# A historical overview of the classification of the Neotropical tribe Zammarini (Hemiptera, Cicadidae) with a key to genera 

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#### Abstract

An overview is given of the past century's confusions concerning some key characters within this Neotropical cicada tribe. The limits of the genera Zammara and Orellana have been redefined and a comprehensive checklist is included for the tribe. An illustrated key to the genera of the tribe Zammarini (Hemiptera: Cicadidae) is provided; this is the first key to both males and females of this tribe. Odopoea perspicua Distant, 1905 is transferred from Zammarini to the African tribe Platypleurini to become Canualna perspicua (Distant, 1905), comb. n.


## Resumen

Se presenta un resumen de las confusiones del siglo pasado sobre algunos caracteres importantes para la delimitación genérica de esta tribu de cigarras neotropicales. Se redefinen los límites taxonómicos de los géneros Zammara y Orellana y se provee una lista exhaustiva de especies pertenecientes a la tribu. Se incluye una clave illustrada para los géneros de la tribu Zammarini (Hemiptera: Cicadidae); esta es la primera clave para machos y hembras de esta tribu. Odopoea perspicua Distant, 1905 es transferida de Zammarini a la tribu africana Platypleurini tomando la nueva combinación Casualna perspicua (Distant, 1905).

## Keywords

Zammarini, Hemiptera, Cicadidae, tarsomeres, Neotropical, identification key, taxonomy, Platypleurini

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## Introduction

The Neotropical tribe Zammarini (Hemiptera: Cicadidae), belongs to the subfamily Cicadinae, the latter characterized by the presence of tymbal covers. Zammarini are easily recognizable by their strongly produced pronotal flanges. Males of this tribe have a more or less bulbous tymbal cover, which is sometimes useful as a specific character.

Over the past century, the tribe Zammarini has been studied and discussed by several hemipterists, probably because these cicadas are relatively large, colorful, and possess unique, strongly produced pronotal flanges.

This paper is the first one in a series of papers dealing with the taxonomy of the tribe Zammarini, with the ultimate goal of publishing a monograph on the tribe based on morphological, molecular, ecologic, biogeographic and acoustic data.

## History of the tribe

The tribe Zammarini was described by Distant (1905) under the "division" name Zammararia. Distant (1905) defined his Zammararia to consist of Zammara Amyot \& Audinet Serville, 1843 (7 spp.), Odopoea Stål, 1861 (13 spp.), two new genera, Orellana and Miranha, which are based on respectively Z. columbia Distant, 1881 and Z. imbellis Walker, 1858, and two new species Orellana brevis and Odopoea perspicua. These 24 species attributed to 4 genera were catalogued a year later in Distant's catalogue (1906a). In 1915, Van Duzee first used the tribal name Zammarini.

Distant (1912) described the genus Uhleroides as a new genus of Zammarini; Uhleroides is restricted to Cuba and Hispaniola. Without explanation, Kato (1932) transferred Uhleroides to the tribe Thophini. Moulds (2001) recently transferred Uhleroides back into Zammarini, based on the following characters: "the presence of transverse grooves towards the distal ends of the postclypeal ridges, an antennal plate that reaches almost to the eyes, fore wings which carry blotch-like infuscations at distal ends of apical veins 1-7 and at base of apical cells 2,3 and 5, a narrow basal cell to the fore wing with veins M and CuA meeting the cell close together and a hind wing anal lobe that is narrow."

Haupt (1918) and Delétang (1919) both described new genera within Zammarini (Adusella and Edholmbergia, respectively); however, both generic names were synonymized to Odopoea by Torres (1945). Distant (1920) described Juanaria, a monospecific Zammarini genus endemic to Cuba. Davis $(1928,1934)$ added two more genera to the tribe, Borencona (a monospecific genus endemic to Puerto Rico) and Chinaria (restricted to Mexico and the Dominican Republic).

The most recent generic addition to Zammarini was made by Boulard and Sueur (1996), who described the monospecific genus Zammaralna (a group endemic to Venezuela) as the "taxon frère de Zammara" [sister taxon to Zammara].

Following Distant's (1905) raising of the tribe, additional new species were described by Distant (1906b, 1906c, 1912), Schmidt (1919), Goding (1925) Davis


Figure I. Accumulation of species / publication year for the tribe Zammarini, since Distant recognized the tribe in 1905.
(1928, 1934, 1939, 1942), Ramos (1983), Boulard and Sueur (1996) and Sanborn (2004, 2007, in press). For an overview, see Figure 1 and Checklist. Thus, at present, the tribe Zammarini consists of 9 genera and 50 described species: Odopoea ( 15 species), Miranha (1), Zammara (15), Zammaralna (1), Juanaria (1), Borencona (1), Chinaria (4), Orellana (5), Ubleroides (7).

## Tarsomeres and head width: contradictions and confusions in the literature

The presence of 2 or 3 tarsomeres, a character that should be easy to evaluate, has led to considerable confusion within Zammarini. Within Cicadidae, a reduction of the number of tarsomeres is an unusual condition; indeed, within Zammarini, Zammara is the only genus with 2 tarsomeres instead of 3. Amyot and Audinet Serville (1843) originally described Zammara as having 2 or 3 tarsomeres; the type species, Z. tympanum (Fabricius, 1803), has 2 tarsomeres. The other species of Zammara described in this work, $Z$. strepens, was stated (erroneously) as having: "les tarses distinctement de trois articles" [tarsi clearly three-jointed].

Distant (1881a) described Z. columbia as having 3 tarsomeres (in error). Later, Distant (1905) erected the genus Orellana, and assigned Z. columbia as the type species of this genus; oddly, he stated clearly in his generic description for Orellana: "tarsi twojointed," based on a type species that he previously described as having 3 tarsomeres. In this same publication, Distant described the species Orellana brevis as having "twojointed tarsi." One year later, Distant (1906a) transferred Z. nigriplaga Walker, 1858 to
the genus Orellana based on having the "head (including eyes) only about two-thirds the breadth of base of mesonotum" in contrast to "about as wide" for Zammara.

Jacobi (1907) suggested that both Distant (1881a), and Amyot and [Audinet] Serville (1843) made errors in interpreting tarsomere morphology for respectively, Orellana columbia and Zammara strepens. Jacobi implied that the errors might have been due to the "nicht ganz gutem lichte und geringeren optischen hilfmitteln" [suboptimal lighting and inferior optical tools] than his "Zeissschen Binokularlupe mit 35 facher vergrösserung." [Zeiss dissecting microscope with $35 \times$ magnification]. He also transferred O. nigriplaga (Walker, 1858) back into Zammara.

Subsequently, Distant (1914) transferred Z. nigriplaga and Z. brevis, again, into Orellana, based on the breadth of the head (as discussed above) and because these species supposedly have 2 tarsomeres, since he described the genus Orellana again as having tarsi "two-jointed."

Schmidt (1919) discussed Jacobi's and Distant's works and moved Z. nigriplaga, Walker 1858 and O. brevis Distant, 1905 (back) to Zammara because both species have 2 tarsomeres. He also moved Z. strepens Amyot \& Audinet Serville, 1843 to Orellana and described the new species Orellana bigibba; additionally, Schmidt suggested that the genus description for Orellana should be changed to "tarsen dreigliedrich" [tarsi three-jointed].

Goding (1925) based the separation of Zammara and Orellana on Distant's (1905) key to genera, namely "head (including eyes) only about two-thirds the breadth of base of mesonotum" for Orellana and "head (including eyes) about as wide as the breadth of base of mesonotum" for Zammara. Based on this separation, Goding transferred Z. nigriplaga and $Z$. brevis again into Orellana and described two more species in the genus: $O$. pulla and $O$. brunneipennis, not mentioning the number of tarsomeres for either species.

Boulard $(1975,1976)$ treated O. brevis, O. bigibba and O. columbia as belonging to Zammara, though without specifically transferring them back into Zammara. It is not clear whether, in doing this, he intended not to recognize Orellana as a valid genus, since by transferring $O$. columbia (the type species of Orellana) back to Zammara, Orellana would become a junior (subjective) synonym of Zammara.

Boulard and Sueur (1996) praised Distant for his insight in the importance of the number of tarsomeres as a generic character, and gave the example where he [Distant] used it to separate Miranha (trimére) and Orellana (dimére). So it can be assumed that Boulard $(1975,1976)$ did not intend to synonymize the genus Orellana with Zammara. Boulard and Sueur (1996) discussed the number of tarsomeres briefly when they erected the new genus Zammaralna, defining it in the following way: "Habitus de Zammara, mais tarses á trois articles; nervures médiane et cubitale naissant du meme angle de la cellule basale et poursuivant, juxtaposes, plus ou moins longuement (pas de tronc commun)" [Similar to Zammara, but with 3 tarsomeres; median and cubital veins arising at the same angle from the basal cell and from there on juxtaposed, over a more or less long distance (no common base)].

## Results

My research for the present paper proves that Jacobi (1907) was correct that the number of tarsomeres in the descriptions of Orellana columbia Distant, 1881 and Zammara strepens Amyot \& Audinet Serville, 1843 are wrong and that in fact Orellana columbia has 3 tarsomeres, while Zammara strepens has 2 tarsomeres. Schmidt (1919) was also correct in that the genus description for Orellana should be changed to "tarsi threejointed" (i.e. having 3 tarsomeres). Furthermore both nigriplaga and brevis should be transferred to Zammara because they each possess 2 tarsomeres. The species bigibba has 3 tarsomeres and therefore should stay in Orellana. I have not seen the types of Orellana pulla, Goding 1925 or Orellana brunneipennis Goding, 1925, nor specimens that belong to either of these species. Because the type specimens have not been located yet, the generic placement of the latter two species is tentative. This is especially so because Goding (1925) separated Zammara and Orellana based on the width of the head, a characteristic not valid to separate these genera. Distant (1905) described Odopoea perspicua and listed the type locality as "Saó Thomé". After seeing pictures of the type, it is clear that this species is misplaced in Zammarini as it clearly belongs to the African tribe Platypleurini. This species is very closely related to Canualna liberiana (Distant, 1912), a species occurring on the island of Saó Thomé (M. Villet, personal communication). Distant erroneously thought that Saó Thomé referred to a location in Brazil, but instead this specimen is almost certainly from the African Island Saó Thomé, even more so because the collector was "Negreiros", a painter born on that island. For the above reasons the species is transferred to Canualna perspicua (Distant, 1905), new combination.

## Checklist of genera and species currently included within the tribe Zammarini.

In the following check-list only the type locality for each species is given, further distribution records will be discussed in future papers.

Cicadidae Latreille, 1802
Cicadinae Latreille, 1802
Zammarini Distant, 1905

Odopoea Stål, 1861: 616 ; Type species: Tettigonia dilatata Fabricius, 1775: 678
Adusella (Haupt, 1918: 84)
Edholmbergia (Delétang, 1919: 70)
azteca Distant, 1881b: 4 (Mexico)
cariboea Uhler, 1892:169 (Hispaniola)
degiacomii Distant, 1912: 644 (Espirito Santo, Brazil)
dilatata (Fabricius, 1775: 678), Tettigonia (Jamaica) plena (Walker, 1850: 38), Zammara (Jamaica)

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cuncta (Walker, 1850: 39), Zammara (Jamaica)
praxita (Walker, 1850: 40), Zammara (Unknown)
erato (Walker, 1850: 41), Zammara (Jamaica)
domingensis (Uhler, 1892: 172), Odopoea (Hispaniola)
diriangani Distant, 1881b: 5 (Chontales, Nicaragua)
funesta (Walker, 1858: 2), Zammara (North America)
insignifera Berg, 1879: 135 (Salta, Argentina)
jamaicensis Distant, 1881a: 629 (Jamaica)
lebruni (Distant, 1906b: 385), Tettigades (Patagonia)
minuta Sanborn, 2007: 2 (Colima, Mexico)
signoreti Stål, 1864: 59 (Mexico)
strigipennis (Walker, 1858: 3), Zammara (Haiti)
suffusa (Walker, 1850: 37), Zammara (Santo Domingo, [Dominican Republic]) vacillans (Walker, 1858: 3), Zammara (Santo Domingo, [Dominican Republic])
venturii Distant, 1906c: 150 (Argentina)
lebruni (Delétang, 1919: 16) Edholmbergia (Catamarca)
signata (Haupt, 1918: 84) Adusella (Catamarca, Argentina)
Miranha Distant, 1905: 381 ; Type species: Zammara imbellis Walker, 1858: 2
imbellis (Walker, 1858: 2), Zammara (Mexico)
Zammara Amyot \& Audinet Serville, 1843: 468 ; Type species: Tettigonia tympanum Fabricius, 1803: 40
brevis (Distant, 1905: 382), Orellana (Colombia)
calochroma Walker, 1858: 4 (Cundinamarca, [Colombia])
erna Schmidt, 1919: 390 (Pucay, Ecuador)
eximia (Erichson, 1848: 616), Cicada (Zammara) (British Guiana)
bertha Schmidt, 1919: 386 (Chanchamayo, Peru( \({ }^{\text {® }}\) ); Canelos, Ecuador ( q ))
intricata Walker, 1850: 35 (Puerto Rico)
lichyi Boulard \& Sueur, 1996: 106 (Aragua, Venezuela)
luculenta Distant, 1883: 187 (Unknown)
medialinea Sanborn, 2004: 367 (Aragua, Venezuela)
nigriplaga Walker, 1858: 4 (South America)
olivacea Sanborn, 2004: 365 (Providencia, Colombia)
smaragdina Walker, 1850: 33 (Unknown)
angulosa (Walker, 1850: 34), Zammara (Mexico)
smaragdula Walker, 1858: 4 (South America)
strepens Amyot \& Audinet Serville, 1843: 469 (Brazil)
tympanum (Fabricius, 1803: 40), Tettigonia (Brazil)
Zammaralna, Boulard \& Sueur,1996: 110 ; Type species: Zammaralna bleuzeni, Boulard \&
Sueur,1996: 110
bleuzeni Boulard \& Sueur, 1996: 110 (Bolivar, Venezuela)
Juanaria Distant, 1920: 455 ; Type species: Juanaria mimica Distant, 1920: 456
poeyi (Guérin-Méneville, 1856: 178), Cicada (Platypleura) (Cuba) mimica (Distant, 1920:456), Juanaria (Cuba)
Borencona Davis, 1928: 31; Type species: Borencona aguadilla Davis, 1928: 31
aguadilla Davis, 1928: 31 (Yauco, Puerto Rico)
Chinaria Davis, 1934: 52; Type species: Chinaria mexicana Davis, 1934: 52
pueblaensis Sanborn, 2007: 5 (Puebla, Mexico)
mexicana Davis, 1934: 52 (Morelos, Mexico)
similis Davis, 1942: 178 (Guerrero, Mexico)
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    vivianae Ramos, 1983: }63\mathrm{ (La Estrella, Dominican Republic)
Orellana Distant, 1905:381; Type species: Zammara columbia Distant, 1881a: }62
    bigibba Schmidt, 1919: }392\mathrm{ (Brazil)
    brunneipennis* Goding, 1925: 27 (El Oriente, Ecuador)
    castaneamaculata Sanborn, 2010: ? (Magdalena[?], Colombia)
    columbia (Distant, 1881a: 628), Zammara (Medellin, Colombia)
    pulla* Goding, 1925: }25\mathrm{ (Ecuador)
Ubleroides Distant, 1912: 644; Type species: Uhleroides cubensis Distant, 1912:}64
    chariclo (Walker, 1850: 146), Cicada (Cuba)
    cubensis Distant, 1912: }645\mathrm{ (Cuba)
    bispaniolae Davis, 1939: }292\mathrm{ (Santo Domingo, [Dominican Republic])
    maestra Davis, 1939: }291\mathrm{ (Santiago de Cuba, Cuba)
    sagrae (Guérin-Méneville, 1856: 178), Cicada (Cuba)
    samanae Davis, 1939: }294\mathrm{ (Santo Domingo, [Dominican Republic])
    walkerii (Guérin-Méneville, 1856: 179), Cicada (Cuba)
*= generic placement uncertain (possibly in Zammara), due to not having seen any
(type) specimens.
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## Platypleurini Schmidt, 1918

Canualna Boulard, 1985: 184; Type species: Platypleura liberiana Distant, 1912: 200 perspicua (Distant, 1905: 380), Odopoea (Saô Thomé)

## Key to the genera of the tribe Zammarini

Below, the first key to both males and females for all (described) species within the Tribe Zammarini is provided.

There are several genera (Plautilla Stål 1865, Procollina Metcalf 1963, Daza Distant 1905, Aragualna Champagnet, Boulard \& Gaiani 2000, Onoralna Boulard 1996) that are at present placed outside of Zammarini, which may prove to be members of the tribe. Currently molecular data and additional morphological data are being collected for each to help determine their taxonomic position within the Cicadidae.

1. Median (M) and anterior cubital ( CuA ) vein arising together from the basal cell (Figs 2 left, 4, 5); 2 or 3 tarsomeres, first tarsomere sometimes strongly reduced (Fig. 3)2

- Median (M) and anterior cubital ( CuA ) vein arising separately from the basal cell, separated by a distance of at least the width of either vein (Fig. 2 right); 3 tarsomeres, first tarsomere sometimes strongly reduced (Fig. 3 right) ..... 4

2. Two tarsomeres, first tarsomere sometimes only visible in ventral view (Fig. 3 left) Zammara

- Three tarsomeres, first tarsomere sometimes only visible in ventral view (Fig 3 right)3


Figure 2. CuA and $M$ veins arising together (left) or separate (right) from the basal cell.


