed across many other moriomorphine taxa, is shared with *Raphetis* Moore of southeastern Australia (Liebherr 2020).

Nomenclatural notes. Although *Tropopterus* Solier (1849) was used by major authorities throughout the 19th century (see synonymy above), Gemminger and Harold's (1868) unjustified emendation *Tropidopterus* was adopted by Enderlein (1909), Moore (1963), and subsequently followed by Baehr (1998). The original spelling of *Tropopterus* has also been used more recently (Straneo 1954; Roig-Juñent and Domínguez 2001; Maddison and Ober 2011; Larochelle and Larivière 2013). Though both variants have been used, the original spelling predominates and so the unjustified emendation *Tropidopterus* cannot be considered “in prevailing usage” (ICZN 1999, Article 33.2.3.1). Thus *Tropidopterus* must be rejected in favor of the original spelling.

In addition to the three *Tropopterus* spp. described by Solier (1849), Germain (1911) listed “*T. plicicollis*” ms. name, as an undescribed species held in the Museo

Nacional de Historia Natural, Santiago, Chile, assigning it his “N.^{os} del Catálogo primitivo” entry 500. This combination was never validly described (Lorenz 2005). However a specimen labelled as per Germain’s protocol (“459 / Catapilcanus / P. G. (ined.)”) was described as *Merizodus catipileanus* by Jeannel (1962). That name is synonymized below with *T. montagnei* Solier. Germain’s (1911) list also includes undescribed specimens labelled with his catalog numbers 458 and 460, bracketing the number assigned to “Catapilcanus.” Germain assigned those numbers to his manuscript names *Trechus ebeninus* and *Trechus araucanus*, with Jeannel subsequently describing those specimens as *Trechisibus araucanus* (Jeannel 1962: 562) and *Trechisibus ebeninus* (Jeannel 1962: 577). Thus, some of the undescribed Germain (1911) material was used by Jeannel as the basis for new species he described in 1962, but there is no evidence that any specimens assigned to “*T. plicicollis*”, catalog entry 500, were part of Jeannel’s working material, nor was Germain’s name validated in any subsequent publication. Thus Germain’s (1911) “*Tropopterus plicicollis* (P. G. ined.)” has no nomenclatural standing.

Straneo (1954) described *Tropopterus peruvianus* from two specimens (Sivia, Peru, 13-v-1936, 520 m el.) collected during the Südperu-Expedition of the Naturhistorisches Museum, Hamburg. Although Straneo’s description was published in 1954, the material had been originally de-

scribed in 1942, with the specimens returned to the Hamburg museum and subsequently destroyed in the Allied firebombing of 1943. That the types of this species were lost in the destruction of the museum was documented by Weidner (1976; Dr. M. Husemann pers. comm.). Straneo (1954) recorded the female type used as the basis for the description as being of 8 mm body length. His diagnosis for *T. peruvianus*, translated from the Italian, follows:

“It differs from *T. giraud[y]i* Sol. by the basally non-sinuate pronotum; it also has distinctly obtuse pronotal basal angles; the 1st stria is strongly impressed from approximately 1/6 of the elytra length, immediately commencing as a distinct impression and not with isolated punctures; the eighth stria is about as long as the 1st; the third interstria has a small puncture present the apical half; the two basal antennal articles extend beyond the pronotal base, etc. From *T. duponcheli[i]* Sol. it differs by the first and second striae stria reaching the elytral base, and because the lateral pronotal [margin] is very gradually enlarged from the anterior setal pore towards the base.”

This diagnosis does not fit any of the species treated below. Indeed the presence of a puncture in the third interval does not fit the diagnosis of *Tropopterus*, suggesting phylogenetic placement outside the presently treated taxa. Thus *T. peruvianus* Straneo is to be treated as an available *nomen dubium* with its identity to be stabilized through new collection and designation of a neotype.

Key to the adults of *Tropopterus* Solier recorded from Chile and Argentina

- 1 Elytral microsculpture of transverse mesh or dense transverse lines, the surface iridescent, or discal surface glossy, sculpticells difficult to discern..... 2
- 1' Elytral microsculpture isodiametric, sculpticells distinct, surface granulate with silvery reflection (Fig. 1A)..... 1. *Tropopterus montagnei* Solier
- 2 At least sutural stria evident in basal half of elytral length, the sutural stria indicated by isolated punctures or distinct punctures connected by longitudinally impressed strial segments..... 3
- 2' All elytral striae reduced, elytra smooth basally; sutural stria represented at most by very small isolated punctures on basal half of length versus very distinct in apical half, with distinct isolated punctures subapically and a deep continuous impression apically (Fig. 1B)..... 2. *Tropopterus giraudyi* Solier
- 3 Body robust, broad, eyes moderately to very convex, MEW/EL = 0.70–0.81, ocular ratio = 1.35–1.50; standardized body length 5.2–8.4 mm (those beetles of *T. robustus*, sp. nov. and *T. canaliculus* sp. nov. that overlap in body length with *T. peckorum*, **sp. nov.** below, differ greatly in MEW/EL and ocular ratios)..... 4
- 3' Body narrow, eyes little convex, MEW/EL = 0.66–0.68, ocular ratio = 1.30–1.33 (Fig. 1C); standardized body length 5.5–6.0 mm..... 3. *Tropopterus peckorum* sp. nov.
- 4 Elytra with well-developed basal groove extended from laterad scutellum to angulate humerus..... 5
- 4' Elytra lacking basal groove, elytra smoothly depressed mesad humeral angles from disc to depressed anterior elytral margin..... 7
- 5 Vertex with indistinct to well-developed transverse mesh microsculpture, the surface glossy to iridescent; pronotum at most moderately transverse, MPW/PL = 1.20–1.33 (Fig. 1E, F)..... 6
- 5' Vertex covered with distinct mesh of isodiametric and transversely stretched sculpticells, the surface appearing granulate; pronotum rather transverse, MPW/PL = 1.36–1.41 (Fig. 1D)..... 4. *Tropopterus robustus* sp. nov.
- 6 Prosternum with deep, narrow, canaliculate depression medially from prosternal process anterad more than half length of prosternum; discal elytral intervals 1–3 with glossy surface, sculpticells difficult to discern except near strial punctures, surface not iridescent (Fig. 1E)..... 5. *Tropopterus canaliculus* sp. nov.
- 6' Prosternum broadly, medially flattened anterad prosternal process, a shallow longitudinal depression present over a portion of the flattened area in some individuals; discal elytral intervals 1–3 covered with dense transverse-line microsculpture, surface iridescent (Fig. 1F)..... 6. *Tropopterus duponcheli* Solier

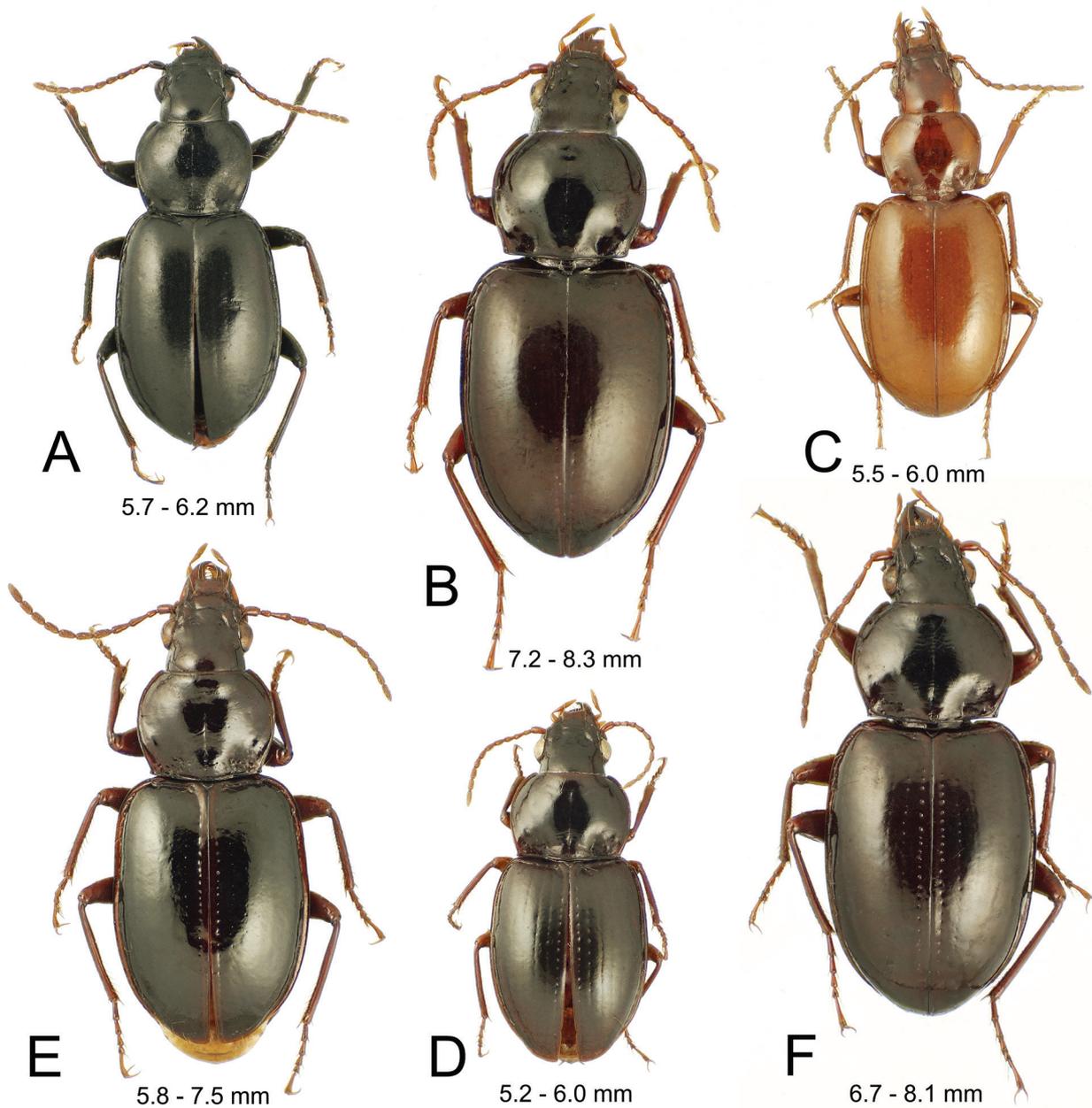


Figure 1. *Tropopterus* spp., dorsal view; range of standardized body lengths in mm. **A.** *T. montagnei* female; Petorca Prov., Q. Tigre Zapallar, Catapilco (MNHN). **B.** *T. giraudyi* female; Valdivia Prov., Chaihuin (EMEC). **C.** *T. peckorum* male; Quillota Prov., P. N. La Campana (FMNH). **D.** *T. robustus* female; Malleco Prov., M. N. Contulmo (FMNH). **E.** *T. canaliculus* female; Malleco Prov., P. N. Nahuelbuta (FMNH). **F.** *T. duponchelii* male; Arauco Prov., Caramavida (MCZ).

- 7 Pronotal basal margin straight, or anteriorly curved laterally so that hind angles lie anterad margin of median base; eyes moderately to very convex, ocular ratio = 1.41–1.45, ocular lobe ratio = 0.85–0.89, juncture of ocular lobe and gena slightly obtuse in dorsal view 8
- 7' Pronotal basal margin trisinate, inflexed anteriorly behind very deep laterobasal depressions, posteriorly expanded laterally to acute hind angles (Fig. 2A); eyes small, little convex, ocular ratio = 1.36, ocular lobe ratio = 0.76–0.81, juncture of ocular lobe and gena very obtuse in dorsal view 7. *Tropopterus trisinuatus* sp. nov.
- 8 Sutural stria deep, narrow, continuous at elytral apex, stria 2 obsolete there except for broad, very shallow depression just mesad apical seta; pronotum more quadrate, MPW/PL = 1.27–1.37 (Fig. 2B)..... 8. *Tropopterus minimicro* sp. nov.
- 8' Both sutural stria 1 and stria 2 impressed at elytral apex, both of them punctate anteapically; pronotum more transverse, MPW/PL = 1.37–1.39 (Fig. 2C)..... 9. *Tropopterus fieldianus* sp. nov.

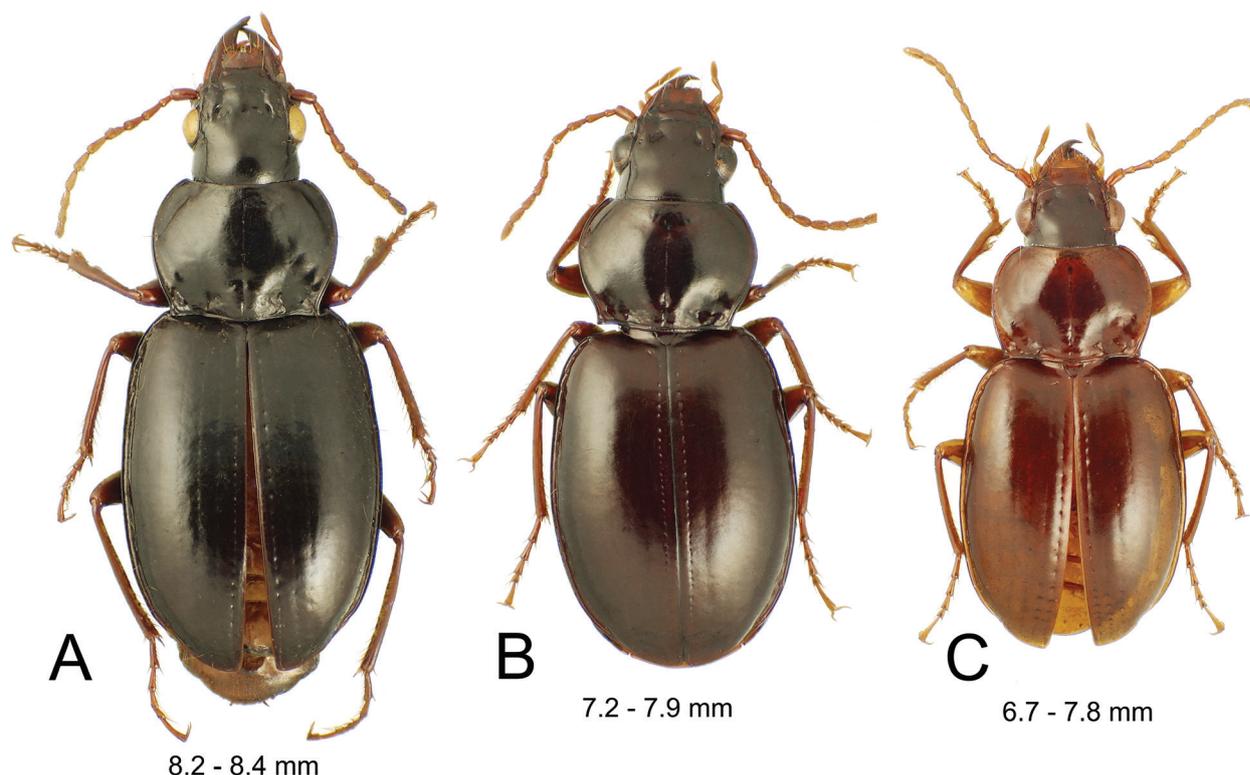


Figure 2. *Tropopterus* spp., dorsal view; range of standardized body lengths in mm. **A.** *T. trisinuatus* female; Cautín Prov., Villarrica (CAS). **B.** *T. minimicro* female; Valdivia Prov., P. N. Oncol (OSAC). **C.** *T. fieldianus* male; Osorno Prov., Maicolpue (FMNH).

1. *Tropopterus montagnei* Solier

Figures 1A, 7A, 8A, 9A, 10

Tropopterus montagnei Solier 1849: 214; Reed 1874: 58.

Tropidopterus montagnei Gemminger and Harold 1868: 385 (unjustified emendation).

Merizodus catapileanus Jeannel 1962: 606 (New synonymy).

Diagnosis ($n = 3$). These somber-colored, small-bodied beetles – standardized body length 5.7–6.2 mm – can be recognized by the isodiametric elytral microsculpture that gives the surface a granulate appearance. The legs are dark, with the femora and tibial apices as dark as the piceous head, pronotum, and elytra. The pronotum is moderately transverse (MPW/PL = 1.21–1.27) with the pronotal hind angle obtuse, the lateral margin straight anterad the hind angle. The elytral striae 1–4 are obsolete, only traceable on the disc and without punctuation. Only the first, sutural stria is \pm traceable on the elytral apex. The eyes are small (ocular ratio = 1.32–1.36) with about 18 ommatidia crossed along a horizontal diameter of the eye. The vertex is glossy, contrasted with the transverse mesh microsculpture of the pronotum, and the granulate isodiametric microsculpture of the elytra. Ventrally the prosternum is broadly flattened to moderately depressed medially from the prosternal process anterad to 2/3 of the prosternal length, and the mesepisternum is smooth, with 2–3 irregular punctures dorso-ventrally arranged on its concave surface.

Female reproductive tract ($n = 1$). Bursa copulatrix columnar, length twice breadth, compressed under microslide cover slip (Fig. 7A), bursal walls relatively thick, translucent; spermatheca globose (separated in single dissection); basal gonocoxite 1 with apical fringe of two setae (Fig. 8A); apical gonocoxite 2 broadly triangular, base extended laterally, with two moderate lateral ensiform setae and one dorsal ensiform seta; apical sensory fossa with two nematiform setae.

Type information. *T. montagnei* lectotype female (MNHN) hereby designated: S. Iago (handwritten on blue label) // MUSEUM PARIS / CHILI / Cl. Gay 1845 (grey label) // 9 45 (round blue label) // TYPE (red label) // *Tropopterus* / *montagnei* / Sol. Sn. Iago (handwritten white label) // *Tropopterus* / Measured / Specimen #1 / det. J.K. Liebherr 2019 // LECTOTYPE / *Tropopterus* / *montagnei* / Solier / des. Liebherr 2019 (black-margined red label). PARALECTOTYPE female (MNHN): MUSEUM PARIS / CHILI / Cl. Gay 1845 (grey label) // 9 45 (round blue label) // *Tropopterus* / Measured / Specimen #2 / det. J.K. Liebherr 2019 // PARALECTOTYPE (as above).

