



The taxonomy, biology and medical importance of *Simulium amazonicum* Goeldi (Diptera: Simuliidae), with a review of related species

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Synopsis

The taxonomy of the species in the *Simulium amazonicum*-group is discussed and keys for the identification of adults and pupae are given. *S. quadrifidum* Lutz is resurrected from synonymy with *S. amazonicum* Goeldi, and *S. nitidum* Malloch is newly synonymized with *S. metallicum* Bellardi. A complete redescription of adults, pupae and larvae of *S. amazonicum* is provided, together with details of its distribution, biology and medical importance in Brazil.

Introduction

The discovery during the last decade of several foci of onchocerciasis in the Brazilian Amazon (Moraes *et al.*, 1979) has led to renewed interest in the region's black-flies. However, considerable difficulty continues to be experienced in identifying Simuliids from this area, as well as from the tropical rain forests of neighbouring countries, because of the lack of keys and inadequate and confused species descriptions. The inchoate state of the taxonomy of South American *Simulium* s.l. has inevitably led to the misidentification of both vector and nuisance species, the most important examples being *S. amazonicum* Goeldi and *S. sanguineum* Knab. The former species is now firmly entrenched in the literature as nominally a vector of *Mansonella ozzardi* in Brazil (Cerqueira, 1959) and more recently, but almost certainly erroneously, of *Onchocerca volvulus* both in Brazil (Rassi *et al.*, 1975) and in Venezuela (Rassi *et al.*, 1977). It is said to have a vast distribution in Central and South America (Pinto, 1932; Vargas, 1945; Vulcano, 1967) and numerous reports have been published on its morphology and biology based on a scanty original description and without reference to type-material. In contrast, *S. sanguineum*, though with a similarly wide putative distribution (Pinto, 1932; Vargas, 1945; Vulcano, 1967), has received less attention, being regarded simply as a biting nuisance. However, recent work in Brazil (Shelley *et al.*, 1979) has shown that a species morphologically closer to *S. sanguineum* than to *S. amazonicum* is the vector of *O. volvulus*, and that although *S. amazonicum* is undoubtedly a vector of *M. ozzardi* (Shelley *et al.*, 1980) its distribution in Brazil is more localized than previously supposed.

Because of the potential importance of human onchocerciasis in the Amazon basin, a region of Brazil destined for future development, a taxonomic study of the black-flies in this part of Brazil has become essential. The redescription of *S. amazonicum* and the key to adults and pupae of species in the *S. amazonicum*-group given here are necessary first steps to this end. Some of the species in this group are the most common and persistently aggravating man-biting black-flies in South America, both in the tropical rain forests and adjacent savanna zones, and taxonomic resolution of this troublesome group of species is a prerequisite for a better understanding of the epidemiology of human onchocerciasis and mansonelliasis, especially in Amazonia and circum-jacent areas.

Material studied

Most of the material examined for this paper is deposited in the Oswaldo Cruz Institute, Rio de Janeiro and the British Museum (Natural History), London. The majority of the *S. amazonicum*-group species examined in the Lutz collection of Simuliidae at the Oswaldo Cruz Institute lacked complete data. Reference is made only to specimens identified by us as species in the *S. amazonicum*-group or to those that have been previously confused with *S. amazonicum*. Collection data for these were found either on the label or, where a specimen only bears a number, in the card index of the Lutz Simuliid collection. These specimens have been relabelled and extra information, extrapolated from Lutz's publications, has been added where possible. Reared specimens of *S. amazonicum*-group species collected by us and used in this study have been deposited in the Oswaldo Cruz Institute and British Museum (Natural History). Although account has been taken of the numerous female specimens, in the collections of these two institutions, that have been collected from human bait, they are not referred to here due to the present difficulty in reliably separating some of the species of the *S. amazonicum*-group on one stage alone.

The following abbreviations are used for depositories of specimens referred to in this paper.

- AMNH American Museum of Natural History, New York, U.S.A.
- BMNH British Museum (Natural History), London, U.K.
- INPA Instituto Nacional de Pesquisas na Amazônia, Manaus, Brazil.
- IOC Instituto Oswaldo Cruz, Rio de Janeiro, Brazil.
- MLP Museo La Plata, La Plata, Argentina.
- MNHN Muséum National d'Histoire Naturelle, Paris, France.

NM Naturhistorisches Museum, Bern, Switzerland.
 USNM United States National Museum, Washington, D.C., U.S.A.

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The *S. amazonicum*-group of species

Shortly after Goeldi's description (1905) of *S. amazonicum* it was already clear that it was difficult to recognize this species reliably. Lutz (1910) observed variability in female scutal patterns that he thought was caused by the different methods of preservation used and by the existence of two similar species which he went on to describe (Lutz, 1917). Similar difficulties were encountered by Cerqueira & Nunes de Mello (1964) who used material that was a mixture of at least three species (see below for evidence for this) in their redescription of *S. amazonicum*. To explain the difficulties involved in identifying *S. amazonicum*, exacerbated by Cerqueira & Nunes de Mello's confused description, it became customary for many entomologists in South America to refer to the *S. amazonicum* species complex, applying the term to any man-biting black-fly collected in the Brazilian Amazon or neighbouring countries that possessed a silver scutum with three black vittae and whose pupae showed a four- or six-filamented gill. Following recent investigations in Brazil and Colombia no sound evidence has been discovered to suggest that *S. amazonicum* is a complex in the strict sense used for *S. damnosum* (World Health Organization, 1977), but it is now known that several closely similar but nevertheless morphologically separable species occur which, for reasons of their homogeneity, form a natural species-group, the *S. amazonicum*-group. Some species within this group are only reliably separable when combinations of characters found in both adults and pupae are used.

DIAGNOSIS. *Female, male.* Sc bare.* Pleural membrane and katapisternum bare. Scales on legs. Eyes dark red or black. *Female.* Fronto-ocular triangle absent. Cibarium armed with two or three rows of teeth. Scutum silver or grey pruinose with three velvet-black vittae, one median and 1 + 1 sublateral. Tarsal claws without teeth (except *S. quadrifidum*). Abdominal tergites 1–5 velvet-black, second segment silver pruinose; tergites 6–9 shiny black. Paraprocts broadly rectangular, cerci semi-oval with concave inner surfaces. Genital fork long and slender with 1 + 1 anterior processes. *Male.* Scutum silver or grey pruinose with three velvet-black vittae, either distinctly separate, or coalescing posteriorly to form an anchor-shaped mark, or coalescing along almost entire length leaving 1 + 1 indistinct silver submedian pruinose bands. Abdominal tergites velvet-black with silver pruinose areas particularly obvious on segments 2 and 6–8. Distimere subtriangular, shorter than subquadrangular basimere, with one apical or subapical spine (except *S. chaquense* which has two). Ventral plate broadly triangular, slightly concave ventrally, with many setae and spines.

Pupa. Cocoon usually slipper-shaped (except *Simulium* sp. (Madeira) which is shoe-shaped) with or without reinforced rim and median projection. Pupal gill with four, six or eight filaments usually shorter than pupa. *Onchotaxy.* Tergites three and four with 4 + 4 simple hooks; tergites 7–9 with spine combs on anterior margins. Sternite four with 1 + 1 hooks, sternites 5–7 with 2 + 2 hooks; posterior sternites with antero-lateral groups of spiny cuticular processes on each segment.

* Coscarón (1971) describes Sc of ♀ *S. chaquense* with 4–5 hairs but the ♀ paratype in the BMNH collection has a bare Sc. Further examination of the type-material in MLP has shown that the Sc is bare (Coscarón, pers. comm.).

The *S. amazonicum*-group contains, according to our studies, the following species.

S. amazonicum Goeldi, 1905

? *S. tallaferoae* Ramírez Pérez, 1971

S. chaquense Coscarón, 1971

S. minusculum Lutz, 1910

? *S. roraimense* Nunes de Mello, 1974

S. quadrifidum Lutz, 1917 sp. rev.

S. sanguineum Knab, 1915

Simulium sp. (Barbacoas). Unidentified species from Barbacoas, Venezuela.

Simulium sp. (Madeira). Unidentified species from the R. Madeira, Brazil.

Previous reference has been made (World Health Organization, 1979; Shelley *et al.*, 1980) to *S. delponteianum* Wygodzinsky as a member of the *S. amazonicum*-group. It is now thought preferable not to include this species in the group at this stage due to its different eye colour and form of the male distimere. Similarly, *S. quadrivittatum* Loew and *S. haematopotum* Malloch are not at present included in the group due to differences in their morphology, despite their superficial resemblance to some of the *S. amazonicum*-group species.

Keys to the species of the *S. amazonicum*-group

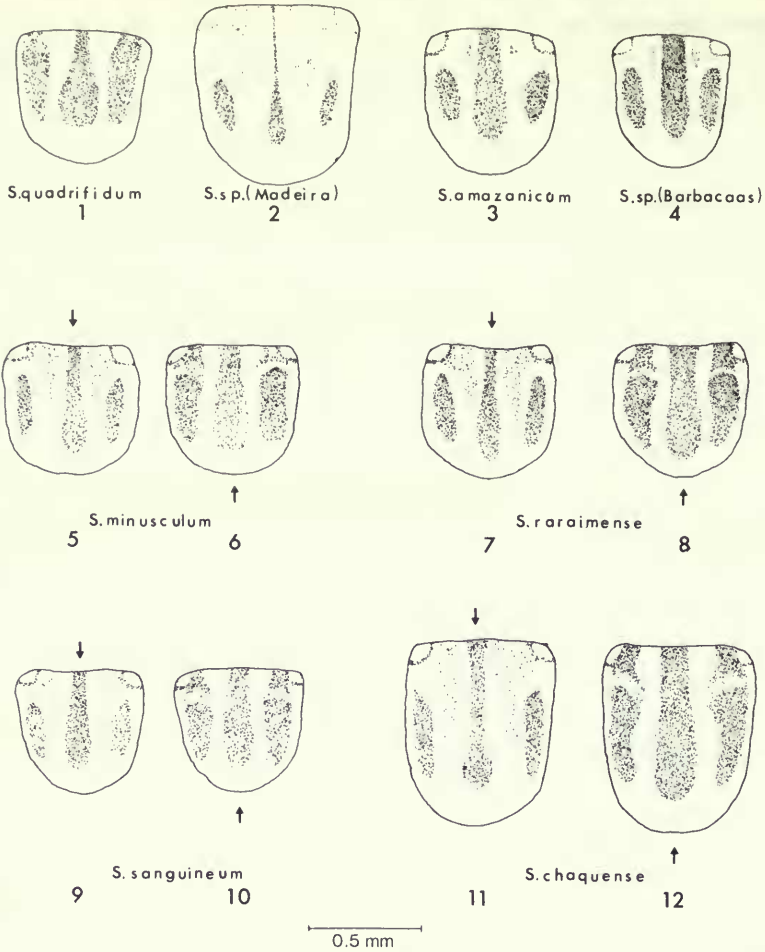
Separate keys are given for females, males and pupae even though it is not usually possible to identify to species when only one stage is available. This arrangement has been used for the sake of clarity, an accurate identification usually only being possible on reared material and using a combination of keys. As the keys have been based mainly on reared material from the Brazilian Amazon this must be borne in mind when they are used for identifying material collected outside this area. They are necessarily preliminary due to the difficulty in obtaining sufficient numbers of immature stages of the anthropophilic members of the group. However, they do provide a basis for more detailed future works and help to clarify the previous confusion surrounding *S. amazonicum* and its relatives.

Although most of the species in this key are clearly separable, future investigation is needed for the element denoted *S. minusculum*. In this paper it is assumed that the circumstantial association of six-filamented pupae with *S. minusculum* females by Lutz (1917) is correct, since females reared by the authors from six-filamented pupae appear conspecific with the *S. minusculum* syntypes. *S. roraimense* is regarded for the purposes of the key as a separate species even though it may only be separated from *S. minusculum* in the male by the absence of posterior merging of the scutal vittae. The variability of this character within *S. minusculum* and *S. roraimense* and hence its validity for separating these two species needs to be investigated. This character is already known to be variable in *S. sanguineum* (Tidwell *et al.*, 1981) and this finding has been confirmed in specimens in the BMNH collection. Where the key to females is used for the identification of Brazilian material, collected from human bait, that shows (with a posterior light source) the presence of intervittal marks and long sublateral vittae extending to the anterior scutal border, the specimens would run out to couplet three and a choice between four species would be obtained. In such a case they should be assigned to *S. minusculum* rather than *S. roraimense*, due to the possible synonymy of the latter species with *S. minusculum* for the reason previously indicated. It is unlikely that such females are *S. sanguineum*, which has a pupa with an eight-filamented gill. Although the two species are indistinguishable as adult females, *S. sanguineum* has only been recorded from north-western Colombia, being replaced in the Colombian Amazon by *S. minusculum*, which has a pupa with a six-filamented gill. Similarly, confusion with *S. chaquense*, which also has a pupa with an eight-filamented gill, is unlikely as this species has only been recorded from a quite different type of habitat in Argentina. Variations in the appearance of the intervittal marks in *S. minusculum* females, including the syntypes, have been regarded as infra-specific as they cannot be associated with either fixed pupal characters, other adult characters or particular localities in Brazil. The significance of these variations at the species level as well as the status of *S. roraimense* may only become apparent once reared *S. minusculum* topotypes have been studied or by cytogenetic or enzymatic means.

The scutal patterns described relate to specimens in a horizontal position with the light source anterior to the specimen unless otherwise indicated. It is essential that undamaged specimens are used and attention paid to the exact positioning of both specimen and light source. For practical reasons scutal patterns referred to in the keys have been regarded as black vittae, in various stages of development, depending on the species, on a silver pruinose background. These patterns may be considered alternatively as silver ornamentations on a black background, but in such a case would unnecessarily complicate the keys due to the lengthier descriptions that would be required. Although variation in scutal pattern has been seen within some species of the *S. amazonicum*-group the patterns described in the three couplets in the key to females are distinctive.

