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The bee genera *Haplomelitta* and *Samba* (Hymenoptera : Anthophila : Melittidae): phylogeny, biogeography and host plants

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Abstract. Recent molecular phylogenetic data showed the Melittidae as the likely sister group to all other bees and indicated that proto-melittids could have been host-plant specialists originating in Africa. However, robust phylogenetic data at generic and species level are now needed for all melittid clades to test these hypotheses and investigate early melittid and bee evolution in general. The bee genera *Haplomelitta* and *Samba*, which comprise the former tribe Sambini (Hymenoptera : Melittidae), are revised here. The genera are endemic to the Afrotropical region, occurring in eastern and southern Africa. Previous studies hypothesised that *Samba* rendered *Haplomelitta* paraphyletic but a conclusive taxonomic decision was not proposed. By performing a comprehensive phylogenetic analysis based on five nuclear genes (28S, CAD, EF-1α (F2 copy), long-wavelength rhodopsin (opsin) and RNA polymerase II (RNAp); total 4179 bp) and morphological characters (34 characters), we here synonymise *Haplomelitta* with *Samba*. The genus is now subdivided into six subgenera containing 10 species, four of which are here described as new, namely: *S. ascheri*, *S. gessorum*, *S. spinosa* and *S. rubigoinis*. Moreover, we also considered biogeography, phenology and floral visitation data. *Samba* seems to have originated in southern Africa and later colonised eastern Africa. The ancestral host-plant foraging strategy was probably specialisation on one plant family (e.g. oligolectism). This result supports the hypothesis that the ancestor of bees arose in Africa and was a host-plant specialist.

Additional keywords: Afrotropical region, host specialisation, new species.

Introduction

Bees constitute a monophyletic group with a recently estimated 19 200 species worldwide (Ascher and Pickering 2010). Seven families are currently acknowledged: Apidae, Andrenidae, Colletidae, Halictidae, Megachilidae, Melittidae and Stenotritidae. Melittidae is one of the most controversial families as both its monophyly and phylogenetic position are debated (Engel 2001; Danforth *et al*. 2006*b*; Michener 2007; Michez *et al*. 2009). Monophyly of the family remains poorly supported, based on studies of larval and adult morphology (Rozen and McGingley 1974; Michener 1981, 2007; Alexander and Michener 1995), and there is no single morphological synapomorphy for the family (Michener 1981, 2007). However, Michener (2007) presented, in a 'traditional' hypothesis, the melittid bees as a monophyletic group morphologically intermediate between the non-melittid short-tongued bees and the long-tongued bees. Given the uncertainty about melittid monophyly, some authors prefer to recognise three families rather than the traditional three subfamilies (Alexander and Michener 1995; Danforth *et al*. 2006*b*). In this latter hypothesis, melittids form a paraphyletic group from which all other bees emerged. Irrespective of previous hypotheses, melittid bees are a key group for understanding the evolution of bees. A comprehensive understanding of melittid relationships and systematics is therefore essential.

Here, three monophyletic subfamilies of melittid bees are recognised: Dasypodainae, Meganomiinae and Melittinae (Michener 2007; Michez *et al*. 2009). The Dasypodainae is the most diverse melittid subfamily and it includes more than 100 species (Michener 2007; Michez *et al*. 2009). Based on molecular and morphological characters, two tribes (Hesperapini and Dasypodaini) were recognised by Michez *et al*. (2009)

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(Fig. 1*B*), whereas Michener (2007) considered three tribes based on morphological features only (Fig. 1*A*). The Dasypodaini *sensu* Michez *et al.* (2009) include three genera: the sister genera *Samba* and *Haplomelitta*, and the genus *Dasypoda*. Although most genera of Dasypodainae have been comprehensively revised in the last decades (Stage 1966; Michez *et al.* 2004*a*, 2004*b*, 2007; Michez and Patiny 2006), *Haplomelitta* and *Samba* remained unrevised.

Haplomelitta and *Samba* share some remarkable features: head wider than long; shallow upper metapleural pit; female mesotibial spur short, robust and strongly hooked apically; terga generally without apical hair bands; male gonocoxite with a medio-apically produced lobe; and male gonostylus enlarged apically (Michener 1981). *Samba*, which includes only one east African species, *S. calcarata* Friese, 1908, shows numerous autapomorphies: mentum membranous, clypeus with prominent median ridge, vertex concave, and female with only one hind tibial spur. Michener (1981) recognised six *Haplomelitta* species from southern Africa: *H. (Atrosamba) atra* Michener, 1981, *H. (H.) ogilviei* Cockerell, 1932, *H. (Haplosamba) tridentata* Michener, 1981, *H. (Metasamba) fasciata* Michener, 1981, *H. (Prosamba) griseonigra* Michener, 1981 and *H. (?) diversipes* (Cockerell, 1932). The monophyly of *Haplomelitta* is dubious due to the lack of synapomorphies (Michener 1981, 2007). Preliminary results of Michez *et al.* (2009) suggested that *Haplomelitta* is rendered paraphyletic by *Samba* (Fig. 1*B*). However, they could not revise the generic status, at that point, without a more detailed and thorough analysis at the species level. Here we present a comprehensive revision for *Samba* and *Haplomelitta* based on the study of 537 specimens. We provide a species level key and a taxonomic review including diagnoses, biogeographical distributions, phenologies and the description of four new species. A cladistic analysis was performed using molecular data (five genes, 4179 base pairs (bp)) and 34 morphological characters allowing us to propose a robust taxonomic hypothesis.

In addition, we aim to fill a gap in our knowledge of *Samba* and *Haplomelitta* life histories. Rozen (1974) carried out the sole study on the biology of *H. ogilviei*. He showed that *H. ogilviei* is solitary and nests in sandy soils like other Dasypodainae. Females dig individual tunnels, with a regular tumulus resulting from the excavation. The provisions of pollen, exclusively from *Monopsis simplex* (Campanulaceae), are moulded into a spherical ball. In a later paper, Gess and Gess (2004) presented floral records for three species of *Haplomelitta*. They confirmed that *H. ogilviei* females collect Campanulaceae pollen. The second and third, undetermined, species of *Haplomelitta* independently foraged on *Indigofera* sp. (Fabaceae) and Crassulaceae. In the present work we collate additional information about floral visits and pollen collection to determine accurately the host-plant range of the group. Based on our new phylogenetic hypotheses we propose a scenario for the evolution of host-plant selection in *Haplomelitta* and *Samba*.

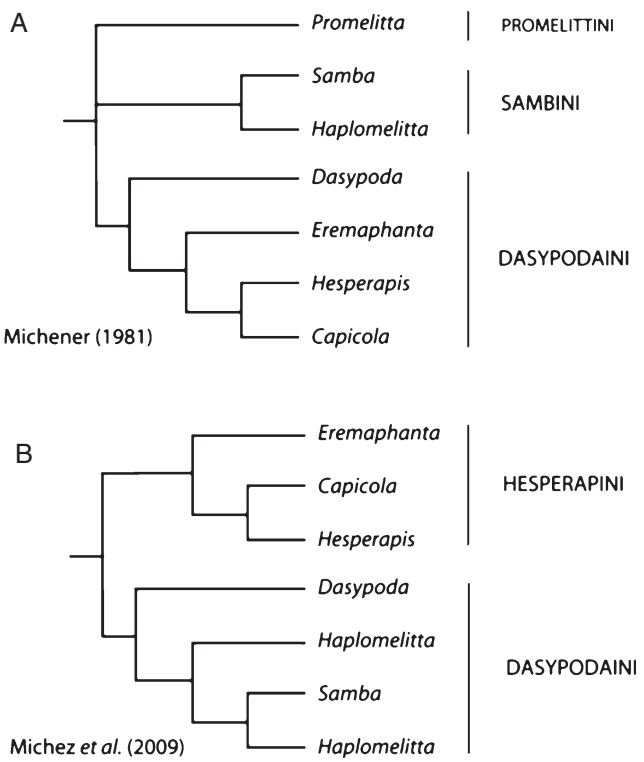

Fig. 1. (*A*) Summary of previous studies on Dasypodainae phylogeny: analysis of morphological data from melittid bees including all *Samba* and *Haplomelitta* (Michener, 1981). (*B*) Analysis of five nuclear genes plus a morphological matrix including seven species of *Samba* and *Haplomelitta* (*Promelitta* is removed to the Melittinae) (Michez *et al.* 2009).

Materials and methods

Studied material

The type material of *Haplomelitta* and *Samba* was examined. The type material and additional specimens examined during this study are held in the following collections: South African National Collection of Insects, Pretoria, South Africa (SANC, 203 specimens); American Museum of Natural History, New York, USA (AMNH, 4 specimens); Albany Museum, Grahamstown, South Africa (AMGS, 151 specimens); Cornell University, Ithaca, USA (CUIC, 5 specimens); Iziko Museum, Cape Town, South Africa (SAMC, 37 specimens); Kuhlmann collection, London, UK (UM, 30 specimens); Natural History Museum, London, UK (NHM, 17 specimens); Oberösterreichisches Landesmuseums, Linz, Austria (OOLL, 69 specimens); Schwarz collection, Ansfelden, Austria (SC, 1 specimen); University of Kansas Museum of Natural History, USA (SEM, 18 specimens); Zoological Institute, St. Petersburg, Russia (ZIL, 2 specimens). All associated biogeographical data were digitised and mapped (Fig. 2).

Taxonomic study

Species concept, morphological terms, descriptions and illustrations

In the present paper we define taxa in the sense of the morphological species concept. We used the glossary of Harris (1979) as a terminological reference for the description of the surface sculpture and Michener (2007) for general morphology. Puncture density is treated in terms of the relationship between puncture diameter (d) and the spaces between them (i), for

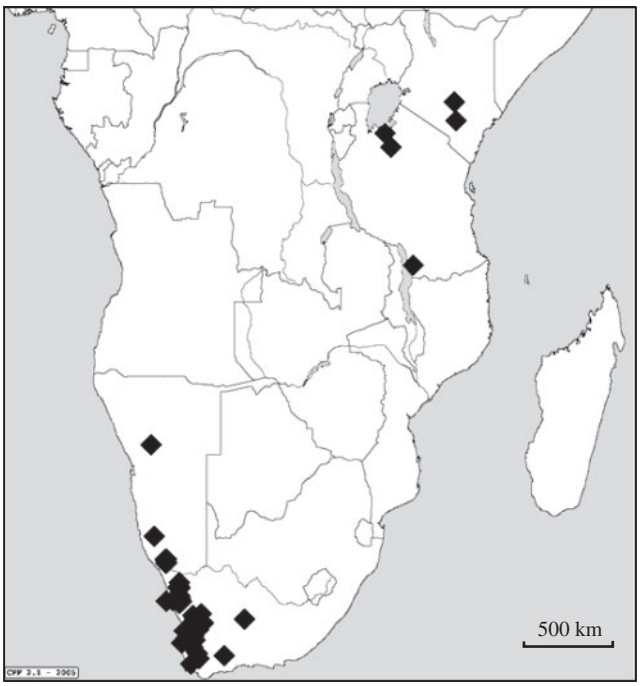

Fig. 2. Collecting localities of the Dasypodaini from eastern and southern Africa (537 specimens).

example i > d. Measurements are all lengths (head, scutum, forewing, body).

The following abbreviations were used for morphological structures: A, antennal segment (A1, scape); Bt, basitarsus; cu-v, cubital–vannal vein; F, femur; L, maximal length; Pp, pygidial plate; Rs, first submarginal crossvein; S, metasomal sternum; Tb, tibia; T, metasomal tergum; W, maximal width.

Integument ultrastructure was studied using a scanning electron microscope (JEOL JSM-6100) associated with the software Semafore (JEOL, Sollentuna, Sweden).

Cladistic analysis

Taxa

The sampled taxon was Dasypodainae. Within the tribe Dasypodaini, all known species belonging to the genera *Haplomelitta* and *Samba* were examined. *Capicola hantamensis* Michez & Kuhlmann, 2007, *Dasypoda hirtipes* (Fabricius, 1793), *Eremaphanta iranica* Schwammberger, 1971 and *Hesperapis regularis* (Cresson, 1878) were used as outgroup taxa (Table 1).

Morphological data

We used the morphological characters proposed in the phylogenetic analyses of Michener (1981) and Roig-Alsina and Michener (1993) and added 10 new characters (8, 11, 14, 15, 17, 21, 22, 26, 27, 32). Thirty-four morphological characters were finally included in the analysis (Table 1).

Female and male:

(*1*) *Paraglossa*: (0) present, smaller than suspensorium; (1) absent.
(*2*) *Maxillary palpus*: (0) nearly hairless; (1) with long setae.
(*3*) *Posterior margin of stipe*: (0) without flange; (1) with flange along posterior margin.
(*4*) *Labrum*: (0) smooth; (1) with strong ridge.
(*5*) *Vertex seen in front*: (0) flat or weakly convex; (1) concave.
(*6*) *Upper metapleural pit*: (0) widely separated from lower pit; (1) very close to lower pit (hardly distinguishable).
(*7*) *Profile of propodeum*: (0) anterior part nearly horizontal, posterior part declivous; (1) anterior and posterior parts slanting (Fig. 7*A*).
(*8*) *Propodeal triangle*: (0) sculptured or carinate (Fig. 7*D*); (1) smooth.
(*9*) *Forewing, second abscissa of Rs*: (0) oblique; (1) at right angles with longitudinal veins.
(*10*) *Hind wing, jugal lobe*: (0) two thirds as long as vannal lobe; (1) about half as long as vannal lobe or less.

Table 1. Character-state matrix for cladistic analysis

Taxa	Characters			
	0000000001 1234567890	1111111112 1234567890	2222222223 1234567890	3333 1234
Outgroup				
Capicola hantamensis	0000000010	0200000000	0000110000	0001
Dasypoda (Dasypoda) hirtipes	0000001011	0000010000	0000100000	0000
Eremaphanta (Eremaphanta) iranica	0000000010	0000000000	0000010000	0000
Hesperapis (Panurgomia) regularis	0000000010	0000000000	1000100000	0000
Ingroup				
Samba (Atrosamba) atra, comb. nov.	1010011101	1100121111	1120011111	1011
S. (Atrosamba) gessorum, sp. nov.	1010011101	1100121111	1120011111	1011
S. (Haplomelitta) ogilviei, comb. nov.	1010111011	1110120111	1120101111	1111
S. (Metasamba) fasciata, comb. nov.	1010011101	0100120111	1021111111	1001
S. (Metasamba) rubigoinis, sp. nov.	1010011101	0101121111	0021111111	1001
S. (Prosamba) griseonigra, comb. nov.	0110011111	0000110111	1100001001	0011
S. (Prosamba) spinosa, sp. nov.	0110011111	0000110111	1100001001	0011
S. (Haplosamba) tridentata, comb. nov.	1010111111	0100120111	0220011101	0111
S. (Samba) ascheri, sp. nov.	1011111101	1111122111	1?????????	????
S. (Samba) calcarata	1011111101	1111122111	0121001111	1111

(*11*) *Basal vein*: (0) more basal than cu-v; (1) interstitial with cu-v or nearly so.
(*12*) *Inner spur on Tb2*: (0) finely serrate or ciliate; (1) coarsely serrate; (2) with sharp outstanding spines (pectinate).