Merizodus catapileanus holotype female (MNHN): Catapilco // 459 // Chili / Aconcagua / Catapilco // *Catapileanus* / P. G. (ined.) / 459 // *Merizodus* / *catapileanus* / m. (hand written cursive) // *Tropidopterus* / *catapileanus* / det. P. M. Johns // 163 // *Tropopterus* / Measured / Specimen #3 / det. J.K. Liebherr 2019 // HOLOTYPE / *Merizodus* / *catapileanus* / Jeannel 1962 (black-margined

red label) // *Tropopterus / montagnei / Solier / det. J.K. Liebherr 2019*. Because Jeannel (1962) stated this species name was based on “une femelle,” he designated a holotype by monotypy. This female was card-mounted with the abdomen missing. As Jeannel routinely mounted dissected genitalia on separate pins (see the *Tropopterus giraudyi* paralectotype) it appears this species was dissected with the abdomen plus genitalia mounted separately, the latter subsequently disassociated. The data on the specimen agree with those provided in Jeannel’s (1962: 606) description. Also, Jeannel’s textual description fits the specimen with regard to size, wing configuration, general habitus, and absence of dorsal elytral setae. However, the illustration accompanying the text deviates significantly from the specimen by showing the penultimate palpomere as setose, and the elytra with eight lateral elytral setae (arranged as 4 + 4). In fact the penultimate palpomere is glabrous, and the lateral elytral setae are arranged as 6 + 1 + 6; i.e. a single seta separated from the anterior and posterior series of six setae each. Admittedly, there was excessive mucilage filling the elytral marginal depression, and so the setae were apparently missed. The consequence of these mistakes was Jeannel’s placement of this species in a genus of the Zolini.

Date locality information for all specimens. Chile: Petorca Prov. (labelled “Aconcagua”), Catapilco, 32°34.10'S, 71°16.52'W, Germain (MNHN, 1); Q. Tigre Zapallar (= Catapilco), 13-vii-1966, Pena (MNHN, 1). Santiago Prov., Santiago (lectotype and paralectotype), 33°26.75'S, 70°40.12'W, Solier (MNHN, 2).

Distribution and habitat. No habitat data are associated with the types of either names representing this species. This species is restricted to the Santiagan entomofaunal region (Fig. 9A; O’Brien 1971).

2. *Tropopterus giraudyi* Solier

Figures 1B, 3A, B, 6A, B, 7B, 8B, 9B, 10

Tropopterus giraudyi Solier 1849: 212 (*Tropoptertus giraudyi*, printer’s error); Reed 1874: 58.

Tropidopterus giraudi Gemminger and Harold 1868: 385 (unjustified emendations).

Diagnosis ($n = 5$). This large-bodied species (standardized body length 7.2–8.3 mm) is easily diagnosed by the smooth elytra with the sutural stria completely effaced to irregularly punctate basally (Fig. 1B), the punctures, when present, broad, very shallow, and irregularly distributed. Conversely, the sutural stria is distinctly punctate behind the elytral midlength, transforming to a very narrow canaliculate depression near the elytral apex. The eyes are moderately convex (ocular ratio = 1.41–1.47) with about 23 ommatidia crossed by a horizontal diameter of the eye. The pronotal hind angles are right to obtuse, sharp, with the lateral margins subparallel anterad the angles. The pronotal apical margin is finely, continuously margined medially, and the pronotum is relatively narrow

(MPW/PL = 1.21–1.25) compared to the similar-appearing *T. duponchelii* (MPW/PL = 1.25–1.32; Fig. 1F) and *T. minimucro* (MPW/PL = 1.27–1.37; Fig. 2B). Ventrally the prosternum is deeply depressed medially, the broad depression extended from the prosternal process more than halfway toward the front margin, and the mesepisternum is broadly punctate, with 8–9 punctures in 2–3 dorsoventral rows. The glossy vertex contrasts with the pronotum that bears a dense, shallow transverse mesh, and the iridescent elytra covered with dense transverse lines.

Male genitalia ($n = 13$). Aedeagal median lobe robust, broad dorsoventrally from base to apex, the broadly rounded apex bearing a well-developed mucro on its ventrobasal aspect (Fig. 3A); internal sac lightly sclerotized (sac not everted), with a sinuous spicular sclerite that would be positioned on the sac apex when everted. Antecostal apodeme of laterotergite IX (Deuve 1993) broadly angulate distally, the apex of the apodeme not extended much beyond lateral arms of the apodeme (Fig. 3B). Right paramere of median lobe elongate, slightly broader medially, with one or two long setae apically, six to eight setae along ventral margin, and several more smaller setae apically (Figs 6A, B); left paramere broad basally, variously narrowed apically into a parallel-sided extension (Fig. 6A), or an evenly narrowed apex (Fig. 6B), the apex of the paramere bearing two or three longer setae plus several shorter subapical setae.

Female reproductive tract ($n = 2$). Bursa copulatrix columnar, length 2.5× breadth, compressed under microslide cover slip (Fig. 7B), bursal walls relatively thick, translucent; spermatheca ovoid; spermathecal gland elongate, broadest distally; spermathecal gland duct entering spermathecal duct basad spermathecal reservoir; basal gonocoxite 1 with two apical fringe setae (Fig. 8B); apical gonocoxite 2 narrowly triangular, base little extended laterally, with one or two (Fig. 8B) lateral ensiform setae, one dorsal ensiform seta, and two apical nematiform setae.

Type information. Lectotype female (MNHN) hereby designated (card mounted): S. Iago (handwritten on blue label) // MUSEUM PARIS / CHILI / Cl. Gay 1845 (grey label) // TYPE (red label) // *Tropopterus / Giraudyi / Sol.* Sn. Iago (handwritten white label) // 9 / 45 (pale blue circle) // LECTOTYPE // *Tropopterus / giraudyi / Solier / des. Liebherr 2019* (black-margined red label). Paralectotype male (MNHN) (card mounted, genitalia dissected and removed): MUSEUM PARIS / CHILI / Cl. Gay 1845 (grey label) // 9 / 45 (pale blue circle) // *Tropidopterus / giraudi Sol.* // PARALECTOTYPE (as above). Male genitalia (card mounted): *Tropidopt. / Giraudi / Chili / '71* // PARALECTOTYPE (as above).

Date locality information for all specimens. Argentina: Neuquén Prov., Pucará to Lago Venados road, Lago Lacar, 40°10.50'S, 71°21.50'W, 24–25-i-1972, Herman (NMNH, 1). Chile: Cautín Prov., Bellavista, Lago Villarrica, 39°12.55'S, 72°08.14'W, 250 m el., 8-i-2006, Will (EMEC, 1); Villarrica, 30 km NE, 39°09.23'S, 71°51.82'W, 1–30-i-1965 (MCZ, 1). Chiloé Prov., Chepu (det. Straneo, see Straneo [1969]), 42°02.03'S,

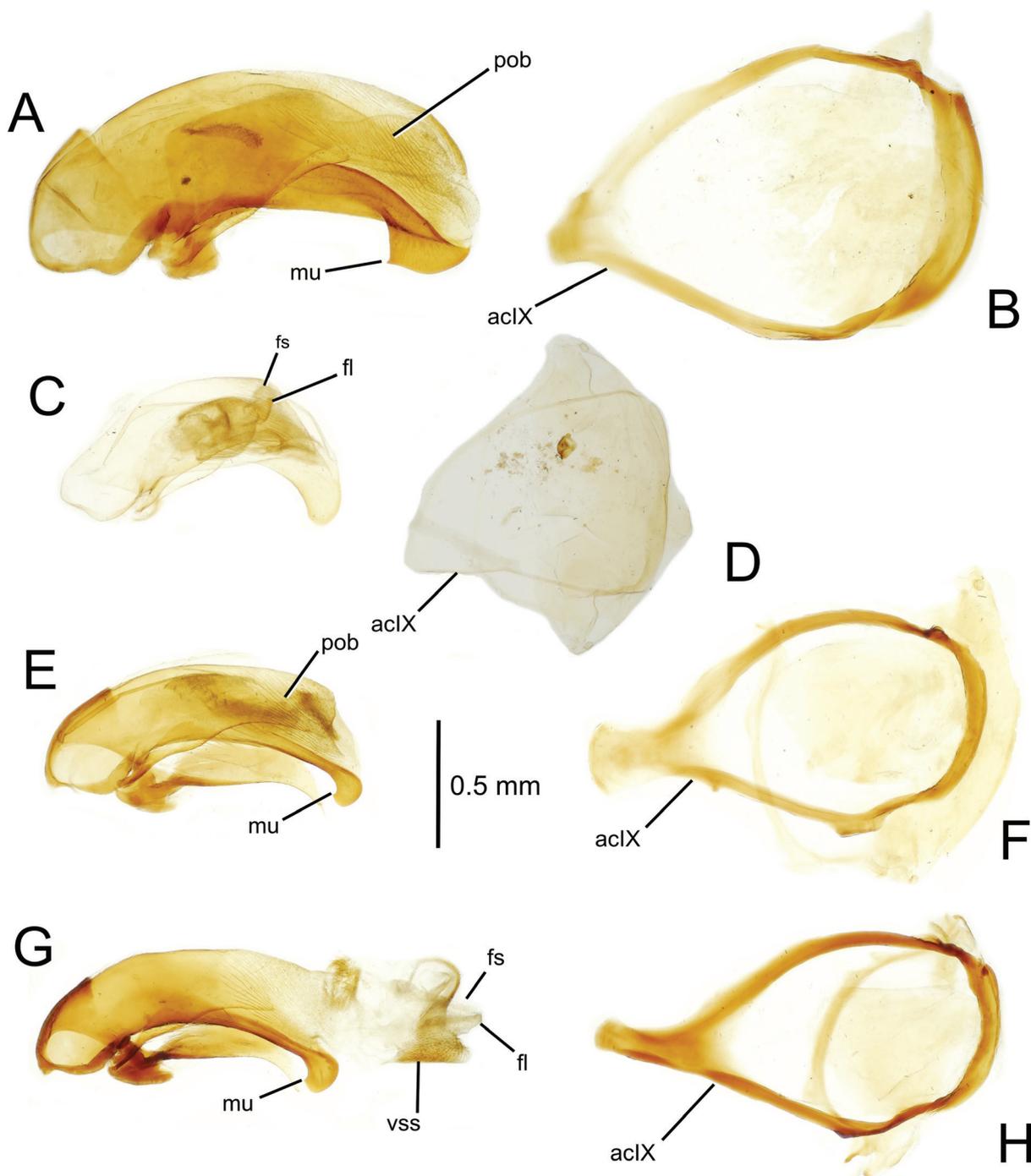


Figure 3. Male aedeagal median lobe, left view, and antecostal apodeme and tergite of abdominal IX, dorsal view. **A–B.** *T. giraudyi*; Chile, “*Tropopterus nitidus* Sol.”, Chaudoir Coll. (MNHN). **C, D.** *T. peckorum*; Quillota Prov., P. N. La Campana (FMNH) (**D** darkened to allow viewing of teneral dissection). **E–H.** *T. robustus*; Malleco Prov., M. N. Contulmo. **E–F.** (CMNH). **G, H.** (FMNH). For abbreviations used to label structures see Table 1.

73°58.31'W, 9-x-1958, Kuschel (MNHN, 1); P. N. Chiloé, under logs/rocks, 42°36.84'S, 74°06.25'W, 20-i-2002, Will & Lew (EMEC, 1), Rio Cipresal, above, lot DRM 06.085, 42°34.70'S, 74°04.98'W, 195 m el., 20–21-i-2006, Maddison & Will (OSAC etoh, 2), Quemchi, 11 km w of, 11 km E Hwy. 5, Valdivian rainforest remnant w/ thick bamboo understory, beating vegetation, 42°10.40'S, 73°35.73'W, 140 m el., 10-

xii-2002, Clarke (FMNH, 3). Llanquihue Prov., P. N. Vicente Pérez Rosales, Ensenada, 9.2 km NE, on road to Petrohué, Valdivian rainforest w/ *Nothofagus* spp., lot 987, pyr.-fogging old logs, 41°10.20'S, 72°27.10'W, 125 m el., 2-i-1997, Newton & Thayer (FMNH etoh, 1), 28-i-1997, Newton & Thayer (FMNH etoh, 1), 4–28-i-1997, Newton & Thayer (DRM DNA voucher DNA0532, FMNH on loan to OSAC, 1), Volcán Osor-

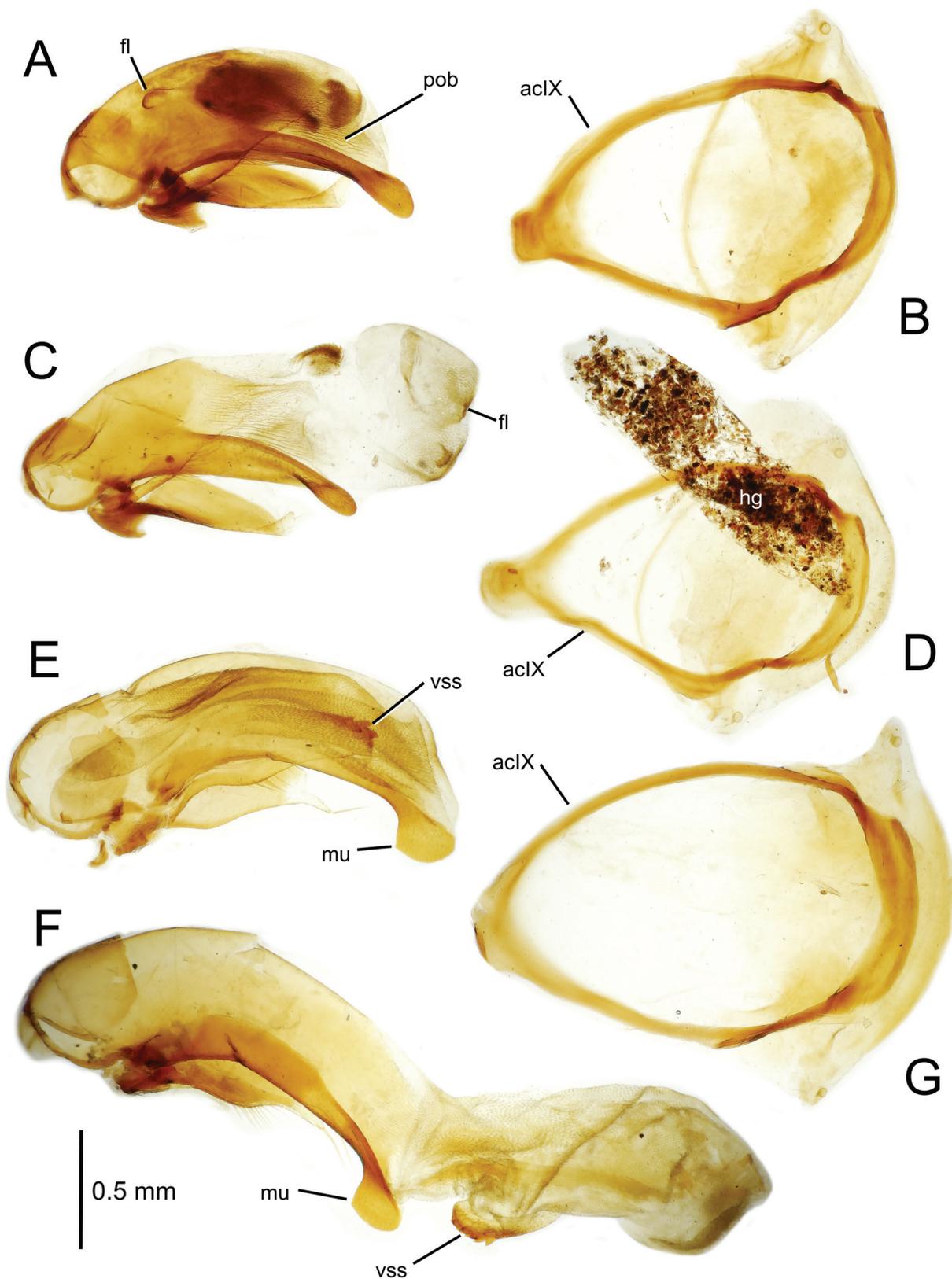


Figure 4. Male aedeagal median lobe, left view, and antecostal apodeme and tergite of abdominal IX, dorsal view. **A–D.** *T. canaliculus*; Malleco Prov., P. N. Nahuelbuta. **A, B.** (FMNH). **C, D.** (OSAC). **E–G.** *T. duponchelii*; Arauco Prov., Caramavida. **E.** (NMNH). **F–G.** (MCZ). For abbreviations used to label structures see Table 1.

