

Revision and phylogenetic systematics of the Neotropical Ceratomerinae (Insecta: Diptera: Empidoidea: Brachystomatidae)

BRADLEY J. SINCLAIR

Canadian National Collection of Insects, Ottawa Plant Laboratory – Entomology, CFIA,
K.W. Neatby Bldg., C.E.F., 960 Carling Ave., Ottawa, ON, Canada K1A 0C6
[bradley.sinclair@inspection.gc.ca]

Received 11.i.2010, accepted 13.iv.2010.

Published online at www.arthropod-systematics.de on 22.06.2010.

> Abstract

Thirteen Neotropical species of *Ceratomerus*, including nine new species (*C. apterus*, *C. argutus*, *C. comarapa*, *C. hibbsi*, *C. irramus*, *C. longicornis*, *C. masneri*, *C. paraconnexus*, *C. penai*) are described and illustrated. One of these species, *C. apterus*, from Ecuadorian páramo above 4000 m, lacks wings and has reduced halteres. A preliminary phylogeny of the genera and species groups of the Ceratomerinae is presented, with a discussion of the generic concept of *Ceratomerus* Philippi. A provisional biogeographic hypothesis of this Gondwanan lineage is discussed. Significant relationships include the Southern Gondwana Pattern, the Inverted Southern Pattern and the Neotropical *C. paradoxus* group evolved within the Australian *C. campbelli* group, illustrating both an intra-generic and intercontinental pattern.

> Key words

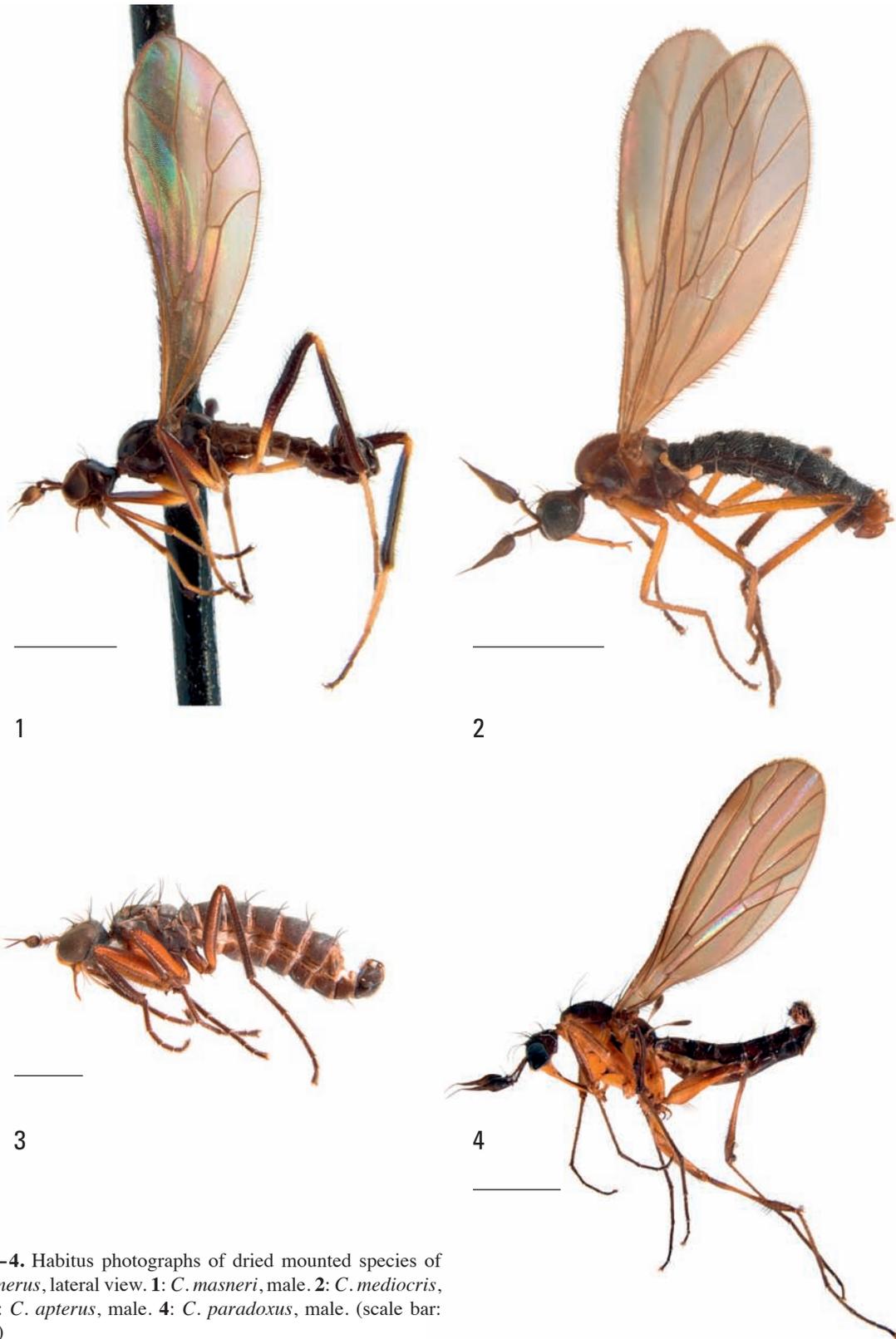
Empidoidea, Brachystomatidae, *Ceratomerus*, Neotropics, Chile, Ecuador, Argentina, Bolivia.

1. Introduction

The family Brachystomatidae is a recently recognized worldwide family, classified into three subfamilies: Brachystomatinae, Ceratomerinae and Trichopezinae (SINCLAIR & CUMMING 2006). This family was recognized for empidoid taxa with modified female terminalia: female tergum 7 often with fringe of setae, and female cercus held upright. There are currently 21 recognized genera and some 163 described species prior to this study (YANG et al. 2007). As in other empidoid families, adults range in size from large and slender species of *Heterophlebus* Philippi, 1865 (10 mm) to *Glyphidopeza* Sinclair, 1997 (2 mm). Species occur in a variety of habitats including arctic tundra (*Heleodromia* Haliday, 1833), Chilean rainforests (*Heterophlebus*), tropical rainforests (*Apalocnemis* Philippi, 1865) and cold temperate streams (*Ceratomerus* Philippi, 1865).

The ceratomerine group was first recognized from the Neotropical Region with the description of the type species, *Ceratomerus paradoxus* by

PHILIPPI (1865), which possesses remarkably modified male legs. COLLIN (1928) first erected the subfamily in recognition of the distinctive conus, a finger-like projection from the pedicel (2nd antennal segment) projecting into the postpedicel (3rd antennal segment), and absence of an anal cell in the wing (except in the New Zealand genus *Glyphidopeza*). Two additional Chilean species were described by COLLIN (1933) and one species by PLANT (1995). Ceratomerinae is confined to the Southern Hemisphere and in addition to South America, is known from Australia, New Zealand and Norfolk Is. The historical classification of the subfamily was more thoroughly reviewed in SINCLAIR (2003a). Currently there are three genera assigned to Ceratomerinae, *Glyphidopeza* (2 spp.), *Icasma* Collin, 1928 (7 spp.) and *Ceratomerus* (36 spp.). The former two genera are endemic to New Zealand, with *Glyphidopeza* confined to small cascading streams and *Icasma* occurring in humid forests, often near streams or



Figs. 1–4. Habitus photographs of dried mounted species of *Ceratomerus*, lateral view. **1:** *C. masneri*, male. **2:** *C. mediocris*, male. **3:** *C. apterus*, male. **4:** *C. paradoxus*, male. (scale bar: 1.0 mm)

small pools (SINCLAIR 1997). *Ceratomerus* appears to occur both in streams and humid forests (SINCLAIR 2003a).

This is the first revision of the Neotropical species of Ceratomerinae based on a large number of specimens; it builds on earlier studies of the Australian

and New Zealand faunas (SINCLAIR 1997, 2003a). The genus *Ceratomerus* exhibits a classic Gondwanan or Trans-Antarctic pattern and this study attempts a first analysis of the biogeographic and phylogenetic relationships among species groups of *Ceratomerus* and genera of Ceratomerinae.

2. Material and methods

2.1. Material

This study is based on some 630 adult specimens of Ceratomerinae borrowed from the following institutions: Biosystematics Laboratory, Kyushu University, Fukuoka, Japan (BLKU); The Natural History Museum, London, England (BMNH); Bernice P. Bishop Museum, Honolulu, USA (BPBM); Canadian National Collection of Insects, Ottawa, Canada (CNC); University of Guelph, Guelph, Canada (DEBG); Kitakyushu Museum of Natural History, Kitakyushu, Japan (KMNH); Museum National d'Histoire Naturelle, Paris, France (MNHN); National Museum of Wales, Cardiff, Wales, U.K. (NMWC); United States National Museum of Natural History, Washington, USA (USNM); Zoological Museum, University of Copenhagen, Denmark (ZMUC). Abbreviations given here are used throughout the text to indicate deposition of specimens.

All dissections were made in glycerin and tissues cleared using hot 85% lactic acid. Terms used for adult structures primarily follow McALPINE (1981), except for the antenna and the wing venation, where the terms of STUCKENBERG (1999) and SAIGUSA (2006) are used, respectively. Homologies of the male terminalia follow those of SINCLAIR & CUMMING (2006). Lists of scutal setae in descriptions refer to one-side only, except scutellum.

Label data for primary types are exactly as they appear. Labels are listed from the top downward, with data from each label enclosed in single quotation marks; lines are delimited by a 'pipe' (|). Additional information is included in [square] brackets.

2.2. Cladistic analysis

Characters were scored for all known genera and representative species groups of the Ceratomerinae and three outgroup genera, two from the Trichopezinae (Brachystomatidae) and *Oreogeton* Schiner, 1860 (Empidoidea, *incertae sedis*). A complete list of exemplars is provided in Tab. 1. Forty-six characters were analyzed in the cladistic analysis, including four multi-state characters (Tab. 2). All characters were treated as unordered with multi-state characters considered as non-additive, and all characters were equally weighted. Character polarity was determined by rooting the tree with the three empidoid outgroups, which together were constrained to be paraphyletic in relation to the ingroup.

Parsimony analysis of the character state matrix (Tab. 3) was performed using the program PAUP* ver-

sion 4.0b10 (SWOFFORD 2002). A heuristic search with stepwise addition was implemented to find the most parsimonious trees using random addition sequence of taxa, tree-bisection-reconnection (TBR) branch swapping and 1000 random replications. *A posteriori* character weighting was implemented using successive approximations according to the rescaled consistency index (RC). Character evolution, character state distributions and alternative tree topologies were examined using the program MacClade 4 (MADDISON & MADDISON 2003). The dataset may be downloaded from the TreeBASE database (URL: <http://purl.org/phylo/treebase/phylo/study/TB2:S10399>).

2.3. Morphological abbreviations

The following abbreviations are used in the species descriptions, material examined sections, and figures:

ad	anterodoral (position of setae/bristles)
alc	alcohol
av	anteroventral (position of setae/bristles)
cerc	cercus
d	discal cell
dc	dorsocentral bristles/setulae
ej apod	ejaculatory apodeme
epand	epandrium
FIT	flight intercept trap
for.	forest
gcx apod	gonocoxal apodeme
hypd	hypandrium
hypd proc	hypandrial process
hyprt	hypoproct
M _{1,2,4}	medial vein
MT	Malaise trap
NP	national park
npl	notopleural bristles
pal	postalar bristle
pd	posterodorsal (position of setae/bristles)
pgt	postgonite
ph	phallus
pprn	postpronotal bristle
presut spal	presutural supra-alar bristles
psut spal	postsutural supra-alar bristles
PT	pan traps
pv	posteroventral (position of setae/bristles)
R _{1,2+3,4,5}	radial vein
Sc	subcostal vein
sctl	scutellar bristles
sur	surstylus
T _{8,10}	tergum
ypans	yellow pan traps

3. Taxonomy

3.1. Genus *Ceratomerus* Philippi

Ceratomerus Philippi, 1865: 765. Type-species *Ceratomerus paradoxus* Philippi (monotypy).

Tomia Paramonov, 1961: 100 nec MARTYNOV (1936: 1262). Type-species *Tomia campbelli* Paramonov (original designation).

Diagnosis. *Ceratomerus* is distinguished by the following combination of characters: posterior ocelli usually widely separated with ocellar bristles inserted anteriorly, postpedicel lengthened and tapered apically, acrostichal setulae present, 2–5 dorsocentral bristles present, Sc complete, R_{4+5} branched or unbranched, cell d emitting 2 veins (M_{1+2} and M_4), cell cua absent, presence of distinct bristles on tibiae, scutum not highly polished.

Remarks. See SINCLAIR (2003a) for full re-description of the genus and notes on synonymy.

3.2. *Ceratomerus apterus* sp.n.

Figs. 3, 5, 6

Material. Holotype ♂, 'Ecuador, Napo/Pichincha, | Papallacta Pass, 4200 m, | 0°19'15S 78°11'51W, | paramo, yellow pans, 29 | Apr-11 May 2002, Marshall & | Buck, debu00202092', 'HOL-OBJECT | *Ceratomerus* | *apterus* | Sinclair [red label]' (CNC). – Paratypes, **ECUADOR:** 1♂, 0°17'S 78°12'W, 4200 m, 1–2.iii.1979, PT, S.A. Marshall (DEBG); 1♂, Prov. Napo, Quito-Baeza Pass, 1 km E, mixed Polylepis litter, 4.xi.1999, R. Anderson, debu00116804 (DEBG); 1♀, Napo/Pichincha, Quito-Baeza Pass, 4000 m, PT in moss, 4–8.xi.1999, S.A. Marshall, debu00140518 (DEBG); 27♂♂, 21♀♀, same data as holotype (CNC, DEBG, USNM).

Recognition. This species is distinguished from all other species of ceratomerines by the absence of wings and halteres.

Description: Male. Head dark brown, face with pale pruinescence, lacking setulae; ocellar triangle with pair of long, divergent bristles, inserted between posterior ocelli; postocellar bristle 0.5 × length of ocellar bristle; 2 pairs of vertical bristles, slightly shorter than ocellars; frons with 2 pairs of dark lateral setulae; postocular bristles erect, 0.2 × width of eye. Antenna short, with scape ca. 0.5 × length of labrum, pedicel oval with posterior fringe of setae; scape sparsely covered by short setae. Postpedicel onion-shaped lacking apical prolongation, covered by dense pruinescence; two-segmented arista-like stylus nearly 2 × length of postpedicel; first segment of stylus not longer than

wide; apex of stylus concolorous with postpedicel. Base of labrum lacking dorsal process; palpus short, pale and slender, 0.2 × length of labrum, with several long, dark setae.

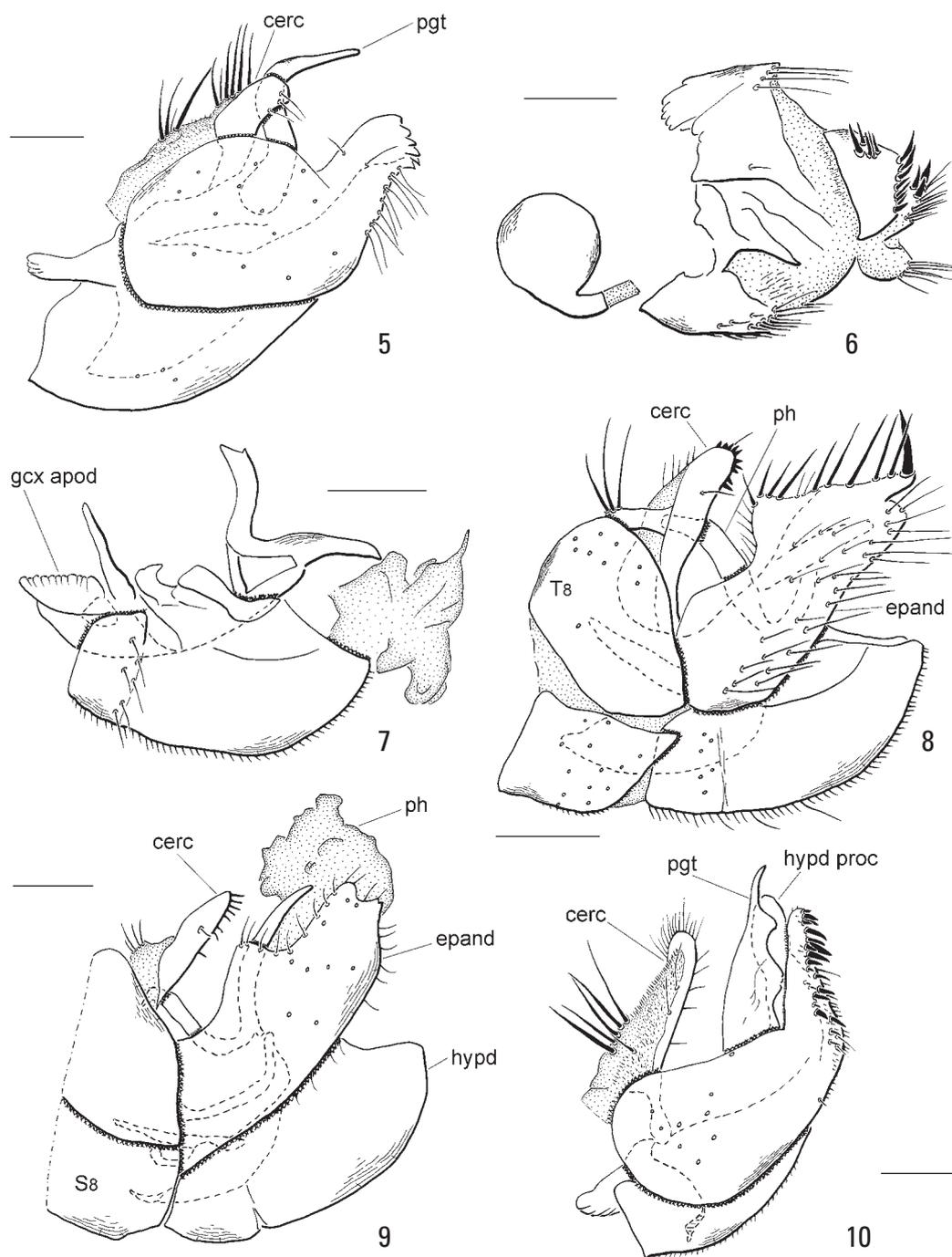
Due to wingless condition, thorax shortened. Mesonotum, postnotum and pleura dark. Acrostichals lacking; 2 dc, with several setulae interspersed; 1 pprn; 1–2 short presut spal; 1 npl; 0 psut spal; 1 pal; 2 sclt; lacking setulae scattered on scutum. Anteprepronotum with pair of short setulae; laterotergite bare.

Wing reduced to mere vestige. Halter reduced to short, pale, knob-like process, bearing long apical seta.

Fore coxa much paler than pleura, remaining coxae slightly paler than pleura; fore and mid femora with light anterior surface and dark brown posterodorsal margin; hind femur and remaining leg segments dark brown; fifth tarsomere dorsoventrally flattened. Fore coxa less than 2 × length of mid coxa, gradually tapering apically, lacking modified setae. Fore trochanter lacking setae. Fore femur distinctly swollen, thickened just after base; pv surface with row of short, dark setulae. Fore tibia slender, slightly arched; subequal in length to femur; apex slightly dilated. First tarsomere 0.5 × length of fore tibia; distal 4 tarsomeres combined longer than first tarsomere. Mid coxa with apical setae only. Mid trochanter unmodified. Mid femur with pv row of short, dark setae. Mid tibia slightly longer than femur; apical third with deep, anterior notch, bordered by 2 upper processes and stout seta. First tarsomere short, slightly longer than tarsomere 4, constricted sub-basally. Hind coxa bearing long apical setae only. Hind trochanter unmodified. Hind femur not greatly swollen, bearing av row of slender setae. Hind tibia subequal in length to femur; 2 ad bristles on distal half; apex slightly dilated, bearing posteroapical comb. Hind tarsomeres longer than tibia; first tarsomere with single short, erect, ventral seta near base.

Abdominal terga and sterna dark brown, with long, stout setae along posterior margin of terga 1–6; tergum 7 desclerotized medially with terminalia arched onto tergum, lacking long posterior setae, not articulated with sternum 8; tergum 8 rectangular. Terminalia (Fig. 5) (not dissected internally): hypandrium with flap-like posterior extensions; pair of heavily sclerotized sickle-shaped postgonites, crossing medially; base of postgonite with short tooth. Surstylus not articulated; apical margin toothed; posterior margin with fringe of long setae. Cercus with apical half heavily sclerotized.

Description: Female. Similar to male except as follows: fore femur with several dark spine-like pv setae, especially at base. Base of mid femur with 4 spine-like av setae at base. Mid tibia with 4–5 stout anterior bristles along entire length; ad bristle at basal third; pd bristle near mid-length; av bristle on either side of



Figs. 5–10. Terminalia of *Ceratomerus*, lateral view. **5:** *C. apterus*, male. **6:** *C. apterus*, female. **7:** *C. argutus*, hypandrium and phallus. **8:** *C. argutus*, male. **9:** *C. comarapa*, male. **10:** *C. connexus*, male. Abbreviations: cerc – cercus, epand – epandrium, gcx apod – gonocoxal apodeme, hypd – hypandrium, hypd proc – hypandrial process, ph – phallus, pgt – postgonite, T – tergum. (scale bar: 0.1 mm)

mid-length. Hind tibia with 3 evenly spaced ad bristles. Apical abdominal segments retracted into segment 7; tergum 7 with posterior fringe of very short golden setulae; lateral margin of sternum 7 straight and arched to posterior margin. Terminalia (Fig. 6): posterior two-thirds of tergum 8 membranous, with anterior fringe of long setae along dorsolateral margin; pair of small, flat lateral sclerites extend into segment 7 from anterior margin of tergum 8; sternum 8 with

ventral setulae; posterior margin invaginated. Tergum 10 split medially into rectangular sclerites, with 3–4 stout ad setae; posterior margin bearing row of 7–9 spine-like setae. Cercus bearing row of 3 spine-like setae; lateral margin with long setulae. Spermathecal receptacle spherical, with broad, short neck.

