Proposal of Karliella gen. n. for the Afrotropical 'Pegomya' sexpunctata Karl, 1935 (Diptera: Anthomyiidae), a Possible Kleptoparasite of Dung-Breeding Beetles

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Source: African Invertebrates, 54(2) : 335-347

Published By: KwaZulu-Natal Museum

URL: https://doi.org/10.5733/afin.054.0205

African Invertebrates Vol. 54 (2): 335–347 Pietermaritzburg 7 August 2013

Proposal of *Karliella* gen. n. for the Afrotropical '*Pegomya*' *sexpunctata* Karl, 1935 (Diptera: Anthomyiidae), a possible kleptoparasite of dung-breeding beetles

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ABSTRACT

The genus *Karliella* Michelsen, gen. n., is described to accommodate *Pegomyia sexpunctata* Karl, 1935 (syn.: *Pegomyia abdominalis* Emden, 1941). The peculiar morphology of *Karliella* makes it difficult to find a closer relationship to any particular anthomyiid genus or group of genera, which suggests that it represents the only extant member of an ancient lineage. The type species and only included species, *Karliella sexpunctata* (Karl, 1935), comb. n., appears to be locally abundant in dry and mesic woodland of Namibia and South Africa, but has also been found in Botswana and Zambia. The larvae probably develop in dung from large herbivorous mammals. The female has been observed laying eggs on newly formed, unburied scarab dung-balls, but whether this is customary behaviour is unknown.

KEY WORDS: Anthomyiidae, *Karliella*, southern Africa, new genus, true flies, dung beetles, kleptoparasitism.

INTRODUCTION

The chapter on the family Anthomyiidae that I am preparing to the forthcoming *Manual of Afrotropical Diptera* will need a key to all regional genera for the adults of both sexes. The Afrotropical anthomyiid fauna appears rather depauperate, with 66 described species recorded to date (Kirk-Spriggs & Stuckenberg 2009). Practically all Afrotropical species known so far may readily be assigned to one of the following 11 genera, originally proposed for Palaearctic species: *Anthomyia* Meigen, 1803, *Botanophila* Lioy, 1864, *Calythea* Schnabl & Dziedzicki, 1911, *Chirosiomima* Hennig, 1966, *Delia* Robineau-Desvoidy, 1830, *Emmesomyia* Malloch, 1917, *Enneastigma* Stein, 1916, *Fucellia* Robineau-Desvoidy, 1841, *Lasiomma* Stein, 1916, *Leucophora* Robineau-Desvoidy, 1830 and *Pegomya* Robineau-Desvoidy, 1830. However, a single species currently assigned to *Pegomya* Robineau-Desvoidy (syn.: *Pegomyia* Macquart, 1835, unjustified emendation) (Pont & Ackland, 1980) and recorded so far from South Africa, Namibia, Botswana and Zambia, is a remarkable exception. It was first described by Karl (1935) as *Pegomyia sexpunctata* from three males and two females from Montrose, South Africa, and subsequently by Emden (1941) as *Pegomyia abdominalis* from two females from Mbala, Zambia, at the Tanzanian border. The species was described at a time when the generic classification of anthomyiid flies was somewhat preliminary, often disregarding the several characters of the male terminalia now considered essential by all students of the family. The yellowish legs and abdomen, bare anepimeron and ventrally setulose vein C are all characters that the currently recognized species shares with most species of *Pegomya* and surely the reason why it was first described in that genus. However, Emden (1941) admitted that it might be "entitled to generic rank" because of the presence of an apical *pv* seta on the hind tibiae.

The present paper reassigns Karl's species *Pegomyia sexpunctata* to a new monotypical genus, *Karliella* gen. n. Morphological evidence in support of this is provided

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in a redescription of the male and female. The coprophagy by the larvae is further incompatible with classification in *Pegomya*, a genus in which the larvae known so far feed on fresh tissue from either plants or fungi.

MATERIAL AND METHODS

The specimens examined in this study belong to the National Museum, Bloemfontein, South Africa (BMSA), National Museum of Namibia, Windhoek, Namibia (NMNW), Natural History Museum, London, UK (BMNH), Natural History Museum of Denmark, University of Copenhagen, Denmark (ZMUC), and Senckenberg Deutsches Entomologisches Institut, Eberswalde, Germany (SDEI). Photographs were taken using a Leica digital camera M205A mounted on a Leica DFC 420 stereomicroscope. Images were processed with a Leica Application Suite program. Stacking and final processing were carried out with Helicon Focus and Adobe Photoshop software. Adult morphological terminology follows Cumming and Wood (2009).

Abbreviations: *a* – anterior, *ad* – anterodorsal, *av* – anteroventral, *d* – dorsal, *p* – posterior, *pd* – posterodorsal, *pv* – posteroventral, *v* – ventral.

TAXONOMY

Genus **Karliella** gen. n.

Type species: *Pegomyia sexpunctata* Karl, 1935.

Etymology: The new genus is named after Otto Karl (1868–1945), the author of the type species. Karl lived in the Pommeranian city of Stolp [now Słupsk], in the north-western part of present-day Poland. As a dipterist, he published faunistic papers on Brachycera from Pommerania and the island of Amrum at the German North Sea coast, but further contributed to the taxonomy of his favourite groups, the present families Muscidae, Fanniidae and Anthomyiidae.

Diagnosis: The following combination of characters will assist in recognition of *Karliella* as being distinct from other anthomyiid genera: femora and tibiae extensively or wholly light-coloured, ochre-brown to yellow; abdomen with paired dark spots at anterior margins of tergites III–V, both laterodorsally and ventrally; arista plumose, longest rays at least ⅔ as long as width of postpedicel; upper occiput bare below postocular setae; vein C bare on the dorsal surface and setulose on the ventral surface; hind tibia with 1–4 *pd* setae, none of them reaching half the length of hind tarsomere 1, and with a short apical *pv* seta.

