Taxonomic description of allodapine bees from the Zanzibar archipelago, genus *Macrogalea* (Hymenoptera: Apidae)

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Recent molecular phylogenetic work on allodapine bees (Apidae, Xylocopinae), reported elsewhere, has shown that the tropical African genus *Macrogalea* is the most basal genus in the tribe Allodapini, and studies on this genus are likely to provide important insights into social evolution in the xylocopine bees. A new species, *Macrogalea magenge* from Pemba Island, Tanzania, and the previously unrecorded male of *M. zanzibarica* are described. Genetic divergence data, from one nuclear and two mitochondrial gene fragments, for *M. candida, M. zanzibarica* and *M. magenge* are compared with intra-generic pairwise distances of other allodapine taxa.

Key words: Anthophoridae, Allodapini, *Macrogalea,* allodapine bees, genetic distance.

INTRODUCTION

The systematics of the bee tribe Allodapini were comprehensively revised by Michener (1965, 1975, 1977a, 2000). However, recent molecular phylogenetic studies of the tribe using one nuclear and two mitochondrial gene fragments (Schwarz *et al.* 2003) showed that the genus *Macrogalea* Cockerell comprises the basal clade and is sister group to the remaining Allodapini. Given the recent discovery of well-developed social behaviour in *Macrogalea zanzibarica* (Tierney *et al.* 2002), evolutionary studies need to focus further on this genus because of its potential usefulness for inferring early stages in the social evolution of the Allodapini.

Macrogalea is restricted to tropical East Africa, Namibia and Madagascar, and currently consists of ten species, three of which are probable social parasites. Initially it was thought only three species existed, and that other forms varying in colour and size did not warrant species status (Michener 1971, 1975), but later revisions of the Malagasy forms identified key characters to distinguish two additional specific taxa (Michener 1977b, c) and uncovered four new species (Pauly *et al.* 2001). Morphologically, *Macrogalea* is one of the most distinctive groups in Allodapini. Adults are large, robust and hairy, larvae are unusual among allodapines in lacking any kind of appendages, and in possessing numerous, densely distributed, short hairs covering all areas of the soma that are often hooked dorsally (Michener 1976).

A new species *Macrogalea magenge* from the Tanzanian island of Pemba, and the male of *M. zanzibarica* Michener from Unguja (Zanzibar Island) are described below. Genetic distance divergence data for *M. candida, M. zanzibarica* and *M. magenge* are compared with other allodapine genera.

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Macrogalea magenge sp. n.

Description

Female. Length 9–10 mm; forewing length 6 mm. Integumental colouration black, except fulvous distitarsis, testaceous tibial spurs and clypeus with whitish mediolongitudinal band. Punctation: clypeal disc dense and coarse, area between punctures less than half puncture diameter (similar to *M. candida*), but punctures not in rows; depression ventrolateral to antennal base similar to surrounding areas; vertex shining and minutely roughened between punctures, between ocelli and summits of eye densely punctate, except shiny areas lateral to posterior ocellus and lateral margins of eye summits. Surface of vertex anterior to preoccipital carina gently convex (resembles *M. zanzibarica*). Flagellum nearly twice as long as scape, segment 1 a little longer than broad, segments 2–3 less than twice as broad as long. Posterolateral angles of sixth tergum sharply angulate (as acute as or more so than *M. zanzibarica*). Pubescence on face white,

vertex and supraclypeus yellow; dorsum of thorax yellow, venter and sides of thorax whitish. Scopa on outer surface of tibia and basitarsis fulvous; bands of white tomentum on lateral thirds of tergum 2, continuous on terga 3–5 (less conspicuous than *M. candida*); hairs of metasomal dorsum between bands on terga 3–6 black to fuscous. Stigma and veins of wings brown (darker than *M. candida,* but paler than *M. zanzibarica*).

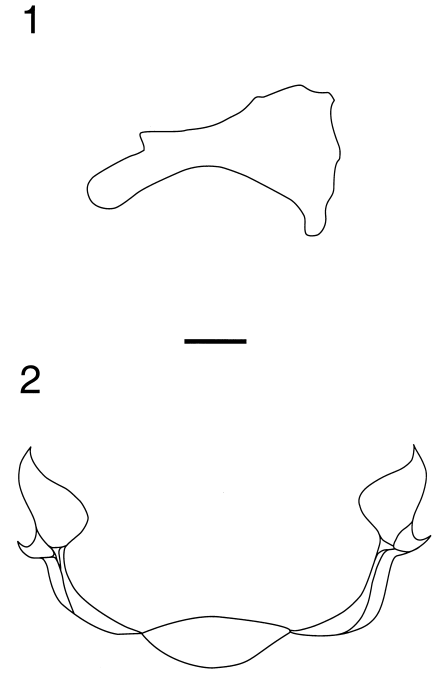
Male. Unknown.

