Studies of Neotropical Caddisflies, LI: Systematics of the Neotropical Caddisfly Genus *Contulma* (Trichoptera: Anomalopsychidae)

RALPH W. HOLZENTHAL
and
OLIVER S. FLINT, Jr.

SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY · NUMBER 575

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ABSTRACT

Holzenthal, Ralph W., and Oliver S. Flint, Jr. Studies of Neotropical Caddisflies, LI: Systematics of the Neotropical Caddisfly Genus *Contulma* (Trichoptera: Anomalopsychidae). *Smithsonian Contributions to Zoology*, number 575, 59 pages, 164 figures, 6 maps, 1 table, 1 cladogram, 1995.—The systematics of the genus *Contulma* (Anomalopsychidae) are reviewed. Morphology of males and females is diagnosed and the immatures are described for the first time. Three previously described species are compared with 18 new species. The 21 species now known in the genus and their distributions are *C. adamsae*, new species (Peru); *C. bacula*, new species (Ecuador); *C. caldensis*, new species (Colombia); *C. cataracta*, new species (Ecuador); *C. colombiensis* Holzenthal and Flint, 1991 (Colombia); *C. costaricensis*, new species (Costa Rica); *C. cranifer* Flint, 1969 (Chile); *C. echinata*, new species (Ecuador); *C. ecuadorensis*, new species (Ecuador); *C. inornata*, new species (Colombia); *C. lanceolata*, new species (Ecuador); *C. nevada*, new species (Colombia); *C. papallacta*, new species (Ecuador); *C. penai*, new species (Ecuador); *C. sancta*, new species (Costa Rica); *C. spinosa* Holzenthal and Flint, 1991 (Colombia, Ecuador); *C. talamanca*, new species (Costa Rica); *C. tapanti*, new species (Costa Rica); *C. tica*, new species (Costa Rica); *C. tijuca*, new species (Brazil); and *C. valverdei*, new species (Costa Rica). A key to males is provided as is a phylogeny of the species. Two monophyletic species groups are recognized: the *cranifer* Group, containing 11 species and characterized by dorsolateral processes on male abdominal segment IX, and the *spinosa* Group, containing 10 species and characterized by mesolateral setae on male segment IX.

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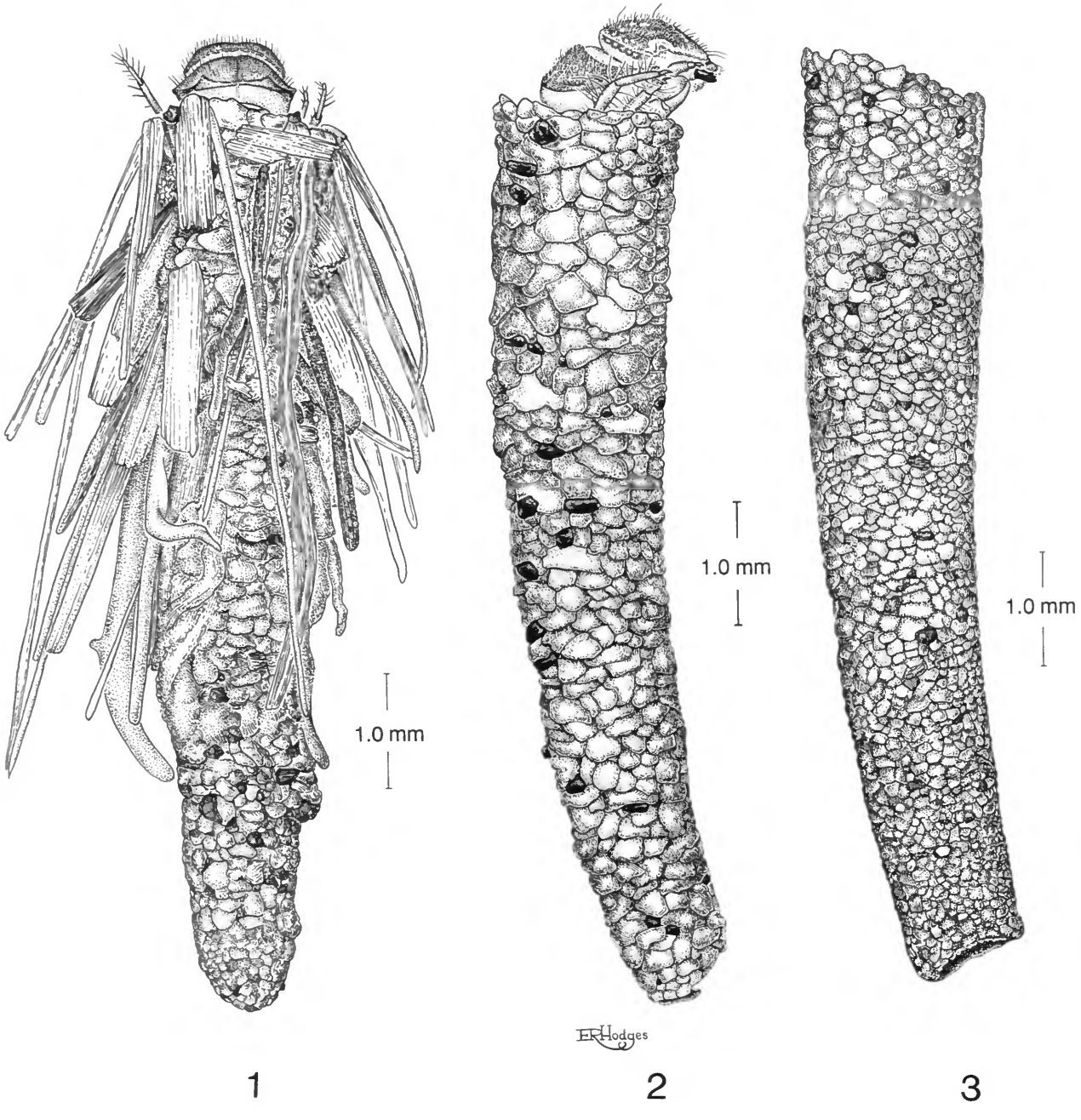
Contents



FRONTISPIECE.—Figure 1, *Contulma penai*, larva in case from near Baños, Ecuador; Figure 2, same from near Medellín, Colombia; Figure 3, *C. spinosa* case from near Cuenca, Ecuador.

Studies of Neotropical Caddisflies, LI: Systematics of the Neotropical Caddisfly Genus *Contulma* (Trichoptera: Anomalopsychidae)

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Introduction

The trichopteran family Anomalopsychidae was erected by Flint in 1981 for two species previously placed in the Sericostomatidae, *Contulma cranifer* Flint, 1969, and *Anomalopsyche minuta* (Schmid), 1957 (as *Myotrichia* = *Anomalopsyche ocellata* Flint, 1967). Until now, only two additional species, both from Colombia, have been added to the family, *Contulma colombiensis* and *Contulma spinosa*, both described by Holzenthal and Flint in Flint's 1991 monograph on the caddisflies of Antioquia. In this paper we describe and illustrate an additional 18 species of *Contulma* from Brazil, Colombia, Costa Rica, Ecuador, and Peru. Also, we provide diagnoses of the previously described species and the first descriptions of the female and immature stages.

Contulma species are generally found associated with the spray and splash zones of waterfalls, small first order streams, and seeps in lush, montane forests. However, Flint has taken some species beside small streams flowing through the Páramo. They probably feed on periphyton and associated fine detritus on the exposed surfaces of rocks. Larvae may be commonly encountered at a site, where adults may also be readily collected during the day with a sweep net. However, unlike most caddisfly adults, those of *Contulma* are not attracted to lights in great numbers. Each mountain habitat sampled seems to have one or two apparently endemic species, suggesting that the genus is much more species rich even than recorded in this paper.

METHODS.—The manner of preparation and study of the specimens utilized in this study are those commonly in use in entomology. The abdomens of the males and females were carefully removed and cleared by immersion in warm KOH until the contents could be easily extracted. The drawings of the genitalia, done by Holzenthal, were made using a camera lucida. The term length, when used in descriptions without modifiers, means that of the forewing. Roman numerals as used in the discussions of the male and female abdomens refer to the segment number, and as used in reference to wing venation refer to the forks.

For discussions of the various computer programs and methods employed, please refer to the pertinent sections under the "Phylogenetic Considerations" portion of the paper.

ACKNOWLEDGMENTS.—Types of the species described in this paper are deposited in the collections of the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (NMNH), the Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica (INBIO), Museu de Zoologia, Universidade de Sao Paulo, Sao Paulo, Brazil (MZUSP), and the University of Minnesota Insect Collection, St. Paul, Minnesota (UMSP), as indicated below.

The authors are indebted to Mrs. Elaine R.S. Hodges for the exquisite illustrations of the larval structures.

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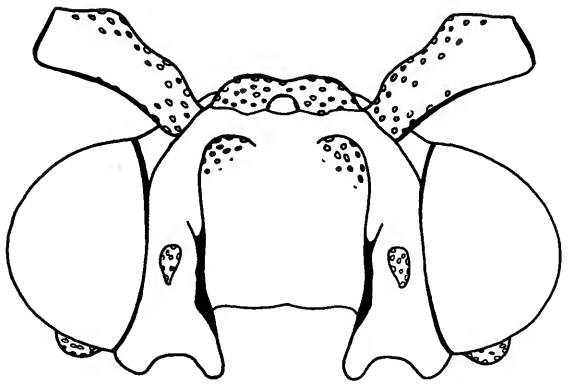

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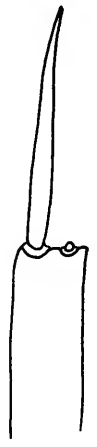

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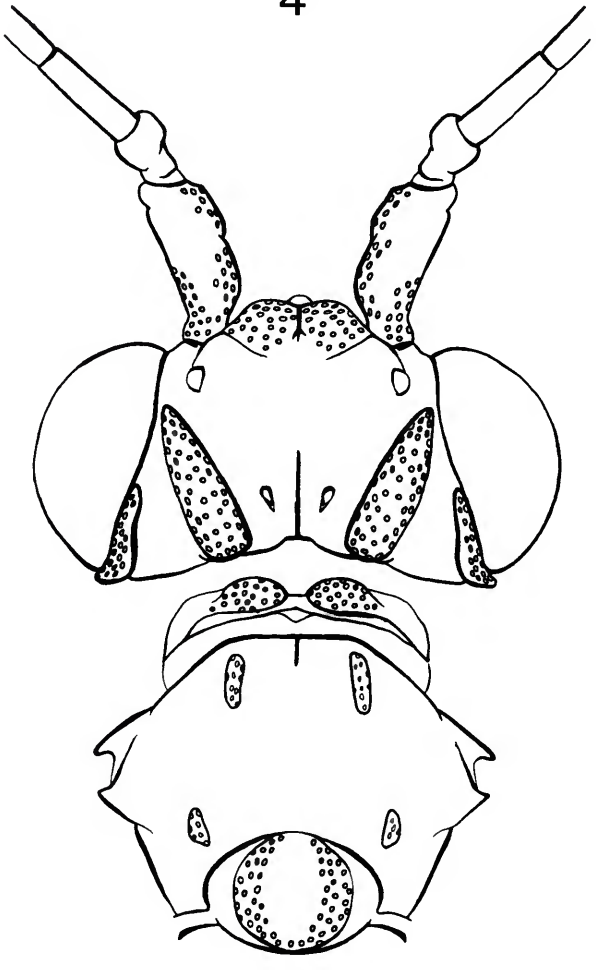

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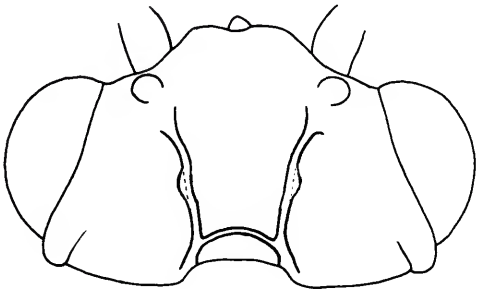

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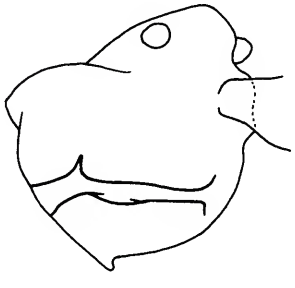

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FIGURES 4–8.—*Contulma colombiensis:* 4, adult head, frontal aspect; 5, head, pro- and mesonotum, dorsal; 6, apex of foretibia showing spurs. *Contulma ecuadorensis:* 7, outline of head showing tentorium, dorsal; 8, same, lateral.

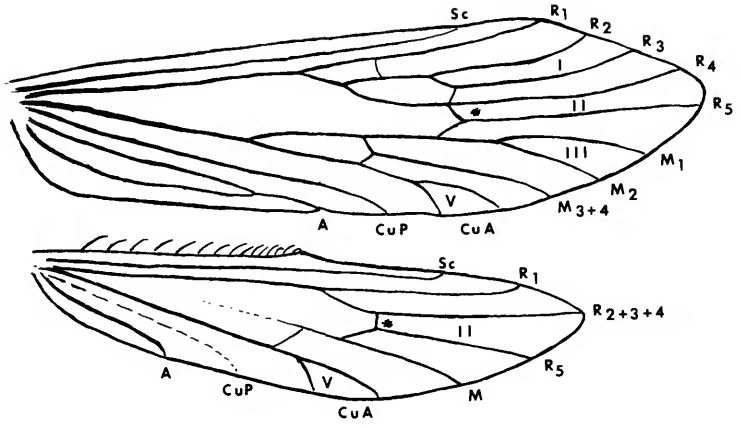

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FIGURE 9.—*Contulma colombiensis*, wing venation.

Smithsonian Institution. Flint's collections from Ecuador were made possible by a grant from the Biological Diversity Programs of the Smithsonian Institution. This is paper number 20,963 of the Scientific Journal Series, Minnesota Agricultural Experiment Station, St. Paul, Minnesota.

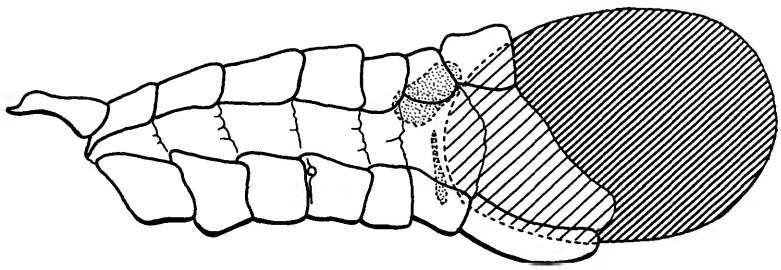
Genus *Contulma* Flint

Contulma Flint, 1969:513 [type species: *Contulma cranifer*, by original designation].

ADULT (Figures 4–9).—Length 4–8 mm. Body and appendages fuscous, forewing of some species with cream-colored patches of setae, especially at arculus. Ocelli 3. Maxillary palpi 5-segmented in both sexes; labial palpi 3-segmented in both sexes. Antennae shorter than forewing; scape cylindrical, three times as long as wide. Head with epicranial suture; frontal setal wart small, ovoid; anteromesal setal wart large, ovoid; posterior setal warts elongate, narrow; posterolateral setal warts small, ovoid. Tentorium simple, with long narrow anterior tentorial arms and narrow, dorsally arching tentorial bridge; dorsal tentorial arms absent. Pronotum with pair of large, elongate-oval warts. Mesonotum with anterior margin shallowly bilobed; mesoscutal setal warts very narrow, elongate; mesoscutellar setal wart large, ovoid. Tibial spurs 2,2,4 (2nd spur of foreleg minute, no longer than wide). Midleg tibia with row of short spines, basal tarsomere with 1 or 2 pairs of ventral spines; all tarsomeres with 2 pairs of apical spines. Forewing with forks I, II, III, and V present; MP fused, hence fork IV absent; large space present between stem of R and M+CuA; discoidal and thyridial cells short, subequal. Hindwing with R 3-branched; M unbranched, CuA branched.

MALE.—Abdominal segments I–VIII without processes, but with posterior halves heavily setose, setae on tergum VIII longest. Genitalia: segment IX complex, synscleritous; usually short dorsally; dorsolateral portion of anterior border extended anteriorly; posterolateral to posteroventral margin extended, forming broad, heavily setose lobe; posterior border of IX often bearing short or broad, setose or spinous, dorsolateral to lateral processes; sternum IX with posteromesal, sclerotized projection. Inferior appendages short, crescent-shaped, apices usually acute, setose, fused together basally and apparently fused to base of posteromesal projection of sternum IX, forming highly complex structure between posterolateral lobes of IX. Pair of very membranous, setose, mound-like or mushroom-like processes apparently associated with subphallic membranes often present above inferior appendages. Segment X small, extending posteriorly over apex of phallus, usually entirely membranous, occasionally with lateral portions very lightly sclerotized, often displaced dorsad by phallus. Phallus often complex; phallobase sclerotized, tubular; phallicata reduced, when present very lightly sclerotized and difficult to distinguish from phallic membranes; endothecal and endophallic membranes often greatly developed, highly convoluted, and bearing sclerotized processes; phallotremal sclerite present or absent.

FEMALE (Figures 10–13).—Abdominal segments II–VIII heavily setose, posterior halves of tergites, sternites, and pleural membranes especially so; sternite V with anterolateral sclerotized area (possibly opening of sternum V gland); sternum VIII broad, rounded, somewhat globose, very heavily setose, with prominent anterolaterally directed apodemes; pleural membranes of segments VII and VIII large, highly folded, heavily setose; segment IX with anterior edge heavily sclerotized; tergum and sternum largely membranous, ventral



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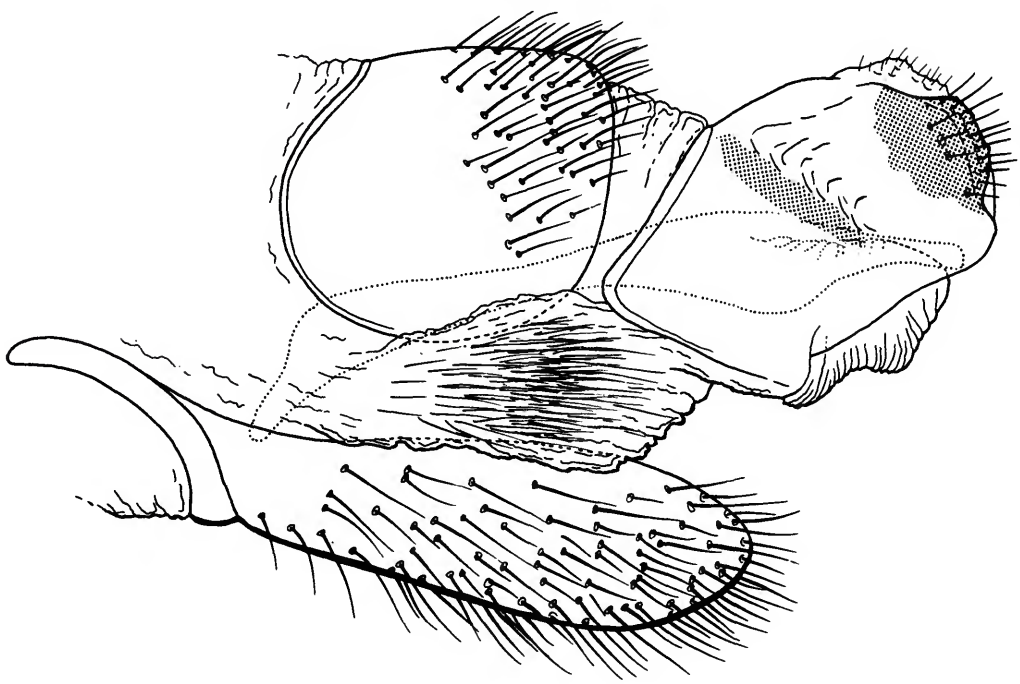

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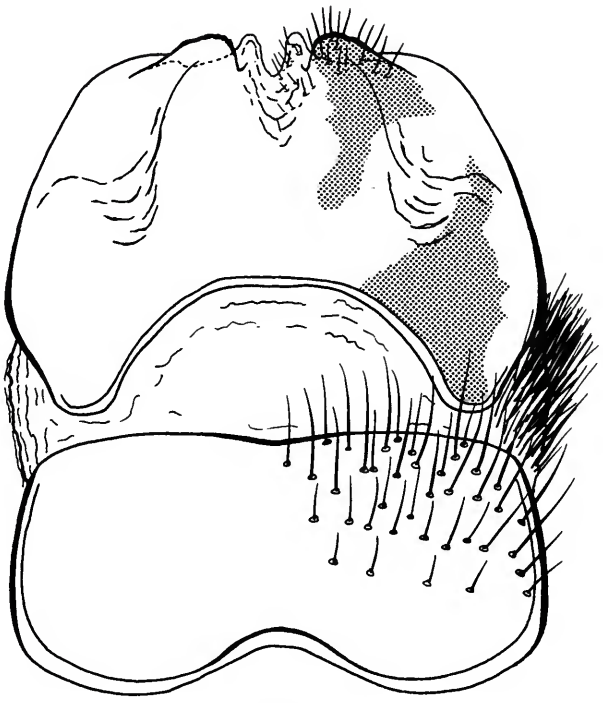
FIGURES 10, 11.—*Contulma* species: 10, female abdomen showing egg mass in situ. *Contulma spinosa:* 11, apex of female abdomen, lateral.

membranes convoluted, dorsal membranes with short setae; anterolateral surfaces with darkly pigmented areas; posterolaterally with pair of sclerotized, setose appendages. Sclerites of vaginal apparatus long, thin, flat in lateral view; in ventral view (Figures 152–163 and insets), generally trident-shaped, with single anterior base, paired midlateral processes, and single medial process; apically with single narrow to broad, sclerotized to semi-membranous process; apical half of vaginal apparatus highly membranous, the membranes apparently joining with those of the medial processes and vaginal chamber. Vaginal apparatus and associated structures apparently highly species specific.

REMARKS.—The adults of *Contulma* are separated from those of *Anomalopsyche,* the only other genus included in the family, by several characteristics of the forewing venation as well as genital structures. In *Contulma* Rs is shorter than either R_{2+3} or R_{4+5}, whereas in *Anomalopsyche* it is several times as long as either following branch. The crossvein from M_{3+4} in *Contulma* joins the stem of CuA well basad of its fork, but in *Anomalopsyche* it joins the anterior branch of CuA, conse-



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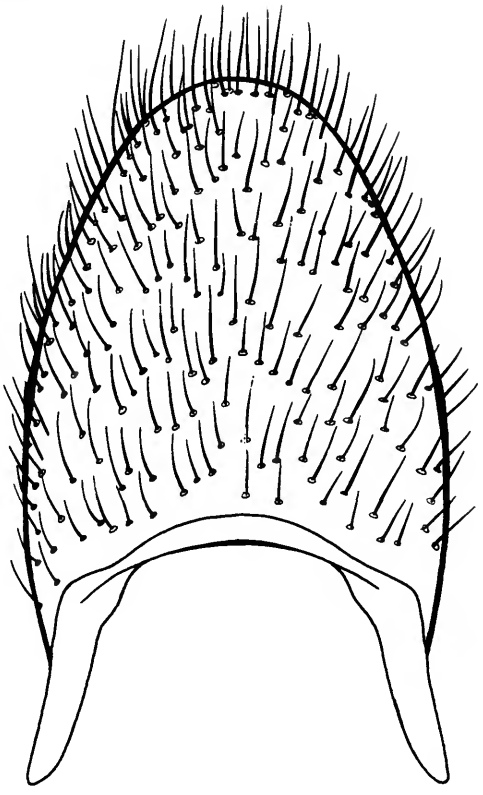

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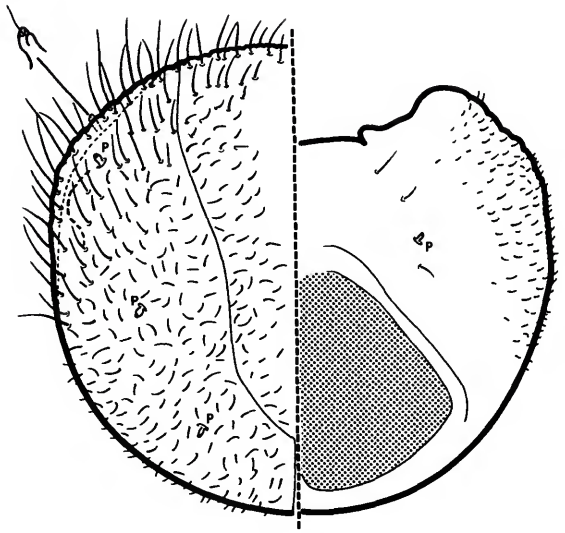
FIGURES 12, 13.—*Contulma spinosa:* 12, apex of female abdomen, dorsal; 13, female sternum VIII, ventral.



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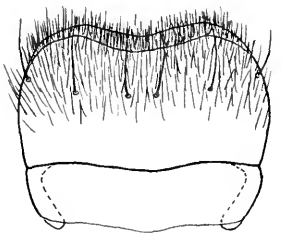

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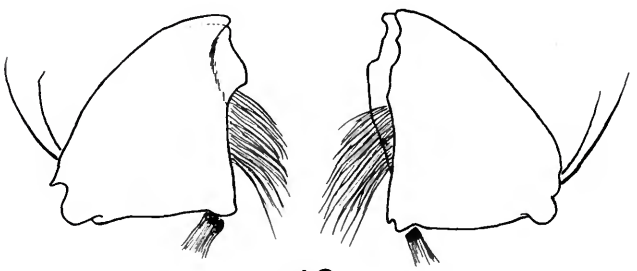

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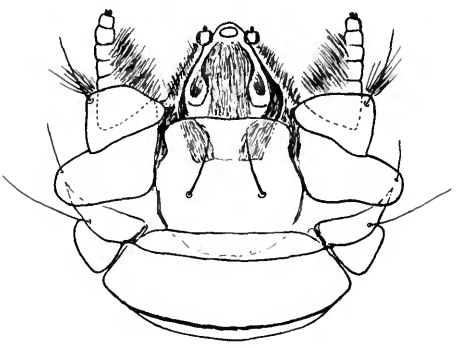

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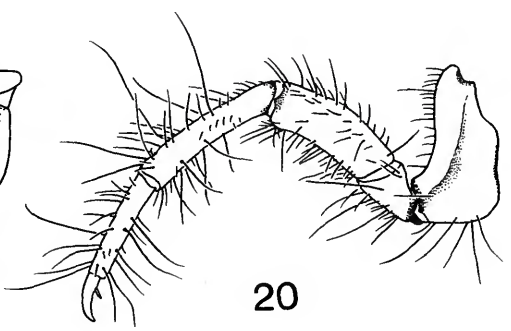

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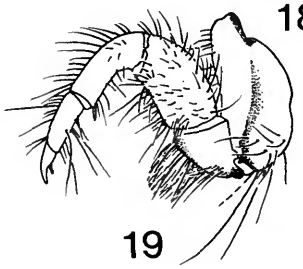

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FIGURES 14–20.—*Contulma valverdei:* 14, larval head, dorso/ventral, inset of antenna greatly enlarged. *Contulma penai,* larva from near Medellín, Colombia: 15, labrum, dorsal; 16, mandibles, ventral; 17, maxillolabium, ventral; 18, foreleg, posterior; 19, midleg, posterior; 20, hindleg, posterior.

quently the thyridial cell in *Contulma* is only about half as long as it is in *Anomalopsyche*. Vein 1A appears to join 2A near the wing margin in *Contulma* but loops up to CuP near its base in *Anomalopsyche*. The hindwing in *Contulma* appears to lack fork I, which is present in *Anomalopsyche*. The male genitalia of the two genera are quite different, especially the inferior appendages, which in *Contulma* are small and highly modified, but in *Anomalopsyche* readily conform to the basic 2-segmented groundplan of the caddisflies. Also segment X is greatly reduced and generally membranous in *Contulma* but sclerotized and elongate in *Anomalopsyche*, also conforming more closely to other male caddisflies. In the female genitalia the vaginal sclerites are quite different in the two. In *Contulma* there is a generally trident-shaped sclerotization in addition to a median anterior base and apical membranes. In *Anomalopsyche* the vaginal sclerites are bipartite and sclerotized with an apical, bell-like portion and an anterior, keyhole-like sclerite.