Karliella sexpunctata (Karl, 1935), **comb. n.**

Figs 1–21

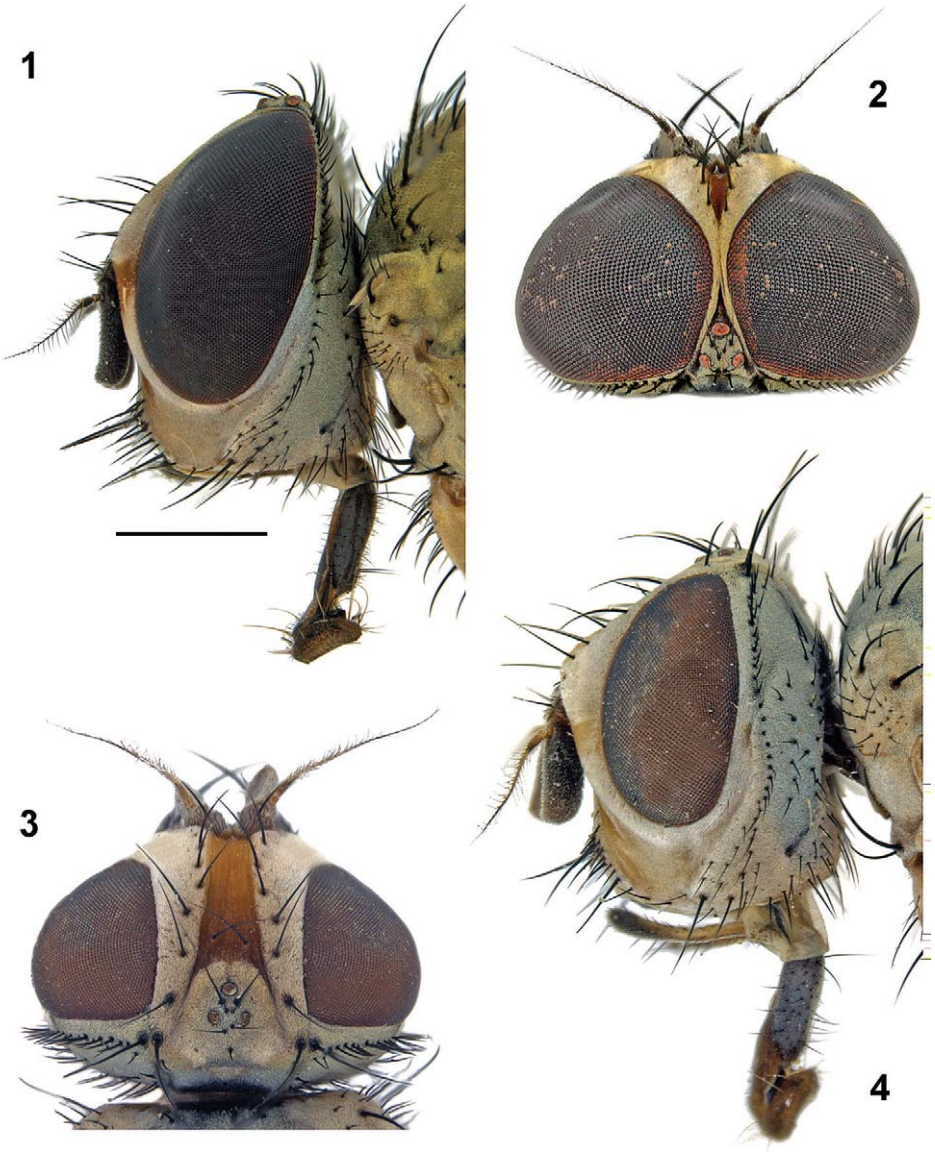
Pegomyia sexpunctata: Karl 1935: 45, fig. 3 (South Africa, ♂ and ♀).
Pegomyia abdominalis Emden, 1941: 263 (Zambia, ♀). Synonymized by Pont and Ackland (1980: 718).

Description:

Size. Both sexes very variable, as indicated by a wing length range of 3.0–5.5 mm.

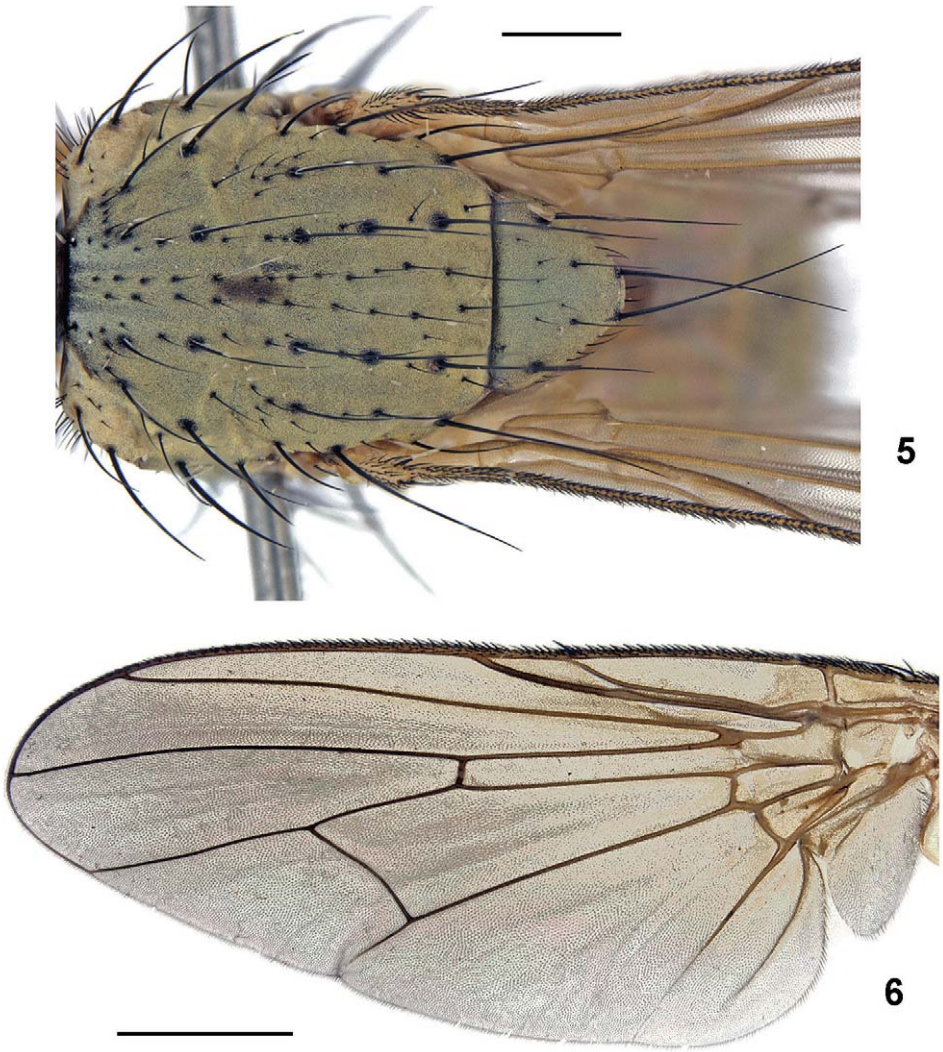
Male.

Head (Figs 1, 2): Ground colour dark on vertex, occiput and postgenae, light ochre-yellow on frons, parafacials and genae, covered in light grey to silvery grey dusting;



Figs 1–4. *Karliella sexpunctata* (Karl): (1, 2) male head, lateral and dorsal views; (3, 4) female head, dorsal and lateral views. Scale bar = 0.5 mm.

