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Simuliidae (Diptera) of the Solomon Islands: new records and species, ecology, and biogeography

D. A. CRAIG[1], R. A. ENGLUND[2] & H. TAKAOKA[3]

[1]*Department of Biological Sciences, University of Alberta, Edmonton, Alberta, T6G 2E9 Canada.*
E-mail: d.craig@ualberta.ca
[2]*Pacific Biological Survey, Bishop Museum, 1525 Bernice Street, Honolulu, Hawai'i, 96817 USA.*
E-mail: englund@bishopmuseum.org
[3]*Department of Infectious Disease Control, Faculty of Medicine, Oita University, Hasama, Yufu City, Oita, 879-5593 Japan. E-mail: takaoka@med.oita-u.ac.jp*

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Abstract

Five species of Simuliidae are reported for the first time from the Solomon Islands of Santa Isabel, Malaita, and Makira, and Kolumbangara and Rendova of the New Georgia Island group. One new

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species, *Simulium* (*Gomphostilbia*) *rhopaloides* Craig, Englund & Takaoka, from Guadalcanal is described. The new material consists mainly of immature larvae, which, while allowing assignment to subgenus, do not always allow identification to species. The probability of other new species is suggested. The record for Makira is the most easterly known for the subgenus *Morops,* as are those for *Gomphostilbia* from Guadalcanal and Malaita. Larval habitats on the islands are illustrated. A brief synopsis of the paleogeology of the Solomon Islands is given as a basis for preliminary comments on distribution and biogeography of the known species of Simuliidae, now 10, for the Solomon Islands.

Key words: Simuliidae, *Morops*, *Gomphostilbia*, ecology, paleogeology, biogeography, Solomon Islands

Introduction

Of major strategic importance during the Second World War, the Solomon Islands comprise the third largest archipelago in the South Pacific. Scattered in a double chain of islands, the archipelago is a mixture of mountainous islands and low-lying coral atolls that stretches between E155.5° and E170.5°, some 1,667 km, in a southeasterly direction from the Shortland Islands to the Santa Cruz Islands (Fig. 1, Table 1) and farther to three remote, tiny outliers, Tikopia, Anuta, and Fataka. From North to South, between the Ontong Java Atoll at latitude S5.2° and the Indispensable Reefs at S12.7°, south of Rennel Island, is ca. 900 km. There are six major and approximately 990 smaller land masses, covering an area of about 28,446 sq km. The biggest islands are, from the west, Choiseul, New Georgia, Santa Isabel, Guadalcanal, Malaita, and Makira (San Cristobal). These larger islands are characterized by thickly forested mountain ranges intersected by deep, narrow valleys.

Bougainville, while politically part of Papua New Guinea, is geologically part of the western Solomon Islands. Similarly, the Santa Cruz Islands, while politically of the Solomon Islands, are geologically part of Vanuatu and are the northern extent of the New Hebrides Arc system.

The presence of simuliids on the Solomon Islands was first noted by Maffi and Sherwood (1970) and that material was described by Stone & Maffi (1971) as *Simulium* (?*Gomphostilbia*) *sherwoodi*; an unknown species near *S. avilae* Smart & Clifford 1965, of New Guinea also was recorded. Crosskey (1989) assigned *S. sherwoodi* to *Morops*. Further material was described as *S.* (*G.*) *hiroshii* by Takaoka (1994) and *S.* (*M.*) *kerei* by Takaoka & Suzuki (1994). A taxonomic revision of simuliids from the Solomon Islands by Takaoka & Suzuki (1995) included five new species: *S.* (*M.*) *kawagishii, S.* (*M.*) *noroense, S.* (*M.*) *pohaense*, *S.* (*M.*) *selwynense*, and *S.* (*M.*) *solomonense*. Along with *S.* (*M.*) *papuense* Wharton 1948, known also from New Guinea, nine species were recognized and the *Morops* species segregated to groups, mainly the *clathrinum* species group, which possesses a distinctive so-called 'pit organ' near the base of the pupal gill. Takaoka & Suzuki (1995) note that the unidentified species, which Stone & Maffi (1971) placed near

S. avilae, at the time, is either *S.* (*M.*) *pohaense* or *S.* (*M.*) *selwynense*.

As originally noted by Stone & Maffi (1971), by Crosskey (1967), and later by Takaoka (1994), assignment of species to subgenus and species group is often difficult with these taxa. Takaoka (2003) transferred *S. sherwoodi*, *S. noroense*, and *S. kerei* — previously ungrouped in *Morops* (Takaoka & Suzuki 1995) — into the *sherwoodi* species group of *Gomphostilbia* and provided a new diagnosis for that subgenus, as well as for *Morops*.

Takaoka (1995) reviewed the simuliids of Bougainville Island, Papua New Guinea, immediately to the west of the Solomon Islands. Seven species were recorded, of which two, *S.* (*G.*) *hiroshii* and *S.* (*G.*) *noroense* (then in *Morops*), were shared with the Solomon Islands. Crosskey (2004) provided amplifying notes on the Bougainville material.

New material was collected by the second author (RAE) in 2005 as part of an archipelago-wide rapid biological assessment of freshwaters, funded by Conservation International and Smithsonian Institution and conducted with the Bishop Museum.

The objectives of this paper are to identify the new material and describe one new species. The paper updates distribution patterns and, along with a synopsis of the paleogeology of the region, provides a basis for a preliminary biogeographical analysis.

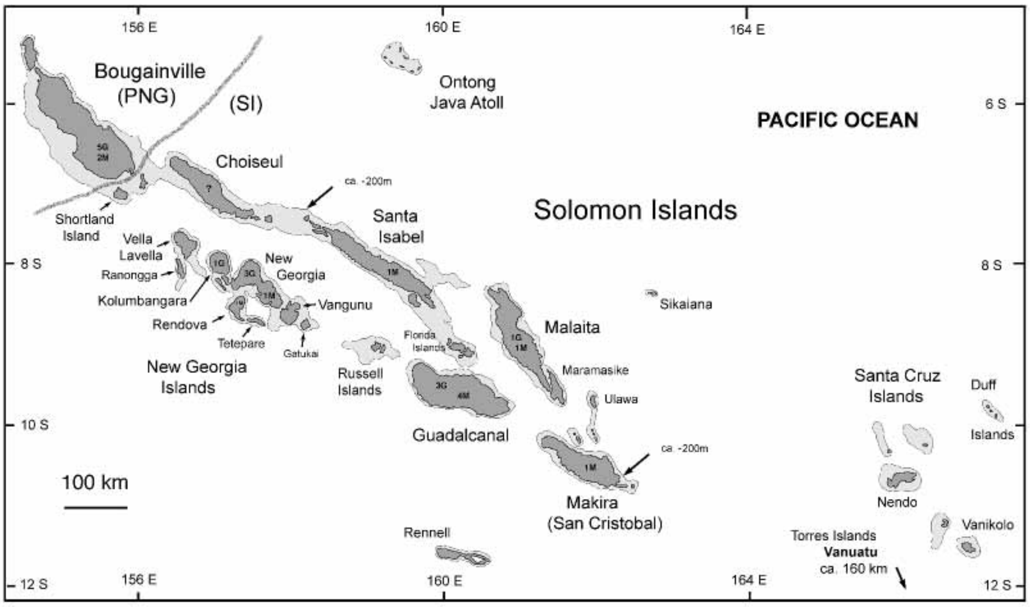

FIGURE 1. Bougainville (PNG) and the Solomon Islands. The 200-m bathymetric contour is indicated. Numbers and letters associated with islands are number of recognised species and subgenus (M = *Morops*, G = *Gomphostilbia*).

TABLE 1. Geographic aspects of the larger Solomon Islands, plus species of Simuliidae.

Island Name	Lat/Long	Area (km2)	Height (m)	Type	Simuliidae species*
Shortland Island	7.00°S 155.75°E	202	237	volcanic/coral	Unknown
Vella Lavella	7.75°S 156.65°E	629	808	volcanic/coral	Unknown
Ranongga	8.05°S 156.55°E	147	869	volcanic/coral	Unknown
Kolumbangara	7.95°S 157.05°E	687	1,768	high volcanic	3
New Georgia	8.25°S 157.60°E	2,036	860	volcanic/coral	1,2,3,9
Rendova	8.55°S 157.30°E	411	1,060	volcanic	nr 8
Tetepare	8.75°S 157.55°E	118	420	volcanic/reef	Unknown
Vangunu	8.60°S 158.00°E	509	1,082	volcanic	Unknown
Choiseul	7.10°S 159.95°E	2,970	1,067	high volcanic	Unknown
Santa Isabel	8.00°S 159.10°E	3,664	1,219	volcanic/coral	8
Malaita	9.00°S 161.00°E	548	1,433	high volcanic	1,7
Maramasike	9.60°S 161.45°E	480	518	raised coral	Unlikely
Guadalcanal	9.60°S 160.20°E	5,352	2,447	Old volcanic	1,4,5,6,7,8,10
Rennell	11.65°S 160.20°E	660	154	raised coral	Unlikely
Makira (San Cristobal)	10.60°S 161.85°E	3,190	1,250	volcanic	nr 7
Nendo (Ndeni)	10.75°S 166.00°E	505	549	volcanic	Unknown
Vanikolo	11.60°S 166.85°E	173	924	recent volcano	Unlikely

Gomphostilbi**a* (*hiroshii* species group): 1. *S. hiroshii*; (*sherwoodi* species group) 2. *S. kerei*, 3. *S. noroense,* 4. *S. rhopaloides*, 5. *S. sherwoodi*. ***Morops (*clathrinum* species group): 6. *S. kawagishii*, 7. *S. pohaense*, 8. *S. selwynense*, 9. *S. solomonense*. ***Morops*** (*papuense* species group):10. *S. papuense*.

