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**Systematics and biogeography of the New World species of
Trichadenotecnum Enderlein (Insecta: Psocodea: 'Psocoptera': Psocidae)**

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Running title: New World *Trichadenotecnum*

Abstract. The taxonomy of the New World species of the genus *Trichadenotecnum* is revised. A total of 44 species, including 29 new species, were treated. These species are classified into 12 monophyletic species groups, eight of them newly proposed here. Two species previously assigned to *Trichadenotecnum*, *T. pichincha* New & Thornton and *T. sylvaticum* Turner, are recognized as not belonging to this genus. Phylogenetic relationships among 16 previously and presently proposed species groups are estimated based on a data matrix of 58 morphological characters. Trees from these analyses support monophyly of *Trichadenotecnum* and the proposed species groups. The New World species were divided into three major clades. Based on the phylogenetic hypothesis and distributional pattern of the species groups, the biogeographic history of the New World *Trichadenotecnum* is discussed.

Additional keywords: asymmetry - Beringia - genitalia - North Atlantic Land Bridge - morphology - new species - phylogeny.

INTRODUCTION

The genus *Trichadenotecnum* Enderlein, 1909 is one of the most diverse genera of the family Psocidae (Insecta: Psocodea: 'Psocoptera') contained ca. 160 named species recorded from all zoogeographic regions, except for the Australian Region (Lienhard & Smithers, 2002; Lienhard, 2003a, b; 2004, 2005, 2006; Yoshizawa & Smithers, 2006). Recent taxonomic and systematic studies on the Old World species of *Trichadenotecnum* revealed that the genus is highly diverse in the Oriental Region (Yoshizawa, 2001, 2003; Li, 2002; Endang, Thornton & New, 2002; Yoshizawa & Lienhard, 2004; Endang & New, 2005). In contrast, alpha-taxonomic studies on the New World species of the genus are scarce. Until now, only 16 species have been recorded from the New World, and half of them are known only from North America (Lienhard & Smithers, 2002). However, biodiversity of the genus might be expected to be higher in the tropics or in subtropical regions (Central and South America) than in the temperate region (North America), as is the case for the Old World (Lienhard & Smithers, 2002). For example, Mockford & García Aldrete (1996) listed 18 species of Mexican *Trichadenotecnum*, but 15 of them were unnamed.

In addition, it has been continuously pointed out that *Trichadenotecnum sensu lato* (e.g., Enderlein, 1909; Thornton, 1961) includes heterogeneous species (Thornton, 1961; New, 1978; Yoshizawa, 1998, 2001). A recent revised definition of the genus was based on the Palearctic and Oriental species (Yoshizawa, 2001, 2003). Some heterogeneous Old World and Australian species were excluded from *Trichadenotecnum*, following the revised definition (Yoshizawa, 1998; Endang et al., 2002; Yoshizawa & Smithers, 2006). However, the generic assignments of the New World species of *Trichadenotecnum* have not been tested critically yet. Particularly *Psocus desolatus* (now *T. desolatum*) was once treated as the type species of

an independent (sub)genus *Trichadenopsocus* (Roesler, 1943; Li, 2002). Although this treatment has been rejected repeatedly (Mockford, 1993; Lienhard, 2003c), the exact systematic placement of *T. desolatum* within *Trichadenotecnum* is still unclear (Mockford, 1993).

Phylogenetic relationships between the Old World and the New World species of the genus are little understood. The revised definition and subdivisions of *Trichadenotecnum* were based on phylogenetic analyses of morphological and molecular data sets (Yoshizawa, 2003, 2004; Yoshizawa & Lienhard, 2004). However, those analyses were based mainly on Japanese species and thus, a more extensive study of the genus is required to test the proposed generic redefinition and the systematic framework of it. Systematic revision of the New World species of *Trichadenotecnum* is especially important for further phylogenetic and biogeographic analyses of the genus worldwide.

In the present paper, we systematically revise the New World species of *Trichadenotecnum*. Purposes of this paper are to get a better understanding of the New World fauna of *Trichadenotecnum*, to estimate their phylogenetic relationships, and to discuss their biogeographic history.

MATERIALS AND METHODS

Most specimens examined here have been preserved in 70-80% ethanol until described.

However, a few specimens were dried and later placed in ethanol, and it is mentioned in the descriptions. A few fresh specimens preserved in 99.5% ethanol and stored frozen were also used.

Males and females of the same species have been collected simultaneously only in limited cases, and this has caused a male-female association problem. Without confident evidence, we did not decide association of sexes. Therefore, 17 of 29 species described in this study are based only on male specimens. Differences in the morphology of the male genitalia are most important for distinguishing species and also have greatest phylogenetic significance. Alternatively, no new species are based solely on females because females are more difficult to diagnose than males and thus there is a higher risk of creating synonymies.

For detailed methods of dissection and illustration, see Yoshizawa (2001). Terminology follows Yoshizawa (2001), but the term pseudoparamere was adopted instead of paramere according to the revised interpretation of the structure by Yoshizawa (2003, 2004). Methods of phylogenetic analysis follow Yoshizawa (2001, 2004). In group diagnoses, apomorphies are given in italics.

Frequently appearing collector and institution names are abbreviated as follows: ANGA: Alfonso Neri García Aldrete; CL: Charles Lienhard; ELM: Edward L. Mockford; ISU: Illinois State University; KY: Kazunori Yoshizawa; MHNG: Museum d'histoire Naturelle, Geneva; SEHU: Systematic Entomology, Hokkaido University; SI: Smithsonian Institution, Washington, D.C.; UNAM: Universidad Nacional Autónoma de Mexico. The specimens from the Río Tambopata Reserve, Madre de Dios, Peru, and from the Waorani Ethnic Reserve, Napo, Ecuador, belong to the Smithsonian Institution, presently on loan to ANGA (UNAM).

KEY TO THE NEW WORLD SPECIES GROUPS OF

TRICHADENOTECHNUM

Males. (The *spiniserrulum* group is not keyed here because the only New World species of this group, *T. pardus*, is considered to be parthenogenetic and thus the male is unknown).

1. Rs fork obtuse (Fig. 5); clunium with postero-lateral process (clunial arm: Fig. 6A) 3
- Rs fork acute (Fig. 1); clunium without postero-lateral process (Fig. 2 A, E)..... 2
2. Forewing extensively covered with small spots (Fig. 1D-F); hypandrium with well developed movable median tongue (Fig. 3 C, G, I)..... *roesleri* group
- Forewing not extensively covered with small spots (Fig. 1A-C); hypandrium without median tongue (Fig. 2 C, G).. *circularoides* group
3. Hypandrium with movable median tongue (Fig. 6 C)..... 4
- Median tongue fused with hypandrium *majus* group (*T. majus*)
4. Hypandrial median tongue well sclerotized (Fig. 6 C)..... 5
- Hypandrial median tongue membranous (Fig. 38 C)... *slossonae* group
5. Hypandrial median tongue long, much longer than basal width (Fig. 6 C) 6
- Hypandrial median tongue short, length almost equal to width (Fig. 43 C)*decui* group
6. 8th sternum fused to hypandrium medially (Fig. 21C)9
- 8th sternum separated from hypandrium (Fig. 6 C) 7
7. Hypandrium asymmetrical (Figs. 6C, 19 C).... 8
- Hypandrium symmetrical *alexandrae* group (*T. alexandrae*)
8. Dorsal surface of hypandrial median tongue with keel medially (Fig. 18 A)

chiapense group (in part)

- Dorsal surface of hypandrial median tongue without keel (Fig. 6 A)*desolatum* group
- 9. Hypandrium asymmetrical (Fig. 21 C) 10
- Hypandrium symmetrical (Fig. 32 C) *concinnum* group
- 10. Hypandrial posterior processes widely separated apically (Fig. 37 C) 11
- Hypandrial posterior processes crossing or closely associated apically (Fig. 21 C)*quaesitum* group
- 11. Hypandrial median tongue broadened apically (Fig. 18 C)*chiapense* group (in part)
- Hypandrial median tongue tapered apically (Fig. 37 C,G)*aconcinnum* group

Females (Some of the species groups proposed below, such as *quaesitum* and *concinnum*, are defined only on male genital apomorphies and are difficult to distinguish on female characters. When males are available, together with females, refer to the male key above. For observation of some key characters, dissection of specimens is required. Females are unknown for *aconcinnum* group, which are expected to fall into couplet 9 by the following key).

- 1. Ventral valve of gonapophyses long, apex far exceeding posterior margin of external valve (Fig. 7 B) 4
- Ventral valve of gonapophyses short, apex not exceeding posterior margin of external valve (Fig. 4B) 2
- 2. Forewing extensively covered with small spots (Fig. 1D-F) 3
- Forewing not extensively covered with small spots (Fig. 1A-C).....*circularoides*

group

3. Forewing Rs fork acute (Fig. 1) *roesleri* group
- Forewing Rs fork obtuse (as in Fig. 5) *spiniserrulum* group (*T. pardus*)
4. Forewing extensively covered with small spots (Figs. 5, 17F-L).... 5
- Forewing not extensively covered with small spots (Fig. 17A-D) 7
5. Egg guide of subgenital plate gradually narrowing to rounded or almost straight distal margin (Fig. 7A) 6
- Egg guide of subgenital plate broadened distally (Fig. 24 A)*quaesitum* group (in part) & *concinnum* group
6. Anterior margin of subgenital plate with broad membranous region medially (e.g., Fig. 20A) *alexandrae* group
- Anterior margin of subgenital plate with narrow membranous region medially (Fig. 7A) *desolatum* group
7. Egg guide of subgenital plate broadened distally (Fig. 24 A) 8
- Egg guide of subgenital plate almost parallel sided or gradually narrowing to distal margin (Fig. 20 A)... 10
8. Egg guide of subgenital plate with sclerotized portion dorsally (Figs. 39 A, 45A)..... 9
- Egg guide of subgenital plate without sclerotized portion dorsally (Fig. 24 A)*quaesitum* group (in part)
9. Internal plate triangular in shape, with rounded or somewhat pointed posterior margin (Fig. 45 C) *decui* group (in part)
- Internal plate with square shaped posterior extension (Fig. 39 C) *slossonae* group
10. Egg guide strongly narrowing distally (Fig. 20 A) 11
- Egg guide almost parallel sided *decui* group (in part, *T. decui*)

- 11. Egg guide without sclerotized portion dorsally *chiapense* group
- . Egg guide with sclerotized portions dorsally *majus* group (*T. majus*)

SYSTEMATICS

Trichadenotecnum Enderlein

See Yoshizawa (2001) for synonymy and Yoshizawa (2001, 2003) for generic definition.

The *circularoides* group

Diagnosis. Small sized psocids, length of forewing ca. 2 mm. *Forewing* (Fig. 1A-C), *not extensively covered with small spots* (secondary reversal); cell a with single marking; opposing spots in cell r absent; Rs fork acute; 3rd section of CuA almost straight, directed posteriorly. *Male terminalia* (Fig. 2): No clunial arm. Epiproct with well expanded lobe. Paraproctal distal lobe small; distal process almost straight. Eighth venter with pair of small sclerites widely separated from hypandrium. Hypandrium asymmetrical, *with lobe-like projection on right side* (= modified right process), *medially with wide membranous region; left process well developed*; median tongue absent. *Phallosome asymmetrical*, broadened posteriorly, with weakly sclerotized pseudoparameres (*sensu* Yoshizawa, 1999; 2005: not Yoshizawa, 2001), postero-lateral corner with extension. *Female genitalia*: Ventral valve of gonapophyses short, not reaching external valve. External valve lacking posterior lobe. Internal plate little

sclerotized.

Remarks. Although Yoshizawa (2001) assigned the parthenogenetic *T. circularoides* into the *spiniserrulum* group, based on the short ventral valve of the gonapophyses, results from molecular analyses showed that the species should be excluded from the *spiniserrulum* group to constitute its own species group (Yoshizawa, 2004). The present morphology-based phylogenetic analysis with bisexual *T. gonzalezi* and *T. peruense*, that are apparently closely related to *T. circularoides*, corroborates the result from the molecular phylogenetic analyses. Especially, lack of the clunial arm and the opposing spots in cell r in the *circularoides* group are important plesiomorphic character states that exclude *T. circularoides* and relatives from the *spiniserrulum* group, although the latter state was considered to be a reversal by Yoshizawa (2001).

Key to Species

1. Forewing discoidal cell with distinct spots (Fig. 1A, B); epiproct lobe bilobed (for *T. gonzalezi*: Fig. 2 B).. 2
- Forewing discoidal cell without distinct spots except for faint markings along veins (Fig. 1C); epiproct lobe not bilobed (Fig. 1F) *T. peruense* sp. nov.
2. Posterior margin of subgenital plate flattened; anterior arms of subgenital plate separated by narrow membranous region *T. gonzalezi* (Williner)
- Posterior margin of subgenital plate slightly hollowed medially; anterior arms of subgenital plate broadly separated by membranous region..... *T. circularoides* Badonnel

***Trichadenotecnum circularoides* Badonnel, 1955**

Trichadenotecnum circularoides Badonnel, 1955: 229; Yoshizawa, 2001: 198.

Material examined. Mexico: 1 female, Tabasco, Villahermosa, Parque Museo la Venta, 30.

VIII. 1994, ANGA (UNAM).

Diagnosis. This species is similar to *T. gonzalezi* (Williner) but can be separated from it by the following character states: darker background color of forewing; apical margin of egg guide slightly bilobed; pigmented arms of subgenital plate broadly separated; ventral valve of gonapophyses shorter (Mockford, 1991). The *T. circularoides* - *T. gonzalezi* complex can be easily distinguished from *T. peruense* sp. nov., the other member of this species group, by the more strongly developed forewing markings. See Badonnel (1955) and Yoshizawa (2001) for further descriptions of *T. circularoides*.

Distribution. North America; Mexico (new record); Northern Brazil; Japan; Malaysia; Angola.

***Trichadenotecnum gonzalezi* (Williner)**

Psocus gonzalezi Williner, 1945: 235.

Trichadenotecnum gonzalezi (Williner): Mockford, 1991: 268.

Material examined. Ecuador: Napo, 1 km S Oncone Gare Camp, Waorani Ethnic Reserve, 220 m, 0°39'10"S: 76°26'W, 8. II. 1995 (SI), 1 male, T. L. Erwin *et al.* (950) (SI); 1 male, same data (968) (SI); 1 male, same locality and collector, 10. II. 1995 (993) (SI); 1 male, same locality and collector, 11. II. 1995 (1022) (SI); 2 females (abdomen missing), same locality and collector, 12. II. 1995 (1041) (SI). Peru: Madre de Dios, Río Tambopata Reserved Zone, 30 km SW Puerto Maldonado, 12°50'S 69°17'W, 16. IX. 1984, 1 female, T. L. Erwin *et al.* (SI).

Description of the male terminalia. As for the group diagnosis. Epiproct lobe (Fig. 2 B) expanded dorsally, bilobed. Paraproct (Fig. 2 A); ventro-lateral band indistinct; distal process long, directed upwards. Hypandrium (Fig. 2 C) with broad, mesal, membranous region; left process well developed, lamellate, triangular; right side of hypandrium with complicated lobe-like projection (=right process), lobe with membranous region, external surface of lobe covered basally by denticles. Phallosome (Fig. 2D): Slightly skewed to left, posterior margin broad, truncated and with papillae, postero-lateral corner with extended process. Phallobase narrowing to somewhat truncated anterior end.

Remarks. This species has been known from the type specimen (sex unknown) and females re-described by Mockford (1991). Examined specimens match the forewing markings of the original description and also the female genital structures in Mockford's re-description.

Distribution. Ecuador, Peru, Brazil, Argentina.

***Trichadenotecnum peruense* sp. nov.**

Material examined. Holotype. Male. Peru: Madre de Dios. Río Tambopata Reserved Zone, 30 km SW Puerto Maldonado, 290m, 6. IX. 1984, T. L. Erwin *et al.* (SI).

Etymology. The specific epithet is taken from the type locality of this species.

Description: Male. Head. Mostly brown; narrow white band between vertical and orbital markings; coronal suture black; frontal suture bordered with brown band; frons with two pairs of white spots, median pair smaller and located dorsally, lateral pair large, extending from dorsal margin of postclypeus to frontal suture; gena white; eye black, small, IO/D = 1.6; ocelli white, ocellar field black; antennal socket bordered with brown band; postclypeus white with T-shaped blackish brown marking on ventral half, dorsal region with ca. six rows of pale brown spots; anteclypeus pale brown. Antenna pale brown. Mouth parts pale brown; 4th segment of maxillary palpus dark brown.

Thorax. Prothorax brown. Mesonotum brown, with white spot posterior to anterior lobe of scutum, lateral lobe of scutum with transversal narrow white line; scutellum blackish brown; postnotum pale brown. Metanotum brown, with white spot at posterior end of anterior lobe of scutum; scutellum blackish brown; postnotum brown. Meso- and metapleurites brown except membranous region white.

Legs. Coxae brown; middle leg pale brown, tibia darker; fore and hind legs missing.

Forewing (Fig. 1C). Spots in cell a₁ not separated. Opposing spots in cell r absent, but similar markings, not homologous, in posterior region of cell r just proximal to proximal band. Proximal band reduced, interrupted beyond CuP and almost absent between M-CuA

fork and basal section of Rs. Median spots almost absent except for some faint markings along discoidal veins. Distal band almost indistinct except for brown spot in cell r3. Spot on roof of cell m3 small, only distinct below distal Ms-CuA fork. Submarginal spots reduced, spots in cell r1 and m3 hardly visible. Marginal clouds almost indistinct except for brown spots on distal ends of vein R2+3, R4+5 and M1. *Hindwing*. Hyaline; veins brown.

Abdomen. White, with sparse minute brown spots. *Terminalia*. Epiproct lobe (Fig. 2EF) expanded antero-dorsally, smoothly rounded, medially with longitudinal swelling. Paraproct (Fig. 2E): ventro-lateral band absent; distal process short, directed posteriorly. Hypandrium (Fig. 2G) with wide membranous region on left side; left process well projected, arched inwardly, cylindrical; right side of hypandrium with lobe-like projection (=right process), lobe with broad membranous region near right edge, external edge of lobe covered by denticles. Phallosome (Fig. 2H) nearly symmetrical, only slightly left-skewed posteriorly, posterior margin wide, with papillae, postero-lateral corner extending. Phallobase narrowing apically, with pair of projections directed anteriorly.

Length. B 1.9; FW 2.0; HW 1.5.

Female. Unknown.

Distribution. Peru.

The *roesleri* group

Diagnosis. Small sized psocids, length of forewing ca. 2 mm. Forewing (Fig. 1D-F) extensively covered with small spots; spots in cell a faint; opposing spots of r absent or only

posterior spot distinct; proximal band only distinct just below fork of M + Cu and along basal section of vein Rs; distal band faint, indistinct in cell r3; submarginal spots sometimes indistinct, especially in cells r1, r3 and m3; marginal clouds only distinct along vein ends; Rs fork acute; third section of CuA almost straight, directed posteriorly. *Male terminalia*. No clunial arm present (Fig. 3 A, E). Epiproct with *keel-like projection posteriorly* (Fig. 3 B, E); epiproct lobe well expanded, *its dorsal margin with some rather long setae* (Fig. 3 B, F). Paraproctal distal lobe small (Fig. 3 A, E); distal process long and almost straight, directed posteriorly. *Eighth venter* (Fig. 3 C, I) with *transversal single sclerite fused with hypandrium posteriorly at middle*. Hypandrium (Fig. 3 C, G, I) symmetrical; median tongue well developed, its ventral surface with denticles. Phallosome (Fig. 3 D, H, J) variable in shape but consistently symmetrical. *Female genitalia* (Fig. 4). Ventral valve short, not reaching external valve.

Key to Species

1. Males 2
- Females 6
2. Hypandrial median tongue long, length > apical width (Fig. 3 C, G) 3
- Hypandrial median tongue short, length $\approx$ apical width (Fig. 3 I) *T. bos* sp. nov.
3. Phallosome without long processes (Fig. 3 D, H) 4
- Phallosome with long processes arising from postero-lateral corners (Fig. 3, J)

T. sinuatum New

4. Phallosome narrowing posteriorly, with pair of short processes postero-medially (Fig. 3D) 5
- Phallosome broadened posteriorly, without pair of processes postero-medially (Fig.

3H) *T. oaxacense* sp. nov.

5. Hyandrial median tongue almost parallel sided..... *T. roesleri* New

-. Hyandrial median tongue strongly constricted medially (Fig. 3C)..... *T.*

tambopatense sp. nov.

6. Body of subgenital plate broad and transverse, anterior margin with shallow and broad invagination of membranous region7

-. Body of subgenital plate sinuate *T. sinuatum* New

7. Anterior margin of body of subgenital plate with narrow notch medially *T.*

tambopatense sp. nov.

-. Anterior margin of body of subgenital plate without narrow notch medially *T.*

roesleri New

***Trichadenotecnum roesleri* New**

Trichadenotecnum roesleri New, 1972: 228.

Remarks. Specimens not examined. Judging from the original description and illustrations by New (1972), this species is similar to *T. oaxacense* and to *T. tambopatense*, both of them newly described below. However, *T. roesleri* differs from *T. oaxacense* in the shape of the phallosome (with a pair of projections posteriorly in *T. roesleri* and with broad and serrated posterior margin in *T. oaxacense*), and from *T. tambopatense* in the shape of the median tongue (nearly parallel sided in *T. roesleri* and strongly constricted medially in *T. tambopatense*).

Distribution. Brazil.

***Trichadenotecnum tambopatense* sp. nov.**

Material examined. *Holotype.* Male. Peru: Madre de Dios. Río Tambopata Reserved Zone, 30 km SW Puerto Maldonado, 290m, 10. IX. 1984, T. L. Erwin *et al.* (SI). *Paratypes.* 1 male, 2 females, same data as holotype, 4. V. 1984 (SI); 1 male, same locality, 6. IX. 1984; 2 males, same data as holotype (SI); 1 male, same locality as holotype, 14. IX. 1984 (SI).

Etymology. The specific epithet is taken from the type locality of this species.

Description: **Male.** *Head.* White in ground color; vertical and orbital markings brown; coronal suture black; frontal suture bordered with narrow pale brown line dorsally; frons with pair of pale brown lines at middle; gena brown in ventral half with white spot ventrally; eye black, IO/D = 1.0; ocelli white, ocellar field pale; antennal socket bordered with narrow brown band; postclypeus with ca. six rows of brown spots, ventral margin blackish brown; anteclypeus brown. Antenna pale brown. Mouth parts pale brown; 4th segment of maxillary palpus darker.

Thorax. Prothorax brown. Mesonotum white in ground color; each lobe of scutum with large brown marking, marking on anterior lobe bilaterally divided by narrow white line, marking on lateral lobe divided in two by narrow white transverse line; scutellum brown, antero-lateral corner blackish brown; postnotum pale brown. Metanotum brown, anterior lobe

paler, lateral lobe with white spot posteriorly; antero-lateral corner of scutellum blackish brown. Meso- and metapleurites brown except membranous region and ventral region of epimeron white.

Legs. Fore- and middle femur, tibiae and tarsi unavailable. All coxae, trochanter and hind leg brown, distal ends of hind femur and tibiae paler.

Forewing (Fig. 1D). Spots in cell a₁ faint, indistinct. Opposing spots in cell r indistinct except for very small posterior spot. Proximal band represented by triangular or semicircular markings just below fork of M + Cu and irregular-shaped marking on basal section of Rs. Distal band indistinct except for faint brown tinge in cell r₅. Spot on roof of cell m₃ small, only distinct on distal Rs-CuA fork. Submarginal spots distinct only for large spots in cells r₅, m₁ and m₂. Marginal clouds indistinct except for brown spots on distal ends of vein R₂ + 3, R₄ + 5 and M₁. *Hindwing.* Hyaline, cell CuP with faint brown markings at distal end; veins brown.

Abdomen. White, sparsely with minute blackish brown spots ventrally. *Terminalia.* Anterior margin of 8th sternum (Fig. 3C) deeply incised by membranous region medially. Epiproct lobe (Fig. 3B) longer than wide, nearly parallel sided and with smoothly rounded dorsal margin, posterior surface shallowly concave. Paraproct (Fig. 3A): ventro-lateral band absent. Hypandrium (Fig. 3C): left and right processes conical, directed posteriorly, basally arranged with many processes of variable size; basal and distal parts of median tongue strongly expanded laterally, apical margin slightly hollowed, with several fine and rather long setae, ventral surface covered with denticles distally and antero-laterally. Phallosome (Fig. 3D): posteriorly with pair of conical processes medially. Phallobase parallel sided distally, then narrowing to rounded anterior end.

Length. B 1.8-2.0; FW 2.3-2.4; HW 1.7-1.8.

Female (available from dissected females only). Color and general morphology almost as in male. IO/D = 2.1. Fore and middle legs brown, distal ends of femur white, tibiae paler.

Genitalia. Egg guide of subgenital plate (Fig. 4A) gradually narrowing to slightly arched distal margin, medially with membranous region; pigmented arms closely approximated basally, antero-internally with extension of sclerite. External valve of gonapophyses (Fig. 4B) small, internal end not reaching internal margin of dorsal valve, posteriorly with weak posterior lobe. Internal plate as in Fig. 4C.

Length. B (unavailable); FW 2.1-2.2; HW 1.6-1.7.

Distribution. Peru.

***Trichadenotecnum oaxacense* sp. nov.**

Material examined. *Holotype.* Male. Mexico: 10 mi NW Tapanatepec, Oaxaca, 20. VIII. 1968, ELM & ANGA (ISU).

Etymology. The specific epithet is taken from the type locality of this species.

Description: Male (based on a weakly colored teneral specimen). *Head.* White in ground color; vertical and orbital markings faint; coronal suture black; frontal suture hardly visible; frons without markings; eye black, small, IO/D = 1.3; ocelli white, ocellar field black; antennal socket bordered with pale band; postclypeus with ca. nine rows of pale brown spots,

ventrally with pale brown oval markings; anteclypeus pale. Antenna pale. Mouth parts pale.

Thorax. Prothorax pale brown. Mesonotum white in ground color; each lobe of scutum with large pale brown markings, marking on anterior lobe bilaterally divided by narrow white line, marking on lateral lobe divided in two by narrow white transverse line; scutellum pale, antero-lateral corner brown; postnotum pale. Metanotum pale brown, anterior lobe paler, lateral lobe with white spot posteriorly; antero-lateral corner of scutellum brown. Meso- and metapleurites pale brown except membranous region white.

Legs. Pale brown.

Forewing (Fig. 1E). Spots in cell a₁ indistinct. Opposing spots in cell r indistinct. Proximal band represented by broad marking just below fork of M + Cu and narrow marking along basal section of Rs. Distal band indistinct except for very faint brown tinge in cell r₅. Spot on roof of cell m₃ narrow, only distinct on distal Rs-CuA fork. Submarginal spots distinct only for faint spots in cells r₅, m₁ and m₂. Marginal clouds indistinct except for faint brown tinge on distal ends of vein R₄ + 5 and M₁. *Hindwing.* Hyaline; veins pale brown.

Abdomen. White, each segment with irregular brown band ventrally. *Terminalia.* Sclerite on eighth venter hardly visible (Fig. 3G). Epiproct lobe (Fig. 3F) nearly parallel sided, almost as long as wide, dorsal margin rounded, posterior surface slightly concave. Paraproct (Fig. 3E): ventro-lateral band indistinct. Hypandrium (Fig. 3G) symmetrical, with pair of weakly sclerotized lobes at base of median tongue; left and right processes conical, well projected and directed posteriorly; median tongue with some fine setae ventro-medially, strongly expanded basally, apical margin serrated and hollowed medially, ventral surface covered with wrinkles except antero-lateral region denticulated. Phallosome (Fig. 3H) with broad and rounded posterior margin, notched medially; postero-dorsal margin with denticles.

Phallobase parallel sided posteriorly, then narrowing to pointed anterior end.

Length. B 1.6; FW 2.0; HW 1.5.

Female. Unknown.

Distribution. Mexico.

***Trichadenotecnum sinuatum* New**

Trichadenotecnum sinuatum New, 1972: 230.

Specimens not examined. See key to species to diagnose this species, and New (1972) for description and illustrations.

Distribution. Brazil.

***Trichadenotecnum bos* sp. nov.**

Material examined. Holotype. Male. Peru: Madre de Dios. Río Tambopata Reserved Zone, 30 km. SW Puerto Maldonado, 290m, 6. IX. 1984, T. L. Erwin *et al.* (SI).

Etymology. The specific epithet is taken from the latin *bos* (= cow), referring to a pair of phallosomal processes that look like cow horns.

Description: Male (available only by partly cleared and dissected specimen). *Head.*

Coloration unavailable. Eye small, IO/D = 1.3.

Thorax. Coloration of prothorax unavailable. Mesonotum white in ground color, each lobe of scutum with large brown marking, marking on anterior lobe divided bilaterally by narrow white line, marking on lateral lobe divided in two by narrow transverse white line; scutellum white, anterior margin brown; postnotum brown. Metanotum brown, median lobe with longitudinal white line medially; lateral lobe with white spot posteriorly; scutellum white; postnotum brown. Meso- and metapleurites brown except membranous region, postero-ventral corner of anepisternum and median part of epimeron white.

Legs. Missing.

Forewing (Fig. 1F). Spots in cell a₁ distinct only for distal small spot. Opposing spots in cell r distinct only for small, semicircular posterior spot. Proximal band represented by circular marking just below fork of M + Cu, narrow marking along basal section of Rs, and faint brown tinge in cell CuP. Distal band almost indistinct except for faint brown tinge in cell r₅. Spot on roof of cell m₃ broad and distinct. Submarginal spots distinct only for large spots in cells r₅, m₁ and m₂. Marginal clouds faint, only visible along distal ends of vein R₂ + 3, R₄ + 5 and M₁. *Hindwing.* Hyaline, cell CuP with faint brownish marking distally; veins brown.

Abdomen. Pregenital segments missing. *Terminalia.* Clunium, epiproct and paraproct missing. Hypandrium (left postero-lateral corner missing, possibly including left process: Fig. 3 I): group of setae at postero-lateral corner; left process unknown; right process reduced to tiny conical process projected from near postero-lateral corner; median tongue short and broad, broadened basally, basal part with two pairs of processes laterally, distal pair smaller

and conical, basal pair larger and covered by denticles, apical margin serrated and hollowed at middle, ventral surface covered by wrinkles and tiny denticles. Phallosome (Fig. 3J): pair of strongly hooked processes (=pseudoparameres?) arising from postero-lateral corner, processes widely separated by aedeagus, this with small notch medially. Phallobase parallel sided, then gradually narrowing to opened anterior tip.

Length. B (unavailable); FW 2.1; HW 1.6.

Female. Unknown.

Distribution. Peru.

The *spiniserrulum* group

See Yoshizawa (2001) for group diagnosis and diagnosis of the following species.

***Trichadenotecnum pardus* Badonnel, 1955**

Trichadenotecnum pardus Badonnel, 1955: 231.

Trichadenotecnum pardidum: Yoshizawa, 2001: 198 (not *Trichadenotecnum pardidum* Thornton, 1961: see Yoshizawa & Lienhard (2004) for further discussion).

Material examined. Mexico: 1 female, Veracruz, 14.7 mi. N. Nautla, Rd. 180, 27. VI. 1962, 1 female, ELM, J. Campbell, F. Hill (ISU); 1 female, 16.7 mi. N. Nautla, Rd. 180, 27. VI. 1962,

ELM & J. Campbell (ISU); 2 females, 23 km N of Alvarado, sea level, 13. III. 1984, ANGA (UNAM); 1 female, Tabasco, Ejido Libertad, 1 mi. SW Frontera, Hwy. 180, 1. IV. 1964, ELM (ISU). Dominican Republic: 2 females, La Vega, 1520 m, NE Jarabacoa, 25. V. 1978, L. B. & C. W. O'Brien (UNAM). Panama: 1 female, Prov. Panama, Dpto. Chepo Isla Majé, in Lago Bayano, 8. VIII. 1992, D. Burckhardt (MHNG). Venezuela: 1 female, Miranda, 400 m, 35 km N. Altagracia Guatopon NP, Agua Blanca, 7-14. VI. 1987, S. & J. Peck (MHNG); 1 female, same locality, 400 - 700 m alt., 3-11. VI. 1987 (MHNG); 1 female, same locality, 700 m alt., 7-14. VI. 1987 (MHNG).

Remarks. This parthenogenetic species is widely distributed throughout the world, and its closest relative (the bisexual *T. pardidum*) is known only from Hong Kong. Therefore, it is likely that the species is not native to the New World but is introduced from the Old World (probably from the Oriental Region).

Distribution. Mexico, North America, Cuba, Puerto Rico, Trinidad, Brazil, Japan, Hong Kong, Malaysia, Angola, Madagascar, Suriname.

The *alexandrae* group

See Betz (1983), Schmidt (1991) and Yoshizawa (2001) for group diagnosis. See Betz (1983) and Mockford (1993) for species key. For descriptions and diagnosis of the species, see literature listed under synonymy.

***Trichadenotecnum alexandrae* Sommerman**

Trichadenotecnum alexandrae Sommerman, 1948: 169; Betz, 1983: 1336; Mockford, 1993: 280; Yoshizawa, 2001: 187.

Distribution. Canada, USA; Japan.

***Trichadenotecnum castum* Betz**

Trichadenotecnum castum Betz, 1983: 1341; Mockford, 1993: 281; Yoshizawa, 2001: 187.

Remarks. Mockford (1993) noted that the spot on the roof of cell m3 is usually extremely narrow in this species, and a well developed condition (as illustrated by Betz, 1983, Fig. 2) is not usual.

Distribution. Canada, USA, Japan, Azores Islands.

***Trichadenotecnum innuptum* Betz**

Trichadenotecnum innuptum Betz, 1983: 1349; Mockford, 1993: 281; Lienhard, 1998: 423.

Distribution. USA., Hungary, Italy, Switzerland.

***Trichadenotecnum merum* Betz**

Trichadenotecnum merum Betz, 1983: 1348; Mockford, 1993: 282.

Distribution. USA.

The *majus* group

See Yoshizawa (2001) and Yoshizawa & Lienhard (2004) for group diagnosis.

***Trichadenotecnum majus* (Kolbe)**

Psocus sexpunctatus var. *majus* Kolbe, 1888: 109.

Trichadenotecnum majus (Kolbe): Enderlein, 1909: 330.

See Mockford (1993) and Lienhard (1998) for diagnosis of this species.

Distribution. Canada, USA (possibly introduced); Europe.

The *desolatum* group

Diagnosis. Forewing (Fig. 5) *extensively covered with small spots* in various degrees (sparse to dense), proximal band narrow and sometimes indistinct, submarginal spots not apparent; Rs fork obtuse; 3rd section of CuA more or less arched. *Male terminalia.* Eighth venter (Fig. 6C) with large transversal sclerite separated from hypandrium. Clunial process (Fig. 6A) developed but *weakly sclerotized* and never forming free process apically, variable in shape. Epiproct (Fig. 6 A, B) chair-shaped, epiproct lobe long, much longer than wide, gradually narrowing to truncate dorsal margin, protruded over clunium. Paraproctal distal process (Fig. 6A) long, directed upwards. Hypandrium (Fig. 6C) asymmetrical, *with narrow longitudinal membranous or weakly sclerotized region anterior to median tongue socket*; left process conical, variable in size; right process distinct, variable in shape and size. Median tongue arising from anterior part of hypandrium, much longer than wide. Phallosome (Fig. 6D) with broad pseudoparameres. *Female genitalia.* Intra-specific variation of gonapophyses not significant (Fig. 7B). Ventral valve of gonapophyses long; posterior lobe of external valve not strongly projected. Internal plate (Fig. 7C) symmetrical or asymmetrical; spermathecal opening surrounded by egg-shaped strongly pigmented sclerite; anterior region almost unpigmented except for weakly pigmented anterior margin.

Remarks. Some species recognized below show considerable variation in some characters such as body size, eye size, wing markings and genital structures. Such variations sometimes exceed the morphological gap between species observed in other species groups (*e.g.*, the *medium* group of eastern Asia: Yoshizawa, 2001). However, each species recognized below can be morphologically united by some features (as indicated in the Key to Species and

species diagnoses), and thus we recognize such morphological groups as distinct species, although some species recognized below may actually include more than one biological unit.

In contrast, some specimens examined in this study and recognized as members of the *desolatum* group are morphologically highly variable in many features and cannot be united morphologically (Fig. 16). Therefore, those specimens probably consist of more than one species. However, such variations are more or less continuous and decision on species boundaries is presently impossible. Therefore, we postpone classifying them as distinct species. To clarify their species boundaries, examination of more specimens, exact understanding of distributional ranges, and probably molecular-based analyses are needed.

Key to Species (Many unidentified specimens are not keyed out and thus will incorrectly fall into identified species. Refer to species diagnoses and illustrations of wing markings and genital structures for exact identification of species.)

1. Males 6
- Females 2
2. Anterior margin of body of subgenital plate apparently hollowed, with broad but relatively shallow (not or slightly exceeding middle of body of subgenital plate) membranous notch medially (Fig. 7A) 3
- Anterior margin of body of subgenital plate almost straight, with relatively deep (far exceeding middle of body of subgenital plate) and narrow membranous notch medially (Fig. 15A) *T. latipenne* sp. nov.
3. Egg guide of subgenital plate nearly parallel sided at apex, with almost straight apical margin (Fig. 7A) 4

- Egg guide of subgenital plate gradually narrowing apically, with rounded apical margin (Fig. 9A)..... *T. acutolingum* sp. nov.
- 4. Egg guide with broad pale pigmented area medially (Fig. 10A) 5
- Egg guide with narrow longitudinal pale pigmented area medially (Fig. 12A) *T. longilingum* sp. nov.
- 5. Body of subgenital plate (excluding postero-lateral extension) shorter than egg guide, postero-lateral part strongly extended posteriorly (Fig. 10A) *T. magnolingum* sp. nov.
- Body of subgenital plate longer than egg guide, postero-lateral part weakly extended posteriorly (Fig. 7A) *T. desolatum* (Chapman)
- 6. Hypandrial right process shorter than or almost equal in length to left process (Fig. 6C) 8
- Hypandrial right process longer than left process (Fig. 8E) 7
- 7. Hypandrial right process conical; hypandrial median tongue constricted medially, apical margin clearly bilobed (Fig. 8E)..... *T. magnolingum* sp. nov.
- Hypandrial right process lamellate; hypandrial median tongue almost parallel sided, apical margin almost straight (Fig. 13B) *T. carinatum* sp. nov.
- 8. Apex of hypandrial median tongue with sharp triangular notch medially (Fig. 6C)10
- Apex of hypandrial median tongue with dull hollow (Figs. 11B, 13E)..... 9
- 9. Hypandrial median tongue long and narrow, more than 4x longer than basal width (Fig. 11)..... *T. longilingum* sp. nov.
- Hypandrial median tongue short and broad, less than 3x longer than basal width (Fig. 13E) *T. tuitense* sp. nov.
- 10. Apex of hypandrial median tongue broad, clearly bilobed (Fig. 6C) 11

- Apex of hypandrial median tongue narrow, almost pointed, with small notch medially (Fig. 8B) *T. acutolingum* sp. nov.
- 11. Epiproct lobe long, as long as or longer than basal width (Fig. 6B)..... 12
- Epiproct lobe short, shorter than basal width (Fig. 14D) *T. latipenne* sp. nov.
- 12. Hypandrial median tongue constricted medially (Fig. 14B) *T. sparsum* sp. nov.
- Hypandrial median tongue parallel sided or gradually narrowing apically (Fig. 6C) *T. desolatum* Chapman

***Trichadenotecnum desolatum* (Chapman)**

Psocus desolatus Chapman, 1930: 236.

Trichadenotecnum (Trichadenopsocus) desolatum: Roesler, 1943: 4.

Material examined. USA: 2 males, 2 females, New Mexico, Lincoln Co., Capitan Gap, Road #56, N. Hwy. 380, E. Capitan, 11. VIII. 1983, ELM (ISU); 1 male, Arizona, Chiricahua Mountains, Turkey Creek, 24. VIII. 2004, KY (SEHU); 1 female, Arizona, Rucker Canyon, 30. VIII. 2004, KY (SEHU).

Diagnosis. This species can be distinguished from the other species of this group by the combination of the following character states of the hypandrium (Fig. 6C): median tongue parallel sided or narrowing apically, with apparent apical notch; left process longer or almost of equal length to right process.

Remarks. Although this species can be characterized by the combination of the above mentioned character states, intra-specific variation is considerable, especially in the shape of the hypandrial median tongue. As mentioned in remarks under the group diagnosis, molecular and morphological examinations based on extensive sampling are required to test its taxonomic status.

Distribution. USA, Mexico.

***Trichadenotecnum acutolingum* sp. nov.**

Material examined. *Holotype.* Male, Mexico: Nuevo León, Galeana, Cerro Potosí, 3090m., 29. VIII. 1979, ANGA & M.C. Herrera (UNAM). *Paratypes.* 3 females, same data as holotype (UNAM).

Etymology. The specific epithet is taken from *the* latin *acutus* (= pointed) + *lingua* (= tongue), referring to the apically pointed hypandrial median tongue of this species.

Description: Male. Head. White in ground color; vertical and orbital markings dark brown; coronal suture black; frontal suture dorsally bordered with pale brown band broadened externally; frons with two pairs of dark brown bands, internal pair darker; ventral half of gena dark brown; eye black, small, IO/D = 1.5; ocelli white, ocellar field black; antennal socket bordered with dark brown band; postclypeus with ca. eight rows of blackish brown spots, fused with each other ventrally forming a large marking, ventro-lateral corner white;

anteclypeus dark brown. Antenna brown, pedicel and scape darker. Mouth parts brown.

Thorax. Prothorax brown. Meso- and metathorax mostly dark brown except membranous region white; mesonotum with white region medially, dorsal surface of anterior lobe and anterior region of lateral lobes of mesoscutum paler.

Legs. Brown; distal half of fore femur and tibiae of all legs paler; middle and hind coxae and hind femur dark brown.

Forewing (Fig. 5B). Moderately spotted. Spots in cell a_1 distinct, distal spot larger. Opposing spots in cell r distinct but anterior one small, widely separated from each other. Proximal band faint, darker and distinct in cell CuP, just below fork of M + Cu and along vein M. Distal band faint but distinct. Spot on roof of cell m_3 small. Submarginal spots hardly distinct, spot in cell r_5 larger and distinct, spots in cells m_1 and m_2 distinct. Marginal clouds indistinct. *Hindwing.* Hyaline, cell CuP with faint sparse spots; veins brown.

Abdomen. White, with sparse blackish brown spots. *Terminalia.* Clunial arm long and broad, distal end straight with short triangular extension dorsally. Epiproct lobe (Fig. 8A) long and broad, slightly shorter than basal width, gradually narrowing to rounded dorsal margin. Hypandrium (Fig. 8B): left process conical, strongly projected posteriorly, slightly curved; right process triangular, dorsally with longitudinal trench; median tongue with broad base, then narrowing to basal fourth, almost parallel sided from basal fourth to distal 1/6 then strongly narrowing to apex, tip with small notch. Phallosome (Fig. 8C): pseudoparameres short and broad, expanded laterally, broadly separated. Phallobase narrowing ventrally, with truncated ventral end.

Length. B 3.2; FW 5.8; HW 4.4.

Female. Color and general morphology almost as in male; eye IO/D = 2.6. *Genitalia:*

Egg guide of subgenital plate broad (Fig. 9A), apically rounded, broader than length, body of subgenital plate with slightly hollowed anterior margin and with rather broad and shallow median membranous notch. Internal plate as in Fig. 9B.

Length. B 3.7; FW 4.8-5.0; HW 3.6-3.7.

Distribution. Mexico.

***Trichadenotecnum magnolingum* sp. nov.**

Material examined. *Holotype.* Male, Mexico: Veracruz, Perote, 2960m, 7. IX. 1977, ANGA (UNAM). *Paratypes.* MEXICO: 1 female, same data as holotype (UNAM); 1 male, Michoacán, Hwy. 15, 17 mi. E. Zacapu, 21. VII. 1963, F. Hill (ISU); 1 male, 11 mi. E. Michoacán-Mexico State Line, Hwy. 15, 23. VII. 1963, ELM & F. Hill (ISU).

Etymology. The specific epithet is taken from latin *magnus* (= large) + *lingua* (= tongue), referring to the large hypandrial median tongue.

Description: Male. Head. White in ground color and extensively marked with dark brown; vertical and orbital markings dark brown; coronal suture black; frontal suture dorsally bordered with broad brown band; frons with pair of U-shaped dark brown markings; gena uniformly dark brown; eye black, IO/D = 1.1-1.7; ocelli white, ocellar field black; antennal socket broadly bordered with dark brown band; postclypeus with ca. ten rows of blackish brown spots at middle, fused with each other ventrally forming a large, T-shaped marking, ventro-lateral corner white; anteclypeus dark brown. Antenna brown, pedicel and scape

darker. Mouth parts brown.

Thorax. Prothorax brown. Meso- and metathorax mostly dark brown except membranous region white; dorsal surface of mesoscutum paler. Mesopleuron with longitudinal white band medially.

Legs. Brown; median part of fore femur and tibiae of all legs except distal tips paler.

Forewing (Fig. 5C). Moderately to rather sparsely spotted. Spots in cell a₁ distinct, basal spot fainter. Opposing spots in cell r distinct, widely separated from each other. Proximal band distinct, faint in posterior half of cell CuP, widely interrupted beyond fork of M+Cu. Distal band broad and distinct. Spot on roof of cell m₃ small and sometimes almost indistinct. Submarginal spots distinct, spot in cell r₅ larger, spots in cell m₃ sometimes hardly distinct. Marginal clouds indistinct. *Hindwing.* Hyaline, basal and distal regions of cell CuP with faint sparse spots; veins brown.

Abdomen. White, ventrally and laterally with irregular brown markings. *Terminalia.* Clunial arm short. Epiproct lobe (Fig. 8D) short and broad, slightly shorter than basal width, sharply narrowing to rounded or truncated narrow dorsal margin. Hypandrium (Fig. 8E): left process conical, strongly projected posteriorly, straight or slightly curved; right process triangular, strongly projected posteriorly, its apex usually exceeding that of the left process; median tongue elongate, broad basally, gradually narrowing to middle, then broadened near apex, apical margin notched. Phallosome (Fig. 8F): pseudoparameres short and broad, expanded laterally, broadly or narrowly separated. Phallobase narrowing ventrally, with triangular ventral end.

Length. B 2.8-3.3; FW 4.3-4.9; HW 3.2-3.7.

Female. Color and general morphology almost as in male; eye IO/D = 2.1. *Genitalia:*

Egg guide of subgenital plate broad (Fig. 10A), anterior margin almost straight, broader than long, anterior margin of body of subgenital plate with shallow circular hollow and relatively broad median notch. Internal plate as in Fig. 10B.

Length. B 3.4; FW 4.6; HW 3.6.

Distribution. Mexico.

***Trichadenotecnum longilingum* sp. nov.**

Material examined. *Holotype.* Male, Mexico: Hidalgo, 15 mi W. Huauchinango Rd. 130, 24. VI. 1962, ELM, J. Campbell, F. Hill (ISU). *Paratypes.* 2 males, 4 females, same data as holotype (ISU).

Etymology. The specific epithet is taken from the Latin *longus* (= long) + *lingua* (= tongue), referring to the narrow and elongate hypandrial median tongue of this species.

Description: Male. Head. White in ground color; vertical and orbital markings dark brown; coronal suture black; frontal suture dorsally bordered with narrow pale brown band; frons with pair of dark brown bands medially and pair of small brown spots laterally; gena mostly brown with white portion medially; eye black, rather large, IO/D = 1.0; ocelli white, ocellar field black; antennal socket bordered with dark brown band; postclypeus with ca. eight rows of brown spots dorsal to median region, ventrally with blackish brown marking medially, ventro-lateral corner white; anteclypeus brown. Antenna pale brown, pedicel and scape

darker. Mouth parts brown.

Thorax. Prothorax brown. Meso- and metathorax mostly dark brown except membranous region white; dorsal surface of mesonotum mostly white, with pale brown markings; mesopleuron with longitudinal white band medially.

Legs. Brown; distal half of fore femur and tibiae of all legs paler.

Forewing (Fig. 5D). Rather sparsely spotted. Spots in cell a_1 distinct, distal spot larger. Opposing spots in cell r indistinct. Proximal band faint, darker and distinct in cell CuP and Rs-M fusion, very narrow in cell CuA. Distal band distinct, broad. Spot on roof of cell m_3 very small, hardly distinct. Submarginal spots distinct, spot in cell r_5 larger, spot in cell m_3 somewhat indistinct. Marginal clouds indistinct except ends of veins. *Hindwing.* Hyaline, cell CuP and distal region of cells r_1 and r_3 with faint sparse spots; veins brown.

Abdomen. White, each segment with broad brown band ventrally. *Terminalia.* Clunial arm long and broad, distal end narrow but rounded. Epiproct lobe (Fig. 11A) broad, shorter than basal width, sharply narrowing to narrow and rounded dorsal margin. Hypandrium (Fig. 11B): left process conical, strongly projected postero-laterally, slightly curved; right process triangular, projected postero-internally; median process long and narrow, broadest at basal 1/9, gradually narrowing to basal third, then nearly parallel sided to apex; apical margin shallowly hollowed. Phallosome (Fig. 11C): pseudoparameres short and broad, expanded laterally, almost fused medially with shallow hollow between them. Phallobase narrowing ventrally, with pointed ventral end.

Length. B 3.1-3.3; FW 4.2-4.4; HW 3.2-3.4.

Female. Color and general morphology almost as in male; eye IO/D = 2.2. *Genitalia:* Egg guide of subgenital plate broad (Fig. 12A), broader than long, anterior margin almost

straight, lateral margins near distal end nearly parallel sided, anterior margin of body of subgenital plate shallowly hollowed, and with rather broad median notch. Internal plate as in Fig. 12B.

