Further Details of the Morphology of the Enigmatic African Fly Mormotomyia hirsuta Austen (Diptera: Mormotomyiidae)

Authors: Kirk-Spriggs, Ashley H., Kotrba, Marion, and Copeland, Robert S.

Source: African Invertebrates, 52(1) : 145-165

Published By: KwaZulu-Natal Museum

URL: https://doi.org/10.5733/afin.052.0107

African Invertebrates Vol. 52 (1) Pages 145–165 Pietermaritzburg June, 2011

Further details of the morphology of the enigmatic African fly *Mormotomyia hirsuta* Austen (Diptera: Mormotomyiidae)

Ashley H. Kirk-Spriggs[1], Marion Kotrba[2] and **Robert S. Copeland[3]**

[1]Department of Entomology, National Museum, P.O. Box 266, Bloemfontein, 9300 South Africa and Department of Zoology & Entomology, University of the Free State, P.O. Box 339, Bloemfontein, 9300 South Africa; ashley.kirk-spriggs@nasmus.co.za

[2]Zoologische Staatssammlung, Muenchhausenstrasse 21, D-81247 Munich, Germany; Marion.Kotrba@zsm.mwn.de

[3]International Centre of Insect Physiology and Ecology, P.O. Box 30772, Nairobi, 00100 Kenya and National Museums of Kenya, P.O. Box 40658, Nairobi, 00100 Kenya; rcopeland@icipe.org

ABSTRACT

Mormotomyia hirsuta Austen, 1936 is one of the most extraordinary and unusual looking Diptera and was placed by E.E. Austen into a family of its own, the Mormotomyiidae, upon its discovery in 1933. Adults superficially resemble small solifugids (sun spiders), having extremely long legs that are clothed, especially in males, in very long, closely-packed brown hair-like setae. The wings are reduced to dysfunctional straps, the halteres to small nodular processes, and the eyes are greatly reduced. *M. hirsuta* is cavernicolous in all life stages and guanobious at least in the larval stages. The phylogenetic position of the family has long been a subject of much speculation and disagreement. Until recently *M. hirsuta* had only been collected on two occasions: in May 1933 and December 1948, although there have been numerous unsuccessful rediscovery attempts. The species is apparently confined to the type locality and is, therefore, widely regarded as the "rarest fly in the world". Here we report the rediscovery of adults, larvae and puparia at the type locality, a cave-like rock fissure at Ukasi Hill, Eastern Province, Kenya, in December 2010. This rediscovery has facilitated a more thorough examination and study of the immature stages using scanning electron microscopy (SEM). This has revealed numerous microstructures not previously described by van Emden in 1950, and the larva and puparium are therefore re-described. An SEM study was conducted of the leg features of adults, specifically the form and structure of the tarsal claw and pulvillus, and these were compared to the same structures in examples of the true bat fly ectoparasitic families Nycteribiidae and Streblidae, and to the phoretic Mystacinobiidae. The basal sclerites of the wing are interpreted for the first time using SEM, the functional morphology of the larva, puparium and adult is discussed and notes are provided on the biology, development and cavernicolous habits of the species. The cuticular parts of the internal female reproductive tract are further described. They comprise a tubular vagina, two sclerotized spermathecae, paired accessory glands, and a small one-chambered sclerotized ventral receptacle. These are compared to species in the Mystacinobiidae, Sphaeroceroidea and Ephydroidea, and it is concluded that the structure of the female reproductive tract lends support to the inclusion of the Mormotomyiidae in the Ephydroidea.

KEY WORDS: Afrotropical, bat fly, cavernicolous, biospeleology, female reproductive tract, functional morphology, guanobious, immature stages, phylogeny, redescription, spermathecae, ventral receptacle.

INTRODUCTION

In 1936, E.E. Austen described the bizarre flightless, cavernicolous fly, *Mormotomyia hirsuta* (Fig. 49), meaning "frightful hairy fly", that he regarded as "… one of the most extraordinary and unusual looking Diptera ever discovered" (p. 426). The disproportionately long legs have numerous extremely long, dense and closely-packed hair-like setae (Figs 38, 49), while the wings are drastically reduced to dysfunctional thin straps and the halteres (Fig. 48) are likewise reduced to small nodular processes. Austen assigned the fly to a family of its own, the Mormotomyiidae.

The Mormotomyiidae are one of four Diptera families with extant species now endemic to the Afrotropical Region, the others being the Glossinidae, Marginidae and Natalimyzidae (Kirk-Spriggs & Stuckenberg 2009). Both the Glossinidae and Natalimyzidae are, however, represented in the fossil record from other zoogeographical

regions of the world: the Glossinidae from North America (e.g., Cockerell 1917; Grimaldi & Engel 2005); and the Natalimyzidae as inclusions in Baltic amber (Tschirnhaus & Hoffeins 2009). The Mormotomyiidae are, therefore, one of only two endemic families occurring solely in the Afrotropics.

Austen considered the Mormotomyiidae as "perhaps distantly related to Borboridae [= Sphaeroceridae]", in the series Acalyptratae. Later, based largely on the study of immature stages, van Emden (1950) took a different view, suggesting placement in the Calyptratae and stating (p. 124) "If *Mormotomyia* belongs to the Calyptrata series or is transitional between it and the Acalyptrata, there can be little doubt that the Cordyluridae [= Scathophagidae] are its closest allies."

Both Hennig (1971: 63–69) and Griffiths (1972) treated the position of Mormotomyiidae in some detail. Notably, Hennig (1971) mentioned the presence of the dorsal seam of the pedicel and suggested that this was not necessarily compelling evidence for its inclusion in the Calyptratae. He extensively discussed the male and female terminalia and noted the presence of two spermathecae in the female.

Pont (1980: 713) was the first to place this family in the superfamily Muscoidea and summarised the systematic positions of Austen, van Emden and Hennig (1971).

Subsequent authors, however, have been in agreement as to its placement in the "Acalyptratae". Griffiths (1972) interpreted the Mormotomyiidae as an aberrant family in his prefamily Tephritoinea. He aligned *Mormotomyia* with the genera *Neossos* Malloch (= *Chiropteromyza* Frey) and *Prosopantrum* Enderlein (= *Cnemospathis* Enderlein), both of which were later transferred to the Heleomyzidae (Sphaeroceroidea) (D.K. McAlpine 1985). In the most recent published interpretation, J.F. McAlpine (1989) concluded that the majority of morphological character states indicated placement in the Acalyptratae, provisionally regarding it as a separate family in the Sphaeroceroidea, probably near the Heleomyzidae.

Austen's original (1936) description was based on two males collected in May 1933 by H.B. Sharpe from Ukasi (as Ukazzi, Garissa District), Kenya (Fig. 50) inhabiting a cave-like cleft "about a yard wide", with its horizontal and oblique side-cracks inhabited by unidentified bats and swifts. Upon entering the cave at Ukasi, Sharpe (cited in Austen 1936) noted that the flies "… came floating down from above like feathers" (Austen 1936: 430); a behaviour later noted by van Emden (1950), who remarked that the fall of the flies is apparently much slowed by the long, shaggy, hair-like body setae and occurs in a slight spiral motion.

Austen's (1936) description was appropriate for its time and he provided line drawings of the male habitus dorsum (fig. 1), the male head lateral (fig. 2), the external features of the male terminalia (fig. 3) the wing (fig. 4) and the hindleg (fig. 5).

In 1950 van Emden described the unknown female, egg, mature larva and puparium, based on material collected at the type locality by V.G.L. van Someren and his son, G.R. Cunningham-van Someren, in December 1948[1]. For adults he provided line drawings (all lateral) of the female head (fig. 1), the female proboscis (fig. 2), the basal two segments of the midtarsus of the male and female (fig. 3), and the male and female terminalia (figs 4–6). For the early stages he included illustrations of the larval habitus lateral (fig. 7)

[1]Letter: G.R. Cunningham-van Someren, to M. De Meyer, dated 5 September 1994 (copy in Archives of Musée Royal de l'Afrique Centrale, Tervuren, Belgium).

and dorsum (fig. 8), the puparial habitus lateral (fig. 9) and anterior end dorsal (fig. 10), the anterior spiracle lateral (fig. 11), the cephaloskeleton lateral (fig. 12), the pseudocephalon lateral (fig. 13), the posterior end of the anal division (with details of the posterior spiracles, the process on the anal pad and the "thumb-like process on ninth abdominal segment") (fig. 14) and the egg dorsal and lateral (fig. 15).

Hennig (1971: 64–67) illustrated the male genitalia (figs 94, 95), the antenna (fig. 96), the ovipositor dorsal (fig. 97) and ventral (fig. 98), the female terminalia ventral (fig. 99) and lateral (fig. 100) with two spermathecae.

Since the second discovery of the species in 1948, at least five unsuccessful attempts have been made to collect specimens at the type locality. The rediscovery of adults, larvae and puparia at the type locality in December 2010 has facilitated detailed examination of the larva and puparium using scanning electron microscopy (SEM), and a redescription of both is provided below. As all adult females collected in 2010 were teneral it was not possible to obtain eggs through dissection, as did van Emden, and a redescription of the egg is not provided here.

An SEM study of leg features of adults, specifically the form and structure of the tarsal claw and pulvillus, was also conducted and these were compared to the same structures in examples of the true bat fly ectoparasitic families Nycteribiidae and Streblidae, and to the phoretic Mystacinobiidae. The basal sclerites of the wing are interpreted for the first time using SEM, the functional morphology of the larva, puparium and adult is discussed and notes are provided on the biology, development and cavernicolous habits of the species.

Current knowledge of the internal female reproductive tract in *Mormotomyia* is limited to the presence of two small, sclerotized spermathecae (Hennig 1971; Griffiths 1972). Here additional morphological details are presented and discussed regarding their phylogenetic implications.

MATERIAL AND METHODS

Specimen preparation and imaging

Living larvae and puparia were removed from guano that had washed from the rock fissure on the north face of Ukasi Hill and had accumulated in a hollow at the base of the cliff face (Fig. 51). A more complete description of the collecting site will be provided at a later stage. Specimens were extracted on 1.xii.2010 and later from a collected guano sample containing living larvae on 5.xii.2010. Each puparium was transferred to an individual glass vial with the date of collection and subsequent adult eclosion recorded. A few puparia were also preserved in 96% ethanol for later study. Larvae were killed in near boiling water and transferred to 96% ethanol. Following cleaning with a fine camel hair brush, some were dehydrated in absolute ethanol, critically-point-dried (CPD) in a ®Tousimis Samdri-795 critical-point-dryer, mounted on stubs using double-sided carbon conductive tape or silver paint, sputter-coated with gold in a ®Bio-Rad SEM Coating System and viewed at a working distance of 17 mm (larvae and puparium) and 30–38 mm (adults) at 5 kV accelerating voltage, in a ®Shimadzu SSX-550 Superscan scanning electron microscope (SEM). Resulting scanning electron micrographs were edited, arranged into plates and labelled using the program ®CorelDraw 14. Cephaloskeletons (Figs 28, 29) were removed from the ventral puparial cap by soaking in water overnight and by subsequent maceration in 10% potassium hydroxide (KOH), mounted on a slide in a

thin film of set glycerin jelly and photographed at a range of focal planes with a ®Nikon TE2000-E compound microscope and digitized using ®Combine ZP Image Stacking Software.

