

Blackflies (Diptera: Simuliidae) of Southern Guyana with Keys for the Identification of Adults and Pupae - A Review

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A revision is made of the previously poorly studied blackfly fauna from the south-western border of Guyana with Brazil. Notes on the biosystematics of the species found are provided, together with keys and illustrations based on their morphology. Of the 14 species recorded, eight are anthropophilic and two of these (Simulium oyapockense s.l. and S. guianense s.l.) are proven vectors of human onchocerciasis in the nearby Amazonia focus of the disease in neighbouring Brazil.

Key words: blackflies - Simuliidae - Neotropical region - taxonomy - Guyana

There have been few studies on the Simuliidae in Guyana and all those that have been made involve the border area with Brazil in the Rupununi District. This has largely been due to the lack of simuliids in the swampy coastal regions, the difficulty of access to the interior of the country and the lack of any pathogenic parasites transmitted by these insects. It was in Guyana (then British Guiana) at the end of the last century that relatively non pathogenic, blood inhabiting microfilariae were sent by Dr Ozzard to Manson, who described them as the new species *Mansonella ozzardi*. It was soon discovered that this filarial species was common in the Caribbean Islands where the vectors were species of *Culicoides* midges. Eighty years later the discovery of simuliids as vectors of *M. ozzardi* in Brazil and Colombia (reviewed in Shelley & Coscarón 2001) prompted the work of Nathan et al. (1982), who discovered that *Simulium oyapockense* s.l. is a vector of *M. ozzardi* in the Rupununi District of Guyana.

At the beginning of the twentieth century studies on anthropophilic Diptera were numerous because of their biting nuisance and, in the case of mosquitoes, their proven role as vectors of pathogenic species of protozoal parasites. The first attempt at study of the Simuliidae in Guyana was made by the government Surgeon General at Georgetown, KS Wise. He had been sent man-biting simuliids by Melville from the upper branches of the Essequibo river (R) (the Rupununi and Siparuni R) and also examined specimens of two species from the same area in the Museum of the Royal Agricultural and Commercial Society of British Guiana in Georgetown. Wise (1911) provided a redescription for one of the species known as the "pium" in Brazil [by the Macuxi indians] and the "cabouri" fly by the Arawak indians in Guyana, and which had already been described in Brazil [by Lutz] as *S. amazonicum*. This species is not *S. amazonicum* but *S. oyapockense* s. l., a species later described in the 1940s

from French Guiana (Shelley et al. 1997) and also known in Brazil as the "pium". Wise described the other species as new, *S. guianense*, which the local indians referred to as the itanimi fly to distinguish it from the smaller pium or cabouri fly. In 1915 Knab described the anthropophilic female, sent to him by Dr Wise from the same area, as the new species *S. limbatum*.

At a time when it was considered that any development of the interior of the country would need to take account of blackfly control, Drs OW Richards and J Smart visited Guyana in 1937. They recorded seven simuliid species from this country and published taxonomic notes and a key to these, as well as other species collected from the Lesser Antilles (Smart 1940). The seven species from Guyana were: *S. amazonicum* (= *S. oyapockense* s.l.), *S. guianense* (= *S. perplexum*), *S. haematopotum* (= *S. oyapockense* s.l.), *S. limbatum*, *S. lutzianum* (= *S. kabanayense*), *S. rubrithorax* (= *S. maroniense* s.l.), *S. sanguineum* (= *S. oyapockense* s.l.). It is now known that these names represent only five distinct species as indicated in brackets. In most cases the misidentifications are completely understandable because at this time many species were poorly defined morphologically. However, an obvious lapse occurred with pupae identified as *S. rubrithorax* (with eight gill filaments), which are *S. maroniense* s.l. (with 18-22 gill filaments). Similarly, the naming of three pupal exuviae (in BMNH collection) as *S. lutzianum* s.l. (with eight gill filaments) was incorrect as the specimens have 10-13 filaments and are of a species later described as *S. kabanayense* (Ramírez Pérez & Vulcano 1973). These three specimens were not referred to in the taxonomic discussion of *S. lutzianum* s.l. in Shelley et al. (1997) because they were known not to be of this species but were not identified at the time. In 1989b Shelley et al. described the new species *S. perplexum* based on specimens identified by Smart (1940) as *S. guianense* Wise.

The collections by the third author, which have been the most comprehensive for the country, were made in the 1970s when the development of the Rupununi savanna for tourism was being contemplated. One of the constraints to this development was the presence of large numbers of anthropophilic simuliids. This work was nec-

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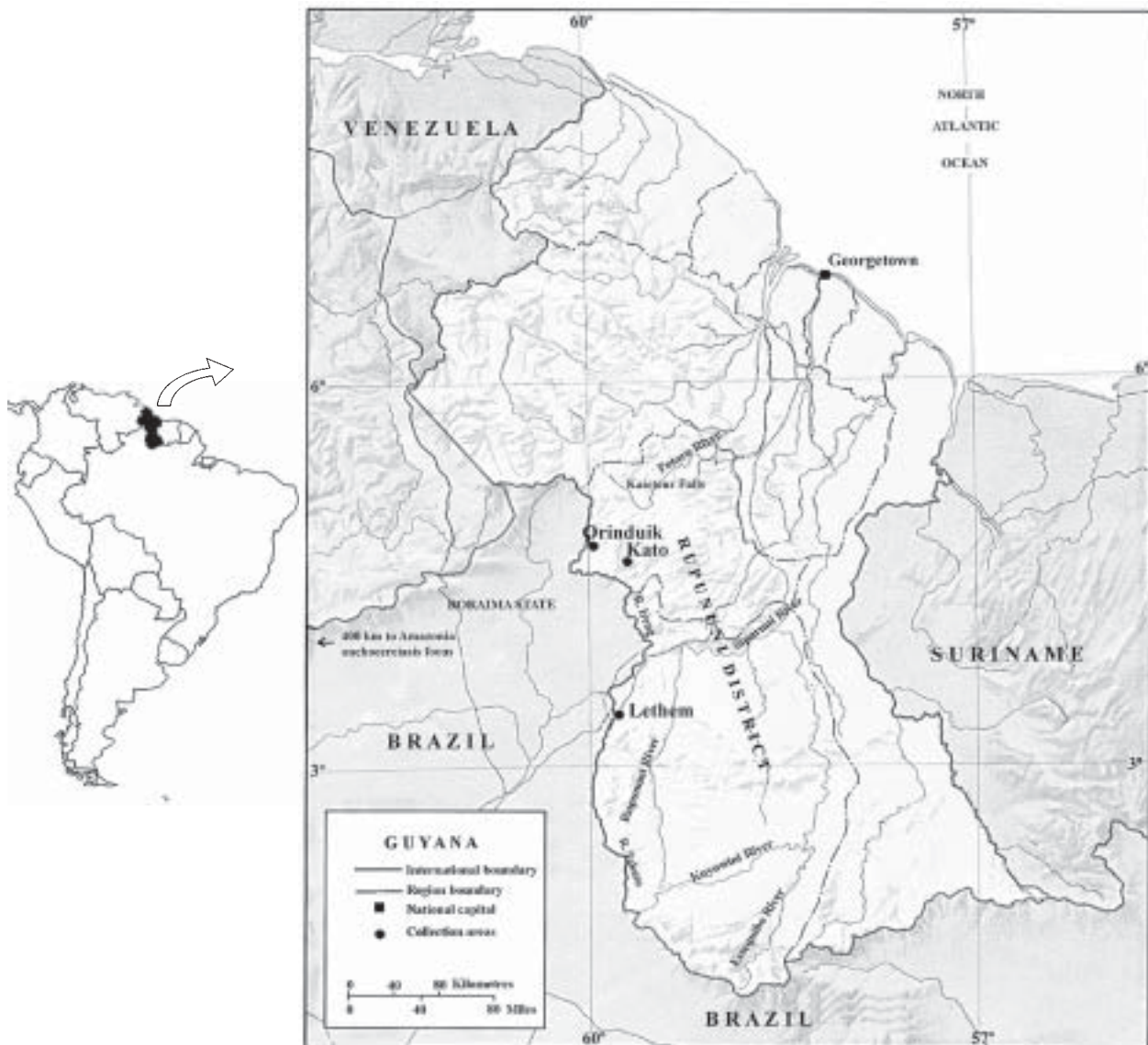
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essary for the development of studies on the biology of and a pilot control project for *S. limbatum* (as *S. incrustatum*) and *S. oyapockense* s.l. (as *S. amazonicum*/*S. sanguineum*, *S. amazonicum* or *S. sanguineum* complexes) (Humphrys et al. 1977, Rambajan 1981a, b). At this time the taxonomy of the Simuliidae of this region of Latin America was relatively unknown, and it was not until the finding of onchocerciasis in the Brazil-Venezuela Amazonia focus some 400km to the west of the Rupununi District that comprehensive taxonomic studies began.

This paper, based on holdings at the Natural History Museum, London (BMNH) mainly including the specimens of Wise, Knab, Smart, and the third author, provides the first modern review of the Simuliidae of Guyana, albeit limited to the south-western frontier area of the country with Brazil. Illustrated keys to the adults and pupae of the 14 species of Guyana are presented, together with bio-systematic notes for each species and a list of material examined.

MATERIALS AND METHODS

Collections were made in 1970 and 1975 in three savanna areas of the Rupununi District on the western border of Guyana with the state of Roraima Brazil (Map). Two are situated in highland areas (400-450 m) around Orinduik on the R Ireng and Kato on the R Chiung, and the other farther south in a more lowland area (145 m) around Lethem on the R Takutu. Rivers, streams (creeks) and drainage channels in these areas were prospected for immature stages of simuliids from which mature pupae were selected and reared to adults, and man-biting females were also collected. Standard techniques for capture, dissection and conservation of material have already been described in Shelley et al. (1997). All material has been deposited in the Department of Entomology of the BMNH. Time constraints have meant that only reared and man-biting specimens have been used in this paper and they are listed under Material Examined. These data, to-



Map of Guyana showing collection areas.

gether with all the original collecting data, are stored at the NHM on a CD. Further material has been examined from Clemson University Arthropod Collection, Clemson University, South Carolina, US (CUAC), Instituto Nacional de Pesquisas da Amazônia, Manaus, Amazonas, Brazil (Inpa) and the Institut Pasteur, Paris, France (IP). Figures of simuliid morphology have been obtained from a Synoptics image capture system as detailed in Shelley et al. (2000). Identification of material has been largely based on papers describing the Venezuelan fauna (Ramírez Pérez 1983) and the Brazilian Amazonia onchocerciasis focus fauna (Shelley et al. 1997), as well as the papers cited in the text. Recent publications from neighbouring French Guiana (Hamada & Fouque 2001) and Venezuela and Brazil (Hamada & Grillet 2001) also provide an insight into simuliid species that may be present in Guyana if more comprehensive surveys are to be carried out in the future.

CHECKLIST OF THE SIMULIIDAE OF GUYANA

Crosskey and Howard's world inventory of the Simuliidae (1997) records 13 species of simuliids from Guyana: *S. cauchense*, *exiguum s.l.*, *guianense s.l.*, *haematopotum*, *incrustatum*, *limbatum*, *oyapockense s.l.*, *perflavum*, *perplexum*, *pulverulentum*, *quadrifidum*, *rorotaense*, and *S. rubrithorax*. Since this publication the taxonomy of the species of the Amazon and surroundings has advanced and so the following comments can be made. The records of *S. rubrithorax* Lutz and *S. haematopotum* Malloch date back to Smart (1940). Their correct identifications (see Shelley et al. 1997, 2002) are *S. maroniense s.l.* Floch & Abonnenc and *S. oyapockense s.l.* Floch & Abonnenc, respectively. *Simulium pulverulentum* Knab was based on a record in Vulcano (1981), but Shelley et al. (2002) in their revision of this species discounted its presence in Guyana based on lack of information on specimens and the known distribution of this species. The record for *S. incrustatum* Lutz refers to the closely related *S. limbatum* Knab (see Shelley et al. 1997 for morphological diagnoses). The origin of the record of *S. exiguum* Roubaud cannot be traced, but the present work confirms its presence in the area studied (see Material Examined). Also *S. rorotaense* should read as *S. maroniense s.l.* Consequently, prior to the present paper only nine simuliid species had been reliably recorded from Guyana. The 14 species now known from the country are listed in alphabetical order by subgenera and by species within each subgenus. Five species, *S. clarki*, *S. kabanayense*, *S. lutzianum s.l.*, *S. spinibranchium*, and *S. subpallidum* represent new country records. Species marked with an asterisk bite man.

- Simulium (Chirostilbia) spinibranchium* Lutz, 1910 *
- Simulium (Chirostilbia) subpallidum* Lutz, 1910
- Simulium (Inaequalium) clarki* Fairchild, 1940 *
- Simulium (Notolepria) exiguum* Roubaud, 1906 (species complex) *
- Simulium (Psaroniocompsa) cauchense* Floch & Abonnenc, 1946
- Simulium (Psaroniocompsa) limbatum* Knab, 1915 *
- Simulium (Psaroniocompsa) oyapockense* Floch & Abonnenc, 1946 (species complex) *

- Simulium (Psaroniocompsa) quadrifidum* Lutz, 1917
- Simulium (Psilopelmia) kabanayense* Ramírez Pérez, 1973
- Simulium (Psilopelmia) lutzianum* Pinto, 1932 (species complex)
- Simulium (Psilopelmia) maroniense* Floch & Abonnenc, 1946 (species complex)
- Simulium (Psilopelmia) perflavum* Roubaud, 1906
- Simulium (Trichodagmia) guianense* Wise, 1911 (species complex) *
- Simulium (Trichodagmia) perplexum* Shelley, Maia-Herzog, Luna Dias & Couch, 1989 *

[It is probable that the anthropophilic species *S. roraimense* Nunes de Mello, 1974, also exists in Guyana - See "Notes on the Biosystematics of Species" under *S. oyapockense s.l.*]

KEYS TO THE SIMULIIDAE OF GUYANA

Morphological characters that are usually observed in un-dissected material were used wherever possible. Scutal patterns described are those seen in specimens placed with their bodies parallel to the microscope stage and with the fibre optic light source immediately in front of the head of the specimen. For the effects of light source direction on scutal patterns see Shelley et al. (1997). Where a species complex occurs the species name is followed by *s.l. [sensu lato]*. *S. kabanayense* was only found in Guyana as pupae and consequently this species has not been included in the adult keys. A description of these stages in this orange species is found in Ramírez Pérez and Vulcano (1973).

FEMALES

- 1. Thorax orange 2
- Thorax grey or black 5
- 2. Thoracic pattern consisting of four, wide, faintly pruinose longitudinal lines; lateral scutal borders greyish (Fig. 2) *subpallidum* (orange form)
- Thorax without a pattern; lateral scutal borders silver pruinose 3
- 3. Humeri orange or yellowish, never pruinose (Fig. 10). Paraprocts sub-quadrangular (Fig. 21) *lutzianum s.l.*
- Humeri orange or yellowish with silver pruinosity in some light incidences (Figs. 11, 12). Paraprocts sub-triangular (Figs 22, 23) 4
- 4. Abdominal tergites shiny black, first two segments silver pruinose *maroniense s.l.*
- Abdominal tergites brown and orange, mottled with no pruinose areas *perflavum*
- 5. Scutum without pattern 6
- Scutum with pattern 8
- 6. Scutum with groups of silvery gold setae appearing green in some lights and arranged in lines diverging from median line (Fig. 5). Nudiocular area absent (Fig. 27)
- *exiguum s.l.*
- Scutum with groups of cream or brass-coloured, fine or scale-like setae in at least anterior two thirds and not arranged in diverging lines (Figs 13, 14). Nudiocular area present (Figs 30, 31) 7

7. Scutal setae arranged irregularly in groups in anterior two thirds and densely and individually on posterior third (Fig. 13). Basal section of radius of wing with single row of setae (Fig. 32). Claws of hind leg without basal teeth (Fig. 34). Paraproct broadly quadrangular with small, internal, membranous extension including anterior tail-like projection (Fig. 24); genital fork with distal ends of lateral arms well developed with small anterior processes (Fig. 40) *guianense s.l.*
 - Scutal setae arranged regularly in small groups, except singly and sparsely on posterior border (Fig. 14). Basal section of radius of wing bare (Fig. 33). Claws of hind leg with basal teeth (Fig. 35). Paraproct broadly rectangular with internal extension well developed, not membranous and lacking anterior tail-like projection (Fig. 25); genital fork with distal ends of lateral arms less developed with larger anterior processes (Fig. 41) *perplexum*
8. Scutal pattern largely black with 1+1 sub-median, posteriorly diverging, silver pruinose lines of varying length (Figs 4, 6, 7) 9
 - Scutal pattern almost equally black and silver pruinose, or mainly silver pruinose (Figs 1, 3, 8, 9) 11
9. Nudiocular area absent (Fig. 28). Cibarium armed with blunt tubercles (Fig. 45) *cauchense*
 - Nudiocular area absent or well developed (Figs 26, 29). Cibarium armed with sharply pointed teeth (Figs 44, 46) 10
10. Cibarial teeth present along anterior margin, including median protuberance, cornuae well developed (Fig. 44). Paraproct well developed, extending beyond ventral edge of cercus by length of cercus (Fig. 17) *clarki*
 - Cibarial teeth present along anterior margin, except for area of median concavity, cornuae poorly developed (Fig. 46). Paraproct small, only slightly protruding beyond ventral edge of cercus (Fig. 18) *limbatum*
11. Scutal pattern composed of black and silver, longitudinal pruinose areas in almost equal proportions (Figs 8, 9). Cibarium armed with teeth or blunt tubercles (Figs 47, 48). Paraprocts poorly developed with little extension beyond ventral surface of cercus (Figs 19, 20) 12
 - Scutal pattern composed of longitudinal, largely pruinose bands and narrow black bands (Figs 1, 3). Cibarium unarmed (Figs 42, 43). Paraprocts well developed with triangular extension beyond ventral margin of cerci (Figs 15, 16) 13
12. Cibarium with rows of sharp teeth along anterior margin (Fig. 47). Genital fork lightly sclerotised with poorly developed terminations to lateral arms (Fig. 38)
 *oyapockense s.l.*
 - Cibarium with blunt tubercles on anterior margin (Fig. 48). Genital fork well sclerotised with well developed terminations to lateral arms (Fig. 39) *quadrifidum*
13. Scutum with 1+1 longitudinal, sub-median bands wide and diverging anteriorly (Fig. 1); scutellum greyish black. Hind legs with distal part of femora yellow and of tibiae dark brown (Fig. 36) *spinibranchium*
 - Scutum with 1+1 longitudinal, sub-median bands converging anteriorly (Fig. 3); scutellum yellowish orange.