Figure 3. Presence of 2 (left) or 3 tarsomeres (right).
3. M and CuA juxtaposed (Figs 2 left, 5); apical $1 / 3$ to $1 / 2$ of fore wing infuscated with wavy pattern of brown and grayish, basal half transparent

## Zammaralna

- $\quad \mathrm{M}$ and CuA juxtaposed or fused (at least at base, Figs 2 left, $4 \& 5$ ); fore wing transparent with scattered infuscations or apical part infuscated but not with wavy pattern

Orellana
4. Both fore and hind wings at least partly infuscated, hind wing sometimes only very small part of apical cells directly bordering apical margin. 5

- At least hind wing completely transparent, i.e., no infuscation present (except for vannal fold, jugum and apical wing margin in some species) (Fig. 4) .... 8

5. Hind wing completely infuscated; fore wing completely opaque. (Restricted to Cuba)

- Hind wing not completely infuscated; at least some areas of fore wing transparent

6. Infuscations of fore wing restricted to apical $1 / 3^{\text {rd }}$, infuscations following veins of apical cells; infuscations of hind wing restricted to apical $1 / 4^{\text {th }}$ (and vannal fold)

Odopoea (in part)

- Infuscations present over whole length of fore wing, infuscations less restricted to wing veins; infuscations of hind wing at least present in apical wing margin and part of apical cells directly bordering apical margin


Figure 4. Hind wing terminology following Moulds (2005).
7. Infuscations of hind wing only present in apical wing margin and part of apical cells directly bordering apical margin (and vannal fold). (Restricted to Mesoamerica).

Miranha

- Infuscations of hind wing present both at apical wing margin (and vannal fold), and at central internal edges of basal cells. (Restricted to Mexico and Dominican Republic)

Cbinaria
8. Width of pronotal flange (Fig. 5) less than half diameter of eye (restricted to Cuba, Haiti and Dom. Rep.)

- Width of pronotal flange (Fig. 5) at least half diameter of eye .................... 9

9. Veins of fore wing evenly striped; width of pronotum (at widest point, including flanges) more than 1.7 times width of head including eyes. (Restricted to Puerto Rico).

- Veins of fore wing evenly colored, not striped; width of pronotum (at widest point, including flanges) less than 1.5 times width of head including eyes....

Odopoea (in part)


Figure 5. Pronotal flange; bracket indicates width of pronotal flange.

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# A preliminary characterization of Bembidion perspicuum LeConte, with a reclassification of related species (Coleoptera, Carabidae) north of México 

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[^1]
#### Abstract

Bembidion perspicuum LeConte is a species distinct from B. transversale Dejean, the names of which have been synonymized in the past. In the United States, B. perspicuum occurs from Oregon through Texas along the shores of rivers and creeks. We show that it is consistently different at 40 bases in DNA sequences of cytochrome oxidase I and 4 bases in 28 r ribosomal DNA, as well as in subtle morphological characters. In addition, we review the classification of related species in the B. transversale and B. mexicanum species groups in America north of México. In the United States and Canada, the B. transversale group includes $B$. transversale, $B$. perspicuum, and B. sarpedon Casey; the $B$. mexicanum group includes $B$. mexicanum Dejean, B. lugubre LeConte, and B. pernotum Casey.


## Keywords

Bembidiini, Ocydromus, COI

## Introduction

Members of the Bembidion transversale group are large ( $6-8 \mathrm{~mm}$ ) Bembidion occurring along creek and river shores throughout much of western North America, east across Canada and adjacent United States to Nova Scotia and Newfoundland. A recent catalogue (1993) lists two species within the group, B. pernotum Casey (known from Colorado and New Mexico) and the widespread B. transversale Dejean.

The related Bembidion mexicanum group contains very similar members whose combined range extends from South Dakota to Central America; in the United States this group is considered to consist of only the nominotypical species (Bousquet and Larochelle 1993).

In sequencing 28 S rDNA (28S) and cytochrome oxidase I (COI) from specimens of the $B$. transversale group from several North American localities, and examination of morphological characters, it became evident that " $B$. transversale" is in reality several species.

This paper is the first of several that will attempt to resolve the complexity of both the $B$. transversale and $B$. mexicanum groups. We herein report the discovery that the common form of the $B$. transversale group throughout much of the southwest United States is a separate species, B. perspicuum LeConte, distinct both morphologically and molecularly from the widespread and more northern $B$. transversale. We also briefly document the other species in the two species groups, so that a revised classification is available for future publications. A later paper (Maddison, in prep.) will revise the group in America north of México, including forms along the west coast of North America, and give a fuller treatment of all species. In advance of this more complete revision, however, we wish to document the distinctiveness of $B$. perspicuum, as this is one of the primary species studied in a forthcoming paper (Wild, Kanda, McKenna, Farrell, and Maddison, in prep.).

## Methods

Members of the B. transversale and B. mexicanum groups were examined from or are deposited in the collections listed below. Each collection's listing begins with the coden used in the text.

DRM David R. Maddison, Department of Zoology, Oregon State University, Corvallis, OR, 97331 U.S.A.
MCZ Museum of Comparative Zoology, Harvard University
MNHN Muséum National d'Histoire Naturelle, Paris
OSAC Oregon State Arthropod Collection, Oregon State University
USNM National Museum of Natural History, Smithsonian Institution
ZMUM Zoological Museum, Moscow State University

Methods for studying adult structures, and terms used, are given in Maddison (1993). Photographs of body parts were taken with a Leica Z6 and JVC KY-F75U camera using Microvision's Cartograph software for extended depth of field (EDF) processing; the images thus potentially have some artifacts caused by the EDF algorithm.

In the section on classification, we do not list which junior synonyms are so considered for the first time. All names listed under $B$. transversale have previously been considered synonyms of $B$. transversale; the same applies to $B$. mexicanum. However, we have not conducted the historical analysis required to determine if any of the names herein considered junior synonyms of $B$. lugubre have ever been considered as such previously, although they and B. lugubre have been considered synonyms of B. mexicanum; the same applies to $B$. perspicuum and $B$. sarpedon (which have been considered synonyms of $B$. transversale, as have all of their synonyms).

Taxon sampling for DNA studies. We sequenced DNA from 28 specimens of the B. transversale group from Nova Scotia, Alberta, British Columbia, as well as 10 states in western U.S.A. (Table 1). We have included one specimen each of $B$. mexicanum, $B$. commotum Casey, and B. sejunctum semiaureum Fall as outgroups to this study. Preliminary analyses of multiple genes across Bembidion (Maddison, unpublished) indicate that the $B$. mexicanum group and $B$. transversale group are closely related, forming a clade along with a few other members of Ocydromus (sens. lat.), including B. commotum and B. sejunctum. Vouchers are housed in the David Maddison voucher collection at Oregon State University.

DNA sequencing. Methods for obtaining DNA sequences are described in Maddison (2008). In brief, we obtained ca. 1000 bases of sequence data in the D1 through D3 domains of 28 S and between 600 and 1400 bases of COI. Fragments for these genes were amplified using the Polymerase Chain Reaction on an Eppendorf Mastercycler Thermal Cycler, using either Eppendorf Hotmaster Taq or TaKaRa Ex Taq and the basic protocols recommended by the manufacturers. Primers and details of the cycling reactions used are given in Maddison (2008). In particular, we used the primer pair LS58F and LS998R and the pair NLF184/21 and LS1041R to amplify and sequence 28 S rDNA. For COI, two amplification strategies were used: amplification with B1490 and Pat, and sequencing with those primers plus Bcoi2R and Jerry (see Maddison, 2008), or amplification and sequencing with the LCO1490 and HCO2198 primers (Hebert et al. 2003). Amplified products were cleaned, quantified, and sequenced at the University of Arizona's Genomic and Technology Core Facility using either a 3730 or 3730 XL Applied Biosystems automatic sequencer.

Assembly of multiple chromatograms for each gene fragment and initial base calls were made with Phred (Green and Ewing 2002) and Phrap (Green 1999) as orchestrated by Mesquite's Chromaseq package (Maddison and Maddison 2009a; Maddison and Maddison 2009b), with subsequent modifications by Chromaseq and manual inspection. Multiple peaks at a single position in both reads were coded using IUPAC ambiguity codes.

Table I. Specimens examined for 28 s rDNA and COI. \#: Maddison lab DNA voucher number. Sex: male (" $m$ ") or female (" f "). St: State or Province.

| Species | \# | Sex | St | Locality | Latitude | Longitude |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| B. transversale | 2161 | m | AB | Lethbridge | $49.7043^{\circ} \mathrm{N}$ | $112.866^{\circ} \mathrm{W}$ |
| B. transversale | 2186 | m | AB | Lethbridge | $49.7043^{\circ} \mathrm{N}$ | $112.866^{\circ} \mathrm{W}$ |
| B. transversale | 2191 | f | BC | Creston | $49.1395^{\circ} \mathrm{N}$ | $116.6489^{\circ} \mathrm{W}$ |
| B. transversale | 2164 | f | ID | Baker Creek | $43.7511^{\circ} \mathrm{N}$ | $114.5627^{\circ} \mathrm{W}$ |
| B. transversale | 2184 | f | ID | Baker Creek | $43.7511^{\circ} \mathrm{N}$ | $114.5627^{\circ} \mathrm{W}$ |
| B. transversale | 2163 | m | MT | Divide Creek | $48.7314^{\circ} \mathrm{N}$ | $113.4216^{\circ} \mathrm{W}$ |
| B. transversale | 2185 | m | MT | Galena Gulch | $46.2562^{\circ} \mathrm{N}$ | $112.1843^{\circ} \mathrm{W}$ |
| B. transversale | 2359 | m | MT | Bozeman | $45.7077^{\circ} \mathrm{N}$ | $110.9743^{\circ} \mathrm{W}$ |
| B. transversale | 2158 | f | NS | Bass River | $45.4125^{\circ} \mathrm{N}$ | $64.0560^{\circ} \mathrm{W}$ |
| B. transversale | 2160 | m | NS | Hantsport | $45.0487^{\circ} \mathrm{N}$ | $64.1835^{\circ} \mathrm{W}$ |
| B. transversale | 2346 | m | NV | Dunphy | $40.7052^{\circ} \mathrm{N}$ | $116.5312^{\circ} \mathrm{W}$ |
| B. transversale | 2183 | f | UT | Diamond Fork | $40.0737^{\circ} \mathrm{N}$ | $111.426^{\circ} \mathrm{W}$ |
| B. transversale | 2251 | f | UT | Diamond Fork | $40.0737^{\circ} \mathrm{N}$ | $111.426^{\circ} \mathrm{W}$ |
| B. transversale | 2097 | m | WY | Laramie | $41.2897^{\circ} \mathrm{N}$ | $105.6224^{\circ} \mathrm{W}$ |
| B. transversale | 2157 | m | WY | Laramie | $41.2897^{\circ} \mathrm{N}$ | $105.6224^{\circ} \mathrm{W}$ |
| B. transversale | 2481 | m | CO | Texas Creek | $38.4106^{\circ} \mathrm{N}$ | $105.5844^{\circ} \mathrm{W}$ |
| B. transversale | 2486 | m | CO | Texas Creek | $38.4106^{\circ} \mathrm{N}$ | $105.5844^{\circ} \mathrm{W}$ |
| B. perspicuum | 2482 | m | CO | Texas Creek | $38.4106^{\circ} \mathrm{N}$ | $105.5844^{\circ} \mathrm{W}$ |
| B. perspicuum | 2485 | m | CO | Texas Creek | $38.4106^{\circ} \mathrm{N}$ | $105.5844^{\circ} \mathrm{W}$ |
| B. perspicuum | 1120 | f | AZ | Charleston | $31.6300^{\circ} \mathrm{N}$ | $110.1774^{\circ} \mathrm{W}$ |
| B. perspicuum | 2156 | m | AZ | McGuireville | $34.6376^{\circ} \mathrm{N}$ | $111.813^{\circ} \mathrm{W}$ |
| B. perspicuum | 2159 | f | AZ | Mammoth | $32.7413^{\circ} \mathrm{N}$ | $110.6458^{\circ} \mathrm{W}$ |
| B. perspicuum | 2182 | m | NM | Gila | $32.9691^{\circ} \mathrm{N}$ | $108.5872^{\circ} \mathrm{W}$ |
| B. perspicuum | 2173 | m | NV | Weeks | $39.2866^{\circ} \mathrm{N}$ | $119.2778^{\circ} \mathrm{W}$ |
| B. perspicuum | 2318 | m | CA | Miller Canyon | $34.2717^{\circ} \mathrm{N}$ | $117.2892^{\circ} \mathrm{W}$ |
| B. perspicuum | 2319 | m | CA | Pine Creek | $32.8548^{\circ} \mathrm{N}$ | $116.5228^{\circ} \mathrm{W}$ |
| B. perspicuum | 2320 | m | CA | Pine Creek | $32.8548^{\circ} \mathrm{N}$ | $116.5228^{\circ} \mathrm{W}$ |
| B. perspicuum | 2321 | m | CA | Pine Creek | $32.8548^{\circ} \mathrm{N}$ | $116.5228^{\circ} \mathrm{W}$ |
| B. mexicanum | 2192 | m | NM | Bonito Creek | $33.4557^{\circ} \mathrm{N}$ | $105.7470^{\circ} \mathrm{W}$ |
| B. commotum | 2136 | m | CA | Sonora Pass | $38.3323^{\circ} \mathrm{N}$ | $119.6401^{\circ} \mathrm{W}$ |
| B. sejunctum | 1817 | f | WA | Ilwaco | $46.29^{\circ} \mathrm{N}$ | $124.08^{\circ} \mathrm{W}$ |

Sequences have been deposited in GenBank with accession numbers GU454737 through GU454797. In addition, the 28 S sequence for $B$. transversale voucher number DNA2157 is from GenBank, number EU677688.

## Alignment and phylogenetic analysis

Alignment was not difficult for either gene, as there was no evidence of insertion or deletions in the history of these sequences. Aligned matrices are available at http:// bembidion.org/transversaleGroup. Three matrices were examined: (1) 28 S rDNA; (2)

COI with all data; (3) COI with only the first ca. 600 bases that were sequenced for all specimens, the so-called "barcode" piece (Hebert, Cywinska, Ball and DeWaard 2003). The second matrix (full-length COI) has the last half of COI missing for 10 of the 28 B. transversale group specimens as well as $B$. sejunctum and $B$. commotum; only $77.7 \%$ of the cells have data in them, as opposed to $98.6 \%$ for the shorter COI matrix and $99.6 \%$ for the 28 matrix. Phylogenetic analysis was conducted using parsimony, likelihood, and Bayesian methods.

Most-parsimonious trees were sought using PAUP* (Swofford 2002). For each search, 4000 replicates were conducted, each beginning with a starting tree formed with the random addition sequence option; each replicate was allowed to save no more than 25 trees. The number of most parsimonious trees found for each matrix ranged from 2 to 63,341 ; shortest trees were found in at least 2000 of the replicates. Bootstrap parsimony analyses were conducted using 1000 bootstrap replicates, with each replicate consisting of five search replicates beginning with starting trees formed with the random addition sequence option, and with each search replicate allowed to save no more than 25 trees.

Models of nucleotide evolution where chosen with the aid of ModelTest (Posada 2005). The model chosen by the Akaike Information Criterion (AIC) for 285 rDNA was an HKY 2-parameter rate matrix with a proportion of sites being invariant (HKY+I). For COI, models were inferred treating each codon position separately as well as pooling all positions; phylogenetic analyses were conducted under both model structures. First positions are best fit by a General Time Reversible (GTR) rate matrix with a proportion of sites being invariant $(\mathrm{GTR}+\mathrm{I})$; second positions a 1-parameter F81 rate matrix with a proportion of invariant sites ( $\mathrm{F} 81+\mathrm{I}$ ), and third positions with an HKY rate matrix and site-to-site rate variation following a gamma distribution $(\mathrm{HKY}+\Gamma)$. If instead all positions were pooled for COI , the model chosen was GTR +I .

Maximum Likelihood analyses were conducted with GARLI version 0.96 (Zwickl 2006). A GTR + I model was used for all COI sites. The maximum likelihood tree was sought using 500 search replicates. Maximum likelihood bootstrap analyses with 500 replicates were also conducted for all three matrices.

Bayesian analyses were conducted using MrBayes version 3.1.2 (Huelsenbeck and Ronquist 2005). For each of the two COI matrices, the analyses were done both with separate models for each codon position, as well as GTR +I for all sites; thus, four Bayesian analyses were conducted for COI and one for 28S. A single MrBayes MCMCMC search was conducted for each analysis, each with two runs of four chains each, for 10 million generations, with trees sampled every 1000 generations. All searches converged, as judged by an average standard deviation of split frequencies of less than 0.006 (Huelsenbeck and Ronquist 2005) and by stabilization of the likelihood scores and all parameter values as judged by visualization tools in Tracer (Rambaut and Drummond 2004), except for the full-length COI matrix with codon positions treated separately. That analysis did not converge after 100 million generations, and was discarded. A burn-in sample of the first 7.5 million generations was excluded from the other analyses; the number of trees sampled for each analysis was thus 5,000 .

