Revision of the *Camponotus fulvopilosus* (De Geer) species-group (Hymenoptera: Formicidae)

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The *Camponotus fulvopilosus* species-group comprises four species: *C. fulvopilosus* (De Geer) (arid and open savanna areas of southern Africa), *C. brevisetosus* Forel (granite outcrops on the Drakensberg escarpment and its foothills), *C. detritus* Emery (dunes of the Namib Desert) and *C. storeatus* Forel (southern Cape). A key to major workers and queens is provided, redescriptions are provided for major workers, and the biology of each species is reviewed. *Camponotus fulvopilosus* comprises three morphological forms that are parapatrically distributed with discernible hybrid zones. The evolution of the four species is discussed on the basis of their biogeography.

Key words: southern Africa, ant systematics, *Camponotus fulvopilosus* species-group, hybrid zones, Namib Desert, Savanna, Karoo.

INTRODUCTION

Members of the *Camponotus fulvopilosus* (De Geer) species-group (Hymenoptera: Formicidae) are easily distinguished from other members of *Camponotus* by the thick blunt hairs on the gaster (Figs 1, 3–5) and the angulate cross-section to the hind tibiae (Fig. 2). In the subgeneric classification presented by Emery (1925), this group was included in the subgenus *Myrmopiromis* (group *fulvopilosus*) along with a number of other species that also have an abundance of blunt hairs on the dorsum of the gaster but which lack the angulate hind tibiae. Robertson (1990) clarified the nomenclature of the *C. fulvopilosus* species-group and provided an abstract to part of the work considered in the present paper. The four species are found mainly in southern Africa, but the distribution of *C. fulvopilosus* extends as far north as Cabinda and Zaïre. The group is composed of the widely distributed *C. fulvopilosus* that occurs in arid and savanna areas of southern Africa and three peripheral species with more limited and habitat-specific distributions. Within *C. fulvopilosus* there are three variants that are geographically distinct with clear transition zones between them, confirming their status as variants and not species. The group therefore provides an ideal model for studying the biogeography of southern African ants and the present paper considers this in part. It is also an initial contribution towards resolving the unsatisfactory state of *Camponotus* taxonomy.

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MATERIAL AND METHODS

The following measurements were taken from each of five major workers per sample (n = 58 samples), using a measuring eyepiece on a Wild stereo microscope: (1) maximum width of head; (2) head length, from a line linking the occipital corners to the midpoint of the clypeal margin; (3) scape length; (4) pronotal width; (5) pronotal length; (6) pronotal angle, *i.e.* the angle of the pronotal humeri, estimated using the cross-hairs on the measuring eyepiece; (7) the lengths of five hairs, arbitrarily selected from the second gastral tergite; (8) the hair densities on the first and second gastral tergites, estimated by counting the number of hairs intersecting the measuring line on the micrometer for a length of 40 micrometer units (0.996 mm); and (9) the width of the hairless patches on the first four gastral tergites (only the width of the second patch is reported here). In addition, the colour of the hairs and cuticle were scored using a Munsell (1954) colour chart. The following indices were derived from the measurements: cephalic index = (head width/head length) × 100; scape index = (scape length/head width) × 100; and pronotal index = (pronotal

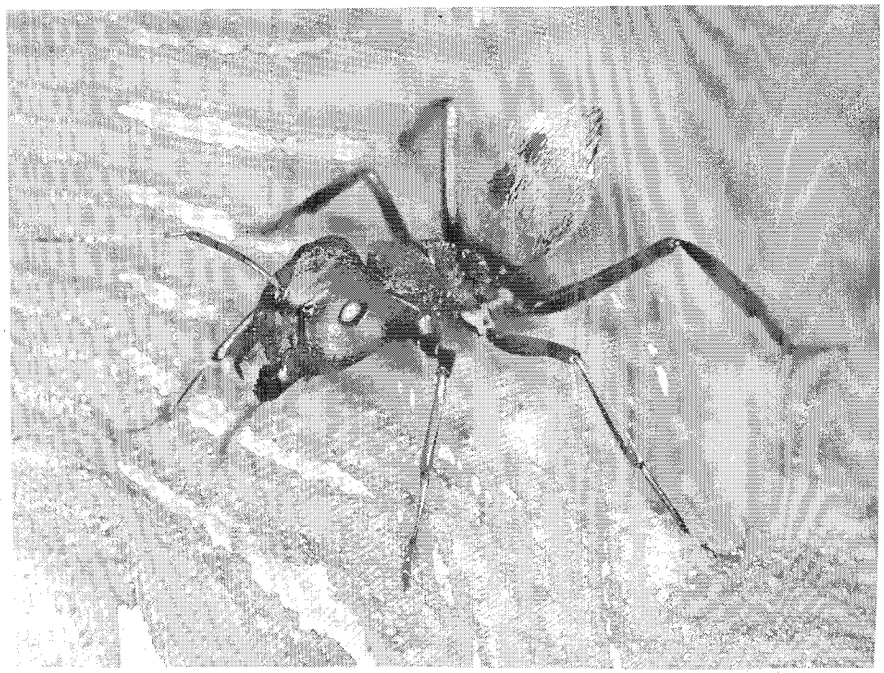


Fig. 1. *Camponotus fulvopilosus* (Karoo form) major worker in aggressive posture, showing the thick blunt hairs on the gaster that are one of the characteristics of the *C. fulvopilosus* species-group.

width/pronotal length) × 100. Eye length was measured later for a random sample of 10 major workers from each species. Collection and identification information on all the specimens examined (both measured and unmeasured) was recorded on a computer database and converted to Genstat 5.3 (Payne *et al.* 1993) for mapping of distributions.

Material examined is in the following collections: Albany Museum, Grahamstown (AMGS); American Museum of Natural History, New York (AMNH); The Natural History Museum, London (BMNH); National Museum, Bloemfontein (BMSA); Muséum d'Histoire Naturelle, Geneva (MHNG); Museo Civico Di Storia Naturelle 'Giacoma Doria', Genoa (MCSN); Museum of Comparative Zoology, Harvard (MCZC); Museum of Zoology, Lund University, Lund (MZLU); South African Museum, Cape Town (SAMC); National Collection of Insects, Biosystematics Division, Plant Protection Research Institute, Pretoria (SANC); National Museum of Namibia, Windhoek (SMWN); Transvaal Museum, Pretoria (TMSA); and Zoologisches Museum der Humboldt-Universität zu Berlin, Berlin (ZMHB).

Key to workers and queens of the *Camponotus fulvopilosus* species-group

1. Dense mat of hairs partly or completely covering the gastral tergites and obscuring the underlying cuticle (Figs 7–9)..... 2
1′. Gastral tergites with regularly spaced, sparsely distributed hairs; underlying cuticle clearly visible (Fig. 6) ..... *C. brevisetosus* Forel
2. Hairless patches on gaster narrow, less than half the width of tergite in major worker (Fig. 8), or absent (Fig. 9)..... 3
2′. Hairless patches on gaster wide, greater than half the width of tergite in major worker (Fig. 7); distribution limited to Namib Desert dune sea .... *C. detritus* Emery
3. Pronotal humerus in major worker acute (Fig. 11); cuticle reddish; distribution limited to southern Cape .... *C. storeatus* Forel

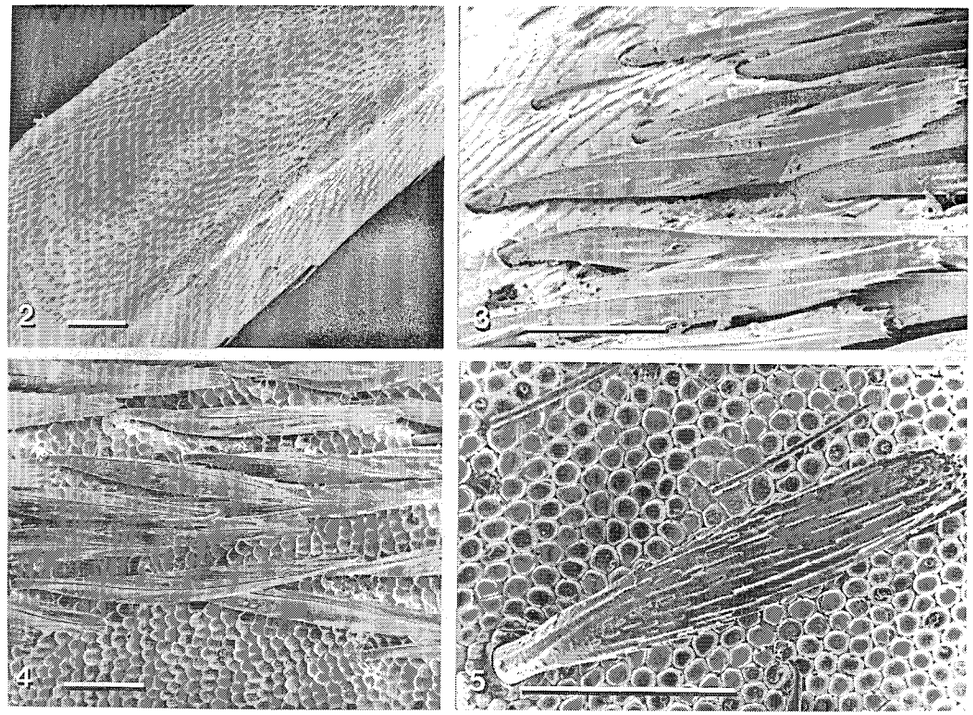


Fig. 2–5. 2, Hind tibia of *Camponotus storeatus* worker showing the quadrate ridges that characterize the *C. fulvopilosus* species-group; **3–5,** scanning electron micrographs of gastral hairs in *C. fulvopilosus* (3–4) and *C. brevisetosus* (5). Scale bar = 0.1 mm.

3′. Pronotal humerus in major worker obtuse (Fig. 10); cuticle usually black; distributed through arid and savanna areas of southern Africa..... *C. fulvopilosus* (De Geer)

In addition to the above key, differences between the species and populations can be discerned using Figs 12–13 and Table 1.

Camponotus brevisetosus Forel, Figs 5–6, 13; Table 1

Camponotus fulvopilosus subsp. *brevisetosus* Forel, 1910: 25.

Camponotus brevisetosus Forel: Robertson 1990: 327.

Diagnosis

Easily distinguished from the other three species by the sparsely distributed spatulate hairs on the gaster (Figs 5–6). It is also smaller than the other species (Table 1).

Redescription of major worker

Colour. Head, alitrunk and petiole dark-red to brown-black, gaster black.