Male:

(*13*) *Bt3*: (0) flat; (1) swollen (Fig. 7*C*).
(*14*) *Sterna 1–5*: (0) black to brownish; (1) orange.
(*15*) *S6*: (0) sparsely hirsute to nearly hairless; (1) with bushy medio-apical hairs (Fig. 7*E*).
(*16*) *S7*: (0) without latero-apical process; (1) with one pair of latero-apical processes (Figs 8*E*, 9*C*); (2) with two pairs of latero-apical processes (Figs 6*A*, *C*, *F*, *J*, 7*F*, 8*A*).
(*17*) *Column of S8*: (0) apically rounded (Figs 6*G*, *K*, 8*F*); (1) apically bifid (Figs 6*B*, 8*B*); (2) apically divided into laterally directed processes.
(*18*) *Gonocoxite*: (0) without medio-apical lobe; (1) with medio-apical lobe (Fig. 7*I*, *J*).
(*19*) *Gonostylus*: (0) not bifurcate apically; (1) bifurcate apically (Figs 6*E*, *I*, *M*, 7*J*, 8*D*, *H*).
(*20*) *Lobes of volsella*: (0) digitis of equal length to cuspis; (1) digitis longer than cuspis (Fig. 7*H*).
(*21*) *Digitis*: (0) apically rounded; (1) apically pointed (Fig. 7*H*).

Female:

(*22*) *Compound eyes*: (0) converging below; (1) parallel; (2) diverging below.
(*23*) *Shape of head*: (0) nearly as long as wide ($1.25 > L/W \geq 0.75$); (1) longer than wide ($L/W > 1.25$); (2) wider than long ($L/W < 0.75$).
(*24*) *Clypeus*: (0) flat; (1) with small or prominent medio-longitudinal ridge.
(*25*) *Integument of paraoccular area*: (0) not differentiated from median part of frons; (1) lateral parts of face with punctures sparser and smaller than on frons.
(*26*) *Legs 2–3*: (0) black; (1) partly reddish.
(*27*) *Base of F2*: (0) with undifferentiated sparse hairs; (1) with a short conspicuous brush of stiff yellow hairs on trochanter and femur.
(*28*) *Apical spur of Tb2*: (0) slender; (1) robust, enlarged basally.
(*29*) *Apical spur of Tb2*: (0) nearly straight; (1) apically hooked.
(*30*) *Shape of Bt3*: (0) over three times as long as wide; (1) 1.6 to 2.9 times as long as wide; (2) 1.5 times as long as wide or less.
(*31*) *Apex of Bt3*: (0) without projection above articulation of second tarsal segment; (1) with projection above articulation of second tarsal segment.
(*32*) *T1–2*: (0) completely black; (1) partly red.
(*33*) *T2–4*: (0) with apical hair bands; (1) without apical hair bands.
(*34*) *Pygidial plate*: (0) flat; (1) with a strongly elevated median area.

Molecular methods

Material for DNA extraction was available in all species of the outgroup and five species of the ingroup (Table 2). Total DNA was extracted from single dry or EtOH-preserved specimens using a phenol/chloroform protocol adapted from Saghai-Maroof *et al*. (1984) (see Danforth 1999). Vouchers were deposited in the Cornell University insect collection and University of Mons collection. Conditions of polymerase chain reaction (PCR) and primer sequences are given in Table 3. The PCR products were purified using a multiscreenTM 96-well plate and sequenced on an automated 3730 DNA Analyzer (Applied Biosystems). The sequences were trimmed and assembled using Sequencher 4.7 (Gene Codes Corporation, www.genecodes.com/). The edited sequences were aligned using MAFFT 6.0 (http://align.bmr.kyushu-u.ac.jp/mafft/online/server/). The resulting alignment was checked by eye and edited manually in Mesquite 2.0 (Maddison and Maddison 2007). *Apis mellifera* was used as a reference for identifying intron/exon boundaries within EF-1α and opsin and for identifying stem and loop regions within 28S (Cameron and Mardulyn 2001).

Molecular data

We generated DNA sequences for five nuclear genes: 28S, CAD, EF-1α (F2 copy), long-wavelength rhodopsin (opsin) and RNA polymerase II (RNAp), all of which, except 28S, are protein coding. These genes have been used in previous studies of bee

Table 2. Description of the molecular dataset

The first column provides the valid names for the sampled species. The second column gives the sampling localities (country and locality; SA = South Africa). The five next columns give the Genbank accession numbers respectively for ribosomal 28S subunit (28S), conserved ATPase domain protein (CAD), Elongation Factor-1α F2 copy (EF-1α), long-wavelength rhodopsin (Opsin) and RNA polymerase II (RNAp)

Taxon	Collection locality	GenBank access numbers				
		28S	CAD	EF-1α	Opsin	RNAp
Outgroup						
C. hantamensis	SA: Calvinia	EF594353	GU945209	EF594329	EF594378	EF599276
D. hirtipes	France: Generac	AY654519	DQ067162	AY585149	DQ116681	AY945113
E. iranica	Oman: Wadi Quibit	GU936605	GU945210	GU936598	GU945206	GU936602
H. regularis	USA: Del Puerto Cyn.	AY654456	DQ067168	AY585151	DQ116692	AY945122
Ingroup						
Samba (Atrosamba) atra	SA: Dassiefontein	GU936606	GU945211	GU936599	GU945207	GU936603
S. (Haplosamba) ogilviei	SA: Nieuwoudtville	EF594364	GU945213	GU936601	EF594388	EF599285
S. (Metasamba) fasciata	SA: Akkedis Pass	GU936607	GU945212	GU936600	GU945208	GU936604
S. (Prosamba) griseonigra	SA: Clanwilliam	AY654524	DQ067164	AY585153	DQ116684	AY945125
S. (P.) spinosa	SA: Nieuwoudtville	EF594365	GU945214	EF594340	EF594389	EF599286

Table 3. PCR conditions and primer sequences

PCR conditions	
28S	
Bel-Mar	94°C/1 min; 65°C/1 min; 72°C/1 min. 35 cycles
CAD	
apCadfor4-ap835rev1amel	94°C/1 min; 58°C/1 min; 72°C/1 min. 35 cycles
CADMegfor1-ap1098rev4a	94°C/1 min; 52°C/1 min; 72°C/1 min30 sec. 35 cycles
EF-1α	
For1deg-F2rev1	94°C/1 min; 94°C/1 min; 52°C/1 min; 72°C/1 min30 sec. 35 cycles
HaF2For1-F2rev1	94°C/1 min; 94°C/1 min; 54°C/1 min; 72°C/1 min30 sec. 35 cycles
HaF2For1-F2rev3	94°C/1 min; 94°C/1 min; 54°C/1 min; 72°C/1 min30 sec. 35 cycles
F3rho-Cho10	94°C/1 min; 94°C/1 min; 58°C/1 min; 72°C/1 min. 35 cycles
Opsin	
For3mod-Revmod	94°C/1 min; 94°C/1 min; 56°C/1 min; 72°C/1 min. 35 cycles
RNAp	
Polfor2a-Polrev2a	94°C/1 min; 94°C/1 min; 52°C/1 min; 72°C/1 min. 35 cycles
Primers	Sequences from 5′ to 3′
28S	
Bel	5′-AGA GAG AGT TCA AGA GTA CGT G-3′
Mar	5′-TAG TTC ACC ATC TTT CGG GTC CC-3′
CAD	
apCADfor4	5′-TGG AAR GAR GTB GAR TAC GAR GTG GTY CG-3′
CADMegfor1	5′-GAG CCY AGT CTC GAY TAY TG-3′
ap1098rev4a	5′-ATA TTR TTK GGC ARY TGD CCK CCC-3′
Ap835rev1amel	5′-GC CAT YAC YTC KCC YAC GCT YTT CAT-3′
EF-1α	
HaF2For1	5′-G GGY AAA GGW TCC TTC AAR TAT GC-3′
For3rho	5′-GGY GAC AAY GTT GTT TTY AAY G-3′
F2rev1	5′-A ATC AGC AGC ACC TTT AGG TGG-3′
F2rev3	5′-GTGAAATCASMAGCACCYYAAGGTGG-3′
Cho10 (mod)	5′-AC RGC VAC KGT YTG HCK CAT GTC-3′
Opsin	
Opsin For3 (mod)	5′-TTC GAY AGA TAC AAC GTR ATC GTN AAR GG-3′
Opsin Rev (mod)	5′-ATA NGG NGT CCA NGC CAT GAA CCA-3′
RNAp	
Polfor2a	5′-AAY AAR CCV GTY ATG GGT ATT GTR CA-3′
Polrev2a	5′-AGR TAN GAR TTC TCR ACG AAT CCT CT-3′

phylogeny at various levels including generic (e.g. Hines *et al*. 2006; Larkin *et al*. 2006), tribal (e.g. Praz *et al*. 2008; Michez *et al*. 2009) and family levels (e.g. Danforth *et al*. 2006*a*, 2006*b*). For the nuclear 28S ribosomal gene we sequenced a ~681 bp fragment in the D2-D3 region (http://www.entomology.cornell.edu/BeePhylogeny). After manual editing, ambiguities remained in the loop regions of the gene (see secondary structure in Kjer 1995). These sites (117 bp) were excluded for the final analysis. CAD is one gene among a tightly linked group of nuclear, protein-coding genes involved in pyrimidine biosynthesis. Our primers were modified versions of primers used by Danforth *et al*. (2006*a*) for the bee families. We sequenced 994 bp but the less conserved intron region (89 sites) was excluded for the final analysis. Two copies of EF-1α occur in bees (Danforth and Ji 1998). Our dataset consisted of a 1562 bp fragment of the F2 copy (Danforth and Ji 1998). The sequenced fragment included two introns, which were aligned manually. The less conserved intron regions (131 sites, mainly AT rich areas) were excluded for the final analysis. We sequenced a 580 bp region of the LW (long-wavelength) opsin paralog, which spanned two introns (Chang *et al*. 1996). We chose to exclude the opsin introns from all analyses because their alignment appeared highly ambiguous. The resulting dataset for LW opsin spanned a 460 bp region of coding sequence. For RNA polymerase II (RNAp) we analysed an 819 bp intron-less region. RNAp has been used in previous studies of family level bee phylogeny (Danforth *et al*. 2006*a*, 2006*b*). Primer sequences, amplification protocols and other additional information on these genes are available at http://www.entomology.cornell.edu/BeePhylogeny.

The final molecular dataset for the present study spanned 4179 aligned nucleotide sites after ambiguities were excluded. Sampling localities and GenBank accession numbers are listed in Table 2.

Phylogenetic analyses

We performed analyses on the dataset based on parsimony (MP), maximum likelihood (ML), and Bayesian methods. For MP and ML we used PAUP 4.0b10 (Swofford 2002), and for Bayesian analyses we used MrBayes 3.1.2 (Huelsenbeck and Ronquist 2001). Bootstrap values were calculated using PAUP 4.0b10.

First we performed a series of MP analyses of: (i) the morphological data partition (14 taxa), (ii) the molecular data

partition (9 taxa), and (iii) the molecular data + morphological data (14 taxa). For all MP analyses, including molecular data, we coded gaps as a fifth state. We performed an heuristic search with 10 000 random sequence additions, using the tree bisection reconnection (TBR) branch swapping. Bootstrap support values were computed using 1000 replicates with 10 random sequence additions per replicate. Winclada (1.00.08) (Nixon 2002) was used for the mapping of characters onto the MP tree (Fig. 3).

Second, we analysed the performance of 56 substitution models using Modeltest 3.7 (Posada and Crandall 1998). The TrN+I+G (Tamura and Nei variable base frequencies with proportion of invariable sites and a gamma distribution for variation among sites) was selected based on its scores in the Akaike information criterion test. The topology obtained by the MP analysis was used as a starting tree for an iterative analysis under maximum likelihood using PAUP 4.0b10 (Swofford 2002). The overall likelihood was estimated on the basis of the selected model and then the topology was submitted to a series of increasingly exhaustive branch-swapping algorithms: nearest neighbour interchange (NNI), subtree pruning regrafting (SPR) and TBR. In each step, the ML parameters were re-estimated based on the trees in memory and applied to the next step of branch swapping (Danforth 1999). We calculated bootstrap support based on a GTR+I+G model and 100 replicates using PAUP 4.0b10 (Swofford 2002).

For Bayesian analyses we partitioned the dataset by gene. For each gene partition we calculated the likelihood score for 24 possible substitution models using MrModeltest 2.2 (Nylander 2004; in MrMTgui 1.01). Models were compared based on the hierarchical likelihood ratio test and the Akaike information criterion. These criteria produced slightly different sets of models. We consequently analysed the datasets using both model combinations. An additional analysis was performed using the site-specific rate model (SSR) model wherein the three codon positions (and introns, when present) were assigned separate rates. This analysis resulted in a model with 14 discrete rate categories. Analysis of the combined molecular and morphological dataset was performed using five molecular partitions (corresponding to each gene). An additional partition was created for the morphological data. The 'standard' model implemented in MrBayes for analysis of the discrete data was used for an analysis of the morphological partition. Five million generations were computed along two simultaneous runs (with four chains each). Parameters and topologies were sampled every 100 generations and two different lengths of 'burn-in' (25% and 50% of the samples) were compared. The 50% majority rule consensus trees are based on 25 000 trees retained after discarding the burn-in (50% of the samples).

