# A Redescription of Merenius alberti Lessert, 1923 (Araneae:Corinnidae), with Remarks on Colour Polymorphism and Its Relationship to Ant Models

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# A redescription of *Merenius alberti* Lessert, 1923 (Araneae: Corinnidae), with remarks on colour polymorphism and its relationship to ant models

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## ABSTRACT

The ant-like sac spider *Merenius alberti* Lessert, 1923, previously known only from South Africa, is redescribed. The species is recorded for the first time from Mozambique, Swaziland and Zimbabwe. While most populations of *M. alberti* conform to the typical black morph of the species, a red morph is also reported here, providing the first case of colour polymorphism in an Afrotropical ant-like castianeirine spider. Spiders were collected by hand, and ants by pitfall trapping in the Ndumo Game Reserve in northern KwaZulu-Natal, South Africa, to identify the potential models of the two colour morphs of *M. alberti*. The ants collected at 20 sites in the reserve suggest that the black morph is a generalised mimic of black ground-dwelling ants, most likely *Camponotus cinctellus* (Gerstäcker, 1859), *Streblognathus peetersi* Robertson, 2002 and *Polyrhachis gagates* F. Smith, 1858, while the red morph is a mimic of *Anoplolepis custodiens* (F. Smith, 1858) ants.
KEY WORDS: Castianeirinae, Formicidae, habitat, mimicry, Ndumo Game Reserve, southern Africa.

## INTRODUCTION

Ant mimicry is a widespread occurrence among many unrelated spider families but is usually only encountered in a small proportion of the species diversity of each (Cushing 1997, 2012). The diversity of mimics is greatest in three families of hunting spiders, the Salticidae (jumping spiders), Corinnidae, especially the subfamily Castianeirinae (ant-like sac spiders), and the Zodariidae, particularly Zodariinae (ant-eating spiders). Despite the development of mimicry devices in many genera of these higher taxa, species of Castianeirinae usually employ one of three mimicry strategies (Reiskind 1969): (1) have a broad-based mimicry strategy, resembling, for example, large brown or black ants; (2) subfamilial or generic ant mimics, and (3) resembling a single species of ant, with which their mimetic modifications are particularly specialised to associate with a particular ant. Little is known of whether castianeirines are aggressive mimics and feed on their models, or whether they are merely Batesian mimics.

During fieldwork in the Ndumo Game Reserve (NGR) in northern KwaZulu-Natal, South Africa, as part of an arachnid biodiversity survey, six species of ant mimicking castianeirine spiders were found (Haddad *et al.* 2006). *Apochinomma formicaeforme* Pavesi, 1881 is an accurate mimic of *Polyrhachis gagates* F. Smith, 1858 ants (Fig. 7), while *Corinnomma semiglabrum* (Simon, 1896) and *C. lawrencei* Haddad, 2006 are inaccurate mimics of *P. gagates* and *Camponotus cinctellus* (Gerstäcker, 1859) (Fig. 8) ants. The two undetermined, possibly new *Castianeira* species recorded from the reserve show contrasting strategies. One species is polymorphic, with a red morph (widespread in southern Africa) that mimics *Anoplolepis custodiens* (F. Smith, 1858) (Fig. 9) ants, and a black morph (widespread in the eastern half of Africa) that mimics *C. cinctellus* ants. The smaller second species seems to be an accurate mimic of *Pheidole* ants. Quite often the distribution of these castianeirines overlaps as populations of their respective models overlap.

The sixth ant-mimicking corinnid species, *Merenius alberti* Lessert, 1921, was the most common castianeirine species occurring in leaf litter in most of the habitats in NGR, particularly in woodlands and sand forest, and is an exclusive ground-dwelling spider. During the first three years of the survey (2000–2002), all specimens collected were of the "typical" colouration that is found in eastern southern Africa, being black with cream or blue-grey markings on the body (Figs 1–3, 5). This morph is an inaccurate mimic that resembles several black ground-dwelling ants, including *P. gagates*, *C. cinctellus* and *Streblognathus peetersi* Robertson, 2002 (Fig. 10). This is the only colour morph observed in museum specimens from more than 50 localities in southern Africa. During 2003 and 2004, two *M. alberti* populations were discovered in NGR (Dipini Hide and Ezikebheni) having a red carapace and grey abdomen with cream markings (Figs 4, 6), which represented the first records of this colour morph. These populations were



Figs 1–6. General habitus of *Merenius alberti* Lessert, 1923 females from Ndumo Game Reserve, South Africa (1, 4–6), iSimangaliso Wetlands Park, South Africa (2) and Sodwana Bay, South Africa (3): (1–3, 5) common black colour morph; (4, 6) scarce red colour morph.
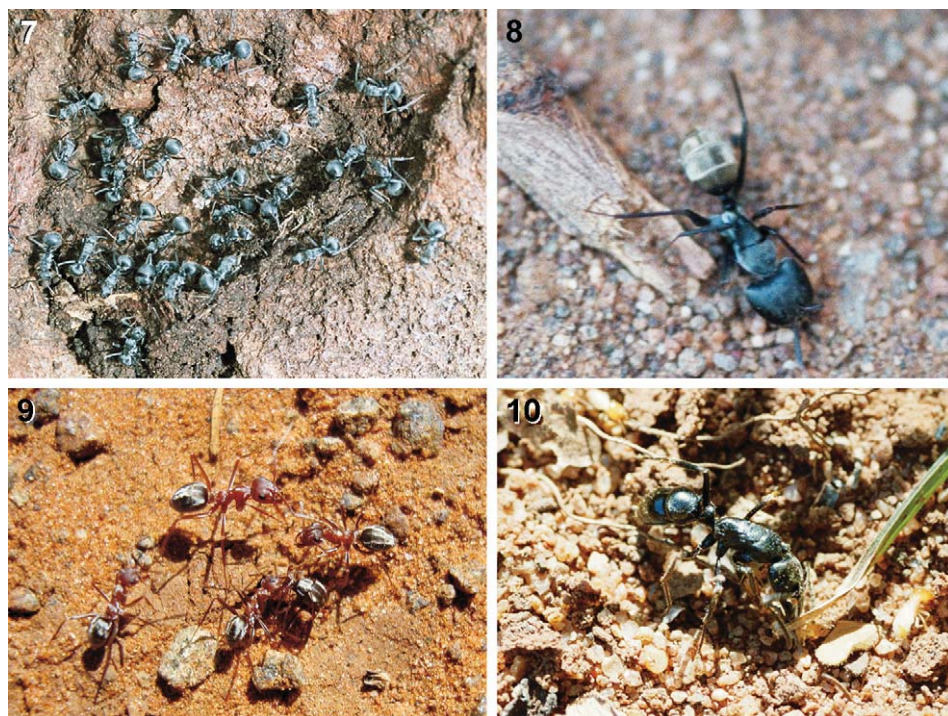
Figs 7–10. General habitus of ants from Ndumo Game Reserve, South Africa: (7) *Polyrhachis gagates* F. Smith, 1858; (8) *Camponotus cinctellus* (Gerstäcker, 1859); (9) *Anoplolepis custodiens* (F. Smith, 1858); (10) *Streblognathus peetersi* Robertson, 2002.

only found in association with colonies of *A. custodiens* ants. Subsequent sampling in the Kruger National Park forming part of an MSc study (Harris 2009; Roberston *et al.* 2011) lead to the discovery of an additional population of the red morph, found amongst specimens of the typical black colour morph. The occurrence of two distinctly different colour morphs mimicking different ants in such close proximity to one another is quite remarkable, and warranted further investigation into the role of ant assemblage composition on the occurrence of each morph.

*Merenius alberti* shows restricted capability to mimicking its models. Adaptations are restricted to the adaptive colouration of their models, as no morphological modifications of the carapace and abdomen are evident, with the exception of gravid females that have a swollen abdomen reminiscent of that of *P. gagates*. The legs of both colour morphs have dark stripes typically found in mimetic castianeirines (Figs 1–6). In contrast, more specialised castianeirine mimics in the genera *Apochinomma* Pavesi, *Mazax* O.P.-Cambridge, *Myrmecium* Latreille, *Myrmecotypus* O.P.-Cambridge, *Pranburia* Deeleman-Reinhold and *Sphecotypus* O. P.-Cambridge (Reiskind 1969; Oliveira 1988; Deeleman-Reinhold 2001) have constricted or elongate carapaces, distinct elongate petioles, and globose or constricted abdomens, sometimes with modified spines or setae. From a behavioural point of view, *M. alberti* runs in rapid short, darting bursts, and when stationary, moves its front legs up and down to simulate movements of the antennae of ants.

In this paper, *M. alberti* is redescribed and scanning electron microscopy is used to provide details of the morphology of the species. Quantitative data on the abundance of the two morphs of *M. alberti* and their potential ant models within NGR is presented to explain the occurrence of each morph. Habitat structure as an influence determining the spatial distribution of ants and their mimics is also considered.

## MATERIAL AND METHODS

*Taxonomy*

All spiders were examined under a Nikon SMZ800 stereomicroscope. Female genitalia were dissected from the abdomen using fine entomological pins, placed in a small vial in 70 % ethanol and cleared for 1 minute in a Labcon 5019U ultrasonic bath. Genitalia were observed for illustrations in 70 % ethanol. Dissected genitalia were placed in microvials together with the specimens from which they had been removed. A range of total length measurements is provided to indicate size variation, and descriptions of the eye arrangements are given for the anterior view of the anterior eye row and dorsal view of the posterior eye row. The length of leg segments is given from the femur to tarsus, and total. All measurements are given in millimetres.

The following abbreviations are used in the redescription: AER – anterior eye row, AL – abdomen length, ALE – anterior lateral eye, ALS – anterior lateral spinneret(s), AME – anterior median eye, AW – abdomen width, CL – carapace length, CW – carapace width, FL – fovea length, MOQAW – median ocular quadrangle anterior width, MOQL – median ocular quadrangle length, MOQPW – median ocular quadrangle posterior width, PER – posterior eye row, PERW – posterior eye row width, PLE – posterior lateral eye, PLS – posterior lateral spinneret(s), PME – posterior median eye, PMS – posterior median spinneret(s), SL – sternum length, ST – spermatheca, SW – sternum width, TL – total length. Leg spination follows the format of Bosselaers and Jocqué (2000) and includes the following abbreviations: do – dorsal, pl – prolateral, plv – prolateral ventral, rl – retrolateral, rlv – retrolateral ventral, vt – ventral terminal.

