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The Simuliidae (Diptera) of the Santiago onchocerciasis focus of Ecuador

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CONTENTS

SYNOPSIS Keys to the adults, larvae and pupae of the seven species of Simuliidae found in the Santiago onchocerciasis focus of Ecuador are provided. Full morphological descriptions of each of these stages are given for each species, together with notes on their taxonomy, distribution and biology. Three new synonyms are established.

INTRODUCTION

The simuliid fauna of Ecuador had been only superficially studied up until 1980 when the discovery of onchocerciasis in the north of the country (Arzube, 1981) emphasised the need for a systematic investigation of the family. Previous taxonomic work on Simuliidae in Ecuador was either of a preliminary nature, consisting of notes on and keys to the then poorly studied fauna in papers that also covered the medical importance of the family (Leon & Wygodzinsky, 1953a, b; Levi-Castillo, 1956), or of a more detailed revisionary nature on certain high altitude temperate climate species of the Andes (e.g. Wygodzinsky, 1971). No studies then existed on the fauna of the lowland tropical forests of northern Ecuador where onchocerciasis is now known to occur. This paper provides the necessary biosystematic data on the Simuliidae of the Santiago onchocerciasis focus that are prerequisites for future longitudinal entomological surveys aimed at providing baseline data for vector control. Only three of the seven species recorded in the Santiago onchocerciasis focus are significantly anthropophilic and two of these, *Simulium exiguum* and *S. quadrivittatum*, have been incriminated as vectors of *Onchocerca volvulus* by Shelley & Arzube (1985).

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All species found in the Santiago onchocerciasis focus belong to the genus *Simulium* and the subgeneric assignments conform to those published in the recent checklist of world blackflies (Crosskey, 1987).

Material examined and terminology

All the material studied from the Santiago onchocerciasis focus was collected in 1981 during investigations into the vector species of the disease. Details of collection sites and the biology and medical importance of the species in the area have already been given by Shelley & Arzube (1985); a summary of this information is given for each species in the current paper. Data on the precise location of the focus shown in Figs 1 and 2, its topography, climate and inhabitants, are given in Arzube (1982) and Guderian *et al.* (1983). Specimens from the 1981 collection and subsequent

Fig. 1 Distribution of onchocerciasis in Ecuador.

collections made in other regions of Ecuador with which this material has been compared are deposited in the British Museum (Natural History), London, U.K. and the Instituto Nacional de Hygiene y Medicina Tropical 'Leopoldo Izquieta Perez', Guayaquil, Ecuador. Material has been conserved in the following ways: larvae, pupae, individually reared adults with their corresponding pupal pelts and females from biting catches – in 80% alcohol; individually reared adults in association with their pupal pelts preserved in glycerine in small polypropylene phials, and females from biting catches – in pinned collection; all stages – on microscope slides mounted in Berlese mountant. Chromosomal preparations from larval silk glands of some of the species are stored on microscope slides with accompanying photographs of some of the karyotypes in the Diptera Section of the Entomology Department of the British Museum (Natural History); larval cadavers from which silk glands have been extracted are preserved in 80% alcohol and on microscope slides. With the increasing need for larval polytene chromosome analysis in taxonomic studies on Neotropical Simuliidae, preservation of samples of larvae in Carnoy's fixative must now become routine. Carnoy's fixative accentuates and in some cases alters the colour pattern of larvae compared to that seen in material preserved in alcohol. Where colour changes occur these are noted at the head of the larval descriptions. Descriptions of adult coloration for each

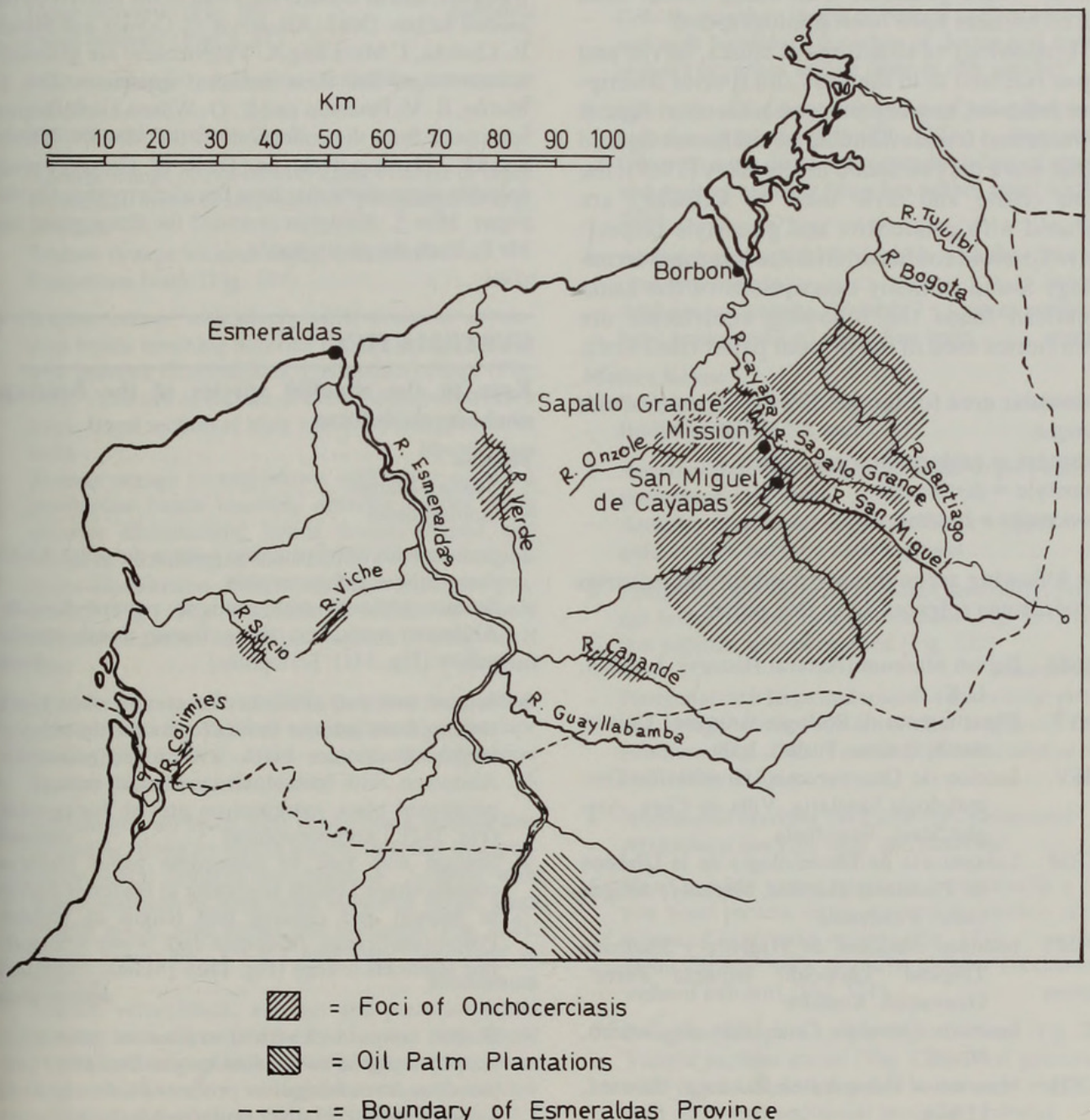

Fig. 2 The onchocerciasis foci of Esmeraldas Province, Ecuador.

species have been based on pinned specimens whereas photographs (Figs 138–153) are from alcohol preserved material prepared in the following way. Legs are removed from the body and directly mounted on a microscope slide in Berlese mounting medium. The wings are removed and discarded and the head, thorax and abdomen are placed in 'Cellosolve' for 12 hours, xylene for 6 hours and then air dried and mounted on a microscope slide using a drop of 'Araldite' epoxy resin. The specimens photographed have been preserved in alcohol for up to seven years and show little or no colour changes from pinned material. However, much of our alcohol material is teneral and hence full adult coloration, particularly of the legs, has not been attained. To obviate differences between descriptions and photographs of each species where possible, man-biting rather than reared females have been photographed.

Terminology of structures in adults, larvae and pupae referred to in the keys and species descriptions follows Crosskey (in press). General figures for male and female Simuliid genitalia not figured in that work may be found in Crosskey (1969); the terms coxite and style used by Crosskey are replaced with gonocoxite and gonostyle respectively. To avoid confusion with the less usual terminology found in many descriptions of the Latin American fauna the following equivalents are given (terms used in the present paper cited first):

nudiocular area (of female head) = fronto-ocular triangle;
paramere = endoparameral organ;
gonostyle = distimere;
gonocoxite = basimere.

The following acronyms are used for depositories of specimens referred to in this paper.

BMNH British Museum (Natural History), London, U.K.
DBAT Dipartimento di Biologia Animale, Universita di Torino, Torino, Italy
DDSV Seccion de Oncocercosis, Division de Dermatologia Sanitaria, Villa de Cura, Aragua State, Venezuela
DERM Laboratorio de Entomologia de la Division de Endemias Rurales, Maracay, Aragua State, Venezuela
INHMT Instituto Nacional de Hygiene y Medicina Tropical 'Leopoldo Izquieta Perez', Guayaquil, Ecuador
IOC Instituto Oswaldo Cruz, Rio de Janeiro, Brazil
MCZH Museum of Comparative Zoology, Harvard, U.S.A.
MLP Museo La Plata, La Plata, Argentina
MNHN Muséum National d'Histoire Naturelle, Paris, France
STMPR Department of Microbiology, School of Medicine, School of Tropical Medicine, San Juan, Puerto Rico
USNM United States National Museum, Washington, D.C., U.S.A.
ZM Zoologisches Museum der Humboldt Universitaet, Berlin, West Germany

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SYSTEMATICS

Keys to the simuliid species of the Santiago onchocerciasis focus

Females

1 Scutum orange 2
– Scutum black 4

2 Scutum with white pruinose pattern dorsally. Abdomen without yellow tergites 3
– Scutum without white pruinose pattern dorsally. Abdomen with first three (rarely four) tergites yellow (Fig. 141). [Zoophilic] ..... ***lewisi***

3 Scutum with pair of submedian greyish white bands running from anterior border for four fifths of scutal length. Postnotum black with silver pruinosity. Abdomen with dorsal chequerboard pattern of prominent black markings on greyish background (Fig. 142). [Anthropophilic] ..... ***escomeli***
– Scutum with pair of submedian white pruinose comma-shaped bands beginning at posterior border of humeri and running half length of scutum. Postnotum orange. Abdomen dark brown with anterior segments orange (Fig. 140). [Mainly zoophilic] ***bipunctatum***

4 Scutum velvet-black with silver pruinose pattern formed by a pair of submedian longitudinal silver pruinose bands reaching silver pruinose hind margin and a pair of sublateral silver pruinose bands. Abdomen black dorsally with transverse silver pruinose bands

on segments of anterior three-quarters (Fig. 145). [Anthropophilic] ..... ***quadrivittatum***
– Scutum shiny black without silver pattern. Abdomen black without transverse silver pruinose bands .. 5

5 Scutal hairs yellowish white. Legs mainly dark; fore tarsi dilated (Fig. 144). Basal section of wing vein *R* with two or three irregular rows of hairs; *Sc* with single row of hairs (Fig. 41). [Zoophilic] ***mexicanum***
– Scutal hairs golden or green (depending on light incidence). Legs mainly pale; fore tarsi not dilated (Figs 138, 139). Basal section of wing vein *R* and *Sc* without hairs. 6

6 Paraproct with long anterior process (Fig. 55). [Anthropophilic] ..... ***exiguum***
– Paraproct with short anterior process (Fig. 56). [Zoophilic] ..... ***gonzalezi***

Males

1 Head dichoptic (Fig. 10) ..... ***gonzalezi***
– Head holoptic (Figs 8, 11) 2

2 Scutum orange or brown. Scutellum orange or yellow 3
– Scutum and scutellum black 5

3 Scutum orange or brown with a pair of silver or black submedian bands in anterior half. Postnotum orange or black 4
– Scutum orange without dorsal ornamentation. Postnotum black (Fig. 149) ..... ***lewisi***

4 Scutum orange with silvery white pruinose submedian bands touching anterior border (most obvious with anterior illumination). Postnotum orange (Fig. 148). Vestiture of scutum of evenly distributed black hairs. Basal section of wing vein *R* with single row of hairs ..... ***bipunctatum***
– Scutum orange to mid-brown with silver pruinose submedian bands touching anterior border using anterior illumination; bands comma-shaped and black, not touching anterior scutal border with posterior illumination. Postnotum black with grey pruinosity (Fig. 150). Vestiture of scutum of evenly distributed golden hairs. Basal section of wing vein *R* bare. ..... ***escomeli***

5 Scutum with a pair of silver pruinose submedian cunae in anterior third of scutum touching anterior border (Fig. 153) ..... ***quadrivittatum***
– Scutum without ornamentation 6

6 Scutum greyish black with velvet-black median line extending along its entire length; anterior and posterior scutal borders not pruinose. Scutum with dense vestiture of long-brass coloured setae. Legs mainly black; tarsi broad and flattened (Fig. 152). Large robust fly, 3.0–4.5 mm long (preserved in alcohol) ..... ***mexicanum***
– Scutum velvet-black; anterior and posterior scutal borders with silver pruinosity. Scutum with dense vestiture of short golden setae with green reflections. Legs mainly yellow or light brown with narrow unflattened tarsi (Figs 146, 147). Small fly 1.3–2.1 mm long (preserved in alcohol) 7

7 Femur of mid leg dark brown to black (Fig. 147). ***gonzalezi***
– Femur of mid leg yellow (Fig. 146) ..... ***exiguum***

Pupae

Gill with six filaments (Fig. 110) ..... ***gonzalezi***
– Gill with more than six filaments 2

2 Gill with twelve filaments (Fig. 115) .. ***mexicanum***
– Gill with eight filaments 3

3 Cocoon white to light brown, thick walled and with a longitudinal dorsal ridge. Gill with most distal bifurcations of dorsal and median primary branches at mid point (Fig. 106) ..... ***lewisi***
– Cocoon brown to grey, thin-walled and without dorsal ridge. Most distal bifurcations of dorsal and median primary branches within basal third of gill 4

4 Gills longer than length of ventral surface of cocoon and with spaced secondary branching (Fig. 116) ***quadrivittatum***
– Gills shorter than length of ventral surface of cocoon and with secondary branches of dorsal and median primary branches arising close to one another .. 5

5 Gill with secondary branching of all primary gill branches in basal eighth (Fig. 112) ... ***bipunctatum***
– Gill with most distal secondary branches of median and ventral primary branches within basal sixth to third 6

6 Abdominal sternite IV with 2 + 2 fine hairs on posterior margin ..... ***exiguum***
– Abdominal sternite IV with 1+1 outer simple or bifid hooks and 1+1 inner fine hairs ..... ***escomeli***

Mature larvae

1 Body length 6.9–9.7 mm ..... ***mexicanum***
– Body length 2.8–5.8 mm 2

2 Anterior abdominal segments white to grey with two prominent dark bands 3
– Anterior abdominal segments white to grey with a pale or dark band on each segment 4

3 Postgenal cleft small and pointed anteriorly; postgenal bridge as long as hypostomium (Fig. 137). Ventral papillae well-developed (Fig. 122) ***quadrivittatum***
– Postgenal cleft large and rounded anteriorly; postgenal bridge about one-tenth the length of hypostomium (Fig. 134). Ventral papillae absent or very small (Fig. 119) ..... ***lewisi***

4 Abdominal marking dark and very prominent .. 5
– Abdominal marking light and indistinct 6

5 Head capsule without pattern (occasionally a positive head pattern or an amorphous darker area in region of head spots occurs) (Fig. 123) .. ***exiguum***
– Head capsule with negative pattern (occasionally without pattern) (Fig. 124) ..... ***gonzalezi***

6 Postgenal bridge as long as hypostomium (Fig. 135). Ventral papillae absent (Fig. 120). Anal gills usually with three simple lobes but outer pair sometimes with up to two additional secondary lobules ***escomeli***

– Postgenal bridge one-third the length of the hypostomium (Fig. 133). Ventral papillae small (Fig. 118). Anal gills with 6–8 secondary lobules on each primary lobe. ..... ***bipunctatum***

Simulium (Notolepria) exiguum Roubaud

(Figs 3, 5, 7, 8, 12–14, 17, 21, 23, 24, 25, 31, 37, 43, 49, 55, 62, 69, 75, 76, 90, 103, 110, 117, 123, 131, 138, 146)

Simulium exiguum Roubaud, 1906: 108. LECTOTYPE ♀, VENEZUELA: Haut Sarare, 1899 (*F. Geay*) (MNHN), here designated. [examined]

Simulium glaucophthalmum Knab, 1914b: 123. Holotype ♀, PERU: Santa Clara, iv.1914 (*C. H. T. Townsend*) (USNM Cat. No. 18494) [examined]. [Synonymy by Wygodzinsky, 1951: 214.]

Simulium delpontei Paterson & Shannon, 1927: 742. Holotype ♀, ARGENTINA: Salta Province, Embarcacion, 4.v.1926 (*Paterson, Shannon & Shannon*) (depository unknown). [Synonymy by Wygodzinsky, 1951: 214.]

DESCRIPTION. *Female*. General body colour black. Body length (alcohol preserved specimens) 1.8–2.7 mm (n = 24), wing length 1.4–2.0 mm (n = 21), wing width 0.7–0.9 mm (n = 19).

Head dichoptic (Fig. 7) with dark red eyes showing green highlights; nudiocular area absent (Fig. 25). Frons, clypeus and occiput black with silver pruinosity. Mouthparts orange-brown. Antennae dark brown with scape, pedicel and first flagellomere orange-brown. Cibarium unarmed (Fig. 31).

Scutum and humeri greyish black with faint silver pruinosity; one median and a pair of posteriorly divergent submedian darker black lines running along whole length of scutum (best seen in specimens devoid of setae and with illumination perpendicular to specimen); scutum also with small velvet-black spot adjoining paranotal folds (= paratergites). Paranotal folds black with silvery grey pruinosity. Scutum with numerous short adpressed dark setae and discrete groups of short flattened brass-coloured setae with greenish reflections (Fig. 138). Pleural region silvery grey pruinose. Scutellum greyish black and faintly pruinose, its vestiture comprised of golden setae longer than those on scutum and a single row of black bristles on posterior margin. Postnotum silvery grey pruinose.

Subcostal wing vein and basal sector of radius bare (Fig. 37). Costal base tuft of dark hairs.

Legs yellow to light brown, except fore tarsi, mid and hind coxae, hind femora and distal three-fourths of hind tibiae black. All femora and tibiae with scales (Fig. 3). Proportions of legs as in Fig. 138. Claws curved and slender, without basal tooth on fore and mid legs but with poorly developed tooth on hind leg (Fig. 43). Halteres pale yellow with light brown stem.

Abdominal tergites shiny brownish black with silver pruinosity on second segment (Fig. 138). Tergal plates well-developed, pattern as in Fig. 4. Sternites brownish black; genitalia light brown. Eighth sternite highly sclerotised with a group of 8–12 stout setae in each sclerotised portion (Fig. 49); gonopophyses small, sclerotised on inner margin, glabrous. Cerci hemispherical, light brown; paraprocts broadly rectangular with pointed anteriorly directed process (Fig. 55). Genital fork (Fig. 62) slender, with sclerotised anteriorly directed processes and stem. Spermatheca oval, highly sclerotised, with no external sculpturing and spicules of inner surface obscured by sclerotisation; width of membranous area of insertion of spermathecal duct large, about half maximum width of spermatheca (Fig. 5).

Male. General body colour black. Body length (alcohol preserved specimens) 1.9–2.1 mm (n = 6), wing length 1.5–1.7 mm (n = 5), wing width 0.7–0.8 mm (n = 5).

Head holoptic (Fig. 8) with dark red eyes; lower, smaller facets with greenish reflections. Clypeus black with silver pruinosity, other head coloration as in female.

Scutum and humeri velvet-black with anterior and posterior margins and anterior two-thirds of lateral margin silver pruinose (Fig. 146). Paranotal folds velvet-black with silvery grey pruinosity. Scutum covered in numerous, short, adpressed, light brown setae interspersed amongst groups of brilliant gold, scale-like setae. Coloration and setation of pleural region, scutellum and postnotum as in female except scale-like setae on scutellum brilliant gold.

Wing venation, leg coloration (Fig. 146) and haltere coloration as in female.

Abdominal tergites velvet-black, basal fringe dark brown with few long hairs. Silver ornamentation as follows: tergites II and VI all silver except sometimes in median area on VI; tergite VII all silver except for median area, some specimens show a pair of lateral silver pruinose patches on posterior margin of tergite VIII. Tergite IX shiny black (Fig. 146). Sternites grey with well-developed velvet-black sternal plates on segments II–VIII (Fig. 6). Genitalia brownish black. Gonocoxite subrectangular, gonostyle small, subtriangular, one-third as long as gonocoxite and with small distal spine (Fig. 69). Ventral plate with reduced basal arms, lightly sclerotised, triangular

with small keel, hairs short, diffuse and mainly occurring around median keel (Figs 75, 76). Median sclerite subrectangular with deep apical incision (Fig. 90). Paramere with several apical spines (as shown in Fig. 97 for *S. gonzalezi*).

Pupa. Cocoon length dorsally 1.6–2.6 mm, ventrally 2.2–3.2 mm; pupa length 1.7–2.3 mm; gill length 1.3–2.1 mm (n = 27).

Cocoon slipper-shaped, mid to dark brown; rim of aperture dark brown, reinforced and without central protuberance (Fig. 103). Cocoon composed of elastic, amorphous substance interwoven with fibres. Gill light brown with eight forwardly directed slender filaments arranged in the vertical plane (Fig. 110), main trunk giving rise to three primary branches, ventral with two filaments and median and dorsal each with three filaments; ventral branch with bifurcation in basal fourth of gill, median branch with first bifurcation in basal fourth and second bifurcation in basal third of gill; dorsal branch with first bifurcation basally at junction of median and dorsal primary branches and second bifurcation within basal fourth of gill; filaments slender with crenate margins and rounded distally, their surfaces covered in fine spicules (Fig. 12). Head (frontoclypeus) with 2 + 2 frontal trichomes of which the more dorsal pair is simple and poorly developed and the more ventral pair well-developed and 2–5 branched, and 1 + 1 well-developed facial trichomes with 2–5 branches; surface of head covered with platelets (Figs 13, 14). Thorax with 5 + 5 antero-dorsal, well-developed trichomes of 2–5 branches. Surface of thorax covered with platelets which are more densely distributed on anterior half (Fig. 17). Abdominal tergite II with 4 + 4 simple hairs in a line on posterior border of segment, III–IV with 4 + 4 simple hooks, VI–IX with patches of poorly developed spine combs on antero-lateral margins, IX with 1 + 1 strong, unbranched spines (Fig. 19); sternite IV with 1 + 1 simple hairs, V with 2 + 2 bifid or trifid hooks, VI and VII with 2 + 2 hooks, the inner pairs being bifid or trifid and the outer pairs simple; 1 + 1 patches of poorly developed spine combs on postero-lateral borders of sternites IV–VIII (Fig. 20).

Mature larva. Body length 3.6–4.4 mm (n = 33). Width of head capsule 0.4–0.5 mm (n = 32). Body usually white with greyish brown markings (Fig. 117), occasionally almost completely white and showing only indistinct grey pigmentation. Coloration in Carnoy's fixative is similar except that the banding patterns are more distinct. Body form as in Fig. 117.

Head yellow with head spots concolorous; occasional specimens with positive head spot pattern as in Fig. 123 or with an amorphous dark area in head spot region that obscures the spots. Head capsule with few, randomly distributed setae on all surfaces. Postgenal cleft as wide as long, rounded anteriorly; postgenal bridge about half as long as hypostomium (Fig. 131). Hypostomium with strongly pigmented anterior margin and nine apical teeth: corner teeth large and blunt, median tooth less developed but larger than subequal intermediate teeth; 4–5 lateral serrations with hindmost about level with first hypostomial seta; 1 + 1 groups of four hypostomial setae lying parallel to lateral margins of hypostomium; surface of hypostomium with a few short setae (Fig. 21). Antennae long, unpigmented with segment ratios 23 : 10 : 12. Mandible (Fig. 23) with first three comb teeth decreasing in size posteriorly and two mandibular serrations of which the anterior is larger. Maxillary palp about twice as long as breadth at base. Cephalic fan with 30–43 rays (n = 10).

Thorax white with grey ring around anterior region and grey pattern dorsally of variable form that almost covers whole area, ventrally with two or three central patches of grey chromatocytes posterior to proleg. Cuticle with occasional small setae dorsally, glabrous ventrally. Proleg plates lightly sclerotised and with about six processes. Pupal respiratory histoblast dark brown, claviform.

Abdomen white with a single complete black or grey ring on each of the four anterior narrow segments; posterior segments grey or black dorsally, white with variable scattered black chromatocytes ventrally. Ventral nerve cord black. Ventral papillae absent. Cuticle with minute hairs dorsally in dark areas, ventral surface glabrous. Anterior perianal area with a group of fine spines. Anal sclerite well sclerotised with posterior arms extending to twelfth row of posterior circlet hooks. Posterior circlet with 70–78 rows of 2–14 hooks (n = 8). Anal gill trilobed, each lobe with 6–8 long finger-like lobules (Fig. 24).

Material Examined

Lectotype ♀, paralectotypes 5 ♀ of *S. exiguum*, **Venezuela**: Sarare, 1899 (*F. Geay*) (BMNH, MNHN). Holotype ♀ of *S. glaucophthalmum*, **Peru**: Santa Clara, 1914 (*C. H. T. Townsend*) (USNM).

Argentina: 3 ♀, Jujuy, xii.1938 (*W. C. Paterson*) (BMNH).

Bolivia: 2 ♀, Covende, 1921–22 (*W. M. M. Mann*) (BMNH); 1 ♀, HuachiBeni, viii.1921–22 (*W. M. M. Mann*) (BMNH).

Brazil: Roraima Territory: 1 ♀, Posto Meva, Rio Auaris, 3.iv.1977 (*R. R. Pinger*) (BMNH); 1

♀, 15 ♀ 6 ♂ (ex pupae), Catrimani Mission, Rio Catrimani, 9.i.1977 and 12, 13.i.1979 (*A. J. Shelley*, and *A. J. Shelley & A. P. A. Luna Dias*) (BMNH); 1 ♀ 1 ♂ (ex pupae), Rio Uraricoeira, 20.i.1979 (*A. J. Shelley & A. P. A. Luna Dias*) (BMNH); 3 ♀ 2 ♂ (ex pupae), Northern Perimeter Road, Rio Agua Preta, 18.xi.1980 (*A. J. Shelley & A. P. A. Luna Dias*); 1 ♀ 1 ♂ (ex pupae), Mucajai Mission, Rio Mucajai, 6.i.1977 (*A. J. Shelley*) (BMNH); 1 ♂, Normandia, Igarapé Inamaru, 3.xii.1980 (*A. J. Shelley & A. P. A. Luna Dias*) (BMNH); 1 ♀, 1 ♀ 5 ♂ (ex pupae), Vila Pereira, Rio Surumu, 25, 26.xi.1980 (*A. J. Shelley & A. P. A. Luna Dias*) (BMNH); 2 ♀ 2 ♂ (ex pupae), nr Bonfim, Rio Arraia, 3.xii.1980 (*A. J. Shelley & A. P. A. Luna Dias*); Amazonas State: 11 ♀, Mission Post, Rio Toototobi, 16.viii. and 24, 25.x.1976 (*R. R. Pinger*) (BMNH); 6 ♀, Rio Ituxi, v.1978 (*D. Roberts*) (BMNH); 6 ♀ 3 ♂ (ex pupae), Mato Grosso, Rio Aripuana, 29.vi.1978 (*J. D. Charlwood*) (BMNH).

