

## Revision of the genus *Culoptila* (Trichoptera: Glossosomatidae)

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## ABSTRACT

The caddisfly genus *Culoptila* is revised to include 17 previously described species and 9 new species. Illustrations of the male genitalia and a key are provided for all species. In addition, illustrations of male head and thoracic features, larval characters and cases, and female genitalia are included. New species described here include: *Culoptila bidentata* (Costa Rica), *C. buenoi* (Mexico), *C. cascada* (Costa Rica), *C. hamata* (Costa Rica), *C. pararusia* (Mexico), *C. plummerensis* (eastern United States), *C. tapanti* (Costa Rica), *C. unispina* (Costa Rica, Panama), and *C. vexillifera* (Guatemala).

**Key words:** Trichoptera, Glossosomatidae, Protoptilinae, *Culoptila*, caddisfly, revision, new species, Neotropics, Nearctic

## INTRODUCTION

The subfamily Protoptilinae of the family Glossosomatidae is species rich and known to contain a number of additional, undescribed species (Flint et al. 1999). There has never been a comprehensive treatment of the subfamily. This paper represents one of a planned series of papers intended to review the genera of this subfamily and to describe the many new species. Although most *Culoptila* species have been reasonably well described, they are difficult to compare due to differences in terminology and different styles of illustration used by various authors. This paper reviews the described species, provides new illustrations, and increases the known diversity of the genus by about a third.

To date, 18 genera and 205 species (including 3 fossil species) are recognized for Protoptilinae. Protoptilinae is most abundantly represented in the Neotropics, both by species and genera. In fact, it is the only subfamily of Glossosomatidae found in the region. Diversification of protoptilines outside the Neotropics is comparatively limited. One genus, *Matrioptila* Ross 1956, with a sole species, is endemic to eastern North America. Seventeen species in 4 genera, *Nepaloptila* Kimmins 1964, *Padunia* Martynov 1910, *Poeciloptila* Schmid 1991 (1990), and *Temburongpsyche* Malicky 1995, are known from Asia.

Within the Neotropics, generic diversification shows an interesting pattern. Three genera, *Campsiophora* Flint 1964, *Cariboptila* Flint 1964, and *Cubanoptila* Sykora 1973

(Botosaneanu & Sykora 1973), are endemic to the greater Antilles, but most of the generic diversity is found in the southern part of the South American continent, primarily in southeastern Brazil and the Chilean subregion, with most genera restricted to either one region or the other. Genera that are largely restricted to the southern Neotropics include *Itauara* Müller 1888, *Merionoptila* Schmid 1959, *Canoptila* Mosely 1939, *Mastigoptila* Flint 1967b, *Tolhuaca* Schmid 1964, and *Scotiotrichia* Mosely 1934. Throughout much of the rest of South America, the species rich genera *Mexitrichia* Mosely 1937, *Mortoniella* Ulmer 1906, and *Protoptila* Banks 1904 are the only ones recorded. Admittedly, many additional species remain to be described from this region and additional genus-level diversity is not impossible.

In Central America only 3 genera are present, *Mexitrichia*, *Protoptila*, and *Culoptila*. The first 2 genera have distributions extending southward to southeastern Brazil and Argentina (but not the Chilean subregion, per se). *Protoptila*, has an additional range extension into the United States and Canada, where it is also widespread and abundant and has a moderate species radiation (13 species). *Culoptila* is the only genus largely endemic to Central America, although it does extend into western and southwestern United States, and disjunctly into the northeastern United States. Morphologically, it is very distinct from the other genera present in Central America, probably having its closest affinity to the Antillean endemic genera.

### **Taxonomic history of Protoptilinae**

The relationship of protoptilines to other glossosomatids was not at first recognized. So small are they (< 5 mm) that many rival Hydroptilidae, commonly referred to as microcaddisflies, for their minuteness. In fact, the first described species of *Protoptila* was placed in the genus *Hydroptila* (Walker 1852). Species of protoptilines continued to be described in the family Hydroptilidae well into the 20th Century, although additional genera were established to recognize some of them. Mosely (1937) began to question this placement and commented that it was open to question whether the species of *Protoptila* he was then describing from Mexico might not better be placed in the subfamily Glossosomatinae of the family Rhyacophilidae, in which glossosomatids were then placed. However, Mosely (1939) continued to place the new genera of protoptilines he described from Brazil in Hydroptilidae. Ross (1938) was the first author to describe species of protoptilines in Glossosomatinae, based in large part on his observations of the similarity of immature stages to other glossosomatids. Ross placed all 4 of his new species in the genus *Protoptila*, which was the only genus he specifically transferred to Glossosomatinae. These new species included 2 now placed *Culoptila* and 1 in *Matrioptila*.

The recognition of protoptiline genera as a specific subgroup within Glossosomatinae, and the inclusion of all genera constituting the group, was formally made by Mosely

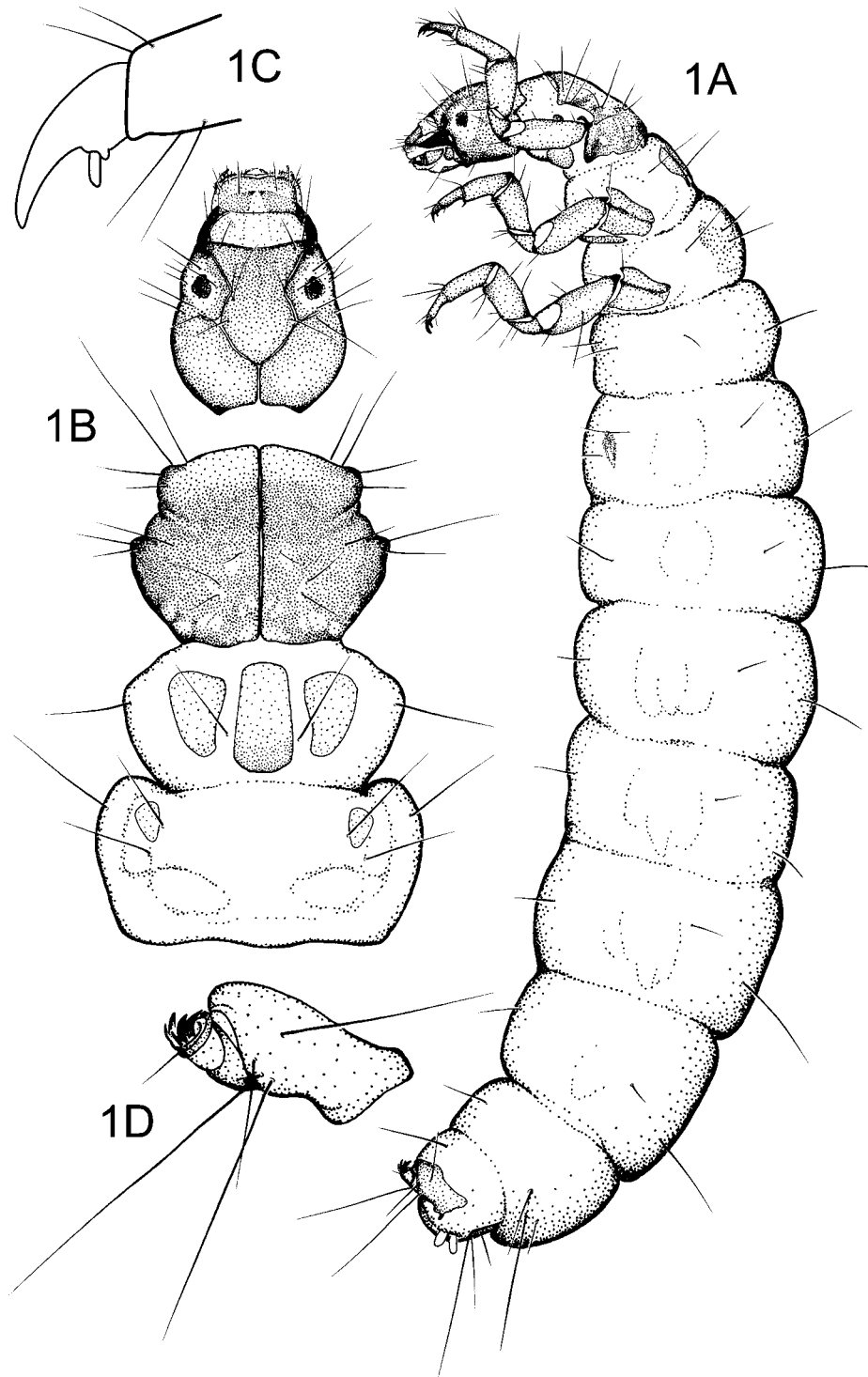
(1954) in a posthumously published paper. He confessed that he had intended to describe the group as a new subfamily within Rhyacophilidae, but subsequently accepted the viewpoint of Ross and Ulmer, who had expressed a similar conclusion in personal correspondence (Mosely 1954), that the taxa were closely related to glossosomatids. Mosely thus defined the *Protoptila* Group as a lineage within the subfamily Glossosomatinae of the family Rhyacophilidae. The recognition of Protoptilinae as a subfamily within Glossosomatidae was left to Ross (1956), coincident with his decision to recognize Glossosomatidae as a family. However, he did not treat the systematics of protoptilines or discuss relationships among the genera in the 1956 work.

In addition to defining the *Protoptila* Group, Mosely (1954) also established the genus *Culoptila* and described 4 species. He neither mentioned the similarity of the 2 *Protoptila* species described by Ross (1938) to species in his new genus, nor did he transfer Ross's species to *Culoptila*. Five additional species of *Culoptila* were subsequently described by Denning (1965) and Flint (1967a, 1974a) before Flint (1974b) recognized that the 2 species described by Ross in 1938 also belong in the genus *Culoptila* and formally transferred them there, and at the same time described 1 additional species. Bueno-Soria & Santiago-Fragoso (1996) subsequently described 5 additional species, bringing to 17 the number of species in the genus. All of these species are here considered valid.

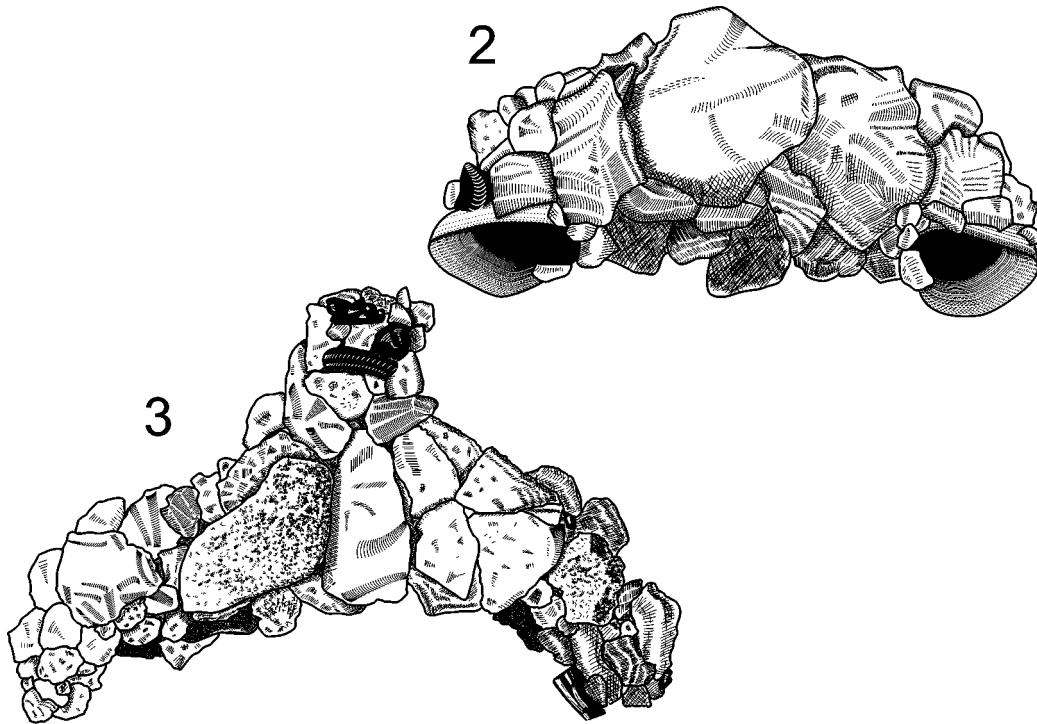
### Life history and larval stages

Life history and larval descriptions are known for only a few species of protoptilines. Wiggins (1996) provided a description of the larva of *Culoptila moselyi* Denning 1965, and Houghton & Stewart (1998a,b) subsequently provided larval instar and pupal descriptions, as well as life history and case-building behavior for *Culoptila cantha* (Ross 1938). We are providing an illustration of an additional, unidentified species from the Río Guineal, Puntarenas Province, Costa Rica (Fig. 1). Generic determination was based on the keys of Wiggins (1996), Flint (1963), and Posada-Garcia & Roldán-Pérez (2003). The primary character currently used to distinguish larvae of *Culoptila* from those of *Protoptila* and *Mexitrichia* is a greatly thickened seta basal to the tarsal claw (Fig. 1C); the Costa Rican species has this character and fits the description provided by Wiggins (1996) for the genus. The same character, or a very similar character state, is shared with *Mortoniella*, an evident sister taxon to *Mexitrichia*. The distributions of *Culoptila* and *Mortoniella* are not yet known to overlap (Flint et al. 1999).

*Culoptila cantha* was found to be multivoltine in the Brazos River of Texas (Houghton & Stewart 1998b) and to construct typical glossosomatid tortoise-case larval retreats, either of uniform small grains of sand, as described by Wiggins (1996) for *Culoptila moselyi*, or with larger lateral stones, similar to cases of species in the genus *Protoptila*. A typical *Culoptila* case, that of *C. moselyi*, is illustrated in Fig. 2. In Costa Rica we have



**FIGURE 1.** *Culoptila* larva, undetermined species from Río Guineal, Puntarenas Province, Costa Rica. 1A—habitus, lateral; 1B—head and thorax, dorsal; 1C—detail of tarsal claw and basal seta, lateral; 1D—detail of anal proleg, lateral.



**FIGURES 2–3.** Larval cases. 2—*Culoptila moselyi* Denning, Arizona, U.S.A. 3—*Culoptila unispina*, new species, Río Cotón, Puntarenas Province, Costa Rica.

found an interesting modification of this basic case architecture (Fig. 3), in which the case is more elongate and possesses a central open turret made with very fine sand grains. The case illustrated is presumptively identified as that of *Culoptila unispina*, n. sp., which was the only species collected from the Río Cotón, Puntarenas, Costa Rica.

Although *Culoptila* is known to occur in large rivers, some species records and collection sites indicate that it is also found in small springs and seepage areas and it is likely that some species will be shown to have a preference for these habitat types.

## MATERIAL AND METHODS

Methods used for preparation of specimens followed those discussed by Blahnik & Holzenthal (2004). Genitalia were cleared in either 12.5% KOH at room temperature for 6–12 hours, or a solution of 85% lactic acid heated to 125°C for about 30 minutes. Pencil drawings of genitalic structures were made by use of an ocular grid and final illustrations of wings, head and thoracic structures, and genitalia were rendered in Adobe Illustrator®.

The interpretation of genitalic structures follows that of Flint (1974a) and terminology for these structures follows Schmid (1996), as shown in Fig. 11A.

Each pinned specimen, or lot of specimens examined during the study was barcoded (4 mil polyester, 8 x 14 mm., code 49) with a unique alphanumeric sequence beginning with the prefix UMSP. The prefix is not meant to imply ownership by the University of Minnesota Insect Collection (UMSP), but only to indicate that the specimen was databased at that collection. Specimen taxonomic and collection data are stored in Biota® (v. 2.0, Sinauer Associates, Inc.) (Colwell 2003). A detailed list of all material examined, including individual barcode numbers, is maintained at UMSP and can be accessed from (UMSP 2006). Additional North American and Mexican distributional records were taken from literature records compiled by Morse (2003) and Bueno-Soria & Flint (1978).

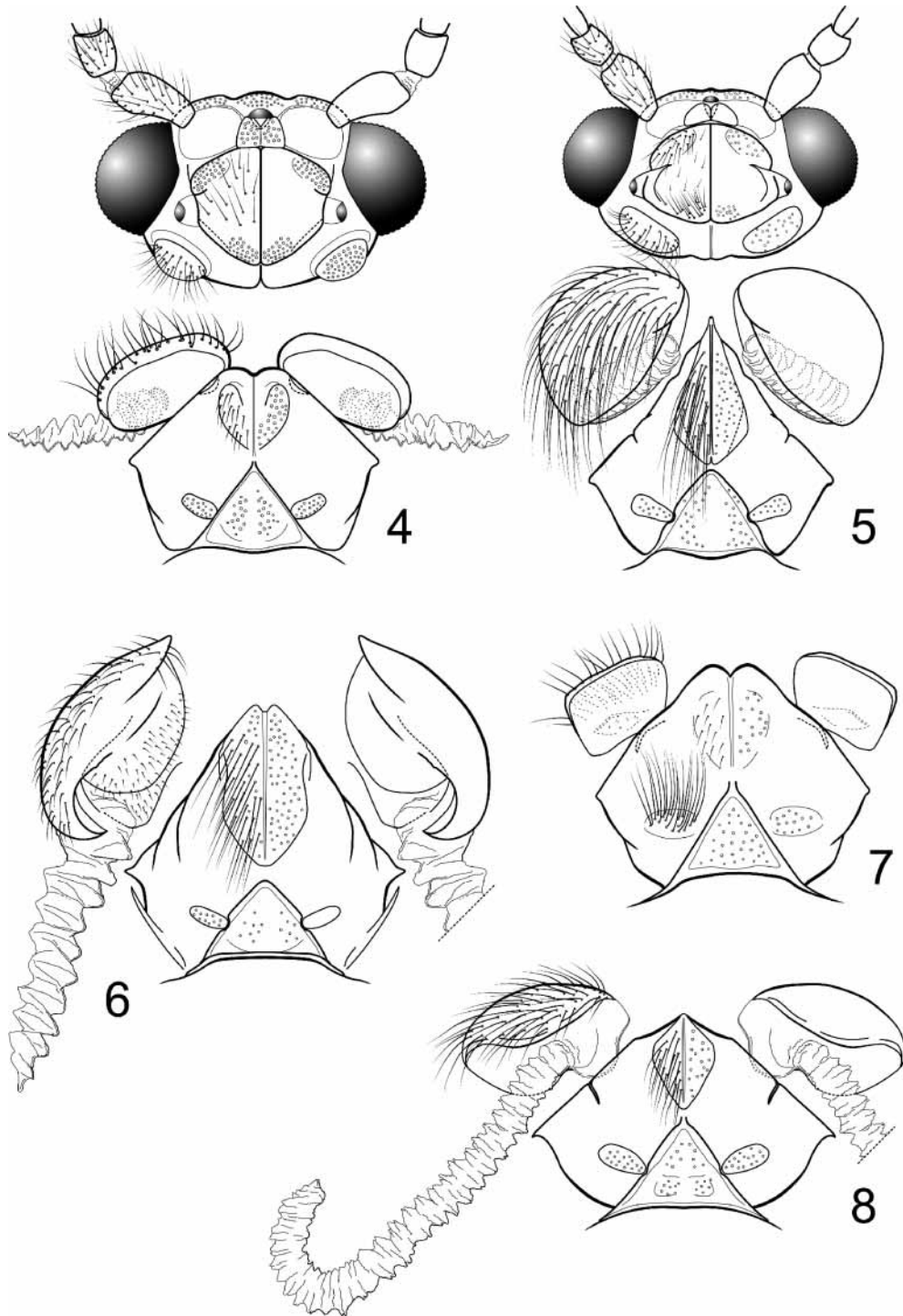
Holotypes are deposited in the collections of the University of Minnesota, St. Paul (UMSP), the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (NMNH), and the Universidad Nacional Autónoma de México (UNAM). Other material examined is deposited in those same institutions and also in the Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica (INBIO). The holotype of *C. amberia* was borrowed from the Natural History Museum, London, England (NHM).