Material and methods

All material was preserved in 80% ETOH and was processed according to the procedures of Craig (2004). Specifically, adults in alcohol were dried via Peldri® and pinned. Genitalia were cleared in potassium hydroxide (KOH), stained in Chlorozoal Black, and examined in glycerine. Pupal gills and thoracic cuticle were mounted in polyvinyl lactophenol, as were larval structures. Gill characteristics are important for identification (Takaoka & Suzuki 1995). However, much of the new material consisted of earlier instar larvae with undeveloped gills, which presented a problem. It was possible, however, to dissect out the developing gills of penultimate larvae and, after staining them in Chlorozoal Black, determine the basic structure and disposition of the gill filaments. Other structures of such larvae, such as the mandible and hypostoma, were not a problem. Photography was with a Nikon CoolPix 4500 digital camera, in manual mode. Whole-body images (e.g., Figs. 2a, 5a) of larvae used a Wild M5 dissecting microscope and others a Wild M20 compound microscope. The dorsal views of larval heads (e.g., Figs. 2e, 5b) were compiled in Photoshop from a series of images at different foci. All habitus images were with the specimens in alcohol. Only new material is illustrated; other Solomon

Islands black fly species are well illustrated in the various works by Takaoka. Terms for morphological structures and format of the taxonomic description follow those of Craig (2004).

For firm identification, last-instar larvae or pupae are usually needed for pupal gill characteristics, in particular for *Morops* in which the 'pit organ' of the pupa can be definitive. But, even in a fully developed pharate pupa, the pit organ is not well sclerotized, or easily observable. Hence, in all instances where we could determine subgenus, it was not possible to make definitive identifications to species for some material. We do, however, suggest the most likely identification and, where appropriate, the probability of new species.

As common for Pacific islands, spelling of names is various (Craig *et al.* 2001). Here we use names from the official WWW page of the Solomon Islands Government.

All the material collected by RAE and dealt with here, is deposited in the Bernice P. Bishop Museum (BPBM), Honolulu, 1525 Bernice Street, Honolulu, Hawai'i, 96817. Below, we deal, island by island, with the new material (Table 2), also noting previously known material.

TABLE 2. Locality data for new material of Simuliidae from the Solomon Islands.

Island name	Locality	Lat/Long	Alt (m)	Date	Material	Habitat type	Figure
Kolumban-gara Island	nr. Ringgi	S8.07240 E157.11998	119	19 iii 2005	Earlier instar larvae	Small forest stream	11a
New Georgia Island	Sakumebure River	S8.40771 E157.69275	190	22 iii 2005	Penultimate & earlier larvae	Small forest stream	11b
Rendova Island	Toropi River	S8.50818 E157.31313	240	21 iii 2005	Full range of larval instars	Small forest stream	11c
Santa Isabel	Garana River	S8.07131 E159.46126	0–11	24 vii 2005	Full range of larval instars	Broad river	11d
Guadalcanal	Charovuga River	S9.59936 E160.12402	510	27 vii 2005	Pupa & full range of larvae	Small rocky river	11e
Malaita Island	Aluta River	S8.69625 E160.83405	75	30 vii 2005	Adults & full range of larvae	Cascade	11f
Makira (San Cristobal)	Puepue River	S10.47786 E161.92592	17–60	10 vii 2005	Two penultimate larvae	Small rocky river	11g

Observations and descriptions

Choiseul

No simuliids are known as yet from this island, but there is little reason for them to be absent. Lack of time to reach suitable habitats during the present survey hindered simuliid searches on Choiseul. Almost equidistant (ca. 60–100 km) from Choiseul are Bougainville

(PNG) immediately to the west, with Santa Isabel to the southeast and the New Georgia Islands to the south. Bougainville possesses two species of *Morops* and five of *Gomphostilbia* (Takaoka 1995). Both *S.* (*G.*) *hiroshii* and *S.* (*G.*) *noroense* are common to Bougainville and the Solomon Islands. New Georgia Islands to the south have four species of simuliids. Further, topographically, Choiseul is mountainous and there are numerous river systems (Google Earth®) quite adequate for simuliids.

New Georgia Islands

Previously, only the island of New Georgia itself was known to possess simuliids: *S.* (*G.*) *hiroshii*, *S.* (*G.*) *kerei*, *S.* (*G.*) *noroense*, and *S.* (*M.*) *solomonense* (Takaoka & Suzuki 1994, 1995). We assign new larval material from Kolumbangara Island and New Georgia to *S.* (*G.*) *noroense*, but note that there are differences in the number of hypostomal teeth and setae, and the head spots are more positive (Figs. 2, 3) in the new material than in the type description from Guadalcanal. These are possibly new species; however, more material will be needed for that to be correctly ascertained.

New material (Fig. 4) from Rendova Island is of *Morops* and, based on pharate pupal gill proportions of gill base to filament length (Fig. 4b), appears to be neither *S.* (*M.*) *solomonense,* known from New Georgia, nor *S.* (*M.*) *kawagishii* from Guadalcanal. Larval characteristics (Figs. 4a, c-g) are similar to those of *S.* (*M.*) *selwynense* or *S.* (*M.*) *pohaense* of Guadalcanal and more so to the former. There is a strong possibility that this *Morops* from Rendova is a new species, but similarly for the new *Gomphostilbia* material from Kolumbangara, more material is need before such a decision can be made.

The simuliid habitat (Fig. 11a) in Kolumbangara was a small, unnamed stream 5.5 km north of Ringgi harbour that flowed through a dense secondary growth forest that was first harvested in the 1970s. The stream here was low gradient with a mixture of riffles and shallow pools with good water clarity and a water temperature of 26ºC. Simuliid larvae were abundant on leaves and rocks in shallow riffle areas.

On the main island of New Georgia, simuliids were collected from the upper Sakumebure River (Fig. 11b) near the former Sakumbare logging camp lying 15.5 km east of Putagita harbour. Water temperature at this site was 26ºC, and the stream had a high silt load (sometimes as deep as knee-level), as the watershed has been heavily logged. The stream had large and striking cascades 3-7 m high, with larval simuliids being collected from leaves in high-velocity riffle areas.

Rendova Island has a particularly rich aquatic insect fauna, with simuliids being collected from a tributary of the upper Toropi River (Fig. 11c) above a road crossing 5.5 km southeast of Kenole. Water temperature here was 26ºC, and the moderately sized and low-gradient stream was shaded and flowed through second-growth forest, and adjacent banana and manioc fields. Water clarity was high, and simuliid larvae were common on leaves in heavily shaded, low-to-moderate gradient riffles.

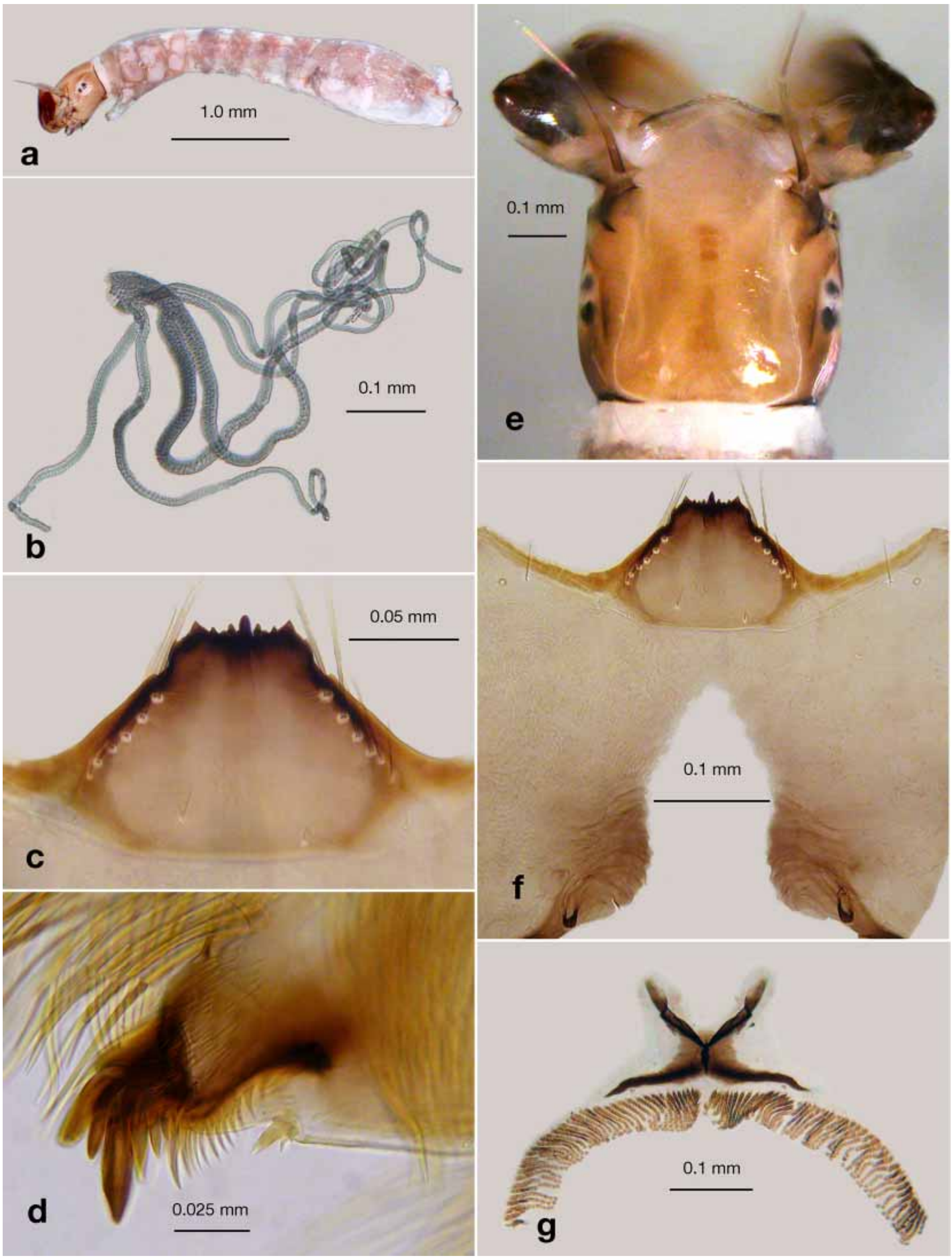

FIGURE 2. *Simulium* (*G.*) *noroense*, Kolumbangara, New Georgia Islands. Penultimate instar larva. **a**, left lateral view. **b**, pharate pupal gill. **c**, hypostomal teeth. **d**, mandible teeth, sensillum, and serration. **e**, dorsal view of head. **f**, hypostoma and postgenal cleft. **g**, anal sclerite and circlet of hooks.

