ZOOTAXA

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A taxonomic revision of the southwestern Pacific subgenus *Hebridosimulium* (Diptera: Simuliidae: *Simulium*)

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Abstract

Sixteen species, of which 13 are new, in the subgenus *Hebridosimulium* Grenier & Rageau are now known. Fiji has only *Simulium laciniatum*, which is widely distributed on five islands. Tahiti has only one species, the enigmatic *S. anatolicum*. The remaining species are in Vanuatu and known from nine islands, ranging the full length and breadth of the archipelago. *Hebridosimulium* species are divided among two species groups. The *callipygium* species group is characterized, in part, by a smooth posterior abdomen in the larvae, and all but one species possess dorsal tubercles on the larval abdomen. *Simulium callipygium* is the type species, with the tuberculate species in a subgroup comprised of *S. banksi*, *S. johnfrumi*, *S. pankumuense*, and *S. tuberculum*. The second species group has larvae with the posteroventral abdomen markedly expanded, and all species lack dorsal tubercles. Constituents of the *steatopygium* species group are *S. anatolicum*, *S. jolyi*, *S. laciniatum*, *S. lucyae*, *S. paradisium*, *S. steatopygium*, *S. subparadisium*, *S. supercilium*, and *S. undulatum*. Two other species of this group, *S. adsonense* and *S. spiroi*, of which larvae have markedly pigmented heads, are assigned to the *adsonense* species subgroup. A chromosome map for *Hebridosimulium* is established for the first time.

Key words: Southwestern Pacific, Simuliidae, *Hebridosimulium*, taxonomy, cytology, ecology

Introduction

Even a century ago, when discovered, Simuliidae from Vanuatu were noted as unusual because of the massive calcipala on the hind legs. Some 60 years later (Crosskey 1967), when much more was known about western Pacific simuliids and the calcipala of some of those were known to also be well developed, simuliids from Vanuatu, and now Fiji, were still considered a distinct segregate of the wider fauna. In the most recent inventory of World Simuliidae (Crosskey & Howard 2004), the *Simulium* subgenus *Hebridosimulium* consists of three nominal species distributed in Vanuatu, Fiji and the Society Islands.

Roubaud (1906) described *Simulium jolyi* from alcohol-glycerine material of female adults collected in 1903 by a Dr. Joly, apparently from Port Sandwich, New Hebrides (now Vanuatu). Roubaud remarked on the large size of the calcipala. No types were designated, although one of five pinned females in the Muséum National d'historie Naturelle, Paris, has a red printed "Type" label. That specimen is accepted here as the Holotype.

The locality of the original collection is of interest in that, while Port Sandwich is on Malekula Island, Grenier & Rageau (1961) in describing new material of all stages of what they considered *S. jolyi*, were quite definite that the type locality was actually Port Vila, Efate (Vate) Island, some 125 km SSE of Malekula. This assumption is not unreasonable because Efate was originally called Sandwich Island by Cook (Cheesman 1933). There is, however, no evidence that Grenier and Rageau examined Roubaud's types. One of the five pinned Roubaud specimens (Paris Museum) has a label that indicates the female came from "Ile Mallicolo" (sic). So, since the other four labels have the same date, albeit only indicating New Hebrides as the locality, it is herein assumed that all specimens were from Port Sandwich, located in southeastern Malekula, adjacent to the town of Lamap. Thence, as demonstrated later, most of Grenier and Rageau's material from Efate was not of *S. jolyi*. After consideration of the relationships of Vanuatu material to other simuliid taxa in the western Pacific, Grenier & Rageau (1961) erected a new genus — *Hebridosimulium*.

Simulium laciniatum from Fiji was described by Edwards (1924), but in 1932 he placed it in synonymy with *S. jolyi*, noting that he had overlooked Roubaud's original description. Crosskey (1967) while recognizing the synonymy, questioned its validity since there were, at that time, no known immature stages from Fiji. These were described by Dumbleton (1973) who recognized *S. laciniatum* as a valid species, albeit with adults very similar to those of *S. jolyi.*

Cheesman (1933, 1960) visited many of the islands in Vanuatu and obtained simuliids as part of her general collections. She provided vivid descriptions of being bitten by adult female simuliids while on Aneityum Island (Craig 2006).

Crosskey (1967), in an examination of *Simulium* from the Western Pacific, relegated *Hebridosimulium* (Fig. 1a, b, c) to subgeneric level and provided a diagnosis. Crosskey (1974) expanded on the description of the Fijian black fly, describing for the first time the male (Fig. 1b). In a detailed consideration, he treated *S. laciniatum* as a subspecies of *S. jolyi*. He also considered the possible origin of *Hebridosimulium* and relationships

between the Fijian and Vanuatuan species, concluding that the Fijian simuliid was more recently derived.

Rothfels (pers. comm. 1981), based on his examination of the polytene chromosomes, noted cytological variation in populations from Fiji, though not sufficiently marked to recognize multiple species. The conspecificity of Fijian populations was upheld in the light of subsequently collected material (see below). Rothfels (1989) also noted cytological variation within and between *Hebridosimulium* populations from Vanuatu (Efate and Espiritu Santo).

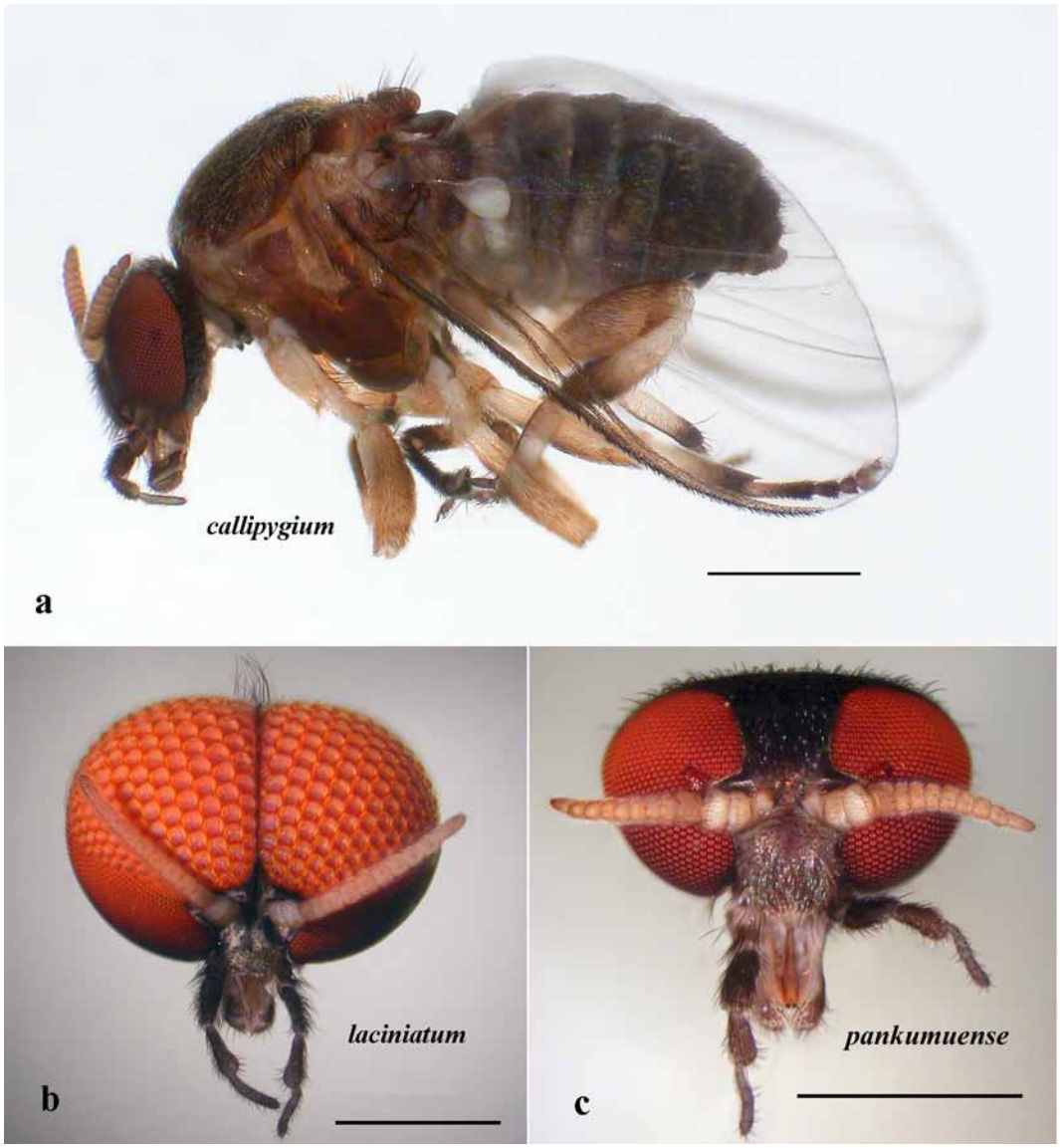

FIGURE 1. Typical examples of *Hebridosimulium*. **a**. Female *Simulium callipygium* (Santo). **b**. Head of male *S. laciniatum* (Fiji). **c**. Head of female *S. pankumuense* (Malekula). Scale bar = 0.5 mm.

Craig (1987) described *S.* (*H.*) *anatolicum* from Tahiti, thereby extending the range of *Hebridosimulium* by some 3,500 km. This species, based on a single reared female, and for which no other material was ever collected (Craig *et al.* 2001), exhibited more similarities to *S. laciniatum* than to *S. jolyi*, as then known. Craig (1987) considered *S. laciniatum* and *S. jolyi* as valid species, as did Crosskey (1987). Rothfels (pers. comm. 1986) commented that *S. anatolicum* might be the cytospecies he had found on Tahiti and termed "forbidden" (*in* Craig 1983, Crosskey & Howard 1997). Apparently "forbidden" and *Hebridosimulium* had similar karyological characteristics.

Preliminary examination of *Hebridosimulium* material for this revision was begun in 2002. The available material, however, varied greatly in quality of preservation and immature stages were sparsely represented. Hence an expedition to Vanuatu and Fiji by the senior author and his wife, Ruth, was undertaken between September and December 2004.

Geographic setting

The nations of Vanuatu and Fiji are, in large part, culturally Melanesian. The Solomon Islands, Vanuatu and Fiji, are all part of the so-called “Ring of Fire” around the Pacific and all have a common paleogeological history (Hall 2002, Craig 2006a).

Vanuatu. This archipelago consists of some 80 islands in a narrow “Y” configuration (Fig. 2). To the north, Hiu Island of the Torres Islands, is within sight of Vanikolo, southernmost of the Santa Cruz Islands of the Solomon Islands. Only 13 Vanuatu islands would be considered major, but there are 9 active volcanoes. The main line of islands runs SSE from the Torres Islands, through the Banks Islands, then Maewo, Ambae, Pentecost, Ambrym, and Epi. On the western arm of the “Y” is Espiritu Santo, the largest island, and then Malekula, the next largest. The junction of the “Y” meets at Efate and continues south to Erromango, Tanna, and Aneityum. Distances between islands are not great.

Fiji. Consisting of some 330 islands in a roughly inverted “U” arrangement (Fig. 3), with 100 inhabited islands, Fiji also includes the Polynesian Rotuma, 650 km NNW of Suva. Viti Levu is by far the largest island followed by Vanua Levu and then the substantially smaller islands of Taveuni, Kadavu, Gau, Koro, and Ovalau. While many of the islands have a volcanic origin, there are no active volcanoes at present. Originally part of the same island arc system as Vanuatu, Fiji has its own later, very complex geological history.

Material and methods

General collecting

During the 2004 expedition to Vanuatu and Fiji, a standard protocol was followed at all collecting sites. The fastest water was located and leaves and trailing roots were

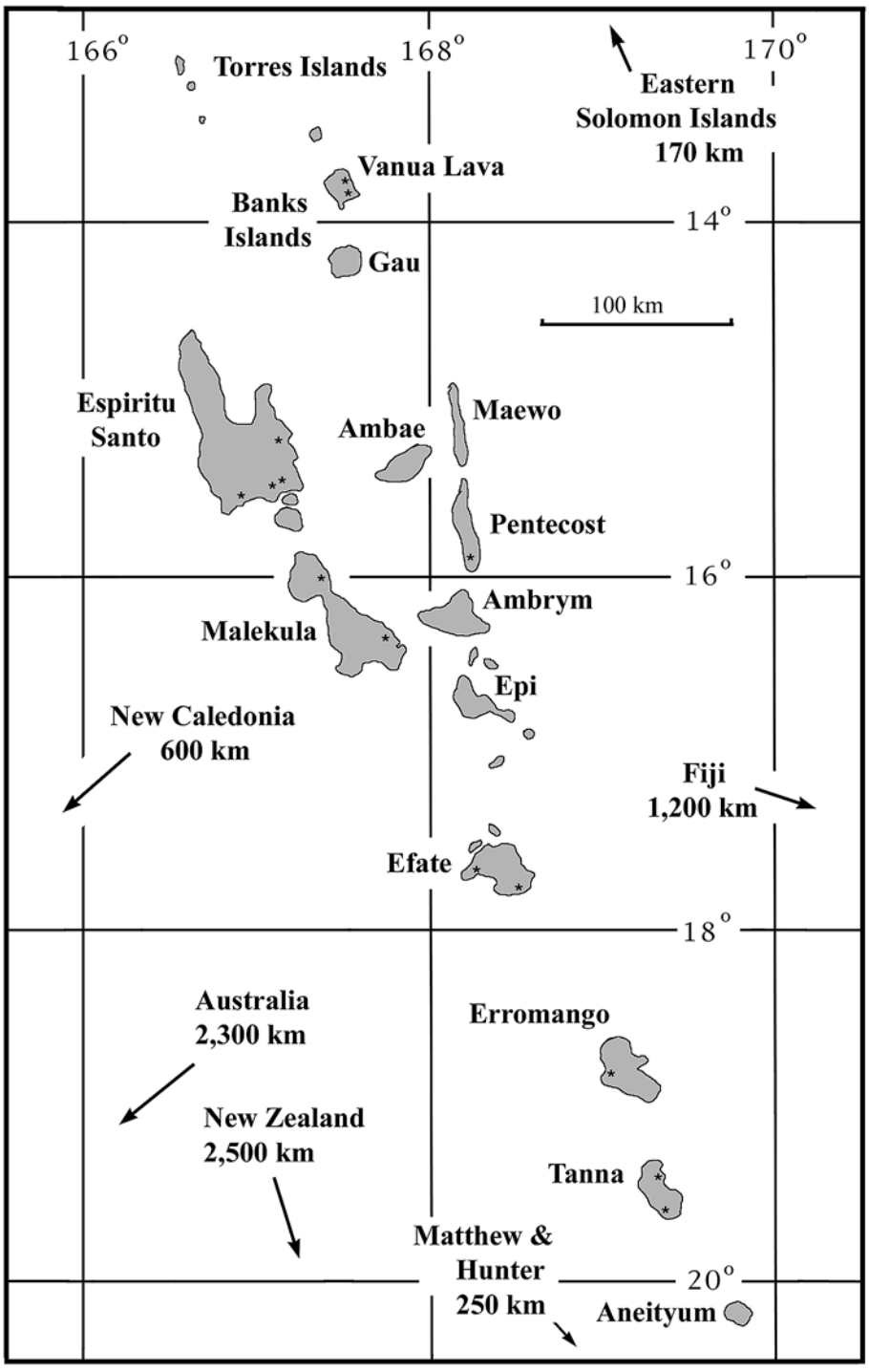

FIGURE 2. Map of Vanuatu (New Hebrides). Approximate distance to other land masses is indicated. Smaller islands omitted. Location of collections in 2004 indicated by asterisks.

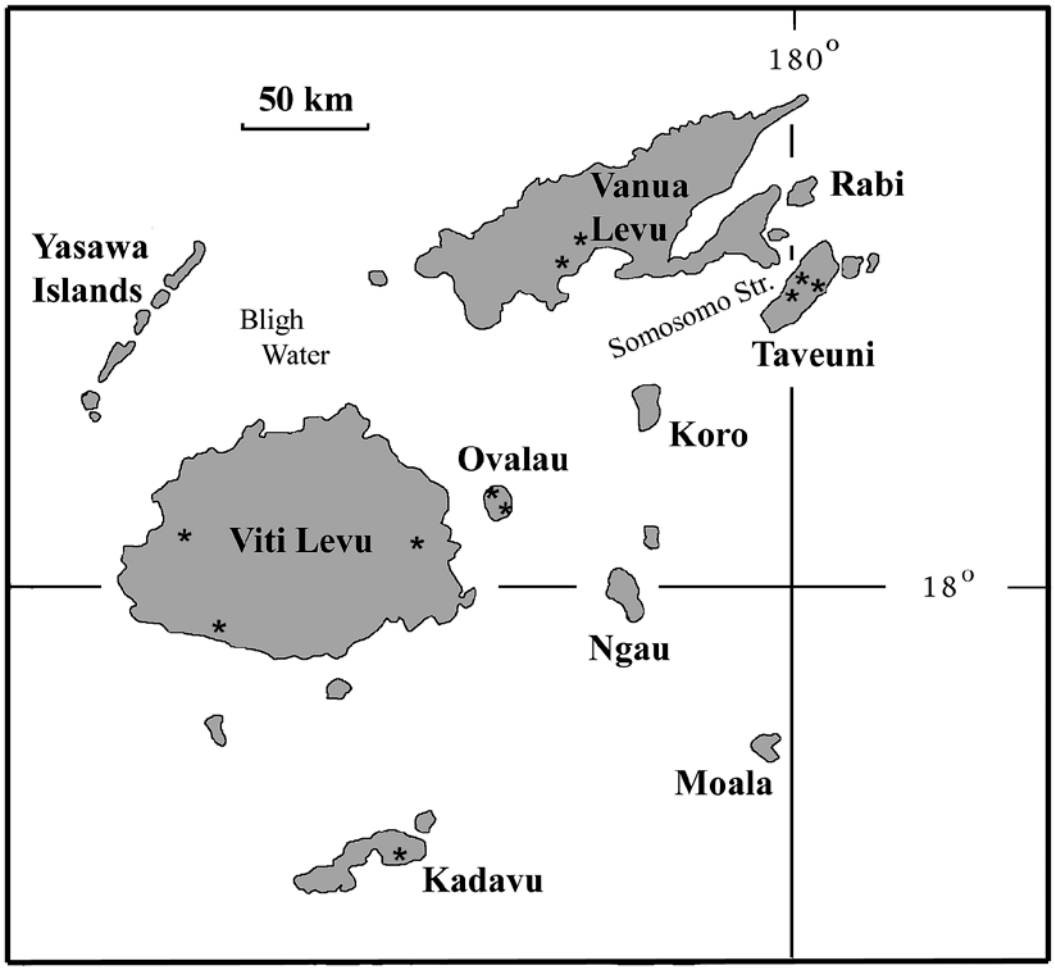

FIGURE 3. Map of Fiji. Smaller islands omitted. Location of collections in 2004 indicated by asterisks.

searched for the presence of simuliid larvae and other aquatic insects, for a minimum of one hour. Further, the rock substrate was wiped with a shaving brush while holding a fine net downstream. Any specimens taken were fixed in 98% ethanol (ETOH) for morphological and molecular analysis and, if enough material was available, some fixed in Carnoy's solution (1:3 of glacial acetic acid to 98% EtOH) for cytological (chromosomal) analysis. Pupae, if present, were taken along with a small portion of underlying substrate and placed in a tube with damp filter paper. On emergence, the adult was allowed to harden for a minimum of two hours prior to fixation. A sweep net was employed to catch flying adults.

Physical parameters recorded (Table 1) were latitude and longitude (Garmin GPS 12XL™), altitude (Thommen™ altimeter), air and water temperature, water conductivity, and pH (Oakton™). Water velocity was determined, general character of the river noted, and photographs of habitats taken (Figs. 23, 24).

TABLE 1. Physical data for collecting localities, Vanuatu and Fiji (2004).

Coll. No.	Date	Island	Location	Fig. No.	Lat/Long	Alt. mabs	Air temp C	Water temp C	Cond. *u*S	pH	Velocity m/s	Habitat*	Simuliid species**	Other insects***
Vanuatu														
1	26-viii-04	Santo	Hydro Stat, Sarakata R	23a	S15.43147° E167.11448°	25	27.5	23.2	250	8.7	1.1	Rock/veg	1, 9	absent
2	27-viii-04	Vanua Lava	Lemourous R	-	S13.88001° E167.55325°	27	26.4	25.2	40	8.4	2.0	Rock/veg	absent	1
3	28-viii-04	Vanua Lava	Tahiti R	23d	S13.84454° E167.52212°	12	28.0	24.5	90	8.3	1.3	Vegetation	1,2,12	absent
4	29-viii-04	Vanua Lava	Nebeseu Str	-	S13.78245° E167.53139°	10	25.3	24.4	100	8.4	0.8	Vegetation	1	absent
5	1-ix-04	Malekula	Orap R	-	S15.98103° E167.32759°	18	29.6	24.7	540	8.3	1.2	Vegetation	4	1, 4
6	2-ix-04	Malekula	Pankumu R	23f	S16.27628° E167.63687°	15	25.0	24.1	320	8.3	1.1	Vegetation	4,6	1
7	2-ix-04	Malekula	Wesso R, cascade	32c	S16.37551° E167.76503°	34	29.7	25.0	300	8.8	1.3	Rock	14	1
8	6-ix-04	Epi	Rovo Bay, spring	-	S16.63378° E168.17086°	225	-	-	-	-	-	Rock	absent	2
9	8-ix-04	Ambrym	No name	-	S16.35022° E168.09779°	25	28.7	25.1	80	8.6	0.7	Rock	absent	1, 5
10	13-ix-04	Santo	Little Cave Str	23b	S15.45547° E167.07158°	192	25.4	22.2	120	8.4	1.7	Veg/rock	1,10	1, 5
11	13-ix-04	Santo	Millennium Cave Str	24e	S15.43839° E167.07425°	126	30.7	24.4	120	9	0.8	Vegetation	1	absent
12	13-ix-04	Santo	Sarakata R., trib, cascade	24b	S15.43224° E167.07600°	217	28.6	23.6	310	8.5	1.0	Rock/veg	8	absent
13	15-ix-04	Santo	Adsone R	24a	S15.55968°	59	32.0	25.6	240	8.9	1.9	Rock	13,1?	1, 5

					E166.96876°									
14	15-ix-04	Santo	Nasouri (Neavu) R	-	S15.58157° E167.02709°	43	30.0	27.0	470	8.1	1.3	Vegetation	1	absent
15	17-ix-04	Santo	Rotal R., Forestry Stat.	-	S15.26410° E167.09851°	100	25.0	23.9	340	8.4	1.0	Vegetation	1	1, 2, 3, 5
16	22-ix-04	Pentecost	Worbat R, Solap	24d	S15.95677° E168.19893°	25	24.1	24.0	270	8.1	1.4	Vegetation	11	1
16a	23-ix-04	Pentecost	Lonpoa R	-	S15.93821° E168.19579°	23	27.0	24.4	270	8.5	1.5	Rock/veg	absent	absent
17	26-ix-04	Erromango	Williams R. Main.	-	S18.81624° E169.03047°	25	28.3	24.2	200	9	1.5	Vegetation	3	1, 4, 5
18	27-ix-04	Erromango	Williams R. Right branch	-	S18.82551° E169.04526°	47	26.0	21.4	140	9.2	1.0	Vegetation	3	1, 3, 4, 5
19	29-ix-04	Tanna	Louniel Village cascade	-	S19.43082° E169.33971°	53	23.9	19.3	220	9.4	1.5	Vegetation	3	1, 5
20	1-x-04	Tanna	7km south of Bethel	23e	S19.58142° E169.31825°	24	28.0	22.3	180	8.4	0.9	Vegetation	3	1, 5
21	5-x-04	Efate	Ewor R., La Cressionnière	23g	S17.71728° E168.56946°	24	29.0	26.0	390	10.2	1.3	Rock/veg	5,10	1, 5
22	6-x-04	Efate	Mele Cascade	24c	S17.67778° E168.25473°	65	27.0	23.1	360	9.9	1.3	Rock/veg	5,10	1, 5
Fiji														
1	17-xi-04	Taveuni	Waitavala Waterslides	-	S16.79613° W179.99058°	45	29.1	25.9	40	9.9	1.7	Veg/rock	7	1, 2, 3, 5
2	18-xi-04	Taveuni	Wainibau River	-	S16.86596° W179.90589°	30	29.1	24.1	30	8.9	ca 1.5	Vegetation	7	absent
3	18-xi-04	Taveuni	Lavena Track cascade	-	S16.87089° W179.89072°	12	-	-	-	-	-	Vegetation	7	absent
4	19-xi-04	Taveuni	Waitavala Waterslides	-	S16.79720° W179.99064°	60	28.8	23.5	50	8.4	ca 1.0	Vegetation	7	1, 2, 3, 5

5	20-xi-04	Taveuni	Upper Wairiki River	24g	S16.81939° W179.99456°	350	26.7	22.7	50	8.9	1.7	Rock/veg	7	1
6	23-xi-04	Vanu Levu	Cross Island road	-	S16.62289° E179.16664°	280	29.7	23.4	90	8.9	1.1	Rock/veg	absent	1, 2, 3, 5
7	23-xi-04	Vanu Levu	Ravini Stream Cascade	25i	S16.65305° E179.22107°	120	30.1	23.2	90	8.9	1.3	Rock/veg	7	1
8	25xi-04	Vanu Levu	Nakasa River	-	S16.67770° E179.19881°	90	26.1	24.1	90	8.9	1.0	Rock/veg	7	1
9	27-xi-04	Kadavu	Wailea Stream Cascade	24h	S19.03674° E178.37830°	10	25.8	23.3	90	8.7	1.5	Rock	7	1
10	28-xi-04	Kadavu	Lambasa Creek	-	S19.04535° E178.35305°	80	26.5	22.0	100	8.5	0.8	Vegetation	7	1
11	2-xii-04	Ovalau	Waitovu Stream Cascade	-	S17.66545° E178.82551°	60	25.7	23.8	75	8.3	0.8	Rock	7	1, 2, 3, 5
12	3-xii-04	Ovalau	Rukuruku Stream	-	S17.65023° E178.76643°	76	27.4	23.8	90	8.1	0.7	Rock	7	1
13	4-xii-04	Viti Levu	Vereni Crk Cascade, Abaca	24f	S17.66866° E177.54200°	510	26.3	23.5	50	8.2	1.5	Rock/veg	7	1
14	5-xii-04	Viti Levu	Uru's Waterfall	-	S17.78154° E178.43657°	120	29.2	24.4	110	8.4	1.3	Rock/veg	7	1
15	6-xii-04	Viti Levu	Savunamatelaya Cascade	-	S18.17973° E177.73834°	100	27.7	24.0	110	8.2	1.0	Rock/veg	7	1
16	7-xii-04	Viti Levu	Savuione Falls, Abaca	-	S17.67429° E177.55430°	600	30.5	21.0	50	/	/	Rock	7	1, 2, 3, 5

*Predominant habitat listed first.

**Simuliid species: 1. *S. callipygium*; 2. *S. banksi*; 3. *S. johnfrumi*; 4. *S. pankumuense*; 5. *S. tuberculum*; 6. *S. jolyi*; 7. *S. laciniatum*; 8. *S. paradisium*; 9. *S. steatopygium*; 10. *S. subparadisium*; 11. *S. supercilium*; 12. *S. undulatum*; 13. *S. adsonense*; 14. *S. spiroi*.

***Other aquatic insect larvae: 1 = Chironomidae; 2 = Trichoptera; 3 = Ephemeroptera; 4 = Odonata; 5 = Lepidoptera.

In Vanuatu, certain island names are spelled variously (e.g., Aneytioum, Aneityum, Anatom; and Mallicolo, Malekula, Malakula), in large part dependent on which of the three languages in Vanuatu is used — English, French, or Bislama. The latter is the official language and based, in part, on pidgin English and French. Here we use names from the Government of Vanuatu Tourist office WWW site, e.g., Aneityum, Malekula, and Erromango.

Fijian place names are less variable; however, older maps use phonetic spellings as in 'Ambatha' and pronounced as such, but now written as 'Abaca'. Similarly, the phonetic spelling of 'Nandi' is now 'Nadi.

Morphology

Material available for this study was highly variable in quality. Much of older pinned material was greasy and covered with mosquito scales. For examination, such specimens were humidified and soaked in water with detergent to remove grease. They were then dehydrated and dried in Peldri II (Brown 1990) and re-pinned. This typically restored the original colour and vestiture. For ethanol-fixed material dried in Peldri, however, colours were of slightly muted tone. For examination of genitalia and other structures, the entire adult was cleared in 10% KOH to the point where there was some material still left in the thorax and abdomen. On transfer to distilled water, the body then expanded and, normally, the genitalia would partially evaginate. The abdomen was then removed and any remaining internal material removed by flushing with a fine hypodermic needle and syringe. For males, this was usually necessary to fully extend the genitalia. These were then stained with aqueous Chlorozal Black, which stains membranous cuticle light blue and is not taken up by sclerotized cuticle and is particularly useful for observing the membranous posterior extension of the female hypogynial valves. Such preparations were examined in glycerine. Genitalia were then placed in a microvial in glycerine and attached to the pin of the dried adult.

Some older collections (e.g., 1971, Natural History Museum, London) of larvae and pupae had been dried at some time. To restore such material it was soaked in a dilute sodium triphosphate solution. However, fine details of abdomen shape and head colour were not recoverable. For mounting structures on slides, these and other larvae were prepared as by Craig (1997).

Terms used for structures follow those of Adler *et al.* (2004). Other terms used are as follows: larvae of *Hebridosimulium* may have the anterior palatal bar (Craig 1974) projecting anteromedially from the labral fan base (e.g., Fig. 13e). This structure, termed the 'striated cuticle band' by Davies (1974), was illustrated by Wood *et al*. (1963), but not identified. Terms for head sensilla, when used, follow the chaetotaxy proposed by Craig (2005). Terms for dorsal head spots (= muscle scars) follow those used by Adler *et al.* (2004); others are designated by position (e.g., anterolateral, posteroventral). On the larval mandible, the edge posterior to the serration and basal sensillum is termed the 'blade' (Fig.

20e). Further, the variable gap between the serration and the subapical teeth, usually overlain by the spinous teeth (Craig 1977), is termed the 'spinous teeth gap'. To define, in part, the shape of the larval hypostoma, the ratio of distance between tips of the lateral hypostomal teeth to that of the width between the posteriormost sublateral setae is given. The Greek term for beautiful rump, "callipygous" is used for a smooth posterior abdomen of a larva (Fig. 12a), with the converse, "steatopygous" used to describe an enlarged posterior (Fig. 12b).

Larvae of *Hebridosimulium* are markedly dimorphic in colour, with males more yellowish and females more grayish (*cf.* Figs. 11i & j). The sex of such colour morphs was confirmed with Feulgen stain (Adler *et al.* 2004). Precursors to gonads are spherical in males and elongate in females. Male larvae tend to be smaller than those of females.

Illustrations

Photographs were taken with a Nikon CoolPix 9500 digital camera. Images were manipulated and plates assembled in Photoshop, as in Craig (1997). In *Hebridosimulium* males, genital parameral spines of all species are essentially identical and borne on a concertina-like cuticular base. The parameres were reflexed anteriorly (i.e., were recoiled) and thus difficult to observe in most specimens. Spines are presented in detail only in Figure 6e.

Taxonomy

Format of taxonomic treatments follows that of Craig (2004), as do labels of types and other material. For recent Fijian material, a label designation (e.g., FBA 010408) refers to Fiji Bioinventory of Arthropods, a Schlinger Foundation project (Evenhuis & Bickle 2005) and the number is unique to that specimen. By agreement, such material is deposited in the Bernice P. Bishop Museum (BPBM). Holotypes are held in trust for the nation of Vanuatu. With the exception of *Simulium spiroi* (see later), new species names are attributed to only the senior author, DAC.

Cytology

The chromosome maps used for this study were recovered from the laboratory of the late Klaus Rothfels, Department of Botany, University of Toronto. Using laboratory notes of Rothfels, now in the possession of DCC and FFH, the chromosome maps were identified as *Simulium* (*H.*) *laciniatum* and *S.* (*H.*) *johnfrumi* (then as *S. jolyi*). The former species was from Waitumbukum Valley, Nandarivatu, Vanu Levu, Fiji, 1980, and the latter from the 2nd Stream, South of Bethel, Tanna, Vanuatu, 1981, and collected according to methods described by Craig (1987) and Craig & Joy (2000). Chromosomes from the larval silk glands were prepared according to the Feulgen technique of Rothfels & Dunbar (1953). Chromosomal terminology, including names of markers, follows that of Rothfels *et al.* (1978). Numbering of the chromosome sections on the map of *S.* (*H.*) *johnfrumi* was completed by dividing the complement into 100 sections, and using the standard map of

Inseliellum (*sensu* Spironello *et al.* 2002) as a guide in determining section limits.

All fixed-inversion differences between *S. johnfrumi* and *S. laciniatum* were resolved. These interspecific inversions were named in the order of their discovery and indicated by brackets on the map for *S. johnfrumi* (Fig. 25).

Deposition of material:

BM Entomology Department, Natural History Museum, Cromwell Road, London, SW7 5BD, England.

BPBM Bernice P. Bishop Museum, 1525 Bernice Street, Honolulu, Hawaii, 96817-2704.

CNCI Canadian National Collection of Insects, Arachnids and Nematodes, Plant Protection Program, Eastern Cereal and Oilseed Research Centre, Agriculture Canada, Ottawa, Canada K1A 0C6.