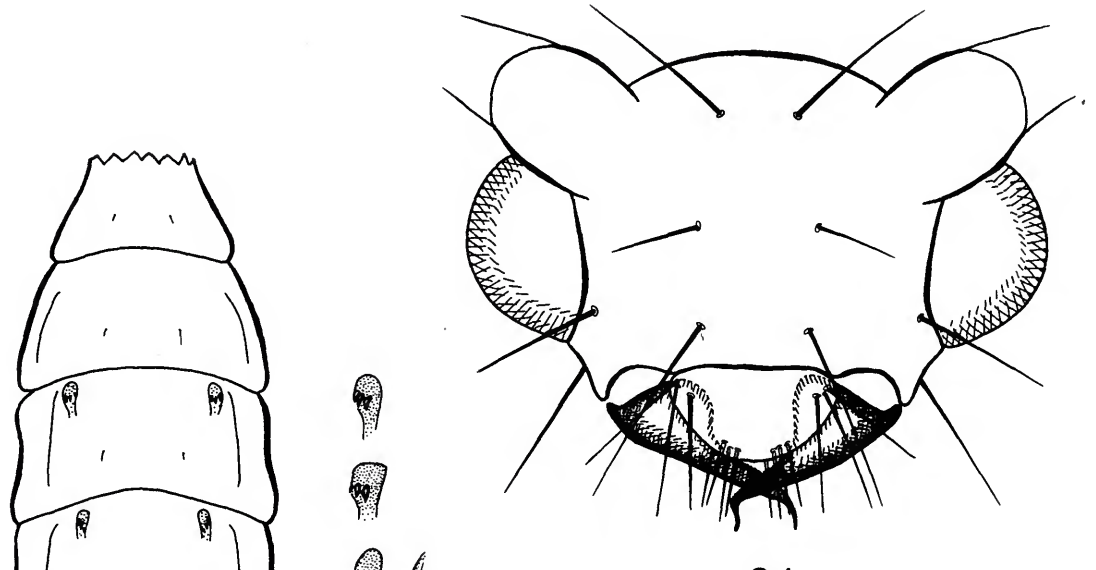
Several female specimens were collected with large, oval egg masses still attached to the end of the abdomen (Figure 10). In these individuals, egg masses were held within the terminalmost abdominal segments, which resulted in extreme stretching of the pleural membranes of abdominal segments VII and VIII and a dorsal and ventral displacement of the terga and sterna of those segments, respectively. The shape and curvature of tergum VIII and the large size and dorsally concave shape of sternum VIII apparently serve to hold the egg mass in place. Pleural membranes tightly envelope the egg mass laterally. At the same time, segment IX+X is pushed back into the abdomen and the vaginal apparatus, which normally lies in a horizontal plane, similarly is displaced posteriorly and comes to be situated vertically. In specimens lacking egg masses, membranes in the region of the vaginal orifice between sternum VIII and segment IX+X were invariably torn. These ruptures could have occurred during the clearing process, but because almost all females thus prepared exhibited some degree of tearing, it seems more likely that these occurred during the formation of the egg mass or its oviposition. Obviously, observation of oviposition in living specimens would better elucidate these conclusions. In any case, the terminal abdominal segments of *Contulma* females appear to be highly unusual within the Trichoptera.

LARVA (Figures 14–20).—Length to 8 mm. Color of sclerites of head and pronotum golden yellow, brown, dark brown, or reddish brown with paler muscle scars; meso- and metanota and legs paler. Labrum with dense brush of setae on anterior half. Mandibles scoop-shaped, with apical margins weakly toothed; each mandible with large brush of long setae mesally. Maxillolabium about as broad as long, with many setae and papillae on inner surface of maxillae, but without large membranous lobes. Antennae short, situated midway between eye and anterior edge of head capsule. Head setation variable, with numerous long setae along anterolateral margin of head capsule in most species, remainder of head covered with short secondary setae or scale-like setae (Figure 14); slight to strong carina around margin, usually interrupted by eye, continuing across anterior margin of frontoclypeus and posteriorly around vertex; dorsum of head, especially frontoclypeus variously ornamented, with rows of spines, cales, large spiny protuberances, pits, depressions, patches of thick, dark setae, etc., depending on species; ventrally head usually pale and lightly sclerotized. Pronotum with carina near posterior margin produced anterolaterally as pointed or rounded, usually serrate lobe; surface often rugose, bearing many short, secondary setae. Prosternal horn absent. Mesonotum with pair of dorsal plates bearing transverse ridge or protuberances at midlength, and numerous short secondary setae or scale-like setae. Metanotum generally with sa1 (sa = setal area) developed as single transverse or oval pale sclerite bearing numerous short setae; sa2 with single seta; sa3 with small sclerite bearing 6–10 or more setae. Legs bearing many setae along ventral halves of femora, tibiae, and tarsi; midleg with well-developed ventral trochanteral brush. First abdominal segment apparently with dorsal hump, but difficult to discern, lateral hump with long, narrow, crescentic sclerite. Abdomen without lateral line and gills; no indication of any bifid tubercles. Tergum IX without sclerotized shield, but with setae posteriorly. Anal proleg and associated lateral sclerites normal, or rarely elongate; anal claw with single basoventral tooth and with dorsal curved process bearing many secondary teeth and resembling a cock's comb.

PUPA (Figures 21–23).—Length to 7 mm. Color white, texture smooth. Mandible broad basally, tapering to slender apical process. Labrum semicircular with 3 dorsal setae in each of anterolateral and basolateral corners. Anterior tentorial pits well marked. With 2 pairs of stout setae on face and between antennae, and 2 pairs below eyes. Legs and abdomen lacking hair fringes. Dorsal abdominal surface with minute spicules from posterior half of segment I to VII; spicules very small, and most conspicuous laterally on terga I and II, and just behind anterior hook plates on terga III–VI. Anterior hook plates on segments III–VI elongate, each with 3 hooks; posterior hook plates on segment V oval, each with 2 small hooks. Apical appendage long, rod-like, upcurved, with several long setae basally and with dorsal surfaces serrate.

CASE (Figures 1–3).—Length large enough only to tightly house larva or pupa. Constructed of small sand grains finely attached by silk, occasionally of larger mineral fragments or with vegetation included laterally and dorsally; tapered and slightly curved posteriad. Anal opening almost closed by silken sheet with ovoid dorsal opening, usually overhung by lip-like silken hood (Figures 138, 155). Pupal case essentially identical, with anterior opening closed by silken sheet with small, elongate openings marginally.

REMARKS.—The larvae of *Contulma*, in spite of their overall similarity to those of *Anomalopsyche* (Flint, 1981), offer a number of distinctive differences. In the mouthparts, the labrum and maxillolabium, although setose, do not bear such large, hirsute, membranous lobes as in *Anomalopsyche*. The



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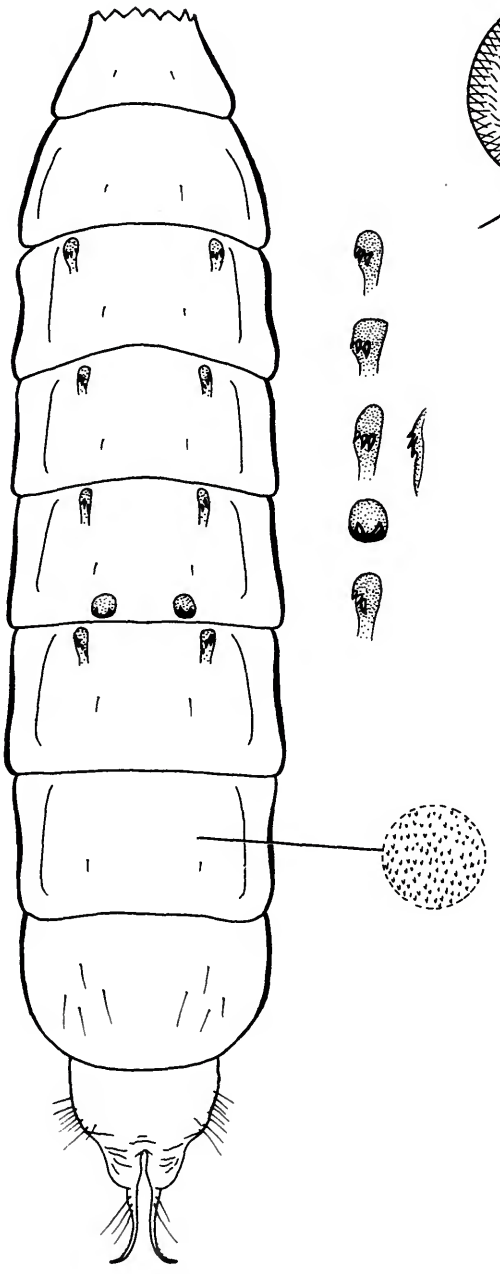

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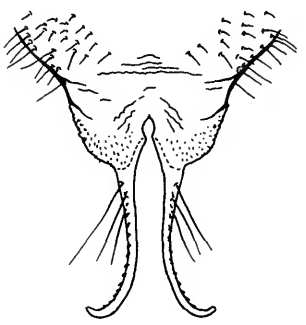

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FIGURES 21-23.—*Contulma adamsae*, pupa: 21, head, frontal; 22, abdomen, dorsal, with inserts of hook plates dorsal view and plate 5A lateral view, and integument of segment VII greatly enlarged; 23, apex of abdomen, dorsal.

mandibles are weakly dentate apically. The head and thoracic nota bear many secondary setae. The mesonotum is transversely divided by a low carina or row of sclerotized projections, and the metanotum bears a transverse sclerite anteromesally. The legs, especially the femora, tibiae, and tarsi, are usually very hairy ventrally and the midtrochanter bears a large brush. The first abdominal segment in *Anomalopsyche* bears a well-developed midventral hump, which is lacking in *Contulma*. The accessory teeth of the anal claw of *Contulma* are borne in large numbers on a lobe arising from the hook, but in *Anomalopsyche* the few teeth are borne in a row from the dorsum of the hook.

As described above and illustrated in Figures 129–164, larvae of the various species reveal a great deal of specific variation. The heads, in their manner of ornamentation, rugosities, and carinae, are grossly different between the species. Also, the appearance of the pro- and mesonota are species specific, although all species have at least a small part of the transverse row of processes on the mesonotum. The degree of development of the accessory tooth process also varies between species. Cases are more nearly uniform among the species, but in at least some species vegetation is incorporated along the sides and top.

The pupae are more similar among the species of *Contulma* than they are to *Anomalopsyche*. The pupa of the species herein described differs from those of *Anomalopsyche* by lacking the strong band of hair basally on the labrum and in having much longer apical processes. The type of respiratory opening left in the anterior pupal closures do appear to be different in the two genera.

Key to Males of *Contulma* Species

1. Posterior margin of segment IX without elongate, dorsolateral processes, although there may be small setose projections [Figures 30, 35] 2
   Posterior margin of segment IX with elongate, dorsolateral processes [Figure 24] 9
2. Segment IX with patch of long, stout, spine-like mesolateral setae [Figure 39] 3
   Segment IX without such setae, although there may be areas of much smaller setae present [Figures 35, 36] 5
3. Phallus with pair of massive, highly convoluted membranous midlateral lobes and pair of large, heavily sclerotized parameres [Figures 39–43] . . . . . ***C. cataracta,*** new species
   Phallus without such large lobes or heavy parameres, although there may be smaller parameres and apical spines present [Figure 97] 4
4. Apex of phallus with series of long spine-like setae; tergum X lightly sclerotized, setose [Figures 94–98] . . . . . ***C. talamanca,*** new species
   Apex of phallus lacking setae, although a pair of parameres present more basally; tergum X membranous, lacking setae [Figures 99–102] . . . . . ***C. tapanti,*** new species
5. Phallus with pair of large, highly convoluted, membranous dorsolateral lobes [Figure 89] 6
   Phallus without such lobes [Figure 38] 7
6. Segment IX with mesolateral patch of small setae on inner surface; apex of phallus with thin, trough-like, apicomesal lobe [Figures 86–89] . . . . . ***C. sancta,*** new species
   Segment IX without such setae; apex of phallus with large, membranous apicomesal lobe [Figures 111–115] . . . . . ***C. valverdei,*** new species
7. Segment X without lightly sclerotized lateral regions that apparently articulate basally with sclerotized projections of dorsolateral corners of segment IX; inferior appendages elongate, crescentic [Figures 35–38] . . . ***C. caldensis,*** new species
   Segment X with lightly sclerotized lateral regions that apparently articulate basally with sclerotized projections of dorsolateral corners of segment IX; inferior appendages short, compact [Figure 48] 8
8. Parameres long, slender; projection of sternum IX truncate apically [Figures 48–51] . . . . . ***C. costaricensis,*** new species
   Parameres short; projection of sternum IX acute apically [Figures 103–106] . . . . . ***C. tica,*** new species

9. Phallus with very large, often massive, convoluted membranous dorsolateral lobes and associated apical to subapical scale-like sclerites and/or setae [Figures 28, 55] 10
Phallus with membranous areas much smaller; phallic sclerites absent, or, if present, smaller and less conspicuous or more tooth-like [Figures 47, 60, 65] 13
10. Segment IX very short dorsolaterally; posteromesal projection of sternum IX only lightly sclerotized, rounded [Figures 52–56] . . . . . ***C. cranifer*** Flint
Segment IX normal dorsolaterally; posteromesal projection of sternum IX heavily sclerotized, rounded or truncate [Figures 24, 91] 11
11. Phallus with lateral and ventrolateral lobes bearing short, black spicules [Figures 24–29] . . . . . ***C. adamsae,*** new species
Phallus without such spicule bearing lobes, but with dorsolateral and mesoventral membranous lobes, each bearing apical, sclerotized, scale-like processes [Figure 34] 12
12. Dorsolateral processes of segment IX broad, curved ventrad apically [Figures 90–93] . . . . . ***C. spinosa*** Holzenthal and Flint
Dorsolateral processes of segment IX slender, straight [Figures 30–34] . . . . . ***C. bacula,*** new species
13. Tergum IX with prominent, posteromesal extension [Figures 61–65] . . . . . ***C. ecuadorensis,*** new species
Tergum IX without posteromesal extension [Figure 44] 14
14. Apex of phallus with pair of large, tooth-like spines and/or with smaller apicoventral spines [Figures 60, 77] 15
Apex of phallus without such spines, although small setae or papillae may be present [Figures 47, 69, 73] 17
15. Apex of phallus without tooth-like spines, but with small subapicoventral spines [Figures 74–77] . . . . . ***C. nevada,*** new species
Apex of phallus with large, tooth-like spines [Figure 60] 16
16. Segment IX with long dorsolateral processes covered with many stout setae; tooth-like spines of phallus small, no other spines on phallus [Figures 78–81] . . . . . ***C. papallacta,*** new species
Segment IX with short dorsolateral processes bearing few blade-like setae; tooth-like spines of phallus very large and phallus with series of apicoventral spines [Figures 57–60] . . . . . ***C. echinata,*** new species
17. Dorsolateral processes of segment IX clothed with short, fine setae; segment IX extended anterodorsally [Figure 44] 18
Dorsolateral processes of segment IX lacking vestiture of fine setae; segment IX only slightly extended anterodorsally, if at all [Figure 66] 20
18. Segment IX posteriorly with both long dorsolateral setose process and long, slender, sharply pointed, ventrolateral process [Figures 70–73] . . . . . ***C. lanceolata,*** new species
Segment IX posteriorly with only single long dorsolateral or lateral setose process [Figure 44] 19
19. Dorsolateral setose processes of segment IX straight, parallel, directed downward, and close together [Figures 82–85] . . . . . ***C. penai,*** new species
Dorsolateral setose processes of segment IX curved mesally, widely separated [Figures 44–47] . . . . . ***C. colombiensis*** Holzenthal and Flint
20. Dorsolateral processes of segment IX short, spatulate, straight [Figures 66–69] . . . . . ***C. inornata,*** new species
Dorsolateral processes of segment IX long, slender, downcurved, their apices rugose [Figures 107–110] . . . . . ***C. tijuca,*** new species

Contulma adamsae, new species

FIGURES 21-29, 116; MAP 1

The male genitalia of this species, especially the phallus, are the most complex known in the genus. The species is easily recognized from all others by the elongate, heavily setose ventrolateral lobes of segment IX and the elongate, fused inferior appendage-IXth sternal complex. The phallus, with its spinose membranous lobes, is unique, but apparently closest to that of *C. cranifer*, possibly indicating a close relationship between these species.

Larvae and female metamorphotypes were taken together with adult males, but the larvae appear to be in the penultimate instar. Because they may change appearance somewhat in the final instar they were not figured, but salient characters, verified by examination of sclerites of the head and pronotum from a metamorphotype, will be mentioned here. The head is not grossly modified, but its surface is rugose, each rugosity bearing a small, pale, decumbent, scale-like seta (as in Figure 130). The surface of the pronotum is modified in the same manner and has the same general shape as in Figure 130, but in lateral aspect the lateral knobby ridge is produced anteriad into a sharp point. The knobby ridge of the mesonotum is complete across the dorsum as in Figure 135, but is slightly sinuate mesally.

MALE.—Length 5.5 mm. Color fuscous, forewing with patch of cream-colored setae at arculus; otherwise, wings badly rubbed. Foretibia with second spur small, about twice as long as wide. Segment IX, short dorsally; in lateral view IX slightly extended anterodorsally; posteriorly with very narrow, elongate, sinuate, sclerotized dorsolateral process; posterolaterally produced into prominent, very heavily setose lobe, its mesal face with thin, sclerotized shelf-like ridge, this lobe more lightly pigmented than remainder of IX; pair of elongate, setose lobes present posteroventrally, setae on their lateral margins directed anteriad; sternum IX with posteromesal, sclerotized, elongate projection, its apicolateral corners very acute. Segment X mound-like, entirely membranous, with single basolateral seta. Inferior appendages elongate, sinuate, terete, each bearing 4 short, stout, apicolateral setae; inferior appendages fused basally and apparently fused to base of IXth sternal projection, together forming highly complex structure that includes pair of narrow, anteriorly directed apodemes as in Figures 24, 27. Processes of subphallic membranes present, but difficult to discern. Phallus very complex; phallobase short, sclerotized; endophallic membranes massive, highly convoluted dorsally, consisting of 2 pairs of ventrolateral membranous lobes bearing numerous small spicules apically; phallicata present, lightly sclerotized, with pair of apical, partially sclerotized lobes bearing minute setae and with mesal ventral sclerotized projection; phallotremal sclerite present, narrow, much wider than long.

FEMALE (pharate).—Size and color apparently as in male. Vaginal apparatus with base short, narrow; midlateral processes short, lanceolate, pointed apically; medial process lanceolate, 1.5 times as long as midlateral processes; medial membranes highly convoluted; apex broad, thumb-like, highly membranous.

MATERIAL EXAMINED.—*Holotype* (male): PERU, CUZCO, Paucartambo, near park entrance station, near km 106, seeps, 3420 m [13°17.43'S, 71°35.95'W], 28 Aug 1989, N. Adams (NMNH).

Paratypes: Same data as holotype, 2♂ (1 teneral), 2♀ metamorphotypes (NMNH); same, except J. Gelhaus #430, 1♂ (UMSP).

Nontypes: Same data as holotype, 3 small larvae, 2 empty pupal cases (NMNH); same, but collected from vertical rock seep, R.A. Faitoute, colln. # 2, 1 small larva (NMNH).

ETYMOLOGY.—We take great pleasure in naming this species for Nancy E. Adams, who collected it and who has assisted the authors in their explorations of the Neotropical caddisfly fauna.

Contulma bacula, new species

FIGURES 30-34; MAP 1

This species is similar to *C. spinosa*, but differs from it in the shape of the dorsolateral processes of segment IX, which are much straighter and narrower in the new species.

MALE.—Length 6 mm. Color brown in alcohol. Foretibia with second spur minute, about as long as wide. Segment IX, short dorsally; posterior border in lateral view extended anterodorsally; posteriorly with heavily sclerotized, rod-like dorsolateral process, its apex only very slightly directed ventrad, bearing few long setae on ventral margin; posterolateral margin of IX a large, roughly triangular, very heavily setose lobe, bearing setae on mesal surface; sternum IX with elongate, posteromesal, sclerotized projection, its apex entire. Segment X membranous, except for very lightly sclerotized lateral region; slightly displaced dorsad by phallus. Inferior appendages long, narrow, pointed, crescentic, bearing short apical setae; fused basally and apparently fused to base of IXth sternal projection, together forming highly complex structure as in Figure 32. Processes of subphallic membranes present. Phallus complex; phallobase elongate, sclerotized; pair of highly convoluted, membranous, dorsolateral lobes present medially, each ending in small, sclerotized, scale-like process; apical half of phallus trough-like, with highly convoluted internal membranes; U-shaped sclerite (possibly phallotremal sclerite) present within these membranes.

MATERIAL EXAMINED.—*Holotype* (male): ECUADOR [NAPO], 1 mi [1.6 km] E of Papallacta, 30 Jan 1958, R.W. Hodges (NMNH).

ETYMOLOGY.—From the Latin word for rod, in reference to the dorsolateral processes of segment IX.

MAP 1.—Known adult distribution of *Contulma adamsae*, *C. bacula*, *C. caldensis*, and *C. costaricensis*.

Contulma caldensis, new species

FIGURES 35–38; MAP 1

This species can be distinguished from other members of the genus by the general absence of prominent spines or processes on segment IX. Instead there are short, spinous projections dorsolaterally on IX and short, inconspicuous setae on the mesolateral surfaces of IX. In addition, the inferior appendages are long and curved, similar to those found in *C. spinosa*.

MALE.—Length 7.5–8.5 mm. Color fuscous, forewing with

three patches of cream-colored setae: at arculus, pterostigma, and apex of discal cell. Foretibia with second spur not apparent. Segment IX, short dorsally; in lateral view, IX extended anterodorsally; posteriorly with short, spinous to serrate, setose dorsolateral processes; posterolateral to posteroventral margin of IX a blunt, very heavily setose lobe, its mesolateral surface excavate and bearing small, inconspicuous, mound-like, setose projections; sternum IX with posteromesal, sclerotized, quadrate projection, its apicolateral corners rounded and its apex slightly excavate mesally. Segment X mound-like, entirely membranous. Inferior appendages elongate, crescentic, curved downward, apically setose; inferior appendages fused basally and apparently fused to base of IXth sternal projection, together forming highly complex structure as in Figure 37. Processes of subphallic membranes present, small, mound-like, setose. Phallus relatively simple; phallobase elongate, sclerotized; phallicata apparently present, but very lightly sclerotized; pair of long, flat, lightly sclerotized parameres; phallus bearing lightly sclerotized, trough-like apex.

MATERIAL EXAMINED.—*Holotype* (male): COLOMBIA, CALDAS, 1.1 km E Termales de Ruíz, 3600 m, 28 Feb 1984, C.M. and O.S. Flint, Jr. (NMNH).

Paratype: COLOMBIA, CALDAS, 0.7 km S entrance Parque Nacional Los Nevados, 4100 m, 28 Feb 1984, C.M. and O.S. Flint, Jr., 1♂ (NMNH).

ETYMOLOGY.—Named for the type locality, the Colombian state of Caldas.

Contulma cataracta, new species

FIGURES 39–43; MAP 2

This species is very similar to *C. spinosa*, but differs from it in several obvious features of the male genitalia. The phallus on the new species bears a pair of large, thick parameres, which are lacking altogether in *C. spinosa*, and segment IX of *C. cataracta*, although bearing a patch of long setae, lacks the large spine-like process seen in *C. spinosa*.

MALE.—Length 4.5 mm. Color fuscous, forewing with three patches of cream-colored setae: at arculus, pterostigma, and apex of discal cell. Foretibia with second spur not apparent. Segment IX, short dorsally; posterior border in lateral view extended anterolaterally; posteroventral margin of IX very heavily setose lobe, its mesodorsal surface bearing patch of long, stout setae and scattered short setae; sternum IX with long, narrow, posteromesal, sclerotized projection. Segment X membranous, except for very lightly sclerotized lateral region; displaced dorsad by phallus. Inferior appendages crescentic, curved downward, bearing short apical setae; fused basally and apparently fused to base of IXth sternal projection, together forming complex structure as in Figure 41. Processes of subphallic membranes present, mushroom-like, setose. Phallus complex; phallobase tubular, sclerotized; with pair of massive, highly convoluted membranous midlateral lobes, each ending in sclerotized, scale-like process; pair of large, heavily sclerotized parameres present midlaterally, their apices somewhat serrate along ventral edges; apical half of phallus (phallicata) lightly sclerotized, trough-like, with membrane dorsally and apically.

MATERIAL EXAMINED.—*Holotype* (male): ECUADOR, NAPO, Río Maspa Chico, 2 km W Cuyuja, 2460 m, 9 Sep 1990, O.S. Flint, Jr. (NMNH).

Paratype: ECUADOR, PICHINCHA, 2.3 km S Tandayapa, 1800 m, 6 Sep 1990, O.S. Flint, Jr., 1 ♂ (UMSP).

ETYMOLOGY.—The specific epithet refers to the cataracts, cascades, and waterfalls frequented by many members of the genus.

MAP 2.—Known adult distribution of *Contulma cataracta*, *C. colombiensis*, *C. echinata*, and *C. tapanti*.

Contulma colombiensis Holzenthal and Flint

FIGURES 4–6, 9, 44–47, 117; MAP 2

Contulma colombiensis Holzenthal and Flint in Flint, 1991:106, figs. 396–399 [male, Colombia: Antioquia (NMNH)].

This species shares with *C. penai* and *C. lanceolata* setose dorsolateral processes on segment IX, but in *C. colombiensis* these processes curve inward apically.

MALE.—Length 4–4.5 mm. Color fuscous, immaculate. Foretibia with second spur minute, barely as long as wide. Segment IX, very short dorsally; in lateral view IX extended anterolaterally; posteriorly with short, dorsolateral, rounded process and larger, apically acute, densely setate, mesally hooked lateral process; posteroventral margin of IX a large, blunt, rounded, very heavily setose lobe; sternum IX with posteromesal, lightly sclerotized, quadrate projection, bearing pair of darkly sclerotized knobs on its ventral surface. Segment X almost entirely membranous, except for very lightly sclerotized apical and lateral regions. Inferior appendages short, thick, crescentic, curved downward; fused basally and apparently fused to base of IXth sternal projection, together forming highly complex structure as in Figure 46. Processes of subphallic membranes apparently absent or very light and not seen in genitalic preparation. Phallus relatively simple; phallobase elongate, sclerotized; phallicata apparently present, but very lightly sclerotized, its apex acute and keel-like; parameres and lateral processes absent; phallotremal sclerite present.

FEMALE.—Size and color as in male. Vaginal apparatus with base narrow, elongate; midlateral processes broad, lightly sclerotized, medial process narrow, sclerotized; apex rounded, sclerotized, acute in lateral view.

MATERIAL EXAMINED.—COLOMBIA, ANTIOQUIA, 12 km N Fredonia, 2000 m, 22 Feb 1983, O.S. Flint, Jr., ♂ holotype, USNM type 104576 (NMNH); same, 1♂; 18 km E San Jerónimo, 23 Feb 1983, C.M. and O.S. Flint, Jr., 1♂, 1♀ paratypes (NMNH); CHOCO, km 114, 6 km E El Siete, 17 Feb 1983, O.S. Flint, Jr., 2♂, 1♀ paratypes (NMNH).

ETYMOLOGY.—The name was proposed in recognition of the country in which the types were found.

Contulma costaricensis, new species

FIGURES 48–51; MAP 1

Contulma costaricensis is a small unadorned species that can be distinguished from other species in the genus by the absence of dorsolateral processes on segment IX, the presence of numerous short setae on the apicolateral and mesal surfaces of segment IX, and by the long, paired, lightly sclerotized parameres of the phallus. It is similar to *C. tica*, but has an apically acute rather than truncate sternal projection of segment IX.

MALE.—Length 4.5 mm. Color fuscous, immaculate. Foretibia with second spur minute, about twice as long as wide. Segment IX, short dorsally; in lateral view extended anterolaterally; posteriorly without dorsolateral processes; posterolateral to posteroventral margin of IX a blunt, very heavily setose lobe, its apicodorsal and apicomesal surfaces bearing numerous setae; sternum IX with posteromesal, sclerotized, triangular projection, its apex narrow and truncate in ventral view and acute and upturned in lateral view. Segment X mound-like, entirely membranous, except for lightly sclerotized lateral portions that apparently articulate basally with sclerotized projections of dorsolateral corners of segment IX. Inferior appendages short, globose, bearing apical setae; fused basally and apparently fused to base of IXth sternal projection, together forming complex structure as in Figure 50. Setose processes of subphallic membranes present. Phallus relatively simple; phallobase elongate, sclerotized; phallicata apparently absent; pair of long, flat, lightly sclerotized parameres present; apical half of phallus membranous.