Females

- 1 Three velvet-black vittae occupying most of width of anterior three-fourths of silver pruinose scutum: median vitta narrow anteriorly, widening posteriorly, drop-shaped; sublateral vittae pointed and narrow posteriorly, widening anteriorly and only joining scutal margin at two points, their form not altered by change in direction of light, intervittal marks absent (Fig. 1); row of silvery gold setae along entire mid line of median vitta giving appearance of two adjacent vittae in perfect specimens.
[Zoophilic species; stream and small-river breeder; pupal gill with four filaments] *quadrifidum* (p. 25)
 - Three velvet-black vittae in anterior three-fourths of silver pruinose scutum: median vitta of varying width, widening posteriorly but never drop-shaped; sublateral vittae of variable length depending on position of light: with light anterior sublateral vittae oblong with rounded extremities not reaching anterior scutal border and indistinct cuneiform marks between median and sublateral vittae (intervittal marks); with light posterior length of sublateral vittae unaltered (short) or sublateral vittae reaching anterior scutal border (long), intervittal marks present or absent; setae not concentrated along mid line of median vitta 2
 - 2 Median vitta narrow, often appearing as thin black line; sublateral vittae narrow, often reduced in length but always wider than median vitta, in median third of scutum diverging anteriorly; cuneiform black intervittal marks with slightly indistinct borders, arising on anterior scutal border and extending for half length of scutum (Fig. 2); with light source posterior scutal pattern similar with short sublateral vittae but intervittal marks indistinct and silvery white pruinose.
[Anthropophilic species; large-river breeder; pupal gill with six filaments] undescribed species (Madeira) (p. 27)
 - Median vitta wider and conspicuous; lateral vittae of approximately same width as median vitta in median third of scutum and diverging anteriorly; black intervittal marks of indistinct form or cuneiform, arising on anterior scutal margin; with light posterior to specimen sublateral vittae long or short, intervittal marks present or absent. 3
 - 3 Sublateral vittae short and intervittal marks of indistinct form irrespective of position of light. In some cases intervittal marks appear to be absent with posterior light source. (Figs 3, 4.)
[Anthropophilic species; large-river breeder; pupal gill with eight filaments.] *amazonicum* (pp. 8, 10)
[Biting habits and habitat details unknown; pupal gill with six filaments.] undescribed species (Barbacoas) (p. 27)
(Species only separable by reference to pupal gill.)
 - Sublateral vittae short, intervittal marks distinct, cuneiform and extending up to half length of scutum; with light posterior sublateral vittae long, inner half of intervittal mark silver pruinose and merging with background scutal pruinosity, outer half dark and merging with sublateral vitta. (Figs 5-12.)
[Anthropophilic species; large-river breeder; pupal gill with six filaments.] *minusculum* (p. 22)
[Anthropophilic species; large-river breeder; pupal gill with six filaments.] *roraimense* (p. 22)
[Anthropophilic species; large-river breeder; pupal gill with eight filaments.] *sanguineum* (p. 26)
[Anthropophilic species; slow-flowing stream breeder; pupal gill with eight filaments.] *chaquense* (p. 22)
- (Further identification only possible by reference to pupal gill; *S. roraimense* may only be separated from *S. minusculum* on male scutal pattern.)



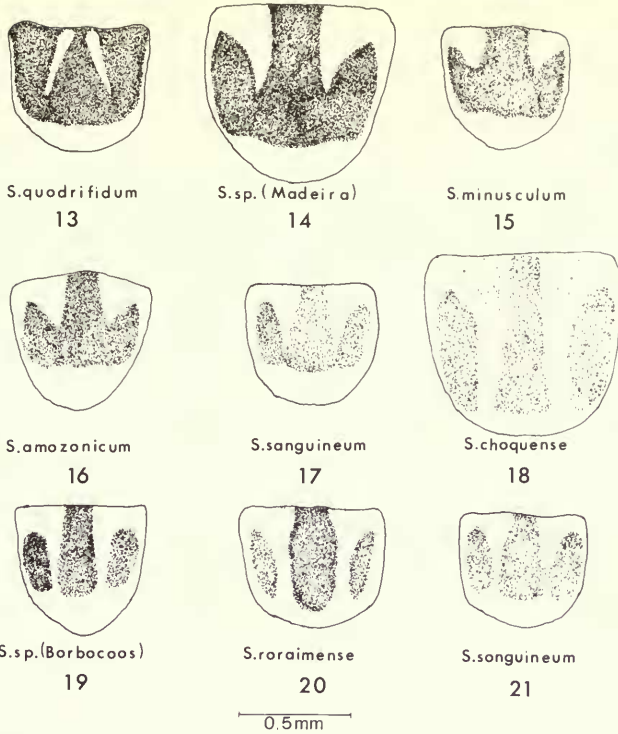
Figs 1-12 Female scutal patterns of *S. amazonicum*-group species. (Arrows indicate direction of light; arrows omitted where scutal pattern not greatly altered by direction of light.)

Males

- 1 Scutum with three velvet-black vittae merged and covering most of scutal area except lateral and posterior borders, and submedian area forming two fine silver pruinose bands diverging posteriorly and not reaching anterior scutal border. (In some specimens these bands are absent). (Fig. 13.)
 - [Pupal gill with four filaments.] *quadrifidum* (p. 25)
- Scutum with three velvet-black vittae either merging posteriorly or distinctly separate 2
- 2 Vittae merging posteriorly and appearing as black anchor on silver pruinose background, no intervittal marks present; distimere of genitalia with one apical spine. (Figs 14-17.)
 - [Pupal gill with six filaments.] undescribed species (Madeira) (p. 27)
 - [Pupal gill with six filaments.] *minusculum* (p. 22)
 - [Pupal gill with eight filaments.] *amazonicum* (pp. 8, 12)
 - [Pupal gill with eight filaments.] *sanguineum** (p. 26)

(Further identification only possible by reference to pupal gill.)
- Vittae distinctly separate; median vitta broad, arising on anterior scutal border and extending three-fourths length of scutum, lateral vittae short, in central half of scutum, intervittal marks present or absent; distimere of genitalia with one or two apical spines (Figs 18-21) 3

* Tidwell *et al.* (1981) comment on the variation in the male scutal pattern of *S. sanguineum*; sublateral vittae may merge at posterior extremity or be separate.

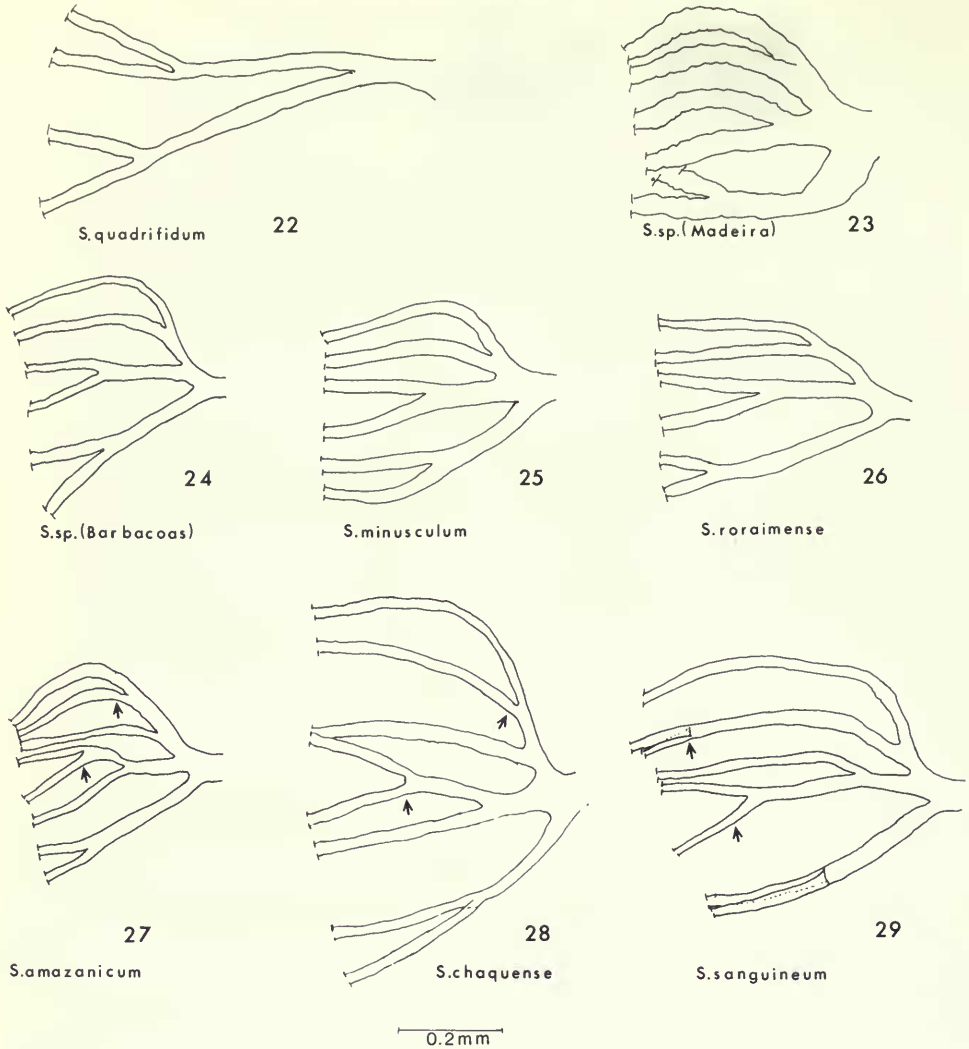


Figs 13–21 Male scutal patterns of *S. amazonicum*-group species.

- 3 Distimere of genitalia with two apical spines.
 [Pupal gill with eight filaments.] *chaquense* (p. 22)
 - Distimere of genitalia with one apical spine.
 [Pupal gill with six filaments.] undescribed species (Barbacoas) (p. 27)
 [Pupal gill with six filaments.] *roraimense* (p. 22)
 [Pupal gill with eight filaments.] *sanguineum** (p. 26)
- (Further identification only possible by reference to pupal gill. *Simulium* sp. (Barbacoas) only separable from *S. roraimense* on female scutal characters.)

Pupae

- 1 Gill with four filaments longer than pupal body; trunk of gill with basal bifurcation, each primary branch having a secondary bifurcation at approximately the same level in basal fifth of gill (Fig. 22); filaments arranged in horizontal plane; cocoon slipper-shaped *quadrifidum* (p. 25)
 - Gill with six or eight filaments shorter than pupal body; branching in basal fourth of gill; filaments arranged in vertical plane; cocoon slipper- or shoe-shaped. 2
 - 2 Gill with six filaments in a 2 : 2 : 2 configuration 3
 - Gill with eight filaments in a 3 : 3 : 2 configuration: dorsal and median primary branches each with three secondary branches, ventral primary branch with a single bifurcation 4
 - 3 Gill about one-third length of pupal body; bifurcation of ventral primary branch always more distal than those on dorsal and median primary branches; filaments wide at base, tapering apically (Fig. 23); cocoon shoe-shaped undescribed species (Madeira) (p. 27)
 - Gill almost as long as pupal body; bifurcations on three primary branches at variable distance from base of gill; width of filaments approximately equal throughout entire length (Figs 24, 25, 26); cocoon slipper-shaped.
 undescribed species (Barbacoas) (p. 27), *minusculum* (p. 22), *roraimense* (p. 22)
- (Further identification only possible by rearing to adult).
- 4 Trifid dorsal and median primary branches with most apical fork on dorsal secondary branch (Figs 27, 28) *amazonicum* (pp. 8, 14), *chaquense* (p. 22)
 - (Further identification only possible by rearing to adult).
 - Trifid dorsal and median primary branches with most apical fork on ventral secondary branch (Fig. 29) *sanguineum* (p. 26)



Figs 22–29 Pupal gills of *S. amazonicum*-group species. (Arrows indicate branch bifurcations referred to in key.)

Simulium amazonicum Goeldi

(Figs 30–94)

Simulium amazonicum Goeldi, 1905: 138; Smart, 1942: 46. Syntypes ♀, BRAZIL: Amazonas, Bom Lugar, R. Purus (BMNH) [examined]. [Application to International Commission on Zoological Nomenclature for setting aside extant syntypes and establishment of neotype under plenary powers (Shelley, 1981).]

? *Simulium tallaferoae* Ramírez Pérez, 1971: 339. Holotype [sex unspecified], VENEZUELA: Guárico, Camaguán (División de Endemias Rurales, Maracay), [not examined; type-material lost or destroyed, see World Health Organization, 1979].

TYPE-MATERIAL OF *S. amazonicum*. Goeldi's description of *S. amazonicum* in 1905 was based on females collected by A. Ducke from Teffé (now Tefé) on the river Solimões (Upper Amazon) and by J. Huber from the rivers Purus and Acre, in the Brazilian state of Amazonas. Goeldi stated in the original description that a series of 'cotypes' was sent to the BMNH but did not indicate their precise provenance nor make reference to other type-series. Some confusion then followed in succeeding publications over the type-locality and status of the BMNH 'cotypes'.

Pinto (1932), in his catalogue of Central and South American Simuliidae, stated that Goeldi's description of *S. amazonicum* was based on specimens collected by Ducke at Tefé, neglecting to mention the material collected by Huber from the two other localities but recording that Goeldi had sent a series of 'cotypes' to the BMNH. Both Smart (1940) and Vargas (1945) erroneously believed that a *S. amazonicum* 'type' (i.e. holotype) had possibly been deposited in the Goeldi collection at the NM and the latter author followed Pinto's citation of the type-locality as Tefé. Smart (1942) discussed Goeldi's meaning of 'cotype', and allowing for its possible sensu stricto use made a slide preparation of one of the BMNH 'cotypes' which he labelled as 'plesio-cotype'; Smart regarded this specimen as a provisional lectotype to be designated, if necessary, once the status of the 'cotypes' had been established. In the same paper Smart gave details of the labels of the BMNH 'cotypes' showing the specimens to have been collected by Huber from Bom Lugar on the river Purus, thus correcting Pinto's inference (1932) that they were collected at Tefé. However, Tefé is still wrongly considered as type-locality by Cerqueira & Nunes De Mello (1964) in their redescription of *S. amazonicum*, and no mention is made by them of the BMNH type-material. A male 'holotype', female 'topotype' and male and female 'paratypes' were designated by these authors from their own material collected at Tefé, regardless of the fact that under the *International Code of Zoological Nomenclature* only the original author of a name can designate or indicate a holotype. Vulcano (1967), however, correctly quotes the three original *S. amazonicum* type-localities in her catalogue of Neotropical Simuliidae, omitting reference to Cerqueira & Nunes de Mello's paper (1964).

