Zootaxa 1063: 53–68 (2005)
www.mapress.com/zootaxa/

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

1063

The Neotropical caddisfly genus *Tolhuaca* (Trichoptera: Glossosomatidae)

DESIREE R. ROBERTSON & RALPH W. HOLZENTHAL

University of Minnesota, Department of Entomology, 1980 Folwell Ave., Room 219, St. Paul, Minnesota 55108, U.S.A. (robe0494@umn.edu; holze001@umn.edu)

ABSTRACT

The caddisfly genus *Tolhauca* Schmid 1964 (Glossosomatidae: Protoptilinae) is diagnosed and discussed in the context of other protoptiline genera, and a review of its taxonomic history is provided. A new species, *Tolhuaca brasiliensis*, from southeastern Brazil, is described and illustrated, and the type species, *Tolhuaca cupulifera* Schmid 1964, from Chile, is redescribed and illustrated. Additionally, females of the genus are described and illustrated for the first time. Characters of the female genitalia, wing venation, and thorax suggest that *Tolhuaca* is more primitive than any other protoptiline genus and probably deserves a basal placement within the subfamily. The genus shows a broadly disjunct distribution perhaps reflecting an ancient southern Gondwana pattern.

Key words: Trichoptera, Glossosomatidae, Protoptilinae, *Tolhuaca*, new species, caddisfly, male genitalia, female genitalia, Neotropics, Southern Cone, Chile, Brazil, phylogeny, biogeography

INTRODUCTION

The genus *Tolhuaca* Schmid 1964, belongs to the saddle-, or tortoise-case making caddisfly family Glossosomatidae. The family contains approximately 500 species worldwide and consists of 3 subfamilies: Agapetinae (~200 spp.), Glossosomatinae (~100 spp.), and Protoptilinae (~200 spp.). Members of the subfamily Protoptilinae, to which *Tolhuaca* belongs, are very minute (1.5–6 mm) and were originally thought to belong to the family Hydroptilidae, the microcaddisflies. Following Mosely's (1937) suggestion, Ross (1938) transferred *Protoptila* Banks 1904, the first genus to be described in the protoptiline group, to Glossosomatinae, at that time a subfamily within Rhyacophilidae. Mosely (1954) later added to the protoptiline group by transferring *Antoptila* Mosely 1939 (junior synonym of *Itauara* Müller 1888), *Canoptila* Mosely 1939, *Culoptila* Mosely 1954, *Mexitrichia* Mosely 1937, and *Mortoniella* Ulmer 1906 from Hydroptilidae, and

Accepted by Z.-Q. Zhang: 28 Sept. 2005; published:14 Oct. 2005

expressed his inclination to form a new subfamily within the Rhyacophilidae to contain these "kindred genera." Consequently, Ross (1956) elevated the "*Protoptila* group" to subfamily status within the family Glossosomatidae.

The subfamily Protoptilinae currently contains 18 genera and has a rather disjunct distribution: 4 genera are restricted to the East Palaearctic and Oriental regions; the remaining genera occur in the Nearctic and Neotropical regions. It is in the Neotropics where the subfamily reaches its greatest diversity, and also exhibits a high degree of endemism at both the genus and species levels (Flint et al. 1999). The Southern Cone region of South America (Argentina, Chile, Uruguay, Paraguay, and Southern Brazil) includes 6 endemic protoptiline genera, among them, *Tolhuaca*.

Until now, the genus *Tolhuaca* contained a single species, *T. cupulifera* Schmid 1964, known only from Chile. A new species, including a female, is now described from southeastern Brazil as a result of a recent survey of that fauna by researchers and students at the University of Minnesota. In addition, *T. cupulifera* is illustrated and redescribed, and a description of the female is provided for the first time.

MATERIALS AND METHODS

Morphological terminology used in this paper for male and female genitalia follows that of Holzenthal (2004) and Nielsen (1980), respectively. For setal warts of the head and thorax, we use the terminology of Wiggins (1996). Terminology for wing venation follows that of Schmid (1998). Procedures for the preparation, examination, and illustration of important taxonomic structures, and construction of species descriptions, followed those outlined in detail by Holzenthal and Andersen (2004). Georeference data (longitude & latitude) for older specimens collected by L.E. Peña was obtained by searching specimen localities through the Alexandria Digital Library Gazetteer (2005). A list of all material examined during this study as well as taxonomic, locality, collection, and individual specimen barcode information can be accessed and downloaded from the University of Minnesota Insect Collection (UMSP) Trichoptera Holdings Biota® database, www.entomology.umn.edu/museum/databases/BIOTAdatabase.html.

Types of the species described in this paper and other material examined are deposited at the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (NMNH), the Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil (MZUSP), and the University of Minnesota Insect Collection, Saint Paul, Minnesota, USA (UMSP) as indicated in the species descriptions.

Position of *Tolhuaca* within the subfamily Protoptilinae

Schmid (1964) originally placed *Tolhuaca* in the family Sericostomatidae, commenting on the similarity of the bifid tergum X of the male genitalia to that of Brachycentridae, at that time a subfamily within Sericostomatidae. Flint (1967) later transferred *Tolhuaca* to Protoptilinae upon discovery that the wing figures in the original description were mislabelled with those of *Austrocentrus griseus* Schmid 1964 (Helicophidae). Since that time, there has been nothing published regarding the placement of *Tolhuaca* in relation to the other protoptiline genera.

When Schmid (1964) first described the genus he wrote, "Dans l'état actuel de nos connaissances, il est impossible d'assigner une position phylétique au genre *Tolhuaca*, dont la nervulation assez complète, surtout aux ailes antérieures, contraste avec l'extrême simplification et spécialisation des génitalia…" ["In the current state of our knowledge, it is impossible to assign a phyletic position to the genus *Tolhuaca*, whose rather complete venation, especially in the forewings, contrasts with the extreme simplification and specialization of the genitalia…" Translation from Schmid (1964)]. The male genitalia (Figs. 5A, 7A) have completely lost both the inferior and preanal appendages, and sternum IX has been reduced to nothing more than a thin, ventral strap. The phallic apparatus (Figs. 5A, 5D, 5F, 7A, 7D) consists of a greatly enlarged, but simple tubular phallobase, and an eversible membranous endotheca. These apparently derived conditions of the male genitalia contrast with other features that imply a basal placement of *Tolhuaca* within Protoptilinae.