Material of both sexes of both colour morphs of *M. alberti* was prepared through a graded ethanol series and then critical point dried in an argon chamber. Material was then mounted on stubs and sputter-coated three times for 3 min. with gold before observation in a JEOL WinSEM 6400 at 10 kV. Digitised micrographs were taken. Digital photographs of the general habitus of males and females of both colour morphs were taken using a Nikon Coolpix 8400 camera mounted on a Nikon SMZ800 stereomicroscope.

Material of *M. alberti* from the following collections was examined or was identified as part of general Corinnidae loans (curators in parenthesis):

MHNG – Museum of Natural History, Geneva, Switzerland (Peter Schwendinger);
MRAC – Royal Museum for Central Africa, Tervuren, Belgium (Rudy Jocqué);
NCA – National Collection of Arachnida, ARC–Plant Protection Research Institute, Pretoria, South Africa (Ansie Dippenaar-Schoeman);
NMSA – KwaZulu-Natal Museum, Pietermaritzburg, South Africa (Audrey Ndaba);
NMZA – National Museum of Zimbabwe, Bulawayo, Zimbabwe (Moira FitzPatrick);
SAMC – Iziko South African Museum, Cape Town, South Africa (Margie Cochrane);
TMSA – Ditsong National Museum of Natural History, Pretoria, South Africa (Robin Lyle).

Sometimes locality co-ordinates were not provided on specimen labels or were not available in the institutional databases, in which case they were traced using the Global Gazetteer Version 2.2 (www.fallingrain.com) and are indicated in square brackets. The distribution map was produced using the online mapping software SimpleMappr (Shorthouse 2010).

*Frequency of colour morphs relative to ant assemblages*

To assess the relationship between the frequencies of the two colour morphs of *M. alberti* relative to the local abundance of potential ant models, sampling was conducted in the NGR, a small savanna reserve (10112 ha or 101 km$^2$) situated on the Maputaland coastal plain in South Africa (Fig. 11). A wide variety of habitats is conserved within the reserve, 16 in total (De Moor *et al.* 1977), including various woodland and savanna types, floodplain habitats and sand forest. The floodplain habitats are of particular importance, and consequently the reserve is considered as a RAMSAR site of international importance (Ramsar 2010). During the arachnid biodiversity survey (Haddad *et al.* 2006), these habitats were grouped into eight broad habitat types, namely: *Acacia tortilis* savanna (AS), *Acacia xanthophloea* forests around pans (AX), Deciduous broadleaf woodland (BW), *Ficus sycomorus* forest (FF), Floodplain vegetation near the Pongola and Usutu rivers (FP), Riparian forests along Pongola and Usutu rivers (RF), Sand forest (SF), and Subtropical bush. For the purposes of the current study, subtropical bush was subdivided into three further habitat types: *Acacia nigrescens* woodland (AW), *Albizia−Euphorbia* thicket (AE), and Mahemane thicket (MT). A base map to indicate the sampling sites was provided by Cathariné Hanekom of Ezemvelo KZN Wildlife.

During June−July (winter) and November−December (summer) 2009, pitfall traps were set out to sample epigeic ants for a period of 10 days at two sites in each of the 10 habitats listed above. The two habitat sampling sites were separated by at least 1 km to avoid pseudoreplication (Fig. 11). Five pitfalls (diameter of 10 cm) were set out 5 m apart in a straight line at each site and filled with 100 ml of ethanediol as a preservative. The collected material from each site was removed after the 10 days of sampling and the ants were extracted from each sample, pooled together by site, and preserved in 70 % ethanol for later identification in the laboratory. Ants were identified using the online resources "The Ants of Africa" (Taylor 2011), which has keys to the subfamilies, genera and species of African ants, and "AntWeb" (Fisher 2002), which provides supplementary figures and original descriptions of ants.

During each of these sampling periods, *M. alberti* were collected at each site by hand in leaf litter, under logs or at the base of grass tussocks. Twenty individuals were collected at each sampling site in the vicinity of the pitfall traps to determine the proportion of red:black variants. Hand collecting for *M. alberti* was preferred to pitfall trapping, as previous experience using pitfalls in NGR yielded very few *M. alberti* individuals relative to sampling effort. Preference was given to adult individuals, but when adults were scarce, subadults or immatures were also collected. If no *M. alberti* were collected during three hours of searching, or if sites were inaccessible due to flooding, a site was abandoned. This was the case at two sites during winter (AN1 and AX1, no *M. alberti*) and four during summer (no *M. alberti* at AS2 and AX1, RF1 and RF2 flooded). Collected individuals were pooled for each site, preserved in 70 % ethanol, and the proportions of each colour morph were noted in the laboratory. The collected material has been deposited in the collection of TMSA (voucher numbers TMSA 24068−24101).

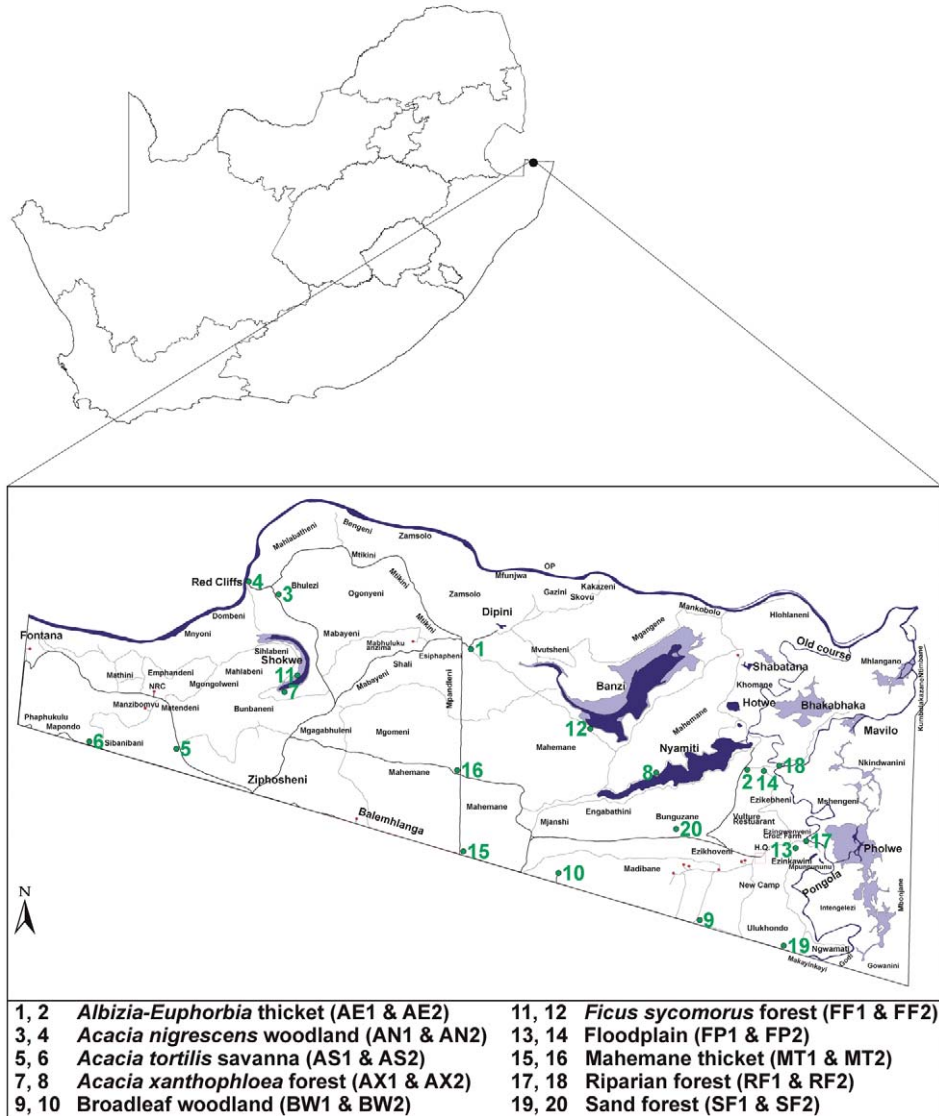| 1, 2 | *Albizia-Euphorbia* thicket (AE1 & AE2) | 11, 12 | *Ficus sycomorus* forest (FF1 & FF2) |
| 3, 4 | *Acacia nigrescens* woodland (AN1 & AN2) | 13, 14 | Floodplain (FP1 & FP2) |
| 5, 6 | *Acacia tortilis* savanna (AS1 & AS2) | 15, 16 | Mahemane thicket (MT1 & MT2) |
| 7, 8 | *Acacia xanthophloea* forest (AX1 & AX2) | 17, 18 | Riparian forest (RF1 & RF2) |
| 9, 10 | Broadleaf woodland (BW1 & BW2) | 19, 20 | Sand forest (SF1 & SF2) |

Fig. 11. Map of South Africa indicating the location of Ndumo Game Reserve, with enlarged map indicating the 20 sites sampled for *Merenius alberti* Lessert, 1923 and the resident ant assemblages that may serve as their models.

RESULTS

*Taxonomy*

Genus *Merenius* Simon, 1910

*Merenius alberti* Lessert, 1923

Figs 1–6, 12–49

*Merenius alberti*: Lessert 1923: 192, figs 38–41.

Redescription:

*Female* (Ndumo, TMSA 24067).

Measurements: CL 4.35, CW 2.65, AL 4.10, AW 2.25, TL 8.15 (6.55–10.05), FL 0.36, SL 1.85, SW 1.36, AME–AME 0.10, AME–ALE 0.03, ALE–ALE 0.42, PME–PME 0.16, PME–PLE 0.14, PLE–PLE 0.73, PERW 0.94, MOQAW 0.37, MOQPW 0.44, MOQL 0.45.

Length of leg segments: I 2.60+1.10+2.25+2.18+1.55=9.68; II 2.33+1.08+1.88+1.96+ 1.37=8.62; III 2.30+1.04+1.67+2.10+1.03=8.14; IV 3.32+1.35+2.93+3.65+1.37= 12.62.