Distribution. This flightless species was collected above 4000 m, in the Andean alpine habitat, páramo.

This habitat is dominated by tussock grasses, mosses and cushion plants.

Remarks. This is the only known case of wing reduction in the Ceratomerinae, but not surprising given the widespread occurrence of flightlessness in the Empidoidea. A second flightless species from this locality in the family Dolichopodidae was collected during the same 1999 survey, *Papallacta stenoptera* Bickel, 2006. BICKEL (2006) reviewed and discussed selective pressures for flightlessness and its occurrence in Dolichopodidae. Wing reduction is reported also in the Tachydromiinae (GROOTAERT & SHAMSHEV 2008), Ocydromiinae (e.g., *Apterodromia* Oldroyd, 1949: SINCLAIR & CUMMING 2000), Hemerodromiinae (e.g., *Drymodromia* Becker, 1914: SMITH 1969) and Clinocerinae (e.g., *Dolichocephala* Macquart, 1823: SINCLAIR 1995). This is the first reported example of wing reduction in the Brachystomatidae.

Etymology. The specific name is derived from the Greek *apteros* (wingless), referring to the absence of wings in this species.

3.3. *Ceratomerus argutus* sp.n.

Figs. 7, 8

Material. Holotype ♂, 'BOLIVIA: Santa Cruz | 32.8 kmNW Comarapa, Kara | Huasi, Yungas de la Siberia | 2400 m, 17°49'20"S 64°42'31"W | 28–30.i.1999, F. Genier, Yungas | ex. FIT, 99-017', 'HOLOTYPE | *Ceratomerus* | *argutus* | Sinclair [red label]' (CNC). – Paratypes, PERU: 1♂, Cusco, Wayqecha Biol. Stn, 9 km NE Challabamba, 2800 m, 13°10'S 71°35'W, 13–15.v.2007, cloud for., S.M. Paiero, debu00303187 (DEBG).

Recognition. This species is distinguished by the mostly shiny head and scutum and apex of epandrium (surstylus) bearing an erect spine-like seta.

Description: Male. Head shiny, dark reddish-brown, vertex to vertical bristles bare, occiput posterior to vertical bristles with pruinescence; face with pale pruinescence, lacking setulae; ocellar triangle with pair of ocellar bristles (missing), inserted between posterior ocelli; 1 pair of postocellar bristles slightly shorter than vertical bristles; 2 pairs of subequal vertical bristle; postocular bristles erect, short and slender. Antenna short, with scape $>0.5 \times$ length of labrum, pedicel oval with posterior fringe of long setae; scape with 1 long ventral seta and several dorsal setae. Postpedicel brown concolorous with basal segments, covered by long, dense pale pruinescence; triangular, strongly tapered on apical two-thirds; two-segmented arista-like stylus slightly longer than postpedicel; first segment of stylus longer than wide; apical half of second segment of stylus paler than base at certain angles, bear-

ing long apical seta-like sensillum. Base of labrum lacking dorsal process; palpus dark brown, short and slender, $0.25 \times$ length of labrum, with several long, pale setae; prementum with short setae only.

Mesonotum shiny, dark reddish-brown; lateral margin of notopleuron, posterior margin of prescutellar depression (mostly obscured by glue), scutellum, pleura, and postnotum clothed in silvery pruinescence, especially dense on upper half of katepisternum. Acrostichals absent; uniserial row of slender, short dc, prescutellar slender and longer; 0 pprn; 0 presut spal; 1 strong npl; 0 psut spal; 1 short pal; 2 very stout sctl; scattered setulae on pprn, pal and sctl. Antepronotum with several pairs of setulae; laterotergite bare.

Wing (length approx. 3 mm) margin lacking posterior incision and appendage, venation unmodified. Pterostigma absent, wing infusate; 1 short costal bristle; costal margin with unmodified setulae, increasing in length along posterior margin. R_{4+5} and M_{1+2} broadly forked; cell d slender, short, rectangular; medial fork basal to radial fork by half length of R_4 . Halter with white knob.

Legs with coxae, trochanters, basal half of femora, fore (except apex) and mid tibiae, base of hind tibia and tarsomeres 1–2 (or 3) yellow; remainder of legs brown to dark reddish-brown; bristles lacking. Fore tibia with small anteroapical comb. Mid femur with biserial row of short, stout setae beneath. Mid tibia with row of short, stout setae beneath. Basal third of hind femur narrowed, apical two-thirds slightly sinuous; av margin with row of long setae nearly as long as width of femur. Posterior surface of hind tibia clothed in long, fine pale setulae; apex not expanded, armed with posteroapical comb. Fifth tarsomere somewhat flattened on all legs.

Abdominal sclerites lightly sclerotized, pale brown, narrow; vestiture short and slender; sclerites of segments 7–8 shiny, sclerites of segment 8 heavily sclerotized; tergum 7 with broad U-shaped membranous cleft on posterior half; sternum 7 longer than preceding segment, posterolateral corner prolonged and articulated with sternum 8; tergum 8 inflated, directed vertically, anterior margin deeply cleft medially. Terminalia (Figs. 7, 8): heavily sclerotized, shiny dark brown; hypandrium broad posteriorly, with wide collar along anterior margin; postgonite digitiform. Phallus with wide, membranous apical sac arising subapically. Epandrium narrow, bearing long stout setae along dorsal margin; surstylus weakly differentiated bearing spine-like apical seta. Cercus held obliquely, thickly sclerotized, apex rounded, $0.5 \times$ length of epandrium; with dense stout posteroapical setae.

Description: Female. Unknown.

Distribution. This species is known only from two localities: Yungas de la Siberia (Bolivia) at 2400 m and Wayqecha Biological Station (Peru) at 2800 m, a region of montane tropical forest.

Etymology. The specific name is from the Latin *argutus* (shiny), referring to its shiny head and mesonotum.

3.4. *Ceratomerus comarapa* sp.n.

Fig. 9

Material. Holotype ♂, 'BOLIVIA: Santa | Cruz, Yungas de | Siberia, 26.0kmNW | Comarapa, FIT | 17°49'S 64°39'W | 2640m, 28–30.i.1999 | R.S. Hanley', 'HOLOTYPE | *Ceratomerus* | *comarapa* | Sinclair [red label]' (CNC). – Paratypes, **BOLIVIA**: 1♂, same data as holotype (CNC).

Recognition. This species is distinguished by the mostly shiny scutum with pruinescence covering at most a narrow central stripe on the prescutellar depression, male terminalia arched anteriorly and the male cercus short, bearing only scattered stout setae.

Description: Male. Head shiny, dark reddish-brown, vertex to vertical bristles bare, occiput posterior to vertical bristles with very sparse pruinescence; face with pale pruinescence, lacking setulae; ocellar triangle with pair of ocellar bristles, inserted between posterior ocelli; 1 pair of postocellar bristles shorter than ocellar bristles; 2 pairs of subequal vertical bristle equal in length to postocellars; postocular bristles erect, short and slender. Antenna short, with scape $>0.5 \times$ length of labrum, pedicel oval with posterior fringe of long setae; scape with 1 long ventral seta and several dorsal setae. Postpedicel brown concolorous with basal segments, covered by long, dense pale pruinescence; triangular, strongly tapered on apical two-thirds; two-segmented arista-like stylus damaged. Base of labrum lacking dorsal process; palpus dark brown, short and slender, $0.25 \times$ length of labrum, with several long, pale setae; prementum with short setae only.

Mesonotum shiny, dark reddish-brown; lateral margin of notopleuron, central stripe or posterior margin of prescutellar depression, scutellum, pleura, and postnotum clothed in silvery pruinescence, especially dense on upper half of katapisternum. Acrostichals absent; uniserial row of slender, short dc, prescutellar slender and longer; 0 pprn; 0 presut spal; 1 fine npl; 0 psut spal; 1 short pal; 2 sctl; scattered setulae on pprn, pal and sctl. Anteprepronotum with several pairs of setulae; laterotergite bare.

Wing (length approx. 3 mm) margin lacking posterior incision and appendage, venation unmodified. Pterostigma absent, wing infuscate; 1 short costal bristle; costal margin with unmodified setulae, increasing in length along posterior margin. R_{4+5} and M_{1+2} broad-

ly forked; cell d slender, short, rectangular; medial fork basal to radial fork by half length of R_4 . Halter with white knob.

Legs (hindlegs missing) with coxae, trochanters, basal half of femora, fore (except apex) and mid tibiae, and tarsomeres 1–2 (or 3) yellow; remainder of legs brown to dark reddish-brown; bristles lacking. Fore tibiae with small anteroapical comb. Mid femur with biserial row of short, stout setae beneath. Mid tibia with row of short, stout setae beneath. Fifth tarsomere somewhat flattened on all legs.

Abdominal sclerites lightly sclerotized, pale brown, narrow; vestiture short and slender; sclerites of segments 7–8 shiny, sclerites of segment 8 heavily sclerotized; tergum 7 with broad U-shaped membranous cleft on posterior half; sternum 7 longer than preceding segment, posterolateral corner prolonged and articulated with sternum 8; tergum 8 inflated, directed vertically, anterior margin deeply cleft medially. Terminalia (Fig. 9): heavily sclerotized, shiny dark brown; hypandrium broad posteriorly, with wide collar along anterior margin; postgonite digitiform. Phallus with wide, membranous apical sac arising subapically. Epandrium narrow, with protuberance near mid-length along dorsal margin; surstylus weakly differentiated lacking stout apical seta. Cercus held obliquely, thickly sclerotized, apex rounded, less than half-length of epandrium; with scattered stout posteroapical setae.

Description: Female. Similar to male (including legs) except as follows: abdominal sclerites largely membranous except for segments 7 and 8; apical segments retracted into segment 7; tergum 7 with posterior fringe of golden setulae; lateral margin of sternum 7 straight. Terminalia (undissected): retracted, not examined.

Distribution. This species is known only from the holotype and female paratype, collected in Yungas de la Siberia (Bolivia) at 2640 m.

Etymology. The specific name is a noun in apposition, named after the nearest population centre.

3.5. *Ceratomerus connexus* Collin

Figs. 10, 11

Ceratomerus connexus Collin, 1933: 320.

Material. Lectotype (here designated) ♂, '♂ | Type [red bordered circle]', '*Ceratomerus* | *connexus*, Collin | Type ♂ [handwritten]', 'Casa Pangué. | 4–10.xii.1926.', 'S.Chile: | Llanquihue prov. | F.& M. Edwards. B.M.1927-63.' (BMNH). My lectotype label 'LECTOTYPE | of *Ceratomerus* | *connexus* Collin | des. B.J. Sinclair 1994 [red label]' has been attached to this specimen. – Paralectotype **CHILE**: Llanquihue Prov., Puerto Varas, 16.xii.1926, F.&M. Edwards, BMNH(E)#248190 (1♀,

BMNH) [= *C. paraconnexus*]. My paralectotype label has additionally been attached to this specimen.

Additional material examined. **CHILE: Chiloé Is.:** 1♀, Senda Darwin, 41°53'00"S 73°40'22"W, Patagonian for., 17 m, 18.i.2006 (NMWC); 2♀♀, (in alc.), Cord. De Piuché, 150–320 m, Los Allerzales Tk., 20–21.i.2006, 42°34'46"S 74°05'02"W, Valdivian & Patagonian for. (NMWC). **Llanquihue:** 1♀, El Chingue, N Correntoso, MT, i.1990 (CNC). **Osorno:** 1♀, 4.1 km E Anticura, 430 m, window trap, 19–26.xii.1982 (USNM). **Valdivia:** 1♂, 2♀♀, 6 km E Anticura, 430 m, 19–25.xii.1982 (CNC).

Recognition. This species is distinguished from *C. mediocris* by the presence of an auxiliary cross-vein between R_4 and R_{2+3} and two notopleural bristles. It is most similar to *C. paraconnexus*, distinguished by the male terminalia (spines along margin of surstylus, not clustered at apex and only posterior margin of cercus sclerotized) and female terminalia with very stout spine-like setae on tergum 10.

Re-description: Male. Head reddish-brown, face pale brown, lacking setulae; ocellar triangle with 1 pair of long, divergent bristles; postocellar bristle reduced to short setula; 1 pair of long vertical bristles; 2 pairs of stout postverticals; postocular bristles short, not overlapping eye. Antenna long, with scape $0.33 \times$ length of proboscis, scape sparsely covered by setulae, with 1 short dorsal seta and 1 long, ventral seta about middle; pedicel oval with posterior fringe of setae. Postpedicel with basal half rectangular, inner ventral margin yellowish; apical half strongly differentiated from base, $1.3 \times$ longer than base; tapered to short two-component arista-like stylus, shorter than basal half of postpedicel; length of first segment of stylus subequal to width; apex of arista concolorous with postpedicel. Base of labrum lacking dorsal process; palpus pale, short and slender, $0.16 \times$ length of labrum, with several long, pale setae.

Thorax reddish-brown; mesonotum with faint, dark, median stripe, broader on prescutellar depression. Acrostichals with anterior pair erect, followed by uniserial row of minute acrostichal setulae to prescutellar depression directed posteriorly; 5 dc, slender and fine, increasing in length posteriorly, prescutellar strong; 1 pprn; 1 presut spal; 2 stout npl; 1 psut spal; 1 pal; 2 sclt, with outer setula. Antepnotum with pair of setae; laterotergite bare.

Wing (length 5–5.4 mm) infuscate; margin lacking posterior incision and appendage, venation unmodified. Pterostigma at apex of cell r_1 , faint, slender; single short costal bristle; costal margin with unmodified setulae. R_{4+5} broadly forked; auxiliary cross-vein from R_4 to R_{2+3} ; cell d short, rectangular; medial fork basal to radial fork by slightly less than half length of R_4 . Halter with pale knob.

Legs yellow, slender, lacking bristles and processes. Tip of hind femora and tibia not darkened, or

at least darkening confined to extreme tip; apical 2 tarsomeres of all legs darkened. Fore tibia with small anteroapical comb. Posterior surface of hind tibia clothed in long, fine pale setulae; apex of hind tibia slightly dilated, with posteroapical comb.

Abdomen dark reddish-brown, somewhat arched; coarsely punctate except hind margins of each segment, with pale setula arising from each puncture, lacking stout setae. Tergum 7 thinly sclerotized, lacking punctations, retracted within segment 6; tergum 8 rectangular, with broad median notch on posterior margin. Terminalia (Fig. 10): hypandrium with sharply pointed posterior process; dorsal surface lacking rudder-shaped process; postgonite articulated, with sculptured posterior margin. Phallus short, surrounded by postgonites. Epandrium linear, lacking narrow sclerotized bridge ventral to cercus. Surstylus broad, gradually tapered; posterior margin lined with stout, blunt, spine-like setae. Posterior margin of cercus sclerotized, apex broadly rounded.

Description: Female. Similar to male except as follows: abdomen broader. Tergum 7 lacking fringe of setae. Terminalia (Fig. 11): tergum 8 widely divided into pair of sclerites, posterior margin with long setae; anterior margin with pair of broad plate-like dorsolateral apodemes. Sternum 9 present as a broad internal, U-shaped sclerite. Tergum 10 divided medially, each half bearing dense cluster of somewhat stout, pale setae, stouter and darker on posterior margin, appearing to form distinct row at lower magnification. Cercus short, bearing many short stout, apical setae similar to those of tergum 10. Spermatheca oval, longer than wide, not flattened and lacking neck.

Distribution. This species and nearly all other ceratomerines from southern South America are confined to the Subantarctic subregion, primarily situated in the Valdivian forest province (*sensu* MORRONE 2006). This region is dominated by temperate broad-leaved mixed forests and hygrophilous vegetation.

3.6. *Ceratomerus deansi* Plant

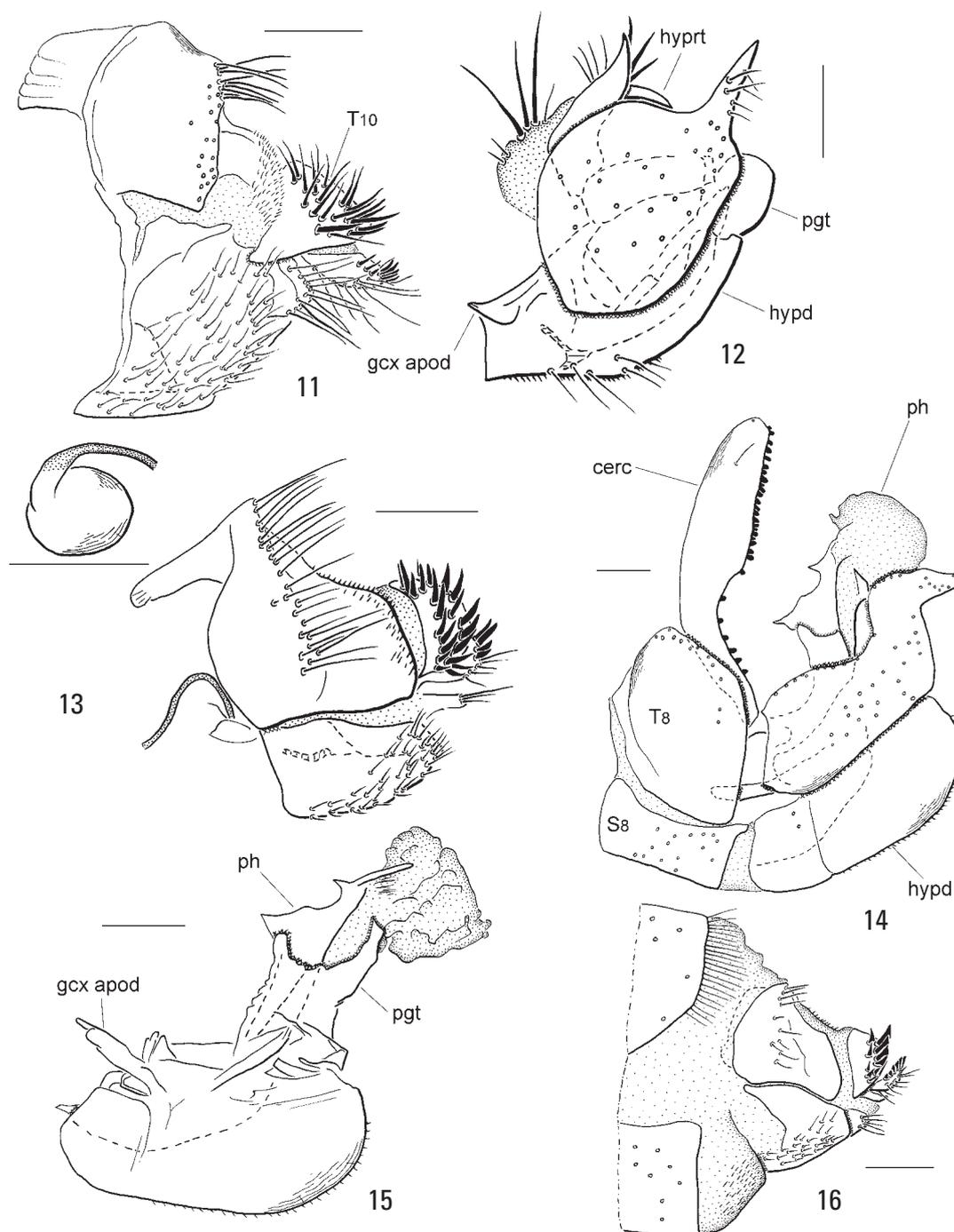
Figs. 12, 13

Ceratomerus deansi Plant, 1995: 123.

Ceratomerus paradoxus Collin *nec* Philippi, 1933: 317. Misidentification.

Material. Holotype ♂, 'CHILE: Alerce NP | Laguna Fria | y.pan tp. rainfor. | 250m; 17.i.1986 | N.A. Deans'; '*Ceratomerus deansi* | HOLOTYPE ♂ | sp.n. Plant 1995', 'BMNH (E) | 1995-230', 'HOLOTYPE | Ceratomerus | deansi Plant [red label]' (BMNH). – Paratype 1♀, same data as holotype (BMNH).

Additional material examined. **ARGENTINA: Neuquén:** 1♀, L. Currhue, Pk. Lanin, 8.xii.1976, Araucarian for. (USNM).



Figs. 11–16. Terminalia of *Ceratomerus*, lateral view. **11:** *C. connexus*, female. **12:** *C. deansi*, male. **13:** *C. deansi*, female. **14:** *C. hibbsi*, male. **15:** *C. hibbsi*, hypandrium and phallus. **16:** *C. hibbsi*, female. Abbreviations: cerc – cercus, epand – epandrium, gcx apod – gonocoxal apodeme, hypd – hypandrium, hyprt – hypoproct, ph – phallus, pgt – postgonite, S – sternum, T – tergum. (scale bar: 0.1 mm)

CHILE: Atacama: 1♂, 2♀♀, Pata de Gallina, 27°21'S 70°31'W, yfans, 10–25.i.1993 [male missing terminalia] (CNC). **Chiloe Is.:** 1♀, Castro, xii.1926 (USNM). **Malleco:** 1♂, 1♀, Region IX, PN Nahuelbuta, 37°49'42"S 73°00'39"W, 1138 m, 8–10.ii.2005, yfans, meadow & along stream, UCR AToL C05-002. **Osorno:** 1♀, Puyehue NP, ca Anticura, 250 m, *Nothofagus*, ii.1988 (CNC). **Valdivia:** 1♀, Las Trancas, 30 kmW La Union, 500 m, *Nothofagus*, 9.ii.1988 (CNC): 1♂, (in alc.), Oncol., ca 490 m, 39°41'59"S 73°19'11"W, 13.i.2006 (NMWC); 1♂, Cima Oncol., 490–650 m, 39°42'09"S 73°18'32"W, 10–11.i.2006 (NMWC).

Notes on synonymy. COLLIN (1933) provisionally assigned a female specimen from the USNM collection to *C. paradoxus*, but it is conspecific with *C. deansi* as suggested by PLANT (1995).

Recognition. This species is distinguished by four strong dorsocentral bristles, with the front bristle out of line with the others bristles, two notopleural bristles, and male legs lacking extreme modifications.