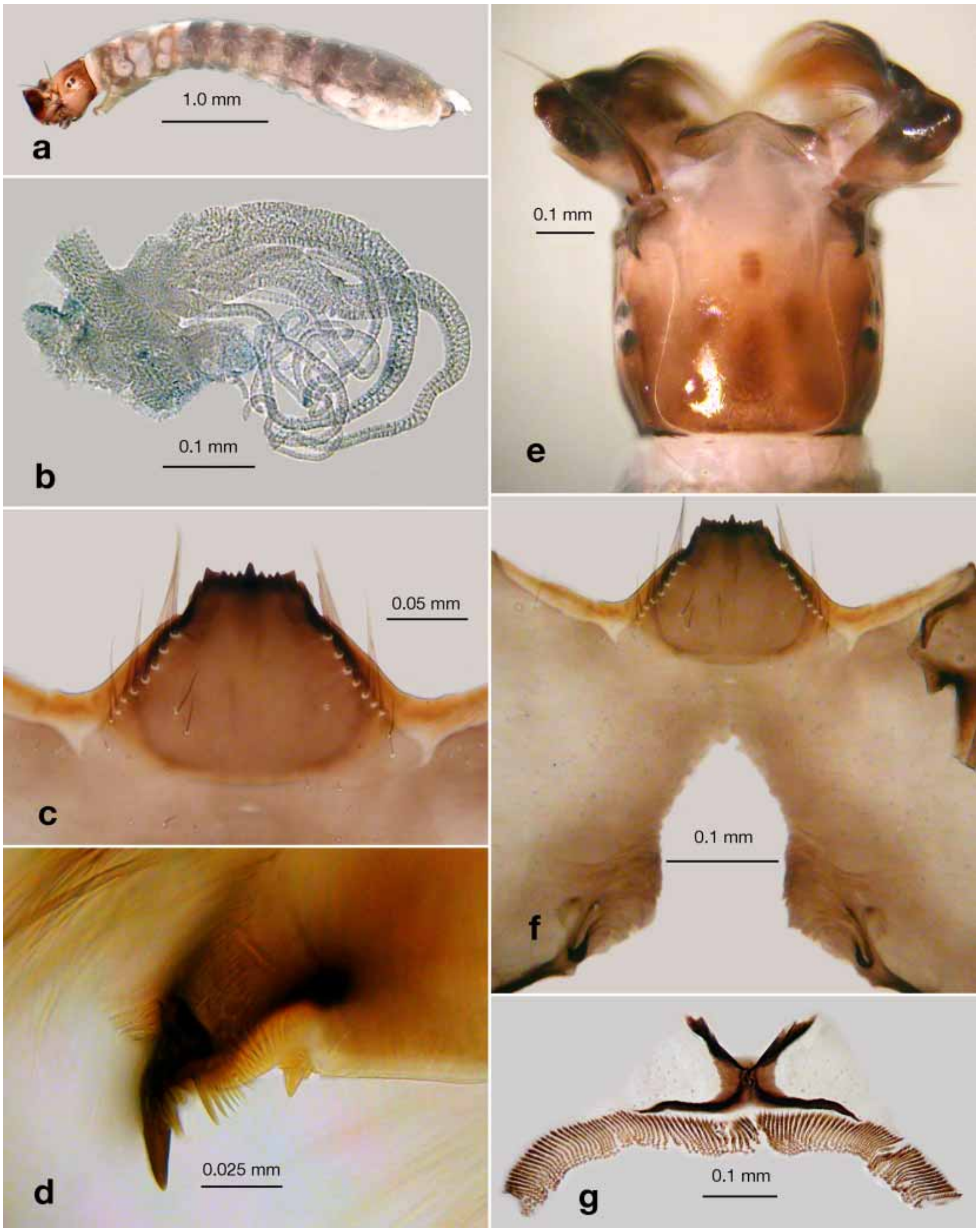

FIGURE 3. *Simulium* (*G.*) *noroense*, New Georgia, New Georgia Islands. Penultimate instar larva. **a**, left lateral view. **b**, pharate pupal gill. **c**, hypostomal teeth. **d**, mandible teeth, sensillum, and serration. **e**, dorsal view of head. **f**, hypostoma and postgenal cleft. **g**, anal sclerite and circlet of hooks.

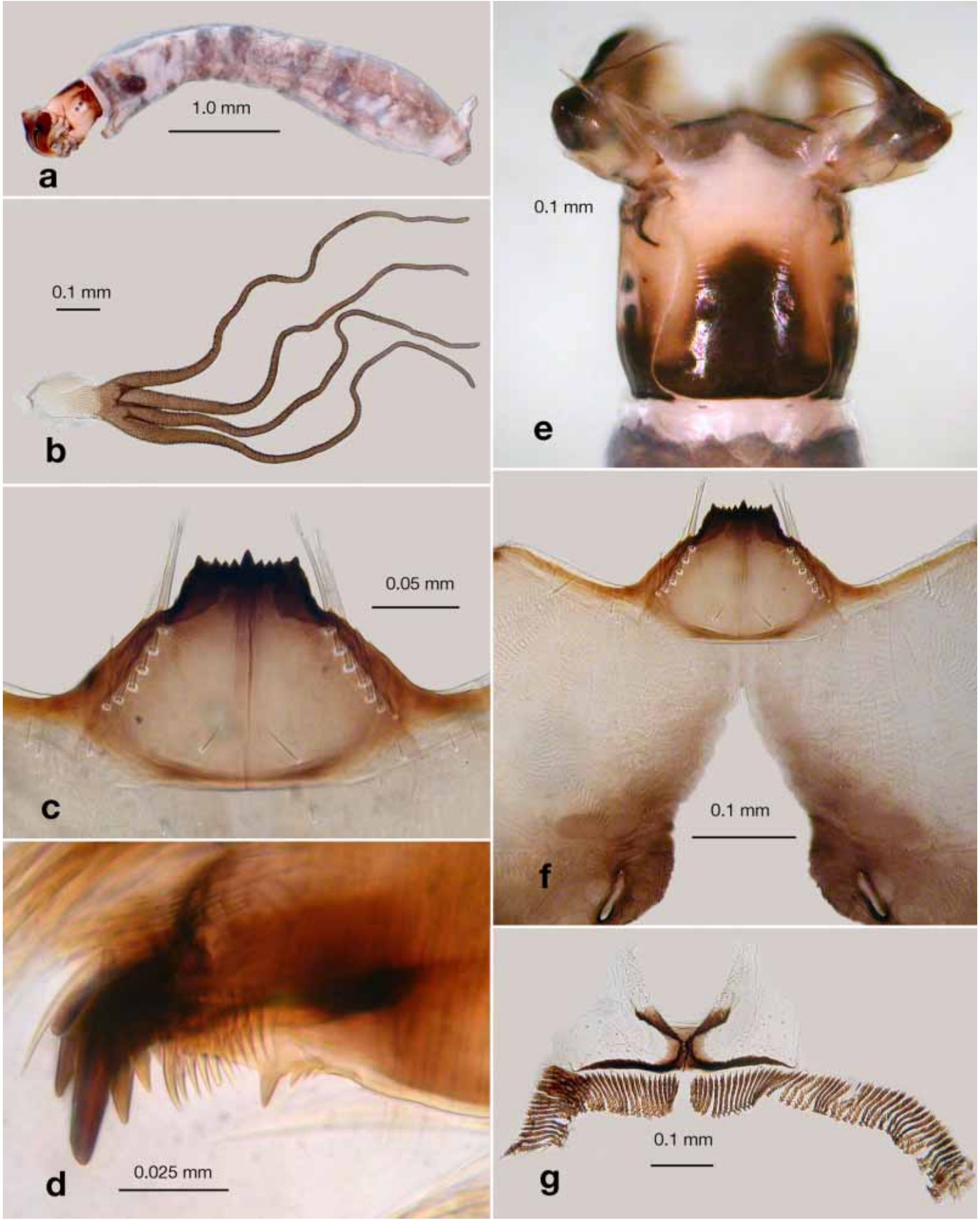

FIGURE 4. *Simulium* (*M.*) nr. *selwynense*, Rendova, New Georgia Islands. Last-instar larva. **a**, left lateral view. **b**, pharate pupal gill. **c**, hypostomal teeth. **d**, mandible teeth, sensillum, and serrations. **e**, dorsal view of head. **f**, hypostoma and postgenal cleft. **g**, anal sclerite and circlet of hooks.