Biogeography, phenology and floral visit

We detail biogeographical, phenological and floral visitation information in the Taxonomy section. The specimen information is quoted using the following standardisation of label data: locality, coordinates (or conventional coordinates in decimal degrees when not given on the label), date, collector, plants visited and depository. The distribution maps (Figs 10–14) illustrate the biogeographical information of the material examined as well as records published with species descriptions. These biogeographical data are included in the

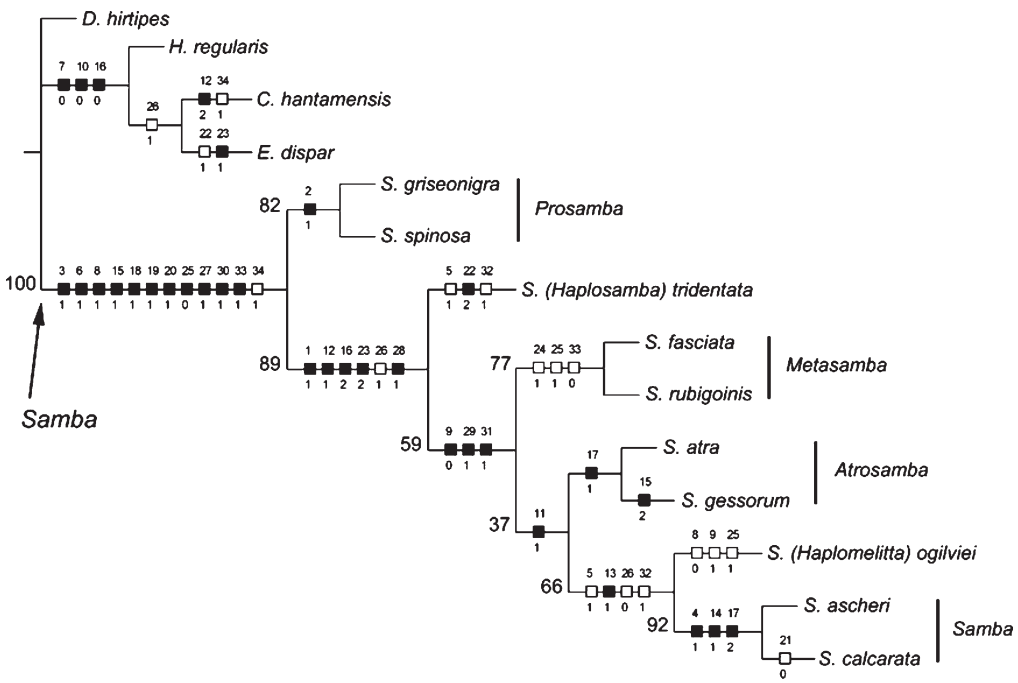

Fig. 3. Single most parsimonious tree based on morphological data from heuristic search for the 14 taxa (length = 55 steps; CI = 0.71; RI = 0.86). The numbers above and under the squares are the character and the character state respectively. Black squares indicate synapomorphies or autapomorphies. White squares indicate homoplasies. Bootstrap values are indicated in front of the nodes.

Banque de données fauniques Gembloux-Mons (BDFGM). They were managed using Data Fauna Flora 2.0 (Barbier *et al*. 2000). Conventional geographic coordinates for the records were obtained from the numeric gazetteer included in the software (CFFGazet). Data were mapped using Carto Fauna Flora 2.0 (Barbier and Rasmont 2000). A Gall geographical projection was used for mapping (Barbier and Rasmont 2000).

Host plants

The label data provided information on the floral visits of 151 specimens. However, several studies showed that field records alone are not reliable for identifying host-plant associations because they rarely distinguish between pollen and nectar foraging (e.g. Westrich and Schmidt 1986; Westrich 1990; Müller 1996; Sipes and Tepedino 2005). We therefore identified the pollen on the scopae of 43 females listed in Table 4. This method provides an accurate and quantitative estimate of host-plant use by bees (Westrich and Schmidt 1986). Pollen analyses allow for discrimination of pollen and nectar hosts, and the detection of inconspicuous floral choices. The pollen was gently removed with a pin and embedded in glycerol gelatine on microscope slides. Pollen samples were identified by light microscopy at a magnification of 400×. Pollen composition was investigated by identification of 400 pollen grains randomly chosen from each sample (Table 4).

Table 4. Palynological analysis (% of pollen type per sample) of pollen extracted from female scopae of *Samba* species

SA = South Africa; *Fil* = degree of filling; As = Asteraceae; Ca = Campanulaceae; Cr = Crassulaceae; Fa = Fabaceae; Ge = Geraniaceae; Sc = Scrophulariaceae; Zy = Zygophyllaceae; Un = unidentified pollen

Taxon	Localities and collection	*Fil*	As	Ca	Cr	Fa	Ge	Zy	Sc	Un
Samba atra (*n* = 7)	SA, Bloukrans Pass, 26.viii.1997, SAMC	*3*	–	–	–	100	–	–	–	–
	SA, Piketberg, 27.ix.1996, SAMC	*5*	–	–	–	100	–	–	–	–
	SA, Piketberg, 03.ix.2001, SAMC	*3*	–	–	–	100	–	–	–	–
	SA, Piketberg, 22.ix.1995, SAMC	*5*	–	–	–	100	–	–	–	–
	SA, Hetkruis, 22.viii.1988, SAMC	*2*	–	–	–	93	3	1	3	–
	SA, Bidouw Valley, 04.ix.1983, SAMC	*3*	–	–	–	100	–	–	–	–
	SA, Nieuwoudtville, SAMC	*4*	–	–	–	100	–	–	–	–
S. fasciata (4)	Namibia, Omaruru, 13.iii.1979, AMNH	*2*	–	–	–	100	–	–	–	–
	Namibia, Omaruru, 13.iii.1979, AMNH	*5*	4	–	–	96	–	–	–	–
	Namibia, Klein Aus Vista, AMGS	*5*	–	–	–	100	–	–	–	–
	SA, Richtersveld, 23–24.viii.2006, SANC	*5*	–	–	–	100	–	–	–	–
S. gessorum (1)	SA, Die Koei River, 11.x.1974, SANC	*5*	–	–	–	100	–	–	–	–
S. griseonigra (7)	SA, Garies, 30.ix.1980, NHM	*5*	–	–	100	–	–	–	–	–
	SA, Garies, 30.ix.1980, NHM	*5*	–	–	100	–	–	–	–	–
	SA, Dassiefontein, 01.ix.1990, SANC	*2*	–	–	100	–	–	–	–	–
	SA, Dassiefontein, 01.ix.1990, SANC	*1*	–	–	100	–	–	–	–	–
	SA, Garies, 30.ix.1980, NHM	*4*	–	–	100	–	–	–	–	–
	SA, Garies, 30.ix.1988, SAMC	*1*	–	–	100	–	–	–	–	–
	SA, Bidouw Valley, 04.ix.1983, SAMC	*5*	–	–	100	–	–	–	–	–
S. spinosa (5)	SA, Clanwilliam, 31.viii.2004, SANC	*4*	–	–	100	–	–	–	–	–
	SA, Clanwilliam, 03.ix.1986, SAMC	*5*	–	–	100	–	–	–	–	–
	SA, Grootfontein, 11.xi.1999, SAMC	*4*	–	–	100	–	–	–	–	–
	SA, Picketberg, 10.xi.2001, SAMC	*5*	–	–	100	–	–	–	–	–
	SA, Sauer, 9.ix.1994, SAMC	*5*	–	–	100	–	–	–	–	–
S. ogilviei (17)	SA, Citrusdal, 27.x.1999, OOLL	*3*	–	100	–	–	–	–	–	–
	SA, Citrusdal, 27.x.1999, OOLL	*1*	100	–	–	–	–	–	–	–
	SA, Citrusdal, 27.x.1999, OOLL	*1*	70	30	–	–	–	–	–	–
	SA, Citrusdal, 27.x.1999, OOLL	*3*	7	28	–	–	–	–	–	65
	SA, Citrusdal, 27.x.1999, OOLL	*2*	3	94	–	–	–	–	–	3
	SA, Citrusdal, 27.x.1999, OOLL	*2*	4	96	–	–	–	–	–	–
	SA, Citrusdal, 27.x.1999, OOLL	*3*	5	95	–	–	–		–	–
	SA, Citrusdal, 27.x.1999, OOLL	*1*	60	40	–	–	–	–	–	–
	SA, Citrusdal, 27.x.1999, OOLL	*2*	14	86	–	–	–	–	–	–
	SA, 15km Citrusdal, 04.x.1990, SANC	*4*	–	100	–	–	–	–	–	–
	SA, Nieuwoudtville, 18–22.xi.1931, NHM	*3*	–	100	–	–	–	–	–	–
	SA, Nieuwoudtville, 18–22.xi.1931, NHM	*2*	–	100	–	–	–	–	–	–
	SA, Nieuwoudtville, 18–22.xi.1931, NHM	*3*	–	100	–	–	–	–	–	–
	SA, Stellenbosen, 10.xii.1984, NHM	*5*	–	100	–	–	–	–	–	–
	SA, 15 km Citrusdal, 04.x.1990, SANC	*1*	–	100	–	–	–	–	–	–
	SA, Kamieskroon, 1–2.x.1990, SANC	*3*	–	100	–	–	–	–	–	–
	SA, Kamieskroon, 1–2.x.1990, SANC	*3*	–	100	–	–	–	–	–	–
S. rubigoinis (1)	SA, Meltonwold, 15.ii.1991, SANC	*1*	100	–	–	–	–	–	–	–
S. tridentata (1)	SA, Wallekraal, SAMC	*2*	–	–	–	–	–	65	–	35

Two different approaches have been proposed to define host-range categories based on pollen load composition. According to the definition of Cane and Sipes (2006), a species is oligolectic if more than 90% of its loads are fully filled by pollen originating from one host-plant family. If not, the species has to be considered as mesolectic (two or three host-plant families) or polylectic (four or more host-plant families) depending on the diversity of the alternative host plants. According to Müller (1996) a species is designated as oligolectic if 95% or more of the all counted pollen grains belong to the same plant family. Müller and Kuhlmann (2008) showed that the two approaches are congruent. We considered both approaches.

Results

Phylogeny and taxonomic implication

Figures 3–5 summarise phylogenetic topologies based on different data matrices (morphological, molecular and mixed data) and different methods (MP, ML, Bayesian). In all analyses the former Sambini (*Haplomelitta* + *Samba*) constituted a monophyletic group with high posterior probabilities and high bootstrap support. The group is supported by 11 synapomorphies among the 34 morphological characters in the MP analysis (Fig. 3). Within this clade, relationships among species differ between the molecular and morphological trees, but the same subgenera were recovered in all analyses. No synapomorphies were found supporting the monophyly of the two genera (i.e. *Samba* and *Haplomelitta*). We therefore consider *Haplomelitta* to be a junior synonym of *Samba* and all *Haplomelitta* species are here transferred to *Samba*. Moreover, we propose six subgenera: *Atrosamba*, *Metasamba*, *Haplomelitta*, *Haplosamba*, *Prosamba* and *Samba* s.str.

Host plants of Samba

Most *Samba* species examined in this study seem to be strictly oligolectic (Table 4). *Samba atra*, *S. fasciata* and *S. gessorum* are probably oligolectic on Fabaceae as females were mainly caught foraging on this family (two females of *S. atra*, 14 of *S. gessorum* and nine of *S. fasciata*), and 11 scopal loads contained 100% Fabaceae pollen. Samples with 93% and 96% Fabaceae could have been contaminated with pollen from other plants visited for nectar. The observation of *S. gessorum* on *Crassula dichotoma* (Crassulaceae) could also be associated with nectar foraging behaviour. Moreover, *S. griseonigra* and *S. spinosa* are oligolectic on Crassulaceae, with field observations (seven females) and pollen samples (12 scopal loads) showing specialisation on Crassulaceae pollen.

The floral choices of *S. ogilviei* are somewhat ambiguous. Rozen (1974) observed *S. ogilviei* foraging only on *Monopsis simplex* (Campanulaceae) and Gess and Gess (2004) collected 38 females on Campanulaceae (observations on *Monopsis debilis*, see Taxonomy section) indicating that *S. ogilviei* is oligolectic. However, C. Eardley collected two females on *Cotula coronopifolia* (Asteraceae; see Material examined for *S. ogilviei* in Taxonomy section), thus raising doubts about *S. ogilviei* being oligolectic. Palynological records presented in this study reveal the same ambiguity (Table 4). Most of the samples (76%) contain Campanulaceae pollen only, and 17% contain mainly Asteraceae pollen. According to the definition of Cane and Sipes (2006), *S. ogilviei* is mesolectic. However, Asteraceae samples originate from less filled scopae. The global ratio of pollen grains is 7% Asteraceae, 90% Campanulaceae and 3% unidentified pollen. According to the definition of Müller and Kuhlmann (2008) *S. ogilviei* is strictly oligolectic on Campanulaceae, with the Asteraceae pollen loads possibly resulting from contamination during nectar foraging.

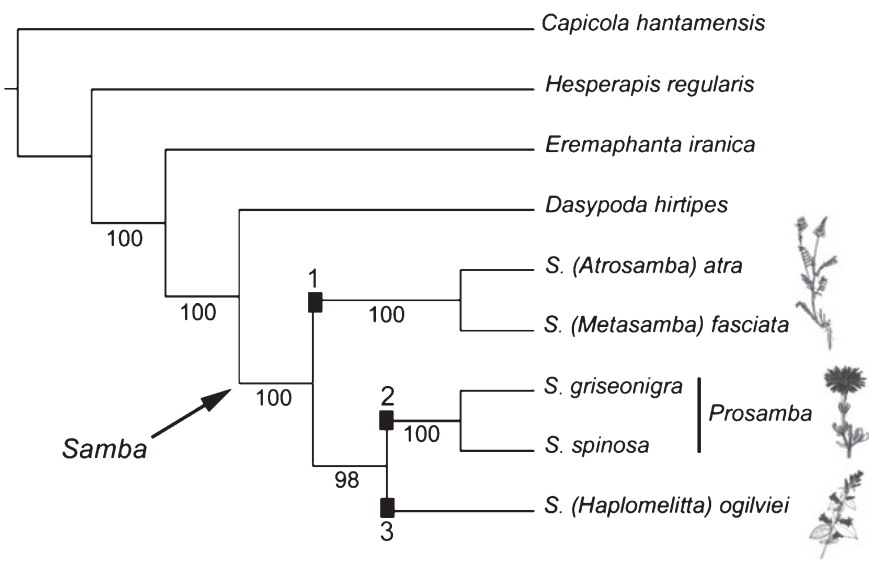

Fig. 4. Maximum likelihood tree based on combined analysis of five genes for nine taxa by using TrN+I+G model and TBR as the branch swapping algorithm. Bootstrap values are indicated below the nodes. 1 = species foraging on Fabaceae. 2 = species foraging on Crassulaceae. 3 = species foraging on Campanulaceae.