Re-description: Male. Head dark brown, dull; face narrow, parallel-sided, less than width of antennal sockets; face white, lacking setulae; ocellar triangle with pair of divergent bristles, inserted anterior to posterior ocelli; pair of postocellar bristles, slender, one-half length of ocellars; 2–3 vertical bristles, shorter than ocellar bristle; postocular bristles erect, shorter than postocellars. Antenna with length of scape $0.33 \times$ longer than height of eye, with 2 long dorsal setae near mid-length, and 1 long ventral seta; pedicel globular, with setae confined to apical fringe. Postpedicel long, clothed in short, dense pruinescence, length $>1.5 \times$ longer than scape, or $0.66 \times$ length of labrum; basal portion rectangular; apical portion ca. $1.5 \times$ longer than base, gradually tapered; two-segmented stylus short, $0.2 \times$ length of postpedicel; apex of stylus concolorous with remaining segments. Base of labrum lacking dorsal process; proboscis long, shorter than fore femur; palpus yellow, slender, $0.2 \times$ length of labrum, with several dark setae; prementum with short setae only.

Thorax brown, dull, except pale antepnotum, postpronotal lobe, anterior portions of notopleural depression and postalar ridge; pleura and lower half of laterotergite yellow, mediotergite brown. Acrostichals biserial, ending at prescutellar depression, directed posteriorly, with long erect anterior pair; 4 dc, increasing in length posteriorly, with posterior bristles long and stout and setae interspersed; first dc incurved and offset from line of others; 1 pprn; 1 presut spal; 1 stout and 1–2 slender lower npl; 2 psut spal; 1 pal; 2 sclt with several pairs of marginal setulae; additional long setulae interspersed among dc and postpronotal lobe. Antepnotum with pair of stout setae.

Wing (length 3–3.8 mm) infusate, membrane with dense microtrichia; pterostigma dark, slender proximally, at apex of cell r_1 ; costal bristle very long, extending nearly to branching of Rs; costal margin with unmodified setulae; posterior margin lacking incision; posterior setal margin complete, setae on wing stem undifferentiated. R_1 reaching costa before middle of wing; R_{2+3} straight, arched smoothly to C; medial fork basal to radial fork; cell d rectangular, slender; auxiliary cross-vein between R_{2+3} and R_4 lacking. Halter with base of shaft pale and knob dark.

Legs with coxae and inner ventral surface of femora pale; apex of hind femur dark; remaining segments dark. Fore coxa slightly shorter than mid and hind coxae combined; apex with 3–4 dark, somewhat stout, inner apical setae. Fore femur with av row of long, slender setae, less defined basally, longer than width of femur, setae at mid-length ca. $2 \times$ width of femur; 1 short, preapical dorsal bristle on apical fourth and 1 dorsal bristle near mid-length. Fore tibia slightly sinuous, shorter than femur; apex with anteroapical comb, swollen laterally; 5–6 stout, erect anterior se-

tae near mid-length; 1 erect, ventral bristle at apical third; 1 short, preapical dorsal bristle. First tarsomere $0.8 \times$ length of fore tibia, with erect ventral setae; all tarsomeres slender. Mid coxa lacking modified seta. Mid femur slightly swollen with av row of setae, less defined basally, longer than base of femur; apical half with pv row of setae, with longest apically. Mid tibia slightly curved near mid-length with 1 long, erect seta just distal to mid-length; ventral margin with several rows of erect fine setae; bristles lacking. First tarsomere shorter than remaining 4 tarsomeres, with 1 long, erect, ventral seta just distal to mid-length. Hind coxa with long pv seta. Hind femur more swollen than other femora, basal third with fringe of erect ad setae; 1 anterior and 1 dorsal preapical bristle. Hind tibia with 3 widely spaced ad bristles and 2 dorsal bristles on apical half; posterior face lacking mat of erect setulae; apex partially dilated, bearing posteroapical comb. Hind tarsomeres longer than tibia; first tarsomere with 1 long erect, ventral seta near base and 1 long, erect posterior seta on basal half.

Abdominal sclerites dark; posteromarginal setae one-half length of sclerite; sterna and terga lacking modified setae and ridges; tergum 7 thinly sclerotized on posterior half, posteromarginal setae confined to lateral margin; sternum 7 subequal in length to preceding sternum, anterolateral margin not produced; tergum 8 U-shaped, $0.5 \times$ length of sternum. Terminalia (Fig. 12): hypandrium convex, truncate apically; gonocoxal apodemes slender, projecting; postgonites divergent, arising from near base of phallus, spatulate apically; phallus arched anteriorly, with narrow, tubular apex. Epandrial lobes round lacking processes; broad bacilliform sclerites present; subepandrial sclerite lacking lobes. Surstylus straight, slender, apex truncate; posterior margin with fringe of short setae. Cercus short, stout, apex sclerotized and pointed; inner apical margin with stout setae; posterior face (hypoproct) with pair of heavily sclerotized, short sickle-shaped processes; inner base of cercus with several setae.

Re-description: Female. Similar to male except as follows: antenna with apical portion of postpedicel slightly longer than basal portion; occasionally dc setulae strongly developed similar to bristles; lacking modified setae on fore femur and fore and midlegs; mid femur with 1 dorsal preapical bristle and 1 pd bristle on apical third. Mid tibia with 2 pairs of ad and pd bristles, with ring of several apical bristles. Apical abdominal segments retracted into segment 7; tergum 7 with posterior fringe of golden setulae; lateral margin of sternum 7 straight. Terminalia (Fig. 13): posterior two-thirds of tergum 8 membranous, with fringe of long setae along lateral margin; pair of small, flat lateral sclerites extend into segment 7 from anterior margin of tergum 8; sternum 8 with ventral setulae;

posterior margin invaginated. Tergum 10 split medially into rectangular sclerites, bearing dense, spine-like setae. Cercus bearing row of similar setae; lateral margin with long setae. Spermathecal receptacle spherical, with broad, short neck.

Distribution. See general notes under *C. connexus*. This species also occurs in the Atacama Region of Chile, which is quite far north from the Subantarctic Subregion of southern South America (Fig. 50).

3.7. *Ceratomerus hibbsi* sp.n.

Figs. 14–16, 34

Material. Holotype ♂, 'ECUADOR: Napo | Oyocachi, 3000m | 0°22'S 78°08'W | 30.iii.–15.iv.1996 | P.J. Hibbs, FIT', 'HOLOTYPE | *Ceratomerus/ hibbsi* | Sinclair [red label]' (CNC). – Paratypes, ECUADOR: 28 ♂♂, 5 ♀♀, same data as holotype, 8.ii.–16.v.1996 (CNC). Selected paratypes also deposited in USNM and BMNH.

Recognition. This species is distinguished by the mostly shiny scutum with pruinescence clothing the width of the prescutellar depression, male terminalia arched anteriorly and the male cercus extending beyond tip of epandrium.

Description: Male. Head shiny, dark reddish-brown with very sparse pruinescence; face with pale pruinescence, lacking setulae; ocellar triangle with pair of divergent ocellar bristles, inserted between posterior ocelli; 1 pair of postocellar bristles subequal in length to ocellars; 2 pairs of subequal vertical bristles; postocular bristles erect, short and slender. Antenna short, with scape $>0.5 \times$ length of labrum, pedicel oval with posterior fringe of long setae; scape with 1 long ventral seta and several dorsal setae. Postpedicel with pale ventrobasal margin, covered by long, dense, pale pruinescence, triangular, strongly tapered; two-segmented arista-like stylus slightly longer than postpedicel; length of first segment of stylus $2 \times$ width; apical half of second segment of stylus paler than base at certain angles, bearing seta-like apex. Base of labrum lacking dorsal process; palpus dark brown, short and slender, $0.25 \times$ length of labrum, with several long, pale setae; prementum with short setae only.

Mesonotum shiny, dark reddish-brown; lateral margin of notopleuron, prescutellar depression, scutellum, pleura, and postnotum clothed in silvery pruinescence, especially dense on upper half of katapisternum. Acrostichals absent; uniserial row of slender, short dc, prescutellar dc slender and longer; 0 pprn; 0 presut spal; 1 strong npl; 0 psut spal; 1 short pal; 2 stout sctl; scattered setulae on pprn, pal and sctl. Anteprepronotum with several pairs of setulae; latero-tergite bare.

Wing (length 5.6–5.8 mm) (Fig. 34) margin lacking posterior incision and appendage, venation unmodified. Pterostigma absent, wing infusate; 1 short costal bristle; costal margin with unmodified setulae, increasing in length along posterior margin. R_{4+5} and M_{1+2} broadly forked; cell d slender, short, rectangular; medial fork basal to radial fork by half length of R_4 . Halter with white knob.

Legs with coxae, trochanters, basal third of femora, basal half of fore and mid tibiae, base of hind tibia and all first tarsomeres yellow, hind first tarsomere especially pale; remainder of legs brown to dark reddish-brown; sometimes tibiae more pale, especially ventrally; bristles lacking. Fore tibia with small anteroapical comb. Mid femur with biserial row of short, stout setae beneath. Mid tibia with row of short, stout setae beneath. Basal third of hind femur narrowed, apical two-thirds slightly sinuous; av margin with row of long setae nearly as long as width of femur. Posterior surface of hind tibia clothed in long, fine pale setulae; apex not expanded, armed with posteroapical comb. Fifth tarsomere somewhat flattened on all legs.

Abdominal sclerites lightly sclerotized, pale brown, narrow; vesture short and slender; sclerites of segments 7–8 shiny, sclerites of segment 8 heavily sclerotized; tergum 7 with broad U-shaped membranous cleft on posterior half; sternum 7 longer than preceding segment, posterolateral corner prolonged and articulated with sternum 8; tergum 8 inflated, directed vertically, anterior margin deeply cleft medially. Terminalia (Figs. 14, 15): heavily sclerotized, shiny dark brown; hypandrium inflated posteriorly, with wide collar along anterior margin; postgonite enclosing base of phallus in dark membranous sheath, anterior margin with pair of narrow sclerites. Phallus with wide, membranous, apical sac arising subapically; anterior margin with median keel; apex in form of arrowhead. Epandrium slender, with apical arched lobes. Surstylus lacking. Cercus held vertically, thickly sclerotized, large flap-like, divergent, longer than epandrium; inner margin armed with rows of stout, blunt, knob-like setae.

Description: Female. Similar to male (including legs) except as follows: sclerites largely membranous except for segments 7 and 8; apical segments retracted into segment 7; tergum 7 with posterior fringe of golden setulae; lateral margin of sternum 7 straight. Terminalia (Fig. 16): posteromedial half of tergum 8 membranous, with sparse fringe of short setae along lateral margin; 2 pairs of flat, lateral sclerites extend into segment 7 from anterior margin of tergum 8; posterior half with internal, medial sclerite. Sternum 8 with ventral setulae; posterior margin invaginated, forming well sclerotized, internal plate. Tergum 10 split medially into rectangular sclerites, bearing double row of

spine-like setae. Cercus bearing row of similar setae; apex with additional spine-like setae; short, slender marginal setae. Spermathecal receptacle spherical, with wide opening for duct.

Distribution. This species is known only from the Ecuadorian province of Napo, above 3000 m.

Etymology. The specific name is a patronym in honour of P.J. Hibbs, the collector of the entire type series.

3.8. *Ceratomerus irramus* sp.n.

Figs. 17, 18

Material. Holotype ♂, 'CHILE : R.X Puyuhue | Anticura, Sendero | Repucura, 40°39'53"S 72°10'02"W | 447 m, 17–18.ii.2005, YPT | *Nothofagus/ Chusquea* for. | UCR AToL C05-022', 'HOLOTYPE | *Ceratomerus | irramus* | Sinclair [red label]' (CNC). – Paratypes. **CHILE: Osorno:** 2♂♂, R.X. PN Puyuhue, Antillanca, trail Lago Paraiso, 40°46'34"S 72°15'47"W, 753 m, 18.ii.2005, SS, *Nothofagus* for., UCR AToL C05-024' (CNC); 2♀♀, same data as holotype (CNC); 1♀, Puyehue NP, 250 m, Anticura, ii.1988, *Nothofagus* for., L. Masner (CNC).

Recognition. Distinguished from all other species of the genus *Ceratomerus* by its small size and unbranched R_{4+5} and differs from *Icasma* by presence of long thoracic bristles, postpedicel long and tapered and pterostigma present (SINCLAIR 1997).

Description: Male. Head dark brown, face with pale pruinescence, lacking setulae; ocellar triangle with pair of divergent bristles, inserted between posterior ocelli; postocellar bristles reduced, slender, $0.33 \times$ length of ocellar bristle; 2 vertical bristles, subequal or longer than length of ocellars; postocular bristles erect, very short and slender. Antenna short, with scape $>0.5 \times$ length of labrum, pedicel oval with posterior fringe of long setae; scape with 1 long ventral seta and numerous dorsal setae. Postpedicel covered by long, dense pale pruinescence; basal half rectangular, apical half very strongly tapered; two-segmented arista-like stylus longer than basal half of postpedicel; first segment of stylus $2 \times$ longer than wide; apex of stylus concolorous with postpedicel. Base of labrum lacking dorsal process; palpus pale, short and slender, $0.14 \times$ length of labrum, with several long, pale setae.

Mesonotum, pleura, and postnotum, light brown; clothed in thin pruinescence. Acrostichals absent; 2 dc, several setulae interspersed; 1 pprn; 0 presut spal; 2 strong npl; 0 psut spal; 1 slender pal; 2 sctl; scattered setulae on pprn, dc and sctl. Anteppronotum with 1 pair of short setulae; laterotergite bare.

Wing (length nearly 2 mm): margin lacking posterior incision and appendage, venation unmodified. Pterostigma present, remainder of wing faintly infusate; single long costal bristle; costal margin with unmodified setulae, increasing in length along posterior incision. R_{4+5} unbranched; cell d slender, short, rectangular; medial fork with long petiole, longer than M_2 . Halter with white knob.

Legs with coxae and femora pale, remaining leg segments increasingly darker apically. Femora with dense white pile beneath. Fore and mid femora with biserial row of short, stout ventral setae. Fore and mid tibiae with biserial row of short, dark ventral setae. Basal two-thirds of hind femur with av row of short stout setae, $0.33 \times$ width of femur.

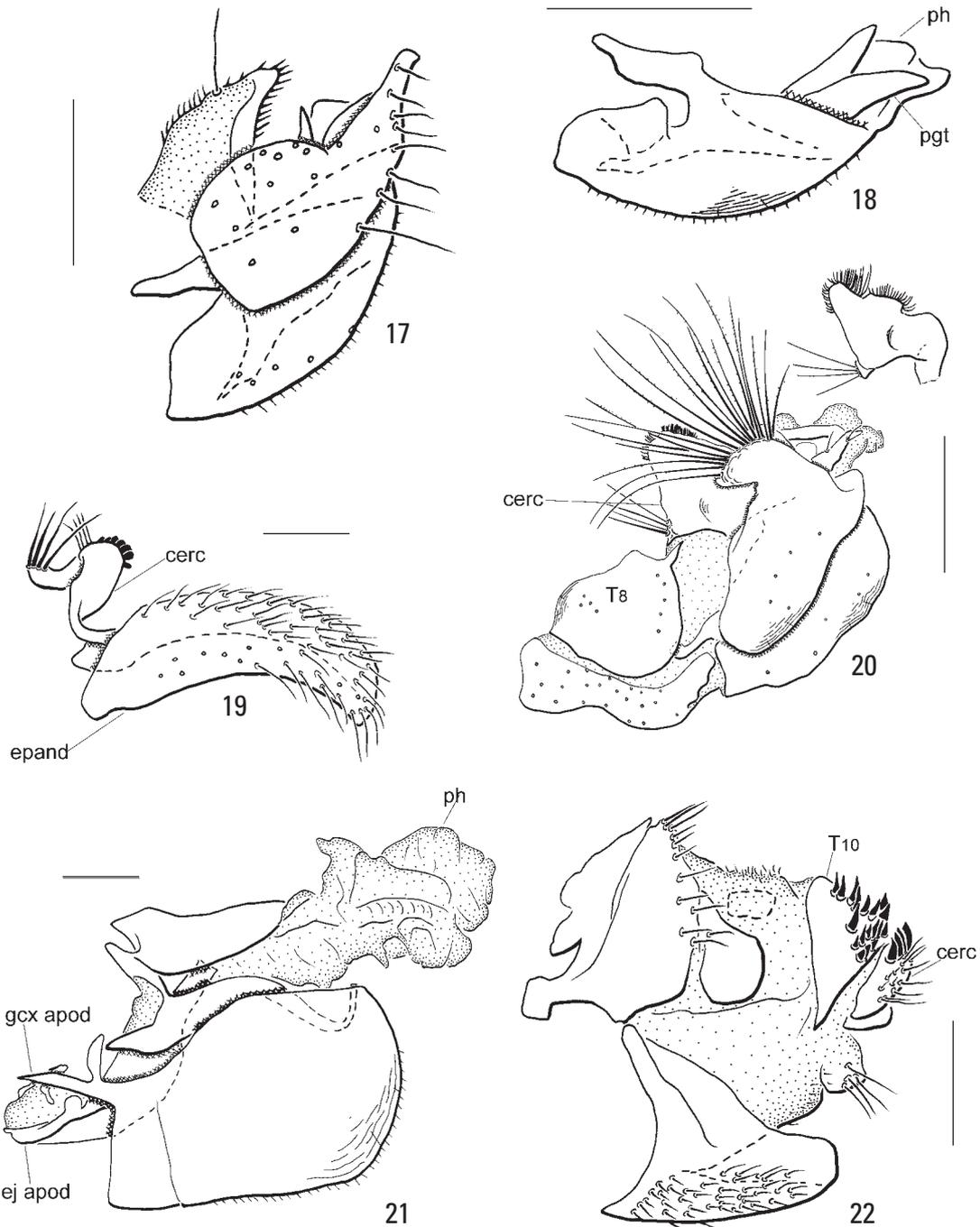
Abdominal terga dark brown, sterna paler; posterior margin of terga 1–6 with outstanding setae; tergum 7 weakly sclerotized on less than posterior half, lacking long posterior setae; sternum 7 not longer than preceding segment, posterodorsal corner not produced and articulated with sternum 8; tergum 8 slender band, ca. $0.16 \times$ length of sternum. Terminalia (Figs. 17, 18): hypandrium lacking posterior flap-like process; arising subapically, short non-articulated pair of slender, triangular postgonites flanking phallus. Phallus with apical pair of arched posterior processes and stout anterior triangular process. Epandrium lacking narrow sclerotized bridge ventral to cercus; posterolateral margin with long setae. Surstylus slender, tapered, with hooked apex. Cercus sclerotized along posterior and posterolateral surfaces, short, apex rounded, bearing fine setulae.

Description: Female. Similar to male except as follows: hind femur lacking row of anteroventral setae. Abdomen with apical segments retracted into segment 7; tergum 7 with posterior fringe of golden setulae; lateral margin of sternum 7 straight. Terminalia (not dissected): posteromedial region of tergum 8 membranous, with fringe of long, lateral setae. Tergum 10 split medially into rectangular sclerites, bearing posterior row of spine-like setae. Cercus bearing row of similar setae.

Distribution. See general notes under *C. connexus*.

Remarks. *Ceratomerus irramus* is characterized by an unbranched radial vein, unique among the Neotropical ceratomerine species (also unbranched in *Icasma* and *Glyphidopeza longicornis* Sinclair).

Etymology. The specific name is from the Latin *ramus* (branch) and the prefix 'ir-' (not, without), referring to the unbranched R_{4+5} vein.



Figs. 17–22. Terminalia of *Ceratomerus*, lateral view. **17:** *C. irramus*, male. **18:** *C. irramus*, hypandrium and phallus. **19:** *C. masneri*, epandrium and cercus, male. **20:** *C. longicornis*, male, inner view of cercus. **21:** *C. masneri*, hypandrium and phallus. **22:** *C. masneri*, female. Abbreviations: cerc – cercus, ej apod – ejaculatory apodeme, epand – epandrium, gcx apod – gonocoxal apodeme, ph – phallus, pgt – postgonite, T – tergum. (scale bar: 0.1 mm)

3.9. *Ceratomerus longicornis* sp.n.

Fig. 20

Material. Holotype ♂, 'ECUADOR: Pichincha | 20.5 km E Pifo, 3700 m | 26–28 Sep 1990 | O.S. Flint, Jr.', 'HOLOTYPE | *Ceratomerus* | *longicornis* | Sinclair [red label]' (USNM). – Paratypes **ECUADOR:** 1♀, Napo, 3800 m, 0°17'S 78°10'W, elfin for., 1.iii.1979, W.R.N. Mason (CNC); 1♀, Napo, 0°20'S 78°10'W, 3950 m, 4–7.iii.1976, G.&M. Wood (CNC).

Recognition. This large brown species is unlike any other species known from Ecuador with its elongate pedicel, nearly two-thirds the length of the scape.

Description: Male. Head dark brown, including face, lacking facial setulae; ocellar triangle with pair of widely spaced, divergent bristles, inserted anteriorly to posterior ocelli; postocellar bristles widely spaced, 0.33–0.5 × length of ocellars; 2 pairs of long verti-

cal bristles, outer 2 pairs extremely long, median pair short; postocular bristles long, overlapping more than half width of eye. Antenna long, with scape subequal to height of head; scape clothed in many short, dorsal setae and 1 long ventral seta, with scattered setulae; pedicel lengthened to $0.66 \times$ length of scape with setae limited to apical fringe of setae; scape covered by short setae. Postpedicel covered by dense pruinescence, shorter than scape; basal half rectangular; apical half strongly differentiated from base, tapered to short two-segmented arista-like stylus, subequal to half length of postpedicel; length of first segment of stylus not longer than wide; apex of stylus concolorous with postpedicel. Base of labrum lacking dorsal process; palpus long, brown, $0.2 \times$ length of labrum, with several long, dark setae.

Mesonotum, postnotum and pleura dark brown. Acrostichals lacking; 4 dc, with setulae interspersed; 1 pprn, with setulae; 1 presut spal; 2 npl, upper long; 1 psut spal; 1 pal; 2 sctl. Anteprepronotum with 2 pairs of short setulae; laterotergite bare; proepisternum with patch of dark setae.