Published works regarding protoptiline phylogeny are few and far between. Morse and Yang (1993) discussed some genera from the East Palaearctic and Oriental regions, and also provided a very useful table comparing wing venation among 15 recognized genera. Ross (1956) provided an early discussion of possible phylogenetic relationships among protoptiline genera and considered the genus *Matrioptila* Ross 1956 to be most primitive based on characteristics of the male genitalia and wing venation. In *Matrioptila*, segment IX is complete and ringlike, tergum X consists of a pair of simple lobes, and inferior appendages are present. Forewing veins Cu1 and Cu2 are often fused in Protoptilinae, but in *Matrioptila*, they are separate and distinct along their entire lengths and in the hind wing, Cu1 is branched. These genitalic and venational characters are primitive according to Ross (1956). Kimmins (1964) described a new genus, *Nepaloptila*, from Nepal and placed it in Protoptilinae. The genus shares some characteristics of the male genitalia with *Matrioptila*, but Kimmins (1964) considered *Nepaloptila* to be more primitive, based on its retention of apical fork V in the forewing, which is usually absent in other Protoptilinae. The venation of *Tolhuaca* (Figs. 3, 4) is quite similar to that of *Nepaloptila* (Kimmins 1964), differing only slightly. In *Tolhuaca*, Sc is distinct from R1 in the forewing, whereas in *Nepaloptila*, Sc and R1 are fused near the wing margin. The 2

genera also differ in the position of crossveins in the forewing: those of *Tolhuaca* form a relatively straight transverse cord along the anastomosis whereas in *Nepaloptila*, they do not. In the hind wing, A2 is present in *Tolhuaca*, but absent in *Nepaloptila*.

Although *Tolhuaca* would seem to have more specialized male genitalia than *Nepaloptila* and *Matrioptila*, other characters suggest *Tolhuaca* is the more primitive genus. In *Nepaloptila* and *Matrioptila*, the foretibial spur has been lost, whereas in *Tolhuaca*, although reduced considerably, the spur is retained (Fig. 2). The genus *Tolhuaca* also has two small setal warts on the mesoscutellum (Fig. 1), which Ross (1956) considered to be primitive; these warts are absent in all other known protoptilines. The female genitalia (Figs. 6, 8) consist of an elongate oviscapt and 2 pairs of long, rod-like apodemes on segments VIII and IX. The presence of these apodemes is pleisiomorphic within Amphiesmenoptera (Kristensen 1984). The retention of the foretibial spur, presence of mesoscutellar setal warts, and the structure of the female genitalia suggest that *Tolhuaca* deserves a basal placement within the subfamily Protoptilinae.

Diagnosis of the genus *Tolhuaca* Schmid

Tolhuaca Schmid, 1964:336 [Type species: *Tolhuaca cupulifera* Schmid 1964, original designation].

Tolhuaca is most similar in wing venation to the genus *Nepaloptila* Kimmins 1964, differing only slightly. In the forewing of *Tolhuaca* Sc is distinct from R1, whereas in *Nepaloptila*, Sc and R1 are fused near the wing margin. The 2 genera also differ in the position of the forewing crossveins: those of *Tolhuaca*, although faint, form a relatively linear transverse cord at the anastomosis; in *Nepaloptila*, the crossveins do not form a line. The hind wing venation of the 2 genera is quite similar as well, each with apical forks II, III, and V present, and differ only in that *Tolhuaca* has retained the A2 vein, while *Nepaloptila* has lost A2. The male genitalia of *Tolhuaca* are slightly similar to *Culoptila* Mosely 1954, in that both genera have a reduced sternum IX, but the 2 genera can be distinguished from each other based on their venation, shape of the sternum VI process, and numerous other characters.

Adult. Forewing length: male 2.7–5.0 mm, female 2.7–5.3 mm. Body, wings, and appendages nearly uniformly fuscous; tibia and tarsi yellowish brown; forewing with erect or retrorse setae along some veins, most noticeably along Cu2. Head (Fig. 1) broader than long, vertex rounded, with pair of small distinct anteromesal setal warts, elongate anterior setal warts, suboval posterior warts, and large subtriangular posterolateral setal warts. Ocelli present. Scape short, but longer than wide. Maxillary palps 5 segmented, 1st and 2nd segments short with elongate setae apically; 2nd segment bulbous; last 3 segments each nearly same length as 1st and 2nd segments combined. Prothorax (Fig. 1) with 2 large subtriangular pronotal setal warts; mesoscutum with 2 pairs of setal warts, elongate

anteromesal pair and smaller oval posterolateral pair; mesoscutellum with pair of small, round, yet distinct setal warts. Forewing (Figs. 3A, 4A) relatively narrow or broad beyond anastomosis, apex rounded. Forewing venation complete; Sc and R1 distinct along their entire lengths; Cu1 and Cu2 distinct along their entire lengths; Cu1 thick in relation to M; A3 looped and intersecting A2; crossveins *r*, *d*, *r-m*, and *m-cu* present, forming a relatively linear transverse cord. Hind wing (Figs. 3B, 4B) narrow or broad; forks II, III, and V present; Sc and R1 either fused basally or converging near wing margin. Tibial spurs 1,4,4, foretibial spur extremely reduced and hairlike (Fig. 2).

Male genitalia extremely simple (Figs. 5, 7). Sixth sternal process associated with oblique apodeme posteriorly. Preanal and inferior appendages absent. Abdominal segment IX well developed dorsally and laterally but extremely reduced ventrally, forming very thin sclerotized ring; anterior margin rounded. Membranous connection between segments IX and X distinct. Tergum X roof-like, excavate apicomesally, setose apically; ventrally with mesal or apicomesal processes. Phallobase large and tubular or bulbous, with apicodorsal projection, lightly sclerotized, diminishing to membrane posteroventrally, with small, stout setae; endotheca membranous and greatly enlarged when evaginated, with sclerotized structures internally.

Female genitalia (Figs. 6, 8) elongate and tubular, with 2 pairs of rod-like internal apodemes, with apparent insertion points near anterior margin of tergum IX and posterior margin of segment VIII and extending anteriorly; pair of thin, short, apodemes apparently inserted at anterior margin of tergum IX and extending posteriorly to segment X. Sternum V with slightly raised, sclerotized linear ridge. Sixth sternal process associated with oblique apodeme. Abdominal segment VIII synscleritous. Segment X digitate or bulbous, bearing cerci.

SPECIES DESCRIPTIONS

Tolhuaca cupulifera Schmid

Figs. 1–3, 5, 6

Tolhuaca cupulifera Schmid, 1964: 337 [Type locality: Chile, Pichinahuel, Arauco; NMNH; male; in Sericostomatidae]. –Flint 1967:52 [correction of transposition of wing figures in original description; to Glossosomatidae, Protoptilinae; distribution].

Tolhuaca cupulifera can be distinguished from *T. brasiliensis*, new species, by the presence of sclerotized, conical, thorn-like spines in the endotheca. Tergum X is also much more excavate apicomesally, while it is shallowly excavate in the new species, *T. brasiliensis*. Tergum X is triangular in lateral view in *T. cupulifera* and quadrate in *T. brasiliensis*. The wings of *T. cupulifera* are broader than the wings of *T. brasiliensis.* The species is known only from Chile.