Measurements

Measurements were calibrated using a graticule eyepiece on a ®Leica Wild M3Z binocular microscope. Measurements of larvae were taken from alcohol-preserved specimens. The body shape of living larvae and specimens killed and preserved using other techniques may differ. Measurements are expressed in millimetres as the range followed by the mean and standard deviation (SD) in brackets. Overall puparial lengths were derived from "unhatched" puparia mounted ventral side up on white mounting cards.

Preparation of female abdomen

The studied specimens (n=3) had been stored in alcohol for a short period prior to dissection. Abdomens were removed and macerated in cold 10 % KOH prior to peeling away the cuticle and freeing the internal female reproductive tract from the surrounding tissue. The specimens were then neutralized with glacial acetic acid and mounted on a microscopic slide in polyvinyllactophenol with an admixture of Chlorazol Black E. The dissections were studied in bright field and DIC contrast using a ®Zeiss Axioskop compound microscope, equipped with ®Zeiss AxioCam digital camera. Figure 30 was combined from a series of digital images captured at different focal planes.

The description is restricted to the morphology of those parts that are internally lined with cuticle and thus persist after maceration. For terminology and a general introduction to the internal female reproductive tract of Diptera see Kotrba (2000). Following common practice the term "sclerotized" is applied to structures consisting of brown cuticle.

Label data, citations and codens

Label data are quoted exactly as they appear. A division slash (/) denotes the commencement of a new line, two division slashes (//) data on a further label. Material used in this study is deposited in the following institutions: BMSA – National Museum, Bloemfontein, South Africa; ZSM – Zoologische Staatssammlung, Munich, Germany.

Descriptive passages

Terminology for larval morphology follows Courtney *et al.* (2000). Abbreviations used in the text and on the figures: *a/mp* – antennal sensillae; *abd 1–7* – abdominal segments 1–7; *acth* – accessory tooth; *ag* – accessory gland; *andi* – anal division; *ant* – antenna; *ant spir* – anterior spiracle; *ap* – anal pad; *axs* – axillary sclerite; *b/ring* – basal ring; *bsc* – basal sclerite; *cib* – cibarium; *clw* – claw; *co* – posterior portion of common oviduct; *d* – dome; *dbr* – dorsal bridge; *dcor* – dorsal cornu; *den* – dental sclerite; *dlp* – dorsolateral pit; *dlt* – dorsolateral tubule; *dmp* – dorsomedial pit; *dslp* – dorso-sublateral pit; *ecds* – ecdysial scar; *emp* – empodium; *epsc* – epistomal sclerite; *fama* – facial mask; *gp* – genital papilla; *insc* – intermediate sclerite; *ko* – Keilen's organ; *llo* – labial lobe; *mhk* – mouth-hook; *msth* – mesothorax; *mtth* – metathorax; *mxp* – maxillary palpus; *mxps* – maxillary palpus sensillae; *pab* – parastomal bar; *pap* – papilla/papillae; *post spir* – posterior spiracle; *psceph* – pseudocephalon; *pstgt* – peristigmal tuft; *pth* – prothorax;

pulv – pulvillus; *sp* – spermatheca; *spiro* – spiracular opening; *stigo* – stigmal opening; *tars 1* – tarsomere 1; *tars 5* – tarsomere 5, *va* – anterior part of vagina; *vcor* – ventral cornu; *vf* – ventral fold; *vlt* – ventrolateral tubule; *vr* – ventral receptacle.

TAXONOMY

Family Mormotomyiidae Austen, 1936

Mormotomyidae: Austen 1936: 426. Type-genus *Mormotomyia* Austen, 1936: 426.

Genus *Mormotomyia* Austen, 1936

Mormotomyia: Austen 1936: 426. Type-species: *Mormotomyia hirsuta* Austen, 1936: 429, by original designation.

Mormotomyia hirsuta Austen

Figs 1–49, 52

Mormotomyia hirsuta: Austen 1936: 429.

Redescription of third-instar larva

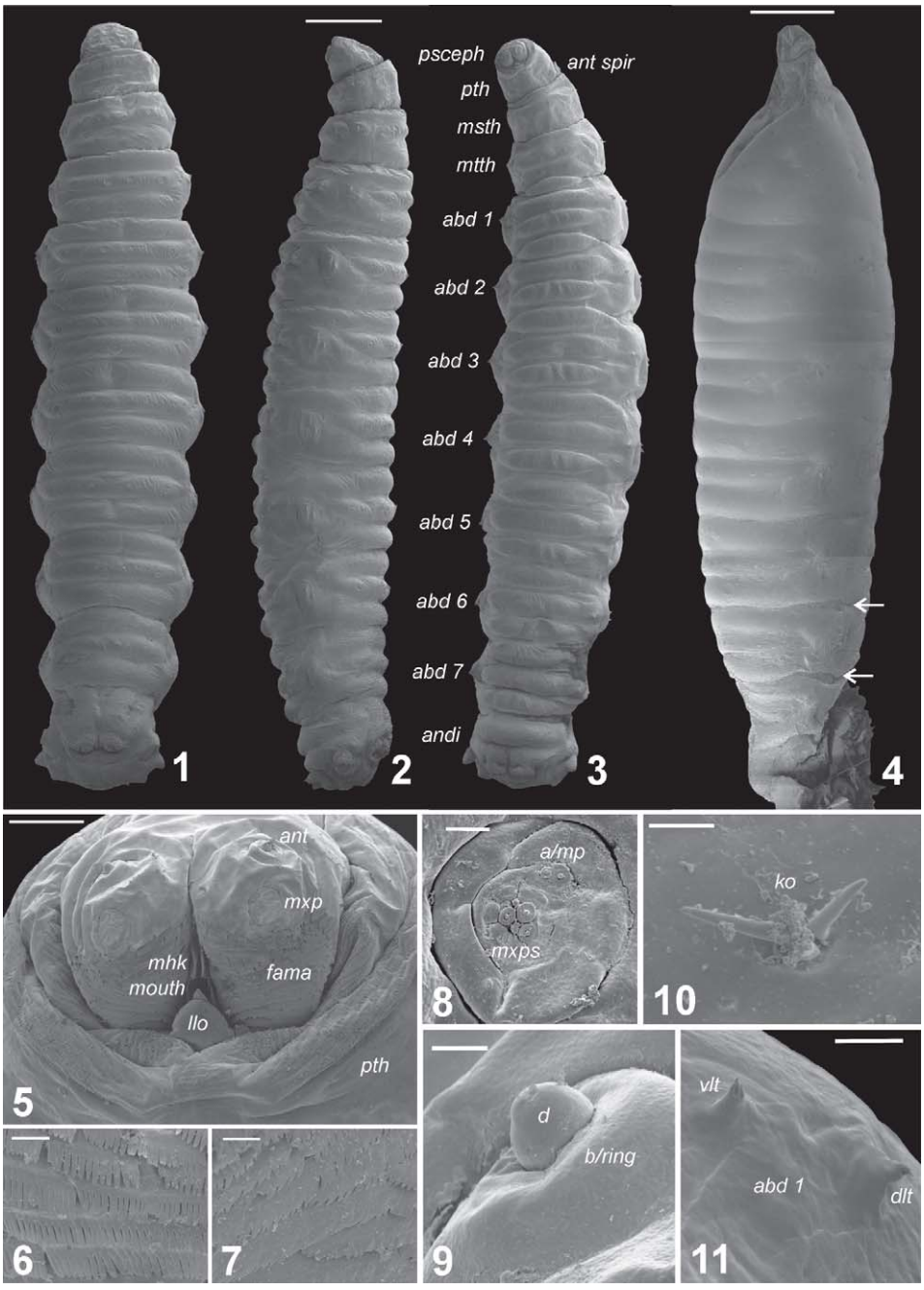
Measurements: Overall length: 9.5–10.2 mm (mean = 10 mm; SD = 0.21 mm; $n = 10$); breadth at widest point (*abd 3*): 1.7–2.6 mm (mean = 1.9 mm; SD = 0.29 mm; $n = 10$).

Colour: Uniformly pure white, except anterior spiracles pale tan-brown and posterior spiracles chestnut-brown around margin of spiracular plate and stigmal openings.

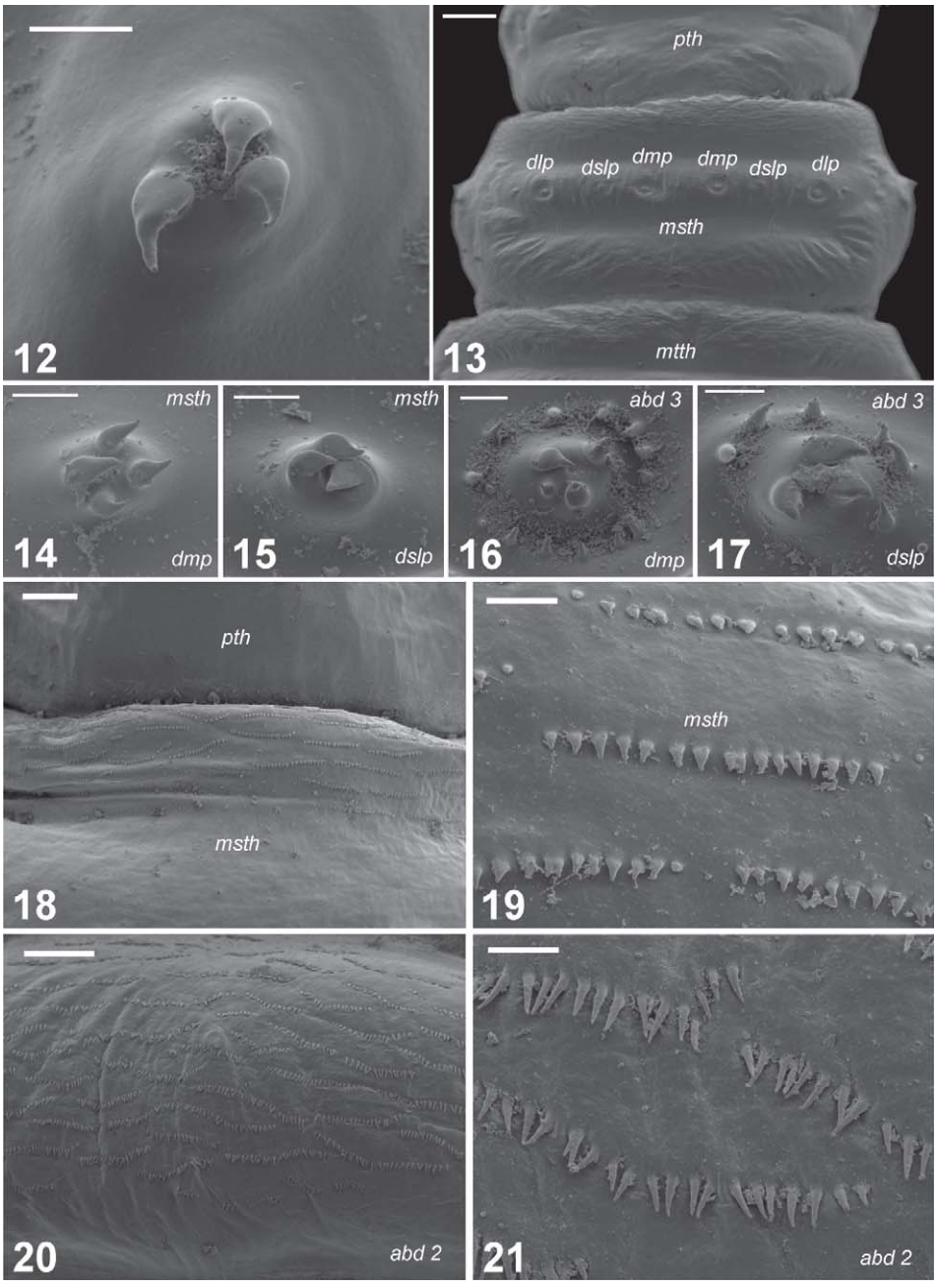
Habitus (Figs 1–3): Cylindrical, slightly flattened dorsoventrally, anteriorly and posteriorly narrowed, posteriorly truncate; body segmentation (as labelled on Fig. 3) of the usual schizophoran arrangement, divided into pseudocephalon, three thoracic, and seven abdominal segments, plus anal division.

