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A detailed description of *Simulium (Meilloniellum) adersi* (Pomeroy) from Mayotte, Comoro islands, with comments on bionomics and biogeography (Diptera: Simuliidae)

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Abstract

All stages of *Simulium (Meilloniellum) adersi* (Pomeroy) from Mayotte, Comoro archipelago are described in detail. This species is widespread on the African mainland and in Madagascar; morphological divergences from African material point towards the Mayotte entity being a separate, but closely related species. Biology of the species overall is reviewed and brief comments are made regarding habitats and biogeography of the Mayotte material.

Key words: Comoro archipelago, Mayotte, Simuliidae, *Simulium*, *Meilloniellum*, *adersi*, black flies

Introduction

Located in the northern Mozambique Channel, 300 km off the north-western tip of Madagascar, the Comoros are a linear array of islands (Fig. 1). Politically, Grand Comore, Mohéli and Anjouan islands form the Union of the Comoro, with Mayotte an independent protectorate of France.

Of relative recent geological age, flora and fauna of the archipelago is generally considered to have resulted from dispersal out of the African mainland and Madagascar (e.g., Vences *et al.* 2003, Johanson and Mary 2009, and others).

Simuliidae are known for the archipelago and Crosskey (2012) published detailed notes with emphasis on Anjouan. Simuliids do not occur on Grande Comore—there is no permanent running water. Anjouan was well collected by Prof. Dr. Ferdinand Starmühlner (Zoologisches Institute der Universität Wien) (1976, 1979) during an Austrian expedition in 1974. That material, now in the Natural History Museum, London, comprises, *Simulium adersi*, *S. ruficorne*, *S. dentulosum* group sp. (sp. new) and an unidentifiable species of the *S. ruficorne* group. Crosskey (*loc. cit.*) noted that the Madagascan subgenus *Xenosimulium* was not collected by Starmühlner. This is of interest since Grenier and Grjebine (1959) found larvae on Mohéli that might have been of *S. (X.) imerinae*. The record by Crosskey and Howard (1997) for *S. imerinae* on Mayotte is in error and refers to Mohéli.

The taxonomic history of *S. adersi* is not particularly complex, but there are considerable disagreements in descriptions between the various accounts—themselves widespread and often disparate in the literature. For that reason, where relevant, we give page and figure numbers for the citations. That disparity between descriptions is a major reason for this complete description of all stages of the Mayotte *S. adersi*.

Freeman and de Meillon (1953) provided a detailed synonymy for *S. adersi* up until 1950. There was an earlier one by Bequaert (1939). We, therefore, comment only on some main items. *Simulium adersi* was originally described by Pomeroy (1922) as a variety of *Simulium hirsutum*, differing mainly in the branching of pupal filaments (his fig. 6). Otherwise, given material available at the time, the two entities were essentially identical. Edwards, though, (in de Meillon 1930) commented that the pupa of *S. hirsutum* var. *adersi* was sufficiently different from *S. hirsutum* that it probably represented a distinct species. Gibbins (1934) had material of sufficient quality that he formally raised *S. adersi* to species status. That work is noteworthy for the fine description and illustrations. An oddity is that Gibbins and Loewenthal (1933), in a paper that was published essentially

simultaneously with that of Gibbins (1934), refer to *S. adersi* at species rank—it appears that this latter paper was expected to be published first. Gibbins (1936) in an extensive work on Uganda simuliids, provided further description and illustration of both *S. hirsutum* and *S. adersi*—in particular the pupal gill and adult male genitalia of *S. adersi*.

Freeman and de Meillon (1953) in an in-depth overview of simuliids from the Ethiopian region, re-described *S. adersi* and provided the detailed synonymy as noted above. *Simulium adersi* was grouped along with seven other species in a Group IV (Group of *S. hirsutum* Pomeroy). The study was well illustrated and of comment is that the cocoon of *S. adersi* was rendered similarly to that shown here (Fig. 21, 22), not as that by Gibbins (1934; his fig. 8). No mention was made regarding the state of setae on the larval head. Gibbins (*loc. cit.*; his fig. 5a) had illustrated the head with distinct setae.

Crosskey (1960) used the species groupings of Freeman and de Meillon (1953) and provided keys, as well as illustrations of some structures of *S. adersi*. Philippon (1981), following Crosskey (*loc. cit.*), provided a key to larvae and used hypostomal teeth and antennal characters to separate *S. adersi* and *S. hirsutum*. Rubtsov (1962: 1496) placed species of the *hirsutum*-group erected by Freeman and de Meillon (1953) along with others into a new genus *Meilloniellum*—with the type species *Simulium hirsutum* Pomeroy.

Crosskey (1969: 74) in his seminal work on African simuliids, reduced *Meilloniellum* to subgeneric status and provided a detailed diagnosis for that segregate. He restricted the subgenus to *S. (M.) adersi* (Pomeroy), *S. (M.) hirsutum* Pomeroy, *S. (M.) sexiense* de Meillon and *S. (M.) urundiense* Fain. Of note was that *S. (M.) adersi* was the only member of the subgenus to possess a haired pleural membrane (*e.g.*, Fig. 12). Crosskey and Büttiker (1982) added *S. (M.) yemenense*. They discussed placement of species within the subgenus and noted that *S. yemenense* was closely related to *S. hirsutum*.

Fain (1950) described *S. adersi* var. *urundiensis*, based on pupae from a single locality in Rwanda. Wanson (1950) also referred to this as a variety of *S. adersi*. Freeman and de Meillon (1953: 113) raised the variety to species level. No mention was made by Crosskey (1960), but he does so in 1969. Further details of the species were given by Elsen and Fain (1981).

Ecologically larvae of *S. adersi* tolerate a wide range of running water habitats. Crosskey (1960: 25) after close examination of the larval material from the shore of Nsazdi Island, Lake Victoria (Gibbins 1934), alluded to the possibility that the tolerance might indicated the species was a complex. Palmer and de Moor (1998) gave considerable ecological details of larval habitats of *S. adersi* and on the basis of that wide range of habitats, also suggested *S. adersi* was likely a complex of species.

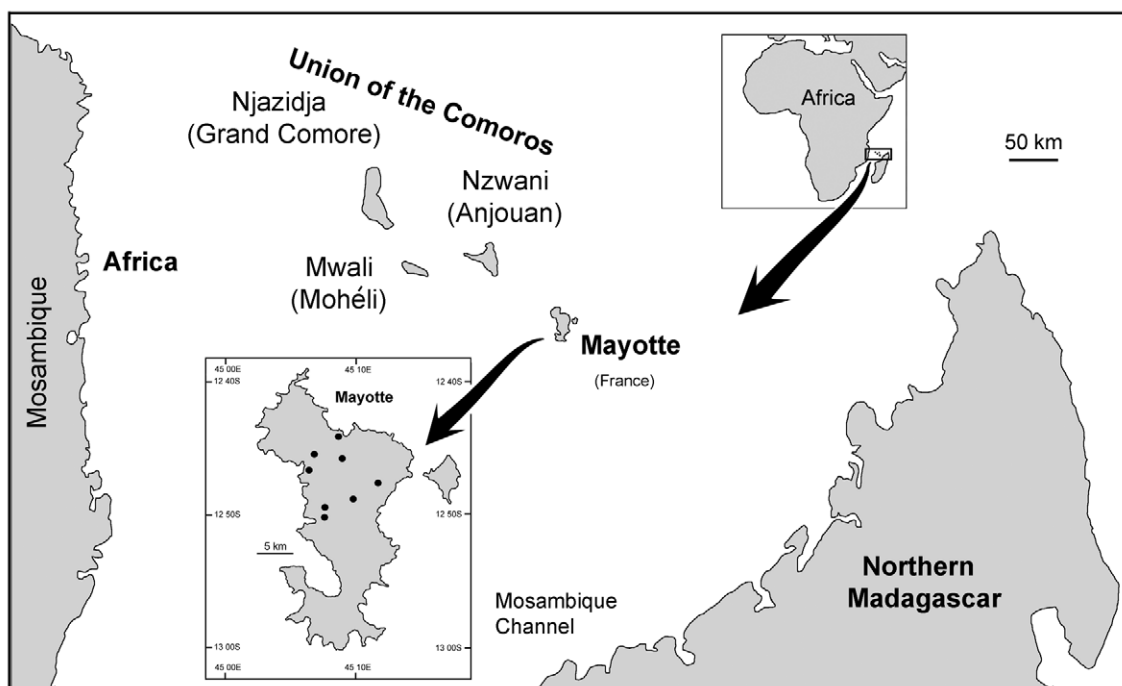


FIGURE 1. Geographic locality of Mayotte (French Protectorate) and the Union of the Comoros. Inset of Mayotte shows general position (dots) of localities for material examined in this study.

de Moor (2003) provided a useful key and notes on biology of simuliids in Southern Africa. *Simulium adersi* is wide spread, occurring in all provinces of South Africa, and is in Angola, Botswana, Malawi, Mozambique, Namibia, Swaziland, Zambia and Zimbabwe. Adler and Crosskey (2012: 50) listed *S. adersi* as also in Tanzania (Zanzibar, mainland); Benin, Burkina Faso, Cameroon, Central African Republic, Chad, Comoro Islands (Anjouan, Mayotte), Congo, Democratic Republic of Congo, Ethiopia, Ghana, Guinea, Guinea-Bissau, Kenya, Liberia, Lesotho, Mali, Mauritius, Niger, Nigeria, Rwanda, Senegal, Sierra Leone, South Sudan, Sudan, Togo and Uganda. Not noted in that world list was the fact that *S. adersi* is well known and widespread in Madagascar (e.g., Elouard 1978, Pilaka and Elouard 1999, Elouard and Pilaka 2000). This is now so noted in Adler and Crosskey (2013: 51)

An online literature search with the simple search string '*Simulium adersi*', returns a large body of information. In the main because of the importance of the species as a vector of leucocytozoons in poultry. Also, that at times, this simuliid seriously bites humans and is a possible vector of the causative agent of onchocerciasis. A major compilation of literature on *S. adersi* is by Travis *et al.* (1967).

The hydrobiological survey that enabled one of us (Nathalie Mary-Sasal) to collect simuliids was conducted in the context of the Water Framework Directive (WFD) adopted in 2000 (Directive 2000/60/EC of the European Parliament and Council of 23, October 2000, establishing a framework for community action in water policy). The main objective of the WFD is to achieve good qualitative and quantitative status of all water bodies by 2015. The studies conducted in October 2008 and April 2009 aimed to provide a basis (implementation, feasibility, logistics, number of stations needed) for establishment of a Surveillance Monitoring program (SM) of running waters in Mayotte. Since 2010, the SM program has 15 sites in rivers and streams that are sampled annually during the lowest water level.

Material and Methods.

Preparation, illustration and terms for structures follow Craig *et al.* (2012).

We did not examine type material. The Mayotte simuliid keys definitively to *S. (M.) adersi* (e.g., Crosskey 1960, 1969, de Moor 2003, and others), so it was deemed un-necessary to look at types. However, numbers of structures not used as key characters do differ from earlier descriptions of this species and it is this aspect that is addressed in detail in this work. Descriptions of colour are from material in ethanol. Sizes are based on measurement of at minimum five specimens.

Simulium (Meilloniellum) adersi (Pomeroy) 1922

Simulium hirsutum var *adersi* Pomeroy 1922: 459. Original description.

Simulium hirsutum var *adersi*, de Meillon 1930: 197.

Simulium adersi, Gibbins and Loewenthal 1933: 493. Referred to at species rank.

Simulium adersi, Gibbins 1934: 57. Detailed description and formal designation.

Simulium adersi, Bequaert 1939: 120.

Simulium adersi, Freeman and de Meillon 1953: 110.

