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Redefining the generic limits of *Winthemia* (Diptera : Tachinidae)

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Abstract. One of the major problems hindering the systematic study of tachinid flies is that genera are often poorly defined, making it difficult to unambiguously assign species among closely related genera. Within the tribe Winthemiini, an example of this problem is represented by the unstable classification of the Afrotropical species most recently classified as *Smidtia capensis* (Schiner). This species has been previously assigned to four different genera on the basis of limited examination and evidence. Here, we evaluate the identity and phylogenetic affinities of this species and other members of the tribe Winthemiini using morphological and molecular phylogenetic analysis. We demonstrate that *S. capensis* actually belongs to the genus *Winthemia* Robineau-Desvoidy. We also find that *Winthemia* is paraphyletic with respect to two monotypic genera, *Crypsina* (type species *Crypsina prima* Brauer & Bergenstamm) and *Hemiwinthemia* (type species *Hemiwinthemia calva* Villeneuve). On the basis of morphological and genetic evidence, we propose to extend the generic limits of *Winthemia* to include *W. londti*, sp. nov. (South Africa), *W. capensis* (Schiner), comb. nov. (South Africa), *W. prima* (Brauer & Bergenstamm), comb. nov. (China, Japan, Australia) and *W. calva* (Villeneuve), comb. nov. (D.R. Congo), thus synonymising with *Winthemia* the generic names *Crypsina*, syn. nov. and *Hemiwinthemia*, syn. nov.

Additional keywords: COI, *Crypsina*, Exoristinae, *Hemiwinthemia*, new species, parasitoid, phylogeny, *Smidtia*, systematics, Winthemiini, 28S rDNA.

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Introduction

The tachinid tribe Winthemiini represents a diverse group of insect parasitoids belonging to the largest subfamily of Tachinidae, the Exoristinae. This tribe includes ~20 genera of oviparous parasitoids distributed across all major zoogeographical regions in the world (Guimarães 1971; Crosskey 1973, 1980; Coelho *et al*. 1989; Shima 1996; O'Hara and Wood 2004; O'Hara and Cerretti 2016). Within this group only two genera, *Winthemia* Robineau-Desvoidy and *Nemorilla* Rondani, are nearly cosmopolitan in distribution and account for more than half of the total species richness of the tribe.

Winthemiines attack mainly lepidopteran larvae, although sawfly larvae also serve as hosts for several species, especially among those assigned to *Smidtia* Robineau-Desvoidy (Herting 1960; Crosskey 1973, 1976, 1984; Arnaud 1978; Tschorsnig and Herting 1994). Several winthemiines are parasitoids of agricultural and forest insect pests and may play an important role in regulating the population dynamics of their hosts. This is true for several species of *Winthemia* that have often been reared from economically important pest species of armyworms (Lepidoptera : Noctuidae) such as the bertha armyworm (*Mamestra configurata* Walker) and the fall armyworm (*Spodoptera frugiperda* (Smith)) (e.g. Ashley 1979; O'Hara 1999; Molina-Ochoa *et al*. 2003; Ruíz-Nájera *et al*. 2007). Despite the importance of winthemiines as parasitoids, the systematics of this group remains unsettled.

Recent phylogenetic reconstructions of the Tachinidae based on morphological (Cerretti *et al*. 2014) and molecular (Stireman 2002; Tachi and Shima 2010) data generally support monophyly of Winthemiini, though not always (see Stireman 2002). The tribe is characterised by having a setose katepimeron, a flattened bacilliform sclerite in the male terminalia, and macrotype plano-convex eggs that are laid unincubated on the host cuticle by means of a telescopic oviscapt (see Tschorsnig 1985; Shima 1996). While this combination of characters clearly defines the group, further relationships within this tribe are less clear. Several winthemiine genera such as *Nemorilla*, *Smidtia* and *Winthemia* have been studied in some detail in the Palaearctic and Nearctic regions (e.g. Mesnil 1949; Guimarães 1972; Herting 1984; Shima 1996); however, the taxonomy of this tribe for all other regions is largely unexplored.

One of the major problems affecting the stability of the systematics of tachinids is that supraspecific groupings are often not defined along phylogenetic lines (e.g. Cerretti *et al*.

2015). This has produced a proliferation of often monotypic genera that are defined by highly specific and typically superficial external features. Within this context, the unambiguous assignment of species among closely related genera is difficult, if not impossible, which perpetuates the taxonomic challenges of working with the family. Within the Winthemiini, an example of this problem is represented by the troublesome classification of '*Smidtia*' *capensis* (Schiner). This species was originally described in the genus *Nemoraea* Robineau-Desvoidy based on a single male from South Africa (Schiner 1868). It was later moved to the winthemiine genus *Nemosturmia* Townsend by Mesnil (1949), the species of which were later transferred to *Timavia* Robineau-Desvoidy (Herting 1974; Mesnil 1975). Crosskey (1980), in his Catalogue of Afrotropical Tachinidae, treated *capensis* under *Timavia*, now junior synonym of *Smidtia* (Wood 1987; Shima 1996). In the most recent revision of *Smidtia*, Shima (1996) treated only the Palaearctic species, and thus circumscribed *Smidtia* without considering characters of *capensis*. A formal placement of *capensis* in *Smidtia* (*sensu* Shima 1996) had not been proposed until recently (see Cerretti *et al*. 2013).

In this study, we use morphological and molecular data to evaluate the relationships among winthemiine taxa and determine the correct taxonomic placement of '*Smidtia capensis*'. Our phylogenetic inferences allow us to unambiguously assign *capensis* and a new closely related species from the Northern Cape (South Africa) to a newly circumscribed genus *Winthemia*, which also includes taxa formerly included in the genera *Crypsina* and *Hemiwinthemia*.

Materials and methods

Adult specimens were examined with a MZ 12.5 stereoscopic microscope (Leica, Germany) equipped with a digital camera DS-L1 Nikon (Nikon, Tokyo). Photographs of male terminalia were taken using a DM LS microscope (Leica, Germany) equipped with the camera described above. To create images with greater depth of field, ~5–15 photographs of each specimen/structure at different focal points were taken. Final photos were combined into a single image using the image stacking software CombineZM (Hadley, UK). Additionally, uncoated male terminalia and whole pinned specimens were examined with a Hitachi TM1000 environmental scanning electron microscope.

Dissections of the male terminalia were performed according to the procedure described by Cerretti and Pape (2012). Briefly, this procedure involves the removal of the abdomen, partial clearing of it in 10% NaOH, dissection of terminalia, reattachment of the abdomen to the specimen and finally storage of the terminalia in a microvial with glycerin. Morphological terminology follows Cumming and Wood (in press) except for costal sections of the wing and for measurements and ratios of the head, which follow Cerretti (2010).

Data from each type specimen are given verbatim, with each line separated by a diagonal slash (/) and information for each individual label enclosed within quotation marks. Additional information not appearing on the label is enclosed within brackets. Finally, the depository is cited in parentheses. Acronyms used in the text for the museums where specimens are deposited appear below.

CNC	Canadian National Collection of Insects, Agriculture and Agri-Food Canada, Ottawa, Canada.
JOSC	J. O. Stireman III Collection, Wright State University, Dayton, Ohio, USA.
MZUR	Museum of Zoology, Università di Roma 'La Sapienza', Roma [Rome], Italy.
NMB	National Museum, Bloemfontein, South Africa.
NMDA	Department of Arthropoda, Natal Museum, Pietermaritzburg, South Africa.
SMNS	Staatliches Museum für Naturkunde, Stuttgart, Germany.
TAU	Tel Aviv University, Tel Aviv, Israel.

Phylogenetic analysis

Morphology

Characters and their states were scored from representatives of the following taxa: '*Crypsina*' *prima* Brauer & Bergenstamm, '*Hemiwinthemia*' *calva* Villeneuve, *Ossidingia cruciata* (Wiedemann), *Rhaphiochaeta breviseta* (Zetterstedt), '*Smidtia*' *capensis*, *Winthemia dasyops* (Wiedemann), *Winthemia londti*, sp. nov., *Winthemia quadrata* (Wiedemann) and *Winthemia venusta* (Meigen) (Appendix 1). We also examined and scored traits using multiple species of the genera *Nemorilla*, *Smidtia* and *Winthemia*, but treated each genus as a single operational taxonomic unit (OTU) in our analysis. The exoristine taxa *Exorista larvarum* (Linnaeus), *Paratryphera barbatula* (Rondani) and *Phorocerosoma* spp. were included as outgroups (Appendix 1). A matrix containing 25 morphological characters was prepared in Mesquite 3.03 (Tables 1, 2) and analysed in TNT 1.1 (Goloboff *et al*. 2008). Multistate characters were treated as unordered and zero-length branches were collapsed. The analysis was run as implicit enumeration with equal weights as well as under implied weights (concavity factor of 1 and higher). No resampling analysis was carried out, as the interpretation of the resulting percentiles when performed on a small and highly selective morphological dataset is uninformative.

