



RESEARCH ARTICLE

Revision of the *Simulium (Simulium) multistriatum* species-group (Diptera: Simuliidae) in Sumatra, Indonesia: Descriptions of three new species and a redescription of the male and pupa of *S. (S.) fenestratum* Edwards

Takaoka, H.^{1*}

¹Higher Institution Centre of Excellence (HiCoE), Tropical Infectious Diseases Research and Education Centre (TIDREC), Universiti Malaya, 50603, Kuala Lumpur, Malaysia

*Corresponding author: takaoka@oita-u.ac.jp

ARTICLE HISTORY

Received: 14 September 2025

Revised: 8 December 2025

Accepted: 10 December 2025

Published: 31 March 2026

The ZooBank registration of this article is [lsid:zoobank.org:pub:2ED826CC-1308-4703-A515-EC45423EC344](https://zoobank.org/pub:2ED826CC-1308-4703-A515-EC45423EC344)

ABSTRACT

Adults and pupae of black flies assigned to the *Simulium (Simulium) multistriatum* species-group collected from Sumatra, Indonesia in 1992 and 1994 were reexamined. As a result, three undescribed species were found besides *S. (S.) fenestratum* Edwards, the only species in this species-group so far described from Sumatra. These undescribed species are described as new: *S. (S.) mutaralamense* sp. nov., which is characterized in the female by the haired basal portion of the radial vein, in the male by the number of upper-eye (large) facets in 18 or 19 vertical columns and 19 or 20 horizontal rows and hind basitarsus entirely darkened, and in the pupa by the gill with eight filaments widely divergent when viewed laterally; *S. (S.) lubuksulasihense* sp. nov., which is similar to *S. (S.) mutaralamense* sp. nov., but differs by the male hind basitarsus yellow on its basal one-third; and *S. (S.) liwaense* sp. nov., which is characterized in the male by the smaller number of upper-eye (large) facets in 14 or 15 vertical columns and 16 horizontal rows, and in the pupa by the gill with eight filaments moderately divergent when viewed laterally, and all three anterodorsal trichomes unbranched on each side of the thorax. Taxonomic notes to distinguish these new species from their related species are given. The male and pupa of *S. (S.) fenestratum* are redescribed.

Keywords: *Simulium*; biodiversity; fauna; taxonomy; pests.

INTRODUCTION

The fauna of black flies (Diptera: Simuliidae) in the Oriental Region is represented by 677 named species, of which 570 species are endemic species with their distributions limited to one country (type country), 62 species are semi-endemic species with their distributions including their neighboring countries, and 45 species are widely distributed beyond their neighboring countries (Adler, 2025; Takaoka, 2024). These widely distributed species include medically and veterinarily important species, such as *Simulium (Simulium) nodosum* Puri, *S. (S.) nigrogilvum* Summers and *S. (Gomphostilbia) asakoeae* Takaoka & Davies, of which the first species is a vector of *Onchocerca* sp., the last species is a vector of an unnamed filaria species, and the second species is a vector of both kinds of filariae, in Thailand (Aupalee *et al.*, 2020; Fukuda *et al.*, 2003; Takaoka *et al.*, 2003). To accurately identify vector species in countries other than the type country, it is prerequisite to investigate whether the putative species is a single species or multiple species. Among such widely distributed species, *S. (S.) nodosum* and *S. (S.) rufibasis* Brunetti, both originally described from India (Brunetti, 1911; Puri, 1933), were recently revised morphologically, molecularly and chromosomally. *Simulium (S.) nodosum* was found

to be a single species widely distributed from India to Taiwan through Myanmar, Thailand and Vietnam, thus a generalist (Low *et al.*, 2015). *Simulium (S.) rufibasis*, once thought to be a generalist distributed in Nepal, Pakistan, Myanmar, China, Vietnam, Taiwan, Korea and Japan, besides India, was discovered to be multiple species, and species once regarded as *S. (S.) rufibasis* were newly described as *S. (S.) langtangense* Takaoka & Shrestha from Nepal (Takaoka *et al.*, 2020), *S. (S.) tenebrosum* Takaoka Srisuka & Saeung from Thailand (Takaoka *et al.*, 2019), *S. (S.) fuscicoxae* Takaoka & Ya'cob from Vietnam (Takaoka *et al.*, 2017), *S. (S.) hehuanense* Takaoka and *S. (S.) xiulinense* Takaoka, from Taiwan (Takaoka *et al.*, 2021), and *S. (S.) yamatoense* Takaoka, Adler & Fukuda from Korea and Japan (Adler *et al.*, 2019). In addition, the species regarded as *S. (S.) rufibasis* in China was suggested to be different from true *S. (S.) rufibasis* because the pupae in China have no terminal hooks (Takaoka, 2024). These recent reviews show the importance of reexamination of widely distributed black flies.

The aim of the current study was to revise *S. (S.) fenestratum* Edwards, a widely distributed putative species, based on adult and pupal specimens collected from Sumatra, Indonesia (type locality of this species), because its female and male were insufficiently described from adults dissected from pupae, although some

important characteristics were shown, in particular the haired basal portion of the female radial vein, male genitalia (ventral view), and eight pupal gill filaments moderately divergent at an angle of about 90 degrees when viewed laterally (Edwards, 1934). This species was later recorded from Japan (Ogata, 1966), Thailand (Takaoka & Saito, 1996) and Laos (Adler & Crosskey, 2017), though the species regarded as *S. (S.) fenestratum* from Japan was described as a new species, *S. (S.) sakishimaense* Takaoka (Takaoka, 1977). The male and pupa of *S. (S.) fenestratum* are here redescribed to be of use in future studies of the species regarded as *S. (S.) fenestratum* from Thailand and Laos. During this study, three undescribed species, which are similar to but different from *S. (S.) fenestratum*, were found in Sumatra. These three undescribed species are described as new.

The biting habits of *S. (S.) fenestratum* and other species of the *S. multistriatum* species-group have not been investigated.

MATERIAL AND METHODS

Adult black flies reared from pupae, together with their pupal exuviae and cocoons, all collected from Sumatra, Indonesia, in 1992 and 1994, by the current author and fixed in 80% ethanol, were morphologically reexamined. The methods of observation under a dissecting microscope and a biological microscope, line-drawings and measurements were the same as those of Takaoka (2003), and terms of morphological features used in this study followed those of Takaoka (2003) and partially those of Adler *et al.* (2004). Colors of all adult specimens were based on specimens in ethanol.

All type specimens are deposited in the Department of Entomology, Queen Sirikit Botanic Garden, Chiang Mai, Thailand.

RESULTS AND DISCUSSION

The present reexamination of adults and their pupal exuviae and cocoons shows that there are four species in the *S. multistriatum* species-group, i.e., *S. (S.) fenestratum* and three new species. These three new species are described herein, and taxonomic notes to separate them from related species are given. The male and pupa of *S. (S.) fenestratum* are redescribed.

Simulium (Simulium) mutaralamense sp. nov.

lsid:zoobank.org:act:BE0F1CB2-42FF-4EDE-AADA-5EB5FD93C0E7

Female (n=8). Body length 2.8–3.0 mm. **Head.** Narrower than thorax. Frons black, shiny, with several dark long stout hairs along each lateral margin and four similar hairs just above lower margin; frontal ratio 1.3–1.4:1.0:1.6–1.7; frons:head ratio 1.0:4.7–5.0. Fronto-ocular area well developed, short, directed laterally and slightly upward. Clypeus black, white pruinose, slightly shiny when illuminated at certain angles, moderately covered with dark-brown long stout hairs along lateral and ventral margins but widely bare on middle portion. Labrum 0.66–0.71 times as long as clypeus. Antenna composed of scape, pedicel and nine flagellomeres, medium to dark brown except scape, pedicel, and base of first flagellomere yellow. Maxillary palpus with five segments, proportional lengths of third, fourth, and fifth segments 1.0:1.1:2.4–2.5; third segment (Figure 1A) somewhat widened apically; sensory vesicle (Figure 1A) small (0.25–0.28 times length of third segment) having moderate or large opening near apex. Maxillary lacinia with 12–14 inner and 13 or 14 outer teeth. Mandible with 24 or 25 inner and 13 outer teeth. Cibarium (Figure 1B) with blunt medial projection on posterior margin and without any minute processes near base of medial projection. **Thorax.** Scutum black, shiny when illuminated at certain angles, densely covered with yellow recumbent short

hairs interspersed with several dark-brown long upright hairs on prescutellar area; when illuminated in front and viewed dorsally, scutum white pruinose, with five longitudinal nonpruinose vittae (one narrow medial vitta, two wider submedial vittae and two wider sublateral vittae though sublateral vittae somewhat wider than submedial ones), all vittae united with broad transverse band on prescutellar area; when illuminated from behind, scutum having reversed color pattern. Scutellum brownish black, covered with dark brown upright long hairs and yellow short hairs. Postnotum black, white pruinose when illuminated at certain angles and bare. Pleural membrane bare. Katepisternum longer than deep, black, shiny and white pruinose when illuminated at certain angles and bare. **Legs.** Foreleg: coxa and trochanter yellow; femur light to medium brown except inner surface of base yellow; tibia white except apical cap brownish black, with shiny sheen widely on outer surface when illuminated at certain angles; tarsus brownish black, with moderate dorsal hair crest; basitarsus greatly dilated, 4.8–4.9 times as long as its greatest width. Midleg: coxa brownish black; trochanter medium brown; femur medium to dark brown; tibia white except apical cap dark brown, and with shiny sheen on posterior surface when illuminated at certain angles; tarsus medium to dark brown except basal one-third to half whitish though its border not well defined. Hind leg: coxa brownish black; trochanter yellow; femur dark brown to brownish-black except base yellow; tibia white except apical one-third dark brown, and with shiny sheen on posterior surface when illuminated at certain angles; tarsus dark brown except basal two-thirds of basitarsus and basal one-third of second tarsomere whitish; basitarsus (Figure 1C) nearly parallel-sided, 5.7–5.9 times as long as wide, and 0.72–0.76 and 0.58–0.63 times as wide as greatest widths of hind tibia and femur, respectively; calcipala (Figure 1C) moderately developed, slightly shorter than basal width, and 0.4 times as wide as basitarsus; pedisulcus (Figure 1C) well developed at basal one-third of second tarsomere; all tarsal claws simple. **Wing.** Length 2.4–2.5 mm. Costa with dark spinules and hairs; subcosta haired except near apex bare; basal section of radial vein haired on apical one-fourth to three-fourths; R₁ with dark spinules and hairs; R₂ with hairs; hair tuft on base of radial vein dark brown; basal cell absent. **Halder.** White with basal portion darkened. **Abdomen.** Basal scale medium brown, with fringe of dark-brown long hairs. Dorsal surface of abdomen brownish-black except basal half of second segment yellowish-white, with short dark hairs; tergite 2 shiny, white iridescent when illuminated at certain angles, and tergites 6–8 shiny. **Terminalia.** Sternite 8 (Figure 1D) bare medially, with 25–38 dark medium-long to long stout hairs on each lateral surface. Ovipositor valves (Figure 1D) triangular though rounded posteromedially, membranous, each moderately covered with microsetae and one dark medium-long hair, except portion along inner margin widely bare, so thin and transparent that it is difficult to discern inner margin. Genital fork (Figure 1E) of inverted-Y form, with narrow well sclerotized stem; arms of moderate width, each with distinct projection directed anterodorsally. Paraproct in ventral view (Figure 1F) nearly quadrate, densely covered with minute setae and with 23–30 short to medium-long hairs on lateral and ventral surfaces except anterolateral corner widely unpigmented and bare; anteromedial surface with four or five short sensilla; paraproct in lateral view (Figure 1G) 0.7 times as long as wide, moderately protruded ventrally beyond ventral margin of cercus. Cercus in lateral view (Figure 1G) short, rounded posteriorly, half as long as wide, and with numerous short to medium-long hairs. Spermatheca (Figure 1H) ellipsoidal, 1.6 times as long as wide, well sclerotized except portion of juncture with duct unsclerotized, with no defined surface patterns, and with internal setae; accessory ducts subequal in thickness to each other, and to major duct.

