

Revision of the southern African genus *Stuckenbergomyia* Smith, 1971 (Diptera, Empidoidea) and proposal of a new subfamily

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Abstract

The genus *Stuckenbergomyia* Smith is revised with the description of a new species from Namibia (*S. namibiensis* **sp. nov.**) and an undescribed species based on females from Western Cape Province of South Africa. The genus is fully illustrated and its phylogenetic relationships within the Hybotidae are discussed with the proposal of a new subfamily, *Stuckenbergomyiinae* **subfam. nov.**

Keywords

Mozambique, Namibia, South Africa, Brandberg, new species, new subfamily

Introduction

The genus *Stuckenbergomyia* Smith, 1971 is an odd genus of the family Hybotidae (Diptera, Empidoidea), characterised by a short spur vein arising from or near cell cua (anterior cubital). The genus is endemic to southern Africa, recorded from Mozambique, South Africa, Zimbabwe and now Namibia. Originally assigned to the Ocydromiinae, the genus is currently placed as *incertae sedis* in the Hybotidae (Sinclair 2003; Sinclair and Cumming 2006; Sinclair and Cumming 2017). Species of *Stuckenbergomyia* are believed to occur in dry montane grasslands (Smith 1969) and the form of the mouthparts suggests that they are flower visitors (Sinclair and Cumming 2017).

Aside from two species of *Ocydromia* Meigen, 1820 (Ocydromiinae) recorded from East Africa and South Africa, *Stuckenbergomyia* is the only other Afrotropical genus of Hybotidae not assigned to the subfamilies Tachydromiinae and Hybotinae (Smith 1969; Sinclair and Cumming 2017). The discovery of newly collected and better preserved specimens initiated this study and facilitated re-examination of the genus and subfamily assignment.

Material and methods

This study is based on material loaned from or deposited in the following institutions: Canadian National Collection of Insects, Ottawa, Canada (CNC); KwaZulu-Natal Museum, Pietermaritzburg, South Africa (NMSA); National Museum of Namibia, Windhoek, Namibia (NMNW).

Terminology used for adult structures follows those of Cumming and Wood (2017). Label data for primary types are presented exactly as they appear. Data are listed from the top downwards on the staging pin, with data from each label enclosed in quotation marks; lines are delimited by a forward slash mark. Additional information is included in square brackets. The repository of each type is given in parentheses. Secondary type data are abridged and listed alphabetically. Photographs were taken with a Leica camera model DFC5400 using Leica Application Suite X. Photo montages were created using Zerene Stacker 1.04. The distribution map was created with Simplemappr (Shorthouse 2010).

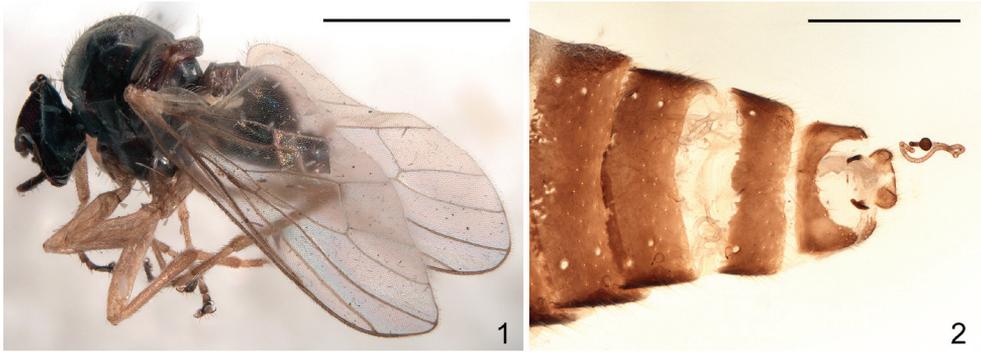
Taxonomy

Stuckenbergomyia Smith, 1971

Stuckenbergia Smith, 1969: 125 [preoccupied by *Stuckenbergia* Tchernychev, 1898: 24 (fossil Porifera)]. Type species: *Stuckenbergia tumbinensis* Smith (original designation). *Stuckenbergomyia* Smith, 1971: 699. Replacement name for *Stuckenbergia* Tchernychev. Other references: Sinclair and Cumming 2006: 77 (classification).

Diagnosis. The genus (as in Figs 1, 10, 20) is characterised by an elongate postpedicel, stout antennal stylus, three complete wing veins from cell dm (discal medial) and a short spur vein, that extends from or near cell cua.

