



## RESEARCH ARTICLE

## Four new species of black flies (Diptera: Simuliidae) from Sumatra, Indonesia

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## ARTICLE HISTORY

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## ABSTRACT

Four new species of black flies are described based on the females, males and pupae from Sumatra, Indonesia, and are assigned to three species-groups in two subgenera of the genus *Simulium* Latreille s. l.: *Simulium (Gomphostilbia) kandisense* sp. nov. in the *S. asakaoae* species-group, *S. (Simulium) kotsuboyui* sp. nov. and *S. (S.) solokense* sp. nov. in the *S. iridescent* species-group, and *S. (S.) bengkuruense* sp. nov. in the *S. striatum* species-group. The two new species in the *S. iridescent* species-group and one new species in the *S. striatum* species-group were formerly regarded as *S. (S.) iridescent* De Meijere and *S. (S.) argyrocinatum* De Meijere, respectively, in Sumatra, although these two species were originally described from Java and later recorded from Sumatra. The number of male upper-eye (large) facets, the presence or absence of tubercles on the pupal head and thorax, and the arrangement and relative thickness of pupal gill filaments were useful for separating these three new species from the two known species. This study increased the number of species of black flies in Sumatra from 27 to 31. However, records of some old species including *S. (S.) iridescent* and *S. (S.) argyrocinatum* should be reconfirmed for their distribution in Sumatra by future surveys.

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

## INTRODUCTION

Black flies (Diptera: Simuliidae) are medically and veterinarily important insects as pests and vectors of parasites in humans and animals (Crosskey, 1990). To accurately identify pest and vector species, exploring the fauna of black flies in the areas concerned is prerequisite.

The black fly fauna of Sumatra, Indonesia was first reported by Edwards (1925, 1934), who recorded nine species. Takaoka & Davies (1995) described a new species, *Simulium (Nevermannia) glatthaari*. Hadi *et al.* (1996) showed that *S. (Simulium) eximium* De Meijere from Sumatra chromosomally differs from that from Java. Takaoka & Sigit (1997) described three new species, *S. (Gomphostilbia) padangense*, *S. (S.) minangkabaum* and *S. (S.) sumatraense*. Takaoka *et al.* (2000) newly recorded 12 species and treated *S. (S.) eximium* from Sumatra as *S. (S.) sp. nr. eximium* based on their surveys carried out in 1992 and 1994. Takaoka (2003) maintained Sumatra as one of the distribution islands of *S. (S.) eximium* in his list of the Oriental black flies. Takaoka *et al.* (2006b) treated *S. (S.) sp. nr. eximium* as a new species and described it as *S. (S.) ranauense*. The black fly fauna of Sumatra is now represented by 27 species of the genus *Simulium* Latreille s. l., which are further classified in three subgenera: 12 species in the subgenus *Gomphostilbia* Enderlein, three species in the subgenus *Nevermannia* Enderlein, and 12 species in the subgenus *Simulium* Latreille s. str. (Adler, 2025; Takaoka, 2024).

The biting habits of black flies in Sumatra are not well documented except for three species, which are also distributed in Java: *S. (G.) atratum* De Meijere, which was feeding on blood of domestic fowl; *S. (S.) argyrocinatum* De Meijere, which was a pest of cattle, water buffalos and horses; and *S. (S.) iridescent* De Meijere, which attacked cattle, all reported from Java by Friederichs (1925).

Four undescribed species of black flies were found when adult black flies reared from pupae collected in Sumatra in 1992 and 1994 were reexamined. These species are described as new species.

## 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 using a camera-lucida (Olympus U-DA) attached to a biological microscope (Olympus BX-50), 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 in vials with 80% ethanol are deposited in the Department of Entomology, Queen Sirikit Botanic Garden, Chiang Mai, Thailand.

## RESULTS AND DISCUSSION

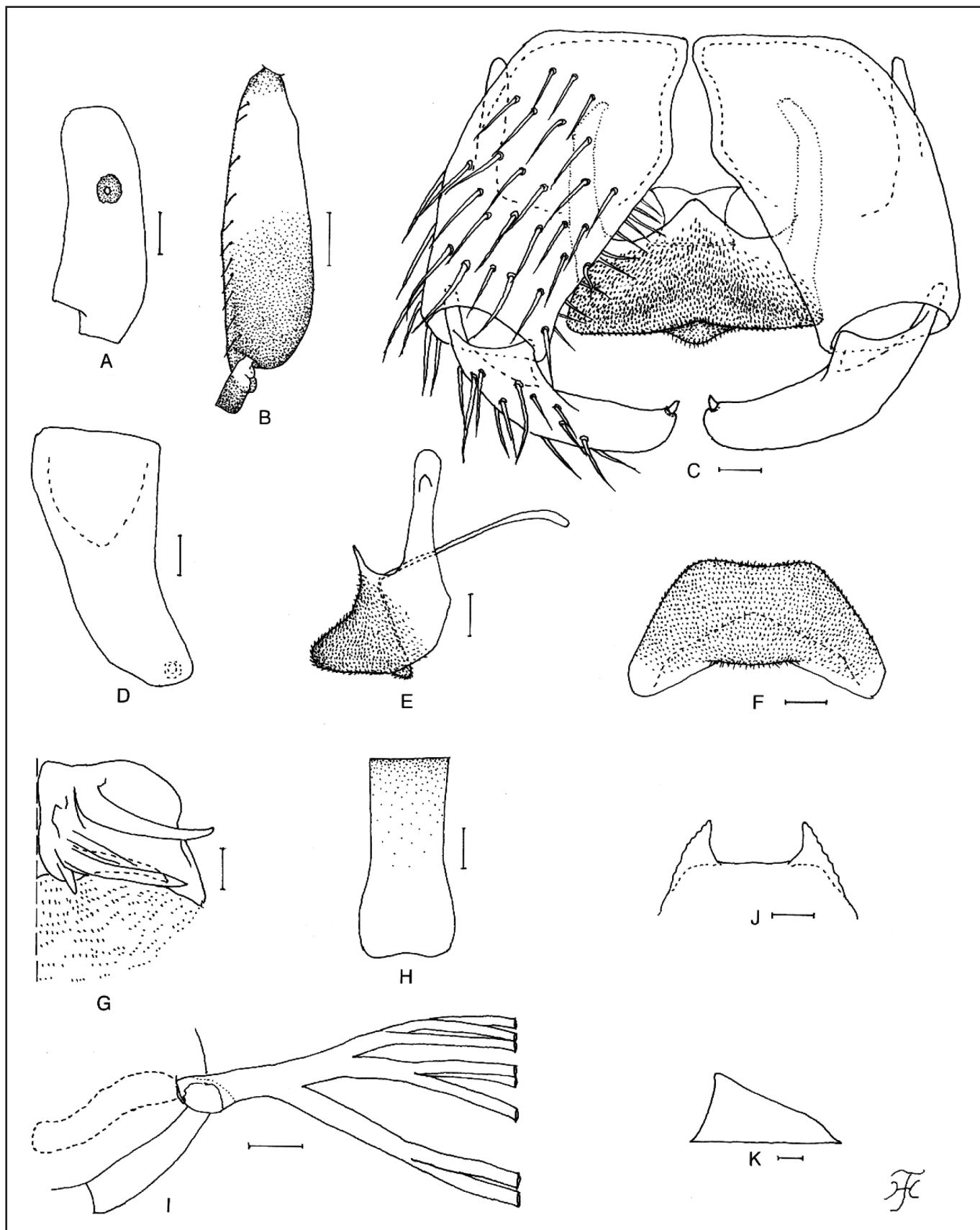
The present reexamination of adults and their pupal exuviae and cocoons shows that there are four new species. They are described herein, and taxonomic notes to separate them from their related species are given.

### *Simulium (Gomphostilbia) kandisense* sp. nov.

**Male (n=1).** Body length 2.2 mm. **Head.** Slightly wider than thorax. Upper eye consisting of 13 vertical columns and 15 horizontal rows of large facets. Face dark brown, whitish pruinose. Clypeus dark brown, whitish pruinose, densely covered with yellow scale-like medium-long hairs (mostly directed upward) interspersed with few light brown unbranched longer hairs. Antenna (color faded) composed of scape, pedicel and nine flagellomeres; first flagellomere elongate, 1.7 times as long as second one. Maxillary palpus light to medium brown, with five segments, proportional lengths of third, fourth, and fifth segments 1.0:1.1:2.4; third segment (Figure 1A) slightly widened apically; sensory vesicle (Figure 1A) globular, small, 0.11 times length of third segment, and with small opening. **Thorax** (color somewhat faded). Scutum light brown, shiny and thinly white pruinose on each shoulder, on broad area along each lateral margin and on prescutellar area when illuminated at certain angles; scutum densely covered with golden-yellow recumbent short hairs. Scutellum light brown, with yellow short hairs and dark brown longer upright hairs along posterior margin. Postnotum light brown, shiny and white pruinose when viewed at certain angles and bare. Pleural membrane bare. Katepisternum light brown, moderately covered with yellow fine hairs mixed with dark brown ones. **Legs** (color partially faded). Foreleg: coxa and trochanter whitish yellow; femur yellow; tibia whitish except apical one-fourth or little more medium brown, and with white sheen on outer surface of basal three-fourths; tarsus medium brown; basitarsus moderately dilated, 6.8 times as long as its greatest width. Midleg: coxa light brown except posterior surface dark brown; trochanter whitish yellow; femur light brown except base yellow (though apical extreme yellow); tibia light to medium brown except basal one-third or little more whitish; tarsus medium brown except basal one-third of basitarsus yellow (though its border not well defined). Hind leg: coxa light brown; trochanter yellow; femur medium brown with base yellow and apical cap dark brown (though apical extreme yellow); tibia medium brown except basal half whitish; tarsus medium brown except basal half of basitarsus (though base darkened) and basal half of second tarsomere yellowish; basitarsus (Figure 1B) enlarged, wedge-shaped, 3.6 times as long as wide, and as wide as greatest width of tibia and femur; calcipala nearly as long as basal width, and 0.2 times as wide as greatest width of basitarsus; pedisulcus well defined. **Wing.** Length 2.2 mm. Costa with rows of dark brown spinules and yellow short hairs except basal short portion with patch of yellow short hairs and lacking dark brown spinules. Subcosta without hairs. Hair tuft on base of radial vein dark brown. Basal portion of radius fully haired;  $R_1$  with dark spinules and hairs;  $R_2$  with hairs only. Basal cell absent. **Halter.** White. **Abdomen.** Basal scale medium brown, with fringe of light brown hairs. Dorsal surface of abdomen medium brown to brownish black, moderately covered with dark-brown short to long hairs; segments 2 and 5–7 each with pair of shiny white dorsolateral or lateral patches. **Genitalia.** Coxite in ventral view (Figure 1C) nearly rectangular, though much narrowed posteriorly, 1.8 times as long as its greatest width. Style in ventral view (Figure 1C) bent inward, nearly parallel-sided, rounded apically and with apical spine; style in ventrolateral view (Figure 1D) 0.9 times length of coxite, 2.2 times as long as its basal width, gently bent inward, and tapered slightly from base toward apex. Ventral plate in ventral view (Figure 1C) with body transverse, 0.6 times as long as wide, with lateral margins somewhat depressed medially, with anterior margin produced anteromedially, and posterior margin slightly concave ventromedially, though convex dorsomedially, and densely covered

with microsetae on ventral surface; basal arms of moderate length, directed forward, then slightly convergent apically; ventral plate in lateral view (Figure 1E) moderately produced ventrally; ventral plate in caudal view (Figure 1F) produced ventrally, its ventral margin slightly depressed medially, and densely covered with minute setae on posterior surface. Median sclerite in caudal view (Figure 1H) thin, plate-like, and wide. Paramere (Figure 1G) of moderate size, with three long and one short stout hooks. Aedeagal membrane (Figure 1G) sparsely setose.

