A revision of the New World genus *Aptilotella* Duda (Sphaeroceridae: Limosininae)

by

Stephen Pui Lam Luk

A Thesis
presented to
The University of Guelph

In partial fulfilment of requirements
for the degree of
Master of Science
in
Environmental Biology

Guelph, Ontario, Canada

© Stephen Pui Lam Luk, December, 2013
ABSTRACT

A revision of the New World genus *Aptilotella* Duda (Sphaeroceridae: Limosininae)

Stephen Pui Lam Luk
University of Guelph, 2013
Advisor: Professor S.A. Marshall

The genus *Aptilotella* Duda (Diptera: Sphaeroceridae: Limosininae) is redefined and revised. The type species, *Aptilotella borgmeieri* Duda is redescribed, and twenty-one species are described as new: *Aptilotella andersoni*, *A. angela*, *A. caerulea*, *A. corona*, *A. diffisa*, *A. ebenea*, *A. gemmula*, *A. germana*, *A. gloriosa*, *A. gracilis*, *A. involucris*, *A. macula*, *A. pennifera*, *A. pichinchensis*, *A. pyropanda*, *A. quadrata*, *A. quatuorchela*, *A. radians*, *A. sphyra*, *A. umbracatus*, and *A. vivus*. A phylogenetic analysis and key to species are presented, with illustrations and notes on distribution.
ACKNOWLEDGEMENTS

I was very privileged to have the opportunity to study insects under the instruction of Dr. Stephen A. Marshall. He guided my choice to take on *Aptilotella* over other sphaerocerid genera, and provided financial support for the duration of this project. Dr. Marshall’s publications and macrophotography have long captivated me, from my childhood explorations in Algonquin Provincial Park in Ontario, to my recent expeditions to the tropical forests of Ecuador.

Part of my entomological training as an undergraduate student came from courses taught by Drs. Gard W. Otis and Paul K. Sibley. They have graciously devoted time as members of my advisory committee, and I value their feedback and guidance.

This revision of *Aptilotella* would not have been possible without the dipterous donations from the Leaf Litter Arthropods of Mesoamerica (LLAMA) project. Dr. Robert S. Anderson (Canadian Museum of Nature) single-handedly contributed over half of the material. His specimens represent every one of the newly described species except *A. caerulea*, and constitute the only material for eight of these species. I named one of them *Aptilotella andersoni* as a tribute to Dr. Anderson’s prolific collecting efforts.

Dr. Sandy Smith (Department of Food Science, University of Guelph) very kindly granted me access to scanning electron microscopy equipment. Dr. Smith walked me through every procedure, and was very delightful to work with.

I have greatly benefited from the support and company of past and present colleagues at the University of Guelph Insect Systematics Lab: Matthew Bergeron, Adam Brunke, David Cheung, Morgan Jackson, Adam Jewiss-Gaines, Joel Kits, Nichelle Lomas, Gil Miranda, Steven Paiero, and Andrew Young. Dave Cheung and Adam Brunke were always thoughtful and enthusiastic
toward my projects, particularly when I was still working on fireflies and other beetles. Steve Paiero and Morgan Jackson assisted in many aspects of curation and computation such as database, mapping, illustration, and phylogenetics software. Joel Kits and Matt Bergeron oriented me to sphaerocerid taxonomy and illustration. Andrew Young was an excellent coworker in the field in Ecuador. Many of these individuals are avid insect photographers, and I have received at least a tip or two from each of them.

I thank my family: my parents Raymond and Gloria, and sisters Stephanie and Angela, for surrounding me with unwavering affection and affirmation, and constantly exhorting me to excellence in faith and character. Thanks likewise to my grandparents Henry and Fanny, and Aunt Grace and Vivian Fung. Uncle Antony would have been thrilled to see this thesis.

I am deeply grateful for my brothers and sisters in Guelph Asian Christian Fellowship, who steadfastly stirred me up to love and good works during my university career.

I am indebted to God, my Lord Jesus Christ, who loved me and gave himself for me. By grace I have been saved through faith (Ephesians 2:8), that I am resolved to live with all my might, soli Deo gloria.
Figure 1 *Aptilotella macula* sp. nov., holotype male.
# TABLE OF CONTENTS

ACKNOWLEDGEMENTS ......................................................................................................................... iii

LIST OF TABLES ........................................................................................................................................ ix

LIST OF MAPS .......................................................................................................................................... ix

LIST OF FIGURES ................................................................................................................................. ix

1. INTRODUCTION ................................................................................................................................. 1
   Natural history of *Aptilotella* ............................................................................................................... 2
   Sphaerocerid taxonomy and *Aptilotella* ........................................................................................... 3
   Research objectives ............................................................................................................................. 5

2. MATERIALS AND METHODS ............................................................................................................. 6
   Sources of material ............................................................................................................................... 6
   Acronyms of depositories ..................................................................................................................... 7
   Specimen preparation .......................................................................................................................... 7
   Illustrations .......................................................................................................................................... 8
   Scanning electron microscopy ............................................................................................................ 9
   Terminology and abbreviations .......................................................................................................... 10
   Measurements and ratios .................................................................................................................... 11
   Distributional records ......................................................................................................................... 12

3. PHYLOGENY .......................................................................................................................................... 12
   Phylogenetic analysis .......................................................................................................................... 12
   Characters used in the phylogenetic analysis of *Aptilotella* ............................................................ 13
   Results of phylogenetic analysis ......................................................................................................... 19
Character evolution and the terricolous existence ........................................... 25

4. ZOOGEOGRAPHY ........................................................................................... 30

5. TAXONOMY .................................................................................................... 32

Generic description ............................................................................................. 32
Identification key .................................................................................................. 35

Key to the described species of Aptilotella ......................................................... 36
Species accounts ................................................................................................. 42

Aptilotella borgmeieri Duda .................................................................................. 42
Aptilotella caerulea sp. nov. .................................................................................. 43

The Aptilotella germana Species Group .............................................................. 46

Aptilotella germana sp. nov. ............................................................................... 47
Aptilotella pyropanda sp. nov. ............................................................................. 49
Aptilotella gracilis sp. nov. .................................................................................. 52
Aptilotella diffisa sp. nov. .................................................................................... 56
Aptilotella involucris sp. nov. ............................................................................. 59

The Aptilotella corona Species Group ................................................................. 62

Aptilotella sphyra sp. nov. .................................................................................. 63
Aptilotella andersoni sp. nov. ............................................................................. 65
Aptilotella quatuorcheula sp. nov. ..................................................................... 68
Aptilotella gloriosa sp. nov. ................................................................................ 71
Aptilotella pennifera sp. nov. ............................................................................. 74
Aptilotella corona sp. nov. .................................................................................. 78
Aptilotella radians sp. nov. ................................................................................ 80
Aptilotella ebenea sp. nov. ................................................................. 84
Aptilotella gemmula sp. nov. ................................................................. 86
The Aptilotella quadrata Species Group .............................................. 89
  Aptilotella quadrata sp. nov. ............................................................ 90
  Aptilotella umbracatus sp. nov. .......................................................... 94
The Aptilotella angela Species Group ................................................. 97
  Aptilotella angela sp. nov. ............................................................... 97
  Aptilotella pichinchensis sp. nov. ....................................................... 100
Aptilotella vivus sp. nov. ................................................................. 102
Aptilotella macula sp. nov. ............................................................... 105

6. CONCLUSION ...................................................................................... 108
  Aptery and the higher classification of Limosininae ......................... 108
  Concluding remarks .......................................................................... 109

7. REFERENCES ...................................................................................... 111

8. MAPS AND FIGURES .......................................................................... 115
LIST OF TABLES

TABLE

1 Character state matrix for *Aptilotella* .......................................................... 18

LIST OF MAPS

MAP

1 Distributions of *Aptilotella* species from Mexico to Honduras ....................... 115
2 Distributions of *Aptilotella* species from Costa Rica to Panama ...................... 116
3 Distributions of *Aptilotella* species (Clade 2) in South America ..................... 117

LIST OF FIGURES

FIGURE(S)

1 *Aptilotella macula* sp. nov., male habitus drawing ........................................ v
2 *Aptilotella angela* sp. nov., male habitus photograph ................................. 2
3 *Aptilotella quadrata* sp. nov., male habitus drawing .................................... 90
4 *Aptilotella umbracatus* sp. nov., male habitus drawing ............................... 93
5 Most parsimonius trees .................................................................................. 118
6 Phylogeny of *Aptilotella* ................................................................................ 120

[Scanning Electron Micrographs]

7–8 *Aptilotella caerulea* sp. nov., male habitus ................................................. 121
9–11 *Aptilotella germana* sp. nov., male: 9–10, habitus; 11, terminalia .............. 122
Aptilotella pyropanda sp. nov., male: 12–13, habitus; 14, terminalia ........... 124

Aptilotella gracilis sp. nov., male: 15–16, habitus; 17, left wing; 18, terminalia


................................. 126

Aptilotella diffisa sp. nov., male: 19–20, habitus; 21, terminalia ............... 128

Aptilotella involucris sp. nov., male: 22–23, habitus; 24, terminalia ........... 130

Aptilotella sphyra sp. nov., male: 25–26, habitus; 27, terminalia ............... 132

Aptilotella andersoni sp. nov., male: 28–29, habitus; 30, terminalia ........... 134

Aptilotella quatuorchenla sp. nov., male: 31–32, habitus; 33, terminalia ...... 136

Aptilotella gloriosa sp. nov., male: 34–35, habitus; 36, terminalia ............. 138

Aptilotella pennifera sp. nov., male: 37–38, habitus; 39, terminalia .......... 140

Aptilotella corona sp. nov., male: 40–41, habitus; 42, terminalia ............... 142

Aptilotella radians sp. nov., male: 43–44 habitus; 45, terminalia .............. 144

Aptilotella gemmula sp. nov., male: 46–47, habitus; 48, terminalia .......... 146

Aptilotella umbracatus sp. nov., male: 49–50, habitus; 51, terminalia ........ 148

Aptilotella pichinchensis sp. nov., male: 52–53, habitus; 54, terminalia ...... 150

Aptilotella vivus sp. nov., male: 55–56, habitus; 57, terminalia ............... 152

Aptilotella macula sp. nov., male: 58–59, habitus; 60, terminalia .......... 154

[Illustrations]

Aptilotella caerulea sp. nov.: 61–67, male genitalia; 68, male left wing; 69–72, female genitalia; 73, head ................................................................. 156

Aptilotella germana sp. nov.: 74–79, male genitalia; 80–83, female genitalia

................................................................................................. 159

x
Aptilotella pyropanda sp. nov.: 84–89, male genitalia; 90–93, female genitalia

Aptilotella gracilis sp. nov.: 94–100, male genitalia; 101, male left wing; 102–105, female genitalia; 106, head

Aptilotella diffisa sp. nov.: 107–112, male genitalia; 113–116, female genitalia

Aptilotella involucris sp. nov.: 117–122, male genitalia; 123–126, female genitalia; 127, male mid leg

Aptilotella sphyra sp. nov.: 128–134, male genitalia; 135, male left wing; 136–139, female genitalia; 140, male mid tibia

Aptilotella andersoni sp. nov.: 141–146, male genitalia; 147–150, female genitalia

Aptilotella quatuorchela sp. nov.: 151–157, male genitalia; 158–161, female genitalia; 162, male mid tibia

Aptilotella gloriosa sp. nov.: 163–168, male genitalia; 169–172, female genitalia

Aptilotella pennifera sp. nov.: 173–178, male genitalia; 179, male left wing; 180–183, female genitalia

Aptilotella corona sp. nov.: 184–189, male genitalia; 190–193, female genitalia; 194, male head

Aptilotella radians sp. nov.: 195–201, male genitalia; 202, head; 203–206, female genitalia
Aptilotella ebenea sp. nov.: 207–212, male genitalia; 213–216, female genitalia ...

Aptilotella gemmula sp. nov.: 217–223, male genitalia; 224–227, female genitalia

Aptilotella quadrata sp. nov., male genitalia .......................................................... 201

Aptilotella umbracatus sp. nov.: 234–239, male genitalia; 240–243, female genitalia .......................................................... 203

Aptilotella angela sp. nov.: 244–249, male genitalia; 250–253, female genitalia

Aptilotella pichinchensis sp. nov.: 254–258, male genitalia; 259–262, female genitalia .......................................................... 209

Aptilotella vivus sp. nov.: 263–267, male genitalia; 269–272, female genitalia ..... .......................................................... 212

Aptilotella macula sp. nov.: 273–278, male genitalia; 279–282, female genitalia .......................................................... 215
1. INTRODUCTION

Sphaeroceridae is a nearly cosmopolitan family of minute (usually 1–3 mm) and typically dull and dark-coloured Diptera. These inconspicuous but ubiquitous flies are associated with sites of organic decay, with many having developed specialized morphologies and lifestyles that enable them to exploit microhabitats ranging from animal burrows to phytotelmata (Marshall & Buck, 2010). A handful of flightless sphaerocerid lineages occur in leaf litter in tropical montane forests worldwide. These flies are usually strikingly beetle-like or ant-like in appearance (Fig. 2). Many have reduced or lost their wings and halteres, with the accompanying atrophy of flight musculature leading to compaction of the thorax (Richards, 1951, 1966; Hackman, 1964). They are also characterized by reduction or loss of chaetotaxy, ocelli, and sometimes the eyes (Richards, 1951, 1967b), and frequently have a broadened prosternum that may serve to support robust legs for running (Richards, 1962, 1967b; Hackman, 1964). Most of these terricolous sphaerocerid taxa are in the large subfamily Limosininae, including the Neotropical genus *Aptilotella* Duda.

The name *Aptilotella* is a combination of the Greek *aptilos*, “unfeathered,” and Latin *tellus*, “[of the] earth,” reflecting both the insects’ aptery and seclusive habits. The genus was erected in 1924 by the German dipterologist Oswald Duda, for a series of unusual apterous sphaerocerids from Petrópolis, Brazil, which he named *Aptilotella borgmeieri* in honour of the discoverer, Thomas Borgmeier. The genus *Aptilotella* is here considered to include several species of strongly brachypterous to apterous flies that are generally less than 2 mm in length, compact and shining, black or bicoloured, and with robust legs and reduced chaetotaxy.
Natural history of Aptilotella

All species of *Aptilotella* inhabit montane cloud forest or páramo in Central and South America, at elevations between 1,400 and 3,500 m above sea level. Collection labels associated with adult specimens record habitats with overstorey compositions dominated by *Alnus*, *Quercus*, *Polylepis*, or species of Bambuseae. In Costa Rica, *Aptilotella involucris* sp. nov. has been sifted from forest litter “adjacent to [a] sphagnum bog,” while a female belonging to an as yet undescribed species was collected along a stream margin. A paratype male of *Aptilotella vivus* sp. nov. was sifted from streamside litter in Venezuela.

Knowledge of *Aptilotella* life history is exceedingly scarce. Labels indicate that adults were mostly sifted from leaf litter, with a few being taken in pan traps baited with dung, carrion, or compost. Immature stages remain unknown, though the larvae probably develop as microbial grazers like other sphaerocerids (Marshall & Richards, 1987; Marshall & Buck, 2010), and the
adults likely stay close to food sources. Marshall et al. (2011) provide a photograph of a female of an undescribed species perched on the gill of a mushroom in Costa Rica. This suggests that at least some species in the genus may be mycophagous, but the observed behaviour might have been entirely incidental. Richards (1951) raised the possibility that species of *Aptilotella* might be myrmecophilus. Comparing the structure of the first antennal flagellomere in *A. borgmeieri* to that of a macropterous ant-loving species of *Anommonia* Schmitz from Africa, he wrote: “*[A. borgmeieri]* of which a single male has been found in Brazil may also be a myrmecophile.” This tenuous connection was followed much later by an unsubstantiated report of *A. borgmeieri* and a homalomitrine sphaerocerid associating with *Eciton* army ants in Brazil (Richards, 1968). Such an association is unlikely *Eciton* species are found in lowland rainforests well below the elevations inhabited by *Aptilotella*.

**Sphaerocerid taxonomy and *Aptilotella***

Sphaerocerid taxonomy commenced early in the 19th century and gained momentum during the 20th century (Roháček et al., 2001). As of four decades ago, the size of the family was unclear, with counts between just 300 described species (Richards, 1967a) up to as many as 700 described species (Hackman, 1969). Roháček et al. (2001) comprehensively catalogued the world fauna, including 111 genera and 1,339 valid species. Within another decade, these totals had grown to 141 genera and 1,550 valid species (Marshall et al., 2011), with new species being added regularly. Nevertheless, the higher classification of the family remains in need of revision (Marshall & Buck, 2010), with many genera, including *Aptilotella*, awaiting proper phylogenetic investigation.
Aptilotella has hardly been mentioned in the published literature since its description, based on one species from Brazil, by Duda (1924). Richards (1967a) first catalogued the genus with Central and South American Sphaeroceridae, whereas Hackman (1969) simply noted its distribution as “Neotropical.” Roháček et al. (2001) provided a thorough catalog entry, with the subsequent catalog update contributing the first photographic record of Aptilotella (Marshall et al., 2011). Richards (1951) briefly described A. borgmeieri in a key to the then-known genera of brachypterous and apterous sphaerocerids, and replicated the couplet in an expanded key (Richards, 1965). Much later, Marshall and Buck (2010) presented a novel key to the Neotropical sphaerocerid genera, with updated characters separating Aptilotella from other apterous genera. They also noted that additional species of Aptilotella have been identified and were awaiting description.

The entirety of published phylogenetic discussion on Aptilotella is encapsulated in one comment by Marshall and Buck (2010): “This might be just an apterous clade of the large genus Pterogramma.” Aptilotella is superficially similar to flightless members of the exceptionally diverse genus Pterogramma, from which it has been separated by the absence of orbital and outer vertical bristles, and sometimes also the reduction of ocellar and inner vertical bristles (Marshall & Buck, 2010). However, these bristles are present in some Aptilotella and many species currently treated as brachypterous Pterogramma, so other characters must be explored to more adequately distinguish the genera. The investigation of the possible affinities between Aptilotella and Pterogramma is central to this thesis, and raises two major questions. Can the monophyly of Aptilotella be supported by synapomorphies independent of Pterogramma? If so, is Pterogramma without Aptilotella a paraphyletic group, or is Aptilotella merely a lineage of the giant genus Pterogramma?
Research objectives

Research objectives were to describe new species of *Aptilotella* and examine their distribution and relationships. Central to the investigation are tests of two hypotheses:

1. *Aptilotella* is monophyletic.
2. *Pterogramma* without *Aptilotella* is monophyletic (i.e., the recognition of *Aptilotella* as a genus does not render *Pterogramma* paraphyletic).

These objectives were met through the following activities:

1. Curation of specimens in the University of Guelph Insect Collection, supplemented by fresh material from the Leaf Litter Arthropods of Mesoamerica (LLAMA) project.
2. Dissection of male and female terminalia for comparison between species of *Aptilotella*, and also to the *Pterogramma* species described by Smith and Marshall (2004).
3. Illustration of genitalia and other characters useful for species identification.
4. Preparation of phylogenetic trees, distributional data, and an identification key to the species.

An additional objective was to perform molecular analysis of ethanol-preserved *Aptilotella* and *Pterogramma* from the LLAMA project. Regrettably, this objective had to be abandoned due to inadequate fresh material, which is necessary because dried specimens 1–2 mm in size rarely yield informative DNA.

Unusual forms and undescribed species continued to accumulate over the course of the study, until it became apparent that a comprehensive revision of *Aptilotella* was not possible within the framework of a time-limited MSc project. Since it was necessary to establish a basic treatment of the genus using an ample selection of species, the project was narrowed to the just over twenty
species that had been adequately examined and illustrated. A list of morphological characters was compiled based on these species, in order to construct the initial phylogeny of *Aptilotella*.

2. MATERIALS AND METHODS

**Sources of material**

Approximately 1,000 specimens of *Aptilotella* and similar Neotropical flightless taxa were examined at the University of Guelph Insect Collection, School of Environmental Sciences, Guelph, Ontario (DEBU). All material is point-mounted with the exception of several specimens in ethanol. This material had largely been processed out of alcohol in a critical point dryer, which enhanced preservation of form and pigmentation (Gordh & Hall, 1979). Non-critical point dried *Aptilotella* were less affected by air drying than most other Limosininae; their heavily sclerotized body resists shrivelling, the minute wings rarely warp, and colour degradation is minimal.

Several *Aptilotella* species treated in this study were collected as early as the 1970s. Since then, taxonomic and geographical coverage of the genus has expanded substantially thanks to intensified collecting and to survey work specifically targeting terricolous insects. Surveys of Neotropical terrestrial invertebrate biodiversity, notably the five-year “Leaf Litter Arthropods of Mesoamerica” (LLAMA) project, contributed the bulk of material used in this study. Berlese funnels and Winkler sifters were highly effective tools for capturing *Aptilotella* specimens. Siftate preserved in alcohol consistently yielded dozens of species of Sphaeroceridae, mostly *Pterogramma* and other common limosinine genera, and usually at least a few brachypterous or apterous sphaerocerids.
In 2011, a search for *Aptilotella* was conducted in two apparently suitable habitats in the Pichincha Province of Ecuador, namely, the Bellavista Cloud Forest Reserve and the Pasachoa Forest Reserve. Two species, *Aptilotella gemmula* sp. nov. and *Aptilotella ebenea* sp. nov., had been previously collected at Bellavista, but no specimens were found during the 2011 attempt.

**Acronyms of depositories**

Note: if no acronym is indicated for material examined, it was deposited in DEBU.

- **DEBU** University of Guelph Insect Collection, School of Environmental Sciences, Guelph, Ontario, Canada
- **INBC** Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica
- **QCAZ** Departamento de Biología, Pontífica Universidad Católica del Ecuador, Quito, Ecuador
- **UNAM** Universidad Nacional Autónoma de México, Mexico City, Mexico
- **UNSP** Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil.

**Specimen preparation**

*Aptilotella* are best studied under high magnification with bright lighting to illuminate fine chaetotaxy. Very high precision is necessary for dissecting the minute genitalia of these flies. Dissection commenced with severing the abdomen from the thorax by applying pressure to its ventral surface with an insect pin or ultra-fine forceps. To prevent particularly rigid specimens from snapping off the point, separation was facilitated by initially cutting with a sharpened probe around a tergite beyond the syntergite. The abdomen was cleared of soft tissue through heating in 10% potassium hydroxide (KOH) for 15 minutes. Thereafter, the abdomen was removed from
the solution, neutralized of remaining KOH by soaking in 10% glacial acetic acid, rinsed in
deionized water, and transferred into glycerin. These steps were frequently repeated to permit
manual removal of excess tissue, since the first heating in KOH did not so much clear the
crushed as it softened the viscera-packed abdomen.

*Aptilotella* terminalia are here defined as the combination of the epandrium and sternites 5
and 6+7, and in the female, segments 8–10 (see for example, Figs. 61–64, 69–71). At no more
than 0.4 mm in diameter, these structures are exceedingly difficult to handle. Fortunately, the
heavily sclerotized *Aptilotella* terminalia are able to withstand moderate manipulation. Even
normally membranous structures such as spermathecae, which tend to collapse upon transfer into
glycerin, hold their shape quite well. Dissections were performed in glycerin on a depression
slide using a bent-tipped size 0 insect pin and a probe made from a 0.1 mm diameter pin inserted
into the end of a matchstick. The male terminalia were teased apart so that each sclerite could be
illustrated individually, whereas the female terminalia were left intact with the spermathecae still
inside the abdomen. The left wing of brachypterous specimens was removed and slide mounted
in glycerin without additional treatment. Dissections are permanently stored in 6 × 12 mm
polyethylene genitalia vials pinned beneath the specimen labels.

**Illustrations**

This project involved the preparation of over 200 detailed illustrations of terminalia as well
as several legs and heads. Drawings were preferred over photographs because they capture fine
details in the subject at a resolution level defined by the illustrator, which is unconstrained by the
magnification and resolution limits of digital photography. They also omit clutter such as soft
tissue remnants, fragments of sclerites, and debris, which are unavoidable in photographs.
The subject to be illustrated was positioned on a depression slide near the margin of the depression, and held in place by a glass coverslip to prevent drifting in the glycerin. Using a Nikon Labophot compound microscope with camera lucida projector, a drawing was traced in pencil on paper. It was subsequently finished with a 0.2 mm ink pen on a sheet of translucent design vellum superimposed over the pencil drawing. The species designation and specimen identifier (DEBU number, if applicable) were recorded on draft and completed drawings.

**Scanning electron microscopy**

Scanning electron microscopy (SEM) was employed to photograph the dorsal and left lateral habitus, and intact male terminalia. This was done using an Emitech K550 sputter coater and a Hitachi S-570 scanning electron microscope at the Department of Food Science, University of Guelph, Guelph, Ontario.

Only male specimens in good condition were selected for imaging. Three species could not be prepared for scanning due to limited stock: *A. ebenea*, *Aptilotella quadrata* sp. nov., and *Aptilotella angela* sp. nov. Each specimen was meticulously cleared of surface debris using the pin-tipped probe. The paper point was then carefully removed from the pin and attached to a piece of double-sided adhesive tape pressed onto an aluminum stub, leaving the specimen suspended over the edge of the stub. This orientation allowed a clear view of the habitus, but required the tip of the point to be temporarily bent upward with fine forceps prior to imaging the terminalia. Specimens were arranged four to a stub, and coated with a 7 nm layer of gold-palladium in the sputter coater. After photography, each sputter-coated point was detached from the stub, rejoined to the original pin and data labels, and returned to the corresponding series.
Terminology and abbreviations

Morphological terminology generally follows the Manual of Central American Diptera (Cumming & Wood, 2009). The term “microptery” was used to describe highly advanced brachyptery (refer to Hackman, 1964). The processes of the postgonite are described based on what they articulate with (“for pregonite” or “for basiphallus”). Distiphalic terminology was adapted from Smith and Marshall (2004). Several new terms were devised to describe structures considered unique to *Aptilotella*, and are defined as follows. The “paired arched sclerites” (Figs. 78, 88) are a pair of confluent ventral sclerites arching through the lateral flanking sclerites. They are unique to the *Aptilotella germana* species group. The “club-shaped sclerite” (Figs. 132, 155, 177) is the elongated basal article of the ventral flanking sclerite, found in members of the *Aptilotella corona* species group. Also in this species group are the “medial paired sclerites” (Figs. 133, 156, 188), a pair of convergent sclerites distal to the lateral flanking sclerites. They are replaced in Clade 2 by the “curved dorsal sclerites” (Figs. 221, 248, 257, 267), which are similar to the medial paired sclerites but ascend nearly vertically and are generally stouter and more sclerotized. In members of the *A. quadrata* species group, the “dorsal sclerite” (Figs. 232, 238) is a heavily sclerotized, rod-shaped structure arising from between the lateral flanking sclerites of the distiphallus.

Abbreviations were used for labelling micrographs and illustrations, following Smith and Marshall (2004).
Measurements and ratios

Measurements and ratios were standardized as follows:

1. Body length: distance from apex of facial tubercle to tip of abdomen.

2. Width of medial stripes on frons: ratio between greatest width of a single stripe and total width of frons between eye margins. The same ratio applies to ocular stripes.

3. Length of ocellar bristle: ratio between length of bristle and medial length of frons from ptinial suture to occipital margin.

4. Shape and size of scutellum: ratios between medial length of disc and greatest width of disc, and between greatest width of disc to width of scutum.

5. Length of scutellar bristles: ratio between length of apical bristle and basal bristle.

6. Male cercus: ratio between basal width, and distance from midpoint of base to tip of cercus.

7. Postgonite: ratio between distance from articulatory process for basiphallus to tip of descending arm, and width from posterior margin perpendicularly to apex of articulatory process for pregonite.

8. Length of female cercus: ratio between length of cercus and its greatest diameter.

9. Length of spermathecal ducts: in the paired spermathecae, ratio between diameter of a fully inflated spermatheca, and distance from attachment point to branching point at the common duct.
Distributional records

The distribution of each *Aptilotella* species was visualized in Google™ Earth software (version 6.1.0.5001; Google Inc., 2010). This platform is practical because the intuitive interface permits instant localization, visualization, and archiving of collection data. It is also ideal for studying species that inhabit high elevations, since the high resolution three-dimensional rendering of terrain facilitates reasonably accurate interpretation of local geography. Each unique collection locality was assigned an individual “placemark” based on the label data, using precise GPS coordinates where these are specified. In spite of its utility, the basic version of Google™ Earth used in this study was unsatisfactory for displaying static maps. Therefore, distribution maps were generated in ArcGIS software (version 9.2, build 1324; ESRI Inc., 1999–2006) using latitude-longitude data exported from Google™ Earth.