## Results of molecular analyses

The two forms, B. transversale and B perspicuum, consistently differ by 4 bases in 28S, and 40 bases in COI (of which 14 fall within the first 600 bases of the gene; Table 2). The base differences in COI yield predictions of two sites at which amino acids differ in the protein. These fixed differences in both genes are also evident between the two specimens of $B$. transversale and two of $B$. perspicuum sampled microsympatrically from the same shore of the Arkansas River at Texas Creek, Colorado ( $38.4106^{\circ} \mathrm{N} 105.5844^{\circ} \mathrm{W}$ ).

As a cautionary note, there is evidence (in the form of double peaks at sites in the chromatograms of both reads) for multiple copies of COI in one Bembidion perspicuum from Arizona (specimen 1120), one B. transversale from Montana (specimen 2163) and another from Utah (specimen 2183). This is likely to indicate nuclear copies of COI, and casts some doubt on the location of any particular sequenced copy. Nonetheless, the consistency within each species in the sequenced COI provides evidence of lack of gene flow even if some copies are nuclear.

The phylogenetic analyses (Fig. 1; Table 3) indicate clearly that the two forms are reciprocally monophyletic. This is supported in all analyses for both genes. The geographic distributions of sequenced individuals of these two forms are shown in Fig. 2.

We should note that while it appears from Fig. 1B that the California specimens of B. perspicuum are distinctive, there are no nucleotide sites in either gene at which there are consistent differences between California specimens and the remainder.

## Morphological differences

Once the two forms became evident from the molecular analyses, specimens were separated and examined for morphological differences. B. transversale shows more contrast in the dorsal color pattern, and B. perspicuum tends to have a more orange hue (Fig. 3).

Table 2. Number of fixed differences between B. transversale and B. perspicuum for each gene. Only those specimens whose sequences were complete for the length indicated where used in the comparison. For example, there are 40 sites in the entire COI gene at which all 13 examined $B$. transversale have a different nucleotide than all 5 examined $B$. perspicuum, and these nucleotide differences imply two consistent differences in amino acids.

|  | $\mathbf{2 8 S}$ | COI <br> (entire) | COI <br> (first portion) |
| ---: | :---: | :---: | :---: |
| B. transversale, $\mathrm{n}=$ | 17 | 13 | 17 |
| Fixed nucleotide differences | 4 | 40 | 14 |
| Fixed amino acid differences | - | 2 | 0 |
| Total nucleotides | 914 | 1417 | 614 |
| B. perspicuum, $\mathrm{n}=$ | 11 | 5 | 11 |

Figure I. Maximum likelihood trees inferred from gene sequences. Branch lengths as reconstructed by Garli. A 28 s rDNA; scale bar 0.001 substitutions per site
B COI, all sites; scale bar 0.01 substitutions per site C COI, first ca. 600 sites; scale bar 0.01 substitutions per site. Asterisks indicate specimens collected microsym-
patrically on a gravel bank along the shores of the Arkansas River at Texas Creek, Colorado ( $38.4106^{\circ} \mathrm{N} 105.5844^{\circ} \mathrm{W}$ ).



Figure 2. Geographic distribution of specimens sampled for DNA sequences. Circles: Bembidion transversale; stars: Bembidion perspicuum. More complete data for these localities are available at http://bembidion.org/transversaleGroup/, as a KML file.

Table 3. Support values for monophyly of each of B. transversale and B. perspicuum. BPP: Bayesian Posterior Probability; ML Boot: likelihood bootstrap percentage; Pars Boot: parsimony bootstrap percentage. "partitioned" indicates those analyses for which the gene was partitioned into codon positions with different models used for first, second, and third positions, as opposed to analyses in which all positions were pooled, and subject to a single model.

|  |  | B. transversale | B. perspicuum |
| :--- | :--- | :---: | :---: |
| $28 S$ | BPP | 0.78 | 0.76 |
|  | ML Boot | 96 | 65 |
|  | Pars Boot | 98 | 65 |
| COI (entire) | BPP (partitioned) | - | - |
|  | BPP (pooled) | 1.00 | 0.99 |
|  | ML Boot | 99 | 95 |
|  | Pars Boot | 100 | 100 |
| COI (partial) | BPP (partitioned) | 1.00 | 0.96 |
|  | BPP (pooled) | 1.00 | 0.72 |
|  | ML Boot | 97 | 68 |
|  | Pars Boot | 100 | 94 |

The most consistent external differences are in the pronotum: $B$. transversale has a slightly more convex and cordate pronotum, with a smoother basal region, in contrast to the flatter pronotum of B. perspicuum, which has less rounded sides, and with the basal region more evidently punctate (Fig. 4). In the localities from which DNA sequences were obtained (Fig. 2), specimens of B. transversale have in addition a very


Figure 3. Adult habitus. A B. transversale, DNA2481, USA: Colorado: Fremont Co., Arkansas River at Texas Creek, $38.4106^{\circ} \mathrm{N} 105.5844^{\circ} \mathrm{W}$ B B. perspicuum, DRM Voucher V100552, USA: Colorado: Huerfano Co., Huerfano River at Badito, $37.7285^{\circ} \mathrm{N} 105.0167^{\circ} \mathrm{W}$. Scale bar is 1 mm .
distinctive mentum, with much reduced lateral lobes (Fig. 5A), in contrast to the more normal mentum and typical lateral lobes of B. perspicuum (Fig. 5B). However, there are specimens in the west (western British Columbia south to California) that match B. transversale in all regards, including in DNA sequences and other morphological characters, and yet have a more typical mentum with large lateral lobes (Maddison, unpublished). In addition to these differences in external traits between $B$. transversale and $B$. perspicuum, the ostial flag of $B$. transversale extends further ventrally and has a more gentle curvature (arrow in Fig. 6A) than that of B. perspicuum (arrow in Fig. 6C).

The differences observed in morphological characters, congruent with the consistent molecular differences between two unlinked genes, even where the two forms are microsympatric in Colorado, provides strong evidence that the two forms are not exchanging genes, and are two different species.

As an aid for identification, Bembidion perspicuum can be incorporated into Lindroth's (1963) key by replacing couplet 145 (on page 223) with the following two couplets:
145. Prothorax (Figs. 168a-b) without or with very faint, oblique latero-basal carina .............................................................................................................................

- Prothorax with latero-basal carina well developed, less oblique................ 146


Figure 4. Dorsal view of pronotum. A B. transversale, DNA2481, USA: Colorado: Fremont Co., Arkansas River at Texas Creek, $38.4106^{\circ} \mathrm{N} 105.5844^{\circ} \mathrm{W}$ B B. perspicuum, DRM Voucher V100552, USA: Colorado: Huerfano Co., Huerfano River at Badito, $37.7285^{\circ} \mathrm{N} 105.0167^{\circ} \mathrm{W}$. Scale bar is 0.25 mm .


Figure 5. Mentum, ventral view. Both specimens from USA: Colorado: Fremont Co., Arkansas River at Texas Creek, $38.4106^{\circ} \mathrm{N} 105.5844^{\circ} \mathrm{W}$. A B. transversale, DRM Voucher V100555 B B. perspicuum, DRM Voucher V100556.


Figure 6. Male aedeagus, left lateral view. All specimens from USA: Colorado: Fremont Co., Arkansas River at Texas Creek, $38.4106^{\circ} \mathrm{N} 105.5844^{\circ} \mathrm{W}$. A Bembidion transversale, DRM Voucher DNA2481 B B. transversale, DRM Voucher DNA2486 C B. perspicuum DRM Voucher DNA2482 D B. perspicuum DRM Voucher DNA2485. All to same scale; scale bar is 0.1 mm . Arrows indicate the ostial flag, which differs in form between the species.

145A. Prothorax slightly more cordate, flatter, with a smoother basal region (this paper, Fig. 4A); aedeagus with ostial flag extending further ventrally, and with gentler curvature (this paper, Fig. 6A) B. transversale

- Prothorax slightly less cordate, with more notable punctures in the basal region (this paper, Fig. 4B); aedeagus with ostial flag more dorsal, and with a more abrupt curve at its anterior end (this paper, Fig. 6B) .... B. perspicuum


## Classification and species notes

Our studies indicate that the Bembidion transversale and B. mexicanum groups contain a combined six species in America north of México:
B. transversale group
B. transversale Dejean
B. perspicuum LeConte
B. sarpedon Casey
B. mexicanum group
B. mexicanum Dejean
B. lugubre LeConte
B. pernotum Casey

## Bembidion transversale Dejean, 1831

Bembidium transversale Dejean, 1831:110. Type locality restricted to Nipigon, Ontario, by Lindroth (Lindroth 1963). Holotype female, in MNHN, examined by Kipling Will, who provided to us photographs, including of the mentum, allowing us to confirm the identification.
Peryphus eros Motschulsky, 1850:10. Type locality California. Lectotype, designated by Bousquet and Larochelle (1993), in ZMUM. Synonymy tentative.
Ochthedromus mannerheimii LeConte, 1852:190. Type locality San Diego, California. Three specimens in the MCZ in the Bembidion transversale unit tray in the LeConte collection have gold discs (signifying California), and include syntypes for this name. The first specimen is a female labeled as follows: [gold dot] / "O. mannerheimii Lec. S. D. transversale $\ddagger$ Man" [in LeConte’s handwriting] / "transversale 27" [handwritten], and is certainly a syntype. The two following specimens, a male and female, are labeled with a gold dot in addition to a label of "transversale 28 " and "transversale 29" respectively, and are quite possibly also syntypes. As the first specimen is the only one that is surely a syntype, it is herein designated as the lectotype, MCZ type number 35571. All specimens externally match the western form (see below) of $B$. transversale. We have examined the aedeagus of the male, and it matches that of $B$. transversale.
Bembidium haplogonum Chaudoir, 1868: 241. Type locality California. Location of types unknown. Synonymy tentative.
Bembidion marinicum Casey, 1918:57. Type locality Marin County, California. Holotype female in USNM (type number 36919), examined. Synonymy tentative.
Bembidion tuolumne Casey, 1924:30. Type locality Tuolumne, California. Lectotype male, designated by Lindroth (1975), in USNM (type number 36917), examined. Synonymy tentative.

As currently conceived, this species is a mix of different forms. The typical form (including the holotype of B. transversale Dejean, and all specimens sequenced for this
study) has an unusual mentum with much-reduced lateral lobes, which do not project anteriorly much beyond the mental tooth (Fig. 5A). This form occurs from Nova Scotia west to Alaska, south through eastern British Columbia, eastern Oregon, Idaho, Nevada, Utah, Colorado, and Wyoming. Western British Columbia, western Oregon, and California contain another form, with no consistent differences in COI or 28 S from the typical form (Maddison, unpublished), with a normal B. transversale pronotum and aedeagus, but with full lateral lobes on the mentum. The mentum of this western form is thus similar to that of B. perspicuum, Fig. 5B, and in contrast to eastern B. transversale. The western form itself is rather variable morphologically, and is being examined in more detail (Maddison, in prep.). It may be a complex of multiple species, and thus the five younger names mentioned above are only tentatively synonymous with $B$. transversale. In addition, while it is clear that the LeConte name and the two Casey names are not synonyms of B. perspicuum, the Motschulsky and Chaudoir names might be junior synonyms of $B$. perspicuum; examination of the types will be required to confirm the synonymies.

Morphological characters distinguishing these species from B. perspicuum are described above, under "Morphological Differences".

## Bembidion perspicuum LeConte, 1848

Ochthedromus perspicuus LeConte, 1848: 466. Type locality "Rocky Mountains". Holotype male, in MCZ (type number 5510), external structure and aedeagus examined. Bembidion acomanum Casey, 1918: 59. Type locality Jemez Springs, New Mexico, so restricted by Lindroth (1975). Lectotype female, designated by Lindroth (1975), in USNM (type number 36916), examined.
Bembidion excursum Casey, 1918: 59. Type locality Tucson, Arizona. Holotype female, in USNM (type 36915), examined.

This species is known from Texas, Kansas, Colorado, New Mexico, Arizona, Utah, Nevada, California, and Oregon. Its range in México has not been examined. Specimens from northern California and Oregon are dark, with only elytral apices being pale. They are thus very similar in appearance to paler specimens of Bembidion lugubre, from which they are most readily distinguished by genitalic characters.

## Bembidion sarpedon Casey 1918

Bembidion sarpedon Casey, 1918: 58. Type locality Cañon City, Colorado. Lectotype male, designated by Lindroth (1975), in USNM (type number 36914); external structure and aedeagus examined.
Bembidion animatum Casey, 1918: 62. Type locality Jemez Springs, New Mexico, so restricted by Lindroth (1975). Lectotype female, designated by Lindroth (1975), in USNM (type number 36918), examined.

This species is known from northeastern Arizona, Utah, northern New Mexico, Colorado, and Wyoming. It is characterized by a shiny, slightly more cordate pronotum than other members of the group, without notable basal punctuation, relatively flat elytral intervals, with small punctures in the elytral striae, and distinctive male genitalia. As first revisers, we choose $B$. sarpedon Casey as the valid name of this species.

## B. mexicanum Dejean, 1831

Bembidium mexicanum Dejean, 1831:126. Type locality México. Lectotype male, designated by Erwin (1982), in MNHN; external structure and aedeagus examined.
Bembidium stabile LeConte, 1879: 508. Type locality La Veta, Colorado. Lectotype male, designated by Erwin (1984), in MCZ; external structure and aedeagus examined.
Bembidion lugubre vafrum Casey, 1918:60. Type locality Arizona. Lectotype male, designated by Erwin (1984), in USNM; external structure and aedeagus examined.
Bembidion badiipenne Casey, 1918: 60. Type locality between Fort Wingate and Jemez Springs, New Mexico. Lectotype female, designated by Erwin (1984), in USNM (type number 36913); external structure examined (spermatheca absent, as most of the abdomen is missing).

This species is known from South Dakota, Colorado, New Mexico, and Arizona, south at least to Guatemala. In the United States, specimens have unicolorous, dark elytra, a smoother pronotum, and tend to be larger than those of B. lugubre; some specimens from México and Central America have pale elytral apices. The two species can only be reliably distinguished by characters of the male genitalia, female spermatheca, or DNA sequences. The two species are microsympatric, occurring together on the same creek or river shore at numerous localities in Arizona and New Mexico.

## B. lugubre LeConte, 1857

Bembidium lugubre LeConte, 1857:6, described as a "variety" of B. mexicanum Dejean. Type locality "Valley of the Rio Grande". Holotype female in MCZ (type number 5511); external structure and spermatheca examined.

Bembidium sallaei Bates, 1882:148. Type locality not specified, with localities specified in several states of México as well as Belize and Guatemala. Lectotype male, designated by Erwin (1982), in MNHN; external structure and aedeagus examined.
Bembidion canonicum Casey, 1918:61. Type locality Arizona. Holotype male in USNM (type number 36920); external structure and aedeagus examined.
Bembidion retectum Casey, 1918:61. Type locality St George, Utah. Lectotype male, designated by Erwin (1984), in USNM (type number 36923); external structure and aedeagus examined.

This species is known from Texas, New Mexico, Arizona, Utah, and California south at least to Oaxaca, México. In the United States specimens of this species tend to be paler than those of $B$. mexicanum, with some specimens having a pale elytral apex, and with more notable punctures at the base of the pronotum. Male genitalia, female spermathecae, and DNA sequences are distinctive.

## B. pernotum Casey, 1918

Bembidion pernotum Casey, 1918: 62. Type locality Jemez Springs, New Mexico. Lectotype female, designated by Erwin (1984), in USNM (type number 36922), examined.

This species is known from northern New Mexico and southern Colorado. Individuals are colored similarly to $B$. transversale, but are brighter and more reddish, and are more convex and shinier than other members of the group, with larger punctures in the elytral striae, and more convex intervals. While their color pattern is similar to members of the $B$. transversale group, male genitalia and DNA sequences indicate a much closer relationship to $B$. mexicanum and $B$. lugubre.

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# Revision of the genus Chiasognathus Stephens of southern South America with the description of a new species (Coleoptera, Lucanidae, Lucaninae, Chiasognathini) 

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#### Abstract

The genus Chiasognathus Stephens is revised and now consists of seven species, all of which are endemic to southern South America. The genus-level names Bomansodus Chalumeau \& Brochier, Carmeniella Molino-Olmedo, and Ramireziella Molino-Olmedo are all confirmed to be synonyms of Chiasognathus. A new species of Chiasognathus is described from the Biobío Region of Chile. The species Chiasognathus mniszechii Thomson is removed from synonymy and is a valid species with Chiasognathus schoenemanni Kriesche as its junior synonym. In order to promote nomenclatural stability, a lectotype is designated for the name Chiasognathus reichei Thomson, and a neotype is designated for the name Chiasognathus pygmaeus Dallas.


## Keywords

Systematics, Lucanidae, Chile, Argentina, Scarabaeoidea, stag beetle

## Introduction

The genus Chiasognathus Stephens (Lucanidae: Lucaninae: Chiasognathini) is distributed in southern South America in Chile with some species extending into Argentina. The latest taxonomic treatment of Chiasognathini was done by Chalumeau and Brochier (1995, 2007), who listed four species in the genus Chiasognathus and one in the genus Bomansodus Chalumeau \& Brochier. Molino-Olmedo (2001, 2002, 2003, 2006) also published a series of recent papers on the phylogeny and classification of Chiasognathus. In spite of the large size and distinct appearance of these beetles, some species are difficult to identify because they exhibit considerable intraspecific variation. As a result, the scientific literature on Chiasognathus is checkered with misidentifications and misinterpretations of species. Although the genus was treated recently, Chalumeau and Brochier (2007) correctly identified only three of the seven species known to us, thus necessitating this revision.