Head. Mandibles finely reticulate-punctate, overlain by regularly spaced large punctures each one smudged apically. Seven teeth, teeth 5 and 6 partly fused. Line of hairs present on dorsal surface of mandible, each hair opposite a tooth. Fringe of hairs on ventral surface of mandibles parallel to apical margin and another parallel to external margin. Eye length 0.68–0.75 mm (n = 10), 0.20–0.23 times head width. Sides of head convex and occipital margin slightly concave. Head finely reticulate, evenly pitted with groups of punctures. Clypeus with short projecting median shelf with rounded corners. Fringe of hairs present along median clypeal border. Pronotum sometimes bearing a hair, up to three hairs on mesonotum, and up to 10 hairs on propodeum.

Thorax and abdomen. Pronotum with distinct humeri forming an angle of 105–128 degrees

Table 1. Measurements of major workers in the four species comprising the *Camponotus fulvopilosus* species-group. The first line of each cell provides the mean ± S.D. and the second line the range of values. The sample size for hair lengths is greater than for other measurements because a number of hairs (usually 5) were measured on each worker.

	C. brevisetosus (*n* = 10)	*C. detritus* (*n* = 10)	*C. fulvopilosus* (*n* = 245)	*C. storeatus* (*n* = 25)
Head width (mm)	3.51 ± 0.15 (3.31–3.73)	3.80 ± 0.24 (3.30–4.11)	4.69 ± 0.57 (3.05–5.79)	4.82 ± 0.55 (3.05–5.47)
Head length (mm)	3.26 ± 0.11 (3.12–3.52)	3.55 ± 0.13 (3.30–3.73)	4.22 ± 0.36 (3.05–4.85)	4.48 ± 0.37 (3.30–5.04)
Cephalic index	107 ± 2 (106–111)	107 ± 3 (100–112)	111 ± 5 (94–121)	107 ± 5 (92–116)
Scape length (mm)	3.08 ± 0.08 (2.98–3.22)	3.19 ± 0.08 (3.05–3.30)	3.50 ± 0.19 (2.12–3.92)	3.72 ± 0.15 (3.23–3.98)
Scape index	88 ± 3 (83–91)	84 ± 4 (80–92)	75 ± 8 (49–108)	78 ± 9 (68–106)
Pronotal index	135 ± 4 (126–139)	128 ± 3 (123–133)	123 ± 6 (103–141)	126 ± 4 (121–135)
Pronotal angle (degrees)	116 ± 7 (105–128)	111 ± 10 (100–122)	125 ± 10 (95–147)	89 ± 7 (75–98)
Lengths of hairs on gaster (mm)	0.28 ± 0.03 (0.21–0.34) (*n* = 50)	0.29 ± 0.03 (0.24–0.36) (*n* = 50)	0.30 ± 0.03 (0.21–0.41) (*n* = 1169)	0.28 ± 0.03 (0.21–0.37) (*n* = 125)
Hair density (hairs/mm)	4.3 ± 1.1 (2.7–5.9)	27.5 ± 2.6 (24.5–31.4)	21.6 ± 2.3 (13.8–28.2)	19.2 ± 2.4 (14.4–23.9)

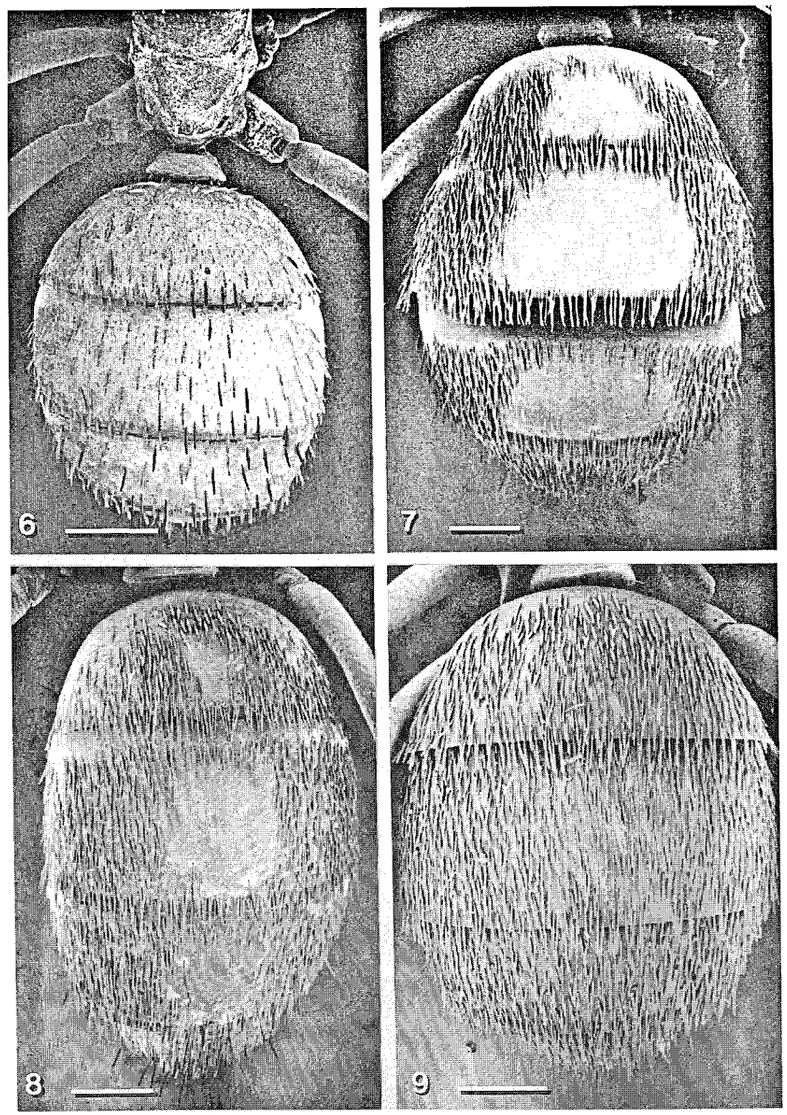
(Table 1). Tibiae angular with two dorsal and two ventral ridges, the surface between the ridges indented. Gaster covered with regularly spaced, blunt, flattened, spatulate hairs (Fig. 5), the distance between adjacent hairs usually greater than half the length of a hair, also with sparse, adpressed silvery pubescence. Gaster uniformly reticulate-punctate, each puncture sharply defined.

Distribution and habitat. The few existing records of *C. brevisetosus* suggest that its distribution is limited to the eastern fringes of the Grassland biome (Rutherford & Westfall 1994) in southern Africa (Fig. 15). In particular, it has been found on the Drakensberg escarpment and foothills at altitudes ranging from 914–1944 m. The location of nests of this species between granite slabs suggests that its distribution might be influenced by the occurrence of granitic outcrops. F. Wilms (ZMHB) recorded this species from Cape Town but the record is doubtful and has been excluded from the distribution map.

Biology. According to M.H. Villet (pers. comm.) the four nests of *C. brevisetosus* that he and R.M. Crewe found at Vernon Crookes Nature Reserve were located between large flakes of pink granite and were all clear of the soil, with the edges of the cavity sealed with matting made from plant fibres. The nests had no internal structure but the brood was clumped. The smallest nest had a queen and about 40 workers, and covered an area of 15 × 5 cm. The other three nests were mature, with hundreds of alates and about 1000 workers. These nests were found on 30 October, so alates occur in nests during early summer. Little is known about the diet of *C. brevisetosus* but De Swart & Louw (1994) recorded it from inflorescences of *Protea roupelliae* Meisn., suggesting that they feed on nectar and possibly flower-inhabiting insects.

Type material examined. Syntype workers, *Camponotus fulvopilosus* subsp. *brevisetosus*. SOUTH AFRICA: 'Natal Alt 3600 Haviland 217', '217 Natal Alt 3600 ft June 1898' (locality too general for coordinates to be determined but specimens were probably collected in the vicinity of Slievyre, 28.56S 29.54E, in the Weenen District where the collector lived) (MHNG).

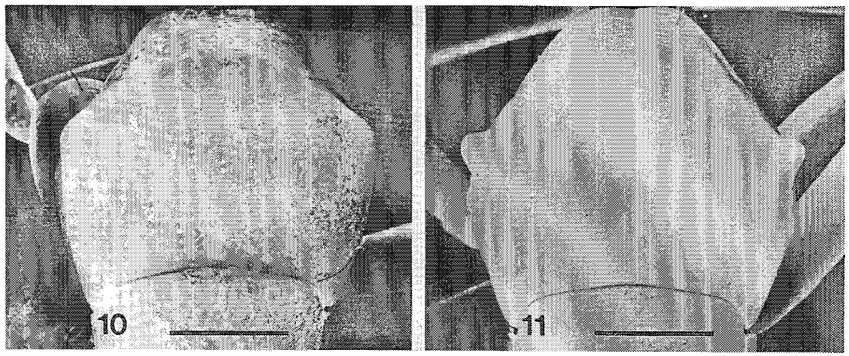
Additional material examined. Specimens from: SOUTH AFRICA: Gustav Klingbiel Nature Reserve, 25.05S 30.32E, 23.xi.1992, D.H.de Swardt (SAMC); Marieps Mountain (24.34S 30.52E), 15.iv.1948, G.van Son (TMSA); Mariepskop, summit (1944m) 24.32S 30.52E, 3.vi.1992, G.Alpert (MCZC); Sterkspruit, 25.07S 30.31E, 23.xi.1992, D.H.de Swardt; Vernon Crookes Nature Reserve, 30.16S 30.35E, 10.ii.1991, M.H.Villet; same locality but 30.x.1991, R.M.Crewe (all SAMC).



Figs 6–9. Dorsal view of gasters. **6**, *Camponotus brevisetosus*; **7**, *C. detritus*; **8**, *C. fulvopilosus* (Karoo form); **9**, *C. storeatus* (southern form). Scale bar = 1 mm.

Camponotus detritus Emery, Figs 7, 12; Table 1

Camponotus detritus Emery, 1886: 357.
Camponotus fulvopilosus subsp. *detritus* Emery: Forel 1910: 26.
Camponotus detritus Emery: Forel 1914: 273.
Camponotus fulvopilosus subsp. *detritus* Emery: Wheeler 1922: 986.
Camponotus detritus Emery: Emery 1925: 128.



Figs 10–11. Pronotum. **10**, *Camponotus fulvopilosus*; **11**, *C. storeatus*. Scale bar = 1 mm.

Diagnosis

Distinguished from the other species by the wide bare patches on gastral tergites 1–3 (Fig. 7).

Redescription

Colour. Head, alitrunk and petiole pale red-brown, gaster black.