As Goeldi (1905), in his description of *S. amazonicum*, made no reference to designating a 'type' the only designation being that of 'cotypes', this series of specimens can only have the status of syntypes under Article 73 of the current *International Code of Zoological Nomenclature*. Whether a 'type' was selected or not by Goeldi, as has been assumed by several authors, would not alter the situation as no published designation was made.

Since the BMNH syntypes are in poor condition, having been preserved in alcohol for three-quarters of a century, attempts were made by the authors to locate other possible syntypes from the two other localities indicated by Goeldi, as he made reference to pinned specimens. No specimens were found in any of the major Brazilian depositories (INPA; IOC; Museu Goeldi, Belém; Museu Nacional, Rio de Janeiro; Museu de Zoologia, São Paulo). However, a series of 27 pinned specimens was located in the NM with the following labels in Goeldi's handwriting: 'Piúm. Purús, schreckliche Landplage am Amazonasstrom' and 'An Austen in London British Museum einsenden zum bestimen trockenens & Spiritusmater'. These have been examined and are also in poor condition. Although not cited as 'cotypes' by Goeldi in his 1905 paper, these 27 specimens were almost certainly examined by him when preparing the *S. amazonicum* manuscript and hence have syntype status.

Reference has already been made to the importance of separating *S. amazonicum* from its related vector and non-vector species in the epidemiology of human filariasis in Brazil. Though this is possible in some instances using the form of the pruinose pattern of the female scutum, reliable separation to species level is often only feasible when pupal characters are also considered. The complete redescription of *S. amazonicum*, necessary as a basis for the elucidation of the *S. amazonicum*-group, could not be made using the poorly preserved syntypes and hence has been based on a reared female (proposed as neotype, Shelley, 1981) and other reared adults and immature stages collected at the type-locality Bom Lugar on the river Purus. Because of the necessity of associating pupae with adults and the poor condition of the extant syntypes, a request has been made to the International Commission on Zoological Nomenclature (Shelley, 1981) to set aside the latter type-material and designate as neotype the principal specimen used in this redescription. A comparison of dissected female topotypes with five of the Goeldi syntypes showed the material to be conspecific.

Bom Lugar, the type-locality, was a rubber collecting community on the river Purus early in this century. It was abandoned in the 1930s when this part of the river formed an oxbow lake, Lagoa Bom Lugar, and the new community of Valparaíso was constructed about 2 km upstream from the original site. Collections made by the authors are labelled Valparaíso, Bom Lugar and Canto Escuro, the community on the opposite bank to Valparaíso.

IMPORTANT MISIDENTIFICATIONS AND NOMENCLATRURAL CHANGES. Because of the incrimination of *S. amazonicum* as a vector of *M. ozzardi* in Brazil, and the incorrect references to it as a vector of *O. volvulus* both in Brazil (Rassi *et al.*, 1975) and Venezuela (Rassi *et al.*, 1977), it became necessary to examine all references to this species in the literature so that the confusion surrounding its identity could be clarified. Only a small proportion of the 30 or so publications are quoted as the majority involves either the description of insignificant morphological details that are impossible to check without reference to the specimens used, or notes on its biology. As far as can be ascertained only Smart (1942) and possibly Cerqueira & Nunes de Mello (1964, female only) were dealing with true *S. amazonicum*, and in the case of the latter authors' description an admixture of at least three species was involved. The main material available to the authors on which a description of *S. amazonicum* had been based, apart from the original syntypes, was that in Lutz's Simuliid collection at the Oswaldo Cruz Institute. Most of the specimens are in bad condition or inadequately labelled, but of those that were identifiable, judging by the scutal vittae, none was *S. amazonicum*. Where possible, specimens labelled by Lutz as *S. amazonicum* or *S. amazonense* (incorrect subsequent spelling by Lutz of *S. amazonicum*; also incorrectly cited in Lutz, 1917) have been assigned to either *S. minusculum* or *S. quadrifidum*.

Nomenclatural changes involving *S. amazonicum* have only been made by Lutz (1917) and Cerqueira & Nunes de Mello (1964). Lutz described two new species, *S. exiguum* (not Roubaud) in 1909 and *S. minusculum* in 1910, only to synonymize them in 1917 with *S. amazonicum*. Our reasons for not accepting these synonymies may be found in the sections on *S. lutzi* and *S. minusculum* respectively. Similarly the reader is referred to the section on *S. metallicum* for details of Lutz's incorrect synonymy (1917) of *S. nitidum* Malloch with *S. amazonicum*. The synonymy of *S. quadrifidum* with *S. amazonicum* and the resurrection of *S. minusculum* by Cerqueira & Nunes de Mello (1964) are dealt with under the sections on *S. quadrifidum* and *S. minusculum*.

DESCRIPTION. *Female*. General body colour black. Length of body 1.2–2.5 mm; alcohol specimens 1.5–2.5 mm, pinned specimens 1.2–2.3 mm. Length of wings 1.2–1.9 mm, breadth of wings 0.6–0.9 mm.

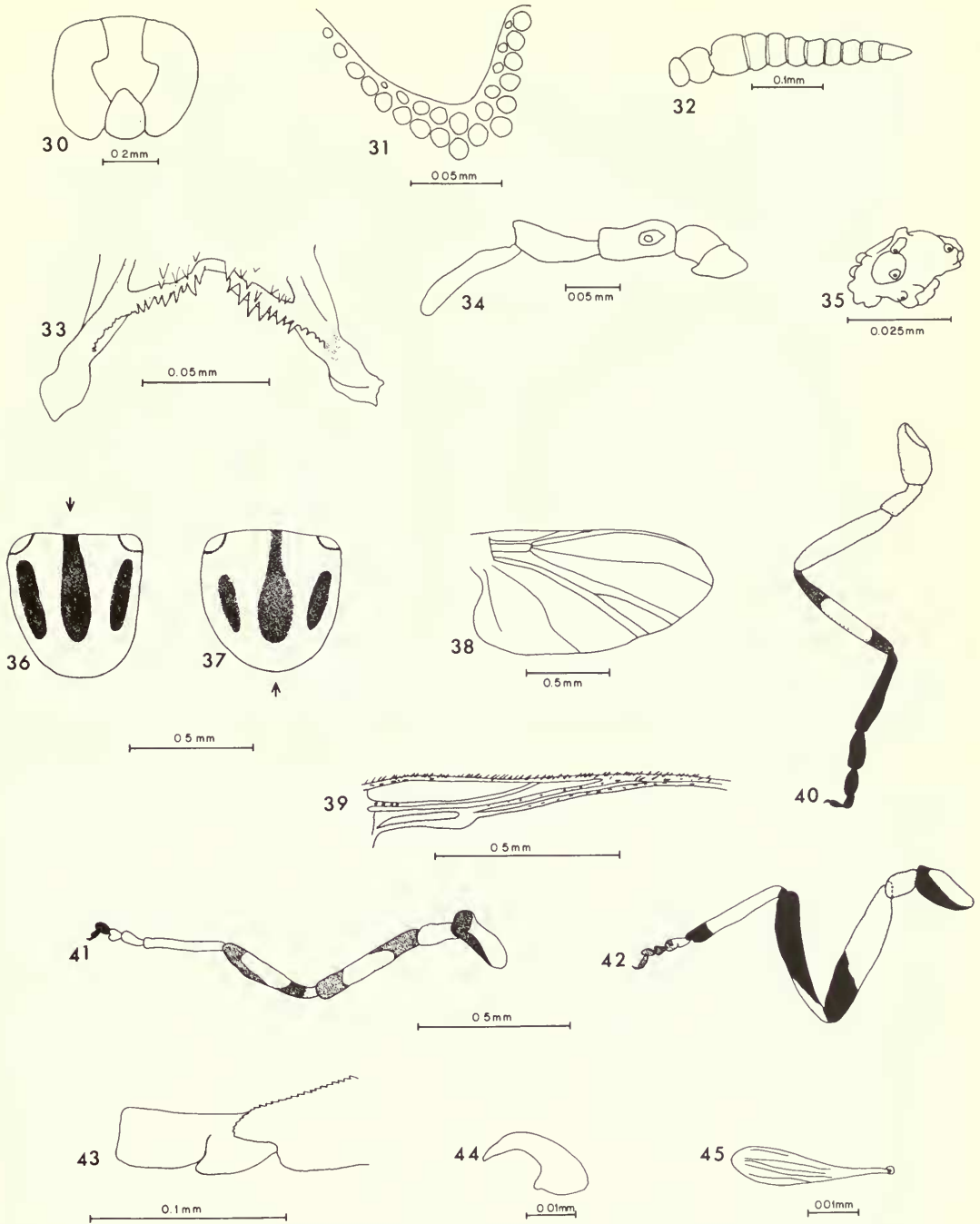
Eyes dark red. Clypeus, frons and occiput black with bluish silver pruinosity. Frons and clypeus with scattered dark brown lateral marginal hair, occiput with denser dark brown hair. Antennae brown to brownish black, pedicel and basal part of scape brownish orange. Mouthparts dark brown.

Frons narrow, about one and a half times as wide at vertex as at narrowest point (Fig. 30). Fronto-ocular triangle absent (Fig. 31). Clypeus slightly longer than broad. Antenna 11-segmented (Fig. 32). Cibarium (Fig. 33) with median margin and cornuae strongly sclerotised; central portion of margin glabrous, submedian and lateral portions with 25–40 sharp and uneven teeth arranged in two to four rows; anterior row of teeth extending to base of cornuae as fine serrations. Maxillary palp with apical segment approximately two-thirds the combined length of the two preceding segments (Fig. 34); sensory vesicle slightly elongate with many tubercles and short neck, its diameter about one-third the width of third segment of maxillary palp (Fig. 35). Maxillae and mandibles with teeth on both margins: maxillae with 16–21 teeth, mandibles with 3–6 poorly developed teeth on outer margin and 28–32 teeth on inner margin.

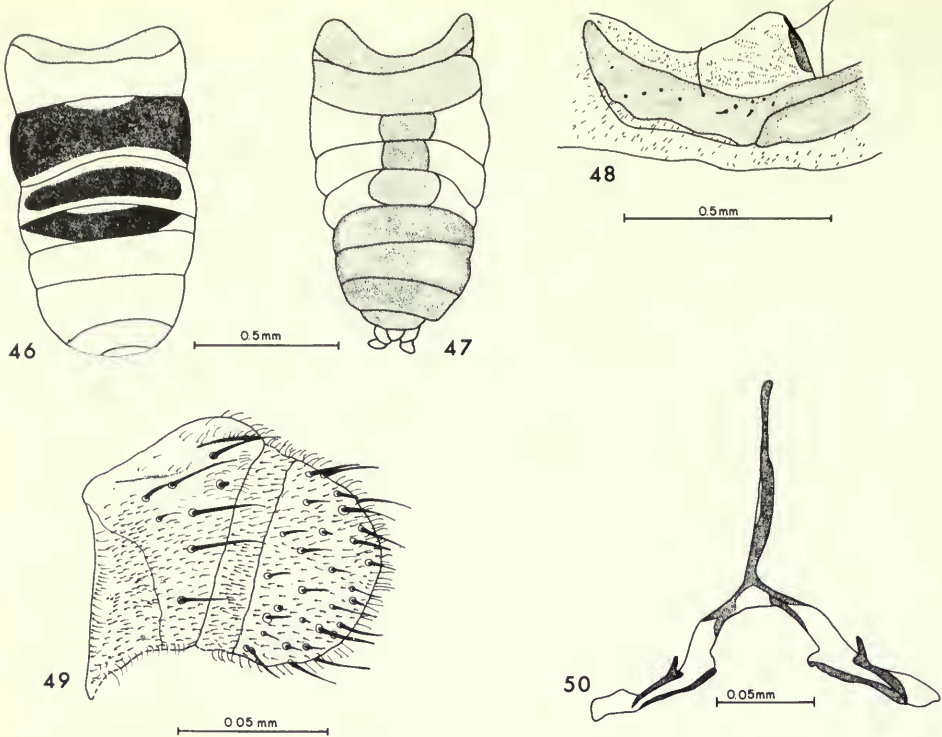
Scutum with pattern appearing variable depending on position of light: when light anterior to specimen scutum black with silver-grey pruinosity and a median black vitta occupying first three-fourths, 1 + 1 sublateral vittae, slightly divergent anteriorly and occupying central third of scutum, and 1 + 1 diffuse dark areas in pruinose region between vittae abutting anterior margin of scutum (Fig. 36); when light posterior to specimen sublateral vittae shorter and median vitta wider posteriorly (Fig. 37); scutal pattern indistinct when light source in other positions; when specimen on its side and anterior margin tilted slightly downwards 1 + 1 fine black bands present close to and running parallel to lateral margin of scutum. Humeri and scutum with dense silver-yellow adpressed hairs. Pleura and sterna greyish black with silver pruinosity; pleural membrane brownish black, bare. Scutellum greyish black with long adpressed brown hairs becoming upright on posterior margin. Postnotum black with silver pruinosity, bare. Mesepimeral sulcus complete, katapisternum bare, longer than deep in profile.

Wing shape and venation as shown in Figs 38 and 39. *C* with hairlike and spiniform macrotrichia; *Sc* with two prominent and 4–6 fine sensillae on basal fifth; basal section of *R* bare, apical section with single row of spiniform macrotrichia; *Rs* simple with single row of hairlike macrotrichia along entire length except for base; *Cu*₂ sinuous.