Length. B 3.2-3.6; FW 4.2-4.6; HW 3.2-3.4.

Distribution. Mexico.

***Trichadenotecnum carinatum* sp. nov.**

Material examined. *Holotype.* Male, Mexico: Oaxaca, 29 km SE Nochixtlán, 21. VIII. 1973, ANGA (UNAM). *Paratypes.* 2 males, same data as holotype (UNAM).

Etymology. The specific epithet is taken from the Latin *carina* (= keel), indicating the keel-like hypandrial right process of this species.

Description. **Male.** *Head.* White in ground color; vertical and orbital markings brown; coronal suture blackish brown; frontal suture pale brown; frons with two pairs of brown bands, lateral pair not reaching frontal suture; gena brown, with paler portion medially; eye black, large, IO/D = 0.9; ocelli white, ocellar field black; antennal socket bordered with dark brown band; dorsal region of postclypeus with ca. eight rows of blackish brown spots, fused with each other ventrally forming large T-shaped marking, ventro-lateral region without markings; anteclypeus brown. Antenna brown, pedicel and scape darker. Mouth parts brown.

Thorax. Prothorax brown. Mesonotum white in ground color; anterior surface of

scutum brown; anterior margin of lateral lobe of scutum black; anterior lobe of scutum with pair of blackish brown spots at posterior end, anteriorly with pair of large oval brown markings narrowly divided by white longitudinal band, each marking with paler region at middle; lateral lobes of scutum mostly brown, with pale region medially; scutellum brown, anterior margin darker, with pair of pale circular areas on posterior margin at middle. Metanotum brown, medially with white portion; lateral lobe with white spot posteriorly; scutellum as in mesonotum. Meso- and metapleurites brown except membranous region white.

Legs. Brown; fore coxa paler; tibiae paler with brown apices; hind femur with pale portion near distal end.

Forewing (Fig. 5E). Rather sparsely spotted. Spots in cell a_1 distinct, basal one smaller. Opposing spots in cell r clear, partly fused with each other. Proximal band narrow but distinct, broadly interrupted just beyond fork of $M + Cu$. Distal band faint, narrow in cell r_5 . Spot on roof of cell m_3 distinct but small. Submarginal spots hardly distinct, spot in cell r_5 large and distinct. Marginal clouds indistinct. *Hindwing.* Hyaline, cell CuP densely covered with pale brown spots distally, much sparser basally; veins brown.

Abdomen. White. *Terminalia.* Clunial arm long, triangular. Epiproct lobe (Fig. 13A) long, longer than wide, gradually narrowing to rounded dorsal margin. Hypandrium (Fig. 13B): left process needle-like, long, strongly projected posteriorly, slightly curved and directed postero-externally at tip; right process less projected, dorsally with longitudinal keel; median tongue of almost same width from base to apex, apical margin with few minute notches. Phallosome (Fig. 13C): pseudoparameres short and broad, broadly separated. Phallobase almost parallel sided on dorsal 2/3, ventral tip with short process.

Length. B 2.3-2.5; FW 3.3-3.7; HW 2.5-2.7.

Female. Unknown.

Distribution. Mexico.

***Trichadenotecnum tuitense* sp. nov.**

Material examined. *Holotype.* Male, MEXICO: Jalisco, ca. 20 km E of El Tuito, road to El Cuale, 3. XII. 1980, ANGA (UNAM).

Etymology. The specific epithet makes reference to the type locality.

Description: **Male.** *Head.* White in ground color; vertical and orbital markings pale brown; coronal suture black; frontal suture bordered with narrow brown band dorsally; frons with two pair of brown bands, median pair paler dorsally, lateral pair darker; gena mostly white, dorsal and ventral margins bordered with brown band; eye black, small, IO/D = 1.6; ocelli white, ocellar field black; antennal socket bordered with brown band; postclypeus with ca. ten rows of blackish brown spots, faint near dorsal margin, fused with each other ventrally forming a T-shaped large marking, ventro-lateral region white; anteclypeus brown. Antenna pale brown, pedicel and scape brown. Mouth parts pale brown.

Thorax. Prothorax brown. Meso- and metathorax mostly brown except membranous regions white; mesoscutum paler; mesopleuron with broad longitudinal white band at middle; dorsal half of meso- and metapleurites darker.

Legs. Brown; all tibiae paler, with darker portions near distal ends.

Forewing (Fig. 5F). Rather sparsely spotted. Spots in cell a₁ distinct, distal one large.

Opposing spots in cell r distinct but small. Proximal band narrow but distinct, paler in cell CuA, broadly interrupted just beyond fork of M + Cu. Distal band faint but distinct. Spot on roof of cell m₃ distinct but small. Submarginal spots apparent; spot in cell r₅ larger than others; spots in cell r₁, m₁ and m₃ small, sometimes indistinct. Marginal clouds almost invisible, slightly distinct at distal end of each vein. *Hindwing.* Hyaline, cell CuP with pale markings basally; veins brown.

Abdomen. White, with brown markings irregularly. *Terminalia.* Clunial arm short and narrow. Epiproct lobe (Fig. 13D) long, almost as long as basal width, almost parallel sided basally, then gradually narrowing to truncate dorsal margin. Paraproct: ventro-lateral band short, triangular; distal process long, directed upward. Hypandrium (Fig. 13E) symmetrical, without narrow membranous region anterior to median tongue socket; left process conical, projected posteriorly; right process less projected; median tongue with broad base, gradually narrowing to distal fourth, then slightly broadened, distal fourth parallel sided, distal margin with broad and shallow notch. Phallosome (Fig. 13F): pseudoparameres short and broad, strongly expanded laterally, broadly separated from each other. Phallobase almost parallel sided on dorsal 2/3, ventral tip with tiny process.

Length. B 2.7; FW 3.1; HW 2.3.

Female. Unknown.

Distribution. Mexico.

***Trichadenotecnum sparsum* sp. nov.**

Material examined. Holotype. Male, Mexico: Durango, Reserva de la Biosfera La Michilía, Trampa Mesa del Burro, 2500m, 26. VIII. 1987, ANGA & IWB Thornton (UNAM).

Paratype. 1 male, same data as holotype (UNAM).

Etymology. The specific epithet is taken from the Latin *sparsus* (= sparse), indicating the sparsely spotted forewing of this species.

Description: Male. Head. White in ground color; vertical and orbital markings dark brown; coronal suture black; frontal suture dorsally bordered with narrow brown band; frons with two pairs of dark brown bands; gena mostly dark brown with white spot medially; eye black, small, IO/D = 1.6; ocelli white, ocellar field black; antennal socket bordered with dark brown band; postclypeus with ca. eight rows of blackish brown spots at middle, fused with each other ventrally forming a large T-shaped marking, ventro-lateral corners white; anteclypeus dark brown. Antenna brown, pedicel and scape darker. Mouth parts dark brown.

Thorax. Prothorax dark brown. Meso- and metathorax mostly dark brown except membranous region white; dorsal surface of mesonotum mostly white, irregularly with some brown spots, anterior lobe with pair of pale brown markings, each with white circular marking medially, posterior margin of lateral lobe pale brown. Mesopleuron with longitudinal white band medially.

Legs. Dark brown; distal half of fore femur and tibiae of all legs except distal tips pale brown.

Forewing (Fig. 5G). Relatively narrow and sparsely spotted. Spots in cell a₁ distinct, nearly equal in size. Opposing spots in cell r small but distinct, widely separated from each other. Proximal band faint, distinct only in cell CuP and around vein Rs-M fusion. Distal band broad, faint to distinct. Spot on roof of cell m₃ variable. Submarginal spots distinct, spot in cell r₅ larger, spots in cells r₁ and m₃ hardly distinct. Marginal clouds indistinct. *Hindwing*. Hyaline, cell CuP with few faint spots; veins brown.

Abdomen. White dorsally, each segment with narrow blackish band, blackish brown ventrally. *Terminalia*. Clunial arm long, distal end pointed. Epiproct lobe (Fig. 14A) long and broad, longer than basal width, gradually narrowing to rounded dorsal margin. Hypandrium (Fig. 14B): left process conical, strongly projected posteriorly; right process small, hardly projected posteriorly; median tongue with broad base, then narrowing to basal fourth, almost parallel sided from basal fourth to distal fourth, then broadened apically; apical margin with deep triangular notch. Phallosome (Fig. 14C): pseudoparameres short and broad, expanded laterally, almost fused medially with shallow hollow between them. Phallobase narrowing ventrally, with pointed anterior end.

Length. B 2.6-2.9; FW 3.8-3.9; HW 2.9-3.0.

Female. Unknown.

Distribution. Mexico.

***Trichadenotecnum latipenne* sp. nov.**

Material examined. Holotype. Male, Mexico, Cañada de Contreras, D. F. Camino a Los Dínamos, 2700m, 29. VI. 1977, ANGA (UNAM). *Paratypes.* Mexico: 2 females, same data as holotype (UNAM); 1 male, 1 female, D. F. Cañada de Contreras, 2600m, 14. VII. 1978, ANGA (UNAM); 1 male, 2 females. Desierto de los Leones, D. F., 23. I. 1972, ANGA (UNAM); 1 male, 1 female. Morelos, 2.4mi W. Huitzilac, 6. VII. 1973, ELM (ISU); 2 males, Estado de Mexico, 2mi W. Río Frío, Hwy. 190, 10. VII. 1973, ELM (ISU); 1 male, 1 female, Hidalgo, Acaxochitlán, carretera 130, 22. V. 1975, ANGA (UNAM).

Etymology. The specific epithet is taken from the Latin *latus* (= broad) + *penna* (= wing), indicating the wide forewing of this species.

Description: Male. Head. White in ground color and extensively marked with dark brown; vertical and orbital markings dark brown; coronal suture black; frontal suture dorsally bordered with dark brown band; frons with two pairs of dark brown bands, lateral pair smaller but darker; gena mostly dark brown with white portion medially; eye black, small, IO/D = 1.1-1.4; ocelli white, ocellar field black; antennal socket bordered with dark brown band; postclypeus with ca. eight rows of blackish brown spots at middle, fused with each other ventrally forming a large T-shaped marking, ventro-lateral corner white; anteclypeus dark brown. Antenna brown, pedicel and scape darker. Mouth parts brown.

Thorax. Prothorax brown. Meso- and metathorax mostly dark brown except membranous region white; dorsal surface of mesonotum paler, median and postero-lateral regions white, with pair of faint blackish spots at posterior end of anterior lobe.

Legs. Brown; median part of fore femur and tibiae of all legs except distal tips paler.

Forewing (Fig. 5H). Somewhat broad, moderately spotted. Spots in cell a_1 distinct, distant spot usually larger or sometimes almost equal in size. Opposing spots in cell r distinct but sometimes faint. Proximal band narrow and faint, darker and distinct in cell CuP, just below fork of $M + Cu$ and around $Rs-M$ fusion. Distal band broad and distinct. Spot on roof of cell m_3 usually small and indistinct in distal half. Submarginal spots distinct, spots in cells r_1 and m_3 fainter and sometimes indistinct. Marginal clouds indistinct. *Hindwing*. Hyaline, cell CuP with faint sparse spots or not; veins brown.

Abdomen. White, each segment with irregular blackish brown band, thicker ventrally and laterally. *Terminalia*. Clunial arm variable in shape but usually short. Epiproct lobe (Fig. 14D) short, shorter than basal width, usually sharply narrowing to rounded or truncate narrow dorsal margin. Hypandrium (Fig. 14E): left process conical, strongly projected postero-laterally, slightly to strongly curved; right process triangular, weakly projected posteriorly; median tongue slightly to moderately constricted near middle, apical margin with triangular notch medially. Phallosome (Fig. 14F): pseudoparameres short and broad, expanded laterally, almost fused medially with shallow hollow posteriorly. Phallobase narrowing ventrally, with triangular ventral end.

Length. B 2.8-3.2; FW 4.6-5.5; HW 3.5-4.2.

Female. Color and general morphology almost as in male; eye IO/D = 2.2-2.3.

Genitalia: Egg guide of subgenital plate (Fig. 15A) broad, broader than long, anterior margin somewhat rounded, anterior margin of body of subgenital plate almost straight, with narrow and deep median notch. Internal plate as in Fig. 15B.

Length. B 3.6-4.0; FW 4.8-5.5; HW 3.6-4.5.

Distribution. Mexico.

***Trichadenotecnum* spp.**

As noted under group remarks, many specimens (all collected in Mexico) examined here and recognized as members of the *desolatum* group are treated as unidentified specimens. Some examples of male genital structures of such unclassified specimens are shown in Fig. 16.

The *chiapense* group

Diagnosis. Forewing (Fig. 17AB) not extensively covered with small spots; Rs fork obtuse; 3rd section of CuA slightly to rather strongly arched. *Male terminalia.* Eighth venter with large transversal sclerite separated from (Fig. 19C) or partly fused with (Fig. 18C) hypandrium. Clunial process well developed (Fig. 18A), long, forming pointed free process apically. Epiproct (Fig. 18AB) chair-shaped, epiproct lobe long and wide, protruded over clunium, its dorsal margin wide and with small projection at middle. Hypandrium (Fig. 18C) asymmetrical; left process long, sometimes lamellate; right process usually shorter than left, *distally lamellate*. Median tongue much longer than wide, dorsally with rounded keel covered by denticles or long spines. Phallosome (Fig. 18D) with broad pseudoparameres, widely separated from each other. *Female genitalia.* Body of subgenital plate (Fig. 20A) with pair of extensions of sclerite antero-medially. Ventral valve of gonapophyses (Fig. 20B) long; posterior lobe of external valve strongly projected. Internal plate (Fig. 20C) symmetrical;

spermathecal opening surrounded by egg-shaped strongly pigmented plate.

Key to Species (female unknown for *T. erwini*)

1. 8th sternum fused with hypandrium postero-medially (Fig. 18C) *T. erwini* sp. nov.
- . 8th sternum separated from hypandrium (Fig. 19C) *T. chiapense* sp. nov.

***Trichadenotecnum erwini* sp. nov.**

Material examined. Holotype. Male. Peru: Madre de Dios. Río Tambopata Reserved Zone, 30 km SW Puerto Maldonado, 290m, 14. IX. 1984, T. L. Erwin *et al.* (SI).

Etymology. The specific epithet honors Dr. Terry L. Erwin, leader of the Smithsonian Institution team that conducted canopy fogging episodes at the Río Tambopata Reserved Zone and at the Waorani Ethnic Reserve, In Napo, Ecuador.

Description: Male. Head. White in ground color; vertical and orbital markings brown; coronal suture dark brown; frontal suture bordered with a narrow brown band dorsally; frons with pair of pale brown bands medially, and with pair of blackish brown spots laterally; gena almost white except ventral and dorsal margins brown; eye black, small, IO/D = 1.5; ocelli white, ocellar field black; antennal socket bordered with broad brown band; postclypeus with ca. eight rows of blackish brown spots, fused with each other ventrally, forming a large circular marking, lateral region white; anteclypeus brown. Antenna pale brown, pedicel and

scape darker. Mouth parts pale brown; 4th segment of maxillary palpus brown.

Thorax. Prothorax brown. Mesonotum pale; anterior surface of anterior lobe of scutum brown, anterior margin of anterior lobe brown and with pale brown marking posteriorly; anterior margin of scutellum blackish brown; postnotum pale. Metanotum pale brown; anterior region of lateral lobe of scutum brown; postnotum pale. Meso- and metapleurites brown, with longitudinal white band medially.

Legs. Coxae brown; fore leg missing; femora brown except distal half of middle femur pale; tibiae pale brown, distal end of hind tibia darker; hind tarsus brown.

Forewing (Fig. 17A). Spots in cell a₁ rather small, basal one paler. Opposing spots in cell r small, broadly separated from each other. Proximal band narrow, its outline indented, broadly interrupted just beyond fork of M + Cu. Median spots sparse, some spots fused with each other. Distal band narrow, faint in cell r₅. Spot on roof of cell m₃ broad. Submarginal spots apparent; spots in cells r₃ and r₅ larger than others, spot in r₅ largest. Marginal clouds apparent, darker in cells r₅ and m₁. *Hindwing.* Hyaline; veins brown.

Abdomen. White, irregularly with blackish brown spots. *Terminalia.* Clunial arm (Fig. 18A) long and narrow, dorsal margin incised by membranous region; needle-like apically, its apical tip free from membrane. Anterior margin of 8th sternum (Fig. 18C) only slightly sinuate, partly fused with hypandrium posteriorly. Epiproct (Fig. 18 A, B) chair-shaped; epiproct lobe long and broad, broader than long, expanded dorsally, dorsal margin almost straight, with small conical process at middle, posterior surface slightly swollen. Hypandrium (Fig. 18C): left process conical, directed posteriorly, slightly sinuate, with small conical process dorso-basally; right process lamellate, apical margin serrated; median tongue constricted at basal third, apical margin denticulate, with shallow rounded notch, dorsal

surface with semicircular keel covered by denticles. Phallosome (Fig. 18D): pseudoparameres broader than long, narrowly separated, apical margin rounded, postero-internal part with few denticles. Phallobase widest near middle, then narrowing to pointed anterior end.

Length. B 2.3; FW 2.5; HW 1.8.

Female. Unknown.

Distribution. Peru.

***Trichadenotecnum chiapense* sp. nov.**

Material examined. Holotype. Male. Mexico: Chiapas, Apicpac, orilla de Presa Malpaso, 53 km N. Ocozocoautla, 1. VII. 1981, ANGA & L. B. Menchaca López (UNAM). *Paratype.* Mexico: 1 male, (no. 96); 2 males, Veracruz, Los Tuxtlas, ca. 25 mi NW of UNAM Field Station., 350 m, 22. XII. 1984, E. L. Mockford *et al.* (UNAM). BELIZE: 1 male, Cayo District, Chiquibul Forest Reserve, Las Cuevas, 9-12. XI. 1994, T. King & A. Howe (UNAM); 1 male, same locality and collectors, 16-17. VI. 1995 (UNAM); 1 male, Cayo District, Chiquibul Forest Reserve, San Pastor, 10-13. XI. 1994, T. King & A. Howe; 1 male, 1 female, same locality and collectors, 23-26. III. 1995 (UNAM); 1 male, 1 female, Cayo District, Chiquibul Forest Reserve, 23. III. 1995, T. King & A. Howe (UNAM); 3 males, MT 11, 10-13. IV. 1996, A. Howe & T. King (UNAM); 2 males, 1 female, MT 14, 10-13. VI. 1996, T. King & A. Howe (UNAM).

Etymology. The specific epithet is the patronymic of 'Chiapas', the state In southern Mexico where the holotype was collected.

Description: Male. Head. White in ground color; vertical and orbital markings blackish brown; coronal suture black; frontal suture bordered with blackish brown broad band dorsally; frons with two pairs of blackish brown bands, median pair narrow and lateral pair broad; gena almost blackish brown except narrow crescent white dorsal region; eye black, IO/D = 1.1; ocelli white, ocellar field black; antennal socket bordered with broad blackish brown band; postclypeus with ca. four rows of blackish brown spots dorsally, fused with each other ventrally forming a large, T-shaped blackish marking, ventro-lateral region white; anteclypeus brown. Antenna pale brown, pedicel and scape darker. Mouth parts brown; 4th segment of maxillary palpus darker.

Thorax. Prothorax blackish brown. Meso- and metathorax mostly blackish brown except membranous regions white; mesoscutum pale, anterior surface of anterior lobe blackish brown, mesopleuron with broad longitudinal white band medially; anterior margins of meso- and metascutum and around notal wing processes of meso- and metanotum blackish brown.

Legs. Pale brown; each tibia with darker portion near distal end; ventral surface of fore and middle femur with pair of blackish brown markings.

Forewing (Fig. 17B). Spots in cell a_1 subequal in size, basal one paler. Opposing spots in cell r large, triangular, narrowly separated from each other. Proximal band broad in cell CuP and posterior half of cell CuA, with large paler spot in cells CuA and CuP, strongly constricted just below fork of $M + Cu$, broadly interrupted just beyond fork of $M + Cu$. Median spots sparse, partly fused with each other. Distal band narrow. Spot on roof of cell m_3 broad. Submarginal spots apparent; spot in cell r_5 larger than others; spot in cell m_3 small and rather faint. Marginal clouds apparent. *Hindwing.* Hyaline; veins brown.

Abdomen. White, with irregular blackish brown markings, 6th to 8th venters blackish brown. *Terminalia.* Clunial arm (Fig. 19A) long and narrow, sickle-like in shape apically, its apical tip pointed forming free process. Eighth venter (Fig. 19C) with transverse sclerite, anterior margin almost straight, free from hypandrium posteriorly. Epiproct (Fig. 19AB) chair-shaped; epiproct lobe long and broad, broader than wide, slightly expanded dorsally, dorsal margin strongly sinuated, with small process at middle, posterior surface slightly swollen. Hypandrium (Fig. 19C): left process with flattened lateral surfaces, directed posteriorly, slightly sinuated, of almost equal width in lateral view from base to apical 2/5 then strongly narrowing to sharply pointed apex; right process much shorter than left process, lamellate, usually serrated apically; median tongue broadened apically, apical margin with or without shallow and broad notch, dorsal surface with semicircular keel covered by long spines. Phallosome (Fig. 19D): pseudoparameres widely separated, narrow, rounded apically, postero-internal part with group of denticles. Phallobase widest near middle, then narrowing to pointed anterior end.

Length. B 2.0-2.4; FW 2.6-2.9; HW 1.8-2.0.

Female. Color and general morphology almost as in male; eye IO/D = 2.0. *Genitalia:* Egg guide of subgenital plate (Fig. 20A) relatively narrow, gradually narrowing apically, apical margin rounded; body of subgenital plate with pair of tongue-shaped extensions of sclerite antero-medially. Dorsal valve of gonapophyses (Fig. 20B) with long distal process; posterior lobe of external valve strongly projected posteriorly. Internal plate as in Fig. 20C.

Length. B 2.5-2.8; FW 3.0-3.3; HW 2.1-2.4.

Distribution. Mexico, Belize.

The *quaesitum* group

Diagnosis. Forewing extensively covered with small spots (Fig. 17F-I) or not (Fig. 17 C, D), submarginal spots usually apparent; Rs fork obtuse; 3rd section of CuA usually arched. *Male terminalia.* Eighth venter (Fig. 21C) with large transversal sclerite, postero-medially fused with hypandrium. Clunial process (Fig. 21A) well developed, long, forming free process apically, antero-ventrally with ball-shaped lobe. Epiproct (Fig. 21 A,B) chair-shaped, epiproct lobe long and wide, protruded over clunium, its dorsal margin wide and with small projection at middle. Paraproctal distal process (Fig. 21A) directed upwards. Hypandrium (Fig. 21C) asymmetrical; left and right processes well developed, conical or needle-like in shape, *right process strongly bent internally near its base and crossing with left process.* Median tongue much longer than wide, broadened to flat or slightly sinuated apical margin, its dorsal surface with keel covered with denticles. Phallosome (Fig. 21D) with broad pseudoparameres. *Female genitalia.* Egg guide of subgenital plate (Fig. 24A) broadened apically, apical margin almost flat or with very shallow notch medially. Ventral valve of gonapophyses (Fig. 24B) long; posterior lobe of external valve strongly projected. Internal plate symmetrical (Fig. 24C) or slightly asymmetrical (Fig. 28C); spermathecal opening surrounded by egg-shaped strongly pigmented plate; anterior region unpigmented or only slightly pigmented.

Key to Species

1. Forewing extensively covered with small spots (Fig. 17F-I) 3
- . Forewing not extensively covered with small spots (Fig. 17 C, D) 2

2. Hypandrial median tongue relatively short, about 3x longer than apical width; hypandrial right process exceeding left one (Fig. 21C)..... *T. quaesitum* (Chapman)
- Hypandrial median tongue relatively long, about 3.5x longer than apical width; hypandrial right arm not exceeding left one (Fig. 22C); female unknown *T. quaesitellum* sp. nov.
3. Hypandrial left process long exceeding apex of right one (Fig. 23C).. 4
- Hypandrial left process short, not reaching right one (Fig. 31C); female unknown *T. brevicornum* sp. nov.
4. Forewing sparsely spotted, areola postica not covered with large brown marking (Fig. 17E) 5
- Forewing densely spotted; distal half of areola postica covered with large brown marking (Fig. 17F) *T. maculatum* sp. nov.
5. Clunial lobe membranous (Fig. 23A); subgenital plate without narrow membranous notch antero-medially (Fig. 24A) 6
- Clunial lobe strongly sclerotized (Fig. 29A); body of subgenital plate with narrow membranous notch antero-medially extending near base of egg guide (Fig. 30A) *T. ericium* sp. nov.
6. Forewing proximal band complete in cell CuA (Fig. 17E); hypandrial median tongue broad, about 2x longer than apical width (Fig. 23C); dorsal margin of epiproct lobe with conical median projection (Fig. 23B) *T. cerrosillae* sp. nov.
- Forewing proximal band narrowly interrupted at median part of cell CuA (Fig. 17G); hypandrial median tongue slender, about 2.5x longer than apical width (Fig. 27C); dorsal margin of epiproct lobe without distinct median projection (Fig. 27B) *T. neoleonense* sp. nov.

***Trichadenotecnum quaesitum* (Chapman)**

Psocus quaesitus Chapman, 1930: 270 (male; not female of *Psocus quaesitum* Chapman, 1930: 270).

Trichadenotecnum slossonae (Banks): Sommerman, 1948: 273 (female).

Trichadenotecnum quaesitum (Chapman): Mockford, 1993: 286.

Material examined. CANADA: 1 male, Quebec, Rd. 18 nr. Mascouche, N. Montreal, 21.

VIII. 1956, ELM (ISU); 1 male, USA: Indiana, Dunes State Park, 6. IX. 1952, ELM (ISU); 1 male, Missouri, Big Spring State Park, Carter Co., 21. VI. 1959, ELM (ISU); 1 male, 1 female, South Carolina, Berkeley Co., Bonneau, 3. X. 1973, ELM (ISU).

Diagnosis. Although considerable variations in body size and some genital characters are recognized, this species can be characterized by the combination of the following character states: forewing not extensively covered with small spots (Fig. 17C); basal lobe of clunial arm weakly sclerotized (Fig. 21A); epiproct lobe nearly parallel sided (Fig. 21B); apex of hypandrial right arm exceeding outer margin of left process; hypandrial median tongue relatively broad, asymmetrical, slightly left skewed (Fig. 21C); pseudoparameres widely separated, aedeagal area wider than basal width of pseudoparamere (Fig. 21D). In contrast, the following intraspecific variations were observed: difference in body size, male forewing length 2.6 - 3.8 mm; some minute differences in hypandrium and phallosome. However, these variations are continuous and intraspecific. It is also possible that these morphological variations indicate genetic isolation between different populations, and further morphological

and molecular analyses are required to clarify it. See Mockford (1993) for further description of the species.

Distribution. Canada, USA, Mexico.

***Trichadenotecnum quaesitellum* sp. nov.**

Material examined. Holotype. Male. Mexico: Tamaulipas, 5.1 mi W. Gómez Farías, 16. VI. 1962, ELM *et al.* (ISU).

Etymology. The specific epithet is taken from *quaesitum* (= specific epithet of *Trichadenotecnum quaesitum*) + *-ellus* (= Latin diminutive). This species is very similar to *T. quaesitum* but smaller.

Description: Male. Head. White in ground color; vertical and orbital markings blackish brown; coronal suture black; frontal suture bordered with narrow brown band dorsally; frons with pair of pale brown bands at middle and with pair of circular markings laterally; eye black, IO/D = 0.6; ocelli white, ocellar field black; gena white; antennal socket bordered with brown band; postclypeus with ca. eight rows of pale brown spots at middle, fused with each other ventrally forming a large marking, ventro-lateral corner white, lateral margin of postclypeus dark brown, dorsal margin without marking; anteclypeus pale brown. Antenna pale brown, pedicel and scape darker. Mouth parts pale brown; 4th segment of maxillary palpus brown.

Thorax. Prothorax brown. Mesonotum pale; anterior surface of scutum brown; lateral lobe of scutum with large pale brown marking; scutellum pale brown, median part darker, anterior margin blackish brown; postnotum brown. Metanotum pale brown, with three whitish oval spots on posterior regions of scutal lobes. Meso- and metapleurites brown, with longitudinal white band medially.

Legs. Pale brown; middle and hind coxae, basal half of middle femur and entire hind femur brown, distal tip of hind tibia darker.

Forewing (Fig. 17D). Not extensively covered with tiny spots. Spots in cell a_1 apparent, nearly of equal size. Opposing spots in cell r distinct. Proximal band broad, narrowly interrupted just beyond fork of $M + Cu$. Distal band distinct. Spot on roof of cell m_3 narrow but distinct. Submarginal spots apparent; spot in cell r_5 elongate. Marginal clouds distinct. *Hindwing.* Hyaline, cell CuP with faint brownish spots in distal half; veins brown.

Abdomen. White, with sparse minute blackish brown spots. *Terminalia.* Clunial arm (Fig. 22A) developed but very weakly sclerotized, not forming free process apically, basally with membranous lobe ventrally covered with short spines. Anterior margin of 8th sternum (Fig. 22C) smoothly arched, fusion with hypandrium narrow. Epiproct lobe (Fig. 22B) broadened dorsally, wider than long, dorsal margin sinuate, posterior surface slightly concave. Paraproct (Fig. 22A); ventro-lateral band short, triangular; distal process long. Hypandrium (Fig. 22C): outer margin of left process slightly arched, directed posteriorly; right process projected outward, then strongly bent postero-internally near base, its apex not exceeding outer margin of left process; median tongue long, slightly constricted medially, apical margin slightly hollowed, dorsal keel rounded. Phallosome (Fig. 22D): pseudoparameres widely separated, long, longer than basal width, directed dorsally, apical margin rounded with tiny

denticles internally. Phallobase widest at ventral third, then narrowing to pointed ventral end.

Length. B 2.3; FW 2.8; HW 2.0.

Female. Unknown.

Distribution. Mexico.

***Trichadenotecnum cerrosillae* sp. nov.**

Material examined. *Holotype.* Male. Mexico: Nuevo León, ca. Cd. Contry, Monterrey, western slope of Cerro de la Silla, 700m, 24. XII. 1980, ANGA (UNAM). *Paratypes.*

Mexico: 1 male, 6.3 mi SW Teziutlán, Puebla, 7000', 19. VIII. 1958, H. Howden (ISU); 1 male, Nuevo León, 9 km NE San Antonio Peña Nevada, 1930m, 25. VIII. 1979, ANGA & M. C. Herrera (UNAM); 1 male, 1 female, Nuevo León, western slope of Cerro de la Silla, path to the Arch, 900 m, 28. VIII. 1982, ANGA (UNAM).

Etymology. The specific epithet derives from 'Cerro de la Silla' (Saddle Mountain), an emblematic feature of Monterrey, Mexico, where the holotype of the species was collected.

Description: **Male.** *Head.* White in ground color; vertical and orbital markings blackish brown; coronal suture black; frontal suture bordered with narrow pale brown band dorsally; frons with pair of blackish brown circular spots laterally; eye black, IO/D = 1.0; ocelli white, ocellar field black; antennal socket bordered with broad blackish brown band; gena blackish brown except rectangular white portion dorsally; postclypeus with ca. eight rows of blackish brown

spots at middle, fused with each other ventrally forming a large marking, ventro-lateral corner white, lateral margin of postclypeus blackish brown, dorsal margin without marking; anteclypeus brown. Antenna pale brown, pedicel and scape brown. Mouth parts blackish brown; third segment of maxillary palpus pale brown.

Thorax. Prothorax brown. Mesonotum white; anterior surface of scutum brown; anterior margin of lateral lobe of scutum black; posterior region of scutum with pair of brown markings at middle; scutellum white, median part and anterior margin brown; postnotum brown. Metanotum brown, with three whitish oval spots on posterior regions of scutal lobes. Meso- and metapleurites brown with longitudinal white band medially.

Legs. Coxae dark brown; femora brown except middle part of fore and middle femora white; tibiae pale brown, with darker portion near distal ends; tarsi brown.

Forewing (Fig. 17E). Rather sparsely covered with small spots. Spots in cell a₁ distinct, distal one larger, basal one paler. Opposing spots in cell r very small but distinct. Proximal band narrow, strongly constricted just beyond fork of M + Cu. Distal band narrow and faint in cell r₅, fragment of band in cell r₃ large. Spot on roof of cell m₃ large and dark. Submarginal spots apparent; spots in cells r₁, r₃ and m₃ small, sometimes indistinct. Marginal clouds faint. *Hindwing.* Hyaline, cell CuP with faint brownish spots; veins brown.

Abdomen. White, each segment with blackish brown band laterally, dorsum sparsely with irregular blackish brown markings, 6th to 8th venters blackish brown. *Terminalia.* Clunial arm (Fig. 23A) long and narrow, slightly sinuated, free from membrane apically, antero-ventrally with membranous lobe covered with fine setae. Anterior margin of 8th sternum (Fig. 23C) with semicircular extension medially; fusion with hypandrium narrow. Epiproct lobe (Fig. 23B) almost as long as wide, dorsal margin strongly sinuated, posterior

surface almost flattened. Paraproct (Fig. 23A): ventro-lateral band indistinct; distal process broad. Hypandrium (Fig. 23C) with rugose region laterally; left process almost straight, directed postero-internally; right process projected outward, then strongly bent postero-internally near base; median tongue broadened apically, apical margin sinuated, dorsal keel triangular. Phallosome (Fig. 23D): pseudoparameres broadly separated, longer than wide, directed dorsally, apical margin rounded or somewhat truncate. Phallobase narrowing to pointed anterior end, anterior end with tiny triangular projection.

Length. B 2.2-2.5; FW 3.0-3.9; HW 2.1-2.9.

Female. Color and general morphology almost as in male; eye IO/D = 2.0. *Genitalia:* Egg guide of subgenital plate (Fig. 24A) broadened at distal end, postero-lateral corners strongly angled, apical margin arched, with very shallow notch at middle; body of subgenital plate with pair of sclerites extending antero-medially. Dorsal valve of gonapophyses (Fig. 24B) with short distal process; posterior lobe of external valve strongly projected posteriorly. Internal plate as in Fig. 24C.

Length. B 2.9; FW 3.1; HW 2.2.

Distribution. Mexico.

***Trichadenotecnum maculatum* sp. nov.**

Material examined. Holotype. Male. Mexico: Nuevo León, 5 km W of Ciénega, hacia Laguna de Sánchez, 1200 m, 25. V. 1977, ANGA (UNAM). *Paratypes.* 1 female, same data as holotype; 1 male, 1 female, Nuevo León, 10 mi. E. Iturbide, Hwy. 60, 13. VI. 1962, J. Campbell, (ISU).

Etymology. The specific epithet is taken from Latin *macula* (= spotted), indicating the heavily spotted forewing in this species.

Description: Male. Head. White in ground color; vertical and orbital markings pale brown; coronal suture black; frontal suture very narrowly bordered with pale brown band dorsally; frons with two pairs of pale brown spots ventrally; eye black, IO/D = 1.0; ocelli white, ocellar field black; antennal socket bordered with dark brown band; postclypeus with ca. eight rows of pale brown spots at middle, fused with each other ventrally forming a large blackish brown marking, ventro-lateral corner white, lateral margin of postclypeus brown, dorsal margin without marking; anteclypeus brown. Antenna pale brown, pedicel and scape darker. Mouth parts dark brown; third segment of maxillary palpus pale brown.

Thorax. Prothorax brown. Mesonotum white; anterior surface of scutum brown; anterior margin of lateral lobe of scutum black; posterior region of scutum with pair of brown markings at middle; scutellum white, median part and anterior margin brown; postnotum brown. Metanotum brown, with pair of whitish oval spots on posterior regions of lobes of scutum, lateral corner white. Meso- and metapleurites brown with longitudinal white band medially.

Legs. Coxae dark brown; femora brown except middle part of fore and middle femora white; tibiae pale brown, with darker portion near distal ends; tarsi brown.

Forewing (Fig. 17F). Densely covered with small spots. Spots in cell a_1 distinct, basal one smaller. Opposing spots in cell r apparent for anterior one but posterior one very small and less distinct. Proximal band broad, strongly constricted around fork of $M + Cu$, with

elongate paler pigmented area in cell CuA. Distal band somewhat indistinct in cell r5, band in cell r3 distinct. Spot on roof of cell m3 large. Submarginal spots diffuse; spot in cell r5 larger than others and distinct; spots in cell m1, m2 and m3 small, sometimes indistinct. Marginal clouds clear, darker along veins. *Hindwing*. Hyaline, extensively covered with pale brown spots, some spots fused with each other to form a large marking in cell CuP; veins brown.

Abdomen. White, each segment with blackish brown band. *Terminalia*. Clunial arm (Fig. 25A) long and narrow, slightly arched, forming pointed free process apically, antero-ventrally with fleshy lobe covered with fine setae. Anterior margin of 8th sternum (Fig. 25C) concave; fusion with hypandrium very narrow. Epiproct lobe (Fig. 25B) expanded dorsally, wider than long, dorsal margin slightly arched, with rounded projection at middle, posterior surface almost flattened. Paraproct (Fig. 25A): ventro-lateral band short, triangular; distal process broad. Hypandrium (Fig. 25C) with weakly rugose region laterally; left process sinuate, directed postero-externally at apex; right process of almost equal width from base to apex, projected outward, then strongly bent postero-internally near base, with few denticles at apex; median tongue narrowing medially, then broadened apically, apical margin almost straight, dorsal keel triangular. Phallosome (Fig. 25D): pseudoparameres widely separated, longer than wide, directed dorsally, apical margin rounded or somewhat truncated. Phallobase widest at ventral 2/5, then narrowing to pointed anterior end.

Length. B 2.6-2.9; FW 3.0-3.7; HW 2.2-2.8.

Female. Color and general morphology almost as in male; eye IO/D = 1.9. *Genitalia*: Egg guide of subgenital plate (Fig. 26A) widened near distal end, postero-lateral corners rounded, apical margin only slightly arched; body of subgenital plate with pair of broad extensions of sclerite antero-medially. Dorsal valve of gonapophyses (Fig. 26B) with long

distal process; posterior lobe of external valve strongly projected posteriorly. Internal plate as in Fig. 26C.

Length. B 2.8-3.0; FW 3.2-3.8; HW 2.1-2.9.

Distribution. Mexico.

***Trichadenotecnum neoleonense* sp. nov.**

Material examined. *Holotype.* Male. Mexico: Nuevo León, Guadalupe, Rancho Alamillos, Ladera E Cerro de la Silla, 620 m, 31. VII. 1979, ANGA (UNAM). *Paratype.* 1 female, same data as holotype; 2 males, 2 females, same locality as holotype, 22. V. 1977, ANGA (UNAM).

Etymology. The specific epithet refers to the Mexican state of Nuevo León, from where this species is only known presently.

Description: **Male.** *Head.* White in ground color; vertical markings brown; orbital markings pale brown; coronal suture black; frontal suture very narrowly bordered with pale brown band; frons with two pairs of spots ventrally, lateral ones small, circular, dark brown, median ones tiny, pale brown; eye black, IO/D = 0.9; ocelli white, ocellar field black; antennal socket bordered with narrow brown band; postclypeus with ten rows of blackish brown spots at middle, fused with each other ventrally forming a large marking, ventro-lateral corner white, dorsal region without marking; anteclypeus brown. Antenna pale brown, pedicel and scape

darker. Mouth parts brown; 4th segment of maxillary palpus darker.

Thorax. Prothorax brown. Meso- and metathorax mostly brown except membranous regions white; mesoscutum pale, anterior surface of anterior lobe brown, mesopleuron with broad longitudinal white band medially; anterior margins of meso- and metascutellum blackish brown; metascutum with white spot medially, anterior part of lateral lobe white, lateral lobe with white spot posteriorly.

Legs. Coxae brown; hind femur brown, fore and middle tibiae brown basally, white distally and each with pair of dark brown spots on ventral surface; tibiae pale brown, with dark brown portion at distal end; tarsi brown.

Forewing (Fig. 17G). Sparsely covered with small spots. Spots in cell a₁ distinct, subequal in size. Opposing spots in cell r distinct, posterior one very small. Proximal band narrow, strongly constricted at middle in cell CuA and just beyond fork of M + Cu. Distal band clear, narrow in cell r₅, broad in cell r₃. Spot on roof of cell m₃ large and dark. Submarginal spots apparent; spot in cell r₅ larger; spot in cell m₃ obscure. Marginal clouds faint, almost invisible except along each vein dark. *Hindwing.* Hyaline, cell CuP with large brown marking and few faint brown spots; veins brown.

Abdomen. White, each segment with blackish brown band except dorsum sparsely with blackish brown spots. *Terminalia.* Clunial arm (Fig. 27A) long and narrow, slightly sinuate, forming pointed free process apically, antero-ventrally with fleshy lobe covered with fine setae. Anterior margin of 8th sternum (Fig. 27C) with triangular extension; fusion with hypandrium broad. Epiproct lobe (Fig. 27B) slightly wider than long, dorsal margin sinuated, posterior surface almost flat. Paraproct (Fig. 27A); ventro-lateral band very short; distal process short. Hypandrium (Fig. 27C) with weakly rugose region laterally; left process

slightly curved at middle, directed posteriorly; right process projected outward, then strongly bent postero-internally near base; median tongue broadened apically, apical margin almost straight, dorsal keel triangular. Phallosome (Fig. 27D): pseudoparameres broadly separated, short and narrow, longer than wide, gradually narrowing to rounded apex. Phallobase widest at ventral third, then narrowing to pointed anterior end.

Length. B 2.6-2.7; FW 2.8-3.2; HW 2.2-2.4.

Female. Color and general morphology almost as in male; eye IO/D = 1.6. *Genitalia:* Egg guide of subgenital plate (Fig. 28A) broadened near distal end, apical margin slightly hollowed; dorsal surface of egg guide sclerotized laterally; body of subgenital plate with pair of tongue-shaped extensions antero-medially. Dorsal valve of gonapophyses (Fig. 28B) with short distal process; posterior lobe of external valve not strongly projected posteriorly. Internal plate as in Fig. 28C.

Length. B 2.7-3.0; FW 3.1-3.5; HW 2.3-2.5.

Distribution. Mexico.

***Trichadenotecnum ericium* sp. nov.**

Material examined. *Holotype.* Male. Mexico: Puebla, ca. Xicotepec de Juárez, 20. III. 1983, H. Brailovsky (UNAM). *Paratypes.* 2 males, 1 female, 4 mi W. Jalacingo, Rd. 131, Veracruz, 29. VI. 1962, ELM, J. Campbell & F. Hill (ISU).

Etymology. The specific epithet is taken from the Latin *ericus* (= spiny), in reference to the

field of spines on the lobes of the clunial arms.

Description: Male. Head. White in ground color; vertical and orbital markings pale brown; coronal suture black; frontal suture bordered with dark brown band dorsally; frons with pair of brown band medially and pair of pale circular spots laterally; gena dark brown, dorsal half paler; eye black, IO/D = 0.9; ocelli white, ocellar field black; antennal socket bordered with dark brown band; postclypeus with ca. eight rows of pale brown spots at middle, fused with each other ventrally forming a large blackish brown marking, ventro-lateral corner white, lateral margin of postclypeus brown, dorsal margin without marking; anteclypeus brown. Antenna pale brown, pedicel and scape darker. Mouth parts dark brown; third segment of maxillary palpus pale brown.

Thorax. Prothorax brown. Mesonotum white; anterior surface of scutum brown; anterior margin of lateral lobe of scutum black; posterior region of scutum with pair of brown markings at middle; scutellum white, median part and anterior margin brown; postnotum brown. Metanotum brown, with pair of whitish oval spots on posterior regions of lobes of scutum, lateral corner white. Meso- and metapleurites brown with longitudinal white band medially.

Legs. Coxae dark brown; femora brown except middle part of fore and middle femora white; tibiae pale brown, with darker portion near distal ends; tarsi brown.

Forewing (Fig. 17H). Sparsely covered with small spots. Spots in cell a₁ apparent, almost equal in size. Opposing spots in cell r large and distinct. Proximal band narrow, broadly interrupted just beyond fork of M + Cu. Distal band narrow in cell r₅, small in cell r₃. Spot on roof of cell m₃ narrow, narrower in distal half. Submarginal spots apparent; spot

in cell r₅ elongate; spots in cells r₁ and m₃ small, almost indistinct. Marginal clouds faint.

Hindwing. Hyaline, cell CuP with faint brownish spots in distal half, cell r₃ with few faint spots, cell r₁ with longitudinal faint marking along R₁ vein; veins brown.

Abdomen. White, with sparse minute blackish brown spots. *Terminalia.* Clunial arm (Fig. 29A) long, rather broad, forming rounded free process apically, antero-ventrally with sclerotized lobe covered with short and thick spines. Anterior margin of 8th sternum (Fig. 29C) irregularly indented; fusion with hypandrium rather broad. Epiproct lobe (Fig. 29B) wider than long, dorsal margin almost straight, with conical projection medially, posterior surface almost flat. Paraproct (Fig. 29A): ventro-lateral band short, triangular; distal process short. Hypandrium (Fig. 29C): left process broad, slightly arched, directed postero-internally; right process projected outward, then strongly bent postero-internally near base; median tongue slightly broadened apically, apical margin slightly hollowed, dorsal keel rounded. Phallosome (Fig. 29D): pseudoparameres widely separated, short, almost as long as wide, directed dorsally, apical margin almost straight with small projection internally. Phallobase widest at ventral third, then narrowing to pointed anterior end.

Length. B 2.6-2.8; FW 3.5-3.7; HW 2.7-2.8.

Female. Color and general morphology almost as in male; eye IO/D = 2.0. *Genitalia:* Egg guide of subgenital plate (Fig. 30A) slightly widened near distal end, apical margin slightly arched and shallowly hollowed at middle; dorsal surface of egg guide sclerotized laterally; body of subgenital plate with pair of triangular extensions antero-medially. Dorsal valve of gonapophyses (Fig. 30B) with short distal process; posterior lobe of external valve not strongly projected posteriorly. Internal plate as in Fig. 30C.

Length. B 3.1; FW 3.9; HW 2.8.

Distribution. Mexico.

***Trichadenotecnum brevicornum* sp. nov.**

Material examined. *Holotype.* Male. Mexico: Chiapas, 4 km N. Tuxtla Gutiérrez, 15. VII. 1962, ELM (ISU).

Etymology. The specific epithet is taken from Latin *brevis* (= short) + *cornu* (=horn), in reference to the short hypandrial left process of this species.

Description: **Male** (teneral). *Head.* White in ground color; vertical and orbital markings pale brown; coronal suture black; frontal suture bordered with narrow pale brown band dorsally; frons with pale brown marking ventro-medially and pair of spots laterally; ventral and dorsal margins of gena pale brown; eye black, IO/D = 0.9; ocelli white, ocellar field black; antennal socket bordered with broad pale brown band; postclypeus with ca. eight rows of pale brown spots, fused with each other ventrally forming a large marking, ventro-lateral corner white, dorsal margin without marking; anteclypeus pale brown. Antenna pale brown, scape brown. Mouth parts white.

Thorax. Prothorax pale brown. Mesonotum white; anterior surface of scutum pale brown; anterior margin of lateral lobe of scutum brown; scutellum white, anterior margin brown; postnotum pale brown. Metanotum pale brown, with three white oval spots on posterior regions of lobes of scutum. Mesopleuron white, except dorsal half pale brown.

Metapleuron brown except membranous region white.

Legs. White; middle and hind coxae pale brown; all femora with blackish brown spot at distal end ventrally; hind femur with slightly darker portion near distal end.

Forewing (Fig. 17 I). Spots in cell a_1 apparent, basal one small. Opposing spots in cell r distinct only for posterior spot, anterior spot indistinct. Proximal band narrow and somewhat indistinct in cell CuA, broadly interrupted just beyond fork of $M + Cu$. Distal band narrow and faint. Spot on roof of cell m_3 narrow but distinct. Submarginal spots apparent; spot in cell r_5 elongate. Marginal clouds faint. *Hindwing.* Hyaline, cell CuP with faint brownish marking; veins pale brown.

Abdomen. White, each segment with blackish brown band. *Terminalia.* Clunial arm (Fig. 31A) weakly developed, with membranous lobe covered with short spines. Anterior margin of 8th sternum (Fig. 31C) with semicircular extension medially, fusion with hypandrium narrow. Epiproct lobe (Fig. 31B) wider than long, dorsal margin slightly concave, with rounded projection medially, posterior surface with swelling medially near dorsal margin. Paraproct (Fig. 31A); ventro-lateral band absent; distal process long. Hypandrium (Fig. 31C): left process short, not reaching right process, conical, curved inwards; right process well developed, projected posteriorly, then strongly bent postero-internally near base; median tongue broadened apically, apical margin with median notch, dorsal keel rounded. Phallosome (Fig. 31D): pseudoparameres widely separated, long, slightly longer than wide, directed dorsally, apical margin rounded, postero-internally with serrated projection. Phallobase nearly parallel sided, then narrowing to pointed ventral end.

Length. B 2.3; FW 2.6; HW 1.9.

Female. Unknown.

Distribution. Mexico.

The *concinnum* group

Diagnosis. Species of this group are similar to those of the *quaesitum* group in many features but can be distinguished by the *symmetrical hypandrium in the male* (Fig. 32C). The female is known only for *T. concinnum*, and it differs from females of the *quaesitum* group in the asymmetrical internal plate with anterior region partly pigmented (Fig. 33C).

Key to Species

1. Clunial arm with well sclerotized and denticulated lobe basally (Fig. 34A); female unknown 2
- Clunial arm with less sclerotized and smooth surfaced lobe basally (Fig. 32A)..... *T. concinnum* sp. nov.
2. Dorsal margin of epiproct lobe deeply hollowed medially, dorso-lateral corner acute (Fig. 35B) *T. nicaraguense* sp. nov.
- Dorsal margin of epiproct lobe shallowly hollowed medially, dorso-lateral corner rounded (Fig. 34B) *T. acutum* sp. nov.