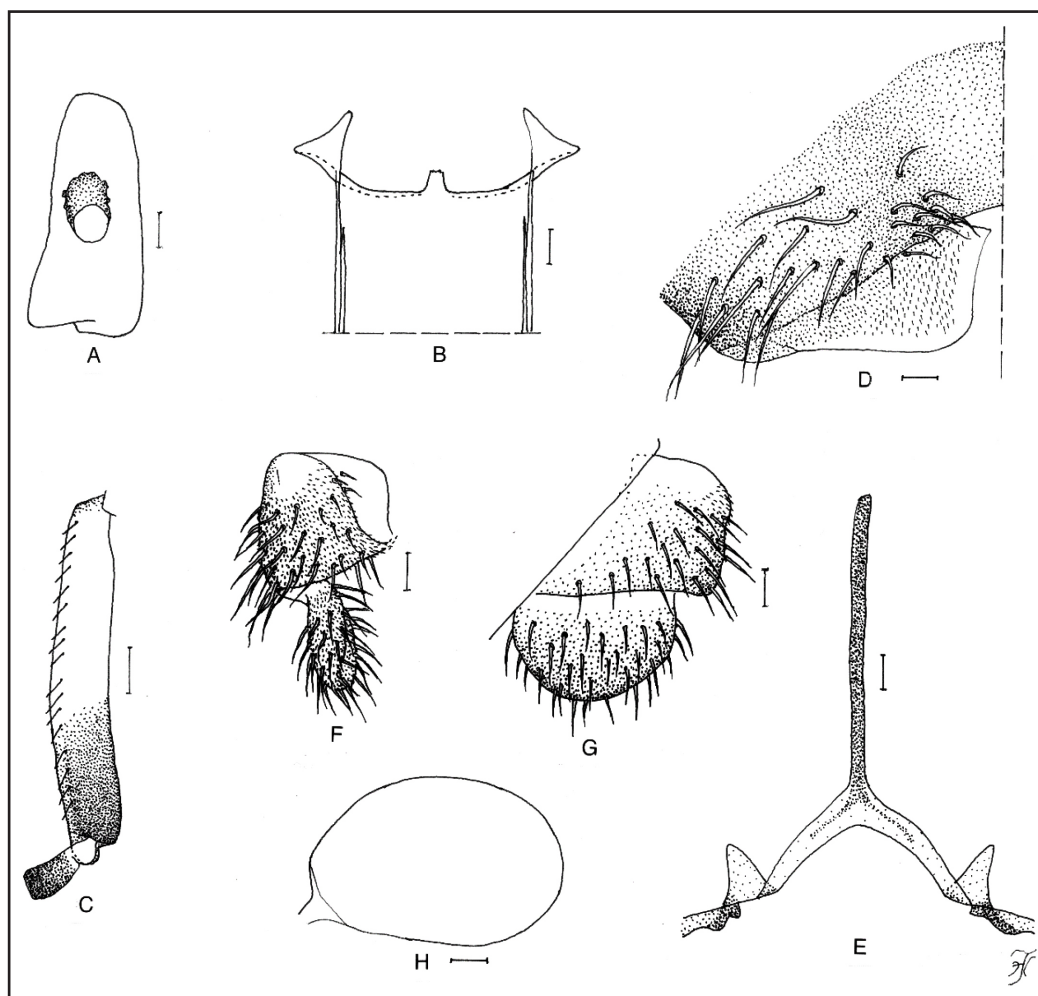


Figure 1. Female of *S. (S.) mutaralamense* sp. nov. A, Third palpal segment with sensory vesicle (left side; front view). B, Cibarium (front view). C, Hind basitarsus and second tarsomere (left side; outer view). D, Sternite 8 and ovipositor valve (right half; ventral view). E, Genital fork (ventral view). F & G, Paraprocts and cerci (right side; F, ventral view; G, lateral view). H, Spermatheca (lateral view). Scale bars. 0.1 mm for C; 0.02 mm for A, B & D–H.

Male (n=8). Body length 2.8–3.0 mm. **Head.** Width slightly wider than that of thorax. Upper eye medium brown, consisting of large facets in 18 or 19 vertical columns and in 19 or 20 horizontal rows. Clypeus black, thickly white pruinose, shiny when illuminated at certain angles, sparsely covered with dark-brown hairs along and near lateral margins (most of central portion of upper half bare). Antenna composed of scape, pedicel and nine flagellomeres, medium to dark brown except scape, pedicel, and base of first flagellomere yellow; first flagellomere elongate, 1.6–1.7 times as long as second one. Maxillary palpus grayish to dark brown, composed of five segments with proportional lengths of third, fourth, and fifth segments 1.0:1.1–1.2:2.3–2.8; third segment (Figure 2A) somewhat widened apically; sensory vesicle (Figure 2A) small (0.17–0.18 times the length of third segment), ellipsoidal, and with small opening. **Thorax.** Scutum black, with white pruinose pattern, i.e., anterior pair of rectangular spots on shoulders extending posteriorly along lateral margins and connected to large transverse spot entirely covering prescutellar area; these pruinose areas shiny and iridescent when illuminated at certain angles; scutum uniformly and densely covered with golden-yellow recumbent short hairs interspersed with dark-brown long upright hairs on prescutellar area. Scutellum brownish black, with several dark long upright hairs and golden-yellow short hairs. Postnotum black, white pruinose when illuminated at certain angles and bare. Pleural membrane bare. Katepisternum longer than deep, brownish black to black, shiny and white pruinose when illuminated at certain angles, and

bare. **Legs.** Foreleg: coxa yellow; trochanter medium brown; femur medium brown with apical cap dark brown; tibia medium to dark brown except outer surface widely white medially, and with white sheen when illuminated at certain angles; tarsus brownish black, with moderate dorsal hair crest; basitarsus moderately dilated, 5.4 times as long as its greatest width. Midleg: coxa brownish black; trochanter and femur dark brown; tibia whitish on basal half and light to medium brown on rest; tarsus dark brown except base of basitarsus dark yellow to light brown. Hind leg: coxa brownish black; trochanter yellow; femur medium to dark brown except extreme base yellow and apical cap brownish black; tibia dark brown to brownish black except basal tip yellow; tarsus (Figure 2B) medium brown to brownish black; basitarsus (Figure 2B) much enlarged, gradually widened from base to apical one-third, then slightly tapered to round apex, 4.0 times as long as its greatest width, and 0.85–0.89 and 0.89–0.92 times as wide as greatest widths of hind tibia and femur, respectively; calcipala (Figure 2B) small, nearly as long as width at base, 0.26 times as wide as greatest width of basitarsus; pedisulcus (Figure 2B) well marked. **Wing.** Length 2.2–2.4 mm. Other features as in female except subcosta and basal section of radial vein bare. **Halter.** White with basal portion darkened. **Abdomen.** Basal scale dark brown to brownish-black, with fringe of dark long hairs. Dorsal surface of abdomen brownish-black to black and covered with dark short hairs; segments 2 and 5–7 each with pair of silvery or bluish iridescent spots dorsolaterally, those on segment 2 connected broadly to each other in middle. **Genitalia.** Coxite in

ventral view (Figure 2C) nearly quadrate, covered with many stout hairs on posterior half. Style in ventral view (Figure 2C) elongate, gradually tapered to middle, then nearly parallel-sided to apex, with apical spine; style in ventrolateral view (Figure 2D) elongate, 2.7 times as long as its greatest width at base, nearly parallel-sided from base to basal one-fourth, then abruptly narrowed to middle, nearly parallel-sided for short length and slightly widened near apex; style in medial view (Figure 2E) spatulate dorsoventrally, 1.5 times as long as coxite, with long horn-like basal protuberance, appearing to have several minute cone-like spines each having microseta on anterior surface (Figure 2F). Ventral plate in ventral view (Figure 2C) with body nearly quadrate (though, slightly shorter than its greatest width, somewhat narrowed basally, and rounded on each posterolateral corner), with ventromedial process directed ventrally, and covered with many minute setae on anteroventral surface, and several ridges in two vertical rows on posterior surface; arms directed forward and

divergent outward from each other; ventral plate in lateral view (Figure 2G) having ventromedial process at about right or slightly more angle against dorsal margin of body, with serrated posterior margin, and bare except anteroventral surface moderately covered with minute setae; ventral plate in caudal view (Figure 2H) having ventromedial process nearly parallel-sided and with round apical tip, 0.4 times as wide as greatest width of ventral plate, and having several ridges in two vertical rows on posterior surface except apical two-fifths without ridges, and no setae on posterior surface. Median sclerite in caudal view (Figure 2I) plate-like, widened from base toward near apex, with round apex, brown basally, but not so well sclerotized apically. Paramere (Figure 2J) with several distinct hooks. Aedeagal membrane (Figure 2K) densely covered with minute fine setae, and with weakly sclerotized dorsal plate in form of horizontal bar.

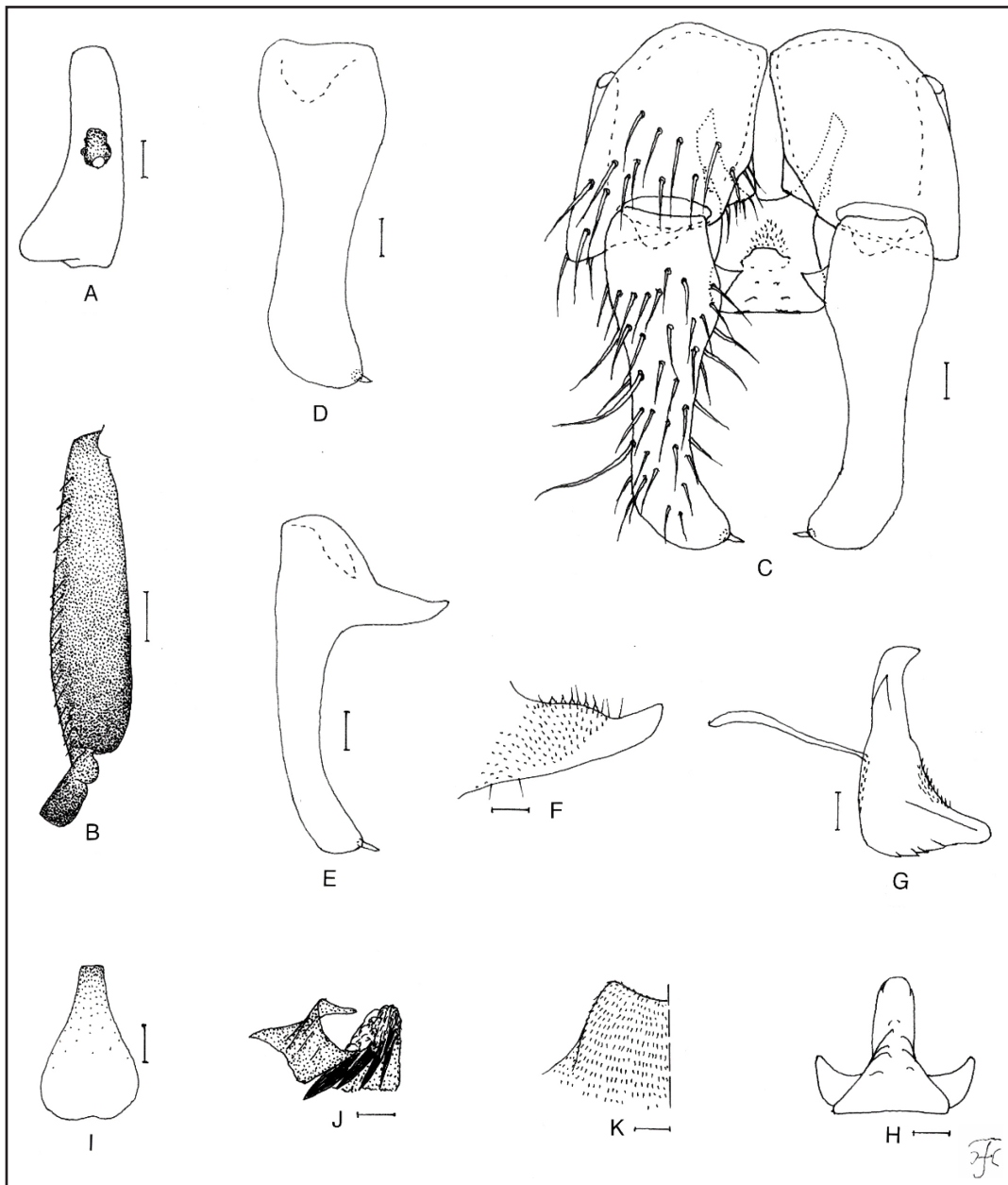


Figure 2. Male of *S. (S.) mutaralamense* sp. nov. A, Third palpal segment with sensory vesicle (left side; front view). B, Hind basitarsus and second tarsomere (left side; outer view). C, Coxites, styles and ventral plate (ventral view). D, Style (right side; ventrolateral view). E, Style (right side; medial view). F, Basal protuberance of style (right side; medial view). G, Ventral plate and median sclerite (lateral view). H, Ventral plate (caudal view). I, Median sclerite (caudal view). J, Paramere (right side; caudal view). K, Aedeagal membrane (right half; caudal view). Scale bars. 0.1 mm for B; 0.02 mm for A, C-E & G-J; 0.01 mm for F & K.