Redescription. *Head:* Holoptic with enlarged facets on upper two-thirds or di-choptic (facets not enlarged); eyes bare (ommatrichia absent). Face nearly completely membranous, U-shaped to base of antennal sockets. Ocellar triangle elevated in hol-optic species; pair of ocellar setae very short, indistinguishable from other setae on tri-angle. Antenna inserted at middle of eye height; scape and pedicel subequal in length;



Figures 1, 2. *Stuckenbergomyia namibiensis* sp. nov. **1** Holotype habitus, lateral view **2** Female abdomen and spermatheca, dorsal view. Scale bars: 1.0 mm (**1**); 0.5 mm (**2**).

scape bare, pedicel with cirlet of subapical setulae; postpedicel elongate, tapered, 2–3× length of scape and pedicel combined; two-articled stylus, with short, apical peg-like receptor. Proboscis (as in Fig. 19) projected forwards, about as long as head. Palpus straight, strap-like; bearing numerous setulae, held obliquely to proboscis, with narrow palpifer (Fig. 10); lacinia absent. Labrum slender, straight without pair of apical epipharyngeal blades. Hypopharynx straight, slender, subequal in length to labrum. Labellum well developed, with pseudotracheae.

Thorax: Moderately to strongly arched. Acrostichals biserial or 4-serial; dorsocentral setae uniserial and better developed posteriorly; numerous postpronotal and notopleural setae; 1 postalar seta; 2 or more pairs of marginal scutellar setae. Prosternum separate; laterotergite bare.

Legs: Lacking modified setae and processes; base of fore tibia with posteroventral gland (Fig. 12). Acropod with broad pulvillus.

Wing (Length 2.5–3.2 mm) (as in Fig. 11): Broad with often well-developed anal lobe; alula developed or undeveloped. Basal costal seta present; pterostigma narrow, at apex of cell sc (subcostal). Costa strongly reduced beyond R_{4+5} or M_1 ; Sc incomplete, reduced at pterostigma; R_{4+5} unbranched terminating at wing apex; cell dm present; M_{1+2} branched, complete; M_4 complete; short spur vein from apex of cells bm (basal medial), cua or between basal cells; CuA+CuP complete, fading towards wing margin.

Abdomen: Sclerites well developed, bearing scattered slender setae; tergite 8 slender medially, strap-like, symmetrical. Segment 8 rotated nearly 45° to right.

Male terminalia: Symmetrical, rotated 45° to right; held apically, upright or arched anteriorly over abdomen. Cercus thinly sclerotised, weakly pigmented, clothed in slender setae; hypoproct broad with fine setae on posterior margin. Epandrial lamellae narrowly joined; surstylus undifferentiated, subapical or broadly articulated. Hypandrium trough-shaped, without apical lobes; postgonite sickle-shaped, slender, closely associated with phallus; ventral apodeme broad, plate-like. Ejaculatory apodeme elongate, narrow. Phallus mostly membranous, with expanded apex.

Female. Similar to male, dichoptic, eye facets not enlarged. Apex of abdomen somewhat truncate with segment 8 partially retracted into segment 7. Female terminalia (based on *S. namibiensis*) (Figs 2, 6): Cercus flattened, quadrate and broad. Epiproct divided into pair of narrow, widely separated sclerites. Hypoproct broad, quadrate. Spermathecal receptacle small, spherical, darkly sclerotised; duct consisting of sclerotised rings, extending 2–3 abdominal segments (Figs 2, 7).

Distribution. Described species of *Stuckenbergomyia* are recorded from Mozambique, Namibia and South Africa. An undescribed female (in Natural History Museum, London), representing an additional species, is recorded from Zimbabwe (Fig. 22) (Umtali [now Mutare], Vumba, 19°05'S, 32°45'E), but the specimen is said to be in poor condition (Smith 1969) and was not examined in the present study.

Remarks. *Stuckenbergomyia* can be identified by using the key to genera in Sinclair and Cumming (2017).

Specimens have only been collected by Malaise traps, yellow pans and light traps and there are no direct observations on habits. Adult mouthpart morphology (i.e. angle of proboscis; absence of epipharyngeal blades) and the observation of pollen grains in the dissected male and female abdomens of *S. namibiensis*, provides evidence that *Stuckenbergomyia* visits flowers and feeds on pollen.