Wing (length ca. 4.5 mm) margin lacking posterior incision and appendage, venation unmodified. Wing darkly infuscate; pterostigma not differentiated; single long costal bristle; costal margin with unmodified setulae. R_{4+5} acutely forked; cell d rectangular; medial fork very long, basal to radial fork by slightly more than half length of R_4 . Halter dark brown.

Legs uniformly dark brown; lacking bristles; fifth tarsomere dorsoventrally flattened. Fore coxa $<0.5 \times$ length of mid coxa, gradually tapering apically lacking modified setae. Fore trochanter lacked setae. Fore femur swollen at mid-length with dense av cluster of long setae, longer than width of femur; pv row of dark, stout setae, with 4 setae opposite cluster, longer than width of femur; basal third with long dorsal setae subequal to width of femur. Fore tibia slender, straight, shorter than femur; apex not dilated. First tarsomere equal to length of remaining tarsomeres. Mid coxa with apical setae only. Mid trochanter unmodified. Mid femur constricted near middle, with apical third distinctly bent; ventral surface with long, stout, basal setae and short swelling basal to constriction, bearing cluster of long stout setae; apical half with long ad setae. Mid tibia strongly arched about corresponding lobe of femur, with dense pv setae; apex flattened with long, shallow excavation, bearing long lateral setae. First tarsomere slightly shorter than remaining tarsomeres. Hind femur curved (bowed) and distinctly laterally flattened, with clusters of short, ad setae. Hind tibia slightly longer than femur, apex dilated, bearing posteroapical comb. Hind tarsomeres longer than tibia; first tarsomere with single short, erect, ventral seta near base.

Abdominal terga and sterna dark brown, with sparse setae; lacking setae along posterior margin of terga. Tergum 7 weakly sclerotized medially with terminalia arched onto tergum; lateral margin with row of long setae; sternum 7 longer than preceding segment, posterodorsal corner produced and articulated with sternum 8; tergum 8 broad, concave, heavily sclerotized, not narrow medially; sternum 8 with sinuous surface. Terminalia (not examined internally) (Fig. 20): epandrium narrow, with anterodorsal crown of long setae, either bead-like or with minute lateral projections. Cercus broad, with apical and median dense clusters of stout setae.

Description: Female. Similar to male except lacking leg modifications; fifth tarsomere slender; proepisternum bare; posterior margin of tergum 7 with fringe of golden setulae. Terminalia (not dissected): tergum 10 divided medially, bearing posterior row of spine-like setae; cercus with apical row of similar shaped setae.

Distribution. This species is known only from high altitude regions of Ecuador, 3700 m to nearly 4000 m. This region is dominated by elfin forest, a region of stunted trees and shrubs.

Remarks. This species is assigned to the *C. ordinatus* species-group of Australia (SINCLAIR 2003a), along with undescribed species 12 from New Zealand (Fig. 49) on the basis of the following characters: pedicel greatly lengthened, postocular setae very long, overlapping eye, ocellar bristles inserted anteriorly to posterior ocellus, legs lacking bristles, pterostigma absent.

Etymology. The species name is an adjective derived from the Latin *longus* (long) and *cornu* (horn), in reference to the long first antennal segment.

3.10. *Ceratomerus masneri* sp.n.

Figs. 1, 19, 21, 22, 35

Material. Holotype ♂, 'ECUADOR Napo | above Papallacata | Feb. 16–21 [19]83 3200m | L.Masner pan tr.', 'HOLOTYPE | *Ceratomerus* | *masneri* | Sinclair [red label]' (CNC). – Paratypes **ECUADOR**: 5♂♂, 2♀♀, same data as holotype (CNC); 24♂♂, 12♀♀, Napo, Oyocachi, 3000 m, 0°22'S 78°08'W, FIT, 18.ii.–16.v.1996, P.J. Hibbs (CNC); 1♂, Pichincha, Quito, 27 km WNW, Campamiento, Pichan (above Nono), 3350 m, 0°7'31"S 78°33'56"W, 24.x.1999, S.A. Marshall, sweeping vegetation (DEBG). Selected paratypes also deposited in USNM and BMNH.

Recognition. This species is distinguished by the pruinose scutum, horizontally oriented male terminalia and very short male cercus.

Description: Male. Head dark reddish-brown with light pruinescence; face with pale pruinescence, lacking setulae; ocellar triangle with pair of divergent ocellar bristles, inserted between posterior ocelli; postocellar bristles very reduced, slender; 2 pairs of short vertical bristles, $<0.5 \times$ length of ocellar bristles; postocular bristles erect, short and slender. Antenna short, with scape $>0.5 \times$ length of labrum, pedicel oval with posterior fringe of long setae; scape with 1 long ventral seta and several dorsal setae. Postpedicel covered by long, dense pale pruinescence; triangular, strongly tapered, paler on inner ventral face; two-segmented arista-like stylus slightly shorter than postpedicel; length of first segment of stylus subequal to width; apex of arista-like stylus concolorous with postpedicel, bearing seta-like apex. Base of labrum lacking dorsal process; palpus brown, short and slender, $0.2 \times$ length of labrum, with several long, pale setae; prementum with short setae only.

Mesonotum, pleura, and postnotum dark reddish-brown; clothed in pruinescence. Acrostichals absent; uniserial row of slender short dc, longer posteriorly; 0 pprn; 0 presut spal; 1 strong npl; 1 slender psut spal; 1 slender pal; 1 pair stout sctl and outer more slender shorter pair; scattered setulae on pprn, presut spal and sctl. Anteprepronotum with several pairs of setulae; laterotergite bare.

Wing (length 5–5.4 mm) margin lacking posterior incision and appendage, venation unmodified. Pterostigma absent, remainder of wing faintly infusate; single short, stout costal bristle; costal margin with unmodified setulae, increasing in length along posterior margin. R_{4+5} broadly forked; cell d slender, short, rectangular; medial fork basal to radial fork by less than half length of R_4 . Halter with white knob.

Legs with coxae, trochanters, basal third of femora and all first tarsomeres yellow; remainder of legs brown to dark reddish-brown; bristles lacking. Fore tibia with small anteroapical comb. Mid femur with biserial row of short, stout setae beneath. Mid tibia with row of short, stout setae beneath. Posterior surface of hind tibia clothed in long, fine pale setulae; apex not expanded, armed with posteroapical comb. Fifth tarsomere somewhat flattened on all legs.

Abdominal sclerites more lightly sclerotized than thorax, narrow; vesture short and slender; tergum 7 with broad U-shaped membranous cleft on posterior half; sternum 7 longer than preceding segment; postero-dorsal corner produced and articulated with sternum 8; sclerites of segment 8 stout; tergum 8 laterally inflated, lying horizontally, posterior margin cleft medially encircling cerci. Terminalia (Figs. 19, 21): hypandrium inflated posteriorly, with wide collar along anterior margin; postgonite horizontal, fused to opposing lobe medially, forming phallic brace, fused to apical shield of phallus. Phallus with wide, membranous apical sac

arising from dorsal shield; base with long keeled apodeme and apical sperm pump. Epandrium slender, parallel-sided, arched lobes; clothed with fine setae; inner apical margin lined by bacilliform sclerite. Surstylus lacking. Cercus thickly sclerotized, forming fist-like lobe, armed with series of stout, blunt, knob-like setae; keel of dorsal shield of phallus articulating between cerci.

Description: Female. Similar to male (including legs) except as follows: apical segments retracted into segment 7; tergum 7 with posterior fringe of golden setulae; lateral margin of sternum 7 straight. Terminalia (Fig. 22): posteromedial three-quarters of tergum 8 membranous, with sparse fringe of short setae along lateral margin; 2 pairs of small, flat lateral sclerites extend into segment 7 from anterior margin of tergum 8; posterior half with internal, medial sclerite. Sternum 8 with ventral setulae; posterior margin invaginated, forming well sclerotized, internal plate. Tergum 10 split medially into rectangular sclerites, bearing double row of spine-like setae. Cercus bearing row of similar setae; apex with additional spine-like setae; short, slender marginal setae. Spermathecal receptacle spherical, with wide opening for duct.

Distribution. This species is known only from the Ecuadorian province of Napo, above 3000 m.

Etymology. The specific name is a patronym in honour of L. Masner, the collector of the holotype, and who has contributed many rare and unusual Diptera through his inventive collecting techniques.

3.11. *Ceratomerus mediocris* Collin

Figs. 2, 23, 24, 26, 36, 39–43

Ceratomerus mediocris Collin, 1933: 318.

C. paradoxus: CHVÁLA 1983: fig. 62 (wing).

Material. Lectotype (here designated) ♂, 'Type | ♂ [red bordered circle]', 'Casa Pangué. | 4–10.xii.1926.', 'S.Chile: | Llanquihue prov. | F.& M. Edwards. B.M.1927-63.' (BMNH). My lectotype label 'LECTOTYPE | of *Ceratomerus* | *mediocris* Collin | des. B.J. Sinclair 1994 [red label]' has been attached to this specimen. – Paralectotypes **CHILE**: Same data as lectotype (2♂♂, 6♀♀, BMNH; 2♂♂, 2♀♀, USNM); Llanquihue, Puerto Varas, 16.xii.1926, F.&M. Edwards (3♂♂, BMNH); same locality, xii.1926, R.&E. Shannon (1♂, USNM); Puerto Montt, 24.xii.1926, F.&M. Edwards (1♂, BMNH); Peulla, 12–13.xii.1926, F.&M. Edwards (3♂♂, BMNH; 1♂, 1♀, USNM); Castro, Chiloe Is., 20–22.xi.1926, F.&M. Edwards (1♂, 1♀, BMNH); same locality, xii.1926, R.&E. Shannon (1♂, USNM); Ancud, Chiloe Is., 17–19.xii.1926, F.&M. Edwards (1♀, BMNH). My paralectotype labels have additionally been attached to these specimens.

Additional material examined. **ARGENTINA: Rio Negro:** 2♂♂, 1♀, Rio Negro 8: Lago Nahuel Haupi, Puerto Blest, 770

m, 1–2.iii.1979 (ZMUC). **Neuquén:** 3♂♂, 1♀, P.N. Lanin Pucará, 8,15.i.1972, 11.iii.–22.iv.1973 (MNHN). **CHILE:** **Arauco:** 5♂♂, 4♀♀, Cord. Nahuelbuta, 41 km E Cañete, 1070 m, 8.ii.1998 (USNM); 4♂♂ (in alc.), Villarrica, R. Pedrogoso, 1134 m, 39°09'58"S 71°59'07"W, 9.i.2006 (NMWC). **Aisén:** 3♂♂, Puerto Cisnes, 1–28.ii.1961 (CNC). **Caramauida:** 1♂, 1♀, Arauco, 25–31.xii.1953 (CNC). **Cautín:** 6♂♂, 1♀, Conguillio NP, 1150 m, ii.1988 (CNC); 2♂♂, 5♀♀, Los Coigues, L. Villarrica, 16–31.xii.1964, 16–25.i.1965 (CNC); 4♂♂ (in alc.), Villarrica, R. Pedrogoso, 1134 m, 39°09'58"S 71°59'07"W, 9.i.2006, A.R. Plant (NMWC). **Chiloé Is.:** 14♂♂, 11♀♀, Ahoni Alto, ii–iii.1988 (CNC); 2♂♂, Ahoni Alto, S. Chonchi, 20–23.ii.1988 (KMNH, MNHP); 1♀ (in alc.), E. Degán, 170 m, 42°10'30"S 73°35'52"W, 18.i.2006 (NMWC); 1♂, San Pedro, Piruquinz, 500 m (KMNH); 13♂♂, 5♀♀, Reserva Costera, Valdiviana, 15.i.2006, 39°59'29"S 73°34'16"W, mixed *Fitzroya*/ *Podocarp* for. (NMWC); 1♂, 3♀♀ (in alc.), ditto, 40°05'18"S 73°33'02"W (NMWC); 1♀ (in alc.), 5.4 km S Huillinco, riverbank, 42°43'08"S 73°53'50"W, 22.i.2006 (NMWC); 11♂♂, 14♀♀ (in alc.), Region X, 22.i.2006, 40°03'43"S 73°05'19"W, 80 m, Valdivian for., 0.6 km W Ruta 5 (NMWC); 2♂♂, 3♀♀ (in alc.), R Negro, 42°48'03"S 73°55'13"W, 22.i.2006 (NMWC); 12♂♂, 2♀♀, Senda Darwin, 18.i.2006, 41°53'00"S 73°40'22"W, Patagonian for., 17 m (NMWC); 4♀♀, Cord. De Piuché, 150–320 m, Los Allerzales Tk., 20–21.i.2006, 42°34'46"S 74°05'02"W, Valdivian & Patagonian for., 17 m (NMWC). **Llanquihue:** 11♂♂, 17♀♀, Carelmapu, 21.ii.–3.iii.1957 (CNC); 3♂♂, 1♀, El Chingue, N. Correntoso, i.1990 (CNC); 7♂♂, 8♀♀, 3 km NW Ensenada, 41°11'S 72°32'W, 29–30.i., 14.ii.1998 (USNM); 1♂, 12 km NW Ensenada, 41°09'S 72°35'W, 14.ii.1998 (USNM); 15♂♂, 8♀♀, Lago Chapo, 200 m, *Nothofagus*, 18.ii.1988 (CNC); 1♂, 1♀, upper R. Tracura, 1250 m, 38°49'47"S 71°24'15"W, 24.i.2006 (NMWC). **Malleco:** 1♂, 1♀, 6.5 km E Malalcahuello, 1080 m, *Nothofagus dombeyi* w/ *Chusquea*, 13–31.xii.1982 (USNM); 1♀, Termas, Tolhuca, 15–20.i.1959 (CNC); 1♂, 3♀♀, Region IX, PN Nahuelbuta [37°48'S 73°01'W], 8.ii.2005, sweep in Araucaria for. Ch-01. **Nuble:** 2♂♂, Las Trancas, 19.5 kmESE Recinto, 1250 m, *Nothofagus*, 10.xii.1982–3.i.1983 (USNM). **Osorno:** 1♂, 1♀, Aguas Calientes, Puyehue, 500 m, 2–6.i.1982 (KMNH); 4♂♂, Puyehue NP, Anticura, 250 m, *Nothofagus*, ii.1988 (CNC); 1♂, Puyehue NP, Aguas Calientes, Sendero El Pionero, Eucryphia/ Bamboo for., 16–17.xi.2000 (CNC); 1♂, PN Puyehue, Anticura, Sendero Repucura, 40°39'53"S 72°10'02"W, 447 m, 17–18.ii.2005, ypan, *Nothofagus*/ *Chusquea* for., UCR ATOLC05-022 (CNC); 10♂♂, 4♀♀, Rio Golgol, 8–11.ii.1957 (CNC); 2♀♀, Rio Negro, 8–11.ii.1957 (CNC). **Valdivia:** 3♂♂, 10♀♀, 6 km E Anticura, 430 m, 19–25.xii.1982 (CNC); 7♂♂, 2♀♀, Enco, 1000 m, 26.ii.1955 (CNC); 2♂♂, 1♀, Las Tablas, W La Union, 500 m, 6–9.ii.1988 (KMNH); 2♂♂, 3♀♀ (in alc.), Oncol, ca 490 m, 39°41'59"S 73°19'11"W, 13.i.2006 (NMWC); 2♂♂, 2♀♀ (in alc.), Cima Oncol, summit, 750 m, 39°41'38"S 73°18'51"W, 12.i.2006 (NMWC); 25♂♂, 13♀♀, Las Trancas, 30 km W La Union, 500 m, ii.1988 (CNC); 1♂, 2♀♀, Neltume, ii.1987 (KMNH); 1♀, Pucatrihue, 42°28'S 73°47'W, 12.iii.1955 (CNC); 1♀ (in alc.), Punta Curinanco, 50–160 m, 39°42'41.59"S 73°24'10.87"W, 13.i.2006 (NMWC); 2♀♀ (in alc.), Reserva Costera Valdiviana, S Chaihuin, 457 m, 40°03'42"S 73°35'18"W, 14.i.2006 (NMWC); 1♀, Rincon de Piedra, 30 m, 20 km SE Valdivia, 24–25.ii.1979 (USNM); 1♂, Rimihue, 24.ii.1955 (CNC).

Recognition. This species is distinguished by the dark, heavily sclerotized abdomen, shortened cell d, one notopleural bristle and base of postpedicel dark.

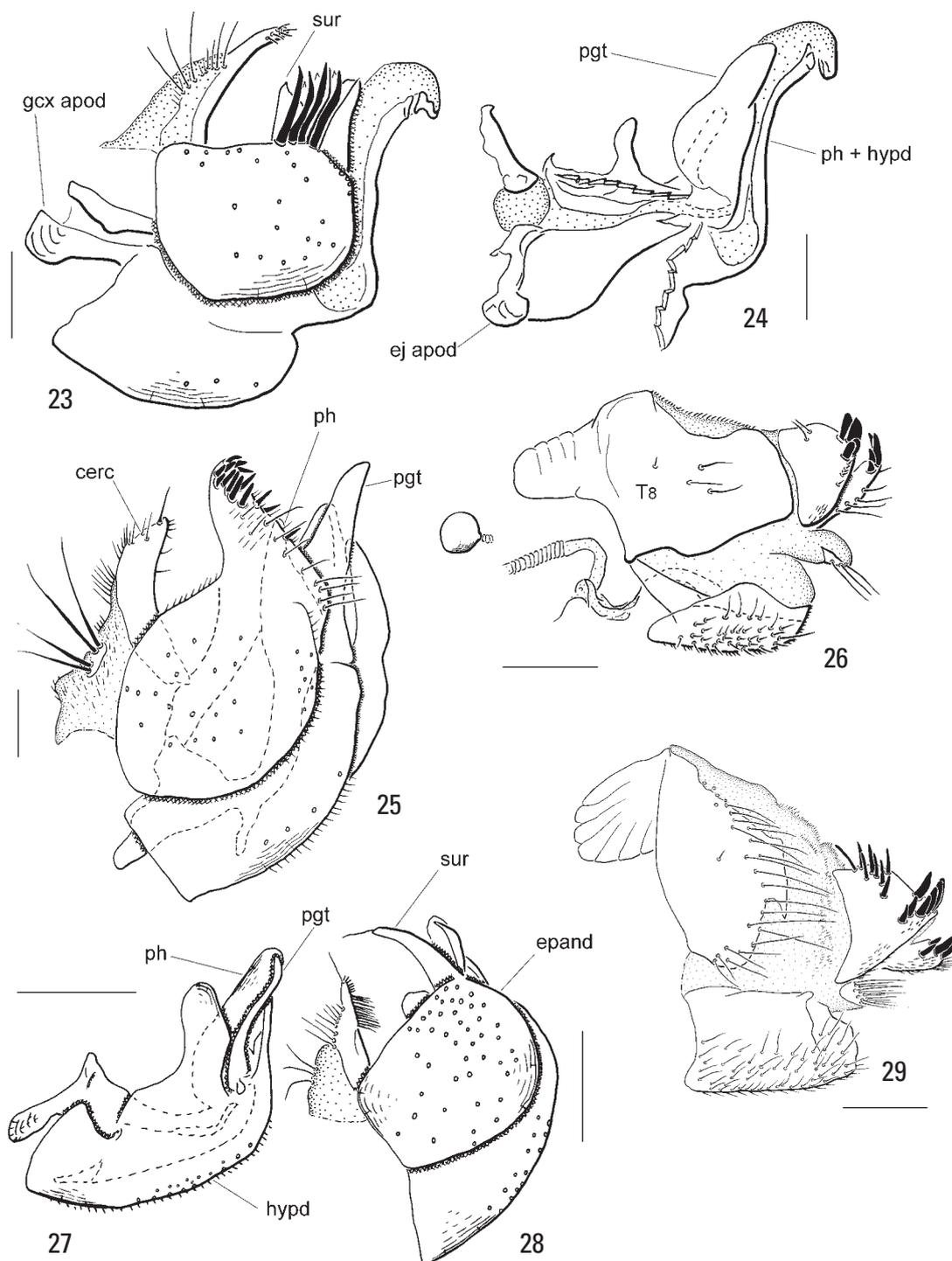
Description: Male. Head (Fig. 42) dark brown, face with pale pruinescence and lacking setulae; ocellar triangle with pair of long, divergent bristles; postocellar bristle slender, 0.5 × length of ocellars; 1 pair of long vertical bristles; postocular bristles erect, very short and slender. Antenna long, with scape <0.5 × length of labrum, pedicel oval with posterior fringe of setae; scape sparsely covered by dorsal setulae, with 1 long, ventral seta at mid-length. Postpedicel covered by long dense pruinescence, basal half rectangular, dark; apical half strongly differentiated from base, tapered to very short two-segmented arista-like stylus, slightly >0.5 × length of base of postpedicel; length of first segment of stylus equal to width; apex of stylus concolorous with postpedicel. Base of labrum lacking dorsal process; palpus pale, short and slender, 0.14 × length of labrum, with several long, pale setae.

Mesonotum and pleura tawny-yellow, often darkened along acrostichals, prescutellar depression, anepisternum, katapisternum, meron, and postnotum dark brown. Uniserial row of minute acrostichal setulae to prescutellar depression; uniserial row of minute dc, prescutellar strong; 0 pprn; 0 presut spal; 1 strong npl; 1 psut spal; 1 pal; 2 sctl, outer pair of small setulae; scattered setulae on pprn and presut spal. Antepronotum with pair of long setae and several setulae; laterotergite bare.

Wing (length 3.2–4.5 mm) (Fig. 36) margin lacking posterior incision and appendage, venation unmodified. Pterostigma absent, remainder of wing infuscate; single short costal bristle; costal margin with unmodified setulae. R₄₊₅ broadly forked; occasional specimen with auxiliary cross-vein from R₄ to R₂₊₃ (generally only on one, sometimes both wings); cell d short, rectangular; medial fork basal to radial fork by slightly less than half length of R₄. Halter with pale knob.

Legs yellow, slender, without distinct bristles and processes; bristles absent. Tips of hind femur, tibia, apical 4 tarsomeres, and apical 3 tarsomeres of fore and midlegs distinctly darkened. Apex of hind tibia dilated, with posteroapical comb; fore tibia with small, anteroapical comb. Fifth tarsomere not flattened (Fig. 43).