Pseudocephalon (Figs 5–9): Retractile, anteriorly bilobed, slightly longer than wide; each cephalic lobe in area of antenna and maxillary palpus smooth; facial mask (Fig. 5, *fama*) comprising extensive series of oral ridges, those on upper part of *fama* (immediately posteriad to maxillary palps) formed of fringes of uniform, closely-abutting finger-like digitations (Fig. 6), those on lower *fama* formed of ratchet-like rows of irregular digitations (Fig. 7), those on lateral sides of cephalic lobes, shorter, rather scallop-like. Labial lobe (Fig. 5, *llo*) in the form of a sub-triangular fleshy, undivided protuberance, posteriad to mouth opening; pseudocephalon separated from *pth* by distinct fleshy fold, the surface of which is clothed in linear, regular to irregular rows of uniform, often partially overlapping, long pointed spinules. Antenna (Fig. 5, *ant*; 9) apparently one-segmented, relatively large, in terminal position, composed of spherical distal dome (Fig. 9, *d*), inserted into basal ring. Maxillary palpus (Fig. 8) ventrolateral to antenna, with maxillary palpus sensillae and antennal sensillae arranged collectively in a ring and surrounded by three elongated fleshy folds; two *a/mp* partially separated from three *mxps, a/mp* slightly larger than *mxps*. Ventral organ not visible on examined specimens.

Cephaloskeleton (Figs 28, 29): Mouth-hooks drawn-out, with posterior dorsal process truncate, ending in a blunt point; deep black basally, pale yellow-brown centrally and apically, with single well-developed, sharp, posteriorly-directed hooked accessory tooth, campaniform sensilla situated laterally at base of accessory tooth, visible as an elliptical "window". Intermediate sclerite roughly wedge-shaped (viewed laterally, Fig. 28), black, slightly paler on dorsal edge, markedly narrowed basally, acutely pointed at point



Figs 1–11. Scanning electron micrographs of third-instar larva and puparium of *Mormotomyia hirsuta*: (1–3) larva habitus, dorsal (1), lateral (2), ventral (3); (4) puparium habitus, lateral (arrows indicate lateral creases allowing articulation); (5–11) larva pseudocephalon, ventral (5), detail of upper oral ridges (6), detail of lower oral ridges (7), maxillary palpus (8), antenna (9); (10) Keilin's organ on prothorax, ventral; (11) ventrolateral and dorsolateral tubules on first abdominal segment. Scale bars: Figs 1–4 = 1 mm; Fig. 5 = 100 µm; Figs 6–9 = 10 µm; Fig. 10 = 5 µm; Fig. 11 = 50 µm.



Figs 12–21. Scanning electron micrographs of third-instar larva of *M. hirsuta*: (12) dorsolateral tubule on first abdominal segment, from above; (13) detail of mesothorax indicating positions of dorsal pits; (14) dorsomedial pit on mesothorax; (15) dorso-sublateral pit on mesothorax; (16) dorsomedial pit on third abdominal segment; (17) dorso-sublateral pit on third abdominal segment; (18) creeping welt at junction on mesothorax, ventral; (19) detail of same; (20) creeping welt on second abdominal segment, ventral; (21) detail of same. Scale bars: Figs 12, 14–17, 19, 21 = 10 µm; Fig. 13 = 200 µm; Figs 18, 20 = 50 µm.

of connection with basal sclerite, markedly widened in basal third, with small ventral spine, tapering to bluntly pointed apex; H-shaped (viewed dorsally, Fig. 29), laterally-expanded and concave at points of connection with mouth-hooks. Basal sclerite (Fig. 28, *bsc*) deep brown-black in area of ventral plate, but becoming markedly paler posteriad to dorsal bridge of dorsal cornu and posterior and lateral regions of the ventral cornu, here weakly sclerotized, in region of cibarium with series of posteriorly-directed lines or ridges. Parastomal bars (Fig. 28, *pab*) attached to basal sclerite, extremely long and narrow for their entire length (needle-like), running above and parallel to dorsal edge of intermediate sclerite. Dorsal bridge (Fig. 28, *dbr*) with cuticular sieve consisting of a network of holes, contiguous with basal sclerite. Dorsal cornu (Fig. 28, *dcor*) broad in region of basal sclerite coming to an acute point, medial margin forming a darker, more heavily sclerotized band or line. Ventral cornu (Fig. 28, *vcor*) broad basally, with dorsally-directed sub-triangular cuticular extension in region of basal plate, more weakly sclerotized centrally, with two acute bars posteriorly, forming dorsal edge of cibarium. Dental sclerite (Fig. 28, *den*) sub-triangular (viewed ventrally), with slight posteroventral indentation, carrying adductor apodemes to mouth-hooks. Epistomal sclerite (Fig. 29, *epsc*) pale black-brown, darker basally and centrally, triangular, with broad, shallow, crescent-shaped excision basally.

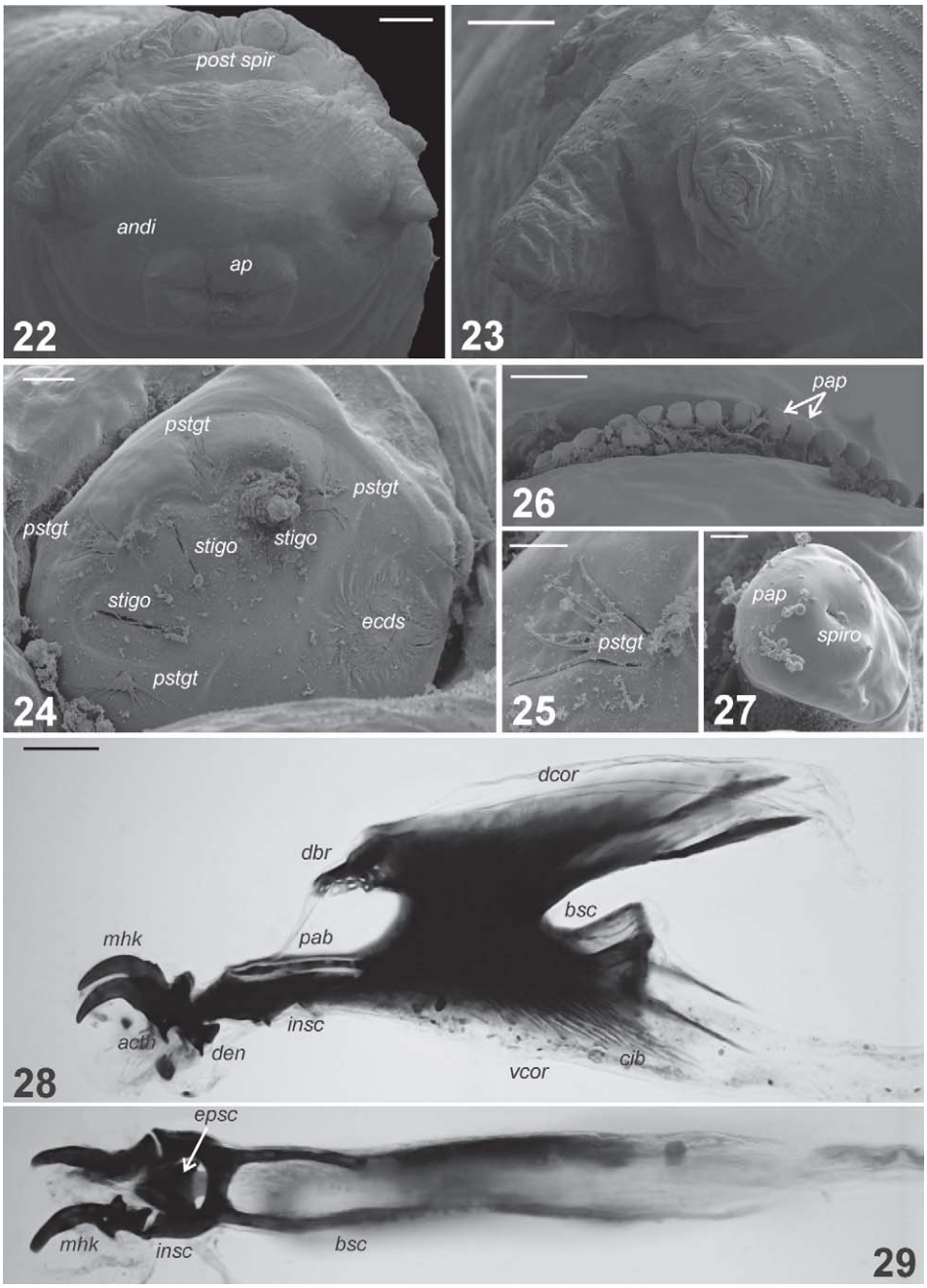
Thoracic and abdominal body segmentation (Figs 1–3, 11–17): Three thoracic segments (Figs 1–3, *pth*, *msth*, *mtth*), each slightly increasing in length posteriad; *abd 1–7* of more-or-less equal length, sub-triangular at lateromedial edges; *msth*, *mtth* and *abd 1–7* each with one dorsolateral and one ventrolateral tubule (Fig. 11), apex furnished with three posteriorly-directed tear-shaped curved processes (Fig. 12); *abd 1–7* subdivided into three distinct transverse dorsal and ventral folds (Figs 1–3, 13), similar, but less pronounced on *msth* and *mtth* (Fig. 1); each medial fold with three or four pits (possibly distended in living larvae as the membranous teats described by van Emden) (Fig. 13), dorsomedial pits on *msth* (Fig. 13, *dmp*) bearing ring of four tear-shaped projections (Fig. 14), dorso-sublateral pits (Fig. 13, *dslp*), with three overlapping leaf-shaped projections arranged in a spiral (Fig. 15); dorsomedial and dorso-sublateral pits on *abd 3* similar, but encircled by a "fairy ring" of incurved, sharp spikelets (Figs 16, 17).