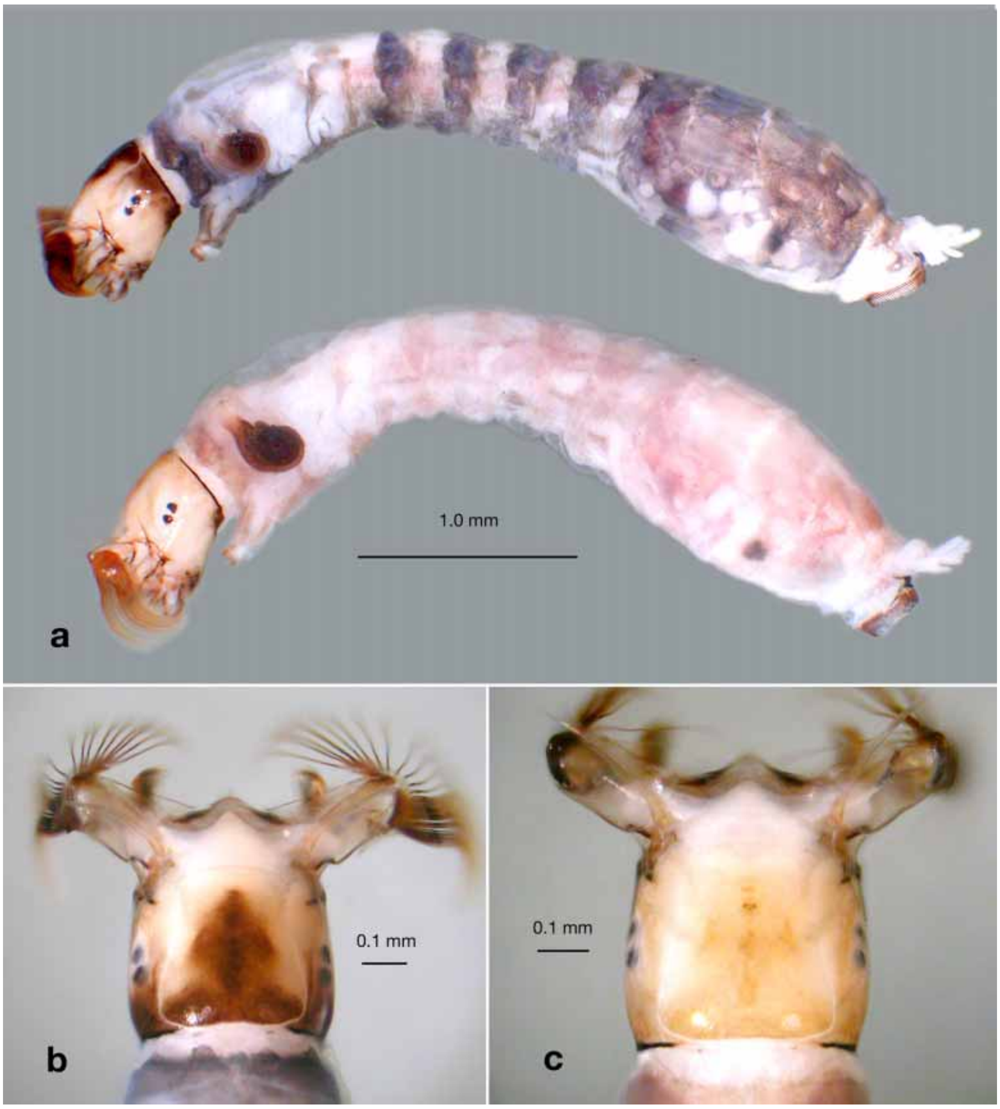

FIGURE 5a–c. *Simulium* (*M.*) nr. *selwynense*, Santa Isobel. Last-instar larvae. **a**, left lateral views, female upper, male lower. **b**, dorsal view of female larva head. **c,** dorsal view of male larva head.

Santa Isabel

Black flies previously were unknown from this island. The newly collected simuliid larvae are clearly of *Morops*. The pharate gill and larval structures (Fig. 5) indicate that the material is either *S.* (*M.*) *selwynense* (previously known only from Guadalcanal) or a closely related species.

Simuliids were collected from a shallow, clear-water riffle 2 km upstream from the ocean in the Garana River (Fig. 11d). In this area, the river flowed through second- growth forest interspersed with small agricultural plots, and was of low gradient but with exceedingly clear water devoid of silt. Judging from the size of the bare cobble sandbars, the Garana River greatly fluctuates in discharge during the wet season. Simuliids were not collected elsewhere on Santa Isabel because of heavy rain.

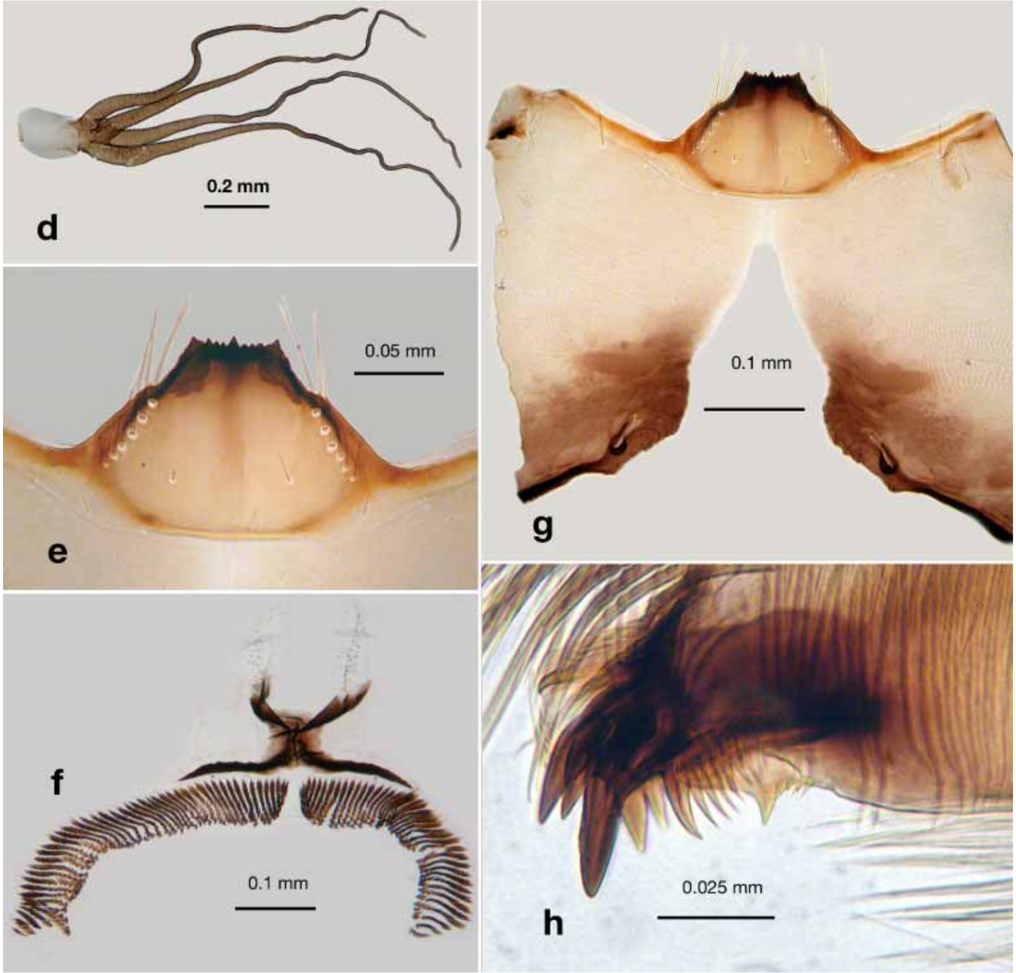

FIGURE 5. *Simulium* (*M.*) nr. *selwynense*, Santa Isobel. Last-instar larvae. **d**, pharate pupal gill. **e**, hypostomal teeth. **f**, anal sclerite and circlet of hooks. **g**, hypostoma and postgenal cleft. **h**, mandible teeth, sensillum, and serrations.

Guadalcanal

This island is relatively well collected and was previously known to have six simuliids of the nine known species of the Solomon Islands (Takaoka 1994, Takaoka & Suzuki 1995): *S.* (*G.*) *hiroshii*, *S.* (*G.*) *sherwoodi*, *S.* (*M.*) *kawagishii*, *S.* (*M.*) *papuense*, *S.* (*M.*) *pohaense*, and *S.* (*M.*) *selwynense*. The new material is of a single pupal exuviae (Fig. 6) and some early-instar larvae of *S.* (*G.*) *sherwoodi*, plus larvae of a new species, assigned to *Gomphostilbia* (*sherwoodi* species group) and described below, to give a total now of seven species for the island.

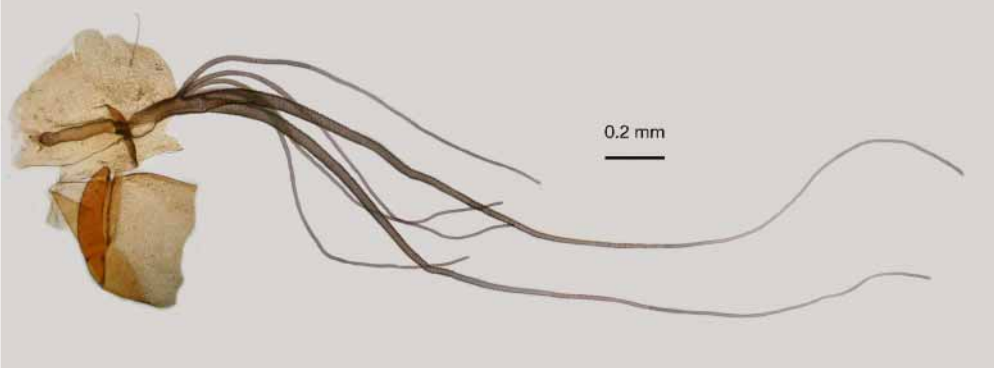

FIGURE 6. *Simulium* (*G.*) *sherwoodi*, Guadalcanal. Pupal gill, thoracic cuticle, and antennal sheath.

Simulium (*Gomphostilbia*) *rhopaloides* Craig, Englund & Takaoka n. sp.
(Fig. 7)

Types

Holotype. Larva: early-last instar on slide. Label data "*Simulium* (*Gomphostilbia*) *rhopaloides*. Solomon Islands, Guadalcanal, Charovuga River upstream of Gold Ridge Mine, S9.59936º E160.12402º, alt 540m. 27.vii. 2005. Coll. R. Englund. HOLOTYPE. No. 16626 (BPBM).

Paratypes. Larvae: seven early last and penultimate instars in alcohol. Label data—as for Holotype, but with "PARATYPE" (BPBM).

Diagnosis

Pupa: Gill filaments modified into single club-like structure with 2 fine nontapered filaments. Larva: anterior cephalic apotome markedly pale, light brown elsewhere; antennae extended well beyond labral fan stalk, hypostomal margins smooth; mandible serration and sensillum forming acute angle with mandible; ventral tubercles present, but not markedly developed.

Description

Adult female: Unknown.

Adult male: Unknown.