MATERIAL EXAMINED.—*Holotype* (male): COSTA RICA, CARTAGO, Reserva Tapantí, unnamed tribs. [Quebrada Palmitos and falls], about 9 km (road) NW tunnel, 9.72°N, 83.78°W, 1400 m, 8–9 Apr 1988, C.M. and O.S. Flint, Jr., Holzenthal. (NMNH).

ETYMOLOGY.—Named for the country of Costa Rica, which harbors a rich and heretofore unknown *Contulma* fauna.

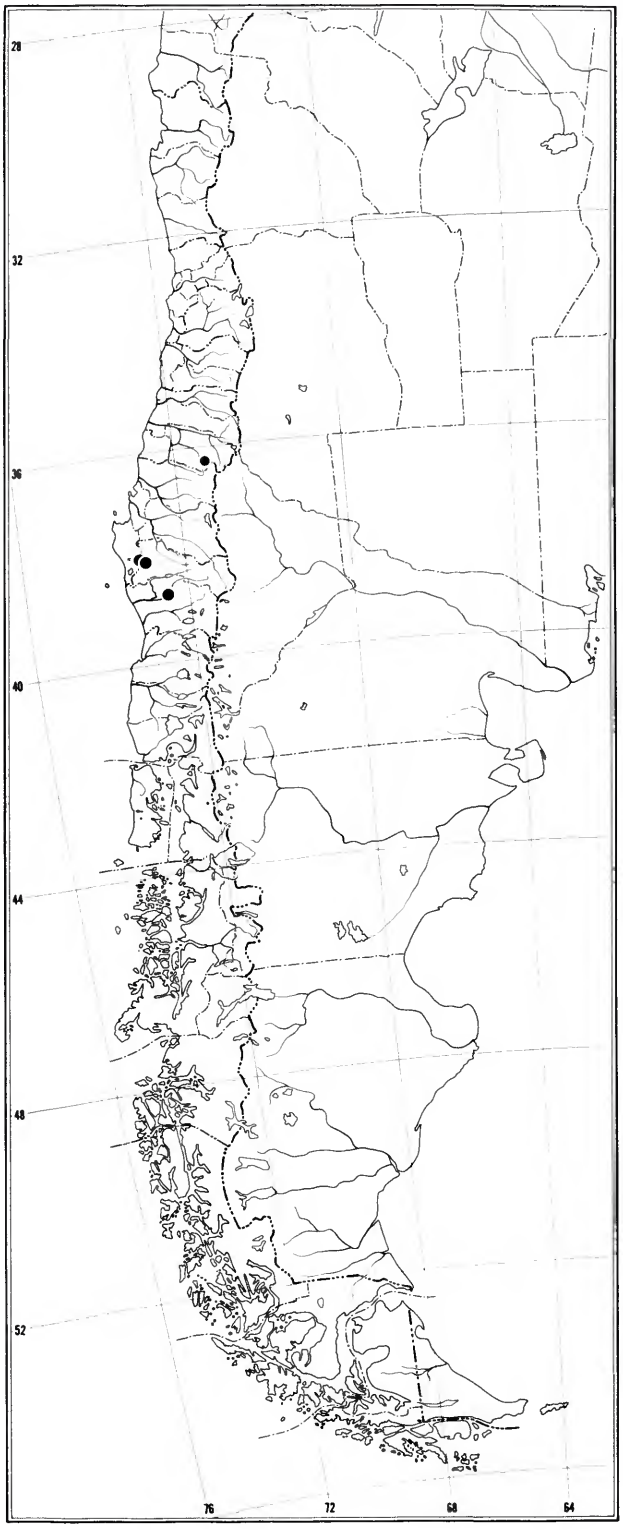
Contulma cranifer Flint

FIGURES 52–56, 118; MAP 3

Contulma cranifer Flint, 1969:513, figs. 41–43 [male, Chile: Malleco (NMNH)]; 1974:91; 1981:82 [transferred to Anomalopsychidae]; 1990:120 [distribution].

The bizarre male genitalia of this, the type species of the genus, are quite different from those of all other *Contulma* species, yet they easily fall within the general groundplan of the *cranifer* Group. The species is recognizable by having a short, strap-like pleural region of segment IX, an elongate, ventrally directed dorsolateral process of segment IX, and a phallus with a massive, convoluted, membranous region and associated sclerotized areas.

MALE.—Length 6–6.5 mm. Color brown, immaculate (specimens examined badly rubbed). Foretibia with second spur small, barely as long as wide. Segment IX, very short dorsally and dorsolaterally; in lateral view, IX much extended anterodorsally; posteriorly with elongate, ventrally directed dorsolateral processes, their apices acute and crossing; posteroventral and ventral margins of IX forming large, blunt, very heavily setose lobes, almost meeting mesoventrally; sternum IX with posteromesal, lightly sclerotized, rounded projection. Segment X membranous, almost obliterated. Inferior appendages short, thick, crescentic, apically acute and bearing subapical setae; fused basally and apparently fused to base of IXth sternal projection, together forming complex structure as in Figure 54. Processes of subphallic membranes



MAP 3.—Known adult distribution of *Contulma cranifer*.

present, small, finger-like, setose, lying laterad of inferior appendages. Phallus very complex; phallobase sclerotized, tubular; phallicata apparently absent or highly membranous and difficult to distinguish from phallic membranes; apical third of phallus bearing large, highly convoluted, folded membranous areas (these membranes appear to be not fully expanded in the specimen figured) with apparently three paired apical areas of varying degrees of sclerotization: dorsal-most sclerites broadly rounded, smooth; median sclerites bearing numerous, small papillae; ventral sclerites bearing both heavily and lightly sclerotized areas.

FEMALE.—Size and color as in male. Vaginal apparatus with base short, broad; midlateral processes broad, lightly sclerotized; medial process narrow, sclerotized; medial membranes heavy, highly convoluted; apex sclerotized, broad, rounded in ventral and lateral views.

MATERIAL EXAMINED.—CHILE, MALLECO, Parque Nacional Contulmo, 2 Jan 1966, Flint and Cekalovic, 2♂, 1♀ paratypes; Río Manzanares [near Purén], 2 Jan 1966, Flint and Cekalovic, 1♂ holotype, 3♀ paratypes. CAUTÍN, Río Cautín, Cajón, 3 Jan 1966, Flint and Cekalovic, 1♀ paratype. LINARES, Embalse Bullileo, 36°18′S, 71°25′W, 11–12 Jan 1994, C.M. and O.S. Flint, Jr., 1♂, 1♀.

Contulma echinata, new species

FIGURES 57–60, 119; MAP 2

As its name implies, *C. echinata*, is distinguished easily from other known species by the presence of distinct spines emanating from a small lateral process on segment IX and by the numerous spines associated with the phallus. The latter character is shared with *C. papallacta* and *C. nevada*.

MALE.—Length 6.5 mm. Color fuscous, forewing with three patches of cream-colored setae: at arculus, pterostigma, and apex of discal cell. Foretibia with second spur minute, barely as long as wide. Segment IX short dorsally; in lateral view, IX extended anterodorsally; posteriorly with long, flat, spatulate dorsolateral process and shorter, more lateral process bearing about 3 long, spine-like setae; posteroventral margins of IX forming large, blunt, very heavily setose lobes; sternum IX with posteromesal, sclerotized projection, its apex deeply cleft mesally, apicolateral corners acute. Segment X entirely membranous. Inferior appendages short, crescentic, bearing apical setae; fused basally and apparently fused to base of IXth sternal projection, together forming complex structure as in Figure 59. Processes of subphallic membranes present. Phallus complex; phallobase tubular, slender, sclerotized; phallicata apparently present, very lightly sclerotized; membranous lobe arising apicodorsally from phallobase and overlying dorsal part of phallicata; apicoventral phallic membranes bearing paired setal areas of about 20 short spine-like setae, about 10-15 longer, spine-like setae, and pair of very large, apical, tooth-like spines.

FEMALE.—Size and color as in male. Vaginal apparatus with

base elongate, narrow, especially medially; midlateral processes sclerotized, curved inward, pointed; medial process elongate, narrow, sclerotized; medial membranes highly convoluted, with pair of small, sclerotized processes; apex heavily sclerotized, tooth-like.

MATERIAL EXAMINED.—*Holotype* (male): COLOMBIA, CALDAS, 5 km W Termales de Ruíz, 3200 m, 27–29 Feb 1984, C.M. and O.S. Flint, Jr. (NMNH).

Paratype: Same data as holotype, 1♀ (NMNH).

ETYMOLOGY.—From the Latin, *echinatus,* in reference to the spines on the phallus.

Contulma ecuadorensis, new species

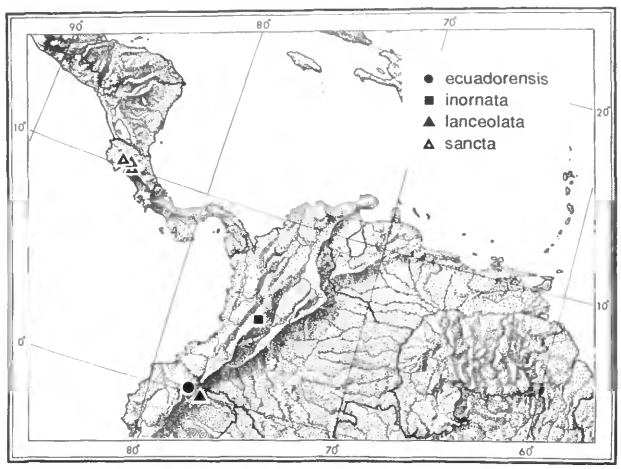
FIGURES 7, 8, 61–65, 120; MAP 4

This species is one of the most distinctive in the genus because of the posteromesal extension of tergum IX, the long, slender, posterolateral processes of IX, and the phallus, with its apical tooth-like processes. Like *C. cranifer* and *C. tijuca,* it has elongate subphallic mushroom-like processes, but is easily distinguished by the posteromesal extension of tergum IX.

MALE.—Length 4.5–5.5 mm. Color fuscous, immaculate. Foretibia with second spur minute, barely as long as wide. Segment IX short dorsally, tergum IX with prominent posteromesal extension; in lateral view, IX extended anterolaterally; posteriorly with long, lateral process, downturned at apex and bearing fine, apicoventral setae; posteroventral margin of IX forming large, rounded, very heavily setose lobe; sternum IX with posteromesal, sclerotized projection; in ventral view its apex broadly excavate mesally, apicolateral corners rounded, in lateral view apex narrow, pointed. Segment X roughly foot-shaped in lateral view, membranous dorsomesally; lateral and ventral portions of X very lightly sclerotized, apex slightly cleft in dorsal view. Inferior appendages short, crescentic, apices acute; fused basally and apparently fused to base of IXth sternal projection, together forming complex structure as in Figure 63. Processes of subphallic membranes present; digitate, setose, as long as inferior appendages. Phallus complex; phallobase tubular, slender, sclerotized; phallicata may be present, but very lightly sclerotized and difficult to distinguish from apical phallic membranes; membranous lobe arising apicodorsally from phallobase and overlying dorsal part of apical half of phallus; apical and apicoventral phallic membranes highly convoluted and appearing as distinct lobes as illustrated in Figures 64, 65; apex of phallus bearing pair of membranous lobes each bearing apical tooth-like spine.

FEMALE.—Size and color as in male. Vaginal apparatus with base very short, about as long as wide; midlateral processes broad basally, narrowed apically; medial process narrow, sclerotized, shorter than midlateral processes; medial membranes lightly sclerotized, convoluted; apex broad, thumb-like, semimembranous.

MATERIAL EXAMINED.—*Holotype* (male): ECUADOR, IMBABURA, Otavalo/Apuila, 2200 m, 8–9 Sep 1977, L.E. Peña G. (NMNH).



MAP 4.—Known adult distribution of *Contulma ecuadorensis, C. inornata, C. lanceolata,* and *C. sancta.*

Paratypes: Same data as holotype, 4♀ (NMNH).

ETYMOLOGY.—Named for the country in which the types were collected.

Contulma inornata, new species

FIGURES 66–69; MAP 4

This species is most similar to *C. colombiensis,* but differs from that species in the absence of setae on the lateral processes of segment IX and in the details of the phallus, among other characters. Three other species, *C. echinata, C. caldensis,* and *C. nevada,* occur within the same region as this new species within the Colombian state of Caldas. They can be separated from each other by characters of the phallus, which is quite similar to that of *C. caldensis,* but lacks the spines found in *C. echinata* and *C. nevada,* by the unadorned lateral process and posteromesal face of segment IX, and by the short posteromesal process of sternum IX, which is only slightly concave apically, rather than several times as long as broad and sometimes bifid apically in the other three species.

MALE.—Length 6.5–7.0 mm. Color fuscous, forewing with large cream-colored spot at arculus. Foretibia with second spur minute, barely as long as wide. Segment IX short dorsally; in lateral view, IX slightly extended anterolaterally; posteriorly with short rounded or pointed dorsolateral, setose process and longer, flat, spatulate lateral process; posteroventral margin of IX forming large, rounded, very heavily setose lobe; sternum IX with short posteromesal, sclerotized projection; in ventral view shallowly excavate apically, in lateral view thin, pointed. Segment X entirely membranous. Inferior appendages short, quadrate, apices blunt, setose; fused basally and apparently fused to base of IXth sternal projection, together forming

complex structure as in Figure 68. Processes of subphallic membranes present, lacking setae. Phallus simple; phallobase tubular, slender, sclerotized; phallicata may be present, but difficult to distinguish from phallobase; apex of phallus with dorsal membranous lobe and ventral, sclerotized, papillate lobe.

MATERIAL EXAMINED.—*Holotype* (male): COLOMBIA, CALDAS, 5 km W Termales de Ruíz, 3200 m, 27–29 Feb 1984, C.M. and O.S. Flint, Jr. (NMNH).

Paratype: Same data as holotype, 1♂ (NMNH).

ETYMOLOGY.—Named for the unadorned processes of segment IX and the phallus.

Contulma lanceolata, new species

FIGURES 70–73; MAP 4

The long, thin, lanceolate processes of segment IX distinguish the male genitalia of this species from the others described in this paper. With respect to the setose dorsolateral processes of IX, this species is most similar to *C. colombiensis* and *C. penai*.

MALE.—Length 4.5 mm. Color fuscous, immaculate. Foretibia with second spur minute, barely as long as wide. Segment IX short dorsally and laterally; in lateral view, IX extended anterodorsally; posteriorly with long, lanceolate, setose dorsolateral process and somewhat shorter, thin, pointed, mesally curved ventrolateral process; posteroventral and ventral margins of IX heavily setose, but not forming large, rounded, lobe; sternum IX with short truncate, posteromesal, sclerotized projection; in ventral view with shallow apical excavation. Segment X large, mostly membranous, but very lightly sclerotized laterally; attenuate in dorsal view; truncate in lateral view. Inferior appendages short, crescentic, apices blunt, setose; fused basally and apparently fused to base of IXth sternal projection, together forming complex structure as in Figure 72. Processes of subphallic membranes present, lacking setae. Phallus relatively simple; phallobase tubular, slender, sclerotized; phallicata may be present, but difficult to distinguish from phallobase; apex of phallus with dorsal membranous lobe and ventral, sclerotized lobe; group of thin setae present apically; phallotremal sclerite apparently present, lightly sclerotized.

MATERIAL EXAMINED.—*Holotype* (male): ECUADOR, NAPO, Baeza (72 km E), in seep at waterfall, 4200 feet [1260 m], 16 May 1975, A.B. Gurney (NMNH).

Paratype: Same data as holotype, 1♂ (NMNH).

ETYMOLOGY.—Named for the long, lanceolate dorsolateral processes of abdominal segment IX.

Contulma nevada, new species

FIGURES 74–77, 121, 129–132; MAP 5

This species is characterized by the short, spatulate, dorsolateral process of segment IX, by the small patch of setae just below this process, and by the patches of small setae located apicoventrally on the phallus. It seems to be closest in general appearance, especially in the latter character, to *C. echinata* and *C. papallacta*.

The very distinctive larva of this species is easily recognized by the short, scale-like hairs of the head and pronotum, which are produced into a large brush centrally on the frontoclypeus and along the anterior margin of the head, and by the vestiture of the mesonotum with only a few dark points laterally. A single early instar larva in the collection lacks the frontoclypeal brush, but agrees in the structure of the thorax and anal prolegs.

MALE.—Length 7.5–8.0 mm. Color fuscous, forewing with three patches of cream-colored setae: at arculus, pterostigma, and apex of discal cell. Foretibia with second spur minute, barely as long as wide. Segment IX short dorsally; in lateral view, IX slightly extended anterolaterally; posteriorly with short, lanceolate, dorsolateral process; posterior and posteroventral margins of IX forming large, rounded, heavily setose lobe, its mesolateral surface excavate and bearing patch of small setae; sternum IX with posteromesal, sclerotized projection; in ventral view with shallow apical cleft and slightly acute apicolateral corners. Segment X large, membranous. Inferior appendages crescentic, apices somewhat pointed, setose; fused basally and apparently fused to base of IXth sternal projection, together forming complex structure as in Figure 76. Processes of subphallic membranes present, digitate, bearing apical setae. Phallus simple; phallobase long, slender, tubular, with small subapicodorsal membranous lobe; apex of phallus very lightly sclerotized, trough-like; apicoventrally with paired group of about 15–20 short, spine-like setae.

FEMALE.—Size and color apparently as in male. Vaginal apparatus with base long; midlateral processes short, slender, pointed apically; medial process lanceolate, longer than midlateral processes; medial membranes convoluted; apex narrow, digitate.

MATERIAL EXAMINED.—*Holotype* (male): COLOMBIA, CALDAS, 0.7 km S entrance Parque Nacional Los Nevados, 4100 m, 28 Feb 1984, C.M. and O.S. Flint, Jr. (NMNH).

Paratypes: Same data as holotype, 5♂ (NMNH), 1♀ (UMSP), 1♂ and 2♀ metamorphotypes (NMNH).

Nontypes: Same data, 21 larvae, 10 pupae (NMNH).

ETYMOLOGY.—Named for the "snows" of the type locality, Parque Nacional Los Nevados.

Contulma papallacta, new species

FIGURES 78–81; MAP 5

This species is similar to *C. echinata*, but differs from it substantially in the nature of the dorsolateral processes of segment IX and the phallus. In *C. papallacta* the more dorsal dorsolateral process is abruptly spatulate apically, whereas in *C. echinata* it is more gradually spatulate. Also, in *C. papallacta*, the ventralmost dorsolateral process is longer and covered with numerous long setae, whereas in *C. echinata* it is shorter and bears from two to three shorter, stouter, spine-like

MAP 5.—Known adult distribution of *Contulma nevada*, *C. papallacta*, *C. penai*, and *C. talamanca*.

setae. Finally the phallic structures of the two species are very similar, but in *C. papallacta* the phallus is much smaller proportionally and lacks the numerous subapical spines found in *C. echinata*.

MALE.—Length 5.5 mm. Color brown in alcohol. Foretibia with second spur minute, about twice as long as wide. Segment IX short dorsally; in lateral view, IX slightly extended anterodorsally; posteriorly with long, flat, abruptly spatulate dorsolateral process and subequal, more lateral process bearing long setae along its entire length; posteroventral margins of IX forming large, blunt, very heavily setose lobes; sternum IX with posteromesal, sclerotized projection, its apex cleft mesally, apicolateral corners rounded. Segment X entirely membranous. Inferior appendages short, curved, bearing apical setae and peg-like setae on ventral edge (Figure 80, inset); fused basally and apparently fused to base of IXth sternal projection, together forming complex structure as in Figure 80. Processes of subphallic membranes present. Phallus complex; phallobase tubular, slender, sclerotized; phallicata apparently present, very lightly sclerotized; membranous lobe arising apicodorsally from phallobase and overlying dorsal part of phallicata; apicoventral phallic membranes bearing pair of large, apical, tooth-like spines.

MATERIAL EXAMINED.—*Holotype* (male): ECUADOR [NAPO], 1 mi [1.6 km] E of Papallacta, 30 Jan 1958, R.W. Hodges (NMNH).

Paratype: Same data as holotype, 1♂ (UMSP).

ETYMOLOGY.—Named for the type locality in Ecuador.

Contulma penai, new species

FIGURES 1, 2, 15–20, 82–85, 122, 133–139; MAP 5

Contulma penai is most similar in overall appearance to *C. colombiensis* in that both species have setose dorsolateral processes of segment IX. However, in the new species, these appendages do not curve mesally and are much closer together basally. Both species have very similar, unadorned phalli, however.

The larva of this species is quite similar to that of *Contulma* species B in the basic structure of the thoracic sclerites and very elongate dorsal comb of the anal proleg. However, the head of *C. penai* is almost evenly convex, without the pair of large, spinose knobs found on the head of species B.

MALE.—Length 5.5–6.0 mm. Color fuscous, forewing with cream-colored spot at arculus. Foretibia with second spur minute, barely as long as wide. Segment IX short dorsally; in lateral view, IX greatly extended anterodorsally; posteriorly with long, pointed, straight setose processes, these processes lie close together basally; posteroventral and ventral margins of IX a blunt, very heavily setose lobe; sternum IX with short, posteromesal, sclerotized, quadrate projection, its apex slightly cleft mesally. Segment X elongate, narrow, entirely membranous. Inferior appendages short, crescentic, curved downward, apically setose; fused basally and apparently fused to base of IXth sternal projection, together forming highly complex structure as in Figure 84. Processes of subphallic membranes present, small, setose. Phallus relatively simple; phallobase short, sclerotized, with small subapicodorsal membranous lobe; apex of phallus elongate, narrow, pointed.

FEMALE.—Size and color as in male. Vaginal apparatus with base narrow, dorsally with lightly sclerotized keel; midlateral processes very lightly sclerotized; medial process narrow, sclerotized; medial membranes light, convoluted; apex lightly sclerotized, broad, with shallow mesal notch.

MATERIAL EXAMINED.—*Holotype* (male): ECUADOR, ZAMORA-CHINCHIPE, 30 km E Loja, 2000 m, 23 Sep 1990, O.S. Flint, Jr. (NMNH).

Paratypes: Same data as holotype, 7♂, 1♀ (NMNH), 3♂, 1♀ (UMSP). ECUADOR, 1977, Peña [no additional data given], 1♂, 1♀ (NMNH).

Nontypes: COLOMBIA, ANTIOQUIA, 18 km E San Jerónimo (road to Medellín), 23 Feb 1984, C.M. and O.S. Flint, Jr., 2 larvae, 1 prepupa, 1 pupa, 2 empty pupal cases (NMNH). ECUADOR, TUNGURAHUA, 13 km E Baños, 1550 m, 15 Sep 1990, O.S. Flint, Jr., 15 larvae (cases incorporating long plant material), ♂ metamorphotype (NMNH); Baños (5 km S), 4 Jun 1977, P.J. Spangler and D.R. Givens, 3 larvae (NMNH); Baños (18 km E), coll. in drainage ditch below seep over rock outcrops, 5130 feet [1539 m], 25 Jan 1976, Spangler et al., 4 larvae, cases (NMNH); Baños (32 km E), seepage over rock outcrops, 28 Jan 1976, Spangler et al., 1 larva, cases (NMNH); ZAMORA-CHINCHIPE, 30 km E Loja, 2000 m, 23 Sep 1990, O.S. Flint, Jr., many larvae, pupae, and cases, ♀ metamorphotype (NMNH).

ETYMOLOGY.—Named in honor of the collector, L.E. Peña, who through his collecting efforts has added greatly to our knowledge of the Neotropical caddisfly fauna.

Contulma sancta, new species

FIGURES 86–89; MAP 4

Contulma sancta is similar to two other species, *C. cataracta* and *C. valverdei*, in that all have membranous dorsolateral lobes and large parameres on the phallus and lack the dorsolateral process of segment IX. *Contulma cataracta* has a patch of large, mesolateral, spine-like setae on segment IX, which setae are much smaller in *C. sancta* and lacking in *C. valverdei*. The apicomesal lobe of the phallus in *C. sancta* is thin and trough-like, but large and membranous in *C. valverdei*.

MALE.—Length 4 mm. Color fuscous, forewing with patches of cream-colored setae at arculus and pterostigma. Foretibia with second spur not apparent. Segment IX short dorsally; in lateral view, IX somewhat extended anterodorsally; posterolateral margin of IX a very heavily setose, obtuse lobe; patch of short, stout setae present mesally on posterolateral lobe of IX; sternum IX with short, quadrate, posteromesal, sclerotized projection, its apex very slightly excavate mesally, apicolateral corners rounded. Segment X membranous, lightly sclerotized laterally. Inferior appendages broadest basally, crescentic, curved downward, apices slightly rugose; fused basally and apparently fused to base of IXth sternal projection, together forming highly complex structure as in Figure 87. Processes of subphallic membranes small, setose. Phallus with phallobase tubular, sclerotized, with pair of subapicodorsal membranous lobes and pair of heavily sclerotized, narrow parameres; apex of phallus thin, lightly sclerotized, trough-like.

MATERIAL EXAMINED.—*Holotype* (male): COSTA RICA, ALAJUELA, Quebrada Virgencita, 10.2 km S Bajos del Toro, 10.168°N, 84.326°W, 1780 m, 5–6 Sep 1990, Holzenthal, Blahnik, Huisman (NMNH).

Paratypes: COSTA RICA, ALAJUELA, Reserva Forestal San Ramón, Río Lorencito and tributaries, 10.216°N, 84.606°W, 980 m, 15 Feb 1994, Holzenthal, Muñoz, 1♂ (UMSP); [PUNTARENAS] 14.1 mi [22.6 km] SE Esparta, 23 Jul 1967, O.S. Flint, Jr., 1♂ (UMSP).

ETYMOLOGY.—The name is proposed in reference to the sanctified Virgin, the basis for the name of the stream at the type locality.

Contulma spinosa Holzenthal and Flint

FIGURES 3, 11–13, 90–93, 123, 140–146; MAP 6

Contulma spinosa Holzenthal and Flint in Flint, 1991:106, figs. 400–403 [male, Colombia: Antioquia (NMNH)].

This species is readily separable from all others based on the structure of the dorsolateral processes of segment IX and the phallus with its huge membranous lobes and their scale-like apical processes. However, in the latter respect, it is similar to *C. cranifer* and, perhaps, *C. ecuadorensis*.

The larva of this species is easily recognized by possessing short hair on the head, having a broad (in lateral aspect) anterolateral lobe of the pronotum, and lacking the transverse row of dark spots on the mesonotum.

MALE.—Length 4.5–5 mm. Color fuscous, immaculate. Foretibia with second spur about $1^1/2$ times as long as wide. Segment IX short dorsally; posterior border in lateral view extended anterodorsally; posteriorly with very heavily sclerotized dorsolateral process, its apex directed ventrad and

MAP 6.—Known adult distribution of *Contulma spinosa*, *C. tica*, *C. tijuca*, and *C. valverdei*.

bearing many spinose setae on ventral margin; posterolateral margin of IX a large, roughly triangular, very heavily setose lobe, bearing smaller setae along dorsomesal edge; sternum IX with elongate posteromesal, sclerotized projection. Segment X membranous, except for very lightly sclerotized lateral region; displaced dorsad by phallus. Inferior appendages long, narrow, pointed, crescentic, bearing short apical setae; fused basally and apparently fused to base of IXth sternal projection, together

forming highly complex structure as in Figure 91. Processes of subphallic membranes present, large, setose. Phallus complex; phallobase elongate, sclerotized; apical half of phallus comprised of pair of massive, highly convoluted membranous dorsolateral lobes and similar mesoventral lobe, each lobe ending in sclerotized, scale-like process.

FEMALE.—Size and color as in male. Vaginal apparatus with base elongate, narrow; midlateral and medial processes narrow, sclerotized, subequal; apex narrow, semimembranous.