***Trichadenotecnum concinnum* sp. nov.**

Material examined. Holotype. Male. Mexico: Veracruz, Santiago Tuxtla, road to cerro El Vigía, 3 km W intersection with Hwy. 180, 13. VII. 1973, ANGA (UNAM). *Paratypes.* Mexico: 1 male, same data as holotype; 1 male, 1 female, Veracruz, road from Catemaco to Coyame, 2.6 mi from Catemaco, 16. VII. 1973, J. R. Taber (ISU); 1 male, 1 female, Veracruz, road to Cerro San Martín from San Andrés Tuxtla, 8 mi from Hwy. 180, 14. VII. 1973, J. R. Taber (ISU).

Etymology. The specific epithet is taken from the Latin *concinus* (= symmetric), indicating the symmetrical hypandrium of this species.

Description: Male. Head. White in ground color; vertical and orbital markings blackish brown; coronal suture black; frontal suture bordered with blackish brown band dorsally; frons with pair of faint brown bands at middle and pair of blackish brown irregular bands laterally; gena white except ventral margin blackish brown; eye black, IO/D = 0.6; ocelli white, ocellar field black; antennal socket bordered with dark brown band; postclypeus with ca. eight rows of pale brown spots dorsally, fused with each other ventrally forming a large blackish brown marking, dorsal margin and ventro-lateral corner without marking; anteclypeus brown.

Antenna pale brown, scape and pedicel darker. Mouth parts pale brown; 4th segment of maxillary palpus dark brown.

Thorax. Prothorax brown. Mesonotum white; anterior surface of scutum pale brown; anterior margin of lateral lobe of scutum black; posterior region of lateral lobe of scutum pale brown; anterior margin of scutellum blackish brown; postnotum white. Metanotum pale brown, with white markings on anterior and posterior regions of lateral lobe of scutum; anterior margin of scutellum blackish brown. Mesopleuron white except dorsal third and ventral margin brown. Metapleuron brown except membranous region white.

Legs. Dark brown; fore femur, distal half of middle femur and all tibiae paler; distal tip of fore and middle femora with blackish brown spots ventrally; middle tibia with dark spot near distal end.

Forewing (Fig. 17J). Spots in cell a_1 apparent, distal spot larger. Opposing spots in cell r large and distinct. Proximal band narrow, narrower in anterior half, with oval lighter pigmented portion in cell CuA. Distal band broad but faint. Spot on roof of cell m_3 small, distal half indistinct. Submarginal spots apparent; spot in cell r_5 larger; spot in cell m_3 indistinct. Marginal clouds faint. *Hindwing.* Hyaline, cell CuP with group of faint brown spots in distal half; veins brown.

Abdomen. White, each segment with blackish brown band. *Terminalia.* Clunial arm (Fig. 32A) weakly sclerotized, not forming a free process apically, basally with membranous lobe. Eighth venter (Fig. 32C) with transverse, triangular sclerite, fused with hypandrium at middle. Epiproct lobe (Fig. 32B) slightly wider than long, slightly narrowing dorsally, posterior surface almost flattened. Paraproct (Fig. 32A): ventro-lateral band indistinct; distal process short. Hypandrium (Fig. 32C): left and right processes well developed, rising from postero-lateral corners, strongly curved, apices pointed and directed postero-internally; median tongue slightly broadened apically, with slight hollow medially on posterior margin, dorsal keel rounded. Phallosome (Fig. 32D): pseudoparameres narrowly separated, broad and short, much wider than long, rounded apically. Phallobase narrowing to pointed anterior end, anterior end with triangular plate.

Length. B 2.2-2.3; FW 2.4-2.8; HW 1.8-2.1.

Female. Color and general morphology almost as in male. IO/D=1.9. *Genitalia:* Egg guide of subgenital plate (Fig. 33A) widened near distal end, postero-lateral corners rounded,

apical margin rounded; body of subgenital plate with pair of broad median extensions anteriorly. Dorsal valve of gonapophyses (Fig. 33B) with long distal process; posterior lobe of external valve strongly projected posteriorly. Internal plate as in Fig. 33C.

Length. B 2.2-2.6; FW 2.9-3.0; HW 2.1-2.3.

Distribution. Mexico.

***Trichadenotecnum acutum* sp. nov.**

Material examined. *Holotype.* Male. Mexico: 40 mi S. Oaxaca City, 19. VIII. 1968, ELM (ISU). *Paratypes.* 2 males, same data as holotype (ISU).

Etymology. The specific epithet is taken from the Latin *acutus* (= sharp), indicating the narrow and pointed clunial arm of this species.

Description: Male. Head. White in ground color; vertical and orbital markings brown; coronal suture black; frontal suture bordered with narrow pale brown band; frons with pair of pale brown bands at middle and with pair of brown spots laterally; gena white; eye black, IO/D = 1.1; ocelli white, ocellar field black; antennal socket bordered with narrow brown band; postclypeus with ca. ten rows of pale brown spots dorsally, fused with each other ventrally to form a large blackish brown marking, lateral margin of postclypeus brown, ventro-lateral corner without marking; anteclypeus brown. Antenna pale brown, pedicel and scape darker. Mouth parts pale brown; 4th segment of maxillary palpus brown.

Thorax. Prothorax brown. Mesonotum pale brown; anterior surface of scutum pale

brown; anterior margin of lateral lobe of scutum black; scutellum brown, anterior margin darker; postnotum white. Metanotum brown, with white spot on posterior region of lateral lobe of scutum; anterior margin of scutellum darker. Mesopleuron white except dorsal third brown. Metapleuron brown except membranous region white.

Legs. Coxae and tarsi of all legs and hind femur brown; fore and middle femora pale brown with white part medially; tibiae pale with brown part near distal end.

Forewing (Fig. 17K). Spots in cell a₁ apparent, distal spot large. Opposing spots in cell r distinct but anterior spot less so. Proximal band narrow, broadly interrupted just beyond fork of M + Cu. Distal band narrow and faint. Spot on roof of cell m₃ distinct. Submarginal spots apparent; spot in cell r₅ larger; spots in cells r₁ and m₃ indistinct. Marginal clouds faint. *Hindwing.* Hyaline, cell CuP with group of faint brown spots in distal half; veins brown.

Abdomen. White, each segment with irregular brown band. *Terminalia.* Clunial arm (Fig. 34A) well sclerotized, apical part long and slender, forming free needle-like process, antero-ventrally with strongly sclerotized lobe covered with denticles. Eighth venter (Fig. 34C) with transversal sclerite, anterior margin rounded, posteriorly fused with hypandrium at middle. Epiproct lobe (Fig. 34B) wider than long, broadened dorsally, dorsal margin with conical process medially, posterior surface almost flattened. Paraproct (Fig. 34A): ventro-lateral band small, rectangular; distal process short. Hypandrium (Fig. 34C): left and right processes well developed, rising from postero-lateral corners, slightly curved, apices directed posteriorly; median tongue constricted medially, posterior margin with rounded notch medially, ventral surface smooth with few wrinkles, dorsal keel shallowly rounded. Phallosome (Fig. 34D): pseudoparameres widely separated, broad and short, wider than long,

rounded apically. Phallobase narrowing to pointed ventral end.

Length. B 2.1-2.3; FW 3.0-3.1; HW 2.3-2.4.

Female. Unknown.

Distribution. Mexico.

***Trichadenotecnum nicaraguense* sp. nov.**

Material examined. *Holotype.* Male. Nicaragua: Granada, Volcán Mombacho, Santa Ana No. 2, 15. VII. 1978, J. M. Maes (UNAM). *Paratypes.* Nicaragua: 1 male, Granada, Volcán Mombacho, 340 m, 15. XII. 1997, J. M. Maes (UNAM); 1 male, Granada, Volcán Mombacho, San Joaquín #1, 16. III. 1998, J. M. Maes (UNAM).

Etymology. The specific epithet derives from Nicaragua, the country of origin of this species.

Description: **Male.** *Head.* White in ground color; vertical and orbital markings blackish brown; coronal suture black; frontal suture bordered with blackish brown band dorsally; frons with pair of faint brown bands at middle and with pair of circular blackish brown spots laterally; gena white dorsally, blackish brown ventrally; eye black, IO/D = 0.6; ocelli white, ocellar field black; antennal socket bordered with dark brown band; postclypeus with ca. eight rows of pale brown spots dorsally, fused with each other ventrally to form a large blackish brown marking, lateral margin of postclypeus brown, dorsal margin and ventro-lateral corner without marking; anteclypeus brown. Antenna brown. Mouth parts pale brown; 4th segment of

maxillary palpus dark brown.

Thorax. Prothorax brown. Mesonotum white; anterior surface of scutum pale brown; anterior margin of lateral lobe of scutum black; posterior region of lateral lobe of scutum pale brown; scutellum dark brown medially, anterior margin blackish brown; postnotum white. Metanotum dark brown, with white markings on anterior and posterior regions of lateral lobe of scutum; anterior margin of scutellum darker. Mesopleuron white, except dorsal third and ventral margin dark brown. Metapleuron brown except membranous region white.

Legs. Dark brown; fore and middle femora with paler region medially; fore and middle tibiae pale brown with blackish brown part near distal end.

Forewing (Fig. 17L). Spots in cell a₁ apparent and narrowly separated from each other, distal spot large. Opposing spots in cell r distinct but posterior spot small. Proximal band narrow, broadly interrupted just beyond fork of M + Cu, with round lighter pigmented portion in cell CuA. Distal band narrow but distinct especially in cell r₅. Spot on roof of cell m₃ broad and distinct. Submarginal spots apparent; spots in cells r₅ and m₁ larger; spot in cell m₃ indistinct. Marginal clouds apparent, darker in cells r₅ and m₁. *Hindwing.* Hyaline, cell CuP with faint brown irregular marking and spots in distal half; veins brown.

Abdomen. White with irregular brown markings. *Terminalia.* Clunial arm (Fig. 35A) well sclerotized, long, forming free process apically, with well sclerotized lobe covered with denticles. Eighth venter (Fig. 35C) with transverse rectangular sclerite, posteriorly fused with hypandrium at middle. Epiproct lobe (Fig. 35B) wider than long, broadened dorsally, dorsal margin deeply hollowed, medially with conical process directed posteriorly, posterior surface swollen. Paraproct (Fig. 35A): ventro-lateral band very short, tongue-shaped; distal process short. Hypandrium (Fig. 35C): left and right processes well developed, rising from postero-

lateral corners, almost straight, apices directed posteriorly; median tongue constricted medially, posterior margin concave, dorsal keel rounded. Phallosome (Fig. 35D): aedeagus unsclerotized; pseudoparameres weakly sclerotized, broadly separated, rounded apically. Phallobase narrowing to pointed ventral end.

Length. B 1.8-2.2; FW 2.6-2.8; HW 2.0-2.2.

Female. Unknown.

Distribution. Nicaragua.

The *aconcinnum* group

Diagnosis. Forewing not extensively covered with small spots (Fig. 36 A, B), marginal clouds apparent and dark; Rs fork obtuse; 3rd section of CuA arched. *Male terminalia.* Eighth venter (Fig. 37 C, G) with large transverse sclerite medially fused with hypandrium. Epiproct (Fig. 37 A, B, E, F) chair-shaped, postero-dorsal margin with projection at middle, epiproct lobe protruded over clunium. Hypandrium (Fig. 37 C, G) asymmetrical, *left process well developed, right process lamellate*. Phallosome (Fig. 37 D, H) *asymmetrical*, pseudoparameres usually needle-like, left one projected posteriorly and *right one projected postero-internally*; aedeagus broadly sclerotized and strongly projected posteriorly. Females of this group are so far unknown.

Key to Species

1. Median tongue relatively long, about 2.5 times longer than wide (Fig. 37C) *T.*

aconcinnum sp. nov.

-. Median tongue relatively short, about 2 times longer than wide (Fig. 37G) *T.*

guttatum sp. nov.

***Trichadenotecnum aconcinnum* sp. nov.**

Material examined. Holotype. Male, Mexico: Chiapas, 7km N. El Bosque, 10 km S. Simojovel, 1050m, 13. VIII. 1975, ANGA & B. García González (UNAM).

Etymology. The specific epithet is taken from the Latin *a* (= not) + *concinnus* (= symmetry), in reference to the asymmetrical hypandrium of this species.

Description: Male. Head. White in ground color; vertical and orbital markings large, blackish brown; coronal suture black; frontal suture bordered with blackish brown band dorsally; frons with two pairs of pale brown bands; gena blackish brown; eye black, IO/D = 1.1; ocelli white, ocellar field black; antennal socket bordered with blackish brown band; postclypeus with eight rows of blackish brown spots, fused with each other ventrally, forming large marking, lateral margin of postclypeus blackish brown; anteclypeus blackish brown. Antenna pale brown, scape and pedicel darker. Mouth parts blackish brown.

Thorax. Prothorax blackish brown. Mesonotum brown; anterior surface of scutum blackish brown; anterior margin of lateral lobe of scutum black; posterior part of median lobe white; lateral lobe with paler oval part medially; anterior margin of scutellum blackish brown; postnotum brown. Metanotum brown, with pale oval part on posterior region of each lateral

lobe of scutum; medial lobe with white spot medially; anterior margin of scutellum blackish brown. Meso- and metapleurites blackish brown except membranous region white and mesopleuron with longitudinal pale brown band.

Legs. Blackish brown; tibiae paler; fore and middle femora with pale brown portions medially.

Forewing (Fig. 36A). Spots in cell a₁ apparent. Opposing spots in cell r large, almost fused with each other. Proximal band broad in cell CuP but narrower in cell CuA, broadly interrupted just beyond fork of M + Cu, cell CuA including pale spot. Median spots dense, some spots fused with each other, forming larger markings. Distal band faint, broad in cell r₅, fragment of band in cell r₃ small. Spot on roof of cell m₃ small, darker than marginal cloud. Submarginal spots apparent; spots in cell r₁ and r₃ smaller than others. Marginal clouds apparent and dark. *Hindwing.* Hyaline with faint brown markings in cell CuP; veins brown.

Abdomen. White. *Terminalia.* Clunial arm (Fig. 37A) long and narrow, sickle-like in shape and forming free process apically. Epiproct (Fig. 37AB) chair-shaped, postero-dorsal margin with strongly projected transversal ridge; epiproct lobe small, much broader than long, narrowing dorsally, posterior surface with well developed swelling. Paraproct (Fig. 37A): ventro-lateral band short, triangular; distal process long, directed upward. Hypandrium (Fig. 37C): left process needle-like, almost straight, directed postero-internally; right process lamellate; median tongue small but long, length/width ≈ 2.5 , gradually narrowing to rounded apex, dorsal surface covered by weak denticles. Phallosome (Fig. 37D): pseudoparameres long, needle-like. Aedeagus strongly projected dorsally, triangular, sclerotized region extending to endophallus opening. Phallobase broadest in the middle, ventral margin rounded.

Length. B 2.5; FW 3.2; HW 2.4.

Female. Unknown.

Distribution. Mexico.

***Trichadenotecnum guttatum* sp. nov.**

Material examined. Holotype. Male. Mexico: Chiapas, Reserva de la Biosfera El Ocote, 6. XII. 1993, G. Ortega & E. Barrera (UNAM). *Paratypes.* Mexico: 1 male, Veracruz, 9.5 mi. E. Orizaba, Rd. 150, 7. VII. 1962, F. Hill, ELM & J. Campbell (ISU); 1 male, Veracruz, Rd. to El Vigía, 4 mi. N Santiago Tuxtla, Hwy 180, 3 mi. from Hwy.180, 13. VII. 1973, ELM (ISU); 1 male, Veracruz, Rd. to Cerro San Martín from San Andrés Tuxtla, 8 mi. from Hwy. 180, 14. VII. 1973, ELM (ISU).

Etymology. The specific epithet is taken from the Latin *guttatus* (= drop), indicating the shape of the hypandrial median tongue.

Description: Male. Head. White in ground color; vertical and orbital markings large, blackish brown; coronal suture black; frontal suture bordered with broad blackish brown band dorsally; frons with two pairs of blackish brown bands, internal pair narrow, external pair broad and not reaching frontal suture; gena blackish brown except eye margin white; eye black, IO/D = 0.7; ocelli white, ocellar field black; antennal socket bordered with blackish brown band; postclypeus with eight rows of blackish brown spots, fused with each other ventrally to form a large marking, ventro-lateral corner white; anteclypeus blackish brown. Antenna brown,

scape darker. Mouth parts blackish brown.

Thorax. Prothorax blackish brown. Mesonotum pale brown; anterior surface of scutum blackish brown; anterior margin of lateral lobe and postero-lateral margin of anterior lobe of scutum black, postero-lateral margin of lateral lobe and posterior part of anterior lobe white; scutellum brown, anterior margin blackish brown; postnotum brown. Metanotum pale brown, anterior lobe of scutum brown with white longitudinal line medially; scutellum brown, anterior margin blackish brown. Meso- and metapleurites blackish brown, with white longitudinal band medially.

Legs. Brown; fore leg except tarsus and hind tibia paler; all femora with pair of blackish brown spots ventrally; all tibiae with blackish brown band near distal end; middle femur with paler region medially.

Forewing (Fig. 36B). Spots in cell a₁ apparent. Opposing spots in cell r large, almost touching each other. Proximal band broad, broadly interrupted just beyond fork of M + Cu, strongly constricted at anterior end in cell CuA, including triangular pale spot. Median spots dense, some spots fused with each other, forming larger markings. Distal band apparent, broad in cell r₅. Spot on roof of cell m₃ apparent and broad. Submarginal spots apparent; spot in cell r₁ and m₃ smaller than others. Marginal clouds apparent and dark. *Hindwing.* Hyaline with faint brown marking in cell CuP; veins brown.

Abdomen. Mostly black ventrally, each segment with blackish band dorsally and laterally. *Terminalia.* Clunial arm long and narrow, sickle-like in shape and forming free process apically. Epiproct (Fig. 37 E, F) chair-shaped, postero-dorsal margin with strongly projected transversal ridge, its median part with square-shaped thin keel; epiproct lobe long

and wide, broader than long, narrowing dorsally, posterior surface slightly swelling.

Paraproct: ventro-lateral band short, triangular; distal process long, directed upward.

Hypandrium (Fig. 37G): left process needle-like, almost straight, directed posteriorly; right process lamellate; median tongue small and short, length/width ≈ 2 , nearly parallel sided and rounded apically, dorsal surface covered by weak denticles. Phallosome (Fig. 37H): pseudoparameres long, needle-like. Aedeagus strongly projected dorsally, rectangular, sclerotized region extending to endophallus opening. Phallobase broadest at the middle, ventral margin rounded.

Length. B 2.5-2.6; FW 3.0-3.2; HW 2.3-2.5.

Female. Unknown.

Distribution. Mexico.

The *slossonae* group

Diagnosis. Forewing (Fig. 36 C-F) not extensively covered with small spots; Rs fork obtuse; 3rd section of CuA more or less arched. *Male terminalia.* Eighth venter with large transverse sclerite broadly fused with hypandrium. Clunial arm (Fig. 38A) well developed, long and broad, with rounded and serrate distal margin, forming free process apically. Epiproct (Fig. 38B) with pair of projections on postero-dorsal margin; epiproct lobe well developed, protruded over clunium, variable in shape (Figs 38B, 40B, 41B, 42B). Paraproct (Fig. 38A): ventro-lateral band short, almost indistinct; distal process long, directed upward. Eighth venter (Fig. 38C) with single transversal sclerite. Hypandrium (Fig. 38C) *symmetrical*,

postero-median region broadly membranous, *dorsally with sclerotized flaps*; left and right processes well developed, long and needle-like (except for *T. simile*), more or less hooked. *Median tongue membranous*, very narrow and long. Phallosome (Fig. 38D) with pair of small processes posteriorly, processes sometimes fused to single process (Fig. 41D). *Female genitalia*. Dorsal surface of egg guide of subgenital plate (Fig. 39A) with median sclerite. Dorsal valve of gonapophyses (Fig. 39B) with short distal process; posterior lobe of external valve not strongly projected. Internal plate (Fig. 39C) symmetrical, broadly sclerotized and pigmented, strongly pigmented around spermathecal opening, posteriorly with square-shaped extension.

Key to Species (Females are known only for *T. slossonae*.)

1. Epiproct lobe bilobed dorsally (Fig. 38B) 3
- Epiproct lobe not bilobed dorsally (Fig. 41B) 2
2. Hypandrial processes short; epiproct lobe semicircular *T. simile* Mockford
- Hypandrial processes long (Fig. 41C); epiproct lobe conical (Fig. 41B)..... *T. denticulatum* sp. nov.
3. Clunial arm broad apically (Fig. 38A) 4
- Clunial arm narrow apically (Fig. 42A) *T. miffy* sp. nov.
4. Dorsal margin of epiproct lobe deeply hollowed medially (Fig. 38B) *T. slossonae* (Banks)
- Epiproct lobe semicircular in posterior view, with pair of small projections dorso-laterally (Fig. 40B) *T. barrerae* sp. nov.

***Trichadenotecnum slossonae* (Banks)**

Psocus slossonae Banks, 1903: 236; Chapman, 1930: 273 (male).

Psocus quaesitus Chapman, 1930: 270 (female).

Trichadenotecnum unum Sommerman, 1948: 167 (synonymy by Mockford, 1993: 287).

Trichadenotecnum slossonae (Banks): Mockford, 1993: 287.

Material examined. USA: 2 females, Virginia, Giles Co., Jeffers National Forest, 8. IX. 1984, CH (MHNG); 1 female, Virginia, Floyd Co., Buffalo Mountain, 9. IX. 1984, CH (MHNG); 2 males 1 female, Virginia, Floyd Co., Indian Ride, 9. IX. 1984, CH (MHNG); 1 male, same locality, 10. IX. 1984, CH (MHNG); 1 male, Virginia, Tazewell Co., Burkes Garden, 11. VII. 1987, V. M. Dalton (MHNG); 1 male 2 females, Virginia, Giles Co., Mountain Lake Scenic Area, 17. IX. 1984, CH (MHNG); 2 male 3 females, Virginia, Blue Ride Parkway, 18. IX. 1984, CH (MHNG); 1 female, Virginia, Madison Co., Oak Park, 10. VIII. 1988, D. Burckhardt (MHNG); 1 male, Virginia, Isle of Wight Co., Blackwater Ecologic Preserve, 1. VII. 1994, S. M. Roble (MHNG); 1 female, Virginia, Augusta Co., Blue Ride Parkway, 16. IX. 1994, S. M. Roble (MHNG); 1 male, Virginia, Wythe Co., Sand Mountain, 23. VII. 1998, S. M. Roble, C. S. Hobson, R. Charles (MHNG); 1 male, Virginia, Brunswick Co., Fort Pickett Military Reservation, 3. X. 2000, A. C. Chazal, S. M. Roble (MHNG); 1 female, Tennessee, Sevier Co., Great Smoky National Park, 14. IX. 1984, CL (MHNG); 2 males 1 female, Tennessee, Unicoi Co., Cherokee National Forest, 16. IX. 1984, CH (MHNG); 1 male, 2 females, Florida, Okaloosa Co., Blackwater River State Forest, Nature Center, 27. X. 1973, ELM (ISU); Mexico: Nuevo León, 20 km south Monterrey, 2 males, 3 females, 1800 m, 25. XII. 1969, ANGA (UNAM).

Diagnosis. This species can be clearly distinguished from the other species of the group by the dorsally broadened and clearly bilobed epiproct lobe in the male (Fig. 38B). Female genital structures are as in Fig. 39.

Distribution. USA, Mexico.

***Trichadenotecnum barrerae* sp. nov.**

Material examined. Holotype. Male, Mexico: Chiapas, Reserva de la Biósfera El Triunfo, Ca. Sta. Rita. Vereda hacia Cañada Honda, 1860m, 6. V. 1993, ANGA & E. Barrera (UNAM).

Etymology. The specific epithet honors Ernesto Barrera (Instituto de Biología, UNAM), one of the holotype collectors, friend and colleague of ANGA.

Description: Male. Head. White in ground color; vertical and orbital markings large, blackish brown; coronal suture black; frontal suture bordered with brown band dorsally; frons with two pairs of pale brown bands; gena blackish brown with white spot medially; eye black, IO/D = 1.2; ocelli white, ocellar field black; antennal socket bordered with blackish brown band; postclypeus with eight rows of faint brown spots, fused with each other ventrally forming a large blackish brown marking, ventro-lateral corner white; anteclypeus blackish brown. Antenna pale brown, scape and pedicel darker. Mouth parts blackish brown.

Thorax. Prothorax blackish brown. Mesonotum pale brown; anterior surface of

scutum blackish brown; anterior margin of lateral lobe of scutum black; anterior margin of scutellum blackish brown; postnotum brown. Metanotum brown, with pale oval spot on posterior region of each lateral lobe of scutum; medial lobe with white spot posteriorly; scutellum blackish brown. Meso- and metapleurites blackish brown except membranous region white.

Legs. Blackish brown; tibiae and fore coxa paler; fore and middle femora with pale brown portions at middle and distal end.

Forewing (Fig. 36D). Spots in cell a_1 small, basal one faint. Opposing spots in cell r large, posterior spot placed proximal to anterior one. Proximal band broad in posterior half, interrupted just beyond fork of $M + Cu$, strongly constricted at anterior end in cell CuA , including circular light area. Median spots sparse. Distal band broad. Spot on roof of cell m_3 broad and dark. Submarginal spots apparent, large; spots in cell r_5 and m_1 larger than others; spot in cell m_3 smaller and paler, partly fused with spot on roof of cell m_3 . Marginal clouds apparent, dark. *Hindwing.* Hyaline with faint brown marking in cell CuP , with longitudinal brown marking in cell r_1 along R_1 ; veins brown.

Abdomen. White, each segment with blackish brown band ventrally, extending to lateral region. *Terminalia.* Clunial arm (Fig. 40A) broad, axe-shaped, distal part covered with small denticles. Anterior margin of 8th sternum (Fig. 40C) with shallow incision at middle, broadly fused with hypandrium posteriorly. Epiproct lobe (Fig. 40B) semicircular in posterior view, dorsal margin with pair of tongue-like lobes projected dorso-laterally. Hypandrium (Fig. 40C): left and right processes long, directed postero-internally, then slightly arched, and directed inward apically, slightly broadened near apices, pointed at apices. Phallosome (Fig. 40DE) with pair of short, needle-like processes closely approximated. Phallobase almost

parallel sided, widest near anterior end, anterior margin slightly concave .

Length. B 2.4; FW 3.5; HW 2.6.

Female. Unknown.

Distribution. Mexico.

***Trichadenotecnum denticulatum* sp. nov.**

Material examined. *Holotype.* Male. Guatemala: 18 km SE of Guatemala, Guatemala C. A., Carretera a Puerto Barrios, 27. VIII. 1973, ANGA (UNAM). *Paratypes.* Honduras: 1 male, Comayagua, 4 km N Lahikostad, 18. VII. 1977, G. B. Marshall; 1 male, D. C., 8 km SE Tamara, Hwy 1, 27. VII. 1977, L. B. O'Brien *et al.* (UNAM); 1 male, Comayagua, 5 km NW Taulabé, 29. VII. 1977, L. B. O'Brien *et al.* (UNAM).

Etymology. The specific epithet refers to the denticles on the edge of the clunial arms and on the apex of the aedeagus.

Description: **Male.** *Head.* White in ground color; vertical and orbital markings large, blackish brown; coronal suture black; frontal suture bordered with brown band dorsally; frons with two pairs of pale brown bands; gena blackish brown with white spot medially; eye black, IO/D = 1.0; ocelli white, ocellar field black; antennal socket bordered with blackish brown band; postclypeus with eight rows of faint brown spots, fused with each other ventrally forming a large, blackish brown marking, ventro-lateral corner white; anteclypeus blackish brown.

Antenna pale brown, scape and pedicel darker. Mouth parts blackish brown.

Thorax. Prothorax blackish brown. Mesonotum pale brown; anterior surface of scutum blackish brown; anterior margin of lateral lobe of scutum black; anterior margin of scutellum blackish brown; postnotum brown. Metanotum brown, with pale oval spot on posterior region of each lateral lobe of scutum; medial lobe with white spot posteriorly; scutellum blackish brown. Meso- and metapleurites blackish brown except membranous region white.

Legs. Blackish brown; tibiae and fore coxa paler; fore and middle femora with pale brown portions at middle and distal end.

Forewing (Fig. 36E). Distal spot in cell a₁ large and dark, basal one small and faint. Opposing spots in cell r apparent but rather small. Proximal band broad but pale in posterior half, strongly constricted at anterior part of cell CuA, broadly interrupted around fork of M + Cu. Median spots sparse, some distal spots fused with each other, forming a large marking. Distal band broad but faint, especially in cell r₅. Spot on roof of cell m₃ small, almost indistinct around M₃ fork. Submarginal spots apparent; spot in cell m₃ smaller and paler. Marginal clouds apparent, darker along each vein. *Hindwing.* Hyaline; veins brown.

Abdomen. White with irregular faint brown markings. *Terminalia.* Clunial arm (Fig. 41A) broad, axe-shaped, distal part with rows of serrations and denticles. Anterior margin of 8th sternum (Fig. 41C) with broad triangular incision at middle, narrowly fused with hypandrium posteriorly. Epiproct lobe (Fig. 41B) long, much longer than wide, conical and pointed dorsally in posterior view. Hypandrium (Fig. 41C): left and right processes long, directed postero-internally, very slightly arched, gradually narrowing to pointed apices. Phallosome (Fig. 41 D,E) with single posterior process apically denticulated. Phallobase

almost parallel sided, widest near anterior end, anterior margin rounded.

Length. B 2.1-2.9; FW 2. 6-3.0; HW 2.0-2.4.

Female. Unknown.

Distribution. Guatemala, Honduras.

***Trichadenotecnum miffy* sp. nov.**

Material examined. *Holotype.* Male. Peru: Madre de Dios. Río Tambopata Reserved Zone, 30 km SW Puerto Maldonado, 290m, 10. V. 1982, T. L. Erwin *et al.* (SI). *Paratypes.* 1 male, same locality and collectors as holotype (SI), 7. XI. 1983; 1 male, same locality and collectors as holotype, 28. XI. 1984 (SI).

Etymology. The specific epithet is taken from Miffy, a picture book character in the form of a small rabbit, referring to the shape of the epiproct lobe.

Description: **Male** (available as dissected and partly cleared specimens only). *Head.*

Coloration not discernible; coronal suture black; eye black, IO/D = 1.0; ocelli white, ocellar field black; postclypeus with rows of faint brown spots, ventral margin blackish brown.

Antenna pale brown. Mouth parts brown, 4th segment of maxillary palpus blackish brown.

Thorax. Prothorax blackish brown. Mesonotum white; anterior surface of scutum brown with longitudinal white line medially; posterior margin of lateral lobe of scutum pale brown; scutellum pale brown, antero-lateral corner blackish brown; postnotum pale brown.

Metanotum white, anterior lobe of scutum and postero-median part of lateral lobe of scutum pale brown; scutellum pale brown, antero-lateral corner blackish brown. Meso- and metapleurites brown except membranous region and ventral part of epimeron white.

Legs. Brown; tibiae pale brown with brown spot near distal end; fore and middle femora with pale brown portions at middle and distal end.

Forewing (Fig. 36F). Distal spot in cell a₁ large and dark, basal one small and faint. Opposing spots in cell r apparent, anterior one smaller, posterior one large, placed proximal to anterior spot. Proximal band broad but pale in posterior half, strongly constricted at anterior part of cell CuA, broadly interrupted just beyond fork of M + Cu. Median spots sparse. Distal band broad but faint, especially in cell r₅. Spot on roof of cell m₃ small but apparent. Submarginal spots apparent; spot in cell r₅ larger, spot in cell m₃ smaller. Marginal clouds apparent, darker in cell r₅. *Hindwing.* Hyaline; cell cup with pale brown marking; veins brown.

Abdomen. White, each segment with pale brown band. *Terminalia.* Clunial arm (Fig. 42A) broad basally, then strongly constricted near apex, onion-shaped and serrated apically. Anterior margin of 8th sternum (Fig. 42D) with broad and deep trapezoidal incision at middle, widely fused with hypandrium posteriorly. Epiproct lobe (Fig. 41B) long, much longer than wide, very deeply incised at middle. Hypandrium (Fig. 41D): left and right processes long, gradually narrowing to pointed apices, directed posteriorly, then strongly arched, with distal tip directed internally. Phallosome (Fig. 41E): posteriorly with pair of rather long conical processes. Phallobase almost parallel sided posteriorly, anterior part gradually narrowing to pointed anterior end.

Length. B (unavailable); FW 2.4-2.5; HW 1.7-1.8.

Female. Unknown.

Distribution. Peru.

***Trichadenotecnum simile* Mockford**

Trichadenotecnum similis Mockford, 1996: 75.

Trichadenotecnum simile: Lienhard & Smithers, 2002: 469.

Trichadenotecnum decui Mockford, 1991: 268 (not *Trichadenotecnum decui* Badonnel, 1987).

Diagnosis. This species can be distinguished from the other species of the *slossonae* group by short left and right processes in the hypandrium. The female of this species is unknown to date. See Mockford (1991) for further description and illustrations of the male (described as *T. decui*).

Distribution. Brazil.

The *decui* group

Diagnosis. Forewing not extensively covered with small spots (Fig. 36G-I), marginal clouds apparent and dark; Rs fork obtuse; 3rd section of CuA arched. *Male terminalia.* Eighth venter (Fig. 44C) with large transverse sclerite medially fused with hypandrium. Epiproct (Fig. 44

A, B) chair-shaped, postero-dorsal margin with projection at middle, epiproct lobe protruded over clunium, variable in shape (Figs 43B, 44B, 46C). Hypandrium (Fig. 44C) *symmetrical*, left and *right processes short*. *Median tongue very short* and rounded. Phallosome (Fig. 43D, 44D, E, 46E, F): pseudoparameres usually needle-like, projected posteriorly; aedeagus usually broadly sclerotized and strongly projected posteriorly. *Female genitalia*. Egg guide of subgenital plate (Fig. 45A) broadened at distal end, dorsal surface with median sclerite. Ventral valve of gonapophyses (Fig. 45B) long; posterior lobe of external valve not strongly projected. Internal plate (Fig. 45C) symmetrical; spermathecal opening surrounded by triangular pigmentation; anterior half with pair of pigmented arms.

Key to Species

1. Males 2
- Females 4
2. Epiproct lobe pointed dorsally (Fig. 44B) 3
- Epiproct lobe with wide dorsal margin (Fig. 43B) *T. decui* Badonnel
3. Hypandrial left and right processes cone-shaped (Fig. 44C) *T. obrienorum* sp. nov.
- Hypandrial left and right processes lamellate (Fig. 46D) *T. cintalapense* sp. nov.
4. Egg guide narrowing apically *T. decui* Badonnel
- Egg guide broadened apically (Fig. 45A) *T. obrienorum* sp. nov.

***Trichadenotecnum decui* Badonnel**

Trichadenotecnum decui Badonnel, 1987: 177; Mockford, 1996: 75. (Not *Trichadenotecnum decui* Mockford, 1991: 268.)

Material examined. 1 male, Venezuela, Trujillo, 7600', Old Road, 44 km E Trujillo, 5. VIII. 1988, C. & L. B. O'Brien & G. Wibmer (UNAM).

Diagnosis. See the original description for female and Mockford (1996) for further description of male.

Remarks. The male specimen examined here agrees completely in morphological characters with the male of *T. decui* described by Mockford (1996). The male specimen examined by Mockford (1996) was collected at the type locality of the species and agrees precisely with the female holotype in forewing markings, on which male-female correspondence by Mockford (1996) was based.

Distribution. Venezuela.

***Trichadenotecnum obrienorum* sp. nov.**

Material examined. *Holotype.* Male, Honduras: Cortés, 20 km N. Cofradía, 4. VII. 1977, L. B. O'Brien *et al.* (UNAM). *Paratypes.* 1 female, same data as holotype (UNAM).

Etymology. The specific epithet honors Lois B. and Charles W. O'Brien, dear friends and colleagues of ANGA, formerly from Florida A. & M. University, presently enjoying retirement in Arizona, collectors of the type specimens.

Description: Male. Head. White in ground color; vertical and orbital markings large, blackish brown; coronal suture black; frontal suture bordered with blackish brown band dorsally; frons with two pairs of pale brown markings; gena blackish brown; eye black, IO/D = 1.0; ocelli white, ocellar field black; antennal socket bordered with blackish brown band; postclypeus with seven rows of blackish brown spots, fused with each other ventrally forming large marking, lateral margin of postclypeus blackish brown; anteclypeus blackish brown. Antenna pale brown, scape and pedicel darker. Mouth parts blackish brown; maxillary palpus paler except for 4th segment blackish brown.

Thorax. Prothorax blackish brown. Mesonotum pale brown; anterior surface of scutum blackish brown; anterior margin of lateral lobe of scutum black; anterior margin of scutellum blackish brown; postnotum brown. Metanotum brown, with whitish oval spot on posterior region of each lateral lobe of scutum; anterior margin of scutellum blackish brown. Meso- and metapleurites blackish brown except membranous region white.

Legs. Blackish brown; tibiae paler; fore and middle femora pale brown medially.

Forewing (Fig. 36H). Spots in cell a₁ apparent, distal spot smaller. Opposing spots in cell r large. Proximal band broad in posterior half, broadly interrupted just beyond fork of M + Cu, strongly constricted near anterior part of cell CuA, including broad light area, band in cell CuP, including longitudinal narrow lighter area. Median spots dense, some spots fused with each other and forming larger spots. Distal band broad in cell r₅, fragment of band in cell

r₃ rather small. Spot on roof of cell m₃ broad, darker than marginal cloud. Submarginal spots apparent; spot in cell r₅ large and elongate; spot in cell m₃ very small. Marginal clouds broad and dark. *Hindwing*. Hyaline with faint brown markings in cell CuP; veins brown.

Abdomen. White, each segment with blackish brown band. *Terminalia*. Clunial arm (Fig. 44A) long, broadened apically, free from membrane at apex, apical tip covered with tiny denticles, postero-dorsal region incised by membrane from dorsal margin to subapical portion. Anterior margin of 8th sternum (Fig. 44C) irregularly indented. Epiproct (Fig. 44AB) chair-shaped, postero-dorsal margin with semicircular keel-like projection at middle, its posterior margin denticulated; epiproct lobe small, conical. Paraproct (Fig. 44A): ventro-lateral band very short, triangular; distal process short, directed upward. Hypandrium (Fig. 44C): left and right processes conical, directed postero-internally; median tongue circular in ventral view. Phallosome (Fig. 44D, E): pseudoparameres long, needle-like, sinuated, pointed apically. Aedeagus strongly extending anteriorly, projected and pointed dorsally. Phallobase widest at ventral third, anterior margin almost straight.

Length. B 2.1; FW 3.3; HW 2.4.

Female. Color and general morphology almost as in male; eye IO/D = 1.6. *Genitalia*: Egg guide of subgenital plate (Fig. 45A) narrowing to distal fourth, then broadened at distal end, apical margin almost flattened; dorsal surface of egg guide with V-shaped sclerite at middle; posterior margin of body of subgenital plate next to egg guide projected posteriorly. Dorsal valve of gonapophyses (Fig. 45B) with rather short distal process; posterior lobe of external valve not strongly projected posteriorly. Internal plate as in Fig. 45C.

Length. B 2.5; FW 3.1; HW 2.4.

Distribution. Honduras.

***Trichadenotecnum cintalapense* sp. nov.**

Material examined. Holotype. Male, Mexico: Chiapas, 35 km south of Cintalapa, 920m. 20. VIII. 1975, ANGA & B. García González (UNAM).

Etymology. The specific epithet is the patronymic of Cintalapa, where the holotype was collected.

Description: Male. Head. White in ground color; vertical and orbital markings large, blackish brown; coronal suture black; frontal suture bordered with blackish brown band dorsally; frons with two pairs of pale brown bands; gena blackish brown; eye black, IO/D = 1.0; ocelli white, ocellar field black; antennal socket bordered with blackish brown band; postclypeus with eight rows of blackish brown spots, fused with each other ventrally forming a large marking, lateral margin of postclypeus blackish brown; anteclypeus blackish brown. Antenna pale brown, scape and pedicel darker. Mouth parts blackish brown.

Thorax. Prothorax blackish brown. Mesonotum brown, medially with longitudinal white band; anterior surface of scutum blackish brown; anterior margin of lateral lobe of scutum black; anterior margin of scutellum blackish brown; postnotum brown. Metanotum brown, medially with longitudinal white band; anterior margin of scutellum blackish brown. Meso- and metapleurites blackish brown except membranous region white.

Legs. Blackish brown; tibiae paler; fore and middle femora with pale brown portions

medially.

Forewing (Fig. 36 I). Spots in cell a₁ apparent, basal one smaller and paler. Opposing spots in cell r apparent, anterior one small. Proximal band broad in posterior half, broadly interrupted just beyond fork of M + Cu, strongly constricted near anterior end in cell CuA, including broad light pigmented area. Median spots dense, some spots fused with each other and forming large marking. Distal band broad but faint. Spot on roof of cell m₃ long.

Submarginal spots apparent; spot in cell r₁ small; spot in cell m₃ paler. Marginal clouds broad and dark. *Hindwing*. Hyaline with faint brown markings in cell CuP; veins brown.

Abdomen. White, sparsely with irregular brown markings. *Terminalia*. Clunial arm (Fig. 46 A, B) broadened and forming free process apically, strongly bent inward near apex, apical region with dorsal tongue-like projection and distal pointed process, distal margin serrated. Anterior margin of 8th sternum (Fig. 46 D) widely but shallowly incised. Epiproct (Fig. 46 A, C) chair-shaped, postero-dorsal margin with small projection; epiproct lobe small, conical. Paraproct (Fig. 46 A): ventro-lateral band broad and short, triangular; distal process long, directed posteriorly. Hypandrium (Fig. 46 D) almost symmetrical; left process conical, directed posteriorly; right process broad and lamellate, trapezoidal, its distal margin slightly sinuated; median tongue square-shaped, slightly wider than long in ventral view. Phallosome (Fig. 46 E, F): pseudoparameres needle-like, rather short. Aedeagus broadly sclerotized, long, strongly projected postero-ventrally, apical region V-shaped in cross section, with two longitudinal rows of denticles at middle.

Length. B 2.5; FW 2.9; HW 2.3.

Female. Unknown.

Distribution. Mexico.

Unplaced species

The following two species do not have autapomorphies of *Trichadenotecnum* and thus are not treated in this study. Further comments are given under each species.

***Trichadenotecnum pichincha* New & Thornton**

Trichadenotecnum pichincha New & Thornton, 1975: 73.

Specimens not examined. Judging from the original description and illustrations, this species from Ecuador does not possess any apomorphic character state of the genus

Trichadenotecnum as designated by Yoshizawa (2001, 2003), particularly, presence of a dorsal clunial flap indicates that this species is not even a member of the tribe Ptyctini. This evidence indicate that the species must be removed from *Trichadenotecnum*. However, this species shows peculiar male genital structures, and there seems to be no appropriate genus to place it. Therefore, we tentatively leave the species in *Trichadenotecnum* and postpone proposing an official nomenclatural change.

Distribution. Ecuador.

***Trichadenotecnum sylvaticum* Turner**

Trichadenotecnum sylvaticum Turner, 1975: 597.

Specimens not examined. Judging from the original description and illustrations, the forewing of this Jamaican species is superficially similar to that of *Trichadenotecnum* spp. in having dense spots. However, wing venation of this species lacks an important apomorphic feature of the genus: the triangular areola postica. Genital structure of this species seems far distant from the other species of the genus, too. Therefore, it is very likely that it does not belong in *Trichadenotecnum*. It is difficult to decide its appropriate systematic position based only on the original description and illustrations. Therefore, we postpone making a nomenclature act for the species, but its systematic position must be revised in the future.

Distribution. Jamaica.

PHYLOGENETIC ANALYSIS

We selected 58 characters which were potentially informative for phylogenetic estimation (Appendices 1, 2). Characters 1-33 were from Yoshizawa (2004), and the others were newly selected for the present study. One character of wing marking was erroneously coded for *T. circularoides* by Yoshizawa (2004) and is corrected here (see below and Appendix 1).

Character 1 (male eye size) was excluded from the analyses because this character is revealed here to be continuous and intraspecific variation is also considerable sometimes. Character 21 (size and shape of the hypandrial right process) was excluded, and the character was re-coded as Characters 45 (size) and 46 (shape). Maximum parsimony analysis of the data matrix with

PAUP 4.0b10 (Swofford, 2002) yielded 92 equally parsimonious trees (L=133, CI=0.44, RI=0.75). Application of successive weighting (Farris, 1969; Carpenter, 1988) reduced the number of trees to one, which was identical to one of the 92 shortest trees estimated by equally weighted analysis. Therefore, the tree estimated from successive weighting of morphological characters was preferred here (Fig. 47).

DISCUSSION

Phylogeny (Fig. 47).

Except for two unclassified species, the New World species of *Trichadenotecnum* can be assigned to the genus *sensu* Yoshizawa (2001, 2003). *Trichadenotecnum desolatum*, which was once treated as the type species of an independent (sub)genus, *Trichadenopsocus* (Roesler, 1943; Li, 2001) is imbedded within *Trichadenotecnum*. Exclusion of *T. desolatum* from *Trichadenotecnum* makes the remaining members of the genus paraphyletic. Therefore, independent (sub)generic status for *T. desolatum* is inappropriate, and synonymy between *Trichadenopsocus* and *Trichadenotecnum* proposed by Mockford (1993) and Lienhard (2003) is justified. The morphological tree is concordant with the previous molecular tree of the genus, which included fewer terminal taxa sampled mostly in Japan (Yoshizawa, 2004).

Apart from the possibly introduced (*T. pardus* and *T. majus*) and two unplaced species, the New World species of *Trichadenotecnum* are divided into three major clades: (1) *circularoides* + *roesleri* groups, (2) *alexanderae* group and (3) *desolatum* + *chiapense* + *concinnum* + *quaesitum* + *aconcinnum* + *slossonae* + *decui* groups. The latter clade, termed here the 'bulky clade', is further divided into three sub-major clades, (3-1) *desolatum*, (3-2)

chiapense + *concinnum* + *quaesitum* and (3-3) *aconcinnum* + *slossonae* + *decui* groups.

Monophyly of all species groups is supported, and their autapomorphies are described under the group diagnoses (see above).

The *circularoides* + *roesleri* clade is the sister group of all other members of the genus *Trichadenotecnum*. In the previous morphological analysis, parthenogenetic *T. circularoides* was imbedded within the *spiniserrulum* group (Yoshizawa, 2004) but, by inclusion of additional characters, examination of closely related bisexual species, and correcting a character coding of wing markings (Appendices 1, 2: Character 3: see also Yoshizawa, 2001, 2004), the species group is now separated from the *spiniserrulum* group, which is in agreement with the molecular phylogeny (Yoshizawa, 2004). Monophyly of *Trichadenotecnum* excluding the *circularoides* + *roesleri* clade is supported by the presence of opposing spots in cell r. The obtuse Rs fork is also an apomorphic condition uniquely observed in *Trichadenotecnum* excluding the *circularoides* and *roesleri* groups, but the acute Rs fork is also observed in *T. germinatum* (the *corniculum* group). Therefore, it is ambiguous whether the obtuse Rs fork is an autapomorphy of *Trichadenotecnum* excluding the *circularoides* and *roesleri* groups or not. Sister group relationship between the *circularoides* and *roesleri* groups is supported by the following synapomorphies: the short male paraproct, short ventral valve of gonapophyses (also observed in some species of the *spiniserrulum*, *vaughani* and *majus* groups) and less developed posterior lobe of the external valve of gonapophyses (also observed in some species of the *spiniserrulum* group).

The *alexandrae* group constitutes its own clade, distantly separated from the other New World species groups. Its monophyly was already discussed before (Betz, 1983; Yoshizawa, 2001). Phylogenetic placement of this group is stable and in agreement with the previous molecular analyses (Yoshizawa, 2004).

Monophyly of the bulky clade is supported by a stable autapomorphy, dorsal surface of the hypandrial median tongue covered with papillae or denticles. The clade is placed as sister of the *sempunctatum* + *medium* clade. Their sister group relationship is supported by a stable autapomorphy, the presence of pseudoparameres. A superficially similar process is also observed in *T. bos* but is considered here to be homoplasy. One additional, homoplastic apomorphy for this clade is the upwardly directed paraproctal distal process.

Subdivision within the bulky clade is also stable in the present analysis. The *desolatum* group is the basal split of the clade, and monophyly of the clade composed of the remaining bulky clade is supported by the fusion of the 8th sternum with the hypandrium. This character state is homoplastic (also observed in the *roesleri* and *spiniserrulum* groups), and reversal is also detected within the bulky clade (*T. chiapense*). Support for monophyly of the *chiapense* + *concinnum* + *quaesitum* subclade is robust, with three autapomorphies, including two non-homoplastic ones: the well developed hypandrial left process (highly homoplastic), presence of a dorsal keel on the hypandrial median tongue, and antero-median extensions of the sclerite on the body of the subgenital plate. Within the clade, the *concinnum* and *quaesitum* groups are considered to be sister groups, supported by a non-homoplastic and prominent synapomorphy, the clunial arm with a basal lobe. Monophyly of the *aconcinnum* + *slossonae* + *decui* subclade is also supported by three autapomorphies, including a non-homoplastic one: the phallosome narrowing posteriorly (secondary reversal), the aedeagal region of the phallosome with an anteriorly extended sclerite, and the egg guide of the subgenital plate with a dorsal sclerite (also observed in the *majus* group). Within the clade the *slossonae* and *decui* groups form a clade supported by one, rather homoplastic character state: symmetrical hypandrium (considered to be a reversal from the asymmetrical form). The *aconcinnum* and *decui* groups share a character state, presence of a keel-like projection on the

postero-dorsal corner of the epiproct, and sister relationship between them is equally parsimonious when all characters were weighted equally. However, successive weighting put heavier weight for the hypandrial symmetry/asymmetry than the epiproctal keel.