***Stuckenbergomyia namibiensis* sp. nov.**

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Figs 1–7, 22

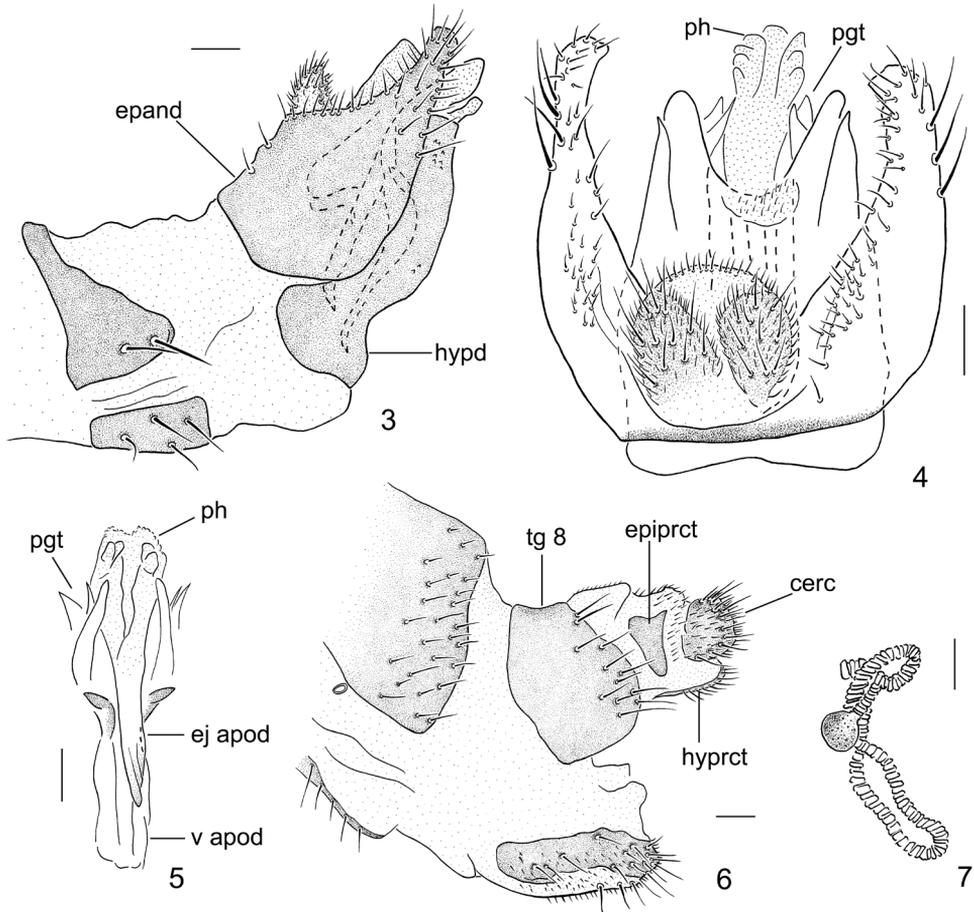
Etymology. The specific epithet refers to the country of origin, Namibia.

Diagnosis. This species is characterised by the pair of dark vittae between acrostichals and dorsocentrals; broad wings, yellow legs and 5–7 pairs of long scutellar setae; male terminalia: nearly symmetrical, held at apex of abdomen, surstyli not clearly differentiated.

Description. Head: Holoptic with enlarged facets on upper two-thirds. Antenna with scape and pedicel paler than dark brown postpedicel; postpedicel length less than 4× basal width; stylus cylindrical, shorter than basal width of postpedicel; apical mechanoreceptor one-third length of stylus.

Thorax: Mostly brown with grey pruinescence. Scutum with pair of dark vittae between acrostichals and dorsocentral rows (viewed anteriorly); anterior margin of postpronotal lobe shiny, lacking pruinescence. Acrostichals 4-serial anteriorly, biserial anterior to prescutellar depression; dorsocentral setae biserial and short anteriorly, longer and uniserial at prescutellar depression; postpronotal setae numerous, short and pale; numerous pale presutural and postsutural supra-alar setae; 3–4 short pale notopleural setae; 1 pale postalar seta; 5–7 pairs of pale scutellar setae, slightly longer than length of scutellum. Proepisternum with a few short, pale setae.

Legs: Yellow, including at least apical half of coxae; apical tarsomeres increasingly darker.



Figures 3–7. *Stuckenbergomyia namibiensis* sp. nov., male and female terminalia. **3** Male, lateral view **4** Male, dorsal view **5** Phallus, dorsal view **6** Female, lateral view **7** Spermatheca, dorsal view. Abbreviations: ej apod – ejaculatory apodeme, epand – epandrium, epiprct – epiproct, hypd – hypandrium, hyprct – hypoproct, pgt – postgonite, ph – phallus, tg – tergite, v apod – ventral apodeme. Scale bars: 0.1 mm.

Wing (2.5–3 mm): Broad, anal lobe nearly right-angled; alula well-developed. Costal margin at humeral crossvein expanded, costal cell broad; costa gradually reduced beyond R_{4+5} ; spur vein arising between cells *bm* and *cua* or from cell *cua*. Halter knob pale.

Abdomen: Dark brown, concolorous with thorax; setae pale; sternites paler than tergites; tergite 8 narrow medially, expanded laterally, bearing pair of setae.

Male terminalia (Figs 3–5): Nearly symmetrical, held at apex of abdomen, not arched over abdomen; rotated 45° to right. Cercus thinly sclerotised, weakly pigmented, clothed in slender setae; hypoproct broad with fine setae on posterior margin. Epandrial lamellae narrowly joined anteriorly; narrowed and tapered on posterior half;

surstylus undifferentiated, apex with flattened dorsal margin. Postgonite with slender, sickle-shaped apex; ventral apodeme broad, rectangular. Ejaculatory apodeme elongate, apex pointed. Phallus mostly membranous, expanded apically.