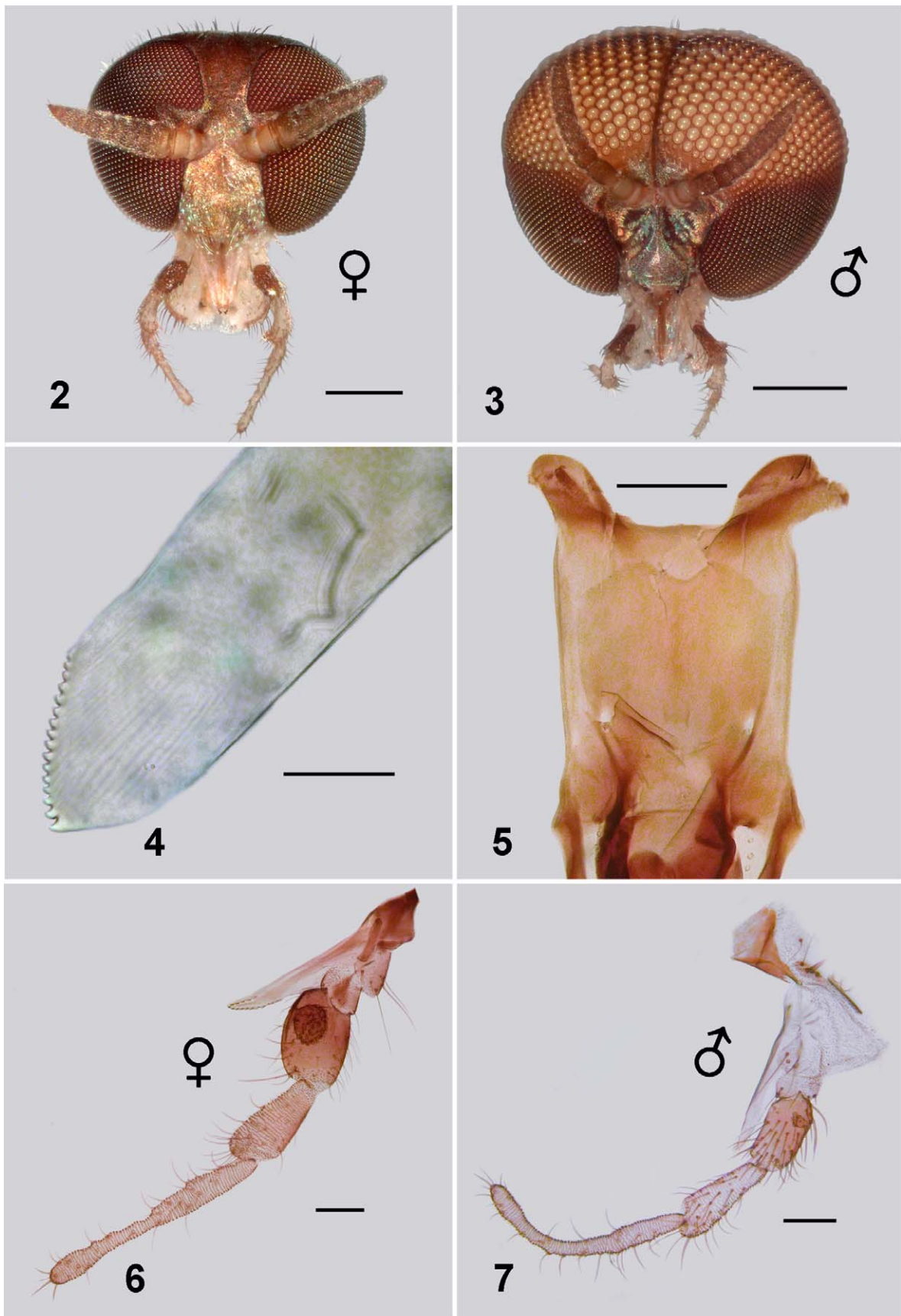
Meilloniellum adersi, Rubtsov 1962: 1,496. Transferred to new genus.

Simulium (Meilloniellum) adersi, Crosskey 1969: 74. Relegated to subgenus.

Simulium (Meilloniellum) adersi, Adler and Crosskey, 2013: 51.

Diagnosis

Adults. Female mandible toothed only on inner side; pleural membrane haired; hind basitarsus with row of stouter setae; calcipala and pedisulcus present; tarsal claw with basal tooth; female abdominal tergites III–V small, rounded; male gonostyli abruptly tapered distally, ventral plate deeply emarginated posteromedially. **Pupa:** thoracic cuticle with small even granules, gill with three basal branches, bifurcating to 11 finely tapered filaments; abdominal sternite IX lacks grapnel hooks. **Cocoon:** silk threads coarse, open weave, slipper shaped, low profile, internal pocket. **Larva:** body pale yellowish grey; head markedly bicoloured, head spot pigmentation negative, figure 8-shaped pattern on cephalic apotome; body cuticle with fine small trichoid setae; posteroventral tubercles poorly developed, rounded; rectal scales present; anal sclerite arms short; accessory sclerites small and distinct.



FIGURES 2–7. *Simulium (Meilloniellum) adersi*. Fig. 2. Frontal view of head of female. Scale bar = 0.2 mm. Fig. 3. Frontal view of head of male. Scale bar = 0.2 mm. Fig. 4. Mandible of female adult. Scale bar = 0.02 mm. Fig. 5. Cibarium of female adult. Scale bar = 0.05 mm. Fig. 6. Maxillary palpus and lacinia of female. Scale bar = 0.05 mm. Fig. 7. Maxillary palpus and lacinia of male. Scale bar = 0.05 mm.

Description

Adult Female.

Body: general body colour in alcohol very dark reddish brown/black; total length 3.3–3.5 mm. **Head** (Fig. 2): width 0.60–0.64 mm; depth 0.47–0.50 mm; frons-head ratio (narrowest width of frons: greatest width of head) 1.0:6.0. **Eye:** interocular distance 0.09–0.11 mm; ommatidia 0.014 mm in diameter; *ca.* 30 rows up and across at mid-eye. **Clypeus:** 0.17–0.19 mm wide; dark brown; vestiture of sparse silvery scales. **Antenna:** length 0.46 mm; not markedly tapered, all nine flagellomeres light brown, subequal in size, wider than long, basal flagellomere larger; scape and pedicel paler. **Mouthparts:** poorly developed, 0.4 length of head depth; cibarium (Fig. 5) broad shallow medial space, armature absent, cornuae short, substantial, rounded; mandible (Fig. 4) narrow and elongate, lacking outer teeth, 16 inner teeth; maxillary palpus (Fig. 6), total length 0.44 mm, third article dark brown, remainder lighter, proportional length of 3rd, 4th and 5th articles 1.0:1.1:2.5; 5th article markedly elongated; sensory vesicle spherical, 0.5 times width of 3rd article, opening 0.25 times width of vesicle, lacinia with 6 inner teeth and 11 outer teeth. **Thorax:** length 0.95–1.2 mm; width 0.71 mm; in alcohol, postpronotal lobes concolourous with scutum, sparse pale hairs; scutum evenly dark shiny brown, vestiture of recumbent flattened silvery hairs (usually rubbed bare), presutellar depression not markedly developed, no vittae visible in alcohol; scutellum slightly lighter than scutum, vestiture of sparse long pale hairs laterally; postnotum concolourous with scutum; pleuron and plural membrane concolourous with scutum, with hairs present, but usually rubbed bare, sockets remain—see male (Fig. 12). **Wing** (Fig. 8): length 1.9–2.1 mm; width 0.9 mm; leading veins poorly pigmented, others virtually not; costa with spines and hairs; radius base haired, and spines more distally; radial sector basally with hairs; small area surrounding campaniform sensilla at junction of radius and median veins distinctly pigmented; vein CuA2 markedly sinuous. **Haltere:** white. **Furcasternum** (Fig. 9): anterior lateral arms flared. **Legs:** bicolourous with darker brown bases to femoral, tibial, and tarsal segments, yellowish-brown elsewhere; fore basitarsus about 5 times as long as its greatest breadth; hind basitarsus about 6 times as long as greatest breadth; hind basitarsus with ventral series of stout spines (Fig. 10); calcipala not markedly developed, half width of hind basitarsus; pedisulcus not markedly indented; tarsal claw elegantly curved, basal tooth moderately developed, cone-shaped, both slightly serrated (Fig. 11). **Abdomen** (Fig. 13): abdominal scale poorly developed with sparse, fine pale hairs, barely extended over 2nd abdominal segment; overall, pale anteriorly and evenly mottled grey elsewhere; cuticle markedly corrugated; tergites not obvious in whole animal; pleurites and sternites not expressed; tergite II broad, 5.6 times wider than long, tergite III–V as long as wide, rounded; tergites VI and VII slightly larger and also rounded; tergite vestiture of very fine sparse hairs, longer hairs on posterior tergites, not dense, but possibly heavily worn. **Genitalia** (Fig. 14, 16, 17): sternite VIII pigmented across, lighter medially, vestiture of longer hairs posterolaterally, medially with triads and arrays of microtrichia; hypogynial valves poorly pigmented, broadly rounded apically, vestiture of microtrichia triads; median depression broad and shallow, smoothly divergent, valves broadly rounded posteroapically; genital fork finely constructed, lateral plate elongated, apodeme not obvious (perhaps is pigmented anterior ledge of the plate), median extension of plate sharply pointed; anal lobe in lateral view bare of microtrichia, but with a few hairs, cercus broadly rounded apically. **Spermatheca** (Fig. 15): slightly ovoid; surface pattern absent as are internal hairs; clear area at junction of duct small. **Eggs:** one female, *ca.* 160 eggs, 0.15 x 0.09 mm in size, subtriangular in shape.

Adult Male.

Body: general colour dark blackish brown; total length 2.5–2.7 mm. **Head** (Fig. 3): width 0.90 mm; depth 0.70 mm. **Eyes:** upper larger ommatidia orange, 0.031 mm in diameter, *ca.* 16 across and 18 down; lower ommatidia dark brown, 0.014 mm in diameter, *ca.* 30 across and 35 down. **Clypeus:** markedly small, dark brown, pollinose in some lighting; 0.20 times as wide as head; no vestiture obvious. **Antenna:** total length 0.58 mm; not tapered, evenly medium brown. **Mouthparts:** poorly developed; length 0.33 times head depth; mandibles insubstantial, broadly tapered with apical hairs; laciniae, finely tapered apically; maxillary palpus (Fig. 7) medium brown basally, pale distally, elongate distally, sensory vesicle markedly small; 0.65 mm long, proportional lengths of 3rd, 4th and fifth articles 1.0:1.4:2.8. **Thorax:** length 0.9–1.2 mm; width 0.7–0.8 mm; scutum evenly dark brown/black, vestiture of sparse recumbent silvery flat hairs—normally rubbed bare; scutellum translucent and pale with sparse, long pale hairs; postscutellum concolourous with scutum; pleural membrane, haired (usually rubbed bare), but sockets remain visible (*e.g.*, Fig. 12). **Wing:** 2.1–2.4 mm in length, 0.9–1.2 mm at maximum width. **Haltere:** white. **Legs:** in mature specimens evenly medium brown, for immature specimens bicolorous yellowish-brown, with darker brown femoral, tibial, and tarsal bases; femur and tibia expanded slightly; hind basitarsus 4.5 times as long