DAC D. A. Craig, Department of Biological Sciences, University of Alberta, Edmonton, Canada. T6G 2E9. Personal collection.

MNHP Département d'entomologie, Muséum National d'historie Naturelle, 45 Rue de Buffon, 75005, Paris, France.

NZAC New Zealand Arthropod Collection, Landcare Research, 231 MorrinRoad, St. Johns, Auckland, New Zealand.

PI Pasteur Institute, 25–28 Rue du Docteur Roux, 75724 Paris Cedex 15, France.

ROM Department of Natural History, Royal Ontario Museum, 100 Queen's Park, Toronto, Ontario, CANADA M5S 2C6

Key to later instar larvae of *Hebridosimulium*

Larvae of *S. lucyae* and *S. anatolicum* are unknown.

1. Posterior abdomen steatopygous (expanded posterolaterally and posteroventrally) (Figs. 11h, 12b), circlet of hooks directed posteriorly, more than 5,000 hooks (Fig. 22b) 2
- Posterior abdomen callipygous (not markedly expanded) (Figs. 11a, 12a), circlet of hooks directed more ventrally, less than 4,000 hooks (Fig. 22a) 3

2 (1). Head darkly pigmented … (*adsonense* subgroup. Figs. 11m, n; 14e, f) 7
- Head pattern with anterior apotome pale or lightly pigmented (Fig. 13) 8

3 (1). Abdomen with dorsolateral tubercles (*tuberculum* subgroup. Figs. 11b–e) 4
- Abdomen lacking dorsolateral tubercles (Fig. 11a)..... *S. callipygium*

4 (3). Head lightly pigmented overall, posteromedial head spots not marked (Fig. 13b) . .....*S. banksi*
- Head pale anteriorly, pigmented posteriorly, head spots more distinct 5

5 (4). Posteromedial head spots in distinct Eiffel Tower configuration, lateral head spots distinct (Fig. 15a. Tanna), or less so (Erromango) ..... *S. johnfrumi*
- Head spot not as above, posterior apotome pigmented, posterolateral head spots

pale (Figs. 13, g, h) 6
6 (5). Abdomen markedly pigmented and banded. Malekula (Fig. 11d) . *S. pankumuense*
- Abdomen paler. Efate (Fig. 11e) ..... *S. tuberculum*
7 (2). Ecdysial lines markedly pale and straight, posterior inflexion sharper (Santo) (Fig. 14e) ..... *S. adsonense*
- Ecdysial lines markedly pale but curved, posterior inflexion more rounded (Malekula) (Fig. 14f) ..... *S. spiroi*
8 (2). Head pale with well-developed posteromedial head spots in Eiffel Tower configuration 9
- Head pale without distinct head spots, or more evenly, heavily pigmented 12
9 (8). Lacking posterolateral pigmentation on apotome (Fig. 13f) ..... *S. jolyi*
- With posterolateral pigmentation on apotome (Figs. 14a, b) 10
10 (9). Head evenly light brown, posterolateral pigmentation not markedly developed (Fig. 14a) ..... *S. steatopygium*
- Head markedly pale with posterolateral pigmentation distinct (Figs. 14b, d) 11
11 (10). Posteromedial head spots in Eiffel Tower configuration, posterior edge of apotome markedly emarginate (Fig. 14d) ..... *S. undulatum*
- Lacking Eiffel Tower configuration, posterior edge of apotome not emarginate (Fig. 14b) ..... *S. subparadisium*
12 (8). Head evenly pigmented, but anterior apotome pale, muscle scars prominent 13
- Head evenly pale, muscle scars not markedly developed (Fig. 14c). Distinct dark line and spot above lateral stemmata (Fig. 15c) ..... *S. supercilium*.
13 (12). Anterior genae pale (Figs. 13g, 15b; Fiji only) ..... *S. laciniatum*
- Anterior genae heavily pigmented (Fig. 13h) ..... *S. paradisium*

Taxonomic treatment

Subgenus *Hebridosimulium* Grenier & Rageau

Hebridosimulium Grenier & Rageau 1961: 96 (as genus). Type species: *Simulium jolyi* Roubaud 1906 (by original designation)
Simulium (Hebridosimulium): Crosskey, 1967: 27 (new status); Crosskey 1974:156; Craig 1987: 381; Crosskey & Howard 2004: 29

Diagnosis (revised)

Adults: wing with basal section of radius haired; vein R_1 with hairs only, spinules absent. Cibarial pump without armature. Mandible lacking outer teeth. Distal article of maxillary palpus short. Base of wing vein Rs slightly pigmented. Pleural membrane haired (Fig. 4), sparsely so in some species. Katepisternum bare. Fore tarsus slender, fore basitarsus about 6–7 times as long as greatest width. Hind basitarsus parallel sided in both sexes, with markedly expanded calcipala extended almost to second hind tarsomere. Scutum without pattern. Female (e.g., Fig. 1a): thorax not markedly domed; tarsal claw

simple, basal tooth absent. Abdomen with thick pale scales laterally, dark scales medially and on terminal segments. Seventh sternite very weakly developed. Genitalia (Fig. 5): hypogynial valves produced apically as flattened membranous processes; anal lobes with anterior extension; spermatheca pigmented with distinct reticulate pattern, small clear area around junction of sperm duct. Male: upper ommatidia enlarged, but not markedly so (Fig. 1c). Genitalia (Fig. 6): gonostyle long, slender, tapered with single apical tooth, slightly shorter than gonocoxa; gonocoxite not produced beyond base of gonostyle, with well-developed anterior apodeme; ventral plate complex, produced medially as large haired spatulate process with constricted neck, anterior arms subparallel to curved; parameres weakly developed, parameral spines well developed, complex, about 10 on each side, 1 larger slightly recurved and 2 narrower apical spines with 6–8 smaller basal spines on concertinaed cuticle; dorsal plate cone- to V-shaped with vestiture of microtrichia; median sclerite variously T-shaped with convex larger end; aedeagal membrane with triads of microtrichia. Cerci: distinct. Pupa: gill approximately half as long as body, with 8 or 10 elongate filaments on each side, occasionally 9, mostly branched in pairs, diverging basally and converging apically, dorsal filaments often shorter than other filaments (Fig. 7). Dorsal thoracic granules generally present, either large and coarsely scattered, or smaller and densely packed, rarely absent (Fig. 8). Abdomen with normal complement of hooks, lacking spinecombs dorsally on terminal segments, second segment dorsally with row of 4 hairs each side; grapnel hooks absent; terminal spines short, thick, smooth laterally. Cocoon: closely woven, no fenestrae; boot-shaped with conspicuous raised anterior margin, or almost slipper-shaped with short raised anterior margin; opening circular (Fig. 7). Larva: head capsule with head spots variable, cephalic apotome sometimes darkened in midline posteriorly and posterolaterally; cephalic setae and sockets small; cuticle smooth; cervical sclerites separate from postocciput or lightly attached. Antenna: distal article extended completely beyond labral fan stalk, or antenna subequal in length to stalk. Mandible without supernumerary serrations. Mandibular phragma lacking ventral extension. Labral fan with 36–53 fine rays, fan stalk markedly unpigmented, with posterobasal notch more or less strongly developed, anterior palatal bar often projected anteromedially. Hypostoma: 11 teeth, either not prominent, or moderately prominent lateral and median teeth and small distinct sublateral teeth; paralateral teeth very poorly developed; hypostomal serrations poorly developed or absent; 9–12 substantial setae subparallel to lateral margin of hypostoma. Postgenal cleft of medium size, acutely V-shaped; longer than postgenal bridge, occasionally with anterior apical extension. Abdomen: posterodorsal cuticle smooth; with or without dorsolateral tubercles; posterior abdomen either callipygous or steatopygous; posteroventral tubercles poorly developed or absent. Rectal papillae: 3 simple lobes. Rectal scales absent. Anal sclerite: X-shaped; anterodorsal arms substantial and splayed at apices; subequal in length to posterolateral arms that extend 0.3 distance around circlet of hooks; accessory sclerite absent (Fig. 22). Posterior circlet with 154–214 rows of 20–35 hooks; directed either ventrally or posteriorly.

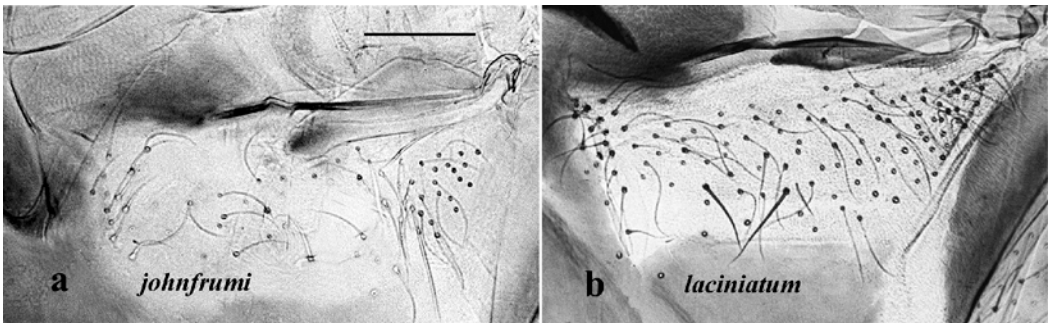

FIGURE 4. *Hebridosimulium.* Female adult right pleural membranes. Dorsal to the left, anterior up. Scale bar = 0.1 mm.

callipygium species group

Diagnosis

Females: stem of genital fork relatively short and thick; medial edges of hypogynial valves concave, occasionally markedly so. Pupae: cocoons more slipper-shaped, basal edges flared laterally. Larvae: hypostomal hairs fewer than 9 per side; abdomen with or without pairs of dorsolateral tubercles; posterior abdomen callipygous; posterior circlet directed more ventrally, with fewer than 4,000 hooks.

Constituents: *S. callipygium, S. banksi, S. johnfrumi, S. pankumuense, S. tuberculum*.

***Simulium* (*Hebridosimulium*) *callipygium* Craig n. sp.**

Figs (1a, 5a, 6a, 7a, 8a, 9a, 11a, 12a, 13a, 16a, 18a, 20a)

Types

Holotype. Larva: mature last instar in alcohol. Label data – "*Simulium* (*Hebridosimulium*) *callipygium*. VANUATU, Santo, Sarakata R, UNELCO Hydrostation, S15.43147° E167.11448°, alt. 25 m, 26.viii.2004. Coll. D. A. & R. Craig. HOLOTYPE No. 16605" (BPBM). **Paratypes.** Adults: two double-pinned reared males, dried from alcohol, with pupal exuviae on point. A third with cleared head, genitalia, thorax, pupal exuviae, and cocoon in glycerine vial. Label data as above. (BPBM). Larvae: mature last and penultimate instars. Label data – as for Holotype, but with "PARATYPE" (DAC, BPBM, LCNZ, ROM). Santo, Nasori/Neavu River, S15.58157° E167.02709°, alt. 43m, 15.ix.2004. Coll. D. A. & R. Craig (DAC).

Diagnosis

Relatively small species. Pupa: cuticle pale brown with sparse fine granules; gill filaments tapered evenly. Larva: anterior cephalic apotome markedly pale, darker

posteriorly; hypostomal teeth distinct; abdomen markedly callipygous, posterodorsal tubercles absent, ventral tubercles directed laterally, posterior circlet directed ventrally.

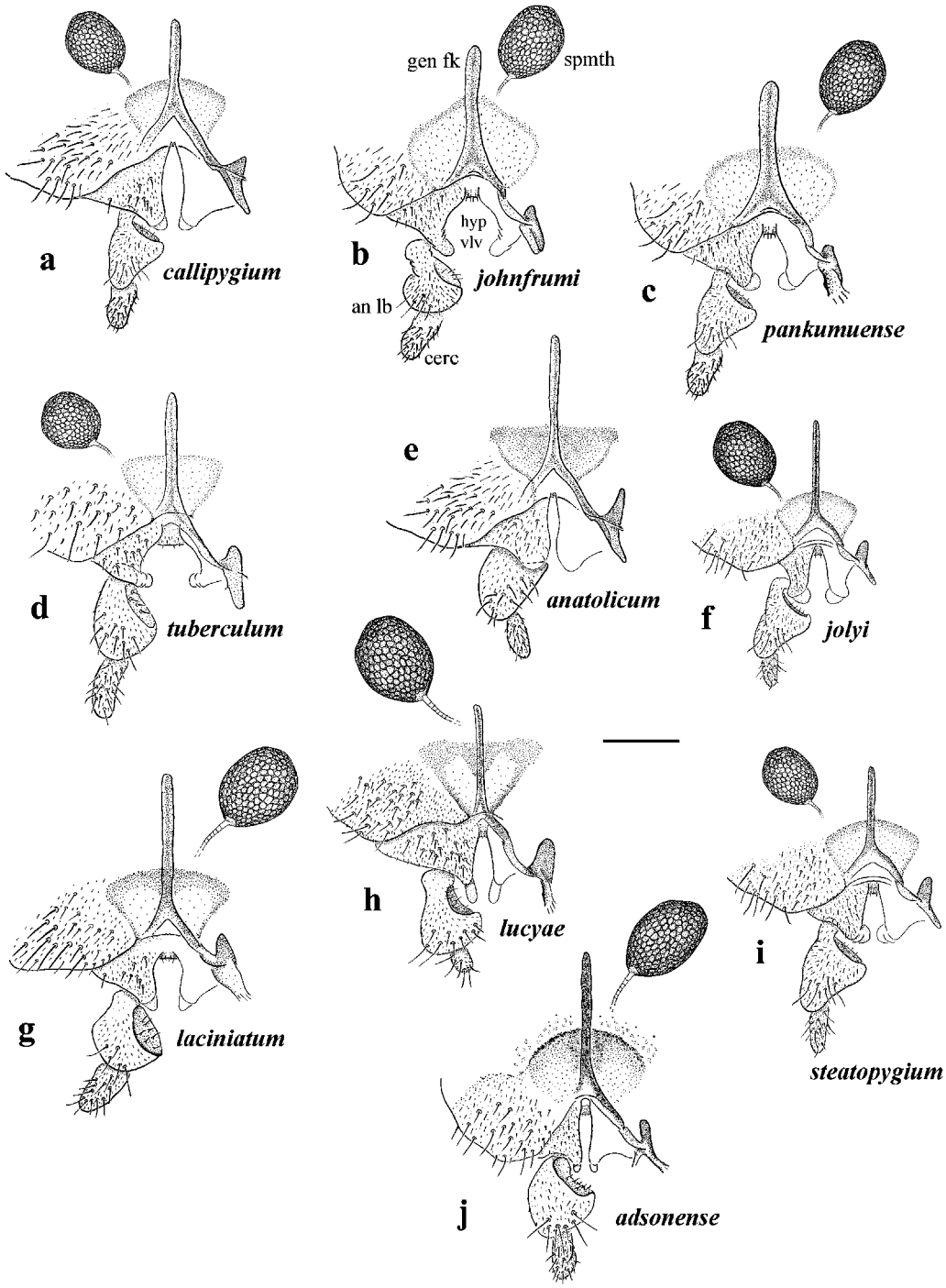

FIGURE 5. *Hebridosimulium.* Female genitalia. **a**–**d** *callipygium* species group, **e**–**j** *steatopygium* species group. **e**. Adapted from Craig (1987). Scale bar = 0.1 mm. Abbreviations: an lb — anal lobe; cerc — cercus; gen fk — genital fork; hyp vlv — hypogynial valve; spmth — spermatheca.

Description

Adult female (based on 2 reared females in alcohol). Body (Fig. 1a): head, thorax, and abdomen concolourous, dark brown; total length 1.9 mm. Head: width 0.65 mm; depth 0.51 mm; postocciput very dark brown, vestiture of distinct black hairs; frons concolourous; frons-head ratio (narrowest width of frons: greatest width of head) 1.0:4.1. Eyes: interocular distance 0.14 mm; ommatidia 0.015 mm in diameter; ca. 30 rows across and 40 down at mid-eye. Clypeus: 0.16 mm wide; concolourous with frons; vestiture of dense black and pale hairs. Antenna: length 0.39 mm; flagellomeres very pale brown; scape, pedicel lighter. Mouthparts: 0.3 length of head depth; mandible well developed with 21 finer adoral teeth decreased in size proximally; lacinia with 10 inner teeth and 14 outer teeth; maxillary palpus markedly short, total length 0.41 mm, uniformly brown, proportional length of 3rd, 4th, and 5th articles 1:1:1.2; sensory vesicle spherical, markedly small, ca. 0.2 times width of 3rd article, opening 0.5 times width of vesicle. Thorax: length 0.97 mm, width 0.7 mm; postpronotal lobes and scutum evenly medium brown, vittae not distinct, vestiture of sparse, very fine pale hairs; scutellum pale, apical angle 120°, vestiture of very sparse substantial black hairs and pale hairs laterally; postnotum concolourous with scutum; pleuron and pleural membrane slightly lighter than scutum. Wing: length 1.8 mm; maximum width 0.9 mm. Legs: fore leg; coxa, trochanter, femur, and most of tibia pale yellow, remainder blackish brown; mid leg, as for fore leg, but femur darker; hind leg as for mid leg except femur darker and tarsus yellow, calcipala and remainder black. Abdomen: overall blackish brown, vestiture of evenly distributed short pale hairs; basal scale brownish black, with fringe of pale hairs. Genitalia (Fig. 5a): sternite VIII deeply indented, broader anteriorly, median region pale; hypogynial valves lightly pigmented with sparse vestiture; medial margins slightly concave, apical membranous extension simple and broad; genital fork substantial with stem short, lateral arms pigmented, anteriorly directed apodeme pointed; anal lobes with anterolateral apodeme and anteromedian concavity markedly developed, rounded posteriorly; cercus broad; spermatheca slightly ovoid.

Adult male (based on 2 reared specimens in alcohol). Body: overall dark brown to black; total length 2.1 mm. Head: width 0.77 mm; depth 0.55 mm. Eyes: division between upper and lower ommatidia distinct; upper ommatidia dark orange, large, 0.057 mm in diameter, ca. 10 across and 15 down; lower ommatidia brown, 0.019 mm in diameter, ca. 21 across and 30 down. Clypeus: dark brown, pruinose, 0.2 times as wide as head; vestiture of medium and short hairs laterally. Antenna: total length 0.38 mm; flagellomeres light yellow, scape, pedicel, and base of first article slightly darker; first flagellomere slightly longer than remainder**.** Mouthparts: short, 0.2 length of head depth; mandibles feebly developed, finely tapered with apical hairs; lacinia broad basally, finely tapered apically with terminal hairs, some tooth-like; maxillary palpus dark, 0.51 mm long, proportional lengths of 3rd, 4th, and 5th articles 1:1.4:1.6, third article hairy, sensory vesicle barrel shaped, occupying 0.33 times width of article, opening 0.33 times width of vesicle. Thorax: length 0.8 mm; width 0.77 mm; broadest anteriorly; postpronotal lobes

pale; scutum evenly blackish brown; vestiture of short pale hairs; scutellum slightly paler than scutum, apical angle distinctly obtuse; vestiture of long black hairs laterally, interspersed with paler hairs; postnotum concolourous with scutum: pleuron concolourous with scutum. Wing: 1.7 mm in length, 0.9 mm at maximum width. Legs**:** markedly bicolourous: tarsal and tibial apices dark brownish black, remainder yellow; pretarsal claws with ca. 17 grappling hooks dorsally. Abdomen: anteriorly pale, remainder brownish black, vestiture of dense fine pale hairs; basal scale black with long, pale yellow hairs. Genitalia (Fig. 6a): gonocoxa narrow, 1.7 times longer than basal width, basal pigmented band narrow, vestiture of markedly substantial hairs, anterolateral apodeme well developed; gonostyle approximately 3 times longer than basal width, subequal in length to gonocoxite, mediobasal strengthening ridge not marked; ventral plate similar to that of *S. laciniatum*, small, sloped laterally, proximal arms distinctly curved medially and finely tapered; median keel flattened apically in ventral view, vestiture of small, evenly spaced hairs; dorsal and median sclerite as for *S. johnfrumi*. Cerci: distinct.

Pupa (based on 10 specimens). Body length: female 2.1–2.9 mm; male 2.2–2.4 mm. Gill (Fig. 9a): dark brown, finally tapered, distinctly annulated; maximum length, 1.6 mm; dorsal gill filaments subequal in length; petioles generally subequal in length, middle petiole occasionally longer, filament branching pattern 2+2+2+2+1+1. Head and anterior thorax with sporadically distributed, sparse, brown granules (Fig. 8a); thoracic trichomes elongate. Cocoon (Fig. 7a): base markedly flared laterally, anterior margin not markedly raised above substrate, both characters variable**.**

Larva (based on numerous mature last-instar larvae). Body (Fig. 11a): relatively small species; total length, female 4.8–5.2 mm, male 3.9–4.6 mm; females grayish, males more yellowish, thorax evenly pigmented, anterior abdominal segments pigmented with intersegmental areas pale, producing marked banded appearance, posterior abdominal segments evenly pigmented. Head (Fig. 13a): anterior frontoclypeal apotome markedly pale; labral fan stalks lightly pigmented; female head spot pattern slightly negative, indistinct in darker individuals, ecdysial lines pale and distinct; width 0.49–0.55 mm, length 0.55–0.58 mm; distance between antennal bases 0.28–0.31 mm; male head overall paler than that of female, with positive head spots in Eiffel Tower configuration, distinct in some specimens, width 0.47–0.52 mm, length 0.51–0.66 mm; distance between antennal bases 0.28–0.30 mm; lateral margins of head evenly convex; ecdysial lines slightly concave, broadly rounded at maximum width; posterior edge of apotome not eroded; cervical sclerites distinct; postocciput not extended medially. Antenna: total length 0.36 mm; distal article 0.35 times as long as basal articles, extended slightly beyond labral fan stalk; distal article and basal portion of medial article brown, distal portion of basal article pale, remainder brown. Labral fan: stalk light brown, anterior palatal bar not markedly protruded anteromedially; 38–43 rays, 0.70 mm in length, 9–11 rays less substantial; microtrichia 0.75 times shorter than ray width, pattern of 6 smaller microtrichia between larger ones. Postgenal cleft (Fig. 16a): V-shaped, 1.6 times deeper than wide with slightly convex edges; posteroventrally elongate muscle spots light brown. Postgenal bridge: 0.25

times as long as cleft depth; genae and postgenae light brown. Hypostoma (Fig. 18a): ratio 4.3; overall shape domed; median tooth prominent, lateral teeth directed laterally, not expanded basally, medial sublateral teeth larger, others smaller; paralateral teeth not apparent; lateral serrations poorly developed; 7–9 hypostomal setae per side. Mandible (Fig. 20a): preapical and apical teeth well developed, subapical teeth less so; 7 spinous teeth in distinct row; spinous teeth gap minor; serration and sensillum broadly based; blade region smooth and straight. Abdomen (Fig. 11a): anterior abdomen narrower than thorax, expanded gradually posteriorly to 5th abdominal segment, then expanded further laterally (Fig. 12a), callipygous posteroventrally; ventral tubercles directed laterally; posterodorsal tubercles absent. Posterior circlet: directed ventrally; 130–135 rows of hooks; 19–23 hooks per row (total ca. 2,700).

Additional material examined

Banks Islands. Vanua Lava, Tahiti River. S13.84454° E167.52212°, alt. 12.5 m, 28.viii.2004. Coll. D. & R. Craig. (larvae. DAC. BPBM). Nebeseu(?) Str., S13.78245° E167.53139°, alt. 5 m. 29.viii.2004. Coll. D. A. & R. Craig. (larva. DAC). **Santo**. Sarakata River, UNELCO Hydrostation. S15.43147° E167.11448°, alt. 25 m, 26.viii.2004. Coll. D. A. & R. Craig. (larvae. DAC). Millennium Cave Stream, S15.45547° E167.07158°, alt. 192 m. 13.ix.2004. Coll. D. & R. Craig (larvae, pupae. DAC). Tafwakar Stream, tributary Sarakata River. S15.43839° E167.07425°, alt. 126m. 13.ix.2004. Coll. D. A. & R. Craig (larvae. DAC). Upper cascade, tributary Sarakata River. S15.43224° E167.07600°, alt. 217 m, 13.ix.2004. Coll. D. A. & R. Craig (larvae. DAC). Nasori/Neavu River, S15.58157° E167.02709°, alt. 43m, 15.ix.2004. Coll. D. A. & R. Craig. Tributary Rotal River, S15.26410° E167.09851°, alt. 165m, 17.ix.2004. Coll. D. A. & R. Craig (larvae. DAC).

Etymology

Named in reference to the elegant shape of the larval posterior abdomen.

Distribution

VANUATU: Vanua Lava (Banks Islands); Santo.

Comments

This species is distributed widely, but in low numbers in streams and rivers (Fig. 23d) in Vanua Lava (Banks Islands) and Santo (Fig 23a). In dorsal view (Fig. 12a), the callipygous posterior abdomen is reminiscent of the amphora shape exhibited by the cascade-dwelling larvae of *Inseliellum* in Tahiti. Craig and Joy (2000) speculated that the condition is an adaptation for reducing drag in fast water. Velocities recorded (0.8–1.3 m/s) for *S. callipygium* larvae are in the typical range for *Hebridosimulium* (see Table 1). Palmer and Craig (2000) suggested a correlation between the number of hooks adorning the posterior circlet and velocity of the habitat, namely that high velocity habitats have larvae with a greater number of hooks. Accordingly, *S. callipygium* larvae, with the lowest number (2700) of hooks for any larva in *Hebridosimulium*, do not support this hypothesis.

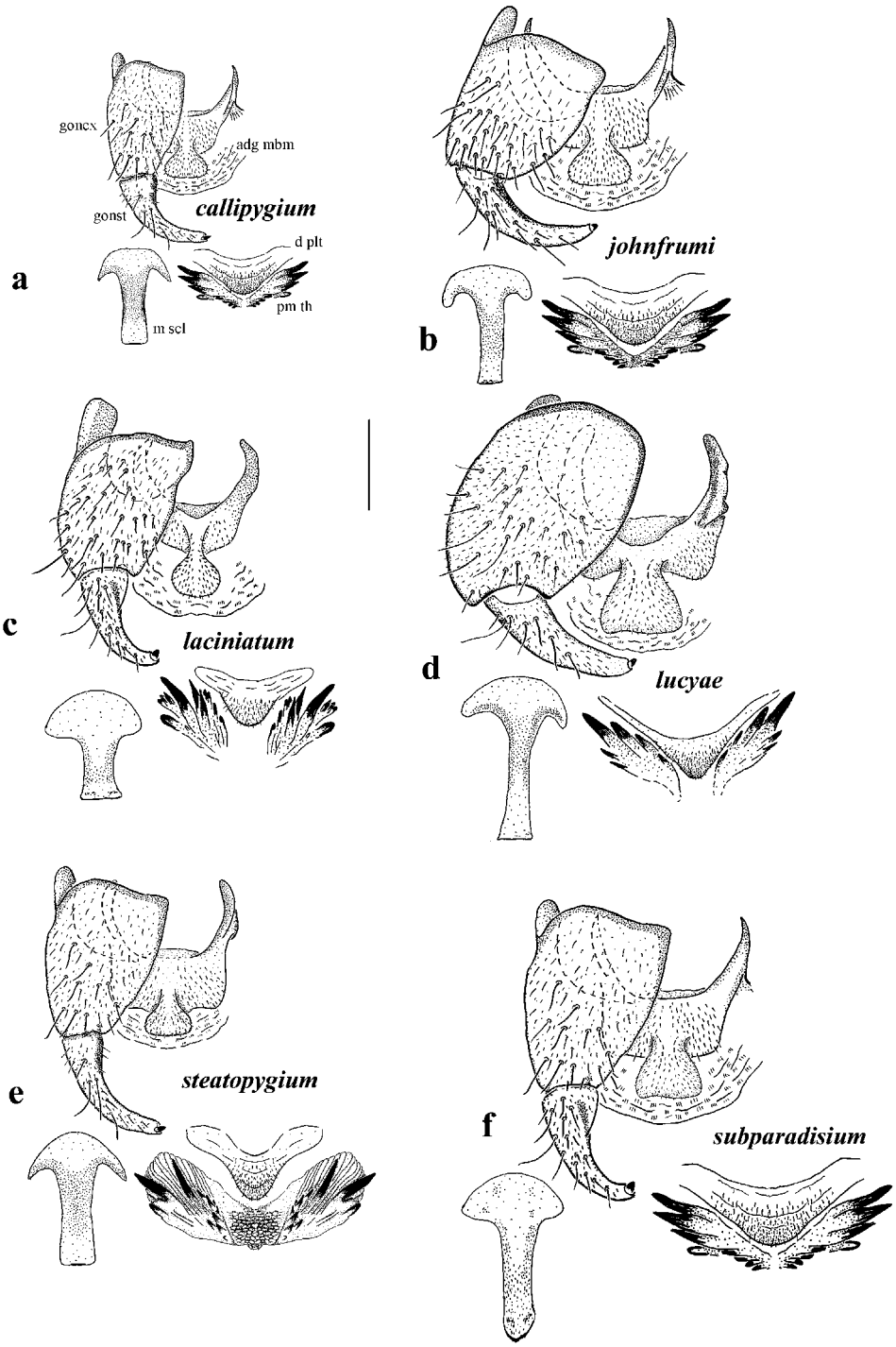

FIGURE 6. *Hebridosimulium.* Male genitalia. **a**–**b** *callipygium* species group, **c**–**f** *steatopygium* species group. **e**. Paramere spines shown in detail. Scale bar = 0.1 mm. Abbreviations: adg mbm — aedeagal membrane; d plt — dorsal plate; goncx — gonocoxite; gonst — gonostyle; m scl — median sclerite; pm th — paramere teeth; v plt — ventral plate.

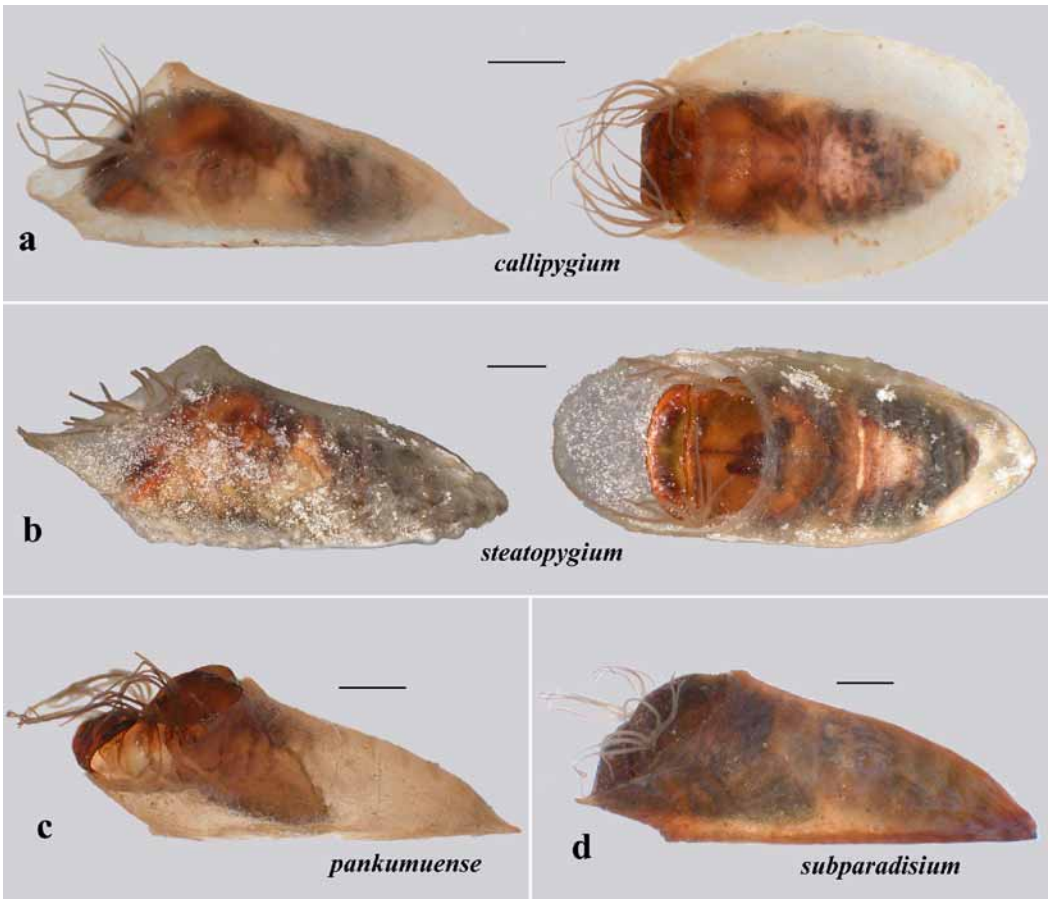

FIGURE 7. *Hebridosimulium.* Pupal cocoons. **a** & **b**. Lateral and dorsal views. **c** & **d.** Lateral view. Scale bar = 0.5 mm.

Simulium callipygium may well be a complex of closely related species. While all larval specimens examined possess, in general, similar morphological characters, there is considerable variation in pupal gill branching pattern and larval head spot pattern.

Larvae from the Banks Islands, while assigned to *S. callipygium*, are problematic in that the material was all prepenultimate larvae. They are, however, markedly callipygous and have the circlet of hooks directed ventrally. Further examination of additional material may show these to be a separate species.

***tuberculum* species subgroup**

Diagnosis

Larva. Three to five pairs of dorsolateral tubercles on abdominal segments II-VI, increasing in size posteriorly.