MATERIAL EXAMINED.—COLOMBIA, ANTIOQUIA, Quebrada La Iguana, 17 km NW Medellín [on road to San Jerónimo], 14–15 Feb 1983, O.S. Flint, Jr., ♂ holotype, USNM type 104575 (NMNH); same data, 1♂ paratype (NMNH); BOYACA, Quebrada El Chuscal, Santuario Iguaque, near Arcabuco, 2650 m, 5 Aug 1988, Luis E. LaRotta, 1♂ paratype (NMNH); same, except Quebrada Colorado, 2700 m, 16 Aug 1988, 1♀ (NMNH); CUNDINAMARCA, 23 km E El Colegio, 9 Mar 1969, P.J. Spangler, 1 larva (NMNH). ECUADOR, AZUAY, Río Llaviuco, 16 km W Cuenca, 3010 m, 18 Sep 1990, O.S. Flint, Jr., 1♂, 4♀, many larvae, pupae, ♂ and ♀ metamorphotypes (NMNH); PICHINCHA, 7 km E Pifo, 2950 m, 26–28 Sep 1990, O.S. Flint, Jr., 1 larva, 1 immature pupa NMNH); 20.5 km E Pifo, 3700 m, 26–28 Sep 1990, O.S. Flint, Jr., 1 larva (NMNH); Quito (64 km SW), base of waterfall, 6 May 1975, Spangler, Gurney, Langly, and Cohen, 1 larva (NMNH); Quito, Mt. Pichincha, brook, 2 Nov 1977, Jos. J. Anderson, 1 small larva (NMNH); TUNGURAHUA, Baños (14 km E), 5380 feet [1614 m], 25 Jan 1976, Spangler et al., 1 larva (NMNH); ZAMORA-CHINCHIPE, 30 km E Loja, 2000 m, 23 Sep 1990, O.S. Flint, Jr., 1♂, 2♀ (NMNH), 1♂, 1♀ (UMSP), many larvae, pupae, and cases, ♂ metamorphotype (NMNH).

ETYMOLOGY.—The name was proposed in recognition of the large patch of spines on the ventral margin of dorsolateral process of segment IX.

Contulma talamanca, new species

FIGURES 94–98, 124; MAP 5

This new species is distinguishable from others in the genus by the patch of long, spine-like setae located on the mesolateral surface of segment IX, which character it shares with *C. tapanti*, and by the excavate, setose mesolateral surfaces of segment IX. The phallus, with its spinous apex, is also unique.

MALE.—Length 4.0–4.5 mm. Color fuscous, immaculate. Foretibia with second spur minute, barely as long as wide. Segment IX longer dorsally than in other species; in lateral view, IX slightly extended anterodorsally; posteriorly without processes or projections; posterolateral and posteroventral margins of IX a very heavily setose lobe, its mesolateral surface greatly excavate and clothed with numerous, long, thin setae; patch of about 15 long, stout, spine-like setae present apicomesally on IX; sternum IX with short, posteromesal, sclerotized projection, its apex slightly cleft mesally, apicolateral corners rounded. Segment X elongate, tubular, lightly sclerotized, covered with short, fine setae; bearing membranous apical lobe. Inferior appendages short, crescentic, curved downward, bearing short apical setae; fused basally and apparently fused to base of IXth sternal projection, together forming highly complex structure as in Figure 96. Processes of subphallic membranes present, mushroom-like, setose. Phallus complex; phallobase tubular, sclerotized; phallus with paired subapicodorsal lightly sclerotized lobes; apex of phallus bearing pair of long, sinuate, lightly sclerotized setae laterally, about 10 heavily sclerotized spine-like setae ventrally and ventrolaterally, and heavily sclerotized apicodorsal wedge-shaped sclerite (phallotremal sclerite?).

FEMALE.—Size and color as in male. Vaginal apparatus with base broad, about as long as wide; midlateral processes lightly sclerotized, narrow; medial process narrow, pointed apically, subequal to midlateral processes; mesal membranes highly convoluted, especially in region at basolateral corners of apical sclerite where there is a small, darkened membranous area; highly folded membranes also underlying base of vaginal apparatus; apex broad, sclerotized, in lateral view, flat, pointed.

MATERIAL EXAMINED.—*Holotype* (male): COSTA RICA, PUNTARENAS, Río Jaba at rock quarry, 1.4 km (air) W Las Cruces, 8.79°N, 82.97°W, 1150 m, 14 Jun 1986, Holzenthal, Heyn, Armitage (NMNH).

Paratypes: Same data as holotype, 5♂, 1♀ (INBIO); same, except 9 Aug 1990, Holzenthal, Blahnik, Muñoz, 38♂, 6♀ (UMSP).

ETYMOLOGY.—Named for the mountain range of the type locality, being the Cordillera de Talamanca of Costa Rica.

Contulma tapanti, new species

FIGURES 99–102, 125; MAP 2

This species is most similar to *C. talamanca*. It is easily distinguished by lacking the excavate, hairy mesolateral surface of segment IX (although it possesses the cluster of spiniform setae) and lacking the spiny apex of the phallus.

MALE.—Length 4.0–4.5 mm. Color fuscous, immaculate. Foretibia with second spur minute, barely as long as wide. Segment IX short dorsally; in lateral view, IX extended anterodorsally; posteriorly with very small, setose dorsolateral process; posterolateral and posteroventral margins of IX a very heavily setose truncate lobe; patch of about 20 long, stout, spine-like setae present apicomesally on IX; sternum IX with posteromesal, sclerotized projection, its apex broadly cleft mesally, apicolateral corners rounded. Segment X large, membranous, lightly sclerotized laterally. Inferior appendages broad, especially basally, crescentic, curved downward, bearing short apical setae; fused basally and apparently fused to base of IXth sternal projection, together forming highly complex structure as in Figure 101. Processes of subphallic membranes small, digitate, setose. Phallus relatively simple; phallobase tubular, sclerotized, with apicodorsal membranous lobe; paired, sclerotized flange-like processes present laterally;

and pair of long, slender, lightly sclerotized parameres.

FEMALE.—Size and color as in male. Vaginal apparatus with base broad, truncate; midlateral processes broad, lightly sclerotized; medial process narrow, sclerotized; apex sclerotized, broad, truncate in ventral and acute in lateral view.

MATERIAL EXAMINED.—*Holotype* (male): COSTA RICA, CARTAGO, Reserva Tapantí, unnamed trib. [Quebrada Palmitos and falls] about 9 km (road) NW tunnel, 9.72°N, 83.78°W, 1400 m, 8–9 Apr 1988, C.M. and O.S. Flint, Holzenthal (NMNH).

Paratypes: Same data as holotype, 1♂, 1♀ (UMSP), 1♂ (INBIO).

ETYMOLOGY.—Named for the Tapantí Wildlife Reserve in the western Talamanca Mountains of Costa Rica. The reserve covers about 5000 hectares of steep forested slopes of the Río Grande de Orosi watershed and harbors an unusually rich and endemic caddisfly fauna.

Contulma tica, new species

FIGURES 103–106; MAP 6

This species is very similar to *C. costaricensis*, but can be separated from it by the shorter phallic parameres and the more acute posteromesal process of sternum IX in the new species.

MALE.—Length 4.0 mm. Color fuscous, immaculate. Foretibia with second spur minute, barely as long as wide. Segment IX very short dorsally; in lateral view, IX only slightly extended anterolaterally; posterolateral margin of IX a very heavily setose truncate lobe; sternum IX with large posteromesal, sclerotized projection, its apex acute. Segment X small, entirely membranous except for lightly sclerotized lateral portion, which apparently articulates basally with sclerotized projection of dorsolateral corners of segment IX; X displaced dorsad by phallus. Inferior appendage broad, hemispherical; bearing short apical setae; fused basally and apparently fused to base of IXth sternal projection, together forming highly complex structure as in Figure 105. Processes of subphallic membranes present, setose. Phallus very simple; phallobase tubular; phallus with highly convoluted internal membranes and short, paired parameres.

MATERIAL EXAMINED.—*Holotype* (male): COSTA RICA, PUNTARENAS, Río Bellavista, about 1.5 km NW Las Alturas, 8.951°N, 82.846°W, 1400 m, 2–3 Aug 1987, Holzenthal, Morse, Clausen (NMNH).

ETYMOLOGY.—Named for the Costa Ricans, or "Ticos," in recognition of the warm hospitality they have extended to the authors during their research in the country.

Contulma tijuca, new species

FIGURES 107–110, 126, 147–150 (probable *tijuca*); Map 6

The complex structure formed by the inferior appendages and posteromesal projection of sternum IX in *Contulma tijuca* is quite different than that found in all other known species. In the new species, the posteromesal projection bears apical, flat, spine-like setae and the inferior appendages are digitate. However, the very reduced nature of tergum X and the elongate, ventrally directed dorsolateral processes of segment IX are similar to those seen in *C. cranifer*.

Two larvae were taken at the same time as the adults and are in all probability the same species, but this is not absolutely confirmed. The larvae have a simple, but hairy head, dark points near the lateral margin of the mesonotum, and a very long anal proleg with a short, rounded, dorsal comb.

MALE.—Length 4.5 mm. Color fuscous, immaculate. Foretibial spurs not evident. Segment IX very short dorsally; in lateral view, anterior margin nearly straight; posteriorly with elongate, curved, ventrally directed dorsolateral process, apically rugose; posteroventral margin of IX forming prominent, acute, very heavily setose lobe; sternum IX with posteromesal, sclerotized projection, apically cleft, anterolateral corners bearing about 4 flat, closely appressed, tooth-like setae; in lateral view this process large, quadrangular. Segment X membranous, almost obliterated. Inferior appendages short, quadrate, apparently fused to base of IXth sternal projection, together forming highly complex structure as in Figure 109. Processes of subphallic membranes present, digitate, apically setose. Phallus relatively simple; phallobase sclerotized, tubular; apex of phallus bearing small dorsal membranous lobe, paired triangular sclerites, and ventral sclerotized, setose lip; phallotremal sclerite present, flat, apically forked.

FEMALE.—Size and color as in male. Vaginal apparatus with base very broad, quadrate; midlateral processes short, narrow, sclerotized; medial process narrow, sclerotized; apex sclerotized, elongate, narrow, curved, especially in lateral view.

MATERIAL EXAMINED.—*Holotype* (male): BRAZIL, RIO DE JANEIRO, Parque Nacional Tijuca, Represa dos Ciganos, 7 Apr 1977, C.M. and O.S. Flint, Jr. (MZUSP).

Paratype: Same data as holotype, 1♀ (MZUSP).

Nontypes: Same data as holotype, 2 larvae (probably this species), empty cases.

ETYMOLOGY.—Named for the type locality, Tijuca National Park, Brazil. Interestingly, the genus is named for Contulmo National Park, Chile.

Contulma valverdei, new species

FIGURES 14, 111–115, 127, 151–156; MAP 6

Contulma valverdei can be diagnosed from its sympatric congeners by the absence of any spines on the dorsolateral or mesal surfaces of segment IX and by its unique, large, complex phallus.

The larvae of this species have an evenly convex head with short setae, except anteriorly, and the dark points of the mesonotum are incomplete middorsally.

MALE.—Length 4.0 mm. Color brown in alcohol. Foretibia

with second spur minute, barely visible. Segment IX short dorsally; in lateral view, IX only slightly extended anterolaterally; posterolateral margin of IX a very heavily setose quadrate, truncate lobe; sternum IX with posteromesal, sclerotized, quadrate projection, its apex only very slightly emarginate. Segment X entirely membranous, except for lightly sclerotized lateral portions. Inferior appendage broad, crescentic; bearing short apical setae; fused basally and apparently fused to base of IXth sternal projection, together forming highly complex structure as in Figure 113. Processes of subphallic membranes present, setose. Phallus complex, very large; phallobase tubular, with highly convoluted internal membranes; pair of subapicodorsal membranous lobes, each ending in sclerotized scale-like process and pair of midlateral, large, heavily sclerotized, striate parameres; apex of phallus trough-like, with highly convoluted membranes; phallotremal sclerite (?) present, large, exact shape difficult to discern.

FEMALE.—Size and color as in male. Vaginal apparatus with base short, broad; midlateral processes narrow, sclerotized; medial process elongate, narrow, sclerotized; medial membranes heavy, highly convoluted; apex heavily sclerotized, very broad.

MATERIAL EXAMINED.—*Holotype* (male): COSTA RICA, CARTAGO, Reserva Tapantí, waterfall, about 1 km (road) NW tunnel, 9.69°N, 83.76°W, 1600 m, 10 Jun 1988, C.M. and O.S. Flint, Jr., Holzenthal (NMNH).

Paratypes: COSTA RICA, CARTAGO, Reserva Tapantí, Río Grande de Orosi, 9.686°N, 83.756°W, 1650 m, 18–21 Mar 1987, Holzenthal, Hamilton, Heyn, 2♀ (UMSP).

Nontypes: COSTA RICA, CARTAGO, Reserva Tapantí, Río Grande de Orosi, 9.686°N, 83.756°W, 1650 m, 18–21 Mar 1987, Holzenthal, Hamilton, Heyn, 48 larvae (UMSP, NMNH); Reserva Tapantí, Río Badilla, 9.688°N, 83.757°W, 1640 m, 21 Mar 1987, Holzenthal and Hamilton, 4 larvae (UMSP).

ETYMOLOGY.—Named in honor of Mr. Ronald Valverde Guillén, Geologist, Instituto Costaricense de Electricidad (ICE), in recognition of his generous hospitality and logistic support during our many pleasant and productive days at ICE's facilities on the Río Grande de Orosi in the Tapantí National Wildlife Reserve.

Contulma species A

FIGURE 128

Although characters have not been found in the female genitalia to separate the species into the same groups as with the males, it seems that this species will be found to belong to the *spinosa* Group based on the similarity of its genitalia to those of *C. talamanca* and *C. valverdei*. In all three species, both the base and apex of the vaginal apparatus are broad.

FEMALE.—Length, 6 mm. Color fuscous. Vaginal apparatus with base short, about as long as wide; midlateral processes long, broad, rounded apically; medial process as long as midlateral processes, narrow, pointed apically; mesal and apical membranes highly convoluted; apex broad, sclerotized, with slight apicomesal emargination, in lateral view, narrow, pointed.

MATERIAL EXAMINED.—*Female:* ECUADOR, NAPO, Sebundoy, 2600 m, 11–15 Sep 1977, L.E. Peña G., 1♀ (NMNH).

Contulma species B

FIGURES 157–161

These larvae are very striking in the possession of a spinose knob posteriorly on each side of the head, but otherwise the structure of the pro- and mesonota and anal claws is very much like that of *C. penai*.

MATERIAL EXAMINED.—ECUADOR, NAPO, Baeza (72 km E), waterfall, 16 May 1975, P.J. Spangler, 2 larvae, 6 cases.

Contulma species C

FIGURES 162–164

This larva is easily distinguished from the other known larvae by the unmodified head that bears pale, decumbent, scale-like setae, the rugose pronotum, the mesonotum covered by short setae and only a few lateral knobs, and a long anal proleg whose claw bears a very large accessory comb. This might be the larva of *C. caldensis* or *C. inornata* whose adults were taken nearby.

A small larva in the collection of *C. nevada* lacks the central brush on the frontoclypeus, and thus its head is quite similar to that of species C. However, the structure of its thorax and anal prolegs is typical of that of *C. nevada*, not that of species C. The larva of species C is also larger than that of *C. nevada*.

MATERIAL EXAMINED.—COLOMBIA, CALDAS, 3.7 km E Termales de Ruiz, 3800 m, 28 Feb 1984, C.M. and O.S. Flint, Jr., 1 larva.

Phylogenetic Considerations

MONOPHYLY OF THE ANOMALOPSYCHIDAE AND THE FAMILY'S POSITION WITHIN THE TRICHOPTERA

Now that the adult and immature stages of *Contulma* are more fully known and described it is possible to offer additional insights into the phylogenetic relationships among the Anomalopsychidae and other case making families. Flint (1981) identified one synapomorphy for the family: the simple, reduced female genitalia, with the large, heavily setose, rectangular sternum VIII. Flint also noted the large membranous connection to sternum IX, forming a gap to hold the egg mass. In addition, female sterna VIII of both *Anomalopsyche* and *Contulma* have prominent anterolaterally directed apodemes and the membranes of the pleural region are large. The two genera perhaps engage in similar oviposition behaviors.

In addition to these female genitalic characters, at least one larval character seems to be synapomorphic. Larvae of both genera have a dorsomesal comb of accessory teeth on the anal

claw, although it is much more developed in *Contulma* (Flint, 1981, fig. 28). Somewhat similar modifications of the anal claw are seen in the Helicopsychidae, but appear to be of a different nature and are not borne on a long extension of the claw (Monson et al., 1988, fig. 2E). A second larval character may be synapomorphic: absence of bifid tubercles dorsolaterally on abdominal segment VIII. Being unable to find any row of bifid tubercles in the larvae of *Contulma,* we have reexamined the larvae of *Anomalopsyche* in this regard. We are unable now to find them in the larvae of the latter genus, and can only conclude Flint (1981) was in error. In some *Contulma* species from Ecuador there are small structures on segment VIII that appear to be minute bifid tubercles, but other species show nothing on this or other segments. The presence, but restriction, of bifid tubercles to segment VIII is considered one of the synapomorphies of the Brevitentoria of Weaver (1984). Their absence in almost all anomalopsychid larvae could represent a derived loss.

If, as it seems, a few of the species of *Contulma* still possess weak bifid tubercles on segment VIII, the family would clearly remain in the Brevitentoria where it was originally placed by Flint (1981) and later substantiated by Weaver (1984). The lack of bifid tubercles in most species would represent further development of a trend within the family. The complete loss of the tubercles, we believe, is a secondarily derived condition that in itself neither speaks for or against the placement of the family, which then must be placed on other evidence. The earlier placement of the Anomalopsychidae within the Brevitentoria by Flint (1981) and Weaver (1984) is further corroborated herein by two apomorphies found in *Contulma* and shared with Brevitentoria: atrophication of adult dorsal tentorial arms and female with ability to form an egg mass and carry it in flight. Later, Weaver and Morse (1986) placed the family in Sericostomatoidea of Brevitentoria, based on Weaver's (1983) contention that included families shared the following synapomorphies: larval abdominal tergite IX reduced and adult tibial spur formula 2,2,4. *Contulma* larvae, as newly described herein, and *Anomalopsyche* both lack a sclerotized tergite IX and although adults of both genera have 2,2,4 tibial spur formulae, the second spur of the foreleg of *Contulma* is present, but rudimentary. In any case, Weaver's (1983) placement of Anomalopsychidae in Sericostomatoidea is corroborated by the larval characters of *Contulma.*

Unfortunately, we are unable to offer further insight into the position of the Anomalopsychidae within the Sericostomatoidea. Flint (1981) suggested that it held a basal position, perhaps related to the Beraeidae and Helicophidae. Weaver (1983) agreed with a basal position, referring to the family's retention of adult ocelli, which are lacking in all other families in the subfamily. The most recent study attempting to analyze cladistically the families of the Sericostomatoidea (Scott and de Moor, 1993) also noted the same primitive trait, and their tree also places the Anomalopsychidae in a basal position in the superfamily. In the three most-parsimonious trees it is found in a basal trichotomy, shared with either the Sericostomatidae, or with the two lineages within the superorder. In any case, the characters described, illustrated, and discussed above for the species of *Contulma* should prove useful to ongoing studies by Weaver (pers. comm.) and others on the relationships among these caddisfly families.

Phylogeny of the Species of *Contulma*

Although the definition of the Anomalopsychidae is based on few synapomorphies and the family's position within the Brevitentoria and Sericostomatoidea may be uncertain, there is no doubt that the genus *Contulma* is monophyletic. This conclusion is based on several characters and these and others were analyzed with the numerical parsimony program PAUP version 3.1.1 (Swofford, 1993) to infer phylogenetic relationships among the species of *Contulma.*

Methods.—Sixteen adult characters, most from the male genitalia, were included in the analysis. Characters were coded as "0" if ancestral and "1," "2," or "3" if derived, depending on the number of derived states (Table 1). All characters were equally weighted and all, except 8, were coded as ordered, based on the assumption that they exhibited linear morphoclines. *Anomalopsyche minuta* was designated the outgroup taxon.

Character Analysis and Polarization.—

Character 1: Forewing cell R. This character, along with characters 2, 3, 5, 11, and 16 were uninformative with regard to species level relationships, but together with characters 4, 9, and 12 strongly support monophyly for *Contulma.* In *Contulma* the space between R and M+Cu1 of the forewing is wide and is interpreted as the derived state of character 1. This character state also can be stated as stem of R very long with first branch (between R and Rs) not occurring until the midlength of the wing. In *Anomalopsyche* (Flint, 1981, figs. 12, 16) and Trichoptera in general, there is not such a large open space or, differently stated, the first branch of R occurs much more basally.

Character 2: Hind wing fork I. The presence of fork I in the hind wing is the primitive condition as seen in *Anomalopsyche* and primitive Trichoptera. Its absence in *Contulma* is regarded as the derived character state. However, the loss of fork I occurs in other genera throughout the order.

Character 3: Male segment VII ventromesal process. The presence of a small ventromesal process on abdominal segment VII is part of the groundplan of the Trichoptera. *Anomalopsyche minuta* has a short, broad ventromesal process. The absence of such a process in *Contulma* is considered to be synapomorphic, but like character 2, this structure is frequently absent throughout the Trichoptera.

Character 4: Male segment IX posterior border. The

TABLE 1.—Character Matrix for *Contulma* Species (0 = plesiomorphic state; 1, 2, 3 = apomorphic states; ? = missing data). ADULT CHARACTERS—Character 1: Space between R and Cu1+M of forewing: 0 = normal, 1 = wide; Character 2: Hind wing fork I: 0 = present, 1 = absent. MALE GENITALIA—Character 3: Segment VII ventromesal process: 0 = present, 1 = absent; Character 4: Segment IX posterior border: 0 = not lobe-like, 1 = very heavily setose, lobe-like, truncate, 2 = extended, acute; Character 5: Sternum IX posteromesal sclerotized projection: 0 = absent, 1 = present; Character 6: Segment IX mesolateral patch of setae: 0 = absent, 1 = present, 2 = present and rod-like; Character 7: Segment IX dorsolateral process: 0 = absent, 1 = present, 2 = present and broad or somewhat spatulate, 3 = broad and setose; Character 8: Posteromesal sclerotized projection of sternum IX: 0 = apically entire or shallowly emarginate, 1 = deeply cleft, 2 = narrow elongate, 3 = short attenuate; Character 9: Segment X sclerotization: 0 = sclerotized, 1 = very membranous, 2 = almost obliterated; Character 10: Segment X lateral articulating sclerites: 0 = absent, 1 = present; Character 11: Inferior appendages: 0 = large, elongate, 1 = small, crescentic; Character 12: Subphallic mushroom-like processes: 0 = absent, 1 = present, 2 = present, elongate; Character 13: Phallus with dorsolateral, highly convoluted, membranous lobes: 0 = absent, 1 = present, membranous apically, 2 = sclerotized apically; Character 14: Phallus apicoventral spines: 0 = absent, 1 = present, 2 = present, prominent; Character 15: Phallus apex: 0 = blunt, 1 = apically narrow, acute. FEMALE GENITALIA—Character 16: Vaginal apparatus: 0 = oval, 1 = trident-shaped.

Taxon	Character															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Anomalopsyche	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0
adamsae	1	1	1	1	1	0	1	0	1	0	1	1	0	0	0	1
bacula	1	1	1	2	1	2	0	2	1	0	1	1	2	0	0	1
caldensis	1	1	1	1	1	1	0	0	1	0	1	1	0	0	0	1
cataracta	1	1	1	2	1	1	0	2	1	0	1	1	2	0	0	1
colombiensis	1	1	1	1	1	0	3	0	1	0	1	?	0	0	1	1
costaricensis	1	1	1	1	1	1	0	3	1	1	1	1	0	0	0	1
cranifer	1	1	1	1	1	0	1	0	2	0	1	2	0	0	0	1
echinata	1	1	1	1	1	1	2	1	1	0	1	1	0	2	0	1
ecuadorensis	1	1	1	1	1	0	1	0	1	0	1	2	0	0	0	1
inornata	1	1	1	1	1	0	2	0	1	0	0	1	1	1	0	0
lanceolata	1	1	1	1	1	0	3	0	1	0	1	1	0	0	0	1
nevada	1	1	1	1	1	1	2	1	1	0	1	1	0	1	0	1
papallacta	1	1	1	1	1	1	2	1	1	0	1	1	0	2	0	1
penai	1	1	1	1	1	0	3	0	1	0	1	1	0	0	1	1
sancta	1	1	1	1	1	1	0	0	1	0	1	1	1	0	0	1
spinosa	1	1	1	2	1	2	0	2	1	0	1	1	2	0	0	1
talamanca	1	1	1	1	1	1	0	0	1	0	1	1	0	0	0	1
tapanti	1	1	1	1	1	1	0	0	1	0	1	1	0	0	0	1
tica	1	1	1	1	1	?	0	3	1	1	1	1	0	0	0	1
tijuca	1	1	1	1	1	0	1	0	2	0	1	2	0	0	0	1
valverdei	1	1	1	1	1	0	0	0	1	0	1	1	2	0	0	1

enlarged, extended, very heavily setose, lobe-like posterior borders of segment IX in male *Contulma* appear to be unique within the Trichoptera. Such lobes certainly do not occur in *Anomalopsyche*. We suspect that these lobes may be functionally equivalent to the inferior appendages in other Trichoptera, which aid in clasping the female during copulation. In *Contulma*, the inferior appendages are small and medially located and may not be capable of clasping, that function being taken over by the IXth segment setose lobes. The very extended, acute nature of these lobes in some *Contulma* species is considered a further derived condition (state 2).

Character 5: Male segment IX posteromesal sclerotized projection. This is a character that occurs uniquely in *Contulma*. The sclerotized projection seems to fuse basally with the inferior appendages and together this character complex is perhaps the most distinctive feature of the male genitalia. Nothing like it appears on *Anomalopsyche* or other Trichoptera.

Character 6: Male segment IX mesolateral setal patch. The presence of these setae on the inner surface of segment IX is interpreted as being derived and was considered to be the first of an ordered multistate transformation series. In *C. bacula* and *C. spinosa*, this patch of setae seems to coalesce into a distinct, extended, rod-like process (state 2). *Anomalopsyche* has no setae in this position and represents the generalized trichopteran condition.

Character 7: Male segment IX dorsolateral process. Many species of *Contulma* have a dorsolateral process on the posterior edge of segment IX. This character was coded as ordered and multistate, depending on whether it

was present, short, and unmodified (state 1), broad and flattened (state 2), or broadened and covered with many small setae (state 3). *Anomalopsyche* does not have such processes.

Characters 8: Male posteromesal sclerotized projection of sternum IX. We assume here that a short, somewhat quadrate, apically entire posteromesal projection of sternum IX represents the primitive condition and the modifications indicated in character 8 are derived. However, because this projection does not occur in *Anomalopsyche*, we have no solid basis for this interpretation. Nevertheless, the species that share these particular modifications are similar in other characters that may suggest that the elongate (state 1), cleft (state 2), and attenuate (state 3) modifications of the posteromesal projection are uniquely derived. No logical morphocline was apparent and the transformation series was coded as unordered.

Character 9: Male segment X sclerotization.

Character 10: Male segment X lateral articulating sclerites. In *Anomalopsyche* and the trichopteran groundplan, segment X is sclerotized and often bears distinctly sclerotized lateral processes (the intermediate appendages). In *Contulma*, segment X is very membranous (character 9, state 1) and in a few species is almost obliterated (state 2). It never has intermediate appendages. In two species, however, segment X retains some lateral sclerotization and this sclerotization seems to be articulated basally with small condyles on the dorsolateral comers of segment IX (character 10). This character, especially evident in *C. costaricensis* and *C. tica*, seems to aid in the dorsal displacement of segment X for extrusion or expansion of the phallus (Figures 84, 139). Other species may possess these lateral sclerites, but throughout the genus segment X is so completely membranous and lightly sclerotized they are difficult to discern.

Character 11: Male inferior appendages. The short, crescentic, basally fused, inferior appendages of *Contulma* are unique to the genus. They are apparently fused to base of the posteromesal projection of sternum IX. The inferior appendages of *Anomalopsyche* are larger and more typical of Trichoptera in general.

Character 12: Male subphallic mushroom-like processes. These very membranous, setose, mound-like or mushroom-like processes, apparently associated with subphallic membranes above inferior appendages, are unique to *Contulma*. They are lacking in *Anomalopsyche* and are unknown in other Trichoptera. In two *Contulma* species they are extended and elongate (state 2).

Character 13: Male phallus with dorsolateral, highly convoluted, membranous lobes (coded as multistate depending on degree of apical sclerotization).

Character 14: Male phallus apicoventral spines (coded as multistate depending on the degree of development).

