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Calyptrate flies in fossil resin from Mexico and Tanzania

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Abstract

Fossil Calyptratae flies are exclusively found in the Cenozoic. Calyptrates arose around the K-T boundary and rapidly diversified in the early Tertiary. Only a few species of fossil Calyptratae are known from fossil resins such as Baltic amber, Dominican amber, and East African copal or Defaunation resin. However, these preserved organisms provide valuable insights into the evolutionary and ecological history of calyptrate flies. In this study, we describe *Mesembrinella guimaraesi* **sp. nov.** (Mesembrinellidae) from Miocene Mexican amber, representing the first record of a calyptrate from this fossiliferous site; and we report *Dichaetomyia immaculiventris* Malloch as the first occurrence of *Dichaetomyia* Malloch (Muscidae) in Tanzanian copal. We also briefly discuss the abundance of calyptrate flies in resins and actualistic experiments.

Keywords: actualistic experiments, amber, copal, Mesembrinellidae, Muscidae, new species

Introduction

Fossil calyptrate flies (Schizophora: Calyptratae) are found only in the Cenozoic. The clade arose around the K-T boundary, and rapid diversification was found in the early Tertiary (Wiegmann *et al*., 2011). Hitherto, 12 calyptrate species are known from amber and copal/Defaunation resin: two Anthomyiidae from Baltic and Dominican amber (Michelsen, 1996, 2000); five Muscidae, three from Dominican amber and two from East African copal/Defaunation resin (Meunier, 1908; Pont & Carvalho, 1997; O'Hara *et al*., 2013); one Mesembrinellidae from Dominican amber (Cerretti *et al*., 2017); one Oestridae from Baltic amber (Berendt, 1830; Townsend, 1921) [probably not an Oestridae species (T. Pape, pers. comm., 17 June 2025)]; one Sarcophagidae from East African copal/Defaunation resin (O'Hara *et al*., 2013); one Streblidae from Dominican amber (Poinar & Brown, 2012); and an extinct family (Hoffeinsmyiidae) from Baltic amber (Michelsen, 2009).

The Mesembrinellidae is a monophyletic family based on morphology and molecular data (Guimarães, 1977; Cerretti *et al*., 2017; Marinho *et al*., 2017). It belongs to the Oestroidea and contains 53 known species with a distribution restricted to the Neotropical region from southern Mexico to Argentina (Bonatto & Marinoni, 2005; Marinho *et al*., 2017; Whitworth & Yusseff-Vanegas, 2019). Mesembrinellids are most abundant in tropical rain and cloud forests (Guimarães, 1977; Vargas & Wood, 2009). In Mexico, six species are known (Jaume-Schinkel, 2021). Cerretti *et al*. (2017) presented a phylogenetic analysis based on morphological and molecular evidence, recommending that all genera included in the family should be synonymized under *Mesembrinella*. Also, Marinho *et al*. (2017) proposed synonyms for some genera, and Whitworth & Yusseff-Vanegas (2019) accepted the synonymization proposed by Marinho *et al*. (2017), leaving the family with 3 subfamilies (Laneellinae, Mesembrinellinae, Souzalopesiellinae) and 3 genera (*Laneella*, *Mesembrinella*, *Souzalopesiella*).

The Muscidae is also a monophyletic family based on morphological and molecular data (Hennig, 1965; Carvalho, 1989; McAlpine, 1989; Kutty *et al*., 2014). It is a cosmopolitan family with 5,218 species and 187 genera (Pape *et al*., 2011). The Muscidae are biologically diverse, although the majority of species feed on decaying animal and vegetal matter (Carvalho & Couri, 2002). The genus *Dichaetomyia* has 88 described species mainly distributed in the Afrotropical region, with a few species also occurring in the Australian, Oriental and Palearctic regions (Couri *et al*., 2006; Evenhuis & Pape, 2024). The larvae are obligate carnivores and have been found in decaying vegetation and dung (Couri *et al*., 2006).

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Amber is well defined as a resin that has existed for millions of years (Grimaldi, 1996; Solórzano-Kraemer *et al*., 2020), while copal can be defined as an ancient resin with an age between 2.58 Ma and 1760 AD, resins younger than 1760 AD are called Defaunation resin (Solórzano-Kraemer *et al*., 2020). The study of these bioinclusions provides data on the evolutionary history of organisms and their behaviour, as well as on the ecology of forest ecosystems in the past, biogeography, climatic changes, among other applications (Grimaldi & Engel, 2005; Solórzano Kraemer *et al*., 2015, 2018, 2020; Penney, 2016; Delclòs *et al*., 2020; Solórzano-Kraemer *et al*., 2020).

The *Hymenaea* trees of different species, *H. mexicana*† Poinar & Brown, 2002; and *H. allendis*† Calvillo-Canadell *et al*., 2010, were the source of the resin that later became the Miocene ambers from Mexico. Trees of this genus were also the source of the resin that later became the copal, and Defaunation resin from East Africa (Delclòs *et al*., 2020; Solórzano-Kraemer *et al*., 2020).

Here, we describe the first species of a Mesembrinellidae found in Mexican amber from Simojovel, Chiapas. We also report for the first time the discovery of *Dichaetomyia immaculiventris* Malloch, 1930 (Muscidae) in Holocene copal from Tanzania and briefly discuss the abundance of Calyptratae flies in copal and actualistic experiments.

Material and methods

The general morphology and abbreviations follow Cumming & Wood (2017). For the description of the Mesembrinellidae specimen, we followed Cerretti *et al*. (2017).

For the identification of the specimen in the copal from Tanzania we followed the key of Afrotropical Muscidae (Couri, 2007), the *Dichaetomyia* key from Afrotropical region (Emden, 1942), the original descriptions of the *Dichaetomyia* species (Couri *et al*., 2006; Zielke, 2020, 2021a, b, c, 2022), and images of *D. immaculiventris* types deposited at National Museum Smithsonian Institution, Washington, USA (USNM).

The Mesembrinellidae specimen is housed in Museo de Palentología 'Eliseo Palacios Aguilera', Tuxtla Gutiérrez, Chiapas, Mexico with the catalogue number IHNFG-6188. It is a female preserved in Mexican amber from Simojovel, Chiapas (Mexico). The age of the Mexican amber has been estimated as Early Miocene (Solórzano Kraemer, 2007). The main deposit, Simojovel, where most of the amber with inclusions comes from, has been dated to 23 Ma (Serrano-Sánchez *et al*., 2015). Syninclusions: one Coleoptera, one Hymenoptera, and plant remains.