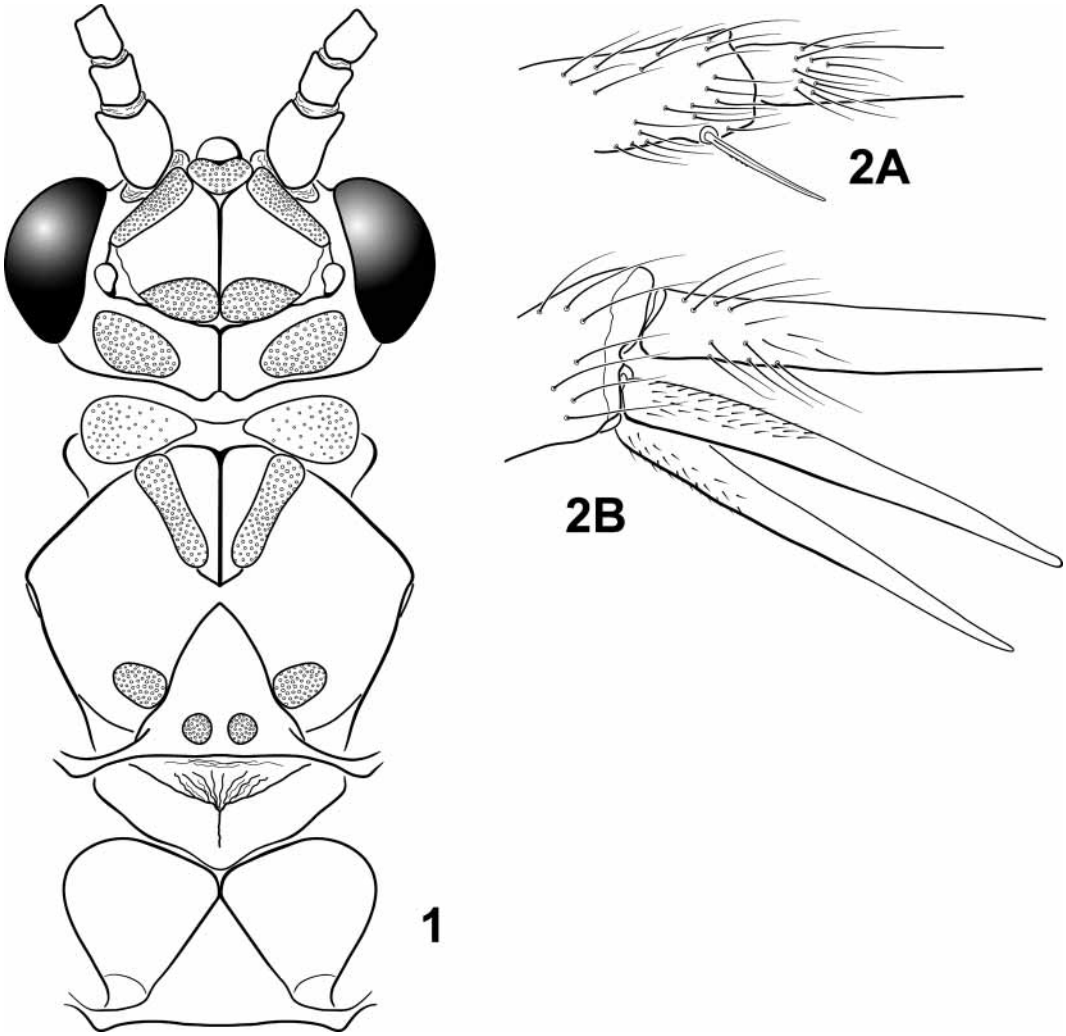

FIGURE 1. *Tolhuaca cupulifera.* Adult: dorsal view of head and thorax.
FIGURE 2. *Tolhuaca cupulifera.* Adult: A—foretibial spur; B—mesotibial spurs, at same scale for comparison.

Adult. Length of forewing: male 4.7–5.0 mm (n=5); female 5.0–5.3 mm (n=3). Body, wings, and appendages nearly uniformly fuscous, tibia and tarsi yellowish brown. Forewing (Fig. 3A) relatively broad, apex blunt; with retrorse setae along veins; Sc incomplete, not reaching anterior margin; fork I emerging at or immediately beyond cord; fork II emerging anteriorly to cord; forks III and IV longer than their stems; A3 forming short loop, intersecting A2 basally; crossveins *r*, *d*, *r-m*, and *m-cu* present, forming a relatively straight line, but with *m-cu* slightly basal to cord. Hind wing (Fig. 3B) relatively broad; Sc converging with R1 near wing margin; fork II about 4 times longer than its stem; fork III longer than its stem; crossveins *r*, *r-m*, and *m-cu* present.