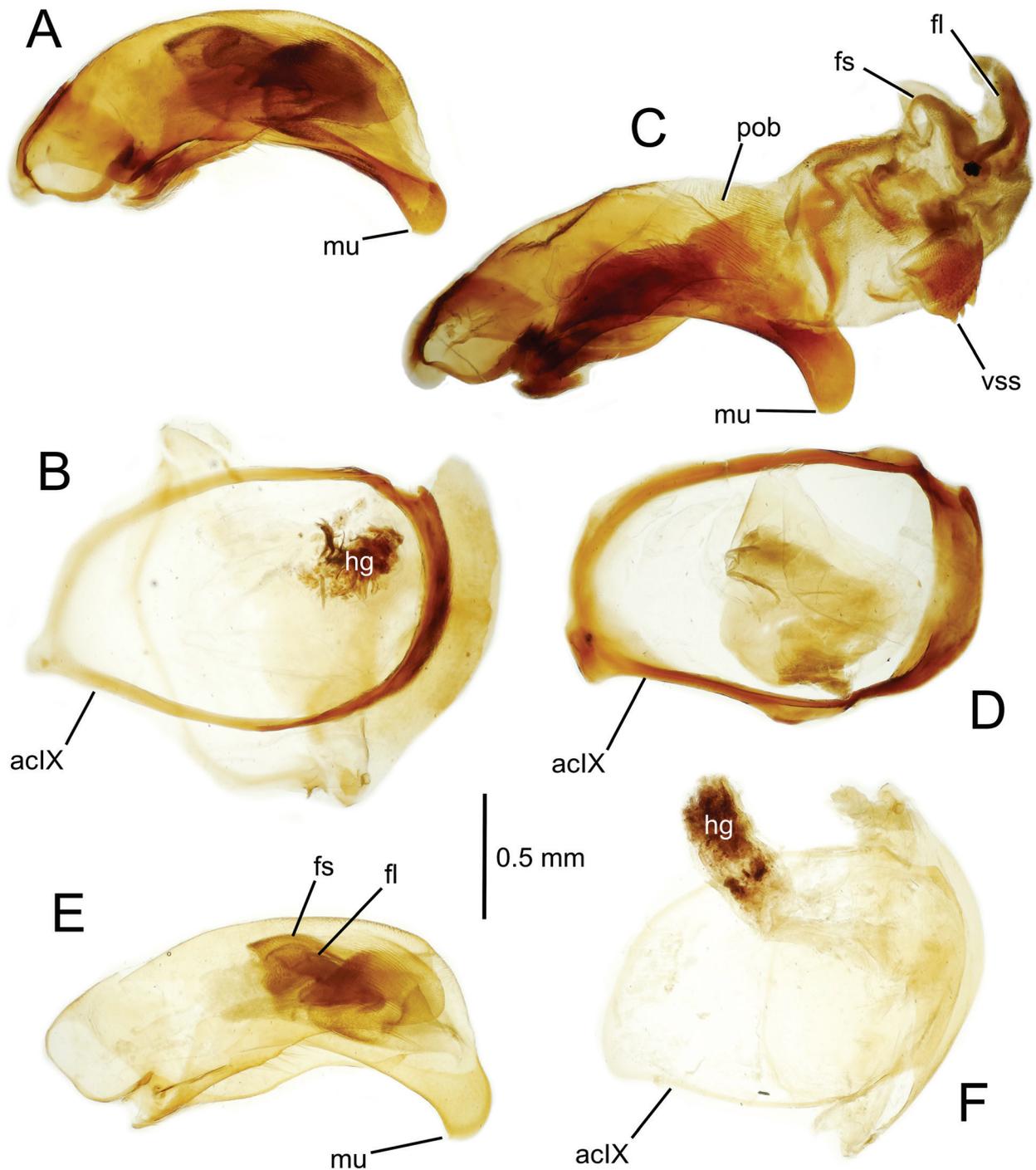


Figure 5. Male aedeagal median lobe, left view, and antecostal apodeme and tergite of abdominal IX, dorsal view. **A–D.** *T. minimucro*. **A, B.** Cautín Prov., Bellavista (EMEC). **C, D.** Llanguihue Prov., P. N. Vicente Pérez Rosales (FMNH). **E, F.** *T. fieldianus*. **E.** Osorno Prov., Maicolpue (FMNH). **F.** Valdivia Prov. La Unión (FSCA). For abbreviations used to label structures see Table 1.

no, SW slope, c. km 11 to La Burbuja, low *Nothofagus dombeyi* w/bamboo & shrub understory, lot 1065, pyr.-fogging old mossy logs, 41°07.9'S, 72°32'W, 1090 m el., 15-xii-2002, Newton & Thayer (FMNH, 3). Malleco Prov.: P. N. Nahuelbuta, Los Portones entrance, 2.3 km W, *Nothofagus dombeyi* + ?*antarctica*, mostly open understory, lot 1057, pyr. fogging old *Nothofagus*

logs, 37°49.41'S, 72°58.95'W, 1150 m el., 25-xii-2002, Newton, Thayer & Chani (FMNH, 1). Osorno Prov., P. N. Puyehue, Aguas Calientes, forest litter on trail, lot P#85-43, sifting 40°43.66'S, 72°18.11'W 500 m el. 20-xii-1984, S. & J. Peck (FMNH, 1), Anticura, 4 km E, 40°39.73'S, 72°08.1'W, 460 m el., 31-xii-1996, Newton & Thayer (DRM 97-021, DNA voucher DNA0459,

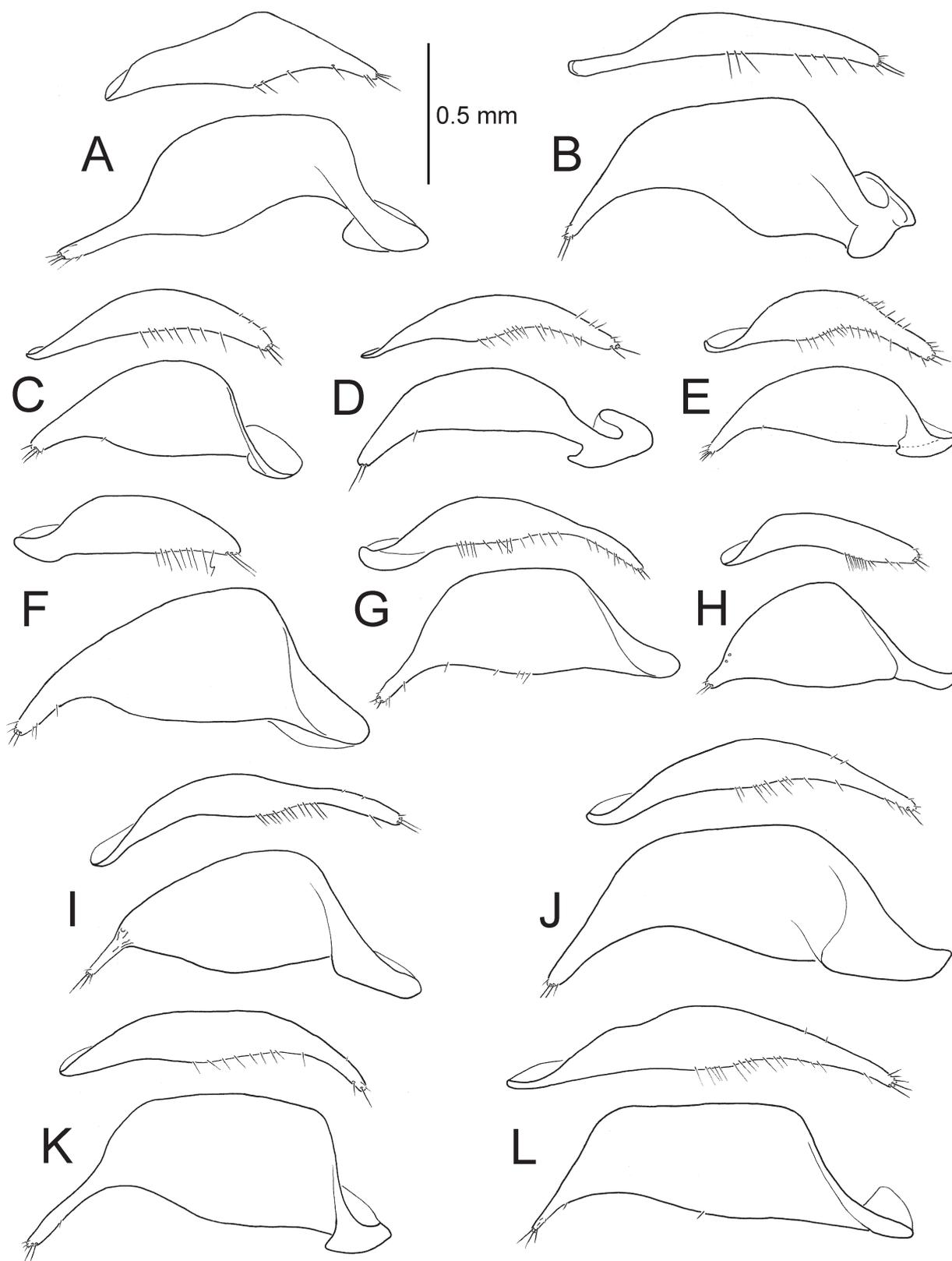


Figure 6. Paired sets of left parameres (above) and right parameres (below), ectal view, for male specimens of *Tropopterus* spp. Parameres are in anatomically correct orientation with ventral surface toward bottom of drawing. **A, B.** *T. giraudyi*. **A.** Malleco Prov., P. N. Nahuelbuta (FMNH). **B.** Chili, “*Tropopterus nitidus* Sol.” [sic], Chaudoir Coll. (MNHN). **C.** *T. peckorum*; Quillota Prov., P. N. La Campana (FMNH). **D, E.** *T. robustus*. **D.** Malleco Prov., P. N. Contulmo (CMNH). **E.** Cautín Prov., Bellavista (CAS). **F, G.** *T. canaliculus*. **F.** Malleco Prov., P. N. Nahuelbuta (FMNH). **G.** Arauco Prov., Caramavida (NMNH). **H–I.** *T. duponchelii*. **H.** Talca Prov., Altos de Vilches (MNHN). **I.** Arauco Prov., Caramavida (MCZ). **J, K.** *T. minimicro*. **J.** Cautín Prov., Bellavista (EMEC). **K.** Llanquihue Prov. P. N. Vicente Pérez Rosales (FMNH). **L.** *T. fieldianus*; Valdivia, La Union (FSCA).

FMNH on loan to OSAC, 1), rainforest w/ large *Saxegothaea*, lot 985-2, pyr.-fogging old logs, 40°39.73'S, 72°08.10'W, 460 m el., 30-i-1997, Newton & Thayer (FMNH etoh, 1), Puyehue, 10 km E, 40°37.00'S, 72°30.68'W, 24-i-1951, Ross & Michelbacher (CAS, 2), 20 km E, 40°36.66'S, 72°24.83'W, 26-i-1951, Ross & Michelbacher (CAS, 1). San Antonio Prov., Santo Domingo, 33°35.50'S, 71°36.33'W, 1-xi-1972 (MNHN, 1). Santiago Prov., Santiago (lectotype, paralectotype), 33°26.75'S, 70°40.12'W, Solier (MNHN, 2). Valdivia Prov., Chaihuin, Res. Costera Valdiviana, lot CH2006.13.H.i.2, 40°03.71'S, 73°35.32'W, 443 m el., 14-i-2006, Will (EMEC etoh, 1), lot CH2006.16.i.2, 40°01.67'S, 73°31.85'W, 511 m el., 16-i-2006, Will (EMEC etoh, 1), headlamp search, 39°58.32'S, 73°39.23'W, 77 m el., 10-xi-2008, Will (EMEC, 1), Corral, 39°53.25'S, 73°25.69'W, xii-1905, Thaxter (MCZ, 3), i-1906, Thaxter (MCZ, 1). Valdivia Prov., P. N. Oncol, Mirador Pilocura, Sendero, 39°41.65'S, 73°18.86'W, 715 m el., 12-i-2006, Will (EMEC, 2), road to P. N. Oncol, 39°41.98'S, 73°20.65'W, 513 m el., 9-xi-2008, Will (EMEC, 1), Cerro Oncol trail, 39°41.89'S, 73°18.07'W, 500 m el., 11-i-2006, Maddison & Seago (OSAC, 2), Puerto Fui, 12 km SSE, Lago Pirehueico, Site F, Coigue-Lenga Forest, *N. dombeyi*, *N. alpina*, *N. pumilio*, under *Nothofagus* bark 39°58'S, 71°50'W, 1030 m el., 10-i-1988, Ashworth, Figiseth & Maliscke (NDSU, 1), Valdivia Res., Punta Curiñanco, CH2006.13.i.2, 39°41.25'S, 73°21.50'W, 150 m el., 13-i-2006, Will (EMEC etoh, 1). No other data except “x-70” (MNHN, 1); “1611”, Chaudoir colln. (MNHN, 1); “Chili // *Tropopterus nitidus* [sic]”, Bates colln. (MNHN, 1).

Distribution and habitat. This is the most widely distributed species of *Tropopterus*. with localities ranging in latitude from 33°27'S–42°37'S (Fig. 9B). Known localities thus occur within the Santiagan, Northern Valdivian, and the northern portion of the Southern Valdivian entomofaunal provinces (O'Brien 1971). Specimens have been collected by sifting in Valdivian rainforest with *Nothofagus*, by pyrethrin fogging of old *Nothofagus* logs, under logs and rocks, and by beating vegetation. *Tropopterus giraudyi* has been contemporaneously collected in localities shared with: *Metacorneolabium exuberatum* Thayer (1985; Argentina: Neuquén Prov., Pucara, 24–25-i-1972, Herman, NMNH); *Glypholoma chepuense* Thayer (1997; Chile: Chiloé Prov., Chepu, MNHN); *Andotypus ashworthi* Spangler (Fikáček et al. 2014; Chile: Llanquihue, P. N. Vicente Pérez Rosales, 9.2 km NE Ensenada on road to Petrohué, FMNH); *Anaballatus chilensis* (Newton et al. 2017; Chile: Cautín Prov., Bellavista, N. shore Lago Villarrica, FMNH); Chile: Malleco Prov., P. N. Nahuelbuta, 2.3 km W Los Portones entrance, FMNH; and Chile: Osorno Prov., P. N. Puyehue, 4.1 km E Anticura, FMNH). The Neuquén Province, Argentina record from Lee Herman, above, represents the only Argentine record for both *Tropopterus* and *Metacorneolabium* Steel (Thayer 1985).

3. *Tropopterus peckorum* sp. nov.

<http://zoobank.org/2E5BF389-1E6B-4C7D-A3CA-5ACF5E7A536F>

Figures 1C, 3C, D, 6C, 9C, 10

Diagnosis ($n = 3$). Beetles of this species are distinguished by their small size (standardized body length 5.5–6.0 mm) and narrow bodies. The latter is evidenced by: very flat eyes, ocular ratio = 1.30–1.33; a narrow, quadrate pronotum, MPW/PL = 1.21–1.31; and narrow, relatively flat elytra, MEW/EL = 0.66–0.68. The pronotal median base is longitudinally wrinkled near the narrow basal marginal bead, whereas the anterior margin is smooth medially, with an anterior marginal bead present only in the lateral half of each side. The sutural stria is evident as a series of minute, isolated punctures on the elytral disc, whereas it is effaced on the elytral apex. The elytral basal groove is present, continuous from laterad the parascutellar seta to the obtuse angle where it joins the lateral marginal depression. Ventrally the prosternum is broadly flattened to slightly depressed medially anterad the prosternal process, and the mesepisternum bears 7 or 8 linearly arranged punctures in the dorsoventral depression. The vertex is glossy, the pronotum glossy with indistinct transverse lines, and the elytral disc is covered with an elongate transverse mesh, the sculpticells 2–4× as broad as long.

Description. Head capsule narrow; eyes flat, ocular lobe little-protruded, compound eye covering 0.82–0.83 length of ocular lobe, 18–20 ommatidia across horizontal diameter of eye; antennomeres broadened apically, moderately elongate, antennomere 9 length 1.83× greatest diameter; mandibles elongate, distance from anterior condyle to apex of left mandible 1.91× distance from condyle to lateroapical margin of labrum; mentum basal breadth 2.86× length from lateral apex to base, paramedial pits deep; ligular apex truncate, broad, two setae separated by three setal diameters; paraglossae extended as far beyond ligular margin as distance from paraglossal base to ligular margin. Pronotum relatively narrow, lateral margins straight to slightly sinuate before right to slightly acute hind angles; anterior transverse impression broad and shallow across width; front angles only slightly protruded; lateral marginal depression narrowest at midlength, slightly broader at front angle, broadened progressively toward hind angle; lateral seta separated from lateral marginal depression by one diameter of articulatory socket; laterobasal depression quadrate, oblique with deep inner groove and upraised tubercle in middle of depression. Elytra smooth, striae 2–4 traceable on disc as longitudinal series of minute lenticular punctures, striae 5–7 obsolete; stria 8 present anteriorly near posterior portion of anterior lateral setal series, very shallow at midlength, and deep, continuous inside posterior setal series; lateral marginal depression broad, lined with transverse sculpticells; subapical sinuation broad, shallow, elytral plica evident in lateral view. Metepisternum equitrapezoidal, the maximal width and lateral length subequal; metasternal process rounded apically, apex

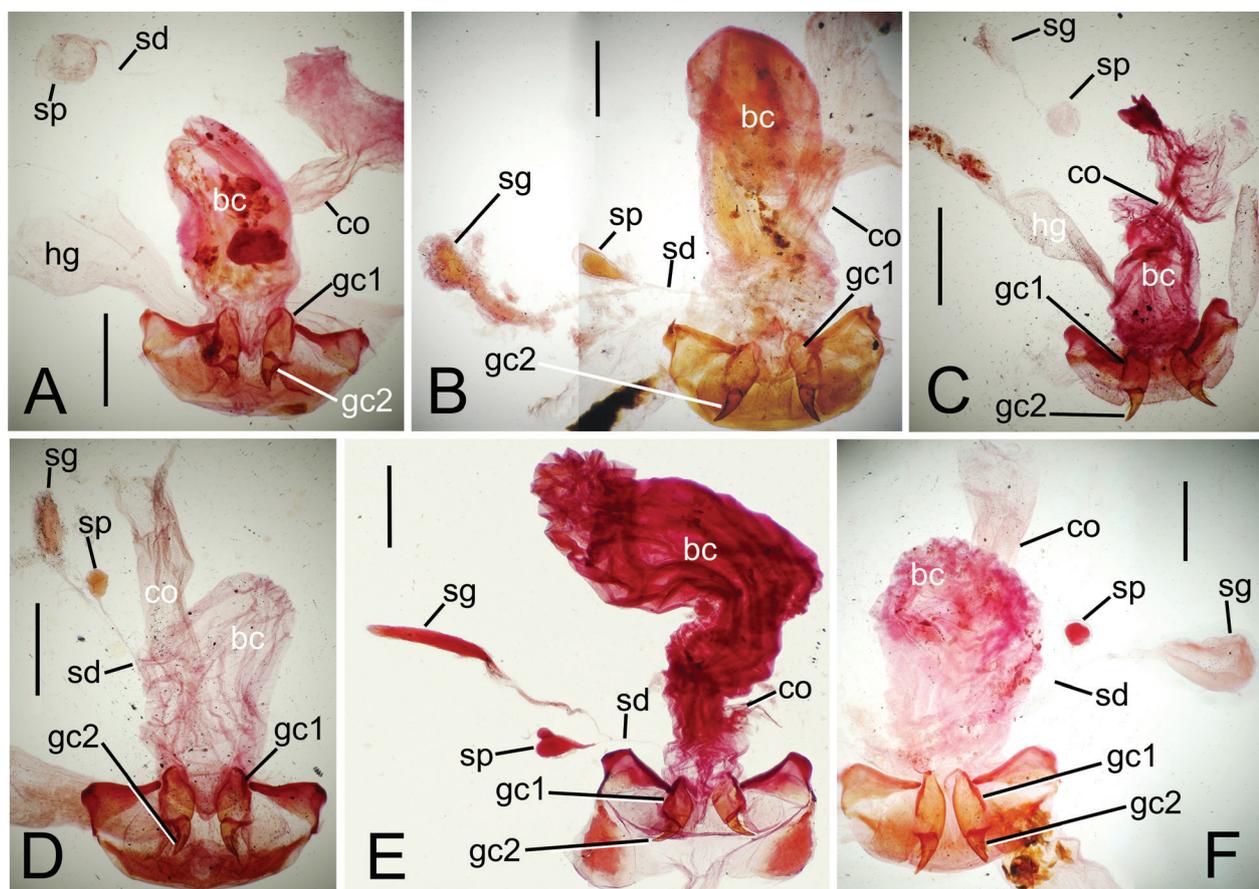


Figure 7. Female reproductive tract and gonocoxae of abdominal segment IX, ventral view. **A.** *T. montagnei*; Petorca Prov., Q. Tigre Zapallar, Catapilco (MNH). Spermatheca disassociated from bursal assemblage. **B.** *T. giraudyi*; Llanquihue Prov., P. N. Vicente Pérez Rosales (FMNH). **C.** *T. robustus*; Malleco Prov., M. N. Contulmo (FMNH). **D.** *T. canaliculus*; Malleco Prov., P. N. Nahuelbuta (FMNH). **E.** *T. duponchelii*; Arauco Prov., Caramavida (MCZ). **F.** *T. minimucro*; Valdivia Prov., P. N. Oncol (EMEC). For abbreviations used to label structures see Table 1. Vertical scale bars: 0.5 mm.

broadly and the side narrowly upraised in a lateral bead. Abdominal ventrites 3–6 broadly depressed laterally, suture between ventrites 1 and 2 nearly straight, surface of ventrite 2 depressed within slight sinuation; anterior margins of ventrites 4–6 depressed, intersegmental membranes punctate; female apical abdominal ventrite with two setae each side, four shorter medial setae arranged in an apically broader trapezoid. Body coloration pale (specimens appear teneral), concolorous rufobrunneous, legs not paler; ventral surface concolorous, with elytral epipleura, metepisternum, and apical half of ventrite 6 paler, rufoflavous.