**Pupa (n=1).** Body length 2.8 mm. **Head.** Integument yellow, moderately covered with small round tubercles; antennal sheath without any protuberances; face with pair of unbranched long trichomes with coiled or uncoiled apices, and frons with three pairs of unbranched long trichomes with coiled or uncoiled apices; three frontal trichomes on each side arising close together, subequal in length to one another and slightly longer than facial one. **Thorax.** Integument yellow, moderately covered with round tubercles except posterior half somewhat sparsely covered with smaller tubercles, with three long dorsomedial trichomes with coiled apices, two long anterolateral trichomes (one with coiled apex, another one with uncoiled apex), one medium-long mediolateral trichome with uncoiled apex, and three ventrolateral trichomes with uncoiled apices (one medium-long, two short) on each side; all trichomes unbranched. Gill (Figure 1I) composed of eight slender thread-like filaments, arranged as (3+3)+2 from dorsal to ventral, with medium-long common basal stalk having somewhat swollen basal fenestra at base; common basal stalk 0.9 times length of interspiracular trunk; dorsal and middle triplets sharing short stalk and each with three filaments arising at almost same level from short stalk; ventral paired filaments with medium-long stalk which is nearly as long as common basal stalk and 0.9 times length of interspiracular trunk; stalk of ventral pair 1.2 times as thick as primary stalk of middle triplet, 1.3 times as thick as primary stalk of dorsal triplet, and 0.9 times as thick as common stalk of dorsal and middle triplets; primary stalk of dorsal triplet lying against stalk of ventral pair at angle of 60 degrees when viewed laterally; all filaments grayish light brown, gradually tapered toward apices; six filaments of middle and dorsal triplets subequal in length (2.1–2.4 mm long including their own stalks, their common stalk and common basal stalk) and thickness to one another (though three filaments of dorsal triplet slightly thinner than those of middle triplet); two filaments of ventral pair subequal in length (2.8 mm long including their own stalk and common basal stalk) and thickness to each other, and 1.25 times as thick as three filaments of middle triplet when compared basally; cuticle of all filaments with well-defined annular ridges and furrows except near apices nearly smooth, and densely covered with minute tubercles. **Abdomen.** Dorsally, segments 1 and 2 not pigmented and without tubercles; segment 1 with one unbranched slender short hair-like seta on each side; segment 2 with one unbranched slender short hair-like seta and five extremely short somewhat spinous setae submedially on each side; segments 3 and 4 each with four hooked spines and one short somewhat spinous seta on each side; segment 5 lacking spine-combs; segments 6–9 each with spine-combs in transverse row and comb-like groups of minute spines on each side; segment 9 with pair of triangular, flat terminal hooks, of which outer margins are 1.6–1.7 times length of inner margins and crenulated (Figure 1J). Ventrally, segment 4 with one unbranched hook and few slender short setae on each side; segment 5 with pair of bifid hooks submedially and few slender short setae on each side; segments 6 and 7 each with pair of bifid inner and unbranched outer hooks somewhat spaced from each other and few unbranched slender extremely short setae on each side; segments 4–8 each with comb-like groups of minute spines. Each side of segment 9 with three grapnel-shaped hooklets. **Cocoon** (Figure 1K). Wall pocket-shaped, thinly and moderately woven, not extended ventrolaterally; anterior margin thickly woven; posterior half with floor roughly or moderately woven; individual threads visible; 3.0 mm long by 1.0 mm wide.



**Figure 1.** Male and pupa of *S. (G.) kandisense* sp. nov. A–H, Male; I–K, Pupa. A, Third segment of maxillary palpus with sensory vesicle (left side; front view). B, Hind basitarsus and second tarsomere (left side; outer view). C, Coxites, styles, ventral plate and median sclerite (ventral view). D, Style (right side; ventrolateral view). E, Ventral plate and median sclerite (lateral view). F, Ventral plate (caudal view). G, Paramere and aedeagal membrane (left side; caudal view). H, Median sclerite (caudal view). I, Basal portion of gill filaments (right side; lateral view). J, Terminal hooks (caudal view). K, Cocoon (lateral view). Scale bars. 0.5 mm for K; 0.1 mm for B & I; 0.02 mm for A, C–H & J.

**Female and Mature larva.** Unknown.

**Type specimen.** Holotype: Male (with its associated pupal exuviae and cocoon) reared from a pupa, collected from a brook (width 1.0 m, exposed to the sun, flow slow, 30 °C, elevation ca. 120 m), at Tigosakato, Tanjung Kandis, Padang, West Sumatra, Indonesia, 10-VIII-1994, by H. Takaoka.

**Biological notes.** The pupa of this new species was collected from a slender plant root in flowing water. Associated species were *S. (G.) friedrichsi* Edwards, *S. (G.) atratum*, and *S. (N.) aureohirtum* Brunetti.

**Etymology.** The species name *kandisense* is after Kandis, a kingdom based in the western-central region of Sumatra in the 14th century.

**Remarks.** This new species is assigned to the *S. asakoae* species-group of the subgenus *Gomphostilbia*, redefined by Takaoka (2024), by having the male fore coxa yellow, hind basitarsus enlarged (Figure 1B), and ventral plate with its lateral margins depressed medially when viewed ventrally (Figure 1C), although the dark brown hair tuft at the base of the radial vein departs from its definition.

Of the 71 species of the *S. asakoae* species-group (Adler, 2025), this new species is exceptional by having a tuft of dark brown hairs at the base of the radian vein, a characteristic shared by only four species, i.e., *S. (G.) nepalense* Lewis from Nepal, *S. (G.) inthanonense* Takaoka & Suzuki from Thailand, *S. (G.) rutengense* Takaoka, Hadi & Sigit from Indonesia, and *S. (G.) yunnanense* Chen & Zhang from China (Takaoka, 2024). However, this new species is easily distinguished from *S. (G.) nepalense* by the male scutum covered with yellow hairs and hind tibia yellow on the basal half (c.f., the male scutum covered with brassy hairs and hind tibia yellow on the basal two-fifths in *S. (G.) nepalense*), and from the three other species by the male upper-eye (large) facets in 13 vertical columns and 15 horizontal rows (c.f., 17 vertical columns and 17 or 18 horizontal rows in *S. (G.) inthanonense*, 11 vertical columns and 13 horizontal rows in *S. (G.) rutengense*, and 11 vertical columns and 14 horizontal rows in *S. (G.) yunnanense*) (Takaoka, 2024).

Apart from the difference in color of wing tuft hairs, this new species appears to be related to the following species by having the similar shape of the ventral plate, i.e., its posterior margin somewhat produced dorsomedially when viewed ventrally (Figure 1C) and its ventral margin depressed medially when viewed caudally (Figure 1F): *S. (G.) confertum* Takaoka & Sofian-Azirun from Vietnam, which is also similar to this new species in having the upper-eye (large) facets in 14 vertical columns and 15 horizontal rows, and pupal terminal hooks with their outer margins 1.8–2.2 times as long as their inner margins, but differs in the male by the spindle-shaped hind basitarsus narrower than the hind tibia, and in the pupa by the extremely short common stalk of the upper and middle triplets of the gill (Takaoka *et al.*, 2015); *S. (G.) phapeungense* Takaoka, Srisuka & Fukuda from Thailand, which has a similar arrangement of the pupal gill but differs in the male by the upper-eye (large) facets in 11 vertical columns and 13 horizontal rows and hind basitarsus 1.2 times as wide as the hind femur, and in the pupa by the terminal hooks with their outer margins 2.5–2.6 times as long as their inner margins; *S. (G.) pitasawatae* Takaoka, Srisuka & Saeung from Thailand, which is also similar in having the upper-eye (large) facets in 13 or 14 vertical columns and 15 horizontal rows and hind basitarsus as wide as the hind tibia and femur, but differs in the male by the narrower fore basitarsus 7.9–8.3 times as long as its greatest width, and in the pupa by the extremely short stalk of the upper triplet of the gill and much wider terminal hooks with their outer margins 3.6–3.9 times as long as their inner margins (Takaoka *et al.*, 2020b); *S. (G.) kiewfinense* Takaoka, Srisuka & Fukuda from Thailand, which is also similar in the arrangement of the pupal gill filaments, but differs in the male by the upper-eye (large) facets in 16 or 17 vertical columns and 16 or 17 horizontal rows and hind basitarsus 0.9 times as wide as the hind tibia and yellow on the basal two-fifths or little less than the basal half, and in the pupa by the terminal hooks with their outer margins 2.3–2.7 times as long as their inner margins (Takaoka *et al.*, 2020b);

and *S. (G.) tanahrataense* Takaoka, Sofian-Azirun & Hashim from Peninsular Malaysia, which has similar male upper-eye (large) facets in 14 vertical columns and 15 horizontal rows and the ventral plate with its ventral margin depressed medially when viewed caudally (though its posterior margin is not produced posteromedially when viewed ventrally) and similar arrangement of the pupal gill filaments, but differs in the male by having the narrower fore basitarsus 7.5–7.7 times as long as its greatest width, hind tibia yellow on the basal one-third or little more and subcosta with 6–12 hairs, and in the pupa by the wider terminal hooks with their outer margins 2.7–2.8 times as long as their inner margins (Takaoka *et al.*, 2014b).

*Simulium (G.) namense* Takaoka from Myanmar has similar male upper-eye (large) facets in 14 vertical columns and 15 horizontal rows but differs from this new species by having a slender male fore basitarsus 9.0 times as long as its greatest width and ventral plate slightly narrowed posteriorly when viewed ventrally (Takaoka, 1989). *Simulium (G.) namense* was wrongly assigned to the *S. asakoae* species-group by Takaoka (2024). It is here transferred to the *S. ceylonicum* species-group based on the shape of the ventral plate, which is slightly narrowed posteriorly when viewed ventrally and has its ventral margin produced medially when viewed caudally (Takaoka, 1989).

This new species is distinguished from the three members of the *S. asakoae* species-group recorded from Indonesia, i.e., *S. (G.) brevilabrum* Takaoka, Sigit & Hadi, *S. gyorkosae* Takaoka & Davies and *S. (G.) rutengense*, in the male by the upper-eye (large) facets in 13 vertical columns and 15 horizontal rows (c.f., 10 or 11 vertical columns and 13 horizontal rows in the three latter species) and ventral plate with its ventral margin depressed medially when viewed caudally (Figure 1F) (c.f., its ventral margin rounded when viewed caudally in the three latter species), and in the pupa from *S. (G.) brevilabrum* by the gill with eight filaments (Figure 1I) (c.f., gill with four filaments in *S. (G.) brevilabrum*), from *S. (G.) rutengense* by the terminal hooks with their outer margins 1.6–1.7 times as long as their inner margins (Figure 1J) (c.f., their outer margins 2.7 times as long as their inner margins in *S. (G.) rutengense* and from *S. (G.) gyorkosae* by the simple wall pocket-shaped cocoon (Figure 1K) (c.f., cocoon with a short anterodorsal projection in *S. (G.) gyorkosae*) (Takaoka & Davies, 1996; Takaoka *et al.*, 2006a).

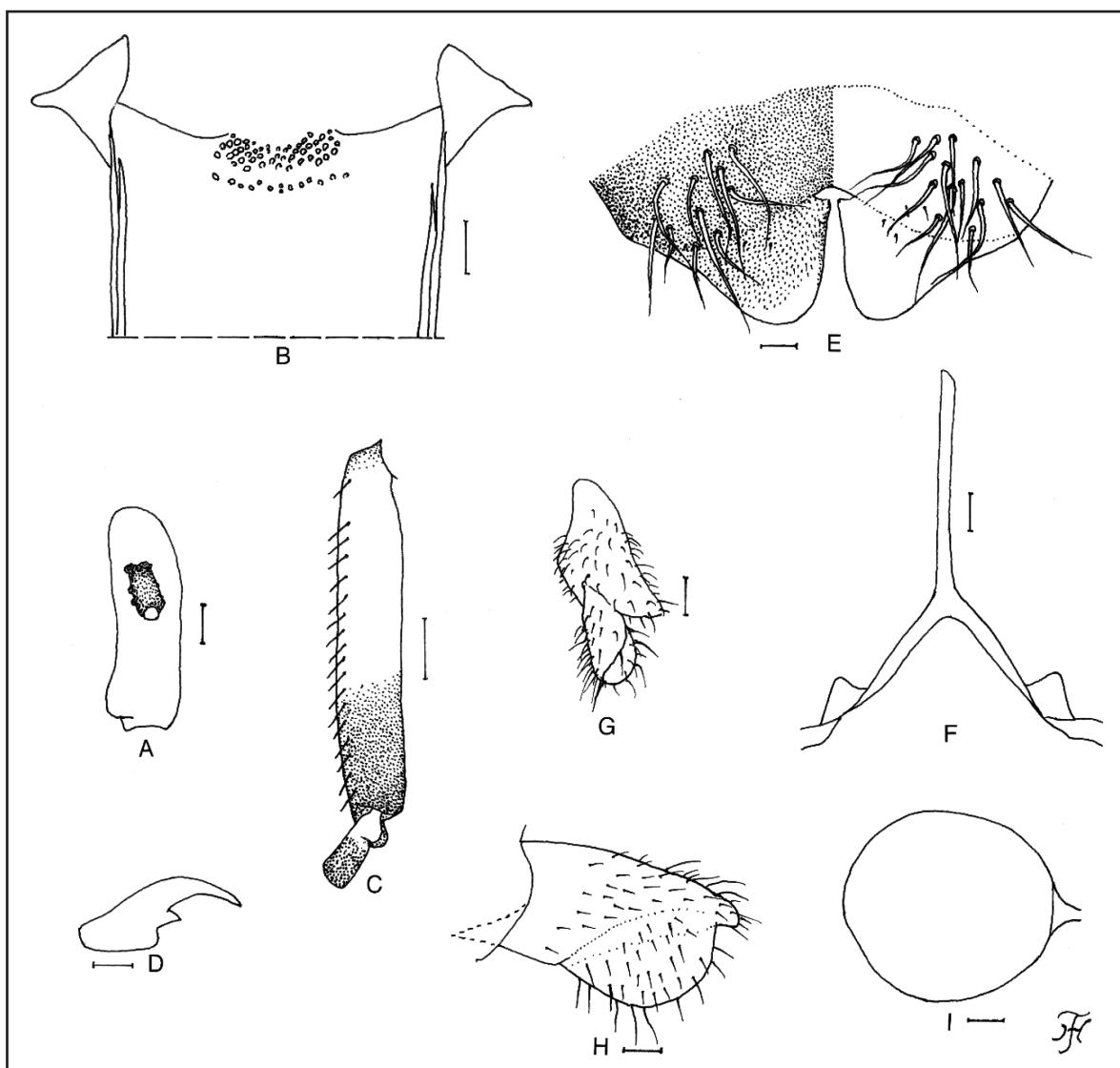
#### *Simulium (Simulium) kotsuboyui* sp. nov.