Catalogs have gone from one extreme to the other, with Benesh (1960) recognizing only three species of Chiasognathus, while Maes (1992) listed six valid species. Some species names have a history of repeatedly being synonymized and revalidated by various authors. We refer the reader to Numhauser (1981) for such details and will focus primarily in this paper on the synonymies recognized within the past three decades.

The genus Chiasognathus forms part of the tribe Chiasognathini, which is distributed in South America and Australia. Smith (2006) considered Chiasognathini a synonym of the subfamily Lucaninae Latreille because of the chaotic state of lucanid classification, especially within the subfamily Lucaninae. However, we reverse this synonymy based on the almost universal recognition of this taxon in the lucanid literature. Chiasognathini was firmly placed in the subfamily Lucaninae by the morphological characters discussed by Holloway $(1960,1968,1997,2007)$ and is treated as such in the most recent lucanid catalogs and checklists (Krajcik 2001; Paulsen 2008). Maes (1992) and Chalumeau and Brochier (2007) both treated Chiasognathini as a subfamily without justification or differentiation from the subfamily Lucaninae.

Chiasognathus grantii Stephens was the first species described in the genus. The males of this species are spectacular (see Figs 1-2), making them one of the most often illustrated lucanids in popular books and websites on insects. This species is highly distinctive, and there is no doubt about its identification, even with the crude drawings of Stephens (1831) in the original description or of the considerably better drawings by Lesson (1833) of Tetropthalma chiloensis Lesson (a junior synonym of C. grantii).

Through the mid to late 1800 s and early 1900s, there was a proliferation of Chiasognathus species described. Reiche (1850a, b) described C. jousselinii, Solier (1851) described C. latreillei, and Parry (1870) described C. impubis - three species that we consider valid. Several species were also described that were later placed in synonymy with C. grantii or C. latreillei, namely: C. affinis Philippi and C. pygmaeus Dallas (synonyms of C. grantii), and C. imberbis Philippi and C. reichei Thomson (synonyms of C. latreillei) (see Philippi 1859; Thomson 1862; Dallas 1933). Thomson (1862) also described C. mniszechii, a species that was later synonymized with C. jousselinii but is


Figures I-2. I Threat display of male Chiasognathus grantii $\mathbf{2}$ Mate guarding posture in C. grantii, adopted here at a light trap.
here removed from synonymy and considered a distinct species based on the examination of the type specimens. Chiasognathus schoenemanni Kriesche was described from an abraded specimen (Kriesche 1919) and subsequently treated as a synonym of C. jousselinii by Krajcik (2001) and Chalumeau and Brochier (2007), but it is actually a synonym of C. mniszechii.

Only a single species of Chiasognathus has been described during the past 75 years: Chiasognathus beneshi Lacroix (Lacroix 1979), a species that is similar to C. latreillei. The immense popularity of this genus makes it surprising that one additional species remained undescribed due to the confusion over synonymies in the genus, and in this paper we remedy that situation with the description of that species as new.

Over the past 15 years, authors have attempted to split Chiasognathus into multiple genera/subgenera. Chalumeau and Brochier (1995) described Bomansodus for the single species C. impubis. Molino-Olmedo (2001) later attempted to erect two new subgenera within Chiasognathus: Carmenia Molino-Olmedo (for C. latreillei) and Ramirezia Molino-Olmedo (for C. jousselinii, C. mniszechii, and C. schoenemanni). Unfortunately, Molino-Olmedo (2001) neglected to explicitly designate type species for his two new subgenera, and so Ramirezia is unavailable from this publication (although Carmenia is available from this publication because the type species was automatically fixed by monotypy). Molino-Olmedo (2002) later published another paper describing the same two subgenera and this time designated type species and properly validated the name Ramirezia. Therefore, Carmenia Molino-Olmedo was made available from the 2001 publication and Ramirezia Molino-Olmedo was made available from the 2002 publication. It is unclear why the author published two very similar papers almost simultaneously in different journals with descriptions of the same new taxa in both papers. In another unfortunate twist, Molino-Olmedo (2003) realized too late that both Carmenia and Ramirezia were permanently invalid names because both are junior homonyms. He proposed Carmeniella and Ramireziella, respectively,
as replacement names (Molino-Olmedo 2003). The two sets of authors who recently erected new genus-group names for Chiasognathus species did not agree with each other. Molino-Olmedo (2006) synonymized Bomansodus with Chiasognathus. Subsequently, Chalumeau and Brochier (2007) resurrected Bomansodus and synonymized Carmeniella Molino-Olmedo and Ramireziella Molino-Olmedo with Chiasognathus. We here consider all of the above genus-level names to be synonyms of Chiasognathus for reasons discussed below.

Despite being treated numerous times, our examination of the type specimens indicated that the identities of some species are confused, even though Chalumeau and Brochier (2007) reported to have also examined type material. The main goal of this paper is to alleviate confusion about the species and circumscription of Chiasognathus by redefining the genus and each of the included species. As mentioned above, the confusion surrounding the nomenclature of Chiasognathus left one species without a formal description, which is rectified in this paper.

The study of the genus has historically been hampered by a few factors, and these were examined in marvelous detail by Numhauser (1981). In addition, our previous revisions of the fauna of this region have taught us that an unusually large number of locality labels from Chile are erroneous. For some taxa in this study, this is a major impediment to determining correct distributions. There are already few specimens available of the more difficult taxa, making the problem of erroneous data even more of an issue. Also, specimens of the variable C. latreillei are available for study only from a handful of widely separated localities. Because of this, we are tentative about our hypothesis concerning this taxon. It is possible that the availability of larger series and specimens from additional localities will make clear if this taxon is one species or a complex of more than one cryptic species.

Chiasognathus larvae have been described and discussed in a few papers. Cekalovic and Castro (1983) first described the larvae of C. grantii based on 16 specimens from various localities. Onore (1994) listed diagnostic characters for Chiasognathini larvae including Chiasognathus. Molino-Olmedo (2005) recently provided an additional description purportedly of C. latreillei.

## Materials and methods

Specimens and Taxonomic Material. Specimens examined for this study were provided by the following institutions and private collections. A total of 445 specimens, including all accessible type material, formed the basis of this research. Acronyms for institutions when available are from Evenhuis (2009).

ABTS Andrew B. T. Smith Collection, Ottawa, Canada
AMNH American Museum of Natural History, New York, NY, USA (Lee Herman)
AUPC Alfredo Ugarte Peña Collection, Santiago, Chile
BMNH The Natural History Museum, London, UK (Max Barclay)

CASC California Academy of Sciences, San Francisco, CA, USA (Jere Schweikert, David Kavanaugh)
CMNC Canadian Museum of Nature, Ottawa, Canada (François Génier)
CNCI Canadian National Collection of Insects, Ottawa, Canada (Patrice Bouchard)
CUMZ Cambridge University Museum of Zoology, Cambridge, UK (William Foster)
EPGC Everardo \& Paschoal Grossi Collection, Nova Friburgo, Brazil
FMNH Field Museum of Natural History, Chicago, IL, USA (James Boone)
JMEC José Mondaca E. Collection, Santiago, Chile
LBC Luca Bartolozzi Collection, Florence, Italy
LEMQ Lyman Entomological Museum, McGill University, Ste. Anne de Bellevue, PQ, Canada (Terry Wheeler, Stéphanie Boucher)
MJPC M.J. Paulsen Collection, Lincoln, NE, USA
MNHN Muséum National d’Histoire Naturelle, Paris, France (Stéphane Boucher, Olivier Montreuil, Thierry Deuve)
MNNC Museo Nacional de Historia Natural, Santiago, Chile (Mario Elgueta)
NHRS Swedish Museum of Natural History, Stockholm, Sweden (Bert Viklund)
SMTD Staatliches Museum für Tierkunde, Dresden, Germany (Olaf Jäger)
UNSM University of Nebraska State Museum, Lincoln, NE, USA (M.J. Paulsen)
ZMHB Zoologisches Museum der Humboldt-Universitat, Berlin (Johannes Frisch)
Morphological characters. Conventions used in the description of morphological characters are as in Paulsen (2005). Mandibular development is sexually dimorphic and varies allometrically within males of each species. Major males are larger-bodied males that possess enlarged mandibles that are more elongate, usually with additional internal teeth. Minor males are smaller-bodied males that often have less-developed mandibular teeth. Female mandibles in Chiasognathus species are similar to those found in all chiasognathine females, with a flattened dorsal surface and usually one internal tooth. We use the term nasus to refer to the projection of the anterior margin of the head when visible in dorsal view, as in Chalumeau and Brochier (2007). The maxilla and labium in Chiasognathus species bear elongated setal brushes that may be diagnostic in length; here we are concerned only with the relative length of the longest setae on these structures, which we term the galeal brush after Nel and Scholtz (1990).

Characters of the pronotum, elytra, male mandibles, legs, vestiture, and genitalia are useful in diagnosing species of Chiasognathus. Chalumeau and Brochier (2007) discounted the usefulness of the male genitalia for species diagnosis, and this is true with respect to the median lobe and parameres that exhibit considerable intraspecific variation. However, a character of the male genitalia that we found to be useful in this genus is the form of the flagellum (the sclerotized, everted internal sac) that is diagnostic in the material studied. The length of the flagellum varies from short $(\sim 1 \mathrm{~mm})$ to extremely long ( $\sim 18 \mathrm{~mm}$; Figs 3-9) depending on the species.


Figures 3-9. Male genitalia of Chiasognathus species. 3 C. grantii 4 C. impubis 5 C. jousselinii 6 C. mniszechii 7 C. sombrus, sp. n. 8 C. beneshi, and 9 C. latreillei. Scale bars $=2 \mathrm{~mm}$.

## Taxonomic Treatment

Tribe CHIASOGNATHINI Burmeister, 1847
Type genus: Chiasognathus Stephens, 1831: 213.

## Genus Chiasognathus Stephens, 1831

Chiasognathus Stephens, 1831: 213. Type species: Chiasognathus grantii Stephens 1831, by monotypy.
Tetropthalma Lesson, 1833: plate 24. Type species T. chiloensis Lesson 1833, by monotypy.
Bomansodus Chalumeau \& Brochier, 1995: 20. Type species Chiasognathus impubis Parry 1870, by original designation. Synonymy reinstated.
Carmenia Molino-Olmedo, 2001: 85. Type species Chiasognathus latreillei Solier, 1851 by monotypy. Junior homonym of Carmenia Roewer, 1915.
Ramirezia Molino-Olmedo, 2002: 124. Type species Chiasognathus jousellinii Reiche, 1850 by original designation. Junior homonym of Ramirezia Zamponi, 1979. Mo-
lino-Olmedo (2001: 85) attempted to describe this generic name earlier but did not designate a type species, and so the name is not available from the 2001 publication. Carmeniella Molino-Olmedo, 2003: 29. Type species Chiasognathus latreillei Solier, 1851 by monotypy. Replacement name for Carmenia Molino-Olmedo 2001. Ramireziella Molino-Olmedo, 2003: 29. Type species Chiasognathus jousellinii Reiche, 1850 by original designation. Replacement name for Ramirezia Molino-Olmedo, 2002.

Description. Length: 16.6-88.0 mm. Width: 8.4-17.0 mm. Color: Light to dark reddish brown, commonly with green to purple metallic reflections. Head: Form subquadrate to subtriangular, narrower than 1 elytron width, shorter than mandibles in both sexes. Disc surface uneven, often with foveae or apparent tubercles. Surface punctate; punctures fine to coarse, generally setose with short to long setae. Ocular canthus well developed, externally rounded, dividing eye completely into upper and lower portions. Temporal process absent. Anterior angles produced, obtuse or acute. Anterior margin of head in dorsal view varying from weakly emarginate to strongly produced into binodose or acute nasus (nasus when present occasionally migrated anteroventrally and obscured in dorsal view); head below anterior margin and nasus declivous and recessed forming more or less vertical intermandibular projection. Labrum scoop-like, lightly sclerotized, vertical, separated from intermandibular projection by a distinct suture; apex of labrum rounded or acute. Male mandibles $2-6 \times$ as long as head, right mandible usually shorter than left, both mandibles with a single, dentate carina (more or less cylindrical, lacking well-defined external or internal carinae present in Sphaenognathus Buquet); dentate carina generally dorsal at base becoming more internal toward apex. Apex abruptly curved, acute. Mandibular surface punctate; punctures generally setose, setae sparse to dense. Female mandible externally weakly rounded to almost straight in dorsal view, never with external tooth; dorsal surface flattened, internally subdentate (acute tooth occasionally present near middle), punctate; punctures setose with short to long setae. Maxilla and labium with long or short galeal brushes, palps elongate. Mentum transverse, subtrapezoidal, anteriorly emarginate, punctate; punctures fine to coarse, pubescent. Antennal club composed of 6 entirely tomentose antennomeres; antennomeres gradually increasing in length distally. Funicle not tomentose, instead pubescent with scattered setae; distal antennomere of funicle produced as in club or not. Scape elongate, longer than funicle and club together, normally with long setae present at enlarged apex. Pronotum: Shape subtrapezoidal, broadest in basal fifth, anteriorly convergent with rounded sides (margin not strongly produced near anterior angles). Anterior margin sinuate. Anterior angles not prominent. Posterior angle and lateral angle variably developed: obsolete, subdentate, to strongly dentate. Lateral margins distinct and crenulate, rarely obsolete anterolaterally. Dorsal surface generally with variably developed longitudinal and transverse ridges surrounding longitudinal, median furrow; when present ridges less punctate than disc; punctures fine to moderate, variably dense, setose; setae short to long. Each side with subcircular fovea; fovea generally impunctate and glabrous. Scutellum: Form broad, rounded. Surface densely to sparsely punctate; punctures setose or not. Elytra: Form broad and short, convex. Surface gener-
ally smooth, occasionally weakly wrinkled, punctate; punctures fine and extremely dense (distance between punctures $\leq 1$ puncture diameter), setose; setae scale-like, microscopic to clearly visible. Humeri broadly rounded. Apex broadly rounded, angulate, or dentate. Epipleuron strongly concave or flat. Wings: Fully developed. Legs: Protibiae dentate or serrate externally from base to 2 larger, apical teeth; ventral surface along internal margin with series of downward-pointing teeth. Mesotibiae and metatibiae with 4-6 external teeth, teeth of metatibiae less distinct, occasionally absent. Onychium of claws with more than 4 setae. Venter: Ventral surface densely pubescent, especially mesosternum. Last abdominal segment distinctly emarginate in males. Male genitalia: Genital capsule simple and parameres of generalized lucanid form. Median lobe strongly sclerotized, form cylindrical or widening apically, with everted internal sac forming flagellum; flagellum simple, length varying from $<1 \mathrm{~mm}$ to 18 mm (Figs 3-9).

Distribution. Chiasognathus species are distributed in Regions VII-XI and XIV of Chile and in adjacent parts of Argentina.

Diagnosis. In the New World lucanine fauna, Chiasognathus species are immediately recognizable as members of the tribe Chiasognathini because their antennal club is composed of six antennomeres; they are the only stag beetles in southern South America to display this character.

Remarks. The following characters were used by Moxey (1962) to distinguish Chiasognathus from the only other genus of South American Chiasognathini, Sphaenognathus (including the subgenus Chiasognathinus Didier): front of head projected (nasus) and usually acute, antennal scape 1.5-3.0 times longer than funicle and club combined, and elytral surface not strongly sculptured. Molino-Olmedo (2001) rightfully questioned each of these characters given the variability of the nasus and elytral sculpture and lack of a demonstrable difference in antennal scape length. However, we feel the recognition of these genera as distinct is warranted, and this is especially true with respect to the biogeography of South America, as all known southern South American lucanids are distinct from their Neotropical relatives at the generic level (Paulsen and Mondaca 2006; Grossi and Paulsen 2009).

There are few reliably expressed characters that can be used to distinguish Chiasognathus and Sphaenognathus, and these unfortunately tend to be observable in only one sex or the other. Male mandibles in Chiasognathus species are rounded externally, not carinate, and therefore appear to be more cylindrical than the mandibles of males of Sphaenognathus species, which are often more triangular in cross section. Importantly, the teeth on Chiasognathus male mandibles are located where the usually toothless (rarely with a single large tooth basally) dorsal carina is found in Sphaenognathus species; the teeth on Sphaenognathus male mandibles are on an internal ventral carina that is not present in Chiasognathus species. Female mandibles are weakly rounded externally in Chiasognathus species, never with an external tooth as in females of some Sphaenognathus species. Male abdominal apices are strongly emarginate in Chiasognathus species but more or less straight or rarely weakly emarginate in Sphaenognathus species. Finally the lateral margin of the pronotum is produced near the anterior angles in females of Sphaenognathus species but is more convergent towards the head in Chiasognathus species females.

Chalumeau and Brochier (2007) emphasized three characters used to differentiate Bomansodus in their earlier work (Chalumeau and Brochier 1995): male mandibular structure, nasus/intermandibular projection, and effaced lateral pronotal margin. We can find no clear discussion of how the mandibular structure of C. impubis differs from its congeners in either work, and our examination of the mandibles indicates that they are of the same basic plan as those of the remaining Chiasognathus species. Only C. grantii and C. mniszechii more or less consistently possess a prominent nasus; therefore, its absence cannot be used to segregate C. impubis from the genus as a whole. Finally, some specimens of C. impubis we have studied do have a distinct lateral pronotal margin. While it is true that the pronotum is overall more rounded and less distinctly ridged in C. impubis, the character is too weak and variable to support a generic distinction. This is especially true with respect to the shared characters of C. impubis and C. mniszechii, namely the strikingly concave epipleuron, similar protibiae, and beaded elytral margin. For these reasons, we reconfirm the synonymy of Bomansodus with Chiasognathus.