The Muscidae specimen is housed in the Senckenberg Research Institute, Frankfurt under the catalogue number SMF Be 2507b. It is a female preserved in Holocene copal (*sensu* Solórzano-Kraemer *et al*., 2020) from Tanzania, dated to 1270 ± 30 BP years, according to ^{14}C analysis. For more information on the provenance of the Tanzanian copal see Solórzano-Kraemer *et al*. (2022). The copal piece also contains one *Plagiozopelma* (Diptera: Dolichopodidae), one Hemiptera: Sternorrhyncha, one Hymenoptera, and one Thysanoptera.

Two studies were performed with commercial yellow sticky traps. One in Madagascar, where the traps were placed around four *Hymenaea verrucosa* Gaertn. in the lowland forest on the northeast side of Madagascar, in the Mananjary region (between Nosy Varika and Ambahy, in 2013). The other one in Niederhof on the east coast of Germany, the yellow sticky traps were placed around four *Fagus sylvatica* (Linné, 1753) in a Cormorant National Park. The Cormorant Park is about 25 hectares and in the year of collection (2024) there were 800 cormorant pairs living there. The traps were deployed, and active capturing organisms, for eight days in all the collecting places. For the sticky traps, the glue was dissolved from the sticky sheets using gasoline to extract their contents. The extracted arthropods from the sticky traps were promptly transferred to containers with alcohol for preservation. For a more detailed description of the methodology, refer to Solórzano Kraemer *et al*. (2018).

Systematic palaeontology

Order Diptera Linnaeus, 1758
Superfamily Oestroidea Leach, 1815
Family Mesembrinellidae Shannon, 1926
Genus *Mesembrinella* Giglio-Tos, 1893

***Mesembrinella guimaraesi* sp. nov.**
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(Figs 1A–C, 2)

Holotype. Female preserved in Mexican amber from Simojovel, Chiapas (Mexico). Deposited in the "Museo de Palentología 'Eliseo Palacios Aguilera', Tuxtla Gutiérrez, Chiapas, Mexico" with the catalogue number IHNFG-6188. Syninclusions: one Coleoptera, one Hymenoptera, and plant remains.

Etymology. The specific name is in honor of the Brazilian entomologist Dr. José Henrique Guimarães, who significantly contributed to the knowledge of several

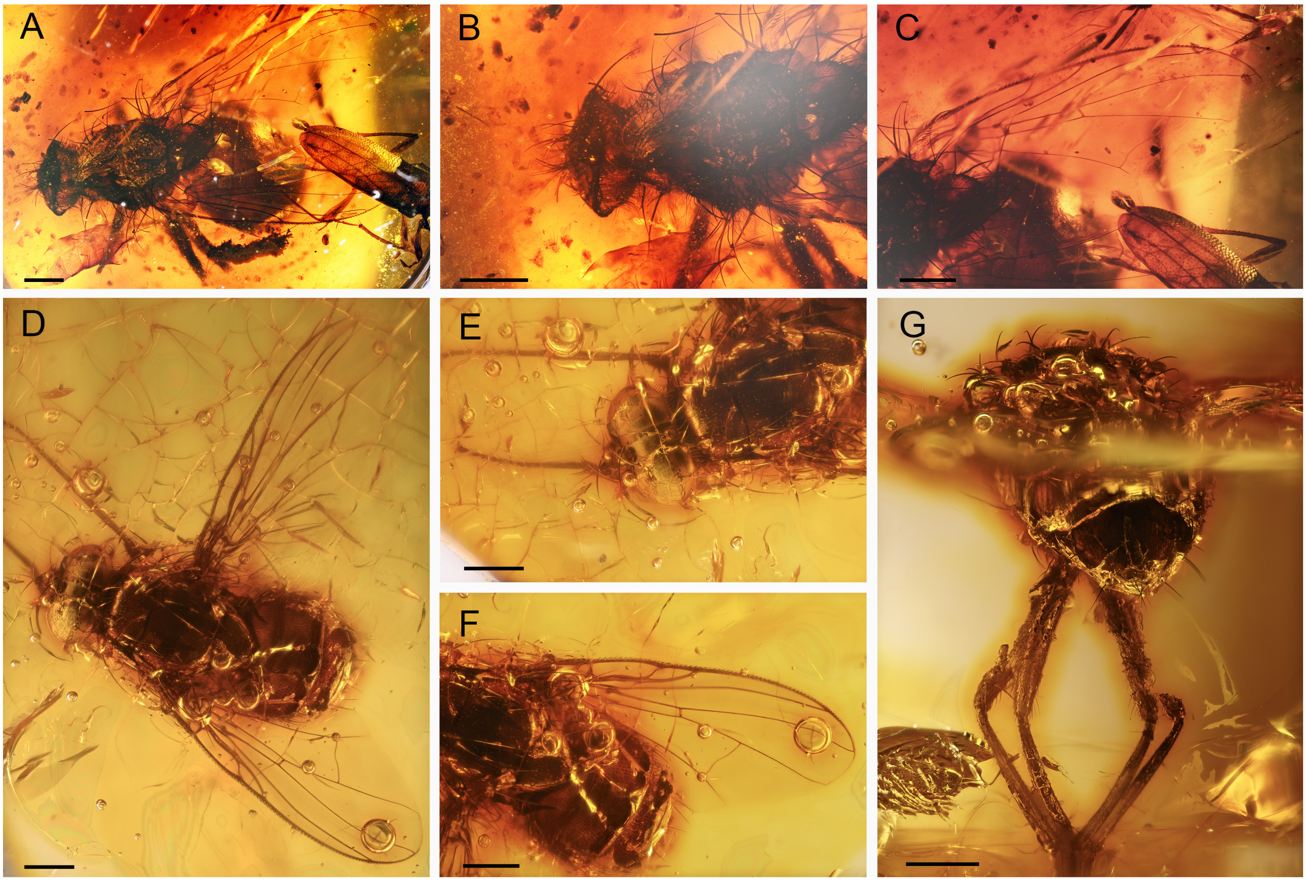

FIGURE 1. *Mesembrinella guimaraesi* (IHNFG-6188) in Miocene Mexican amber from Simojovel (**A**–**C**) and *Dichaetomyia immaculiventris* (catalog number SMF Be 2507b) in Holocene copal from Tanzania (**D**–**G**). **A**, Habitus dorsal view. **B**, Head and thorax, dorsal view. **C**, Wing. **D**, Habitus, dorsal view. **E**, Head and thorax, dorsal view. **F**, Wing, dorsal view. **G**, Habitus, posterior view. Scale bars: 1 mm.