Coxa, trochanter and femur of fore leg light brown; tibia light brown with basal and apical fourths mid-brown; tarsus black. Coxa of mid leg dark brown, faintly pruinose; trochanter light brown with basal articulation yellow; femur and tibia light brown with basal and apical fourths dark except at articulation



Figs 30–45 *S. amazonicum* female. 30, head, anterior view; 31, fronto-ocular triangle; 32, antenna; 33, cibarium; 34, maxillary palp; 35, sensory vesicle of maxillary palp; 36, colour pattern of scutum with anterior light source; 37, colour pattern of scutum with posterior light source; 38, wing; 39, anterior veins of wing; 40, fore leg; 41, mid leg; 42, hind leg; 43, apex of posterior basitarsus with second tarsal segment; 44, claw of hind leg; 45, scale from hind leg.



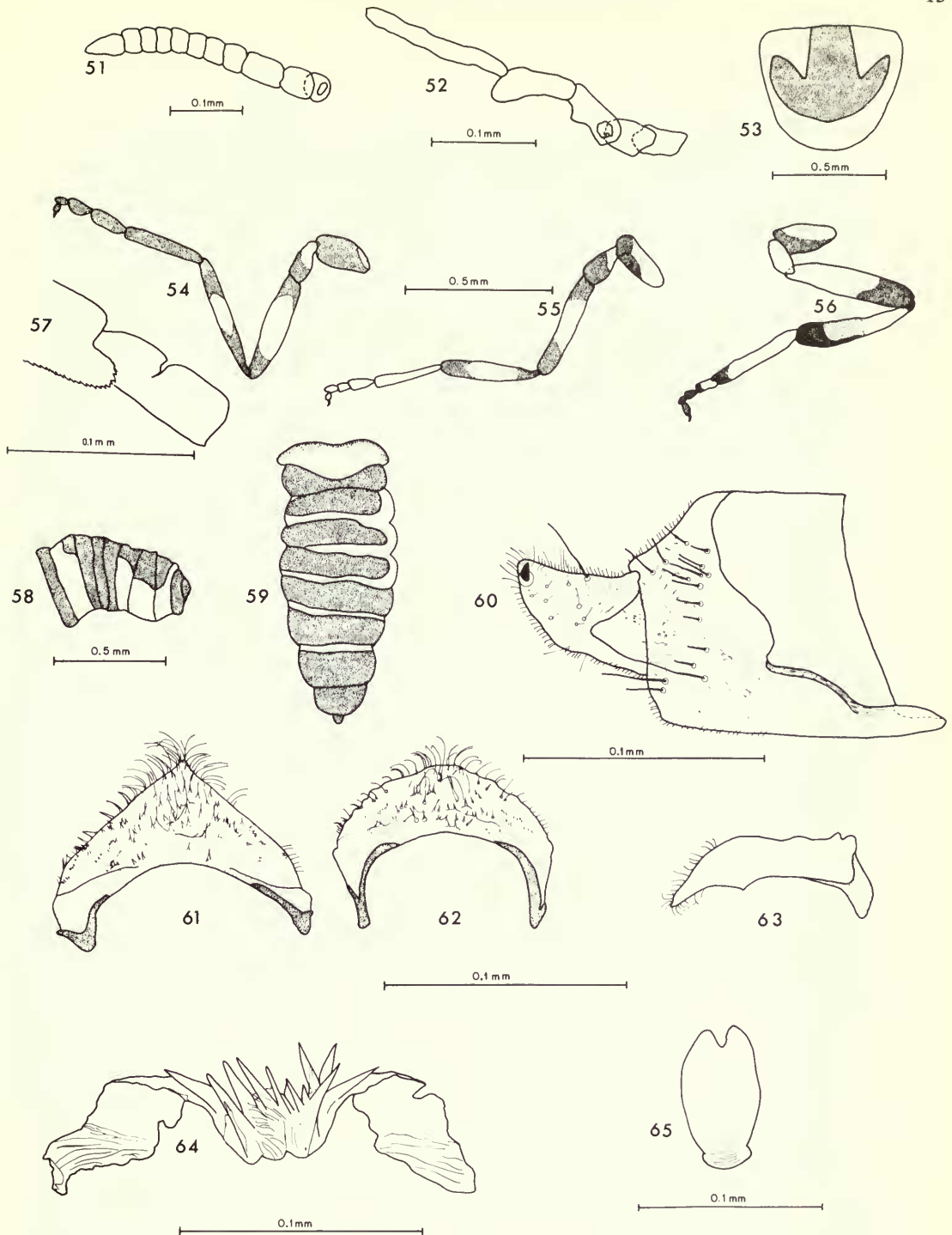
Figs 46–50 *S. amazonicum* female. 46, dorsal view of abdomen showing colour pattern; 47, dorsal view of abdomen showing tergal plates; 48, part of eighth sternite with gonopophysis; 49, paraproct and cercus; 50, genital fork.

points; first three tarsomeres light brown, rest dark brown. Hind leg coxa dark brown, faintly pruinose; trochanter light brown with basal articulation orange brown; femur light to mid brown with distal third dark brown; tibia dark brown with basal fourth to half cream, and basal articulation dark brown; basitarsus cream with basal articulation and apical fourth mid to dark brown, basal half of second tarsomere cream, apical half mid to dark brown, third tarsomere cream to light brown, fourth and fifth tarsomeres mid to dark brown. Leg shapes and proportions as in Figs 40–42, first and second fore tarsomeres slightly flattened. Calcipala as long as wide, extending almost to base of pedisulcus (Fig. 43). Claws without teeth (Fig. 44). Femur and tibia of mid and hind legs with scattered scales (Fig. 45). Haltere with capitulum and distal tip of pedunculus pale yellow, rest of pedunculus light brown.

Abdomen with first tergite brownish black, basal fringe with dark brown hair; second tergite velvet-black with silver pruinosity; third to fifth tergites velvet-black, anterior and posterior margins silver pruinose; sixth to ninth tergites shiny black (Fig. 46). Terminalia and sternites brownish black. Tergal plates well developed, covering almost entire surface in segments 2 and 6–9, but only median part of segments 3–5 (Fig. 47). Eighth sternite strongly sclerotised with about 12 + 12 setae, gonopophyses broadly subtriangular with sclerotised median borders and numerous scattered hairs (Fig. 48). Cerci and paraprocts with strong spines and numerous hairs, cerci semi-oval and slightly concave on inner surface, paraprocts broadly rectangular (Fig. 49). Genital fork with slender heavily pigmented stem, posterior arms long and slender with median and sublateral sections of posterior margin pigmented; fine pigmented anterior processes arising from broad pigmented base (Fig. 50). Spermatheca oval, externally smooth, internally with needle-like spicules of varying size, arranged in groups of 6–8 in regular rows in anterior three-fourths of spermatheca; spermathecal duct and its area of insertion membranous.

Male. General body colour black. Length of body 1.3–2.4 mm; alcohol specimens 1.5–2.4 mm, pinned specimens 1.3–1.9 mm. Length of wings 1.2–1.6 mm, breadth of wings 0.5–0.9 mm.

Eyes red. Coloration of head as in female, antennae dark brown. Length of antennae as in female except pedicel and first flagellomere longer (Fig. 51). Single vertical row of hairs between eyes. Maxillary palp as shown in Fig. 52, sensory vesicle oval, smaller, and with fewer tubercles than in female.



Figs 51–65 *S. amazonicum* male. 51, antenna; 52, maxillary palp; 53, colour pattern of scutum; 54, fore leg; 55, mid leg; 56, hind leg; 57, apex of posterior basitarsus with second tarsal segment; 58, lateral view of abdomen showing colour pattern; 59, dorsal view of abdomen showing colour pattern; 60, paramere, ventral view; 61, ventral plate, dorsal view; 62, ventral plate, ventral view; 63, ventral plate, profile; 64, endoparameral organ; 65, median sclerite.

Scutum black with silver-blue pruinosity; three velvet-black vittae merge posteriorly to form an anchor-shaped area almost filling scutum (Fig. 53). Rest of thorax as in female.

Wing shape and venation as in female, Sc with 2–3 sensillae on basal fifth.

Coxa of fore leg mid brown; trochanter yellow-brown on basal half, light brown on apical half; femur yellow-brown, generally with basal fourth light brown; tibia cream to mid brown with basal and apical articulations darker brown, anterior face white pruinose; tarsus dark brown to black. Mid leg coxa dark brown; trochanter mid brown with basal half and articulation light brown; femur and tibia mid to dark brown with darkened basal and apical articulations; basitarsus cream to light brown, rest of tarsus cream to dark brown. Coxa and trochanter of hind leg light to dark brown; femur light to dark brown with apical third dark brown to black; basal half of tibia cream, apical half light to dark brown, basal articulation dark brown; basitarsus cream with apical fourth light to dark brown, second tarsomere cream basally becoming light to dark brown apically, other tarsal segments light brown. Leg shape and proportions as shown in Figs 54–56. Calcipala and pedisulcus as in Fig. 57. Legs scaled on fore tibia, mid trochanter, femur and tibia, and hind femur and tibia. Haltere with capitulum lemon-yellow, pedunculus grey with faint silver pruinosity.

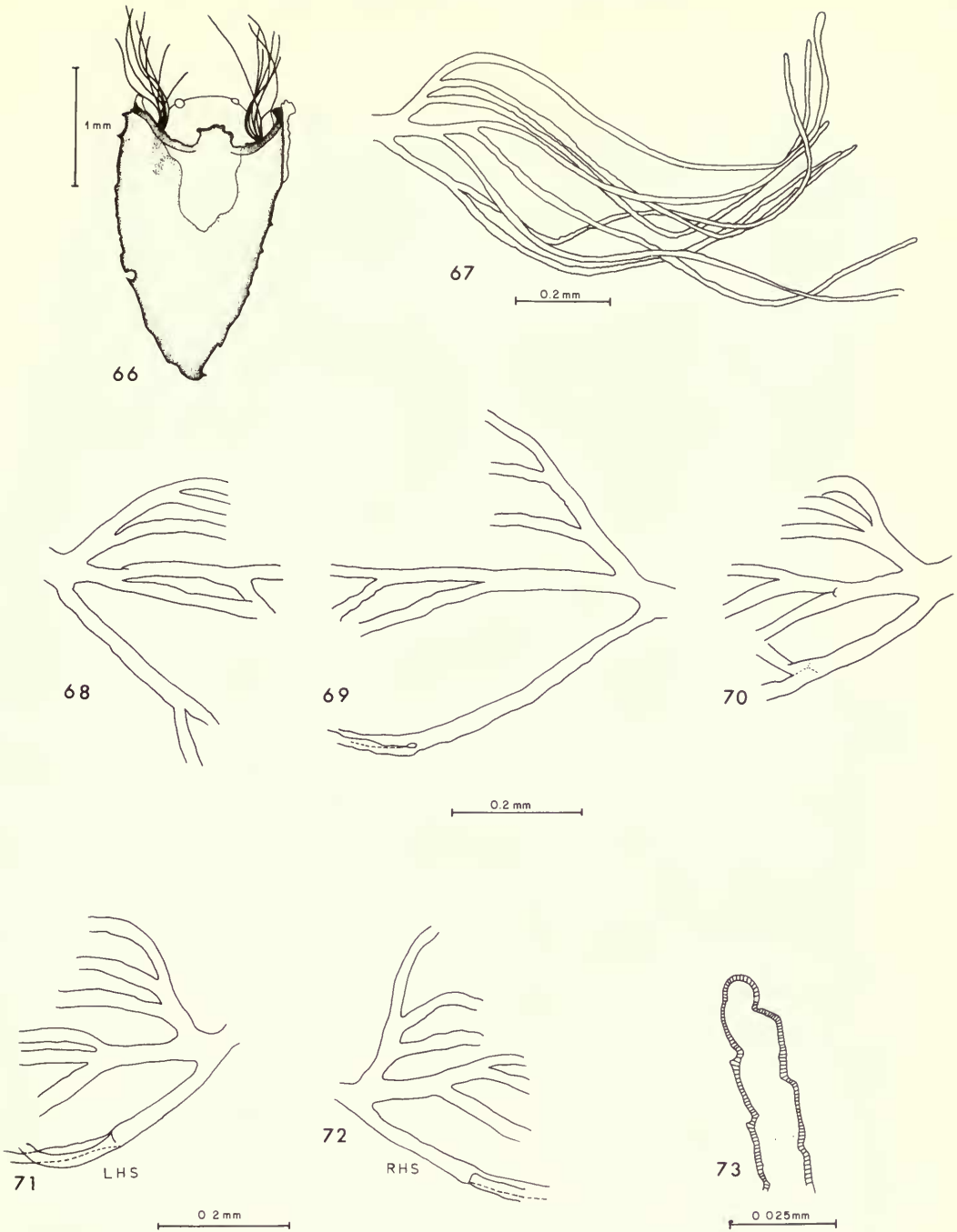
Abdominal tergites velvet-black, basal fringe with long black hair. Tergites with pruinose areas as follows: tergite 2 silver pruinose except median black spot on posterior margin; tergites 6–8 with 1 + 1 lateral silver pruinose bands as shown in Fig. 58. Terminalia black with faint silver pruinosity. Sternites velvet-black. Paramere black, setose, with faint silver pruinosity. Tergal plates on segments 2–9 well developed (Fig. 59), rectangular plates on central portions of sternites 3–8. Basimere almost as long as wide, distimere conical, shorter than basimere and with blunt subapical spine (Fig. 60). Ventral plate subtriangular with numerous setae and spines, apex slightly concave ventrally (Figs 61, 62), profile as shown in Fig. 63, basal arms pigmented; endoparameral organ as in Fig. 64; median sclerite (Fig. 65) with distal incision.

Pupa. Length of cocoon dorsally 1.6–2.3 mm, ventrally 2.0–2.7 mm; length of pupa 1.6–2.5 mm; length of gill 1.0–1.5 mm.