General appearance as in Fig. 12. Carapace dark brown, eye region darker, with black striae radiating from fovea; surface finely granulate, densely setose, white feathery setae forming broad median stripe from cephalic region, narrowed towards posterior margin, black feathery setae forming paired stripes mediolaterally from ⅓ carapace length to posterior, lateral margins with white feathery setae; several long curved setae on clypeus, eye region and along midline posterior to PER; carapace oval-elongate, broadest at posterior of coxae II, highest at ⅔ carapace length, eye region slightly narrowed; fovea distinct, short and narrow; posterior margin slightly concave. All eyes with black rings; AER procurved, laterals slightly larger than medians; AME separated by distance approximately ¾ their diameter; AME separated from ALE by distance approximately ¼ AME diameter; clypeus height approximately double AME diameter; chilum single, triangular; PER slightly recurved, nearly straight, medians very slightly larger than laterals; PME separated by distance slightly larger than their diameter; PME separated from PLE by distance equal to PLE diameter; CW:PERW = 2.82:1. Chelicerae dark
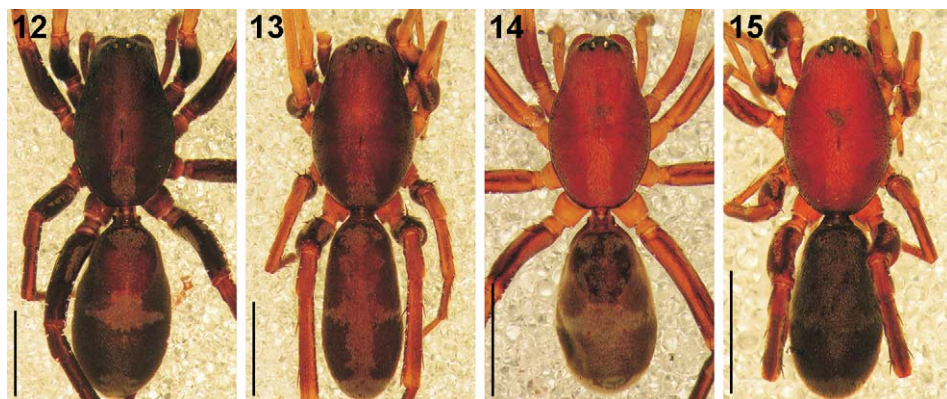


Figs 12–15. Light microscope photographs of *Merenius alberti* Lessert from Ndumo Game Reserve: (12) female, black morph; (13) male, black morph; (14) female, red morph; (15) male, red morph. Scale bars = 2.0 mm.

orange-brown with black mottling, paler proximally retrolaterally, distally prolaterally and on posterior surface of paturon, with long, erect straight setae on anterior surface and pectinate curved setae on fang promargin (Fig. 16); three teeth on promargin, distal tooth smallest, median tooth largest; median and distal teeth adjacent; retromargin with two teeth, distal tooth slightly smaller than proximal tooth. Endites dark yellow-brown with black mottling, white at distinct serrula and maxillar hair tuft; labium yellow-brown,
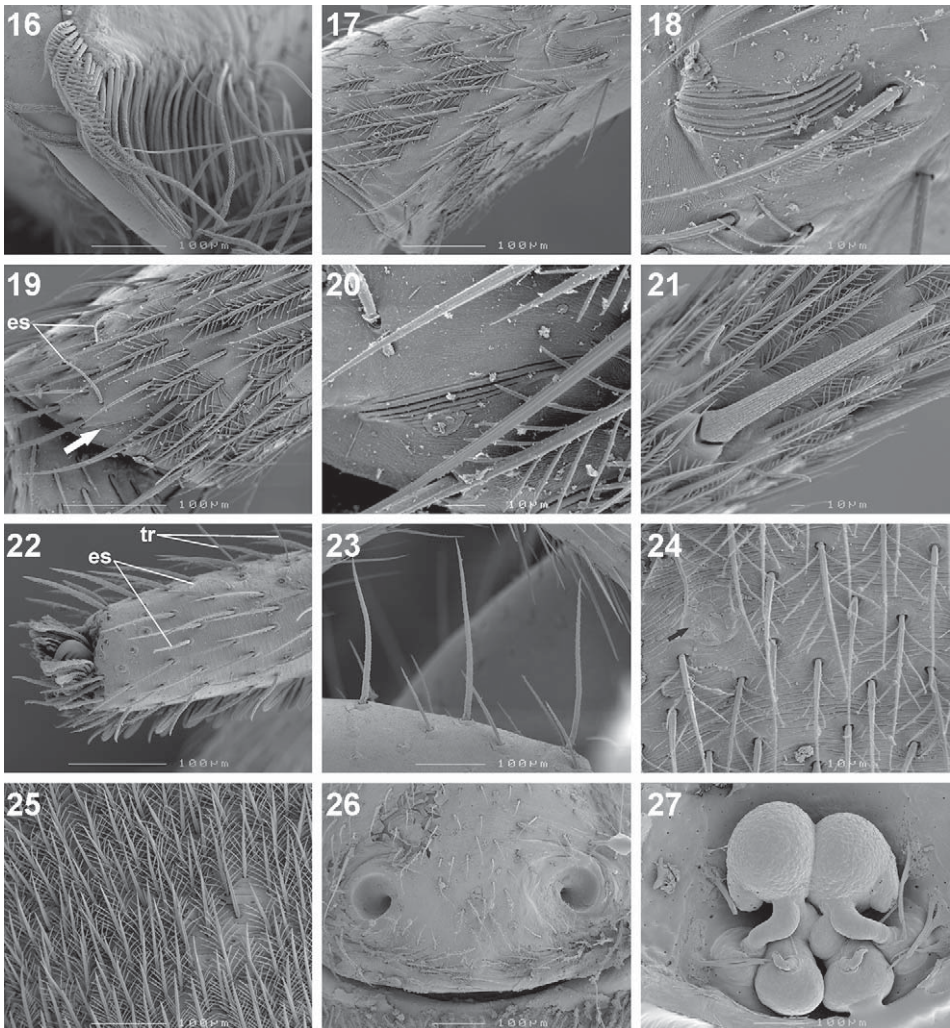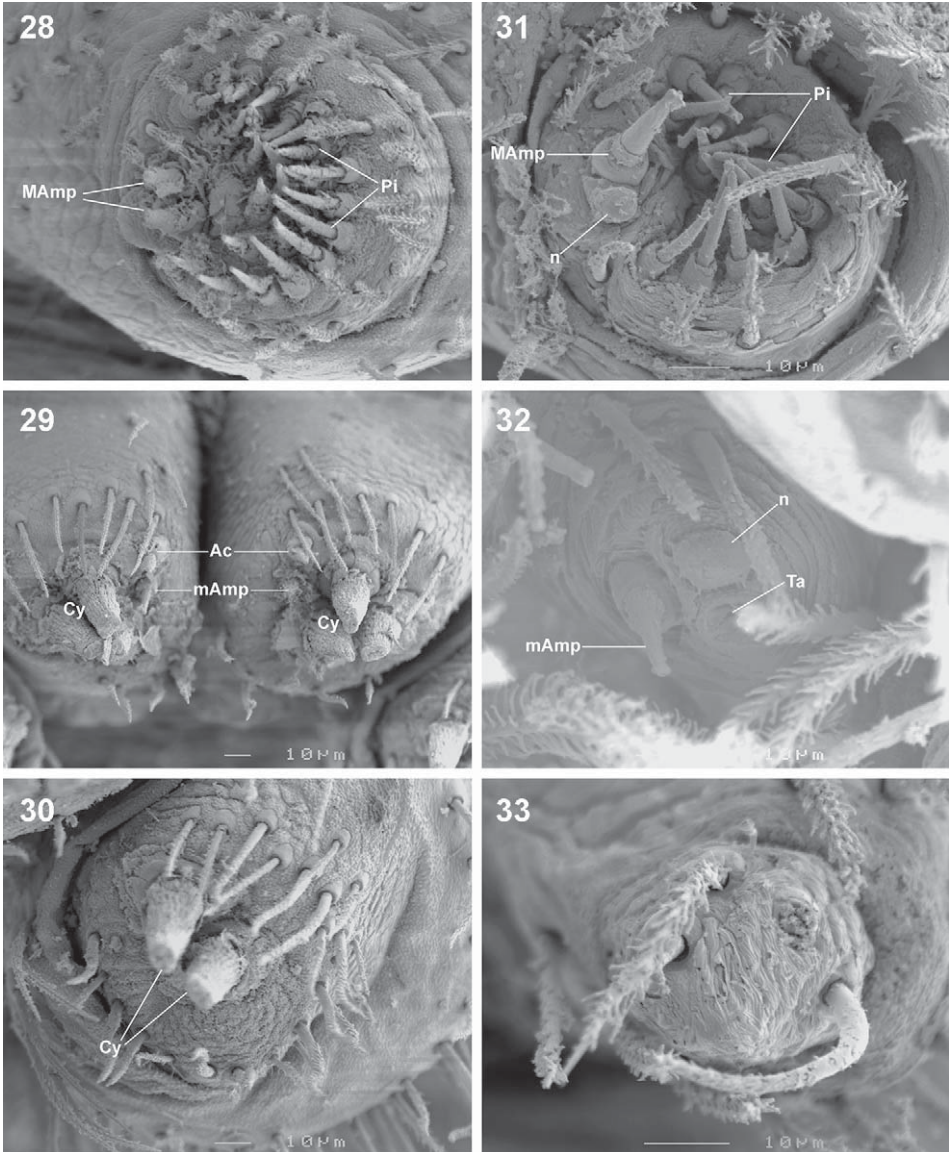


Figs 16–27. Scanning electron microscope photographs of *Merenius alberti* Lessert female: (16) cheliceral promarginal bent setae, anterior view; (17) leg I, patellar indentation (PI); (18) same, detail of proximal end of PI; (19) tibiae I, retrolateral view, indicating slit sensilla (arrow) and short erect setae (es); (20) same, detail of slit sensilla; (21) metatarsus III, spine and feathery setae; (22) tarsus II, indicating short erect setae (es) and trichobothria (tr); (23) palpal femur, erect ventral setae; (24) dorsal abdominal setae, arrow indicating sigillum; (25) same; (26) epigyne, ventral view; (27) same, dorsal, slightly lateral view.