Hind leg yellowish with distal articulations of femora and tibiae dark brown (Fig. 37) *subpallidum* (dark form)

MALES

1. Thorax orange 2
 - Thorax grey or black 5
2. Scutum with 1+1 large, silver pruinose patches on anterior third of scutum beginning at anterior margin [best seen when specimen tilted] (Fig. 50). Gonostyle sub-triangular with no terminal spine, shorter than gonocoxite (Fig. 66); ventral plate wider than long with poorly developed keel and basal arms (Fig. 79)
 *subpallidum* (orange form)
 - Scutum without pattern (Figs 60-62). Gonostyle elongate with prominent terminal spine, as long as gonocoxite (Figs 73-75); ventral plate as wide as long or longer than wide, with or without well developed . keel and with well developed inwardly curved basal arms (Figs 86-88) 3
3. Keel of ventral plate slightly developed (Fig. 86). Legs distinctly dark brown except for most of basitarsi of mid and hind legs, which are yellow (Fig. 93) ... *lutzianum s.l.*
 - Keel of ventral plate well developed (Figs 87, 88). Legs distinctly yellowish or pale brown, including basitarsi of mid and hind legs (Figs 94, 95) 4
4. Keel of ventral plate with upright hairs (Fig. 87). Sc of wing with setae (see Fig. 32 for location of vein Sc on wing) *maroniense s.l.*
 - Keel of ventral plate with adpressed hairs (Fig. 88). Sc of wing without setae *perflavum*
5. Scutum without pattern 6
 - Scutum with pattern 9
6. Scutum with setae short and arranged in small packets or groups (Figs 53, 64) 7
 - Scutum with setae long and not arranged in small packets or groups (Figs 54, 58) 8
7. Gonostyle conical and shorter than gonocoxite (Fig. 68); ventral plate wider than long with triangular keel and reduced basal arms (Fig. 81) *exiguum s.l.*
 - Gonostyle sub-rectangular and as long as gonocoxite (Fig. 77); ventral plate wider than long with concavity in place of keel and well developed basal arms (Fig. 90)
 *perplexum*
8. Paramere with poorly developed spines (Fig. 91)
 *cauchense*
 - Paramere with well developed spines (Fig. 92)
 *quadrifidum*
9. Scutal pattern in anterior third of scutum consisting of 1+1 divergent, well defined, sub-median cunae or vittae (Figs 55-57, 59). Ventral plate sub-triangular or arcuate (Figs 82-85) 10
 - Scutal pattern consisting of extensive areas of white pruinosity in anterior third of scutum or black and white pruinose pattern involving whole scutum (Figs 49, 51, 52, 63). Ventral plate sub-triangular (Fig. 80), arcuate (Figs 78, 79) or H shaped (Fig. 89) 13
10. Scutum with sub-median cunae (Figs 56, 57). Gonostyle sub-quadrangular or conical with central



1



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4



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7

Colour patterns of the female thorax (anterior illumination). Fig.1: *Simulium spinibranchium*. Fig. 2: *S. subpallidum* (orange form). Fig. 3: *S. subpallidum* (dark form). Fig. 4: *S. clarki*. Fig. 5: *S. exiguum* s.l. Fig. 6: *S. cauchense*. Fig. 7: *S. limbatum*



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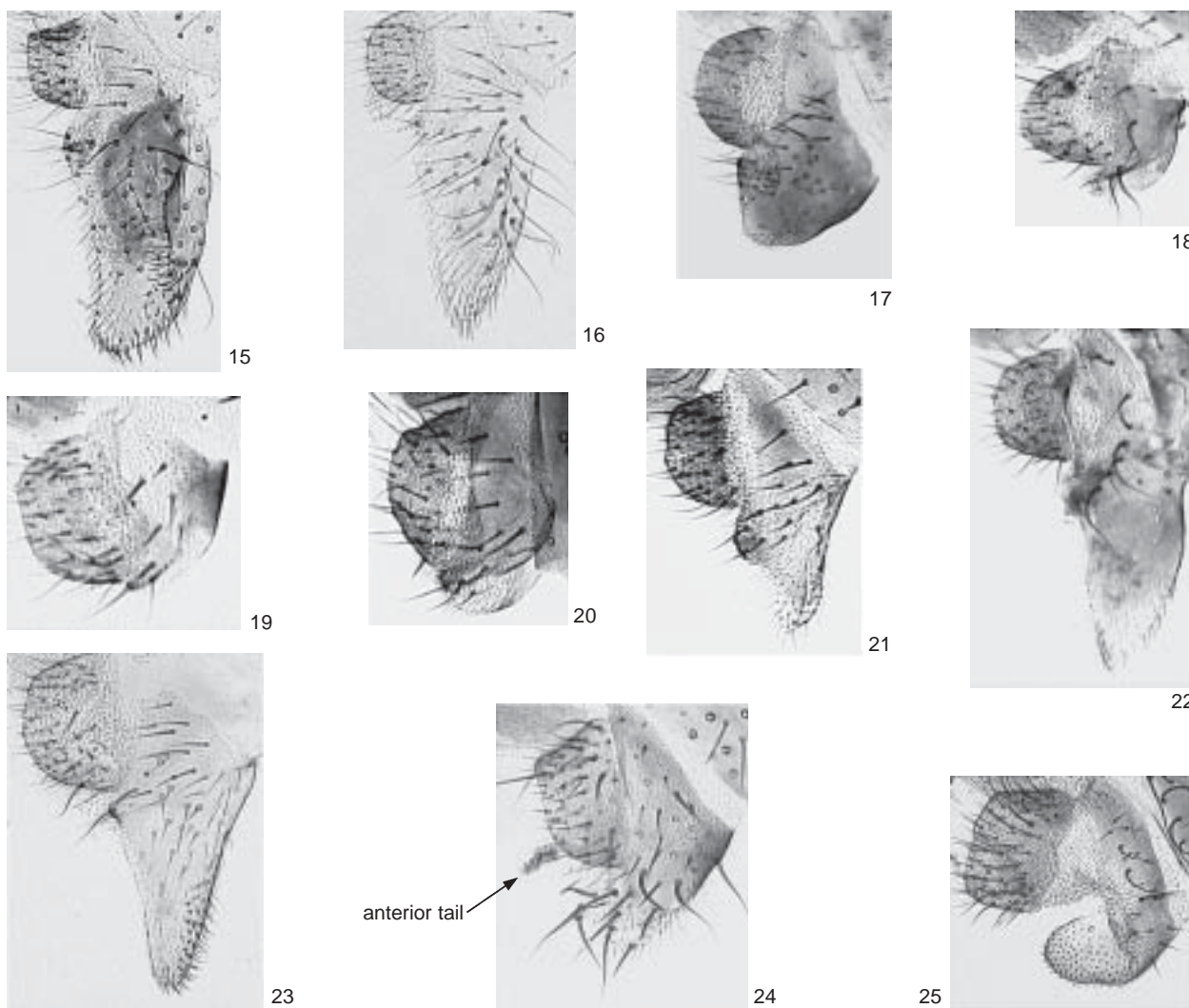


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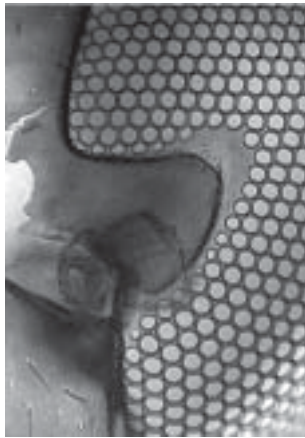
Colour patterns of the female thorax (anterior illumination). Fig. 8: *Simulium oyapockense* s. l. Fig. 9: *S. quadrifidum*. Fig. 10: *S. lutzianum* s.l. Fig. 11: *S. maroniense* s.l. Fig. 12: *S. perflavum*. Fig. 13: *S. guianense* s.l. Fig. 14: *S. perplexum*

or terminal spine and considerably shorter than gonocoxite (Figs 70, 71) 11
 - Scutum with sub-median thin vittae (Figs 55, 59).
 Gonostyle conical with terminal spine and about as long as gonocoxite (Figs 69, 72) 12
 11. Sub-median cunae each with smaller black cuna within (Fig. 56). Gonostyle sub-quadrangular with central spine (Fig. 70) *limbatum*
 - Sub-median cunae with no internal black cunae (Fig. 57).
 Gonostyle conical with terminal spine (Fig. 71)
 *oyapockense s.l.*
 12. Paramere with poorly developed spines (Fig. 91)
 *cauchense*
 - Paramere with well developed spines (Fig. 92)
 *quadrifidum*
 13. Scutal pattern consisting of thick black median vitta extending for three fourths scutal length and 1+1 lateral, wide, black vittae in middle portion of scutum (Fig. 63).

Gonostyle conical with terminal spine and twice as long as gonocoxite (Fig. 76); ventral plate H-shaped with central prominence (Fig. 89) *guianense s.l.*
 - Scutal pattern consisting of extensive areas of white pruinosity in anterior third of scutum (Figs 49, 51, 52).
 Gonostyle conical or sub-quadrangular, with or without terminal spine and as long as or shorter than gonocoxite (Figs 65-67); ventral plate triangular or arcuate (Figs 78-80) 14
 14. Scutal pattern of 1+1, sub-median, broad, white pruinose bands on anterior scutal margin (Fig. 52). Gonostyle conical with terminal spine, shorter than gonocoxite (Fig. 67); ventral plate triangular (Fig. 80) *clarki*
 - Scutal pattern consisting of white pruinose band along anterior scutal margin (Figs 49, 51). Gonostyle sub-quadrangular or conical with no spine and shorter than gonocoxite (Figs 65, 66); ventral plate arcuate (Figs 78, 79) 15



Cercus and paraproct. Fig. 15: *Simulium spinibranchium*. Fig. 16: *S. subpallidum*. Fig. 17: *S. clarki*. Fig. 18: *S. limbatum*. Fig. 19: *S. oyapockense s.l.* Fig. 20: *S. quadrifidum*. Fig. 21: *S. lutzianum s.l.* Fig. 22: *S. maroniense s.l.* Fig. 23: *S. perflavum*. Fig. 24: *S. guianense s.l.* Fig. 25: *S. perplexum*



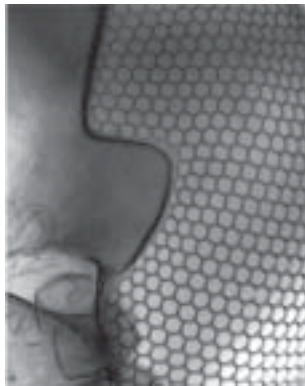
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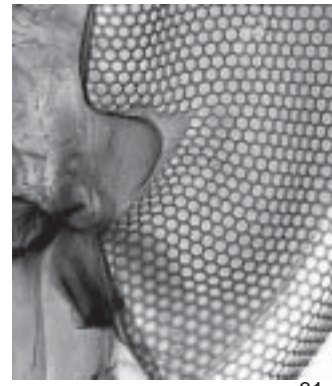
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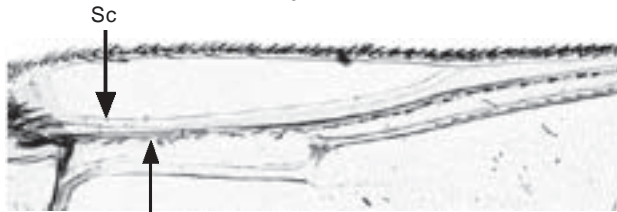
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Sc
basal section of R

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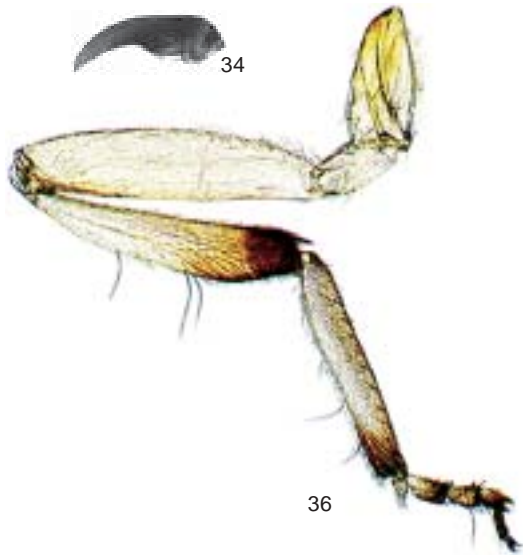
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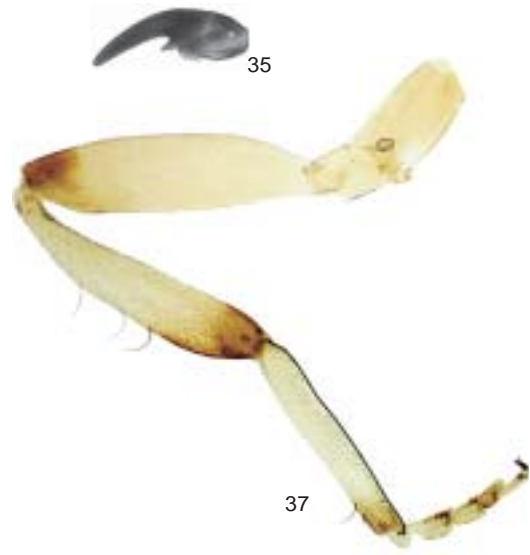
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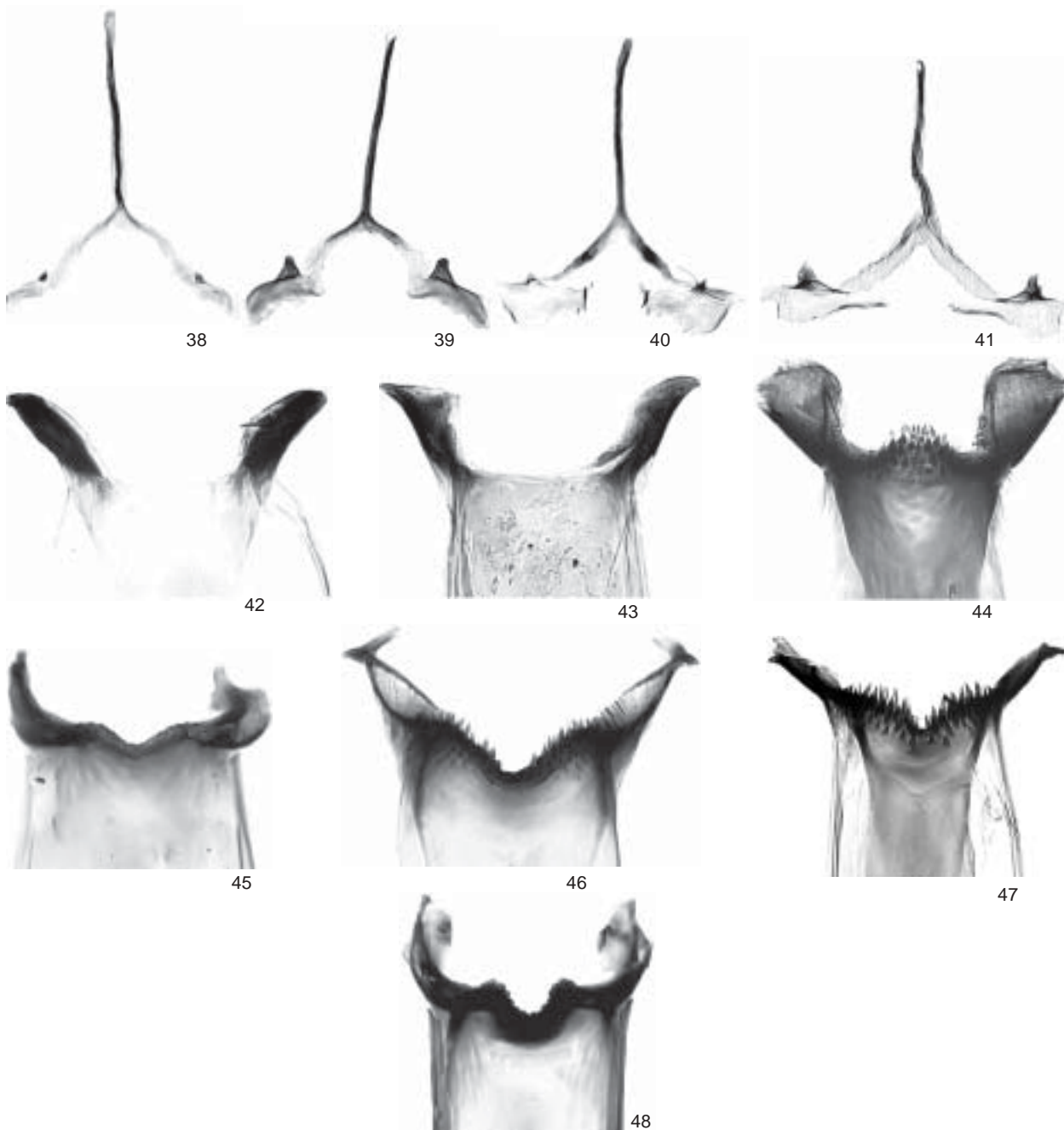
Nudiocular area. Fig. 26: *Simulium clarki*. Fig. 27: *S. exiguum s.l.* Fig. 28: *S. cauchense*. Fig. 29: *S. limbatum*. Fig. 30: *S. guianense s.l.* Fig. 31: *S. perplexum*. Wing. Fig. 32: *S. guianense s.l.* Fig. 33: *S. perplexum*. Hind leg claws. Fig. 34: *S. guianense s.l.* Fig. 35: *S. perplexum*. Colour pattern and proportions of female legs. Fig. 36: *S. spinibranchium*. Fig. 37: *S. subpallidum* (dark form). Sc: subcosta; R: radius