## GENERIC DESCRIPTION

### *Culoptila* Mosely 1954: 336

Type species: *Culoptila aluca*, original designation.

As discussed by Mosely (1954), the most distinctive feature of *Culoptila* is the modification of the tegulae of males. The tegulae are moderately to greatly enlarged in most species and cover an extensible glandular structure, which Mosely (1954) aptly described as being concertina-like. The length of this glandular structure varies among species and is difficult to compare directly, since it is only fortuitously expanded during the clearing of some specimens (Figs. 4–8). In a few species, most especially *C. thoracica* (Fig. 5), the tegulae are so enlarged that they affect the shape of the thorax, which is consequently very narrowed anteriorly. Despite this, the possession of modified tegulae and associated glands is not completely diagnostic for the genus, since a few species either lack these structures, or they are minimally developed and inconspicuous. An additional character discussed by Mosely (1954) as diagnostic for *Culoptila* is the structure of the ventral process of abdominal segment VI (Fig. 28C). The process is short, rounded to subtruncate apically, and unusual in that the posterior margin is only narrowly attached to a sclerotized, diagonal apodeme (present on sternum VI of all protoptilines). The anterior part of the ventral process sits in a small depression, so that it is not immediately apparent that the process is only narrowly attached, and thus it is not actually as peculiar appearing as in the diagrammatic illustrations of Mosely (1954).



**FIGURES 4-8.** Head, mesothorax, and tegular structures, dorsal. 4—*Culoptila hamata*, new species. 5—*Culoptila thoracica* (Ross). 6—*Culoptila aluca* Mosely. 7—*Culoptila cantha* (Ross). 8—*Culoptila moselyi* Denning.



*Culoptila* is further characterized by the male genitalia. A distinctive character is the apparent absence of a sternum IX. In a few species it is obvious that the ventral part of tergum IX is reduced to a very narrow, membranous band that subtends the phallobase. Probably, this occurs in all species, even when the membranous connection is not obvious. A similar reduction of the sternum occurs in the Antillean genera *Campsiophora*, *Cariboptila*, and *Cubanoptila*, and also occurs in the genus *Tolhuaca* (Robertson & Holzenthal 2005). Also characteristic of *Culoptila* is a projecting tergum X with a pair of ventrolateral processes. Tergum X varies greatly in length and shape among the different species and is often nearly diagnostic in and of itself. Perhaps the most unusual and diagnostic structure of the genitalia is the phallobase, which consists of a large inflated bag, open posteriorly, often nearly membranous in appearance, with a more or less rounded opening on the anterior or anteroventral margin through which the sperm duct probably enters the chamber. On its ventral surface is a pair of reduced inferior appendages, which are fused to the structure (absent in *Culoptila cantha* and *C. plummerensis*, n. sp.). It is notable that neither Ross (1938) nor Denning (1965) chose to illustrate the inflated phallobase as part of the genitalia, although it was discussed in their species descriptions. Although Mosely (1954) clearly illustrated the structure, he also did not consider it part of the phallic apparatus, but instead referred to the 2 internal spines as the “penis and penis sheath.” In some species only a single internal spine is found. The phallobase has a sclerotized, extending, posterodorsal apex, varying in shape, length, and the angularity of its inflection among the different species. The phallobase also often has a narrow sclerotized ridge running along the dorsal and ventral margins, which helps to give the overall structure a defined shape and size. This sclerotized ridge is more noticeable in some species (and probably also some specimens) than in others, and appears to be absent in some species. In dorsal or ventral views the phallobase of some species, particularly those with dorsal and ventral sclerotized ridges, shows varying degrees of lateral compression.

Another diagnostic feature of the phallic apparatus is an apical structure of variable sclerotization, which we have interpreted as the phallotremal sclerite. This fairly large structure is sometimes faintly sclerotized and difficult to see, or obscured by other structures. The overall structure is broadly tubular or trough-like, usually with 2 curved, finger-like, more prominently sclerotized apicodorsal projections. Because the structures of the phallotremal sclerite are often difficult to see, they may not always be precisely and accurately rendered in the accompanying illustrations. Generally, these are not features that a person identifying *Culoptila* is likely to focus on and, for most species, the phallotremal sclerite is not discussed in the species diagnoses or descriptions.

Adult. Forewing length 2.0–3.8 mm, females slightly larger than males. Coloration from pale to dark brown, appendages usually paler. Anastomosis of forewing complete and nearly linear, usually marked by pale venation, sometimes with overlying whitish band of setae, or a whitish setal spot at the arculus. Forewing (Fig. 9A) with forks I–IV

present, fork V absent; fork II sessile or petiolate; Cu1 incomplete, not reaching wing margin; Cu2 thickened, with row of stiff setae; 3A apparently absent (or possibly weakly developed). Hind wing (Fig. 9B) with only forks II and III present; crossveins absent (or possibly very weakly developed). Tegulae of males usually enlarged (minimally or not modified in some species) (Figs.4–8), either flattened or inflated and rounded; ventrally with glandular structure of variable development, often elongate and concertina-like. Mesothorax unmodified or narrowed anteriorly (in species with greatly enlarged tegulae). Mesoscutum short and heart-shaped, or elongate and narrowed anteriorly (in species with greatly enlarged tegulae); scutellar warts small, ovoid, contiguous with mesoscutellum. Sternum VI of both males (Fig 28C) and females (Fig. 16A) with short, apically rounded or subtruncate ventral process; process only narrowly attached posteriorly to sclerotized segmental apodeme.

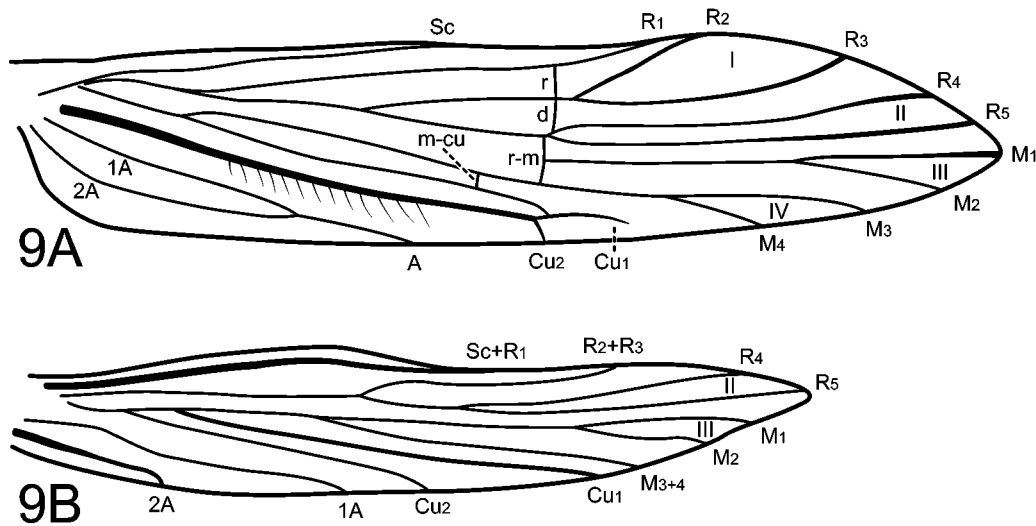


FIGURE 9. *Culoptila hamata*, new species, wings. 9A—forewing; 9B—hind wing.

Male genitalia (Fig. 11). Tergum IX with ventral margin usually rounded, occasionally acutely narrowed; sternum IX absent. Tergum X with apex variably developed, acute, truncate, or incised mesally; apicolaterally with sclerotized processes; processes setose, usually mesally curved apically. Preanal appendages absent. Inferior appendages fused to ventral surface of phallobase, usually short and linear, sometimes more elongate and curved mesally, apparently absent in *C. cantha* and *C. plummerensis*. Phallobase very large and rounded, weakly sclerotized (apparently membranous), with small rounded aperture in anterior or anteroventral margin; posterodorsally with sclerotized, projecting apex of variable development. Phallic spines 1 or 2, of variable length and development. Phallotremal sclerite fairly large, but often weakly sclerotized and inconspicuous, usually with more conspicuously sclerotized, paired, fingerlike posterodorsal processes.

Female genitalia. (Females unknown for many species). Segment VIII usually short

and synscleritous (Fig. 16A, B), deeply incised midlaterally on posterior margin. Tergum IX short, with pair of elongate, narrow apical cerci; sternum IX very short. Vaginal apparatus with distinctive, elongate, sclerotized, keyhole sclerite. Extraordinarily, as in Figs. 23A, B (*C. hamata*), with segment VIII not synscleritous and with tergum IX narrowed and elongate.

## SPECIES DESCRIPTIONS

### *Culoptila acaena* Bueno-Soria & Santiago-Fragoso

Fig. 10A, B

*Culoptila acaena* Bueno-Soria & Santiago-Fragoso 1996: 448.

This is a distinct species, most easily diagnosed by its unusual, short, rounded phallobase and the structure of the phallic spine, which is short and bears numerous accessory spine-like projections. In the latter character, it may show some relationship to *Culoptila kimminsi* Denning 1965 and *C. buenoi*, n. sp. Additional characters useful in identifying the species are the shape of the inferior appendages, which are more arched and laterally displaced than most species of *Culoptila*, and also the relatively short tergum X, which is either slightly incised or nearly acute apically.

Adult. Length of forewing: male 3.3 mm. Color yellowish-brown in alcohol, appendages paler. Mesothorax of male not noticeably modified; mesoscutal wart prominent, subtriangular, wide at anterior margin. Mesothoracic tegulae of male rounded, slightly enlarged; tegular gland very short, with several concertina-like folds.

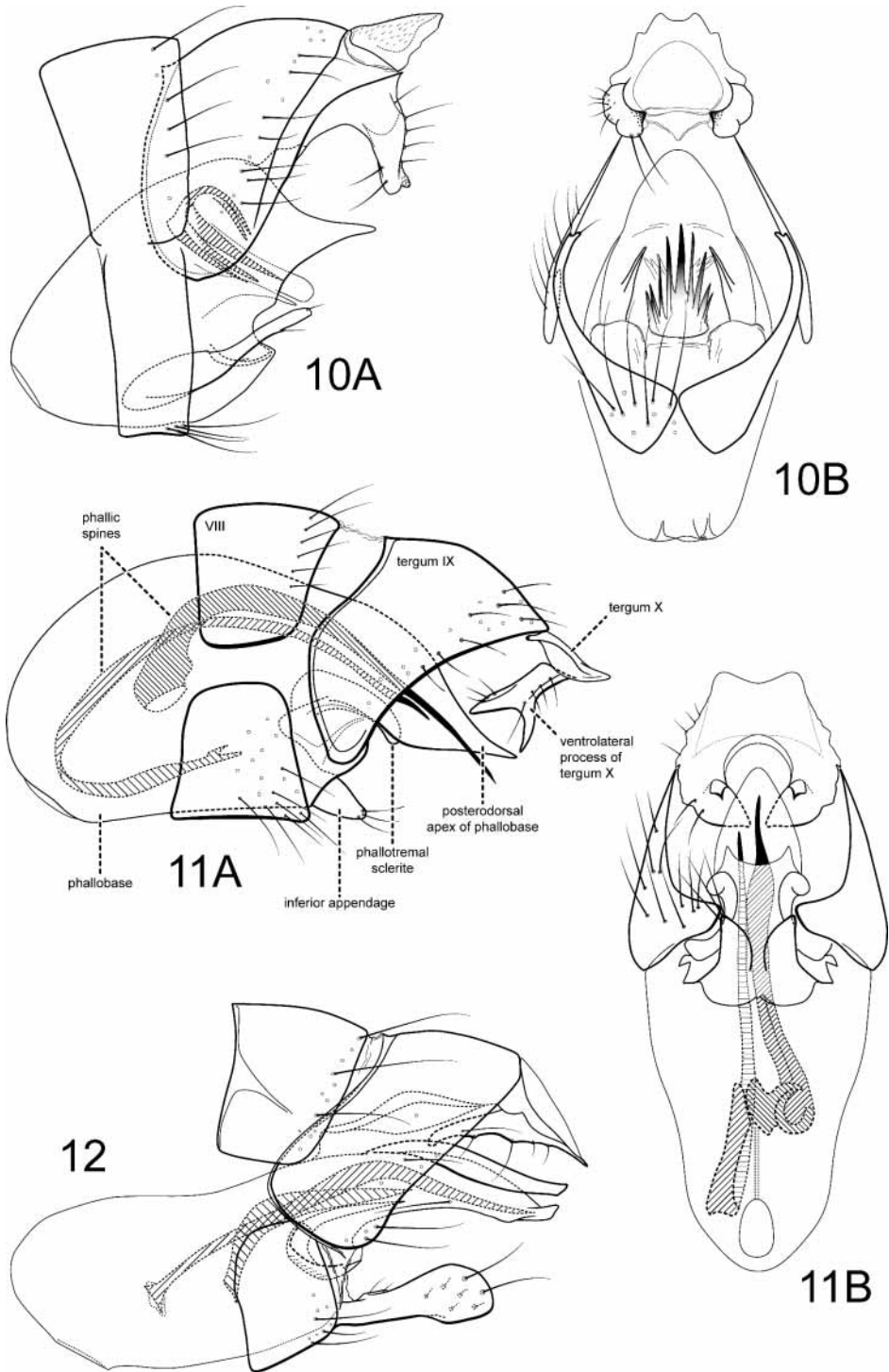
Male genitalia. Sternum VI process short, rounded. Tergum IX ventral margin broadly rounded, not produced posteroventrally. Inferior appendages moderately long, narrow apically, divergent basally, curving mesad apically. Tergum X short, about as long as wide, apex in ventral view variable, subacute or weakly incised mesally; ventrolateral processes with apices incurved, nearly planar in caudal view, mesal margin acute; apices not or scarcely posteriorly bent. Phallobase short, rounded in lateral view, apicodorsal projection short, with very distinct inflection at base, apex rounded. Phallic apparatus with only 1 apparent phallic spine, spine relatively short and divided into a number of accessory spines of varying lengths.

#### *Material examined*

**MEXICO: Guerrero:** NW Zihuatanejo, km 80, Ruta 130, 1200 m, 7.vi.1984 (Bueno & Barrera) — male holotype, 2 male paratypes, 1 male (UNAM).

#### *Distribution*

MEXICO (Guerrero).



**FIGURES 10–12.** Male genitalia. 10. *Culoptila acaena* Bueno-Soria & Santiago-Fragoso: 10A—lateral; 10B—ventral. 11. *Culoptila aluca* Mosely: 11A—lateral; 11B—ventral. 12. *Culoptila amberia* Mosely—lateral.

***Culoptila aluca* Mosely**

Figs. 6, 11A, B

*Culoptila aluca* Mosely 1954: 337.

This species is very similar to *Culoptila azulae* Bueno-Soria & Santiago-Fragoso 1996, and also to *C. bidentata*, n. sp. It differs from either of these by its shorter inferior appendages and also by the apical fork of the lateral process of tergum X, which is absent in *C. azulae* and less distinctly branched in *C. bidentata*. All of these species have a short, subtruncate tergum X and an inflated and much rounded phallobase with 2 prominent spines, 1 of which is much enlarged and heavily sclerotized basally. In *Culoptila aluca* the longer spine is the one without a prominent enlarged base, whereas the opposite is true in the other 2 species. In both *C. aluca* and *C. azulae* the tegulae of the males are much enlarged and the shape of the anterior margin of the thorax is consequently much narrowed (a character shared with a number of other species); in *C. bidentata* the tegulae of the males are only moderately enlarged and the shape of the thorax is not greatly modified.

One examined specimen of *C. aluca* had inferior appendages similar in size and shape to *C. azulae*. The form of the apicolateral process of tergum X and the shape and relative lengths of the phallic spines were otherwise typical of *C. aluca*.

Adult. Length of forewing: male 2.0–2.8 mm. Color yellowish-brown in alcohol, appendages paler. Mesothorax of male narrow and greatly acute anteromesally; mesoscutal wart elongate, narrowed, rounded anteromesally; mesoscutal setae long. Mesothoracic tegulae of male rounded, greatly enlarged; tegular setae long; tegular gland elongate, pleated, concertina-like.

Male genitalia. Sternum VI process short, rounded. Tergum IX ventral margin rounded, tapered from anterolateral margin, slightly produced posteroventrally. Inferior appendages short, subtruncate apically. Tergum X short, about as long as wide, apex in ventral view truncate to subtruncate; ventrolateral processes with apices incurved, nearly planar in caudal view, mesal margin acute; apices not or scarcely posteriorly bent, with prominent, diverging fork or branch from posterior margin, forming acute spine-like projection. Phallobase large, broadly rounded in lateral view, apicodorsal projection short, with slight inflection at base, apex subacute. Phallic apparatus with 2 phallic spines, one greatly elongate and narrow, strongly recurved at base, without basal enlargement, the other shorter, stouter, extending over 2/3 length of phallobase, basally greatly enlarged.