3. PHYLOGENY

Phylogenetic analysis

The twenty-one newly described species of *Aptilotella* were scored for 46 morphological characters, mostly from chaetotaxy and male genitalia. *Aptilotella borgmeieri* was scored for 18 external characters based on Duda’s (1924) description. Characters were polarized using the functional in-group and functional out-group criterion (Waltrous & Wheeler, 1981; Maddison et al., 1984), based on a hypothetical ancestor of *Aptilotella*, and with reference to *Pterogramma*. Two members of the Central American *Pterogramma madare* species group were selected for the out-group: *Pterogramma madare* (Spuler, 1925) and *Pterogramma meridionale* (Malloch, 1914). These species were used because they are morphologically similar to *Aptilotella*. Many
Pterogramma species were simply incompatible with the matrix and could not be scored for genitalic characters.

A character matrix (Table 1) was generated using Mesquite phylogenetics software (version 2.75; Maddison & Maddison, 2011) and exported for phylogeny construction in Tree Analysis Using New Technology software (TNT Willi Hennig Society Edition, version 1.1; Goloboff et al., 2008). Tree analysis parameters were set to do a traditional search with memory space for 90,000 trees and 5,000 replicates. The strict consensus tree was constructed with default parameters on. Trees were imported back into Mesquite for optimization, and finalized in Adobe Illustrator CS4 (version 14.0.0; Adobe Systems Inc.).

Characters used in the phylogenetic analysis of Aptilotella

The 46 morphological characters are organized by body region and sex. Character states were scored as plesiomorphic (0), apomorphic (1), or multistate (1–3). Unordered multistate characters are marked with an asterisk (*).

Habitus

1. Body texture: 0 – pruinose; 1 – polished

Head

2. Orbital bristles: 0 – one, distinctly stronger than orbital setulae; 1 – absent

3. Interfrontal setae: 0 – three or more pairs; 1 – two pairs, less frequently one pair only; 2 – absent

4. Ocellar bristle length: 0 – subequal to or longer than frons; 1 – two-thirds or less than the length of frons; 2 – ocellar bristle absent
5. Ocelli: 0 – present; 1 – absent

6. Frons, stripes: 0 – one pair on interfrontal sutures and usually also an orbital pair; 1 – none

7. Frons, pale pruinose spots: 0 – none; 1 – one in each ocular emargination; 2 – one in each ocular emargination and elsewhere on frons

8. Facial excavation*: 0 – bare; 1 – lower margin with a pruinose silvery-white band; 2 – with pruinose silvery-white or iridescent spots (Fig. 194)

9. Genal chaetotaxy: 0 – lower margin setaceous; 1 – vibrissa only, and rarely one or two setae behind

Thorax

10. Pruinose pleural stripe: 0 – none; 1 – one or two longitudinally on anepisternum

11. Scutal markings: 0 – none; 1 – with pruinose longitudinal vittae

12. Scutal microtrichosity: 0 – uniform, at least medially; 1 – none, except marginally

13. Scutellar microtrichosity: 0 – uniform, at least on disc; 1 – none, except marginally

14. Scutellar bristles: 0 – apical pair at least twice as long as basal; 1 – apical pair not more than twice as long as basal; 2 – subequal in length

15. Mid tibial bristles: 0 – three anterodorsal and one distal posterodorsal; 1 – two anterodorsal and one distal posterodorsal; 2 – one or two anterodorsal only

16. Male fore femur, ventral setal comb: 0 – absent; 1 – present

17. Ventral modified chaetotaxy on male mid leg: 0 – present on tibia, also on trochanter and/or femur (Fig. 127); 1 – at least some on tibia or femur (Fig. 162); 2 – absent

18. Wings: 0 – macropterous; 1 – brachypterous, at least in male; 2 – micropterous; 3 – rudimentary
Abdomen

19. Lateral remnant of syntergite 1: 0 – fused to syntergite; 1 – partially separated from syntergite as a small square disc (Fig. 3)

20. Tergal setae: 0 – uniform; 1 – only one or two sparse distal rows

21. Tergal microtrichosity: 0 – uniform; 1 – along basal margin only; 2 – none

Male terminalia

22. Posteromedial tab-like piece of sternite 5*: 0 – absent; 1 – strong and bridging sternite 5 and synsternite 6+7 (Fig. 144); 2 – conical and articulating with posteromedial process of sternite 5 (Figs 96, 98)

23. Posteromedial margin of sternite 5*: 0 – at most shallowly emarginate and flat, or strongly lobed (Figs. 231, 275); 1 – strongly emarginate and raised (Fig. 110); 2 – nearly or completely divided by emargination (Figs. 77, 87); 3 – twice emarginate (Fig. 198)

24. Posteromedial processes of sternite 5*: 0 – absent; 1 – single process present (Fig. 266); 2 – paired and heavily sclerotized and clasper-like (Figs. 97, 131)

25. Synsternite 6+7*: 0 – simple; 1 – medial bridge very narrow; 2 – medial bridge flanked by arching lobes (Fig. 246); 3 – medial bridge flanked by prominent prongs (Fig. 96)

26. Cercal chaetotaxy*: 0 – with normal or sensory setae only; 1 – with at least one very long seta and sometimes one or more shorter setae adjacent (Fig. 163); 2 – with a long seta and thickened setae (Fig. 196); 3 – with a large claw-like seta (Fig. 264)

27. Cercal setulae: 0 – clothing most of outer surface (Fig. 42); 1 – present, scattered or basal (Fig. 45); 2 – absent

28. Hypandrium: 0 – symmetrical; 1 – hypandrium weakly asymmetrical; 2 – hypandrium and prehypandrial sclerites strongly asymmetrical
29. Ejaculatory apodeme*: 0 – discoid or inconspicuous; 1 – columnar (Fig. 88); 2 – spindle-shaped (Fig. 238)

30. Basiphallus: 0 – square (Fig. 132); 1 – cylindrical (Fig. 248); 2 – arched (Fig. 188)

31. Ventrobasal sclerite: 0 – divided (Fig. 111); 1 – single (Fig. 221); 2 – absent

Distiphallus

32. Dorsal sclerite: 0 – absent; 1 – present (Fig. 238)

33. Lateral flanking sclerites: 0 – ventrobasally separate; 1 – ventrobasally fused

34. Membranous sacs*: 0 – absent; 1 – sheet-like, between lateral flanking sclerites (Fig. 277); 2 – paired, arising at distal margin of lateral flanking sclerites (Fig. 199)

35. Dorsal dentition*: 0 – absent; 1 – clothing the membranous sacs, lateral flanking sclerites, or other dorsal surfaces (Figs. 111, 257); 2 – crowning the club-shaped sclerite of distiphallus (Fig. 188)

36. Ventral flanking sclerites*: 0 – two or fewer articles (Fig. 211); 1 – tripartite, articles separate (Fig. 248); 2 – tripartite, with the basal and medial articles ascending (Fig. 188); 3 – tripartite, with the medial and distal articles fused (Fig. 238)

37. Basal article of ventral flanking sclerite: 0 – absent; 1 – simple and fused to lateral flanking sclerite (Fig. 111); 2 – fused to lateral flanking sclerite and bearing a dorsal arm (Fig. 248); 3 – modified into a club-shaped sclerite ascending through lateral flanking sclerite (Fig. 188)

38. Medial paired sclerites*: 0 – absent; 1 – arising from between ventral flanking sclerites, slender distal portion parallel (Fig. 188); 2 – arising from between ventral flanking sclerites, distal portion spatulate (Fig. 99)
39. Curved dorsal sclerites*: 0 – absent; 1 – arising from between lateral flanking sclerites, slender and twisting (Fig. 248); 2 – arising from between lateral flanking sclerites, club-shaped (Fig. 221)

40. Paired arched sclerites: 0 – absent; 1 – arching through lateral flanking sclerites and with an elaborate terminus (Fig. 78)

41. Ventral sclerites: 0 – absent; 1 – a pair below ventral flanking sclerites (Fig. 121)

42. Descending medial sclerite*: 0 – absent; 1 – rod-shaped, descending distal to lateral flanking sclerites (Fig. 121); 2 – stalked with a saddle-shaped terminus (Fig. 111)

Female terminalia

43. Epiproct: 0 – sclerotized; 1 – indistinct or reduced

44. Hypoproct*: 0 – indistinct or reduced; 1 – reduced to a pair of setaceous discs (Fig. 182); 2 – divided into two narrow strips (Fig. 92)

45. Spermathecae: 0 – pear-shaped or modified (Fig. 206); 1 – finely ridged (Fig. 262); 2 – simple (Fig. 172)

46. Spermathecal ducts: 0 – shorter than one spermathecal diameter and very stout (Fig. 206); 1 – shorter than two spermathecal diameters; 2 – longer than two spermathecal diameters
Table 1 Character state matrix for *Aptilotella*. Two *Pterogramma* species were included for the out-group. 0 = plesiomorphic; 1 = apomorphic; 1–3 = multistate; ? = data unavailable

<table>
<thead>
<tr>
<th>Species</th>
<th>Character numbers</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1</td>
</tr>
<tr>
<td>1234567890</td>
<td></td>
</tr>
<tr>
<td>ancestor</td>
<td>0000000000</td>
</tr>
</tbody>
</table>
| *P. madare*       | 0011001000 | 0001000000 | 0000010?21 | 00?0101000 | 00?????
| *P. meridionale*  | 1001010000 | 0101001000 | 1010210?00 | 0011100000 | 000121 |
| *A. caerulea*     | 1011001200 | 0021011100 | 0001110220 | 0010000000 | 001000 |
| *A. germana*      | 1011011101 | 0112101200 | 0020011111 | 0011000001 | 001222 |
| *A. pyropanda*    | 1011011010 | 0110201300 | 2020011011 | 0010000001 | 001222 |
| *A. gracilis*     | 1011011010 | 0102002100 | 0211310101 | 0001112000 | 001022 |
| *A. diffisa*      | 1011000100 | 0002102300 | 0012211202 | 0012111000 | 121021 |
| *A. involucris*   | 1001010100 | 0002100301 | 0020111011 | 0012121100 | 001122 |
| *A. sphyra*       | 1011010100 | 0010011100 | 0012011000 | 0010223100 | 001021 |
| *A. andersoni*    | 1011001100 | 0001102300 | 1120001102 | 0012231000 | 001022 |
| *A. quattuorhela* | 1011001100 | 0001101300 | 0110010102 | 0010223100 | 001122 |
| *A. gloriosa*     | 1011000100 | 0100101300 | 1110011102 | 0012231000 | 001022 |
| *A. pennifera*    | 1011001100 | 0110101100 | 1110010102 | 0012231000 | 001121 |
| *A. corona*       | 1011000210 | 0112101301 | 2110010102 | 0012231000 | 001122 |
| *A. radians*      | 1001000010 | 1111102300 | 1030121101 | 1012010000 | 001000 |
| *A. ebenea*       | 1011000010 | 0101112300 | 0001112021 | 1002011000 | 001012 |
| *A. gemmula*      | 1111100011 | 1101112300 | 0001010021 | 1010010020 | 001012 |
| *A. quadrata*     | 1101101011 | 0112012311 | 2000120210 | 2110131000 | 00???? |
| *A. umbracatus*   | 1111100011 | 0100202311 | 2000012021 | 2110131000 | 001010 |
| *A. pichinchensis*| 1110100010 | 0101123000 | 1000212001 | 1010120100 | 001012 |
| *A. angela*       | 1110100010 | 0112123000 | 1000212001 | 1010012010 | 001012 |
| *A. borgmeieri*   | 1110110101 | 011221230? | 2????????? | ?????????? | ????? |
| *A. macula*       | 1100112011 | 0112202300 | 0000000101 | 0011120010 | 001012 |
| *A. vivus*        | 0122110011 | 0111212200 | 0001131001 | 1010002010 | 011012 |
Results of phylogenetic analysis

Nine most parsimonious trees were retained from the analysis (Fig. 5). Figure 6 displays the strict consensus tree. Most of the species resolve to Clade 1, which contains *Aptilotella diffisa* sp. nov., *A. involucris*, and the *Aptilotella corona* species group, or to Clade 2, which contains the *Aptilotella quadrata* and *Aptilotella angela* species groups. *Aptilotella caerulea* sp. nov., the *Aptilotella germana* species group, *Aptilotella gracilis* sp. nov., and *Aptilotella radians* sp. nov. do not belong in either clade.

All *Aptilotella* have a strong anterodorsal ocular emargination as in *Pterogramma*, and two of the synapomorphies of *Pterogramma* identified by Smith and Marshall (2004): an excavated face with a tubercle between the antennae, and a single apical bristle on the maxillary palp. Many *Aptilotella* retain a single orbital bristle (character 2) and have simplified mid tibial chaetotaxy apparently derived from the *Pterogramma* arrangement of three anterodorsal bristles and one distal posterodorsal bristle (character 15). Several elements of the *Aptilotella* aedeagus are shared at least with the *P. madare* species group: divided ventrobasal sclerites (character 31, state 0), lateral flanking sclerites, and simple ventral flanking sclerites (character 36, state 1). It is evident from these characters that *Aptilotella* may be a lineage of *Pterogramma*, which would suggest a paraphyletic interpretation of *Pterogramma*.

The genus *Aptilotella* is diagnosed by the compact and shiny body (character 1), zero to two pairs of interfrontal setae (character 3), shortened ocellar bristle (character 4), reduced mid leg chaetotaxy (characters 15, 17), and very short to rudimentary wings (character 18). These characters loosely unify all *Aptilotella* and distinguish them from short-winged *Pterogramma*, which possess a heavily pruinose body in which the thorax is noticeably longer than wide and the wings have partial but distinctive venation. The definitive character of *Aptilotella* is the pair of
ventral flanking sclerites of the distiphallus (character 36, states 1–3). During the evolution of the genus, these have subdivided into three articles, which have become modified via elongation and branching. Other genitalic characters tend to be reduced in *Aptilotella*; for example, the ejaculatory apodeme (character 29, state 0) has degenerated to a small disc that is often hard to see, though it has evolved a columnar shape in the *A. germana* species group and a spindle shape several times. Females have a reduced or indistinct epiproct (character 43) and sclerotized, spherical spermathecae (character 45, states 1–2).

The basal polytomy gives rise to *P. meridionale*, *P. madare*, *A. caerulea*, and the remaining *Aptilotella*. *Aptilotella caerulea* possesses a very simple aedeagus (characters 30, 36, 37, all state 0; Figs. 65, 66) with a rather strongly asymmetrical hypandrium (character 28, state 2). Females have a sclerotized epiproct (character 43; Fig. 69) and pear-shaped spermathecae (character 45, state 0). Together with the orbital bristle (character 2) and small ocelli (character 5), these conditions suggest that *A. caerulea* is closer than other *Aptilotella* to the ancestral *Pterogramma*. It is here treated as a species of *Aptilotella* given the compact and shiny body with reduced chaetotaxy and strongly reduced wings (character 18, state 2; Fig. 68).

The *A. germana* species group lacks ventral flanking sclerites of the distiphallus (character 36, state 0), a plesiomorphic condition in the genus. It is unequivocally monophyletic given the dramatically modified terminalia: the nearly or fully divided male sternite 5 (character 23, state 2; Figs. 77, 87), a columnar ejaculatory apodeme (character 29, state 1; Figs. 78, 88), and paired arched sclerites of the distiphallus (character 40; Figs. 78, 88). In females, the hypoproct is distinctly divided into two narrow strips (character 44, state 2; Figs. 82, 92). The mid tibia uniquely bears two short, subequal anterodorsal bristles (character 15, state 2). The two pruinose
stripes (character 10) on the pleuron of *Aptilotella germana* sp. nov. probably originated independently of the single stripe located on the same pleurites in Clade 2 species.

Tripartite ventral flanking sclerites are present in *A. gracilis*, which is arguably the most bizarre member of the genus. This species resembles a “chimaera” of various *Aptilotella* (6, 9, 14, 18, 36) and *Pterogramma* (15, 33) characters, yet is exceptionally autapomorphic, with extremely slender surstyli (Fig. 95), prominent posterior prongs on synsternite 6+7 (character 25, state 3; Fig. 96), and spatulate medial paired sclerites of the distiphallus (character 38, state 2; Fig. 99). Also unique to *A. gracilis* is the semi-conical tab-like piece of male sternite 5 (character 22; Figs. 96, 98), akin to the structure found in the *A. corona* species group, but differing in that it fits neatly into a clasper-like process (character 24; Fig. 97) stemming from the same sternite.

The monophyly of Clade 1 is supported mainly by the progressive modification of the posteromedial margin of male sternite 5, which bears a paired or single process that apparently functions partly to conceal the cerci (Figs. 24, 30, 33, 39). Paired clasper-like processes (character 24, state 2; Figs. 110, 120, 131) appear in *A. diffisa*, *A. involucris*, and *Aptilotella sphyra* sp. nov. They are quite likely symplesiomorphic, being replaced by a single tab-like piece (character 22, state 1) in the *A. corona* species group, possibly through fusion of the elements. This event evidently occurs somewhere between *A. sphyra* and the remaining *A. corona* group species, and is accompanied by arching of the basiphallus (character 30, state 2; Figs. 121, 145, 167) and development of medial paired sclerites in the distiphallus (character 38, state 1; Figs. 121, 133, 189). In the ventral flanking sclerite of the *A. involucris* distiphallus, the basal and medial articles appear to rise slightly (character 36, state 2; Fig. 121), a condition that becomes pronounced in the *A. corona* species group. The hypoproct (character 44, state 1; Figs. 125, 149,
has degenerated into a pair of setaceous discs, which can be lost (Fig. 138) as in other
*Aptilotella*.

On the other hand, *A. diffisa* and *A. involucris* differ significantly from the *A. corona* species
group in possessing asymmetrical prehypandrial sclerites of the hypandrium (character 28, state
2). Moreover, the convoluted distiphallus (Figs. 111, 121) has paired sclerites below the ventral
flanking sclerite (character 41)—though oddly, these are also present in *Aptilotella andersoni* sp.
nov.—and a miscellany of smaller sclerites internally and beneath, such as the saddle-shaped
sclerite (character 42, state 2) in *A. diffisa*. Each lateral flanking sclerite bears a finely denticulate
(character 35, state 1) apical membranous pouch (character 34, state 2). These two species
definitely belong in Clade 1, but may not be sister species since they differ markedly in body
form (Figs. 19, 20, 22, 23) and distiphallic structure.

The *A. corona* species group is clearly monophyletic. In the distiphallus, the basal article of
the ventral flanking sclerite has developed a clubbed shape and a cap of denticles (characters 37,
state 3, and 35, state 2, respectively; Figs. 132, 155, 177, 188), while the medial paired sclerites
(character 38, state 1) have increased in size and narrowed and converged at their midlength. The
latter is considered to be a synapomorphy unrelated to superficially similar structures in *A.
ebenea* (Fig. 211). While *A. sphyra* resolves as the basal species because of its clasper-like
processes and a squared basiphallus (character 30, state 0; Fig. 132), the rest of the group forms a
polytomy. The closely related *A. andersoni*, *Aptilotella quatuorchela* sp. nov., and *Aptilotella
gloriosa* sp. nov. are distinguishable by phylogenetically uninformative chaetotaxic and colour
characters. The sister species *Aptilotella corona* sp. nov. and *Aptilotella pennifera* sp. nov. are
distinguished by the elbowed club-shaped sclerite of the distiphallus (Figs. 177, 188).
The sister group to Clade 2 is *A. radians*, which exhibits characters consistent with the clade, such as reduction of the orbital bristle (character 2; Fig. 202) and chaetotaxy of the gena (character 9), and the single ventrobasal sclerite in the aedeagus (character 31, state 1). It is nonetheless excluded from Clade 2 on the basis of strongly inconsistent characters of the terminalia: a twice posteriorly emarginate male sternite 5 (character 23, state 3; Fig. 198) and ventrally pronged cercus bearing thickened setae (character 26, state 2; Fig. 196), as well as pear-shaped spermathecae with very short ducts (characters 45, 46, all state 0; Fig. 206).

Clade 2 is characterized by loss of the ocelli (character 5) and of cercal setulae (character 27, state 2), and absence of a ventral setal comb in the male fore femur (character 16). The orbital bristle (character 2) is also lost, though not entirely in the basal *A. ebenea*. The hypandrium is symmetrical (character 28, state 0) except for a weak asymmetry in *Aptilotella macula* sp. nov., and the ventrobasal sclerite (character 31) is reduced to one piece or absent. The distiphallus has tripartite ventral flanking sclerites (character 36, state 1) as in Clade 1. Denticles (character 35) have been repeatedly lost and regained, appearing in the *A. quadrata* species group on the dorsal sclerite (character 32; Figs. 238, 248), on the lateral flanking sclerite in *Aptilotella pichinchensis* sp. nov., and as scales covering the membranous sheet (character 34, state 1) between the lateral flanking sclerites in *A. macula*. The spermathecae (character 45, state 1; Figs. 216, 253, 272, 282) are finely ridged. A pruinose stripe is visible on the pleuron (character 10) except in the *A. quadrata* species group.

An enigma in Clade 2 is the relationship between the basal taxa *A. ebenea* and *A. gemmula*. These purported sister species are sympatric and nearly identical externally with the exception of an orbital bristle in the former, but the genitalia share very little in common. The distiphallus of *A. ebenea* (Fig. 211) has a pair of medial paired sclerites (character 38, state 1), and the lateral
flanking sclerites, each with a finely ridged apical membranous sac (character 34, state 2), are ventrally separate (character 33). Except for the lateral flanking sclerites, these characters are all but absent in the distiphallus of *A. gemmula* (Fig. 221), which has the striking apomorphies of a robust and club-shaped curved dorsal sclerite (character 39, state 2) and a pair of internal sclerites. Until additional data (i.e., genetic, broader sampling) become available, two hypotheses are raised to explain this mystery: *A. ebenea* and *A. gemmula* have either diverged drastically from a common ancestral genitalic morphology, or they have spectacularly converged in appearance from unrelated sympatric lineages.

Members of the *A. quadrata* species group possess just one or two enlarged bristles on the mid tibia (character 15, state 2), a character shared with the remainder of Clade 2. On its own, the species group is unequivocally monophyletic. The fully separated lateral remnant of tergite 1 (character 19) is a strong synapomorphy, as is the dorsal sclerite of the distiphallus (character 32; Figs. 232, 238), in which the ventral flanking sclerites have fused medial and distal articles (character 36, state 3). The ventrobasal sclerite is lost in this group alone (character 31, state 2).

The *A. angela* species group and the *A. borgmeieri* cluster together form a monophyletic assemblage based on a pair of synapomorphies in the distiphallus (Figs. 248, 257, 267, 277): slender curved dorsal sclerites (character 39, state 1), and the dorsally branched basal article of the ventral flanking sclerite (character 37, state 2). In members of this clade, the posteromedial margin of male sternite 5 is protruded (character 23, state 0; Figs. 247, 256, 276). No clear synapomorphies have been identified for the *A. angela* species group specifically; however, its members appear to be related based on the arched lobes of synsternite 6+7 (character 25, state 2; Fig. 246), aedeagal morphology (Figs. 248, 257), loss of the pruinose pleural stripe (character 10), and body shape and colouration. The *borgmeieri* polytomy is probably paraphyletic. The
three species are broadly distributed (see section 4 “Distribution”) and have no uniting characters other than their being bare and especially compact, which is attributable to homoplasy.

**Character evolution and the terricolous existence**

The terricolous lifestyle involves inevitable wear and tear, and problems for sensing and locomotion. *Aptilotella* have responded through evolutionary reduction or loss of characters that are disadvantageous to survival. Heavy sclerotization of the cuticle, resulting in a polished, scratch-resistant body (character 1), is a key modification seen in *Aptilotella* and superficially similar limosinine genera such as *Aptilotus* and *Myrmolimosina* Marshall. There is bewildering plasticity in the development of chaetotaxy in *Aptilotella*. Since hairs are easily abraded and may hinder navigation, they are probably subjected to high selective pressure. On the head, genal setae (character 9) are lost in Clade 2 and in *A. gracilis* and *A. corona*, while the ocellar bristles (character 4, state 1) are shortened, or lost as in *A. vivus*, lengthening again only in more derived Clade 2 species. Scutal microtrichosity (character 12) are all gone but for a sparse coat in Clade 1, whereas scutellar microtrichosity (character 13) are more conserved, undergoing independent losses in the *A. germana* species group, *A. corona* and *A. pennifera*, *A. radians*, and most of Clade 2. Scutellar bristles (character 14) seem to have shortened and lengthened randomly, with the apical pair averaging 1.4 to 1.7 times the length of the basal pair. Abdominal chaetotaxy has also tended toward reduction or loss across the genus (characters 20, 21). Tergal setation is dramatically reduced to two rows in the *A. quadrata* species group; *A. involucris* and *A. corona* also possess two rows of regular, albeit unmodified setae. Even cercal setulae (character 27) are gradually lost, completely so in much of Clade 2.
The most interesting chaetotaxic modifications are observed in the mid leg. Strong setae (character 17, state 0; Figs. 127, 140, 162) are rare, appearing extensively only in *A. involucris*, at some length on the tibia in the *A. germana* species group, and on the tibia or femur in most of the *A. corona* species group. The mid tibial bristles (character 15) sequentially depart from the *Pterogramma* arrangement of three anterodorsal bristles and one distal posterodorsal bristle. The middle anterodorsal bristle is always first to disappear, followed by the distal posterodorsal bristle, and then by the proximal anterodorsal bristle as in *A. quadrata* and *A. angela*. The two-bristle arrangements in Clade 2 and the *A. germana* species group are interpreted as independent synapomorphies, since the *A. germana* species group seems to have merely lost two bristles, whereas the loss in Clade 2 is accompanied by enlargement of the remaining bristles.

Flightlessness has evolved many times across diverse dipteran lineages and is common in the Sphaeroceridae. *Aptilotella* may have become flightless as a consequence of specialization for a terricolous lifestyle. Elevation is a possible influence on the evolution of flightlessness in *Aptilotella*. The efficiency of flight decreases with increasing altitude, as air pressure drops and cool temperatures prevail (Hackman, 1964). Large insects compensate behaviourally by basking or thermogenesis, or via physiological or anatomical adaptations such as longer wings with increased surface area in some flies. Roff (1990) suggested that a lower susceptibility to overheating may permit smaller flying insects to physiologically adapt more readily to low ambient temperature, but also stressed the difficulty of testing this. This does not exclude the fact that getting and staying airborne in the thin mountain air is an energetically costly activity for small insects such as *Pterogramma*, which must boost already high wingbeat frequencies to generate sufficient lift. In any case, these constraints by themselves are insufficient to account for the loss of flight, since cloud forests teem with minute flying insects.
Habitat homogeneity also confers pressures leading toward flightlessness (Roff, 1990). The leaf litter blanket of montane forests is fairly stable and uniform, and is insulated from seasonal climatic changes and the elements (Hackman, 1964). Resources are probably uniformly distributed but concealed and, therefore, more efficiently located on foot. There is thus less incentive for flying long distances between patches of suitable habitat (Roff, 1990). Hence, terricolous flies would have secretive habits, which Hackman (1964) insisted are connected with the loss of wings. He observed that, even among some cloud forest Sphaeroceridae and Ephydridae that are fully capable of flight but live near the ground, individuals are not often inclined to fly. It is likely that there is a lack of selection for wings, flight muscles, and halteres in terricolous Diptera. In an environment where the ability to run and jump is advantageous over flying, energy invested into building and nourishing flight organs is better utilised for foraging, mating, and reproduction. Since smaller wings allow more resources to be devoted to functions that enhance fitness, a population would gradually be driven towards aptery.