Pupa (n=10). Body length 2.9–3.2 mm. **Head.** Integument ochreous, densely and elaborately covered with small round tubercles; antennal sheath bare except basal portion covered with small tubercles; frons with two unbranched slender short trichomes with uncoiled apices (Figure 3A) on each side; face with one unbranched short trichome with uncoiled apex (Figure 3B) on each side. **Thorax.** Integument dark yellow to ochreous, densely and elaborately covered with small round tubercles; thorax on each side with three anterodorsal trichomes with uncoiled apices (all bifid or trifid, or anterior trichome bifid and middle and posterior ones unbranched) (Figure 3C), two unbranched anterolateral trichomes with uncoiled apices (anterior trichome short, posterior one medium-long) (Figure 3D), one unbranched medium-long mediolateral trichome with uncoiled apex (Figure 3E), and three unbranched ventrolateral trichomes with uncoiled apices (one short and slender, two others medium-long and stout) (Figure 3F). Gill (Figure 3G) with eight slender thread-like short filaments arranged as 2+(2+2)+2 from dorsal to ventral, arising from extremely short common basal stalk; all pairs short-stalked; gill filaments widely divergent basally, stalk of dorsal pair forming an obtuse angle of 130–140 degrees against stalk of ventral pair when viewed laterally; filaments subequal in length to one another, though upper filament of dorsal pair probably longest (about 1.7 mm long); relative thickness of eight filaments from dorsal to ventral when basal portions were compared 1.4–1.5:1.3–1.4:1.0–1.1:1.0–1.2:1.3–1.4:1.1–1.2:1.0:1.0; all filaments medium to dark brown,

tapered toward apex, with distinct annular ridges and furrows forming definite reticulate surface patterns, and densely covered with minute tubercles. **Abdomen.** Dorsally, segment 1 ochreous, and other segments unpigmented except basal portion of spine-combs on segment 8 yellow; segment 1 with one unbranched slender short seta (Figure 3H) on each side; segment 2 with one unbranched slender short seta and five short spinous setae, of which four are relatively stouter than remaining one (Figure 3I) on each side; segments 3 and 4, each with four distinct hooked spines and one unbranched short seta on each side; segments 5, 6, 7 and 9 lacking spine-combs, though one pupa with one spine (Figure 3J) on left side; segment 8 with distinct spine-combs in transverse row (Figure 3K) on each side; segments 5–9 each with comb-like groups of minute spines on each side; segment 9 without terminal hooks. Ventrally, segments 3–9 unpigmented, each (except segment 9) with comb-like groups of minute spines; segment 4 with few unbranched slender minute setae on each side; segment 5 with pair of bifid stout hooks submedially and few unbranched short setae on each side; segments 6 and 7 each with pair of bifid inner and unbranched outer stout hooks somewhat separated from each other, and few unbranched short setae on each side. Grapnel-shaped hooklets absent on each side of segment 9. **Cocoon** (Figure 3L, M). Wall-pocket-shaped or shoe-shaped with narrow anteroventral collar, tightly and thickly woven, ochreous to dark brown, with medium-sized anterolateral window on each side, and not extended ventrolaterally; individual threads invisible; 3.8–4.0 mm long by 1.4–1.6 mm wide.

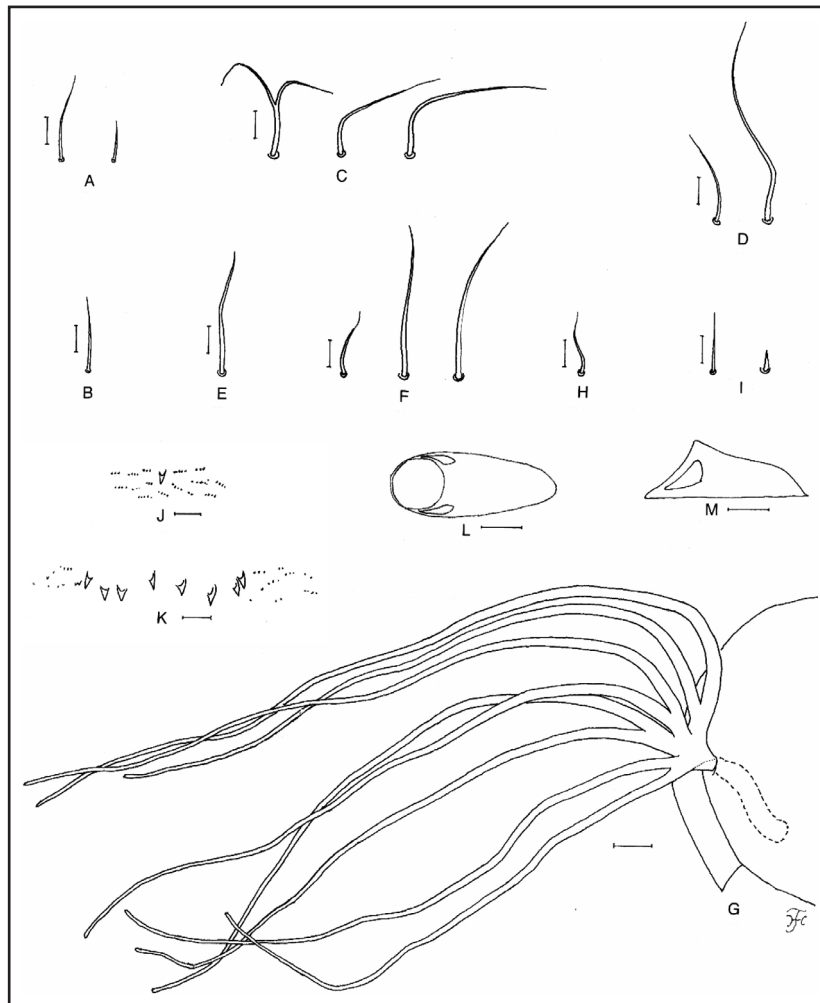


Figure 3. Pupa of *S. (S.) mutaralamense* sp. nov. A, Frontal trichomes. B, Facial trichome. C–F, Thoracic trichomes (C, anterodorsal; D, anterolateral; E, mediolateral; F, ventrolateral). G, Gill filaments (left side; outer view). H, Slender seta on abdominal segment 1. I, Slender seta and stout seta on abdominal segment 2. J, Spine and comb-like microspines on right side of abdominal segment 7. K, Spine-combs and comb-like microspines on right side of abdominal segment 8. L & M, Cocoons (L, dorsal view; M, lateral view). Scale bars. 1.0 mm for L & M; 0.1 mm for G; 0.02 mm for A–F & H–K.

Mature larva. Unknown.

Type materials. HOLOTYPE: Male (with its pupal exuviae and cocoon), reared from a pupa collected from an irrigation ditch (width 1.0 m, 23.0°C, exposed to the sun, elevation 900 m) slowly flowing in a paddy field at Batu Kebayan, Mutaralam, Lampung, South Sumatra, 30-VII-1992, H. Takaoka. PARATYPES: Eight females and seven males (with their pupal exuviae and cocoons), reared from pupae, same data and date as those of the holotype.

Biological notes. The pupae of *S. (S.) mutaralamense* sp. nov. were collected from grass leaves, stalks and roots trailing in flowing water. Associated species were *S. (Gomphostilbia) atratum* De Meijere, *S. (G.) gyorkosae* Takaoka & Davies, *S. (Nevermannia) aureohirtum* Brunetti, and *S. (S.) nobile* De Meijere.

Etymology. The species name *mutaralamense* refers to the district name, Mutaralam, where this new species was collected.

Remarks. *Simulium (S.) mutaralamense* sp. nov. is assigned to the *S. multistriatum* species-group of the subgenus *Simulium* s. str. defined by Takaoka & Davies (1996), based on the female scutum with five longitudinal vittae, female cibarium with a dorsomedian projection (Figure 1B), female claw simple, female ovipositor valves thin and unpigmented along inner margins (Figure 1D), male style with an elongate basal protuberance (Figure 2E), pupal gill with eight filaments (Figure 3G), and cocoon with an anterolateral open space on each side (Figure 3M).

This new species is characterized by the haired basal portion of the radial vein of the female wing, a characteristic found in five species of this species-group: *S. (S.) chaliowae* Takaoka & Boonkemtong described from Thailand (Takaoka & Kuvangkadilok, 1999), *S. (S.) fenestratum* described from Sumatra (Edwards, 1934), *S. (S.) hirtinervis* Edwards described from Peninsular Malaysia (Edwards, 1928; Takaoka & Davies, 1995), *S. (S.) lacduongense* Takaoka & Ya'cob described from Vietnam (Takaoka *et al.*, 2015) and *S. (S.) sakishimaense* Takaoka described from Japan (Takaoka, 1977).

Simulium (S.) chaliowae is similar to this new species by having the entirely darkened male hind basitarsus and widely divergent pupal gill filaments, but differs from this new species by the number of male upper-eye (large) facets in 17 vertical columns and 18 horizontal rows, ventral plate with its ventromedial process tapered toward the ventral tip when viewed caudally, and cocoon shoe-shaped and without an anterolateral open space on each side. *Simulium (S.) fenestratum* differs from this new species in the male by the number of upper-eye (large) facets in 16 vertical columns and 17 horizontal rows, hind basitarsus dark yellow on its basal one-third (Figure 9B), ventral plate slightly longer than wide when viewed ventrally (Figure 9C), and ventromedial process about half as wide as the greatest width of the ventral plate when viewed caudally (Figure 9G) (according to the result of the current study); and in the pupa by the gill filaments moderately divergent basally by about 90 degrees when viewed laterally (Figure 10G). *Simulium (S.) hirtinervis* differs by the number of male upper-eye (large) facets in 14 vertical columns and 13 horizontal rows, and ventromedial process of the ventral plate much constricted basally when viewed posteriorly. *Simulium (S.) lacduongense* is most similar to this new species by having a similar number of male upper-eye (large) facets in 19 vertical columns and 20 horizontal rows and widely divergent pupal gill filaments, but differs from this new species by having the medium-sized female sensory vesicle (0.33–0.41 times as long as the third palpal segment), male fore basitarsus 6.1 times as long as its greatest width, male hind basitarsus dark yellow or grayish yellow on its basal half, and ventromedial process of the ventral plate not parallel-sided and slightly constricted basally when viewed caudally. *Simulium (S.) sakishimaense* differs by the basal portion of the female radial vein partially haired only near its apex, number of male upper-eye (large facets) in 17 vertical columns and 17 horizontal

rows (according to the current author's recent reexamination), male fore basitarsus 6.7 times as long as its greatest width (according to the current author's recent reexamination), male hind basitarsus clear yellow on its basal two-fifths, and gill filaments moderately divergent basally by about 90 degrees when viewed laterally.

***Simulium (Simulium) lubuksulasihense* sp. nov.**

Isid:zoobank.org:act:5E9AAC2F-6B2A-4042-9ABA-E3F0825F3E8F

This species is similar to *S. (S.) mutaralamense* sp. nov. in many characteristics, thus only different characteristics are noted, although most numerical characteristics are shown.

Female (n=4). Body length 2.6–3.0 mm. **Head.** Frontal ratio 1.4:1.0:1.7–1.8; frons:head ratio 1.0:4.7–5.5. Labrum 0.71–0.72 times as long as clypeus. Maxillary palpus: proportional lengths of third, fourth, and fifth segments 1.0:1.1:2.1–2.4; sensory vesicle (Figure 4A) of moderate size (0.30–0.35 times length of third segment) having moderate or large opening. Maxillary lacinia with 10 or 11 inner and 13–15 outer teeth. Mandible with 23 or 24 inner and 11–13 outer teeth. Cibarium (Figure 4B) with blunt medial projection on posterior margin. **Legs.** Foreleg: basitarsus 4.8–5.1 times as long as its greatest width. Hing leg: tarsus dark brown except basal two-thirds or little less of basitarsus and basal half of second tarsomere whitish; basitarsus (Figure 4C) 5.7–6.1 times as long as wide, and 0.71–0.72 and 0.59–0.60 times as wide as greatest widths of hind tibia and femur, respectively; calcipala (Figure 4C) slightly shorter than basal width, and 0.4 times as wide as basitarsus. **Wing.** Length 2.5–2.6 mm; basal section of radial vein haired on apical half to three-fourths. **Terminalia.** Sternite 8 (Figure 4D) bare medially, with 26–36 dark medium-long to long stout hairs on each lateral surface. Ovipositor valves (Figure 4D) each moderately covered with microsetae and one or two dark medium-long hairs. Genital fork as in Figure 4E. Paraproct in ventral view (Figure 4F) with 21 or 22 short to medium-long hairs on lateral and ventral surfaces except anterolateral corner widely unpigmented and bare; anteromedial surface with six or seven short sensilla; paraproct in lateral view (Figure 4G) 0.6 times as long as wide. Cercus in lateral view (Figure 4G) 0.45 times as long as wide. Spermatheca (Figure 4H) ellipsoidal, 1.14–1.28 times as long as wide.