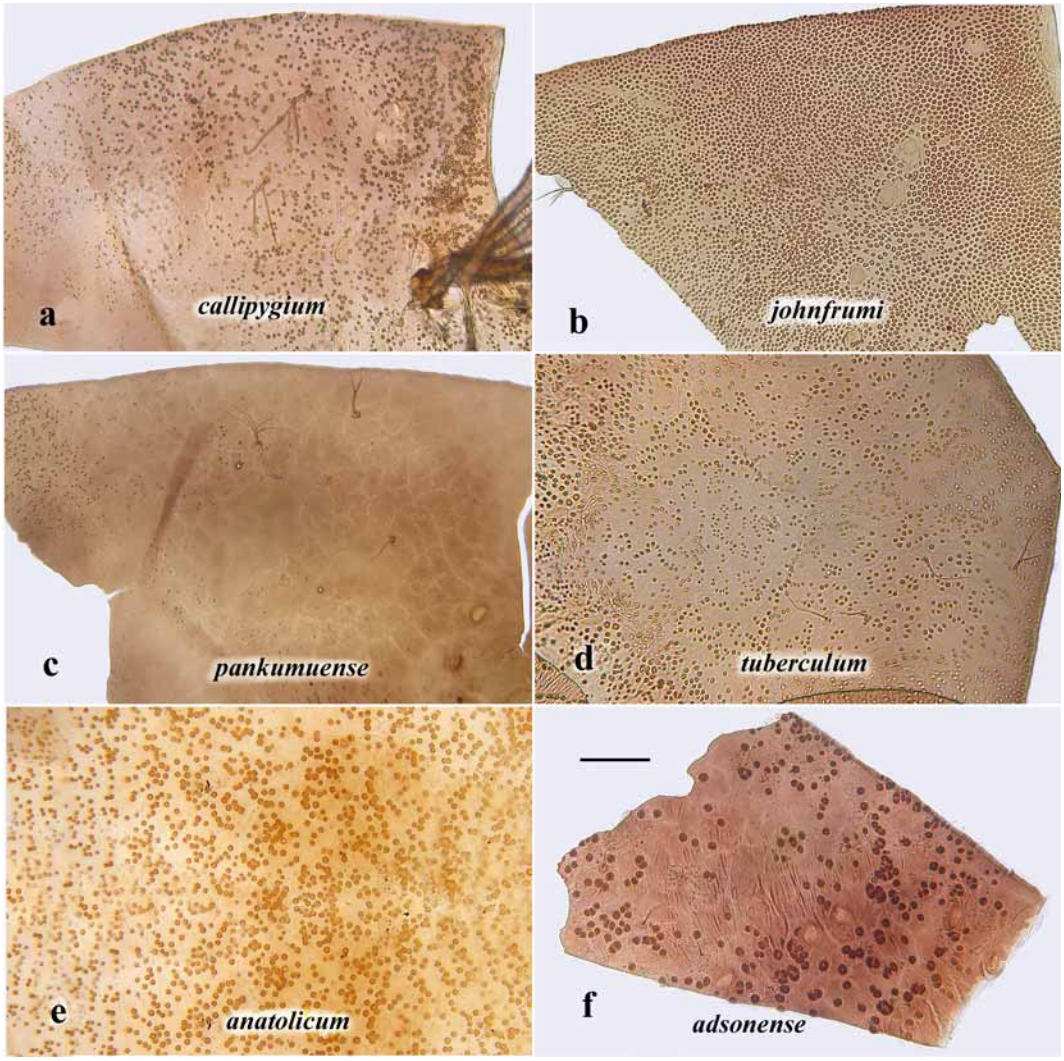

FIGURE 8. *Hebridosimulium.* Pupal thoracic cuticle. Scale bar = 0.1 mm.

***Simulium* (*Hebridosimulium*) *banksi* Craig, n. sp.**
(Figs. 9b, 11b, 13b, 16b, 18b, 20b, 22a,)

Types

Holotype. Larva: last instar larva in alcohol. Label data – "*Simulium* (*Hebridosimulium*) *banksi*, Vanuatu, Banks Islands, Vanua Lava, Tahiti River. S13.84727° E167.52191°, alt. 12.5 m, 28.viii.2004. Coll. D. & R. Craig. HOLOTYPE #16607" (BPBM). **Paratypes.** Larvae: last and penultimate larvae in alcohol. Label data – as for Holotype, but with "PARATYPE" (larvae; BPBM, DAC, ROM).

Diagnosis

Relatively small species. Pupa: gill with short dorsal filaments, short petioles. Larva: head with distinct spot below stemmata; hypostomal median and lateral teeth not well developed, sublateral teeth small; fan rays ca. 37; abdomen callipygous, dorsolateral tubercles present. Posterior circlet with ca. 2,800 hooks.

Description

Adult female. Unknown.

Adult male. Unknown.

Pupa (based on 1 pharate specimen). Thorax: cuticle with sparse small granules. Gill (Fig. 9b): dorsal filaments shorter; arising from short petioles, branching pattern (2+2)+2+2+1+1; filaments evenly tapered, brown; maximum length 1.3 mm.

Larva (based on 5 last-instar specimens with immature pharate pupal gills). Body (Fig. 11b): length 5.4–5.6 mm; mottled dark grey, with paler intersegmental regions; males slightly more yellowish and smaller than females; females darker. Head (Fig. 13b): light brown, paler anteriorly; labral fan stalks pale; head spots essentially neutral, slightly positive medially, posterolateral spots slightly negative; width 0.58 mm; length 0.64 mm; distance between antenna bases 0.11 mm; lateral margins convex; ecdysial lines straight, diverging posteriorly, broadly rounded at maximum width; posteromedial edge of apotome darker brown; posterior edge of apotome slightly eroded, cervical sclerites distinct, postocciput not extended to cervical sclerites; distinct brown spot anterodorsal of stemmata. Antenna: total length 0.50 mm; distal article 0.3 times as long as basal articles, subequal in length to labral fan stalk; basal and distal article pale brown, median article pale. Labral fan: stalk clear to pale brown, anterior palatal bar not markedly developed; 33–35 fine rays, 0.63 mm in length, 6–8 rays less substantial; microtrichia fine and elongate, 1.5 time longer than ray width, no distinctive pattern. Postgenal cleft (Fig. 16b): deeply V-shaped, slightly concave margins 1.5 times as long as width. Postgenal bridge: 0.3 times as long as cleft depth; genae evenly light brown; elongate ventrolateral muscle scars slightly positive. Hypostoma (Fig. 18b): ratio 5.4; overall shape domed; teeth well developed, but not prominent; lateral teeth short, sharp, scalloped medially, directed laterally; sublateral teeth small; paralateral teeth small but obvious; lateral serrations poorly developed; 8 or 9 hypostomal setae per side. Mandible (Fig. 20b) preapical and subapical teeth poorly developed; 5 or 6 spinous teeth, gap absent; serration and sensillum fused basally and markedly pointed, blade region concave and smooth. Abdomen: thorax and anterior abdomen subequal in width, expanded gradually posteriorly to maximum width, callipygous; tergites II–V with dorsolateral tubercles increased in size posteriorly. Anal sclerite (Fig. 22a). Posterior circlet: directed ventrally; 131 rows of hooks; 21–23 hooks per row (total ca. 2,880).

Additional material examined

Vanua Lava, Tahiti River. S13.84727° E167.52191°, alt. 12.5 m, 28.viii.2004. Coll. D. & R. Craig (immature larvae; DAC).

Etymology

In honour of Joseph Banks, botanist on Captain James Cook's first voyage to the Pacific (1768–1771) and after whom the Banks Islands were named, although he never visited Vanuatu.

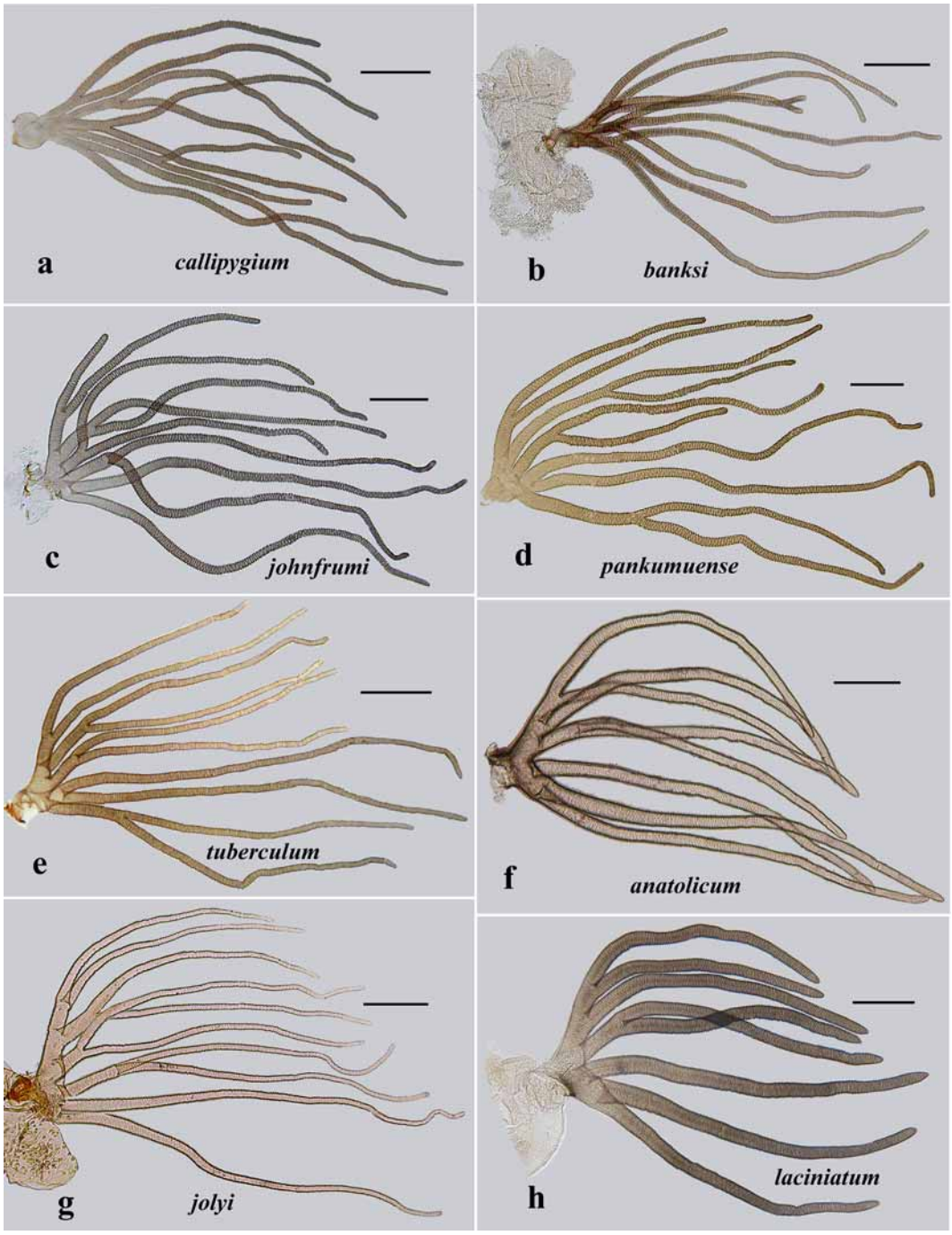

FIGURE 9. Pupal gill filaments of *Hebridosimulium* species. Scale bar = 0.2 mm.

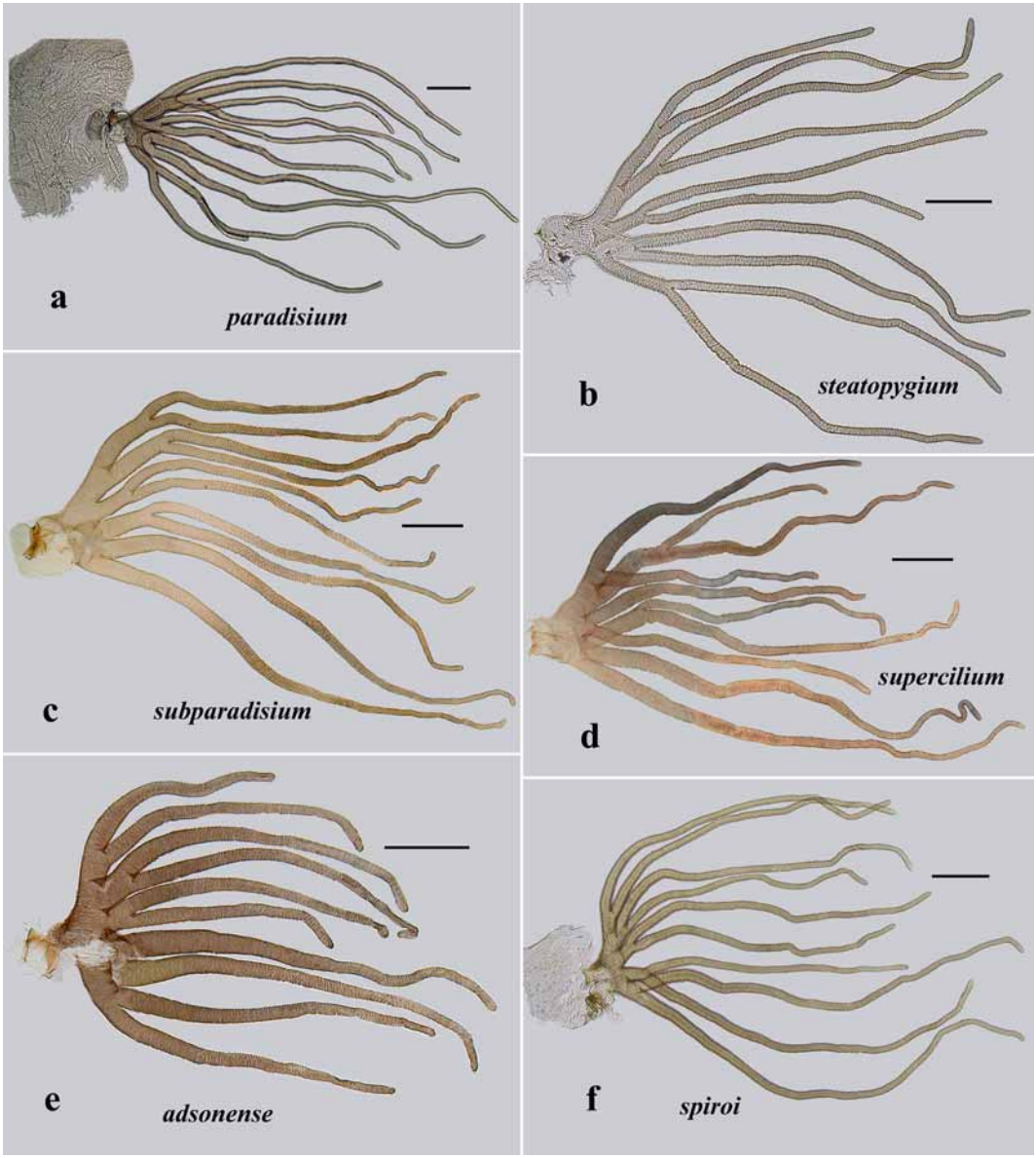

FIGURE 10. Pupal gill filaments of *Hebridosimulium* species (continued). Scale bar = 0.2 mm.

Distribution

VANUATU: Vanua Lava (Banks Islands).

Comments

This callipygous species is assigned to the *tuberculum* species subgroup on the basis of the dorsal paired tubercles on the larval abdomen. Larvae differ from others in the group in possessing smaller hypostomal teeth, distinct lateral head-spot pattern and a deeper postgenal cleft. The type habitat of *S. banksi* larvae is somewhat unusual for a member of

the *tuberculum* species subgroup in that it was a moderately sized river (Fig. 23d), although larvae attach themselves to vegetation in typical fashion.

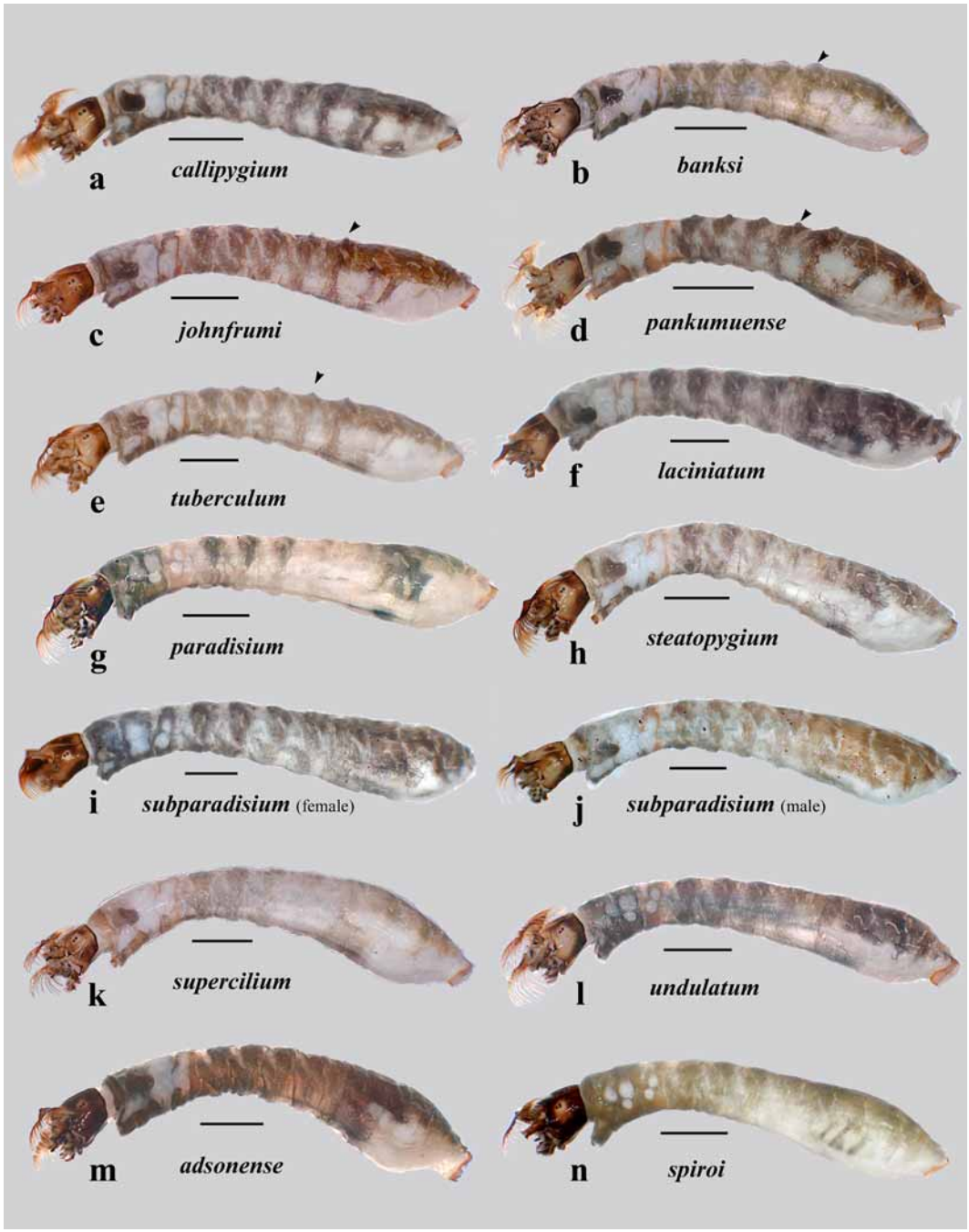

FIGURE 11. Left lateral views of *Hebridosimulium* species larvae. Last-instar larvae, except **l** & **n**, which are penultimate. Arrowheads indicate dorsal tubercles. Scale bar = 1.0 mm.

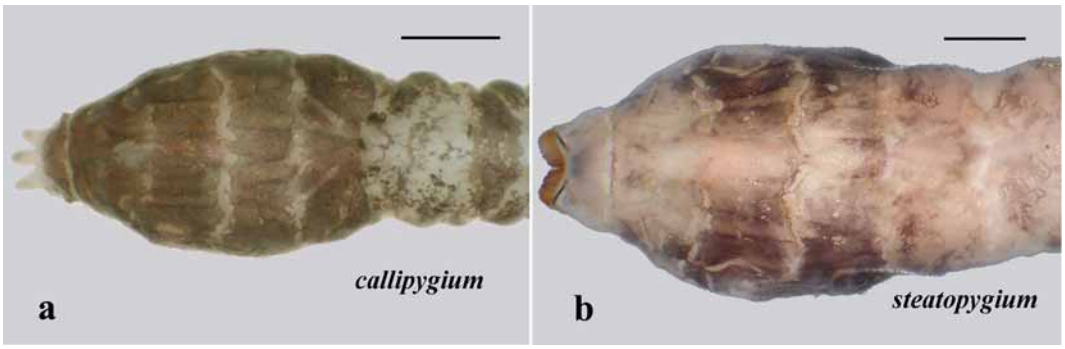

FIGURE 12. Posterior abdomens of larvae of *Hebridosimulium*. Dorsal views. Scale bar = 0.5 mm.

***Simulium* (*Hebridosimulium*) *johnfrumi* Craig, n. sp.**
(Figs. 4a, 5b, 6b, 8b, 9c, 11c, 13c, 15a, 16c, 18c, 20c)

Types

Holotype. Adult: double-pinned reared male, dried from alcohol. Label data—"*S.* (*H.*) *johnfrumi*. VANUATU. Tanna. 2nd strm, S of Bethel. 2m abs. 19.vi.1981, Coll. D. A. Craig", "Holotype" (BM). Pupal exuviae and cocoon as subsidiary material. **Paratypes**. Adults: Nine double-pinned reared males, dried from alcohol. Two pinned, cleared and in glycerine vials. Label data—as for Holotype. Pupal exuviae and cocoon on points (4 BM, 3 BPBM, 2 DAC). One pinned female, cleared and in glycerine vial (BM). Double-pinned reared female, dried from alcohol. Label data—as above, but with "S19.58429° E169.31089°, alt. 24 m. 1.x.2004. Coll. D. A. & R. Craig". Right wing on slide (DAC). Alcohol material. Label data—as for Holotype (larvae; BM, BPBM. larvae, pupae, reared males; DAC). Label data—"Vanuatu, Tanna, Louniel Village Casd, north of Point Lenamblain. S19.43082° E169.33971°, alt. 53m. 29.ix.2004. Coll. D. A. & R. Craig" (larvae; DAC).

Diagnosis

Relatively small species. Adults: thorax relatively light in colour. Female: palpal sensory vesicle markedly small; pleural membrane with sparse fine hairs; genital fork stem thickened, hypogynial valves markedly divergent, anal lobe small. Male: ventral plate keel large. Pupa: dense, small thoracic granules. Cocoon: slightly flared basally. Larva: head with distinct spot below stemmata; hypostomal median and lateral teeth distinct, paralateral teeth developed but small; fan rays ca. 37; abdomen callipygous, dorsolateral tubercles present.

Description

Adult female (based on 2 reared specimens in alcohol). Body: head and abdomen very

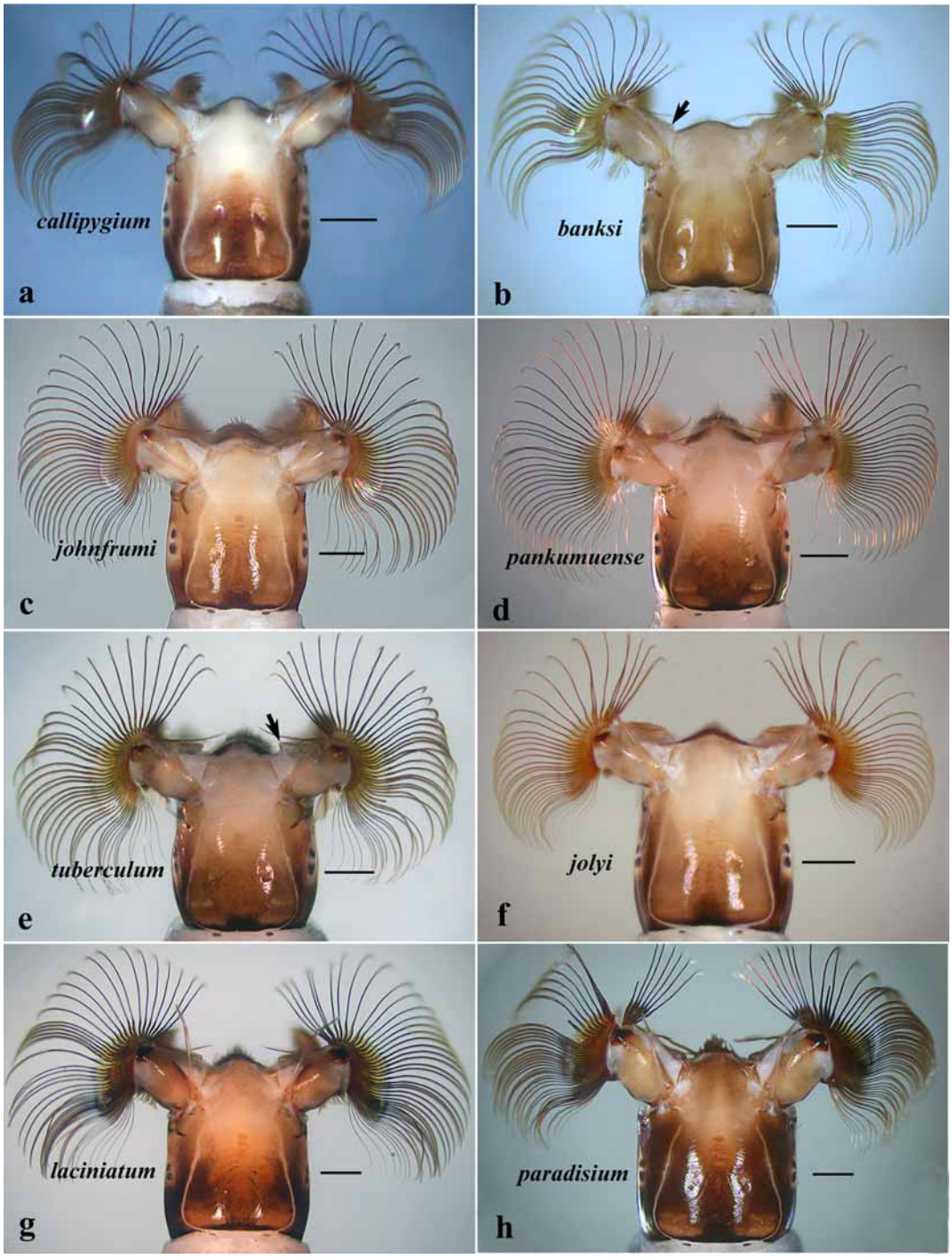

FIGURE 13. Dorsal views of larval heads of *Hebridosimulium* species. **a**–**e.** *callipygium* species group, **f**–**h.** part of *steatopygium* species group. Last instars, except **f** & **h**, which are penultimate instars. Arrows (**b** & **e**) indicate anterior palatal bar. Scale bar = 0.2 mm.

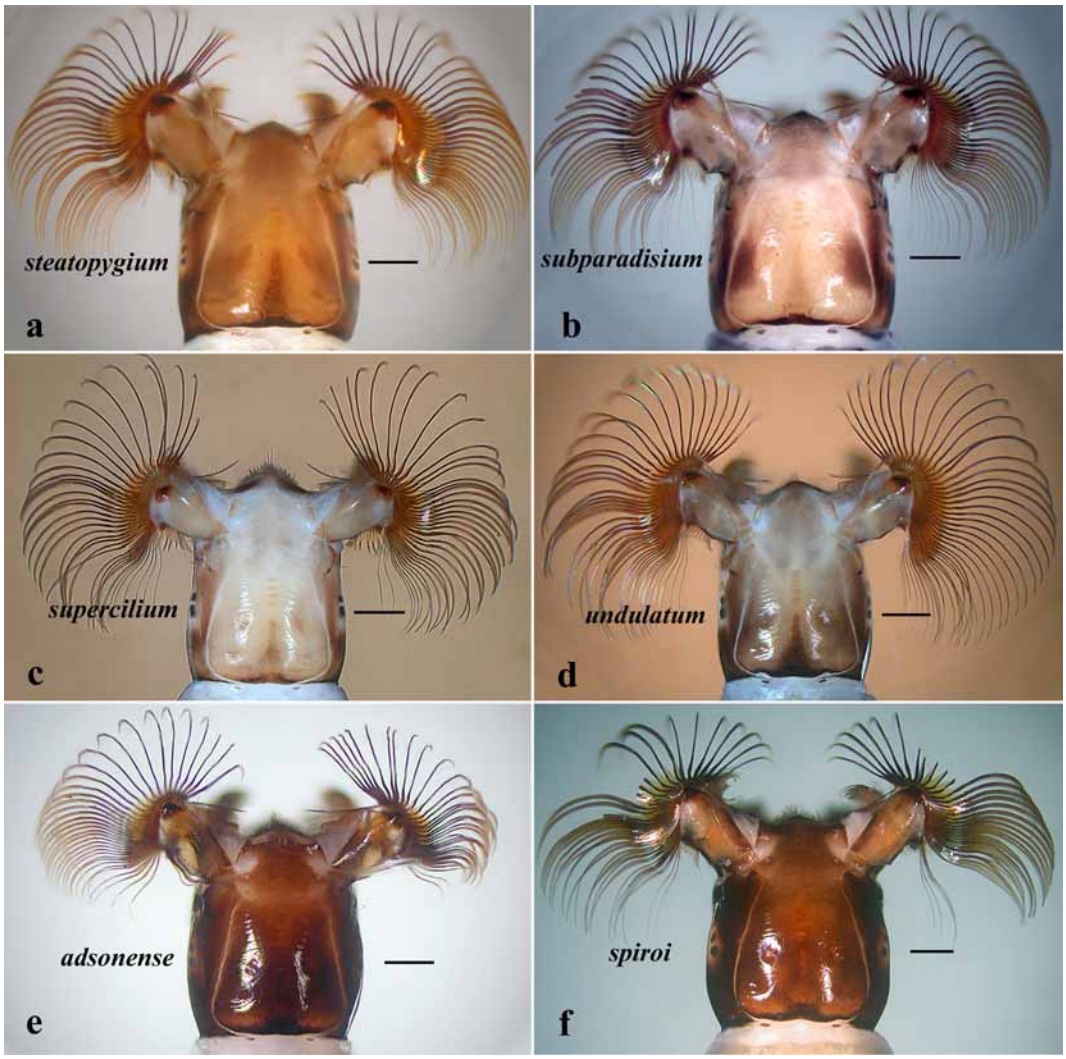

FIGURE 14. Dorsal views of larval heads of *Hebridosimulium* species. *steatopygium* species group. Last instars, except **d** & **f**, which are penultimate instars. Scale bar = 0.2 mm.

dark blackish brown; thorax light brown; total length 2.2–2.4 mm. Head: width 0.80–0.83 mm; depth 0.51–0.57 mm; postocciput black, vestiture of dense short hairs; frons paler ventromedially; frons-head ratio (narrowest width of frons: greatest width of head) 1.0:4.2. Eye: interocular distance 0.19 mm; ommatidia 0.019 mm in diameter; 29 rows across, 35 rows down. Clypeus: 0.22 mm wide; concolourous with ventral region of frons; vestiture of black and pale hairs. Antenna: length 0.48–0.51 mm; flagellomeres grayish-yellow, scape and pedicel pale yellow. Mouthparts: 0.5 times length of head depth, substantial; mandible shorter than lacinia, poorly sclerotized with 23 fine inner teeth; lacinia with 9 inner teeth and 14 outer teeth; maxillary palpus, total length 0.55 mm; with all articles evenly brown, proportional length of 3rd, 4th, and 5th articles 1.0:0.9:1.4; sensory vesicle

ovoid, less than 0.3 times width of 3rd article, opening 0.5 times width of vesicle. Thorax: length 1.1–1.2 mm; width 0.89–0.99 mm; postpronotal lobe paler than scutum; scutum evenly medium brown, vittae not distinct, vestiture of very sparse, fine pale hairs, with few longer darker hairs posteriorly; scutellum markedly pale, vestiture of few long black hairs and shorter pale hairs laterally, apical angle 120°, rounded; postnotum concolourous with scutum; pleural membrane (Fig. 4a), pale and with markedly fine pale hairs (barely observable at 50x in alcohol). Wing: length 2.2–2.3 mm; width 1.1 mm. Legs: overall appearance light brown and pale yellow; coxae light brown; femorae pale brown basally, yellow distally; tibiae yellow basally, brown distally; fore tibiae brown; mid tibiae yellow basally, brown distally; hind tibiae yellow. Abdomen: overall blackish brown; basal scale dark brown with fringe of long pale hairs; anterior tergites concolourous with scutum; tergite II 4 times wider than long, tergite III 2 times wider than long, both with vestiture of sparse fine pale hairs, tergites IV–VII and VII wider, with vestiture of longer fine pale hairs, tergite VIII paler. Sternum: paler anteriorly, concolourous with tergum posteriorly. Genitalia (Fig. 5b): sternite VIII pale, not deeply indented; hypogynial valves lightly pigmented with sparse vestiture; median edges concave and widely divergent, membranous apices directed medially, genital fork with stem short and substantial, posterolateral arms lightly pigmented, anterolateral extension rounded apically, small; anal lobes with anterolateral apodeme not markedly developed, median depression not strongly developed; cercus elongated.