white distally, trapezoidal with slightly concave distal margin; sternum shield-shaped, rebordered, orange-brown with black mottling, with scattered long erect and short straight setae and white feathery setae; intercoxal sclerites present between all coxal pairs; precoxal triangles present; pleural bars isolated. Leg formula 4123; legs covered in black and white feathery and short straight setae corresponding with markings, with short leg spines on femora, tibiae and metatarsi, and trichobothria and short erect white setae on tibiae, metatarsi and tarsi (Figs 17–21); feathery setae absent on tarsi, claw tufts dense (Fig. 22); coxae finely granulate, yellow-brown with black mottling, coxae I and IV slightly darker; femora black, yellow distally, with prolateral, retrolateral and ventral white stripes, markings fused proximally on ventral side; patellae I and II yellow with black mottling dorsally, proximally and laterally; patellae III and IV yellow-brown with black mottling, III with broken white prolateral stripe and unbroken white retrolateral stripe along length of patella, IV with unbroken white stripes pro- and retrolaterally along length of patella; patellar indentation narrow, broadened proximally (Figs 17, 18); tibiae I and II uniform yellow, with dorsal, prolateral ventral and retrolateral ventral black stripes, fainter on tibia I; tibia III yellow with black mottling, with dorsal, prolateral ventral and retrolateral ventral black stripes; tibia IV yellow-brown, distal end yellow, with prolateral and retrolateral black stripes; tibiae with distal retrolateral slit sensilla (Figs 19, 20); metatarsi I and II uniform yellow; metatarsus III yellow and IV yellow-brown, both with black mottling, with retrolateral black stripe running the length of metatarsi; tarsi all uniform yellow. Leg spination: femora: I pl 1 do 3, II pl 1 do 3, III pl 2 do 3 rl 1, IV pl 2 do 3 rl 1; patellae: all with single long fine distal seta; tibiae: I plv 2 rlv 1, II rlv 1, III pl 2 do 1 rl 2 plv 2 rlv 2 vt 2, IV pl 2 do 1 rl 2 plv 2 rlv 2 vt 2; tibiae I and II with single long fine seta near distal end; metatarsi: I plv 2 rlv 2, II plv 2 rlv 2, III pl 3 rl 3 plv 1–2 rlv 2 vt 3, IV pl 3 rl 3 plv 2 rlv 2 vt 3. Palpal spination: femora: pl 1 do 2, with rlv 7 erect ventral spines (Fig. 23); patellae: pl 1; tibiae: pl 1 do 2 plv 1; tarsi: pl 1 rl 1 plv 2 rlv 1. Abdomen oval, with short sclerotised petiole, three pairs of erect setae on anterior margin and red-brown dorsal scutum extending 0.4 abdomen length; two pairs of distinct sigilla present (Fig. 24), first just behind margin of scutum and second at 0.6 abdomen length; dorsum black, with broad symmetrical irregular cream marking medially, broken at ¾ abdomen length (sometimes not in several specimens), triangular posterior cream marking and white spot of dense setae above spinnerets; sides of abdomen black, with triangular cream marking above epigastric furrow, fused to diamond-shaped median marking; dorsum densely covered in black and cream feathery setae corresponding to markings, with scattered short straight setae; venter pale mottled grey, covered in short straight black setae with sparse feathery setae; ventral sclerite absent, post-epigastric and inframamillary sclerites present, weakly sclerotised; two paired rows of tiny sclerites from epigastric furrow to spinnerets, outer row much smaller and less sclerotised. Spinnerets: ALS with two major ampullate gland spigots and many piriform gland spigots (Fig. 28); PMS with three large cylindrical gland spigots, one small minor ampullate gland spigot and one aciniform gland spigot (Fig. 29); PLS with two large cylindrical gland spigots only (Fig. 30). Epigyne with small circular coiled epigynal ridges with prolateral copulatory openings (Figs 26, 46); copulatory ducts short, sharply bent medially before entering ST II along their posterior margin; anterior ST II round, with posterolateral projection of varying size, broadly connected to smaller kidney-shaped posterior ST I; ST I clearly narrower than ST II (Figs 27, 47).

*Male* (Ndumo, TMSA 24067).

Measurements: CL 3.35, CW 2.10, AL 3.50, AW 1.72, TL 6.60 (5.80–9.60), FL 0.23, SL 1.48, SW 1.15, AME–AME 0.07, AME–ALE 0.02, ALE–ALE 0.33, PME–PME 0.13, PME–PLE 0.09, PLE–PLE 0.54, PERW 0.74, MOQAW 0.30, MOQPW 0.38, MOQL 0.39.



Figs 28–33. Scanning electron microscope photographs of *Merenius alberti* Lessert female (28–30) and male (31–33) spinneret morphology: (28, 31) anterior lateral spinneret; (29, 32) posterior median spinneret; (30, 33) posterior lateral spinneret. Abbreviations: Ac – aciniform gland spigot(s); Cy – cylindrical gland spigot(s); MAmp – major ampullate gland spigot(s); mAmp – minor ampullate gland spigot(s); n – nubbin; Pi – piriform gland spigot; ta – tartipore.

Length of leg segments: I 1.88+0.76+1.68+1.66+1.31=7.29; II 1.73+0.73+1.38+1.41+ 1.06=6.31; III 1.70+0.75+1.25+1.56+0.84=6.10; IV 2.50+0.98+2.20+2.73+1.20=9.61. General appearance as in Fig. 13, more slender than female. Carapace dark brown, nearly black, eye region darker, with black mottling and striae radiating from fovea; markings, setae and carapace proportions as for female. All eyes with black rings; AER procurved, laterals slightly larger than medians; AME separated by distance slightly larger than ½ their diameter; AME separated from ALE by distance approximately ¼ AME diameter; clypeus height slightly more than double AME diameter (Fig. 34);
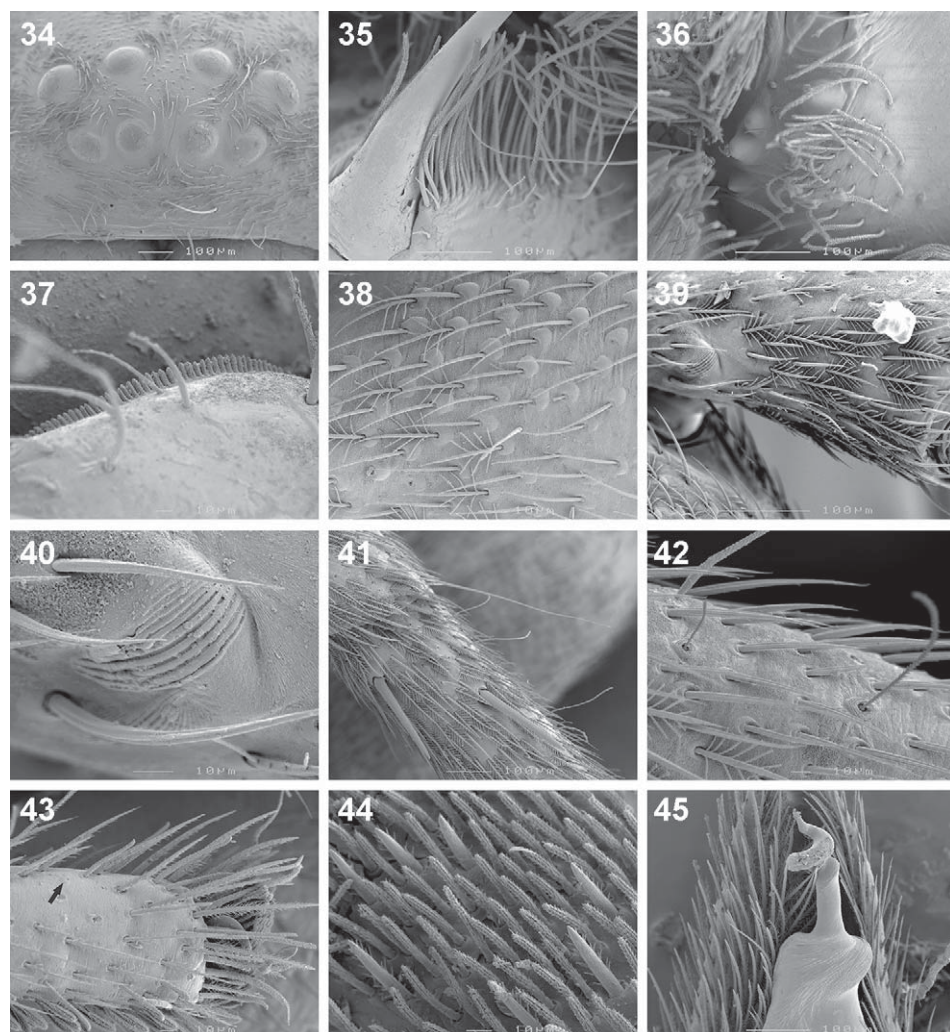


Figs 34–45. Scanning electron microscope photographs of *Merenius alberti* Lessert male: (34) eye region, anterior view; (35) promarginal bent setae, anterolateral view; (36) chelicera, ventral view; (37) serrula; (38) femur I, feathery setae; (39) leg II, patellar indentation (PI); (40) same, detail of proximal end of PI; (41) patella and tibia III setae and spines; (42) metatarsus I trichobothria and setae; (43) tarsus II, arrow indicating tarsal organ; (44) distal section of palpal cymbium; (45) embolus.

chilum single, triangular; PER slightly recurved, nearly straight, medians very slightly larger than laterals; PME separated by distance slightly less than their diameter; PME separated from PLE by distance equal to 0.6 PME diameter; CW:PERW = 2.84:1. Chelicerae dark red-brown with black mottling, yellow proximally retrolaterally, distally prolaterally and on posterior surface of paturon, with scattered long, erect straight setae on anterior surface and curved setae on fang promargin not pectinate (Fig. 35); cheliceral dentition (Fig. 36) as for female. Endites dark orange-brown with black mottling, yellow at distinct serrula (Fig. 37) and maxillar hair tuft; labium dark brown, cream distally, trapezoidal with slightly concave distal margin; sternum shield-shaped, rebordered, dark red-brown with black mottling, with dense white feathery setae and scattered long erect setae; intercoxal sclerites present between all coxal pairs; precoxal triangles present; pleural bars isolated. Leg formula 4123; leg setae, spines and claw tuft (Figs 38–43) and markings as for female, except colouration darker and more intense. Leg spination: femora: I pl 1 do 3, II pl 1 do 3, III pl 2 do 3 rl 1, IV pl 2 do 3 rl 1; patellae: all with single long fine distal seta (Fig. 41); tibiae: I plv 2 rlv 1, II rlv 1, III pl 2 do 1 rl 2 plv 2 rlv 2 vt 2, IV pl 2 do 1 rl 2 plv 2 rlv 2 vt 2; tibiae I and II with single long fine seta near distal end; metatarsi: I plv 2 rlv 2, II plv 2 rlv 2, III pl 3 rl 3 plv 2 rlv 2 vt 3, IV pl 3 rl 3 plv 2 rlv 2 vt 3. Palpal spination: femora: pl 1 do 2; patellae: pl 1; tibiae: pl 1 plv 1; tarsi: plv 2. Abdomen narrow, elongate-oval, with short sclerotised petiole (longer than in female), three pairs of erect setae on anterior margin and deep red-brown scutum
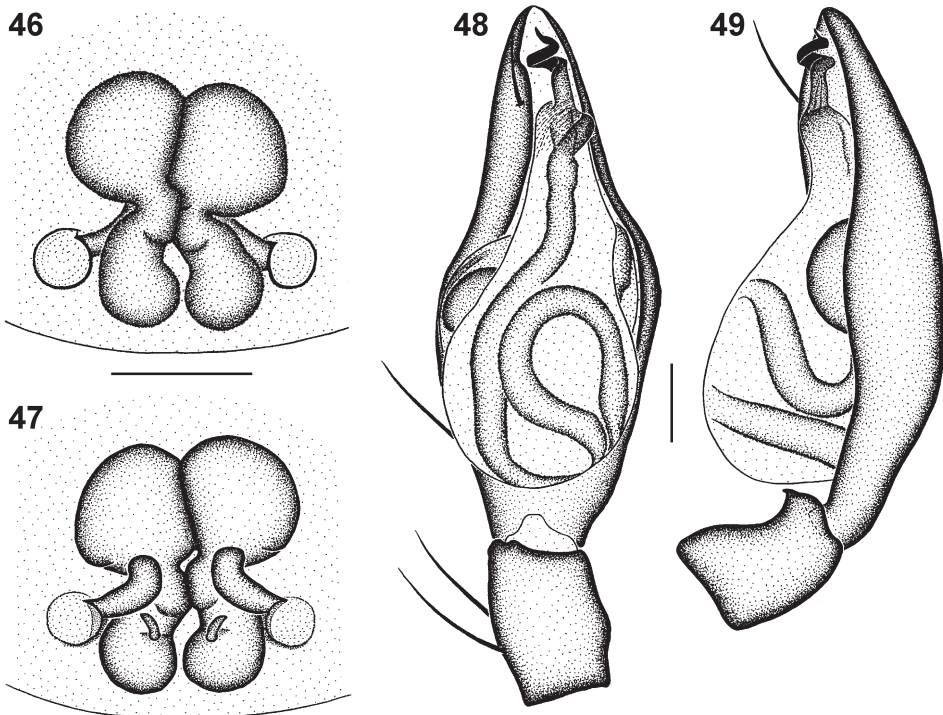


