


**Taxonomy, phylogeny and biogeography of seed-harvesting
ants in the *Tetramorium solidum*-group
(Hymenoptera:Formicidae)**

*Thesis presented in partial fulfilment of the requirements for the
degree Masters of Science in the Department of Botany and
Zoology at Stellenbosch University*



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Declaration

I hereby declare that that the work presented in this thesis is my own original work and has not previously been submitted in entirety or in part at any university for any other degree.

Nokuthula Mbanyana

Date: 14 December 2012

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Preamble and thesis outline

Ants emerged during the Cretaceous Period more than 100 million years ago (Grimaldi & Engel 2005; Perrichot *et al.* 2008) and diversified independently on different landmasses following the Early Cretaceous fragmentation of Pangaea (Grimaldi & Agosti 2000). Today, ants represent one of the most ecologically successful groups globally (Wilson 1987), and their diversity far exceeds that of other social insects (Hölldobler & Wilson 1990). Currently 21 subfamilies, 305 genera and 12465 recorded ant species exist (Bolton 2012).

Ants occur in almost all terrestrial habitats (Brown 2000) and are not uniformly distributed across regions, biomes and continents. As with all other taxa, historical abiotic factors have played a major role in their diversification and biogeographic structure (Tolley *et al.* 2006), including climatic changes (Hölldobler & Wilson 1990) and the necessity to adapt to new environmental conditions (Tolley *et al.* 2006).

Many global areas still lack data on regional biodiversity and the historical processes that may have shaped it. This is particularly so for southern Africa where the ant fauna is still relatively poorly known (Robertson 2000) and where there have been no published biogeographic analyses for any ant taxon.

There is a highly endemic ant fauna that has evolved in the dry regions of southern Africa, which shows unique adaptations to the extreme thermal niches of these regions. For example, ants in the genus *Ocymyrmex* have adapted to forage on barren ground at temperatures as high as 67 °C, when most insects and other arthropods are unable to survive (Marsh 1985). *Ocymyrmex* have long legs and usually hold the head, thorax and gaster high above the substrate, which helps with body temperature regulation. These ants are most active at the hottest time of the day and they move very rapidly. For example, *O. barbiger* has been observed running at speeds of 23 m/min (Marsh, 1985). In some ant species such extreme temperatures may limit foraging activity (Ward, 2007) but, in the

case of *Ocymyrmex*, adaptations to this extreme thermal niche allowed exploitation of resources (dead and heat stressed arthropods). Moreover, these ants have subterranean nests that are ideal to escape environmental extremes and to move their brood deeply under the ground (Marsh, 1985). The distribution of some ant taxa in these dry regions closely reflects borders between particular biomes. For instance, in South Africa the ponerine ant, *Pachycondyla hottentota*, and the sugar ant, *Camponotus storeatus*, follow the borders of the Nama and Succulent Karoo biomes respectively (Robertson 2000).

In the light of this background the overall objective of this study is to revise the taxonomy and determine the historical drivers of diversification in an important group of arid-adapted ants, the *Tetramorium solidum*-group, which is mainly restricted to dry semi-desert areas in southern Africa. Members of the *Tetramorium solidum*-group are commonly encountered seed harvesters yet despite their apparent ecological importance, their taxonomy and biogeography remains largely unresolved. Thirty years elapsed since the last revision of the group by Bolton (1980) and since, ant surveys have considerably expanded the material available for study and provide an opportunity for a fresh perspective on this group. The specific aims of this project were twofold: 1) to revise the species of the *Tetramorium solidum*-group; and 2) to explore the phylogenetic relationships among members of the group and the bioclimatic factors restricting their current distributional ranges in southern Africa. My study is timely, as to date no attempt has been made to unravel the history of arid-adapted ant diversification in southern Africa. Such information is much needed for identifying areas of high species diversity and endemism (Azuma *et al.* 2006) and prioritizing areas for conservation (Faith 1992).

The thesis consists of three chapters. In chapter one I use morphological characters to review the current taxonomy of the *Tetramorium solidum*-group. From these data I have compiled an updated identification key for the group and described five new species. In chapter two I have constructed a fossil-calibrated dated phylogeny for *Tetramorium*

solidum-group species in order to explore the historical processes that may have contributed in structuring the current distribution patterns and endemism within and among the species of the group. In this chapter I also explore bioclimatic factors that may restrict the current distribution of members on the *Tetramorium solidum*-group, using correlative bioclimatic modeling approaches. Chapter three provides a brief and overall conclusion to the study.

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Chapter 1

A taxonomic review of seed-harvesting ants in the *Tetramorium solidum*-group (Hymenoptera: Formicidae)*

This chapter will form the basis of a paper that will be submitted to *Zootaxa* for publication.

Abstract

The *Tetramorium solidum*-group occurs in Africa, with the vast majority of species endemic to the arid regions of southern Africa. In the more than 30 years since the first revision of the genus by Bolton (1980), ant surveys have considerably expanded the amount of material available, including surveys conducted specifically for this study. This review, based on both morphological and genetic data, has expanded the number of known species from 14 (Bolton 1980) to 19, constituting an increase of 36%.

Keywords: *Tetramorium solidum*-group; Afrotropical region; arid regions; Nama Karoo, Succulent Karoo, new species; rainfall.

Introduction

The genus *Tetramorium* Mayr, 1855 is widespread species-rich with approximately 465 described species (Bolton, 2012). The genus has been recorded in most zoogeographical regions of the world, but its highest diversity lies in the Afrotropical region with about 230 described species (Hita Garcia *et al.* 2010a, 2010b, 2010c).

Members of the *Tetramorium solidum*-group are ground nesting, seed harvesting ants mainly restricted to dry semi-desert areas in southern Africa. Two species in the group have a wider distribution and are found further north in Africa. Bolton (1980) revised the group and listed 14 species. Other than this revision and the recording of particular species in various surveys of ants (e.g. Robertson 2000; Parr *et al.* 2002; Netshiliphala *et al.* 2005), very little has been published on the *Tetramorium solidum*-group despite its

apparent ecological importance in terms of seed predation in semi-arid habitats in southern Africa. In the nearly 30 years since Bolton's revision, ant surveys have considerably expanded the material available for study and provide an opportunity for a fresh perspective on this group.

The species of *Tetramorium solidum*-group can be distinguished from other groups of *Tetramorium* by the median notch or impression on the anterior clypeal margin, which is often broad and deeply indented, combined with the presence of ammocheate hairs on the ventral side of the head (Bolton 1980). Bolton (1980) grouped the species of *T. solidum*-group into three complexes based on the form of pilosity. The first complex comprises *T. peringueyi*, *T. rothschildi* and *T. dichroum*. These three species are characterized by the presence of abundant hairs on the dorsal surfaces of the head and body. *Tetramorium rothschildi* is distinguished from the other two species by the presence of branched hairs on the dorsal surfaces of head and body, whereas the other two species have simple hairs. The second complex comprises *T. clunum*, *T. galoasanum* and *T. setuliferum*. These three species lack erect hairs on the dorsal surface of mesosoma, pedicels, petiole, postpetiole and first gastral tergite. They have bizarre pilosity, which consists of short, broad, blunted, much flattened and strongly appressed glittering silvery hairs. The third complex consists of *T. barbigerum*, *T. glabratum*, *T. grandinode*, *T. jordani*, *T. pogonion*, *T. rufescens*, *T. signatum*, and *T. solidum*, in which the body is hairless or nearly so. Only *T. solidum* have few hairs on the mesosoma. The members of this complex show the well-developed psammophore (Bolton 1980).

Using a wide range of morphological characters, this study will provide an updated taxonomic revision for the *Tetramorium solidum*-group.

Materials and methods

Sample collection

Sampling was undertaken in the Northern Cape and Western Cape Provinces of South Africa, as well as Namibia. Ants were collected by hand, including digging up nests. Sampled ants were preserved in ethanol (96%) for future DNA research. Representatives of each sample were mounted and labelled and incorporated into the Entomology Collection at Iziko South African Museum, Cape Town. For long-term storage, all remaining material was preserved and stored in 96% alcohol. Specimens already housed in the Entomology Collection at the South African Museum were also included in all analyses, along with further material loaned from the Natural History Museum London, The California Academy of Sciences and Stellenbosch University.

Morphological variation

Morphological characters of adult workers were examined using a Leica MZ16A stereomicroscope, and all the measurements were taken with an ocular micrometer. Based mainly on the morphological terminology of Bolton (1980), the following measurements were taken:

- 1) HL (Head Length): the length of the head proper, excluding the mandibles, measured in a full-face view, in a straight line from the anterior-most point of the median clypeal margin to the mid-point of the occipital margin.
- 2) HW (Head Width): the maximum width of the head in full-face view, behind the eyes.
- 3) HW1 (Head Width 1): the maximum width of the head in full-face view, including the eyes.
- 4) EL (Eye Length): the maximum diameter of the eye.

- 5) SL (Scape Length): the maximum straight line measurement of the antennal scape excluding the condylar bulb.
- 6) PW (Pronotal Width): the maximum width of the pronotum in dorsal view.
- 7) NW1 (Petiole node width): the maximum width of the petiole in dorsal view.
- 8) NW2 (Postpetiole node width): the maximum width of the postpetiole in dorsal view.
- 9) NL1 (Petiole node length): the length of the petiole in lateral view.
- 10) NL2 (Postpetiole node length): the length of the postpetiole in lateral view.
- 11) ML (Mesosoma Length): the length of the mesosoma (= alitrunk) in lateral view from the anterior-most point of the pronotum to the posterior base of the propodeal lobes.
- 12) CI (Cephalic Index): $HW \text{ divided by } HL, \times 100.$
- 13) SI (Scape Index): $SL \text{ divided by } HW, \times 100.$
- 14) EI (Eye Index): $EL \text{ divided by } HW, \times 100.$

Results

Key to identification of species in the *Tetramorium solidum* group (workers)

The key below is based on that presented in Bolton (1980).

1. Dorsum of mesosoma in profile without any erect hairs, with appressed pubescence only (Fig. 1A) 2

Dorsum of mesosoma in profile with erect hairs, which are longer than broad (Fig. 1B)

..... 13

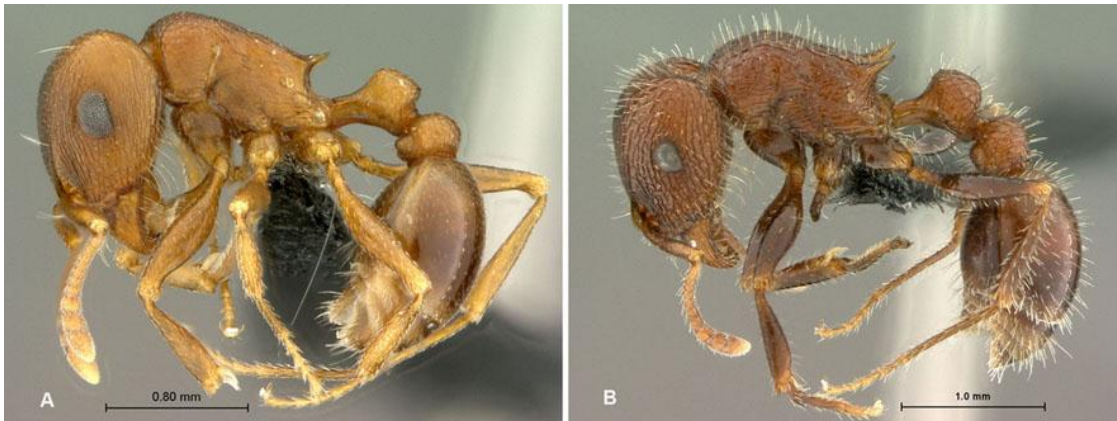


FIGURE 1. Lateral view of: *T. rufescens* worker (A), showing absence of erect hairs, and *T. peringueyi* worker (B) showing presence of erect hairs on mesosoma.

2. Propodeum armed with a pair of elongate spines or short triangular teeth (Fig. 2A)...

.....3

Propodeum unarmed, angulate or with a pair of minute tubercles (Fig. 2B) ***jordani***

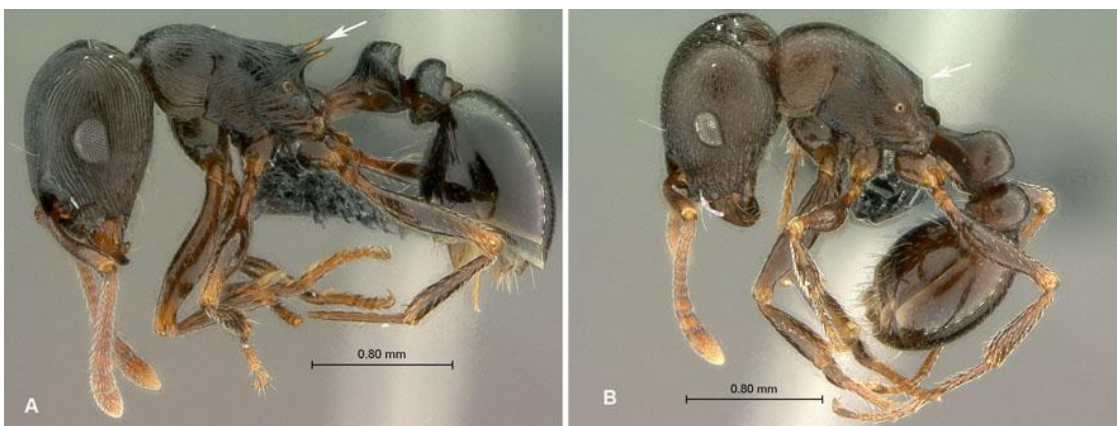


FIGURE 2. Lateral view of: *T. grandinode* worker (A) with propodeal spines (indicated by arrow) and *T. jordani* worker (B) with propodeum unarmed.

3. Dorsum of head and body with short, broad, blunted, much flattened and strongly appressed glittering silvery hairs (Fig. 3A).....4

Dorsum of head and body without such hairs, with only sparse simple appressed pubescence present (Fig. 3B)..... 6

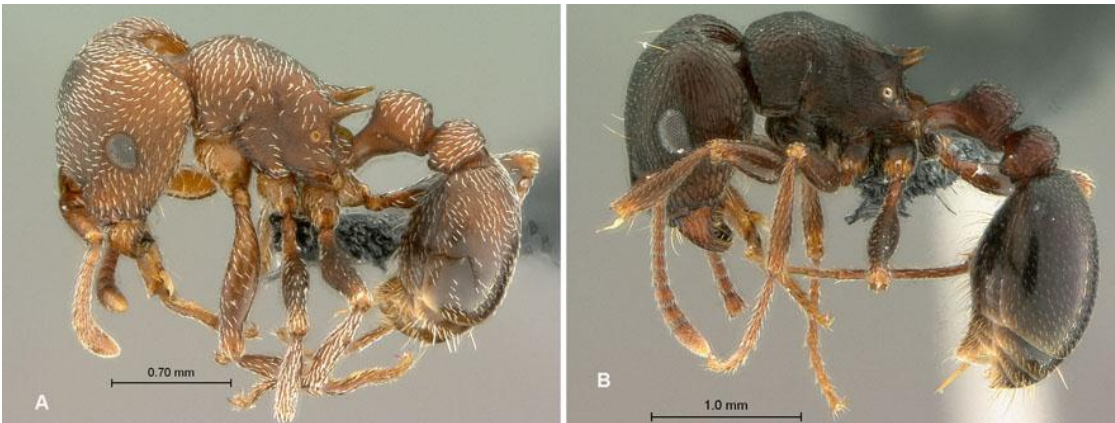


FIGURE 3. Lateral view of *T. setuliferum* worker (A) showing appressed silvery hairs, and *T. signatum* worker (B) showing only sparse simple pubescence.