Molino-Olmedo $(2001,2006)$ accepted (but later rejected) Bomansodus and created additional subgenera with the result of placing almost all species in their own genus or subgenus. There is little justification for such over-splitting of a small, clearly related group based on what amount to species-level characters. We agree with the arguments presented by Chalumeau and Brochier (2007) against the validity of the Molino-Olmedo subgenera. Our greatest concern is that the work was premature given that it was not preceded by a careful revision of the group and was, therefore, founded on an incomplete understanding of the taxonomy of the genus. Thus, we include the seven species in a single genus and are confident that our taxonomic treatment of the species will provide a foundation for future research into the relationships and evolution of Chiasognathus.

## Key to Adults of Chiasognathus Species

1. Apex of elytra spinose. Males with large tooth projecting ventrally from each mandible, females with ridge or large tubercle in the same spot ... C. grantii Stephens

- Apex of elytra not spinose, either subdentate or rounded. Males and females at most with small ventral tooth at base of mandible. 2

2. Epipleuron strongly concave in basal third of elytra. Elytral apex with beaded margins to just before apex..

- Epipleuron more or less flat in basal third of elytra. Elytral apex thickened, with margin lacking bead. 4

3. Prothorax with lateral margin obsolete anteriorly. Elytra distinctly shiny; surface glabrous in males, with long scattered bristles in females. ........ C. impubis Parry

- Prothorax with lateral margin strongly indicated throughout, crenulate. Elytra usually densely squamose (rarely abraded).... C. mniszechii Thomson

4. Dorsal surface entirely squamose with short scales....... C. jousselinii Reiche

- Dorsal surface (especially pronotum) more or less glabrous........................ 5

5. Mesotibia thickened (Fig. 10). Specimens known only from Nuble Province (VIII Región del Biobío, Chile) .......... C. sombrus Paulsen \& Smith, sp. n.

- Mesotibia not thickened (Fig. 11). Specimens from farther south .............. 6


Figures I0-II. 10 Robust right mesotibia of $C$. sombrus, ventral view. II. Slender right mesotibia of $C$. latreillei, ventral view. Scale bars $=5 \mathrm{~mm}$.
6. Males with median mandibular teeth directed internally, apex usually simply acute. Flagellum of male genitalia extremely short (Fig. 9). Specimens from Biobío to Los Lagos (VIII-X Regiones) in Chile and Neuquén to Chubut in Argentina.

- Males with median mandibular teeth directed dorsally, apex surrounded by additional dorsal and ventral teeth. Flagellum of male genitalia moderately long (Fig. 8). Specimens from Aisén (XI Región, Chile). $\qquad$ C. beneshi Lacroix


## Chiasognathus beneshi Lacroix, 1978

Figs 8, 12, 27
Chiasognathus beneshi Lacroix, 1978: 250. Type material: Holotype reportedly deposited in the J. P. Lacroix collection. Lacroix is deceased, and the Lacroix collection is not available for study and is in an unknown state of preservation. Type locality: "Chili, Province d'Aysen: Río Manihuales".

Description. Length: 21.7-28.0 mm. Width: $10.0-12.6 \mathrm{~mm}$. Color: Reddish brown with weak green or purple metallic reflections. Head: Form subquadrate. Surface punctate; punctures fine to coarse, generally setose with short to long setae. Anterior margin of head rounded or concave, not strongly produced beyond anterior angles, lacking median nasus. Anterior angles obtusely rounded in dorsal view. Male mandibles cylindrical, $1.5-2 \times$ as long as head, externally almost straight until internally curved apex. Dentate carina beginning with basal tooth on dorsal surface, continuing along internal edge, not becoming internal; dorsal and ventral teeth present either side of apex resulting in scoop-like appearance; apex lacking
patch of setae. Base of mandibles lacking ventral tooth. Female mandible externally rounded in basal third, dorsally flattened, with median internal tooth. Galeal brush moderately long, $2 \times$ longer than mentum. Antennal scape with sparse area of long setae present in males, or setae absent. Pronotum: Posterior and lateral angles dentate, posterior angle more strongly so in males, or angles obsolete. Lateral margins distinct, crenulate. Dorsal surface with transverse ridge, longitudinal median furrow broad, weak depressions indicated either side of disc before middle in most specimens. Surface near margins with distinct, moderately long setae in females, glabrous in males examined. Elytra: Surface weakly shiny, appearing wrinkled, densely punctate, setose; setae scale-like, often abraded except on lateral elytral declivity; females lacking distinct, scattered, longer bristle-like setae. Apex rounded, lacking spine. Epipleuron flat. Legs: Protibiae short, serrate externally; ventral surface along internal margin with 2-5 small teeth. Male genitalia: Flagellum moderately long, subequal in length to basal piece (Fig. 8).

Distribution. Specimens were examined only from Aisén, Chile (Fig. 27).
CHILE (6): Aisén (6): Caleta Tortel, Coihaique, Lago Yulton, Río Correntoso.
Temporal distribution. January (3), February (3).
Diagnosis. This species, although externally nondescript (Fig. 12), can be separated from the C. latreillei complex by the longer flagellum of the male genitalia and by its geographic distribution.

Remarks. The amateur entomologist J. P. Lacroix described this species. Most taxa named by Lacroix, especially in the Chiasognathini, are now considered synonyms, including eight of twelve available Lacroix names in Sphaenognathus (Chalumeau and Brochier 2007; Paulsen 2008). The type specimen was not deposited in an institution and is unavailable for study, but we have examined specimens from near the type locality in Aisén that display mandibles identical to those drawn for the holotype of $C$. beneshi. These specimens have a distinctly longer flagellum of the male genitalia than do C. latreillei. Because this character appears to be useful in separating other species in the genus, we have refrained from synonymizing C. beneshi at this time. However, externally there are few strong morphological characters to support the distinction, in part because the C. latreillei complex is so variable and possibly composed of multiple taxa. The median teeth of the male mandibles in C. latreillei generally point distinctly inward, while in the $C$. beneshi material studied the teeth remain more or less vertical. The apex of the male mandible in C. beneshi generally has a strong tooth above and below the apex, giving a scoop-like appearance, and the mandibles overall are more cylindrical and curved internally at the apex. Most specimens of C. latreillei have externally straighter mandibles with a simple apex. Unfortunately, a few specimens of the C. latreillei complex have mandibles similar to those of $C$. beneshi. The specimens treated as C. beneshi by some authors (Mizunuma and Nagai 2001; Chalumeau and Brochier 2007) represent an undescribed species that we describe below. Chiasognathus beneshi was previously recorded from Biobío (Las Trancas) but this locality is erroneous due to the misapplication of the name - this species is only known to occur in Aisén region of Chile.


Figures 12-13. Dorsal habitus of Chiasognathus species, males. I2 C. beneshi, and I3 C. latreillei.

## Chiasognathus grantii Stephens, 1831

Figs 1-3, 14-15, 28
Chiasognathus grantii Stephens, 1831:214. Type material: holotype male (CUMZ) labeled a) red label "Chiasognathus / grantii Stephens, 1831 / HOLOTYPE [male symbol] / Det: M.J. Paulsen \& A.B.T. Smith". Type locality: "Island of Chiloe."
Tetropthalma chiloensis Lesson, 1833: plate 24. Type material: lectotype designated by Chalumeau and Brochier (2007) using the original illustration in Lesson (1833) under ICZN Article 74.4. The original specimen could not be located in the MNHN and has presumably been lost. Type locality: "l'̂lle de Chiloë."
Chiasognathus affinis R. Philippi in F. Philippi, 1859: 658. Type material: Lectotype male (MNNC) designated by Chalumeau and Brochier (1995) labeled a) handwritten "Chiasognathus / affinis Phil."; b) orange label "LECTOTYPE"; c) handwritten "Chiasognathus / affinis Phil. / det F. Chalumeau / \& B. Brochier '94"; d) Chiasognathus grantii / Stephens / Dét. det F. Chalumeau / \& B. Brochier ‘94"; e) red label "Chiasognathus / affinis / Philippi [male symbol] / LECTOTYPE / A.B.T.

Smith"; f) "Chiasognathus / grantii / Stephens, 1831 / det. M.J. Paulsen 2010". Type locality: "cerca del Corral."
Chiasognathus pygmaeus Dallas, 1933: 74. Type material: Holotype lost - reportedly deposited in the Dallas collection (Dallas 1933). Primary types should be deposited in legitimate institutional collections so they have a good chance of being available for study by taxonomists. Neotype male, (MNNC) HERE DESIGNATED, labeled a) handwritten "Aysen / I-37"; b) "['95] / Chiasognathus grantii / Stephens / Dét. Chalumeau \& B. Brochier / [var. pygmaea]"; c) red label "Chiasognathus / pygmaeus Dallas male symbol / NEOTYPE / Paulsen \& Smith"; d) "Chiasognathus / grantii / Stephens, 1831 / det. M.J. Paulsen 2010". A neotype is designated in order to preserve the stability of nomenclature by selecting one specimen as the sole, name-bearing type of this taxon because the original name-bearing type specimen(s) was lost or destroyed. The neotype specimen serves to tie the published name to an actual specimen and as a reference standard for the taxon. This is important because there has been confusion in the literature regarding this name with disagreement whether it is a valid species, synonym of C. grantii, or synonym of C. latreillei. Type locality: "Chile".

Description. Length: 24.5-88.0 mm. Width: 9.5-17.0 mm. Color: Light to dark reddish brown, everywhere with green, gold, or purple metallic reflections. Pronotum with metallic coloration gold/green on disk, becoming purple near margins, lateral fovea darker bluish-green. Elytra with disc greenish-brown due to weak green and purple metallic reflections, lateral margin darker metallic green. Head: Form subquadrate in minor males and females, subtriangular in major males. Surface punctate; punctures fine to coarse, generally setose with short to long setae. Anterior margin of head produced beyond anterior angles and always with median nasus, nasus variably binodose or simply obtuse. Anterior angles produced ventrally, acute in dorsal view. Male mandibles $2-6 \times$ as long as head, externally sinuate, arched and somewhat flattened in lateral view; dentate carina internally on dorsal margin for entire length of mandible; teeth variable along mandible, large basal tooth followed by serrate margin in basal third and more widely spaced, peg-like teeth in apical two-thirds. Apex abruptly curved, distally acute and hooked upwards in male majors, male majors with patch of setae inside apex. Base of mandibles with large, ventral tooth always present, in male majors longer than head; tooth internally serrate. Female mandible externally rounded, never with median internal tooth, but with strongly produced internal carina ventrally near base. Galeal brush elongate, $2-3 \times$ longer than mentum. Antennal scape with well-developed area of long setae present at apex in males. Pronotum: Posterior angle and lateral angle strongly dentate, especially in males; posterior angle uncinate and somewhat curved anteriorly in major males. Lateral margins distinct, weakly crenulate. Dorsal surface not strongly ridged, longitudinal median furrow distinct basally. Elytra: Surface shiny, appearing smooth, actually densely punctate, setose; setae scale-like, microscopic, often broken off. Apex spinose with acute spine. Epipleuron flat. Legs: Protibiae elongate, dentate externally; ventral surface along internal margin with teeth well developed.


Figures 14-15. Dorsal habitus of C. grantii. $1 \mathbf{4}$ male, and $\mathbf{1 5}$ female.

Male genitalia: Flagellum long, length more than $2 \times$ length of parameres and basal piece together (Fig. 3).

Distribution. This species is found in central Chile and neighboring areas of Argentina (Fig. 28).

ARGENTINA (38): Chubut (9): Lago Puelo, Parque Nacional Los Alerces; Neuquén (26): Parque Nacional Lanín, Pucará, San Martín de los Andes; Río Negro (3): El Bolsón, Lago Guillelmo.

CHILE (123): Biobío (5): La Invernada, Nuble, Las Trancas; La Araucanía (11): Cherquenco, Curacautín, Parque Nacional Huerquehue, Malleco, Villarrica; Los Ríos (9): Monumento Nacional Alerce Costero, Llifen, Valdivia; Los Lagos (36): Ahoni, "Chiloe", Dalcahue, Lago Chapo, Llanquihue, Palena, Puerto Varas, Parque Nacional Puyehue; Aisén (62): Aisén, Coihaique. No data (6).

Temporal distribution. January (32), February (119), March (7), June (1), November (4), December (5).

Diagnosis. This species is the most readily identifiable in the genus (Figs 14-15). The large ventral tooth on the mandibles of males, smooth and apparently glabrous
elytra, and spinose elytral apex in both sexes are diagnostic. Male majors, with their extremely elongate mandibles and large size, cannot be confused with any other species.

Remarks. Stephens (1831) described C. grantii based on a single holotype specimen. This specimen was found in the University of Cambridge Museum of Zoology, U.K. The holotype was likely part of the Stephens collection that was acquired by the Cambridge Philosophical Society. The entire insect collection of the Cambridge Philosophical Society was turned over to the University of Cambridge in 1865 as the foundation of a museum collection at the university. Unfortunately, none of the Stephens specimens were properly labeled so we had to match the attributes of this particular specimen to the original illustrations of Stephens (1831) to verify that it is the holotype. The male mandibles of this species can display great variation in their length, thickness, and curvature, and this specimen perfectly matches the specific curving and unusually large and thick mandibles of the original illustration. Specimens of such great size are relatively rare, and the general way the specimen is mounted also closely matches the original illustrations. The fact that this specimen was the only $C$. grantii specimen found in the University of Cambridge Museum of Zoology (the subsequent depository of Stephens' collection) and that it matches the original description and illustrations gives us enough evidence to state that this specimen is the holotype. Stephens (1831) reported that a Chilean collected this specimen in January on Chiloé Island and gave it to Dr. Grant, who was the surgeon on board the H.M.S. Forte.

The immense variation in size in this species has prompted the continued use of the name 'pygmaeus' for the smaller males despite any evidence that would suggest distinct populations or genetic uniqueness. The idea remains tempting to amateur collectors, possibly because even these smaller males are of a similar size (and show the same amount of allometric development) as male majors of other species such as $C$. mniszechii. The development of male majors in C. grantii that are twice-again as large, and how this relates to the breeding behavior of the species, is something that deserves to be studied in more detail.

Benesh (1960), and thus Krajcik (2001), listed C. pygmaeus under synonymy with C. latreillei despite the photograph in the original that clearly depicts a small C. grantii. Nevertheless, this demonstrates the existence of some confusion about the taxon and that the designation of a neotype is warranted.

Natural History. Grant's stag beetle, sometimes referred to as Darwin's stag beetle, is the largest species in the genus and one that commands a great deal of attention. Other common names for the species include ciervo volante, llico-llico, and cantábria. The species was observed by Darwin in Chile (Darwin 1871): "The male Chiasognathus grantii of South Chili - a splendid beetle ... has enormously-developed mandibles; he is bold and pugnacious; when threatened on any side he faces round, opening his great jaws, and at the same time stridulating loudly; but the mandibles were not strong enough to pinch my finger so as to cause actual pain." Darwin's observations were expanded by Joseph (1928) and Hamilton (2000) with further discussion on the behavior of C. grantii males. To this we add our own observations made while collecting in Chile. Males of C. grantii are energetic and will attempt to pinch with their elongate mandibles when handled. As
noted by Arrow (1951), the bite of a female would be much more painful, although the sharp mandibular apex of males can draw blood (ABTS, personal observation). Males will raise up on their middle and hind legs when threatened or when approached by another male (Fig. 1). When another male is introduced, the two individuals will move together and adopt this aggressive posture and will then battle each other. Each will attempt to grip with their mandibles around the lateral teeth of the pronotum of their opponent. Once a strong grip is established there is an attempt to lift the opponent and drop it to the ground. When a female is introduced, the successful combatant will adopt an apparent mate-guarding stance with his mandibles and legs arched over the female (Fig. 2) and will battle any other males that approach. Hamilton (2000) reported that male combat occurs either in trees, where the females feed on sap, or among the flowers of the native canelilla, a climbing hydrangea (Hydrangea serratifolia (H. et A.) F. Phil (Hydrangeaceae)). Adults have been reported to feed on the sap of Nothofagus betuloides (Mirbel) Oersted, N. nitida (Phil.) Krassen, N. obliqua (Mirbel) Oersted (Fagaceae), and Weinmannia trichosperma Cav. (Cunoniaceae) (Joseph 1928; Vergara and Jerez 2009). As with other chiasognathines, larvae live in the soil (Joseph 1928). Adults may be seen flying just before dark and are attracted to light.

Arrow (1904) discussed the stridulatory mechanism present in adults of both sexes of C. grantii, and that it is composed of a ridged elytral margin and corresponding grooves on the hind femora. These modifications are not present in the other species in the genus, thus sound production in the adult appears to be an autapomorphy of this species that may be related to the larger size and threat display behavior.

## Chiasognathus impubis Parry, 1870

Figs 4, 16-17, 29
Chiasognathus impubis Parry, 1870: 68, original combination. Type material: Lectotype male (BMNH) designated by Chalumeau and Brochier (1995) labeled a) circular label "Mendoza"; b) handwritten on blue-gray paper "C. impubis Ph."; c) red circled label "Type"; d) bordered label "Bomansodus impubis ["93] / (Parry) / Det. F. Chalumeau \& B. Brochier." Paralectotype male (MNHN) labeled a) "impubis Parry, Chili / [ex. Musaeo E.D. Brown] / [ex. R. Oberthür]. Type locality: "Chili... Mendoza, on the eastern side of the Cordillera."