Head. Mandibles finely reticulate basally, striate apically, with regularly spaced faint impressions. Seven mandibular teeth, teeth 5 and 6 partly fused, sometimes appearing as one tooth. Line of hairs present on dorsal surface of mandible, each hair facing into the cavity between two teeth. Fringe of hairs on ventral surface of mandibles parallel to apical margin and another parallel to external margin. Eye length 0.90–0.97 mm (n = 10), 0.23–0.26 times head width. Sides of head convex and occipital margin slightly concave. Head finely reticulate with regularly spaced superficial impressions. Clypeus with short projecting median shelf with rounded corners. Fringe of hairs present along median clypeal border.

Thorax and abdomen. Alitrunk uniformly reticulate-punctate, each puncture sharply defined. A maximum of two erect hairs on pronotum, up to three on mesonotum and up to 13 on propodeum. Pronotum with obtuse humeri forming an angle of 100–122 degrees (Table 1). Tibiae angular with two dorsal and two ventral ridges, with surfaces between the ridges indented. Scale-like petiolar node with convex dorsal rim. A line of blunt hairs situated just posterior to dorsal rim. Gastral dorsum with mat of blunt, thick, off-white hairs, interrupted by wide median bare patches (1.89–3.26 mm wide on second tergite (Fig. 12)) that reveal the underlying black cuticle. Gastral dorsum with fine, sharply defined, reticulate punctation and with no pubescence.

Distribution and habitat. Camponotus detritus is found exclusively on sparsely vegetated dunes in the Namib Desert dune sea (Fig. 15). This band of dunes extends from the Kuiseb River to Lüderitz, and is about 130 km broad at its widest point (Curtis & Seely 1987).

Biology. The biology of *C. detritus* has been studied by Curtis (1985a–e, 1988, 1990; Curtis & Seely 1987) and respiration in this species has been investigated by Lighton (1989). Nests were found under perennial vegetation on dunes and consisted of numerous interconnecting passages 9–22 mm in diameter, linking chambers that were 30–88 mm in diameter and rarely exceeded a depth of 0.4 m (Curtis 1985b). Some of the chambers and passages were 'lined with a pliable viscous substance that hardened to form rigid tunnels', and chambers were often lined with detritus and bird droppings. Colonies consisted of 1–5 nests, with sister nests 0.5–100 m apart. There are aggressive territorial interactions between colonies and the greatest territory size recorded was 5.5 ha for a three-nest colony (Curtis 1985a). Nests are large, and Curtis (1985b) recorded a mean of 3404 workers and a maximum of 15670 workers. The latter nest had a sister nest and the total colony size recorded was 20 038 workers. Curtis (1985a) recorded alates in nests from December to June and a mid-morning alate flight in April, the day after 3 mm of rain had fallen. This is the only nuptial flight recorded for a member of the *C. fulvopilosus* species-group, but unfortunately no mating was observed. *Camponotus detritus* has independent colony foundation and Curtis (1985a) recorded a development time (egg to eclosion) of just over two months for the nanitic workers. Of 10 nests excavated that contained queens, seven had one queen, two contained two queens, and one (the largest nest) contained eight wingless queens. It is not known whether all queens laid eggs in these polygynous colonies. The apparent polygyny might have been due to virgin queens losing their wings or might have been genuine polygyny presumably arising from pleometrosis, or newly-mated queens joining an established nest, or by fusion of colonies, factors that have been implicated in polygyny of other ant species (Hölldobler & Wilson 1990).

The major food source recorded by Curtis (1985c) for *C. detritus* was honeydew from scale insects on the perennial dune vegetation but this was also supplemented by insects and arachnids. Movement between nests and honeydew sources occurred from 06:00–13:00 and from 15:00–20:00, therefore only occurring during the cooler daylight hours. However, workers were found patrolling scale insects at all times of the day and night.

Type material examined. Camponotus detritus, Syntype workers. NAMIBIA: 'Damaraland Péringuey' (MCSN); 'Damaraland' (ZMHB).

Additional material examined. Specimens from: NAMIBIA: Namib Naukluft Park: Gobabeb (23.33S 15.02E), 20.x.1972, Swift & Kistner (BMNH); same locality but (TMSA); same locality but v.1959, R.F.Lawrence (SAMC); Homeb, 10mi ESE Gobabeb (23.38S 15.11E), 23.i.1972 (BMNH); Khomabes, 23.33S 14.59E, 9.ix.1987, 7.iii.1988, 9.iii.1988, H.G.Robertson (SAMC); near 'big slip face', 23.39S 15.20E, 11.ix.1987, H.G.Robertson (SAMC); Numabis Pan, 25.31S 15.35E, 7.iv.1986, J.Irish (SMWN); Sandwich Bay (23.20S 14.30E), v.1959, R.Paulian (TMSA); Sossusvlei, 24.42S 15.17E, 12.ix.1971; Tiras dunes, 26.01S 16.07E, 8.iv.1986, J.Irish; Tsondabvlei SE at 23.59S 15.27E, 25.viii.1989, J.Irish & E.Marais; Witberg, 24.48S 15.20E, 8.iv.1974, W.Wendt & H.Roth; same locality but 11.v.1969, 'CGC'; dunes W of Sossusvlei, 24.53S 15.08E, 13–14.ix.1971 (all SMWN). Rooibank (23.10S 14.39E), 4.v.1905, L.Schultze (ZMHB); Walfish Bay (22.59S 14.28E) (SAMC); same locality but xi.1891, Cleverley (SAMC); same locality but 1885, Nightingale (SAMC).

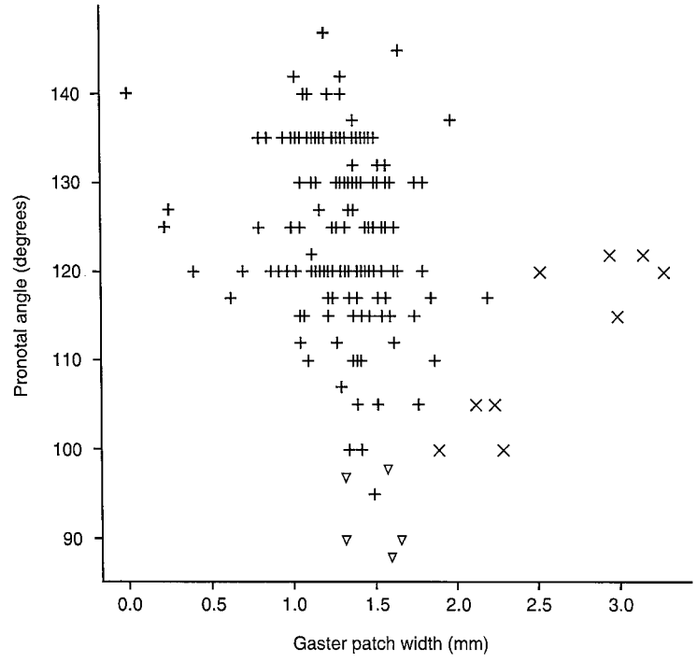


Fig. 12. Relationship between pronotal angle and gaster patch width for those species or populations that have distinct hairless patches on the gaster: *Camponotus detritus* (×); *C. fulvopilosus* (Karoo form) (+); *C. storeatus* (northern form) (▽).

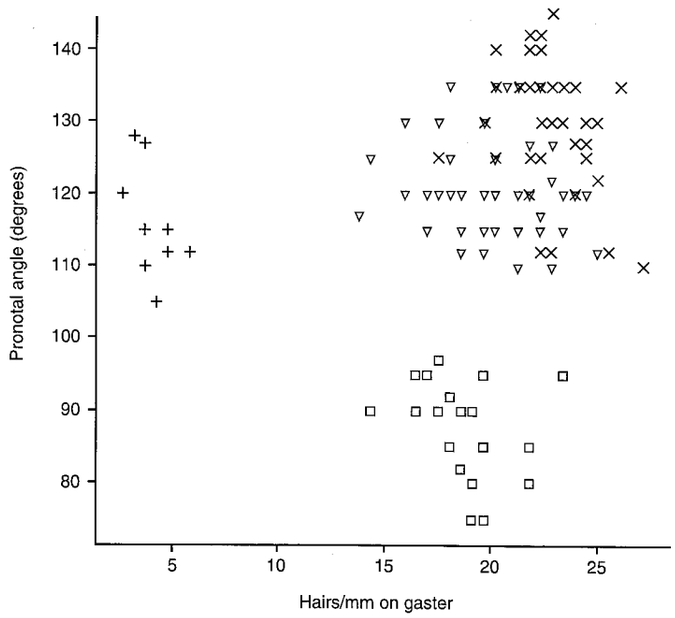


Fig. 13. Relationship between pronotal angle and gastral hair density for those species or populations that do not have distinct hairless patches on the gaster: *Camponotus brevisetosus* (+); *C. fulvopilosus* (savanna form) (▽); *C. fulvopilosus* (Cape West Coast form) (×); *C. storeatus* (southern form) (❑).

Camponotus fulvopilosus (De Geer), Figs 1, 8, 10, 12, 13

Formica fulvopilosa De Geer, 1778: 613. Major worker described by Forel (1879: 108) and male by Forel (1910: 25).

Formica pilosa Olivier, 1792: 498; Lepeletier 1835: 213.

Formica rufiventris Fabricius, 1804: 409; Lepeletier 1835: 213.

Camponotus fulvopilosus var. *detritoides* Forel, 1910: 25; Robertson 1990: 327.

Camponotus fulvopilosus var. *flavopilosus* Emery, 1895: 54; Robertson 1990: 327.

Diagnosis

Does not have the sharply angled pronotal humeri found in *C. storeatus* (Fig. 10). Gastral hairless patches are not as wide as in *C. detritus* (Fig. 8) or are absent. Hairs much more densely distributed on gaster than in *C. brevisetosus* (Fig. 8). Head and alitrunk usually black or brownish-black (except in Skeleton Coast population) whereas in the other three species they are usually brownish-red.

Redescription

Colour. Cuticle black to uniformly brownish-black except in some individuals from Skeleton Coast in which the head and alitrunk are reddish-brown.

Head. Mandibles finely reticulate basally, striate apically, with regularly-spaced, smeared foveae that are indistinct in some individuals. Eight mandibular teeth with teeth 5 and 6 partly fused. Line of hairs present on dorsal surface of mandible, each hair opposite a tooth. Fringe of hairs on ventral surface of mandibles parallel to apical margin and another parallel to external margin. Eye length 0.98–1.16 mm (n = 10), 0.19–0.21 times head width. Sides of head convex, occipital margin slightly concave. Head finely reticulate to reticulate-punctate and evenly pitted with groups of punctures that are faint to absent on occiput. Clypeus with short projecting median shelf with rounded corners. Fringe of hairs along median clypeal border.