Asymmetry of the Male Genitalia.

Within the Psocodea, asymmetry of male genital structures is most frequently observed in the family Psocidae. Because all subfamilies and tribes of Psocidae include both symmetrical and asymmetrical forms, it is obvious that asymmetric forms evolved independently in several lineages (Yoshizawa & Johnson, 2007). Asymmetry of the hypandrial structures in Psocidae has been well known, but its evolutionary patterns and processes have not been explicitly discussed because of lack of a reliable phylogenetic hypothesis. Among Psocidae, *Trichadenotecnum* shows the highest variation of male genital structure, and both symmetrical and asymmetrical forms are observed within the genus. Based on the previous (Yoshizawa, 2004) and present trees, it is possible to hypothesize the origins of asymmetrical male genitalia in *Trichadenotecnum*.

Although not clearly stated, independent origins of asymmetry in *Trichadenotecnum* were already apparent from the previous studies (Yoshizawa, 2001, 2003, 2004). Among the taxa studied by Yoshizawa (2004), asymmetry of the hypandrium is observed in the *corniculum*, *majus*, *medium* and *sempunctatum* groups and in *T. falx*. The hypandrium of *T. falx* is more or less symmetrical and significant asymmetry is observed only in the median tongue of the hypandrium, whereas in the above-mentioned groups, the hypandrium is significantly asymmetrical with completely symmetrical median tongue. Therefore, different origins of asymmetry are obvious also from a morphological point of view. The *majus*, *medium*, and *sempunctatum* groups form a monophyletic group, and the *corniculum* group is

distantly related to them. In summary, an asymmetric hypandrium has been known in three different clades within *Trichadenotecnum*.

In the present study, several additional asymmetric clades were detected (Fig. 47, Character 41). The most ancestral condition of *Trichadenotecnum* is presently unclear due to uncertainty of its sister taxon. If the symmetric condition is ancestral, at least four independent origins of asymmetry can be assumed. In addition, the present study detected evidence for independent reversals from asymmetry to symmetry (*i.e.*, *concinnum*, *slossonae* and *decui* groups: indicated by open triangles in Fig. 47, Character 41). The alternative interpretation, *i.e.* independent origins of asymmetry with no reversal, required three more steps to explain evolution of asymmetry (9 gains vs. 4 gains + 2 reversals). Although phylogenetic analysis of morphology-independent data (*i.e.*, molecular phylogenetic analysis) is required for final conclusion, male genital structure of *Trichadenotecnum* may provide interesting examples of asymmetry to symmetry reversals in the evolution of insect genitalia.

The present study also reveals the first examples of asymmetry in the phallosome in *Trichadenotecnum* (Figs. 2 D, H; 37 D, H). Asymmetry in the phallosome is rare even in Psocidae and only known for *Indiopsocus*, *Ptycta* (note that this genus includes a lot of heterogeneous species: Lienhard & Smithers, 2002), *Steleops* (tribe Ptyctini), *Hyalopsocus*, *Psocus* (tribe Psocini) and *Atrichadenotecnum* (tribe Atrichadenotecnini: Yoshizawa & Johnson, 2007). Asymmetry of the phallosome is restricted in some species of the distantly related groups, the *circularoides* (Fig. 2 D, H) and *aconcinnum* groups (Fig. 37 D, H), and thus the independent origins of this character state within *Trichadenotecnum* are obvious. Detailed morphological analysis including the functional aspects and establishment of a robust phylogenetic hypothesis for Psocidae are required for further discussion.

Biogeography (Fig. 48)

The New World *Trichadenotecnum* are divided into three major clades, and each clade probably has very different histories of invasion and diversification in the New World.

The bulky clade is monophyletic and endemic to the New World. Distributional range of its sister group, the *sempunctatum* + *medium* clade, is restricted to the Oriental and Palearctic regions. The *majus* + *vaughani* groups are possible sister groups for the *sempunctatum* + *medium* + bulky clade, and they are also distributed in the Oriental and Palearctic Regions. Therefore, the bulky clade can be considered to originate from a single ancestral species that invaded the New World from the Palearctic region via Beringia or the North Atlantic Land Bridge. This supposition indicates that the ancestral species of the bulky clade first invaded North America, but now the center of its diversity is Central America. This pattern of diversification is probably derived from the Pleistocene glaciations (2 Myr -10000 yr). During the glaciations, most areas of North America were covered by ice sheets and were not suitable for *Trichadenotecnum* (Sanmartín, Enghoff & Ronquist, 2001), and the distributional range of the genus was probably restricted to Central America. Re-colonization to North America was probably possible only in the temperate Holocene (10000 yr). This prediction is also supported by the distributional patterns of some species or species groups in Central and North America. For example, *T. quaesitum* (North America and Mexico) has sparsely spotted forewings, whereas most other species of the *quaesitum* group and all species of its sister group, the *concinnum* group, (all distributed in Central America) have extensively spotted forewings. The sparsely spotted condition is only known for *T. quaesitum* and its possible sister, *T. quaesitellum* in Mexico. It indicates that sparsely spotted forms were derived from the extensively spotted ancestor after diversification of extensively spotted species in Central America, and divergence of *T. quaesitum* and *T. quaesitellum* was a

recent event. Two other North American species, *T. desolatum* and *T. slossonae*, are also distributed in Mexico, and their close relatives are most diversified in Central America. Therefore, it is reasonable to consider that these North American species were divergent in Central America and dispersed to North America recently, probably after the end of the Pleistocene glaciations.

The South American fauna of the bulky clade is relatively poorly diversified as compared to the Central American, although there were refugia suitable even for tropical and subtropical insects in South America during the Pleistocene glaciations (Brown, Sheppard & Turner, 1974; Dietz, 1994). As mentioned above, the common ancestor of the bulky clade probably first colonized North America and further dispersed to South America through Central America. There was a geographic barrier between Central and South America, and their connection is considered not to have been established until the Pliocene (3 Myr), which probably prohibited dispersal of insects between those two areas. These geographic and climatic histories probably explain the present distributional and diversification pattern of the bulky clade of *Trichadenotecnum* in the New World.

In contrast, the *alexandrae* group is distributed in both the Nearctic and Palearctic Regions. Especially, *T. alexandrae* and *T. castum* are recorded from North America and Japan, and both populations are morphologically indistinct. Molecular analysis also showed that the North American and Japanese populations of the species complex are genetically close (only 1.7% differences in mitochondrial COI gene). Close relatives of the *alexandrae* complex (*sensu* Betz, 1983), *T. biternatum* (Li, 1995), *T. aduncatum* (Li, 2001) and *T. trichotomum* (Li, 2001) (all newly assigned to the *alexandrae* group on the basis of apomorphies detected by Yoshizawa, 2001, 2004), are known from China. Therefore, the origin of this species group is also considered to be in the eastern Palearctic Region, and

divergence between North American and Japanese populations of the *alexanderae* complex is considered to be a recent event, possibly trans-Beringia during the Quaternary or even recent introduction by humans.

Divergence of the *circularoides* + *roesleri* clade is considered to have occurred at the most basal node of *Trichadenotecnum*. The distributional range of the clade is restricted to Central and South America (except for widely distributed and probably artificially introduced *T. circularoides*), and they are most diversified in South America. Its sister clade, the remaining *Trichadenotecnum*, is considered to be of Old World origin. Such distributional pattern and their deep branching seems to indicate a Gondwanan origin of the *circularoides* + *roesleri* clade. However, native species of *Trichadenotecnum* are not known from Australia, New Zealand and Chile, where many relicts of Gondwanan biota are distributed (*e.g.*, southern beech genus *Nothofagus*: Swenson et al., 2001; hemipteran suborder Coleorrhyncha: Austin et al., 2004), and the oldest fossil record of the family Psocidae only dates back to the Oligocene (Carpenter, 1992). These forms of evidence contradict the Gondwanan origin of the clade.

The present phylogenetic analysis is based only on morphological characters and thus dating of divergent times is impossible. In addition, although the present distributional pattern of the bulky clade provides a relatively reasonable story for the biogeographical history of the clade, we did not include the western Palearctic species of *Trichadenotecnum* in the present analysis. That would be important for deciding the dispersal route of the ancestor of the bulky clade from the Palearctic Region to the Nearctic Region (Beringia or North Atlantic Land Bridges). To test and corroborate the above hypotheses on the biogeographical history of *Trichadenotecnum*, examination of the western Palearctic species and extensive molecular-based phylogenetic analyses are required. Furthermore, phylogenetic and biogeographical

analyses of the family Psocidae in whole is required to estimate the origin and the most basal divergence of the genus *Trichadenotecnum*.

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REFERENCES

Austin AD, Yates DK, Cassis G, Fletcher MJ, La Salle J, Lawrence JF, McQuillan PB, Mound LA, Bickel DJ, Gullan PJ, Hales DF, Taylor GS. 2004. Insects 'Down-Under'

- Diversity, Endemism and evolution of the Australian insect fauna: examples from selected orders. *Australian Journal of Entomology* **43**: 216-234.
- Badonnel A. 1955.** Psocoptères de l'Angola. *Publicações culturais da Companhia de Diamantes de Angola* **26**: 1-267.
- Badonnel A. 1987.** Psocoptères de Venezuela et de la République Argentine. In Decu V. et al. ed. *Fauna hipogea y hemiedáfica de Venezuela y de otros países de America del Sur*. Bucharest, 173-182.
- Banks N. 1903.** Some new Neuropteroid insects. *Journal of the New York Entomological Society* **11**: 236-243.
- Betz BW. 1983.** Systematics of the *Trichadenotecnum alexanderae* species complex (Psocoptera: Psocidae) based on an investigation of modes of reproduction and morphology. *Canadian Entomologist* **115**: 1329-1354.
- Brown KS, Sheppard PM, Turner JRG. 1974.** Quaternary refugia in tropical America: evidence from race formation in *Heliconius* butterflies. *Proceedings of the Royal Society of London (B)* **187**: 369-378.
- Carpenter FM. 1992.** Superclass Hexapoda. In Kaesler RL ed. *Treatise on Invertebrate Paleontology, Part R, Arthropoda 4, Volumes 3 & 4*. Kansas: The Geological Society of America.
- Carpenter JM. 1988.** Choosing among equally parsimonious cladograms. *Cladistics* **4**: 291-296.
- Chapman PJ. 1930.** Corrodentia of the United States of America: I. suborder Isotecnomera. *Journal of the New York Entomological Society* **38**: 219-403.
- Dietz RE. 1994.** Systematics and biology of the genus *Macrocneme* Hübner (Lepidoptera: Ctenuchidae). *University of California Publications in Entomology* **113**: 1-121, 27 maps +

236 figs (not paginated).

Endang SK, Thornton IWB, New TR. 2002. The Psocidae (Insecta: Psocoptera) of Java and the eastern islands of Indonesia. *Invertebrate Systematics* **16**: 107-176.

Endang SK, New TR. 2005. The genus *Trichadenotecnum* (Insecta: Psocoptera: Psocidae) in Sumatra, Indonesia, with description of thirteen new species. *Records of the Australian Museum* **57**: 15-38.

Enderlein G. 1909. Neue Gattungen und Arten nordamerikanischer Copeognathen. *Bulletino del Laboratorio di Zoologia generale e agraria della R. Scuola Superiore d'Agricoltura in Portici* **3**: 329-339.

Farris JS. 1969. A successive approximations approach to character weighting. *Systematic Zoology* **26**: 269-276.

Johnson KP, Yoshizawa K, Smith VS. 2004. Multiple origins of parasitism in lice. *Proceedings of the Royal Society of London (B)* **271**: 1771-1776.

Kolbe HJ. 1880. Monographie der deutschen Psociden mit besonderer Berücksichtigung der Fauna Westfalens. *Jahresbericht des Westfälischen Provinzial-Vereins für Wissenschaft und Kunst* **8**: 73-142.

Li F. 1995. Psocoptera. In Wu H. ed. *Insects of Bashanzu Mountain, Eastern China*. Beijing: Forestry Publishing House, 142-210.

Li F. 2002. *Psocoptera of China*. Beijing: Science Press.

Lienhard C. 1998. Psocopterès euro-méditerranéens. *Faune de France* **83**: 1-517.

Lienhard C. 2003a. Additions and corrections (part 1) to Lienhard & Smithers, 2002:

'Psocoptera (Insecta) - World catalogue and bibliography'. *Psocid News* **4**: 2-24.

Lienhard C. 2003b. Additions and corrections (part 2) to Lienhard & Smithers, 2002:

'Psocoptera (Insecta) - World catalogue and bibliography'. *Psocid News* **5**: 2-37.

- Lienhard C. 2003c.** Nomenclatural amendments concerning Chinese Psocoptera (Insecta), with remarks on species richness. *Revue suisse de Zoologie* **110**: 695-721.
- Lienhard C. 2004.** Additions and corrections (part 3) to Lienhard & Smithers, 2002: 'Psocoptera (Insecta) - World catalogue and bibliography'. *Psocid News* **6**: 1-23.
- Lienhard C. 2005.** Additions and corrections (part 4) to Lienhard & Smithers, 2002: 'Psocoptera (Insecta) - World catalogue and bibliography'. *Psocid News* **5**: 1-16.
- Lienhard C. 2006.** Additions and corrections (part 5) to Lienhard & Smithers, 2002: 'Psocoptera (Insecta) - World catalogue and bibliography'. *Psocid News* **8**: 1-18.
- Lienhard C, Smithers CN. 2002.** *Psocoptera (Insecta): World catalogue and bibliography*. Instrumenta Biodiversitatis 5. Genève: Muséum d'Histoire Naturelle.
- Mockford EL. 1991.** New species and records of Psocoptera (Insecta) from Roraima State, Brazil. *Acta Amazonica* **21**: 211-317.
- Mockford EL. 1993.** *North American Psocoptera (Insecta)*. Flora and Fauna Handbook, no. 10. Gainesville, FL: Sandhill Crane Press.
- Mockford EL. 1996.** New species and records of Psocoptera from northern Venezuela. *Tropical Zoology, Special Issue* **2**: 1-98.
- Mockford EL, García Aldrete AN. 1996.** Psocoptera. In Bousquets et al., ed. *Biodiversidad, taxonomía y biogeografía de Artrópodos de Mexico: Hacia una síntesis de su conocimiento*. Mexico: UNAM, 175-205.
- New TR. 1972.** A collection of Psocidae (Psocoptera) from Central Brazil. *Arquivos de Zoologia, S. Paulo* **22**: 1-111.
- New TR. 1978.** Notes on the Oriental species of *Trichadenotecnum* Enderlein s. l. *Oriental Insects* **12**: 33-41.
- New TR, Thornton IWB. 1975.** Psocomorpha (Psocoptera) collected on recent expeditions

- to South America. *Journal of Entomology (B)* **44**: 27-80.
- Roesler R. 1943.** Über einige Copeognathengenera. *Stettiner Entomologische Zeitung* **104**: 1-14.
- Sanmartín I, Enghoff H, Ronquist F. 2001.** Patterns of animal dispersal, vicariance and diversification in the Holoarctic. *Biological Journal of the Linnean Society* **73**: 345-390.
- Sommerman KM. 1948.** Two new nearctic psocids of the genus *Trichadenotecnum* with a nomenclatural note on a third species (Corrodentia). *Proceedings of the Entomological Society of Washington* **50**: 165-173.
- Swenson U, Backlund A, McLoughlin S. Hill RS. 2001.** *Nothofagus* biogeography revised with special emphasis on the enigmatic distribution of subgenus *Brassospora* in New Caledonia. *Cladistics* **17**: 28-47.
- Swofford, D. L. 2002.** *PAUP*: phylogenetic analysis using parsimony (*and other methods), version 4 beta*, MA: Sinauer.
- Thornton IWB. 1961.** The *Trichadenotecnum* group (Psocoptera: Psocidae) in Hong Kong, with descriptions of new species. *Transactions of the Royal Entomological Society of London* **113**: 1-24.
- Turner BD. 1975.** The Psocoptera of Jamaica. *Transactions of the Royal Entomological Society of London* **126**: 522-609.
- Williner GJ. 1945.** Corrodentidos del Brasil (Corrodentia: Psocidae et Caecilidae). *Acta Zoologica Lilloana* **3**: 231-234.
- Yoshizawa K. 1998.** A new genus, *Atrichadenotecnum*, of the tribe Psocini (Psocoptera: Psocidae) and its systematic position. *Entomologica scandinavica* **29**: 199-209.
- Yoshizawa K. 2001.** Systematic revision of Japanese *Trichadenotecnum* Enderlein (Psocodea: 'Psocoptera': Psocidae: Ptyctini), with redefinition and subdivision of the

genus. *Invertebrate Taxonomy* **15**: 159-204.

Yoshizawa K. 2003. Two new species that are likely to represent the most basal clade of the genus *Trichadenotecnum*. *Entomological Science* **6**: 301-308.

Yoshizawa K. 2004. Molecular phylogeny of major lineages of *Trichadenotecnum* and a review of diagnostic morphological characters (Psocoptera: Psocidae). *Systematic Entomology* **29**: 383-394.

Yoshizawa K, Johnson KP. 2007. Molecular systematics of the barklouse family Psocidae (Insecta: Psocodea: 'Psocoptera') and implications for morphological and behavioral evolution. *Molecular Phylogenetics and Evolution* doi:10.1016/j.ympev.2007.07.011.

Yoshizawa K, Lienhard C. 2004. Systematics of *Trichadenotecnum* (Psocoptera: Psocidae) in Hong Kong. *Publicaciones Especiales, Instituto de Biología, UNAM. México* **20**: 121-149.

Yoshizawa K, Smithers CN. 2006. Systematic position of *Trichadenotecnum enderleini* (Roesler) (Psocodea: 'Psocoptera': Psocidae). *Records of the Australian Museum* **58**: 411-415.

Appendix 1. Characters used in the cladistic analysis.

1. *Male eye*: (0) large, IO/D < 1; (1) small, IO/D > 1. (excluded from the analyses).
2. *Six submarginal spots on forewing*: (0) absent; (1) present. L = 1; RC = 1.
3. *Opposing spots in cell r of forewing*: (0) absent; (1) present. L = 1; RC = 1.
4. *Proximal band of forewing*: (0) running from base of pterostigma to distal end of cell sup;
(1) running from base of pterostigma to distal 1/3 of cell cup. L = 1; RC = 1.
5. *Spots in cell a of forewing*: (0) absent; (1) present. L = 1; RC = 1.
6. *Forewing*: (0) not extensively covered with spots; (1) extensively covered with spots. L = 7; RC = 0.08.
7. *Male eighth sternum*: (0) single sclerite; (1) two sclerites. L = 3; RC = 0.27.
8. *Male eighth sternum and hypandrium*: (0) separated; (1) fused. L = 4; RC = 0.2.
9. *Male clunial arm*: (0) absent; (1) present. L = 1; RC = 1.
10. *Male epiproct lobe*: (0) not broadly expanded; (1) broadly expanded. L = 4; RC = 0.17.
11. *Male epiproct lobe*: (0) without process; (1) with processes covered by papillae or denticles. L = 1; RC = 1.
12. *Dorsal surface of male epiproct*: (0) almost flattened; (1) greatly swelling and forming conical epiproct. L = 1; RC = 1.
13. *Male paraproctal basal process*: (0) absent; (1) present. L = 1; RC = 1.
14. *Male paraproctal trichobothrial process*: (0) absent; (1) present. L = 1; RC = 1.
15. *Male paraproctal distal process*: (0) directed posteriorly; (1) directed upwardly. L = 3; RC = 0.29.
16. *Hypandrial median tongue*: (0) absent; (1) present. L = 5; RC = 0.04.
17. *Hypandrial median tongue*: (0) unmovable; (1) movable. L = 3; RC = 0.11.
18. *Lateral corner of hypandrium*: (0) not denticulated; (1) denticulated. L = 2; RC = 0.25.

19. *Hypandrial left process*: (0) absent or less developed; (1) well developed. L = 6; RC = 0.1.
20. *Hypandrial left distal lobe*: (0) absent or less developed; (1) well developed. L = 2; RC = 0.42.
21. *Hypandrial right process*: (0) absent or less developed; (1) cone-like; (2) lamellate.
(excluded from analyses: re-coded as characters 45 and 46).
22. *Hypandrial right arm*: (0) absent; (1) present. L = 1; RC = 1.
23. *Hypandrial right arm*: (0) almost straight; (1) hooked. L = 1; RC = 1.
24. *Keel-like process of hypandrium*: (0) absent; (1) present. L = 1; RC = 1.
25. *Pseudoparamere*: (0) absent; (1) present. L = 2; RC = 0.46.
26. *Width of pseudoparamere*: (0) narrow, much narrower than long; (1) broad, as wide as long or even wider. L = 3; RC = 0.11.
27. *Anterior margin of phallosome*: (0) rounded; (1) pointed. L = 4; RC = 0.18.
28. *Shape of phallosome*: (0) narrowing posteriorly; (1) broadened posteriorly. L = 3; RC = 0.29.
29. *Posterior margin of phallosome*: (0) well sclerotized; (1) weakly sclerotized or membranous. L = 3; RC = 0.
30. *Subgenital plate*: (0) without median sclerotized band; (1) with median sclerotized band.
L = 1; RC = 1.
31. *Ventral valve of gonapophyses*: (0) long; (1) short. L = 4; RC = 0.13.
32. *Posterior lobe of external valve of gonapophyses*: (0) well developed; (1) less developed.
L = 2; RC = 0.40.
33. *Internal plate*: (0) single plate; (1) clearly divided into two. L = 1; RC = 1.
34. *Rs fork in forewing*: (0) acute; (1) right angle to obtuse. L = 2; RC = 0.43.
35. *Direction of 3rd section of CuA in forewing*: (0) posteriorly; (1) posteroproximally. L = 2;

RC = 0.46.

36. *Development of clunial arm*: (0) less developed, weakly sclerotized; (1) well developed, strongly sclerotized. L = 3; RC = 0.28.

37. *Basal lobe of clunial arm*: (0) absent; (1) present. L = 1; RC = 1.

38. *Keel-like projection on posterodorsal margin of epiproct*: (0) absent; (1) present. L = 4 ; RC = 0.10.

39. *Dorsal margin of epiproct lobe*: (0) bare; (1) setose. L = 1; RC = 1.

40. *Distal lobe of male paraproct*: (0) long; (1) short. L = 1; RC = 1.

41. *Hypandrium*: (0) symmetrical; (1) asymmetrical. L = 6; RC = 0.10.

42. *Anteromedian slit on hypandrium*: (0) absent; (1) present. L = 1; RC = 1.

43. *Hypandrial median membranous region*: (0) absent; (1) present. L = 2; RC = 0.25.

44. *Dorsal flap of hypandrium*: (0) absent; (1) present. L = 1; RC = 1.

45. *Hypandrial right process*: (0) absent or less developed; (1) well developed. L = 6; RC = 0.1.

46. *Shape of hypandrial right process*: (0) conical; (1) lamellate; (2) lobe-like. L = 5; RC = 0.25.

47. *Shape of hypandrial left process*: (0) conical; (1) lamellate. L = 3; RC = 0.

48. *Hypandrial left and right processes*: (0) not crossing; (1) crossing. L = 1; RC = 1.

49. *Length of hypandrial median tongue*: (0) long, much longer than wide; (1) short, almost as long as wide. L = 3; RC = 0.17.

50. *Dorsal surface of hypandrial median tongue*: (0) smooth; (1) covered with denticles or spines; (2) papillae. L = 2; RC = 1.

51. *Dorsal keel of hypandrial median tongue*: (0) absent; (1) present. L = 1; RC = 1.

52. *Hypandrial median tongue*: (0) sclerotized; (1) membranous. L = 1; RC = 1.

53. *Hypandrial median tongue*: (0) not setose; (1) setose. L = 1; RC = 1.
54. *Phallosome*: (0) symmetry; (1) asymmetry. L = 3; RC = 0.11.
55. *Aedeagal region of phallosome*: (0) narrowly sclerotized; (1) broadly sclerotized. L = 1;
RC = 1.
56. *Egg guide of subgenital plate*: (0) gradually narrowing apically; (1) constricted medially. L
= 5; RC = 0.09.
57. *Dorsal surface of egg guide of subgenital plate*: (0) without sclerite; (1) with sclerites. L =
2; RC = 0.4.
58. *Body of subgenital plate*: (0) without pair of anteromedian extensions of sclerites; (1) with
pair of anteromedian extensions of sclerites. L = 1; RC = 1.

Appendix 2. Data matrix for the cladistic analysis. 0-2, character states; &, 1 or 2; ?, inapplicable data; -, excluded character (see Phylogenetic Analysis section).

	1	2	3	4	5
Characters	0	0	0	0	0
Atrichadenotecnum quadripunctatum	-00000000000000?000-0?00?0000000000000000??0?0?710000				
Symbiosocus hastatus	-0000000000000010000-0?00?0000000000000000??0?0?000000				
Loensia variegata	-000010000000000?000-0?00?0000000000000000??0?0?7000000				
T. gonzalezi	-10110000000000?010-0?00?100011000000011010120?????10000				
T. peruense	-101100000000010?010-0?00?1000???000000110101210?????10???				
T. tambopatense	-?011111010000011000-0?00?0000110000011100000000000100000				
T. bos	-?&11111010000011000-0?01?0100110000011100000000000100000				
T. corniculum	-111110001000100?000-0?00?00000001000000100011?0?0?00000				
T. germinatum	-1111100010001010000-0?00?0? ??????0100000100011?0?0?000000				
T. furcilingum	-1111111100110011000-0?00?1000110101000000000000000000100				
T. falx	-1111111100110011000-0?00?10001101010000100000000000000000				
T. ianobidensis	-1111111100100011000-0?00?10000101010000000010000000000100				
T. castum	-11110?????????????-?????00000110?????????????????0000				
T. alexandrae	-1111010110000011000-0?00?10000011010000000010000000000000				
T. iani	-1111010110000011010-0?00?11101001110100100011100000000000				
T. yamatomajus	-1111010100000100011-0?00?110000011100001000110001000000010				
T. nothoapertum	-1111010101000000001-0?00?1110100111000010101100?0?00010				
T. mixtum	-1111000110000111001-1001011010001100000100000000000000000				
T. latebrachium	-1111000110000111101-1001011010001100000100000001000000000				
T. sp. (ca. medium)	-1111100110000111101-1001011010001100000100000001000000000				
T. incognitum	-1111000110000111011-1111110000011100001000100000000000000				
T. album	-1111000110000111011-1111110000011100001000100000000000000				
T. desolatum	-1111110110000111000-0?01111000001100000110000000100000000				
T. tuitense	-1111110110000111000-0?01011000001100000110000000100000000				
T. slossonae	-1111011110000111000-0?0?00000001110000000110000?01001110				
T. miffy	-1111011110000111000-0?0?710000001110000000110000?01001110				
T. aconcinnum	-1111011110000111010-0?010000????1110100100011000100011???				
T. decui	-1111011110000011000-0?010000000011101000000000100001010				
T. obrienorum	-1111011110000111000-0?0100000000111010000000001100001110				
T. chiapense	-1111010110000111010-0?01011000001110000100011100210000001				
T. erwini	-1111011110000111110-0?010110? ???1110000100011000110000???				
T. concinnum	-1111111110000111010-0?01111000001111000000010000110000101				
T. nicaraguense	-1111111110000111010-0?010111????1111000000010000110000???				
T. quaesitum	-1111011110000011010-0?01011000001110001000010010110000101				
T. brevicornum	-1111111110000111010-0?01011000001111000100010010110000101				

Figure captions

Figure 1. Forewings of *Trichadenotecnum circularoides* (A), *T. gonzalezi* (B), *T. peruense* (C), *T. tambopatense* (D), *T. oaxacense* (E) and *T. bos* (F).

Figure 2. Male terminalia structures of *Trichadenotecnum gonzalezi* (A-D) and *T. peruense* (E-H), showing terminalia in lateral view (A, E), epiproct in posterior view (B, F), hypandrium in ventral view (C, G) and phallosome in ventral view (D, H).

Figure 3. Male terminalia structures of *Trichadenotecnum tambopatense* (A-D), *T. oaxacense* (E-H) and *T. bos* (I, J), showing terminalia in lateral view (A, E), epiproct in posterior view (B, F), hypandrium in ventral view (C, G, I) and phallosome in ventral view (D, H, J).

Figure 4. Female genitalia of *Trichadenotecnum tambopatense*, showing subgenital plate (A), gonapophyses (B) and internal plate (C) in ventral view.

Figure 5. Forewings of *Trichadenotecnum desolatum* (A), *T. acutolingum* (B), *T. magnolingum* (C), *T. longilingum* (D), *T. carinatum* (E), *T. tuitense* (F), *T. sparsum* (G) and *T. latipenne* (H).

Figure 6. Male terminalia structures of *Trichadenotecnum desolatum*, showing terminalia in lateral view (A), epiproct in posterior view (B), hypandrium in ventral view (C) and phallosome in ventral view (D).

Figure 7. Female genitalia of *Trichadenotecnum desolatum*, showing subgenital plate (A), gonapophyses (B) and internal plate (C) in ventral view.

Figure 8. Male genitalia of *Trichadenotecnum acutolingum* (A-C) and *T. magnolingum* (D-F), showing epiproct in posterior view (A, D), hypandrium in ventral view (B, E) and phallosome in ventral view (C, F).

Figure 9. Female genitalia of *Trichadenotecnum acutolingum*, showing subgenital plate (A)

and internal plate (B) in ventral view.

Figure 10. Female genitalia of *Trichadenotecnum magnolingum*, showing subgenital plate (A) and internal plate (B) in ventral view.

Figure 11. Male genitalia of *Trichadenotecnum longilingum*, showing epiproct in posterior view (A), hypandrium in ventral view (B) and phallosome in ventral view (C).

Figure 12. Female genitalia of *Trichadenotecnum longilingum*, showing subgenital plate (A) and internal plate (B) in ventral view.

Figure 13. Male genitalia of *Trichadenotecnum carinatum* (A-C) and *T. tuitense* (D-F), showing epiproct in posterior view (A, D), hypandrium in ventral view (B, E) and phallosome in ventral view (C, F).

Figure 14. Male genitalia of *Trichadenotecnum sparsum* (A-C) and *T. latipenne* (D-F), showing epiproct in posterior view (A, D), hypandrium in ventral view (B, E) and phallosome in ventral view (C, F).

Figure 15. Female genitalia of *Trichadenotecnum latipenne*, showing subgenital plate (A) and internal plate (B) in ventral view.

Figure 16. Hypandrium (left) and epiproct (right) of some unidentified specimens of the *desolatum* group: *Trichadenotecnum* sp. 32 (A), *T. sp. 35* (B), and *T. sp. 3* (C).

Figure 17. Forewings of *Trichadenotecnum erwini* (A), *T. chiapense* (B), *T. quaesitum* (C), *T. quaesitellum* (D), *T. cerrosillae* (E), *T. maculatum* (F), *T. neoleonense* (G), *T. ericium* (H), *T. brevicornum* (I), *T. concinnum* (J), *T. acutum* (K), and *T. nicaraguense* (L).

Figure 18. Male terminalia structures of *Trichadenotecnum erwini*, showing terminalia in lateral view (A), epiproct in posterior view (B), hypandrium in ventral view (C) and phallosome in ventral view (D).

Figure 19. Male terminalia structures of *Trichadenotecnum chiapense*, showing terminalia in

lateral view (A), epiproct in posterior view (B), hypandrium in ventral view (C) and phallosome in ventral view (D).

Figure 20. Female genitalia of *Trichadenotecnum chiapense*, showing subgenital plate (A), gonapophyses (B) and internal plate (C) in ventral view.

Figure 21. Male terminalia structures of *Trichadenotecnum quaesitum*, showing terminalia in lateral view (A), epiproct in posterior view (B), hypandrium in ventral view (C) and phallosome in ventral view (D).

Figure 22. Male terminalia structures of *Trichadenotecnum quaesitellum*, showing terminalia in lateral view (A), epiproct in posterior view (B), hypandrium in ventral view (C) and phallosome in ventral view (D).

Figure 23. Male terminalia structures of *Trichadenotecnum cerrosillae*, showing terminalia in lateral view (A), epiproct in posterior view (B), hypandrium in ventral view (C) and phallosome in ventral view (D).

Figure 24. Female genitalia of *Trichadenotecnum cerrosillae*, showing subgenital plate (A), gonapophyses (B) and internal plate (C) in ventral view.

Figure 25. Male terminalia structures of *Trichadenotecnum maculatum*, showing terminalia in lateral view (A), epiproct in posterior view (B), hypandrium in ventral view (C) and phallosome in ventral view (D).

Figure 26. Female genitalia of *Trichadenotecnum maculatum*, showing subgenital plate (A), gonapophyses (B) and internal plate (C) in ventral view.

Figure 27. Male terminalia structures of *Trichadenotecnum neoleonense*, showing terminalia in lateral view (A), epiproct in posterior view (B), hypandrium in ventral view (C) and phallosome in ventral view (D); everted endophallus is not illustrated in D.

Figure 28. Female genitalia of *Trichadenotecnum neoleonense*, showing subgenital plate (A),

gonapophyses (B) and internal plate (C) in ventral view.

Figure 29. Male terminalia structures of *Trichadenotecnum ericum*, showing terminalia in lateral view (A), epiproct in posterior view (B), hypandrium in ventral view (C) and phallosome in ventral view (D).

Figure 30. Female genitalia of *Trichadenotecnum ericum*, showing subgenital plate (A), gonapophyses (B) and internal plate (C) in ventral view.

Figure 31. Male terminalia structures of *Trichadenotecnum brevicornum*, showing terminalia in lateral view (A), epiproct in posterior view (B), hypandrium in ventral view (C) and phallosome in ventral view (D).

Figure 32. Male terminalia structures of *Trichadenotecnum concinnum*, showing terminalia in lateral view (A), epiproct in posterior view (B), hypandrium in ventral view (C) and phallosome in ventral view (D).

Figure 33. Female genitalia of *Trichadenotecnum concinnum*, showing subgenital plate (A), gonapophyses (B) and internal plate (C) in ventral view.

Figure 34. Male terminalia structures of *Trichadenotecnum acutum*, showing terminalia in lateral view (A), epiproct in posterior view (B), hypandrium in ventral view (C) and phallosome in ventral view (D).

Figure 35. Male terminalia structures of *Trichadenotecnum nicaraguense*, showing terminalia in lateral view (A), epiproct in posterior view (B), hypandrium in ventral view (C) and phallosome in ventral view (D).

Figure 36. Forewings of *Trichadenotecnum aconcinnum* (A), *T. guttatum* (B), *T. slossonae* (C), *T. barrerai* (D), *T. denticulatum* (E), *T. miffy* (F), *T. decui* (G), *T. obrienorum* (H) and *T. cintalapense* (I).

Figure 37. Male terminalia structures of *Trichadenotecnum aconcinnum* (A-D) and *T.*

guttatum (E-H), showing terminalia in lateral view (A), epiproct in posterior view (B, E), epiproct in lateral view (F), hypandrium in ventral view (C, G) and phallosome in ventral view (D, H).

Figure 38. Male terminalia structures of *Trichadenotecnum slossonae*, showing terminalia in lateral view (A), epiproct in posterior view (B), hypandrium in ventral view (C) and phallosome in ventral (D) and lateral views (E).

Figure 39. Female genitalia of *Trichadenotecnum slossonae*, showing subgenital plate (A), gonapophyses (B) and internal plate (C) in ventral view.

Figure 40. Male terminalia structures of *Trichadenotecnum barrerae*, showing terminalia in lateral view (A), epiproct in posterior view (B), hypandrium in ventral view (C) and phallosome in ventral (D) and lateral views (E); everted endophallus is not illustrated in D and E.

Figure 41. Male terminalia structures of *Trichadenotecnum denticulatum*, showing terminalia in lateral view (A), epiproct in posterior view (B), hypandrium in ventral view (C) and phallosome in ventral (D) and lateral views (E); everted endophallus is not illustrated in D and E.

Figure 42. Male terminalia structures of *Trichadenotecnum miffy*, showing clunial arm in lateral view (A), epiproct in posterior view (B), paraproct in lateral view (C), hypandrium in ventral view (D) and phallosome in ventral (E).

Figure 43. Male terminalia structures of *Trichadenotecnum decui*, showing terminalia in lateral view (A), epiproct in posterior view (B), hypandrium in ventral view (C) and phallosome in ventral view (D).

Figure 44. Male terminalia structures of *Trichadenotecnum obrienorum*, showing terminalia in lateral view (A), epiproct in posterior view (B), hypandrium in ventral view (C) and

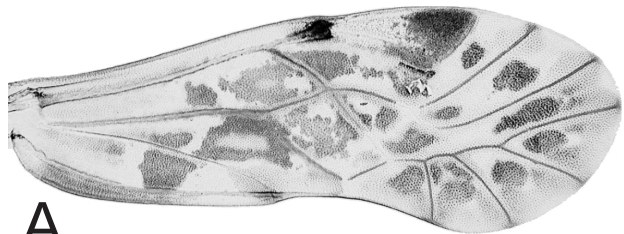
phallosome in ventral (D) and lateral views (E).

Figure 45. Female genitalia of *Trichadenotecnum obrienorum*, showing subgenital plate (A), gonapophyses (B) and internal plate (C) in ventral view.

Figure 46. Male terminalia structures of *Trichadenotecnum cintalapense*, showing terminalia in lateral view (A), clunial arm in posterolateral view (B), epiproct in posterior view (C), hypandrium in ventral view (D) and phallosome in ventral (E) and lateral views (F).

Figure 47. Preferred cladogram of *Trichadenotecnum* and most parsimonious reconstruction of character states. Character 41 is highlighted (see text).

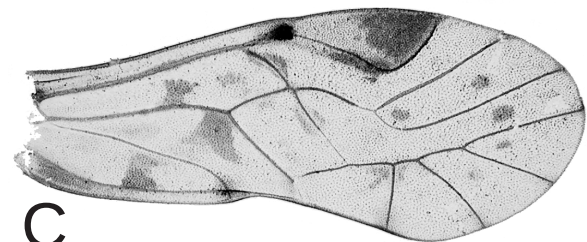
Figure 48. Phylogenetic relationships among species-groups of *Trichadenotecnum*. Thick nodes indicate New World distribution and thick broken node indicate Holarctic distribution.



A



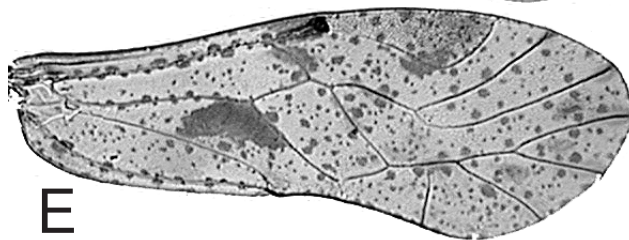
B



C



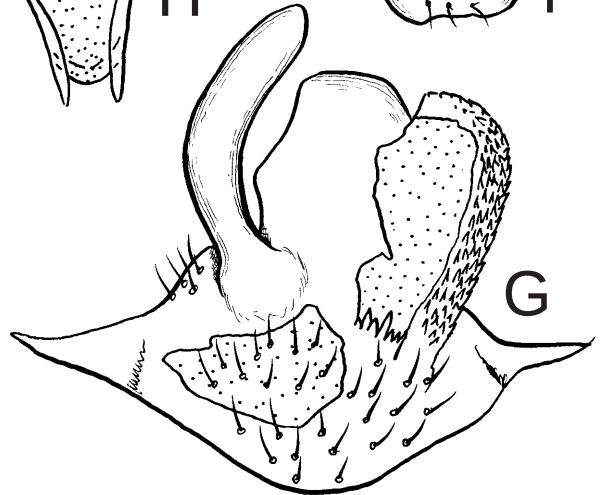
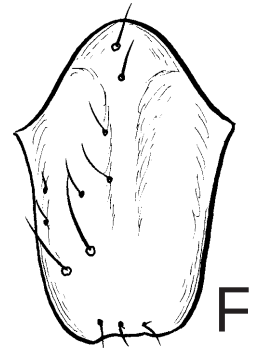
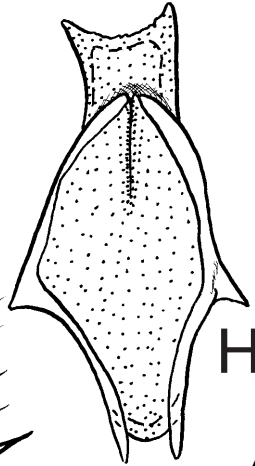
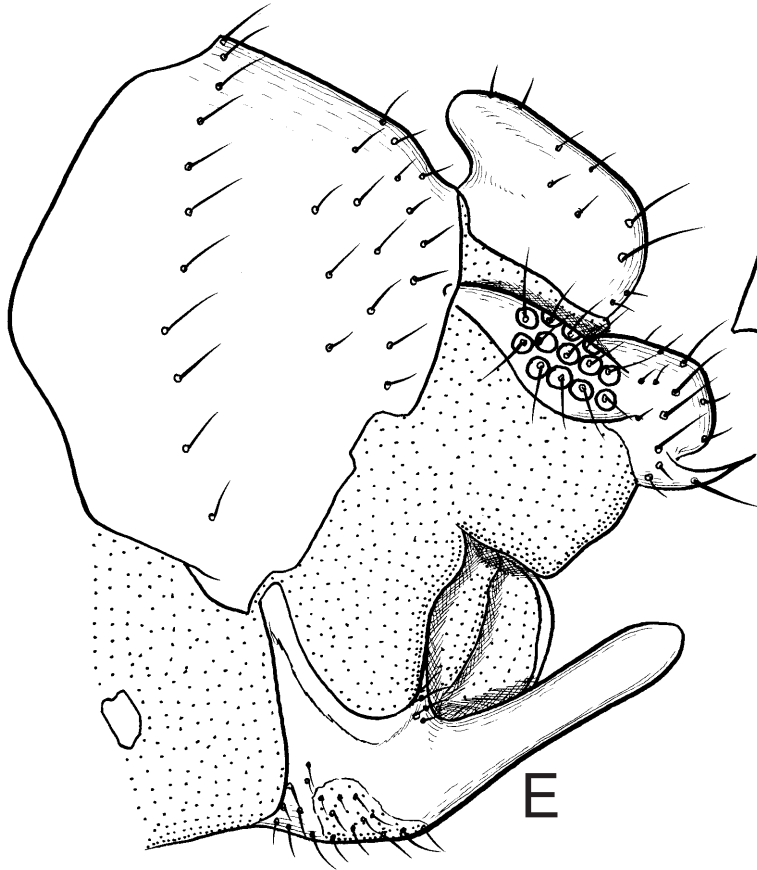
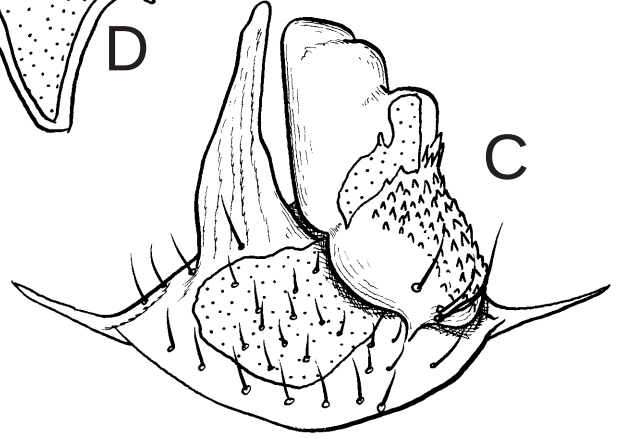
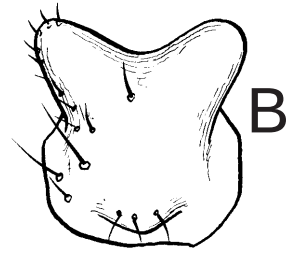
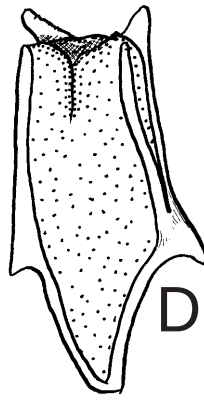
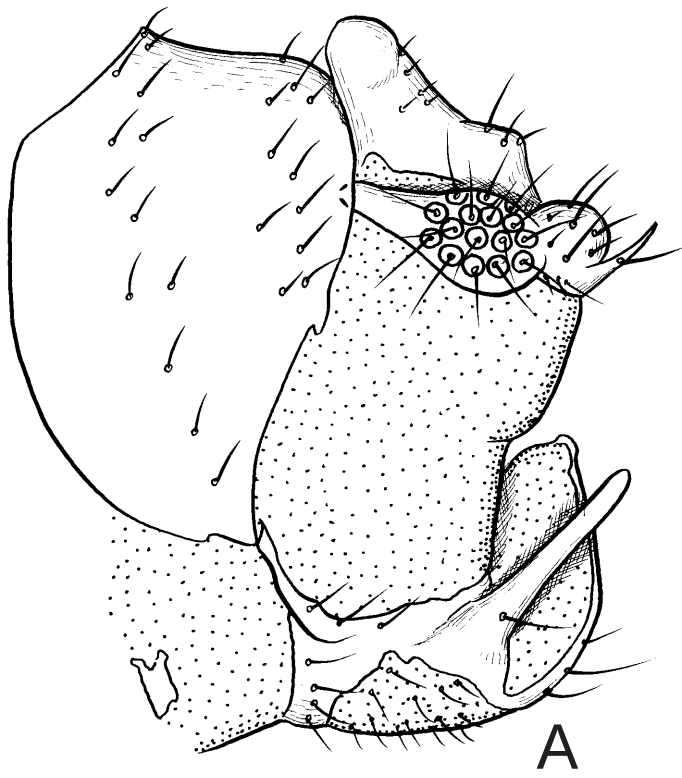
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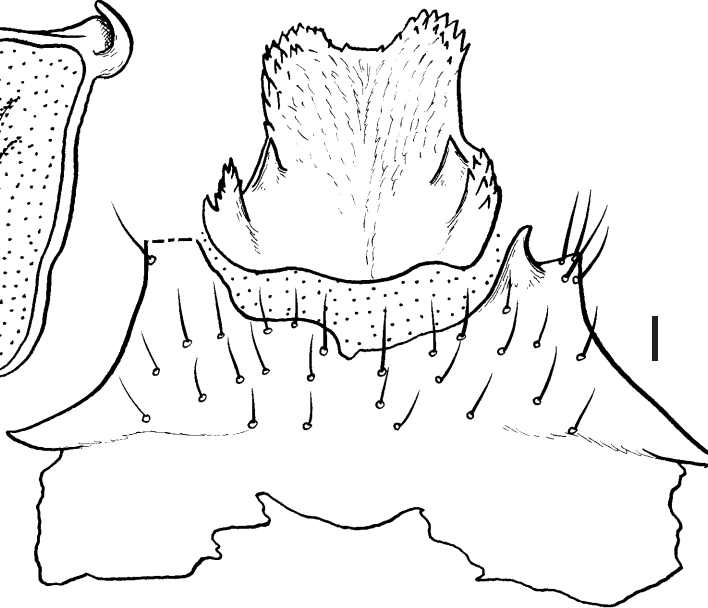
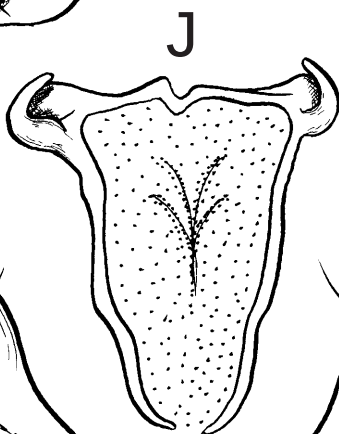
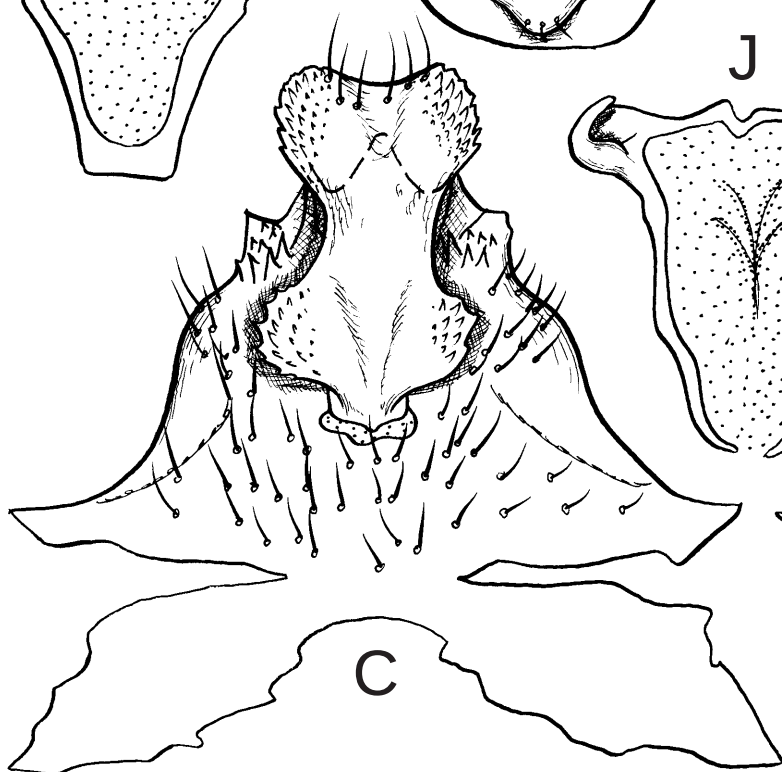
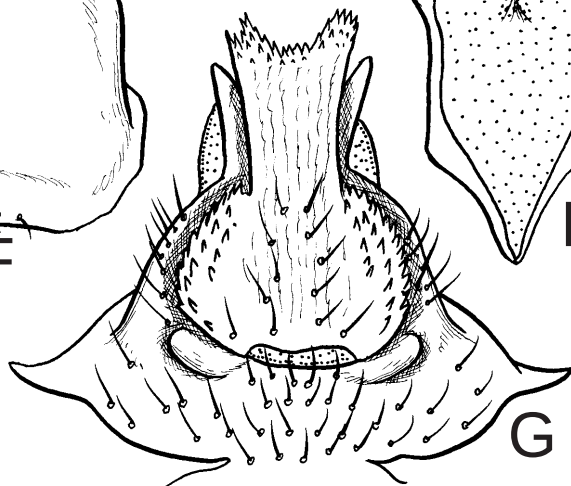
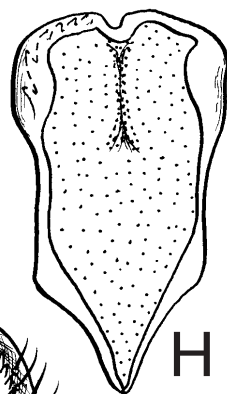
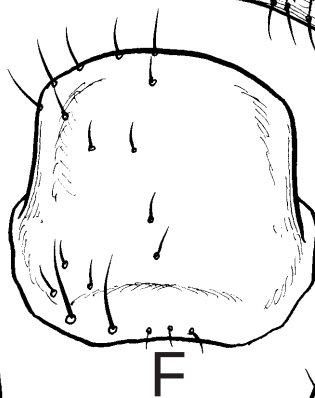
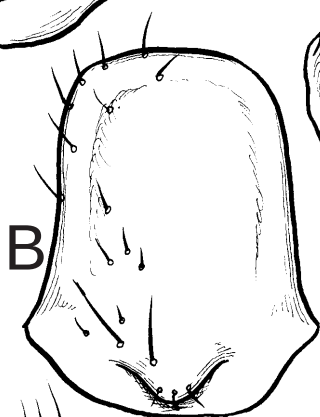
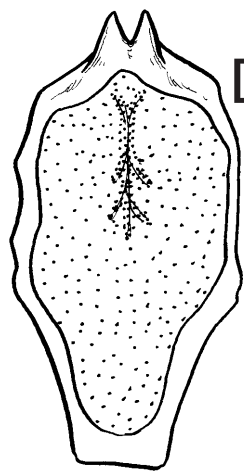
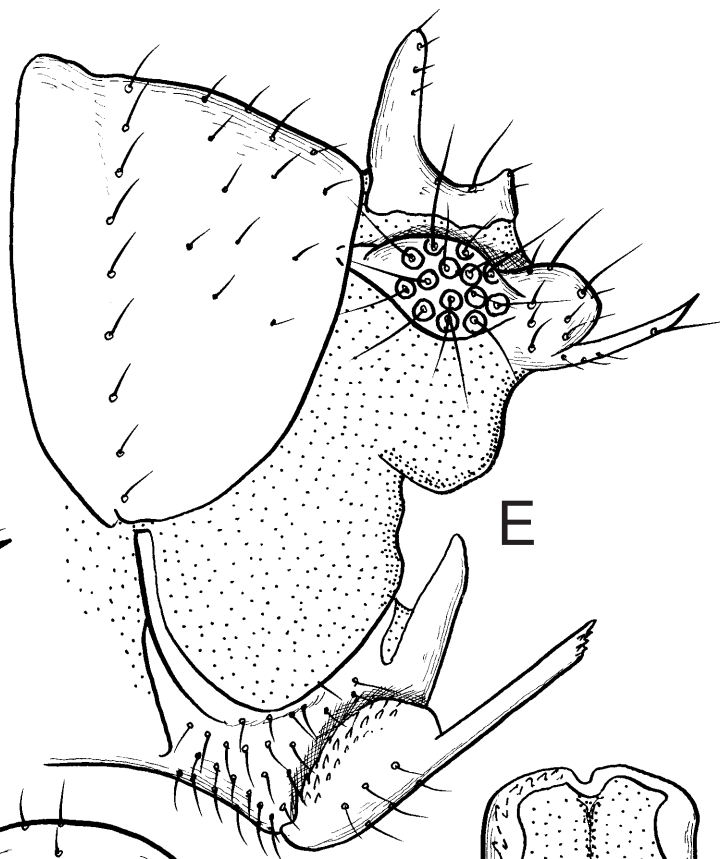
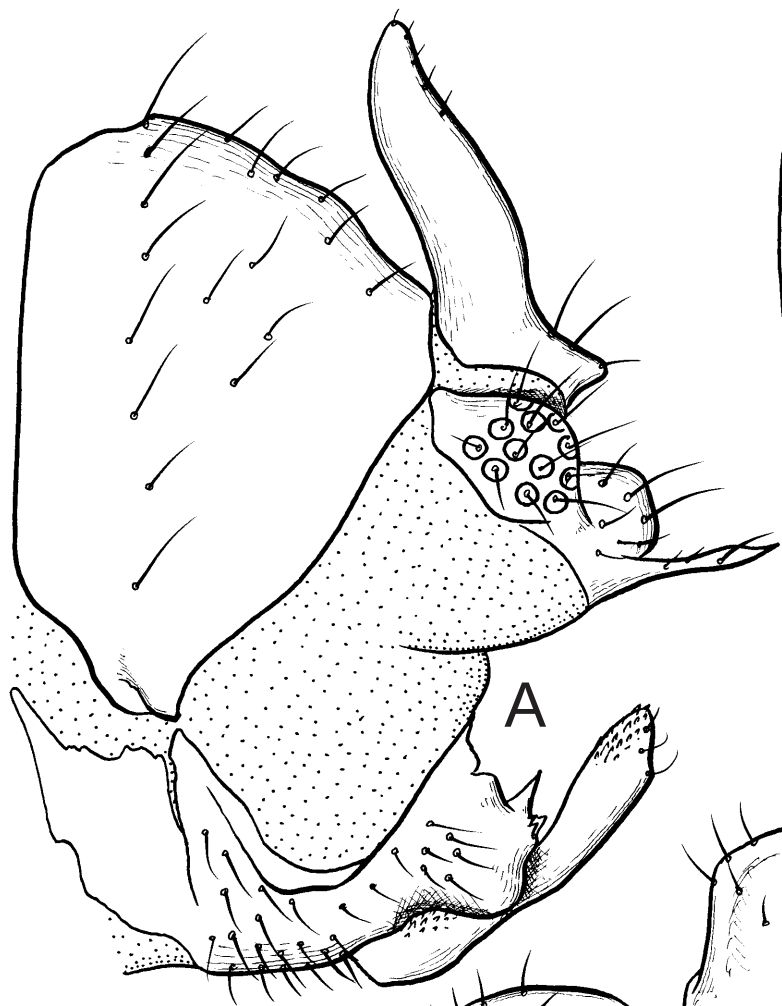