*Simulium (Simulium) iridescent* (nec De Meijere), part: Takaoka *et al.*, 2000: 163.

**Female** (n=6). Body length 2.3–2.5 mm. **Head.** Slightly narrower than thorax. Frons brownish black, shiny, with several dark stout hairs along lateral margin on each side and near antennal base; frontal ratio 1.2:1.0:1.1; frons:head ratio 1.0:4.1–4.2. Fronto-ocular area of moderate size, rounded apically. Clypeus brownish black, shiny, moderately covered with dark brown medium-long hairs. Labrum 0.72–0.75 times length of clypeus. Antenna composed of scape, pedicel and nine flagellomeres, and light to medium brown except scape, pedicel and base of first flagellomere yellow. Maxillary palpus with five segments, light brown; proportional lengths of third, fourth, and fifth segments 1.0:1.0–1.2:1.9–2.2; third segment (Figure 2A) slender, with sensory vesicle (Figure 2A) medium-sized, ellipsoidal, 0.22–0.29 times length of third segment, having small opening. Maxillary lacinia with 11 or 12 inner and 14 or 15 outer teeth. Mandible with 27 or 28 inner and 11 or 12 outer teeth. Cibarium (Figure 2B) with 56–61 round processes near posterodorsal margin; each cornua triangular. **Thorax.** Scutum brownish black, shiny, unpatterned, densely covered with coppery fine recumbent short hairs interspersed with several dark brown long upright hairs on prescutellar area. Scutellum dark brown, covered with dark brown upright relatively long hairs. Postnotum dark brown and bare. Pleural membrane bare. Katepisternum brownish black, longer than deep and bare. **Legs.** Foreleg: coxa yellowish white; trochanter light brown; femur medium brown; tibia dark brown, with large outer median portion white; tarsus brownish black, with thick dorsal

hair crest; basitarsus greatly dilated, 3.6–3.8 times as long as its greatest width. Midleg: coxa dark brown with posterolateral surface brownish black; trochanter medium brown; femur dark brown with apical cap brownish black; tibia dark brown to brownish black except base white, though basal one-third or little more of posterior surface white; basitarsus yellowish white except apical tip light brown, other tarsomeres light to medium brown except basal half of second tarsomere yellowish white. Hind leg: coxa dark brown; trochanter light to medium brown; femur medium to dark brown with apical cap brownish black; tibia dark brown to brownish black except base white, though basal one-third to two-fifths of posterior surface white; tarsus medium brown except basal two-thirds or little more of basitarsus and basal half of second tarsomere white; basitarsus (Figure 2C) nearly parallel-sided, 5.6 times as long as wide, and 0.7–0.8 and 0.6–0.7 times as wide as greatest widths of hind tibia and femur, respectively; calcipala (Figure 2C) moderately developed, nearly as long as basal width, and 0.4 times as wide as greatest width of basitarsus; pedisulcus (Figure 2C) well developed. Tarsal claw with small subbasal tooth (Figure 2D). **Wing.** Length 2.1 mm. Costa with dark spinules and hairs; subcosta bare; basal section of radial vein bare;  $R_1$  with dark brown spinules and hairs;  $R_2$  with dark brown hairs; hair tuft on stem vein dark brown; basal cell absent. **Halter.** White except base darkened. **Abdomen.** Basal

scale medium brown, with fringe of dark fine hairs. Dorsal surface of abdomen medium to dark brown, with light to dark brown short hairs; tergite 2 shiny and silvery iridescent when illuminated at certain angles and tergites 5–8 shiny. **Terminalia.** Sternite 8 (Figure 2E) bare medially but with 10–13 stout medium-long and long hairs and few short hairs on each lateral surface. Ovipositor valves (Figure 2E) rounded posteromedially, membranous except narrow area along inner margins somewhat sclerotized, each covered with few short hairs and numerous microsetae; inner margins slightly concave from base to middle, then nearly straight or slightly convex apically, and moderately separated from each other. Genital fork (Figure 2F) of inverted-Y form, with narrow well sclerotized stem; arms of narrow width, each with short and broad projection directed anterodorsally. Paraproct in ventral view (Figure 2G) elongate, with many short hairs on ventral and outer surfaces; paraproct in lateral view (Figure 2H) about half as long as wide, and protruding ventrally beyond ventral margin of cercus. Cercus in lateral view (Figure 2H) short, about half as long as wide, with posterior margin somewhat rounded, and with numerous short hairs. Spermatheca (Figure 2I) nearly globular, 1.1 times as long as wide, well sclerotized and pigmented except duct and portion of junction with duct narrowly unpigmented, with weakly defined reticulate patterns on its surface; internal setae present.



**Figure 2.** Female of *S. (S.) kotsuboyui* 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, Claw (lateral view). E, Sternite 8 and ovipositor valves (ventral view). F, Genital fork (ventral view). G & H, Paraprocts and cerci (right side; G, ventral view; H, lateral view). I, Spermatheca (lateral view). Scale bars. 0.1 mm for C; 0.02 mm for A, B & E-I; 0.01 mm for D.

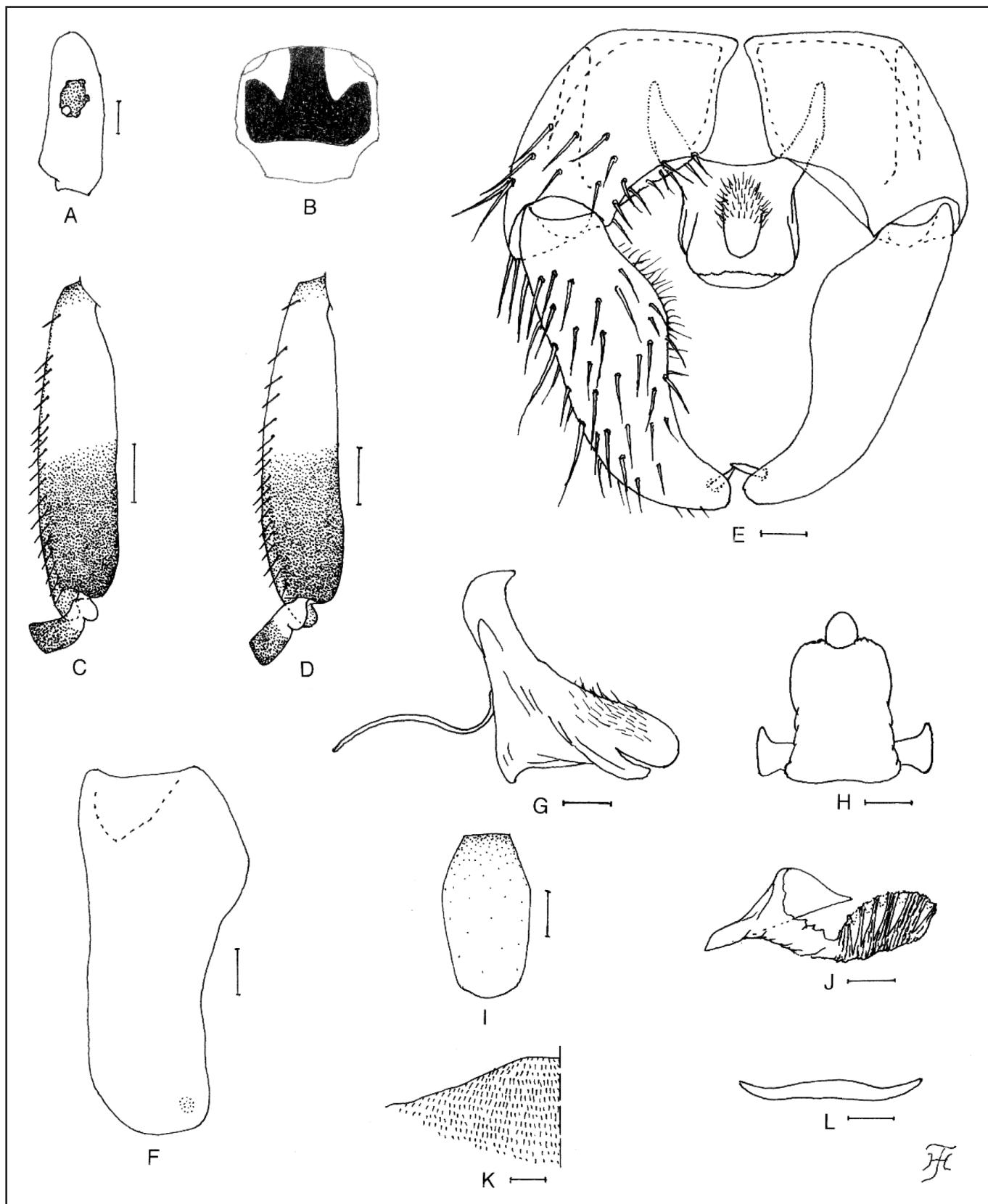
**Male** (n=7). Body length 2.4–2.7 mm. **Head**. Slightly wider than thorax. Upper-eye (large) facets in 17 or 18 vertical columns and 17 or 18 horizontal rows. Clypeus black, thickly white pruinose and iridescent when illuminated at certain angles, with dark brown hairs along and near lateral margins. Antenna composed of scape, pedicel and nine flagellomeres, medium to dark brown except base of first flagellomere yellow; first flagellomere elongate, 2.1–2.3 times length of second. Maxillary palpus with five segments, medium-brown except first and second segments ochreous; proportional lengths of third, fourth, and fifth segments 1.0:1.2–1.3:2.3–2.6; third segment (Figure 3A) narrow; sensory vesicle (Figure 3A) globular or ellipsoidal, 0.18–0.23 times length of third segment, and with small opening. **Thorax**. Scutum brownish black to black, with whitish-pruinose pattern (Figure 3B), i.e., anterior pair of large triangular spots on shoulders extended posteriorly along lateral margins and connected to large transverse spot entirely covering prescutellar area, anterior pair of large spots on shoulders partially disappear depending on direction of lighting; all spots brilliantly iridescent when illuminated at certain angles; scutum uniformly and moderately covered with coppery fine recumbent short hairs and with several dark brown long upright hairs on prescutellar area. Scutellum medium brown, with dark brown long upright hairs. Postnotum brownish black, shiny and whitish pruinose when illuminated at certain angles and bare. Pleural membrane bare. Katepisternum longer than deep, brownish black, and bare. **Legs**. Color nearly as in female except mid tibia entirely dark brown to brownish black (or with extreme base whitish or light brown), mid tarsus medium brown except basal four-fifths to two-thirds of basitarsus and base of second tarsomere whitish yellow, hind tibia dark brown to brownish black except extreme base whitish yellow, and hind tarsus medium to dark brown except little more than basal half of basitarsus and basal half of second tarsomere whitish yellow. Fore basitarsus greatly dilated, 3.9–4.1 times as long as its greatest width; hind basitarsus spindle-shaped (Figure 3C) or gradually widened from base to apical one-third (Figure 3D), 4.1 times as long as wide, and 0.8–0.9 and 0.9 times as wide as greatest widths of hind tibia and femur, respectively; calcipala (Figure 3C, D) small, nearly as long as its basal width, and 0.3 times as wide as greatest width of basitarsus; pedisulcus (Figure 3C, D) well developed. **Wing**. Length 2.0–2.1 mm. Other characteristics as in female. **Halter**. As in female. **Abdomen**. Basal scale brownish black, with fringe of dark brown long hairs. Dorsal surface of abdomen dark brown to brownish black, moderately covered with dark brown short to medium-long hairs; segments 2 and 4–7 each with pair of white-pruinose dorsolateral spots (brilliantly iridescent when illuminated at certain angles), those on segment 2 broadly connected in middle to each other. **Genitalia**. Coxites, styles and ventral plate in ventral view as in Figure 3E. Coxite in ventral view (Figure 3E) 1.4 times as long as wide. Style in ventrolateral view (Figure 3F) 1.5 times length of coxite, 2.2 times as long as its greatest width at basal one-third, somewhat narrowed from basal one-third to basal half, then nearly parallel-sided, and with subapical spine. Ventral plate in ventral view (Figure 3E) nearly quadrate, though posterodorsal margin slightly to somewhat rounded, with prominent median process narrowed to round apical tip and moderately covered with minute setae centrally on anteroventral surface except apical tip of median process bare; arms short, stout, divergent; ventral plate in lateral view (Figure 3G) triangular, with median process having round apical tip, produced beyond ventral tip of posterior margin, covered with minute setae centrally, and with stout arms; ventral plate in caudal view (Figure 3H) nearly quadrate, bare, with ventral margin slightly to somewhat concave medially, and irregularly and weakly dentate, and lateral margins somewhat concave. Median sclerite in lateral view (Figure 3G) arising from anteromedian portion of ventral plate and bent

dorsally in middle; median sclerite in caudal view (Figure 3I) wide, plate-like. Paramere (Figure 3J) enlarged basally, with at least five hooks apically. Aedeagal membrane (Figure 3K) densely covered with extremely minute setae; dorsal plate (Figure 3L) weakly sclerotized, in form of narrow transverse bar.