Pupa (based on poorly developed pharate pupal gill). Gill with club-like structure and 2 fine filaments (Fig. 7b).

Larva (based on early last-instar larvae). Body: total length 5.3 mm, overall greyish, thorax evenly pigmented, paler dorsally, posterior abdomen darker dorsally, pale ventrally (Fig. 7a). Head (Fig. 7e): lateral margins convex; anterior frontoclypeal apotome markedly pale, lighter brown elsewhere; antero- and posteromedial head spots positive and distinct, anterolateral head spots positive and distinct, posterolateral head spots positive and

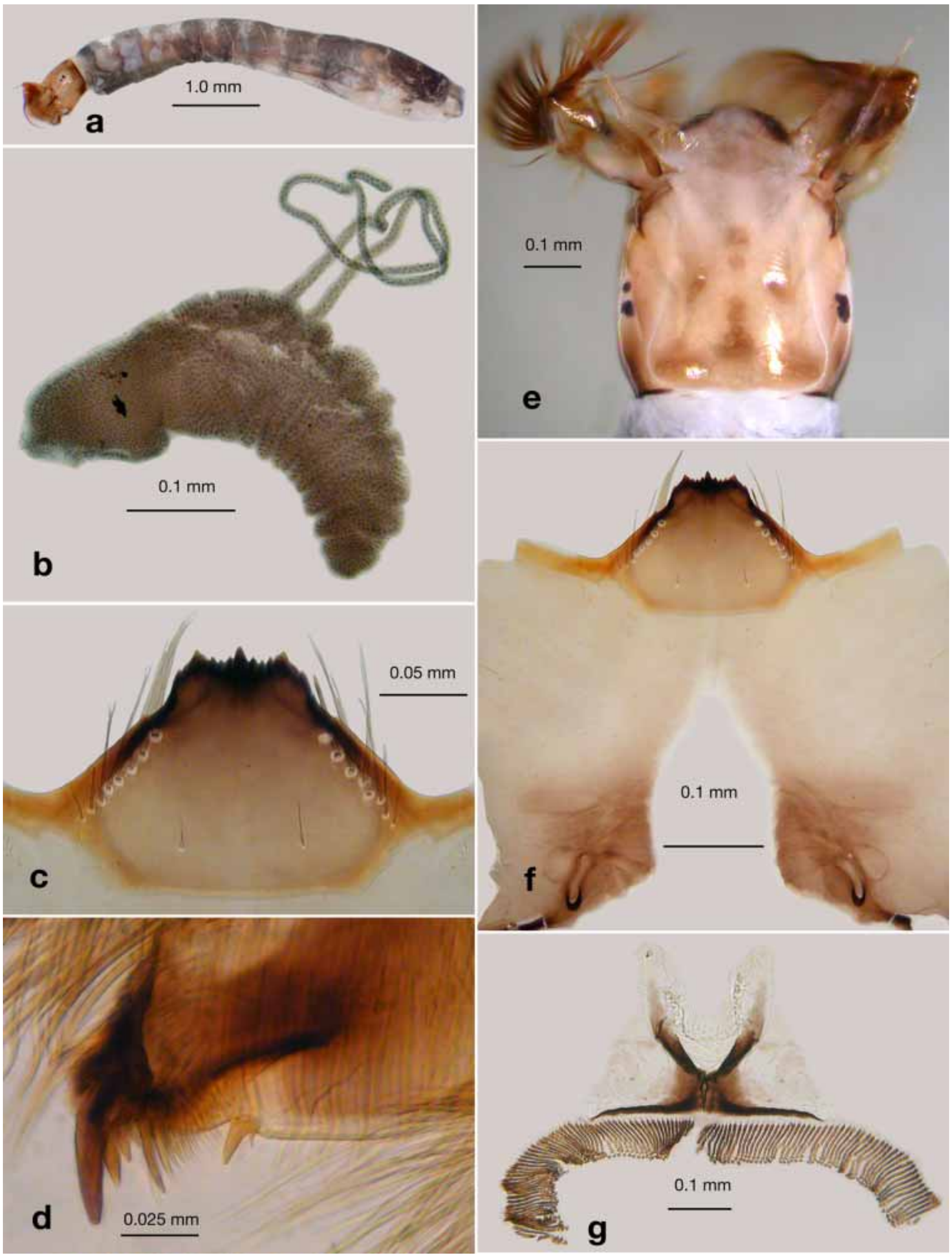

FIGURE 7. *Simulium* (*G.*) *rhopaloides* **n. sp.** Guadalcanal. Early last instar larva, Holotype. **a**, left lateral view. **b**, pharate pupal gill. **c**, hypostomal teeth. **d**, mandible teeth, sensillum, and serrations. **e**, dorsal view of head. **f**, hypostoma and postgenal cleft. **g**, anal sclerite and circlet of hooks.

surrounded by diffuse light brown; ecdysial lines pale and distinct, broadly rounded posteriorly; fan stalks translucent; width 0.51 mm, length 0.61 mm; distance between antennal bases 0.25 mm; cervical sclerites distinct; postocciput not extended medially. Antennae: total length 0.41 mm; proportions of articles 1.0:1.0:1.1; distal article extended half length beyond labral fan stalk; distal article and proximal portion of medial article brown, distal portion of basal article pale, remainder distinctly brown. Labral fan: stalk with anterior palatal bar not markedly protruded; 43 rays, 0.55 mm in length, 5 rays less substantial; microtrichia 1.75 times longer than ray width, distinct pattern of 5 or 6 smaller microtrichia between larger ones. Hypostoma (Fig. 7c): median tooth and lateral teeth equally developed, not prominent, lateral teeth broadly based, sublateral teeth distinct, but not markedly so; paralateral teeth poorly developed; 1 lateral serration poorly developed, otherwise smooth; 8 hypostomal setae per side. Postgenal cleft (Fig. 7f): arrowhead-shaped, 1.5 times deeper than wide, posterior margins vertical for half of depth, remainder V-shaped with slightly rounded margins; posteroventrally elongate muscle spots light brown. Postgenal bridge: 0.3 times as long as cleft depth; genae and postgenae markedly light brown. Mandible (Fig. 7d): preapical and apical teeth well developed but not markedly, subapical teeth less so; 7 and more spinous teeth decreased in size markedly; sensillum markedly developed and forming acute angle with anterior blade of mandible, serration single, distinct, but not well developed. Abdomen: anterior abdomen narrower than thorax, expanded smoothly posteriorly to 5th abdominal segment, then expanded markedly smoothly. Anal sclerite (Fig. 7g): rectal scales well developed; anterior arms slightly longer than ventral arms, central junction broad. Posterior proleg circlet of hooks: 118 rows of hooks; 15-16 hooks per row (total ca. 1,800).

Etymology

The name is in reference to the club-like pupal gill.

Comments

Larval characteristics clearly place this material in *Gomphostilbia*. The pupal gill is, however, unusual with a club-like structure and only two fine filaments (Fig. 7b)—a unique arrangement for that subgenus. There are, however, gills with some thickened filaments in the *sherwoodi* species group (e.g., *S.* (*G.*) *kerei* and *S.* (*G.*) *pangunaense*) and the *batoense* species group (*S.* (*G.*) *padangense*), albeit the number of slender filaments is four in the former two species and seven in the last. Elsewhere in *Gomphostilbia*, four gill filaments are also found in *S.* (*G.*) *palauense*, *S.* (*G.*) *mogii*, *S.* (*G.*) *gimpuense*, and *S.* (*G.*) *brevilabrum*. We consider the gill of *S.* (*G.*) *rhopaloides* the extreme of such examples and within the *sherwoodi* species group.

All types are deposited in the Bishop Museum.

Although Guadalcanal is the largest and most geographically complex of the Solomon Islands, it was not emphasized during the present survey, and was little sampled. Because few roads extend into the backcountry, with the notable exception of the Gold Ridge Mine area, gaining access to higher-elevation stream areas is problematic. However, we were able to sample upstream of the influence of the large Gold Ridge Mine on the Charovuga River (Fig. 11e), at elevations above 500 m. There the Charovuga River is moderately sized, but heavily sedimented in places because of many small-scale gold diggings being done by squatters. However, the river has numerous tributaries and cascades feeding it at this elevation, many of which appear to run through undisturbed forest. Water temperatures were 23.5ºC and aquatic habitats were highly varied, ranging from small seeps and cascades to riffles and pools. *Simulium* (*G.*) *rhopaloides* larvae were collected from rocks in small riffles in the main portion of the river.

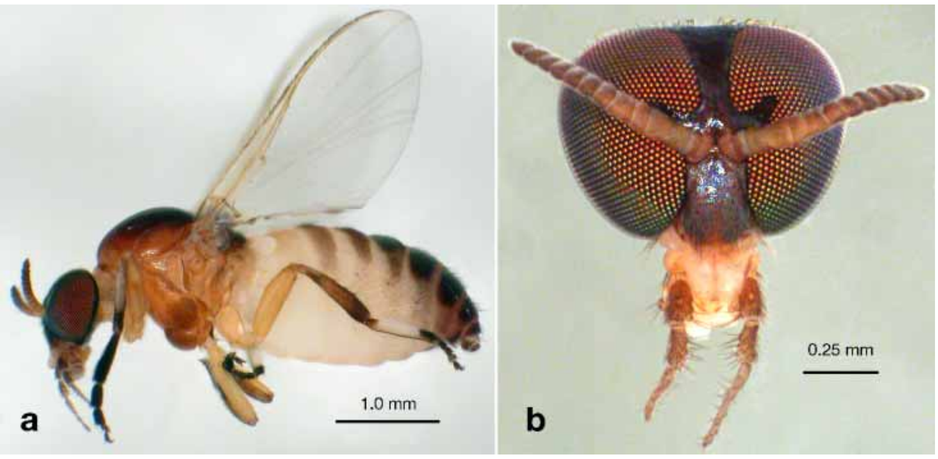

FIGURE 8. *Simulium* (*G.*) *hiroshii*, Malaita. Female adult. **a**, left lateral view. **b**, frontal view of head. Specimen in alcohol.