Abdomen dark reddish-brown, shiny, somewhat arched; coarsely punctate except hind margins of each segment, with pale setula arising from each puncture, lacking stout setae (Figs. 40, 41). Tergum 7 thinly sclerotized along posterior margin, lacking punctations, retracted within segment 6; tergum 8 rectangular, with broad median cleft. Terminalia (Figs. 23, 24): hypandrium with posterior flap-like process attached to apex of phallus; dorsal surface with rudder-shaped process; broad, paired articulated postgonites flanking phallus. Phallus sickle-shaped, with long basal rod bearing central apodeme; sperm pump with paired, rod-like apodemes. Epandrium lacking narrow sclerotized bridge ventral to cercus; long, blade-like setae at base



Figs. 23–29. Terminalia of *Ceratomerus*, lateral view. **23:** *C. mediocris*, male. **24:** *C. mediocris*, phallus and postgonite, male. **25:** *C. paraconnexus*, male. **26:** *C. mediocris*, female. **27:** *C. paradoxus*, male, hypandrium and phallus. **28:** *C. paradoxus*, male. **29:** *C. paraconnexus*, female. Abbreviations: cerc – cercus, ej – ejaculatory apodeme, epand – epandrium, gcx apod – gonocoxal apodeme, hypd – hypandrium, ph – phallus, pgt – postgonite, sur – surstylus, T – tergum. (scale bar: 0.1 mm)

of surstylus. Surstylus broad, thumb-shaped. Posterior margin of cercus sclerotized, tapering to narrow apex bearing setulae.

Re-description: Female. Similar to male except as follows: Abdomen more broad; apical segments retracted into segment 7; segment 7 reddish; tergum

7 with fringe of very short, fine setulae on posterior margin. Terminalia (Figs. 26, 39): tergum 8 widely divided by deep U-shaped membranous zone from posterior margin; 3 short, lateral setae; anterior margin with pair of lateral sclerites extending into segment 7. Tergum 10 divided medially, bearing posterior row of 4–5 stout spine-like setae, with several fine medial

setae. Cercus short, bearing 4 spine-like apical setae similar to those of tergum 10. Spermatheca receptacle small, spherical; neck very short.

Distribution. This is the most commonly collected species of Neotropical Ceratomerinae, collected in Valdivian and Patagonian forests of Chile and Argentina, including coastal *Aextoxicicon punctatum* forest (Aextoxicaceae), *Araucaria* forest (Araucariaceae), *Fitzroya cupressoides* forest (Cupressaceae), and stream side and dense or stunted forests. See general notes under *C. connexus*.

3.12. *Ceratomerus paraconnexus* sp.n.

Figs. 25, 29, 37

Material. Holotype ♂, 'CHILE: Prov. Llanquihue | 3 km NW Ensenada | 41°11'S, 72°32'W | 30 Jan 1998 | N. E. Woodley', 'HOLOTYPE | *Ceratomerus* | *paraconnexus* | Sinclair [red label]' (USNM). – Paratypes, ARGENTINA: **Rio Negro:** 1♂, Lago Nahuel Huapi, Puerto Blest, 770 m, 2.iii.1979, Mision Científica Danesa (ZMUC). **CHILE: Chiloé Is.:** 1♂, (in alc.), E of Degân, 18.i.2006, 42°10'30"S 73°35'52"W, 170 m, Valdivian for., A.R. Plant (NMWC); 1♂, 1♀, (in alc.), Cord. De Piuché, 150–320 m, Los Allerzales Tk., 20–21.i.2006, 42°34'46"S 74°05'02"W, Valdivian & Patagonian for., A.R. Plant (NMWC); 1♂, (in alc.), 22.i.2006, 40°03'43"S 73°05'19"W, 80 m, Valdivian for., 0.6 km W Ruta 5, A.R. Plant (NMWC). **Concepcion:** 1♀, S. Concepcion, Laraquete, 10–25.i.1993, P. Salinas (CNC). **Llanquihue:** 1♀, same data as holotype (USNM). **Osorno:** 1♀, Aguas, Calientes, Puyehue, 500 m, 12–17.xii.1981, L.E. Pena (KMNH); 1♂, P.N. Pyehue, 60 m, Ag. Calientes to 2 km S, 10–22.ii.1979, D.&M. Davis & B. Akerbergs (USNM). **Mal-leco:** 1♀, Region IX, PN Nahuelbuta, 37°48'10"S 73°01'27"W, 1327 m, 8–10.ii.2005, ypan, Araucaria/Chusquea forest, UCR AToL C05-004. **Valdivia:** 1♂, (in alc.), Oncol., ca 550 m, 39°41'S 73°W, 10–23.i.2006, MT over stream in Valdivian for. (NMWC); 1♀, 30 km W La Union, Las Trancas, 500 m, *Nothofagus*, 7–11.ii.1988, L. Masner (CNC). Additional material examined. **CHILE: Llanquihue:** Puerto Varas, 16.xii.1926, F.&M. Edwards, BMNH(E)#248190 (1♀, BMNH = paralectotype of *C. connexus*).

Recognition. This species is very similar to *C. connexus*, but distinguished readily by male terminalia (cluster of spines at apex of surstylus and heavily sclerotized cercus) and female terminalia with numerous pale, setae on tergum 10.

Description: Male. Head reddish-brown, postocular region darker, face pale brown, lacking setulae; ocellar triangle with pair of long, divergent bristles; postocellar bristle reduced to short setula; 1 pair of long vertical bristles; 2 pairs of stout postverticals; postocular bristles very short, not overlapping eye. Antenna long, with scape 0.33 × length of proboscis, scape sparsely covered by setulae, with 1 short dorsal seta and 1 long, ventral seta about middle; pedicel oval with posterior fringe of setae. Postpedicel with basal half rect-

angular, inner ventral margin yellowish; apical half strongly differentiated from base, tapered to short two-segmented arista-like stylus, shorter than basal half of postpedicel; length of first segment of stylus not longer than wide; apex of stylus concolorous with postpedicel. Base of labrum lacking dorsal process; palpus pale, short and slender, 0.16 × length of labrum, with several long, pale setae.

Thorax reddish-brown; mesonotum with distinct, wide (nearly extending to base of dc), dark, median stripe along entire length. Uniserial row of minute acrostichal setulae to prescutellar depression directed posteriorly; 5 dc, slender and fine, increasing in length posteriorly, prescutellar strong; 1 pprn; 0 presut spal; 2 stout npl; 1 psut spal; 1 short pal; 2 sctl and 1 pair of outer setulae. Antepnotum with pair of setae; laterotergite bare.

Wing (length 5–5.2 mm) (Fig. 37) margin lacking posterior incision and appendage, venation unmodified. Pterostigma at apex of cell r_1 , faint, slender; remainder of wing infusate; single short costal bristle; costal margin with unmodified setulae. R_{4+5} broadly forked; auxiliary crossvein from R_4 to R_{2+3} ; cell d short, rectangular; medial fork basal to radial fork by slightly less than half length of R_4 . Halter with pale knob.

Legs yellow, slender, without distinct bristles and processes. Tip of hind femur and tibia not darkened, or at least darkening confined to extreme tip; tarsomeres of all legs darkened. Fore tibia with small anteroapical comb. Posterior surface of hind tibia clothed in long, fine, pale setulae; apex of hind tibia slightly dilated, with posteroapical comb.

Abdomen dark reddish-brown, somewhat arched; coarsely punctate except hind margins of each segment, with pale setula arising from each puncture, lacking stout setae. Tergum 7 thinly sclerotized, lacking punctations, retracted within segment 6; tergum 8 rectangular. Terminalia (Fig. 25): hypandrium with sharply pointed posterior process; dorsal surface lacking rudder-shaped process; lateral process arising at mid-length of posterior process; postgonite articulated, triangular, flanking phallus. Phallus with short, blade-like apex. Epandrium round, lacking narrow sclerotized bridge ventral to cercus. Surstylus articulated, broad, gradually tapered; posterior margin lined with stout, blunt, spine-like setae, more dense apically. Posterior margin of cercus with wide sclerotized margin, apex broadly rounded.

Description: Female. Similar to male except as follows: abdomen more broad; apical segments retracted into segment 7; tergum 7 lacking a fringe of setae. Terminalia (Fig. 29): tergum 8 widely divided into pair of sclerites, posterior margin with long setae; anterior margin with pair of broad plate-like dorsolateral

apodemes. Sternum 9 present as a broad internal, U-shaped sclerite. Tergum 10 divided medially, each half bearing posterior row of 6 stout spine-like setae; anterior half with cluster of 8 straight, stout setae. Cercus short, bearing 4 stout, apical setae similar to those of tergum 10. Spermatheca oval, longer than wide, not flattened and lacking neck.

Distribution. See general notes under *C. connexus*.

Etymology. The specific name is from the Greek *para* (near), reflecting its similarity to *C. connexus*.

3.13. *Ceratomerus paradoxus* Philippi

Figs. 4, 27, 28, 30, 38, 44–48

Ceratomerus paradoxus Philippi, 1865: 766.

Material. Some parts of the Philippi insect collection (e.g., Tabanidae), although unlabelled, have been found in the collections at the Natural History Museum, Santiago (EVENHUIS 1999). Consequently the holotype of *C. paradoxus* may possibly be discovered among this collection. The identity of this species was based on the original illustration (poor but adequate) and the description.

Additional material examined. **CHILE:** **Aisén:** 2♂♂, Puerto Cisnes, 44°45'S 72°40'W, 1–28.ii.1961 (CNC); 1♂, Rio Manihuales, 26–28.i.1961 (CNC). **Chiloé Is.:** 6♀♀, Ahoni Alto, 70 m, ii–iv.1988 (CNC); 2♂♂, 5♀♀, Ahoni Alto, S. Chonchi, 20–23.ii.1988 (KMNH); 1♂, 1♀, (in alc.), Cord. De Piuché, Los Allerzales Tk., 20–21.i.2006, 42°34'S 74°05'W, stream in Valdivian for. (NMWC); 1♂, 2♀♀, (in alc.), Cord. De Piuché, 150–320 m, Los Allerzales Tk., 20–21.i.2006, 42°34'46"S 74°05'02"W, Valdivian & Patagonian for. (NMWC); 2♀♀, Miraflores, Pte. Rio Negro, 42°48'05"S 73°55'15"W, 50 m, 13.ii.2006, creek, ypan, UCR ATOL C05-014 (CNC); 18♂♂, 4♀♀, San Pedro, Piruquinz, 500 m (KMNH). **Llanquihue:** 1♀, El Chingue, N. Correntoso, i.1990 (CNC); 2♂♂, 5♀♀, N. Correntoso, N.E. Puerto Montt, iv–vii.1989 (CNC). **Osorno:** 1♂, Aguas Calientes, 7.ii.1978 (USNM); 2♂♂, 1 km W Anticura, 430 m, 1–3.ii.1978 (USNM); 1♀, Pucatrihue Costa, 28–30. iv.1968 (MNH); 2♀♀, Puyehue NP, 600 m, Ag. Calientes, 10–22.ii.1979 (USNM). **Palena:** 1♂, Rio Amarillo, ca. 28 km SE Chaiten, 23.i.1987 (USNM). **Valdivia:** 1♀, 2.6 km W El Mirador along rd to M.N. Alerce Costero, 40°12.5'S 73°24.0'W, 630 m, MT, 3–4.ii.1999 (USNM); 7♂♂, 3♀♀, Enco, 5–600 m, 2–9.iii.1955 (CNC); 6♂♂, 10♀♀, 36 km W La Union, 25–26.ii.1987 (BLKU); 1♂, Neltume, ii.1987 (KMNH); 1♂, 3♀♀, Rio Chaquigua, iii.1955 (CNC).

Recognition. The species is distinguished from *C. penai* by the narrow, pale lateral band on the mesonotum, prescutellar depression lacking stripe or with a very pale stripe, male mid femur with narrow tubercle bearing setae, and male hind femur greatly swollen.

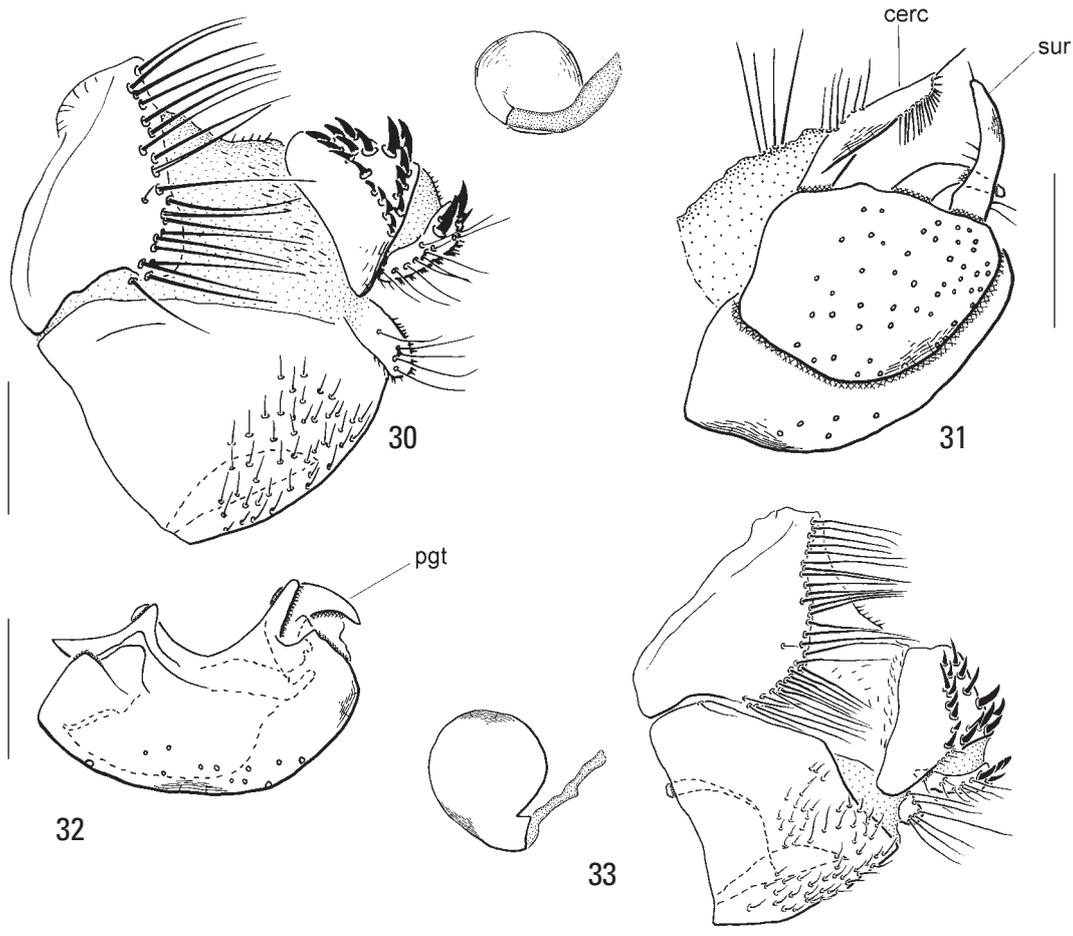
Re-description: Male. Head (Fig. 4) dark brown, face with pale pruinescence and 2 pairs of long setulae below antenna; frons lacking setae; ocellar triangle with pair of long, divergent bristles; postocellar bristle

0.5 × length of ocellar bristle; 2 pairs of long vertical bristles, 0.66 × length of ocellar bristle; postocular bristles erect, 0.33–0.5 × width of eye. Antenna long, with scape subequal to half length of labrum, pedicel oval with posterior fringe of setae; scape sparsely covered by setulae, with 2 long, dorsal setae and 1 ventral seta. Postpedicel 1.3 × length of scape; covered by long, dense pruinescence, basal half rectangular; apical half strongly differentiated from base, tapered to short two-segmented arista-like stylus, ca. to 0.5 × length of postpedicel; length of first segment of stylus 1.5 × width; apex of stylus concolorous with postpedicel. Base of labrum lacking dorsal process; palpus pale, short and slender, 0.16 × length of labrum, with several long, dark setae.

Mesonotum, mediotergite dark brown, with prescutellar depression pale and lightly dusted with pruinescence; pleura, postnotum, postpronotal lobe, lower margin of notopleuron, scutellum yellow to yellowish-brown. Acrostichals uniserial, alternate setulae divergent to prescutellar depression; 3 dc, posterior seta short and slender; 1 pprn; 1 presut spal; 1 npl; 2 psut spal, lower near wing base; 1 pal; 2 sctl; numerous setulae scattered on scutum, particularly on pprn, among dc and npl. Antepronotum with 2 pairs of short setulae; laterotergite bare.

Wing (length 4–5.3 mm) (Fig. 38) margin lacking posterior incision and appendage, venation unmodified. Pterostigma at apex of cell r_1 broad, dark, remainder of wing infusate; single long costal bristle; costal margin with unmodified setulae, increasing in length along posterior incision. R_{4+5} acutely forked; cell d rectangular; medial fork basal to radial fork by slightly more than half length of R_4 . Halter with dark knob.

Legs (Figs. 44–48) with coxae concolorous with pleura. Fore coxa less than twice length of mid coxa, greatly inflated basally, inner surface deeply concave; armed with stout, subapical seta and pair of short setae on lateral margin near base. Fore trochanter lacking setae. Fore femur twisted, with light anterior margin and dark brown posterior margin; large modified seta (similar to a collapsed sac) inserted before deep constriction at base; apical fifth with row of av setae, length less than width of femur. Fore tibia equal in length to femur, with dark outer dorsal surface; small, round av subbasal tubercle; anterior surface clothed densely with fine, short setae; apex slightly dilated bearing anteroapical comb. Tarsomeres dark brown; first tarsomere subequal in length to fore tibia, bearing long ventral basal seta; distal 4 tarsomeres shorter than first tarsomere; fifth tarsomere weakly flattened. Mid coxa with row of apical setae. Mid trochanter with long, flattened, basoventral seta; apicoventral patch of long setulae; several long, stout av setae. Basal half of mid femur compressed dorsoventrally; apical half with large, darkly tinted, pointed tubercle, sub-



Figs. 30–33. Terminalia of *Ceratomerus*, lateral view. **30:** *C. paradoxus*, female and spermatheca. **31:** *C. penai*, male. **32:** *C. penai*, hypandrium and phallus. **33:** *C. penai*, female and spermatheca. Abbreviations: cerc – cercus, pgt – postgonite, sur – surstylus. (scale bar: 0.1 mm)

equal to width of femur; anterior margin of tubercle fringed with long, flattened setae terminating in large spur; ventral region of femur flat, bearing av fringe of broad, blade-like setae of various lengths, with long erect stout seta at mid-length. Mid tibia shorter than femur, dorsal surface darkly coloured, dorsoventrally compressed, with lateral margins fringed with broad, flattened setae. Tarsomeres much longer than femur and tibia combined; first tarsomere longer than remaining 4 tarsomeres, bearing long pv setae near base. Hind coxa bearing 4 long anterior setae; inner surface with large tubercle at base, bearing long, flattened seta with curled tip. Inner margin of hind trochanter with long, flattened setae, similar to mid trochanter. Hind femur greatly enlarged, apical third darkened, $< 2 \times$ length of fore femur; bearing oblique row of posterior setae near base. Hind tibia longer than femur, apical half swollen and apex dilated, bearing posteroapical comb; apical half with perpendicular row of ad setae, longer than width of tibia; subapically with dense pd row of setae, ending with long, curved stout seta. Hind tarsomeres longer than tibia; first tarsomere lacking seta near base.

Abdominal terga and sterna dark brown, with long, stout setae along posterior margin of terga 1–6; tergum 7 with deep U-shaped membranous region of posterior half, lacking long posterior setae; sternum 7 slightly longer than preceding segment, posterodorsal corner produced and articulated with sternum 8; tergum 8 rectangular, with median notch, $0.25 \times$ length of sternum. Terminalia (Figs. 27, 28): hypandrium with posterior flap-like process; hypandrial lobe broad, $0.33 \times$ length of phallus, not articulated; postgonite flanking phallus, erect, somewhat S-shaped. Phallus with apical pair of articulated, divergent processes. Epandrium lacking narrow sclerotized bridge ventral to cercus; posterolateral margin with very long setae encircling hypandrium. Surstylus slender, tapered, with minute apical setula. Cercus heavily sclerotized, short, apex acute, with subapical cluster of stout setae on posterior margin.

Re-description: Female. Similar to male except as follows: postpedicel slightly longer than scape; 4 dc. Legs lacking modified appendages and setae; apical 4 tarsomeres of fore and midlegs and tips of hind fe-

mur, tibia and all tarsomeres darkened; apex of fore tibia not expanded. Mid tibia with 1 long ventroapical bristle and 1 pv bristle on apical third; 2 ad bristles on apical half and 1 dorsal bristle on basal third. Hind tibia with 3 ad and 2 dorsal bristles on apical half. Apical segments retracted into segment 7; tergum 7 with posterior fringe of golden setulae; lateral margin of sternum 7 jagged. Terminalia (Fig. 30): posterior three-quarters of tergum 8 membranous, with dense fringe of long setae along lateral margin; pair of small, flat lateral sclerites extend into segment 7 from anterior margin of tergum 8; sternum 8 with ventral setulae; posterior margin invaginated, forming well sclerotized, internal plate. Tergum 10 split medially into rectangular sclerites, bearing posterior and oblique median rows of spine-like setae. Cercus bearing row of similar setae; apex with additional spine-like setae; short, slender marginal setae. Spermathecal receptacle spherical, with broad, short neck.

Distribution. See general notes on biogeographic sub-region under *C. connexus*. Collection records indicate that both *C. paradoxus* and *C. penai* are likely closely associated with forest streams as are related species (i.e., *C. campbelli* group) from Australia (SINCLAIR 2003a).

Remarks. *Ceratomerus paradoxus* is the sister species of *C. penai* as resolved in the phylogenetic analysis (Fig. 49) with both species characterized by a large modified collapsed sac-like seta on the male fore femur and highly modified male midlegs.

3.14. *Ceratomerus penai* sp.n.