Colombia: Sierra Nevada de Santa Marta: 3 ♀, Ariguani, 20.xii.1963 (*J. P. Lee-Potter*) (BMNH); 1 ♀, Meollaca, 22.xii.1963 (*J .P. Lee-Potter*), 2 ♀, Valledupar, 15.i.1963 (*J. P. Lee-Potter*) (BMNH); 2 ♀, Department of Valle, Tunselas, 16.iii.1977 (*J. Ardila*) (BMNH).

Ecuador: numerous man-biting females, reared adults, pupae and larvae from the following localities in the Santiago onchocerciasis focus in Esmeraldas Province: R. Cayapa, San Miguel de Cayapas, 18–21.vi.1981 (*A. J. Shelley & M. Arzube*) (BMNH, INHTM); R. Grande (Cayapa), Viruela and Calle Mansa, 26–27.v.1981 (*A. J. Shelley & M. Arzube*) (BMNH, INMHT); R. Sapallo Grande, Tumbaviro, 18.vi.1981 (*A. J. Shelley & M. Arzube*) (BMNH, INHTM); numerous man-biting females, reared adults and larvae from the Canandé peripheral onchocerciasis focus in Esmeraldas Province, R. Canandé, Naranjal, 25.ix.1983 and 21–24.vi.1985 (*A. J. Shelley & M. Arzube*) (BMNH, INHMT); 1 ♀, 1 ♀ (ex pupa), 1 larva, Esmeraldas Province, nr Concordia, road to Puerto Quito, R. Caoni, 24.ix.1983 (*A. J. Shelley & M. Arzube*) (BMNH); 2 ♀ 1 ♂ (ex pupa), nr Concordia, road to Puerto Quito, Rio Salazar, 28.ix.1983 (*A. J. Shelley & M. Arzube*) (BMNH, INMHT); 5 ♀ 3 ♂ (ex pupae), nr Concordia, road to Puerto Quito, R. Blanco, 28.ix.1983 (*A. J. Shelley & M. Arzube*) (BMNH); 1 ♀ (ex pupa), Santo-Domingo-Esmeraldas road, Rio Sapotal, 26.ix.1983 (*A. J. Shelley & M. Arzube*) (BMNH); 1 ♀, Imbabura Province, Salinas road, R. Tahuando, 8.ix.1983 (*A. J. Shelley & M. Arzube*) (BMNH); 3 ♀, 5 ♀ 3 ♂ (ex pupae), Salinas-Lita road, San Juan del Hacha, R. Mira, 11.ix.1983 (*A. J. Shelley & M. Arzube*) (BMNH); 1 ♀ (ex pupa), Salinas-Lita road, R. San Pedro, 11.ix.1983 (*A. J. Shelley & M. Arzube*) (BMNH); 13 ♀, 16 ♀ 12 ♂ (ex pupae), Napo Province, nr Lago Agrio, Rio San Miguel, 9.xii.1982 (*A. J. Shelley & M. Arzube*) (BMNH); 1 ♀, nr Lago Agrio, Posto 19, R. Tarapa, 9.xii.1982 (*A. J. Shelley & M. Arzube*) (BMNH); 1 ♀, nr Lago Agrio, Rio Teteye, 9.xii.1982 (*A. J. Shelley & M. Arzube*) (BMNH); 15 ♀, 8 ♀, 6 ♂ (ex pupae), nr Lago Agrio, Dureno, R. Aguarico, 10–13.xii.1982 (*A. J. Shelley & M. Arzube*) (BMNH, INHMT); 8 ♀, nr Tena, Misahualli, R. Napo, 7.vi.1985 (*A. J. Shelley & M. Arzube*) (BMNH); 6 ♀, 1 ♀ (ex pupa), El Oro Province, Machala-Naranjal road, canal de riego, Rio Bucay, 12.vi.1984 (*A. J. Shelley & M. Arzube*) (BMNH); 4 ♀, Machala-Uzcurume road, nr Pasaje, Rio Guesha, 20.vi.1984 (*A. J. Shelley & M. Arzube*) (BMNH); 1 ♀ (ex pupa), Machala-Uzcurume road, near Pasaje, Rio Jubones, 20.vi.1984 (*A. J. Shelley & M. Arzube*) (BMNH); 2 ♀, 4 ♀ 2 ♂ (ex pupae), Machala-Pinas road, Rio Carne Amarga, 21.vi.1984 (*A. J. Shelley & M. Arzube*) (BMNH); 2 ♀, Pastaza Province, Tena-Puyo road, Rio Mira Valle, 8.vi.1985 (*A. J. Shelley & M. Arzube*) (BMNH); 1 ♀, Puyo, Shell-Mera road, confluence of Rios Alpayacu and Pastaza, 10.vi.1985 (*A. J. Shelley & M. Arzube*) (BMNH); 6 ♀, 5 ♀ 2 ♂ (ex pupae), Cotopaxi Province, Quevedo-La Mana-Pilalo road, Rio San Pablo, 8.vi.1984 (*A. J. Shelley & M. Arzube*) (BMNH, INHMT); 1 ♂ (ex pupa), Quevedo-La Mana-Pilalo road, Recinto Beles, Rio San Pablo, 8.vi.1984 (*A. J. Shelley & M. Arzube*) (BMNH); 6 ♀, 1 ♂ (ex pupa), Manabi Province, Santo Domingo-El Carmen road, Rio Suma, 7.vi.1984 (*A. J. Shelley & M. Arzube*) (BMNH); 2 ♀, Los Rios Province, Babahoyo-Montalvo road, Rio Cristal, 10.vi.1984 (*A. J. Shelley & M. Arzube*) (BMNH); 3 ♀, Bolivar Province, Babahoyo-Balzapamba-Aguaranda road, Rio Chanpiaco, 10.vi.1984 (*A. J. Shelley & M. Arzube*) (BMNH); 39 ♀, 2 ♀ 2 ♂ (ex pupae), Guayas Province, Naranjal-Machala road, Via Cooperativa 11 de Agosto, Rio Bucay, 19.vi.1984 (*A. J. Shelley & M. Arzube*) (BMNH); 14 ♀, 2 ♀ (ex pupae), Loja Province, Loja-La Toma road, Hacienda Monterey, Rio Guayabal, 23.vi.1984 (*A. J. Shelley & M. Arzube*) (BMNH).

Venezuela: numerous man-biting females from the Caripe onchocerciasis focus, Monagas State, San Antonio de Maturin (nr Caripe) and Caripe area, 7.iv.1981 and iv.1981 (*D. J. Lewis*) (BMNH); 3 ♀ 5 ♂ (ex pupae), Yaracuy State, Rio Yaracuy (no collection date) (*J. Ramirez Perez*) (BMNH); 1 ♀ with associated pupal case, Miranda State, Tacata (no collection date) (*J. Ramirez Perez*) (BMNH); 1 ♀ 2 ♂ (ex pupae),

Trujillo State, Carache (no collection date) (*J. Ramirez Perez*) (BMNH).

TAXONOMIC DISCUSSION. *Simulium exiguum* was described by Roubaud from a series of females (one specimen pinned and an undisclosed number preserved in alcohol) sent from Sarare [presumably the upper reaches of the R. Sarare in Arauca State in northern Venezuela, where *S. exiguum* is commonly found today] by F. Geay. No type designations were made in the paper so the specimens have syntype status. Vargas (1945) incorrectly refers to their status as a type [= holotype] in the MNHN and a probable paratype in the BMNH. Six pinned specimens from the original material have been located in the BMNH and MNHN, each bearing a printed label of the Paris Museum as follows: 'Museum Paris, Venezuela, Sarare, Geay 1899'. One of the five specimens in the MNHN bears a 'type' label and a handwritten label with the following details '*S. exiguum* Roubaud n.sp. Bull.Mus. 1906'. This specimen is in relatively good condition, is here designated lectotype and has been labelled accordingly. The other four specimens in the MNHN appear to have been recovered from alcohol and have been labelled as paralectotypes. The single specimen in the BMNH had been previously recovered from alcohol and although in poor condition is recognisable as *S. exiguum*. It bears two labels in Austen's hand indicating the collection locality and that it was donated by Roubaud, and it has now been labelled as a paralectotype.

In Wygodzinsky's revision (1951) of *S. exiguum* two nominal species, *S. glaucophthalmum* Knab collected in Peru and *S. delpontei* Paterson & Shannon from Argentina, are synonymised with *S. exiguum*. His synonymy of *S. glaucophthalmum* was based on an examination of types and Knab's description (1914b) but no reasons were given for the synonymy of *S. delpontei* with *S. exiguum*. We here confirm the former synonymy following dissection of the *S. glaucophthalmum* holotype and comparison of its paraprocts with those of *S. exiguum*. Although Paterson & Shannon's description (1927) of *S. delpontei* clearly indicates it to be within the subgenus *Notolepria* its synonymy with *S. exiguum* or the closely related *S. gonzalezi* or *S. paraguayense* may only be clarified once the form of its paraproct is known. Coscaron & Wygodzinsky (1975) continue to cite *S. delpontei* as a synonym of *S. exiguum* in a paper devoted to comparing the latter with *S. paraguayense*. We also recommend that the value of the characters, principally the female paraproct, used for the separation of *S. paraguayense, S. exiguum* and *S. gonzalezi* are investigated in conjunction with chromosomal analyses in 'genetically monomorphic' populations in order to clarify the taxonomic status of these three species.

Simulium exiguum is one of the more commonly encountered anthropophilic South American simuliids and hence has been well described and cited in numerous publications. The most complete taxonomic works on the species are Wygodzinsky (1951) and Coscaron & Wygodzinsky (1975). *Simulium exiguum* is the type species of the subgenus *Notolepria* and is closely related to *S. paraguayense* from southern South America, from which it is distinguished by adult leg coloration and the morphology of the male and female genitalia (Coscaron & Wygodzinsky, 1975). Another close relative, *S. gonzalezi* Vargas & Diaz Najera, occurs sympatrically in Ecuador with *S. exiguum* from which it may be distinguished by adult leg coloration, the form of the female paraproct and the number of pupal gill filaments. Takaoka (1983) confirmed Dalmat's finding in 1955 that in Guatemala this latter character is variable within *S. gonzalezi* and cannot therefore be used for accurate species determination there. Similar observations on the form of the paraproct for distinguishing *S. exiguum* from *S. gonzalezi* were made by Lewis & Lee-Potter (1964). They noted differences in the paraproct of *S. exiguum* from the Sierra Nevada de Santa Marta in northern Colombia compared with typical *S. exiguum* from northern Venezuela. Lewis (1963) also refers to the presence of eight-filamented pupae of *S. gonzalezi* in Antigua but no material has been found in the BMNH collections. In Ecuador separation of *S. exiguum* and *S. gonzalezi* has been based on the form of the paraproct in females in conjunction with the number of filaments in the gill of the pupa. No variation in gill filament number was observed, pupae with eight-filamented gills always producing females with *S. exiguum* type paraprocts and those with six filaments females with *S. gonzalezi* type paraprocts. Adult females collected biting man and horses were identified as *exiguum* or *gonzalezi* based on paraproct form, and similar identifications of males were based on the gill form of pupae from which they were reared.

Only male *S. exiguum* with holoptic heads were recorded in the Santiago onchocerciasis focus but a dichoptic form occurs in Venezuela (Vargas & Diaz Najera, 1953b; Lewis 1963) and Darien Province, Panama (material collected by Dr J. Petersen and examined by senior author).

The recent discovery (Procunier *et al.*, 1985 and Procunier, pers. comm.) that *S. exiguum* is a complex of at least four sibling species in Ecuador now suggests the need for integrated morphological

and cytological studies when investigations on the biology and medical importance of the sibling species in South America are made.

DISTRIBUTION. In Ecuador *S. exiguum* is found in most provinces on both the east and west of the Andean cordillera. It occurs at both the main onchocerciasis focus in the Santiago river basin and at the peripheral focus at the R. Canandé.

Simulium exiguum occurs in the following South American countries: Argentina, Bolivia, Brazil, Colombia, Peru and Venezuela. It has also been recently collected in southern Panama (Dr J. Petersen, pers. comm.). Records of its occurrence in other Central American countries, especially Guatemala and Mexico, need to be verified because in many cases these refer to *S. gonzalezi* (Vargas & Diaz Najera, 1953b; Dalmat, 1955; Takaoka, 1983). Further details of its distribution and bionomics may be obtained in Shelley (in press b).

BIOLOGY. In Ecuador *S. exiguum* is the most common man-biting species in the lowland tropical forests of the eastern and western slopes of the Andes, where, typically at altitudes of 100–500 m, high biting rates of up to 2200 flies/man/day occur in some localities (Procunier *et al.*, 1985; Shelley & Arzube, 1985, unpublished data); in these areas horses, when present, are also favoured as a blood source. Similar host preferences have been noted for this species in northern Venezuela in an area where it is a suspected sporadic vector of onchocerciasis (Lewis & Ibañez de Aldecoa, 1962) and in Colombia where it attacks man, horses and cattle in large numbers (Guttman, 1972), showing a preference for animal hosts in some localities (Trapido *et al.*, 1971). *Simulium exiguum* bites man in large numbers in Argentina (Coscaron & Wygodzinsky, 1975) but in contrast it may be almost entirely zoophilic in some localities in northern Brazil (Shelley, 1988). In Bolivia it has been recorded biting tapirs (Vargas & Diaz Najera, 1953b).

Apart from being a biting nuisance, *S. exiguum* is a primary vector of onchocerciasis in Ecuador (Shelley & Arzube, 1985) and Colombia (Tidwell *et al.*, 1980) and a suspected sporadic vector in northern Venezuela (Lewis & Ibañez de Aldecoa, 1962). A review of its biology in relation to onchocerciasis transmission in Latin America may be found in Shelley (1988). In Colombia, *S. exiguum* is also suspected of being involved in the transmission of Venezuelan Equine Encephalitis (Sanmartin *et al.*, 1973), although more recent work (Homan *et al.*, 1985) showing no viral replication in *S. metallicum* Bellardi and *S. mexicanum* also suggests that *S. exiguum* may only be involved in mechanical transmission.

Simulium exiguum favours open, sunlit rivers from 5–100 m wide for breeding grounds in Ecuador; larvae are found on fallen leaves and submerged tree branches in shallow shingle beds as well as in deeper parts of the river. Large rivers are the breeding sites of this species in other countries of South America (Coscaron & Wygodzinsky, 1975).

Simulium (Notolepria) gonzalezi Vargas & Diaz Najera

(Figs 9–11, 56, 63, 77–79, 91, 97, 104, 111, 124, 132, 139, 147)

Simulium gonzalezi Vargas & Diaz Najera, 1953b: 235. Syntypes ♀, ♂ and pupae, MEXICO and GUATEMALA (more precise information on localities, collection date, collectors and depository not given).

DESCRIPTION. *Female*. General body colour black. Body length (alcohol preserved specimens) 1.5–2.6 mm (n = 44), wing length 1.2–1.7 mm (n = 22), wing width 0.6–0.8 mm (n = 20).

Coloration and morphology as in *S. exiguum* except femora and inner surface of tibiae of mid leg and coxae of fore leg brownish black (Fig. 139). Tergal plates wider than in *S. exiguum* and paraproct with short anteriorly directed process (Fig. 56).

Male. There are two forms of the male: the predominant dichoptic form (Fig. 10) and the holoptic form (Fig. 11) (in the proportion 44 : 5, n = 49).

Dichoptic form. Body length (alcohol preserved specimens) 1.3–1.9 mm (n = 18), wing length 1.1–1.3 mm (n = 8), wing width 0.5–0.6 mm (n = 6).

Coloration and form of head as in female except head small relative to that of female and holoptic male (Figs 9–11). Frons at narrowest point about one-eighth width of head at that point compared to about one-sixth in the female. Antennae of dichoptic males longer in proportion to depth of head (ommatidial area) (1.25 : 1) than in females (0.9 : 1), and the antennae of these males are thinner.

Coloration and setation of thorax and appendages as in female except claws of male type (Fig. 147).

Coloration of abdomen as in *S. exiguum* male except central area of tergite V silver. Basal fringe short as in female *S. gonzalezi*. Genitalia as in male *S. exiguum* except ventral plate more rectangular than triangular and basal arms more

developed (Figs 77, 78) and median sclerite narrower at base (Fig. 91).

Holoptic form. Body length (alcohol preserved specimen) 2 mm (n = 1). Coloration and morphology as in male *S. exiguum* except in the single specimen dissected ventral plate shows a small protuberance adjacent to basal arms (Fig. 79).

Pupa. Female and dichoptic male pupae: cocoon length dorsally 1.5–2.4 mm, ventrally 1.9–2.7 mm; pupa length 1.4–2.2 mm; gill length 1.1–1.8 mm (n = 41). Holoptic male pupae: cocoon length dorsally 1.6–2.2 mm, ventrally 2.2–2.6 mm; pupa length 1.6–2.2 mm; gill length 1.0–1.4 mm (n = 5)

Cocoon as in *S. exiguum* (Fig. 104). Pupal morphology of female and both male forms as in *S. exiguum* except for gill. Gill light brown with six forwardly directed slender filaments arranged irregularly in a vertical plane (Fig. 111); main trunk giving rise to three primary branches each of which bears a single bifurcation. Dorsal branch with basal bifurcation at about one-tenth length of total gill, ventral bifurcation the most distal occurring at about a fourth the length of the gill and median bifurcation between those of the dorsal and ventral primary branches, although it may occasionally arise at the same distance from the gill base as that on the ventral branch.

Mature larva. Body length 2.8–4.6 mm (n = 43). Width of head capsule 0.3–0.4 mm (n = 43). Body colour and form as *S. exiguum*. *S. gonzalezi* may be distinguished from *S. exiguum* by the negative head pattern (Fig. 124) although the concolorous state typical of *S. exiguum* sometimes occurs.

MATERIAL EXAMINED

Belize: 23 ♀, nr Caya, Augustine, 27.vii.1981 (*D. J. Lewis*) (BMNH).

Ecuador: numerous reared adults, pupae and larvae from the following localities in the Santiago onchocerciasis focus in Esmeraldas Province: R. Cayapa, San Miguel de Cayapas, 17–19.vi.1981 (*A. J. Shelley & M. Arzube*) (BMNH, INHMT); R. San Miguel, San Miguel de Cayapas, 17.vi.1981 (*A. J. Shelley & M. Arzube*) (BMNH, INHMT); R. Sapallo Grande, Tumbaviro, 26.v. and 18.vi.1981 (*A. J. Shelley & M. Arzube*) (BMNH, INHMT); R. Grande (Cayapa), Viruela and Calle Mansa, 24–27.v.1981 (*A. J. Shelley & M. Arzube*) (BMNH, INHMT); numerous reared adults, pupae and larvae from the Canandé peripheral onchocerciasis focus in Esmeraldas Province, R. Canandé, Naranjal, 25.ix.1983 and 21–24.vi.1985 (*A. J. Shelley & M. Arzube*) (BMNH, INHMT).

Guatemala: 3 ♀, Departamento Chimaltenango, Finca Sibaja, 6.xi.1974 (*R. Garms*) (BMNH).

Mexico: 1 ♀, Tamazunchale, SLP, ix.1944 (*M. Macias*) (BMNH).

TAXONOMIC DISCUSSION. *Simulium gonzalezi* is most closely related to *S. exiguum* and *S. paraguayense* Schrottky as detailed in the taxonomic discussion on *S. exiguum*.

In the Santiago onchocerciasis focus, as well as in the Canandé peripheral onchocerciasis focus, the dichoptic form of the male head is the more prevalent. A similar situation has already been reported for this species from a locality in the Oaxaca onchocerciasis focus in Mexico, where Dampf (1944) recorded this species (as *exiguum*). In the Yepocapa onchocerciasis focus in Guatemala, however, the holoptic male condition is more prevalent (Dalmat, 1955; Takaoka, 1983).

DISTRIBUTION. In Ecuador *Simulium gonzalezi* has only been recorded from the main Santiago and peripheral Canandé onchocerciasis foci. It is also known from many localities in southern Mexico (Vargas & Diaz Najera, 1957), Guatemala (Dalmat, 1955) and Belize (BMNH collection). Lewis (1963) records an eight-filamented pupa of *S. gonzalezi* from Antigua but there is insufficient evidence presented for this species determination.

BIOLOGY. In Ecuador *S. gonzalezi* appears to be totally zoophilic although its main host has not yet been determined; using a horse as bait 401 *S. exiguum* and one *S. gonzalezi* were collected in two hours at the Canandé peripheral onchocerciasis focus (Shelley & Arzube, unpublished data). Though biting a variety of animals in Central America it will often attack man in large numbers there. Dalmat (1955) records *S. gonzalezi* (as *S. exiguum*) as being mainly zoophilic with a preference for large domestic stock (bovines and equines) but in the lower altitudes (under 800 m) of the Yepocapa onchocerciasis focus it is the dominant man-biter (Gibson & Dalmat, 1952, as *S. exiguum*). In Mexico *S. gonzalezi* probably shows similar biting habits (Shelley, 1988) and specimens (now in BMNH) have been obtained biting both man and mules in Belize.

Simulium gonzalezi is found in similar breeding grounds to those of *S. exiguum* in Ecuador but, as in Guatemala (Dalmat, 1955), shows a preference for larger rivers over 10 m wide.

Although not a vector of onchocerciasis in Ecuador because of its zoophilic habit, *S. gonzalezi* is nevertheless an important species because of its sympatry with and similarity to the primary vector *S. exiguum*. In Mexico and Guatemala it is suspected as a secondary vector of onchocerciasis because of its man-biting habit in the onchocerciasis foci and the finding of filarial larvae in wild females (Shelley, 1988).

Simulium (Psilopelmia) bipunctatum Malloch

(Figs 26, 32, 38, 44, 50, 57, 64, 70, 80, 81, 92, 98, 105, 112, 118, 125, 133, 140, 148)

Simulium bipunctatum Malloch, 1912: 650. Holotype ♀, PERU: Rio Charape, 13.ix.1911 (*C. H. T. Townsend*) (USNM, Cat. No. 15305) [examined]. [Synonymised with *S. dinellii* Joan by Knab, 1913: 155; revalidated by Coscaron, 1985: 320.]

Simulium antillarum Jennings, 1915: 200. Lectotype ♂, VIRGIN ISLANDS: St Croix Island, 1.5 miles west of West End, Frederiksted, 24.xi.1913 (*A. H. Jennings*) (USNM Cat. No. 19997) by designation of Stone (1969: 313) [examined]. **Syn. n.**

Simulium wolcotti Fox, 1953: 138. Holotype ♂, PUERTO RICO: Henry Barracks, near Cayey, 1950 (*I. Fox*) (STMPR). [Synonymised with *S. antillarum* Jennings by Stone, 1969: 313.] **Syn. n.**

Simulium pseudoantillarum Ramirez Perez & Vulcano, 1973: 379. Syntypes 1 ♀, 1 ♂, VENEZUELA: Monagas State, San Antonio de Maturin, (no collection date) (*Ramirez Perez & Vulcano*) (DDSV). **Syn. n.**

DESCRIPTION. *Female*. General body colour orange. Body length (alcohol preserved specimens) 2.1–3.5 mm (n = 30), wing length 1.7–2.7 mm (n = 30), wing width 0.9–1.2 mm (n = 30).

Head dichoptic with red eyes; nudiocular area poorly developed (Fig. 26). Frons, clypeus and occiput black with silver pruinosity. Mouthparts black. Antennae orange with distal third to half dark brown. Cibarium with central trough unarmed and sclerotised and a group of about 20 small teeth forming a protuberance on each side of trough that do not reach the sclerotised cornuae (Fig. 32).

Scutum dirty yellow with three prominent longitudinal orange bands that coalesce posteriorly; median band commences on anterior border of scutum and occupies three-quarters of its length; the pair of lateral bands commence in the second quarter of the scutum and continue to posterior margin. Scutum with a pair of submedian silver comma-shaped marks commencing at interface between yellow anterior margin and orange area and running half length of scutum. Lateral margins of scutum yellow and faintly pruinose (not obvious as in *S. lewisi*). Paranotal folds orange-brown in fresh specimens, often becoming dark brown in preserved material. Scutum with numerous adpressed black setae lying singly. Pleural region varying from light orange to mid brown with faint silver pruinosity. Scutellum and postnotum orange; posterior margin of scutellum with erect black bristles (Fig. 140).

Subcostal wing vein with line of setae almost to distal extremity, basal section of *R* with two or three irregular rows of setae. Costal base tuft dark brown (Fig. 38).

Fore leg coxae, trochanters and femora of all legs orange to light brown; coxae of mid and hind legs light brown on anterior half, dark brown on posterior half; tibiae and tarsi of all legs dark brown. Mid and hind leg femora and tibiae with darker distal articulations. Claws curved with large basal tooth (Fig. 44). Proportions of legs as in Fig. 140. Halteres yellow with light brown stems.

Abdominal tergites from orange to brown depending on age of specimen and whether it has blood fed; older blood fed specimens tend to become dark brown. Tergites I–IV usually mottled light brown and yellow but can be yellowish orange, particularly in reared material, occasionally mid brown; tergite V usually matt grey but sometimes matt black; tergites VI–IX dull mottled mid and light brown but sometimes completely shiny brown or black (Fig. 140). Tergal plates (Fig. 4) well-developed and generally light brown, sometimes dark brown. Sternites and genitalia orange to light brown becoming dark brown in preserved specimens. Eighth sternite usually lightly sclerotised with 20–24 setae on each side; gonopophyses small, membranous with minute hairs on inner margin (Fig. 50). Cerci hemispherical; paraprocts with pronounced ventral extension (Fig. 57). Genital fork slender with well-developed triangular anterior processes (Fig. 64). Spermatheca similar to that of *S. exiguum* (Fig. 5), oval, sclerotised, with surface covered in regular rounded depressions and spicules of inner surface randomly arranged; area of insertion of spermathecal duct membranous and a third as wide as maximum width of spermatheca.

Male. General body colour orange. Body length (alcohol preserved specimens) 2.0–3.4 mm (n = 15); wing length 1.8–2.4 mm (n = 15); wing width 0.9–1.0 mm (n = 15).

Head holoptic with red eyes. Clypeus black with silver pruinosity. Rest of head coloration as in female.

Coloration and hairing of scutum, pleural region, scutellum and postnotum as in female (Fig. 148).

Subcostal wing vein bare or with variable number of setae (1–7) in central portion, basal section of *R* with a single row of setae.

Leg (Fig. 148) and haltere coloration as in female.

Abdominal tergites I–IV mottled orange and light brown; tergites V–IX and genitalia light brown; basal tuft of light orange hairs. Silver ornamentation as follows: tergites VI and VII with a pair of submedian silver pruinose patches, anterior margin of tergite II and all of tergite IX faintly pruinose (Fig. 148). Sternites I–IV light orange, V–IX dark brown; sternal plates well-developed only on segments V–VIII (cf. Fig. 6). Genitalia orange to light brown. Gonocoxite longer than wide; gonostyle small, half the length of the gonocoxite, curved and conical with apical spine (Fig. 70). Ventral plate (Figs 80, 81) with reduced and lightly sclerotised basal arms and a small keel; hairs long and covering most of ventral plate. Median sclerite (Fig. 92) slightly longer than wide with deep apical incision occupying about half the length of the sclerite. Paramere as in Fig. 98 with few, well-developed, mainly apical spines and several smaller spines.

Pupa. Length of cocoon dorsally 2.1–3.2 mm, ventrally 2.8–4.2 mm; length of pupa 2.0–3.3 mm; length of gill 2.5–3.2 mm (n = 38).