FIGURE 15. Left lateral views of larval heads of *Hebridosimulium* species. Left labral fan removed for clarity. Last instars except **c**, which is penultimate. Scale bar = 0.2 mm.

Adult male (based on 5 reared specimens in alcohol). Body: overall dark brown to black; total length 2.4–2.6 mm. Head: width 0.85–0.92 mm; depth 0.58–0.63 mm. Eyes: upper ommatidia orange, 0.042 mm in diameter, ca. 15 across and 13 down; lower ommatidia dark brown, 0.018 mm in diameter, ca. 24 across and down. Clypeus: brown, paler medially; 0.2 times as wide as head; vestiture of long fine pale hairs. Antenna: total length 0.52 mm; pale yellow. Mouthparts: length 0.38 times head depth; mandibles insubstantial, finely tapered with apical hairs; lacinia broad basally, finely tapered apically with terminal hairs; maxillary palpus dark brown, 0.49 mm long, proportional lengths of 3rd, 4th, and 5th articles 1.0:0.9:1.7, third article darker and markedly hairy, sensory vesicle spherical, occupying 0.33 times width of article, opening 0.25 times width of vesicle.

Thorax: length 1.0–1.1 mm; width 0.8 mm; postpronotal lobes and scutum evenly light brown; scutum with 2 barely visible vittae; vestiture of even, small fine pale hairs;

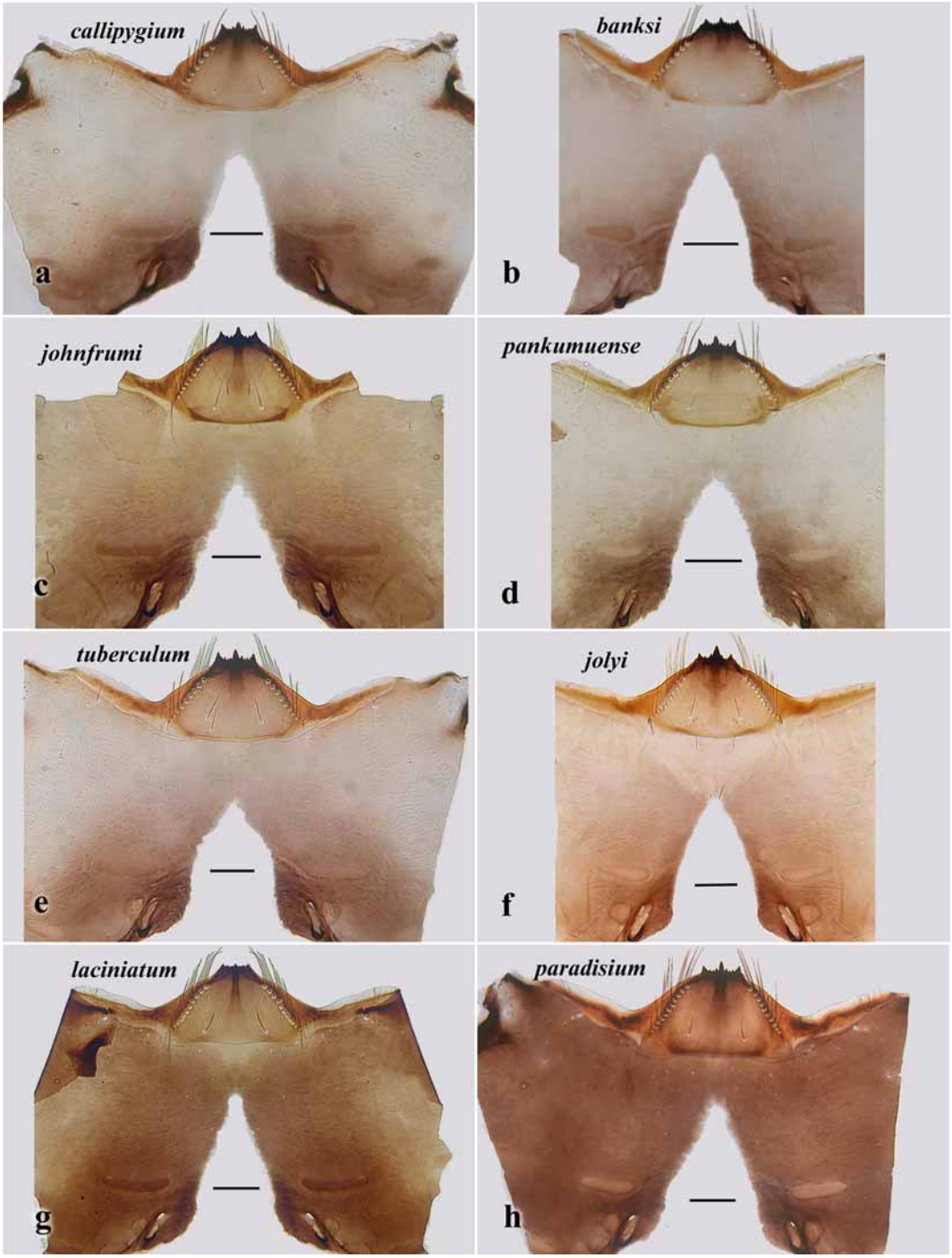

FIGURE 16. Postgenal clefts and hypostoma of larvae of *Hebridosimulium* species. **a**–**e** *callipygium* species group, **d**–**h** *steatopygium* species group. Last instar, except **b**, which is penultimate. Scale bar = 0.1 mm.

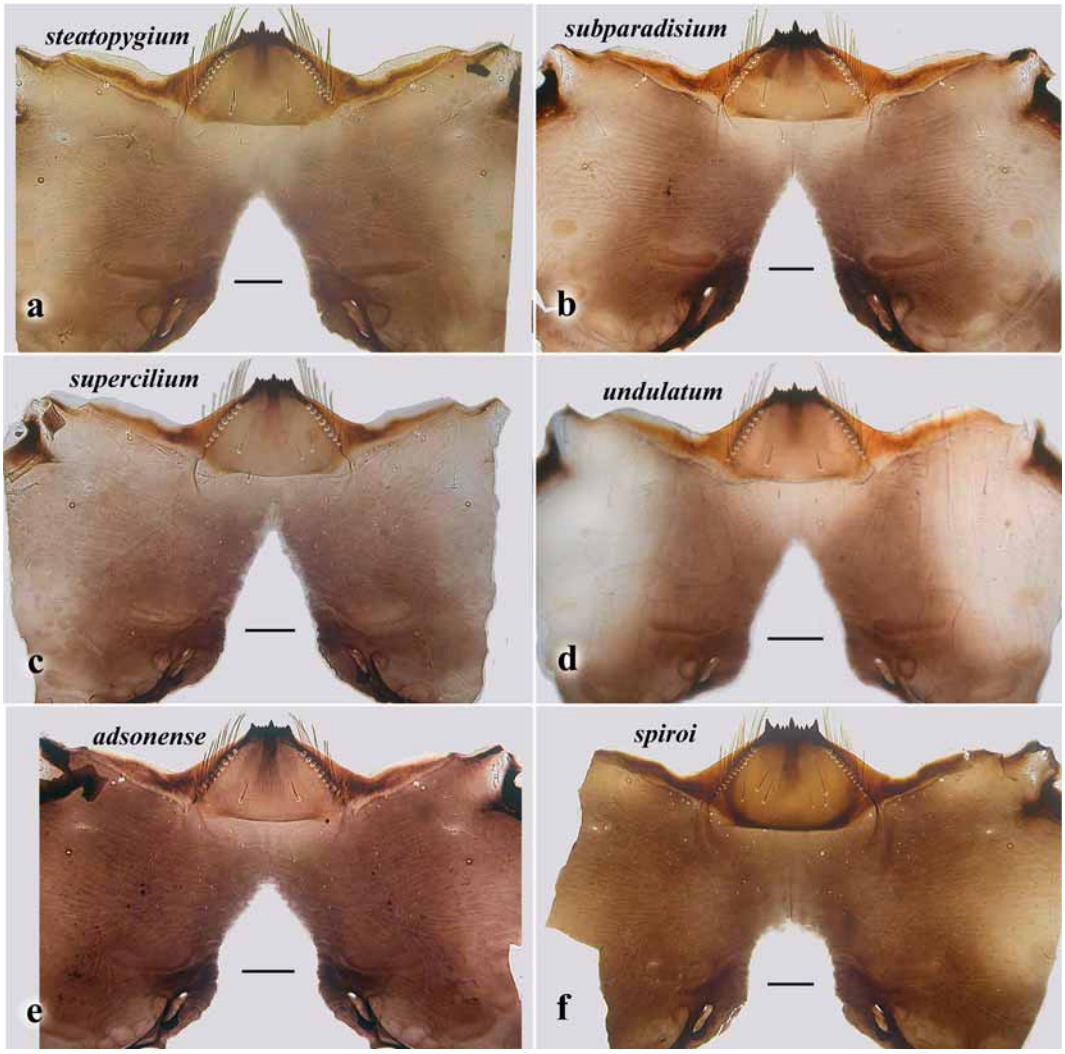

FIGURE 17. Postgenal clefts and hypostoma of larvae of *Hebridosimulium* species. Last instar except **b**, **d**, & **f**, which are penultimate. Scale bar = 0.1 mm.

scutellum pale, apical angle 100°; vestiture of few black hairs laterally, remainder pale; postnotum concolourous with scutum, shiny: pleuron and pleural membrane concolourous with scutum; pleural membrane with hairs, but not visible at 50x in alcohol. Wing: 2.1–2.2 mm in length, 0.96–1.1 mm at maximum width. Legs: mainly yellowish; coxae and trochanters yellow; fore femur light brown, distal region of tibia and all of tarsus dark brown; mid leg as for foreleg; hind leg with femur pale and tibia hairy and pigmented distally, both swollen and flattened, width to length ca. 0.35, pretarsal claw with ca. 19 grappling hooks dorsally. Abdomen: dark brown; basal scale well developed and black, hairs markedly long, fine, and pale, extended to beyond 2nd segment; 1st and 2nd segment paler brown, remainder dark brown; vestiture of sparse pale hairs. Genitalia (Fig. 6b): gonocoxa

1.3 times longer than basal width, brown, with long black hairs on distal half; gonostyle paler, approximately 3.3 times longer than basal width, strengthening ridge not marked;

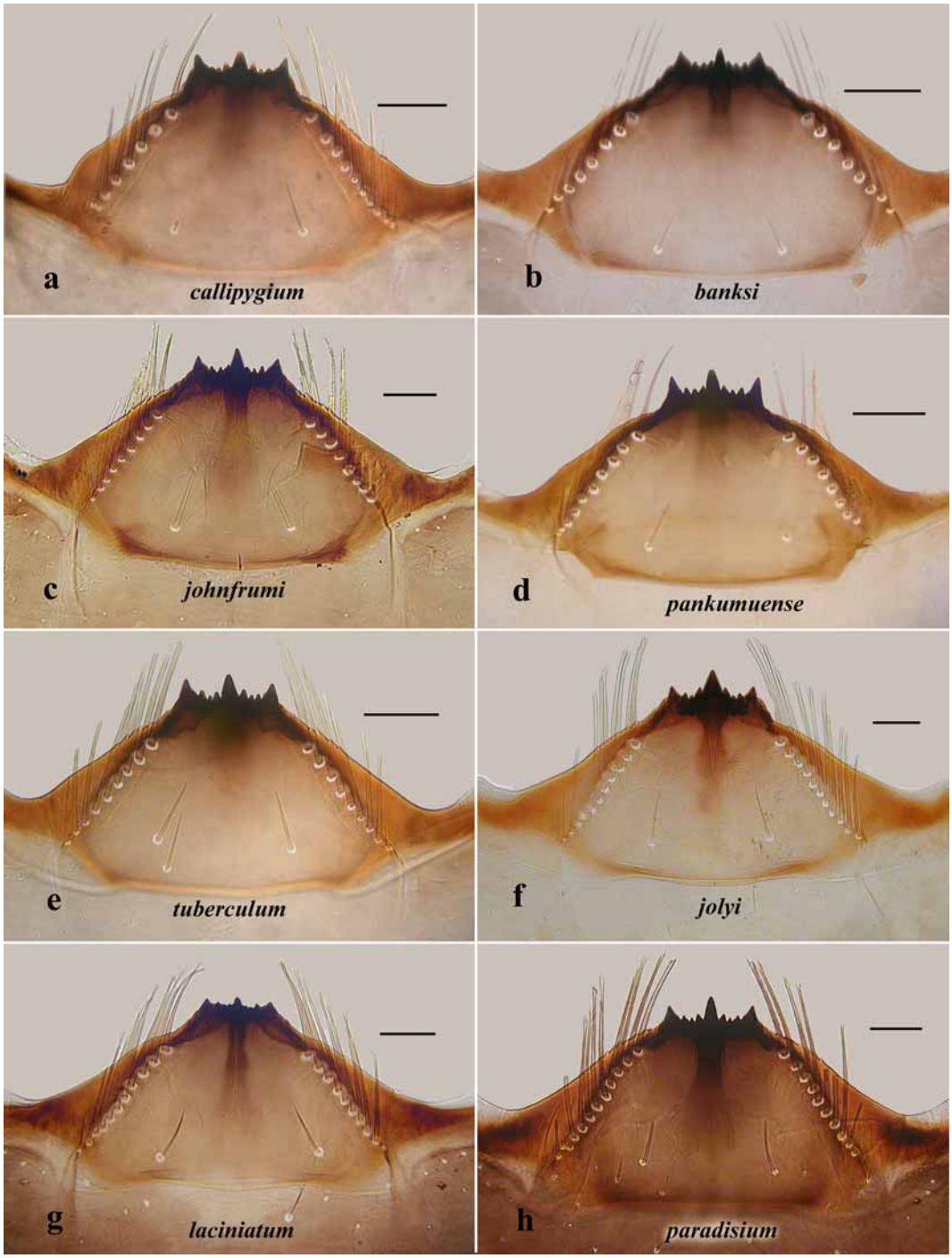

FIGURE 18. Hypostomal teeth of larvae of *Hebridosimulium* species. Last instar. Scale bar = 0.05 mm.

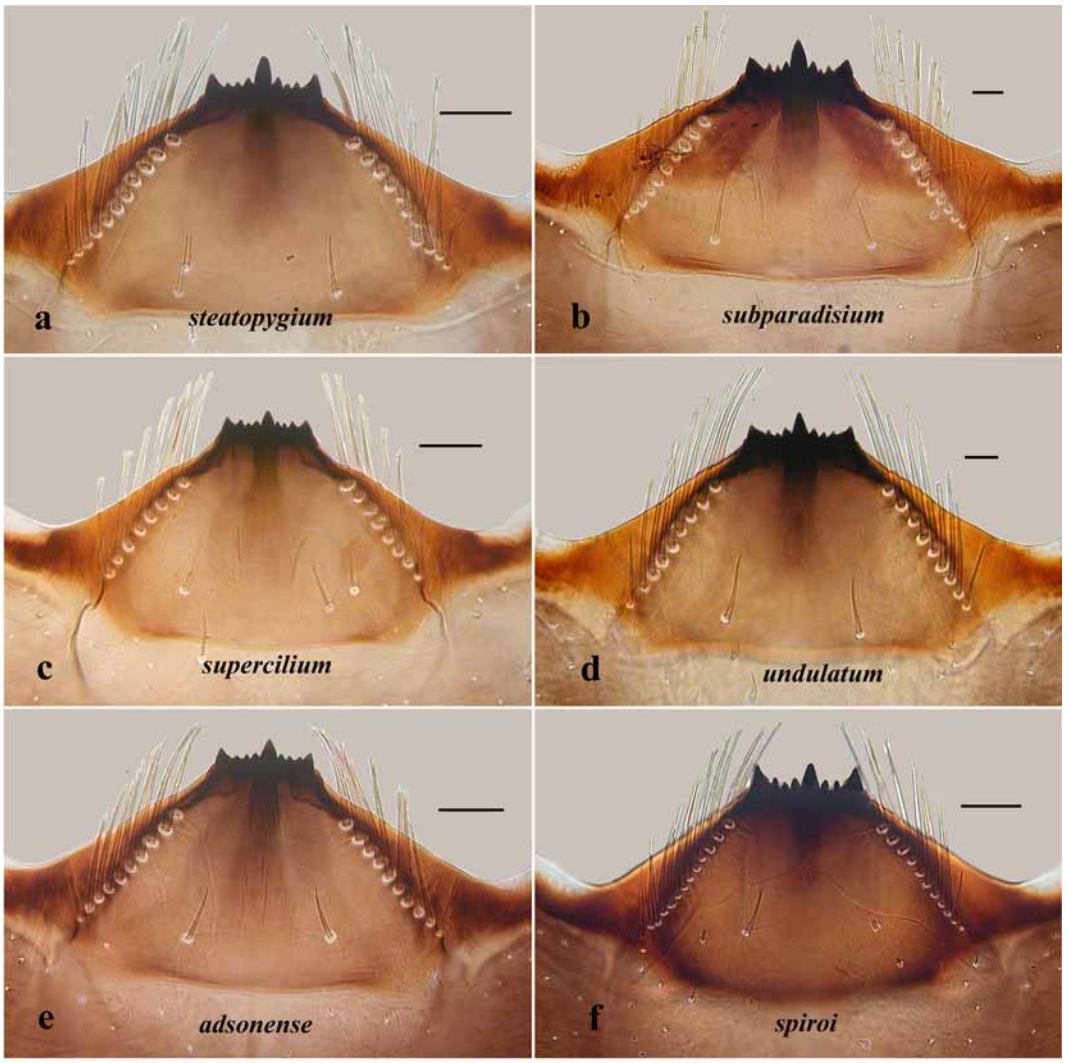

FIGURE 19. Hypostomal teeth of larvae of *Hebridosimulium* species. Last instar, except **d** & **f**, which are penultimate. Scale bar = 0.05 mm.

ventral plate angulate laterally, proximal arms finely tapered, median keel subequal in length to remainder of plate, flattened apically; dorsal sclerite well developed and broadly V-shaped; median sclerite with stem 1.3 times as long as crosspiece length. Cerci: essentially absent.

Pupa (based on 10 specimens). Body length: female 2.3–3.0 mm, male 2.4–2.7 mm. Head and thoracic cuticle light brown, covered with dense small granules (Fig. 8b). Gill (Fig. 9c): 6 dorsal filaments subequal in length and shorter than remainder, occasionally dorsalmost filament markedly shorter; branching pattern (2+2)+2+2+2, often (2+2)+2+2+1+1; arising from short petioles; grayish brown, not markedly tapered; maximum length 1.4 mm. Cocoon: in females not completely covering pupa, in males

occasionally extended part way along gills; anterior collar not well developed in Tanna specimens, well extended in those from Erromango; opening width less than basal width of cocoon; slightly flared basally.

Larva (based on numerous mature last-instar larvae). Body (Fig. 11c): total length 5.3–6.9 mm, females mottled dark grey, with paler intersegmental regions; males smaller, slightly more yellowish. Head (Fig. 13c): evenly light brown, slightly darker posteriorly; width 0.58–0.64 mm; length 0.70–0.83 mm; distance between antennal bases 0.35–0.40 mm; lateral margins of head subparallel (Tanna), more convex (Erromango); apotome pale anteriorly, darker posteriorly, ecdysial lines straight, diverging posteriorly, very broadly rounded at maximum width; anteromedial head spots slightly positive, posteromedial and posterolateral spots slightly negative; area surrounding stemmata pale with marked posterodorsal extension; distinct brown spot ventral to stemmata (Fig. 15a), less well developed in specimens from Erromango (such specimens with lateral head spots reminiscent of *S. supercilium*, Banks Islands); posterior edge of apotome slightly emarginate; postocciput with fine medial extension to cervical sclerites (Tanna), or marginally so (Erromango). Antenna: total length 0.45 mm; distal article 0.3 times as long as basal articles, markedly longer than labral fan stalk; basal and distal article pale brown, median article pale. Labral fan: stalk light brown and clear; 36–38 fine rays, 0.70 mm in length, 8–10 rays less substantial; microtrichia markedly fine and elongate, 2 times longer than ray width, 4 or 5 finer microtrichia between thicker ones, pattern not distinct. Postgenal cleft (Fig. 16c): sharply V-shaped, 1.3 times deeper than wide; posteroventral elongate muscle scars light brown. Postgenal bridge: 0.3 times as long as cleft depth; genae evenly light brown. Hypostoma (Fig. 18c): ratio 4.8; overall cone-shaped; median tooth sharp, prominent, extended well beyond other teeth; lateral teeth deltoid; sublateral teeth small, medial teeth barely present; paralateral teeth absent; 3 or 4 markedly small lateral serrations; 8 or 9 hypostomal setae per side. Mandible (Fig. 20c): all apical teeth well developed; 5 or 6 clumped spinous teeth, small gap; serration and sensillum sharply cone-shaped, occasionally 2 sensilla, blade region smooth, essentially straight. Abdomen: thorax and anterior abdomen subequal in width, expanded evenly posteriorly to maximum width, callipygous, more so for Erromango material; dorsolateral tubercles present, increased in size posteriorly; pale posteroventrally with marked diagonal gray band, more so for Tanna material. Posterior circlet: directed posteriorly (Tanna) or more ventrally (Erromango); 154 rows of hooks; 24–28 hooks per row (total ca. 4,000).

Additional material examined

Tanna. Tannus (sic), ?.x.1930, Coll. L. E. Cheesman (male, female; BM). Lenakel, 0–150 m, ?.iii.1970; 0–200 m, ?.i.1973. Coll. N. H. L. Krause (2 females; BPBM). Nr. Imalo, 22.ii.1985. Coll. B. S. Batson (larvae-in poor condition. DAC). Louniel Village cascade. S19.43082° E169.33971°, alt. 53m. 29.ix.2004. Coll. D. A. & R. Craig. (larvae; DAC). Stream south of Bethel. S19.58429° E169.31089°, alt. 24 m. 1.x.2004. Coll. D. A.

& R. Craig (larvae; DAC). **Erromango.** ?.viii.1930. Coll. L. E. Cheesman (4 females; BM). 8–11 km W of Ipota, 100–200 m. ?.iii.1970. Coll. N. H. L. Krause (8 females-2 in vials; BPBM). Dillons Bay, Williams River, main channel. S18.82137° E169.03061°, alt. 25m. 26.ix.2004. Coll. D. A. & R. Craig (larvae, pupae, reared adults; DAC, BPBM). Williams River, right channel. S18.82596° E169.004445°, alt. 47m. 27.ix.2004. Coll. D. A. & R. Craig (larvae; DAC).

Etymology

Named after John Frum, of dubious existence, but integral to the so-called 'cargo cults' on Tanna.

Distribution

VANUATU: Tanna, Erromango.

Comments

This species is closely related to *S. tuberculum* in Efate. Larvae of both species possess dorsolateral tubercles, a callipygous abdomen and generally ventrally directed posterior circlet, but they differ in larval head-spot pattern and armature on the dorsum of the pupa. Adults of *S. johnfrumi* are slightly smaller and more yellow than those of *S. lucyae* (Aneityum). While females have substantial mouthparts, the mandible is not highly sclerotized. Whether they bite, as do females of *S. lucyae*, is moot. Certainly, there are no records of simuliids biting humans on either Tanna or Erromango. Streams and rivers in Tanna and Erromango are not travertine as are those of the more northern islands. At the type locality, a typical Tanna stream (Fig. 23e), larvae and pupae of *S. johnfrumi* were taken from small basalt rocks and leaves in moderate velocity (ca. 80 cm/s). At the Louniel Village cascade, larvae and the pupa were found exclusively on trailing vegetation and leaves in fast velocity (1.5 m/s). There are differences in the abdomen of larvae of *S. johnfrumi*; they are less callipygous in populations from Tanna than those from Erromango. Similarly, there are differences in larval head-spot pattern. The pupae and adult male genitalia are, however, identical. Further analysis may show the Tanna and the Erromango material to be separate species, but they will be closely related.

***Simulium* (*Hebridosimulium*) *pankumuense* Craig, n. sp.**
(Figs. 1c, 5c, 7c, 8c, 9d, 11d, 13d, 16d, 18d, 20d)

Types

Holotype. Adult: double-pinned reared male, dried from alcohol. Label data – "*S.* (*H.*) *pankumuense,* Vanuatu, Malekula, Pankumu River, S16.27629º E167.63687º, alt. 15 m, 2.ix.2004. Coll. D. A. & R. Craig. HOLOTYPE. No. 16608". (BPBM). Pupal exuviae and cocoon as subsidiary material on point. **Paratypes**. Adults: double pinned; 2 reared males,

3 females; pupal exuviae and cocoons as subsidiary material on points. Label data – as for Holotype, but with 'PARATYPE'. Alcohol material: last-instar larvae, pupal exuviae, and reared adults (male and female). Label data – as for Holotype, but with 'PARATYPE'. (larvae, pupae, adults; BPBM, DAC, LCNZ, ROM).

Diagnosis

Pupa: cuticular granules absent, petioles of gills elongate. Larva: labral fan stalk clear; head markedly pale anteriorly, darker posteriorly, head-spot pattern mainly negative; genal cleft arrowhead shaped, median and lateral hypostomal teeth well developed; abdominal dorsolateral tubercles present, abdominal posterior circlet directed ventrally.

Description

Adult female (based on 6 reared specimens in alcohol). Body: overall dark brown, head blackish brown, thorax dark brown, abdomen blackish brown; total length 2.3–2.5 mm. Head (Fig. 1c): width 0.75–0.79 mm; depth 0.48–0.50 mm; postocciput black, vestiture of dense, black hairs; frons vestiture of smaller fine pale hairs and longer sparser black hairs; frons-head ratio (narrowest width of frons: greatest width of head) 1.0:6.0. Eye: interocular distance 0.13 mm; ommatidia 0.015 mm in diameter; ca. 35 rows across and down at mid eye. Clypeus: 0.21–0.23 mm wide; concolourous with frons; vestiture of dense fine pale hairs and long black hairs ventrally. Antenna: length 0.39–0.41 mm; flagellomeres pale yellow, scape and pedicel markedly pale. Mouthparts: relatively large, 0.4 length of head depth; mandible with 24 inner teeth; lacinia with 11 inner teeth and 13 outer teeth; maxillary palpus with all articles evenly dark brown, proportional length of 3rd, 4th, and 5th articles 1.0:0.9:1.2; sensory vesicle small and spherical, ca. 0.3 times width of 3rd article, opening 0.25 times as wide as vesicle. Thorax: length 1.1–1.3 mm; width 0.83–0.85 mm; postpronotal lobes markedly paler than scutum; scutum evenly dark brown medially, with 2 indistinct lateral vittae in alcohol specimens, vestiture of dense, very fine pale hairs; scutellum more or less concolourous with scutum, vestiture of long black hairs and pale hairs laterally, markedly obtuse; postnotum concolourous with scutum; pleuron evenly dark brown; pleural membrane slightly paler with fine sparse hairs. Wing: length 2.1–2.3 mm; width 1.0–1.1 mm. Legs: as for male, but darker. Abdomen: overall black; vestiture of dense silver hairs, long laterally, with few black hairs; basal scale black with pale hairs. Genitalia (Fig. 5c): similar to those of *S. johnfrumi* with, however, anterior margin of medial region of sternite VIII not angulate and darker; genital fork stem short and substantial, anteriorly directed apodeme of lateral arm truncated and flattened, spermatheca ovoid, markedly dark.

Adult male (based on 5 reared specimens in alcohol). Body: relatively small, total length 1.9–2.3 mm. Head: width 0.79–8.6 mm; depth 0.57–0.61 mm. Eyes: upper ommatidia dark orange, large, 0.027 mm in diameter, ca. 14 across and down; lower ommatidia brown, 0.017 mm in diameter, ca. 26 across and 27 down. Clypeus: black, pruinose 0.2 times as wide as head; sparse short black hairs laterally. Antenna: total length

0.49–0.54 mm; flagellomeres light yellow, proximal one slightly darker and longer than remainder, scape, pedicel markedly paler. Mouthparts: short, length 0.25 times head depth; mandibles insubstantial, finely tapered with apical hairs; lacinia broad basally, finely tapered apically with terminal hairs, some tooth-like; maxillary palpus dark, 0.45 mm long, proportional lengths of 3rd, 4th, and 5th articles 1.0:0.9:1.6, third article distinctly hairy, sensory vesicle spherical, occupying 0.4 times width of article, opening 0.25 times width of vesicle. Thorax: length 0.8–1.0 mm; width 0.8–0.9 mm; broadest anteriorly; postpronotal lobes slightly paler than evenly medium brown scutum, vestiture of short pale hairs, dense posteriorly; scutellum lighter than scutum, apical angle distinctly obtuse; vestiture of markedly long stiff black hairs, interspersed with paler hairs; postnotum concolourous with scutum: pleuron concolourous with scutum, membrane paler with markedly fine pale hairs. Wing: 1.8–2.0 mm in length, 0.8–1.0 mm at maximum width. Legs: markedly bicolourous; foreleg with coxa, trochanter, femur, and proximal half of tibia pale, remainder black; mid leg coxa brown, trochanter, and proximal half of femur pale, distal half brown, remainder of leg black; hind leg coxa brown, trochanter pale, femur light brown, proximal 2/3 of tibia pale and remainder black, middle portion of tarsus pale, remainder black; pretarsal claws with ca. 21 grappling hooks dorsally. Abdomen: anteriorly yellowish, remainder brownish black, vestiture of dense fine pale hairs; basal scale with markedly long, pale yellowish hairs. Genitalia: essentially as for *S. johnfrumi* (e.g., Fig. 6b), ventral plate keel enlarged and flattened apically, ventral plate markedly angulate laterally.

Pupa (based on 12 specimens). Body length, male and female, 2.9 mm in length; dorsal cuticle lacking larger rounded, raised granules, minute granules adjacent to gill base and on posterior thorax, otherwise smooth (Fig. 8c). Gill (Fig. 9d): dorsal filaments 0.4 times length of longer ventral filaments; branching pattern (2+2)+2)+2+1+1; dorsal filaments with elongated petioles; filaments not markedly tapered, light brown; annulations distinct; maximum length 1.7 mm. Cocoon: not flared laterally, anterior collar distinct, but not markedly so (Fig. 7c).

Larva (based on 8 mature last-instar larvae). Body (Fig.11d): total length 5.3–5.7 mm, males smaller than females; females mottled light to dark grayish brown, with paler intersegmental regions, males lighter gray and more yellowish orange; prothorax gray, mesothorax pale, metathorax orange, more so in males. Head (Fig. 13d): anterior apotome markedly pale; width 0.57–0.58 mm; length 0.65–0.71 mm; distances between antennal bases 0.31–0.38 mm; lateral margins of head slightly convex; ecdysial lines straight, markedly diverged posteriorly, very broadly rounded at maximum width; posterior apotome mottled brown; medial head spots essentially neutral to slightly positive, lateral head spots markedly negative laterally; posterior genae darker brown than posterior apotome, remainder of genae pale; cervical sclerites distinctly separate from evenly curved apotome posterior edge and non-extended postocciput. Antenna: total length 0.35–0.44 mm; distal article 0.25 times as long as basal articles, extended just beyond labral fan stalk; basal article pale, medial and distal articles light brown; distance between antennal

bases 0.35mm. Labral fan: stalk markedly clear, posterobasal notch and anterior palatal bar not markedly developed; 38–40 fine pale rays, finely tapered, 0.85 mm in length, 7–9 rays less substantial; microtrichia markedly obvious, subequal in length to ray width, distinctive pattern with 6 or 7 slightly shorter microtrichia between those more substantial. Postgenal cleft (Fig. 16d): arrowhead shaped with evenly convex sides, 1.5 times as deep as wide. Postgenal bridge: 0.6 times length of cleft depth; genae pale, posteroventral elongate muscle spot negative. Hypostoma (Fig. 18d): ratio 5.2; overall shape domed; median tooth prominent, longer than sharp deltoid lateral teeth; sublateral teeth small but distinct; paralateral teeth absent; 4 or 5 markedly small, low, lateral serrations; only 8 or 9 hypostomal setae per side. Mandible (Fig. 20d): all apical teeth well developed; 5 or 6 spinous teeth, gap essentially absent; serration and sensillum cone-shaped, markedly developed; blade smooth, slightly convex. Abdomen: thorax marginally wider than head, anterior abdomen (segments I–IV) narrower, gradually expanding to maximum width at segments VI–VII; expanded gradually to maximum width, markedly callipygous; dorsolateral tubercles present: single diagonal band of muscle markedly pigmented. Posterior circlet: markedly directed ventrally; 134 rows of hooks; 20–21 hooks per row (total ca. 2,700).

Additional material examined

Malekula, Pankumu River, S16.27629º E167.63687º, alt. 15 m. 2.ix.2004. Coll. D. A. & R. Craig (larvae, pupae, reared adults; DAC). Orap River, S15.98335° E167.32998°, alt. 5m. 1.ix.2004. Coll. D. A. & R. Craig (immature larvae; DAC).

Etymology

Named for the type locality, the Pankumu River, east-central Malekula Island, Vanuatu.

Distribution

VANUATU: Malekula.

Comments

A tuberculate Vanuatuan species, *S. pankumu* is known mainly from a single location, the sizable Pankumu River (Fig. 23f). Larvae and pupae were on trailing grass leaves and roots in moderately fast flow (1.1 m/ sec). The Orap River, so called, is more of a stream and the few larvae therein were immature and assigned to *S. pankumuense*, mainly on the basis of abdominal characteristics. Larvae are markedly callipygous and the posterior circlet is directed more ventrally than for other larvae (*rf.* Fig. 11d), an orientation previously observed in African simuliid larvae that are phoretic (Crosskey 1990). The number of hooks on the posterior circlet is thought to correlate to water velocity of the habitat (Crosskey 1990, Palmer and Craig 2000); however, *S. pankumuense* with its relatively low number of hooks, does not show a correlation with the relatively high velocity of the habitat.