Figs 46–49. Genitalic morphology of *Merenius alberti* Lessert: (46, 47) female epigyne, ventral (46) and dorsal (47) views; (48, 49) male palp, ventral (48) and retrolateral (49) views. Scale bars = 0.25 mm.

covering entire dorsum; two pairs of distinct sigilla present, first at 0.4 and second at 0.6 abdomen length; dorsal and lateral setae and markings as for female; venter dark grey, covered in short straight black setae with sparse feathery setae; ventral sclerite present, deep red-brown, subrectangular, nearly extending to spinnerets; post-epigastric and inframamillary sclerites distinct, quite strongly sclerotised. Spinnerets: ALS with single major ampullate gland spigot, single large adjacent nubbin and many piriform gland spigots (Fig. 31); PMS with one minor ampullate gland spigot, one tartipore and one nubbin, without aciniform gland spigots (Fig. 32); PLS without functional spigots (Fig. 33). Male palpal cymbium dark brown, nearly black, densely setose, with many short thickened black rod-like setae in distal third dorsally (Fig. 44); palpal tegulum dark orange-brown with deep red-brown ducts; embolus with broad base, long stalk-like proximal section and single compressed distal coil (Figs 45, 48, 49).

Variation: The typical colour variant (black morph) of *M. alberti* described above consists of dark brown to black specimens that have cream or blue-grey markings comprising modified feathery setae (Figs 1–3, 5, 12, 13). A second colour variant reported here for the first time has a bright orange to deep red carapace with black integumental markings and cream markings identical to the black morph described above. The abdomen of the red morph is grey in colour and has cream markings identical to those of the black morph (Figs 4, 6, 14, 15). Juveniles with a light to dark brown carapace that were reared to maturity in the laboratory moulted into adults of the black morph, while juveniles with a bright yellow or orange carapace matured as the red morph, and thus the two colour forms can be recognised during all of their life stages.

Lectotype (here designated): ♀ SOUTH AFRICA: *KwaZulu-Natal*: Durban, Umbilo [29°53'S 30°59'E], L. Bevis (NMSA 18851).

Paralectotypes: 1♂ same data as lectotype (NMSA 18851); 1♂ palp 2♀ same data as lectotype (MHNG).

Other material examined: MOZAMBIQUE: 1♂ 2♀ 2 imm. Bilene, Praia do Bilene, 25°15.649'S 33°17.659'E, 27 m, leaf litter, coastal forest, 20.xii.2007, C. Haddad, R. Lyle & R. Fourie (NCA 2008/215); 1♂ Inhaca Island, 26°01'S 32°54'E, open parkland, 25.xii.1993–8.i.1994, T. Steyn, pitfalls (MRAC 209694); 1♂ same locality, wetland, 24.i–7.ii.1994, T. Steyn, pitfalls (MRAC 208955); 1♂ same data, 13–27.xii.1993 (MRAC 208967); 2♀ same data, 9–23.vii.1994 (MRAC 209210); 1♀ same data, 13–29.xi.1993 (MRAC 209314); 1♀ same data, 27.xii–10.i.1994 (MRAC 209361); 1♂ same data, 28.v–19.vi.1994 (MRAC 209720); 1♂ same data, 8–23.iv.1994 (MRAC 209744); 2♂ same data, 23–30.iv.1994 (MRAC 209788); 1♀ same data, 19–25.vi.1994 (MRAC 209797); 1♂ same data, 14–28.v.1994 (MRAC 209812); 1♂ same data, 30.iv–14.v.1994 (MRAC 209904); 1♀ same data, 25–30.viii.1994 (MRAC 215901); 1♀ same data, xii.1954, R.F. Lawrence (NMSA 7004); 1♀ near Marrucuene, Blue Anchor Inn, 25°35.124'S 32°39.568'E, 50 m, sifting leaf litter, savanna, 28.xi.2007, C. Haddad & R. Fourie (NCA 2008/170); 1♂ 1♀ 2 imm. near Marrucuene, Marrucuene Lodge, 25°46.379'S 32°41.046'E, 12 m, leaf litter, riverine forest, 1.xii.2007, C. Haddad (NCA 2008/172); 2♂ 3♀ 1 imm. Xai-Xai, Montego's Camp, 25°03.659'S 33°40.633'E, 28 m, leaf litter, dune forest, 2.xii.2007, C. Haddad (NCA 2008/182). SOUTH AFRICA: *Eastern Cape*: 2♂ Coffee Bay, 31°59.148'S 29°09.076'E, 5 m, base of grass tussocks, 9.i.2011, C. Haddad (NCA 2010/2745); 1♀ 3 imm. Cwebe Nat. Res., The Haven, 32°14.497'S 28°54.653'E, grassy litter behind dunes, 30.x.2006, C. Haddad (NCA 2007/247); 2♀ East London, 33°01'S 27°54'E, 15.iii.1985, D. Keetch, pitfalls (NCA 95/313); 1♀ 1 imm. Mazeppa Bay, 32°28.476'S 28°38.873'E, grassy litter, *Acacia* thicket behind dunes, 28.x.2006, C. Haddad (NCA 2007/202); 1♀ same locality, leaf litter, coastal dune forest, 28.x.2006, C. Haddad (NCA 2007/223); 1♀ Mkhambathi Nat. Res., 31°17.429'S 30°00.672'E, 16 m, grassland, 29.i.2008, Inland Invertebrate Initiative−University of KwaZulu-Natal, pan traps (NCA 2010/240); 1♂ 1♀ 1 imm. near Mazeppa Bay, 32°26.495'S 28°36.968'E, leaf litter, *Eucalyptus* plantation, 28.x.2006, C. Haddad (NCA 2007/277). *Gauteng*: 1♀ 1 imm. Johannesburg, Florida, 26°30'S 27°54'E, xii.1918, R. Tucker (SAMC ENW-C005347). *KwaZulu-Natal*: 1♂ Cathedral Peak, 28°58.054'S 29°15.832'E, 1910 m, active ground searching, 19.xi.2005, Maluti-Drakensburg Transfrontier Project staff (NCA 2008/1912); 1♀ Charter's Creek, Lake St Lucia, 28°12'S 32°26'E, forest, 19–21.xi.1985, J. Doyen & C. & T. Griswold (NMSA 22032); 1♂ same data, moulted in captivity (NMSA 22033); 2♀ Charter's Creek camp, Lake St Lucia, 2832Ab, 60 m, 3–11.x.1977, J.G.H. Londt (NMSA 22029); 1♂ 3♀ Dukuduku Forest [28°22'S 32°19'E], xi.1957, R.F. Lawrence (NMSA 6966);