Molecular

DNA was extracted from the right legs of the following winthemiines: *Avibrissosturmia* sp., *Hemisturmia scissilis* (Reinhard), '*Smidtia*' *capensis*, *Smidtia conspersa* (Meigen), *Winthemia aureonigra* Thompson, *Winthemia quadrata*, *Winthemia rufiventris* (Macquart), *Winthemia rufopicta* (Bigot), *Winthemia sinuata* Reinhard and *Winthemia* sp. (Appendix 1). In addition, we extracted DNA from *Tachinomyia nigricans* Webber, *Phorocera slossonae* (Townsend) and *Paratryphera barbatula* (Appendix 1), which were included as outgroup taxa as they lie outside of the Winthemiini but within the Exoristinae, and they share similar macrotype, unembryonated eggs with Winthemiini. For DNA extraction we used the Puregene Core Kit A (QIAGEN Sciences Inc., Germantown, MD, USA) following the manufacturer's protocols. The mitochondrial gene COI and the nuclear gene

Table 1. Characters and character states used in the phylogenetic analysis

1. Length of arista: (0) at least as long as antenna; (1) at most as long as postpedicel.
2. Thickened portion of arista: (0) at most on proximal 2/3; (1) on proximal 3/4 or more.
3. Parafacial: (0) bare; (1) setose.
4. Setulae in front of the anteroventral corner of compound eye between the parafacial and the gena: (0) absent; (1) present.
5. Male, upper reclinate orbital setae: (0) present; (1) absent.
6. Seta on facial ridge: (0) decumbent and confined on lower 1/5–1/3; (1) erect, robust and extended on lower 3/4 or more.
7. Black setae behind the postocular row: (0) absent; (1) at most one irregular row; (2) more than one row.
8. Number postsutural dorsocentral setae: (0) 4; (1) 3.
9. Katepisternal setae: (0) 2; (1) 3 or more.
10. Katepimeron: (0) entirely setose; (1) only with a few hairs anteriorly.
11. Lower calypter: (0) non-convex; (1) convex.
12. Number of anterodorsal setae on mid tibia: (0) 1; (1) 2; (2) 3 or more.
13. Anterodorsal comb-like setae on hind tibia: (0) with at least two long setae; (1) close set of setae uniform in length and thickness or at most with a single larger seta.
14. Number of preapical setae on hind tibia: (0) 2; (1) 3.
15. Discal setae on abdominal t3 and t4: (0) absent; (1) present.
16. Male, sixth abdominal tergite: (0) present, well developed; (1) reduced or absent.
17. Male, sixth abdominal tergite: (0) plate-like, i.e. not indented anteriorly; (1) divided into two hemitergites, or if not divided indented anteriorly.
18. Shape and size of the membranous extension of dorsal sclerite of distiphallus: (0) short and spine-like; (1) long and flag-like, well developed.
19. Membranous extension of dorsal sclerite of distiphallus: (0) absent; (1) present.
20. Epiphallus: (0) well developed; (1) reduced or absent.
21. Position of epiphallus: (0) in dorsobasal position; (1) in dorsomedial or dorsodistal position.
22. Bacilliform sclerite: (0) flattened dorsoventrally and expanded medially; (1) rod-shaped; (2) flattened dorsoventrally but not expanded medially.
23. Oviscapt: (0) not elongated; (1) elongated.
24. Female, 7th sternite: (0) normally developed; (1) reduced; (2) strongly reduced to virtually absent.
25. Female, 8th tergite: (0) normally developed; (1) strongly reduced; (2) absent.

Table 2. The resulting matrix used in the phylogenetic analysis

When two or more states occur in a single terminal taxon, they are separated by a diagonal slash (/). The first three taxa (grey shading) were used as outgroups

Taxa	Characters																								
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Exorista larvarum	0	0	0	0	0	0	0	0	1	1	0	2/3	0	0	0	0	1	?	0	0	0	2	0	0	0
Paratryphera barbatula	0	0	0	0	0	0	0/1	0	1	0	1	0/1	0	0	0/1	0	0	?	0	1	0	1	0	0	2
Phorocerosoma spp.	0	0	0	0	1	0	0	0	1	0	1	3	0	0	0	0	1	0	1	1	0	1	0	0	?
'*Crypsina*' *prima*	0	0	1	0	1	0	2	0	0	0	0	1/2	1	0	0	0	0	0	1	1	?	0	1	2	1
'*Hemiwinthemia*' *calva*	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	1	0	?	?	?
Nemorilla spp.	0	0	0/1	0	1	0	0	0	0/1	0	0	0	0	0	1	0	1	0	1	0	1	0	1	1	0
Ossidingia cruciata	0	0	0/1	0	1	0	0	1	1	0	0	1	0	0	1	0	1	0	1	0	1	0	1	1	0
Rhaphiochaeta breviseta	1	1	1	0	0	0	1/2	1	1	0	0	2/3	0	1	0	1	1	1	1	0	1	0	1	1	0
'*Smidtia*' *capensis*	0	0	0	1	1	0	1	0	1	0	0	2/3	0	0	0	0	1	0	1	0	1	0	1	2	1
Smidtia spp.	0	0	1	0	0	0	0/1	0/1	1	0	0	2	0	0	0	1	?	1	1	0	1	0	1	1	0
Winthemia dasyops	0	0	1	0	1	0	0	0	0	1	1	0	1	0	0	0	1	0	1	0	1	0	1	2	1
Winthemia londti	0	0	0	1	1	0	1	0	1	0	0	2/3	1	0	0	0	1	0	1	0	1	0	?	?	?
Winthemia quadrata	0	0	1	0	1	1	0	0	0	0	1	2	1	0	0	0	1	0	1	0	1	0	1	2	1
Winthemia spp.	0	0	1	0	1	0	0	0	0	0	0	1	1	0	0	0	1	0	1	0	1	0	1	2	1
Winthemia venusta	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	1	0	1	2	1

28S were amplified using the primers LepF1 and LepR1 (see Smith *et al*. 2006) and 28SF and 28SR (see Winkler *et al*. 2015). For the PCR amplification, the general procedure described in Winkler *et al*. (2015) was followed. In particular, PCRs were performed in 30-µL reaction volumes using a thermocycling profile of one cycle of 2 min at 94°C; 36 cycles of 30 s at 94°C, 60 s at 45°C, and 60 s at 72°C; and a final cycle of 6 min at 72°C. The PCR products were sent to the University of Arizona Genetics Core, where the samples were run on an Applied Biosystems 3730XL DNA Analyzer in 96-well format.

Sequences were manually aligned and edited using CodonCode Aligner 3.5 (CodonCode Corporation, Dedham, MA, USA). For the 28S gene, 20 highly variable sites were omitted from the final dataset due to difficulty in inferring homology. Final aligned sequence lengths were 601 bp for COI and 1319 bp for 28S. In addition, 13 sequences were obtained from the NCBI GenBank database (Benson *et al*. 2013), and seven sequences were obtained from the BOLDsystems (Barcode Of Life Database) database (http://www.boldsystems.org). All new sequence data generated in this study have been uploaded to the GenBank database and their respective accession numbers are reported in Appendix 1. Maximum Likelihood (ML) phylogenetic analyses of each gene dataset were conducted separately as well as a concatenated dataset of both genes for a subset of taxa in RAxML (Stamatakis 2014) implemented via the CIPRES Science Gateway (Miller *et al*. 2010; https://www.phylo.org). ML analyses used a GTR+I +G model of nucleotide substitution with 1000 bootstrap replicates.

Results

Morphological analysis

The parsimony analysis resulted in one most parsimonious cladogram (Fig. 1) with a tree length of 46 steps, a consistency index of 0.67 and a retention index of 0.72. In this reconstruction, Winthemiini are retrieved as monophyletic on the basis of three non-homoplasious apomorphies (21 : 1, epiphallus in dorsomedial or dorsodistal position; 23 : 1, females with elongate oviscapt; 24 : 1, hypandrial arms posteriorly not fused). These three character states are found in other tachinid lineages, thus becoming homoplasious in a more comprehensive analysis. The tribe is divided into two main subclades: Clade A (*Smidtia* + *R. breviseta*) and Clade B (all other winthemiines taxa sampled) (Fig. 1).

The sister group relationships between *Smidtia* and *R. breviseta* (Clade A) is supported by one homoplasious (3 : 1) and two non-homoplasious apomorphies (16 : 1, sixth abdominal tergite in males not reduced; 18 : 1, presence of a long membranous extension on dorsal sclerite of distiphallus). Monophyly of Clade C (*Nemorilla* + *O. cruciata*) is supported by one non-homoplasious apomorphy (15 : 1, presence of discal setae on tergites 3 and 4). Clade D comprises the sister groups Clade E (‘*Smidtia*’ *capensis* + *W. londti*, sp. nov.) and Clade F (‘*Hemiwinthemia*’ *calva* + (*W. venusta* + (*W. quadrata* + *W. dasyops*) + (*Winthemia* + ‘*Crypsina*’ *prima*)) based on two non-homoplasious apomorphies (24 : 2, strong reduction of the 7th abdominal sternite in females; 25 : 1, strong reduction of the 8th abdominal tergite in females). Within this reconstruction we did not find any autapomorphic support for OTUs *Smidtia*, *Nemorilla* and *Winthemia*, nor any evidence supporting assignment of *capensis* to *Smidtia*.