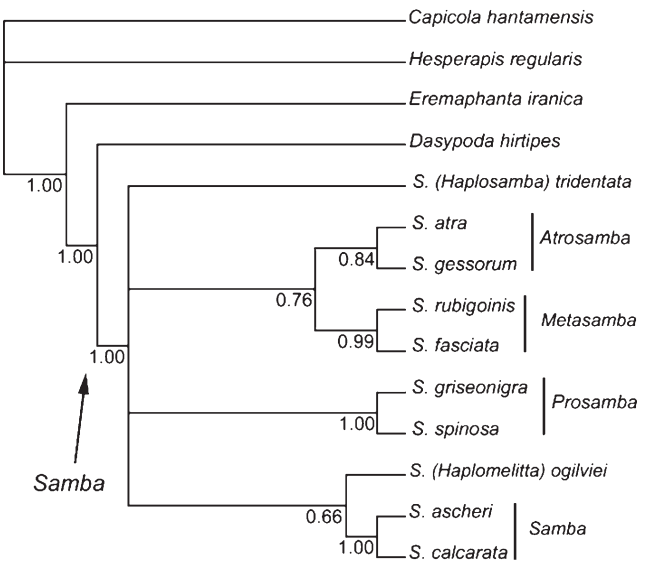

Fig. 5. Majority rule consensus of trees in the Bayesian analysis based on combined dataset of five genes and morphology for 14 taxa. Posterior probabilities are indicated below the nodes.

This is confirmed by field observations by two of the authors (KT and MK).

There is little information on the host plants of *S. tridentata* and *S. rubigoinis*. The only pollen sample of *S. tridentata* suggests that this species is mesolectic on Zygophyllaceae and an unidentified pollen source. *Samba rubigoinis* could be oligolectic on Asteraceae, however the small number of samples and the low degree of scopal filling of the two samples do not allow for reliable conclusions. There is no available host-plant data for *S. ascheri* or *S. calcarata*.

Discussion

Michener (1981, 2007) and Michez *et al*. (2009) suggested that recognising *Samba* as a valid genus could render *Haplomelitta* paraphyletic. By exploring an extensive dataset, the present study confirms this hypothesis (Figs 3, 5), and therefore we make *Haplomelitta* a junior synonym of *Samba*. The generic diversity of Dasypodainae is therefore reduced to five genera: *Capicola*, *Dasypoda*, *Eremaphanta*, *Hesperapis* and *Samba*.

Samba is endemic to the Afrotropical region, presenting a bipolar distribution with a large disjunction between south-west African and east African species (Fig. 2). However, this disjunction could be an artefact resulting from insufficient sampling, because several other bee groups with similar macro-ecological patterns (i.e. *Ceylalictus*, *Meliturgula*) have a continuous range between southern Africa and the area east of the Rift Valley (Patiny 2004; Pesenko and Pauly 2005). Notably, this pattern of continuous distribution explains the occurrence of several typical southern African species in Saharan Africa (Pauly 1990; Patiny 2004; Patiny and Michez 2007). For these latter species (i.e. *Ceylalictus*, *Meliturgula*), as in many other insect groups, eastern Africa played the role of a xeric corridor allowing for north–south dispersal (Bobe 2006). Independent of a possible disjunction, the origin of the genus *Samba* is probably southern Africa with subsequent east African colonisation. Two elements, at least, suggest such a biogeographical scenario: (i) most subgenera are restricted to southern Africa (Figs 10–14), and (ii) the only group endemic to east Africa is possibly the most derived (i.e. *Samba* s.str.) (Fig. 3).

Like most melittid bees (Michez *et al*. 2008), *Samba sensu lato* species mainly show specialised behaviour in their host-plant foraging, with six species collecting pollen from just one plant family. The diversity of host-plant use is, however, surprising. They apparently forage on unrelated and morphologically divergent host plants: Campanulaceae (Asteridae, Asterales), Crassulaceae (Rosidae, Saxifragales) and Fabaceae (Rosidae, Fabales). These three host plants are included in three distant clades in the angiosperm phylogeny (Stevens, 2001). Therefore, there is no link between plant cladogenesis and *Samba* phylogeny. Moreover, at some level, host-plant choices of *Samba* seem to be inherited from a common ancestor, as host-plant choice is similar inside each of the three well supported clades (Fig. 4). As far as is known, species from the clade of *S. atra* forage on Fabaceae while the *S. griseonigra* clade forages on Crassulaceae and *S. ogilviei* forages on Campanulaceae. This rare pattern has been described in other Melittidae in the genera *Capicola*, *Hesperapis* and *Melitta* (Michez and Eardley 2007; Michez *et al*. 2007, 2008), and from a few non-melittid taxa such as *Colletes* or *Dufourea* (Ebmer 1984; Müller and Kuhlmann 2008; Patiny *et al*. 2008). At this time no study has explored the proximal or ultimate causes of these kinds of host-plant shifts. The widespread distribution and diversity of the host plants used by *Samba* species suggest that they are ecological opportunists but their physiological abilities are unknown.

Danforth *et al*. (2006*b*) showed that Dasypodainae is probably the sister group to all other bee families. Moreover, inside the Dasypodainae, Michez *et al*. (2009) described the phylogenetic position of *Samba* as basal. Based on these to papers, the genus *Samba* could be considered as one of the most plesiomorphic genera inside the bee clade. As we show in the present paper that (i) the ancestral host-plant foraging strategy of *Samba* was probably specialist and (ii) the genus is endemic in Africa, our results support the hypothesis that the ancestor of bees was African and a host-plant specialist (Danforth *et al*. 2006*b*).

Taxonomy

Family **MELITTIDAE** Schenck, 1860

Subfamilly **DASYPODAINAE** Börner, 1919

Genus ***Samba*** Friese, 1908

Samba Friese, 1908: 568.
Type species: *Samba calcarata* Friese, 1908, monobasic.
Haplomelitta Cockerell, 1934: 446.
Type species: *Rhinochaetula ogilviei* Cockerell, 1932, by original designation. **Syn. nov.**

Diagnosis

Like other Dasypodainae, *Samba* species share a short, pointed glossa with all segments of the labial palpus similar to one another, one subantennal suture, forewing with straight to gently curved basal vein and two submarginal cells. *Samba*

species have a black head that is wider than long, shallow upper metapleural pit, short hooked mesotibial spur and male gonocoxite with meso-apically produced lobe.

Included species

Samba ascheri, sp. nov., *S. atra*, comb. nov., *S. calcarata*, *S. fasciata*, comb. nov., *S. gessorum*, sp. nov., *S. griseonigra*, comb. nov., *S. ogilviei*, comb. nov., *S. rubigoinis*, sp. nov., *S. spinosa*, sp. nov. and *S. tridentata*, comb. nov.

The study of the type series of *Haplomelitta diversipes* (Cockerell) revealed that this species belongs to the genus *Scrapter* (Colletidae). *Samba* is divided into six subgenera: *Atrosamba*, *Haplomelitta*, *Haplosamba*, *Metasamba*, *Prosamba* and *Samba*.

Key to the species of *Samba*

1. Antenna 13 segmented. Hind leg without scopa. Apex of metasoma with genitalia. Male 2
   Antenna 12 segmented. Hind leg with scopa. Apex of metasoma with a sting. Female 11
2. Labrum carinate, with strong ridge. S1–5 orange. S8 apically divided into laterally directed processes. T1–6 with broad depressed marginal zones, narrow sub-laterally, broad medially, premarginal line and marginal zone orange. Bt3 swollen 3
   Labrum flat, smooth, without ridge. S1–5 reddish to black. S8 apically indented. Marginal zone of T1–6 flat, black, reddish or red. Bt3 flat or swollen 4
3. Bt3 with hairy pocket. Clypeus with median ridge *S. (Samba) calcarata*
   Bt3 without hairy pocket. Clypeus without median ridge ..... *S. (Samba) ascheri*
4. S7 with a pair of long and narrow latero-apical structures, longer than disc width (Fig. 8*A*). Inner apex of Tb3 with small patch of long hairs on the base of the spurs 5
   S7 latero-apical structures different (Figs 6*A*, *C*, *F*, *J*, 7*F*, 8*E*). Inner apex of Tb3 either without patch or with wider patch of hairs 6
5. Metasoma black. Terga with strong apical hair bands. Inner spur of Tb3 curved backward and elongated ..... *S. (Samba) fasciata*
   Metasoma reddish. Terga without strong hair bands. Inner spur of Tb3 straight and only slightly longer than the outer spur ..... *S. (Samba) rubigoinis*
6. T1–3 red 7
   T1–3 black 8
7. Propodeal triangle strongly differentiated, rugose basally (Fig. 7*D*). Bt3 swollen, wider than Tb3 (Fig. 7*C*) ..... *S. (Haplomelitta) ogilviei*
   Propodeal triangle weakly differentiated, smooth basally. Bt3 slender, narrower than Tb3 ..... *S. (Haplosamba) tridentata*
8. Basal segments of maxillary palpus nearly hairless. Second submarginal cell about as long as the first. S7 with two pairs of pedunculated lobes (Fig. 6*A*, *C*). Bt3 with apical spine projecting above segment 2. Basal vein interstitial with cu-v or nearly so. Inner surface of Tb3 with erect setae 9
   Basal segments of maxillary palpus with long setae. Second submarginal cell distinctly shorter than first. S7 with one pair of pedunculated lobes and one pair of narrow hairy lobes (Figs 8*E*, 9*C*). Bt3 flattened without apical projection. Basal vein distinctly basal of cu-v. Inner surface of Tb3 smooth and hairless 10
9. Head, mesepisternum, legs and T2–3 extensively clothed with white pubescence; tarsi orange ..... *S. (Atrosamba) atra*
   Head, mesepisternum, legs and T2–3 mostly with black pubescence; tarsi blackish ..... *S. (Atrosamba) gessorum*
10. Hind trochanter with a strong spine on ventral surface (Fig. 9*A*). Flagellum brown. F1–2 black. Basitibial plate punctuate ..... *S. (Prosamba) spinosa* sp. nov.
    Hind trochanter gently curved below, with short spine (Fig. 9*D*). Flagellum yellow. F1–2 with reddish spots. Basitibial plate smooth ..... *S. (Prosamba) griseonigra*
11. One hind tibial spur. Vertex strongly concave in frontal view. Clypeus with strong median ridge ..... *S. (Samba) calcarata*
    Two hind tibial spurs. Vertex not or slightly concave. Clypeus smooth, without ridge 12
12. Terga with apical hair bands. Clypeus with small medio-longitudinal ridge 13
    Terga without apical hair bands. Clypeus flat 14
13. T1–4 black ..... *S. (Metasamba) fasciata*
    T1–4 red ..... *S. (Metasamba) rubigoinis* sp. nov.
14. Mandible tridentate ..... *S. (Haplosamba) tridentata*
    Mandible bidentate 15
15. Propodeal triangle well differentiated, posteriorly smooth, basally with short longitudinal carinae. T1–4 red. S1 strongly reduced with large, bifurcate tubercle postero-medially ..... *S. (Haplomelitta) ogilviei*
    Propodeal triangle differentiated only by weak lines, smooth basally. T1–4 black. S1 normal 16
16. Basal segments of maxillary palpus nearly hairless. Second submarginal cell about as long as first. First recurrent and first transverse cubital veins well separated. Jugal lobe of hind wing about half as long as vannal lobe 17
    Basal segments of maxillary palpus with long setae. Second submarginal cell distinctly shorter than first. First recurrent and first transverse cubital veins close together. Jugal lobe of hind wing less than half as long as vannal lobe 18
17. Large bee ~11 mm long. Antennal flagellum orangish below. Bt2–3 orange ..... *S. (Atrosamba) atra*
    Small bee ~9 mm long. Antennal flagellum completely black. Bt2–3 black ..... *S. (Atrosamba) gessorum* sp. nov.
18. Antennal flagellum entirely brown. Pronotum with black vestiture laterally ..... *S. (Prosamba) spinosa* sp. nov.
    Antennal flagellum yellowish below. Pronotum with greyish vestiture laterally ..... *S. (Prosamba) griseonigra*

Subgenus ***Atrosamba*** Michener, 1981

Atrosamba Michener, 1981: 65–66.
Type species: *Haplomelitta atra* Michener, 1981.

Diagnosis

Integument mostly black, tibia sometimes orange. Pubescence mostly black, sometimes pallid on mesosoma and orange on tibiae and tarsi. Basal segments of maxillary palpus nearly hairless. Mandible of female bidentate. Labrum half as long as clypeus. Clypeus of female sparsely punctate, glabrous between punctures. Propodeal triangle smooth, short and glabrous. Wings brown. Second submarginal cell about as long as first. First recurrent vein not interstitial with first transverse cubital vein. Jugal lobe of hind wing about half as long as vannal lobe. Female Bt3 with apical spine projecting above segment 2. Male Bt3 flat. Terga without apical fringes. Male S7 with two pairs of pedunculate membranous lobes, which differ between species in their hairiness (Fig. 6*A*, *C*). S8 weakly bifid apically, column about circular (Fig. 6*B*).

Included species

Samba atra and *S. gessorum*.