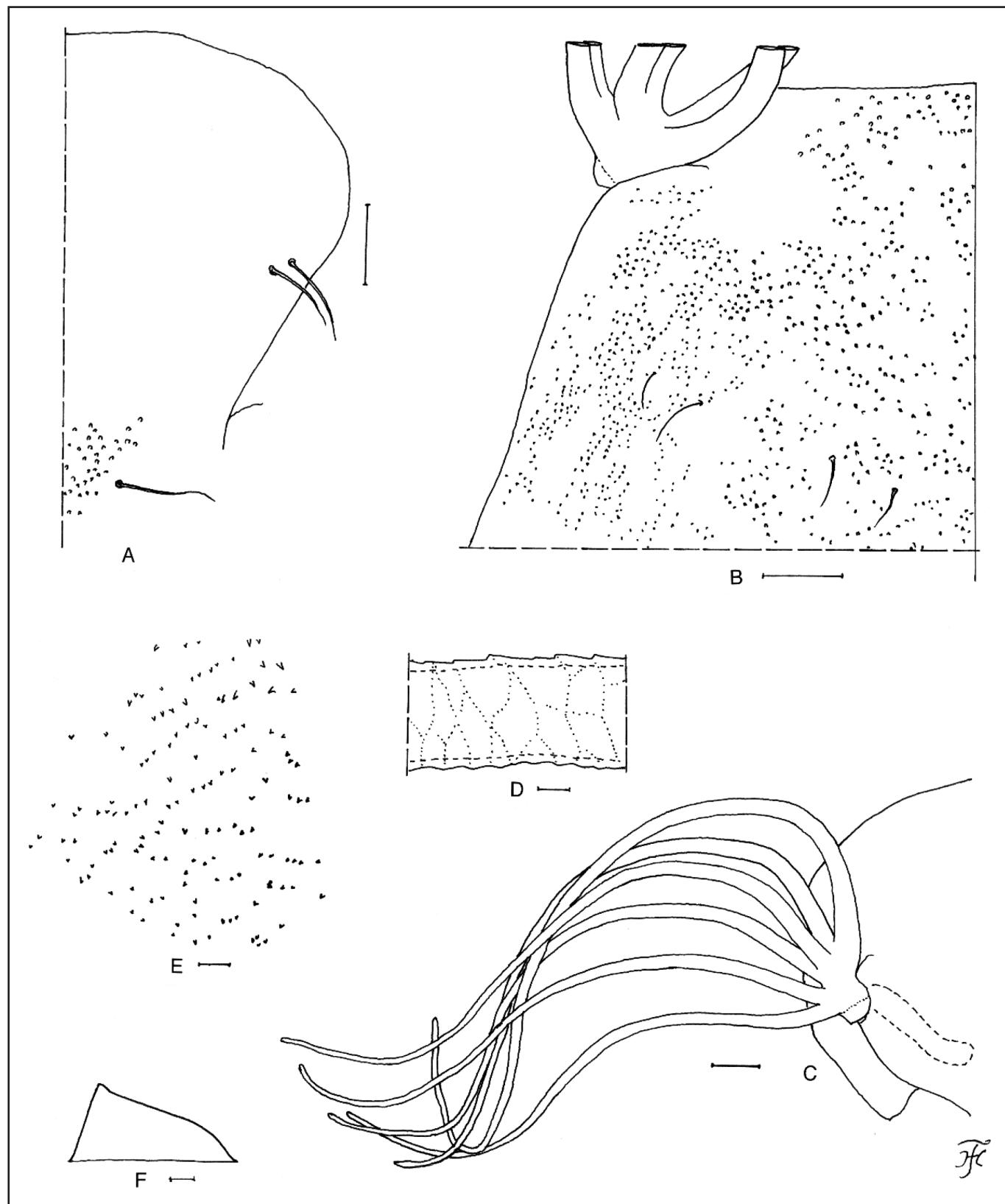
**Pupa** (n=13). Body length 2.5–3.0 mm. **Head**. Integument ochreous, bare except small area between facial trichomes with round tubercles (Figure 4A); frons with two unbranched short slender trichomes (Figure 4A) on each side; face with one unbranched short slender trichome (Figure 4A) on each side. **Thorax**. Integument (Figure 4B) ochreous, moderately covered with round tubercles except posterodorsal surface with conical tubercles; thorax on each side with two short trichomes (Figure 4B) dorsomedially, two short trichomes (Figure 4B) anterolaterally, one short trichome mediolaterally, and three trichomes (one short, and two medium-long) ventrolaterally; all unbranched. Gill (Figure 4C) with six thread-like filaments arranged as 2+2+2 from dorsal to ventral; dorsal and ventral pairs extremely short-stalked and middle pair almost sessile; all filaments subequal in length to one another (1.1–1.3 mm); relative thickness of filaments from dorsal to ventral when measured basally 1.3–1.6:1.0–1.4:1.2:1.0–1.1:1.0:1.0; upper filament of dorsal pair thickest and two filaments of ventral pair thinnest; all filaments 0.6–1.1 times as thick as interspiracular trunk; all filaments ochreous, covered with sharply-pointed annular ridges and furrows and densely covered with minute tubercles; annular ridges forming reticulate patterns (Figure 4D). **Abdomen**. Dorsally, segment 1 ochreous and without tubercles, with one unbranched short slender seta on each side; segment 2 ochreous on anterior one-fourth, with one unbranched short slender seta, five minute spinous setae, and comb-like groups of microspines (Figure 4E) submedially on each side; segments 3 and 4 each with 4 distinct hooks and one short seta on each side; all setae and hooks unbranched; segments 5, 6, and 9 lacking spine-combs; segments 7 and 8 each with distinct spine-combs in transverse row; segments 6–9 each with comb-like groups of microspines on each side; segment 9 without terminal hooks. Ventrally, segments 4–8 transparent, each with comb-like groups of minute spines; segment 5 with pair of bifid stout hooklets submedially and few unbranched short setae on each side; segments 6 and 7 each with pair of bifid inner and unbranched outer stout hooklets somewhat separated from each other and few unbranched short setae on each side. **Cocoon** (Figure 4F). Medium to dark brown, wall pocket-shaped, strongly and tightly woven, with distinct thick anterior rim; posterior half with floor; individual threads invisible; 2.8–3.0 mm long by 1.0–1.3 mm wide.

#### Mature larva. Unknown.

**Type specimens.** Holotype: Male (with its associated pupal exuviae and cocoon), reared from a pupa, collected from a river (width ca.10 m, exposed to the sun, moderately or rapidly flowing, 20 °C, elevation ca. 560 m), at Airmancur, along the road from Kayutanam to Padangpanjang, Bukittinggi, West Sumatra, Indonesia, 14-VIII-1994, by H. Takaoka. Paratypes: Five females, four males (with their associated pupal exuviae and cocoons), same place and date as those for the holotype; one female with its associated pupal exuviae and cocoon) reared from a pupa collected from a stream (width ca. 1.0 m, flow moderate, exposed to the sun, 19 °C, elevation 980 m) along the road from Lubukbargalung to Lubuksulasih, West Sumatra, 8-VIII-1994, by H. Takaoka; two males (with their associated pupal exuviae and cocoons) reared from pupae collected from a river (width 10–15 m, partially shaded, flow moderate to fast, 23 °C, elevation ca. 340 m) in Pasaman, halfway between Bonjol and Lubuksikaping, along the road from Bukittinggi to Lubuksikaping, West Sumatra, 18-VIII-1994, by H. Takaoka.



**Figure 3.** Male of *S. (S.) kotsuboyui* sp. nov. A, Third palpal segment with sensory vesicle (left side; front view). B, Scutum (dorsal view). C & D, Hind basitarsi and second tarsomeres (left side; outer view). E, Coxites, styles and ventral plate (ventral view). F, Style (right side; ventrolateral 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 (left half; caudal view). L, Dorsal plate (ventral view). Scale bars. 0.1 mm for C & D; 0.02 mm for A, E-J & L; 0.01 mm for K.



**Figure 4.** Pupa of *S. (S.) kotsuboyui* sp. nov. A, Frons and upper part of face (left half; frontal view). B, Anterior half of thorax (left half; dorsal view). C, Gill filaments (left side; outer view). D, Enlargement of part of uppermost filament at basal one-third. E, Group of microspines on dorsum of abdominal segment 2 (left side; dorsal view). F, Cocoon (lateral view). Scale bars. 0.5 mm for F; 0.1 mm for A-C; 0.01 mm for D & E.

**Biological notes.** The pupae of this new species were collected from slender plant roots trailing in flowing water. Associated with this new species were *S. (G.) parahiyangum* Takaoka & Sigit, *S. (G.) whartoni* Takaoka & Davies, *S. (N.) aureohirtum*, *S. (S.) bengkuruense* sp. nov., *S. (S.) fenestratum* Edwards, *S. (S.) tani* Takaoka & Davies complex, *S. (S.) nobile* De Meijere, *S. (S.) ranauense* Takaoka, Hadi & Sigit, and *S. (S.) solokense* sp. nov.

**Etymology.** The species name *kotsuboyui* is in honor of Mr. Yu Kotsubo, M. Ag., Deputy Editor, Department of Science and Technology News Section, The Asahi Shimbun (Newspaper), Tokyo, Japan, for his great contribution in highlighting the importance of biodiversity, conservation of the natural environment and the One Health concept.

**Remarks.** The females, males and their pupal exuviae and cocoons of the species, which were regarded as *S. (S.) iridescent* De Meijere in Sumatra, Indonesia by Takaoka *et al.* (2000), were reexamined and found to consist of two new species.

*Simulium (S.) kotsuboyui* sp. nov. is placed in the *S. iridescent* species-group of the subgenus *Simulium* s. str., defined by Takaoka (2017), by the characteristic shape of the female paraproct (Figure 2G, H) and male ventral plate (Figure 3E, G, H). This species-group is small, consisting of only two species, *S. (S.) iridescent* and *S. (S.) javaense* Takaoka & Hadi, both from Sunda Archipelago (Takaoka, 2024).

This new species is similar to *S. (S.) iridescent* in many characteristics including the female terminalia and male genitalia, but is distinguished from the latter species in the female and male by the mid and hind femora entirely darkened [c.f., brownish black except the base yellow in *S. (S.) iridescent*], in the male by the upper-eye (large) facets in 17 or 18 vertical columns and hind basitarsus slightly narrower than the hind tibia and femur [c.f., upper-eye (large) facets in 13 or 14 vertical columns and hind basitarsus slightly wider than the hind tibia and femur in *S. (S.) iridescent*]; and in the pupa by the frons nearly bare (Figure 4A) [c.f., covered with tubercles moderately on the lower half and sparsely on the upper half in *S. (S.) iridescent*] and gill filaments each with the interridge distances relatively long (Figure 4D) [c.f., interridge distances relatively short in *S. (S.) iridescent*].

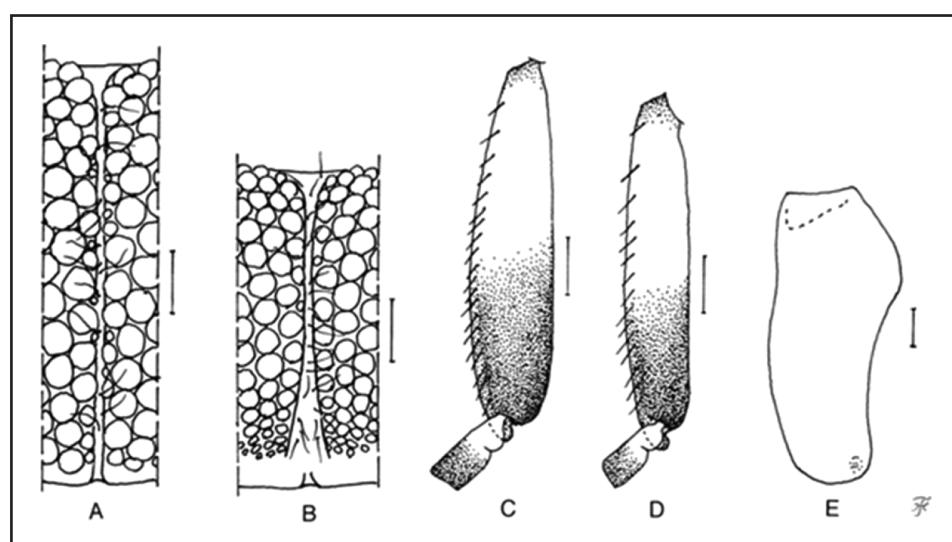
#### *Simulium (Simulium) solokense* sp. nov.

*Simulium (Simulium) iridescent* (nec De Meijere), part: Takaoka *et al.*, 2000: 163.

The morphological characteristics of the female and male of this new species are mostly omitted because they are extremely similar to those of *S. (S.) kotsuboyui* sp. nov. Only numerical characteristics are shown although almost indistinguishable from those of *S. (S.) kotsuboyui* sp. nov.