Molecular analysis

Each of the ML phylogenetic analyses, COI mtDNA, 28S rDNA, and the concatenated dataset, resulted in similar topologies, with ‘*Smidtia*’ *capensis* being reconstructed as sister to members of the genus *Winthemia*, and this group, ‘*Smidtia*’ *capensis* + *Winthemia*, as sister to *Nemorilla* (Fig. 2). In contrast, representatives of the genus *Smidtia* are reconstructed in a separate clade (COI, Fig. 2*a*; concatenated, Fig. 2*c*), or as more basal lineages within the tribe (28S, Fig. 2*b*). For COI, bootstrap support for ‘*Smidtia*’ *capensis* + *Winthemia* is relatively weak (60% bootstrap support (bs)), however, the more inclusive clade with

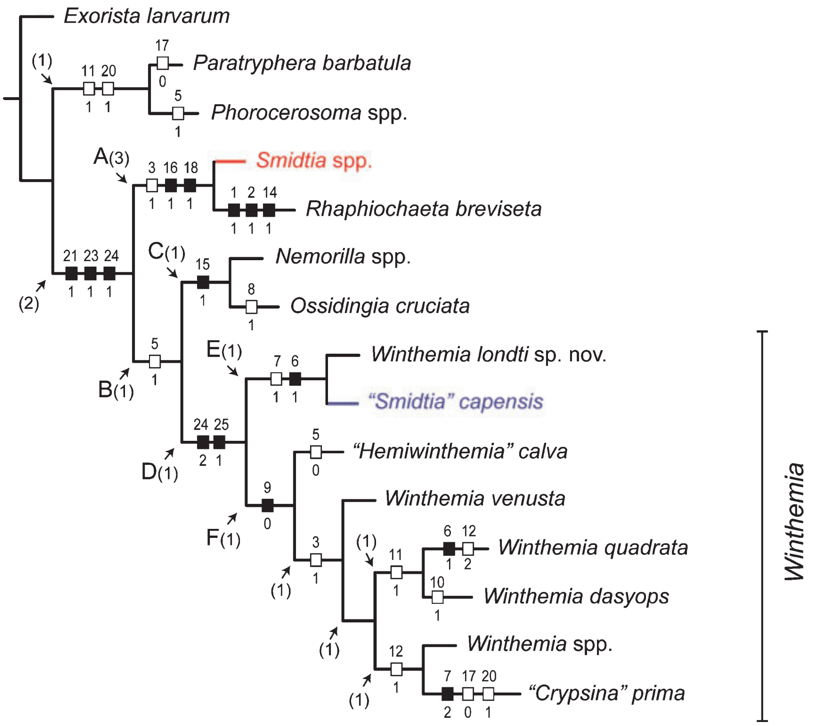

Fig. 1. The most parsimonious cladogram of Winthemiini (total length = 46 steps). Open squares represent homoplastic synapomorphies, while filled squares represent uniquely derived synapomorphies. Clades discussed in the text are labelled with letters. Numbers within parentheses indicate Bremer support values. ‘*Smidtia*’ *capensis* and *Smidtia* spp. are in bold and their positions are highlighted by blue and red branches/text, respectively (online version).

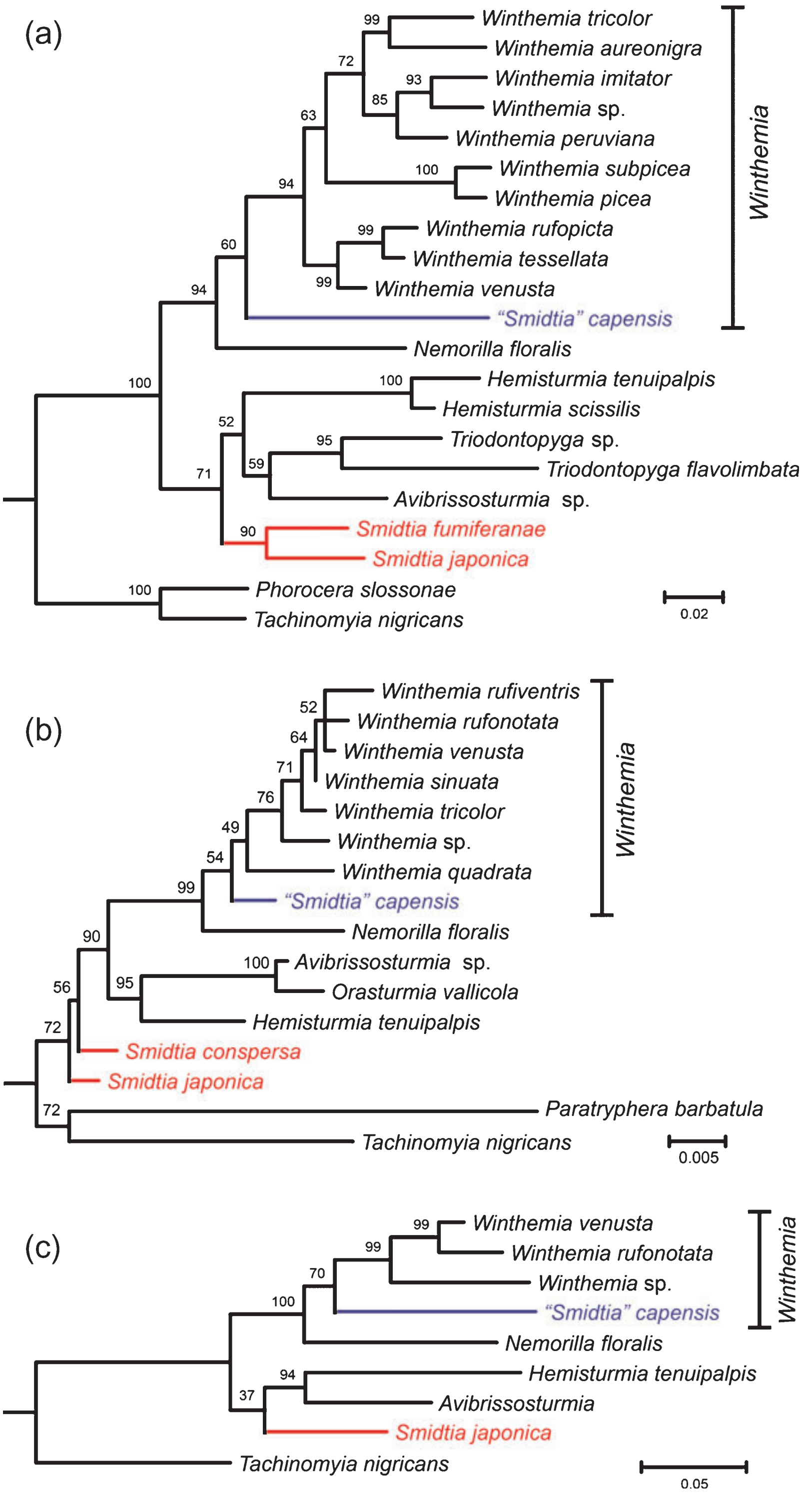

Fig. 2. Maximum-likelihood trees of representative Winthemiini based on: (*a*) COI, (*b*) 28S rDNA, and (*c*) a concatenated dataset of both genes for a limited set of taxa. '*Smidtia*' *capensis* and *Smidtia* spp. are in bold and their positions are highlighted by blue and red branches/text, respectively (online version). Numbers above branches indicate bootstrap support (%). Scale bars below trees indicate ML distances.

Nemorilla is strongly supported (94% bs; Fig. 2*a*). In this reconstruction, the two *Smidtia* species are placed in a separate clade with the New World genera *Hemisturma*, *Avibrissosturmia*, and *Triodontopyga* (70% bs; Fig. 2*a*). We note that the monophyly of *Winthemia* is well supported in this tree (94% bs).

Very similar patterns are found for the reconstruction based on 28S rDNA, with limited support for '*Smidtia*' *capensis* + *Winthemia* (54% bs) and very strong support for *Nemorilla* + '*Smidtia*' *capensis* + *Winthemia* (99% bs; Fig. 2*b*). In contrast to the COI tree, the New World winthemiine genera *Hemisturma* and *Avibrissosturmia*, as well as *Orasturmia*, join this group with high support (90% bs), leaving *Smidtia* as a paraphyletic basal grade (among the taxa sampled). The reduced taxon concatenated dataset generally conforms to the COI tree, with 100% bootstrap support for *Nemorilla* + '*Smidtia*' *capensis* + *Winthemia*, substantial support for '*Smidtia*' *capensis* + *Winthemia* (70% bs) and a weakly supported (37% bs) clade comprising *Smidtia* and the New World genera mentioned above (Fig. 2*c*).

Systematics

Genus ***Winthemia*** Robineau-Desvoidy, 1830

(Figs 3–10)

Winthemia Robineau-Desvoidy, 1830: 173. Type species: *Musca quadripustulata* Fabricius, 1794, by subsequent designation of Desmarest *in* d'Orbigny (1849: 301) (see Evenhuis & Thompson, 1990: 239) [Palaearctic].