Male (n=4). Body length 2.8–3.0 mm. **Head.** Upper eye medium brown, with large facets in 17 or 18 vertical columns and in 18 horizontal rows. Antenna medium to dark brown except scape, pedicel, and base of first flagellomere yellow; first flagellomere elongate, 1.8 times as long as second one. Maxillary palpus: proportional lengths of third, fourth, and fifth segments 1.0:1.3:3.2; sensory vesicle (Figure 5A) small (0.21–0.26 times the length of third segment), globular or ellipsoidal, and with small opening. **Legs.** Foreleg: basitarsus moderately dilated, 5.9 times as long as its greatest width. Midleg: tibia whitish on basal two-thirds to three-fourths and light to medium brown on rest; tarsus dark brown except basal one-third of basitarsus whitish yellow. Hind leg: tarsus (Figure 5B) medium brown to brownish black except basal one-third of basitarsus and basal half of second tarsomere yellow; basitarsus (Figure 5B) 3.8 times as long as its greatest width, and 0.93–0.96 and 0.89–0.93 times as wide as greatest widths of hind tibia and femur, respectively; calcipala (Figure 5B) small, slightly shorter than width at base, 0.32 times as wide as greatest width of basitarsus. **Wing.** Length 2.2–2.3 mm. **Genitalia.** Coxite in ventral view (Figure 5C) nearly quadrate, covered with many stout hairs on posterior half to one-third. Style in ventral view (Figure 5C) gradually tapered from basal one-third to middle, then slightly widened to apex; style in ventrolateral view (Figure 5D) 3.2 times as long as its greatest width at base, gradually narrowed from basal one-fourth to middle, then slightly widened to apex; style in medial view (Figure 5E) 1.6 times as long as coxite. Ventral plate in ventral view as in Figure 5C; ventral plate in lateral view (Figure 5F) having ventromedial process

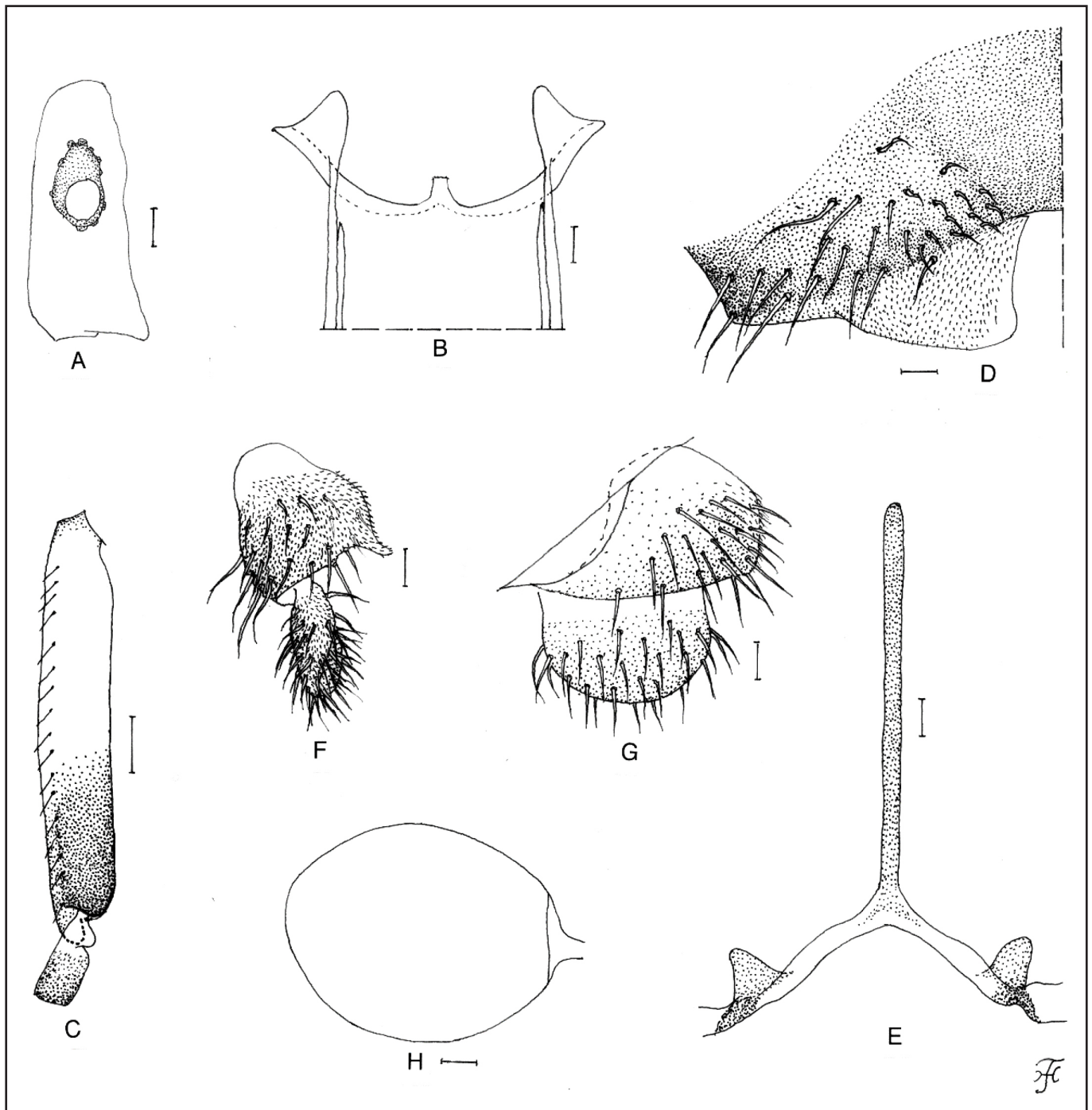


Figure 4. Female of *S. (S.) lubuksulasihense* sp. nov. A, Third palpal segment with sensory vesicle (right side; front view). B, Cibarium (front view). C, Hind basitarsus and second tarsomere (left side; outer view). D, Sternite 8 and ovipositor valve (right half; ventral view). E, Genital fork (ventral view). F & G, Paraprocts and cerci (right side; F, ventral view; G, lateral view). H, Spermatheca (lateral view). Scale bars. 0.1 mm for C; 0.02 mm for A, B & D–H.

somewhat inclined posteriorly against dorsal margin of body; ventral plate in caudal view (Figure 5G) having ventromedial process 0.3 times as wide as greatest width of the ventral plate.

Pupa (n=10). Body length 2.9–3.2 mm. **Head.** Frons with two unbranched slender short trichomes with uncoiled apices (Figure 6A) on each side; face with one unbranched short trichome with uncoiled apex (Figure 6B) on each side. **Thorax.** Thorax on each side with three anterodorsal trichomes (anterior and middle trichomes bifid or trifold, and posterior ones unbranched) (Figure 6C), two unbranched anterolateral trichomes (anterior trichome shorter than posterior one) (Figure 6D), one unbranched or bifid medium-

long mediolateral trichome (Figure 6E), and three unbranched ventrolateral trichomes (one short and slender, two others medium-long and stout) (Figure 6F); all trichomes with uncoiled apices. Gill (Figure 6G) with eight slender thread-like short filaments arranged as 2+(2+2)+2 from dorsal to ventral; all pairs short-stalked; gill filaments widely divergent basally, stalk of dorsal pair forming obtuse angle of about 140 degrees against stalk of ventral pair when viewed laterally; filaments subequal in length to one another; relative basal thickness of eight filaments from dorsal to ventral 1.7–1.9:1.3–1.7:1.0–1.6:1.1–1.3:1.2–1.6:1.1–1.6:1.0:1.0. **Cocoon.** 3.8–4.5 mm long by 1.5–1.8 mm wide.

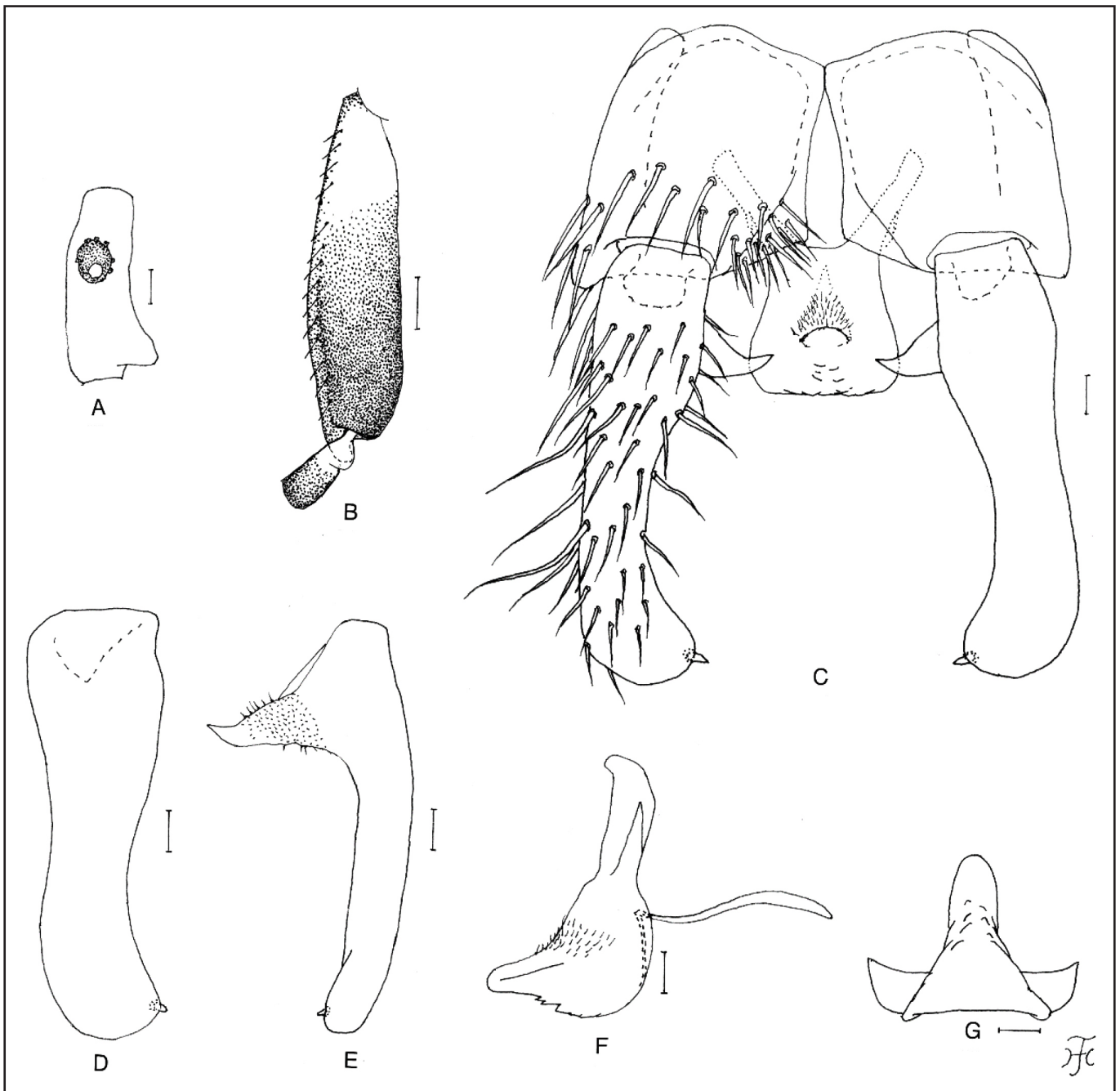


Figure 5. Male of *S. (S.) lubuksulasihense* sp. nov. A, Third palpal segment with sensory vesicle (right side; front view). B, Hind basitarsus and second tarsomere (left side; outer view). C, Coxites, styles and ventral plate (ventral view). D, Style (right side; ventrolateral view). E, Style (left side; medial view). F, Ventral plate and median sclerite (lateral view). G, Ventral plate (caudal view). Scale bars. 0.1 mm for B; 0.02 mm for A & C–G.

Mature larva. Unknown.