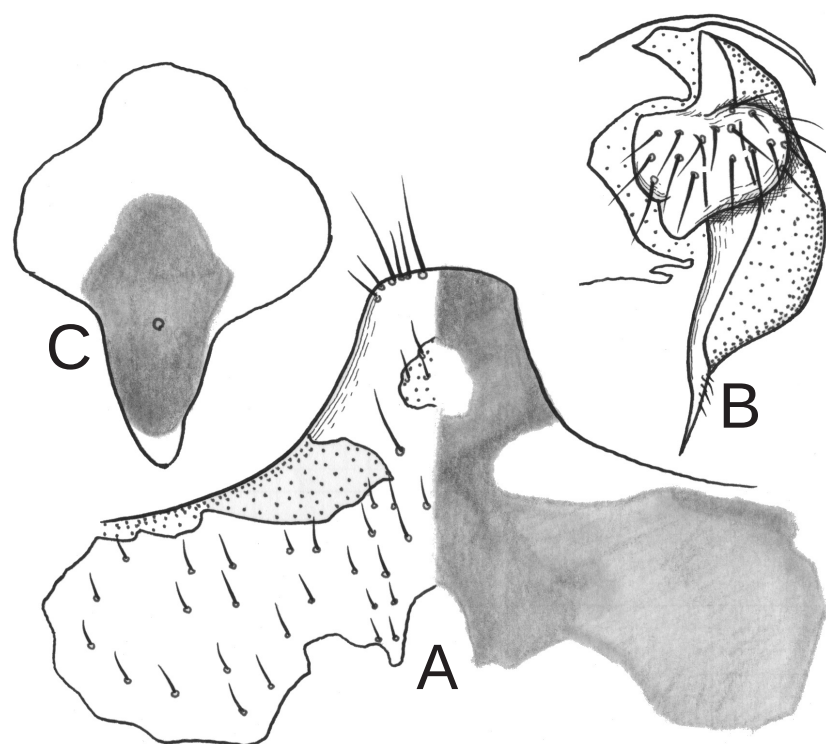
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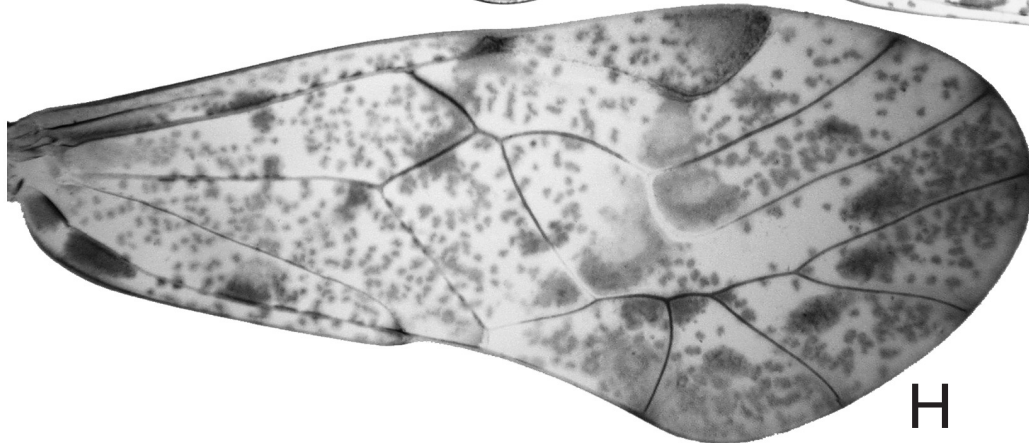
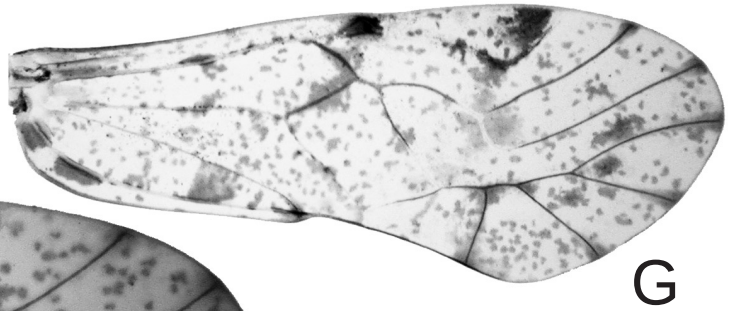
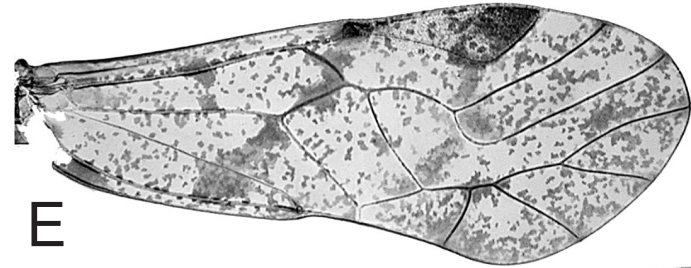
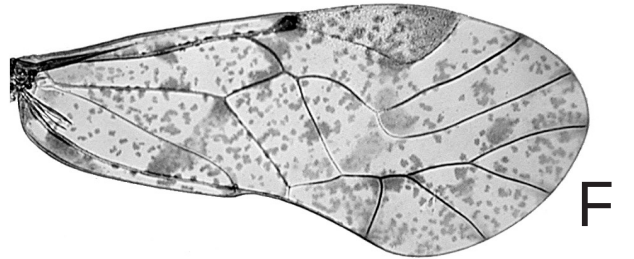
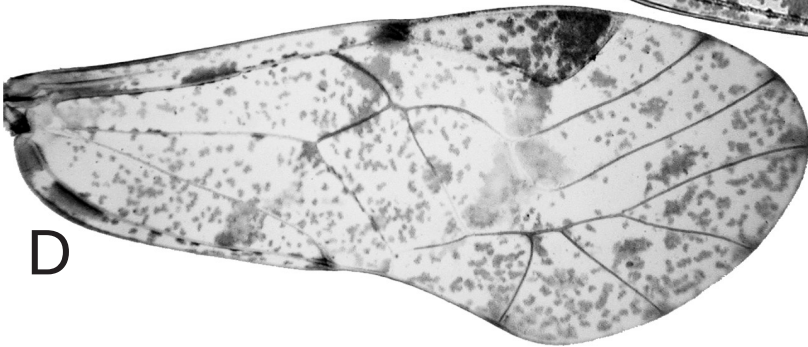
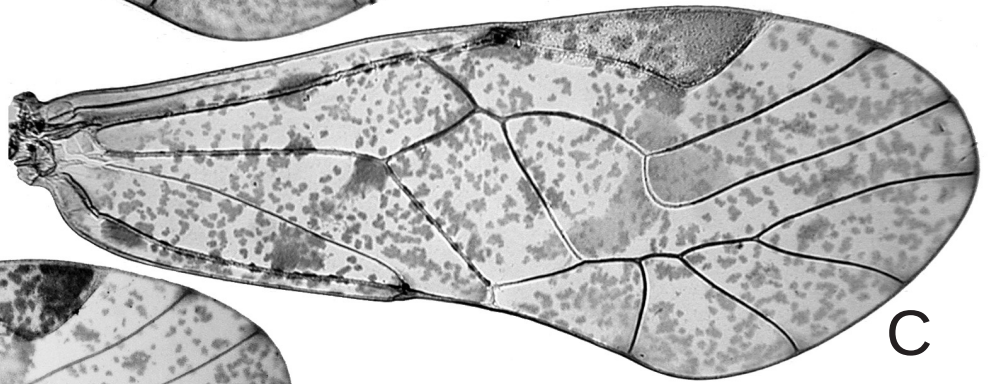
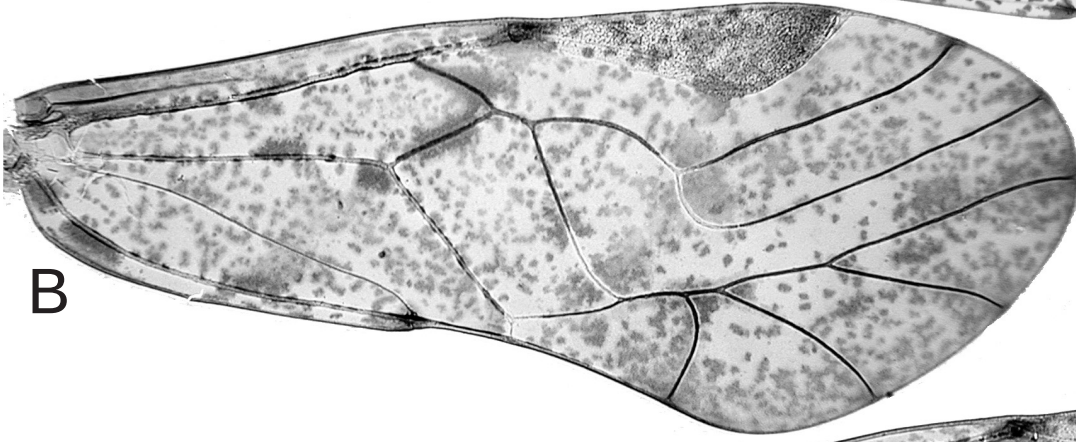
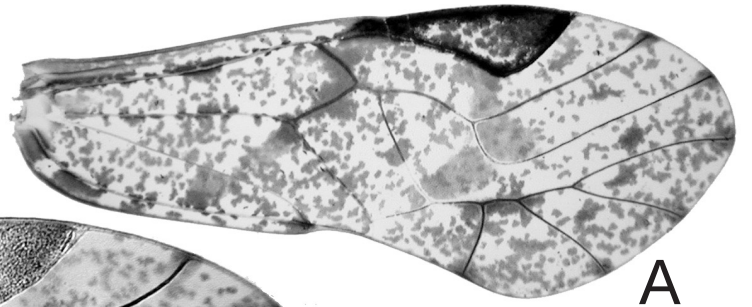


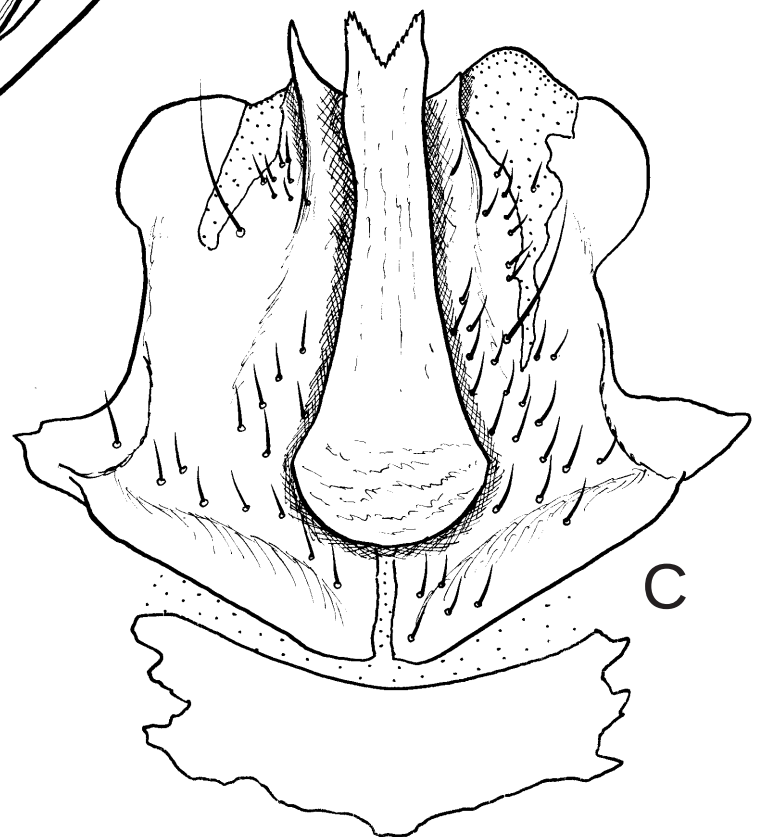
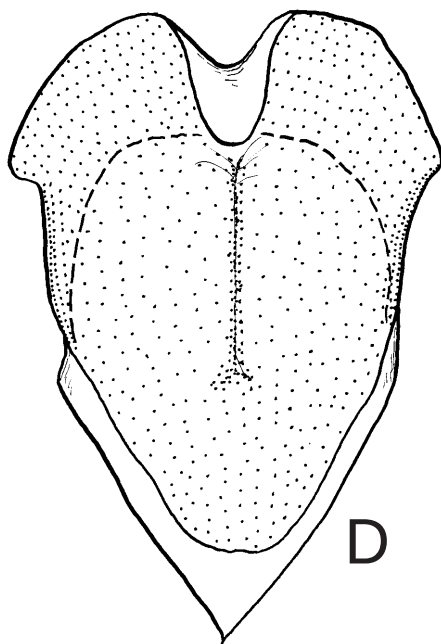
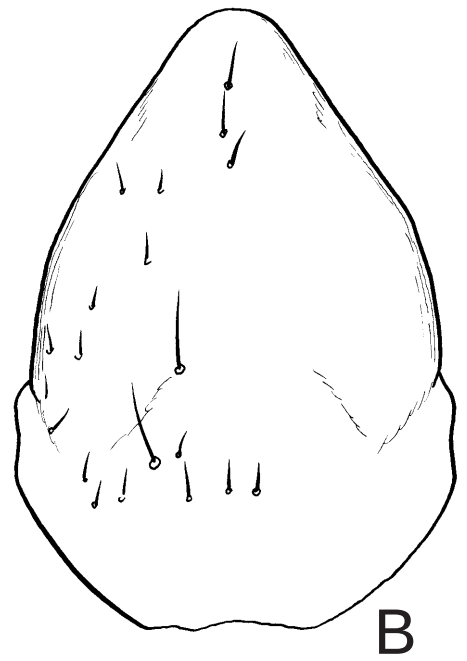
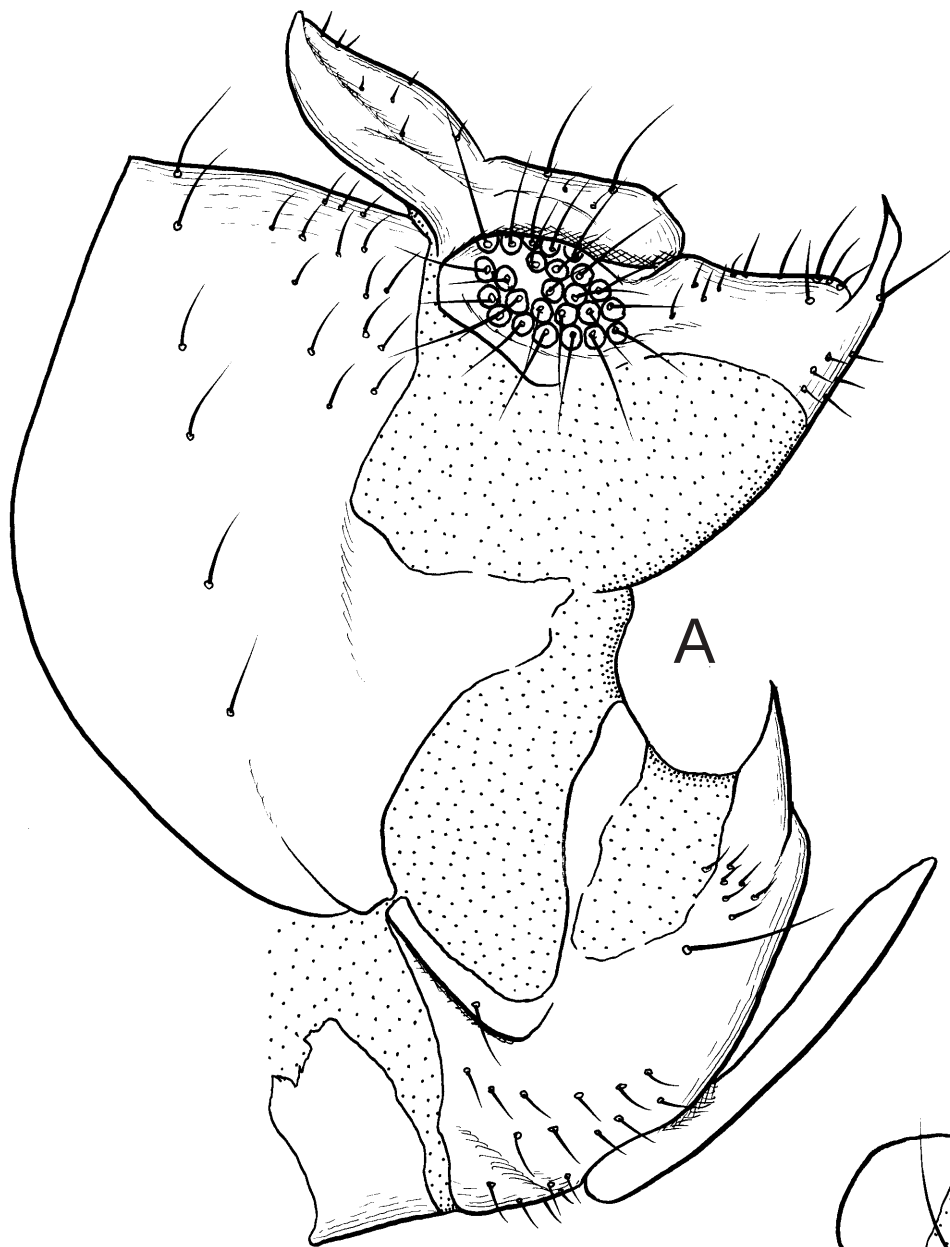
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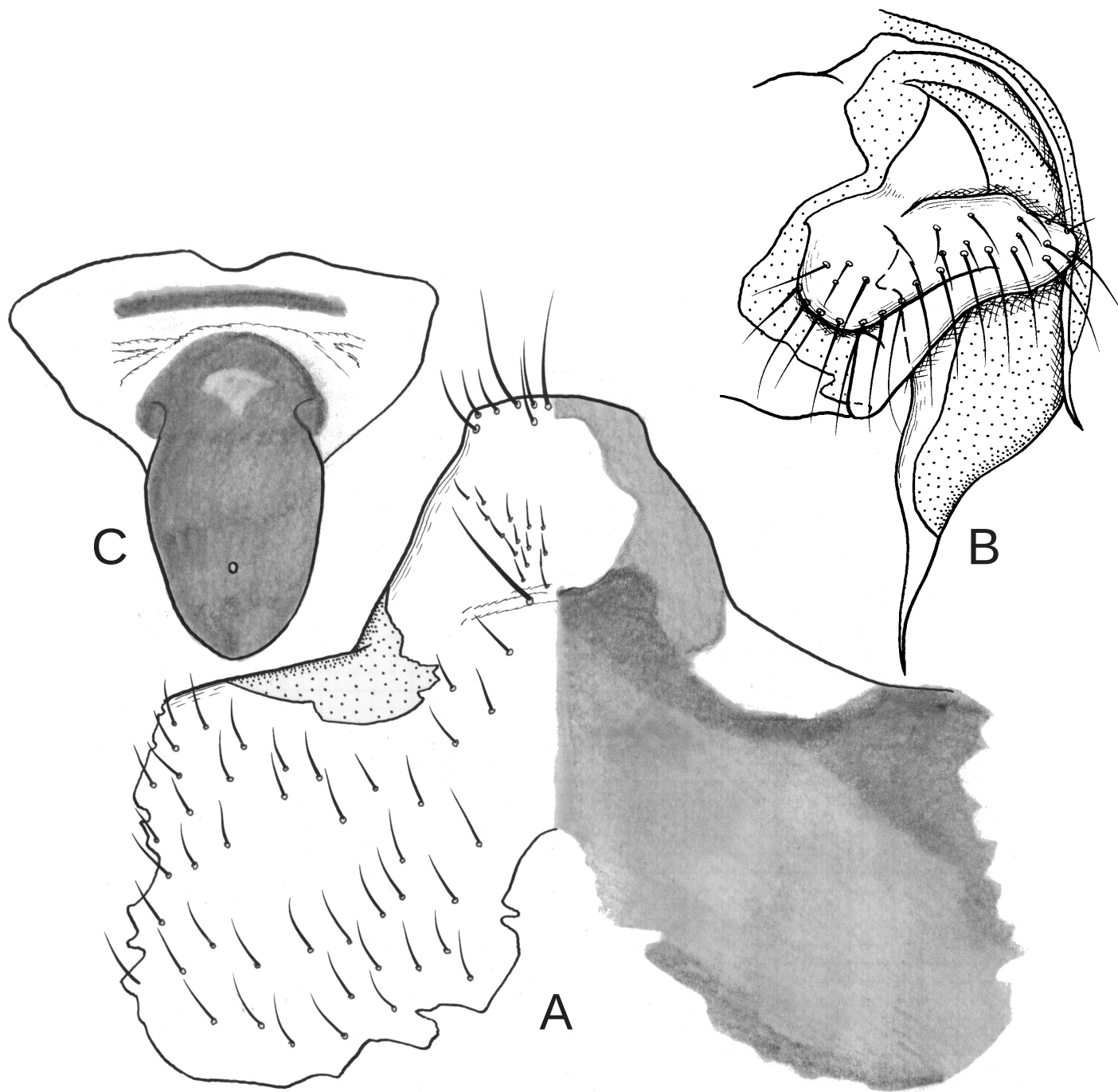


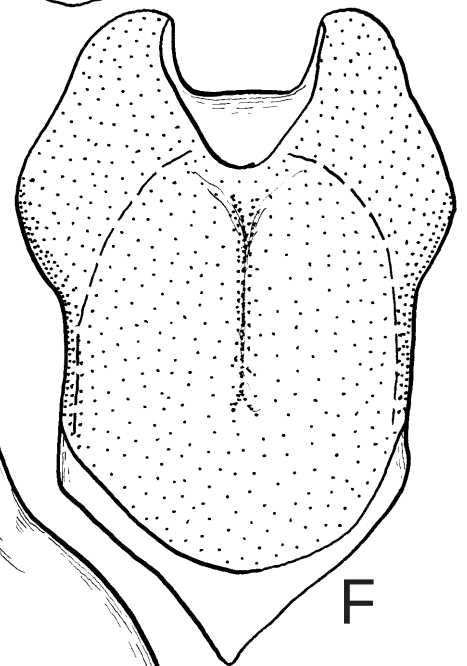
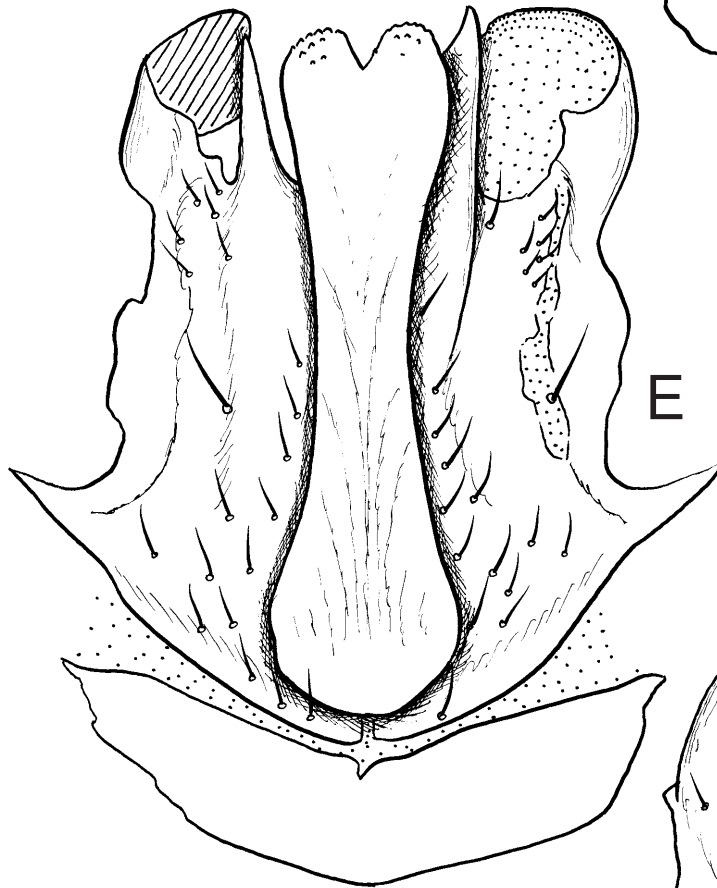
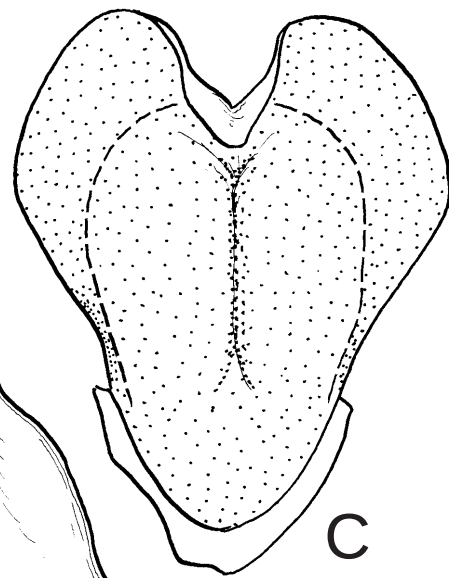
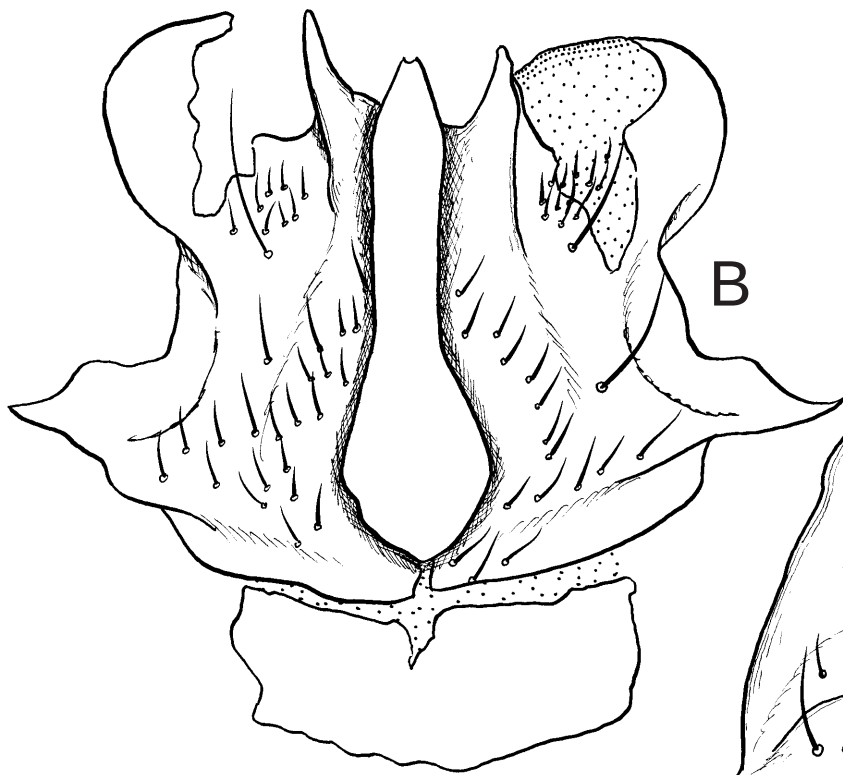


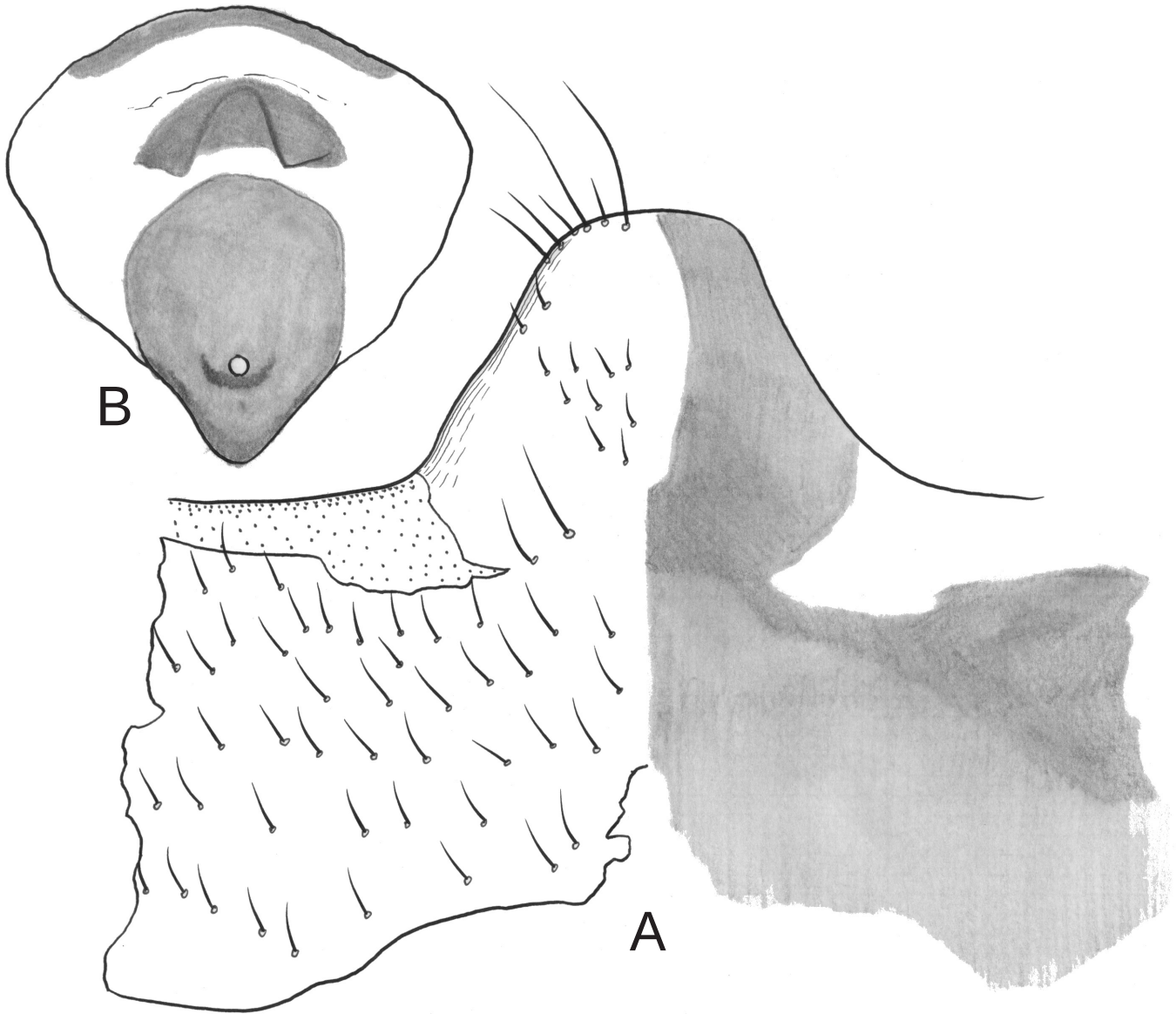


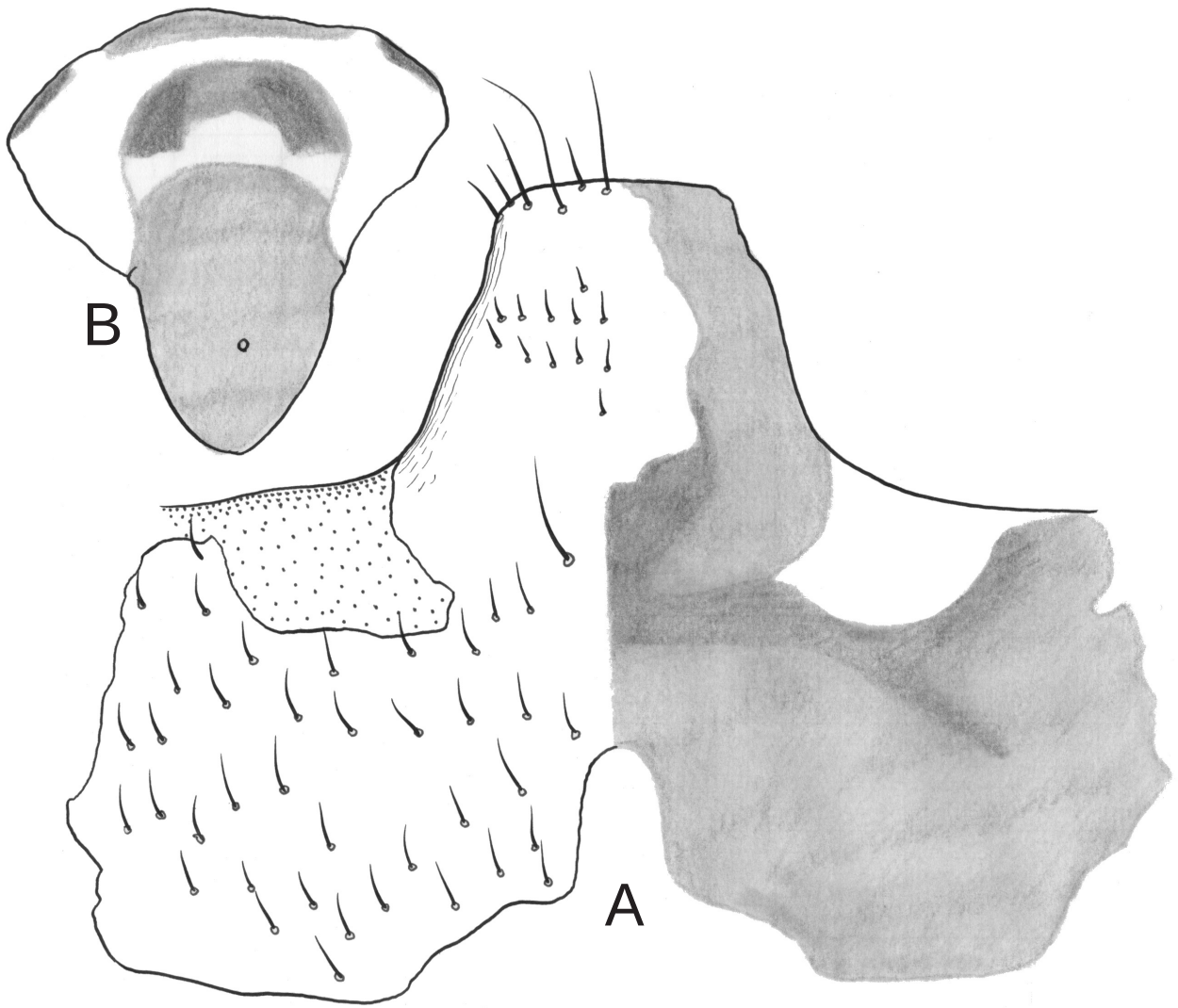


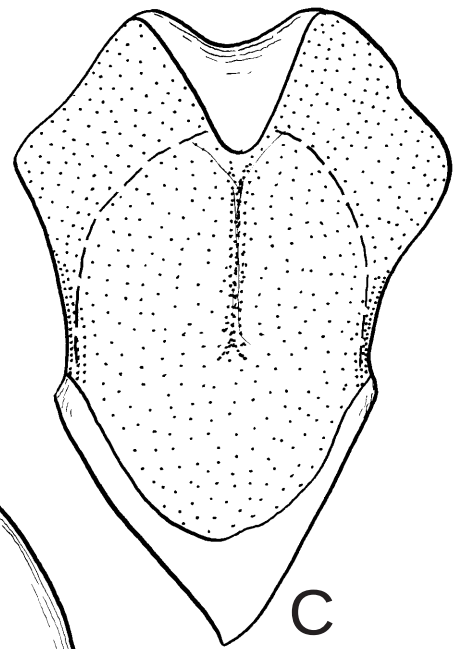
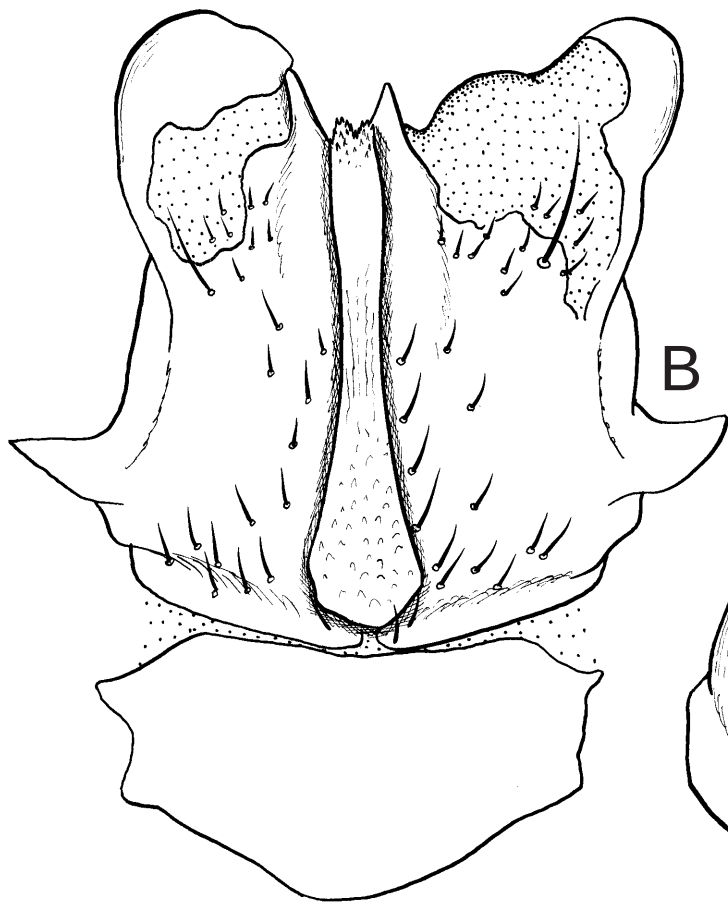


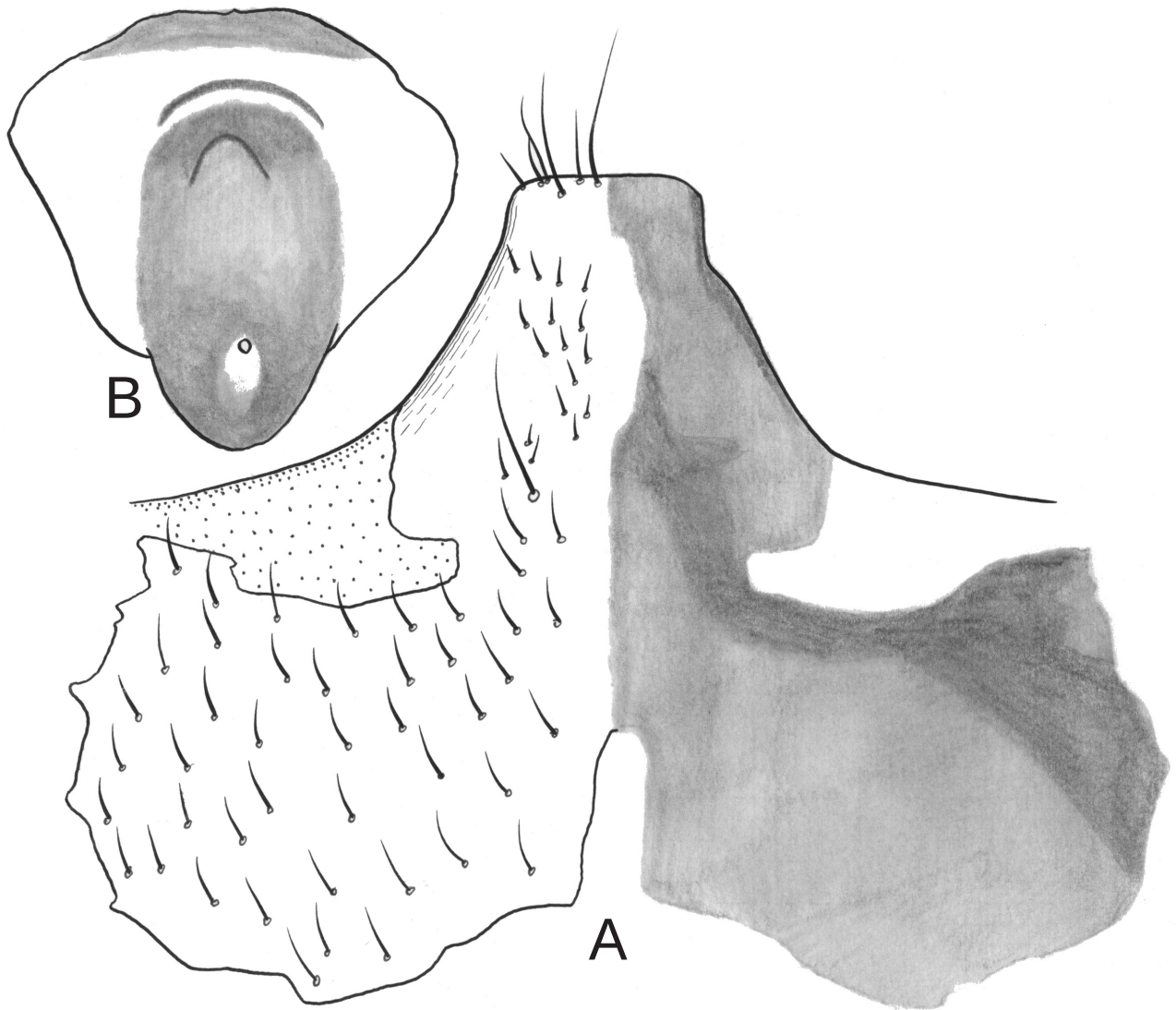


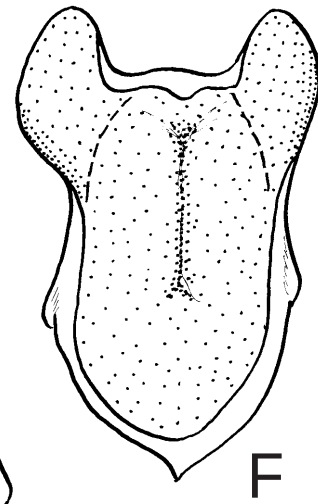
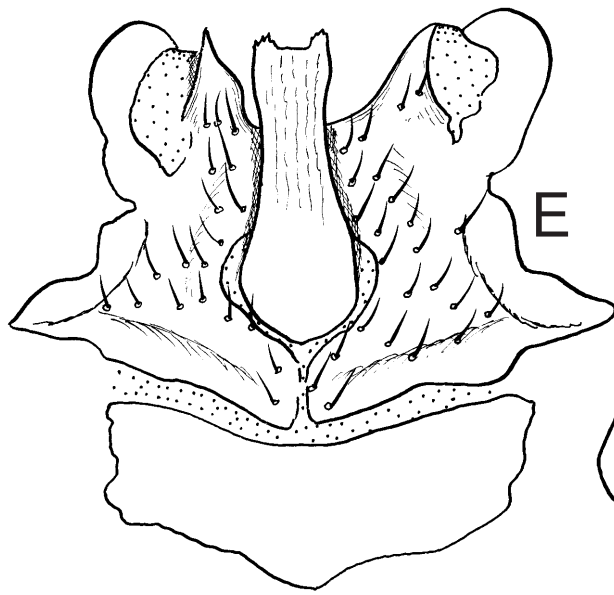
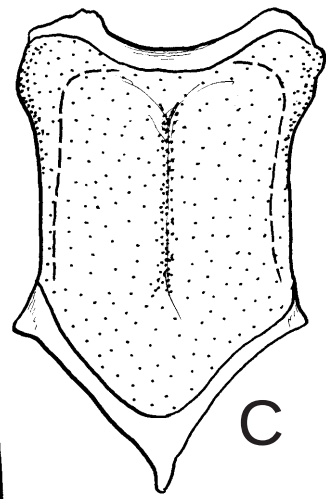
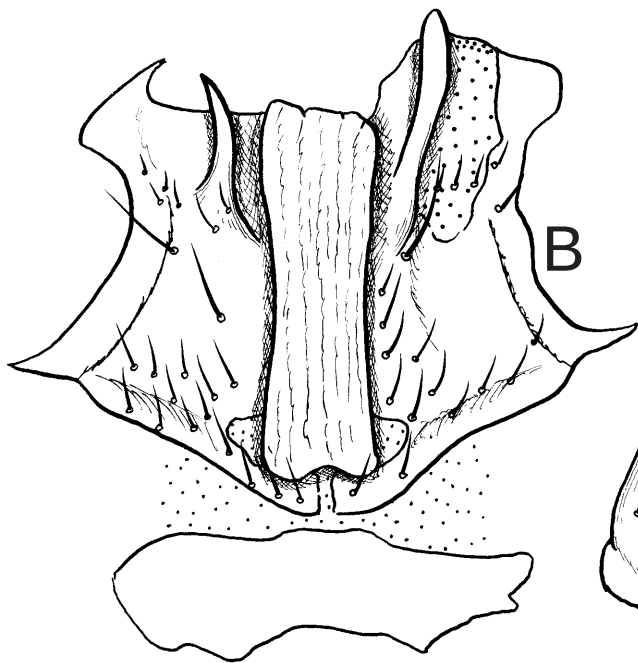