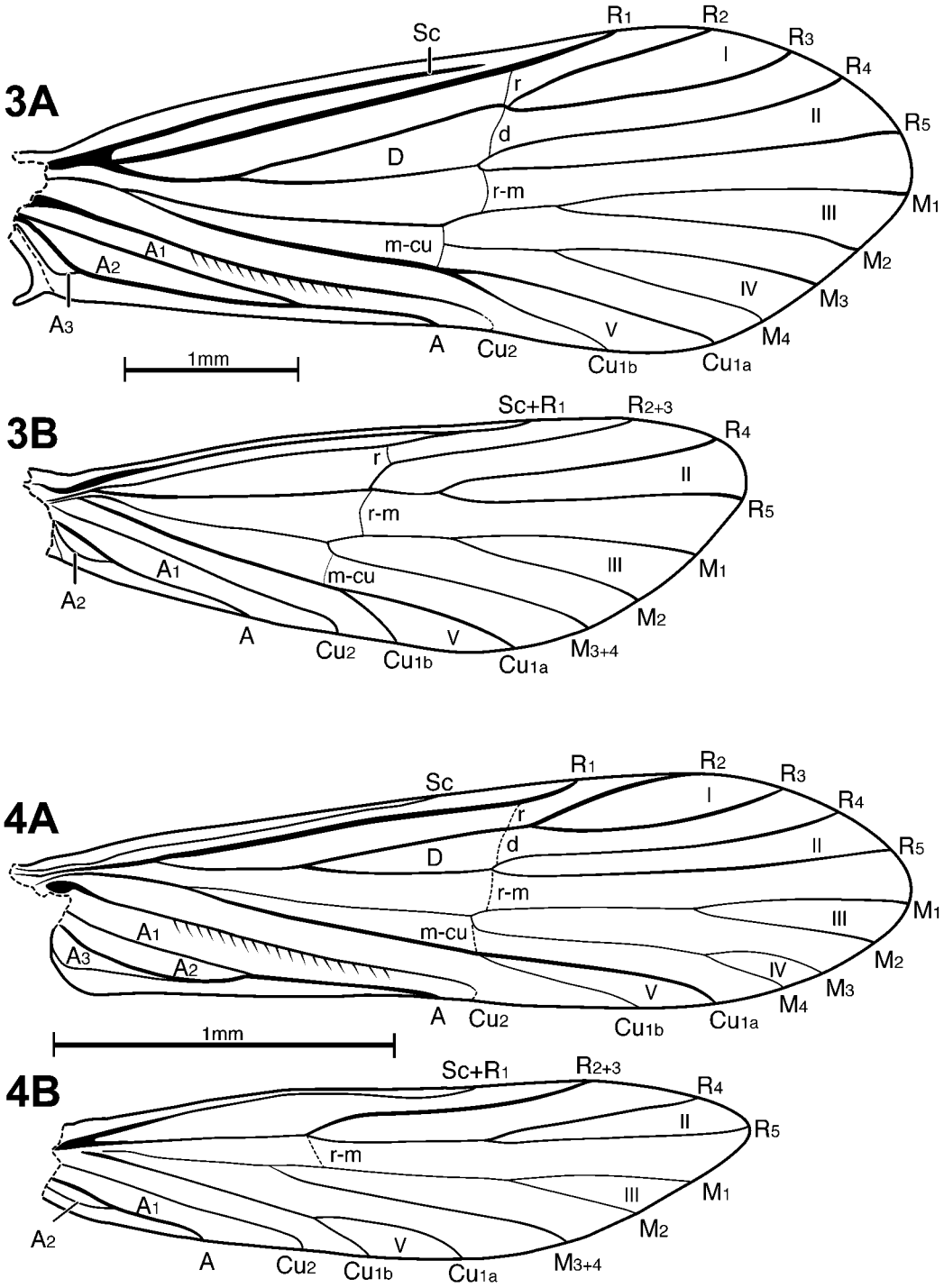

FIGURE 3. *Tolhuaca cupulifera* Schmid. Wings: A—forewing; B—hind wing.
FIGURE 4. *Tolhuaca brasiliensis*, new species. Wings: A—forewing; B—hind wing.

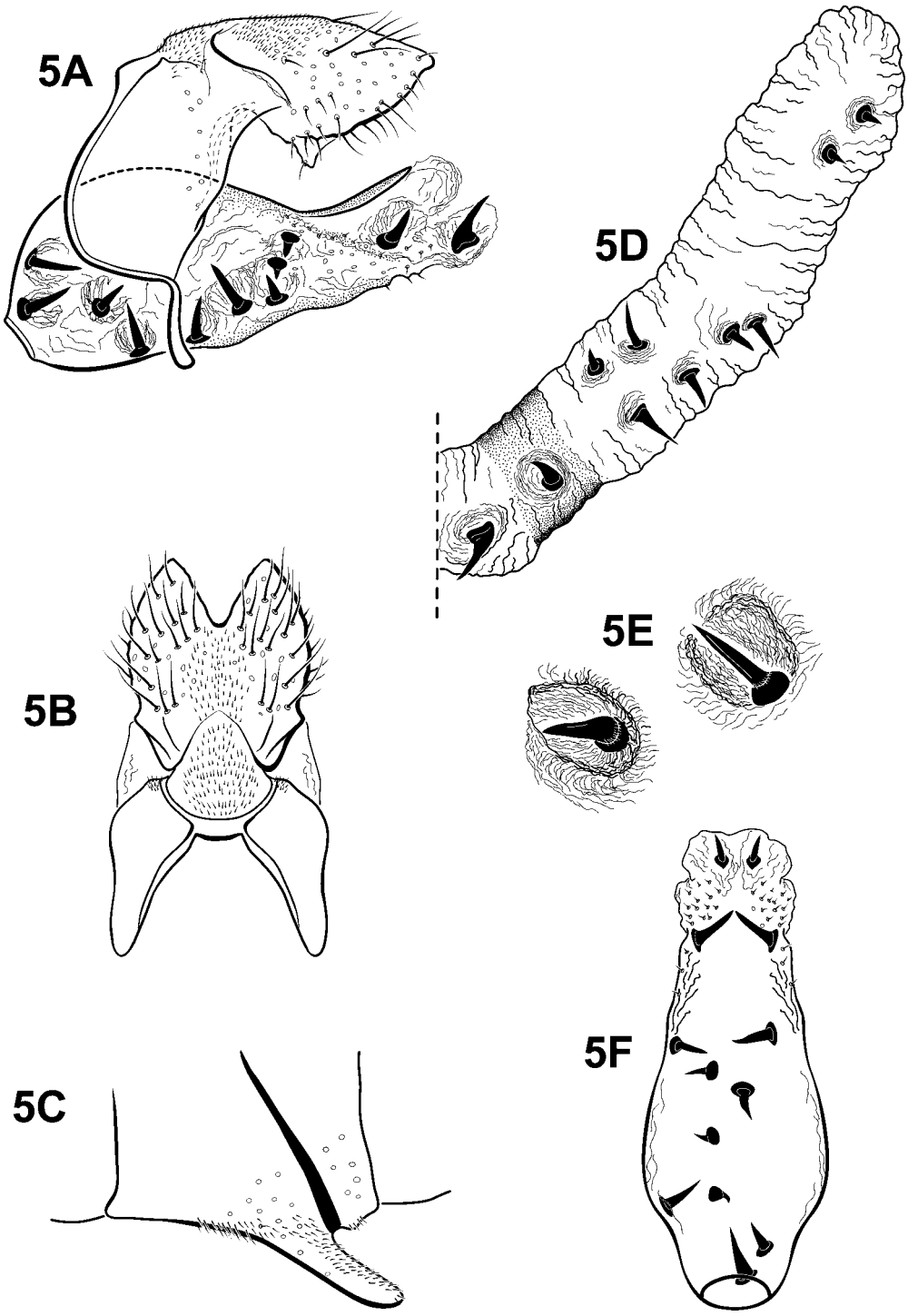

FIGURE 5. *Tolhuaca cupulifera* Schmid. Male genitalia: A—lateral; B—dorsal; C—process of sternum VI; D—endotheca fully everted as observed in holotype; E—detail of endothecal thorn-like spines; F—ventral view of phallobase.