Cocoon slipper-shaped, dark brown; rim of aperture dark brown, reinforced and usually without median protuberance (Fig. 105). Cocoon composed of thick threads producing an open weave, particularly laterally at point of adhesion to substrate. Gill light brown with eight forwardly directed slender filaments arranged irregularly in a vertical plane (Fig. 112): main trunk giving rise to three primary branches, ventral with two filaments and median and dorsal each with three filaments; filaments arise basally on all primary branches; filaments slender with crenated margins and rounded distally, their surfaces covered with fine spicules as in *S. exiguum* (Fig. 12). Head similar to that of *S. exiguum* (Fig. 13) with 2 + 2 frontal and 1 + 1 facial bifid or trifid well-developed trichomes; surface of head with sparsely distributed platelets. Thorax similar to *S. exiguum* (Fig. 17) with 5 + 5 trichomes on anterior border, each with two to five trichomes, 1 + 1 postero-dorsal and 1 + 1 ventral unbranched trichomes. Surface of thorax covered with platelets mainly concentrated around the dorsal region. Abdominal tergites II–IV with 4 + 4 simple hooks, more weakly developed on segment II, VI–IX with spine combs on anterior margins, tergite IX with 1 +1 strong unbranched spines (Fig. 19); sternite IV in female with 2 + 2 simple hooks, in male reduced to fine setae, sternites V–VII with 2 + 2 simple to bifid hooks; 1 + 1 patches of spine combs on postero-lateral borders of sternites IV–VIII (Fig. 20).

Mature larva. Body length 3.8–5.8 mm (n = 46). Width of head capsule 0.4–0.6 mm (n = 46). Body colour grey in both alcohol and Carnoy's preserved specimens. Body form as in Fig. 118.

Head yellow with brown markings and several scattered minute setae on all surfaces. Head pattern negative as in Fig. 125, consisting of a central clear area and 1 + 1 antero-lateral and 1 + 1 postero-lateral clear areas of head spots within a dark background confined to the posterior half of the cephalic apotome. More rarely the head pattern may be positive (Fig. 126) and this form has also been recorded outside the focus. Postgenal cleft large, longer than wide, with pointed anterior margin; postgenal bridge short, one-third as long as hypostomium (Fig. 133). Hypostomium of type seen in *S. exiguum* (Fig. 21). Antennae long, brown and with segment ratios 12 : 14 : 17. Mandible as in *S. exiguum* (Fig. 23) with one to three mandibular serrations, of which anterior is usually larger. Maxillary palp short, about twice as long as breadth at base. Cephalic fan with 34–42 rays.

Thorax whitish grey dorsally, darker grey ventrally, either diffuse or concentrated into one to three central patches posterior to the proleg. Cuticle with minute scattered hairs on dorsal and lateral surfaces. Proleg plates lightly sclerotised with 10–12 processes. Pupal respiratory histoblast dark brown and claviform.

Abdomen whitish with four grey bands encircling the body on the four (narrow) anterior segments, bands more obvious dorsally; posterior (wide) segments of abdomen brownish grey dorsally and whitish laterally and ventrally. Ventral papillae small (Fig. 118). Cuticle with minute scattered hairs on dorsal and lateral surfaces as in thorax but in greater density on postero-dorsal region. Anal sclerite well sclerotised with posterior arms extending to twelfth row of posterior circlet hooks. Posterior circlet with about 62–71 rows of 1 to 12 hooks. Anal gill tri-lobed as in *S. exiguum* (Fig. 24), each lobe with 4–7 short, secondary lobules.

Material examined

Holotype ♀ of *S. bipunctatum*, **Peru**: Rio Charape, 13.ix.1911 (*C. H. T. Townsend*) (USNM); paratype ♀ (collection data as for holotype) (BMNH). Lectotype ♂, paralectotype ♀, various topotypic pupae of *antillarum*, **St Croix Island**: Frederiksted, 24.xi.1913 (*A. H. Jennings*) (USNM).

Brazil: 3 ♀, Roraima, MEVA Mission post, Auaris, 7.vii.1976 (*A. J. Shelley*) (BMNH); 10 ♀, Amazonas, R. Vaupes, Igarapé Tiquié, 15. xii.1977 (*C. Vicente*) (BMNH, IOC).

Colombia: 3 ♀, Norte de Santander,

Arboledas, Siravita, La Esperanza, 25.xi.1984 (*B. Alexander*) (BMNH).

Dominica: 6 ♀, Roseau, 7.vii.1974 (*L. J. Charles*) (BMNH).

Ecuador: numerous reared adults, pupae and larvae from following localities in the Santiago onchocerciasis focus, Esmeraldas Province, R. Cayapa, 18–21.vi.1981 (*A. J. Shelley & M. Arzube*) (BMNH, INMHT); R. Cayapa, stream 4 km below San Miguel de Cayapas, 17.vi.1981 (*A. J. Shelley & M. Arzube*) (BMNH, INHMT); R. Cayapa, above Sapallo Grande Mission, 28.v.1981 (*A. J. Shelley & M. Arzube*) (BMNH, INMHT); R. San Miguel, small stream 100 m above San Miguel de Cayapas, 17.vi.1981 (*A. J. Shelley & M. Arzube*) (BMNH, INHMT); R. San Miguel de Cayapas, Estero Hacha, 26.v.1981 (*A. J. Shelley & M. Arzube*) (BNMH, INMHT).

Jamaica: 8 ♀, Loaf Water, 6.iii.1958 (*D. J. Lewis*) (BMNH); 2 ♀ 2 ♂ (ex pupae), Pindars River, near Kellits, 17.vii.1970 (*Clarendon*) (BMNH).

Montserrat: 4 ♀, Montserrat Woodlands, 20.ix.1938 (*F. A. S.*) (BMNH).

Venezuela: 8 ♀, 10 pupae, Monagas State, localities near San Antonio de Maturin, v.1961 (*D. J. Lewis*) (BMNH) [labelled by Lewis as sp. D and regarded by Ramirez Perez as *S. pseudoantillarum*].

The following specimens of two species closely related to *S. bipunctatum* were examined and are referred to in the following taxonomic discussion.

Simulium dinellii Joan

Argentina: 27 ♀, Jujuy (collection date unkown) (*W. C. Paterson*) (BMNH).

Peru: 19 ♀, Apurimac, Cuzco-Abancay road, Apurimac crossing at Cuya, 7.viii.1971 (*C. & M. Vardy*) (BMNH).

Simulium ochraceum Walker

Guatemala: 3 ♀, Department Chimaltenango, Finca Sta. Anita, 8.iii.1974 (*R. Garms*) (BMNH); 1 ♀ , 2 ♂, Department Chimaltenango, Acantenango, 2.x.1948, 8.vi.1949 (*H. Dalmat*) (BMNH).

Mexico: 3 ♀, Chalchihuitan, 4.xii.1940 (*J. Parra*) (BMNH); 10 ♀, Chiapas State, Huixtla, x.1958 (*R. W. Crosskey*) (BMNH).

Panama: 1 ♀, Chiriqui Province, Los Planes de Hornito, 12.ix.1978 (*J. Petersen*) (BMNH).

Taxonomic discussion. *Simulium bipunctatum* was first described by Malloch (1912) from females collected in Peru (and presumably biting man) in a survey for the possible transmitters of pellagra. This name was then synonymised by Knab (1913) with *S. dinellii* Joan from Argentina after he had compared the holotype of *S. bipunctatum* with the original description of the former. He neglected to observe that Malloch named *S. bipunctatum* after the two submedian, white comma-shaped marks on the female scutum whilst Joan (1912) had clearly noted the absence of scutal patterns in *S. dinellii*. Wygodzinsky (1950) questioned Knab's synonymy of *bipunctatum* with *dinellii* in a paper redescribing the latter species. Recently, Coscaron (1985) recalled *S. bipunctatum* from synonymy after examining the holotype in the USNM and topotypic material. His study confirmed the distinctness in scutal patterns of the two species and also revealed differences in the morphology of the paraproct. We support this revalidation after comparing a paratype of *S. bipunctatum* donated to the BMNH by the USNM, with specimens of *S. dinellii* in the BMNH collection that correspond to Joan's original description and the more detailed description of Wygodzinsky (1950). We base our synonymy of *S. antillarum* Jennings with *S. bipunctatum* on a comparison of the male lectotype and a female paralectotype (USNM) of the former with the holotype of the latter. Examination of large numbers of specimens of '*antillarum*' from the Caribbean Islands and Ecuador showed variation in the sclerotisation and dentition of the female cibarium, characters which Coscaron (1985) uses to separate it from *bipunctatum*. The detailed descriptions and comments of Coscaron, (1985), Diaz Najera (1961), Floch & Abonnenc (1946), Jennings (1915), Rubtsov & Garcia Avila (1972), Smart (1940) and Vargas & Diaz Najera (1951) for *S. antillarum* and the original description of *S. bipunctatum* by Malloch (1912) were consulted.

We accept Stone's (1969) synonymy of *S. wolcotti* with *S. antillarum* because of his comparison of topotypes of the former with the original syntype series of *S. antillarum*, which did not confirm Diaz Najera's observations (1961) supporting the validity of *S. wolcotti* based on coloration. Following our synonymy of *S. antillarum* with *S. bipunctatum*, *S. wolcotti* becomes a new junior synonym of *S. bipunctatum*. Coscaron (1985) omits *S. wolcotti* from his revision of the subgenus *Ectemnaspis*.

The synonymy of *S. pseudoantillarum* Ramirez Perez & Vulcano is based on the following observations. *Simulium pseudoantillarum* was described by Ramirez Perez & Vulcano (1973) from collections that they had made in the region of the onchocerciasis foci of northern Venezuela. The specimens are listed as paratypes but as no holotype was designated they have syntype status. The authors cite the BMNH as a depository but no

specimens have yet been received and all type material is presumed to be in the 'Seccion de Oncocercosis, Villa de Cura, Venezuela'. This species corresponds with '*Simulium* sp. D' of Lewis (1963) who had previously collected in the same area and made a preliminary description. Ramirez Perez & Vulcano (1973) state that *S. pseudoantillarum* is closely related to *S. antillarum* but can be distinguished from it by differences in size, the form of the pedisulcus and calcipala in the female and in the more distal bifurcation of pupal gill filaments. Their conclusions are stated to have been made after a comparison of *S. antillarum* types in the BMNH and of descriptions of this species by Jennings (1915), Diaz Najera (1961) and Floch & Abonnenc (1946). We have no record of the *S. antillarum* types having been on loan to the BMNH from their depository the USNM. We have examined topotypic material collected by Lewis in Venezuela in 1961 and identified as *Simulium* sp. D (Lewis, 1963) and found that the figure of a pupal gill with the relatively distal bifurcations of filaments arising on the median primary gill branch is atypical for the sample, the majority of the specimens having a gill form as in *S. antillarum* (Fig. 112). Ramirez Perez & Vulcano (1973: 380, fig. 2) copied Lewis figure of the gill (Lewis, 1963: 57, fig. 3H) but mistakenly state that it is a more detailed figure of their figure 1, which is obviously of another specimen. In later works Ramirez Perez (1983) and Ramirez Perez *et al.* (1982) figure the gill of *S. pseudoantillarum* with basal branching typical of *S. antillarum*. Taking into account the natural variation in adult size, the lack of detectable difference in the form of calcipala and pedisulcus, and the natural variation in gill configuration, we consider *S. pseudoantillarum* to be conspecific with *S. antillarum* and hence synonymous with *S. bipunctatum*. Coscaron (1985) suggests that *S. pseudoantillarum* may fall within the natural variation of *S. antillarum*.

We retain *Simulium bipunctatum* in the subgenus *Psilopelmia* and do not follow Coscaron's inclusion (1985) of this species in *Ectemnaspis*. It is morphologically most closely related to *S. ochraceum* which differs in its dark postnotum and legs. Simuliid species with orange coloration preserve badly, both as pinned and alcohol specimens, and female coloration can be influenced by whether the specimen is blood fed or not. Variation in coloration of the key characters of the thorax and abdomen in both species is apparent in the specimens in the BMNH collection. The distinctness of the two species needs to be more thoroughly investigated to take into account intraspecific variation by using both morphological and cytological methods on long series of specimens from different localities.

DISTRIBUTION. Distribution of *S. bipunctatum* is based upon the BMNH collections and Stone (1969, as *antillarum*). In Ecuador *S. bipunctatum* has only been reported in Esmeraldas Province. Its distribution in South America includes northern Brazil, Colombia, Peru and northern and southern Venezuela. In Central America it has been reported from the following Caribbean Islands: Cuba, Dominica, Guadeloupe, Jamaica, Montserrat, Puerto Rico, St Croix, and Trinidad as well as from mainland Mexico.

BIOLOGY. *Simulium bipunctatum* will bite man to varying degrees in different localities. In the onchocerciasis focus of Ecuador (Shelley & Arzube, 1985) and in the majority of the Caribbean Islands and Mexico (Stone, 1969; Rubtsov & Garcia Avila, 1972) it is mainly zoophilic, only rarely coming to bite man. It is, however, markedly anthropophilic in the Upper Amazon region of Brazil along the R. Vaupes but only occasionally bites man (possibly due to small fly populations rather than zoophilic tendencies) farther north in the Amazonia onchocerciasis focus of Brazil and Venezuela (Ramirez Perez *et al.*, 1982; Shelley, 1988; Shelley & Luna Dias, unpublished data). In parts of Guadeloupe it can also be a biting nuisance (Floch & Abonnenc, 1946).

Simulium bipunctatum breeds in shaded, slow-flowing streams in lowland forest of Ecuador (Shelley & Arzube, 1985) and in fast flowing small streams in St Croix and Jamaica (Jennings, 1915). In Cuba (Rubtsov & Garcia Avila, 1972) it occurs in small streams up to an altitude of 1200 m throughout the year. In the Amazonia onchocerciasis focus of Brazil and Venezuela it occurs in slow flowing streams (1 m wide, Ramirez Perez *et al.*, 1982) and larger rivers (up to 20 m wide, Shelley & Luna Dias, unpublished data) in highland forested areas.

Simulium (Psilopelmia) lewisi Ramirez Perez

(Figs 27, 33, 39, 45, 51, 58, 65, 71, 82, 83, 93, 99, 106, 113, 119, 127, 134, 141, 149)

Simulium lewisi Ramirez Perez, 1971: 349. Holotype ♀, VENEZUELA: Miranda State, Panaquire (No collection date; collector presumably *J. Ramirez Perez*) (DERM).

Simulium iguazuense Coscaron 1976a: 147. Holotype [sex unspecified], ARGENTINA: Parque Nacional Iguazu, route 101, in unnamed stream or Arroyo Nandu [not specified], 17.x.1974 (*S. Coscaron*) (MLP). [Synonymised with *S. lewisi* by Coscaron, 1985: 304.]

DESCRIPTION. *Female*. General body colour orange and black. Body length (alcohol preserved specimens) 1.6–2.3 mm (n = 11); wing length 1.8–2.1 mm (n = 10), wing width 0.8–1.0 mm (n = 10).

Head dichoptic with dark red eyes; nudiocular area poorly developed (Fig. 27). Frons, clypeus and occiput black with silver pruinosity. Mouthparts mid brown, maxillary palps dark brown. Antennae dark brown with scape and pedicel and first flagellomere orange. Cibarium with five irregular rows of blunt tubercles in area of central trough and a group of about 20–30 minute teeth between this and each cornua; anterior margin of cibarium sclerotised (Fig. 33).

Scutum orange, humeri yellow to light orange, lateral scutal margins yellowish orange with brilliant white pruinosity. Paranotal folds dark brown with silver pruinosity. Scutum with numerous adpressed dark brown hairs lying singly. Pleural region mainly dark brown with faint silver pruinosity although in some specimens orange to light brown areas may occur in the area adjacent to the paranotal folds. Scutellum orange with erect brown hairs on posterior margin. Postnotum dark brown with faint silver pruinosity (Fig. 141).

Subcostal wing vein usually with one to six setae in the median third of the vein, in some cases without setae; basal section of *R* with single row of setae to base of vein (Fig. 39). Costal base tuft of dark brown setae.

Legs black except basal two-thirds of mid and hind basitarsi which are white (Fig. 141). Claws curved, each with a small tooth as in Fig. 45. Proportions of legs as in Fig. 141. Halteres yellow with light brown stems.

Abdominal tergites I–III bright yellow, sometimes orange, tergite IV velvet-black, tergites VI–IX shiny black or mottled brown and black (Fig. 141). Occasionally specimens occur in which tergites I–IV are yellow, in which case tergite V is velvet-black. Tergal plates (Fig. 4) well developed on segments IV–IX. Sternites I–III yellowish brown, rest mid brown, genitalia dark brown. Eighth sternite well sclerotised with about 15–18 setae on each side; gonopophyses small, membranous with minute hairs (Fig. 51). Cerci hemispherical; paraprocts with pronounced ventral extension (Fig. 58). Genital fork slender with sclerotised, triangular anteriorly-directed processes (Fig. 65). Spermatheca similar to that of *S. exiguum* (Fig. 5), oval, sclerotised, with no external sculpturing and randomly distributed spicules on internal surface. Area of insertion of spermathecal duct membranous, one-third as wide as maximum width of spermatheca.

Male. General body colour orange and black. Body length (alcohol preserved specimens) 1.9–2.8 mm (n = 15), wing length 1.7–2.1 mm (n = 15), wing width 0.8–1.0 mm (n = 15).

Head holoptic with dark red eyes. Coloration of rest of head as in female.

Coloration and hairing of thorax and its appendages as in female (Fig. 149) except subcostal vein of wing devoid of setae. Morphology of legs as in Fig. 149.

Abdominal tergites I–III yellow, rest of tergites and genitalia velvet-black; basal fringe of long black hairs. Silver ornamentation on tergites as follows: tergite II faintly silver pruinose and tergites VI, VII and IX with obvious silver patches laterally (Fig. 149). Sternites I–III orange, IV–IX dark brown with well-developed sternal plates (Fig. 6) on segments IV–VIII. Gonocoxite longer than wide, gonostyle with distal spine longer than wide and about half length of gonostyle (Fig. 71). Ventral plate membranous with lightly sclerotised, reduced basal arms, a small keel and hairs covering most of its surface (Figs 82, 83). Median sclerite pyriform with small apical incision (Fig. 93). Paramere as in Fig. 99 with few distal spines of varying sizes.

Pupa. Cocoon length dorsally 1.9–2.7 mm, ventrally 2.3–3.0 mm; pupa length 1.6–2.5 mm; gill length 2.2–2.7 mm (n = 32).

Cocoon slipper-shaped, white under natural conditions and light brown in alcohol; rim of aperture thickened and without median protuberance, median thickened dorsal ridge connecting with rim of aperture (Fig. 106). Cocoon very thick, composed of amorphous elastic substance containing fibres which are only apparent under higher magnification. Gill light brown with eight forwardly directed slender filaments arranged in a vertical plane (Fig. 113); main trunk giving rise to three primary branches, ventral with two filaments and median and dorsal each with three filaments; ventral branch bifurcation at limit of basal third of total gill length, first division of median and dorsal branches arise in the same region but individual specimens vary in the exact position – some showing divisions at the same distance from the gill base in all three branches while in others these divisions occur at different points on each branch, the most dorsal of the two filaments arising from this division in the median and dorsal primary branches again bifurcate, usually at the same level on each branch, at the mid point of the gill; filaments slender with crenate edges, rounded distally, their surfaces covered in spicules as in *S. exiguum* (Fig. 12). Head as in Figs 13, 14 of *S. exiguum* with 2 + 2 frontal trichomes usually with 4–6 branches but sometimes up to

eight and 1 + 1 facial trichomes with 2–4 branches, trichomes well-developed; surface of head with few platelets mainly concentrated around the facial trichomes. Thorax as in *S. exiguum* (Fig. 17) with 5 + 5 well-developed trichomes with 6–8 branches on anterior margin of thorax. Anterior half of surface of thorax with scattered platelets. Abdominal tergite II with 4 + 4 simple hairs, III–IV with 4 + 4 simple hooks, VI–IX with spine combs on anterior margins, tergite IX with 1 + 1 unbranched spines (Fig. 19); sternite IV in both sexes with 1 + 1 inner simple or bifid hooks and 1 + 1 outer fine setae (developed as hooks in *bipunctatum*), V–VII with 2 + 2 hooks with 1 to 3 branches; 1 + 1 patches of spine combs on postero-lateral borders of sternites IV–VIII (Fig. 20).

Mature larva. Body length 3.7–4.9 mm (n = 23). Width of head capsule 0.4–0.5 mm (n = 23). Body colour white with either greyish purple or green markings. These colour variations are not sex linked (W. S. Procunier, pers. comm.). In Carnoy's fixative markings are bright purple or green and more distinct. Body form as in Fig. 119.

Head yellow with scattered minute setae on all surfaces. Head spots generally indistinct being the same colour as the rest of the head capsule, but in some specimens a negative pattern occurs (Fig. 127). Postgenal cleft large, longer than wide, with rounded anterior margin; postgenal bridge short, about one-tenth as long as hypostomium (Fig. 134). Membrane within postgenal cleft containing green or grey chromatocytes that obscure the outline of the cleft. Hypostomium of type figured for *S. exiguum* (Fig. 21). Antennae long, light brown, with segment ratios 14 : 13 : 12. Mandible as in *S. exiguum* (Fig. 23) except second comb tooth shorter than the first or third. Maxillary palp short, about twice as long as width at base. Cephalic fan with 30–34 rays.

Thorax whitish grey with few scattered dark greyish purple spots dorsally and two central greyish purple patches ventrally posterior to the proleg. In some specimens green replaces the grey coloration. Cuticle with scattered small hairs on ventral and lateral surfaces but densely distributed on the dorsum. Proleg plate lightly sclerotised with about twelve processes. Pupal respiratory histoblasts dark brown and ovoid. Abdomen whitish grey with a prominent dark greyish purple band at the anterior end and at the posterior end of the narrow abdominal segments, posterior (wide segments) of abdomen with four dorsal dark greyish purple bands that often coalesce and scattered patches of grey pigment laterally and ventrally. Pigment in some specimens is green. Ventral papillae absent or very reduced and indistinct. Cuticle with densely distributed minute hairs on dorsum, more scattered laterally and absent ventrally. Anal sclerite well sclerotised with posterior arms extending to the twelfth row of posterior circlet hooks. Posterior circlet with 56–60 rows of 4–14 hooks. Anal gill trilobed as in *S. exiguum* (Fig. 24), median lobe with 6–7 secondary lobules, lateral lobes with 8–11 secondary lobules.

MATERIAL EXAMINED

Paratypes of *S. lewisi*, **Venezuela**: 1 ♀ (ex pupa), Miranda State, Panaquire (no collection date) (*J. Ramirez*) (BMNH); 1 ♀ (ex pupa), Miranda State, Acevedo District, Panaquire, Rio Yaguapo, (no collection date) (*J. Ramirez*) (BMNH); 1 ♀ (ex pupa), Carabobo State, Virigima (no collection date) (*J. Ramirez*) (BMNH); 1 ♂ (ex pupa), Barinas State, Rio Socopo (no collection date) (*J. Ramirez*) (BMNH).

Ecuador: numerous reared adults, pupae and larvae from the following localities in the Santiago onchocerciasis focus of Esmeraldas Province: San Miguel de Cayapas, Rio San Miguel, 25, 26.v. & 17.vi.1981 (*A. J. Shelley & M. Arzube*) (BMNH, INMHT); Tumbaviro, R. Sapallo Grande, 26.v. & 18–25.vi.1981 (*A. J. Shelley & M. Arzube*) (BMNH, INMHT); San Miguel de Cayapas and Calle Mansa, Rio Cayapa, 27.v. & 17.vi.1981 (*A. J. Shelley & M. Arzube*) (BMNH); numerous reared adults, pupae and larvae from the Canandé peripheral onchocerciasis focus in Esmeraldas Province, Naranjal, Rio Aguas Negras, Naranjal and Canandé, 23–25.vi.1983 (*A. J. Shelley & M. Arzube*) (BMNH, INMHT); 1 ♀ (ex pupa), Esmeraldas Province, Tululbi (Ricaurte), Rio Bogota, 13.ix.1983 (*A. J. Shelley & M. Arzube*) (BMNH); 3 ♀ (ex pupae), Tululbi (Ricaurte), Riachuelo Nadadeiro, 14.ix.1983 (*A. J. Shelley & M. Arzube*) (BMNH, INMHT); 2 ♂ (ex pupae), Santo Domingo-Esmeraldas road, R. Caoni, 24.ix.1983 (*A. J. Shelley & M. Arzube*) (BMNH, INHMT); 3 ♀ 2 ♂ (ex pupae), Pichincha Province, Quito-Santo Domingo road, Rio Tanti, 28.ix.1983 (*A. J. Shelley & M. Arzube*) (BMNH); pupae, Napo Province, near Lago Agrio, 14.xii.1982 (*A. J. Shelley & M. Arzube*) (BMNH, INMHT).

Venezuela: 1 ♀ (ex pupa), Miranda State, Acevedo District, El Clavo, Rio Sapo (no collection date) (*J. Ramirez*) (BMNH); 2 ♀ 1 ♂, [Aragua State], Altagracia, Quebrada Caranacare, 28.vi.1961 (*D. J. Lewis*) (BMNH); 1 ♀ [Aragua State], Tucuyito, Rio Aguacatal, 14.vi.1961 (*D. J. Lewis*) (BMNH).

The following closely related species were also examined and are referred to in the taxonomic discussion.

S. alirioi Ramirez-Perez & Vulcano

Venezuela: 2 ♂, Monagas State, San Antonio de Maturin, Rio Negro, 23.v.1961 (*D. J. Lewis*) (BMNH); 4 pupae, Paratebueno, v.1961 (*D. J. Lewis*) (BMNH).

S. gabaldoni Ramirez-Perez

Paratypes 2 ♀ (ex pupae), **Venezuela**: Monagas State, San Francisco (no collection date) (*J. Ramirez*) (BMNH).

Venezuela: 1 ♂ (ex pupa), Monagas State, San Antonio (no collection date) (*J. Ramirez*) (BMNH).

S. lutzianum Pinto

Ecuador: 1 ♀ (ex pupa), Imbabura Province, Salinas-Lita road, 54 km from Ibarra, Rio San Pedro, 11.ix.1983 (*A. J. Shelley & M. Arzube*) (BMNH); 10 ♀ 4 ♂ (ex pupae), Pichincha Province, Quito-Santo Domingo road, Rio Tanti and Riachuelo Lelia, 28 & 29.ix.1983 (*A. J. Shelley & M. Arzube*) (BMNH); 1 ♂ (ex pupa), Manabi Province, Chone-Santo Domingo road, Rio Maceto, 10.xii.1984 (*M. Arzube*) (BMNH); 2 ♀ 2 ♂ (ex pupa), Pastaza Province, Tena-Puyo road, Rio Puyo, Rio Mira Valle and Riachuelo Huamayacu, 8 & 9.vi.1985 (*A. J. Shelley & M. Arzube*) (BMNH); 3 ♀ (ex pupae), Cotopaxi Province, Quevedo-La Mana-La Pilalo road, Rio San Pablo, 8.vi.1984 (*A. J. Shelley & M. Arzube*) (BMNH).

Venezuela: 1 ♀ 1 ♂ (ex pupa), Carabobo State, Montalban (no collection date) (*J. Ramirez*) (BMNH); 2 ♀ 1 ♂ (ex pupae), Aragua State, Rancho Grande (no collection date) (*J. Ramirez*) (BMNH); 4 ♂ (ex pupae), Merida State, Merida & Timotes (no collection date) (*J. Ramirez*) (BMNH); 5 ♀ 6 ♂ (ex pupae), Miranda State, Guarenas, Rio Izcaragua, Guatire (no collection dates) (*J. Ramirez*) (BMNH).

TAXONOMIC DISCUSSION. Attention was first drawn to *S. lewisi* by Lewis (Lewis, 1963; Lewis & Ibañez de Aldecoa, 1962) during a survey of simuliids as potential vectors of *O. volvulus* in the human onchocerciasis foci in northern Venezuela. Lewis was unable to identify this species due to the inchoate state of the taxonomy of Neotropical Simuliidae at the time and designated it as species A. During his revisionary work on the Venezuelan fauna Ramirez Perez collected *Simulium* species A of Lewis and described it as a new species, *S. lewisi* (Ramirez Perez, 1971). The depository of the holotype is presumed to be the 'Division de Endemias Rurales, Maracay, Venezuela' since the other cited depository, the BMNH, contains only paratypes. Further descriptions and distributional records of *S. lewisi* were subsequently given by Ramirez Perez (1983) and Coscaron (1985).