Thorax and abdomen. Alitrunk uniformly reticulate-punctate, each puncture sharply defined. One hair occasionally present on pronotum, up to five on mesonotum and up to 19 on propodeum. Pronotum with obtuse humeri forming angles of

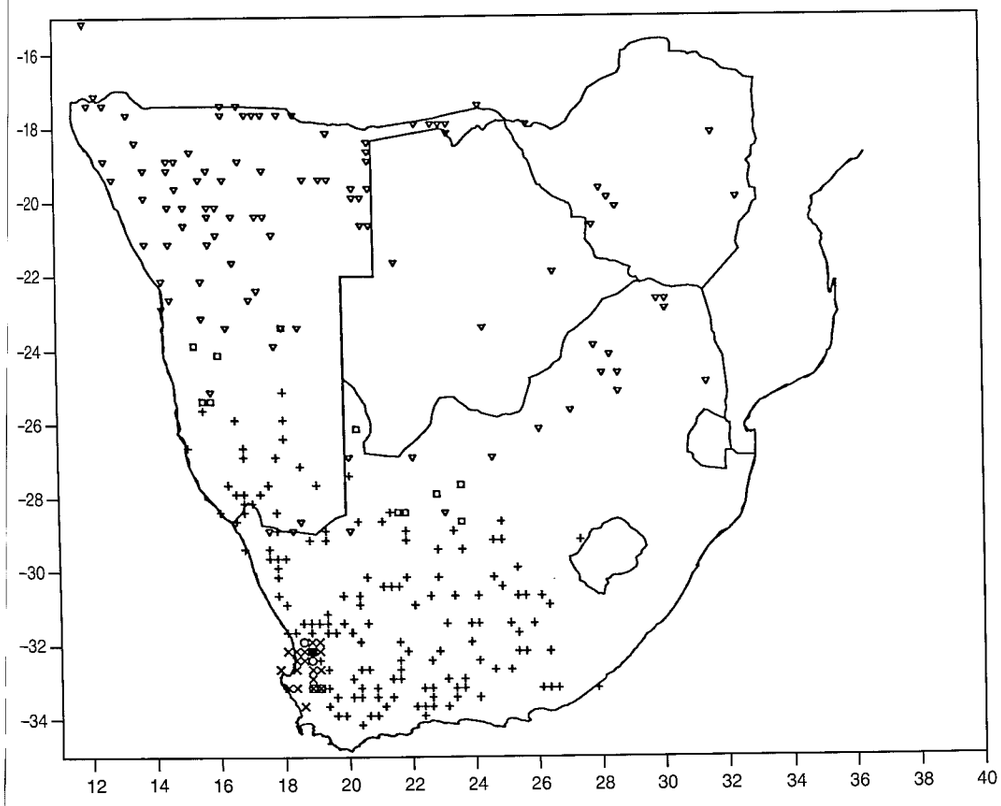


Fig. 14. Distribution of *Camponotus fulvopilosus* in southern Africa showing the main forms and intergrades between them: Cape West Coast form (×); Cape West Coast - Karoo intergrade (○); Karoo form (+); Karoo - savanna intergrade (❑); savanna form (▽).

95–147 degrees (Table 1). Tibiae angular with two dorsal and two ventral ridges, the surfaces between the ridges indented. Scale-like petiolar node with convex or slightly indented, blunt dorsal rim. A line of blunt hairs situated just posterior to dorsal rim. Gastral dorsum with mat of blunt, thick hairs, the distance between adjacent hairs less than half the length of a hair.

Remarks. Camponotus fulvopilosus has differentiated into three main forms (Fig. 14) over its distribution range. Karoo forms (Figs 1, 8) almost invariably have median bare patches on first, second (up to 2.19 mm wide; only one specimen with no patch) (Fig. 12) and third gastral tergites, while in Savanna and Cape West Coast forms, the entire gastral dorsum is usually covered with hairs (a few specimens have small gastral patches). In Cape West Coast forms the gastral hairs are a rich dark-golden-yellow, in Karoo forms the hairs range from golden-yellow to pale-yellow while in the Savanna forms they are off-white to pale-yellow. Gastral dorsum with fine, sharply defined, reticulate punctation and with little or no pubescence.

Distribution and habitat. Camponotus fulvopilosus is widely distributed throughout most of the arid, savanna and woodland areas of southern Africa (Fig. 14) but is limited to areas where the soils have a high sand content. Its distribution in savanna evidently extends as far north as Cabinda (Angola) and Zaïre (Wheeler 1922) but we were unable to trace any specimens north of the Cunene and Zambesi Rivers other than a few records from southern Angola and southern Zambia. Figure 14 shows only a few records from Botswana but this

is because of limited collecting and it is probably common throughout this region. It is absent from: grasslands; all types of fynbos except Dry Mountain Fynbos; Renosterbosveld; Indigenous Evergreen Forest; Valley Bushveld; and the Namib dune sea between Walvis Bay and Lüderitz (although it is found on the periphery of this region). It has not been recorded in northern KwaZulu-Natal despite this area containing open woodlands on sandy soils, seemingly favourable for *C. fulvopilosus*.

The Savanna form of *C. fulvopilosus* is found in the savanna and woodland areas as well as in the northern Namib. The transition zone between this form and the Karoo form corresponds closely with the transition between Savanna and Karoo biomes as shown by Rutherford & Westfall (1994). The Cape West Coast form seems to have differentiated as a result of isolation from the Karoo form by the Bokkeveld and Cedarberg mountain ranges.

Biology. Considering the abundance and wide distribution of *C. fulvopilosus*, it is remarkable that the only substantial research that has been conducted on this species is that of Lighton (1989), on their respiratory physiology. However, information on its biology is available from miscellaneous observations by ourselves and others. Nests are constructed in the soil under a large rock or fallen tree (Arnold 1924) or at the base of a small bush; they are not found in exposed ground although there might be bare ground nearby. They have independent claustral colony foundation, the queen initially producing small nanitic workers. The nests may become fairly large, occupying an area of about 40 × 30 cm and reaching a depth of about 30 cm. The nest is made up of galleries linked by short tunnels. When a nest is broken open, the workers stream towards the excavator with mandibles open and gasters cocked upwards (Fig. 1) and when close enough bend the gaster under the legs and spray formic acid that can be propelled over 15 cm through the air (this can be seen under special lighting conditions). They will unhesitatingly bite and the major workers can draw blood. Major workers function as soldiers and the ratio of majors to minors is highest when excavation begins, decreasing as the lower brood galleries are uncovered. The full excavation of a nest is best achieved by digging a pit in front of the nest and then excavating forward so that the pit separates the excavator from the workers streaming forward.

In Savanna, *C. fulvopilosus* workers forage in trees, presumably for honeydew from Homoptera. Workers in laboratory colonies of *C. fulvopilosus* feed on caterpillars, cockroaches, grasshoppers and mealworm larvae.

There are no known observations of mating flights in *C. fulvopilosus*. Most species of *Camponotus* seem to have crepuscular or nocturnal flights, judging from the large numbers of alates taken in light-traps. However, there are no records of *C. fulvopilosus* from light-traps, and as the closely related *Camponotus detritus* has been observed flying in mid-morning (Curtis 1985a), *C. fulvopilosus* is probably similar. As in most other *Camponotus* species, flights probably occur after rain. *Camponotus fulvopilosus* alates have been collected from nests during the months of October to March, with a peak in January (six of the 16 records), followed by December (four records), and October (three records). There are two records of males and winged queens without workers (suggesting that they were out of the nest) and these are both from January. Dealate queens have been recorded in April and May and a queen with three nanitic workers was collected on 27 August. Based on these observations, it seems that in most areas alates accumulate in nests in early summer between October and early February and that the alate flights occur mainly in late January. The only two March records of alates in nests were recorded simultaneously from the Namib Desert which usually receives late rains. Two of the three October records were from the Northern Province, South Africa, and Zimbabwe and alate flights perhaps occur earlier than January in these mesic savanna areas, where it is warmer and summer rains are earlier.

Type material examined. Formica fulvopilosa. Specimen not found in Naturhistoriska Riksmuseet, Stockholm, Sweden, and presumed to have been lost because it is not mentioned in an 1810 catalogue of De Geer's collection (P.I. Persson, pers. comm.). The type specimen was probably collected by Anders Sparrman in 1775–1776, as shortly after this trip to the 'Cape of Good Hope' he went to visit Baron Charles de Geer (Rookmaaker 1989).

Camponotus fulvopilosus var. *detritoides.* Syntype workers. SOUTH AFRICA: 'Glatkop S. Afr. (Schultze)'. 'No 551'. 'Coll. A. Forel' (29.23S 17.41E) (MHNG).

Camponotus fulvopilosus var. *flavopilosus.* Syntype workers. SOUTH AFRICA: 'De Aar Cape, C. Simon' (30.39S 24.01E) (MCSN).