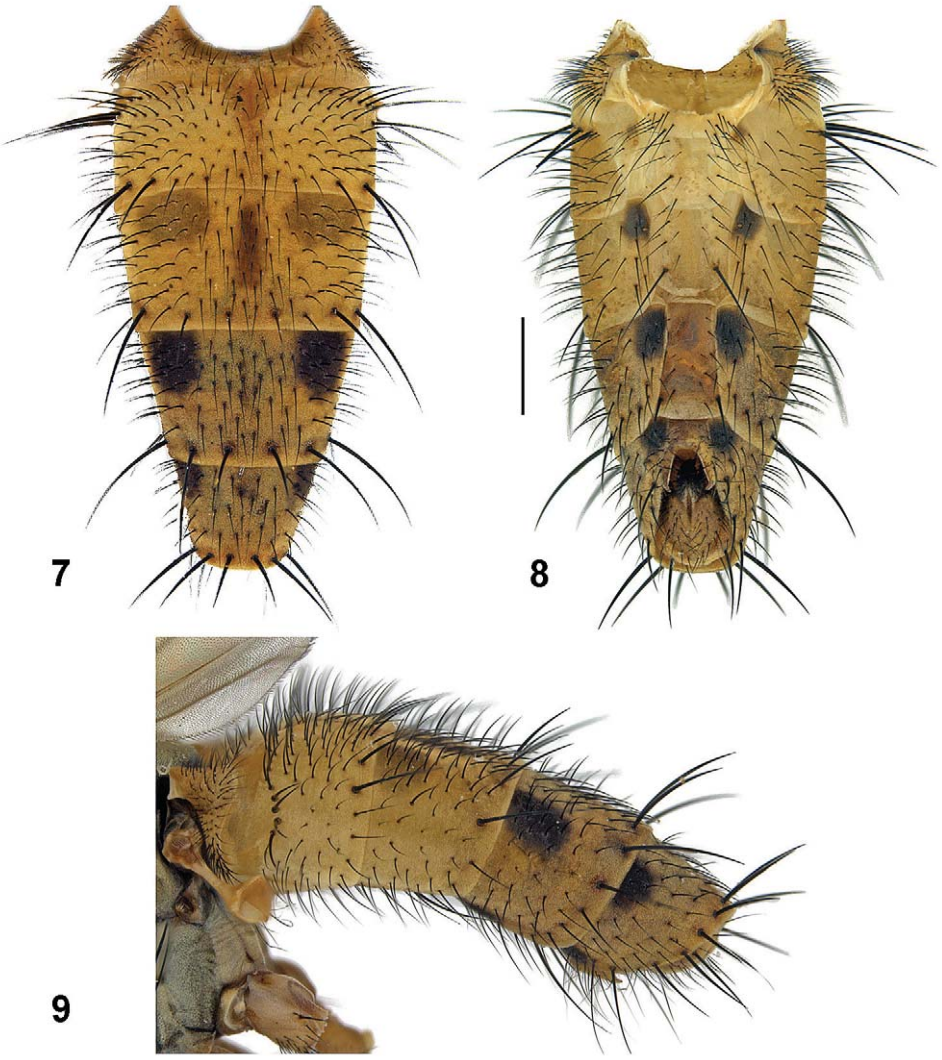
antennae brownish black or to varying extent orange-brown to orange-yellow on scape, pedicel and basal part of postpedicel; palpi brownish black, on basal half often ochre-yellow dorsally. Antennae distinctly shorter than comparatively deep face; plumose arista abruptly thickened basally; longest aristal rays ⅔ to fully as long as width of postpedicel. Proboscis short, with relatively slender haustellum and small labella; palpi slender, slightly longer than haustellum. Frons on upper part narrow, with contiguous



Figs 5, 6. *Karliella sexpunctata* (Karl): (5) male thorax, dorsal view; (6) male wing, ventral view. Scale bars: Fig. 5 = 0.5 mm, Fig. 6 = 1.0 mm.

parafrontalia, bare except for 2 or 3 pairs of frontals well below middle. Gena in profile 0.12–0.21× as deep as eye height, proportionately wider in large specimens; short genal setae arranged in single row but more abundant on aristal angle. Upper occiput without setulae below short postoculars.

Thorax (Fig. 5): Ground colour wholly dark or to varying extent ochre-yellow on prothoracic parts, covered in thick light grey to olive-grey dusting, on middle third of mesonotum sometimes with a median brown vitta. Prosternum bare. Dorsocentral setae 2+3; acrostichals, except near scutellum, setulose, abundant and arranged in two close-set rows. Prealar seta about the same length as but weaker than posterior notopleural seta.

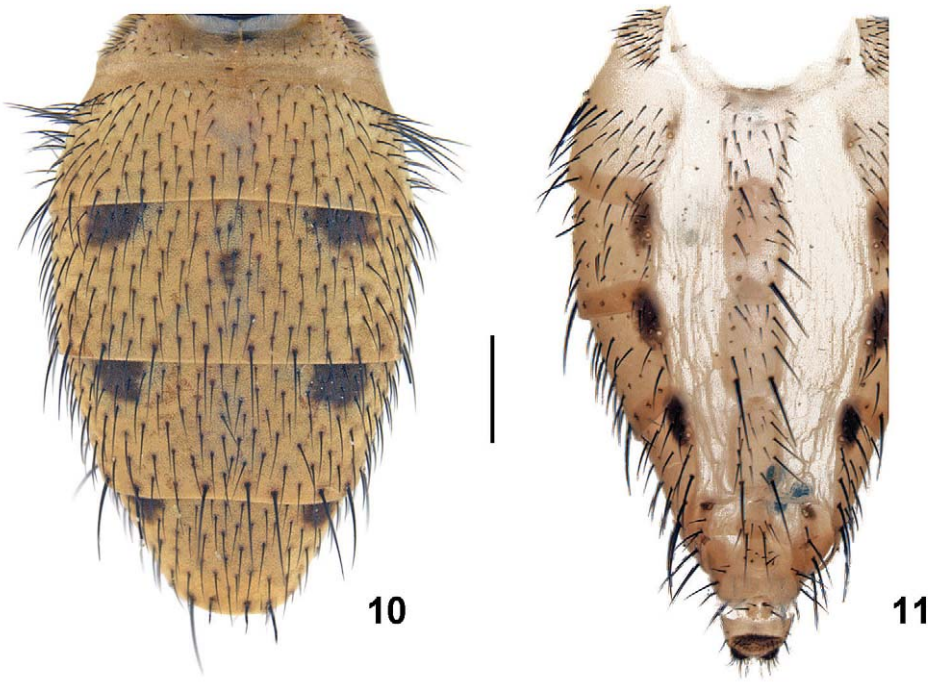


Figs 7–9. *Karliella sexpunctata* (Karl), male abdomen, dorsal (7), ventral (8) and lateral (9) views. Scale bar = 0.5 mm.

Scutellum with minute hair-like setulae beneath tip. Proepisternals 2, proepimerals (1–)2. Anepisternum with anterodorsal seta; katepisternal setae 1–2+2. Anepimeron, katepimeron and metapleuron bare.