Wing loss is a frequent homoplasy in Aptilotella. At least three transitions from strong brachyptery to aptery (character 18) have occurred independently in taxa with both apterous and brachypterous forms: the A. germana species group, the A. corona species group, and Clade 2. Brachypterous wings (state 1) are present in A. gracilis (Fig. 101) and A. sphyra (Fig. 135), and in males only in A. caerulea (Fig. 68) and A. pennifera (Fig. 179), exhibiting three very different morphologies. Two occurrences and types of micropterous wings (state 2) are known. The first is in A. germana as a dark and thickened bud (Fig. 9). The second, in A. vivus, is pale and narrowly lance-shaped (Fig. 56), and might be better described as “micro-stenopterous.” In the apterous species, all that remains of the wing is a minute, pale rudiment (state 3). There is no trace of halteres in all of the Aptilotella species. These complex gyroscopic organs are critical to the
maintenance of equilibrium and maneuverability in dipteran flight (Fraenkel, 1939; Pringle, 1948). The general rule has thus been established that, if flight is lost and the wings are consequently reduced or lost, the halteres will correspond in reduction or loss (Bezzi, 1917; Fraenkel, 1939; Hackman, 1964). This is true for *Aptilotella*, but prominent halteres are retained in the apterous and similarly terricolous *Howickia* Richards, which is essentially the Indopacific counterpart of *Aptilotella*.

The ocelli (character 5) are often lost along with wings and halteres. These photoreceptors have been shown to mediate phototaxis through integration with the compound eyes in light detection (Kalmus, 1945; Cornwell, 1955; Hu & Stark, 1980). Like halteres, ocelli may contribute to orientation in take-off and flight (Kalmus, 1945). Where present in *Aptilotella*, they are always minute, and their loss in Clade 2 is due perhaps to flightlessness as well as life in the undergrowth. Ocelli, although superior to compound eyes in photosensitivity (Cornwell, 1955), are probably less efficacious in the constantly dim environment. Perhaps like wings and halteres, the maintenance of ocelli contributes negatively to the fitness of a flightless fly, so that these organs tend to disappear as well.

One more question for consideration is why many *Aptilotella* are brilliantly marked. A red or orange head and thorax may enhance the ant-like appearance of flies traversing a sunlit patch, or camouflage them against variably coloured detritus, but is inconspicuous beneath the cover of leaf litter. Stripes on the frons (character 6), which are common in *Pterogramma*, are retained in *Aptilotella* but also repeatedly lost, as in *A. gracilis, A. involucris, A. sphyra*, and the *A. borgmeieri* cluster. Even more remarkable is the reflective pruinosity that adorns half of the species. Silvery-white spots (character 7, states 1–2) are present in the ocular emarginations of *A. gracilis* (Fig. 106), *A. andersoni, A. quatuorchela, A. pennifera, A. quadrata*, and the strikingly
diademed *A. macula* (Fig. 1). Others “wear” a mask over the facial excavation (character 8, states 1–2)—a broad silvery-white band in Clade 1 and the *A. germana* species group, or a pair of “headlights” developed in *A. corona* (Fig. 194). These markings may function in intraspecific communication, possibly in the ultraviolet (UV) range. UV-detecting photoreceptors have been documented in the eyes of a few insect orders, and in Diptera at least among the lower Brachycera (Bishop, 1974). UV-reflecting pruinosity in Diptera (see Silberglied, 1979) has been investigated in an ephyrid fly (Deonier, 1974; Steinly et al., 1978). Hinton (1973) postulated that the white spots and bands on the body and legs of Culicidae function in UV as disruptive patterning. *Aptilotella* pruinosity appears similar in composition. When specimens of Clade 1 species are exposed to a blacklight, weak fluorescence of the pruinosity can be observed, particularly in *A. corona*. Whether apterous sphaerocerids communicate using UV-reflecting pruinosity would be a fascinating hypothesis to test, and may potentially shed light on the significance of *Aptilotella* colouration.
4. DISTRIBUTION

Maps 1–3 depict the distributions of the newly described species of *Aptilotella* based on available collection data. The genus occurs in Central America from central Mexico to Panama, and parts of South America from Venezuela to Bolivia. The known distributions are mostly consistent with the phylogenetic patterns, notably at the species group level.

Both members of the *A. germana* species group occur along the northerly slopes of the Mexican Sierra Madre de Chiapas (Map 1), isolated from the *A. corona* species group except in western Guatemala near the Mexican border where the distribution of *Aptilotella pyropanda* sp. nov. overlaps with that of the *A. corona* species group. Map 1 also depicts the distribution of *A. gracilis* in the Sierra Madre Oriental Mountains in east-central Mexico, which is farther north than all other Central American species, as well as the isolation of *A. radians* in south-central Mexico, which agrees with the exclusion of this species from Clade 2.

The *A. corona* species group occurs in southern portions of the Sierra Madre de Chiapas Mountains from extreme southeastern Mexico to Honduras (Map 1). Near the border of Mexico and Guatemala, *A. andersoni, A. quatuorchela,* and *A. gloriosa* are clustered on the southerly face of the range. These species may have diverged due to the formation of sufficiently isolative geographical barriers, such as the rich network of river valleys in this region that empty into the Pacific. Similar mechanisms were implied by Richards (1957, 1962) to explain the diversification of almost parapatric apterous sphaerocerids inhabiting African montane forests. East of the three species, the well-resolved sister species *A. pennifera* and *A. corona* are almost parapatric in south-central Guatemala. The purported basal species of the group is found further southeast, where the range of *A. sphyra* overlaps the junction of the borders of Guatemala, El Salvador, and Honduras. Over 700 kilometres southeast of the *A. corona* species group, *A.
*involucris* and *A. diffisa* occur largely sympatrically in the Cordillera de Talamanca of central Costa Rica (Map 2), and are also sympatric with the unrelated *A. quadrata*.

Clade 2 is well represented in the northern Ecuadorian Andes (Map 3, inset). There, the *A. angela* species group is scattered across roughly one hundred kilometres, *A. pichinchensis* being sympatric with *A. ebenea* and *A. gemmula*, the nearly identical species which are probably related to each other. The *A. quadrata* species group is the only taxon of the clade found outside of South America, occurring along the Cordillera de Talamanca of Costa Rica and Panama (Map 2). The widely separated species of the *A. borgmeieri* cluster are morphologically convergent as already discussed. In northern South America, *A. macula* and *A. vivus* inhabit western Bolivia and northwestern Venezuela (Map 3), respectively, separated by close to 3,600 km over the Andean topography. Even more isolated is *A. borgmeieri* in the Serra Da Mantiqueira Mountains along the southeastern coast of Brazil, which is remote from the Andean distribution of the South American members of Clade 2.
5. TAXONOMY

Generic description

Genus *Aptilotella* Duda, 1924

Body length 0.9–1.6 mm. Strongly brachypterous to apterous, beetle-like Limosininae with a shining, uniform dark reddish-brown to black or bicoloured body and no halteres.

**HEAD.** Wider than long; ground colour typically pale yellow to orange. Eye large, reniform, with prominent anterodorsal emargination; finely hairy. Frons flat, finely rugose, sometimes with shining posterior portion of orbital plate; frequently marked with a pair of medial brown stripes on the interfrontal sutures and brown orbital stripes along eye margin; ocular emargination sometimes with a pale pruinose spot. Ocellar triangle levelled or reduced to a slightly raised tubercle; ocelli minute or absent; ocellar bristles divergent, two-fifths to subequal to length of frons. Interfrontal setae minute to scarcely visible, in 0–4 convergent pairs on anterior third of interfrontal suture. Orbital setulae minute to inconspicuous, in 2–7 pairs along eye margin. Orbital bristle present or absent. Internal vertical bristles long, slightly convergent. Face shining; when marked, usually with a pruinose silvery-white band as in the *A. corona* and *A. germana* species groups, sometimes spotted or barred. Gena bare or setaceous, infrequently with darkened posteroverentral margin. Antennae separated by less than the diameter of their sockets; typically pale; first flagellomere conical, apically hairy and sometimes darker; arista approximately twice as long as frons and sparsely hairy.

**THORAX.** Approximately as broad as head, cuboid. Scutum convex; microtrichose or bare; uniformly setose and with only one pair of posterior dorsocentral (prescutellar) bristles and a long postalar seta. Scutellum lunate and often very broad, but rarely more than two-thirds width of scutum; microtrichose or bare, with densely tomentose margin. Scutellar bristles in two
marginal pairs; the apical pair long, varying from three times as long as to subequal to basal pair, and subequal to length of scutum. Pleuron dull, unicolored or with dark lower third; uniformly, finely pruinose, occasionally with one or two pale pruinose stripes on anepisternum. Katepisternum with one posterodorsal bristle. Legs robust, typically pale with darker tibiae, and at least mid and hind coxae dark; banded in the A. angela species group; fore tarsus contrasting white in A. gracilis. Mid femur with anteroapical seta; fore tibia with apicodorsal seta; mid tibia with small apicoventral seta, and one to three anterodorsal bristles and usually one distal posterodorsal bristle. Wing generally rudimentary, but paddle-shaped in several species. Haltere entirely absent.

**ABDOMEN.** Round, shining. Tergal setation varying from one or two rows of sparse setae to uniformly setaceous; microtrichosity uniform, confined to basal margin, or absent. Lateral remnant of tergite 1 fused to syntergite except in the A. quadrata species group. Sternites uniformly microtrichose, setae uniform or confined to distal margin.

**MALE TERMINALIA.** Sternite 5 rectangular or lunate; posteromedial margin shallowly to strongly emarginate and frequently concave, or nearly to completely divided as in the A. germana species group; occasionally with a single or paired sclerotized process. In the A. corona species group, a tab-like piece originating from sternite 5 lies perpendicularly with sternite 5 and synternite 6+7. Synternite 6+7 relatively unmodified except in A. gracilis, although in a few species the medial bridge is relatively narrow or flanked by arching lobes. Cerci separated, typically straight or gently curved outward, usually with one very long seta and additional setae of various lengths as well as sensory setae; may or may not be partially clothed in setulae. Surstylus varying from rectangular to saddle-shaped, generally consisting of a conical base modified with lobes or tubercles arrayed with setae and sensory setae. Hypandrium symmetrical
in Clade 2; left pregonite weakly asymmetrical in the *A. corona* species group, and strongly asymmetrical in *A. diffisa* and *A. involucris*. Postgonite gradually curved with a slender and tapering descending arm, or very broad as in the *A. germana* species group; articulatory process for pregonite usually triangular; articulatory process for basiphallus undeveloped or knobbed as in the *A. corona* species group. Basiphallus usually cylindrical, but may be square or stout, or compressed and arched as in the *A. corona* species group. Ejaculatory apodeme discoid and not very prominent in most species, but columnar in the *A. germana* species group and spindle-shaped in the *A. quadrata* species group, *A. gemmula* and *A. ebenea*. Ventrobasal sclerite usually present as a broad or weakly divided, curved band.

Distiphallus with lateral flanking sclerites typically ventrobasally fused; distal margin sometimes giving rise to paired membranous sacs; dorsum sometimes denticulate. A dorsal sclerite arises from between the lateral flanking sclerites in the *A. quadrata* species group. Ventral flanking sclerites tripartite, although the medial and distal articles may be fused as in the *A. quadrata* species group; the basal article generally fused to lateral flanking sclerite, bearing a dorsal arm in Clade 2, modified into a club-shaped sclerite in the *A. corona* species group; the medial article generally elongate, ascending with the club-shaped sclerite in the *A. corona* species group; the distal article usually weaker and expanded. Medial paired sclerites arise from between ventral flanking sclerites in Clade 1. In Clade 2, curved dorsal sclerites arise from the same region. In the *A. germana* species group, paired arched sclerites pass through the lateral flanking sclerites and end in an elaborate terminus. Ventral paired sclerites and various other sclerites of uncertain affinity are present in *A. diffisa* and *A. involucris*, and rarely in the *A. corona* species group.
FEMALE TERMINALIA. Epiproct (tergite 10) reduced, lightly sclerotized to absent, usually clothed in microtrichosity. Each half of tergite 8 strongly sclerotized, convex and rounded or angled, uniformly or marginally setaceous. Hypoproct lightly sclerotized, varying from rectangular to divided into two setaceous discs or rods. Sternite 8 lunate or triangular. Cercus small and fusiform, lightly sclerotized; clothed in small setulae, setaceous in distal half. Spermathecae three in number, with two paired by a short to very long duct to a common duct; relatively sclerotized, spherical or rarely pear-shaped.

Identification key

The draft key by Smith (1994) relies chiefly on colouration and chaetotaxy for the identification of a large number of undescribed brachypterous Pterogramma, including several species here treated as Aptilotella. The following phylogeny-based key is completely reworked for identification of the species of Aptilotella, and includes genitalic characters in addition to external morphology. Aptilotella borgmeieri is included in Clade 2 (see discussion in species account) based on Duda’s (1924) description. Many species remain to be described, so it is advisable to check all determinations against the species-specific characters in the species descriptions. Since the key follows the hypothesized clades and species groups of the genus (Fig. 6), undescribed species are likely to key out to species group or clade at least.
Key to the described species of *Aptilotella*

1 Face with a pair of iridescent bluish-gray bars enveloping a brown square spot at oral margin (Fig. 73); distiphallus simple, with only two pairs of triangular lobes (Fig. 66) .................

................................................................. *A. caerulea* sp. nov. [Dominican Republic]

1’ Face plain or with pruinose silvery-white markings; distiphallus well-developed, with many sclerites ................................................................. 2

2 Fore tarsus white, contrasting with dark fore tibia; frons orange, with three narrow silvery stripes and a large silvery spot in each ocular emargination (Fig. 106); synsternite 6+7 with an asymmetrical pair of large curved processes (Fig. 96); surstylus much longer than epandrium, twisting and tapering to a point (Fig. 95) .............. *A. gracilis* sp. nov. [Mexico]

2’ Fore tarsus dull and not contrasting with fore tibia; frons unmarked or with brown stripes, or with silvery spots only; synsternite 6+7 at most with arched lobes; surstylus short ........... 3

3 Facial excavation pruinose silvery-white at least along oral margin (except in females of *A. involucris*); genal margin typically setaceous; ventrobasal sclerite of aedeagus divided ...... 4

3’ Facial excavation and gena bare; ocelli absent (vestigial in *A. radians*); ventrobasal sclerite of aedeagus single or absent; spermathecae finely ridged ........................................ 13

4 Body stout; mid tibia lacking distal posterodorsal bristle; male sternite 5 very deeply emarginate or divided (Figs. 77, 87); postgonite very broad (Figs. 79, 89); distiphallus with prominent paired arched sclerites passing through lateral flanking sclerites (Figs. 78, 88) ......

.......................................................................................................................... 5 (*A. germana* species group)
4’ Body relatively slender; mid tibia with or without posterodorsal bristle; male sternite 5
shallowly to moderately emarginate, with a single or paired sclerotized process; postgonite
slender; distiphallus without paired arched sclerites ........................................ 6 (Clade 1)

5 Thorax dark brown with two pale pruinose stripes on anepisternum and a dark wing bud (Fig.
9); paired arched sclerites of distiphallus terminating in a lunate process and flanked on each
side by a chain of trifid denticles (Fig. 78) .........................  A. germana sp. nov. [Mexico]

5’ Thorax entirely red-orange, wing buds absent; distiphallus with bilobed distal dorsal sclerite,
paired arched sclerites basally with a pair of triangular lobes and terminating in a sickle-
shaped process (Fig. 88) .........................  A. pyropanda sp. nov. [Mexico, Guatemala]

6 Male sternite 5 with a pair of cercal claspers (Fig. 24); distiphallus containing several pairs of
internal sclerites and a descending ventral sclerite flanked by paired triangular sclerites (Figs.
111, 121) .................................................................................................................. 7

6’ Male sternite 5 with a tab-like piece or paired processes not clasping the cerci (Fig. 30, 33,
42); distiphallus with medial paired sclerites, tripartite ventral flanking sclerite with the basal
article developed into a club-shaped sclerite (as in Fig. 188) ...... 8 (A. corona species group)

7 Body stout, length 1.3 mm; frons striped; male mid femur unmodified; male cercal claspers
curved (Fig. 110); distiphallus ventrally with an asymmetrical saddle-shaped sclerite (Fig.
111) ..........................................................................................................................  A. diffisa sp. nov. [Costa Rica]

7’ Body slender (Figs. 22, 23), length 1.7 mm; frons unmarked; male mid femur swollen (Fig.
127); male cercal claspers bulbous, with a small hook (Figs. 24, 120); distiphallus with
ventral paired sclerites ending in a leaf-shaped sclerite (Fig. 121) ............................
..........................................................................................................................  A. involucris sp. nov. [Costa Rica]
8 Frons unmarked; thorax orange except for dark brown katepisternum; cercus axe head-shaped (Figs 27, 129); basiphallus squared (Fig. 132); distiphallus with hammer-like club-shaped sclerite (Fig. 132) .......................... \textit{A. sphyra sp. nov.} [Honduras, El Salvador]

8’ Frons with brown stripes; thorax orange or brown; cercus slender; basiphallus arched (as in Fig. 188); club-shaped sclerite of distiphallus not hammer-shaped ............................... 9

9 Body strikingly bicoloured, with orange thorax and pleuron dark brown in lower third; ocular emargination lacking pruinose spot; tab-like piece fused to male sternite 5 and antler-like (Figs. 36, 166); club-shaped sclerite of distiphallus bare ........ \textit{A. gloriosa sp. nov.} [Mexico]

9’ Body dark coloured; ocular emargination typically with small pale pruinose spot; male sternite 5 with detached tab-like piece; club-shaped sclerite of distiphallus capped with denticles .............................................................. 10

10 Body and legs completely dark brown; male mid leg without modified or long setae; tab-like piece of male sternite 5 U-shaped (Figs. 30, 144) ............. \textit{A. andersoni sp. nov.} [Mexico]

10’ Legs orange or brown; male mid leg ventrally either with long setae on femur or stout apical setae on tibia (as in Fig. 162); tab-like piece of male sternite 5 bilobed or clasper-like ..... 11

11 Thorax dark reddish-brown, legs orange in male or dark brown with pale tarsi in female; distiphallus with short medial paired sclerites not extending beyond it, ventral flanking sclerite with pincer-like distal article (Fig. 156) ........... \textit{A. quatuorchela sp. nov.} [Mexico]

11’ Legs uniformly brown or reddish-brown in both sexes; distiphallus with long medial paired sclerites, dorsal margins of lateral flanking sclerites meeting only in basal fifth, and elbowed club-shaped sclerites (Figs. 177, 188) ................................................................. 12
12  Thorax black; male with clavate wing pad (Figs. 39, 179); male sternite 5 with a pair of 
sclerotized processes (Figs. 39, 176); basiphallus obtusely arched (Fig. 177); ventral flanking 
sclerite of distiphallus with an apically spatulate medial article, club-shaped sclerite with 
minute denticles (Fig. 177) .................................................  A. pennifera sp. nov. [Guatemala]

12’ Thorax and legs reddish-brown; both sexes apterous; face with a pair of silvery-white spots 
(Fig. 194); tab-like piece of male sternite 5 two-pronged (Figs. 42, 186); basiphallus with 
right-angled arch (Fig. 188); ventral flanking sclerite of distiphallus with apically narrow 
medial article, club-shaped sclerite crowned with large denticles (Fig. 188) ....................

..........................................................  A. corona sp. nov. [Guatemala]

13  Face with a pair of dark brown bars (Fig. 202); scutum with 3 or 5 bold pruinose vittae; 
cercus with a curved ventral prong (Figs. 45, 196) ..............  A. radians sp. nov. [Mexico]

13’ Face and scutum unmarked; pleuron with a pruinose stripe (except in the A. angela species 
group); cercus simple and without setulae ....................................................  14 (Clade 2)

14  Orbital bristle absent or present; thorax squat, half as long as wide (Fig. 47); mid tibia with 
two or three anterodorsal bristles and one distal posterodorsal bristle; abdomen with bluish 
iridescence, uniformly densely setose and microtrichose ........................................  15

14’ Orbital bristle absent; thorax usually at least two-thirds as long as wide; mid tibia with only 
one or two anterodorsal bristles (except in A. pichinchensis); abdomen iridescent or not, but 
never uniformly densely microtrichose ........................................................................  16

15  Orbital bristle present; surstylus bent at a right angle in profile (Fig. 208); male sternite 5 
posteromedia1y shallowly emarginate (Fig. 210); distiphallus with wrinkled membranous 
sacs and medial paired sclerites (Fig. 211) .........................  A. ebenea sp. nov. [Ecuador]
15’ Orbital bristle absent; surstylus triangular in profile (Fig. 218); male sternite 5 posteromedially with a pair of truncate, setaceous tubercles (Figs. 48, 220); distiphallus with club-shaped and knobby curved dorsal sclerites (Figs. 221, 222) ...................................................

.......................................................... A. gemmula sp. nov. [Ecuador]

16 Body relatively bare; legs unicolorous; lateral remnant of tergite 1 separate from syntergite (Figs. 3, 4); aedeagus without ventrobasal sclerite; distiphallus with prominent dorsal sclerite (Figs. 232, 238), ventral flanking sclerite with fused medial and distal articles ............... 

.......................................................... 17 (A. quadrata species group)

16’ Body with regular setae; legs variously coloured; lateral remnant of tergite 1 never fully separate from syntergite; aedeagus with ventrobasal sclerite; distiphallus without dorsal sclerite, ventral flanking sclerite with dorsal arm rising from basal article ............... 18

17 Frons with orange-bordered medial stripes; scutum and scutellum black; male sternite 5 with long, rounded lobes (Fig. 231); dorsal sclerite of distiphallus laterally raised (Fig. 232) 

................................. A. quadrata sp. nov. [Costa Rica]

17’ Frons with brown medial stripes; scutum and scutellum reddish brown, anterior margin of scutum medially and laterally with a minute tomentose patch; male sternite 5 weakly emarginate (Fig. 237); dorsal sclerite of distiphallus with rudder-like ventral keel (Fig. 238)  

................................. A. umbracatus sp. nov. [Costa Rica, Panama]

18 Body highly compact and ovular, length 0.9 mm; frons with either ocellar or vertical bristles, never both; male sternite 5 posteromedially notched and with a hammer-shaped process (Fig. 266; undescribed in A. borgmeieri) .......................................................... 19
18’ Body more teardrop shaped, length 1.3–1.5 mm; frons with both ocellar and vertical bristles; male sternite 5 posteromedially slightly produced (Figs. 247, 256, 275) ...................... 21

19  Body black and shining; frons black with a pair of gray stripes, with ocellar bristles; clypeus and gena black; syntergite as long as other tergites combined … A. *borgmeieri* Duda [Brazil]

19’ Body bluish-gray pruinose with a weak iridescent sheen; frons yellow-orange, all chaetotaxy lost except for outer vertical bristles (Fig. 57); clypeus and gena yellow-orange; syntergite no longer than combined length of tergites 3 and 4 …………….. A. *vivus* sp. nov. [Venezuela]

20  Head with a silvery spot at each corner and in center of frons, and one on lunule (Fig. 1); tibiae unicolorous; abdomen with metallic sheen; surstylus broad, boomerang-shaped (Figs. 60, 273, 274); lateral flanking sclerites of distiphallus supporting a membranous sheet studded with elongate sclerotized scales (Fig. 277) ……………. A. *macula* sp. nov. [Bolivia]

20’ Frons with a pair of straight, narrow, brown medial stripes (Fig. 2); antenna dark brown; pleuron bare, lacking a pruinose stripe; tibiae banded; abdomen not metallic; surstylus rectangular in profile (Figs. 245, 255); distiphallus with neither a membranous sheet nor scales …………………………………………………………… 21 (A. *angela* species group)

21  Thorax black; mid tibia with a single distal anterodorsal bristle; distiphallus with curved dorsal sclerites directed upward, basal article of ventral flanking sclerite with straight dorsal arm (Fig. 248) …………………………………………………………… A. *angela* sp. nov. [Ecuador]

21’ Thorax reddish-brown; mid tibia with two anterodorsal bristles and one distal posterodorsal bristle; distiphallus with curved dorsal sclerites and dorsal arm of basal article both strongly curved (Fig. 257) ……………………………………… A. *pichinchensis* sp. nov. [Ecuador]
Species Accounts

The order of the new species accounts follows the results of the phylogenetic analysis (Fig. 6).

*Aptilotella borgmeieri* Duda 1924

*Aptilotella borgmeieri* Duda, 1924: 74.

Since the type series of *Aptilotella borgmeieri* has apparently been lost, the following redescription of the male is adapted from Duda’s original German description in 1924.

Gapasin (1972) and Smith (1994) both redescribed *A. borgmeieri* based on Duda (1924) and specimens that originated from “a long series in São Paulo [UNSP]” collected by F. Plaumann on an unknown date at 300–600 m in Nova Teutonia (abbreviated NT), Brazil. The structural characters recorded from this specimen by Smith (1994) are inconsistent with Duda’s description, including a reduced orbital bristle and double rows of interfrontal setae. Gapasin (1972) examined a single female from the NT series and illustrates a pair of bean-shaped spermathecae. No such spermathecal morphology is known in other *Aptilotella*. It is possible that Gapasin (1972) illustrated the deflated paired spermathecae, while the third spermatheca was either lost or overlooked. The NT series originated from Serra Geral, a mountain range separate from the Serra Da Mantiqueira Mountains in which the type locality of *A. borgmeieri* is situated. Because of uncertainty about the identity of the species described by Gapasin (1972) and Smith (1994), their notes are not reflected in the redescription below.

**DESCRIPTION.** Body length 0.9 mm. Head ground color dark brown. Frons black, shining; with a pair of narrow, parallel grey stripes. Ocelli absent; ocellar bristle three quarters the length of frons. Interfrontal setae minute, in two or three pairs. Several pairs of orbital setulae present.
Orbital and vertical bristles absent. Face and gena shining; lunule, clypeus, and gena black. Body black, shining. Scutum twice wider than long; sparsely microtrichose. Scutellum approximately twice wider than long. Pleuron black. Legs brown; tarsi light brown; mid tibia with two anterodorsal bristles. Wings absent. Abdomen with large syntergite approximately the length of the other tergites combined.

**TERMINALIA.** Duda (1924) vaguely noted synsternite 6+7 and the epandrium, but did not describe any genitalic characters or dissect any specimens.

**TYPE MATERIAL.** Holotype ♂ (UNSP, not examined and probably lost). BRAZIL: Petrópolis, T. Borgmeier.

**COMMENTS.** Duda’s original description is nebulous, but seems to be consistent with Clade 2. *Aptilotella borgmeieri* most closely resembles *A. vivus*, from which it differs by the shining black body, dark colouration of the frons and gena, long ocellar bristle, and a few pairs of interfrontal setae and orbital setulae. In *A. borgmeieri*, the enlargement of the syntergite is far more pronounced than in other *Aptilotella* species. This is somewhat also noticeable in *A. vivus*.

This species is the only South American *Aptilotella* known outside of the Andes. The type locality, near the eastern coast of Brazil, is more than 2,200 km from that mountain range.

*Aptilotella caerulea* sp. nov.

(Figs. 7, 8, 61–73)

**DESCRIPTION.** Habitus as in Figures 7 and 8. Body length 1.2 mm. Head (Fig. 73) ground color brown. Frons finely rugose, weakly shining; pale areas bluish-gray, the lateral pair attaining front margin of frons and sharply converging on occiput; dark brown medial stripes
each about one-fourth the width of frons, tapering anteriorly; dark brown orbital stripes each narrower than medial stripe, lightening to amber anteriorly; ocular emargination with narrow pale border. Ocellar tubercle slightly raised; ocelli present; ocellar bristle two-fifths the length of frons. Interfrontal setae in two pairs. Orbital setulae in three pairs. Face weakly shining; facial excavation bordered by a pair of iridescent bluish-gray bars, each interjected at oral margin by a brown square spot; gena dull, finely rugose, with a pale pruinose stripe along anterior ocular margin. Antenna brown. Occiput dark brown. Scutum and scutellum dark brown, weakly shining, uniformly densely microtrichose. Scutum deeply creased along posterolateral margin; uniformly setose. Scutellum flat, 1.7 times wider than long, 0.6 times the width of scutum. Scutellar bristles subequal in length, approximately two-thirds the length of scutum. Pleuron black. Legs dark brown; coxae black; distal two-thirds of fore femur and tarsi light brown; fore and hind tibiae with orange medial band, the latter much darker; mid tibia with two anterodorsal and one distal posterodorsal bristle; male mid femur with a setal comb in ventrobasal third. Wing pad (Figs. 8, 68) brown in male and similar in size to scutellum; reduced in female to a small, brown stub with several long apical setae. Abdomen black, shining, uniformly setose and microtrichose. Cercus and surstylus yellow.