Figs. 31–33

Material. Holotype ♂, 'CHILE : Chiloe I. | Ahoni Alto 70m | April .1988 | L.E. Pena, MT [malaise] | primary forest', 'HOLOTYPE | *Ceratomerus | penai* | Sinclair [red label]' (CNC). – Paratypes, CHILE: Aisén: 2♂♂, Puerto Cisnes, 44°45'S 72°40'W, 1–28.ii.1961, L.E. Pena (CNC). Chiloé Is.: 4♂♂, 7♀♀, Ahoni Alto, 70 m, ii.iv.1988, primary for., L.E. Pena (CNC); 2♂♂, Miraflores, Pte. Rio Negro, 42°48'05"S 73°55'15"W, 50 m, 13.ii.2006, L. Masner, creek, ypan, UCR AToL C05-014; 2♂♂, San Pedro, Piquin, 500 m, L.E. Pena (KMNH). Llanquihue: 1♂, N. Correntoso, N.E. Puerto Montt, iv–vii.1989, L.E. Pena (CNC). Valdivia: 1♀, Las Trancas, 30 km W La Union, 500 m, *Nothofagus*, 25.ii.1988, L. Masner (CNC); 2♂♂, 36 km W La Union, 26–28.ii.1987, L.E. Pena (BLKU).

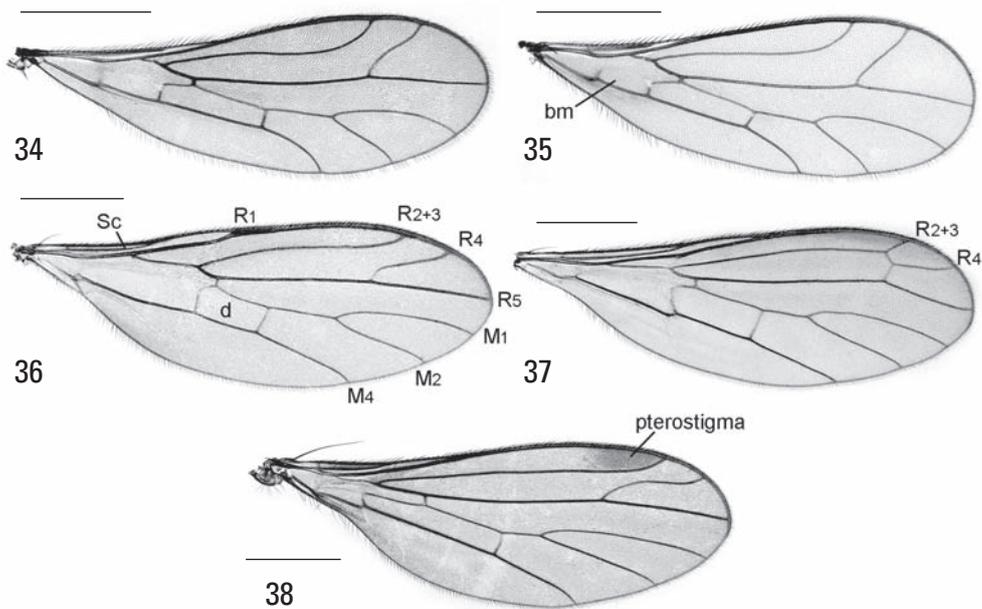
Recognition. This species is distinguished from *C. paradoxus* by the broad yellow band extending from the anterior margin of scutum to the postalar ridge, prescutellar depression with narrow yellow stripe extending from second dorsocentral bristles to scutellum, male mid femur with setose ridge not produced into a distinct lobe, and male hind femur slender.

Description: Male. Head dark brown, face with pale pruinescence and pair of long setulae below antenna; ocellar triangle with pair of long, divergent bristles; postocellar bristle 0.33 × length of ocellar bristle; 2 pairs of long vertical bristles, 0.66 × length of ocellars; postocellar bristles erect, 0.33 × width of eye. Antenna long, with scape subequal to half length of labrum, pedicel oval with posterior fringe of setae; scape sparsely covered by setulae, with 2 long, dorsal setae and 1 ventral seta. Postpedicel covered by long, dense pruinescence, base rectangular; apical two-thirds strongly differentiated from base, tapered to short two-segmented arista-like stylus, ca. 0.5 × length of postpedicel; length of first segment of stylus 3 × width; apex of stylus concolorous with postpedicel. Base of labrum lacking dorsal process; palpus pale, short and slender, 0.16 × length of labrum, with several long, dark setae.

Mesonotum dark brown with yellow vittae along postsutural supralar, prescutellar depression and from postpronotal lobe to notopleuron; postnotum and pleura yellow, scutellum yellow-brown, mediotergite dark brown. Acrostichals uniserial, alternate setae divergent, to prescutellar depression; 3 dc, posterior seta short and slender; 1 pprn; 1 presut spal; 1 npl; 2 psut spal, lower near wing base; 1 pal; 2 sclt; numerous setulae scattered on scutum, particularly on pprn, among dc and npl. Antepronotum with 2 pairs of short setulae; laterotergite bare.

Wing (length 4.5–5.2 mm) margin lacking posterior incision and appendage, venation unmodified. Pterostigma at apex of cell r_1 broad, dark, remainder of wing infusate; single long costal bristle; costal margin with unmodified setulae, increasing in length along posterior incision. R_{4+5} acutely forked; cell d rectangular; medial fork basal to radial fork by slightly more than half length of R_4 . Halter with dark knob.

Legs with coxae concolorous with pleura. Fore coxa <2 × length of mid coxa, greatly inflated basally, inner surface deeply concave; armed with pair of strongly, curved setae on lateral margin near base; inner margin with fine setae on apical third. Fore trochanter lacking setae. Fore femur twisted laterally, with light anterior margin and dark brown posterior margin; large modified seta (similar to a collapsed sac) inserted before shallow constriction at base; 3–4 long, posterior setae near mid length, 2 × width of femur; apex with very long, wavy, pv seta, 0.75 × length of tibia. Fore tibia equal in length to femur, with dark outer dorsal surface; base strongly constricted, with small, round subbasal, av tubercle; row of long pv setae, 1.5 × width of tibia; anterior surface densely clothed with fine, short setae; dark tinted apex slightly dilated bearing anteroapical comb. Tarsomeres dark brown; first tarsomere slightly longer than fore tibia; distal 4 tarsomeres shorter than first tarsomere; fifth



Figs. 34–38. Wings of *Ceratomerus*. **34:** *C. hibbsi*, male. **35:** *C. masneri*, male. **36:** *C. mediocris*, female. **37:** *C. paraconnexus*, female. **38:** *C. paradoxus*, female. Abbreviations: bm – basal medial cell, d – discal cell, M_{1,2,4} – medial vein, R_{1,2,3,4,5} – radial vein, Sc – subcostal vein. (scale bar: 1.0 mm)

tarsomere not strongly flattened. Mid coxa with row of apical setae. Mid trochanter with long, flattened, basoventral seta; apicoventral region with scattered setulae; several av setae. Basal half of mid femur compressed dorsoventrally; apical half with small, darkly tinted, pointed tubercle, subequal to width of femur; anterior margin of tubercle fringed with long, flattened setae terminating in large spur; ventral region of femur flat, bearing av fringe of broad, blade-like setae of various lengths. Mid tibia shorter than femur, dorsal surface darkly coloured, dorsoventrally compressed, with lateral margins fringed with broad, flattened setae. Tarsomeres much longer than femur and tibia combined; first tarsomere longer than remaining 4 tarsomeres, bearing long, pv setae near base. Hind coxa bearing 4 short, anterior setae; inner surface with small tubercle at base, bearing long, flattened, convoluted seta. Inner margin of hind trochanter with long, stout setae, similar to mid trochanter. Hind femur not greatly enlarged, evenly shaded; row of 4–5 pv setae near base. Hind tibia longer than femur, apex dilated, bearing posteroapical comb; apical half with 3 ad bristles; apical third with av setae increasing in length distally. Hind tarsomeres longer than tibia; first tarsomere with 1 short, erect, ventral seta near base.

Abdominal terga dark brown, sterna pale; long, stout setae along posterior margin of terga 1–6; tergum 7 weakly sclerotized on posterior half, lacking long posterior setae; sternum 7 not longer than preceding segment, posterodorsal corner produced and articulated with sternum 8; tergum 8 rectangular, with swollen median notch; 0.25 × length of sternum. Terminalia (Figs. 31, 32): hypandrium with poste-

rior flap-like process; lateral hypandrial lobe narrow, short, not articulated; pair of slender, sickle-shaped postgonites flanking phallus (visible in anterior view). Phallus with apical pair of articulated, sickle-shaped processes, arching posteriorly. Epandrium lacking narrow sclerotized bridge ventral to cercus; posterolateral margin with very long setae encircling hypandrium. Surstylus slender, tapered, with minute apical setula. Cercus heavily sclerotized, short, apex acute, with cluster of stout setae on posterior margin.

Description: Female. Similar to male except as follows: postpedicel slightly longer than scape; first segment of stylus 2 × longer than wide; vittae reduced on mesonotum, with median pale stripe from scutellum to suture, faint lateral vitae along psut spal ridge; 4 dc. Legs lacking modified appendages and setae; apical 4 tarsomeres of fore and midlegs and tips of hind femur, tibiae and all tarsomeres darkened; apex of fore tibia not expanded. Mid tibia with 1 long ventroapical bristle; 2 ad bristles on apical half and 1 dorsal bristle on basal third. Apical segments retracted into segment 7; tergum 7 with posterior fringe of golden setulae; lateral margin of sternum 7 jagged. Terminalia (Fig. 33): posterior three-quarters of tergum 8 membranous, with dense fringe of long setae along lateral margin; pair of small, flat lateral sclerites extend into segment 7 from anterior margin of tergum 8; sternum 8 with ventral setulae; posterior margin invaginated, forming well sclerotized, internal plate. Tergum 10 split medially into rectangular sclerites, bearing posterior and oblique median rows of spine-like setae. Cercus bearing row of similar setae; apex with additional spine-

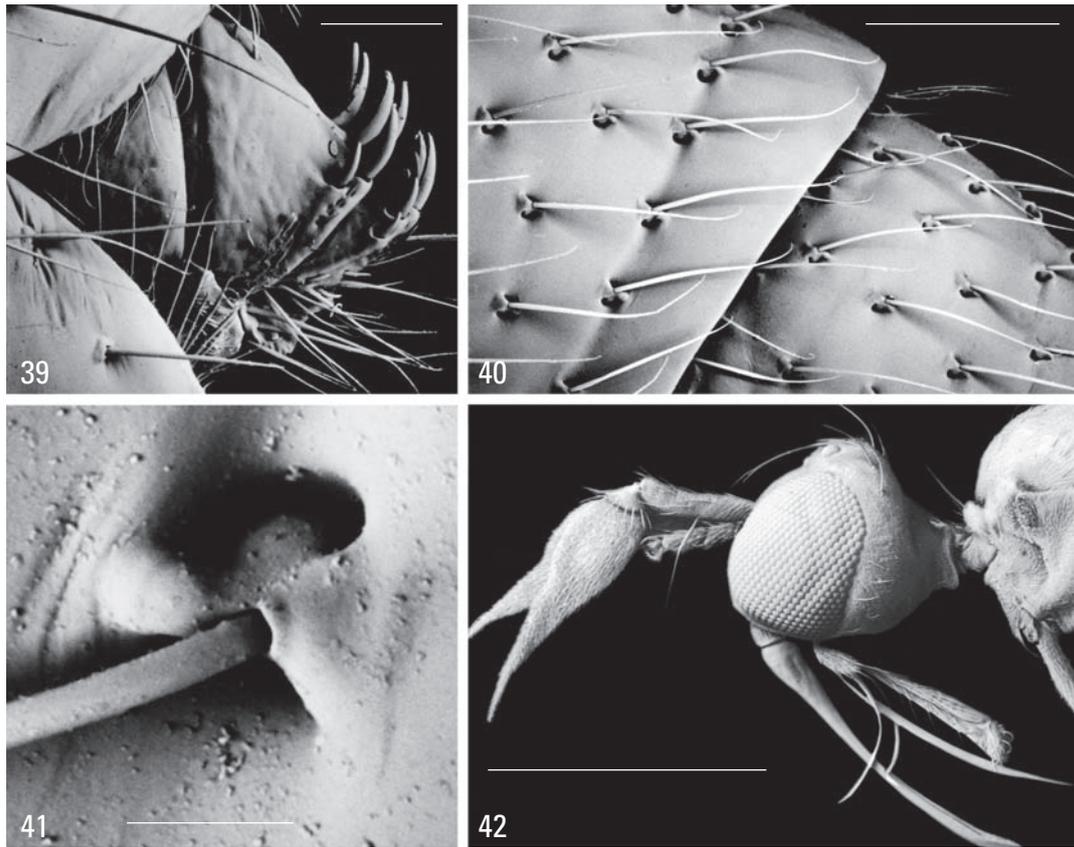
like setae; short, slender marginal setae. Spermathecal receptacle spherical, with broad, short neck.

Distribution. See general notes on biogeographic sub-region under *C. connexus* and see discussion under *C. paradoxus*.

Etymology. Named in honour of L.E. Peña, in recognition to his irreplaceable collections of Chilean empidoids.

4. Key to Neotropical species of *Ceratomerus*

1. Wings present **2**
 - Wings absent (Fig. 3) (Ecuador) *C. apterus* sp.n.
2. R₄₊₅ unbranched; two dorsocentral bristles (Chile) *C. irramus* sp.n.
 - R₄₊₅ branched (Figs. 34–38); more than two dorsocentral bristles **3**
3. Pedicel (second antennal segment) cylindrical, nearly subequal in length to scape (Ecuador) *C. longicornis* sp.n.
 - Pedicel globular, <0.33 × length of scape (Fig. 42) **4**
4. Abdomen heavily sclerotized, coarsely punctate (Figs. 2, 40) (*C. mediocris* group) **5**
 - Abdomen not heavily sclerotized, lacking punctate pattern **7**
5. Auxiliary crossvein between R₂₊₃ and R₄ lacking (occasionally present on one wing) (Fig. 36); one distinct notopleural bristle; base of postpedicel brown; apex of hind femur and tibia generally dark brown in contrast to remaining pale legs (Argentina, Chile) *C. mediocris* Collin
 - Auxiliary crossvein between R₂₊₃ and R₄ present (Fig. 37); two distinct notopleural bristles; base of postpedicel pale; apex of hind femur and tibia not distinctly darker than remaining legs (females of following species indistinguishable on basis of external or non-genitalic characters) **6**
6. Male cercus sclerotized on posterior margin only (Fig. 10); postgonite with narrow, curved pointed apex; female tergum 10 with dense cluster of stout setae, stouter and darker on posterior margin, but not spine-like (Fig. 11) (Chile) *C. connexus* Collin
 - Male cercus sclerotized laterally (Fig. 25); postgonite triangular, gradually tapered apically; female tergum 10 with row of 6 stout, spine-like setae on posterior margin (Fig. 29) (Argentina, Chile) *C. paraconnexus* sp.n.
7. Postpedicel slender and tapered apically (Fig. 4); 3–4 dorsocentral bristles present; scutum not polished; pterostigma present or absent **8**
 - Postpedicel pointed ovate (Fig. 1); dorsocentral bristles reduced to row of fine pale setulae; scutum polished; pterostigma absent (*C. masneri* group) **10**
8. First dorsocentral bristle offset from others; pterostigma tapered proximally; males and females with four well developed dorsocentral bristles; scutellum dark (Argentina, Chile) *C. deansi* Plant
 - First dorsocentral bristle in-line with others; pterostigma truncate proximally; males with three and females with four well developed dorso-central bristles; scutellum pale (*C. paradoxus* group) ... **9**
9. Notopleural depression with broad yellow band extending to notopleural bristle; prescutellar depression with narrow yellow stripe extending from second dorsocentral bristle to scutellum; male mid femur with setose ridge; male hind femur slender (Chile) *C. penai* sp.n.
 - Notopleural depression with narrow yellow band not extending to notopleural bristle; prescutellar depression lacking stripe or with very pale stripe; male mid femur with narrow tubercle bearing setae (Figs. 45–46); male hind femur greatly swollen (Chile) *C. paradoxus* Philippi
10. Scutum clothed in thin pruinescence; male cercus very short, inconspicuous, <0.33 × length of epandrium (Fig. 19); male terminalia lying obliquely posteriorly, not arched over abdomen (Ecuador) *C. masneri* sp.n.
 - Scutum lacking pruinescence, except prescutellar depression; male cercus large, conspicuous, at least 0.5 × length of epandrium (Figs. 8, 9, 14); male terminalia upright, somewhat arched over abdomen **11**
11. Pruinescence filling width of prescutellar depression (between dorsocentral bristles); male cercus longer than epandrium, bearing stout knob-like setae only on entire inner face (Fig. 14); apex of epandrium arched subapically and tapered to narrow apex (Ecuador) *C. hibbsi* sp.n.
 - Pruinescence covering at most only centre of prescutellar depression; male cercus slightly >0.5 × length of epandrium, lacking knob-like setae (Figs. 8, 9); epandrium with dorsolateral triangular expansion near mid-length, not arched or tapered **12**
12. Epandrium (surstylus) bearing spine-like apical seta; male cercus with dense stout posteroapical setae (Fig. 8) (Bolivia) *C. argutus* sp.n.
 - Epandrium lacking spine-like apical seta, apex with pair of short prolongations; male cercus with scattered stout setae (Fig. 9) (Bolivia) *C. comarapa* sp.n.



Figs. 39–42. Scanning electron micrographs of *Ceratomerus mediocris*, female. **39:** Terminalia, lateral view (scale bar: 0.05 mm). **40:** Abdominal terga, dorsolateral view (scale bar: 0.1 mm). **41:** Abdominal seta, dorsal view (scale bar: 0.01 mm). **42:** Head, lateral view (scale bar: 0.5 mm).

5. Biology

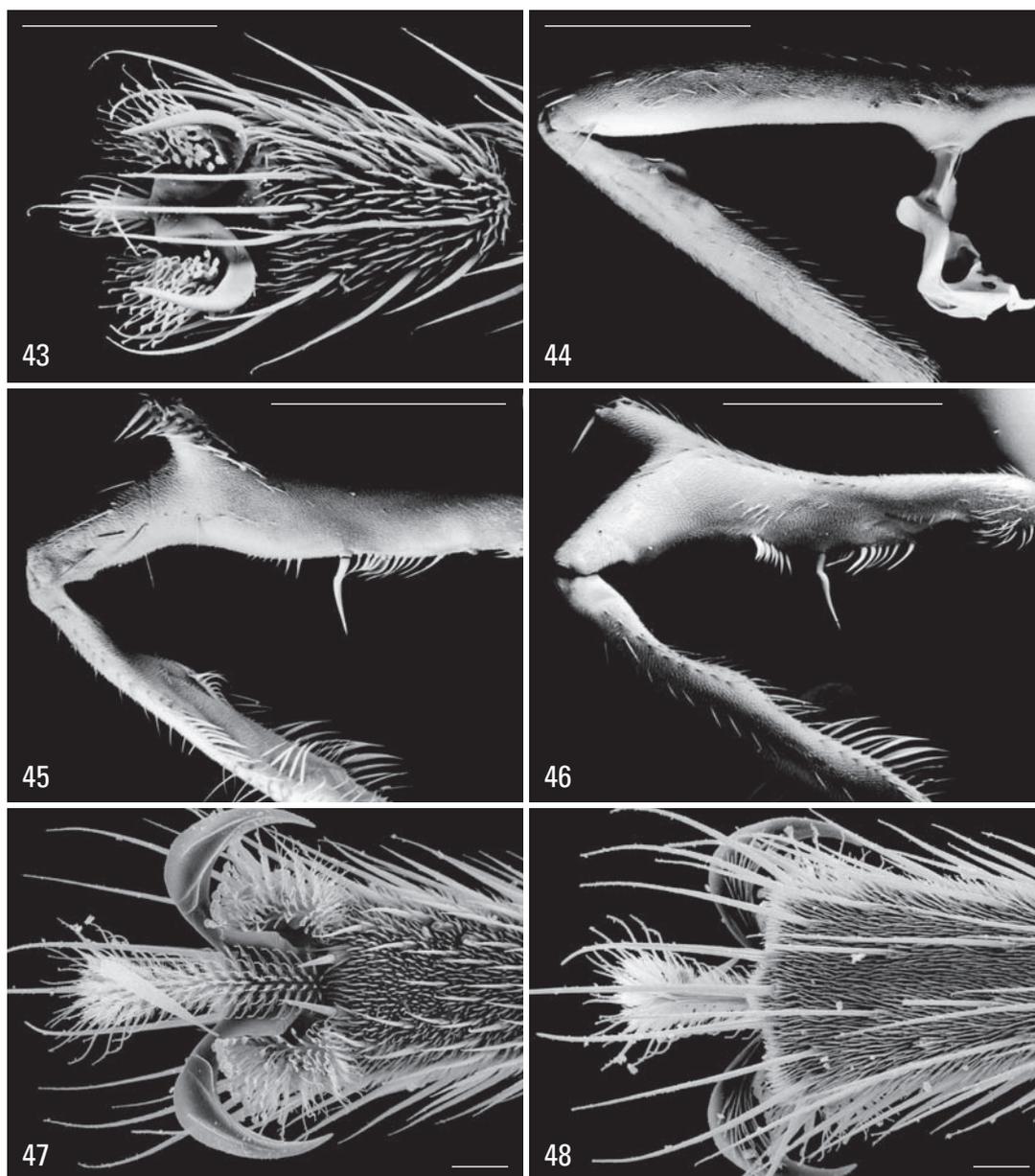
In Australia, species of *Ceratomerus* are assumed to primarily have aquatic larvae and pupae, with adults collected on emergent rocks in shaded rocky streams and rivers or on riparian vegetation. Only *C. albistylus* Hardy, 1930 was collected more distant from streams and likely breeds in damp soil (SINCLAIR 2003a). In the Neotropical region, the habitat associations have not been as clearly determined. Many species appear to be associated with temperate forests, e.g., *C. mediocris*, the most commonly collected Neotropical ceratomerine. The Chilean species *C. paradoxus* and *C. penai* have been hand collected in streams or using yellow pans associated with streams and this is presumably the breeding habitat. Clarification through hand collection of adults and emergence traps are required to make comparable observations to species in Australia and New Zealand.