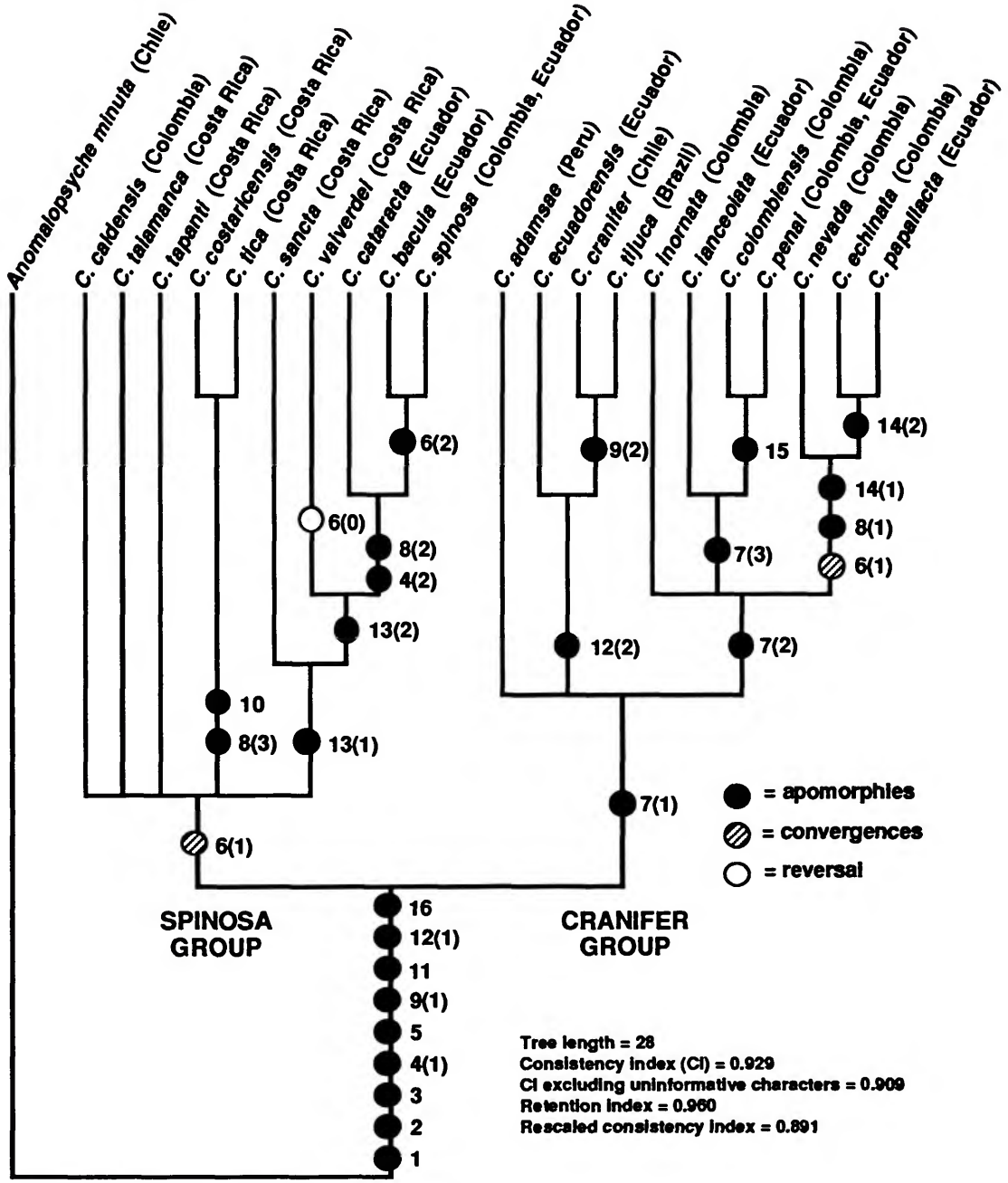
Character 15: Male phallus apex. The structure of the phallus of *Contulma* species varies greatly ranging from a fairly simple tube to a complex structure with large lobes and spines. The phallus of *Anomalopsyche* is simple and tubular with a C-shaped phallotremal sclerite and represents the primitive condition. We interpret the modifications described in characters 13, 14, and 15 to be derived.

Character 16: Female vaginal apparatus. The vaginal apparatus of *A. minuta* is simple, oval, and more closely resembles the general condition found in other case-making Trichoptera. The trident-shaped condition in *Contulma* is considered to be derived.

RESULTS AND DISCUSSION.—A single most-parsimonious tree was found using PAUP's Branch and Bound tree searching routine under both ACCTRAN and DELTRAN optimization with the Collapse Option in effect. The tree had a length of 28 steps, an overall consistency index (C.I.) of 0.929, and a C.I. excluding uninformative characters of 0.909. Other tree statistics are included on the cladogram.

Monophyly of *Contulma* is supported by nine characters of adult wing venation and male and female genitalia. The unique similarities among the genitalia of both sexes provides especially strong evidence that the genus is monophyletic. Both sexes contain characters that are seen nowhere else in Trichoptera. These include the posteromesal sclerotized projection/inferior appendage complex of the male and the trident-shaped sclerites of the vaginal apparatus of the female. Larvae also have several potential synapomorphies, including the structure of the maxillolabium, the weakly dentate mandibles, the head and thoracic nota with great numbers of secondary setae, the mesonotum transversely divided by a low carina or row of sclerotized projections, the legs, especially the femora, tibiae, and tarsi usually very hairy ventrally and the midleg with a large trochanteral brush, the shape of the sclerotized area laterally on the first abdominal segment, and the accessory teeth and processes on the anal claw. These characters were not included in the PAUP analysis because so few larvae are positively associated and their inclusion would not have affected the tree topology.

Within *Contulma*, two large monophyletic clades can be recognized, although one is defined by a homoplasic character. The first group, herein designated the *spinosa* Group and containing 10 species from Costa Rica, Colombia, and Ecuador, possesses a mesolateral patch of setae on segment IX (character 6). This patch of setae is secondarily absent in *C. valverdei*, but also occurs convergently in *C. nevada*, *C. echinata*, and *C. papallacta*. Within the *spinosa* Group, *C. costaricensis* and *C. tica*, both very similar overall, share two apomorphies: short, attenuated posteromesal sclerotized pro-



CLADOGRAM.—Hypothetical phylogeny for species of *Contulma*. Numbers correspond to those used in the "Character Analysis and Polarization" section of the text and Table 1.

jections of sternum IX (character 8, state 3) and lateral articulating sclerites on segment X (character 10). Also, within the *spinosa* Group, *C. sancta, C. valverdei, C. cataracta, C. bacula,* and *C. spinosa* possess uniquely derived, highly convoluted, dorsolateral membranous lobes on the phallus (character 13, state 1). In all species except *C. sancta* these lobes are sclerotized apically (character 13, state 2). *Contulma cataracta, C. bacula,* and *C. spinosa* have narrow elongate posteromesal sclerotized projections of sternum IX (character 8, state 2) and the posterior borders of segment IX are heavily

setose and extended (character 4, state 2). Finally, the mesolateral patch of setae on IX is interpreted as becoming coalesced and rod-like in *C. bacula* and *C. spinosa* (character 6, state 2). *Contulma nevada* and *C. echinata* also possess what appear to be setae or spines mesolaterally on IX and *C. papallacta* possesses a setose extension approaching that seen in *C. spinosa*. These features are interpreted as convergent evolutionary developments in these two groups of species. Relationships among other species in the *spinosa* Group are unresolved.

The remaining 11 species in the genus, distributed in Brazil, Chile, Colombia, Ecuador, and Peru and herein designated the *cranifer* Group, all have synapomorphic dorsolateral processes on abdominal segment IX (character 7). Within this species group, *C. ecuadorensis, C. cranifer,* and *C. tijuca* share elongate mushroom-like, subphallic processes (character 12, state 2) and *C. cranifer* and *C. tijuca* share the apomorphic obliteration of segment X (character 9, state 2). The relationship of *C. adamsae,* the most aberrant species in the *cranifer* Group, to other members of the group is unresolved. The dorsolateral processes of segment IX in their broad, somewhat spatulate state (character 7, state 2) define a monophyletic group of species that includes *C. inornata, C. lanceolata, C. colombiensis, C. penai, C. nevada, C. echinata,* and *C. papallacta*. Within this group of 7 species the relationship of *C. inornata* to the others is not resolved, but *C. lanceolata, C. colombiensis,* and *C. penai* all share minutely setose dorsolateral processes of IX (character 7, state 3) and *C. colombiensis* and *C. penai* have synapomorphic apically acute phalli (character 15). Also, within the larger group of 7 species, *C. nevada, C. echinata,* and *C. papallacta* possess a synapomorphic, deeply cleft, posteromesal projection of segment IX (character 8, state 1) and apicoventral spines on the phallus (character 14, state 1). The latter character, in its more derived condition (state 2), indicates a sister group relationship between *C. echinata* and *C. papallacta*.

This first assessment of the phylogenetic relationships of the species of *Contulma* contains some homoplasy and several unresolved relationships. Discovery of additional sets of characters from newly discovered species and from females and larvae as they become discovered and associated will test and refine our hypothesis. We suspect that we have captured only a small sample of the actual species richness in this most interesting genus of caddisflies.

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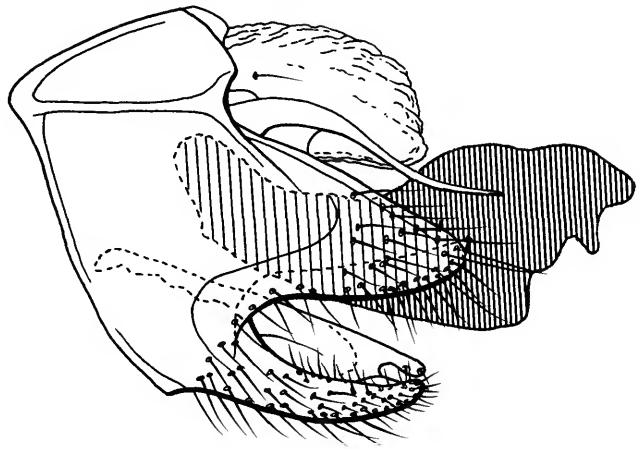

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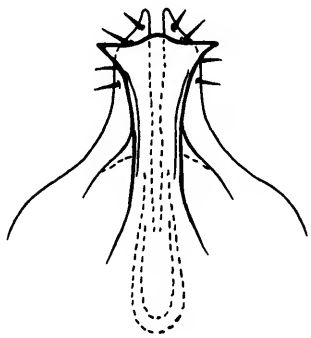

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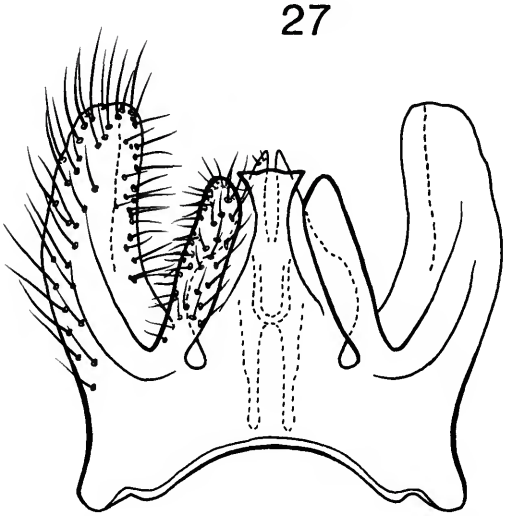

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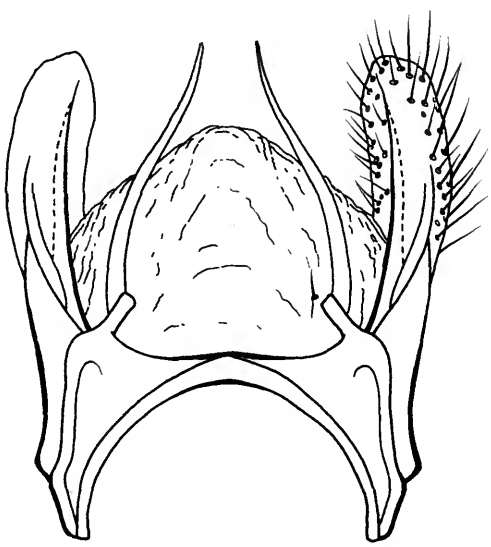

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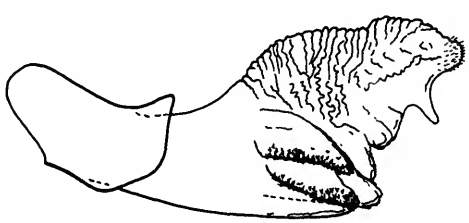

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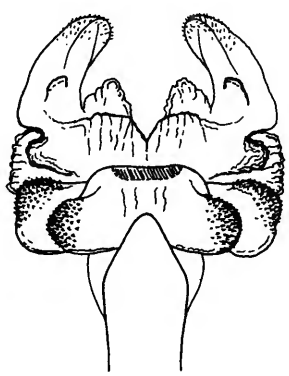
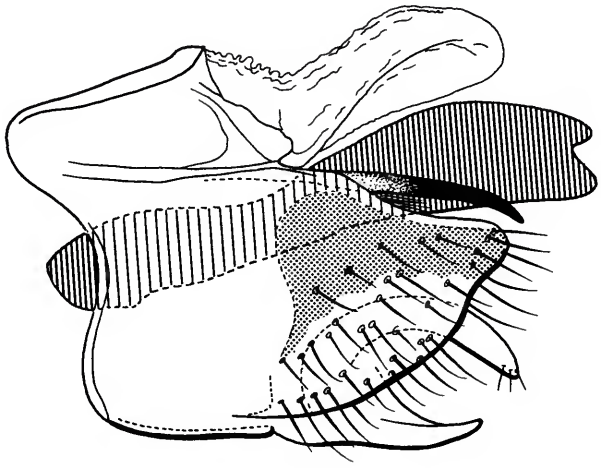


29

FIGURES 24–29.—*Contulma adamsae*, male genitalia: 24, lateral; 25, dorsal; 26, ventral; 27, fused inferior appendages and posteromesal projection of sternum IX; 28, phallus, lateral; 29, same, dorsal.



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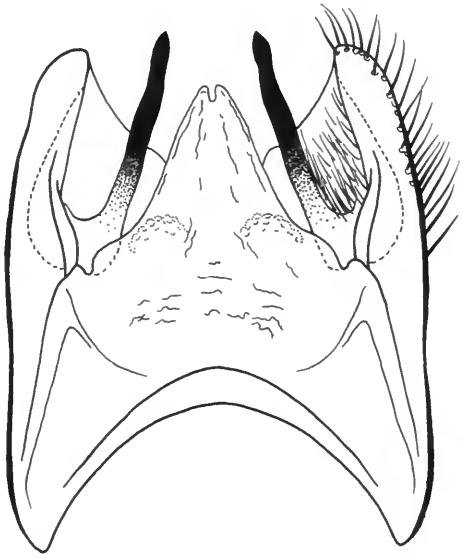

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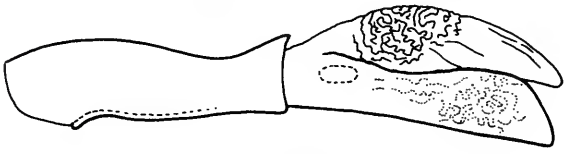

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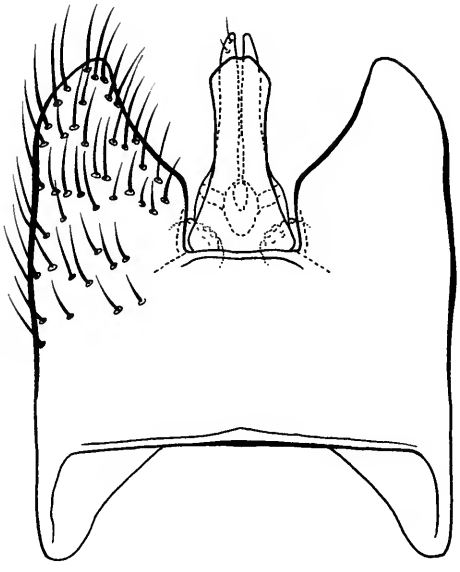

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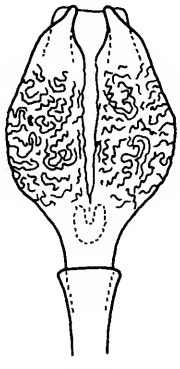
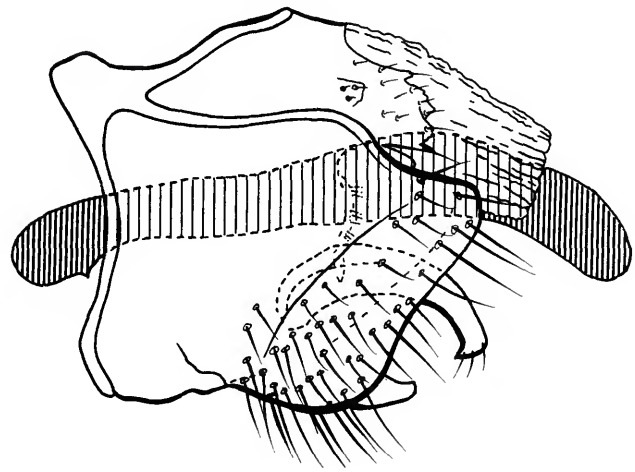


34

FIGURES 30–34.—*Contulma bacula*, male genitalia: 30, lateral; 31, dorsal; 32, ventral; 33, phallus, lateral; 34, same, dorsal.



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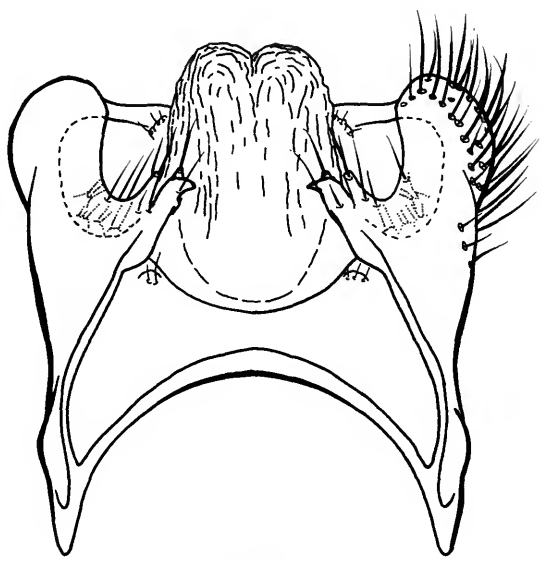

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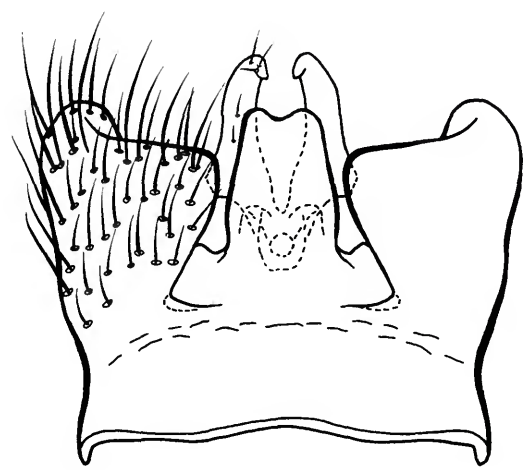

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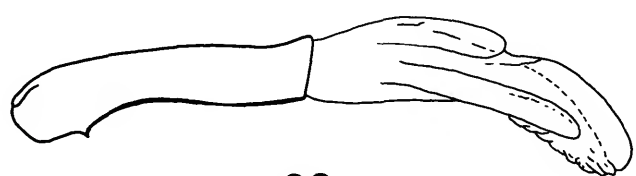
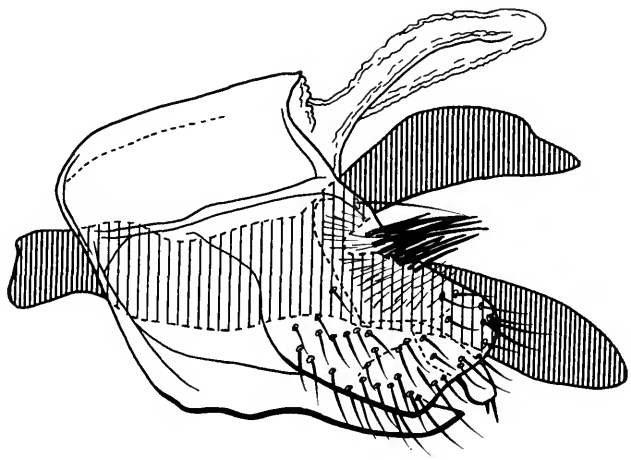


38

FIGURES 35–38.—*Contulma caldensis*, male genitalia: 35, lateral; 36, dorsal; 37, ventral; 38, phallus, lateral.



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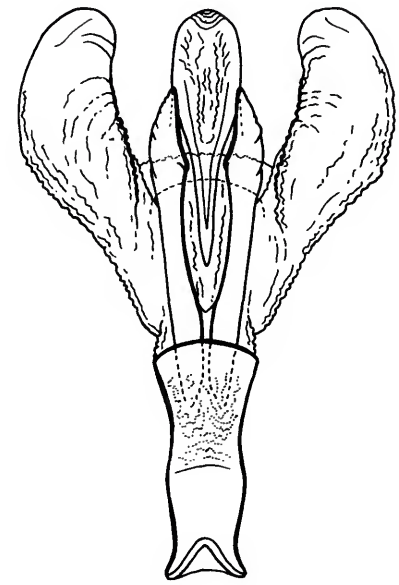

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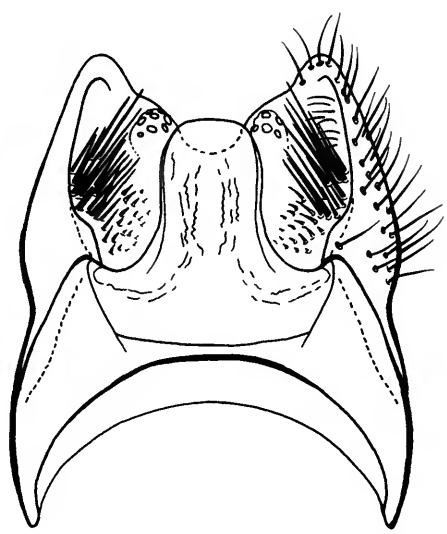

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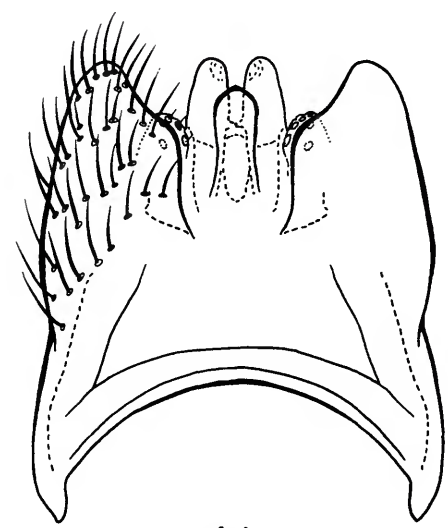

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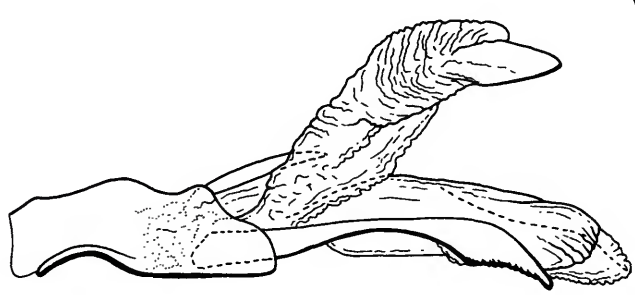
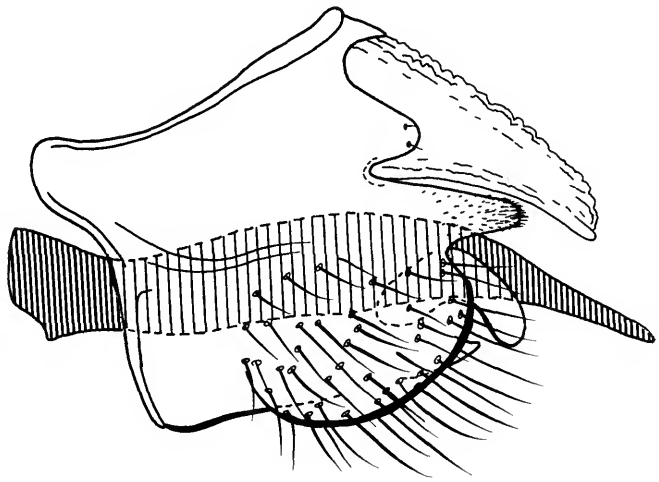


42

FIGURES 39–43.—*Contulma cataracta*, male genitalia: 39, lateral; 40, dorsal; 41, ventral; 42, phallus, lateral; 43, same, dorsal.



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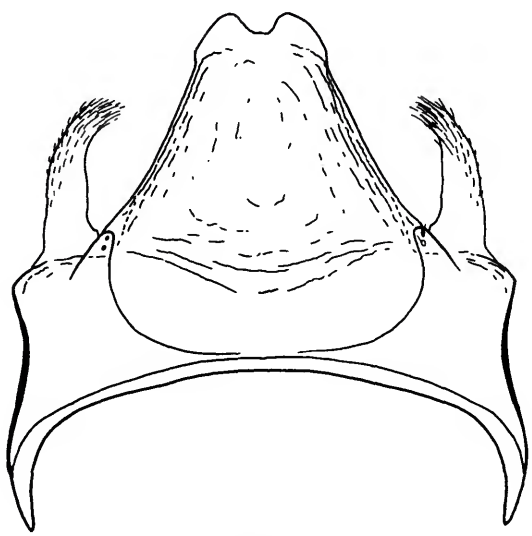

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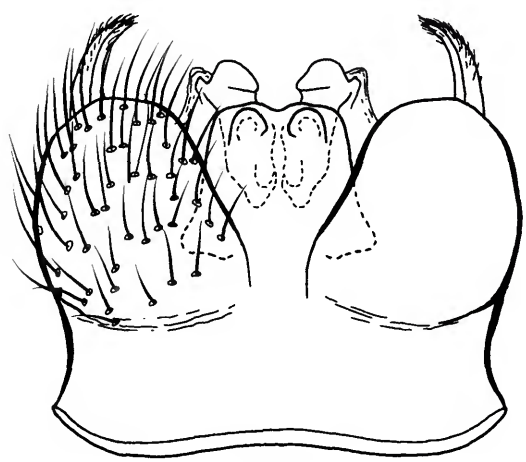

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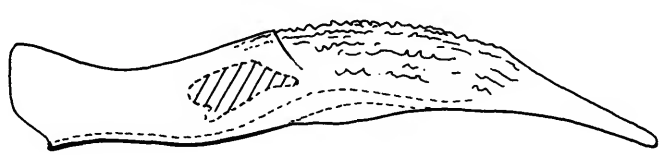
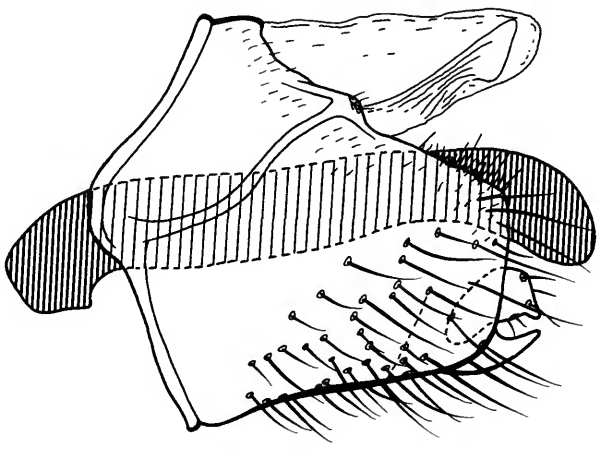


47

FIGURES 44–47.—*Contulma colombiensis*, male genitalia: 44, lateral; 45, dorsal; 46, ventral; 47, phallus, lateral.