Material examined. Holotype: Australian National Insect Collection, CSIRO, Canberra (ANIC), 1♀: Chwaka, Pemba Island, Tanzania (4°57′S 39°46′60″E), January 2001 (S.M. Tierney). Paratypes: 3♀, locality as for holotype. South African National Collection of Insects, ARC-Plant Protection Research Institute, Pretoria (SANC); Nairobi Museum (NM), South Australian Museum, Adelaide (SAM).

Remarks. This species appears to be most similar to *M. candida* and *M. zanzibarica* as opposed to the Malagasy forms, and differs from both in the paler leg colouration, dimensions of flagellum segments 1–3, and acute apicolateral angles of tergum 6. Clypeal colouration and punctation are most similar to *M. candida,* with vertex and preoccipital carina as in *M. zanzibarica*.

Distribution and habits. The species is known only from the type locality. Pemba is the northern neighbouring island to Unguja and these comprise the two largest islands of the Zanzibar archipelago. Pemba is geologically older than Unguja and thought to have separated from mainland Tanzania ~ 6 Mya (Griffiths 1993). It is geographically very different from Unguja, with a higher relief, undulate landscape and is more heavily forested, with similar vegetation to that of mainland East Africa. Nests were found in dead stems and lacked constructed entrance collars, similar to many other Allodapini and Ceratinini (Michener 1970). Life history and social habits are unknown, though nest contents for one nest (two below) suggest that the species may be social (*cf.* Tierney *et al.* 2002). Three nests of this species were collected in mid afternoon: 1) one adult female, one medium larva and one small larva; 2) four adult females, two callow females, five female pupae, one pre-pupa, six large larvae, five medium larvae and six eggs; 3) one adult female and one large larva.

Etymology. This species is named for the 'Magenge', the Swahili name for the legendary giant people of Pemba.



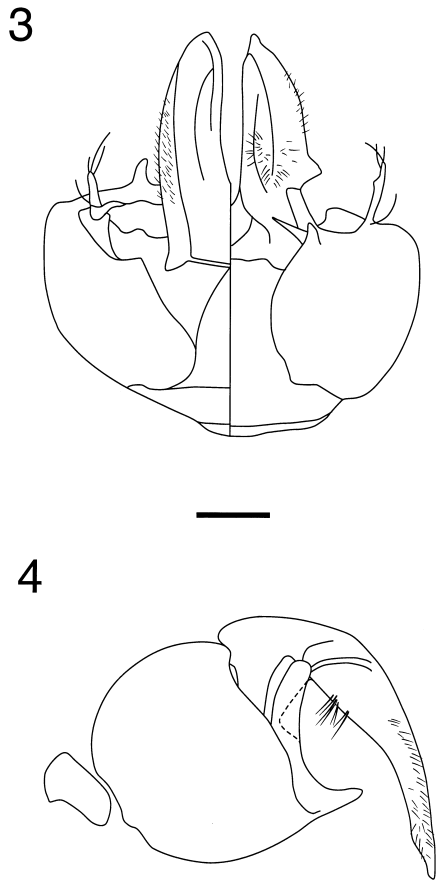
Figs 1–2. *Macrogalea zanzibarica* male. **1**, Left mandible; **2**, sclerotic bands of the eighth tergum. Scale bar = 0.2 mm.

Macrogalea zanzibarica Michener, Figs 1–4

Macrogalea zanzibarica Michener, 1977c, p. 429.
Macrogalea candida Michener, 1975, p. 231 (misidentification of Zanzibar specimens).

Type material. Holotype: British Museum 1♀, Nazi Moja, Zanzibar (Unguja), Tanzania, October–December 1924 (H. J. Snell). Paratypes: 2♀ British Museum; 1♀ Kansas University – collection locality as for holotype.

After revision of the Malagasy *Macrogalea,* Michener (1977c) elevated the Zanzibar form of *M. candida* to that of a valid species. Prior to this change in status *M. zanzibarica* was regarded as an intermediate form between mainland *M. candida* and the Madagascan *M. ellioti* (Michener 1975). Males of *Macrogalea* are not commonly found and male specimens of *M. zanzibarica* were not available to Michener. The only other descriptions for males of this genus are for *M. candida* (Michener 1971, 1975), *M. ellioti* and *M. scaevolae* (Pauly *et al.,* 2001). The following description is comparable to those of Michener (1971, 1975) and uses male *M. candida* collected from Meru National Park, Kenya (M.P. Schwarz) for comparison.



Figs 3–4. *Macrogalea zanzibarica*, male genitalia. **3**, Lateral view; **4**, dorsal/ventral view. Scale bar = 0.2 mm.