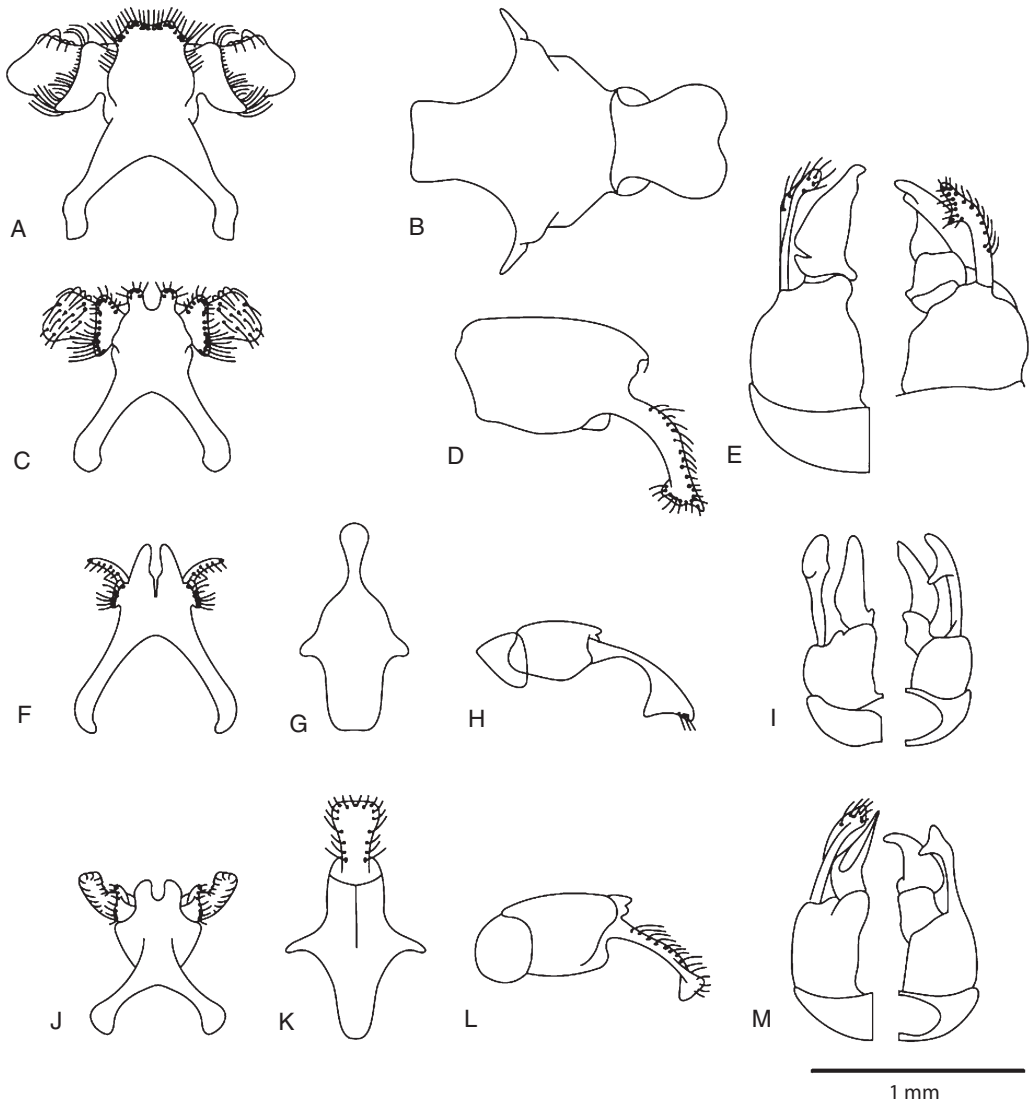

Fig. 6. Hidden sterna and genitalia of *Samba* male. (*A, B*) *S. atra*, sterna 7–8. (*C*) *S. gessorum*, sternum 7. (*D, E*) *S. atra*, genitalia. (*F–I*) *S. ogilviei*, sterna 7–8 and genitalia. (*J–M*) *S. tridentata*, sterna 7–8 and genitalia.

Samba (Atrosamba) atra (Michener, 1981), comb. nov.

(Fig. 6*A*, *B*, *D*, *E*)

Haplomelitta (*Atrosamba*) *atra* Michener, 1981: 128–129.

Material examined

Type material. Holotype♀, 2♀/1♂ paratypes, **South Africa:** Springbok, 29.67°S 17.88°E, 07.ix.1966, leg. Michener, SEM and SAMC; 2♀ paratypes, Nieuwoudtville, 31.38°S 19.10°E, ix.1961, leg. SAMC expedition, SAMC; 1♀ paratype, Kamieskroon, 30.20°S 17.93°E, ix.1930, leg. SAMC expedition, SAMC.

Additional material examined. **South Africa:** 1♀, Worcester, 33.65°S 19.43°E, 7.ix.1966, leg. Michener, SEM; 1♂, Ladismith, 33.48°S 21.27°E, 09.ix.1948, leg. Guillarmod, SEM; 2♀/1♂, Farm Dassiefontein, near Kamieskroon, 30.09°S 17.59°E, 01.x.1990, leg. Eardley, SANC; 2♂, idem, 16.ix.2007, SANC; 1♀, Bidouw Valley, 32.03°S 19.40°E, 04.ix.1983, leg. Whitehead, SAMC; 1♀, Hetkruis, 32.60°S 18.75°E, 22.viii.1988, on *Indigofera procubens*, leg. Whitehead, SAMC; 1♀, Piketberg, 32.9°S 18.76°E, 03.ix.2001, on *Indigofera* sp., leg. Whitehead, SAMC; 1♀, idem, 22.ix.1995, SAMC; 1♀, idem, 03.ix.2001, SAMC; 1♀/2♂, Bloukrans Pass, 31.66°S 19.75°E, 26.viii.1997, leg. Whitehead, SAMC.

Redescription of female

Body size measurements: head 2.8 mm; scutum 2.2 mm; forewing 8.1 mm; body 9.7 mm. Vestiture mostly black, whitish around antennal sockets, on vertex, forepart and sides of mesosoma, disc of T1; keirotrichia orangish, tarsi bright orange below. Antennal flagellum orangish below. Tarsi integument orange. Vertex nearly straight, frontal view. Head and mesosoma moderately punctate (i = d), clypeus very sparsely punctate, almost smooth medially (i > d). Metasomal dorsum moderately punctate (i = d), shiny between punctures. Bt2–3 long (L/W = 1/0.38; 1/0.25). S1 gently convex, weakly concave medio–distally. Marginal zones of T2–4 smooth, longer medially.

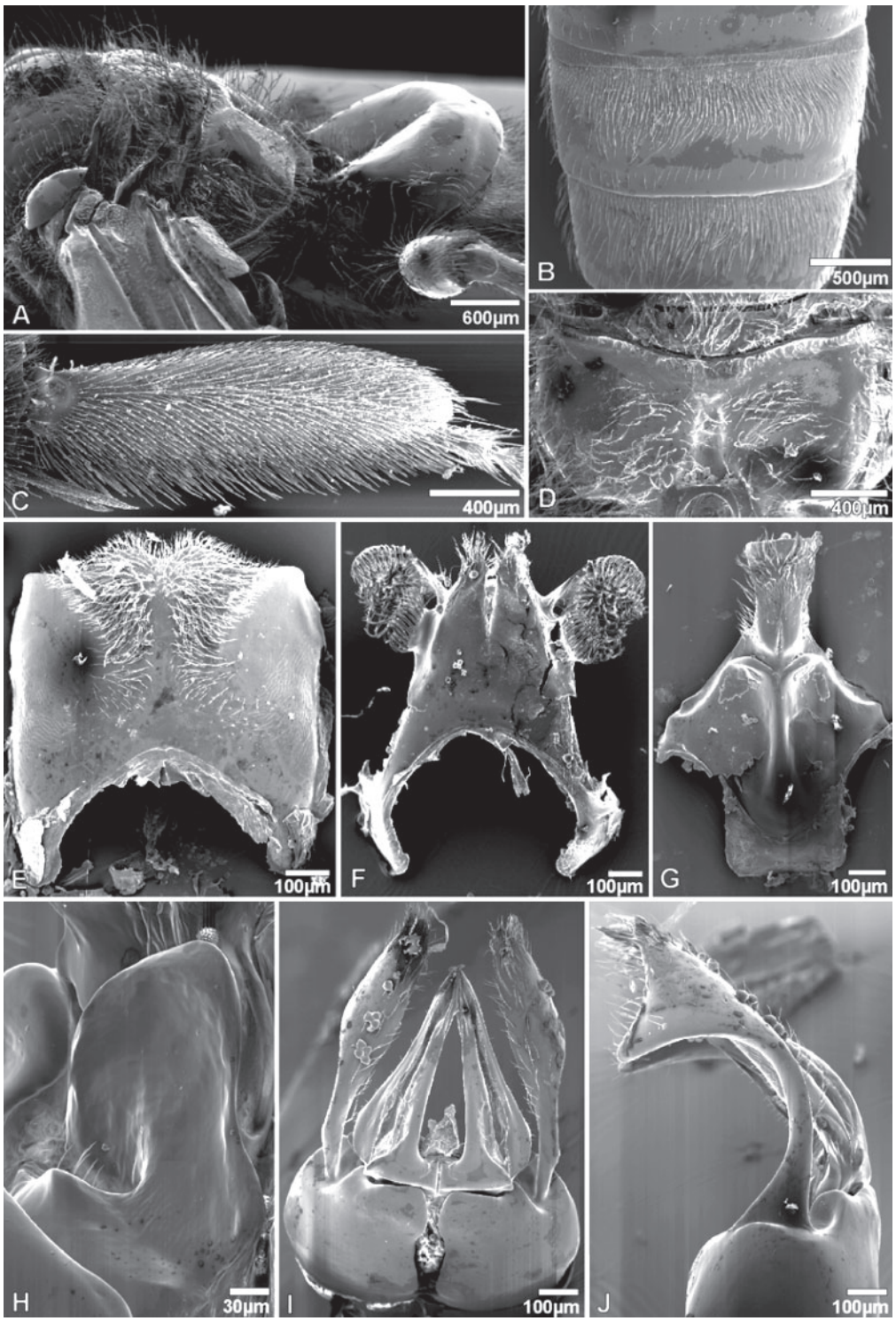

Fig. 7. *Samba ogilviei* male. (*A*) Lateral view of propodeum. (*B*) Tergum 2. (*C*) Hind basitarsus swollen. (*D*) Dorsal view of propodeum. (*E*) Ventral view of sternum 6. (*F*) Ventral view of sternum 7. (*G*) Ventral view of sternum 8. (*H*) Volsella. (*I*) Ventral view of genitalia. (*J*) Lateral view of genitalia.

Redescription of male

Clypeus covered with appressed white hair. Lateral part of face with black vestiture. Inner surface of Tb3 with erect black setae. Disc of T4–5 with black vestiture. Tb3 slender. Inner spur of Tb3 elongated, curved backward, hairy, with short sharp spines. Bt3 flat. Basitibial plate punctate. S7 with discs of membranous lobes

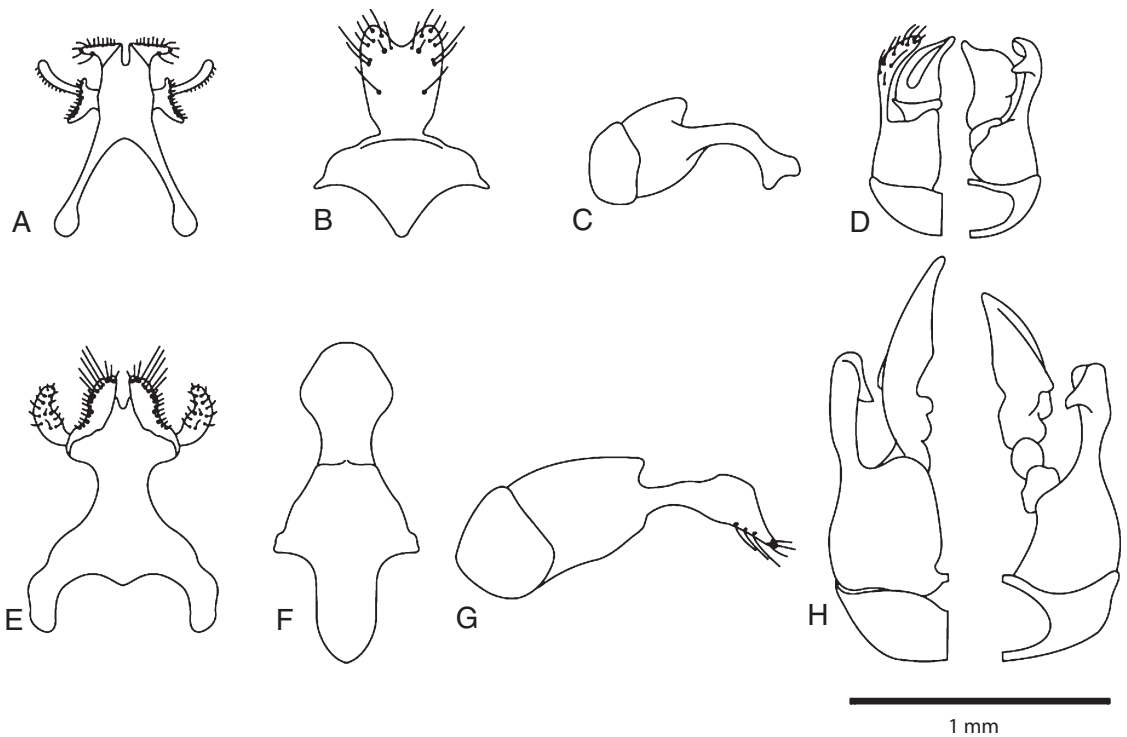

Fig. 8. Hidden sterna and genitalia of *Samba* male. (*A–D*) *S. fasciata*, sterna 7–8 and genitalia. (*E–H*) *S. griseonigra*, sterna 7–8 and genitalia.

nearly hairless (Fig. 6*A*). S8 apically bifid (Fig. 6*B*). Genitalia as in Fig. 6*D*, *E*.

Distribution

South Africa, in the western regions of Northern and Western Cape provinces in Fynbos and Nama Karoo biomes of the winter rainfall area (Fig. 10).

Phenology

Collected from the end of August to the beginning of October.

Samba (Atrosamba) gessorum Eardley, sp. nov.

(Fig. 7*C*)

Material examined

Type material. Holotype ♀, **South Africa:** Richtersveld, National Park, Die Koei River, 28.28°S 17.02°E, 11.x.1974, leg. R. Watmough, SANC. Paratypes 14♀/12♂, South Africa, Richtersveld, National Park, Koeroegabvlakte, 28.21°S 17.03°E, 17–24.ix.1995, on *Indigofera* sp., leg. S., F. and R. Gess, AMGS.

Additional material. 3♀, Sors Sors, 9 km NE Kamieskroon, 30.15°S 18.02°E, 17.ix.1992, on *Crassula dichotoma*, leg. F. and S. Gess, AMGS; 1♀, Zoekoevlei, 20 km W Clanwilliam, 32.18°S 18.9°E, 17.x.1989, F. and S. Gess, AMGS; 1♀, Goegap, near Kraaiwater, 29.37°S 18.00°E, 3–4.x.1994, F. and S. Gess, AMGS.