Diptera families, including an important revision of Mesembrinellidae.

Diagnosis. Acrostichals 4+4. Dorsocentrals 2+3. Intra-alars 2+2. Supra-alars 2+3. Three postpronotal setae, the anterior one shorter with about half the length of the other two. Wing hyaline. Stem vein and base of R_{4+5} bare. Meeting point of R_{2+3} and R_{4+5} with one dorsal and one ventral setulae. Hind coxa posteriorly bare. Tarsal claws proximally light and distally dark.

Type locality and horizon. Simojovel de Allende, Chiapas, Mexico.

Description. Female. Holotype. Body length: *ca.* 10.0 mm. Wing length: 7.0 mm.

Head. Dichoptic. Eyes bare. Frons wide, with about a third of the head width [head partially collapsed]. Two long fronto-orbital setae proclinate [the lower one longer, about a third longer than the upper one] and one reclinate. Occiput with a well-defined row of fine and long postocular setae alternating in size. Eight pairs of frontal setae; the upper two shorter, with about a third of the length of the others. Parafacial and fronto-orbital plate bare. One pair of interfrontal setae crossed. Ocellar triangle with a pair of long proclinate [and apparently divergent] ocellar and a pair of parallel post-ocellar seta. Outer vertical setae divergent. Inner vertical setae long convergent, twice as long as the outer vertical seta. Post-ocular setae dark, homogeneously distributed up to middle of eyes. Vibrissae crossed, long and thick, arising at level of lower facial margin. Four short setulae above vibrissae. Lower facial margin warped forward. Pedicel and postpedicel not visible, arista long plumose and ticked proximally [partially visible]. Palpi and proboscis not visible.

Thorax. Prosternum not visible. Anterior spiracle not visible. Posterior spiracle apparently without setae [not visible]. Mesonotum dark. Legs dark. Proepisternum with hair-like setulae [apparently]. Three postpronotal setae, the anterior one shorter with about half length of the other two. Two notopleural setae, posterior one slightly longer. Postpronotal lobe and notopleuron covered by long setulae. Setulae of postpronotum, scutum and scutellum relatively long and suberect. One post-humeral seta. Acrostichals 4+4, the anterior presutural one is short, about half as long as the others. Dorsocentrals 2+3. Intra-alars 2+2. Supra-