Male genitalia ($n = 1$). Aedeagal median lobe broadest dorsoventrally at base, narrowed slightly to a narrowly rounded apex (Fig. 3C); internal sac with a sclerotized flagellar complex (teneral specimen), with a putative, short flagellum visible. Antecostal apodeme of abdominal IX narrowly rounded, the apex not extended beyond lateral arms (Fig. 3D, although teneral specimen may not have sclerotized fully to attain mature configuration; e.g. Song 2004). Right paramere elongate, slightly broader at midlength with broadly rounded apex, two longer apical

setae complemented by eight setae along ventral margin and several very small setae on the dorsoapical surface (Fig. 6C); left paramere broad basally, with short narrow apical extension that bears two longer apical setae plus several very small subapical setae.

Holotype male (FMNH): CHILE: Quillota Prov. / Olmue, La Campana / N.P., 2.XII.1984 // FMHD#85-889, / hygrophilous forest / leaf litter, S.&J. / Peck, P#85-4, Berlese / FIELD MUSEUM NAT. HIST. // Tropopterus / Measured / Specimen #2 / det. J.K. Liebherr 2019 // HOLOTYPE / Tropopterus / peckorum/ J.K. Liebherr 2019 (black-margined red label).

Paratypes: Chile: Quillota Prov., P. N. La Campana (Sector Granizo), Cajón La Opositora, 685 m el., 32°58.80'S, 71°06.93'W, 29.xi–29.xii.2002, sclerophyll forest, ?w/*Nothofagus obliqua*, FMHD#2002-019, flight intercept trap, Thayer, Newton, Solodovnikov, 1045, FIELD MUSEUM NAT. HIST. (FMNH, 2)

Etymology. This species is named to honor Stewart Peck and Jarmila Kukalova-Peck for their immense contributions to systematic entomology, and their numerous discoveries of Austral biodiversity.

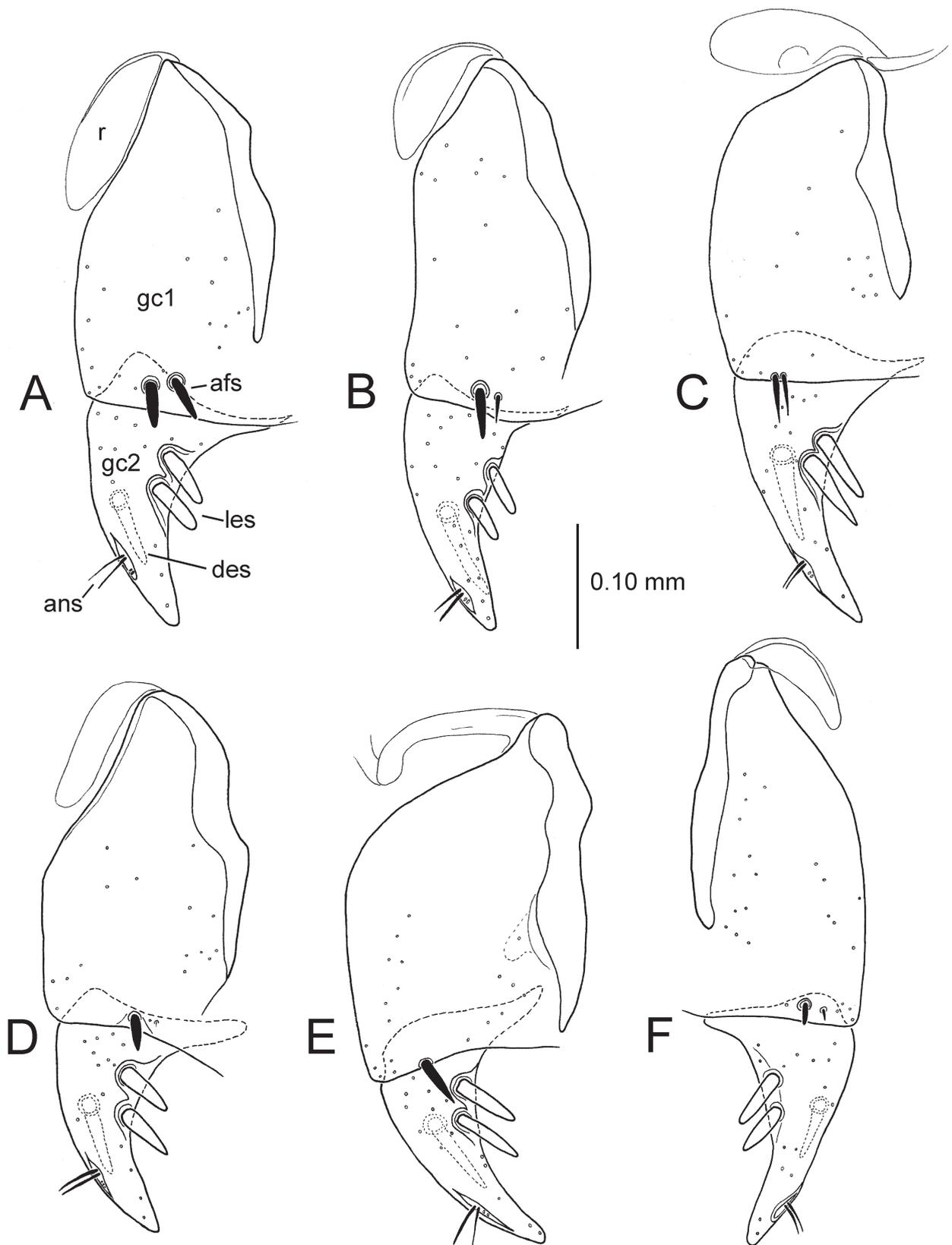


Figure 8. Left gonocoxa (except where noted), ventral view, for *Tropopterus* spp. Specimen information is parallel to that in Figure 7A–F. For abbreviations used to label structures see Table 1. **A.** *T. montagnei*. **B.** *T. giraudyi*. **C.** *T. robustus*. **D.** *T. canaliculus*. **E.** *T. duponchelii*. **F.** *T. minimucro* (right gonocoxa).

Distribution and habitat. This species is known from localities in the Santiagan entomofaunal province (O'Brien 1971) at latitudes near 33°S (Fig. 9C). Both collecting events are associated with ground-level microhabitats, either in forest litter via Berlese sifting, or in an octopus-baited carrion trap in sclerophyll forest with *Nothofagus obliqua* (Brisseau de Mirbel).

4. *Tropopterus robustus* sp. nov.

<http://zoobank.org/A6E5A597-16AB-45C9-BBC8-7F6448078F50>

Figures 1D, 3E–H, 6D–E, 7C, 8C, 9D, 10

Diagnosis ($n = 5$). The combination of small, very broad body, and punctate discal elytral striae 1 and 2 (Fig. 1D) diagnoses this species: standardized body length 5.2–6.0 mm; pronotal MPW/PL = 1.36–1.41; and elytral MEW/EL = 0.74–0.81. The pronotal hind angle is right to acute, the apex of the angle denticulate, and the lateral margins convergent just before the angles. The pronotum anterior margin is beaded only along the lateral 1/3 to 1/4 each side. The parascutellar striole is absent, and instead the sutural stria continues to the well-developed basal groove laterad the scutellum. These small beetles have the most well-developed elytral striae in the genus, striae 3–7 traceable on the disc, and the sutural stria is narrowly and smoothly grooved apically. Ventrally the prosternum is deeply depressed medially from the prosternal process 2/3 of the way to the anterior prothoracic margin. The mesepisternum is mostly smooth, with only 2 or 3 punctures in a furrow at the deepest part of the sclerite's concave surface. And the metepisternum and metepimeron are fused along the lateral margins of those sclerites; a derived character otherwise only observed in *T. fieldianus*. The microsculpture is distinctive, with the vertex covered with well-developed isodiametric to slightly transverse microsculpture, the pronotum covered with a dense transverse mesh, sculpticell breadth 3–4× length, and the elytral disc covered with dense transverse lines connected into a mesh over only portions of the surface.

Description. Head capsule broad, eyes moderately convex, ocular ratio 1.35–1.48, eyes covering most of moderately protruded ocular lobe, ocular lobe ratio 0.90–0.92, horizontal diameter of eye crossing 20 ommatidia; antennae relatively stout, antennomere 9 length 1.67× maximal diameter; mandibles short, distance from anterior condyle to apex of left mandible 1.67× distance from condyle to lateroapical margin of labrum; mentum basal breadth 2.75× length from lateral apex to base, paramedial pits moderately deep; ligular apex truncate, two setae separated by four setal diameters, paraglossae elongate, extended beyond ligular apex more than distance from base to ligular margin. Pronotum broad, lateral margins convergent before minutely denticulate hind angles; basal margin lined with well-developed marginal bead, median base anterad bead longitudinally, shallowly strigose medially, minutely punctate laterally; median longitudinal impression with

elongate lenticular pit at front of median base, narrow and shallow on disc, deep near anterior transverse impression; anterior transverse impression broad and shallow across width; anterior margin beaded only in lateral 1/3 to 1/4 each side, smooth medially; front angle protruded, subangulate mesally, rounded laterally; lateral seta separated from very narrow lateral marginal depression by two diameters of setal articulatory socket; laterobasal depression broadly subquadrate, central tubercle connected anteriorly to disc, mesal surface irregular near punctate median base. Elytra broadly hemiovoid, basal groove deep, slightly irregular at bases of striae, angle with lateral marginal depression obtuse-rounded; sutural stria deeply punctate on disc, the punctures isolated, smooth and moderately deep apically, the sutural striae of the two elytra bordering an upraised sutural callus at conjoined elytral apices; stria 8 deep mesad anterior and posterior series of lateral setae, shallow at midlength, variously interrupted there; lateral elytral setal series variable, with either: anterior series of 5 setae, 2 intermediate setae, and 6 apical setae; or 6 anterior setae, 2 intermediate setae, and 6 posterior setae; or 7 anterior setae, 2 intermediate setae, and 4 posterior setae; lateral marginal depression narrow anteriorly, broadened in apical half, lined with transverse sculpticells apically; subapical sinuation distinctly concave, elytral plica visible in dorsolateral view. Metepisternum slightly elongate, maximal width 0.82× lateral length. Abdomen with visible ventrites 3–6 broadly depressed laterally; suture between ventrites 1 and 2 nearly straight, ventrite 2 depressed within slight sinuation; anterior margins of ventrites 4–6 slightly depressed, but no punctures visible along suture; female apical abdominal ventrite with two setae each side, four shorter medial setae arranged in an apically broader trapezoid. Coloration of dorsal surfaces rufopiceous to piceous with silvery reflection; palpomeres, antennae, legs, and pronotal and elytral margins rufobrunneous; ventral body surface rufopiceous, though proepipleuron dark rufous, elytral epipleuron dark anteriorly and rufobrunneous posteriorly, and apical half of ventrite 6 rufobrunneous.

Male genitalia ($n = 5$). Aedeagal median lobe broad dorsoventrally, apex broadly downturned apicad ostium, with a small mucro on ventrobasal face of apex (Fig. 3E); internal sac with sclerotized spicular fields (Fig. 3E), including a ventrobasal spicular sclerite (Fig. 3G); short flagellum and flagellar sheath both present. Antecostal apodeme of abdominal IX extended distally, the extension ranging from broad and expanded distally (Fig. 3D), to narrow and parallel-sided (Fig. 3H). Right paramere varying slightly in length, the ventral surface lined with many (14–18) setae, the apex bearing two longer setae, and the apicodorsal surface lined with five to eight small setae (Fig. 6D, E); left paramere broadly rounded dorsally, with length varying in concert with right paramere (Fig. 6D, E), apex of variable length and breadth, bearing two longer apical setae and also small subapical setae of variable position and number.

Female reproductive tract ($n = 1$). Bursa copulatrix broader basally, with narrow apex, length twice breadth, compressed under microslide cover slip (Fig. 7C), surface relatively thick, translucent; spermatheca globose; spermathecal gland ovoid; spermathecal gland duct entering spermathecal duct basad spermathecal reservoir; basal gonocoxite 1 with apical fringe of two slender setae (Fig. 8C); apical gonocoxite 2 triangular, base moderately extended laterally, with two lateral ensiform setae, one dorsal ensiform seta, and two apical nematiform setae.

Holotype male, dissected (FMNH): CHILE: Malleco Prov., / Puren Nat. Mon. / Contulmo, 350 m, / 13.II.1985 // FMHD#85-1001, mixed / forest litter, S. & J. / Peck, P#85-118. / berlese / FIELD MUSEUM NAT. HIST. // dissection vial // *Tropopterus / robustus / Liebherr* ♂4 / J.K. Liebherr 2019 // HOLOTYPE / *Tropopterus / robustus / J.K. Liebherr* 2019 (black-margined red label).

Paratype: Chile: Cautín Prov., Bellavista, Lago Villarrica, N shore, Berlese wet forest litter, 39°12.55'S, 72°08.14'W, 30-i-1986, Platnick & Schuh (CAS, 1), Villarrica, upper Flor del Lago, lot CH2002/3.41, 39°10.00'S, 71°59.07'W, 700 m el., 12-i-2003, Will (EMEC etoh, 5), Villarrica, 15 km S, *Nothofagus* woods, 39°24.62'S, 72°13.69'W, 14-ii-1993, Ward (CMNH, 2). Malleco Prov., M. N. Contulmo, Sendero Lemu Mau, *Nothofagus obliqua-Eucalyptus cordifolia* ++ w/ fern & bamboo understory, lot 1059, FMHD#2002-063, Berlese leaf and log litter, 38°00.74'S, 73°11.13'W, 410 m el., 8-xii-2002, Newton & Thayer (FMNH, 13), lot 1059, FMHD#2002-061, Flight intercept trap, 38°00.74'S, 73°11.13'W, 410 m el., 8-24-xii-2002, Thayer, Newton, Solodovnikov, Chani & Clarke (FMNH, 1), M. N. Puren, Contulmo, lot FMHD#85-1001, Berlese mixed forest litter, 38°00.90'S, 73°13.76'W, 13-ii-1985, S. & J. Peck (FMNH, 1), no other data, lot CH2002/3.124, Will (EMEC etoh, 1). Valdivia Prov., Huilohuilo, Neltume, 1 km WSW, Site B, Valdivian Rain Forest, leaf litter, sifting/photoeclector, 39°51'S, 71°57'W, 390 m el., 28-xi-1987, Ashworth, Figiseth & Maliscke (NDSU, 1), 7-i-1988, Ashworth, Figiseth & Maliscke (NDSU, 1), Pte. Blanco, Choshuenco, 8 km NW, Site A, Valdivian Rain Forest, leaf litter, sifting/photoeclector, 39°48'S, 72°05'W, 180 m el., 25-xi-1987, Ashworth, Figiseth & Maliscke (NDSU, 1).

Etymology. The adjectival species epithet *robustus* is used to denote the broad body form of beetles of this species.

Distribution and habitat. This species is distributed from latitude 38°S–39°51'S (Fig. 9D), within the Northern Valdivian entomofaunal province (O'Brien 1971). It has been recovered from Berlese samples of mixed forest litter, wet forest litter, or combined leaf and log litter. One specimen was collected in a ground-level collecting pan associated with a flight intercept trap. This species has been collected contemporaneously with the leiodid beetle *Anaballatus chilensis* (Newton et al. 2017: Chile: Cautín Prov., Bellavista, N shore Lago Villarrica, FMNH; and Chile: Malleco Prov., N. M. Contulmo, Sendero Lemu Mau, FMNH).

5. *Tropopterus canaliculus* sp. nov.

<http://zoobank.org/93355D10-1B12-42EA-9907-ED6D43477E92>

Figures 1E, 4A–D, 6F, G, 7D, 8D, 9E, 10

Diagnosis ($n = 5$). Both this species and *T. duponchelii* exhibit subparallel elytra with the sutural stria represented by a series of isolated punctures on the disc, and the second stria much reduced though still visible as a series of minute punctures (Fig. 1E, F). Individuals of *T. canaliculus* with more reduced second elytral striae could be confused with those of *T. minimucro*; however, that species is characterized by the absence of a basal elytral groove, the elytral surface smoothly convex inside the humeral tooth at the anterior end of the lateral marginal depression (compare Figs 1E, 2B). Compared to *T. duponchelii*, *T. canaliculus* can be characterized by the prosternum bearing a median, canaliculate depression that extends from the ventral face of the prosternal projection 2/3 the distance toward the anterior pronotal margin, whereas the prosternum of *T. duponchelii* is medially flattened to broadly depressed, not narrowly canaliculate. The two species can also be told by individuals of *T. canaliculus* exhibiting a narrower pronotum (MPW/PL = 1.20–1.25 versus 1.25–1.32 for *T. duponchelii*) and a glossier upper body surface. *Tropopterus canaliculus* has the vertex glossy with indistinct transverse sculpticells over portions of the surface, the pronotum also glossy, and the elytral disc glossy with indistinct transverse sculpticells visible near depressed portions of the surface such as the stria punctures, and minute micropunctures regularly distributed across the glossy surface. The dorsal microsculpture of *T. duponchelii* is much more developed, with both the pronotum and elytra bearing dense transverse lines that cause iridescence of the latter. In this species the pronotum is sparsely punctate in the laterobasal depressions and lateral portions of the median base, versus smooth in *T. duponchelii*, and the anterior pronotal margin is completely beaded, versus smooth and unmarginated across the median half in *T. duponchelii*. The standardized body length = 5.8–7.5 mm; a smaller though not diagnostic range of sizes compared to *T. duponchelii* (below).