Female. Similar to male, except dichoptic; frons broad with thick grey pruinescence; abdomen truncate apically (Fig. 6) (see generic description).

Type locality. NAMIBIA: Brandberg, Mason Shelter, 21°04'42"S 14°35'33"E (Fig. 22).

Type material. Holotype ♂, labelled: "Namibia: BRANDBERG / Mason Shelter / 21°04'42"S 14°35'33"E / 05–14.iii.2002, 1750 m [elev.] / A.H. Kirk-Spriggs / light trap sample"; "HOLOTYPE / *Stuckenbergomyia* / *namibiensis* / Sinclair [red label]" (NMNW) (Fig. 1).

Paratypes: NAMIBIA: 1♂, 1♀, same data as holotype (CNC); 3♀, same data as holotype (NMNW).

Remarks. This species was not included in the original list of Empidoidea from the Brandberg Massif (Sinclair 2000), because these specimens were collected subsequent to the initial surveys.

Stuckenbergomyia secunda (Smith, 1969)

Figs 8–14, 19, 22

Stuckenbergia secunda Smith, 1969: 128. Type locality: Pietermaritzburg, KwaZulu-Natal, South Africa.

Stuckenbergomyia secunda: Smith, 1980: 436 (catalogue).

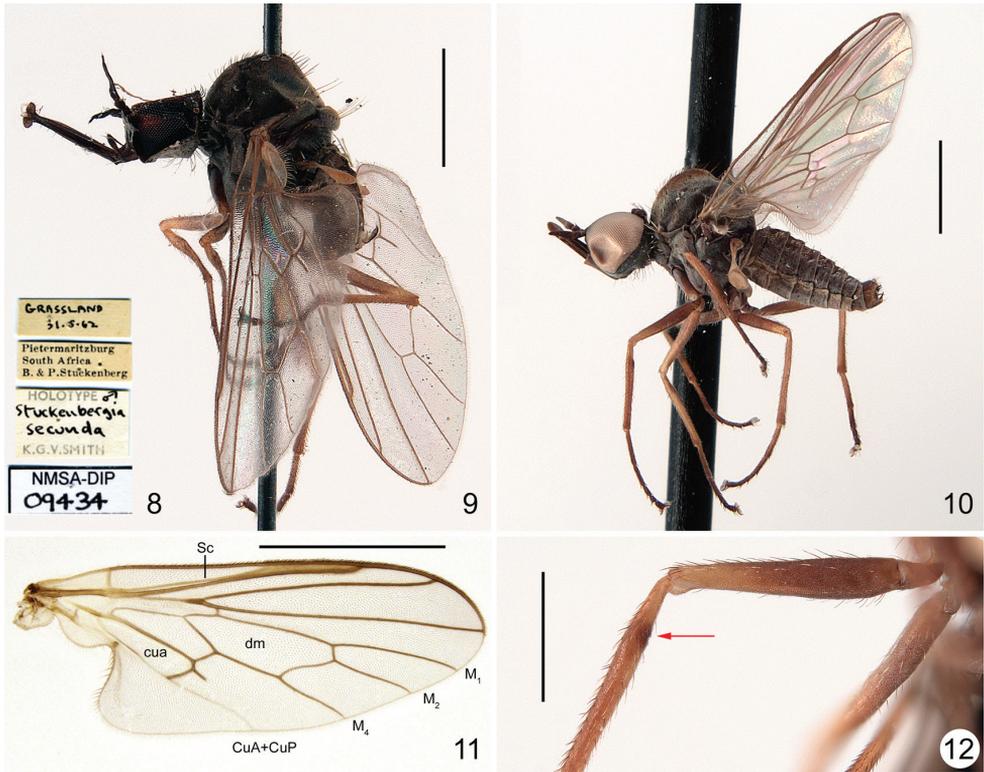
Diagnosis. This species is characterised by the faint brown vittae beneath acrostichals and dorsocentrals; broad wings and 4 pairs of long scutellar setae; male terminalia: symmetrical, held at apex of abdomen, surstyli broadly articulated lobes.

Redescription. Head: Holoptic with enlarged facets on upper two-thirds. Antenna dark brown; postpedicel length ca. 4× basal width; stylus cylindrical, about as long as basal width of postpedicel; apical mechanoreceptor one-third length of stylus.

Thorax: Mostly dark greyish pruinescence. Scutum with brownish vittae below acrostichals and dorsocentral rows (viewed anteriorly); anterior margin of postpronotal lobe shiny, lacking pruinescence. Acrostichals 4-serial anteriorly, biserial anterior to prescutellar depression; dorsocentral setae biserial and short anteriorly, longer, darker and uniserial at prescutellar depression; postpronotal setae numerous, long and pale; numerous pale presutural and postsutural supra-alar setae; 4 pale notopleural setae; 1 pale postalar seta; 4 pairs of pale scutellar setae, longer than length of scutellum. Proepisternum with several long, pale setae.