4. Appressed silvery hairs long, dense and strap-like, overhanging one another especially on mesosoma. Sculpture on the first gastral tergite mostly obscured by size and density of the hairs***galoasanum***

Appressed hairs sparse and spaced out, not strap-like and not overlapping (Fig. 3A) 5

5. The base of the first tergite in profile forming a thick, laterally projecting down-curved flange, which obscures the tergosternal suture basally and base of the sternite. First gastral tergite sculptured only at the base. Reddish-brown or red species (Fig. 4A).
..... ***setuliferum***

The base of the first tergite in profile not projecting as above, the tergosternal suture and base of the sternite clearly visible. First gastral tergite finely sculptured from base to apex. Blackish brown to black species (Fig. 4B).....***clunum***



FIGURE 4. Lateral view of *T. setuliferum* worker (A) showing the base of the first tergite in profile obscuring the tergosternal suture (arrow), and *T. clunum* worker (B) showing first gastral tergite without the overhanging tergosternal suture (arrow).

- 6. Postpetiole with lateral extensions (Fig. 5A) 7
- Postpetiole globular or subglobular, without lateral extension (Fig. 5B) .. 8

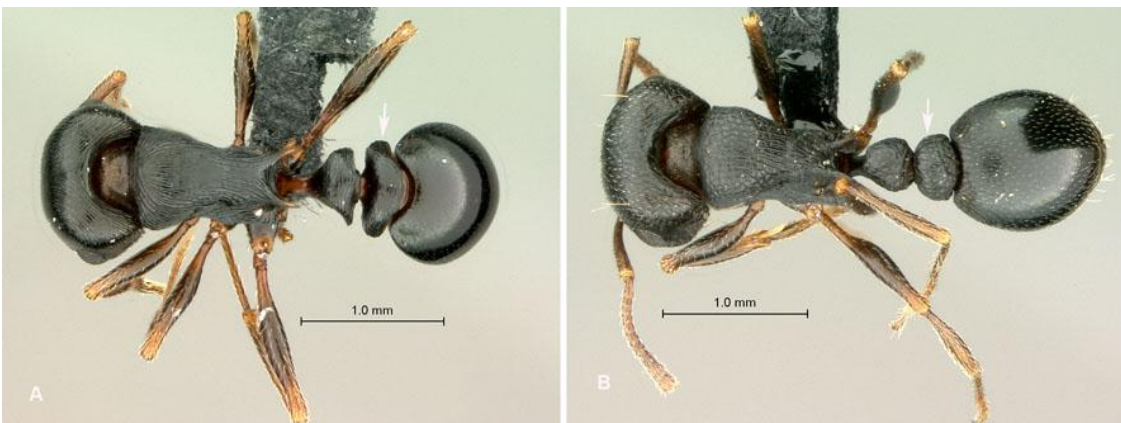


FIGURE 5. Dorsal view of: *T. grandinode* worker (A) showing lateral extension on the postpetiole node (arrowed), and *T. signatum* worker (B), which does not have lateral extensions of the postpetiole node.

- 7. In dorsal view petiole node very much broader than long. Dorsal surface of the mesosoma with fine longitudinal rugulae and glossy appearance in-between (Fig. 6A) ***grandinode***

In dorsal view only the posterior face of the petiole node slightly broader than the anterior face, with an angled corner in lateral view. Dorsum of mesosoma with reticulate ground-sculpture overlaid by short fine longitudinal striations (Fig. 6B)

.....**sp. nov. 4**



FIGURE 6: Dorsal view of: *T. grandinode* worker (A), showing broad petiole node, and *Tetramorium* sp.nov. 4 worker (B) showing petiole node.

- 8. Colour orange-brown to brick red (Fig.7A)..... 9
- Colour black to blackish brown (Fig.7B) 10

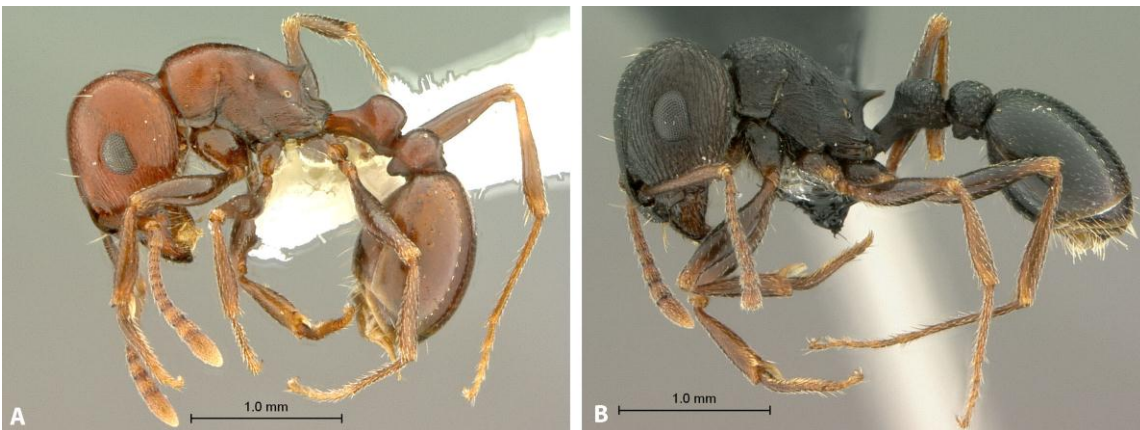


FIGURE 7: Lateral view of red-coloured *T. glabratum* (A) and black-coloured *T. signatum* (B).

- 9. Propodeal spines short and broad, triangular and acute, the basal width of each spine greater than its length (Fig. 8A) **glabratum**

Propodeal spines long, each spine distinctly much longer than its basal width (Fig. 8B)..... *rufescens*

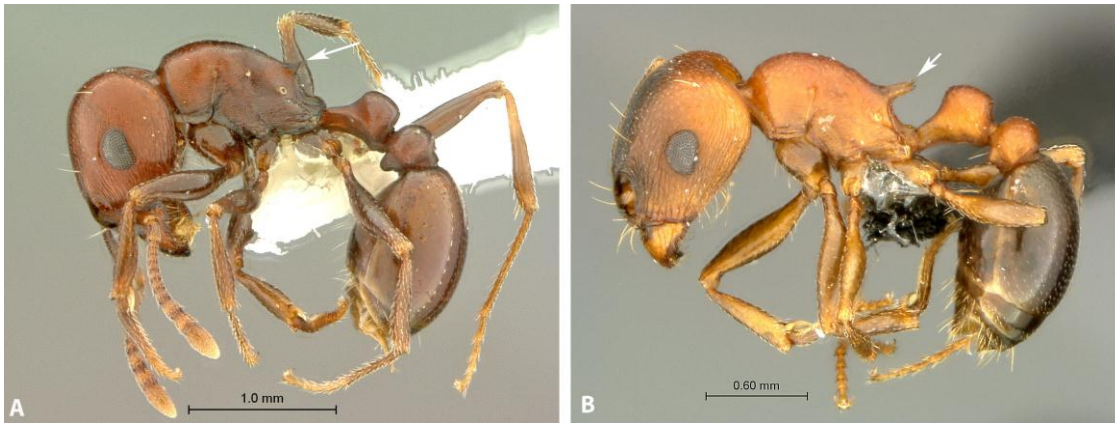


FIGURE 8: Lateral view of *T. glabratum* (A) showing reduced propodeal spines (arrowed), and *T. rufescens* (B) showing elongate propodeal spines.

10. Anterior clypeal margin with an extensive broad, deeply concave median impression, which occupies almost half the width of the margins (Fig 9A)..... 11

Anterior clypeal margin with a very shallow median impression (Fig. 9B)..12

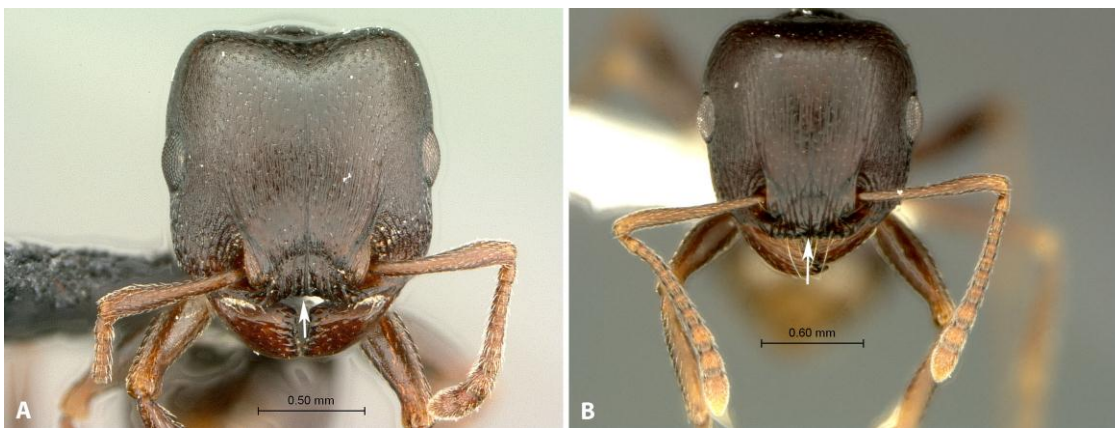


FIGURE 9. Dorsum of head of: *Tetramorium* sp. nov. 3 (A) showing massive median impression of the anterior clypeal margin (arrowed), and *T. barbigerum* (B) showing a shallow median impression of the anterior clypeal margin.

11. Petiole in dorsal view broadened with lateral flanges on the sides (Fig. 10A). **sp. nov.**

3

Petiole in profile strongly nodiform, without any lateral extensions (Fig. 10B)..... ..

signatum

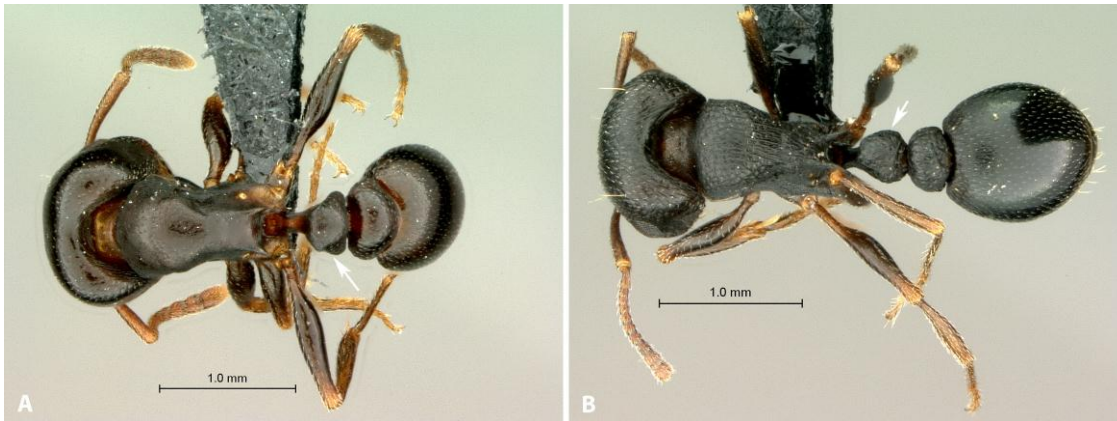


FIGURE 10. Dorsal view of: *Tetramorium* sp. nov. 3 (A) showing posterior flanges to petiole node (arrowed); and *T. signatum* (B) where flanges are absent.

12. Head in full-face view narrowing anteriorly, narrower in front of eyes than behind. Costulate sculpture of dorsal head very feeble, fading out behind level of eyes and replaced by fine superficial punctulation. ***barbigerum*** (Fig. 11A)

Head in full-face view as broad or broader in front of eyes as behind. Costulate sculpture of dorsal head fine, reaching to occipital margin
 ***pogonion*** (Fig. 11B)

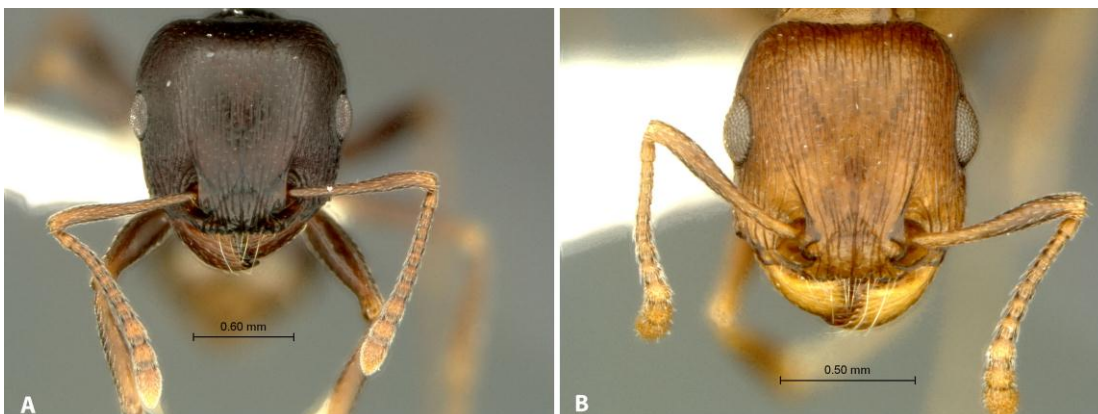


FIGURE 11. Dorsum of head of *T. barbigerum* (A) showing head narrowing anteriorly and *T. pogonion* (B) with head slightly broader in front of the eyes than behind.

13. Abundant erect hairs on all dorsal surfaces of head and body (Fig. 12A)... 14

Only a few hairs present on the dorsum of mesosoma, 1-4 pairs (Fig. 12B) 18



FIGURE 12. Lateral view of: *T. dichroum* worker (A) showing abundant erect hairs on all body surfaces; and *T. solidum* worker (B) showing sparse hairs on the mesosoma.

14. Head and mesosoma with branched pilosity (Fig. 13A)..... ***rothschildi***

Head and mesosoma with simple pilosity (Fig. 13B) 15



FIGURE 13. Lateral view of *T. rothschildi* worker (A) showing branched hairs covering the entire body, and *T. peringueyi* worker (B) showing simple hairs covering all the surfaces of the body.

15. Antennal scapes with erect hairs, similar to those on the outer surface of hind tibia (Fig. 14A)..... 16

Antennal scapes without erect hairs, only with pubescence (Fig.14B) . 17

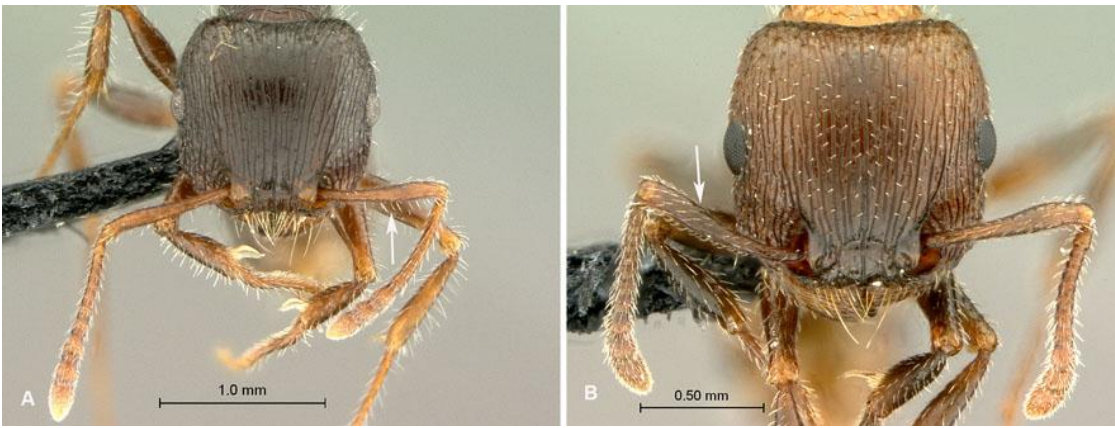


FIGURE 14. Dorsum of head of *Tetramorium* sp. nov. 1 worker (A) showing erect hairs on the antennal scapes, and *T. dichroum* worker (B) showing appressed pubescence on the antennal scapes.

16. Dorsal surface of mesosoma predominantly with irregular longitudinal rugulose and irregular reticulum pattern. Colour orange (Fig. 15A)..... *peringueyi*

Dorsal surface of mesosoma with short longitudinal striations and fine reticulate ground sculpture in places. Colour uniformly black (Fig. 15B)... **sp. nov. 1**



FIGURE 15. Dorsal view of *T. peringueyi* (A) showing dorsum of mesosoma with irregular longitudinal rugulose and irregular reticulum pattern, and *Tetramorium* sp. nov. 1 (B) showing dorsum of mesosoma with short longitudinal striation and fine reticulate ground sculpture in places.