Type materials. HOLOTYPE: Male (with its pupal exuviae and cocoon), reared from a pupa collected from a stream (width ca. 1.0 m, partially shaded, 20°C, elevation ca. 950 m) moderately flowing in an open land, at Lubuksulasih, Padang, West Sumatra, 8-VIII-1994, by H. Takaoka. PARATYPES: Five females and three males (with their pupal exuviae and cocoons), reared from pupae, same data as those of the holotype.

Biological notes. The pupae of *S. (S.) lubuksulasihense* sp. nov. were collected from grass leaves and stalks trailing in flowing water. Associated species were *S. (G.) atratum*, *S. (G.) minangkabaum* Takaoka & Sigit, and *S. (S.) nobile*.

Etymology. The species name *lubuksulasihense* refers to the name of the city Lubuksulasih, where this new species was collected.

Remarks. *Simulium (S.) lubuksulasihense* sp. nov. is assigned to the *S. multistriatum* species-group of the subgenus *Simulium* s. str., like *S. (S.) mutaralamense* sp. nov.

This new species is similar to *S. (S.) mutaralamense* sp. nov. in many characteristics including the number of male upper-eye (large) facets, but differs in the female by the medium-long sensory vesicle (0.30–0.35 times as long as the third palpal segment) (Figure 4A), in the male by the mid tibia whitish on the basal two-thirds to three-fourths, and hind basitarsus yellow on its basal one-third (Figure 5B).

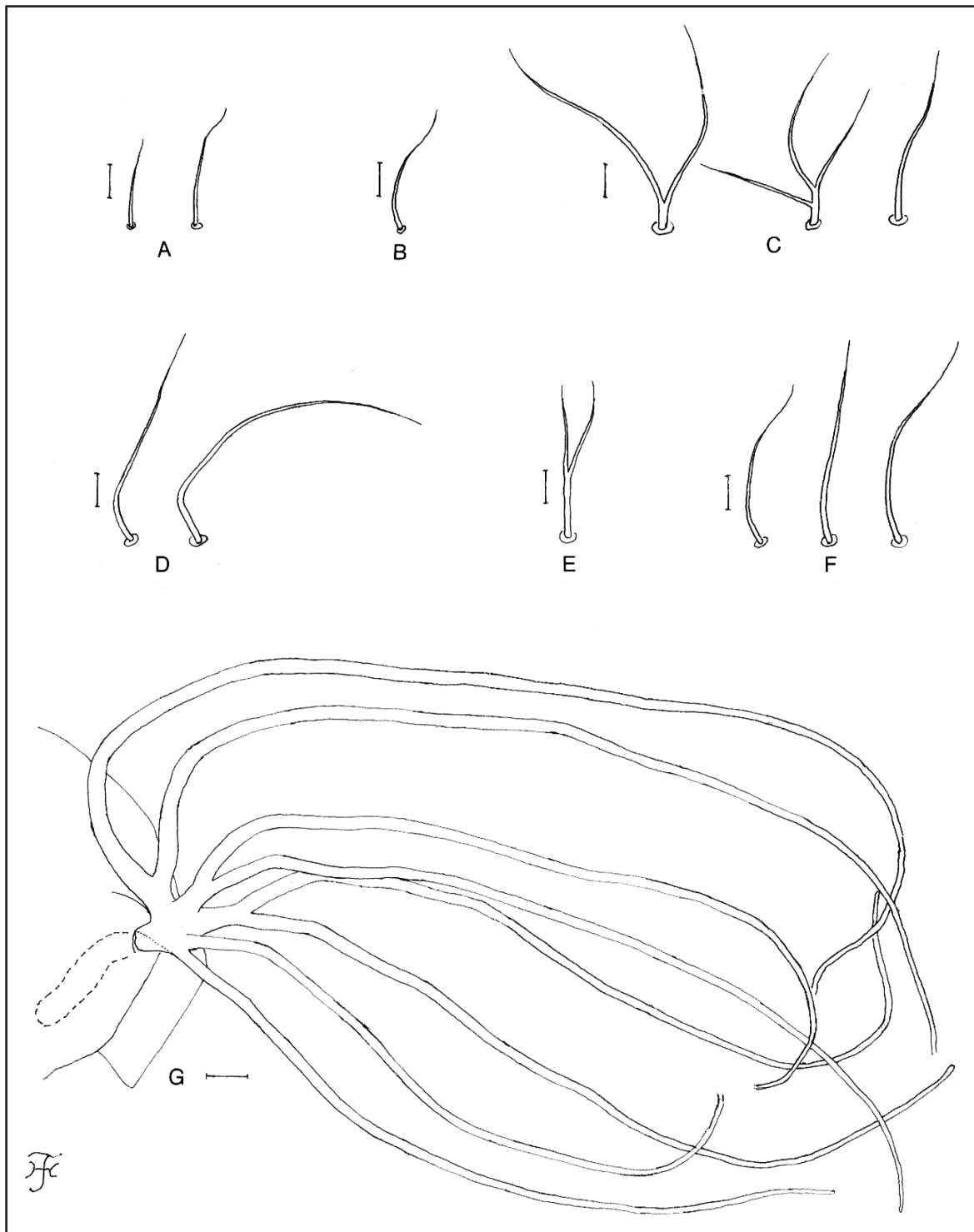


Figure 6. Pupa of *S. (S.) lubuksulasihense* sp. nov. A, Frontal trichomes. B, Facial trichome. C–F, Thoracic trichomes (C, anterodorsal; D, anterolateral; E, mediolateral; F, ventrolateral). G, Gill filaments (right side; outer view). Scale bars. 0.1 mm for G; 0.02 mm for A–F.

This species is distinguished from the five other species of the *S. multistriatum* species-group, which are characterized by the haired basal portion of the radial vein of the female wing as follows: from *S. (S.) chaliowae* from Thailand (Takaoka & Kuvangkadilok, 1999); by the male hind basitarsus yellow on the basal one-third (Figure 5B) and cocoon with an anterolateral window on each side; from *S. (S.) fenestratum* from Sumatra (Edwards, 1934), *S. (S.) hirtinervis* from Peninsular Malaysia (Edwards, 1928; Takaoka & Davies, 1995), and *S. (S.) sakishimaense* from Japan (Takaoka, 1977) by the higher number of the male upper-eye (large) facets in 17 or 18 vertical columns

and 18 horizontal rows and pupal gill filaments widely divergent (Figure 6G); and *S. (S.) lacduongense* from Vietnam (Takaoka *et al.*, 2015) by the smaller number of male upper-eye (large) facets in 17 or 18 vertical columns and 18 horizontal rows (19 vertical columns and 20 horizontal rows in *S. (S.) lacduongense*), male hind basitarsus 3.8 times as long as its greatest width (c.f., 4.4 times as long as its greatest width in *S. (S.) lacduongense*), and ventral plate with its ventromedial process parallel-sided when viewed caudally (c.f., not parallel-sided, and somewhat constricted basally in *S. (S.) lacduongense*).

***Simulium (Simulium) liwaense* sp. nov.**

lsid:zoobank.org:act:1FC13DA6-764C-4615-8172-F55C295FAD20

This new species is represented by two pharate males with their pupal exuviae and cocoons, and one pupal exuviae with its cocoon. The wings and hind basitarsi of the males were not yet extended, but the coloring of the legs of one male was almost completed. This species is similar to *S. (S.) mutaralamense* sp. nov. in many characteristics; thus, only different characteristics are noted, although most numerical characteristics are shown.

Male (n=2). Body length 2.8 mm. **Head.** Upper eye consisting of large facets in 14 or 15 vertical columns and in 16 horizontal rows. Antenna: first flagellomere twice as long as second one. Maxillary palpus: proportional lengths of third, fourth, and fifth segments 1.0:1.2:2.8–2.9; sensory vesicle (Figure 7A) small (0.17–0.20 times the length of third segment), globular, and with medium-sized or large opening. **Legs.** Foreleg: basitarsus somewhat enlarged, 6.3

times as long as its greatest width. Hind leg: basitarsus yellowish on basal one-third and dark brown on rest; basitarsus (Figure 7B) enlarged, 0.9 times as wide as hind tibia and femur.

Genitalia. Coxite in ventral view (Figure 7C) nearly quadrate, covered with many stout hairs on posterior half. Style in ventrolateral view (Figure 7D) 3.4 times as long as its greatest width at base, nearly parallel-sided from base to basal one-third, then abruptly narrowed to middle, slightly widened to apical one-fourth, then nearly parallel-sided; style in medial view (Figure 7E) 1.9 times as long as coxite; ventral plate in ventral view (Figure 7C) with body nearly quadrate (though slightly shorter than its greatest width); ventral plate in lateral view (Figure 7F) having ventromedial process at about right angle against dorsal margin of body; ventral plate in caudal view (Figure 7G) having ventromedial process 0.36 times as wide as greatest width of ventral plate.

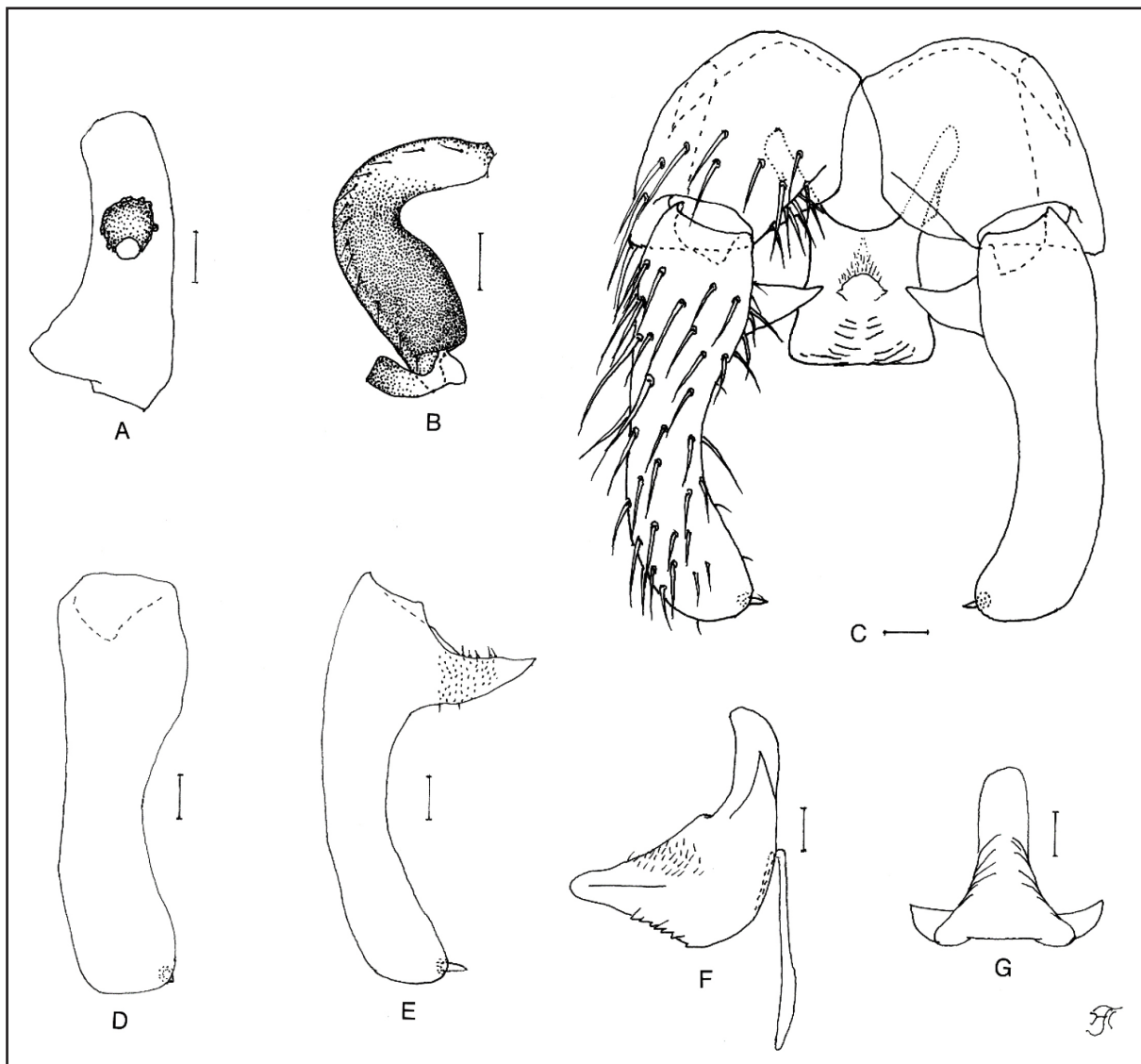


Figure 7. Male of *S. (S.) liwaense* sp. nov. A, Third palpal segment with sensory vesicle (left side; front view). B, Hind basitarsus and second tarsomere (left side; outer view). C, coxites, styles and ventral plate (ventral view). D & E, Styles (right side; D, ventrolateral view; E, medial view). F, Ventral plate and median sclerite (lateral view). G, Ventral plate (caudal view). Scale bars, 0.1 mm for B; 0.02 mm for A & C–G.