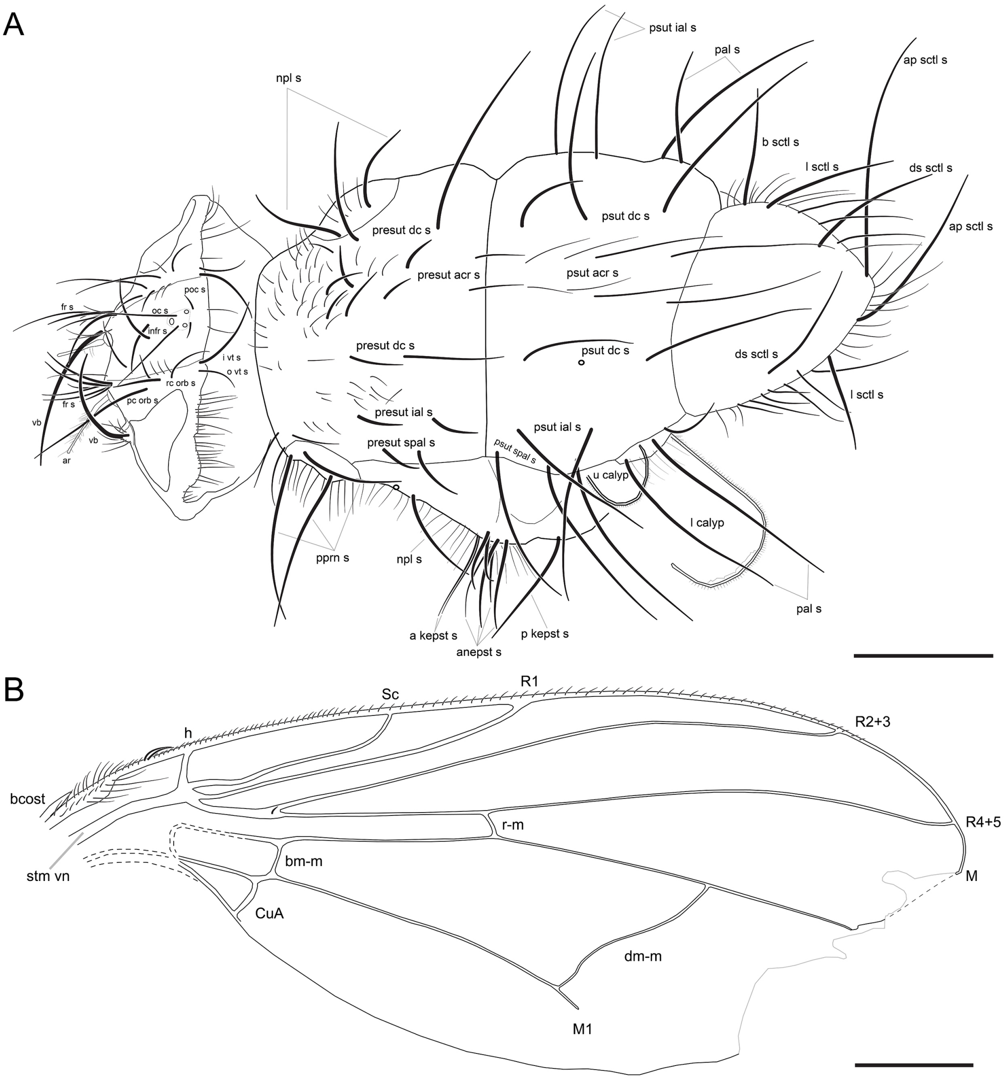

FIGURE 2. *Mesembrinella guimaraesi* **sp. nov.** (IHNFG-6188). **A**, Head and thorax, dorsolateral view. **B**, Right wing, dorsal view. Abbreviations: acr s, acrostichal seta; a kepst s, anterior katepisternal seta; anepst s, anepisternal seta; ap sctl s, apical scutellar seta; ar, arista; b sctl s, basal scutellar seta; ds sctl s, discal scutellar seta; fr s, frontal seta; infr s, interfrontal seta; i vt s, inner vertical seta; l calyp, lower calypter; l sctl s, lateral scutellar seta; npl s, notopleural seta; oc s, ocellar seta; o vt s, outer vertical seta; pal s, postalar seta; pc orb s, proclinate orbital seta; poc s, postocellar seta; p katepst s, posterior katepisternal seta; pprn s, postpronotal seta; presut acr s, presutural acrostichal seta; psut acr s, postsutural acrostichal seta; presut dc s, presutural dorsocentral seta; psut dc s, postsutural dorsocentral seta; presut ial s, presutural intra-alar seta; psut ial s, postsutural intra-alar seta; rc orb s, reclinate orbital seta; spal s, supra-alar seta; u calyp, upper calypter; vb, vibrissa; bcosta, basicosta; bm-m, basal medial crossvein; CuA, anterior branch of cubital vein; stm vn, stem vein; h, humeral crossvein; Sc, subcostal vein; M_1, first branch of media; dm-m, discal medial crossvein; R_1, anterior branch of radius; R_{2+3}, second branch of radius; R_{4+5}, third branch of radius; M, medial vein; r-m, radial-medial crossvein. Scale bars: 1.0 mm.

alars 2+3. Two postalar setae, with an additional shorter seta posteriorly. One intrapostalar seta. Scutellum with three pairs of marginal setae (apical, basal, and lateral), and one pair of discal setae; the apical pair a third longer than the basal pair. Ventrolateral setulae dark, covering the entire margin of scutellum. Two proepimeral setae [apparently, not completely visible]. Six anepimeral setae; anepimeron covered by fine setulae [partially visible]. Katepisternals 2+1. Meron with a row of setae. Post-alar wall with setulae. Anatergite, katatergite, katepimeron, suprasquamal ridge and subscutellum not visible.

Wing. Hyaline without spots. Tegula and basicosta light. Tegula bare [apparently]. Basicosta bare. Subcostal sclerite and stem vein bare. Costal spine twice as long as costal setae. Subcostal vein with a distinct concavity before the node with R_1. Base of R_{4+5} bare. Meeting point of R_{2+3} and R_{4+5} with one dorsal and one ventral setulae. Section of vein M between crossvein r-m and dm-m distinctly longer than section between dm-m and bend of M. Bend of M broadly rounded, forming an obtuse angle; postangular section of M very close to and parallel with wing margin [apparently, due to both wings have part of the apex missing]. Vein CuA+CuP not reaching wing margin. Alula well developed. Upper calypter light, with light edge. Lower calypter dark with dark edge; enlarged, with the apex almost reaching the scutellum apex; Posterolateral margin of lower calypter with long trichia.

Legs. Fore femur with a row of long setae on posterodorsal and posteroventral surfaces; several setae on posterior surface; and five long setae on anterodorsal surface. Fore tibia not clearly visible, it is only possible to see a posterior median seta and a dorsal preapical seta. Mid femur with [at least] two long anterodorsal and anteroventral setae on basal half; and two long posterior preapical setae. Mid tibia with submedian seta on anterodorsal, dorsal, posterior, and ventral surfaces [apparent positions, not clearly visible]; long apical seta on anterior, anterodorsal, dorsal, posterodorsal, posteroventral, and ventral surfaces. Hind femur with a row of long anterodorsal and anteroventral setae. Hind tibia with three anterodorsal seta (two supramedian and one median); one supramedian posterodorsal seta; and two dorsal [or anterodorsal, not clearly visible] (one submedian and one preapical seta). Hind coxa bare on posterior margin. Claws and pulvilli as long as fifth tarsomere, claws proximally light and distally dark.

Abdomen. Broadly oval. Light and not metallic [apparently]. Syntergite 1+2 without setae [apparently]. Tergite 1+2, tergite 3 and tergite 4 without median marginal setae. Tergite 3 with six [at least] lateral marginal setae. Tergite 4 with a row of marginal setae, absent on median region. Tergite 5 with a row of erect marginal setae. Discals absent [apparently]. Mid-dorsal depression of syntergite 1+2 not visible. Syntergite 1+2 without median marginal setae and with several short, lateral marginal setae. Abdominal setulae sub-erect. Sternite 1 not clearly visible. Sternite 2–3 rectangular, longer than wide, with long setae on lateral and distal regions. Sternite 4–5 quadrangular, with long setae on lateral and distal regions. Sternites 2–5 with rounded edges and with two [at least] lateral setae and four [at least, not clearly visible] distal setae.

Terminalia. Cercus, epiproct, hypoproct, and spermathecae not visible.

Remarks. The head of the specimen is collapsed, deformed, and visibly hollow. The abdomen is slightly flattened dorsoventrally. A cloudy substance in the amber obscures some body structures in lateral and ventral views.

Order Diptera Linnaeus, 1758
Infraorder Schizophora Becher, 1882
Parvorder Calyptratae Robineau-Desvoidy, 1830
Family Muscidae Latreille, 1802
Genus *Dichaetomyia* Malloch, 1921

***Dichaetomyia immaculiventris* Malloch, 1930**
(Figs 1 D–G, 3)

Diagnosis. [adapted from Malloch (1930) and Emden (1942)] Body shining testaceous-yellow. Antennae and palpi yellow. Gena, frons and occiput black with silver pruinosity. Thorax and abdomen dorsally pale without dark marks. Thorax with white pruinosity dorsally, forming three subvittae. Dorsocentrals 2+3. Infra-alar bulla setulose. Legs yellow, tarsi apically slightly darkened. Wing yellowish hyaline. Fore tibia without a submedian posterior seta. Tergite 5 with discal setae.

Type locality and horizon. Burundi, Ethiopia, ? Malawi, Mozambique, South Africa, Tanzania, and Zimbabwe (Couri *et al*., 2013).

Remarks. First record from Tanzanian copal.

Muscidae in Tanzanian copal

The Muscidae specimen belongs to the genus *Dichaetomyia* Malloch, 1921, which is widespread in the Afrotropical region with more than 70 species (Couri *et al*., 2012; Zielke, 2020, 2021a, b, c, 2022). Following the key of Emden (1942) and studies by Zielke (2020, 2021a, b, c, 2022), the species has been identified as *Dichaetomyia immaculiventris* Malloch, 1930 (Fig. 3). However, some uncertainties remain due to the coloration and color pattern of the body, which are very important for the identification of the species within this genus, but unfortunately not preserved or visible in our specimen.