Creeping welts (Figs 1–3, 18–21): Encircling all body compartments on anterior sixth, those on thoracic compartments less pronounced than on abdominal compartments; ventral thoracic welts (e.g., Figs 3, 18) in semi-regular, but widely-spaced crescent-shaped rows, formed of short, blunt, undivided spinules (Fig. 19); ventral abdominal creeping welts (e.g., Figs 3, 20) in similar crescent rows, on broad, raised medial fleshy folds, each comprising closely-packed long-pointed spinules (Fig. 21).

Anterior spiracles (Figs 26, 27): Fan-shaped, located on *pth,* normally consisting of 18 short, oblong papillae on a broad laterally-expanded lobe-like fleshy projection (retracted into cuticle in Fig. 26), each papilla with a slit-like spiracular opening (Fig. 27, *spiro*); ecdysial scar not visible in examined specimens.

Keilin's organs (Fig. 10, *ko*): On *pth* closely-separated, consisting of two relatively long, slender, rigid and divergent spike-like sensillae.

Anal division (Figs 22, 23): Large, projecting laterally as three large, cone-shaped projections on either side, surface with multiple and numerous rows of long, pointed spinules, similar to those on ventral creeping welts of *abd 1–7* (Fig. 23). Anal pad (Fig. 22, *ap*) transverse, elongate, sub-rectangular, anus surrounded by large, raised, fleshy



Figs 22–29. Scanning electron and light micrographs of third-instar larva of *M. hirsuta*: (22) anal division, posterior; (23) detail of lateral process on anal division, posterior; (24) posterior spiracular plate, dorsal; (25) detail of peristigmal tuft; (26) anterior spiracle between prothorax and mesothorax laterally; (27) detail of papilla on anterior spiracle; (28) light micrograph of cephaloskeleton, lateral; (29) same, dorsal. Scale bars: Fig. 22 = 200 µm; Figs 23, 28 = 100 µm; Fig. 24 = 20 µm; Fig. 25 = 10 µm; Fig. 26 = 50 µm; Fig. 27 = 5 µm.

folds, either side of which has a raised, prominent, medially-directed tubule, encircled with regular, closely-packed rows of brown, long-pointed spinules (these not clearly visible on Fig. 22).

Posterior spiracles (Figs 24, 25): On extremely short stigmatophores, each with three radiating, elliptical, long and narrow stigmal openings (*stigo*) in a shamrock-shaped cuticular depression, surface between them smooth, positioned on a sub-triangular spiracular plate, ecdysial scar large, rounded and conspicuous; with four peristigmal tufts (Figs 24, 25, *pstgt*), inserted between stigmal openings on spiracular plate, broad and blade-like basally with 5–7 long, narrow undivided filaments.

Redescription of puparium (Fig. 4)

As described for third-instar larvae, but with following differences.

Overall length ("unhatched" puparia): 6.9–9.5 mm (mean = 7.8 mm; SD = 1.16 mm; $n = 10$); width at widest point (*abd 2*): 1.6–2.6 mm (mean = 2.1 mm; SD = 0.37 mm; $n = 10$).

Male: Overall length (with partially opened puparial caps following eclosion): 8.1–9.7 mm (mean = 8.7 mm; SD = 0.73 mm; $n = 10$); width at widest point (*abd 2*): 2.1–2.7 mm (mean = 2.4 mm; SD = 0.17 mm; $n = 10$).

Female: Overall length (with partially opened puparial caps following eclosion): 6.7–6.9 mm (mean = 7 mm; SD = 0.41 mm; $n = 4$); width at widest point (*abd 2*): 1.7–2.2 mm (mean = 1.9 mm; SD = 0.22 mm; $n = 4$).

Shape ($n = 10$), broad, cylindrical, strongly dorsoventrally flattened and markedly wider at anterior end in region of *abd 1* and *abd* 2 (*abd 2* normally widest), posteriorly narrowed at *abd 7* and *andi*, posterior end truncate (all puparia examined with a semi-pliable, waxy substance adhering to posterior end, presumably secreted from anus during pupariation), transverse folds, and creeping welts on *msth*, *mtth* and *abd 1–7* apparent, but less pronounced than larva; dorsal pits, and lateral processes indistinct; deep, lateral, crease-like indentations (allowing articulation) strongly developed between *abd 5 & 6* and *abd 6 & 7* (Fig. 4, indicated with arrows), and two less distinct crease-like clefts on ventral surface of *abd 6 & 7*. Colour ($n = 10$) pale tan-brown to deep chestnut-brown (pale yellow-brown immediately following pupariation); surface matt, sub-shiny, usually brighter and shinier on thoracic region. Anterior spiracles black basally, with papillae dirty yellow. Posterior spiracles concolourous with rest of puparium. Processes to either side of anal pad, black, strongly developed into hook-like structures, terminal rows of spinules strongly developed.

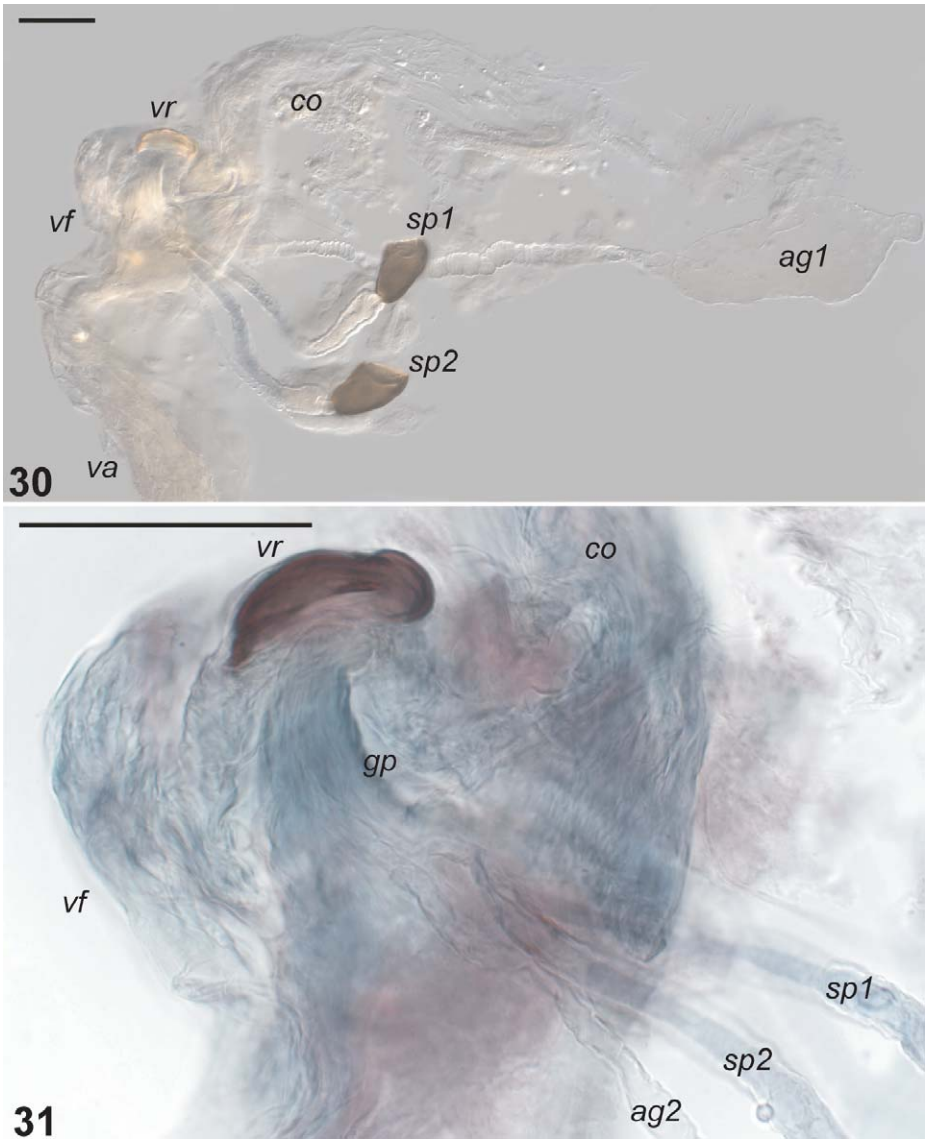
Description of female reproductive tract

The posterior part of the common oviduct (Figs 30–32, *co*), is lined with membranous cuticle along a considerable portion of its length. This opens anterodorsally into the wide anterior part of the tubular vagina (Figs 30, 32, *va*). Posterior to this, the paired spermathecae and accessory glands open adjacent to each other into the dorsal vaginal wall.

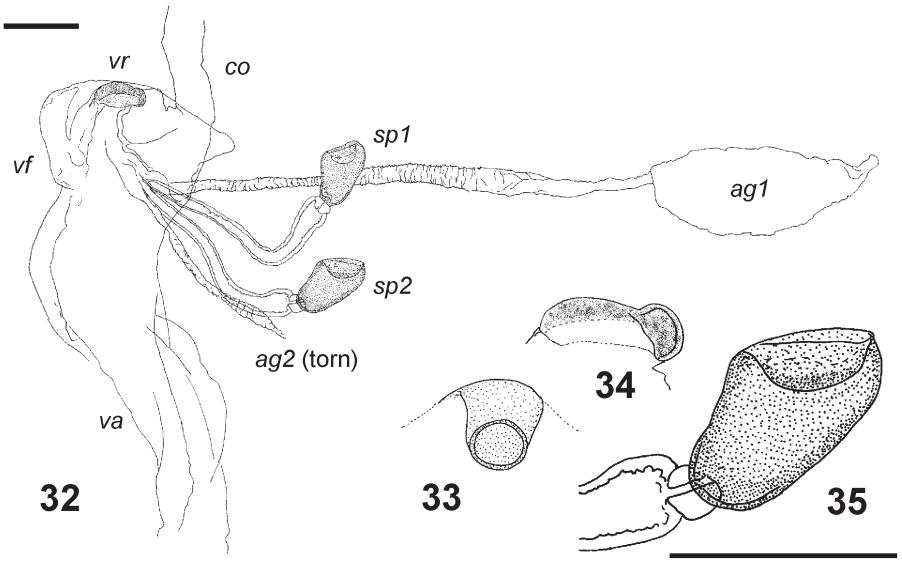
Each of the two spermathecae (Figs 30, 32, *sp1*, *sp2*; 35), consists of a pear-shaped sclerotized chamber, approx. 100 μm in length and 60 μm in width. The surface (Fig. 35) is smooth, with tiny wart-like protrusions, bearing the delicate cuticular end apparatus of epithelial gland cells. The wider apical portion of the spermatheca bears a circular invagination. No introvert is present at the base, but there is a valve-like structure at the insertion of the ducts.