1♀ Durban, Stella Bush [29°51'S 31°00'E], i.1915, W. Bell Marley (SAMC B891); 1♀ E side of Lake Sibaya [27°22'S 32°42'E], nest under bark of trees, 27.vi.1967, B.H. Lamoral (NMSA 9570); 1♂ Empangeni, 28°45'S 31°54'E, 2.iv.1979, P. Reavell (NMSA 12765); 1♀ same locality, pool, 27.iii.1983, P. Reavell (NMSA 22026); 1♂ same locality, in garden, xii.1986, P. Reavell (NMSA 22030); 1♀ same locality, leaf litter in garden, 30.iv.1988, P. Reavell (NMSA 22031); 1♂ 1♀ Enseleni Nat. Res., 28°41'S 32°03'E, *Ficus-Barringtonia* swamp forest, 19.i.1986, C.E. Griswold & T. Meikle-Griswold (NMSA 22028); 1♂ 1♀ Gwaliweni, north of Jozini Dam, 27°23'S 32°03'E, ii.1957, R.F. Lawrence (NMSA 6887); 2♀ Hluhluwe [28°02'S 32°17'E], x.1953, R.F. Lawrence (NMSA 6872); 2♀ 3 imm. Hluhluwe-Imfolozi Park, Hilltop Research Station, 28°04.680'S 32°02.472'E, leaf litter, Afromontane forest, 20.iv.2006, C. Haddad (NCA 2006/770); 1♀ 1 imm. Howick, Shooter's Hill [29°26'S 30°19'E, 790 m], xii.1937, R.F. Lawrence (NMSA 2129); 1♀ Ingwavuma [27°07'S 31°59'E], 12.vii.1951, R.F. Lawrence (NMSA 5569); 1♀ iSimangaliso Wetlands Park, Cape Vidal, 28°07'S 32°33'E, sifting leaf litter, 18.iv.1992, A. Leroy (NCA 93/317), 1♀ (NCA 93/321); 1♀ same locality, 18.iv.1992, A. Leroy, by hand (NCA 93/355); 1♀ same locality, Fanie's Island, 28°06'S 32°25'E, by hand in rotting log, 22.vii.1990, M. Filmer (NCA 91/726); 1♀ same locality, Fanie's Island, 28°32'S 32°24'E, 22.vii.1990, M. Alderweireldt & R. Jocqué, by hand (MRAC 172654); 2♂ 9 imm. 3♀ same locality, Gwala-Gwala Forest, 28°23.042'S 32°24.436'E, leaf litter, coastal forest, 21. iv.2006, C. Haddad (NCA 2006/723); 2♀ same locality, Hell's Gate block A, 28°00'S 32°28'E, 15.xi.2004, J. Esterhuizen, tsetse fly traps (NCA 2010/283); 2♀ 1 imm. same data, 19.i.2003 (NCA 2004/820); 3♀ same data, 2.ix.2003 (NCA 2004/825); 1♀ same data, 29.ix.2003 (NCA 2004/824); 1♀ same data, 17.xi.2003 (NCA 2004/826); 1♀ same data, 24.xi.2003 (NCA 2004/823); 1♀ same data, 2.ii.2004 (NCA 2004/822); 1♂ 1♀ Lake Sibaya, 27°20'S 32°42'E, i.1968, B. Lamoral (NMSA 12363); 1♂ Mapelaan [28°23'S 32°25'E], dune forest, 12.ii.1980, P. Reavell (NMSA 13197); 1♀ Mevamhlope area near old Eshowe road [28°43'S 31°49'E], on *Acacia*, *Aloe* and *Euphorbia*, 28.ix.1979, P. Reavell (NMSA 12783), 1♂ 1♀ (NMSA 12783); 3♀ Mfongosi [27°18'S 32°10'E], ii.1918, W.C. Jones (SAMC ENW-C005349); 1♀ Mkhuze Game Reserve, Inhlonhlela Pan road off main reserve road, 27°37.358'S 32°11.113'E, 95 m, 6–7.viii.2007, C. Smith, pitfalls (NCA 2008/2908); 1♀ Mtunzini, "Twin Streams" Farm (I.F. Garland), 28°57'S 31°46'E, coastal dune forest, 19–20.i.1984, T. & C. Griswold, P. Croeser & P. Reavell (NMSA 22034); 1♂ 1♀ Ndumo Game Reserve, Broadleaf woodland, 26°54.417'S 32°19.207'E, under logs, with ants, 29.xi.2000, C. Haddad (NCA 2002/399); 1♂ same data, under rocks, 7.vii.2002 (NCA 2002/404); 1♀ same locality, broadleaf woodland, 26°55.275'S 32°17.947'E, leaf litter, 6.ii.2005, C. Haddad (NCA 2005/38); 4♀ same locality, Crocodile farm, 26°54.426'S 32°19.185'E, under rocks, 12.i.2007, C. Haddad (NCA 2007/3066); 1♂ same data, 8–23.i.2002, pitfalls (NCA 2002/401); 1♂ 3♀ same data, leaf litter under fig tree, 7.vii.2002 (NCA 2002/405); 2♂ 1♀ same locality, E shore of Shokwe Pan, 26°52.516'S 32°12.407'E, 8–23.i.2002, C. Haddad, pitfalls (NCA 2002/400); 2♀ same data, leaf litter, 25.i.2006 (NCA 2008/1959); 2♂ 1♀ same locality, E shore of Shokwe Pan, 26°52.516'S 32°12.407'E, grass at tree bases, 24.i.2006, C. Haddad & R. Lyle (NCA 2006/836); 2♂ same locality, Game count transect 4, near Dipini Hide, 26°52.052'S 32°15.320'E, on ground with *Anoplolepis custodiens* ants, 3.vii.2003, C. Haddad (TMSA 24102); 1♂ same locality, near Fontana Camp, 26°52.072'S 32°09.545'E, under rocks, *Acacia tortilis* woodland, 2.vii.2002, C. Haddad (NCA 2002/403); 8♂ 14♀ same locality, Pongola River floodplain, 26°53.362'S 32°18.892'E, leaf litter, 9.ii.2005, C. Haddad (NCA 2005/47); 6♀ 3 imm. same locality, Pongola River floodplain, 26°53.384'S 32°19.097'E, leaf litter, riverine forest, 16.i.2006, C. Haddad (NCA 2006/704); 4♀ same locality, Pongola River floodplain, Ezikebheni, 26°53.389'S 32°18.878'E, on ground with *Anoplolepis custodiens* ants, 9.ii.2004, C. Haddad (TMSA 24103); 1♂ 1♀ same locality, Pongola River floodplain, near pump, 26°54.323'S 32°19.435'E, leaf litter, riparian forest, 9.i.2002, C. Haddad (TMSA 24067); 2♂ 3♀ same locality, southern boundary fence, 26°55.664'S 32°19.038'E, leaf litter, sand forest, 9.ii.2005, C. Haddad (NCA 2005/44); 1♂ same locality, W shore of Shokwe Pan, 26°52.013'S 32°12.982'E, leaf litter, *Ficus sycomorus* forest, 19.i.2002, C. Haddad (NCA 2002/402); 1♀ Nfuli River Hillside, semi-arid *Acacia* veld, under log, 21.i.1980, P. Reavell (NMSA 13002); 2♂ Ngome State Forest, 27°46'S 31°27'E, grass-layer, 1.ii.1992, M. van der Merwe, pitfalls (NCA 94/460); 1♂ same data, 1.ix.1992 (NCA 94/453), 1♂ (NCA 94/455); 2♂ same data, 1.x.1992 (NCA 94/450); 1♂ same data, 1.xi.1992 (NCA 94/452), 2♂ (NCA 94/458); 2♂ 1♀ same data, 1.xii.1992 (NCA 94/457), 1♀ (NCA 94/461); 1♂ same data, 1.i.1993 (NCA 94/454), 1♂ (NCA 94/456), 3♂ (NCA 94/459); 3♂ same locality, grass-layer, 1.x.1992, M. van der Merwe, beating (NCA 94/451); 1♂ 2♀ Ngoye Forest [28°50'S 31°42'E], ii.1953, R.F. Lawrence (NMSA 5928); 1♀ Nkhandla Forest [28°44'S 31°08'E], i.1937, R.F. Lawrence (NMSA 1397), 1♀ (NMSA 1379); 1♂ 2 imm. Ophathe game Reserve, 4×4 trail near Imfolozi River, 28°22.555'S 31°23.993'E, under rocks, 5.vii.2007, C. Haddad & R. Fourie (NCA 2007/2991); 1♂ 1 imm. same locality, game drive trail, rocky outcrop, 28°23.182'S 31°22.213'E, under rocks, 5.vii.2007, C. Haddad & R. Fourie (NCA 2007/2985); 2♂ 12 imm. same locality, montane grassland, 28°25.344'S 31°23.957'E, 897 m, sifting leaf litter, 4.x.2008, C. Haddad (NCA 2008/3911); 2♀ 1 imm. same locality, Ophathe River bed, 28°22.693'S 31°24.442'E, leaf litter, river bank, 5.vii.2007, C. Haddad & R. Fourie (NCA 2007/2970); 1♂ 2♀ 1 imm. same locality, Ophathe River bed, 28°23.727'S 31°23.643'E, 455 m, active searching, 2.x.2008, C. Haddad (NCA 2008/4221); 2♀ 1 imm. same data, 30.ix–4.x.2008, pitfalls (NCA 2008/4244); 1♀ 4 imm.
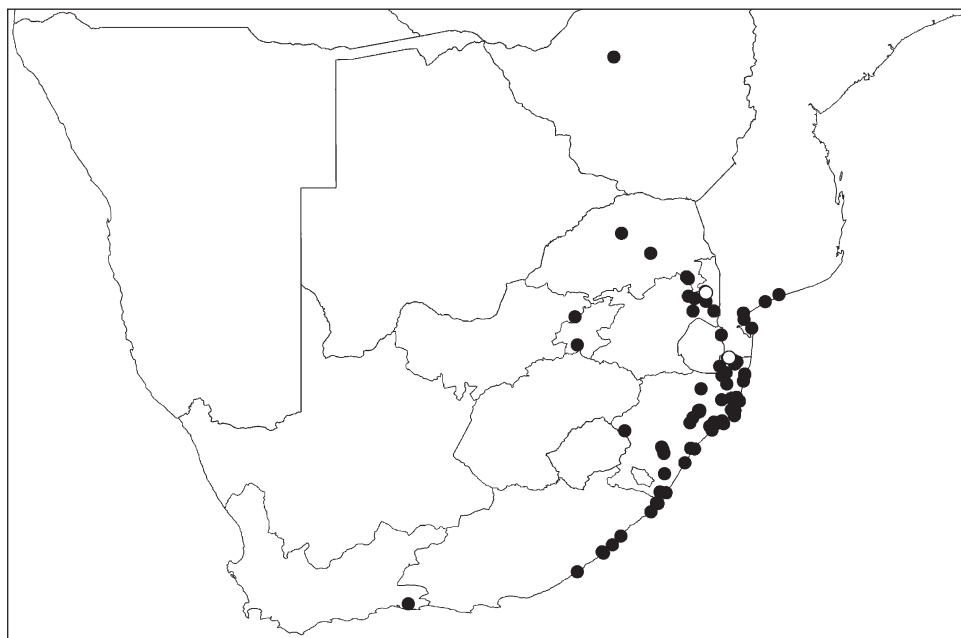
Fig. 50. Distribution of *Merenius alberti* in southern Africa: black circles – black morph; white circles – red morph.