Wings (Fig. 6): Wing and calypteres with a light brown tinge; haltere ochre-yellow. Vein C with short spinules in *ad* and *av* rows, bare on dorsal surface but with short setulae in two irregular rows ventrally. Lower calypter the same size as and thus distinctly projecting behind upper calypter in lateral view.

Legs: Ochre-yellow except for blackish tarsi, or sometimes (especially in small specimens) femora and hind tibia extensively brownish infuscated. Fore femur without *a*

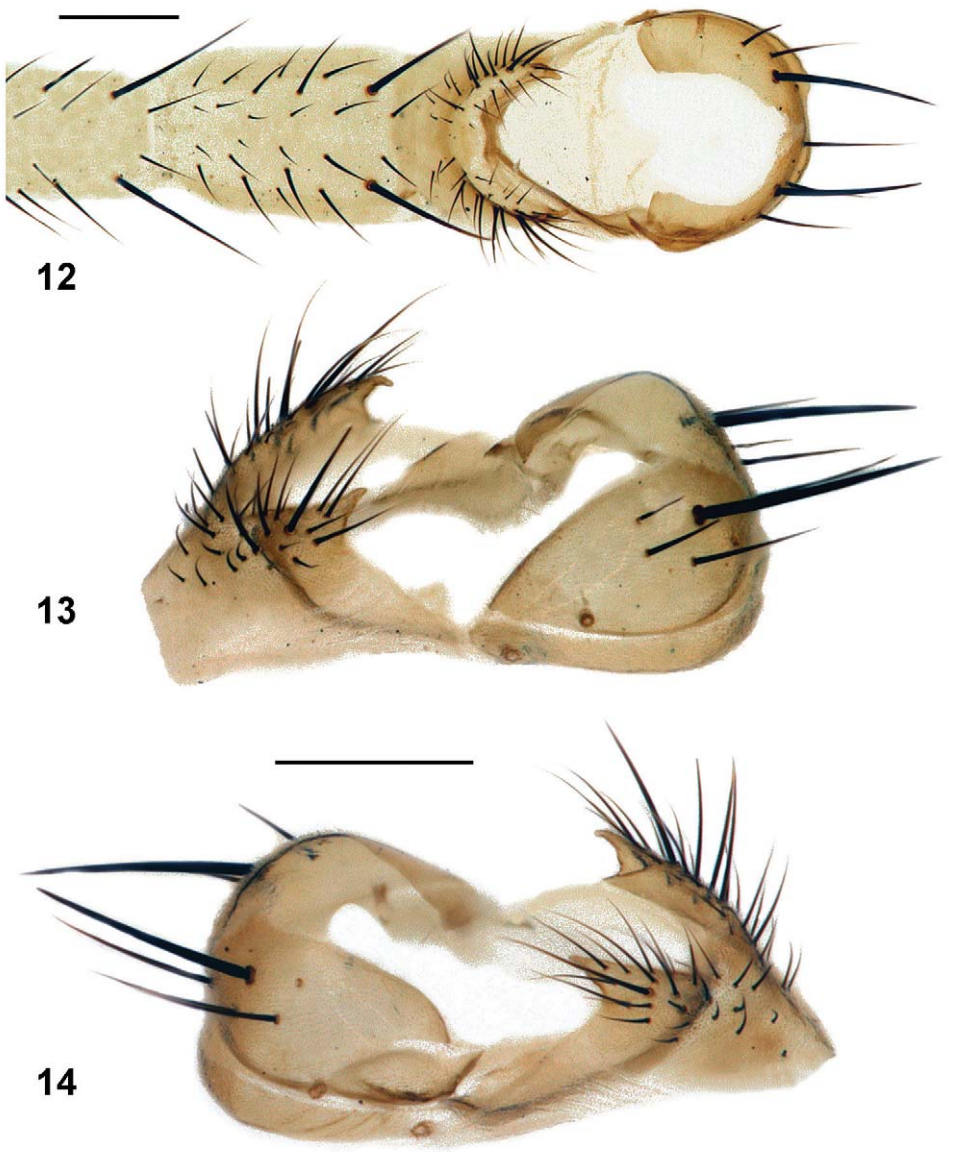


Figs 10, 11. *Karliella sexpunctata* (Karl), female abdomen, dorsal and ventral views. Scale bar = 0.5 mm.

setae; fore tibia with a weak (sometimes absent) *pv* seta in middle, apically with *d* seta flanked by short *ad* and *pd* setae. Mid femur without *av* setae, but with 2 short *pv* setae near base; mid tibia with a small *ad* seta on distal third, 1 *pd* and 1 *p* setae on middle third. Hind femur has, in addition to sub-basal *v* seta, 3 or 4 short *av* setae on at least distal half and a few short *pv* setae on middle third and apically; hind tibia with 1–3 *av*, 2–4 *ad*, 1–4 (normally 2–3) *pd* setae, 0–1 *p* seta near middle, and an apical *pv* seta about the same length as sub-basal *v* seta on hind tarsomere 1.

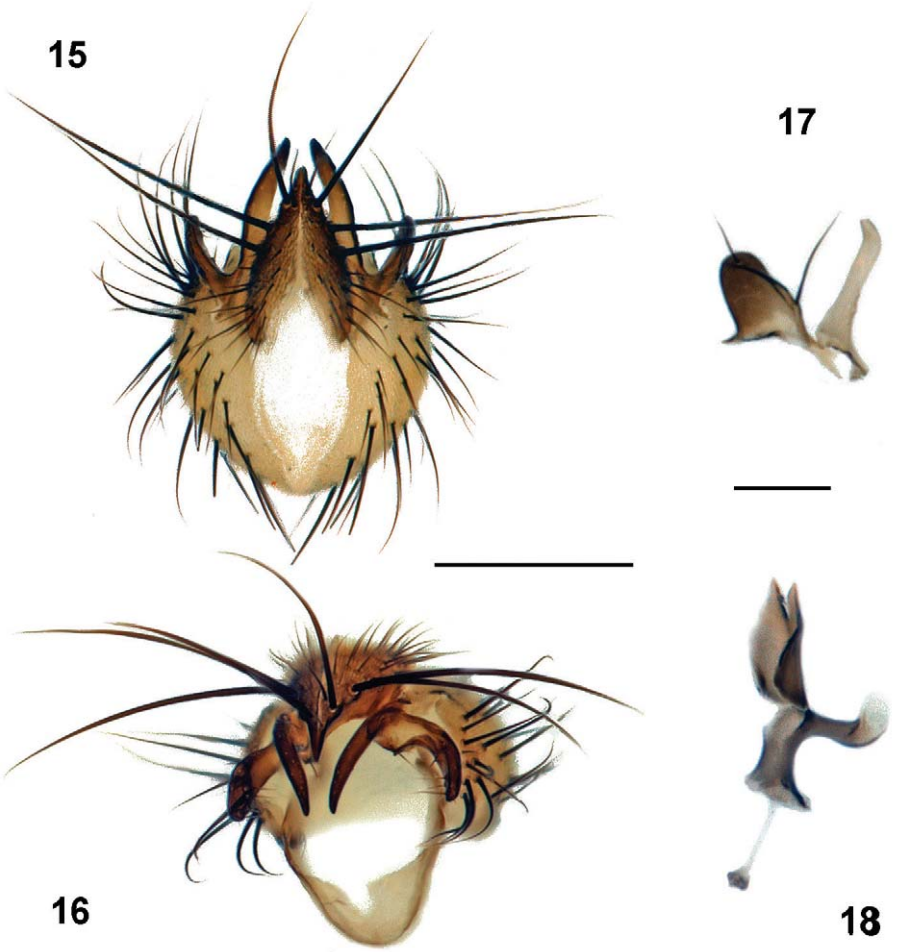
Abdomen (Figs 7–9, 12–14): Slender, conical, subcylindrical, rather tapering, with small terminalia. Covered in thin silvery grey dusting over pale ochre-yellow ground colour except for paired brown to blackish rounded spots laterodorsally and ventrally at anterior margins of tergites III–V, sometimes even with indications of a median dark stripe on tergites II and III; caudal parts of abdomen often darkened to a varying extent, especially in small specimens. Robust hind marginal setae present laterally on tergites II and III and forming complete rows on tergites IV and V; discal setae absent. Tergite VI short, bare, incorporating spiracles VI near lateral margins; syntergosternite VII+VIII with pair of strong setae and some setulae. Sternite I setulose; sternites II–V at fore margin each with a widely spaced pair of alpha-sensilla; sternites III and IV with a pair of strong hind marginal setae. Sternite V small, cordiform, with short, sharply tapering posterior lobes.