Muscidae are rare in copal from Tanzania, with only two other species reported, *Aethiopomyia gigas* (Stein, 1906) (O'Hara *et al*., 2013) and *Pyrellia viridissima* Meunier, 1908 (Meunier, 1908).

Actualistic experiments

In actualist experiments in a *Hymenaea* forest in Madagascar and around *Fagus sylvatica* in a Cormorant National Park, Calyptrate flies have also been caught in sticky traps (Fig. 4). However, in the *Hymenaea* forest, calyptrates are not as abundant as other Diptera (Fig. 4A, B). From a total of more than 1000 flies only 10 are calyptrates. These are rare around *Hymenaea* but extremely abundant in the Cormorant National Park (Fig. 4C, D).

Discussion

The new mesembrinellid species, *M. guimaraesi* **sp. nov.**, is morphologically similar to *M. caenozoica* Cerretti *et*

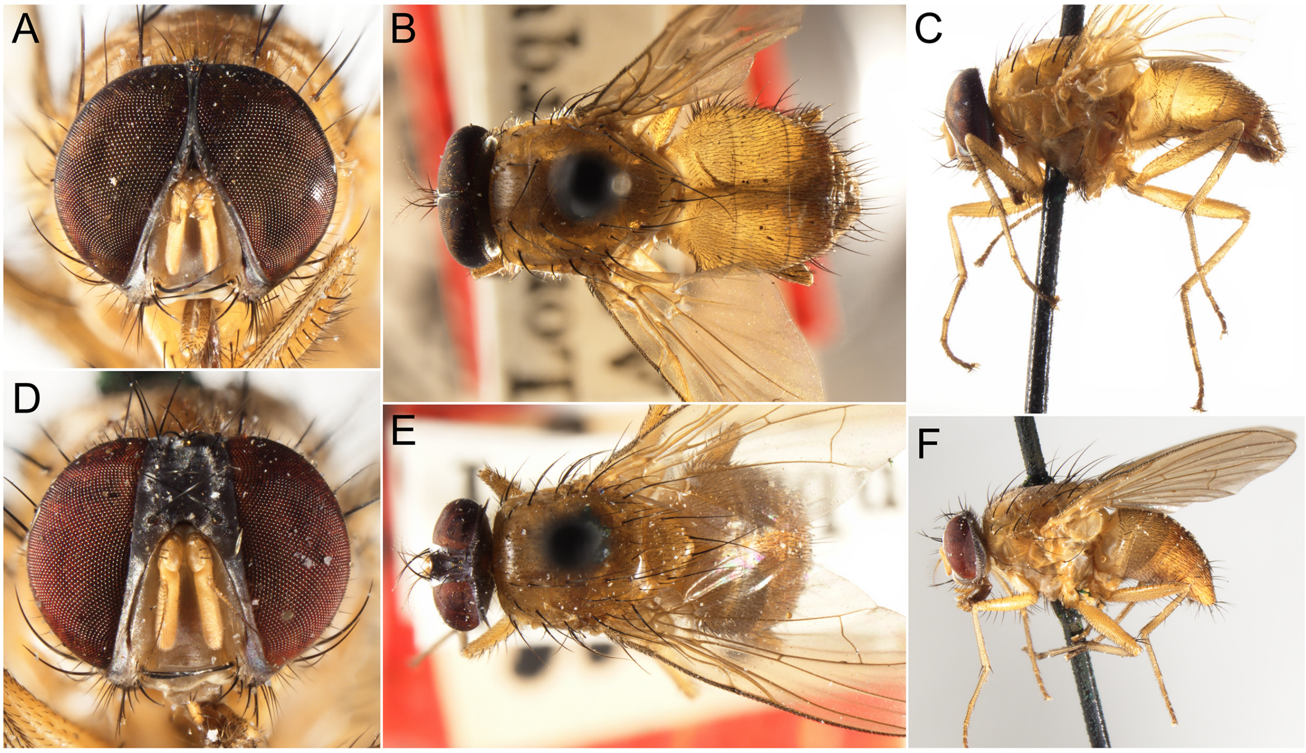

FIGURE 3. *Dichaetomyia immaculiventris* Malloch, 1930. **A–C**, Male holotype (USNM). **A**, Head, frontal view. **B**, Habitus, dorsal view. **C**, Habitus, lateral view. **D–F**, Female paratype (USNM). **D**, Head, frontal view. **E**, Habitus, dorsal view. **F**, Habitus, lateral view.

al., 2017 and *M. facialis* (Aldrich, 1922). Cerretti *et al*. (2017) indicated *M. caenozoica* as sister to *M. facialis* based on the presence of narrow lateroventral projections of the distiphallus. Even without analysing this and other characters based on male terminalia, we also observed similarities between the new species and *M. caenozoica* and *M. facialis*, as the body is not metallic [apparently in *M. guimaraesi* **sp. nov.**], three post-pronotal setae, and stem vein bare (Guimarães, 1977; Cerretti *et al*., 2017).

Additionally, both fossil species (*M. guimaraesi* **sp. nov.** and *M. caenozoica*) present the acrostichal setae with 3+3 conformation (Cerretti *et al*., 2017), differing from all other known Mesembrinellids (Guimarães, 1977; Wolff, 2013; Wolff *et al*., 2014; Whitworth & Yusseff-Vanegas, 2019). Another remarkable difference is seen in the abdominal sternites. The new species and *M. caenozoica* have sternites with long, thin, normally developed setae, whereas *M. facialis* has long, thick, spine-like setae on both male and female sternites (Whitworth & Yusseff-Vanegas, 2019).

Mesembrinella guimaraesi **sp. nov.** has the base of R_{4+5} bare, as in *M. facialis*, both species differ from *M. caenozoica*, which has a row of fine setulae on the dorsal side of vein R_{4+5} extending from the base to about ⅔ of the distance to crossvein r-m; a unique and likely derived character state among Mesembrinellidae indicated by Cerretti *et al*. (2017). Also, the tarsal claws of *M. guimaraesi* **sp. nov.** are light proximally and dark distally, as in *M. facialis*, while *M. caenozoica* has claws uniformly dark (Guimarães, 1977; Cerretti *et al*., 2017).

Mesembrinella guimaraesi **sp. nov.** was probably a stenotopic, silvicolous and shade-loving species, as hypothesized for *M. caenozoica* (Cerretti *et al*., 2017), living in a lowland coastal area with tropical dry forest and mangrove vegetation during the Cenozoic (Langenheim, 1967; Solórzano Kraemer, 2007).