15. Gonostyle sub-quadrangular, less than half as long as gonocoxite (Fig. 65) *spinibranchium*
 - Gonostyle conical, almost as long as gonocoxite (Fig. 66) *subpallidum* (dark form)

PUPAE

- 1. Gill with 4 to 8 filaments 2
- Gill with 10 or more filaments 11
- 2. Gill with 4 filaments 3
- Gill with 6 to 8 filaments 4
- 3. Primary branching of gill in vertical plane; gill branch

bifurcations usually not at same level at mid point of gill (Fig. 100). Abdominal tergite V without spines or spines combs *cauchense*
 - Primary branching of gill in horizontal plane; gill branches usually bifurcate at same level in basal 1/5 of gill (Fig. 103). Abdominal tergite V with weak sub-median row of spines (usually present) along anterior border terminating in weak patch of spines combs at margins *quadrifidum*
 4. Gill with 6 filaments 5
 - Gill with 8 filaments 7



Genital fork. Fig. 38: *Simulium oyapockense* s.l. Fig. 39: *S. quadrifidum*. Fig. 40: *S. guianense* s.l. Fig. 41: *S. perplexum*. Cibarium. Fig. 42: *S. spinibranchium*. Fig. 43: *S. subpallidum*. Fig. 44: *S. clarki*. Fig. 45: *S. cauchense*. Fig. 46: *S. limbatum*. Fig. 47: *S. oyapockense* s.l. Fig. 48: *S. quadrifidum*

5. Gill approximately half length of pupa (gill length - \bar{x} = 1.0 mm, range 0.8-1.5 mm, n = 10; pupa length - \bar{x} = 1.9 mm, range 1.5-2.1 mm, n = 10*), with basal branching and gill trunk dividing into three primary branches (Fig. 102) *oyapockense* s.l.
 - Gill almost as long as or longer than pupa, gill branching varying from basal to most distal at mid point of gill and gill trunk dividing into two or three primary branches (Figs 98, 101) 6

6. Gill slightly longer than pupa (gill length - \bar{x} = 3.3 mm, range 2.4-4.1 mm, n = 10; pupa length - \bar{x} = 2.9 mm, range 2.2-3.5 mm, n = 10); gill branching basal and gill trunk dividing into three primary branches (Fig. 98) *clarki*
 - Gill almost as long as pupa (gill length - \bar{x} = 2.4 mm, range 2.1-2.8 mm, n = 10; pupa length - \bar{x} = 2.6 mm, range 1.8-3.6 mm, n = 10); gill branching varying from basal to most distal at mid point of gill and gill trunk dividing into two primary branches (Fig. 101) *limbatum*

7. Gill filaments broadest at base and becoming progressively finer towards tip, thereby resembling stag's antler (Fig. 96) *spinibranchium*
 - Gill filaments narrow along entire length 8

8. Gill filaments arranged in bunch with all secondary branches arising very near gill base (Fig. 108) *perflavum*
 - Gill filaments not arranged in a bunch with only some secondary branches arising very near gill base (Figs 97, 99, 104) 9

9. Gill trunk bifurcating near base (Fig. 104).....*lutzianum* s.l.
 - Gill trunk dividing into three primary branches near base (Figs 97, 99) 10

10. Cocoon with closely meshed fibres (Fig. 113). Trichomes of frontoclypeus bifid to 5-branched and tubercles sparsely distributed (Fig. 115) *subpallidum*
 - Cocoon with open weave (Fig. 114). Trichomes of



49



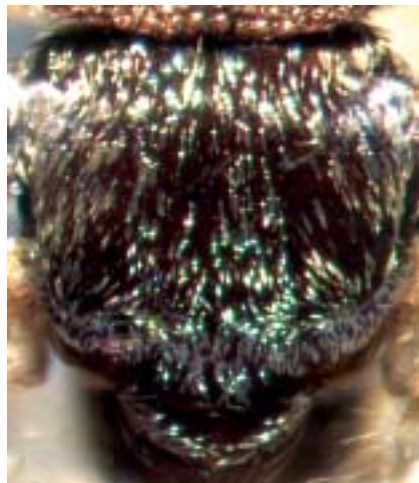
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Colour patterns of the male thorax (anterior illumination). Fig. 49: *Simulium spinibranchium*. Fig. 50: *S. subpallidum* (orange form). Fig. 51: *S. subpallidum* (dark form). Fig. 52: *S. clarki*. Fig. 53: *S. exiguum* s.l. Fig. 54: *S. cauchense* (without cunae)

frontoclypeus simple or bifid (rarely with 3 branches) and tubercles densely distributed (Fig. 116) *exiguum s.l.*

11. Gill with 10-14 filaments (Figs 105, 106, 109, 111) .. 12
- Gill with 17-23 filaments (Fig. 107) *maroniense s.l.*

12. Gill with 10-14 long, fine filaments rounded apically; gill trunk branching basally into 10 primary branches, some of which may have secondary bifurcations (Figs 105, 106) *kabanayense*
- Gill with 12 short, pointed filaments; gill trunk branching basally to form four primary branches (Figs 109, 111) 13

13. Gill filaments with annulations on distal part of gill less accentuated with spicules (Fig. 110) *guianense s.l.*
- Gill filaments with annulations on distal parts of gill accentuated by forwardly directed processes (Fig. 112)
..... *perplexum*

*data from Shelley et al. (1997)

NOTES ON THE BIOSYSTEMATICS OF SPECIES

Simulium (Chirostilbia) spinibranchium Lutz

This species is dealt with in Coscarón (1991), Py-Daniel & Shelley (1980) and Shelley et al. (2000). It is an uncom-

mon highland species previously only recorded from Brazil and Southern Venezuela. In Guyana (see Material Examined) it was collected in the mountainous area of the Orinduik region near the R Ireng. Pupae were collected in small waterfalls, and on rocks covered with red algae and attached to dead leaves. It has been collected at similar sites on the Brazilian side of the R Ireng (R Maú in Brazil) where females voraciously bite man (AJ Shelley & APA Luna Dias, unpublished data).

Simulium (Chirostilbia) subpallidum Lutz

A full description is given by Coscarón (1991) and Shelley et al. (2000); the latter authors summarise the relevant literature. Over its range this species varies in scutal coloration from faded orange to light grey. Black specimens were also recorded in the present work. It is common and widespread throughout neighbouring Brazil and also occurs in Venezuela, Argentina, and Paraguay. Pupae were collected on vegetation in rivers 3-50 m wide, with rocky beds, in the Rupununi District.

Simulium (Inaequalium) clarki Fairchild

Since the original description by Fairchild (1940) based on specimens from Panama the species has had no full taxonomic treatment. It has also been recorded from Brazil



Colour patterns of the male thorax (anterior illumination). Fig. 55: *Simulium cauchense* (with cunae). Fig. 56: *S. limbatum*. Fig. 57: *S. oyapockense s.l.* Fig. 58: *S. quadrifidum* (without cunae). Fig. 59: *S. quadrifidum* (with cunae)

and Venezuela and now in the northern Rupununi District of Guyana, where it was anthropophilic and found breeding in 50 m wide rivers. In the neighbouring part of Brazil it was also collected biting man and found breeding in smaller streams (AJ Shelley & APA Luna Dias, unpublished data).

Simulium (Notolepria) exiguum Roubaud
(species complex)

Shelley et al. (1997, 2000) reviewed the taxonomy of this widespread, commonly occurring Neotropical species. Many populations of this species complex are anthropophilic and some are vectors of human onchocerciasis, but in some areas almost total zoophily occurs. *S. exiguum s.l.* has been collected breeding on vegetation in the R Takutu (R Tacutu in Brazil) on the border between Brazil and Guyana.

Simulium (Psaroniocompsa) cauchense
Floch & Abonnenc

This zoophilic species has been reviewed in Shelley et al. (1997) and occurs in Brazil, French Guiana and Venezu-

ela. In Guyana *S. cauchense* was collected in 15-50 m wide rivers, attached to leaves and submerged vegetation.

Simulium (Psaroniocompsa) limbatum Knab

S. limbatum is a voracious, anthropophilic species occurring in the Guianas, Venezuela, and Brazil and has frequently been confused with *S. incrustatum*, which it greatly resembles. It is generally associated with small to medium flowing rivers in flat savanna areas. Shelley et al. (1997) described the morphological differences and previous taxonomic confusion surrounding these two species. In the present survey *S. limbatum* was collected from the southern Rupununi District biting man and breeding on leaves in 1.5 m to 10 m wide rivers. All the specimens previously identified by Davies (1973) as *S. incrustatum* are *S. limbatum*. Preliminary studies on its man-biting densities and insecticide trials with temephos have been reported (Humphrys et al. 1977, Rambajan 1981 ab). Shelley et al. (1987) showed that this species is capable of acting as a host to *Onchocerca volvulus* outside the Amazonia onchocerciasis focus in Brazil and hence it may be a vector of *M. ozzardi* in Guyana.



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Colour patterns of the male thorax (anterior illumination). Fig. 60: *Simulium lutzianum s.l.* Fig. 61: *S. maroniense s.l.* Fig. 62: *S. perflavum*. Fig. 63: *S. guianense s.l.* Fig. 64: *S. perplexum*

Simulium (Psaroniocompsa) oyapockense Floch & Abonnenc (species complex)

This species was originally described from French Guiana and is now known to be common and widespread in South America. Shelley et al. (1997) reviewed its complicated taxonomy and provided a full description of all stages. *S. oyapockense s.l.* is a species complex in which most populations are anthropophilic and is closely related to the anthropophilic *S. roraimense* Nunes de Mello. The two species can only be separated morphologically in the male and pupa and hence man-biting females of the two species cannot be distinguished. In neighbouring Brazil both species occur, often sympatrically, and an atypical form of male *S. oyapockense s.l.* occurs where the scutal cunae are extended into tails. This atypical form also occurs in Guyana (Fig. 57), but no *S. roraimense* has yet been recorded. Most of the specimens from Guyana were collected biting man and have been recorded as *S. oyapockense s.l.* However, it is likely that *S. roraimense* will be found in this country and at such a time the status of these females will need to be re-examined. *S. oyapockense s.l.* was commonly found in the Rupununi District of Guyana biting man (Material Examined). Its breeding grounds are often difficult to locate and tend to be in rapids in larger, fast running rivers. Humphrys et al. (1977) and Rambajan (1981b) made observations on the biting habits of this species around the town of Lethem in the southern Rupununi District (Map). *S. oyapockense s.l.* is medically important because of its role as a vector of two filarial species that infect man. In the Rupununi District and in the adjacent savanna region of Brazil it is a vector of *M. ozzardi* (Nathan et al. 1982, Moraes et al. 1985) and in the Amazonia onchocerciasis focus in Brazil it is the primary vector of *O. volvulus* (Shelley et al. 1997).

Simulium (Psaroniocompsa) quadrifidum Lutz

This zoophilic species has been covered in Shelley et al. (1997) and is found in Bolivia, Brazil, Ecuador, Surinam, and Venezuela. *S. quadrifidum* was collected attached to dead leaves in small rapids, in 10 m wide rivers in the southern part of the Rupununi District.

Simulium (Psilopelmia) kabanayense Ramírez Pérez & Vulcano, 1973

Only three pupal exuviae of this species exist in the BMNH collection. They were originally identified as *S. lutzianum* (Smart 1940), but have now been identified as *S. kabanayense*, a presumably zoophilic species only previously recorded from Venezuela (Ramírez Pérez & Vulcano 1973, Ramírez Pérez 1983, Hamada & Grillet 2001). The specimens from Guyana were collected from a small stream in northern Rupununi District.

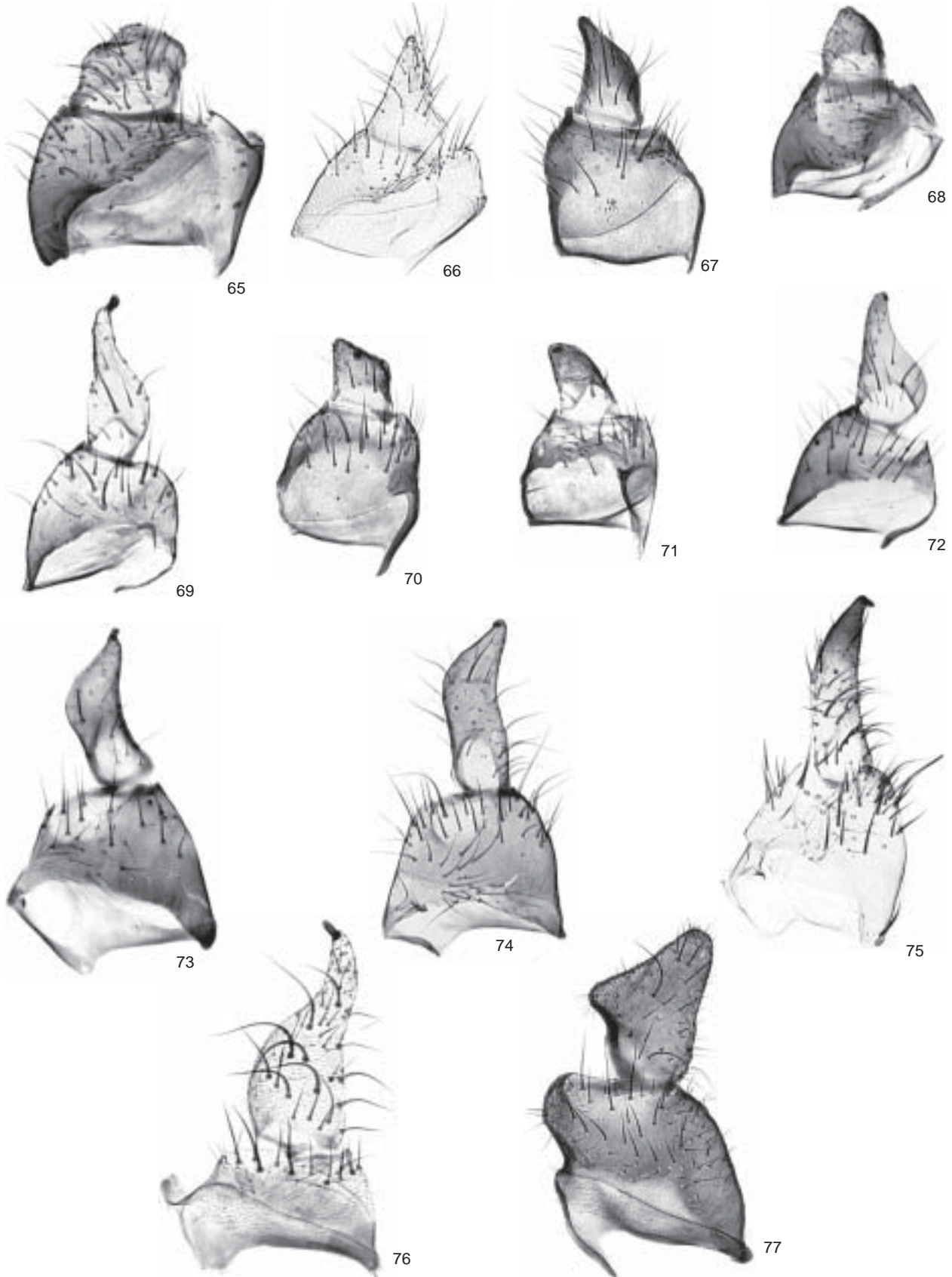
Simulium (Psilopelmia) lutzianum Pinto, 1932 (species complex)

The species is dealt with in Sawyer (1991) and Shelley et al. (1989a, 1997) and occurs in Argentina, Bolivia, Brazil, Colombia, Ecuador, Peru, and Venezuela. It is usually zoophilic, but has been recorded biting man in Southern Brazil (Shelley et al. 2000). In Guyana pupae were col-

lected on vegetation in small rapids in 15 m wide rivers.