*Material examined*

**MEXICO: Guerrero:** Zihuaquio, km 95, ruta Ciudad Altamirano-Zihuatanejo, 24.vii.1985 (R. Barba) — 2 males (NMNH), 9 males (UNAM); Acahuizotla, 4.v.1982 (Barrera & Brailovsky) — 1 male (UNAM); **Morélos:** San Rafael V. Aranda, 26.iii.1982 (H. Velasco) — 1 male (UNAM); Vicente Aranda, Río Amacuzac, 26.ii.1986 (H. Velasco) — 37 males (NMNH), 303 males (UNAM); 2.5 km N of Huautla, Estación

C.E.A.M.I.S.H., 18°27'40"N, 099°02'29"W, 940 m, 14.ii.1996 (E. Gonzalez) — 3 males (UNAM); **Oaxaca**: Candelaria de Loxicha, Finca Pacífica, 510 m, 2.vi.1985 (E. Mariño) — 1 male (UNAM).

*Distribution*

MEXICO (Guerrero, Michoacán, Morélos, Oaxaca).

***Culoptila amberia* Mosely**

Fig. 12

*Culoptila amberia* Mosely 1954: 338.

This species is only known from the holotype male, and its relationship to other described species is not immediately evident. The most diagnostic character is the shape of the inferior appendages, which are relatively elongate and enlarged and rounded apically. Other useful characters for distinguishing this species include the shape of the phallobase, which is relatively parallel sided and has an arched, longitudinally subdivided apex, and the shape and relative lengths of the included spines.

Adult. Length of forewing: male 2.8 mm. Color not evident (microscope preparation). Mesothorax of male not present on slide preparation.

Male genitalia. Sternum VI process short, subtruncate. Tergum IX ventral margin subtruncate rounded, not produced posteroventrally. Inferior appendages long, narrowed basally, rounded apically. Tergum X short, about as long as wide, apex in ventral view broadly rounded (specimen mounted on slide in fixed lateral view); ventrolateral processes with apices incurved, nearly planar in caudal view, mesal margin acute; apices not or scarcely posteriorly bent. Phallobase elongate, dorsal and ventral margins subparallel in lateral view, apicodorsal projection arched, subdivided apically, apicodorsal projection elongate, apex subacute. Phallic apparatus with 2 phallic spines, one elongate, narrow, extending about 3/4 length of phallobase, sinuous, somewhat widened at middle, basally with abrupt sclerotized enlargement, the other spine much shorter, stouter, about 1/2 length of longer spine, without distinct basal enlargement.

*Material examined*

**MEXICO**: Liquidamber, 19.iii.1931 (A. Dampf) male holotype (NHM).

*Distribution*

MEXICO (Chiapas).

***Culoptila azulae* Bueno-Soria & Santiago-Fragoso**

Fig. 13A, B

*Culoptila azulae* Bueno-Soria & Santiago-Fragoso 1996: 451.

This species is most similar to *Culoptila aluca*, as discussed under that species, and is also similar to *C. bidentata*, n. sp. All of these species have a short, subtruncate tergum X and an inflated and much rounded phallobase with 2 prominent spines, one of which is enlarged and sclerotized basally. Both *C. azulae* and *C. aluca* have males with greatly enlarged tegulae, affecting the shape of the anterior margin of the thorax, which is consequently much narrowed; *C. bidentata* has only moderately enlarged tegulae and the shape of the thorax is not greatly modified. The most distinct differences of *C. azulae* from *C. aluca* include the longer inferior appendages, absence of an apparent apical fork on the lateral processes of tergum X, and the relative lengths of the included spines of the phallic apparatus. The shorter phallic spine in *C. azulae* is the one that lacks a pronounced basal enlargement. The form of the phallic spines is, however, very similar to *C. bidentata*, which differs in that the lateral processes of tergum X are forked, although less distinctly than in *C. aluca*, and also in having a shorter tergum X than *C. azulae*.

Adult. Length of forewing: male 2.0–2.2 mm. Color yellowish-brown in alcohol, appendages paler. Mesothorax of male narrow and greatly acute anteromesally; mesoscutal wart elongate, narrowed, rounded anteromesally. Mesothoracic tegulae of male rounded, greatly enlarged; tegular gland elongate, pleated, concertina-like.

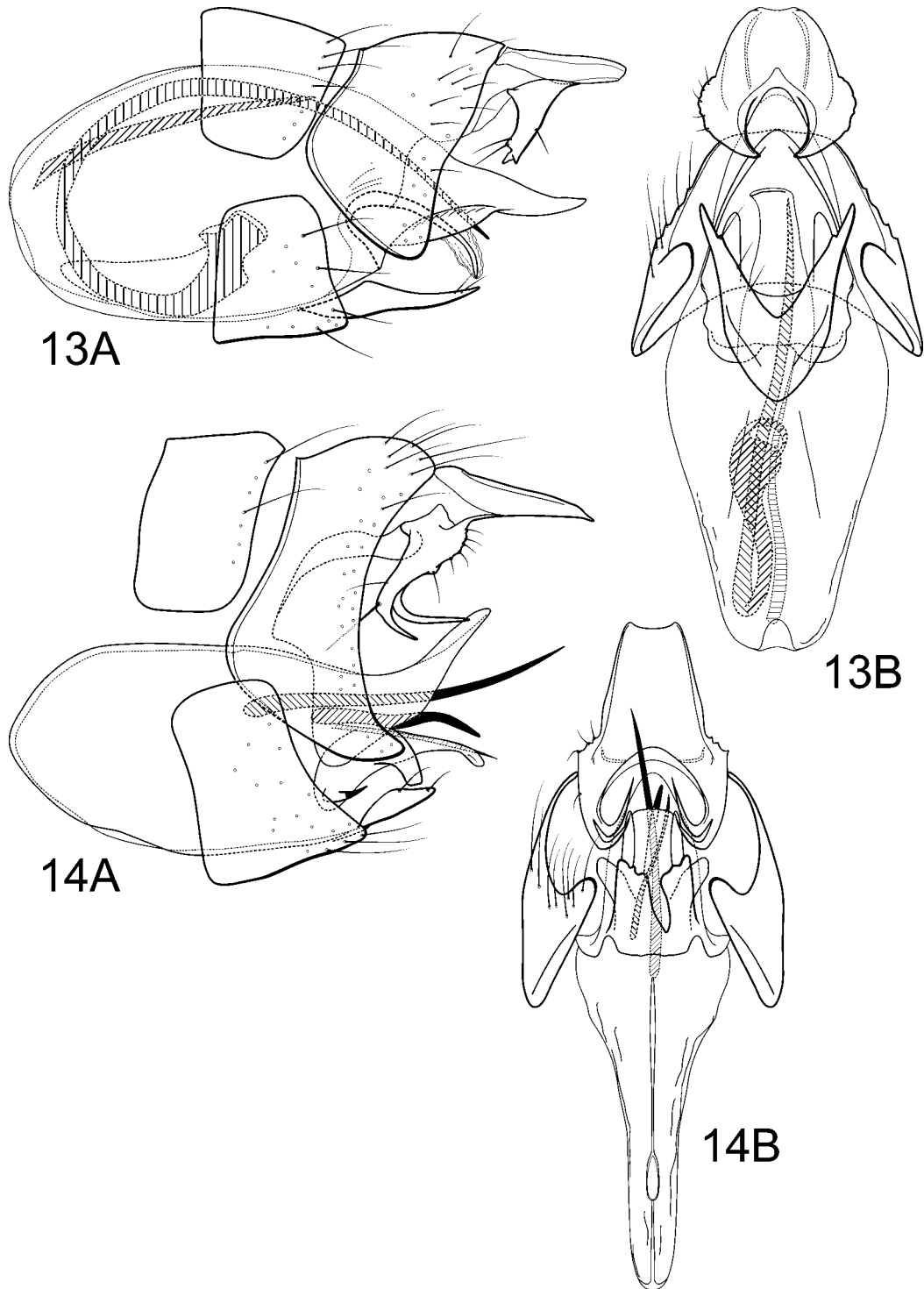
Male genitalia. Sternum VI process short, subtruncate. Tergum IX ventral margin rounded, tapered from anterolateral margin, slightly produced posteroventrally. Inferior appendages long, narrow apically, divergent from base. Tergum X short, about as long as wide, apex in ventral view broadly rounded to subtruncate; ventrolateral processes with apices incurved, nearly planar in caudal view, mesal margin acute; apices not or scarcely posteriorly bent. Phallobase large, broadly rounded in lateral view, apicodorsal projection short, with slight inflection at base, apex subacute. Phallic apparatus with 2 phallic spines, one greatly elongate, overall length exceeding length of phallobase, narrow, strongly recurved at base, basally greatly enlarged, sclerotized, the other spine elongate, about 1/2 length of phallobase, narrow, nearly straight, without basal enlargement.

*Material examined*

**MEXICO: Chiapas:** Ocosingo, Reserva Montes Azules, 29.iv.1986 (R. Barba, et al.) — 1 male (NMNH), male holotype, 4 male paratypes (UNAM).

*Distribution*

MEXICO (Chiapas).



**FIGURES 13–14.** Male genitalia. 13. *Culoptila azulae* Bueno-Soria & Santiago-Fragoso: 13A—lateral; 13B—ventral. 14. *Culoptila barrerai* Bueno-Soria & Santiago-Fragoso: 14A—lateral; 14B—ventral.



***Culoptila barrerai* Bueno-Soria & Santiago-Fragoso**

Fig. 14A, B

*Culoptila barrerai* Bueno-Soria & Santiago-Fragoso 1996: 448.

This distinctive species is not obviously similar to any other described species. It can be readily diagnosed by the elongate, apically truncate tergum X and the curved, acute, bifid apex of the lateral process of the same structure.

Adult. Length of forewing: male 2–2.6 mm. Color yellowish-brown in alcohol, appendages paler. Mesothorax of male slightly narrowed anteromesally; mesoscutal wart short, heart-shaped. Mesothoracic tegulae of male rounded, distinctly enlarged; tegular setae short; tegular gland short, pleated, concertina-like.

Male genitalia. Sternum VI process short, subtruncate. Tergum IX ventral margin rounded, tapered from anterolateral margin, distinctly produced posteroventrally. Inferior appendages short, subtruncate apically. Tergum X long, length greater than width, apex in ventral view truncate to subtruncate; ventrolateral processes with apices strongly curved and bifid, forming paired spine-like structures, both oriented posteriorly. Phallobase moderate in size, rounded in lateral view, apicodorsal projection moderately elongate, with very distinct upward inflection at base, apex rounded. Phallic apparatus apparently with three phallic spines, one elongate narrow, only slightly curved, slightly more than 1/2 length of phallobase, second narrow, slightly curved, about 1/2 length of longer spine, third spine about same length as second, very fine and needle-like (possibly part of phallosomal sclerite complex).

*Material examined*

**MEXICO: Oaxaca:** Pochutla, Finca Progreso, 2.vi.1987 (E. Barrera) — male holotype, 4 male paratypes (UNAM); Loxicha, 450 m, 22.x.1982 (J. Bueno-Soria) — 2 males (UNAM); Finca Pacifica, 2.vi.1985 (E. Barrera) — 5 male paratypes (NMNH).

*Distribution*

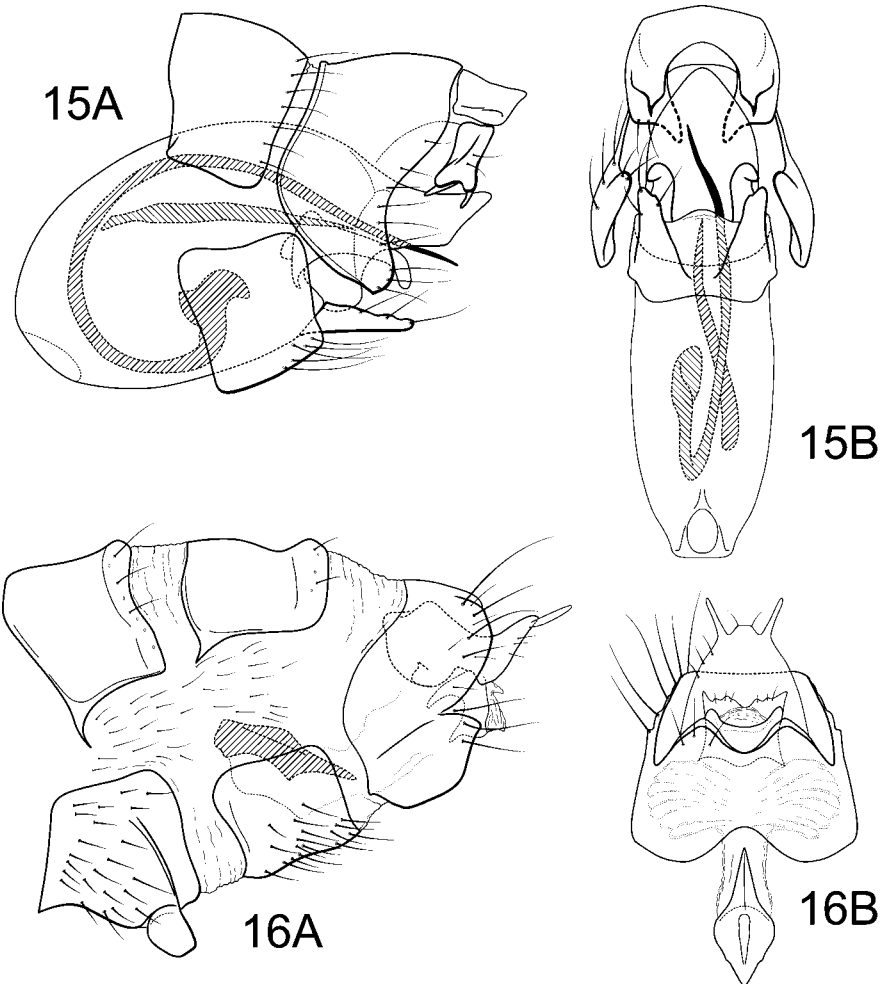
MEXICO (Oaxaca).

***Culoptila bidentata*, new species**

Figs. 15A, B, 16A, B

This species is probably closely related to *C. aluca* and *C. azulae*, agreeing in having an inflated phallobase with 2 prominent spines, one strongly curved and with a greatly enlarged base. In general form it probably most closely resembles *C. azulae* in that the longer spine is the one with the enlarged base and the inferior appendages are nearly as elongate. It differs from either of those species in being smaller overall, and with a shorter

tergum X. The apicolateral process of tergum X bears a prominent apical spine, somewhat like *C. aluca*, but not so enlarged and differently oriented.



**FIGURES 15–16.** *Culoptila bidentata*, new species. 15. Male genitalia: 15A—lateral; 15B—ventral. 16. Female genitalia: 16A—lateral; 16B—ventral.

Adult. Length of forewing: male 2–2.2 mm.; female 2.2–2.5 mm. Color brown in alcohol. Mesothorax of male not noticeably modified; mesoscutal wart prominent, subtriangular, wide at anterior margin. Mesothoracic tegulae of male flattened and weakly cupped, distinctly enlarged; tegular setae short; tegular gland short, pleated, concertina-like.

Male genitalia. Sternum VI process short, subtruncate. Tergum IX ventral margin rounded, tapered from anterolateral margin, slightly produced posteroventrally. Inferior appendages moderately long, narrow apically, divergent from base. Tergum X very short, length much less than width, apex in ventral view truncate to subtruncate; ventrolateral processes with apices incurved, slightly narrowed and anteriorly bent, and with diverging

fork or branch from posterior margin, forming acute spine-like projection. Phallobase large, broadly rounded in lateral view, apicodorsal projection short, with slight inflection at base, apex subacute. Phallic apparatus with 2 phallic spines, one greatly elongate, overall length exceeding length of phallobase, narrow, strongly recurved at base, basally greatly enlarged, sclerotized, the other spine elongate, narrow, nearly straight, about 1/2 length of phallobase, without basal enlargement.

*Material examined*

**Holotype male: COSTA RICA: Alajuela:** Río Pizote, ca. 5 km N Dos Rios, 10°56'53"N, 085°17'28"W, 470 m, 9.iii.1986 (Holzenthal & Fasth) (UMSP000018803) (UMSP).

**Paratypes: COSTA RICA: Alajuela:** same data as holotype — 1 male, 6 females (UMSP); Río Pizote, ca. 5 km (air) S Brasilia, 10°58'19"N, 085°20'42"W, 390 m, 12.iii.1986 (Holzenthal & Fasth) — 7 males (UMSP, NMNH, INBIO).

*Etymology*

The name *bidentata* was suggested by the bidentate apex of the lateral lobes of tergum X of this species.

***Culoptila buenoi*, new species**

Fig. 17A, B

This species is closely related to *Culoptila kimminsi* and together they form a distinctive species pair. They are similar in the general shape of the phallobase and its posterodorsal apex, and in the possession of a curved phallic spine with numerous smaller accessory spines. This curved phallic spine is apparently united basally with a 2nd, elongate spine, which is nearly straight and lacks accessory spines. A distinctive and diagnostic difference between *C. buenoi* and *C. kimminsi* is the shape of the inferior appendages. In both species they are relatively elongate and curved, but they are much more prominent and apically widened in *C. buenoi*.

Adult. Length of forewing: male 3 mm. Color brown in alcohol. Mesothorax of male narrow anteromesally; mesoscutal wart elongate, narrowed, rounded anteromesally; mesoscutal setae long. Mesothoracic tegulae of male rounded, distinctly enlarged; tegular setae long; tegular gland present, length not ascertained because gland not everted.

Male genitalia. Sternum VI process short, subtruncate. Tergum IX ventral margin acutely angled, tapered from anterolateral margin, not produced posteroventrally. Inferior appendages very long, wide apically, divergent basally, sharply curving mesad apically. Tergum X short, about as long as wide, apex in ventral view broadly rounded to subtruncate; ventrolateral processes with apices incurved, nearly planar in caudal view, mesal margin nearly orthogonal; apices not or scarcely posteriorly bent. Phallobase

moderate in size, rounded, anterior end narrowed, apicodorsal projection weakly arched, apicodorsal projection moderately elongate, apex subacute. Phallic apparatus with 2 phallic spines, phallic spines united basally, shorter spine much thickened, sinuously twisted around longer spine, with numerous, overlapping accessory spines, longer spine about 3/4 length of phallobase, weakly curved, apically narrowed, acuminate.

*Material examined*

**Holotype male: MEXICO: Puebla:** 26 km N Xicotepec de Juárez, km 93, Rta 130, 23.i.1985 (Bueno-Soria) (UMSP000092422) (UNAM).

Additional material examined: same data as holotype, 1 larva, 1 pupa (without abdomen), 2 male pupae, 1 female pupa (UNAM).