Pupa (n=3). Body length 2.8–3.0 mm. **Head.** Frons with two unbranched slender short trichomes of different length (Figure 8A) on each side; face with one unbranched short trichome (Figure 8B) on each side. **Thorax.** Thorax on each side with three stout anterodorsal trichomes (anterior and middle trichomes long, posterior trichome medium-long (Figure 8C), two anterolateral trichomes (anterior one medium-long and slender, posterior one long and stout) (Figure 8D), one medium-long stout mediolateral trichome (Figure 8E), and three ventrolateral trichomes (one short and slender, two others long and stout) (Figure 8F); all trichomes unbranched and with uncoiled apices. Gill (Figure 8G) with eight slender thread-like short filaments arranged as 2+(2+2)+2 from dorsal to ventral, arising from extremely short common basal stalk; all pairs short-stalked, though ventral pair with extremely short

stalk; gill filaments moderately divergent basally, stalk of dorsal pair forming angle of 90 degrees against stalk of ventral pair when viewed laterally; upper filament of dorsal pair longest, two filaments of ventral pair shortest, and four filaments of middle two pairs intermediate in length; relative basal thickness of eight filaments from dorsal to ventral 1.6–1.8:1.6–1.7:1.2–1.4:1.2–1.6:1.4:1.0–1.2:1.0–1.2:1.0; all filaments medium brown, with distinct annular ridges and furrows forming definite reticulate surface patterns (except basal parts of ventral paired filaments with no annular ridges and furrows). **Abdomen.** Dorsally, spine-combs only on each side of dorsum of segment 8, and one of five short spinous setae on each side of dorsum of segment 2 slender, and four others relatively stout (Figure 8I). **Cocoon.** 3.0 mm long by 1.0–1.2 mm wide.

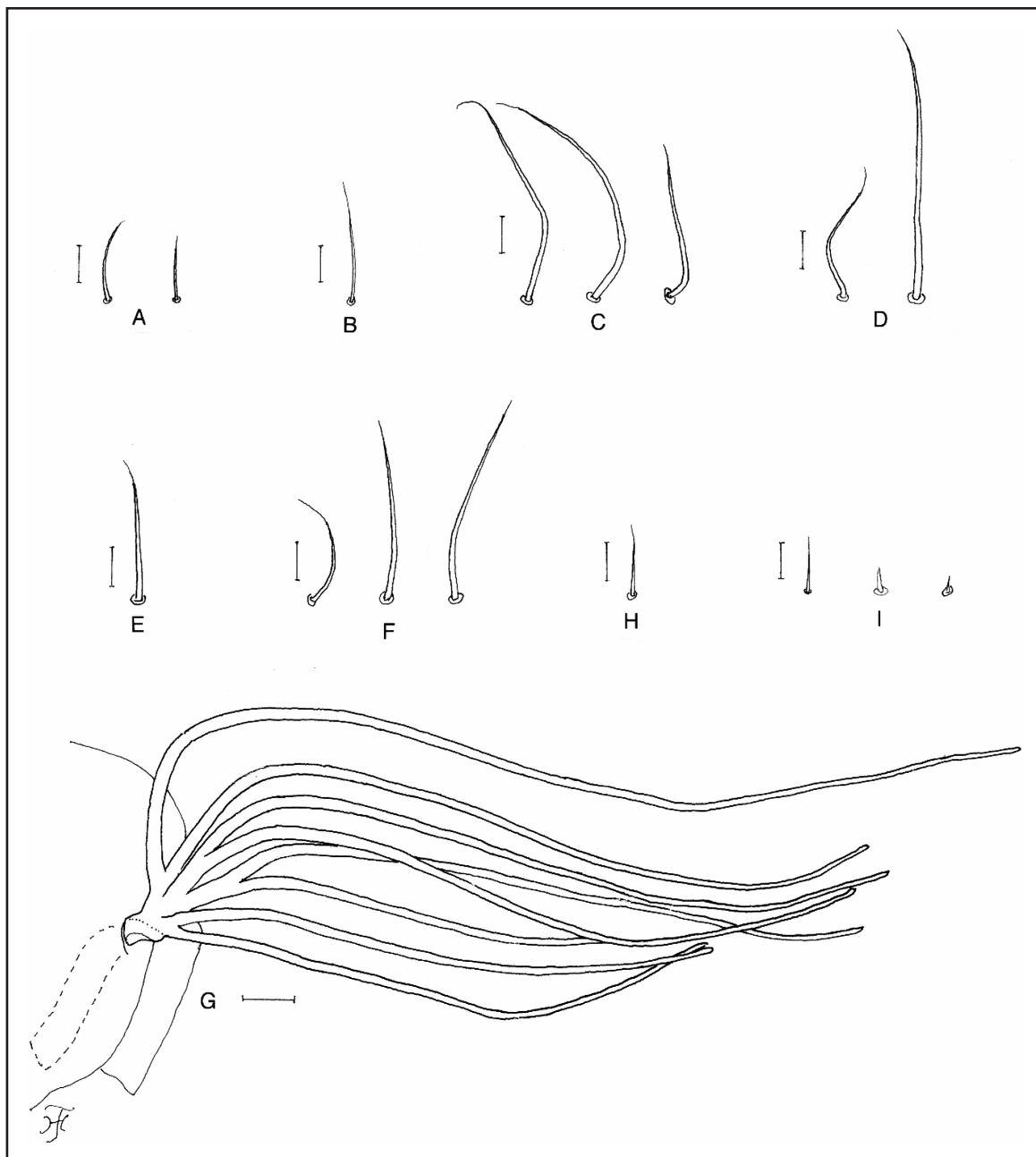


Figure 8. Pupa of *S. (S.) liwaense* sp. nov. A, Frontal trichomes. B, Facial trichome. C–F, Thoracic trichomes (C, anterodorsal; D, anterolateral, E, mediolateral, F, ventrolateral). G, Gill filaments (right side; outer view). H, short seta on each side of dorsum of abdominal segment 1. I, short seta and two spinous setae on each side of dorsum of abdominal segment 2. Scale bars. 0.1 mm for G; 0.02 mm for A–F, H & I.

Female and Mature larva. Unknown.

Type materials. HOLOTYPE: Pharate male (with its pupal exuviae and cocoon), reared from a pupa, collected from a brook (width 1.0 m, 20.0°C, partially shaded, elevation 950 m) slowly flowing into Lake Toba, Sualan, Prapat, Middle Sumatra, 27-VIII-1994, by H. Takaoka. PARATYPES: One pharate male (with its pupal exuviae and cocoon), collected from a creek (width 2.0–3.0 m, flow moderate or rapid, bottom stones, 22.0°C, partially shaded, elevation ca. 900 m) along the road between Liwa and Gunungkemala, in the Barisan Range, Liwa, Lampung Province, South Sumatra, 30-VII-1992, by H. Takaoka; and one pupal exuviae and cocoon, same data as the holotype.

Biological notes. The pupae of *S. (S.) liwaense* sp. nov. were collected from grass roots trailing in flowing water. Associated species were *S. (G.) atratum*, *S. (S.) fenestratum* and *S. (S.) barisanense* Takaoka.

Etymology. The species name, *liwaense*, is based on the city name, Liwa, where one of two pupae of this new species was collected.

Remarks. *Simulium (S.) liwaense* sp. nov. is assigned to the *S. multistriatum* species-group based on the male style with a long basal protuberance (Figure 7E), pupal gill with eight filaments (Figure 8G), and cocoon with an anterolateral open space on each side.

This new species is characterized in the male by the smaller number of upper-eye (large) facets in 14 or 15 vertical columns and 16 horizontal rows; and in the pupa by the gill with eight filaments moderately divergent vertically (an angle formed by the stalk of the dorsal pair and that of the ventral pair is 90 degrees) (Figure 8G), and anterodorsal trichomes on each side of the thorax all unbranched (Figure 8C).

Simulium (S.) ubonae Thajjarern *et al.* from Thailand has a similar number of male upper-eye (large) facets in 15 vertical columns and 15 or 16 horizontal rows, but differs from this new species in the male by the ventral plate with a few setae on its ventral surface and its arms not so divergent; and in the pupa by having eight gill filaments widely divergent at an angle of about 180 degrees when viewed laterally, and three anterodorsal trichomes on each side of the thorax, of which at least one is bifid (Thajjarern *et al.*, 2019).

Simulium (S.) hirtinervis has a smaller number of male upper-eye (large) facets in 14 vertical columns and 13 horizontal rows, but differs from this new species by the ventromedial process of the ventral plate much constricted basally when viewed caudally (Takaoka & Davies, 1995).

Simulium (S.) bifengxiaense Huang, Zhang & Chen from China shares one of the two pupal characteristics of this new species, i.e., all three unbranched anterodorsal trichomes on each side of the thorax, but differs in the male by the number of upper-eye (large) facets in 18 vertical columns and 17 horizontal rows, and ventral plate rounded when viewed ventrally (Huang *et al.*, 2013).

Simulium (S.) fenestratum from Sumatra is similar in the pupal gill filaments moderately divergent at an angle of about 90 degrees when viewed laterally (Figure 10G) to this new species, but differs in the male by the number of upper-eye (large) facets in 16 vertical columns and 17 horizontal rows, and the shape of the ventral plate, which is longer than wide when viewed ventrally (Figure 9C), with its ventromedial process somewhat wider, about half as wide as the greatest width of the ventral plate when viewed caudally (Figure 9G); and in the pupa by having one or two bifid anterodorsal trichomes on each side of the thorax (Figure 10C).

***Simulium (Simulium) fenestratum* Edwards**

Simulium (Simulium) fenestratum Edwards, 1934: 110–111 (female, male, pupa and larva).

Only one adult male with its pupal exuviae and cocoon, one pupa with its cocoon, and one pupal exuviae with its cocoon were identified as *S. (S.) fenestratum* among adult and pupal specimens of the *S. multistriatum* species-group collected from Middle Sumatra [type locality of *S. (S.) fenestratum*]. The identification was based on the following two characteristics: the pupal gill with eight filaments moderately divergent (at an angle of about 90 degrees) when viewed laterally, as originally illustrated in Figure 18 of Edwards (1934), and the ventral plate with its ventromedial process about half or slightly more times as wide as the greatest width of the ventral plate when viewed caudally, as originally illustrated in Figure 8 of Edwards (1934).

This species is similar in many characteristics to *S. (S.) mutaralamense* sp. nov. described above. Thus, only the morphological characteristics of this species, which are different from those of *S. (S.) mutaralamense* sp. nov., are shown, although most numerical characteristics are presented.

Male (n=1). Body length 2.8 mm. **Head.** Upper eye consisting of large facets in 16 vertical columns and in 17 horizontal rows. Antenna dark brown except base of first flagellomere yellow; first flagellomere 1.8 times as long as second one. Maxillary palpus: proportional lengths of third, fourth, and fifth segments 1.0:1.4:2.9; sensory vesicle (Figure 9A) small (0.23 times length of third segment), ellipsoidal, and with small opening. **Legs.** Foreleg: basitarsus moderately dilated, 5.3 times as long as its greatest width. Midleg: tibia whitish on little more than basal half and light to medium brown on rest; tarsus dark brown except base of basitarsus yellow. Hind leg: femur medium to dark brown except base yellow and apical cap brownish black; tarsus dark brown to brownish black except basal one-third of basitarsus dark yellow; basitarsus (Figure 9B) 3.9 times as long as its greatest width, and 0.90 and 0.90 times as wide as greatest widths of hind tibia and femur, respectively. Calcipala 0.9 times as long as basal width and 0.23 times as long as greatest width of basitarsus. **Wing.** Length 2.1 mm. **Genitalia.** Coxite in ventral view (Figure 9C) nearly quadrate. Style in ventrolateral view (Figure 9D) 3.1 times as long as its greatest width at basal one-fourth, nearly parallel-sided from base to basal one-fourth, then abruptly narrowed to middle, then nearly parallel-sided toward apex; style in medial view (Figure 9E) 1.8 times as long as coxite. Ventral plate in ventral view (Figure 9C) with body nearly rectangular, 1.1 times as long as its greatest width; ventral plate in lateral view (Figure 9F) having ventromedial process slightly inclined posteriorly against dorsal margin of body; ventral plate in caudal view (Figure 9G) having ventromedial process nearly parallel-sided, with round apical tip, and about half as wide as greatest width of ventral plate.