Additional material examined. SAVANNA FORM, specimens from: ANGOLA: Lobito Bay (12.17S 13.32E), iv.1925 (AMNH). BOTSWANA: Ghanzi (21.34S 21.42E), 4.vi.1926, J.Maurice (BMNH); Kuke Pan (23.19S 24.27E), 21.iii.1930, Vernay-Lang Kal Exp (TMSA); Smiti (21.53S 26.38E), 15.ix.1975, A.Russell-Smith (BMNH). NAMIBIA: Aha-hills, 19.37S 20.58E, 9–28.i.1991, E.Marais; Auses waterhole, Hoanib River, 19.23S 12.53E, 7.xii.1971, 'MSP'; Botswana-SWA border, 2km S north Vet fence, 20.33S 20.59E, 20.xi–16.xii.1988, M.Paxton & E.Marais (all SMWN); Brandberg, parking area for White Lady Rock Painting, 21.06S 14.40E, 7–8.iii.1995, H.G.Robertson (SAMC); Bushmanland, 19.22S 19.36E, 8.i–1.ii.1991, E.Marais (SMWN); Christirina Farm, 23.20S 18.00E, iv.1992, C.R.Dickman (SAMC); 5km NE Dikweya, 17.41S 18.32E, 14–27.i.1993, E.Marais; 21km S Eenhana, 17.39S 16.16E, 25.i.1993, E.Marais; Edimba, 17.28S 16.23E, 14–26.i.1993, E.Marais; Enyana, 17.37S 17.25E, 14–27.i.1993, E.Marais (all SMWN); Etosha National Park, Bloubokkiedraai, 18.52S 16.58E, 13.x.1986, E.Marais & E.Griffin; Dorsland, 18.45S 14.48E, 8.x–14.xi.1986, E.Griffin; Dorsland, 18.46S 14.44E, 14.v–16.vi.1986, E.Griffin; Duikersdrink, 19.04S 14.43E, 8.x–14.xi.1986, E.Griffin; Gobaub, 19.18S 16.25E, 11.iv.1989, J.Irish & E.Marais; Ondundozonananandana Mountains, 19.15S 15.43E, 10.x–30.xi.1986, E.Griffin; Paradys Perdekamp, 18.38S 15.16E, 3.v.1987, J.Irish & E.Marais; Etudilondjaba, 17.36S 17.36E, 14–27.i.1993, E.Marais; Fransfontein, 20.13S 15.01E, 6.v.1986, J.Irish; Gwaa-nwi, 19.42S 20.24E, 8–30.i.1991, E.Marais; Hereroland West, 20.27S 17.34E, 19.vi–25.vii.1991, M.Pusch (all SMWN); Kalkveld, 40m NNW Okahandja (20.53S 16.11E), 18.ii.1963, F.Gaerdes; Kamanjab (19.38S 14.50E), i.1925, S.A.M.Expedition; same locality but 12.ix.1967, F.Gaerdes; Kaoko Otavi (18.18S 13.39E), iii.1926, S.A.M.Expedition (all SAMC); Kaokoland, dunes SW of 17.15S 12.10E, 17.x.1988, E.Griffin; Kaudom Game Reserve at 18.56S 20.57E, 11–30.i.1991, E.Marais; Kaudom River at 18.29S 20.56E, 12–30.i.1991, E.Marais; 2km S Kaudom River, 18.31S 20.56E, 12–30.i.1991, E.Marais (all SMWN). Khumib Valley, 8 mi inland, about 110 mi SW Ohopoho (18.49S 12.31E), 10.vi.1951, P.Brinck & G.Rudebeck (MZLU); Klaarwater Farm, 20.55S 17.46E, iv.1992, C.R.Dickman (SAMC); 26 km W Kongola, 17.48S 23.05E, 30.x–5.xi.1987, E.Marais; Koreangab Dam (not located), 12.ii.1971; 3km W Kuru, 19.56S 20.38E, 9–28.i.1991, E.Marais (all SMWN); 6km NW Leonardville (23.29S 18.43E), 15.v.1981, V.B.Whitehead (SAMC); M'Bela Farm, 23.45S 17.50E, iv.1992, C.R.Dickman (SAMC); Menziasubila Mulopo, 17.51S 23.27E, 25.xi.1991–5.i.1992, E.Marais; Mudumu National Park, 18.08S 23.26E, 25.xi–4.xii.1991, E.Marais; Münsterland 113 at 20.14S 15.53E, 8.ii.1986, J.Irish (all SMWN); Namib Naukluft Park, Ganab Campsite, 23.07S 15.33E, 12.ix.1987, 14.iii.1988, H.G.Robertson (SAMC); Nangera, 17.37S 18.08E, 14–27.i.1993, E.Marais (SMWN); Narugas (=Nurugas) (19.16S 18.46E), i.1919 (SAMC); Navachab 67, 22.01S 15.44E, iii.1988–24.iv.1988, S.Schubert; Neudamm (=Neudamm Experimental Farm) (22.26S 17.20E), 9.ii.1971; Northern Namib at 17.11S 12.17E, 24.iv.1991, E.Marais; Northern Vet. fence on Gam road, 20.31S 20.42E, 19.xi–15.xii.1988, M.Paxton & E.Marais; Odila River at 17.29S 16.51E, 23.i.1992, E.Marais; Okakutuwo, 17.27S 12.42E, 7–18.v.1991, E.Griffin; Omaruru River Mouth, 22.04S 14.17E, 22.vii.1971, M.-.L.Penrith & 'L.C.'; 2km W Omatako, 19.16S 19.18E, 8.i–1.ii.1991, E.Marais; Onamihongwa, 17.36S 17.02E, 14–26.i.1993, E.Marais (all SMWN); Ongombeanavita (21.34S 16.32E), 14.ii.1963 & 18.v.1963, F.Gaerdes (SAMC); Ongongo (=Warmquelle), 19.10S 13.49E, 9.iii.1995, H.G.Robertson (SAMC); Otjiveze, 17.38S 13.27E, 5–11.xi.1989, C.S.Roberts (SMWN); Outjo (20.07S 16.09E), i.1925, S.A.M.Expedition (SAMC); Palmwag, 19.53S 13.56E, 9.iii.1995, H.G.Robertson (SAMC); Rasputin 137, 20.15S 15.54E, 8–9.ii.1986, J.Irish (SMWN); 10km S Rundu, 18.00S 19.41E, 12.i.1993, E.Marais (SMWN); Sandfontein (28.42S 18.33E), i.1926, S.Gillman (SAMC); Sebraskop 410, 20.44S 15.09E, 13.iv.1987, J.Irish & E.Marais (SMWN); Swakopmund, 10mi ex, on Swakop River (22.38S 14.43E), 25.ii.1965, P.Lotter (SAMC); Te-Barku, 19.51S 20.26E, 9–30.i.1991, E.Marais (SMWN); Tsumeb (19.14S 17.43E), 1920, E.Kochig (SAMC); Verdeel 319, 20.14S 15.52E, J.Irish (SMWN); Walfish Bay (22.59S 14.28E), Nightingale (SAMC); Warmbad (19.13S 13.53E), ii.1925, S.A.M.Expedition (SAMC); Waterberg Plateau Park, 20.19S 17.20E, 18.vi–24.vii.1991, M.Pusch; Weissenfels 22, 23.16S 16.27E, 19.v.1972, H.Strauss & de Quarto; Weissenfels 35 at 21.04S 15.59E, 11.ii.1986, J.Irish; Welkom 680, 20.09S 14.35E, 29–31.x.1985, J.Irish; West Caprivi Park, 3km NE Chwaha River, 17.58S 22.28E, 4–10.iv.1990, E.Marais; 2km SE Qeya River, 17.54S 22.50E, 4–

10.iv.1990, E.Marais (all SMWN). Windhoek (22.34S 17.06E), 1.xii.1959, F.Honiball (SAMC); Wolwedans 144, 25.06S 15.59E, 12–18.iii.1992, E.Griffin (SMWN). SOUTH AFRICA: Bezuidenhoutskraal (25.08S 28.44E), 12.xii.1957, J.J.Nel; Boschdraai Farm, NE Vaalwater, 24.12S 28.17E, 13.vi.1987, H.G.Robertson; Goodhouse (28.54S 18.15E), xi.1936, S.A.M.Expedition; 2km W Mpzema, Venda, 22.56S 30.09E, 20.x.1987, H.G.Robertson; Naboomspruit (24.31S 28.43E), 14.xii.1963, M.Johannsmeier; Nylsvley, 24.40S 28.43E, 16.iv.1987, H.G.Robertson; Poffadder (28.51S 20.04E), 26.ix.1968, A.A.Boonzaaier; Postmasburg (28.19S 23.04E), x.1939, S.A.M.Expedition; Rietfontein, Kalahari (26.45S 20.02E), 23.vii.1963, F.Gaerdes (all SAMC); Surprise 33, Kuruman, 26.56S 22.05E, 1–3.vii.1986, N.M.B. Entomology Dept. (BMSA); Vioolsdrift (28.46S 17.38E), 27.ix.1968, A.A.Boonzaaier; Vryburg (26.58S 24.44E), 1904, F.W.Jones (SAMC). ZAMBIA: Livingstone (17.51S 25.51E), Powell (SAMC); Sesheke - Katima Molilo (=Katima Mulilo) (17.27S 24.15E), 25.vii.1905, Seiner (ZMHB). ZIMBABWE: Birchenough Bridge (19.57S 32.20E), 27.ix.1949, Nat Mus S Rhodesia; Bulawayo (20.10S 28.43E), v.1917, R.W.E.Tucker; Nyamandhlovu (19.50S 28.16E), 25.iii.1961, Nat Mus S Rhodesia; Plumtree (20.30S 27.50E), 17.xii.1911, G.Arnold; Sawmills, Umgusa River (19.31S 28.02E), 1.v.1917, Rhodesia Museum; Springvale (18.10S 31.37E), 12.xi.1911, G.Arnold; Victoria Falls (17.56S 25.50E), xii.1914 & ii.1957, Rhodesia Museum; same locality but vii.1911, L.A.Péringuey; same locality but i.1957, iii.1957, G.Arnold (all SAMC).

SAVANNA - KAROO TRANSITION. NAMIBIA: Blässkranz 7 at 24.06S 16.14E, 12–14.x.1984, J.Irish; Christirina 259, Nouas, 23.25S 18.03E, 21.xi.1989, C.S.Roberts; Gorrasis 99 (=Gorasis), 25.18S 15.56E, 12–15.ii.1973; Haibvlakte, 25.29S 15.42E, 5–6.iv.1986, J.Irish; Tsondabvlei SE, 23.59S 15.27E, Namib Naukluft Park, 25.viii.1989, J.Irish & E.Marais (all SMWN). SOUTH AFRICA: Dingle, 29mi from Olifantshoek on Kuruman road (27.49S 22.56E), 21.x.1963, J.J.Cillie; Kamqua, Kalahari Gemsbok Park (26.01S 20.24E), 10.viii.1964, A.J.Prins; Karreeboom vlakte, 43mi from Upington on Kuruman road (28.18S 21.58E), 21.x.1963, A.J.Prins; Klippan, 17mi from Papkuil on Griekwastad road (28.38S 23.31E), 22.x.1963, J.J.Cillie; 15mi from Kuruman on Griekwastad road (27.40S 23.31E), 22.x.1963, J.J.Cillie; 22mi from Upington on Kuruman road (28.22S 21.36E), 19.x.1963, A.J.Prins (all SAMC).