*Etymology*

We take great pleasure in naming this species for Dr. Joaquin Bueno-Soria, in honor of his many contributions to the taxonomy and systematics of Neotropical caddisflies.

***Culoptila cantha* (Ross)**

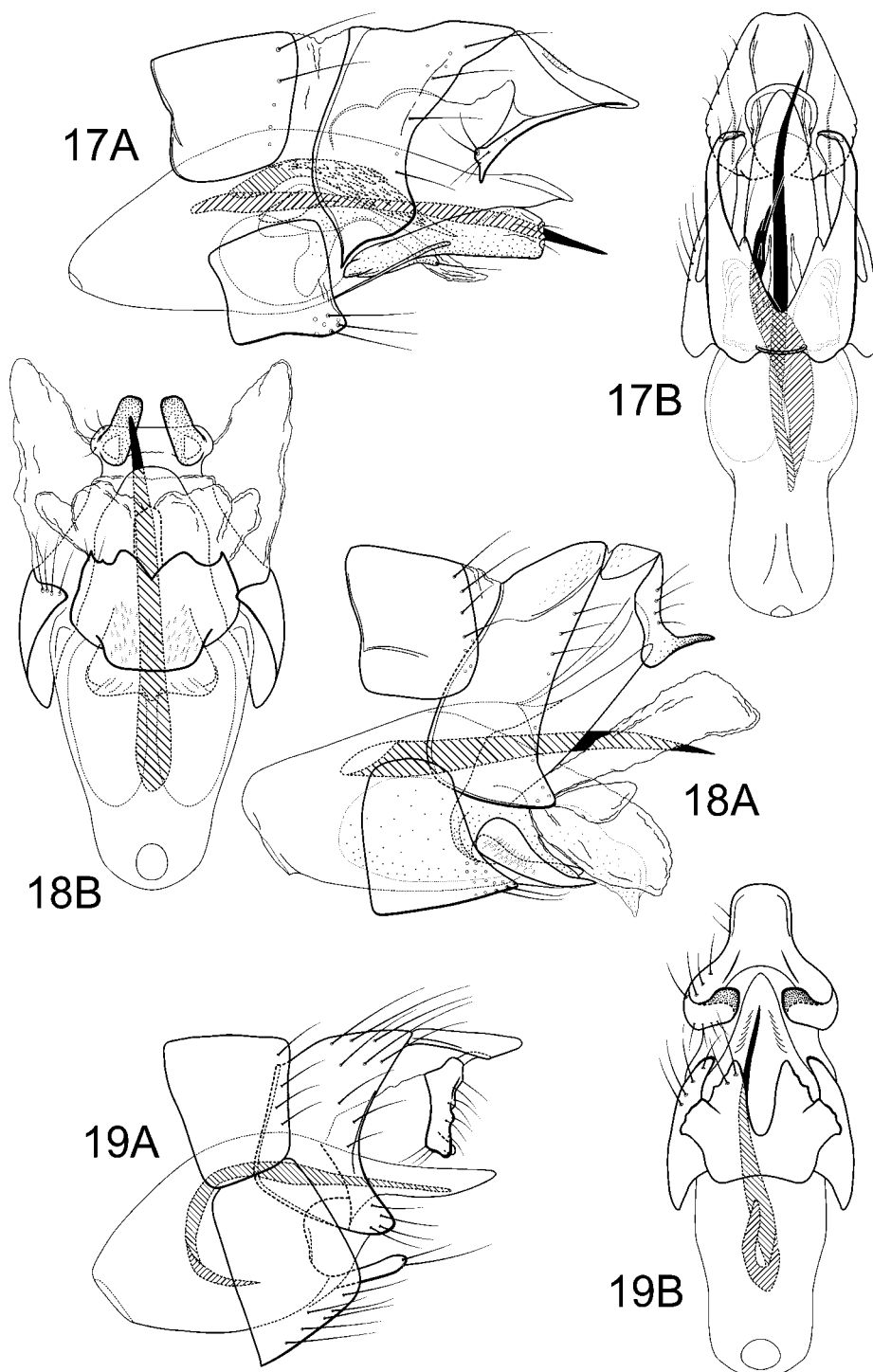
Figs. 7, 18A, B

*Protophila cantha* Ross 1938: 113.

*Culoptila cantha*—Flint 1974b; Schmid 1982; Houghton & Stewart 1998a, b.

This species is similar only to *C. plummerensis*, n. sp. and together comprise a distinctive species pair. In both species the phallobase is relatively short and bears a single stout phallic spine. Both species are also unusual in that the inferior appendages are apparently absent (or possibly reduced and fused to the phallostremal sclerite). Also, in both species the tegulae of the males are only minimally modified, and the associated glandular structures tiny. *Culoptila cantha* differs from *C. plummerensis* by the possession of numerous minute spines on the dorsal surface of the ventral plate of the phallostremal sclerite. Other diagnostic genitalic differences include the structure of tergum X, which is short and truncate in *C. cantha* and short, but apically acute in *C. plummerensis*, and the shape of the apex of the apicolateral process of tergum X, which is more distinctly and prominently bent in *C. cantha*. In addition to their structural differences, the species can be diagnosed by their distributions, eastern United States for *C. plummerensis* and west and southwestern United States for *C. cantha*.

Adult. Length of forewing: male 2.4–3 mm; female 2.5–3.2 mm. Color brown; wing chord evident, but scarcely paler in coloration. Mesothorax of male not noticeably modified; mesoscutal wart short, heart-shaped; mesoscutal setae short. Mesothoracic tegulae of male flattened, only slightly enlarged; tegular setae short; tegular gland present, very small, minimally developed.



**FIGURES 17–19.** Male genitalia. 17. *Culoptila buenoi*, new species: 17A—lateral; 17B—ventral. 18. *Culoptila cantha* (Ross): 18A—lateral; 18B—ventral. 19. *Culoptila cascada*, new species: 19A—lateral; 19B—ventral.

Male genitalia. Sternum VI process very short, rounded. Tergum IX ventral margin subtruncately rounded, slightly produced posteroventrally. Inferior appendages not evident, apparently absent, but phallosomal sclerite complex forming a distinctive, sclerotized ventral plate with minute spines on its dorsal surface. Tergum X very short, length much less than width, apex in ventral view truncate to subtruncate; ventrolateral processes with apices incurved and posteriorly bent, bend very prominent, approximately right angle, mesal margin of apex bluntly rounded, not acute. Phallobase relatively short, widening from base, dorsal and ventral margins more or less straight in lateral view, apicodorsal projection moderately elongate, with slight upward inflection at base, apex subacute. Phallic apparatus with 1 phallic spine, nearly length of phallobase, straight, often slightly recurved at base, stout at base, strongly tapered apically.

*Material examined*

**UNITED STATES: Arizona:** Clear Cr. Cmp., SE Camp Verde, 17.vi.1968 (Flint & Menke) — 1 male, 4 females (NMHH); Greenlee Co., Lower Blue River, F.R. 475, 33°17'00"N, 109°11'00"W, 1280 m, 21.vi.1999 (D.C. Houghton,) — 12 males (UMSP); Mohave Co., Hackberry, 14.vii.1975 (Cross) — 1 male, 12 females (NMNH); **Colorado:** Mesa Co., Colorado River, Hwy 6 nr. DeBeque, 11.viii.1973 (Baumann & Stark) — 1 male (NMNH); Moffat Co., Yampa River, below Maybell, 3.viii.1973 (Baumann & Stark) — 7 males, 2 females (NMNH); Yampa R., Maybell (Baumann & Stark) — 1 male, 1 female (NMNH); **New Mexico:** Grant Co., Grapevine Cmgd., Gila N.F., Rt. 15, 33°10'42"N, 108°12'18"W, 26.vii.2001 (C. & O. Flint,) — 1 male, 2 females (NMNH); Taos Co., Rio Grande, 6.vii.1953 (W.W. Wirth,) — 1 male (NMNH); **Texas:** Medina R., above Riomedina, 10.v.1960 (Flint & Collette) — 1 male (NMNH); **Wyoming:** Teton Co. Yellowstone National Park, Madison R., 23.v.1992 (G. Roemhild) — 33 males, 9 females (NMNH); same, except T135 R5E S36, 29.vi.1964 (J.R. Heaton) — 2 males, 12 females (NMNH).

*Distribution*

CANADA (Saskatchewan); UNITED STATES (Arizona, Colorado, Idaho, Montana, New Mexico, Texas, Utah, Washington, Wyoming).

***Culoptila cascada*, new species**

Fig. 19A, B

This species shows an evident similarity to *Culoptila hamata*, *C. tapanti*, and *C. unispina*, all also new species from Costa Rica. All of these species have a single phallic spine and a phallobase with a relatively elongate, extended dorsal apex. *Culoptila cascada* differs from any of those species by the shape of the phallobase, which is short and rounded in *C. cascada*, but elongate and parallel-sided in the other species. It also differs from these

other species by the shape of tergum X (short and subtruncate in *C. cascada*, but short and acute or subacute in *C. unispina*, elongate and acute in *C. hamata*, and elongate and deeply incised mesally in *C. tapanti*).

Adult. Length of forewing: male 2.5–3.2 mm; female 3.5 mm. Color dark brown; fore wing unmarked, marginal setae with bluish highlights at some light angles. Mesothorax of male not noticeably modified; mesothoracic wart and tegular structures not modified or not apparently so (only pinned specimens available).

Male genitalia. Sternum VI process short, subtruncate. Tergum IX ventral margin rounded, tapered from anterolateral margin, distinctly produced posteroventrally. Inferior appendages short, subacute apically. Tergum X short, about as long as wide, apex in ventral view truncate to subtruncate; ventrolateral processes with apices incurved and posteriorly bent, bluntly rounded, as viewed ventrally. Phallobase short, rounded in lateral view, apicodorsal projection moderately elongate, straight, apex acute. Phallic apparatus with 1 phallic spine, elongate, about 3/4 length of phallobase, narrow, strongly recurved basally.

#### *Material examined*

**Holotype male: COSTA RICA: Cartago:** Reserva Tapantí, Quebrada Palmitos & falls, ca. 9 km (road) NW tunnel, 09°43'12"N, 083°46'48"W, 1400 m, 1–2.viii.1990 (Holzenthal, Blahnik, & Muñoz) (UMSP000000495) (UMSP).

**Paratypes: COSTA RICA: Cartago:** same data as holotype, except 8–9.vi.1988 (C. & O. Flint, Holzenthal) — 3 males, 4 females (NMNH); same data as holotype — 2 males (UMSP, INBIO); Reserva Tapantí, waterfall, ca. 1 km (road) NW tunnel, 09°41'24"N, 083°45'36"W, 1600 m, 24.iii.1991 (Holzenthal, Muñoz, Huisman) — 1 male, 1 female (UMSP).

#### *Etymology*

The name *cascada*, Spanish for falls, was given to this species because all of the type material was collected in the vicinity of small falls or cascades.

#### *Culoptila costaricensis* Flint

Fig. 20A, B

*Culoptila costaricensis* Flint 1974a: 9.

This species is superficially most similar to *C. unispina*, n. sp. Both species have a similarly shaped phallobase, elongate and parallel-sided with an elongate projecting posterodorsal apex, and also a relatively short, apically acute tergum X. It differs from *C. unispina* in possessing 2 phallic spines rather than 1, and also by possessing shorter inferior appendages and a slightly shorter tergum X.

Adult. Length of forewing: male 3.5 mm. Color yellowish-brown in alcohol, appendages paler. Mesothorax of male not noticeably modified; mesoscutal wart short, heart-shaped; mesoscutal setae short. Mesothoracic tegulae of male rounded, small, unmodified; tegular setae short; tegular gland not discernable.

Male genitalia. Sternum VI process short, subtruncate. Tergum IX ventral margin rounded, tapered from anterolateral margin, distinctly produced posteroventrally. Inferior appendages short, subacute apically. Tergum X short, about as long as wide, apex in ventral view narrowed, subacute; ventrolateral processes with apices incurved and posteriorly bent, bend preapical and relatively weak, inner margin of apex subacute. Phallobase elongate, dorsal and ventral margins subparallel in lateral view, apicodorsal projection elongate, straight, apex acute. Phallic apparatus with 2 phallic spines, elongate, about 3/4 length of phallobase, narrow, subequal in length, one nearly straight, the other strongly recurved at base.

*Material examined*

**COSTA RICA: Cartago:** Ojo de Aqua, Route. 2, km 75, 20.vii.1967, (O.S. Flint), male holotype (USNM Type No. 72732) (NMNH).

*Distribution*

COSTA RICA.

***Culoptila denningi* Bueno-Soria & Santiago-Fragoso**

Fig. 21A, B

*Culoptila denningi* Bueno-Soria & Santiago-Fragoso 1996: 451.

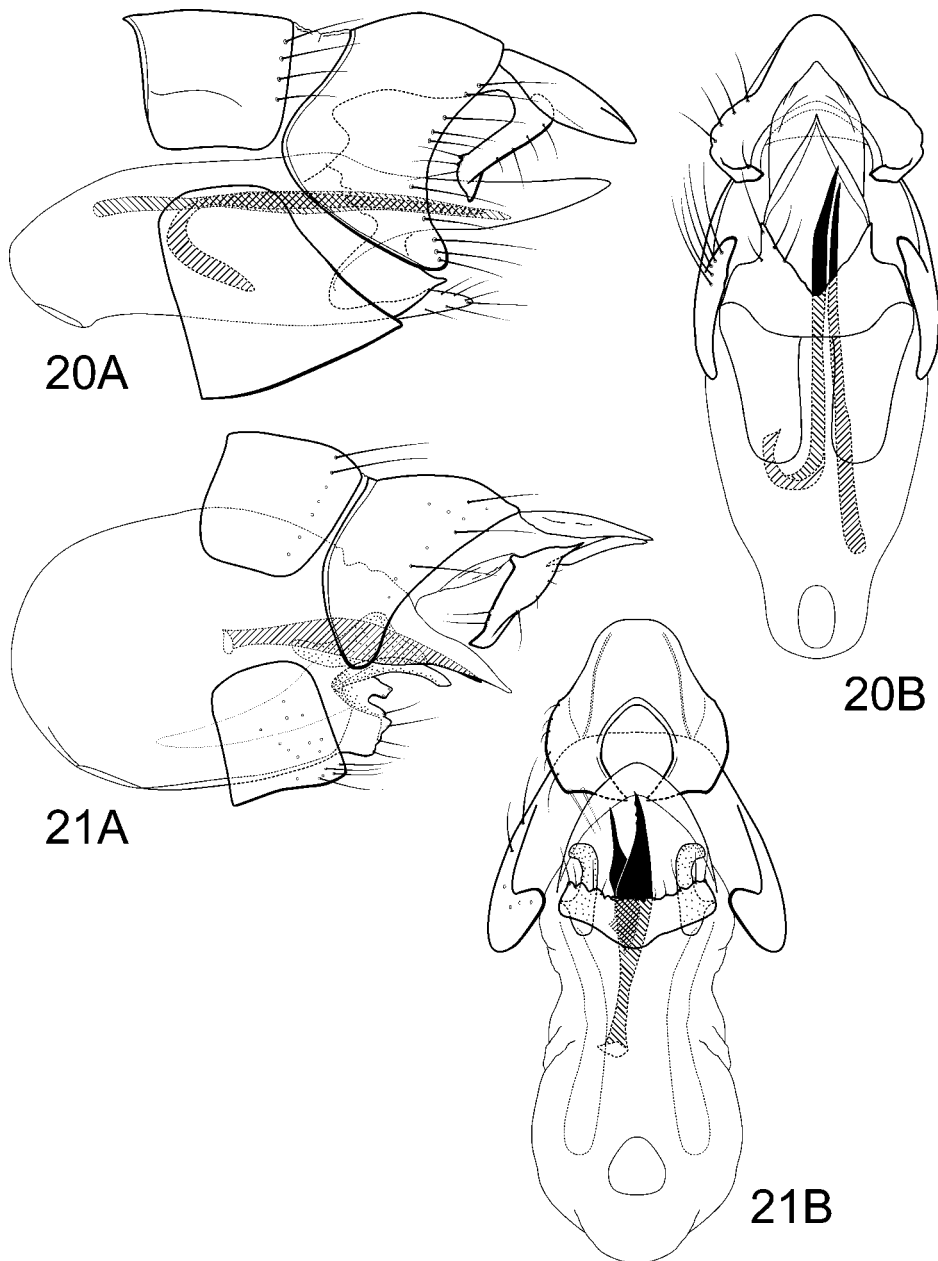
*Culoptila denningi* is not obviously similar to any other species of *Culoptila*. It is easily diagnosed by the shape of the phallobase, which is short and bulbously rounded and possesses 2 short and characteristically shaped phallic spines, the larger one much thickened at its center and the smaller one a mere sclerotized curl, so small that it could easily be missed. The short, subtruncate tergum X and short inferior appendages are also useful diagnostic characters.

Adult. Length of forewing: male 3 mm. Color yellowish-brown in alcohol, appendages paler. Mesothorax of male narrow anteromesally; mesoscutal wart short, heart-shaped. Mesothoracic tegulae of male rounded, greatly enlarged; tegular gland elongate, pleated, concertina-like.

Male genitalia. Sternum VI process short, subtruncate. Tergum IX ventral margin rounded, tapered from anterolateral margin, slightly produced posteroventrally. Inferior appendages very short, truncate apically. Tergum X short, about as long as wide, apex in ventral view broadly rounded to subtruncate; ventrolateral processes with apices incurved,



nearly planar in caudal view, mesal margin acute; apices not or scarcely posteriorly bent. Phallobase short, rounded in lateral view, apicodorsal projection weakly arched, apicodorsal projection short, apex rounded. Phallic apparatus with 1 apparent phallic spine and remnant of second; larger spine nearly straight, about 1/2 length of phallobase, thick, widened at middle, slightly enlarged basally, second (remnant?) spine easily missed, very short, flattened basally and wrapped around larger spine.



**FIGURES 20–21.** Male genitalia. 20. *Culoptila costaricensis* Flint: 20A—lateral; 20B—ventral. 21. *Culoptila denningi* Bueno-Soria & Santiago-Fragoso: 21A—lateral; 21B—ventral.

*Material examined*

**MEXICO: Guerrero:** NW Zihuatanejo, km 80, Ruta 130, 1200 m, 7.vi.1984 (Bueno & Barrera) — male holotype (UNAM); 1 male (NMNH).

*Distribution*

MEXICO (Guerrero).