17. Propodeum armed with acute spines. Colour light brown, with gaster a little bit darker compared to the mesosoma (Fig. 16A)..... *dichroum*

Propodeum with short propodeal teeth. Colour reddish brown, with gaster black (Fig. 16B)..... **sp. nov. 5**



FIGURE 16. Lateral view of: *T. dichroum* (A) showing propodeum armed with acute spines and, and *Tetramorium* sp. nov. 5 (B) showing short propodeal teeth (photo taken by B. Braschler).

18. Propodeum with elongate and acute spines. (Fig. 13A)..... **solidum**

Propodeum with short triangular teeth. (Fig. 13B)... .. **sp. nov. 2**



FIGURE 17. Lateral view of *T. solidum* worker (A) showing elongate spines (arrowed), and *Tetramorium* sp. nov. 2 worker (B) showing short propodeal teeth.

Species descriptions

***Tetramorium barbigerum* Bolton, 1980**

(Figures 8A, 11A, 18 A-C)

Measurements (workers)

HL 1.013-1.279, HW 1.003-1.240, HW1 1.101-1.318, CI 95-101, SL 0.767-0.891, SI 67-77, PW 0.669-0.806, NW1 0.315-0.384; NW2 0.433-0.472; NL1 0.325-0.384; NL2 0.295-0.403; ML 1.131-1.356, EL 0.285-0.323, EI 24-28 (9 measured)

Diagnosis

Tetramorium barbigerum is easily distinguished from all the species in *T. solidum*-group by its shape of head, which is narrow in front of the eyes (Figure 11A). Morphologically this species is similar to *T. jordani* and *T. signatum* in that they are all black in colour and lack erect hairs on the mesosoma but the sculpture in *T. signatum* is much stronger compared to *T. jordani* and *T. barbigerum*. *Tetramorium barbigerum* and *T. jordani* have feeble cephalic sculpture, fading out at the level of the eyes and replaced by fine superficial punctuation (Figures 18A and 23A). These two species can be easily distinguished by the lack of propodeal spines in *T. jordani* (Figure 23B).

Notes

Only known from type locality, Okombaha in Namibia.

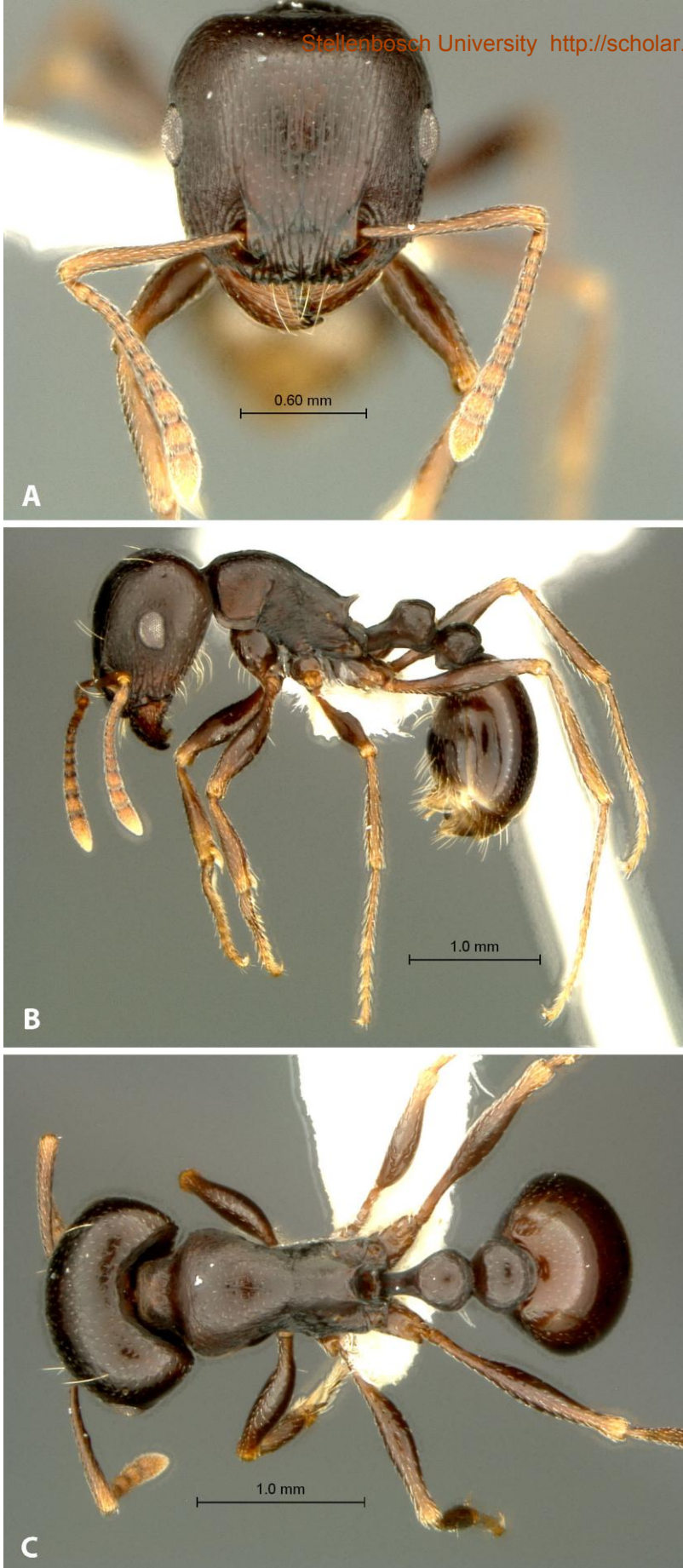


FIGURE 18. A worker of *T. barbigerum*: A. head in full face view; B. lateral view and C. dorsal view.

Tetramorium clunum Forel, 1913

(Figures 4B, 19A-C)

Measurements (workers)

HL 0.905-1.062, HW 0.934-1.090, HW1 1.009-1.147, CI 101-105, SL 0.688-0.747, SI 68-77, PW 0.566-0.669, NW1 0.301-0.381; NW2 0.382-0.472; NL1 0.282-0.340; NL2 0.187-0.246; ML 0.915-1.023, EL 0.207-0.266, EI 22-27 (13 measured)

Diagnosis

In the *Tetramorium solidum*-group there are only three species with short, broad, much flattened and strongly appressed glittering silvery hairs covering the body (Figures 4A & 4B), namely, *Tetramorium setuliferum*, *Tetramorium clunum* and *Tetramorium galoasanum*. *Tetramorium galoasanum* is distinguished from the other two species by its long, dense, overlapping strap-like hairs, whereas in the other two species these hairs are sparse and spaced out. *Tetramorium clunum* is separated from *T. setuliferum* by the following characters: (1) first gastral tergite does not overhang the tergo-sternal suture in profile (Figure 4B); (2) first gastral tergite is sculptured throughout whereas in *T. setuliferum* only the base is sculptured; (3) dorsum of head behind clypeus with at least one pair of erect hairs (Figure 4B), whereas *T. setuliferum* lacks elongate erect hairs on the dorsum of head; and (4) tergum of postpetiole without lateral alar prominences (Figure 19C); whereas *T. setuliferum* has these present.

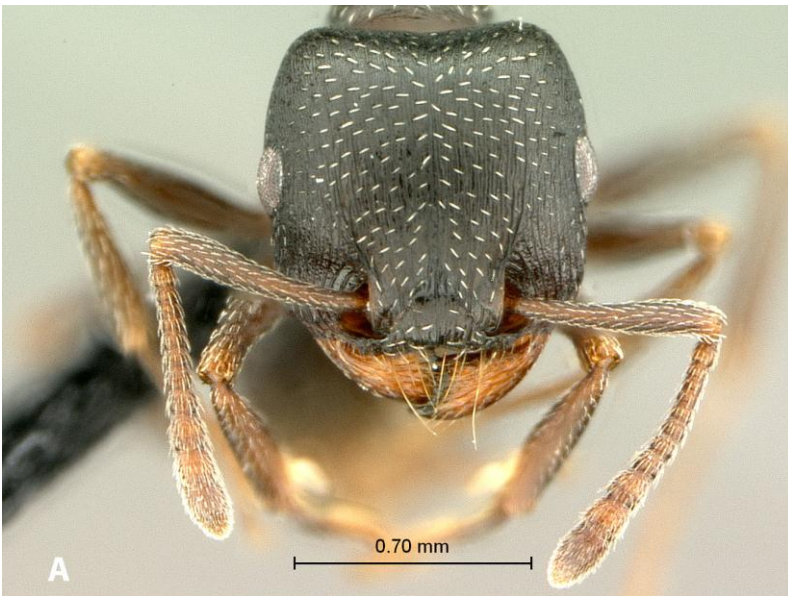


FIGURE 19. A worker of *T. clunum*: A. head in full face view; B. lateral view and C. dorsal view.

Notes

Tetramorium clunum has been recorded from South Africa (Eastern Cape, Western Cape, and Northern Cape) and Namibia. This is a ground-nesting species, sometimes with part of the nest underneath rocks. It has been recorded nesting in deep soils. Nothing is known about its feeding behavior but presumably feeds on seeds, as this is recorded for other species of this group. Yellow pan trap, pitfall trap and turning the stones are the methods that have been used to collect this species.

Tetramorium dichroum Santschi ,1932

(Figures 12A, 14B, 20A-C)

Measurements (workers)

HL 0.989-1.023, HW 0.983-1.072, HW1 1.042-1.118, CI 100-105, SL 0.688-0.747, SI 66-93, PW 0.614-0.669, NW1 0.325-0.372; NW2 0.382-0.454; NL1 0.315-0.344; NL2 0.252-0.295; ML 0.934-1.121, EL 0.230-0.248, EI 23-25 (8 measured)

Diagnosis

Tetramorium dichroum is the only species in this *solidum*-group lacking ammochaete hairs. In the *solidum*-group, there are five species with abundant hairs covering the dorsal surfaces of the whole body, namely, *T. rothschildi*, *T. peringueyi*, *T. dichroum*, *T. sp. nov. 1* and *T. sp. nov. 5*. *Tetramorium rothschildi* is easily separated from these species by having branched hairs. *Tetramorium dichroum* is morphologically similar to *T. peringueyi*,

T. sp. nov. 1 and *T. sp. nov. 5* in that they are the only species in the *solidum*-group that have simple abundant hairs covering the entire body. These are the only four species in the group that have erect hairs on the dorsal surfaces of the hind tibia. *Tetramorium dichroum* can be easily distinguished from *T. peringueyi* and *Tetramorium sp. nov. 1* by the absence of erect hairs on the antennal scapes (Figures 14B), whereas in *T. peringueyi* and *Tetramorium sp. nov. 1*, erect hairs are present on the scapes (Fig.14A), similar in appearance to those on the tibiae. *Tetramorium dichroum* is separated from *Tetramorium sp. nov. 5* on basis of spine length: in *T. dichroum* spines are long and acute whereas *Tetramorium sp. nov. 5* has propodeal teeth (Fig. 16B).

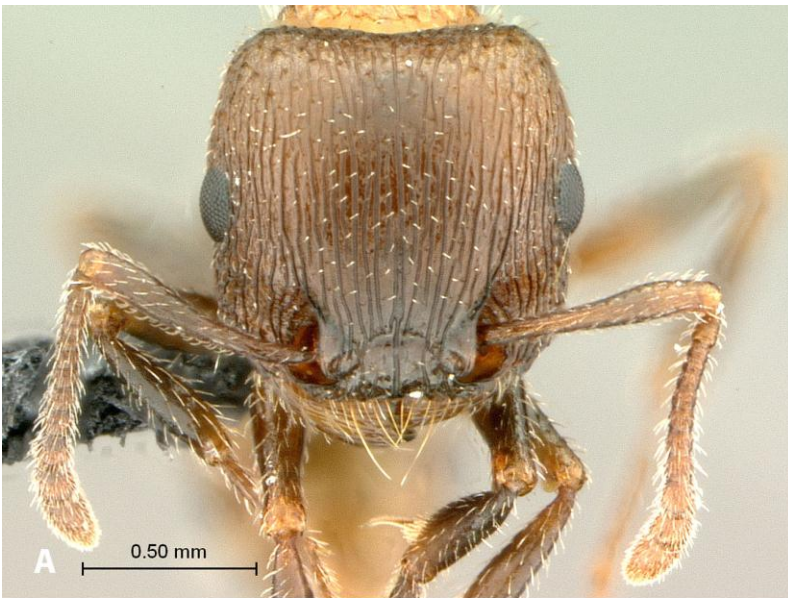


FIGURE 20. A worker of *T. dichroum*: A, head in full face view; B, lateral view and C, dorsal view.

Notes

Tetramorium dichroum has been recorded from South Africa (Eastern Cape, southern parts of the Free State, Northern Cape and Western Cape). It has been recorded from grassland with trees, and also in Karoo vegetation. This species nests in the soil and feeds on seeds. Pitfall trapping and turning over rocks have been used to collect these ants.

Tetramorium galoasanum Santschi, 1910

Diagnosis (information from Bolton, 1980)

HL 1.42-1.152, HW 1.44-1.58, CI 101-105, SL 0.96-1.04, SI 66-68, PW 0.90-1.02, ML 1.44-1.56 (from Bolton, 1980)

Tetramorium galoasanum looks similar to *T. clunum* and *T. setuliferum*. They are the only species in *solidum*-group with glittering hairs. *Tetramorium galoasanum* (HW1.44-1.58) is larger than *T. clunum* (HW 0.934-1.090) and *T. setuliferum* (HW 0.964-1.277). The glittering hairs are much denser in *T. galoasanum* compared to the other two species and almost overlap each other in places (Bolton 1980).

Notes

Tetramorium galoasanum has been recorded only from the Congo. Nothing is known about the habitat and biology of this species.

***Tetramorium glabratum* Stitz, 1923**

(Figures 7A, 8A, 21A-C)

Measurements (workers)

HL 1.095-1.141, HW 1.031-1.082, HW1 1.128-1.158, CI 94-100, SL 0.757-0.806, SI 73-78, PW 0.667-0.738, NW1 0.315-0.384; NW2 0.423-0.475; NL1 0.266-0.295; NL2 0.246-0.266; ML 1.072-1.175, EL 0.295-0.315 EI 28-29 (6 measured)

Diagnosis

Tetramorium glabratum looks similar to *T. rufescens* in that they both lack pilosity on the dorsum of the mesosoma and on the first gastral tergite and are both reddish coloured. *Tetramorium glabratum* can be distinguished from the latter by the short and broad propodeal spines (Figure 8A), whereas these are long and narrow in *T. rufescens* (Figure 8B).

Notes

This species occurs in South Africa (Northern Cape and Western Cape) and Namibia.