Description

Male. Length ~10 mm; forewing length 6 mm. Integumental colouration as in female but clypeus without mediolongitudinal line; flagellum light brown. Labrum flat, subtriangular (base not as acute as *M. candida*), one third wider than long. Flagellum twice as long as scape; first segment 1.5 times longer than wide, segments 8–9 each a little wider than long. Outer surface of mandible visible when head is viewed perpendicular to face (similar to *M. candida*), subapical tooth on dorsal surface well developed, basal tooth rounded distally and condyle well developed (Fig. 1), (subapical tooth and condyle more prominent and apex broader than in *M. candida*). Preoccipital carina absent. Pubescence on subapical mandible tooth pallid (unlike *M. candida* in that there are no dark hairs and pubescence is less dense). Hair on head, mesosoma and first two metasomal terga mostly yellowish, plumose, long and dense; long simple black hairs around eye margins (slightly shorter than those of *M. candida*), clypeus with dense, erect white pubescence; summits of mesepisternum yellowish; legs with long hair, black to dark brown on hind tibiae and tarsi; terga 3–6 with short erect black hairs dorsally; tergum 7 naked dorsally; terga 6–7 with whitish hairs laterally and posteriorly; tomentum absent on tergum 3, on terga 4–6 patchy, not forming distinct bands and weak laterally; sterna with long brownish-white hair. Veins and stigma of wings dark brown. Lateral sclerotic bands of terga 8 enlarged, reaching triangular inward angled areas anteriorly; bands with distinct ridge lines (Fig. 2). Gonocoxite wider than long; midventral inward projection of ventroapical plate at gonocoxite base, extended and acute; gonostylus with 1–3 bristles at posterior end (otherwise similar to *M. candida*); penis valves enormous (similar to *M. candida* and with similar setae); angular lateral projections at base of penis enlarged and pronounced (Figs 3 & 4).

Material examined. Four ♂, Jambiani, Unguja, Tanzania (6°19′S 39°32′6″E), December 2000 (M.P. Schwarz & S.M. Tierney). ANIC, SANC, NM, SAM.

Remarks. This species differs from *M. candida* in the more elaborate mandibles, penis valves, eighth tergum, broader labrum, and slight variations in plumage length and colouration. Examination of male characters further verifies Michener's (1977c) elevation of *M. zanzibarica* to specific status.

Distribution and habits. This species is endemic to Unguja (Zanzibar Is.), known from Nazi Moja east of Stone Town and the east coast villages of Jambiani and Matemwe. Nests collected by the authors were found in coastal shrubs just above the high tide mark at the last two villages. Tierney *et al.* (2002) examined the biology of *M. zanzibarica,* which represents the most comprehensive study of sociality for this genus. Sociality and life history is similar to that of tropical halictines (Michener & Bennett 1977), with continuous brood development and alloparental care. Molecular justification for the basal phylogenetic position of *Macrogalea* combined with the discovery of well-developed sociality, *M. zanzibarica* displays the most female-biased sex ratios of any allodapine studied to date, greatly altered the view of allodapine social evolution (Schwarz *et al.* 2003; Tierney *et al.* 2002). Where it was previously assumed that social

behaviour evolved from within the extant members of the tribe, it became apparent that complex social interactions were attained prior to the radiation of the contemporary representatives. It is likely then that allodapine social behaviour is of ancient origin and has persisted for an extensive period.

Molecular evidence for species status

Initial reviews of *Macrogalea* and other African taxa (Michener 1971, 1975) suggested only three species, *M. candida* and its social parasite *M. mombasae,* both from mainland East Africa, and a single species *M. ellioti* from Madagascar. A later revision of Malagasy allodapines (Michener 1977b) recognized a second species, *M. infernalis,* and subsequent work by Pauly *et al.* (2001) described a further four novel species from that island, *M. scaevolae, M. antanosy* and probable parasites *M. berentyensis* (host *M. ellioti*), *M. maizina* (host *M. antanosy*). Michener (1971) discussed the existence of problematic morphotype complexes where species distinctness is not clear and this problem also exists for some Australian exoneurine groups (M.P. Schwarz, pers. obs.). It therefore seems advisable to determine whether apparent species distinctiveness, based on morphological characters, is supported by DNA sequence data.