***Culoptila hamata*, new species**

Figs. 9A, B, 4, 22A, B, 23A, B

This species is probably most closely related to *Culoptila tapanti*, n. sp. Both species are similar in having an elongate curved tergum X, a phallobase that is relatively parallel-sided, with an elongate, acute posterodorsal apex, and also in the possession of a single phallic spine, which is somewhat inflated mesally and tapers to a very fine needle-like apex. *Culoptila hamata* differs most notably *C. tapanti* in the form of the apex of tergum X (narrowed and acute in *C. hamata* and deeply emarginate in *C. tapanti*).

Adult. Length of forewing: male 2.2–3.2 mm; female 2.4–3.2 mm. Color brown; forewing with small whitish mark at arculus on wing margin. Mesothorax of male slightly narrowed anteromesally; mesoscutal wart short, heart-shaped. Mesothoracic tegulae of male rounded, distinctly enlarged; tegular setae short; tegular gland short, pleated, concertina-like.

Male genitalia. Sternum VI process short, subtruncate. Tergum IX ventral margin subtruncate rounded, slightly produced posteroventrally. Inferior appendages moderately long, subacute apically. Tergum X very elongate, narrow, strongly curved, apex in ventral view acute; ventrolateral processes with apices incurved and posteriorly bent, bluntly rounded and distinctly sclerotized. Phallobase elongate, dorsal and ventral margins subparallel in lateral view, apicodorsal projection very elongate, straight, apex acute. Phallic apparatus with 1 phallic spine, narrow and needle-like, about 1/2 length of phallobase, with rather abrupt, bulbous expansion in basal half.

*Material examined*

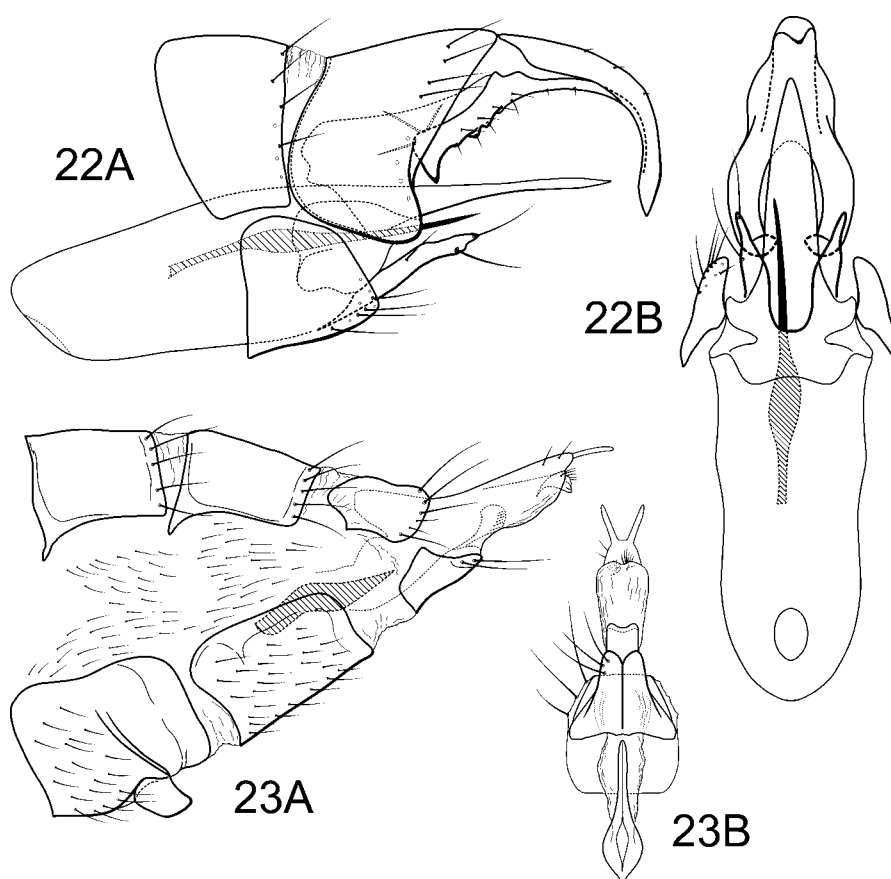
**Holotype male: COSTA RICA: Alajuela:** Río Toro, 3.0 km (road) SW Bajos del Toro, 10°12'14"N, 084°18'58"W, 1530 m, 3–4.ix.1990 (Holzenthal, Blahnik, & Huisman) (UMSP000000386) (UMSP).

**Paratypes: COSTA RICA: Alajuela:** same data as holotype — 1 male (UMSP); Río Sarapiquí, ca. 2 km SE Cariblanco, 10°17'56"N, 082°10'19"W, 710 m, 22.vi.1986 (Holzenthal, Heyn, & Armitage) — 15 males (UMSP); Reserva Forestal San Ramón, Río San Lorencito & tribs., 10°12'58"N, 084°36'25"W, 980 m, 30.iii.–1.iv.1987 (Holzenthal, Hamilton, & Heyn) — 951 males, 1044 females (UMSP, INBIO); same, 13–16.vi.1988 (C. & O. Flint, Holzenthal) — 92 males, 59 females (NMNH); same, 1–4.v.1990 (Holzenthal

& Blahnik) — 176 males, 138 females (UMSP); same, 28–30.viii.1990 (Holzenthall, Blahnik, & Muñoz) — 6 male (UMSP); same, 6–10.iii.1991 (Holzenthall, Muñoz, Huisman) — 59 males, 51 females (UMSP); Quebrada Latas, 8.9 km NE Bajos del Toro, 10°16'08"N, 084°15'36"W, 1030 m, 6.ix.1990 (Holzenthall, Blahnik, & Huisman) — 3 males, 3 females (UMSP); Reserva Bosque Nubosa Monte Verde, Río Peñas Blancas, 10°18'00"N, 084°44'24"W, 950 m, 1.iii.1986 (Holzenthall & Fasth) — 4 males, 15 females (UMSP); **Guanacaste:** Parque Nacional Guanacaste, Río Tempisquito, Maritza, 10°57'29"N, 085°29'49"W, 550 m, 30–31.viii.1990 (Huisman, Blahnik, & Quesada) — 60 males, 37 females (UMSP); same, 13–16.vii.1992 (F. Munoz) — 2 males (INBIO); Río Tempisquito Sur, Maritza, 10°57'00"N, 085°28'48"W, 600 m, 30.viii.1990 (Huisman & Quesada) — 172 males, 34 females (UMSP); ca. 0.7 km N Est. Maritza, 10°57'36"N, 085°30'00"E, 550m , 31.viii.1990 (Huisman & Quesada) — 16 males, 3 females (UMSP).

#### *Etymology*

This species is named *hamata*, from the Latin *hamus*, meaning hooked, in reference to the elongate, curved, or hooked apex of tergum X of this species.



**FIGURES 22–23.** *Culoptila hamata*, new species. 22. Male genitalia: 22A—lateral; 22B—ventral. 23. Female genitalia: 23A—lateral; 23B—ventral.

*Culoptila jamapa* Bueno-Soria & Santiago-Fragoso

Fig. 24A, B

*Culoptila jamapa* Bueno-Soria & Santiago-Fragoso 1996: 446.

This is a distinctive species, most readily diagnosed by its phallic spines, both of which are elongate and narrow, and one of which has a row of spaced accessory spines near its apex and also a characteristic, enlarged, sclerotized base. The elongate, arched dorsal apex of the phallobase is also distinctive. The species is also characterized by males with only minimally developed tegulae and tegular glands.

Adult. Length of forewing: male 2.8–3.8 mm; female 3.2–3.8 mm. Color yellowish-brown in alcohol, appendages paler. Mesothorax of male not noticeably modified; mesoscutal wart short, subtriangular, wide at anterior margin. Mesothoracic tegulae of male flattened, only slightly enlarged; tegular gland present, very small, minimally developed.

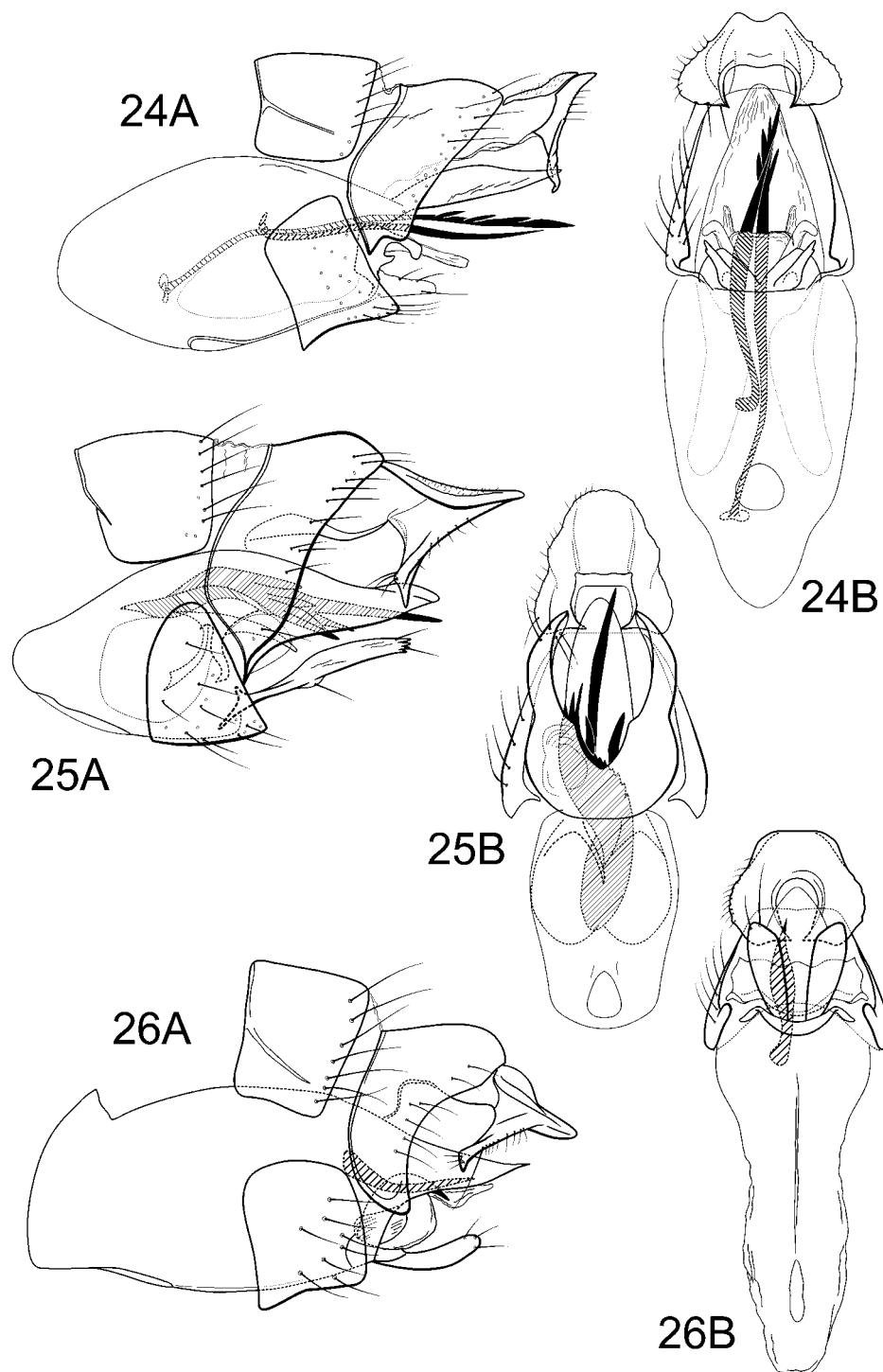
Male genitalia. Sternum VI process short, subtruncate. Tergum IX ventral margin acutely angled, tapered from anterolateral margin, not produced posteroventrally. Inferior appendages short, narrow apically, divergent from base. Tergum X short, length slightly less than width, apex in ventral view subtruncate, slightly concavely rounded; ventrolateral processes with apices incurved, nearly planar in caudal view, mesal margin acute; apices not or scarcely posteriorly bent. Phallobase moderate in size, rounded in lateral view, apicodorsal projection arched, apicodorsal projection elongate, apex subacute. Phallic apparatus with 2 phallic spines, both very narrow and elongate, only slightly, sinuously curved; longer spine about 3/4 length of phallobase, shorter spine about 2/3 length of longer one; longer spine in apical 1/3 with row of short accessory spines, subequal in length, basally with abrupt sclerotized enlargement.

*Material examined*

**MEXICO: Puebla:** Puente Apulco, 1400 m, 1.v.1987 (J. Bueno-Soria) — 2 male paratypes (UNAM); 20 km de Zacatlan, 1.v.1987 (J. Bueno-Soria) — 1 male paratype (UNAM); **Veracruz:** Río Jamapa, 6 km N Coscomatepec, 26.v.1981 (C. & O. Flint) — 7 males, 1 female (NMNH); Río Jamapa, ca. Coscomatepec, 26.v.1981 (J. Bueno-Soria) — 1 male (UNAM); Las Minas, 12.ix.1986 (J. Bueno-Soria) — 1 male (UNAM); Las Minas, ca. Perote, 20 km SW, 6.ix.1977 (J. Bueno-Soria) — 1 male paratype (UNAM); Río La Perla at La Perla, 14.xi.1993 (R. Baumann) — 4 males, 8 females (UNAM).

*Distribution*

MEXICO (Puebla, Veracruz).



**FIGURES 24–26.** Male genitalia. 24. *Culoptila jamapa* Bueno-Soria & Santiago-Fragoso: 24A—lateral; 24B—ventral. 25. *Culoptila kimminsi* Denning: 25A—lateral; 25B—ventral. 26. *Culoptila montanensis* Flint: 26A—lateral; 26B—ventral.

***Culoptila kimminsi* Denning**

Fig. 25A, B

*Culoptila kimminsi* Denning 1965: 270.

This species is closely related to *Culoptila buenoi* and together they comprise a distinctive species pair. They are similar in the general shape of the phallobase and its posterodorsal apex, and in the possession of a curved phallic spine with numerous smaller accessory spines. This curved phallic spine is apparently united basally with a 2nd, elongate spine, which is nearly straight and lacks accessory spines. A distinctive difference between *C. kimminsi* and *C. buenoi* is in the shape of the inferior appendages. In both species they are relatively elongate and curved, but they are much narrower in *C. kimminsi*.

Adult. Length of forewing: male 3.2–3.6 mm; female 3.2 mm. Color light brown; wing with nearly complete, linear whitish bar at wing anastomosis. Mesothorax of male narrow anteromesally; mesoscutal wart elongate, narrowed, rounded anteromesally; mesoscutal setae long. Mesothoracic tegulae of male rounded, greatly enlarged; tegular setae short; tegular gland large, rounded, with several pleated folds.

Male genitalia. Sternum VI process short, subtruncate. Tergum IX ventral margin acutely angled, tapered from anterolateral margin, not produced posteroventrally. Inferior appendages very long, narrow apically, divergent basally, curving mesad apically. Tergum X short, about as long as wide, apex in ventral view broadly rounded to subtruncate; ventrolateral processes with apices incurved, nearly planar in caudal view, mesal margin acute; apices not or scarcely posteriorly bent. Apicodorsal projection arched, moderately elongate, apex subacute. Phallic apparatus with 2 phallic spines, phallic spines united basally, shorter spine much thickened, sinuously twisted around longer spine, with numerous, overlapping accessory spines, longer spine about 2/3 length of phallobase, weakly curved, apically narrowed, acuminate.

*Material examined*

**UNITED STATES: Arizona:** Cochise Co., S.W.R.S., 5 mi W Portal, 1646 m, 7.iv.1965 — 1 male (NMNH); same, 23.v.–5.vi.1967 (C.W. Sabrosky,) — 2 males, 3 females (NMNH).

*Distribution*

UNITED STATES (Arizona).

***Culoptila montanensis* Flint**

Fig. 26A, B

*Culoptila montanensis* Flint 1967: 2.

This species is most similar to *Culoptila vexillifera*, n. sp. In both species the large, inflated phallobase has a laterally flattened apodeme extending from its anterodorsal margin. This apodeme is short and subtriangular in *C. montanensis*, but very elongate and rounded in *C. vexillifera*. An additional difference is that the phallic spine of *C. montanensis* is considerably shorter than *C. vexillifera*.

Adult. Length of forewing: male 3.5 mm. Color dark brown; wing with small whitish mark at arculus, anastomosis indistinctly marked. Mesothorax of male not noticeably modified; mesoscutal wart obscured by pin. Mesothoracic tegulae of male with elongate setae, not evidently modified (specimen on pin); tegular gland not discernable.

Male genitalia. Sternum VI process short, subtruncate. Tergum IX ventral margin rounded, tapered from anterolateral margin, distinctly produced posteroventrally. Inferior appendages moderately long, subtruncate apically. Phallosomal sclerite heavily sclerotized. Tergum X short, length slightly less than width, apex in ventral view truncate to subtruncate; ventrolateral processes with apices incurved, nearly planar in caudal view, mesal margin acute; apices not or scarcely posteriorly bent. Phallobase large, broadly rounded in lateral view, anterior margin compressed and keel-like, extending dorsally to form acute, trianguloid projection, apicodorsal projection moderately elongate, straight, apex subacute. Phallic apparatus with 1 phallic spine, very short, about 1/4 length of phallobase, weakly sinuous, widened at middle.

#### *Material examined*

**GUATEMALA: El Progreso:** Finca la Cajeta, 12–20.viii.1965 (Flint & Ortiz) — male holotype (UNSM Type No. 69569) (NMNH).

#### *Distribution*

GUATEMALA.

#### ***Culoptila moselyi* Denning**

Figs. 2, 8, 27A, B

*Culoptila moselyi* Denning 1965: 269; Wiggins 1996.

This species bears a general similarity to a number of species, but can be diagnosed by several characters taken in combination. The short, but subacute apex of tergum X is particularly diagnostic and will distinguish it from most other species with which it might be confused. An acute apex of tergum X is also typical of *C. rusia* and *C. pararusia*, n. sp., but in these species the apex is longer and more curved. Additional characters useful in diagnosing *C. moselyi* include an inflated phallobase with an arched posterodorsal apex and 2 relatively straight and prominent included spines, and very short rounded inferior appendages. The divided and arched apicodorsal projection of the phallobase is similar to

that of *C. amberia*, which, however, differs in a number of other points, including its much longer inferior appendages.

Adult. Length of forewing: male 2.8–3.8 mm; female 3.2–3.8 mm. Color light brown; wing with complete, linear whitish bar at wing anastomosis. Mesothorax of male narrow and greatly acute anteromesally; mesoscutal wart short, diamond-shaped, sharply angulate anteromesally; mesoscutal setae short. Mesothoracic tegulae of male rounded, greatly enlarged; tegular setae short; tegular gland elongate, pleated, concertina-like.