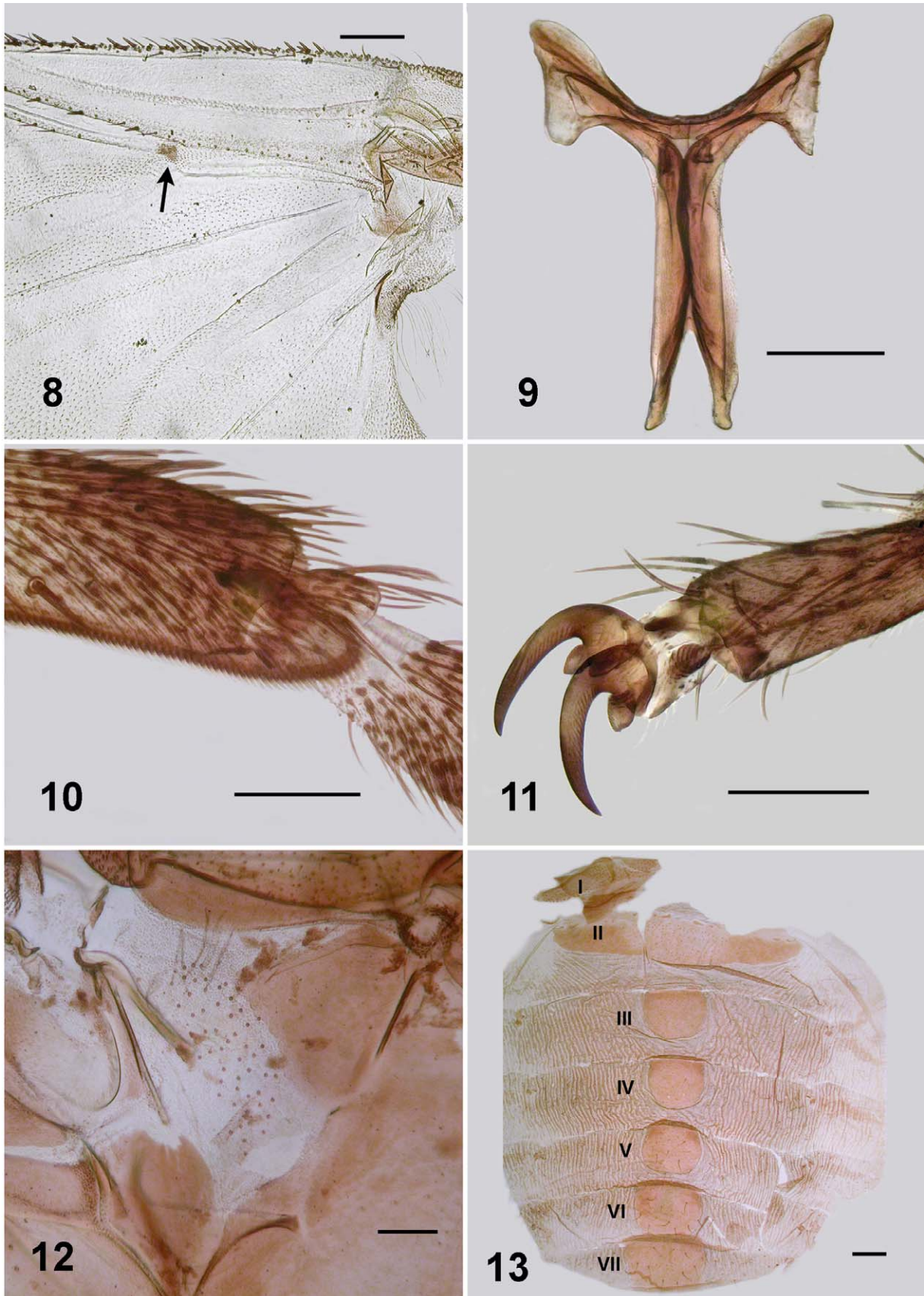
as greatest breadth; with row of stout spines; tarsal claw partially covered by grappling pad of 24–26 teeth. **Abdomen:** overall dark blackish brown; tergites occupy whole width of dorsum, more pigmented areas laterally; small pleurites and sternites posteriorly; vestiture of sparse pale hairs. **Genitalia** (Fig. 18, 19, 20): gonocoxa curved and smoothly tapered posteriorly, 1.3 times longer than basal width, extensive medial crenulated region posterior of base, dark brown posteriorly, pale medially, vestiture of sparse, coarse black hairs medially; gonostylus approximately 2.8 times longer than basal width, abruptly decreased in size 2/3 from base apically with single spine; ventral plate broad with major medial depression apically, moderately haired, proximal arms short, substantial; small central keel; median sclerite well expressed, narrow, slightly T-shaped posteriorly; parameres of a thin curved rod basally, thickening to terminate in substantial tooth; aedeagal membrane bare.

Pupa: Body length; male 2.8–2.9 mm, female 2.2–2.5 mm. **Head:** evenly tuberculate, including the ocular region; facial and frontal setae present, the former double, epicranial setae apparently absent; cephalic apotome of female short and broad, more tuberculate medioventrally, ratio of basal width to length 1:1.5 (Fig. 27); apotome of male ovoid, ratio of basal width to length 1:2.5 (Fig. 28); muscle scars not tuberculate. **Thorax** (Fig. 24). mesonotum finely tuberculate; no distinct pattern; dorsocentral setae simple, elongate. **Gill** (Fig. 21, 23): maximum length 2.0–2.3 mm; basal trunk short, three branches rapidly bifurcated to produce 11 smoothly tapered filaments; ventral filaments up to half length shorter than dorsal filaments; filament surface pseudoannulated (Fig. 25). **Abdomen** (Fig. 26): cuticle pale and membranous; spine combs absent; posterior setae on tergite II trichoid, sparse microtubercles anteriorly; setae on tergite III and IV short curved and spine-like, microsculpture absent; setae on tergite V trichoid; tergites VI–VIII with anterior small spines directed posteriorly, lateral microsculpture of scales; sternite III with trichoid setae, sternite IV with one bifurcated spine-like seta; sternite V with two; sternites VI and VII with one bifurcated seta and one single; grapnel hooks on sternite IX absent; terminal spines short and blunt.

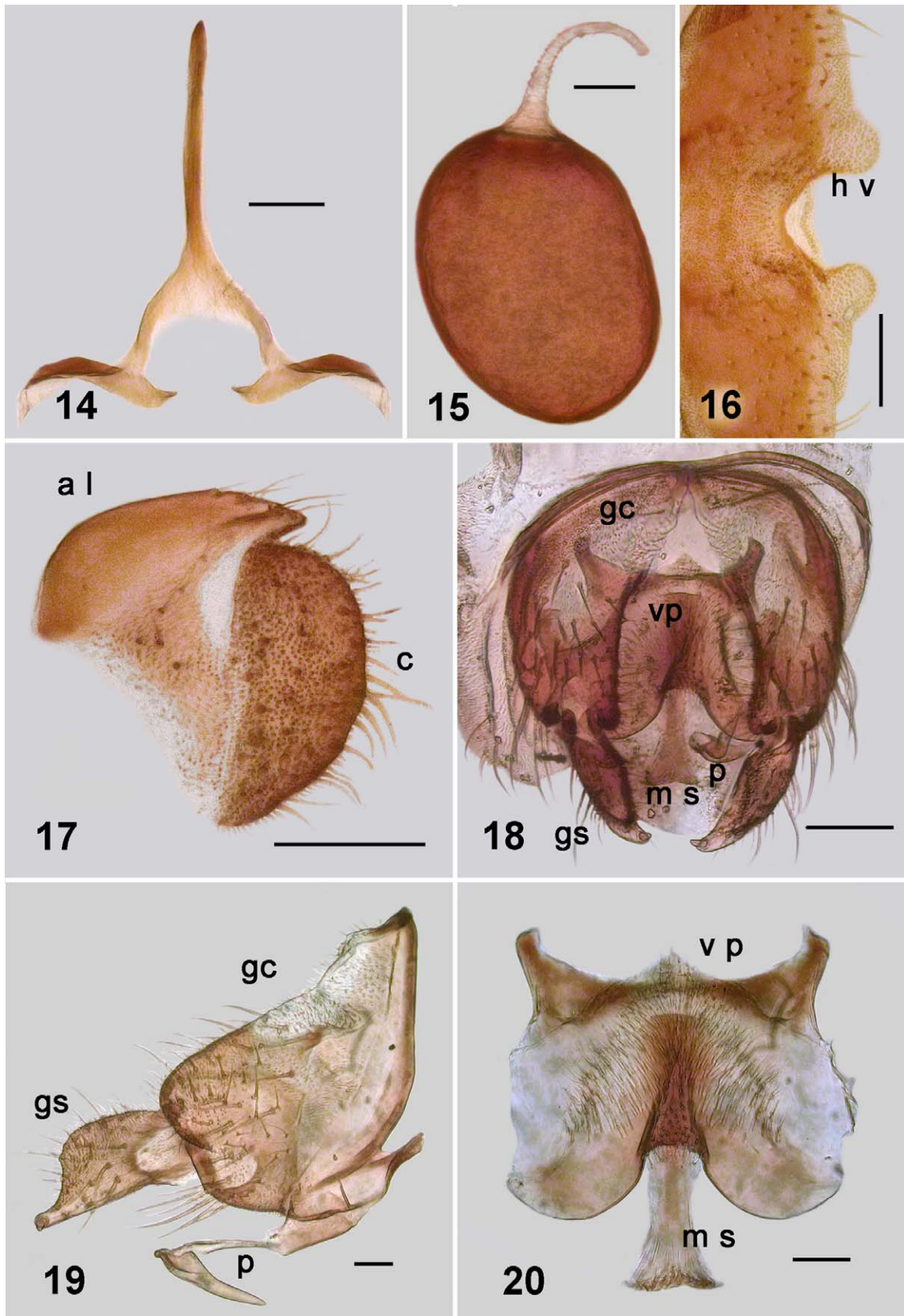
Cocoon (Fig. 21, 22): slipper shaped; of markedly thickened dark brown silk threads, loosely woven; inner pocket more closely woven than remainder of cocoon, with distinct anterior edge and occasional indication of dorsomedial projection; lateral extremities of cocoon either with distinct edge, or individual anchor points for silk threads.

Larva (last instar).