Crypsina Brauer & Bergenstamm, 1889: 97. Type species: *Crypsina prima* Brauer & Bergenstamm, 1889, by original designation, **syn. nov.**

Hemiwinthemia Villeneuve, 1938: 4. Type species: *Hemiwinthemia calva* Villeneuve, 1938, by monotypy, **syn. nov.**

New combinations:

Winthemia calva (Villeneuve, 1938), **comb. nov.**

Winthemia capensis (Schiner, 1868), **comb. nov.**

Winthemia prima (Brauer & von Bergenstamm, 1889), **comb. nov.**

See Mesnil (1949), Guimarães (1971, 1972), Crosskey (1973, 1980), Coelho *et al*. (1989), Shima (1996), O'Hara and Wood (2004), and O'Hara and Cerretti (2016) for a full list of species, synonymies and selected references.

Recognition of Winthemia

Compound eye covered with long ommatrichia; parafacial setose or bare (two species have a patch of a few small setulae between parafacial and gena near the lower anterior margin of compound eye (Fig. 4)); upper reclinate orbital seta absent, or indistinguishable from dorsalmost frontal setae (one seta differentiated only in *W. calva*); occiput flat or slightly concave with at most one row of black setulae behind postocular row. Postpronotum with the 3 strongest basal setae arranged in a triangle or, more rarely, in a straight line; prosternum setose; first postsutural supra-alar seta at most as long as notopleural setae and usually shorter than first postsutural dorsocentral seta; 2 or (rarely) 3 katepisternal setae; katepimeron setose; hind tibia with a row of close-set comb-like anterodorsal setae, rarely interspersed with one or two slightly longer setae. Mid-dorsal depression of abdominal syntergite 1+2 extending posteriorly to hind margin of syntergite; abdominal tergites without median discal setae. Male: no proclinate orbital setae; abdominal tergite 6 usually divided into two hemitergites, rarely plate-like (*W. prima*); membranous extension of dorsal sclerite of distiphallus present, but short; epiphallus usually well developed (reduced only in *W. prima*). Female: two proclinate orbital setae; sternite 7 and tergite 8 strongly reduced; ovisac relatively short; plano-convex macrotype egg, whitish to yellow in colour.

Winthemia londti Inclán & Cerretti, sp. nov.

(Figs 3–6)

http://zoobank.org/urn:lsid:zoobank.org:act: 9073C9C3-8F38-4E63-B463-03040B2D7F70

Material examined

Holotype. ♂: 'R.SA [Republic of South Africa]: N [Northern] Cape #83/ 2 km S [South] of Nababeep/ 29°37′S: 17°48′E 810 m [altitude]/ Date: 24.viii.1995/ Coll: J. & A. Londt/ Stream edge Flowers' (NMDA).

Paratype. 1 ♂: 'STH AFRICA [Republic of South Africa]: N Cape/ 7 km SSE Nababeep/ 29°37′13″S: 17°50′29″E/ 24.viii.2002 JGH Londt/ 1020 m [altitude] Rocky hillside/ with sandy areas below' (MZUR). Terminalia are detached from the paratype and stored in glycerin in a microvial pinned below the specimen.

Diagnosis

Scutum heavily covered with grey microtomentum, except on four presutural dark vittae. Abdominal tergites 3 and 4 with 2 large black patches each emerging from dense, silver-grey reflecting microtomentum. Distal half of abdominal tergite 5 shiny black with remaining dorsal surface covered with silver-grey reflecting microtomentum (Fig. 3*c*). Parafacial bare, with a few small setulae (<12) between parafacial and gena, near lower anterior margin of compound eye (Fig. 4).

Description

Male

Body length: 14.9–15.4 mm.

Coloration: Head black, covered with dense grey reflecting microtomentum. Antenna mainly black or dark brown except distal end of pedicel and inner proximal portion of postpedicel light brown to yellowish. Palpus light brown or yellowish. Thorax (including legs) black; scutum with 4 black presutural vittae standing out against silver-microtomentose scutum; scutellum varying from entirely yellowish to mostly black, but yellowish apically. Tegula black; basicosta reddish-yellow. Wing membrane hyaline. Haltere brownish. Abdominal tergites 3 and 4 densely covered with silver microtomentum with two relatively large black spots close to posterior margin (Fig. 3*c*). Distal half of abdominal tergite 5 shiny black with the remaining dorsal surface covered with silver microtomentum.

Head: Compound eye covered with very long ommatrichia, distinctly longer than 4 eye facets. Ocellar setae well developed and proclinate. Frons at its narrowest point 0.75–0.78 times as wide as compound eye in dorsal view. Outer vertical seta small, but differentiated from postocular setae. Frontal setae descending on parafacial to base of arista (or slightly below). Fronto-orbital plate with several medioclinate setulae, more or

Fig. 3. Male of *Winthemia londti*, sp. nov. (*a*) Habitus in lateral view, (*b*) head in lateral view, (*c*) abdomen in dorsal view.

less arranged into two irregular rows, between frontal row and compound eye margin. Upper reclinate orbital seta absent. Proclinate orbital setae absent in male, 2 proclinate orbital setae in female. Parafacial mostly bare below lowest frontal seta, but with a patch of hair-like setulae (5–12) arising close to lower margin of compound eye (Fig. 4). Parafacial at its narrowest point 1.2−1.3 times wider than width of postpedicel at midlength. Facial ridge with short, recumbent setae on its lower 1/4–1/3. Vibrissa arising above level of lower facial margin. Face and lower facial margin not protruded, though lower facial margin slightly visible in lateral view in front of vibrissal insertion. Genal dilation well developed and covered with robust black setulae. Postgena and lower occiput covered with mostly pale setulae. Upper occiput with 1 irregular row of black setulae behind postocular row. Gena ~0.17−0.19 times as high as compound eye. Postpedicel ~1.43−1.67 times as long as pedicel. Postpedicel distally rounded. Arista apparently bare, thickened approximately on proximal 1/2−3/5. First aristomere distinctly shorter than wide. Second aristomere at least about as long as wide. Prementum 3−4 times as long as wide. Palpus almost filiform, slightly enlarged apically.

Thorax: Prosternum setulose. Proepisternal depression bare. Postpronotum with 5−6 setae, 3 strongest basal arranged more or less in a straight line. Scutum with 2 posthumeral setae; 3 (presutural) + 3 (postsutural) acrostichal setae; 3 + 4 dorsocentral setae; 1 + 3 intra-alar setae; 3 postsutural supra-alar setae, first postsutural supra-alar seta at least as long and robust as posterior notopleural seta and distinctly longer than first postsutural dorsocentral seta. Two notopleural setae. Three katepisternal setae. Katepimeron setulose on at least anterior 2/3. Anepimeral seta present and well differentiated from general anepimeral setulae. Scutellum with 3 pairs of marginal setae (basal, subapical and apical). Apical scutellar setae crossed and tilted upwards to ~30° from horizontal. Subapical scutellar setae robust and reaching at least as far as apical setae. Anatergite bare below lower calypter. Second costal sector bare ventrally. Costal spine generally undifferentiated from costal setulae. Vein R_{4+5} with only a few setulae at base, not extending beyond basal 1/3.

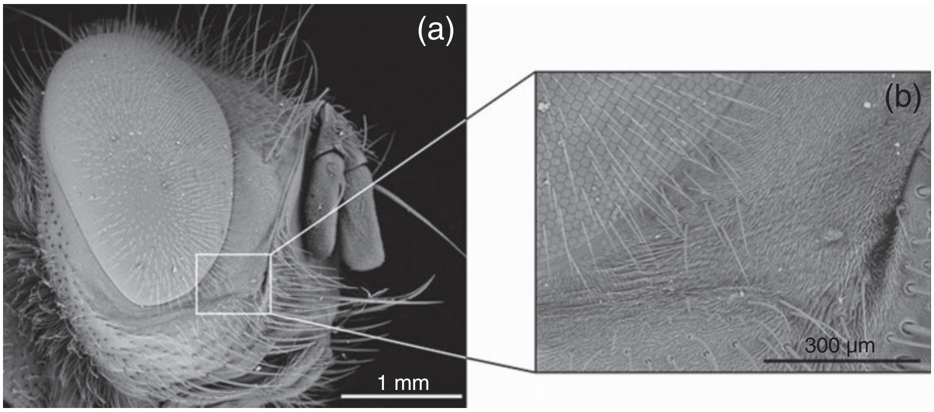

Fig. 4. Male of *Winthemia londti*, sp. nov. (*a*) Head in lateral view, (*b*) close-up of the small setae between parafacial and the gena near the lower anterior margin of compound eye.