**MALE TERMINALIA.** Sternite 5 (Fig. 64) shallowly emarginate in posteromedial one-fourth; fringed with a membranous lining clothed in small hairs; flanked on each side with a patch of setae. Synsternite 6+7 (Fig. 63) reduced; arm of sternite 7 very slender and apically hooked; medial bridge extremely narrow; posteromedially giving rise to a bulbous sclerite with a flared base. Anal aperture very large. Cercus (Figs. 61, 62) approximately twice wider than long; the broad base laterally articulating with a notch in the epandrium; the slender portion bent near apex, with two long basal setae, three medial setae, and two preapical sensory setae. Surstylus
(Figs. 61, 62) saddle-shaped; posterior margin straight, setaceous; anterior margin sinuate.

Postgonite (Fig. 67) rounded; descending arm slender, half the total length and of uniform width, with two anterior and one posterobasal strong marginal sensory setae; posterior margin giving rise to a rounded projection before descending arm; articulatory processes for pregonite and basiphallus both undeveloped and rounded. Aedeagus as in Figures 65 and 66. Basiphallus compressed, squared; posteroventrally humped; articulatory margin with distiphallus straight; anterior margin articulating with aedeagal apodeme; articulatory process for postgonite reduced. Ejaculatory apodeme sinuate, basal half broader and with two sensory pores. Ventrobasal sclerite divided. Lateral flanking sclerite broadly fused ventrobasally; dorsal margin straight, medially fused into a chisel-shaped tab; distal margin slanted. Ventral flanking sclerite rod-shaped, distally expanding outward into a triangular lobe. Dorsal triangular sclerites arising from inside the distal margin of lateral flanking sclerite, expanding outward like ventral flanking sclerites.

FEMALE TERMINALIA. Tergite 7 (Fig. 69) posteromedially shallowly emarginate. Epiproct (Figs. 69, 70) rectangular; medially microtrichose, with two lateral pre-marginal setae. Each half of tergite 8 (Figs. 70, 71) weakly convex, rounded; with setae near margins; lower third shining. Cercus two times as long as wide; with one long apical seta and several other setae. Epiproct very indistinct. Hypoproct (Figs. 70, 71) triangular, apically with four setae. Spermathecae (Fig. 72) finely ridged; with conical invagination; collar ringed by several stubs; sclerotized ducts very short, less than the diameter of a spermatheca.

VARIATION. The iridescent bars may attain an intense cerulean blue colour, while the brown square spot varies significantly in size.

ETYMOLOGY. *Aptilotella caerulea* is named for its vivid facial pruinosity.
TYPE MATERIAL. Holotype ♂. DOMINICAN REPUBLIC: Independencia, 32 km NW La Descrubierta Sabana Real, 1800 m, 26.xi.-5.xii.1991, cloud forest, carrion traps, S. and J. Peck.

PARATYPES. DOMINICAN REPUBLIC: Independencia, 30 km NW La Descrubierta Sabana Real, 1646 m, 25.xi.-5.xii.1991, cloud forest, dung traps (3♂; 9♀); same label but from carrion (4♀); same label as holotype (7♂; 10♀); same label as holotype but dated 26.ix.1991, forest moss and litter (4♂; 4♀).

COMMENTS. This primitive species of Aptilotella possesses orbital bristles and small ocelli, and a very simple distiphallus. The brilliant facial pruinosity is diagnostic.

The Aptilotella germana Species Group

DIAGNOSIS. Members of this species group are defined by the nearly or fully divided male sternite 5, columnar ejaculatory apodeme, and paired arched sclerites of the distiphallus. Additional diagnostic genitalic characters include: postgonite broad with short descending arm; basiphallus squat; and lateral flanking sclerite of distiphallus with posterior descending tab. At first glance, these Aptilotella may be confused with members of the A. corona species group, but are stouter in form and have unicolorous legs. The mid tibia possesses two short, subequal anterodorsal bristles, and in the male bears a row of 5–6 stout peg-like setae in the ventrodistal third. Two species are described from extreme southeastern Mexico and adjacent Guatemala.
**Aptilotella germana sp. nov.**

(Figs. 9–11, 74–83)

**DESCRIPTION.** Habitus as in Figures 9 and 10. Body length 1.0 mm. Head ground color yellow. Frons finely rugose; pale areas silvery-blue; brown medial stripes each about one-fourth the width of frons, diffuse along the anterior margin; brown orbital stripes each half the width of medial stripe; ocular emargination with small pale spot. Ocellar tubercle scarcely raised; ocelli present; ocellar bristle two-fifths the length of frons. Interfrontal setae in two pairs. Orbital setulae minute, in five pairs. Lunule polished; face shining; facial excavation with a silvery-white band continuing onto anterior half of gena; gena weakly shining, setaceous. Antenna brown. Scutum and scutellum dark reddish-brown, shining. Scutum creased along posterolateral margin; uniformly setose. Scutellum bare; flat, 2.4 times wider than long, 0.6 times the width of scutum. Apical scutellar bristles 1.4 times as long as basal. Pleuron dark reddish-brown; with two pale pruinose stripes, the first on upper half of the anepisternum and anepimeron, the second fainter, at margin with katepisternum. Legs yellow ochre; mid and hind coxae brown; mid tibia with two anterodorsal bristles, in male with row of five stout setae in ventrodistal third. Wing pad (Fig. 9) small, dark brown. Abdomen black, shining; tergites each with two rows of setae, three rows on syntergite; sternites finely microtrichose. Epandrium and synsternite 6+7 dark reddish-brown; cercus and surstylus yellow-orange.

**MALE TERMINALIA.** Sternite 5 (Figs. 11, 77) completely divided, the inner margins concave posteriorly and flanked by setae. Synsternite 6+7 as in Figure 76. Cercus (Figs. 11, 74, 75) compressed, 3.5 times as long as basal width; base triangular, clothed in setulae; apex rounded, thickened; midlength with one long seta reaching apex, distally with several evenly spaced marginal setae and preapical sensory setae. Surstylus (Figs. 11, 74, 75) a half-cone;
posteromedia weakly humped and bearing several long setae; apex round and flexed up.

Postgonite (Figs. 11, 79) broad; descending arm short, slender and curved forward; articulatory process for pregonite undeveloped, truncate; lower portion before descending arm acutely angled; articulatory process for basiphallus knobbed with blunt anterior and posterior teeth.

Aedeagus as in Figure 78. Basiphallus stout, cylindrical; posterodorsally humped; articulatory process for postgonite truncate, curved upward. Ejaculatory apodeme pale, with the disc embedded midway. Ventrobasal sclerite divided. Lateral flanking sclerite broadly fused posteriorly, with a narrow descending tab; deeply indented at level of basiphallus; fused dorsally until distal third, where it darkens and tapers to a blunt apex. Paired arched sclerites very dark, originating at descending tab of lateral flanking sclerite; their trunks bearing a truncate lateral process, ascending between lateral flanking sclerites and descending ventrodistally, becoming depressed before merging into a prominent process; this process lunate, broadly rounded, basally formed into a sharp thorn. Paired dorsal sclerites slender, originating within dorsal division of lateral flanking sclerite, apically bearing a club of denticles. Lateral flanking sclerite giving rise to a pair of stubs beneath paired dorsal sclerites, capped in trifid denticles, which descend in a line next to lunate process, broadening and curving posteriorly to the level of its thorns.

**FEMALE TERMINALIA.** Epiproct (Fig. 80) indistinct, triangular; microtrichose. Each half of tergite 8 (Figs. 80–82) convex; apex truncate; distal half setose. Cercus three times as long as wide; with one long apical seta and several preapical setae. Hypoproct (Figs. 81, 82) reduced to a pair of curved, convergent rods; apically microtrichose and with two pairs of setae. Spermathecae (Fig. 83) simple; sclerotized ducts very long, five times the diameter of a spermatheca.
ETYMOLOGY. The species epithet is from the Latin *germanus*, “having the same parents,” since this species and its relatives is characterized by the unmistakable aedeagal morphology.

TYPE MATERIAL. Holotype ♂ (UNAM). MEXICO: Chiapas, Cerro El Calvario, near Tapalapa, 17°11’12″N, 93°7’21″W, 2200 m, 23.vii.2003, wet cloud forest litter, R.S. Anderson.

PARATYPES. MEXICO: Chiapas, same label as holotype (9♂, 10♀); Cerro de Tapalapa, 17°11’16″N, 93°7’23″W, 2260 m, 27.v.2008, cloud forest, ex. sifted leaf litter, R.S. Anderson (♂); Cerro de Tapalapa, 17°11’30″N, 93°7’4″W, 2240 m, 27.v.2008, oak-pine forest, ex. sifted leaf litter, R.S. Anderson (♀).

COMMENTS. The aedeagus of *Aptilotella germana* is incredibly autapomorphic and character-rich. This species differs subtly from all other *Aptilotella* in possessing a minute, dark brown, thickened wing “bud.” Several undescribed species have somewhat larger and triangular wing “buds.”

*Aptilotella pyropanda* sp. nov.

(Figs. 12–14, 84–93)

DESCRIPTION. Habitus as in Figures 12 and 13. Body length 1.1 mm. Head ground color light brown. Frons finely rugose; pale areas silvery; dark brown medial stripes each about one-fourth the width of frons, narrowing toward the anterior margin then diffusing; dark brown orbital stripes each one-third the width of medial stripe; ocular emargination with silvery-white spot. Ocellar tubercle slightly raised, orange; ocelli present; ocellar bristle two-fifths the length of frons. Interfrontal setae, in two pairs. Orbital setulae minute, in three pairs. Lunule with silvery-white spot; face shining; facial excavation with a silvery-white band continuing through ocular margin of gena; clypeus dark brown; gena brown but appearing dark brown from the
front, weakly shining, setaceous. Antenna brown. Scutum and scutellum red-orange, shining. Scutum uniformly setose. Scutellum darker, bare; flat, 2.5 times wider than long, 0.6 times the width of scutum. Apical scutellar bristles twice as long as basal. Pleuron orange. Legs orange; fore femur, tibiae, and tarsi darker; mid tibia with two anterodorsal bristles, in male with row of six stout peg-like setae in ventrodistal third (compare to Figure 127). Wing rudiment brown. Abdomen black, shining; tergites each with two rows of long setae; sternites finely microtrichose. Epandrium and synsternite 6+7 dark reddish-brown; cercus and surstylus dull yellow.

MALE TERMINALIA. Sternite 5 (Figs. 14, 87) deeply emarginate in posteromedial seventh and lined by two rows of thick setae. Synsternite 6+7 (Fig. 86) with slightly arched medial bridge, giving rise to a pair of small sclerites. Cercus (Figs. 14, 84, 85) compressed, four times as long as basal width; base setulose, lateral margin carinate; apex rounded, with two sensory setae; margin at midlength with one long seta and an adjacent sensory seta, and two setae in distal quarter. Surstylus (Figs. 84, 85) saddle-shaped; posteroventral ridge bearing long setae. Postgonite (Fig. 59) broad; descending arm very short and curved forward, with two inner sensory setae; articularatory process for pregonite undeveloped, angular; articularatory process for basiphallus knobbed. Aedeagus as in Figure 88. Basiphallus stout, cylindrical; anterior margin weakly arched; postero-dorsally with a truncate tubercle; articularatory process for postgonite truncate, curved upward. Ejaculatory apodeme columnar, appearing spongy and borne on a disc with four sensory pores. Ventrobasal sclerite divided. Lateral flanking sclerite broadly fused posteriorly, with a broad, curved descending tab; deeply indented at level of basiphallus; fused dorsally until halfway, where it darkens laterally, then dilates and descends, initially nearly converging, then twisting outward and tapering to a point. Paired arched sclerites very dark,
originating at descending tab of lateral flanking sclerite; their trunks basally with an interior protuberance and a large, finely-pointed and convergent triangular outer lobe; ascending and barely entering lateral flanking sclerites before descending again, becoming depressed and merging into a sickle-shaped, twice laterally frilled portion, which gently curves up between the apices of lateral flanking sclerites. Distal dorsal sclerite broad, originating at dorsal division of lateral flanking sclerite; dorsal surface dark and gradually curved; lateral margins straight; distally split into two divergent, upwardly curved lobes.

**FEMALE TERMINALIA.** Epiproct (Figs. 90, 91) triangular, apically rounded and microtrichose. Each half of tergite 8 (Figs. 90–92) convex; margin rounded; sparsely setaceous. Cercus three times as long as wide; with several scattered setae. Hyoproct (Figs. 91, 92) reduced to a pair of curved, convergent rods; apically with a patch of microtrichosity and two pairs of setae. Spermathecae (Fig. 93) simple; sclerotized ducts long, three times the diameter of a spermatheca.

**ETYMOLOGY.** The species epithet is derived from the Greek *pyros*, “fire,” and Latin *pandus*, “bent, curved,” in reference to the fiery colour of the thorax, and the paired arched sclerites of the distiphallus, a defining character of this species and its relatives.

**TYPE MATERIAL.** Holotype ♂ (UNAM). MEXICO: Huixtán, Bazóm, 16°44′19″N, 92°29′18″W, 2450 m, 9.vii.2003, mixed magnolia/oak forest litter, R.S. Anderson.

**PARATYPES.** MEXICO: Chiapas, same label as holotype (4♂; 3♀); San Cristóbal, 15 km E, 16°44′49″N, 92°29′23″W, 2800 m, 29.v.2008, cloud forest, ex. sifted leaf litter (♂, 2♀). GUATEMALA: Huehuetenango, Max, 15°30′24″N, 91°21′52″W, 2750 m, 14.ix.2008, oak/cloud forest, ex. sifted leaf litter, R.S. Anderson (3♂); Todos Santos, 4.4 km W, 15°30′24″N, 91°38′41″W, 2800 m, 14.ix.2008, cloud forest, ex. sifted leaf litter, M.G. Branstetter (♀).
COMMENTS. *Aptilotella pyropanda* is readily recognized by the fiery orange thorax and legs. In dorsal view, the highly reflective silvery-white spots of the ocular emarginations and lunule give the fly an appearance of having three “headlights.” It has a relatively broad range with at least two populations along the Sierra Madre de Chiapas Mountains, one in the extreme Mexican southeast and the other in western Guatemala.

*Aptilotella gracilis* sp. nov.

(Figs. 15–18, 94–106)

**DESCRIPTION.** Habitus as in Figures 15 and 16. Body length 1.3 mm. Head (Fig. 106) ground color orange. Frons finely rugose; with three silvery stripes that are most conspicuous from behind—a very narrow medial stripe from the anterior margin to ocellar tubercle, and a pair of broader lateral stripes not attaining either margins; ocular margin darkened between eye and lateral stripe; ocular emargination with a large silvery spot. Ocellar tubercle raised; ocelli present; ocellar bristle approximately two-thirds the length of frons. One pair of interfrontal setae. Orbital setulae minute, in five pairs. Face shining; lower corners of facial excavation diffuse brown; gena paler, weakly shining. Antenna yellow-orange. Scutum orange with diffuse brownish medial stripe and lateral margins, shining, finely rugose; uniformly setose. Scutellum brown, lightly microtrichose, finely rugose; twice wider than long, 0.7 times the width of scutum. Scutellar bristles subequal in length. Pleuron dull orange, with diffuse yellow stripe running through middle; katepisternum and meron dark brown. Legs yellow ochre; coxa dark brown; fore tibia and first tarsal segment dark brown; fore tarsus off-white; mid tibia with three anterodorsal and one distal posterodorsal bristle. Wing (Figs. 17, 101) paddle-shaped, setaceous.
Abdomen black, shining; tergites finely rugose, uniformly densely microtrichose, each with two rows of setae; sternites setose and finely microtrichose.

**MALE TERMINALIA.** Sternite 5 (Figs. 18, 97) concave in posteromedial third and with three scalloped emarginations; the outer two flanked by regular setae and four long marginal setae, one of which is borne on a slender tubercle; the area between the emarginations projecting beyond margin and bearing a pair of hoof-shaped processes, joined by a membrane lining the middle emargination. Synsternite 6+7 (Figs. 18, 96) giving rise to a pair of large, heavily sclerotized, asymmetrically curved processes on either side of medial bridge. Tab-like piece (Fig. 98) resembling half of a hollow cone with foot-like extensions from its basal corners; the top of the cone articulates neatly with the hoof-shaped processes. Cercus (Figs. 18, 94, 95) 3.5 times as long as wide, uniform in thickness except for toothed base and tapered apex; medially slightly bent inward, with long outer seta; apex sloped inward, with two sensory setae; clothed in setulae; outer surface with scattered small setae. Surstylus (Figs. 94, 95) extremely long, nearly twice the length of cercus; base conical; slender portion compressed, twisting and tapering to a point; basally with scattered sensory setae. Postgonite (Fig. 100) broad; descending arm short, slightly curved forward and tapering, with several marginal sensory setae; articulatory process for pregonite truncate; articulatory process for basiphallus short-stalked, knobbled. Aedeagus as in Figure 99. Basiphallus compressed, squared; anterior margin weakly arched; articulatory process for postgonite apically dilated, directed anteriorly. Ejaculatory apodeme indistinct, with two sensory pores. Ventrobasal sclerite divided. Lateral flanking sclerite not fused ventrobasally; dorsal margin rolled, straight then diverging, tapering to a sharp point with ventral margin. Ventral flanking sclerites very dark; the bilobed basal article originating along but separate from ventral margin of lateral flanking sclerite, projecting an equal length beyond and apicodorsally
densely clothed in suspended minute denticles, the inner medial lobe parallel, its dilated apex extending beyond even the distal article; the very dark medial article as long as lateral flanking sclerite, needle-tipped, its base dilated and articulating with ventral margin of lateral flanking sclerite below basal article; the depressed distal article originating from below midpoint of medial article, apex slightly lobed inward. Medial paired sclerites originating between medial and distal articles; dorsally with a posteriorly directed tooth; twisting inward and terminating in a spade-shaped apex.

**FEMALE TERMINALIA.** Epiproct (Figs. 102, 103) very pale, triangular; apically finely hairy. Each half of tergite 8 (Figs. 102–104) convex, its margins straight, rounded apically; upper two-thirds setaceous. Cercus three times as long as wide; with one long apical seta and several preapical setae. Sternite 8 (Figs. 103, 104) triangular; with four preapical setae. Spermathecae (Fig. 105) simple; length of sclerotized ducts approximately twice the diameter of a spermatheca.

**VARIATION.** The scutum and scutellum occasionally have a more uniform orange wash. The facial excavation is entirely orange in some specimens.

**ETYMOLOGY.** The species epithet refers to the unusually slender surstyli.

**TYPE MATERIAL.** Holotype ♂ (UNAM). MEXICO: Tamaulipas, Joya de Manantiales, 23°0’30”N, 99°17’6”W, 1430 m, 22.viii.2009, mesophyll forest, ex. sifted leaf litter, M.G. Branstetter.

**PARATYPES.** MEXICO: Tamaulipas, Gomez Farias, Rancho del Cielo, near Cabins, 23°6’4”N, 99°11’32”W, 1200 m, 17.vii.2006, mixed oak forest, ex. sifted leaf litter, R.S. Anderson (♀); El Cielo, near Alta Cima, 23°3’55”N, 99°12’16”W, 980 m, 21.viii.2009, riparian wet forest, ex. sifted leaf litter, L. Sáenz (♂); same label as holotype (♂; ♀); same label as holotype but collected by L. Sáenz (♂); El Cielo, 1.8 km NW La Gloria, 23°3’31”N,
99°15′48″W, 2030 m, 23.viii.2009, mesophyll forest, ex. sifted leaf litter, M.G. Branstetter (♀); Querétaro, Pinal de Amoles, Huasquiloc, 21°9′39″N, 99°34′27″W, 1750 m, 28.vii.2006, hardwood forest, ex. sifted leaf litter, R.S. Anderson (♀); Pinal de Amoles, 2 km W San Pedro Escanela, 29.vii.2006, ex. sifted leaf litter, R.S. Anderson (♂); Pinal de Amoles, 1.9 km NE, 21°8′59″N, 99°36′57″W, 2250 m, 18.viii.2009, oak–pine forest, ex. sifted leaf litter, M.G. Branstetter (♂); Pinal de Amoles, 7 km NE, 21°10′34″N, 99°34′24″W, 1700 m, 18.viii.2009, disturbed mesophyll forest, ex. sifted litter, M.G. Branstetter (♀); Pinal de Amoles, 4.6 km SW, 21°9′53″N, 99°35′39″W, 1960 m, disturbed mesophyll forest, ex. sifted litter, M.G. Branstetter (♂; 5♀); San Luis Potosi, Xilitla, 7.2 km NE, 21°25′42″N, 98°56′28″W, 180 m, 19.viii.2009, disturbed tropical forest, ex. sifted litter, M. Vásquez-Bolaños (♂; ♀).

**COMMENTS.** *Aptilotella gracilis* has the northernmost distribution of any *Aptilotella* species, and is also among the most distinctive looking. Males of this strongly apomorphic species are unmistakable, with extremely slender cerci, asymmetrical posterior prongs on synsternite 6+7, and the sclerite complex in sternite 5. The fore leg is boldly patterned in both sexes, and is strikingly similar to that of the apterous limosinine *Myrmolimosina andersoni* Marshall and even a brachypterous *Aluligera* from Africa (Richards, 1955). Field observations could yield insight into the potential behavioural functions of these remarkably convergent fore limbs.
**Aptilotella diffisa sp. nov.**

(Figs. 19–21, 107–116)

**DESCRIPTION.** Habitus as in Figures 19 and 20. Body length 1.3 mm. Head ground color yellow-orange. Frons finely rugose; pale areas silvery, the lateral pair sharply converging on occiput; brown medial stripes each about one-fourth the width of frons, converging along the anterior margin, darkening posteriorly; brown orbital stripes each half the width of medial stripe. Ocellar tubercle slightly raised; ocelli present; ocellar bristle two-fifths the length of frons. Interfrontal setae in two pairs. Orbital setulae minute, in seven pairs. Face weakly shining; facial excavation with a broad silvery-white band, margin with a small medial notch; gena dull, finely rugose, lower margin darkened and setaceous. Antenna yellow. Occiput brown. Scutum and scutellum dark reddish-brown, shining. Scutum convex, deeply creased along posterolateral margin; uniformly setose, microtrichose except for crease. Scutellum uniformly microtrichose; flat, twice wider than long, 0.7 times the width of scutum. Scutellar bristles subequal in length. Pleuron dark brown, weakly shining. Legs yellow; coxae and mid and hind femora dark brown; mid tibia with two anterodorsal and one distal posterodorsal bristle. Wing rudiment brown. Abdomen black, shining; tergites uniformly setose and microtrichose; sternites finely microtrichose. Epandrium and synsternite 6+7 dark reddish-brown; cercus yellow.

**MALE TERMINALIA.** Sternite 5 (Figs. 21, 110) lunate, anteromedially grooved; posteromedial third concave and emarginate, bearing stout setae, flanked by numerous long and short setae, and lined by a hair-fringed membrane; periphery of emargination giving rise to a pair of curved cercal claspers. Synsternite 6+7 (Fig. 109) posteriorly with two triangular lobes arching over medial bridge; posteromedially with a free, two-armed structure with hooked ends. Anal aperture (Fig. 107) closed by narrow bridge. Cercus (Figs. 21, 107, 108) slender, shallowly
S-shaped as in profile of sternite 5; seta at mid-length about half as long as the cercus; outer margin with five evenly spaced setae between long seta and apex. Surstylus (Figs. 107, 108) saddle-shaped; ventral face with several setae; posteriorly with a protuberance bearing 6-7 setae. Postgonite (Fig. 112) cylindroid, 1.3 times as long as wide; descending arm very short, slightly curved, with several marginal sensory setae; articulatory process for pregonite reduced; articulatory process for basiphallus only slightly protruding. Aedeagus as in Figure 111. Basiphallus cylindrical, arched; articulatory process for postgonite twisted and divergent. Ventrobasal sclerite divided. Lateral flanking sclerite fused ventrobasally by a very narrow bridge; dorsal margin rolled, straight; basal and distal margins excavated; distal margin giving rise to an open-ended, membranous sac clothed in dense rows of denticles. Ventral flanking sclerites with the basal article fused along entire ventral margin of lateral flanking sclerite, bearing a ventrodistal tooth and a weak dorsal arm; the dark cylindrical medial article broadened basally to articulate with basal article and meeting ventral margin of lateral flanking sclerite; the membranous distal article irregularly spade-shaped, with sclerotized elliptical plate articulating with medial article. Triangular dorsal sclerites originating from above membranous sac and similarly clothed in denticles, with two more pairs of internal sclerites (not illustrated) beneath them. Triangular internal sclerites articulating with asymmetrical saddle-shaped sclerite, which descends between the distal articles of ventral flanking sclerites. Ventral plate-like sclerites (not illustrated) diamond-shaped, posterior to saddle-shaped sclerite.

**FEMALE TERMINALIA.** Epiproct (Figs. 113, 114) rectangular, sclerotized. Each half of tergite 8 (Figs. 114, 115) weakly convex; apex triangular, rounded; with several setae. Tergite 7 posteromedially notched. Cercus 3.5 times as long as wide; with one long apical seta and several preapical setae. Hypoproct (Figs. 114, 115) very pale, medially microtrichose and with two setae.
Spermathecae (Fig. 116) simple; length of sclerotized ducts less than twice the diameter of a spermatheca.

**VARIATION.** Teneral specimens have a uniformly reddish-brown body. The silvery facial stripe occasionally diffuses into the gena. Tergite 8 in some females is broadly rounded rather than triangular.

**ETYMOLOGY.** The species epithet is from the Latin *diffido*, “to distrust,” referring to the uncertainty of its classification.

**TYPE MATERIAL.** Holotype ♂ (INBC). COSTA RICA: Cartago, Llano Bonito, trail to Cerro Chirripó, 27.vi.1999, cloud forest, leaf litter, R.S. Anderson.

**PARATYPES.** COSTA RICA: Cartago, same label as holotype (4♂, ♀); San José, km 117, Pan American Highway, 19 km N San Isidro, 9°28’N, 83°40’W, 26.vi.1997, cloud forest, litter, R.S. Anderson (3♂, 5♀); same locality as previous label, 1800 m, 20.vi.1997, R.S. Anderson (5♂, 3♀); same locality as previous label but without coordinates, 15.ii.1998 (♀); Estación Cuerici, 4.6 km E Villa Mills, 2600 m, 9°34’N, 83°40’W, 26.vi.1997, oak forest, litter, R.S. Anderson (2♀); same data as previous label but from mixed oak *Alnus* forest (3♂, ♀).

**COMMENTS.** *Aptilotella diffisa* closely resembles members of the *A. corona* species group, but its aedeagus bears little commonality. The complex distiphallus is comparable to that of *A. involucris*, particularly in the arrangement of ventral sclerites. The lopsided saddle-shaped sclerite is unique to this species. Aside from the hypandrium, asymmetrical elements are rare in *Aptilotella* genitalia.
Aptilotella involucris sp. nov.

(Figs. 22–24, 149–159)

DESCRIPTION. Habitus as in Figures 22 and 23. Body length 1.7 mm. Head ground color yellow-orange. Frons finely rugose. Ocellar triangle slightly raised; ocelli present; ocellar bristle two-thirds the length of frons. Interfrontal setae in three pairs. Orbital setulae in four pairs. Face weakly shining and pale in males, with a broad white band in facial excavation; shining in females; gena dull, lower margin setaceous. Antenna orange, first flagellomere brown. Scutum and scutellum black, shining, finely rugose and microtrichose. Scutum uniformly setose. Scutellum trapezoidal, 1.6 times wider than long, 0.6 times the width of scutum. Apical scutellar bristles subequal in length. Pleuron black. Legs yellow-orange; mid and hind coxae and tarsi dark brown; femora brown basally; mid tibia with two anterodorsal and one distal posterodorsal bristle. Male mid leg (Figs. 22, 127) modified: trochanter ventrally with a comb of strong setae; mid femur swollen in distal half, ventrally with long setae and stout setae before base; tibia with a ventrodistal comb. Wing rudiment dark brown. Abdomen black, shining, finely rugose and microtrichose; tergites each with two rows of setae, which become longer with each segment. Cercus orange, surstylus brown.