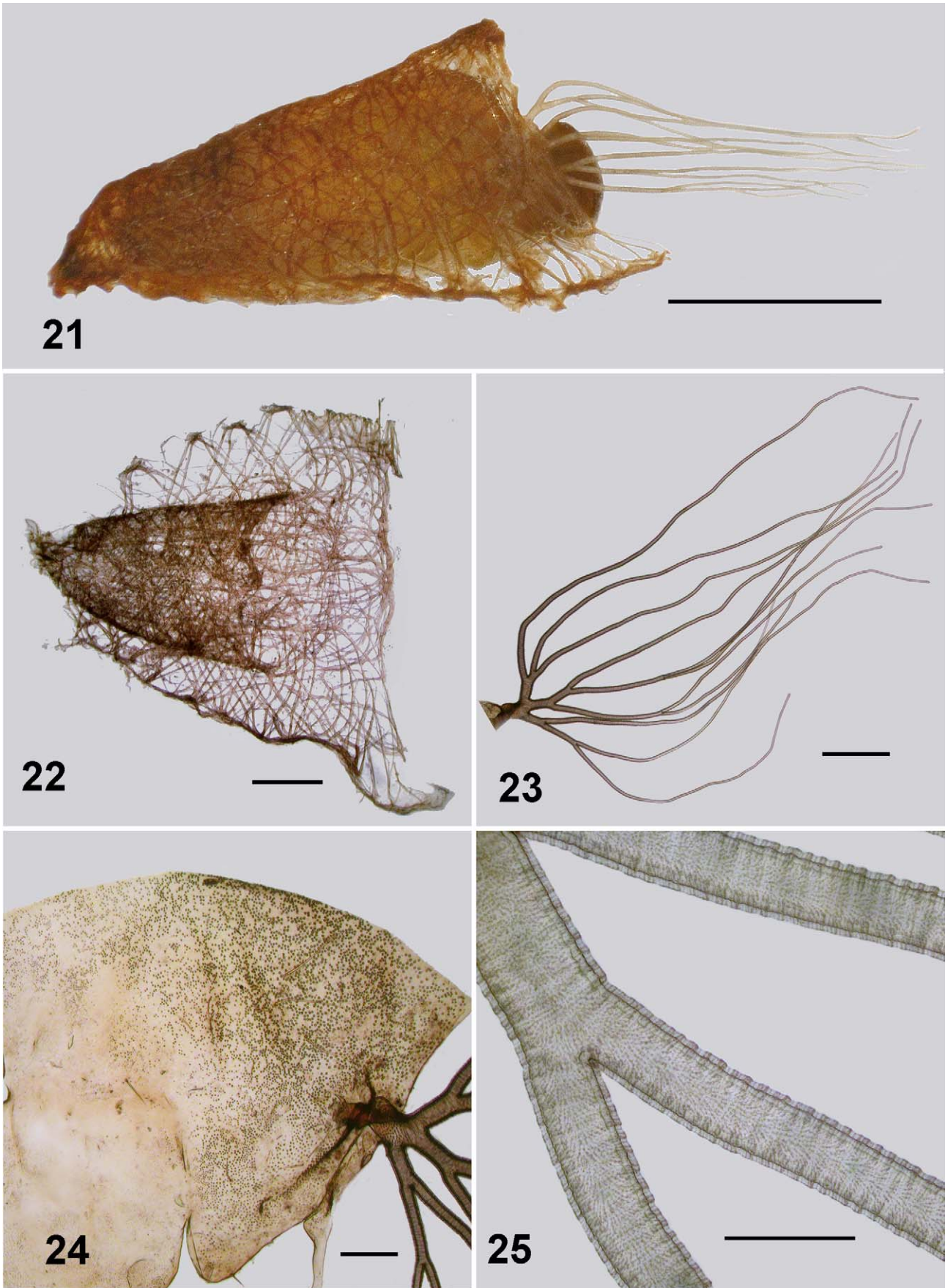
Body (Fig. 29): total length 4.3–4.5 mm. **Head** (Fig. 30): markedly bicoloured; length 0.51–0.65 mm, width 0.54–0.55; distance between antennal bases 0.36–0.38 mm; lateral margins of head smoothly convex; cephalic apotome translucent and pale yellow, median head spots negative, surrounded by rich brown pigmentation, producing marked figure-of-8 shape; cuticle slightly corrugated, no extra vestiture beyond normal array of setae; ecdysial lines narrowed slightly anterior of stemmata, expanded posteriorly to curve broadly posteriorly; cervical sclerites, separate, not markedly developed, poorly pigmented. **Antenna** (Fig. 32): articles evenly light brown, medial article slightly paler; 0.35 mm total length, extended just beyond apex of fan stalk; ratio of length of apical, medial and basal articles 1:1.6:1.2, length of basal article 4.8 times width. **Labral fan:** stalk clear and relatively short; 40–46 short, substantial rays, 0.56 mm in length, 0.012 mm in width at mid length; distinct pattern of microtrichia, longer microtrichia 0.8 times longer than ray width, interspersed with *ca.* 8 smaller microtrichia. **Postgenal cleft** (Fig. 33): markedly rounded, posterior tentorial pit region not markedly sclerotized and pigmented. **Postgenal bridge:** subequal in length to hypostoma, slightly paler than dark genae, elongated posteroventral muscles spots not visible. **Hypostoma** (Fig. 34): 11 teeth, median tooth shorter than lateral teeth, the latter broadly based, sublateral teeth small and directed laterally; one paralateral tooth; 5–6 small but distinct lateral serrations; 5 hypostomal setae per side, subparallel to edge of hypostoma. **Mandible** (Fig. 35, 36): normal development, brushes not markedly produced; outer teeth poorly developed; apical tooth well developed; three subapical teeth not substantial decreased in size proximally and then 5–6 spinous teeth (markedly few); serration well developed and sensillum distinct; blade region elongated and smooth. **Thorax:** wider than anterior abdomen, markedly pale dorsally, pale yellowish brown otherwise; pharate pupal gill histoblast (Fig. 31) with filaments in broad L-shape; directed ventrally then curved posteriorly to then curve dorsally again and coil back towards the gill base. **Abdomen:** clear pale yellowish grey, intersegmental regions pale producing slightly banded appearance; abdominal segments I–IV narrowed, expanded laterally at 5th segment—producing a slight amphora shape, but not ventrally; ventral tubercles poorly developed and rounded; cuticle with minute but distinct simple setae, more dense on posterior segments (Fig. 37). **Anal sclerite:** anterior and posterior arms short, robust, both abruptly tapered; accessory sclerites small, distinct and sometimes comma-shaped with the tail directed ventrally (Fig. 29, 37). Rectal scales present and interspersed with the abdominal setae (Fig. 38). **Rectal papillae:** three simple lobes with rarely a small basal lobe on the lateral papillae. **Posterior proleg circlet of hooks** (Fig. 29, 37): directed posteriorly; 75–80 rows of hooks, 12–14 per row (total *ca.* 1 000).



FIGURES 8–13. *Simulium (Meilloniellum) adersi*. Fig. 8. Wing base of female. Scale bar = 0.1 mm. Arrow indicates pigmented area. Fig. 9. Metathoracic furcasternum of female. Scale bar = 0.05 mm. Fig. 10. Distal hind basitarsus of female. Scale bar = 0.05 mm. Fig. 11. Tarsal claw of female. Scale bar = 0.05 mm. Fig. 12. Pleural membrane of male showing sparse, fine hairs and sockets. Scale bar = 0.05 mm. Fig. 13. Tergites I (abdominal scale) to VII of female abdomen. Scale bar = 0.1 mm.



FIGURES 14–20. *Simulium (Meillonium) adersi*. Fig. 14. Genital fork. Scale bar = 0.05 mm. Fig. 15. Spermatheca. Scale bar = 0.02 mm. Fig. 16. Ventral view of hypogynial valves (h v). Scale bar = 0.05 mm. Fig. 17. Lateral view of anal lobe (a l) and cercus (c). Scale bar = 0.05 mm. Fig. 18. Male genitalia, ventral view (gc—gonocoxa; gs—gonostylus; v p—ventral plate; m s—median sclerite; p—paramere). Scale bar = 0.05 mm. Fig. 19. Gonocoxa (gc), gonostylus (gs) and paramere (p), lateral view. Scale bar = 0.02 mm. Fig. 20. Ventral view of ventral plate (v p) and median sclerite (m s). Scale bar = 0.02 mm.



FIGURES 21–25. *Simulium (Meilloniellum) adersi*. Fig. 21. Female pupa, right lateral view. Scale bar = 1.0 mm. Fig. 22. Cocoon, dorsal view. Scale bar = 0.5 mm. Fig. 23. Lateral view, right pupal gill. Scale bar = 0.25 mm. Fig. 24. Right thoracic pupal cuticle. Scale bar = 0.1 mm. Fig. 25. Surface structure of pupal gill filaments. Scale bar = 0.05 mm.

Etymology: Not specifically mentioned by Pomeroy, but implicitly for William Mansfield Aders (Crosskey and Davies 2012).

Material examined: Full array of eggs, larvae, pupae, male and female adults.

Mayotte, Comoro Archipelago. Ouroveni, 2-x-2008, S12.80831° E45.12761°; Bouyouni, 5-x-2008, S12.74036° E45.14258°; Batirini, 5-x-2008, S12.76047° E45.11183°; Coconi, 6-x-2008, S12.83481° E45.12827°; Combani, 7-x-2008, S12.77144° E45.14753°; Koualé, 8-x-2008, S12.80542° E45.16381°; Chirini, 8-x-2008, S12.77769° E45.10456°; Koualé, 9-x-2008, S12.79714° E45.18572°. All collected by N. M-S.

Deposited in the Strickland Museum, Department of Biological Sciences, University of Alberta, Edmonton, CANADA. Other material is in the personal collection of N. M-S.

Comments. Below we discuss differences between the original descriptions by Pomeroy (1922), Gibbins (1934), Freeman and de Meillon (1953), Crosskey (1960), Rubtsov (1962) and Crosskey (1969) of African mainland *S. adersi* and the Mayotte material as given above.

Adults. The Mayotte adults of *S. adersi* show little difference to previous descriptions of the species. A character, however, apparently not noted elsewhere is the distinct pigmented region around the campaniform sensory organs on the wing at the junction of the radial sector (Rs) vein and 1st radial (R1) vein (Fig. 8).

We make the point, already known, that the mandible of the female has teeth only on one side (Fig. 4). This was described by Freeman and de Meillon (1953: 111) who described 18 small teeth on the inner surface only. The Mayotte material has 16. It is perhaps surprising that more importance has not been assigned to this character state. We comment because in simuliids, teeth on both sides of the mandible is plesiomorphic. The one-sided condition is known for *Austrosimulium* (Craig *et al.* 2012) where it is a diagnostic character for that genus in the Australasian region. Further, for *Austrosimulium* it is known to be a derived character—reverting to a two-sided condition in gynandromorphs (Craig and Crosby 2008). Otherwise teeth on one side of the mandible is sporadic in Simuliidae (*e.g.*, *Gomphostilbia*, Takaoka and Davies 1995, Bentinck 1955). Is it possible that a one-sided mandible is diagnostic for *Meilloniellum*? We did not investigate further.

The lacinia in the Mayotte material has reduced numbers of recurved teeth with only 5 inner and 12 outer teeth (Fig. 6). For other *S. adersi* material, Freeman and de Meillon (1953) describe 9 and 13 teeth respectively

The rather finely crafted mandible and reduced number of teeth on the lacinia along with the relatively short mouthparts tend to indicate that *S. adersi* would be a bird feeder—in agreement with the similar mouthparts in *Austrosimulium*. Bird feeding in *S. adersi* is well confirmed, but such mouthparts do not preclude feeding on humans and other mammals, as this simuliid is known to do readily (Gibbins 1934, Bequaert 1939, Palmer and de Moor 1998).

Simulium adersi is the only species of *Meilloniellum* that possesses a haired pleural membrane (Crosskey 1969). Of fine nature this vestiture is difficult to observe and also the hairs dislodge easily, usually leaving only the sockets visible (Fig. 12).

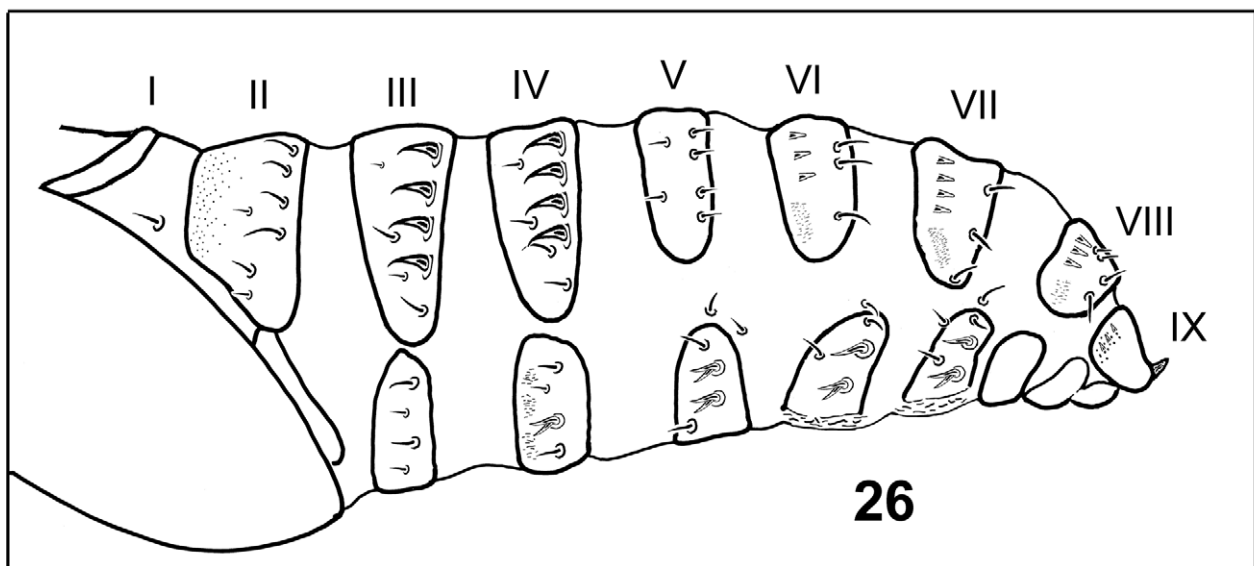


FIGURE 26. *Simulium (Meilloniellum) adersi*. Pupal abdominal armature. Structures not to scale.

There is little difference in adult legs between localities. Mayotte females, however, have a calcipala (Fig. 10) that is slightly more elongate than that illustrated by Gibbins (1934; his fig. 2e) and the membranous area of the pedisulcus less extensive.

Crosskey (1969) described the abdomen of the *Meilloniellum* species as thickly and evenly covered with pale scales. Freeman and de Meillon (1953) describe the abdomen as black with dense silvery and yellow scales. The Mayotte material is not black and while there are pale scales, these are sporadic. However, the available females and males give every impression of having been worn and they perhaps are not showing the original vestiture.

Pupae. Difference between pupae of Mayotte *S. adersi* and those from elsewhere show in the gills and the cocoon. The cocoon as first illustrated by Gibbins (1934; his fig. 8) shows it to be apparently of close weave. Another illustration by Freeman and de Meillon (1953; their fig. 32h) shows the weave to be more open—similar to the Mayotte material (Fig. 21). Not mentioned, or illustrated previously, is the internal pouch shown clearly here (Fig. 22). The gills of the Mayotte pupae have the same number of filaments and branching pattern, but are noticeable longer overall, with relatively shorter ventral filaments. Gibbins (1934; his fig. 7; 1936; his fig. 5a), shows the total length of the gill to be *ca.* 1.2 mm. with the ventral filaments slightly shorter than the others, as does Crosskey (1969; his fig. 194). The Mayotte material has gill length of *ca.* 2.1 mm (Fig. 23).