Description of female

Body size measurements: head 1.7 mm; scutum 1.4 mm; forewing 6.5 mm; body 6.9 mm. Vestiture largely black, with a little white on vertex, anterior region of scutum, pronotal lobes and T1; orange under foretarsus. Tarsi integument orange. Vertex straight, frontal view. Head and mesosoma moderately punctate (i = d), clypeus sparsely punctate. Metasomal dorsum moderately punctate (i = d), shiny between punctures. Bt2–3 long (L/W = 1/0.32; 1/0.25). S1 gently convex, weakly concave medio–distally. Marginal zones of T2–4 smooth, longer medially.

Description of male

Body size measurements: head 2.0 mm; scutum 1.5 mm; forewing 6.7 mm; body 8.5 mm. Vestiture largely black, clypeus and supraclypeus covered with appressed white hair, vertex, mesosomal dorsum and tibia with white intermixed with black, dorsal surface of T1 and T2 white, ventral surfaces of tarsi orange. Inner spur of Tb3 elongated, curved backward, with short sharp spines. Bt3 flat. Basitibial plate punctate. Tb3 slender. S6 with bushy medio-apical hairs. S7 with discs of membranous lobes hairy (Fig. 7*C*). Genital capsule similar to *S. atra*.

Remarks

This species is most closely related to *S. atra.* The females differ most strikingly in that *S. atra* is distinctly larger than *S. gessorum*, and the integument of the tarsi is orangish-black. The males of *S. atra* and *S. gessorum* are similar in size, but *S. atra* has extensive white vestiture on the face, mesosomal pleuron and T2–3, whereas these areas are mostly black in *S. gessorum*. In *S. gessorum* the pedunculate membranous lobes of S7 are hairier than in *S. atra*.

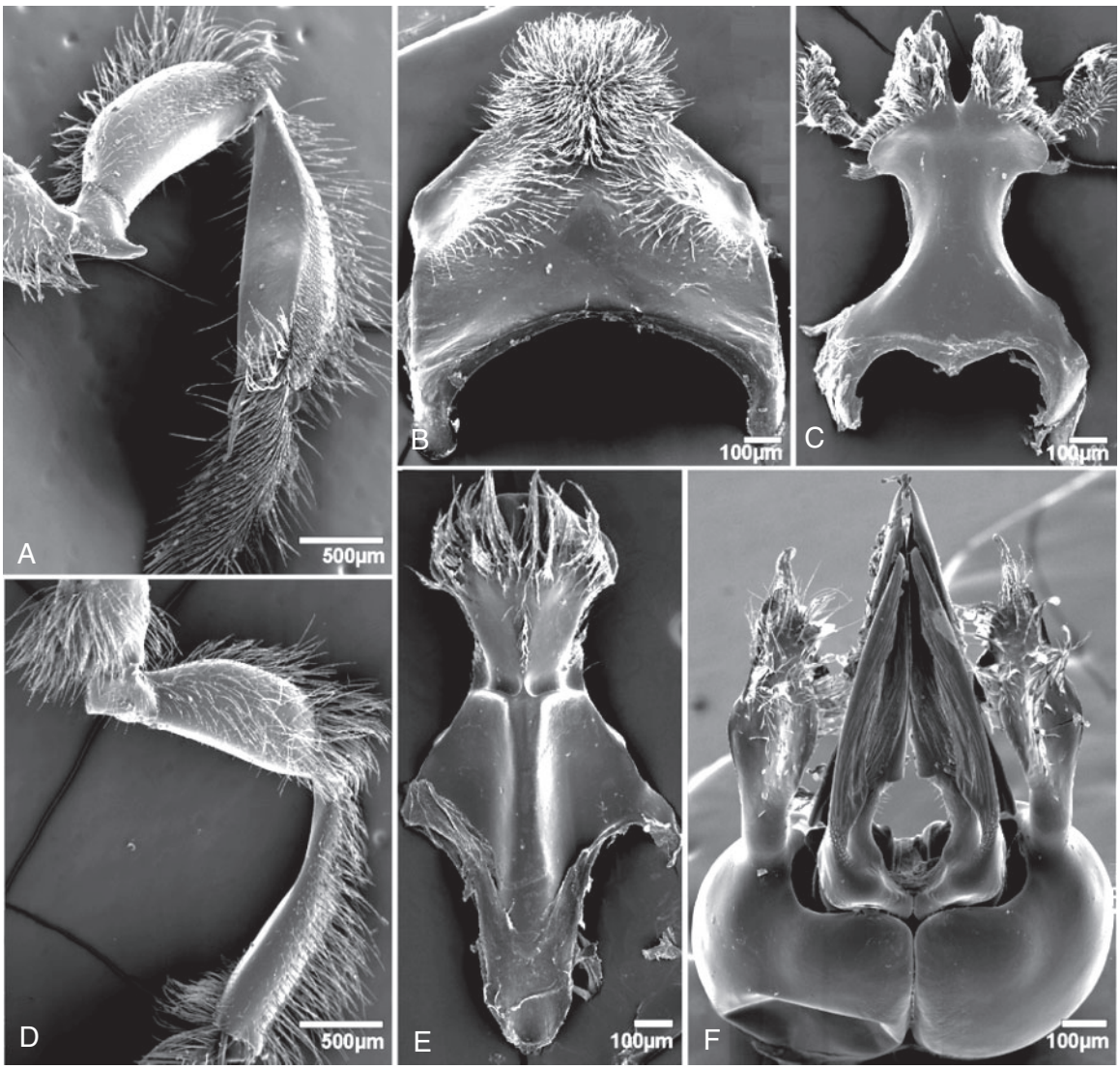

Fig. 9. (*A*) *Samba spinosa*, outer view of male hind leg. *Samba griesonigra* male: (*B*) ventral view of sternum 6; (*C*) ventral view of sternum 7; (*D*) outer view of hind leg; (*E*) ventral view of sternum 8; and (*F*) ventro-apical view of genitalia.

Distribution

South Africa, in the western regions of Northern and Western Cape provinces (Fig. 11).

Phenology

Collected during late September and early October.

Etymology

Named for Sarah and Fred Gess, who collected much of the type series.

Subgenus ***Haplomelitta*** Cockerell, 1934

Haplomelitta Cockerell, 1934: 446.
Type species: *Rhinochaetula ogilviei* Cockerell, 1932.

Diagnosis

Integument of head and mesosoma mostly black, metasoma mainly red, distal segments red. Basal segments of maxillary palpus nearly hairless. Mandible of female bidentate. Labrum half as long as clypeus. Clypeus of female smooth. Propodeal triangle strongly differentiated, smooth posteriorly (Fig. 7*D*), faintly sculptured anteriorly. Wings brown. Second submarginal cell a little shorter than first. First recurrent vein not interstitial with first transverse cubital vein. Jugal lobe of hind wing less than half as long as vannal lobe. Bt3 of female with small apical projection. Bt3 of male swollen, wider than Tb3 (Fig. 7*C*). Terga without apical fringes (Fig. 7*B*).

Included species

Samba ogilviei.

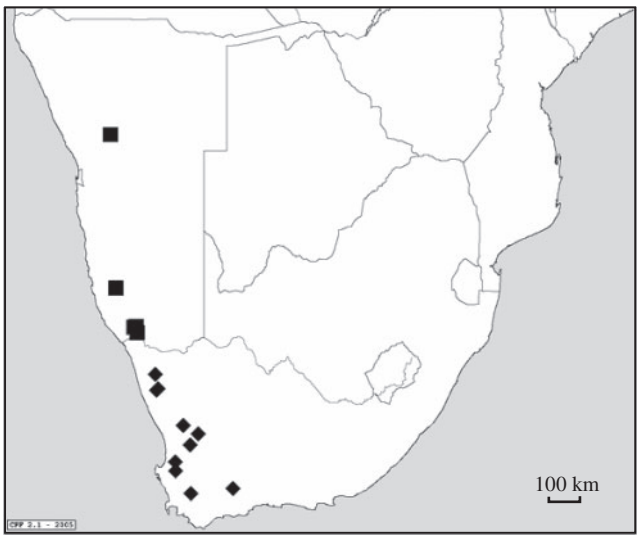

Fig. 10. Distribution of *Samba atra* (solid diamonds, 22 specimens) and *Samba fasciata* (solid squares, 31 specimens).

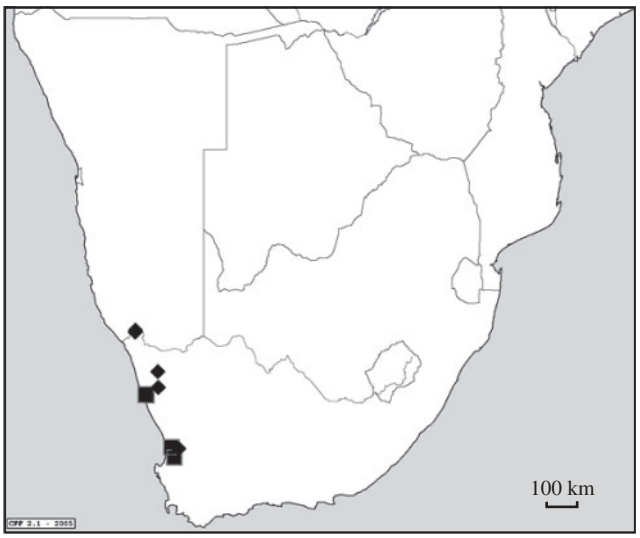

Fig. 11. Distribution of *Samba gessorum* (solid diamond, 32 specimens) and *Samba tridentata* (solid squares, 3 specimens).

Samba* (*Haplomelitta*) *ogilviei (Cockerell, 1932), comb. nov.

(Figs 6*F–I*, 7*A–J*)

Rhinochaetula ogilviei Cockerell, 1932: 454–455.

Material examined

Type material. Holotype ♀, 1♂/1♀ paratypes, **South Africa:** Nieuwoudtville, 31.38°S 19.1°E, 20–22.X, leg. Cockerell, NHM.

Additional material examined. **South Africa:** 2♂, Stellenbosch, 33.93°S 18.85°E, 07.x.1925, leg. Nel, NHM; 1♀, idem, 10.xii.1984, NHM; 4♀/1♂, Nieuwoudtville, 31.38°S 19.1°E, 18–22.xi.1931, NHM; 2♀, Ceres, 33.36°S 19.31°E, leg. Turner, NHM; 1♂, Clanwilliam, 32.18°S 18.9°E, 14.x.1981, leg. Whitehead, NHM; 1♀, Nieuwoudtville, 31.38°S 19.1°E, 18–22.xi.1931, ZIL; 1♀, Clanwilliam, 32.18°S 18.9°E, 19.ix.1966, SEM; 1♀/1♂, 28 km E Velddrif, 32.78°S 18.17°E, leg. Rozen, SEM; 2♀, Nieuwoudtville, 31.38°S 19.10°E, leg. Ogilvie, SEM; 5♂, 15 km Nieuwoudtville Farm Engelsepunt, 31°14′30″S 18°59′13″E, 830m, 10.x.2006, leg. Kuhlmann, UM; 4♂, 15 km Nieuwoudtville Farm Engelsepunt, 31°14′30″S 18°59′13″E, 830m, 14.x.2006, leg. Kuhlmann, UM; 1♂, 5 km E Graafwater, 32°08.93′S 18°40.27′E, 22.ix.2001, leg. Danforth, CUIC; 2♀/32♂, Clanwilliam district, Biedou Valley, 32.08°S 19.14°E, ix.1990, on *Cotula coronopifolia*, leg. Eardley, SANC; 3♂, Farm Dassiefontein, near Kamieskroon, 30.09°S 17.59°E, 1.X.1990, leg.and Eardley, SANC; 24♀/39♂, Farm Arkoep, 6 km N Kamieskroon, 30.19°S 17.56°E, 1–2.x.1990, leg. Eardley, SANC; 2♀/10♂, 15 km E Citrusdal, 32.37°S 19.08°E, 4.x.1990, leg. Eardley, SANC; 1♂, Graafwater, 32.09°S 18.37°E, 14.ix.1987, leg. Eardley, SANC; 28♀/41♂, W. Cape, 20 km Citrusdal, 32.60°S 19.02°E, 27.X.1999, leg. Halada, OOLL; 2♀/12♂, Springbok, Hester Malan Nature Reserve, 29.67°S 18.03°E, 10–12.X.1988, F. and S. Gess, AMGS; 30♀/2♂, Citrusdal, 32, 4.X.1990, on *Monopsis debilis*, F. and S. Gess, AMGS; 12♀/7♂, 11 km W Clanwilliam, 32.18°S 18.9°E, 2–3.X.1990, F. and S. Gess, AMGS; 8♀/7♂, Nature Reserve Kraaiwater, 29.38°S 18.00°E, 29.ix.1997, on *Monopsis debilis*, F. and S. Gess, AMGS; 5♂, between Taaiboskraal and Anegas, 30.07S 18.01E, 3.X.1995, F. and S. Gess, AMGS; 10♀, Goegap, near Kraaiwater, 29.37S 18.00E, 3–4.X.1994, F. and S. Gess, AMGS.

Redescription of female

Body size measurements: head 1.9 mm, scutum 1.3 mm, forewing 6.3 mm, body 7.7 mm. Vestiture on head and mesosomal dorsum mostly black, white on pronotum, pronotal lobes and behind wings, mesosomal venter white with black hairs intermixed, legs with black and white patches, ventral surfaces of tarsi black and orange, metasoma white, except segments 5–6 black. Flagellum orangish below. Tarsi with integument blackish orange. Clypeus flat. Vertex distinctly concave, frontal view. Head mesosoma and metasomal dorsum sparsely punctate (i > d). Bt2–3 long (L/W = 1/0.50; 1/0.29). Marginal zone of terga smooth and wide, much like rest of terga.

Redescription of male

Body size measurements: head 1.6 mm, scutum 1.1 mm, forewing 5.7 mm, body 6.5 mm. Vestiture mostly white, except black on upper region of head, scutum, propodeum and distal region of metasomal dorsum, pale yellow under tarsi. Hind trochanter gently curved below. F3 and Tb3 slender. Basitibial plate punctate. Inner spur of Tb3 a little shorter than outer spur. S7 with two pairs of hairy, narrow membranous lobes (Figs 6*F*, 7*F*). Column of S8 elongate, curved (Figs 6*G*, 7*G*). Genitalia as in Figs 6*H*, *I*, 7*I*, *J*.

Distribution

South Africa, Western and Northern Cape provinces (Fig. 12).