The spermathecal ducts are comparatively short, lined with thick colourless cuticle and are dilated apically, i.e., near the spermathecae and may be slightly sclerotized at their bases.

The accessory glands (Fig. 32, *ag1*, *ag2*) are almost twice as long as the spermathecae. The large membranous gland lumina receive the delicate end apparatuses of gland cells very similar to those of the spermathecae. The thin-walled ducts are densely pleated, especially towards their bases.



Figs 30–31. Light micrographs of internal female reproductive tract of *M. hirsuta*: (30) cuticular parts, left lateral (one accessory gland lost during dissection); (31) anterior part of vagina with genital papilla, left lateral. Scale bars = 100 μm.



Figs 32–35. Line illustrations of internal female reproductive tract of *M. hirsuta*: (32) cuticular parts, left lateral (one accessory gland lost during dissection); (33) ventral receptacle, dorsal; (34) same, lateral; (35) spermatheca. Scale bars = 100 μm.

The anteroventral vaginal wall is enlarged to form a deep transversal pouch-like fold (Figs 30–32, *vf*). A small one-chambered, sclerotized ventral receptacle is embedded between this fold and the oviduct (Figs 30–34, *vr*). It arises from the anteroventral portion of the vagina and curves dorsally where it ends in a round chamber. The total length is approx. 70 μm. Only the anterior and dorsal portions of the ventral receptacle are sclerotized. Its shape thus resembles a slipper (Fig. 34) and is reminiscent of a small ephydroid ventral receptacle without operculum.

Where the spermathecal and accessory gland ducts open into the dorsal wall of the vagina, it is drawn out to form a large genital papilla (Fig. 31, *gp*). This papilla protrudes ventrally towards and into the entrance of the ventral receptacle and thus, as long as the vagina is empty, the internal openings of the ducts are in close contact with this organ.

Other than the structures described above, the delicate cuticle of the tubular vagina is devoid of any sclerotized and/or pigmented elements. Posteriorly the vagina opens to the exterior behind sternite 8.

Material examined: *Larvae* (all labelled "*Mormotomyia* / *hirsuta* Austen, 1936 / det. A.H. Kirk-Spriggs 2011"): 42 "KENYA: Eastern Prov. / Ukazi [= Ukasi] Hill at: / 00˚49.028'S 38˚32.535'E / 29.xi–1.xii.2010, 720 m / A.H. Kirk-Spriggs // Extracted from / accumulated bat guano / (1.xii.2010) washed from / rock fissure // Property of the / National Museums / of Kenya, Nairobi [yellow card]" [36 preserved in 96% ethanol; 6 critically-point-dried, mounted on cards; 5 sputter-coated with gold] // BMSA(D) / 26135–26141"; 34 (alcohol-preserved) same except: "Extracted from / accumulated bat guano / (5.xii.2010) washed from / rock fissure // BMSA(D) / 26142" (all BMSA).

Puparia only (all "unhatched" puparia, labelled "*Mormotomyia* / *hirsuta* Austen, 1936 / det. A.H. Kirk-Spriggs 2011"): 16 "KENYA: Eastern Prov. / Ukazi [= Ukasi] Hill at: / 00˚49.028'S 38˚32.535'E / 29.xi–1.xii.2010, 720 m / A.H. Kirk-Spriggs // Extracted from / accumulated bat guano / (1.xii.2010) washed from / rock fissure // Property of the / National Museums / of Kenya, Nairobi [yellow card]" [all card-mounted; 1 critically-point-dried, sputter-coated with gold; specimens individually numbered "BMSA(D) / 26119–26134"] (all BMSA).

Reared adults (all with associated puparia glued to card pinned beneath; labelled "*Mormotomyia* [♂ or ♀] / *hirsuta* Austen, 1936 / det. A.H. Kirk-Spriggs 2010"): 1♂ "KENYA: Eastern Prov. / Ukazi [= Ukasi] Hill at: / 00˚49.028'S 38˚32.535'E / 29.xi–1.xii.2010, 720 m / A.H. Kirk-Spriggs // bat guano washed / from rock fissure // Puparium extracted / from guano: 1.xii.2010 / eclosion: 5.xii.2010 // Property of the / National Museums / of Kenya, Nairobi [yellow card]"; 1♂, 1♀, same, except: extracted: 1.xii.2010, eclosion: 6.xii.2010; 1♂, 1♀, same, except: extracted: 1.xii.2010, eclosion: 7.xii.2010; 2♂, same, except: extracted: 1.xii.2010, eclosion: 8.xii.2010; 3♂, 1♀, same, except: extracted: 5.xii.2010, eclosion: 5.xii.2010; 3♂, 1♀, same, except: extracted: 5.xii.2010, eclosion: 5.xii.2010; 6♂, same, except: extracted: 5.xii.2010, eclosion: 6.xii.2010; 3♂, same, except: extracted: 5.xii.2010, eclosion: 7.xii.2010; 1♂, 3♀, same, except: extracted: 5.xii.2010, eclosion: 8.xii.2010; 2♂, same, except: extracted: 5.xii.2010, eclosion: 13.xii.2010 [specimens individually numbered "BMSA(D) / 26093–26118"] (all BMSA).

Adult material: 3♀ "KENYA: Eastern Prov. / Ukazi [= Ukasi] Hill at: / 00˚49.028'S 38˚32.535'E / 29.xi–1.xii.2010, 720 m / R.S. Copeland" (ZSM).

DISCUSSION

Biology and functional morphology of immature stages

Van Emden (1950: 123) concluded that the larvae of *M. hirsuta* are saprophagous, rather than predatory, and pointed out a number of larval characteristics indicative of saprophagy/coprophagy. In addition to those cited by van Emden, other larval features indicating this include: the extensive, overlapping and fringed oral ridges on the facial mask of the larva (Figs 5–7); and the presence of a cuticular sieve on the cephaloskeleton (Fig. 28). Fragments of guano are also present in the cibarium of cephaloskeletons removed from puparia (e.g., Fig. 28, *cib*).

The peristigmatic tufts of *M. hirsuta* (Figs 24, 25, *pstgt*) are extremely small in overall size and are comprised of a flat blade-like structure basally, with a few short terminal filaments. Kirk-Spriggs *et al*. (2002) note that the size of the peristigmal tufts is related to the feeding substrate of larvae. These tufts are water-repellent and are used to maintain, or establish contact with atmospheric air in very moist or even liquid media. It is significant that the peristigmatic tufts of *M. hirsuta* are extremely similar to, although smaller than, those of *Katacamilla cavernicola* Papp (Camillidae) (Kirk-Spriggs *et al*. 2002, fig. 19), which is also cavernicolous and guanobious in the larval stages and occurs in the xeric caves of Namibia. These structures are also very small in described species of *Curtonotum* Macquart (Curtonotidae) (Kirk-Spriggs 2008; Meier *et al*. 1997).

Egg hatching in *M. hirsuta* is probably triggered by precipitation. The three occasions on which flies have been observed were all following heavy downpours that resulted in guano being washed from either the north or south clefts of the rock fissure. Evidence from rearing experiments with *Katacamilla cavernicola* (Kirk-Spriggs *et al*. 2002), revealed that eggs remain dormant in bat guano for extended periods during dry conditions. Adults of *K. cavernicola* were successfully reared from guano samples collected dry and moistened four and six months after collection, followed by very rapid larval development. The same may apply in *M. hirsuta.* Larvae of *M. hirsuta* were in an advanced stage of development when sampled at Ukasi in December 2010, but puparia, some of which were quite fresh, were extracted at the sampling site and reared in the laboratory. The dates of collection and eclosion (see material examined above) reveal a puparial period of only ±8 days. Bat guano is an extremely rich medium for larval development and flies of six other families were reared from a guano sample with a dry weight of 150.20 grams (including some sand), collected at the same site (Fig. 51), i.e., Chloropidae (?*Meijerella* sp.) (693 specimens), Milichiidae (*Leptometopa* sp. n.) (263),

Muscidae (*Musca domestica* L.) (43), Camillidae (*Katacamilla* sp. n.) (19), Fanniidae (*Fannia* sp.) (3) and Chyromyidae (1).

Van Emden (1950: 123) noted that: "When full-grown, the larvae leave the substrate and pupate on nearby stones in an upright position, in which they are securely fixed by the spinulose thumb-shaped processes on either side of the anus in collaboration with the aspirate prominence behind the anus…". Although puparia were present in guano examined at the sampling site, this had been washed from the rock fissure in an exposed situation, so conditions were not normal. All puparia examined as part of this study ($n=42$) had a semi-pliable, white waxy substance adhering to the anal division. Microscopic examination of this substance indicates that it is exuded from the anus during pupariation and is used (in combination with the ventral processes described by van Emden), to cement the posterior end of the larvae (and later the puparium) to the rock surface (e.g., Fig. 52, indicated with arrow). Examination of alcohol-preserved puparia also revealed that these have crease-like indentations strongly developed between *abd 5 & 6* and *abd 6 & 7* (Fig. 4, indicated with arrows), serving as points of articulation and allowing the puparium to move dorsoventrally. This articulation presumably prevents puparia from being dislodged by the movement of bats and swifts that inhabit the rock fissure. The size of the puparia vary in the two sexes, with those of males considerably larger than females (overall length of male 8.1–9.7 mm, female 6.7–6.9 mm). These sizes correspond with sexual dimorphism in the overall size of adult flies, and smaller puparia in general may result from the food source drying out prematurely, thus leading to early pupariation of third-instar larvae and correspondingly smaller puparia and adults.