same data, sifting leaf litter, 2.x.2008 (NCA 2008/2879); 2 imm. 1♀ same locality, overgrazed savanna, 28°22.135'S 31°23.363'E, 560 m, sifting leaf litter, 1.x.2008, C. Haddad (NCA 2008/4074); 1♂ 1♀ 1 imm. same data, 29.ix–3.x.2008, pitfalls (NCA 2008/4098); 2♂ 2♀ 3 imm. same locality, rocky mountainside, 28°23.202'S 31°24.077'E, 505 m, 29.ix–3.x.2008, C. Haddad, pitfalls (NCA 2008/4012); 1♀ Oribi Gorge Nat. Res., open grassland patch, 30°43.079'S 30°16.381'E, 315 m, base of grass tussocks, 13.i.2011, C. Haddad (NCA 2010/2746); 1♀ Otto's Bluff [29°30'S 30°21'E], under stones, x.1942, R.F. Lawrence & W.G. Rump (NMSA 3822); 1♂ Pietermaritzburg [29°37'S 30°23'E], vii.1913, C. Akerman (NMSA 2065); 1♀ Pietermaritzburg, Town Bush [29°36'S 30°23'E], x.1936, R.F. Lawrence (NMSA 1368); 1♂ Port Edward [31°03'S 30°13'E], i.1986, J. Stannard (NMSA 18469), 1♂ (NMSA 18471); 1♀ Port Edward district, Blencanthra Farm, 5 km NW of Port Edward, 31°02'S 30°10'E, 335 m, viii.1983, J. Stannard (NMSA 22027); 2♀ Port Shepstone [30°45'S 30°27'E], ix.1905, W.F. Purcell (SAMC 150750); 10♂ Richards Bay, 28°46'S 32°06'E, by hand, 6.xi.1983, R. Oberprieler (NCA 95/187); 1♀ same data, 6.ix.1985 (NCA 91/411); 1♀ Sani Pass, Site 8c, 30°12'S 30°24'E, 900 m, 1.i.2009, University of Pretoria students, pitfalls (NCA 2011/778); 2♀ 2 imm. Sodwana Bay National Park, Hiking trail, 27°32.609'S 32°39.851'E, leaf litter, coastal forest, 17.iv.2006, C. Haddad (NCA 2006/738); 2♂ 2♀ Tembe Elephant Park, Deep sand forest, 27°02.030'S 32°24.784'E, leaf litter, 6.i.2002, C. Haddad (NCA 2002/408); 2♂ same data, 10.i.2002 (NCA 2002/409); 2♂ same data, 3–23.i.2002, pitfalls (NCA 2002/406); 1♀ same locality, 27°02'S 32°24'E, leaf litter, sand forest, 15.iii.2003, A. Honiball (NCA 2004/265); 1♀ same locality, Manungu Picnic spot, open woodland/sand, 26°58.991'S 32°28.335'E, searching under logs, 9.i.2006, C. Haddad & R. Lyle (NCA 2007/3513); 4♂ 5♀ 2 imm. same locality, open woodland/sand, near offices, 27°03'S 32°25'E, sifting leaf litter, 8.ii.2005, C. Haddad (NCA 2007/3609); 2♂ 1♀ same data, 3–23.i.2002, pitfalls (NCA 2002/407); 1♂ 3♀ same data, leaf litter, 14.i.2002 (NCA 2002/410); 1♀ same locality, Picnic spot, 26°57.505'S 32°24.437'E, at base of grasses, 12.iv.2006, C. Haddad (NCA 2006/872); 1♂ same locality, sand forest near viewing tower, 27°01.713'S 32°24.559'E, active searching, leaf litter, 10.i.2002, C. Haddad (NCA 2007/3100); 1♂ 6♀ 1 imm. Umhlali [29°28'S 31°09'E], ii.1940, R.F. Lawrence (NMSA 2938), 1♀ (NMZA 277); 3♂ 2♀ 2 imm. Umhlali, Sheffield Beach [29°29'S 31°16'E], i.1937, R.F. Lawrence (NMSA 1416); 3♂ same data, vii.1937 (NMSA 1555); 1♂ 1♀ same data, x.1938 (NMSA 2435); 1♀ Umziki Pan Game Reserve, near Hluhluwe [28°02'S 32°19'E], sandveld forest, xii.1999 (NMSA 22037); 1♀ 'Zululand', 28°35'S 31°13'E, 12.ii.2009, J. Pryke (NCA 2011/908). *Limpopo Province*: 1♀ Klaserie, Bokmakierie Game Farm, tent camp, 24°33'S 31°02'E, open sandy area, dry river bed, 11.iv.2001, R. Jocqué, hand collecting (MRAC 210081); 3♂ 1 imm.

Magoebaskloof [23°52'S 30°00'E], 5000 ft, iii.1960, R.F. Lawrence (NMSA 7956); 1♂ Westphalia, 23°18'S 29°10'E, 27.v.1983, R. Harris, by hand (NCA 95/174). *Mpumalanga*: 1♂ 1♀ Acornhoek [24°36'S 31°05'E], ii.1918, R. Tucker (SAMC ENW-C005346); 1♀ Burgershall [25°06'S 31°05'E], citrus orchard, 21.i.1989, M. van den Berg, beating (NCA 2008/2774); 1♀ Crocodile River Gorge, 25°32'S 31°13'E, running in leaf litter, 18.xi.2007, J. Leroy (NCA 2008/1988); 3♂ 3♀ Komatipoort, 25°31.593'S 31°49.171'E, in cultivated flower garden near farmhouse, 9.ii.2005, J. Horn (NCA 2007/1308); 1♀ same locality, xi.1918, R. Tucker (SAMC B4342); 1♂ Kruger National Park, near Skukuza, 25°00.342'S 31°35.165'E, medium *Opuntia* infestation, 1.v.2006, K. Harris, pitfalls (NCA 2007/3124); 1♂ same locality, near Skukuza, 25°00.352'S 31°35.106'E, heavy *Opuntia* infestation, 29.xi.2005, K. Harris, pitfalls (NCA 2007/3125); 1♀ same locality, near Skukuza, 25°00.286'S 31°35.186'E, no *Opuntia* infestation, 5.iv.2006, K. Harris, pitfalls (NCA 2007/3126); 1♀ same locality, Pretoriuskop Camp, 25°10'S 31°16'E, in humus, 2.xii.1963, R.F. Lawrence (NMSA 22036); 1♂ same locality, Skukuza, 25°00'S 31°36'E, 1200 ft, 14–18.xii.1984, C. Griswold, T. Meikle-Griswold, F. & J. Wright (NMSA 22035); 1♂ same locality, Sabie River, 16.ii.1962, R.F. Lawrence (NMSA 18472); 1♀ near Graskop, Sabie River, Lisbon Farms, 24°58'S 31°34'E, leaf litter, 16.xi.1993, A. Dippenaar-Schoeman (NCA 2007/1139). *North-West*: 1♂ near Skeerpoort [25°42'S 27°50'E], in *Acacia caffra*, shaded, 10.xii.1977, P. Reavell (NMSA 13337). *Western Cape*: 1♂ 1♀ 2 imm. Terblans trail, near Grootdraai picnic site [33°56'S 23°03'E], indigenous evergreen forest, 14.x.1996, H.G. Robertson (SAMC ENW-C006108). SWAZILAND: 1♂ Mlawula Nat. Res., 26°13'S 32°02'E, running on hot stones with ants, 13.v.1988, A. Leroy, by hand (NCA 91/351). ZIMBABWE: 1♀ Gokwe, 18°14'S 28°57'E, vii.1964, W. Lawson (NMSA 12267).

Distribution: Widespread throughout the eastern half of southern Africa, extending southwards along the South African coast as far as the vicinity of Knysna in the Western Cape Province. Most records are of the black morph; the red morph has so far only been recorded from two localities, Ndumo Game Reserve and the Kruger National Park in South Africa (Fig. 50).

Biology: *M. alberti* is an exclusive ground-dwelling spider and has mainly been collected by pitfall traps, litter sifting or by hand from the soil surface, under rocks and logs. Only on very rare occasions have specimens been collected by sweeping or beating. Typical of castianeirines, this species constructs an egg sac with a basal plate and a dome-shaped cover of papery silk, which is usually placed on the underside of dead leaves, rocks and logs on the ground. Egg sacs are 7.4–7.8 mm in diameter and contain 17–26 eggs each (n=6).

Prey capture involves a rapid leap when contact is made with a prey arthropod, and the front legs and palps form a basket used to hold the prey securely while being sedated. Observed prey items in the field include cockroach and cricket nymphs, termites, and other spiders (Lycosidae, Salticidae and Theridiidae). This species was not observed feeding on ants in the field, but in the laboratory the black morph would capture *Anoplolepis custodiens* ants, which serve as the model of the red morph (<5 observations). The black morph did not capture its potential models *Camponotus cinctellus* and *Polyrhachis gagates* under laboratory conditions. Further study is necessary to determine whether this species feeds on ants preferentially, and if so, whether its models or only other non-model species are fed on.

*Frequency of colour morphs relative to ant assemblages*

During the pitfall trapping survey, 16 species of medium to large ants were collected, representing four subfamilies of Formicidae (Table 1). Of these, nine species were considered not to be potential models for either of the two morphs of *M. alberti* due to their small size, slender bodies and inappropriate colouration. Two species of Formicinae and three of Ponerinae could possibly be models for the black morph, while *A. custodiens* is the model of the red morph. A second species, possibly *Atopomyrmex mocquerysi* André, 1889 (Myrmicinae), could possibly also serve as a model for the red morph in

TABLE 1

Checklist of medium to large ants (Hymenoptera: Formicidae) collected by pitfall traps in 10 habitats in the Ndumo Game Reserve in 2009. Species that are potential models for the black morph of *Merenius alberti* Lessert, 1923 are highlighted in dark grey, those of the red morph in light grey, and species considered not being models are not highlighted.

| Subfamily/Genus/Species | Total | % | Reasons for inclusion/ omission as model |
|---|---|---|---|
|  |  |  |  |
| **DORYLINAE** |  |  |  |
| *Dorylus helvolus* (Linneaus, 1764)? | 4 | 0.24 | Too small (<4 mm); colouration inconsistent with mimic |
|  |  |  |  |
| **FORMICINAE** |  |  |  |
| *Anoplolepis custodiens* (F. Smith, 1858) | 402 | 24.33 | Colouration and size consistent with mimic |
| *Camponotus cinctellus* (Gerstaecker, 1859) | 127 | 7.69 | Colouration and size consistent with mimic |
| *Camponotus* sp. 1 (*maculatus* group) | 38 | 2.30 | Colouration inconsistent with mimic |
| *Polyrhachis gagates* F. Smith, 1858 | 17 | 1.03 | Colouration and size consistent with mimic |
|  |  |  |  |
| **MYRMICINAE** |  |  |  |
| *Atopomyrmex mocquerysi* André, 1889? | 10 | 0.61 | Colouration and size consistent with mimic |
| *Crematogaster* sp. | 17 | 1.03 | Too small (<4 mm); colouration inconsistent with mimic |
| *Myrmicaria natalensis* (F. Smith, 1858) | 71 | 4.30 | Colouration and ventrally-pointing abdomen inconsistent with mimic |
| *Ocymyrmex fortior* Santschi, 1911 | 48 | 2.91 | Body too slender; colouration inconsistent with mimic |
| *Pheidole* sp. | 558 | 33.78 | Too small (<4 mm); colouration inconsistent with mimic |
| *Tetramorium quadrispinosum* Emery, 1886 | 6 | 0.36 | Too small (<4 mm); colouration inconsistent with mimic |
|  |  |  |  |
| **PONERINAE** |  |  |  |
| *Leptogenys havilandi* Forel, 1901 | 2 | 0.12 | Body too slender |
| *Odontomachus troglodytes* Santschi, 1914 | 28 | 1.69 | Colouration and size consistent with mimic |
| *Pachycondyla caffraria* (F. Smith, 1858)? | 40 | 2.42 | Colouration and size consistent with mimic |
| *Pachycondyla tarsata* (Fabricius, 1798) | 61 | 3.69 | Too large (>16 mm) |
| *Streblognathus peetersi* Robertson, 2002 | 223 | 13.50 | Colouration consistent with mimic, size considerably larger |

the absence of *A. custodiens*, sharing similar size and colouration, but this is unlikely due to the low activity densities of this species in the pitfall traps.