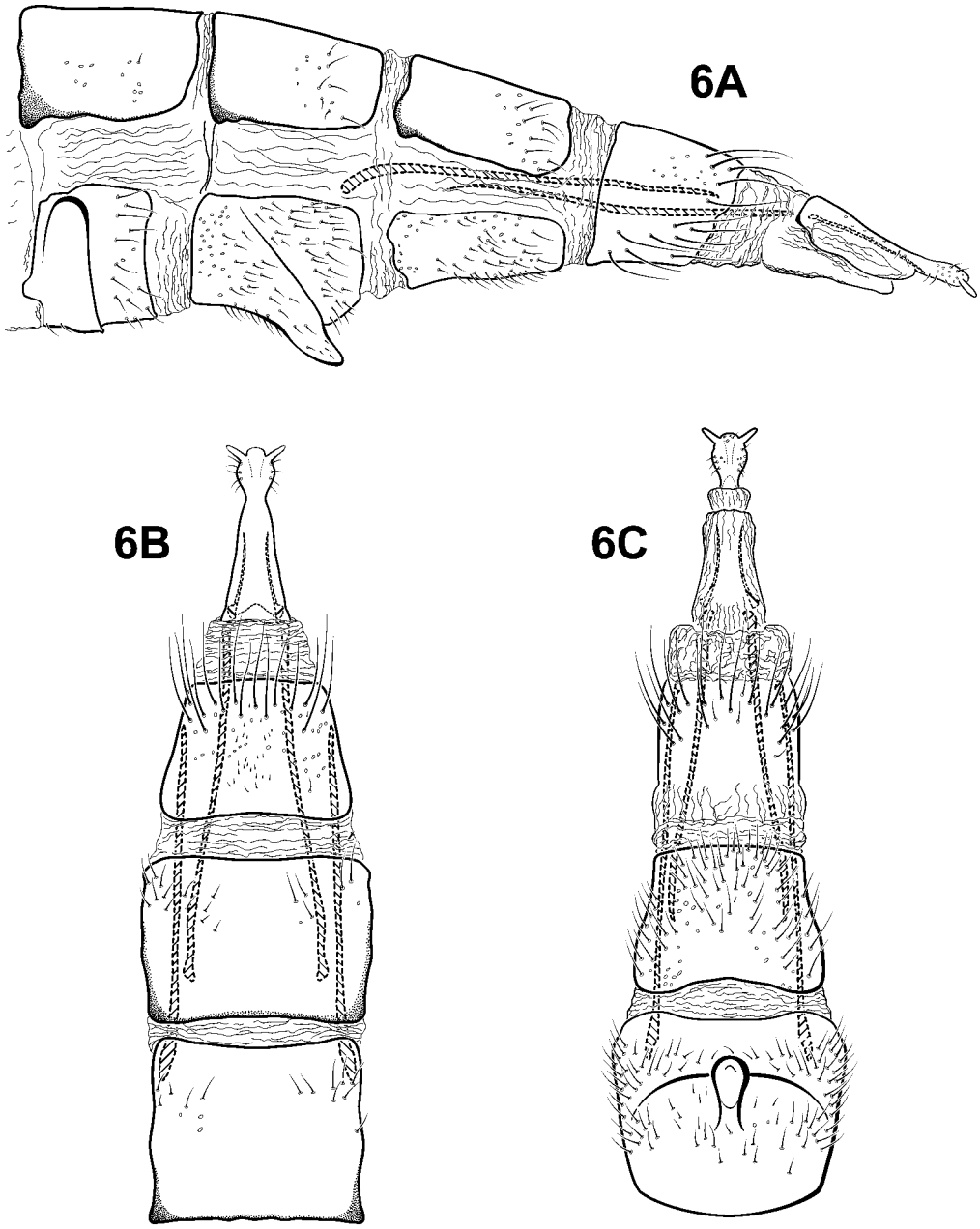

FIGURE 6. *Tolhuaca cupulifera* Schmid. Female genitalia: A—lateral; B—dorsal; C—ventral.

Male genitalia (Fig. 5). Sternum VI (Fig. 5C) with thin, digitate mesal process, projecting caudally. Abdominal segment IX (Fig. 5A) well developed dorsally and laterally, but extremely reduced ventrally, forming very thin sclerotized strap; anterior margin slightly rounded; tergum IX, in dorsal view (Fig. 5B), with posteromesal margin triangular, covered with fine microtrichia; membranous connection between segments IX and X distinct. Tergum X (Figs. 5A, 5B) covered with fine microtrichia; in lateral view

(Fig. 5A), triangular, apex rounded, setose dorsally to ventrally, with acute ventromesal process; in dorsal view (Fig. 5B), with lateral margins slightly sinuous; apex strongly excavate medially. Phallobase (Figs. 5A, 5F) large and bulbous, projecting apicodorsally, lightly sclerotized, with small, stout setae at posterior end, running transversally from dorsum to venter; endotheca (Figs. 5A, 5D) membranous except for lightly sclerotized sub-basal ring, greatly enlarged and tubular when evaginated, with 12 or 13 heavily sclerotized conical, thorn-like spines with enlarged bases, each sitting within membranous ovoid cupule (Figs. 5A, 5D, 5E).

Female genitalia (Fig. 6). Sternum V with slightly raised, sclerotized linear mesal ridge running parallel to anterior and posterior margins. Sternum VI process associated with strongly oblique apodeme. Segment VII normally developed. Abdominal segment VIII synscleritous, more distinctly sclerotized along anterior margin, venter lightly sclerotized, becoming membranous posteroventrally. Tergum IX lightly sclerotized. Segment X, in lateral view, elongate, digitate; in dorsal and ventral views, bulbous, bearing cerci.

Material examined: **CHILE: Bío-Bío:** Arauco, Pichinahuel, [ca. 37º47’52”S, 073º02’37”W], 1–30.i.1959, Peña — 1 male (holotype) (UMSP000115157) (NMNH); **Bío-Bío:** Estero Pichinahuel, 2 km W Parque Nacional Nahuelbuta entrance, 37°47'52"S, 073°02'37"W, 1070 m, 11–12.ii.2005, Holzenthal, Blahnik, Chamorro — 1 female, 4 males (UMSP); **Malleco:** Cord. Nahuelbuta, Cabreria, [37º49’30”S, 073º01’00”W], 1100 m, 9–15.i.1977, Peña — 1 female (NMNH); same except 15–20.i.1977, Peña — 1 male (NMNH).

Distribution. Chile. This species occurs in the Cordillera Nahuelbuta region and extends south to Valdivia based on records provided by Flint (1967).

Tolhuaca brasiliensis, new species

Figs. 4, 7, 8

This new species lacks the sclerotized conical endothecal spines found in *T. cupulifera*. Tergum X is quadrate in lateral view, whereas in *T. cupulifera* it is triangular. Tergum X is also shallowly excavate apicomesally, while it is deeply excavate in *T. cupulifera*. *Tolhuaca brasiliensis* is about half the size of *T. cupulifera* and also has narrower wings. The species is known only from southeastern Brazil.

Adult. Length of forewing: male 2.7–2.8 mm (n=2), female 2.7 mm (n=1). Body, wings, and appendages nearly uniformly fuscous, tibia and tarsi yellowish brown. Forewing (Fig. 4A) narrow, margins nearly parallel; with erect setae along Cu2; Sc reaching anterior margin; fork I emerging beyond cord; fork II emerging at cord; forks III and IV shorter than their stems; A3 gradually intersecting A2; crossveins *r*, *d*, *r-m*, and *m-cu* faintly visible, forming nearly straight line. Hind wing (Fig. 4B) relatively narrow, tappering slightly past anastomosis, subacute apically; Sc and R1 fused; fork II subequal to its stem; fork III shorter than its stem; crossvein *r-m* faintly visible, *r* and *m-cu* absent.