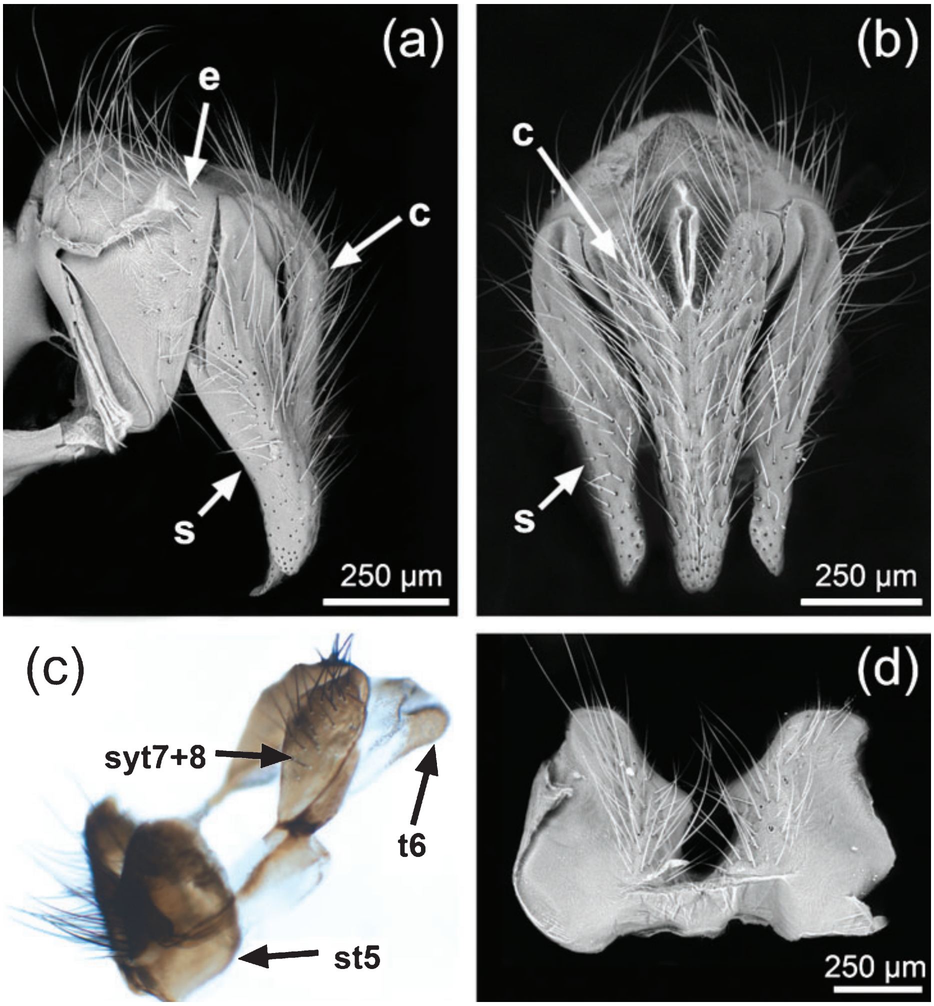

Fig. 5. Male terminalia of *Winthemia londti*, sp. nov. (*a*) Cercus and surstylus in lateral view, (*b*) cerci and surstyli in posterior view, (*c*) tergite 6, syntergite 7+8 and sternite 5, (*d*) sternite 5. Abbreviations: c, cerci; s, surstylus; st5, sternite 5; syt 7+8, syntergite 7+8; t6, tergite 6.

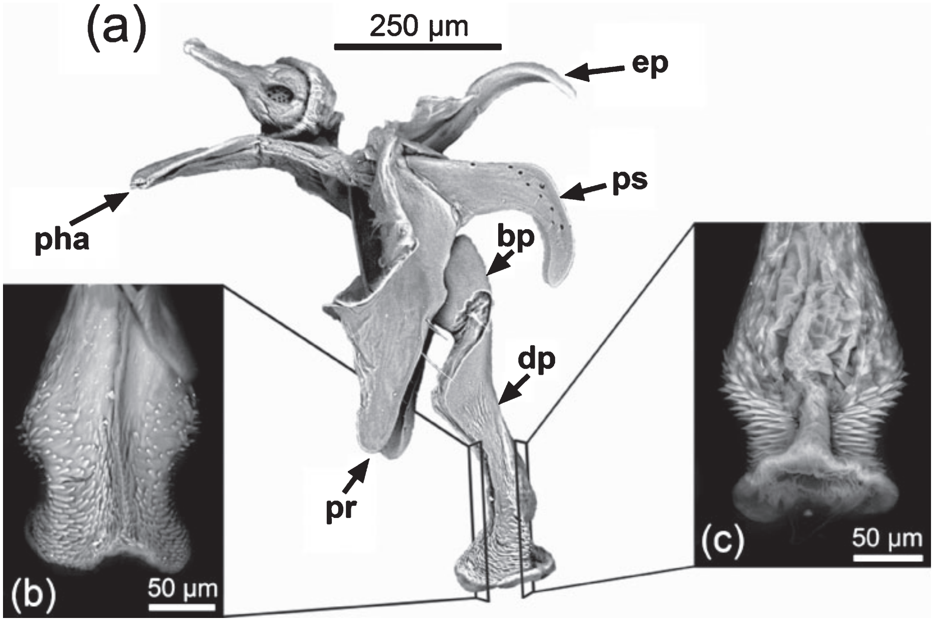

Fig. 6. Male phallus of *Winthemia londti*, sp. nov. (*a*) Phallus in lateral view, (*b*) distiphallus in ventral view, (*c*) distiphallus in dorsal view. Abbreviations: bp, basiphallus; dp, distiphallus; ep, epiphallus; pha, phallapodeme; pr, pregonite; ps, postogonite.

Bend of vein M_1 obtuse. Sector of M_1 between crossveins r-m and dm-m visibly longer than sector between dm-m and bend of M_1. Cell r_{4+5} open. Preapical anterodorsal seta of fore tibia as long as or longer than preapical dorsal seta. Mid tibia with 3–4 anterodorsal setae. Hind tibia with 2 dorsal preapical setae. Preapical posteroventral seta of hind tibia distinctly longer than preapical anteroventral seta. Hind tibia with a row of anterodorsal setae varied from regular to irregular, but never forming close-set comb-like setae as in other *Winthemia*.

Abdomen: Mid-dorsal depression of syntergite 1+2 extending back to hind margin of that segment. Syntergite 1+2 with 1 pair of marginal setae. Tergite 3 with 1 pair of median marginal setae. Tergite 3 with a row of 4 marginal setae, tergite 4 usually with a row of 6 marginal setae. Tergites 3 and 4 without median discal setae. Tergite 5 with irregular rows of marginal and discal setae. Tergite 5, in dorsal view, narrowed posteriorly and about as long as tergite 4 measured at mid-length. Sternites 3 and 4 covered by lateroventral edges of corresponding tergites.

Male terminalia: Anterior margin of sternite 5 nearly straight, posterior margin with a deep median cleft, smoothly U-shaped. Lateral lobe of sternite 5 rounded apically and covered with several strong setae along medial margin. Basal section of sternite 5 shorter than length of apical lobes. Tergite 6 bare, divided into two small hemitergites (Fig. 5*c*). Sternite 6 asymmetrical and right side connection to segment 7 membranous. Epandrium broad and convex. Anterior epandrial process scarcely developed and lateral epandrial lobe moderately developed. Cerci in posterior view subtriangular, narrowed towards apex, completely fused medially (Fig. 5*b*). Cerci in lateral view, almost straight with apex hooked ventrally (Fig. 5*a*). Upper lobes of cerci ~1/3 of total length of cerci. Surstylus in lateral view, concave along its anterior and posterior margins, ending in a lobe-like apex; surstylus not fused with epandrium. Bacilliform sclerites dorsoventrally flattened and medially fused. Hypandrial arms not fused posteromedially. Pregonite well developed, 0.9 times as long as distiphallus, triangular in shape, ending in a lobe-like apex and provided with fine setulae. Postgonite well developed, slightly narrowed towards its apex, strongly curved, hook-shaped. Intermedium present, normally developed. Basal processes of basiphallus present. Epiphallus well developed and apically hooked. Distiphallus ~1.5 times as long as basiphallus. Lateroventral region of distiphallus well developed, strongly sclerotised with robust spines lateroventrally that are concentrated on distal 1/3. Membranous extension of dorsal sclerite of distiphallus absent (Fig. 6).

Female

Unknown.

Etymology

We are pleased to dedicate this species to Jason Gilbert Hayden Londt, who has greatly contributed to knowledge of the Afrotropical Diptera, and has extensively collected flies in South Africa, including the holotype and paratype of this species.

Winthemia capensis (Schiner, 1868), comb. nov.

(Figs 7–10)

Holotype. ♂: South Africa, Western Cape, Cape of Good Hope [as 'Cap']. (type specimen not located)

Material examined

Hemiwinthemia francoisi Verbeke, 1973: 4. *Holotype*. ♀ (IRSNB). Type locality: Western Cape, Ceres District, Michell's Pass. Examined by PC (see O'Hara and Cerretti, 2016).