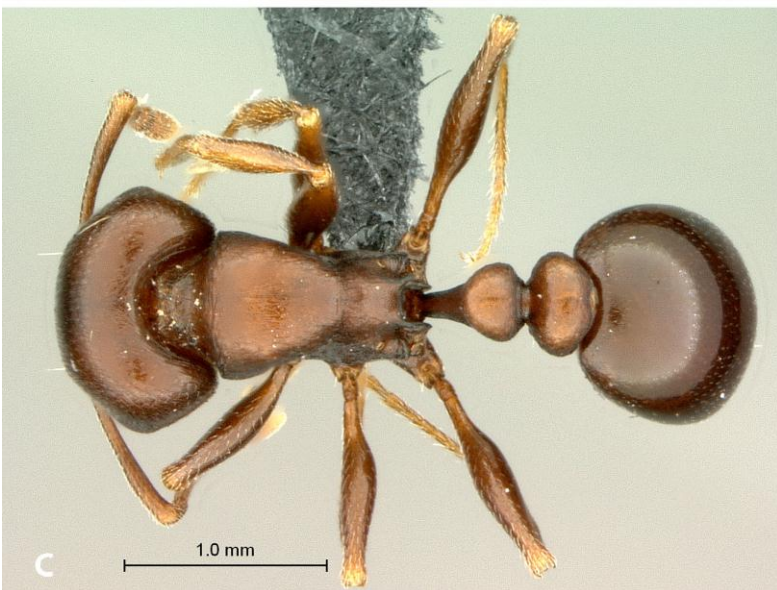
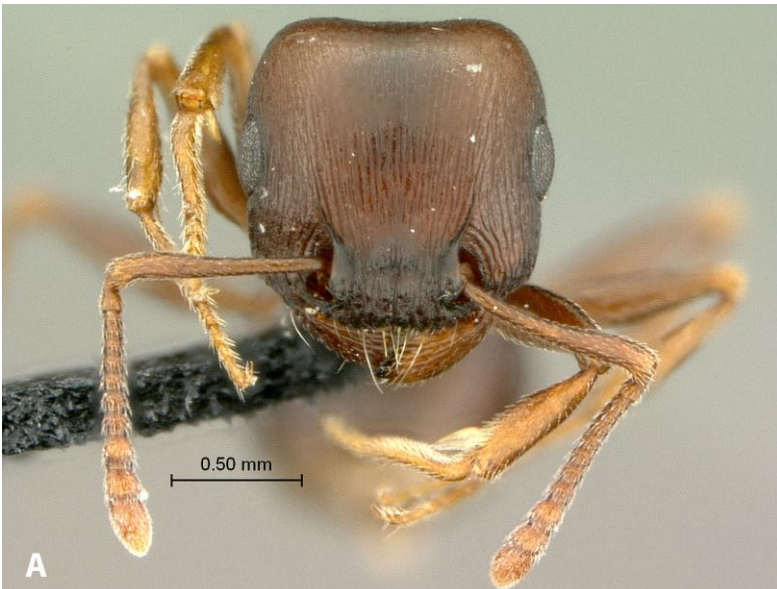


FIGURE 21. A worker of *T. glabratum*: A. head in full face view; B. lateral view and C. dorsal view.

Tetramorium grandinode Santschi, 1913

(Figures 2A, 5A, 6A, 22A-C)

Measurements (workers)

HL 0.993-1.225, HW 0.952-1.173, HW1 1.019-1.305, CI 94-103, SL 0.747-0.895, SI 70-80, PW 0.656-0.843, NW1 0.490-0.641; NW2 0.590-0.875; NL1 0.246-0.315; NL2 0.211-0.295; ML 1.072-1.382, EL 0.246-0.344, EI 24-29 (27 measured)

Diagnosis

The remarkable lateral extension of the postpetiole node (NW2 [node width of postpetiole] 0.590-0.875) (Figures 5A & 22B) distinguishes *T. grandinode* from all other species in the *Tetramorium-solidum* group. This species has superficial similarities with *Tetramorium* sp. nov. 4 in that *T. sp. nov. 4* also has broader postpetiole but to a lesser extent (NW2 0.413-0.555) compared to *T. grandinode*. These two species can be separated on basis of sculpture on the mesosoma. In *T. grandinode*, the dorsal surface of mesosoma has fine longitudinal rugulae and glossy appearance in-between, whereas in *T. sp. nov. 4* dorsum of mesosoma has a reticulate ground-sculpture overlaid by short fine longitudinal striations. Also, *T. grandinode* has a much broader petiole node when viewed dorsally compared to *Tetramorium* sp. nov. 4 (Fig. 10B).

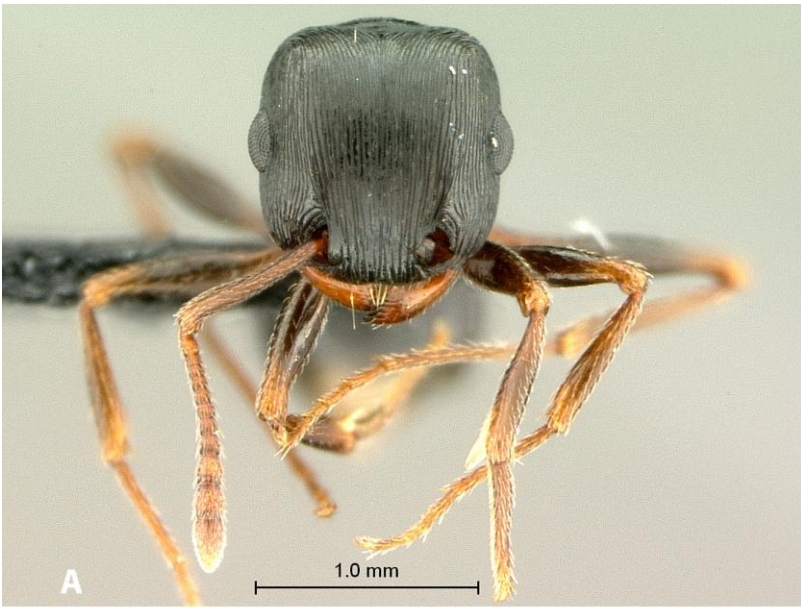


FIGURE 22. A worker of *T. grandinode*: A. head in full face view; B. lateral view and C. dorsal view.

Notes

Tetramorium grandinode is known to occur in South Africa (Northern Cape, Western Cape) and Namibia. This species has been recorded from the following habitats: Karoo (sandy plain next to dry river bed; dolerite hills; and rocky ridges with sparsely distributed shrubs; and Koedoesberge-Moordenaars karoo), and Plain Gariep desert.

It has been recorded nesting in deep soil on a flood plain. Specimens of these species were collected using pitfall traps, tuna bait, sugar bait, and cookie bait.

Tetramorium jordani Santschi, 1937

(Figures 2B, 23A-C)

Measurements (workers)

HL 1.013-1.169, HW 0.957-1.141, HW1 1.028-1.305, CI 94-101, SL 0.777-0.846, SI 70-82, PW 0.593-0.734, NW1 0.305-0.388; NW2 0.438-0.511; NL1 0.285-0.315; NL2 0.256-0.319; ML 1.072-1.182, EL 0.246-0.275, EI 23-27 (14 measured).

Diagnosis

Tetramorium jordani is the only species in the *solidum*-group with a combination of the following characters: lack of propodeal spines (the propodeum is only angulated), and hairless body (Figures 2B & 23B)). In the *Tetramorium solidum*-group, there are only two species that have no propodeal spines, namely, *T. jordani* and *Tetramorium* sp. nov. 5. The latter species can be separated from *T. jordani* by the presence of erect hairs covering the entire body.

Notes

This species has been recorded from arid regions of South Africa (Western Cape and Northern Cape) and Namibia in the following habitats: Succulent Karoo, sand dunes, grasslands, sand plain fynbos, fynbos on limestone, rehabilitated mine dump, rehabilitated slimes dam, Strandveld,. The species nests in sandy soils, with nests located either at the base of the plants or with the entrance in the open, away from plants. The nest usually has a crater of soil around the entrance. In sand dunes of the Namib Desert, the tunnels inside the nest have crust-like walls to stop sand from falling in, and the entrance of one nest observed was funnel shaped due to the crust-like lining and the fact that the loose sand around the entrance was blown away by wind. The species has been collected using yellow pan traps, pitfall traps, and hand-collecting. It feeds on seeds.

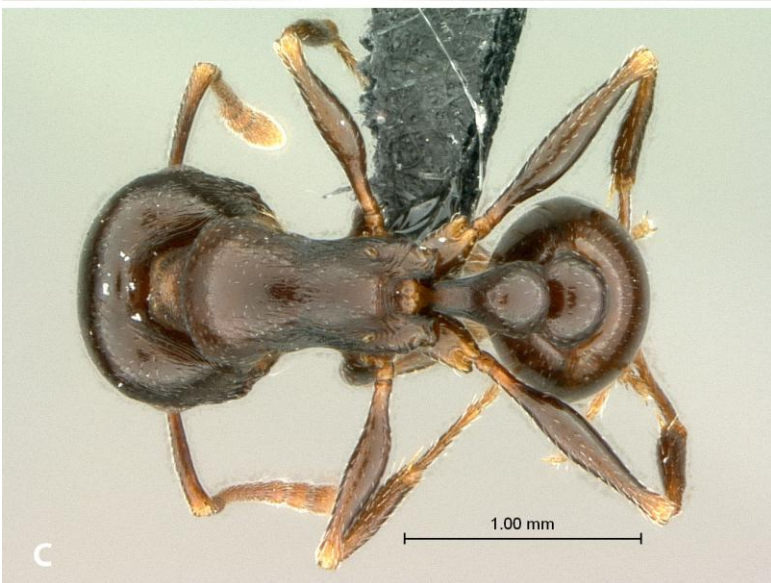


FIGURE 23. A worker of *T. jordani*: A, head in full face view; B, lateral view and C, dorsal view.

***Tetramorium peringueyi* Arnold, 1926**

(Figures 1B, 13B, 15A, 24A-C)

Measurements (workers)

HL 0.983-1.175, HW 1.040-1.199, HW1 1.081-1.275, CI 99-109, SL 0.777-0.885, SI 69-76, PW 0.649-0.769, NW1 0.344-0.460; NW2 0.415-0.587; NL1 0.320-0.399; NL2 0.256-0.393; ML 1.050-1.408, EL 0.199-0.271, EI 19-23 (17 measured).

Diagnosis

Tetramorium peringueyi is morphologically similar to *T. dichroum*, *Tetramorium* sp. nov. 1 and *Tetramorium* sp. nov. 5 in that they have numerous simple, erect hairs covering the body (Figure 24B). This species is separated from *T. dichroum* and *T. sp. nov. 5* by the presence of erect hairs on leading edges of the antennal scapes, whereas the other two species only have sub-erect pubescence. *Tetramorium peringueyi* and *T. sp. nov. 1* are the only species in *solidum*-group with erect hairs on the leading edges of the antennal scapes but the two can be distinguished based on colour. *Tetramorium peringueyi* is orange to light-brown (Fig. 15A) whereas *T. sp. nov. 1* is black (Fig. 15B).

Notes

Tetramorium peringueyi is known to occur in South Africa (Western Cape, Northern Cape and Eastern Cape), Namibia and Botswana. It has been recorded from grasslands, open Karoo, highland savanna, Kimberley Thornveld, Gariiep Rocky Desert, and Gariiep Plain Desert. *Tetramorium peringueyi* has been found nesting in sandy soils and in deep

dolerite reddish soils. The nests normally have more than one entrance, occurring either in open areas at the basal parts of plants. There is often a crater of soil round the nest entrance. This species feeds on seeds and stores them inside the nest - seed stores have been recorded within 8 cm of the soil surface. In one of the samples collected, the larvae and alates were found at about 22cm down. Pitfall trapping and sugar bait have been used to collect this species.

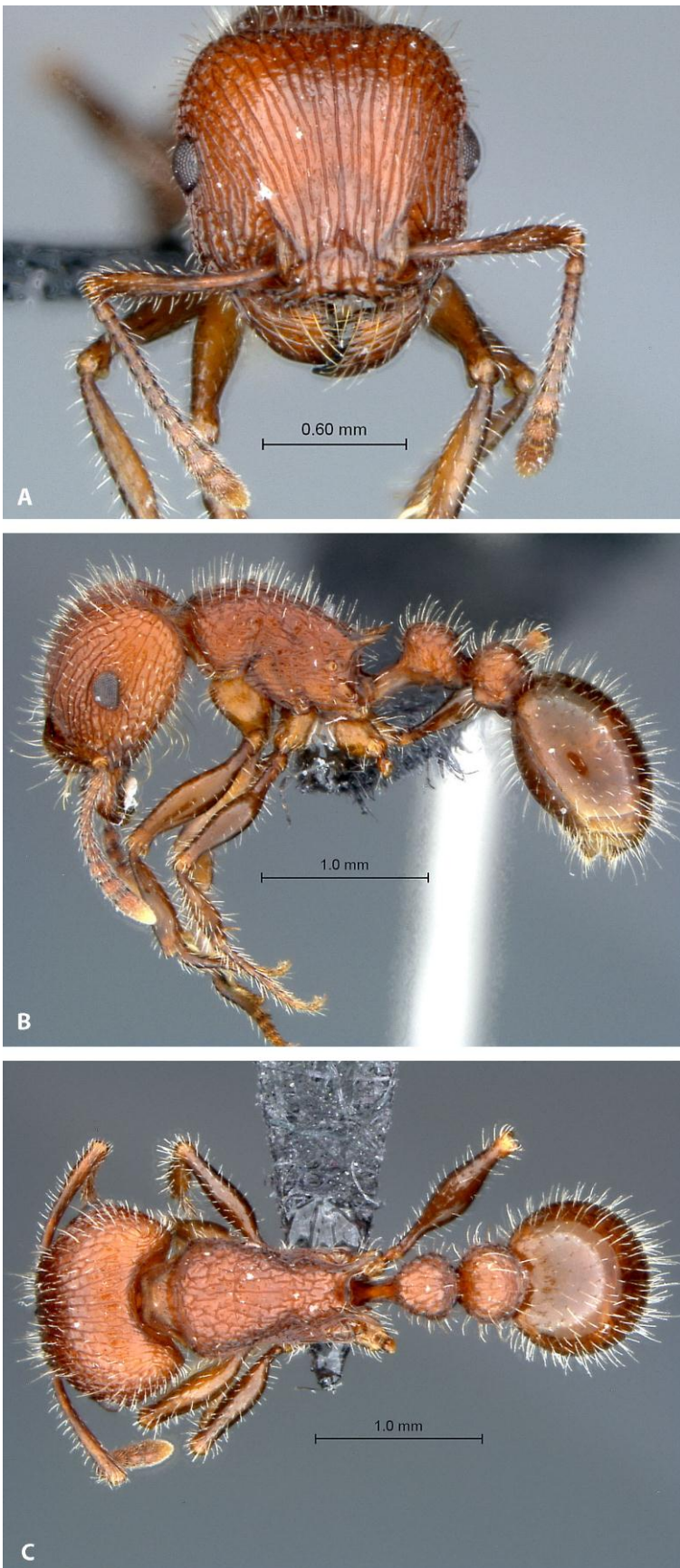


FIGURE 24. A worker of *T. peringueyi*: A. head in full face view; B. lateral view and C. dorsal view.

Tetramorium pogonion Bolton, 1980

(Figures 11B, 25A-C)

Measurements (workers)

HL 0.924-1.072, HW 0.856-0.993, HW1 1.266-1.343, CI 91-95, SL 0.688-0.806, SI 79-85, PW 0.580-0.659, NW1 0.275-0.295, NW2 0.344-0.374; NL1 0.275-0.295; NL2 0.246-0.295; ML 0.954-1.292, EL 0.246-0.285, EI 27-32 (6 measured).

Diagnosis

Tetramorium pogonion is the smallest species in the *Tetramorium solidum*-group.

Notes

Only known from the type locality Aus, Namibia. Nothing is recorded about the habitat and biology of this species.