Male genitalia. Sternum VI process short, subtruncate. Tergum IX ventral margin acutely angled, tapered from anterolateral margin, not produced posteroventrally. Inferior appendages very short, truncate apically. Tergum X moderately long, length greater than width, apex in ventral view narrowed, subacute; ventrolateral processes with apices incurved, nearly planar in caudal view, mesal margin acute; apices not or scarcely posteriorly bent. Phallobase large, broadly rounded in lateral view, apicodorsal projection arched, subdivided apically, apicodorsal projection elongate, apex subacute. Phallic apparatus with 2 phallic spines, both elongate narrow, relatively straight; longer spine about 2/3 length of phallobase, shorter spine about 2/3 length of longer one.

#### *Material examined*

**UNITED STATES: Arizona:** Oak Creek Canyon, Halfway Camp, 18.vi.1968 (Flint & Menke) — 1 adult (missing abdomen), 7 males, 10 females (NMNH); Chiricahua Mts., E. Turkey Cr., 9.vi.1968 (Menke & Flint) — 1 male, 3 larvae, 2 pupae (NMNH); Apache Co., South Fork Little Colorado River, F.R. 560, nr S. Fork Cpgrd, 34°04'41"N, 109°24'38"W, 2347 m, 27.vi.1999 (D.C. Houghton) — 5 males (UMSP). **New Mexico:** Catron Co., Whitewater Canyon, 1.vi.1972 (W.W. Wirth) — 2 males (NMNH); Willow Crk., @ Willow Crk. Cmp. Gnd., 11.vi.1974 (W.P. Stark) — 2 males (NMNH); Whitewater Ck., Catwalk Picnic Area (W.P. Stark,) — 1 male, 1 female (NMNH).

#### *Distribution*

UNITED STATES (Arizona, New Mexico).

#### ***Culoptila nahuatl* Flint**

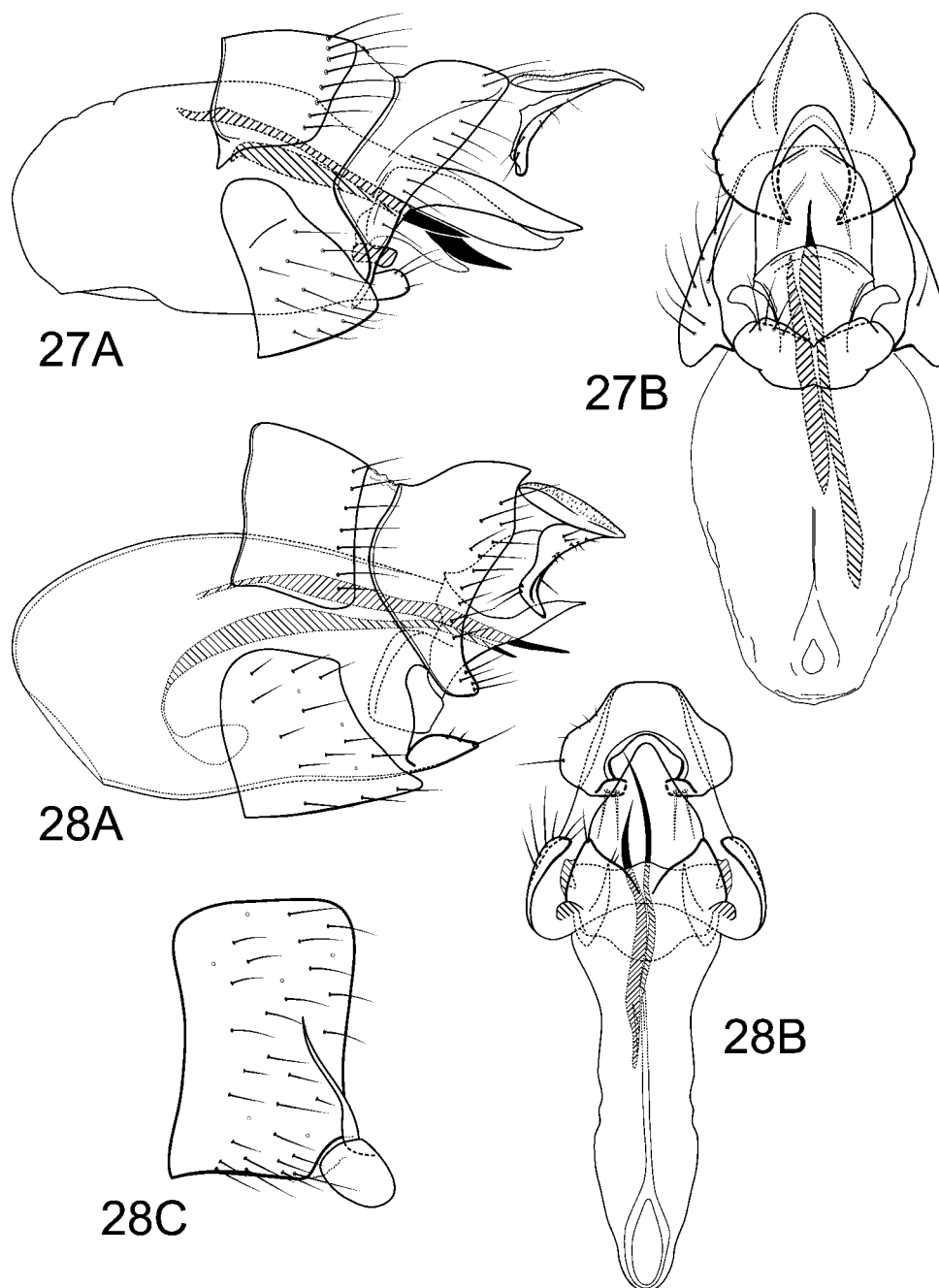
Fig. 28A–C

*Culoptila nahuatl* Flint 1974a: 8.

This species is similar to *Culoptila aluca*, *C. azulae*, and *C. bidentata*, agreeing in having a relatively short, subtruncate tergum X and an inflated phallobase with 2 prominent, curved spines. In *C. nahuatl*, however, the curved phallic spine, while enlarged basally, does not have the basal enlargement strongly sclerotized. *Culoptila nahuatl* differs most from *C. aluca* and *C. azulae* in having the posterodorsal apex of the phallobase distinctly upturned,



and by the very narrow ventral margin of tergum IX. It differs from *C. aluca* and *C. bidentata* by the absence of a strong spine (and apparent fork) of the ventrolateral processes of tergum X, and from *C. azulae* and *C. bidentata* by its shorter inferior appendages.



**FIGURES 27–28.** Male Genitalia. 27. *Culoptila moselyi* Denning: 27A—lateral; 27B—ventral. 28. *Culoptila nahuatl* Flint: 28A—lateral; 28B—ventral; 28C—ventral process of sternum VI, lateral.

Adult. Length of forewing: male 2.5 mm. Color light brown; wing without markings, anastomosis only indistinctly evident. Mesothorax of male narrow and greatly acute anteromesally; mesoscutal wart short, diamond-shaped, sharply angulate anteromesally. Mesothoracic tegulae of male rounded, greatly enlarged; tegular gland large, concertina-like, with small number of pleats (ca. 8–10).

Male genitalia. Sternum VI process short, subtruncate. Tergum IX ventral margin rounded, tapered from anterolateral margin, distinctly produced posteroventrally. Inferior appendages short, subacute apically. Tergum X short, length slightly less than width, apex in ventral view truncate to subtruncate; ventrolateral processes with apices incurved, mesal margin acute, or nearly so, apices slightly posteriorly bent, apical bend near apex and relatively weak, mesal margin of apex bluntly rounded, not acute. Phallobase large, broadly rounded in lateral view, apicodorsal projection short, with very distinct upward inflection at base, apex subacute. Phallic apparatus with 2 phallic spines, both elongate, narrow, weakly sinuous; longer spine about 2/3 length of phallobase, basal part distinctly recurved, with weakly sclerotized basal enlargement; shorter spine subequal, but lacking recurved base and basal enlargement.

#### *Material examined*

**MEXICO: Veracruz:** Fortín de las Flores, 17.v.1964 (Blanton et al.) — 32 male paratypes, 9 female paratypes (NMNH); same, except 24.vii.1966 (Flint & Ortiz) — male holotype (USNM Type No. 72731) (NMNH); Barranca de Metlac, ca. Fortín de las Flores, 30.iii.1976 (J. Bueno-Soria) — 129 males, 33 females (UNAM).

#### *Distribution*

MEXICO (Veracruz).

#### *Culoptila pararusia*, new species

Fig. 29A, B

This species is obviously very closely related to *Culoptila rusia* and resembles that species in the shape of tergum X, which is moderately elongate, curved, and acutely tapered apically. On average, the length of tergum X is slightly greater in *C. pararusia* (but not nearly so long as in *C. hamata* of Costa Rica). Primary differences are in the shape of the phallic spines, which are stout, straight, and subequal in length in *C. pararusia*, and always with 1 spine strongly curved in *C. rusia* and with the other elongate and very narrowly tapered apically. Also, the inferior appendages are acute apically in *C. rusia* and bluntly rounded in *C. pararusia*. The differences do not seem to be strictly geographical, since the distributions of the 2 species overlap.

Adult. Length of forewing: male 2–2.6 mm.; female 2.2–2.8 mm. Color yellowish-brown in alcohol, appendages paler. Mesothorax of male not noticeably modified;

mesoscutal wart short, heart-shaped. Mesothoracic tegulae of male flattened and weakly cupped, distinctly enlarged; tegular setae long; tegular gland short, pleated, concertina-like.

Male genitalia. Sternum VI process short, subtruncate. Tergum IX ventral margin subtruncately rounded, slightly produced posteroventrally. Inferior appendages short, subtruncate apically. Tergum X long, length greater than width, and distinctly curved, apex in ventral view acute; ventrolateral processes with apices incurved and posteriorly bent, bend prominent and strong, approximately right angle; apices of lateral processes much narrowed, inner margin of apex bluntly rounded, not acute. Phallobase large, broadly rounded in lateral view, apicodorsal projection elongate, straight, apex subacute. Phallic apparatus with 2 phallic spines, both elongate, about 3/4 length of phallobase, narrow, straight, subequal.

#### *Material examined*

**Holotype male: MEXICO: Chiapas:** trib. to Rio de Teapa on Mex.195, 1.5 mi. N Ixhuatan, 23.xii.1983 (Hamilton, Holzenthal, & Kovach) — (NMNH).

**Paratypes: MEXICO: Chiapas:** trib. to Rio de Teapa on Mex.195, 1.5 mi. N Ixhuatan, 23.xii.1983 (Hamilton, Holzenthal, & Kovach) — 6 males (NMNH); Ixtacomitan, 10.xii.1985 (R. Barba) — 6 males, 1 female (NMNH); 100 males, 2 females (UNAM); **Oaxaca:** San Mateo, Yetla Arroyo Virgen, km 50, Rta 175, 10.vii.1996 (Barba & Rojas) — 2 males (UNAM); **Veracruz:** Río Tacolapan, 25–26.vii.1966 (Flint & Ortiz) — 276 males, 942 females (NMNH), 10 males, 10 females (UMSP); Fortín de las Flores, 22.v.1965 (Rabago) — 4 males (NMNH); Barranca de Metlac, ca. Fortín de las Flores, 30.iii.1976 (J. Bueno-Soria) — 1 male (UNAM); Río Tlacotalpan, km 551, 26.vii.1966 (Flint & Ortiz) — 8 males, 14 females (UNAM); Los Tuxtlas, Río La Palma, ca. Estación de Biologica, 14.ix.1978 (J. Bueno-Soria) — 1 male (UNAM); Río Tecolapa, ca. Santiago Tuxtla, 28.vii.1976 (J. Bueno-Soria) — 65 males, 1 female (UNAM).

#### *Etymology*

This species is named *pararusia* (near *rusia*) because it was confused with *Culoptila rusia* in the material examined.

#### ***Culoptila plummerensis*, new species**

Fig. 30A, B

*Protophila cantha* Ross 1938 (in part); Blicke & Morse 1966.

This species is obviously very closely related to *Culoptila cantha* and was included among the paratype material of that species when it was described. Differences include the shape of tergum X, which is shorter and apically truncate in *C. cantha* and has its ventrolateral

processes more abruptly curved apically, and the structure of the ventral plate of the phallosomal sclerite. The latter is differently shaped in the 2 species and has numerous distinct small spines in *C. cantha*, which are absent in *C. plummerensis*. These differences are consistent among populations. *Culoptila cantha* is nearly constant in morphology over its wide distribution in the western United States, and populations of *C. plummerensis* from Maryland and Maine were also very similar to each other.

Adult. Length of forewing: male 2.5–2.9 mm; female 2.7–3.4 mm. Color light brown; wing chord evident, but scarcely paler in coloration. Mesothorax of male not noticeably modified; mesoscutal wart short, heart-shaped; mesoscutal setae short. Mesothoracic tegulae of male slightly flattened, minimally modified; tegular setae short; tegular gland possibly present (if so, only minimally developed).

Male genitalia. Sternum VI process short, subtruncate. Tergum IX ventral margin subtruncate rounded, slightly produced posteroventrally. Inferior appendages not evident, apparently absent, but phallosomal sclerite complex forming a distinctive, sclerotized ventral plate, lacking minute spines on its dorsal surface. Tergum X very short, length much less than width, apex in ventral view narrowed, subacute; ventrolateral processes with apices incurved and posteriorly bent, bend very prominent, slightly obtuse, mesal margin of apex bluntly rounded, not acute. Phallobase relatively short, widening from base, dorsal and ventral margins more or less straight in lateral view, apicodorsal projection moderately elongate, with slight upward inflection at base, apex subacute. Phallic apparatus with 1 phallic spine, nearly length of phallobase, straight, often slightly recurved at base, stout at base, strongly tapered apically.

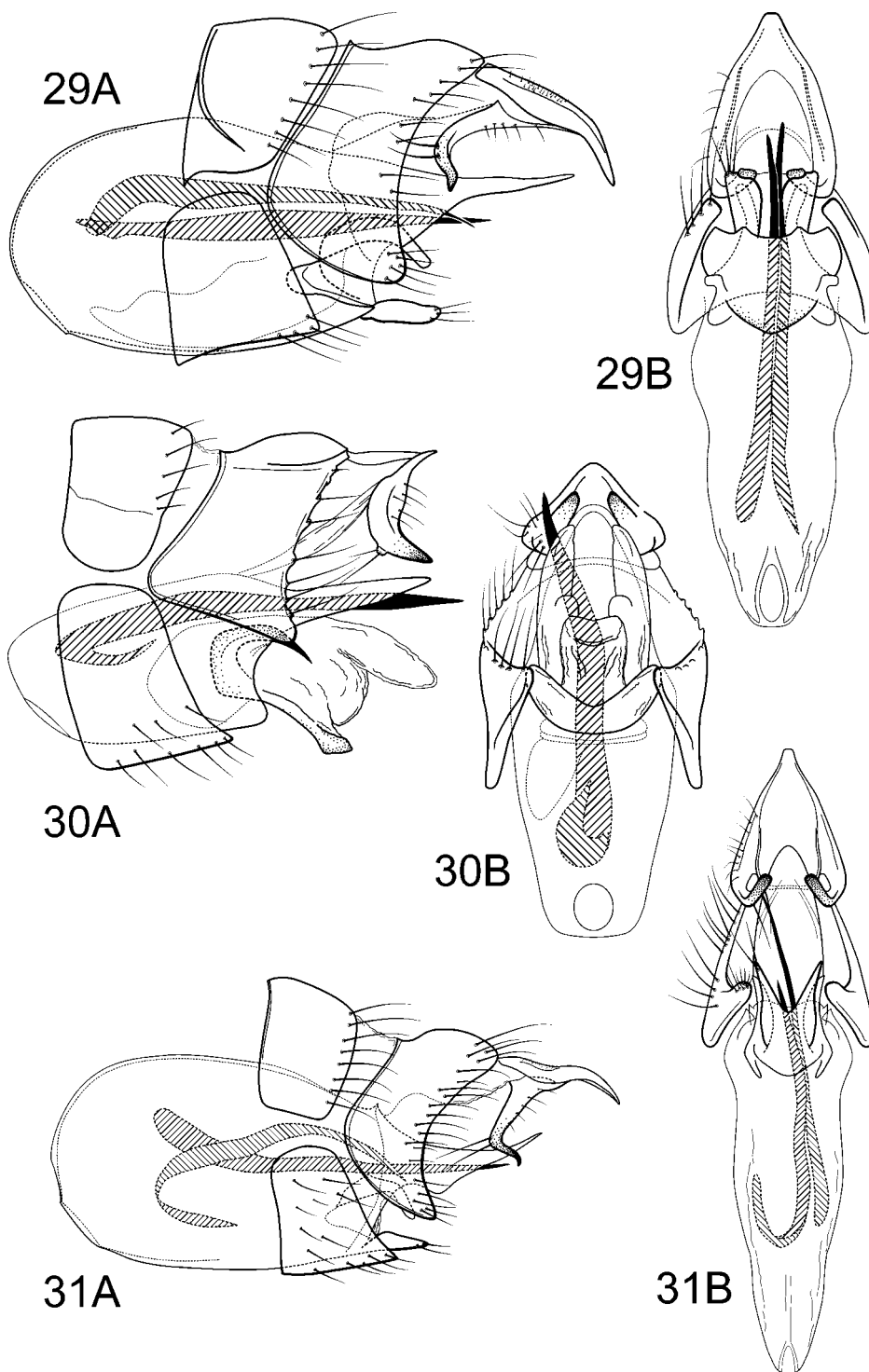
#### *Material examined*

**Holotype male: UNITED STATES: Maryland:** Plummers Island, 24.vi.1902 (R.P. Currie) (paratype of *C. cantha*) (UMSP000206886) (NMNH).

**Paratypes: UNITED STATES: Maine:** Lincoln, 8.vii — 1 male (NMNH); Big Black River (T15R13), 25.vii.1961 (A. Brower) — 32 males, 27 females (NMNH); **Maryland:** Plummers Island, (H.S. Barber) — 1 adult, 2 males (paratypes of *C. cantha*);— 1 male (paratype of *C. cantha*) (NMNH); 28.viii.1902 (Barber & Schwartz) — 1 male (paratype of *C. cantha*) (NMNH); 20.v.1903 (W.V. Warner) — 1 female (NMNH); Stubblefield Falls of Potomac (near Plummer's Island), 24.vi.1982 (H.S. Barber) — 45 males, 4 females (NMNH).