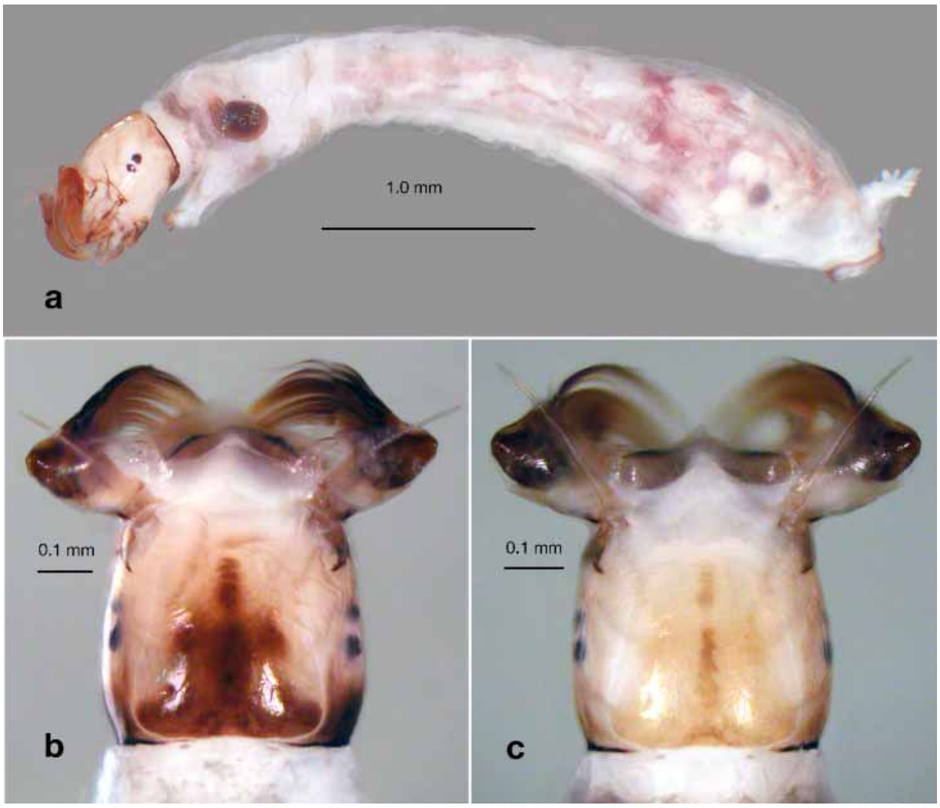

FIGURE 9a–c. *Simulium* (*M.*) nr. *pohaense*, Malaita. Last instar larva. **a**, left lateral view, male. **b**, dorsal view, female larva head. **c**, dorsal view, male larva head.

Malaita

Simuliids have not previously been known from this island. Five female adults are of *S.* (*G.*) *hiroshii* (Fig. 8), previously known only from Guadalcanal (Takaoka 1994) and New Georgia (Takaoka & Suzuki 1995). We note, however, that these adults are slightly larger in body length and size of the maxillary palp sensory vesicle than given in the original description. The adults were not biting, and apparently are not pests of humans, as no bites were reported by any of the survey crew there, or elsewhere in the Solomon Islands.

The new larval material (Fig. 9) is of *Morops*, and is similar to *S.* (*M.*) *selwynense* and to *S.* (*M.*) *pohaense*, both from Guadalcanal. Given the extreme sex-related dimorphism in colour (Fig. 9b, c), we assign this material to *S.* (*M.*) *pohaense*.

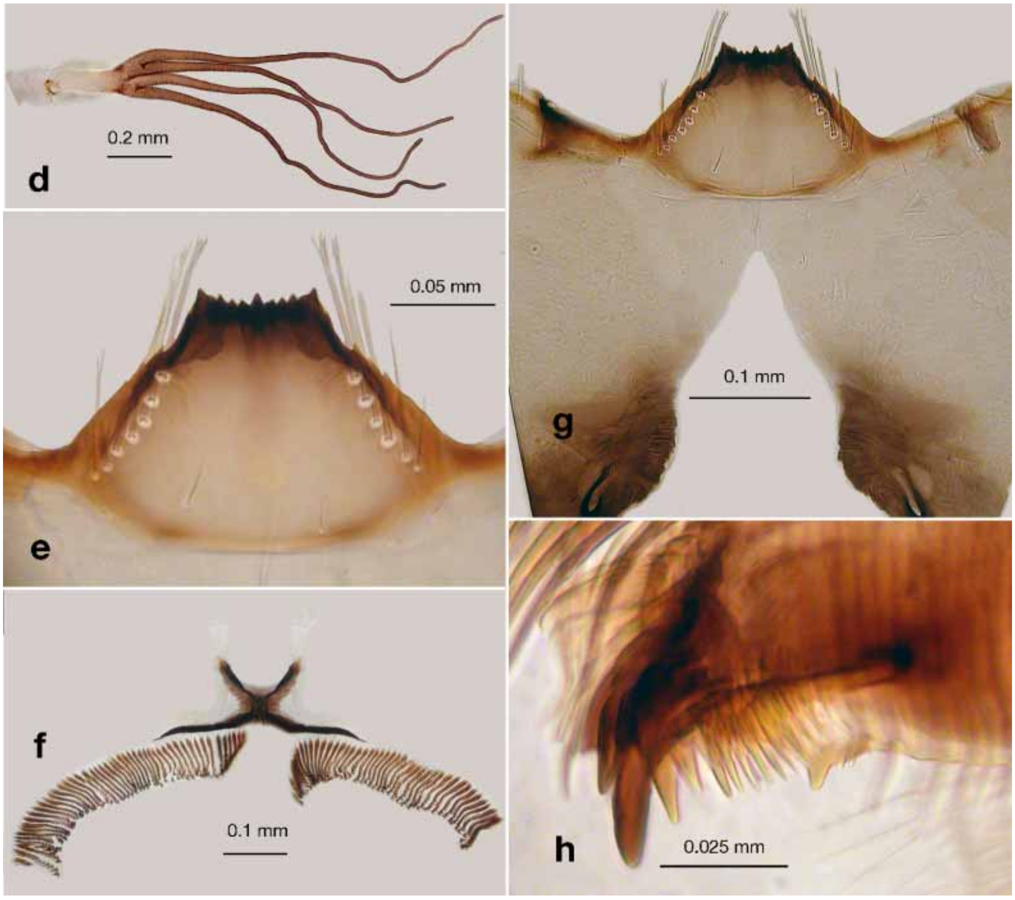

FIGURE 9d–h. *Simulium* (*M.*) nr. *pohaense*, Malaita. Last instar larva. **d**, pharate pupal gill. **e**, hypostomal teeth. **f**, anal sclerite and circlet of hooks. **g**, hypostoma and postgenal cleft. **h**, mandible teeth, sensillum, and serrations

Streams on Malaita are well developed and often have large travertine waterfalls, such as the Aluta River with its spectacular Kwaisale waterfall complex (Fig. 11f) where the simuliids were collected. Water here flowed over a series of 10-50 m travertine cascades, separated by riffles and pools up to 2m deep. Smaller tributaries flowed into the main stream as large cascades or waterfalls, producing a complex of aquatic habitats. Simuliid larvae were collected from rocks and leaves, and the adults were collected by sweeping around the cascade and riffle areas. Water in this stream was clear, reflecting the largely undisturbed nature of the surrounding watershed. Water temperature was 25.5ºC.