Phenology

Collected from the beginning of September to the middle of December.

Subgenus ***Haplosamba*** Michener, 1981

Haplosamba Michener, 1981: 66–67.
Type species: *Haplomelitta tridentata* Michener, 1981.

Diagnosis

Head black to reddish-black (especially clypeus), mesosoma black, legs and metasoma mainly reddish, distal metasomal segments black. Basal segments of maxillary palpus nearly

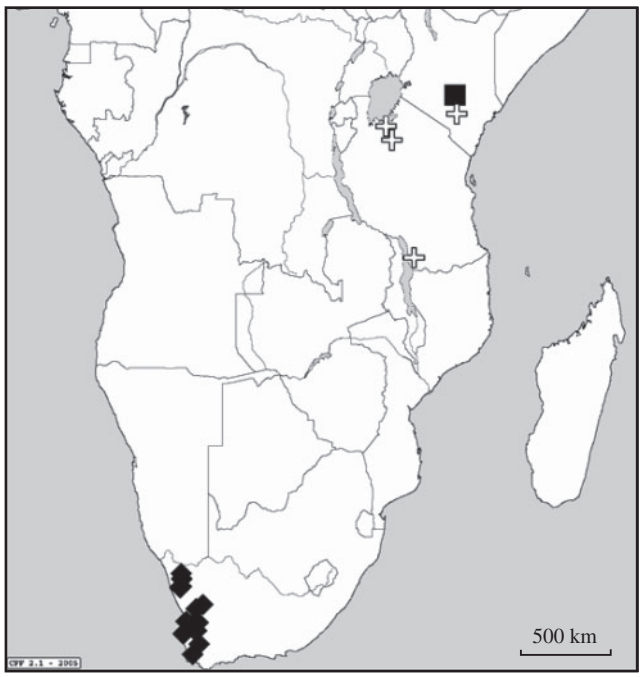

Fig. 12. Distribution of *Samba ogilviei* (solid diamonds, 299 specimens), *Samba ascheri* (solid square, 1 specimen) and *Samba calcarata* (open crosses, 9 specimens).

hairless. Female mandible tridentate. Labrum two third as long as clypeus. Clypeus of female flat and smooth. Propodeal triangle short and smooth. Wings brown. Second submarginal cell shorter than first. First recurrent vein not interstitial with first transverse cubital vein. Jugal lobe of hind wing less than half as long as vannal lobe. Female Bt3 without apical spine. Male Bt3 flat. Terga without apical fringes.

Included species

Samba tridentata.

Samba* (*Haplosamba*) *tridentata (Michener, 1981), comb. nov.

(Fig. 6*J–M*)

Haplomelitta (*Haplosamba*) *tridentata* Michener, 1981: 129–130.

Material examined

Type material. Holotype ♀, **South Africa**, Wallekraal, 30.38°S 17.5°E, X.1950, leg. SAM expedition, SAMC.

Additional material examined. We examined two males in the SAMC, which allow us to describe hereafter the previously unknown sex of *S. tridentata*. These males were respectively caught in Graafwater, 32.15°S 18.60°E, and Paleisheuwel, 32.46°S 18.72°E . They are not associated with female but they share with the examined female holotype numerous non sexual features: wing venation, red metasoma, structures of clypeus, propodeum and labrum.

Redescription of female

Body size measurements: head 2.6 mm, scutum 1.9 mm, forewing 7.4 mm, body 10.3 mm. Vestiture on head, mesosoma and metasoma mostly black, keirotrichia and ventral surfaces of tarsi orange. Flagellum orangish below. Clypeus flat. Vertex slightly concave, frontal view. Head clypeus almost without punctures, glabrous, rest of head and mesosoma moderately punctate (i = d), metasomal dorsum sparsely punctate (i > d). Bt2–3 long (L/W = 1/0.45; 1/0.21). Marginal zone of terga smooth and wide, unlike rest of terga that are punctate. Tarsi with integument blackish orange.

Description of male

Body size measurements: head 2.2 mm, scutum 1.7 mm, forewing 7.4 mm, body 8.0 mm. Vestiture mostly black, scutum white, pale yellow under tarsi. Hind trochanter gently curved below. F3 and Tb3 slender. Basitibial plate glabrous. Inner spur of Tb3 a little shorter than outer spur. S7 with two pairs of hairy, membranous lobes, dorsal lobe slender and projecting downwards (Fig. 6*J*). Column of S8 slender, curved (Fig. 6*K*). Genitalia as illustrated (Fig. 6*L*, *M*).

Distribution

South Africa, Northern Cape Province in the Nama Karoo biome in the winter rainfall area (Fig. 11)

Phenology

Only found in October.

Subgenus ***Metasamba*** Michener, 1981

Metasamba Michener, 1981: 69–70.

Type species: *Haplomelitta fasciata* Michener, 1981.

Diagnosis

Head and mesosoma black, legs blackish proximally, orange distally, metasoma black or red. Basal segments of maxillary palpus nearly hairless. Mandible of female bidentate. Labrum short. Clypeus of female with a small medio-longitudinal ridge. Propodeal triangle short and smooth. Second submarginal cell shorter than first. First recurrent vein not interstitial with first transverse cubital vein. Jugal lobe of hind wing about half as long as vannal lobe. Female Bt3 with apical spine projecting above segment 2. Terga with apical fringes. Male inner apex of Tb3 with small patch of long hairs on base of spurs. Male S7 with a pair of latero-apical structure long and narrow, longer than disc width (Fig. 8*A*).

Included species

Samba fasciata and *S. rubigoinis*.

Samba* (*Metasamba*) *fasciata (Michener, 1981), comb. nov.

(Fig. 8*A–D*)

Haplomelitta (*Metasamba*) *fasciata* Michener, 1981: 130–131.

Material examined

Type material. Holotype ♀, 1♀ paratype, Namibia, 61 km W Omaruru, 21.43°S 15.93°E, 21.iii.1979, leg. Rozen, AMNH; 2♀/2♂ paratypes, same data but different dates, SEM and AMNH; 3♀ paratypes, 32 km W of Omaruru, 15.iii.1979, on *Indigofera*, leg. Rozen, AMNH.

Additional material examined. Namibia: 3♀/11♂, SW Klein-Aus-Vista, 26°44′10″S 16°09′50″E, 24.ix.2003, on Fabaceae, leg. Gess and Gess,

AMGS. **South Africa:** 1♂, Richtersveld National Park, near Potjies, 28.04°S 16.57°E, 23–24.viii.2006, leg. Eardley, SANC; 1♀, idem, near Oena Mine, 28.03°S 17.03°E, 23–24.viii.2006, leg. Eardley, SANC; 2♀/7♂, Richtersveld National Park, near Koeroegabvlakte, 28.11°S 17.03°E, 24.ix.1995, on *Indigofera* sp., leg. Gess and Gess, AMGS.

Redescription of female

Body size measurements: head 1.9 mm, scutum 1.5 mm, forewing 5.1 mm, body 7.4 mm. Vestiture mostly white; orange on parts of legs and under tarsi, distal end of metasoma black. T3–4 with white basal tomentum. Antennal flagellum blackish red below; integument of segments 2–5 of foretarsus, middle tarsus and hind tibia and tarsus blackish-orange; metasoma black. Vertex straight, frontal view. Head and mesosoma moderately punctate (i = d). Jugal lobe of hind wing about half as long as vannal lobe. Metasomal dorsum moderately punctate (i = d), shiny between punctures. Bt2–3 long (L/W = 1/0.30; 1/0.29). S1 gently convex and concave medio-distally. Marginal zone of terga hirsute.

Redescription of male

Body size measurements: head 1.8 mm, scutum 1.3 mm, forewing 4.8 mm, body 6.5 mm. Vestiture mostly white, orange on vertex and ventral surfaces of tarsi. Integument of fore and middle tibiae orange-black proximally, orange distally, hind tibia completely orange, all tarsi orange, metasoma black. Inner spur of Tb3 elongated, curved backward, with short sharp spines. Hind trochanter gently curved below. Tb2–3 strongly swollen. Bt3 flat. Basitibial plate punctate and hairy. S7 with two pairs of slightly hairy, membranous lobes, dorsal lobe thread-like, distal end of disc hammate (Fig. 8*A*). Column of S8 strongly curved downwards, mostly bifid distally (Fig. 8*B*), sometimes rounded distally in some specimens. Genitalia with bulbous penis valve, gonostylus apically bifid (Fig. 8*C*, *D*).

Remarks

Some male specimens differ slightly from the paratypes in the shape of the distal end of S8. The typical form has S8 apically rounded, as illustrated by Michener (1981), while some specimens have S8 apically bifid (Fig. 8*B*). Without further evidence this variation is considered to be intraspecific. Moreover, the females of these two species are indistinguishable.

Distribution

Desert regions of north-western South Africa and western Namibia (Fig. 10).

Phenology

Collected during August and September.

Samba* (*Metasamba*) *rubigoinis Eardley, sp. nov.

Material examined

Type material. Holotype ♀, 3♀ paratypes, **South Africa**, Meltonwold, near Victoria West, 31.27°S 22.45°E, 15.ii.1991, leg. C. Eardley, SANC. 1♂ paratype, Namibia, Karibib district, 50 km SW Usakos, 21.ii.1990, leg. Pulawski, CAS.

Description of female

Body size measurements: head 2.0 mm, scutum 1.6 mm, forewing 5.2 mm, body 7.0 mm. Wings weakly infuscated. Basal segments of maxillary palpus nearly hairless. Second submarginal cell shorter than first. Jugal lobe of hind wing less than half as long as vannal lobe. Integument of head, mesosoma, coxae 1–3, trochanters 1–3 and F1–3 and T5–6 mostly black; antennal flagellum, tibiae and tarsi and metasoma mostly orange. Vestiture mostly white, orange under tarsi, distal end of metasoma black, T4–5 with distal fringes. Clypeus with small medio-longitudinal ridge. Vertex about straight, frontal view. Head and mesosoma moderately punctate (i = d). Bt1 short, Bt2 long (L/W = 1/0.48; 1/0.29). Bt2–3 with small apical spine projecting above segment 2. Metasomal dorsum punctate (i = d), shiny between punctures. Marginal zone of terga hirsute. S1 gently convex and slightly concave medio-distally.

Description of male

Body size measurements: head 1.9 mm, scutum 1.5 mm, forewing 6.2 mm, body 7.0 mm. Vestiture white on legs, vertex, scutum and prepygidial fimbria. Inner apex of Tb3 with small patch of long hairs on base of spurs. Bt3 with long lateral white hairs. Basal segments of maxillary palpus nearly hairless. Body integument black except reddish on apical tarsi and metasoma. Antenna brown. Wings brownish. Labrum smooth. Vertex straight in frontal view. Clypeus flat. Scutum deeply punctate, smooth between punctures. Propodeal triangle short and smooth. Bt1–3 flat. Bt1 short, Bt2 wide (L/W = 1/0.45; 1/0.5). Inner spur of Tb3 straight, sligthly longer than outer spur. Second submarginal cell shorter than first. Median and lateral length of terga marginal zones subequal. S5–6 with apical bushy hairs. S7 with pair of latero-apical structure long and narrow, longer than disc width. S8 strongly curved downwards, bifid distally. Genitalia with bulbous penis valve, gonostylus apically bifid.

Remarks

S. rubigoinis is morphologically similar to *S. fasciata* but the former species presents the metasoma mostly reddish, the vanal lobe smaller and the hind basitarsus with smaller apical spine. Moerover *S. rubigoinis* male does not have strong apical hair bands on terga and its inner spur of Tb3 is straight, slightly longer than the outer spur.

Distribution

South Africa, in the central Karoo, a semi-desert that receives summer rainfall. The distribution area is widely separated from the *Samba* species of the winter rainfall region (Fig. 13).

Phenology

The type material and additional male were collected in February.

Etymology

Named for the rust coloured metasoma, which is diagnostic.

Subgenus ***Prosamba*** Michener

Prosamba Michener, 1981: 63–65.
Type species: *Haplomelitta griseonigra* Michener, 1981.

Diagnosis

Metasoma black. Basal segments of maxillary palpus with long setae. Mandible of female bidentate. Labrum short. Clypeus of female flat. Propodeal triangle short and smooth. Wings brown to hyaline. Second submarginal cell distinctly shorter than first. First recurrent vein interstitial with first transverse cubital vein. Jugal lobe of hind wing less than half as long as vannal lobe. Bt3 of female without apical spine. Bt3 of male flat. Terga without apical fringes.

Included species

Samba griseonigra and *S. spinosa*.

Samba (Prosamba) griseonigra (Michener, 1981), comb. nov.

(Figs 8*E–H*, 9*B–F*)

Haplomelitta (*Prosamba*) *griseonigra* Michener, 1981: 126–127.

Material examined

Type material. Holotype ♀, 4♀ paratypes, South Africa, Kamieskroon, 30.2°S 17.93°E, SEM and SAMC.

Additional material examined. **South Africa:** 1♂, Bowesdorp, 30.15°S 17.93°E, leg. S.A. museum, SEM; 2♀/2♂, 5 km S Clanwilliam, 32°11.4′S 18°52.5′E, 07.ix.2001, on *Crassula dichotoma*, leg. B. Danforth, CUIC; 2♀/1♂, Garies, 30.55°S 17.98°E, leg. Whitehead, NHM; 61♀/2♂, farm Dassiefontein, 30.09°S 17.59°E, 01.ix.1990, leg. Eardley, SANC; 3♀, Kamiesberg, 30.10°S 18.01°E, 11.ix.1987, leg. Eardley, SANC; 1♀/1♂, Farm Arkoep, 6 km N Kamieskroon, 30.19°S 17.56°E, 1–2.X.1990, leg. Eardley, SANC; 1♀, Doring Kraal farm, 30.55°S 17.98°E, 29.ix.1988, on sand, leg. Whitehead, SAMC; 1♀, idem, on *Crassula* sp., SAMC; 1♀/1♂, Welkom farm, 30.45°S 18.15°E, 30.ix.1988, on *Crassula* sp., leg. Whitehead, SAMC; 1♀, Nieuwoudtville, 31.38°S 19.10°E, 28.ix.1995, on *Crassula dichotoma*, leg. Whitehead, SAMC; 1♂, Kamieskroon, 30.20°S 17.93°E, SAMC; 1♀, Bidouw valley, 32.03°S 19.40°E, 04.ix.1983, leg. Whitehead, SAMC; 1♀/1♂, Kamiesberg, 30.13°S 18.03°E, 28.ix.1995, leg. Gess and Gess, AMGS; 5♀/3♂, Studer's Pass, near Garies, 30.26S 17.03E, 16.ix.2007, C. Eardley, SANC.