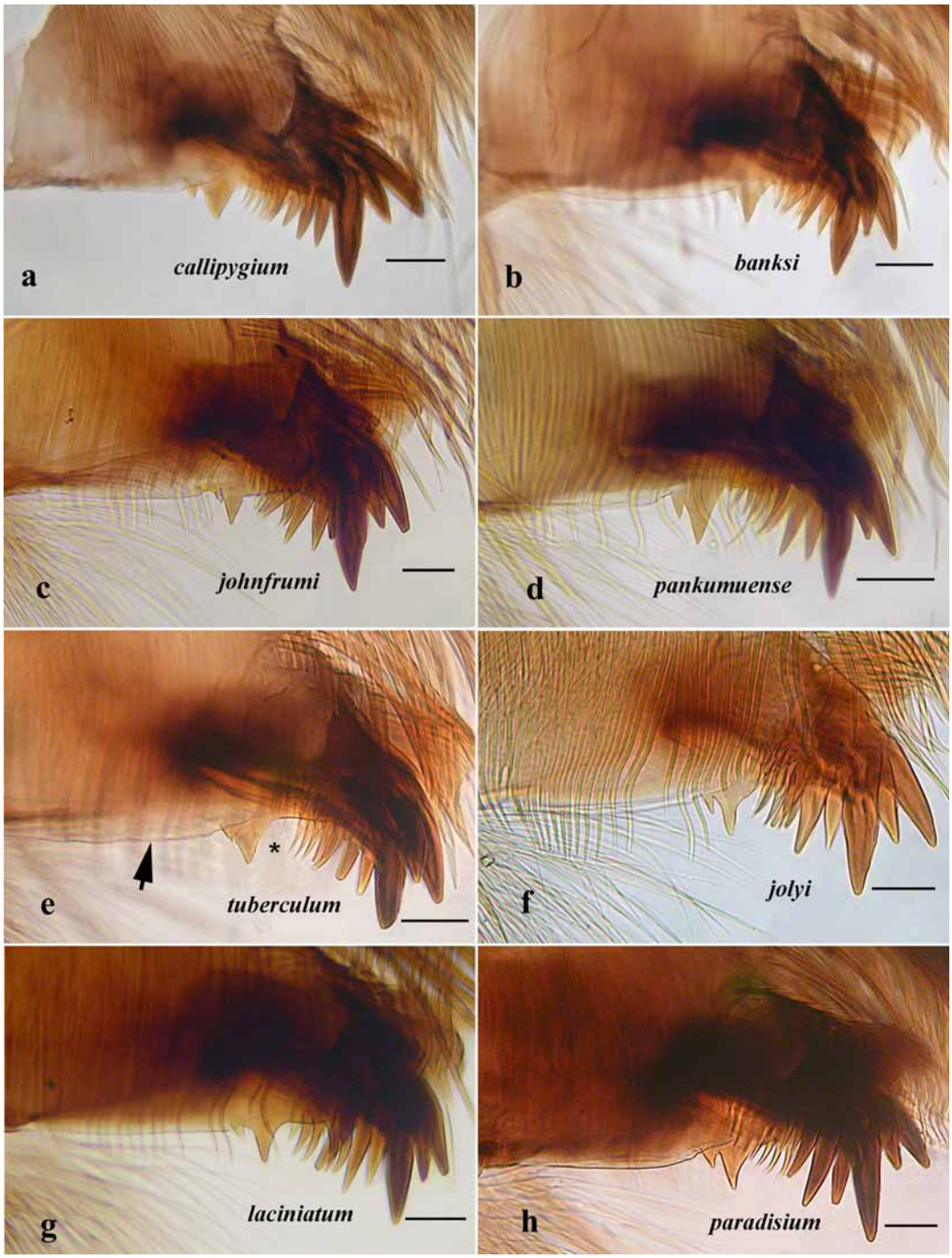

FIGURE 20. Mandibular teeth of larvae of *Hebridosimulium* species. **a**–**e** *callipygium* species group, **f**–**h** *steatopygium* species group. Last instar, except **b**, which is penultimate. Arrow (**e**) indicates the blade region; asterisk the spinous teeth gap. Scale bar = 0.025 mm.

FIGURE 21. Mandibular teeth of larvae of *Hebridosimulium* species, *steatopygium* species group. Last instar, except **d** & **f**, which are penultimate. Scale bar = 0.025 mm.

Mouthparts of the female adult are moderately substantial and the number of mandibular and lacinial teeth is similar to that of species known to bite, namely *S. laciniatum* and *S. lucyae*. The sensory vesicle on the maxillary palpus is, however, small. There are no records of simuliids biting on Malekula, and locals are not aware of biting flies fitting the description of female black flies. Cheesman collected simuliids from Malekula and nearby Achin Island, but makes no mention of any biting simuliids in the vicinity (Cheesman 1933, 1957a, 1960).

Closely related to *S. johnfrumi* in genitalic characters, *S. pankumuense* differs from that and other tuberculate species in lacking pupal cuticular granules (Fig. 8). In the Pankumu River, *S. pankumuense* larvae occur with those of *S. jolyi*.

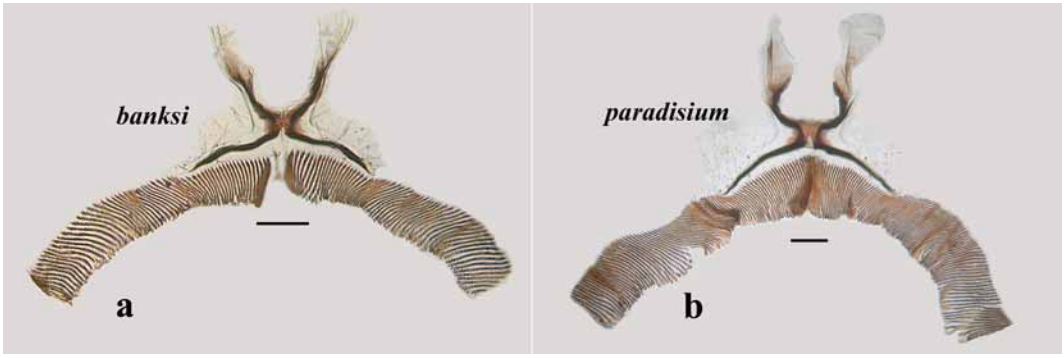

FIGURE 22. Anal sclerite and circlet of hooks of larvae of *Hebridosimulium* species. Last instar. Ca. 2800 and 7300 hooks, respectively. Scale bar = 0.2 mm.

***Simulium* (*Hebridosimulium*) *tuberculum* Craig. n. sp.**
(Figs. 5d, 8d, 9e, 11e, 13e, 16e, 18e, 20e)

Hebridosimulium jolyi: Grenier and Rageau (1961: 96) not Roubaud 1906.
Simulium (*Hebridosimulium*) *jolyi*: Crosskey (1967:27) in part not Roubaud 1906.

Types

Holotype. Adult: pinned reared female, dried from alcohol. Label data— "*Simulium* (*Hebridosimulium*) *tuberculum*, VANUATU, Efate, Ewor R., La Cressionnière, 16.vi.1981, Coll. D. A. Craig", "Holotype". Pupa and cocoon as subsidiary material (BM). **Paratypes**. Adults: Six pinned reared females (4 BM, 2 BPBM), one reared male (BM). Label data— as for Holotype, but with "Paratype". Six reared females, two males, label data— "*S.* (*H.*) *tuberculum* , Ewor River, La Cressionnière. S17.71728° E168.56946°, alt. 24m, 5.x.2004. Coll. D. A. & R. Craig. Paratype" (BM, BPBM). **Alcohol**: label data— as for Holotype, but with "21.vi.1981" and 'PARATYPE' (larvae; BM, BPBM. Pupae, reared adults; DAC).

Diagnosis

Pupa: thoracic cuticle with sparse, unevenly distributed granules. Cocoon: relatively small and not completely covering pupa, with tendency to be flared basally. Larva: lateral head spot beneath stemmata absent, dorsolateral tubercles present.

Description

Adult female (based on numerous specimens). Body: head and abdomen very dark brownish black, thorax evenly light brown; total length 2.1–2.6 mm. Head: width 0.72–0.83 mm; depth 0.57 mm; postocciput black, vestiture of dense short black hairs; frons paler ventromedially; frons-head ratio (narrowest width of frons: greatest width of

head) 1.0:4.0. Eye: interocular distance 0.18–0.21 mm; ommatidia 0.026 mm in diameter; 35 rows up and across at mid eye. Clypeus: 0.22 mm wide; concolourous with ventral region of frons; vestiture of black and pale hairs. Antenna: length 0.48 mm; flagellomeres light brown, scape and pedicel pale yellow. Mouthparts: 0.3 length of head depth; mandible shorter than lacinia, poorly sclerotized with 20 inner teeth, larger distally, poorly developed basally; lacinia with 11 inner teeth and 11 outer teeth; maxillary palpus, all articles evenly brown, proportional length of 3rd, 4th, and 5th articles 1.0:0.8:1.3; sensory vesicle ovoid, less than 0.3 times width of 3rd article, opening 0.5 times width of vesicle. Thorax: length 1.1–1.2 mm; width 0.94 mm; postpronotal lobes paler than scutum; scutum evenly medium brown, vestiture of very sparse, fine pale hairs, with few longer darker hairs posteriorly; scutellum pale, vestiture of few black hairs and pale hairs laterally, apical angle 120°, rounded and bare; postnotum concolourous with scutum; pleural membrane, pale brown and with markedly fine pale hairs (not observable at 50x in alcohol). Wing: length 1.6–2.1 mm; width 0.9–1.1 mm. Legs: as for *S. johnfrumi*. Abdomen: as for *S. johnfrumi*. Genitalia (Fig. 5d): similar to *S. johnfrumi*; sternite VIII pale, not deeply indented; hypogynial valves lightly pigmented with sparse vestiture; median edges markedly concave and divergent, membranous apex ridged, markedly directed medially; genital fork with stem thickened, posterolateral arms lightly pigmented, anteriorly directed apodeme of lateral arm rounded and smaller than posterior portion; anal lobes with anterior extension not markedly developed, median depression not strongly developed; cercus elongated.

Adult male (based on 9 reared specimens). Generally as for *S. johnfrumi*, but smaller. Body: total length 1.9–2.0 mm. Head: width 0.77–0.82 mm; depth 0.47–0.53 mm. Eyes: upper ommatidia orange, 0.039 mm in diameter, ca. 13 across and 16 down; lower ommatidia dark brown, 0.018 mm in diameter, ca. 24 across and down. Clypeus: brown, paler medially; 0.2 times as wide as head; vestiture of long fine pale hairs. Antenna: total length 0.44 mm; flagellomeres pale brown, scape and pedicel yellow. Mouthparts: length 0.34 times head depth; mandibles insubstantial, finely tapered with apical hairs; lacinia broad basally, finely tapered apically with terminal hairs; maxillary palpus dark brown, 0.38 mm long, proportional lengths of 3rd, 4th, and 5th articles 1.0:0.8:1.1, 3rd article darker and markedly hairy, sensory vesicle spherical, occupying 0.33 times width of article, opening 0.25 times width of vesicle. Thorax: as for *S. johnfrumi*, but smaller, length 0.86–0.93 mm; width 0.8 mm. Wing: 1.6–1.9 mm in length, 0.77–0.83 mm at maximum width. Legs: essentially as for *S. johnfrumi*, but hind leg with femur and tibia not as swollen and flattened, width to length ca. 0.22, and pretarsal claw with ca. 23 grappling hooks dorsally. Abdomen: dark brown; basal scale well developed and dark, hairs markedly long, fine and pale, extended beyond 2nd segment; 1st and 2nd segment paler brown, remainder dark brown; vestiture of sparse pale hairs. Genitalia: as for *S. johnfrumi* (e.g., Figs. 6b).

Pupa (based on numerous specimens). Generally as for *S. johnfrumi*, but with coarser

thoracic granules (Fig. 8d). Body length: male 2.2–2.4 mm, female 2.6–2.9 mm. Gill (Fig. 9e): petioles moderately elongate except for 1 ventral pair, but variable; 6 dorsal filaments subequal in length, 0.6–0.8 length of ventral filaments; branching pattern of filaments (2+2)+2+2+2; annulations fine. Cocoon: shoe shaped, as for *S. johnfrumi*; in males flared basally more often than not, less so in females.

Larva (based on numerous mature last-instar larvae). Body (Fig. 11e): generally as for *S. johnfrumi*; male yellowish, females grayish; total length, male 4.7–5.9 mm, female 5.6–6.4 mm. Head (Fig. 13e): overall as for *S. johnfrumi* but slightly darker; male length 0.74–0.83 mm, width 0.58–0.66, distance between antennal bases 0.32–0.34; female length 0.73–0.86 mm, width 0.55–0.65, distance between antennal bases 0.35–0.37; lateral margins of head more convex than for *S. johnfrumi*; head-spot pattern less distinct than for *S. johnfrumi,* lacking distinct lateral head spot beneath stemmata (similar to *S. johnfrumi* from Erromango); ecdysial lines markedly broadly rounded at maximum width; posterior margin of apotome very slightly emarginate; postocciput finely extended between cervical sclerite and apotome. Antenna as for *S. johnfrumi*. Labral fan: anterior palatal bar on stalk markedly developed; 38–41 rays, 1.0 mm in length, 5 or 6 rays less substantial, distinct pattern of microtrichia, with 6 smaller, decreasing in size between those longer. Postgenal cleft (Fig. 16e): arrowhead shaped, 1.5 times deeper than wide, posteroventral elongated muscle spots neutral. Postgenal bridge: 0.5 times as long as cleft depth; genae and postgenae evenly light brown. Hypostoma (Fig. 18e): overall cone-shaped; ratio 4.7; median and lateral teeth distinct, subequal in length, latter slightly scalloped medially, sublateral teeth usually small, but individual teeth variably occasionally larger; paralateral teeth not apparent, lateral serrations barely visible; 8 or 9 hypostomal setae per side, medial setae markedly substantial. Mandible (Fig. 20e): apical and subapical teeth substantial as are the few spinous teeth, gap marked; sensillum fused to serration; blade region smooth and convex. Abdomen: as for *S. johnfrumi,* but lighter in colour. Posterior circlet: directed slightly ventrally; 160 rows, 23–26 hooks (total ca. 3,800).

Additional material examined

Efate. Fourteen slide mounts, including 11 “plesiotypes” with round green labels, variously labeled, Klem (sic) River, 26.v.1958, Coll. J. Rageau (larvae, pupae, adults; PI). Klem (sic) River, 26. v. 1958, 5.vi.1958, Coll. J. Rageau (larvae — numerous, pupae, adults; BM, PI). Klehm Cascade, 17.vi.1981. Coll. D. A. Craig (larvae; DAC). Ewor River, La Cressionnière, alt. 10m, 16.v.1981. Coll. D. A. Craig (reared adults; DAC); 21.vi.1981 (larvae, pupae; ANIC, BM, BPM, DAC, HT, PI); 23.ii.1985, Coll. B. S. Batson (larvae; DAC). Ewor River, La Cressionnière. S17.71728° E168.56946°, alt. 24m. 5-x-2004. Coll. D. A. & R. Craig (larvae (some in Carnoy’s), pupae, reared adults; BPBM, DAC, LCNZ, ROM). Mele Cascade. S17.67778° E168.25473°. alt. 65m. 6.x.2004. Coll. D. & R. Craig. (larvae, pupae, reared adults; DAC).

Etymology

Named for the dorsolateral abdominal tubercles on the larva.

Distribution

VANUATU: Efate.

Comments

Problems associated with the work of Grenier & Rageau (1961) on Efate material were discussed earlier. *Simulium tuberculum* is, in great part, that described by these authors as *S. jolyi*, Efate. Although *S. johnfrumi* is very similar to *S. tuberculum*, it differs markedly by lacking lateral head spots in the larva and possessing coarser dorsal thoracic granules in the pupa. The highly variable pupal gill-filament branching patterns might indicate that *S. tuberculum* is a complex of species.

Ontogenetically, the four pairs of dorsolateral tubercles on abdominal segments II–V are derived. Earlier instars lack them and they develop from approximately the 5th instar onwards. This applies to all the *tuberculum* species subgroup larvae.

Many streams in Efate flow over raised fossilized coral and the water is hard (Table 1), with calcium deposits or travertine (tufa) (Hynes 1970) common. Both the Mele (or Klehm) Cascade and the Ewor River at La Cressionnière have such (Figs. 23g, 24c). Larvae could be taken in astronomical numbers from travertine surfaces and vegetation in fast flow. Pupae were mainly taken from trailing vegetation, with the cocoon normally encrusted with travertine (e.g., Fig. 7b). At La Cressionnière, large collections by DAC, June, 1981, were entirely of *S. tuberculum*; however, in January, 1985, B. S. Batson collected a few *S. steatopygium* larvae in an otherwise monospecific population of *S. tuberculum*. Rageau's material from the Klehm (sic) River (or Mele Cascade) in May/June 1958 was almost entirely *S. tuberculum*. Again, in 2004, larvae from La Cressionnière were solely *S. tuberculum*, suggesting seasonal differences in species as well as probable habitat preferences.

***steatopygium* species group**

Diagnosis

Females: genital fork stem long and thin; medial edges of hypogynial valves more-or-less parallel. Pupae: cocoon more shoe-shaped, generally not flared laterally on basal edges Larvae: anterior apotome normally pale to lightly pigmented; hypostomal hairs more than 10; posterior abdomen more-or-less steatopygous; paired dorsolateral tubercles absent; posterior circlet directed more posteriorly, more than 5,000 hooks.

Constituents: *S. anatolicum, S. jolyi, S. laciniatum, S. paradisium, S. steatopygium, S. subparadisium, S. supercilium, S. undulatum, S. adsonense, S. spiroi.*

***Simulium* (*Hebridosimulium*) *anatolicum* Craig**
(Figs. 5e, 8e, 9f).

S. (*Hebridosimulium*) *anatolicum* Craig 1987: 382. Crosskey & Howard (2004: 29)

Type

Holotype. Female: pinned; reared, with pupal cocoon and exuviae as subsidiary material. Label data – "Holotype, *Simulium* (*H.*) *anatolicum* Craig, det. D.A. Craig 1986, Tahiti, Mahaena, Mahape R., 17° 34' 00" S. 149° 20' 33" W. alt. 700m. 14.vi.1980, D.A. & R.E.G. Craig. Stat. #6." (MNHP). Head, genitalia and pupal exuviae in vial on pin. Left gill of pupa as slide mount, same data as adult (MNHP).

Diagnosis

Large species. Adult female: yellowish; mandibles small; veins R_1 and Sc lacking hair; hypogynial valves with apical membranous region not extended. Pupa: sternite V hooks, close-set. Cocoon: anteroventral edge with small fenestrae.

Redescription

Adult female (Holotype). Body: generally yellowish-brown, total length 2.5 mm. Head: grayish-brown, width 0.98 mm, depth 0.69 mm; frons bulging ventrally over sunken antennal bases, densely covered with silver scale-like hairs, frons-head ratio 1:6.1. Eyes: interocular distance 0.16 mm; yellowish-gray; frontal angle, 115 degrees; ommatidia 0.014 mm in diameter, ca. 34 and 45, respectively, across and down at mid-eye. Clypeus: 0.22 mm wide; concolourous with ventral region of frons, slightly longer than wide, densely covered with silver hairs medially; lateral hairs dark, extended beyond bases of maxillary palpus. Postocciput: densely covered with silver hairs extended to eye margin, scattered long black hairs extended over posterior margin of eye. Antenna: length 0.63 mm; flagellomeres and basal articles yellowish. Mouthparts: 0.5 length of head depth; mandibles with ca. 30 very fine teeth; lacinia with ca. 25 pronounced teeth; maxillary palpus (distal articles absent from specimen) with basal articles flattened and densely covered with black hairs; sensory vesicle of third article elongated, occupying 0.5 width of article, opening of vesicle 0.66 width of vesicle. Thorax: rich brown; length 1.4 mm, width 1.1 mm; postpronotum and contiguous area of scutum creamy, remainder of scutum uniformly brown, moderate vestiture of silver hair, in some views 3 darker vittae; scutellum yellowish, with sparse black and golden hairs; postnotum brown medially and posteriorly, yellow laterally; pleural membrane with distinct pale yellow flattened hairs, as for *S. laciniatum* (e.g., Fig. 4b). Wing: length 2.9 mm, maximum width 1.3 mm; veins pale yellow, hairs black. Legs: coxae, femora, and tibiae yellow, distal portion of tibiae brown; fore basitarsus 6 times longer than wide, brown anteriorly; hind basitarsus parallel sided, 7 times longer than wide; calcipala enormously extended to 0.66 times length of 2nd tarsomere. Abdomen: overall black with dense dark scales anteriorly, pale scales

posteriorly on each segment; basal fringe of shiny dark golden hairs extended to 2nd abdominal segment; tergites III–VII lighter in colour than others; sternite VII distinct, narrower anteriorly; pleural regions with dense silver scales. Genitalia (Fig. 5e): sternite VIII not deeply indented, broader anteriorly, dark brown; hypogynial valves lightly pigmented, sparse vestiture, medial edges slightly concave, not divergent, rounded apically, membranous, but not extended; genital fork with stem narrow, posterolateral arms pigmented, with anteriorly directed apodeme on lateral arm large and cone-shaped; anal lobe rounded with marked anterolateral apodeme, median depression not developed; cercus ovoid; spermatheca (destroyed during preparation for illustration): dark brown (probably reticulated).

Adult male: Unknown.

Pupa (based on exuviae). Body length. 3.6 mm. Gill (Fig. 9f): 8 filaments, maximum length 1.4 mm, petioles moderately elongate, branching pattern (2+1)+2+2+1, dorsal filaments subequal in length, markedly shorter than ventral filaments, evenly tapered, annulations fine. Thorax: dorsal cuticle with dense rounded granules (Fig. 8e), those more lateral and posterior, pointed and hooked. Cocoon: shoe shaped, 4.6 mm long, 1.6 mm wide, basal edges not flared, anteroventral edge rough, with small fenestrae.

Distribution

POLYNESIA. Tahiti.

Comments

The pupa from which the adult was reared came from grass trailing in a small, rapidly flowing, open stream. Velocity was ca. 80cm/s and temperature 29°C. Larvae of *Simulium tahitiense* and *S. lotii* were taken from the same locality (Craig 1987).

This single specimen from a subgenus unexpected in Tahiti, was initially thought by Craig (1987) to be a contaminant from collections made either in Fiji or Vanuatu. However, *Simulium anatolicum*, while very similar to *S. jolyi* and *S. laciniatum*, shows differences in the wings and genitalia and is considered here a valid species. The pupa of *S. anatolicum* has eight filaments, indicating that it is more closely related to the Fijian *S. laciniatum.* No new material has ever been found in Tahiti despite extensive searching (Craig *et al.* 2001), so *S. anatolicum* remains enigmatic.

***Simulium* (*Hebridosimulium*) *jolyi* Roubaud.**
(Figs. 5f, 9g, 13f, 16f, 18f, 20f)

Simulium jolyi: Roubaud 1906: 142
S. (*Hebridosimulium*) *jolyi*: Crosskey (1967: 27); Crosskey (1974: 150); Crosskey & Howard (2004: 29) in part not Roubaud 1906.

Types

Holotype. Adult: female on standard pin (dried from alcohol and glycerine). Label data – "TYPE (red, printed), Museum-Paris. Nouv.-Hébrides. Dr. Joly 1903". Condition excellent. Left hind tarsus missing. **Paratypes**. Adults: four females double pinned (dried from alcohol). Three with label data – "Museum-Paris. Nouv.-Hébrides. Dr. Joly 1903", (two re-pinned with cleared, stained genitalia in glycerin vials on the pin), one with label data- "Museum Paris. Nouv.-Hébrides. Ile Mallicolo. Port Sandwich. Dr. Joly 1903", "Museum Paris (printed). N^{elles} Hébrides. Port Sandwich, Dr. Joly 1903. Simulium jolyi Roub. Avril 1903 (pencil)".

Diagnosis

Female: lighter in colour than *S. laciniatum* and *S lucyae*; genital fork stem long and thin, hypogynial valves flexed laterally, spermatheca large and darkly pigmented. Pupa: 10 gill filaments, petioles moderately elongate, filament branching pattern ((2+2)+2)+2+1+1, thoracic cuticle with sparse granules; anterior collar of cocoon well developed. Larva: median hypostomal tooth extended beyond lateral teeth; posterior abdomen steatopygous; posterior circlet of ca. 7,200 hooks.

Description

Adult female (based on type material). Body: head and abdomen very dark brown, thorax light brown; length 2.0–3.6 mm. Head: width 0.71–0.93 mm; depth 0.47–0.67 mm; postocciput very dark brown, vestiture of sparse, silvery, small hairs; frons lighter; frons-head ratio (narrowest width of frons: greatest width of head) 1.0:4.0. Eye: interocular distance 0.2 mm; ommatidia 0.019 mm in diameter; 45 rows across and 42 down at mid-eye. Clypeus: 0.25 mm wide; concolourous with frons; vestiture of dense black and pale hairs. Antenna: length 0.46–0.54 mm; flagellomeres pale yellow; scape, pedicel, and first flagellomere slightly darker than remainder. Mouthparts: 0.40 length of head depth; mandible well developed with 15 inner teeth decreased in size proximally; lacinia with 10 inner teeth and 16 outer teeth; maxillary palpus evenly dark brown**,** proportional length of 3rd, 4th, and 5th articles 1.0:0.8:1.4; sensory vesicle spherical, ca. 0.3 times width of 3rd article, opening 0.8 times width of vesicle. Thorax: length 0.99–1.22 mm; width 0.85–0.96 mm; postpronotal lobes concolourous with scutum (Malekula); scutum evenly medium brown, vittae not distinct, vestiture of sparse, very fine pale hairs; scutellum pale, vestiture of stiff long black hairs and pale hairs laterally, apical angle 90°, very sparse black hairs; postnotum concolourous with scutum; pleural membrane pale and with very small hairs. Wing: length 1.7–2.8 mm; maximum width 0.96–1.2 mm. Legs: fore leg, coxa, trochanter, and femur dark brown, basal tibia yellow, remainder dark; mid leg, coxa, trochanter, and basal femur yellow, distal femur black, basal tibia yellow, remainder black; hind leg as for mid leg except tarsus yellow with calcipala and remainder black; some specimens with legs darker overall. Abdomen: overall blackish brown; basal scale brownish black, with

fringe of long pale hairs; vestiture of evenly distributed short dark hairs. Genitalia (Figs 5f): sternite VIII deeply indented, broader anteriorly, median region pale; hypogynial valves lightly pigmented with sparse vestiture; median edges slightly concave, diverged, more so posteriorly, apical membranous extension broadly rounded and insubstantial, directed medially; genital fork stem narrow, lateral arms lightly pigmented, anteriorly directed apodeme well developed and rounded; anal lobes with anterolateral apodeme and anteromedian concavity not markedly developed; cercus not markedly developed.

Adult male. Unknown.

Pupa (based on pharate specimens). Gill (Figs. 9g): maximum length 1.4–1.5 mm; petioles moderately elongate, branching pattern variable, e.g., ((2+2)+2)+2+2 or ((2+2)+2)+2+1+1; dorsal filaments shorter, but not markedly more so than others, fine, similar in thickness; light grey.

Larva (based on numerous last-instar larvae (previously dried) and a few fresher penultimate instars). Body (not illustrated): total length 5.5–6.7 mm; probable females mottled dark grey, with paler intersegmental regions, probable males pale yellow. Head (Fig. 13f): evenly medium brown, some evenly pale yellow; width 0.58–0.78 mm; length 0.74–1.0 mm; lateral margins of head subparallel to slightly convex; frontoclypeal apotome pale anteriorly, darker posteriorly; ecdysial lines straight, diverged posteriorly, maximum width at posterior; anteromedian head spots slightly positive to give Eiffel Tower configuration**.** Antenna: total length 0.49 mm; distal article 0.28 times as long as basal articles, 0.5 length of distal article extended beyond labral fan stalk; evenly very pale yellowish brown. Labral fan: stalk markedly clear, neither posterobasal notch nor anterior palatal bar markedly developed; 40–42 fine rays, 0.75–0.81 mm in length, 10–14 rays less substantial, 2 or 3 very fine; microtrichia markedly fine and elongate, 2 time longer than ray width, indistinct pattern of 4 or 5 small microtrichia between those longer. Postgenal cleft (Fig. 16f): deeply arrowhead-shaped, slightly concave edges; 1.5 times as long as maximum width. Postgenal bridge: 0.4 times as long as cleft depth; genae more or less evenly lightly pigmented, posterolateral elongated muscle scars neutral to negative. Hypostoma (Fig. 18f): overall cone-shaped; ratio 5.0; median tooth markedly prominent; adjacent sublateral teeth larger than others and elevated on median tooth base, other sublateral teeth depressed, lateral teeth sharp, slightly scalloped medially and directed laterally; paralateral teeth very poorly developed, essentially absent, 3 or 4 very small irregular lateral serrations; 11 or 12 substantial hypostomal setae per side. Mandible (Fig. 20f): preapical and subapical teeth well developed; apical tooth prominent; 5 or 6 clumped spinous teeth, spinous teeth gap absent; serration and sensillum with distinct concave sides and unusual domed anterior base; blade region evenly convex. Abdomen: thorax and anterior abdomen subequal in diameter, steatopygous posteriorly but not markedly so; dorsal tubercles absent. Anal sclerite: anterodorsal arms subequal in length to posterolateral arms, splayed at apices and paler; medial strut extended; posterolateral arms tapered evenly to 0.4 times distance around circlet of hooks. Posterior circlet: apparently

directed more posteriorly; 206–210 rows of hooks; 33–37 hooks per row (total ca. 7,200).

Additional material examined

Malekula. Nr. Port Stanley, alt. 10 & 200 ft. 1–4.x.1971. Coll. J. Smart (2 tubes larvae, pupae in alcohol — previously dried; BM). Pankumu River, S16.27629º E 167.63687º, alt. 15m. 2.ix.2004. Coll. D. A. & R. Craig (penultimate instar larvae; DAC).

Distribution

VANUATU: Malekula.

Comments

As noted above, Roubaud (1906) did not designate a Holotype. The specimen with the "TYPE" label is, however, accepted here as such.

Assigning material to *S. jolyi* has been difficult. Although the five female types are in good physical shape, albeit over 100 years old, the colours are muted in tone, in large part probably because the specimens were originally in an alcohol-glycerine mixture. Further, genitalic and other characters of female *Hebridosimulium* are conservative and of not great use in diagnosing species. Adult material from Malekula, mainly collected by Cheesman in the 1930s and with better colour preservation is not placed in *S. jolyi*, because recent material of immatures from Malekula shows at least three species of *Hebridosimulium* on that island, with no clear indication of which is *S. jolyi*. Two of these species are designated as *S. pankumuense* and *S. spiroi* (see later), both larvae of which are clearly specialized for the hydraulic conditions of large rivers and cascades. The validity of these two species were subsequently confirmed by mitochondrial CO1 DNA analysis (A. Cywinska, unpublished data). A third entity is of earlier collected larvae and pupae taken by the Royal Society-Percy Sladen Expedition to Vanuatu in 1971 (Corner and Lee 1975) from streams near Port Stanley, east central Malekula, and deposited in the BM. That material had been allowed to dry and is in no condition for DNA analysis and is barely useable for morphological examination. Further, no new material of any stage of *S. jolyi* has been taken from the type locality, Port Sandwich, Malekula, where maps show two small streams flowing into the harbour. An assumption is made here that *S. jolyi* larvae inhabit such streams. Accordingly, the 1971 immatures taken by the Royal Society are assigned to *S. jolyi*. A small number of immature larvae from the Pankumu River, Malekula, that lack dorsal tubercles are also assigned to *S. jolyi*. This is an unsatisfactory situation that will require further detailed collection of material from Malekula.

***Simulium* (*Hebridosimulium*) *laciniatum* Edwards**
(Figs. 1b, 4b, 5g, 6c, 9h, 11f, 13g, 15b, 16g, 18g, 20g)

Simulium laciniatum: Edwards 1924:572
Simulium jolyi: Edwards (1932:103) not Roubaud 1906
Hebridosimulium jolyi: Grenier & Rageau (1961: 96) not Roubaud 1906
Simulium (*Hebridosimulium*) *jolyi*: Crosskey (1967: 30) in part not Roubaud 1906
Simulium (*Hebridosimulium*) *laciniatum*: Dumbleton (1973: 453) revalidation
Simulium (*Hebridosimulium*) *jolyi laciniatum*: Crosskey (1974: 150)
Simulium (*Hebridosimulium*) *laciniatum*: Craig (1987: 383); Crosskey (1987: 451); Crosskey (1989: 223); Crosskey & Howard (2004: 29)

Types

Holotype. Adult. Pinned female. Label data – "W Greenwood/ Mt Evans/ Lautoka, Fiji/ 2500 ft. 11.5.19." (BM). **Paratype**. Adult. Pinned female. Label data – "W Greenwood/ Mt Evans. Fiji/ 18.6.1922" (BM).