Simulium (Psilopelmia) maroniense Floch & Abonnenc, 1946 (species complex)

This is a species found in the R Orinoco tributaries of Southern Venezuela, the northern tributaries of the R Amazon in Brazil and in the Guianas. There have been some taxonomic problems concerning this species and the closely related *S. rorotaense* described by Floch and Abonnenc (1946) in the same paper. In a paper reviewing the taxonomy of several Neotropical species Shelley et al. (1984) regarded *S. maroniense s.l.*, *S. wuayaraka* Ortiz, 1957, *S. fulvinotum* Cerqueira & Nunes de Mello in Cerqueira, 1967 and *S. ignacioi* Ramírez Pérez and Vulcano, 1973 as synonyms of *S. rorotaense*. During the publication of this paper Ramírez Pérez (1983) was issued in which *S. maroniense s.l.* and *S. rorotaense* were treated as valid species, *S. wuayaraka* was considered a synonym of *S. maroniense s.l.* and *S. ignacioi* a synonym of *S. rorotaense*. A discussion of these actions and subsequent treatment of these names by other reviewers is given in Shelley et al. (1997), who maintained their original synonymy list under *S. rorotaense* as expounded in their 1984 paper. Since then Hamada and collaborators have carried out more extensive morphological and cytological work and concluded that both *S. maroniense s.l.* and *S. rorotaense* are valid species. Hamada and Adler (1998) were unable to find differences between adult *S. maroniense s.l.* and *S. rorotaense*, but in specimens collected from the Brazilian Amazon were able to distinguish pupae in the following ways. *S. maroniense s.l.* has thicker, more darkly pigmented gills, dorsal filaments shorter than ventral and more basal branching. The filaments form a rosette in *S. maroniense s.l.*, but are bunched forwards in *S. rorotaense*. Trichome branching and tubercle density in pupae were variable in each species [as we also found], but generally tubercles were larger and more densely distributed in *S. maroniense s.l.* In this paper they considered *S. ignacioi* to be a valid species, but provided no evidence to support this view and apparently did not examine type material. In their key the pupa is recorded as indistinguishable from that of *S. rorotaense*, with which Ramírez Pérez (1983) had synonymised it, based on the original description of *S. ignacioi* by Ramírez Pérez and Vulcano (1973). A later paper by Hamada and Grillet (2001) with keys to species in two adjacent regions of Southern Venezuela and Northern Brazil stated that Hamada and Adler (1998) had based their recognition of species status for *S. ignacioi* on gill filament numbers and chromosomal configuration [although not stated in the paper]. In their key to last instar larvae, Hamada and Grillet (2001) recorded the gill histoblast of *S. ignacioi* with 14-17 filaments (usually 16) [the original description of Ramírez Pérez and Vulcano (1973) recorded 17-20 filaments in 8 specimens examined] compared to *S. maroniense s.l.* and *S. rorotaense* with 17-23 filaments (usually 18-21). The pupa of *S. ignacioi* is again keyed out with that of *S. rorotaense*, having 17-23 thin, lightly pigmented filaments, not arranged in the form of a rosette [In couplet 17 of the key an error exists where specimens with gills with "10-17



Gonocoxite and gonostyle. Fig. 65: *Simulium spinibranchium*. Fig. 66: *S. subpallidum*. Fig. 67: *S. clarki*. Fig. 68: *S. exiguum* s.l. Fig. 69: *S. cauchense*. Fig. 70: *S. limbatum*. Fig. 71: *S. oyapockense* s.l. Fig. 72: *S. quadrifidum*. Fig. 73: *S. lutzianum* s.l. Fig. 74: *S. maroniense* s.l. Fig. 75: *S. perflavum*. Fig. 76: *S. guianense* s.l. Fig. 77: *S. perplexum*

filaments" are compared to those with gills "with more than 17 filaments"]. In the key to pupae they also recorded *S. ignacioi* and *S. rorotaense* as having lateral fenestrations in the cocoon, that are absent in *S. maroniense s.l.* We examined pupae of *S. maroniense s.l.* collected and identified by Hamada and Xavier from Brazil and *S. rorotaense* collected by Hamada and Fouque from French Guiana (see Material Examined) and both species showed lateral fenestrations in the cocoon. Hamada and Adler (1999) provided cytological evidence supporting the validity of *S. maroniense s.l.*, which was recorded as having four cytotypes in Brazil compared to the single cytotype of *S. rorotaense*. The two species were separated by the presence of the fixed terminal inversion IIIIL-5 in *S. maroniense s.l.* Chromosomal evidence was also used to support the synonymy of *S. fulvinotum* (Py-Daniel 1982, Shelley et al. 1984, 1997) with *S. rorotaense*, but insufficient material was available for comment on the status of *S. ignacioi* and *S. wuayaraka*. Subsequently, Hamada and Fouque (2001) showed a similar karyotype for *S. rorotaense* topotypes from French Guiana, but were unable to obtain *S. maroniense s.l.* from its type locality because of the construction of a dam in the area. Scarpassa and Hamada (2003) were unable to find diagnostic loci between *S. rorotaense* and a cytotype of *S. maroniense s.l.* in recent studies on isoenzyme variation of several species from the Brazilian Amazon.

We have now re-examined the type specimens of *S. maroniense s.l.* and *S. rorotaense*, examined named specimens of the two species loaned by Dr Neusa Hamada from the Inpa collection, specimens from the BMNH collection, kindly reviewed by Dr Neusa Hamada, and from CUAC. We have the following comments. We were only able to locate the lectotypes and paralectotypes of the two species in the IP in Paris. The other paralectotypes referred to in the original publication and assumed by Shelley et al (1984) to be in the IP, French Guiana could not be located there and are presumed lost (N Hamada, pers. commun.). The difficulty in establishing whether *S. maroniense s.l.* is a synonym of *S. rorotaense* still lies in the fact that the slide of the reared female lectotype of the former species lacks the pupal exuviae and of the male paralectotype all but the abdomen of the pupal exuviae, the stage in which the only significant interspecific characters occur. Recourse has therefore had to be made to the authors' original descriptions and subsequent work by Hamada and collaborators. The original authors (Floch & Abonnenc, 1946) described *S. maroniense s.l.* as a species distinct from *S. rorotaense* based on differences between the female genitalia and cibarium and between pupae. Later, Coscarón (1990) distinguished the two species based on the size of the sensory organ in the maxillary palp, the size of the nudiocular triangle and minor differences in pupal morphology, all of which are intraspecific variations. Our re-examination of the adult types and specimens recorded in "Material Examined" revealed no differences in adult morphology. In the pupae the original authors referred to the presence of the following characters in *S. rorotaense* with observations for *S. maroniense s.l.* in brackets - 2-3 branched trichomes (3-6), largely unpigmented thorax and gill (finely pigmented), small and

sparsely distributed tubercles (strong and densely distributed) and no great difference in gill filament lengths (shorter dorsally) and some secondary gill branches not basal (relatively basal). We recorded the following for the female lectotype of *S. rorotaense*- the thoracic trichomes vary from single to at least 5 branched (trichome broken) and of the head bifid to 4-branched, no pigmentation is evident and tubercles are relatively small and sparsely distributed, gill filaments are approximately of equal length and secondary branching can occur up to the middle part of the gill. Pupae in the BMNH collection and loaned from the Inpa collection (see Material Examined) for *S. maroniense s.l.* showed thoracic trichomes with 1-9 branches, pigmented thorax and gills, well developed, densely distributed thoracic tubercles, dorsal gill filaments shorter than ventral and branching always basal. The principal character of the rosette form of the *S. maroniense s.l.* gill and its shorter dorsal filaments, both not present in *S. rorotaense*, was efficient in separating most specimens. However, in some (even preserved in spirit) it was difficult to make an accurate identification, which might suggest the presence of a cline with the rosette and forward bunched forms of the filaments representing either extreme. Consequently, we agree with the re-validation of *S. maroniense s.l.*, but advocate an examination of larger series of specimens to assess the variability of the form of the gill in different localities.

Our recognition of the type status of *S. maroniense s.l.* now opens the question of which names are synonymous with which species. It is now known from cytological evidence that *S. fulvinotum* is a synonym of *S. rorotaense* (Hamada & Adler, 1999). We previously regarded *S. ignacioi* and *S. wuayaraka* as synonyms of *S. rorotaense* (Shelley et al. 1984, 1997), while Ramírez Pérez (1983) synonymised *S. ignacioi* with *S. rorotaense* and *S. wuayaraka* with *S. maroniense s.l.* The types of *S. ignacioi* and *S. wuayaraka* are now lost to science [The private collection of Dr Ramírez Pérez is now in such a poor condition as to be of limited value (E Grillet, pers. commun.) and is not freely accessible; the private collection of Dr Vulcano is not available for examination and the other depositories cited in the original descriptions have lost the specimens]. Therefore, we can only consider the original descriptions of the two species concerned, taking into account the comments made in Shelley et al. (1997) in relation to subsequent publications by Ramírez Pérez on *S. maroniense s.l.* and *S. rorotaense*. In addition to these we agree that the figure of the gill of *S. maroniense s.l.* in Ramírez Pérez (1983) is of this species because of the shorter dorsal filaments and the gill of *S. rorotaense* appears to be of this species. The recent work by Hamada and Grillet (2001) revealed only *S. maroniense s.l.* in several watercourses in the Gran Sabana area of Venezuela and no *S. rorotaense*, but higher sample numbers are required before any conclusions on distribution patterns may be drawn. *S. ignacioi* is difficult to place because figures of the original description (Ramírez Pérez & Vulcano 1973) are different for this species in Ramírez Pérez et al. (1983), which also has a more complete description. In the latter publication the male scutal pattern, gill, female and male genitalia have all been redrawn and these figures are

replicated to illustrate *S. rorotaense* (with which *S. ignacioi* is synonymised) in Ramírez Pérez (1983). The latter paper figures the male scutum with 1+1 sub-median, comma-shaped marks on the anterior scutal border, but no mention of these is made in the text. We have now examined further material of *S. maroniense s.l.* from the R Mucajai in Brazil and of *S. rorotaense* from the Reserva Ducke, near Manaus in Brazil and have noted the presence of these marks in one male of each species. They are of a lighter orange than the rest of the scutum and are only visible when the light is anterior to the specimen with the thorax tilted to an almost lateral position. We still regard *S. ignacioi* as a synonym of *S. rorotaense* because the figure of Ramírez Pérez and Vulcano (1973) shows secondary branching of the gill filaments less basal than in *S. maroniense s.l.* and no evidence of the dorsal filaments being shorter than the ventral, two of the main features typical of *S. rorotaense*. *S. wuayaraka* was described from 16 man-biting females, whose description is similar to those of *S. maroniense s.l.* and *S. rorotaense*, and so in the absence of pupae no objective decision may be made on synonymy. The distribution of *S. maroniense s.l.* and *S. rorotaense* is not sufficiently known to use this as a basis for synonymy. Therefore, for taxonomic simplicity we accept the synonym of *S. wuayaraka* with *S. maroniense s.l.* recorded by Ramírez Pérez (1983).

Distribution records for *S. maroniense s.l.* and *S. rorotaense* recorded in Shelley et al. (1997) are accordingly amended as shown in the "Material Examined". Those for Ramírez Pérez (1983) need to be verified.

Coscarón (1990) placed *S. maroniense s.l.* and *S. rorotaense* in the subgenus *Ectemnaspis*.

Simulium (Psilopelmia) perflavum Roubaud, 1906

Morphological descriptions and taxonomic details of this species may be found in Coscarón (1990, 1991) and Ramírez Pérez (1983). Rambajan (1979) described *S. nilesi* from the southern Rupunini District, but this name was later synonymised with *S. perflavum* by Py-Daniel (1989). The zoophilic species occurs in Argentina, Brazil, Paraguay, and Venezuela (Crosskey & Howard 1997). In Guyana *S. perflavum* was collected in muddy, slow flowing rivers of 1-5m wide with pupae attached to leaves and submerged grasses.

Simulium (Trichodagmia) guianense Wise, 1911
(species complex)

This anthropophilic species, which is a primary vector of human onchocerciasis in Brazil and Venezuela, has been revised by Shelley et al. (1997). Since then four pinned females have been found in the Nearctic accessions of the BMNH. These are the four missing specimens of the 11 sent by Melville to Wise (Wise 1911). These were presented by Dr KS Wise and bear printed labels, but not labels in the hand of Wise (see Material examined for details). Extra labels have been added to the lectotype and original paralectotypes indicating Melville as collector (Wise had used his own name on the labels) and extra details have been added to the four paralectotypes recently found in the BMNH. All four specimens are *S. guianense s.l.* and the genitalia of two confirmed this iden-

tification. They are undoubtedly paralectotypes and have been labelled accordingly. This species is also found in Brazil, the other Guianas and Venezuela. *S. guianense s.l.* was collected on submerged vegetation, especially of the "Orin Weed" of the family Podostemaceae, in fast flowing stretches close to waterfalls or steep rapids of 50 m wide rivers with rocky beds.

Simulium (Trichodagmia) perplexum Shelley,
Maia-Herzog, Luna Dias & Couch, 1989

This anthropophilic species is only known from its type locality at the Kaieteur Falls, Potaro R. Pupae of *S. perplexum* were collected attached to submerged vegetation in the family Podostemaceae by Smart (1940), who identified it as *S. guianense s.l.* to which it is closely related. A full description of this species is found in Shelley et al. (1989b).

MATERIAL EXAMINED

Simulium (Chirostilbia) spinibranchium Lutz, 1910

GUYANA
PINNED

Rupununi, Orinduik, ADC's Creek, [site 32, (GUY 79/1c, GUY 79/2, GUY 74/4)], 4°43'N 60°02.9'W, 450 m; 3.xii.1970, (*JB Davies*) - 3 females, 1 male (reared, 1 without pupa) (BMNH, B.M. 1999-16, specimen nos. 151227, 151228 151231). Rupununi, Orinduik, ADC's Creek, [site 32, (GUY 70/1a)], 4°43'N 60°02.9'W, 450 m; 3.xii.1970, (*JB Davies*) - 1 male (reared) (BMNH, B.M. 1999-16, specimen no. 151226).

SPIRIT

Rupununi, Orinduik, ADC's Creek, [site 32, (GUY 70)], 4°43'N 60°02.9'W; 2.xii.1970, (*JB Davies*) - 1 pupa (BMNH, B.M. 1999-16, sample no. 151158). Rupununi, Orinduik, ADC's Creek, (site 32, [GUY 70/6]), 4°43'N 60°02.9'W, 450 m; 2.xii.1970, (*JB Davies*) - several pupae (BMNH, B.M. 1999-16, sample no. 151165).