**Female** (n= 8). Body length 2.2–2.5 mm. **Head.** Frontal ratio 1.2:1.0:1.2; frons:head ratio 1.0:4.2–4.4. Labrum 0.69–0.71 times length of clypeus. Maxillary palpus: proportional lengths of third, fourth, and fifth segments 1.0:1.0–1.2:1.8–2.2; sensory vesicle 0.28–0.31 times length of third segment, having medium-sized opening. Maxillary lacinia with 11 or 12 inner and 14 or 15 outer teeth. Mandible with 27–30 inner and 12 or 13 outer teeth. Cibarium with 51–56 round processes near posterodorsal margin. **Legs.** Foreleg: basitarsus moderately dilated, 3.8–3.9 times as long as its greatest width. Hind leg: basitarsus 5.6 times as long as wide, and 0.7–0.8 and 0.6–0.7 times as wide as greatest widths of hind tibia and femur, respectively. **Wing.** Length 2.1 mm. **Terminalia.** Sternite 8 with 10–14 stout medium-long and long hairs and few short hairs on each lateral surface. Paraproct in lateral view 0.6 times as long as wide. Cercus in lateral view 0.6 times as long as wide. Spermatheca ovoid, 1.3 times as long as wide.

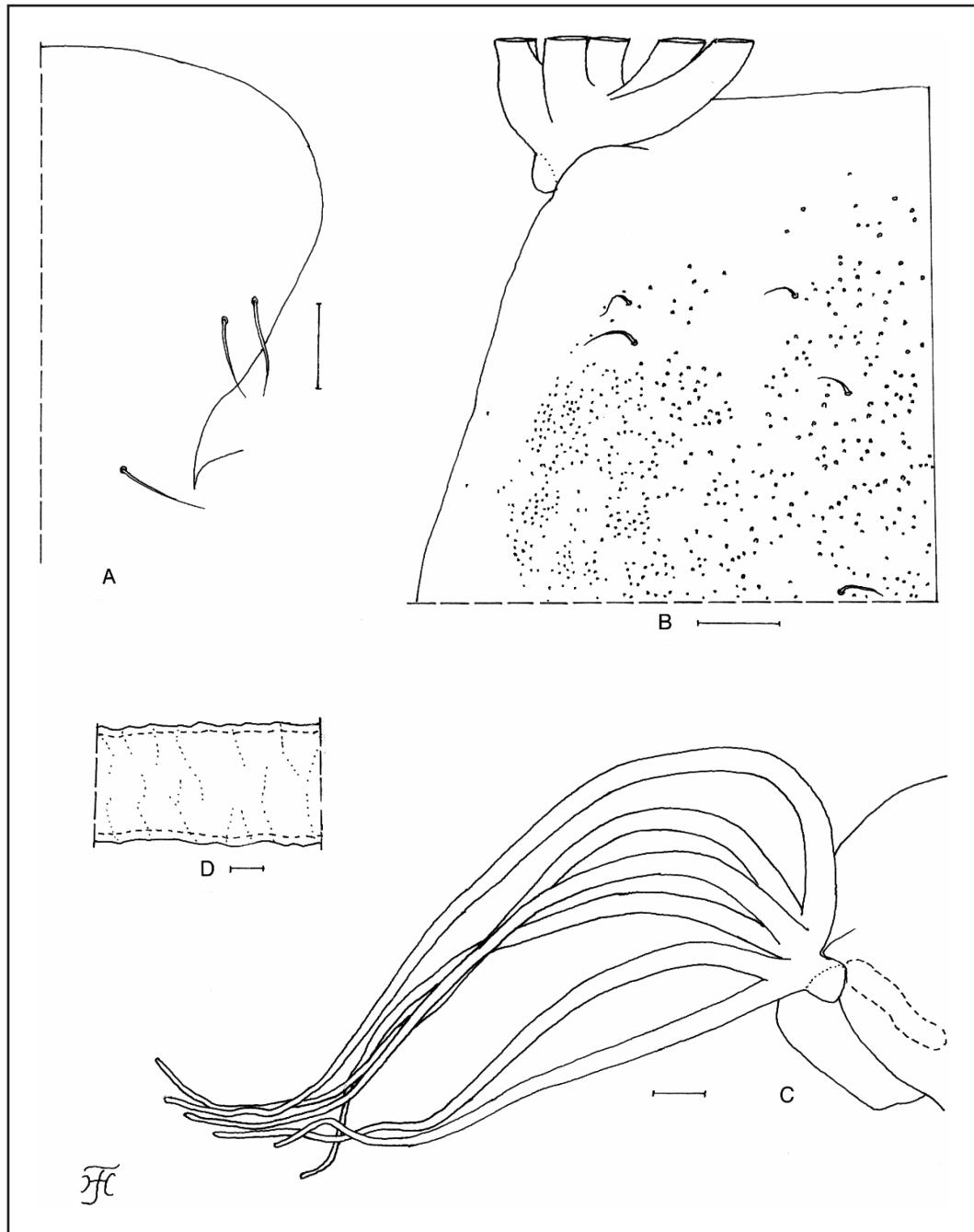
**Male** (n=11). Body length 2.5–2.8 mm. **Head.** Upper-eye (large) facets in 16–18 vertical columns and 16–18 horizontal rows. Antenna: first flagellomere elongate, 1.8–2.1 times length of second. Maxillary palpus: proportional lengths of third, fourth, and fifth segments 1.0:1.1–1.2:2.2–2.6; sensory vesicle globular or ellipsoidal, 0.17–0.22 times length of third segment. **Legs.** Foreleg: basitarsus greatly dilated, 4.5 times as long as its greatest width. Hind leg: basitarsus (Figure 5C) 4.2–4.5 times as long as wide, and 0.8 and 0.9 times as wide as greatest widths of hind tibia and femur, respectively. **Wing.** Length 2.0–2.1 mm. **Genitalia.** Coxite in ventral view 1.4 times as long as wide. Style in ventrolateral view (Figure 5E) 1.5 times length of coxite, 2.5 times as long as its greatest width at basal one-third, and slightly narrowed from basal one-third to apical tip.



**Figure 5.** Male of *S. (S.) solokense* sp. nov. A & B, Middle parts of heads showing frons (dorsal view; A, normal male; B, aberrant male). C & D, Hind basitarsi and second tarsomeres (C, normal male; D, aberrant male). E, Style (right side; ventrolateral view). Scale bars. 0.1 mm for A–D; 0.02 mm for E.

**Pupa** (n=20). Body length 2.9–3.2 mm. **Head.** Integument (Figure 6A) ochreous and bare; frons with two unbranched short slender trichomes (Figure 6A) on each side; face with one unbranched short slender trichome (Figure 6A) on each side. **Thorax.** Integument (Figure 6B) ochreous, moderately (or sparsely) covered with round tubercles except area along anterior margin narrowly (or widely) bare, and posterodorsal area with cone-like tubercles; thorax on each side with two or three short trichomes (Figure 6B) dorsomedially, two short trichomes (Figure 6B) anterolaterally, one short trichome mediolaterally, and three trichomes (one short, and two medium-long) ventrolaterally; all unbranched. Gill (Figure 6C) with six thread-like filaments arranged as 2+2+2 from dorsal to ventral; dorsal and ventral pairs

extremely short-stalked and middle pair almost sessile; all filaments subequal in length to one another (1.1–1.3 mm); relative thickness of filaments from dorsal to ventral when measured basally 1.3–1.4:1.1:1.1:1.0:1.0; upper filament of dorsal pair thickest and two filaments of ventral pair thinnest; all filaments 0.90–1.25 times as thick as interspiracular trunk; all filaments ochreous, irregularly covered with weakly developed annular ridges forming indefinite reticulate patterns (Figure 6D), and densely covered with minute tubercles. **Abdomen.** Nearly as in *S. (S.) kotsuboyui* sp. nov. **Cocoon.** Similar to that of *S. (S.) kotsuboyui* sp. nov., though some cocoons somewhat extended ventrolaterally when attached on flat dead tree leaves in flowing water; 2.8–3.0 mm long by 1.2–1.8 mm wide.



**Figure 6.** Pupa of *S. (S.) solokense* sp. nov. A, Frons and upper part of face (left half; frontal view). B, Anterior half of thorax (left half; dorsal view). C, Gill filaments (left side; outer view). D, Enlargement of part of uppermost filament at basal one-third. Scale bars. 0.1 mm for A–C; 0.01 mm for D.

**Mature larva.** Unknown.

**Type specimens.** Holotype: Male (with its associated pupal exuviae and cocoon) reared from a pupa collected from a stream (width ca. 10 m, flow moderate, exposed to the sun, 19 °C, elevation 980 m) along the road from Lubukbargalung to Lubuksulasih, Solok, West Sumatra, 8-VIII-1994, by H. Takaoka. Paratypes: Five females and four males (with their associated pupal exuviae and cocoons), same data and date as those for the holotype; two females and three males (with their associated pupal exuviae and cocoons), reared from pupae collected from a river (width 4.0–5.0 m, flow moderate, exposed to the sun, 20 °C, elevation 970 m) flowing in a paddy field, near Talang, along the road from Lubuksulasih to Talang, West Sumatra, 8-VIII-1994, by H. Takaoka; one pupa collected from a stream (width 0.4–1.0 m, flow moderate, exposed to the sun, 20 °C, elevation 1,090 m) between Alahanpanjang and Surian, West Sumatra, 11-VIII-1994, by H. Takaoka; one female and three males (with their associated pupal exuviae and cocoons), reared from pupae collected from a river (width 4.0–6.0 m, flow moderate, shaded, 22 °C, elevation 880 m) flowing in a forest, at Bandar Baru, Sibolangit, North Sumatra, 25-VIII-1994, by H. Takaoka.

**Biological notes.** The pupae of this new species were collected from slender plant roots and dead tree leaves in flowing water. Associated with this new species were *S. (G.) parahiyangum*, *S. (S.) bengkuruense* sp. nov., *S. (S.) fenestratum*, *S. (S.) kotsuboyui* sp. nov. and *S. (S.) tani* complex.

**Etymology.** The species name *solokense* is given after the locality, Solok, where this new species was collected.

**Remarks.** Like *S. (S.) kotsuboyui* sp. nov., this new species is also assigned to the *S. iridescent* species-group of the subgenus *Simulium* s. str.

This new species is similar to *S. (S.) javaense* described from East Java (Takaoka & Hadi, 1991) and recorded from Bali (Takaoka *et al.*, 2017) in many characteristics including the female terminalia, male genitalia and pupal frons and face without tubercles (Figure 6A), but differs from the latter species by the pupal thorax bare narrowly near the anterior margin (Figure 6B) (c.f., bare widely on the anterior half of the dorsal surface in the latter species) and gill filaments thread-like, 0.9–1.25 times as thick as the interspiracular trunk (Figure 6C) and irregularly with annular ridges faintly forming reticulate patterns (Figure 6D) (c.f., inflated, 1.3–3.6 times as thick as the interspiracular trunk, and without annular ridges and reticulate patterns in the latter species).

This new species is almost indistinguishable in the female and male from *S. (S.) kotsuboyui* sp. nov., though the male style (Figure 5E) appears to be slightly different in the shape when viewed ventrolaterally (ratio of the length of the style relative to its greatest width: 2.5 in this new species vs. 2.2 in *S. (S.) kotsuboyui* sp. nov.). On the other hand, it is distinguished in the pupa from *S. (S.) kotsuboyui* sp. nov. by the frons and face entirely bare (Figure 6A) [c.f., pupal frons bare but face with tubercles (Figure 4A) in the latter species], thorax narrowly bare near the anterior margin (Figure 6B) [thorax entirely covered with tubercles (Figure 4B) in the latter species], and gill filaments each irregularly with weakly-defined annular ridges (Figure 6D) [c.f., pupal gill filaments each regularly with well-defined annular ridges (Figure 4D) in the latter species].

Three relatively small males (body length 2.5 mm) of *S. (S.) solokense* sp. nov. collected from North Sumatra showed the heads differing from those (Figure 5A) of normal male specimens: i.e., the frons slightly widened basally (Figure 5B) and the reduced number of the upper-eye (large) facets in 14 vertical columns and 14 or 15 horizontal rows on each side, though large facets in the upper-eye region are not so clearly separated from small ones; and two of them showed the hind basitarsus narrow and parallel-sided (Figure 5D), which is 5.3–5.5 times as long as its widest, and 0.66–0.70 and 0.70–0.74 times as wide as the hind tibia and femur, respectively. Since most of their other characteristics as well as those of their pupal exuviae are almost the same as those (as described above)

of typical specimens of this new species, these three males are considered aberrant forms of *S. (S.) solokense* sp. nov. They were, thus, not designated as paratypes.

Finally, whether *S. (S.) iridescent* is distributed in Sumatra should be confirmed in future surveys.