Hypopygium (Figs 15–18): Epandrium small, rather shallow, with a loose tuft of long-ish setulae at lower lateral sides; cercal plate on distal ⅔ forming an acutely pointed,



Figs 12–14. *Karliella sexpunctata* (Karl): (12) male sternites III–V and pregenital segments VI–VIII; (13, 14) male sternite V and pregenital segments VI–VIII, right and left lateral views. Scale bars = 0.25 mm.

beak-like process extending freely between surstyli and bearing three pairs of robust setae; a narrow, sclerotized bridge is formed between basal opposing parts of each cercus and surstylus; surstyli of unusual shape, split deeply into two slender arms; a narrow, sclerotized extension from epandrium unites with dorsobasal part of surstylus; bacilliform sclerites short, fused with ventrobasal extensions of surstyli; pregonites

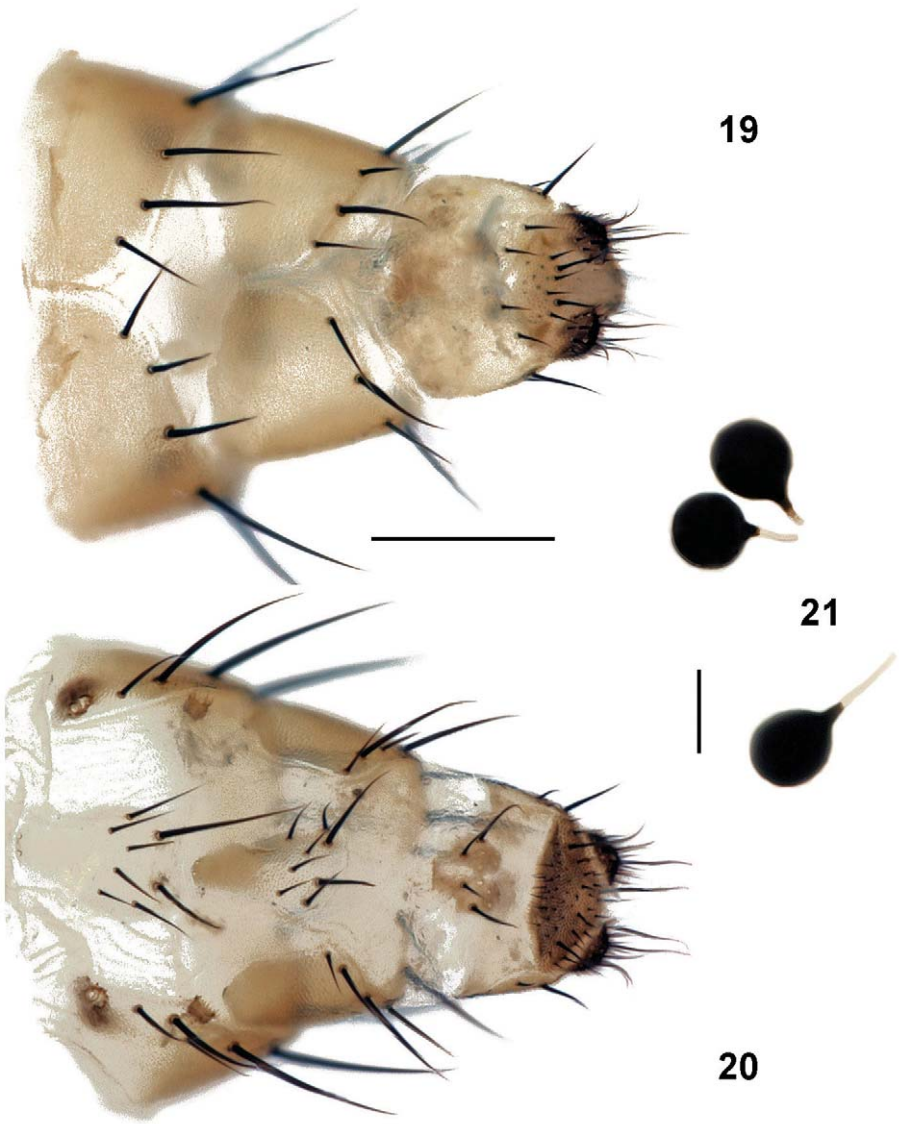


Figs 15–18. *Karliella sexpunctata* (Karl): (15, 16) hypopygium, posterior and ventral views; (17) pre- and postgonite, lateral view; (18) phallus and ejaculatory apodeme, anterolateral view. Scale bars: Figs 15, 16 = 0.25 mm, Figs 17, 18 = 0.1 mm.

with two setulae, at outer basal margin articulated with central plate of hypandrium; postgonites slender and bare except for group of sensilla sub-basally; outer extension of phallapodeme detached from hind margin of hypandrial plate and from inner bases of pregonites; basiphallus with epiphallic extension and articulating with a short, sessile distiphallus without paraphallic processes or sclerotized acrophallus; ejaculatory apodeme notably small.

Female. Resembles male, except for the usual sexual differences.