Description. Head capsule broad basally, eyes moderately convex, ocular ratio 1.40–1.50; eyes covering much of abruptly protruded ocular lobe, ocular lobe ratio 0.85–0.90; horizontal diameter of eye crossing 25 ommatidia; antennomeres moderately elongate, length of antennomere 9 2.0× maximal diameter; mandibles moderately elongate, distance from anterior condyle to apex of left mandible 1.81× distance from condyle to lateroapical margin of labrum; mentum basal breadth 2.86× length from lateral apex to base, deep paramedial pits laterad base of mentum tooth; ligular apex broad, truncate, two setae separated by four setal diameters; paraglossae extended as far beyond ligular margin as distance from their base to ligular margin. Pronotal lateral margins convex, hind angles distinctly denticulate; basal margin with complete marginal bead, median base sparsely punctate across breadth, the punctures continuing across lateroba-

sal depressions; median longitudinal impression with lenticular depression at front of median base, narrow and deep on disc; anterior transverse impression broad and shallow medially, traceable to front angles, anterior callosity broadly convex; anterior margin completely beaded, the bead continuous medially; front angle slightly protruded, right angled; lateral marginal depression very narrow in apical half, broadened from lateral seta to laterobasal depression; lateral seta separated from lateral marginal depression by the diameter of setal articulatory socket; laterobasal depression rugosely punctate, surface upraised in middle of depression; surface of proepisternum slightly irregular, as if beaten by a ball-peen hammer. Elytra broad, sides subparallel, humeri broad; basal groove deep, continuous from anterad parascutellar seta to tightly rounded humeral angle; parascutellar striole absent, sutural stria reaching basal margin mesad parascutellar seta; sutural stria a series of isolated punctures on disc, continuous and smooth apically, the striae of both elytra bordering upraised sutural callus associated with conjoined elytra; surface of elytra depressed mesad subapical and apical elytral setae; stria 8 continuous throughout length; lateral marginal depression broad, lined with transverse sculpticells; subapical sinuation broad, moderately excavated, elytral plica evident in dorsolateral view. Mesepisternum with broad vertical depression lined with ~8 punctures in 2 or 3 vertical rows; metasternal process narrowly rounded apically, apex broadly and sides more narrowly upraised; metepisternum somewhat elongate, maximal width 0.78× lateral length. Abdomen with ventrites 3–6 broadly depressed laterally, suture between ventrites 1 and 2 nearly straight, ventrite 2 depressed within slight sinuation; anterior margins of ventrites 4–6 depressed, intersegmental membranes punctate; apical female abdominal ventrite with 2 setae each side, plus a median group of two to four setae, subequal in length; if two nearly in line with lateral setae, if four aligned in an apically broader trapezoid. Coloration of dorsal body surface subtly tricolored, head and pronotum dark rufous, elytra darker, rufopiceous, elytral lateral marginal depressions translucent rufobrunneous; antennae, mouthparts, and legs rufobrunneous; ventral body surface rufopiceous, apex of elytral epipleuron slightly paler, apex of abdominal ventrite 6 narrowly paler to concolorous.

Male genitalia ($n = 8$). Aedeagal median lobe broad dorsoventrally, but with sclerotized ventral surface of shaft narrow and terminated in a narrow, smooth, spoon-like apex (Fig. 4A, C); internal sac with flagellum small, apical. Antecostal apodeme of abdominal IX broadly angulate distally, the short distal extension very broad (Fig. 4B, D). Right paramere of variable length, length not associated with length of left paramere (Fig. 6F, G), ranging from shorter and broader to more elongate with an attenuated apical extension, the ventral surface bearing from 8–20 setae, two longer setae present near or at apex; left paramere much broader basally, with apical extension ranging from an evenly narrowed projection (Fig. 6F) to a narrow, parallel digitiform extension (Fig. 6G),

two longer setae present at apex, plus a variable number of subapical and ventral setae.

Female reproductive tract ($n = 1$). Bursa copulatrix columnar, broadly rounded apically, length 1.75× breadth, compressed under microslide cover slip (Fig. 7D), bursal walls thin, nearly transparent; spermatheca globose; spermathecal gland elongate-ovoid; spermathecal gland duct entering spermathecal duct basad spermathecal reservoir; basal gonocoxite 1 with one large apical fringe seta, a second small seta also present unilaterally (Fig. 8D); apical gonocoxite 2 falciform, base extended laterally, with two lateral ensiform setae, one dorsal ensiform setae, and two apical nematiform setae.

Holotype male dissected (CAS): Crest of Sierra / Nahuelbuta / Elev. 1200 m // W. of Angol / CHILE, I-3-51 // Ross and / Michelbacher / Collectors // dissection vial // *Tropopterus* / canaliculus / Liebherr ♂4 // HOLOTYPE / *Tropopterus* / canaliculus / J.K. Liebherr 2019 (black-margined red label). The type locality is in Malleco Prov., with geographic coordinates estimated to be 37°47.76'S, 73°02.27'W.

Paratypes. Chile: Arauco Prov., San Alfonso, Carmañavida, above, 37°42.75'S, 73°09.00'W, 16–17-x-1969, Flint & Barria (NMNH, 1). Malleco Prov., P. N. Nahuelbuta, lot DRM 06.046, DRM DNA2200, 37°48.98'S, 73°05.7'W, 1312 m el., 7-i-2006, Maddison (OSAC, 1), Los Portones entrance, 4.5 km W, emergent *Nothofagus* spp., *Araucaria aurucana*, *Chusquea* understory, lot 975, pyr.-fogging old logs, 37°49.25'S, 72°59.82'W, 1300 m el., 7-ii-1997, Newton & Thayer (FMNH etoh, 1), Guarderia Pichinahuel, E of, *Araucaria-Nothofagus dombeyi* w/ *Chusquea* bamboo, lot 1054, in rotten logs, 37°48.20'S, 73°01.41'W, 1290 m el., 7-xii-2002, Clarke & Solodovnikov (FMNH, 5), lot 1054, pyr. fogging live *Araucaria*, 37°48.20'S, 73°01.41'W, 1290 m el., 24-xii-2002, Newton & Solodovnikov (FMNH, 1), lot 1054, FMHD#2002-094, Berlese debris under bark large *Araucaria* log, 37°48.20'S, 73°01.41'W, 1290 m el., 24-xii-2002, Newton & Solodovnikov (FMNH, 4), Los Portones entrance, 2.3 km W, *Nothofagus dombeyi* + ?*antarctica*, mostly open understory, lot 1057, pyr. fogging old *Nothofagus* logs, 37°49.41'S, 72°58.95'W, 1150 m el., 25-xii-2002, Newton, Thayer & Chani (FMNH, 6).

Etymology. The species epithet *canaliculus* references the narrow, deep median prosternal depression present in these beetles. The epithet is to be treated as a noun.

Distribution and habitat. This species' distribution lies near 38°S (Fig. 9E) in the Northern Valdivian entomofaunal province (O'Brien 1971). Most records are from forest-floor microhabitats, either by pyrethrin fogging of old, rotten *Nothofagus* logs, or in Berlese siftate from under bark of a large *Araucaria* log. One specimen was collected via pyrethrin spraying onto a live *Araucaria* trunk. This species was collected with *Anaballatus chilensis* at two sites (Newton et al. 2017: Chile: Malleco Prov., P. N. Nahuelbuta, 2.3 km W Los Portones entrance, FMNH, and P. N. Nahuelbuta, E of Guarderia Pichinahuel, FMNH).

6. *Tropopterus duponchelii* Solier

Figures 1F, 4E–H, 6G, I, 7E, 8E, 9F, 10

Tropopterus duponchelii Solier 1849: 213; Reed 1874: 58.

Tropidopterus duponcheli Gemminger and Harold 1868: 385 (unjustified emendations).

Tropopterus nitidus Solier 1849: 213 (synonymy Chaudoir 1876: 124).

Diagnosis ($n = 5$). To distinguish this species from *T. canaliculus* see that species' diagnosis above. From all others, this species can be recognized by the medially, broadly flattened to broadly depressed prosternum, the depression not narrow and deep. The elytra bear a well-developed, dense, transverse-line microsculpture that results in a distinctly iridescent surface, whereas the vertex is covered with a shallow isodiametric mesh transversely stretched in parts, and the pronotum is covered with shallow transverse lines that result in only subtle iridescence. The eyes are moderately convex, ocular ratio = 1.37–1.46, with 20–25 ommatidia crossed by a horizontal diameter of the eye. The pronotal hind angles are obtuse and sharp, with the lateral margins slightly sinuate before the angles, and the pronotal median base and laterobasal depressions are smooth (Fig. 1F). The elytra are broad basally, with the basal groove well developed and meeting the lateral marginal depression at a distinct, obtuse angle, with a minute tooth projected posterad from that juncture. The mesepisternum is smooth throughout the dorsoventral depression of that sclerite. Standardized body length = 6.7–8.1 mm.

Male genitalia ($n = 4$). Aedeagal median lobe broad dorsoventrally to broadly rounded apex, the apex with broad, blunt mucro on ventrobasal surface (Fig. 4E, F); aedeagal internal sac with stout, serrate ventrobasal spicular sclerite and elongate, moderately sclerotized flagellum. Antecostal apodeme of abdominal IX rounded distally, the juncture of the lateral arms only slightly broader (Fig. 4G). Right paramere of variable length, ranging from short and broadly parallel-sided, to more elongate with an apical attenuated apex (Fig. 6H, I), ventral surface with about 13 setae in apical half, apex with two longer setae, and apicodorsal surface with several very small setae of variable position; left paramere varying in length in concert with right paramere, ranging from short and stout with a very short apical extension, to longer with a narrow, digitiform extension connected to body of paramere by semiflexible membrane, two longer apical setae present plus one to several short subapical setae.

Female reproductive tract ($n = 1$). Bursa copulatrix elongate, broader distally, length nearly 4× breadth, compressed under microslide cover slip (Fig. 7E); spermatheca an ovoid heart-shape; spermathecal gland elongate, fusiform; spermathecal gland duct entering spermathecal duct basad spermathecal reservoir; basal gonocoxite 1 with single apical fringe seta (Fig. 8E); apical gonocoxite 2 falciform, base extended laterally, with two lateral ensiform setae, one dorsal ensiform seta, and two apical nematiform setae.

Type information. *Tropopterus duponchelii* lectotype female (MNHN) hereby designated: S. Iago (handwritten on blue label) // MUSEUM PARIS / CHILI / Cl. Gay 1845 (grey label) // 9 45 (round blue label) // TYPE (red label) // *Tropopterus / Duponchelii / Sol.* Sn. Iago (handwritten white label) // LECTOTYPE / *Tropopterus / duponchelii / Solier / des.* Liebherr 2019 (black-margined red label). *Tropopterus nitidus* lectotype female (MNHN) hereby designated (pinned specimen with mouthparts mounted beneath on point): S. Iago (handwritten on blue label) // MUSEUM PARIS / CHILI / Cl. Gay 1845 (grey label) // 9 45 (round blue label) // TYPE (red label) // *Tropopterus / nitidus Sol. / Sn.* Iago (handwritten white label) // LECTOTYPE / *Tropopterus / nitidus / Solier / des.* Liebherr 2019 (black-margined red label). The types would have come into the Chaudoir Collection in 1876 directly from Philibert Germain (Ball and Erwin 1982). Given Chaudoir's interest in mouthpart characters (Basilewsky 1982), and his synonymization of *T. nitidus* under *T. duponchelii* in that year, it seems likely that the mouthpart dissection of the *T. nitidus* lectotype was made by Chaudoir himself.

Date/locality information, all specimens: Chile: Arauco Prov., Caramavida, Nahuelbuta (W), 37°40.99'S, 73°21.00'W, 750 m el., 25–31-xii-1953, Peña (MCZ, 2; MNHN, 1); Curanilahue, 37°28.58'S, 73°20.58'W, 10-xii-1967, Cekalov[ic] (MNHN, 1); San Alfonso, above Caramavida, 37°42.75'S, 73°09.00'W, 16–17-x-1969, Flint & Barria (NMNH, 1). Santiago Prov., Santiago, 33°26.75'S, 70°40.12'W, Solier (lectotypes *T. duponchelii* plus *T. nitidus*), 33°26.75'S, 70°40.12'W, Solier (MNHN, 1). Talca Prov., Altos de Vilches, 35°36.25'S, 71°04.30'W, 19-ix-1968, Ramirez (MNHN, 1), 26-i-1969, Valencia (MNHN, 1), 11-x-1971, Valencia (MNHN, 1). No data except “81”, Chaudoir Colln. (MNHN, 1).

Distribution and habitat. This species is distributed from 33°27'S–37°41'S (Fig. 9F), spanning the Santiagan and Northern Valdivian entomofaunal provinces (O'Brien 1971). Specimens have been found by sifting litter in Valdivian rainforest with *Nothofagus*, via pyrethrin fogging of old *Nothofagus* logs, under logs and rocks, and by beating vegetation. Thus this species is most often encountered in ground-level microhabitats; however, there is evidence that the beetles can climb onto vegetation. *Tropopterus duponchelii* and the leiodid beetle *Anaballatus chilensis* are both known from Alto de Vilches, Talca Prov., Chile (Newton et al. 2017).

7. *Tropopterus trisinuatus* sp. nov.

<http://zoobank.org/CF674F9C-289B-49FE-A307-0B0478E28DCE>

Figures 2A, 9G, 10

Diagnosis ($n = 2$). Although the pronota of all *Tropopterus* have the basal margin slightly undulated and medially convex, beetles of this species exhibit an exaggeration of this situation, with the base profoundly concave just mesad the acute hind angles in association with the deep

laterobasal depressions (Fig. 2A). This *Tropopterus* also exhibits the largest body size; standardized body length of 8.2–8.4 mm larger than all but the largest individuals of *T. giraudyi*. The eyes are large in diameter though little convex, with an ocular ratio = 1.36 and a horizontal diameter crossing the eye intersecting 25–26 ommatidia. The sutural stria is punctate, the isolated punctures joined in part by indistinctly depressed strial connections, and the parascutellar striole is absent, the sutural stria vaguely continued to the elytral base as a broad depression. The outer elytral striae are progressively reduced, with striae 2 and 3 traceable as a series of minute, isolated punctures, and a very few minute punctures visible in the position of stria 4. Stria 8 just dorsad the lateral elytral setae is continuous throughout its length. As in *T. minimucro* and *T. fieldianus*, the elytral basal groove is absent; the elytral surface evenly and smoothly convex inside the anterior termination of the lateral marginal depression at the toothed humerus. Ventrally, the prosternum is broadly and deeply depressed from the prosternal process anterad 2/3 the distance to the pronotal anterior margin, and the mesepisternum is punctate, with ~18 punctures arranged in 2 or 3 vertical rows broadly distributed across its surface. Microsculpture of the vertex is an evident isodiametric mesh with sculpticells arranged in transverse rows in part. The pronotum is covered with a dense transverse mesh with sculpticells of breadth 3–4× length, complemented by transverse lines, and the elytra are covered with dense transverse lines producing iridescence.

Description. Head capsule broad, ocular lobe little protruded; antennae moderately robust, length of antennomere 9 2.0× maximal diameter; mandibles elongate, but given large head, distance from anterior condyle to apex of left mandible only 1.80× distance from that condyle to lateroapical margin of labrum; mentum basal breadth 3.05× length from lateral apex to base, very deep paramedial pits laterad base of mentum tooth; ligular apex broad, truncate, two setae separated by four setal diameters; paraglossae extended beyond ligular margin slightly more than distance from their base to ligular margin. Pronotum moderately transverse, lateral margins distinctly sinuate anterad right to slightly acute hind angles; base with complete marginal bead, median base smooth medially, with approximately eight small punctures each side mesad laterobasal depression; median longitudinal impression with lenticular depression on median base, finely etched on disc; anterior transverse impression traceable medially, broad and shallow laterally; anterior margin smooth in medial 1/3, margined in lateral 1/3 each side; front angle protruded, subangulate; lateral marginal depression narrow from apex to lateral seta, widened in basal 1/3 of length; lateral seta separated from lateral marginal depression by diameter of setal articulatory socket; laterobasal depression margined medially by deep, sinuous impression, an upraised tubercle in middle of depression; proepisternum smooth dorsally, with broad irregular punctures near prosternal suture. Elytra broad basally, sides sub-

parallel; humerus angulate with short extension of basal groove mesad angle; sutural stria with closely set yet isolated punctures on disc, punctures larger toward apex, but stria deep, narrow and smooth distad subapical situation; stria 8 deep and continuous throughout length; seven or eight anterior lateral elytral setae, six posterior setae; lateral marginal depression very narrow anteriorly, broader in apical half, lined there with transverse sculpticells; subapical situation broad and shallow, elytral plica visible in lateral view. Metepisternum equitrapezoidal, maximal width subequal to lateral length; metasternal process with a rounded apical knob, the lateral margins narrowly upraised. Abdomen with ventrites 3–5 longitudinally depressed laterally; suture between ventrites 1 and 2 sinuate, ventrite 2 depressed posterad situation; ventrites 4–6 depressed basally, the intersegmental membranes minutely punctate; female apical ventrite with two setae laterally each side and an elongate quadrangle of subequally-lengthed setae medially. Coloration of body dark, head, pronotal disc and elytra piceous, the latter with iridescent surface; antennae, mouthparts and legs brunneous; ventral surface piceous, pterothoracic and abdominal ventrites, and elytral epipleura iridescent, only apical 1/6 of apical abdominal ventrite paler, rufobrunneous.

Female reproductive tract ($n = 2$; females not dissected, only accessible gonocoxal characters described). Basal gonocoxite 1 with one apical fringe seta; apical gonocoxite 2 narrowly triangular, base not extended laterally, with two lateral ensiform setae, one dorsal ensiform seta, and two apical nematiform setae.

Holotype female (CAS): CHILE: Cautin Province, / Villarrica, 1250 m, trap / site 653, 15 – 29 Jan 1982 / *Nothofagus domb.-pumilio* / forest w/ *Chusquea* / A.F. Newton & M.K. Thayer // *Tropopterus* / *trisinuatus* / sp. nov. ♀ 1 photo / det. J.K. Liebherr 2019 // *Tropopterus* / Measured / Specimen #1 / det. J.K. Liebherr // HOLOTYPE *Tropopterus* / *trisinuatus* / J.K. Liebherr 2019 (black-margined red label). The type locality is Volcán Villarrica, 1250 m el.; geographic coordinates 39° 22.8'S, 71° 56.4'W (A.F. Newton, pers. comm.).

Paratype with identical data (CAS, 1).

Etymology. The adjectival species epithet *trisinuatus* signifies the trisinate basal pronotal margin that unique characterizes this species among those known.

Distribution and habitat. This species is known only from the type locality in the Northern Valdivian entomofaunal province (O'Brien 1971). The two specimens were collected in a mixed forest of large *Nothofagus dombeyi* (Brisseau de Mirbel), *N. pumilio* (Poepig and Endlicher), and *Chusquea* bamboo. The forest was near a recent lava flow, and the soil was thin. The specimens were collected from the ground-level microhabitat, either in a flight intercept trap catch pan, or in a leaf litter sift sample. The two types were collected at the same place and time as part of the type series of the oribatid mite *Novonothrus puyehue* Casanueva and Norton (1997).

8. *Tropopterus minimicro* sp. nov.