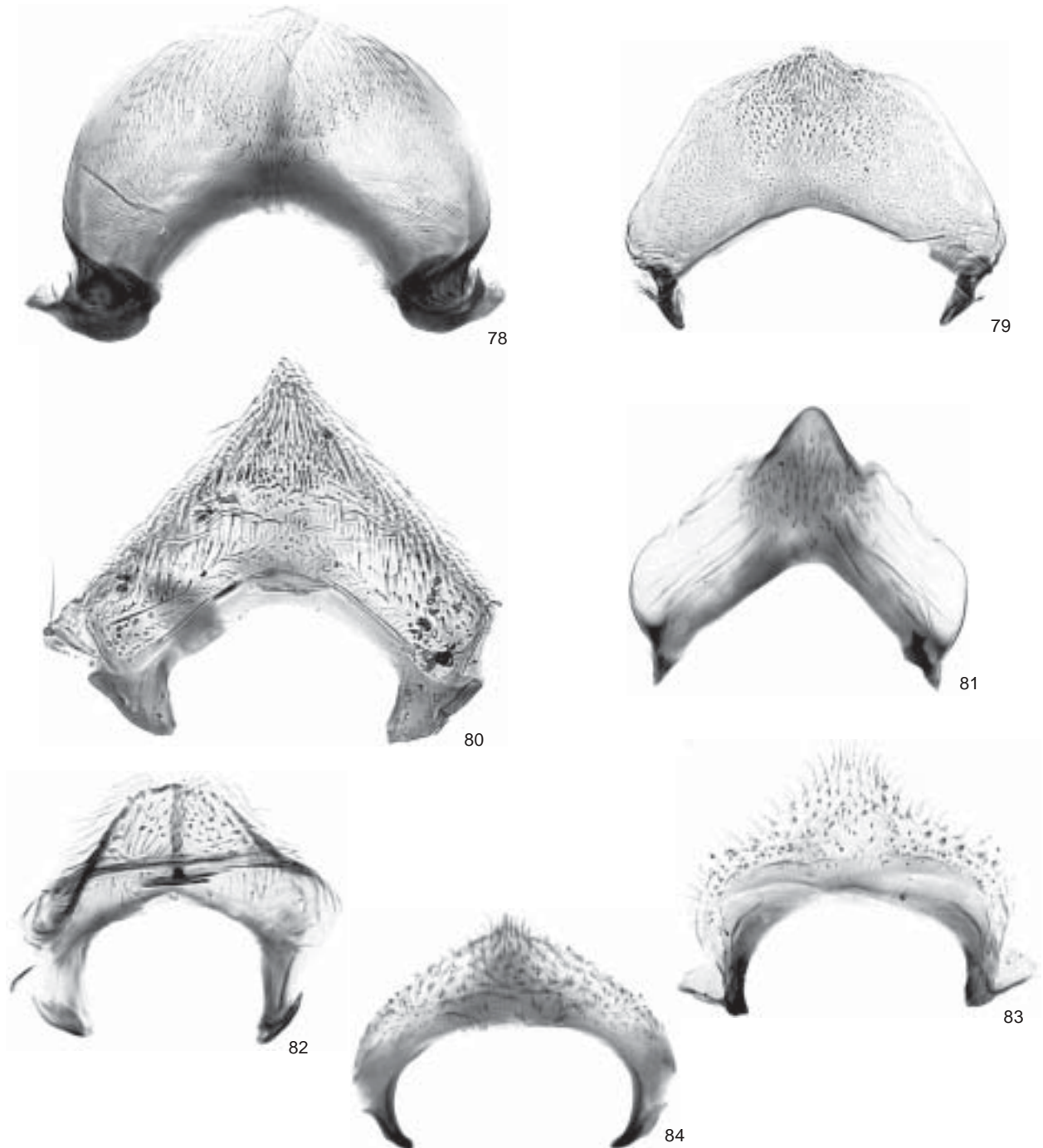
Simulium (Chirostilbia) subpallidum Lutz, 1910

GUYANA
PINNED

Rupununi, Orinduik, R. Ireng, [site 13, (GUY 22/1; 23/2, 4; 25/1)], 4°44'N 60°02.9'W, 450 m; 23.iii.1970, (*JB Davies*) - 2 females, 2 males (reared) (BMNH, B.M. 1999-16, specimen no. 151212, 151215, 151224, 151243). Rupununi, Orinduik, R. Ireng, (site 10, [GUY 16/20]), 4°44.5'N 60°02.4'W, 460 m; 23.iii.1970, (*JB Davies*) - 1 male (reared) (BMNH, B.M. 1999-16, specimen no. 151210). Rupununi, Orinduik, R. Ireng, [site 11, (GUY 19/3)], 4°44.3'N 60°02.3'W, 460 m; 22.iii.1970, (*JB Davies*) - 1 male (reared) (BMNH, B.M. 1999-16, specimen no. 151211). Rupununi, Orinduik, R. Ireng, (GUY 23/1), 4°44'N 60°02'W, 450 m; 23.iii.1970, (*J.B. Davies*) - 1 male (BMNH, no. 141214). Rupununi, Orinduik, un-named stream (site 12, GUY 64/6; 68/2; GUY 66/1), 4°44.5'N 60°02'W, 455-460 m; 1.xii.1970, (*JB Davies*) - 2 males (reared, but not associated with pupa) (BMNH, B.M. 1996-16, no. 141218; 151259). Rupununi, Orinduik, near R. Ireng crossing, un-named stream [site 30, (GUY 64/3-48-9)], 4°44.5'N 60°02.8'W, 460 m; 23.iii.1970, (*JB Davies*) - 4 females, 1 male (reared, two but not associated with pu-

pae) (BMNH, B.M.1999-16, sample no.151216-21). Rupununi, Orinduik, ADC's Creek, [site 32, (GUY 70/2)], 4°43'N 60°02.9'W; 2.xii.1970, (JB Davies) - 1 female (reared) (BMNH, B.M.1999-16, specimen no. 151225). Rupununi, Orinduik, R Tumong, (site 33, [GUY 70]), 4°42.8'N 60°02.4'W; 2.xii.1970, (JB Davies) - 1 female (reared, but not associated with pupa) (BMNH, B.M.1999-16, specimen no. 1511223). Rupununi, Orinduik, R Chiung, [site 41, (GUY 80/3a, 4)], 4°39.3'N 59°50.5'W; 5.xii.1970, (JB Davies)

- 1 female, 1 male, (reared, but not associated with pupae) (BMNH, B.M.1999-16, specimen no. 151222). Rupununi, Orinduik, R Chiung, [site 46, (GUY 80/3a; 88/7-8)], 4°39.2'N 59°50.5'W; 7.xii.1970, (JB Davies) - 4 females, 2 males, (reared, but not associated with pupa) (BMNH, B.M.1999-16, specimens no. 151238, 151282-86). R Kumu, [site 58, (GUY 105)], 3°19'N 59°46.5'W, 143m; 17.ii.1975, (JB Davies) - 1 male (reared, but not associated with pupa) (BMNH, B.M.1999-16, specimen no.151271).



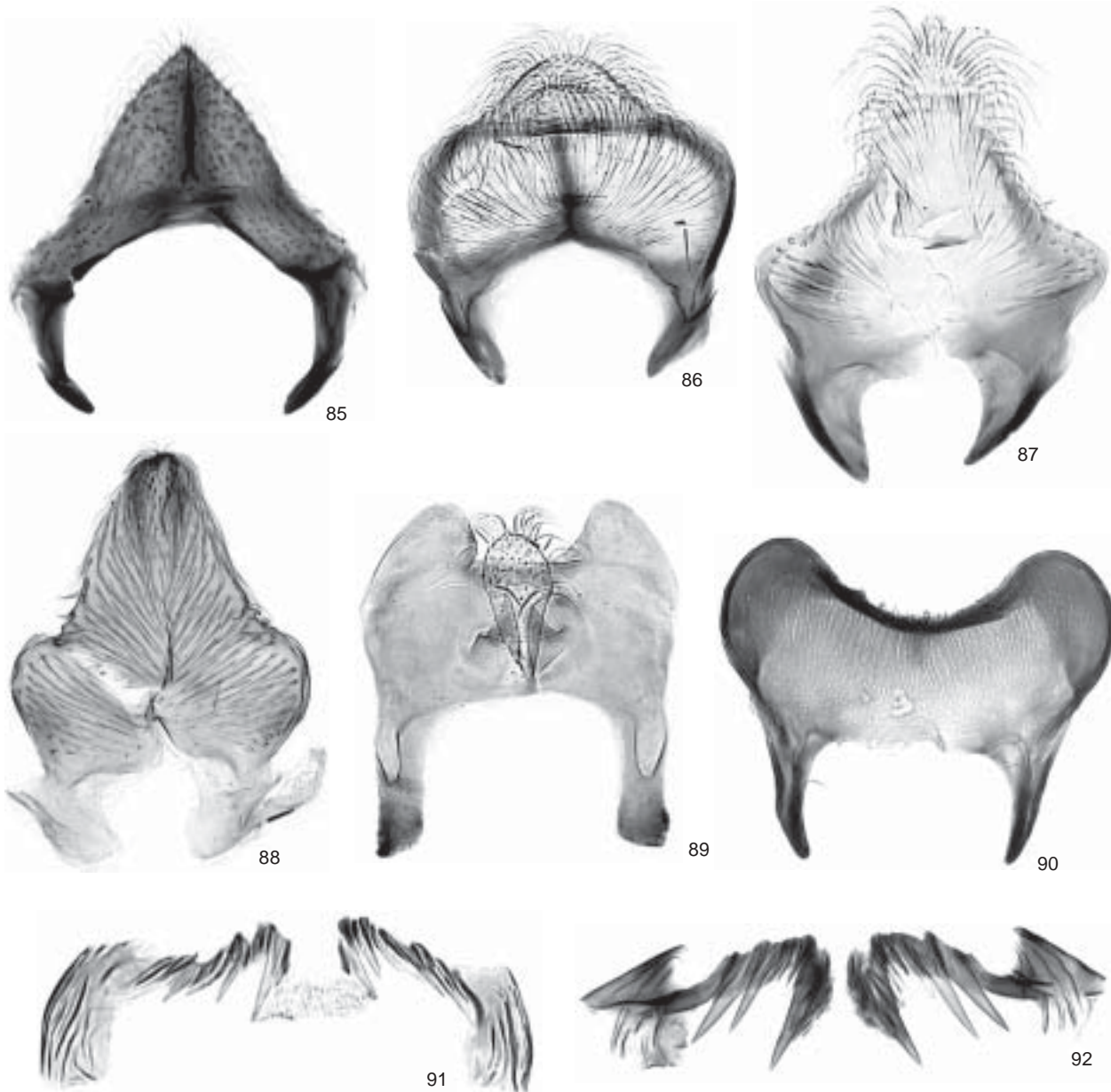
Ventral view of ventral plate. Fig. 78: *Simulium spinibranchium*. Fig. 79: *S. subpallidum*. Fig. 80: *S. clarki*. Fig. 81: *S. exiguum s.l.* Fig. 82: *S. cauchense* Fig. 83: *S. limbatum*. Fig. 84: *S. oyapockense s.l.*

Simulium (Inaequalium) clarki Fairchild, 1940

GUYANA
PINNED

R Tumong, 3.xii.1970, (*JB Davies*) - 4 females (man-biting) (BMNH). Orinduik, Sagars' house, 4°44'N60°2'W; 28.vii.1969, (*Sagar*) - 19 females (man-biting) (BMNH). Creek near District Commissioner's house, 4°42'N60°1'W; 3.xii.1970, (*JB Davies*) - 15 females (man-biting) (BMNH). Orinduik, R Ireng, 4°44'N60°2'W; 23.iii.1970, (*JB Davies*) - 1 female (man-biting) (BMNH). Kato, R. Chiung, 4°44'N60°2'W; 5.xii, 7.xii.1970, (*JB Davies*) - 14 females (man-biting) (BMNH). Kurubakaru, R. Tumong, 4°38'N59°52'W; 2.xii.1970, (*JB Davies*) - 5 females (man-biting) (BMNH). R Tumong, between Habec crossing and

Santa Maria; 2.xii.1970, (*JB Davies*) - 1 female (man-biting) (BMNH). R Tumong, lower falls; 2.xii.1970, (*JB Davies*) - 1 female (man-biting) (BMNH). Kato, water falls behind school, 4°40'N59°41'W; 10.iii.1970, (*JB Davies*) - 12 females (man-biting) (BMNH). Orinduik, R. Ireng; 11.vii.1957, (*R. McConnell*) - 4 females (BMNH). Rupununi, Kato, R Chiung, [site 46, (GUY 89/1-2, 4)], 4°39.3'N59°50.5'W, 460 m; 7.xii.1970, (*JB Davies*) - 3 females (man-biting) (BMNH, specimens no. 151291-92, 94). Rupununi, Kato, R Chiung, [site 48, (GUY 91/2)], 4°38.9'N59°49.6'W, 460 m; 8.xii.1970, (*JB Davies*) - 1 female (man-biting) (BMNH, specimens no. 151287). Rupununi, Kato, R Ireng, [site 11, (GUY 17/4)], 4°44.3'N60°02.3'W, 460 m; 21.iii.1970, (*JB Davies*) - 1 female (man-biting) (BMNH, specimens no. 151296).



Ventral view of ventral plate. Fig. 85: *Simulium quadrifidum*. Fig. 86: *S. lutzianum* s.l. Fig. 87: *S. maroniense* s.l. Fig. 88: *S. perflavum*. Fig. 89: *S. guianense* s.l. Fig. 90: *S. perplexum*. Parameres. Fig. 91: *S. cauchense*. Fig. 92: *S. quadrifidum*

SLIDES

Kato, R Chiung, 4°44'N60°2'W; 5.xii, 7.xii.1970, (*JB Davies*) - 2 females (man-biting) (BMNH). Creek near District, Commissioner's house, 4°42'N60°1'W; 3.xii.1970, (*JB Davies*) - 1 female (man-biting) (BMNH). Kato, tributary of R Kowa; 6.xii.1970, (*JB Davies*) - 1 female (man-biting) (BMNH). R Tumong, between Habec crossing and Santa Maria; 2.xii.1970, (*JB Davies*) - 1 female (man-biting) (BMNH). R Tumong, Kurubakaru trail; 3.xii.1970, (*JB Davies*) - 1 female (man-biting) (BMNH). Rupununi, Orinduik, R Ireng, [site 1, (GUY 17/2)], 4°44.3'N60°02.3'W, 460 m; 21.iii.1970, (*JB Davies*) - 1 female (reared but not associated with pupa) (BMNH, B.M. 1999-16, specimen no. 151290). Rupununi, Kato, R Chiung, [site 46, (GUY 89/3)], 4°39.3'N59°50.5'W, 460 m; 7.xii.1970, (*JB Davies*) - 1 female (man-biting) (BMNH, specimen no. 151293). Rupununi, Orinduik, R Ireng, [site 15, (GUY 28/1)], 4°43.1'N60°03'W, 450 m; 23.iii.1970, (*JB Davies*) - 1 female (man-biting) (BMNH, B.M. 1999-16, specimen no. 151288). Rupununi, Orinduik, R Ireng, [site 11, (GUY 17/1)], 4°44.3'N60°02.3'W, 460 m; 21.xi.1970, (*JB Davies*) - 1 female (man-biting) (BMNH, B.M. 1999-16, specimen no. 1511289). Orinduik, R Tumong; 12.xii.1970, (*JB Davies*) - 3 females (man-biting) (BMNH). Rupununi, Kato, un-named river, [site 49, (GUY 92)], 4°40.3'N45°42.9'W; 10.xii.1970, (*JB Davies*) - 1 female (man-biting) (BMNH, B.M. 1999-16, specimen no. 151178).

SPIRIT

Orinduik, R Tumong; 12.xii.1970, (*JB Davies*) - 12 females (man-biting) (BMNH).

Simulium (Notolepria) exiguum Roubaud, 1906
(species complex)

BRAZIL

State of Roraima

PINNED

Rio Tacutu, (site 1315); 28.xi.1994, (*S Luz & APA Luna Dias*) - 1 female, 2 males (reared) (BMNH).

Simulium (Psaroniocompsa) cauchense Floch & Abonnenc, 1946

GUYANA

PINNED

Rupununi, Orinduik, R Ireng, [site 10, (GUY 16/13,14, 16a, 17)], 4°44.5'N60°02.4'W, 460 m; 21.iii.1970, (*JB Davies*) - 6 females, 1 male (reared) (BMNH, B.M. 1996-16, specimen nos. 151180, 151182, 151200, 151201, 151181-83). Rupununi, Orinduik; 22.iii.1970, (*JB Davies*) - 1 female (BMNH). Rupununi, Orinduik, R Ireng, [site 11, (GUY 19/1,6,8)], 4°44.3'N60°02.3'W, 460 m; 22.iii.1970, (*JB Davies*) - 2 males (reared) (BMNH, B.M. 1996-16, specimens no. 151185-86, 88). Rupununi, Orinduik, R Tumong, [site 31, (GUY 65/1)], 4°42.4'N60°02.8'W, 450 m; 1.xii.1970, (*JB Davies*) - 1 male (reared but associated with pupae) (BMNH, B.M. 1996-16, specimen no. 151206). Rupununi, Orinduik, R Tumong, [site 33, (GUY 72/6)], 4°42.8'N60°02.4'W, 450 m; 2.xii.1970, (*JB Davies*) - 1 male (reared but not associated pupa) (BMNH, B.M. 1996-16, specimen no. 151190). Creek on route to R Kowa, un-named river, [site 43, (GUY 83/1)], 4°38.3'N59°48.8'W, 460 m; 6.xii.1970, (*JB Davies*) - 1 male

(reared but without pupa) (BMNH, B.M. 1996-16, specimen no.151260). Rupununi, Kato, R Chiung, [site 41, (GUY 80/2a; 83/2)], 4°30.3'N59°50.5'W, 460 m; 3.xii.1970, (*JB Davies*) - 2 males (reared, but not associated with pupae) (BMNH, B.M. 1996-16, specimens no. 151209, 151261). Rupununi, Lethem, R Mocomoco, [site 3, (GUY 102)], 3°21.3'N49°47.4'W, 140 m; 10.i.1970, (*JB Davies*) - 1 male (reared) (BMNH, B.M. 1996-16, specimen no. 151263). Rupununi, Lethem, R Burru, [site 3, (GUY 102)], 3°17.6'N59°49.3'W, 145m; 13.i.1975, (*JB Davies*) - 1 male (reared) (BMNH, B.M. 1996-16, specimen no. 151269).