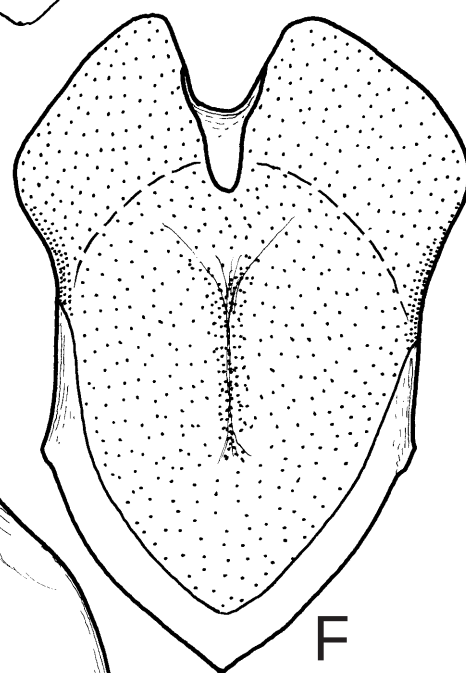
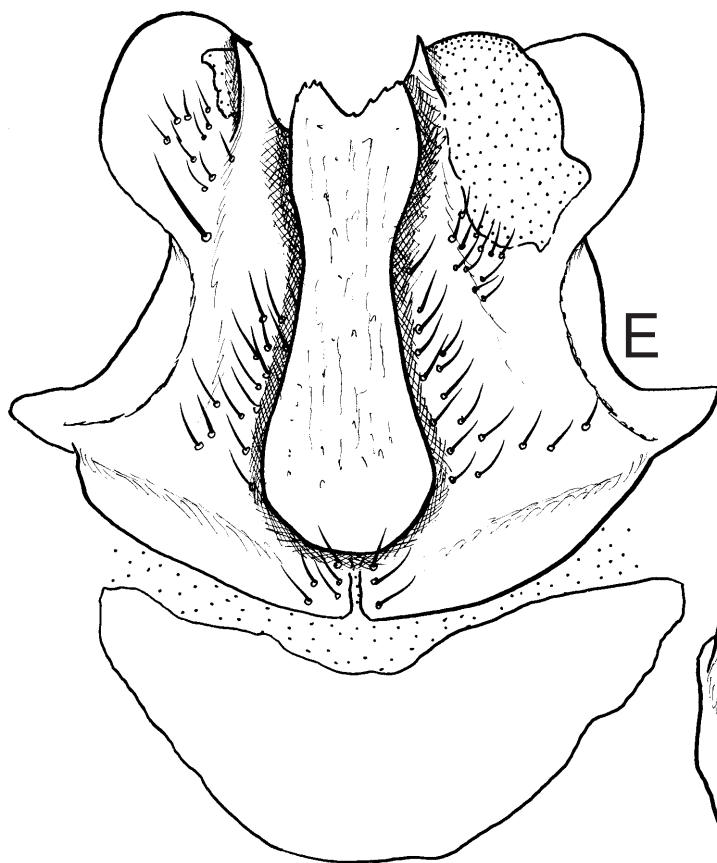
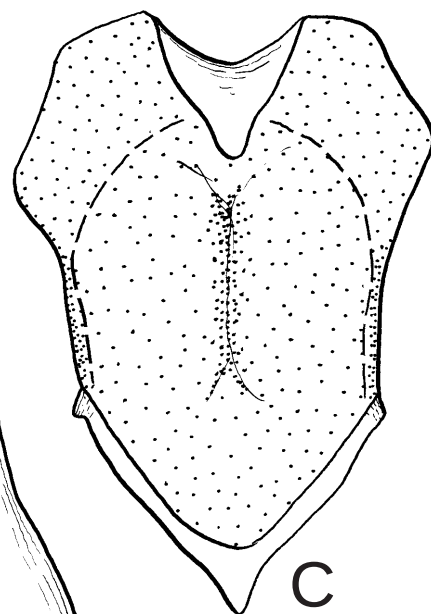
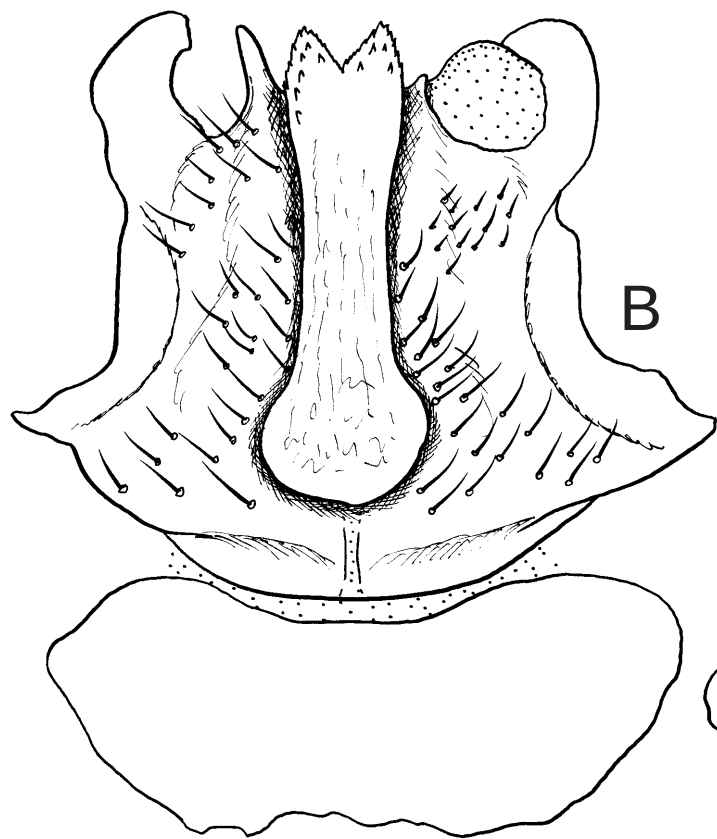


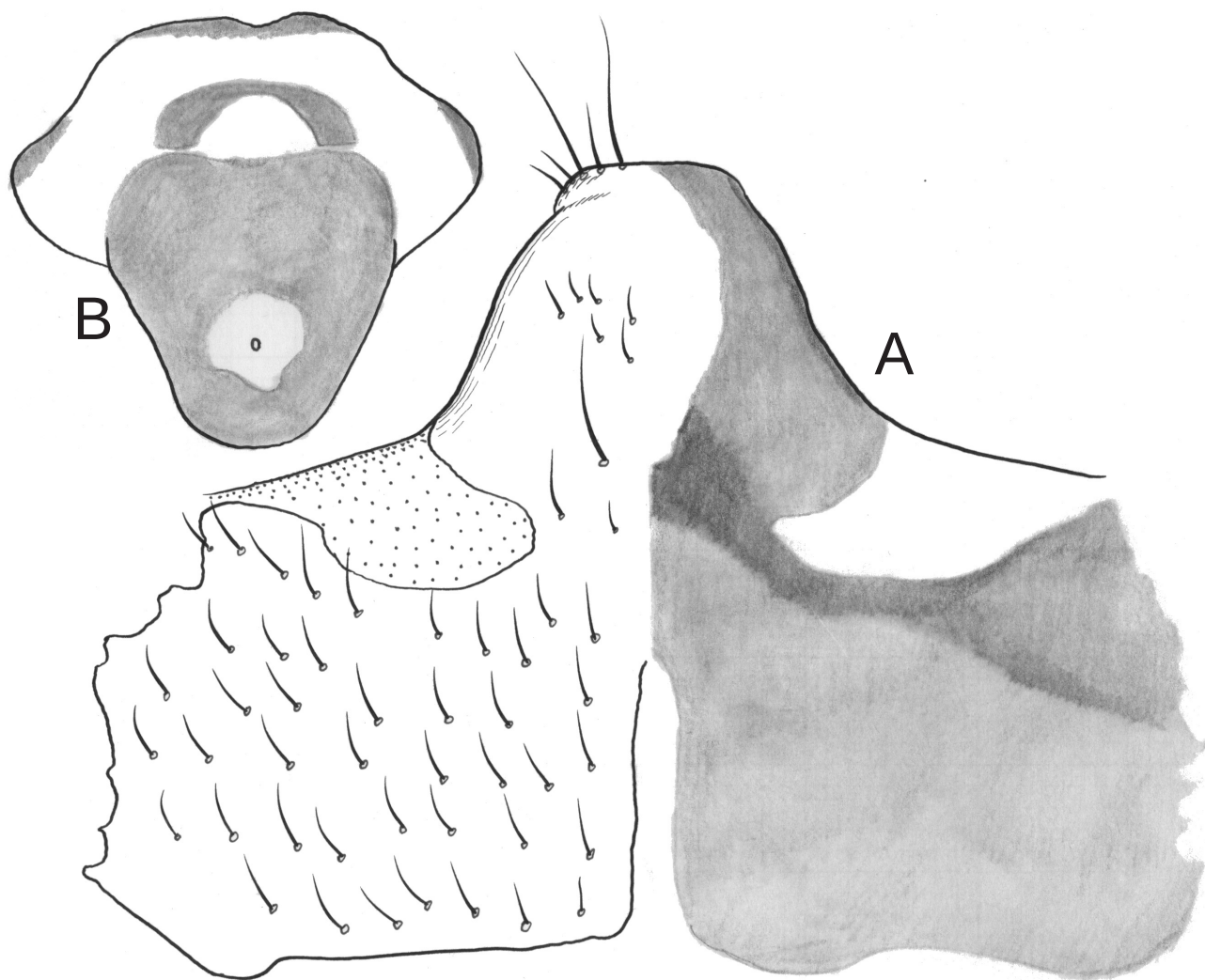


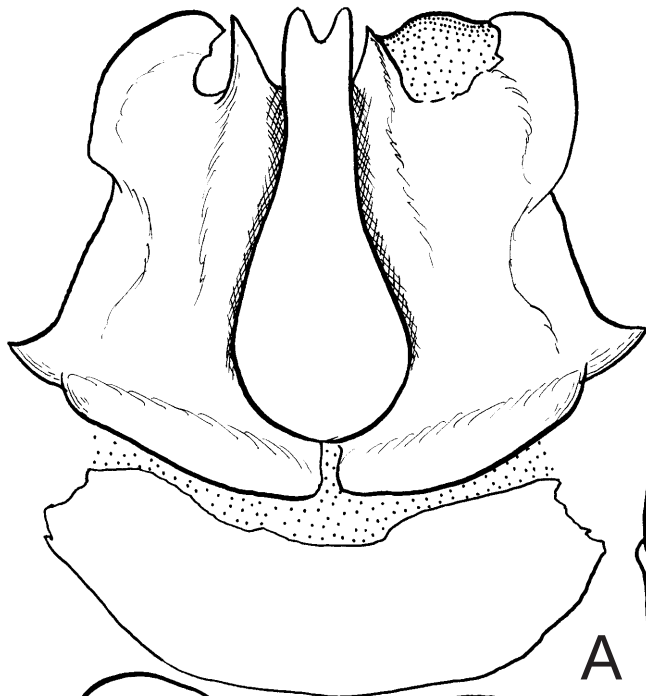




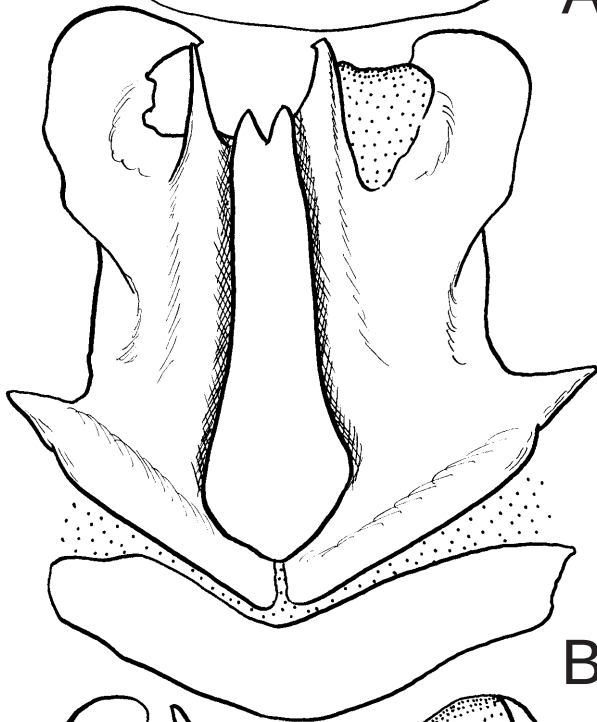
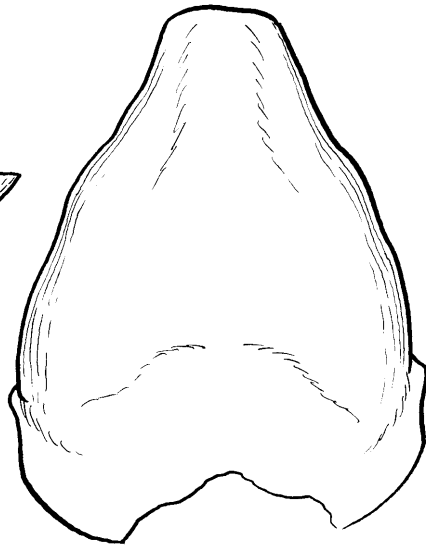




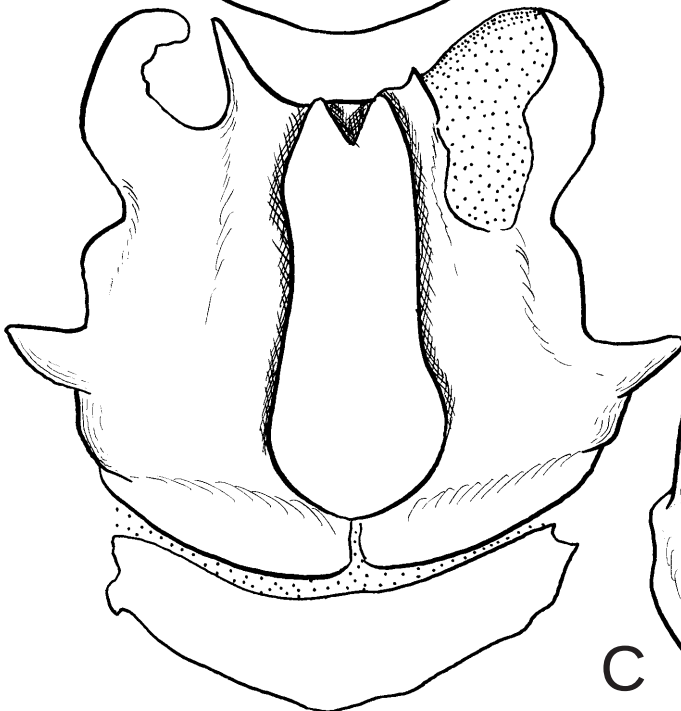
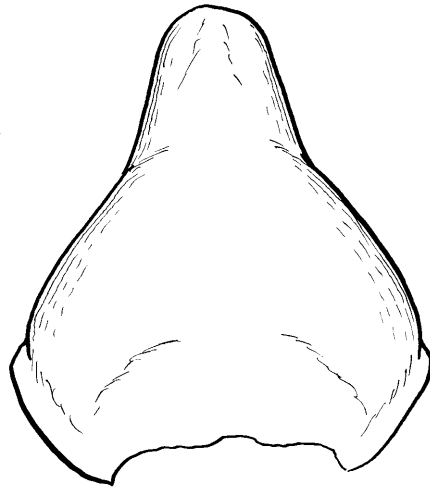




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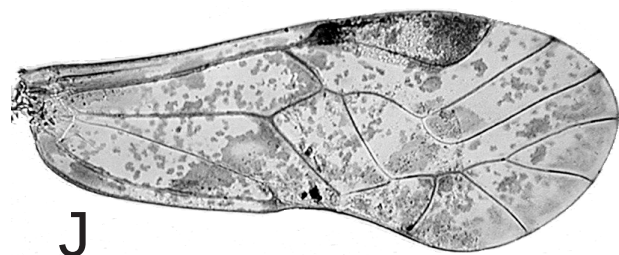
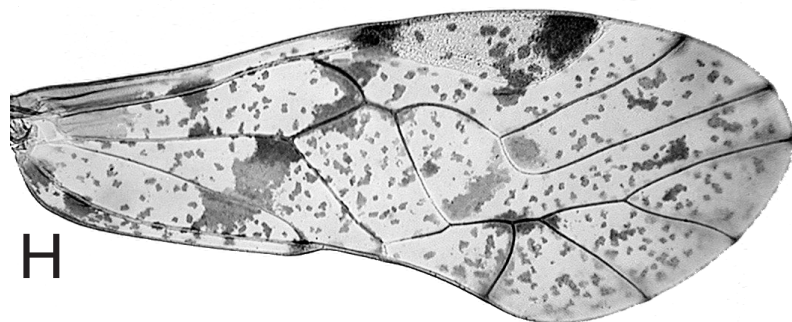
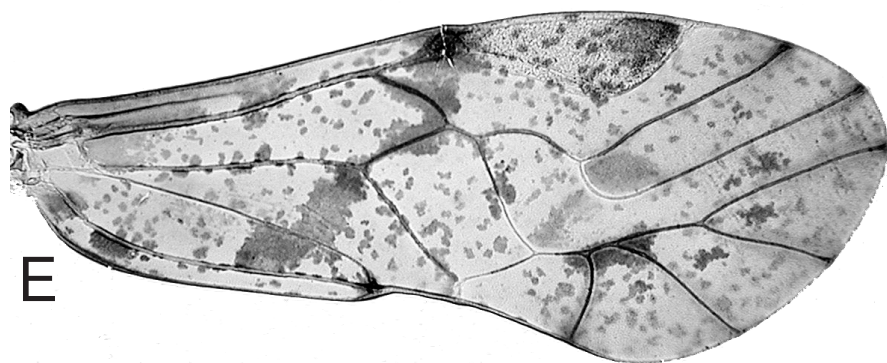
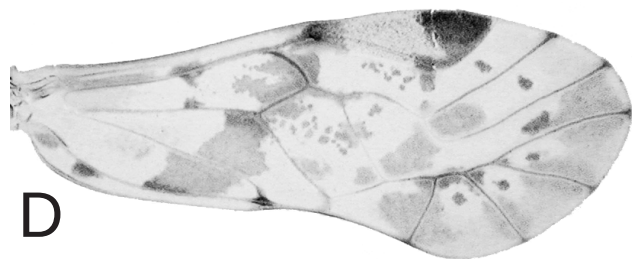
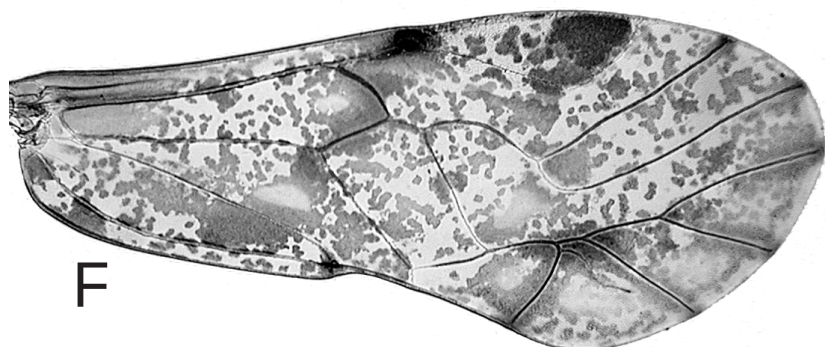
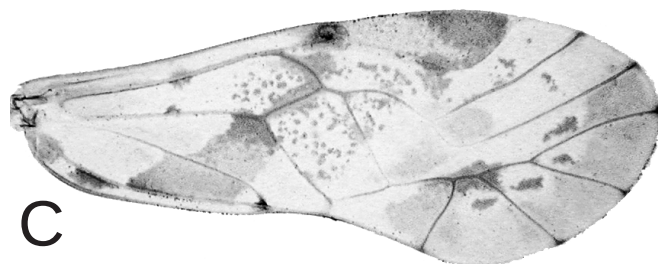
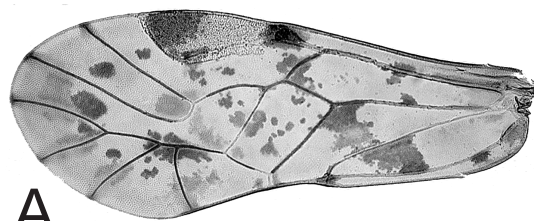


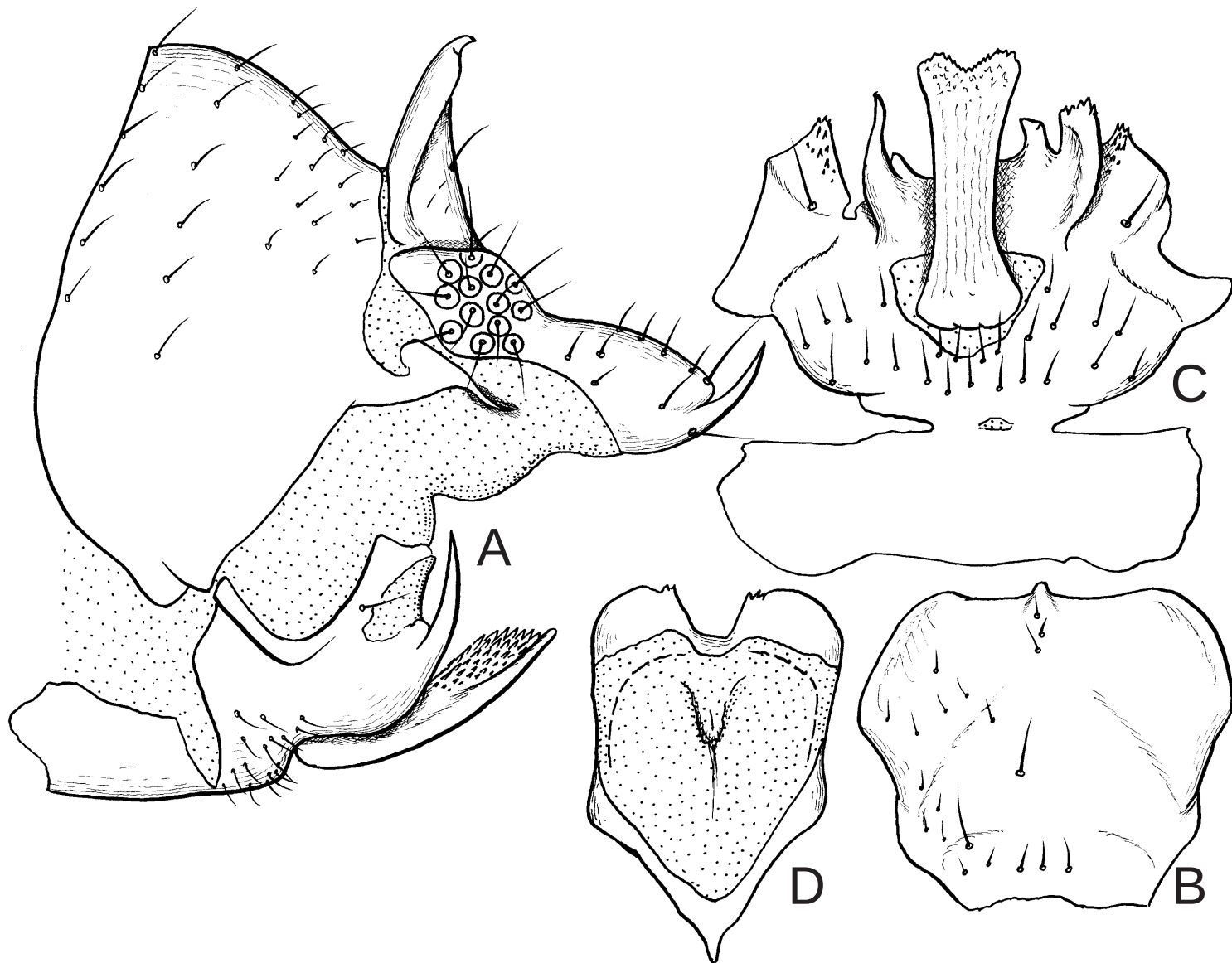
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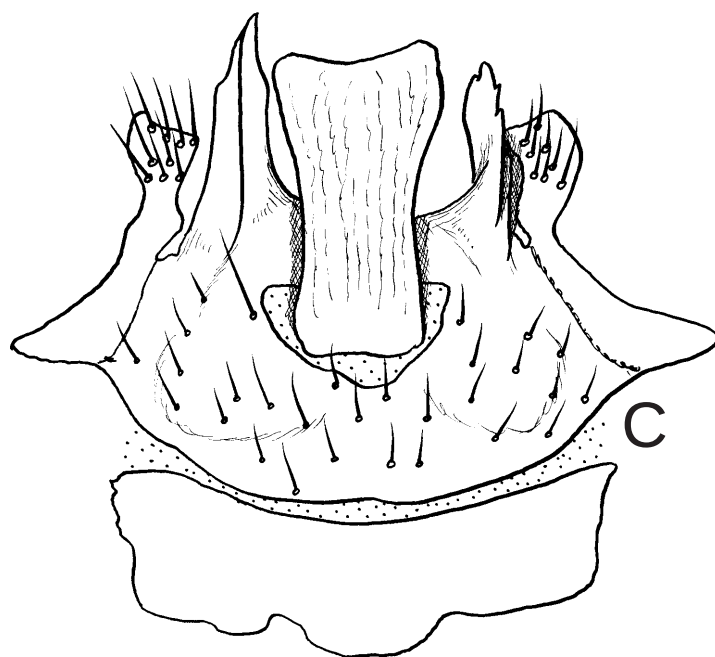
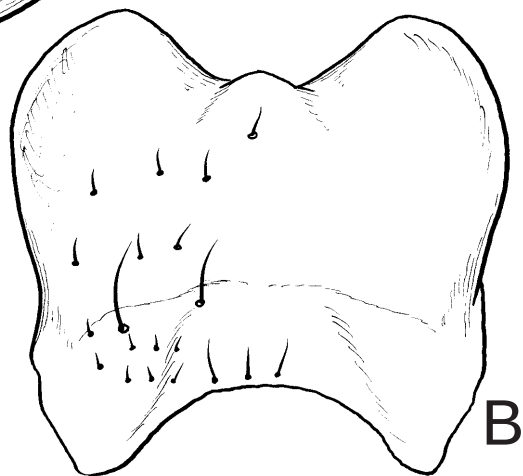
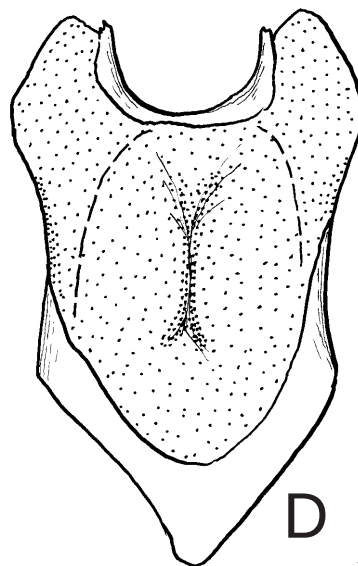
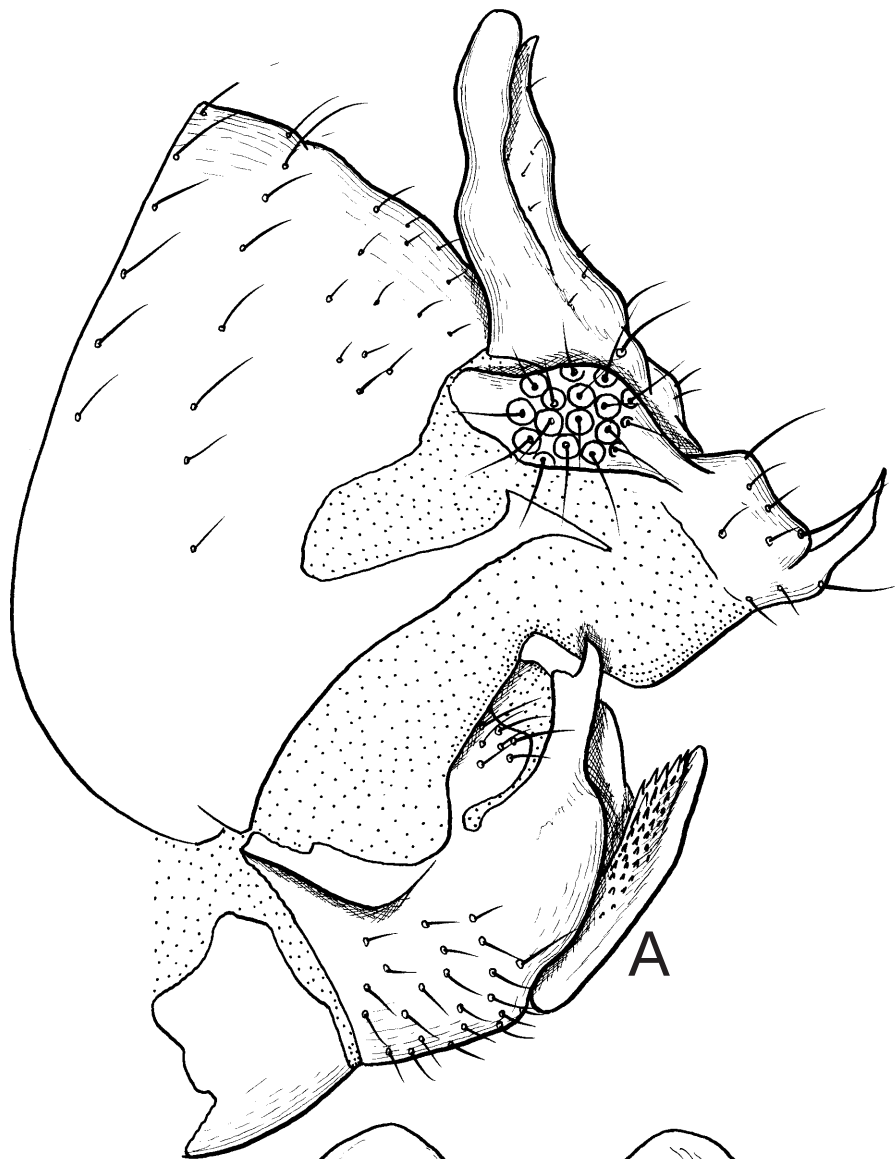


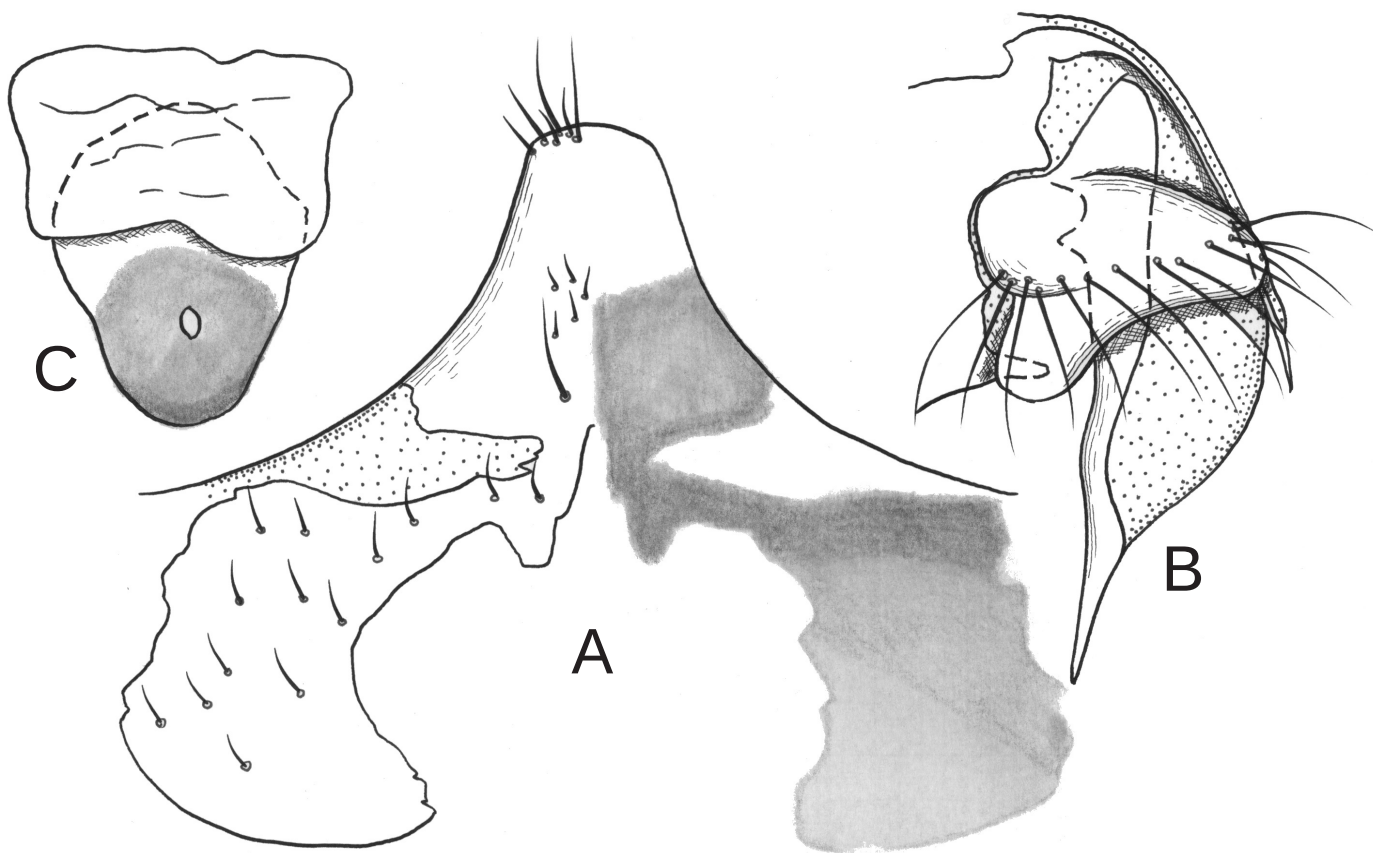
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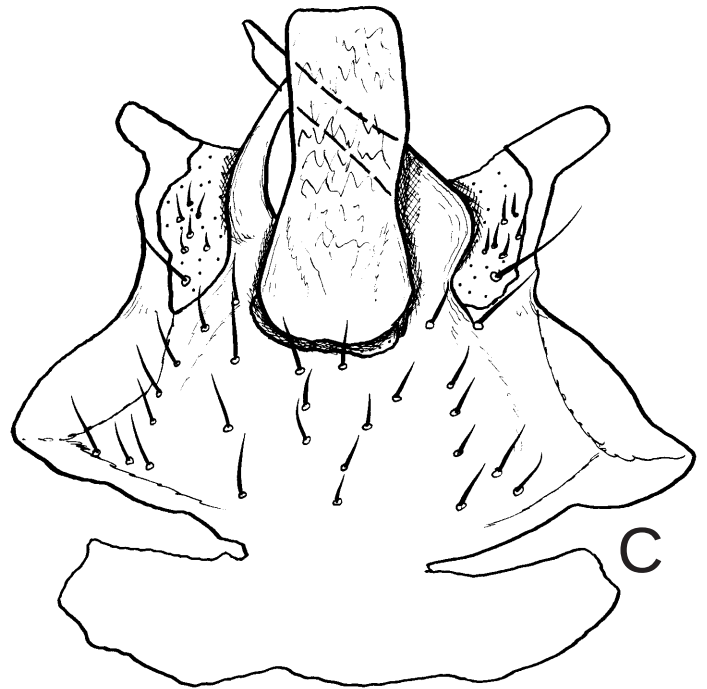
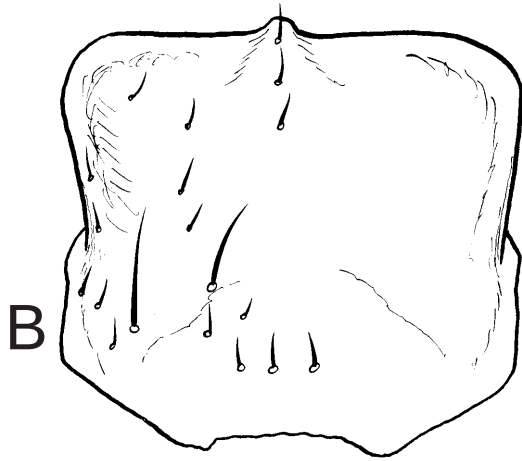
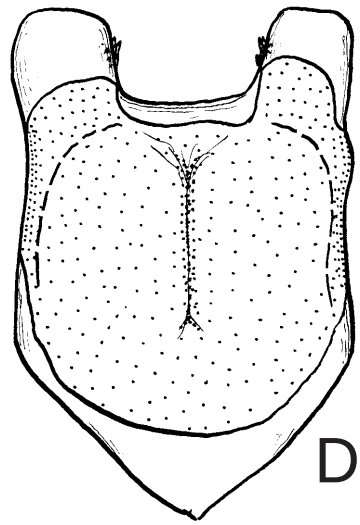
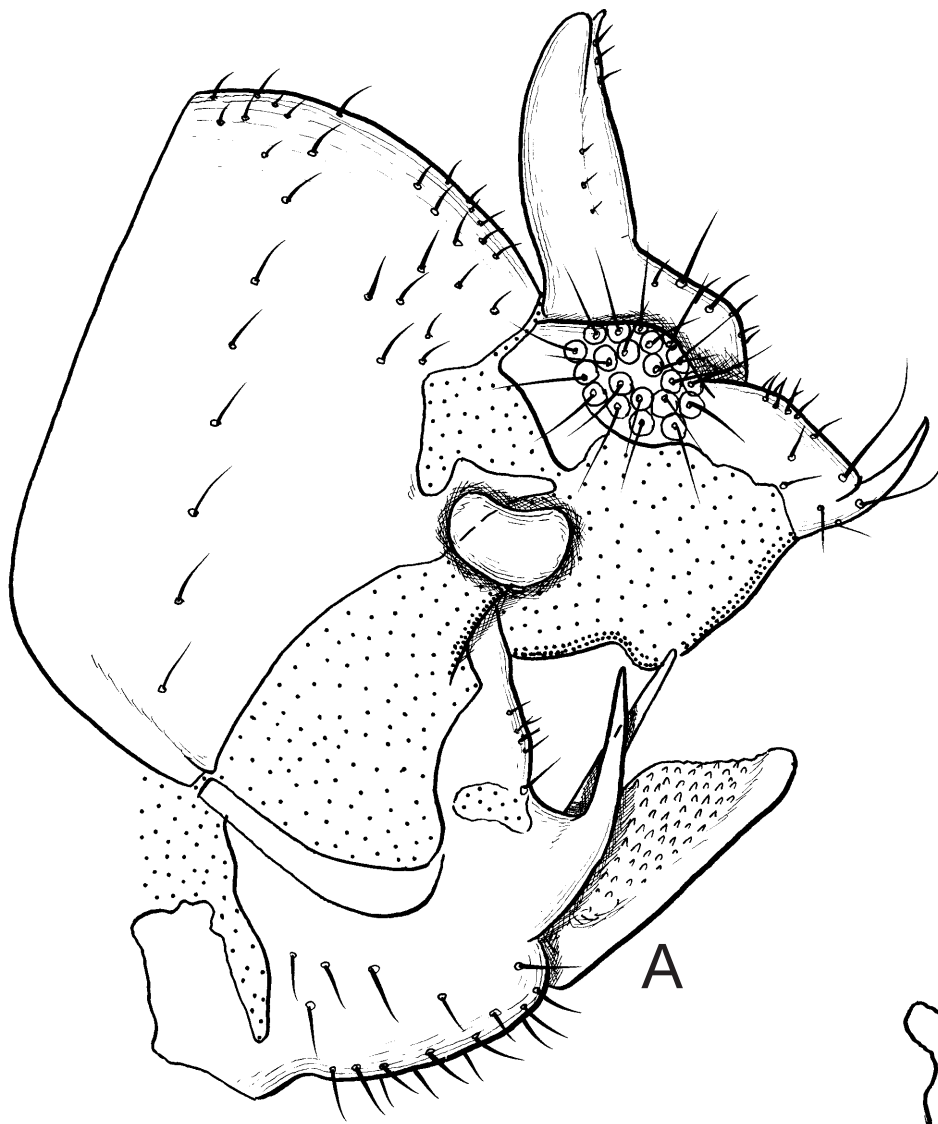