Larvae. Gibbins (1934; his fig. 5a) specifically illustrated the cephalic cuticle of the larva as armed with minute spines, and mentioned a pigmented area below the stemmata as also spined. Such has not been commented on by following workers and the Mayotte material has merely normal chaetotaxy (Fig. 30, 31) as detailed for simuliids by Craig (2005). Pigmentation pattern of the head, namely the negative head-spots is similar for all material (Crosskey 1960; his fig. 21), however the trident-shaped lateral pigmentation posterior to the stemmata is overall slightly darker in the Mayotte material. The rendition of the lateral head in Crosskey's figure appears to show the spined region noted by Gibbins (1934).

Aspects of the ventral head capsule of the larvae are similar in all material. Shape of the postgenal cleft and postgenal bridge (Crosskey 1960; his fig. 38; 1969; his fig. 250) agree with the Mayotte material (Fig. 33). However, that of Mayotte have hypostomal teeth (Fig. 34) not as prominent as otherwise illustrated (Gibbins 1934; his fig. 6; Crosskey 1960; his fig. 57). In particular the median tooth does not protrude beyond the lateral teeth.

Crosskey (1960) described the larval antenna of *S. adersi* as having the basal article (his first segment) 6.0 times as long as broad. That of the Mayotte material is only 4.8 times as long as broad. Further, Crosskey (*loc. cit.*; his figure 79) gave proportions of the three articles as 1.0:1.25:1.28, those for the Mayotte material are 1.0:1.47:1.18 (Fig. 32) where the median article is relatively longer.

Labral fan ray number is variable. Gibbins (1934) stated that there were 28–32, but Crosskey's (1960) re-examination of type material showed there to actually be 38–41. Overall, Crosskey (*loc. cit.*) reported 38–47 rays, with 44 the mean. The Mayotte material has 40–46 rays. Whether the minor difference in number is taxonomically useful is moot. Fan ray number is known to be phenotypically plastic—dependent on nutrition and velocity of water (Zhang 2006).

Crosskey (1960; his fig. 90) illustrated three basic conditions of larval mandible for African simuliids. That of *S. adersi* were of the more common condition (Fig. 35). For Mayotte material, however, the mandibular serration and sensillum are larger and more closely applied (Fig. 36) than illustrated by Crosskey (*loc. cit.*; his fig. 104). Gibbins (1934; his fig. 5d) illustration appears somewhat stylized, and the mandibular sensillum is rendered as markedly small and the serration smaller too.

Crosskey (1960; his fig. 126) illustrated the maxillary palpus and described it as 3.1 times as long as the basal width, not including the apical sensilla. The palpus of the Mayotte larvae is only 2.5 times as long as the basal width.

Overall shape of the posterior abdomen and relative size of the ventral tubercles of Mayotte *S. adersi* last instar larvae agrees closely with the illustration by Crosskey (1960; his fig. 157), but that illustration lacked any accessory sclerite. The anal sclerite is very similar (Fig. 37) to that shown by Crosskey (*loc. cit.*; his fig. 164), but again his material lacked the accessory sclerite(s). Never-the-less, Crosskey (1969) stated that there are accessory sclerites as "sometimes only minute weakly sclerotized trace". Mayotte material has a small, but distinct, accessory sclerite on each side (Fig. 37).

Rectal scales were not mentioned by Gibbins (1934, his fig. 5c) and are notably absent from the illustration. Rubtsov (1962), in his key to larvae, divided *Meilloniellum* species into those with and without rectal scales. Crosskey (1969) in his revision of *Meilloniellum* has rectal scales as a diagnostic character for the subgenus. The Mayotte larvae clearly possess these structures (Fig. 37, 38)

Gibbins (1934) describes the rectal papillae as trilobed and each with smaller secondary appendages. Freeman and de Meillon (1953) merely refer to *S. adersi* rectal papillae as trifid—there is no mention of lateral lobes. Rubtsov (1962) describes *Meillonium* with branched rectal papillae. Crosskey (1960) describes the papillae as having several secondary lobes each. The Mayotte material are basically simple trifid structures with, very rarely, a slight indication of secondary lobules (poorly visible in Fig. 29).

The number of hooks comprising the circlet of hooks on the posterior proleg is variable. Gibbins (1934) stated there were *ca.* 120 rows of 19–25 hooks for the Nsadzi larvae. Crosskey (1960) gave a much lower number of 69–75 rows with 9–15 hooks. The Mayotte larvae have some 75–80 rows of 12–14 hooks. These characters states are phenotypically plastic, and Palmer and Craig (2000) showed a clear correlation between velocity of water in the habitat of the larva and total number of hooks. Of relevance here too is that the original larval material of *S. adersi* from Nsadzi Island in Lake Victoria were larger (5.8–6.0 mm in length. Gibbins 1934) than other known larvae (Crosskey 1960. 4.5–5.0 mm in length). The Mayotte larvae are of the latter size.

Overall, the disagreement in morphological character states between Mayotte *S. adersi* and those from the African mainland, suggest that the Mayotte entity is a separate species. Before, however, that is formally done, the material needs to be compared with *S. adersi* from Madagascar. Indeed, the whole complex needs further examination, including using molecular and cytological methods.

General biology of *Simulium adersi*

Commonly mentioned in the literature regarding *S. adersi* is that the immature stages have a remarkable range of habitat. Gibbins (1934) commented about larvae being found on the wave-swept shore of islands in Lake Victoria, in particular Nsadzi Island—a most unusual habitat for simuliid larvae. Immature stages have been found in almost every type of running water, from large rivers to small runnels, high conductivity, estuarine (Crosskey 1960), and less so, high quality water (Palmer and de Moor 1998; de Moor 2003). Oddly, because of that latter aspect, *S. adersi* has been investigated as a possible indicator of water quality in the Buffalo River, South Africa (Palmer *et al.* 1996).

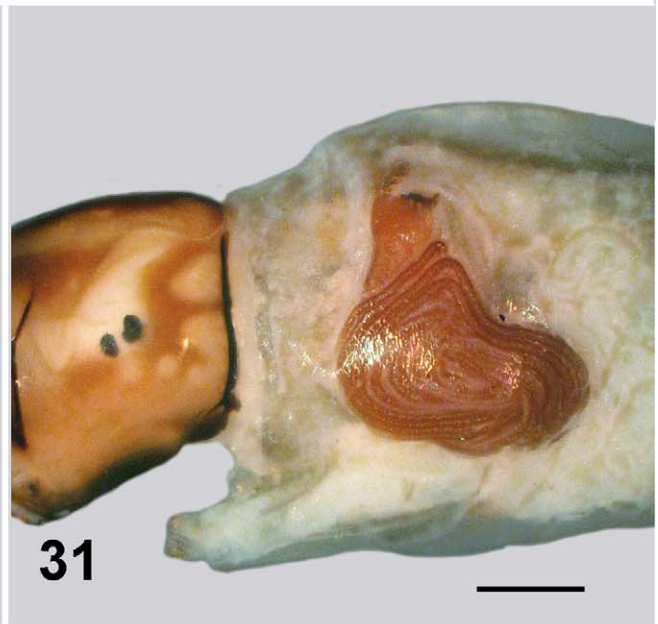
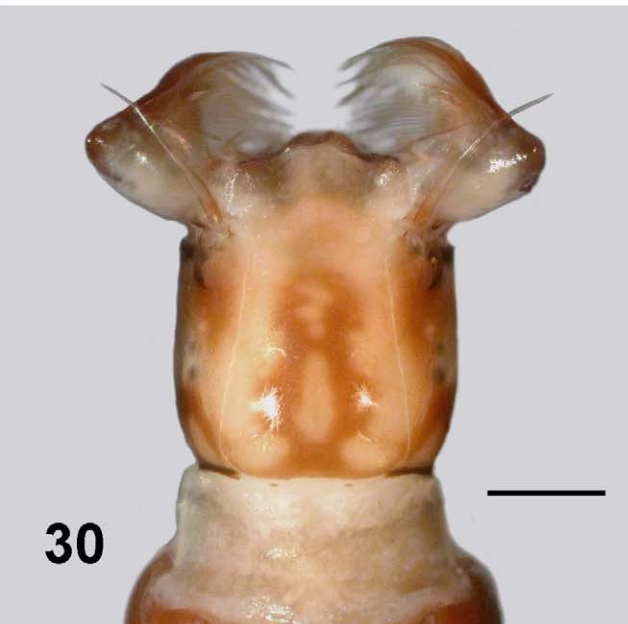
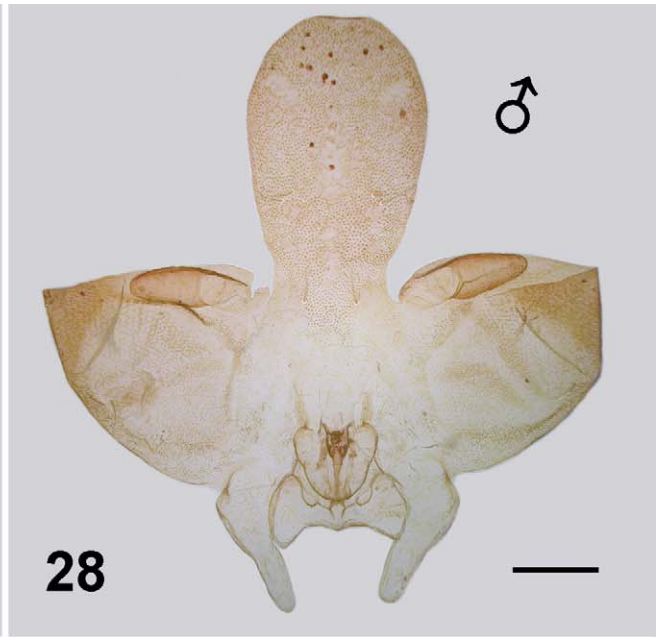
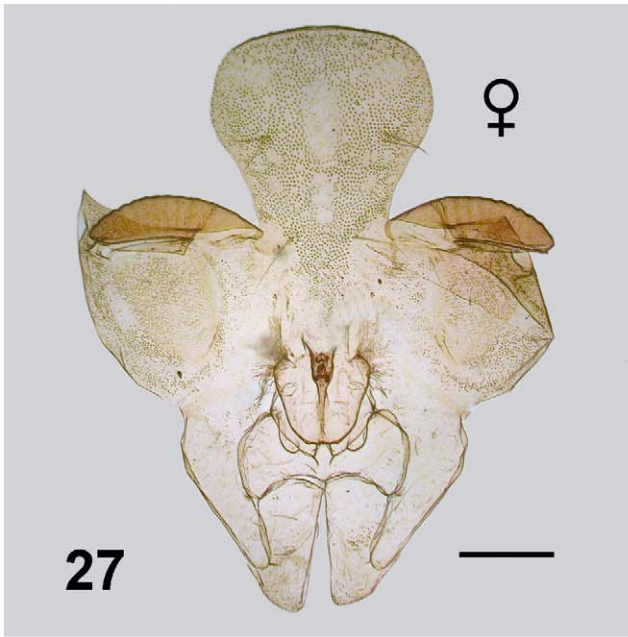
Of economic importance was replacement of *S. adersi* and *S. nigrifurcata*, both relatively non-pest species, with the seriously biting *S. chutteri* as a result of interbasin water transfer projects involving the Vaal, Orange and Great Fish rivers (*e.g.*, O'Keeffe and de Moor 1988). Effects of these projects are still of considerable interest (Rivers-Moore *et al.* 2007, Gupta and van der Zaag 2008, de Beer and Green 2012).