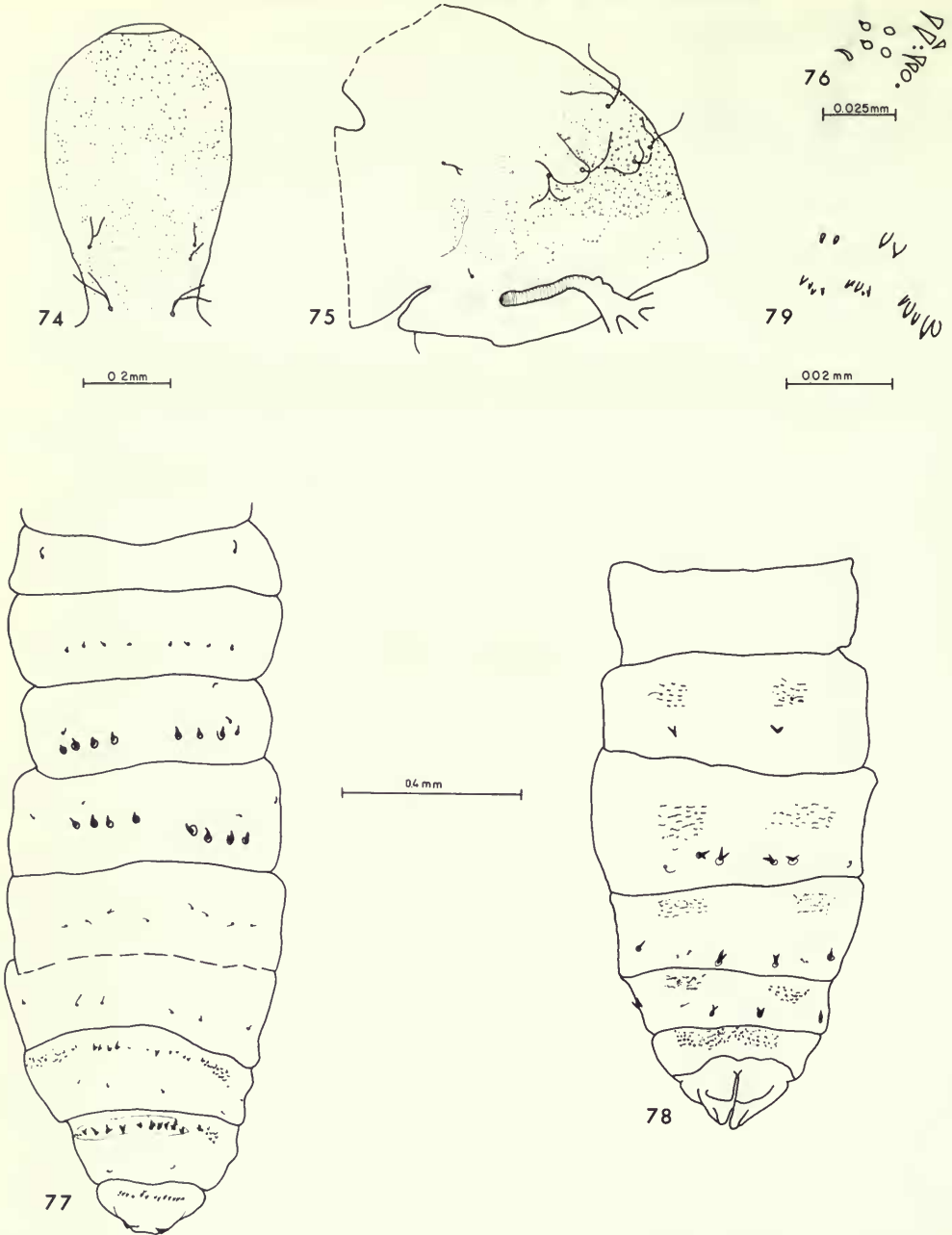
Cocoon slipper-shaped, mid brown; rim of aperture dark brown, reinforced and usually with small median projection (Fig. 66). Cocoon surface composed of fine threads, more loosely woven ventrally and only occupying distal half of cocoon. Gill light brown with eight forwardly directed filaments arranged irregularly in a vertical plane (Fig. 67): main trunk gives rise to three primary branches, ventral with two filaments, median and dorsal each with three filaments; filaments of all primary branches arise basally but branch height varies (Figs 68–70) even in same specimen (Figs 71, 72); filaments slender with crenated margins and rounded distally, their surfaces covered with fine spicules (Fig. 73). Head with 2 + 2 frontal and 1 + 1 facial trichomes; surface of head with numerous irregularly arranged platelets and fine spines (Fig. 74). Thorax with 5 + 5 dorsal trichomes each with 2–4 branches, 1 + 1 unbranched or bifid lateral trichomes, and 1 + 1 latero-ventral unbranched trichomes (Fig. 75). Surface of thorax with platelets, densely distributed and in area of dorsal trichomes interspersed with spinules (Fig. 76); 1 + 1 groups of dense platelets and fine spines ventral to lateral trichomes on slight cuticular prominence. Onchotaxy of abdomen as illustrated in Figs 77 and 78: tergite 1 with 1 + 1 lateral hairlike setae; tergite 2 with 4 + 4 spine-like setae; tergite 3 with 4 + 4 simple hooks and 1 + 1 hair-like setae; tergite 4 with 4 + 4 simple hooks and 2 + 2 simple hair-like setae; tergite 5 with 4 + 4 simple or bifid hair-like setae; tergite 6 with 3 + 3 hair-like setae; tergite 7 with 2 + 2 simple hair-like setae; tergite 8 with 1 + 1 simple hair-like setae. Tergites 7–9 with anterior margins faintly pigmented and with spine combs; tergites 7 and 8 with 1 + 1 antero-lateral groups of spiny cuticular processes; apex of abdomen with 1 + 1 well-sclerotised pointed tubercles. Sternite 4 with 1 + 1 bifid hooks; sternite 5 with 2 + 2 adjacent bifid to quadrid hooks and 1 + 1 hair-like setae; sternite 6 with 2 + 2 well-spaced hooks, lateral simple and median bifid to quadrid, and 2 + 2 hair-like setae; sternite 7 with 2 + 2 well-spaced hooks, median bifid and lateral simple, and 1 + 1 simple hair-like setae. Sternites 4–7 with 1 + 1 antero-lateral groups of backwardly directed spiny cuticular processes; sternite 8 with band of these processes on anterior margin (Fig. 79).

Mature larva. Length 3.8–4.3 mm. Width of head capsule 0.38–0.45 mm. Body colour varying from yellow to brown with grey mottling. Ventral nerve cord grey. Body form as in Fig. 80.

Head yellow to light brown with faint positive pattern on cephalic apotome consisting of an antero-medial group of three spots, 1 + 1 antero-lateral group of two or three spots, and 1 + 1 postero-lateral head spots (Fig. 81). Head spots only visible in spirit material with anterior part of head tilted downwards. Scattered spines on head capsule, densest on cephalic apotome. Postgenal cleft large, broader than long with rounded anterior margin (Fig. 82); postgenal bridge short, one-third as long as hypostomium. Hypostomium (Fig. 83) with nine apical teeth: corner teeth large and blunt, median tooth less developed but slightly larger than subequal intermediate teeth: 6–7 lateral serrations with hindmost serration lying posterior to first hypostomial seta; 1 + 1 groups of 3–4 hypostomial setae lying parallel to lateral margins of hyposto-

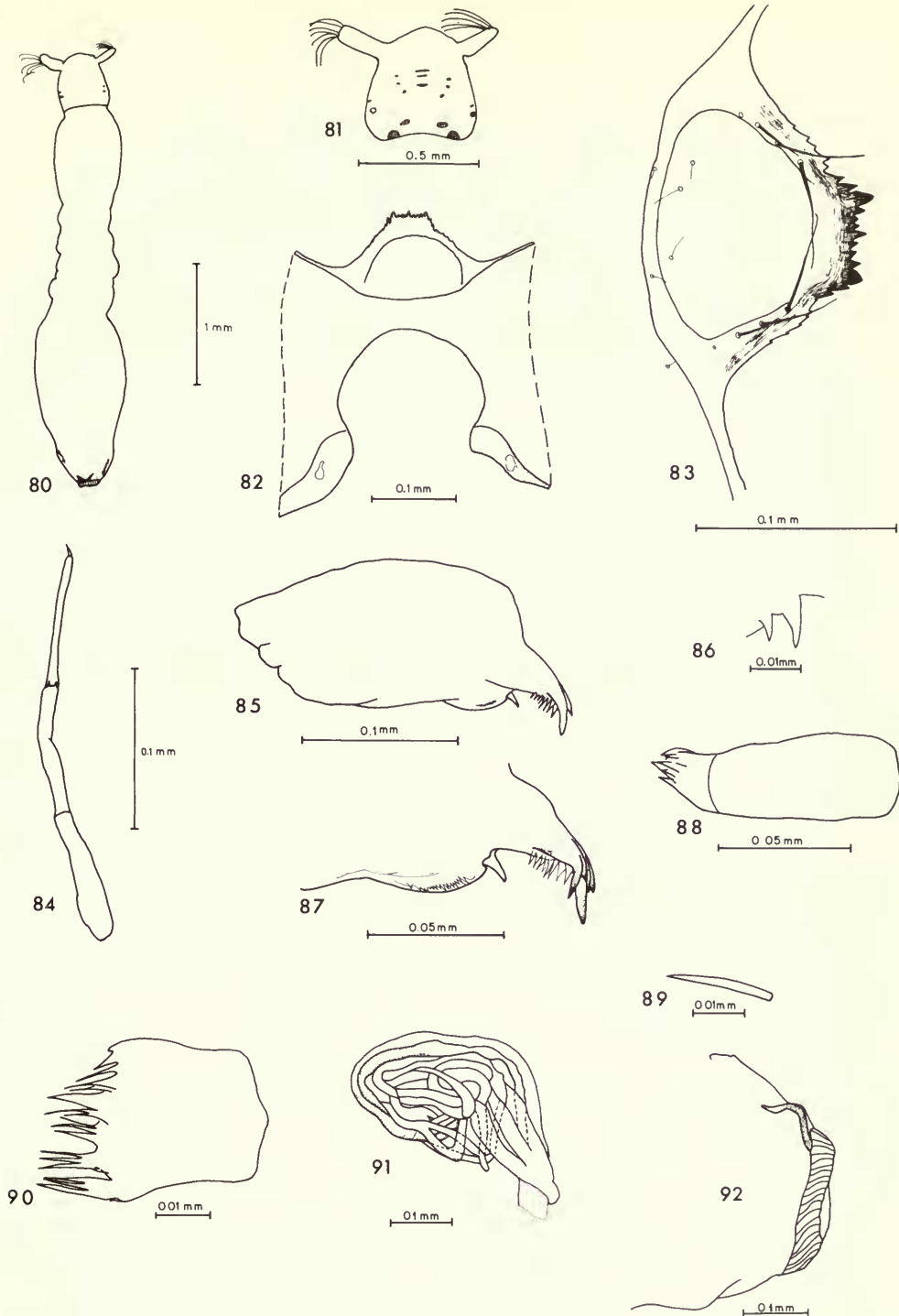


Figs 66–73 *S. amazonicum* pupa. 66, cocoon and pupa, dorsal view; 67, gill; 68–70, variations in branching pattern of gill; 71, 72, variations in branching pattern of gill of one specimen (LHS = left-hand side, RHS = right-hand side); 73, gill filament, detail of distal part.

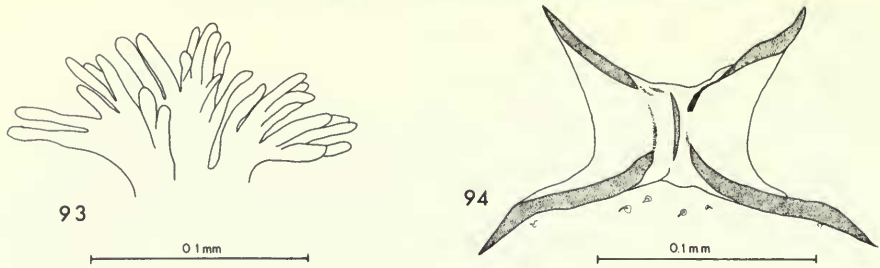


Figs 74-79 *S. amazonicum* pupa. 74, frontoclypeus; 75, thorax; 76, platelets and spinules of thorax; 77, abdomen, dorsal view; 78, abdomen, ventral view; 79, spiny cuticular processes of eighth sternite.

mium: distance between apex of corner tooth and first hypostomial seta slightly less than that between corner teeth. Antenna long (Fig. 84), unpigmented; first segment about five times as long as broad, segment length ratios about 5 : 4.8 : 5.5 (only one antenna examined). Mandible (Fig. 85) with one narrow elongate mandibular serration, sometimes with small serration posterior to this (Fig. 86); first three comb teeth equal in size; ventral margin of mandible posterior to mandibular serration with row of saw-like serrations (Fig. 87). Maxillary palp short, about three times as long as breadth at base (Fig. 88). Cephalic fan with 12-15 rays.



Figs 80–92 *S. amazonicum* larva. 80, larva, dorsal view; 81, head, dorsal view; 82, head, ventral view (flattened); 83, hypostomium; 84, antenna; 85, mandible; 86, mandibular serrations; 87, mandible, ventral margin showing saw-like serrations; 88, maxillary palp; 89, cuticular spine; 90, lateral sclerite of proleg; 91, pupal respiratory histoblast; 92, posterior end of abdomen, lateral view, showing ventral papillae.



Figs 93, 94 *S. amazonicum* larva. 93, anal gills; 94, anal sclerite.

Thorax yellow to light brown with scattered dark mottling of variable form dorsally and one or two central patches posterior to proleg ventrally. Cuticle of dorsal surface densely covered with fine spines (Fig. 89), lateral surface with scattered spines and ventral surface bare. Proleg circlet with about 22 rows of 1–6 hooks, lateral sclerite faintly pigmented with about eight processes (Fig. 90). Pupal respiratory histoblast (Fig. 91) with eight tightly coiled filaments divided into three primary branches near base.