Pairwise uncorrected 'p' distances were calculated, using PAUP* 4.0b9 (Swofford 1999), between *M. magenge, M. candida* and *M. zanzibarica* for each of three gene fragments from cytochrome oxidase I (*COI*), cytochrome oxidase *b* (*Cyt b*) and elongation factor 1-α (*EF1-α*) and compared with intra-generic species pairwise distances for several other allodapine genera. Gene fragments were 620, 429 and 457 nucleotides in length, respectively. Primers, DNA extraction, purification, and sequencing protocols are described in Schwarz *et al.* (2003). In order to compare genetic distances between *Macrogalea* species with those of other allodapine taxa, 18 species from *Allodape (A. exoloma, A. mucronata, A. skaifeorum), Braunsapis (B. paradoxa, B. pictarsis, B. protuberans, B. trochanterata, B. unicolor, B. vitrea), Brevineura (B. froggatti, B. ploratula, B. xanthoclypeata), Exoneura (E.angophorae, E. robusta),* and *Exoneurella (E. eremophila, E. lawsoni, E. setosa, E. tridentata)* were chosen, allowing 31 intra-generic pairwise comparisons. Of these genera, we chose only species where morphological characters clearly indicate species distinctness. DNA sequences for taxa used in this study are registered with GenBank: *Macrogalea magenge* EF1-α, AY245174; COI, AY245175; Cyt *b*, AY245176; see Schwarz *et al.* (2003) for accession numbers of remaining species.

Table 1. Base pair distance matrix (uncorrected 'p' values) for nuclear (*EF1-α*) and mitochondrial (*COI* & *Cyt b*) gene fragments of *Macrogalea magenge, M. candida* and *M. zanzibarica.*

		COI & *Cyt b*		
		M. magenge	*M. candida*	*M. zanzibarica*
EF1-α	*M. magenge*		0.05681; 0.08647	0.06159; 0.07710
	M. candida	0.00656		0.04382; 0.06077
	M. zanzibarica	0.00875	0.00221	

The genetic distances between *M. magenge* and *M. candida* or *M. zanzibarica* are greater than between *M. candida* and *M. zanzibarica* for both nuclear and mitochondrial regions, which is concordant with phylogenetic studies (Schwarz *et al.* 2003) showing that *M. magenge* is the basal-most species among these three. As expected from previous work on relative nucleotide substitution rates in allodapine bees (Schwarz *et al.* 2003), genetic distances are greatest for *Cyt b* and smallest for the nuclear gene *EF1-α*. Table 1 shows that for mitochondrial sequences, *M. magenge* differs from *M. candida* and *M. zanzibarica* by 5.7 % and 6.2 % for *COI*, and 8.6 % and 7.7 % for *Cyt b,* while for the same regions *M. candida* and *M. zanzibarica* differ by only 4.4 % and 6.1 %, respectively. The same trend can also be seen for the slower evolving *EF1-α*, where *M. magenge* differs more from *M. candida* (0.7 %) and *M. zanzibarica* (0.9 %) than the latter two differ from each other (0.2 %).

While there is no consensus on what degree of genetic distance is expected for biological species, and any measure of base pair divergence will clearly vary across genes and gene regions, intra-generic pairwise comparisons within the tribe Allodapini are likely to be useful in deciding whether species divergences in one genus are comparable with those for other genera. Figure 5 shows the range of distance values found within five allodapine genera, using data from Bull *et al.*'s (2003) study. These genera represent the full geographic range of Allodapini: *Macrogalea* + *Allodape* are restricted to Africa; *Brevineura* + *Exoneurella* + *Exoneura* are endemic to Australia; with representative *Braunsapis* taxa present in

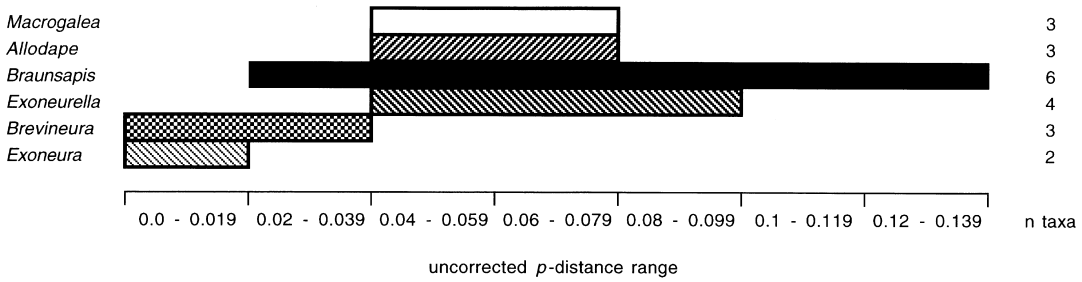


Fig 5. Intra-generic genetic distance ranges of allodapine bees. Representative taxa from Africa (*Macrogalea*, *Allodape*), Australia (*Exoneurella*, *Brevineura* and *Exoneura*) and the widely distributed *Braunsapis* are included. The number of taxa from each genus is indicated at the far right of the figure and species names are listed in the text.

both these continents and South East Asia. For the limited taxon set used here, *Braunsapis* exhibits the greatest intra-generic variation, the Australian exoneurines show the least divergence, and the endemic African clades are intermediate (Fig. 5). Intra-generic distance values for *Macrogalea* exist within the mid-range of other intra-generic pairwise comparisons where species distinctness based on morphological taxonomy (Michener 1965, 1975, 2000) is very clear.

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