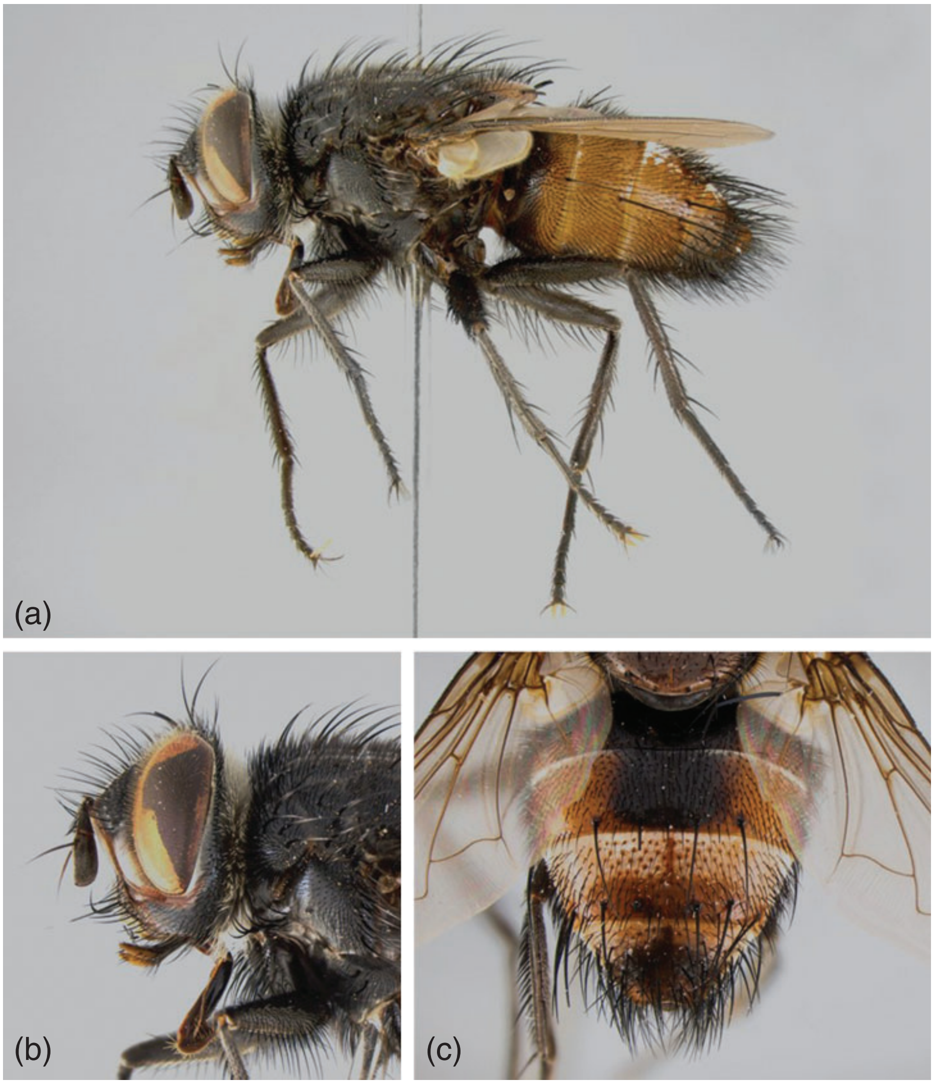

Fig. 7. Male of *Winthemia capensis*, comb. nov. (*a*) Habitus in lateral view, (*b*) head in lateral view, (*c*) abdomen in dorsal view.

Other material examined. 18 ♂ and 1 ♀: 1 ♂: 'R.SA [Republic of South Africa]: W [Western] Cape #45/ Bloukrans Forest Reserve/ 33°58′S: 23°37′E 330 m [altitude]/ Date: 21.x.1996/ Coll: J. & A. Londt/ Stinkhoud Kloof Trail' (NMDA). 1 ♂: 'SOUTH AFRICA: W. CAPE/ West Coast National Park/ 33°10′09″S: 18°07′57″E 60 m [altitude]/ JGH & A Londt 8.ix.2001/ Thick bushy area along road' (NMDA). 1 ♀ as previous except for: '33°07′31″S: 18°03′38″E 30 m/ JGH & A Londt 13.ix.2001/ Seeberg area, lagoon bush' (NMDA). 1 ♂: 'SOUTH AFRICA: W. CAPE/ Table Mountain Nat. Park/ Silvermine 11.x.2006 470 m/ 34°04.684′S 018°23.912′E/ JGH Londt Rocky area with/ *Erica*, *Protea*, *Berzelia* etc.' (NMDA). 12 ♂: 'SOUTH AFRICA: Western Cape/ Gamkaskloof (Die Hel) at:/ 33°22′5.90″S 21°37′19.43″E/ 17–18.X.2012, 336 m (hilltop)/ P. Cerretti, J. Stireman, J. O'Hara,/ I. Winkler & A.H. Kirk-Spriggs' (MZUR), 1 specimen with the terminalia stored in glycerin in a microvial pinned below specimen. 3 ♂ as previous except for: 'Ladismith, 30 km SW (R62) hilltop/ 33°37′44.50″S 21°2′58.04″E/ 21. X.2012, 385 m' (MZUR). 1 ♂: 'SOUTH AFRICA: Western Cape/ Anysberg Nature Reserve at:/ 33°26.612′S 20°47.497′E/ 14.X.2012 842 m hilltop/ P. Cerretti, J. Stireman, & I. Winkler', 'IZK03' (JOSC). This specimen is the source of the CO1 and 28S sequence data.

Diagnosis

Scutum with weak grey reflecting microtomentum, appearing almost entirely black. Laterodorsal section of abdomen covered with weak microtomentum, not covering the reddish ground coloration. Mid-dorsal section of syntergite 1+2 and tergite 3 usually black. Parafacial bare, rarely with one or two small setae between parafacial and gena, near to lower margin of compound eye.

Redescription

Body length: 9.9–12.4 mm.

As described for *W. londti*, sp. nov. except as follows:

Coloration: Palpus dark brown proximally, shading into yellowish towards apex. Presutural portion of scutum weakly covered with grey microtomentum, with 4 barely visible black vittae. Scutellum mostly red or yellowish. Abdomen largely reddish at least latero-dorsally, usually with a black median

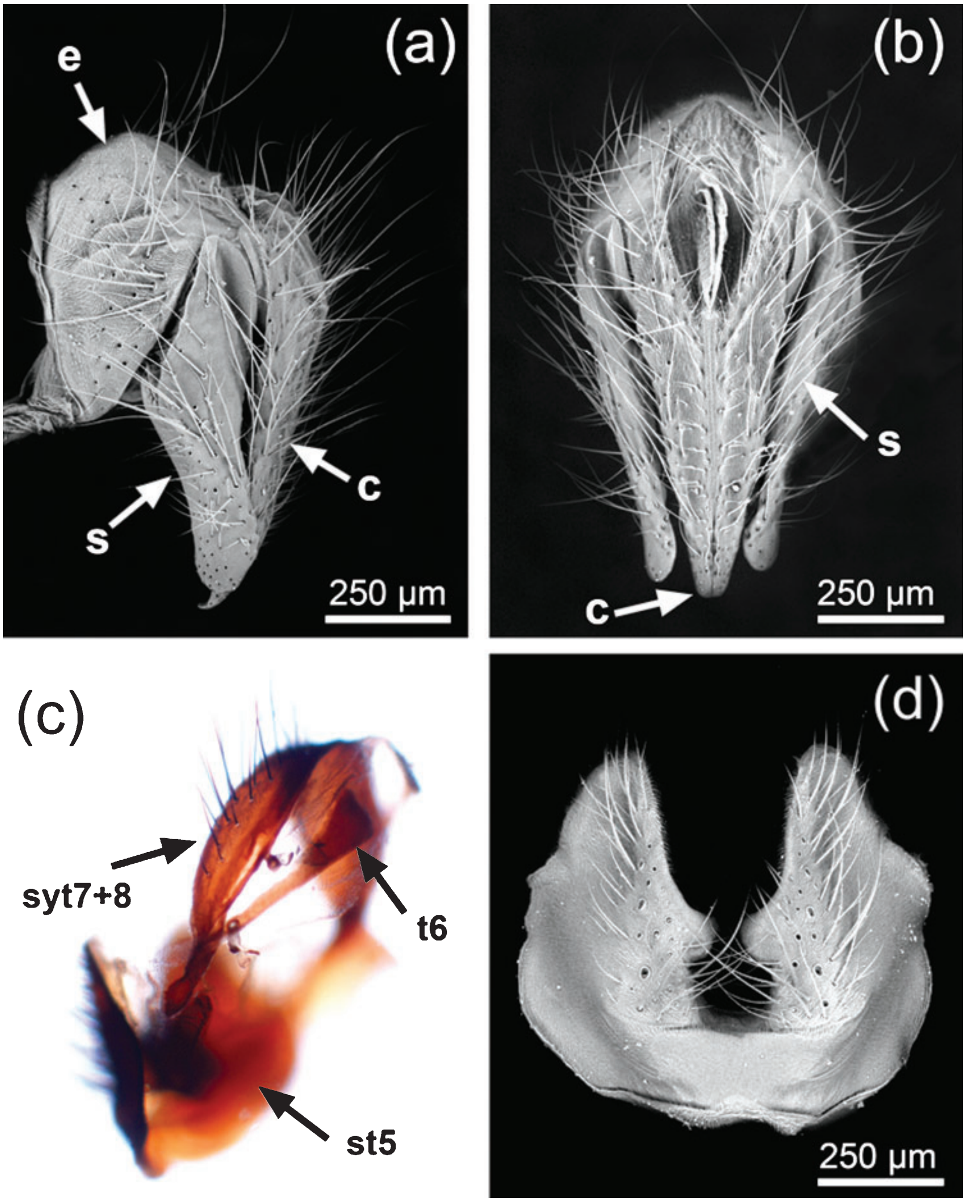

Fig. 8. Male terminalia of *Winthemia capensis*, comb. nov. (*a*) Cercus and surstylus in lateral view, (*b*) cerci and surstyli in posterior view, (*c*) tergite 6, syntergite 7+8 and sternite 5, (*d*) sternite 5. Abbreviations: c, cerci; s, surstylus; st5, sternite 5; syt 7+8, syntergite 7+8; t6, tergite 6.

dorsal vitta extending on syntergite 1+2 and tergite 3. Abdominal microtomentum forming weak bands along anterior margin of syntergite 1+2 and tergite 3, and covering more than anterior 1/3 of tergites 4 and 5 (Fig. 7*c*).