Abdomen yellow to brown with grey annular mottling on four anterior segments and varying patterns on other segments. Cuticle with spines arranged as on thorax except scattered spines present ventrally also. Ventral papillae small (Fig. 92). Scattered short spines on anterior fold of anus, tri-lobed rectal gills with about eight secondary lobules on each lobe (Fig. 93). Anal sclerite (Fig. 94) with arms strongly sclerotised; posterior arm extending to between ninth and twelfth rows of posterior circlet hooks. Posterior circlet with about 54–56 rows of 2–12 hooks. 2 + 2 (sometimes 1 + 1) mid-dorsal and 1 + 1 lateral strongly developed setae between posterior arms of anal sclerite and posterior circlet.

MATERIAL EXAMINED

Syntypes ♀, **Brazil**: Amazonas, Bom Lugar, R. Purus, v.1904 (*Huber*) (25 ♀ in alcohol, pinned or as slide preparations, BMNH; 27 ♀, pinned, NM). [The International Commission on Zoological Nomenclature has been requested to set aside these syntypes under their plenary powers (Shelley, 1981).]

Brazil: 1 ♀, Amazonas, Valparaiso (near Lagoa Bom Lugar), R. Purus, approx. 8°42'S 67°22'W, approx. elevation 120 m, ex pupa, 22.xi.1977 (*Shelley*) (BMNH). [The International Commission on Zoological Nomenclature has been requested to designate this specimen as a neotype under their plenary powers (Shelley, 1981).]

Topotypes. 18 ♀, ex pupae (pinned and as slide preparations); 31 ♂, ex pupae (pinned and as slide preparations); 16 pupae (in alcohol); 10 larvae (slide preparations); data as for proposed neotype. Numerous ♀, collected from human bait and horse (pinned, in alcohol, slide preparations); data as for proposed neotype. (AMNH, BMNH, IOC, MLP, USNM.) Numerous ♀, collected from human bait (pinned, in alcohol); locality data as for proposed neotype, 29.xi.–3.xii.1976, 17–19.vi.1977 (*Arouck*) (BMNH, IOC). 1 ♂, Amazonas, Igarapé Escondido (Lagoa Bom Lugar), R. Purus, ex pupa, 17.xi.1977 (*Shelley*) (BMNH).

DISTRIBUTION. Because of the previously confused situation over the identity of *S. amazonicum* the confirmed distribution of this species is based only on material studied by the authors for the present work. The distribution of this species in relation to other species in the *S. amazonicum*-group that occur in Brazil is shown in Fig. 95. *S. amazonicum* was found at the following localities in addition to the type-locality on the Purus river system, the specimens having been deposited in the BMNH and IOC: several ♀, Boca de Acre, confluence of R. Acre and R. Purus, 8°45'S 67°24'W, 24.xi.1977 (*Shelley*); numerous ♀, Labrea, R. Purus, 7°14'S 64°50'W, 8.x.1973 (*Shelley*); numerous ♀, Capacini, near Labrea, R. Purus, 25.ix.1976 (*Shelley*); numerous ♀, Parana do Ituxi, confluence of R. Ituxi with R. Purus, near Labrea, 30.ix.1976 (*Shelley*).

Specimens tentatively determined as *S. amazonicum* have also been collected biting man at the following localities (slight scutal variations are apparent from the Bom Lugar form but their significance cannot be decided until immature stages and males have been examined).

Numerous ♀, Amazonas State, Feijoal, R. Solimões, 4°10'S 69°25'W, 5.x.1979 (*Shelley & Luna Dias*); numerous ♀, Tefé, R. Solimões, 3°22'S 64°43'W, 8.x.1978 (*Shelley & Luna Dias*); numerous ♀, Roraima Territory, Km 50, Northern Perimeter Road (BR 210), R. Ajarani, 1, 2°01'N 61°28'W, 16.i.1979 (*Shelley & Luna Dias*).



Fig. 95 The distribution of species of the *S. amazonicum*-group in Brazil. Inset: detail of Roraima Territory. (Based on reared specimens and type-material.)

BIOLOGY. Although various aspects of the biology of *S. amazonicum* have already been investigated by several workers in Brazil and neighbouring countries their value is dubious as it is probable that other species were involved. Studies on the biology of this species as well as other anthropophilic species in the *S. amazonicum*-group that are large-river breeders are hampered by the difficulties involved in sampling for immature stages. Breeding grounds, even in localities where adults attack man in enormous numbers, are difficult to find. Apart from the more obvious difficulties involved in sampling large rivers, such as water depth, current speed and the time and manpower needed to examine vast areas of substrate for larvae and pupae, account must be taken of the large fluctuation in river depth over a short period of time principally in the rainy season. Even large rivers in the Amazon basin may rise by as much as a metre over night as a result of rainfall often some considerable distance away.

Detailed investigations at Valparaiso, near Bom Lugar, the type-locality of *S. amazonicum*, were not possible and hence only brief comments are made mainly on larval and pupal habitat. However a study made some years ago at Capacini, also on the R. Purus, by one of the authors (A.J.S.) is cited, now that the correct identity of *S. amazonicum* has been established.

Studies at Valparaiso. The river Purus at Valparaiso is about 100 m wide, has a fast current and few suitable objects for mooring a boat to facilitate sampling. The banks of the river, with its many meanders, are either steep and devoid of vegetation, in the form of sandy spits, or marshy and covered with herbaceous vegetation and scattered bushes. Immature stages of *S. amazonicum* were found only on a small submerged wild guava bush near the river bank in strong current up to 1.5 m below the water surface. This was the only breeding ground found after four days of searching in the river Purus at a time of the year when swarms of *S. amazonicum* attack man at the river's edge throughout the day. Pupae were found mainly on small branchlets but sometimes attached to leaves, and were usually covered in sediment. No pupae or mature larvae of other *Simulium* species were found. Collections from several forest streams draining into the R. Purus or into Lagoa Bom Lugar produced large numbers of immature stages of *S. quadrifidum* but only one male *S. amazonicum* pupa. In a collection from human bait several thousand *S. amazonicum* females were identified as well as one female *Simulium* sp. (Madeira), which has been shown to be a vector of *M. ozzardi* on the R. Solimões (Shelley *et al.*, 1980). *S. amazonicum* was also collected feeding on a horse at Valparaiso.

Studies at Capacini. Aspects of the biology of *S. amazonicum* were studied at Capacini, a small rubber collecting community near Labrea on the R. Purus, in low lying (altitude 60 m) tropical rain forest. The observations were made during investigations into the vector of *M. ozzardi* at this locality (Shelley & Shelley, 1976) but not hitherto published because of uncertainty as to the identity of the species. Reexamination of voucher specimens (deposited in the BMNH and IOC) has confirmed that true *S. amazonicum* is the species involved.

Only *S. quadrifidum* was found in the two local streams, Igarapé Capacini and Igarapé Ca-Te-Espera, and no immature stages were found in the R. Purus. Studies were therefore confined to adult *S. amazonicum*, the only anthropophilic black-fly found in the area.

To discover the resting sites of *S. amazonicum* searches with a sweep net were made in potential resting sites alongside the river and at the forest's edge by the two streams. Host preference was determined by making a 12-hour catch using baits of man, cow, sheep, dog, monkey and chicken. These were positioned, 10 m apart, in bean fields at the edge of the river and three collectors captured all flies biting from 06.00 to 18.00 hrs; two further collectors captured flies biting a human and a bovine bait in the cattle pastures above the bean fields. To determine the biting pattern of *S. amazonicum* five collections were made from human volunteers clad in shorts and seated in the bean fields for three consecutive days. One collector was assigned to each bait and commenced capturing flies at 06.00 hrs (dawn) until midday; he was replaced by another collector who worked from midday to 18.30 hrs (dusk). Flies were collected directly into alcohol, a small number being set aside for taxonomic studies, the rest being dissected later for filariae. Daily records of temperature and relative humidity were kept.

No *S. amazonicum* were found on vegetation at the forest edge but 29 females were collected from long grass in the cattle pasture and 15 females from cracks in the soil in the bean fields. *S. amazonicum* showed a marked preference for human blood although the cow could be an important secondary host in the area (Table 1). During the three consecutive days of the biting catch

Table 1 Biting preferences of *S. amazonicum* at Capacini

Bait	Bean fields		Pasture	
	No. collected	% of total catch	No. collected	% of total catch
Man	794	90.7	1292	80.1
Cow	80	9.1	321	19.9
Sheep	1	0.1	0	—
Dog	0	—	0	—
Monkey	0	—	0	—
Chicken	0	—	0	—
Totals	875	99.9	1613	100.0

SIMULIUM AMAZONICUM GOELDI

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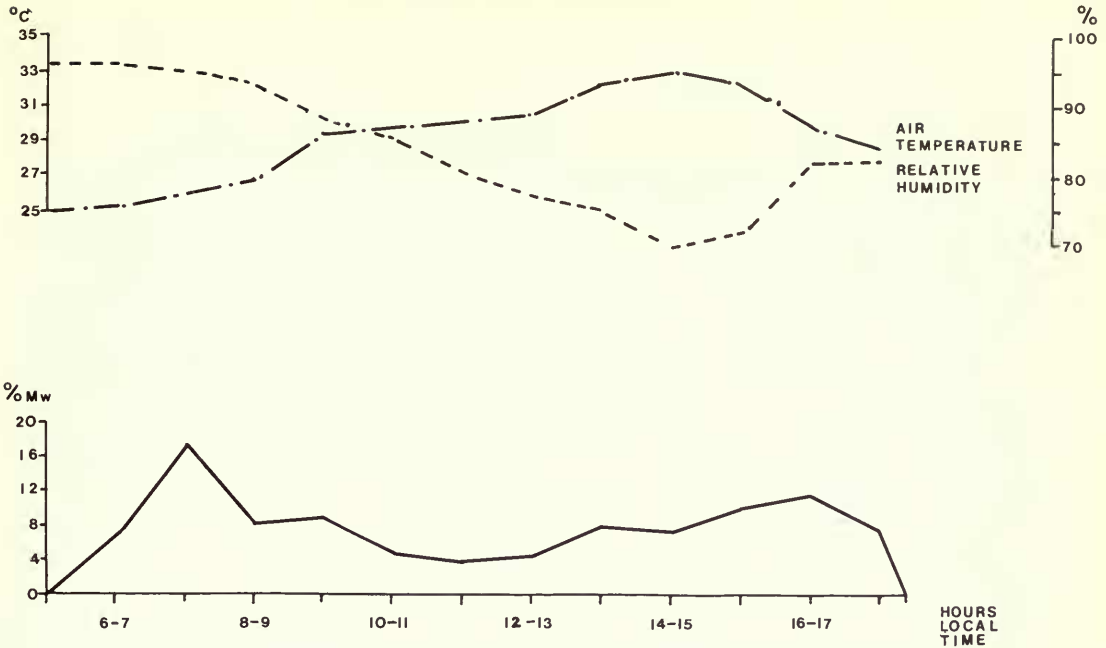


Fig. 96 The biting cycle of *S. amazonicum* at Capacini.

3 400 *S. amazonicum* were collected from the human baits. The biting pattern is shown in Fig. 96 where the geometric mean hourly catch (M_w , after Williams) expressed as a percentage of the total days' catch (% M_w) is plotted against time. Biting occurred between dawn and dusk with the main peaks at 07.00–08.00 and 15.00–18.00 hrs local time.

MEDICAL IMPORTANCE. Formerly *S. amazonicum* was considered to be a noxious man-biting species in several countries in South America and many published reports concerning this exist in the literature. It is impossible to establish which, if any, of these reports actually refer to *S. amazonicum* as specimens were not deposited in collections at the time. However, investigations have been made where this species has been cited as a vector of pathogens to man. Only two have been found, both involving human filariae. In Brazil Cerqueira (1959) named *S. amazonicum* as the vector of *M. ozzardi* at Codajas on the R. Solimões. No critical analysis of Cerqueira's data had been made until Shelley *et al.* (1980) challenged his conclusions on the data that he had presented, as well as on his identification of the vector. Specimens from Codajas identified by Cerqueira as *S. amazonicum* have now been determined (A.J.S.) as an undescribed species of the *S. amazonicum*-group referred to in this paper as *Simulium* sp. (Madeira) (p. 27). That this species is a vector of *M. ozzardi* in Brazil has now been confirmed by these authors (Shelley *et al.*, 1980) at Feijoal on the river Solimões. They also showed that *S. amazonicum*, a less common species at this locality, is also a vector of this filaria. This species is responsible for transmission of mansonelliasis along the river Purus as Shelley & Shelley (1976) found a female *S. amazonicum* naturally infected with *M. ozzardi* at Capacini, and more recently an infective larva of this filaria was recovered from an experimentally infected fly that had previously fed on a person with mansonelliasis at Valparaiso (A.J.S., unpublished data). The supposed incrimination of *S. amazonicum* as a vector of onchocerciasis at the R. Toototobi in Brazil by Rassi *et al.* (1975) is an error stemming from their misidentification of *S. minusculum* as *S. amazonicum*. A summary of the distribution, host preference and vector capacity of species in the *S. amazonicum*-group is given in Table 2.

Table 2 The distribution, host preference and vector capacity of species in the *S. amazonicum*-group (based on a report by the World Health Organization, 1979).

Species	Distribution	Host preference		Vector of	
		Man	Animal	<i>M. ozzardi</i>	<i>O. volvulus</i>
<i>S. amazonicum</i>	Brazil	+	+	+	—
	? Colombia	+	—	+	—
<i>S. chaquense</i>	Argentina	? +	—	—	—
<i>S. minusculum</i>	Brazil	+	—	—	+
	Colombia	+	—	+	—
	Guyana	+	—	—	—
	Venezuela	+	—	—	+
<i>S. quadrifidum</i>	Brazil	—	+	—	—
<i>S. sanguineum</i>	Colombia	+	—	+	—
<i>Simulium</i> sp. (Barbacoas)	Venezuela	?	?	—	—
<i>Simulium</i> sp. (Madeira)	Brazil	+	—	+	—
	Colombia	+	—	+	—

Taxonomic notes on other species in the *S. amazonicum*-group

Simulium chaquense Coscarón

Simulium chaquense Coscarón, 1971: 33. Holotype ♀, ARGENTINA: Chaco, Arroyo Zapirain, approx. 27°S 59°W, ex pupa (MLP) [examined]. [Coscarón (1971) gives the type-locality as Formosa Province. Arroyo Zapirain is a stream running through a small farm crossed by Route 11 on the border of Chaco and Formosa Provinces; the actual collection site is in Chaco Province (Coscarón, pers. comm.).]