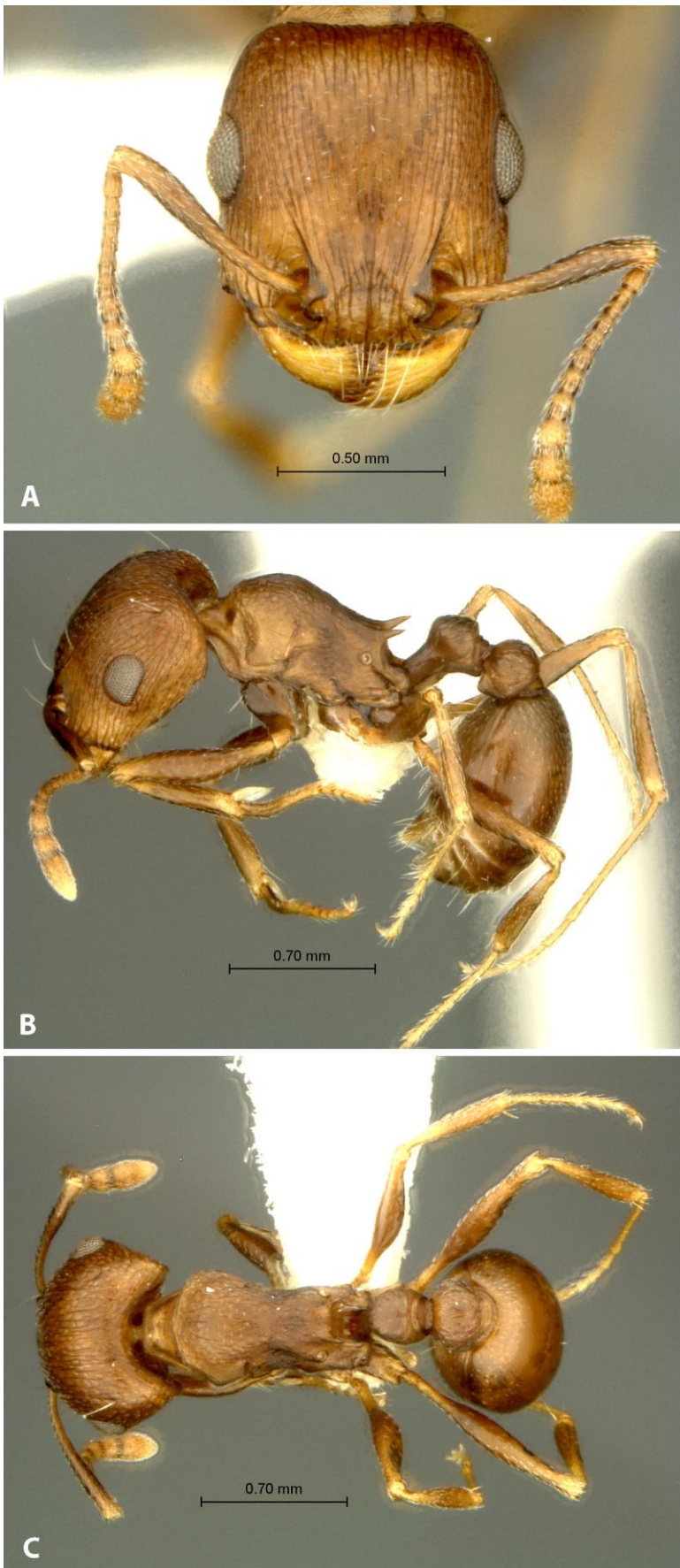


FIGURE 25. A worker of *T. pogonion*: A. head in full face view; B. lateral view and C. dorsal view.

Tetramorium rothschildi Forel, 1907

(Figures 13, 26A-C)

Measurements (worker)

HL 1.062-1.121, HW 1.111-1.170, HW1 1.131-1.192, CI 104-105, SL 0.757-0.767, SI 66-68, PW 0.708-0.747, NW1 0.384-0.403; NW2 0.443-0.482; NL1 0.334-0.344; NL2 0.275-0.285; ML 1.111-1.175, EL 0.236-0.275, EI 20-25 (2 measured).

Diagnosis

Tetramorium rothschildi is the only species in the *Tetramorium solidum*-group with branched hairs (Figures 26A-C).

Notes

Tetramorium rothschildi was first placed in the genus *Triglyphothrix* because of its branched pilosity (Bolton 1976). After (Bolton, 1985) revised the *Tetramorium solidum*-group, he placed this species under *Tetramorium solidum*-group because of the deep indentation on the anterior clypeal margin. This species has been recorded from Ethiopia, Uganda, Kenya, Ghana and Tanzania. It has been found in grassland and open woodland areas with laterite soil. *Tetramorium rothschildi* has been found nesting in red laterite soils; sometimes nests have grass husks around the entrance. Pitfall traps have been used to collect this species.

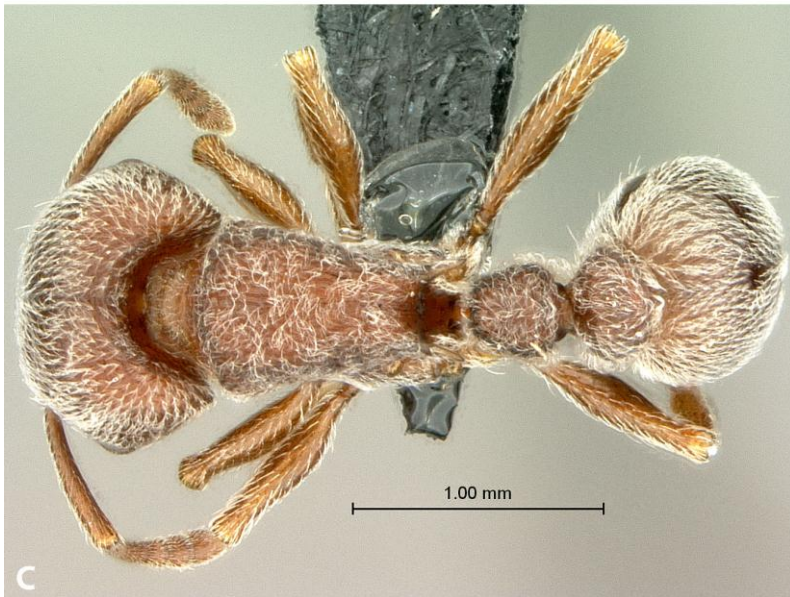


FIGURE 26. A worker of *T. rothschildi*: A. head in full face view; B. lateral view and C. dorsal view.

Tetramorium rufescens Stitz, 1923

(Figures 8B, 27 A-C)

Measurements (worker)

HL 0.924-1.253, HW 0.875-1.201, HW1 0.940-1.301, CI 92-108, SL 0.688-0.865, SI 72-82, PW 0.561-0.816, NW1 0.275-0.475; NW2 0.402-0.610; NL1 0.256-0.384; NL2 0.246-0.344; ML 0.950-1.356, EL 0.246-0.334, EI 24-31 (24 measured).

Diagnosis

Tetramorium rufescens is the only species in the *solidum*-group with the combination of long thin spines and orange-red colour. The other orange-red species in group either have very short and broad spines (*glabratum*) or ones that are medium length and broad (*T. signatum* Kalahari form).

Notes

Tetramorium rufescens has been recorded from South Africa (Western Cape, Northern Cape, Gauteng, Eastern Cape and KwaZulu Natal); and Namibia. This species has been found in thorn bush savanna, highland savanna, dwarf shrub savanna, dry forest savanna and semi-desert areas. *Tetramorium rufescens* has been found nesting in open savanna in red clay soils, sometimes in termite mounds or in soil next to the rocks, with the nest entrance in the open or at the base of the rock. Nests have also been collected in deep soils on flood plains. Feeds on seeds, with seed stores recorded in the

nest at about 10cm below the ground surface. It has been collected using pitfall trapping, tuna baits, cookie baits, sugar baits, and hand collecting.



FIGURE 27. A worker of *T. rufescens*: A. head in full face view; B. lateral view and C, dorsal view.

***Tetramorium setuliferum* Emery, 1895**

(Figures 3A, 4A, 28A-C)

Measurements (worker)

HL 0.964-1.199, HW 0.964-1.277, HW1 1.013-1.314, CI 100-108, SL 0.698-0.865, SI 66-69, PW 0.610-0.806, NW1 0.329-0.433; NW2 0.401-0.620; NL1 0.295-0.413; NL2 0.236-0.354; ML 0.983-0.993, EL 0.220-0.275, EI 20-24 (13 measured).

Diagnosis

Tetramorium setuliferum is morphologically similar to *Tetramorium clunum*. The two species are separated by the characters listed under *T. clunum*.

Notes

This is a widespread and common species in savanna and grassland regions of southern Africa, including: South Africa (Western Cape, Northern Cape, Eastern Cape, KwaZulu-Natal, Mpumalanga, Limpopo, Gauteng, North West, Free State), Zaire; Mozambique, Angola, Zimbabwe, Tanzania, Namibia, Zambia, Botswana, Lesotho and Malawi. It has been collected in grasslands, forest clearings, in weedy areas, in savanna on white clay soil, dry forest savanna, thornveld savanna, Kimberley Thornveld, Miombo woodland, riverine-grassveld, old tobacco fields, sandy soil areas dominated by shrubs, and in citrus orchards. The species normally nests in sandy to loamy soils, with nest entrances found in open areas, away from the basal parts of plants or at the base of a grass tuft. There can be more than one nest entrance per colony. Circles of grass seed

husks, piles of small stones or scattered soil particles have been found around nest entrances. Seeds are regularly found in nests. Reproductive forms have been collected from nests between October and February. Collected using pitfall traps, tuna baits, and sugar baits.

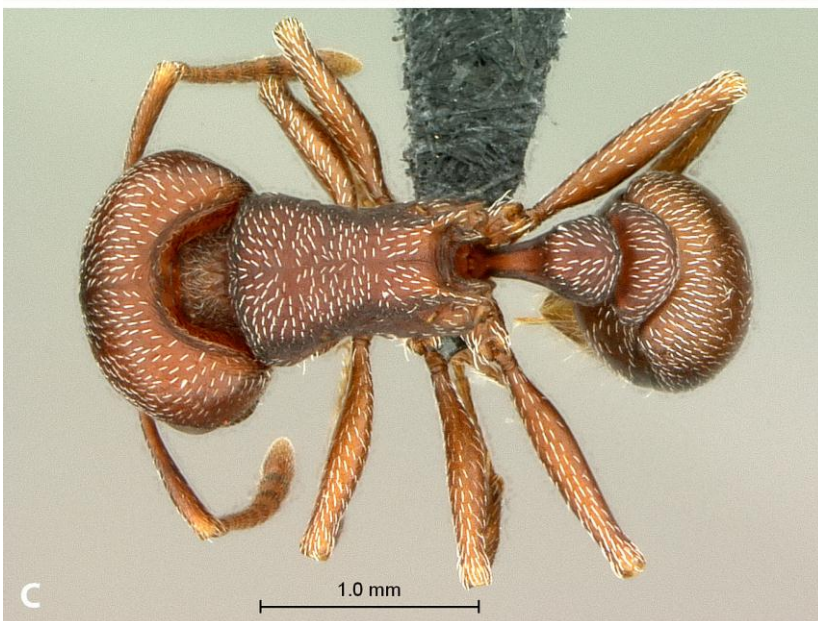


FIGURE 28. A worker of *T. setuliferum*: A. head in full face view; B. lateral view and C, dorsal view.

Tetramorium signatum Emery, 1895

(Figures 5B, 29A-C)

Measurements (worker)

HL 0.895-1.240, HW 0.811-1.192, HW1 0.903-1.308, CI 91-102, SL 0.679-0.930, SI 70-84, PW 0.561-0.816, NW1 0.270-0.433; NW2 0.325-0.521; NL1 0.244-0.384; NL2 0.226-0.334; ML 0.924-1.493, EL 0.246-0.349, EI 26-31 (45 measured).

Diagnosis

Tetramorium signatum is morphologically similar to *T. barbigerum* and *T. jordani* in that they are all black in colour and lack erect hairs on the mesosoma but the sculpture in the last two species is weaker compared to *T. signatum*. *Tetramorium jordani* is distinguished from other species by lacking propodeal spines.

Notes

The material observed matched mostly Bolton's description. The following differences were noted: Interestingly, the colour variation in this species is explained by geographical distribution. It looks like there are two forms, the Karoo form and the Kalahari sand form. The specimens collected in the Karoo region mainly in South Africa are brown to black in colour. The specimens collected from red sand dunes (Northern Cape- Dregghorn and Cullinan Farm and parts of southern Namibia) are reddish in colour. There is also variation in sculpture pattern. In black coloured specimens, the mesosoma has strong irregular

sculpture on the pronotum and short longitudinal striations on the mesonotum with punctulate sculpture in between. The nodes have punctulate sculpture overlaid by irregular striations. First gastral tergite punctulate or shagreened at the base. In the reddish specimens, most of the specimens have strong irregular sculpture on the pronotum and short longitudinal striations on the mesonotum with punctulate sculpture in between, and in few specimens, the nodes are predominantly smooth with only reticulate sculpture. The spine length varies in all forms from medium spines which are broad at the base to very short spines.

This species has been recorded from South Africa (Eastern Cape, Western Cape, and Northern Cape), Namibia and Angola. It has been found in the following habitats: Nama Karoo (including Koedoesberge-Moordenaars Karoo), Succulent Karoo, open rocky savanna, Kimberley Thornveld, open Mopane savanna on granite derived gravel soils, on sandy soil near river, Gariep rocky desert, on rocky ridges with sparsely distributed shrubs, Strandveld, Gariep Plain Desert, and Eastern Gariep Plain Desert. This species nests in sandy to loamy soils, with nests sometimes partly under rocks. Up to three entrances have been recorded per nest and entrances sometimes have craters of soil around them. Alates have been collected from nests in December. Two nests were found with Thysanura inquilines. Collected using pitfall traps, yellow pan traps, tuna baits, sugar baits, cookie baits and by hand-collecting.

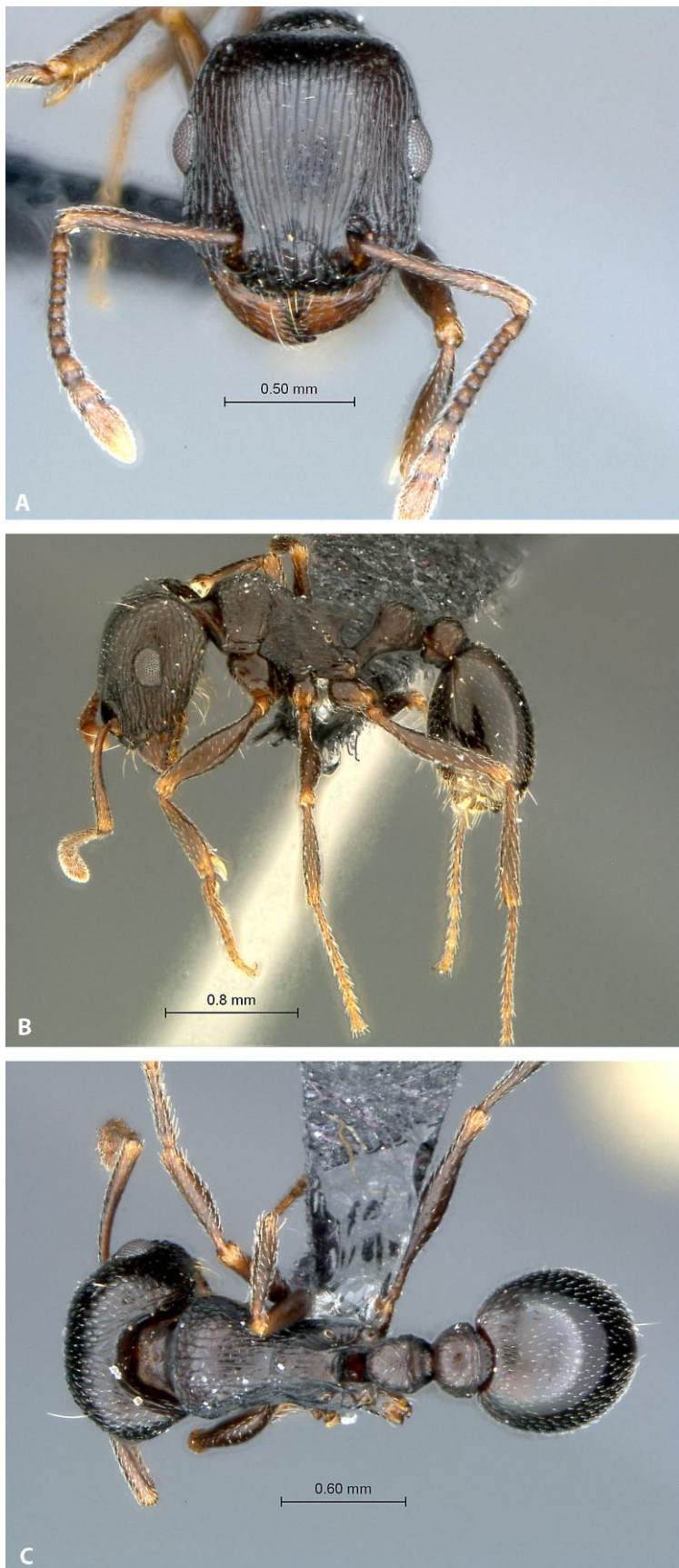


FIGURE 29. A worker of *T. signatum*: A. head in full face view; B. lateral view and C, dorsal view.