Based on observations on Australian taxa (SINCLAIR 2003a), it is assumed that adults of all Neotropical species are predacious on small flying insects in streams and forests. *Ceratomerus mediocris* is the most commonly collected species and collection records indicate that the flight period is at least from November to

April (late spring to early autumn). There are too few records for the remaining ceratomerine species to estimate flight period. Among the clinocerines, *Clinocera oriunda* (Collin, 1933) has a similar long flight period (SINCLAIR 2008). *Ceratomerus mediocris* has been collected in a variety of humid temperate forests, by sweep net, yellow pan traps and Malaise traps.

6. Phylogeny

A cladistic analysis was performed on the character state matrix (Tab. 3), which generated 121 most parsimonious trees (tree length = 104; CI = 0.52; RI = 0.73; RC = 0.38). Strict consensus of these trees produced a mostly unresolved tree with nearly all ingroup taxa (exclusive of *Glyphidopeza*) depicted as a large polytomy (except: *deansi* + *dorsatus*; *paradoxus* + *penai*; *crassinervis* + (*prodigiosus* + *brevifurcatus*); *falcatus* + sp. 12 + *longicornis* species pairings). Using successive approximations resulted in three weighted trees, of which the least resolved cladogram (i.e., most polytomies) was selected for discussion of character evolution and biogeographic scenarios (Fig. 49). This



Figs. 43–48. Scanning electron micrographs of *Ceratomerus*. **43:** *C. mediocris*, fifth tarsomere, dorsal view (scale bar: 0.05 mm). **44:** *C. paradoxus*, male foreleg, posterior view (scale bar: 0.5 mm). **45:** *C. paradoxus*, male midleg, anterior view (scale bar: 0.5 mm). **46:** *C. paradoxus*, male midleg, posterior view (scale bar: 0.5 mm). **47:** *C. paradoxus*, fifth tarsomere (scale bar: 0.02 mm), ventral view. **48:** *C. paradoxus*, fifth tarsomere, dorsal view (scale bar: 0.02 mm).

cladogram is two steps longer than the initial 121 most parsimonious trees. This tree should be viewed as preliminary, while most groupings are well supported; the relationships between them remain equivocal.

The monophyly of Ceratomerinae is very strongly supported by five synapomorphies [dichoptic male (1.1); scape more than twice as long as pedicel (2.1); conus present (3.1); pterostigma at apex of cell r_1 (27.1); epandrial lamellae separate dorsally (42.1)]. The genus *Glyphidopeza* remains the sister group to the remaining Ceratomerinae as first proposed by SINCLAIR (1997). The remaining Ceratomerinae form another very well supported clade on the basis of six synapomorphies [inner basal face of scape flattened

(5.1); pseudotracheae absent (15.1); four dorsocentral bristles (21.2); M_{1+2} petiolate, two veins emitted distally from cell d (33.1); cell bm poorly defined or absent (34.1); anal cell (= cua) absent (35.1)].

Obviously, the results of this analysis are somewhat disappointing, with species and genus level relationships within the Ceratomerinae remaining inconclusive. Successive approximations (Fig. 49), failed to clearly define the genus *Ceratomerus* from other possible generic groupings, including *Icasma*, and the *C. masneri* and *C. mediocris* groups (see below for definitions of species groups). *Ceratomerus* is clearly paraphyletic in relation to *Icasma* (see SINCLAIR 1997). Despite several morphologically distinct

Tab. 1. List of exemplar taxa.

Taxon	Collection locality
<i>Ceratomerus albistylus</i> Hardy, 1930	Australia, NSW, Blue Mountains National Park
<i>Ceratomerus apterus</i> sp.n.	Ecuador, Napo
<i>Ceratomerus attenuatus</i> Sinclair, 2003	Australia, VIC, Burrow-Pine National Park
<i>Ceratomerus brevifurcatus</i> Plant, 1995	New Zealand, Waipoua Forest Park
<i>Ceratomerus campbelli</i> (Paramonov, 1961)	Australia, TAS, Mt. Bobs Range
<i>Ceratomerus connexus</i> Collin, 1933	Chile, Valdivia, Anticura
<i>Ceratomerus crassinervis</i> Malloch, 1931	New Zealand, Abel Tasman National Park
<i>Ceratomerus deansi</i> Plant, 1995	Chile, Pata de Galina
<i>Ceratomerus dorsatus</i> Collin, 1928	New Zealand, Hinewai Reserve
<i>Ceratomerus falcatus</i> Sinclair, 2003	Australia, NSW, Border Ranges National Park
<i>Ceratomerus irramus</i> sp.n.	Chile, Puyuhue National Park, Antillanca
<i>Ceratomerus longicornis</i> sp.n.	Ecuador, Pichincha
<i>Ceratomerus masneri</i> sp.n.	Ecuador, Napo
<i>Ceratomerus mediocris</i> Collin, 1933	Chile, Chiloé I., Ahoni Alto
<i>Ceratomerus orientalis</i> Sinclair, 2003	Australia, NSW, Border Ranges National Park
<i>Ceratomerus paraconnexus</i> sp.n.	Chile, Osorno, Puyehue National Park
<i>Ceratomerus paradoxus</i> Philippi, 1865	Chile, Aysen, Puerto Cisnes
<i>Ceratomerus penai</i> sp.n.	Chile, Chiloé I., Ahoni Alto
<i>Ceratomerus prodigiosus</i> Collin, 1928	New Zealand, Westland National Park
<i>Ceratomerus victoriae</i> Sinclair, 2003	Australia, VIC, Warburton, Cement Creek
<i>Ceratomerus</i> sp. 12	New Zealand, Hwy 40, west of Ohura
<i>Ceratomerus</i> sp. 23	New Zealand, Cloustonville, Akatarawa Valley
<i>Glyphidopeza fluviatilis</i> Sinclair, 1997	New Zealand, Jones Creek
<i>Icasma setosa</i> Sinclair, 1997	New Zealand, Abel Tasman National Park
Outgroup	
<i>Oreogeton obscurus</i> (Loew, 1864)	Canada, Cape Breton Highlands National Park
<i>Anomalempis archon</i> Melander, 1945	Canada, Yukon, Dempster Hwy
<i>Heterophlebus versabilis</i> (Collin, 1933)	Chile, Magellanes, Lag Amarga, Natales

Tab. 3. Character state matrix for cladistic analysis of Neotropical and major groups of Ceratomerinae. Inapplicable characters are indicated by “-”, and unknown data by “?”.

Taxon	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	3	3	3	3	3	3	3	4	4	4	4	4	4																
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6																	
<i>Oreogeton obscurus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0															
<i>Anomalempis archon</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0													
<i>Heterophlebus versabilis</i>	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0													
<i>Glyphidopeza fluviatilis</i>	1	1	1	0	0	0	0	0	2	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	-	-	1	0	1	0	0	0	0	0	0	0	1	1	1	0	0	1										
<i>Icasma setosa</i>	1	1	1	0	1	0	1	0	1	0	1	0	0	0	1	0	0	1	0	0	2	0	0	0	1	-	-	0	1	1	0	1	1	0	0	0	0	1	0	1	0	0	0										
<i>Ceratomerus albistylus</i>	1	1	1	0	1	1	0	0	0	0	1	0	0	0	1	0	0	1	1	0	2	0	0	1	0	0	1	1	0	0	1	1	1	0	0	0	1	1	1	0	0	0	1										
<i>Ceratomerus apterus</i>	1	1	1	0	1	0	1	1	1	0	1	0	0	0	1	2	0	1	0	0	1	0	1	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	1	1	1	0	0	0						
<i>Ceratomerus attenuatus</i>	1	1	1	0	1	0	0	1	1	0	0	0	0	0	1	1	0	1	1	0	2	0	1	0	0	1	1	0	0	1	1	0	0	0	1	1	0	1	1	1	0	1	0	1	0	1							
<i>Ceratomerus brevifurcatus</i>	1	1	1	0	1	1	0	1	1	0	0	0	1	1	1	0	0	0	0	2	0	0	1	1	-	-	1	0	1	0	1	1	1	0	1	0	1	1	1	1	0	0	0	1	1	1	0	0					
<i>Ceratomerus campbelli</i>	1	1	1	0	1	0	0	1	1	0	0	0	0	1	1	0	1	1	0	2	0	0	1	0	1	0	0	1	1	0	1	0	1	1	0	1	1	1	1	0	0	1	1	1	0	0	1						
<i>Ceratomerus connexus</i>	1	1	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	5	0	0	0	0	1	0	0	0	0	1	1	1	0	0	0	0	1	0	1	1	0	0	0	1	0	1	0	0					
<i>Ceratomerus crassinervis</i>	1	1	1	0	1	0	0	1	1	0	0	1	0	0	1	0	0	0	0	2	0	0	1	0	1	-	-	1	0	1	0	1	1	1	0	0	0	0	1	1	1	0	0	0	1	1	0	0	0				
<i>Ceratomerus deansi</i>	1	1	1	0	1	0	0	1	1	0	1	0	0	0	1	0	0	1	0	2	0	0	1	0	0	0	1	1	1	1	0	0	0	0	0	1	1	1	0	0	0	1	1	1	0	0	0						
<i>Ceratomerus dorsatus</i>	1	1	1	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	1	3	0	0	1	0	0	2	0	0	0	1	1	1	1	0	0	0	0	1	1	1	0	0	0	1	1	1	0	0	0				
<i>Ceratomerus falcatus</i>	1	1	1	1	1	0	0	1	1	1	0	0	0	0	1	0	0	1	0	2	0	0	0	0	1	-	-	0	0	1	0	1	1	1	0	0	0	0	1	1	1	0	1	0	0	1	0	0					
<i>Ceratomerus irramus</i>	1	1	1	0	1	0	0	0	0	0	1	0	0	0	1	2	0	1	0	1	1	1	0	0	0	1	1	0	0	1	1	0	0	0	0	1	1	1	0	0	0	1	1	1	0	0	0	1	1	0	0		
<i>Ceratomerus longicornis</i>	1	1	1	1	1	0	0	1	3	1	0	0	0	0	1	2	0	0	0	2	0	0	0	1	-	-	0	0	1	0	1	1	1	0	0	0	0	1	1	1	0	0	0	1	1	1	0	0	0				
<i>Ceratomerus masneri</i>	1	1	1	0	1	0	0	0	0	0	1	0	0	0	1	2	0	1	0	4	1	0	0	0	1	-	-	0	0	1	0	1	1	1	0	0	0	0	1	0	1	1	0	0	0	1	0	1	0	0			
<i>Ceratomerus mediocris</i>	1	1	1	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	5	0	0	0	0	1	0	0	0	0	0	1	1	1	0	0	0	0	1	0	1	1	0	0	0	1	0	1	1	0	0	0		
<i>Ceratomerus orientalis</i>	1	1	1	0	1	0	0	1	1	0	1	0	0	1	1	0	1	1	0	2	0	0	1	0	0	1	1	0	0	1	0	1	1	1	0	0	0	0	1	1	1	0	0	0	1	1	1	0	0	0	1		
<i>Ceratomerus paraconnexus</i>	1	1	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	5	0	0	0	0	1	0	0	0	0	0	1	1	1	0	0	0	0	1	0	1	1	0	0	0	1	0	1	1	0	0	0		
<i>Ceratomerus paradoxus</i>	1	1	1	0	1	0	0	1	1	0	0	1	0	0	1	0	0	1	1	2	0	0	0	0	1	0	0	1	1	0	1	0	1	1	0	1	0	1	1	1	1	0	1	1	1	0	0	0	1	1	1	0	0
<i>Ceratomerus penai</i>	1	1	1	0	1	0	0	1	1	0	0	1	0	0	1	0	0	1	1	2	0	0	0	0	1	1	0	0	1	1	0	1	1	1	0	1	0	1	1	1	1	0	1	1	1	0	0	0	1	1	1	0	0
<i>Ceratomerus prodigiosus</i>	1	1	1	0	1	1	0	1	1	0	0	0	1	1	1	0	0	0	0	2	0	0	1	1	-	-	1	0	1	0	1	1	1	1	0	1	0	1	1	1	1	0	0	0	1	1	1	0	0	0	1		
<i>Ceratomerus victoriae</i>	1	1	1	0	1	0	0	1	1	0	0	0	0	0	1	1	0	1	1	2	0	0	1	0	0	1	1	0	0	1	0	1	1	1	0	0	0	1	1	1	1	0	0	1	1	1	0	0	1	1	1	0	0
<i>Ceratomerus</i> sp. 12	1	1	1	1	1	0	1	3	1	0	0	0	1	1	0	0	0	0	2	0	0	0	0	1	-	-	0	0	1	0	1	1	1	0	0	1	0	1	1	1	0	0	1	1	1	0	1	0	0	1			
<i>Ceratomerus</i> sp. 23	1	1	1	0	1	0	0	0	2	1	0	0	0	0	1	0	0	0	0	2	0	1	1	0	1	-	-	0	0	1	0	1	1	1	0	0	0	0	1	0	1	1	0	0	0	1	0	1	0	0	0		

Tab. 2. Characters used in the phylogenetic analysis.

- Head**
01. *Male eye contiguity*: holoptic (0); dichoptic (1).
 02. *Dimensions of the scape*: equal or slightly longer than pedicel (0); more than 2 times as long as pedicel (1).
 03. *Conus*: absent (0); present (1).
 04. *Dimensions of the pedicel*: at most twice as long as wide (0); 3–4 times longer than wide (1).
 05. *Base of scape*: cylindrical (0); flattened (1).
 06. *Shape of male postpedicel*: gradually tapered from base onwards (0); apical portion slender and tapered, at least two times as long as base (1).
 07. *Arista-like stylus (2nd + 3rd flagellomeres)*: shorter than postpedicel (0); equal to or longer than postpedicel (1).
 08. *Ocelli*: all three ocelli equidistantly separated (forming equilateral triangle) (0); posterior ocelli more widely separated than distance from anterior ocellus (1).
 09. *Position of ocellar bristles*: inserted anteromedially to posterior ocelli (0); inserted anterior to posterior ocelli (1); inserted near margin of eye, anterior to anterior ocellus (2); inserted outside ocellar triangle and anterior to posterior ocelli (3).
 10. *Condition of postocular setae*: erect, not lying and overlapping compound eye (0); oblique, overlapping almost half width of eye (1).
 11. *Width of face*: wide, at least somewhat divergent from antennal sockets (0); narrower than antennal sockets (1).
 12. *Face*: Bare (0); lower half setose (1).
 13. *Male palpus form*: setae fine, evenly dispersed (0); modified with tufts of setae and/or long stout setae (1).
 14. *Orientation of male palpus*: palpus held obliquely to proboscis (0); palpus held parallel to proboscis (1).
 15. *Pseudotracheae*: present (0); absent (1).
- Thorax**
16. *Acrostichal setae*: acrostichals sloping posteriorly (0); acrostichals directed anteriorly (1); absent (2).
 17. *Postpronotal bristles*: one (0); two (1).
 18. *Notopleural bristles*: two or more stout bristles (0); one stout bristle (1).
 19. *Length of prescutellar bristles relative to other dorsocentral bristles*: prescutellar pair longest (0); prescutellar pair shortest (1).
 20. *Position of first pair of dorsocentral bristles*: in-line with remaining bristles (0); off-line from remaining pairs, often considered intrahumeral bristles (1).
 21. *Number of dorsocentral bristles*: 6 or more (0); 2 (1); 4 (2); 5 (3); 0, but as row of setulae (4); 1, remaining are setulae or setae (5).
 22. *Presutural supra-alar bristle (posthumeral)*: present (0); absent (1).
 23. *Postsutural supra-alar bristles*: present (0); absent (1).
 24. *Antepronotum vestiture*: numerous setae (0); pair of bristle-like setae only (1).
 25. *Male posterior basalare*: flat, not projecting (0); elevated as shiny lobe (1).
- Wing**
26. *Pterostigma*: present (0); absent (1).
 27. *Position of pterostigma*: overlapping apex of R_{1+2} , extending into cell r_1 (0); positioned at apex of cell r_1 (1); positioned near middle to end of cell r_1 (2).
 28. *Shape of pterostigma*: elliptical (0); proximal end truncate (1).
 29. *Anterior margin of costa*: costa with longitudinal rows of simple setae (0); costa with stout, erect setae interspersed along costa (1).
 30. *Subcosta*: complete, reaching wing margin (0); incomplete, ending short of wing margin (1).
 31. *R_1 termination*: distal to mid-length of wing (0); proximal to mid-length of wing (1).
 32. *Basal costal bristle length*: shorter than scutal bristles and not reaching apex of Sc vein (0); longer than scutal bristles and reaching apex of Sc vein (1).
 33. *Medial branching pattern*: three veins emitted distally from cell d (0); M_{1+2} petiolate, two veins emitted distally from cell d (1); occasionally obscured in males and then based on female, which is more stable.
 34. *Cell bm*: present (0); very faintly defined or lacking (1).
 35. *Cell cua (= cup)*: present (0); absent, CuA absent (1).
 36. *Posterior margin of male wing base*: unmodified (0); concave, sclerotized “pocket” (1).
- Legs**
37. *Male fore coxae, inner apical margin*: straight (0); concave (1).
 38. *First tarsomere of male foreleg*: cylindrical, without groups of erect setae (0); slightly sinuous, bearing groups of erect setae (1).
 39. *Male midleg*: cylindrical (0); greatly distorted with tubercles and lobes, modified setae on femur, and tibia flattened with lateral lobes and setae (1).
 40. *Hind tibia vestiture*: lacking pile (0); posterior face with fine, erect pile (setulae) (1).
 41. *Hind first tarsomere basal vestiture*: no ventral seta(e) at base (0); 1–2 ventral seta(e) at base (1).
- Terminalia – Male**
42. *Epandrium*: U-shaped with sclerotized dorsal bridge (lobes connected) (0); lobes separate, not connected dorsally (1).
- Terminalia – Female**
43. *Flattened apodeme on anterolateral margin of tergum 8*: absent (0); present (1).
 44. *Flattened apodeme on anterior margin of tergum 8*: absent (0); present (1).
 45. *Rod-shaped apodeme on anterior margin of tergum 8*: absent (0); present (1).
 46. *Spermathecal receptacle*: unflattened (0); flattened (1).

species groups within *Ceratomerus*, I am reluctant to erect new genera at this time because of the inability to clearly define *Ceratomerus* with the remaining species. It is hoped that an ongoing revision of the New Zealand taxa and inclusion of additional data may help to resolve the relationships among the species groups of *Ceratomerus*.

The clade, *C. deansi* + *C. dorsatus* (the latter species representing the New Zealand *dorsatus* group), is sister group to all remaining ceratomerine taxa and is

defined by two synapomorphies [postpronotum with two bristles (17.1); long basal costal bristle (32.1)].

The remaining ceratomerine taxa are supported also by two synapomorphies [dorsocentral bristles align in straight line (20.0); posterior face of hind tibia with erect pale setulae (40.1)]. The remaining taxa are divided into several clades. The genus *Icasma* is grouped with several of the most distinctive *Ceratomerus* species groups (i.e., *C. mediocris* and *C. masneri* groups) that also could easily be recognized

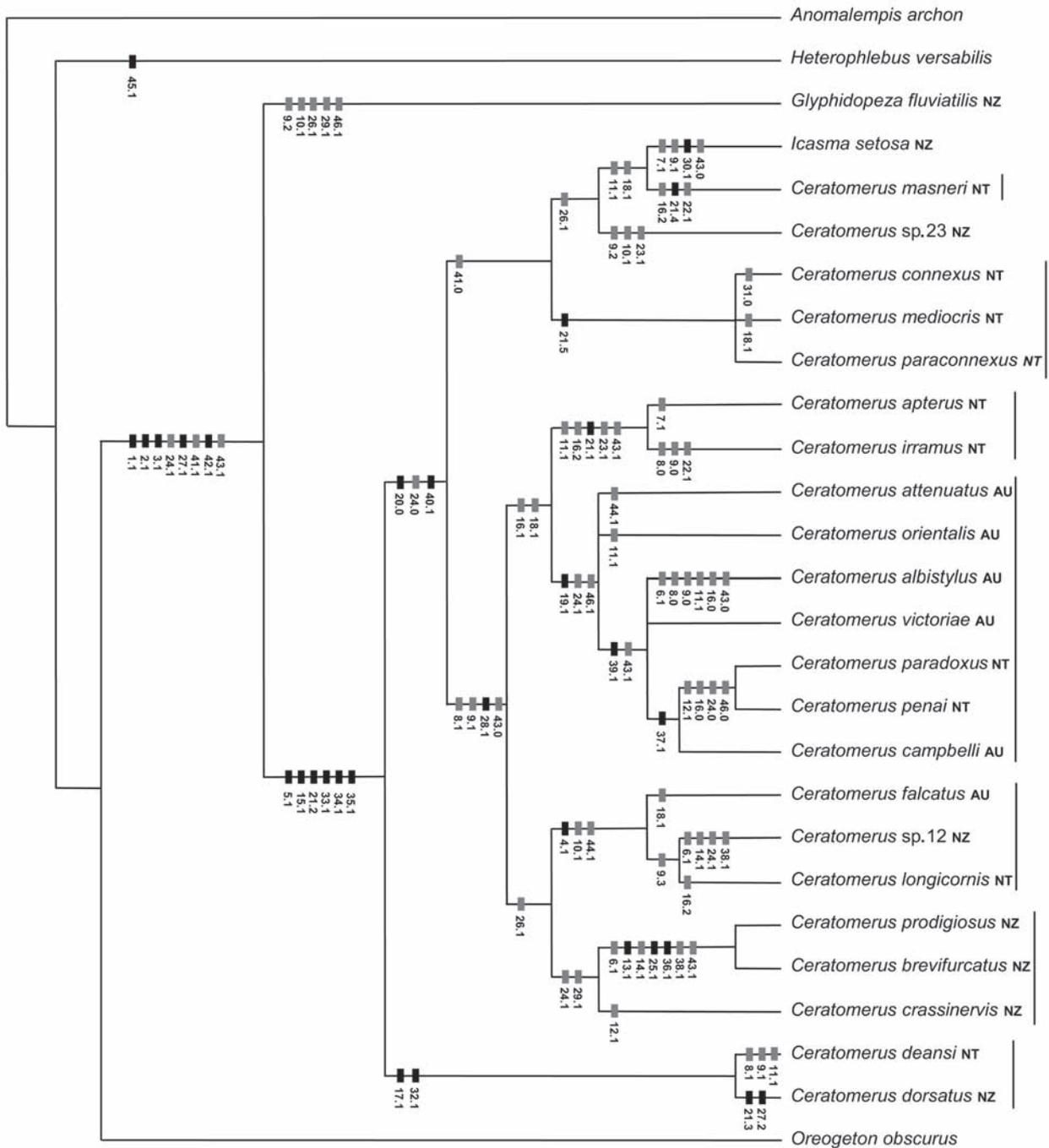


Fig. 49. One of three most parsimonious cladograms produced by analysis of the data matrix (Tab. 3) and successive approximations (tree length = 106). Character distributions shown by black hash marks for uniquely derived states and grey hash marks for homoplasious states. AU – Australia; NT – Neotropics; NZ – New Zealand. Vertical line to the right of terminal taxa depicts species groups.

as distinct genera if examined in isolation (e.g., few specimens) and without consideration of the monophyly of the remaining species of *Ceratomerus*. Alternatively and most parsimoniously, *Icasma* could be sunk within *Ceratomerus*. This clade is weakly supported by the absence of basal setae on the hind first tarsomere (41.0). The *C. mediocris* group is herein defined and includes three species (*mediocris*, *connexus*, *paraconnexus*) and is the most readily recognized species group on the basis of their darkly pigmented,

heavily sclerotized and punctate abdomen (Figs. 4, 40, 41), shortened cell d and single prescutellar bristle (21.5). This species group is endemic to southern South America. The *C. masneri* group is herein defined and includes four species (*argutus*, *comarapa*, *hibbsi*, *masneri*) and is clearly distinguished by the reduced thoracic chaetotaxy (21.4), wing shape, widely divergent R₄ and R₅ (Figs. 34, 35) and form of the postpedicel (Fig. 1). This species group is endemic to Ecuador and Bolivia.