KAROO FORM. NAMIBIA: Aukam 104, 26.49S 16.56E, 7–19.viii.1990, C.S.Roberts & E.Marais; Berseba 170, 25.12S 18.03E, 7–29.xi.1992, E.Marais; Blinkoog, 27.40S 19.04E, 14–17.x.1971; Boomrivier, 28.01S 17.04E, 13–26.xi.1992, E.Marais; Dassiefontein 87, 27.13S 18.35E, 7–27.xi.1992, E.Marais; Gemsbokberg, 28.23S 17.48E, 9–26.xi.1992, E.Marais; Hobas 374, 27.37S 17.43E, 19.i–16.ii.1985, J.le Roux; Khabus 146, 26.17S 18.14E, 13.ii–14.iii.1988, 14.iii–14.iv.1988, 8.xii.1988–6.i.1989, N.Olivier & G.Olivier; Mara 114, 27.54S 17.19E, 24.xi.1992, E.Marais; Namuskluft 88, 27.55S 16.49E, 10.x.1970 & 11–13.x.1970; Numabis Pan, 25.31S 15.35E, 7.iv.1986, J.Irish; Obib dunes at 27.58S 16.31E, 15.xi.1992, Huns Exp. '92; E of Oranjemund, 28.23S 16.08E, 8–11.xi.1986, E.Griffin; 10km NW Rosh Pinah, 27.54S 16.42E, 13.viii.1990, C.S.Roberts & E.Marais; Sendelingsdrift, 28.07S 16.50E, 14–29.ix.1994, E.Marais; Swartkop, 28.20S 16.46E, 14–29.ix.1994, E.Marais; 9km W Tses, 25.53S 18.03E, 7–29.xi.1992, E.Marais (all SMWN). SOUTH AFRICA: Aberdeen (32.29S 24.01E), 26.v.1987, A.J.Prins & A.Roux; same locality but xi.1935, S.A.M.Expedition; 80km SE Aberdeen, 33.00S 23.33E, 5.ix.1988, H.G.Robertson; Aggenys (29.12S 18.51E), 8–9.ii.1989, 22.ix.1989, W.R.J.Dean (all SAMC); Allemans Drift 37, 30.33S 25.23E, 15–17.vii.1975, G.W.Ferreira (BMSA); Augusfontein (=Augustfontein), Calvinia (31.37S 19.21E), ix.1947, S.A.M.Expedition; Barrydale (33.54S 20.44E), 15.iv.1960, F.W.Gess; 2mi from Barrydale on Ladismith road (33.53S 20.45E), 5.v.1966, A.J.Prins; Baviaanskop, near Jackalswater (28.56S 17.50E), ix.1939, R.H.N.Smithers; Beaufort West (32.21S 22.35E), iv.1984, A.J.Prins; Beaufort West, Nieuwveldt (32.21S 22.35E), xi.1935, S.A.M.Expedition; Beaufort West, Oukloof (32.10S 21.46E), i.1949, H.Zinn & A.J.Hesse; Beauvillan, 'plaas langs Oranje Rivier' (nr Alexander Bay) (28.31S 16.38E), 10.ix.1968, A.J.Prins; Blokzynkolk, 33mi from Brandvlei on Kenhardt road (30.03S 20.40E), 18.x.1963, A.J.Prins; Blomplaas, 60km SE Aberdeen, 32.52S 23.40E, 5.ix.1988, H.G.Robertson; Bloutoring Station, 30mi E Touws River (33.29S 20.19E), xii.1962, S.A.M.Expedition; Bontebok National Park (34.04S 20.27E), 8.xi.1964, J.J.Cillie; same locality but 18.vi.1964, A.J.Prins; Brandkop, 9mi from Nieuwoudtville on Loeriesfontein road (31.15S 19.12E), 22.iv.1963, J.J.Cillie & A.J.Prins; Brandvlei (30.31S 20.29E), 28.v.1986, A.J.Prins; 3mi from Brandvlei on Williston road (30.31S 20.27E), 23.iv.1963, J.J.Cillie; 2mi from Britstown on Vosburg road (30.35S 23.28E), 14.i.1958, J.H.Grobler;

Calvinia (31.25S 19.45E), v.1986, A.J.Prins; same locality but 1876, J.G.Gamble; same locality but 1903, G.French; 14mi from Calvinia on Nieuwoudtville road (31.30S 19.34E), 4.i.1962 & 6.i.1962, J.J.Cillie; 32mi from Calvinia on Niewhoudtville road (31.28S 19.19E), 6.i.1962, A.J.Prins; 76mi from Ceres on Sutherland road (32.48S 20.14E), 28.viii.1962, A.A.Boonzaaier; Clanwilliam (32.09S 18.57E), 1897, L.Malley; 23mi from Colesberg on Petrusville road (30.28S 24.52E), 19.iii.1969, A.A.Boonzaaier; Constable (33.14S 20.17E), xii.1962, S.A.M.Expedition; Cradock (32.11S 25.38E), 22.xi.1960, A.J.Prins (all SAMC); Dassiefontein & Sneeukop, 30.09S 17.59E, 20–22.ix.1988, J.Irish & E.Marais (SMWN); De Aar (30.39S 24.01E), vii.1925, F.Beyers (SAMC); De Doorns (33.29S 19.41E), 17.v.1960, A.J.Prins (SAMC); De Kalk 71, 29.02S 24.58E, 16–18.xi.1981, S.Louw & Gaaje (BMSA); 2mi from De Rust on Oudtshoorn road (33.31S 22.30E), 21.xi.1962, A.J.Prins; 3mi from De Rust on Prince Albert road (33.27S 22.34E), 21.xi.1962, J.J.Cillie; 30mi from De Rust on Uniondale road (33.30S 23.00E), 6.viii.1965, A.A.Boonzaaier; Dikbome, Die Koup (32.54S 21.22E), iv–v.1950, H.Zinn; Dreunberg, Burgersdorp (30.58S 26.23E), xi.1959, S.A.M.Expedition; Fraserburg (31.55S 21.31E), xii.1927, A.J.Hesse; same locality but i.1930, A.J.Hesse; Garies (30.33S 17.59E), vi.1930, S.A.M.Expedition; same locality but 5.x.1959, A.J.Prins; Gough (=Die Koup) (32.45S 21.40E), ix.1937, S.A.M.Expedition; 20mi from Grahamstown on Bedford road (33.13S 26.23E), 18.xi.1965, A.A.Boonzaaier; Groenfontein, 20mi from Ceres on Citrusdal road (33.07S 19.21E), 30.viii.1962, A.J.Prins (all SAMC); Groenkloof 294, 29.02S 27.24E, 18–29.ix.1978, N.M.B. Museum Staff (BMSA); Grootfontein Agricultural College, Middelburg (31.29S 25.01E), 24.vii.1968, A.A.Boonzaaier (SAMC); Hardevlak, 29.25S 23.36E, 7.ix.1993, J.Irish (BMSA); Hex River (33.41S 19.27E), xii.1884; Jagersfontein, Fauresmith (29.46S 25.26E), 28.xii.1962, F.Honiball; Jakopsplaas, 21mi from Williston on Calvinia road (31.23S 20.37E), 23.iv.1963, J.J.Cillie; Kimberley (28.44S 24.46E), 1920, J.H.Power; 37mi from Kimberley on Hopetown road (29.13S 24.31E), 19.vii.1968, A.A.Boonzaaier; Klaarstroom, Prince Albert (33.20S 22.32E), x.1952, S.A.M.Expedition; Knersvlakte (31.23S 18.38E), x.1950, S.A.M.Expedition; Koup Siding (33.08S 21.16E), x.1952, S.A.M.Expedition; Kromrivier Farm, Cedarberg, 32.32S 19.17E, 13.viii.1989, H.G.Robertson; Laingsburg (33.12S 20.51E), 17.v.1960, A.J.Prins; Lammerskraal (33.01S 22.36E), ix.1947, S.A.M.Expedition; Langvlei, Worcester (33.46S 19.44E), 18.v.1960, A.J.Prins; Lekkeroog, 40mi from Loeriesfontein on Brandvlei road (30.44S 19.59E), 22.iv.1963, J.J.Cillie; Liebendal (31.35S 18.26E), xi.1956, S.A.M.Expedition; Merweville (32.40S 21.31E), i.1959, H.Zinn; Middelburg (31.29S 25.01E), 23.xi.1960, A.J.Prins; Middelplaas, 7mi from Springbok on Gamoep road (29.43S 17.59E), 20.iv.1963, A.J.Prins; 2mi from Middelpos on Sutherland road (31.55S 20.15E), 24.iv.1963, J.J.Cillie; Modderfontein Farm, 21km SW Willowmore on R57, 33.25S 23.20E, 7.ix.1988, H.G.Robertson; Mountain Zebra National Park (32.14S 25.28E), 24.v.1987, A.J.Prins & A.Roux; Nababeep (29.35S 17.47E), 6.vii.1960, A.J.Prins; Niekerkshoop (29.19S 22.50E), x.1939, S.A.M.Expedition; Nieuwoudtville (31.23S 19.06E), 15.i.1958, J.H.Grobler; Nieuwoudtville, Brandkop (31.15S 19.12E), ix.1941, S.A.M.Expedition; 7mi from Nieuwoudtville on Vanrhynsdorp road (31.23S 19.01E), 15.i.1958, J.H.Grobler (all SAMC); Obobogorop, 120mi NW Upington (27.18S 20.04E), 14–19.xi.1950, P.Brinck & G.Rudebeck (MZLU); 2mi SE Olifants River Mouth (31.43S 18.14E), 17.xi.1962, R.Matthews; Onder-Downes (31.37S 20.07E), 24.iv.1963, A.J.Prins & J.J.Cillie; Onseepkans (28.45S 19.19E), 26.ix.1968, A.A.Boonzaaier; Ooskloof - Tussen die Randte, Jagersfontein (29.46S 25.25E), 18.xii.1963, F.Honiball; Oudtshoorn (33.35S 22.12E), 14.v.1960, A.J.Prins; Oudtshoorn, Zebra (33.46S 22.19E), x.1951, S.A.M.Expedition; Papendorp (31.42S 18.13E), x.1950, S.A.M.Expedition; 5mi from Petrusville on Colesberg road (30.08S 24.41E), 19.iii.1969, A.A.Boonzaaier; Pienaarsfontein, 61mi from Ceres on Sutherland road (32.47S 20.03E), 28.viii.1962, A.A.Boonzaaier (all SAMC); Pofadder (29.08S 19.24E), 10.xi.1950, P.Brinck & G.Rudebeck (MZLU); Poortje, 49mi from Prieska on Carnavon road (30.14S 22.46E), 23.x.1963, A.J.Prins; Port Nolloth (29.17S 16.51E), viii.1890, R.M.Lightfoot; same locality but A.J.Prins; Prince Albert Road Station (32.59S 21.41E), vii.1945, A.J.Hesse; Putsonderwater (29.14S 21.53E), x.1939, S.A.M.Expedition; Richmond (31.25S 23.57E), 23.xi.1960, A.J.Prins & J.J.Cillie; same locality but 13.xii.1962, F.Honiball; Riemhoogte on N1 highway, 32.09S 22.53E, 5.vii.1987, H.G.Robertson; Rietbron (32.54S 23.09E), 12.vii.1962; Rietfontein Oos, 21mi from Williston on Calvinia road (31.23S 20.37E), 23.iv.1963, A.J.Prins; Robertson (33.48S 19.53E), 18.v.1960, J.J.Cillie; Rooidam, 56mi from Calvinia