Tetramorium solidum Emery, 1886

(Figures 12B, 17A, 30A-C)

Measurements (worker)

HL 0.905-1.082, HW 0.905-1.151, HW1 0.954-1.175, CI 95-107, SL 0.669-0.831, SI 71-81, PW 0.575-0.708, NW1 0.305-0.396; NW2 0.379-0.482; NL1 0.256-0.315; NL2 0.236-0.325; ML 0.964-1.153, EL 0.207-0.275, EI 23-25 (12 measured).

Diagnosis

In the *Tetramorium solidum*-group only *T. solidum* and *T. sp. nov. 2* have sparse hairs that are only restricted to the mesosoma and petiole; the rest either have abundant hairs covering the whole body or lack erect hairs. *Tetramorium solidum* has very long and acute propodeal spines whereas in *Tetramorium sp. nov. 2* the propodeal spines are very short (Figures 17A and 17B).

Notes

Tetramorium solidum has been recorded from South Africa (Western Cape and Northern Cape) in Strandveld and transformed lands on tillite shales. It has been found nesting in clays soils, with craters of soil around nest entrances. Females were collected in April and males collected in September from nests. Seed stores have been found in nests. Specimens were collected using pitfall traps and yellow pan traps.

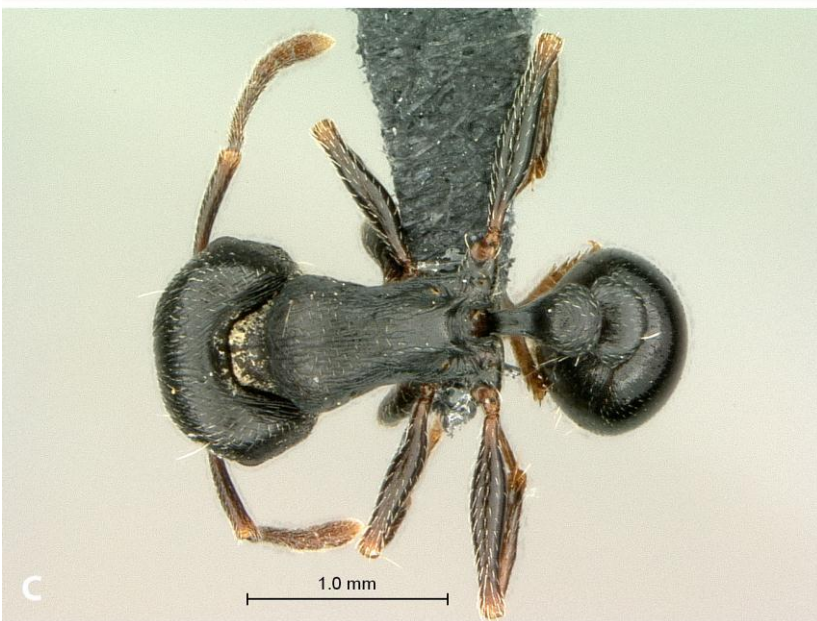
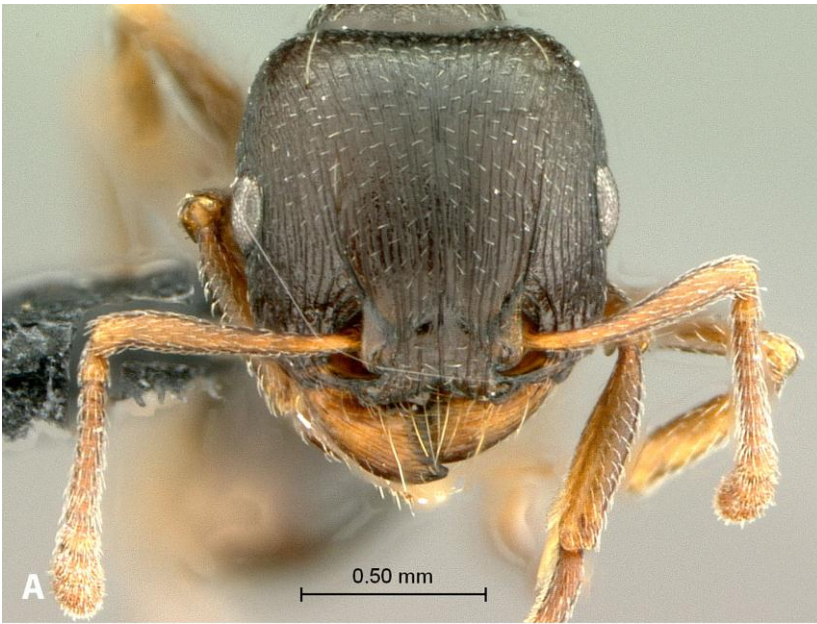


FIGURE 30. *Tetramorium solidum* worker: A. head in full face view; B. lateral view and C. dorsal view.

***Tetramorium* sp. nov. 1**

(Figures 14A, 15B, 31A-C)

Holotype: **South Africa: Northern Cape:** Road between Karsten Farms and Good house, Kokerboom site, Klein Pella, 29.06211°S and 18.97985° E, elevation 832m, collected from Gariep Rocky Desert with Kokerboom and *Euphorbia*, 16 December 2007, N. Mbanyana and HG Robertson, KP-01-P06, SAM-HYM-C019829.

Measurements (workers): HL 1.059-1.163, HW 1.137-1.279, HW1 1.188-1.330, CI 107-110, SL 0.775-0.930, SI 66-74, PW 0.710-0.827, NW1 0.388-0.452; NW2 0.478-0.543; NL1 0.388-0.426; NL2 0.362-0.388; ML 1.201-1.356, EL 0.245-0.258, EI 20-23 (6 measured).

Holotype description (worker): Mandibles with longitudinal striations. Anterior clypeal margin with an extensive, semicircular indentation. Frontal carinae extending back from the frontal lobes as fine ridges that end at about the level of the anterior margins of the eyes. Eyes with 16 ommatidia in the longest row. Propodeum armed with a pair of medium length propodeal spines, which are longer than the basal width. Metapleural lobes low with an angled corner. Peduncle with a prominent keel-shaped subpetiolar process. Petiolar node in profile nodiform, with the posterior face slightly more steeply angled than anterior face; anterior face rounding into dorsum but with slightly angled corners as seen in the dorsal view. Postpetiolar node low and rounded. Dorsal surfaces of head with longitudinal striations, the spaces between them with superficial reticulate ground-sculpture. Dorsum of mesosoma with short longitudinal striations, with superficial ground-

sculpture inbetween them. Petiole and postpetiolar nodes with fine reticulate sculpture, which is overlaid by irregular striations. Gastral tergite with fine, superficial reticulate pattern. All dorsal surfaces of head and body with abundant fine erect short hairs. The tibia of middle and hind legs with numerous short, stout, erect hairs. Ventral surface of head with strongly developed psammophore. Colour uniformly black.

Diagnosis

Tetramorium sp. nov. 1 belongs to the *peringueyi*-complex. Morphologically, it appears to be closely related to *T. peringueyi*, *T. dichroum* and *T. sp. nov. 5* in that these are the only species in the *solidum*-group with erect simple hairs covering the entire body. This species can be separated from the latter on basis of colour, as it is black, whereas other species are orange to light brown.

Notes

Known from South Africa (Western Cape, Northern Cape and Eastern Cape).

Material examined

Paratypes: **South Africa: Northern Cape:** Road between Karsten Farms and Good house, Kokerboom site, Klein Pella, 29.06211°S and 18.97985° E, elevation 832m, collected from Gariep rocky Desert with Kokerboom and *Euphorbia*, 16 December 2007, N. Mbanyana and HG Robertson, KP-01-P06, SAM-HYM-C019829; KP-01-P11, SAM-HYM-C019830; KP-02-P09, SAM-HYM-C019831; KP-02-P11, SAM-HYM-C019832; KP-01-P12, SAM-HYM-C019833, KP-02-P16, SAM-HYM-C019835; KP-02-P03, SAM-HYMC-19836; KP-01-P12, SAM-HYM-C019833; KP-02-P16, SAM-HYM-C019835; NC07-005, SAM-HYM-C019838; NC07-012, SAM-HYM-C019839; KP-01-P07, SAM-HYM-C019828.

Other material: **Western Cape:** Tierberg, near Prince Albert, 33°10'S and 22°16'E, 14 February 1995, H. Adie, Ref. no. 065; SAM-HYM-C008443; 6KM from Prince Albert on Leeu Gama road, 33°09'S and 22°02'E, 10-19 October 1996, T.E. Tshiguvho, SAM-HYM-C009333; 27KM from Prince Albert on Leeu Gama road, 33°09'S and 22°02'E, 10-19 October 1996, T.E. Tshiguvho; **Eastern Cape:** Kudu Reserve in Great Fish River, 33°07'42"S and 26°41'32"E, 25-30 April 2005, T. Jordan, H2S139T4AK, Grassland, SAM-HYM-C018977.

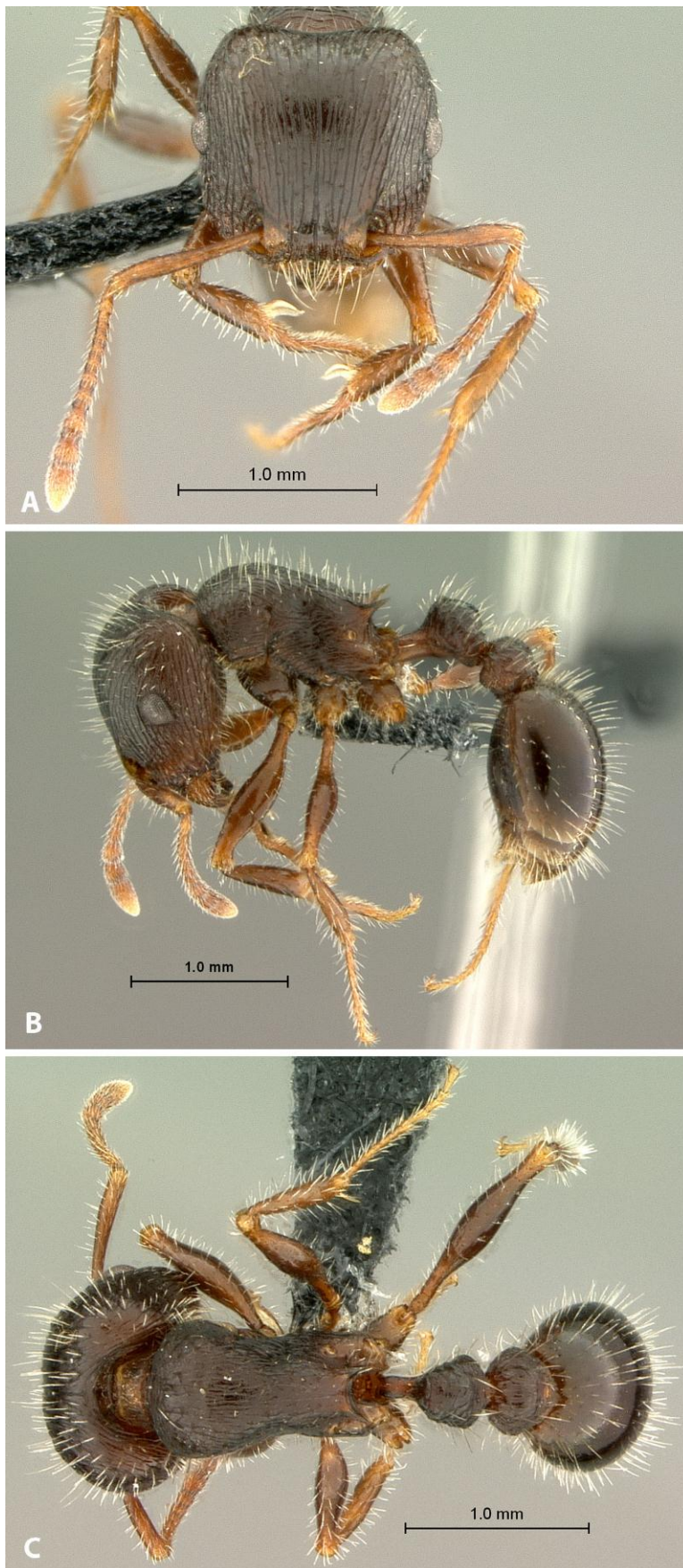


FIGURE 31. A worker of *Tetramorium* sp. nov. 1- holotype : A. head in full face view; B. lateral view and C. dorsal view.

***Tetramorium* sp. nov. 2**

(Figures 17B, 32A-C)

Holotype: **South Africa: Western Cape:** Abrahamskraal, 32.92560° S and 22.01319° E, elevation 516m, collected on a flood plain of dry river bed with *Salsola aphylla* and *Acacia karoo*, in deep finely grained soils, 15 April 2008, N. Mbanyana and HG Robertson, WC08-AK1-P18, SAM-HYM-C020292.

Measurements (workers): HL 0.915-1.101; HW 0.934-1.134; HW1 0.981-1.180; CI 100-106; SL 0.649-0.806; SI 68-74; PW 0.561-0.738; NW1 0.305-0.364; NW2 0.393-0.482; NL1 0.246-0.328; NL2 0.256-0.344; ML 0.993-1.227; EL 0.228-0.285; EI 22-26 (15 measured).

Holotype description (worker): Mandibles with fine longitudinal striations. Anterior clypeal margin with an extensive, semicircular indentation. Frontal carinae extending back from the frontal lobes as fine ridges, which end at about the level of the anterior margins of the eyes. Eyes with 16 ommatidia in the longest row. Propodeum armed with a pair of short triangular teeth. Metapleural lobes low and rounded. Peduncle with a prominent keel-shaped subpetiolar process. Petiolar node in profile nodiform, with the posterior face slightly more steeply angled than anterior face; anterior face also rounding into dorsum but with slightly angled corners as seen in the dorsal view. Postpetiolar node low and rounded. Dorsal surfaces of head and mesosoma with finely reticulate ground-sculpture, which is overlaid by longitudinal striations. Petiole and postpetiolar nodes with fine reticulate sculpture, which is overlaid by irregular transverse striations. Gastral tergite with fine, superficial reticulate pattern. Numerous long hairs on the clypeus. Ventral surface with prominent psammophore. Erect hairs distributed as follows elsewhere: dorsum of head with four pairs; dorsum of mesosoma three pairs (two on the humeri and one on the

mesonotum); one pair on the petiolar node; and numerous hairs on the gastral sternite. Postpetiolar node and gastral tergites without erect hairs, with pubescence only, which is present everywhere. Colour uniformly black.

Paratypes and other material examined: Same as holotype, with the following differences: Three to five pairs of long erect hairs on the dorsum of mesosoma, arranged as follows; two to four pairs along anterior margin of pronotum and one pair on the mesonotum. Eyes with 15-16 ommatidia on the longest row.

Diagnosis

Morphologically, *T. sp. nov. 2* appears to be closely related to *Tetramorium solidum* in that these are the only species in the group with sparse simple erect hairs that are restricted to the mesosoma and petiole only. These two species can be separated on basis of the length of propodeal spines. In *Tetramorium sp. nov. 2*, the propodeum is only armed with very short propodeal teeth (Figure 17B), which are shorter than their basal width, whereas in *T. solidum* the propodeum is armed with elongate and acute spines (Fig. 17A).

Notes

Known from South Africa (Western Cape and Northern Cape) and Namibia, from the Nama-Karoo and highland savannah. Specimens were collected from pitfall traps.