Description. Length: 24.5-34.5 mm. Width: 11.5-14.9 mm. Color: Reddish brown, everywhere with weak green or purple metallic reflections. Pronotum, head, and scutellum with stronger reflections. Head: Form subquadrate. Surface punctate; punctures fine to coarse, generally setose with short to long setae. Anterior margin of head sinuate, not strongly produced beyond anterior angles, lacking median nasus (anterior margin at middle rarely weakly binodose). Anterior angles obtusely rounded in dorsal view. Male mandibles cylindrical, $1.5-2 \times$ as long as head, externally almost straight until curving internally abruptly before apex. Dentate carina internally on dorsal mar-
gin only in basal half (in basal half variably reduced to $1-2$ teeth or low carina), becoming internal in apical half; additional dorsal tooth occasionally present near apex in male majors; apex not hooked upwards, lacking patch of setae. Base of mandibles lacking ventral tooth. Female mandible externally straight, dorsally flattened, with median internal tooth. Galeal brush elongate, $2-3 \times$ longer than mentum (except labial palps of females subequal to mentum). Antennal scape with sparse area of long setae present in males. Pronotum: Posterior and lateral angles dentate, lateral angle more strongly so in males. Lateral margins indistinct, often obsolete anteriorly (occasionally distinct in major males). Dorsal surface nearly evenly convex, not strongly ridged, longitudinal median furrow weak, weak depressions indicated either side of disc before middle in most specimens. Surface with distinct, moderately long setae in females, short setae in depressions and long setae along anterior margin in males. Elytra: Surface shiny, appearing smooth, actually densely punctate, weakly wrinkled, setose; setae scale-like, microscopic, often abraded; females with scattered longer bristle-like setae as on pronotum, bristles distinct macroscopically. Apex obtusely angulate, lacking spine. Epipleuron strongly concave. Legs: Protibiae elongate, serrate externally; ventral surface along internal margin with teeth well developed in males, lacking in females. Male genitalia: Flagellum long, length more than $3 \times$ length of parameres and basal piece together (Fig. 4).

Distribution. This species is distributed widely in central Chile (Fig. 29). Chalumeau and Brochier (2007) listed specimens from Lago Chapo and Llanquihue in Región X Los Lagos, but we did not examine any specimens from these localities.

CHILE (51): Biobío (7): "Arauco"; La Araucanía (44): Cherquenco, Cunco, Curacautín, Las Raíces, Lonquimay, Malalcahuello, Cordillera de Malleco, Manzanar, Nahuelbuta, Victoria; Villarrica. Los Ríos (1): "Valdivia". No data (2).

Temporal distribution. January (13), February (8), June (3), July (2), October (1), November (7), December (13).

Diagnosis. Males of this species can be distinguished by the shiny pronotum and elytra (Fig. 16) in combination with the apex of the elytron being angulate (not spinose or rounded). Often the lateral margin of the pronotum is obsolete in the apical half, but in larger males the margin may be distinct. The long male protibiae, long flagellum of the male genitalia, and the distinctly visible bristles scattered on the elytra of females (Fig. 17) will easily separate this species from C. latreillei.

Remarks. The identity of C. impubis is often incorrect in collections, and the species is generally treated as C. latreillei by commercial dealers and in Mizunuma and Nagai (2001). Based on examination of the lectotype, Chalumeau and Brochier (2007) correctly determined the identity of this species but placed it in their genus Bomansodus. The characters on which the genus are based are not robust, especially the effaced lateral margin of the pronotum, which is not consistently expressed even within the species. Furthermore, the shape of the protibiae, epipleuron, elytral margin, and mandibles of both sexes argue for a close relationship with C. mniszechii, and, to a lesser extent, C. grantii and C. jousselinii. Females of C. impubis are the only ones in the genus to have macroscopically visible scattered bristles on the elytra.


Figures 16-17. Dorsal habitus of $C$. impubis. 16 male, and 17 female.
Other species may have scattered bristles, but when present they can only be seen under magnification.

The lectotype was reported from "Chili... Mendoza, on the eastern side of the Cordillera" (Parry 1870), a somewhat nonsensical combination that could correspond to the area east of Volcán Chillán. This area is currently in Chile, but is depicted as being in Mendoza on maps dated slightly earlier (Greenleaf 1840). Ocampo and Paulsen (2008) followed Maes (1992) and listed the species from Argentina. While it is probable that the species occurs in eastern Neuquén Province, we do not know of any recent records of this species from Argentina.

## Cbiasognathus jousselinii Reiche, 1850

Figs 5, 18, 20, 22, 27
Chiasognathus jousselinii Reiche, 1850: 259, original combination. Type material: holotype male (MNHN) labeled: a) bordered label "Ex-Musæo / Mniszech"; b)
handwritten "Jousselini / Reiche"; c) handwritten "Chiazognathus / Jousselini"; d) "MUSÉUM PARIS / [2810]"; e) red paper, "TYPE"; f) handwritten "Chiasognathus. / jousselini . Reich. / Det: JP. LACROIX."; g) handwritten "Figure I. 1969 / JP. LACROIX."; h) bordered label "Southern Neotropical Scarabs / database \# AS2618225 / Chiasognathus jousselinii / Reiche, 1850 [male symbol] / DET: A.B.T. SMITH 2009"; i) red label "Chiasognatbus / jousselinii [male symbol] / Reiche, 1850 / HOLOTYPE / Det. M.J. Paulsen". The holotype was fixed by monotypy when Reiche (1850a, b) explicitly indicated that only one specimen was used to describe this species. Type locality: "versant oriental des Andes du Chili" (Reiche 1850b).

Description. Length: 22.0-33.9 mm. Width: 10.0-13.1 mm. Color: Reddish brown, with weak metallic reflections, appearing lighter from dense covering of light brown, scale-like setae. Head: Form subquadrate. Surface punctate; punctures fine to coarse, generally setose with short to long setae, especially laterally. Anterior margin of head roundly produced beyond anterior angles and with median nasus; nasus composed of 2 rounded teeth. Anterior angles obtusely rounded in dorsal view. Male mandible (Fig. 20) setose, cylindrical, robust, $2-3 \times$ as long as head, weakly rounded externally until abruptly, internally curved at apex; apex curved weakly upward, lacking patch of setae. Dentate carina with 4-10 obtuse teeth; teeth variably reduced, almost obsolete. Base of mandibles without ventral tooth. Galeal brush long, longer than first and second labial palpomeres combined. Antennal scape in males with sparse area of long setae at apex. Pronotum: Posterior and lateral angles subdentate (angulate in small males). Lateral margins distinct, crenulate. Disc with central area raised and with strong transverse ridge either side of broad median longitudinal depression; depressed areas variably setose, setae moderately long in males (shorter than length of distal antennomere of antennal club), lacking scattered longer setae. Elytra: Surface rough, slightly wrinkled, generally obscured by dense cover of short scale-like setae. Apex rounded to subdentate, lacking spine; elytral margin thickened, without bead. Epipleuron flat. Legs: Protibiae elongate, dentate basally with 4-6 small teeth (Fig. 18); ventral surface along internal margin with teeth well developed. Male genitalia: Flagellum moderately long, longer than length of parameres and basal piece together (Fig. 5). Females unknown.

Distribution. Only known from the west side of the Nahuelbuta Cordillera (Fig. 27).
CHILE (9): Biobío (5): Cañete, "Concepción". No data (4).
Temporal distribution. December (4). No data (5).
Diagnosis. This species can be readily distinguished from the other squamose species, C. mniszechii, by the shorter, more robust and less strongly dentate mandibles in males (Fig. 20), dentate rather than serrate protibiae (Fig. 18), flat epipleuron, pronotum lacking long scattered setae, and thickened elytral apices that lack a marginal bead apically. The flagellum of the male genitalia is nearly twice as long in C. jousselinii as it is in C. mniszechii (Figs 5-6). With only nine male specimens located in collections, the female of this species remains unknown.

Remarks. The fact that the holotype of C. jousselinii is clearly not conspecific with the more common C. mniszechii was recognized by Lacroix (1979), but this species has otherwise been confused with C. mniszechii (Krajcik 2001; Molino-Olmedo 2001, 2002; Chalumeau and Brochier 2007). The two species are easily separated when the appropriate characters are examined. Very few specimens of C. jousselinii are known, which has not helped to alleviate the confusion. We were able to study specimens graciously loaned by Alfredo Ugarte Peña that were collected in Cañete, and they


Figures 18-24. I8-I9 Right protibia of males. 18 C. jousselinii, and 19 C. mniszechii. Scale bar $=2 \mathrm{~mm}$. 20-21 Right mandibles of males. $\mathbf{2 0}$ C. jousselinii, and 21 C. mniszechii. Scale bar $=5 \mathrm{~mm} .22-24$ Dorsal habitus of Chiasognathus species. $\mathbf{2 2}$ C. jousselinii, male, $\mathbf{2 3}$ C. mniszechii, male, and $\mathbf{2 4}$ C. mniszechii, female.
remain the only specimens known with reliable locality information. It is likely that this species is restricted to the western side of the Nahuelbuta Cordillera, where other rarely encountered and potentially threatened stag beetles are also found: Pycnosiphorus franzae (Weinreich) and Hilophyllus penai (Martínez). Very little of this habitat is currently protected, and it is instead being logged at an alarming rate (Smith-Ramirez 2004). Thus, the future of these three species is in doubt, and their need for conservation should be studied in detail.

## Chiasognathus latreillei Solier, 1851

Figs 9, 11, 13, 30
Chiasognathus latreillei Solier, 1851: 42, original combination. Type material: Lectotype female (MNHN) labeled a) green circular label with underside " $15 / 43$ "; b) "MUSEUM PARIS / CHILI / GAY 15-43"; c) red letters "TYPE"; d) handwritten "Chiasognathus / rufpennis Latreillei / Gay-Sol."; e) "MUSÉUM PARIS / [Type. 290D.]"; f) bordered label "Southern Neotropical Scarabs / database \# AS2618224 / Chiasognathus latreillei / Solier, 1851 [female symbol] / DET: A.B.T. SMITH 2009"; g) red label "Chiasognathus / latreillei [female symbol] / Solier, 1851 / LECTOTYPE / Det. M.J. Paulsen". Lectotype designated by Chalumeau and Brochier (1995) by inference under ICZN Article 74.6 when they referred to the specimen as the holotype. Solier (1851) gave no definitive indication that there was only one specimen in the type series. Type locality: "Chile."
Chiasognathus imberbis R. Philippi in F. Philippi, 1859: 657. Type material: Lectotype male (MNNC) designated by Chalumeau and Brochier (1995) labeled a) handwritten "261."; b) "CH. [schönemanni] male symbol / \#2 det. J. Numhauser. VII1993 / genitalia dissect. J.N."; c) handwritten "Chiasognathus / imberbis PHIL. / dét. F. Chalumeau / \& B. Brochier '94"; d) red paper "LECTOTYPE"; e) "Chiasognathus latreillei / Solier / Dét. F. Chalumeau \& B. Brochier / ['94]; f) red, bordered label "Chiasognathus / imberbis / Philippi, 1859 [male symbol] / Lectotype / A.B.T. Smith. Two male paralectotypes (MNNC). Type locality: "Chile."

Chiasognathus reichei Thomson, 1862: 407. Type material: Lectotype male, HERE DESIGNATED (MNHN) labeled a) black-bordered "Th. / TYPE"; b) handwritten "Reichei / Type Thoms. / I, 1862 Chile"; c) "Ex-Musæo / JAMES THOMSON"; d) "MUSÉUM PARIS / [291D]; e) handwritten "Chiasognathus / latreillei Solier / Det: JP. Lacroix"; f) "Chiasognathus latreillei / Solier / Dét. F. Chalumeau \& B. Brochier ['94]"; g) red label "Chiasognathus reichei / Thomson, 1862 [male symbol] / LECTOTYPE / Det. M.J. Paulsen". The length was given as a range in the original description indicating that more than one specimen was used (Thomson 1862), thus the MNHN specimen is considered the lectotype. Type locality: "Chili."

Description. Length: 16.6-29.9 mm. Width: 8.4-13.0 mm. Color: Reddish brown with or without green, blue, or purple metallic reflections. Head: Form subquadrate.

Surface punctate; punctures fine to coarse, generally setose with short to long setae. Anterior margin of head rounded or concave, not strongly produced beyond anterior angles, with or without median nasus; nasus variable, unidentate or bidentate, frequently migrated below anterior margin of head. Anterior angles obtusely rounded in dorsal view. Male mandibles usually strongly narrowed to apex, $1.5-2 \times$ as long as head, externally almost straight until internally curved apex. Dentate carina beginning with basal tooth on dorsal surface, continuing with median teeth becoming internal; dorsal and ventral teeth usually absent either side of apex; apex lacking patch of setae. Base of mandibles with or without ventral tooth. Female mandible elongate, externally almost straight, dorsally flattened, with median internal tooth. Galeal brush short, less than $1.5 \times$ as long as mentum. Antennal scape with sparse area of long setae present in males, rarely only 1-2 setae present. Pronotum: Posterior and lateral angles subdentate or obsolete, rarely distinctly dentate. Lateral margins distinct, crenulate. Dorsal surface generally weakly defined with transverse ridge, broad longitudinal median furrow broad, and depressions indicated either side of disc before middle in most specimens. Surface near margins with distinct, moderately long setae and short bristles, glabrous in some males examined. Elytra: Surface weakly shiny, appearing wrinkled, densely punctate, setose; setae scale-like, often abraded except on lateral and apical elytral declivities; females lacking scattered longer bristle-like setae. Apex rounded, lacking spine. Epipleuron flat. Legs: Protibiae short, serrate externally; ventral surface along internal margin with 2-5 small to large teeth. Mesotibiae slender (Fig. 11). Male genitalia: Flagellum short, shorter than length of basal piece (Fig. 9).

Distribution. Central Chile and adjacent Argentina (Fig. 30).
ARGENTINA (48): Chubut (44): El Turbio, Los Alerces; Neuquén (3): Huahum, Lago Lolog; Río Negro (1): Llao Llao Península.

CHILE (37): La Araucanía (12): Caramavida, Cherquenco, Curacautín, Parque Nacional Huerquehue, Malleco, Volcán Llaima; Los Ríos (1): Parque Nacional Mocho Choshuenco; Los Lagos (22): Correntoso, Cucao, Hornohuinco, Lago Chapo, Llanquihue, Osorno, Parque Nacional Puyehue (Antillanca, Volcán Casa Blanca); No data (2).

Temporal distribution. January (9), February (5), April (1), October (43), November (8), December (11). No data (7).

Diagnosis. This species is not easy to characterize externally (Fig. 13) but can be best distinguished by the characters given in the key. The genitalia of all male specimens examined have a short flagellum (Fig. 9).

Remarks. The lectotype of C. latreillei is a female, and it is difficult to match with any of the eight females from known localities that are on hand. The male lectotype specimens of C. imberbis and C. reichei are both similar to more recent specimens from the Lago Chapo/Puyehue area based on mandibular form and overall coloration. However, the disparate dentition of the male mandibles with respect to disjunct localities in the specimens examined indicates this taxon may represent a complex of more than one cryptic species. More specimens from additional localities are necessary to get a better picture of the specific limits. The specimens examined from Llao Llao

Península (CASC), Caramavida (CASC), and Osorno (SMTD) exhibit enough variation to make their association with C. latreillei uncertain. Nothing is known about the life history of these beetles.

## Chiasognathus mniszechii Thomson, 1862

Figs 6, 19, 21, 23-24, 31
Chiasognathus mniszechii Thomson, 1862: 406, revised status. Type material: Lectotype male (MNHN) labeled: a) bordered label "Ex-Musæo / Mniszech"; b) bordered label "Th. / TYPE"; c) handwritten "Mniszechii / Type Thoms / 4.1862 Chili / [300]"; d) "MUSÉUM PARIS / [280D.]"; e) red paper, "TYPE"; f) "[1993] / Chiasognathus jousselinii / Reiche / Det: F. Chalumeau \& B. Brochier"; g) handwritten "Chiasognathus. / jousselini. Reich. / Det: JP. LACROIX."; h) bordered label "Southern Neotropical Scarabs / database \# AS2618226 / Chiasognathus mniszechii / Thomson, 1862 [male symbol] / DET: A.B.T. SMITH 2009"; i) red label "Chiasognathus / jousselinii [male symbol] / Thomson, 1862 / LECTOTYPE / Det. M.J. Paulsen". Lectotype designated by Chalumeau and Brochier (1995) by inference under ICZN Article 74.6 when they referred to the specimen as the holotype. Thomson (1862) gave no definitive indication that there was only one specimen in the type series. Type locality: "Chili."
Chiasognathus schoenemanni Kriesche, 1919: 94, new synonymy. Type material: Lectotype male (SMTD) designated by Chalumeau and Brochier (1995) labeled a) handwritten "Chile / Bader von Longavi, / Parral"; b) handwritten "Chiasognathus / schoenemanni / Cotyp!"; c) "sammlung KRIESCHE / Ankauf 1974"; d) red label "Typ"; e) "Staatl. Museum für / Tierkunde. Dresden"; f) bordered "[-93] / Chiasognathus / schoenemanni / dés. F. Chalumeau \& / B. Brochier"; f) "[-94] / Chiasognathus jousselinii / Reiche / Dét. F. Chalumeau \& B. Brochier". g) red label "Chiasognathus / schoenemanni [male symbol] / Kriesche, 1919 / LECTOTYPE / Det. M.J. Paulsen". Five paralectotype males (ZMHB).Type locality: "Chile, Bäder von Longavi, Parral."