Head (Figs 3, 4): Frons rather narrow, less than 0.4× of total head width; frontal vitta markedly narrowing downwards: on upper part more than ⅓ of frontal width, above lunule much narrower than parafrontalia. Parafrontalia with (2–)3 orbital setae, 3(–4) frontal setae, without additional setulae; frontal vitta with pair of crossed interfrontal



Figs 19–21. *Karliella sexpunctata* (Karl): (19, 20) oviscapt, dorsal and ventral views; (21) spermathecae. Scale bars: Figs 19, 20 = 0.25 mm, Fig. 21 = 0.1 mm.

setae. Gena in profile 0.18–0.31× as deep as eye height, proportionately wider in large specimens.

Legs: Femora wholly ochre-yellow, with at the most tips of mid- and hind-femora narrowly infuscated. Fore tibia with larger *pv* seta and small *ad* seta on distal third. Mid tibial *ad* seta more robust. Hind femur with fewer (2–3) *av* setae confined to distal third, and only 2 *pv* setae, one near middle and one apically; hind tibia with fewer submedian setae: 1 *av*, 2–3 *ad*, 1–2 *pd* and 0 *p*.

Abdomen (Figs 10, 11, 19, 20): Sternite I bare. Sternites II–VII with paired alpha-sensilla at anterior margins. Oviscapt (6th and following segments) very short, barely ⅓ as long as rest of abdomen, thick, moderately tapering. Spiracles VI situated within anterolateral margins of tergite VI; spiracles VII situated in membrane immediately behind lateral hind margins of tergite VI. Tergites VI and VII fully divided mid-dorsally, tergite VIII only with a posterior notch. Short cerci and hypoproct with dense cuticular pubescence, other sclerites of oviscapt only with dusting. Three spermathecae (Fig. 21), smooth and globular, with a distinct neck.

Larvae and puparium. Unknown.

Egg. Creamy white, 1.1×0.4 mm, in shape of a thick banana, being more tapered at the anterior (micropylar) end than posteriorly. Chorion throughout very finely porous ('matt'), dorsally with two broad, parallel flanges running the length of the egg and delimiting a hatching pleat with coarse hexagonal ornamentation of raised ridges; chorion outside the flanges more or less longitudinally folded.

Type material: *Pegomyia sexpunctata* Karl, 1935. Syntypes 3♂ 2♀ (SDEI, examined by D.M. Ackland in 1975). SOUTH AFRICA: All specimens are labelled 'Montrose N.-Transv. Lingnau leg. 1926' and 'Pegomyia sexpunctata Karl.'. 1♂ also labelled '12.I.26' and 'Pegomyia sexpunctata n. sp./ det. O. Karl. Stolp i Pom', has been labelled as lectotype by D.M. Ackland, a designation presently effectuated. The remaining 2♂ 2♀ are paralectotypes and have been labelled accordingly by D.M. Ackland. 1♂ labelled '15.I.26', and the other paralectotypes '12.I.26'.

Pegomyia abdominalis Emden, 1941. Holotype ♀ and paratype ♀ (BMNH, examined). Mounted together on the same pin (larger lower specimen the holotype). ZAMBIA: Labelled '26.2.23. Loveridge/ Seemed to be oviposit-/ ing in dung ball of beetles. Mbala. 26/2/23'; 'TANGANYIKA T./ A. Loveridge.'; 'Pegomyia/ abdominalis sp. n./ van Emden det. 1940'; 'type the lower specimen'.

Other material examined (in BMSA, NMNW, ZMUC & BMNH): BOTSWANA: 1♂ 1♀ 29 km NE Kalkfontein, 12–13.iv.1972, Southern African Exp., BMNH; 1♀ Kuke Pan, 20°59'S 22°25'E, 14–15.iv.1972, Southern African Exp., BMNH; 1♂ L. Ngami, 19 km NE Sehithwa, 16–17.iv.1972, Southern African Exp., BMNH. NAMIBIA: *Bwabwata Park*: 2♂ 8♀ Bum Hill campsite (Kwando R.), 17°46'52"S 23°20'28"E, 10–13.ii.2004, A.H. Kirk-Spriggs, Malaise trap. *Eenhana dist.*: 1♂ 29 km E Okongo, 17°37'22"S 17°28'44"E, 14–15.x.1999, A.H. Kirk-Spriggs, T. Pape & W. Hauwanga, Malaise trap, dry woodland. *Etosha National Park*: 1♂ 2 km E Renostervlei, 19°09'59"S 14°33'12"E, 26–27.xii.1998, E. Marais, D.J. Mann & D. Newman, Malaise trap. *Gobabis dist.*: 2♂ 22♀ De Hoek, 21°56'26"S 20°58'55"E, 3–6.ii.2001, A.H. Kirk-Spriggs & E. Marais, Malaise trap; 17♂ 40♀ Somerkoms, 22°01'59"S 19°57'22"E, 6–8.ii.2001, A.H. Kirk-Spriggs & E. Marais, Malaise trap. *Grootfontein dist.*: 1♀ Toggenburg campsite, 19°28'32"S 17°58'04"E, 18–20.ii.2004, A.H. Kirk-Spriggs, Malaise trap. *Karibib dist.*: 4♂ Ameib Farm, 31 km NW Karibib, 31.i–2.ii.1972, Southern African Exp., BMNH. *Katima Mulilo dist.*: 3♂ 1♀ Salambala camp site, 17°50'01"S 24°36'09"E, 22–24.ii.2001, A.H. Kirk-Spriggs & E. Marais, Malaise trap, 8–10.ii.2004, A.H. Kirk-Spriggs, Malaise trap; 47♂ 17♀ Salambala forest, 17°50'02"S 24°36'20"E, 23–29.xii.2002, A.H. & M.K. Kirk-Spriggs, Malaise trap; 1♀ Salambala pan, 17°50'00"S 24°35'58"E, 1–4.iii.2001, A.H. Kirk-Spriggs, Malaise trap; 4♂ Kubunyana camp, Kwando River, 17°87'S 23°33'E, 28–30.x.2003, A.H. & M.K. Kirk-Spriggs, Malaise trap; 5♂ 10♀ near Mutonga village, 17°43.747'S 24°32.384'E, 930 m, 20–23.ii.2012, A.H. Kirk-Spriggs; 1♀ Hippo Lodge, Zambezi R., 17°29'45"S 24°20'03"E, 6–7.ii.2004, A.H. Kirk-Spriggs, Malaise trap. *Kaudom Game Park*: 9♀ 10 km W of Dussi, 18°48'32"S 20°43'57"E, 29–30.xii.1998, E. Marais, A.H. Kirk-Spriggs & D.J. Mann, Malaise trap. *Mukwe dist.*: 5♀ Dijuvo, Okavango River, 18°04'04"S 21°28'51"E, 1.i.1999, A.H. Kirk-Spriggs, E. Marais & D.J. Mann, Malaise traps and sweeping; 2♂ 4♀ Popa Falls Restcamp, 18°07'17"S 21°34'59"E, 13–16.ii.2004, A.H. Kirk-Spriggs, Malaise trap, riverine forest. *Okahandja distr.*: 2♂ 1♀ Okahandja, 2–4.ii.1972, Southern African Exp., BMNH. *Omaruru dist.*: 1♀ Weissenfels, 21°04'S 15°59'E, 11.ii.1986, J. Irish. *Otjinene dist.*: 1♂ 9♀ 3 km N Epikuro River, 21°22'26"S 20°06'09"E, 9–11.ii.2001, A.H. Kirk-Spriggs & E. Marais, Malaise trap. *Otavi dist.*: 3♀ 29 km SW Otavi, 6.iv.1972, Southern African Exp., BMNH. *Otjiwarongo dist.*: 1♀ Abachaus, xii.1951, G. Hobohm. *Rundu dist.*: 22♂ 80♀ Simanya, Okavango River, 17°33'17"S 18°32'30"E, 23–24.i.1998, A.H. Kirk-Spriggs & E. Marais, Malaise trap, riverine forest; 1♀ Katara, Okavango River, 17°48'56"S 18°53'38"E, 20–23.i.1998, A.H. Kirk-Spriggs & E. Marais, Malaise trap; 4♂ 5♀ 1 km S of Katara, 17°50'25"S 18°54'26"E, 22–23.i.1998, A.H. Kirk-Spriggs & E. Marais, Malaise trap, primary forest; 1♂ 3♀ Hamoye National Forest, 18°12'S 19°43'E, 5–8.iii.1999, E. Marais, Malaise trap; 1♀ Mile 46, 18°18'39"S 19°15'29"E, 25–27.iii.2003, A.H. Kirk-Spriggs, Malaise