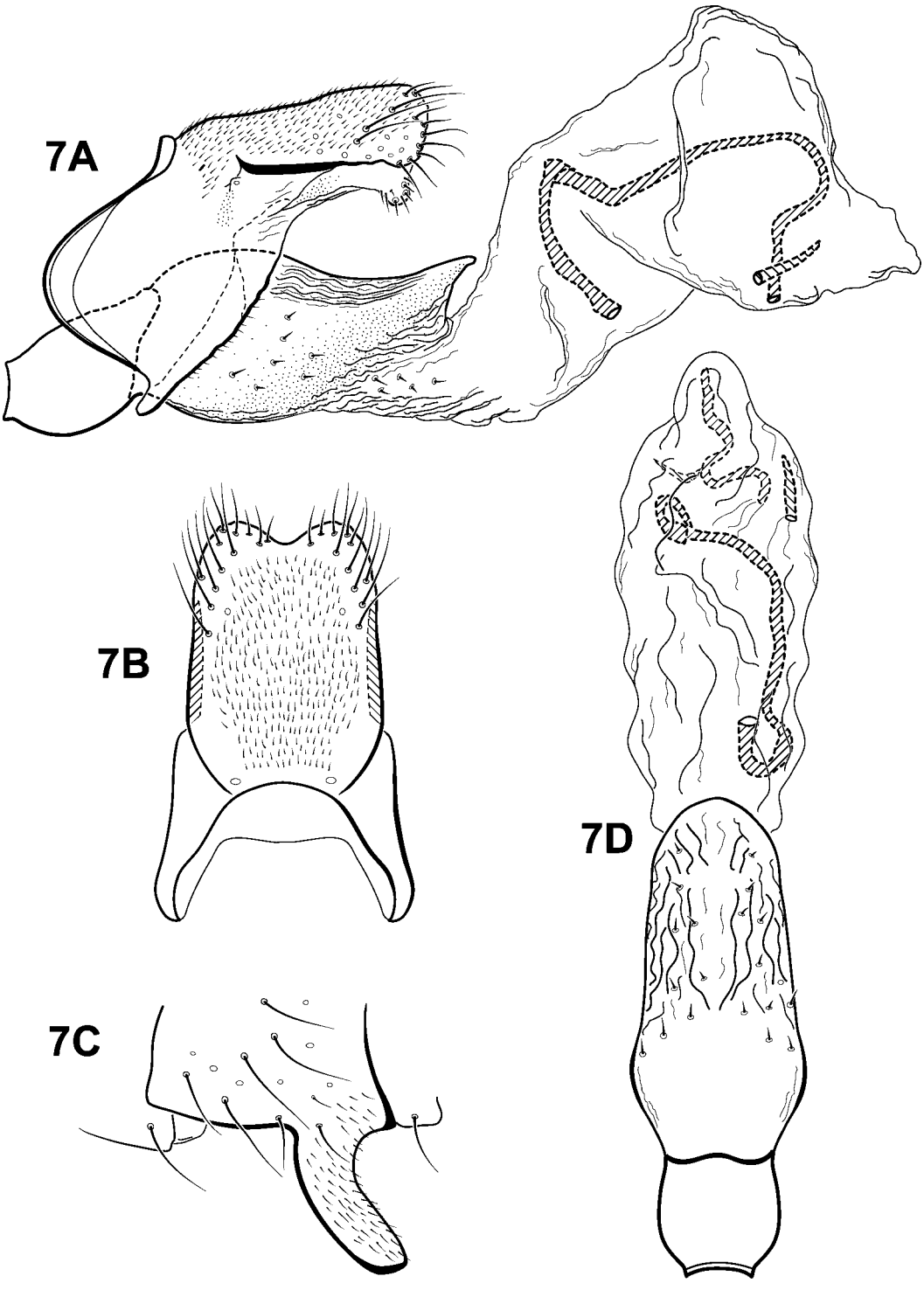

FIGURE 7. *Tolhuaca brasiliensis*, new species. Male genitalia: A—lateral; B—dorsal; C—process of sternum VI; D—ventral view of phallobase.

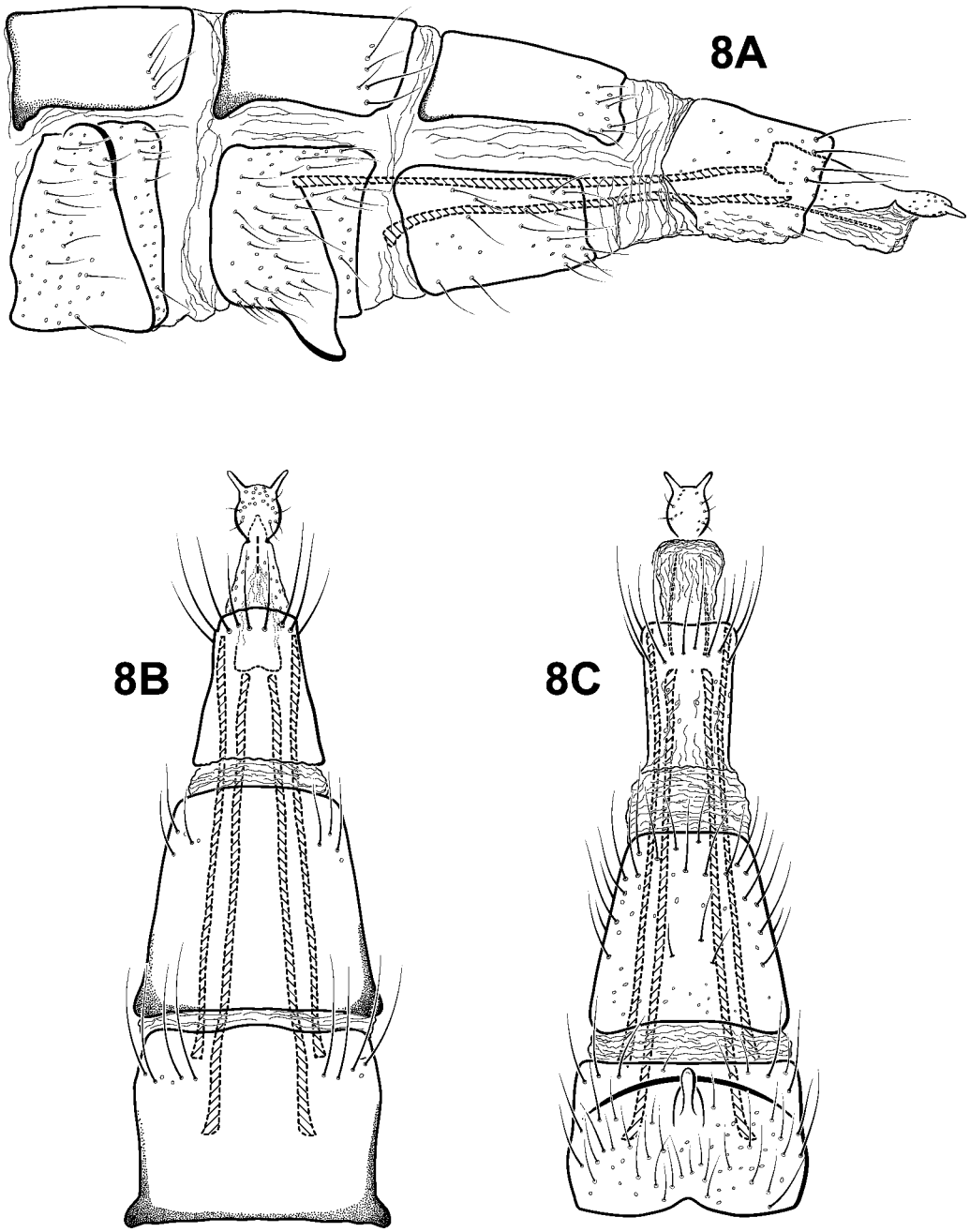

FIGURE 8. *Tolhuaca brasiliensis*, new species. Female genitalia: A—lateral; B—dorsal; C—ventral.