Material examined

Paratypes: **South Africa: Western Cape:** Abrahamskraal, 32.92560°S 22.01319°E, elevation 516m, 15 April 2008, N. Mbanyana and HG Robertson, WC08-AK1-P18, SAM-HYM-C020292; WC08-AK1-P02, SAM-HYM-C020288; WC08-AK1-P06, SAM-HYM-C020289; WC08-AK1-P16, SAM-HYM-C020290; WC08-AK1-P17, SAM-HYM-C020291;

WC08-AK1-P07, SAM-HYM-C020316; WC08-AK1-P04, SAM-HYM-C020329; **Northern Cape:** Melton Wold, 31.46741°S and 22.72155°E, elevation 1333m, 07 January 2009, N. Mbanyana and HG Robertson, NC09-MW2-P15, SAM-HYM-C023306; NC09-MW2-P16, SAM-HYM-C023313.

Other material: **South Africa: Northern Cape:** Sakrivier, 23 April 1963, A.J. Prins, AcAX 2224, SAM-HYM-C019290; Onder-downs, 24 April 1963, A.J. Prins, AcAX 2201-1, SAM-HYM-C019306; Kortkop farm near Strydenburg, 30°09'S and 23°44'E, from a pitfall trap, Karoo vegetation, 17 June 1995, B. Chambers, SAM-HYM-C008783; Hopetown Municipal Farm, 4km East of Hopetown, 15 February 1997, B. Chambers, Ant46, SAM-HYM-C010847; Prieska, 2myl vanaf Prieska na Canarvon, 23 October 1963, AJ Prins, AcAX2966, SAM-HYM-C015044; **Western Cape:** 36km from Prince Albert on Leeu Gama road, 32°54'S and 21°59'E, 10 – 19 October 1996, T.E. Tshiguvho, Site 35, SAM-HYM-C009335; 21km from Prince Albert on Leeu Gama road, 33°02'S and 22°00'E, 10 – 19 October 1996, T.E. Tshiguvho, Site 17 Trap 8, SAM-HYM-C009336.

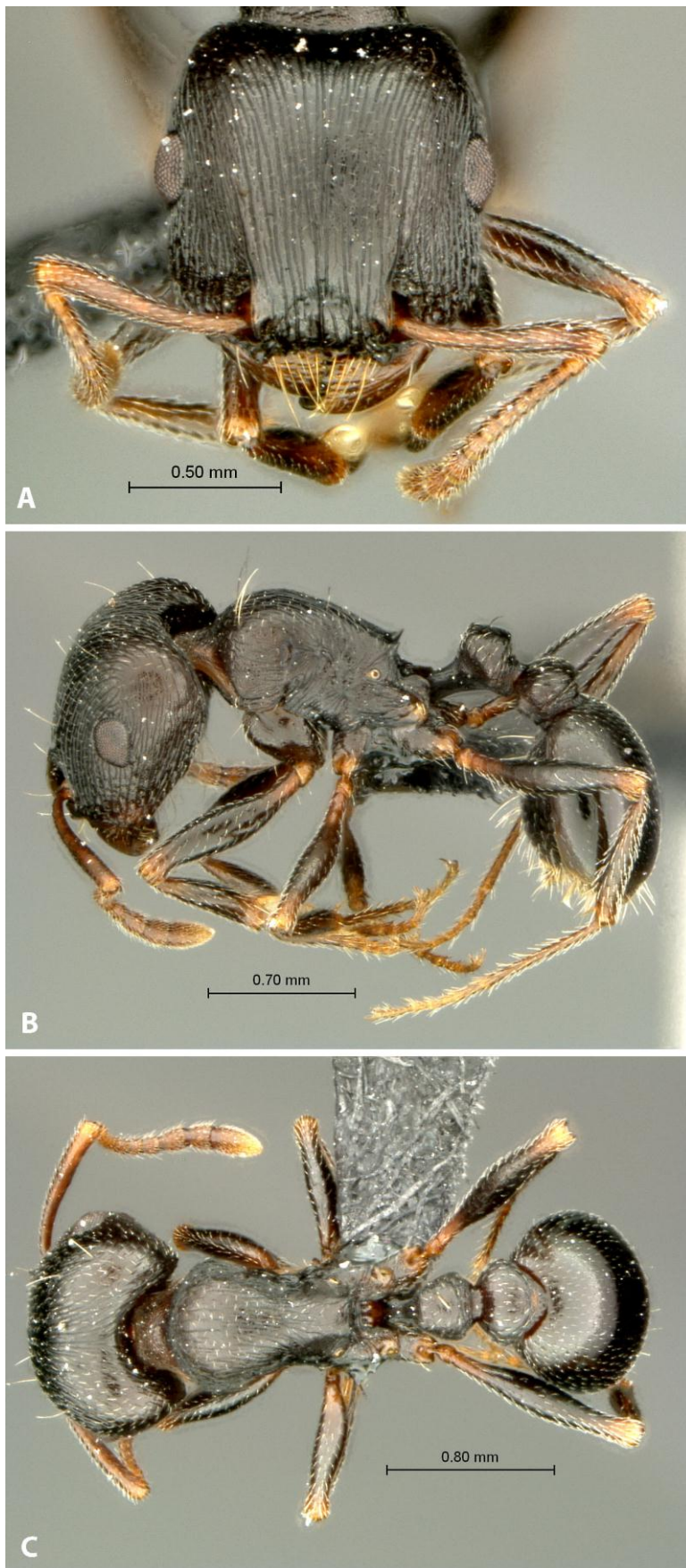


FIGURE 32. A worker of *Tetramorium* sp. nov. 2 - holotype : A. head in full face view; B. lateral view and C. dorsal view.

***Tetramorium* sp. nov. 3**

(Figures 9A, 10A, 33A-C)

Holotype: **South Africa: Northern Cape:** Melton Wold, 31.46741° S and 22.721550° E, elevation 1333m, 07 January 2009, N. Mbanyana and HG Robertson, NC09-MW2-P16, SAM-HYM-C023330.

Worker measurements: HL 1.072-1.227; HW 1.052-1.221; HW1 1.101-1.395; CI 98-106; SL 0.728-0.827; SI 63-69; PW 0.659-0.775; NW1 0.423-0.478; NW2 0.539-0.607; NL1 0.299-0.362; NL2 0.315-0.478; ML 1.151-1.266; EL 0.266-0.310; EI 23-26 (5 measured).

Holotype description (worker): Mandibles predominantly smooth with fine striations basally. Anterior clypeal margin with an extensive and deep indentation. Frontal carinae absent. Eyes with 15 ommatidia in the longest row. Propodeal spines long and acute. Metapleural lobes low and rounded. Peduncle with a broad keel-shaped subpetiolar process. Petiole in profile nodiform, with the anterior face slightly more steeply angled with blunt corners. In dorsal view, petiolar node shaped almost like a rectangle, which is broad posteriorly with rounded corners and narrowing anteriorly with prominent blunt corners. Postpetiole low and rounded both in dorsal view and in profile. Dorsum of head with fine longitudinal striations. Spaces between the striations with very fine reticulate ground sculpture. Dorsal surfaces of mesosoma and petiole with fine reticulate sculpture. Postpetiolar node predominantly smooth, with fine reticulate sculpture in places. Gastral tergite with fine reticulate sculpture. Numerous hairs on the anterior clypeal margin. Dorsum of head with two pairs of erect hairs. Dorsum of mesosoma, nodes and first gastral tergite without any erect hairs, with only sparse white pubescence. Ventral surface of head with psammophore. Colour uniformly black.

Diagnosis

Tetramorium sp. nov. 3 is distinguished from all other species of *Tetramorium solidum*-group by its unique petiole node, which has posterior, lateral, rounded extensions. In posterior view, the dorsal margin straight and angulate with respect to lateral margin (Figure 10A & 33C).

Notes

This species is only known from Melton Wold near Victoria West in the Northern Cape and from Oranjekrag in the Free State, South Africa. It is a ground nesting species and has been collected from pitfall traps.

Material examined

Paratypes: **South Africa: Northern Cape:** Melton Wold, 31.46741° S and 22.721550° E, elevation 1333m, 07 January 2009, N. Mbanyana and HG Robertson, NC09-MW2-P16, SAM-HYM-C023329.

Other material: **Orange Free State:** Oranjekrag, 30°36'0"S and 25°30'0"E, 20 March 1969, AA Boonzaaier, AcAX4877, SAM-HYM-C015315.

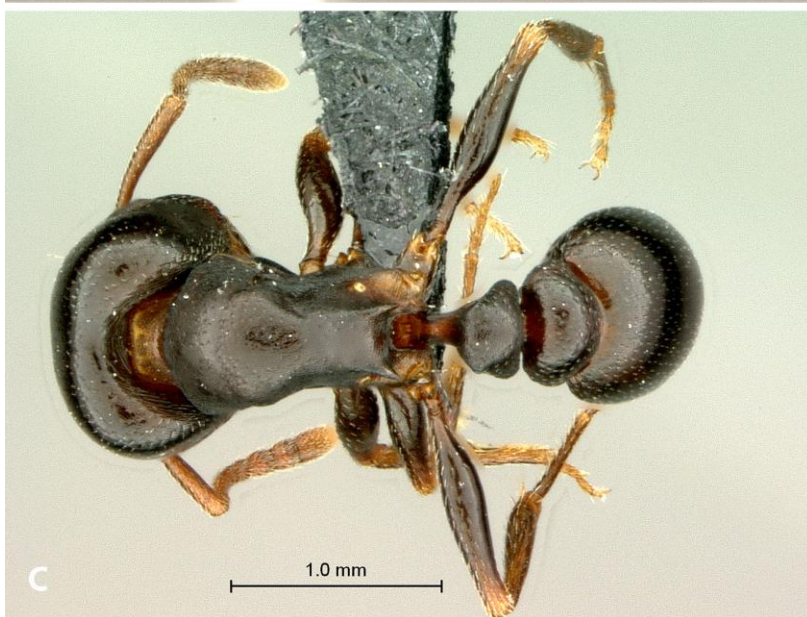
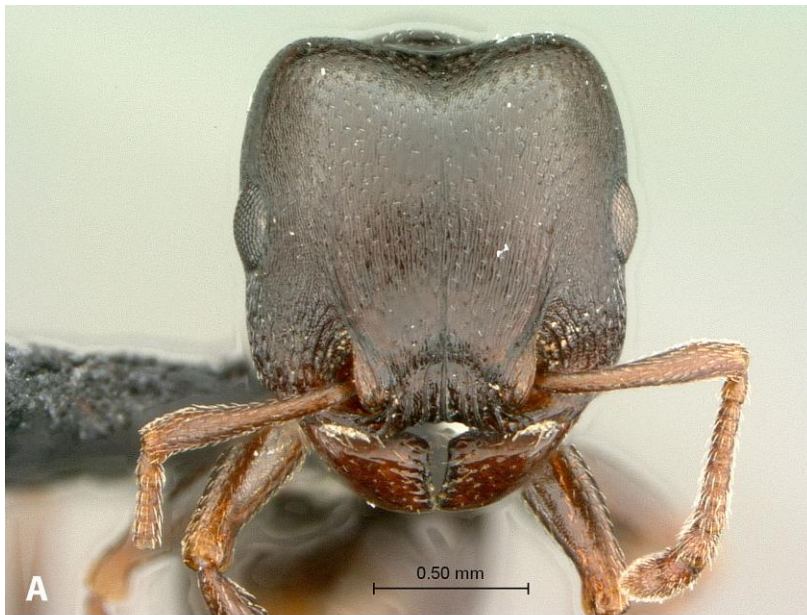


FIGURE 33. A worker of *Tetramorium* sp.nov. 3 - holotype : A. head in full face view; B. lateral view and C, dorsal view.

***Tetramorium* sp. nov. 4**

(Figures 6B, 34A-C)

Holotype: **Namibia:** Withuis, 11 km North of Grunau on B1, S27°36.447 and E18°23.920°, elevation 1243m, 03 April 2011, N. Mbanyana and HG Robertson, NAM2011-035, SAM-HYM-C027003.

Measurements (workers): HL 1.033-1.266; HW 1.033-1.266; HW1 1.150-1.356; CI 97-100; SL 0.723-0.865; SI 68-75; PW 0.672-0.840; NW1 0.323-0.413; NW2 0.413-0.555; NL1 0.297-0.336; NL2 0.284-0.336; ML 1.072-1.382; EL 0.297-0.362; EI 27-31 (5 measured).

Holotype description (worker): Mandibles with fine longitudinal striations. Anterior clypeal margin with a conspicuous, semicircular indentation. Frontal carinae fades before reaching the back from the posterior margins of the eyes. Eyes with 16 ommatidia in the longest row. Propodeum armed with a pair of long spines. Metapleural lobes low, rounded. Peduncle lacking a subpetiolar process. Petiolar node in profile nodiform, with the anterior face rounding into dorsum and dorsum forming an acute angle with the posterior face. Postpetiolar node low and rounded. Dorsal surfaces of head with longitudinal striations, the spaces between them with superficial ground-sculpture. Dorsum of mesosoma with short longitudinal striations, with a shiny superficial ground-sculpture inbetween them. Petiole and postpetiolar nodes with fine reticulate sculpture, which is overlaid by a few irregular striations. Gastral tergite with fine, superficial reticulate pattern. Dorsum of head

with four long erect pairs of hairs. Ventral surface of head with strongly developed psammophore. Remaining dorsum of the body without any hairs. Colour uniformly black.

Diagnosis

Tetramorium sp. nov. 4 belongs to the *barbigerum*-complex. Morphologically, it looks similar to *T. signatum* and *T. grandinode*. This species can be distinguished from all other species in the group by the acute angle between the dorsum of the petiole and the posterior face when viewed laterally.

Notes

Only known from Namibia. Specimens were collected from the nests.

Material examined

Paratypes: **Namibia:** Withuis, 11 km North of Grunau on B1, S27°36.447 and E18°23.920°, elevation 1243m, 03 April 2011, N. Mbanyana and HG Robertson, NAM2011-035, SAM-HYM-C027003; Withuis, 11 km North of Grunau on B1, S27°36.666 and E18°23.726°, elevation 1241m, 02 April 2011, N. Mbanyana and HG Robertson, NAM2011-027; Withuis, 11 km North of Grunau on B1, S27°36.447 and E18°23.920°, elevation 1243m, 03 April 2011, N. Mbanyana and HG Robertson, NAM2011-034.

Other material: **Namibia:** Kyffhauser, S24°28.708' and E16°20.148', elevation 1381m, 06 April 2011, N. Mbanyana and HG Robertson, NAM2011-068; 132km from Mariental on M29, S25°16.795' and E18°37.635', 18 April 2011, N. Mbanyana and HG Robertson, NAM2011-282; Wolwedans 144, Maltahohe district, 25°06'S and 15°59'E, 12-18 March 1992, Pitfall traps, Chauveau dune, E. Griffin, 30027; **South Africa: Northern Cape:** Breckkierie dunes, 30°07'S and 21°33'E, 04 May 1985, M.A. Macpherson, SAM-HYM-C001771; Kortkop farm near Strydenburg, 30°09'S and 23°44'E, 17 June 1995, B. Chambers, SAM-HYM-C008763.



FIGURE 34. A worker of *Tetramorium* sp. nov. 4 - holotype : A. head in full face view; B. lateral view and C, dorsal view.

***Tetramorium* sp. nov. 5**

(Figures 35A-C)

Holotype: **South Africa: Northern Cape:** Near Augrabies Falls National Park, on R359 past turnoff for Augrabies National Park, -28.623 and 20.328, elevation 639m, 13 December 2011, Brigitte Braschler, ASA_NC_44_01.

Holotype description (worker): Mandibles with fine longitudinal striations. Anterior clypeal margin with an extensive and deep indentation. Frontal carinae extending back to the posterior margins of the eyes. Eyes with 16 ommatidia in the longest row. Propodeum armed with a pair of short propodeal spines, which are longer than the basal width. Metapleural lobes low rounded. Peduncle with a prominent keel-shaped subpetiolar process. Petiolar node in profile nodiform, with the posterior face slightly more steeply angled than anterior face; anterior face rounding into dorsum but with slightly angled corners as seen in the dorsal view. Postpetiolar node low and rounded. Peduncle lacking a subpetiolar process. Dorsal surfaces of head and mesosoma with longitudinal striations, the spaces between them with superficial ground-sculpture. Petiole and postpetiolar nodes with fine reticulate sculpture, which is overlaid by few irregular transverse striations. Gastral tergite with longitudinal short striations basally and the remaining part with fine reticulate pattern. The antennae with sub-erect pubescence. The tibia of middle and hind legs with numerous short, stout, erect hairs. Ventral surface of head with strongly developed psammophore. Head and mesosoma light brown in colour and gaster black.