Legs: Mostly brown, with apex of femora and base of tibiae yellowish (Fig. 10).

Wing (2.7–3 mm) (Fig. 11): Broad, anal lobe nearly right-angled; alula well-developed. Costal margin at humeral crossvein expanded, costal cell broad; costa strongly reduced beyond R₄₊₅; spur vein arising from cell cua. Halter knob pale.



Figures 8–12. *Stuckenbergomyia secunda* (Smith). **8** Holotype labels (upper label is reverse side of second label) **9** Holotype habitus, lateral view **10** Male habitus, Louwsberg specimen **11** Wing **12** Male foreleg, arrow pointing to fore tibial gland, posterior view. Abbreviations: cua – anterior cubital cell, CuA+CuP – anterior branch of cubital vein + posterior branch of cubital vein, dm – discal medial cell, M_1 – first branch of media, M_2 – second branch of media, M_4 – fourth branch of media, Sc – subcostal vein. Scale bars: 1.0 mm (**8–11**); 0.5 (**12**).

Abdomen: Slightly paler than thorax; setae pale; sternites paler than tergites; tergite 8 narrow medially, expanded laterally, bearing pair of setae.

Male terminalia (Figs 13, 14): Symmetrical, held at apex of abdomen, directed dorsally, not arched over abdomen; rotated 45° to right. Cercus quadrate, thinly sclerotised, weakly pigmented, clothed in slender setae; hypoproct broad with fine setae on posterior margin, arched medially. Epandrial lamellae very narrowly joined; surstylus broadly articulated with sickle-shaped, arched posterior process. Hypandrium with pair of setae; postgonite consisting of 2 pairs of sickle-shaped, slender, processes; ventral apodeme broad, plate-like. Phallus and ejaculatory apodeme not examined.

Female. Unknown.

Type locality. SOUTH AFRICA, Pietermaritzburg [29°36'S, 30°22'E] (Fig. 22).

Type material examined. Holotype ♂, labelled (Fig. 8): “Pietermaritzburg / South Africa / B. & P. Stuckenberg”; “grassland/ 31.5.62 [underside of label]”;

“HOLOTYPE ♂ / *Stuckenbergia* / *secunda* / K.G.V. SMITH”; “NMSA-DIP-09434” (NMSA) [dissected, genitalia mounted on microslide beneath specimen] (Fig. 9).

Additional material examined. SOUTH AFRICA: 2♂ [NMSA-DIP 092039, NMSA-DIP 092040], KwaZulu-Natal: Louwsberg, Sanyati Farm, 1090 m elev., 27°34'90"S, 31°17.9'E, 11–13.vii.2006, YPT, M. Mostovski, leg (NMSA).

***Stuckenbergomyia tumbinensis* (Smith, 1969)**

Figs 15–18, 22

Stuckenbergia tumbinensis Smith, 1969: 126. Type locality: Tumbine Mountains, Mozambique.

Stuckenbergomyia tumbinensis: Smith, 1980: 436 (catalogue).

Diagnosis. This species is characterised by the biserial acrostichals and uniserial dorso-central setae; narrow wings with undeveloped alula and 2 pairs of long scutellar setae; male terminalia: very large, symmetrical, held erect over right side of abdomen.

Redescription. Head: Dichoptic with facets not enlarged. Antenna with scape and pedicel paler than dark brown postpedicel; postpedicel length slightly longer than 4× basal width; stylus cylindrical, about as long as basal width of postpedicel; apical mechanoreceptor one-half length of stylus.