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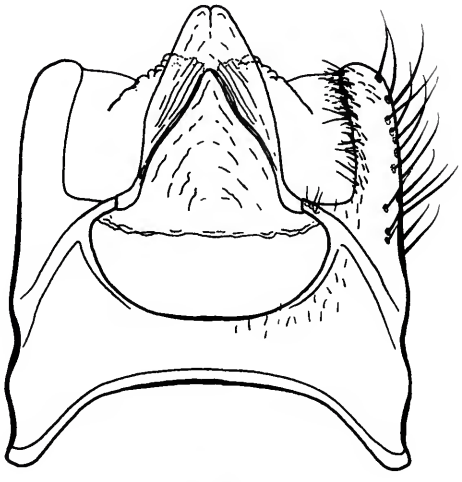

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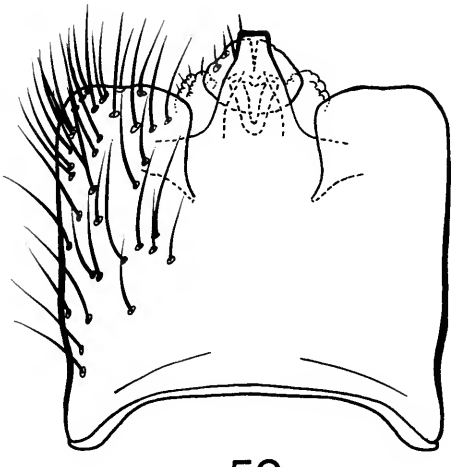

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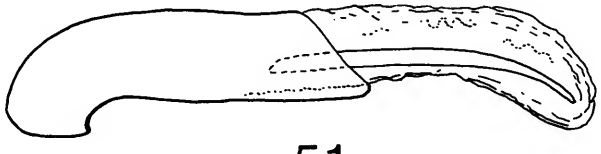
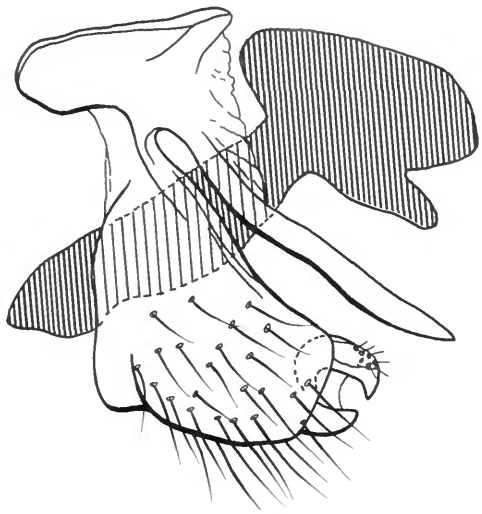


51

FIGURES 48–51.—*Contulma costaricensis*, male genitalia: 48, lateral; 49, dorsal; 50, ventral; 51, phallus, lateral.



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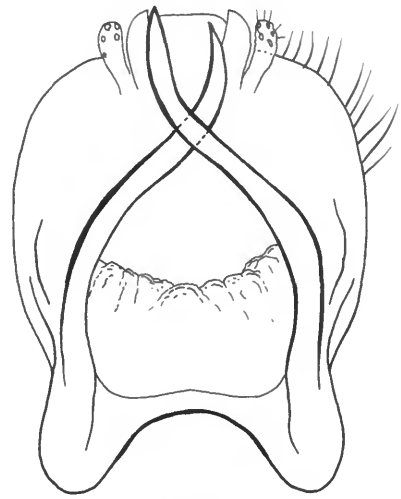

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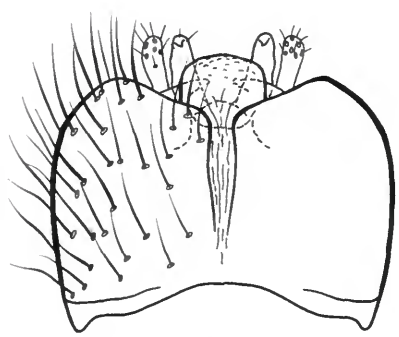

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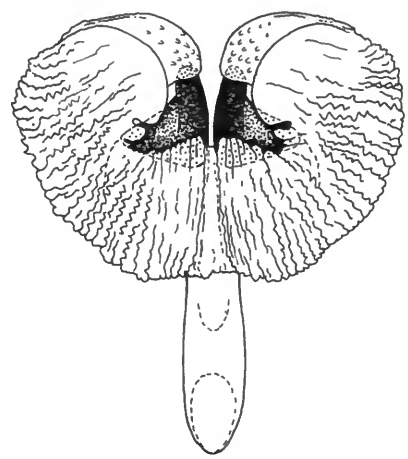

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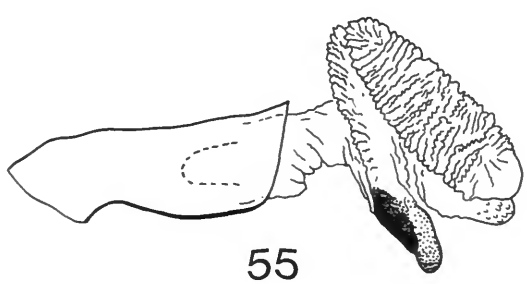
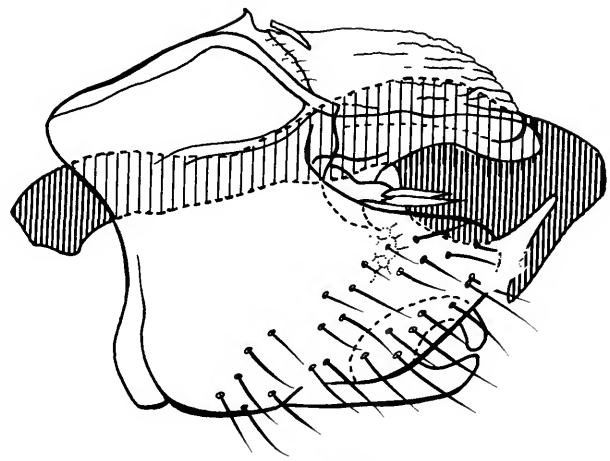


55

FIGURES 52–56.—*Contulma cranifer*, male genitalia: 52, lateral; 53, dorsal; 54, ventral; 55, phallus, lateral; 56, same, dorsal.



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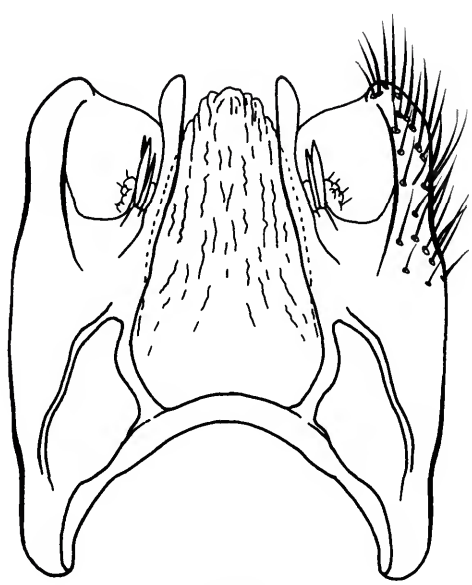

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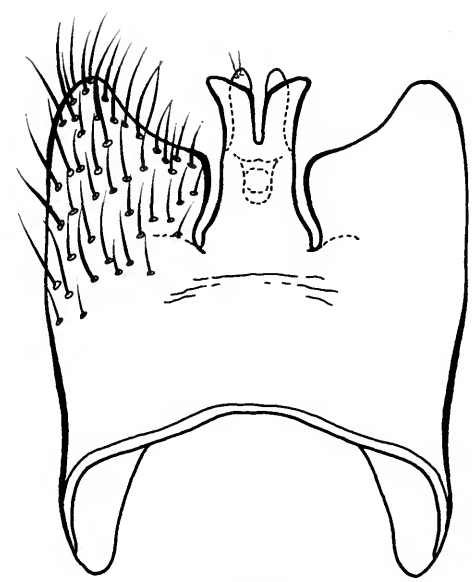

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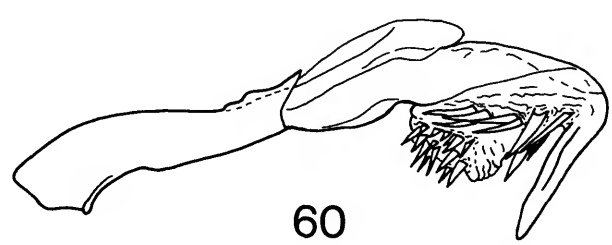
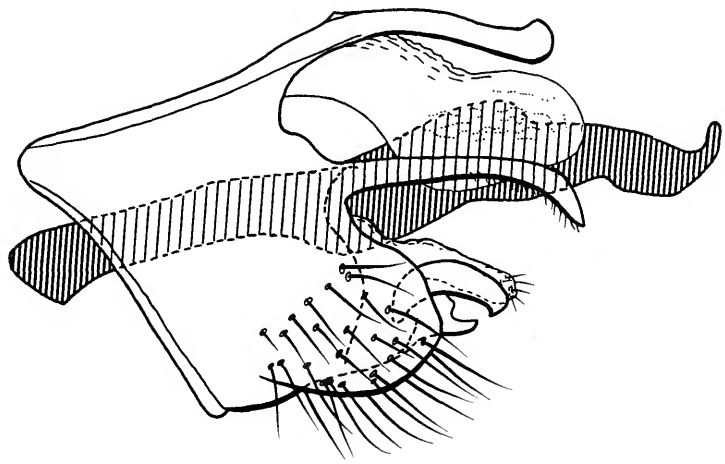


60

FIGURES 57–60.—*Contulma echinata*, male genitalia: 57, lateral; 58, dorsal; 59, ventral; 60, phallus, lateral.



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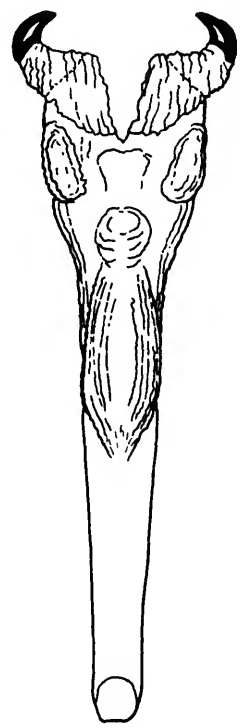

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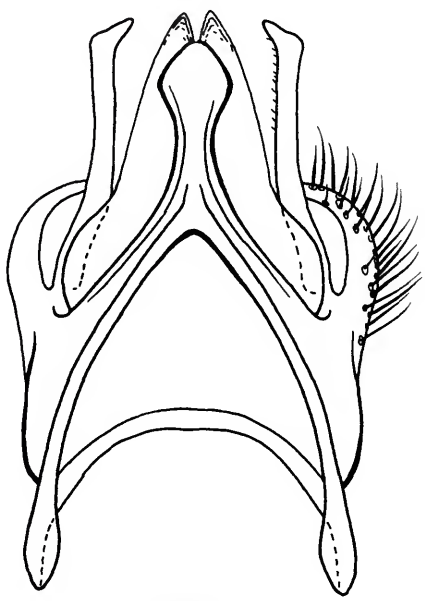

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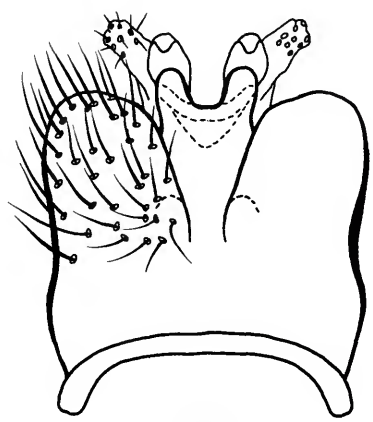

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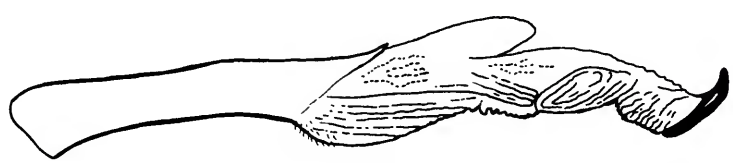

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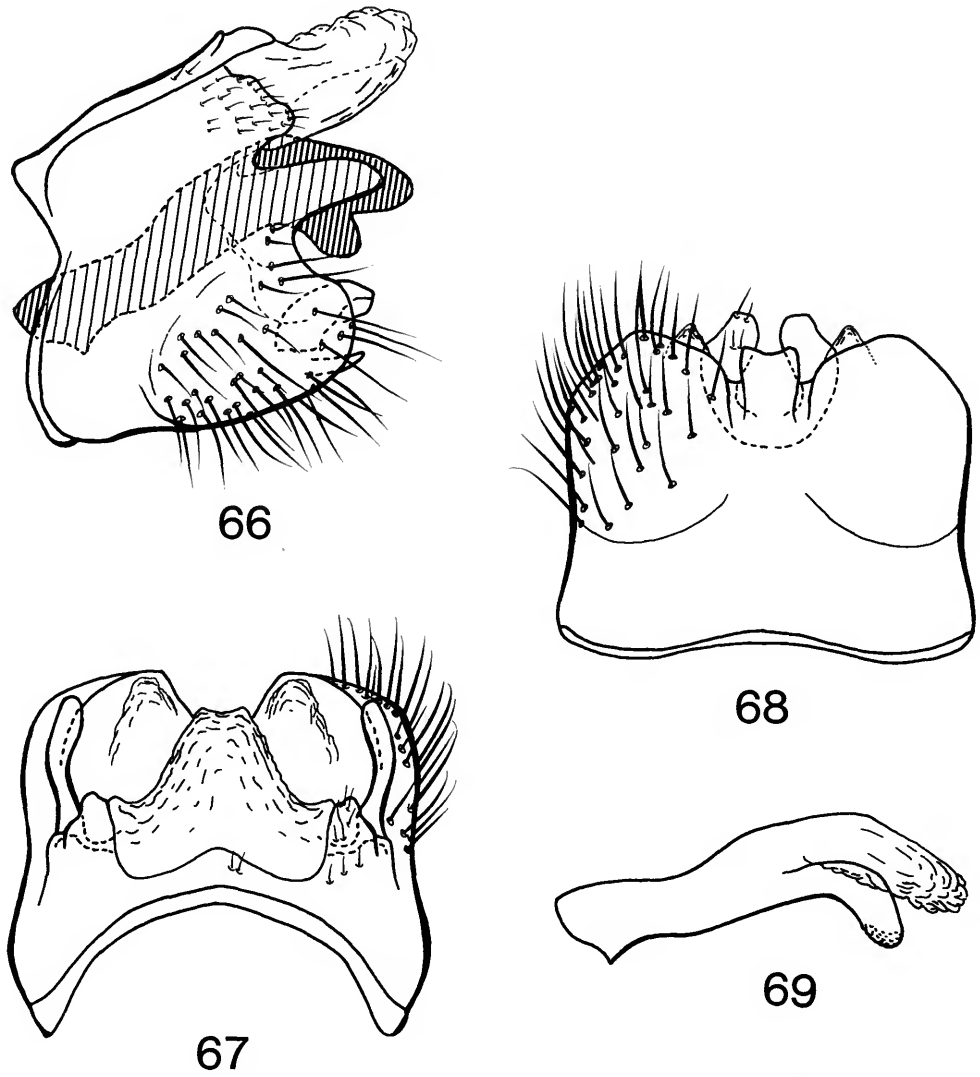
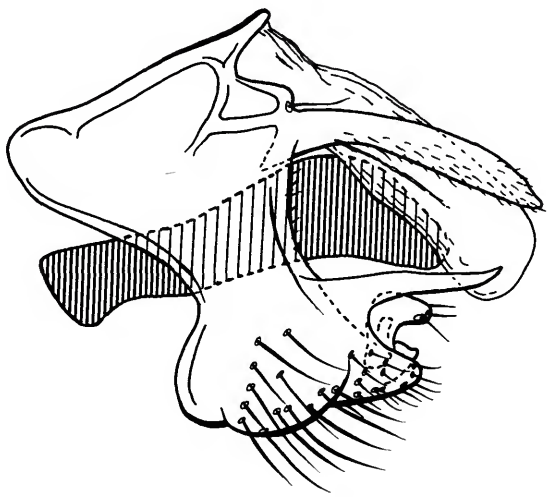
FIGURES 61–65.—*Contulma ecuadorensis*, male genitalia: 61, lateral; 62, dorsal; 63, ventral; 64, phallus, lateral; 65, same, dorsal.



FIGURES 66–69.—*Contulma inornata*, male genitalia: 66, lateral; 67, dorsal; 68, ventral; 69, phallus, lateral.



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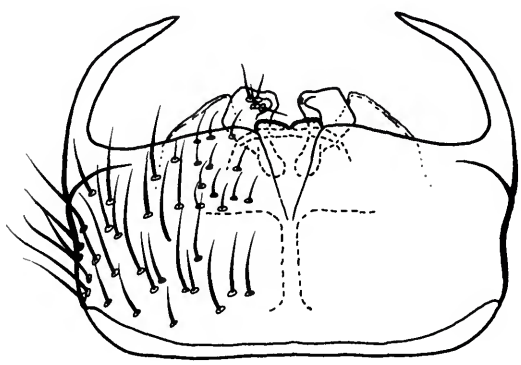

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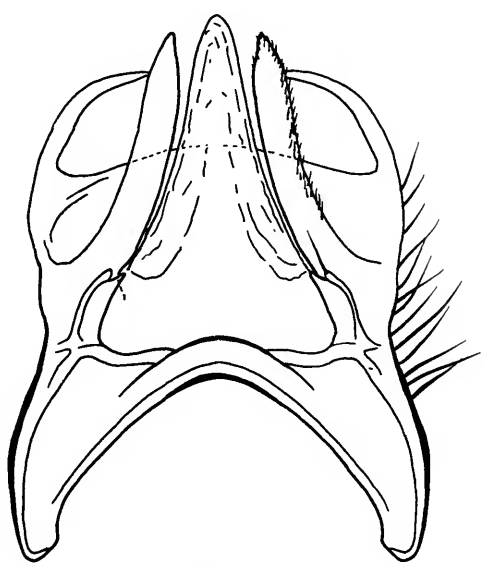

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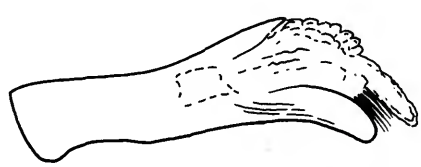
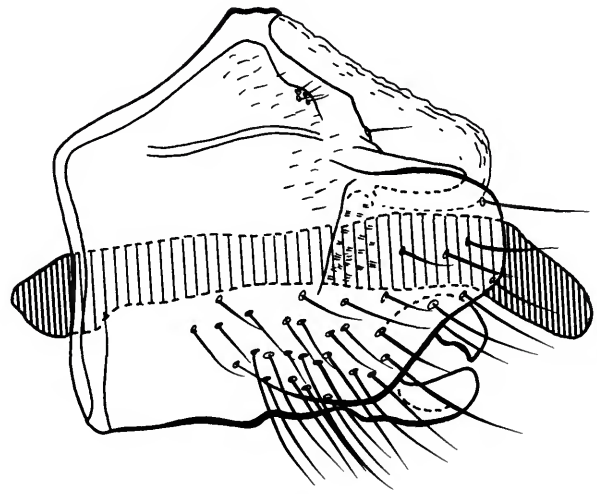


73

FIGURES 70–73.—*Contulma lanceolata*, male genitalia: 70, lateral; 71, dorsal; 72, ventral; 73, phallus, lateral.



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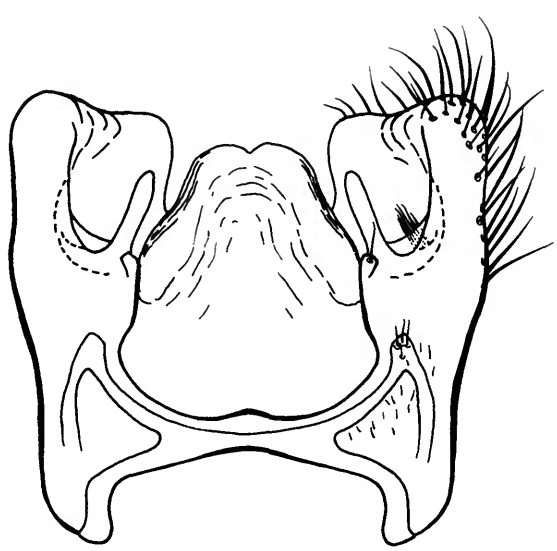

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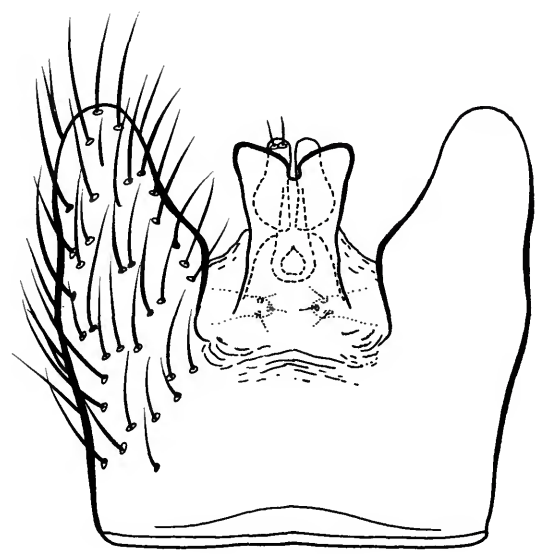

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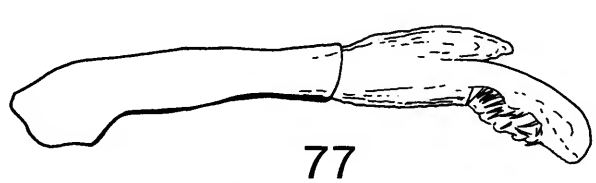

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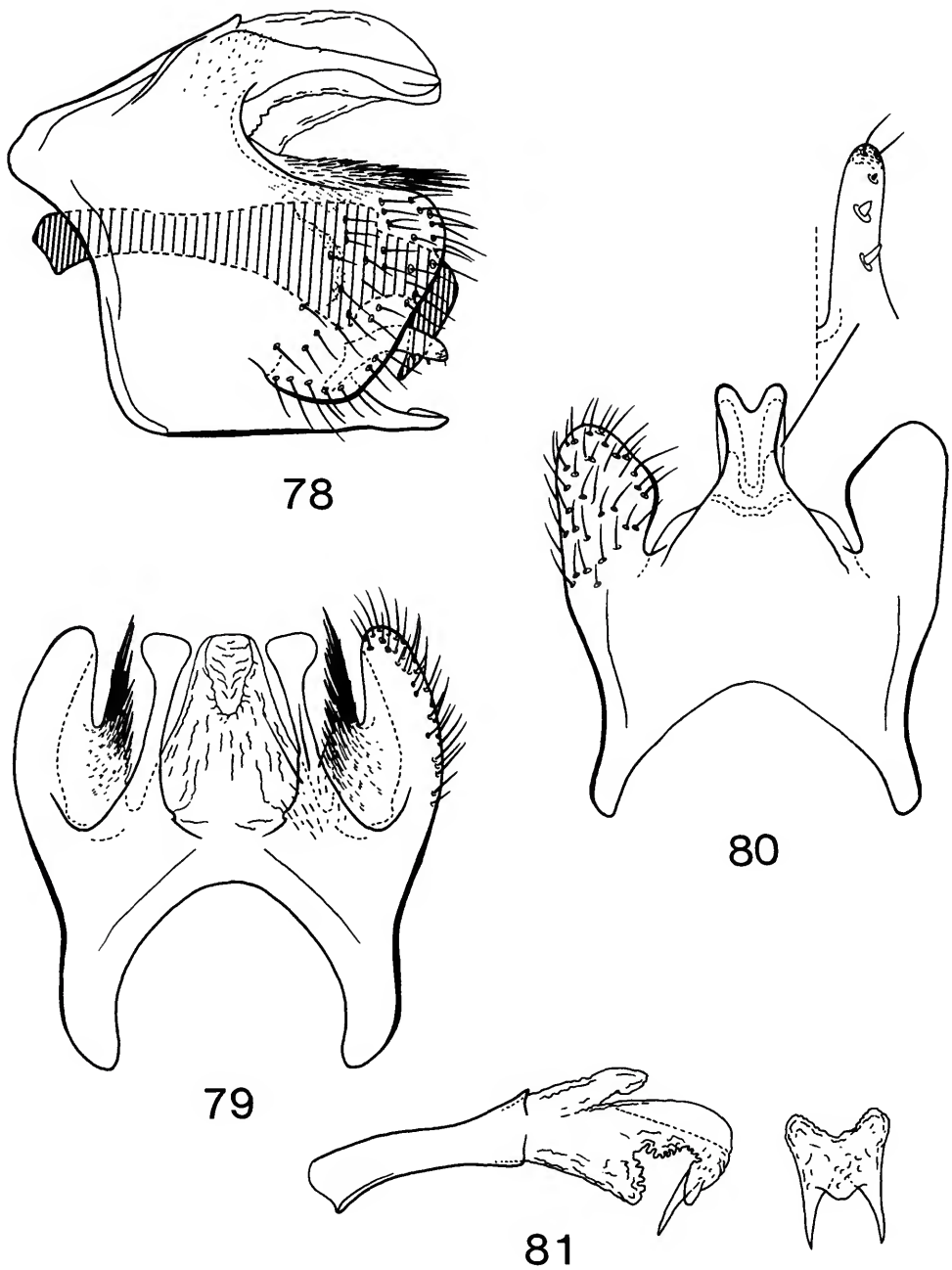
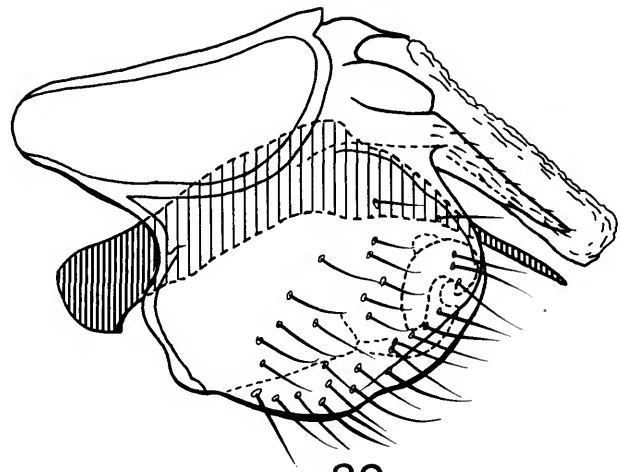
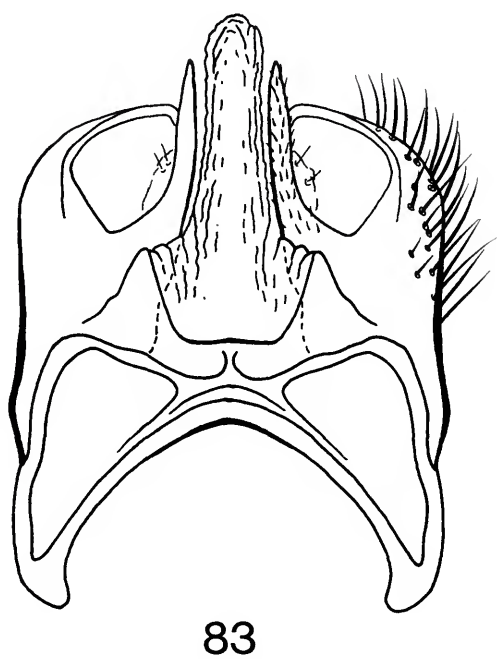
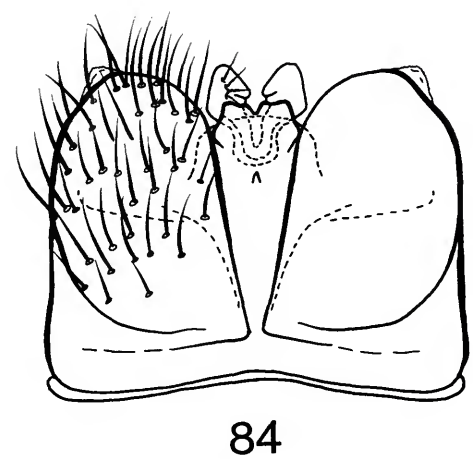
FIGURES 74–77.—*Contulma nevada*, male genitalia: 74, lateral; 75, dorsal; 76, ventral; 77, phallus, lateral.

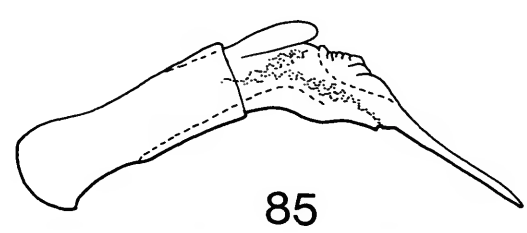


FIGURES 78–81.—*Contulma papallacta*, male genitalia: 78, lateral; 79, dorsal; 80, ventral, inset of inferior appendage greatly enlarged; 81, phallus, lateral, inset of apex, posterior.