While providing considerable details about water quality, velocity, substrates, and density of aquatic insects, Starmühler (1976, 1979) did not identify Simuliidae except to Family, so nothing can be said regarding ecological requirements of *S. adersi* on Anjouan. Considerable ecological data on the streams sampled in Mayotte was compiled during the Surveillance Monitoring programme in 2008 and 2009. Most localities were forested in one manner or other (*e.g.*, Fig. 39, 40). For the localities from which we examined material, larvae of *S. adersi* were normally found on vegetation in situations where the water velocity was fast. No exact velocity measurements were made. Most sites had substrates of cobble or boulders (*e.g.*, Fig. 39), but occasionally solid rock (*e.g.*, Fig 40). Water temperatures ranged from 22–31°C, conductivity from 129–394 µS/cm and oxygen saturation 21–93%. Water was generally clear, but there was considerable anthropogenic impact from washing, excrement and garbage. Details of all sites can be obtained directly from N. M-S.

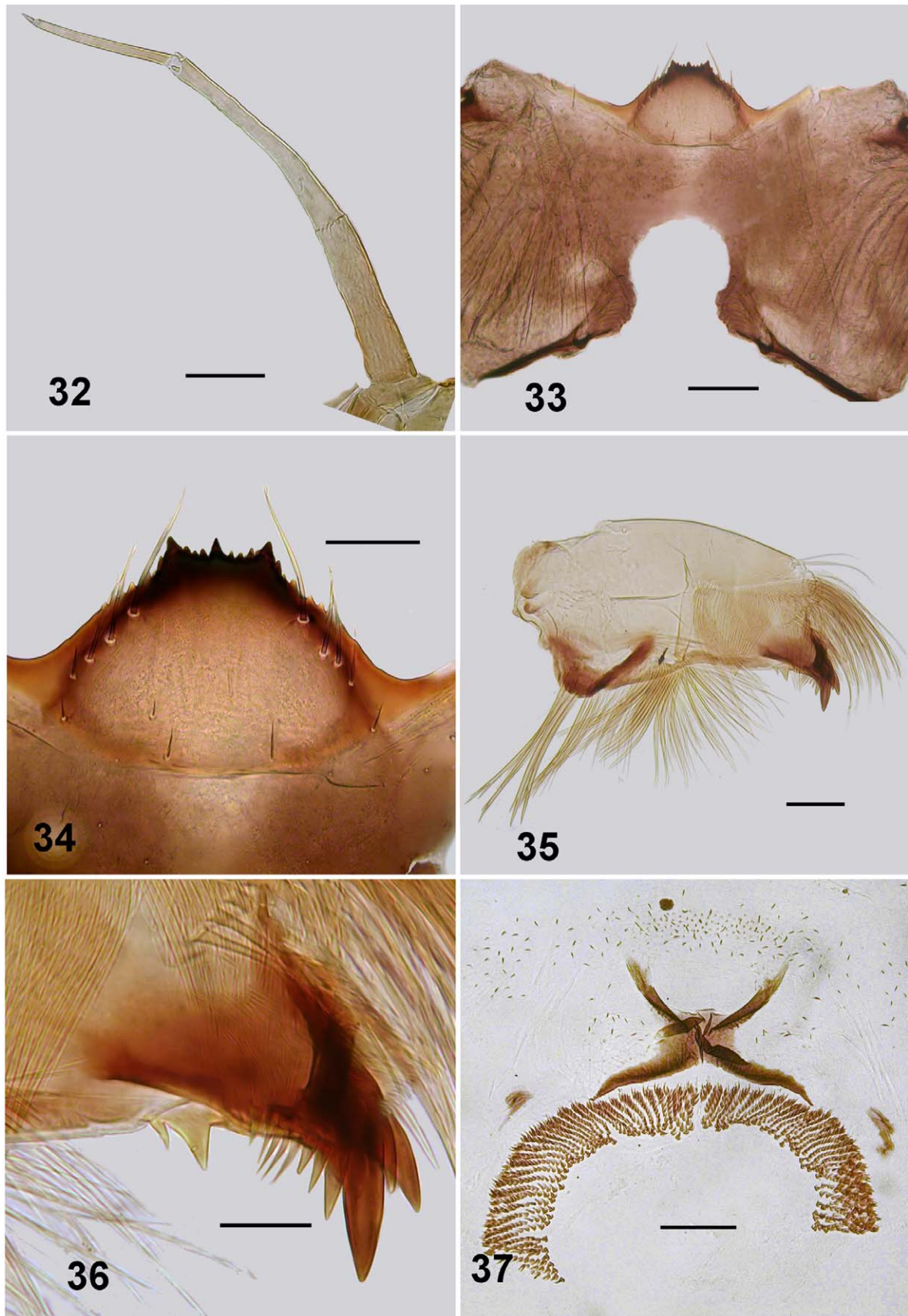
There appears to be no information on nuisance value of *S. adersi* in Mayotte. Certainly no biting was recorded by people involved in the Surveillance Monitoring programme.

Palmer and de Moor (1998) report that *S. adersi* females lay some 400 eggs, considerably more than for the single example of Mayotte *S. adersi*. Furthermore, the eggs were larger. Perhaps this indicates that the Mayotte female had not blood-fed, as suggested by observations by N. M-S. on lack of biting. Oviposition by *S. adersi* takes place underwater (Gillet and Lebied 1959, Balay 1964, Crosskey 1969) with eggs clustered on hard substrates. Laboratory studies show that the eggs take 13 days to hatch at *ca.* 25°C and the larvae a minimum of 17 days to pupae at the same temperature (Begemann 1980). Seven larval instars were convincingly demonstrated for *S. adersi* by Elouard (1987)—in full agreement with the modal number known for Simuliidae (Adler *et al.* 2004).

Parasitoids are known for larvae of *S. adersi*; two genera, *Caudospora* and *Weiseria* spp. were reported by Jamnback (1970).



FIGURES 27–31. *Simulium (Meilloniellum) adersi*. Fig. 27. Female pupal cephalic exuviae. Scale bar = 0.2 mm. Fig. 28. Male pupal cephalic exuviae. Scale bar = 0.2 mm. Fig. 29. Left lateral habitus view of last instar larva. Scale bar = 1.0 mm. Fig. 30. Dorsal view of last instar larval head. Scale bar = 0.2 mm. Fig. 31. Pupal gill histoblast. Scale bar = 0.2 mm.



FIGURES 32–37. *Simulium (Meilloniellum) adersi*. Fig. 32. Antenna of last instar larva. Scale bar = 0.05 mm. Fig. 33. Postgenal cleft, bridge and hypostoma, last instar larva. Scale bar = 0.1 mm. Fig. 34. Hypostoma of last instar larva. Scale bar = 0.05 mm. Fig. 35. Mandible of last instar larva. Scale bar = 0.05 mm. Fig. 36. Mandible apex. Scale bar = 0.02 mm. Fig. 37. Abdominal setae, anal sclerite, accessory sclerites and posterior proleg hooks. Scale bar = 0.05 mm.

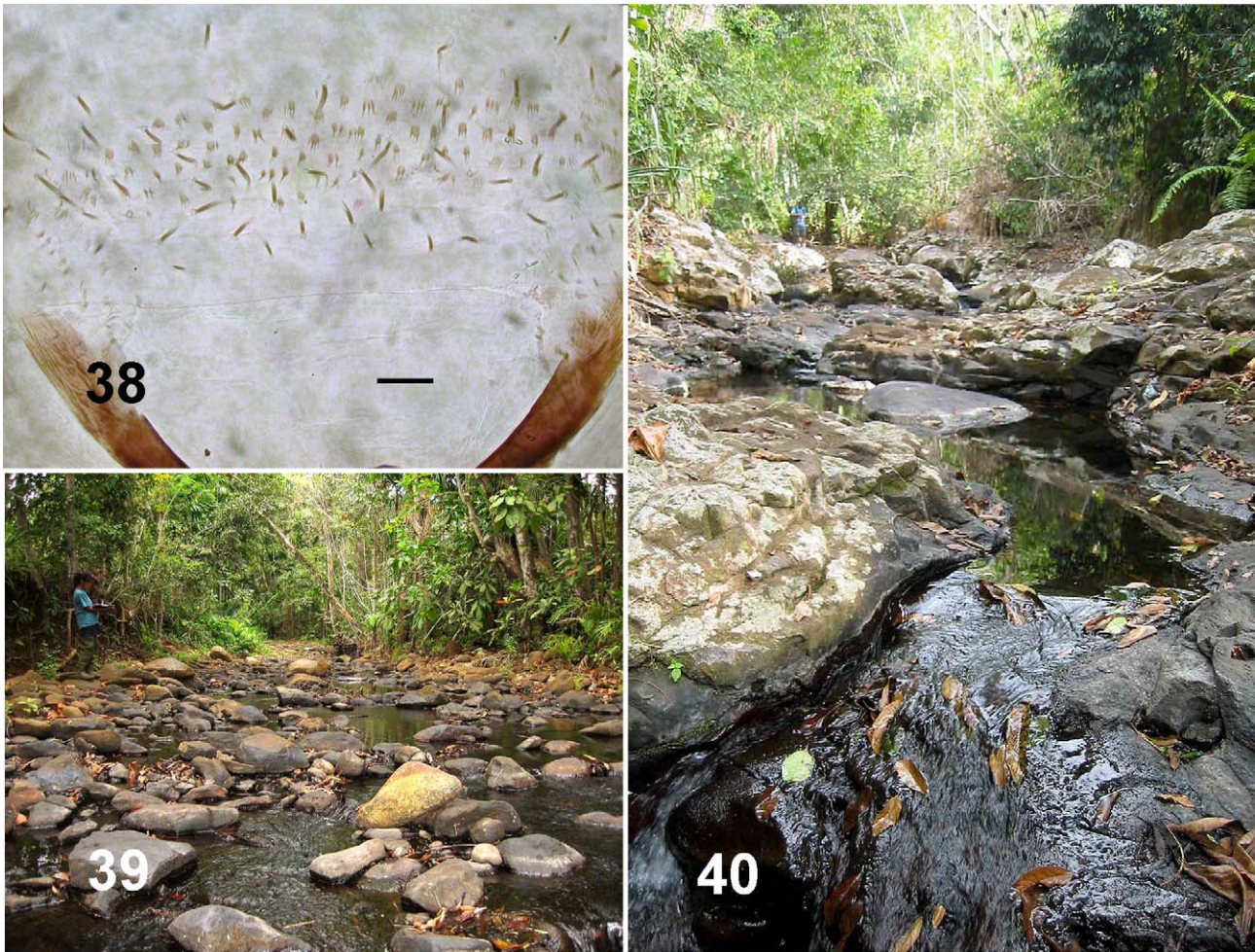


FIGURE 38–40. Fig. 38. *Simulium* (*Meillonium*) *adersi*. Rectal scales and posterior abdominal setae. Scale bar = 0.02 mm. Figs. 39 & 40. Representative habitats on Mayotte. Fig. 39. Bouyouni Stream, 5-x-2008. Fig. 40. Gouloué Stream, 7-x-2008.

Female adults *S. adersi* are primarily bird feeders and a pest of poultry, but are well known to bite sheep, goats and humans (Bequaert 1939). On humans the neck, head and ears are preferred. Fallis and Raybold (1975) convincingly showed that *S. adersi* females were attracted to carbon dioxide exhalations and not silhouettes alone of animals. Oddly, even recently, *S. adersi* was still referred to as non-anthropophilic (e.g., Mbah *et al.* 2003),

Simulium adersi females are known vectors of haematozoa in poultry and transmission of *Leucocytozoon neavei* and *Leucocytozoon schoutedeni* was investigated by Fallis *et al.* (1973a). Transmission of *Trypanosoma numidae* from *S. adersi* to birds was also experimentally demonstrated by Fallis *et al.* (1973b). Because of the nuisance value of that biting, and the transmission of haematozoans, *S. adersi* has been the subject of control proceedings (e.g., Car 1984, Myburgh and Neville 2010), using the organophosphate Temophos™ and *Bacillus thuringiensis israelensis* (Bti). Similarly, because of the possibility that *S. adersi* might be involved in vectoring *Onchocerca volvulus*, the causative agent of onchocerciasis, *S. adersi* was early involved in research related to that disease (e.g., Wanson 1950). *Simulium adersi* could be a potential vector of *O. volvulus* (Wegesa 1970) and is still considered so (e.g., Lamontellerie 1963, Johnson *et al.* 1982, Roberts and Irving-Bell 1996).