Simulium (Psaroniocompsa) limbatum Knab, 1915

TYPE MATERIAL

GUYANA

PINNED

Rupununi District, R Rupununi; ix.1913, (*KS Wise*) - 1 female [HOLOTYPE], 5 females [PARATYPES] (BMNH).

OTHER MATERIAL

PINNED

Rupununi, Orinduik, R.D.C's, [site 32, (GUY 79/1, 1b)], 4°44'N 60°02'W, 450 m; 3.xii.1970, (*JB Davies*) - 2 males (BMNH, no. 151229-30). Rupununi, Lethem, R Tabatinga, [site 22, (GUY 45/1-2)], 3°22.5'N59°47.6'W, 145m; 27.xii.1970, (*JB Davies*) - 2 females (man-biting) (BMNH, B.M. 1996-16, specimen nos. 151298-99). Rupununi, Lethem, R Mocomoco, [site 21, (GUY 43/1)], 3°20.9'N 59°46.8'W, 145m; 7.xii.1970, (*JB Davies*) - 1 female (man-biting) (BMNH, B.M. 1996-16, specimen nos. 151272). Rupununi, Lethem, un-named creek, [site 27, (GUY 55/1)], 3°23.5'N 59°46'W, 144m; 28.xi.1970, (*JB Davies*) - 1 female (reared but not associated with pupa) (BMNH, B.M. 1996-16, specimen no. 151323). Rupununi, Lethem, R Burru, [site 8, (GUY 51/1-10)], 3°17.6'N 59°49.3'W, 145m; 28.xi.1970, (*JB Davies*) - 4 females, 6 males (reared but not associated with pupae) (BMNH, B.M. 1996-16, specimen nos. 151304-13). Manari; 14.vii, 1975, (*E.S.Tikasingsh*) - 2 females (BMNH). Rupununi Lethem, R Kumu, [site 7, (GUY 49/4, 6)], 3°18.3'N 59°48.8'W, 145m; 28.xi.1970, (*JB Davies*) - 2 males (reared but not associated with pupae) (BMNH, B.M. 1996-16, 151274, 151276). St Ignatius, R. Mocomoco, (site 14); 20.iii.1970, 10.i.1975, (*JB Davies*) - 11 females (man-biting), 2 males (reared) (BMNH). Bridge at R. Mocomoco; 11.i.1975, (*JB Davies*). Lethem, 1 mile above St Ignatius crossing, R Mocomoco, 27.xi.1970, (*JB Davies*) - 3 females, 2 males (reared) (BMNH). Cen. Ranch, R Kuma; 17.i.1975, (*JB Davies*) - 4 females (reared) (BMNH). Francis' Ranch, R. Kuma; 17.i.1975, (*JB Davies*) - 1 female (reared) (BMNH). Bridge at R Kuma (sites 11 & 12); 20.iii.1970, 28.xi.1970, (*JB Davies*) - 14 females (man-biting), 2 males (reared) (BMNH). R Burru, at crossing, (site 13); 20.iii.1970, (*JB Davies*) - 2 females (man-biting) (BMNH). MEP (Malaria Eradication Programme) Camp, R Kumu; 28.xi.1970, (*JB Davies*) - 40 females (man-biting) (BMNH). R Burru; 13.i.1970, (no collector's name)-2males (reared) (BMNH). Near Lethem, R Burru, at crossing, 3°17'N59°49'W; 28.xi.1970, (*JB Davies*) - 10 females (man-biting). Near Lethem, confluence of R Ireng with R Tabatinga, 3°23'N59°47'W; 27.xi.1970, (*JB Davies*) - 10 females (man-biting). Near Lethem, R Tabatinga, 3°21'N59°48'W;

27.xi.1970, (*JB Davies*) - 17 females (man-biting) (BMNH). Near Lethem, Manari Creek; 16.vi.1977, (*A.J.Shelley*) - 5 females (man-biting) (BMNH, B.M. 1979-580).

SPIRIT

Rupununi District, bridge at R Kumu; 20.iii.1970, 28.xi.1970, (*JB Davies*) - 1 female (man-biting), 1 female, 1 male (reared) (BMNH).

Simulium (Psaroniocompsa) oyapockense Floch & Abonnenc, 1946 (species complex)

GUYANA

PINNED

British Guiana (no locality, but probably Rupununi or Siparuni rivers); 1908, (*KS Wise* on label probably *Melville*)

- 5 females (man-biting) (BMNH, B.M. 1908-207). Rupununi, Orinduik, R Ireng, [site 15, (GUY 28/2)], 4°43.1'N60°03'W, 450 m; 23.iii.1970, (*JB Davies*) - 1 female (man-biting) (BMNH, B.M. 1999-16, specimen no. 151297). Itanimi Creek; 1908, (*KS Wise*) - 11 females (BMNH). British Guiana; (no date), (*Wise*) - 2 females (BMNH, B.M. 1939-586). Tukeit; 31.viii.1937, (*Richards & Smart*) - 3 females (man-biting) (BMNH, B.M. 1937-776). Warratuk; 31.viii.1937, (*Richards & Smart*) - 6 females (man-biting) (BMNH, B.M. 1937-776). Kaieteur savannah; 1, 4. & 6.i.1937, (*Richards & Smart*) - 3 females (man-biting) (BMNH, B.M. 1937-776). Orinduik Falls, R Ireng; 2.viii.1957, (*R. McConnell*) - 2 females (BMNH). Orinduik, R Ireng, 4°44'N60°2'W; 23.iii.1970, (no collector's name) - 105 fe-



Colour pattern and proportions of male legs. Fig. 93: *Simulium lutzianum* s.l. Fig. 94: *S. maroniense* s.l. Fig. 95: *S. perplexum*

males (man-biting) (BMNH). Rupununi District, Orinduik, R Ireng, 4°44'N60°2'W; 23.iii.1970, (*JB Davies*) - 12 females (man-biting) (BMNH). Orinduik, near ADC's house, 4°42'N60°1'W; 3.xii.1970, (*JB Davies*) - 41 females (man-biting) (BMNH). Rupununi District, Orinduik, below lower fall; 24.iii.1970, (*JB Davies*) - 3 females (man-biting) (BMNH). Rupununi District, Orinduik, above and below falls; 24.iii.1970, (*JB Davies*) - 7 females (man-biting) (BMNH). Rupununi District, R Tumong; 24.iii.1970, (*JB Davies*) - 3 females (man-biting) (BMNH). Rupununi District, Kurukabaru Trail, R Tumong, 4°47'N59°58'W; 3.xii.1970, (*JB Davies*) - 22 females (man-biting) (BMNH). Rupununi District, between Habec crossing and Santa Maria, R Tumong; 2 & 3.xii.1970, (*JB Davies*) - 15 females (man-biting) (BMNH). Rupununi District, Lower Falls, R Tumong; 2.xii.1970, (*JB Davies*) - 17 females (man-biting) (BMNH). Rupununi District, Kato, R Chiung, 4°38'N59°52'W; 5 & 7.xii.1970, (*JB Davies*) - 17 females (man-biting) (BMNH). Rupununi, Apoteri, R Essequibo, ix-x.1926, (*LD Cleare*) - 20 females (man-biting) (BMNH). Rupununi, Karanambu; viii.1959, (*E McTurk*) - 4 females (on same pin, man-biting) (BMNH). British Guiana; (no date), (*KS Wise*) - 4 females (BMNH). British Guiana, (no. 1611); ix.1913, (*KS Wise*) - 10 females (man-biting) (BMNH, B.M. 1990-107, ex. Wellcome Coll.). Lethem; 15.viii.1975, (*ES Tikasingh*). Lethem Hospital, R Takatu; 21.vi.1977, (*AJ Shelley*) - 7 females (man-biting) (BMNH, B.M. 1979-580). Lethem, rest house, R Takatu; 14.vi.1977, (*AJ Shelley*) - 6 females (man-biting) (BMNH, B.M. 1979-580). Rupununi District, Dadanawa, R Rupununi; 19.vi.1977, (*AJ Shelley*) - 2 females (man-biting) (BMNH, B.M. 1979-580). Rupununi District, Lethem, Bon Fim, R Takatu; 13.vi.1977, (*AJ Shelley*) - 2 females, 2 males (reared, pupa on slides) (BMNH, B.M. 1979-580).

SLIDES

Rupununi District, Lethem, Bon Fim, R Takatu; 13.vi.1977, (*AJ Shelley*) - 2 females, 2 males (pupa, adult pinned) (BMNH, B.M. 1979-580).

SPIRIT

Orinduik, R Ireng, (coll. No. 21/1); 22.iii.1970, (*JB Davies*) - several females (man-biting) (BMNH). Orinduik, R Ireng, 2.iii.1969, (*JB Davies*) - several females (man-biting) (BMNH). Orinduik, creek behind house of ADC; 22.iii.1969, 24.iii.1970, (*JB Davies*) - several females (man-biting) (BMNH). Orinduik, beach, below falls, R Ireng, (coll. 28); 2.iii.1969, (*JB Davies*) - 4 females (man-biting) (BMNH). (No locality); 19.ix.1980, (*M Nathan*) - 2 females (man-biting) (BMNH). Rupununi, Karanambu; viii.1959, (*E McTurk*) - several females (man-biting) (BMNH). Takatu River; 4.21.1970, (no collector's name) - several females (man-biting, from 4-6 pm) (BMNH). R Takatu, crossing at Bon Fim; 13.i.1975, (*JB Davies*) - 3 females (man-biting). Nr. Uiramutã, R Ireng, (Brazilian side of river); 31.x.1997, (*AJ Shelley & APA Luna Dias*) - numerous females (man biting) (BMNH). Lethem, behind government house, (FR4-19); 15.viii.1975, (*ES Tikasingh*) - several females (man-biting) (BMNH). Orinduik, (col. 126); 16.iv.1968, (*J Darlington*) - several females (man-biting) (BMNH). (No locality given); 25.ix.1980, (*M Nathan*) - 2 females (man-biting) (BMNH).

Simulium (Psaroniocompsa) quadrifidum Lutz, 1917

GUYANA

PINNED

Rupununi, Lethem, R Mocomoco, [site 26, (GUY 104)], 3°18.5'N59°43'W, 146 m; 13.i.1975, (*JB Davies*) - 1 female (reared) (BMNH, B.M. 1999-16, specimen no. 1511270).

SPIRIT

Rupununi Lethem, R Mocomoco, [site 53, (GUY 10)], 3°18.8'N59°40'W, 144 m; 14.i.1970, (*JB Davies*) - 1 male (reared) (BMNH, B.M. 1999-16, specimen no. 151127). Rupununi, Lethem, R Tumong, [site 16, (GUY 32)], 4°42.9'N60°02.2'W, 450 m; 24.iii.1970, (*JB Davies*) - 3 pupae (BMNH, B.M. 1999-16, sample no. 151148).

Simulium (Psilopelmia) kabanayense Ramírez Pérez & Vulcano, 1973

GUYANA

SLIDES

(Originally identified as *Simulium lutzianus*): Kaieteur savanah, small stream; 6.ix.1937, (*S. Smart*) - 3 pupae (on same slide) (BMNH, B.M. 1937-778).

Simulium (Psilopelmia) lutzianum Pinto, 1932
(species complex)

GUYANA

PINNED

Rupununi, Orinduik, R Tumong, [site 16, (GUY 30/3a; 77/3)], 4°42.9'N 60°02.2'W, 450 m; 24.iii., 3.xii.1970, (*JB Davies*) - 2 females (reared, but not associated with pupae) (BMNH, B.M. 1996-16, specimen no. 151213, 151236). Rupununi, Orinduik, R Tumong, [site 33, (GUY 72/8)], 4°42.8'N 60°02.4'W, 450 m; 2.xii.1970, (*JB Davies*) - 1 female (reared, but not associated with pupa) (BMNH, B.M. 1996-16, specimen no. 151237). Rupununi, Kato, R Kowa (Seyun), [site 44, (GUY 85/1-3, 5)], 4°69'N59°48'W, 400 m; 6.xii.1970, (*JB Davies*) - 3 females, 1 male (reared but not associated with pupae) (BMNH, B.M. 1996-16, specimen no. 151232-33, 151281). Kaieteur savannah; 4.ix.1987, (no collector's name) - 1 male (at light trap) (BMNH).

Simulium (Psilopelmia) maroniense Floch & Abonnenc, 1946 (species complex)

Note: most specimens from the BMNH collection recorded as *S. rorotaense* in Shelley et al. (1997) are now placed as *S. maroniense s.l.*

TYPE MATERIAL

FRENCH GUIANA

SLIDES

Coeur Maroni; 12.viii.1945, (*no collector's name*) - 1 female (reared, pupal pelt missing) (LECTOTYPE, no. 709), 1 male (reared, pupal thorax and cocoon missing) (PARALECTOTYPE, no. 708) (IP).

OTHER MATERIAL

BRAZIL

State of Amazonas

PINNED

Km 26 Estr. Manaus, Ducke Reserve, Igarapé Acará; 20.i.1976, (*Faustino*) - 1 female (reared) (BMNH).

State of Mato Grosso

PINNED

Dardanelos Falls, R Aripuanã, 10°11'S 59°48'W; 22.iii.1977, (no collector's name) - 2 man-biting females, (BMNH).

State of Pará

SPIRIT

Carajás District; vi.1983 (*L Ryan*) - 1 female (man-biting) (BMNH).

State of Roraima

PINNED

Pacaraima, BR 174, tributario do Igarapé Sargento Ávila, 04° 26'N 61° 07' W; 6.vi.1996, (*N Hamada*) - 2 females 2 males (reared) (INPA). Mission post, R Auaris; 31.iii.1977, (*RR. Pinger*) - 1 female (reared), 1 male (reared), (BMNH, B.M.1979-580). Mission post, R Mucajaí, (site 285c); 6.i.1977, B.M.1979-580 (*AJ Shelley & APA Luna Dias*) - 1



Pupal gill. Fig. 96: *Simulium spinibranchium*. Fig. 97: *S. subpallidum*. Fig. 98: *S. clarki*. Fig. 99: *S. exiguum* s.l. Fig. 100: *S. cauchense*. Fig. 101: *S. limbatum*

female (reared, pupal exuviae on slide) (BMNH). R Mucajaí, 200 m below Igarapé Coroconá, 21.vii.1984 (*AJ Shelley & APA Luna Dias*) - 2 females (reared), 2 males (reared, fore leg claw mounted), (BMNH). Near mission post, R Mucajaí, Igarapé Coroconá, 21.vii.1984 (*AJ Shelley & APA Luna Dias*), 1 male (reared) (BMNH). R Preto, tributary of R Ajarani; 28-29.iv.1979, (*R.W Crosskey & AJ Shelley*) - 1 female (reared) (BMNH, B.M.1979-258). Cachoeira, R Cauamé; 29.iv.1982 (*APA Luna Dias & R Malaguti*) - 2 females (reared), 1 male (reared) (BMNH). Boa Vista-Sta. Helena road, Igarapé Ávila; 29.xi.1980 (*AJ Shelley & APA Luna Dias*) - 1 female (reared; fore leg claw mounted) (BMNH).

SLIDES

Pacaraima do Samã, (no. 88); 6.vi.1996, (*N. Hamada*) - 2 females, 1 male (reared) (Inpa). Pacaraima, BR 174, Igarapé Sargento Alves, 04°26'N61°07'W; 14.i.1996, (*N Hamada*) - several pupae (on three slides) (Inpa). Surucucus, Igarapé Falemu (above hydroelectric dam), (site 791); 10.xii.1986 (*AJ Shelley & APA Luna Dias*) - 1 female (reared) (BMNH). Surucucus, Dalem; 11.xii.1986 (*AJ Shelley & APA Luna Dias*) - 1 female (reared) (BMNH). Mission post, R Mucajaí, 6.i.1977, (*AJ Shelley*) - 1 pupa (adult pinned) (BMNH, B.M.1979-580). Near mission post, R Mucajai, Igarapé Coroconá; 21.vii.1984 (*AJ Shelley & APA Luna Dias*) - 1 female (reared), 1 pupa, 3 larvae (BMNH). R Mucajai, 200 below Igarapé Coroconá, (site 675-1); 21.vii.1984 (*AJ Shelley & APA Luna Dias*) - 1 male (reared) (BMNH). Mission post, R Auaris, 7.vii.1976, (*AJ Shelley*) - 1 pupa, (BMNH, B.M.1979-580). Surucucus, Cachoeira 2 km from Funai Post, (site 613); 7.v.1982, (*APA Luna Dias & R. Malaguti*) - 2 males (reared) (BMNH). Surucucus, Igarapé Falemu (above hydroelectric dam), (site 791); 10.xii.1986 (*AJ Shelley & APA. Luna Dias*) - 2 males (reared) (BMNH). Uiramutã, Cachoeira do Urucá, (site 1303); 13.x.1997, (*AJ Shelley & APA Luna Dias*) - 1 male (reared) (BMNH).