Diagnosis

Large species. Adults: black; pleural membrane with distinct yellow hairs; legs markedly bicolourous. Pupa: 8 gill filaments, shorter and thicker than in other species; branching pattern (2+1)+2+2+1. Larva: hypostomal teeth poorly developed; postgenal cleft with marked anterior extension; posterior abdomen steatopygous; dorsal tubercles absent.

Redescription

Adult female (based on numerous topotypical specimens in alcohol). Body: head blackish brown, thorax dark brown, abdomen blackish brown; total length 2.6–3.2 mm. Head: width 0.94–1.0 mm; depth 0.58–0.64 mm; postocciput black, vestiture of dense, black hairs; frons thickly golden haired and pruinose, slightly protruded; frons-head ratio (narrowest width of frons: greatest width of head) 1.0:5.8. Eye: interocular distance 0.17 mm; ommatidia 0.020 mm in diameter; ca 40 rows across and down at mid-eye. Clypeus: 0.21–0.28 mm wide; concolourous with frons; vestiture of dense black and pale hairs, less so in specimens from Taveuni. Antenna: length 0.51–0.61 mm; flagellomeres grayish yellow; slightly darker basally and apically, scape and pedicel pale yellow. Mouthparts: length 0.3 times head depth; mandible with 30–35 markedly fine inner teeth; lacinia with 15 inner teeth and 10 outer teeth; maxillary palpus with all articles evenly dark brown, proportional length of 3rd, 4th, and 5th articles 1.0:0.9:1.4; sensory vesicle markedly elongate, ca. 0.3 times width of 3rd article, opening 0.8 times as wide as vesicle. Thorax: length 1.3–1.5 mm; width 1.0–1.2 mm; postpronotal lobes markedly paler than scutum; scutum evenly medium brown in dry specimens, but 2 lateral vittae in alcohol specimens, vestiture of dense, very fine pale hairs, longer dark hairs posteriorly; more evenly coloured and less hairy in Taveuni specimens; scutellum more or less concolourous with scutum, vestiture of long black hairs and pale hairs laterally, apical angle 125°; postnotum concolourous with scutum; pleuron evenly dark brown; pleural membrane slightly paler and with distinct yellow hairs (Fig. 4b). Wing: length 2.7–2.9 mm; width 1.2 –1.4 mm.

Legs: coxae light brown; trochanters paler; fore leg femur light brown, remainder of leg black; mid leg femur darker brown with dense black vestiture, remainder of leg as for fore leg; hind leg femur as for mid leg, tibia pale basally, tarsus pale except for calcipala, tarsomere black. Abdomen: overall black; vestiture of dense silver hairs, long laterally, with few black hairs; basal scale black with golden hairs; hairs dark and sparser in specimens from Taveuni. Genitalia (Fig. 5g): median region of sternite VIII moderately depressed and pale medially; hypogynial valves with vestiture of sparse short hairs; median edges concave, short, membranous apical extension cone-shaped and posteriorly directed; genital fork stem narrow, lateral arms with small clear region, anteriorly directed apodeme cone-shaped; anal lobes rounded with few longer hairs posteriorly, anterior anterolateral apodeme not well developed, anteromedian concavity distinct with numerous hairs; cercus broad; spermatheca ovoid, reticulate pattern, moderately pigmented.

Adult male (based on numerous topotypical specimens in alcohol). Body: overall dark brown to black; total length 2.7–3.5 mm. Head (Fig. 1b): width 0.86–1.2 mm; depth 0.71–0.82 mm. Eyes: upper ommatidia dark orange, large, 0.057 mm in diameter, ca. 13 across and 16 down; lower ommatidia brown, 0.019 mm in diameter, ca. 26 across and 35 down. Clypeus: dark brown, pruinose 0.17 times as wide as head; vestiture of medium and short hairs laterally. Antenna: total length 0.66–0.70 mm; flagellomeres light yellow, scape, pedicel, and base of first flagellomere slightly darker than remainder; first flagellomere slightly longer than remainder. Mouthparts: short, length 0.2 times head depth; mandibles insubstantial, finely tapered with apical hairs; lacinia broad basally, finely tapered apically with terminal hairs, some tooth-like; palpus dark, 0.58 mm long, proportional lengths of 3rd, 4th, and 5th articles 1.0:1.4:1.6, 3rd article distinctly hairy, sensory vesicle barrel shaped, occupying 0.33 times width of article, opening 0.33 times width of vesicle. Thorax: length 1.2–1.4 mm; width 0.8–1.1 mm; broadest anteriorly; postpronotal lobes and scutum evenly medium brown; vestiture of short pale hairs often rubbed clear; scutellum lighter than scutum, apical angle distinctly obtuse; vestiture of markedly long stiff black hairs laterally, interspersed with paler hairs; postnotum concolourous with scutum; pleuron concolourous with scutum. Wing: 2.4–2.6 mm in length, 1.3–1.5 mm at maximum width. Legs: markedly bicolourous, tarsi and tibial apices dark brownish black, remainder yellow or reddish yellow; pretarsal claws with ca. 25 grappling hooks dorsally. Abdomen: anteriorly yellowish, remainder brownish black, vestiture of dense fine yellow hairs, markedly longer laterally; basal scale with markedly long, pale yellowish hairs. Genitalia (Fig. 6c): gonocoxa 1.3 times longer than basal width, vestiture of numerous substantial hairs, anterolateral apodeme well developed; gonostyle approximately 2.5 times longer than basal width, subequal in length to gonocoxa, distinct mediobasal strengthening ridge; ventral plate small, sloped laterally, proximal arms distinctly curved medially and tapered; median keel slightly angulate apically and laterally, stem narrow, vestiture of markedly small, evenly spaced hairs; parameral spines as for other species; dorsal sclerite broadly rounded apically, less V-shaped than other

species; median sclerite short, slightly longer than apical width. Cerci: distinct.

Pupa (based on numerous topotypical specimens in alcohol). Body length: 2.8–3.8 mm. Gill (Fig. 9h): maximum length 1.28 mm, 8 filaments occasionally 9th as stump, evenly thick, light grey; petioles short, branching pattern (2+1)+2+1+2. Head and thorax with evenly distributed sparse, dark brown rounded granules. Cocoon: markedly boot shaped, anterior collar well raised above substrate, occasionally lower, opening equal to, or slightly narrower than, cocoon base, with marked edge, not flared laterally.

Larva (based on numerous topotypical mature last-instar larvae). Body (Fig. 11f): total length 6.3–7.9 mm; female evenly mottled gray, male yellowish-gray with paler intersegmental regions. Head (Fig. 13g): female medium to dark brown posteriorly extended anteriorly to apotome, males with posterior pigmentation lighter and apotome pale; width 0.62–0.71 mm; length 0.79–0.96 mm; distance between antennal bases 0.33–0.43 mm; lateral margins of head subparallel; ecdysial lines straight, diverged strongly posteriorly; head spots not distinct, anteromedial spots slightly positive, posteromedial and anteromedial spots similarly, but surrounded with pale aureole, posterior head spots negative; anterior genae pale, darkly pigmented posteriorly (Fig. 15b); posterior edge of apotome not emarginated, postocciput not extended between cervical sclerites and apotome. Antenna: evenly pale; total length 0.58 mm; distal article 0.24 times as long as basal articles, extended well beyond labral fan stalk**.** Labral fan: stalk moderately pigmented, anterior palatal bar moderately well developed; 45–50 fine rays, 0.74 mm in length, 8–10 rays less substantial; microtrichia markedly fine and elongate, 2 time longer than ray width, pattern distinct, with 6 or 7 shorter microtrichia between those longer. Postgenal cleft (Fig. 16g): narrowly V-shaped, edges straight. Postgenal bridge: 0.3 times as long as cleft depth; genae evenly pigmented light brown, posterolateral elongated muscle spots positive. Hypostoma (Fig. 18g): overall broadly cone-shaped; ratio 6.6; median tooth and lateral teeth poorly developed, latter teeth broad and subequal in length to median tooth; sublateral teeth very small; paralateral teeth and lateral serrations essentially absent; 9–11 very substantial hypostomal setae per side (12 or 13 in Kadavu larvae). Mandible (Fig. 20g): all apical teeth well developed; 3 or 4 substantial spinous teeth, gap small but distinct; serration and sensillum distinctly separated, but not markedly developed. Abdomen: thorax and anterior abdomen subequal in width, expanded gradually posteriorly; moderately steatopygous. Posterior circlet: directed posteriorly; 160–165 rows of hooks; 20–25 hooks per row (total ca. 3,700).

Additional material examined

Kadavu. Solodamu, E178.11° S19.06°, alt. 128m, 25.viii–23.x.2003. Coll. H. Erwin, E. Schlinger, M. Tokota'a (3 females, 1 male; FBA 010408. BPBM). Kadavucoro Village, Wailea Waterfall, S19.03674° E178.37830°, alt. 10m, 27.xi.2004. Coll. D. & R. Craig (larvae, pupae; DAC). Nacomoto Village, Lambasa Waterfall, S19.04535° E178.35305°, alt. 100m, 28.xi.2004. Coll. D. & R. Craig (larvae; DAC). Matava Resort, S19.04507°

E178.39946°, alt. 33 m, 28.xi.2004. Coll. D. & R. Craig. Attempting to bite (2 females; DAC). **Ovalau**. Mt. Vuma, 700', vii.14.38. Coll. E. C. Zimmerman (female; BPBM). Draiba Trail, alt. 600–800 ft. viii.8.38. Coll. E. C. Zimmerman (4 females; BPBM). Lovoni Val. alt. 50–200 m. 27.xii. 69. Coll. N. H. L. Krause (2 females; BPBM). Levuka, alt. 0–200 m. ?.xii.78. Coll. N. H. L. Krause (7 females; BPBM). Levuka, Totonga Creek, alt.70m alt., 17.viii.1980. Coll. D. A. Craig (larvae, pupae, reared adults; DAC). Waitovu Village, stream cascade, S17.66545° E178.82551°, alt. 50–74 m, 2.xii.2004. Coll. D. & R. Craig (larvae, pupae; DAC). Near Rukuruku, Stream junction, S17.65023° E178.76643°, alt. 76m, 2.xii.2004. Coll. D. & R. Craig (larvae, pupae; DAC). **Taveuni.** Waiyevo. 21.vi.1924. Coll. H. S. Evans. (female; BM). Alt. 0–100m, i.1972. Coll. N. H. L. Krause (2 females; BPBM). Caukadrove Prov. Devo Peak Radio Tower. S 16° 51' E 179° 58', alt. 1200m, 10–17.x.2002. Malaise in rain forest. Coll. M. E. Irwin, E. I. Schlinger, M. Tokota'a. (14 females, male (slightly lighter, smaller and less hairy than other males in Fiji); FBA027946. BPBM). Caukadrove Prov. Devo Forest reserve. S16° 50' E179° 59', alt. 800 m, 10–17.x.2002. Malaise in rain forest. Coll. M. E. Irwin, E. I. Schlinger, M. Tokota'a. (adults; FBA 027947. BPBM). Devo Peak Radio Tower, W179.97° S16.85°, alt. 1200m, 2–10.x.2002. Coll. M. E. Irwin, E. I. Schlinger, M. Tokota'a (1 female, missing wings; FBA021367. BPBM). 13–20.x.2002. Coll. M. E. Irwin, E. I. Schlinger, M. Tokota'a (7 females. FBA020047. BPBM). 25.ix–2.x.2002. Coll. M. E. Irwin, E. I. Schlinger, M. Tokota'a (4 females. FBA012575. BPBM). Waitavala Water Slides, S16.79613° W179.99058°, alt. 45m, 17.xi.2004. Coll. D. & R. Craig (larvae, pupae; DAC). Wainibau Falls, S16.86596° W179.90589°, alt. 30m, 18.xi.2004. Coll. D. & R. Craig (larvae; DAC). Small waterfall 30 mins. on track from Lavena. S16.87089° W179.89072°, 18.xi.2004. Coll. D. & R. Craig (larvae; DAC). Above Waitavala Water Slides, S16.79720° W179.99064°, alt. 60m,19.xi.2004. Coll. D. & R. Craig (larvae, pupae; DAC). Devo Peak, Trib. Wairiki Str., S16.81939° W179.99456°, alt. 350m, 20.xi.2004. Coll. D. & R. Craig (larvae, pupae; DAC). **Vanua Levu**. Savusavu, alt. 100m, ?.iii.1978. Coll. N. Krause (female; BPBM). Cascade, 2 km towards Savusavu from Nambalembala, alt. 10m, 21.viii.1980. Coll. D. A. Craig (larvae; DAC). Cross Island Road, 1st cascade, 21.viii.1980, alt. 270m, Coll. D. A. Craig (larvae, pupae; DAC). Near Savusavu, alt. 300m, 15.vii.1980. Coll. T. K. Crosby & P. A. Ryan. Basasega Crk. alt. 100m, 16.vii.1980. Coll. B. Cowey (larvae; DAC). New Waisala Rain Forest Waterfall, Ravini Stream, Trib. of the Narakariwai River. 27 km from Savusavu, S16.65305° E179.22107° (est.), alt. 95–170m, 23.xi.2004. Coll. D. & R. Craig (larvae, pupae; DAC). Savusavu Bay west road, Nakasa Water Fall, S16.67770° E179.19881°, alt. 90m, 25.xi.2004. Coll. D. & R. Craig (larvae, pupae; DAC). **Viti Levu**. Mt. Lautoka, 1.v.1919. Coll. W. Greenwood (female; BM); 10.v.1919. Coll. W. Greenwood (2 females; BM). Korovou, Tailevu, viii.1937. Coll. J. M. Valentine (female; BPBM). Navia Mill, nr Nadarivatu, alt. 2500', ix.17.1938. Coll. E. C. Zimmerman (female; BPBM); alt. 800–900m, 3.iv.1973; alt. 700–800m, 29.iv.1973; Coll. N. H. L. Krause (4 females; BPBM). Nadarivatu, ix.3.1938; alt. 3700', ix.10.1938; alt.

2700', ix.13.1938; viii.31.1938. Coll. E. C. Zimmerman (5 females; BPBM); alt. 300', 7.iii.54. Coll. M. Laird (female; BM); alt. 850m, 8–13.iii.1963. Coll. C. M. Yosimoto (2 females; BPBM); alt. 810m, vi.27.viii.4.1958. Coll. B. Malkin (female; BPBM). Suva, 1955. Coll. H. W. Simmonds (3 females; BM). Nausori Highland, alt. 500–700m, 1.x.70. alt. 500–600m. 9.xi.1971. Coll. N. L. H Krause (8 females; BPBM). Tholo-i-Suva. ?.i.1958. Coll. N. H. L. Krause (female; BPBM); 15.xi.1970. Coll. H. S. & G. S. Robinson (1 female, 2 males; BM), 21.xii.1970, Coll. H. S. & G. S. Robinson (larvae, pupae; BM). Nandala Riv., alt. 2,400', 13.vi.1971. Coll. M. E. & N. H. Hynes (larvae, pupae adults; BM). Monasavu Riv., nr Nadarivatu. ?.ix.1978. Coll. M. A. Rao (larvae, pupae, adult; BM). Nanuku Crk, alt. 700m, 2.vi.1980. Coll. B. Cowey and P. A. Ryan (larvae, biting females; DAC). Tholo-i-Suva, upper stream 14.viii.1980. Coll. D. A. Craig (pupae, adults; DAC); lower stream 15.viii.1980. Coll. D. A. Craig (pupae, adults; DAC); 8.ix.1984, 23.viii.1984. Coll. B. S. Batson (larvae, pupae; DAC). Nasivis R, trib, cascade nr, Waikumbukumba Vill, alt. 20m, 24.viii.1980. Coll. D. A. Craig (larvae, pupae; DAC). Nakorowabama R, trib, 27.5 km from Suva, alt. 40m, 17.viii.1980, Coll. D. A. Craig (larvae, pupae, reared adults; DAC). Kings Highway 0.1 km South, Wailota No. 1, 22.viii.1980. Coll. D. A. Craig (larvae, pupae, reared adults; ANIC, DAC. HT). Nadarivatu, Tumbeindreketi Creek, alt. 633m, 23.viii.1980. Coll. D. A. Craig (larvae, pupae; DAC). Lautoka, Vitonga Crk, alt. 150m, 24.viii.1980. Coll. D. A. Craig (larvae, pupae, reared adults; DAC); 29.vi.1981. 26.xi.1998 Coll. D. A. Craig (larvae, pupae, reared adults; DAC). Lami, alt. 20–200m, ?.iii.1976; alt. 0–200m, ?.ii.1977; alt. 0–100m, ?.iii.1978; alt. 0–200m, ?.ii.1981; alt. 0–200m, ?.iii.1984; Coll. N. H. L. Krause (6 females; BPBM). Monasavu, alt. 81m, 9.x.1980, 24.x.1980. Coll. B. Cowey (larvae; DAC). Nadarivatu, Waikubkukubu creek, "Governor's pool", 7.iii.1981. Coll. M. Goettel (larvae, pupae, adults; DAC). Nadarivatu, Nadala Creek, 8.iii.1981. Coll. M. Goettel (larvae, pupae; DAC). Namosi Rd, 8 km N Queens Highway, alt. 320m. 3–7.xi.1981. Coll. B. H. & W. E. Gagne (8 females; BPBM). Wainimala R. trib, 10.ix.1984. Coll. B. S. Batson (larvae; DAC). Waindina R. 21.viii.1984. Coll. B. S. Batson. (larvae, pupae; DAC). Wainalithi Riv., trib. 6.ix.1984. Coll. B. S. Batson (larvae, pupae; DAC). Waivaka, Waindwa R, trib, 8.ix.1984. Coll. B. S. Batson (larvae; DAC). Naitisiri Prov., Logging Rd, below Mt. Nakobalevu. E178° 25', S 18° 13', alt. 340m. 22.ix.2002. Colls. E. I. Schlinger, Moala (1 female, 1 male; FBA 027948, BPBM). Mt. Nakobalevu, Logging road behind Suva; in rain forest. S18° 3', E 178° 25'. alt. 340m.13.xii.2002. "Biting collector on hand". Coll. E. I. Schlinger (6 females; FBA 027949, BPBM). Navai Village, alt. 700m. 6.vi.2003. "Moss on wet log". Coll. E. I. Schlinger (2 females; FBA 027950, BPBM). Koroyanitu Reserve, S17° 39' E177° 32', alt. 450m. 3.vi.2003, Coll. E. I. Schlinger (16 females; FBA 027951, BPBM). Near Lautoka, Abaca Village, Vereni Creek Waterfall. S17.66866° E177.54200°, alt. 510m, 4.xii.2004. Coll. D. & R. Craig (larvae, pupae; DAC). King's Highway, Uru's Waterfall, Waindaithi River. S17.66879° E177.54954°, alt. 120m, 5.xii.2004. Coll. D. & R. Craig (larvae, pupae; DAC). Coral Coast, Queen's

Highway, Biasevu Village, Savunamatelaya Water Fall, S18.17973° E177.73834°, alt. 88–105m, 6.xii.2004. Coll. D. & R. Craig (larvae, pupae; DAC). Near Lautoka, Abaca Village, Savuione Falls, S17.67429° E177.55430° (est.), alt. ca. 600m, 7.xii.2004. Coll. D. & R. Craig (larvae, pupae; DAC).

Distribution

FIJI: Kadavu, Ovalau, Taveuni, Vanu Levu, Viti Levu.

Comments

The taxonomic history of *S. laciniatum* has been confused ever since the name was proposed by Edwards (1924), in large part because original material from both Fiji and Vanuatu was mainly female adults, the morphological structures of which are highly conserved. It was not until larvae and pupae of the species were available from Fiji that Dumbleton (1973) recalled the name *S. laciniatum* from synonymy with *S. jolyi*. However, even then this action was contended by Crosskey (1974).

A certain degree of inter- or intra-island morphological divergence might be expected among Fijian simuliids given the diversity of running-water habitats and occurrence on five islands, albeit four of these are adjacent to each other. However, there is little evidence of such divergence. In comparison to material from the type locality area of *S. laciniatum*, (Mount Koroyanitu region — old Mount Evans, Lautoka, Viti Levu), adult females from Kadavu Island (the most remote) have a less hairy clypeus than do those from Viti Levu, and their legs are darker, although the colour pattern is the same. There are minor colour differences in adults from other islands, but colour is variable and appears in large part to depend on preservation. Pupae show no differences in gill arrangement (Fig. 9h) or granule pattern on the cuticle. Larvae from Kadavu have markedly more hypostomal setae (13 vs. 8 or 9) than those from elsewhere; however, they exhibit no other obvious differences. On balance we concluded that Fijian simuliids are exclusively *S. laciniatum*. Independent, preliminary COI mitochondrial DNA analysis also shows Fijian simuliids to consist of one species, with complete lack of clustering of variants, for either islands or habitats (A. Cywinska; unpublished data).

Larvae taken from trailing vegetation typically exhibit marked sexually dimorphic colour, i.e., females with evenly dark brown heads and grey bodies, and males with anterior head pale and body yellowish-orange. Larvae taken from rocky surfaces, and often in large numbers, tend not to show the colour patterns as above, but are rather intermediate in colour, i.e., grayish bodies, lighter head. The male: female ratio of all larvae sexed was normal.

Habitat preferences of larvae are rather varied. Localities where conditions appear to be favourable, such as the edges of waterfalls and large rocks with fast flow may yield no larvae or pupae at all. Rather, larvae in such circumstances are found exclusively on trailing roots or leaves. Other localities, however, have the reverse situation, with larvae

exclusively on rock and commonly in large numbers. Some localities with fast flow and hard rock, but with no vegetation, lacked simuliids entirely. At a typical locality on Viti Levu, such as Vitongo Stream, inland from Lautoka at an altitude of 150 m, the velocity was 1.79 cm/s, water temperature 24.5 C, pH 8.5, and conductivity 90 µS. Larvae here were found in small numbers in full sunlight on rock. At Vereni Creek Cascade, altitude 510 m (Fig. 24f), adjacent to Abaca Village (Holotype region), the velocity was 0.7 m/s, water temperature 23.5 C, conductivity 50 µS and pH 8.1. Larvae here were found exclusively on vegetation. Details for other localities are given in Table 1 and other ecological details are dealt with under 'Ecological Considerations'.

It is not clear if these marked differences in habitat preferences are determined by local ecological conditions, such as presence of other insects or petrolithic algae, or is an indication of genetic divergence between populations, but the DNA analysis indicates otherwise (A. Cywinska; unpublished data). Noticeable at the time of collection, however, was that simuliid larvae were not usually associated with other aquatic insects. The aquatic larvae of the pyralid moth *Nymphula*, often present in large numbers on hard substrates, are aggressive. It is not known if this Fijian *Nymphula* preys on simuliid larvae, but Gorayeb & Pinger (1978) reported that larvae of *Simulium rorotaense* (as *S. fulivinotum*) are preyed on by South American *Nymphula*. Net-building caddisfly larvae (*Abacaria fijiana*), mayfly nymphs (*Cloeon*, *Pseudocloeon*), and chironomid larvae also are often abundant on rock habitats and are generally absent from vegetation, so perhaps there is competition for space on hard substrates.

There is one report of *S. laciniatum* larvae living phoreticaly on atyid shrimp in Ovalau (Crosskey 1987). The phoretic behaviour of simuliid larvae is well documented elsewhere (Crosskey 1990).

Simulium laciniatum exhibits marked separation of cohorts. Collections of larvae on all islands normally consisted of a narrow range of instars. At Lambasa Waterfall, Kadavu, astronomical numbers of early instars (3rd or 4th) were found on leaves. Neither empty pupal exuviae nor flying adults were collected, both indicative of a prior generation. Physical data (Table 1) indicate that the stream is not unusual.

Although *S. laciniatum* is known now from five Fijian islands, we expect that it will occur on other high islands such as Gau, Koro, and Rabi, if suitable habitats of fast-flowing water are present.

Simulium laciniatum can be acutely anthropophilic. Crosskey (1974) notes that, although the species has been considered a minor pest for many years, there are examples of it being a vicious biter. Ryan (2000) recounts one such example and gives the Fijian common name for simuliids as "navanava". There is no record of ornithophily by females of *S. laciniatum*, nor for that matter, by any of the other species of *Hebridosimulium*, in agreement with the lack of a basal tooth on the pretarsal claws; a basal tooth typically indicates a history of blood feeding on birds (Adler *et al.* 2004).

***Simulium* (*Hebridosimulium*) *lucyae* Craig. n. sp.**
(Figs. 5h, 6d)

Types

Holotype. Adult: double-pinned female. Label data— "NEW HEBRIDES/ Aneityum I./Agathis Camp/ 1150 ft./19.21.vii.1971", "Holotype (red)". Coll. G. S. Robinson. (BM). Condition excellent. **Paratypes**. Adults: two pinned males; one cleared and in glycerine vial. Label data— as for Holotype, but with "Paratype (yellow)". One female; double pinned. Label data— as for males. Condition excellent. Ten females; label data— "L.E. Cheesman./B.M. 1955-217", "NEW HEBRIDES:/ Aneityum./ Red Crest, 1,200ft./3m. N.E. of Anelgauhat./ i.1955", "Paratype". One cleared and in glycerine vial, two with genitalia in glycerine vials, remainder on original points in water-soluble glue. Condition variable. (BM). One pinned female. Label data— "NEW HEBRIDES:/ Aneityum I:/ Anelgauhat/ 0–200m, XI.1978", "N. H. L. Krause Coll./ BISHOP MUSEUM". Two pinned females; as previously, but with "Acc. #1978. 465". Condition excellent (BPBM).

Diagnosis

Large species. Adults: evenly very dark brown to black. Female: mouthparts substantial, with large mandibles; maxillary palpal sensillum large; scutum markedly broad; genitalia with median region of sternite VII markedly pale, hypogynial valve densely haired, membranous apex pale, narrow, markedly extended dorsomedially. Male: gonocoxa rounded; ventral plate essentially as keel only; dorsal plate shallowly V-shaped; median sclerite stem narrow; cerci distinct.

Description

Adult female (based on numerous pinned specimens). Body: black to very dark brown; total length 2.6–2.9 mm. Head: width 0.90 mm; depth 0.55 mm; postocciput black with sparse vestiture of silvery hairs; frons very dark brown, slightly pruinose; frons-head ratio (narrowest width of frons: greatest width of head) 1.0:4.7. Eye: interocular distance 0.19 mm; ommatidia 0.017 mm in diameter; ca. 34 rows across and 38 down at mid eye. Clypeus: 0.25 mm wide; concolourous with frons; pruinose, vestiture of dense black and pale hairs. Antenna: length 0.66 mm; flagellomeres dark brown; scape and pedicel slightly lighter. Mouthparts: 0.58 length of head depth; mandible distinctly longer than lacinia, well sclerotized with 24 inner teeth; lacinia with 9 inner teeth and 14 outer teeth, robust and larger apically; maxillary palpus evenly dark brown, total length 0.58 mm, proportional length of 3rd, 4th, and 5th articles 1.0:1.0:1.1, sensory vesicle ovoid, 0.6 times width of 3rd article, opening 0.5 times width of vesicle. Thorax: length 1.28 mm; width 1.03 mm; postpronotal lobes slightly paler than scutum; remainder of scutum evenly dark brown to black, vestiture of sparse, short pale hairs; scutellum concolourous with scutum, vestiture of long black hairs, apical angle 110°; postnotum concolourous with scutum; pleural membrane dark brown with sparse, fine pale hairs. Wing: length 2.6–2.7

mm; maximum width 1.2 mm; anterior veins markedly dark. Legs: overall dark brown and black; coxae dark brown; fore leg evenly dark brown except for basal portion of tibia; mid legs, trochanter brownish yellow, remainder dark brown to black; hind leg trochanter brownish yellow, femur darker brown, tarsus with basal region paler, remainder dark brown, tarsus pale yellow, distal region and tarsomeres black. Halter: light brown. Abdomen: overall evenly black; vestiture of moderately dense, long, pale hairs; basal scale dark brown with fringe of pale hairs extended over segment I. Genitalia (Fig. 5h): median portion of sternite VIII triangular, as deep as wide, markedly depressed, posterior region pale; hypogynial valves with medial edges slightly concave and divergent, vestiture of dense microtrichia and substantial short hairs, membranous apex very thin and directed posteriorly; genital fork stem narrow, lateral arms clear distally, anteriorly directed apodeme markedly developed and dome-shaped; anal lobes with anterolateral apodeme broadly developed, anteromedian concavity deep; cercus short; spermatheca darkly pigmented.

Adult male (based on 2 pinned specimens). Body: overall black; large, total length 2.97 mm. Head: width 0.87 mm; depth 0.64 mm. Eyes: upper ommatidia orange, 0.047 mm in diameter, ca. 11 across and 13 down; lower ommatidia dark brown, 0.012 mm in diameter, ca. 25 across and down. Clypeus: black, 0.10 times as wide as head; vestiture of sparse substantial black hairs. Antenna: total length 0.57 mm; evenly dark brown. Mouthparts: 0.34 length head depth; mandibles insubstantial, finely tapered with apical hairs; lacinia broad basally, finely tapered apically with terminal hairs; maxillary palpus evenly very dark brown, 0.53 mm long, proportional lengths of 3rd, 4th, and 5th articles 1.0:1.1:1.7, sensory vesicle spherical, occupying 0.5 times width of article, opening 0.3 times width of vesicle. Thorax: length 0.89 mm; width 0.93 mm; postpronotal lobes and scutum evenly very dark brown; vestiture of small fine pale hairs; scutellum concolourous with scutum, apical angle 100°; vestiture of long black hairs with few pale; postnotum concolourous with scutum, shiny; pleuron and pleural membrane medium brown; pleural membrane with fine hairs, not visible at 50x in alcohol. Wing: 2.6 mm in length, 1.2 mm at maximum width. Halter: light brown. Legs: overall dark brown; fore leg coxa, trochanter, femur, and basal half of tibia medium brown, remainder dark brown/black; mid leg coxa brown, trochanter pale brown, remainder dark brown/black; pretarsal claw with ca. 25 grappling hooks dorsally. Abdomen: concolourous with scutum; anterior vestiture of long pale hairs, markedly hirsute laterally, hairs black posteriorly; basal scale dark, hairs markedly long, fine, pale, extended to beyond 2nd segment. Genitalia (Fig. 6d): gonocoxa rounded, 1.3 times longer than basal width, markedly pigmented, with long black hairs on distal half, anterolateral apodeme small; gonostyle dark, approximately 3.3 times longer than basal width; mediobasal strengthening ridge not developed; ventral plate reduced, angulate laterally, proximal arms substantial with lateral flange, median keel massive with broad connection to plate, flattened apically; dorsal sclerite thin and more angulate apically**;** median sclerite elongate with stem 6 times longer than cross piece width. Cerci:

markedly developed.

Pupa. Unknown.

Larva. Unknown.

Additional material examined

Aneityum. ?.x.1930. Coll. L. E. Cheesman (16 females; BM); on the hills, 500–1000 ft, ?.xi.1954. Coll. L. E. Cheesman (9 females on 3 pins; BM).

Etymology

Named for Lucy Evelyn Cheesman, whose account of severe biting by females of this species, while she was stationed in Aneityum, is a classic story of the horrors of blood-thirsty simuliids (Cheesman 1957a, Craig 2006).

Distribution

VANUATU: Aneityum.

Comments

Simulium lucyae, along with *S. subparadisium* of Santo, have the largest adults of any simuliid species in Vanuatu. Consistent with the reported vicious biting by females, mandibles of *S. lucyae* are markedly developed. The females also differ from those of other species in that the scutum is noticeably broader and flattened. The male is easily diagnosed by the unique characteristics of the genitalia. Although an expectation might be that *S. lucyae* is related to *S. johnfrumi* of nearby Tanna and Erromango, with no larvae or pupae to indicate otherwise, placement of *S. lucyae* in the *steatopygium* species group is based on details of the female genitalia, namely the elongated genital fork stem, enlarged anteriorly directed apodeme, and straightened medial edges of the hypogynial valves. Discovery and characterization of the immature stages of *S. lucyae* will be of biogeographic interest, because Cheesman (1957b) suggested that the southern three islands of Vanuatu, in particular that of Aneityum, are biogeographically distinct from the others.

***Simulium* (*Hebridosimulium*) *paradisium* Craig. n. sp.**
(Figs. 10a, 11g, 13h, 16h, 18h, 20h, 22b)

Types

Holotype. Larva: last instar in alcohol. Label data – "*Simulium* (*Hebridosimulium*) *paradisium*, Vanuatu, Santo, upper cascade, trib. Sarakata River, S15.43224° E167.07600°, alt. 217m. 13.ix.2004. Coll. D. A. & R. Craig. HOLOTYPE. No. 16609" (BPBM). **Paratypes**. Larvae: last instars in alcohol (larvae; BPBM, DAC, LCNZ). Penultimate and earlier instars in alcohol (larvae; BPBM, DAC, ROM). Label data – as for

Holotype, but with “PARATYPE”.

Diagnosis

Pupa: cuticle with numerous granules; gills branched basally, petioles short; filaments thin, finely tapered. Larva. Head: evenly dark brown, head spots negative, appendages dark brown; body markedly pale, posterolateral diagonal grey stripes on sixth segment.

Description

Adult female. Unknown.

Adult male. Unknown.

Pupa (based on pharate material). Gill (Fig. 10a): filaments fine, gradually tapering, petioles short ((2+2) +2 +2 +2); maximum length 1.4–1.8 mm. Thorax: cuticle with numerous distinct granules.