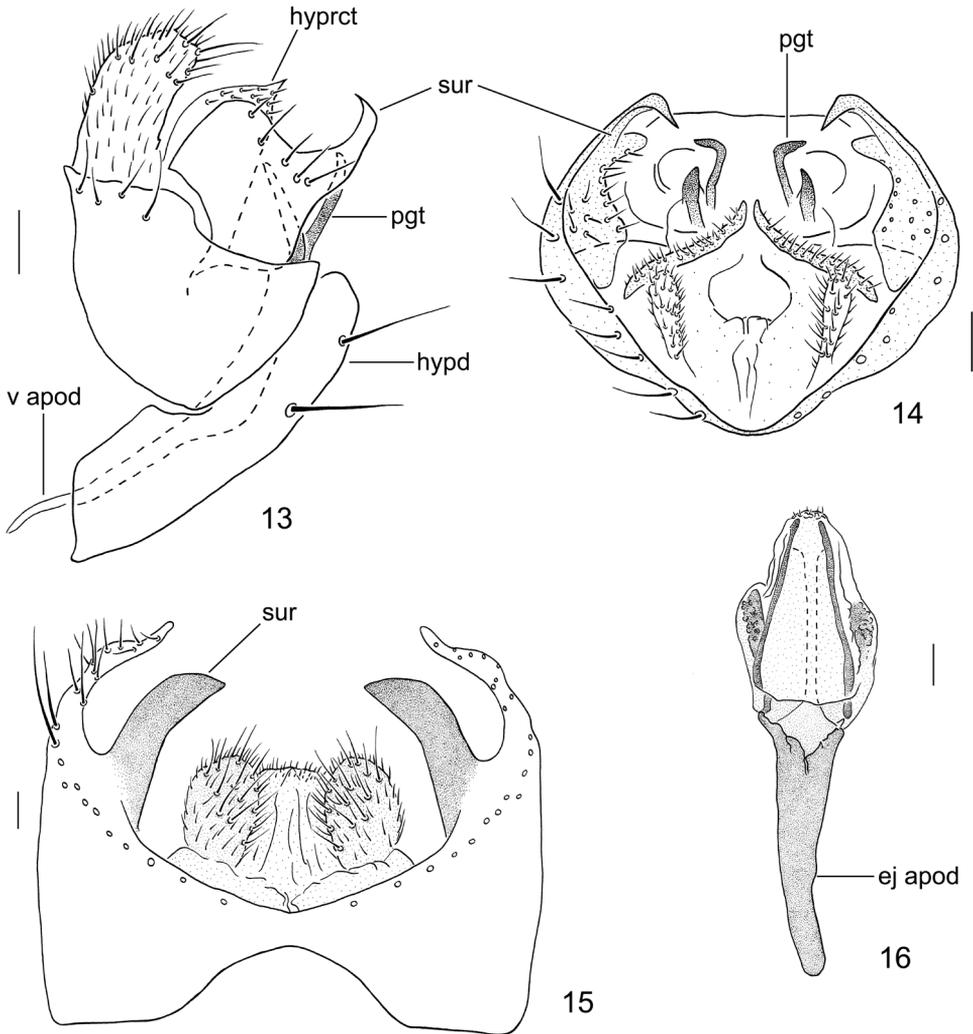
Thorax: Mostly dark with thin greyish pruinescence. Scutum with narrow brownish vittae between acrostichals and dorsocentral rows (viewed posteriorly). Acrostichals biserial; dorsocentral setae uniserial, longer, darker posteriorly; postpronotal setae numerous, long and pale; numerous pale presutural and postsutural supra-alar setae; 3 pale notopleural setae; 1 pale postalar seta; 2 pairs of pale scutellar setae, longer than length of scutellum. Proepisternum with several long, pale setae.

Legs: Yellowish-brown; femora darkened about middle; tibia and tarsi darker; basal half of tarsomere 1 yellowish (Fig. 17).

Wing (3–3.2 mm): Narrow, anal lobe obtuse, not sharply angled; alula undeveloped. Costal margin at humeral crossvein not expanded; costa gradually reduced beyond M_1 ; spur vein arising from between cells bm and cua . Halter knob pale.

Abdomen: Dark brown, concolorous with thorax; setae pale; tergite 8 narrow medially, expanded laterally, bearing 3 setae.

Male terminalia (Figs 15, 16): Very large, symmetrical, held erect over right side of abdomen, as long as half shrunken abdomen; rotated 45° to right. Cercus thinly sclerotised, weakly pigmented, clothed in slender setae, rounded apically; hypoproct broad with fine setae on posterior margin. Epandrial lamellae narrowed anteriorly, with row of setae on posterior margin, prolonged posteriorly, tapered into slender, medially arched extension; surstylus subapical, not articulated, strongly sclerotised and pigmented, arched medially. Postgonite forming phallic sheath, with short, triangular process apicolaterally; ventral apodeme absent? Ejaculatory apodeme elongate, narrow. Phallus membranous apically, expanded with pair of dorsal rods.