Coscaron's subsequent descriptions and nomenclatural changes concerning *S. lewisi* and its near relatives *S. iguazuense* and *S. lutzianum* (Coscaron, 1976a, 1985) have caused uncertainty over the status of these three species. The confusion concerns the coloration of the abdominal tergites, which is the only character used to distinguish them. In 1976 Coscaron described the new species *S. iguazuense*, noting the possibility that it might not be distinct from *S. lutzianum*; the females of *S. iguazuense* were described as having the first three abdominal tergites yellowish brown (similar to *S. lewisi*) whereas in males no abdominal segments were yellow (as in *S. lutzianum*). Coscaron (1985) later synonymised *S. iguazuense* with *S. lewisi*, believing that the abdominal tergite coloration of males of these two species varies intraspecifically. In this later paper he records a greater variation in abdominal coloration of male *S. lewisi* but it is not clear in which localities this occurs, and there are inconsistencies in the descriptions of both sexes of this species in the text and keys. Female *S. lewisi* are said to have the first three abdominal segments yellow, whereas in the key segments I–II or III (presumably meaning I–II or I–III) are yellow or yellowish brown. Similarly, male *S. lewisi* are described as having segments I, I–II, II–III or none yellow, whereas in the key I, I–II, or I–III are recorded as yellow. Similar inconsistencies are seen with *S. lutzianum*. The first two abdominal segments of the female are described as light brown in the text whereas in the key the first segment is said to be yellow; in males tergite I is described as brown in the text but light brown in the key. Considering the confusion over this character it is unclear why Coscaron chose *S. lewisi* as the senior synonym of *S. iguazuense* rather than synonymising both *S. iguazuense* and *S. lewisi* with *S. lutzianum*. While we accept his synonymy at this stage the reliability of such colour differences for species separation needs confirmation by using morphological and cytological methods before the status of *S. iguazuense*, *S. lewisi* and *S. lutzianum* is decided.

Variation in abdominal coloration of both female and male *S. lewisi* was seen in our material, usually the first three and rarely the fourth abdominal segments in both sexes being yellow to orange. The male paratype of *S. lewisi* in the BMNH collection shows orange coloration on the first four abdominal segments. The closest relative to *S. lewisi* is *S. lutzianum*, which differs by the presence of yellow coloration only on the first

tergite of the female abdomen and none on the male abdomen. Other closely related species showing coloration differences in the thorax or in pupal gill filament number are *S. alirioi*, *S. gabaldoni*, *S. romanai* Wygodzinsky and *S. adolfolutzi* Wygodzinsky.

Coscaron (1985) includes *S. lewisi* in the subgenus *Ectemnaspis* but we prefer to place it in the closely related subgenus *Psilopelmia*. Whether these taxa should be maintained as valid subgenera awaits further integrated morphological and cytological studies.

DISTRIBUTION. In Ecuador *S. lewisi* is a common species of the onchocerciasis foci and circumjacent lowland areas on the eastern and western foothills of the Andean cordillera.

Simulium lewisi is widespread in northern Venezuela (Ramirez Perez, 1983). Coscaron (1985) reports *S. lewisi* from Argentina, Bolivia and Peru but the records might refer in some cases to *S. lutzianum* (see taxonomic discussion).

BIOLOGY. In Ecuador *S. lewisi* occurs in small shaded streams and in rivers up to 100 m wide in lowland tropical forest either side of the Andean cordillera (Shelley & Arzube, 1985, unpublished data), and in rivers in lowland areas in central and western Venezuela (Ramirez Perez, 1971). The species is apparently totally zoophilic in Ecuador (Shelley & Arzube, 1985) and there are no records of it attacking man elsewhere.

Simulium (Psilopelmia) escomeli Roubaud

(Figs 28, 34, 40, 46, 52, 59, 66, 72, 84, 85, 94, 100, 107, 114, 120, 128, 135, 142, 143, 150, 151)

Simulium escomeli Roubaud, 1909: 428. Syntypes ♀, PERU: Arequipa (no collection date) (*Escomel*) (deposited in MNHN but now lost).
Simulium rufidorsum Enderlein, 1934: 283. Holotype ♀, PERU: (no locality except 'highland area', collection date and collector unknown) (ZM). [Synonymised with *S. escomeli* by Vargas & Dias Najera 1953a: 146.]

DESCRIPTION. *Female*. General body colour brown and grey. Body length (alcohol preserved specimens) 2.1–3.0 mm (n = 24), wing length 2.0–2.5 mm (n = 24), wing width 1.0–1.2 mm (n = 24).

Head dichoptic with red eyes; nudiocular area poorly developed (Fig. 28). Frons, clypeus and occiput grey pollinose. Mouthparts dark brown. Antennae dark brown with basal fourth light brown. Cibarium with unarmed, lightly sclerotised central trough and a group of about 20 fine teeth in two protuberances lateral to this and extending in a single line along base of each sclerotised cornua (Fig. 34).

Scutum chestnut-brown with two submedian vittae, posterior margin and posterior two-thirds of lateral margins of scutum grey pruinose; anterior third of lateral margins of scutum, humeri and anterior scutal border between these and the submedian vittae light brown; the 1 + 1 cunae in the anterior margins of the submedian vittae appear brown with an anterior light source and white pruinose with posterior lighting. Paranotal folds grey pruinose. Scutum with numerous adpressed golden hairs (Fig. 142). Pleural region with light and dark brown areas with faint silver pruinosity. Specimens from high altitudes are darker; the chestnut-brown of the scutum is darker brown, often with areas of black at the interfaces with the grey pruinose areas, and the whole of the pleural region is dark brown with grey pruinosity (Fig. 143). (Similar findings on high altitude Peruvian specimens are reported in Knab (1914a, b).) Scutellum light brown with adpressed golden hairs and an uneven row of upright dark brown hairs on posterior margin. Postnotum dark brown with silvery grey pruinosity.

Subcostal wing vein usually bare but sometimes with up to two hairs on median section, basal section of radius bare (Fig. 40). In specimens from highland areas *Sc* with 4–6 hairs on median section, basal section of *R* usually bare but occasionally with a single hair on median section of vein. Costal base tuft of dark setae.

Legs yellowish with the following areas dark brown: distal articulation of tibia and whole of tarsus of fore leg, external face of tibia faintly pruinose; coxa, distal articulations of femur and tibia, distal half of basitarsus, second tarsomere and rest of tarsus of mid leg; coxa, distal fourth of femur, distal half of tibia, distal half of basitarsus and second tarsomere and rest of tarsus of hind leg. Proportions of legs as in Fig. 142. Claws slender, slightly curved and lacking a basal tooth (Fig. 46). Halteres white with yellowish stem.

Abdominal tergites yellowish grey. Tergal plates (Fig. 4) not obviously developed. Tergite II with median dark brown amorphous spot, tergites III–VI with well-defined central subrectangular black spots; tergites III–VII with pairs of submedian black spots and tergites II–VII with pairs of indistinct sublateral black spots (Fig. 142). Sternites greyish, genitalia brown. Eighth sternite highly sclerotised with a group of 20–25 hairs on each side; gonopophyses small, glabrous, with light sclerotisation on inner margin. Cerci hemispherical, paraprocts with pronounced anterior extension (Fig. 59). Genital fork with well-developed sclerotised anteriorly directed processes and sclerotised stem (Fig. 66). Spermatheca oval as in *S. exiguum* (Fig. 5), highly

sclerotised with no external sculpturing and spicules of inner surface randomly distributed; area of insertion of spermathecal duct membranous, about a third as wide as spermatheca at widest point.

Male. General body colour brown and black, showing variations in different localities. Populations from lowland localities have orange thoraces and in those from highland areas these are generally black but in some instances orange. Body length (alcohol preserved specimens) 2.3–2.8 mm (n = 5), wing length 2.0–2.6 mm (n = 5), wing width 1.0–1.2 mm (n = 5).

Head holoptic with red eyes. Coloration of rest of head as in female except specimens from highland areas which have black antennae with the scape and pedicel orange-brown.

Scutum-orange brown to chestnut in lowland localities. Anterior border of scutum, except for central area and humeri and lateral margins yellowish, posterior margin black as is interface between yellow lateral margin with orange-brown of scutum; a pair of submedian, comma-shaped marks occupy the anterior half of the scutum (Fig. 150). Direction of light source affects the coloration of some of the scutal patterns; with light source posterior to specimen the pair of submedian, comma-shaped marks appear black, curved and almost reach the anterior border but with light source anterior to specimen they appear silver pruinose, are more triangular and adjoin the anterior scutal margin; with light source perpendicular the posterior and lateral margins of the scutum appear silver pruinose. In some specimens the black posterior margin of the scutum extends anteriorly to join the commas. Paranotal folds black. Scutum with adpressed golden hairs. In specimens from most highland localities the orange-brown areas of the scutum are velvet-black (Fig. 151). Pleural region with superior part light brown with faint silver pruinosity and inferior part grey and strongly pruinose. Scutellum light brown with adpressed yellowish hairs and an uneven row of upright dark brown hairs on posterior margin. Postnotum black with silver pruinosity.

Subcostal wing vein and basal section of radius bare. Costal base tuft of dark setae.

Coxa, trochanter, femur and tibia of fore leg light brown, tarsus black; external face of tibia white pruinose. Coxa of mid leg dark brown, trochanter, femur, basal half of basitarsus and of second tarsomere light brown, rest dark brown to black. Coxa of hind leg black, trochanter, basal two-thirds of femur, proximal fourth of tibia and basal half of basitarsus light brown, rest black. Proportions of legs as in Fig. 150. Haltere coloration as in female.

Abdomen and genitalia velvet-black, except tergite II and lateral margins of tergite III which are brown. Basal fringe of first tergite light brown. Silver ornamentation as follows: tergite II silvery white pruinose except for central black spot, tergite V with a pair of submedian silvery white spots, tergite VI silver pruinose and lateral margins of tergite VII silvery pruinose (Fig. 150). In males from highland localities the silvery white areas on tergite V are usually absent. Sternites dull brown with poorly developed sternal plates (Fig. 6) on segments IV–VIII. Gonocoxite one and a half times as long as wide; gonostyle subrectangular, half as long as gonocoxite and with a distal spine (Fig. 72). Ventral plate lightly sclerotised, subrectangular, with well-developed basal arms and a small keel; hairs long and densely distributed over most of ventral plate (Figs 84, 85). Median sclerite elongate, subquadrangular, with a deep incision in apical third (Fig. 94). Paramere with numerous large spines (Fig. 100).

Pupa. Cocoon length dorsally 2.0–3.0 mm, ventrally 2.8–3.4 mm; pupa length 2.0–3.0 mm; gill length 1.6–2.4 mm (n = 40) (all lowland populations).

Cocoon slipper-shaped, dark brown; rim of aperture dark brown, reinforced and without median protuberance (Fig. 107). Cocoon surface of thin, amorphous, elastic substance containing loosely interwoven fibres visible at higher magnifications. Gill light brown with eight, forwardly-directed, slender filaments arranged irregularly in a vertical plane; main trunk giving rise to three primary branches, ventral with two filaments and median and dorsal each with three filaments; ventral branch with bifurcation in basal fourth of gill, median branch with first bifurcation in basal fourth and second bifurcation in basal third of gill; dorsal branch with first bifurcation basally at junction of median and dorsal primary branches and second bifurcation within basal fourth of gill (Fig. 114); filaments slender with crenate margins and rounded distally, their surfaces covered in fine spicules as in *S. exiguum* (Fig. 12). Head as in *S. exiguum* (Fig. 13) with 2 + 2 frontal trichomes, the most dorsal being simple and the more ventral 1–4 branched both poorly developed and 1 + 1 simple or bifid facial trichomes that are small and difficult to distinguish; surface of head covered with platelets as in *S. exiguum*. Thorax as in *S. exiguum* (Fig. 17) with 5 + 5 antero-dorsal poorly developed trichomes with 2–5 branches. Surface of thorax covered with platelets. Abdominal tergite II with 4 + 4 simple hairs, III–IV with 4 + 4 simple hooks,

VI–IX with spine combs on anterior margins, IX with 1 + 1 strong unbranched spines (Fig. 19); sternite IV with 1 + 1 simple or bifid, well-developed outer hooks and 1 + 1 fine inner hairs, V with 2 + 2 simple hooks, VI with 2 + 2 simple hooks, inner pair sometimes bifid and VII with 2 + 2 simple hooks, 1 + 1 patches of spine combs on postero-lateral borders of sternites IV–VIII (Fig. 20).

Mature larva. Body length 4.5–5.3 mm (n = 20). Width of head capsule 0.4–0.5 mm (n = 20). Body colour white with indistinct grey markings (Fig. 120). In specimens preserved in Carnoy's the grey markings appear greyish green. Body form as in Fig. 120.

Head yellow with dark brown markings and occasional setae on all surfaces. Typical head pattern negative as in Fig. 128, with dark areas in form of ring surrounding a median clear area and 1 + 1 postero-lateral clear areas of head spots. Postgenal cleft rounded anteriorly and small relative to the other *Psilopelmia* species (*lewisi* and *bipunctatum*) in the locality; postgenal bridge almost as long as hypostomium (Fig. 135). Hypostomium of type seen in *S. exiguum* (Fig. 21). Antennae long, brown and with segment ratios 12 : 14 : 20. Mandible as in *S. exiguum* (Fig. 23), with two mandibular serrations, the posterior being the larger. Maxillary palp about twice as long as breadth at base. Cephalic fan with 30–32 rays.

Thorax white dorsally, sometimes with a grey band around anterior margin; ventrally with two median patches posterior to proleg. Cuticle glabrous. Proleg plate lightly sclerotised with about ten processes. Pupal respiratory histoblast mid brown and ovoid.

Abdomen white with 1 + 1 dorso-lateral grey patches on first six abdominal segments (5 narrow, 1 wide), posteriorly patches coalesce and cover whole of dorsum of expanded region. Ventrally patches form indistinct bands on anterior six abdominal segments. Ventral nerve cord grey. Occasionally larvae are white and lack grey ornamentation. Larvae from highland localities where dark male forms occur are more variable in coloration; they are darker than those from lowland localities where orange males occur and in some cases the grey patches on the thorax and abdomen coalesce to form a totally grey larva. Cuticle with scattered fine hairs on dorsal surface of posterior segments. Ventral papillae absent. Anal sclerite well sclerotised with posterior arms extending to twelfth row of posterior circlet hooks. Posterior circlet with about 60 rows of 4–14 hooks. Anal gill trilobed as in *S. exiguum* (Fig. 24), usually without secondary lobules; if present, secondary lobules short and up to two on each lateral lobe.

MATERIAL EXAMINED

Chile: 1 ♀, Valle de Azapa, vi.1912 (*C. E. Porter*) (BMNH); 3 ♀, Valle de Lluta, vi.1912 (*C. E. Porter*) (BMNH).

Ecuador: 3 ♀, Santiago onchocerciasis focus, Rio Onzole, v.1982 (*I. Mera & Platon*) (BMNH); 2 ♀ 4 ♂ (ex pupae), numerous pupae, 4 larvae, Esmeraldas Province, Santo Domingo-Esmeraldas road, Rio Chigwe, 26.ix.1983 (*A. J. Shelley & M. Arzube*) (BMNH, INHMT); 1 ♀ 1 ♂ (ex pupae), 8 pupae, 5 larvae, Santo Domingo-Esmeraldas road, Rio Capli, 26.ix.1983 (*A. J. Shelley & M. Arzube*) (BMNH, INHMT); 1 ♀ 1 ♂ (ex pupae), 8 pupae, 10 larvae, Santo Domingo-Esmeraldas Road, R. Tatica, 26.ix.1983 (*A. J. Shelley & M. Arzube*) (BMNH, INHMT); numerous pupae, Santo Domingo-Esmeraldas Road, R. Achioti, 26.ix.1983 (*A. J. Shelley & M. Arzube*) (BMNH, INHMT); numerous pupae, 2 larvae, Santo Domingo-Esmeraldas road, R. Tabuchi, 26.ix.1983 (*A. J. Shelley & M. Arzube*) (BMNH, INHMT); 1 ♀, near Concordia, road to Puerto Quito, Rio Blanco, 28.ix.1983 (*A. J. Shelley & M. Arzube*) (BMNH); 3 ♂ (ex pupae), numerous pupae and larvae, Esmeraldas-Atacames road, R. Tasechi, 27.ix.1983 (*A. J. Shelley & M. Arzube*) (BMNH, INHMT); 13 ♀ 7 ♂ (ex pupae), Imbabura Province, Salinas road 20 km north of Ibarra, R. Tahuando, 8.ix.1983 (*A. J. Shelley & M. Arzube*) (BMNH, INHMT); numerous females, 15 km south of Juncal on Ibarra road, R. Chota, 7.ix.1983 (*A. J. Shelley & M. Arzube*) (BMNH, INHMT); numerous females, 17 km south of Juncal on Ibarra road, at Engeno Tababuelo, R. Chota, 7.ix.1983 (*A. J. Shelley & M. Arzube*) (BMNH, INHMT); 7 ♀ 5 ♂ (ex pupae), numerous pupae and larvae, Otovalo-Ibarra road, stream opposite Cotacachi turn off, 10.ix.1983 (*A. J. Shelley & M. Arzube*) (BMNH); 1 ♀, Salinas-Lita road, San Juan del Hacha, R. Mira, 11.ix.1983 (*A. J. Shelley & M. Arzube*) (BMNH); 9 ♀, Palacara river, 9.ix.1983 (*A. J. Shelley & M. Arzube*) (BMNH, INHMT); 1 ♀ 2 ♂ (ex pupae), numerous larvae and pupae, nr Ibarra, tributary stream of R. Salado, 11.ix.1983 (*A. J. Shelley & M. Arzube*) (BMNH); 1 ♀ 4 ♂ (ex pupae), numerous larvae and pupae, irrigation canal on Salinas road 4 km from turnoff on Ibarra-Tulcan road, 9.ix.1983 (*A. J. Shelley & M. Arzube*) (BMNH); 1 ♂ (ex pupa), Salinas-Lita road 54 km from Ibarra, R. San Pedro, 11.ix.1983 (*A. J. Shelley & M. Arzube*) (BMNH); numerous pupae, 4 km from Ibarra-Tulcan road, Salinas road, 9.ix.1983 (*A. J. Shelley & M. Arzube*) (BMNH, INHMT); numerous pupae, Salinas-Lita road, 11.ix.1983 (*A. J. Shelley & M. Arzube*) (BMNH, INHMT).

Peru: 15 ♀, Arequipa, [1922] (*Escomel*) (MNHN); 2 ♀, Arequipa (no collection date) (*Escomel*) (BMNH) [presented by E. Roubaud (1923.185)]; 1 ♀ (no collection date or collector's name, but presumed to be Escomel) (BMNH) [presented by Dr Escomel (1919: 259)].

Taxonomic discussion. *Simulium escomeli* was first described by Roubaud (1909) from three female syntypes collected by Escomel in Arequipa, Peru. Roubaud comments on the poor condition of these specimens, which he intended to describe in detail at a later stage once Escomel had obtained more material. The fifteen pinned females in the MNHN are regarded as topotypes as they bear labels indicating the collection locality as Arequipa, the collector E. Escomel and the date 1922; no syntypes were located in this collection and are presumed lost. The two females collected by Escomel from Arequipa and deposited in the BMNH by Roubaud in 1923 (No.1923.185) as well as a third female from the same locality presented in 1919 (No. 1919: 259) are also topotypes.

Later, Enderlein (1934a) gave a superficial description of the nominally new species *S. rufidorsum* from an unnamed highland locality in Peru. Enderlein comments that the holotype was 'through Staudinger'. Staudinger was a lepidopterist and entomological dealer and not the collector (K. S. Sattler, pers. comm.). *Simulium rufidorsum* was synonymised with *S. escomeli* by Vargas & Diaz Najera (1953b) after examination of the holotype female and dissection of its genitalia, which conform to those of *S. escomeli*.

Since Roubaud's preliminary description *S. escomeli* has been redescribed by many authors. The most detailed is that by Wygodzinsky (1971) who lists references to all previous descriptions. (In his work reference to positive head spots on the larval cephalic apotome should read negative.) Wygodzinsky's (1971) work is based on specimens collected in Chile, Peru and Ecuador at high altitude localities. His description completely coincides with the one presented here except that males always possessed black scuta. The colour dimorphism described in this paper, particularly in males, is apparently loosely linked to altitude and appears to be intraspecific; preliminary analysis of polytene chromosomes of larvae from localities pure for males of either colour indicate no obvious differences in their banding patterns (W. S. Procunier, pers. comm.). Further detailed chromosome analysis is underway and will be reported shortly. Although no males, pupae or larvae were found in the lowland forests of the onchocerciasis focus we presume that males are identical to those from adjacent lowland areas and have taken account of this in the identification keys.

Simulium escomeli is the type species of the subgenus *Psilopelmia* Enderlein.

Distribution. *Simulium escomeli* is a common species throughout Ecuador, as indicated by the list of material examined. It is also common in association with the Andean cordillera of western South America in Peru, Chile and Colombia (Knab 1914a; Wygodzinsky, 1971, collections of BMNH, INHMT).

Biology. In Ecuador *Simulium escomeli* bites man voraciously in higher altitude localities but rarely in the western lowlands – despite its omnipresence in the slow-flowing lower reaches of the smaller rivers. In the onchocerciasis focus its breeding grounds have not been located. In higher altitudes it occurs attached to trailing vegetation in both slow – and fast – running small streams.

Simulium escomeli has also been recorded biting man in Chile and Peru where it also breeds in small streams and rivers (Coscaron, 1976b; Wygodzinsky, 1971).

Simulium (Hemicnetha) mexicanum Bellardi

(Figs 15, 16, 18, 22, 29, 35, 41, 47, 53, 60, 67, 73, 86, 87, 95, 101, 108, 115, 121, 129, 136, 144, 152)

Simulium mexicanum Bellardi, 1862 (appendix to part 2): 6. LECTOTYPE ♀, Mexico: Veracruz State, Tuxpango, near Orizaba (collection date and collector unknown) (DBAT), here designated [examined].

Simulium aureopunctatum Malloch, 1914: 27. Holotype ♀, Guatemala: Livingston (6.v. or 5.vi. year not given) (*Barber & Schwarz*) (USNM Cat. No. 15406) [examined]. [Synonymy by Strong *et al.*, 1934: 208.]

Simulium placidum Knab, 1915: 281. Holotype ♀, Trinidad: Arima river, 31.xii.1913 (*F. W. Urich*) (BMNH) [examined]. [Synonymy by Vargas & Diaz Najera, 1951b: 133.]

Simulium lugubre Lutz & Nunez Tovar *in* Lutz, 1928: 46. Syntypes ♀, ♂, l, p, Venezuela: Aragua, Rio de Maracay, La Trinidad, 28.viii.1925 (*A. Lutz & Nunez Tovar*) (IOC) [examined]. [Synonymy by Fairchild, 1940: 708.]

Simulium turgidum Hoffmann, 1930: 298. Syntypes ♀, Mexico: Chiapas State, Soconusco District, Finca Santa Anita (vii.1930) (collector and depository unknown). [Synonymy by Strong *et al.*, 1934: 208.]

DESCRIPTION. *Female*. General body colour black. Body length (alcohol preserved specimens) 3.2–4.0 mm (n = 24). Wing length 2.2–3.6 mm (n = 24), wing width 1.0–1.6 mm (n = 24).

Head dichoptic with red eyes; nudiocular area well-developed (Fig. 29). Frons, clypeus and occiput black with grey pruinosity, covered in numerous black bristles that are longer and denser on upper margin of clypeus and occiput. Proboscis light brown, maxillary palps black. Antennae dark brown with scape, pedicel and first flagellomere orange. Cibarium with large central trough, unarmed; cornuae well-developed and sclerotised (Fig. 35).

Scutum, humeri and paranotal folds black with grey pruinosity. Scutum with numerous, adpressed, short, black setae becoming longer and upright on posterior border, interspersed with clumps of adpressed, brass-coloured scale-like setae (Fig. 144). Pleural region dark brown with grey pruinosity. Scutellum dark brown to black with grey pruinosity and with scattered upright black bristles on whole surface except anterior border and brass-coloured, adpressed, scale-like setae over whole surface. Postnotum black with grey pruinosity.

Subcostal wing vein with an irregular row of setae over entire length; basal section of *R* with three irregular rows of setae along entire length (Fig. 41). Costal base tuft of dark brown setae.

Fore legs with coxae, trochanters, and femora light brown, tibiae white pruinose with apical third and inner margin black, tarsi black. Mid leg coxae dark brown with grey pruinosity, trochanters and femora black, tibiae black with up to basal third light brown, basal two-thirds of basitarsus light brown, rest black, other tarsal segments black. Hind leg coxae dark brown with grey pruinosity, trochanters light brown, femora black, basal third of tibiae white merging to black on apical two-thirds, basal half of basitarsus white, distal half black, rest of tarsi black. Colour and proportions of legs as in Fig. 144. The flattened and widened fore tarsi, mid and hind basitarsi and hind femora and tibiae are typical of *S. mexicanum* and several other species of *Hemicnetha*. Claws curved with subbasal tooth (Fig. 47). Halteres white with black stems.

Basal scale of abdomen (tergite I) velvet-black with long brass-coloured basal fringe, tergite II mottled brown and black with grey pruinosity, tergites III–V velvet-black, tergites VI–IX shiny black (Fig. 144). Tergal plates (Fig. 4) highly sclerotised especially on tergite II. Sternites I and II light brown, rest black. Genitalia black. Eighth sternite well sclerotised with 4–6 setae on each side, gonopophyses well-developed, subtriangular, totally membranous and covered with fine setae (Fig. 53). Cerci hemispherical; paraprocts large and subquadrangular with long bristles and short thick setae (Fig. 60). Genital fork short, strongly sclerotised and with highly developed lateral arms (Fig. 67). Spermatheca oval as in *S. exiguum* (Fig. 5), strongly sclerotised with no external sculpturing and spicules on inner surface randomly distributed; width of membranous area of insertion of spermathecal duct large, about half maximum width of spermatheca.

Male. General body colour black. Body length (alcohol preserved specimens) 3.1–4.5 mm (n = 20), wing length 2.6–3.5 mm (n = 20), wing width 1.1–1.6 mm (n = 20).

Head holoptic with red eyes. Clypeus black with grey pruinosity. Rest of head coloration as in female.

Coloration and setation of scutum, humeri, paranotal folds, pleural region, scutellum and postnotum as in female, except scale-like setae golden and thin dark median line running whole length of scutum, free of these scales (Fig. 152).

Subcostal wing vein and basal section of *R* bare.

Leg coloration and form (Fig. 152) as in female except white area of hind tibia reduced to point of articulation with femur. Halteres as in female.

Basal scale of abdomen (tergite I) velvet-black with dense basal tuft of long black hairs. Tergites II–IX velvet-black with the following silver pruinose ornamentation: tergite II covering whole segment, tergite IV covering anterior border except for median portion, tergites V–VII completely covered except for median triangle on posterior border of each tergite, tergite VIII with a small lateral area on anterior margin of tergite (Fig. 152). Sternites mottled brown and black with poorly developed sternal plates (Fig. 6). Genitalia velvet-black. Gonocoxite rectangular, wider than long, gonostyle elongate with a weakly developed subterminal spine (Fig. 73). Ventral plate rectangular with sclerotised, poorly developed basal arms and a large keel; ventral plate densely covered with fine setae and small spines (Figs 86, 87). Median sclerite elongate with apical depression (Fig. 95). Paramere (Fig. 101) with enlarged basal process and few stout spines apically.

Pupa. Cocoon length 2.5–3.6 mm, ventrally 3.3–4.4 mm; pupa length 3.2–4.3 mm; gill length 1.6–2.5 mm (n = 35).