Larva (based on numerous mature last-instar larvae). Body (Fig. 11g): relatively large species; total length 6.4–7.3 mm; colour: no obvious sexual dimorphism, prothorax and mesothorax completely light gray, metathorax very pale yellowish orange, abdominal segments I–III pale medially, light gray laterally, pale ventrally, segments IV & V pale, remainder of abdomen gray dorsally, laterally with 3 distinct grey diagonal bands. Head (Fig. 13h): overall dark brown; anterior apotome markedly pigmented, unusual pale region medial of fan stalk bases, sensilla 5 and 6 bases markedly pale; dorsal head spots negative and markedly distinct; width 0.69–0.73 mm; length 0.73–0.86 mm; distance between antennal bases 0.43–0.44 mm; ecdysial lines irregular, diverging strongly posteriorly, inflexion at maximum width broadly rounded; lateral margins of head subparallel; posterior edge of apotome slightly emarginated, postocciput not extended between cervical sclerites and apotome. Antenna: total length 0.45 mm; distal article 0.30 times as long as basal articles; longer than labral fan stalk, distal article brown, remainder light brown to pale. Labral fan: stalk moderately pigmented, anterior palatal bar noticeable, but not markedly protrusive; 57–60 dark rays, 0.75–0.84 mm in length, medial rays 0.015 mm in width, 10–12 posterolateral rays finer than others; microtrichia well developed, subequal in length to ray width, pattern distinct, with 5–7 shorter microtrichia between those longer. Postgenal cleft (Fig. 16h): V-shaped; 1.2 times longer than maximum width. Postgenal bridge 0.25 time as long as cleft depth; genae evenly dark brown, paler around stemmata; posteroventral elongated muscle scar markedly negative. Hypostoma (Fig. 18h): overall dome-shaped; ratio 4.8; median tooth markedly prominent, lateral teeth smaller but also prominent, scalloped medially, directed laterally, sublateral teeth distinct; paralateral teeth essentially absent, lateral serrations slightly developed; 11 or 12 hypostomal setae per side. Mandible (Fig. 20h): preapical teeth poorly developed, apical tooth and subapical teeth prominent; spinous teeth substantial, gap absent; serration and sensillum prominent, but not markedly developed; blade region smooth and slightly convex. Abdomen: thorax and anterior abdominal segments subequal in width, expanded

gradually to maximum width, markedly steatopygous; posterodorsal tubercles absent. Posterior circlet (Fig. 22b): directed posteriorly; 208–214 rows of hooks, 34–36 hooks per row (total hooks ca. 7,300).

Additional material examined

Penultimate and earlier larvae. Same label data as Types (larvae; DAC).

Etymology

Named for the paradise-like beauty of the type locality.

Distribution

VANUATU: Santo, Millennium Cave area.

Comments

Known so far only from the Millennium Cave area (Sarakata River watershed) on Santo, the larvae of *S. paradisium* are habitat specialists of fast, shallow water. They were taken in moderately large numbers from smooth travertine substrate in fast flow (1.5 m/s), along with low numbers of larvae of *S. steatopygium* and *S. callipygium*. Larvae show steatopygous modification to the abdomen in addition to possessing, by far, the largest number of hooks comprising the posterior circlet of any Vanuatu simuliid — both structural attributes known as adaptations to fast-flowing water (Palmer and Craig 2000, Craig 2003). Larvae of *S. paradisium* notably do not twist the body to place the labral fans into the mainstream flow — again, a known adaptation to thin films of fast water (Crosskey 1990, Craig 1997).

Of all the Vanuatu simuliids, *S. paradisium* has perhaps the most colourful larvae, with multiple colours of the head spots set off against a dark brown background and with a pale body. The spectacular colouration of the larva seems appropriate, given the stunning beauty of its type locality, a true jungle paradise (Fig. 24b).

***Simulium* (*Hebridosimulium*) *steatopygium* Craig n. sp.**
(Figs. 5i, 6e, 7b, 10b, 11h, 12b, 14a, 17a, 19a, 21a,)

Types

Holotype. Adult: double-pinned reared male, dried from alcohol. Label data – "*Simulium* (*Hebridosimulium*) *steatopygium*, VANUATU. Efate, Mele Cascade. S17.67778° E168.25473°, alt. 65m. 6.x.2004. Coll. D. & R. Craig. HOLOTYPE. No. 16610" (BPBM). Right upper eye and anterior margin region damaged. Pupal exuviae and cocoon as subsidiary material. Cocoon covered with travertine deposits. **Paratypes**. Adults: double-pinned reared adults, dried from alcohol. Label data – as for Holotype, but with "PARATYPE" (1 male, 2 females; BPBM). As for above but date "25.vi.1981" (3

males, 6 females; ROM). Colours muted in tone. All pinned Paratypes have pupal exuviae and cocoon (some with travertine material) as subsidiary material on points. Alcohol material: label data – as for Holotype (larvae; BPBM, LCNZ, ROM. larvae, pupae, reared males; DAC).

Diagnosis

Adults: males markedly small; female genital fork stem narrow, hypogynial valves with inner edges straight, anal lobe triangular; male ventral plate keel smaller. Pupa: sparse thoracic granules. Cocoon: smaller and not completely covering female pupa. Larva: head spots and pigmentation forming distinct Eiffel Tower configuration on posteromedial apotome; abdomen markedly steatopygous, dorsolateral tubercles absent.

Description

Adult female (based on numerous reared specimens). Body: head, thorax and abdomen concolourous, very dark brown; total length 2.5–3.6 mm. Head: width 0.8–0.9 mm; depth 0.6–0.7 mm (larger in specimens from Santo); frons and postocciput with vestiture of sparse silvery small hairs; frons-head ratio (narrowest width of frons: greatest width of head) 1.0:3.6. Eye: interocular distance 0.24 mm; ommatidia 0.018 mm in diameter; 45 rows across and 42 down at mid-eye. Clypeus: 0.22–0.25 mm wide; vestiture of dense pale hairs, black ventrally. Antenna: length 0.46–0.54 mm; flagellomeres light brown; scape and pedicel pale. Mouthparts: 0.43 length of head depth; mandible well developed with 18 inner teeth decreased in size proximally; lacinia with 9 inner teeth and 14 outer teeth; maxillary palpus evenly black, proportional length of 3rd, 4th, and 5th articles 1.0:0.6:1.2; sensory vesicle spherical, ca. 0.3 times width of 3rd article, opening 0.8 times width of vesicle. Thorax: length 1.15–1.22 mm; width 0.93–0.96 mm; postpronotal lobes markedly paler than scutum**;** scutum evenly dark brown, vittae absent, vestiture of sparse, very fine golden hairs; scutellum light brown, vestiture of stiff long black and pale hairs laterally, apical angle 120° (Santo); postnotum concolourous with scutum; pleural membrane pale and with sparse long golden hairs. Wing: length 2.3–2.8 mm; maximum width 1.1–1.2 mm. Legs: fore leg, coxa, trochanter, and proximal femur pale, dark brown distally, proximal tibia yellow, remainder of leg black; mid leg, coxa, trochanter, and proximal femur pale, distal femur black, proximal tibia yellow, remainder of leg black; hind leg as for mid leg except coxa, trochanter, and tarsus yellow, with calcipala and remainder of leg black; some specimens with legs darker overall. Abdomen: overall blackish brown; basal scale brownish black, with fringe of pale hairs; vestiture of evenly distributed short dark and golden hairs, dense laterally. Genitalia (Fig. 5i): overall vestiture of coarse black hair; sternite VIII deeply indented, broader anteriorly (Santo), densely pigmented anteriorly, paler posteriorly; hypogynial valves lightly pigmented with sparse vestiture; median edges straight (Efate), slightly concave (Santo), apical membranous extension corrugated (Efate), markedly directed medially and insubstantial

(Santo); genital fork with stem narrow, posterolateral arms lightly pigmented, anteriorly directed apodeme rounded; anal lobes with anterolateral apodeme and anteromedian notch small (Efate) or markedly developed (Santo), posteriorly triangular (Efate), or less so (Santo); cercus elongated.

Adult male (based on 4 reared specimens). Body: length 2.4–2.6 mm. Head: width 0.85–0.92 mm; depth 0.58–0.63 mm. Eyes: upper ommatidia orange, 0.042 mm in diameter, ca. 15 across and 13 down; lower ommatidia dark brown, 0.018 mm in diameter, ca. 24 across and down. Clypeus: brown, paler medially; 0.23 times as wide as head; vestiture of long, fine, pale hairs. Antenna: total length 0.52 mm; all pale yellow. Mouthparts: length 0.38 times head depth; mandibles insubstantial, finely tapered with apical hairs; lacinia broad basally, finely tapered apically with terminal hairs; maxillary palpus dark brown, 0.49 mm long, proportional lengths of 3rd, 4th, and 5th articles 1.0:0.9:1.6, 3rd article darker and markedly hairy, sensory vesicle spherical, occupying 0.33 times width of article, opening 0.25 times width of vesicle. Thorax: length 1.0–1.1 mm; width 0.8 mm; postpronotal lobes and scutum evenly light brown; scutum with 2 barely visible vittae; vestiture of even, small, fine silvery hairs; scutellum pale, apical angle 100°; vestiture of few black hairs laterally, remainder pale; postnotum concolourous with scutum, shiny: pleuron and pleural membrane concolourous with scutum; pleural membrane with hairs, barely visible at 50x magnification. Wing: 2.1–2.2 mm in length, 0.96–1.1 mm at maximum width. Legs: markedly bicolourous, yellow and black; all coxae and trochanters yellow; fore femur light brown, distal region of tibia and all of tarsus black; mid leg as for foreleg; hind leg with femur and tibia pale yellow proximally, black distally, both swollen and flattened, width to length ca. 0.35, tarsomeres black; pretarsal claw with ca. 19 grappling hooks dorsally. Abdomen: dark brown; basal scale well developed and dark, hairs markedly long, fine, pale, extended to beyond 2nd segment; 1st and 2nd segments paler brown, remainder dark brown; vestiture of sparse pale hairs. Genitalia (Fig.6e): gonocoxa 1.3 times longer than basal width, brown, with long black hairs on distal half; gonostyle paler, approximately 3.3 times longer than basal width; ventral plate angulate laterally, proximal arms finely tapered, median keel subequal in length to remainder of plate, flattened apically; dorsal sclerite well developed and broadly V-shaped; median sclerite with stem 1.3 times as long as crosspiece length. Cerci: essentially absent.

Pupa (based on 8 specimens — in alcohol). Body length: 2.3–3.0 mm. Gill (Fig. 10b): maximum length 1.4 mm, filaments fine, light grey; subequal in length except longer ventral filament and usually slightly shorter dorsal filament; branching pattern (2+2)+2+2+2 arising from petioles, usually 0.25 times length of filament, although rather variable; annulations fine. Head and thorax: cuticle light brown; covered with small granules, variable, from almost absent to evenly dispersed. Cocoon (Figs. 7b): distinctly shoe-shaped; opening well defined; in females not completely covering pupa, in males occasionally extended partway along gills; cocoon occasionally flared laterally.

Larva (based on numerous mature last-instar larvae). Body (Fig. 11h): total length, male 6.5–6.7 mm, females 6.6–7.8 mm; overall mottled grey, with paler intersegmental regions, producing striped appearance, metathoracic segment pale orange, evenly mottled gray brown (female) more yellowish (male). Head (Fig. 14a): overall light brown (darker in Efate specimens), and as wide as long; male width 0.68–0.72 mm; length 0.62–0.71 mm, female width 0.71–0.73 mm, length 0.69–0.81mm; lateral margins of head subparallel to slightly convex; apotome evenly light brown, ecdysial lines straight, diverging posteriorly, maximum width well posterior, broadly rounded inflexion; first and second anterolateral head spots positive, anteromedial and posteromedial head spots positive, posterior ones connected by broad band of similar colour to darker pigmentation on the posteromedial edge of the apotome, producing a distinctive Eiffel Tower configuration, first posterolateral spots positive, second posterolateral spots slightly negative to neutral, all spots surrounded by pale triangular nimbus; head lighter and spots more distinct in Santo larvae; genae anterior of stemmata pale, posterior margin of apotome slightly emarginated; postocciput with narrow extension between cervical sclerites and apotome. Antenna: total length 0.4 mm; distal article 0.3 times as long as basal articles and extended beyond labral fan stalk; basal and distal articles pale brown, median article pale. Labral fan: stalk light brown, anterior palatal bar variously developed; 48–50 rays, 0.80 mm in length; 15–19 rays less substantial; ray width, 0.02 mm; microtrichia with no distinctive pattern, subequal in length to ray width. Postgenal cleft (Fig. 17a): broadly V-shaped, slightly concave margins; 1.5 times as deep as wide. Postgenal bridge: 0.5 times as long as cleft depth, paler than genae, which are evenly medium brown; posteroventral elongated lateral muscle scars positive. Hypostoma (Fig. 19a): overall broadly cone-shaped; ratio 4.7; median tooth markedly prominent; lateral scalloped medially, slightly directed laterally; three small sublateral teeth; paralateral teeth poorly developed; 3 or 4 small lateral serrations; 11 or 12 substantial hypostomal setae per side. Mandible (Fig. 21a): all apical teeth well developed; 4 or 5 spinous teeth, gap absent; serration and sensillum distinct, blade region smooth and slightly convex. Abdomen: thorax and anterior abdomen subequal in width, expanded rapidly laterally at segment VI, markedly steatopygous (Fig. 12b); dorsolateral tubercles absent. Posterior circlet: directed posteriorly; 180 rows of hooks; 34–35 hooks per row (total ca. 6,200).

Additional material examined

Santo Apouna Riv., Camp 2, 450', 26–27.viii.1971. Coll. G. S. Robinson (larvae, pupae; BM); Camp 3, 950', 11.ix.1971. Coll. G. S. Robinson (larvae, adults; BM); 9–11.ix.1971. Coll. G. S. Robinson (adults; BM). Vonalolu, Adsone Riv., 20 m alt. 23.vi.1981. Coll. D. A. Craig (larvae, pupae, reared adults; DAC); 19.ii.1985 Coll. B. S. Batson (larvae, dried; DAC). Nr. Sareti Village, Vonalolu Str., trib., Adsone Riv., 22–23.iv.1981, alt. 20m, Coll. D. A. Craig (larvae; BM, BP, ANIC, DAC, NZ, PI). Adsone River, S15.55968° E166.96876°, alt. 59m. 23.vi.1981, 15.ix.2004. Coll. D. A. Craig

(larvae; DAC). Sarakata R, UNELCO Hydrostation, S15.43147° E167.11448°, alt. 25 m, 26.viii. 2004. Coll. D. A. & R. Craig (larvae; DAC). **Efate** Ewor River, La Cressionnière, S17.71728° E168.56946°, alt. 24m. 16.v.1981. Coll. D. A. Craig (larvae; DAC). 23.ii.1985. Coll. B. S. Batson (larvae; DAC). Neslep Riv., 2 km S of Epao Village. 16.vi.1981. Coll. D. A. Craig (larvae, pupae, reared adults; DAC). Mele Cascade, west of Port Vila, S17.67778° E168.25473°. alt. 65m. 17.vi.1981, 25.vi.1981, 6.x.2004. (larvae, pupae, pinned reared adults; BM, BPBM, CNCI, DAC, PI).). ?.xi.1981, L. Swillen, (larvae; BM, CNCI, DAC, NZ, PI). 21–23.ii.1985. Coll. B. S. Batson (larvae; DAC).

Etymology

Named after the markedly expanded posterior abdomen of the larva.

Distribution

VANUATU: Santo, Efate.

Comments

Widely distributed in Santo, *S. steatopygium* is by far the most common and numerous species encountered, although less so in Efate. On the basis of larval head pattern, (*cf.* Figs. 13f, 14a), this species appears closely related to *S jolyi*, from which it differs mainly in the more marked steatopygy of the larval abdomen. Female genitalia show minor differences in form between Santo and Efate. As well, pupae show considerable variation in gill-branching pattern, all possible indications that *S. steatopygium* is a complex of species, in particular the material from Santo.

***Simulium* (*Hebridosimulium*) *subparadisium* Craig. n. sp.**
(Figs. 6f, 7d, 10c, 11i&j, 14b, 17b, 19b, 21b)

Types

Holotype. Larva: last instar in alcohol. Label data – "*S.* (*Hebridosimulium*) *subparadisium*, Vanuatu, Santo, Millennium Cave Stream, S15.45547° E167.07158°, alt. 192 m. 13.ix.2004. Coll. D. & R. Craig. HOLOTYPE. No. 16611" (BPBM). **Paratypes**. Adults: one double-pinned male dried from alcohol; one partially dissected and cleared male in genitalic tube on pin. Label data – as for Holotype, but with "PARATYPE". Both with pupal exuviae and cocoon as subsidiary material (males; BPBM). Larvae and pupae: in alcohol. Label data – as above. (larvae, pupae; DAC. larvae; BPBM, LCNZ, ROM).

Diagnosis

Large species. Larva: female, head, dark brown with pale nimbus surrounding semi-neutral head spots; male head light brown with blackish lateral areas on apotome. Abdomen: female evenly mottled grey; male pale anteriorly, evenly yellow-grey

posteriorly**.** Pupa: cuticle with numerous dark granules; gill filament petioles elongated; filaments finely tapered.

Description

Adult female. Unknown.

Adult male (based on 2 reared individuals). Body: overall rich dark brown; total length 3.4 mm. Head: width 1.0 mm; depth 0.83 mm. Eyes: interocular hairs markedly long and black; upper ommatidia dark orange, large, 0.06 mm in diameter, ca. 14 across and 15 down, decreasing is size towards smaller ommatidia; lower ommatidia brown, darker ventrally, 0.015 mm in diameter, ca. 26 across and 35 down. Clypeus: dark brown, pruinose, 0.24 times as wide as head; vestiture of sparse black hairs. Antenna: total length 0.63 mm; all parts light yellow. Mouthparts: length 0.3 times head depth; mandibles insubstantial, finely tapered with apical hairs; lacinia broad basally, finely tapered apically with terminal hairs; palpus dark, 0.6 mm long, proportional lengths of 3rd, 4th, and 5th articles 1.0:0.8:1.0, sensory vesicle barrel shaped, occupying 0.25 times width of article, opening 0.33 times width of vesicle. Thorax: length 1.2 mm; width 0.9 mm; postpronotal lobes pale; anterior scutum evenly rich brown, darker posteriorly, faint vittae; vestiture of fine pale hairs; anterior scutellum lighter than scutum, concolourous posteriorly, apical angle distinctly obtuse; vestiture of thin pale hairs and markedly long stiff black hairs laterally; postnotum mottled brown; pleuron concolourous with scutum, pleural membrane well haired. Wing: 2.6 mm in length, 1.2 mm at maximum width. Legs: markedly bicolourous, tarsi and tibial apices black, remainder yellow; pretarsal claws with ca. 25 grappling hooks dorsally. Abdomen: anterior segments pale, remainder medium grey, vestiture of dense, fine, pale hairs; basal scale black with markedly long, pale yellowish hairs. Genitalia (Fig. 6f): gonocoxa 1.5 times longer than basal width, basal pigmented band narrow than in other species, vestiture of numerous substantial hairs, anterolateral apodeme not well developed; gonostyle approximately 3.0 times longer than basal width, subequal in length to gonocoxa, mediobasal strengthening ridge not distinct; ventral plate small, sloped laterally, proximal arms distinctly curved medially and evenly tapered; median keel relatively large, in ventral view flattened, markedly angulate in posterior view, stem broad, vestiture of markedly small, evenly spaced hairs; parameral spines as for other species; dorsal sclerite broadly rounded apically, less V-shaped than other species; median sclerite 1.8 times as long as apical width, stem expanded apically, sclerotized irregularly. Cerci: distinct.

Pupa (based on 1 female and 2 males). Body length: female 3.9–4.2mm, male 3.7 mm. Cuticle with numerous dark granules, those anterior rounded, posterior sharply pointed. Gill (Fig. 10c): filaments fine, gradually tapering, dorsal filaments subequal in length, petioles 0.3 time length of filaments; branching pattern ((2+2) +2) +2 +1+1; maximum length 1.4–1.8 mm; annulations fine. Cocoon (Fig. 7d): distinctly shoe shaped, of substantial construction; not splayed laterally at base.

Larva (based on 8 mature last-instar larvae). Body (Fig. 11i, j): total length, female 8.2–8.7 mm, male 7.4–8.3 mm; female, evenly granular light gray, continuous posteroventrally, male prothorax orange-brown, mesothorax pale, metathorax markedly orange coloured, remainder evenly yellowish brown. Head (Fig. 14b): female, width 0.76–0.79 mm; length 0.71–0.81 mm; distance between antennal bases 0.45–0.46 mm; male, width 0.66–0.74 mm; length 0.74–0.83 mm; distance between antennal bases 0.41–0.44 mm; colour: female markedly bicolourous, anterior apotome pale brown, lateral apotome dark brown, medial spots slightly positive, surrounded by pale yellow nimbus, posterior spots negative; male, apotome yellow with lateral dark brown region, medial head spots slightly positive, ecdysial lines irregular, inflexion at maximum width broadly rounded, posterior margin of apotome slightly emarginate; genae dark brown laterally; lateral margins of head slightly convex; postocciput extended finely between cervical sclerites and apotome. Antenna: total length, female 0.46–0.55 mm, male 0.43–0.50 mm; distal article 0.28 times as long as basal articles; longer than labral fan stalk; distal article light brown, remainder pale. Labral fan: stalk lightly pigmented, anterior palatal bar well developed, 47–51 dark rays, 0.78–0.81 mm in length, medial rays 0.018 mm in width, 10–14 posterolateral rays finer than others; microtrichia well developed, subequal in length to ray width, pattern not distinct. Postgenal cleft (Fig. 17b): sharply V-shaped with slightly concave edges; 1.3 times longer than maximum width; postgenal bridge 0.4 time as long as cleft depth, pale; genae pale laterally, medium brown ventrally, posteroventral elongated muscle spots positive. Hypostoma (Fig. 19b): overall broadly cone-shaped; ratio 1:4.7; median tooth markedly prominent, lateral teeth broadly based, sublateral teeth small; paralateral teeth absent, lateral serrations absent; 10 or 11 hypostomal setae per side; supernumerary hairs on hypostomal base substantial. Mandible (Fig. 21b): apical teeth prominent, but not markedly developed; spinous teeth clumped, gap absent; serration and sensillum normally developed; blade region slightly irregular, but straight. Abdomen: thorax decreased in size to abdomen; anterior segments subequal in width, expanded gradually to maximum width, markedly steatopygous; posterodorsal tubercles absent. Posterior circlet: directed posteriorly; 208–210 rows of hooks, 33–36 hooks per row (total hooks ca. 7,100).

Additional material examined

Santo, Millennium Cave Stream, S15.45547° E167.07158°, alt. 192 m. 13.ix.2004. Coll. D. & R. Craig (larvae; DAC, ROM). Tafwakar Str. trib Sarakata River, S 15.43839° E167.07425°, alt. 126m. 13.ix.2004. Coll. D. A. & R. Craig (larvae; DAC).

Etymology

Named for its apparent close relationship to *S. paradisium*.

Distribution

VANUATU: Santo, Millennium Cave region.

Comments

Known, so far, only from the Millennium Cave region (Sarakata River watershed) on Santo, the larvae of *S. subparadisium* are similar to those of *S. paradisium* in that they are habitat specialists of fast water (Fig. 24e). Larvae were taken in moderately large numbers from smooth basalt substrate in fast flow (1.7 m/s), along with those of *S. steatopygium* and *S. callipygium*. Larvae show marked steatopygy of the abdomen, in addition to possessing, along with larvae of *S. paradisium*, a large number of hooks on the posterior circlet. Both of these attributes are adaptations to fast-flowing water (Craig 2003, Palmer and Craig 2000). Similar to larvae of *S. paradisium*, those of *S. subparadisium* possess a large number of substantial labral fan rays and are highly colourful, albeit less so. It is not known if larvae of *S. subparadisium* lack the ability to twist their bodies, as is characteristic of *S. paradisium*.

***Simulium* (*Hebridosimulium*) *supercilium* Craig. n. sp.**
(Figs. 10d, 11k, 14c, 15c, 17c, 19c, 21c)

Types

Holotype. Larva: last-instar male, in alcohol. Label data – "*Simulium* (*Hebridosimulium*) *supercilium*. Vanuatu, Pentecost, Warbot River. S15.96069° E168.19755°, alt. 25m. 22.ix.2004. Coll. D. A. & R. Craig. HOLOTYPE. No. 16612" (BPBM). **Paratypes**. Larva and pupae: in alcohol. Label data – as for Holotype, but with "PARATYPE". (BPBM, DAC, LCNZ, ROM).

Diagnosis

Smaller species. Pupa: thoracic cuticle with sparse, coarse granules. Cocoon: less shoe shaped than other species; anterior collar not raised markedly above substrate; base not flared laterally. Larva: posterior abdomen slightly steatopygous; dorsolateral tubercles absent; head-spot pattern not markedly distinct, males with Eiffel Tower spot pattern, females darker and pattern ill defined; eyebrow stripe dorsal of ocelli marked, ending in distinct small dark head spot; postgenal bridge markedly small, postgenal cleft deep; fewer sublateral setae than in other species of *Hebridosimulium*.

Description

Adult female. Unknown.

Adult male. Unknown.

Pupa (based on 2 mature specimens). Length 2.9–3.3 mm. Thoracic granules normal. Cocoon covering pupa, base not flared laterally, shoe-shaped. Gills: branching pattern (2+2)+2+2+1+1, maximum length 1.3 mm, petioles short, but variable. (Fig. 10d); annulations fine.

Larva (based on 5 mature last-instar larvae). Body (Fig. 11k): total length, male

6.1–6.2 mm; female 6.8–7.2mm; females evenly mottled grey-brown, males yellowish grey-brown; expanded gradually posteriorly, very slightly steatopygous, (essentially callipygous in earlier instars). Head (Fig. 14c): noticeably longer than wide; female overall medium brown, darker posteriorly, head spots lightly positive, anteromedial spots with paler nimbus, posteromedial spots with darker aureole, male head lighter in colour with head spots forming Eiffel Tower configuration; both sexes with distinct black mark anterior of eyebrow stripe, dorsal of pale ocellar area; head spot ventral of ocelli positive, as are posterolateral spots, surrounded by pale nimbus, producing distinct pattern (lateral head spots not well developed in earlier instars); male head width 0.58–0.63 mm; length 0.74 mm; distance between antennal bases 0.33 mm; female width 0.67–0.73 mm; length 0.75–0.79 mm; distance between antennal bases 0.37 mm; lateral margins of head subparallel; frontoclypeal apotome lateral margins straight, diverging evenly posteriorly, maximum width well posterior; dorsal head spots not distinct, but occasionally in Eiffel Tower configuration; small, distinct black spot anterodorsal of stemmata (Fig. 15c); distinct cervical sclerites separated from apotome by extension of postocciput, posterior edge of apotome not eroded. Antenna: distal and medial articles brown, remainder pale; total length 0.42 mm; distal article 0.24 times as long as basal articles, subequal in length to labral fan stalk. Labral fan: anterior palatal bar well developed; stalk lightly pigmented, 37–43 fine rays, 1.4 mm in length, 8 rays less substantial; microtrichia fine, subequal in length to ray width, pattern indistinct, with 3 or 4 slightly shorter microtrichia between longer ones. Postgenal cleft (Fig. 17c): deeply V-shaped. Postgenal bridge: yellow; 0.2 times as long as cleft depth; genae evenly pigmented light brown, lateral elongate muscle spots negative. Hypostoma (Fig. 19c): overall broadly cone-shaped; ratio 5.3; teeth array smaller and slightly protruding anteriorly; median and lateral teeth not markedly developed, latter smaller than former; sublateral teeth small; paralateral teeth not obvious; lateral serrations poorly developed; 8 or 9 hypostomal setae per side. Mandible (Fig. 21c: preapical and subapical teeth not well developed; spinous teeth not markedly developed, space absent; serration and sensillum well developed, blade region smooth and convex. Abdomen: expanded gradually to maximum width, dorsolateral tubercles absent, slightly steatopygous posteroventrally**.** Posterior circlet: directed posteriorly; 160–163 rows of hooks; 23–25 hooks per row (total ca. 3,800).

Additional material examined

Pentecost, Warbot River. S15.96069° E168.19755°, alt. 25m. 22.ix.2004. Coll. D. A. & R. Craig (immature larvae; DAC).

Etymology

Named for the distinct eyebrow-shaped mark, terminated at a black spot, dorsal to the stemmata in the larvae.

Distribution

VANUATU: Pentecost.

Comments

Pentecost is little collected and future surveys of that island are warranted. The nearby island of Maewo, which is also known to support simuliids because of Cheesman's early collections, is also in need of study. Two other Pentecost rivers (Lonpoa, Oubouen) were examined at the coast, but both lacked simuliids and other macroinvertebrates. The mountainous interior of the island will no doubt be more fruitful.

Found exclusively on trailing vegetation in fast flow (Fig. 24d), *S. supercilium* does not exhibit conspicuous adaptations to life at high velocities. Fan rays are fine in structure, the number of hooks in the posterior circlet is relatively few, and the abdomen is not markedly steatopygous. With adults unknown, the assignment of *S. supercilium* to the *steatopygium* species group is based solely on the character states of the immature stages, viz, the small number of hypostomal hairs and number of hooks in the posterior circlet. Nonetheless, *S. supercilium* would fit almost equally well in the *callipygium* species group. Does the generalized nature of this species perhaps indicate that it is a basal taxon in *Hebridosimulium*?

***Simulium* (*Hebridosimulium*) *undulatum* Craig. n. sp.**
(Figs. 11i, 14d, 17d, 19d, 21d)

Types

Holotype. Larva: Pre-penultimate instar larva in alcohol. Label data – "*Simulium* (*Hebridosimulium*) *undulatum*. Vanuatu, Banks Islands, Vanua Lava, Tahiti River. S13.84727° E167.52191°, alt. 12.5m, 28.viii.2004. Coll. D. & R. Craig. HOLOTYPE. No. 16613" (BPBM). **Paratypes**. Larvae: Prepenultimate instar larvae on slide. Label data as for Holotype, but with "PARATYPE" (larva; BPBM).

Diagnosis

Larva: anterior cephalic apotome markedly pale anteriorly, head spot pattern in Eiffel Tower configuration; posterior edge of cephalic apotome markedly emarginated, postocciput extended between cervical sclerites and apotome, hypostomal teeth not markedly developed; abdomen moderately steatopygous, posterior circlet directed posteriorly; dorsal tubercles absent.

Description

Adult female. Unknown.

Adult male. Unknown.

Pupa. Unknown.

Larva (based on 1 penultimate and numerous prepenultimate instar larvae). Body (Fig. 11i): total length ca. 6.1 mm; females evenly mottled grey, with metathoracic segment slightly orange, males more yellowish. Head (Fig. 14d): anterior frontoclypeal apotome markedly pale; labral fan stalks pale to light brown; head-spot pattern positive, medial head spots in Eiffel Tower configuration, ecdysial lines pale and distinct; width 0.62 mm, length 0.65 mm; distance between antennal bases 0.38 mm; lateral margins of head subparallel; posterior edge of apotome markedly emarginated; postocciput extended between distinct cervical sclerites emarginated apotome. Antenna: distal article light brown, remainder pale; total length 0.44 mm; distal article 0.3 times as long as basal articles, extended well beyond labral fan stalk. Labral fan: stalk very light brown, anterior palatal bar markedly developed; 47 rays, 0.70 mm in length, 16–19 rays less substantial; microtrichia 1.3 times longer than ray width, distinct pattern of 6 smaller microtrichia to 1 larger one. Postgenal cleft (Fig. 17d): arrowhead shaped, 1.3 times deeper than wide with slightly convex edges; posteroventral elongated muscle spots positive. Postgenal bridge: 0.4 times as long as cleft depth, bridge pale yellow; ventral genae and postgenae light brown. Hypostoma (Fig. 19d): overall cone-shaped; ratio 4.4; teeth not markedly protruded anteriorly; median tooth prominent, lateral teeth small, directed anteriorly, but scalloped medially; medial sublateral teeth larger, others smaller with subsidiary basal tooth; paralateral teeth just apparent; lateral serrations essentially absent; 9 hypostomal setae per side. Mandible (Fig. 21d): apical teeth normally developed, 6 spinous teeth; spinous teeth gap normal; serration and sensillum broadly based and distinct; blade region smooth and straight. Abdomen: expanded evenly posteriorly to 5th abdominal segment, slightly steatopygous; posterodorsal tubercles absent. Posterior circlet: directed posteriorly; 180 rows of hooks; 28–30 hooks per row (total ca. 5,200).

Additional material examined

Vanuatu, Banks Islands, Vanua Lava, Tahiti River. S13.84727° E167.52191°, alt. 12.5m. 28.viii.2004. Coll. D. & R. Craig (early instar larvae; DAC).

Etymology

Named in reference to the emarginated posterior edge of the larval cephalic apotome.

Distribution

VANUATU: Vanua Lava (Banks Islands).

Comments

This species is found in the same riverine habitat as *S. banksi* (Fig. 23d). Although described only from one penultimate instar larva and some earlier instar larvae, *S. undulatum* is considered here a separate species — one related to the *steatopygium* species group. *Simulium undulatum* has a markedly emarginated apotome posteriorly. It is

expected that in the last-instar larva, the emarginations will be even more developed, because they increase in size from earlier to later larval instars. With lack of reared adult material from the Banks Islands simuliids (*S. banksi, S. callipygium, S. undulatum*), adults collected by Cheesman in the late 1920s from Vanua Lava and deposited in the BM, cannot as yet be assigned to species (see *Incertae sedis*).