SPIRIT

Surucucus, water-fall 2 km from Funai post; 7.v.1982 (*APA Luna Dias & R. Malaguti*) - 2 females (reared), 7 males (reared), 3 pupae, (BMNH). Surucucus, Igarapé Falemu (above hydroelectric dam); 10.xii.1986 (*AJ Shelley & APA Luna Dias*) - 2 males (reared) (BMNH). Near mission post, R Mucajaí, Igarapé Coroconá; 21.vii.1984 (*AJ Shelley & APA Luna Dias*) - 8 pupae, numerous larvae, (BMNH). Mucajaí mission, Igarapé Coroconá; 6.i.1977 (*AJ Shelley*) - 1 pupa, (BMNH). Mucajaí, 200 m below Igarapé Coroconá, 21.vii.1984 (*AJ Shelley & APA Luna Dias*) - 1 male (reared), 9 pupae, 18 larvae, (BMNH). Boa Vista-Sta. Helena road, Boca da Mato, Igarapé Cunaen; 11.viii.1984 (*AJ Shelley & APA Luna Dias*) - 1 male, 3 pupae, 6 pupal exuviae, (BMNH). Boa Vista-Sta. Helena road, Boca da Mato, Igarapé Cunaen, small stream; 11.viii.1984 (*AJ Shelley & APA Luna Dias*) - 3 females (mass reared), 1 pupa, (BMNH). Auaris mission post, Igarapé; 9.vii.1979, (*AJ Shelley*) - 1 pupa, (BMNH, B.M.1979-580). Mission post, R Auaris; 7.vii.1976, (*AJ Shelley*) & 8.xii.1986 (*AJ Shelley & APA Luna Dias*) - 1 male (reared), 1 pupal exuviae, 3 larvae, (BMNH, B.M.1979-580). Tributário do Ig. Samã, antes da casa da D. Alade, (site 88); 6.vi.1996, (*N Hamada.*) - several pupae (INPA). Igarapé do Banana;

04°25'N 61°13'W; 14.i.1996, (*N Hamada*) - several pupae (CUAC). Igarapé Sargento Ávila; 04°26'N 61°07'W; vi.1996, (*N Hamada*) - several pupae (CUAC).

GUYANA

PINNED

Rupununi, Lethem, R Mocomoco, [site 6, (GUY 9/1-9)], 3°17.5'N59°37.8'W, 146 m; 19.iii.2970, (*JB Davies*) - 4 females, 4 males (reared, 1 male without associated pupa) (BMNH, B.M. 1999-16, specimens nos. 151191-98). (Previously identified as *S. rubrithorax.*) Kaieteur, Savannah; 6.ix.1937, (*Richards & Smart*) - 1 female (at light trap) (BMNH).

SPIRIT

Rupununi, Lethem, R Nappi, [site 1, (GUY 1)], 3°21'N59°28'W, 146 m; 18.iii.1970, (*JB Davies*) - 1 pupa (BMNH, B.M. 1999-16, sample no. 151101). Rupununi, Lethem, R Nappi, [site 1, (GUY 3)], 3°21'N59°28'W, 146m; 18.iii.1970, (*JB Davies*) - numerous pupae (BMNH, B.M. 1999-16, sample no. 151103). Rupununi, Lethem, R Nappi, [site 2, (GUY 2)]; 18.iii.1970, (*JB Davies*) - 4 pupae (BMNH, B.M. 1999-16, sample no. 151108). Rupununi, Lethem, R Mocomoco, [site 6, (GUY 9/11)], 3°17.5'N59°37.8'W, 146 m; 19.iii.2970, (*JB Davies*) - 1 female 3 males, numerous pupae (BMNH, B.M. 1999-16, sample no. 151108).

SLIDES

[Originally identified as *S. rubrithorax*]: Kaieteur, savannah; 4.i.1937, (*J Smart*) - 1 male (only genitalia) (BMNH, B.M. 1937-778). [Originally identified as *S. rubrithorax*]: Kaieteur, savannah; 4 ix.1937, B.M. (*J Smart*), 1 male (genitalia and single hind leg only) (BMNH, 1937-778). [Originally identified as *S. rubrithorax*]: High forest, sandstone bed of stream, Kaieteur/Tukeit Trail, 9.ix.1937, (*J. Smart*) - 3 males (dissected from pupae) (BMNH, B.M.1937-778).

VENEZUELA

Amazonas Territory

PINNED

[Originally identified as *S. wuayaraka* Ortiz]: Parima, 18.iv.1980, (*no collector's name*) - 1 male (reared) (BMNH).

Bolivar State

PINNED

[Originally identified as *S. ignacioi* Ramírez Pérez & Vulcano]: Wonaven, (*no date or collector stated*) - 1 male (reared) (BMNH).

Simulium (Psilopelmia) rorotaense Floch and Abonnenc, 1946

TYPE MATERIAL

FRENCH GUIANA

SLIDES

Rorota; 31.v.1946, (*no collector's name*)-1 female (reared) [LECTOTYPE, no. 751], 1 male (reared but without pupa) [PARALECTOTYPE, no. 752] (IP).

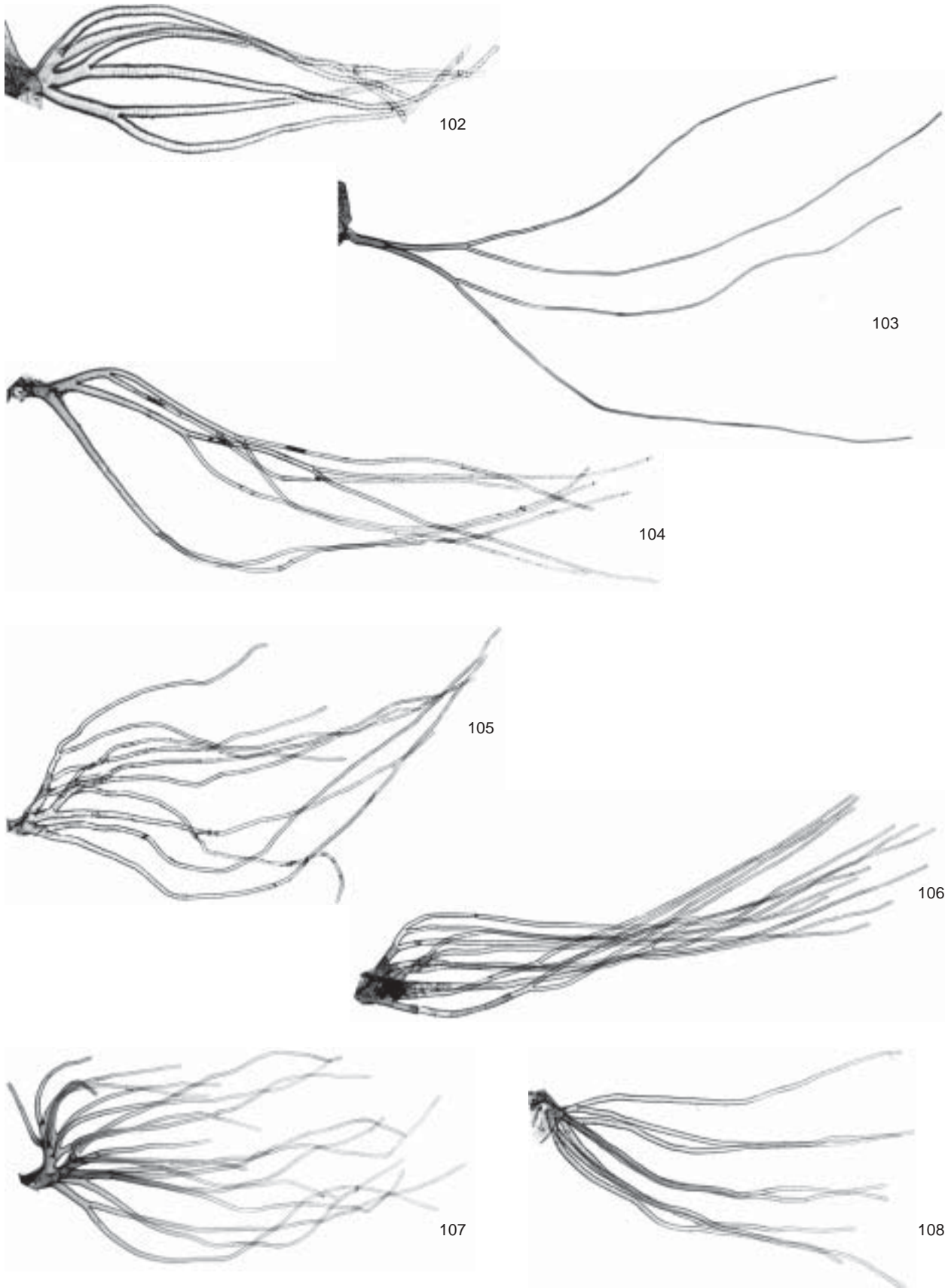
OTHER MATERIAL

BRAZIL

State of Amazonas

PINNED

Manaus, Reserva Ducke, Am 010-km 22, Igarapé Barro



Pupal gill. Fig. 102: *Simulium oyapockense* s.l. Fig. 103: *S. quadrifidum*. Fig. 104: *S. lutzianum* s.l. Fig. 105: *S. kabanayense* (10 filament form). Fig. 106: *S. kabanayense* (13 filament form). Fig. 107: *S. maroniense* s.l. Fig. 108: *S. perflavum*

Branco, 2°55' S 59° 59' W; 18.xi.1998, (*N. Hamada*) - 1 female, 2 males (reared but not associated with pupae) (Inpa). Manaus, Reserva Ducke, Inpa, Ig. Acará, 2°57'S59°57'W; 11.vii.1995 (*N. Hamada*) - 1 female (reared, head, wings, legs and genitalia on slide, rest of body pinned) (BMNH), 1 female, 1 male (reared) (CUAC). P Figueiredo, BR 174, Igarapé Lajes, Balneário, (site 69), 01°59'S 60° 01' 29' W; 19.vii.1996, (*N. Hamada*) - 1 male (reared, genitalia and wings on slide) (BMNH). Manaus-Itacoatiara road, Reserva Ducke, Ig. Acará; 20.i.1976, (*Faustino*) - 1 female (reared) (BMNH.)

SLIDES

Manaus, Reserva Ducke, Am 020, km 26, Igarapé Acará; 21.vi.1996, (*N. Hamada*) - several pupae (Inpa). P Figueiredo, BR 174, Igarapé Lajes, Balneário, (site 69), 01°59'S 60° 01' 29' W; 19.vii.1996, (*N. Hamada*) - 1 male (reared) (genitalia and wings on slide, rest pinned) (BMNH). Presidente Figueiredo, Am 240, pequeno Igarapé, acima da caverna da Maruaza, 02°02'S59°58'W; 22.vi.1996, (*N. Hamada*) - several pupae (Inpa). Manaus, Reserva Duke, 03°00'N59°56'W; 21.vi.1996, (*N. Hamada*) - 1 female, 1 male (mass reared), 2 pupae (BMNH), 1 female, 1 male (mass reared), 2 pupae (CUAC).

SPIRIT

Manaus, Reserva Duke, 03°00'N59°56'W; 21.vi.1996, (*N. Hamada*) - 1 male, several pupae (BMNH), several females, males, several pupae (CUAC).

State of Pará

SLIDES

Estrada Santarém, Cuiabá, BR 163, 28 km do Ramal da Jahoti, 02°53'S54°45'W; 2.viii.1996, (*N. Hamada*) - several pupae (Inpa).

FRENCH GUIANA

SPIRIT

Montagne du Mahery, Rorota; 21.6.1999, (*N. Hamada & F. Fourque*) - several pupae (Inpa).

Simulium maroniense s.l./ Simulium rorotaense

Specimens under this title are from localities where no reared material is available to provide a more precise identification.

BRAZIL

State of Mato Grosso

PINNED

Dardanelos Falls, Rio Aripuanã, (site 307), 10°11'S 59°48'W; 22.iii.1977, (*no collector name*) - 2 females (man-biting) (BMNH).

State of Pará

SLIDE

Carajas District, vi.1983, (*L. Ryan*), - 1 female (man-biting), (BMNH).

State of Roraima

PINNED

Arabobo Mt., (no. 3325); 24.xi.1952, (*JG Myers*) - 1 female (reared) (BMNH).

GUYANA

PINNED

Kutari Sources; i.ii.1936, (*GA Hudson*) - 1 male (reared, but no associated with pupa) (BMNH, B.M. 1956-360).

Simulium (Psilopelmia) perflavum Roubaud, 1906

GUYANA

PINNED

Rupununi, Lethem, R Burru, [site 8, (GUY 13/1-4)], 3°17.6'N59°49.3'W, 145 m; 20.iii.1970, (*JB Davies*) - 1 female, 3 males (reared) (BMNH, B.M. 1999-16, specimens no. 151239, 151240, 151241, 151242). Rupununi, Lethem, R Burru, [site 8, (GUY 51/11-18)], 3°17.6'N59°49.3'W, 145m; 28.iii.1970, (*JB Davies*) - 6 females, 2 males (reared, but not associated with pupa) (BMNH, B.M. 1999-16, specimens no. 151314-151320). Rupununi, Lethem, small stream nr. St. Ignatius, un-named river, [site 25, (GUY 52/1-10, 12)], 3°20.6'N59°47.8'W, 145m; 28.iii.1970, (*JB Davies*) - 6 females, 4 males (reared, but not associated with pupa) (BMNH, B.M. 1999-16, specimens nos. 151322, 151328-151330, 151331-151336, 151338, 151242). Rupununi, Orinduik, Creek behind ADC's house, un-named river, (site 12, (GUY 66/3-8; 68/1)), 4°43.8'N60°02'W, 455m; 1.xii.1970, (*JB Davies*) - 6 females, 1 male (reared, but not associated with pupa) (BMNH, B.M. 1999-16, specimens no. 151157, 151251-52, 151254-57). Rupununi, R Tabatinga, (site 22, (GUY 66/3-8; 68/1)), 3°22.3'N59°47.6'W, 145m; 10.i.1975, (*JB Davies*) - 1 female (reared) (BMNH, B.M. 1999-16, specimens no. 151262). Rupununi, R Burru, [site 8, (GUY 103/1)], 3°17.6'N59°47.3'W, 145m; 13.i.1975, (*JB Davies*) - 3 females, 2 males (reared) (BMNH, B.M. 1999-16, specimens no. 151264-268).

SLIDES

Rupununi, Lethem, small stream nr. St. Ignatius, un-named river, [site 25, (GUY 52/6, 11, 13-14)], 3°20.6'N59°47.8'W; 28.iii.1970, (*JB Davies*) - 2 females, 2 males (reared, but not associated with pupae) (BMNH, B.M. 1999-16, specimen nos. 151322, 15137, 151339-151340).

Simulium (Trichodagmia) guianense Wise, 1911
(species complex)

TYPE MATERIAL

GUYANA

PINNED

Lower Rupununi R; 1908, (*KS Wise* on label, but actually collected by *Melville*) - 1 female (man-biting) [LECTOTYPE, head, abdomen, and two legs on slides], 3 females (man-biting) [PARALECTOTYPES, 1 specimen with abdomen and leg on slide] (BMNH). British Guiana (no locality, but probably the Lower Rupununi R); 1908, (*KS Wise* on label, but actually collected by *Melville*) - 4 females (man-biting) (PARALECTOTYPES, genitalia of two of the females on slides) (BMNH, B.M. 1908-207).