#### *Etymology*

This species is named for Plummer's Island, Maryland, where the holotype specimen was collected. The holotype specimen was selected from among specimens designated as paratypes for *Protoptila cantha* (now *Culoptila cantha*) by Ross (1938).



**FIGURES 29–31.** Male genitalia. 29. *Culoptila pararusia*, new species: 29A—lateral; 29B—ventral. 30. *Culoptila plummerensis*, new species: 30A—lateral; 30B—ventral. 31. *Culoptila rusia* Mosely: 31A—lateral; 31B—ventral.

*Culoptila rusia* Mosely

Fig. 31A, B

*Culoptila rusia* Mosely 1954: 341.

This is a distinctive species, most similar to *C. pararusia*. In both species tergum X is distinctly curved and apically acute, and the apices of the ventrolateral processes are also sclerotized and strongly bent or curved. Both species also have the phallobase inflated and possessing 2 long internal spines. Primary differences are in the shape of the phallic spines, which are stout, straight, and subequal in length in *C. pararusia*, and always with one spine strongly curved in *C. rusia* and with the other elongate and very narrowly tapered apically. Also, the inferior appendages are acute apically in *C. rusia* and bluntly rounded in *C. pararusia*. Among Costa Rican species with an apically acute tergum X, only *C. costaricensis* has 2 phallic spines. It differs in the shape and length of the spines, as well as in the shape of the phallobase.

Adult. Length of forewing: male 2.5–3 mm; female 2.7–3 mm. Color light brown; wing with only indistinctly evident crossband at anastomosis. Mesothorax of male not noticeably modified; mesoscutal wart short, heart-shaped; mesoscutal setae short. Mesothoracic tegulae of male flattened and weakly cupped, distinctly enlarged; tegular setae long; tegular gland short, pleated, concertina-like.

Male genitalia. Sternum VI process short, subtruncate. Tergum IX ventral margin rounded, tapered from anterolateral margin, distinctly produced posteroventrally. Inferior appendages short, subacute apically. Tergum X long, length greater than width, and distinctly curved, apex in ventral view acute; ventrolateral processes with apices incurved and posteriorly bent, bend prominent and strong, approximately right angle; apices of lateral processes much narrowed, inner margin of apex bluntly rounded, not acute. Phallobase large, broadly rounded in lateral view, apicodorsal projection elongate, with slight upward inflection at base, apex subacute. Phallic apparatus with 2 phallic spines, both elongate narrow, about 2/3 to 3/4 length of phallobase, one nearly straight, other with recurved base and distinct sinuous curvature.

*Material examined*

**GUATEMALA:** Chimaltenango, 19–20.viii.1965 (P.J. Spangler) — 71 males, 66 females (NMNH). **MEXICO: Chiapas:** Río Mixcum, Cocahuatan, 23.iii.1985 (H. Velasco) — 4 males (NMNH); Unión Juárez, Puente Colorado, ca. Tapachula, 14.iii.1984 (J. Bueno-Soria) — 7 males, 2 females (UNAM); Tapachula, Río Mixcum, 26.iii.1985 (H. Velasco) — 10 males (UNAM); **Veracruz:** Pte. Tacolapan, E. Tejada, 4.xii.1975 (C. & O. Flint) — 1 male (NMNH).

*Distribution*

MEXICO (Chiapas, Veracruz); GUATEMALA.

***Culoptila saltena* Mosely**

Fig. 32A, B

*Culoptila saltena* Mosely 1954: 342.

This is a distinct species, probably most closely related to *C. nahuatl*. Like that species, it has the posterodorsal apex of the phallobase strongly inflected and also the ventrolateral margin of tergum IX much narrowed. It is easily distinguished from any other species by the shape of tergum X, which is short, but deeply excavated mesally. Other distinguishing characters of *C. saltena* include the shape of the phallobase (parallel-sided), the phallic spines (1 elongate, 1 very short), and the acute apices of the inferior appendages.

Adult. Length of forewing: male 2–2.7 mm; female 2.5–3 mm. Color brown; wing with indistinct whitish wing bar at anastomosis. Mesothorax of male narrow anteromesally; mesoscutal wart elongate, narrowed, rounded anteromesally; mesoscutal setae long. Mesothoracic tegulae of male rounded, greatly enlarged; tegular setae short; tegular gland elongate, pleated, concertina-like.

Male genitalia. Sternum VI process short, subtruncate. Tergum IX ventral margin rounded, tapered from anterolateral margin, distinctly produced posteroventrally. Inferior appendages short, subacute apically. Tergum X short, length slightly less than width, apex in ventral view with deep, broadly rounded mesal incision, apicolateral margins acute; ventrolateral processes with apices incurved, nearly planar in caudal view, apices only weakly bent, mesal margin subacute, slightly rounded. Phallobase elongate, dorsal and ventral margins subparallel in lateral view, apicodorsal projection short, with very distinct upward inflection at base, apex subacute. Phallic apparatus with 2 phallic spines, one elongate and prominent, about 2/3 length of phallobase, narrow, gradually curved, other short and inconspicuous, 1/3 or less length of other spine.

*Material examined*

**GUATEMALA: El Progreso:** San Augustin Ac., 11–21.viii.1965 (Flint & Ortiz) — 1 male (NMNH); **Suchitepequez:** Puente Ixtacapa, 18–19.vi.1966 (Flint & Ortiz) — 1 male, 1 female (NMNH); same, except 28.vi.1966 (Flint & Ortiz) — 1 male, 3 females (NMNH). **HONDURAS:** Pespire, 1.viii.1967 (O.S. Flint) — 1 male (NMNH); El Zamorano, 28–29.i.1966 (G.F. Freytag) — 16 males, 4 females (NMNH); same, except 16.iv.1966 (G.F. Freytag) — 2 males (NMNH); Río Humuya, NW Comayagua, 3.viii.1967 (O.S. Flint) — 43 males, 6 females (NMNH), 2 males (UNAM). **MEXICO: Chiapas:** Tapachula, Río Izapa, 21.iv.1983 (Bueno & Arce) — 1 male (UNAM).

*Distribution*

MEXICO (Chiapas, Morelos); GUATEMALA; HONDURAS.

*Culoptila tapanti*, new species

Fig. 33A, B

This species is probably most closely related to *Culoptila hamata*. Both species are similar in having an elongate curved tergum X, a phallobase that is relatively parallel-sided, with an elongate, acute posterodorsal apex, and also in the possession of a single phallic spine, which is inflated mesally and tapers to a very fine needle-like apex. *Culoptila tapanti* differs from *C. hamata* (and all other species of *Culoptila*) by the shape of tergum X, which is not only elongate, but also deeply incised mesally.

Adult. Length of forewing: male 3–3.3 mm. Color brown; forewing with small whitish mark at arculus on wing margin. Mesothorax of male slightly narrowed anteromesally; mesoscutal wart short, heart-shaped; mesoscutal setae short. Mesothoracic tegulae of male flattened and weakly cupped, distinctly enlarged; tegular setae short; tegular gland short, pleated, concertina-like.

Male genitalia. Sternum VI process short, subtruncate. Tergum IX ventral margin subtruncately rounded, slightly produced posteroventrally. Inferior appendages moderately long, subacute apically. Tergum X long, length greater than width, and distinctly curved, apex in ventral view with deep, broadly rounded mesal incision, apicolateral margins acute; ventrolateral processes with apices incurved and posteriorly bent, bluntly rounded and distinctly sclerotized. Phallobase elongate, dorsal and ventral margins subparallel in lateral view, apicodorsal projection very elongate, straight, apex acute. Phallic apparatus with 1 phallic spine, narrow, needle-like, less than 1/2 length of phallobase, with abrupt, bulbous expansion in basal half.

*Material examined*

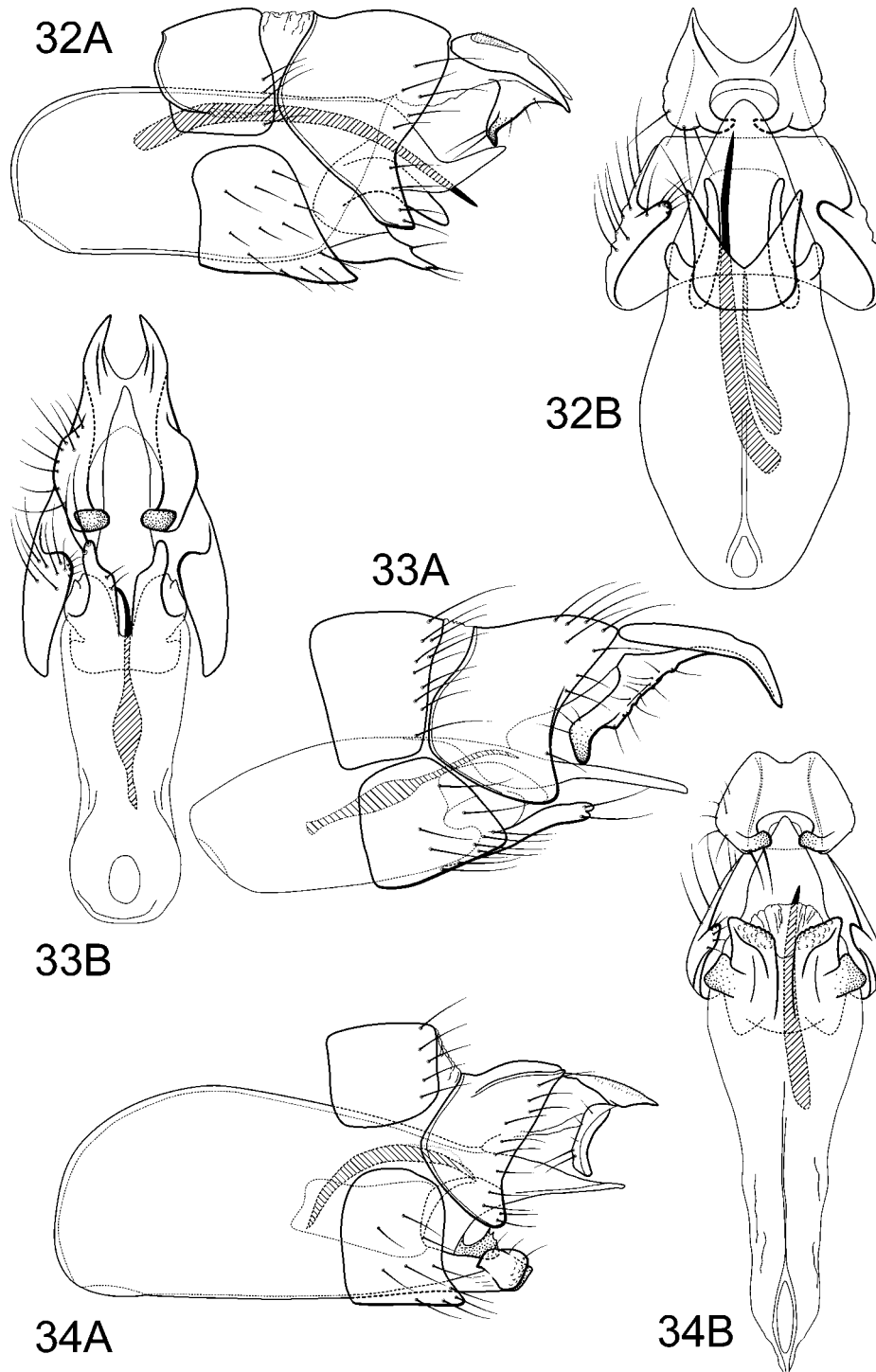
**Holotype male:** COSTA RICA: Cartago: Reserva Tapantí, Río Grande de Orosí, 09°41'10"N, 083°45'22"W, 1650 m, 18–21.iii.1987 (Holzenthal, Hamilton, & Heyn) (UMSP000000484) (UMSP).

**Paratypes:** COSTA RICA: Cartago: same data as holotype — 9 males (UMSP); Lago Orosi, 1.9 km SE Ujarrás, 09°49'26"N, 083°49'30"W, 980 m, 29.i.1986 (Holzenthal, Morse, & Fasth) — 2 males (UMSP); Quebrada Segunda @ administration building, 09°45'40"N, 083°47'13"W, 1250 m, 9–10.v.1990 (Holzenthal & Blahnik) — 1 male; Turrialba, 26.viii.1972 (G.F. & S. Hevel) — 3 males, 2 females (NMNH).

*Etymology*

This species is named *tapanti* for Tapantí National Park, the nearly pristine and beautiful site in Costa Rica where the type specimens were collected.





**FIGURES 32–34.** Male genitalia. 32. *Culoptila saltena* Mosely: 32A—lateral; 32B—ventral. 33. *Culoptila tapanti*, new species: 33A—lateral; 33B—ventral. 34. *Culoptila tarascanica* Flint: 34A—lateral; 34B—ventral.

***Culoptila tarascanica* Flint**

Fig. 34A, B

*Culoptila tarascanica* Flint 1974a: 9.

This is in some respects a relatively nondescript species of *Culoptila*, with a short tergum X, only very slightly incised apically, and short, blunt inferior appendages. The most diagnostic characters are the shape of the phallobase, which is more or less inflated basally and has a straight-projecting posterodorsal apex, and the possession of a single short curved phallic spine.

Adult. Length of forewing: male 2.7–3 mm. Color brown; wing nearly uniformly colored, indistinctly marked at anastomosis by paler coloration, wingbar scarcely evident. Mesothorax of male narrow anteromesally; mesoscutal wart elongate, narrowed, rounded anteromesally; mesoscutal setae long. Mesothoracic tegulae of male flattened and weakly cupped, distinctly enlarged; tegular setae long; tegular gland present, length not ascertained because gland not everted.

Male genitalia. Sternum VI process short, subtruncate. Tergum IX ventral margin rounded, tapered from anterolateral margin, distinctly produced posteroventrally. Inferior appendages short, truncate apically. Tergum X short, length slightly less than width, apex in ventral view subtruncate, slightly concavely rounded; ventrolateral processes with apices incurved, mesal margin acute, or nearly so, apices slightly posteriorly bent. Phallobase large, very broadly rounded anteriorly, narrowing slightly posteriorly, lateral margins distinctly compressed in ventral view, apicodorsal projection moderately elongate, straight, apex subacute. Phallic apparatus with 1 phallic spine, short, about 1/4 length of phallobase, curved.

*Material examined*

**MEXICO: Michoacán:** Carapan, Rt. 15, km. 431, 16.vii.1966 (Flint & Ortiz) — male holotype (USNM Type No. 72730), 2 male paratypes (NMNH).

*Distribution*

MEXICO (Michoacán).

***Culoptila thoracica* (Ross)**

Figs. 5, 35A, B

*Protoptila thoracica* Ross 1938: 114.*Culoptila thoracica*—Flint 1974b.

Perhaps the most immediately distinctive character of this species is the very enlarged

tegulae of the male (more so than any other species of *Culoptila*), which are accompanied by a correspondingly acutely narrowed mesothorax. In this respect it is similar to *C. nahuatl*, *C. tarascanica* and *C. saltena*, all of which also have enlarged tegulae and anteriorly narrowed thoraces, but it differs from those species in the details of the male genitalia. Unlike *C. saltena*, tergum X is short and truncate apically rather than deeply incised, and the apex of the phallobase is not nearly so abruptly upturned. It differs from *C. tarascanica* in having a phallobase with 2 included phallic spines, rather than 1; and it differs from *C. nahuatl* in the shape of its phallobase and phallic spines, as well as in having the posterodorsal apex of the phallobase less distinctly inflected.

Adult. Length of forewing: male 2.8–3.2 mm; female 3.2–3.8 mm. Color yellowish-brown in alcohol, appendages paler; wing uniformly colored, without evidence of cross bar. Mesothorax of male narrow and greatly acute anteromesally; mesoscutal wart elongate, narrowed, sharply angulate anteromesally; mesoscutal setae long. Mesothoracic tegulae of male rounded, greatly enlarged; tegular setae long; tegular gland elongate, pleated, concertina-like.

Male genitalia. Sternum VI process short, subtruncate. Tergum IX ventral margin rounded, tapered from anterolateral margin, slightly produced posteroventrally. Inferior appendages short, subtruncate apically. Tergum X short, about as long as wide, apex in ventral view truncate to subtruncate; ventrolateral processes with apices incurved, nearly planar in caudal view, mesal margin acute; apices not or scarcely posteriorly bent. Phallobase large, rounded anteriorly, with dorsal and ventral margins subparallel, apicodorsal projection short, with slight upward inflection at base, apex subacute. Phallic apparatus with 2 phallic spines, subequal in length, about 1/2 length of phallobase, strongly sinuously curved.

#### *Material examined*

**MEXICO: Chihuahua:** Río Gavilan, Gavilan Ranch (B. Kondratieff) — 1 male, 6 females (NMNH); **Michoacán:** Pedernales, El Salitre (E. Barrera) — 1 male (UNAM). **UNITED STATES: Arizona:** Apache Co: East Fork Black River, F.R. 276, nr. Aspen Cpgrd, 33°48'16"N, 109°19'10"W, 2286 m, 25.vi.1999 (D.C. Houghton) — 12 males, 5 females (UMSP); Greenlee Co: Lower Blue River, F.R. 475, 33°17'00"N, 109°11'00"W, 1280 m, 21.vi.1999 (D.C. Houghton) — 3 males; **Colorado:** Eagle Co: Eagle River, Gypsum, 10.viii.1973 (Baumann & Stark) — 3 males, 3 females (NMNH); Grand Co: Fraser R., Granby, 4.viii.1973 (Baumann & Stark) — 2 males (NMNH); Colorado River, nr. Hot Sulphur Springs (Baumann & Stark) — 1 male (NMNH); **New Mexico:** Catron Co: Whitewater Ck., Catwalk Picnic Area, 11.vi.1974 (W.P. Stark) — 9 males, 34 females (NMNH).

#### *Distribution*

UNITED STATES (Arizona, Colorado, New Mexico, Utah, Wyoming); MEXICO (Chihuahua, Michoacán). [Also reported by Wray (1950) for North Carolina, but this

record is unconfirmed and suspect because of its very disjunct distribution; it may be in error or refer to *C. plummerensis*, n. sp. We were unable to check the identity of Wray's specimens as they could not be located in the North Carolina Department of Agriculture Collection (Bob Blinn, personal communication).]