Biogeography

There has been much written about biota of hot-spot islands, in particular that of Hawai'i (e.g., Wagner and Funk 1995; Losos and Ricklefs 2010). A parsimonious explanation for insect biota of such islands is by wind dispersal and this is the explanation suggested for Simuliidae on islands in Polynesia, and the Gulf of Guinea. (e.g., Craig 2003, Mustapha *et al.* 2006). For the Comoros, wind patterns could indicate an origin from the African mainland. From October to April there is a wet season (Kashkasi) with predominantly strong, consistent north to northwesterly monsoon winds off the Indian Ocean. A dryer season (Kusi) is from May to September with less intense southerly winds.

Given that the Comoro islands are situated essentially midway between Mozambique on the African mainland and northern Madagascar (Fig. 1), such wind dispersal out of Africa to the west would not be unreasonable, but *S. adersi* occurs in Madagascar (Pilaka and Elouard 1999) and that cannot be ignored as the possible source population. Furthermore if presence of *S. (Xenosimulium) imerinae* on Mohéli (Adler and Crosskey 2013; Crosskey 2012) can be confirmed, such would indicate that origin of Comoro simuliids was more likely that of Madagascar. The subgenus *Xenosimulium* is endemic to Madagascar (Adler and Crosskey 2013).

Simulium adersi is widespread in Madagascar (Pilaka and Elouard 1999). While Elouard and Pilaka (2001; their Fig. b) provide keys and distribution maps of Madagascan simuliids and list some 27 species from the island, detailed description of *S. adersi* from there is not yet available, so resolving the question of origin of the Mayotte *S. adersi* will require that examination. With *S. adersi* on both Mayotte and Anjouan, an expectation might be that the two simuliid faunas would be closely related. It could be though, that the islands were colonized from separate sources, or dispersal events (see below). Nothing, however, is known about long range dispersal ability of this species.

Other species known for Comoro islands (Crosskey 2012) only partially help with historical biogeography of simuliids of the archipelago. *Simulium ruficorne* is markedly widespread in the region, occurring in Africa, the Comoros, Madagascar, and elsewhere, so gives no indication of origin. However, *Simulium dentulosum*, widespread in Africa is apparently absent from Madagascar (Elouard and Pilaka 2001), so this indicates dispersal from the west to Anjouan, at least for that species.

The Comoro appears typical of hot-spot island arrays. Geologically, the western island of Grand Comore is the youngest and still is volcanically active at Karthala volcano; ages increase eastwards through Mohéli, Anjouan, with Mayotte the oldest island. The lineage appears to have been formed as the Somali Plate drifted over a magma hot spot at *ca.* 50–70 mm/ yr. (Hajash and Armstrong 1972; Emerick and Duncan 1982). They estimated for Mayotte that shield building began 5.4 million years ago, with post erosional magma from 3.8–2.4 million year ago and then later flows at 1.5 million. Anjouan had only one date known and that was for 1.2 million years ago. Mohéli commenced shield building at 2.8 million years ago, with other flows at 1.9–1.6 million and more recently at 0.8–0.7. Shield-building of Grand Comore started merely 0.1 million years ago.

Mayotte appears to have followed the basic formation pattern known for Polynesian hot spot islands (Duncan and McDougall 1976; Duncan *et al.* 1994; Craig 2003), where, following shield-building volcanics, erosion allows further magma eruptions, often at regular intervals. Later there can be 'rejuvenating flows' of magma, but eventually the island becomes submerged and forms a guyot. In the Nosy region, northwestern Madagascar, volcanics are dated at 10 million years old. Bathymetry shows flat-topped submerged sea-mountains (guyots), the Banc du Geysier, between the Nosy region (NW Madagascar) and Mayotte (Taiwan Ocean Research Institute URL—<http://cmtt.tori.org.tw/>)—consistent with islands forming prior to that of Mayotte, which as such may have provided stepping stones for biota to reach the present Comoro islands.

However, Nougier *et al.* (1986), in a detailed review of geochronology of the archipelago suggest that Mayotte was *ca.* 8 million years of age, with Anjouan 11.1–3.9 mya, Moheil 5.0–3.2 mya, and Grande Comore perhaps 0.01–0.13 mya. They also question the hot spot hypothesis for formation of the array of islands; suggesting instead that volcanism of the Comoros was controlled by old and deep lithospheric fractures that have been reactivated at different times.

Perhaps pertinent to origin of simuliids on Comoro islands is an in-depth study of dispersal of frogs in the Indian Ocean region and in particular those of Mayotte (Vences *et al.* 2003). These frogs require fresh water. Phylogenetic analysis involving calibration from geological, morphological and molecular data indicates that a *Boophilis* and a *Mantidactylus* species, found only on Mayotte, dispersed from Madagascar in independent transmarine events less than 8.7 my ago. For simuliids an expectation might be an age less than that, since permanent running water takes time to develop (Craig 2003).

With the rates of divergence now known for simuliids on Tahiti (Joy *et al.* 2007) and New Zealand (Craig *et al.* 2012), the probable ages of Mayotte give ample time for allopatric divergence of *S. adersi* from its precursor, either from the African mainland, or Madagascar.

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References

- Adler, P.H. & Crosskey R.W. (2012) World Blackflies (Diptera: Simuliidae): a comprehensive revision of the taxonomic and geographic inventory. Available from <http://www.clemson.edu/cafls/departments/esps/biomia/pdfs/blackflyinventory.pdf> (accessed 4 March 2013).
- Adler, P.H. & Crosskey, R.W. (2013) *World blackflies (Diptera: Simuliidae): a comprehensive revision of the taxonomic and geographical inventory [2013]*. 120 pp. Available from <http://www.clemson.edu/cafls/departments/esps/biomia/pdfs/blackflyinventory1.pdf> (accessed 4 March 2013)
- Adler, P.H., Currie, D.C. & Wood, D.M. (2004) *The Black Flies (Simuliidae) of North America*. Cornell University Press, Cornell, 941 pp.
- Balay, G. (1964) Observations sur l'oviposition de *Simulium damnosum* Theobald et *Simulium adersi* Pomeroy (Diptera, Simuliidae) dan l'est de la Haute-Volta. *Bulletin de la Société de Pathologie exotique*, 56, 588–611.
- Begemann, G.J. (1980) Laboratory studies on the biology of *Simulium nigritarse* Coquillett and *Simulium adersi* Pomeroy (Diptera: Simuliidae). *Onderstepoort Journal of Veterinary Research*, 47, 203–211.
- Bequaert, J.C. (1939) Part IV: The Black-Flies, or Simuliidae, of the Belgian Congo *American Journal of Tropical Medicine and Hygiene*, s1–19, No 6 Suppl., 116–136.
- Bentinck, W. (1955) *The black flies of Japan and Korea*. 406th Medical General Laboratory, Tokyo, Japan, 56 pp.
- Car, M. (1984) Laboratory and field trials with two *Bacillus thuringiensis* var. *israelensis* products for *Simulium* (Diptera: Nematocera) control in a small polluted river in South Africa. *Onderstepoort Journal of Veterinary Research*, 51, 141–144.
- Craig, D.A. (2003) Geomorphology, development of running water habitats and evolution of black flies on Polynesian islands. *BioScience*, 53, 1079–1093.
[http://dx.doi.org/10.1641/0006-3568\(2003\)053\[1079:GDORWH\]2.0.CO;2](http://dx.doi.org/10.1641/0006-3568(2003)053[1079:GDORWH]2.0.CO;2)
- Craig, D.A. (2005) A chaetotaxy for cephalic sensilla in larval Simuliidae (Diptera). *Canadian Journal of Zoology*, 83, 344–357.
<http://dx.doi.org/10.1139/z05-023>
- Craig, D.A. & Crosby T.K. (2008) Gynandromorphs of New Zealand *Austrosimulium* spp. (Diptera: Simuliidae). *Zootaxa*, 1811, 57–68.
- Craig, D.A. & Cywinska, A. (2012) Molecular analysis of New Zealand *Austrosimulium* (Diptera: Simuliidae) species. In: Craig, D.A., Craig, R.E.G. Crosby, T.K. (2012): Simuliidae (Insecta: Diptera) Fauna of New Zealand, 68, pp. 60–65, 205–208, 298–301.
- Craig, D.A., Craig, R.E.G. & Crosby, T.K. (2012) Simuliidae (Insecta: Diptera). *Fauna of New Zealand*, 68, 1–336.
- Crosskey, R.W. (1960) A taxonomic study of the larvae of West African Simuliidae (Diptera: Nematocera) with comments on the morphology of the larval black-fly head. *Bulletin of the British Museum (Natural History)*, 10, 1–74.
- Crosskey, R.W. (1962) The identification of the larvae of African *Simulium*. *Bulletin of the World Health Organization*, 27, 483–489.
- Crosskey, R.W. (1969) A re-classification of the Simuliidae (Diptera) of Africa and its islands. *Bulletin of the British Museum (Natural History), Entomology*, Supplement 14, 1–195.
- Crosskey, R.W. (2012) Notes on simuliids in the Comoro Islands with particular reference to Anjouan. *British Simuliid Group Bulletin*, 37, 4–7.
- Crosskey, R.W. & Howard, T.M. (1997) *A new taxonomic and geographical inventory of world blackflies (Diptera: Simuliidae)*. The Natural History Museum, London, 144 pp.
- Crosskey, R.W. & Büttiker, W. (1982) Insects of Saudi Arabia. Diptera: Fam. Simuliidae. *Fauna of Saudi Arabia* 4: 398–446.
- Crosskey, R.W. & Davies, J. (2012) Who was ...? Honorific names: more mini-biographies. *British Simuliid Group Bulletin*, 37, 8–12.
- de Beer C.J. & Green, K.K. (2012) Survey of blackfly (Diptera: Simuliidae) annoyance levels and abundance along the Vaal and Orange Rivers, South Africa. *Journal of the South African Veterinary Association*, 83, 1–6.