Cocoon shoe-shaped, mid brown; rim of aperture mid brown, reinforced and without festoons as seen in other *Hemicnetha* species (Fig. 108). Cocoon surface of thin, amorphous, translucent, elastic substance in which thick, interwoven fibres are sometimes visible. Gill light to dark brown,

generally protruding beyond collar of cocoon, with 12 short, forwardly-directed filaments arranged in a bunch. Main trunk of gill giving rise to an inner primary branch bearing five filaments and an outer branch with seven filaments. The filaments arise basally on the gill (Fig. 115), are slender with crenate margins and rounded distally, their surfaces covered with fine spicules as in *S. exiguum* (Fig. 12). Head with 2 + 2 frontal and 1 + 1 facial trichomes, all poorly developed and unbranched; surface of head with platelets which in the frontal region are scattered, enlarged and highly sclerotised and in the facial region are dense and of normal size (Figs 15, 16). Thorax with 5 + 5 antero-dorsal, poorly developed unbranched trichomes. Surface of anterior region of thorax covered in well-developed highly sclerotised platelets which extend to posterior border of thorax either side of raphe and in a pair of submedian and lateral bands to posterior thoracic border which is densely covered by normal size platelets. Ventral surface of thorax without platelets (Fig. 18). Abdominal tergite II with 3 + 3 well-developed simple hooks and 1 + 1 simple fine hairs external to these, III–IV with 4 + 4 simple hooks, IX with no spines, II–IX with 1 + 1 well-developed areas of spine combs on anterior margins and I and II with groups of spine combs on posterior margins (Fig. 19); sternite IV with no hooks or hairs, V–VII with 2 + 2 simple hooks, 1 +1 patches of spine combs on anterior borders of sternites IV–VIII (Fig. 20).

Mature larva. Body length 7.0–9.7 mm (n = 14). Width of head capsule 0.7–0.8 mm (n = 14). Body colour grey in specimens preserved in both alcohol and Carnoy's fixative. Form as in Fig. 121.

Head yellow with dark brown markings and occasional setae on all surfaces. Head pattern positive as shown in Fig. 129, surrounded by dark pigmentation. Occasionally the 1 + 1 lateral groups of head spots are negative in relation to the dark pigmentation of the cephalic apotome in this region. Postgenal cleft bell-shaped and rounded anteriorly (Fig. 136); postgenal bridge almost as long as hypostomium (Fig. 136). Hypostomium (Fig. 22) rounded anteriorly with strongly pigmented anterior margin and nine poorly developed apical teeth; median tooth the most developed with blunt apex, corner teeth smaller and blunt and intermediate teeth poorly defined; 4–5 lateral serrations, hindmost level with first hypostomial seta; 1 + 1 lines of 9–10 hypostomial setae. Antennae long and faintly pigmented with segment ratios 8 : 15 : 10. Mandible with subequal comb teeth and one well-developed backwardly-slanting mandibular serration; a second short mandibular serration sometimes present posterior to the first. Maxillary palp heavily pigmented, brown, about twice as long as width at base. Cephalic fan with 48–60 rays.

Thorax grey dorsally, white ventrally with a large greyish brown patch occupying ventral surface of proleg and a median patch posterior to this. Cuticle with occasional fine hairs on dorsal and ventral surfaces. Proleg plate well sclerotised with about 20 processes. Pupal respiratory histoblast dark brown, claviform.

Abdomen greyish brown dorsally, usually overall, but in some specimens in indistinct bands in anterior constricted abdominal segments; ventrally whitish with irregular grey patches. Ventral nerve cord greyish. Ventral papillae absent (Fig. 121). Cuticle with occasional fine hairs on dorsal and ventral surfaces. Anal sclerite well sclerotised with posterior arms extending to about 65th row of posterior circlet hooks. Posterior circlet with 214– 228 rows of 31–40 hooks. Anal gill trilobed with 12–15 lobules of which one on each lobe is larger than the rest.

Material examined

Lectotype ♀, paralectotype ♀ of *S. mexicanum*, **Mexico**: Veracruz State, Tuxpango, near Orizaba (collection date and collector unknown) (DBAT). Holotype ♀ of *S. aureopunctatum*, **Guatemala**: Livingston, 6.v. or 5.vi. [no year given] (*Barber & Schwarz*) (USNM). Holotype ♀, paratype ♀ of *S. placidum*, **Trinidad**: Arima River, 31.xii.1913 (*E. W. Urich*) (BMNH). Syntypes pupae and larva of *S. lugubre* [only remaining material of syntype series], **Venezuela**: Rio Limon, Maracay (7 pupae), 28.viii.1925 (*A. Lutz & Nunez Tovar*) (IOC, Cat. Nos. 12134, 12173, 12193–12197); Rio Suaire, Caracas (2 pupae), 1925 (*A. Lutz & Nunez Tovar*) (IOC, Cat. No. 12198); no data on label but part of Lutz collection from Venezuela (1 larva) (IOC, Cat. No. 12207).

Belize: 2 ♀ 2 ♂, Hell's Teeth, 15.ii.1958 (*P. C. C. Garnham & D. J. Lewis*) (BMNH).

Colombia: 3 ♀, Norte de Santander, Arboledas, Siravita, La Esperanza, 26.vii.1986 (*B. Alexander*) (BMNH).

Ecuador: 8 ♀ 8 ♂ (ex pupae), 10 larvae, Esmeraldas Province, various localities in the Santiago onchocerciasis focus, San Miguel de Cayapas, Casacadita, R. Cayapa, 17.vi. & 26.v.1981 (*A. J. Shelley & M. Arzube*) (BMNH, INHMT); 1 ♀ (ex pupa), Agua Blanca, R. Cayapa, 15.vii.1986 (*P. Beech-Garwood*) (BMNH); 8 ♀ 10 ♂ (ex pupae), numerous pupae and larvae, Esmeraldas Province, Santo Domingo-Esmeraldas road, Rio Achioti, 26.ix.1983 (*A. J. Shelley & M. Arzube*) (BMNH, INHMT);

numerous pupae and larvae, Santo Domingo-Esmeraldas road, R. Tabuchi, 26.ix.1983 (*A. J. Shelley & M. Arzube*) (BMNH, INHMT); 4 ♀ 2 ♂ (ex pupae), numerous pupae and larvae, Imbabura Province, stream at 40 km from Ibarra on Salinas-Lita road, 11.ix.1983 (*A. J. Shelley & M. Arzube*) (BMNH); 3 ♀ 9 ♂ (ex pupae), numerous pupae and larvae, Salinas-Lita road, R. San Pedro, 11.ix.1983 (*A. J. Shelley & M. Arzube*) (BMNH, INHMT); 1 ♀ 5 ♂ (ex pupae), numerous pupae and larvae, Pichincha Province, Quito-Santo Domingo road, Riachuelo Lelia, 29.ix.1983 (*A. J. Shelley & M. Arzube*) (BMNH, INHMT); numerous pupae and larvae, Quito-Santo Domingo road, R. Toachi, 28.ix.1983 (*A. J. Shelley & M. Arzube*) (BMNH, INHMT).

Guatemala: 1 ♀, Yepocapa onchocerciasis focus, Chimaltenango, Rio Chusita, Finca Chusita, 26.viii.1948 (*H. Dalmat*) (BMNH); 2 ♂, Acatenango, Chimaltenango, Rio El Arco, Finca Chantunjay, 23.x. and 20.xi.1948 (*H. Dalmat*) (BMNH).

Honduras: 2 larvae, Departamento de Cortes, 5 m stream, El Cacao, treatment point, 23.iii.1984 (*L. Lacey*) (BMNH).

Mexico: 2 ♀, Chiapas State, Escuintla, Jalapa aldeia, xi.1935 (collector unknown) (BMNH).

Panama: 12 larvae and 6 pupae, Chiriqui Provence, Boquete, 5.i.1983 (*R. A. Cheke*) (BMNH); 1 pupa, Chiriqui Province, Rio Chiriqui Viejo, 25.ix.1975 (*M. Kerner*) (BMNH); 1 ♂ (ex pupa), 12 larvae and 5 pupae, Cocle Province, El Valle, Rio Anton, La Mapolo, 1–6.vii.1985 (*A. J. Shelley*) (BMNH).

Trinidad: 3 ♀, Naranja, Tucucha Trail, 30.ix.1937 (*J. Smart*) (BMNH); 4 ♀, Blanchisseuse road, 31.x.1937 (*J. Smart*) (BMNH).

Tobago: 5 ♀, Pigeon Peak, 16.x.1937 (*J. Smart*) (BMNH).

Venezuela: 2 ♀, 3 ♂, [northern Venezuela,] La Puerta, 21.v.1961 (*D. J. Lewis*) (BMNH); 1 ♀ 1 ♂, [northern Venezuela,] Rio Aguacatal, 14.vi.1961 (*D. J. Lewis*) (BMNH); 1 ♀, [northern Venezuela,] Monte Oscuro, 6.v.1961 (*D. J. Lewis*) (BMNH); 2 ♀, [northern Venezuela,] Altamira, x.1969 (*W. Büttiker*) (BMNH); 1 ♀ (ex pupa), Carabobo State, Birigina (no collection date) (*J. Ramirez*) (BMNH); 1 ♂ (ex pupa), Lara State, Rio Tocuyo (no collection date) (*J. Ramirez*) (BMNH); 2 ♂ (ex pupae), Federal District, Hacienda El Limon, Divisa Colonia Tovar (no collection date) (*J. Ramirez*) (BMNH).

Taxonomic discussion. Bellardi's description (1862) of *Simulium mexicanum* gives insufficient detail to be able to determine the sex of the material, which he indicates as being male with no reference to number of specimens. The type status of the specimens (holotype or syntypes) is not, therefore, known. No subsequent authors have examined this material because the depository was not known. However, many descriptions of all taxonomically important stages have since been produced, of which that of Dalmat (1955) is the most complete.

Bellardi's collection of Neotropical simuliids has now been located in the University of Turin. *Simulum mexicanum* is represented by two female specimens which are both covered in fungal hyphae but otherwise well preserved; they are easily recognisable as what is currently regarded as this species. The better specimen bears one label with the word 'Tuxpango' and has been designated as lectotype and labelled accordingly. The other specimen with a single label bearing the number '193' has been labelled as paralectotype. It is apparent that Bellardi had confused the sex of his type specimens.

Simulium mexicanum shows little morphological variation given its wide distribution; only the branching height of pupal gills, though basal, can vary within populations.

The synonymies of *S. turgidum* and *S. aureopunctatum* with *S. mexicanum* were first established by Strong *et al.* (1934) although no reasons were given. Hoffmann's description (1930) of *turgidum* and Malloch's (1914) of *aureopunctatum* are sufficiently detailed to show them to be conspecific with the distinctive *S. mexicanum*. An examination of the well-preserved female holotype of *S. aureopunctatum* showed this specimen to completely correspond with our modern concept of *S. mexicanum*, thus confirming their synonymy. The synonymy of *S. lugubre* with *S. mexicanum* is first listed in Fairchild (1940). We have examined the only remaining syntypes (larvae & pupae) in the IOC, which together with the figures and descriptions given by Lutz & Nunez Tovar (Lutz, 1928) all support this synonymy. Vargas & Diaz Najera (1951b) synonymised *S. placidum* with *S. mexicanum* following a comparison of two specimens in the BMNH identified by Smart as *S. placidum* with specimens of *S. mexicanum* from various Latin American localities. Our examination of the holotype of *S. placidum* confirms this synonymy.

In 1934 Enderlein (1934b) described a new species from Mexico as *Hemicnetha mexicana*. Vargas (1942a) did not accept Enderlein's generic classification of the Simuliidae, regarding *Hemicnetha* as a subgenus of *Simulium*, and published the name *paynei* as a replacement name for *mexicanum* Enderlein (junior secondary homonym of *mexicanum* Bellardi).

Simulium mexicanum belongs to the subgenus *Hemicnetha* and is closely related to *S. smarti* Vargas, although females superficially resemble *S. guianense* Wise and *S. orbitale* Lutz in coloration.

DISTRIBUTION. In Ecuador *S. mexicanum* has been found from the western lowlands of the Andes to higher altitudes in the north of the country.

Elsewhere it has been recorded from Belize, Bolivia, Colombia, Guatemala, Mexico, Panama, Tobago, Trinidad and Venezuela (Barreto *et al.*, 1970; Dalmat, 1955; Fairchild, 1940; Knab, 1915; Lewis, 1963; Ramirez Perez, 1983; Smart, 1940; Strong *et al.*, 1934; Vargas, 1945; Vargas & Diaz Najera, 1957; Vargas *et al.*, 1946; Vulcano, 1967).

BIOLOGY. *Simulium mexicanum* is a zoophilic species (Strong *et al.*, 1934; Lewis, 1963; Shelley & Arzube, 1985) which has been reported to bite man occasionally in Colombia (Barreto *et al.*, 1970) and Venezuela (BMNH collection). In Trinidad it bites mules and donkeys (Knab, 1915). *Simulium mexicanum* and *S. metallicum* were originally thought to be associated with the regular transmission of Venezuelan Equine Encephalitis in Colombia (Sanmartin *et al.*, 1973; Zuluaga & Yuill, 1978) but recent evidence (Homan *et al.*, 1985) suggests that at most they only occasionally transmit the virus mechanically.

Simulium mexicanum breeds, often in enormous numbers, in small, fast-flowing streams at both low and high altitudes usually in, or in close proximity to, waterfalls (Barreto *et al.*, 1970; Shelley & Arzube, 1985).

Simulium (Psilopelmia) quadrivittatum Loew

(Figs 30, 36, 42, 48, 54, 61, 68, 74, 88, 89, 96, 102, 109, 116, 122, 130, 137, 145, 153)

Simulium quadrivittatum Loew, 1862: 186. LECTOTYPE ♀, CUBA: (collection date unknown) (*Gundlach*) (MCZH, Cat. No. 12533), here designated [examined].

Wilhelmia mallochi Enderlein, 1925: 208. LECTOTYPE ♀, COSTA RICA: La Palma, 6.v. (no year cited) (*Biolley*) (USNM, Cat. No. 8998, Type No. 41595), here designated [examined]. [Synonymy by Vargas, 1945: 189.]

Simulium fairchildi Vargas, 1942b: 458. LECTOTYPE ♀, PANAMA: Juan Mina Station, Rio Chagres, 8.xi.1939 (*G. B. Fairchild*) (MCZH), here designated [examined]. [Replacement name for *S. haematopotum* Malloch sensu Fairchild, 1940.] [Synonymised with *S. quadrivittatum* by Fairchild, 1943: 574.]

DESCRIPTION. *Female*. General body colour black. Body length (alcohol preserved specimens) 2.0–2.7 mm (n = 55), wing length 1.6–2.2 mm (n = 55), wing width 0.7–1.0 mm (n = 55).

Head dichoptic with red eyes; nudiocular area well-developed (Fig. 30). Frons, clypeus and occiput black with silver pruinosity. Mouthparts dark brown. Antennae orange-brown. Cibarium with sclerotised posterior margin armed with teeth; median area of margin concave with three stout teeth, a pair of submedian groups of about six well-developed teeth with the central being longer and up to tricusped; posterior margin of cibarium between these teeth and cornuae occupied by three to five smaller teeth; cornuae well-developed and sclerotised (Fig. 36).

Scutum velvet-black with silver pruinose ornamentation, which varies in form depending on angle of illumination. With light source anterior to specimen silver ornamentation as follows: a pair of parallel, submedian bands narrowing posteriorly and running from the anterior scutal border and coalescing with the silver pruinose posterior border, a pair of dull grey cunae in form of equilateral triangles present in anterior section of these bands; a pair of sublateral parallel bands beginning at the golden pruinose humeri and extending to posterior pruinose margin of scutum (Fig. 145). With light source posterior to specimen the grey cunae become silver and merge with the submedian bands, the rest of the pattern being identical to that seen with an anterior light source. Irrespective of direction of light source *S. quadrivittatum* is unique in that the submedian pruinose bands show a constriction at the posterior border of the cunae, which readily distinguishes it from *S. haematopotum* and similarly ornamented species of the *amazonicum* group. Paranotal folds black with silver pruinosity. Scutum with numerous adpressed golden hairs. Pleural region dark brown with faint silver pruinosity. Scutellum velvet-black with an uneven row of long black bristles on posterior border and a group of these bristles on each postero-lateral corner. Postnotum black with grey pruinosity.

Subcostal vein of wing usually bare but sometimes with up to two hairs on median section and more rarely a single hair at base of vein amongst sensilla; basal section of radius bare (Fig. 42). Costal base tuft of dark setae.

Legs dark brown with coxae lightly grey pruinose; distal tip of femur and basal tip of tibia light brown at articulation on fore leg; distal tip of femur of mid leg and basal half of basitarsi and second tarsomeres cream; basal articulation of tibiae, basal half to two-thirds of basitarsi and basal half of second tarsomeres of hind leg cream. Proportions of legs as in Fig. 145. Femora and tibiae of all legs and trochanters of fore and hind

legs with numerous scales scattered amongst hairs as in *S. exiguum* (Fig. 3). Claws curved with subbasal tooth (Fig. 48). Halteres bright yellow with light brown base.

Abdominal tergites black. Tergal plates slightly developed (Fig. 4). Basal scale (tergite I) velvet-black, sometimes with faint silver pruinosity in central part; tergite II black with silver pruinosity; tergites III–V velvet-black with posterior margins faintly silver pruinose; tergites VI–IX shiny black. Sternites and genitalia dull black (Fig. 145). Eighth sternite sclerotised with a group of 8–10 setae on each side, gonopophyses large, subquadrangular with numerous minute setae (Fig. 54). Cerci hemispherical, paraprocts small and subrectangular (Fig. 61). Genital fork stout with well-sclerotised stem, expanded arms and well-developed lateral wings with sclerotised anterior processes (Fig. 68). Spermatheca as in *S. exiguum* (Fig. 5), oval, sclerotised with no external sculpturing and spicules of inner surface arranged in groups of three. Area of insertion of spermathecal duct membranous and about one-third maximum width of spermatheca.

Male. General body colour black. Body length 2.6 mm (alcohol preserved specimen) (n = 1), wing length 1.8 mm (n = 1), wing width 0.9 mm (n = 1).

Head holoptic with dark red eyes. Clypeus black with silver pruinosity. Rest of head coloration as in female.

Scutum velvet-black with a pair of submedian silver cunae extending from anterior scutal border for about two-thirds of its length (most easily seen with light source anterior to specimen). Posterior border and anterior three-fourths of lateral border of scutum silver pruinose. Scutum with adpressed golden hairs. Paranotal fold velvet-black (Fig. 153). Coloration and setation of pleural region, scutellum and postnotum as in female.

Subcostal vein and basal section of *R* bare.

Leg coloration as in females, proportions as in Fig. 153. Scale distribution on legs as in female. Haltere coloration as in female.

Abdominal tergites velvet-black, basal fringe of long black hairs. Silver pruinose ornamentation as follows: tergite II completely silver, tergites III, V and VI completely silver except for median dark patch (Fig. 153). Sternites and genitalia dark brown, sternal plates not examined (lack of material). Gonocoxite slightly longer than wide; gonostyle subtriangular, about half length of basimere, with subterminal, rounded spine (Fig. 74). Ventral plate as in Figs 88, 89 with highly developed lightly sclerotised basal arms and poorly developed keel; hairs long and restricted to keel; median plate slightly pyriform with small apical incision (Fig. 96). Paramere as in Fig. 102 with several well-developed distal spines.

Pupa. Cocoon length dorsally 1.8 mm, ventrally 2.6 mm; pupa length 2.5 mm; gill length 3.6 mm (n = 1).

Cocoon slipper-shaped, dark brown opaque; rim of aperture dark brown, reinforced and sometimes with dorsal protuberance (Fig. 109). Cocoon surface of thin, densely interwoven fibres. Gill mid brown with eight, forwardly-directed, long, slender filaments; primary branches arise in the vertical plane with filaments arranged in the horizontal plane. The gill configuration description is from a slide-mounted specimen (Fig. 116); main trunk giving rise to three primary branches, inner (= ventral) with two filaments and median and outer (= dorsal) each with three filaments; inner branch with bifurcation at basal sixth of gill, median branch with first bifurcation at basal sixth and second at basal third, outer branch with first bifurcation at basal tenth and second bifurcation at basal sixth of gill; filaments slender with crenate margins and rounded distally, their surfaces covered with fine spicules as in *S. exiguum* (Fig. 12). Head as in *S. exiguum* (Figs 13, 14) with 2 + 2 bifid frontal and 1 + 1 simple well-developed facial trichomes; surface of head glabrous with few platelets. Thorax as in *S. exiguum* (Fig. 17) with 5 + 5 well-developed, bifid, antero-dorsal trichomes. Surface of thorax with few platelets. Abdominal tergite II with a line of 4 + 4 fine hairs, III–IV with 4 + 4 simple hooks, IX with 1 + 1 well-developed spines, VI–IX with a row of well-developed spine combs on anterior margins of segments (Fig. 19); sternite IV with 2 + 2 simple or bifid well-developed hooks, V–VII with 2 + 2 bifid or trifid hooks, sternite VIII with 1 + 1 antero-median patches of spine combs (Fig. 20).

Mature larva. Body length 3.4–4.5 mm (n = 6). Width of head capsule 0.4 mm (n = 6). Body colour white with grey banding (Fig. 122). Body form as in Fig. 122. This species is easily confused with *S. lewisi* but can be distinguished by the form of the postgenal cleft and the presence of ventral papillae. Larval coloration in Carnoy's fixative was not observed due to paucity of material.

Head yellow with head spots concolorous or forming a positive pattern as in Fig. 130 and with sparsely distributed setae on all surfaces. Postgenal cleft small, triangular with thickened lateral margins; postgenal bridge as long as hypostomium (Fig. 137). Hypostomium as in *S. exiguum* (Fig. 21). Antennae long, yellow to pale brown with

segment ratios 15 : 20 : 25. Mandible as in *S. exiguum* (Fig. 23). Maxillary palp over three times as long as width at base. Cephalic fan with 36–40 rays. Thorax white with black collar anteriorly, amorphous, grey patches dorsally and several small, black patches ventrally posterior to proleg. Cuticle glabrous ventrally but with occasional setae dorsally. Proleg plate not observed (insufficient specimens). Pupal respiratory histoblast dark brown and claviform.

Abdomen white with a single black ring on first abdominal segment and on last narrow abdominal segment, intermediate segments with incomplete rings usually more obvious dorsally; posterior segments of abdomen with dark patches distributed randomly, but dorsally these coalesce. Ventral nerve cord grey. Cuticle with scattered setae on dorsal surface of anterior (narrow) constricted segments, more densely distributed on posterior (wide) segments, glabrous ventrally. Ventral papillae well-developed (Fig. 122). Anal sclerite well sclerotised with posterior arms extending to twelfth row of posterior circlet hooks. Posterior circlet with 58 rows of 10–11 hooks. Anal gill trilobed as in *S. exiguum* (Fig. 24) with six short lobules on each lobe.

MATERIAL EXAMINED

Lectotype ♀ and paralectotype ♀ of *S. quadrivittatum*, **Cuba**: collection date unknown (*Gundlach*) (MCZH). Lectotype ♀ and paralectotype ♀ of *Wilhelmia mallochi*, **Costa Rica**: La Palma, 6.v. (no year given) (*Biolley*) (USNM) and 2 paralectotype ♀ of *Wilhelmia mallochi*, **Cuba**: Cayamas, 6.vi., 10.vi. (no year given) (*E. A. Schwarz*) (USNM). Lectotype ♀ and 4 paralectotype ♀ of *S. fairchildi*, **Panama**: Juan Mina, Rio Chagres, Canal Zone, 8.xi.1939 (*G. B. Fairchild*) (MCZH), 2 paralectotype ♀ and 1 paralectotype ♂ of *S. fairchildi*, **Panama**: Summit, Canal Zone, 9.i.1940 (*G. B. Fairchild*) (MCZH) and the following female paralectotypes of *S. fairchildi*, **Panama**: 2 ♀, Forest Reserve, Canal Zone, 11.x.1939; 1 ♀, Las Guacas, Panama Republic, 4.i.1940; 1 ♀, Chilibre, Panama Province, Panama Republic, 23.xi.1939 (all *G. B. Fairchild*) (MCZH).

Belize: 46 ♀, Privation Creek, 31.ii.1958 (*D. J. Lewis*) (BMNH); 3 ♀, Cool Shade, 11.i.1958 (*D. J. Lewis & P. C. C. Garnham*) (BMNH); 6 ♀, Middlesex, 8 & 17.ii.1958 (*D. J. Lewis*) (BMNH), 1 ♀, North Branch, 10.ii.1958 (*D. J. Lewis*) (BMNH); 3 ♀, Rio Frio, 5.ii.1958 (*P. C. C. Garnham & D. J. Lewis*) (BMNH); numerous females, near Cayo, Augustine, 27.vii.1961 (*D. J. Lewis*) (BMNH).

Colombia: 1 ♀, Choco, El Tigre, x.1959 (*P. C. C. Garnham*) (BMNH).

Costa Rica: 5 ♀, Env. da Cartago & La Palma, 1500 m, 1906 (*Biolley*) (MNHN) [1 ♀ in BMNH from Env. da Cartago presented by Roubaud with incomplete data but almost certainly from the series deposited by Biolley in MNHN]; 1 ♀, Talamanca, 22.iv.1917 (*C. B. Williams*) (BMNH); 4 ♀, Orosi, 6.i.1938 (*K. W. Kamm*) (BMNH).

Ecuador: 9 ♀, Esmeraldas Province, various localities in the Santiago onchocerciasis focus, San Miguel de Cayapas, R. Cayapa 18–21.vi.1981 (*A. J. Shelley & M. Arzube*) (BMNH, INHMT); 7 ♀, R. Cayapas, 28.vi.1980 (*M. Arzube*) (BMNH, INHMT); 5 ♀, San Miguel de Cayapas, R. Cayapa, 28–30.vi.1980 (*M. Arzube*) (BMNH, INHMT); 6 larvae, San Miguel de Cayapas, Estero Hacha, 26.v.1981 (*A. J. Shelley & M. Arzube*) (BMNH); 1 ♀ (ex pupa), San Miguel de Cayapas, R. Cayapa, Cascadita, 17.vi.1981 (*A. J. Shelley & M. Arzube*) (BMNH); 1 ♂ (ex pupa), 500 m above San Miguel de Cayapas, feeder stream of R. San Miguel, 17.vi.1981 (*A. J. Shelley & M. Arzube*) (BMNH); 1 ♀, Sapallo Grande Mission, R. Cayapa, 28.v.1981 (*A. J. Shelley & M. Arzube*) (BMNH); 3 ♀, Naranjal, R. Canandé, 25.ix.1983 (*A. J. Shelley & M. Arzube*) (BMNH); 1 ♀ (ex pupa), 2 larvae, Naranjal (R. Canandé), R. Aguas Negras, 23.vi.1985 (*A. J. Shelley & M. Arzube*) (BMNH); 1 ♀, 1 ♀ (ex pupa), Cotopaxi Province, Quevedo-La Mana-Pilalo road, La Germania, Riachuelo, 9.vi.1984 (*A. J. Shelley & M. Arzube*) (BMNH); 1 ♀, Manabi Province, Santa Domingo-El Carmen road, km 40, 2 km past El Carmen, Rio Suma, 7.vi.1984 (*A. J. Shelley & M. Arzube*) (BMNH); 2 ♀, El Oro Province, Machala-Naranjal road, Rio Bucay, 12.vi.1984 (*M. Arzube*) (BMNH).

Jamaica: 1 ♀, (no locality or collection date) (*H. G. Johnston*) (BMNH).

Mexico: 1 ♀ 1 ♂, Las Chuapas, ii.1947 (*J. Parra*) (BMNH).