on Brandvlei road (30.58S 20.19E), 17.x.1963, J.J.Cillie; Rooinek (33.20S 20.55E), i.1949, H.Zinn & A.J.Hesse; Scheurfontein, 23mi from Richmond (31.18S 24.08E), 5.xii.1960, A.de Weerdt; Spectakel (29.39S 17.35E), x.1890, R.M.Lightfoot; Spektakel Myn, 30mi from Nababeep (29.39S 17.35E), 6.vii.1960, A.J.Prins; Springbok (29.40S 17.53E), 2.i.1954, Nat Mus S Rhodesia; same locality but 6.x.1959, A.J.Prins (all SAMC); Steinkopf (29.18S 17.43E), viii.1904, L.Schultze (ZMHB); Steynsburg (31.18S 25.50E), 27.ix.1960, P.de Weerdt; Strausspplaas, 12mi from Calvinia on Ceres road (31.42S 19.44E), 25.viii.1962, A.A.Boonzaaier; Tankwa Karoo (32.38S 20.23E), i.1949, H.Zinn & A.J.Hesse; Tarkastad (32.01S 26.16E), 22.xi.1960, A.J.Prins & J.J.Cillie; Touws River (33.20S 20.03E), 17.v.1960, A.J.Prins; same locality but 16.x.1966, S.A.M.Expedition; 18mi E Touws River on Hondewater road (33.27S 20.17E), xii.1962, S.A.M.Expedition; Tussen Die Riviere, near camp site, 30.30S 26.07E, 31.iii.1987, H.G.Robertson; Upington (28.27S 21.15E), 10–12.x.1966, S.A.M.Expedition; 15mi from Upington on Kuruman road (28.23S 21.29E), 19.x.1963, J.J.Cillie; 16mi from Upington on Kakamas road (28.39S 21.02E), 25.ix.1968, A.A.Boonzaaier; Van der Kloofdam, Hopetown (30.00S 24.44E), 19.iii.1969, A.A.Boonzaaier; Van Rhyn's Pass (31.23S 19.01E), x.1961, S.A.M.Expedition; 5mi S Van Rhyn's Pass (31.26S 18.59E), viii.1961, S.A.M.Expedition; 5mi from Vanrhynsdorp on Nieuwoudtville road (31.34S 18.49E), 24.viii.1962, A.A.Boonzaaier; Vanwyksvlei district, north (30.08S 21.53E), 2.ii.1989, W.R.J.Dean; 6mi from Vanwyksvlei on Brandvlei road (30.23S 21.44E), 18.viii.1964, A.J.Prins; 31mi from Vanwyksvlei on Brandvlei road (30.23S 21.24E), 18.viii.1964, J.J.Cillie; 56mi from Vanwyksvlei on Brandvlei road (30.23S 21.02E), 18.viii.1964, A.J.Prins; Venterstad region (30.53S 25.53E), x.1935, S.A.M.Expedition; Verlatenkloof, 23mi from Sutherland on Matjiesfontein road (32.32S 20.36E), 29.viii.1962,. A.J.Prins; Verwoerddam, (30.38S 25.30E), 20.iii.1969, A.A.Boonzaaier; Victoria West district (31.23S 23.08E), iii.1931, S.A.M.Expedition; 12mi from Vosburg on Calvinia road (30.39S 22.42E), 14.i.1958, J.H.Grobler; Vrolikheid Nature Reserve (33.55S 19.52E), 5.xii.1988, P.D.Theron; Willowmore (33.18S 23.29E), 1.i.1914, Rhodesia Museum; 12km N Willowmore, 33.11S 23.26E, 8.ix.1988, H.G.Robertson; 6 km N Willowmore, 33.13S 23.28E, 8.ix.1988, H.G.Robertson; 16 km N Willowmore on Brakfontein Farm, 33.09S 23.26E, 5.ix.1988, H.G.Robertson; 2mi 'van Worcester naby indraai na nasionale pad' (33.38S 19.25E), 27.viii.1962, A.A.Boonzaaier; Wuppertal, 32.16S 19.13E, 9.viii.1989, H.G.Robertson; near Doornbosch (33.26S 24.08E), ix.1961, S.A.M.Expedition (all SAMC).

KAROO - CAPE WEST COAST TRANSITION. SOUTH AFRICA: Blikhuis, 12mi from Porterville on Gouda road (33.05S 18.59E), 7.xii.1962, J.J.Cillie; 13mi from Citrusdal on Clanwilliam road (32.25S 18.58E), 17.vi.1960, A.J.Prins; Clanwilliam (32.09S 18.57E), 17–18.vi.1960, A.J.Prins; 10mi from Clanwilliam on Vanrhynsdorp road (32.04S 18.49E), 18.vi.1960, A.J.Prins; Pakhuis Pass E (32.08S 19.08E), ix.1947, S.A.M.Expedition; Kleinbergrivier, 12mi from Gouda on Porterville road (33.11S 19.10E), 9.viii.1963, J.J.Cillie; Zwartdorings, 26mi from Clanwilliam on Vanrhynsdorp road (31.52S 18.38E), 19.iv.1963, J.J.Cillie (all SAMC).

WEST COAST FORM. SOUTH AFRICA: Aurora (32.42S 18.29E), 5.xii.1962; Blikhuis, 10mi from Porterville on Gouda road (33.05S 18.59E), 23.viii.1962, A.J.Prins; Bulhoek (=Bulshoek), Klaver (31.59S 18.47E), x.1950, S.A.M.Expedition; Citrusdal (32.36S 19.01E), xi.1948, S.A.M.Expedition; 8mi N Citrusdal (32.30S 19.00E), ix.1961, S.A.M.Expedition; Clanwilliam (32.09S 18.57E), 16.i.1958, J.H.Grobler; 1mi from Clanwilliam on Cape Town road (32.10S 18.52E), 4.i.1962, J.J.Cillie; 2mi from Clanwilliam on Springbok road (32.09S 18.52E), 18.iv.1963, J.J.Cillie; 3mi from Clanwilliam on Graafwater road (32.10S 18.50E), 17.vi.1960, A.J.Prins; 7mi from Clanwilliam on Calvinia road (32.08S 18.57E), 4.i.1962, A.J.Prins; 7mi from Clanwilliam on Lamberts Bay road (32.10S 18.49E), 16.i.1958, J.H.Grobler; Dassenberg, Kalabaskraal (33.34S 18.39E), 17.x.1960, A.A.Boonzaaier & J.J.Cillie; Doringbos, 23mi from Clanwilliam on Calvinia road (31.58S 19.14E), 5.i.1962, J.J.Cillie; Elands Bay (32.18S 18.21E), 7.xii.1962; Graafwater (32.09S 18.36E), x.1947, S.A.M.Expedition; 2mi from Graafwater on Clanwilliam road (32.09S 18.38E), 3.i.1962, A.J.Prins (all SAMC); Grey's Pass, 5mi SW Citrusdal (32.37S 18.58E), 7.xi.1950, P.Brinck & G.Rudebeck (MZLU); Halfmanshof, 10mi from Porterville on Gouda road (33.08S 18.27E), 23.viii.1962, J.J.Cillie; Het Kruis (32.36S 18.45E), x.1947, S.A.M.Expedition; Kleinbergrivier, 12mi from Gouda on Porterville road (33.11S 19.10E), 9.viii.1963, A.J.Prins; Lamberts Bay (32.06S 18.19E), 17.vi.1960, A.J.Prins; Leipoldtville, Eland's Bay (32.14S 18.29E), xi.1948, S.A.M.Expedition; Narsdou Pass, 8mi from Clanwilliam to Van Rhynsdorp (32.02S 18.48E), 4.i.1962, A.J.Prins; Olifants River, between Citrusdal and Clanwilliam (32.25S 18.58E), iii.1935, S.A.M.Expedition; Pakhuis, 16mi from Clanwilliam on Calvinia road (32.07S 19.03E), 5.i.1962, A.J.Prins; Pakhuis Pass (32.09S 18.06E), ix.1961, S.A.M.Expedition; Paleisheuwel (32.28S 18.43E), xi.1948, S.A.M.Expedition; Philadelphia (33.40S 18.35E), 27.x.1959, A.J.Prins; Piquetberg (32.55S 18.45E), vi.1886; same locality but 2.xi.1961, A.A.Boonzaaier; 1mi from Redelingshuis on Piketberg road (32.29S 18.34E), 7.xii.1962; Saldanha Bay (33.00S 18.03E), ix.1960, S.A.M.Expedition; Stompneusbaai (32.44S 17.58E), 13.i.1965, J.J.Cillie (all SAMC).

Camponotus storeatus Forel, Figs 9, 11–13

Camponotus fulvopilosus subsp. *storeatus* Forel, 1910: 26.

Camponotus storeatus Forel: Robertson 1990: 327.

Diagnosis

Major workers distinguished mainly by the acute pronotal humeri. Within its geographical range, *C. storeatus* can be distinguished from *C. fulvopilosus* by having cream-coloured hairs on the gaster rather than the yellow hairs found in the Karoo form of *C. fulvopilosus*, and by having a reddish rather than black head and alitrunk. The southern form of *C. storeatus* also lacks median bare patches on the gaster, as found in the Karoo form of *C. fulvopilosus*. *Camponotus fulvopilosus* specimens from the Skeleton Coast in Namibia closely resemble *C storeatus* because they have a reddish cuticle and cream-coloured hairs but the majors are still distinguished by the angle of the pronotal humeri. However, queens of *C. fulvopilosus* from this region are virtually indistinguishable from the southern form of *C. storeatus*.

Redescription

Colour. Head, alitrunk and petiole brick-red to dark-red to brown-black, gaster black.

Head. Mandibles finely reticulate basally, striolate apically, with regularly spaced, smeared foveae. Eight mandibular teeth with some of teeth 4–8 partly fused. Line of hairs present on dorsal surface of mandible, each hair facing into the cavity between two teeth. Fringe of hairs on ventral surface of mandibles parallel to apical margin and another parallel to external margin. Eye length 1.04–1.14 mm (n = 10), 0.21–0.24 times head width. Sides of head convex and occipital margin slightly concave. Head finely reticulate and evenly pitted with groups of punctures. Clypeus with short projecting median shelf with rounded corners. Fringe of hairs present along median clypeal border.

Thorax and abdomen. Alitrunk uniformly reticulate-punctate, each puncture sharply defined. Up to three erect hairs on pronotum, up to five on mesonotum and up to 10 on propodeum (in many specimens there are no hairs on the propodeum). Pronotum with distinct humeri forming an angle of 75–98 degrees (Table 1). Tibiae angular with two dorsal and two ventral ridges, the dorsal and lateral surfaces indented. Scale-like petiolar node with convex or slightly indented blunt dorsal rim. A few blunt hairs situated just posterior to dorsal rim. Gastral dorsum with mat of blunt, thick hairs, the distance between adjacent hairs less than half the length of a hair. Northern forms have median bare patches on second tergite (1.32–1.66 mm wide) and third tergite of gaster, while in southern forms the entire gastral dorsum is covered with hairs. Gastral dorsum with fine, sharply defined, reticulate punctation and with no pubescence.