Description. Length: 22.0-42.2 mm. Width: 10.7-14.8 mm. Color: Brown to reddish brown, with weak metallic reflections, appearing gray from dense covering of scale-like setae (Figs 23-24); setae variably abraded or greased. Head: Form subquadrate. Surface punctate; punctures fine to coarse, generally setose with short to long setae, especially laterally. Anterior margin of head roundly produced beyond anterior angles and with median nasus; nasus variable with two distinct or conjoined teeth or reduced to a single process, in females nasus migrated downward from anterior margin. Anterior angles obtusely rounded in dorsal view. Male mandible (Fig. 21) setose, cylindrical, narrow, $2-3 \times$ as long as head, externally sinuate until abruptly, internally curved at apex; apex curved weakly upward, lacking patch of setae. Dentate carina of 15-20 peg-like teeth beginning on dorsal margin in basal third (in basal third teeth
variably reduced to form low carina), becoming internal in median third, but dorsal again in apical third. Base of mandibles with acute ventral tooth; tooth occasionally obsolete. Female mandible as long as head, externally weakly rounded, dorsally flattened, with median internal tooth. Galeal brush short, shorter than first and second labial palpomeres combined. Antennal scape in males with sparse area of long setae at apex. Pronotum: Posterior and lateral angles obtusely angulate (rarely subdentate), posterior angle more strongly so in males, both angles almost obsolete in females. Lateral margins distinct, crenulate. Dorsal surface with strong transverse ridge either side of triangular median longitudinal furrow, weak depressions indicated either side of disc before middle in most specimens; furrow and depressions variably setose; setae short to long in males ( $3 \times$ longer than length of distal antennomere of club), short in females. Elytra: Surface rough, slightly wrinkled, generally obscured by dense cover of scale-like setae (especially in males). Apex subdentate, but lacking spine; elytral margin narrow, beaded. Epipleuron strongly concave. Legs: Protibiae elongate, serrate externally (Fig. 19); ventral surface along internal margin with teeth well developed in males, variably developed in females. Male genitalia: Flagellum short, shorter than length of parameres and basal piece together (Fig. 6).

Distribution. Central Chile and adjacent Neuquén, Argentina (Fig. 31).
ARGENTINA (2): Neuquén (2): Parque Nacional Lanín.
CHILE (60): Maule (1): Estero Leiva; Biobío (24): Atacalco, Cordillera Chíllan, Las Trancas, Pemehue; La Araucanía (35): Cherquenco, Cunco, Curacautín, Las Raíces, Manzanar.

Temporal distribution. January (6), February (32), March (1), December (23).
Diagnosis. This is the most commonly encountered species with dense, velvety pubescence on the elytra of males. If the scales are abraded, males of this species can still be recognized because they have narrower, more sinuate mandibles than the other species in the genus (Fig. 21). In addition, C. mniszechii differs from the other densely scaled species, C. jousselinii, in having the basal part of the protibiae serrate instead of dentate (Fig. 19), strongly concave epipleura, and a marginal bead on a narrow elytral margin apically.

Remarks. This species is one of the more commonly collected and widespread species in the genus, and it has been collected at mercury vapor lights. Because the species has for so long been incorrectly synonymized under C. jousselinii, all distributional records or information previously published for C. jousselinii (e.g., Benesh 1960; Ocampo and Paulsen 2008) is likely to apply instead to C. mniszechii.

## Chiasognathus sombrus Paulsen \& Smith, sp. n.

urn:lsid:zoobank.org:act:B61FBC6C-2A89-427C-BD90-59FBED9DB91B
Figs 7, 10, 25-26, 32
Type Material. Holotype male deposited at MNNC, labeled a) "CHILE: NUBLE PROV. / El Marchant / 26-XI-2004 / leg. Sergio Ocares"; b) red label "Chiasognathus /
sombrus (male symbol) / Paulsen \& Smith / HOLOTYPE." Allotype female deposited at MNNC, labeled a) "CHILE: REGÍON BIO-BIO / Prov. Nuble, El Marchant / 15-XI-2006 / leg. Sergio Ocares"; b) red label "Chiasognathus / sombrus (female symbol) / Paulsen \& Smith / ALLOTYPE." Two male paratypes (MNNC) same data as holotype. One male paratype (MNNC) labeled a) "Cord. Chillan / Las Trancas / 12.90 / coll. G. Moreno"; b) "Chiasognathus latreillei / Solier / Dét. F. Chalumeau \& B. Brochier / ['95]". Ten male, two female paratypes (JMEC, MJPC, UNSM) same data as allotype. Eleven male, three female paratypes (JMEC, MJPC, EPGC) labeled "CHILE, Región del Biobío, Las Trancas, 18-X-1998, leg. S. Ocares". Eight male paratypes (JMEC, MJPC, EPGC, BMNH) labeled "CHILE, Región del Biobío, El Marchant, 20-X-2006, leg. S. Ocares". Four male paratypes (JMEC) labeled "CHILE, Región del Biobío, El Marchant, 26-XI2004, leg. S. Ocares." One female paratype (JMEC) labeled "Chile, Región del Biobío, N̄uble, Los Lleuques, 13/10/2006, leg. S. Ocares". Four male paratypes (MJPC) labeled "CHILE REGIÓN BIO-BIO / Prov. Nuble, Atacalco / 12-X-2005 / leg. S. Ocares". One male paratype (MJPC) labeled a) "CHILE: Biobio / Chillan; X.2006"; b) orange label "DNA VOUCHER / P67 2009 / MJ PAULSEN - UNSM". One male paratype (LBC) labeled "CHILE - BIO BIO / OCTOBER 2004 / LEG. THOMSON". Six male paratypes (AUPC, ABTS) labeled "Las Trancas / Chillan / Enero- 1992 / leg. S. Figueroa". One male, three female paratypes (AUPC, ABTS) labeled "Las Trancas, / Chillan . XI-90". One female paratype (AUPC) labeled "Andes, Nuble / CHILE, Dec. 91". One female paratype (CASC) labeled "CHILE / Nubles / Nov. 91". Two male paratypes (SMTD) labeled a) "CHILI / NUBLE, CHILLAN / NOV. 1993 / LEG. PENA"; b) "Chiasognathus beneshi / Lacroix / Dét. F. Chalumeau \& B. Brochier / ['95]". One male paratype (SMTD) labeled as previous except "Dec. 1991". One male paratype (SMTD) labeled "CHILE / Nubles / Nov. 91". One male paratype (CMNC) labeled "CHILE: REGIÓN VIII (BIOBÍO) / Ñuble Prov., Atacalco / 20 October 2005, S. Ocares".

Description, holotype male (Fig. 25). Length: 30.7 mm. Widtb: 13.5 mm. Color: Dark reddish brown, pronotum with gold metallic reflections on disc, reflections becoming purple laterally and blue at margin; scutellum with greenish blue and purple metallic reflection; elytra with disc greenish brown due to weak green and purple metallic reflections, lateral margin with darker green reflection; head, mandibles at base, venter, and legs with green metallic reflection except tarsi, distal third of tibiae, and entire ventral surface of protibiae lacking metallic reflection. Head: Form almost semicircular. Surface punctate; punctures fine to coarse, some punctures with short setae. Anterior margin of head rounded, produced beyond rounded anterior angles, lacking median nasus. Mandibles almost $2 \times$ as long as head, externally rounded, robust (not flattened in lateral view); dentate carina on dorsal margin only in basal third, then continuing on internal face to below apex; teeth of carina variable along mandible with large basal tooth, large tooth in basal third, and 5 more or less conjoined teeth in apical half. Apex curved inwards, distally acute and hooked upwards, lacking patch of setae inside apex. Base of mandibles lacking ventral tooth. Galeal brush elongate, $2-3 \times$ longer than mentum. Scape without well-developed area of long setae. Right antennal club missing. Pronotum: Posterior angle strongly dentate, acute; lateral angle almost obsolete. Lateral margins distinct, weakly
crenulate. Dorsal surface with weak transverse ridge medially and distinct longitudinal median depression. Lateral fovea distinct, circular, impunctate. Elytra: Surface appearing rough macroscopically, not shiny, wrinkled on disc, punctate, setose; setae of 2 types: scattered bristle-like, erect setae and flattened, scale-like setae, scale-like setae apparently abraded except in rugae. Apex rounded. Epipleuron flat. Legs: Protibiae not elongate, dentate externally; ventral surface along internal margin with teeth weakly developed. Mesotibia thickened and appearing bent outwards at large external tooth (Fig. 10).

Description, allotype female (Fig. 26). Length: 28.1 mm. Width: 13.4 mm. Differs from holotype male in the following characters. Color: Metallic reflection dorsally muted except on scutellum at base. Head: Mandibles triangular with flat dorsal surface, densely punctate, with single internal tooth at distal third and internal margin bladelike in distal third. Pronotum: Posterior angles lacking tooth, lateral angles prominent.

Description, variation in paratype males. Length: 23.1-31.2 mm. Width: 11.4 13.3 mm . Differ from holotype male in the following characters. Head: Rounded anterior margin of head occasionally appearing weakly binodose. Mandibles with dorsal surface proximal to apex with additional weak tooth. Pronotum: Lateral angle variably developed from almost obsolete to distinct. Male genitalia: Flagellum moderately long, subequal in length to parameres and basal piece together (Fig. 7).


Figures 25-26. Dorsal habitus of C. sombrus, sp. n. $\mathbf{2 5}$ holotype male, and $\mathbf{2 6}$ allotype female. Scale bar $=5 \mathrm{~mm}$.


Figures 27-32. Distribution of Chiasognathus species. Regions of Chile and Provinces of Argentina indicated on Figure 32 as follows: VII Maule, VIII Biobío, IX La Araucanía, X Los Lagos, XI Aisén, XIV Los Ríos, Q Neuquén, R Rio Negro, U Chubut, Z Santa Cruz. All localities indicated with circles except for C. jousselinii (triangle). $\mathbf{2 7}$ C. beneshi, C. jousselinii $\mathbf{2 8}$ C. grantii $\mathbf{2 9}$ C. impubis $\mathbf{3 0}$ C. latreillei 31 C. mniszechii, and $\mathbf{3 2}$ C. sombrus.

Description, variation in paratype females. Length: $22.6-30.0 \mathrm{~mm}$. Width: $11.8-15.7 \mathrm{~mm}$. Female paratypes do not differ significantly from the allotype.

Distribution. The species is only known from Nuble Province, VIII Región del Biobío, Chile (Fig. 32).

CHILE (66): Biobío (66): Atacalco, "Chillán", El Marchant, Las Trancas, Los Lleuques, "Nuble".

Temporal distribution. October (29), November (28), December (2), January (6).
Diagnosis. This species is distinguished by its darker coloration, thickened and bent mesotibiae, and long galeal brush in both sexes. The scattered elytral bristles, although not distinct macroscopically, are more prominent in this species than in all others except C. impubis.

Remarks. This species was mistakenly treated as C. beneshi in Mizunuma and Nagai (2001) and Chalumeau and Brochier (2007). It has been referred to as C. schoenemanni in collections and by commercial dealers; however, examination of the holotype of $C$. schoenemanni revealed that name to be a synonym of $C$. mniszechii.

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# On Scaphidium grande-complex (Coleoptera, Staphylinidae, Scaphidiinae) 

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#### Abstract

The Scaphidium grande-complex is defined and six new species of the complex are described: S. longum sp. n. from Hainan Province, S. spinatum sp. n., from Anhui Province, S. laxum sp. n. and S. inflexitibiale sp. n. from Yunnan Province, $S$. reni sp. n., from Guizhou Province, and $S$. liui sp. n., from Xizang Autonomous Region. Their diagnostic characters are illustrated and a key to Scaphidium grande-complex is provided.


## Keywords

Coleoptera, Staphylinidae, Scaphidium grande-complex, new species

## Introduction

Scaphidium grande Gestro, 1880 is a common species widely distributed in south Asia. It can be easily distinguished from the thus far known congeners by its large body size, the strongly convex pronotum, and the black body with reddish fascia on mesofemora and metafemora. None of the previously described species was considered as closely related to S. grande.

Recently, we have examined many specimens of Scaphidium collected in China and, surprisingly, found six new species closely related to S. grande. Thus, Scaphidium grande forms with its allies, a monophyletic complex that is defined by the following characters: body large, length: 5.9-9.5 mm; body color: black, sometimes with faint blue luster; legs entirely black or with reddish fascia on the mesofemora and metafemora; antennal club broad, $11^{\text {th }}$ segment more or less asymmetric; head, pronotum, and elytra distinctly punctuate, elytra without clearly punctate rows (in rare case, blurry punctate rows can be found in S. grande); male metasternum with well developed setal patch; male pronotum more raised above elytra and relatively slightly longer than that of female; male protarsi without dense setae on ventral side, male protibiae more or less incurved with apical or/and subapical projections on inner side, male profemora without/with projection on inner side, tubercles present on both inner sides of protibiae and ventral sides of profemora; aedeagus with parameres slightly incurved, internal sac of median lobe with sclerites of characteristic structure.

The structure of internal sac is diagnostic in many taxa of the subfamily Scaphidiinae. In the Scaphidium grande-complex, it is composed of five parts (from apex to base): longitudinal bands, apical sclerotized rods, median sclerite, subbasal sclerite, and basal sclerotized plates. The longitudinal bands can usually be hardly observed in the aedeagi of Scaphidium, but they are very distinct in species of this complex, and even appear to be sclerotized. The shape of the apical sclerotized rods is less important for identification, since it is usually similar in different species and not clearly delimited. The median sclerite is trapeziform with sides curved or prominent in different degrees. The subbasal sclerite has a wing-like shape and is close to the basal sclerotized plates. The basal sclerotized plates are paired and spread out.

The Scaphidium grande-complex is possibly one of the more complicated groups in the genus. At present, only males can be identified. Detailed knowledge of the distribution of each species may also be helpful for identification, but presently the distribution gaps are too significant, as is evident from information given below. Scaphidium grande is a widely distributed species in South-east Asia and all its Chinese relatives seem to be endemic species restricted to mountain areas. Some species appear parapatric with S. grande, but the latter probably occurs only in lower altitudes. This may explain why so many members of the $S$. grande-complex remained hitherto unnoticed. It may be that additional species will be discovered with further field work, in particular in high mountains close to the Himalayas. A biogeographic analysis of the group will also likely provide interesting results but it considered premature at present.

## Material and methods

Specimens examined in this paper were collected in China by hand on decayed wood and fungi in deciduous forests and killed with ethyl acetate. For examination of male genitalia, the last two abdominal segments were detached from the body after softening in hot water. The aedeagus was separated, placed in glycerin in a cavity of plastic slide, and sealed by a glass slide. Photos of aedeagi were taken with an Olympus DP71

CCD attached to Olympus SZX 16 stereoscope; other photos were taken with a Cannon macro photo lens MP-E 65 mm attached to a Cannon EOS40D camera.

The following abbreviation is used for body measurements:
BL body length, measured from the anterior margin of clypeus to the apex of abdomen.
ED distance between eyes at narrowest point
FL length of male profemur
FW width of male profemur
PL length of pronotum along the median line
PW width of pronotum
The type material and additional material treated in this study are deposited in following localities:
HBUM Museum of Hebei University, P. R. China (G.-D. Ren)
SEM Shanghai Entomology Museum, the Chinese Academy of Science, P. R. China (X.-W. Liu)
SHNU Department of Biology, Shanghai Normal University, P. R. China (L. Tang)

## Results

## Key to the species of Scaphidium grande-complex

1. Mesofemora and metafemora black with reddish fascia ............................. 2

- Mesofemora and metafemora totally black without reddish fascia ............. 6

2 Distinctly elongated body form; male profemora slender (Fig. 22), FW/ FL=0.14. Habitus (Figs 4, 5), aedeagus (Figs 19, 20). BL: 7.5-9.9 mm. China (Hainan) S. longum

- Stout body form; male profemora stout, FW/FL >0.155............................ 3

3. Smaller body size, BL<7.4 mm; male profemora (Fig. 26) with an acute angle at apical third, protibiae (Fig. 26) with a blunt angle before apical angle. Habitus (Figs 6, 7), aedeagus (Figs 23, 24). 5.9-7.3 mm. China (Anhui)....S. spinatum

- Larger body size, BL>8.4 mm .................................................................... 4

4. Wider body form, PL/PW of male no more than 0.75 , PL/PW of female no more than 0.69 ; lateral sides of pronotum shallowly incurved near antebasal row of punctures; male protibia incurved 5

- Narrower body form, PL/PW of male: $0.79-0.84$, PL/PW of female: $0.75-$ 0.77; lateral sides of pronotum almost straight near antebasal row of punctures; male protibia (Fig. 18) almost straight. Habitus (Figs 1-3), aedeagus (Figs 14-16, also see Fig. 71 in Löbl, 1992 and Fig. 10 in He et al., 2008). BL: 8.4-9.4 mm. China (Yunnan, Guangxi, Guangdong, Fujian, Hunan, Guizhou, Sichuan, Chongqing, Hainan, Taiwan), Burma, India, Indonesia, Laos, Malaysia, Thailand, Vietnam
S. grande

5. Male profemora strongly swollen at basal $2 / 3$ forming a blunt angle at apical third, protibiae $=2.8 \mathrm{~mm}$ (Fig. 30). Habitus (Figs 8, 9), aedeagus (Figs 27, 28). BL: 8.9-9.4 mm. China (Yunnan)
S. laxum

- Male profemora not swollen, protibiae $=3.6 \mathrm{~mm}$ (Fig. 34). Habitus (Figs 10, 11), aedeagus (Figs 31, 32). BL: 10.1 mm . China (Yunnan) .... S. inflexitibiale

6. Last antennal segment (Fig. 41) light brown in about apical third. Habitus (Fig. 2 in He, 2009, regarded as S. dureli), aedeagus (Figs 39, 40). BL: $8.0-9.1 \mathrm{~mm}$. China (Xizang) S. liui

- Last antennal segment (Fig. 37) entirely blackish. Habitus (Figs 12, 13), aedeagus (Figs 35, 36). BL: 6.8-9.5 mm. China (Guizhou) ..................S. reni


## Scaphidium grande Gestro, 1880

Figs 1-3, 14-18

Scaphidium grande Gestro, 1879: 50; Pic, 1915: 3, 1920: 189; Achard, 1924: 91; Löbl, 1992: 488; He et al., 2008: 181.