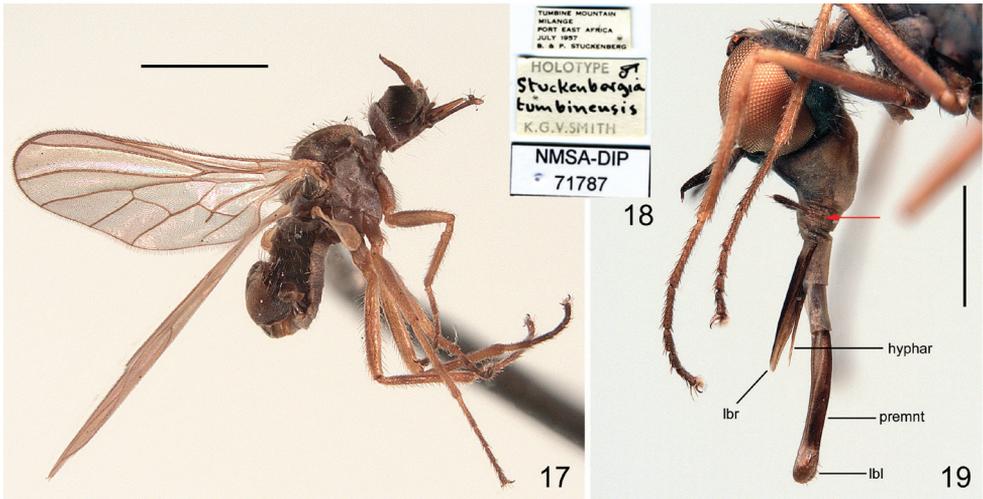
Figures 13–16. *Stuckenbergomyia* species, male terminalia. **13** *S. secunda* (Smith), lateral view **14** *S. secunda*, dorsal view **15** *S. tumbinensis* (Smith), epandrium and proctiger, dorsal view **16** *S. tumbinensis*, phallus, dorsal view. Abbreviations: ej apod – ejaculatory apodeme, hypd – hypandrium, hypcrct – hypoproct, pgt – postgonite, sur – surstylus, v apod – ventral apodeme. Scale bars: 0.1 mm.

Female. Unknown.

Type locality. Mozambique: Zambezia Province, Milange, Tumbine Mountain [16°2'36"S, 36°47'41"E] (Fig. 22).

Type material examined. **Holotype** ♂, labelled (Fig. 18): “TUMBINE / MILANGE/ PORT EAST AFRICA [Mozambique]/ JULY 1957/ B. & P. Stuckenberg”; “HOLOTYPE ♂/ Stuckenbergia/ tumbinensis/ K.G.V.SMITH”; “NMSA-DIP-71787” (NMSA) (Fig. 17).

Paratypes: MOZAMBIQUE: 2♂, same data as holotype, NMSA-DIP-71786, NMSA-DIP-09435 (NMSA).



Figures 17–19. *Stuckenbergomyia* species. **17** *S. tumbinensis* (Smith), holotype habitus, lateral view **18** Holotype labels **19** *S. secunda* (Smith), mouthparts, arrow pointing to palpifer. Abbreviations: hyphar – hypopharynx, lbl – labellum, lbr – labrum, premnt – prementum. Scale bars: 1.0 mm (**17**); 0.5 mm (**19**).

Stuckenbergomyia species A

Figs 20–22

Diagnosis. This species is characterised by a narrow pair of vittae between acrostichals and dorsocentrals and broader brown vittae along supra-alars; broad wings and 7 pairs of whitish scutellar setae.

Description. Head: Dichoptic without enlarged facets. Frons parallel-sided with dense grey pruinescence; brownish stripe medially; ocellar triangle blacking. Antenna with scape and pedicel paler than dark brown postpedicel; postpedicel length less than 4× basal width; stylus cylindrical, shorter than basal width of postpedicel; apical mechanoreceptor one-third length of stylus.

Thorax: Dense grey pruinescence. Scutum with pair of narrow dark brown vittae between acrostichals and dorsocentral rows (viewed anteriorly) (Fig. 21); broader brown stripe extending along supra-alar region; anterior margin of postpronotal lobe shiny, lacking pruinescence; prescutellar depression with light brown stripe medially. Chaetotaxy whitish; acrostichals multi-serial anteriorly, biserial on prescutellar depression; dorsocentral setae multi-serial and short anteriorly, longer and 4-serial at prescutellar depression; postpronotal setae numerous and long; numerous presutural and postsutural supra-alar setae; 3–4 notopleural setae; 1 postalar seta; 7 pairs of scutellar setae, slightly longer than length of scutellum. Proepisternum with several pale setae.

Legs: Brown, apex of femora, base of tibiae and proximal half of tarsomere 1 yellowish; apical tarsomeres increasingly darker (Fig. 20).

Wing (2.6–3 mm): Broad, anal lobe nearly right-angled; alula well-developed. Costal margin at humeral crossvein expanded, costal cell broad; costa gradually reduced beyond M_1 ; spur vein arising from cell bm . Halter knob pale.



Figures 20, 21. *Stuckenbergomyia* sp. A., female. **20** Habitus, lateral view **21** dorsal view. Scale bars: 1.0 mm.