Male genitalia (Fig. 7). Sternum VI (Fig. 7C) with somewhat thickened, basally curved, mesal process, projecting downward. Abdominal segment IX (Fig. 7A) well developed dorsally and laterally, but extremely reduced ventrally, forming very thin

sclerotized strap; anterior margin broadly rounded; tergum IX, in dorsal view (Fig. 7B), with posteromesal margin rounded; membranous connection between segments IX and X distinct. Tergum X (Figs. 7A, 7B) covered with fine microtrichia; in lateral view (Fig. 7A), parallel sided, with broad lateral flange, setose apically and laterally, with rounded apicoventral processes, apex subtruncate; in dorsal view (Fig. 7B), with lateral margins nearly straight and subparallel; apex slightly excavate medially. Phallobase (Figs. 7A, 7D) large and tubular, projecting apicodorsally, with basal extension and apparent suture and constriction medially; lightly sclerotized, but rugose ventrally and dorsally, with small, stout setae laterally and ventrally; endotheca (Figs. 7A, 7D) entirely membranous, greatly enlarged and convoluted when evaginated, with 3 convoluted tubular sclerites of varying lengths.

Female genitalia (Fig. 8). Sternum V with oblique, slightly raised, sclerotized mesal linear ridge. Sternum VI process associated with slightly oblique apodeme. Segment VII normally developed. Abdominal segment VIII synscleritous, anterior margin membranous and receding ventrally, merging with intersegmental membrane, posterodorsal and posteroventral margins distinct and lightly sclerotized. Tergum IX lightly sclerotized. Tergum X, in lateral view, elongate, slightly bulbous; in dorsal and ventral views, bulbous, bearing cerci.

Holotype male: BRAZIL: São Paulo: Parque Estadual de Campos do Jordão, 1st order trib. to Rio Galharada, 22°41'40"S, 045°27'47"W, 1530 m, 14–16.ix.2002, Blahnik, Prather, Huamantinco (UMSP000087908) (MZUSP).

Paratypes: BRAZIL: same data as holotype — 1 female (UMSP); same except Rio Galharada, 13–15.ix.2002, Blahnik, Prather, Melo, Huamantinco — 1 male (UMSP).

Distribution. Brazil. This species is known only from the type locality in the Serra da Mantiqueira.

Etymology. Named for the type locality, in recognition of first species of the genus *Tolhuaca* to be discovered in Brazil.

BIOGEOGRAPHICAL CONSIDERATIONS

Ross (1956) proposed 2 major protoptiline lineages, 1 represented by *Itauara*, which occurs in central South America, and the other containing *Matrioptila*, from southeastern North America. He hypothesized that the subfamily first arose in North America, and dispersed quickly to South America, giving rise to the *Itauara* line (Ross 1956). Therefore, the genus *Itauara* represented the base of an evolutionarily divergent clade, and *Matrioptila* was an archaic remnant of an earlier, more widespread protoptiline ancestor (Ross 1956). Based on the discovery of a protoptiline caddisfly occurring outside of the New World, and of a genus perhaps more primitive than *Matrioptila*, Marshall (1979) encouraged a re-examination of Ross's North American center of origin hypothesis. This evaluation of another primitive protoptiline, *Tolhuaca*, from southern South America, is

further incentive to revisit Ross's hypothesis. However, until the phylogeny of Protoptilinae is better understood through modern phylogenetic analysis, we can only speculate on the evolutionary history of this group. Nonetheless, some observations regarding the biogeography of the genus *Tolhuaca* and possible implications for protoptiline evolution are worthwhile.

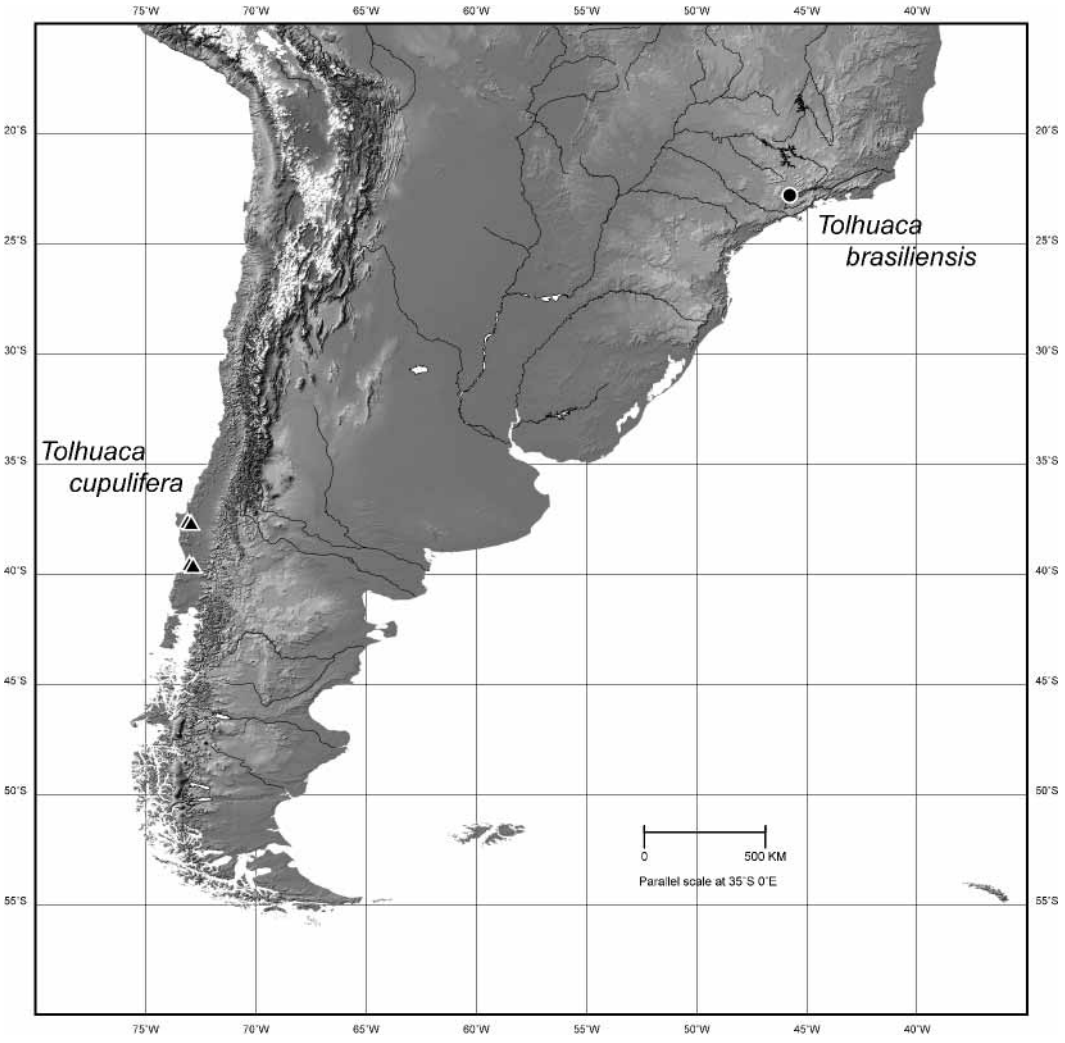

FIGURE 9. Distribution of *Tolhuaca* in southern South America. Triangle—*Tolhuaca cupulifera* Schmid; Circle—*Tolhuaca brasiliensis*, new species.