trap. *Steinhausen dist.*: 1♀ 24 km N Witvlei, 22°16'S 18°26'E, 18.iii.1984, J.G.H. Londt & B. Stuckenberg, acacia thornveld & grassy verge of road. *Tsumkwe dist.*: 5♀ Nama, 19°54'34"S 20°44'08"E, 20–22.xii.1998, A.H. Kirk-Spriggs, E. Marais & D.J. Mann, Malaise trap; 1♀ 3 km N of Kano Vlei, 19°17'15"S 20°21'03"E, 19.xii.1998, A.H. Kirk-Spriggs, E. Marais & D.J. Mann, at light, dry woodland; 1♀ Aha Hills, 19°47'36"S 20°59'51"E, 21–25.xii.1998, A.H. Kirk-Spriggs, E. Marais & D.J. Mann, Malaise trap; 1♀ 2 km W Xawasha pan, 19°09'57"S 20°52'55"E, 26–27.xii.1998, A.H. Kirk-Spriggs & D.J. Mann, Malaise trap; 1♂ Homasi, 19°40'39"S 20°37'08"E, 24.xii.1998, A.H. Kirk-Spriggs, E. Marais & D.J. Mann, ex fallen Baobab tree branch. *West Caprivi Park*: 1♀ Kwando River, Susuwe, 17°45'37"S 23°20'55"E, 28.ix–2.x.1998, A.H. Kirk-Spriggs, Malaise trap, dry woodland; 8♂ 18♀ 5 km N Nova, 18°09'56"S 21°44'31"E, 16–18.xii.1999, E. Marais, D.J. Mann & D. Newman, Malaise trap, MV/UV light; 9♀ 4 km W Immelman air strip, 17°46'36"S 24°16'30"E, 14.xii.1999, E. Marais, D.J. Mann & D. Newman, UV/MV light. SOUTH AFRICA: *KwaZulu-Natal*: 1♂ 2♀ Mkuzi Game Reserve, main camp park area, 25°35'S 32°13'E, 100 m, 1.ii.1988, J.G.H. Londt; Ndumo Game Reserve, camp & riverine bush, 1♂ 4–9.x.1982, J.G.H. Londt; 6♂ 22♀ Ndumo Game Rreserve, main camp area, 26°54.652'S 32°19.719'E, 27–30.xi.2009, A.H. Kirk-Spriggs, Malaise traps, broad-leafed deciduous woodland; 1♂ 19♀ Ndumo Game Reserve, Shokwe area, 26°52.125'S 32°13.731'E, 30.xi–4.xii.2009, A.H. Kirk-Spriggs, Malaise traps, broad-leafed deciduous woodland; 21♂ 66♀ Ndumo Game Reserve, main road, 26°54.288'S 32°17.974'E, 4–8.xii.2009, A.H. Kirk-Spriggs, Malaise traps, sand & broad-leafed deciduous forest; 1♂ 4♀ Ndumo Game Reserve, pan, 26°54.288'S 32°17.974'E, 9–10.xii.2009, A.H. Kirk-Spriggs, Malaise traps, grassy floodplain. *Mpumalanga*: 1♀ Kruger National Park, Skukuza, 23.iii.1952, A.J.T. Janse & L. Vari; 1♂ same locality, 23.xi.1959, F. Zumpt; 1♂ Machadodorp, ii.1969, F. Zumpt.

Distribution: Apparently endemic to the southern part of the African continent, where it has so far been found in South Africa, Namibia, Botswana and Zambia.

Biology: Dissection of a large gravid female revealed 55 eggs, about one-third of them fully developed. There was no sign of a developing larva in a mature egg that was projecting from the vaginal opening, which indicates that *Karliella sexpunctata* is an obligate oviparous species.

The larvae are probably coprophagous, as judged by a published observation of a female apparently laying eggs on a scarab dung ball (Emden 1941). Dung from herbivorous mammals dessicates quickly in warm and dry climates. Accordingly, some Diptera have evolved the habit of making their offspring feed on dung buried by scarab beetles (see Sivinski *et al.* 1999, and references therein), despite the obvious challenge of sharing this resource with the beetle offspring. It is of course too early to say whether this kleptoparasitic behaviour on the part of *Karliella sexpunctata* is obligate or facultative. Whatever the case may be, the pronounced variation observed in adult body size suggests that the larvae sometimes face serious limitations in food supply.

DISCUSSION

The new genus *Karliella* is established for a single species endemic to but apparently widespread in the central and southern parts of the African continent. It unquestionably belongs to the calyptrate family Anthomyiidae because of the following combination of characters: (1) head holoptic in male, dichoptic in female; (2) female with a pair of crossed interfrontal setae; (3) lower calypter well developed; (4) tiny hair-like setulae present beneath tip of scutellum; (5) vein A1 extended to wing margin as a weak fold; (6) male surstyli and cerci united by vertical sclerotized connections immediately distal to lateral cercal apodemes; (7) spiracles VI and VII present in female abdomen. Beyond that, as indicated below, morphology provides no obvious clues as to the closest relationships of this taxon.