This is a recently described species only known from one locality in northern Argentina. It has most of the characters of the *S. amazonicum*-group but is exceptional in having two distal spines on the male distimere whereas all other species in the group possess one. The extent to which *S. chaquense* feeds on man is uncertain but it does not appear to be of medical importance.

MATERIAL EXAMINED

Simulium chaquense Coscarón, holotype ♀ (ex pupa), ARGENTINA: Chaco, Arroyo Zapirain, 14.vii.1971 (Coscarón) (MLP).

ARGENTINA: 5 ♀, 2 ♂ (ex pupae), data as for holotype (2 ♀, 1 ♂ in BMNH; 3 ♀, 1 ♂ in MLP); 1 ♀ (ex pupa), Corrientes, Arroyo Santa María, 9.vii.1971 (Coscarón) (MLP) (all paratypes of *Simulium chaquense* Coscarón).

Simulium minusculum Lutz

Simulium minusculum Lutz, 1910: 253. Syntypes ♀, BRAZIL: Minas Gerais, Lassance, Rio das Velhas (IOC) [examined]. [Synonymised with *S. amazonicum* Goeldi by Lutz, 1917: 64; resurrected from synonymy by Cerqueira & Nunes de Mello, 1964: 102.]

Simulium minusculum: Malloch, 1912: 653. [Incorrect subsequent spelling.]

[*Simulium amazonicum* Goeldi sensu Lutz, 1917: 63 and subsequent authors except Smart, 1942: 46 and Cerqueira & Nunes de Mello, 1964: 102 (♀ only). Misidentifications.]

? *Simulium roraimense* Nunes de Mello, 1974: 45. Holotype ♂, BRAZIL: Roraima, Cachoeira, R. Cauamé, ex pupa (INPA) [not examined, unlocated in type-depository].

S. minusculum is the common Brazilian species of lowland tropical forest that has been most often confused with *S. amazonicum*. The three most significant contributors to the morphology and medical importance of *S. minusculum* (as *S. amazonicum*) have been Lutz, Porto and Rassi. Each is dealt with separately.

LUTZ. The major Brazilian contribution to the morphology of the species that we regard as *S. minusculum* in this paper was made by Lutz who believed that he was dealing with *S. amazonicum*. Because of the rather involved nature of Lutz's taxonomic studies on *S. minusculum* and allied species, a summary of his work covered by his 1909, 1910 and 1917 papers is given followed by our interpretation of his findings.

His first reference (Lutz, 1909) to *S. amazonicum* simply quoted Goeldi's original description (1905) and described a new species, *S. exiguum* (Lutz, not Rouband) from females collected at the R. Grande, near Franca in São Paulo state. This was followed in 1910 by a description of a new species, *S. minusculum*, from females sent in alcohol by Chagas from Lassance, Minas Gerais. In the same paper he compared these with specimens, also sent in alcohol, from the Madeira-Mamoré region in Rondônia and judged them to be conspecific, but at the same time noting differences in the pruinose pattern of the female scutum due, possibly, to different storage times in alcohol of the material from these two localities. He also noted that, apart from leg coloration, *S. minusculum* closely resembles *S. amazonicum*, and suggested their possible synonymy. Pupae with four gill filaments, collected from a stream near the Madeira-Mamoré railroad and assumed to be *S. minusculum*, were described. Having examined more specimens of '*S. amazonicum*' from localities in the Territory of Rondônia, states of Bahia and Minas Gerais, as well as the river Tocantins (state not indicated), Lutz (1917) observed that the angle of incident light affects the form of the pruinose scutal pattern and that this pattern is altered by alcohol preservation and hence is only clear in fresh or dried material. He also noted that darkening of tissues, particularly in the legs, occurs following a blood meal. He therefore attributed the differences previously noted between *S. minusculum* and *S. amazonicum* to these causes, sank the former species as a synonym of *S. amazonicum* and suggested the possible synonymy of *S. exiguum* (Lutz, not Roubaud) with this species. Furthermore, he sank *S. nitidum* Malloch, from Huancabamba, Peru, as a synonym of *S. amazonicum* after examining specimens but not the 'type' from this locality. As his previous description of '*S. amazonicum*' in 1910 was based on spirit material, Lutz (1917) redescribed both the female and pupa of '*S. amazonicum*' from fresh material obtained by mass rearing six-filamented pupae collected at Sant'Anna de Sobradinho on the R. São Francisco above Joazeiro, Bahia. The four-filamented pupa collected at Madeira-Mamoré and previously attributed (Lutz, 1910) to *S. amazonicum* was given the name *S. quadrifidum*.

The synonymy (Lutz, 1917) of *S. minusculum* with *S. amazonicum* cannot be upheld. Apart from coloration Lutz's main criterion for erecting *S. minusculum* in 1910 was its small size (body length 1.00–1.25 mm). Thirteen of Lutz's original series of pinned syntypes from Lassance, Minas Gerais (nos. 12552–12555, 12558) have been examined and the body length (eight specimens measured) found to range from 1.4–2.1 mm; the scutal pattern, only discernible in the better preserved specimens, is distinct from that of *S. amazonicum* but similar to that of the *S. sanguineum* holotype, with which the specimens were compared. Three of Lutz's slides were also examined: no. 12001 with two six-filamented pupae from Madeira-Mamoré, labelled as *S. amazonicum* but not referred to in any of his papers, no. 12005 with a male and pupal pelt, and no. 12007 with eight six-filamented pupae from Sant'Anna do Sobradinho labelled as *S. amazonense* (error for *S. amazonicum* used by Lutz, 1917), which in 1917 he considered conspecific with the *S. minusculum* specimens from Lassance. In their redescription of *S. amazonicum* Cerqueira & Nunes de Mello (1964) referred to Lutz's material and revalidated *S. minusculum* for the specimens reared from six-filamented pupae collected at Sant'Anna do Sobradinho as well as the females from the type-locality at Lassance, but considered the females collected at Madeira-Mamoré as *S. amazonicum*. Until reared material is available from Lassance it is convenient to accept Cerqueira & Nunes de Mello's revalidation of *S. minusculum* for Lutz's material collected from the first two localities as well as the females and six-filamented pupae in the Lutz collection from Madeira-Mamoré. Cerqueira & Nunes de Mello regarded material from the last locality as *S. amazonicum* but they had confused three species of the *S. amazonicum*-group in their 1964 redescription. Our collections of six-filamented pupae from the R. Jacu Parana in the Madeira-Mamoré region gave rise to females indistinguishable from Lutz's *S. minusculum* from Lassance. As *S. sanguineum* s.str., which at present is only distinguishable from *S. minusculum* by

its eight-filamented pupa, has not been recorded in Brazil, females from Brazil without associated pupal pelts that key out to *S. sanguineum* or *S. minusculum* are provisionally regarded as *S. minusculum*. *S. chaquense* and *S. roraimense*, also inseparable from *S. minusculum* in the female, are also excluded due to the restricted distribution and the uncertainty surrounding the validity of the species respectively. The main vector of *O. volvulus* at Toototobi, tentatively determined as *S. sanguineum* (Shelley *et al.*, 1979) and subsequently, when the pupa of *S. sanguineum* became known, as *S. sanguineum* s.l. (Shelley *et al.*, 1980) until it could be assigned to a species, now falls provisionally under *S. minusculum*.

PORTO. Porto (1939) accepted Lutz's synonymy (1917) of *S. minusculum* with *S. amazonicum* as he believed the morphological variations described by Lutz in his material not to be interspecific. Although Porto (1939) did not see type-material of *S. amazonicum* he redescribed this species from females collected in the states of Mato Grosso and Bahia, which are now in the Public Health Faculty of São Paulo University (see Forattini *et al.*, 1971). Vulcano examined them as well as additional specimens from other states in 1943, and concluded that all were two infra-specific taxa of *S. amazonicum* which she labelled with (unpublished) manuscript varietal names. The senior author examined this material and recognized three species among the pinned specimens, none of which is *S. amazonicum*: specimen nos. 4345–4348 and 4350–4352 from Rio das Mortes, Mato Grosso as well as no. 1157 from Rio de Cobre, Salvador, Bahia were provisionally determined as *S. minusculum*; specimen nos. 4330–4340 from Rio das Mortes, Mato Grosso are of an undetermined species. The additional material determined as *S. amazonicum* by Vulcano and also included in the Forattini *et al.* catalogue (1971) are as follows: specimen nos. 4554–4555 from Acre state are now provisionally determined as *S. minusculum*; specimen nos. 4309–4312 from Porto Cabral, São Paulo, 4313–4316 from Rio Claro, São Paulo, 4321–4323 from Dourados, Mato Grosso and 4324–4326 from Juquia, São Paulo and Itatiaia and Teresopolis, Rio de Janeiro are now determined as *S. incrustatum*.

RASSI. Rassi's two publications, resulting from a visit in 1974 to the Brazilian onchocerciasis foci, are important as they refer to *S. amazonicum* as a vector of *O. volvulus* in Brazil. The flimsy evidence provided by Rassi *et al.* (1975) for this incrimination has been discussed elsewhere (Shelley *et al.*, 1979). In his earlier paper Rassi (1974) refers to *S. amazonicum* as a vector but acknowledges the difficulties involved in the identification of this species, which he considers to be a complex. He recognizes two species of this 'complex', which he separates on female size, to be widespread in the Brazilian Amazon, including the onchocerciasis foci. The commoner and smaller species he refers to as *S. amazonicum* Goeldi Lutz (1910, 1917), which he maintains corresponds to *S. minusculum* and *S. quadrifidum* as described by Lutz, and the larger as *S. amazonicum* Goeldi as described by its original author. A redescription of the smaller species is given and it is this species that Rassi (1974) and Rassi *et al.* (1975) believe to be the vector of *O. volvulus* in Brazil. In this redescription based on material collected at Toototobi, females were found to have a body length of 1.0–1.5 mm compared to Goeldi's reference to 2.06 mm body length for *S. amazonicum*. Pupae with four gill filaments, assumed to be of the smaller species, were found by Rassi (1974) in the Toototobi river. He also assumes that the larger species, of which no body length measurements or description are given, has a six-filamented pupa, presumably based on Lutz's description (1917) of '*S. amazonicum*'.

We made collections of man-biting black-flies as well as larvae and pupae from the river Toototobi and surrounding forest streams on eight occasions over three years in both wet and dry seasons, but were unable to find the two species of the '*S. amazonicum* complex' detailed by Rassi (1974). Only one anthropophilic species of the *S. amazonicum*-group, now provisionally assigned to *S. minusculum* until the status of *S. roraimense* is confirmed, was found by us at this locality where it was shown to be a vector of onchocerciasis (Shelley *et al.*, 1979). This was the most common black-fly in the area and showed considerable variation in female body length in February 1976: 1.2–2.0 mm for dried females (101 specimens measured) and 1.7–2.7 mm for females preserved in alcohol (210 specimens measured) with a normal distribution for body length. A zoophilic species, *S. quadrifidum*, was reared from four-filamented pupae collected in the

river Toototobi. It is apparent that Rassi (1974) misidentified both *S. minusculum* and *S. quadrifidum* as *S. amazonicum*. The vector of *O. volvulus* in the Upper Orinoco region of Venezuela, adjacent to the Toototobi in Brazil, indicated as *S. amazonicum* by Rassi *et al.* (1977) has probably been similarly misidentified.

Variations in the scutal pattern of female *S. minusculum* collected by us from different localities in Amazonia as well as in Lutz's syntype-series from Minas Gerais have been noted. Due to the paucity of reared material from these localities and the total lack of such material from the type-locality, it cannot at this stage be decided whether *S. minusculum* is a polymorphic species or whether more than one species is being assigned to this name. A further complication is seen in the case of *S. roraimense*. Although we have examined reared topotypes the only means of separating this species from *S. minusculum* is by the form of the male scutal pattern. The validity of the presence or absence of merging of the three scutal vittae as an interspecific character for separating these two species is not known. As this is the only apparent difference and since *S. sanguineum* males show variation in the extent of merging of these vittae (Tidwell *et al.*, 1981), *S. roraimense* is tentatively treated as a synonym of *S. minusculum* in this paper. This may be confirmed only when reared *S. minusculum* topotypes are available and more reared material has been collected to examine the degree of variation in this character.

MATERIAL EXAMINED

Simulium minusculum Lutz, 16 ♀ syntypes, **Brazil**: Minas Gerais, Lassance, Rio das Velhas. 17°53'S 44°34'W 3.iv.1910 (*Chagas*) (IOC, nos. 12552, 12554 & 12558) [labelled by Lutz as *S. minusculum*].