<http://zoobank.org/115C452A-2872-4623-A3C6-67178AB5F548>

Figures 2B, 5A–D, 6J–K, 7F, 8F, 9H, 10

Diagnosis ($n = 5$). These larger sized beetles – standardized body length = 7.2–7.9 mm – can be distinguished by the closely punctate sutural stria which becomes a fine, narrow impression on the elytral apex, and the broadly impressed and smooth stria 2 which is obsolete apically (Fig. 2B). The basal elytral groove is absent across most of the elytral base, though it extends for a short distance medially from the elevated humeral tooth at the base of the elytral lateral marginal depression. The pronotum is moderately transverse (MPW/PL = 1.27–1.37) and the pronotal base is smooth except for 5–8 shallow punctures mesad the laterobasal depression. The parascutellar striole is present as a broad smooth groove mesad the parascutellar seta, the groove not continuous with the base of the sutural stria. Ventrally the prosternum is broadly and deeply depressed medially from the prosternal process ventral face anterad 2/3 toward the prothoracic anterior margin, and the mesepisternum is irregularly punctate with 8–9 punctures in 2 or 3 vertical rows. The dorsal body surface bears well-developed microsculpture: 1, the vertex with an evident isodiametric mesh in transverse rows; 2, the pronotum with a dense transverse mesh, sculpticell breadth 2–3× length, accompanied by transverse lines over portions of the surface; and 3, the elytra with dense transverse lines resulting in iridescence.

Description. Head capsule broad with moderately convex eyes, ocular ratio = 1.41–1.45, 25 ommatidia crossed by a horizontal diameter of eye; ocular lobes slightly protruded, their posterior margin obtusely meeting gena, ocular lobe ratio 0.85–0.89; antennae elongate, antennomere 9 length 2.30× maximal diameter; mandibles moderately elongate, distance from anterior condyle to apex of left mandible 1.76× distance from condyle to lateroapical margin of labrum; mentum basal breadth 2.8× length from lateral apex to base, very deep paramedial pits laterad base of mentum tooth; ligular apex broad, truncate, two setae separated by 4 setal diameters; paraglossae extended beyond ligular margin slightly more than distance from their base to ligular margin. Transverse pronotum with sides sinuate before acute, projected and denticulate hind angles; median base completely margined, base smooth medially anterad marginal bead, with ~8 minute punctures each side mesad laterobasal depressions; median longitudinal impression with deep, lenticular depression on median base, finely engraved on disc; anterior transverse impression broad and shallow medially, deeper laterally toward front angles; anterior margin smooth medially, margined in outer half of breadth each side; front angles only slightly protruded, rounded; lateral marginal depression very narrow in anterior 2/3 of length, gradually widened to hind angle; lateral setae separated from lateral marginal depression by diameter of articulatory socket; laterobasal depression subquadrate, a smooth tubercle upraised in middle of depression. Elytra broader

in apical half, humeri narrowly rounded; lateral marginal depression ended blindly at humerus; parascutellar striole absent, sutural stria indicated by series of isolated punctures, those punctures more closely spaced in apical half, the stria smooth, narrow and deep on apex; subapical and apical setae together in depressed remnant of stria 7; stria 8 greatly reduced, broad and shallow among anterior lateral elytral setae, absent to shallow medially, and shallow, interrupted to deeper and continuous between setae of posterior series; lateral marginal depression moderately broad, lined with transverse sculpticells; subapical sinuation broad and shallow, elytral plica evident in lateral view. Metepisternum slightly elongate, maximal width 0.83× lateral length. Abdomen with ventrites 3–6 broadly depressed laterally; suture between ventrites 1 and 2 slightly sinuate, ventrite 2 depressed within sinuation; base of ventrites 4–6 depressed, no evidence of punctures associated with the intersegmental membranes; female apical ventrite with two long setae each side and four shorter setae in a more basally situated transverse row medially. Coloration of dorsal body dark rufous, antennae, mouthparts and legs rufobrunneous; ventral body surface also dark rufous, proepipleuron and elytral epipleuron concolorous to paler, rufobrunneous, apex of abdomen not paler.

Male genitalia ($n = 10$). Aedeagal median lobe broad dorsoventrally, the ostial opening narrowed to a rounded apex that bears a very small mucro on the ventrobasal surface (Fig. 5A, C); a large, distally serrate ventrobasal spicular sclerite present (Fig. 5C); flagellum elongate, associated with membranous flagellar sheath. Antecostal apodeme of abdominal IX broadly rounded distally, juncture of two lateral arms asymmetrically offset toward left side, the distal extension short. Right paramere elongate with narrow apical extension (Fig. 6J, K), ventral surface lined with 10–14 small setae, one or two larger setae at apex, and from one to several small setae on dorsoapical surface; left paramere broad basally, the apex ranging from a gradually narrow apex (Fig. 6J) to a very narrow, digitiform extension (Fig. 6K), two longer apical setae accompanied by several short setae.

Female reproductive tract ($n = 1$). Bursa copulatrix ovoid, expanded apically, length about 1.6× greatest breadth, compressed under microslide cover slip (Fig. 7F); spermatheca globose; spermathecal gland large, ovoid; spermathecal gland duct entering spermathecal duct basad spermathecal reservoir; basal gonocoxite 1 with apical fringe of one larger seta and one smaller seta (Fig. 8F); apical gonocoxite 2 broadly triangular, base moderately extended laterally, with two lateral ensiform setae, one dorsal ensiform seta, and two apical nematiform setae.

Holotype male, dissected (MCZ): PucaTrihue / Orsono Prov. / III-23-62 / CHILE Pena // dissection vial // *Tropopterus* / *minimicro* / Liebherr ♂2 / det. J.K. Liebherr 2019 // HOLOTYPE / *Tropopterus* / *minimicro* / J.K. Liebherr 2019 (black-margined red label). The geo-

graphic coordinates for the type locality are 40°32.10'S, 73°41.53'W.

Paratypes: Chile: Cautín Prov., Bellavista, Lago Villarrica, 39 12.55'S, 72 08.14'W, 250 m el., 8-i-2006, Will (EMEC, 4). Chiloé Prov., Degán, 10.3 km E, rte. W33, lot CH2006.18.1.1, 42°10.37'S, 73°36.72'W, 166 m el., 18-i-2006, Will (EMEC etoh, 1), Huillinco, 5.4 km S, Rio Terahuin, 42°43.12'S, 73°53.87'W, 36 m el., 22-i-2006, Will (EMEC, 2), P. N. Chiloé, Cucao, lot CH2002/3.53, 42°38.47'S, 74°07.00'W, 23 m el., 20-i-2003, Will (EMEC etoh, 3). Llanquihue Prov., Lago Chapo, near SE end, km 9.9 on road to Rollizo, Valdivian rainforest on steep slope, lot 989; pyr.-fogging old logs, 41°30.63'S, 72°23.98'W, 385 m el., 26-i-1997, Newton & Thayer (FMNH etoh, 1), P. N. Vicente Pérez Rosales, Volcán Osorno, SW slope ca. km 11 to La Burbuja, low *Nothofagus dombeyi* w/ mixed understory, lot 1005, FMHD #97-35, Berlese leaf and log litter, 41°07.91'S, 72°32.16'W, 1065 m el., 27-i-1997, Newton & Thayer (FMNH, 1), Ensenada, 9.2 km NE, on road to Petrohué, Valdivian rainforest with *Nothofagus* spp., lot 987, pyr.-fogging old logs, 41°10.20'S, 72°27.10'W, 125 m el., 28-i-1997, Newton & Thayer (FMNH etoh, 1), Volcán Osorno, SW slope c. km 11 to La Burbuja, low *Nothofagus dombeyi* w/bamboo & shrub understory, lot 1065, pyr.-fogging old mossy logs, 41°07.9'S, 72°32'W, 1090 m el., 15-xii-2002, Newton & Thayer (FMNH, 1). Osorno Prov., P. N. Puyehue, lot CH2002/3.192, 40°40.22'S, 72°10.07'W, 300 m el., 23-i-2003, Will (EMEC etoh, 1), lot CH2002/3.187, 40°40.22'S, 72°10.07'W, 300 m el. 23-i-2003, Will (EMEC etoh, 2), P. N. Puyehue, Anticura, Repucura Tr., lot P#85-113, FMHD #85-996, Berlese forest litter, 40°39.97'S, 72°10.47'W, 500 m el., 6-ii-1985, S. & J. Peck (FMNH, 2), Volcán Casablanca, E shore Lago Puyehue, Site 36, tundra-forest transition, 40°44'S, 72°10'W, 1270 m el., 18-xii-1977, Ashworth, Hoganson & Mooers (NDSU, 1), Osorno, 40°34.50'S, 73°07.00'W, xii-1977 (NMNH, 2). Valdivia Prov., Curiñanco, road to, 39°42.90'S, 73°23.77'W, 112 m el., 9-xi-2008, Will (EMEC, 1), La Union, 34 km WNW, lot P#85-36, FMHD #85-921, Berlese mixed forest litter, 40°15.00'S, 73°23.75'W, 700 m el., 17-xii-1984, S. & J. Peck (FMNH, 1), P. N. Oncol, Cerro Oncol trail, lot DRM 06-044, 39°41.89'S, 73°18.07'W, 525 m el., 10-i-2006, Maddison & Will (OSAC, 1; OSAC etoh, 1), lot DRM 06.045, 39°41.89'S, 73°18.07'W, 500 m, 11-i-2006, Maddison & Seago (OSAC etoh, 1), Sendero Oncol, 39°41.50'S, 73°18.25'W, 600 m el., 10-i-2006, Will (EMEC, 1), lot CH2006.10.i.2, 39°41.50'S, 73°18.25'W, 600 m el., 10-i-2006 (EMEC etoh, 2), 39°41.65'S, 73°18.86'W, 715 m el., 12-i-2006, Will (EMEC, 8), pitfall trap, 39°41.55'S, 73°18.86'W, 690 m el., 10-23-i-2006, Will et al. (EMEC, 2), 39°41.67'S, 73°18.25'W, 513 m el., 9-xi-2008, Will (EMEC, 2), 600 m el., 8-xi-2008, Will (EMEC, 1), Puerto Fui [sic Fuy], 14 km SE, Lago Pirehueico, Site G, Lenga Forest, *Nothofagus pumilio*, standard pitfall trap, 39 58'S, 71 48'W, 1230 m el., 5-xii-1987, Ashworth, Fugiseth & Maliscke (NDSU, 1), leaf litter, photoelector, 39°58'S,

71°48'W, 1230 m el., 11-i-1988, Ashworth, Fugiseth & Maliscke (NDSU, 1), window/pitfall trap, 39°58'S, 71°48'W, 1230 m el., 11-i-1988, Ashworth, Fugiseth & Maliscke (NDSU, 1), standard pitfall trap, 39°58'S, 71°48'W, 1230 m el., 15-i-1988, Ashworth, Fugiseth & Maliscke (NDSU, 1).

Etymology. The species epithet *minimucro* describes the very small mucro on the apex of the male aedeagal median lobe, that character amply diagnosing this species. The name is to be treated as a noun.

Distribution and habitat. All records for this species are clustered from 39°13'S–42°39'S (Fig. 9H), straddling the transition between the Northern and Southern Valdivian entomofaunal provinces (O'Brien 1971). Collecting sites range from 23 m elevation on Isla Chiloé to 1270 m elevation in the forest-tundra transition zone on Volcán Casablanca (Ashworth and Hoganson 1987). Beetles have been found in Berlese siftate of mixed forest litter, leaf and log litter, and via pyrethrin fogging of old logs with or without moss. The species is broadly sympatric with the southern portion of the range of *T. giraudyi*. Moreover, both *T. minimucro* and *T. giraudyi* have been collected during the same collecting events four different times, suggesting intense sympatry at both macro- and microsympatric scales. The four identical collecting series include: Cautín Prov., Bellavista, Lago Villarrica, 39°12.55'S, 72°08.14'W, 250 m el., 8-i-2006, Will (EMEC); Valdivia Prov., P. N. Oncol, Mirador Pilocura, Sendero, 39°41.65'S, 73°18.86'W, 715 m el., 12-i-2006, Will (EMEC); Llanquihue Prov., P. N. Vicente Pérez Rosales, Volcán Osorno, SW slope c. km 11 to La Burbuja, low *Nothofagus dombeyi* w/bamboo & shrub understory, lot 1065, pyr.-fogging old mossy logs, 41°07.9'S, 72°32'W, 1090 m el., 15-xii-2002, Newton and Thayer (FMNH); and Llanquihue Prov., P. N. Vicente Pérez Rosales, Ensenada, 9.2 km NE on road to Petrohué, Valdivian rainforest with *Nothofagus* spp., lot 987, pyr.-fogging old logs, 41°10.20'S, 72°27.10'W, 125 m el., 28-i-1997, Newton and Thayer (FMNH). *Tropopterus minimucro* has been collected alongside the leiodid *Anaballetus chilensis* two times (Newton et al. 2017; Chile: Cautín Prov., Bellavista, N shore Lago Villarrica, FMNH; and Chile: Valdivia Prov., La Union, 34 km WNW, FMNH).

9. *Tropopterus fieldianus* sp. nov.

<http://zoobank.org/2358ECB7-472F-4371-9FF2-26D51633AFF4>

Figures 2C, 5E–F, 6L, 9I, 10

Diagnosis ($n = 2$). Like *T. minimucro* this species lacks the basal elytral groove and has the sutural stria punctate on the elytral disc. But unlike that species, *T. fieldianus* has both elytral stria 1 and 2 punctate subapically: stria 1 is deeply and narrowly impressed at the apex, whereas stria 2 is broadly, shallowly continuous there. The pronotum of this species is broad (MPW/PL = 1.37–1.39) and rather quadrate, broad basally with MPW/BPW = 1.18–1.25 (compared to the basally narrowed, more cordate prono-

tum of *T. minimucro*; MPW/BPW = 1.24–1.33). The eyes are very convex with 26 ommatidia intersected by a horizontal diameter, and an eye convexity ratio, $EyL/EyD = 2.4$. The pronotal median base is rugosely punctate mesad the laterobasal depressions, and the anterior pronotal margin is smooth medially and margined along the outer 1/3 of each side. Ventrally the prosternum is broadly, moderately depressed medially, the depression extended 2/3 the distance from prosternal process to anterior margin, with the depression shallow and broad between the coxae. The mesepisternum bears a single dorsoventral row of 4–6 punctures, and the metepisternum and metepimeron are fused laterally, the suture difficult to trace except mesally near the metacoxa. Dorsally the head is glossy with very shallow isodiametric sculpticells visible across the surface, and the pronotum and elytra bear dense elongate transverse sculpticells and transverse lines resulting in iridescence. Standardized body length = 6.7–7.8 mm.

Description. Head capsule broad, eyes convex, ocular ratio = 1.42–1.44; antennae moderately elongate, antennomere 9 length $1.96\times$ maximal diameter; mandibles elongate, distance from anterior condyle to apex of left mandible $1.96\times$ distance from condyle to lateroapical margin of labrum; mentum basal breadth $3.0\times$ length from lateral apex to base, very deep paramedial pits laterad base of mentum tooth; ligular apex broad, truncate, two setae separated by 4 setal diameters; paraglossae extended beyond ligular margin as far as distance from their base to ligular margin. Pronotum transverse, lateral margins nearly straight basally, briefly concave anterad right to slightly obtuse, denticulate hind angles; basal marginal bead complete, well developed medially; median base smooth; median longitudinal impression continued to basal marginal bead, lenticularly depressed near front of median base, finely inscribed on disc; anterior transverse impression obsolete medially, broad and shallow approaching front angle; front angles slightly protruded, obtuse-rounded; lateral marginal depression narrow in anterior half of length, evenly broadened from lateral seta to base; lateral seta separated from lateral marginal depression by diameter of setal articulatory socket. Elytra broad, lateral margins subparallel; parascutellar striole absent, sutural stria interrupted basally, terminated in broad, irregular depression surrounding parascutellar seta; stria 8 present near posterior setae of anterior lateral elytral setal series, shallow and interrupted near midlength, deep and continuous mesad posterior setal series; lateral marginal depression moderately broad from humerus to midlength, gradually narrowed to subapical situation; subapical situation broadly concave, moderately deep, plica well evident in dorsolateral view. Metepisternum slightly elongate, maximal width $0.83\times$ lateral length. Abdomen with ventrites 3–6 longitudinally depressed laterally; suture between ventrites 1 and 2 slightly sinuate laterally, ventrite 2 depressed within slight situation; abdominal ventrites 4–6 depressed basally, minutely strigose along intersegmental membranes; male apical abdominal ventrite with two setae each side, in one specimen median two setae more basally positioned, in

the other two bilateral pairs of apical setae complemented by three shorter medial setae in the position usually observed in female specimens. Coloration (based on apparently, slightly teneral individuals) paler, head capsule rufopiceous, pronotum and elytra rufobrunneous; legs paler, rufoflavous; thoracic and abdominal ventrites brunneous, proepipleuron and elytral epipleuron paler, rufoflavous.

Male genitalia ($n = 2$). Aedeagal median lobe broad dorsoventrally with broadly rounded apex, a minute mucro on the ventrobasal margin of the apex (Fig. 5E); internal sac armature including flagellum and flagellar sheath. Antecostal apodeme of abdominal IX broadly rounded distally, with juncture of two lateral arms asymmetrically offset toward left side, distal extension broadly rounded (teneral specimen). Right paramere elongate, broader near midlength, narrowed evenly to apex, ventral surface lined with 16 small setae, two larger setae at apex, three subapical setae, and two very small setae on dorsal surface; left paramere very broad for much of length, terminated apically by a evenly narrowed projection with two larger apical setae, a third smaller subapical seta, plus several very small setae on apical process or ventral margin.

Holotype male (FMNH), point mounted with left mesotarsomeres glued to point: CHILE: Osorno Prov., 3 / km S Maicolpue, Bahia / Mensa, 200 m, / 21.XII.1984 // FMHD#85-933, mixed forest litter, S. & J. / Peck, P85-48 / berlese / FIELD MUSEUM NAT. HIST. // *Tropopterus* / Measured / Specimen #1 / det. J.K. Liebherr 2019 // dissection vial // *Tropopterus* / fieldianus / Liebherr ♂1 / det. J.K. Liebherr 2019 // HOLOTYPE / *Tropopterus* / fieldianus / J.K. Liebherr 2019 (black-margined red label).

Paratype: CHILE: Valdivia, 35 km WNW La Union, 7.xi.1985, 700m el., Mixed forest, S. Peck, P#85-114, FIELD MUSEUM (FSCA, 1)

Etymology. The species epithet *fieldianus* combines the noun *field* with the adjectival ending *-anus*, thereby signifying that this species belongs to the Field Museum. This “belonging” is based on the Field Museum’s institutional dedication to Coleoptera systematics signified by a long succession of beetle curators: John E. Liljeblad, Rupert L. Wenzel, Henry S. Dybas, Harry G. Nelson, Larry E. Watrous, Steve Ashe, Alfred F. Newton, and Margaret K. Thayer.