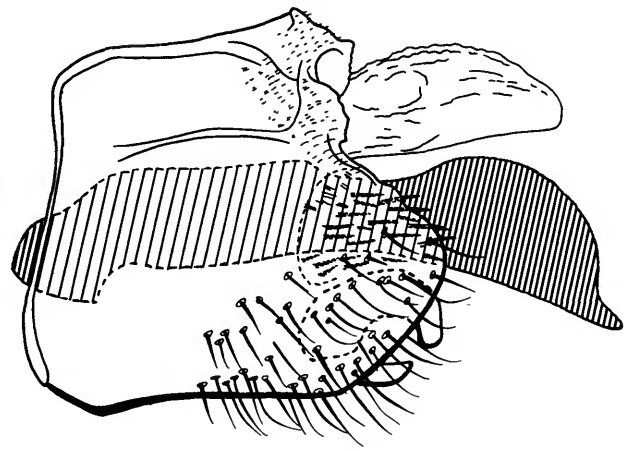








FIGURES 82–85.—*Contulma penai*, male genitalia: 82, lateral; 83, dorsal; 84, ventral; 85, phallus, lateral.



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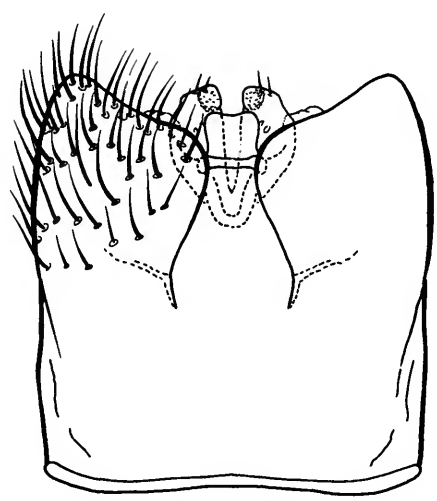

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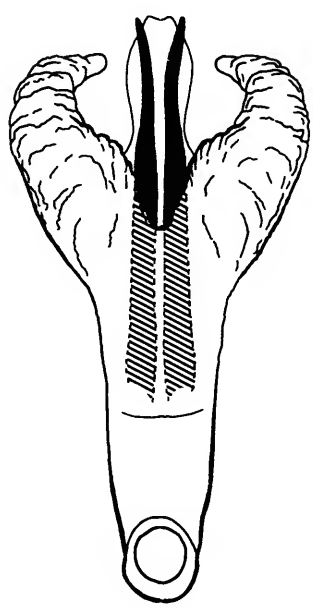

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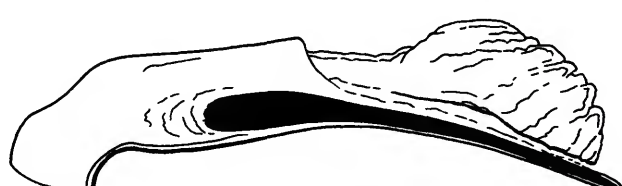

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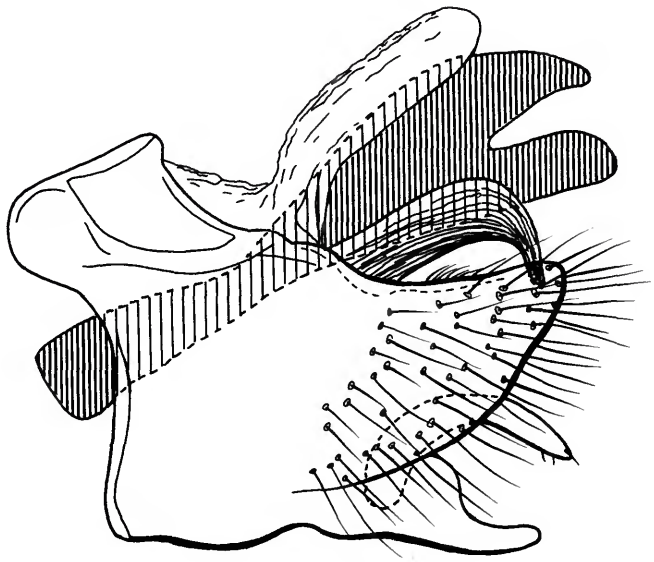
FIGURES 86–89.—*Contulma sancta*, male genitalia: 86, lateral; 87, ventral; 88, phallus, lateral; 89, same, dorsal.



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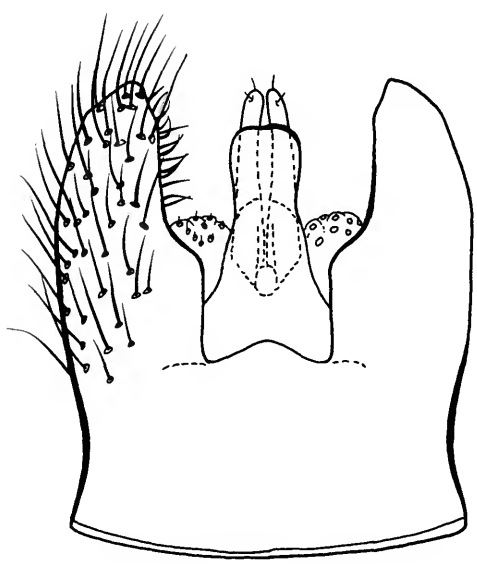

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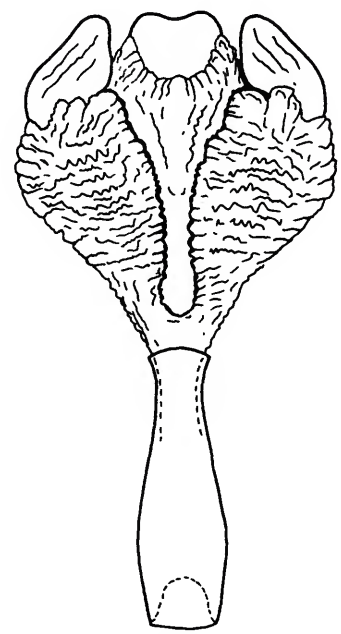

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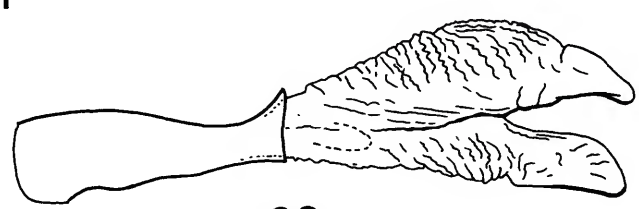

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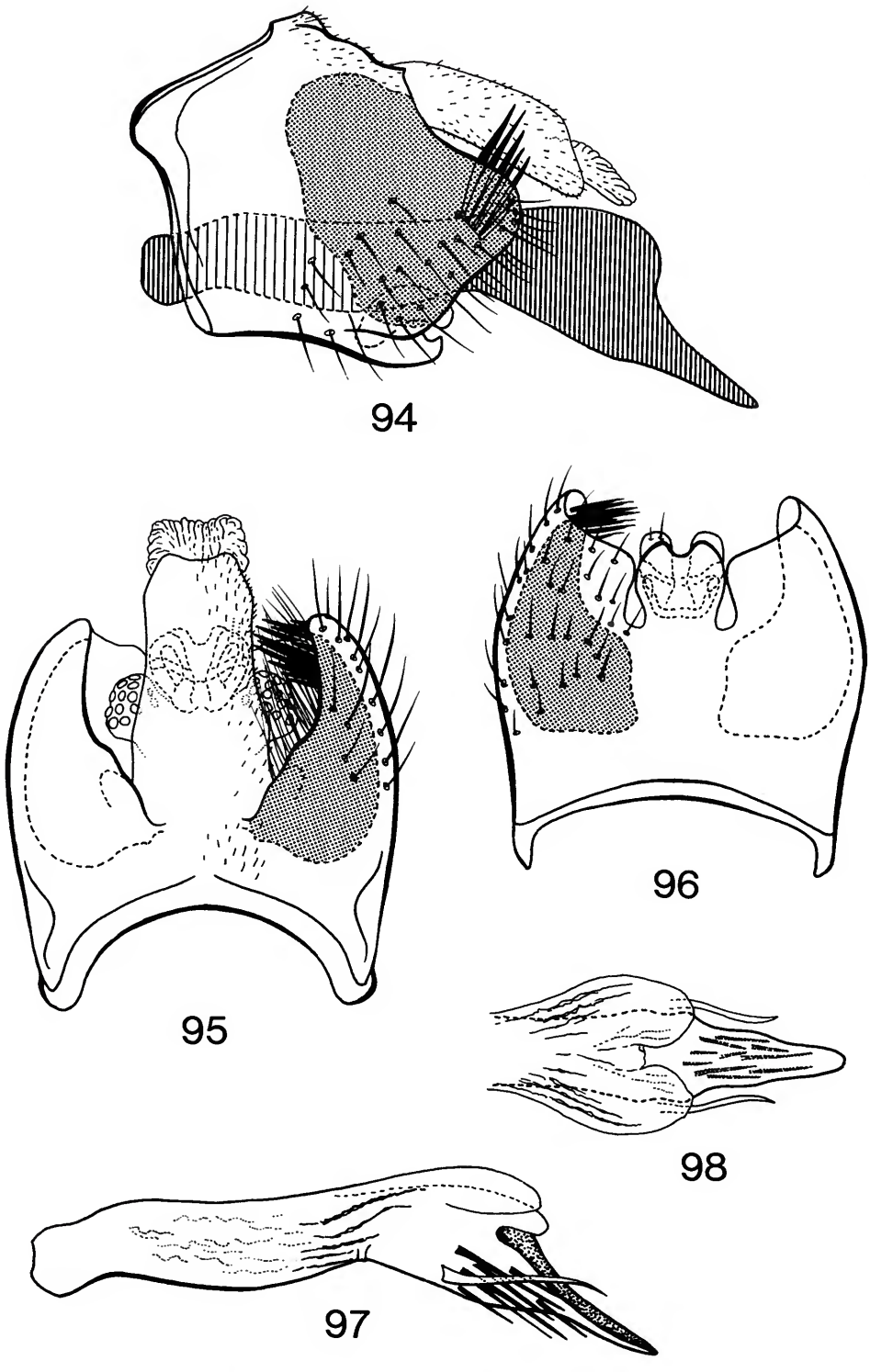
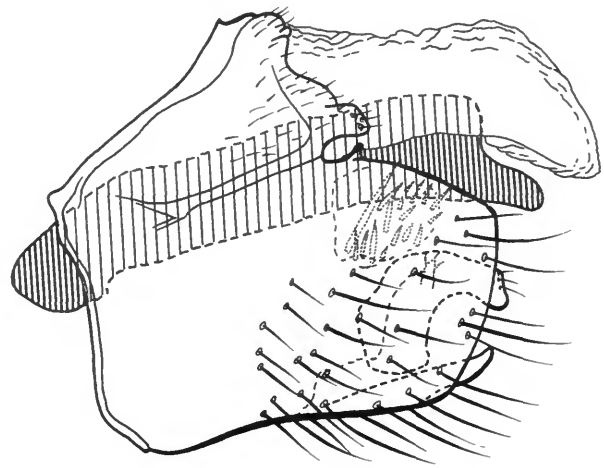
FIGURES 90–93.—*Contulma spinosa*, male genitalia: 90, lateral; 91, ventral; 92, phallus, lateral; 93, same, dorsal.



FIGURES 94–98.—*Contulma talamanca*, male genitalia: 94, lateral; 95, dorsal; 96, ventral; 97, phallus, lateral; 98, apex of same, dorsal.



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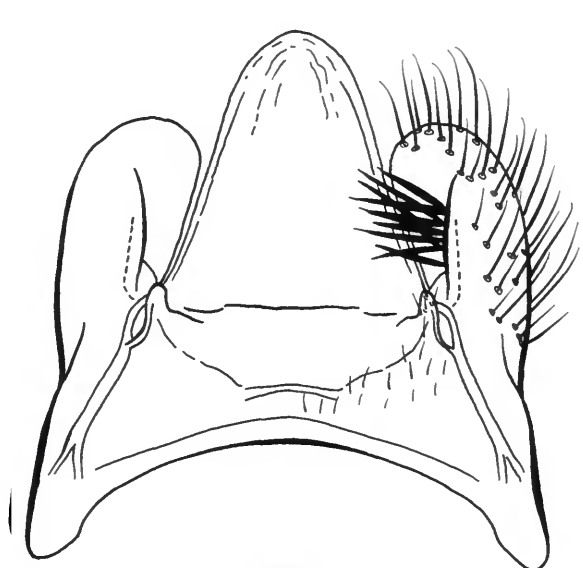

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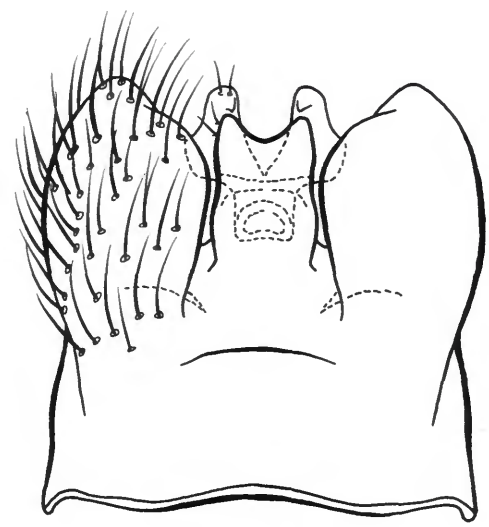

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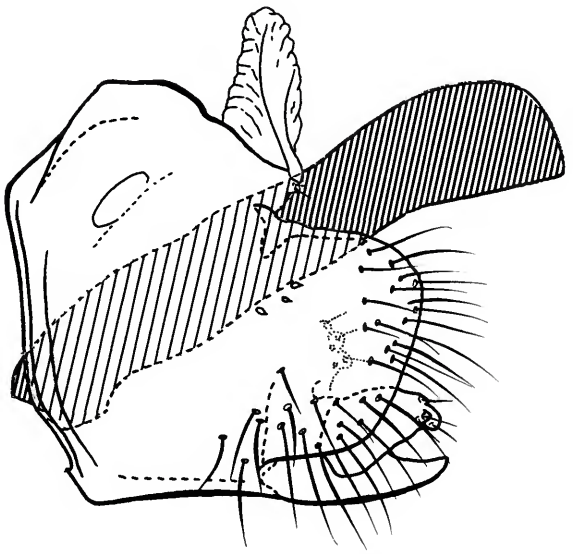
FIGURES 99–102.—*Contulma tapanti*, male genitalia: 99, lateral; 100, dorsal; 101, ventral; 102, phallus, lateral.



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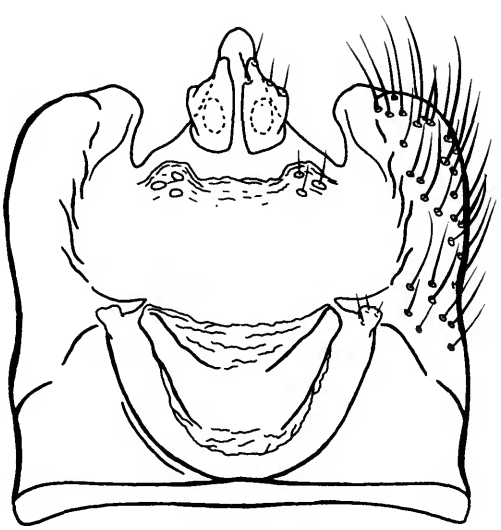

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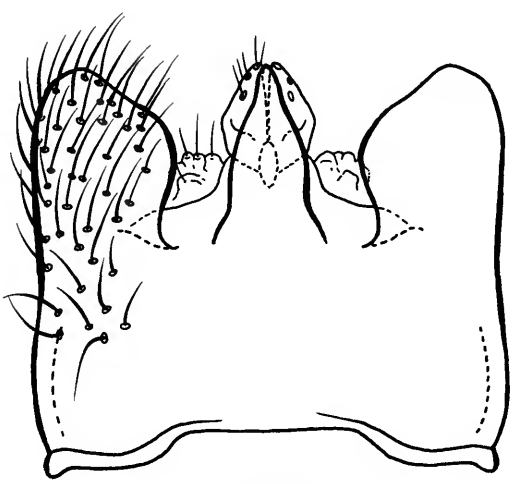

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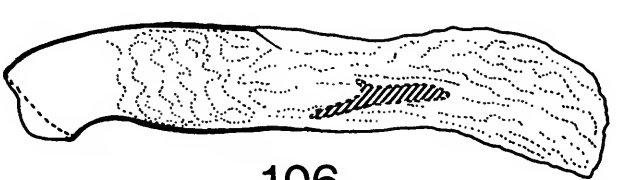

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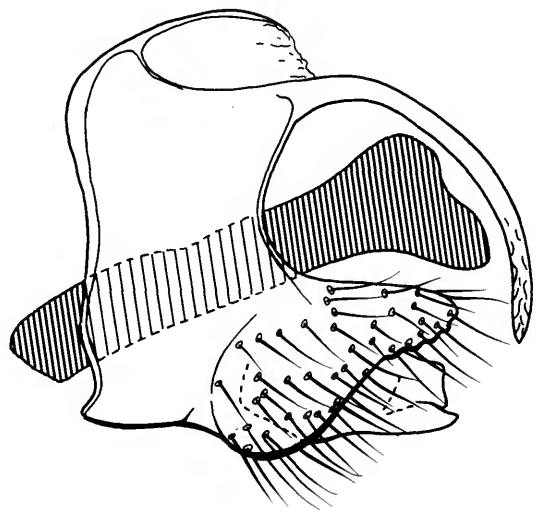
FIGURES 103–106.—*Contulma tica*, male genitalia: 103, lateral; 104, dorsal; 105, ventral; 106, phallus, lateral.



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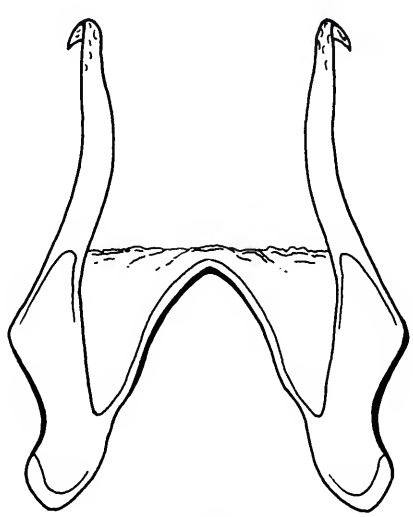

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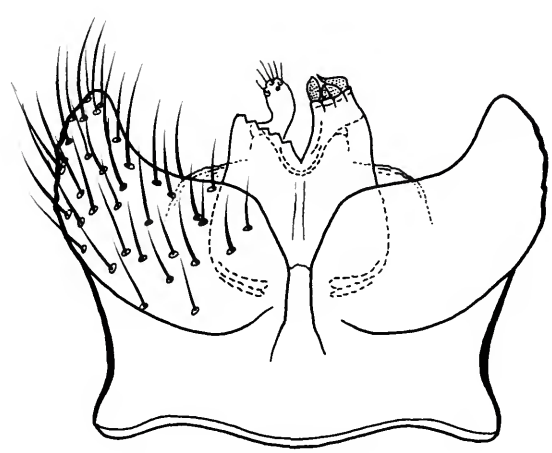

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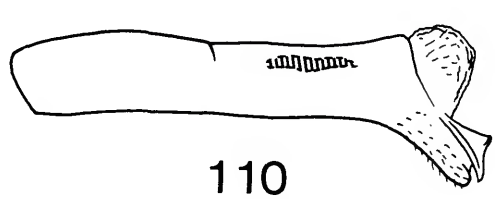

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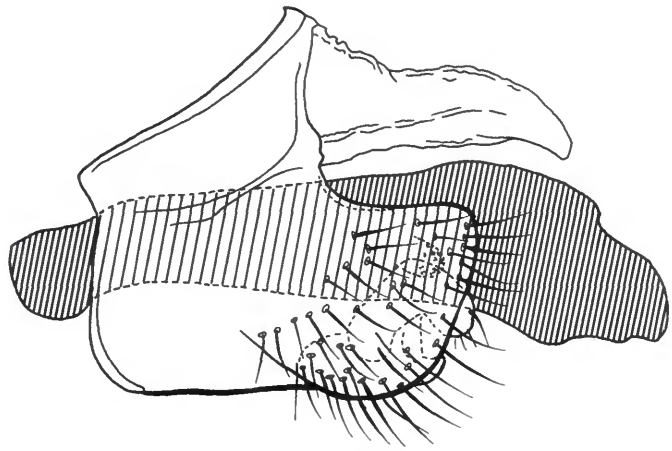
FIGURES 107–110.—*Contulma tijuca*, male genitalia: 107, lateral; 108, dorsal; 109, ventral; 110, phallus, lateral.



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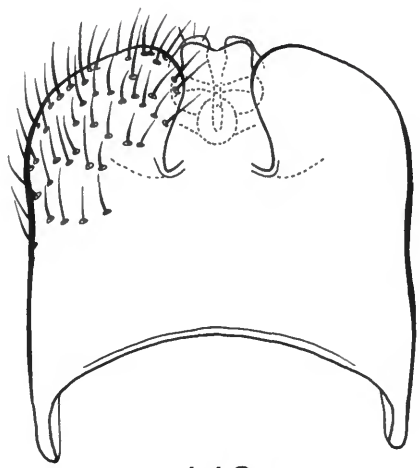

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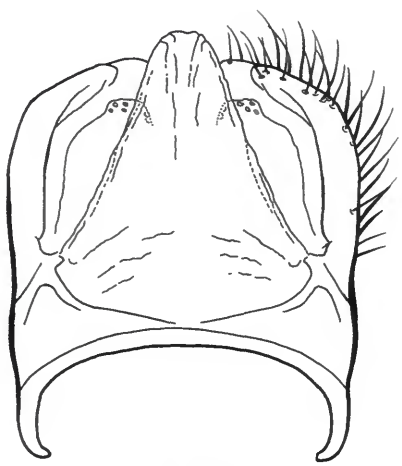

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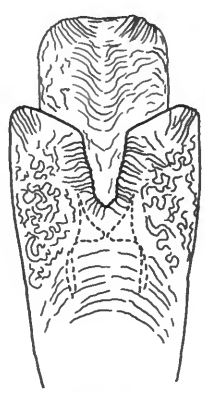

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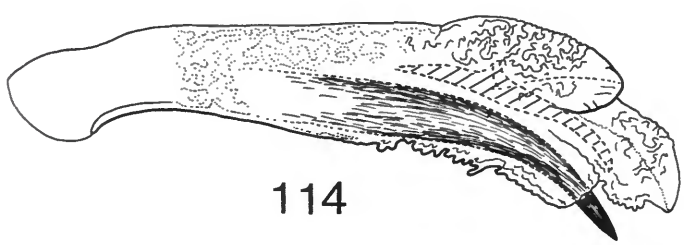

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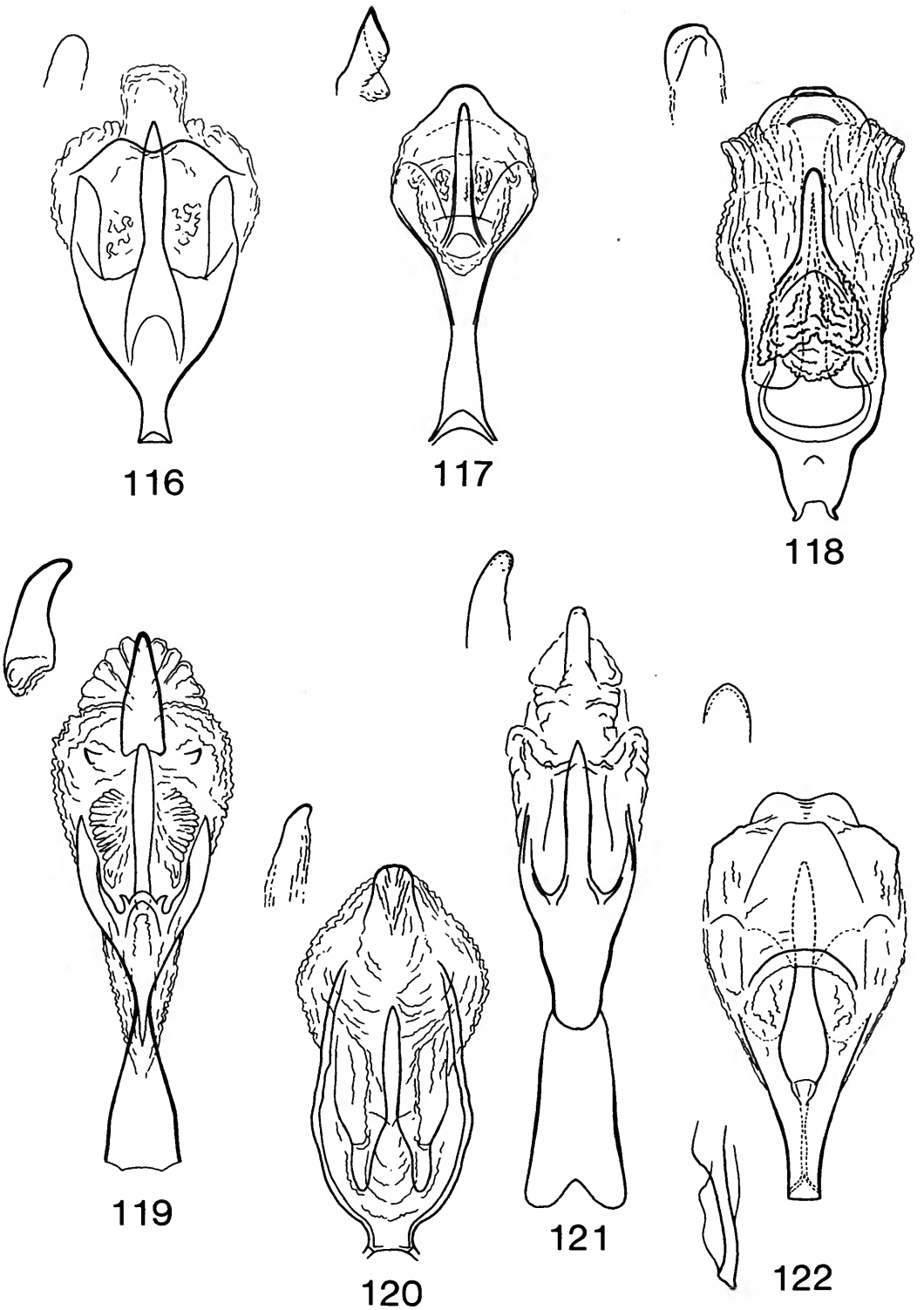
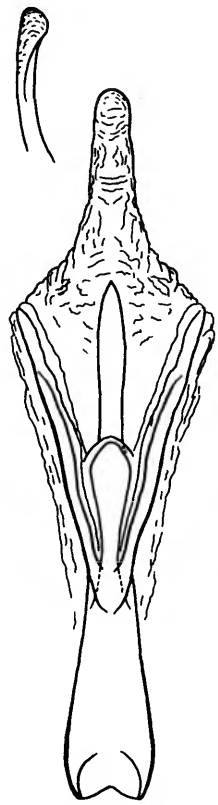
FIGURES 111–115.—*Contulma valverdei*, male genitalia: 111, lateral; 112, dorsal; 113, ventral; 114, phallus, lateral; 115, apex of same, dorsal.



FIGURES 116–122.—Female vaginal apparatus, ventral (anterior end downward), with inset of tip of apical process in lateral aspect of *Contulma* species: 116, *C. adamsae*; 117, *C. colombiensis*; 118, *C. cranifer*; 119, *C. echinata*; 120, *C. ecuadorensis*; 121, *C. nevada*; 122, *C. penai*, with additional inset of base of apparatus.