The deeply biramous surstyli in combination with the apically projecting and very pointed cerci armed with three pairs of giant setae are diagnostic male characters not seen in other anthomyiid genera. The paired dark spots found on the ventro-flexed

lateral parts of tergites III–V in both sexes also represent a unique condition among anthomyiid flies.

A narrow and flexible sclerotized bridge connects the surstyli with the epandrium in male *Karliella* flies. Similar articulations between the surstyli and epandrium are found in the majority of anthomyiid genera including *Anthomyia*, *Botanophila* and *Delia*. However, as first pointed out by Hennig (1976), some anthomyiid genera differ by having a small sclerite inserted at the articulations between the surstyli and epandrium. Among Afrotropical Anthomyiidae, this is seen in *Pegomya*, *Emmesomyia*, *Calythea* and *Enneastigma*.

Dissection of pregnant female anthomyiids of species known to breed in decomposing substrates often reveals the presence of an incubated egg in the uterus with a fully developed larva capable of hatching during or immediately after oviposition (pers. observ.). Because the remaining eggs are unincubated, this condition has been classified as simultaneous viviparity (Meier *et al.* 1999). To what extent this is a facultative or obligate habit among different species of anthomyiids is an open question, but it has evidently been attained through homoplasy in various anthomyiid lineages. The anthomyiid oviscapt (postabdomen) is as regards the ground plan undoubtedly slender, well set off from and hardly shorter than the preabdomen, and has slender cerci with projecting, cylindrical apices. In *Karliella*, the oviscapt is rather thick, only about one-third as long as the preabdomen, and with very short cerci. Despite the apparent larval coprophagy and notably short oviscapt, it seems that *Karliella sexpunctata* is an obligate oviparous species.

The possible kleptoparasitic habits of *Karliella* involve dung-storing Coleoptera as hosts. Kleptoparasitism is further known as an obligate habit in the anthomyiid genera *Leucophora* and *Eustalomyia* Kowarz, 1873, in which the females lay eggs in the borrows of solitary and presocial pollen- or flesh-storing aculeate Hymenoptera (Amiet & Volkart 1983; Meyer-Holzapfel 1986; Polidori *et al.* 2005, and references therein). The overall structure of the male terminalia suggests that these two genera are closely related to each other and to *Delia*. They all share slender male surstyli without the typical anthomyiid trait of a subdistal, mesal incision. *Karliella* differs fundamentally from these by having male surstyli that are deeply incised and biramous.

The reason for the absence of characters in support of a very close relationship between *Karliella* and any other known anthomyiid genus or group of genera might well be that it represents the only extant member of a relict lineage with remote ties to other extant Anthomyiidae. A comparable case is the putatively old Neotropical lineage represented by the genera *Phaonantho* Albuquerque, 1957, *Coenosopsia* Malloch, 1924 and *Coenosopsites* Michelsen, 1996 (extinct; from Dominican amber) as recognized by Michelsen (1991, 1996, 2000). Both relict lineages actually share in the male sex a rather tapering, subcylindrical abdomen, with the terminalia and sternite V notably small, more reminiscent of Muscidae and Fanniidae than Anthomyiidae. That similarity is probably to be ascribed to symplesiomorphy, alternatively homoplasy. Hopefully, molecular studies will soon throw more light on the relationships of *Karliella*.

ACKNOWLEDGEMENTS

I thank Ashley Kirk-Spriggs (National Museum, Bloemfontein) for arranging loans of specimens belonging to the National Museum of Namibia, Windhoek, and his own institution; and Nigel P. Wyatt (Natural History Museum, London) for loaning types and other relevant material. Michael Ackland (Oxford University Museum of Natural History, Oxford) generously gave me access to his unpublished notes from 1975 on the type specimens of *Pegomyia sexpunctata* Karl and let me take over a loan of Anthomyiidae from the National Museum of Namibia.

REFERENCES

Amiet, F. & Volkart, H.D. 1983. Fliegen der Gattung *Eustalomyia* (Dipt., Anthomyiidae) als Brutparasiten von Grabwespen (Hym., Sphecidae). *Mitteilungen der Entomologischen Gesellschaft Basel* **33**: 39−44.

Cumming, J.M. & Wood, D.M. 2009. Adult morphology and terminology. *In*: Brown, B.V. *et al.*, eds, *Manual of Central American Diptera*. Vol. 1. Ottawa: NRC Research Press, pp. 9–50.

Emden, F.I. van. 1941. Keys to the Muscidae of the Ethiopian Region: Scatophaginae, Anthomyiinae, Lispinae, Fanniinae. *Bulletin of Entomological Research* **32**: 251–275.

Hennig, W. 1976. 63a. Anthomyiidae. *In*: Lindner, E., ed., *Die Fliegen der Palaearktischen Region*. Bd 7 (1), pt. 1. Stuttgart: E. Sweizerbart'sche Verlagsbuchhandlung, pp. i–lxxviii.

Karl, O. 1935. Aussereuropäische Musciden (Anthomyiden) aus dem Deutschen Entomologischen Institut. *Arbeiten über morphologische und taxonomische Entomologie aus Berlin-Dahlem* **2**: 29–49.

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

Meier, R., Kotrba, M. & Ferrar, P. 1999. Ovoviviparity and viviparity in the Diptera. *Biological Reviews* **4**: 199−258.

Meyer-Holzapfel, M. 1986. Vergleichende Betrachtung des Verhaltens brutparasitischer Fliegen aus zwei Familien bei solitären Aculeaten Hymenopteren (Methodische Kritik). *Mitteilungen der Schweizerischen entomologischen Gesellschaft* **59**: 95–110.

Michelsen, V. 1991. Revision of the aberrant New World genus *Coenosopsia* (Diptera: Anthomyiidae), with a discussion of anthomyiid relationships. *Systematic Entomology* **16**: 85–104.

———1996. First reliable record of a fossil species of Anthomyiidae (Diptera), with comments on the definition of recent and fossil clades in phylogenetic classification. *Biological Journal of the Linnean Society* **58**: 441–451.

———2000. Oldest authentic record of a fossil calyptrate fly (Diptera): a species of Anthomyiidae from early Coenozoic Baltic amber. *Studia Dipterologica* **7**: 11–18.

Polidori, C., Scanni, B., Scamoni, E., Giovanetti, M., Andrietti, F. & Paxton, R.J. 2005. Satellite flies (*Leucophora personata*, Diptera: Anthomyiidae) and other dipteran parasites of the communal bee *Andrena agilissima* (Hymenoptera: Andrenidae) on the island of Elba, Italy. *Journal of Natural History* **39**: 2745−2758.

Pont, A.C. & Ackland, D.M. 1980. Family Anthomyiidae. *In*: Crosskey, R.W., ed., *Catalogue of the Diptera of the Afrotropical Region.* London: British Museum (Natural History), pp. 715–718.

Sivinski, J., Marshall, S. & Petersson, E. 1999. Kleptoparasitism and phoresy in the Diptera. *Florida Entomologist* **82**: 179–197.