Brazil: 2 ♀, 1 ♂, 1 ♂ (ex pupa), 8 pupae, Bahia, Sant'Anna do Sobradinho, R. São Francisco, 9°23'S 40°50'W, 25.vi.1912 (*Lutz*) (IOC, nos. 12005, 12007, 12461, 12462) [labelled by Lutz as *S. amazonicum*, *S. amazonense* or *S. minusculum (amazonicum)*]; 2 pupae, Rondônia, Madeira-Mamoré region, R. Madeira. 1910 (*Cruz*) (IOC, no. 12001) [labelled by Lutz as *S. amazonicum*]; 5 ♀, 5 ♂ (ex pupae), Madeira-Mamoré region, Jacy Parana, R. Jacy Parana, 9°15'S 64°24'W, 16.x.1978 (*Shelley & Luna Dias*) (BMNH & IOC); 34 ♀, 34 ♂ (ex pupae), Roraima, Cachoeira Bem Querer, R. Branco, 1°58'N 61°00'W, 16.i.1979 (*Shelley & Luna Dias*) (BMNH & IOC); 4 ♂ (ex pupae), Northern Perimeter Road (BR 210), R. Ajarani 1, 2°01'N 61°28'W, 16.i.1979 (*Shelley & Luna Dias*) (BMNH & IOC); 1 ♀ (ex pupa), 8 ♀, 8 ♂ (ex pupae), Boa Vista-Venezuela road, R. Uraricoera, 3°03'N 60°30'W, 20.i.1979 (*Shelley & Luna Dias*) (BMNH, IOC); 1 ♀ (ex pupa), near Boa Vista, R. Cauamé, 2°52'N 60°38'W, 16.viii.1977. (*Shelley*) (BMNH); 4 ♀, 5 ♂ (ex pupae), Amazonas, R. Ituxi, 7°18'S 64°52'W, 30.ix.1978 (*Shelley*) (BMNH, IOC). **Guyana**: 2 ♀, 2 ♂ (ex pupae), Bonfim, R. Takutu. 3°21'N 59°50'W, 13.i.1975 (*Davies*) (BMNH). **Venezuela**: 2 ♀, 3 ♂ (ex pupae), Bolivar, R. Cuyuni, between Guyana & Anacoco [no collection date] (*Ramirez Pérez*) (BMNH).

The following material provisionally placed as *S. minusculum* corresponds to the description of *S. roraimense* given by Nunes de Mello (1974).

Brazil: 27 ♀, 15 ♂ (ex pupae), Roraima, Cachoeira, R. Cauamé [type-locality of *S. roraimense*], 2°52'N 60°39'W, 19.i.1979 (*Shelley & Luna Dias*) (BMNH, IOC); 13 ♀, 18 ♂ (ex pupae), Catrimani Mission Post, R. Catrimani, 1°44'N 62°17'W, 9.i.1977 & 13.i.1979 (*Shelley*) (BMNH, IOC); 1 ♀, 1 ♂ (ex pupae), Amazonas, Toototobi Mission Post, R. Toototobi, 1°47'N 63°37'W, 2.xii.1976 (*Shelley*) (BMNH).

Simulium quadrifidum Lutz sp. rev.

Simulium quadrifidum Lutz, 1917: 66. Syntypes ♂ and pupae, **BRAZIL**: Rondônia, Madeira-Mamore region (IOC) [examined]. [Here resurrected from synonymy with *S. amazonicum* Goeldi (Cerqueira & Nunes de Mello, 1964).]

This name was proposed by Lutz (1917) for the four-filamented pupae from the Madeira-Mamoré region of Rondônia Territory that he had previously assigned to *S. amazonicum* in 1910. The species is listed in all the earlier catalogues of the region's Simuliidae (Pinto, 1932; Smart, 1945; Vargas, 1945) but is sunk as a synonym of *S. amazonicum* by Cerqueira & Nunes de Mello (1964). Vulcano (1967) omits this synonym in her catalogue. We have reared adults from four-filamented pupae collected from streams in the Madeira-Mamoré region, as well as some of the localities sampled by Cerqueira & Nunes de Mello for their 1964 paper, and

compared them with Lutz's material; no differences were apparent and we consider our specimens to be true *S. quadrifidum*. The slide preparation of a male (no. 12310) and four pupae (nos. 12307–12309) of *S. quadrifidum* made by Lutz have syntypic status.

The synonymy of *S. quadrifidum* with *S. amazonicum* and the resurrection of *S. minusculum* contained in Cerqueira & Nunes de Mello's paper (1964) have already been discussed and it therefore only remains to decide on which species these authors were basing their redescription of '*S. amazonicum*'. In our own collections from the three streams at Tefé indicated in the 1964 paper only four-filamented pupae were found and these were reared to adults. Both pupae and adults were readily distinguishable from *S. amazonicum* topotypes. Pupae were also indistinguishable from those described by Cerqueira & Nunes de Mello (1964) and determined by them as *S. amazonicum*, and were conspecific with *S. quadrifidum* syntypes. Our collections from many other Amazonian localities showed *S. amazonicum* to breed almost exclusively in large rivers whereas *S. quadrifidum* is found principally in small shaded forest streams, as are those at Tefé. It is therefore probable that the larvae and males described and figured by Cerqueira & Nunes de Mello (1964) as *S. amazonicum* are also in fact *S. quadrifidum* that have been misidentified. It is also not known whether their description and figures of the female of *S. amazonicum* are based on correctly identified specimens since we have found both *S. amazonicum*-like and *Simulium* sp. (Madeira) females biting man at Tefé. As previously mentioned by Shelley *et al.* (1980) specimens of the latter species misidentified as *S. amazonicum* by Cerqueira are deposited in both the BMNH and INPA collections.

MATERIAL EXAMINED

Simulium quadrifidum Lutz, 1 ♂, 4 pupae syntypes, **Brazil**: Rondônia, Madeira-Mamoré region, 1910 (Cruz) (IOC).

Brazil: 10 ♀, 10 ♂ (ex pupae), Rondônia, Madeira-Mamoré region, Igarapé Caracol, 9°13'S 64°20'W, 16.x.1978 (Shelley & Luna Dias) (BMNH & IOC); 6 ♀, 1 ♂ (ex pupae), Madeira-Mamoré region, Jacy Parana, R. Jacy Parana, 9°15'S 64°24'W, 16.x.1978 (Shelley & Luna Dias) (BMNH, IOC); 1 ♂ (ex pupa), Roraima, Km 104, Northern Perimeter Road (BR 210), R. Ajarani 2, 1°56'N 61°58'W, 16.i.1979 (Shelley & Luna Dias) (BMNH); 2 ♀, 1 ♂ (ex pupae), stream at Km 96, Northern Perimeter Road (BR 210), 1°57'N 61°53'W, 16.i.1979 (Shelley & Luna Dias) (BMNH, IOC); 4 ♀ (ex pupae), stream at Km 211, Northern Perimeter Road (BR 210), 1°20'N 63°10'W, 12.i.1979 (Shelley & Luna Dias) (BMNH, IOC); 4 ♀, 3 ♂ (ex pupae), stream near Cachoeira Bem Querer, R. Branco, 1°58'N 61°00'W, 29.iv.1979 (Crosskey & Shelley) (BMNH); 11 ♀, 7 ♂ (ex pupae), Amazonas, Toototobi Mission Post, R. Toototobi, 1°47'N 63°37'W, 26.ii.1976, 11.iii.1976, 3.xii.1977 (Shelley) & 14.viii.1976 (Pinger) (BMNH, IOC); 10 ♀, 8 ♂ (ex pupae), Igarapé Tarumazinho (near Manaus), 2°58'S 60°04'W, 28.x.1976 (Pinger) & 2.v.1979 (Crosskey & Shelley) (BMNH, IOC); 2 ♀, 1 ♂ (ex pupae), Feijoa, Igarapé São Jorge (R. Solimões), 4°10'S 69°25'W, 3.x.1978 (Shelley & Luna Dias) (BMNH, IOC); 29 ♀, 26 ♂ (ex pupae), Tefé, R. Bauana, 3°29'S 64°58'W, 10.x.1978 (Shelley & Luna Dias) (BMNH, IOC); 11 ♀, 7 ♂ (ex pupae), Tefé, Igarapé Repartimento, 3°22'S 64°43'W, 22.vii.1976 (Shelley) (BMNH, IOC); 22 ♀, 13 ♂ (ex pupae), Bom Lugar, R. Purus, Igarapé Escondido, 8°42'S 67°22'W, 17.xi.1977 (Shelley) (BMNH, IOC); 1 ♀ (ex pupa), R. Ituxi, 7°18'S 64°52'W, 30.ix.1976 (Shelley) (BMNH); 39 ♀, 13 ♂ (ex pupae), Capacini, R. Purus, 7°18'S 64°58'W, 25.ix.1976 (Shelley) (BMNH, IOC).

Simulium sanguineum Knab

Simulium sanguineum Knab, 1915: 279. Holotype ♀, **COLOMBIA**: Chocó, Boca de Arquia, R. Atrato (BMNH) [examined].

This species is only known from northern Colombia where it attacks man. Little is known of its distribution due to the previous confusion with *S. amazonicum*. It is not thought to occur in the tropical forests of southern Colombia where *S. minusculum* is present.

MATERIAL EXAMINED

Simulium sanguineum Knab, holotype ♀, **Colombia**: Chocó, Boca de Arquia, R. Atrato, 6°14'N 76°44'W, v.1914 (Balfour) (BMNH).

Colombia: 1 ♀, data as for holotype (USNM) (paratype of *Simulium sanguineum* Knab); 9 ♀, 1 ♀ (ex pupa), 7 ♂, 3 pupae, R. Tagachi, near R. Atrato, 12.ix.1978 (Tidwell) (BMNH).

Simulium sp. (Barbacoas)

Reared specimens from Barbacoas, Venezuela in the BMNH collection could not be assigned to any named species in the *S. amazonicum*-group. Although in poor condition females resemble *S. amazonicum* while males are nearer *S. sanguineum* or *S. roraimense*. The pupal gill with its six filaments in combination with the adult characters separates this material from the other species of the group. Further collection of material is required before the status of this species can be clarified.

MATERIAL EXAMINED

Venezuela: 3 ♀, 5 ♂ (ex pupae), Guárico, Barbacoas, 9°31'N 66°57'W [no collection date] (*Ramírez Pérez*) (BMNH).

Simulium sp. (Madeira)

This species, as yet undescribed, is found along the river Madeira and river Solimões in Brazil. Cerqueira & Nunes de Mello (1964) were probably dealing with a mixture of this species and *S. amazonicum* in their redescription of female *S. amazonicum*. *Simulium* sp. (Madeira) has been shown to be a vector of *M. ozzardi* in Brazil (*Shelley et al.*, 1980, as *Simulium* n. sp.).

MATERIAL EXAMINED

Brazil: 6 ♀, 6 ♂ (ex pupae), Rondônia, Cachoeira Teotônio, R. Madeira, 8°50'S 64°05'W, 10.x.1978 (*Shelley & Luna Dias*) (BMNH, IOC); 1 ♀, Amazonas, Codajás, R. Solimões, 3°55'S 62°00'W, 21.vii.1958 (*Antonio*) (BMNH) [identified by Cerqueira as *S. amazonicum*].

Other species previously confused with *S. amazonicum**Simulium lutzi* Knab

Simulium exiguum Lutz, 1909: 141. Syntypes ♀, BRAZIL: São Paulo, Franca, R. Grande (IOC) [examined]. [Junior primary homonym of *Simulium exiguum* Roubaud, 1906.] [First recovered from synonymy with *S. amazonicum* Goeldi and correctly cited as *S. lutzi* Knab by Pinto, 1932: 705; recovery here confirmed after examination of syntypes.]

Simulium exigum: Lutz, 1910: 234. [Incorrect subsequent spelling.]

Simulium minutum Surcouf & Gonzalez-Rincones, 1911: 290. [Replacement name for *Simulium exiguum* Lutz, 1909.] [Junior primary homonym of *Simulium minutum* Lugger, [1897].]

Simulium lutzi Knab, 1913: 155. [Replacement name for *Simulium minutum* Surcouf & Gonzalez-Rincones, 1911.]

Simulium luzti: Pinto, 1932: 705. [Incorrect subsequent spelling.]

In 1917 Lutz suggested the possible synonymy of *S. exiguum* Lutz with *S. amazonicum*, apparently being unaware of either Roubaud's species of this name or of Knab's new name. This synonymy was followed in the catalogues of Smart (1945), Vargas (1945) and Vulcano (1967), but Pinto (1932) preferred to maintain *S. lutzi* as a valid name in his catalogue of Central and South American Simuliidae.

Two pinned females in Lutz's collection (no. 12519) from R. Grande on the Minas Gerais/São Paulo state border were badly greased and consequently no scutal pattern was discernible. These have now been cleaned in 'Cellosolve'—both are in poor condition, but in one specimen the thorax appears black with silver pruinose lateral and posterior borders and fits the description of *S. lutzi* given by Lutz (as *S. exiguum*) in his 1910 paper. However, four other specimens (no. 12459) from the same locality are now placed as *S. minusculum*. Apparently Lutz assumed that all specimens from the R. Grande were conspecific even though the scutal patterns of some were obscured due to greasing. Three further females mounted on slide no. 12520 and labelled as *S. exiguum* Lutz have cerci distinct from those of *S. exiguum* Roubaud, but are similar in form to species in the *S. amazonicum*-group to which they possibly belong. We are therefore unable to support Lutz's synonymy of *S. lutzi* (as *S. exiguum* Lutz) with *S. amazonicum* and maintain *S. lutzi* for the two specimens numbered 12519.

Knab's description of *S. lutzii* (1913), based on material sent by Urich from Trinidad, does not agree with either of Lutz's descriptions (1909; 1910 as *S. exiguum* Lutz) nor with the syntype (no. 12519) mentioned above, but suggests that he may have been dealing with *S. incrustatum* or a closely related species because of his reference to two large triangular iridescent white spots on the anterior scutal margin. The single specimen in the BMNH which is one of the series sent to Knab has been examined and placed as *S. incrustatum*.

MATERIAL EXAMINED

Simulium exiguum Lutz, 2 ♀ syntypes, **Brazil**: São Paulo, near Franca, R. Grande, 23.ix.1903, (Lutz) (IOC).

Simulium metallicum Bellardi

Simulium metallicum Bellardi, 1859: 14; 1861: 214. Type(s) ♂, **MEXICO**: locality unspecified (MNHN) [not examined, presumed lost].

Simulium nitidum Malloch, 1912: 652. Holotype ♀, **PERU**: Huancabamba (USNM) [examined]. [Synonymised with *S. amazonicum* Goeldi by Lutz, 1917: 64.]. **Syn. n.**

As previously mentioned Lutz based his synonymy of *S. nitidum* with *S. amazonicum* on examination of material from Huancabamba but did not consult the holotype of *S. nitidum*. This has now been done and the species is undoubtedly a synonym of *S. metallicum*.

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