Wing structure and "sessile knobs"

The male wing of *M. hirsuta* was described and figured by Austen (1936, fig. 4). He interpreted this as consisting of the vestiges of five longitudinal veins in addition to the costa, compacted together, with no trace of a wing membrane and ending in a blunt, narrow point. The base of the female wing was studied with SEM and the basal sclerites are interpreted in Fig. 47. These consist of a tegula, basicosta and four axillary sclerites. The basicosta is constricted medially and terminates at the costagial break, as indicated by the presence of several moderately strongly developed setae. The costal vein is clearly discernable for a short distance after the costagial break, but is then evanescing. The upper calypter is reduced and modified to carry a number of long, ventrally-directed spines, prominent posteriorly, and the lower calypter is scale-like with a fringe of setae similar to the shorter setae on the upper calypter.

Austen (1936: 426) noted that *M. hirsuta* is: "… devoid of ocelli and halteres (though the latter may perhaps be represented by a pair of small sessile knobs)". It has therefore been perpetuated in the literature that the halteres are entirely absent in *M. hirsuta* (e.g., Kirk-Spriggs & Stuckenberg 2009; Matile 1994). These "sessile knobs" were re-examined using SEM (Fig. 48), and given their structure and points of insertion, immediately to the base of the wings, these are here interpreted as being homologous with the halteres of other Diptera, although much reduced and highly modified, commensurate with similar reduction and modification of the wings. The haltere stem is extremely short and laterally-expanded at the base and is devoid of setation; the knob is elongated and somewhat capsulate in profile, and is clothed in moderately long, fine and curved apically-directed setae and some widely-spaced extremely long and thick setae.

Functional morphology of adult and host association

Sexual dimorphism in the leg structure of *M. hirsuta* was noted by van Emden (1950), who illustrated tarsomere 1 of the male and female midleg (fig. 3), but gave no explanation of the possible function of this structure in the male. Tarsomere 1 in the male (Fig. 36, *tars 1*), is slightly curved dorsally, the posterior angle is produced and sub-triangular, and the apical angle is wider than tarsomere 2. The ventral edge is broadly excavated, with irregular crenulations in the posterior half to two-thirds. The ventral edge is also furnished with overlapping, erect, slightly apically-directed strong spines throughout its length, being especially prevalent in the regions of the posterior and apical angles (Fig. 37). Tarsomere 1 of the female is straight, unmodified, and lacks the conspicuous spines present in the male. This structure probably serves in clasping the female during copulation, although this has yet to be observed, or may alternatively serve a grooming function.

Adaptive features associated with a cave-dwelling existence represent regressive evolution and include: reduced eyes and wings (or loss of wing functionality), absence of ocelli, and loss of cuticular pigmentation (Matile 1994; Vandel 1965). In addition, Bezzi (1914, cited in Austen 1936) mentions elongation of the arista, thickening of the proboscis, and development of the abdominal integument.

Austen (1936) briefly discussed structural adaptations for a cave-dwelling existence in *M. hirsuta* and noted some similarities with the structure of *Crumomyia* (as *Speomyia*) *absoloni* (Bezzi, 1914) (Sphaeroceridae) (see Matile 1994: 341, fig. 1), notably the swollen proboscis, the absence of ocelli, reduced eye size, the prominent epistoma, reduced thoracic setae, wings strongly truncated and narrow, and legs elongate.

Although *M. hirsuta* exhibits most of the adaptive features noted above, it remains unclear whether these represent adaptations to a cave-dwelling existence alone or whether there is any true association with Chiroptera, either as ectoparasites or phoretically.

Two families of Diptera, the Nycteribiidae and Streblidae, are known to be obligate ectoparasites of Chiroptera, while a third superficially similar family, the Mystacinobiidae (a monotypic family restricted to New Zealand), is phoretic. These three families represent only two origins; one in Mystacinobiidae (Kutty *et al*. 2010) and one in Nycteribiidae and Streblidae (see Dittmar *et al*. 2006; Petersen *et al*. 2007). Some authors even lump the last two mentioned families into the Hippoboscidae. Nycteribiidae and Streblidae are hematophagous with piecing mouthparts (Holloway 1976; Hutson & Oldroyd 1980*a*, *b*), but adults of Mystacinobiidae feeds on guano and are merely phoretic on bats (Holloway 1976). In reference to the mouthparts of *M. hirsuta*, van Emden (1950: 123) noted: "The lack of prestomal teeth and the large soft labella of the mouthparts (fig. 2) indicate that the adults must feed on readily-available liquid or semi-liquid matter, such as the juices of the excrement and perhaps sweat of the bats." There is, therefore, no evidence to suggest hematophagy in *M. hirsuta*. In the three families noted above the cuticle is thick and leathery and the legs are stout, a presumed adaptation to prevent removal and damage by the host (e.g., Marshall 1981), whereas in *M. hirsuta* the cuticle is thin and the legs long, fragile and easily broken.

The enlarged tarsal claws of *M. hirsuta* are long, smooth and strongly but evenly curved (Figs 39, 40, *clw*; 41), the puvilli are connected to tarsomere 5 basolaterally and consist of narrow, acutely-pointed blades with an arrangement of branched, regular Velcro-like hooks (Figs 39, 40, *pulv*; 41), the empodium is style-like, acutely-pointed

and clothed in short spines (Figs 39, 40, *emp*; 41), and tarsomere 5 is furnished with an very long, downcurved dorsal pre-apical seta.

The tarsal claws of Nycteribiidae and Strebilidae (Figs 43, 45, *clw*) are strongly folded with a narrow cleft. Although these structures could not be studied with SEM for *Mystacinobia zelandica* Holloway (Mystacinobiidae), figures presented by Holloway (1976, figs 20, 21) indicate that the same case applies. This narrow cleft is an adaptation to clinging to the host's fur and to prevent flies being dislodged by the action of the host. The pulvilli of Nycteribiidae and Strebilidae (Figs 44, 46) are composed of long narrow, closely-packed linear structures; in Nycteribiidae apically-expanded and in Strebilidae forming a mat of "hairs". Fig. 20 in Holloway (1976) indicates that the pulvilli of Mystacinobiidae may be similar to those in the Nycteribiidae.

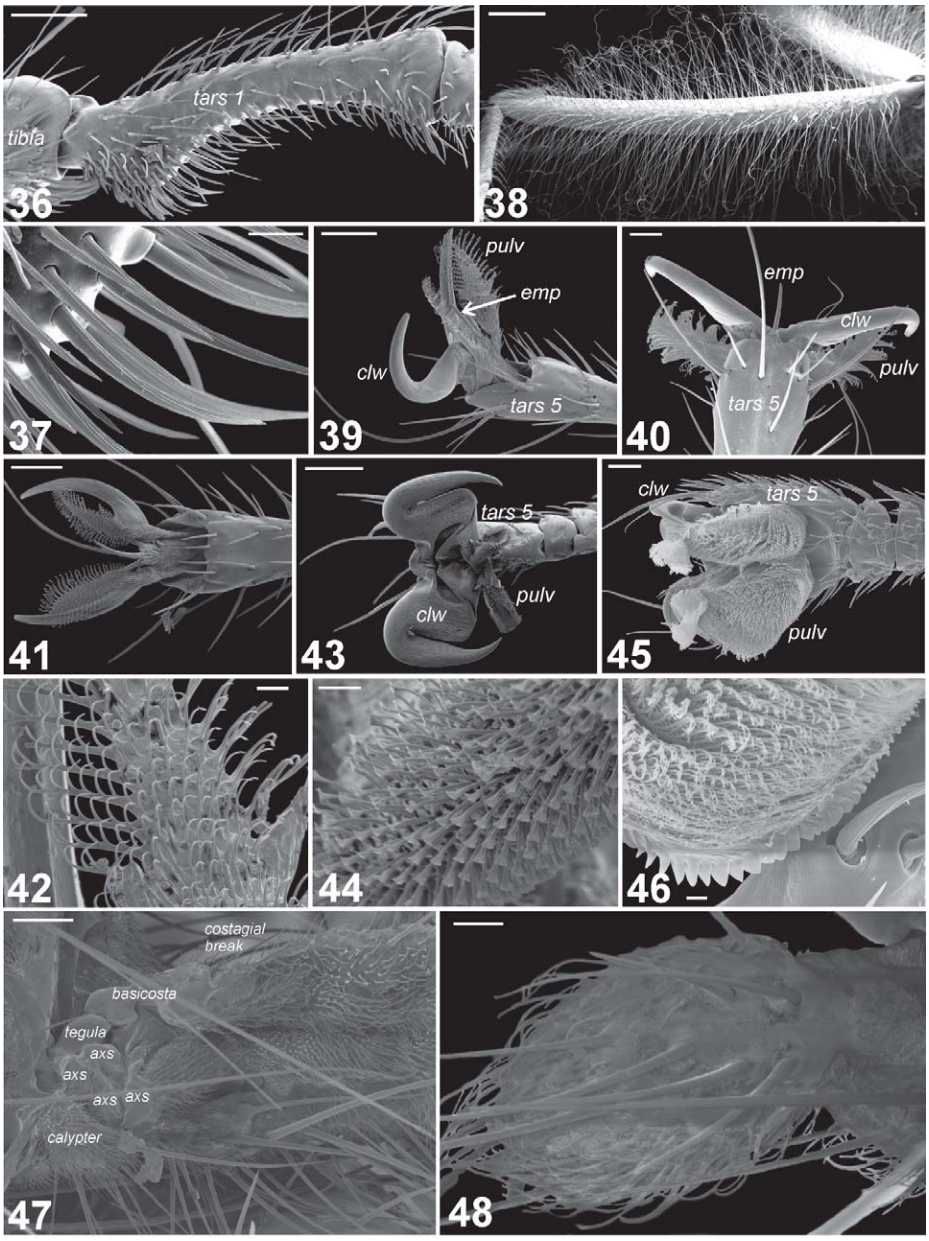
The structure of the tarsal claws of *M. hirsuta* are indicative of free-living habits and the Velcro-like processes on the pulvillus are too diminutive to serve any host-gripping function and are probably more conducive to adhering to the rock walls. We suggest then that *M. hirsuta* does not occur routinely on Chiroptera, either as ectoparasites or phoretically, and that van Emden's (1950) suggestion that flies may feed on the sweat of bats is probably not the case. Ultimately, this can only be confirmed by the collection of living Chiroptera, to assess the presence or absence of flies.

Phylogenetic implications of female reproductive tract

The morphology of *Mormotomyia* differs in many ways from that of the superficially similar bat fly, *Mystacinobia zelandica*, known only from New Zealand. *Mystacinobia* is a calyptrate taxon probably affiliated with Oestroidea (Gleeson *et al*. 2000; Kutty *et al*. 2010). As opposed to *Mormotomyia* it has three spermathecae, with long ducts and a large unsclerotized anteroventral "bursal pouch", with a field of brown armature anterodorsally adjacent to its entrance (Holloway 1976). This structure may be homologous with the dome-shaped fertilization chamber of *Musca domestica* (L.) (Leopold *et al*. 1978) and *Scatophaga stercoraria* (L.) (Arthur *et al*. 2008), or with the spiny area in the anteroventral vaginal wall of *Glossina austeni* Newstead (Pollock 1974). This interpretation remains speculative, however, and these structures require further detailed study in the Mystacinobiidae before homology can be verified.