***adsonense* species subgroup**

Diagnosis

Larva: anterior apotome and remainder of head evenly and deeply pigmented; abdomen not markedly steatopygous.

***Simulium* (*Hebridosimulium*) *adsonense* Craig n. sp.**

(Figs. 5j, 8f, 10e, 11m, 14e, 17e, 19e, 21e)

Types

Holotype. Adult: female, double pinned. Label data – "*Simulium* (*Hebridosimulium*) *adsonense*. VANUATU, Santo, Adsone River, S15.55968° E166.96876°, alt. 59m, 15.ix.2004. Coll. D. A. & R. Craig. HOLOTYPE, #16572" (BPBM). Genitalia in glycerine vial. Pupal cocoon and exuviae as subsidiary material on point; right gill missing. **Paratypes**. Alcohol material: Pupae: exuviae (BPBM, DAC). Larvae: later instars (BPBM, DAC, LCNZ, ROM). Label data as for Holotype, but with "PARATYPE".

Diagnosis

Relatively large species. Adults: black; pleural membrane with distinct yellow hairs; legs markedly bicolourous. Pupa: cuticle medium brown with coarse granules, gill petioles essentially absent, filaments tapered markedly. Larva: head dark brown, anterior cephalic apotome medium brown; hypostomal teeth distinct; abdomen only slightly steatopygous; abdominal dorsolateral tubercles absent.

Description

Adult female (based on 1 reared specimen). Body: head, thorax and abdomen blackish brown; total length 2.6 mm. Head: width 0.85 mm; depth 0.55 mm; postocciput, vertex and frons black, vestiture of sparse, erect, black hairs; frons-head ratio (narrowest width of frons: greatest width of head) 1.0:3.4. Eye: interocular distance 0.16 mm; ommatidia 0.015 mm in diameter; ca 35 rows across and down at mid-eye. Clypeus: 0.24mm wide, concolourous with frons. Antenna: length 0.47 mm; flagellomeres blackish brown, scape and pedicel pale. Mouthparts: 0.4 length of head depth; mandible with ca. 28 fine inner teeth; lacinia with 17 inner teeth and 12 outer teeth; maxillary palpus with total

length 0.45 mm, all articles evenly dark brown, proportional length of 3rd, 4th, and 5th articles 1.0:0.8:1.5; sensory vesicle elongate, ca. 0.3 times width of 3rd article, opening 0.8 times as wide as vesicle. Thorax: length 1.3 mm; width 1.1 mm; postpronotal lobes slightly paler than scutum; scutum evenly very dark brownish black, vestiture of sparse silver hairs; scutellum more or less concolourous with scutum, vestiture of long black hairs and pale hairs laterally, apical angle 125°; postnotum concolourous with scutum; pleuron evenly dark brown; pleural membrane slightly paler and with distinct yellow hairs. Wing: length 2.7 mm; width 1.1 mm. Legs: coxae pale brown**;** fore leg, femur brown, tibia pale proximally, remainder of leg black; mid leg femur brown medially, tibia pale proximally, remainder of leg black; hind leg as for mid leg. Abdomen: anterior light gray, remainder brownish black; vestiture of dense silver hairs, long laterally, with few black hairs**;** basal scale of golden hairs. Genitalia (Fig 5j): median region of sternite VIII moderately depressed and pale posteromedially**;** hypogynial valves with vestiture of sparse short hairs; medial edges essentially parallel, posterolateral edges concave, membranous apical extensions rounded and simple; genital fork with stem long and markedly narrow, posterolateral arms with medial constriction, anteriorly directed apodeme rounded; anal lobes rounded with sparse longer hairs posteriorly, anterior anterolateral apodeme not well developed, anteromedian concavity distinct with sparse hairs; cercus narrow; spermatheca ovoid, moderately pigmented.

Adult male. Unknown.

Pupa (based on 4 specimens). Body length: 3.0 mm. Gill (Fig. 10e): maximum length of female 1.2–1.5 mm, male 1.1 mm; petioles short, branching pattern (2+2)+2+2+2, light brown, thickest proximally, tapered rapidly. Head and anterior thorax with evenly distributed sparse, dark brown, large, irregular granules, cuticle medium brown (Fig. 8f). Cocoon: markedly boot shaped, base not flared laterally, anterior collar well raised above substrate; length of female 3.8–3.9 mm long, 1.5–1.7 mm wide; male 2.8–3.0 mm long, 1.4–1.8 mm wide.

Larva (based on 3 mature last-instar larvae). Body (Fig. 11m): relatively large; total length 6.9–7.1 mm: females overall grey, males with orange tinge, thorax evenly pigmented, anterior abdominal segments pigmented with intersegmental areas pale, producing banded appearance, posterior abdominal segments evenly pigmented. Head (Fig. 14e): both sexes with dark brown pigmentation, lighter anteriorly on frontoclypeal apotome, more so in males; fan stems light brown, triangular region anterior and basal on stem markedly pale, as is region medial of antennal bases and sockets of trichoid sensilla pair 5 and 6, medial of antennal base; head-spot pattern negative, but indistinct; ecdysial lines pale and straight, diverging; width 0.65 mm, length 0.71 mm; distance between antennal bases 0.36 mm; lateral margins of head evenly convex; posterior edge of apotome not emarginate; postocciput finely extended between cervical sclerites and apotome. Antenna: total length 0.83 mm; distal article 0.33 times as long as basal articles, extended barely beyond labral fan stalk, distal article medium brown, distal portion of basal article

concolourous, remainder paler. Labral fan: stalk medium brown, anterior palatal bar markedly protruded anteromedially; 37–45 rays, 0.70 mm in length, 10–12 rays less substantial; microtrichia 0.5 times length of ray width, pattern indistinct. Postgenal cleft (Fig. 17e): markedly arrowhead shaped, slightly deeper than wide with convex edges; posteroventral elongated muscle spots neutral. Postgenal bridge: 0.6 times as long as cleft depth; genae and postgenae dark brown. Hypostoma (Fig. 19e): overall cone-shaped; ratio 5.1; median tooth prominent, lateral teeth smaller and scalloped medially, splayed laterally; sublateral teeth small, well spaced and equal in size; paralateral teeth not obvious; lateral serrations absent; 9–11 substantial hypostomal setae per side. Two substantial hairs situated medially. Mandible (Fig. 21e): apical tooth markedly developed; 4–6 spinous teeth, largely covered by subapical teeth; spinous teeth gap small; serration and sensillum distinct; blade region smooth, barely convex. Abdomen: anterior abdomen subequal in width to thorax, expanded gradually posteriorly to 5th abdominal segment then slightly steatopygous. Posterior circlet: directed posteriorly; 175–180 rows of hooks; 29–31 hooks per row (total ca. 5,300).

Additional material examined

Santo, Adsone River, S15.55968° E166.96876°, alt. 59 m, 15.ix.2004. Coll. D. A. & R. Craig. (immature larvae; DAC).

Etymology

Named after the type locality river, but based on an older spelling, Adson, rather than the modern spelling, Adsone.

Distribution

VANUATU: Santo, Adsone River.

Comments

Simulium adsonense is found in Santo only, along with small numbers of *S. steatopygium* larvae. Association of larvae and pupae of *S. adsonense* was confirmed by comparison of pupal cuticle (Fig. 8f) and gills (Fig. 10e) of pharate pupae in the mature last-instar larvae, to the mature pupae. The type locality (Fig. 24a) is shallow, with very fast water (respectively ca. 5 cm and 1.8 m/s) on an old concrete causeway. Larvae and pupae were also recovered from a riffle upstream. Larvae exhibit behaviours similar to those of *Inseliellum* in Polynesia that are adapted to shallow fast water (Craig 1997), namely, even spacing of larvae and lack of body twisting, so that the ventral surface of the labral fans are directed towards the substrate. The latter behaviour is similar to that observed for larvae of *S. paradisium*. The number of hooks on the posterior circlet is also higher, again in keeping with adaptation to high-velocity habitats.

With the larva not markedly steatopygous and the pupal cuticle unique, placement of

S. adsonense in the *steatopygium* species group was based solely on the genitalia of the single female adult. The relationship of this species may have to be reconsidered once additional material comes to hand.

***Simulium* (*Hebridosimulium*) *spiroi* Craig, Currie & Hunter, n. sp.**
(Figs. 10f, 11n, 14f, 17f, 19f, 21f)

Types

Holotype. Larva: last instar in alcohol. Label data – "*Simulium* (*Hebridosimulium*) *spiroi*. VANUATU, Malekula, Wesso River Cascade. S16.37880° E167.76663°, alt. 34 m, 2.ix.2004. Coll. D. A. & R. Craig. HOLOTYPE. No. 16606" (BPBM). **Paratypes**. Larvae: last instars in alcohol (BPBM, DAC, ROM). Penultimate and earlier instar in alcohol (BPBM, DAC, LCNZ, ROM). Label data as for Holotype, but with "PARATYPE".

Diagnosis

Larva: head evenly dark brown; body markedly lighter gray, posterolateral diagonal gray stripes on sixth segment. Pupa: gill petioles short.

Description

Adult female. Unknown.

Adult male. Unknown.

Pupa (based on pharate material). Thorax: cuticle with numerous granules present. Gill (Fig. 10f): petioles short and thick; branching pattern (2+2) +2 +2 +2, occasionally (2+2) +2 +2 +1+1; filaments noticeably tapered; maximum length 1.4–1.8 mm.

Larva (based on 6 mature last-instar larvae). Body (Fig. 11n): total length 6.5–6.9 mm; females evenly pale grey dorsally, males pale yellowish-grey with paler intersegmental regions, difference not marked. Head (Fig. 14f): both sexes evenly dark brown including labral fan stalks; dorsal head spots negative, but not distinct; sockets of trichoid sensilla pair 5 and 6 markedly pale, darkly aureolate; width 0.74–0.82 mm; length 0.79–0.82 mm; distance between antennal bases 0.39–0.41 mm; ecdysial lines slightly convex, diverged markedly posteriorly, broadly rounded at maximum width; lateral margins of head convex, especially posteriorly; posterior edge of cephalic apotome slightly emarginate; postocciput with fine medial extension. Antenna: total length 0.36 mm; distal article 0.22 times as long as basal articles; markedly shorter than labral fan stalk; distal article dark brown, remainder pale. Labral fan: stalk heavily pigmented anteriorly, anterior palatal bar noticeable, but not markedly protrusive; 39–43 substantial rays, 0.84 mm in length, medial rays 0.02 mm in width, 8–10 posterolateral rays finer than others; microtrichia substantial, subequal in length to ray width, pattern distinct, with 4 or 5 shorter microtrichia between those longer. Postgenal cleft (Fig. 17f): markedly arrowhead shaped; posterior edges parallel, sharply tapered at mid-length to pointed apex,

1.5 times longer than width; postgenal bridge subequal in length to cleft depth; genae evenly pigmented dark brown, paler around stemmata; ventrolateral elongate muscle spots partially negative. Hypostoma (Fig. 19f): ratio 4.2; median tooth and lateral teeth prominent, latter slightly scalloped medially occasionally directed more laterally, sublateral teeth distinct; paralateral teeth and lateral serrations not obvious; 11–13 substantial hypostomal setae per side. Mandible (Fig. 21f): apical tooth markedly prominent, preapical and subapical teeth not so; spinous teeth small, gap distinct; serration and sensillum robust and fused basally; blade region smooth and slightly convex. Abdomen: thorax and anterior abdominal segments subequal in width, expanded gradually to maximum width, callipygous posteroventrally; colour pale laterally and ventrally, marked diagonal gray banding laterally on sixth segment; posterodorsal tubercles absent. Posterior circlet: directed ventrally; 170–175 rows of hooks, 29–35 hooks per row (total ca. 5,500).

Additional material examined

Last and earlier instar larvae in Carnoy's fixative. Label data – as for types (larvae; DAC).

Etymology

Dedicated to the memory of Mike "Spiro" Spironello.

Distribution

VANUATU: Malekula.

Comments

Known only from the type locality (Fig. 23c) on Malekula, larvae of *S. spiroi* appear to be habitat specialists. They were taken in moderately large numbers only from smooth travertine substrate in fast flow (1.3 m/s; Table 1). However, larvae exhibit little structural adaptation to that habitat beyond the scarcely steatopygous abdomen and a relatively large number of hooks in the posterior circlet. Superficially similar to *S. adsonense* in possessing a darkly pigmented larval head and lighter coloured body (*rf.* Figs. 11m, n), *S. spiroi* differs in the structure of the pupal gill filaments (cf. Figs. 10e, f), size and shape of the postgenal cleft, and markedly larger hypostomal teeth. Although grouped together with *S. adsonense* from Malekula, we are of the opinion that the body shape and the head colour in both species may be independent adaptations to full sunlight in shallow, fast water. Dark pigmentation of larval heads is a known adaptation to full insolation (Craig 1997) and most likely is protective against UV light (Donahue & Schindler 1998). Preliminary CO1 mitochondrial DNA analysis indicates that *S. spiroi* and *S. adsonense* are not genetically close (A. Cywinska, unpublished data).

Incertae sedis

Because of difficulty in distinguishing adults of the various species, the following pinned material, mainly older, has not been assigned to species:

Banks Islands. Vanua Lava. ?.xi.1929. Coll. L. E. Cheesman (8 females; BM).

Maewo Sounwari, S15° 23' E168° 07', alt. 0–360m. 4–5.ix.1979. Coll. W. C. Gagne, G. M. Nishida, G. A. Samuelson (7 females; BPBM).

Espiritu Santo ?.vii.1929. Coll. L. E. Cheesman (female; BM); ?.viii.1929. Coll. L. E. Cheesman. (male; BM); ?.viii–ix.1929. Coll. L. E. Cheesman (5 females; BM). SW of Namatasopa, alt. 300m. 29.viii.1957, alt. 400m. 29. viii. 1958. Coll. J. L. Gressitt (6 males; BPBM). Sarautu River, 17.vi.1958. Coll. J. Rageau (adults – damaged; PI). Narango, alt. 900 m. ?.vi.1960; alt. 90m. ?.vii.1970. Coll. W. W. Brandt (male, 4 females, others dry in vials; BPBM). Mt. Tabwemasana. alt. 3,500–4,500 ft. 1–4.ix.1971. Coll. G. S. Robinson (3 males, 3 females; BM).

Malekula. Ouna, ?.ii.1929. Coll. L. E. Cheesman (6 females; BM). Malua Bay, ?.vii.1929. Coll. L. E. Cheesman (26 females on acetate; BM). Atchin Island, ?.vii.1929. Coll. L. E. Cheesman (female; BM). Malekula, ?.iv.1939. Coll. L. E. Cheesman (4 females; BM). Southwest Bay, alt. 1300'. 12.x.1971. Coll. G. S. Robinson (3 females; BM).

Efate. Mt. Bernier, alt. 479m. 24.viii.1979. Coll. G. M. Nisheda (5 females; BPBM). 8 km W Forari (Radier), alt. 175–220m. 21. viii.1979. Coll. G. M. Nisheda (1 female, 2 males; BPBM). Mele Cascade. S17.67778° E168.25473°. alt. 65m. 6.x.2004. Coll. D. & R. Craig. A single, pinned large female adult. The associated pupal exuviae lacks cuticular granules, the cuticle is clear and markedly corrugated. The first two characters are reminiscent of *S. pankumuense* (Malekula) (female; DAC).

Cytology

General Chromosome structure of S. johnfrumi *and* S. laciniatum

The two species had three pairs of chromosomes with homologous chromosomes paired tightly. No chromocenter or B chromosomes were present. Only the chromosomes of *S. johnfrumi* are illustrated here (Fig. 25), with, however, differences in those of *S. laciniatum* indicated. Each chromosome is described individually.

Chromosome I

Chromosome I (IS, IL) was the longest and metacentric. The centromere (CI) was identified (as a highly condensed region) in section 22. A chromosomal landmark, the nucleolar organizer (NO) was located adjacent to the centromere, near the base of the long arm (IL).

Chromosome II

Chromosome II (IIS, IIL) was submetacentric. The centromere (CII) was identified in section 54. The IIS arm was recognized by the Ring of Balbiani (RB, section 46) and Shoestring (SS, end of section 46). The IIL arm was recognized by the Parabalbiani marker (PB, section 58).

Chromosome III

Chromosome III (IIIS, IIIL) was the shortest chromosome and was submetacentric. The centromere (CIII) was not as well defined as in chromosomes I and II, but it was identified in section 83. The IIIS arm was recognized by the "flare" at the end of IIIS (section 72?), and the Blister landmark (BL) in section 78 (Fig. 5). The IIIL arm contained no landmarks.

Interspecific differences

The banding sequences of *S. laciniatum* differed from *S. johnfrumi* by the presence of four inversions. The IL-1 inversion was recognized with breakpoints slightly beyond the 31/32 and 34/35 section limits. On chromosome II, the IIS-1 inversion was originally identified as "extra bands", but later recognized as a pericentric inversion at the centromere within sections 54 and 55. The IIL-1 inversion was the largest interspecific difference, with breakpoints between sections 62 to 67. On chromosome III, the IIIL-1 inversion, of similar size to the IIL-1 inversion, was located near the centromere, between the midpoints of sections 84 to 90.

Ecological aspects

Larvae of *Hebridosimulium* species are found more typically on vegetation than on rocky substrates (Table 1). Trailing roots and leaves of grasses are common habitats, but leaves held on the substrate by fast flow in riffles and cascades are markedly preferred. For *Inseliellum* of Polynesia such habitats are known to be plesiotypic and are important for basal lineages to colonize islands, because on a new island, the first running-water habitat available is small streams overhung by vegetation (Craig *et al*. 2001, Craig 2003a).

Habitat choice by larvae of *S. laciniatum* is puzzling. At some localities (e.g., Waitavala Water Slides, Taveuni.) where conditions appeared to be ideal, no larvae were found on the smooth, solid rock substrate, whereas leaves were frequently populated by larvae. On the other hand, at the Upper Wairiki River, Devo Peak (Fig. 24g), massive numbers of larvae were taken from the rock substrate, with few found on leaves. Crosskey (1990) illustrates a rocky ledge of a stream as a typical habitat for *S. laciniatum*, but this is now not necessarily so.

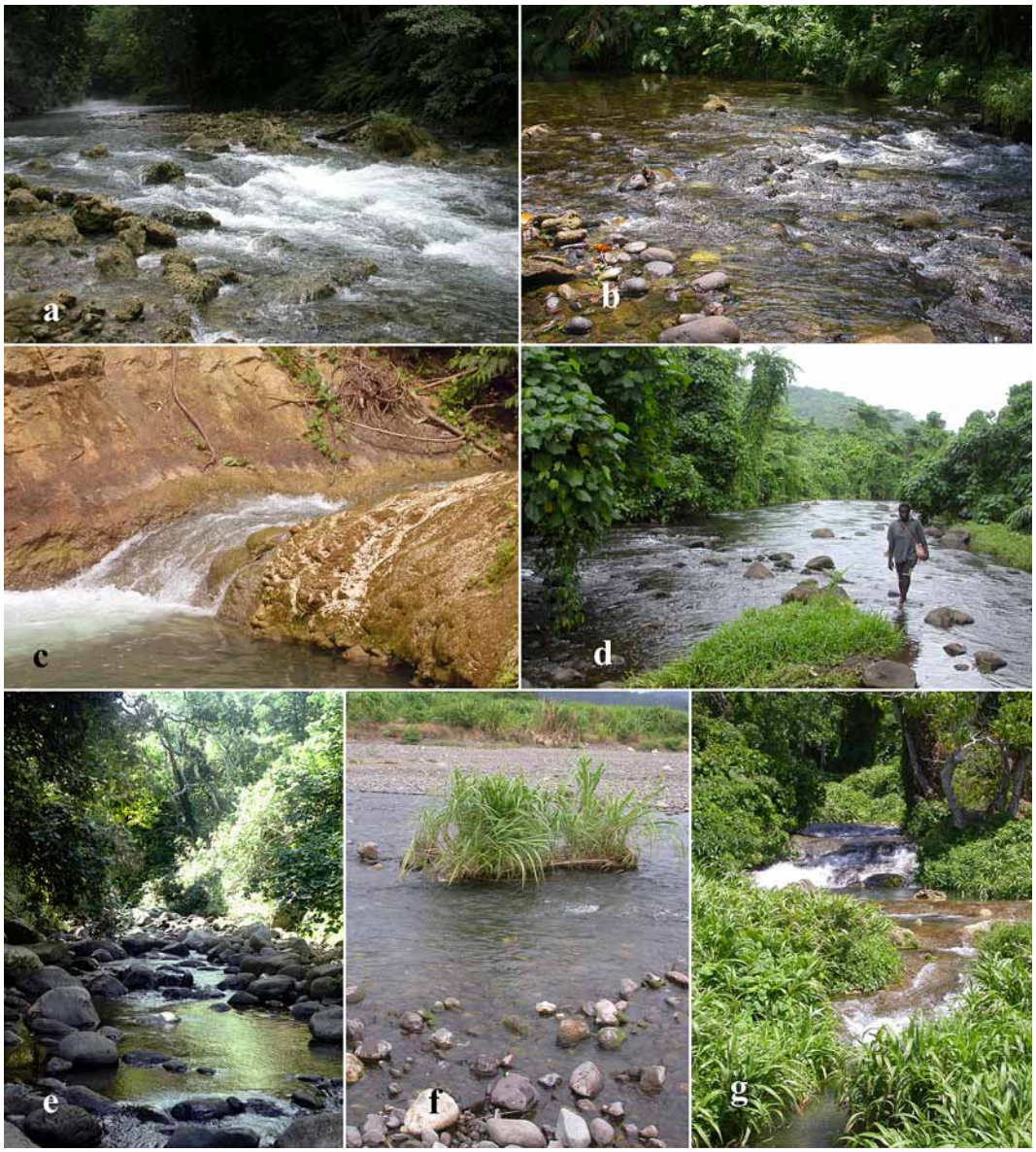

FIGURE 23. Habitats of larvae of *Hebridosimulium* species, Vanuatu. **a**. Santo, Sarakata River, UNELCO Hydro Station. Type locality of *S. callipygium*. Note limestone substrate. **b**. Santo, Upper Sarakata River, Millennium Cave region. Typical habitat of *S. callipygium* and *S. subparadisium*. **c**. Malekula, Wesso River, downstream of cascade. Type locality of *S. spiroi*. Note travertine substrate. **d**. Banks Islands, Vanua Lava, Tahiti River. Type locality of *S. banksi* and *S. undulatum*. **e**. Tanna, stream south of Bethel. Type locality of *S. johnfrumi*. **f**. Malekula, Pankumu River. Type locality of *S. pankumuense*. **g**. Efate, Ewor River, La Cressionnière. Type locality of *S. tuberculum*. Note the travertine terraces.

FIGURE 24. Habitats of larvae of *Hebridosimulium* species. **a**–**e.** Vanuatu. **a**. Santo, Adsone River. Type locality of *S. adsonense*. **b**. Santo, upper cascade, tributary of Sarakata River. Type locality of *S. paradisium*. **c**. Efate, Mele Cascade. Type locality of *S. steatopygium.* Note travertine terraces. **d**. South Pentecost, Warbot River. Type locality of *S. supercilium*. **e**. Santo, small stream, Millennium Cave region. Typical locality of *S. subparadisium*. **f**–**i.** Fiji. Habitats of *S. laciniatum* larvae. **f**. Viti Levu, Abaca Village, above Vereni Falls. Type region. **g**. Taveuni, Wairiki, Devo Peak, looking down water slide. **h**. Kadavu, Kadavacoro Village, Wailea Waterfall. **i**. Vanu Levu, Waisala Rain Forest Reserve, Ravini River.

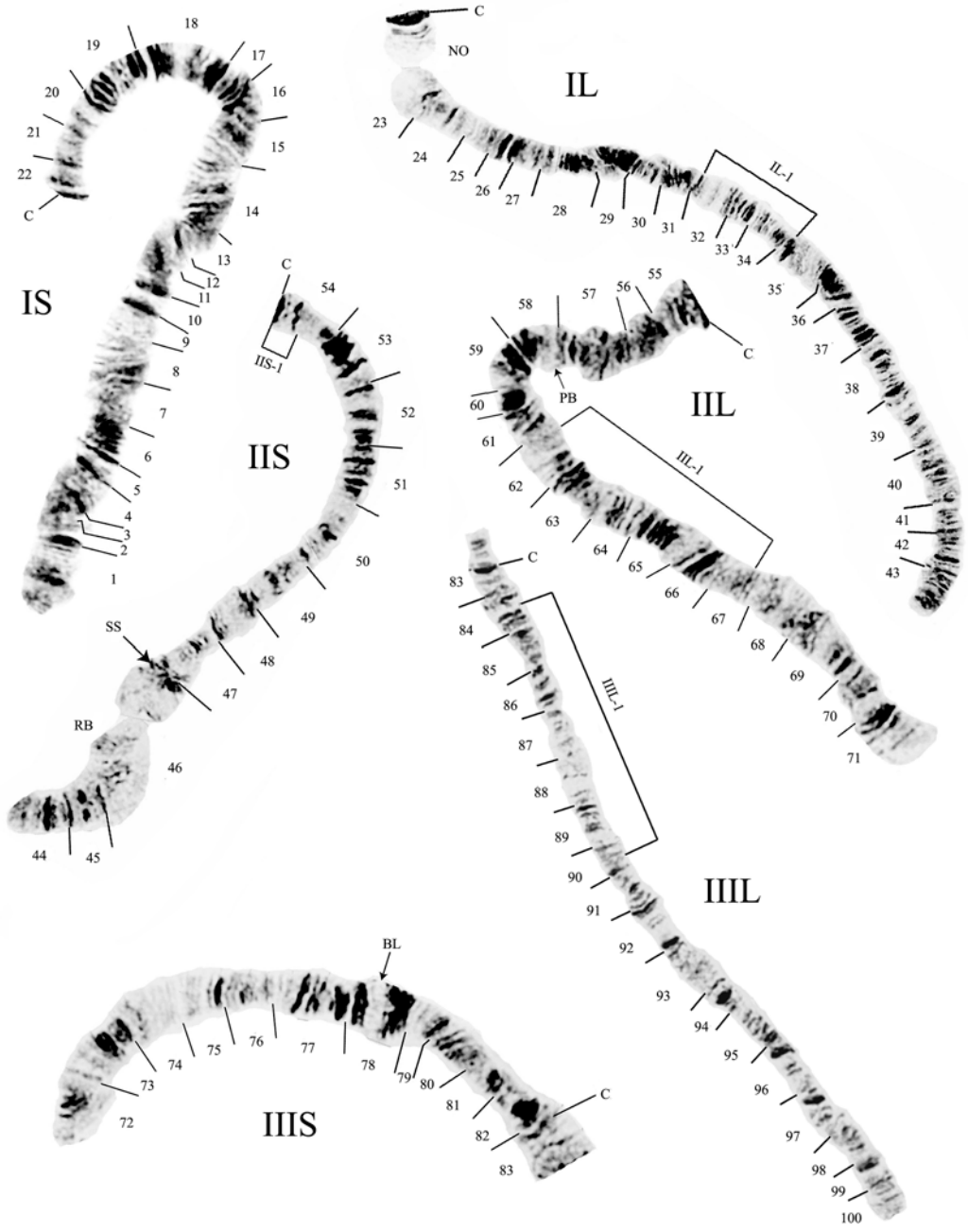

FIGURE 25. Chromosomes of *S. johnfrumi*. The short arm (S) of chromosomes I, II, and III are on the left, the long arm (L) on the right. Banding sequences that differ (fixed inversions) from *S. laciniatum* are indicated by square brackets. Abbreviations: C—centromere; NO — nucleolar organizer; RB — ring of Balbiani; SS — shoestring; PB — Parabalbiani; BL — blister.

Why should there be such a dichotomy of habitat preferences in a known homogeneous, albeit widespread, species? There appears to be no significant difference in physical characteristics of the water between sites (*rf.* Table 1). However, the aquatic pyralid moth *Nymphula* occurs abundantly on rock substrates in running water habitats in Fiji. Noticeably aggressive, *Nymphula* larvae feed on simuliid larvae (Gorayeb & Pinger 1978). Is it possible that simuliids are excluded from some rocky habitats by predation? Alternatively, the dichotomy of habitats may be a precursor to evolution of separate habitat requirements. This latter hypothesis might be tested by conducting comprehensive molecular or cytological analyses.

Another puzzling ecological question concerns cohorts. For *Inseliellum* in Polynesia, lower altitude species are multivoltine, as might be expected for tropical insects. In contrast, higher altitude sites showed evidence of cohorts among *Inseliellum* species (Craig 1997). Certain *Hebridosimulium* species also exhibit evidence of marked cohorts. Those that appear to be multivoltine are *S. tuberculum, S. steatopygium* (Efate), and *S. callipygium* (Santo), for which all stages are common and occur at different times of the year. Marked cohorts of larvae and a total absence of mature last instar-larvae and pupae were seen in *S. spiroi* (Malekula), *S. adsonense*, and *S. paradisium* (Santo). Such apparent differences in life history may eventually be of taxonomic utility. Life history characteristics of other species of *Hebridosimulium* are not known.

One extreme example of cohorts was for *S. laciniatum* at Lambasa Creek, Kadavu, Fiji. Only the larval stage was present; astronomical numbers of 3rd or 4th instar larvae were on leaves. There was no sign of even old pupal cocoons. This is puzzling given that at the same time, the Wailea Stream (Fig. 24h), a mere 4 km distant, supported a full range of larval instars.

There is some evidence for seasonality in species occurrence. Collections of larvae from the Mele Cascade, Efate, by Grenier & Rageau (1961) in May-June, 1958, are almost all *S. tuberculum*, with a few *S. steatopygium*. In June, 1981, almost all material (DAC) was of *S. steatopygium*, with only a few larvae of *S. tuberculum*; in November (Swillen), all were of *S. steatopygium*. In December, 2004, almost all larvae (DAC) were *S. tuberculum*.

Collections made in 1971 in Santo include female simuliids taken while biting humans (G. Robinson pers. com. 2002) and similarly in 1981 by DAC (pers. obs.). This provided clear evidence that females of Santo simuliids bite; however, the identity of these females is not known. Grenier & Rageau (1961) commented that people on Efate were unaware of simuliids, indicative that Efate simuliids do not bite, and this was confirmed by DAC (pers. obs. 1981, 2004). With the exception of well-recorded, serious biting by females of *S. lucyae* on Aneityum (Cheesman 1957a, 1960, Craig 2006), there are no other records of Vanuatu *Hebridosimulium* blood feeding on humans. There are no records of blood feeding on any other animals, and there is no common name for simuliids among the Ni-Vanuatu. Shown reared simuliid adults, locals stated that in Bislama, the official language

of Vanuatu, such flies would be termed “Little Black Fellas”.

On the other hand, in Fiji, females of *S. laciniatum* are well known as serious biters of humans (Crosskey 1974, Ryan 2000, Craig, pers. obs. 2004) and they are known by the common name “Navanava”. Again, however, there are no records of *S. laciniatum* feeding on other animals.

As noted by Craig (2003), because of the time taken for erosion to form a channel network and development of the large catchment area on islands, larger rivers are the more recently developed habitat. Accordingly, species with larvae that exhibit adaptations to fast deep water of larger rivers are probably more derived.

General comments

Cytology

With only two species of *Hebridosimulium* examined cytologically, it is not possible to make statements regarding relationships within the subgenus. In comparison to *Inseliellum*, the nucleolar organizer (NO) of *Hebridosimulium* is located on chromosome I (L), the same region as in the majority of *Inseliellum* species (Spironello et al. 2002). There is no indication that the NO is ‘displaced’, as it is in a basal clade (Austral/Cook/Marquesas Islands) of *Inseliellum*, where the NO is in chromosome arm IIL (Craig 1983, Craig & Craig 1986). Further, there are no fixed inversions or polymorphisms shared between *S. johnfrumi*, *S. laciniatum*, and species of *Inseliellum*. Unlike *Inseliellum* and a few other unrelated simuliids worldwide (Rothfels 1989, Craig & Currie 1999) that are heterogametic (XY) in the female, *Hebridosimulium* is typical (XX). Accordingly, contrary to earlier reports (Craig 1983, Craig 2003), there is, at present, no cytological evidence that *Hebridosimulium* and *Inseliellum* are closely related.

Taxonomy

This work should be considered a preliminary revision only. Morphologically, *Hebridosimulium* is markedly conservative and determining species limits, using adults, is difficult. Females show subtle, albeit consistent differences in genitalia and these have been invoked for the groupings recognized here. Males show no consistent characters. With adults of many species unknown, current groupings may change once the missing adults are described. Pupae show some useful characteristics, such as granulation on the dorsal cuticle, but these are of little use beyond species diagnoses. Gill branching patterns are of minor use, but again, there is much intraspecific variation, similar to the situation with cocoons. The larvae are the most useful for specific discrimination and recognition of taxonomically higher categories. While there are body shape and colour differences, the head pattern is most useful for species discrimination. Nonetheless, problems occur with sexually dimorphic colour where bodies of male larvae tend to be lighter and yellower, with those of the females darker and greyer; such differences are accompanied by marked

variation in head colour pattern. Modification of the posterior abdomen seems to correlate well with habitat, which in turn may promote parallel development in body form, a caveat being that such modifications may well have occurred more than once.

Lack of particular life-history stages for some species, and lack of material from some islands, are further impediments to higher-taxon groupings. These problems are exacerbated by absence of collections from multiple habitats in the interior of islands and of the narrow temporal mien of collections currently available. Cytological and molecular analyses would no doubt flesh out this preliminary taxonomy.

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