Redescription of female

Body size measurements: head 2.4 mm, scutum 1.7 mm, forewing 5.6 mm, body 8.1 mm. Vestiture mostly white, often intermixed with black hairs, orange on parts of legs and always under tarsi, distal end of metasoma black (disc of T4–5 with whitish vestiture). Wings brown. Antennal flagellum orange below. Tarsal segments 2–5 orange. Vertex nearly straight, frontal view. Clypeus flat and smooth, with a few punctures. Bt1 short, Bt2 long (L/W = 1/0.43; 1/0.26). Metasomal dorsum moderately punctate (i = d), shiny between punctures. Marginal zone of terga smooth and wide. S1 gently convex with medio-distal region slightly concave.

Redescription of male

Body size measurements: head 2.2 mm, scutum 1.5 mm, forewing 5.9 mm, body 8.1 mm. Wings transparent. Vestiture white, except ventral surfaces of tarsi orange, T6–7 black. Antennal flagellum orangish. Inner spur of Tb3 unmodified. Hind trochanter gently curved to weakly angulate below (Fig. 9*D*). Hind femur and tibia moderately swollen. Bt2–3 flattened without apical projection, Bt1 elongate, Bt2 long (L/W = 1/0.2; 1/0.25). Basitibial plate smooth. Inner surface of hind tibia smooth and hairless. Terga without apical fringe. Hind tibia moderately swollen (L/W = 1/0.3). S7 with one pair of membranous latero-apical processes (Figs 8*E*, 9*C*). S8 as Figs 8*F*, 9*E*. Genitalia as Figs 8*G*, *H*, 9*F*.

Distribution

South Africa, in the western regions of Northern and Western Cape provinces, in Fynbos and Nama Karoo biomes of the winter rainfall area (Fig. 14).

Phenology

This species has only been found to be active during September.

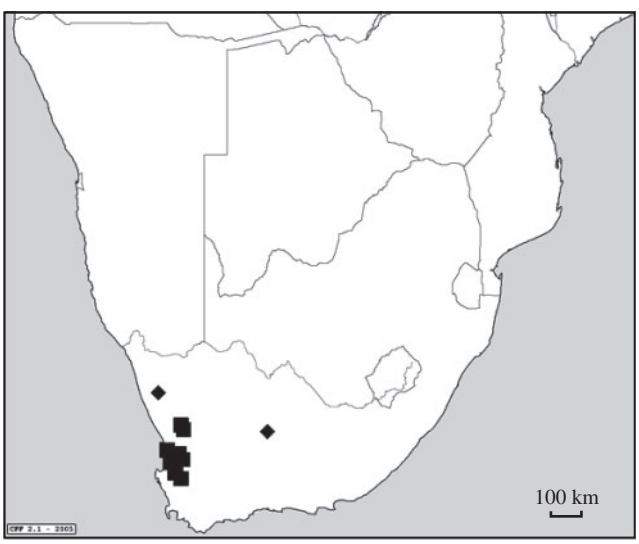

Fig. 13. Distribution of *Samba rubigoinis* (solid diamonds, 3 specimens) and *Samba spinosa* (solid squares, 46 specimens).

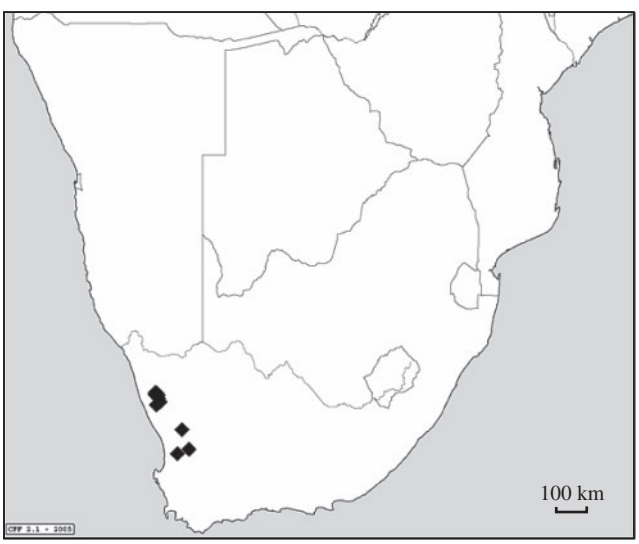

Fig. 14. Distribution of *Samba griseonigra* (98 specimens).

Samba (Prosamba) spinosa Eardley, sp. nov.

(Fig. 9*A*)

Material examined

Type material. Holotype ♂, 2♀ paratypes, **South Africa**, 10 km W Algeria, Clanwilliam Road, 32.21°S 19.03°E, 4.ix.1987, leg. Eardley, SANC; 4♀/2♂ paratypes, Near Clanwilliam, 32.11°S 18.52°E, 01.viii.2004, leg. Eardley, SANC; 1♀/1♂ paratypes, 5 km S Clanwilliam, 32.11°S 18.52°E, 07.ix.2001, leg. Eardley, SANC; 1♂ paratype, Nieuwoudtville, Botanic Gardens, 31.22°S 19.07°E, 09.ix.1987, leg. Eardley, SANC.

Additional material examined. **South Africa:** 3♂, 15 km Nieuwoudtville, Farm Engelsepunt, 31°14′31″S 18°59′08″E, 830 m, 07.X.2003, leg. Timmermann, UM; 2♀, 15 km Nieuwoudtville, Farm Engelsepunt, 31°14′31″S 18°59′08″E, 830 m, 24.ix.2003, leg. Timmermann, UM; 8♀, 15 km Nieuwoudtville, Farm Engelsepunt, 31°14′31″S 18°59′08″E, 830 m, 06.X.2003, leg. Timmermann, UM; 2♀/1♂, 15 km Nieuwoudtville, Farm Engelsepunt, 31°14′30″S 18°59′13″E, 830 m, 10.X.2006, Kuhlmann, UM; 2♀/2♂, 15 km Nieuwoudtville, Farm Engelsepunt, 31°14′30″S 18°59′13″E, 830 m, 29.ix.2006, Kuhlmann, UM; 2♀/1♂, 15km Nieuwoudtville, Farm Engelsepunt, 31°14′30″S 18°59′13″E, 830 m, 14.X.2006, Kuhlmann, UM; 1♀, Suurfontein, 32.06°S 18.40°E, 09.ix.1994, on *Crassula dichotoma*, leg. Whitehead, SAMC; 1♀, idem, 01.ix.1994, SAMC; 1♂, Redelinghuys, 32.48°S 18.53°E, 28.ix.1988, on *Crassula dichotoma*, leg. Whitehead, SAMC; 1♀, 7 km S Clanwilliam, 32.18°S 18.90°E, 03.ix.1986, on *Crassula dichotoma*, leg. Whitehead, SAMC; 1♀/1♂, Porterville, 33.01°S 18.98°E, 11.xi.1999, on *Crassula dichotoma*, leg. Whitehead, SAMC; 1♀/1♂, Piketberg, 32.83°S 18.75°E, 10.xi.2001, on *Crassula dichotoma*, leg. Whitehead, SAMC; 1♂, Piketberg Banghoek, 32.83°S 18.75°E, 20.ix.1991, on *Crassula dichotoma*, leg. Whitehead, SAMC; 1♂, Voorste valley, 32.83°S 18.73°E, 19.ix.1987, on *Crassula dichotoma*, leg. Whitehead, SAMC; 1♂, Nieuwoudtville Oorlog Kloef, 31.38°S 19.10°E, 24.ix.1986, on *Crassula dichotoma*, leg. Whitehead, SAMC; 1♂, Nieuwoudtville Camp Ground, 31.38°S 19.10°E, 20.xi.1996, leg. Whitehead, SAMC; 1♂, idem, 28.ix.1985, on *Crassula dichotoma*, leg. Whitehead, SAMC.

Description of female

Body size measurements: head 2.5 mm, scutum 1.6 mm, forewing 6.2 mm, body 8.1 mm. Vestiture mostly black, white on vertex, pronotal lobe, dorsal surface of fore tibia (intermixed with black hairs), antero-dorsal regions of middle tibia and basitarsus, antero-dorsal region of T1, anterior regions of T2, orange under tarsi. Vertex nearly straight in frontal view. Integument black, antennal flagellum blackish, distal tarsal segments orange. Clypeus flat and glabrous. Bt1 short, Bt2 long (L/W = 1/0.43; 1/0.26). Metasomal dorsum sparsely punctate (i > d), shiny between punctures. Marginal zone of terga smooth and wide S1 gently convex and slightly concave medio-distally.

Description of male

Body size measurements: head 2.2 mm, scutum 1.6 mm, forewing 6.2 mm, body 8.1 mm. Vestiture white, except ventral surfaces of tarsi orange, T6–7 black, S4–7 black. Inner spur of Tb3 unmodified. Wings transparent. Integument black, antennal flagellum blackish. Hind trochanter distinctly spinose (Fig. 9*A*). Hind femur and tibia moderately swollen. Bt2–3 flattened without apical projection, Bt1 elongate, Bt2 long (L/W = 1/0.2; 1/0.25). Basitibial plate smooth. Inner surface of hind tibia smooth and hairless. Terga without apical fringe. Hind tibia moderately swollen (L/W = 1/0.3). S7, S8 and genital capsule similar to *S. griseonigra*.

Remarks

Male and female of *S. spinosa* are similar to *S. griseonigra* but they show reddish-black antennal flagellum. Moreover female presents some additional diagnostic features: (i) the vestiture is mostly black but white on vertex, pronotal lobe, parts of dorsal surfaces of fore and middle tibiae and tarsi and T1–2; (ii) the vestiture is orange under tarsi. The main morphological difference between *S. spinosa* and *S. griseonigra* is the well developed spine on the ventral surface of male hind trochanter.

Distribution

South Africa, in the western regions of Northern and Western Cape provinces, in Fynbos and Nama Karoo biomes of the winter rainfall area (Fig. 13).

Phenology

This species appears to be active during August to November.

Etymology

Named for the spine on the male hind trochanter.

Subgenus ***Samba*** Friese

Samba Friese, 1908: 568.
Type species: *Samba calcarata* Friese, 1908.

Diagnosis

Metasoma mainly red. Basal segments of maxillary palpus nearly hairless. Mandible of female bidentate. Labrum four times as wide as long, with strong transverse median ridge. Propodeal triangle short and smooth. Second submarginal cell as long as first. First recurrent vein not interstitial with first transverse cubital vein. Jugal lobe of hind wing less than half as long as vannal lobe. Bt3 of female with apical spine. Bt3 of male swollen, wider than Tb3. Terga without apical fringes. Disc of terga centrally black, premarginal line and marginal zone orange.

Included species

Samba ascheri and *S. calcarata*.

Samba (Samba) ascheri Michez & Patiny, sp. nov.

Material examined

Type material. Holotype ♂, Kenya, Mwingi, 0.93°S 38.07°E, 04.xii.1997, leg. Snizek, SC.

Desctiption of holotype

Body size measurements: head 1.7 mm, scutum 1.6 mm, forewing 7.5 mm, body 7.9 mm. Vestiture mostly white including prepygidial fimbria. Marginal zone of terga hairless. Wings brown. Integument of head, antennal flagellum, mesosoma, coxae 1–3, trochanters 1–3, F1–3 and Tb1–3 black; tarsi 1–3 and S1–5 orange; disc of terga centrally black, premarginal line and marginal zone orange. Basal segments of maxillary palpus nearly hairless. Labrum with strong transverse median ridge. Vertex slightly concave, frontal view. Head and mesosoma deeply and densely punctate (i < d). Propodeal triangle short and smooth. Second submarginal cell shorter than first cell.

Jugal lobe of hind wing less than half as long as vannal lobe. F3 and Tb3 slender. Basitibial plate punctate. Inner spur of Tb3 shorter than outer spur. T1–6 with broad depressed marginal zones, narrow sub-laterally but broad medially. S6 with apical bushy hairs. S7 with two pairs of hairy membranous latero-apical lobes, one sessile, other pedonculate. Column of S8 dividing apically into laterally directed processes. Gonocoxite with medio-apical lobe. Gonostylus longer than gonocoxite, apically bifid.

Distribution

East Africa, Kenya (Fig. 12).

Phenology

The holotype was collected in December.

Etymology

Named for J. S. Ascher, who identified the type specimen as a new species of *Samba sensu lato*.

Samba (Samba) calcarata Friese, 1908

Samba calcarata Friese, 1908: 569.

Material examined

Type material. Holotype ♀, Kenya, Ikutha, 02.07°S 38.18°E, NHM.

Additional material examined. Tanzania: 1♀/3♂, Terr. Ukerewe, 02.80°S 33.00°E, leg. Conrad, SEM; 1♀, idem, ZIL; 1♂, Shinyanga, 03.67°S 33.43°E, leg. Burtt., NHM.

Redescription of female

Body size measurements: head 2.3 mm, scutum 1.9 mm, forewing 8.3 mm, body 10.1 mm. Vestiture mostly white, pygidial fimbriae medially black. Integument of head and mesosoma black. Flagellum orangish below. Tarsi and sterna orange. Disc of terga centrally black, premarginal line and marginal zone orange. Head wider than thorax. Labrum with strong transverse median ridge. Clypeus with median ridge. Vertex distinctly concave. Tb3 with only one apical spur. Bt2–3 long (L/W = 1/0.6; 1/0.4). T1–6 with broad depressed marginal zones, narrow sub-laterally but broad medially.

Redescription of male

Body size measurements: head 1.9 mm, scutum 1.7 mm, forewing 8.3 mm, body 9.4 mm. Vestiture whitish. Integument of head and mesosoma black. Head as wide as thorax. Disc of terga centrally black, premarginal line and marginal zone orange. S1–5 orange. Labrum with strong transverse median ridge. Clypeus with median ridge. Bt3 swollen, with white hairy pocket. T1–6 with broad depressed marginal zones, narrow sub-laterally, broad medially. S7 with two pairs of hairy membranous latero-apical lobes, one sessile, other pedunculate. Column of S8 dividing apically into laterally directed processes. Gonostylus longer than gonocoxite, apically bifid.

Distribution

East Africa, Kenya and Tanzania (Fig. 12).

Phenology

Unknown.

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