Three spermathecae belong to the ground plan of Diptera in general (Hennig 1973) and Schizophora specifically (Hennig 1958; J.F. McAlpine 1989). Two spermathecae, as found in *Mormotomyia hirsuta*, commonly occur in acalyptrate families and this condition belongs to the ground plan of the superfamilies Carnoidea, Ephydroidea and Opomyzoidea (Kotrba & Baptista 2002; J.F. McAlpine 1989; Meier *et al*. 1997). In the Sphaeroceroidea, however, the plesiomorphic condition of three spermathecae is preserved in the ground plan (J.F. McAlpine 1989), although the number is reduced to two repeatedly within the superfamily.

As opposed to the inconspicuous dome-shaped fertilization chamber that occurs in the calyptrates (e.g., Arthur *et al*. 2008; Leopold *et al*. 1978), a distinct ventral receptacle is only known to occur in acalyptrate families (Kotrba 2000; J.F. McAlpine 1989). Large and heavily sclerotized forms typically occur in families of the superfamily Ephydroidea, namely in the Ephydridae (including *Risa* Becker), Diastatidae, Camillidae (in part) and Curtonotidae (in part) (see references in Kotrba & Mathis (2009)). Sclerotized forms also occur as analogous features in Agromyzidae (e.g., Sasakawa 1958), and in



Figs 36–48. (36–42) Scanning electron micrographs of adult male *M. hirsuta*: (36) tarsomere 1, lateral; (37) same, detail of setation; (38) foretibia, dorsolateral; (39) tarsal claw and pulvillus of foreleg, ventrolateral; (40) same, dorsal; (41) tarsal claw and pulvillus of hindleg, ventral; (42) same, detail of pulvillus, ventrolateral; (43–46) SEMs of Nycteribiidae and Streblidae: (43) Nycteribiidae, tarsal claw and pulvillus of foreleg, ventral; (44) same, detail of pulvillus, ventral; (45) Streblidae (*Nycteribosca* sp.), tarsal claw and pulvillus of foreleg, ventral; (46) same, detail of pulvillus, ventral; (47, 48) SEMs of female *M. hirsuta*: (47) wing base, dorsal; (48) halter, dorsal. Scale bars: Fig. 36 = 200 μm; Figs 37, 45, 48 = 20 μm; Fig. 38 = 500 μm; Figs 39, 41, 43 = 100 μm; Figs 40, 47 = 50 μm; Fig. 42 = 10 μm; Fig. 44 = 5 μm; Fig. 46 = 2 μm.

various smaller families, such as the Tanypezidae and Strongylophthalmiidae (Steyskal 1987*a*, *b*), the Lonchaeidae, Clusiidae and some others. Most notably, to our knowledge, a sclerotized ventral receptacle has not been described in any family of the Sphaeroceroidea.

Neither the presence of two spermathecae nor the sclerotized ventral receptacle supports the placement of the Mormotomyiidae in the Sphaeroceroidea. Instead, the slipper-shaped, sclerotized ventral receptacle present in the Mormotomyiidae (Fig. 34) is reminiscent of small-sized camillid or ephydrid ventral receptacles (albeit lacking the operculum). The placement of the Mormotomyiidae within the Ephydroidea would also be consistent with the presence of two spermathecae.

A recent extensive molecular study of the Schizophora indicates that the superfamily Ephydroidea comprises seven families, namely Braulidae, Camillidae, Cryptochaetidae, Curtonotidae, Diastatidae (including *Campichoeta* Macquart), Drosophilidae and Ephydridae (Wiegmann *et al*. 2011), two of these taxa (Braulidae and Cryptochaetidae) being transferred to the Ephydoidea as a direct result of the study. Remarkably, both these last-named taxa are described as having a single, relatively weakly sclerotized spermatheca (J.F. McAlpine 1987; Peterson 1987). Further studies of these groups are required to establish whether this structure may represent a misinterpreted ventral receptacle, while the spermathecal capsules are completely reduced, as is common in part of the Ephydroidea (Camillidae (in part), Diastatidae, Ephydridae; see references in Meier *et al*. 1997).

The evidence presented above provides some support for the inclusion of the Mormotomyiidae in the Ephydroidea. Additional studies using molecular methods are currently underway.

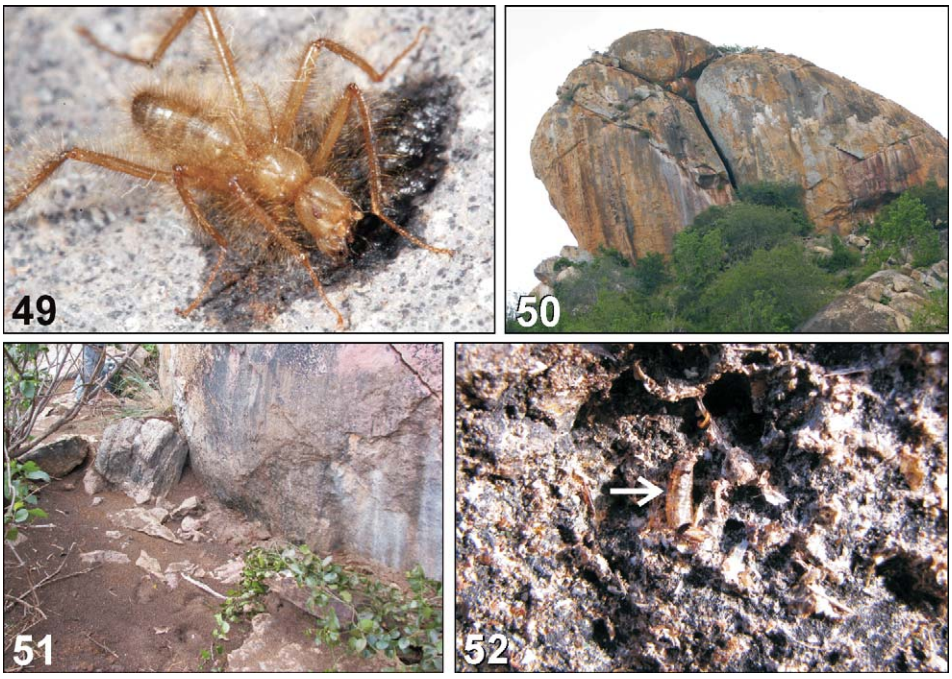
Cavernicolous association

In biospeleology a distinction is made between those species occurring in, and restricted to, the dark zone and those occurring in the parietal (shaded) zone. Vandel (1965: 185–186) regarded true troglobites as rare in the Diptera; those that do exhibit such habits being restricted to ancient, near-basal groups.

Diptera occurring in the parietal zone are far more numerous and better documented, and include examples in the families Camillidae, Milichiidae, Phoridae and Sphaeroceridae, *etc*. Due largely to the lack of phenotypic modifications (Culver 1982: 15–16) and published accounts of larval associations of many of these groups, these are frequently ranked as "troglophiles" rather than proper troglobites (e.g., Vandel 1965).

In the most recently published review of cavernicolous Diptera, Matile (1994: 342) took the more pragmatic view that troglobites represent obligate, cave-inhabiting species that are unable to survive above ground ("Un troglobie est un cavernicole obligatoire, qui ne pourrait survivre ailleurs que dans le milieu hypogé.").

Séguy (1963) did not recognise *M. hirsuta* as a true troglobite and classified it as a troglophile. Vandel (1965), however, who was apparently unaware of Séguy's work, classified the species as a troglobite. Matile (1994) regarded *Mormotomyia* as a true troglobite, but stated (p. 346): "Ils ne sont placés ici dans les troglobies qu'avec hésitation, et seulement en raison de leur isolement géographique et phylogénétique; le groupe-frère des Mormotomyiidae est probablement représenté par la famille des Heleomyzidae …" [They are placed here as troglobians with hesitation, and only because



Figs 49–52. (49) Living male of *Mormotomyia hirsuta*; (50) Ukasi Hill (north face), Kenya, type locality of *M. hirsuta*, illustrating rock fissure in which flies normally reside; (51) Accumulated deposit of damp bat guano washed from rock fissure on north face of Ukasi Hill, breeding site from which larvae and puparia were extracted; (52) Empty puparium of *M. hirsuta* (arrowed) attached to fissure wall *c*. 0.3 metres from substrate. Figs 49, 52 © R. Copeland, Figs 50, 51 © A.Kirk-Spriggs.

of their geographical and phylogenetic isolation; the sister group of Mormotomyiidae is probably represented by the family of Heleomyzidae …].

The type locality of *M. hirsuta* is not a cave in the true sense, but comprises an outcrop of granitic and biotitic feldsparic gneiss that split vertically, forming a narrow rock fissure that transects the outcrop from north to south and from top to bottom (Fig. 50). The orientation of the rock fissure allows light to penetrate to ground level, even at two-thirds of the distance through the fissure, and conditions within this cleft must, therefore, be regarded as parietal. Despite the fact that the habitat is parietal, the presumed restrictive microclimatic conditions prevalent deep within the cleft, the larval dependency on bat guano and the inability of adults to fly and disperse, coupled with other morphological adaptations to a cavernicolous lifestyle, clearly indicate that *M. hirsuta* is a true troglobite (*sensu* Matile 1994).

ACKNOWLEDGEMENTS

Scanning electron micrographs were captured by kind arrangement with the Centre for Microscopy (University of the Free State, Bloemfontein, South Africa); Pieter van Wyk and Beanélri B. Janecke are thanked for their assistance with specimen preparation and imaging. AHK-S's participation in the "*Mormotomyia* Expedition 2010" was supported by the National Research Foundation Incentive Funding for Rated Researchers (IFR2010041300021). Muscidae were identified by Márcia Couri, Chloropidae by John

Ismay and Milichiidae by John Swann. We thank Chief Benjamin Musoo for generously allowing us to explore the Ukasi area. The following individuals also participated in the expedition and are thanked for their assistance in the field: Bruno Leru, Leonard Ngala Mmasava, Christophe Plantamp (all ICIPE) and Juliet Muriuki. F. Christian Thompson provided details of nomenclature. Thomas Papp supplied literature, information and images of the tarsal claw and puvulli of Streblidae (Figs 45, 46). Jeff Cumming assisted with the interpretation of wing sclerites and gave advice on terminology. Marc De Meyer, Rudolf Meier, John Irish, Wayne Mathis, Steve Gaimari and Ray Miller are thanked for their useful corrections and suggestions.