MALE TERMINALIA. Sternite 5 (Figs. 24, 120) anteromedially grooved; posteromedial third projected and raised, flanked by setae, its margin medially excavated and sunken, and giving rise to a pair of very dark, compressed, knobby processes with a large inner tooth which clasps the cercus. Synsternite 6+7 as in Figure 119. Anal aperture dorsally deeply emarginate. Cercus (Figs. 24, 117, 118) gradually tapering, twice as long as basal width; base swollen and setulose; apex sloped inward; distal third bearing several sensory setae, three stout setae and a long seta next to the middle stout seta. Surstylus (Figs. 117, 118) semi-cylindrical, twice as long
as wide; posterior margin setaceous, basally tuberculate; distal third with several sensory setae. Postgonite (Fig. 122) curved with strongly concave anterior margin; descending arm half the total length, gradually tapering, with two basal sensory setae; articulatory process for pregonite triangular and rounded; articulatory process for basiphallus a small knob on a broad stalk. Aedeagus as in Figure 121. Basiphallus arched, with prominent posterior hump; articulatory process for postgonite slender, directed forward. Ejaculatory apodeme round with a descending apical stalk. Ventrobasal sclerite divided. Lateral flanking sclerite darkened and dorsally emarginate in distal third; dorsal margin rolled, straight; basal margin slanted; distal margin rounded, supporting in dorsal half a membranous sac clothed in fine rows of minute denticles. Ventral flanking sclerites with the basal article fused posteroventrally and along ventrodistant margin of lateral flanking sclerite, distally tapering to a point; the medial article confluent with basal article, ascending and ending beneath membranous sac; the distal article articulating with ventrodistant margin of basal article, ladle-shaped and opening outward. Medial paired sclerites originating from inside distal margin of lateral flanking sclerites, slender portion convergent and protruding between membranous sacs. Distal oval sclerites flanking slender portion of medial paired sclerites. Ventral paired sclerites descending between ladle-shaped distal articles; apically with a leaf-shaped sclerite, flanked ventrally by a rod-shaped sclerite and ventrolaterally by triangular ventral plate-like sclerites.

**FEMALE TERMINALIA.** Epiproct (Figs. 123, 124) subpentagonal, with indented basal margin; medially densely microtrichose. Each half of tergite 8 (Figs. 123–125) subpentagonal, convex; apex rounded; distal half setose. Tergite 7 (Fig. 123) anteromedially notched. Cercus 1.5 times as long as wide; with several preapical setae. Hypoproct (Figs. 124, 125) reduced to a pair
of lightly sclerotized, microtrichose discs. Spermathecae (Fig. 126) simple; length of sclerotized ducts approximately twice the diameter of a spermatheca.

**ETYMOLOGY.** The manuscript name used for this species by Smith (1994) is here retained. It is derived from the Latin *involucr*, “unable to fly.”


**PARATYPES.** COSTA RICA: Cartago, same label as holotype (5♀); Cerro Chirripó, trail to, 2800 m, 27.vi.1999, mixed oak forest, leaf litter, R.S. Anderson (♂); San José, km 74 SE San José, 25.ii.1984, dung trap, H. Howden (4♂; 4♀); same label as previous but from flight intercept trap (♀); Pan-American Highway, km 95, 3200 m, 13.iv.1985, oak cloud forest, L. Masner (♀); km 68, Tres de Junio Bog, 2600 m, 10.i.1996, litter ex forest adjacent to sphagnum bog, R.S. Anderson (♂); km 87, near Cerro Buenavista, 9°36′30″N, 83°46′W, 3150 m, 8.vi.1997, mixed elfin forest litter, R.S. Anderson (♂; ♀); km 71, near Tres de Junio, 23.vi.1999, wet cloud forest leaf litter, R.S. Anderson (2♂; ♀); km 78, near Ojo de Agua, 8.vii.1999, cloud forest leaf litter, R.S. Anderson (♀); Cerro de la Muerte, 3200 m, 3.iv.1985, cloud forest, pan traps, L. Masner (♀); Cerro de la Muerte, 7-13.iv.1985, oak cloud forest, L. Masner and H. Goulet (♂); Heredia Porrosati, 6 km N San José de la Montaña, 10°5′30″N, 84°7′W, 1900 m, 21.vi.1997, montane forest litter, R.S. Anderson (♀).

**COMMENTS.** *Aptilotella involucris* is a highly apomorphic and sexually dimorphic species that is readily recognized by its large and slender form. The distiphallus is arrayed with internal and ventral sclerites of uncertain affinities. Females possess a strongly domed tergite 7 which
may initially be mistaken for an epandrium, but examination of the unmodified mid leg and non-pruinose face should eliminate confusion as to the sex of the individual.

The *Aptilotella corona* Species Group

**DIAGNOSIS.** Members of this species group are defined by the very dark, shiny tab-like piece of male sternite 5 that articulates perpendicularly with the posteromedial margins of sternite 5 and synsternite 6+7. This structure apparently serves in part to conceal the cerci when they are not in use. The defining character of the distiphallus is the prominent dark club-shaped sclerite of the ventral flanking sclerite, which often bears a crown of denticles. The aedeagus is rich in additional, diagnostic characters. The basiphallus is strongly compressed and arched and, with the exception of *A. sphyra*, possesses erect articulatory processes for the postgonite. In the ventral flanking sclerites, the medial article is dorsally elongated, and the strongly lobed distal article is arched or coiled inward. Medial paired sclerites arise convergently distal to the medial article of the ventral flanking sclerites and are confluent in the slender distal half.

Both sexes possess a broad silvery-white band on the lower margin of the facial excavation, a character shared with the squatter flies of the *A. germana* species group. The exceptions are *A. corona*, which has white spots instead, and *A. sphyra*, in which the band is faint in the male and lacking in the female. Six species are described from Central America.
Aptilotella sphyra sp. nov.

(Figs. 25–27, 128–140)

DESCRIPTION. Habitus as in Figures 25 and 26. Body length 1.3 mm. Head ground color yellow-orange. Frons shining except for interfrontal suture and lateral portion of orbital plate. Ocellar tubercle slightly raised; ocelli present; ocellar bristle two-thirds the length of frons. Interfrontal setae in two pairs. Orbital setulae minute, in two pairs. Face and gena weakly shining; in males, excavation with a broad silvery band; lower margin of gena setaceous. Antenna yellow-orange. Scutum and scutellum orange, shining. Scutum uniformly setose, densely microtrichose. Scutellum partly microtrichose; trapezoidal in males, rounder in females; 1.7 times wider than long, 0.6 times the width of scutum. Apical scutellar bristles 1.2 times as long as basal. Pleuron orange, with yellow stripe running through middle; katepisternum and lower half of meron dark brown. Legs yellow ochre; coxa brown; mid tibia with three anterodorsal and one distal posterodorsal bristle, in male with an unequal pair of flattened, iridescent, overlapping preapical anteroventral setae (Fig. 140). Wing pad (Figs. 26, 135) clavate in male, reduced and spear-shaped in female. Abdomen black, shining, densely microtrichose; tergites and sternites each with a distal row of setae. Epandrium and synsternite 6+7 reddish-brown.

MALE TERMINALIA. Sternite 5 (Fig. 131) shallowly emarginate in posteromedial sixth, flanked by setae, with the strongest setae nearest the margin, and giving rise to a pair of very dark, clasper-like processes. Synsternite 6+7 (Fig. 130) with narrow medial bridge; posteromedially with a membranous pouch bearing minute spinules. Cercus (Figs. 27, 128, 129) ax-head shaped, thick but narrow at base, the blade compressed and most expanded distally; outer margin bearing several widely-spaced setae, and a longer seta at mid-length. Surstylus
(Figs. 27, 128, 129) about 3.5 times as long as wide; posterior margin irregular, setaceous; anterior margin angled; apex rounded. Postgonite (Fig. 134) curved; descending arm slender, of uniform width, with three basal sensory setae; articulatory process for pregonite undeveloped, rounded; articulatory process for basiphallus slender. Aedeagus as in Figures 132 and 133. Basiphallus compressed, squared; posteroventrally with a small hump; anterior margin arched; articulatory process for postgonite rod-shaped, erect. Ventrobasal sclerite divided. Lateral flanking sclerite fused ventrobasally by a narrow bridge; dorsal margin nearly straight, diverging and sinuous beyond basal third, medially with a patch of minute spinules. Ventral flanking sclerites darker; the club-shaped sclerite fused along ventral margin of lateral flanking sclerite, distally abruptly bent upward into a hammer-shaped process bearing numerous suspended minute denticles; the medial article sharply pointed beneath, confluent with ventral margin of lateral flanking sclerite then ascending with club-shaped sclerite and terminating beyond in a rounded apex; the broad distal article ventrally with a triangular lobe curling inward and converging in the middle. Medial paired sclerites originating from inside of medial article of ventral flanking sclerite, sharply bent upward, convergent and tapered between and above club-shaped sclerites.

**FEMALE TERMINALIA.** Epiproct apparently absent. Each half of tergite 8 (Figs. 136–138) convex, its outer margins rounded; with several setae. Cercus three times as long as wide; with one long apical seta and two preapical setae. Hypoproct (Fig. 138) very pale, narrowly ring-shaped. Spermathecae (Fig. 139) simple; sclerotized ducts slightly longer than the diameter of a spermatheca.
**VARIATION.** Abdominal colouration is dark brown in lighter individuals. Females tend to be darker; the legs, which are unicolorous in the males, may have contrasting brown tibiae in females.

**ETYMOLOGY.** The species epithet is Latin for “hammer,” describing the club-shaped process of the distiphallus.

**TYPE MATERIAL.** Holotype ♂. HONDURAS: Guisayote, 20.5 km E Ocotepeque, 2170 m, 14.vi.1994, cloud forest litter, R.S. Anderson.

**PARATYPES.** HONDURAS: Ocotepeque, same label as holotype but dated 13.vi.1994 (4♂); same label as holotype (5♂; 4♀); same label as holotype but dated 16.vi.1994 (2♂; 6♀); Nueva Ocotepeque, 13 km E, 14°25′11″N, 89°4′10″W, 2190 m, 26.v.2010, cloud forest leaf litter (♀). EL SALVADOR: Chalatenango, El Pital, 13.1 Km N, San Ignacio, 2850 m, 28.viii.1994, cloud forest litter Berlese, R.S. Anderson (4♂; ♀).

**COMMENTS.** Aptilotella sphyra exhibits sexual dimorphism in wing shape; however, in contrast to other species, females are not entirely wingless but retain small wing pads. This species shares similar distiphallic structures with A. pennifera, but is unusual in the A. corona species group in possessing an unusually large, square basiphallus. The combination of bicoloured body and unmarked frons is unique to this species.

*Aptilotella andersoni* sp. nov.

*(Figs. 28–30, 141–150)*

**DESCRIPTION.** Habitus as in Figures 28 and 29. Body length 1.5 mm. Head ground color dull orange. Frons finely rugose except for shiny base of inner vertical bristle; pale areas silvery, the lateral pair converging on occiput; dark brown medial stripes each about one-fourth the width
of frons, narrowing toward the anterior margin, then diffusing; dark brown orbital stripes each half the width of medial stripe; ocular emargination with pale spot. Ocellar tubercle slightly raised; ocelli present; ocellar bristle two-fifths the length of frons. Interfrontal setae in two pairs. Orbital setulae minute, in four pairs. Lunule with silvery spot; face weakly shining; facial excavation with a broad silvery-white band continuing onto anterior half of gena; clypeus dark brown; gena dull, setaceous. Antenna brown. Occiput dark brown. Scutum dark reddish-brown, shining, creased along posterolateral margin; uniformly setose, microtrichose except for area behind the crease. Scutellum black, shining, finely microtrichose; flat, twice wider than long, 0.6 times the width of scutum. Apical scutellar bristles 1.5 times as long as basal. Pleuron dark brown. Legs dark brown; trochanter yellow; fore femur apically orange; fore tibia and tarsi light brown; mid tibia with two anterodorsal and one distal posterodorsal bristle. Wing rudiment light brown. Abdomen black, shining; tergites each with two rows of long yellow setae, syntergite with three rows, basal margin densely microtrichose; sternites setose and finely microtrichose. Cercus and surstylus dull yellow.

MALE TERMINALIA. Sternite 5 (Fig. 144) shallowly emarginate in posteromedial sixth, bordered by many long setae. Synsternite 6+7 (Fig. 143) with arched medial bridge. Tab-like piece (Figs. 30, 144) a single U-shaped piece with a cylindrical base. Cercus (Figs. 30, 141, 142) tapering, twice as long as basal width; base clothed in setulae, bearing two long setae, the lower one reaching apex; apex truncate; distal half with three thick setae and an apical sensory seta. Surstylus (Figs. 30, 141, 142) subquadrate; ventral face shallowly concave and bearing long setae; posteriorly with protuberance bearing an apical and preapical ventral seta; anteriorly truncate and upwardly curved, bearing one long apical seta and a preapical sensory seta. Postgonite (Fig. 146) curved; descending arm straight, tapering to a point, basally with three
marginal sensory setae; articulatory process for pregonite triangular; articulatory process for 
basiphallus stalked, knobbed with blunt anterior tooth. Aedeagus as in Figure 145. Basiphallus 
compressed, strongly arched, flared at articulation with distiphallus; articulatory process for 
postgonite slender and erect. Ventrobasal sclerite divided. Lateral flanking sclerites broadly 
fused ventrobasally; convex; margins gradually converging. Ventral flanking sclerites darker; the 
spade-shaped sclerite distally compressed, fused to one another, and apically supporting a 
suspended crown of fine denticles; the medial article sharply pointed beneath basal article, 
laterally diverging, overlapping basal article and ascending; the distal article originating 
ventromedially to medial article, extending beyond spade-shaped sclerites, and apicoventrally 
hooked downward. Paired medial sclerites similar to distal article of ventral flanking sclerite and 
originating interiorly to it, apically pointed, dorsal margin more strongly sclerotized. An 
additional pair of triangular ventral sclerites present beneath ventral flanking sclerites. 

**FEMALE TERMINALIA.** Epiproct (Figs. 147, 148) indistinct, triangular and rounded 
apically; finely microtrichose. Each half of tergite 8 (Figs. 147–149) weakly convex, rectangular; 
margin rounded, meeting at dorsal and ventral corners; setaceous near margin. Cercus three 
times as long as wide; with one long apical seta and several scattered setae. Hypoproct (Figs. 
148, 149) reduced to a pair of convergent rods; apex microtrichose and with a pair of setae. 
Spermathecae (Fig. 150) simple; sclerotized ducts long, more than three times the diameter of a 
spermatheca. 

**VARIATION.** Females tend to be darker than males in overall colouration. Teneral 
specimens have a uniformly brown body. 

**ETYMOLOGY.** This species is named in honour of Robert S. Anderson, whose leaf litter 
sampling provided much of the material which made this study possible.

**PARATYPES.** MEXICO: Chiapas, same label as holotype (16♂, 20♀); 2 km NE, 15°28’14”N, 92°16’48”W, 2800 m, 27.vii.2005, mixed shrub and forest litter, R.S. Anderson (♂).

**COMMENTS.** The fully dark brown body, legs and antennae of *Aptilotella andersoni* distinguish it as the dullest member of the *A. corona* species group. This species is known from coastal cloud forest some 60 km apart from its closest known relatives, *A. gloriosa* and *A. quatuororchela*.

*Aptilotella quatuororchela* sp. nov.

(Figs. 31–33, 151–162)

**DESCRIPTION.** Habitus as in Figures 31 and 32. Body length 1.3 mm. Head ground color orange. Frons finely rugose except for shining posterior quarter of orbital plate; pale areas silvery, not attaining the anterior margin, the lateral pair converging on occiput; brown medial stripes each about one-fourth the width of frons; brown orbital stripes each half the width of medial stripe; ocular emargination with small silvery spot. Ocellar tubercle slightly raised; ocelli present; ocellar bristle two-fifths the length of frons. Interfrontal setae in two pairs. Orbital setulae minute, in three pairs. Lunule with silvery spot; face shining; facial excavation with a broad silvery-white band continuing onto anterior half of gena; clypeus brown; gena weakly shining, margin dark, setaceous. Antenna orange. Scutum and scutellum dark reddish-brown, shining. Scutum deeply creased along posterolateral margin; uniformly setose, microtrichose except for crease. Scutellum finely microtrichose; flat, twice wider than long, 0.6 times the width
of scutum. Apical scutellar bristles 1.4 times as long as basal. Pleuron dark brown. Legs orange in males, dark brown with light brown tarsi in females; mid and hind coxae black; mid tibia with two anterodorsal and one distal posterodorsal bristle, in males with a posteroventral comb of stout setae (Fig. 162). Wing rudiment light brown. Abdomen black, shining; uniformly finely microtrichose; tergites each with two rows of long yellow setae; sternites with shorter setae. Epandrium and synsternite 6+7 dark reddish-brown; cercus and surstylus orange.

**MALE TERMINALIA.** Sternite 5 (Figs. 33, 154) posteromedially with a V-shaped marginal notch inside a lightly sclerotized concavity, this area surrounded by many setae and a marginal sclerotized stub. Synsternite 6+7 (Fig. 153) very robust, 0.8 times as long as wide; medial bridge broad, posteromedial margin with a membranous protuberance. Tab-like piece (Figs. 33, 154) consisting of a pair of heavily sclerotized saddle-shaped processes fused by a broad, thin strap that articulates within the notch of sternite 5. Cercus (Figs. 33, 151, 152) gradually tapering, 2.5 times as long as basal width; apex truncate; clothed in setulae; one long seta present at base, another near lateral margin at the basal third, distal half toward apex with 4–5 setae of decreasing size. Surstylus (Figs. 33, 151, 152) a compressed cone, posteriorly expanded into a broadly rounded lobe bearing setae of various sizes; base above the lobe with elongate protuberance bearing several small ventral setae, one long lateral seta, and one apical seta. Postgonite (Fig. 157) curved; descending arm slender, slightly sinuous, anterior margin with three evenly spaced sensory setae; articulatory process for pregonite triangular; articulatory process for basiphallus stalked, knobbed with small anterior bump. Aedeagus as in Figures 155 and 156. Basiphallus compressed, arched; articulatory process for postgonite broad and erect. Ejaculatory apodeme discoid, apically slightly upturned. Ventrobasal sclerite divided. Lateral flanking sclerites broadly fused ventrobasally; dorsal margin rolled, straight; distal margin
squarely excavated in middle. Ventral flanking sclerites heavily sclerotized; the spade-shaped sclerite distally compressed, fused to one another by a sclerotized U-shaped belt, and dorsally supporting a loose suspension of small denticles; the elongate medial article sharply pointed before ventromedial margin of spatulate sclerite and rising next to it; the bilobed distal article originating from beneath medial article, pincer-like in appearance due to the inward arching of the broad outer lobe against the slimmer inner lobe, the latter bearing a prominent triangular lobe on its outer face. Paired medial sclerites originating from beneath spatulate sclerite, similarly shaped but slimmer.

**FEMALE TERMINALIA.** Epiproct (Figs. 158, 159) triangular, apically rounded and microtrichose. Each half of tergite 8 (Figs. 158–160) convex, upper third bent and shining; margin rounded, dorsally indented to align with epiproct; sparsely setaceous. Cercus 2.5 times as long as wide; with one long apical seta and several preapical setae. Hypoproct (Fig. 160) very pale, triangular, basal corners laterally drawn out into triangular lobe; apex microtrichose and with two pairs of setae. Spermathecae (Fig. 161) simple; length of sclerotized ducts more than twice the diameter of a spermatheca.

**VARIATION.** The colouration of the legs is generally considerably darker and contrasting in the females, compared to uniform orange in most, but not all males. Teneral specimens have a uniformly brown body.

**ETYMOLOGY.** The species epithet is derived from the Latin *quattuor,* “four,” and *chela,* “claw,” a description of the claw-like array club-shaped sclerites, paired medial sclerites, and the distal article of each ventral flanking sclerite in the distiphallus.

**PARATYPES.** MEXICO: Chiapas, same label as holotype (16♂, 9♀); Custepec, 3.5 km ESE, 15°43’N, 92°56’W, 1800 m, 17.vii.2007, M.G. Branstetter (♂); Custepec, 4 km SE, 15°42’37”N, 92°55’56”W, 1960 m, 18.v.2008, mixed hardwood forest, ex. sifted leaf litter, R.S. Anderson (♂); Custepec, 4 km SE, 15°42’28”N, 92°55’52”W, 2150 m, 21.v.2008, ridge oak forest, ex. sifted leaf litter, R.S. Anderson (♀).

**COMMENTS.** *Aptilotella quatuorchela* and *A. gloriosa* occur sympatrically and appear to be equally common within their range. The male genitalia of *A. quatuorchela* differs from that of its boldly coloured cousin and *A. andersoni* by the long and stout cercus, fused saddle-shaped tab-like piece of sternite 5, weakly arched basiphallus, and ventral flanking sclerites with strongly ascending articles and a chelate distal article. This is also the only species of the three to possess a posteroventral setal comb on the male mid tibia. The sexes are readily distinguished by the leg colour, which is orange in males and dark brown with brown tarsi in females.

*Aptilotella gloriosa* sp. nov.

(Figs. 34–36, 170–179)

**DESCRIPTION.** Habitus as in Figures 34 and 35. Body length 1.3 mm. Head ground color yellow-orange. Frons finely rugose except for shining posterior third of orbital plate; pale areas silvery, most conspicuously at the anterior end of the lateral pair; brown medial stripes each about one-fourth the width of frons, diffuse along the anterior margin; brown orbital stripes each half the width of medial stripe, continuing into ocular emargination. Ocellar tubercle slightly
raised; ocelli present; ocellar bristle two-fifths the length of frons. Interfrontal setae in two pairs.

Orbital setulae minute, in three pairs. Lunule with silvery spot; face shining; facial excavation
with a broad silvery-white band continuing onto anterior half of gena; gena weakly shining,
setaceous. Antenna brown. Scutum yellow-orange, shining, deeply creased along posterolateral
margin; uniformly setose. Scutellum brown, shining, finely microtrichose; flat, 2.2 times wider
than long, 0.6 times the width of scutum. Apical scutellar bristles twice as long as basal. Pleuron
dark brown, with broad yellow stripe through middle, appearing continuous with gena. Legs
yellow ochre; mid and hind coxae and basal half of hind femur dark brown; mid tibia with two
anterodorsal and one distal posterodorsal bristle; male mid femur with a ventrobasal setal comb.
Wing rudiment brown. Abdomen black, shining; tergites each with two rows of long yellow
setae, basal half densely microtrichose; sternites setose and finely microtrichose. Cercus and
surstylus orange.

**MALE TERMINALIA.** Sternite 5 (Figs. 36, 166) twice deeply excavated in posteromedial
quarter, the outer margin of each excavation lobed and lined with setae; the node between the
excavations narrowing to a stem bearing a pair of curved setae and fused to the tab-like piece.
Synsternite 6+7 (Fig. 165) robust, 0.8 times as long as wide; medial bridge short,
posteromedially with a lightly-sclerotized tubercle clothed in minute bumps, resting on a free
process resembling half of a hollow cone. Tab-like piece (Figs. 36, 166) antler-like, consisting of
a pair of flattened curved branches, basally joined to a heavily sclerotized tubercle bearing a
darker, shorter pair of branches. Cercus (Figs. 36, 163, 164) bladelike, strongly compressed with
gently curving posterior margin; 3.5 times as long as basal width; base only one-fifth of the
length but bearing a very long outer seta that nearly reaches the apex; distal half toward apex
with three evenly spaced setae of decreasing size. Surstylus (Figs. 36, 163, 164) saddle-shaped,
ventral face shallowly concave and bearing long setae; anteriorly upturned. Postgonite (Figs. 36, 168) curved; descending arm tapered to a point, medially with three sensory setae; articulatory process for pregonite triangular and rounded; articulatory process for basiphallus short-stalked, knobbed with blunt anterior tooth. Aedeagus as in Figure 167. Basiphallus compressed, strongly arched, flared at articulation with distiphallus; articulatory process for postgonite slender, erect. Ventrobasal sclerite divided. Lateral flanking sclerites broadly fused ventrobasally; dorsal margin darker, rolled, meeting ventral margin at a blunt point. Ventral flanking sclerites with very broad club-shaped sclerite, occupying most of ventral surface, not fused to and projecting beyond lateral flanking sclerite; the medial article sharply pointed beneath basal article and broadly lobed dorsally; the twisting distal article originating from below distal portion of medial article and ascending as a prominent, strongly arched lobe. Medial paired sclerites originating distally to medial article of ventral flanking sclerite, slender portion convergent and ascending.

**FEMALE TERMINALIA.** Epiproct (Figs. 169, 170) triangular, finely microtrichose. Each half of tergite 8 (Figs. 169–171) convex, with a shallow ridge in ventral half; margin rounded and creased to align tightly dorsally; with a row of setae. Cercus three times as long as wide; with one longer apical and several scattered setae. Hypoproct (Fig. 171) very pale, triangular; finely microtrichose and with two pairs of setae. Spermathecae (Fig. 172) simple; length of sclerotized ducts more than twice the diameter of a spermatheca.

**VARIATION.** Females are often darker, with the femora dark brown in the basal half. One male specimen has a yellow scutellum.

**ETYMOLOGY.** *Aptilotella gloriosa* is named for its splendid colouration.

PARATYPES. MEXICO: Chiapas, same label as holotype (17♂, 22♀).

COMMENTS. The striking orange-and-black colour scheme of Aptilotella gloriosa immediately distinguishes it from its dark brown sympatric relatives, and is matched only by A. sphyra, which has paddle wings and an unmarked frons. This is also the only member of the A. corona species group in which the tab-like piece is fused to male sternite 5. The very thin bladelike cercus is also distinctive.

Aptilotella pennifera sp. nov.

(Figs. 37–39, 173–183)

DESCRIPTION. Habitus as in Figures 37 and 38. Body length 1.3 mm. Head ground color dull yellow. Frons finely rugose except for shiny base of inner vertical bristle; pale areas silvery, the lateral pair attaining occiput and sharply converging behind; dark brown medial stripes each about one-fourth the width of frons, meeting along the anterior margin; dark brown orbital stripes each half the width of medial stripe, scarcely reaching ocular emargination; ocular emargination with pale silvery spot. Ocellar tubercle raised; ocelli present; ocellar bristle two-fifths the length of frons. Interfrontal setae in two pairs. Orbital setulae minute, in three pairs. Face shining; lunule silvery; facial excavation with a broad silvery-white band continuing onto anterior two-thirds of gena; clypeus and lower margin of gena dark brown; gena setaceous. Antenna light tan. Scutum and scutellum black with reddish-brown tinge, shining. Scutum uniformly setose. Scutellum bare; flat, twice wider than long, 0.6 times the width of scutum.
Apical scutellar bristles 2.3 times as long as basal. Pleuron dark brown. Legs brown; mid and hind coxae black; tarsi light brown; mid tibia with two anterodorsal and one distal posterodorsal bristle; male mid femur ventrally with long setae. Wing pad (Figs. 38, 179) clavate in male, length subequal to width of scutellum; reduced in female to brown stub. Abdomen black, shining; tergites each with two rows of long setae, microtrichose basally except on syntergite; sternites finely microtrichose, with longer setae posteriorly.