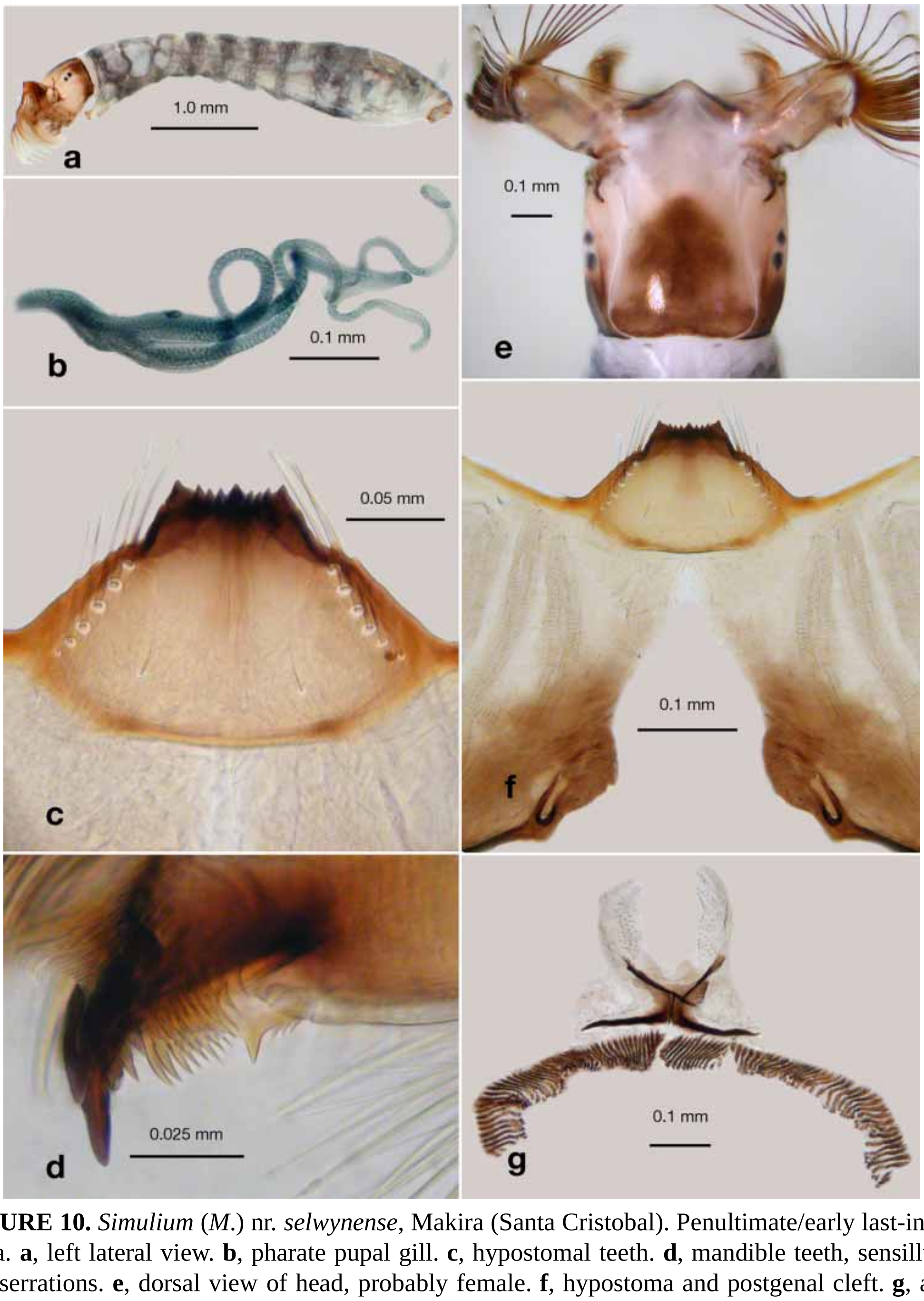

FIGURE 10. *Simulium* (*M.*) nr. *selwynense*, Makira (Santa Cristobal). Penultimate/early last-instar larva. **a**, left lateral view. **b**, pharate pupal gill. **c**, hypostomal teeth. **d**, mandible teeth, sensillum, and serrations. **e**, dorsal view of head, probably female. **f**, hypostoma and postgenal cleft. **g**, anal sclerite and circlet of hooks.

Makira (San Cristobal)

The island of Makira was not previously known to possess simuliids. The new material (Fig. 10), two penultimate larvae only, is of *Morops* and apparently closely related to *S.* (*M.*) *selwynense* or *S.* (*M.*) *pohaense*, again, both of Guadalcanal. We note that the rectal scales of the larvae are better developed when compared to other *Morops* material, and the head-spot pattern more subdued. These differences may indicate a new species; however, more material will be needed to confirm the taxonomic status of this simuliid. The subdued head-spot pattern of the larvae suggests that this material is related to *S.* (*M.*) *selwynense*. This record of *Morops* from Makira represents the most easterly extent for the subgenus.

The simuliid habitat on Makira was the high-gradient Puepue River (Fig. 11g) and tributaries, located 3 km south of Kirakira village. The river flowed through pristine uncut forest and was heavily shaded. There were large limestone boulders and side tributaries with a series of 40-m high cascades. Water temperature of the main stream area was 26ºC. The two larvae were collected from a rock and a leaf in a riffle and cascade, respectively.

General comments

The new material is a major increase in the known distribution of simuliids across the Solomon Islands. Given that a distinctive new species, *S.* (*G.*) *rhopaloides*, is described from Guadalcanal, an island that has previously been moderately well collected (Takaoka & Suzuki 1995), perhaps indicates other unknown simuliids on the Solomon Islands, besides those suggested above. As well, there might be seasonal differences to consider. Previous material (Takaoka & Suzuki 1995) was, in large part, taken in August and September. The new material was taken in March from the New Georgia Islands and Makira, and July from the other islands (Table 2).

Ecological considerations

From the literature (e.g., Takaoka 1995), habitat preference for larvae of the *sherwoodi* species group of *Gomphostilbia* (*S. kerei*, *S. noroense*, *S. sherwoodi*) is almost without exception small, fast-flowing, forested streams, in full agreement with habitats of the new material considered here (Table 1, 2; Fig. 11a, b, c, e). *Simulium* (*G.*) *sherwoodi* has been collected also from rivers. The new species, *S. rhopaloides*, described above and assigned to this group, also comes from a small, fast-flowing, rocky stream (Fig 11e). *Simulium* (*G.*) *hiroshii* (*hiroshii* species group), like *S. noroense* above, found on both Bougainville and the Solomon Islands, is known only from small streams. For the *Morops* species of the *clathrinum* species group, (*S. kawagishii, S. pohaense, S. selwynense, S. solomonense*), the preferred larval habitat tends towards rivers, in agreement with that of the new material.

Simulium solomonense is known only from streams and occasionally so is *S. selwynense*. *Simulium* (*M.*) *papuense* (*papuense* species group) (PNG and the Solomon Islands) is known only from streams.

FIGURE 11. Localities of new Simuliidae material from the Solomon Islands. **a**, Stream near Ringgi, Kolumbangara, New Georgia Islands. **b**, Upper Sakumbare River, New Georgia, New Georgia Islands. **c**, Upper Toropi River, Rendova, New Georgia Islands (J. Polhemus in background). **d**, Garana River (3 km inland), Santa Isabel. **e**, Charovuga River, Guadalcanal. **f**, Aluta River, cascade, Malaita (R. Englund in background). **g**, Puepue River, Makira.

We note that rivers can be among the most recent habitats on an island. Erosion necessary to form the catchment area to produce larger discharges of water takes time (Craig *et al.* 2001, Craig 2003).

None of the known species of *Gomphostilbia* or *Morops* in the Solomon Islands appears to be modified for specialized habitats such as seen in the cascade-dwelling Polynesian simuliids (*Inseliellum*) or in the deep, fast-flowing river species of Tahiti. Instead, in the Solomon Islands, all larvae have a rather generalized body shape, not unlike that of the basal lineages known for *Inseliellum*, and in particular for *S.* (*I.*) *malardei*, the apparent original simuliid colonist of the Society Islands (Craig *et al.* 2001).

Larvae of *S.* (*M.*) *pohaense* from the cascades of the Aluta River, Malaita (Fig 11f), show no modifications for such an extreme habitat. Such lack of modification could be interpreted as indicating recent arrival in the Solomon Islands. For the Polynesian simuliids, Craig *et al.* (2001) and Craig (2003) postulated that species colonizing the islands would possess generalized morphology and ecological requirements allowing their larvae to make use of any available running water habitat. Specialization by *Inseliellum* in cascade habitats took place rapidly in Tahiti, less than 1.8 Mya. On balance, we consider that the generalized nature of the larval bodies and ecological requirements indicate that simuliids colonized the Solomon Islands relatively recently, with *Morops* being more derived because their larvae tend to inhabit rivers.

Paleogeological considerations

The paleogeological history of the Solomon Islands and that of Vanuatu and Fiji is of a complexity second to none on earth (Dickinson 2001). For reasons given below, there is much interest in this region of the Pacific and consequently the literature is considerable, with many different models proposed for formation of the Solomon region. The brief synopsis below is based mainly on Coulson (1985), Petterson *et al.* (1999), and Hall (2002) and provides a simplistic framework for a following preliminary biogeographic consideration of the simuliids of the region.

The Solomon Island archipelago is a double island arc system formed as the result of interaction of the Pacific Plate moving northwestward at 10.7 cm/yr and the Australian Plate moving northeastward at 7 cm/yr and, in particular, the collision of the Ontong Java Plateau (OJP) with the arc. In the Mid Eocene (ca. 40 Mya), the Pacific Plate was subducting beneath the Australian Plate, along what is termed the Vitiaz Trench, producing a typical volcanic island arc. This Stage 1 volcanism began to cease by the early Mid Miocene (ca. 20 Mya), perhaps as a result of the approaching OJP. There is then evidence of erosion, subsidence, and sedimentation into adjacent basins. With the arrival of the OJP and its coupling with the then Solomon Islands a bit later in the Miocene (ca. 18 Mya), the original subduction largely ceased. There was then reversal of subduction about the early Late Miocene (ca. 12 Mya), with the Australian Plate beginning to plunge under the Pacific Plate. This event produced what is termed Stage 2 volcanism that produced a second island arc resulting in the double island arc seen today. For more general details, see Polhemus (1996) and Hall (2002). The animated reconstructions associated with Hall's work are recommended viewing. Formation was, however, complex, and so the Solomon Islands have been considered previously as three geological provinces, each with its own distinct paleogeology (e.g., Coulson 1985).

Currently, however, with more data available, particularly from the Deep Sea Drilling Program, the original three provinces are now subdivided into five terrains, including some with islands that involve terranes from the OJP. Again, each of the five terrains has a complex history. Three of them have Cretaceous origins. The two others are more recent and date from only a few million years ago. Of particular interest to geologists are the portions of OJP that have obducted (uplifted/overridden) onto the Solomon Islands and which are now exposed. Recent interest in the origins of the Solomon Islands is, in the main, focussed on the OJP.

The South Solomon Terrain (Guadalcanal, Choiseul) has Cretaceous (ca. 92 Mya) underpinnings, but also shows Stage 1 volcanism (24 Mya). There is then evidence of subsidence and considerable sedimentation. Renewal of volcanic activity commenced at the Late Miocene/Pliocene (6.4 & 3-1 Mya) with the Stage 2 arc volcanism. Again, there is evidence for sedimentation. For Guadalcanal, Quaternary and Recent alluvial sediments were probably from material eroded off the volcanic northern part of the island associated with a marked uplift (> 2 km) of the south, commencing in the Pliocene (1.8 Mya). By the end of the Pleistocene (0.0115 Mya), Guadalcanal was essentially in its modern form. In general, there has probably been subaerial land in this position since the Miocene (ca. 6 Mya). Choiseul has thousands of meters of sediment over its basement rocks, but was probably emergent in early Mid Miocene or later Mid Miocene (ca. 20–12 Mya), as evidenced by fossil coral/algal reefs that fringed higher adjacent land; so the island is probably of similar age or a bit older than Guadalcanal with regard to subaerial existence.