Distribution and habitat. Camponotus storeatus occurs in the southern Cape (Fig. 15), mainly in the Karoo on north-facing slopes. There are few records of the northern form of *C. storeatus* and from the distribution map, it is uncertain whether it actually has a distribution north of the southern form. With the exception of an easterly record of minor workers from near Doornbosch, all the records for the northern form are west of the records for the southern form. We have yet to discover a transition zone between the two forms and there is a possibility that they are separate species.

Camponotus storeatus and *C. fulvopilosus* occur sympatrically at some sites. At Gwarriepoort, 21 km southwest of Willowmore, we found *C. storeatus* on the north-facing slope that was covered with large rocks embedded in fairly hard, clay soils and which had succulents such as *Euphorbia* spp. *Camponotus fulvopilosus*, on the other hand, was found only on the river floodplain, at the base of the slope, which had sandy soils. Neither the south-facing slope, covered mainly by renosterbos *Elytropappus rhinocerotis* (L.f.), nor a patch of *Acacia karoo* Hayne woodland

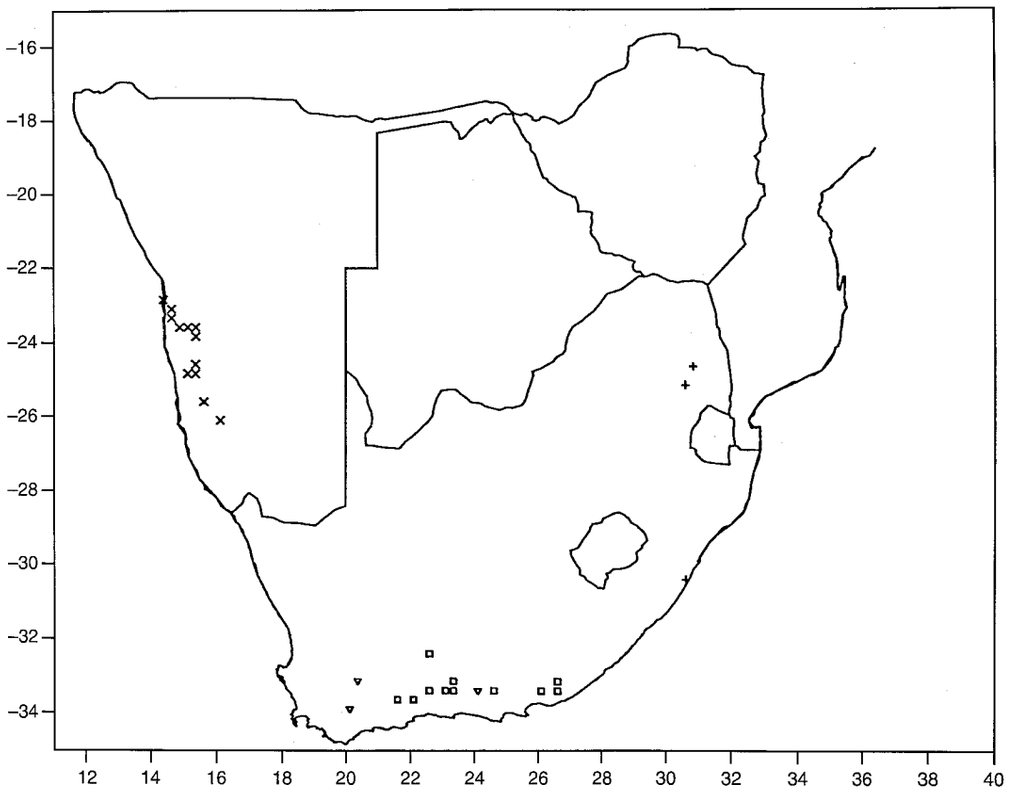


Fig. 15. Distribution of *Camponotus brevisetosus* (+); *C. detritus* (×); *C. storeatus* (northern form) (▽); *C. storeatus* (southern form) (❑).

on the north-facing slope, harboured the two *Camponotus* species. Soil type was possibly the main factor separating the two species at this site, *C. fulvopilosus* preferring the more sandy soils. Another site, north of Willowmore, had large numbers of *Euphorbia mauritanica* L. bushes which were in full flower with *Camponotus* workers of both species feeding on them. Of 25 bushes examined, 10 harboured only *C. fulvopilosus*, 11 attracted only *C. storeatus*, and four had both species present. Perhaps the soils here were possibly a sufficient mix of sand and clay to be suitable for both species.

In September 1995, one of us (HGR) found *C. fulvopilosus* and the northern form of *C. storeatus* in the vicinity of the old fort in Kogmanskloof, southwest of Montagu. *Camponotus fulvopilosus* colonies were found on a northwest-facing slope and *C. storeatus* on a northeast-facing slope. The northeastern slope was slightly more vegetated and rocky than the northwestern slope but otherwise there were no obvious differences between them.

Biology. There are no records of alates from nests of *C. storeatus* so timing of nuptial flights is unknown. Two wingless queens were collected in June and a queen with nanitic workers was collected in early September so nuptial flights could occur in late summer. At Gwarriepoort, five large nests were found, each under a large embedded rock and with well defined, closely packed galleries.

Type material examined. Camponotus fulvopilosus subsp. *storeatus*. Holotype minor worker. SOUTH AFRICA: 'Willowmore Cape Colony Brauns' (33.18S 23.29E) (MHNG).

Additional material examined. SOUTHERN FORM. Specimens from: SOUTH AFRICA: Alicedale (33.19S 26.05E), 15.viii.1914, F.Cruden (AMGS); Beaufort West, Nieuwveldt (32.21S 22.35E), xi.1935, S.A.M.Expedition; 3mi from De Rust on Prince Albert road (33.27S 22.34E), 21.xi.1962, J.J.Cillie; Grahamstown (33.18S 26.32E), ii.1933, R.F.Lawrence (all SAMC); Huisriver Pass, 5mi SW Calitzdorp (33.30S 21.37E), 13–15.xi.1972, J.van Reenen & Mathabathe (TMSA); Klaarstroom (33.20S 22.32E), 21.i.1964, A.J.Prins; same locality but x.1952, S.A.M.Expedition; Meiringspoort, 13mi from De Rust on Klaarstroom road (33.24S 22.34E), 21.i.1964, A.J.Prins; Modderfontein Farm, 21km SW Willowmore on R57, 33.25S 23.20E, 7.ix.1988, H.G.Robertson; Oudtshoorn (33.35S 22.12E), 21.xi.1962, J.J.Cillie; Pluto's Vale, near Grahamstown, 33.14S 26.42E, 31.x.1992, M.H.Villet; Uniondale District (33.23S 23.08E), x.1952, S.A.M.Expedition; Waaipoort, 33.16S 24.30E, 7.vii.1995, H.G.Robertson; Willowmore (33.18S 23.29E), 6.i.1914, G.Arnold; same locality but 8.ix.1988, H.G.Robertson; Willowmore, Vondeling (33.20S 23.08E), x.1952, S.A.M.Expedition; 12km N Willowmore, 33.11S 23.26E, 8.ix.1988, H.G.Robertson; 6km N Willowmore, 33.13S 23.28E, 8.ix.1988, H.G.Robertson (all SAMC).

NORTHERN FORM. SOUTH AFRICA: Constable (33.14S 20.17E), xii.1962, S.A.M.Expedition; Kogmanskloof, 33.48S 20.06E, 15.ix.1995, H.G.Robertson; Kraairivier, 24mi from Matjiesfontein, Ceres Karoo (33.07S 20.21E), viii.1950, H.Zinn; Montagu (33.47S 20.07E), i.1920, C.P.van der Merwe (all SAMC).

DISCUSSION

Members of the *C. fulvopilosus* species-group are large, colourful and conspicuous and have therefore been collected more thoroughly than is usual for African ants. These factors, as well as the wealth of new material that we have been able to obtain from pitfall trapping by staff at the National Museum of Namibia and from the collecting efforts of A.J. Prins, have enabled us to analyse the distribution of this species-group in considerably greater detail than has previously been possible for any other African ant group.

Camponotus detritus, *C. storeatus*, and *C. brevisetosus* probably arose from small peripheral isolates of *C. fulvopilosus*. Speciation of the Namib species, *C. detritus*, may have occurred in a small population of *C. fulvopilosus* that became separated from the parent population by newly formed inhospitable dune systems. *Camponotus detritus* does not exist on the large dunes themselves but only in the valleys between dunes where grasses with associated Homoptera are present. *Camponotus fulvopilosus* has been collected from dunes in the Skeleton Coast region, where *C. detritus* does not occur, but it has never been found in the main dune sea south of the Kuiseb River, although it occurs on the gravel plains immediately adjacent to these dunes. *Camponotus detritus* possibly has a competitive advantage over *C. fulvopilosus* within the dune sea and excludes it from this habitat.

In *C. storeatus*, speciation probably took place in a peripheral population of *C. fulvopilosus* that became isolated within a valley or valleys of the Cape Fold Mountains. This isolation was possibly created by the alternating wet and dry spells that occurred in the Cape during the Cenozoic (Tyson 1987). Subsequent to the speciation of *C. storeatus*, it seems that dispersal occurred over the Cape Fold Mountains to suitable habitats within the southern part of the Great Karoo and resulted in differentiation of the northern form of this species.

The speciation of *C. brevisetosus* possibly resulted from isolation of a population of *C. fulvopilosus* within the mountains of the Drakensberg Escarpment. Our knowledge of its distribution is the poorest of the four species but it has clearly become a specialist, occurring in grasslands on mountains and hilltops that have granite in which the ants can nest.

The Savanna and Karoo forms of *C. fulvopilosus* are aptly named, as the hybrid zone between the two forms follows closely the demarcation between Savanna and Karoo as portrayed in Rutherford & Westfall (1994). Zones of overlap between races of a species are often associated with an environmental transition (Hewitt 1989). Isolation between populations of *C. fulvopilosus* might partly be caused by differences in rainfall patterns resulting in different times for the release of winged reproductives. Isolation of the Western Cape form of *C. fulvopilosus* seems to be the result of the Bokkeveld and Cedarberg mountains that are a barrier between it and the parent population rather than of habitat differences.

While we now have a fairly sound knowledge of the distribution of *C. fulvopilosus* within southern Africa, we still know very little about its distribution and morphological differentiation north of the Zambesi and Cunene Rivers.

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