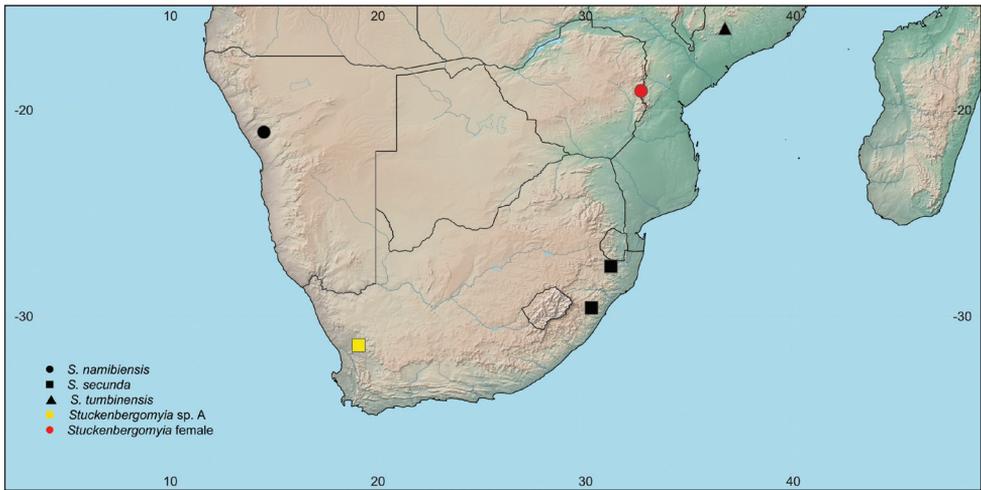


Figure 22. Distribution of *Stuckenbergomyia* in Southern Africa.

Abdomen: Brown with thin grey pruinescence; setae pale. Female terminalia (undissected): Cercus short, truncate; hypoproct paler than cercus.

Male. Unknown.

Material examined. SOUTH AFRICA: 2♀, [Northern Cape], Farm Glenlyon, Camel Koppie, MT, 781 m elev., 31.41324°S 19.15802°E [31°24'47.664"S 19°9'28.872"E], 3–24.x.2005, J. Schmidt, leg. (CNC) (Fig. 22).

Remarks. Formal naming of this species should await association of male specimens.

Key to species of *Stuckenbergomyia*

- 1 Alula undeveloped; acrostichals biserial; scutellum with two pairs of setae; males dichoptic..... ***S. tumbinensis***
- Alula developed (Fig. 11); acrostichals 4-serial; scutellum with four or more pairs of setae; males holoptic (unknown for *Stuckenbergomyia* species A)..... **2**
- 2 Scutum with 3 broad, brown faint stripes beneath acrostichals and dorsocentrals; scutellum with four pairs of setae, much longer than length of scutellum; legs brown with pale “knees” ***S. secunda***
- Scutum with pair of dark vittae between rows of acrostichals and dorsocentral setae (Fig. 21); scutellum with more than four pairs of setae, slightly longer than length of scutellum; legs yellow or yellowish-brown **3**
- 3 Legs yellow (Fig. 1); scutum brownish with grey pruinescence; chaetotaxy yellowish..... ***S. namibiensis* sp. nov.**
- Legs yellowish-brown (Fig. 20); scutum with thick grey pruinescence; chaetotaxy whitish (Fig. 21)..... ***Stuckenbergomyia* species A** (females only)

Phylogenetic affinities

The subfamily assignment of *Stuckenbergomyia* has been problematic since the recognition of this enigmatic genus. Smith (1969) originally assigned this genus to the Ocydromiinae, but at that time, this subfamily included all genera not assigned to the other two subfamilies, the Hybotinae and Tachydromiinae. *Stuckenbergomyia* is currently un-assigned to subfamily in the family Hybotidae (Sinclair and Cumming 2006). The L-shaped male tergite 8 suggests affinities to Atelestidae, but *Stuckenbergomyia* is clearly correctly assigned to the Hybotidae due to the presence of a palpifer (sclerotised plate at base of palpus) (Fig. 19) and fore tibial gland (Fig. 12), in addition to the plate-like ventral apodeme (Fig. 5) (Sinclair and Cumming 2006). The combination of a truncate cell cua, shortened stylus, three veins emitted from cell dm, obliquely directed mouthparts and pollen feeding also suggests affinities with the Oedaleinae, but female segment 8 is not elongate and the epiproct is separate from the female cercus in *Stuckenbergomyia* (Fig. 6). In addition, despite feeding on pollen, epipharyngeal blades are present in the Oedaleinae, but absent in *Stuckenbergomyia*.

In all studied genera of Hybotidae, the spermatheca is stated to be either absent (i.e. not readily observed) or is membranous and unpigmented (Sinclair and Cumming 2006). The discovery of a sclerotised, pigmented spermathecal receptacle and duct in *Stuckenbergomyia* (Figs 2, 7) is the first time this plesiomorphic form has been observed in the family and suggests that the genus could be the sister group to the remaining Hybotidae. In the absence of additional phylogenetic informative characters, a new monotypic subfamily is proposed, *Stuckenbergomyiinae* subfam. nov. (type genus: *Stuckenbergomyia* Smith, 1971). The subfamily is named to provide stability in Hybotidae nomenclature and to highlight the importance of including this clade in future molecular and morphological phylogenetic studies.

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