Panama: 8 ♀, Canal Zone, 1932 (*L. H. Dunn*) (BMNH); 3 ♀, 1 ♀ (ex pupa), Chiriqui Province, Fortuna hydroelectric station, Arroyo 47, Q10 E27 and Q47 CUSA, 18.x.1979, 18.iii.1980 & 22.i.1981 (*J. L. Petersen*) (BMNH).

TAXONOMIC DISCUSSION. *Simulium quadrivittatum* was described by Loew (1862) from females collected in Cuba, with no details of the number of specimens examined or their depository. However, Smart (1942) noted the presence of two syntypes in the MCZH (depository incorrectly cited as in Berlin and not Harvard) where all of Loew's New World Diptera types were deposited. This material has now been examined and the better

specimen designated as lectotype and labelled accordingly. Many descriptions and misidentifications of *S. quadrivittatum* have been made and these are listed with the most complete descriptions of this species by Wygodzinsky (1953), Rubtsov & Garcia Avila (1972) and Fox (1953). *Simulium quadrivittatum* is most closely related to *S. haematopotum* in the subgenus *Psilopelmia* and in female coloration resembles *S. marathrumi* Fairchild, *S. oyapockense* Floch & Abonnenc, *S. roraimense* Nunes de Mello and *S. sanguineum* Knab of the subgenus *Psaroniocompsa*.

In his revision of the Simuliidae of the Americas, Malloch (1914) gave a detailed description of *S. quadrivittatum* based on material from Cuba, Costa Rica, Puerto Rico and Panama in the USNM. Enderlein (1925) later described the specimens from Cuba and Costa Rica as a new species, *Wilhelmia mallochi*, although it is unclear whether he saw Malloch's material. *Wilhelmia mallochi* was later synonymised with *S. quadrivittatum* by Vargas (1945) but with no explanation for this action. Pinned specimens of *W. mallochi* in the USNM have now been examined. They consist of two females labelled as cotypes from La Palma, Costa Rica, collected by Biolley, a female 'cotype' from Cayamas, Cuba, collected by Schwarz in June (specimen and collection year missing), and two further females from Cayamas collected in the same period by Schwarz but with no 'cotype' labels. The better specimen from La Palma of these four syntypes has been designated lectotype. The lectotype and paralectotypes of *Wilhelmia mallochi* have been compared with the lectotype of *S. quadrivittatum* and are conspecific. The specimens in the BMNH and MNHN collected in La Palma by Biolley are almost certainly from the same collection as those examined by Malloch in the USNM. However, they did not form part of the syntype series of *W. mallochi* because they were not cited by Malloch (1914) on which publication Enderlein (1925) presumably based his new species. In Fairchild's (1940) revision of the Simuliidae of Panama a description of the female, male and pupa of *S. haematopotum* were given although the author discussed the possibility that this was a misidentification. He noted differences between his material and the figures of this species by Dyar & Shannon (1927), the similarity of his material to *S. pseudohaematopotum* Hoffmann, and that a previous worker in the area had identified this species as *S. quadrivittatum*. Later, Vargas (1942b) proposed the name *fairchildi* for Fairchild's specimens because of differences they showed in the genital fork and claw with *S. haematopotum* and in the genital fork of *S. haematopotum*. Fairchild (1943) later examined true *S. haematopotum* and concluded that *S. fairchildi* should be regarded as a synonym of *S. quadrivittatum* until material from the type locality (Cuba) of the latter species could be examined. Vargas (1945) maintained this synonymy. Fairchild's description and figures of *S. fairchildi* (as *S. haematopotum* in Fairchild, 1943) indicates *S. quadrivittatum* and not *S. haematopotum* with reference to the toothed claw and pupal gill. Fairchild's material has now been examined and currently comprises the material listed as *S. fairchildi* under material examined. A lectotype from Juan Mina, Rio Chagres has been selected from this syntype series and together with the paralectotypes is conspecific with the lectotype of *S. quadrivittatum*. The male paralectotype of *S. fairchildi* from Summit, Panama, has been compared with a reared *S. quadrivittatum* from Ecuador and is conspecific. We therefore agree with the synonymy of *S. fairchildi* with *S. quadrivittatum* first proposed by Fairchild (1943). Various other misidentifications of *S. quadrivittatum* as *S. haematopotum* are listed by Vulcano (1967) and Wygodzinsky (1953).

Distribution. In Ecuador *S. quadrivittatum* inhabits lowland forested areas and plantations to the west of the Andean cordillera and only occurs in large numbers in the onchocerciasis focus in the north of the country (Shelley & Arzube, 1985; Leon & Wygodzinsky 1953a, b; Wygodzinsky 1953). Outside Ecuador *S. quadrivittatum* has been recorded from Belize (Lewis & Garnham, 1960), Colombia (BMNH), Costa Rica (Roubaud, 1906), Cuba (Rubtsov & Garcia Avila, 1972), Jamaica (BMNH), Mexico (Vargas & Diaz Najera, 1957), Panama (Petersen *et al.*, 1983) and Puerto Rico (Fox, 1953), sometimes at high altitudes (Lewis & Garnham, 1960; Petersen *et al.*, 1983). The inclusion of Venezuela by Vargas (1945) in his distribution list for *S. quadrivittatum* is presumably based on Ortiz (1944). However, Ramirez Perez (1983) believes that a member of the *S. amazonicum* group (subgenus *Psaroniocompsa*) and not *S. quadrivittatum* was involved.

Biology. *Simulium quadrivittatum* is highly anthropophilic in Ecuador (Shelley & Arzube, 1985) and Central America (Fox, 1953; Lewis & Garnham, 1960; Rubtsov & Garcia Avila, 1972; Petersen *et al.*, 1983), but also bites equines (Vargas, 1945). *Simulium quadrivittatum* is only of medical importance in Ecuador where it is a vector of human onchocerciasis (Shelley, 1988; Shelley & Arzube, 1985). In Panama it was a biting nuisance during the construction of a dam in Chiriqui Province (Petersen *et al.*, 1983), and has been shown to be a suitable experimental host to

Guatemalan *O. volvulus* (Schiller *et al.*, 1984), although human onchocerciasis has not been recorded from Panama. It breeds in slow-flowing streams and shows population peaks in the wet season (Lewis & Garnham, 1960; Petersen *et al.*, 1983; Rubtsov & Garcia Avila, 1972; Shelley & Arzube, 1985).

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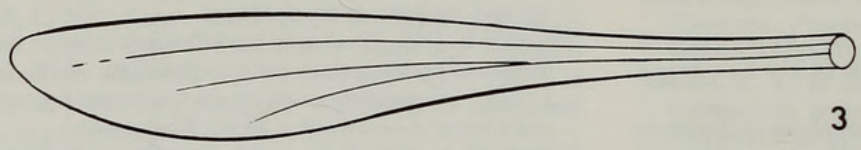
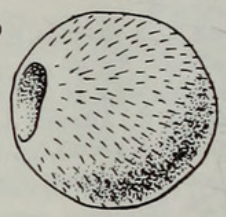
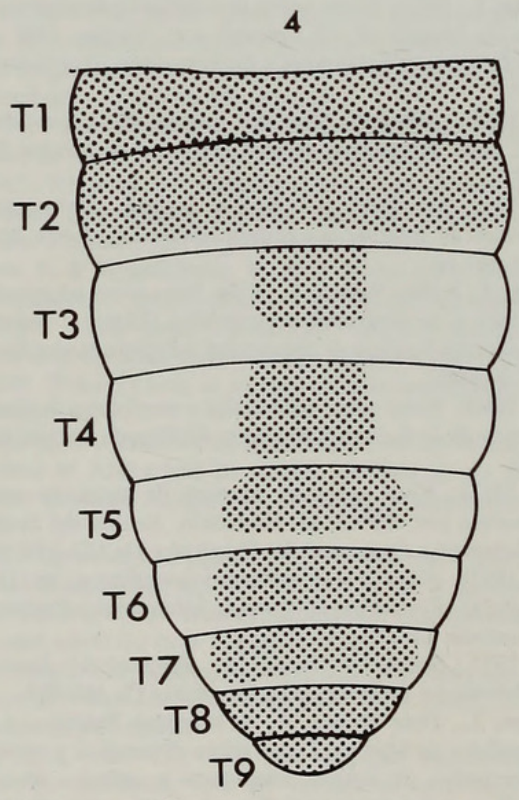
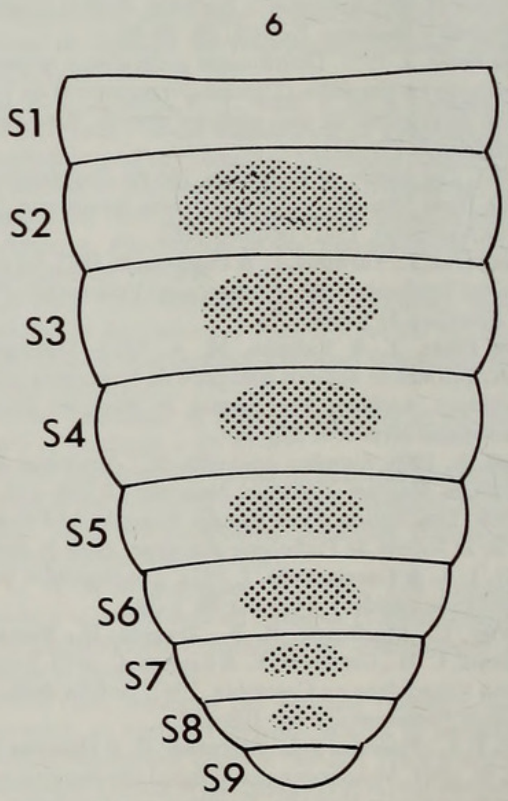
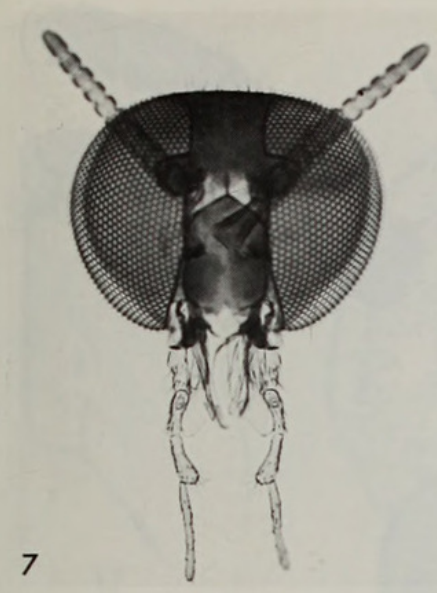


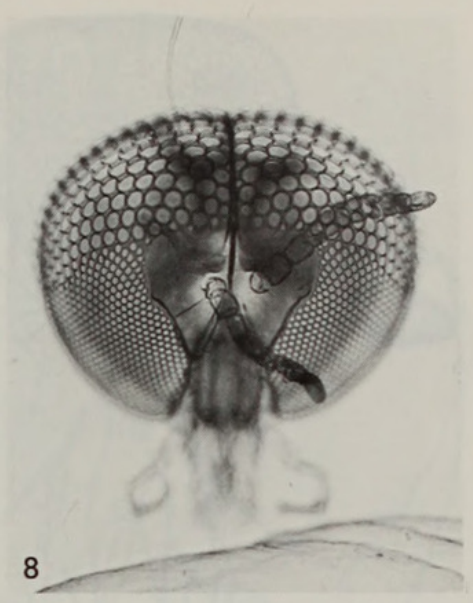


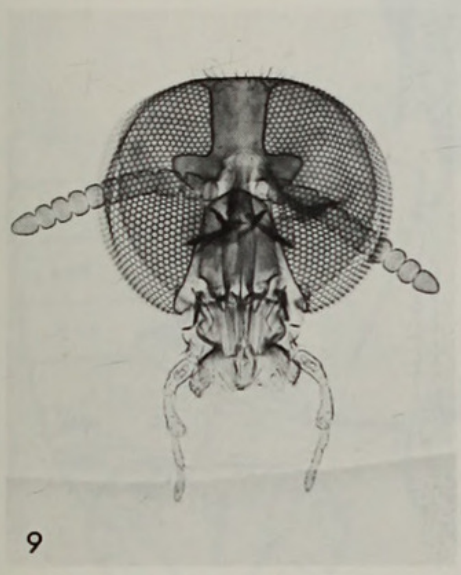


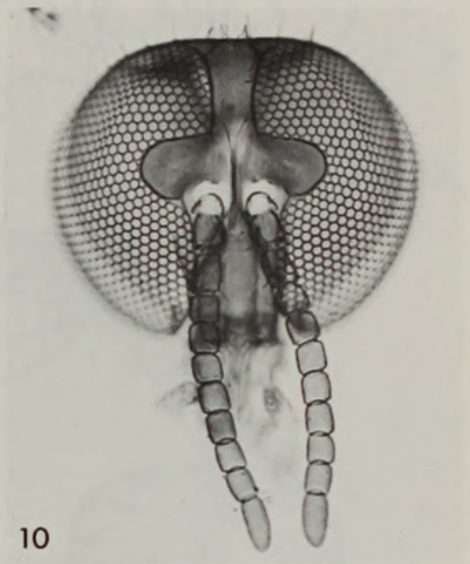


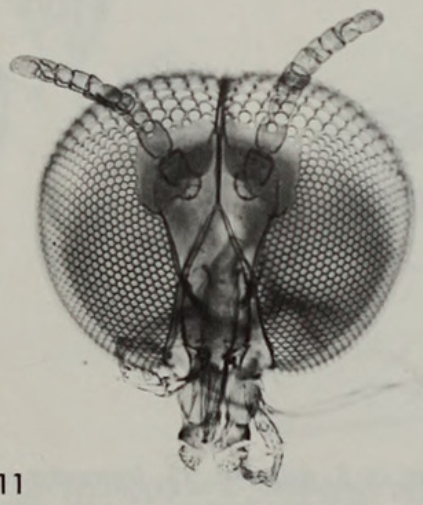
Figs 3–6 3, scale of leg of female *S. exiguum*. 4, dorsal view of female abdomen of *Simulium* showing position of tergal plates (shaded). 5, spermatheca of female *S. exiguum*. 6, ventral view of male abdomen of *Simulium* showing position of sternal plates (shaded).



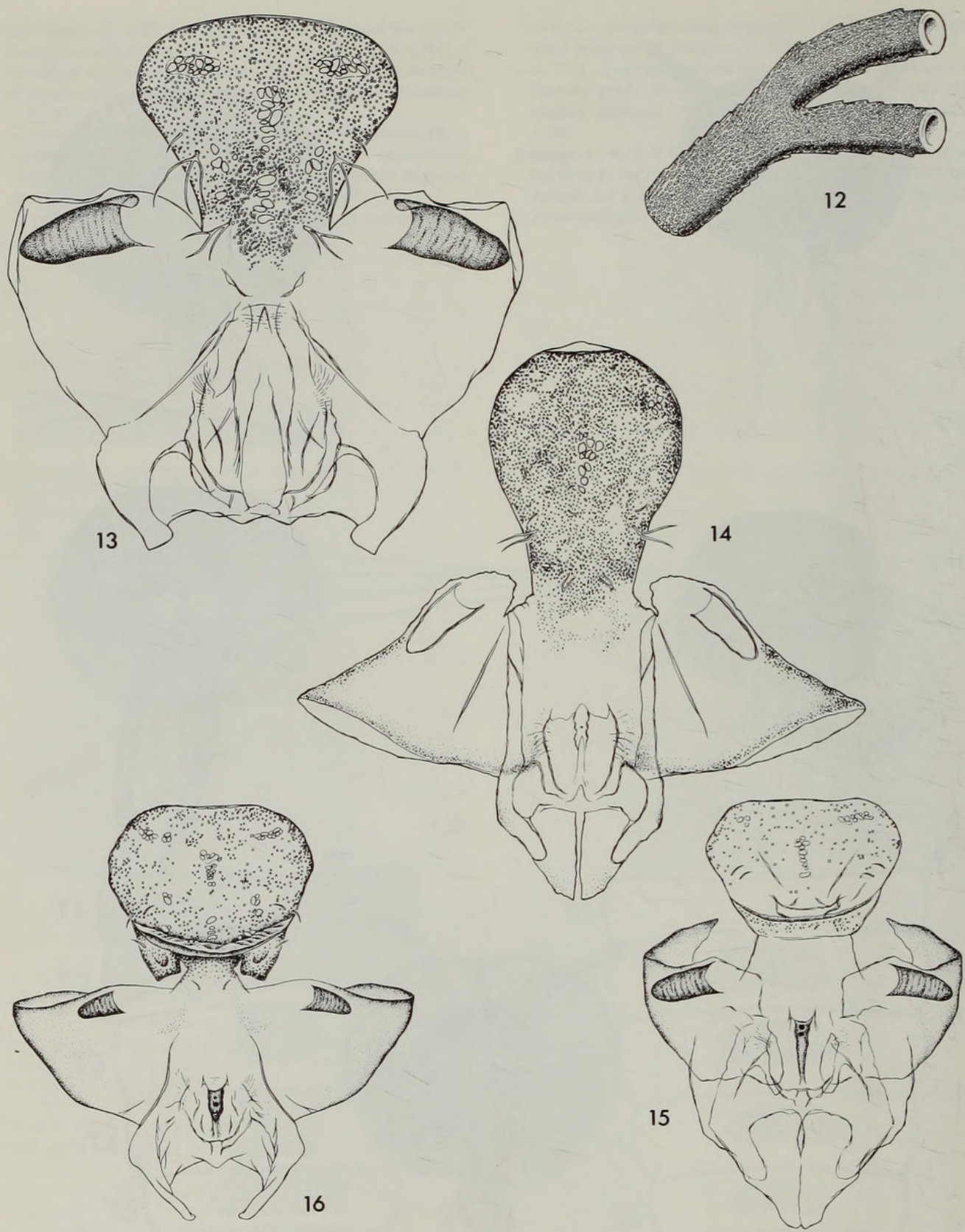








Figs 7–11 Anterior view of head of: (7) dichoptic female *S. exiguum*; (8) holoptic male *S. exiguum*; (9) dichoptic female *S. gonzalezi*; (10) dichoptic male *S. gonzalezi*; (11) holoptic male *S. gonzalezi*.



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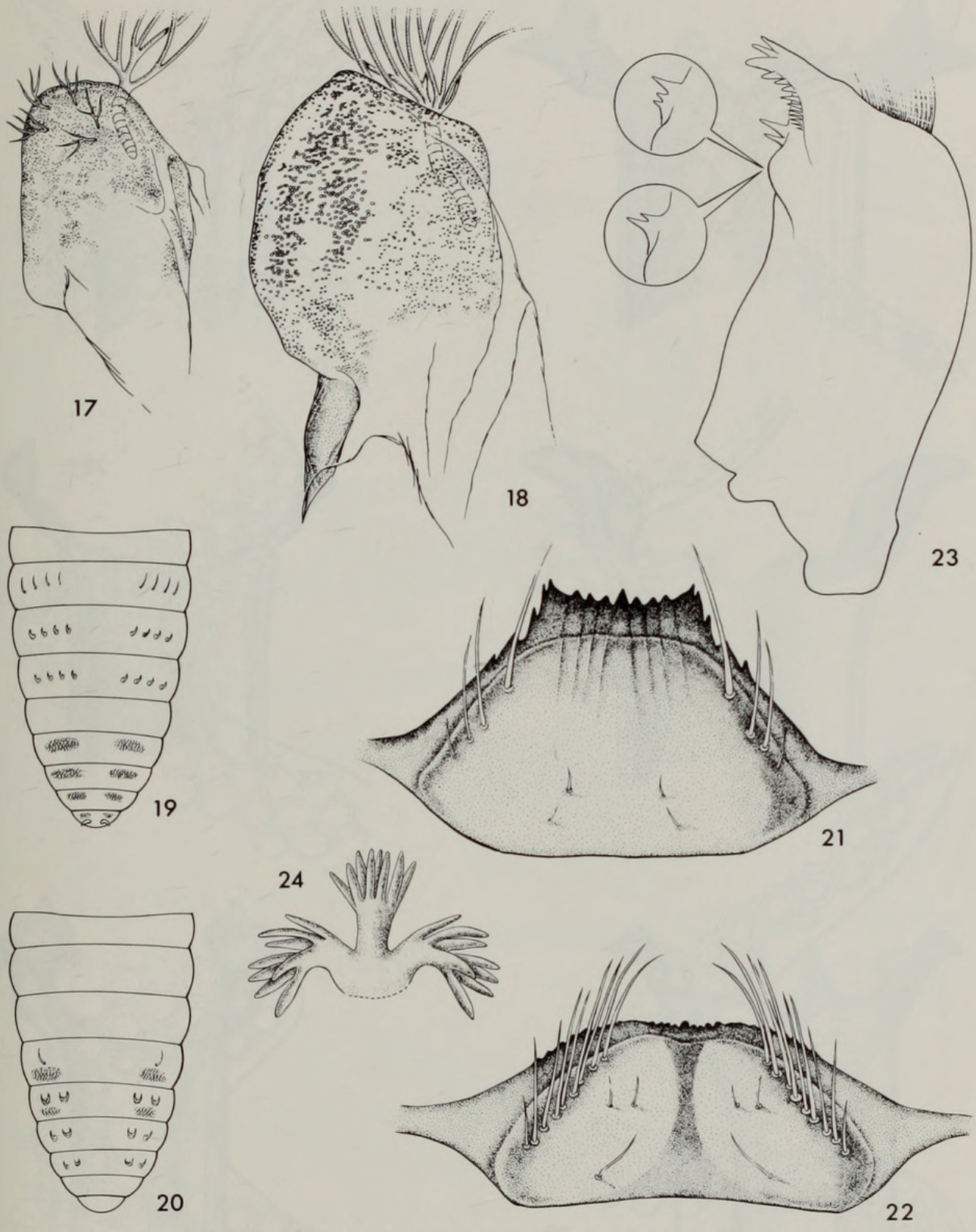

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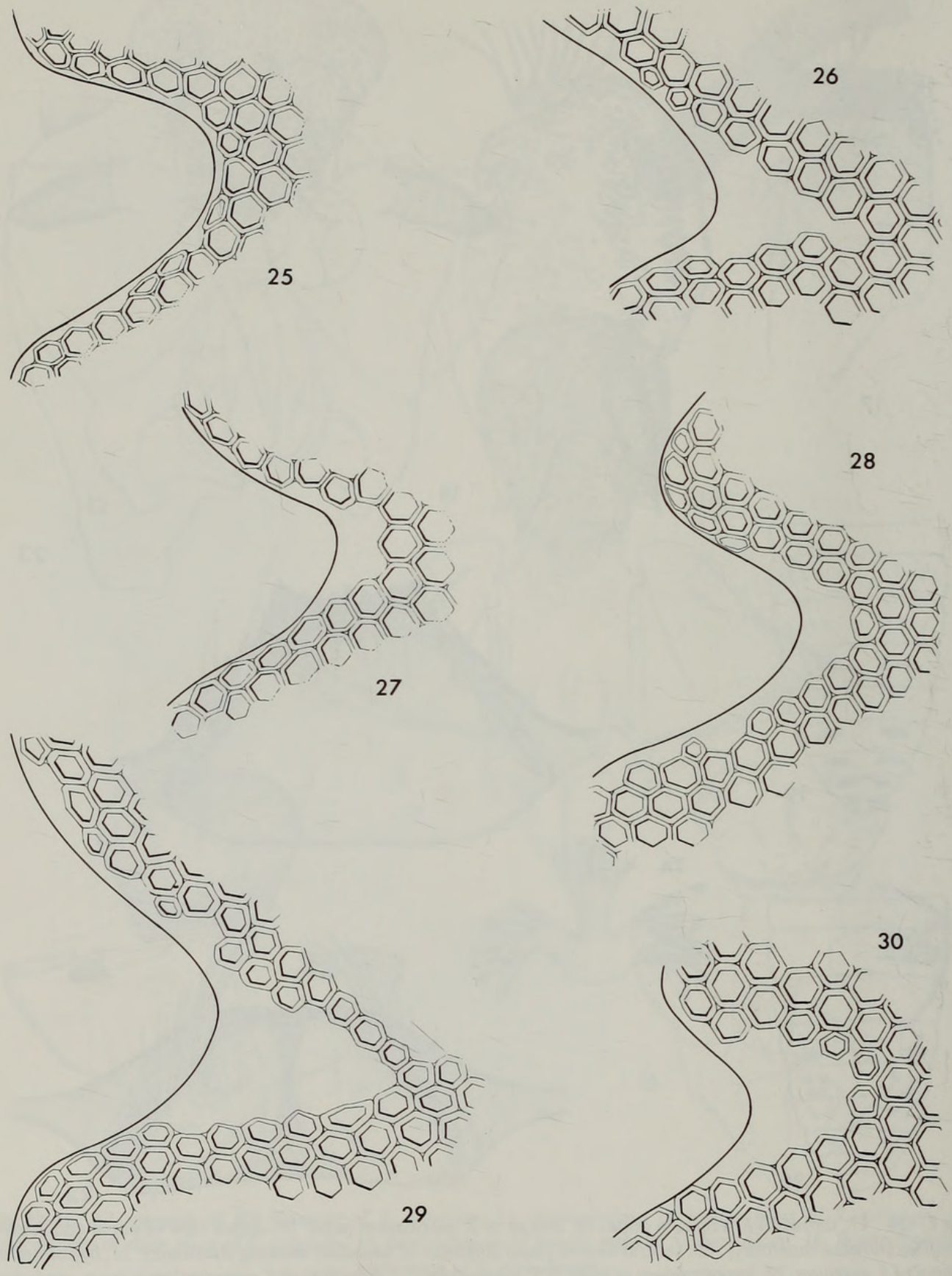

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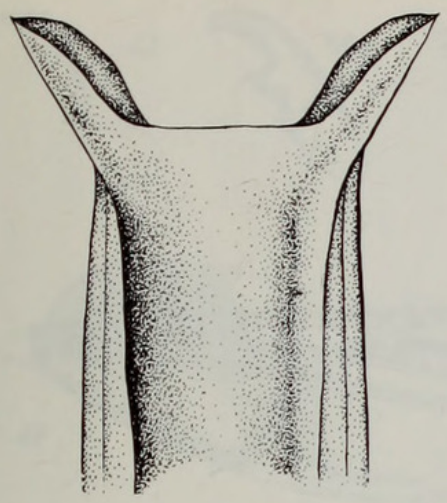

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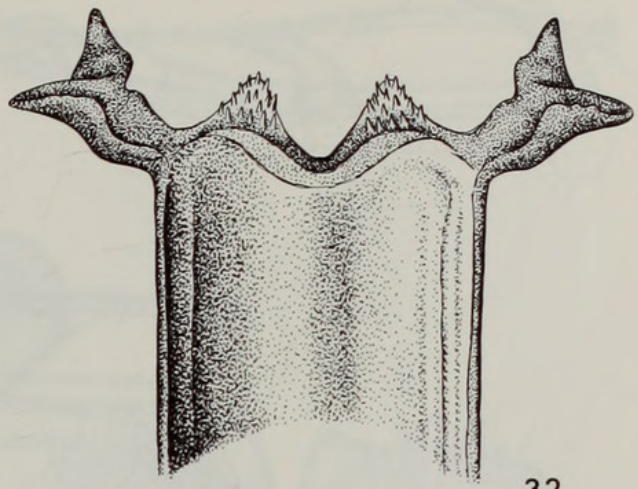

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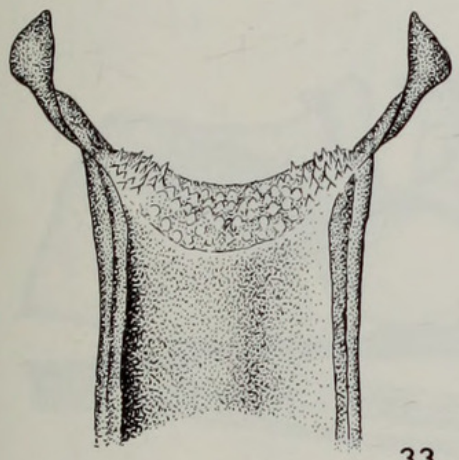