**MALE TERMINALIA.** Sternite 5 (Figs. 39, 176) posteromedially emarginate, with a very dark, slender medial protuberance; the raised margins of emargination bearing thick setae, surrounded by numerous short and long setae. Synsternite 6+7 as in Figure 175. Tab-like piece (Figs. 39, 176) a pair of dark, sclerotized processes each bearing two truncate lobes. Cercus (Figs. 39, 173, 174) 3.5 times as long as basal width; gradually compressed distally, but apex dilated and truncate; basal third with a long outer seta reaching apex; outer margin from midlength to apex bearing four widely-spaced setae. Surstylus (Figs. 39, 173, 174) rectangular, about twice as long as wide; posterior face bearing numerous long setae. Postgonite (Fig. 178) curved; descending arm gradually tapering to a point, medially with one sensory seta; articulatory process for pregonite undeveloped; articulatory process for basiphallus knobbed with large anterior tooth. Aedeagus as in Figure 177. Basiphallus compressed, arched; articulatory process for postgonite broad and erect; posterovertrally humped. Ventrobasal sclerite divided. Lateral flanking sclerites broadly fused ventrobasally; basal margin medially deeply excavated; dorsal margins widely spaced, meeting only in basal fifth, medially with a patch of minute spinules. Ventral flanking sclerites with a hatchet-shaped and heavily sclerotized club-shaped sclerite, crowned with dense suspended rows of minute trifid denticles; the arched medial article pointed beneath and broad, with a narrow and arching ascending arm terminating in an elliptical
dilation; the broad distal article terminating in a round, folded lobe, ventrally with a rounded lobe curling inward and converging in the middle, on itself. Medial paired sclerites originating distally to the bend of the club-shaped sclerite and ascending with it, then leveling and terminating in a truncated, slightly upwardly curved apex.

**FEMALE TERMINALIA.** Epiproct inconspicuous. Each half of tergite 8 (Figs. 180–182) shallowly convex, subquadrate; with a few setae near margin. Tergite 7 (Fig. 180) posteromedially notched. Cercus three times as long as wide; with one long apical seta and several preapical setae. Hypoproct (Figs. 181, 182) reduced to two discs, each densely microtrichose and with two setae. Spermathecae (Fig. 183) simple; length of sclerotized ducts less than twice the diameter of a spermatheca.

**VARIATION.** Females tend to be darker in overall colouration, having especially dark legs with pale “knees,” ranging from reddish brown to dark brown, and even black in the hind femur. Setal insertions are pronounced in a few specimens, giving the scutum a punctured appearance.

**ETYMOLOGY.** The species epithet is derived from the Latin *penna*, “feather, wing,” and Latin *fero*, “bear,” because of the delicate feather-shaped wing pad of the male fly.


**PARATYPES.** GUATEMALA: El Progreso, Cerro Pinalón, 15°4’57’’N, 89°56’31’’W, 2560 m, 17.ix.2008, cloud forest, ex. sifted leaf litter, M.G. Branstetter (♀); same label as holotype (7♂; 4♀); 15°5’3’’N, 89°56’34’’W, 2570 m, 21.ix.2008, cloud forest, ex. sifted leaf litter, L. Sáenz (♂); 15°5’2’’N, 89°56’40’’W, 2560 m, 30.iv.2009, cloud forest, ex. sifted leaf litter (♀); same as previous label but at 15°5’3’’N, 89°56’44’’W (17♂; 21♀); same as previous label but at 15°5’14’’N, 89°56’39’’W, 2550 m (2♀); 15°5’3’’N, 89°55’57’’W, 2715 m, 1.v.2009, cloud forest,
ex. sifted leaf litter (♀); same as previous label but at 15°5′4″N, 89°56′17″W, 2640 m (♂; 6♀); same as previous label but at 15°4′59″N, 89°55′20″W, 2845 m (3♂; 2♀); same as previous label but at 15°5′1″N, 89°57′11″W, 2500 m, 2.v.2009 (♂; 3♀); 15°5′7″N, 89°57′3″W, 2465 m, 2.v.2009, cloud forest, ex. sifted leaf litter, R.S. Anderson (♀); peak, 15°4′52″N, 89°55′15″W, 2900 m, 1-5.v.2009, litter under shrubs, R.S. Anderson (♀); trail to peak, 15°5′3″N, 89°55′57″W, 2700 m, 1-5.v.2009, mixed oak litter, R.S. Anderson (♂; 4♀); 15°5′5″N, 89°56′6″W, 2680 m, 1-5.v.2009, cloud forest litter, R.S. Anderson (♀); near Peña del Ángel, 15°5′1″N, 89°57′11″W, 2500 m, 1-5.v.2009, mixed oak litter, R.S. Anderson (♂); trail to Peña del Ángel, 15°5′3″N, 89°57′0″W, 2520 m, 1-5.v.2009, mixed oak litter, R.S. Anderson (2♀); Baja Verapaz, Biotopo El Quetzal, 15°12′33″N, 90°13′17″W, 1940 m, 7.v.2009, cloud forest, ex. sifted leaf litter (3♂; ♀); same as previous label but at 15°12′24″N, 90°13′37″W, 2120 m, R.S. Anderson (2♂; 3♀); 15°12′26″N, 90°13′45″W, 2150 m, 7.v.2009, ridge oak forest, ex. sifted leaf litter, R.S. Anderson (3♂; 3♀).

**COMMENTS.** *Aptilotella pennifera* is apparently parapatric with its sister species, *A. corona*, inhabiting closely situated montane cloud forests in south-central Guatemala.

This sexually dimorphic species has paddle-winged males and apterous females, and is similar in external appearance to *A. andersoni* and *A. quatuorchela*. Since both sexes in these species are apterous, only female *A. pennifera* are likely to be misidentified, but the posteromedial notch of tergite 7 is diagnostic.
**Aptilotella corona** sp. nov.

(Figs. 40–42, 202–212)

**DESCRIPTION.** Habitus as in Figures 40 and 41. Body length 1.5 mm. Head (Fig. 194) ground color yellow-orange. Frons finely rugose; pale areas silvery; dark brown medial stripes each about one-fourth the width of frons, outer border orange; dark brown orbital stripes each half the width of medial stripe, continuing into ocular emargination. Ocellar tubercle slightly raised; ocelli present; ocellar bristle two-fifths the length of frons. Interfrontal setae yellow, in two pairs. Orbital setulae minute, in three pairs. Face shining; facial excavation with a pair of elliptical silver spots, smaller in females; clypeus brown; gena weakly shining, dark brown except along ocular margin, which is silvery in its posterior half. Antenna orange. Scutum and scutellum reddish-brown, shining. Scutum uniformly setose. Scutellum darker, bare; flat, twice wider than long, 0.6 times the width of scutum. Scutellar bristles subequal in length. Pleuron reddish-brown. Legs dark reddish-brown; front tibia orange; tarsi paler; mid tibia with two anterodorsal and one distal posterodorsal bristle. Male mid leg modified: mid femur ventrobasally with a row of stout setae; tibia apicoventrally with a stout, peg-like seta. Wing rudiment brown. Abdomen black, shining; tergites each with two rows of yellow setae; sternites and epandrium finely microtrichose. Epandrium and synsternite 6+7 dark reddish-brown; cercus and surstylus yellow.

**MALE TERMINALIA.** Sternite 5 (Figs. 42, 187) irregularly emarginate in posteromedial third; margins bulging and bearing five claw-like setae in two rows, flanked by long and short setae. Synsternite 6+7 as in Figure 186. Tab-like piece (Figs. 42, 186) very dark and two-pronged, consisting of two diverging flukes rising medially from a subpentagonal, scalloped plate. Cercus (Figs. 42, 184, 185) 2.5 times as long as basal width; interior and exterior margin of
base excavated; outer margin medially with a seta about half as long as the cercus; apical third bearing four sensory setae. Surstylus (Figs. 42, 184, 185) lunate; outer face anteriorly expanded into a convex, rounded rectangular plate; lower half setose. Postgonite (Figs. 42, 189) curved; descending arm straight, gradually tapering, basally with three sensory setae; articulatory process for pregonite undeveloped, obtuse; articulatory process for basiphallus short-stalked, knobbed with anterior bump. Aedeagus as in Figure 188. Basiphallus compressed, strongly arched, flared at articulation with distiphallus; articulatory process for postgonite spatulate and erect. Ventrobasal sclerite divided. Lateral flanking sclerites broadly fused ventrobasally; dorsal margins widely spaced, meeting only in basal fifth. Ventral flanking sclerites with a hatchet-shaped and heavily sclerotized club-shaped sclerite, wearing a suspended crown of strong denticles; the triangular medial article bearing a prominent dorsal arm which narrows in the apical third; the membranous distal article broad, distally curling in on itself, interior margin projected into a triangular ascending lobe. Medial paired sclerites originating distally to the bend of the club-shaped sclerite, slender portion convergent and ascending, with a ventral preapical dilation.

**FEMALE TERMINALIA.** Epiproct apparently absent. Each half of tergite 8 (Figs. 190, 191) rectangular, weakly convex; margin creased to align tightly dorsally; setose. Tergite 7 (Fig. 190) less sclerotized in posteromedial third, resulting in a paler, medially pointed, lunate area. Cercus 2.5 times as long as wide; with one long apical seta and several scattered setae. Hypoproct (Figs. 191, 192) indistinct with faint parenthesis-shaped margin; medially with two discs, each densely microtrichose and with two setae. Spermathecae (Fig. 193) simple; length of sclerotized ducts less than twice the diameter of a spermatheca.
VARIATION. One aberrant specimen has two orbital bristles on one side of the frons. The mid femur is orange in some specimens. Teneral specimens have a uniformly brown body.

ETYMOLOGY. The species epithet describes the “crown-of-thorns” on the club-shaped sclerite of the distiphallus.

TYPE MATERIAL. Holotype ♂. GUATEMALA: 7 km N San Lorenzo, 2000 m, 10-17.vi.1993, dung, B.D. Gill.

PARATYPES. GUATEMALA: Zacapa, 5 mi N San Lorenzo, 13.vii.1986, flight intercept trap, J.M. Campbell (♀); 5 mi W, 18.vii.1986, sifted piles of pine, J.M. Campbell (♀); same label as holotype (17♂, 26♀); Cerro de los Monos, 15°6’48”N, 89°40’41”W, 2284 m, 6.vii.2007, mixed oak-cloud forest, ex. sifted leaf litter, R.S. Anderson (♀).

COMMENTS. Aptilotella corona is a readily recognizable member of the A. corona species group, with a reddish-brown thorax and a pair of elliptical silver spots on the facial excavation. The distiphallus is equally distinctive due to the crown of large denticles on the club-shaped sclerite.

Aptilotella radians sp. nov.

(Figs. 43–45, 195–206)

DESCRIPTION. Habitus as in Figures 43 and 44. Body length 1.4 mm. Head (Fig. 202) ground color yellow. Frons finely rugose except for smooth pale area of interfrontal plate; dark brown stripes each about one-fourth the width of frons; orbital stripes darker and confined to posterior corners of frons. Ocellar tubercle slightly raised; ocelli present; ocellar bristle approximately two-thirds the length of frons. Interfrontal setae small, in four pairs. Orbital
setulae small, in two pairs. Face and gena shining, with a brown stripe from ventral margin of eye to oral margin between excavation and gena, continuing onto clypeus; clypeus broad. Maxillary palps brown. Antenna yellow, pedicel brown. Occiput dark brown, as well as a narrow strip on gena below the eye. Scutum dark reddish-brown, shining except for pruinose medial half and broken patches of pruinosity along the lateral margins; pruinose area with one medial and two bordering narrow longitudinal vittae, of which only the medial vitta attains the entire length of scutum; uniformly setose; supra-alar strong, subequal to the length of scutum. Scutellum black, convex, bare; twice wider than long, 0.6 times the width of scutum. Apical scutellar bristles 1.7 times as long as basal. Pleuron black; proepisternum and anepisternum mostly orange. Legs dark brown; mid and hind coxae black; fore femur brown; tarsi and distal third of mid and hind femora yellow; mid tibia with two anterodorsal and one distal posterodorsal bristle. Wing rudiment yellowish. Abdomen black, shining; tergites uniformly setose, basal margin microtrichose except for syntergite; sternites finely microtrichose. Epandrium and synsternite 6+7 reddish-brown; cercus and surstylus dull yellow.

**MALE TERMINALIA.** Sternite 5 (Figs. 45, 198) with two semicircular emarginations at each third of posterior margin, into which the cerci retract; setose and marginally microtrichose in between. Synsternite 6+7 (Fig. 197) with extremely narrow medial bridge, lined interiorly by a broad membrane. Cercus (Figs. 45, 195, 196) triangular, compressed; apex irregularly truncate and bearing four blunt claw-like spines, and a long seta anterior to them; basal two-thirds of ventral margin forming a curved process extending beyond apex. Surstylus (Figs. 45, 195, 196) three-sided, each face concave; anterobasally compressed into a truncate lobe; posteroventral face densely setaceous. Postgonite (Fig. 201) broad, 1.5 times as long as wide; posterior margin medially with a truncate hump; apex calloused; articulatory process for pregonite truncate;
articulatory process for basiphallus stalked, knobbled with strong ventral tooth; margin slanted between the two processes. Aedeagus as in Figures 199 and 200. Basiphallus cylindrical; posteroventrally humped, appearing boot-shaped in lateral profile; articulatory process for postgonite rounded and divergent. Ejaculatory apodeme discoid with four sensory pores, arising on a slender stem. Ventrobasal sclerite very narrow. Lateral flanking sclerite divergent, fused ventrobasally by a broad bridge which has a posteromedial truncate lobe; dorsal margin slightly rolled, basally produced into a triangular tooth; apex round and slightly dilated, its lower margin supporting a wrinkled and lightly membranous sac. Ventral flanking sclerites dark; the slender basal article fused along ventral margin of lateral flanking sclerite, apically elongated into a descending arm; the warped spindle-shaped distal article tapered and converging basally, its dorsal margin roughly following the contour of basal article, laterally with pale, warped, and rounded outer lobe and a larger inclined and triangular inner lobe.

**FEMALE TERMINALIA.** Epiproct (Figs. 203, 204) very pale, subpentagonal; with a patch of setae and microtrichosity. Each half of tergite 8 (Figs. 203–205) convex; apex drawn out and rounded; dorsal half microtrichose and with several setae. Tergite 7 (Fig. 203) divided; each half densely covered in curled setulae and laterally with four long marginal setae. Cercus 2.5 times as long as wide; with one long apical seta and three preapical setae. Hypoproct (Figs. 204, 205) a semicircular band; margin more sclerotized and weakly microtrichose. Spermathecae (Fig. 206) pear-shaped, finely ridged; apex invaginated, internally with several stubs; collar with a ring of stubs; ducts short, less than the length of a spermatheca, and lightly sclerotized.

**VARIATION.** Some darker specimens have a fainter pleural stripe, while often having somewhat broader scutal stripes. The marginal pruinosity may form a complete stripe in boldly marked specimens, giving the scutum a five-striped appearance.
**ETYMOLOGY.** The species epithet is Latin for “beaming, shining,” a reference to its bold thoracic markings.

**TYPE MATERIAL.** Holotype ♂ (UNAM). MEXICO: Oaxaca, Valle Nacional, 47.5 km SW, km 100.5, 2125 m, 26.vii.1992, wet oak forest leaf litter, R.S. Anderson.

**PARATYPES.** MEXICO: Oaxaca, same label as holotype (♂, ♀); same label as holotype but from Berlese (♀); 48 km E, km 97, 2012 m, 25.vi-2.viii.1983, montane oak flight intercept trap, S. Peck (♀); 35 mi S, 8000’, 10-12.viii.1970, oak, dense thicket, human dung, A. Newton (2♂, ♀); 29.7 mi S, 6800’, 11-17.viii.1973, cloud forest dung, A. Newton (♂); same label as previous but from carrion (♀); 13.2 km SW, 17°39’34”N, 96°20’3”W, 1360 m, 11.viii.2009, tropical wet forest, ex. sifted leaf litter, M.G. Branstetter (♀); 26 km SW, 17°35’12”N, 96°26’58”W, 2160 m, 11.viii.2009, mixed pine-oak forest, ex. sifted leaf litter, M.G. Branstetter (♂, ♀); 20.5 km SW, 17°36’20”N, 96°23’2”W, 1770 m, 12.vii.2009, mesophyll forest, ex. sifted leaf litter, M.G. Branstetter (♂, 3♀); 27.4 km SW, 17°35’47”N, 96°28’28”W, 2280 m, 12.vii.2009, mesophyll forest, ex. sifted leaf litter, M.G. Branstetter (♂, 2♀); 14.8 km SSW, 17°38’41”N, 96°20’11”W, 1370 m, 13.vii.2009, disturbed mesophyll forest, ex. sifted leaf litter, M.G. Branstetter (♀); 22.4 km SW, 17°35’28”N, 96°23’29”W, 1990 m, 13.vii.2009, cloud forest, ex. sifted leaf litter, M.G. Branstetter (♀).

**COMMENTS.** The pruinose scutal vittae of *Aptilotella radians* resemble the scutal pattern of the *Pterogramma vittatum* species group, although these markings are relatively bolder in *A. radians*. Features of the distiphallus reveal nothing in common between these two taxa, and the similarity in scutal pattern is unlikely to be homologous. The colouration of *A. radians* readily distinguishes it from all other *Aptilotella* species.
**Aptilotella ebenea sp. nov.**

(Figs. 207–216)

**DESCRIPTION.** Habitus as in *Aptilotella gemmula* (Figs. 46, 47). Body length 1.0 mm. Head ground color yellow-orange. Frons finely rugose; brown medial stripes each about two-fifths the width of frons, becoming orange-bordered along the anterior margin; orbital stripes brown, confined to posterior corners of frons. Ocellar tubercle scarcely raised; ocellar bristle two-thirds the length of frons. Interfrontal setae in two pairs. Orbital setulae minute, in four pairs. Face shining; facial tubercle narrow; clypeus brown; gena dull, ventral margin brown, setaceous. Antenna brown, first flagellomere darker. Scutum and scutellum black, shining. Scutum uniformly setose; short, twice wider than long. Scutellum uniformly microtrichose; flat, 3.5 times wider than long, 0.6 times the width of scutum. Apical scutellar bristles 1.7 times as long as basal. Pleuron black; upper half of anepisternum with faint reflective pruinose stripe visible from an oblique angle. Legs yellow-orange; fore and mid tibiae dark brown, hind tibia faintly banded; mid tibia with two anterodorsal and one distal posterodorsal bristle. Wing rudiment yellow. Abdomen black with bluish iridescence; tergites uniformly setose and microtrichose; sternites finely microtrichose. Epandrium dark reddish brown; cercus and surstylus dull yellow.

**MALE TERMINALIA.** Sternite 5 (Fig. 210) lunate; posteromedial third shallowly emarginate, giving rise to a membranous fringe with lobed corners and weak marginal setulae, and four medial sensory setae. Synsternite 6+7 (Fig. 209) with extremely narrow medial bridge; posteriorly with a broad membranous lining, giving rise to a medial trunk, and a lobe on each side bearing a dense hair comb. Cercus (Figs. 207, 208) triangular, its base greatly dilated into anal aperture; laterally projected into a sharply-pointed triangular articulation with a rounded...
epandrial cusp; one long median seta arising basal to the projection, and a small seta above it; apex tapering and slightly curved, with several small setae. Surstylus (Figs. 207, 208) triangular in cross-section; posteriorly with inner and medial rows of small setae; descending, bent at midpoint at a right angle, then continuing to a rounded apex; interiorly with a rounded preapical tooth. Postgonite (Fig. 212) 1.5 times as long as wide; descending arm short, straight, basally with three sensory setae; articulatory process for pregonite undeveloped, triangular; articulatory process for basiphallus long stalked, apically truncate. Aedeagus as in Figure 211. Basiphallus cylindrical; articulatory process for postgonite truncate. Ejaculatory apodeme spindle-shaped, with four basal sensory pores and a short apical stalk. Ventrobasal sclerite present. Lateral flanking sclerite subquadrate, ventrobasally separate; dorsal margins well separated and divergent; distal margin giving rise to a membranous sac with a fish-scale texture. Ventral flanking sclerites darker; the basal article fused diagonally across lateral flanking sclerite; the elongate distal article nearly twice the length of lateral flanking sclerite, sharply pointed beneath basal article, apex pointed. Medial paired sclerites originating beyond distal margin of lateral flanking sclerite, slender portion convergent and ascending.

**FEMALE TERMINALIA.** Epiproct (Figs. 213, 214) rectangular with rounded corners, distal margin medially shallowly indented. Each half of tergite 8 (Figs. 213–215) triangular, convex; ventral corners broadly rounded and converging; distal half microtrichose. Tergite 7 medially narrowed. Cercus 2.5 times as long as wide; with one long apical seta and several scattered setae. Hypoproct (Figs. 214, 215) rectangular; densely microtrichose and medially with a pair of premarginal setae. Spermathecae (Fig. 216) finely ridged; sclerotized ducts very long, five times the diameter of a spermatheca.
ETYMOLOGY. *Aptilotella ebenea* is named for the iridescent black colouration of the abdomen, which is reminiscent of polished ebony.

TYPE MATERIAL. Holotype ♂ (QCAZ). ECUADOR: Pichincha, Bellavista Cloud Forest Reserve, 12 km S Nanegalito, 2150 m, 30.x.1999, cloud forest, leaf litter, R.S. Anderson.

PARATYPES. ECUADOR: Pichincha, Bellavista Cloud Forest Reserve, 12 km S Nanegalito, 28.x.1999, cloud forest, ridge trail leaf litter, R.S. Anderson (♂, ♀); same label as holotype (♂, 2♀).

COMMENTS. See *Aptilotella gemmula* for notes on identification and distribution.

*Aptilotella gemmula* sp. nov.  
(Figs. 46–48, 217–227)

DESCRIPTION. Habitus as in Figures 46 and 47. Body length 1.0 mm. Head ground color yellow-orange. Frons finely rugose; brown medial stripes each about two-fifths the width of frons, broadening posteriorly, diffuse along the anterior margin; orbital stripes brown, narrow. Ocellar tubercle scarcely raised; ocellar bristle two-thirds the length of frons. Interfrontal setae in two pairs. Orbital setulae minute, in four pairs. Face shining; facial tubercle narrow; excavation and clypeus brown; gena dull, with brown ventral margin. Antenna brown, first flagellomere darker. Scutum and scutellum black, shining. Scutum uniformly setose; short, twice wider than long. Scutellum uniformly microtrichose; flat, 3.5 times wider than long, 0.6 times the width of scutum. Apical scutellar bristles 1.7 times as long as basal. Pleuron black, upper half of anepisternum with reflective pruinose stripe visible from an oblique angle. Legs brown; fore and mid tibiae dark brown, hind tibia faintly banded; mid tibia with two anterodorsal and one distal
posterodorsal bristle. Wing rudiment grayish. Abdomen black with bluish iridescence; tergites uniformly setose and microtrichose; sternites finely microtrichose. Epandrium dark reddish brown; cercus and surstylus dull yellow.

**MALE TERMINALIA.** Sternite 5 (Figs. 48, 220) lunate; posteromedial fifth emarginate, the outer margins lobed inward and bearing 3-4 setae; emargination medially giving rise to a triangular process, basally to a pair of densely setaceous stubs, with a membranous lining fringed with several rows of spinules and medially bearing a pair of long medial setae. Synsternite 6+7 as in Figure 219. Cercus (Figs. 217, 218) stout and densely clothed in setulae; basal margin with one long seta medially and several setae in distal half; apex claw-like, with a preapical sensory seta. Surstylus (Figs. 217, 218) cylindroid; distally flattened and broad, anteriorly sharply pointed and medially with a blunt marginal tooth; ventral face with scattered setae. Postgonite (Fig. 223) curved; descending arm straight, slightly tapering, with two anterior marginal sensory setae; articulatory process for pregonite undeveloped, triangular; articulatory process for basiphallus stalked, apically dilated. Aedeagus as in Figures 221 and 222. Basiphallus short, cylindrical; articulatory process for postgonite pointed, short. Ventrobasal sclerite present. Lateral flanking sclerite partitioned in two; the basal half darker, square and fused ventrobasally by a narrow bridge; the smaller distal half pale, irregularly subquadrate, its dorsal margins divergent and with a medial tooth. Ventral flanking sclerites supporting a sail-like membrane; the slender basal article descending and with threadlike attachment to ventral corner of lateral flanking sclerite; the short medial article arising midway along the basal article; the distal article similar to basal article but ascending. Internal sclerite club-shaped, articulated with apicoventral margin of lateral flanking sclerite. Curved dorsal sclerite club-shaped, originating from inside distal ventral margin of lateral flanking sclerite; apex rough and knobby.
**FEMALE TERMINALIA.** Epiproct (Fig. 224) subpentagonal, with a pair of marginal teeth. Each half of tergite 8 (Figs. 224–226) triangular, rather small and weakly convex. Cercus three times as long as wide; with one long apical seta and three shorter preapical setae. Hypoproct (Fig. 226) rectangular; more sclerotized laterally, thus appearing divided; finely hairy, with four basal sensory setae. Spermathecae (Fig. 227) finely ridged; sclerotized ducts very long, four times the diameter of a spermatheca.

**VARIATION.** Colouration varies, with dark or pale stripes on the frons, and legs either uniformly or contrastingly coloured. Teneral individuals are light to reddish brown but possess the distinct iridescence.

**ETYMOLOGY.** The species epithet is Latin for “a small gem,” given in reference to its iridescent abdomen, and elusive habits. Both authors searched intensively for this species at the type locality in 2009, but found only one specimen.

**TYPE MATERIAL.** Holotype ♂ (QCAZ). ECUADOR: Pichincha, Bellavista Cloud Forest Reserve, 12 km S Nanegalito, 28.x.1999, cloud forest, ridge trail leaf litter, R.S. Anderson.

**PARATYPES.** ECUADOR: Pichincha, same label as holotype (7♂, 8♀); same locality as holotype label, 2150 m, 30.x.1999, cloud forest, leaf litter, R.S. Anderson (4♂, 6♀); same locality as holotype label, 0°1’13"S, 78°40’30"W, 2200 m, 9-13.v.2009, S.A. Marshall (♀); Nono, 14 km NW, 2000 m, 24.x.1999, montane forest, leaf litter, R.S. Anderson (2♂, 2♀).

**COMMENTS.** *Aptilotella gemmula* and *A. ebenea* are easily confused, externally differing solely by the presence of orbital bristles in the latter. The distiphallus of *A. gemmula*, however, has a prominent club-shaped sclerite, paired internal sclerites, and membrane-bearing ventral flanking sclerites, all of which are absent in *A. ebenea*. Additionally, each half of the female tergite 8 is much smaller and rounded compared to *A. ebenea.*
Collection data suggest that in the type locality, *A. gemmula* may be commoner than *A. ebenea*, on average outnumbering the latter at least twofold. These species are also sympatric with *A. pichinchensis*, a distantly related species which differs by its larger size, the lack of iridescent colouration, hooked curved dorsal sclerites and well-developed tripartite ventral flanking sclerites.

**The *Aptilotella quadrata* Species Group**

**DIAGNOSIS.** The monophyly of this species group is established on the complete separation of the lateral remnant of tergite 1 from the syntergite, and the prominent dorsal sclerite which is T-shaped in cross-section and originates from between the lateral flanking sclerites (Figs. 232, 238). Other defining aedeagal characters include the fused medial and distal articles of the spoon-shaped ventral flanking sclerites; the loss of the ventrobasal sclerite; and a spindle-shaped ejaculatory apodeme with four sensory pores. Externally, these species are recognizable by their very shiny, nearly hairless body and unicolorous legs. The frons typically has brown medial stripes. Orbital bristles are absent. The mid tibia has one or two anterodorsal bristles. The *A. quadrata* species group is distributed throughout the Central American isthmus.
**Figure 3** *Aptilotella quadrata* sp. nov., holotype male.

*Aptilotella quadrata* sp. nov.  
(Figs. 3, 228–233)

**DESCRIPTION.** Habitus as in Figure 3. Body length 1.6 mm. Head ground color yellow. Frons finely rugose; pale areas attaining the occiput but not the anterior margin; brown medial stripes each about one-seventh the width of frons, with narrow orange borders; dark brown orbital stripes confined to posterior corners of frons, their orange borders confluent with the medial stripes; ocular emargination with pruinose patch. Ocellar tubercle scarcely raised; ocellar
bristle two-thirds the length of frons. Interfrontal setae inconspicuous, in three pairs. Orbital setulae inconspicuous, in two pairs. Face shining; facial tubercle bulbous; gena with black ventral margin. Antenna brown, first flagellomere paler in basal half. Occiput with dark brown margin. Scutum and scutellum black, shining. Scutum with only a few short setae. Scutellum bare; 2.4 times wider than long, 0.6 times the width of scutum. Apical scutellar bristles 2.5 times as long as basal. Pleuron black; anepisternum and anepimeron with pale pruinose stripe. Legs orange; coxa black; femur dark orange, basal half of hind femur brown; mid tibia dark brown, with a single proximal anterodorsal bristle. Wing rudiment dark brown. Abdomen black, shining; tergites distally with a row of evenly-spaced, short setae; sternites microtrichose. Cercus and surstylus orange.