Distribution and habitat. This species is known only from two localities (Fig. 9I) distributed near latitude 40°S in the northern portion of the Southern Valdivian entomofaunal province (O’Brien 1971). It has been recovered from Berlese siftate of mixed forest litter. At the La Union site in Valdivia Prov., it was collected alongside the leiodid species *Anaballetus chilensis* (Newton et al. 2017).

Cladistic analysis

Submitting the 10 taxon by 37 ordered-character data matrix to Winclada running NONA for 200 ratchet runs results in one tree of step-length = 97; CI = 57, RI = 47 (Fig. 10). This identical tree is returned when 1000 ratch-

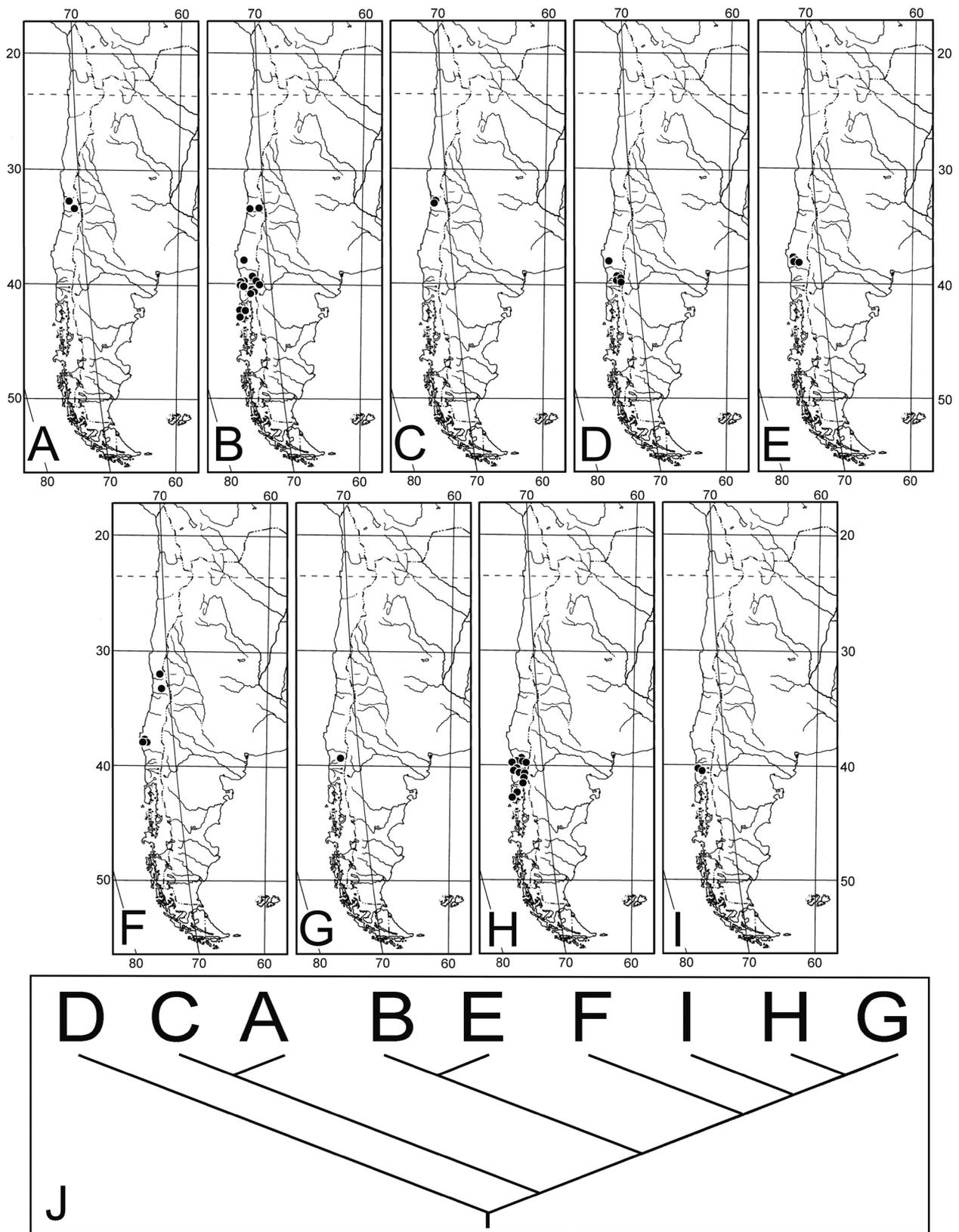


Figure 9. A–I. Geographic distributions of *Tropopterus* spp. A. *T. montagnei*. B. *T. giraudyi*. C. *T. peckorum*. D. *T. robustus*. E. *T. canaliculus*. F. *T. duponchelii*. G. *T. trisinuatus*. H. *T. minimicro*. I. *T. fieldianus*. J. Geographical distributions of *Tropopterus* spp., labeled as per figures above, hierarchically arranged by phylogenetic relationships of the taxon cladogram, Fig. 10.

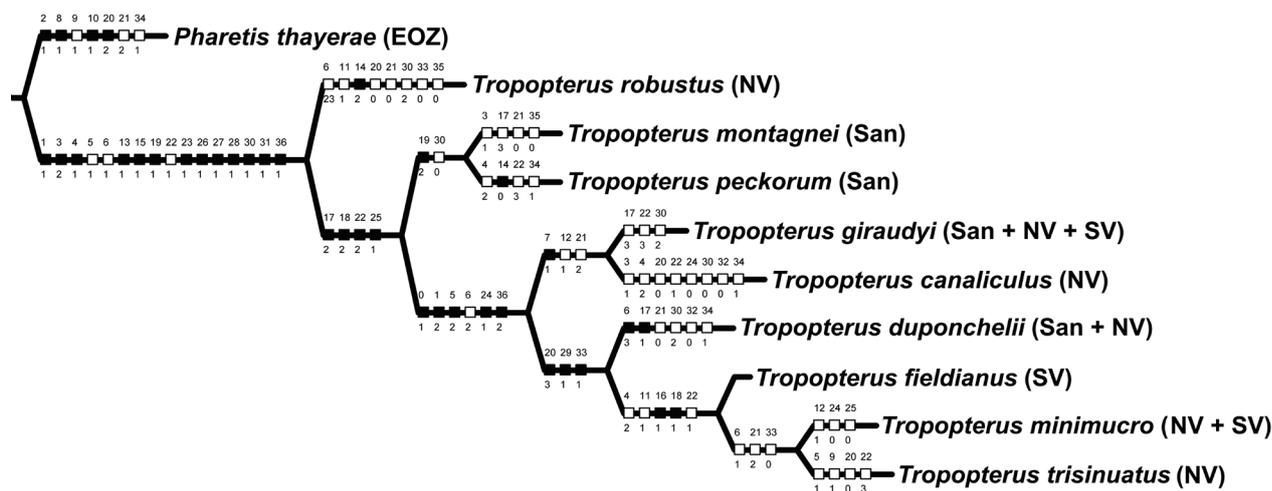


Figure 10. Cladogram returned under all cladistic protocols described in text; tree length = 97, CI = 57, RI = 47, fast character optimization shown. Outgroup choice of *Pharetis thayerae* based on results in Liebherr (2020). Geographic region abbreviations after taxon name include: eastern Australia (EOZ); Santiagan entomofaunal province (San); Northern Valdivian entomofaunal province (NV); Southern Valdivian Entomofaunal province (SV).

et replicates are run using NONA within Winclada. The outgroup *Pharetis thayerae* establishes the root of the *Tropopterus* phylogeny between *T. robustus* and the remaining eight species. Monophyly of *Tropopterus* relative to *Pharetis* is supported by 15 unambiguously optimized synapomorphies, most of which are presented in the generic diagnosis: **1**, mentum paramedial depressions deep (character 3, state 2); **2**, scutellum little projected onto elytral disc (13, 1); **3**, elytral humerus tightly rounded to angulate (15, 1); **4**, sutural stria modified apically (19, 1); **5**, metepisternum foreshortened (22, 1); **6**, male apical ventrite bisetose each side (26, 1); **7**, metatarsomere 4 emarginate apically (27, 1); **8**, male aedeagus inverted (28, 1); and **9**, male aedeagal median lobe with pleated ostial border (31, 1). Five other synapomorphies relative to the *Pharetis* outgroup include three associated with larger eyes; **1**, 18 or more ommatidia (character 1, state 1); **2**, ocular ratio > 1.30 (5, 1), and **3**, ocular lobe ratio > 0.76 (6, 1). The two additional synapomorphies include: **4**, labrum apical margin moderately concave (4, 1); and **5**, body size larger than 5.0 mm (36, 1). A final character listed on the cladogram edge leading to *Tropopterus* (aedeagal median lobe with mucro; character 30, state 1)—is reversed in *T. peckorum* and *T. canaliculus*, or not known in *T. montagnei* or *T. trisinuatus* for which we lack male specimens. In addition, all *Tropopterus* beetles are vestigially winged; a condition more derived than the stenopterous flight wing condition of *Pharetis thayerae* (character 23). However, given *P. thayerae* as the lone outgroup, that character cannot be unambiguously polarized on this cladogram except under fast optimization.

Several character transformation series support the present phylogenetic hypothesis of *Tropopterus* spp. (Fig. 10). Elytral striation is least reduced in *T. robustus* (characters 17, 18, states 0; Fig. 1D), supporting its placement

as adelphotaxon to the other seven *Tropopterus* (Figs 1A–C, E, F, 2). Eye size (character 1) increases during *Tropopterus* phylogeny, with all *Tropopterus* exhibiting larger eyes than the outgroup *Pharetis*, and species of the clade bracketed by *T. giraudyi* and *T. trisinuatus* exhibiting the largest number of ommatidia; 23–26 ommatidia (character 1, state 2). Within this crown clade of six species, the sister species status of *T. giraudyi* and *T. canaliculus* is supported by a pronotal anterior margin that is completely beaded side to side (character 7, state 1). Monophyly of their respective sister group of four species is supported by the synapomorphic, distally rounded antecostal apodeme of the male abdominal ventrite IX (character 29, state 1), though our lack of knowledge regarding males of *T. trisinuatus* must invoke the prediction that those males, when examined, will also exhibit the distally rounded antecostal apodeme. Monophyly of the three-species clade of *T. fieldianus* + (*T. minimucro* + *T. trisinuatus*) is supported by shared loss of the elytral basal groove (character 16, state 1; Fig. 2). Several other characters may represent attributes phylogenetically associated with the reduction of metathoracic flight wings. Body size (character 36, states 1, 2) increases throughout *Tropopterus* phylogeny, consistent with the evolutionary trend observed across brachypterous carabid beetle taxa (Liebherr 1988). The six-taxon *T. giraudyi*–*T. trisinuatus* clade is characterized by the largest body sizes, with the single exception being broad body size variation within *T. canaliculus*, where the smallest males of that species fall near the top of the body-size range for *T. robustus*, *T. montagnei*, and *T. peckorum*. Associated with this phyletic increase in body size is the reduction of the metepisternum (character 22, states 1, 2), though that character is highly homoplasious, changing states six times within *Tropopterus*. Also, the antennae are more elongate (char-

acter 0, state 1) within the larger-bodied *T. giraudyi*–*T. trisinuatus* clade, a finding in keeping with allometric increase in antennal length as body size increases.

Discussion

Tropopterus diversity (Fig. 9A–I) is centered in the Northern Valdivian and the northern portion of the Southern Valdivian entomofaunal regions (O’Brien 1971). The ranges of two of the geographically more widespread species, *T. giraudyi* (Fig. 9B) and *T. minimucro* (Fig. 9H), extend the furthest south, into the North Patagonian Rain Forest (Clarke 1964) and onto Isla Chiloé. Where recorded, the ecological associates of these species include *Nothofagus dombeyi*, *Chusquea* bamboo, and the podocarp *Saxegothaea conspicua* Lindley. To the north, four species have been recorded from the more mesic Santiagan entomofaunal province, though the Solier type localities “near Santiago” for *T. montagnei*, *T. giraudyi*, and *T. duponchellii* (Fig. 9A, B, F) have not been recently corroborated. Northern localities within N. P. La Campana have recently produced *T. peckorum*, with this species found in *Nothofagus obliqua* forest.

That our knowledge of the generic distributional range of *Tropopterus* is more or less accurate can be ascertained by the combination of: syntopic collections of *Tropopterus* beetles and other Coleoptera within the known *Tropopterus* range; and absence of *Tropopterus* beetles from samples outside the known range that comprise beetle species found in sympatry with *Tropopterus*. For example, *T. giraudyi* was collected at Chepu, Chiloé by W. Kuschel, 9-x-1958, and he collected *Glypholoma pustuliferum* Jeannel the day before at the same locality (Thayer 1997). *Tropopterus* is not found further south than Chiloé, though *G. pustuliferum* has been collected, using similar methodology, at numerous localities further south in Magallanes and Tierra del Fuego Provinces. Other entomological survey programs in southern Chile have also not recovered any *Tropopterus* species south of localities presented here (Fig. 9A–I) (Domínguez et al. 2006; Niemalä 1990).

Tropopterus sympatry is greatest near 40°S, with seven of the nine species distributed near this latitude (Fig. 9). Thus any attempt to hypothesize past episodes of allopatric speciation are complicated by secondary sympatry. A limited amount of information suggests that speciation has occurred across relatively limited geographic distances in this group. The three sister-species pairs (Fig. 9J), one in the northern sclerophyllous forest (Fig. 9A, C) and the two in the Valdivian forest (Fig. 9B, E, and 9G, H, respectively), all exhibit little geographic isolation between the paired species. In the two southern examples, both sister-species pairs consist of a more widespread species (Fig. 9B, H) plus a geographically restricted sister (Fig. 9E, G). In the northern sister-species pair, both species are known from a limited range, although agricultural land conversion in this region (O’Brien 1971) may have

greatly reduced primordial distributions. Sympatry is also observed within the three-species clade of *T. fieldianus* + (*T. minimucro* + *T. trisinuatus*) (Fig. 9G–I), though their sister, *T. duponchellii* (Fig. 9F), exhibits narrow allopatry based on its more northerly distribution within the Northern Valdivian and Santiagan entomofaunal regions.

Pleistocene glaciation has influenced geographical distributions of both plants and animals in the region of highest diversity near 40°S. The beetle fauna of the lowland Lake Region (latitude 40°S–42°S) consisted of cold-adapted species immediately following glacial retreat 19,500 yr B.P., with fossils from older assemblages comprising species typical of both forest and more open riparian habitats: for Carabidae this included *Bembidion* Latreille spp. (tribe Bembidiini) (Hoganson and Ashworth 1992). More recent stratigraphic layers from 13,000 yr B.P. to the present yielded forest-adapted species representing genera such as *Ceroglossus* Solier (tribe Carabini), *Cascellius* Curtis (tribe Broscini), *Parhyptes* Motschulsky & *Trirammatus* Chaudoir (tribe Pterostichini), and *Bradycellus* Erichson & *Pelmatellus* Bates (tribe Harpalini) (Ashworth and Hoganson 1987, Ashworth and Markgraf 1989, Hoganson and Ashworth 1992). The Quaternary pollen record synchronously reflects this warming, with the increase of Chenopodiaceae and Amaranthaceae pollen, indicative of warmer conditions, increasing dramatically in the Lake Region from 14,500 yr B.P. to the present (Heusser 1983). Along with the warming came dramatic increases in charcoal deposition during the past 6,000 years, indicating human modification of the landscape.

Tropopterus is the only polytypic taxon within Moriomorphini to uniformly exhibit antisymmetric male genitalia; i.e., the orientation of the male aedeagus is inverted 180° from the plesiomorphic condition in the tribe, and indeed the entire family Carabidae, wherein the anatomical right side is oriented ventrally when the genitalia are in repose within the abdomen (Jeannel 1955: 75). *Mecyclothorax punctipennis* MacLeay exhibits infraspecific variation in male genitalic orientation, with populations in Western Australia variably polymorphic for either the normal left-everting aedeagus (right side ventral), or the inverted right-everting (left side ventral) condition (Liebherr and Will 2015). Just as in *M. punctipennis*, the male genitalic inversion of *Tropopterus* is not reflected in inverted orientation of the female reproductive tract. *Tropopterus* females retain the plesiomorphic condition of the spermathecal duct entering the bursal–common oviduct juncture from the right side (Fig. 7). From a genetic viewpoint then, the orientation of the male and female genitalia are decoupled. Moreover, any functional difference in the inverted male aedeagus is not associated with change from the plesiomorphic condition in the female reproductive tract.

How inverted male genitalia originated in this geographically disjunct clade remains an open question. Liebherr and Will (2015) argued that the antisymmetric genitalic orientation of *Tropopterus* supported the

hypothesis of colonization of Chile over water, assuming a small colonizing propagule became fixed for the alternative, apomorphic left side ventral genitalic orientation during founding of the initial population. However, knowledge that the adelphotaxon *Pharetis* retains the plesiomorphic right side ventral orientation (Liebherr 2020) begs the question of how the switch in orientation might have occurred. If it happened after colonization in a polymorphic population, why was the plesiomorphic condition lost from South America? In Western Australia, maximally 58% of *Mecyclothorax punctipennis* individuals in population samples exhibit antisymmetric genitalia. What conditions would drive the plesiomorphic condition to zero in the primordial Chilean *Tropopterus* population? Moreover, the only other moriomorphine species to monomorphically exhibit antisymmetric male genitalia, *Mecyclothorax storeyi* Moore (1963), evolved the condition on Mt. Bellenden Ker in the Queensland Alps. Closely related species exhibiting the plesiomorphic genitalic orientation occupy adjacent mountains (Baehr 2003), showing that such a transition can occur over limited distances within a terrestrial situation. Given these questions and contradictions, it seems best to consider the origin of antisymmetry agnostic with regard to the history of *Tropopterus* in South America.