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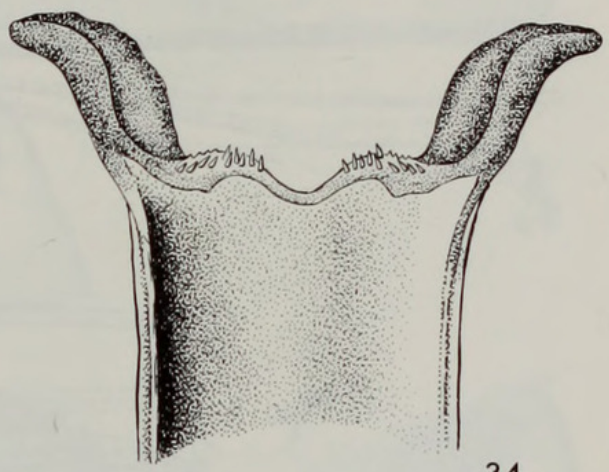

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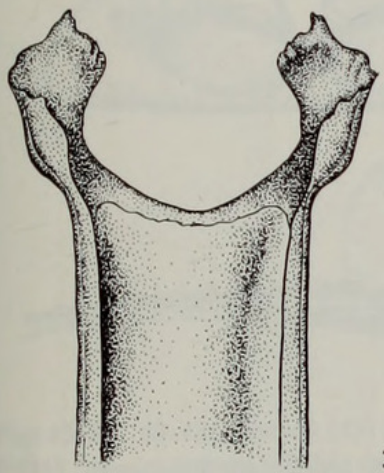

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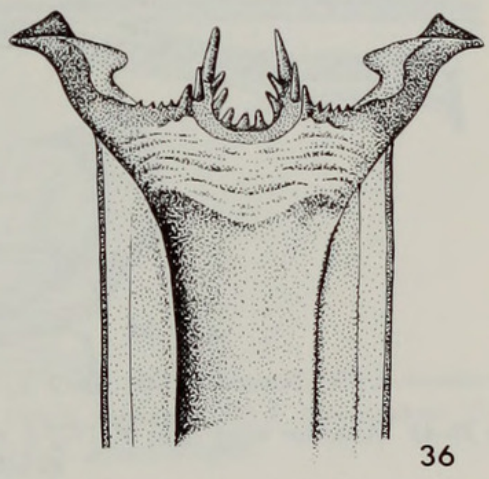

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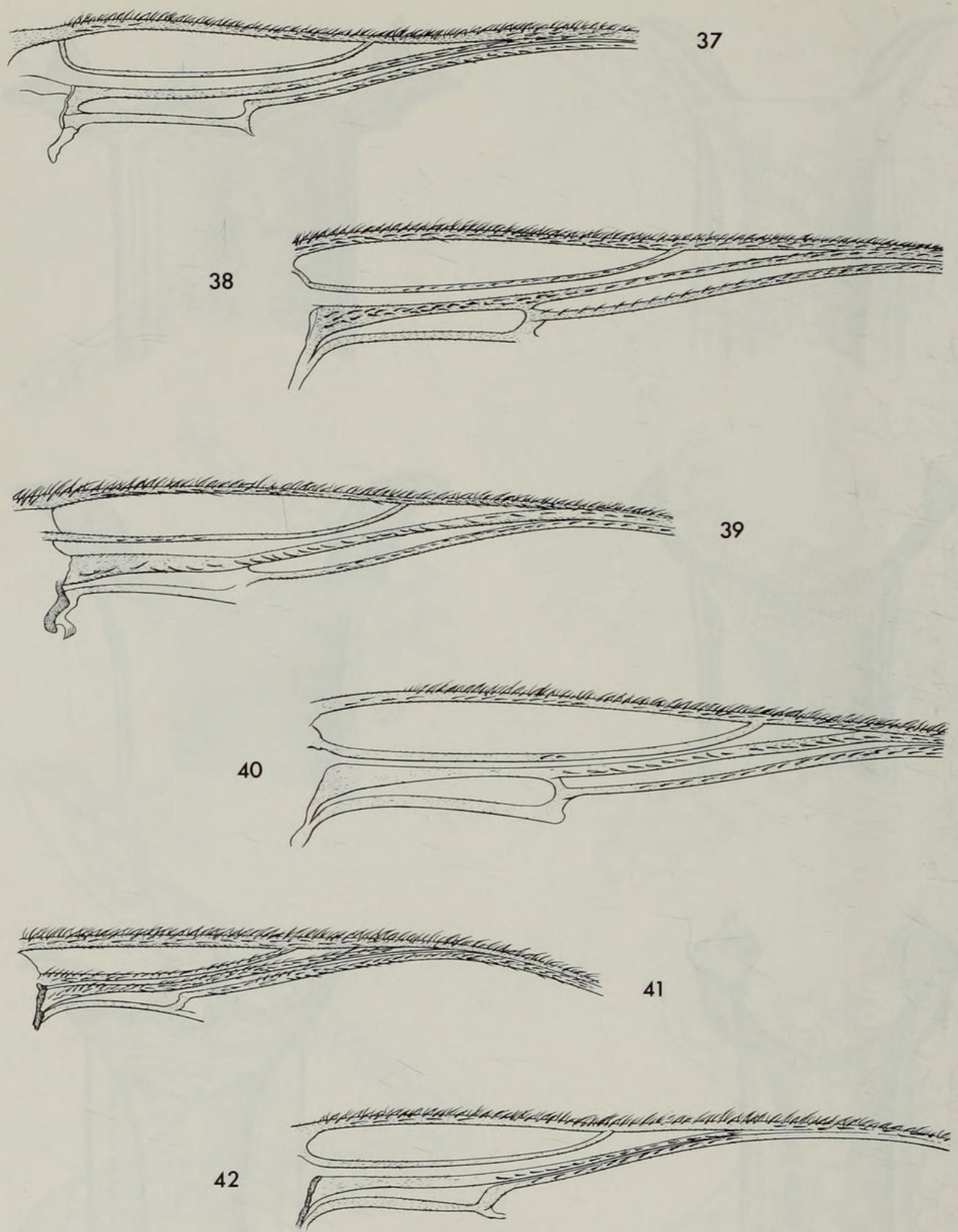

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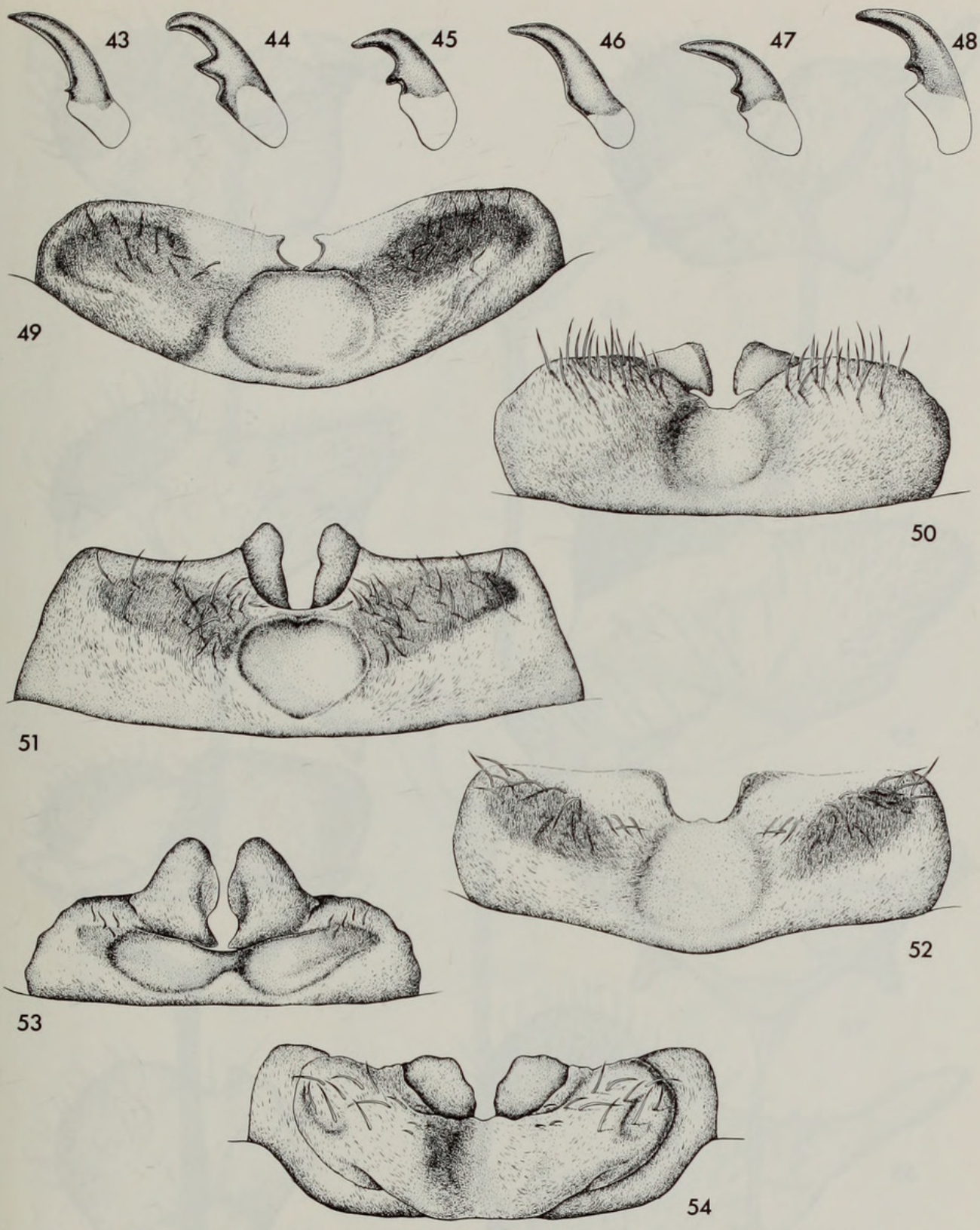

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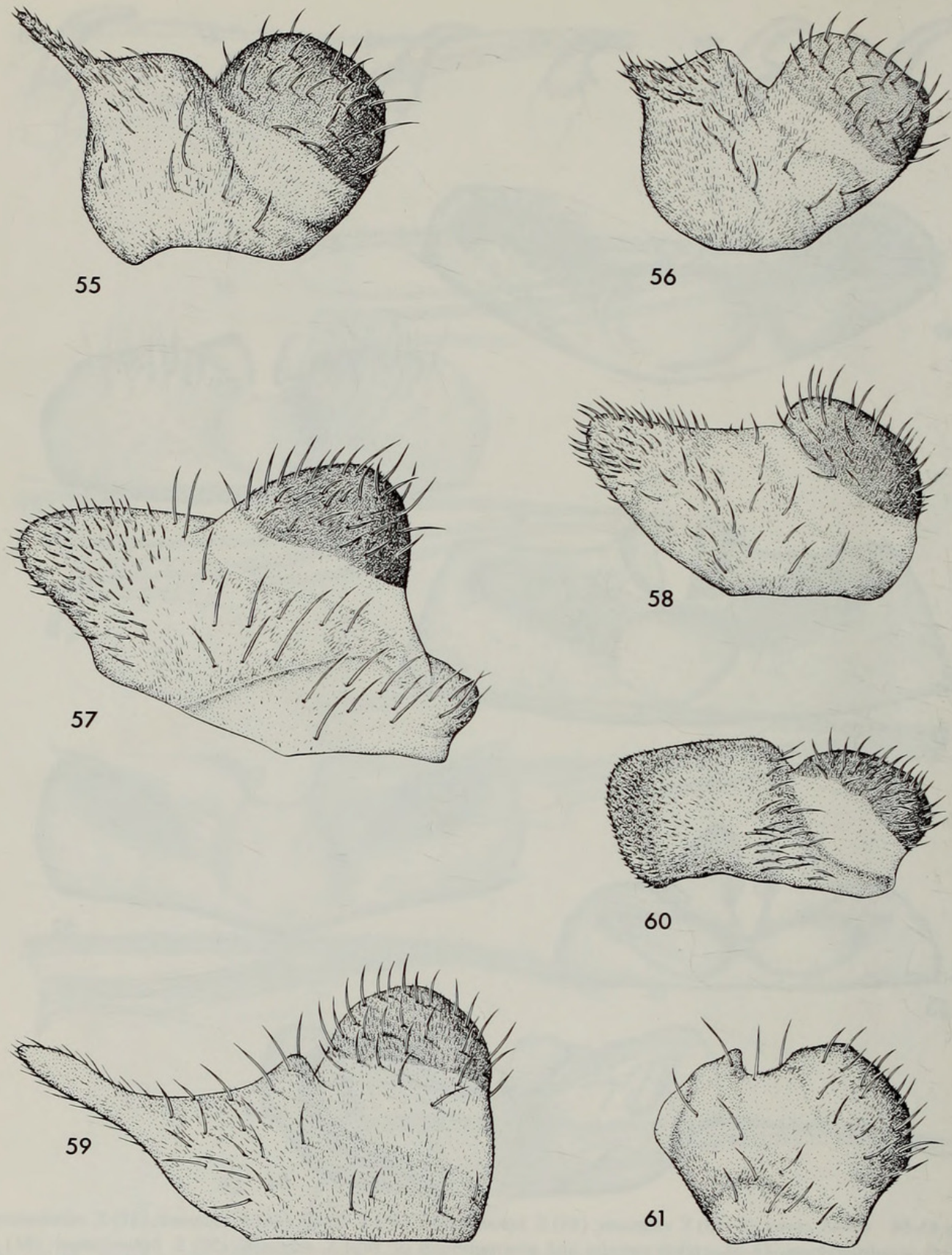

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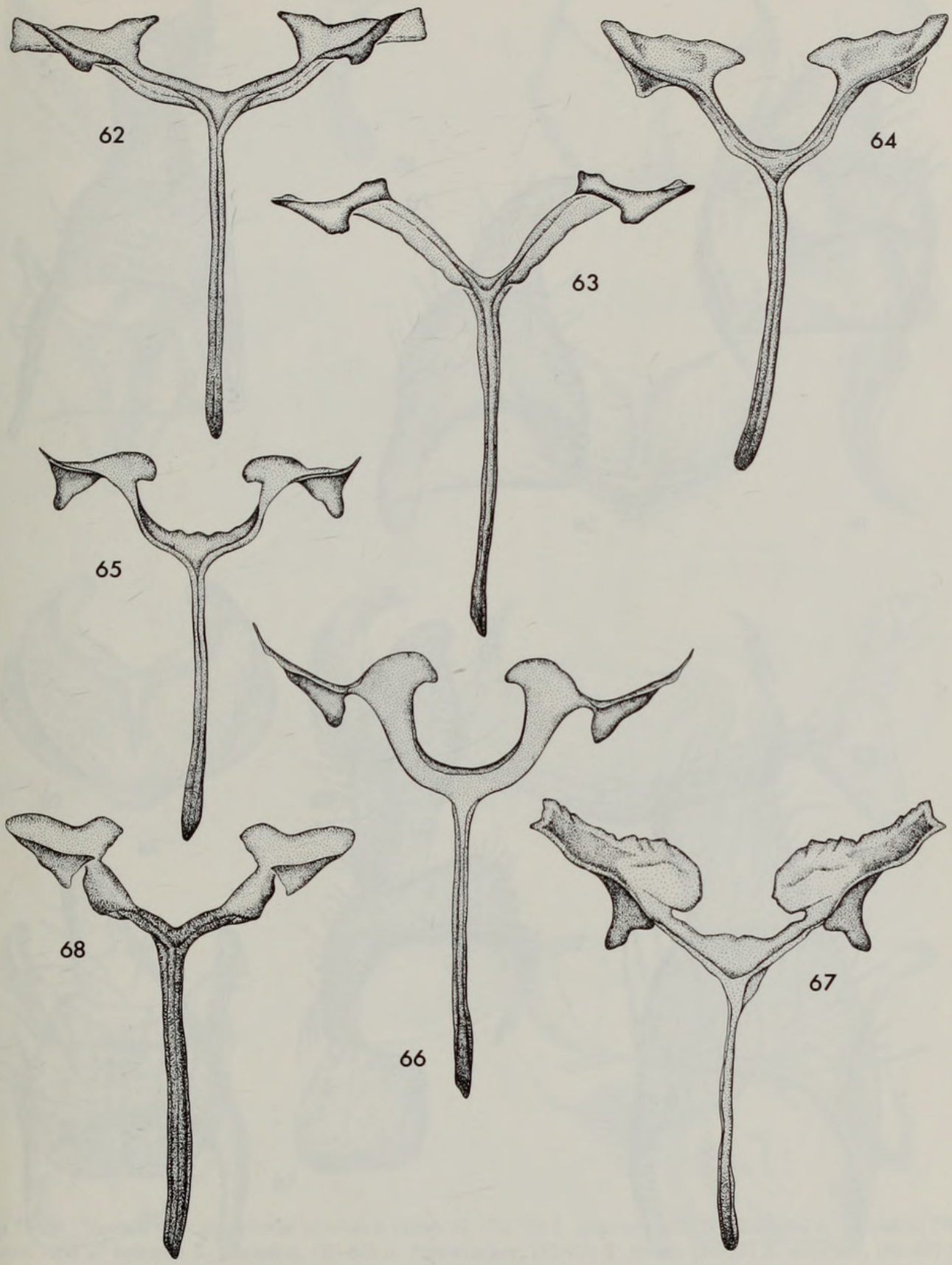

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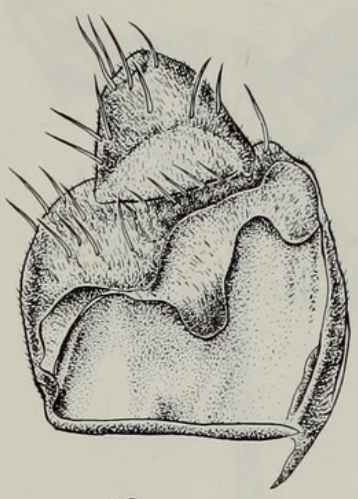

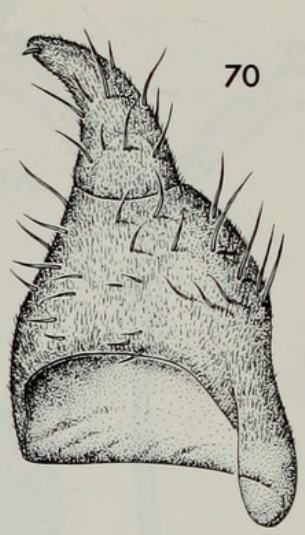

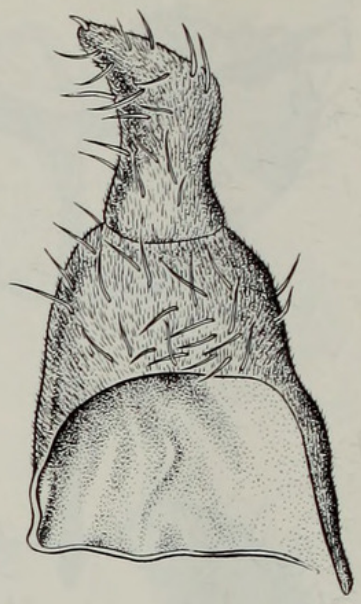

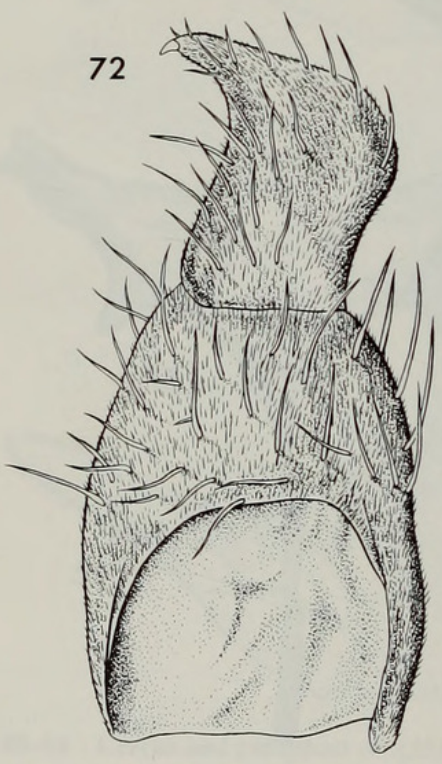

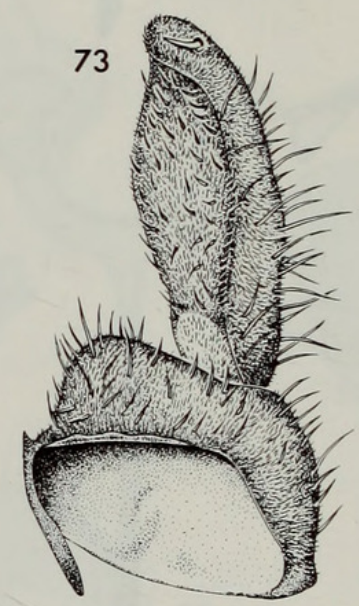

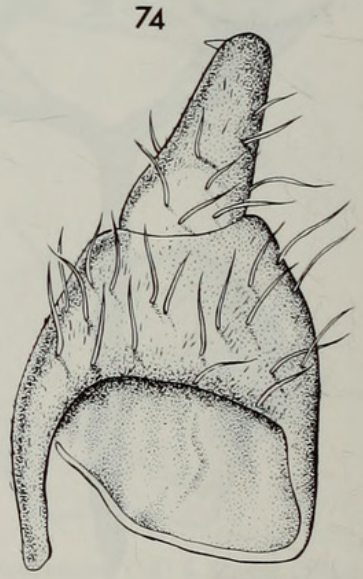

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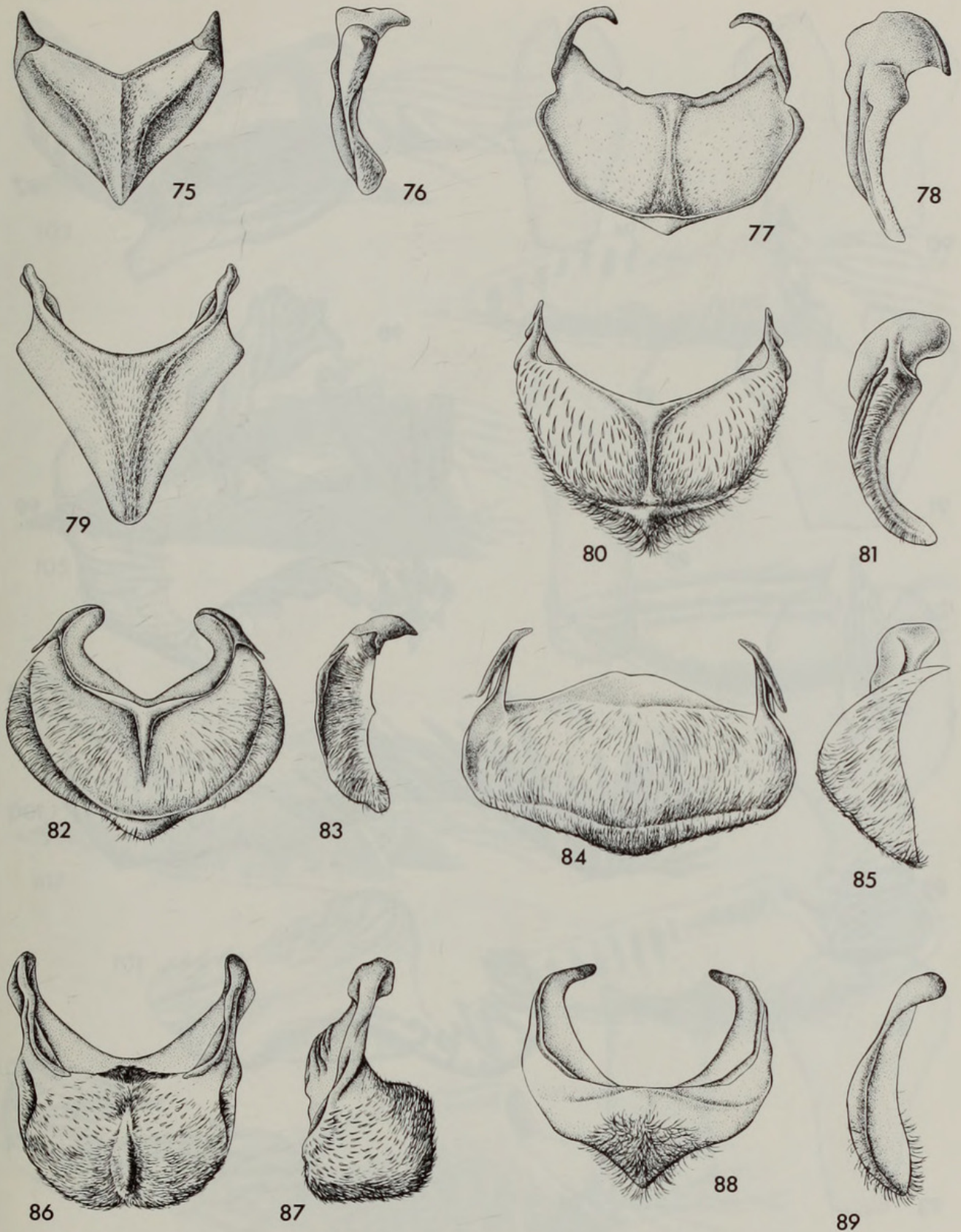

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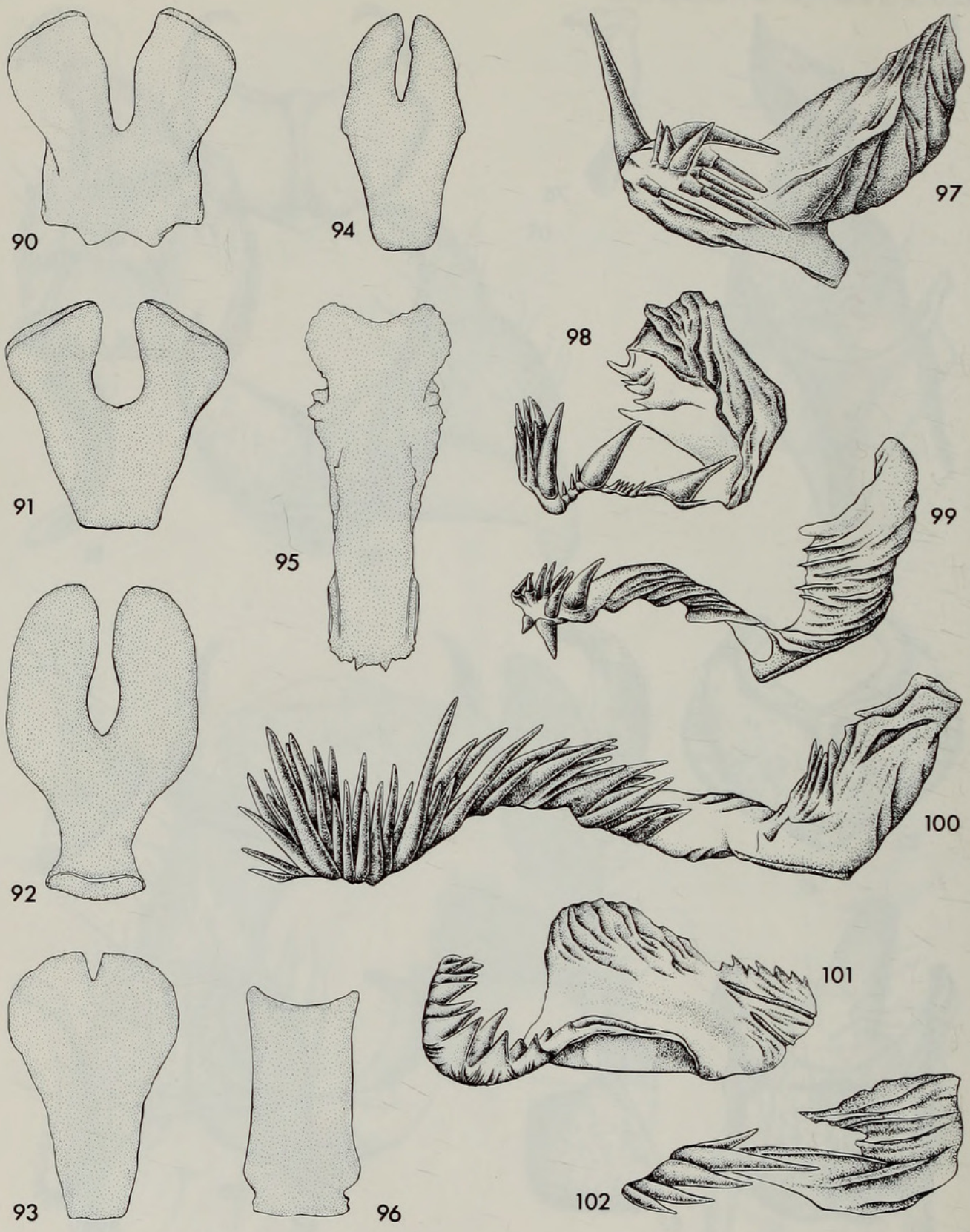