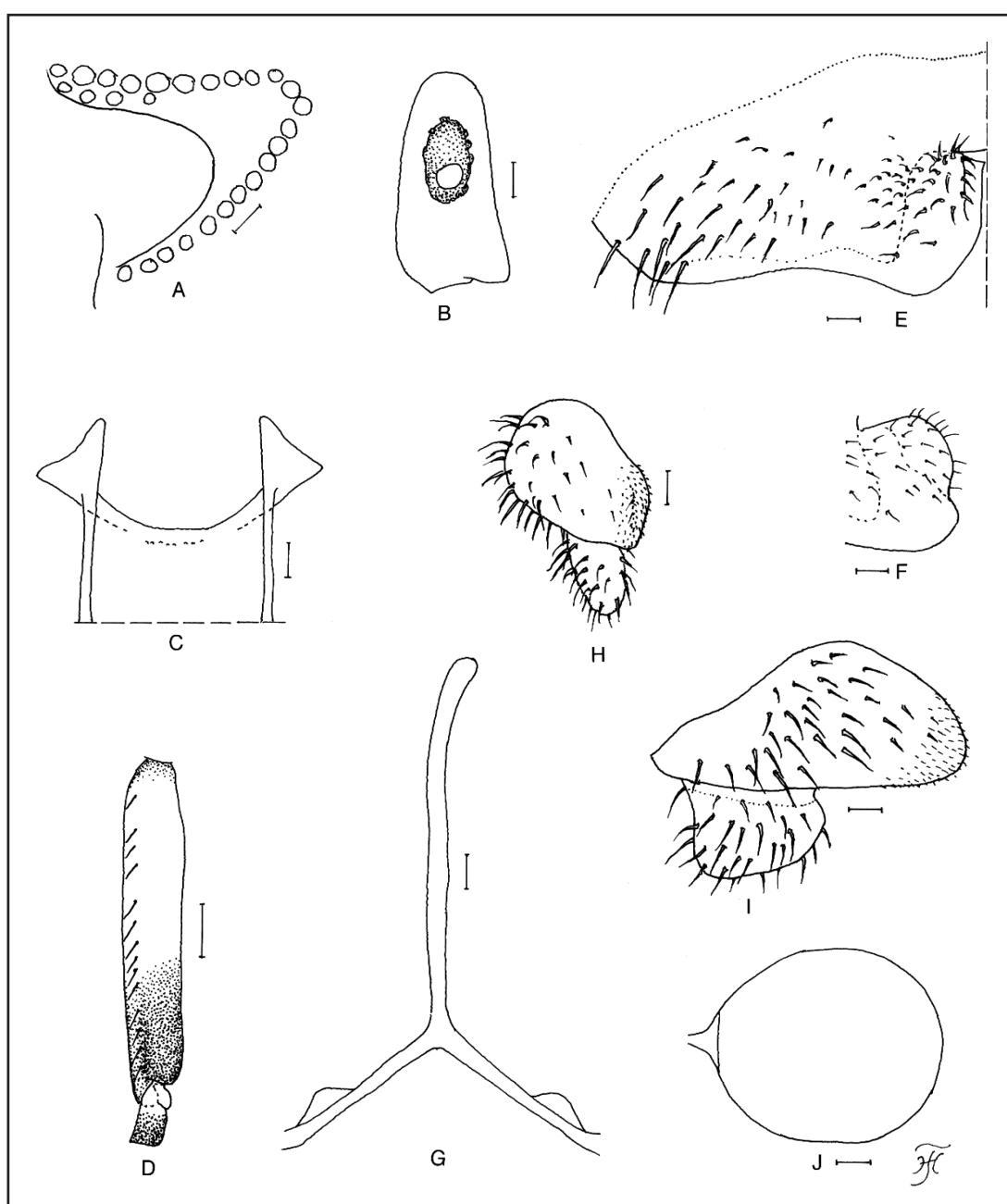
***Simulium (Simulium) bengkuruense* sp. nov.**

*Simulium (Simulium) argyrocinatum* (nec De Meijere): Takaoka *et al.*, 2000: 163.0

**Female** (n=5). Body length 2.7–2.8 mm. **Head.** Slightly narrower than thorax. Frons brownish black, shiny, with several dark stout hairs along lateral margin on each side and near antennal base; frontal ratio 1.3–1.4:1.0:1.5–1.6; frons:head ratio 1.0:4.2–4.9. Fronto-ocular area of moderate size, rounded apically (Figure 7A). Clypeus brownish black, shiny, moderately covered with dark brown medium-long hairs. Labrum 0.6 times length of clypeus. Antenna composed of scape, pedicel and nine flagellomeres, and light to medium brown except scape, pedicel and basal half of first flagellomere yellow when viewed dorsally, though first flagellomere yellow entirely when viewed ventrally. Maxillary palpus with five segments, light brown; proportional lengths of third, fourth, and fifth segments 1.0:1.0–1.1:2.4; third segment slightly widened apically (Figure 7B), with sensory vesicle (Figure 7B) medium-sized, ellipsoidal, 0.3–0.4 times length of third segment, having medium-sized or large opening. Maxillary lacinia with 12–15 inner and 13–15 outer teeth. Mandible with 24–27 inner and 11 or 12 outer teeth. Cibarium (Figure 7C) with eight or nine tiny processes near posterodorsal margin; each cornua triangular. **Thorax.** Scutum brownish black, shiny, densely covered with whitish yellow, fine recumbent short hairs intermixed with light brown similar fine short hairs near anterior and lateral margins, and interspersed with few dark brown long upright hairs on prescutellar area; scutum gray pruinose with five non-pruinose longitudinal vittae (one medial, two submedial, and two lateral), all vittae united with transverse non-pruinose band on prescutellar area, when illuminated in front and viewed dorsally; scutum gray pruinose except four non-pruinose longitudinal vittae, when illuminated posteriorly and viewed dorsally. Scutellum dark brown, covered with dark brown upright long hairs and whitish yellow short hairs. Postnotum dark brown, shiny, gray pruinose when illuminated at certain angles, and bare. Pleural membrane bare. Katepisternum brownish black, longer than deep, shiny, gray pruinose when illuminated at certain angles, and bare. **Legs.** Foreleg: coxa and trochanter yellowish white; femur light to medium brown, though basal one-third or little more of inner surface yellow; tibia dark brown; tarsus brownish black, with moderate dorsal hair crest; basitarsus moderately dilated, 4.9–5.4 times as long as its greatest width. Midleg: coxa dark brown with posterolateral surface brownish black; trochanter medium brown; femur dark brown; tibia dark brown except base white, though one-third or little more of posterior surface white; basitarsus yellowish white except apical one-fifth light brown, other tarsomeres light to medium brown except base of second tarsomere white. Hind leg: coxa dark brown; trochanter yellowish white; femur dark brown except extreme base yellowish white; tibia dark brown except base white, though one-third or little more of posterior surface white; tarsus medium brown except basal two-thirds or little less of basitarsus and basal one-third of second tarsomere white; basitarsus (Figure 7D) nearly parallel-sided, 5.1–5.5 times as long as wide, and 0.6–0.7 and 0.5–0.6 times as wide as greatest widths of hind tibia and femur, respectively; calcipala (Figure 7D) moderately developed, slightly shorter than basal width, and 0.44 times as wide as greatest width of basitarsus; pedisulcus (Figure 7D) well developed. Tarsal claw simple, without tooth. **Wing.** Length 2.3–2.4 mm. Costa with dark spinules and hairs; subcosta haired except near apex bare; basal section of radial vein haired;  $R_1$  with dark brown spinules and hairs;  $R_2$  with dark brown hairs; hair tuft on stem vein dark brown; basal cell absent. **Halter.** White except base darkened. **Abdomen.**

Basal scale medium brown, with fringe of whitish yellow fine hairs. Dorsal surface of abdomen medium to dark brown, with light to dark brown short hairs; tergite 2 shiny and silvery iridescent when illuminated at certain angles and tergites 6–9 shiny. Ventral surface of seventh segment with pair of weakly sclerotized submedian sternal plates. **Terminalia.** Sternite 8 (Figure 7E) with posterior margin concave medially in form of inverted-U shape, bare medially, with 28–30 medium-long hairs (except 13–15 short hairs near ovipositor valve) on each lateral surface. Ovipositor valves (Figure 7E) rounded posteriorly, each with ventrally produced lobe (Figure 7F) near inner margin, membranous except narrow area along inner margin somewhat sclerotized, covered with 17–21 short hairs and numerous minute setae; inner margins slightly concave from base to middle, then nearly straight or slightly convex apically, and widely separated apically from each other. Genital fork (Figure 7G) of inverted-Y form,

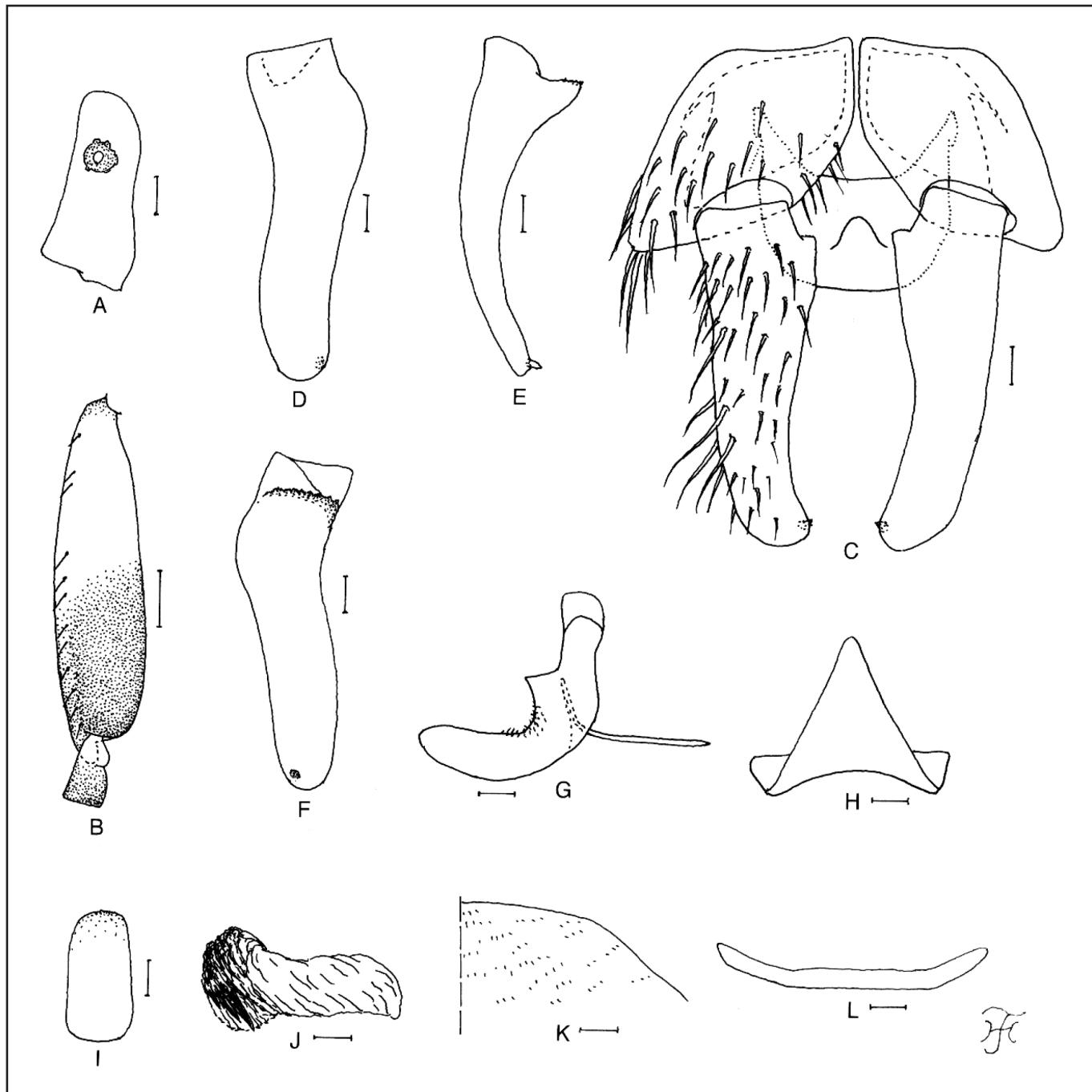
with narrow well sclerotized stem; arms of moderate width, each with short and broad projection directed anterodorsally. Paraproct in ventral view (Figure 7H) rounded, nearly as long as its greatest width, strongly pigmented on anterior surface, with ca. 30 short to medium-long hairs on lateral surface; paraproct in lateral view (Figure 7I) nearly half as long as wide, and much protruding ventrally beyond ventral margin of cercus. Cercus in lateral view (Figure 7I) short, 0.6 times as long as wide, with posterior margin somewhat rounded or nearly straight, and with numerous short to medium-long hairs. Spermatheca (Figure 7J) nearly ellipsoidal, 1.2 times as long as wide, well sclerotized and pigmented except portion of junction with duct somewhat widely unpigmented, with weakly defined reticulate patterns on its surface; internal setae present; accessory ducts subequal in thickness to each other, and slightly thicker than major duct.



**Figure 7.** Female of *S. (S.) bengkuruense* sp. nov. A, Fronto-ocular area (left side). B, Third palpal segment with sensory vesicle (right side; front view). C, Cibarium (front view). D, Hind basitarsus and second tarsomere (left side; outer view). E, Sternite 8 and ovipositor valve (right side; ventral view). F, Ventrally-produced lobe of ovipositor valve (right side; lateral view). G, Genital fork (ventral view). H & I, Paraprocts and cerci (right side; H, ventral view; I, lateral view). J, Spermatheca (lateral view). Scale bars. 0.1 mm for D; 0.02 mm for A–C & E–J.