**MALE TERMINALIA.** Sternite 5 (Fig. 231) narrow and asymmetrical; posteromedial half shallowly emarginate; two long, apically rounded lobes arising in posteromedial quarter, their interior margin setaceous. Synsternite 6+7 (Fig. 230) with humped margin before medial bridge; interior surface of medial bridge with free, saddle-shaped sclerite. Cercus (Figs. 228, 229) curved, twice as long as basal width; base triangular, with four long setae near outer margin, and a much longer marginal seta subequal to the length of cercus; distal three-fifths slender, bearing two small, well-separated sensory setae. Surstylus (Figs. 228, 229) horseshoe-shaped, basally enlarged; anterior lobe apically dilated and truncate, with scattered sensory setae; posterior lobe with setaceous outer margin, apically bearing three large, articulated, claw-like spines. Postgonite (Fig. 233) sinuate; descending arm 0.6 times the total length, of uniform width and slightly bent midway, with two distal sensory setae; articulatory process for pregonite broad, rounded; articulatory process for basiphallus knobbed. Aedeagus as in Figure 232. Basiphallus compressed, arched, basal lobe projecting into distiphallus; articulatory process for postgonite
pointed, erect. Ejaculatory apodeme short. Lateral flanking sclerites with dark dorsal and ventral margins, broadly fused both ventro- and dorsobasally; apicodorsally armed with minute sclerotized teeth. Dorsal sclerite constricted medially, its sides forming a channel; apex laterally lobed and bearing minute sclerotized teeth. Ventral flanking sclerites with the basal article fused along ventrodistal margin of lateral flanking sclerite; the spatulate medial article sharply pointed beneath the basal article; the concave distal article fused to the medial article and sharply pointed over it.

**FEMALE TERMINALIA.** Not examined; retracted from view in the single female specimen.

**VARIATION.** The two specimens from the “trail to Cerro Chirripó” have the dark genal band continuing through the clypeus, a thick dark band across the facial excavation, dark brown legs, and two anterodorsal bristles on the mid tibia. Although otherwise identical to the type material, both are females and cannot be positively identified as *Aptilotella quadrata*.

**ETYMOLOGY.** The species epithet describes the roughly squared tergite 1 plate, a defining character of this species and other members of the *A. quadrata* species group.

**TYPE MATERIAL.** Holotype ♂ (INBC). COSTA RICA: Highway 2, km 96, 3200 m, 7-13.iv.1985, cloud forest (oak), pan trap, H. Goulet and L. Masner.

**PARATYPES.** COSTA RICA: San José, 2 km E Villa Mills, 9°33’30”N, 83°42’W, 2800 m, 26.vi.1997, second growth oak forest litter, R.S. Anderson (♀); same as previous label but at 2750 m, 15.ii.1998 (♂); Cerro Chirripó, Base Crestones, 3350 m, 25.vi.1999, elfin forest, leaf litter, R.S. Anderson (♂).

**OTHER MATERIAL EXAMINED.** COSTA RICA: Cartago, Cerro Chirripó, trail to, 2800 m, 27.vi.1999, mixed oak forest, leaf litter, R.S. Anderson (2♀).
**COMMENTS.** Few members of the genus are as large and robust as *Aptilotella quadrata*, and not even the more slender *A. involucris* possesses such a prominently bilobed male sternite 5 as found in this species. A female superficially similar to *A. quadrata*, but probably belonging to a closely-related species, lacks markings on the frons and has been collected at carrion with *A. umbracatus* in Panama.

*Figure 4* *Aptilotella umbracatus* sp. nov., paratype male.
Aptilotella umbracatus sp. nov.

(Figs. 4, 49–51, 234–243)

DESCRIPTION. Habitus as in Figures 4, 49, and 50. Body length 1.3 mm. Head ground color yellow. Frons finely rugose, its pale areas uniformly constricted by brown stripes; medial brown stripes broad, each approximately one-quarter the width of frons, diffuse along the anterior margin; orbital stripes darker, ending at ocular emargination. Ocellar tubercle slightly raised and overlapping medial stripes; ocellar bristle two-thirds the length of frons. Interfrontal setae minute, in two pairs. Orbital setulae inconspicuous, in three pairs. Facial tubercle, excavation and gena shining. Antenna yellow, first flagellomere brown in distal two-thirds. Scutum and scutellum dark reddish-brown to black, shining. Scutum uniformly, sparsely setose, with minute patch of tomentosity on anterior margin laterally and medially; posterior margin tomentose. Scutellum microtrichose; 2.5 times wider than long, 0.7 times the width of scutum. Apical scutellar bristles 2.5 times as long as basal. Pleuron black; anepisternum sometimes with a faint pruinose stripe. Legs yellow; fore coxa brown, mid and hind coxae dark brown; mid tibia and tarsus darker; mid tibia with two anterodorsal bristles. Wing rudiment yellowish. Abdomen black, shining; tergites distally with a row of evenly-spaced setae, syntergite with 2 rows; sternites finely microtrichose, with rows of longer setae posteriorly. Terminalia reddish-brown; epandrium densely microtrichose; cercus and surstylus yellow.

MALE TERMINALIA. Sternite 5 (Fig. 237) irregularly shallowly excised in posteromedial third, with a simple membranous lining. Synsternite 6+7 (Figs. 51, 236) densely microtrichose, with a field of minute spinules on medial bridge. Cercus (Figs. 51, 234, 235) 1.3 times as long as basal width; base triangular, with two inner setae; distal half narrow and curved, basally with a long seta half the length of cercus, and a shorter seta below. Surstylus (Figs. 51, 234, 235)
irregularly angular; posteromedially with a large setaceous tubercle, beneath which are four stout setae of which the anterior one is largest; distal margin squared, with a few small sensory setae.

Postgonite (Figs. 51, 239) sinuous posteriorly, descending arm one-third the total length, with a basal sensory seta; articulatory process for pregonoite hooked upward and truncate; articulatory process for basiphallus reduced to a small knob. Aedeagus as in Figure 238. Basiphallus cylindrical;posteroventrally humped, appearing boot-shaped in lateral profile; articulatory process for postgonite rounded and divergent. Ejaculatory apodeme very slender-tipped. Lateral flanking sclerites with dark dorsal and ventral margins, very narrowly fused posterodorsally and more broadly posteroventrally; dorsum densely armed with heavily-sclerotized teeth. Dorsal sclerite very dark; flattened; apex curved upwards and broadly rounded, with a rudder-like ventral keel. Ventral flanking sclerites paddle-shaped; the triangular medial article sharply pointed beneath the basal article; the distal article darkest and irregularly ovate.

**FEMALE TERMINALIA.** Tergite 7 divided medially; distal half densely microtrichose, with several marginal setae. Epiproct semicircular. Each half of tergite 8 (Figs. 240–242) rhomboid, with a weak medial ridge. Cercus three times as long as wide; truncate. Hypoproct a narrow band. Spermathecae (Fig. 243) ridged; collar with two rings of minute stubs; sclerotized ducts very short, less than the diameter of a spermatheca.

**VARIATION.** Some series consist of darker and barer individuals. These specimens, while possessing the unmistakable dorsal sclerite which characterises *Aptilotella umbracatus*, differ by most to all of the following: darker overall colour; legs dull yellow to orange, often paler distally; all coxae dark; scutum lacking anteromedial patch of tomentosity; scutellum lacking microtrichosity.
ETYMOLOGY. The species epithet is derived from the Latin *umbra*, “shadow,” and *acatus*, “a boat or light vessel,” in reference to the starkly contrasting, rudder-like dorsal sclerite of the distiphallus.

TYPE MATERIAL. Holotype ♂. PANAMA: Chiriqui, 4.5 km E Cerro Punta, 2500 m, 23-28.v.1977, carrion, S. Peck.

PARATYPES. PANAMA: Chiriqui, same label as holotype (9♂, 4♀); 2 km E Cerro Punta, 2200 m, 28.v.-8.vi.1977, dung traps, S. Peck (2♂, ♀); same locality as previous label, 1-8.vi.1977, carrion traps, S. Peck (♂, ♀); Boquete, 5.7 km NE, 1500 m, 19.vi.1995, mixed oak forest, leaf litter, R.S. Anderson (♂, ♀); Boquete, 5.8 km NE, 14.vi.1996, oak forest, leaf litter, R.S. Anderson (♀); Volcán Barú National Park, 5.9 km E Cerro Punta, 2400 m, 14.vi.1995, oak ridge-bamboo forest, litter, R.S. Anderson (♂, ♀); same as previous label but at 2150 m, riparian alder forest (♀); Volcán Barú National Park, 11 km W Boquete, 2150 m, 18.vi.1995, mixed oak forest, leaf litter, R.S. Anderson (3♂, 4♀); Cerro Pando, 12 km NE Santa Clara, 2120 m, 17.vi.1996, wet cloud forest, leaf litter, R.S. Anderson (♀); Hartmann’s Finca, 30.7 km W Volcán, 1800 m, 16.vi.1995, mixed oak forest, leaf litter, R.S. Anderson (♂); La Fortuna area, Finca La Suisse, 1450-1600 m, 11.vi.1995, oak ridge forest, litter, R.S. Anderson (2♂, ♀); La Fortuna area, Finca La Suisse, 1450 m, 12.vi.1995, wet montane forest, leaf litter, R.S. Anderson (♀). COSTA RICA: Limón, Valle del Silencio, La Estación, 9°6’37”N, 82°57’43”W, 2473 m, 26-27.ii.2005, forest litter, R.S. Anderson (4♂, 2♀).

COMMENTS. *Aptilotella umbracatus* has a known range occupying the southerly slopes of the Cordillera de Talamanca in Panama and neighbouring Costa Rica. This species is
significantly smaller than *A. quadrata* and not as boldly marked. The scutal tomentosity and rudder-like dorsal sclerite of the distiphallus are diagnostic.

**The *Aptilotella angela* Species Group**

**DIAGNOSIS.** This is a monophyletic species group presently known from two closely-allied species from northern Ecuador. Adults are somewhat rotund in appearance, and have banded legs and straight, narrow brown medial stripes on the frons. The distiphallus, as in other members of Clade 2, has curved dorsal sclerites and tripartite ventral flanking sclerites with a dorsally branched basal article.

*Aptilotella angela* sp. nov.

(Figs. 2, 244–253)

**DESCRIPTION.** Habitus as in Figure 2. Body length 1.5 mm. Head ground color yellow-orange. Orbital plate shining, darkened behind antennal insertions, with a somewhat paler spot in ocular emargination; interfrontal plate finely rugose; brown medial stripes each approximately one-fifth the width of frons, diffuse along the anterior margin. Ocellar tubercle raised, shining; ocellar bristle subequal to the length of frons. Interfrontal setae long, in two pairs. Orbital setulae small, in four pairs. Face shining; facial tubercle conical, excavation very shallow, with slightly infuscated margin; gena paler, weakly shining and finely rugose. Antenna black, first flagellomere brown. Occiput black. Scutum and scutellum black, shining. Scutum uniformly, sparsely setose. Scutellum bare; three times wider than long, two-thirds the width of scutum. Apical scutellar bristles 1.4 times as long as basal. Pleuron black. Legs bicoloured; coxa black;
trochanter orange; femur black except for orange “knee”; fore and mid tibiae black, orange basally and apically; hind tibia black except for broad orange band basally and along mid-length; tarsus orange, darkening distally; mid tibia with a single distal anterodorsal bristle. Wing rudiment brown. Abdomen black, shining; tergites uniformly setose, basal margin densely microtrichose except for syntergite; sternites finely microtrichose, with rows of setae posteriorly. Cercus red-orange.

**MALE TERMINALIA.** Sternite 5 (Fig. 247) medially with a field of minute spinules; posteromedial margin giving rise to a somewhat membranous, shallowly concave shelf, covered in rows of bifid or trifid spinules, flanked on each side by a setal cluster. Synsternite 6+7 (Fig. 246) flanked on each side of medial bridge by a curved arm, posteromedially with pouch-like membrane attaching to the marginal shelf of sternite 5. Cercus (Figs. 244, 245) slender, curved, three times as long as basal width; base dilated, margin interiorly deeply excavated; inner basal margin with three long setae in a row and one long seta adjacent to the basal two, this seta two-thirds the length of cercus; apex bearing a stout, recurved seta. Surstylus (Figs. 244, 245) conical; outer face anteriorly expanded into a rounded rectangular plate, about 1.5 times as long as the height of cone, bearing scattered sensory setae, and with a tuberculate posteroventral corner bearing numerous divergent setae. Postgonite (Fig. 249) sinuate; descending arm gradually curving and tapering, with several marginal sensory setae; articulatory process for pregonite triangular and rounded; articulatory process for basiphallus short-stalked and knobbed. Aedeagus as in Figure 248. Basiphallus cylindroid; articulatory process for postgonite pointed and anteriorly directed. Ventrobursal sclerite broad. Lateral flanking sclerite fused ventrobasally by a narrow bridge; dorsal margin rolled, straight and nearly parallel, then irregular diverging and ascending in distal third. Ventral flanking sclerites darker; the slender basal article fused
along ventral margin of lateral flanking sclerite, preapically giving rise to a slender dorsal arm; the chevron-shaped medial article meeting the basal article interiorly; the rounded distal article with a darkened dorsal margin leading a triangular lobe inward and upward. Curved dorsal sclerite originating from inside distal ventral margin of lateral flanking sclerite and abruptly ascending.

**FEMALE TERMINALIA.** Epiproct (Fig. 250) very pale, subpentagonal; finely hairy, with four basal setae. Each half of tergite 8 (Figs. 250–252) strongly convex, its outer margin concave; with several setae. Cercus three times as long as wide; with two long apical setae. Hypoproct (Fig. 252) triangular with rounded apex; finely hairy, with two preapical sensory setae. Spermathecae (Fig. 253) finely ridged; sclerotized ducts very long, four to five times the diameter of a spermatheca.

**VARIATION.** Some specimens have a slightly reddish tinge in the scutum.

**ETYMOLOGY.** The species epithet is a reference to the Ecuadorian city near the páramo habitat where the type series was collected.

**TYPE MATERIAL.** Holotype ♂ (QCAZ). ECUADOR: Carchi, Páramo El Ángel, 14.1 km NW El Ángel, 3450 m, 2.xi.1999, mixed *Polylepis* litter, R.S. Anderson.

**PARATYPES.** ECUADOR: Carchi, same label as holotype (2♂, 2♀); Guandera Forest Reserve, 15 km E San Gabriel, 3300 m, 1.xi.1999, mixed riparian forest, leaf litter, R.S. Anderson (♀).

**OTHER MATERIAL EXAMINED.** ECUADOR: Carchi, Páramo El Ángel, 18.8 km NW El Ángel, 3300 m, 31.x.1999, mixed *Polylepis* litter, R.S. Anderson (♀).

**COMMENTS.** *Aptilotella angela* is known from the northernmost slopes of the Ecuadorian Andes, and its distribution may possibly extend into Colombia. In an aberrant female specimen
from 18.8 km northwest of El Ángel, the frons is faded, the thorax is dull dark grey, the fore tibia is orange, and the mid tibia is more heavily banded. Although it fits within the range of *A. angela*, it cannot be ruled out that this individual may belong to an undescribed species.

*Aptilotella pichinchensis* sp. nov.

(Figs. 52–54, 254–262)

**DESCRIPTION.** Habitus as in Figures 52 and 53. Body length 1.3 mm. Head ground color yellow ochre. Orbital plate shining except for pruinose anterior third; interfrontal plate slightly raised, finely rugose; dark brown medial stripes each about one-fifth the width of frons, diffuse along the anterior margin up to ocular emargination. Ocellar tubercle slightly raised, shining; ocellar bristle subequal to the length of frons. Interfrontal setae long, cruciate, in two pairs. Orbital setulae minute, in three pairs. Face and gena shining. Antenna dark brown, first flagellomere brown. Scutum orange, shining; uniformly, sparsely setose. Scutellum dark brown, bare, flattened; twice wider than long, half the width of scutum. Apical scutellar bristles 2.5 times as long as basal. Pleuron orange, anepisternum paler. Legs dull orange; coxa brown; fore tibia dark brown, mid and hind tibiae with dark brown basal and preapical bands; tarsus brown; mid tibia with two anterodorsal and one distal posterodorsal bristle. Wing rudiment dull yellow. Abdomen black, shining; tergites uniformly setose, evenly microtrichose except distally and dorsum of syntergite; sternites finely microtrichose.

**MALE TERMINALIA.** Sternite 5 (Fig. 256) lunate; posteromedial margin with a small bump bearing minute, thorn-like spines, flanked on each side by a field of setae. Synsternite 6+7 (Fig. 256) also bearing thorn-like spines along posterior arm; medial bridge posteromedially giving rise to a conical sclerite. Cercus (Figs. 54, 254, 255) 1.7 times as long as basal width; base
broad with a medial conical tubercle and three setae along its lower margin, the outermost seta longest, about half the length of cercus; the distal two-thirds compressed and curved, apex blunt, inner margin continuous with base. Surstylus (Figs. 54, 254, 255) cylindrical, flat-bottomed except for descending anterior lobe; ventral margin setaceous. Postgonite (Fig. 258) sinuate posteriorly; descending arm half total length, very slender, gently curved and tapering; articulatory process for pregonite rounded; articulatory process for basiphallus stalked and knobbed. Aedeagus as in Figure 257. Basiphallus cylindroid, weakly arched, posteroventrally humped; articulatory process for postgonite small and diverging. Ventrobasal sclerite single but lightly sclerotized medially. Lateral flanking sclerite broadly fused ventrobasally; dorsal margin darkened, straight, then diverging and folding inward in distal third; distal third clothed in fine spinules. Ventral flanking sclerites darker; the basal article fused along ventral margin of lateral flanking sclerite, with a sickle-shaped dorsal arm arising preapically; the medial article trapezoidal; the elongate distal article pointed and sinuate, internal margin medially giving rise to a pale triangular lobe. Curved dorsal sclerite slender, originating inside distiphallus above distal article of ventral flanking sclerite.

**FEMALE TERMINALIA.** Epiproct very pale and inconspicuous. Each half of tergite 8 (Figs. 260, 261) rounded and strongly convex. Cercus three times as long as wide; with three long apical setae. Sternite 8 (Fig. 261) very narrow and boomerang-shaped. Hyproct (Fig. 260–261) triangular, apically finely hairy. Spermathecae (Fig. 262) finely ridged; sclerotized ducts 1.5 times the diameter of a spermatheca.

**ETYMOLOGY.** *Aptilotella pichinchensis* is named for the Pichincha Province of Ecuador, from which the species is described.
**TYPE MATERIAL.** Holotype ♂ (QCAZ). ECUADOR: Pichincha, Campamento Pichan, ~27.5 km NW Quito, 3350 m, 22.x.1999, cloud forest, leaf litter, R.S. Anderson.

**PARATYPES.** ECUADOR: same label as holotype (9♂, 7♀); near Nono, 24.x.1999, green leaf litter, S.A. Marshall (2♀).

**COMMENTS.** *Aptilotella pichinchensis* occurs farther south than its sister species, *A. angela*, from which it differs by the brighter thoracic colouration and the strong curvature of the curved dorsal sclerites and dorsal arm of the basal article of the ventral flanking sclerite. See comments on *A. gemmula* for notes on sympatry with this species and *A. ebenea*.

*Aptilotella vivus* sp. nov.

(Figs. 55–57, 263–272)

**DESCRIPTION.** Habitus as in Figures 55 and 56. Body length 0.9 mm. Head ground color yellow-orange. Frons finely rugose; completely flat and featureless except for inner vertical bristles. Face and gena shining; face narrow, 1.5 times higher than wide. Antenna light tan, separated by half the diameter of their sockets. Body pruinose; entirely bluish-gray with a weak iridescent sheen, and occasionally a purplish tinge. Scutum uniformly setose. Scutellum bare; three times wider than long, 0.6 times the width of scutum. Apical scutellar bristles 1.5 times as long as basal. Lower anepisternum and anepimeron with a very pale pruinose stripe. Legs yellow-orange; mid and hind coxae dark brown; fore and mid tibiae and tarsi brown, distal third of fore tibia shining dark brown; mid tibia with two anterodorsal bristles. Wing rudiment lanceolate, gray. Tergites uniformly setose; sternites finely microtrichose. Epandrium, synsternite 6+7, and female sternite 8 reddish-brown. Synsternite 6+7 bare and shining.
**MALE TERMINALIA.** Sternite 5 (Figs. 57, 266) with broad membranous shelf along posterior margin, indented medially and clothed in minute spinules; margin posteromedially with a deep circular notch flanked on each side by a stout seta, interiorly giving rise to a free, pickaxe or hammer-shaped sclerite. Synsternite 6+7 (Figs. 57, 265) fairly broad across but with an extremely narrow medial bridge, appearing thus to have a deep groove, which is densely coated in marginal spinules, and containing a membranous pouch. Cercus (Figs. 57, 263, 264) triangular, curved, 1.5 times as long as basal width; base connected to epandrium by a meandering strap; inner margin with many short and one long spinule; apex bearing a stout crowbar-shaped process flanked by two long setae. Surstylus (Figs. 57, 263, 264) bulbous basally and setaceous; whip-like distal portion lightly sclerotized, membranously lobed, the apex hooked and truncate. Postgonite (Fig. 268) curved; descending arm straight, truncate apically, anterior margin medially with three sensory setae; articulatory processes undeveloped. Aedeagus as in Figure 267. Basiphallus with bulbous articulation with aedeagal apodeme; articulatory process for postgonite short, pointed and divergent. Ventrobasant sclerite present. Lateral flanking sclerite lightly sclerotized, dorsal margin scalloped, apically with slender projection. Ventral flanking sclerites darker; the basal article broadly fused ventrally and along entire ventral margin of lateral flanking sclerite, dorsobasal corner lobed, with very slender and curving preapical dorsal arm; the elongate distal article curved and as long as lateral flanking sclerite, basally with two lateral teeth. Curved dorsal sclerites slender, S-shaped, rising near distal margin of the basal article of ventral flanking sclerite. Distomedial sclerite depressed, membranous, as long as ventral flanking sclerite; descending from level of distal margin of lateral flanking sclerite.

**FEMALE TERMINALIA.** Epiproct (Fig. 269) triangular; margin pointed apically, sinuate, setaceous. Each half of tergite 8 (Figs. 267–271) slightly convex with nearly straight margin;
distal half setaceous. Cercus dark brown, shining; four times as long as wide; with several preapical setae. Sternite 8 (Figs. 270, 271) triangular with rounded apex. Hypoproct (Figs. 270, 271) indistinct; finely hairy. Spermathecae (Fig. 272) finely ridged; sclerotized ducts long, twice the diameter of a spermatheca.

**VARIATION.** Two aberrant individuals collected in the same region as the type locality, in upper montane forest, differ from all other specimens examined. The male specimen is teneral but is assumed to be similar to the female, which has a reddish frons, a shiny black body, and finely punctured abdominal tergites. It is unclear whether these are conspecifics or another species.

**ETYMOLOGY.** The species epithet is Latin for “lively,” because its body colouration stands out among its congeners.

**TYPE MATERIAL.** Holotype ♂. VENEZUELA: Mérida, Sierra Nevada National Park, La Mucuy, 7 km E Tabay, 2520 m, 24.v.1998, cloud/bamboo forest, litter, R.S. Anderson.

**PARATYPES.** VENEZUELA: Mérida, same label as holotype (13♂, 14♀); Páramo La Culata, 18.5 km NE Mérida, 2950 m, 25.v.1998, páramo, streamside, shrub litter, R.S. Anderson (♂).

**OTHER MATERIAL EXAMINED.** VENEZUELA: Mérida, Sierra Nevada National Park, La Mucuy, 7 km E Tabay, 2340 m, 24.v.1998, upper montane forest, leaf litter, R.S. Anderson (♂, ♀).

**COMMENTS.** The smallest of all the described *Aptilotella* species, *A. vivus* is instantly recognizable by its compact, pruinose and iridescent bluish-gray body. Similar but polished forms have been examined from Guatemala and southern Ecuador, but are unlikely to be related to *A. vivus*. This species has the northernmost distribution of any *Aptilotella* in continental South
America, and is the only member of the genus known from the Cordillera de Mérida of the northeastern Andes.

*Aptilotella macula* sp. nov.

*(Figs. 1, 58–60, 273–282)*

**DESCRIPTION.** Habitus as in Figures 1, 58, and 60. Body length 1.4 mm. Head ground color orange. Frons finely rugose, with five silvery spots: one before each ocular emargination, one diffusely at each hind corner and slightly on occiput, and one on interfrontal plate before tubercle. Ocellar tubercle scarcely raised, with minute medial seta; ocellar bristle greater than the length of frons. Interfrontal setae in three pairs. Orbital setulae inconspicuous, in four pairs. Face shining; lunule with silver spot; gena finely rugose, posterior margin black. Antenna yellow, distal half of first flagellomere brown, scape black. Scutum and scutellum black, with metallic sheen. Scutum uniformly, sparsely setose; posterior dorsocentral bristles as long as scutum. Scutellum bare; three times wider than long, 0.8 times the width of scutum; margins carinate. Scutellar bristles subequal in length. Pleuron black, weakly shining; upper anepisternum and anepimeron with pale pruinose stripe. Legs brown; mid and hind coxae black; front and mid femora and distal half of hind femur orange; hind tarsus light brown; mid tibia with two anterodorsal bristles. Wing rudiment black. Abdomen black, with metallic sheen; tergites setose, densely microtrichose; sternites finely microtrichose. Cercus and surstylus brown.

**MALE TERMINALIA.** Sternite 5 (Fig. 275) lunate; posteromedial third weakly dilated, concave and polished, flanked by a patch of setae and four strong marginal setae, medially with four marginal setae. Synsternite 6+7 as in Figure 276. Cercus (Figs. 60, 273, 274) stout,
triangular, apically truncate; inner margin setulose. Surstylus (Figs. 60, 273, 274) basally swollen and divergent, bending at a nearly right angle at midpoint, then rounded and upwardly curved apically; base setulose; inner margin with scattered rows of sensory setae before the bend. Postgonite (Figs. 60, 278) 1.8 times as long as wide; posterior margin medially with large tooth-like projection; preapically with three sensory setae; articulatory processes rounded, each with an internal tooth; margin shallowly concave between the two processes. Aedeagus as in Figure 277. Basiphallus stout, cylindrical; articulatory process for postgonite short, divergent; articulation with distiphallus dorsally projected. Ventrobasal sclerite weakly divided. Lateral flanking sclerites very narrowly fused ventrobasally; dorsal margin slightly curved, diverging beyond basal two-fifths and descending, then hooked upward and cradling a membranous sheet in between; the sheet laterally lobed and studded with numerous round or elongate sclerotized scales. Ventral flanking sclerites darker; the basal article fused along ventral margin of lateral flanking sclerite, medially bearing a dorsal arm; the triangular medial article articulating with basal article, its inner corner sharply pointed, its top corner rising to just beneath the hooked portion of lateral flanking sclerite; the membranous distal article with a darker, sickle-shaped ascending arm. Curved dorsal sclerites dark, originating from within hooked portion of lateral flanking sclerite, curving inward and converging, their slightly swollen apices protruding between membranous sheet.

**FEMALE TERMINALIA.** Epiproct (Fig. 279, 280) semicircular. Each half of tergite 8 (Figs. 279, 280) triangular with broadly rounded apex, convex; dorsal half with several long setae. Cercus 2.5 times as long as wide; with two long preapical setae. Sternite 8 (Figs. 280, 281) divided; each half boomerang-shaped, apically microtrichose and with one preapical seta.
Spermathecae (Fig. 282) finely ridged; sclerotized ducts extremely long, six to seven times the diameter of a spermatheca.

**VARIATION.** The reflectiveness of the silvery spots varies from faint to very strong. Infrequently, the hind femur is more or fully orange. Teneral specimens have a brownish body but retain the metallic sheen.