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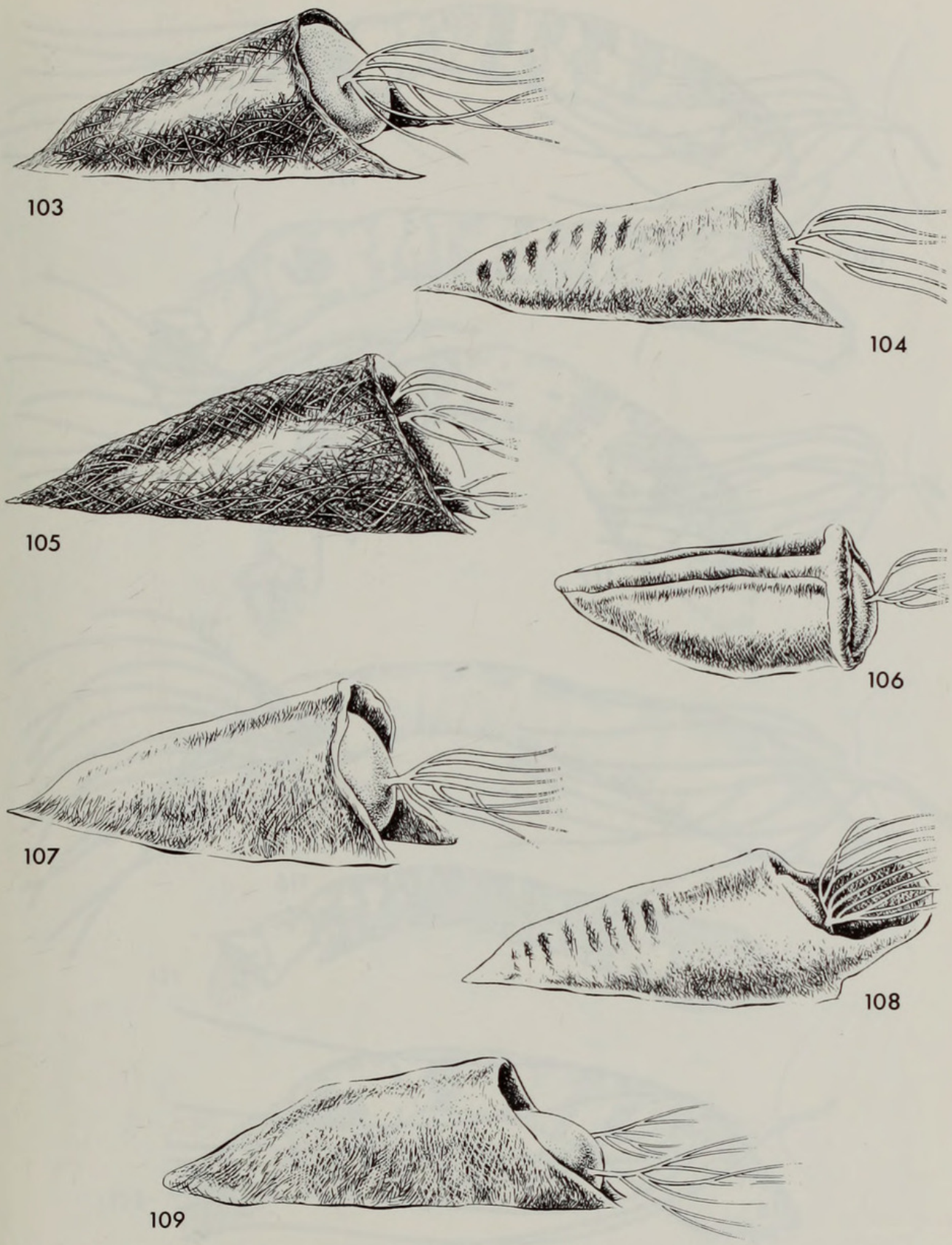

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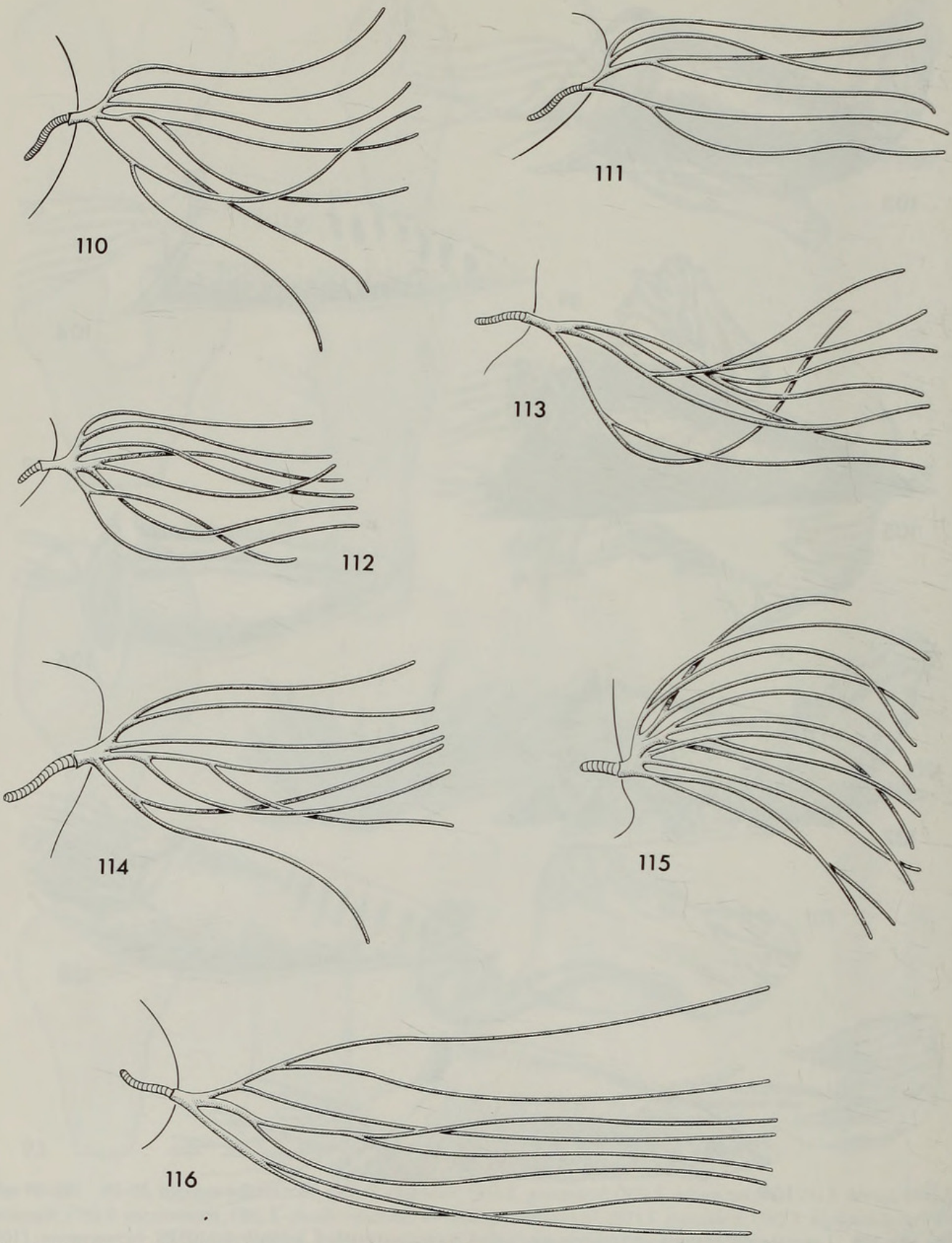

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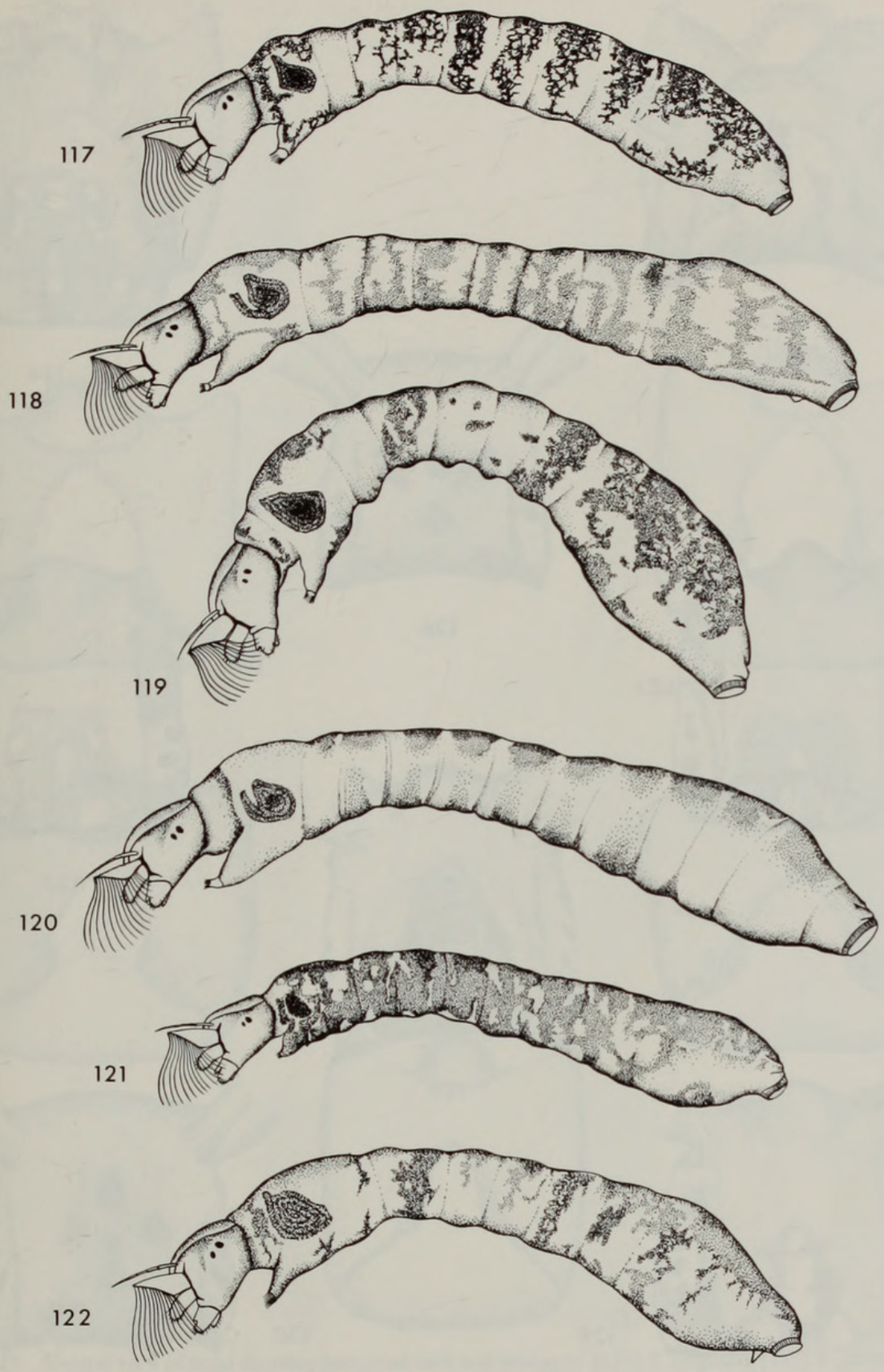

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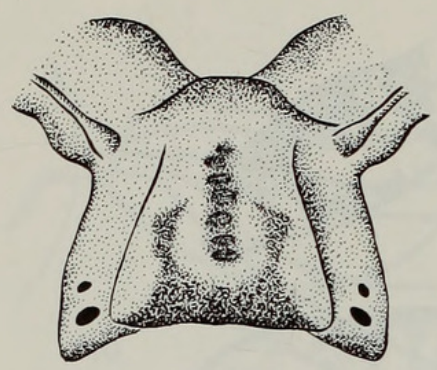

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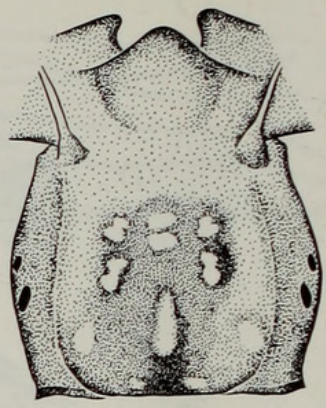

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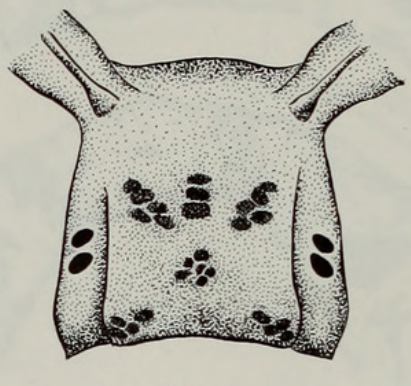

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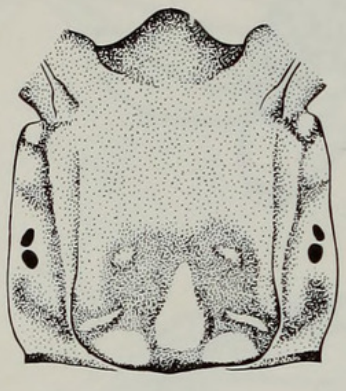

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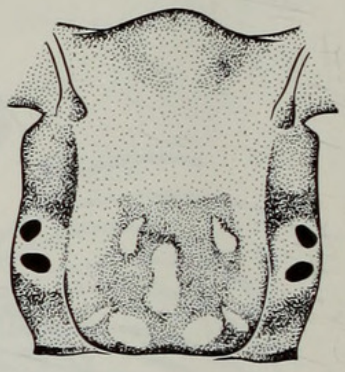

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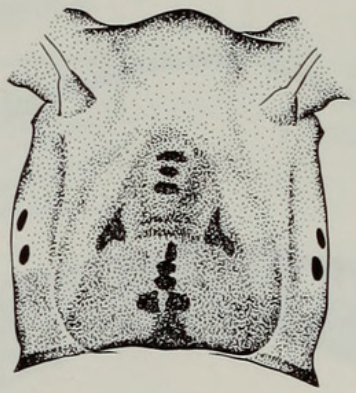

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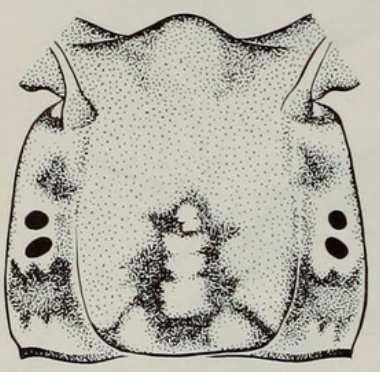

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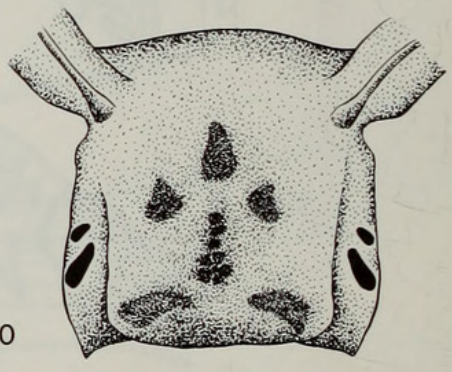

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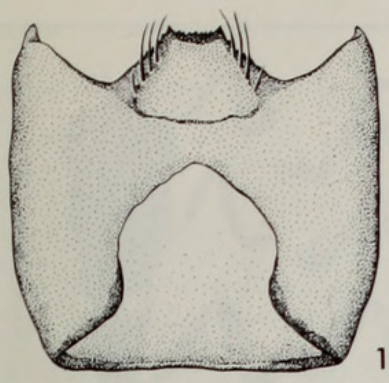
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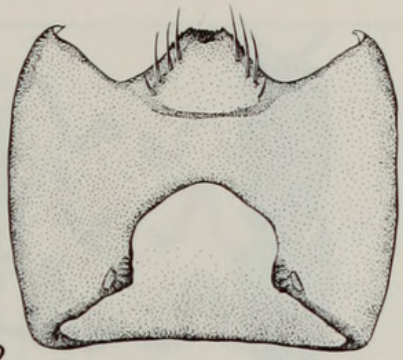
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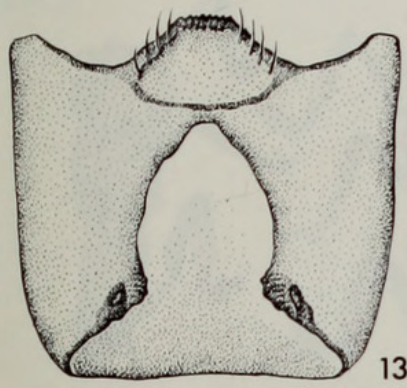
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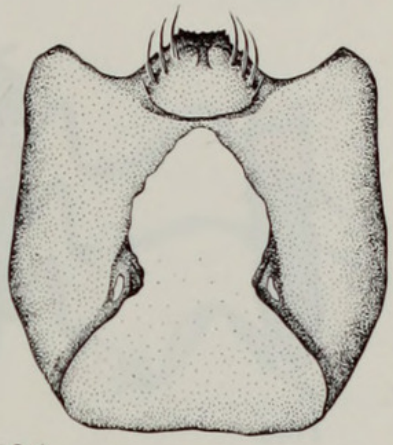
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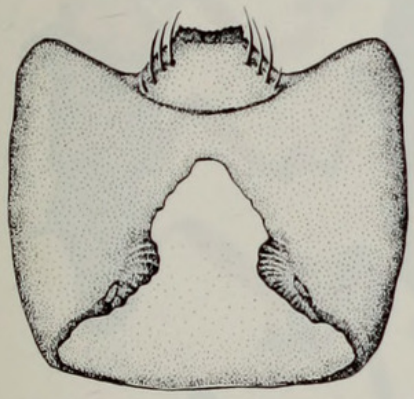
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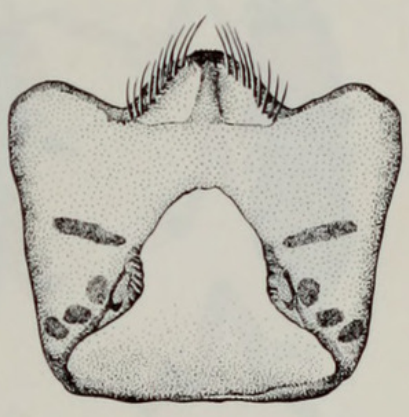
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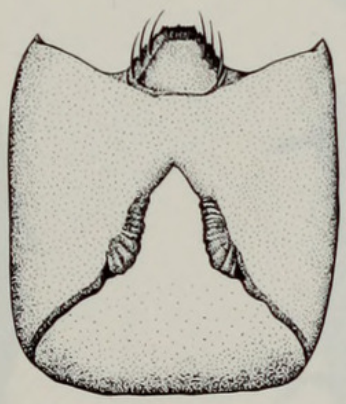
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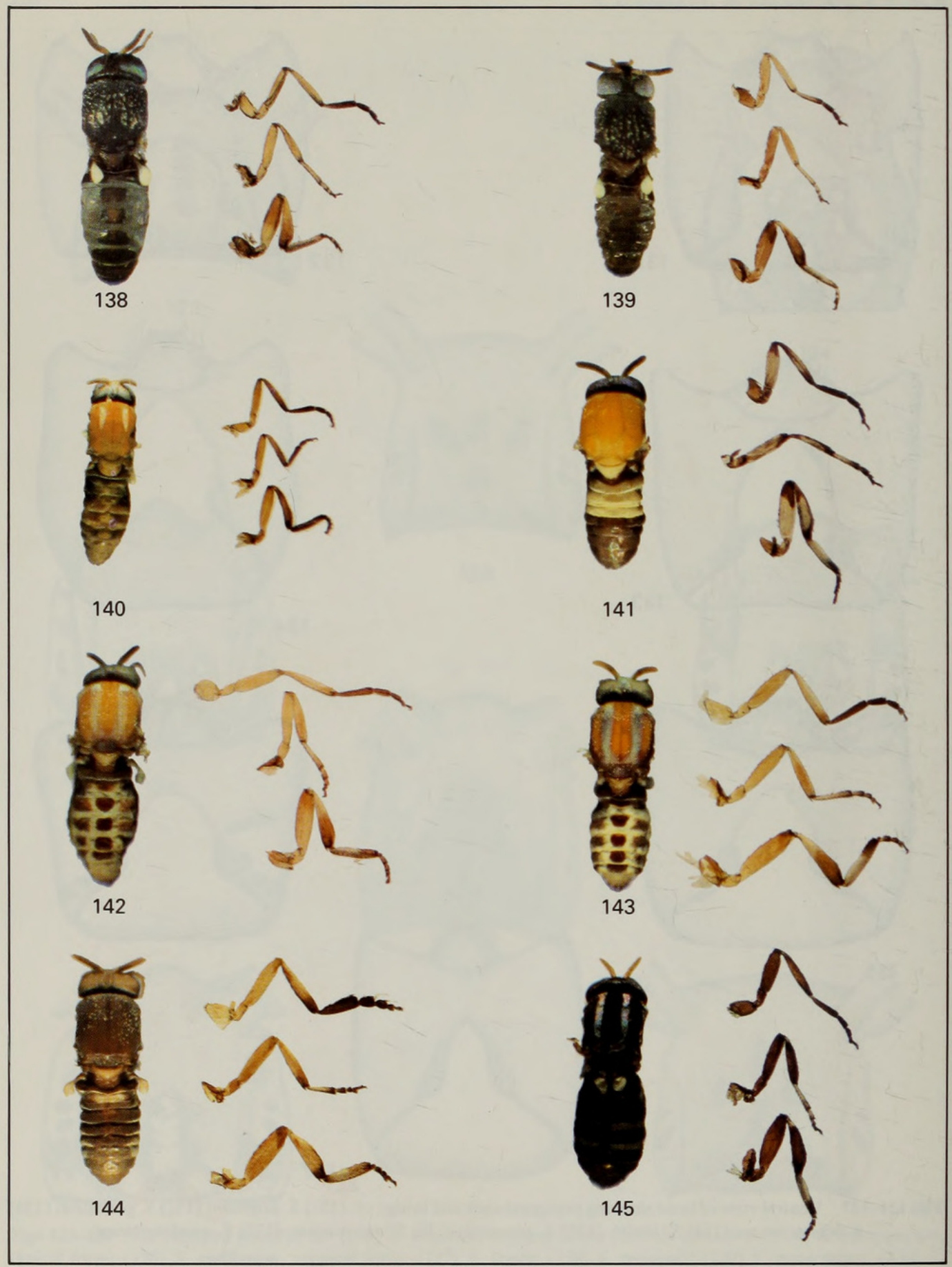

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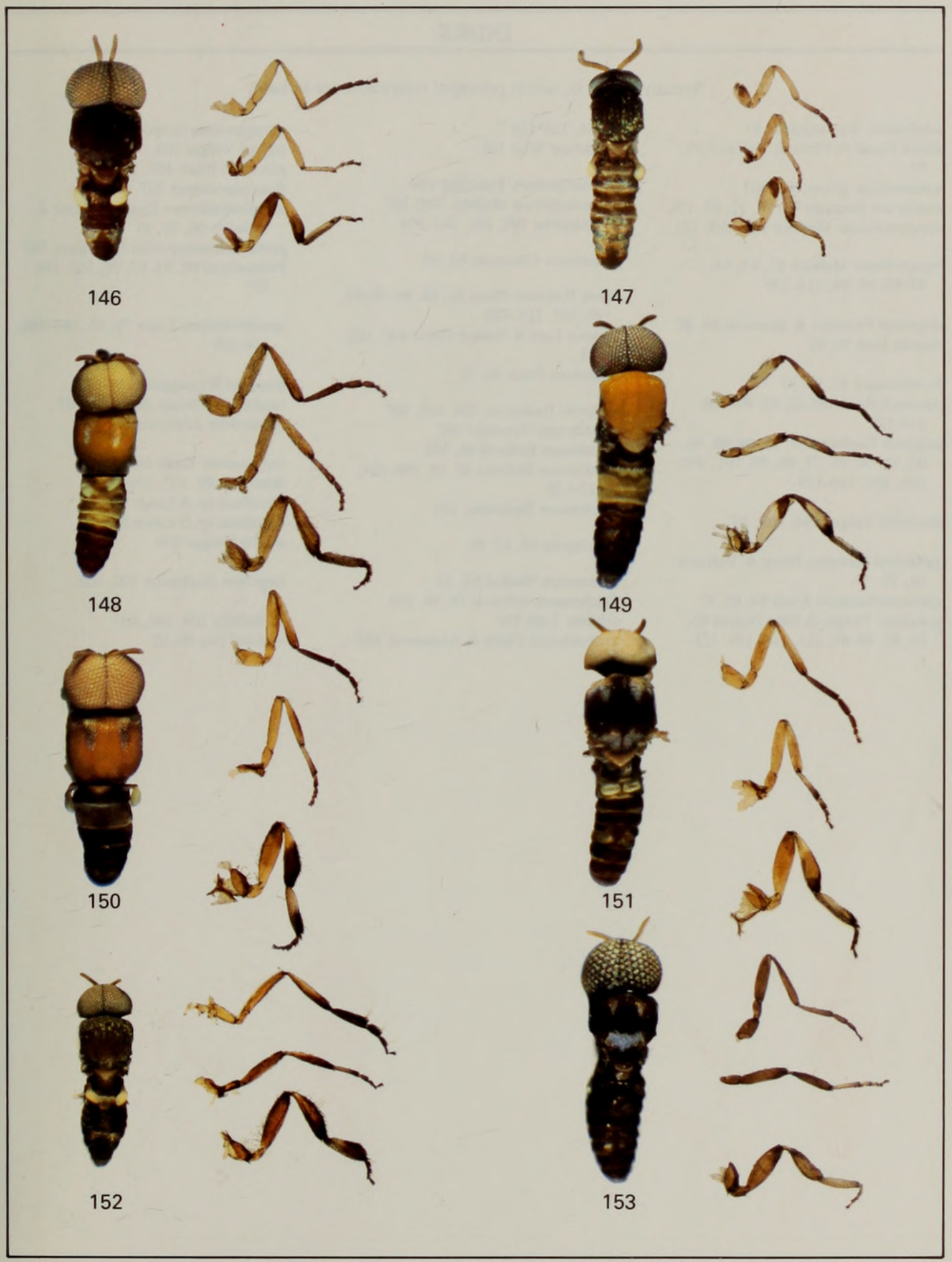

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Shelley, A J, Arzube, M., and Couch, C A. 1989. "The Simuliidae (Diptera) of the Santiago onchocerciasis focus of Ecuador." *Bulletin of the British Museum (Natural History) Entomology* 58, 79–130.

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