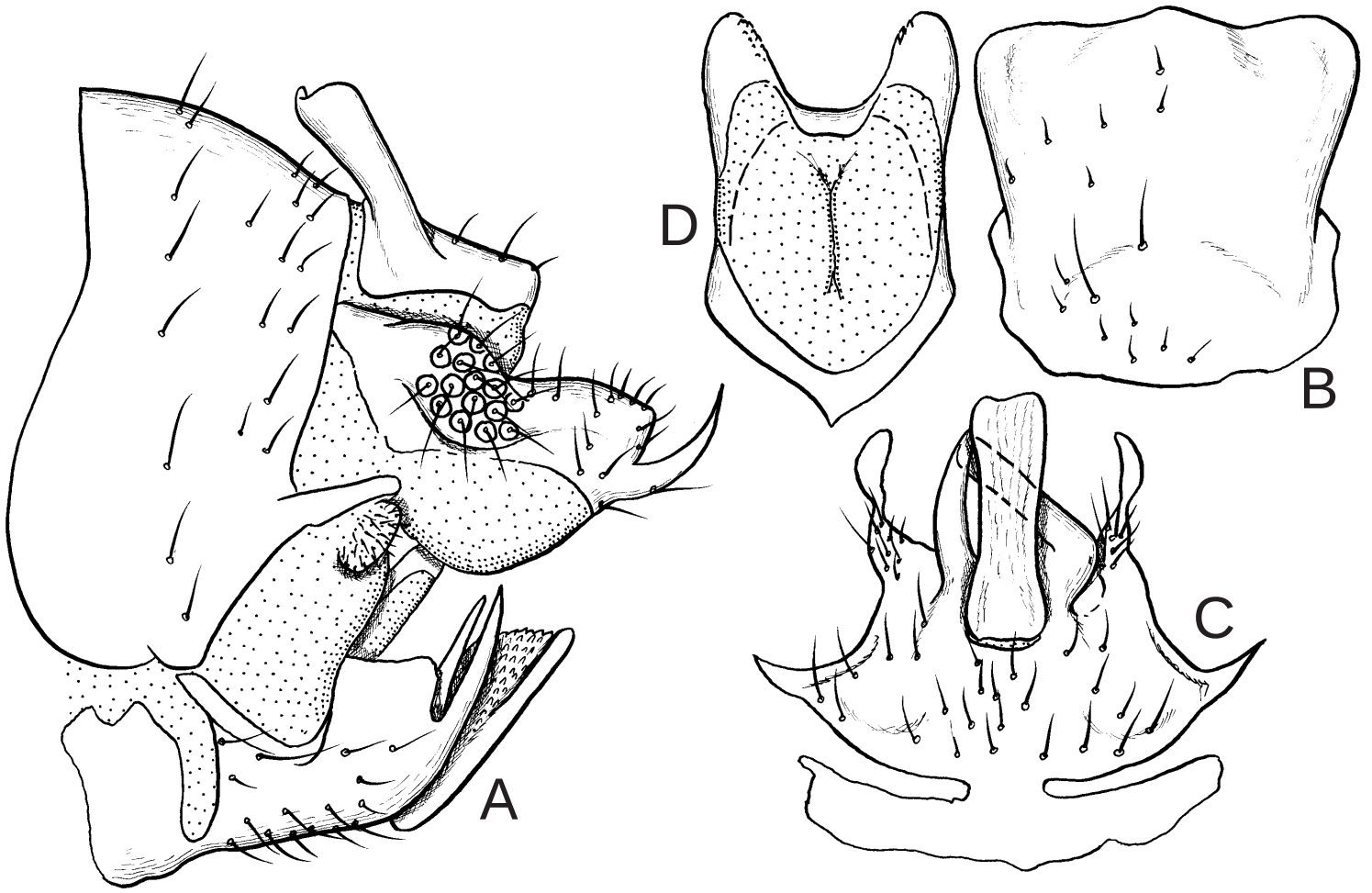


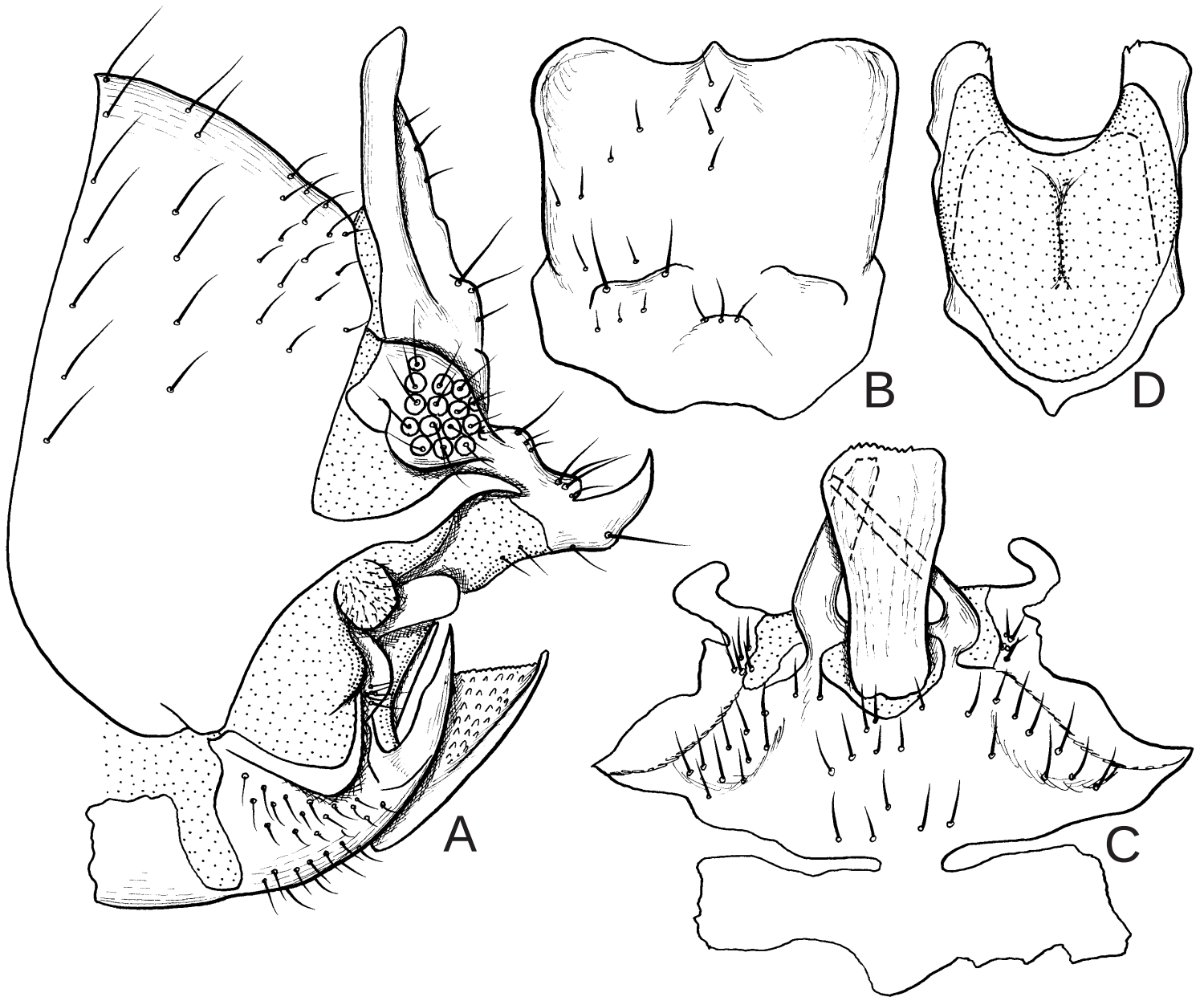


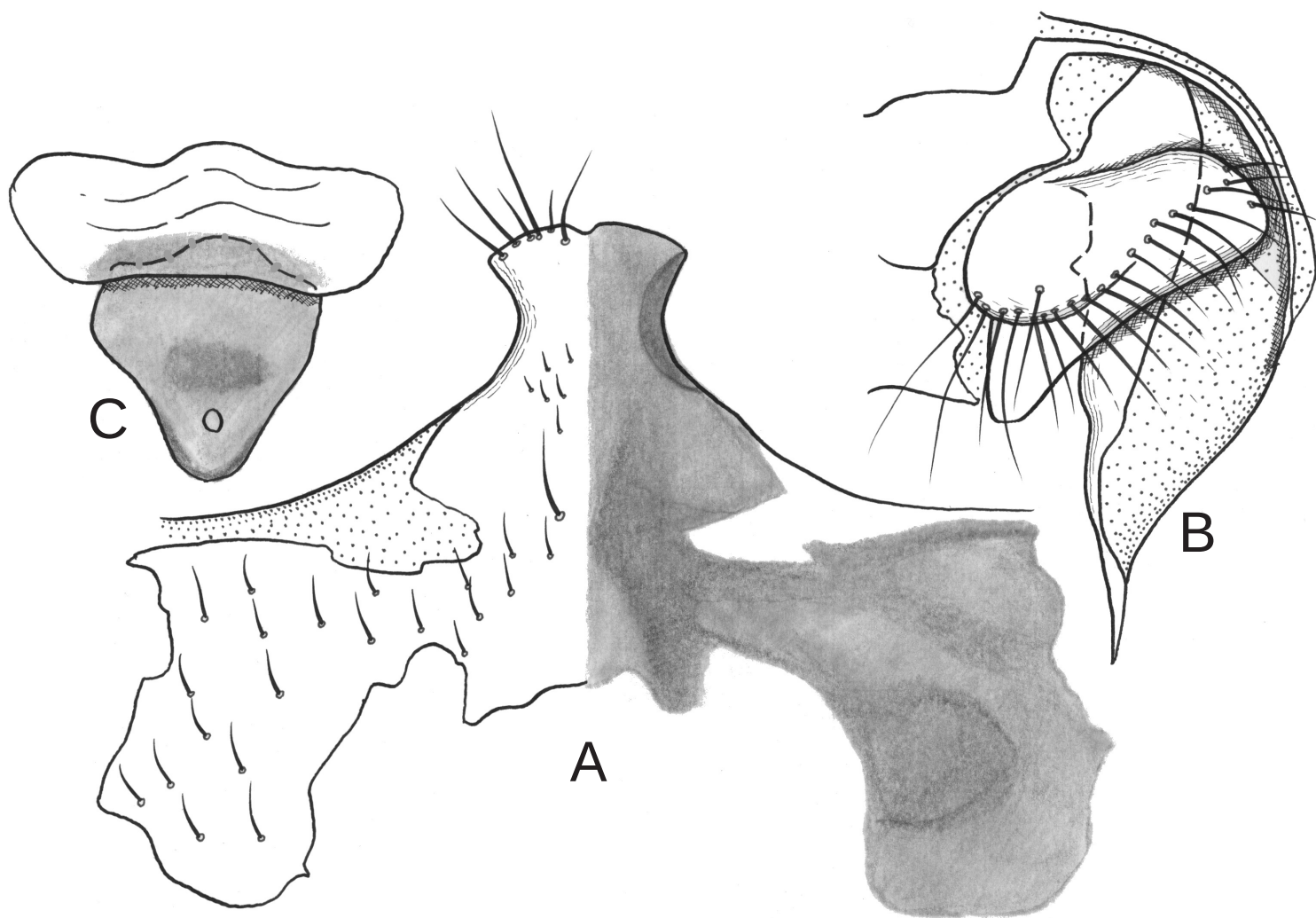


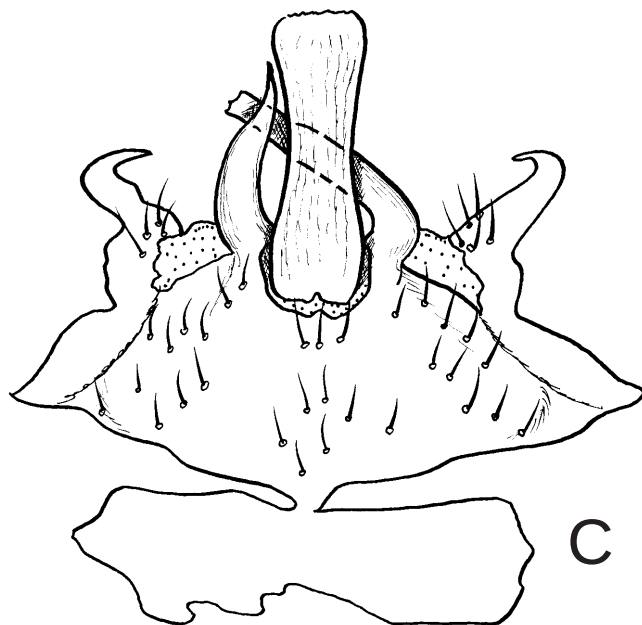
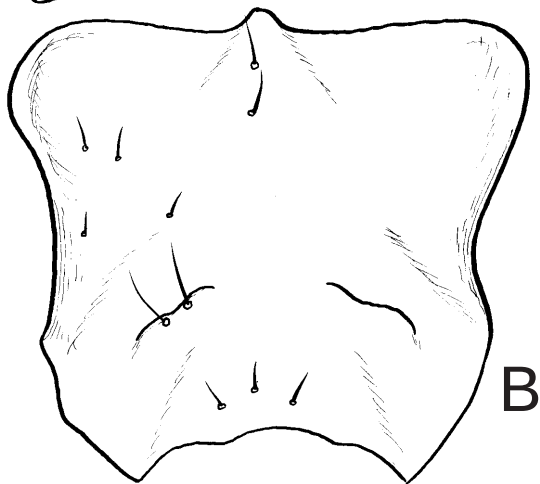
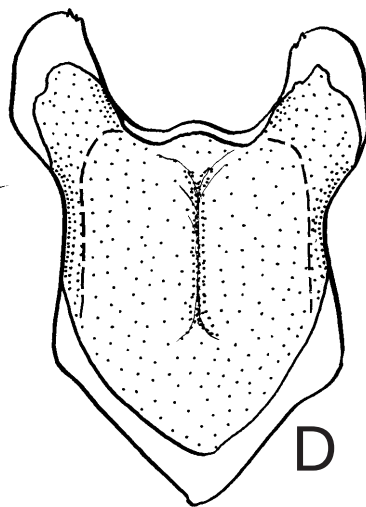
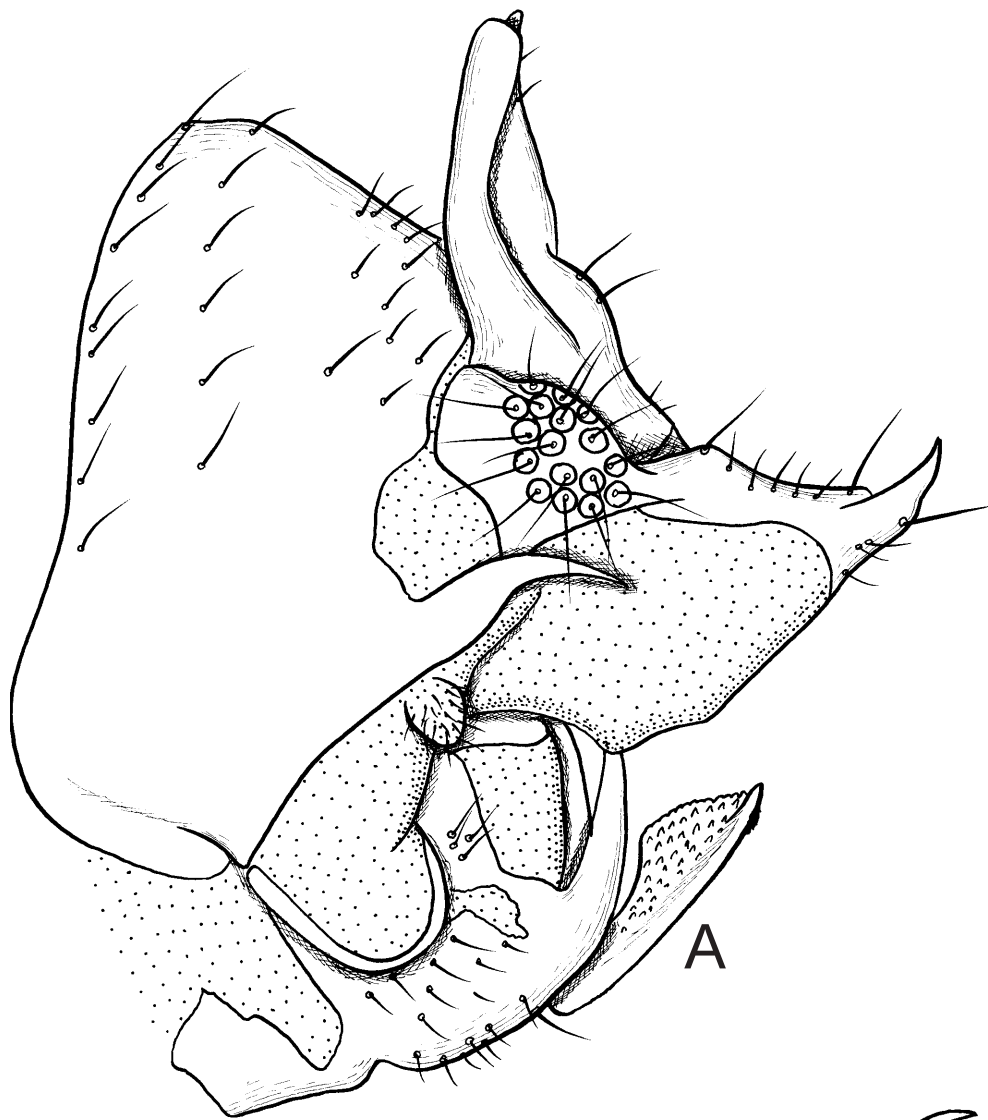


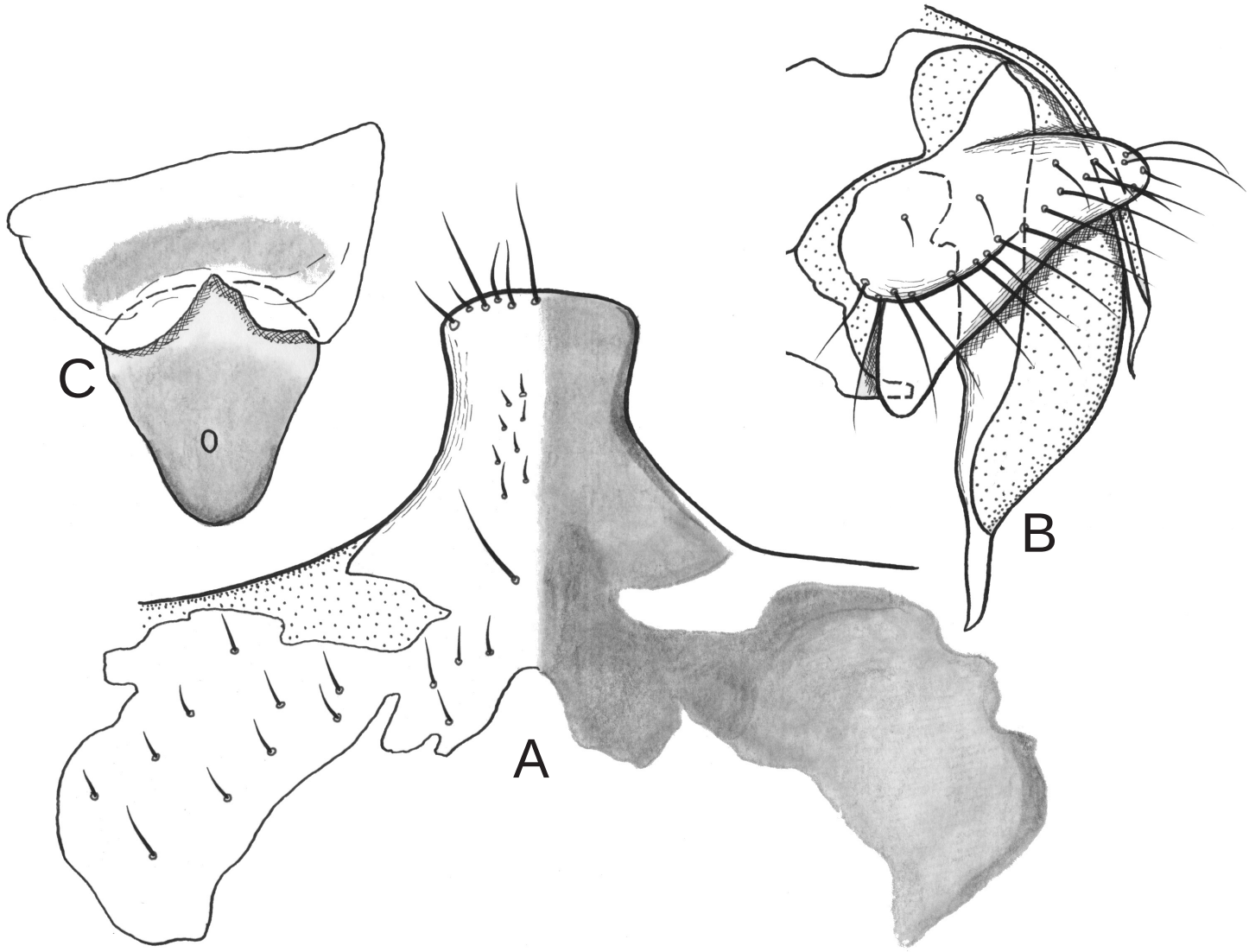


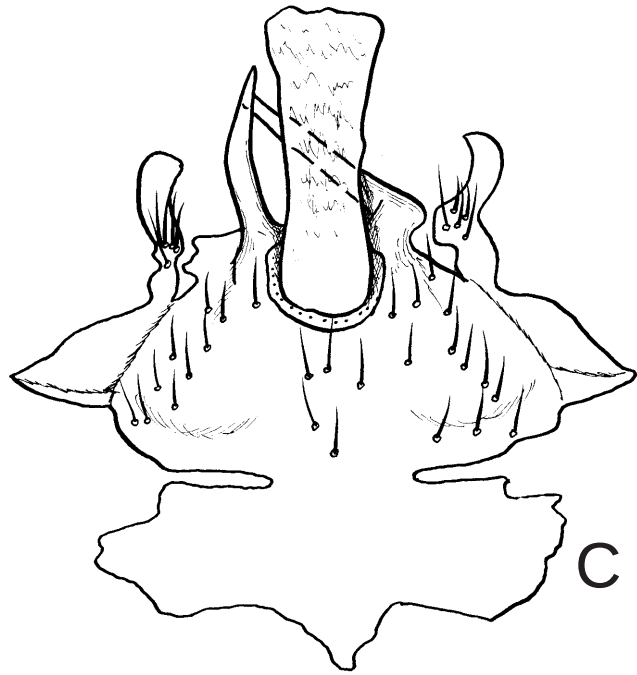
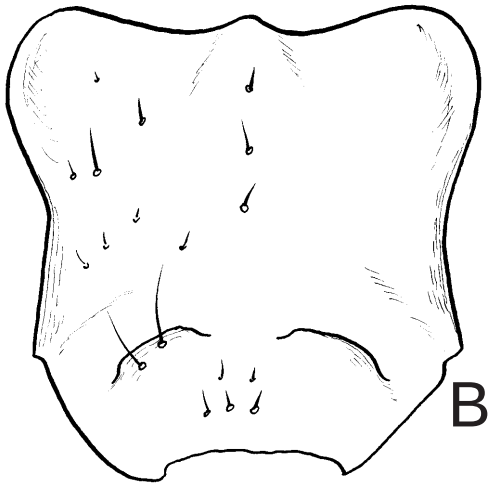
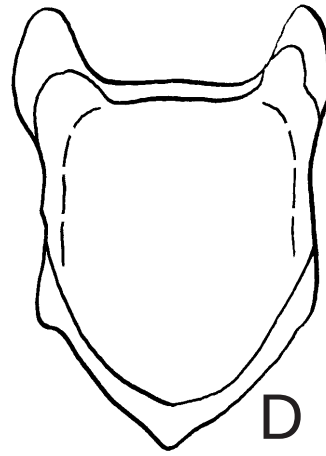
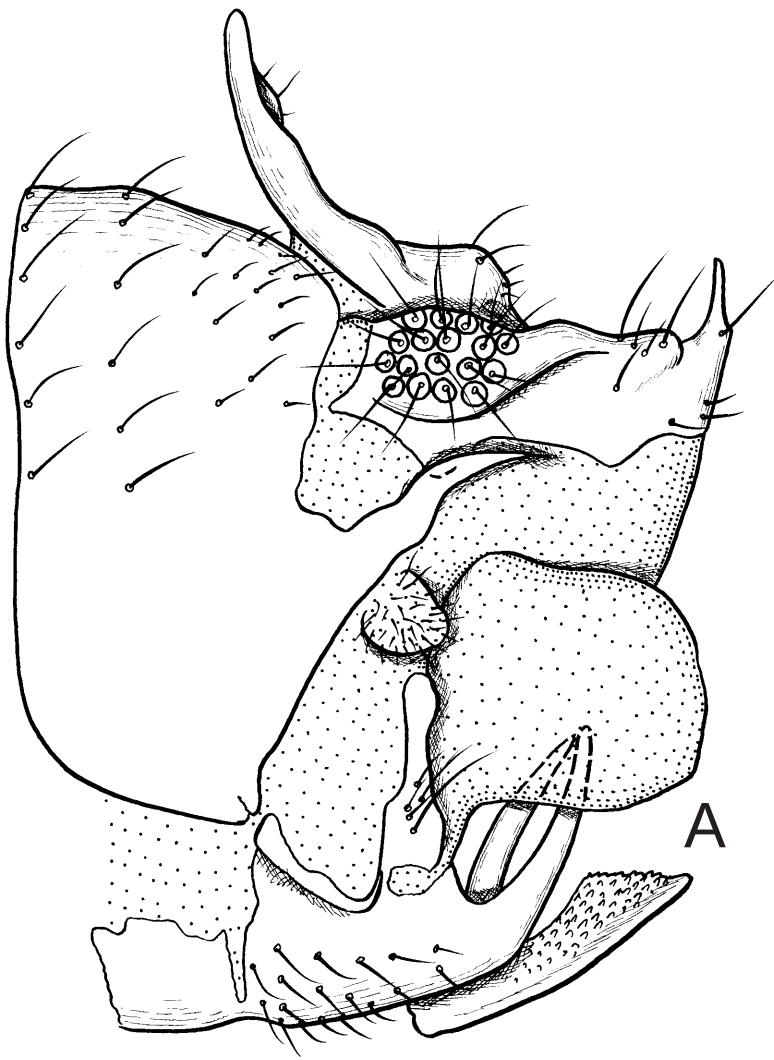


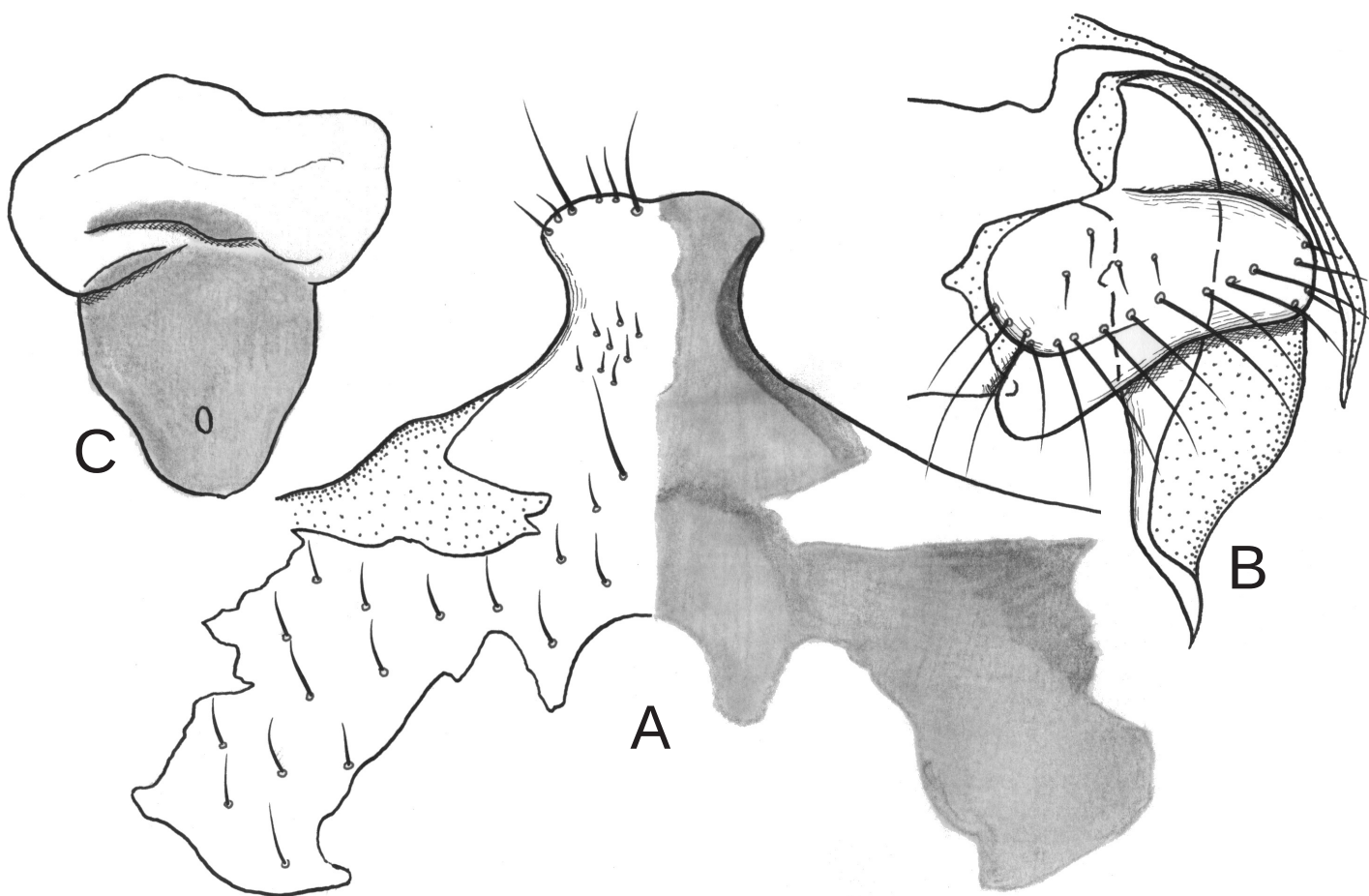


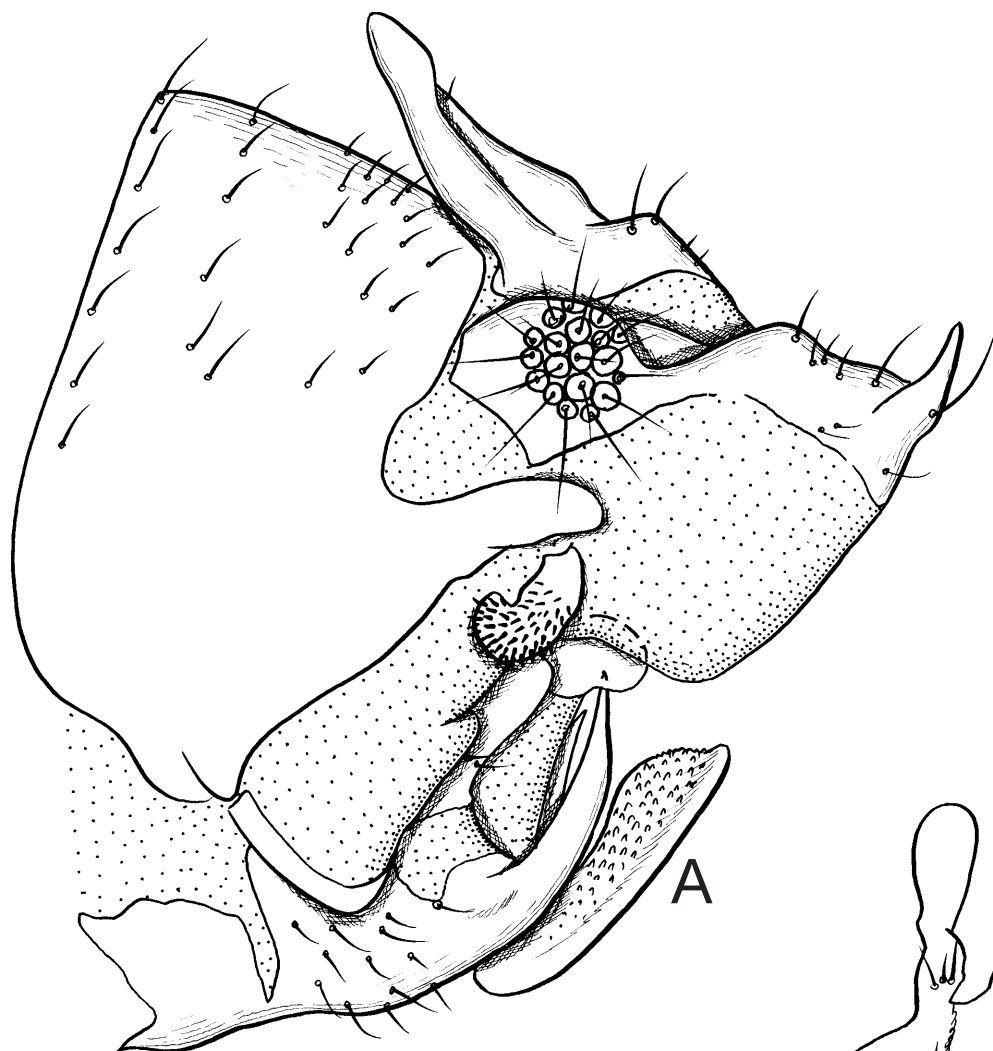




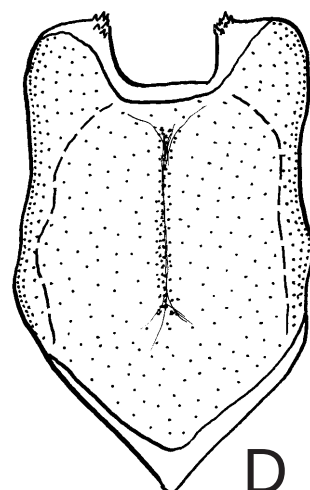




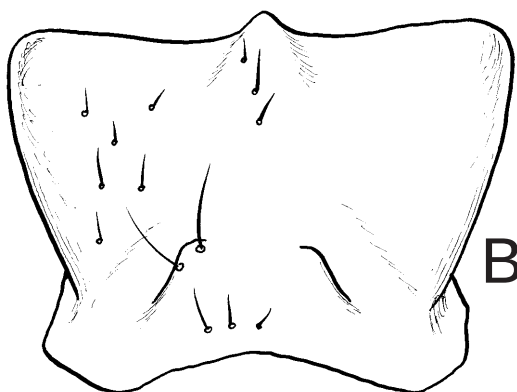




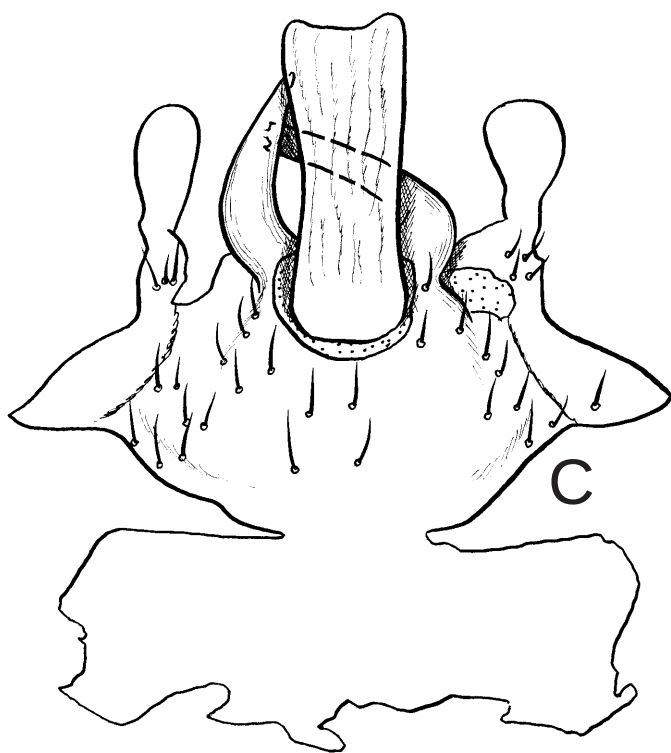
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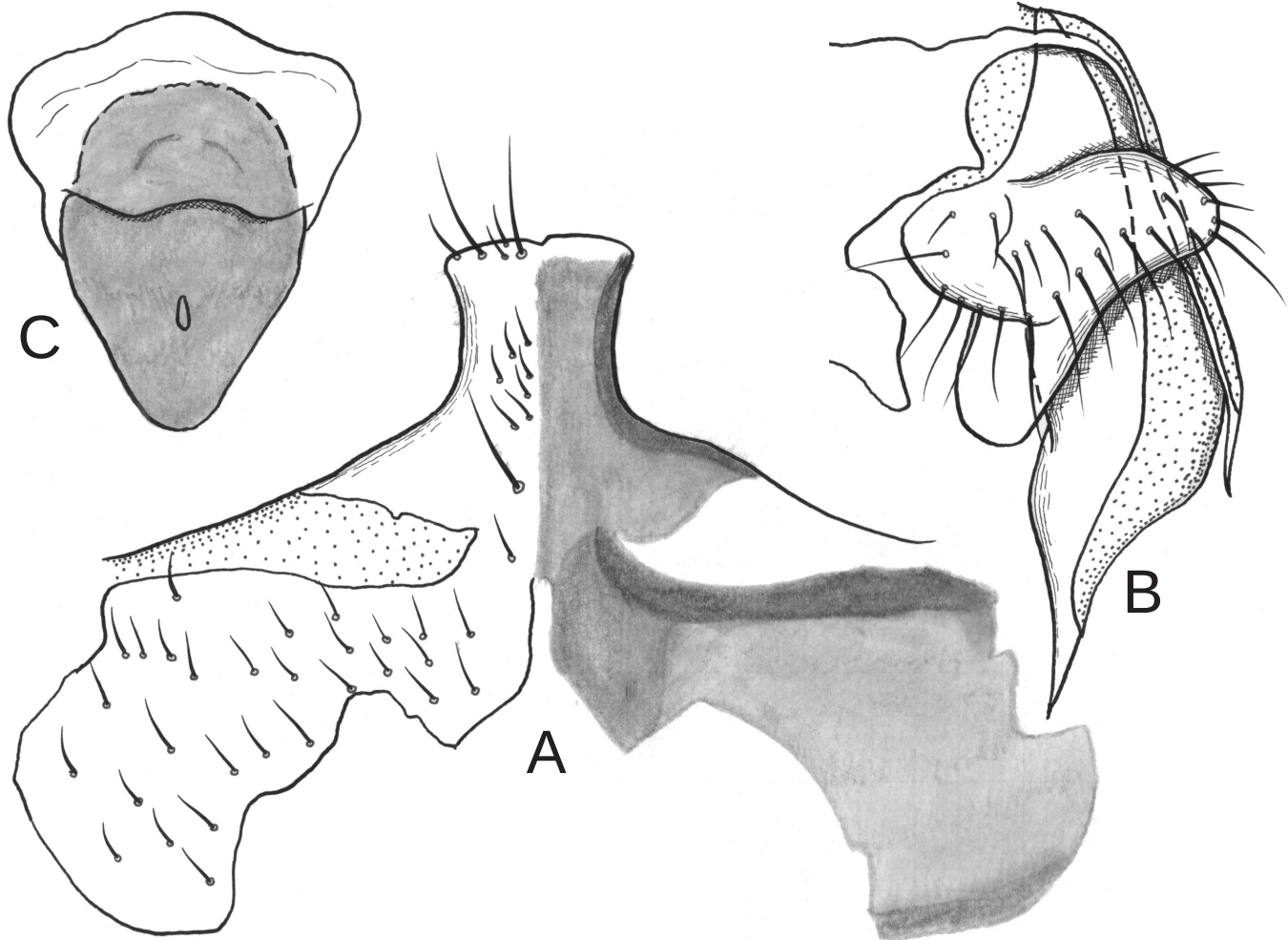
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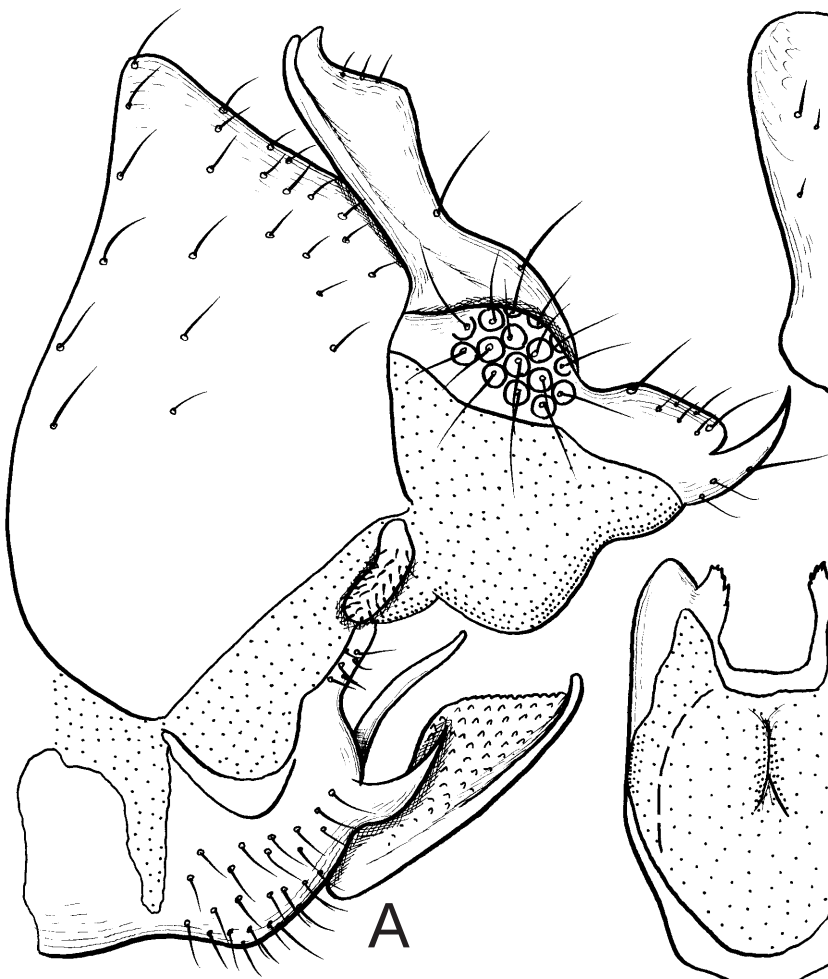


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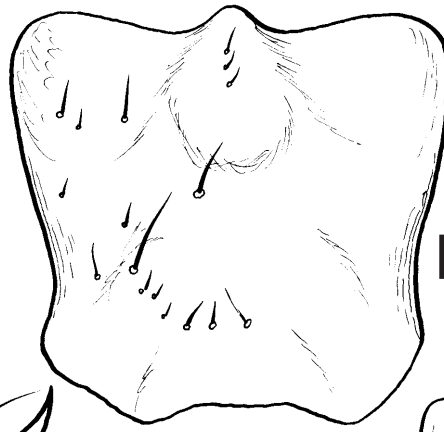


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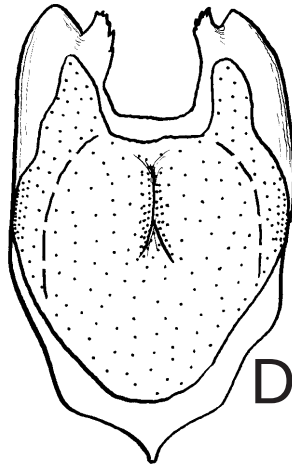




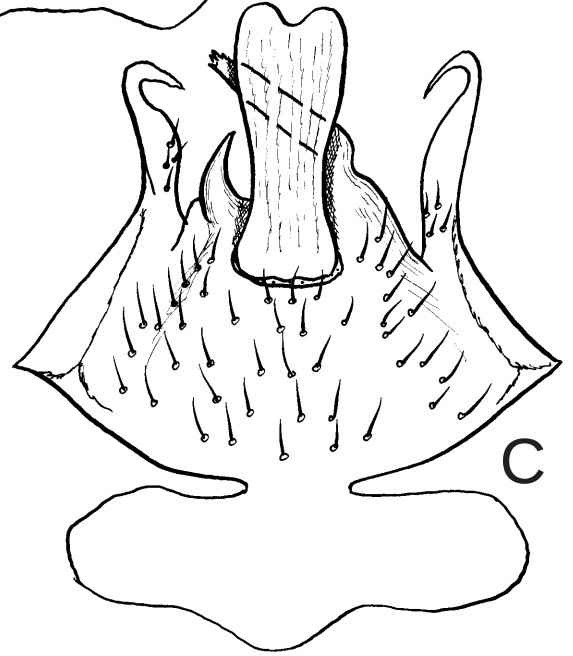
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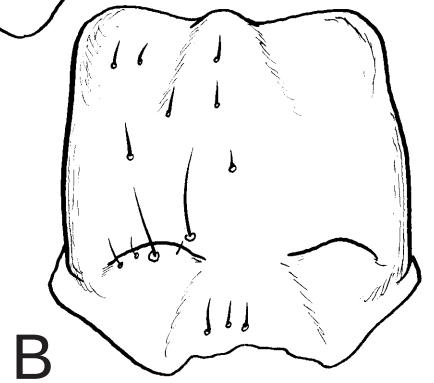
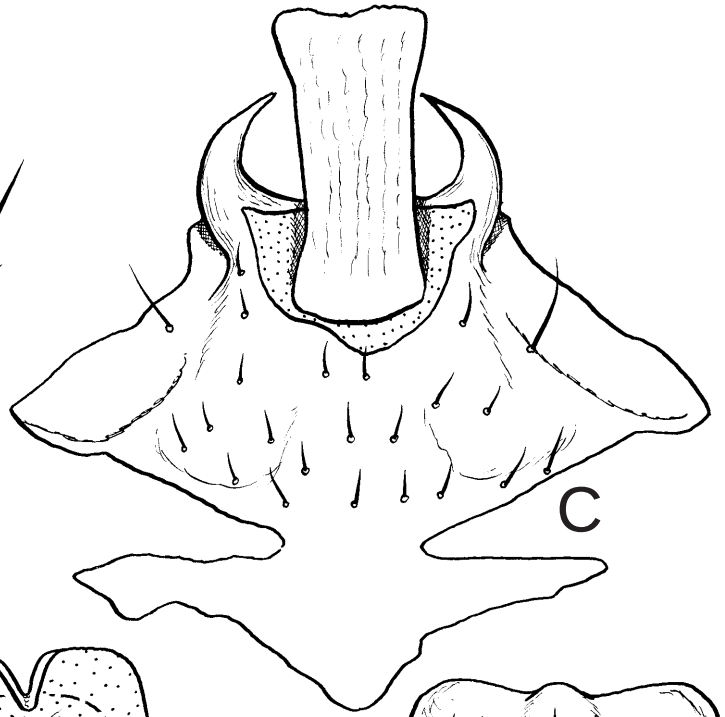
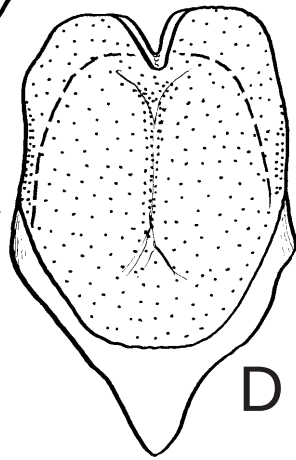
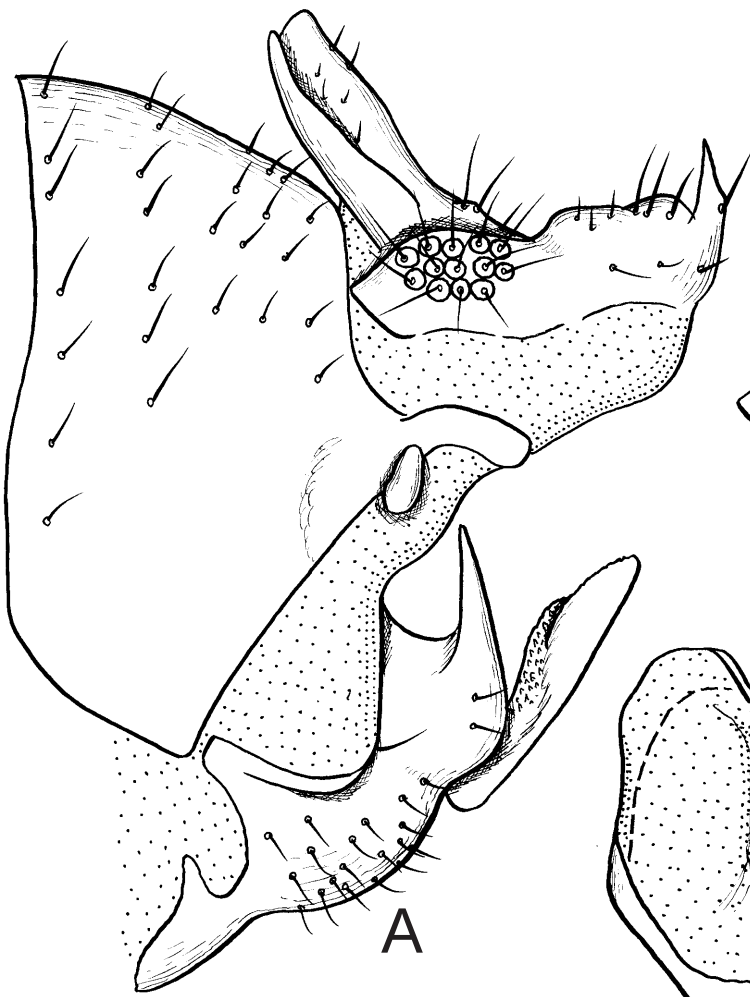
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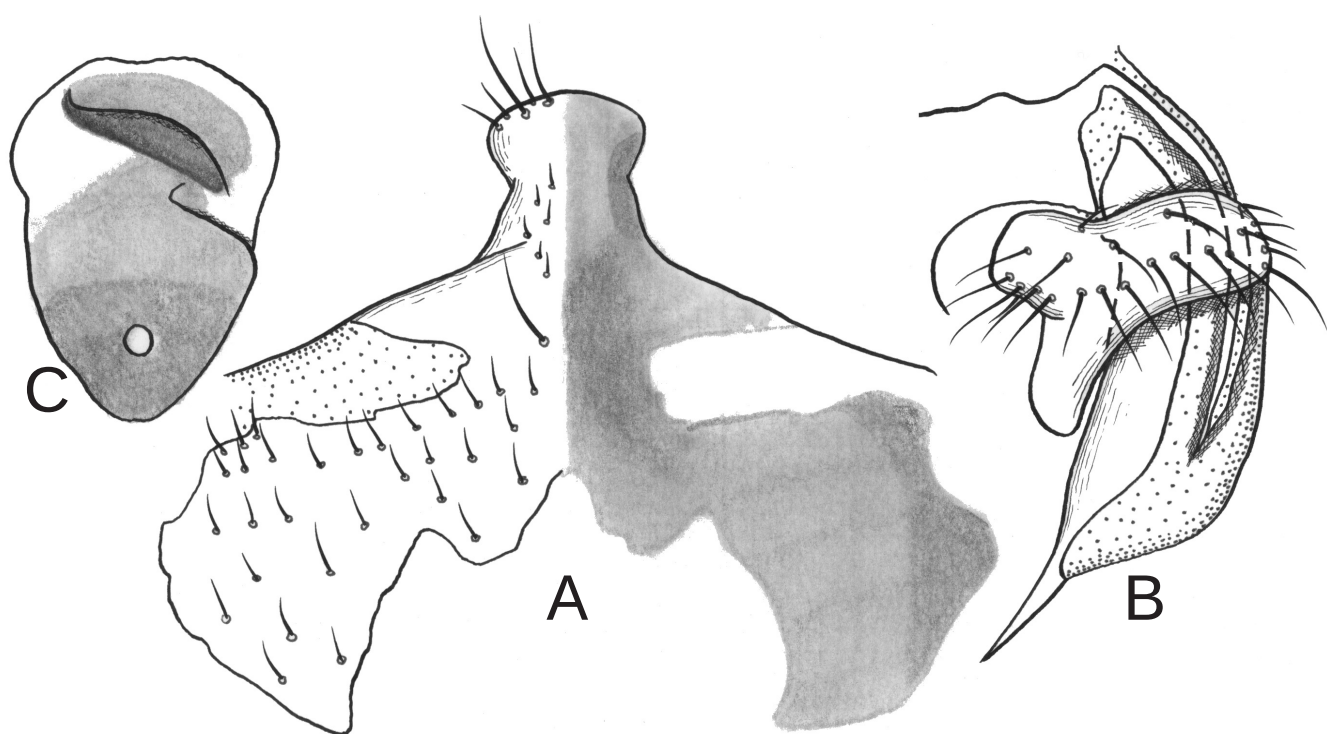