Head: Frons at its narrowest point 0.65–0.70 times as wide as compound eye in dorsal view in males, 1.1 in females. Parafacial usually entirely bare, rarely with 1–2 small setae close to lower margin of compound eye. Parafacial at its narrowest point 1.2–1.3 times as wide as width of postpedicel at mid-length in males, about as wide in single female (0.95). Dorsal part of occiput with only a few black setae behind postocular row. Gena ~0.15–0.20 times as high as compound eye in lateral view. Postpedicel ~1.7–2.3 times as long as pedicel in males, 1.6 in single female.

Thorax: Postpronotum usually with 5 setae, the 3 strongest basal arranged more or less in a straight line. Anterodorsal setae on hind tibia forming an irregular row of setae both in length and thickness.

Male terminalia: Anterior margin of sternite 5 concave (Fig. 8). Pregonite well developed, 0.95 times as long as distiphallus. Postgonite well developed, smoothly curved and somewhat hook-shaped. Epiphallus strongly apically hooked. Distiphallus with robust spines that are concentrated on less than its distal 1/3 (Fig. 9).

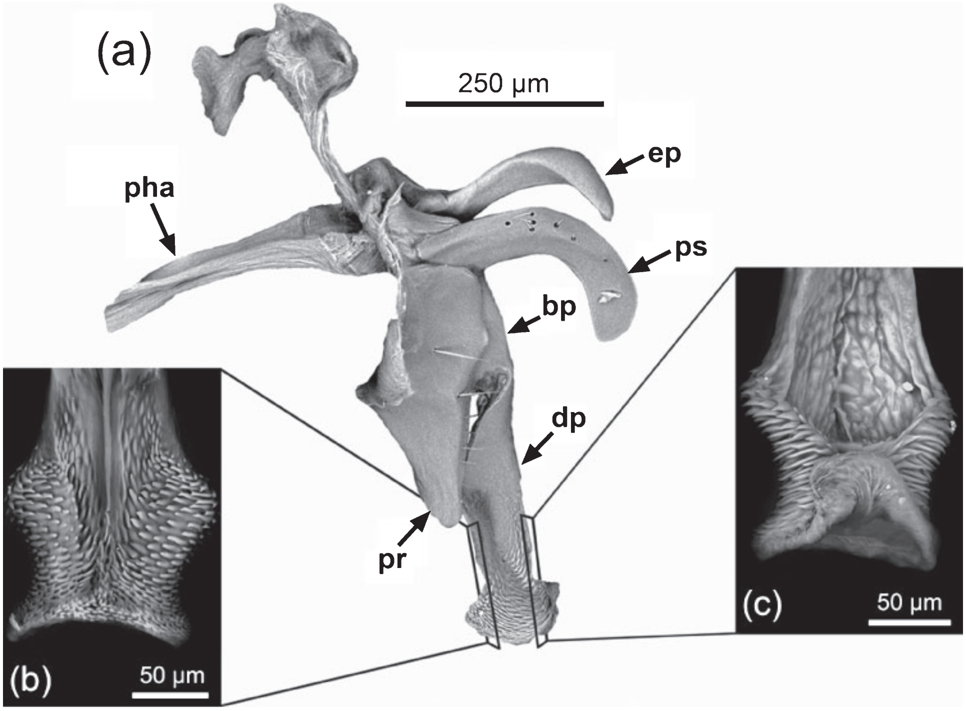

Fig. 9. Male phallus of *Winthemia capensis*, comb. nov. (*a*) Phallus in lateral view, (*b*) distiphallus in ventral view, (*c*) distiphallus in dorsal view. Abbreviations: bp, basiphallus; dp, distiphallus; ep, epiphallus; pha, phallapodeme; pr, pregonite; ps, postogonite.

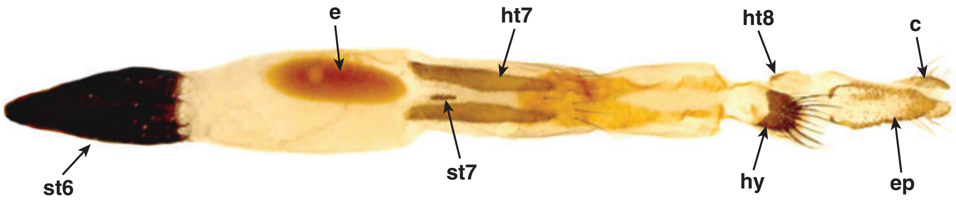

Fig. 10. Female terminalia of *Winthemia capensis*, comb. nov in ventral view (note that due to transparency some of the dorsal structures are also visible). Abbreviations: c, cercus; e, egg; ep, epiproct; ht7, hemitergite 7; ht8, hemitergite 8; hy, hypoproct; st6, sternite 6; st7, sternite 7.

Female terminalia: Hemitergite 6 narrowed towards its posterior 1/2, hemitergite 7 short and narrow, and hemitergite 8 indistinct. Sternite 6 broad, sternite 7 strongly reduced. Epiproct with fine apical setae (Fig. 10).

Discussion

All our analyses consistently recovered *Winthemia capensis* nested within the Winthemiini, thus confirming the previous tribal placement based on morphological evidence (Shima 1996; O'Hara and Cerretti 2016). Both morphological and molecular phylogenetic analyses agreed in recovering *W. capensis* and *Smidtia* spp. in clearly diverging positions within the tribe. Moreover, the overall genetic distances between *W. capensis* and the two *Smidtia* species sequenced is greater than the distance between *W. capensis* and the other *Winthemia*. The cladistic analysis reconstructed *W. capensis* as sister to *W. londti* and this clade clearly does not share any of the autapomorphies supporting the clade *Smidtia* + *R. breviseta* (Clade A).

The backbone of the cladogram obtained from morphological characters largely agrees with that of Shima (1996), though the lack of autapomorphies supporting *Winthemia* spp. and *W. venusta* in our tree suggests the need to redefine this genus based on cladistic arguments. Therefore, we propose to extend the generic limits of *Winthemia* to include *Hemiwinthemia calva*, *Crypsina prima* as well as the former *Nemoraea capensis*, and the new species *Winthemia londti*, sp. nov. Specifically, we propose to define *Winthemia* at the level of Clade D (Fig. 1) on the basis of two non-homoplasious apomorphies, i.e. the strong reduction of the 7th abdominal sternite (24 : 2) and 8th abdominal tergite (25 : 1) in females.

Previous authors have already contemplated an expanded concept of *Winthemia* to include *Hemiwinthemia* spp. and *Crypsina prima*. Specifically, Crosskey (1984: 274) considered *Hemiwinthemia* '… of dubious status and probably should not be maintained distinct from *Winthemia*', although he did not examine any of the three species assigned to this genus at that time (i.e. *H. calva*, *H. francoisi* Verbeke and *H. stuckenbergi* Verbeke: see O'Hara and Cerretti 2016). Similarly, Mesnil (1949) synonymised *Crypsina* with *Winthemia*, but this action was later reversed by Crosskey (1973).

A setose parafacial is widely used by tachinid workers as one of the main features to recognise *Winthemia* within winthemiines, though this condition is here interpreted as a weak homoplasious synapomorphy supporting monophyly of only a subset of *Winthemia* species. Crosskey (1984) already recognised in his key the presence of unidentified specimens with bare parafacials apparently belonging to *Winthemia*. Interestingly, *W. londti*, sp. nov. and some specimens of *W. capensis* have a patch of setae on the anteroventral corner of the compound eye between the parafacial and gena (Fig. 4), which is a very rare condition among tachinids. This patch of setae has been here reconstructed as a non-homoplasious apomorphy supporting a sister-group relationship between *W. londti* and *W. capensis*.

With over 120 species (Wood and Zumbado 2010), the genus *Winthemia* has successfully radiated in all the zoogeographic regions (Guimarães 1971; Crosskey 1973, 1980; Coelho *et al*. 1989; Shima 1996; O'Hara and Wood 2004; O'Hara and Cerretti 2016), being particularly species rich in tropical and subtropical areas of the world. However, the Afrotropical *Winthemia* exhibit a tremendous morphological variability involving several key characters, including: parafacial (bare or setose), facial ridge (bare or with a row of erect setae), arrangement of three basal postpronotal setae (in a line or in a triangle), lateral margin of lower calypter (normal or strongly convex), and bee mimicry. Although we have examined only a few species of *Winthemia*, all of our analyses reconstructed the Afrotropical *Winthemia* species as sister to the remaining congeners (Figs 1, 2), suggesting an Afrotropical phylogenetic origin of this widespread and diverse lineage.