SLIDES

Lower Rupununi R; 1908, (*KS Wise* on label, but actually collected by *Melville*) - 1 female (man-biting) (LECTOTYPE, head, abdomen and two legs). Lower Rupununi River; 1908, (*KS Wise* on label, but actually collected by *Melville*) - 1 female (man-biting) [PARALECTOTYPE, abdomen, wing and hind leg] (BMNH). British Guiana (no locality, but probably the Lower Rupununi R); 1908, (*KS*

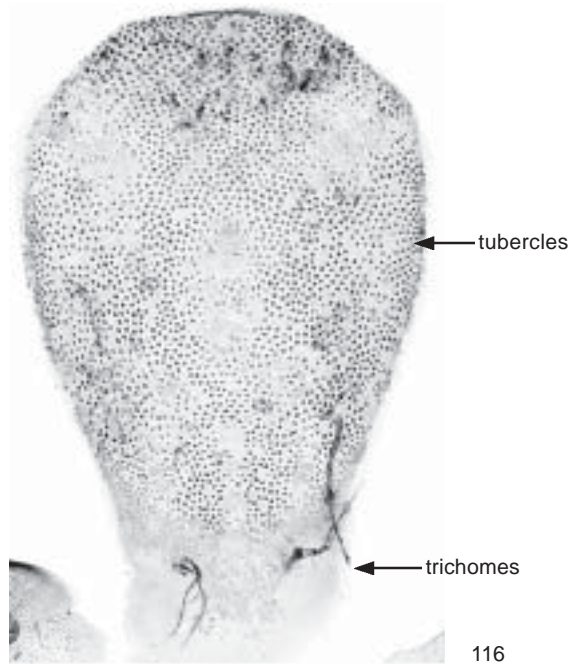
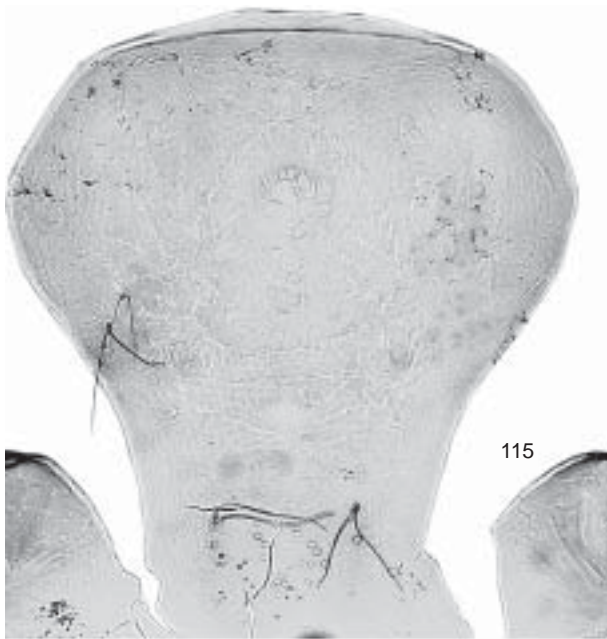
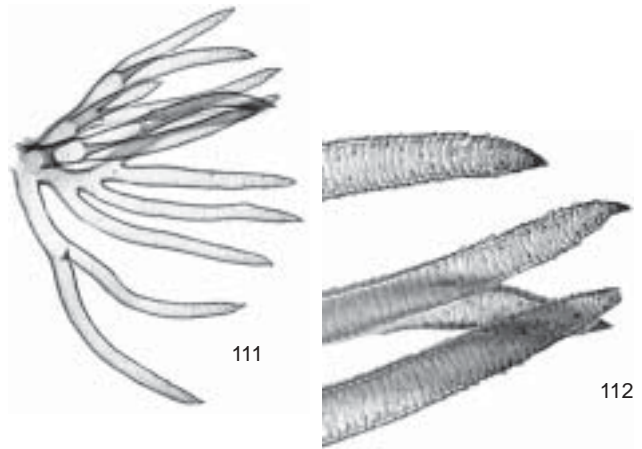
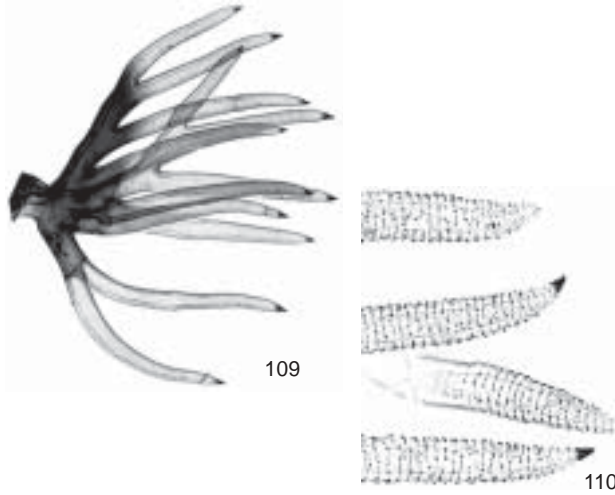
Wise on label, but actually collected by *Melville*) - 2 females (man-biting) [PARALECTOTYPES, only genitalia on slide, adults pinned] (BMNH, B.M. 1908-207).

OTHER MATERIAL

PINNED

Rupununi, Orinduik, R Ireng [site 11, (GUY 17/2, 58/2-5, 59/1-2, 4-5)], 4°44.3'N60°02.3'W, 460 m; 30.xi., 1.xii.1970, (*JB Davies*) - 3 females, 4males (reared, but not associated

with pupa), 1 female (man-biting) (BMNH, B.M. 1999-16, specimen nos., 151248, 151249, 151295, 1511300 - 1511303, 151324 - 151327). Rupununi, Orinduik, R Ireng [site 16, (GUY 16/2, 7, 10)], 4°44.6'N60°02.4'W, 460 m; 21.iii.1970, (*JB Davies*) - 1 female, 2 males (reared) (BMNH, B.M. 1999-16, specimen no. 151245 - 47). Rupununi, Orinduik, R Ireng [site 13, (GUY 61/1-3)], 4°44'N60°02.9'W, 450 m; 1.xi.1970, (*JB Davies*) - 1 female (reared) (BMNH, B.M. 1999-16, specimen no. 151277 - 79).



Pupal gill. Figs 109-110. *Simulium guianense* s.l. Figs 111-112. *S. perplexum*. Cocoon weave. Fig.113: *S. subpallidum*. Fig. 114: *S. exiguum* s.l. Frontoclypeus. Fig. 115: *S. subpallidum*. Fig. 116: *S. exiguum* s.l.

SLIDES

Orinduik, R Tumong, (coll. 74); 2.xii.1970, (*JB Davies*) - 6 females (man-biting) (BMNH). Rupununi Orinduik, R Ireng, [site 16, (GUY 16/12)], 4°44.5'N60°02.4'W, 460 m; 21.iii.1970, (*JB Davies*) - 4 females, 4 males (reared but not associated with pupae), 2 pupae (BMNH, B.M. 1999-16, specimen no. 151134).

SPIRIT

Orinduik, R Tumong; 2.xii.1970, (*JB Davies*) - numerous females (man-biting) (BMNH). Orinduik, R Ireng [site 13, (GUY 61)], 4°44'N60°02.9'W, 450 m; 1.xii.1970, (*JB Davies*) - 1 female, 2 males (reared but not associated with pupa), numerous pupae (BMNH, B.M. 1999-16, sample no. 151152). Rupununi, Orinduik, R Ireng, [site 11, (GUY 58)], 4°44.3'N60°02.3'W, 460 m; 30.xi.1970, (*JB Davies*) - numerous pupae (BMNH, B.M. 1999-16, sample no. 151150). Rupununi, Orinduik, R Ireng, (site 10, (GUY 16/8)), 4°44.5'N60°02'W, 460 m; 1.ii.1970, (*JB Davies*) - 1 pupa (BMNH, B.M. 1999-16, sample no. 151135). Rupununi, Orinduik, R Ireng, (site 10, (GUY 16/8)), 4°44.5'N60°02'W, 460 m; 21.iii.1970, (*JB Davies*) - 1 male (reared) (BMNH, B.M. 1999-16, sample no. 151133). Rupununi, Orinduik, R Ireng, (site 16, (GUY 16/12)), 4°44.5'N60°02.4'W, 460 m; 21.iii.1970, (*JB Davies*) - several females and males (reared but not associated with pupa), numerous pupae (BMNH, B.M. 1999-16, sample no. 151134). Rupununi, Orinduik, R Ireng, [site 19, (GUY 19/20)], 4°44.3'N60°02.3'W, 460 m; 22.iii.1970, (*JB Davies*) - several pupae (BMNH, B.M. 1999-16, sample no. 151139). Rupununi, Orinduik, R. Ireng, [site 11, (GUY 59/20)], 4°44.3'N60°02.3'W, 460 m; 1.xii.1970, (*JB Davies*) - numerous pupae (BMNH, B.M. 1999-16, sample no. 151151).

Simulium (Trichodagmia) perplexum Shelley,
Maia-Herzog, Luna Dias & Couch, 1989

TYPE MATERIAL

GUYANA

PINNED

Kaieteur Falls (Potaro R 5°09'N59°29'W); 1.ix.1937, (*OW Richards & Smart*) - 1 female [HOLOTYPE, BMNH, B.M. 1937-776]. Same locality and collector as holotype; 1..4. & 9.ix.1937- 13 females, 11 males [PARATYPES, B.M. 1937-776]. Amatuk Falls (Potaro River); 31.viii.1937, (*OW Richards & Smart*) - 1 female [PARATYPE, BMNH, B.M. 1937-776]. Warratuk Falls (Potaro River); 31.viii.1937, (*OW Richards & Smart*) - 3 females [PARATYPE, BMNH, B.M. 1937-776].

SLIDES

Kaieteur Falls (Potaro R, 5°09'N59°29'W); 1., 9.ix.1937, (*OW Richards & Smart*) - 3 females, 3 males (only abdomen, legs and genitalia) [PARATYPES, BMNH, B.M. 1937-776]. Kaieteur, savannah; 6.ix.1937, (*Richards and Smart*) - 1 female (man-biting) (BMNH, B.M. 1937-776).

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REFERENCES

- Coscarón S 1990. Taxonomía y distribución del subgénero *Simulium* (*Ectemmaspis*) Enderlein (Simuliidae, Diptera, Insecta). *Iheringia sér Zool* 70: 109-170.
- Coscarón S 1991. *Fauna de Agua Dulce de la República Argentina*. 38. *Insecta, Diptera*. 2. *Simuliidae*. vi+7-304 [+ 67 figures on unnumbered pages], Fundación para la Educación, la Ciencia y la Cultura, Buenos Aires.
- Crosskey RW, Howard TM 1997. *A New Taxonomic and Geographical Inventory of World Blackflies (Diptera: Simuliidae)*. The Natural History Museum, London, 144 pp.
- Davies JB 1973. Kabowra flies of the Rupununi district, Guyana. *West Indian Med J* 22: 199.
- Fairchild GB 1940. Notes on the Simuliidae of Panama (Dipt., Nematocera). *Ann Entomol Soc Am* 33: 701-719.
- Floch H, Abonnenc E 1946. Simulidés de la Guyane Française. I. *S. Guianense* Wise 1911, *S. Rorotaense* n. sp., *S. Maroniense* n. sp. *Pub l'Inst Pasteur de la Guyane et du Territoire de l'Inini* 136: 1-20.
- Hamada N, Adler PH 1998. Taxonomy of the *Simulium perflavum* species-group (Diptera: Simuliidae) with description of a new species from Brazil. *Insecta Mundi* 12: 207-226.
- Hamada N, Adler PH 1999. Cytotaxonomy of four species in the *Simulium perflavum* species group (Diptera: Simuliidae) from Brazilian Amazonia. *Syst Entomol* 24: 273-288.
- Hamada N, Fouque F 2001. Black flies (Diptera: Simuliidae) of French Guiana: cytotaxonomy and preliminary list of species. *Mem Inst Oswaldo Cruz* 96: 955-959.
- Hamada N, Grillet ME 2001. Black flies (Diptera: Simuliidae) of the Gran Sabana (Venezuela) and Pacaraima region (Brazil): Distributional and identification keys for larvae and pupae. *Entomotropica* 16: 29-49.
- Humphrys E, Tikasingh ES, Davies JB 1977. The *Simulium* blackfly problem in Guyana, South America [p. 41]. *Proceedings of the Symposium "Man-made lakes and human health"*, Paramaribo, Suriname, October 23-25, 73 pp.
- Knab F 1915. Some new Neotropical Simuliidae. *Bull Entomol Res* 6: 279-282.
- Moraes MAP, Shelley AJ, Luna Dias APA 1985. *Mansonella ozzardi* no Território Federal de Roraima, Brasil. Distribuição e achado de um novo vetor na área do Rio Surumu. *Mem Inst Oswaldo Cruz* 80: 395-400.
- Nathan MB, Tikasingh ES, Munroe P 1982. Filariasis in Amerindians of western Guyana with observations on transmission of *Mansonella ozzardi* by a *Simulium* species of the *amazonicum* group. *Tropenmed Parasit* 33: 219-222.
- Py-Daniel V 1982. Prosimuliini (Diptera: Simuliidae) Neotropical 1- *Kempfsimulium* V. Py-Daniel & J. A. Nunes de Mello n.gen; *K. simplicicolor* (Lutz, 1910) n. comb.; *Lutsimulium flavopubescens* (Lutz, 1910) n. comb.; *Mayacnephia muzquicensis* (Díaz Nájera, 1971) n. comb. *Amazoniana* 7: 293-333.
- Py-Daniel V 1989. Novas sinonímias e correções em *Simulium* com a revalidação de *S. pruinatum* Lutz, 1904 (Culicimor-

- pha, Simuliidae). *Rev Saúde Públ São Paulo* 23: 254-257.
- Py-Daniel V, Shelley AJ 1980. Revisão do *Simulium spinibranchium* Lutz, 1910 (Diptera: Simuliidae), com a primeira descrição dos adultos e larva, e redescricao da pupa. *Acta Amazonica* 10: 213-223.
- Rambajan I 1979. A new species of *Simulium* (Simuliidae: Diptera) from the Lethem area, Rupununi District, Guyana, South America. *J Guyana Museum and Zoo, South America* 45: 63-77.
- Rambajan I 1981a. Abate for the control of blackfly larvae in the river Burru, Lethem area, Rupunini District, Guyana. *Trop Geogr Med* 33: 55-57.
- Rambajan I 1981b. Some observations on the biting habits of *S. incrustatum* and *S. amazonicum* complex in the Lethem area, Rupunini district, Guyana, South America. *Trop Geogr Med* 33: 58-60.
- Ramírez Pérez J 1983. *Los Jejenes de Venezuela*, Simposio de oncocercosis americana. Caicet. Puerto Ayacucho, 15-17 Octubre 1983, 156 pp.
- Ramírez Pérez J, Vulcano MA 1973. Descripción y redescrpciones de algunos simúlidos de Venezuela (Diptera: Simuliidae). *Arch Ven Med Trop Parasitol Méd* 5: 375-399.
- Sawyer J 1991. *A Comparison of Taxonomic Techniques in the Identification of Sibling Species of South American Simuliidae*, PhD Thesis, University of Salford, UK, 216 pp.
- Scarpassa MV, Hamada N 2003. Isozyme variation in four species of the *Simulium perflavum* species group (Diptera: Simuliidae) from the Brazilian Amazon. *Gen Mol Biol* 26: 39-46.
- Shelley AJ, Coscarón S 2001. Simuliid blackflies (Diptera: Simuliidae) and ceratopogonid midges (Diptera: Ceratopogonidae) as vectors of *Mansonella ozzardi* (Nematoda: Onchocercidae) in Northern Argentina. *Mem Inst Oswaldo Cruz* 96: 451-458.
- Shelley AJ, Arzube M, Couch CA 1989a. The Simuliidae (Diptera) of the Santiago onchocerciasis focus in Ecuador. *Bull Brit Mus Nat Hist (Entomol series)* 58: 79-130.
- Shelley AJ, Hernández LM, Penn M 2002. A biosystematic revision of the blackflies (Diptera: Simuliidae) of Belize, Central America. *Bull Nat Hist Mus London (Entomol series)* 71: 135-271.
- Shelley AJ, Lowry CA, Maia-Herzog M, Luna Dias APA, Moraes MAP 1997. Biosystematic studies on the Simuliidae (Diptera) of the Amazonia onchocerciasis focus of Brazil. *Bull Nat Hist Mus London (Entomol series)* 66: 1-121.
- Shelley AJ, Luna Dias APA, Maia-Herzog M 1984. New specific synonymy in Neotropical *Simulium s.l.* (Diptera: Simuliidae). *Mem Inst Oswaldo Cruz* 79: 143-161.
- Shelley AJ, Luna Dias APA, Moraes MAP, Procuier WS 1987. The status of *Simulium oyapockense* and *S. limbatum* as vectors of human onchocerciasis in Brazilian Amazonia. *Med Vet Parasitol* 1: 219-234.
- Shelley AJ, Maia-Herzog M, Lowry CA, Luna Dias APA, Garritano PR, Shelley A, Camargo M, Carter HG 2000. The Simuliidae (Diptera) of the secondary onchocerciasis focus at Minaçu in central Brazil. *Bull Brit Mus Nat Hist Entomol* 69: 171-221.
- Shelley AJ, Maia-Herzog M, Luna Dias APA, Couch CA 1989b. Description of the adults and pupa of *Simulium (Trichodagnia) perplexum*, new species (Diptera: Simuliidae). *Mem Inst Oswaldo Cruz* 84: 343-349.
- Smart J 1940. Simuliidae (Dipt.) from British Guiana and the Lesser Antilles. *Trans R Entomol Soc London* 90: 1-11.
- Vulcano MA 1981. Simuliidae. In SH Hurlbert, G Rodriguez, N Dias dos Santos (eds), *Aquatic Biota of Tropical South America. Part 1. Arthropoda*, San Diego State University, California, p. 275-285.
- Wise KS 1911. The Simuliidae of British Guiana. *Timehri* 1: 248-254.