Dichaetomyia immaculiventris is a species with a wide distribution in the Afrotropical region (Couri *et al*., 2013). According to the ^{14}C results, the Holocene copal that contains the specimen of *D. immaculiventris* was most likely produced around the year 772–885 *cal* AD and has an age of 1270 ± 30 BP years. Inclusions in copal or Defaunation resin are not commonly described because most palaeontologists focus their attention on evolutionarily interesting species rather than on more recent inclusions that may contain extant species. However, the study of such specimens can be useful to understanding the diversity that existed in some places before the onset of the Anthropocene biodiversity crisis.

Because of their young age, calyptrate flies could not be expected to be common in amber, however a few species could easily have been present with large populations. In copal and Defaunation resin they would be expected to be more abundant. However, this does not seem to

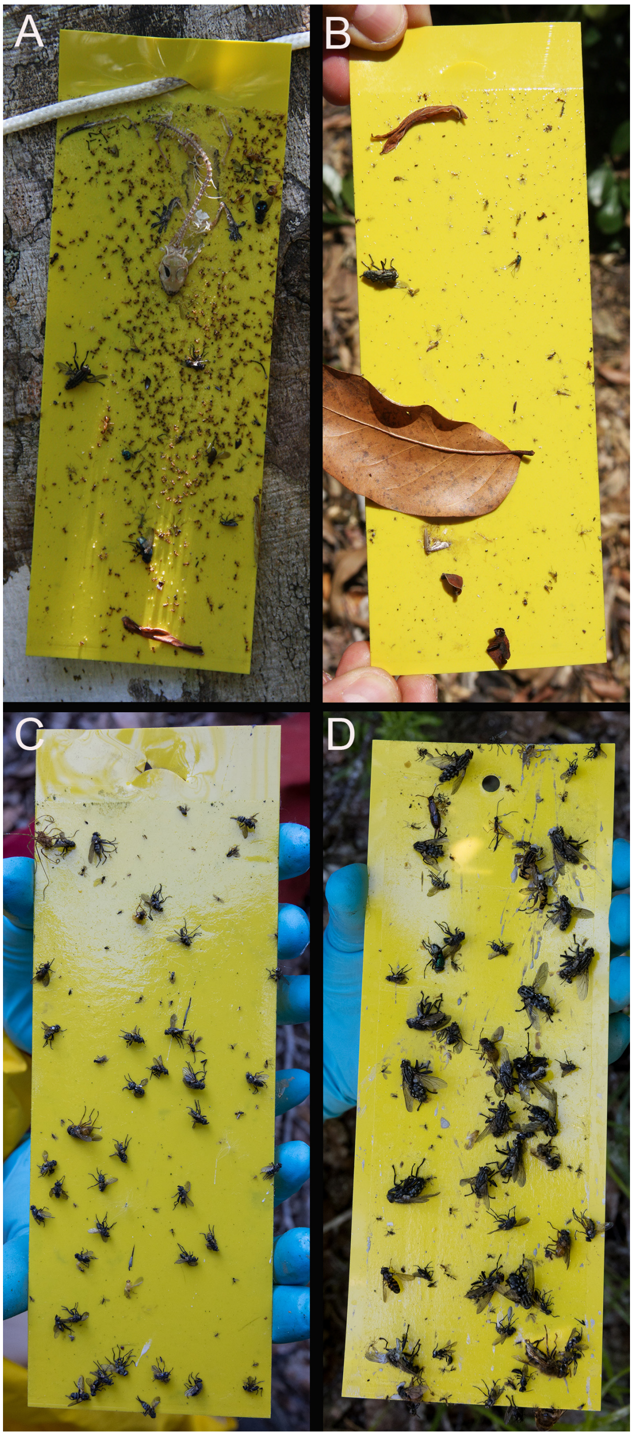

FIGURE 4. Yellow sticky traps with insects, plants, and gecko. **A**, **B**, Yellow sticky traps collocated around *Hymenaea verrucosa* in Nosy Varika, Mananjary region, Madagascar. **C**, **D**, Sticky traps collocated around *Fagus sylvatica* in Niederhof, Germany.

be the case. The size of these large flies is also unlikely to have played a role in their capture in the resin that later became copal or amber, because even if the sticky traps can catch large animals such as small vertebrates as geckos or medium to big invertebrates as calyptrate flies, the latter are rare around *Hymenaea* trees but extremely abundant around *Fagus* (Fig. 4C, D) in a Cormorant National Park. The calyptrates are ecologically diverse, with several species associated with decaying animal matter (Cerretti *et al*., 2017; Marinho *et al*., 2017). We hypothesize that the few calyptrates trapped in resins are more likely to be linked to flies resting on the tree trunks, and to the absence of decaying animal matter near resin sources. However, further actualistic studies are necessary to better understand this influence.

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References

Aldrich, J.M. (1922) The Neotropical muscoid genus *Mesembrinella* Giglio-Tos and other testaceous muscoid flies. *Proceedings of* *the United States National Museum*, 62, 1–36. https://doi.org/10.5479/si.00963801.62-2457.1

Berendt, G.C. (1830) *Die Insekten im Bernstein. Ein Beitrag zur Tiergeschichte der Vorwelt*. Erstes Heft. Nicolai, Danzig [= Gdansk], 30 pp.

Bonatto, S.R. & Marinoni, L. (2005) Gêneros e espécies novos de Mesembrinellinae (Diptera, Calliphoridae) da Costa Rica e Venezuela. *Revista Brasileira de Zoologia*, 22, 883–890. https://doi.org/10.1590/S0101-81752005000400012

Calvillo-Canadell, L., Cevallos-Ferriz, S.R. & Rico-Arce, L. (2010). Miocene *Hymenaea* flowers preserved in amber from Simojovel de Allende, Chiapas, Mexico. *Review of Palaeobotany and Palynology*, 160 (3-4), 126–134. https://doi.org/10.1016/j.revpalbo.2010.02.007

Carvalho, C.J.B. de (1989) Classificação de Muscidae (Diptera): Uma proposta através da análise cladística. *Revista Brasileira de Zoologia*, 6 (4), 627–648. https://doi.org/10.1590/S0101-81751989000400009

Carvalho, C.J.B. de & Couri, M.S. (2002) Part I, Basal Muscidae. *In*: Carvalho C.J.B. de (Ed.), *Muscidae (Diptera) of the Neotropical Region: Taxonomy*. Editora Universidade Federal do Paraná, Curitiba, pp. 17–132.