During winter, an adequate number of *M. alberti* were collected at 18 of the 20 sampling sites, while no *M. alberti* could be found at two sites (AN1 and AX1). Of the 360 *M. alberti* collected, 306 were juveniles (85.0 %), 26 were males (7.2 %) and 28 were
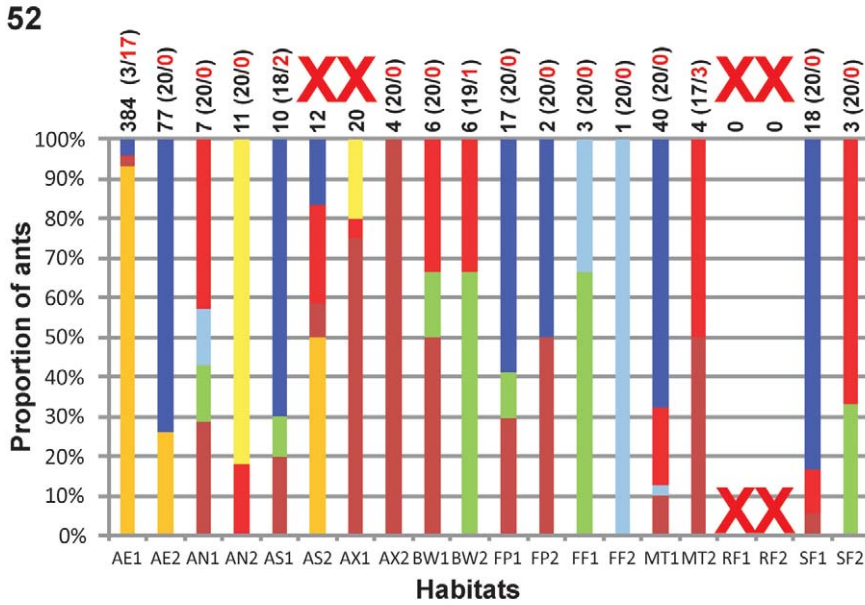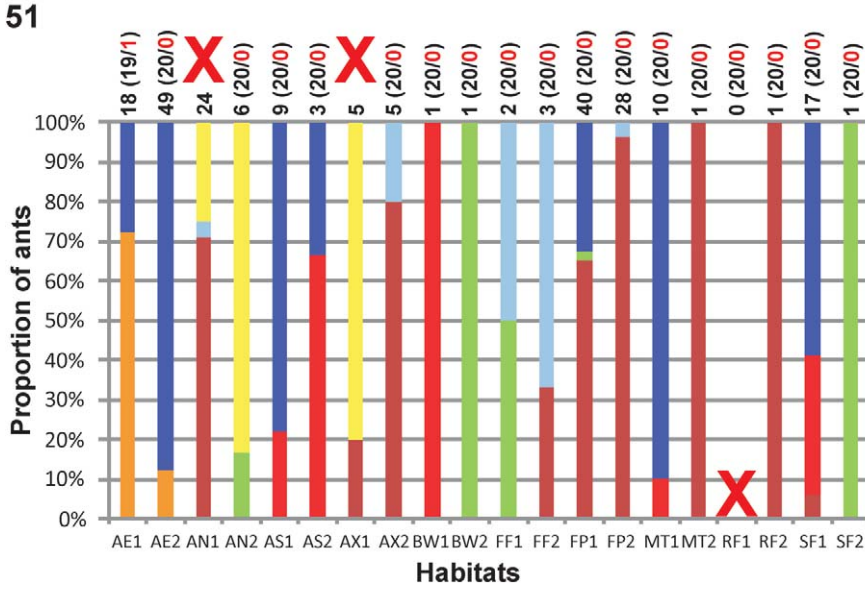
Figs 51, 52. Ant species collected from 20 sites sampled in the Ndumo Game Reserve during June–July (51) and November–December 2009 (52) by pitfall trapping over a 10-day period that may be potential models for *Merenius alberti* Lessert, 1923. Numbers above each column indicate the total number of potential model ants sampled (Table 1), followed in parenthesis by the number of black and red morphs of *M. alberti* collected by hand at each site. Red crosses indicate sites where no potential ant models or *M. alberti* were collected. Blue bars – *Streblognathus peetersi* Robertson, 2002; orange bars – *Anoplolepis custodiens* (F. Smith, 1858); maroon bars – *Camponotus cinctellus* (Gerstäcker, 1859); turquoise bars – ?*Atopomyrmex mocquerysi* André, 1889; yellow bars – *Odontomachus troglodytes* Santschi, 1914; green bars – *Polyrhachis gagates* F. Smith, 1858; red bars – ?*Pachycondyla caffraria* (F. Smith, 1858).

females (7.8%). Of these, only a single adult of the red morph was collected at AE1; all of the remaining individuals were of the black morph (Fig. 51). This individual was collected at the site where *A. custodiens* densities were highest.

Summer sampling of *M. alberti* could only be conducted at 18 of the 20 sites due to extensive flooding of the two riparian forest sites along the Pongola River, thereby ruling out sampling of ants and spiders at RF1 and RF2. Of these remaining 18 sites, *M. alberti* was only collected at 16 sites; no specimens were collected at AS1 and AX1 during three hours of searching. Of the 320 *M. alberti* collected, 168 were juveniles (52.5%), 60 were males (18.8%) and 92 were females (28.7%). Thus, the proportion of adults collected was more than three times higher during summer than winter, providing some indication of the phenology of this species. The red morph was collected in four of the 16 sites where adequate *M. alberti* were collected, but at only one site (AE1) did it represent the majority of *M. alberti* collected (85%).

Regarding ant sampling, 223 potential model ants were collected from 19 of the 20 sampled sites during winter; at one site (RF1) no potential models were collected (Fig. 51). Ant densities were generally highest in the AE and FP habitats. During summer, ant activity densities were nearly three times higher than winter (n=623). Almost two-thirds of the ants collected during summer were *A. custodiens* collected at AE1 (n=382). Ant activity densities were second highest at AE2, not due to high *A. custodiens* densities but rather due to dominance of *Streblognathus peetersi*.

In comparing the proportion of the two *M. alberti* morphs relative to ant assemblages, it is evident that the red morph may be present at sites where its supposed model (*A. custodiens*) may not be active (Fig. 52). However, given the short span of the pitfall trapping (10 days), it is plausible that this ant may be present at these sites but was not actively foraging during the period of sampling. However, when *A. custodiens* densities are very high then the resident *M. alberti* population is strongly dominated by the red morph, e.g. at site AE1 (Fig. 52).

Conversely, even when *A. custodiens* is present in low densities relative to that of some black models, the red morph may be absent (e.g. AE2 in summer). Since no species of potential black models were found at all of the sites, no species can be identified as the sole model of the black morph. Instead it is likely that the black morph is a generalized mimic of black ground-dwelling ants, while the red morph is specifically associated with *A. custodiens* ants. Based on the abundance of different black potential models, the most likely models for the black morph are *C. cinctellus* and *S. peetersi*.

DISCUSSION

Polymorphism amongst corinnid spiders, particularly castianeirines, is a relatively scarce and poorly studied phenomenon. In her review of myrmecomorphy and myrme-cophagy, Cushing (1997) reported that four of the 23 castianeirine species studied were either polymorphic (different colour morphs) or showed transformational mimicry, i.e. different models during different stages of development. According to the definitions of Edmunds (2000), two of these mimics could be considered good or specific mimics (*Myrmecium* spp.) while the other two are poor or general mimics (*Castianeira* spp.). The current study provides the first report of polymorphism in an ant-mimicking African castianeirine, *M. alberti*, which can be considered a general (poor) mimic. Based on the present evidence, the common black morph is a generalised mimic of black ground-

dwelling ants while the scarce red morph is specifically associated with *A. custodiens* ants. As the main driving force behind mimicry is avoiding predation by being mistaken for an unpalatable model by potential predators (Reiskind 1969), polymorphism provides additional protection to the mimic in the presence of ant assemblages with contrasting species compositions, while specialised mimics are more strictly required to associate with a particular model species for this protection.

The red morph was first discovered at site AE1 during 2003 (specimens TMSA 24102), where *A. custodiens* was the dominant actively foraging ant. The specimens collected at this site during 2009 indicate that the colonies of the ant model have remained consistently in this habitat during this period, explaining in part the dominance of the red morph in the summer samples (Fig. 52). However, only a single red morph specimen was collected at the same site during winter, when *A. custodiens* densities were considerably lower. The factors responsible for this dramatic change in the representation of the two morphs requires further investigation, but two possibilities exist: (1) that *M. alberti* possesses ommachromes, as in the case of some crab spiders (e.g. Insausti & Casas 2008, 2009; Théry & Casas 2009; Riou & Christidès 2010), which may facilitate changes in the colour of the integument according to the densities of particular model ants, or (2) that observed changes in the morph ratio are the result of differential predation, i.e. when *A. custodiens* activity at these sites is reduced then the red morph stands out from the foraging black ants and is more susceptible to predation, resulting in a relative decrease in the proportion of red morphs occurring at a particular site.

The incidence of colour polymorphism in *M. alberti* is most likely determined on a microscale by the local abundance of particular ant models. The *A. custodiens* ants that serve as a model to the red morph are widely distributed throughout southern and central Africa (Prins 1982), but *M. alberti* is not, being restricted mainly to the eastern half of southern Africa (Fig. 50). Despite their sympatric occurrence throughout most of the range of *M. alberti*, only two populations of the red morph have been recorded so far. Is the red morph just generally scarce despite the wide distribution of its model, or is the apparent scarcity of the red morph an artefact of collecting effort? The latter seems unlikely as considerable sampling has been done through large parts of KwaZulu-Natal, in particular, and additional populations would likely have been sampled had they been present. The apparent scarcity of the red morph could be tested for by sampling *M. alberti* specifically in the vicinity of *A. custodiens* colonies and determining the ratio of black:red morphs. As *A. custodiens* is very widespread and often very abundant (e.g. Parr 2008; Sithole *et al.* 2010) in the savanna habitats dominating the distribution range of *M. alberti*, identifying suitable sites for such sampling should be relatively easy.

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