**Male (n=7).** Body length 2.9–3.0 mm. **Head.** Slightly wider than thorax. Upper-eye (large) facets in 16 (rarely 17) vertical columns and 16 or 17 horizontal rows. Clypeus black, thickly white pruinose and iridescent when illuminated at certain angles, with dark brown hairs along and near lateral margins (most of central portion bare). Antenna composed of scape, pedicel and nine flagellomeres, medium to dark brown except scape and pedicel light brown and base of first flagellomere yellow; first flagellomere elongate, 1.4–1.5 times length of second. Maxillary palpus with five segments, medium-brown except first and second segments ochreous; proportional lengths of third, fourth, and fifth segments 1.0:1.3–1.4:3.1–3.2; third segment (Figure 8A) slightly widened apically; sensory vesicle (Figure 8A) globular, 0.2 times length of

third segment, and with small opening. **Thorax.** Scutum brownish black to black, with whitish-pruinose pattern, i.e., anterior pair of large spots on shoulders extended posteriorly along lateral margins and connected to large transverse spot entirely covering prescutellar area, anterior pair of large spots divided into anterior half and posterior half, either of which disappears depending on direction of lighting; all spots brilliantly iridescent when illuminated at certain angles; scutum uniformly and moderately covered with yellow fine recumbent short hairs intermixed with dark brown short hairs near anterior and lateral margins and with several dark brown long upright hairs on prescutellar area. Scutellum medium brown, with dark brown long upright hairs and dark brown short hairs. Postnotum brownish black, shiny and whitish pruinose when



**Figure 8.** Male of *S. (S.) bengkuruense* 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–F, Styles (right side; D, ventrolateral view; E, medial view; F, dorsolateral view). G, Ventral plate and median sclerite (lateral view). H, Ventral plate (caudal view). I, Median sclerite (caudal view). J, Paramere (left side; caudal view). K, Aedeagal membrane (left half; caudal view). L, Dorsal plate (ventral view). Lc, Dorsal plate (caudal view). Scale bars. 0.1 mm for B; 0.02 mm for A, C–J & L; 0.01 mm for K.

illuminated at certain angles and bare. Pleural membrane bare. Katepisternum longer than deep, brownish black, and bare. **Legs.** Color nearly as in female except fore trochanter dark yellow to light brown, mid second tarsomere medium brown except base whitish yellow, posterior surface of mid and hind tibiae white only on base, and hind basitarsus and second tarsomere medium to dark brown except basal half whitish yellow. Fore basitarsus moderately dilated, 5.7–5.9 times as long as its greatest width; hind basitarsus (Figure 8B) slightly widened from base to apical one-third, 3.5–3.9 times as long as wide, and 0.9 and 0.9–1.0 times as wide as greatest widths of hind tibia and femur, respectively; calcipala (Figure 8B) small, nearly as long as its basal width, and 0.25 times as wide as greatest width of basitarsus; pedisulcus (Figure 8B) well developed. **Wing.** Length 2.1 mm. Other characteristics as in female except subcosta and basal portion of radial vein without hairs. **Halter.** White except base darkened. **Abdomen.** Basal scale brownish black, with fringe of dark brown long hairs. Dorsal surface of abdomen dark brown to brownish black, moderately covered with dark brown short to medium-long hairs; segments 2, 5, 6 and 7 each with pair of whitish pruinose spots (brilliantly iridescent when illuminated at certain angles) dorsolaterally, those on segment 2 broadly connected in middle to each other. **Genitalia.** Coxites, styles and ventral plate in ventral view as in Figure 8C. Style in ventrolateral view (Figure 8D) 1.7 times length of coxite, 3.3 times as long as its greatest width at basal one-fourth, somewhat narrowed from basal one-fourth to basal half, then nearly parallel-sided, and with subapical spine; style in medial view (Figure 8E) somewhat flattened dorsoventrally, with short triangular basal protuberance directed dorsomedially; style in dorsomedial view (Figure 8F) with basal protuberance having saw-like anterior margin. Ventral plate in ventral view (Figure 8C) with body broad, having anterior margin nearly straight or slightly concave, and posterior margin nearly straight or slightly rounded; body bearing prominent median process sharply narrowed to round tip and moderately covered with minute setae on anteroventral surface; arms short, stout, divergent; ventral plate in lateral view (Figure 8G) with median process abruptly bent ventrally at nearly right angle, and with stout arms; ventral plate in caudal view (Figure 8H) in form of equilateral triangle, and bare. Median sclerite in lateral view (Figure 8G) arising from anteromedian portion of ventral plate and abruptly bent dorsally at basal one-third; median sclerite in caudal view (Figure 8I) wide, plate-like. Paramere (Figure 8J) enlarged basally, with at least three hooks apically. Aedeagal membrane (Figure 8K) very sparsely covered with extremely minute setae; dorsal plate (Figure 8L) weakly sclerotized, in form of narrow transverse bar.

**Pupa** (n=16). Body length 3.0–3.2 mm. **Head.** Integument yellow to ochreous, moderately covered with round tubercles of various sizes, each without secondary projections (Figure 9A); frons with two unbranched short slender trichomes (Figure 9B) on each side; face with one unbranched short slender trichome (Figure 9C) on each side. **Thorax.** Integument yellow to ochreous, moderately covered with round tubercles without secondary projections except conical tubercles on posterodorsal surface; thorax on each side with three long trichomes, each with two to five branches (Figure 9D) dorsomedially, two bifid or trifid medium-long trichomes (Figure 9E) anterolaterally, one unbranched or bifid medium-long trichome (Figure 9F) mediolaterally, and three trichomes (one unbranched long, one bifid medium-long, and one unbranched or bifid short) (Figure 9G) ventrolaterally. Gill (Figure 9H–J) with 10 thread-like filaments arranged as 2+[(2+1)+(2+1)]+2 (Figure 9H), or rarely 2+[(2+1)+3]+2 (Figure 9I), or 2+(2+1+2+1)+2 (Figure 9J) from dorsal to ventral; stalks of dorsal and ventral pairs short; longest filament 1.1–1.3 mm; relative thickness of filaments from dorsal to ventral when measured basally 1.0–1.2:1.0–1.2:0.8–1.1:0.8–1.0:0.9–1.1:1.1:0.9–1.1:1.0–1.1:1.0; lower filament of ventral pair not thickest; angle between stalks of dorsal and ventral paired filaments 140–180 degrees when viewed laterally;

all filaments ochreous, covered with sharply-pointed annular ridges and furrows and densely covered with minute tubercles. **Abdomen.** Dorsally, nearly transparent; segment 1 without tubercles, with one unbranched or bifid short slender seta (Figure 9K) on each side; segment 2 with one unbranched short slender seta and five minute spinous setae on each side; segments 3 and 4 each with 4 distinct hooks and one short seta on each side; all setae and hooks unbranched; segments 5, 6, 7 and 9 lacking spine-combs; segment 8 with distinct spine-combs in transverse row; segments 8 and 9 each with comb-like groups of microspines on each side; segment 9 with pair of cone-like terminal hooks (Figure 9L). Ventrally, segments 4–8 transparent, each with comb-like groups of microspines; segment 5 with pair of bifid stout hooklets submedially and few unbranched short setae on each side; segments 6 and 7 each with pair of bifid inner and unbranched outer stout hooklets somewhat separated from each other and few unbranched short setae on each side. **Cocoon** (Figure 9M). Light ochreous to medium brown, shoe-shaped, with several small to medium-sized open spaces anterolaterally on each side, strongly woven; posterior half with floor; individual threads on anterior portion visible; 3.7–4.0 mm long by 1.2–1.3 mm wide.

#### Mature larva. Unknown.

**Type specimens.** Holotype: Male (with its associated pupal exuviae and cocoon), reared from a pupa, collected from a river (width ca.10 m, exposed to the sun, flow moderate to rapid, 20 °C, elevation ca. 560 m), at Airmancur, along the road from Kayutanam to Padangpanjang, Bukittinggi, West Sumatra, Indonesia, 14-VIII-1994, by H. Takaoka. Paratypes: Five females, four males (with their associated pupal exuviae and cocoons), and five pupal exuviae and cocoons, same place and date as those for the holotype; two males (with their associated pupal exuviae and cocoons), collected from a creek (called Air Mujin) (width 2.0–3.0 m, partially shaded, flow moderate, 24 °C, elevation ca. 500 m) flowing down to Lake Lanau at Tanjung jati, along the road between Simpangsender and Liwa, Bengkuru, Sumatra, Indonesia, 29-VII-1992, by H. Takaoka.

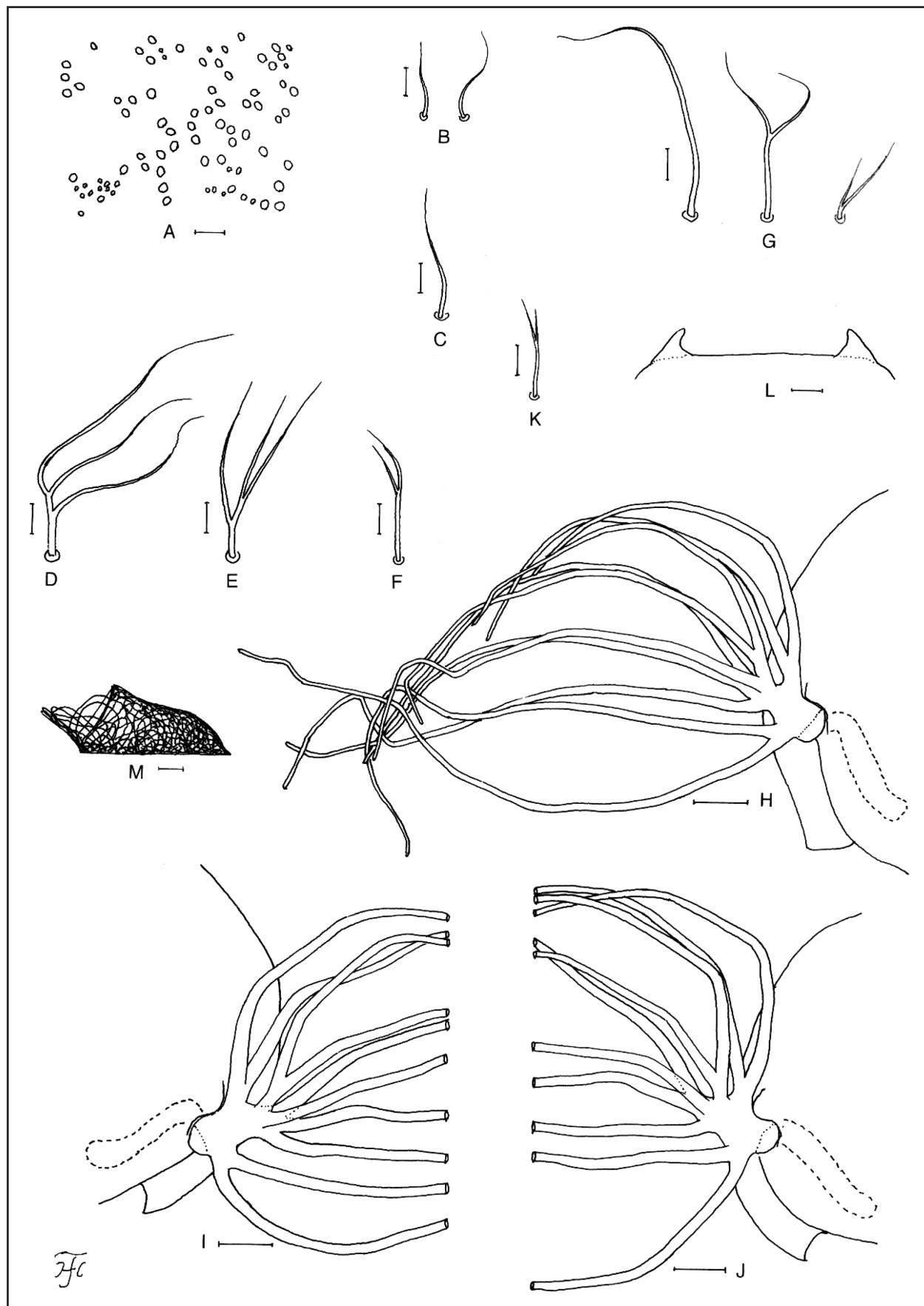
**Biological notes.** The pupae of this new species were collected from slender plant roots trailing in flowing water. Associated with this new species were *S. (S.) fenestratum*, *S. (S.) kotsuboyui* sp. nov., *S. (S.) minangkabauum* Takaoka & Sigit, *S. (S.) nobile*, *S. (S.) ranauense* and *S. (S.) solokense* sp. nov.

**Etymology.** The species name *bengkuruense* is after the locality name, Bengkuru, one of two localities where this new species was collected.

**Remarks.** The females, males and their pupal exuviae and cocoons of the species, which were regarded as *S. (S.) argyrocinatum* from Sumatra, Indonesia by Takaoka *et al.* (2000), were reexamined and found to be a new species.