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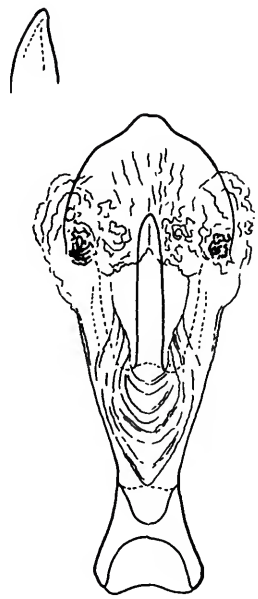

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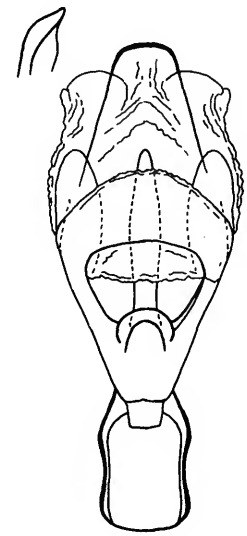

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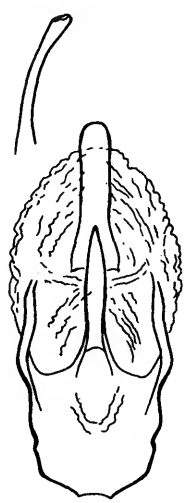

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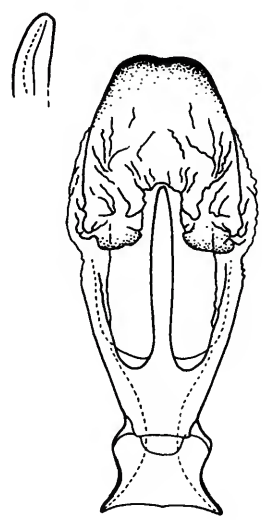

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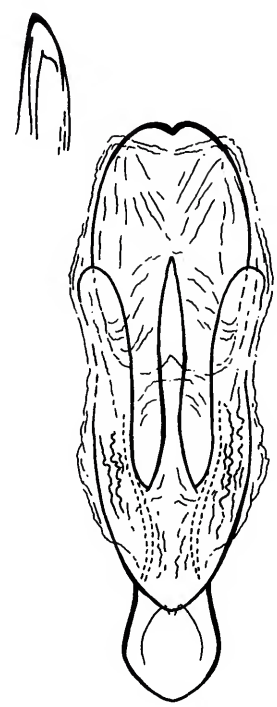

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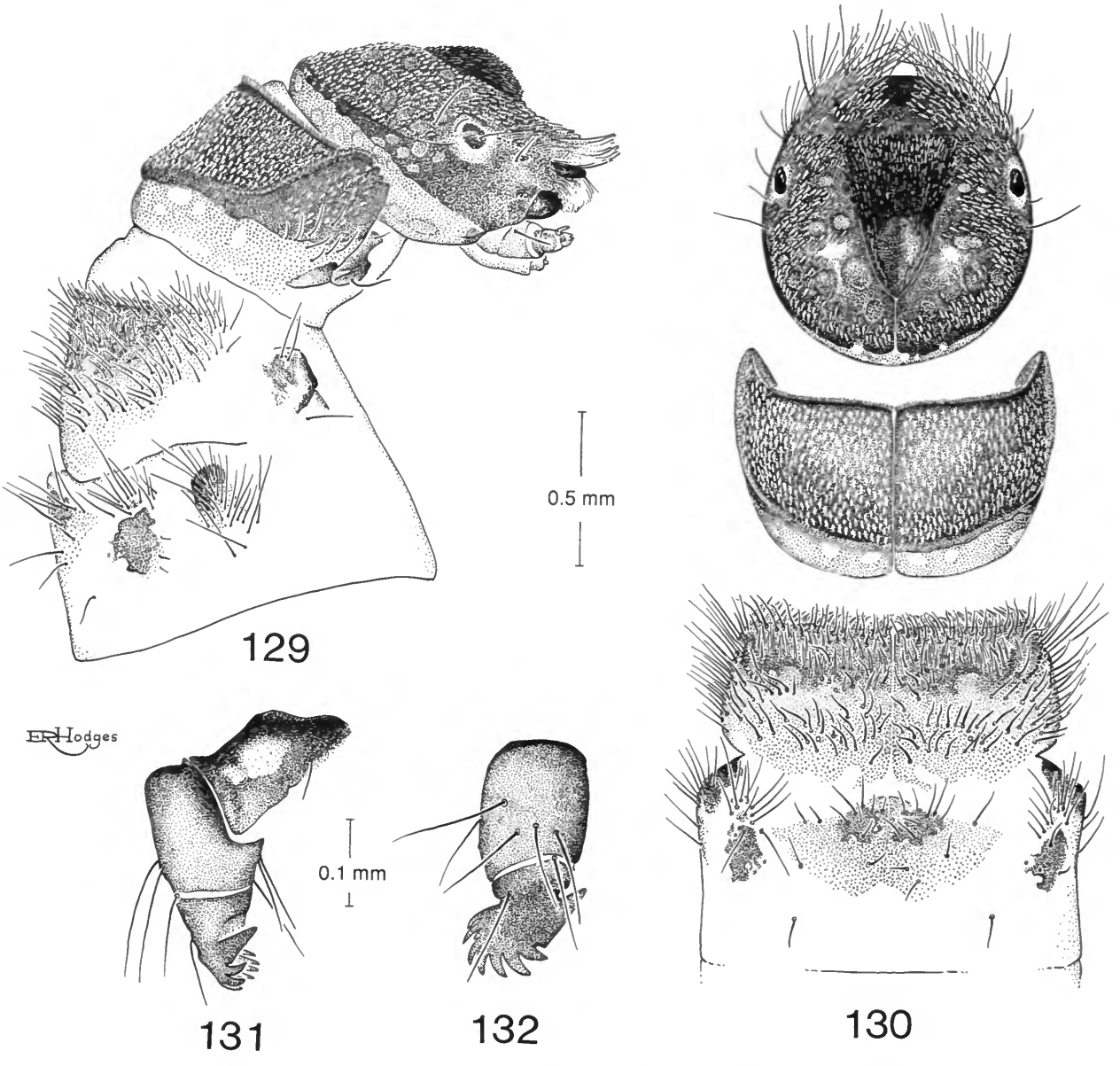
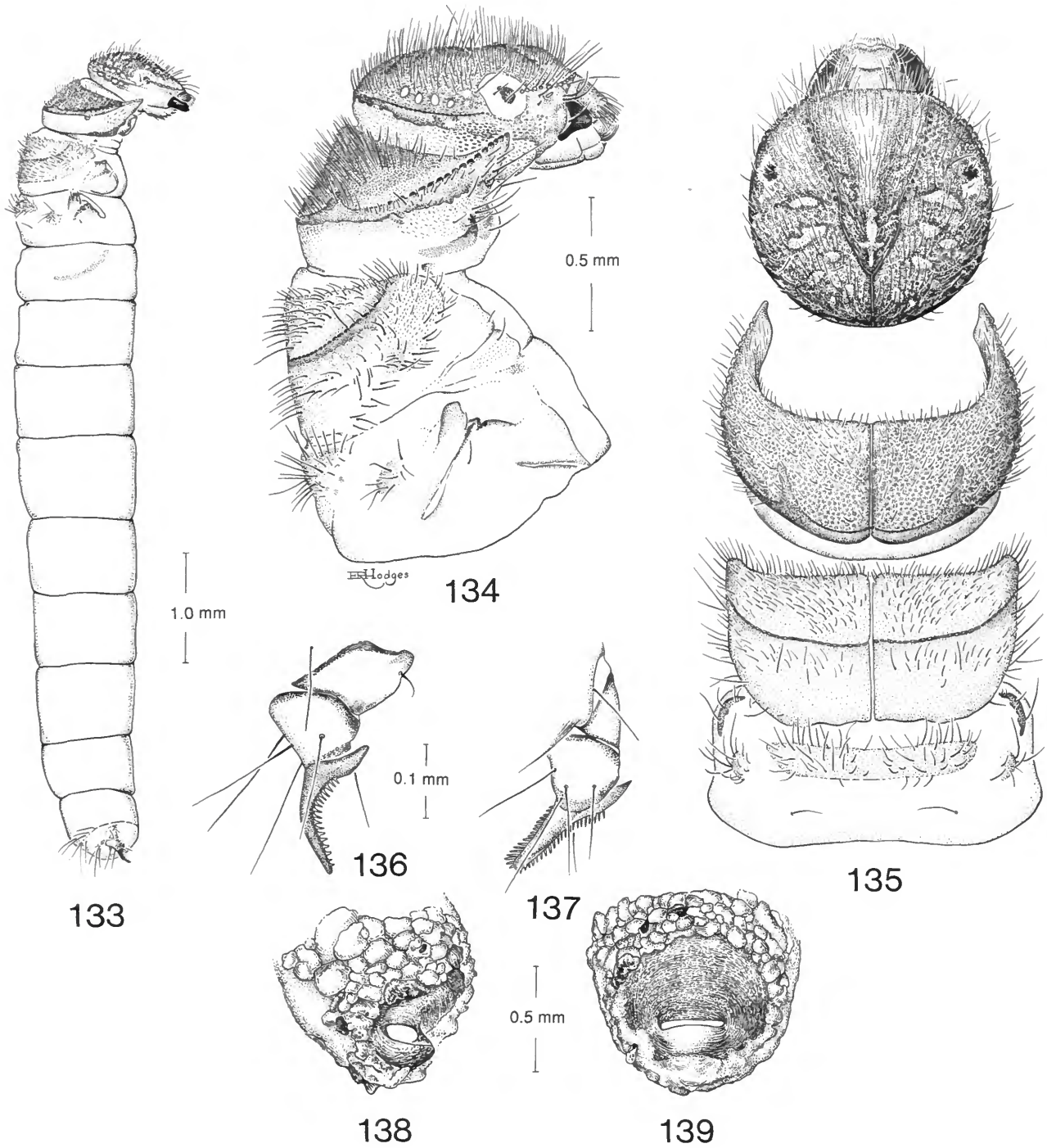
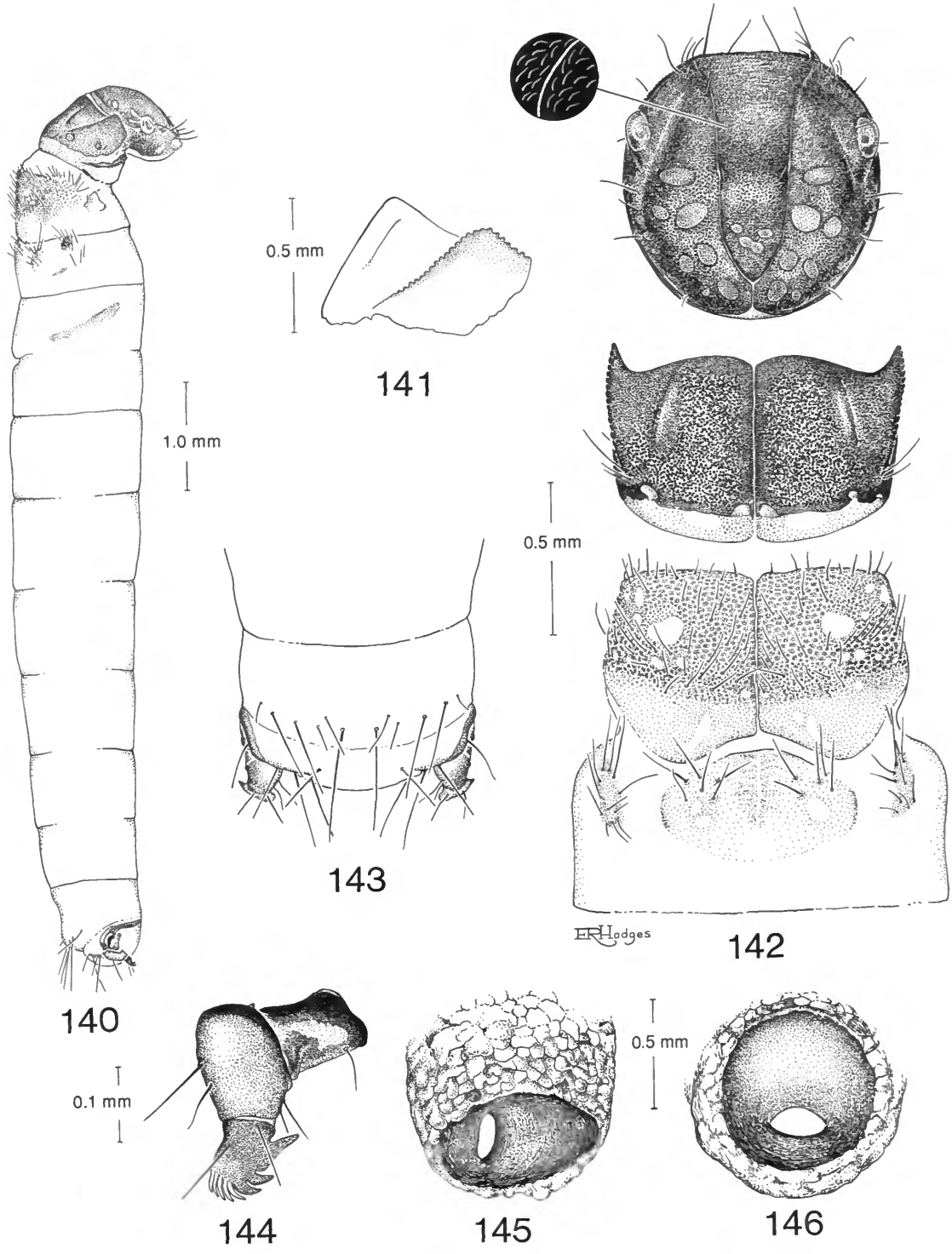
FIGURES 123–128.—Female vaginal apparatus, ventral (anterior end downward), with inset of tip of apical process in lateral aspect of *Contulma* species: 123, *C. spinosa*; 124, *C. talamanca*; 125, *C. tapanti*; 126, *C. tijuca*; 127, *C. valverdei*; 128, *C.* species A.



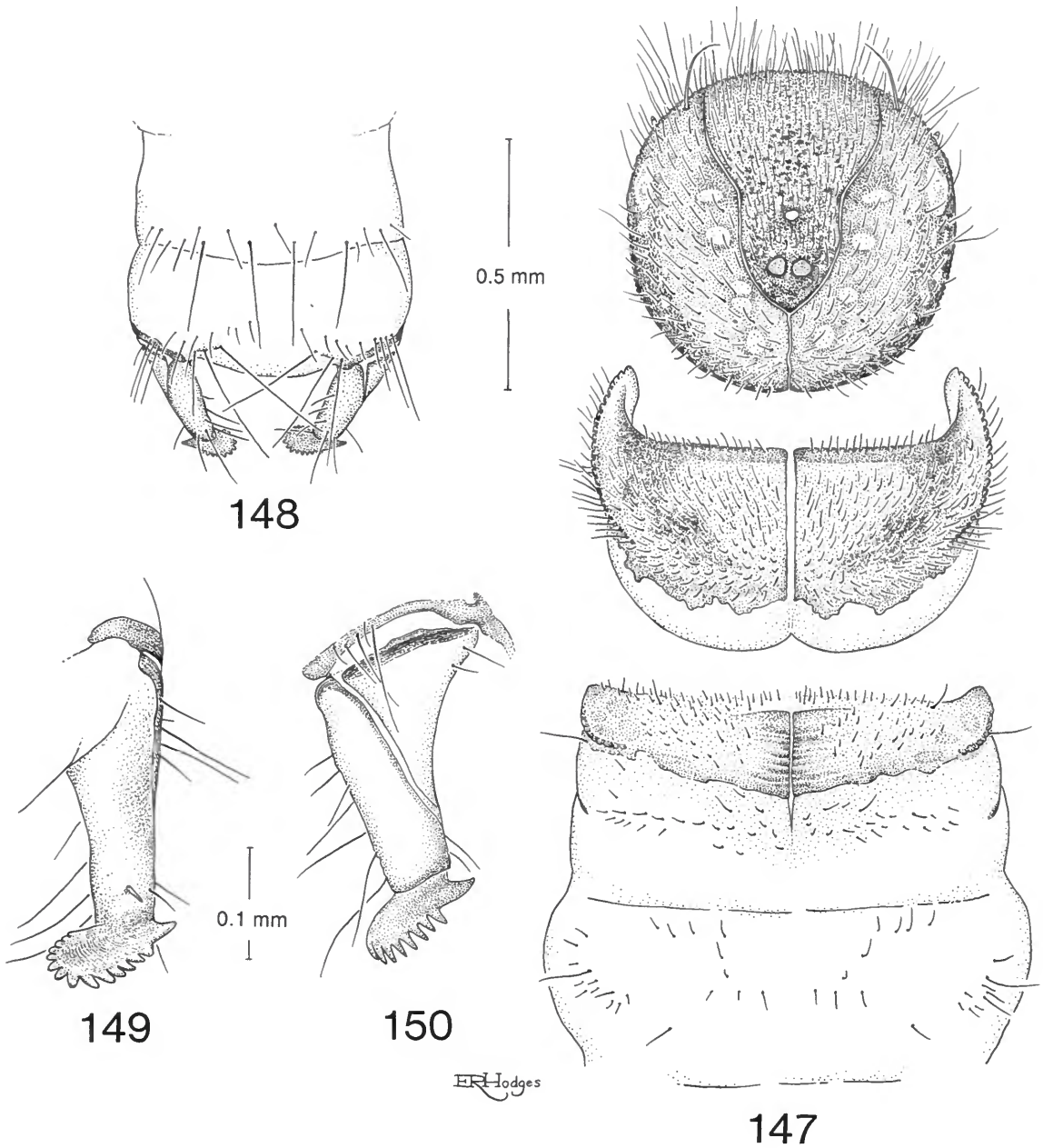
FIGURES 129–132.—*Contulma nevada*, larva: 129, head and thorax, lateral; 130, head and thorax, dorsal; 131, anal claw, lateral; 132, anal claw, dorsal.



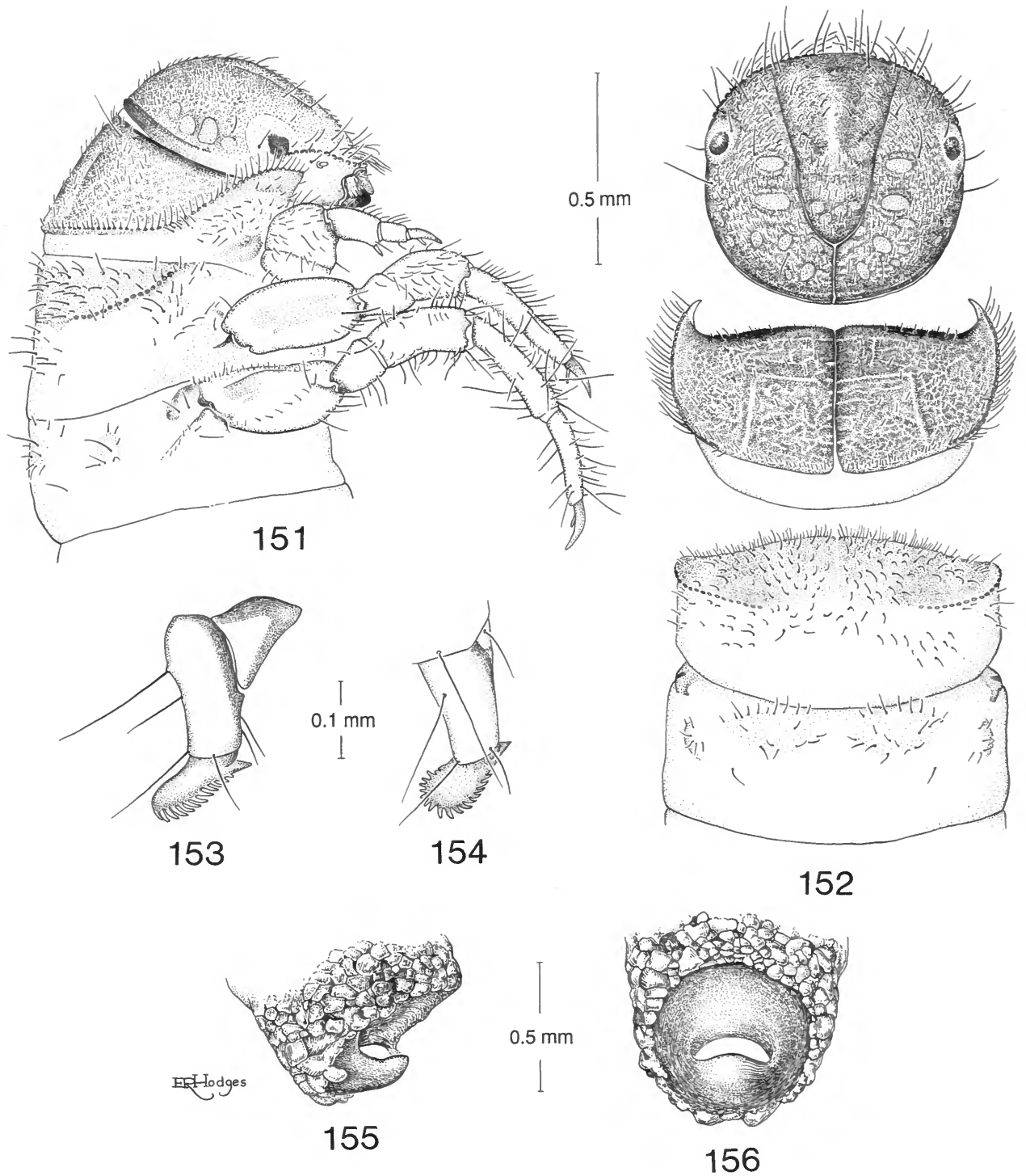
FIGURES 133-139.—*Contulma penai*, larva from near Medellín, Colombia: 133, lateral; 134, head and thorax, lateral; 135, head and thorax, dorsal; 136, anal claw, dorsal; 137, anal claw, lateral; 138, apex of larval case, obliquely posterolateral; 139, same, posterior.



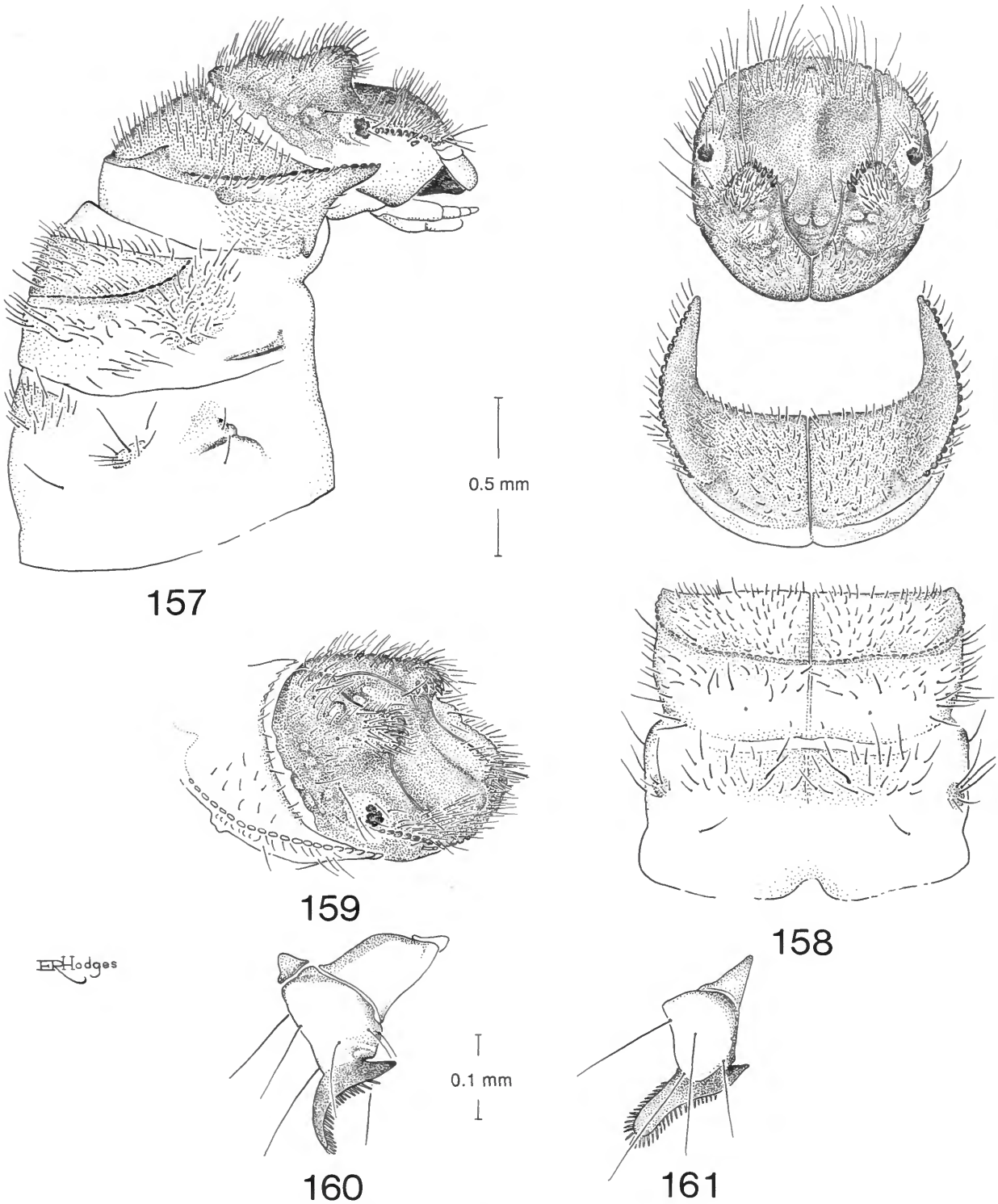
FIGURES 140–146.—*Contulma spinosa*, larva from near Cuenca, Ecuador: 140, lateral; 141, pronotum, lateral; 142, head and thorax, dorsal, with inset of integument showing fine, decumbent setae greatly enlarged; 143, apex of abdomen, dorsal; 144, anal proleg, lateral; 145, apex of larval case, obliquely posterolateral; 146, same, posterior.



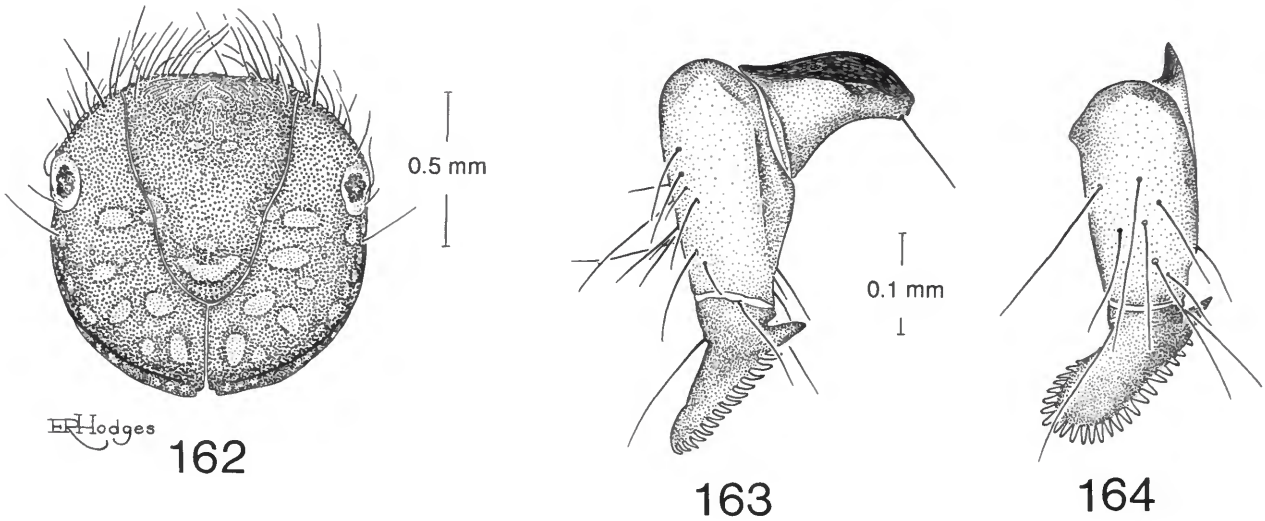
FIGURES 147–150.—*Contulma*, probably *tijuca*, larva: 147, head and thorax, dorsal; 148, apex of abdomen, dorsal; 149, anal claw, dorsal; 150, anal claw, lateral.



FIGURES 151–156.—*Contulma valverdei*, larva: 151, head and thorax, lateral; 152, head and thorax, dorsal; 153, anal claw, lateral; 154, anal claw, dorsal; 155, apex of larval case, obliquely posterolateral; 156, same, posterior.



FIGURES 157–161.—*Contulma* sp. B, larva: 157, head and thorax, lateral; 158, head and thorax, dorsal; 159, head and pronotum, obliquely frontolateral; 160, anal claw, lateral; 161, anal claw, dorsal.



FIGURES 162–164.—*Contulma* sp. C, larva: 162, head, dorsal; 163, anal claw, lateral; 164, anal claw, dorsal.

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