- <http://dx.doi.org/10.4102/jsava.v83i1.5>
- de Meillon, B. (1930) On Ethiopian Simuliidae. *Bulletin of Entomological Research*, 21, 185–200.
<http://dx.doi.org/10.1017/S0007485300021714>
- de Moor, F. (2003) Chapter 5, Simuliidae. In: Day, J.A., Harrison A.D. & de Moor, I.J. (Eds.), *Guides to the Freshwater Invertebrates of Southern Africa. Vo. 9. Diptera. Water Research Commission, Report No. TT201/02*. Gezina, Pretoria, South Africa, pp 75–109.
- Duncan, R.A. & McDougall, I. (1976) Linear volcanism in French Polynesia. *Journal of Volcanology and Geothermal Research*, 1, 197–227.
[http://dx.doi.org/10.1016/0377-0273\(76\)90008-1](http://dx.doi.org/10.1016/0377-0273(76)90008-1)
- Duncan, R.A., Fisk, M.R., White, W.M. & Nielsen, R.L. (1994) Tahiti: Geochemical evolution of a French Polynesian volcano. *Journal of Geophysical Research*, 99, (B12), 24,341–24,357.
<http://dx.doi.org/10.1029/94JB00991>
- Emerick, C.M. & Duncan, R.A. (1982) Age progressive volcanism in the Comoros Archipelago, western Indian Ocean and implications for Somali plate tectonics. *Earth and Planetary Science Letters*, 60, 415–428.
[http://dx.doi.org/10.1016/0012-821X\(82\)90077-2](http://dx.doi.org/10.1016/0012-821X(82)90077-2)
- Elouard, J.M. (1978) Identification biométrique des stade larvaires de *S. damnosum* s.l. et de *S. adersi* (Diptera: Simuliidae). *Tropenmedizin und Parasitologie*, 29, 183–187.
- Elouard, J.M. & Pilaka, T. (2001) Diptères Simuliidae. In Elouard, J.M., & Gibon F.M. (Eds.), *Biodiversité et biotypologie des eaux continentales de Madagascar*. Institut de Recherche pour Développement. Montpellier, pp. 213–226.
- Elsen, P. & Fain, A. (1981) Description de la larve et de la femelle *Simulium (Meilloniellum) urundiense* Fain 1950 comparaison avec *S. (Meilloniellum) hirsutum* Pomeroy, 1922. *Revue de Zoologie Africaine*, 95, 618–622.
- Esson, J., Flower, M.F.J., Strong, D.F., Upton, G.J. & Wadsworth, W.J. (1970) Geology of the Comoros Archipelago, Western Indian Ocean. *Geological Magazine*, 107, 549–557.
- Fain, A. (1950) Simulies nouvelles du Ruanda Urundi. *Revue de Zoologie et de Botanique Africaine*, 43, 101–123.
- Fallis, A.M. & Raybould, J.N. (1975) Response of two African Simuliids to silhouettes and carbon dioxide. *Journal of Medical Entomology*, 12, 349–351.
- Fallis, A.M., Jacobson, R.L. & Raybould, J.N. (1973a) Experimental Transmission of *Trypanosoma numidae* Wenyon to Guinea Fowl and Chickens in Tanzania. *Journal of Eukaryotic Microbiology*, 20, 436–437.
<http://dx.doi.org/10.1111/j.1550-7408.1973.tb00917.x>
- Fallis, A.M., Jacobson, R.L. & Raybould, J.N. (1973b) Haematozoa in domestic chickens and guinea fowl in Tanzania and Transmission of *Leucocytozoon neavei* and *Leucocytozoon schoutedeni*. *Journal of Eukaryotic Microbiology*, 20, 438–442.
<http://dx.doi.org/10.1111/j.1550-7408.1973.tb00918.x>
- Freeman, P. & de Meillon, B. (1953) *Simuliidae of the Ethiopian region*. British Museum Natural History, London, 224 pp.
- Gibbins, E.G. (1934) Further studies on Ethiopian Simuliidae. *Transaction of the Royal Entomological Society of London*, 82, 51–97.
<http://dx.doi.org/10.1111/j.1365-2311.1934.tb00028.x>
- Gibbins, E.G. (1936) Uganda Simuliidae. *Transaction of the Royal Entomological Society of London*, 85, 217–242.
<http://dx.doi.org/10.1111/j.1365-2311.1936.tb00422.x>
- Gibbins, E.G. & Loewenthal, L.J.A. (1933) Cutaneous onchocerciasis in a *Simulium damnosum*-infested region of Uganda. *Annals of Tropical Medicine and Parasitology*, 27, 489–496.
- Gillet, J. & Lebled, B. (1959) Observation sur *Simulium medusaeforme* var. *hargreavesi* (Gibbins) et *Simulium adersi* (Pomeroy) faits a Bukavu-Kivu, Congo belge. *Annales de la Société belge de médecine*, 39, 823–830.
- Grenier, P. & Grjebine, A. (1959) Remarques morphologique et biologiques concernent les “Mouka-Fouhi” (*Simulium neireti* Roubaud, *S. imerinae* Roubaud) de Madagascar et *S. ambositrae* nom. nov. *Bulletin de la Société de Pathologie exotique*, 51, 981–991. (1958)
- Gupta, J. & van der Zaag, P. (2008) Interbasin water transfers and integrated water resources management: Where engineering, science and politics interlock. *Physics and Chemistry of the Earth, Parts A/B/C* 33, Issues 1–2, 28–40.
<http://dx.doi.org/10.1016/j.pce.2007.04.003>
- Hajash, A. & Armstrong, R.L. (1972) Paleomagnetic and radiometric evidence for the age of the Comoros Islands, west central Indian Ocean. *Earth and Planetary Science Letters*, 16, 231–236.
[http://dx.doi.org/10.1016/0012-821X\(72\)90195-1](http://dx.doi.org/10.1016/0012-821X(72)90195-1)
- Jamback, H.A. (1970) *Caudospora* and *Weiseria*, two genera of microsporidia parasitic in blackflies. *Journal of Invertebrate Pathology*, 16, 3–13.
[http://dx.doi.org/10.1016/0022-2011\(70\)90200-4](http://dx.doi.org/10.1016/0022-2011(70)90200-4)
- Johanson, K.A. & Mary, N. (2009) Description of three new caddisfly species from Mayotte Island, Comoros Archipelago (Insecta: Trichoptera). *Zootaxa*, 2089, 1–9.
- Johnson, C.G., Crosskey, R.W. & Davies, J.B. (1982) Species composition and cyclical changes in numbers of savanna blackflies (Diptera: Simuliidae) caught by suction traps in the Onchocerciasis Control Programme area of West Africa. *Bulletin of Entomological Research*, 72, 39–63.
<http://dx.doi.org/10.1017/S0007485300050276>

- Joy, D.A., Craig, D.A. & Conn, J.E. (2007) Genetic variation tracks ecological segregation in populations of Pacific island black flies. *Hereditary*, 99, 452–459.
<http://dx.doi.org/10.1038/sj.hdy.6801023>
- Lamontellerie, M. (1963) Observations sur *Simulium adersi* Pomeroy en zone de savane seche (Region de Garango, Haute-Volta). *Bulletin de l'Institut Français d'Afrique Noire*, (A) 25, 467.
- Lévêque, C. (1989) The use of insecticides in the onchocerciasis control programme and aquatic monitoring in West Africa. In: Bourdeau, P., Haines, J.A., Klein, W. & Krishna Murti, C.R. (Eds.), *Ecotoxicology and Climate*. Wiley & Sons Ltd., pp. 317–335.
- Losos, J.B. & Ricklefs, R.E. (2010) *The theory of island biogeography revisited*. Princeton University Press, New Jersey, 476 pp.
- Mbah, C.E., Nock, I.H. & Vajime, C.G. (2003) Laboratory rearing and distribution of the breeding sites of *Simulium* species in Kaduna State. *Journal of Aquatic Sciences*, 18, 131–139.
<http://dx.doi.org/10.4314/jas.v18i2.19955>
- Myburgh, E. & Nevill, E.M. (2010) Review of blackfly (Diptera: Simuliidae) control in South Africa. *Onderstepoort Journal of Veterinary Research*, 70, 307–316.
<http://dx.doi.org/10.4102/ojvr.v70i4.295>
- Mustapha, M., McCall, P.J., Cheke, R.A. & Post R.J. (2006) The blackflies (Diptera: Simuliidae) of Bioko (Republic of Equatorial Guinea) and the Gulf of Guinea with a description of the larvae of the 'Pomeroy' form of *Simulium cervicornutum*. *Systematic Entomology*, 34, 611–620.
<http://dx.doi.org/10.1111/j.1365-3113.2006.00330.x>
- Nougier, J., Cantagrel, J.M. & Karche, J.P. (1986) The Comores archipelago in the western Indian Ocean: volcanology, geochronology and geodynamic setting. *Journal of African Earth Sciences*, 5, 135–145.
[http://dx.doi.org/10.1016/0899-5362\(86\)90003-5](http://dx.doi.org/10.1016/0899-5362(86)90003-5)
- O'Keeffe, J.H. & de Moor, F.C. (1988) Changes in the physico-chemistry and benthic invertebrates of the Great Fish River, South Africa, following an interbasin transfer of water. *Regulated Rivers: Research & Management*, 2, 39–55.
<http://dx.doi.org/10.1002/rrr.3450020105>
- Palmer, R.W. (1991) Descriptions of the larvae of seven species of blackflies (Diptera: Simuliidae) from southern Africa, and a regional checklist of the family. *Journal of the Entomological Society of Africa*, 54, 197–219.
- Palmer, R.W. & Craig, D.A. (2000) An ecological classification of primary labral fans of filter-feeding black fly (Diptera: Simuliidae) larvae. *Canadian Journal of Zoology*, 78, 199–218.
<http://dx.doi.org/10.1139/cjz-78-2-199>
- Palmer, R.W. & de Moor, F.C. (1998) Annotated records of blackfly (Diptera: Simuliidae) distribution in southern Africa. *African Entomology*, 6, 223–251.
- Palmer, C.G., Maart, B., Palmer, A.R. & O'Keeffe, J.H. (1996) An assessment of macroinvertebrate functional feeding groups as water quality indicators in the Buffalo River, eastern Cape Province, South Africa. *Hydrobiologia*, 318, 153–164.
<http://dx.doi.org/10.1007/BF00016677>
- Philippon, B. (1981) Simuliidae. In: Durand, J.R. & Lévêque, C. (Eds.). *Flore et Faune aquatiques de l'Afrique sahélo-soudanaise*. ORSTOM Press, Paris, pp 643–659.
- Pilaka, T. & Elouard, J.M. (1999) Chapter 8. Aquatic biodiversity of Madagascar: *Simulium* (Diptera: Simuliidae) from the reserve naturelle intégrale d' Andohahela and surrounding areas. In: Goodman S.M. (Ed.), *A floral and faunal inventory of the reserve naturelle intégrale d' Andohahela, Madagascar: with reference to elevational variation*. Fieldian: Zoology, N.S. 94. Field Museum of Natural History, Chicago, pp. 125–128.
http://horizon.documentation.ird.fr/exl-doc/pleins_textes/pleins_textes_7/b_fdi_53-54/010021242.pdf
- Pomeroy A.W.J. (1922) New species of African Simuliidae and further studies of the early stages. *Bulletin of Entomological Research*, 12, 457–463.
<http://dx.doi.org/10.1017/S0007485300045107>
- Rivers-Moore, N.A., de Moor, F.C., Morris, C. & O'Keeffe, J. (2007) Effect of flow variability modification and hydraulics on invertebrate communities in the great fish river (Eastern Cape province, South Africa), with particular reference to critical hydraulic thresholds limiting larval densities of *Simulium chutteri* Lewis (Diptera, Simuliidae). *River Research and Applications*, 23, 201–222
<http://dx.doi.org/10.1002/rra.976>
- Roberts, D.M. & Irving-Bell, R.J. (1996) Effect of weather conditions on the flight activity of Nigerian blackflies (Diptera: Simuliidae). *Medical and Veterinary Entomology*, 10, 137–144.
<http://dx.doi.org/10.1111/j.1365-2915.1996.tb00719.x>
- Rubtsov, I.A. (1962) Genera of buffalo-gnats (Fam. Simuliidae) in the fauna of the Ethiopian Region. *Zoologicheskyy Zhurnal*, 41, 10, 1488–1502. (in Russian)
- Starmühler, F. (1976) Contribution to the knowledge of the freshwater-fauna of the Isle of Anjouan (Comores). *Cahiers O.R.S.T.O.M. (Série Hydrobiologique)*, 10, 255–265.
- Starmühler, F. (1979). Results of the Austrian Hydrobiological Mission, 1974 to the Seychelles-, Comoros- and Mascarene archipelagos: Part I: Preliminary Report, Introduction, Methods, General situation of the Islands with description of the stations and general comments on the distribution of the fauna in the running waters of the islands. *Annalen des*

Naturhistorisches Museum in Wien, 82, 621–742.

- Takaoka, H. & Davies, D.M. (1995) *The black flies (Diptera: Simuliidae) of West Malaysia*. Kyushu University Press, Fukuoka, 175 pp.
- Travis, B.V., Mendoza, C.E. & Labadan, R.M. (1967) B. Black Flies. In: *Arthropods of medical importance in Africa. Part 2. Data on arthropods other than mosquitoes*. United States Army Natick Laboratory Technical report 67-55-ES, pp. 359–396.
- Vences, M., Vieites, D.R., Glaw, F., Brinkmann, H., Kosuch, J., Veith, M. & Meyer, A. (2003) Multiple overseas dispersal in amphibians. *Proceedings of the Royal Society B*, 270, 2435–2445.
<http://dx.doi.org/10.1098/rspb.2003.2516>
- Wagner, W.L. & Funk, V.A. (1995) *Hawaiian biogeography. Evolution on a hot spot archipelago*. Smithsonian Institution Press, Washington, DC, 467 pp.
- Wanson, M. (1950) Contribution à l' étude de l'Onchocercose africaine humaine (Problèmes de prophylaxie à Leopoldville.) *Annales de la Société belge de médecine tropicale*, 30, 667–863.
- Wegesa, P. (1970) *Simulium nyalalandicum* (Amani form) and *S. adersi*, two new potential vectors of *Onchocerca volvulus* in the Eastern Usam-baras, North-Eastern Tanzania. *East African Medical Journal*, 47, 364–367.
- Zhang, Y. (2006) Balancing food availability and hydrodynamic constrain: phenotypic plasticity and growth in *Simulium noelleri* blackfly larvae. *Oecologia*, 147, 39–46
<http://dx.doi.org/10.1007/s00442-005-0243-9>