***Culoptila unispina*, new species**

Figs. 3, 36A, B

This species is probably most closely related to *Culoptila hamata* and *C. tapanti*, agreeing in the shape of the phallobase (elongate and parallel-sided), and in the possession of a single phallic spine. It differs from either of those species in that the phallic spine is not inflated mesally and additionally in that tergum X is acute and only moderately elongate, as opposed to very elongate in the other 2 species (acute in *C. hamata*, deeply incised in *C. tapanti*). *Culoptila unispina* also bears a general similarity to *C. costaricensis*, which differs, however, in having 2 phallic spines, a shorter tergum X and also shorter inferior appendages.

Adult. Length of forewing: male 2.9–3.2 mm; female 3.2–4 mm. Color dark brown; forewing with small whitish mark at arculus on wing margin. Mesothorax of male not noticeably modified; mesoscutal wart short, heart-shaped; mesoscutal setae short. Mesothoracic tegulae of male flattened and weakly cupped, distinctly enlarged; tegular setae short; tegular gland short, pleated, concertina-like.

Male genitalia. Sternum VI process short, subtruncate. Tergum IX ventral margin subtruncate rounded, slightly produced posteroventrally. Inferior appendages moderately long, acute apically. Tergum X long, length greater than width, apex in ventral view narrowed, subacute; ventrolateral processes with apices incurved and posteriorly bent, bluntly rounded and distinctly sclerotized. Phallobase elongate, dorsal and ventral margins subparallel in lateral view, apicodorsal projection elongate, straight, apex subacute. Phallic apparatus with 1 phallic spine, elongate, more than 1/2 length of phallobase, narrow, weakly sinuously curved.

*Material examined*

**Holotype male:** COSTA RICA: **Puntarenas:** Río Bellavista, ca. 1.5 km NW Las Alturas, 08°57'04"N, 082°50'46"W, 1400 m, 10–11.viii.1990 (Holzenthal, Blahnik, & Muñoz) (UMSP000000497) (UMSP).

**Paratypes:** COSTA RICA: **Puntarenas:** same data as holotype, 1 female (UMSP); same, except 8–9.iv.1987 (Holzenthal, Hamilton, & Heyn) — 3 males (UMSP); Río Cotón, in Las Alturas, 08°56'17"N, 082°49'34"W, 1360 m, 16.ii.1986 (Holzenthal, Morse, & Fasth) — 2 males (UMSP); Zona Protectora Las Tablas, Río Cotón, Sitio Cotón, 08°56'28"N, 082°47'13"W, 1460 m, 15.iv.1989 (Holzenthal & Blahnik) — 5 males, 3 females (UMSP); **San José:** Río Chirripó Pacífico, 9.5 km NE Rivas, 09°28'12"N,

083°35'28"W, 1370 m, 23.ii.1986 (Holzenthal, Morse, & Fasth) — 1 male (UMSP).  
**PANAMA: Chiriquí:** Boquete, brook at Hotel Fundadores, 1200 m, 29.v.1983 (Spangler, Faitoute, & Steiner) — 4 males; 52 females (NMNH).

#### *Etymology*

This species is named *unispina* (1 spine) for its single phallic spine, which distinguishes it most readily from *Culoptila costaricensis*, with which it might otherwise be confused.

#### *Culoptila vexillifera*, new species

Fig. 37A, B

This species is most similar to *Culoptila montanensis*. Both species have a large and inflated phallobase with a laterally flattened apodeme extending from the anterodorsal margin. This apodeme is short and subtriangular in *C. montanensis*, but very elongate and rounded in *C. vexillifera*. An additional difference is that the phallic spine of *C. vexillifera* is considerably longer than *C. montanensis*.

Adult. Length of forewing: male 3.7 mm. Color dark brown; wing with small whitish mark at arculus, anastomosis indistinctly marked. Mesothorax of male not noticeably modified; mesoscutal wart short, heart-shaped; mesoscutal setae short. Mesothoracic tegulae of male with elongate setae, not evidently modified (specimen on pin); tegular gland not discernable.

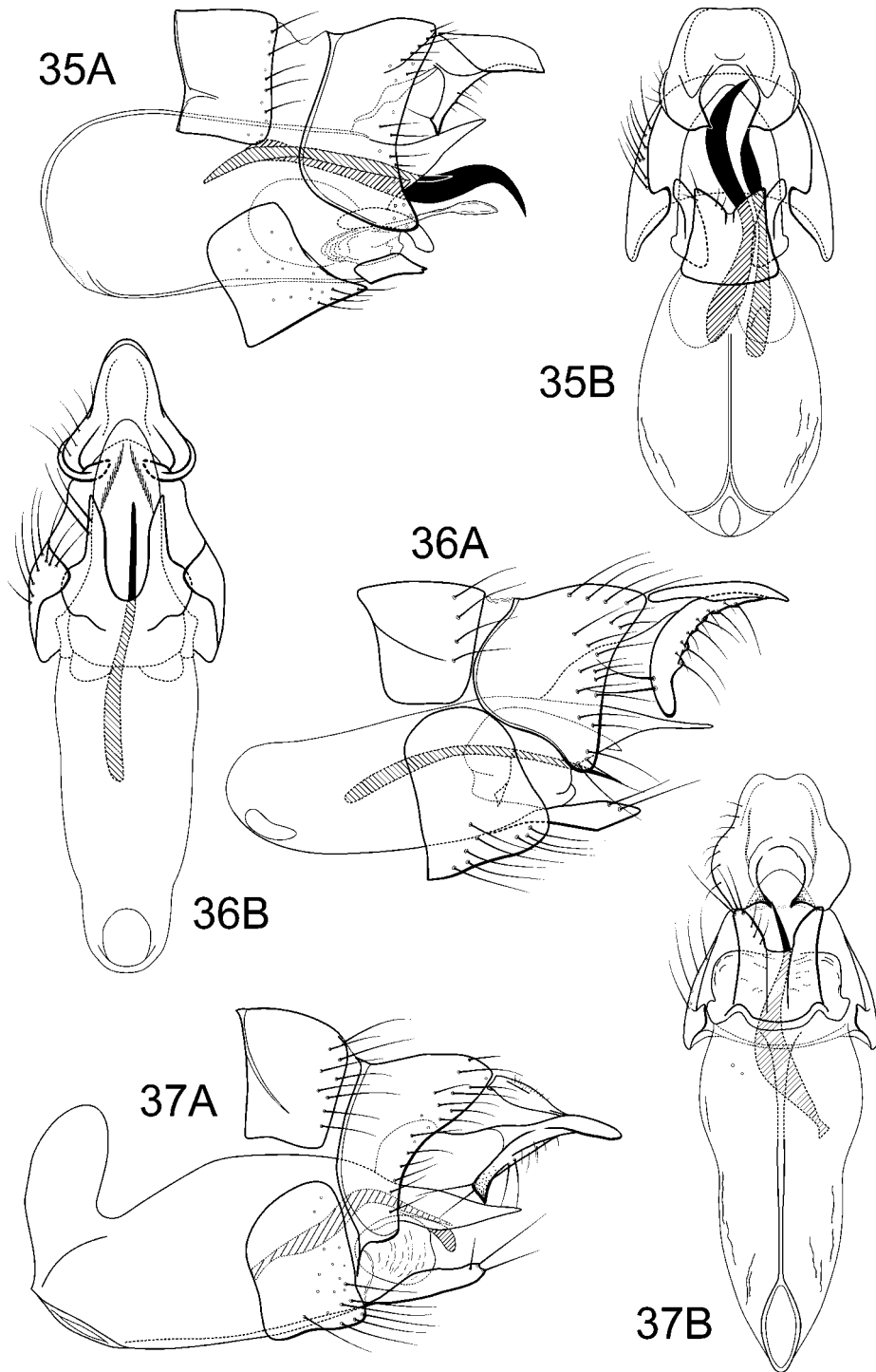
Male genitalia. Sternum VI process short, subtruncate. Tergum IX ventral margin acutely angled, tapered from anterolateral margin, slightly produced posteroventrally. Inferior appendages moderately long, subacute apically. Phallosclerite heavily sclerotized and somewhat rugose. Tergum X short, about as long as wide, apex in ventral view truncate to subtruncate; ventrolateral processes with apices incurved, nearly planar in caudal view, mesal margin acute; apices not or scarcely posteriorly bent. Phallobase large, broadly rounded in lateral view, anterior margin compressed and keel-like, extending dorsally to form prominent, rounded projection, apicodorsal projection moderately elongate, straight, apex subacute. Phallic apparatus with 1 phallic spine, short, less than 1/2 length of phallobase, distinctly sinuous, widened at middle.

#### *Material examined*

**Holotype male: GUATEMALA:** Chimaltenango, 19–20.viii.1965 (Spangler) (UMSP000206898) (NMNH).

#### *Etymology*

This species is named *vexillifera*, from the Latin *vexillum*, meaning banner or flag, in reference to the large apodeme at the base of the phallobase of this species.



**FIGURES 35–37.** Male genitalia. 35. *Culoptila thoracica* (Ross): 35A—lateral; 35B—ventral. 36. *Culoptila unispina*, new species: 36A—lateral; 36B—ventral. 37. *Culoptila vexillifera*, new species: 37A—lateral; 37B—ventral.

It should be possible to identify most species simply by direct comparison to illustrations and reference to the species diagnoses and descriptions. The following key is provided to help the user focus on characters most useful in identifying species. These include, especially, the shape of tergum X and its ventrolateral processes, the shape of the phallobase and its posterodorsal apex, the number, shape, and development of the included phallic spines, and the shape and length of the inferior appendages. A few species are keyed out more than once in the key. This was done when a character used was either variable within a species or likely to be misinterpreted by the user. The key should always be used in conjunction with the illustrations and diagnoses. Attention should also be given to the provenance of the specimens, bearing in mind that the distributional data for many species is incomplete.

- 1 Apex of tergum X distinctly acutely narrowed in ventral view (Figs. 20B, 22B, 30B) ..... 2  
 Apex of tergum X rounded, truncate, or incised medially in ventral view (Figs. 11B, 13B, 32B) ..... 10
- 2(1) Phallic spine divided into a number of short accessory spines (Fig. 10) [apex of tergum X occasionally subacute, variable in specimens examined].....  
 ..... *C. acaena* Bueno-Soria & Santiago-Fragoso  
 Phallic spines 1 or 2, entire, not subdivided ..... 3
- 3(2) One phallic spine ..... 4  
 Two phallic spines ..... 7
- 4(3) Tergum X very elongate and strongly curved (Fig. 22)..... *C. hamata*, new species  
 Tergum X short or only moderately elongate (Figs. 30, 36)..... 5
- 5(4) Tergum X very short, apices of ventrolateral processes strongly bent (lateral view); phallic spine large and prominent and nearly straight, nearly length of phallobase (Fig. 30) (NE United States)..... *C. plummerensis*, new species  
 Tergum X moderate in length, apices of ventrolateral process less distinctly bent; phallic spine much shorter than phallobase (Fig. 36), or strongly recurved (Fig. 19) (Costa Rica)..... 6
- 6(5) Phallobase (lateral view) elongate, parallel-sided; phallic spine not greatly recurved basally (Fig. 36A)..... *C. unispina*, new species  
 Phallobase (lateral view) short, rounded; phallic spine strongly recurved at base (Fig. 19A) [apex of tergum X subtruncate rather than acute, but distinctly narrowed]..... *C. cascada*, new species
- 7(3) Phallobase (lateral view) nearly parallel sided (Fig. 20A) (Costa Rica) .....  
 ..... *C. costaricensis* Flint  
 Phallobase (lateral view) more rounded (Figs. 27A, 29A) (United States, Mexico, Guatemala)..... 8

- 8(7) Tergum X short, apices of ventrolateral processes not strongly bent; inferior appendages very short (Fig. 27) (United States—Arizona, New Mexico) .....  
 ..... *C. moselyi* Denning  
 Tergum X more elongate, apices of ventrolateral processes strongly bent; inferior appendages more elongate (Figs. 29, 31) (Mexico, Guatemala) ..... 9
- 9(8) Phallic spines both nearly straight; apices of inferior appendages subtruncate (Fig. 29)..... *C. pararusia*, new species  
 One phallic spine distinctly curved and twisted; apices of inferior appendages acutely narrowed (Fig. 31)..... *Culoptila rusia* Mosely
- 10(1) At least 1 phallic spine with accessory spines (Figs. 10A, 17A, 24A) ..... 11  
 Phallic spine or spines simple, without accessory spines ..... 14
- 11(10) Phallobase greatly shortened, dorsum bulged before apex (Fig. 10A); phallic spine(s) forming shortened structure, much shorter than phallobase .....  
 ..... *C. acaena* Bueno-Soria & Santiago-Fragoso  
 Phallobase not greatly shortened, apex emerging more linearly (Figs. 17A, 24A); phallic spines elongate, more than 1/2 length of phallobase ..... 12
- 12(11) Phallic spines both very narrow, 1 with enlarged base and row of accessory spines near apex; inferior appendages short (Fig. 24) .....  
 ..... *C. jamapa* Bueno-Soria & Santiago-Fragoso  
 Phallic spines more robust, 1 with many overlapping accessory spines, sinuously wrapped around other spine; inferior appendages elongate (Fig. 17) ..... 13
- 13(12) Inferior appendages narrow, not greatly widened at apex (Fig. 25) .....  
 ..... *C. kimminsi* Denning  
 Inferior appendages broad, widened at apex (Fig. 17) ..... *C. buenoi*, new species
- 14(10) One phallic spine ..... 15  
 Two phallic spines ..... 23
- 15(14) Tergum X deeply or distinctly incised apicomesally (Fig. 32B, 33B) ..... 16  
 Tergum X not incised apicomesally (at most, only weakly concave) (Figs. 10B, 11B, 34B)..... 17
- 16(15) Tergum X elongate, apex deeply incised mesally; apex of phallobase nearly straight, without inflection (Fig. 33B)..... *C. tapanti*, new species  
 Tergum X short, apex distinctly, but less deeply incised; apex of phallobase with very distinct preapical inflection (Fig. 32B) [with 2 phallic spines, one very short]  
 ..... *C. saltena* Mosely
- 17(15) Phallic spine elongate, stout, and nearly straight, nearly length of phallobase; apices of ventrolateral processes of tergum X (lateral view) strongly bent (Figs. 18A, 30A) ..... 18  
 Phallic spine much shorter than length of phallobase (Fig. 21A), or strongly recurved (Fig. 19A); apex of ventrolateral process of tergum X (lateral view) mesally curved (Fig. 37), or weakly bent (Figs 19, 34)..... 19



- 18(17) Basal plate of phallotremal sclerite with many small spines; tergum X very short, apex distinctly truncate; apex of ventrolateral processes of tergum X strongly angulate (Fig. 18) (western and southwestern United States) ..... *C. cantha* (Ross)  
 Basal plate of phallotremal without small spines; tergum X very short, apex rounded to subacute; apex of ventrolateral processes of tergum X less angulate (Fig. 30) (eastern United States) ..... *C. plummerensis*, new species
- 19(17) Phallobase basodorsally with angulate, laterally flattened apodeme (Figs. 26A, 37A) ..... 20  
 Phallobase rounded basally, without basodorsal apodeme (Fig. 34A) ..... 21
- 20(19) Basodorsal apodeme of phallobase small, subtriangular; phallic spine short (Fig. 26A) ..... *C. montanensis* Flint  
 Basodorsal apodeme of phallobase large, prominent; phallic spine more elongate and distinctly sinuous (Fig. 37A)..... *C. vexillifera*, new species
- 21(19) Phallic spine prominent, recurved basally, more than 1/2 length of phallobase; apex of tergum X abruptly narrowed and subtruncate (Fig. 19) (Costa Rica).....  
 ..... *C. cascada*, new species  
 Phallic spine not recurved basally, 1/2 or less of length of phallobase; apex of tergum X not abruptly narrowed (Figs. 21, 34) (Mexico) ..... 22
- 22(21) Phallobase short, rounded; apex of tergum X rounded (Fig. 21A) [with 2 phallic spines, one very short] ..... *C. denningi* Bueno-Soria & Santiago-Fragoso  
 Phallobase elongate, inflated basally; apex of tergum X weakly concave (Fig. 34) ..... *C. tarascanica* Flint
- 23(14) Tergum X distinctly elongate, truncate apically; apex of ventrolateral process of tergum X bifid, with both branches strongly posteriorly hooked (Fig. 14) .....  
 ..... *C. barrerae* Bueno-Soria & Santiago-Fragoso  
 Tergum X short or moderate in length, truncate or not (Figs. 11B, 21B); apex of ventrolateral process of tergum X, if branched, with apices diverging (Fig. 11A) or not posteriorly hooked (Fig. 15A) ..... 24
- 24(23) Apex of tergum X distinctly incised; apex of phallobase with strong preapical inflection (Fig. 32) ..... *C. saltena* Mosely  
 Apex of tergum X truncate or rounded; apex of phallobase inflected or not (Figs. 11, 28) ..... 25
- 25(24) Inferior appendages elongate, with apices enlarged and rounded .....  
 ..... *C. amberia* Mosely  
 Inferior appendages short (Fig. 11) or elongate, tapered (Fig. 13), not distinctly expanded apically ..... 26
- 26(25) Ventrolateral processes of tergum X distinctly bifurcate (Figs. 11A, 15A)..... 27  
 Ventrolateral process of tergum X not bifurcate (Figs. 13A, 21A)..... 28
- 27(26) Bifurcate apices of ventrolateral processes of tergum X distinctly diverging; phallic spine without enlarged base as long as or longer than spine with enlarged base;

- apex of tergum X moderate in length; inferior appendages short (Fig. 11) (Mexico) ..... *C. aluca* Mosely
- Bifurcate apices of ventrolateral processes of tergum X less distinctly diverging; phallic spine without enlarged base much shorter than spine with enlarged base; apex of tergum X very short; inferior appendages more elongate (Fig. 15) (Costa Rica)..... *C. bidentata*, new species
- 28(26) Inferior appendages elongate, acute apically (Fig. 13).....  
..... *C. azulae* Bueno-Soria & Santiago-Fragoso
- Inferior appendages short or very short, acute apically or not (Figs. 21, 28)..... 29
- 29(28) Phallic spines short or very short, one inflated mesally (2nd small enough to be easily missed) (Fig. 21)..... *C. denningi* Bueno-Soria & Santiago-Fragoso
- Phallic spines both relatively elongate, neither inflated mesally (Figs. 28, 35) ... 30
- 30(29) Apex of phallobase sharply inflected; ventral margin of segment IX very narrow; 1 phallic spine with recurved base (Fig. 28)..... *C. nahuatl* Flint.
- Apex of phallobase less distinctly inflected; ventral margin of segment IX not distinctly narrowed; neither phallic spine recurved basally (but one sinuously curved apically) (Fig. 35) ..... *C. thoracica* (Ross)

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