The genus *Tolhuaca* is restricted to the southern region of South America and the 2 known species have disjunct, non-overlapping distributions (Fig. 9). *Tolhuaca cupulifera* occurs in the Cordillera Nahuelbuta region of Chile, which has a temperate climate, while *T. brasiliensis* is only known from the subtropical Serra da Mantiqueira region of Brazil.

Interestingly, this biogeographic pattern is congruent to that of the tree genus *Araucaria* (Araucariaceae) which has a highly disjunct and recognizably trans-Antarctic distribution: Chile, Argentina, southern Brazil, New Caledonia, Norfolk Island, Australia, and New Guinea (de Laubenfels 1988). This distribution is well known in the literature and is generally recognized to be the result of the Mesozoic geological break-up of southern temperate Gondwana (Crisci et al. 1991, Sanmartín & Ronquist 2004). *Tolhuaca*'s broadly disjunct distribution perhaps suggests that it is an isolated relict of a more widespread protoptiline ancestor with an ancient southern Gondwana pattern. Although we do not yet know the sister genus of *Tolhuaca*, if it follows this pattern, we might expect to find related groups in the other Gondwanan regions.

ACKNOWLEDGMENTS

We thank Dr. Roger J. Blahnik, University of Minnesota, for lively discussions of protoptiline evolution and morphology, and for advice regarding early drafts of this manuscript. We express our appreciation to 2 anonymous reviewers for their helpful comments. We are grateful to Dr. Oliver S. Flint, Jr., Smithsonian Institution, for generously providing material, including types, for examination and inclusion in this study. In addition, Dr. Philip J. Clausen, Lourdes Chamorro-Lacayo, Henrique Paprocki, Anne Wasmund, and Laura Freund provided assistance throughout this study. D.R.R gratefully acknowledges financial support from the Bell Museum of Natural History, University of Minnesota (Dayton-Wilkie Natural History Funds). This material is based upon work supported by the National Science Foundation grant nos. DEB 9971885 & 0117772.

REFERENCES

Alexandria Digital Library Gazetteer. (2005) Santa Barbara CA: Map and Imagery Lab, Davidson Library, University of California, Santa Barbara. Copyright UC Regents.
Available from http://middleware.alexandria.ucsb.edu/client/gaz/adl/index.jsp (accessed 29 April 2005)

Banks, N. (1904) A list of new Neuropteroid insects, exclusive of Odonata, from the vicinity of Washington, D.C. *Proceedings of the Entomological Society of Washington*, 6, 201–217.

Crisci, J.V., Cigliano, M.M, Morrone, J.J., & Roig-Juñent, S.R. (1991) Historical biogeography of southern South America. *Systematic Zoology*, 40(2), 152–171.

de Laubenfels, D.J. (1988) Coniferales. *In*: Van Steenis, C.G.G.J., & de Wilde, W.J.J.O. (Eds.), *Flora Malesiana, Series I, Spermatophyta*. 10(3). Dordrecht: Kluwer Academic Publishers. Boston, Massachusetts, pp. 337–453.

Flint, O.S., Jr. (1967) Studies of Neotropical caddis flies, II: Trichoptera collected by Prof. Dr. J. Illies in the Chilean Subregion. *Beiträge zur Neotropischen Fauna*, 5, 45–68.

Flint, O.S., Jr., Holzenthal, R.W., & Harris, S.C. (1999) *Catalogue of the Neotropical Caddisflies (Insecta: Trichoptera)*. Special Publication, Ohio biological Survey. Columbus, Ohio, 239 pp.

Holzenthal, R.W. (2004) Three new species of Chilean caddisflies (Insecta: Trichoptera). *Proceedings of the Entomological Society of Washington*, 106(1), 110–117.

Holzenthal, R.W. & Andersen, T. (2004) The caddisfly genus *Triaenodes* in the Neotropics (Trichoptera: Leptoceridae). *Zootaxa*, 511, 1–80.

Kimmins, D.E. (1964) On the Trichoptera of Nepal. *Bulletin of the British Museum (Natural History) Entomology Series*, 15(2), 35–55.

Kristensen, N.P. (1984) Studies on the morphology and systematics of primitive Lepidoptera (Insecta). *Steenstrupia*, 10, 141–191.

Marshall, J.E. (1979) A review of the genera of the Hydroptilidae (Trichoptera). *Bulletin of the British Museum (Natural History) Entomology Series*, 39(3), 135–239.

Morse, J.C. & Yang, L. (1993) Higher classification of the Chinese Glossosomatidae (Trichoptera), *In:* Otto, C. (Ed.), *Proceedings of the 7th International Symposium on Trichoptera*. Backhuys Publishers, Leiden, The Netherlands, pp. 139–148.

Mosely, M.E. (1937) Mexican Hydroptilidae (Trichoptera). *Transactions of the Royal Entomological Society of London*, 86, 151–190.

Mosely, M.E. (1939) The Brazilian Hydroptilidae (Trichoptera). *Novitates Zoologicae*, 41, 217–239.

Mosely, M.E. (1954) The *Protoptila* group of the Glossosomatinae (Trichoptera: Rhyacophilidae). *Bulletin of the British Museum (Natural History) Entomology Series*, 3(9), 317–346.

Nielsen, A. (1980) A comparative study of the genital segments and the genital chamber in female Trichoptera. *Biologiske Skifter*, 23(1), 1–200.

Ross, H.H. (1938) Descriptions of Nearctic caddis flies (Trichoptera), with special reference to Illinois species. *Illinois Natural History Survey Bulletin*, 21(4), 101–183.

Ross, H.H. (1956) *Evolution and Classification of the Mountain Caddisflies.* University of Illinois Press, Urbana, Illinois, 213 pp.

Sanmartín, I. & Ronquist, F. (2004) Southern Hemisphere biogeography inferred by event-based models: plant versus animal patterns. *Systematic Biology*, 53(2), 216–243.

Schmid, F. (1964) Contribution à l'ètude des Trichoptères nèotropicaux V. *Tijdschrift voor Entomologie*, 107, 307–339.

Schmid, F. (1998) *Genera of the Trichoptera of Canada and adjoining or adjacent United States.* NRC Research Press, Ottawa, Ontario, 319 pp.

Ulmer, G. (1906) Neuer Beitrag zur Kenntnis aussereuropaeischer Trichopteren. *Notes from the Leyden Museum*, 28, 1–116.

Wiggins, G.B. (1996) Trichoptera families. *In:* Merritt, R.W. & Cummins, K.W. (Eds.), *An Introduction to the Aquatic Insects of North America, 3rd Edition*. Kendall/Hunt Publishing Company, Dubuque, Iowa, pp. 309–349.