Conversely, knowledge of the community within which *Tropopterus* occurs may be more relevant to understanding its colonization history in South America. *Tropopterus* beetles have been collected syntopically with *Glypholoma* staphylinid beetles (Thayer 1997), *Andotypus* hydrophilid beetles (Fikáček et al. 2014), and *Anaballetus* leiodid fungus beetles (Newton et al. 2017), establishing a modern ecological association. The middle Jurassic fossil species, *Juroglypholoma antiquum* Cai et al. (2012) dates the origin of the Glypholomatinae to before 165 Myr ago, supporting placement of *Glypholoma* in Australia and southern South America prior to Gondwanan vicariance. *Andotypus* and its sister genus *Austrotypus* also exhibit an Austral disjunction (Fikáček et al. 2014) involving Australia and western South America, supporting a trans-Antarctic vicariant relationship. The leiodid genus *Anaballetus* is hypothesized to be most closely related to presently undescribed taxa from Australia and New Zealand (Newton et al. 2017). Colloff (2011) explicated a trans-Antarctic area relationship involving Chile, Tasmania, and New South Wales for the *Novonothrus puyehue* species group (Acari, Oribatida); litter-inhabiting mites resident in cool temperate *Nothofagus* Rain Forest. Type specimens of *Novonothrus puyehue* Casanueva and Norton (1997) were collected syntopically and synchronically with the two type specimens of *Tropopterus trisinuatus*. The moss-inhabiting hemipterous Peloridiidae represent another taxon of *Nothofagus* associates exhibiting Austral disjunctions consistent with Gondwanan vicariance, with specimens of several species of *Peloridora* China

(Burkhardt 2009) collected at localities represented by *Tropopterus* collections reported above. All of these taxa represent the long-recognized Austral-disjunct Western Antarctic biogeographical track that housed *Nothofagus* forest (Schlinger 1974; Humphries et al. 1986). The modern crown groups of *Nothofagus* began diversifying 55–40 Myr ago (Cook and Crisp 2005), well before the break up of Australia, Antarctica, and South America via vicariance across the Tasman Sea and Drake Passage (San Martín and Ronquist 2004; Livermore et al. 2005). This history is consistent with the broad distribution of specialist *Nothofagus* herbivorous taxa across the range of *Nothofagus* (McQuillan 1993), and the lack of any significant overlap between the herbivore faunas of the *Nothofagus* and *Eucalyptus* dominant communities in Australia. Burgeoning fossil evidence verifies the presence of an Eocene to Late Eocene flora on the Antarctic Peninsula that consisted of *Nothofagus* dominated vegetation with some podocarp conifers (Dawson et al. 2014; Warny et al. 2019). That forest was extremely similar in composition to the Valdivian and North Patagonian forest assemblages found in Chile today (Clarke 1964). The concordance between the ecological distribution of *Tropopterus* and its leaf-litter associates in South American *Nothofagus* forest, and the Austral biogeographical disjunction shown by *Tropopterus* and its New South Wales sister group, *Pharetis*, supports a legacy membership for *Tropopterus* in this vicariant, Austral *Nothofagus* forest community.

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References

- Ashworth AC, Hoganson JW (1987) Coleoptera bioassociations along an elevational gradient in the Lake Region of southern Chile, and comments on the postglacial development of the fauna. *Annals of the Entomological Society of America* 80: 865–895. <https://doi.org/10.1093/aesa/80.6.865>
- Ashworth AC, Markgraf V (1989) Climate of the Chilean channels between 11,000 to 10,000 yr B.P. based on fossil beetle and pollen analyses. *Revista Chilena de Historia Natural* 62: 61–74.
- Baehr M (1998) A preliminary survey of the classification of Psydrinae (Coleoptera: Carabidae). In: Ball GE, Casale A, Vigna Taglianti V (Eds) *Phylogeny and classification of Caraboidea (Coleoptera: Adepaga)*. Atti Museo Regionale di Scienze Naturali, Torino, 359–368.
- Baehr M (2003) Psydrine ground beetles (Coleoptera: Carabidae: Psydrinae), excluding Amblytelini, of eastern Queensland rainforests. *Memoirs of the Queensland Museum* 49: 65–109. <https://www.biodiversitylibrary.org/part/243680>
- Ball GE, Erwin TL (1982) The Baron Maximilien de Chaudoir: inheritance, associates, travels, work, and legacy. *The Coleopterists Bulletin* 36: 475–501.
- Basilewsky P (1982) Baron Maximilien de Chaudoir (1816–1881). *The Coleopterists Bulletin* 36: 462–474.
- Bates HW (1874) On the geodephagous Coleoptera of New Zealand. *Annals and Magazine of Natural History (series 4)* 13: 233–246, 270–277. <https://doi.org/10.1080/00222937408680859>
- Broun T (1880) *Manual of the New Zealand Coleoptera (Part I)*. Government Printer, Wellington, 651 pp. <https://doi.org/10.5962/bhl.title.32505>
- Broun T (1882) On the New Zealand Carabidae. *New Zealand Journal of Science (Dunedin)* 1: 215–227.
- Burkhardt D (2009) Taxonomy and phylogeny of the Gondwanan moss bugs or Peloriidiidae (Hemiptera, Coleorrhyncha). *Deutsche Entomologische Zeitschrift* 56: 173–235. <https://doi.org/10.1002/mmnd.200900019>
- Cai C, Huang D, Thayer MK, Newton AF (2012) Glypholomatine rove beetles (Coleoptera: Staphylinidae): a southern hemisphere recent group recorded from the Middle Jurassic of China. *Journal of the Kansas Entomological Society* 85: 239–244. <https://doi.org/10.2317/JKES120531.1>
- Casanueva ME, Norton RA (1997) New nothroid mites from Chile: *Novonothrus covarrubiasi* n. sp. and *Novonothrus puyehue* n. sp. (Acari: Oribatida). *Revista Chilena de Historia Natural* 70: 435–445.
- Chaudoir M de (1876) Notes et additions au mémoire de M Reed sur les Carabiques du Chile inséré dans les Proceedings of the Zoological Society of London. *Annales de la Société entomologique de Belgique* 19: 105–124.
- Clarke D (1964) The forests of southern Chile and the Argentine (2). *Quarterly Journal of Forestry* 58: 120–134.
- Colloff MJ (2011) A review of the oribatid family Nothridae in Australia, with new species of *Novonothrus* and *Trichonothrus* from rain forest and their Gondwanan biogeographical affinities (Acari: Oribatida). *Zootaxa* 3005: 1–44. <https://doi.org/10.11646/zootaxa.3005.1.1>
- Cook LG, Crisp MD (2005) Not so ancient: the extant crown group of *Nothofagus* represents a post-Gondwanan radiation. *Proceedings of the Royal Society B* 272: 2535–2544. <https://doi.org/10.1098/rspb.2005.3219>
- Dawson M, Francis J, Carpenter R (2014) New views of plant fossils from Antarctica: a comparison of X-rays and neutron imaging techniques. *Journal of Paleontology* 88: 702–707. <https://doi.org/10.1666/13-124>
- Deuve T (1993) L'abdomen et les genitalia des femelles de Coléoptères Adepaga. *Mémoires du Muséum national d'Histoire naturelle, Serie A, Zoologie* 155: 1–184.
- Domínguez MC, Roig-Juñent S, Tassin JJ, Ocampo FC, Flores GE (2006) Areas of endemism of the Patagonian steppe: an approach based on insect distributional patterns using endemicity analysis. *Journal of Biogeography* 33: 1527–1537. <https://doi.org/10.1111/j.1365-2699.2006.01550.x>
- Enderlein G (1909) 9. Des Insektenfauna der Insel Neu-Amsterdam. In Enderlein G (ed). *Die Insekten des Antarktischen Gebietes*, 10. Druck und Verlag von Georg Reimer, Berlin: 486–492.
- Fikáček M, Minoshima YN, Newton AF (2014) A review of *Andotyplus* and *Austrotypus* gen. nov., rygmoline genera with an austral disjunction (Hydrophilidae: Rygmolinae). *Annales Zoologici* 64: 557–596. <https://doi.org/10.3161/000345414X685893>
- Gemminger M, Harold B de (1868) Cicindelidae–Carabidae. *Catalogus Coleopterorum* 1, 424 pp. [+ 8 pp index]
- Germain P (1911) *Catalogo Coleopteros Chilenos del Museo Nacional*. Boletín del Museo Nacional de Historia Natural, Chile 3: 47–73.
- Goloboff PA (1999) NONA (NO NAME). Tucumán, Argentina, Published by the author. <http://www.softpedia.com/get/Science-CAD/NONA.shtml> [accessed 6-ix-2016]
- Heusser CJ (1983) Quaternary pollen record from Laguna de Tagua Tagua, Chile. *Science* 219: 1429–1431. <https://doi.org/10.1126/science.219.4591.1429>
- Hlavac T F (1971) Differentiation of the carabid antennal cleaner. *Psyche* 78: 51–66. <https://doi.org/10.1155/1971/927545>
- Hoganson JW, Ashworth AC (1992) Fossil beetle evidence for climatic change 18,000–10,000 years B.P. in south-central Chile. *Quaternary Research* 37: 101–116. [https://doi.org/10.1016/0033-5894\(92\)90009-8](https://doi.org/10.1016/0033-5894(92)90009-8)
- Humphries CJ, Cox JM, Nielsen ES (1986) *Nothofagus* and its parasites: a cladistic approach to coevolution. In: Stone AR, Hawksworth DL (Eds) *Coevolution and Systematics*. The Systematics Association Special Volume No. 32. Oxford University Press, New York, NY, 55–76.
- ICZN [International Commission on Zoological Nomenclature] (1999) *International Code of Zoological Nomenclature*. Fourth Edition. The International Trust for Zoological Nomenclature, London, 306 pp. <http://iczn.org/iczn/index.jsp> [accessed 26-vi-2018]
- Jeannel R (1955) L'Édage, initiation aux recherches sur la systématique des coléoptères. *Publications du Muséum national d'Histoire naturelle no. 16*: 155 pp.
- Jeannel R (1962) Les tréchides de la Paléantarctide occidentale. In: Debutteville CD, Rapoport E (Eds) *Biologie de l'Amérique Australe I: Etudes sur la faune du sol*. Éditions du Centre national de la Recherche scientifique, Paris, 527–655.
- Larochelle A, Larivière M-C (2013) Carabidae (Insecta: Coleoptera): synopsis of species, Cicindelinae to Trechinae (in part). *Fauna of New Zealand / Ko te Aitanga Pepeke o Aotearoa* 69: 193 pp.
- Lieberr JK (1988) Brachyptery and phyletic size increase in Carabidae (Coleoptera). *Annals of the Entomological Society of America* 81: 157–163. <https://doi.org/10.1093/aesa/81.2.157>

- Liebherr JK (2012) The first precinctive Carabidae from Moorea, Society Islands: new *Mecyclothorax* spp. (Coleoptera) from the summit of Mont Tohiea. *ZooKeys* 224: 37–80. <https://doi.org/10.3897/zookeys.224.3675>
- Liebherr JK (2013) The *Mecyclothorax* beetles (Coleoptera, Carabidae, Moriormorphini) of Tahiti, Society Islands. *ZooKeys* 322: 1–170. <https://doi.org/10.3897/zookeys.322.5492>
- Liebherr JK (2015) The *Mecyclothorax* beetles (Coleoptera, Carabidae, Moriormorphini) of Haleakalā, Maui: Keystone of a hyperdiverse Hawaiian radiation. *ZooKeys* 544: 1–407. <https://doi.org/10.3897/zookeys.544.6074>
- Liebherr JK (2018a) Cladistic classification of *Mecyclothorax* Sharp (Coleoptera: Carabidae: Moriormorphini) and taxonomic revision of the New Caledonian subgenus *Phacothorax* Jeannel. *Deutsche Entomologische Zeitschrift* 65: 1–63. <https://doi.org/10.3897/dez.65.21000>
- Liebherr JK (2018b) Taxonomic review of Australian *Mecyclothorax* Sharp (Coleoptera: Carabidae: Moriormorphini) with special emphasis on the *M. lophoides* (Chaudoir) species complex. *Deutsche Entomologische Zeitschrift* 65: 177–224. <https://doi.org/10.3897/dez.65.27424>
- Liebherr JK (2020) Phylogenetic placement of the Australian *Pharetis*, gen. nov. and *Spherita*, gen. nov., in a revised classification of the circum-Antarctic Moriormorphini (Coleoptera: Carabidae). *Invertebrate Systematics*. [in press]
- Liebherr JK, Will KW (1998) Inferring phylogenetic relationships within Carabidae (Insecta, Coleoptera) from characters of the female reproductive tract. In: Ball GE, Casale A, Vigna Taglianti V (Eds) *Phylogeny and classification of Caraboidea* (Coleoptera: Adephaga). *Atti Museo Regionale di Scienze Naturali, Museo Regionale di Scienze Naturali, Torino*, 107–170.
- Liebherr JK, Will KW (2015) Antisymmetric male genitalia in Western Australian populations of *Mecyclothorax punctipennis* (Coleoptera: Carabidae: Moriormorphini). *Insect Systematics & Evolution* 46: 393–409. <https://doi.org/10.1163/1876312X-45042124>
- Livermore R, Nankivell A, Eagles G, Morris P (2005) Paleogene opening of Drake Passage. *Earth and Planetary Sciences Letters* 236: 459–470. <https://doi.org/10.1016/j.epsl.2005.03.027>
- Lorenz W (2005) *Nomina Carabidarum*, a directory of the scientific names of ground beetles. Published by the author, Tutzing, Germany, 993 pp.
- Maddison DR, Baker MD, Ober KA (1999) Phylogeny of carabid beetles as inferred from 18S ribosomal DNA (Coleoptera: Carabidae). *Systematic Entomology* 24: 103–138. <https://doi.org/10.1046/j.1365-3113.1999.00088.x>
- Maddison DR, Kanda K, Boyd OF, Faille A, Porch N, Erwin TL, Roig-Juñent S (2019) Phylogeny of the beetle supertribe Trechitae (Coleoptera: Carabidae): unexpected clades, isolated lineages, and morphological convergence. *Molecular Phylogenetics and Evolution* 132: 151–176. <https://doi.org/10.1016/j.ympev.2018.11.006>
- Maddison DR, Ober KA (2011) Phylogeny of minute carabid beetles and their relatives based upon DNA sequence data (Coleoptera, Carabidae, Trechitae). *ZooKeys* 47: 229–260. <https://doi.org/10.3897/zookeys.147.1871>
- McQuillan PB (1993) *Nothofagus* (Fagaceae) and its invertebrate fauna – an overview and preliminary synthesis. *Biological Journal of the Linnean Society* 49: 317–354. <https://doi.org/10.1111/j.1095-8312.1993.tb00910.x>
- Moore BP (1963) Studies on Australian Carabidae (Coleoptera) – 3. The Psydrinae. *Transactions of the Royal Entomological Society of London* 115: 277–290. <https://doi.org/10.1111/j.1365-2311.1963.tb00810.x>
- Newton AF, Švec Z, Fikáček M (2017) A new genus and two new species of Leiodinae from Chile, with keys to world genera of Sogdini and Leiodinae from Chile and Argentina (Coleoptera: Leiodidae). *Acta Entomologica Musei Nationalis Pragae* 57: 121–140. <https://doi.org/10.1515/aemnp-2017-0061>
- Niemälä J (1990) Habitat distribution of carabid beetles in Tierra del Fuego, South America. *Entomologica Fennica* 1: 3–16. <https://doi.org/10.33338/ef.83348>
- Nixon KC (1999) The parsimony ratchet, a new method for rapid parsimony analysis. *Cladistics* 15: 407–414. <https://doi.org/10.1111/j.1096-0031.1999.tb00277.x>
- Nixon KC (2002) WinClada. Ithaca, NY. Published by the author. <http://www.softpedia.com/get/Science-CAD/WinClada.shtml> [accessed 16-ix-2016]
- O'Brien CW (1971) The biogeography of Chile through entomofaunal regions. *Entomological News* 82: 197–207.
- Reed EC (1874) 7. On the Coleoptera Geodephaga of Chile. *Proceedings of the Zoological Society of London* 1874: 48–70. [+ 1 pl.] <https://doi.org/10.1111/j.1096-3642.1874.tb02451.x>
- Roig-Juñent S, Domínguez MC (2001) Diversidad de la familia Carabidae (Coleoptera) en Chile. *Revista Chilena de Historia Natural* 74: 549–571. <https://doi.org/10.4067/S0716-078X2001000300006>
- Sanmartín I, Ronquist F (2004) Southern hemisphere biogeography inferred by event-based models: plant versus animal patterns. *Systematic Biology* 53: 216–243. <https://doi.org/10.1080/10635150490423430>
- Schlinger EI (1974) Continental drift, *Nothofagus*, and some ecologically associated insects. *Annual Review of Entomology* 19: 323–343. <https://doi.org/10.1146/annurev.en.19.010174.001543>
- Sloane TG (1898) On Carabidae from West Australia, sent by Mr A M Lea (with descriptions of new genera and species, synoptic tables, &c.). *Proceedings of the Linnean Society of New South Wales* 23: 444–520.
- Sloane TG (1903) *Studies in Australian Entomology*. no. XII. New Carabidae (Panageini, Bembidiini, Pogonini, Platysmatini, Platynini, Lebiini, with revisional lists of genera and species, some notes on synonymy, &c.). *Proceedings of the Linnean Society of New South Wales* 28: 566–642.
- Solier AJJ (1849) Orden III. Coleopteros. In: Gay C (Ed.). *Historia Física y Política de Chile* 4: 105–508. En Casa del Autor, Paris; Museo de Historia Natural de Santiago, Chile.
- Song H (2004) Post-adult emergence development of genitalic structures in *Schistocerca* Stål and *Locusta* L. *Proceedings of the Entomological Society of Washington* 106: 181–191.
- Straneo SL (1954) Pterostichini e Tropopterini (Col. Carabidae). In: Titschack E (Ed.) *Beiträge zur Fauna-Perus*, Jena 4: 95–108. [G. Fischer, Jena]
- Straneo SL (1969) Sui Carabidi del Chile, raccolti dal Dr Holdgate della Royal Society Expedition (1958–1959) e dal Prof Kuschel. *Annales de la Société entomologique de France (NS)* 5: 951–974.

- Thayer MK (1985) Revision, phylogeny and biogeography of the austral genus *Metacorneolabium* Steel (Coleoptera: Staphylinidae: Omaliinae). In: Ball GE (Ed.) Taxonomy, Phylogeny and Zoogeography of Beetles and Ants. Dr W Junk Publishers, Dordrecht, 113–179.
- Thayer MK (1997) *Proglypholoma aenigma* gen. et sp. nov., *Glypholoma* spp. nov. and new records, and a phylogenetic analysis of Glypholomatinae (Coleoptera: Staphylinidae). *Annales Zoologici* 47: 157–174.
- Warny S, Kymes CM, Askin R., Krajeski KP, Tatur A (2019) Terrestrial and marine floral response to latest Eocene and Oligocene events on the Antarctic Peninsula. *Palynology* 43: 4–21. <https://doi.org/10.1080/01916122.2017.1418444>
- Weidner H (1976) Die Entomologischen Sammlungen des Zoologischen Instituts und Zoologischen Museums der Universität Hamburg, IX Teil, Insecta VI. Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut 73: 87–264.

Supplementary material 1

Cladistic analysis of *Tropopterus* spp.

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Data type: phylogenetic data

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