Pupa (n=3). Body length 3.0 mm. **Head.** Frons with two unbranched slender short trichomes with uncoiled apices (Figure 10A) on each side; face with unbranched medium-long trichome with uncoiled apex (Figure 10B) on each side. **Thorax.** Thorax on each side with three anterodorsal trichomes (anterior and middle trichomes long, of which one or both bifid, and posterior one medium-long and unbranched) (Figure 10C), two anterolateral trichomes (anterior trichome medium-long and unbranched, posterior one long and unbranched or bifid) (Figure 10D), one unbranched medium-long mediolateral trichome (Figure 10E), and three unbranched ventrolateral trichomes (one short or medium-

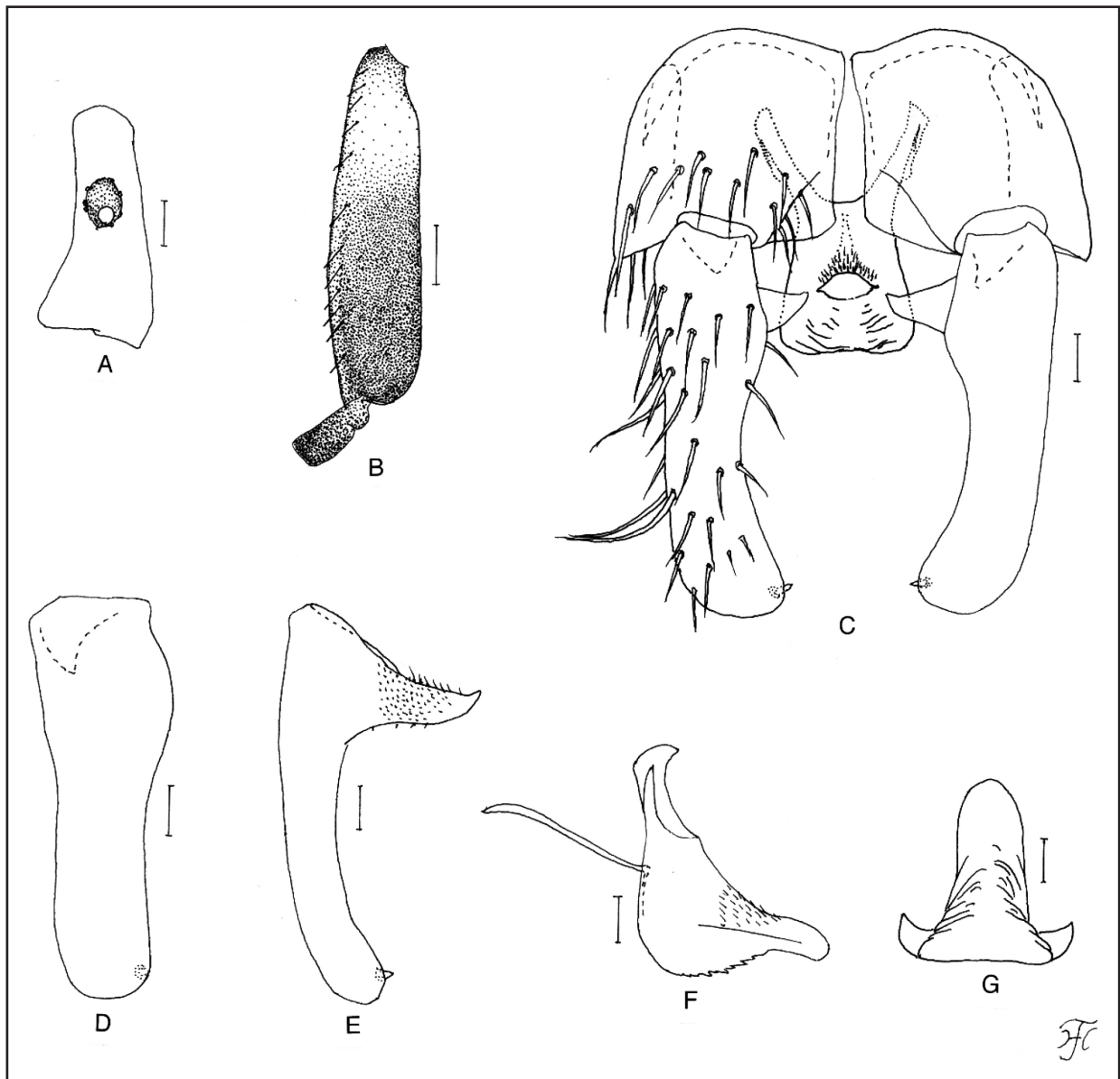


Figure 9. Male of *S. (S.) fenestratum*. A, Third palpal segment with sensory vesicle (left side; front view). B, Hind basitarsus and second tarsomere (left side; outer view). C, coxites, styles and ventral plate (ventral view). D & E, Styles (right side; D, ventrolateral view; E, medial view). F, Ventral plate and median sclerite (lateral view). G, Ventral plate (caudal view). Scale bars, 0.1 mm for B; 0.02 mm for A & C–G.

long, and two others long and stout) (Figure 10F); all with uncoiled apices. Gill (Figure 10G) with eight slender thread-like short filaments arranged as 2+(2+2)+2 from dorsal to ventral, arising from extremely short common basal stalk; gill filaments moderately divergent basally (stalk of dorsal pair forming angle of about 90 degrees against stalk of ventral pair when viewed laterally); upper filament of dorsal pair longest, gradually becoming short from dorsal to ventral and lower filament of ventral pair shortest; relative basal thickness of eight filaments from dorsal to ventral 1.7–18:1.7–1.8:1.3–1.4:1.2–1.3:1.3–1.4:1.2–1.3:1.0–1.2:1.0; all filaments with distinct annular ridges and furrows forming definite reticulate surface patterns, though ventral paired filaments without annular ridges and furrows for short distance from base. **Abdomen.** Spine-combs usually only on segment 8 but also present on each side of segment 7 in one pupa and on one side of segment 7 in another pupa, though number of spines fewer than that on segment 8. **Cocoon.** Wall-pocket-shaped and moderately woven, with medium-sized anterolateral open space on each side; 3.0 mm long by 1.1 mm wide.

Specimens examined: One male (with its pupal exuviae and cocoon), reared from a pupa, one pupa and two pupal exuviae collected from a brook (width 1.0 m, 20.0°C, partially shaded, elevation 950 m) slowly flowing into Lake Toba, Sualan, Prapat, Middle Sumatra, 27-VIII-1994, by H. Takaoka; one pupa collected from a creek (width 4.0–6.0 m, 22.0°C, shaded, elevation 880 m) moderately flowing in a forest, Bandar Baru, Sibolangit, Middle Sumatra, 25-VIII-1994, by H. Takaoka; one pupal exuviae collected from a creek (width 4.0 m, 21.0°C, exposed to the sun, elevation 920 m) moderately flowing in a rice paddy field, Lunbanjulu, Porsea, Middle Sumatra, 26-VIII-1994, by H. Takaoka.

Biological notes. The pupae of *S. (S.) fenestratum* were collected from grass leaves and roots trailing in flowing water. Associated species were *S. (G.) atratum*, *S. (G.) sheilae* Takaoka & Davies, *S. (Nevermannia) feuerborni* Edwards, *S. (S.) ranauense* Takaoka, Hadi & Sigit, and *S. (S.) nobile*.

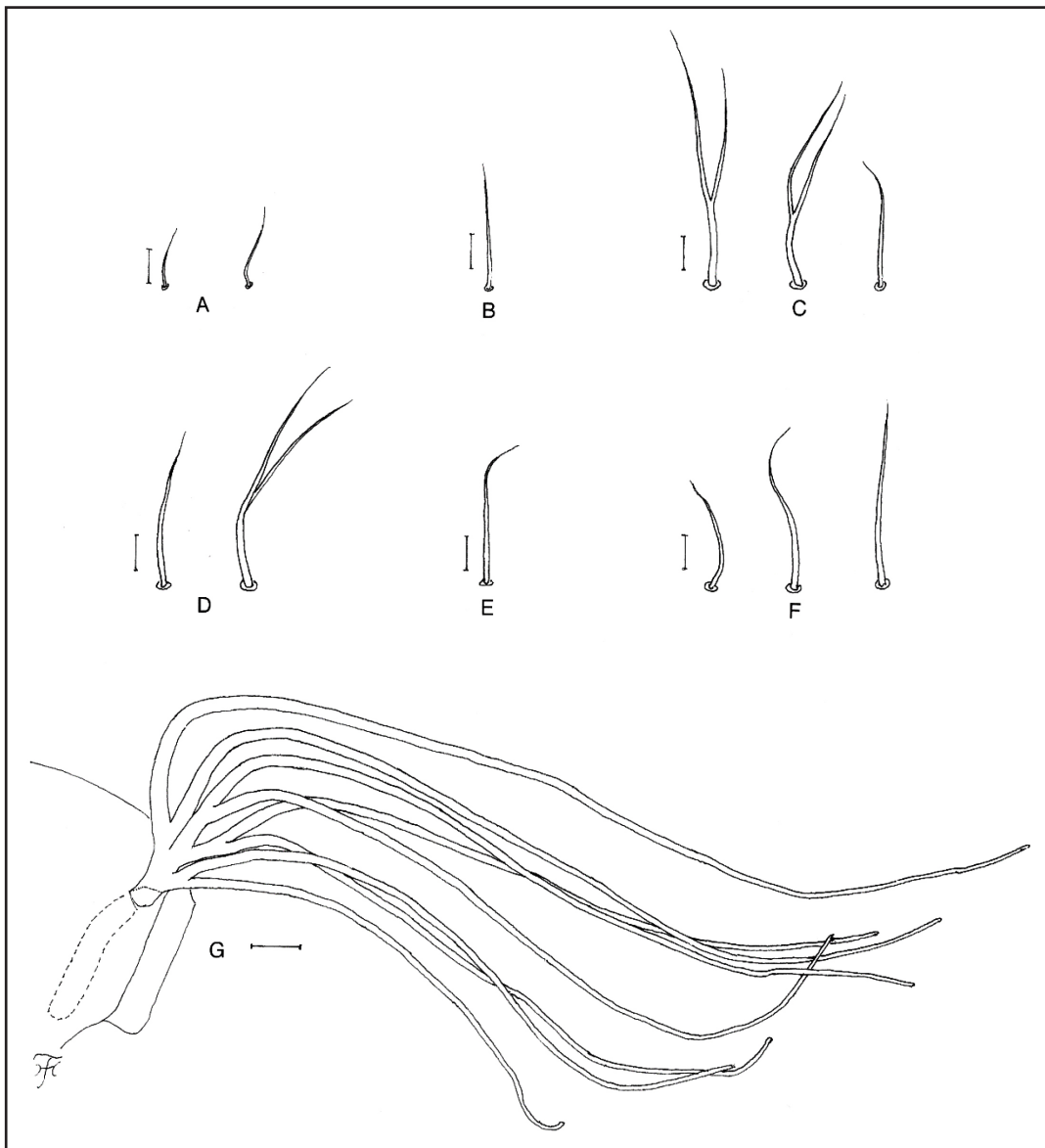


Figure 10. Pupa of *S. (S.) fenestratum*. A, Frontal trichomes. B, Facial trichome. C–F, Thoracic trichomes (C, anterodorsal; D, anterolateral, E, mediolateral, F, ventrolateral). G, Gill filaments (right side; outer view). Scale bars. 0.1 mm for G; 0.02 mm for A–F.

Remarks. *Simulium (S.) fenestratum* was described based on adult females and males (dissected from pupae), pupae and mature larvae from Middle Sumatra, Indonesia by Edwards (1934), and later recorded from the Nansei Islands in Japan, Thailand and Laos. The species regarded as *S. (S.) fenestratum* from the Nansei Islands by Ogata (1966) was found to be a new species and described as *S. (S.) sakishimaense* by Takaoka (1977). The population of this species from Thailand was recently reported to be genetically different from that from Sumatra by Hew *et al.* (2023). This species was suspected to be a species-complex based on the findings that there were two types in the male and larva in Sumatra: i.e., the male hind basitarsus is entirely darkened in one type, but dark except its basal portion yellow in the other type, and the larval abdomen is furnished with paired protuberances dorsally in one type but without such protuberances in the other type (Takaoka *et al.*, 2000).