*Simulium (S.) bengkuruense* sp. nov. is placed in the *S. striatum* species-group of the subgenus *Simulium* s. str., defined by Takaoka & Davies (1996), by having the characteristic shape of the female sternite 8 and ovipositor valves (Figure 7E) and male ventral plate (Figure 8C).

This new species is characterized by a combination of three characteristics, i.e., female radial vein with its basal portion haired, male upper-eye (large) facets in 16 or 17 vertical columns and 16 or 17 horizontal rows, and pupal gill with 10 filaments arranged mainly as two pairs plus two triplets (Figure 9H). In sharing these characteristics, this new species is similar to *S. (S.) grisescens* Puri from India (Takaoka *et al.*, 2020a), *S. (S.) perakense* Takaoka, Ya'cob & Sofian-Azirun from Peninsular Malaysia (Takaoka *et al.*, 2018), *S. (S.) poolpholi* Takaoka, Srisuka & Saeung from Thailand (Srisuka *et al.*, 2023), *S. (S.) taythienense* Takaoka, Sofian-Azirun & Ya'cob from Vietnam (Takaoka *et al.*, 2014a), *S. (S.) yanpingense* Takaoka & Huang from Taiwan and *S. (S.) tanegashimaense* Takaoka & Otsuka from Japan (Takaoka *et al.*, 2022).



**Figure 9.** Pupa of *S. (S.) bengkuruense* sp. nov. A, Tubercles on frons. B, Frontal trichomes. C, Facial trichome. D–G, Thoracic trichomes (D, dorsomedial; E, anterolateral; F, mediolateral; G, ventrolateral). H–J, Gills (H & J, left side; I, right side; H, arranged as  $2+[(2+1)+(2+1)]+2$  from dorsal to ventral; I, arranged as  $2+[(2+1)+3]+2$  from dorsal to ventral; J, arranged as  $2+(2+1+2+1)+2$  from dorsal to ventral). K, Slender short seta on dorsum of abdominal segment 1. L, Terminal hooks (caudal view). M, Cocoon (lateral view). Scale bars. 0.5 mm for M; 0.1 mm for H–J; 0.02 mm for A–G & K; 0.01 mm for L.

**Table 1.** Comparison of morphological characteristics of *S. (S.) bengkuruense* sp. nov. with those of its related species

Simulium species	Female	Male		Pupa		
	Length of frons against its narrowest width	Color of short hairs on scutum	Length of hind basitarsus against its greatest width	Secondary projections on relatively large tubercles on frons	Overlapping of two triplets of gill filaments	Lowest gill filament
<i>S. bengkuruense</i> sp. nov.	1.5–1.6	yellow	3.5–3.9	absent	+	not thickest
<i>S. grisescens</i>	1.2	brassy	4.2	present	+	thickest
<i>S. perakense</i>	1.2	brassy	3.6–4.1	absent	+	thickest
<i>S. poolpholi</i>	1.5–1.6	brassy	5.2–5.3	absent	+	not thickest
<i>S. tanegashimaense</i>	1.2–1.4	yellow	3.5–3.7	present	–	not thickest
<i>S. taythienense</i>	1.4	brassy	4.4–4.6	absent	–	not thickest
<i>S. yanpingense</i>	1.2	brassy	4.0–4.3	absent	–	not thickest

Morphological characteristics of this new species that differ from those of these known species are summarized in Table 1. This new species is distinguished in the female from *S. (S.) grisescens*, *S. (S.) perakense* and *S. (S.) yanpingense* by the relatively high length ratio of the frons against its narrowest width (1.5–1.6 in this new species vs. 1.2 in the latter three species); in the male from all these species [except *S. (S.) tanegashimaense*] by the color of short hairs on the scutum (yellow in this new species vs. brassy in the latter five species) and from *S. (S.) poolpholi* by the relative length of the hind basitarsus against its greatest width (3.5–3.9 in this new species vs. 5.2–5.3 in the latter species); and in the pupa from *S. (S.) grisescens* and *S. (S.) tanegashimaense* by the absence of the secondary projections on the relatively large tubercles on the frons (present in the latter two species), from *S. (S.) tanegashimaense*, *S. (S.) taythienense*, and *S. (S.) yanpingense* by the overlapping of the two middle triplets of the gill filaments (not overlapping in the latter three species), from *S. (S.) grisescens* and *S. (S.) perakense* by the relative thickness of the lower filament of the ventral paired filaments when compared basally (not thickest in this new species vs. thickest of all in the latter two species), and from *S. (S.) poolpholi* by the frons moderately covered with tubercles (densely covered with tubercles in the latter species), and gill filaments regularly with sharply pointed annular ridges (irregularly with ill-developed annular ridges in the latter species).

From Indonesia, two species of the *S. striatum* species-group are recorded, i.e., *S. (S.) argyrocinctum* and *S. (S.) baliense* Takaoka & Sofian-Azirun (De Meijere, 1913; Edwards, 1934; Takaoka & Davies, 1996; Takaoka *et al.*, 2017). This new species is distinguished from both known species by the 10 pupal gill filaments arranged as two pairs plus two triplets (Figure 9H, I) or four pairs and two individuals (Figure 9J) (c.f., arranged as five pairs in the latter two species), and two filaments of the ventralmost pair not thinnest (c.f., thinnest in the latter two species); from *S. (S.) argyrocinctum* by the length ratio of the male fore basitarsus against its greatest width (5.7–5.9 in this new species vs. 6.5 in the latter species), and pupal frons moderately covered with round tubercles of different sizes (Figure 9A) (c.f., densely covered with round tubercles of almost the same size in the latter species); and from *S. (S.) baliense* by the length ratio of the female fore basitarsus against its greatest width (4.9–5.4 in this new species vs. 6.5 in the latter species), and the number of male upper-eye (large) facets (16 or 17 vertical columns and 16 or 17 horizontal rows in this new species vs. 14 or 15 vertical columns and 15 horizontal rows in the latter species).

The pupa regarded as that of *S. (S.) argyrocinctum* by Edwards (1934) appears to be that of *S. (S.) bengkuruense* sp. nov. because its description and illustration were based on pupal specimens from

South Sumatra, and the gill illustrated in Figure 17 in Edwards (1934) is almost the same in the arrangement as one of the arrangements of the pupal gill filaments of this new species, 2+(2+1+2+1)+2 from dorsal to ventral (Figure 9J). The standard arrangement (2+2+2+2+2 from dorsal to ventral) of the pupal gill filaments of *S. (S.) argyrocinctum* from West Java, the type locality, had been unknown until it was shown by Takaoka & Davies (1996).

Whether *S. (S.) argyrocinctum* is distributed in Sumatra should be reconfirmed in future surveys.

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## 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., Currie, D.C. & Wood, D.M. (2004). The black flies (Simuliidae) of North America. New York: Cornell University Press, Ithaca, pp. xv+941.
- Crosskey, R.W. (1990). The natural history of blackflies. England, Chichester: John Wiley & Sons Inc., pp. ix+711.
- De Meijere, J.C.H. (1913). Studien ber S. döstasiatische Dipteren II. *Tijdschrift voor Entomologie* **56**: 317–354.
- Edwards, F.W. (1925). Diptera nematocera from Dutch East Indies. *Treubia* **6**: 154–157.
- Edwards, F.W. (1934). The simuliidae (Diptera) of Java and Sumatra. Deutsche Limnologische Sunda-Expedition. *Archiv für Hydrobiologie* **13**: 92–138.
- Friederichs, K. (1925). Beobachtungen an Simuliiden in Ost-Java. *Archiv für Schiffs und Tropenhygiene* **29**: 119–125.

Hadi, U.K., Takaoka, H., Kondo, K. & Hirai, H. (1996). Larval salivary gland chromosomes of *Simulium (Simulium) eximium* (Diptera: Simuliidae) from Java and Sumatra, Indonesia, with implication of sibling speciation. *Medical Entomology and Zoology* **47**: 139-144.  
<https://doi.org/10.7601/mez.47.139>

Srisuka, W., Takaoka, H., Aupalee, K. & Saeung, A. (2023). Discovery of a new black fly species in the *Simulium (Simulium) striatum* species-group (Diptera: Simuliidae) from northeastern Thailand and phylogenetic relationships within its species-group. *Acta Tropica* **238**: 106790.  
<https://doi.org/10.1016/j.actatropica.2022.106790>

Takaoka, H. (1989). Notes on blackflies (Diptera: Simuliidae) from Myanmar (formerly Burma). *Japanese Journal of Tropical Medicine and Hygiene* **17**: 243-257. <https://doi.org/10.2149/tmh1973.17.243>

Takaoka, H. (2003). The black flies (Diptera: Simuliidae) of Sulawesi, Maluku and Irian Jaya. Japan, Fukuoka: Kyushu University Press, pp. xxii+581.

Takaoka, H. (2017). Morphotaxonomic revision of species-groups of *Simulium (Simulium)* (Diptera: Simuliidae) in the Oriental Region. *Zootaxa* **4353**: 425-446. <https://doi.org/10.11646/zootaxa.4353.3.2>

Takaoka, H. (2024). The black flies of Subtropical and Tropical Asia: taxonomy and biology. Singapore: Springer, pp. xiv+751.

Takaoka, H. & Davies, D.M. (1995). A new black fly species of *Simulium (Nevermannia)* from Sumatra, Indonesia. *Japanese Journal of Tropical Medicine and Hygiene* **23**: 127-131.  
<https://doi.org/10.2149/tmh1973.23.127>

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. & Hadi, U.K. (1991). Two new blackfly species of *Simulium (Simulium)* from Java, Indonesia (Diptera: Simuliidae). *Japanese Journal of Tropical Medicine and Hygiene* **19**: 357-370.  
<https://doi.org/10.2149/tmh1973.19.357>

Takaoka, H., Hadi, U.K. & Sigit, S.H. (2006a). The black flies (Diptera: Simuliidae) of Flores and Timor, Indonesia. *Medical Entomology and Zoology* **57**: 1-26. [https://doi.org/10.7601/mez.57.1\\_1](https://doi.org/10.7601/mez.57.1_1)

Takaoka, H., Hadi, U.K. & Sigit, S.H. (2006b). A new species of *Simulium (Simulium)* from Sumatra, Indonesia (Diptera: Simuliidae). *Medical Entomology and Zoology* **57**: 27-34.  
[https://doi.org/10.7601/mez.57.27\\_1](https://doi.org/10.7601/mez.57.27_1)

Takaoka, H., Shrestha, S. & Dangi, N. (2020a). A new species and a new record of the *Simulium (Simulium) striatum* species-group (Diptera: Simuliidae) from Nepal. *Medical Entomology and Zoology* **71**: 91-100.  
<https://doi.org/10.7601/mez.71.91>

Takaoka, H., Otsuka, Y., Huang, Y.T., Low, V.L., Fukuda, M. & Ya'cob, Z. (2022). Descriptions of two new species of the *Simulium (Simulium) striatum* species-group (Diptera: Simuliidae) from Taiwan and Japan, and a revised description of *S. (S.) quinquestriatum* (Shiraki). *Acta Tropica* **227**: 106293.  
<https://doi.org/10.1016/j.actatropica.2021.106293>

Takaoka, H. & Sigit, S.H. (1997). Three new black fly species of *Simulium* (Diptera: Simuliidae) from Sumatra, Indonesia. *Japanese Journal of Tropical Medicine and Hygiene* **25**: 69-80.  
<https://doi.org/10.2149/tmh1973.25.69>

Takaoka, H., Sofian-Azirun, M., Ya'cob, Z., Chen, C.D., Lau, K.W. & Pham, H.T. (2014a). New species and records of blackflies (Diptera: Simuliidae) from Vinh Phuc Province, Vietnam. *Zootaxa* **3838**: 347-366.  
<https://doi.org/10.11646/zootaxa.3838.3.6>

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. & Suana, I.W. (2017). The black flies (Diptera: Simuliidae) of the Lesser Sunda Archipelago, Indonesia. *Acta Tropica* **169**: 170-186.  
<https://doi.org/10.1016/j.actatropica.2017.01.016>

Takaoka, H., Sofian-Azirun, M., Ya'cob, Z. & Hashim, R. (2014b). Two new species of *Simulium (Gomphostilbia)* (Diptera: Simuliidae) from Cameron's Highlands, Peninsular Malaysia, with keys to 21 species of the *Simulium asakoae* species-group. *Zootaxa* **3765**: 54-68.  
<https://doi.org/10.11646/zootaxa.3765.1.3>

Takaoka, H., Srisuka, W., Fukuda, M. & Saeung, A. (2020b). Twenty-one new species of the *Simulium (Gomphostilbia) asakoae* species-group (Diptera: Simuliidae) in Thailand, with their genetic relationships. *ZooKeys* **950**: 51-152. <https://doi.org/10.3897/zookeys.950.51298>

Takaoka, H., Ya'cob, Z. & Sofian-Azirun, M. (2018). Classification, annotated list and keys for the black flies (Diptera: Simuliidae) in Peninsular Malaysia. *Zootaxa* **4498**: 1-65. <https://doi.org/10.11646/zootaxa.4498.1.1>

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>