The Ontong Java Plateau Terrain (Malaita, North Santa Isabel, Ulawa) is of much interest to geologists and planetary scientists. The underpinning of this terrain is the OJP itself, formed far to the west in the Pacific. This Alaska-sized plateau is the largest such oceanic structure. Formed mainly during the Cretaceous, it has anomalously thick pelagic sediments, plus basalt, acquired during the Paleocene/Miocene. With approach of the OJP to the Solomon Islands from the Late Miocene to Recent, southern portions of the plateau have been obducted onto the archipelago. Malaita has Cretaceous base rock of 125–120 Mya overlain by deep sedimentary sequences that can clearly be equated to sequences in drill cores taken from the OJP proper. Unlike islands elsewhere in the Solomon Islands, Malaita has undergone little geochemical evolution. Uplifted and subaerial for some 4–2 Mya, it is heavily eroded.

The majority of Santa Isabel is also of OJP origin and similar to Malaita. Neither of these islands shows any indication of Solomon Island Arc volcanic activity. The island of Ulawa is not of concern here.

The Makira Terrain consists solely of the island of Makira. This is a special case within the Solomon block, for while it shows OJP material dating back to 90 Mya, there is little or no pelagic sedimentation, as would be expected, suggesting deep erosion of a subaerial edifice. There is abundant evidence for what appears to be Stage 2 arc activity, but there are no volcanic structures preserved. The island has probably been subaerial since the late Pliocene (ca. 3 Mya).

The Central Solomon Terrain (Florida Islands, south Santa Isabel, Shortland Islands) is more recent and the underpinnings of the constituent islands date in large part from the Stage 1 arc magmatism. There are no dates for the Shortland Islands, but ages of 44 and 35 Mya are known for the Florida Islands. In general, the genesis stage was Eocene-Early Miocene (ca. 40–20 Mya), but the southern part of Santa Isabel has Paleocene-age (60–55 Mya) material. It has been suggested (Coulson 1985) that the Florida Islands were emergent in the Late Oligocene and Early Miocene (ca. 23–20 Mya), but then there was widespread sedimentation indicative of subsidence. So, although of ancient mien, the Florida Islands probably became subaerial again with the general uplift of the Solomon Islands from the Late Pliocene to Recent.

The New Georgia Terrain consists of the New Georgia Islands, Russell Islands, Kavachi and Savo. All are volcanic, formed by Stage 2 arc activity. Exact dates are few, ranging from 4.5–1.4 Mya. These are the islands that define when Stage 2 volcanism of the Solomon Arc commenced with the reversal of subduction of the two tectonic plates. While it has been suggested that that took place 12 Mya, there is no evidence apparently that volcanism commenced earlier than the Late Miocene (ca. 8 Mya).

The volume of the New Georgia Islands volcanics is enormous and so subaerial land of some kind could be suggested as being from the very Late Miocene (ca. 7 Mya) to Recent.

While the ages of some Solomon Islands are considerable, probably of more importance biogeographically is the major uplift that accompanied the Stage 2 arc activity that has continued since the Late Pliocene. For example, in the New Georgia Islands, foraminifera indicate that there has been 2–3 km of uplift since the Pliocene (1.8 Mya). Similarly, for Guadalcanal there are Pleistocene (>1.6 Mya) coral limestones some 200 m above sea level and similar aged marine deposits of 800 m altitude. So, the simuliid fauna of the Solomon Islands is probably not older than a maximum of a few million years. Also of possible biogeographic importance were ice ages over the last 500,000 yrs, when sea level depression reached 150 m below present (Rohling *et al.* 1998). The 200-m bathymetric contour (Fig. 1) suggests that that Bougainville, Choiseul, Santa Isabel, and the Florida Islands were probably connected. Only a narrow channel separated them from Guadalcanal. Irrespective of the exact connections, an expectation would be for these islands to have a similar simuliid fauna. The New Georgia Islands were similarly connected and their simuliid fauna should be closely related.

The volcanically recent Santa Cruz islands to the east, while politically of the Solomon Islands, are not strictly part of the Solomon terrains; rather, they are the northernmost extent of the New Hebrides Arc and are geologically related to Vanuatu islands. Of particular interest is whether Santa Cruz Islands possess simuliids. Although Nendo is a small island (Table 1), its topography (Google Earth®) indicates that there might be sufficient running water to sustain a population of simuliids. The main question is whether such simuliids are of *Hebridosimulium*, widespread in Vanuatu and known from the northerly Banks Islands (Cheesman 1933), albeit not Torres Islands, or are of *Gomphostilbia* and *Morops*, both of which populate the other Solomon Islands.

Biogeographical considerations

Within *Gomphostilbia*, the *hiroshii* species group (*S. hiroshii*) on Bougainville (PNG), New Georgia, Malaita, and Guadalcanal (Solomon Islands), is the most widespread *Gomphostilbia* in the region of concern. With the probable connection between these islands during ice ages (Fig. 1), we expect *S. hiroshii* to occur on Choiseul and Santa Isabel, as well as on other islands of the New Georgia Islands.

Simulium (*G.*) *noroense* previously known on Bougainville and New Georgia is now known from Kolumbangara. As suggested for *S. hiroshii*, it is possible that *S. noroense* also occurs on Choiseul and Santa Isabel. *Simulium* (*G.*) *kerei* is so far known only from New Georgia. Both *S. noroense* and *S. kerei* are of the *sherwoodi* species group (Takaoka 2003), and elsewhere the group is found on Guadalcanal as *S.* (*G.*) *sherwoodi* and *S.* (*G.*) *rhopaloides.*

With the exception of *S.* (*M.*) *papuense*, (*papuense* species group), known from Seram, Irian Jaya, PNG, and Guadalcanal, all other *Morops* belong to the *clathrinum* species group, which is widespread westward to Halmahera and south into Australia. In the New Georgia Islands, *S.* (*M.*) *solomonense* is known only from New Georgia with a possible new species, *S.* (*M.*) nr. *selwynense*, from Rendova. *Simulium* (*M.*) *selwynense*, or entities closely related, is also known from Santa Isabel, Guadalcanal, and Makira. Therefore, as presently recognized, it is the most widely distributed *Morops* in the eastern Solomon Islands. Two other species, *S.* (*M.*) *kawagishii* and *S.* (*M.*) *pohaense*, are known only from Guadalcanal.

Why Guadalcanal has the most species (Table 1) is moot. As the largest and highest of the Solomon Islands, Guadalcanal might be expected to have the most species because of the availability of habitats vis-à-vis area (Craig 2003); however, it is also the most intensively collected, with access to higher regions. We expect that with more detailed collecting on other large islands, numbers of species will increase. Low species number on small islands is to be expected on biogeographic principles (Craig 2003, Spironello & Brooks 2003, Adler *et al.* 2005). Both Ranongga and Tetepare, while visited, were not sampled for simuliids, but are expected to have them because there are streams. Further, these islands are respectively 147 and 118 km^2 in area and 727 and 869 m in altitude, and considerably larger than Bora Bora (30 km^2, 727m alt), the smallest island in the Society islands to posses a species of black fly (*S.* (*Inseliellum*) *malardei*), or the markedly small Mohotana (12.2 km^2, alt 520) in the Marquesas, where there is, again, a single species, *S.* (*I.*) *englundi*. Tetepare is a nature preserve that has never been logged, and, as one of the largest uninhabited islands in the Pacific, should contain pristine aquatic habitats.

The original diagnoses of *Gomphostilbia* and *Morops* were given by Crosskey (1967), but the two subgenera are difficult to separate and are generally considered closely related. Takaoka (2003) redefined the two taxa as noted earlier, and transferred certain *Morops* species into *Gomphostilbia*.

Gomphostilbia is widespread in Southeast Asia and further west and north. Highly speciose, at present it consists of nine species groups. The distributions of these species groups tend to overlap in the Philippines, so the subgenus appears to have originated, or radiated, in the western Pacific. Takaoka (1995) suggested that because of close similarities of the constituent species and their distributions (Bougainville and the Solomon Islands), the *sherwoodi* species group of *Gomphostilbia* was precinctive in origin. He further suggested that pupal gill-filament characteristics indicate that *S. noroense* and *S. sherwoodi* are relatively basal species, with the others more derived. *Morops,* also speciose and with six species groups, has a more restricted Australasian distribution (Takaoka 2003). The majority of species center on New Guinea – indicative also of possible precinctive evolutionary radiation and dispersal from New Guinea.

Because *Gomphostilbia* extends into the Palaearctic, the subgenus was considered by Adler *et al.* (2004) in a morphological phylogenetic analysis of simuliid subgenera of the region. *Gomphostilbia* falls into a generally unresolved clade, along with eight other subgenera, including *Nevermannia*, all linked by a synapomorphy involving the adult male parameral spines. *Wallacellum*, another Southeast Asian subgenus that extends north also is in that clade.

There are no phylogenetic analyses at the species level for either *Gomphostilbia* or *Morops*; hence, little can be concluded regarding the historical biogeography of the Solomon Islands Simuliidae. There is, however, little doubt that this fauna is derived from sources farther west because it is the easternmost extent, by far, for both subgenera.

Age of colonization of the Solomon Islands is moot. The above taxonomic, morphological, ecological, and paleogeological information could be interpreted as indicative of relatively recent arrival of a few million years, or less.

Concluding remarks

Because collecting simuliids was not emphasized during these Solomon Islands aquatic biodiversity surveys, further collections from the Solomon Islands will be necessary to consolidate knowledge of the regional simuliid fauna. Conservation of all freshwater taxa in the Solomon Islands is a challenge for the future. Logging and conversion of native forest to large-scale palm plantations, plus invasive species, are some of the primary threats to native aquatic species. Many of the streams sampled had evidence of heavy sediment inputs as a result of logging. Filter-feeding simuliid larvae are particularly vulnerable to this type of disruption.

Additional new species probably will be discovered; and other islands, in particular Choiseul, are expected to have a simuliid fauna. With a plethora of different-sized islands of various distances apart and all within a similar climatic region, knowledge of the simuliid fauna, which must have only a western source area, will be useful for testing biogeographic principles. In particular, why are Simuliidae, which are worldwide and highly vagile (Crosskey 1990), locally gene-flow restricted at <100–500 km distance (Craig *et al.* 2001, Craig 2003, Spironello & Brooks 2003, Adler *et al.* 2005)?

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