The pterostigma with proximal end truncate (28.1), anteriorly directed acrostichal setulae (16.1) and single notopleural bristle (18.1) unite most Australian ceratomerines (except *C. falcatus* group) and several Neotropical species. Within this clade, *C. irramus* and *C. apterus* are sister species, supported by two dorsocentral bristles (21.1). However, the apparent synapomorphies may result from the reduced size of the thorax in the latter species due to loss of wings which has possibly resulted in reduced number of scutal bristles. The Neotropical *C. paradoxus* group is herein defined and includes two species (*paradoxus*, *penai*) and is resolved within the Australian *C. campbelli* group (SINCLAIR 2003a), most closely related to the Tasmanian species, *C. campbelli*. The species of this large clade are defined by shortened prescutellar bristles (19.1).

The remaining *Ceratomerus* species groups are characterized by the loss of the pterostigma (26.1), and divided into two distinctive clades. The Ecuadorian species, *C. longicornis* forms a clade with *C. falcatus* (representing the *C. ordinatus* group of Australia (SINCLAIR 2003a)) and *Ceratomerus* sp. 12 from New Zealand on the basis of a lengthened pedicel (4.1). The *C. prodigiosus* group is weakly supported in the present analysis, but the phylogeny of the New Zealand species of *Ceratomerus* will be more thoroughly examined in an ongoing revision of this group.

7. Biogeography

7.1. Continental patterns

Probable transantarctic relationships within the Ceratomerinae were first suggested by PARAMONOV (1959) and SINCLAIR (2003a) proposed several species pairings among New Zealand / Australian / South American taxa. These relationships are more fully analyzed in the present study, updating these earlier statements. Additional empidoid genera also demonstrate transantarctic patterns, e.g., *Asymphyloptera* Collin, 1933 (SINCLAIR 1995); *Proagomyia* Collin, 1933; *Apalocnemis* Collin; *Heterophlebus* Philippi and the recently analyzed *Empis macrorrhyncha* group (DAUGERON et al. 2009).

No ceratomerine fossils are known and the subfamily is absent from the African continent (SINCLAIR 2003b). Given that the Ceratomerinae is most closely related to the Trichopezinae, with the latter possibly paraphyletic in relation to the ceratomerines (SINCLAIR & CUMMING 2006), the discovery of a Santonian-age (76–80 MYA) fossil of the trichopezine genus *Apalocnemis* (GRIMALDI & CUMMING 1999), provides a mini-

imum age for the Ceratomerinae. Based on this dating, it is hypothesized that the Ceratomerinae were likely widespread in former Gondwanan continents following the separation of southern South America from Africa in the Early Cretaceous (135 MYA).

The circumantarctic pattern of the Ceratomerinae illustrates a temperate amphinotic track; i.e., a temperate transantarctic track excluding South Africa (MATILE 1990; CRANSTON 2005; AMORIM et al. 2009). In an attempt to identify true Gondwanan groups, AMORIM et al. (2009) divided circumantarctic distributions into four categories, of which the Ceratomerinae would be classified as category 4 (neither Jurassic fossils nor southern African representatives). Although taxa in category 4 are less probable to correspond to true Gondwanan groups, the restriction of this group to the southern continents and the estimated minimum age supports the assumption that the Ceratomerinae are true Gondwanan taxa. This is in contrast to the genus *Clinocera* Meigen, another empidoid taxon that is also assigned to category 4, but is a post Gondwanan element having arrived in southern Gondwanan areas via north to south expansion from North America in the Cretaceous (SINCLAIR 2008; AMORIM et al. 2009).

In the present study, the intercontinental relationships among ceratomerine species groups and genera are generally congruent with the classic Southern Gondwana Pattern (SGP) as analyzed by SANMARTÍN & RONQUIST (2004). This is the sequential geological break-up of the Gondwanan landmass of southern continents: Africa (New Zealand (southern South America, Australia)). This biogeographic pattern or area relationships has been discussed and observed in several Diptera and other insect studies (e.g., BRUNDIN 1966; CRANSTON et al. 1987; CRANSTON & EDWARD 1992, 1999) (see SANMARTÍN & RONQUIST 2004 for many additional examples). It is generally accepted that complete continental separation of New Zealand from the other southern continents occurred some 80 MYA and complete terrestrial separation of Australia from Antarctica + southern South America or transantarctic faunal exchange was not broken until the late Eocene (35 MYA) (McLOUGHLIN 2001).

In addition to the SGP, an Inverted Southern Pattern (ISP) is also resolved in the Ceratomerinae (*C. deansi* + *C. dorsatus* group), which is incongruent with the geological scenario. In the ISP, area relationships are: (Australia (southern South America, New Zealand)). This is the same relationship BRUNDIN (1966) proposed for Chironomidae in the amphinotic tract, and additional taxa showing this track are listed by MATILE (1990) and CRANSTON (2005). The New Zealand + southern South America scenario may reflect an ancient relationship of faunal connections through West Antarctica. A number of potential barriers between West and East Antarctica could have

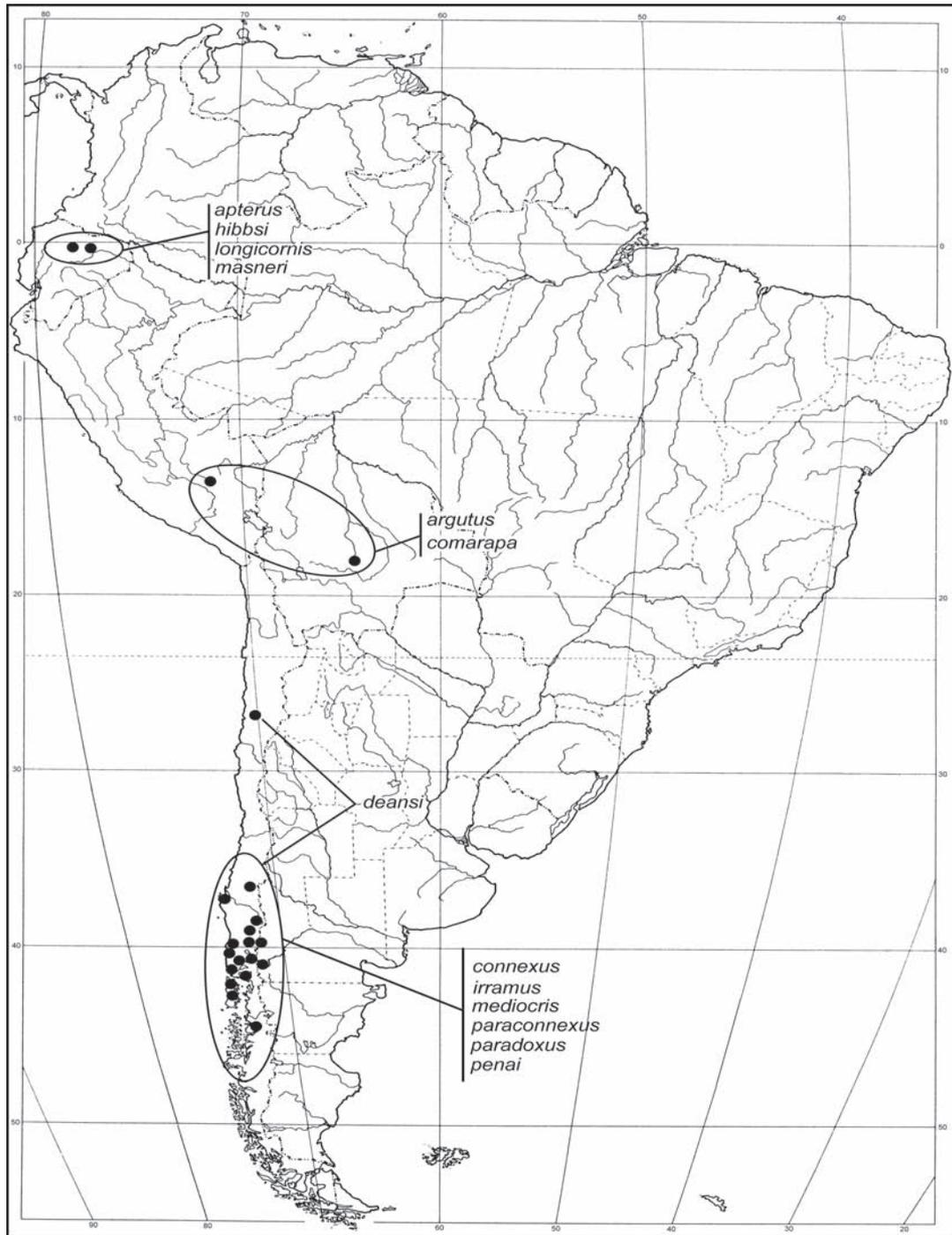


Fig. 50. Known distribution of Ceratomerinae in South America.

resulted in the isolation of this group from Australia (e.g., Transantarctic Mountains, epicontinental seas; MATILE 1990; STUMP & FITZGERALD 1992; FITZGERALD 2002). An alternative model of the opening and expansion of the Pacific Ocean described by MCCARTHY (2005) can explain an exclusive New Zealand – southern South America or southeast Australia – southern South America tract.

The placement of the Neotropical *C. paradoxus* group within the Australian *C. campbelli* group (see Section 6) illustrates both an intra-generic and inter-

continental pattern of great significance. This phylogenetic pattern means that *Ceratomerus* was so well distributed and diversified that species groups occurred across Gondwana before the breakup, and that these species groups must be very old and the genus older still (D. Bickel pers. comm. 2010).

The complex geographic history of New Zealand will be the focus of an on-going revision of the Ceratomerinae from these islands by this author. Many relict empidooids have clearly survived in this region, including the endemic genus, *Glyphidopeza*.

7.2. South American regional patterns

The South American species of Ceratomerinae, based on current records, occur primarily in three biogeographic provinces (Fig. 50) (MORRONE 2006) and may be more widespread with greater collecting efforts in the gap regions. Species of the *C. paradoxus* and *mediocris* groups, as well as *C. irramus* and most records of *C. deansi* are confined to the Subantarctic Subregion, primarily situated in the Valdivian Forest and Maule provinces (*sensu* MORRONE 2006). *Ceratomerus medicris* is also known from the Santiago Province of the Central Chilean Subregion. *Ceratomerus deansi* is also known from the Atacama Province of the South American transition zone. The second known region of South American ceratomerines occurs in the Napo Province of the Amazonian Subregion. The third region of South American ceratomerines is at the eastern edge of the Yungas Province of the Amazonian Subregion. This province consists of the western slopes of the Andes up to an altitude of 3500 m (MARRONE 2006).

8. Acknowledgements

I am indebted to the following curators and their respective institutions for the loan of specimens: T. Saigusa (BLKU), J. Chainey and E. McAlister (BMNH), N.L. Evenhuis (BPBM), S.A. Marshall (DEBG), K. Ueda (KMNH), C. Daugeron (MNHN), A.R. Plant (NMWC), N.E. Woodley (USNM), T. Pape (ZMUC). Scanning electron micrographs were taken by G. Avern (Australian Museum, Sydney) and Ako & Takuji Tachi (Kyushu University, Fukuoka). S.E. Brooks (CNC) provided technical assistance in creating the cladograms and habitus photos. Klaus Klass is thanked for his critical comments on an earlier draft. D. Bickel (Australian Museum) and T. Dikow (Field Museum, Chicago) kindly reviewed the manuscript.

9. References

- AMORIM D.S., SANTOS C.M.D., DE OLIVEIRA S. 2009. Allochronic taxa as an alternative model to explain circumantarctic disjunctions. – *Systematic Entomology* **34**: 2–9.
- BICKEL D.J. 2006. *Papallacta* (Diptera: Dolichopodidae), a new stenopterous genus from the páramo of Ecuador. – *Tijdschrift voor Entomologie* **149**: 209–213.
- BRUNDIN L. 1966. Transantarctic relationships and their significance as evidenced by chironomid midges with a monograph of the subfamilies Podonominae and Aphroteniinae and the austral Heptagyiae. – *Kungliga Svenska Vetenskaps-Akademiens Handlingar Ser. 4* **11**: 1–472 + 30 plates.
- COLLIN J.E. 1928. New Zealand Empididae based on material in the British Museum (Natural History). – *British Museum (Natural History)*, London. 110 pp.
- COLLIN J.E. 1933. Empididae. – *Diptera of Patagonia and South Chile* **4**: 1–334.
- CRANSTON P.S. 2005. Biogeographic patterns in the evolution of Diptera. Pp. 274–311 in: YEATES D.K., WIEGMANN B.M. (eds.), *The Evolutionary Biology of Flies*. – Columbia University Press, New York.
- CRANSTON P.S., EDWARD D.H.D., COLLESS D.H. 1987. *Archaeochlus* Brundin: a midge out of time (Diptera: Chironomidae). – *Systematic Entomology* **12**: 313–334.
- CRANSTON P.S., EDWARD D.H.D. 1992. A systematic reappraisal of the Australian Aphroteniinae (Diptera: Chironomidae) with dating from vicariance biogeography. – *Systematic Entomology* **17**: 41–54.
- CRANSTON P.S., EDWARD D.H.D. 1999. *Botryocladius* gen.n.: a new transantarctic genus of orthocladine midge (Diptera: Chironomidae). – *Systematic Entomology* **24**: 305–333.
- DAUGERON C., D'HAESE C.A., PLANT A.R. 2009. Phylogenetic systematics of the Gondwanan *Empis macrorrhyncha* group (Diptera, Empididae, Empidinae). – *Systematic Entomology* **34**: 635–648.
- EVENHUIS N.L. 1999. *World Catalog of Bee Flies (Diptera: Bombyliidae)*. – Backhuys Publishers, Leiden. xlviii + 756 pp.
- FITZGERALD P.J. 2002. Tectonics and landscape evolution of the Antarctic plate since Gondwana breakup, with an emphasis on the West Antarctic rift system and the Transantarctic Mountains. Pp. 453–469 in: GAMBLE J.A., SKINNER D.N.B., HENRYS S. (eds.), *Antarctica at the Close of a Millennium. Proceedings of the 8th International Symposium on Antarctic Earth Science*. – The Royal Society of New Zealand Bulletin **35**.
- GRIMALDI D., CUMMING J. 1999. Brachyceran Diptera in Cretaceous ambers and Mesozoic diversification of the Eremoneura. – *Bulletin of the American Museum of Natural History* **239**: 1–124.
- GROOTAERT P., SHAMSHEV I. 2008. Notes on the halobiont genus *Chersodromia* (Diptera: Hybotidae) from Tunisia with the descriptions of a new brachypterous species and notes on brachyptery in empidoids – *Bulletin Société Royale Belge d'Entomologie* **144**: 57–63.
- MADDISON W.P., MADDISON D.R. 2003. *MacClade 4: Analysis of phylogeny and character evolution. Version 4.06*. – Sinauer Associates, Sunderland, Massachusetts.
- MARTYNOV A.V. 1936. On some new materials on the arthropods from Kuznetsk basin. – *Izvestiyn Akademii nauk SSR, ser. Biol. No. 6*: 1251–1264 [In Russian with English summary].
- MATILE L. 1990. Recherches sur la systématique et l'évolution des Keroplatidae (Diptera, Mycetophiloidea). – *Mémoires Museum National d'Histoire Naturelle série A*, **148**: 1–682.
- MCALPINE J.F. 1981. Morphology and terminology – Adults [Chapter] 2. Pp. 9–63 in: MCALPINE J.F., PETERSON B.V., SHEWELL G.E., TESKEY H.J., VOCKEROTH J.R., WOOD D.M. (coords.), *Manual of Nearctic Diptera, Volume 1. Agriculture Canada Monograph 27*. – Supply and Services Canada, Hull.
- MCCARTHY D. 2005. The trans-Pacific zipper effect: disjunct sister taxa and matching geological outlines that link the Pacific margins. – *Journal of Biogeography* **30**: 1545–1561.
- MCLOUGHLIN S. 2001. The breakup history of Gondwana and its impact on pre-Cenozoic floristic provincialism. – *Australian Journal of Botany* **49**: 271–300.
- MORRONE J.J. 2006. Biogeographic areas and transition zones of Latin America and the Caribbean Islands based on panbiogeographic and cladistic analyses of the entomofauna. – *Annual Review of Entomology* **51**: 467–494.

- PARAMONOV S.J. 1959. X. Zoogeographical aspects of the Australian Diptero fauna. Pp. 164–191 in: KEAST A., CROCKER R.L., CRISTIAN C.S. (eds.), *Biogeography and Ecology of Australia. Monographiae biologicae* 8. – Dr W. Junk, The Hague.
- PARAMONOV S.J. 1961. Notes of Australian Diptera (XXXII–XXXVI). XXXIII. A new genus of Empididae from Tasmania. – *Annals and Magazine of Natural History* (13) **4**: 100–102, pls. V–VI.
- PHILIPPI R.A. 1865. Aufzählung der chilenischen Dipteren. – *Verhandlungen der kaiserlich-königlichen zoologisch-botanischen Gesellschaft in Wien* **15**: 595–782.
- PLANT A.R. 1995. A new species of *Ceratomerus* Philippi (Dipt., Empididae, Ceratomerinae) from Chile. – *Entomologist's Monthly Magazine* **131**: 123–125.
- SAIGUSA T. 2006. Homology of wing venation of Diptera. – A handout distributed at the 6th International Congress of Dipterology, Fukuoka, Japan. 26 pp.
- SANMARTÍN I., RONQUIST F. 2004. Southern hemisphere biogeography inferred by event-based models: Plant versus animal patterns. – *Systematic Biology* **53**: 216–243.
- SINCLAIR B.J. 1995. Generic revision of the Clinocerinae (Empididae), and description and phylogenetic relationships of the Trichopezinae, new status (Diptera: Empidoidea). – *The Canadian Entomologist* **127**: 665–752.
- SINCLAIR B.J. 1997. *Icasma* Collin and an allied new genus, *Glyphidopeza* from New Zealand (Diptera: Empidoidea; Ceratomerinae). – *Records of the Australian Museum* **49**(2): 195–211.
- SINCLAIR B.J. 2000. 1.2. Morphology and terminology of Diptera male terminalia. Pp. 53–74 in: PAPP L., DARVAS B. (eds.), *Contributions to a Manual of Palearctic Diptera, Volume 1. General and Applied Dipterology*. – Science Herald, Budapest. 978 pp.
- SINCLAIR B.J. 2003a. Taxonomy, phylogeny and zoogeography of the subfamily Ceratomerinae of Australia (Diptera: Empidoidea). – *Records of the Australian Museum* **55**: 1–44.
- SINCLAIR B.J. 2003b. Southern African Empidoidea (Diptera): phylogenetic patterns and biogeographic implications. – *Cimbebasia* **19**: 205–213.
- SINCLAIR B.J. 2008. The systematics of New World *Clinocera* Meigen (Diptera: Empididae: Clinocerinae). – NRC Research Press, Ottawa. viii + 245 pp.
- SINCLAIR B.J., CUMMING J.M. 2000. Revision of the genus *Apterodromia* (Diptera: Empidoidea), with a redefinition of the tribe Ocydromiini. – *Records of the Australian Museum* **52**: 161–186.
- SINCLAIR B.J., CUMMING J.M. 2006. The morphology, higher-level phylogeny and classification of the Empidoidea (Diptera). – *Zootaxa* **1180**: 1–172.
- SMITH K.G.V. 1969. The Empididae of Southern Africa (Diptera). – *Annals of Natal Museum* **19**: 1–347.
- STUCKENBERG B.R. 1999. Antennal evolution in the Brachycera (Diptera), with a reassessment of terminology relating to the flagellum. – *Studia Dipterologica* **6**: 33–48.
- STUMP E., FITZGERALD G.P. 1992. Episodic uplift of the Transantarctic Mountains. – *Geology* **20**: 161–164.
- SWOFFORD D.L. 2002. PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods), Version 4.0b10. – Sinauer Associates, Sunderland, Massachusetts.
- YANG D., ZHANG K., YAO G., ZHANG J. 2007. *World Catalog of Empididae (Insecta: Diptera)*. – China Agricultural University Press, Beijing. vi + 599 pp.