Integrating results from morphological and molecular analysis, we are able to redefine the generic limits of *Winthemia*, proposing a new monophyletic concept of this genus. Our analyses also point to the need to revise the generic limits of *Smidtia* and *Nemorilla* as well. However, we should note that only a sampling of winthemiine taxa were included in these analyses, and both more taxa and more data will be needed to fully understand the relationships of taxa within the tribe Winthemiini.

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We thank the editor, James O'Hara, and the two anonymous reviewers for their insightful comments which considerably improved the quality of the manuscript. This work was supported by a PhD Fellowship from the CARIPARO Foundation to DJI and by USA NSF DEB-1146269 to principal investigator JOS and to major collaborator PC.

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Appendix 1. Tachinid taxa included in the morphological and molecular phylogenetic analyses

Tribe	Species	Locality [Collection]^A	Specimens examined	Analysis: molecular (28S, CO1), morphological (Mor.)	References/ Genbank accessions^B
Ethillini	*Paratryphera barbatula* (Rondani)	Finland [JOSC]	1♂	28S	KU171086
Ethillini	*Paratryphera barbatula* (Rondani)	Italy [MZUR]	3♂, 3♀	Mor.	–
Exoristini	*Exorista larvarum* (L.)	Italy [MZUR]	3♂, 3♀	Mor.	–
Exoristini	*Exorista larvarum* (L.)	–	–	Mor.	Tachi and Shima (2008)
Exoristini	*Phorocera slossonae* (Townsend)	Canada [JOSC]	1♂	CO1	KU171084
Exoristini	*Phorocerosoma* sp1	Australia [MZUR]	1♂	Mor.	–
Exoristini	*Phorocerosoma* sp2	Mozambique [MZUR]	1♀	Mor.	–
Exoristini	*Tachinomyia nigricans* Webber	USA [JOSC]	1♂	28S	KU171085
Exoristini	*Tachinomyia nigricans* Webber	USA [JOSC]	1♂	CO1	KU171083
Winthemiini	*Avibrissosturmia* sp.	Costa Rica [JOSC]	1♂	28S/CO1	KU171087/KU171079
Winthemiini	*Hemisturmia scissilis* (Reinhard)	USA [JOSC]	1♀	CO1	KU171078
Winthemiini	*Hemisturmia tenuipalpis* (Wulp)	Genbank sequence	–	28S/CO1	EF189700/EF181327
Winthemiini	*Nemorilla floralis* (Fallén)	Genbank sequence	–	28S/CO1	AB466091/JF439545
Winthemiini	*Nemorilla* spp.	–	–	Mor.	Cerretti (2010), Tschorsnig (1985), Shima (1996)
Winthemiini	*Nemorilla* spp. [unidentified]	Italy, South Africa [all in MZUR]	9♂, 5♀	Mor.	–
Winthemiini	*Orasturmia vallicola* Reinhard	Genbank sequence	–	28S	AF366682
Winthemiini	*Ossidingia cruciata* (Wiedemann)	South Africa [MZUR]	9♂, 7♀	Mor.	–
Winthemiini	*Ossidingia cruciata* (Wiedemann)	South Africa [NMB]	3♂, 1♀	Mor.	–
Winthemiini	*Ossidingia cruciata* (Wiedemann)	Malawi [TAU]	2♀	Mor.	–
Winthemiini	*Ossidingia cruciata* (Wiedemann)	Uganda [TAU]	1♂	Mor.	–
Winthemiini	*Rhaphiochaeta breviseta* (Zetterstedt)	Germany [SMNS]	1♂	Mor.	Tschorsnig (1985), Shima (1996)
Winthemiini	*Rhaphiochaeta breviseta* (Zetterstedt)	–	–	Mor.	♀ from Shima (1996)
Winthemiini	*Rhaphiochaeta breviseta* (Zetterstedt)	Germany [SMNS]	1♂	Mor.	–
Winthemiini	*Smidtia conspersa* (Meigen)	Italy [JOSC]	1♂	28S	KU171088
Winthemiini	*Smidtia fumiferanae* (Tothill)	Genbank sequence	–	CO1	HQ107803
Winthemiini	*Smidtia japonica* (Mesnil)	Genbank sequence	–	28S/CO1	AB700003/AB700040
Winthemiini	*Smidtia* spp.	–	–	Mor.	Cerretti (2010), Tschorsnig (1985), Shima (1996).
Winthemiini	*Smidtia* spp. [*amoena* (Meigen), *conspersa* (Meigen), *laticauda* (Mesnil), *zimini* (Mesnil)]	Italy, Italy, Italy, Turkey [all in MZUR]	15♂, 9♀	Mor.	–
Winthemiini	*Triodontopyga flavolimbata* (Bigot)	BOLD sequence	–	CO1	ASTAR268-07*
Winthemiini	*Triodontopyga* sp.	Costa Rica [JOSC]	1♂	CO1	KU171077

(*continued next page*)

Appendix 1. (*continued*)

Tribe	Species	Locality [Collection][A]	Specimens examined	Analysis: molecular (28S, CO1), morphological (Mor.)	References/ Genbank accessions[B]
Winthemiini	*Winthemia aureonigra* Thompson	BOLD sequence	–	CO1	ASTAW533-08*
Winthemiini	*Winthemia calva* (Villeneuve)	Uganda [CNC]	1♂	Mor.	–
Winthemiini	*Winthemia capensis* (Schiner)	South Africa [JOSC]	1♂	28S/CO1	KU171092/KU171081
Winthemiini	*Winthemia capensis* (Schiner)	South Africa [MZUR]	16♂, 1♀	Mor.	–
Winthemiini	*Winthemia capensis* (Schiner)	South Africa [NMDA]	2♂, 1♀	Mor.	–
Winthemiini	*Winthemia dasyops* (Wiedemann)	Kenya [MZUR]	1♂, 1♀	Mor.	–
Winthemiini	*Winthemia imitator* Reinhard	BOLD sequence	–	CO1	ASTA1026-07*
Winthemiini	*Winthemia londti* sp. nov.	South Africa [MZUR]	2♂	Mor.	–
Winthemiini	*Winthemia peruviana* (Townsend)	BOLD sequence	–	CO1	ASTAV081-06*
Winthemiini	*Winthemia picea* (Walker)	BOLD sequence	–	CO1	ASTAC834-06*
Winthemiini	*Winthemia prima* (Brauer and Bergenstamm)	Australia [MZUR]	1♂	Mor.	–
Winthemiini	*Winthemia prima* (Brauer and Bergenstamm)	–	–	Mor.	♀ from Shima (1996, as *Crypsina prima*)
Winthemiini	*Winthemia quadrata* (Wiedemann)	South Africa [MZUR]	1♂	28S	KU171093
Winthemiini	*Winthemia quadrata* (Wiedemann)	South Africa [MZUR]	1♂[same as above], 1♀	Mor.	–
Winthemiini	*Winthemia rufiventris* (Macquart)	Italy [JOSC]	1♂	28S	KU171090
Winthemiini	*Winthemia rufonotata* (Bigot)	Genbank sequence	–	28S	AF366691
Winthemiini	*Winthemia rufopicta* (Bigot)	USA [JOSC]	1♀	CO1	KU171082
Winthemiini	*Winthemia sinuata* Reinhard	USA [JOSC]	1♀	28S	KU171089
Winthemiini	*Winthemia* sp.	Costa Rica [JOSC]	1♂	28S/CO1	KU171091/KU171080
Winthemiini	*Winthemia* spp.	–	–	Mor.	Cerretti (2010), Guimarães (1972), Tschorsnig (1985), Shima (1996).
Winthemiini	*Winthemia* spp. [*cruentata* (Rondani), *jacentkovskyi* Mesnil, *quadripustulata* (Fabricius), *rufiventris* (Macquart)]	Italy [all in MZUR]	12♂, 9♀	Mor.	–
Winthemiini	*Winthemia subpicea* (Walker)	BOLD sequence	–	CO1	ASTAC898-06*
Winthemiini	*Winthemia tessellata* (Wulp)	BOLD sequence	–	CO1	ASTAC722-06*
Winthemiini	*Winthemia tricolor* (Wulp)	Genbank sequence	–	28S/CO1	EF183817/EF182571
Winthemiini	*Winthemia venusta* (Meigen)	Genbank sequence	–	28S/COI	AB466092/AB700039
Winthemiini	*Winthemia venusta* (Meigen)	Italy [MZUR]	1♂, 1♀	Mor.	–

[A] The locality is given only for the examined material, otherwise it refers to the molecular data depository. In the case of morphological data retrieved only from literature, see the reference section.

[B] Genbank accession numbers, except for BOLD COI sequences marked by an asterisk, in which case the BOLD reference numbers are given.