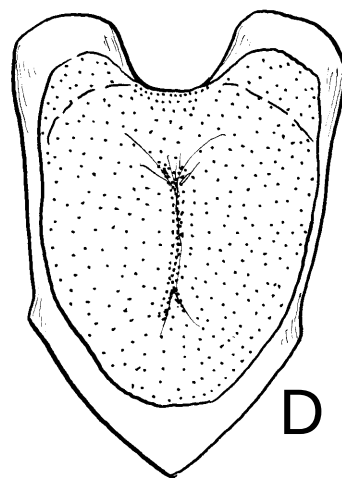
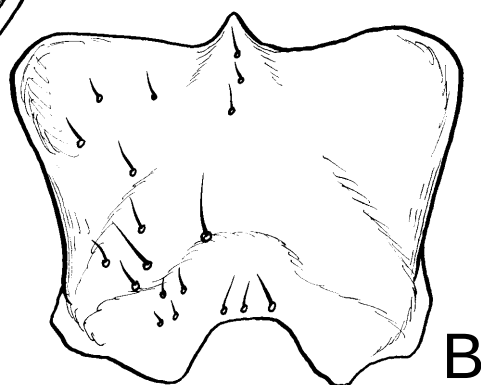
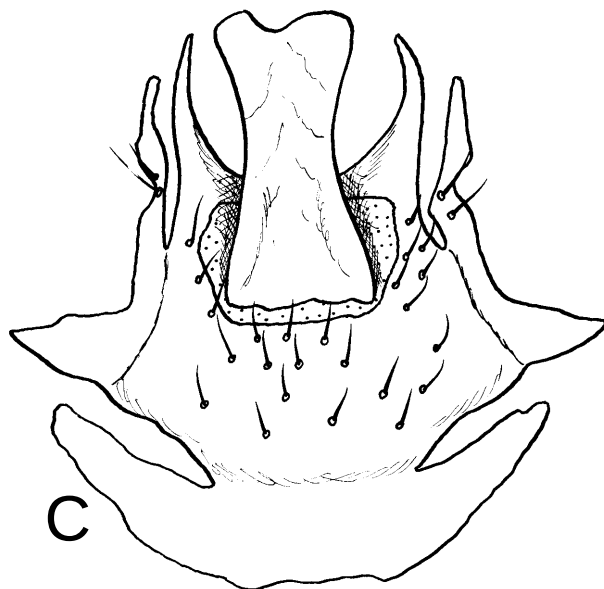
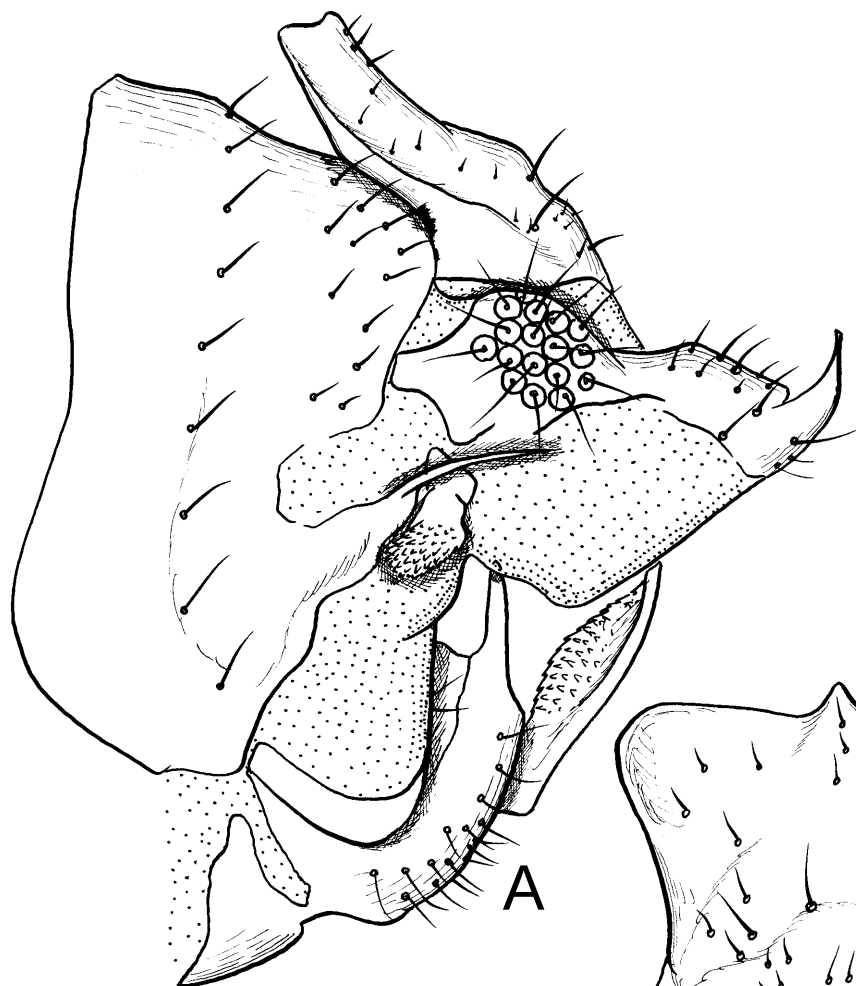
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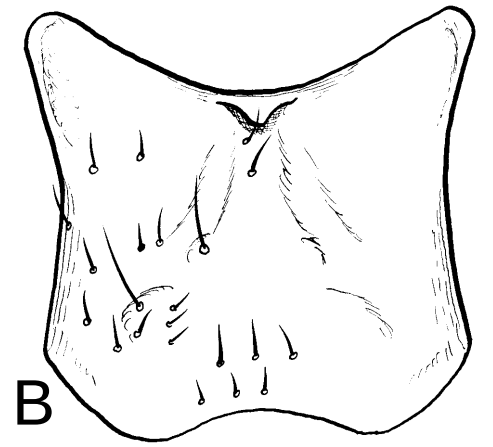
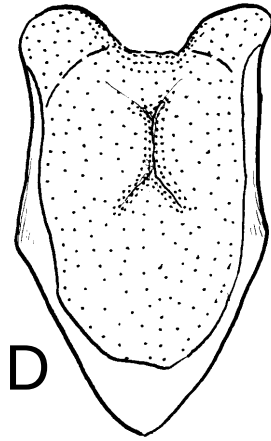
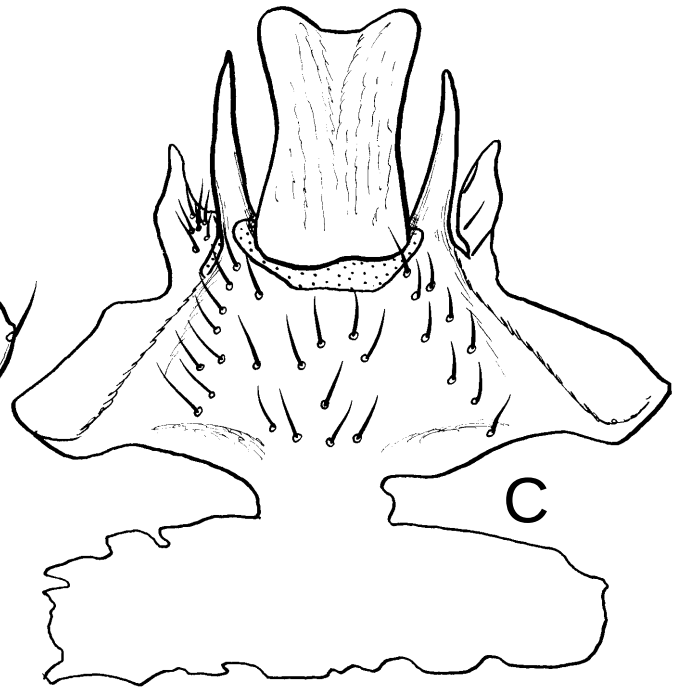
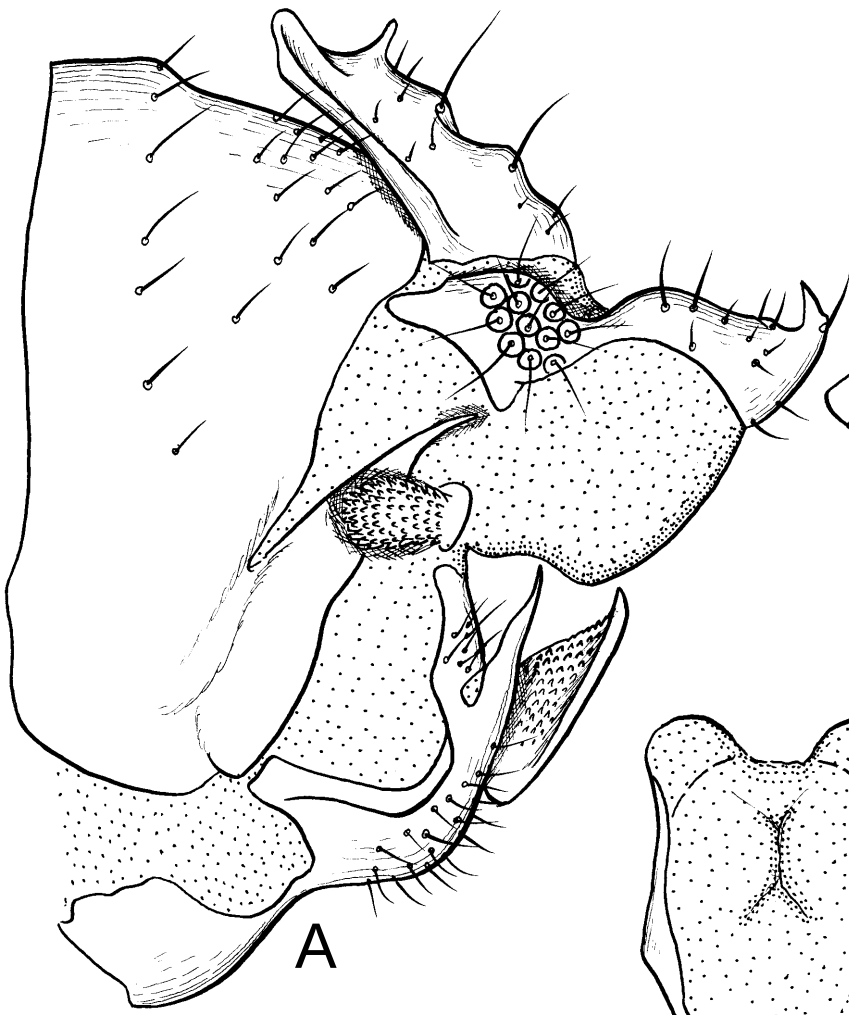


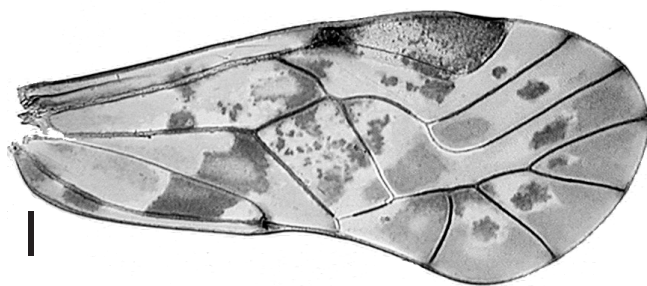
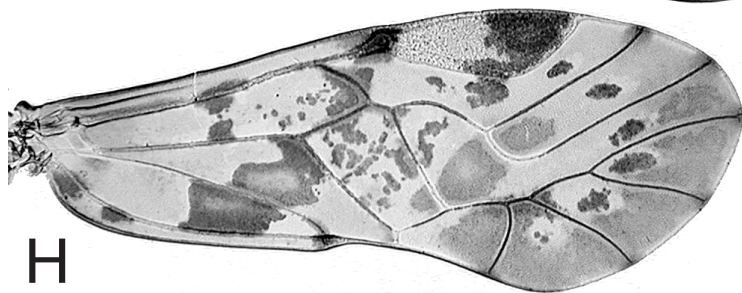
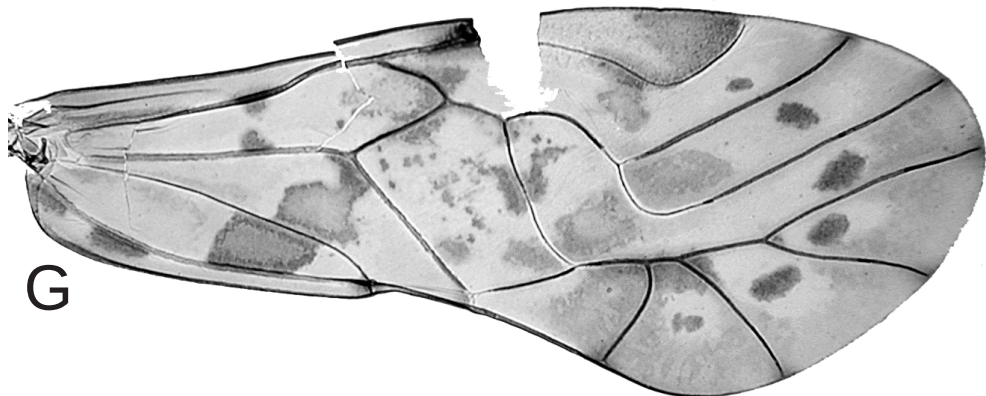
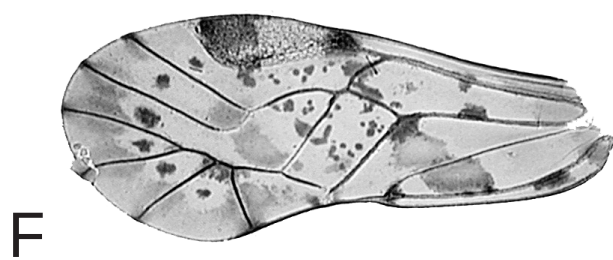
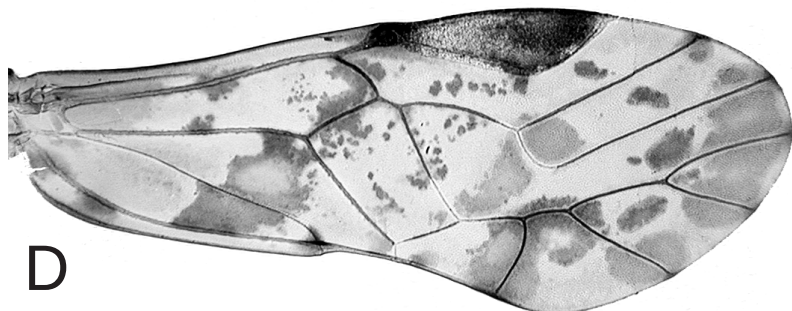
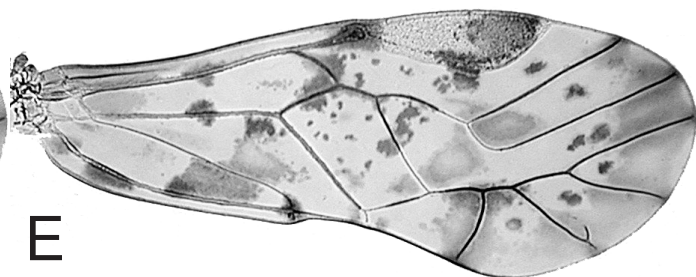
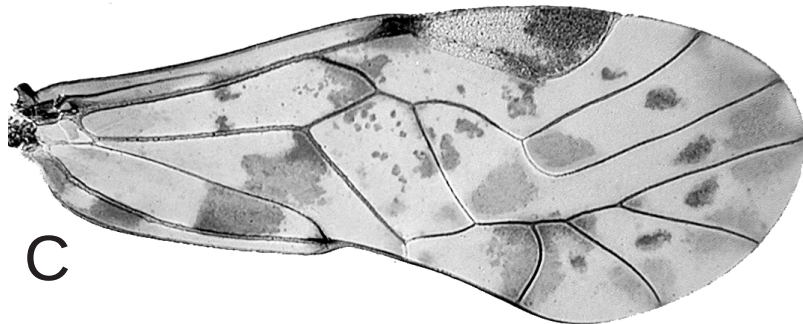
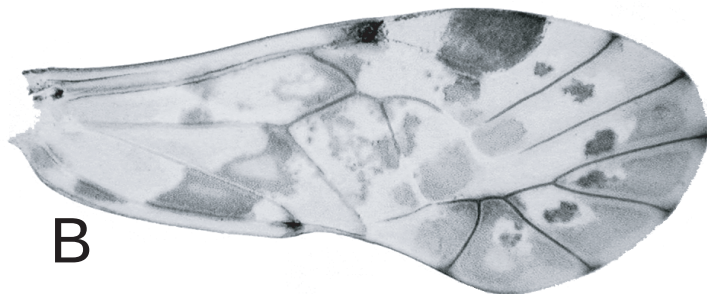
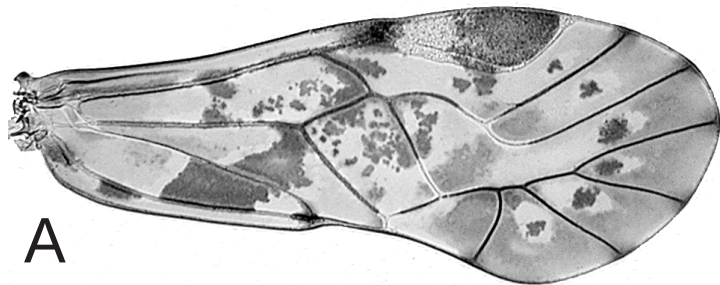
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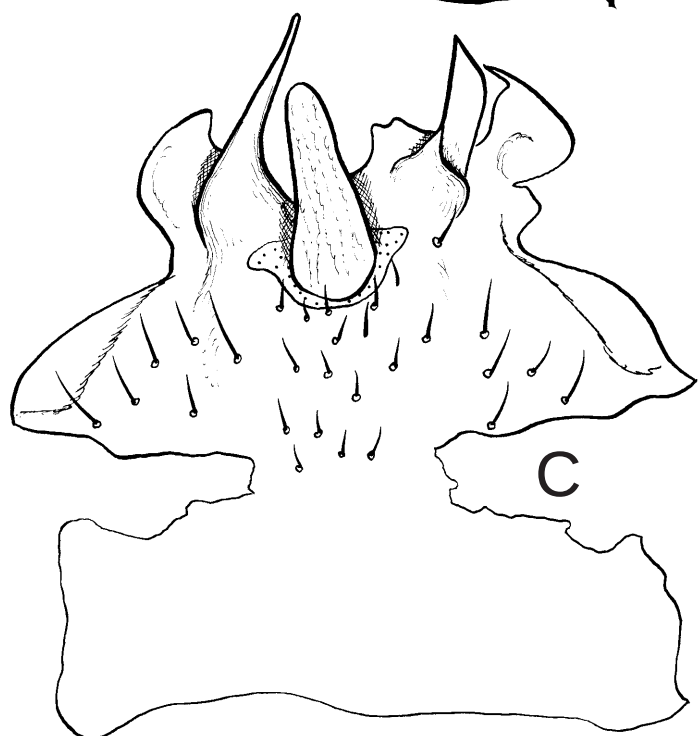
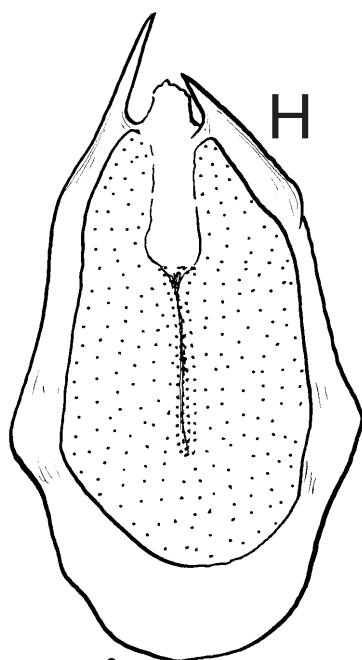
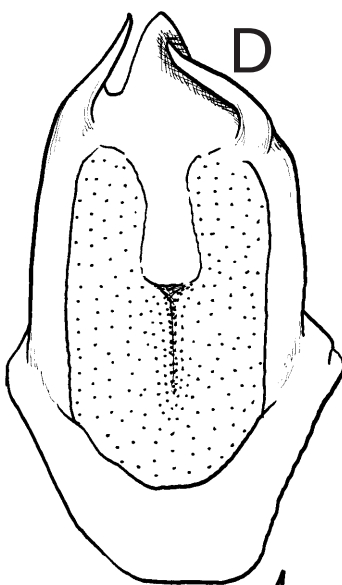
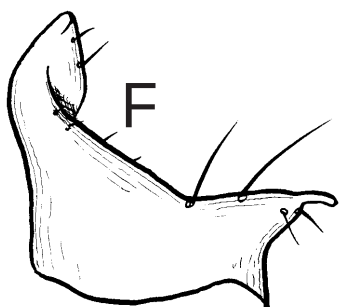
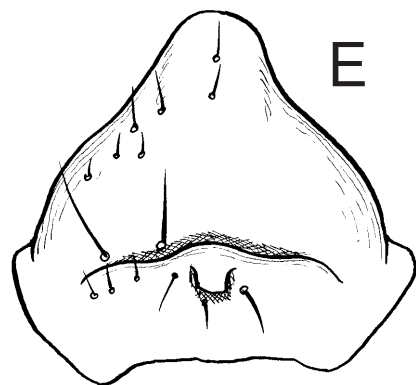
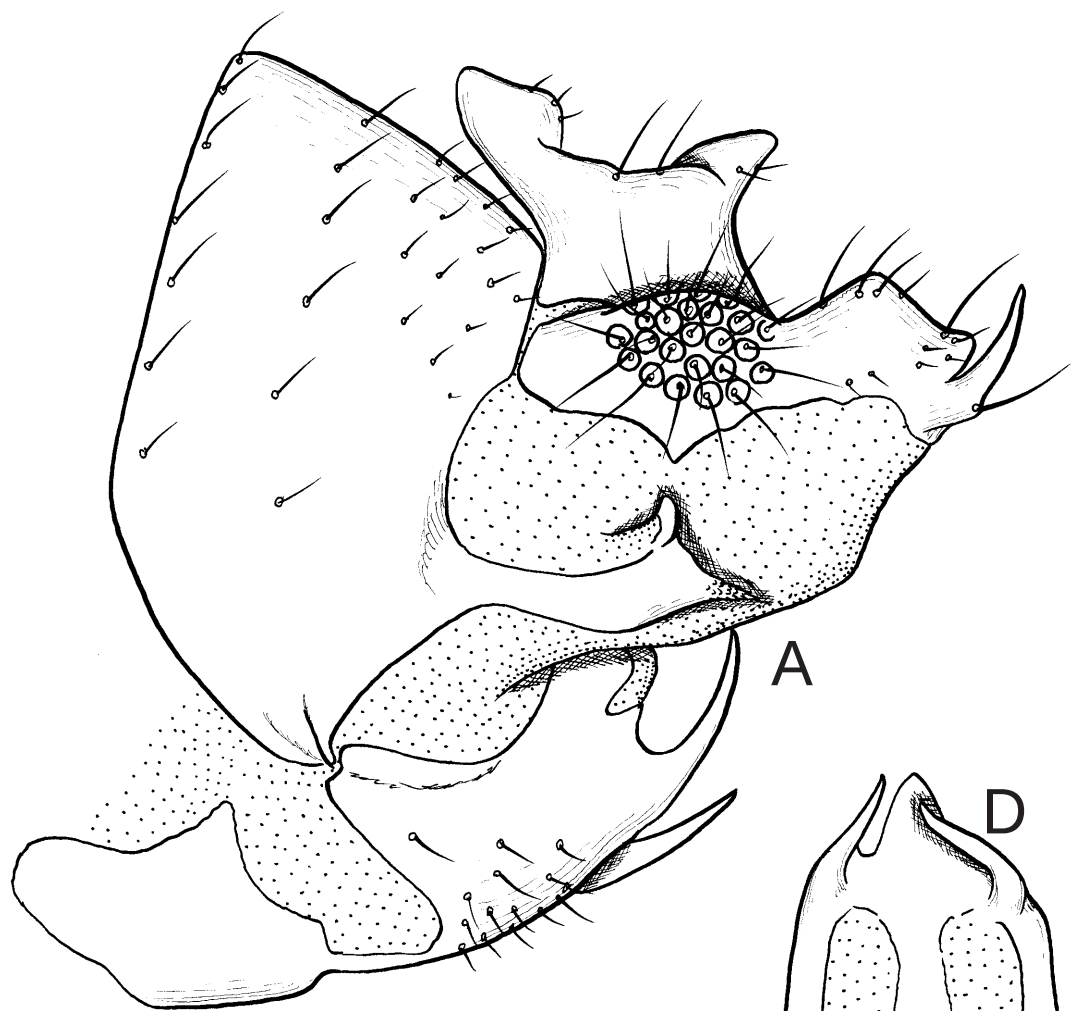


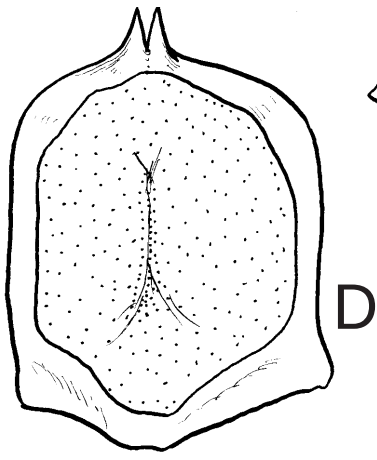
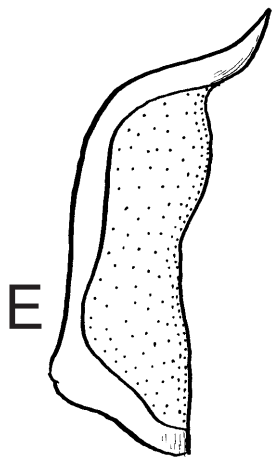
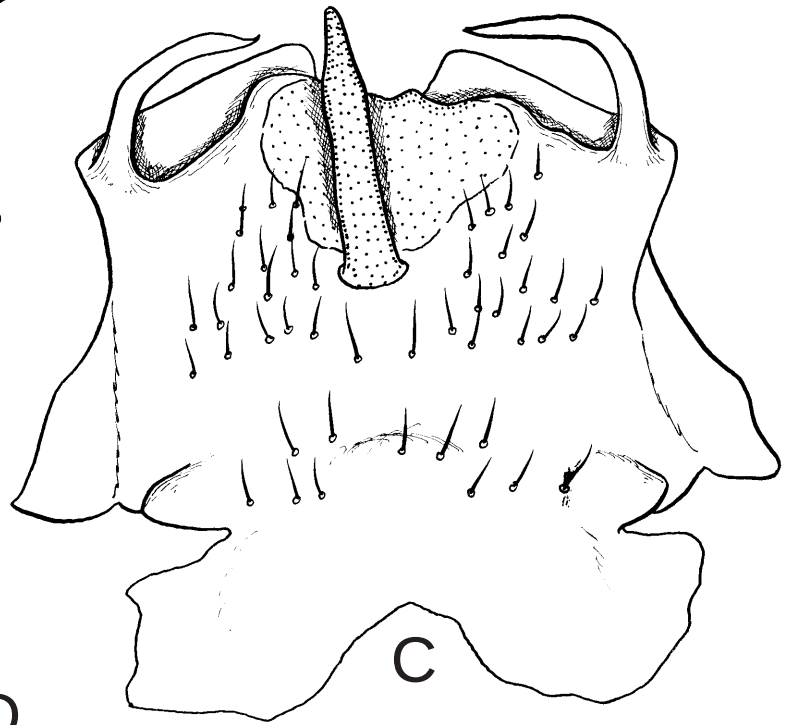
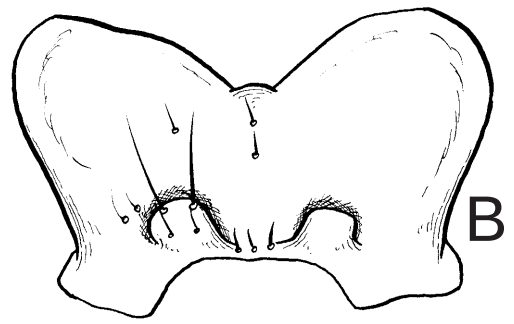
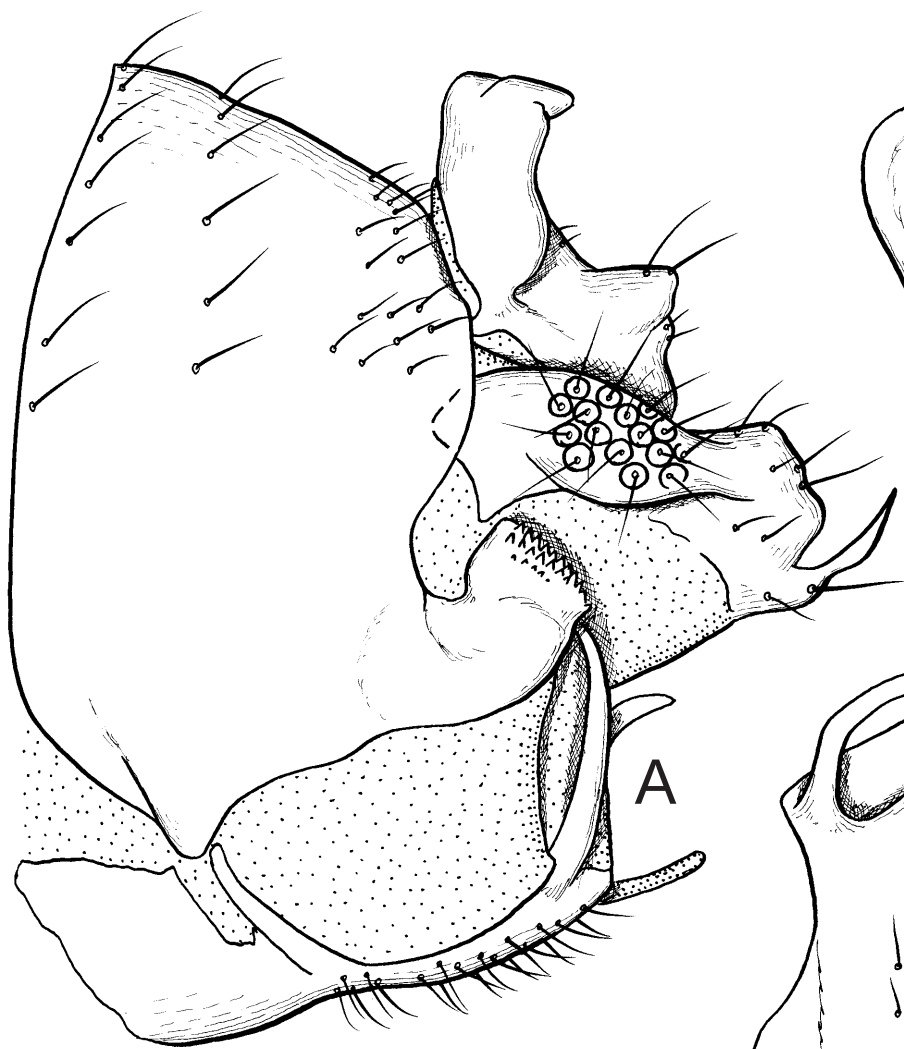


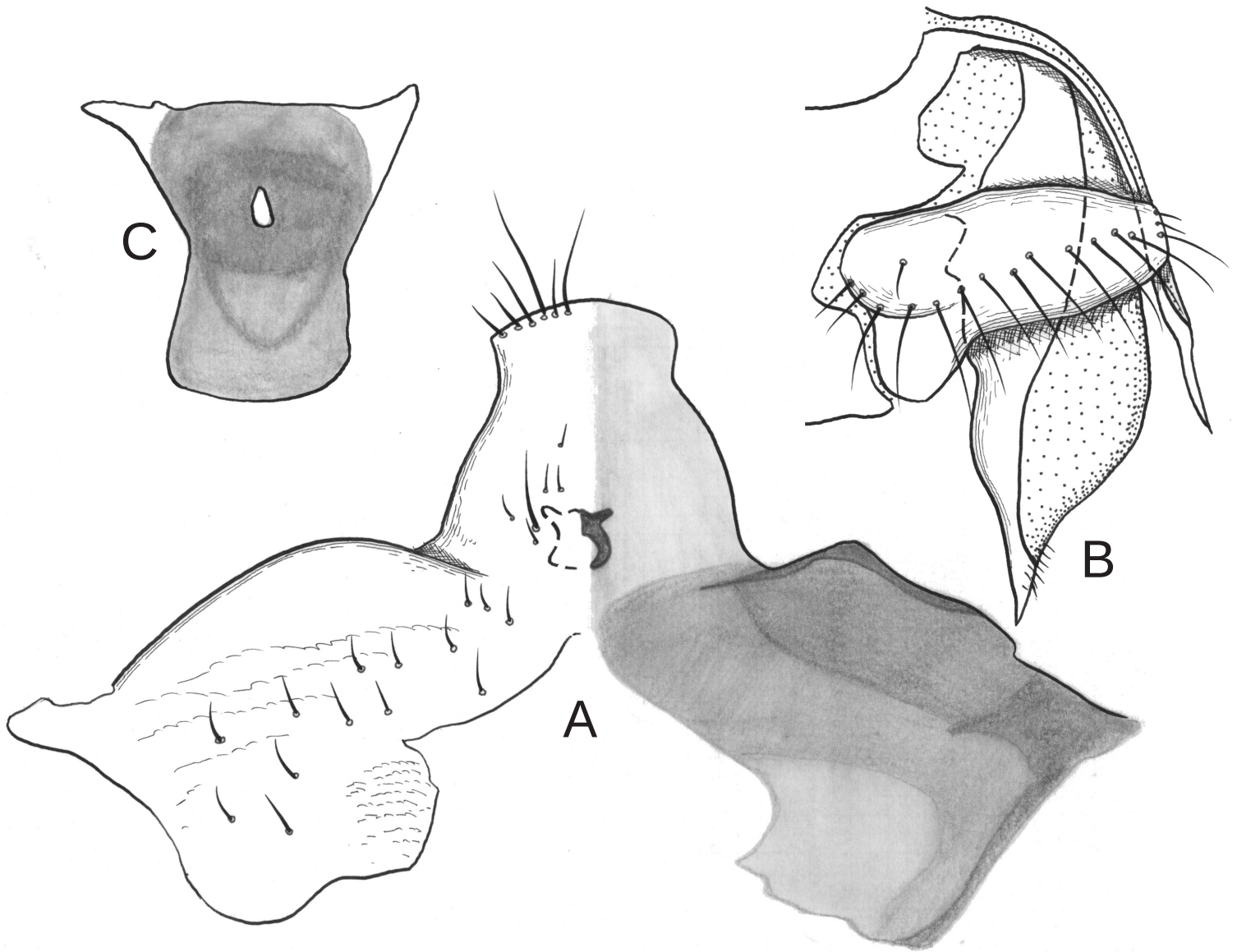


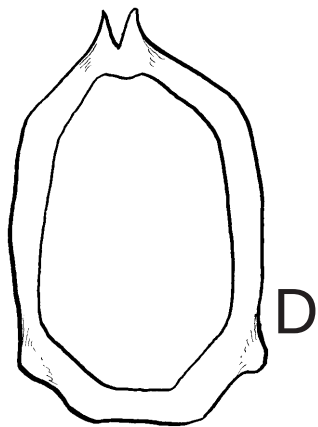
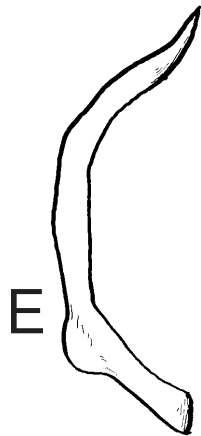
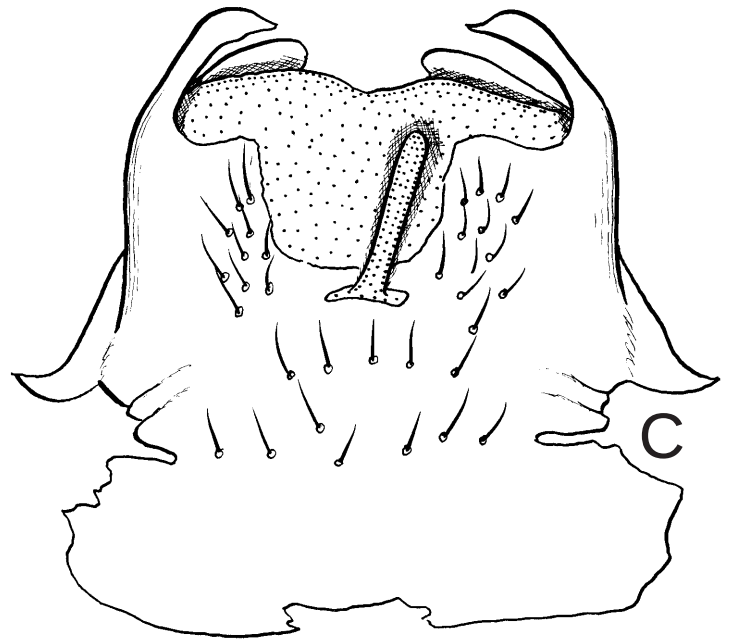
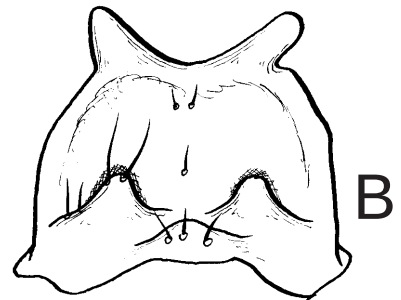


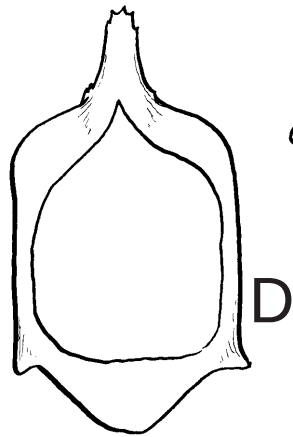
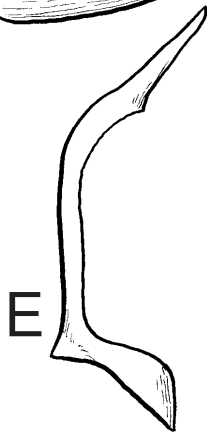
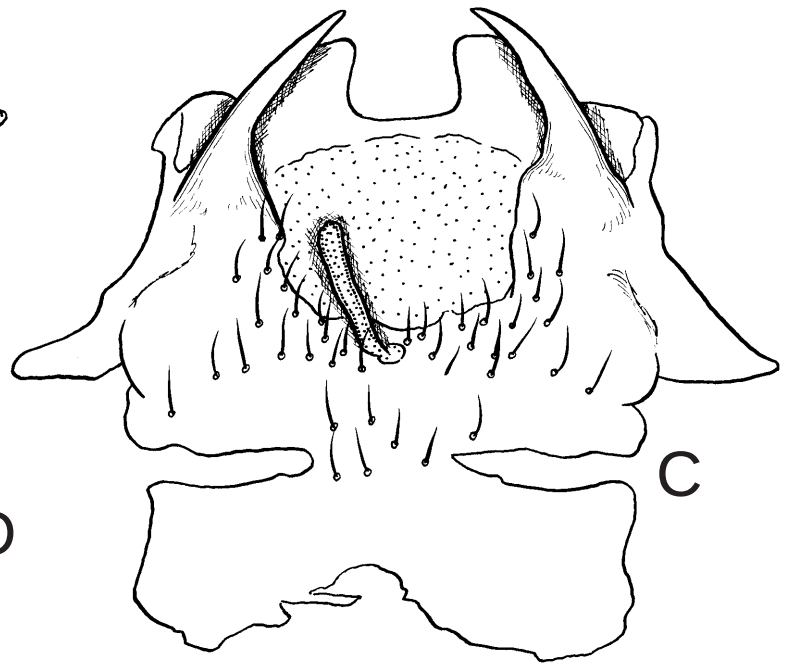
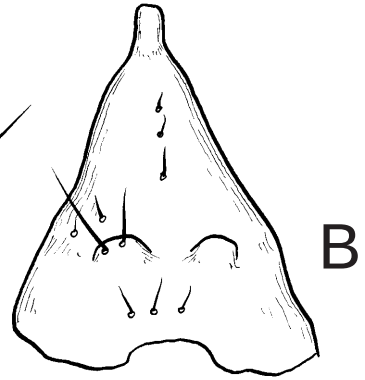


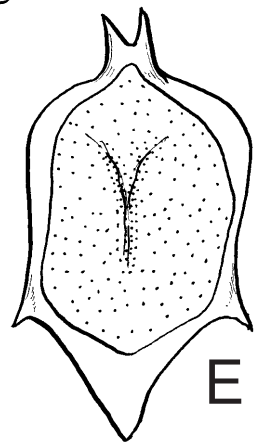
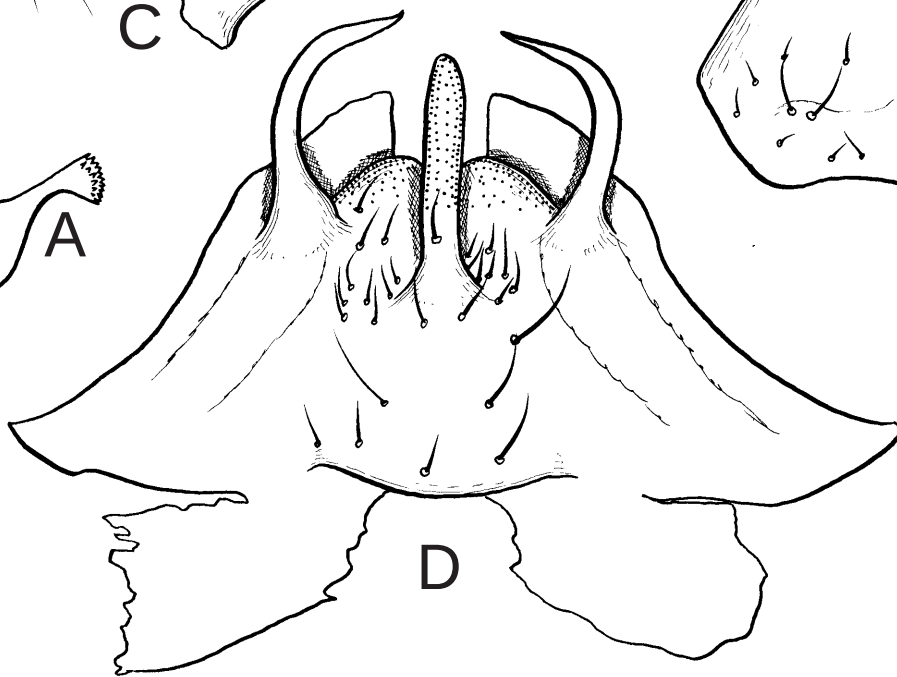
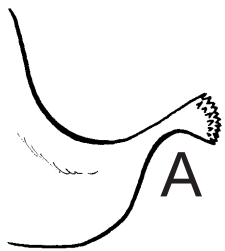
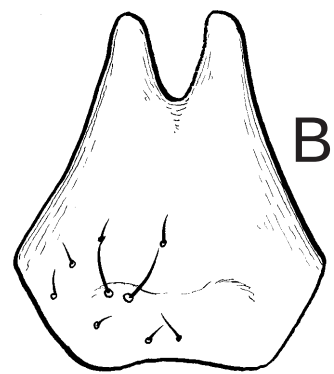
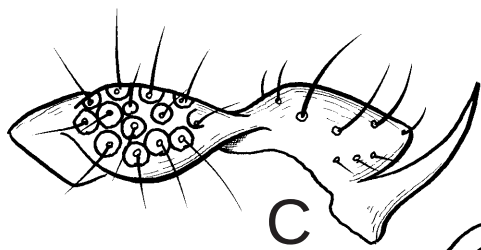






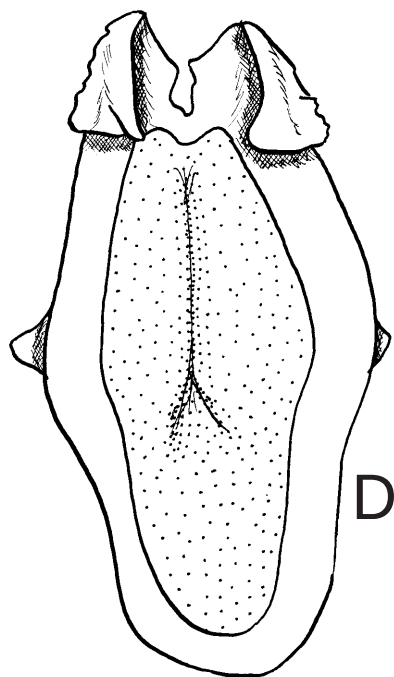




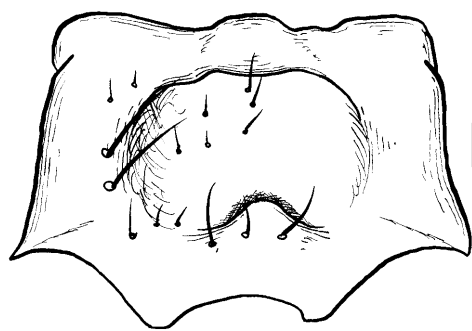




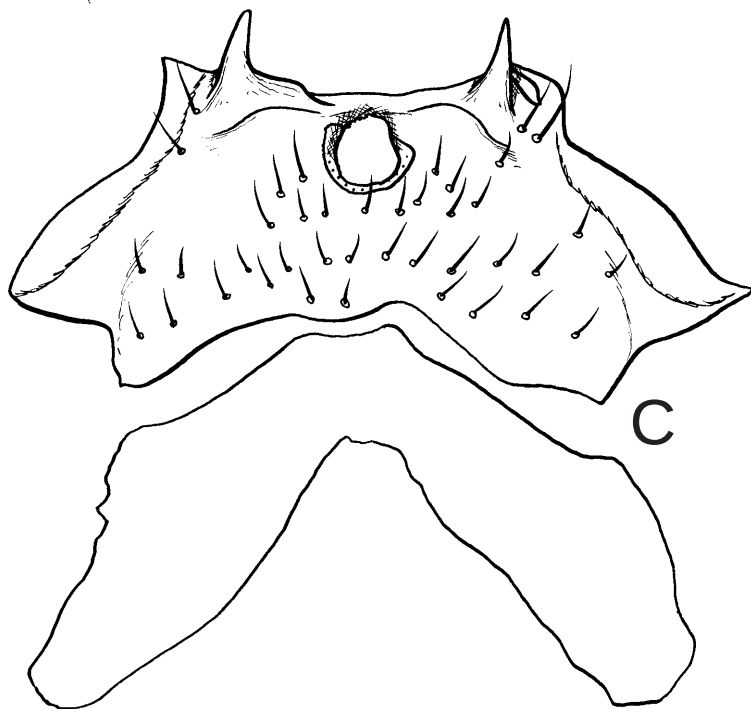
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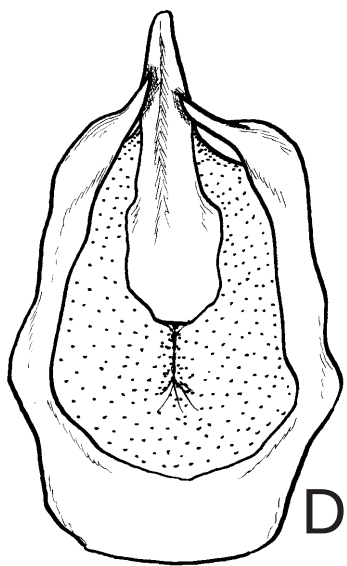
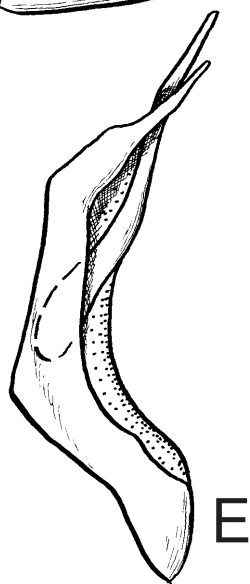
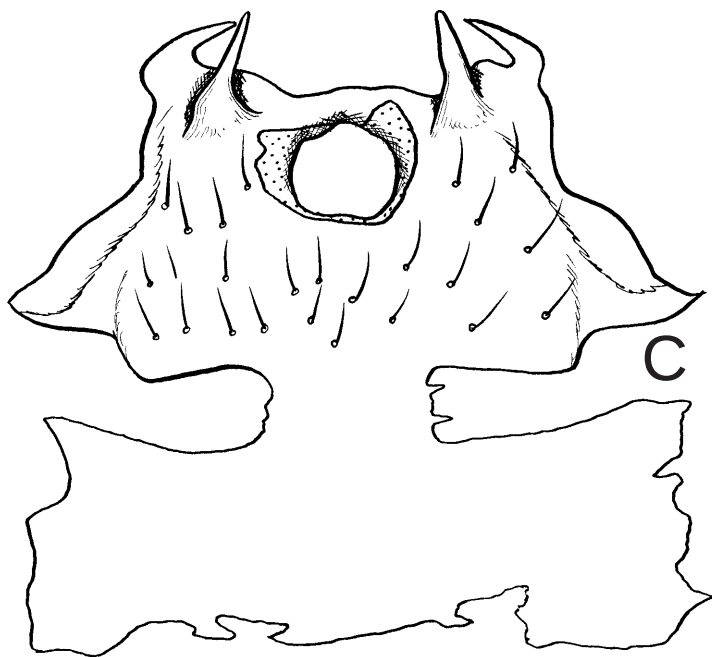
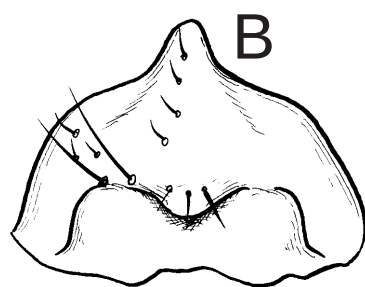
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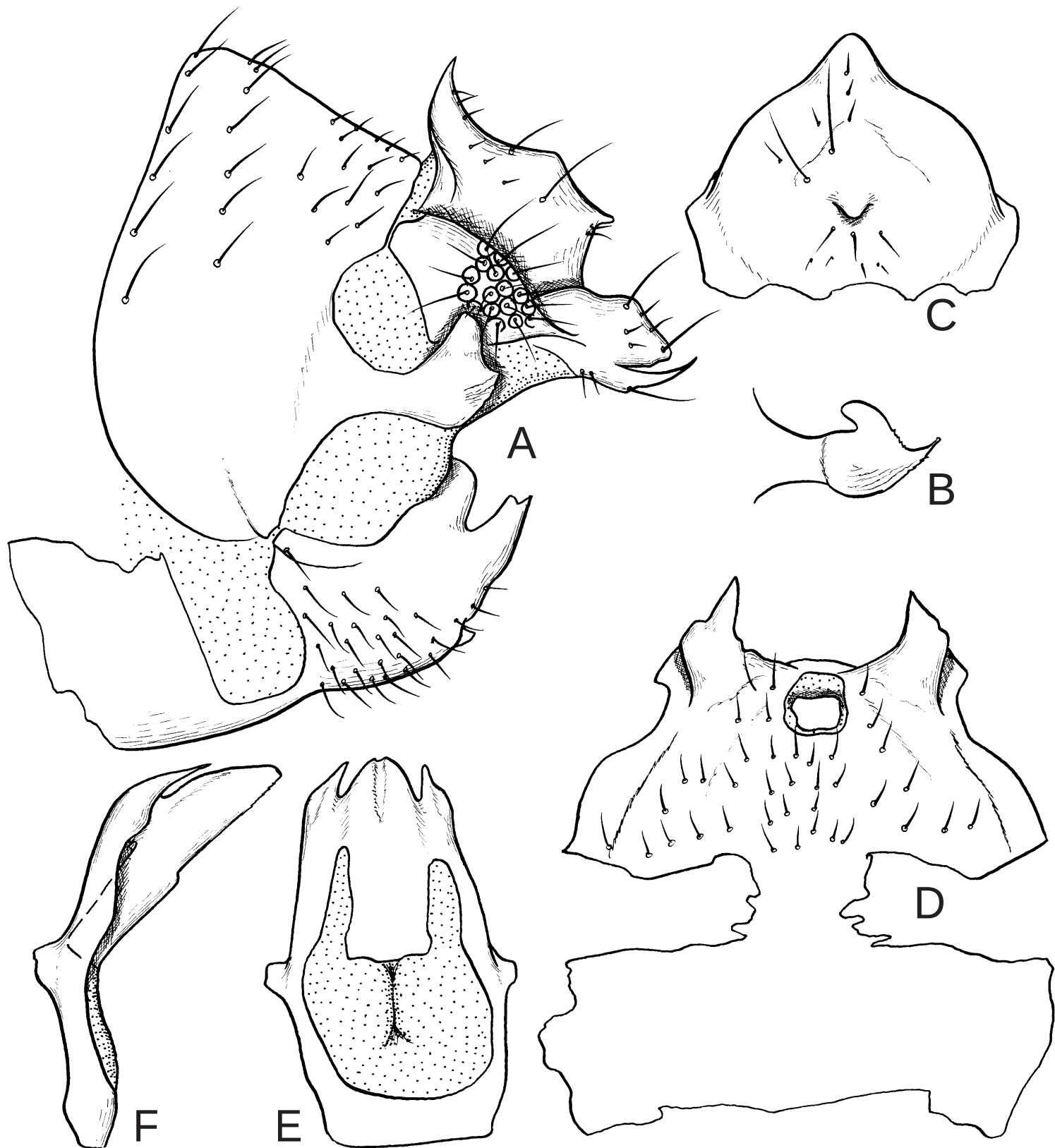
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C







Atrichadenotecnum quadripunctatum

Symbiopsocus hastatus

Loensia variegata