Cerretti, P., Stireman, J.O.III., Pape, T., O'Hara, J.E., Marinho, M.A.T., Rognes, K. & Grimaldi, D.A. (2017) First fossil of an oestroid fly (Diptera: Calyptratae: Oestroidea) and the dating of oestroid divergences. *PLoS ONE*, 12 (8), e0182101. https://doi.org/10.1371/journal.pone.0182101

Couri, M.S., Pont, A.C. & Penny, N.D. (2006) Muscidae (Diptera) from Madagascar: Identification keys, descriptions of new species, and new records. *Proceedings of the California Academy of Sciences*, 57 (29), 799–923.

Couri, M.S. (2007) A key to the Afrotropical genera of Muscidae (Diptera). *Revista Brasileira de Zoologia*, 24, 175–184. https://doi.org/10.1590/S0101-81752007000100022

Couri, M.S., de Carvalho, C.J.B. & Pont, A.C. (2012) Taxonomy of the Muscidae (Diptera) of Namibia: A key to genera, diagnoses, new records and description of a new species. *African Invertebrates*, 53 (1), 47–67. https://doi.org/10.5733/afin.053.0103

Couri, M.S., Kirk-Spriggs, A.K. & Pont, A.C. (2013) New distribution records of Afrotropical Muscidae (Diptera) based on material at the National Museum, Bloemfontein. *Navorsinge*, 29 (1), 1–17.

Cumming, J.M. & Wood, D.M. (2017) Chapter 3. Adult morphology and terminology. *In*: Kirk-Spriggs, A.H. & Sinclair, B.J. (Eds), *Manual of Afrotropical Diptera*. Vol. 1. *Suricata* 4. South African National Biodiversity Institute, Pretoria, pp. 89–133.

Delclòs, X., Peñalver, E., Ranaivosoa, V. & Solórzano-Kraemer, M.M. (2020) Unravelling the mystery of "Madagascar copal": Age, origin and preservation of a Recent resin. *PLoS ONE*, 15 (5), e0232623. https://doi.org/10.1371/journal.pone.0232623

Emden, F.I. van. (1942) Keys to the Muscidae of the Ethiopian Region. *Dichaetomyia*-group. *Annals and Magazine of Natural History*, 9, 673–701. https://doi.org/10.1080/03745481.1942.9755515

Evenhuis, N.L. & Pape, T. (2024) Systema Dipterorum, version 5.3, 14 July 2024. Available from: http://www.diptera.org/ (Accessed 10 September 2024).

Giglio-Tos, D.E. (1893) Diagnosi di nuovi generi e di nuove specie di Ditteri. *Bollettino dei Musei di Zoologia ed Anatomia comparata della Reale Università di Torino*, 8, 1–14. https://doi.org/10.5962/bhl.part.27226

Grimaldi, D.A. (1996) *Amber: window to the past.* Harry N. Abrams, in association with the American Museum of Natural History, New York, 216 pp.

Grimaldi, D.A. & Engel, M.S. (2005) *Evolution of the insects*. Cambridge University Press, New York and Cambridge, xv + 755 pp.

Guimarães, J.H. (1977) A systematic revision of the Mesembrinellidae, stat. nov. (Diptera, Cyclorrhapha). *Arquivos de Zoologia*, 29, 1–109. https://doi.org/10.11606/issn.2176-7793.v29i1p1-109

Hennig, W. (1965) Vorarbeiten zu einem phylogenetischen System der Muscidae (Diptera: Cyclororrapha). *Stuttgarter Beiträge zur Naturkunde*, 141, 1–100.

Jaume-Schinkel, S. (2021) New geographical records of Mesembrinellidae (Diptera: Oestroidea) in Mexico. *Revista chilena de Entomología*, 47 (4), 741–746. https://doi.org/10.35249/rche.47.4.21.11

Kutty, S.N., Pont, A.C., Meier R. & Pape T. (2014) Complete tribal sampling reveals basal split in Muscidae (Diptera), confirms saprophagy as ancestral feeding mode, and reveals an evolutionary correlation between instar numbers and carnivory. *Molecular Phylogenetics and Evolution*, 78, 349–364. https://doi.org/10.1016/j.ympev.2014.05.027

Langenheim, J.H. (1967) Preliminary investigations of *Hymenaea courbaril* as a resin producer. *Journal of the Arnold Arboretum*, 48 (3), 203–230. https://doi.org/10.5962/p.185723

Linné, C. (1753) *Species plantarum*. 2. Laurentii Salvii, Holmiae [= Stockholm]. https://doi.org/10.5962/bhl.title.11179

Malloch, J.R. (1921) Exotic Muscaridae (Diptera). I. *Annals and Magazine of Natural History*, (9) 7, 161–173. https://doi.org/10.1080/00222932108632501

Malloch, J.R. (1930) XLII.—Exotic Muscaridae (Diptera).—XXIX. *Annals and Magazine of Natural History*, (10) 5, 465–484. https://doi.org/10.1080/00222933008673157

Marinho, M.A.T., Wolff, M., Ramos-Pastrana, Y., Azeredo-Espin, A.M.L. de & Amorim, D.S. (2017) The first phylogenetic study of Mesembrinellidae (Diptera: Oestroidea) based on molecular data: clades and congruence with morphological characters. *Cladistics*, 33 (2), 134–152. https://doi.org/10.1111/cla.12157

McAlpine, J.F. (1989) Phylogeny and classification of the Muscomorpha. *In*: McAlpine, J.F. & Wood, D.M. (Eds), *Manual of Nearctic Diptera*. Vol. 3. Research Branch, Agriculture Canada, Ottawa, pp. 1382–1391.

Meunier, F. (1908) Sur quelques diptères (Muscinae, Ortalinae, Helomyzinae) du copal Récent de Zanzibar. *Annales de la Société Scientifique de Bruxelles*, 32, 252–256

Michelsen, V. (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 (4), 441–451. https://doi.org/10.1111/j.1095-8312.1996.tb01445.x

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

Michelsen, V. (2009) Hoffeinsmyiidae, a new extinct family of Schizophora (Diptera) from Baltic amber. *Studia Dipterologica*, 15 (1-2), 211–222.