REFERENCES

Arthur, B.I. Jr., Sbilordo, S.H., Pemberton, A.J. & Ward, P.I. 2008. The anatomy of fertilization in the yellow dung fly *Scathophaga stercoraria*. *Journal of Morphology* **269**: 630–637.

Austen, E.E. 1936. A remarkable semi-apterous fly (Diptera) found in a cave in East Africa, and representing a new family, genus, and species. *Proceedings of the Zoological Society of London* [**1936**]: 425–431.

Bezzi, M. 1914. *Speomyia absoloni*, n.g., sp.n. (Dipt.), eine degenerierte Höhlengliege aus dem herzegovinisch-montenegrinosohen Hochgebirge. *Zoologischer Anzeiger* **44**: 504–507.

Cockerell, T.D.A. 1917. A fossil *tsetse* fly and other Diptera from Florissant, Colorado. *Proceedings of the Biological Society of Washington* **30**: 19–22.

Courtney, G.W., Sinclair, B.J. & Meier, R. 2000. 1.4. Morphology and terminology of Diptera larvae. *In*: Papp, L. & Darvas, B., eds, *Contribution to a manual of Palaearctic Diptera (with special reference to flies of economic importance), Volume 1. General and applied dipterology.* Budapest: Science Herald, pp. 85–161.

Culver, D.C. 1982. *Cave life evolution and ecology*. Cambridge, MA: Harvard University Press.

Dittmar, K., Porter, M.L., Murray, S. & Whiting, M.F. 2006. Molecular phylogenetic analysis of nycteribiid and streblid bat fies (Diptera: Brachycera, Calyptratae): Implications for host associations and phylogeographic origins. *Molecular Phylogenetics and Evolution* **38**: 155–170.

Gleeson, D.M., Howitt, R.L.J. & Newcomb, R.D. 2000. The phylogenetic position of the New Zealand batfly, *Mystacinobia zelandica* (Mystacinobiidae; Oestroidea) inferred from mitochondrial 26S ribosomal DNA sequence data. *Journal of the Royal Society of New Zealand* **30**: 155–168.

Griffiths, G.C.D. 1972. *The phylogenetic classification of Diptera Cyclorrhapha, with special reference to the structure of the male postabdomen*. The Hague, Holland: W. Junk.

Grimaldi, D. & Engel, M.S. 2005. *Evolution of the insects*. Cambridge: Cambridge University Press.

Hennig, W. 1958. Die Familien der Diptera Schizophora und ihre phylogenetischen Verwandtschaftsbeziehungen. *Beiträge zur Entomologie* **8**: 505–688.

———1971. Neue Untersuchungen über die Familien der Diptera Schizophora (Diptera: Cyclorrhapha). *Stuttgarter Beiträge zur Naturkunde* **226**: 1–76.

———1973. 31. Ordnung Diptera (Zweiflügler). *In*: *Handbuch der Zoologie*. IV. Band: Arthropoda – 2. Hälfte: Insecta (Zweite Auflage). 2. Teil: Spezielles. Berlin: W. De Gruyter.

Holloway, B.A. 1976. A new bat-fly family from New Zealand (Diptera: Mystacinobiidae). *New Zealand Journal of Zoology* **3**: 279–301.

Hutson, A.M. & Oldroyd, H. 1980*a*. 88. Family Streblidae. *In*: Crosskey, R.W., ed., *Catalogue of the Diptera of the Afrotropical Region*. London: British Museum (Natural History), pp. 772–774.

———1980*b*. 89. Family Nycteribiidae. *In*: Crosskey, R.W., ed., *Catalogue of the Diptera of the Afrotropical Region*. London: British Museum (Natural History), pp. 775–778.

Kirk-Spriggs, A.H. 2008. A contribution to the knowledge of the immature stages of *Curtonotum* (Diptera: Curtonotidae), from Africa and the Middle East, with a discussion of relationships to other known Ephydroidea larvae. *African Entomology* **16**: 226–243.

Kirk-Spriggs, A.H., Barraclough, D.A. & Meier, R. 2002. The immature stages of *Katacamilla cavernicola* Papp, the first described for the Camillidae (Diptera: Schizophora), with comparison to other known Ephydroidea larvae, and notes on biology. *Journal of Natural History* **36**: 1105–1128.

Kirk-Spriggs, A.H. & Stuckenberg, B.R. 2009. Afrotropical Diptera – rich savannas, poor rainforests. *In*: Bickel, D., Pape, T. & Meier, R., eds, *Diptera diversity: status, challenges and tools*. Leiden: Brill Academic Publishers, pp. 155–196.

Kotrba, M. 2000. 1.3. Morphology and terminology of the female postabdomen. *In*: Papp, L. & Darvas, B., eds, *Contributions to a Manual of Palaearctic Diptera.* Vol. 1. Budapest: Science Herald, pp. 75–84.

KOTRBA, M. & BAPTISTA, A. 2002. The internal female reproductive tract of Opomyzidae (Diptera, Schizophora). *Studia dipterologica* **9**: 57–71.

KOTRBA, M. & MATHIS, W.N. 2009. The internal female reproductive tract of the enigmatic genus *Risa* (Diptera: Schizophora: Ephydroidea) and its phylogenetic implications. *Proceedings of the Entomological Society of Washington* **111**: 627–640.

KUTTY, S.N., PAPE, T., WIEGMANN, B.M. & MEIER, R. 2010. Molecular phylogeny of the Calyptratae (Diptera: Cyclorrhapha) with an emphasis on the superfamily Oestroidea and the position of Mystacinobiidae and McAlpine's fly. *Systematic Entomology* **35**: 614–635.

LEOPOLD, R.A., MEOLA, S. & DEGRUGILLIER, M.E. 1978. The egg fertilization site within the house fly, *Musca domestica* (L.) (Diptera: Muscidae). *International Journal of Insect Morphology and Embryology* **7**: 111–120.

MARSHALL, A.G. 1981. *The ecology of ectoparasitic insects*. London: Academic Press.

MATILE, L. 1994. Les Dipteres cavernicoles. *In*: Juberthie, C. & Decu, V., eds, *Encycloépaedia biospeologica*. 1. Moulis. Bucarest: Société de Biospéologie, pp. 341–357.

MCALPINE, D.K. 1985. The Australian genera of Heleomyzidae (Diptera: Schizophora) and a reclassification of the family into tribes. *Records of the Australian Museum* **36**: 203–251.

MCALPINE, J.F. 1987. Chapter 100. Cryptochaetidae. *In*: McAlpine, J.F. *et al*., eds, *Manual of Nearctic Diptera*. Vol. 2. Ottawa: Agriculture Canada, Biosystematics Research Centre, Monograph 28, pp. 1069–1072.

MCALPINE, J.F. 1989. Phylogeny and classification of the Muscomorpha. *In*: Borkent, A., McAlpine, J.F., Wood, D.M. & Woodley, N.E., eds, *Manual of Nearctic Diptera.* Vol. 3. Ottawa: Agriculture Canada, Biosystematics Research Centre, Monograph 32, pp. 1397–1518.

MEIER, R., KOTRBA, M. & BARBER, K. 1997. On the natural history and morphology of the egg, first instar larva, puparium, and female reproductive system of *Curtonotum helvum* (Curtonotidae; Ephydroidea; Diptera). *American Museum Novitates* **3219**: 1–20.

PETERSEN, F.T., MEIER, R., KUTTY, S.N. & WIEGMANN, B.M. 2007. The phylogeny and evolution of host choice in the Hippoboscoidea (Diptera) as reconstructed using four molecular markers. *Molecular Phylogenetics and Evolution* **45**: 111–122.

PETERSON, B.V. 1987. Chapter 81. Braulidae. *In*: McAlpine, J.F. *et al*., eds, *Manual of Nearctic Diptera*. Vol. 2. Ottawa: Agriculture Canada, Biosystematics Research Centre, Monograph 28, pp. 913–918.

POLLOCK, J.N. 1974. Anatomical relations during sperm transfer in *Glossina austeni* Newstead (Glossinidae, Diptera). *Transactions of the Royal Entomological Society of London* **125**: 489–501.

PONT, A.C. 1980. Superfamily Muscoidea. 81. Mormotomyiidae. *In*: Crosskey, R.W., ed., *Catalogue of the Diptera of the Afrotropical Region*. London: British Museum (Natural History), p. 713.

SASAKAWA, M. 1958. The female terminalia of the Agromyzidae, with description of a new genus (I). *Scientific Reports of the Saikyo University, Agriculture, Kyoto* **10**: 133–150.

SÉGUY, E. 1963. Diptères hypogés recueillis par M. Paul A. Rémy en Yougoslavie. *Memoires du Muséum nationale d'histoire naturelle, Série A Zoologie* **18**: 187–229.

STEYSKAL, G.C. 1987*a*. Chapter 58. Tanypezidae. *In*: McAlpine, J.F. *et al*., eds, *Manual of Nearctic Diptera*. Vol. 2. Ottawa: Agriculture Canada, Biosystematics Research Centre, Monograph 28, pp. 773–776.

———1987*b*. Chapter 59. Strongylophthalmyiidae. *In*: McAlpine, J.F. *et al*., eds, *Manual of Nearctic Diptera*. Vol. 2. Ottawa: Agriculture Canada, Biosystematics Research Centre, Monograph 28, pp. 777–779.

TSCHIRNHAUS, M., von & HOFFEINS, Ch. 2009. Fossil flies in Baltic amber – insights in the diversity of Tertiary Acalyptratae (Diptera, Schizophora), with new morphological characters and a key based on 1,000 collected inclusions. *Denisia* **26**: 171–212.

VANDEL, A. 1965. *Biospeleology, the biology of cavernicolous animals*. International Series of Monographs in Pure and Applied Biology, 22. London: Pergamon Press.

VAN EMDEN, F.I. 1950. *Mormotomyia hirsuta* Austen (Diptera) and its systematic position. *Proceedings of the Royal Entomological Society of London (B)* **19**: 121–128.

WIEGMANN, B.M., TRAUTWEIN, M.D., WINKLER, I.S., BARR, N.B., KIM, J., LAMBKIN, C., BERTONE, M.A., CASSEL, B.K., BAYLESS, K.M., HEIMBERG, A.M., WHEELER, B.M., PETERSON, K.J., PAPE, T., SINCLAIR, B.J., SKEVINGTON, J.S., BLAGODEROV, V., CARAVAS, J., KUTTY, S.N., SCHMIDT-OTT, U., KAMPMEIER, G.E., THOMPSON, F.C., GRIMALDI, D.A., BECKENBACH, A.T., COURTNEY, G.W., FRIEDRICH, M., MEIER, R. & YEATES, D.K. 2011. Episodic radiations in the fly tree of life. *Proceedings of the National Academy of Sciences United States* **108**. (doi: 10.1073/pnas.1012675108)