**ETYMOLOGY.** *Aptilotella macula* is named for the unique patterning of the frons.


**PARATYPES.** BOLIVIA: La Paz, Coroico, same label as holotype (25♂, 18♀); Cerro Uchumachi, 16°12′43″S, 67°42′49″W, 2550 m, 28.i.2001, cloud forest, leaf litter, R.S. Anderson (♂); same locality as previous label, 5-6.iv.2011, S.A. Marshall (6♂, 4♀).

**COMMENTS.** *Aptilotella macula* is readily recognized by the uniquely five-spotted frons and very shiny metallic body. The male distiphallus is distinctive for the scale-studded membranous sheet between the lateral flanking sclerites, and the claw-like fused medial and distal articles of the ventral flanking sclerites.

Two males collected 50 km south of the type locality have four spots evenly spaced along the anterior margin of the frons, and similarly curved but rod-shaped surstyli. Until verified by dissection, these are thought to be distinct from *A. macula*, possibly rendering a complex of recently diversified species.

Besides this, *A. macula* is the remotest and southernmost member of the genus. Its type locality in the Bolivian Altiplano is over 2,100 km southeast of the Pichincha province of Ecuador, the next closest distributional record for a described *Aptilotella* species.
6. CONCLUSION

Aptery and the higher classification of Limosininae

Some 40 genera and 100 species of brachypterous or apterous sphaerocerids have been described (Marshall, 2000), and there are undoubtedly many more, as demonstrated by this study. The tremendous puzzle that looms over the subject of aptery in the Limosininae is the extraordinary morphological congruence among widely separated Neotropical and Old World genera. These similarities presumably are the result of homoplasy, with wingless forms having descended from separate winged ancestors and converged. Under this interpretation, *Aptilotella* has closer evolutionary affinity to other Neotropical Limosininae than to superficially similar Old World or Pacific taxa such as *Howickia*.

A beetle- or ant-like apterous morphology appears in at least two other Neotropical limosinine genera, *Aptilotus* and *Myrmolimosina* (Marshall & Buck, 2010). *Aptilotus* is a Holarctic genus represented in the Neotropics by three species described by Marshall (1997) from a páramo-like site on Cerro de la Muerte, Costa Rica. These apterous *Aptilotus* seem to be a distinct clade, weakly supported by the shape of the male sternite 5 and reduced female sternite 8, as well as the disjunct distribution from the North American species. They are not closely related to the predominantly Neotropical *Pterogramma* and strictly Neotropical *Aptilotella*, differing by the genitalia and chaetotaxy, including the plesiomorphic condition of having two orbital bristles (Marshall, 1997). In contrast, the remarkably ant-like *Myrmolimosina andersoni* shares chaetotaxic characters with *Aptilotella* such as one orbital bristle, two interfrontal bristles, maxillary palpus with one apical bristle, and long presutural dorsocentral bristles (Marshall, 2000). Yet again, the structure of the genitalia, such as unmodified cerci that are connected to the
epandrium, elongated distiphallus, and transverse hypandrium, fail to support a close affinity between the two genera (Marshall, 2000).

Among the Indopacific Limosininae, brachypterous members of the genus *Biroina* Richards are superficially similar to the wingless *Howickia*, forming a phylogenetic puzzle that nearly parallels that of *Pterogramma* and *Aptilotella*. *Howickia* is virtually identical to *Aptilotella*, but differs in the number and arrangement of mid tibial bristles, presence of halteres, and genitalic structure (Richards, 1951; Harrison, 1959). This appears to be a remarkable example of extreme convergence between distantly related lineages.

Several superficially similar flightless lineages also occur in Africa, notably in the vicinity of Mount Elgon and Mount Ruwenzori; these were extensively studied by Richards (see for example, 1951, 1955, 1957, 1962, 1965). Tracing the relationships among lineages will involve not only the wingless forms, but also numerous macropterous taxa.

**Concluding remarks**

This first revision of the genus *Aptilotella* has elevated the genus from monotypy to a present total of twenty-two described species in two clades and four species groups. Sufficient evidence was found to support the newly redefined and expanded genus *Aptilotella* as a monophyletic taxon. The phylogenetic analysis also provided evidence that *Aptilotella* is descended from *Pterogramma*, thus rendering *Pterogramma* paraphyletic.

At least two dozen undescribed *Aptilotella* species within DEBU still need to be studied. The majority of this material is composed of species represented by one or a few specimens, often mostly females. Further undescribed species undoubtedly reside in other collections. It is likely that as more species are examined, new species groups will be erected in addition to the four that
I have established, and a clearer definition or redefinition of Clade 2 is anticipated given the myriad of South American species that await formal description. I am optimistic that new data and refinement of the character list will clarify the phylogenetic understanding of *Aptilotella*.

I could not afford to travel to many field sites in Latin America, but additional sampling will help to expand both the taxonomic and geographical coverage of *Aptilotella*. I was frustrated with my failure to observe *A. gemmula* in its type locality in Ecuador, but remain confident that with persistent field work, living flies will eventually be re-encountered. Future forays for *Aptilotella* could be accompanied by attempts to record their behaviour, and it would be worthwhile to look for immature stages. A small sample of freshly collected adult flies should also be preserved in 90% ethanol for later DNA analysis.

Of particular interest would be the rediscovery of *A. borgmeieri*—admittedly a slim possibility, as cloud forests are steadily dwindling due to human exploitation. Flightless sphaerocerids tend to have restricted distributions and are sensitive to disturbance. Thus, Kits and Marshall (2011) pointed to the genus *Frutillaria* as an example of a potentially significant taxon for identifying habitats of conservation concern. *Aptilotella* may be of similar importance, but it is probable that species such as *A. borgmeieri* have already disappeared with their former haunts. Perhaps Duda implied this when he wondered in 1924, “whether this easily overlooked species of fly will ever be found again.”

The future study of *Aptilotella* as a whole is not nearly as bleak as for *A. borgmeieri*. This is a particularly diverse and fascinating genus of flightless sphaerocerids. The advancement of limosinine taxonomy through their study promises to be an exciting and gratifying endeavour.
7. REFERENCES


Map 2 Distributions of *Aptilotella* species in Central America from Costa Rica to adjacent Panama. Legend: circle (●) = *A. diffisa*, hollow diamond (◊) = *A. involucris*, triangle (▲) = *A. quadrata*, star (★) = *A. umbracatus*. 
Map 3 Distributions of *Aptilotella* species (Clade 2) in South America, with the inset showing the species from northern Ecuador. Legend: diamond (♦) = *A. ebenea* and *A. gemmula*, hollow diamond (◊) = *A. gemmula* only, circle (●) = *A. angela*, star (★) = *A. pichinchensis*, plus sign (+) = *A. vivus*, pentagon (▲) = *A. macula*. 
Figure 5 Nine most parsimonius trees retained by analysis in Tree Analysis using New Technology (TNT, Willi Hennig Society Edition, version 1.1), with traditional search and 5000 replicates, and optimized in Mesquite software (version 2.75).
Figure 6 Strict consensus tree of Aptilotella. A solid circle indicates a synapomorphy, an empty circle a homoplasy, and a crossed-out circle a reversal. Numbers above correspond to the character number; numbers below the circle indicate the state for multistate characters.
Figures 7–8 *Aptilotella caerulea* sp. nov., male: 7 – habitus, left lateral; 8 – habitus, dorsal.
Figures 9–10 *Aptilotella germana* sp. nov., male: 9 – habitus, left lateral; 10 – habitus, dorsal. Abbreviation: WP = left wing pad.
Figure 11 Aptilotella germana sp. nov., male terminalia. Abbreviations: CER = cercus, DS5 = division of sternite 5, PG = postgonite, SUR = surstylus.
Figures 12–13 *Aptilotella pyropanda* sp. nov., male: 12 – habitus, left lateral; 13 – habitus, dorsal.
**Figure 14** *Aptilotella pyropanda* sp. nov., male terminalia. **Abbreviations:** CER = cercus, PG = postgonite, SEM = emargination of sternite 5.
Figures 15–17 *Aptilotella gracilis* sp. nov., male: 15 – habitus, left lateral; 16 – habitus, dorsal; 17 – left wing.
Figure 18 Aptilotella gracilis sp. nov., male terminalia. **Abbreviations:** CER = cercus, HSP = hoof-shaped process of sternite 5, LCP = left curved process of synsternite 6+7, RCP = right curved process of synsternite 6+7.
Figures 19–20 *Aptilotella diffisa* sp. nov., male: 19 – habitus, left lateral; 20 – habitus, dorsal.
Figure 21 *Aptilotella diffisa* sp. nov., male terminalia. **Abbreviations:** CER = cercus, CLP = clasper-like process of sternite 5.
Figures 22–23 Aptilotella involucris sp. nov., male: 22 – habitus, left lateral; 23 – habitus, dorsal.
Figure 24 *Aptilotella involucris* sp. nov., male terminalia. **Abbreviations:** CER = cercus, CLP = clasper-like process of sternite 5, SUR = surstylus.
Figures 25–26 *Aptilotella sphyra* sp. nov., male: 25 – habitus, left lateral; 26 – habitus, dorsal.
Figure 27 *Aptilotella sphyra* sp. nov., male terminalia. **Abbreviations:** CER = cercus, SUR = surstylus.
Figures 28–29 *Aptilotella andersoni* sp. nov., male: 28 – habitus, left lateral; 29 – habitus, dorsal.
**Figure 30** *Aptilotella andersoni* sp. nov., male terminalia. **Abbreviations:** CER = cercus, SUR = surstylus, TLP = tab-like piece of sternite 5.
Figures 31–32 *Aptilotella quatuorchela* sp. nov., male: 31 – habitus, left lateral; 32 – habitus, dorsal.
Figure 33 *Aptilotella quatuorchela* sp. nov., male terminalia. **Abbreviations:** CER = cercus, MBS = marginal lobe of sternite 5, SUR = surstylus, TLP = tab-like piece of sternite 5.
Figures 34–35 *Aplitoletella gloriosa* sp. nov., male: 34 – habitus, left lateral; 35 – habitus, dorsal.
Figure 36 *Aptilotella gloriosa* sp. nov., male terminalia. **Abbreviations:** CER = cercus, PG = postgonite, MBS = marginal lobe of sternite 5, SUR = surstylus, TLP = tab-like piece of sternite 5.
Figures 37–38 *Aptilotella pennifera* sp. nov., male: 37 – habitus, left lateral; 38 – habitus, dorsal.
Figure 39 Aptilotella pennifera sp. nov., male terminalia. Abbreviations: CER = cercus, PG = postgonite, PTU = posteromedial tubercle of sternite 5, SUR = surstylus, TLP = tab-like piece of sternite 5, TSS = thickened setae of sternite 5.
Figures 40–41 Aptilotella corona sp. nov., male: 40 – habitus, left lateral; 41 – habitus, dorsal.
Figure 42 *Aptilotella corona* sp. nov., male terminalia. Abbreviations: CER = cercus, PG = postgonite, CLS = claw-like setae of sternite 5, SUR = surstylus, TLP = tab-like piece of sternite 5.
Figures 43–44 *Aptilotella radians* sp. nov., male: 43 – habitus, left lateral; 44 – habitus, dorsal.
Figure 45 *Aptilotella radians* sp. nov., male terminalia. **Abbreviations:** CER = cercus, SUR = surstylus.
Figures 46–47 Aptilotella gemmula sp. nov., male: 46 – habitus, left lateral; 47 – habitus, dorsal.
Figure 48 *Aptilotella gemmula* sp. nov., male terminalia. **Abbreviations:** TPS = posteromedial triangular process of sternite 5, TUB = paired posteromedial tubercles of sternite 5.
Figures 49–50 *Aptilotella umbracatus* sp. nov., male: 49 – habitus, left lateral; 50 – habitus, dorsal.
Figure 51 Aptilotella umbracatus sp. nov., male terminalia. **Abbreviations:** CER = cercus, PG = postgonite, SPN = spinules of synsternite 6+7, SUR = surstylus, VFS = ventral flanking sclerites of distiphallus.
Figures 52–53 Aptilotella pichinchensis sp. nov., male: 52 – habitus, left lateral; 53 – habitus, dorsal.
Figure 54 Aptilotella pichinchensis sp. nov., male terminalia. Abbreviations: CER = cercus, SUR = surstylus.
Figures 55–56 *Aptilotella vivus* sp. nov., male: 55 – habitus, left lateral; 56 – habitus, dorsal.
Figure 57 *Aptilotella vivus* sp. nov., male terminalia. **Abbreviations:** CER = cercus, SPN = spinulose groove of synsternite SUR = surstylus, TAB = posteromedial tab of sternite 5.
Figures 58–59 *Aptilotella macula* sp. nov., male: 58 – habitus, left lateral; 59 – habitus, dorsal.
Figure 60 *Aptilotella macula* sp. nov., male terminalia. **Abbreviations:** CER = cercus, PG = postgonite, SUR = surstylus.
Figures 61–64 Aptilotella caerulea sp. nov.: 61 – male terminalia, posterior; 62 – male terminalia, left lateral; 63 – male synsternite 6+7; 64 – male sternite 5.
Figures 65–68 *Aptilotella caerulea* sp. nov.: 65 – aedeagus with postgonites removed; 66 – distiphallus, dorsal; 67 – left postgonite; 68 – male left wing. **Abbreviations:** BP = basiphallus, CST = chistle-shaped tab of lateral flanking sclerite, DTS = dorsal triangular sclerite, LFS = lateral flanking sclerite, VBS = ventrobasal sclerite, VFS = ventral flanking sclerite.
**Figures 69–73** *Aptilotella caerulea* sp. nov.: 69 – female terminalia, dorsal; 70 – female terminalia, left lateral; 71 – female terminalia, ventral; 72 – spermathecae; 73 – head.

**Abbreviation:** EP = epiproct, HP = hypoproct, IP = iridescent patch.
Figures 74–77 *Aptilotella germana* sp. nov.: 74 – male terminalia, posterior; 75 – male terminalia, left lateral; 76 – male synsternite 6+7; 77 – male sternite 5.
Figures 78–79 *Aptilotella germana* sp. nov.: 78 – aedeagus with postgonites removed; 79 – left postgonite. **Abbreviations:** BP = basiphallus, DTP = descending tab of paired arched sclerites, LFS = lateral flanking sclerite, PAS = paired arched sclerites, PDS = paired dorsal sclerites, TBS = tooth-bearing stubs, VBS = ventrobasal sclerite.
Figures 84–87 *Aptilotella pyropanda* sp. nov.: 84 – male terminalia, posterior; 85 – male terminalia, left lateral; 86 – male synsternite 6+7; 87 – male sternite 5.
Figures 88–89 Aptilotella pyropanda sp. nov.: 88 – aedeagus with postgonites removed; 89 – left postgonite. Abbreviations: BP = basiphallus, DTP = descending tab of paired arched sclerites, LFS = lateral flanking sclerite, PAS = paired arched sclerites, PTL = paired triangular lobes of paired arched sclerites, VBS = ventrobasal sclerite.
Figures 94–98 Aptilotella gracilis sp. nov.: 94 – male terminalia, posterior; 95 – male terminalia, left lateral; 96 – male synsternite 6+7; 97 – male sternite 5; 98 – tab-like piece.
Figures 99–101 *Aptilotella gracilis* sp. nov.: 99 – aedeagus with postgonites removed; 100 – left postgonite; 101 – male left wing. **Abbreviations:** BP = basiphallus, LFS = lateral flanking sclerite, MPS = medial paired sclerites, VBA = basal article of ventral flanking sclerite, VBS = ventrobasal sclerite, VDA = distal article of ventral flanking sclerite, VMA = medial article of ventral flanking sclerite.
Figures 102–106 *Aptilotella gracilis* sp. nov.: 102 – female terminalia, dorsal; 103 – female terminalia, left lateral; 104 – female terminalia, ventral; 105 – spermathecae; 106 – head.

**Abbreviation:** EP = epiproct, S8 = sternite 8.
Figures 111–112 Aptilotella diffisa sp. nov.: 111 – aedeagus with postgonites removed; 112 – left postgonite. Abbreviations: BP = basiphallus, LFS = lateral flanking sclerite, MS = membranous sac, SSS = saddle-shaped sclerite, TDS = triangular dorsal sclerite, TIS = triangular internal sclerite, VBA = basal article of ventral flanking sclerite, VBS = ventrobasal sclerite, VDA = distal article of ventral flanking sclerite, VMA = medial article of ventral flanking sclerite.
Figures 113–116 *Aptilotella diffisa* sp. nov.: 113 – female terminalia, dorsal; 114 – female terminalia, left lateral; 115 – female terminalia, ventral; 116 – spermathecae. **Abbreviations:** EP = epiproct, HP = hypoproct.
Figures 117–120 *Aptilotella involucris* sp. nov.: 117 – male terminalia, posterior; 118 – male terminalia, left lateral; 119 – male synsternite 6+7; 120 – male sternite 5.
Figures 121–122 *Aplitotella involucris* sp. nov.: 121 – aedeagus with postgonites removed; 122 – distiphallus, dorsal. Abbreviations: BP = basiphallus, LFS = lateral flanking sclerite, LLS = leaf-like sclerite of ventral paired sclerites, MPS = medial paired sclerites, MS = membranous sac, VBA = basal article of ventral flanking sclerite, VBS = ventrobasal sclerite, VDA = distal article of ventral flanking sclerite, VMA = medial article of ventral flanking sclerite, VPS = ventral paired sclerite, VRS = ventral rod-like sclerite.
Figures 123–127 Aptilotella involucris sp. nov.: 123 – female terminalia, dorsal; 124 – female terminalia, left lateral; 125 – female terminalia, ventral; 126 – spermathecae; 127 – male mid trochanter, femur and tibia, anterior. **Abbreviations:** EP = epiproct, HP = hypoproct.
Figures 128–131 *Aptilotella sphyra* sp. nov.: 128 – male terminalia, posterior; 129 – male terminalia, left lateral; 130 – male synsternite 6+7; 131 – male sternite 5.
Figures 132–135 *Aptilotella sphyra* sp. nov.: 132 – aedeagus with postgonites removed; 133 – distiphallus, dorsal; 134 – left postgonite; 135 – male left wing. **Abbreviations:** BP = basiphallus, CSS = club-shaped sclerite, LFS = lateral flanking sclerite, MPS = medial paired sclerites, VBS = ventrobasal sclerite, VDA = distal article of ventral flanking sclerite, VMA = medial article of ventral flanking sclerite.
Figures 141–144 Aptilotella andersoni sp. nov.: 141 – male terminalia, posterior; 142 – male terminalia, left lateral; 143 – male synsternite 6+7; 144 – male sternite 5.
Figures 145–146 *Aptilotella andersoni* sp. nov.: 145 – aedeagus with postgonites removed; 146 – left postgonite. **Abbreviations:** BP = basiphallus, CSS = club-shaped sclerite, LFS = lateral flanking sclerite, MPS = medial paired sclerites, VBS = ventrobasal sclerite, VDA = distal article of ventral flanking sclerite, VMA = medial article of ventral flanking sclerite.
Figures 147–150 *Aptilotella andersoni* sp. nov.: 147 – female terminalia, dorsal; 148 – female terminalia, left lateral; 149 – female terminalia, ventral; 150 – spermathecae. **Abbreviation:** EP = epiproct, HP = hypoproct.
Figures 151–154 *Aptilotella quatuorchela* sp. nov.: 151 – male terminalia, posterior; 152 – male terminalia, left lateral; 153 – male synsternite 6+7; 154 – male sternite 5.
Figures 155–157 Aptilotella quatuorchela sp. nov.: 155 – aedeagus with postgonites removed; 156 – distiphallus, dorsal; 157 – left postgonite. Abbreviations: BP = basiphallus, CSS = club-shaped sclerite, LFS = lateral flanking sclerite, MPS = medial paired sclerites, VBS = ventrobasal sclerite, VDA = distal article of ventral flanking sclerite, VMA = medial article of ventral flanking sclerite.
Figures 158–162 *Aptilotella quatuorchela* sp. nov.: 158 – female terminalia, dorsal; 159 – female terminalia, left lateral; 160 – female terminalia, ventral; 161 – spermathecae; 162 – male mid tibia, anterior. **Abbreviation:** EP = epiproct, HP = hypoproct.
Figures 163–166 *Aptilotella gloriosa* sp. nov.: 163 – male terminalia, posterior; 164 – male terminalia, left lateral; 165 – male synsternite 6+7; 166 – male sternite 5.
Figures 167–168 Aptilotella gloriosa sp. nov.: 167 – aedeagus with postgonites removed; 168 – left postgonite. **Abbreviations:** BP = basiphallus, CSS = club-shaped sclerite, LFS = lateral flanking sclerite, MPS = medial paired sclerites, VBS = ventrobasal sclerite, VDA = distal article of ventral flanking sclerite, VMA = medial article of ventral flanking sclerite.
Figures 173–176 Aptilotella pennifera sp. nov.: 173 – male terminalia, posterior; 174 – male terminalia, left lateral; 175 – male synsternite 6+7; 176 – male sternite 5.
Figures 177–179 *Aptilotella pennifera* sp. nov.: 177 – aedeagus with postgonites removed; 178 – left postgonite; 179 – male left wing. **Abbreviations:** BP = basiphallus, CSS = club-shaped sclerite, LFS = lateral flanking sclerite, MPS = medial paired sclerites, VBS = ventrobasal sclerite, VDA = distal article of ventral flanking sclerite, VMA = medial article of ventral flanking sclerite.
Figures 184–187 *Aptilotella corona* sp. nov.: 184 – male terminalia, posterior; 185 – male terminalia, left lateral; 186 – male synsternite 6+7; 187 – male sternite 5.
Figures 188–189 *Aptilotella corona* sp. nov.: 188 – aedeagus with postgonites removed; 189 – left postgonite. **Abbreviations:** BP = basiphallus, CSS = club-shaped sclerite, DE = denticles, LFS = lateral flanking sclerite, MPS = medial paired sclerites, VBS = ventrobasal sclerite, VDA = distal article of ventral flanking sclerite, VMA = medial article of ventral flanking sclerite.
Figures 190–194 *Aptilotella corona* sp. nov.: 190 – female terminalia, dorsal; 191 – female terminalia, left lateral; 192 – female terminalia, ventral; 193 – spermathecae; 194 – male head.

Abbreviation: HP = hypoproct.
Figures 195–198 *Aptilotella radians* sp. nov.: 195 – male terminalia, posterior; 196 – male terminalia, left lateral; 197 – male synsternite 6+7; 198 – male sternite 5.
Figures 199–202 *Aptilotella radians* sp. nov.: **199** – aedeagus with postgonites removed; **200** – distiphallus, dorsal; **201** – left postgonite; **202** – head. **Abbreviations:** BP = basiphallus, LFS = lateral flanking sclerite, MS = membranous sac, VBS = ventrobasal sclerite, VBA = basal article of ventral flanking sclerite, VDA = distal article of ventral flanking sclerite.
Figures 207–210 *Aptilotella ebenea* sp. nov.: 207 – male terminalia, posterior; 208 – male terminalia, left lateral; 209 – male synsternite 6+7; 210 – male sternite 5.
Figures 211–212 *Aptilotella ebenea* sp. nov.: 211 – aedeagus with postgonites removed; 212 – left postgonite. **Abbreviations:** BP = basiphallus, LFS = lateral flanking sclerite, MPS = medial paired sclerites, MS = membranous sac, VBS = ventrobasal sclerite, VBA = basal article of ventral flanking sclerite, VDA = distal article of ventral flanking sclerite.
Figures 217–220 *Aptilotella gemmula* sp. nov.: 217 – male terminalia, posterior; 218 – male terminalia, left lateral; 219 – male synsternite 6+7; 220 – male sternite 5.
Figures 221–223 *Aptilotella gemmula* sp. nov.: 221 – aedeagus with postgonites removed; 222 – distiphallus, dorsal; 223 – left postgonite. **Abbreviations:** BP = basiphallus, CDS = curved dorsal sclerite, IS = internal sclerite, LFS = lateral flanking sclerite, VBS = ventrobasal sclerite, VFS = ventral flanking sclerite.
Figures 228–231 *Aptilotella quadrata* sp. nov.: 228 – male terminalia, posterior; 229 – male terminalia, left lateral; 230 – male synsternite 6+7; 231 – male sternite 5.
Figures 232–233 Aptilotella quadrata sp. nov.: 232 – aedeagus with postgonites removed; 233 – left postgonite. Abbreviations: BP = basiphallus, DS = dorsal sclerite, LFS = lateral flanking sclerite, VFS = ventral flanking sclerite.
Figures 234–237 *Aptilotella umbracatus* sp. nov.: 234 – male terminalia, posterior; 235 – male terminalia, left lateral; 236 – male synsternite 6+7; 237 – male sternite 5.
Figures 238–239 *Aptilotella umbracatus* sp. nov.: 238 – aedeagus with postgonites removed; 239 – left postgonite. **Abbreviations:** BP = basiphallus, DS = dorsal sclerite, LFS = lateral flanking sclerite, VFS = ventral flanking sclerite.
Figures 244–247 Aptilotella angela sp. nov.: 244 – male terminalia, posterior; 245 – male terminalia, left lateral; 246 – male synsternite 6+7; 247 – male sternite 5.
Figures 248–249 *Aptilotella angela* sp. nov.: 248 – aedeagus with postgonites removed; 249 – left postgonite. **Abbreviations:** BA = basiphallus, CDS = curved dorsal sclerite, LFS = lateral flanking sclerite, VBA = basal article of ventral flanking sclerite, VBS = ventrobasal sclerite, VMA = medial article of ventral flanking sclerite, VDA = distal article of ventral flanking sclerite.
Figures 250–253 *Aptilotella angela* sp. nov.: 250 – female terminalia, dorsal; 251 – female terminalia, left lateral; 252 – female terminalia, ventral; 253 – spermathecae. **Abbreviations:** EP = epiproct, HP = hypoproct, S8 = sternite 8.
Figures 254–256 *Aptilotella pichinchensis* sp. nov.: 254 – male terminalia, posterior; 255 – male terminalia, left lateral; 256 – male sternite 5 and synsternite 6+7.
Figures 257–258 *Aptilotella pichinchensis* sp. nov.: 257 – aedeagus with postgonites removed; 258 – left postgonite. **Abbreviations:** BP = basiphallus, CDS = curved dorsal sclerite, LFS = lateral flanking sclerite, VBA = basal article of ventral flanking sclerite, VBS = ventrobasal sclerite, VDA = distal article of ventral flanking sclerite.
Figures 259–262 Aptilotella pichinchensis sp. nov.: 259 – female terminalia, dorsal; 260 – female terminalia, left lateral; 261 – female terminalia, ventral; 262 – spermathecae.

Abbreviations: HP = hypoproct, S8 = sternite 8.
Figures 263–266 *Aptilotella vivus* sp. nov.: 263 – male terminalia, posterior; 264 – male terminalia, left lateral; 265 – male synsternite 6+7; 266 – male sternite 5.
Figures 267–268 *Aptilotella vivus* sp. nov.: 267 – aedeagus with postgonites removed; 268 – left postgonite. **Abbreviations:** BP = basiphallus, CDS = curved dorsal sclerite, LFS = lateral flanking sclerite, DMS = distomedial sclerite, VBA = basal article of ventral flanking sclerite, VBS = ventrobasal sclerite, VDA = distal article of ventral flanking sclerite.
Figures 273–276 *Aptilotella macula* sp. nov.: 273 – male terminalia, posterior; 274 – male terminalia, left lateral; 275 – male synsternite 6+7; 276 – male sternite 5.
Figures 277–278 *Aptilotella macula* sp. nov.: 277 – aedeagus with postgonites removed; 278 – left postgonite. **Abbreviations:** BP = basiphallus, CDS = curved dorsal sclerite, LFS = lateral flanking sclerite, MS = membranous sheet, VBA = basal article of ventral flanking sclerite, VBS = ventrobasal sclerite, VMA = medial article of ventral flanking sclerite, VDA = distal article of ventral flanking sclerite.
Figures 279–282 *Aptilotella macula* sp. nov.: 279 – female terminalia, dorsal; 280 – female terminalia, left lateral; 281 – female terminalia, ventral; 282 – spermathecae. **Abbreviations:** EP = epiproct, S8 = sternite 8.