O'Hara, J.E., Raper, C.M., Pont, A.C. & Whitmore, D. (2013) Reassessment of *Paleotachina* Townsend and *Electrotachina* Townsend and their removal from the Tachinidae (Diptera). *ZooKeys*, 361, 27–36. https://doi.org/10.3897/zookeys.361.6448

Pape, T., Blagoderov, V. & Mostovski, M.B. (2011) Order Diptera Linnaeus, 1758. *In*: Zhang, Z.Q. (Ed.), Animal biodiversity: An outline of higher-level classification and survey of taxonomic richness. *Zootaxa*, 3148 (1), 222–229. https://doi.org/10.11646/zootaxa.3148.1.9

Penney, D. (2016) *Amber Palaeobiology: Research trends and perspectives for the 21st century*. Siri Scientific Press, Rochdale, 128 pp.

Pont, A.C. & Carvalho, C.J.B. de (1997) Three species of Muscidae (Diptera) from Dominican amber. *Studia Dipterologica*, 4, 173–181.

Poinar, G.O. Jr. & Brown, A.E. (2002) *Hymenaea mexicana* sp. nov. (Leguminosae: Caesalpinioideae) from Mexican amber indicates Old World connections. *Botanical Journal of the Linnean Society*, 139 (2), 125–132. https://doi.org/10.1046/j.1095-8339.2002.00053.x

Poinar, GO., Jr. & Brown, A. (2012) The first fossil streblid bat fly, *Enischnomyia stegosoma* n. g., n. sp. (Diptera: Hippoboscoidea: Streblidae). *Systematic Parasitology*, 81, 79–86. https://doi.org/10.1007/s11230-011-9339-2

Serrano-Sánchez, M.L., Hegna, T.A., Schaaf, P., Pérez, L., Centeno-García, E. & Vega, F.J. (2015) The aquatic and semiaquatic biota in Miocene amber from the Campo La Granja mine (Chiapas, Mexico): paleoenvironmental implications. *Journal of South American Earth Sciences*, 62, 243–256. https://doi.org/10.1016/j.jsames.2015.06.007

Solórzano Kraemer, M.M. (2007) Systematic, palaeoecology, and palaeobiogeography of the insect fauna from the Mexican amber. *Palaeontographica, Abteilung A*, 282, 1–133. https://doi.org/10.1127/pala/282/2007/1

Solórzano Kraemer, M.M., Kraemer, A.S., Stebner, F., Bickel, D.J. & Rust, J. (2015) Entrapment bias of arthropods in Miocene amber revealed by trapping experiments in a tropical forest in Chiapas, Mexico. *PLoS ONE*, 10, e0126046. https://doi.org/10.1371/journal.pone.0118820

Solórzano Kraemer, M.M., Delclòs, X., Clapham, M.E., Arillo, A., Peris, D., Jäger, P., Stebner, F. & Peñalver, E. (2018) Arthropods in modern resins reveal if amber accurately recorded forest arthropod communities. *Proceedings of the National Academy of Sciences of the United States of America*, 115, 6739–6744. https://doi.org/10.1073/pnas.1802138115

Solórzano-Kraemer, M.M., Delclòs, X., Engel, M.S. & Peñalver, E. (2020) A revised definition for copal and its significance for palaeontological and Anthropocene biodiversity-loss studies. *Scientific reports*, 10 (1), 1–12. https://doi.org/10.1038/s41598-020-76808-6

Solórzano-Kraemer, M.M., Kunz, R., Hammel, J.U., Peñalver, E., Delclòs, X. & Engel, M.S. (2022) Stingless bees (Hymenoptera: Apidae) in Holocene copal and Defaunation resin from Eastern Africa indicate Recent biodiversity change. *The Holocene*, 32 (5), 414–432. https://doi.org/10.1177/09596836221074035

Stein, P. (1906) Die afrikanischen Anthomyiden des Königl. Zoologischen Museums zu Berlin. *Berliner Entomologische Zeitschrift*, 51, 33–80. https://doi.org/10.1002/mmnd.47919060104

Townsend, C.H.T. (1921) Some new muscoid genera ancient and recent. *Insecutor Inscitiae Menstruus*, 9, 132–134.

Vargas, J. & Wood, D.M. (2009) Calliphoridae (blow flies). *In:* Brown, B.V., Borkent, A., Cumming, J.M., Wood, D.M., Woodley, N.E. & Zumbado, M.A. (Eds), *Manual of Central American Diptera*. Vol. 2. NRC Research Press, Ottawa, pp. 1297–1304.

Whitworth, T.L. & Yusseff-Vanegas, S. (2019) A revision of the genera and species of the Neotropical family Mesembrinellidae (Diptera: Oestroidea). *Zootaxa*, 4659 (1), 1–146. https://doi.org/10.11646/zootaxa.4659.1.1

Wiegmann, B.M., Trautwein, M.D., Winkler, I.S., Barr, N.B., Kim, J.W., 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.H., 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*, 108 (14), 5690–5695. https://doi.org/10.1073/pnas.1012675108

Wolff, M. (2013) A new species of *Mesembrinella* (Diptera: Calliphoridae: Mesembrinellinae) from Colombia. *Revista Colombiana de Entomología*, 39, 120–124.

Wolff, M., Bonatto, S.R. & Carvalho, C.J.B. de (2014) Review of *Thompsoniella* Guimarães with description of a new species from Colombia (Diptera, Calliphoridae, Mesembrinellinae). *Revista Brasileira de Entomologia*, 58 (4), 319–325. https://doi.org/10.1590/S0085-56262014005000002

Zielke, E. (2020) Correction proposals for some Madagascan *Dichaetomyia* species identified in earlier years, and descriptions of six new species of the genus (Diptera: Muscidae). *Entomologist's Monthly Magazine*, 156, 209–241. https://doi.org/10.31184/M00138908.1564.4045

Zielke, E. (2021a) Descriptions of five new shiny *Dichaetomyia* species from Madagascar (Diptera: Muscidae). *Entomologist's Monthly Magazine*, 157, 81–103. https://doi.org/10.31184/M00138908.1572.4066

Zielke, E. (2021b) Five new species of *Dichaetomyia* from the Malagasy subregion (Diptera: Muscidae). *Historia Naturalis Bulgarica*, 42, 65–78. https://doi.org/10.48027/hnb.42.092

Zielke, E. (2021c) Four new *Dichaetomyia* species from Madagascar (Diptera: Muscidae). *Journal of Entomology and Zoology Studies*, 9, 105–114.

Zielke, E. (2022) On Madagascan *Dichaetomyia* species (Diptera: Muscidae): Description of four new species. *Journal of Entomology and Zoology Studies*, 10 (4), 18–30. https://doi.org/10.22271/j.ento.2022.v10.i4a.9022