Material examined. CHINA: Hainan: male, Wuzhishan City, Shuiman, 2325.V.2007, coll. Ba Yi-Bing \& Lang Jun-Tong (HBUM); female, Lingshui County, Diaoluoshan, 1100m, 29.III.1999, Zhou Wen-Yi leg. (SHNU); Taiwan: female, Xinzhu County, Jianshi, 13.VI.1993, coll. Chen Chang-Chin (SHNU); Yunnan: male, Menla, alt. 670m, 21.IV.1982, coll. Zhang Hong-Liang; male, Jinghong City, 11.VI.1973, coll. Jin Gen-Tao (NO. 24038143, SEM); male, Nabanhe N. R., Manfei, alt. 630 m, 29.VII.2005, coll. LI Jin-Wen \& LI Li-Zhen (SHNU); male and female, Menlun, Xipian, alt. $985 \mathrm{~m}, 1 . \mathrm{IV} .2009$, coll. Yin Zi-Wei (SHNU); male and female, Menla, Wangtianshu, alt. 600m, 5.IV.2009, coll. Yin Zhi-Wei (SHNU); Guangxi: male, Rong'an County, Xishan Forest Farm, Hongchagou, 26.VII.2006, coll. LI Li-Zhen (SHNU); female, Shangsi County, Pinglongshan, 6.IV.2002, alt. 350-500m, coll. Shi Ai-Ming (HBUM); Guangdong: male, Nanling N. R., Waterfall group, VII.2006, coll. Wang Zi-Chen (SHNU); male, Nanxiong City, Yuntan street, 3.V.2007, coll. Huang BaoPing (SHNU); Fujian: male, Yong'an County, Xiyang, 19.IV.1962, coll. JIN Gen-Yao (NO. 24110832, SEM); female, Fuzhou City, Shoushan, Beifeng, V.2004, coll. Li Min (SHNU); female, Wuyishan, 27.V.2002, Li Li- Zhen leg. (SHNU); Hunan: female, Tongdao County, Shangyan, 24.VII.2004, coll. Wang Ji-Liang (HBUM); Guizhou: Fanjingshan, Heiwan Reiver, 800m, 3.VIII.2001, Ma jing leg. (SHNU); Sichuan: female, Luding, Moxi, alt. 1300m, 20.V.2009, He Wen-Jia leg. (SHNU); Chongqing: male, Jiangjin, Simianshan, 10.VII.2005, coll. Zhang Wei-Wei (SHNU).

BL: $8.4-9.4 \mathrm{~mm}$, ED: $0.23-0.26 \mathrm{~mm}$, PL/PW of male: $0.79-0.84$, PL/PW of female: 0.75-0.77.

Body black and glossy, mesofemora and metafemora with reddish fascia. Frons densely punctuate with an impunctate portion on vertex, punctures mostly elongate and slightly confluent. Pronotum raised above elytra, with lateral edges slightly sinu-


Figures I-5. Adult habitus of Scaphidium. I-3 S. grande 4, $\mathbf{5}$ S. longum. Scales $=1 \mathrm{~mm}$.
ate. Antebasal row of punctures impressed; disc densely punctuate, punctures round and well delimited, puncture intervals mostly a little larger than diameters. Elytra with humeral protuberance indistinct, apical portion moderately impressed; discal punctation similar to that of pronotum, punctures on apical portion slightly larger; discal row of punctures absent; basal stria row impressed, with punctures about as coarse as those of pronotal antebasal row; sutural stria row of punctures relatively fine. Prohypomera smooth with very fine and sparse punctures mainly on outer half. Mesepisterna smooth with moderately dense, moderately fine, and very shallow punctures. Exposed abdominal sternites and tergites with coarse and relatively sparse punctures and densely reticulate microsculpture. Legs long, mesotibiae and metatibiae slightly curved.

Male. Metasternum impressed in middle, with long semi-erect pubescence. Profemora (Fig. 18) with tubercles arranged in three rows on ventral side. Protibiae (Fig. 18) slightly incurved with a small apical angle and tubercles on inner side. Variation of internal sac of aedeagus as in Figs 14-16.

Distribution. China (Yunnan, Guangxi, Guangdong, Fujian, Hunan, Guizhou, Sichuan, Chongqing, Hainan, Taiwan), Burma, India, Indonesia, Laos, Malaysia, Thailand, Vietnam.

Diagnoses. This is a rather variable species, especially in body size and punctuation (Löbl 1992). Among the material we examined was one male from Hainan Prov. with three blurry rows of puncture consisting of coarse punctures.

Scaphidium longum Tang \& Li, sp. n.
urn:lsid:zoobank.org:act:B319E6AD-2948-454E-84DE-BC9B76FBB269
Figs 4, 5, 19-22
Type material. Holotype. China: Hainan: male, glued on a board with labels as follows: "China, Hainan, Limu Shan, alt. 800m, 20.IV.2009, Zhu Xiao-Yu leg." "Holotype / Scaphidium longum / Tang \& Li"[red handwritten label] (SHNU). Paratypes. 9 males and 10 females, alt. 800m, 20.IV.2009, Zhu Xiao-Yu leg. (SHNU)

BL: $7.5-9.9 \mathrm{~mm}$, ED: $0.31-0.39 \mathrm{~mm}$, PL/PW of male: $0.82-0.86$, PL/PW of female: 0.77-0.80.

Similar to $S$. grande in most respects, but differs in the following characters: body form distinctly elongate; pronotum more convex; antennal club (Fig. 21) slenderer; male metasternum with larger setal patch; punctation of pronotum slightly finer and sparser; male profemora (Fig. 22) longer and slenderer, tubercles smaller; male protibiae (Fig. 22) longer and more incurved with a small subapical expansion and an apical angle on inner side; internal sac of aedeagus as in Figs 19, 20.

Diagnoses. This species can be easily distinguished from other related species by the elongate body.

Etymology. The Latin adjective "longum" refers to the elongate body and male legs of the new species.

Biological notes. All specimens were collected from a log covered with white fungus (Fig. 43). Territorial behavior of the male was observed by the collector, and it was described as follows: Each male occupies a small area on the fungi. Normally they highly raise bodies upon their long legs and they can shake their bodies up and down rapidly. Once, a small male was too close to a large one, the large male rushed to it immediately and the small male retreated quickly, without having body contact.

## Scaphidium spinatum Tang \& Li, sp. n.

urn:lsid:zoobank.org:act:8943975D-58F1-4FD0-825D-C0FD1E29A77E
Figs 6, 7, 23-26

Type Material. Holotype. China: Anhui: male, glued on a board with labels as follows: "Yuexi Couty, Yaoluoping Village, 17.VII.2007-4.VIII.2007, coll. Ba Yi-Bing, Lang Jun-Tong \& Wang Feng-Yan ""Holotype / Scaphidium spinatum / Tang \& Li"


Figures 6-9. Adult habitus of Scaphidium. 6, 7 S. spinatum 8,9 S. laxum. Scales $=1 \mathrm{~mm}$.
[red handwritten label] (HBUM). Paratypes. 6 males, 12 females, same data as for the holotype (male, female in SHNU, rest in HBUM).

BL: $5.9-7.3 \mathrm{~mm}$, ED: $0.27-0.32 \mathrm{~mm}$, PL/PW of male: $0.78-0.80$, PL/PW of female: 0.75-0.79.

Similar to $S$. grande in most respects, but differs in the following characters: antennal club (Figs 25) relatively stouter; most punctures on head well delimited, connected by weakly confluent traces; apical portion of elytra indistinctly impressed; male profemora (Figs 26) with inner side expanded gradually from base forming an acute angle at apical third, tubercles smaller and sparser; male tibiae (Figs 26) with two widest points forming a blunt and a sharp angle on inner side at about apical $1 / 5$ and apical end respectively; internal sac of aedeagus as in Figs 23, 24.

Distribution. China (Anhui).

Diagnoses. This species can be easily distinguished from other member of the species complex by its small body size.

Etymology. The Latin adjective "spinatum" refers to the spined male profemora of the new species.

Biological notes. All specimens were collected from a log covered with fungi.

Scaphidium laxum Tang \& Li, sp. n. urn:lsid:zoobank.org:act:4A4DCB65-F331-4D60-82DB-ECBD517ED629
Figs 8, 9, 27-30

Type Material. Holotype. China: Yunnan: male, glued on a board with labels as follows: "China, Yunnan, Nabanhe N. R., Benggangxinzhai, alt. 1750 m, 3.V.2009, Hu Jia-Yao \& Yin Zi-Wei leg" "Holotype / Scaphidium laxum / Tang \& Li" [red handwritten label] (SHNU). Paratype. female, same as for the holotype. (SHNU)

BL: 8.9-9.4 mm, ED: $0.33-0.35 \mathrm{~mm}$, PL/PW of male: 0.75 , PL/PW of female: 0.69 .

Similar to $S$. grande in most respects, but differs in the following characters: body form slightly wider, posterior-lateral angles of pronotum more prominent; male profemora (Figs 30) with inner side expanded gradually from base to form a blunt angle at apical third, tubercles smaller and sparser; male tibiae (Figs 30) more incurved; internal sac of aedeagus as in Figs 27, 28.

Etymology. The Latin adjective "laxum" refers to the broad body form of the new species.

Biological notes. Specimens were collected from a log covered with white fungi while mating (Fig 44).

Scaphidium inflexitibiale Tang \& Li, sp. n. urn:lsid:zoobank.org:act:6795EADC-717B-4025-8826-F5D69F740FFF
Figs 10, 11, 31-34
Type Material. Holotype. China: Yunnan: male, glued on a board with labels as follows: "China, Yunnan, Hekou, Yaoshan, N22́49'435", E $103^{\circ} 44^{\prime} 611^{\prime}$ ", alt. 1345 m , 22.VII.2006, Huang Hao leg. " "Holotype / Scaphidium inflexitibiale / Tang \& Li" [red handwritten label] (SHNU).

BL: $10.1 \mathrm{~mm}, \mathrm{ED}: 0.33 \mathrm{~mm}, \mathrm{PL} / \mathrm{PW}$ of male: 0.75 .
Similar to S. grande in most respects, but differs in the following characters: body form slightly wider, posterior-lateral angles of pronotum more prominent; male profemora (Figs 34) longer, tubercles smaller, ventral row of tubercles indistinct; male tibiae (Figs 34) longer and more incurved; internal sac of aedeagus as in Figs 31, 32.

Etymology. The specific name is a combination of the Latin words "inflexi" and "tibia" referring to the incurved male tibia.


Figures I0-I3. Adult habitus of Scaphidium. IO, II S. inflexitibiale II, I2 S. reni. Scales $=1 \mathrm{~mm}$.

Scaphidium reni Tang \& Li, sp. n.
urn:lsid:zoobank.org:act:B307CAE3-DBDF-40D1-93F8-29FCA873FE79
Figs 12, 13, 35-38
Type Material. Holotype. CHINA: Guizhou: male, glued on a board with labels as follows: "China, Guizhou, Leigongshan N. R., Lianhuaping, alt. 1550-1680m, 13-14.IX.2005, coll. Zhou Zhong-Hui" "Holotype / Scaphidium reni / Tang \& Li" [red handwritten label] (SHNU). Paratypes. CHINA: Guizhou: 6 males, 4 females, Leigongshan N. R., Linchang, 13-14.IX.2005, coll. Liu Hao-Yu, Wang Ji-Liang \& Gao Chao (male, female in SHNU, rest in HBUM).


Figures 14-22. I4-I8 Scaphidium grande 19-22 S. longum. $\mathbf{1 4}$ aedeagus (Yunnan) $\mathbf{1 5}$ internal sac in detail (Hainan) $\mathbf{1 6}$ internal sac in detail (Fujian) $\mathbf{1 7}, \mathbf{2 1}$ antenna 18,22 male front leg in ventral view $\mathbf{1 9}$ aedeagus $\mathbf{2 0}$ internal sac in detail. Scales $=0.25 \mathrm{~mm}(\mathbf{I 4 - 1 6}, \mathbf{1 9}, \mathbf{2 0})$, scales $=1 \mathrm{~mm}(\mathbf{I 7}, \mathbf{1 8}, \mathbf{1 9}, \mathbf{2 0})$.

BL: $6.8-9.5 \mathrm{~mm}$, ED: $0.29-0.37 . \mathrm{mm}, \mathrm{PL} / \mathrm{PW}$ of male: $0.76-0.79$, PL/PW of female: 0.72-0.75.

Similar to S. grande in most respects, but differs in the following characters: mesofemora and metafemora black without reddish fascia; body form a little wider; male profemora (Figs 38) with smaller tubercles; male tibiae (Figs 38) more incurved; internal sac of aedeagus as in Figs 35, 36.

Distribution. China (Guizhou).
Diagnoses. Scaphidium reni is extremely similar to the following new species $S$. liui; for differences see description of the latter. This species may be easily distinguished from other members of grande-complex by mesofemora and metafemore totally black without reddish fascia.


Figures 23-30. 23-26 Scaphidium spinatum 27-30 S. laxum. 23, $\mathbf{2 7}$ aedeagus 24, $\mathbf{2 8}$ internal sac in detail 25, 29 antenna 26, $\mathbf{3 0}$ male front leg in ventral view. Scales $=0.25 \mathrm{~mm}(\mathbf{2 3}, \mathbf{2 4}, \mathbf{2 7}, \mathbf{2 8})$, scales $=$ $1 \mathrm{~mm}(\mathbf{2 5}, \mathbf{2 6}, \mathbf{2 9}, \mathbf{3 0})$.

Etymology. This species is named in honor of Prof. Dr. Ren Guo-Dong, who kindly provided specimens of Scaphidium.

Scaphidium liui Tang \& Li, sp. n.
urn:Isid:zoobank.org:act:940ED9AD-9D44-444F-9628-7384469AE8D6
Figs 39-42
Type Material. Holotype: CHINA: Xizang: male, glued on a board with labels as follows: "Xizang, Motuo County, Yadong, alt. 1250m, 25.V.1980, coll. Jin Gen-Tao \& Wu Jian-Yi " "NO. 24205538 " "Holotype / Scaphidium liui / Tang \& Li" [red


Figures 3I-38. 3I-34 Scaphidium inflexitibiale 35-38 S. reni. 3I, $\mathbf{3 5}$ aedeagus 32, $\mathbf{3 6}$ internal sac in detail 33, $\mathbf{3 7}$ antenna $\mathbf{3 4}, \mathbf{3 8}$ male front leg in ventral view. Scales $=0.25 \mathrm{~mm}(\mathbf{3 I}, \mathbf{3 2}, \mathbf{3 5}, \mathbf{3 6})$, scales = $1 \mathrm{~mm}(33,34,37,38)$.
handwritten label] (SEM). Paratypes. CHINA: Xizang: female, Motuo Couty, Kabu, 1070m, 14.V.1980, coll. Jin Gen-Tao \& Wu Jian-Yi (NO. 24205537, SEM).

BL: $8.0-9.1 \mathrm{~mm}$, ED: $0.36-0.40 \mathrm{~mm}, \mathrm{PL} / \mathrm{PW}$ of male: 0.79 , PL/PW of female: 0.76 .

Extremely similar to S. reni sp. n., differing only in the following characters: body form slightly narrower; last antennal segment light brown in about apical third; apical portion of elytra indistinctly impressed; internal sac of aedeagus as in Figs 39, 40.

Distribution. China (Xizang).
Diagnoses. This new species was wrongly recorded as S. dureli Achard, 1922 in He et al., 2009. Scaphidium dureli is now known only from the type locality "British


Figures 39-42. Scaphidium liui. $\mathbf{3 9}$ aedeagus $\mathbf{4 0}$ internal sac in detail $\mathbf{4 I}$ antenna $\mathbf{4 2}$ male front leg in ventral view. Scales $=0.25 \mathrm{~mm}(\mathbf{3 9 , 4 0})$, scales $=1 \mathrm{~mm}(\mathbf{4 1}, 42)$.


Figures 43, 44. 43 Host fungus of S. longum (Photo by Mr. Zhu Xiao-Yu) 44 S. laxum mating on a log with fungi (Photo by Mr. Hu Jia-Yao).

Bootan Padong". It can be easily distinguished from members of the S. grande-complex by the last antennal segments being entirely ochreous and by the absence of sexual characters on the male profemora.

Etymology. This species is named in honor of Prof. Liu Xian-Wei who kindly provided the Scaphidium specimens.

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