This species is characterized in the male by the number of upper-eye (large) facets in 16 vertical columns and 17 horizontal rows, hind basitarsus dark brown to brownish black except its basal one-third dark yellow, 3.9 times as long as its greatest width (Figure 9B), and slightly narrower than the hind tibia and femur, and ventral plate slightly longer than wide when viewed ventrally (Figure 9C), with its ventromedial process parallel-sided and about half as wide as

the greatest width of the ventral plate when viewed caudally (Figure 9G); and in the pupa by the gill with eight filaments moderately divergent when viewed laterally (Figure 10G) and anterodorsal thoracic trichomes, of which one or two are branched (Figure 10C).

This species is similar in the male to *S. (S.) sakishimaense* from Japan (Takaoka, 1977) in many characteristics including the number of upper-eye (large) facets in 16 vertical columns and 17 horizontal rows (17 vertical columns and 17 horizontal rows in *S. (S.) sakishimaense*), and the hind basitarsus slightly narrower than the hind tibia and femur, but differs from the latter species by the fore basitarsus 5.3 times as long as its greatest width (6.7 times in *S. (S.) sakishimaense*), hind basitarsus dark yellow on the basal one-third (clear yellow on the basal two-fifths in *S. (S.) sakishimaense*), and ventral plate longer than wide when viewed ventrally (Figure 9C), with its ventromedial process about half as wide as its greatest width of the ventral plate when viewed caudally (Figure 9G) (ventral plate slightly shorter than wide, and its ventromedial process 0.4 times as wide as the greatest width of the ventral plate in *S. (S.) sakishimaense*).

The species regarded as *S. (S.) fenestratum* from Thailand and Laos should be reexamined in future studies.

Table 1. Comparisons of male and pupal morphological characteristics of four species of the *S. multistriatum* species-group in Sumatra, Indonesia

Species names	Male			Pupa		
	Numbers of large facets in vertical columns (V) and horizontal rows (H)	Color of hind basitarsus	Relative length of body of ventral plate to its width when viewed ventrally	Relative width of ventromedial process to width of ventral plate when viewed caudally	Angle formed between stalks of dorsal and ventral pairs of filaments when viewed laterally	Shapes of anterodorsal trichomes on thorax
<i>S. mutaralamense</i> sp. nov.	18 or 19 V, 19 or 20 H	Entirely dark	Slightly shorter than wide	0.4	130–140°	Bifid, trifid and unbranched
<i>S. lubuksulasihense</i> sp. nov.	17 or 18 V, 18 H	Dark except basal 1/3 yellow	Slightly shorter than wide	0.3	140°	Bifid, trifid and unbranched
<i>S. liwaense</i> sp. nov.	14 or 15 V, 16 H	Dark except basal 1/3 yellow	Slightly shorter than wide	0.36	90°	All three unbranched
<i>S. fenestratum</i>	16 V, 17 H	Dark except basal 1/3 dark yellow	1.1 times as long as wide	0.5	90°	Bifid and unbranched

SUMMARY

The aim of this study to revise the morphology of *S. (S.) fenestratum*, a widely distributed species, based on specimens collected from Sumatra (its type locality) was not completed because its male and pupal specimens were scarce, and its female and larval specimens were not available. However, morphological characteristics of its male and pupa revised here are hopefully helpful in future studies on the species regarded as *S. (S.) fenestratum* in Thailand and Laos.

In the course of this study, three new species in the *S. multistriatum* species-group were found, unveiling the species diversity of this species-group in Sumatra. All three new species and one known species, *S. (S.) fenestratum*, are similar in many characteristics but are distinguished from one another by the subtle differences of a few morphological features, such as the number of male upper-eye (large) facets, color of the male hind basitarsus, shape of the ventral plate and its ventromedial process, and the extent of the divergence of the pupal gill filaments (Table 1), suggesting a common ancestor.

DNA sequence-based and chromosomal analyses for the phylogenetic relationships of these four species, as well as observations of morphological characteristics of the larval stage of each species, remained to be done in future studies.

ACKNOWLEDGEMENTS

I am most grateful to Dr. P.H. Adler, Professor Emeritus, Clemson University, U.S.A. for his kindness in reading the draft and providing valuable suggestions. Thanks are due to Dr. M. Fukuda, Oita University, for scanning line-drawings, and Dr. V.L. Low, Executive Director, Higher Institution Centre of Excellence (HiCoE), Tropical Infectious Diseases Research and Education Centre (TIDREC), Universiti Malaya, who helped in the submission of the manuscript to Tropical Biomedicine. This study was supported by Indonesian Institute of Sciences (LIPI) and by the Ministry of Education, Science and Culture, Japan (grant no. 03041065 to Prof. I. Miyagi, and grant no. 11670246 to H. Takaoka).

Declaration of Competing Interest

I declare that this is my original work. It has not been published elsewhere and I have no conflicts of interest concerning the work reported in this paper. The author has contributed to this study throughout the study design, field work, data collection, data analyses and data interpretation.

REFERENCES

- Adler, P.H. (2025). World blackflies (Diptera: Simuliidae): a comprehensive revision of the taxonomic and geographical inventory [2025]. <https://biomia.sites.clemson.edu/pdfs/blackflyinventory.pdf>
- Adler, P.H. & Crosskey, R.W. (2017). World blackflies (Diptera: Simuliidae): a comprehensive revision of the taxonomic and geographical inventory [2017].
- Adler, P.H., Currie, D.C. & Wood, D.M. (2004). The black flies (Simuliidae) of North America. New York: Cornell University Press, Ithaca, pp. xv+941.
- Adler, P.H., Fukuda, M., Takaoka, H., Reeves, W.K., Kim, S.K. & Otsuka, Y. (2019). Revision of *Simulium rufibasis* (Diptera: Simuliidae) in Japan and Korea: chromosomes, DNA, and morphology. *Journal of Medical Entomology* **57**: 388-403. <https://doi.org/10.1093/jme/tjz197>
- Aupalee, K., Saeung, A., Srisuka, W., Fukuda, M., Streit, A. & Takaoka, H. (2020). Seasonal filarial infections and their black fly vectors in Chiang Mai Province, northern Thailand. *Pathogens* **9**: 512. <https://doi.org/10.3390/pathogens9060512>
- Brunetti, E. (1911). New Oriental Nematocera. *Records of Indian Museum* **4**: 282-288.
- Edwards, F.W. (1928). Diptera Nematocera from the Federated Malay States Museums. *Journal of Federated Malay State Museum* **14**: 1-139.
- Edwards, F.W. (1934). The Simuliidae (Diptera) of Java and Sumatra. *Deutsche Limnologische Sunda-Expedition. Archiv für Hydrobiologie* **13**: 92-138.
- Fukuda, M., Choochote, W., Bain, O., Aoki, C. & Takaoka, H. (2003). Natural infections with filarial larvae in two species of black flies (Diptera: Simuliidae) in northern Thailand. *Japanese Journal of Tropical Medicine and Hygiene* **31**: 99-102. <https://doi.org/10.2149/tmh1973.31.99>
- Hew, Y.X., Ya'cob, Z., Adler, P.H., Chen, C.D., Lau, K.W., Sofian-Azirun, M., Muhammad-Rasul, A.H., Putt, Q.Y., Izwan-Anas, N., Hadi, U.K. *et al.* (2023). DNA barcoding of black flies (Diptera: Simuliidae) in Indonesia. *Parasites & Vectors* **16**: 248. <https://doi.org/10.1186/s13071-023-05875-1>
- Huang, L., Zhang, C.L. & Chen, H.B. (2013). A new species of the genus *Simulium* from Sichuan, China. *Acta Zootaxonomica Sinica* **38**: 368-371.
- Low, V.L., Adler, P.H., Sofian-Azirun, M., Srisuka, W., Saeung, A., Huang, Y.T., Hadi, U.K., Pham, X.D. & Takaoka, H. (2015). Tests of conspecificity for allopatric vectors: *Simulium nodosum* and *Simulium shirakii* (Diptera: Simuliidae) in Asia. *Parasites & Vectors* **8**: 295. <https://doi.org/10.1186/s13071-015-0911-5>
- Ogata, K. (1966). Additional notes on Simuliidae of the Ryukyu Islands (Diptera). *Kontyu* **34**: 123-130.
- Puri, I.M. (1933). Studies on Indian Simuliidae. Part VII. Descriptions of larva, pupa and female of *Simulium nodosum* sp. nov. with an appendix dealing with *S. novolineatum* nov. nom. (= *S. lineatum* Puri). *Indian Journal of Medical Research* **20**: 813-817.

- Takaoka, H. (1977). Studies on blackflies of the Nansei Islands, Japan (Simuliidae; Diptera). III. On six species of the subgenus *Simulium* Latreille. *Japanese Journal of Sanitary Zoology* **28**: 193-217. <https://doi.org/10.7601/mez.28.193>
- Takaoka, H. (2003). The black flies (Diptera: Simuliidae) of Sulawesi, Maluku and Irian Jaya. Japan, Fukuoka: Kyushu University Press, pp. xxii+581.
- Takaoka, H. (2024). The black flies of Subtropical and Tropical Asia: taxonomy and Biology. Singapore: Springer, pp. xiv+751.
- Takaoka, H., Choochote, W., Aoki, C., Fukuda, M. & Bain, O. (2003). Black flies (Diptera: Simuliidae) attracted to humans and water buffalos and natural infections with filarial larvae, probably *Onchocerca* sp., in northern Thailand. *Parasite* **10**: 3-8. <https://doi.org/10.1051/parasite/2003101p3>
- Takaoka, H. & Davies, D.M. (1995). The black flies (Diptera: Simuliidae) of West Malaysia. Japan, Fukuoka: Kyushu University Press, pp. viii+175.
- Takaoka, H. & Davies, D.M. (1996). The black flies (Diptera: Simuliidae) of Java, Indonesia. U.S.A., Honolulu: Bishop Museum Press, Bishop Museum Bulletin in Entomology 6, pp. viii+81 pp.
- Takaoka, H. & Kuvangkadilok, C. (1999). Four new species of black flies (Diptera: Simuliidae) from Thailand. *Japanese Journal of Tropical Medicine and Hygiene* **27**: 497-509. <https://doi.org/10.2149/tmh1973.27.497>
- Takaoka, H., Low, V.L., Huang, Y.T., Fukuda, M. & Ya'cob, Z. (2021). Two new black fly species of the *Simulium* (*Simulium*) *rufibasis* subgroup (Diptera: Simuliidae) from Taiwan. *Tropical Biomedicine* **38**: 403-412. <https://doi.org/10.47665/tb.38.3.081>
- Takaoka, H. & Saito, K. (1996). A new species and new records of black flies (Diptera: Simuliidae) from Thailand. *Japanese Journal of Tropical Medicine and Hygiene* **24**: 163-169. <https://doi.org/10.2149/tmh1973.24.163>
- Takaoka, H., Shrestha, S. & Dangi, N. (2020). Four new species of the *Simulium* (*Simulium*) *tuberosum* species-group (Diptera: Simuliidae) from Nepal. *Medical Entomology and Zoology* **71**: 307-328. <https://doi.org/10.7601/mez.71.307>
- Takaoka, H., Srisuka, W., Low, V.L. & Saeung, A. (2019). Morphological and molecular analyses of *Simulium rufibasis* (Diptera: Simuliidae) in Thailand. *Journal of Medical Entomology* **56**: 408-415. <https://doi.org/10.1093/jme/tjy180>
- Takaoka, H., Sofian-Azirun, M., Ya'cob, Z., Chen, C.D., Lau, K.W. & Pham, X.D. (2015). The black flies (Diptera: Simuliidae) from Thua Thien Hue and Lam Dong Provinces, Vietnam. *Zootaxa* **3961**: 1-96. <https://doi.org/10.11646/zootaxa.3961.1.1>
- Takaoka, H., Sofian-Azirun, M., Ya'cob, Z., Chen, C.D., Lau, K.W., Low, V.L., Pham, X.D. & Adler, P.H. (2017). The black flies (Diptera: Simuliidae) of Vietnam. *Zootaxa* **4261**: 1-165. <https://doi.org/10.11646/zootaxa.4261.1.1>
- Takaoka, H., Yunus, M., Hadi, U.K., Sigit, S.H. & Miyagi, I. (2000). Preliminary report of faunistic surveys on black flies (Diptera: Simuliidae) in Sumatra, Indonesia. *Japanese Journal of Tropical Medicine and Hygiene* **28**: 157-166. <https://doi.org/10.2149/tmh1973.28.157>
- Thajjarern, J., Wongpakam, K., Kangrang, A. & Pramual, P. (2019). A new species of black fly (Diptera: Simuliidae) in the *Simulium* (*Simulium*) *multistriatum* species-group from Thailand. *Zootaxa* **4586**: 461-474. <https://doi.org/10.11646/zootaxa.4586.3.4>