Diagnosis

Tetramorium sp. nov. 5 belongs to the *peringueyi*-complex. Morphologically, it appears to be closely related to *T. peringueyi*, *T. dichroum* and *Tetramorium* sp. nov. 1 in that these are the only species in the complex with abundant erect hairs covering the entire body. *Tetramorium* sp. nov. 5 can be separated from these species on basis of propodeal spine length. This is the only species in this complex with short propodeal teeth. All other species in *peringueyi*-complex have medium to long spine lengths. This species can also be easily distinguished from all other species in the *solidum*-group by the fact that this is the only one with a combination of short propodeal teeth and abundant hairs covering the entire body.

Notes

Known from one specimen which was collected from pitfall traps in the Northern Cape.



FIGURE 35. A worker of *Tetramorium* sp.nov. 5 - holotype : A. head in full face view; B. lateral view and C, dorsal view. (Photo taken by B. Braschler)

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Chapter 2

Unraveling the biogeographic history of the *Tetramorium solidum* group (Hymenoptera: Formicidae) in southern Africa

Part of this work will form the base of a paper that will be submitted to the *Journal of Biogeography*

Abstract

Background The diversification of many taxa has been influenced by historical climatic changes. This often leads to multiple and unrelated taxa showing similar patterns of evolutionary diversification within the same geographic region. Ants in the arid regions of southern Africa display interesting biogeographic patterns but the factors and processes underlying these patterns have never been assessed.

Aim Here I aim to reconstruct a dated phylogeny for southern African ants belonging to the *Tetramorium solidum*-group in order to assess the nature and timing of historical processes that may have led to the diversification of this group.

Location Ants were sampled from the dry regions of the Northern Cape and Western Cape Provinces in South Africa, and Namibia.

Methods The cytochrome oxidase 1 (*CO1*) mitochondrial gene was sequenced to reconstruct phylogenetic relationships among selected *Tetramorium* taxa using Bayesian inference. Divergence date estimates among included taxa were estimated by including a dated fossil record for taxa in the genus *Tetramorium* and a relaxed molecular clock as implemented in BEAST. In order to better understand the ecological factors that restrict the

current distribution of the *T. solidum*-group, species distribution models were developed using various modeling approaches implemented in BIOMOD.

Results From the 10 species of *T. solidum*-group included in our analysis (excluding outgroups); we identified 15 clades, including five possible new species that is in agreement with morphological data (see Chapter 1). Geographically widespread *T. setuliferum* was basal to the phylogeny. The dating analysis suggests that the *Tetramorium solidum*-group diverged from other taxa within the genus about 30 Million Years Ago (MYA) (Oligocene) and that radiation within the group occurred from 24 MYA (Miocene). Species distribution models suggest that the current distribution of the group is profoundly influenced by rainfall whereby almost all species occur only in the drier western half of southern Africa, avoiding the moist regions, with the Nama-Karoo ecoregion being the center of species diversity and endemism.

Conclusion The diversification of *Tetramorium solidum*-group taxa coincides with the Miocene during a period characterized by the onset of aridification, open grassland vegetation and winter-rainfall regimes in south western Africa. The phylogenetic analysis further suggests that *T. setuliferum*, which is the only species occurring in eastern tropical region of Africa is the basal species in the dated phylogeny, and possibly the group originated from the eastern parts of southern Africa before diversifying to the western region.

Keywords: *Tetramorium solidum*-group, southern Africa, Miocene, species diversity, aridification, winter rainfall, Nama Karoo.

Introduction

Understanding the processes that underpin species' natal ranges and the evolutionary histories that shaped them has long interested biogeographers, ecologists and phylogeographers alike. From a phylogeographic perspective, delineating genetic relationships among taxa is potentially informative about the historical processes that impacted on patterns of gene flow, local adaptation and, ultimately, speciation. Paleoclimatic changes are considered to be one of the most important drivers of past speciation events (Hewitt, 2011) and therefore emphasize the need for a resolved phylogeny in order to infer when and how historical processes influenced particular taxa. An understanding of how these processes produced current biodiversity patterns is not only of theoretical interest, but is also relevant to the effective manage given the challenges faced by global biodiversity (Byrne *et al.*, 2008).

Intuitively, not all taxa within the same geographical region experience similar selection pressures over time. For example, in south western Africa the replacement of forests by open grasslands due to increased and ongoing aridification during Miocene has led to the rapid diversification of many arid-adapted fauna (Jansson and Dynesius, 2002). Most taxa in this region responded to these vegetation shifts, for example, dwarf chameleons in southern Africa radiated during Miocene in response to increasing C4 grassland habitats during Miocene (Tolley *et al.*, 2008). Historical climate changes also led to contractions and expansions of many species ranges (Hewitt, 2011), for example, the shift in the Sahara from a tropical to an arid environment led to the divergence of the elephant shrews, *Elephantulus rozeti* and its sister taxa *Petrodromus tetradactylus* during mid to late Miocene (11.6 MYA) (Douady *et al.*, 2003). After the major climatic changes that are known from Miocene epoch, which include climate optimum during Mid-Miocene (about 16-14 MYA) (Hewitt, 2011), there were minor reversals over the years, which included continuation of cooling during the Pliocene (5.3 MYA) and the Pleistocene (2.6

MYA) accompanied by growth of the Arctic Ice Cap (Hewitt, 2011). The climate cycles during the Plio-Pleistocene created habitat heterogeneity and also affected the diversification of many taxa; for example, the species complex of fiscal shrike (*Lanius collaris*) in Africa started to diversify around 2.2 MYA (Fuchs *et al.*, 2011).

There is a highly endemic ant fauna that has evolved in arid regions of southern Africa. For instance, the genus *Ocymymex* comprises 37 described species and is restricted to the Afrotropical regions. Its distribution extends through the dry savannah regions to extreme desert regions of the eastern and southern part of the Afrotropical region. *Ocymymex* ants do not occur in the rain forests of West and Central Africa and neither are they in the Sahelian zone of the Sahara region (Bolton and Marsh, 1989). The highest diversity of *Ocymymex* lies in the arid regions of Namibia, where 17 species have been recorded (11 endemic) and South Africa, also with 17 species recorded of which seven are endemic. The species occurring in the eastern side of the Afrotropical region belong in a single species-group (*weitzackeri*-group), which is also widespread in other parts of southern Africa (Bolton and Marsh, 1989).

In addition to *Ocymymex*, the following ant genera are also dominant in the arid regions of southern Africa: *Monomorium salomonis*-group (32 species); *Monomorium setuliferum*-group (6 species); *Nesomyrmex* (20 species); *Messor* (7 species); *Camponotus fulvopilosus*-group (4 species); and *Camponotus mystaceus*-group (around 8 species) (Robertson, 2000). Despite their impressive diversity, there has been no attempt to analyse the evolutionary systematics and biogeography of these arid-adapted taxa. It is possible that the aridification processes which led to vegetation changes have contributed to the high endemism of ants in these dry regions. For example, in the Namib Desert more than 95 % of the total forage biomass is made up of harvester ants, with seeds making up a substantial part of their diet (Hölldobler and Wilson, 1990). Despite their ecological

importance very little is known about the distribution and phylogeography of ants, and therefore the processes that may have led to their diversification.

Here I investigate the geographical and historical context of diversification of ants within the *Tetramorium solidum*-group. These ants are mainly restricted to the dry regions of southern Africa (Bolton, 1980), although there are two species are found further north in Africa in sub-tropical habitats. Currently the group comprises 19 recognized species (see Chapter 1) in southern Africa, almost all the species in this group occur in the western parts, with the exception of *T. setuliferum*, which is the most abundant species in the group and is the only species that extends its distribution to the wetter regions of the eastern parts of southern Africa. Specifically, using a dated phylogenetic analysis and species distribution modeling, I inferred the role of historical events and current climatic factors in shaping the distribution and diversification of the members of the group.

Materials and methods

Sampling

Ants were sampled throughout their known distributional ranges in the Northern Cape and Western Cape Provinces in South Africa, and Namibia. Individuals were collected by hand, including digging up nests. Ants from the samples were preserved in ethanol 96% prior to DNA extraction. Representatives for each putative species were mounted and labelled and voucher specimens deposited in the dry collection at Iziko South African Museum, Cape Town. For long-term storage all remaining material was preserved and stored in 96% ethanol.

Geographical distribution and species distribution modeling

To visualize species richness and distribution, maps were produced for all the species in the *Tetramorium solidum*-group by overlaying known point locality records onto ecoregional maps of southern Africa using Arc GIS version 9.2.

All available presence records for species of the *Tetramorium solidum*-group were extracted from the ant database of Iziko Museums of South Africa. All records contained information on locality, year of collection with some records having information on habitat. *Tetramorium* species with 12 or fewer records were not included in further analyses.

A set of species distribution models (SDMs) was developed for the 11 *Tetramorium* species that met the selection criteria, with sufficient occurrence data using a randomly-generated set of 20 000 pseudo-absences, and six different environmental factors. Using the strategy of Webber *et al.* (2011), pseudo-absences for each species were randomly chosen within Köppen-Geiger climate zones (sourced from the CliMond 10' historical climate dataset; Kriticos, *et al.*, 2011) within which presence records for the species in question occurred. Only 10 000 pseudo-absence points were used for each model run, but these were randomly selected from the 20 000 points generated for each species to investigate the influence of pseudo-absence selection.

The environmental variables believed to be ecologically important for *Tetramorium* distributions were selected for the SDMs and included four of 19 WorldClim bioclimatic variables [mean annual temperature, mean annual precipitation, maximum temperature of the warmest month and the mean temperature of the wettest quarter (Hijmans *et al.*, 2005) and two of six soil variables from the Harmonized World Soil -Database (percentage clay in the top 30 cm of the soil horizon and percentage clay in the soil horizon from 30 to 100 cm; FAO/IIASA/ISRIC/ISS-CAS/JRC, 2009). To account for co-linearity, environmental variables were compared in a pair-wise correlation and those with pair-wise correlations of less than 0.6 retained for further analyses.

Four different modelling methods available in the BIOMOD package (Thuiller *et al.*, 2009) were used to build SDMs in R (R Development Core Team, 2012) for each *Tetramorium* species: (1) a regression method, Generalised Additive Models (GAM; Hastie and Tibshirani, 1990), with a maximum of three degrees of freedom; (2) Boosted Regression Trees (BRT; Ridgeway, 1999), with the optimal number of trees selected by five cross validations and an upper limit of 3 000 trees; (3) a machine-learning method, Artificial Neural Networks (ANN; Ripley, 1996), with five cross validations; and (4) a classification tree method, randomForest (RF; Breiman, 2001). A randomly-selected subset of 70% of the data was used for model calibration, and the remaining 30% for model evaluation using the area under the receiver operating characteristic curve (AUC; Swets, 1988). AUC values were calculated twice for each species and for each model, by randomly selecting two different calibration and evaluation datasets.

Predicted distributions for each species were obtained through an ensemble forecasting technique (Araújo and New, 2007; Thuiller *et al.*, 2009). All modelling results, including those of model repetitions using different calibration and pseudo-absence datasets, were combined into a single predicted probability of occurrence map for each species by weighting each model by its corresponding AUC value.

Molecular bench work

Mitochondrial DNA was extracted from the ethanol-preserved adult worker using Glass Fiber Plates DNA extraction following manufacturer's protocol (Ivanova *et al.*, 2006). This gene region is often used for phylogenetic and phylogeographic studies in animals as it is haploid, uniparentally inherited and lacks recombination (Avise, 2000). Moreover, relative high mutation rates mean that mitochondrial are more suitable to track shallow/recent evolutionary events than nuclear gene locus (Yoke *et al.*, 2006), including ants (e.g. Azuma *et al.* 2006). Here the mitochondrial cytochrome oxidase subunit 1 gene

(*COI*) was amplified and sequenced using the following primers: LEP-F1 and LEP-R1 as described by Herbet *et al.* (2004). Polymerase chain reactions (PCR) were carried out in reaction volumes of 12.5 μ L containing 2 μ L template DNA, 10 μ M of each of the forward and reverse primers, 10 mM dNTP's, 50 mM MgCl₂, 10 x Buffer, 10% trehalose, 5 U/ μ L Taq DNA polymerase and distilled water. The following PCR thermocycle was used: initial denaturation for 1 min at 94 °C, six cycles of 1 min at 94°C, 1 min and 30 sec at 45°C, and 1 min and 15 sec at 72°C, followed 36 cycles of 1 min at 94°C, 1 min and 30 sec at 51°C, and 1 min and 15 sec at 72°C, with a final step of 5 min at 72°C. PCR products were visualized using agarose gels electrophoresis. PCR products were purified using Sephadex® clean-up following the manufacturer's protocol (Pharmacia Biotech Inc., New Jersey, USA.). Purified products were sequenced in one direction using LEP-F1 primer using Dye terminator sequencing and a 3730xl DNA Analyzer (Applied Biosystems, CA, USA).

Phylogenetic analysis

Bayesian analyses

Contiguous sequences were constructed, edited and aligned using BioEdit version 7.0.5 (Hall, 1999). All edited sequences will be deposited in GenBank (<http://www.ncbi.nlm.nih.gov>). Sequences for five *Temnothorax ambiguus* were obtained from Genbank and used as outgroups. The following species of *Tetramorium* from different species groups were also downloaded from Genbank and added to the alignment: *Tetramorium caespitum*, *T. kelleri*, *T. severini*, *T. delagoense*, *T. tosii*, *T. simillimum*, *T. pleganon*, *T. pacificum*, *T. lanuginosum*, *T. humbloti*, *T. bessonii*, *T. cognatum*, *T. scytalum*, *T. hispidum*, *T. sericeiventre* and *T. quadrispinosum*. Bayesian inference was performed in MrBayes version 3.1.2 (Ronquist and Huelsenbeck, 2003) to estimate tree

topology and branch lengths. The best-fitting model was selected using jModelTest (Posada, 2008) under the Akaike information criterion (AIC). The standard four chain (one cold and three hot) search parameter in two simultaneous runs was implemented, with a burnin value of 20 000 trees (discarded before sampling) and a sample frequency of 10; each chain was run for 4 million generations until the average standard deviation of split frequencies was well below the standard value of 0.01. Confidence in tree topologies was assessed as posterior probabilities calculated for each node as implemented in MrBayes. All Trees were visualised in TreeEdit version 1.0a1-19 (<http://evolve.zoo.ox.ac.uk/software/TreeEdit/main.html>).

Dating analysis

Divergence estimates among species of the *Tetramorium-solidum* group were estimated using uncorrelated lognormal relaxed clock with Yule process as the tree prior in BEAST v1.7.1 (Drummond *et al.*, 2012). Bayesian MCMC analyses were performed using the best fitting model identified by jModelTest (Posada, 2008): Hasegawa-Kishini-Yano (HKY) model of evolution with gamma site heterogeneity model. For calibration, the normal prior age distribution was assigned to the root node of *Tetramorium* using the prior knowledge of the fossil age of *Tetramorium*, which is estimated to 44 MYA (Dlussky, 1997). Markov chain Monte Carlo search was run for 40 million generations, sampling every 8000 generations. Convergence and effective sample size (ESS) values were visualized in Tracer v1.5 (Rambaut and Drummond, 2007). The first 250 trees were discarded as burn-in and the maximum clade credibility tree was produced in TreeAnnotator v1.7.1 (Drummond *et al.*, 2012). The results after burn-in were assessed and visualized with FigTree v1.3.1. (Rambaut and Drummond, 2009).

Results

Species richness and distribution modeling

Mapping of occurrence records indicates that most parts of southern Africa are suitable for members of the *Tetramorium solidum*-group, containing at least one species (Fig. 36). The highest species diversity is evidently in the arid western half of South Africa, in the Nama-Karoo region (13 species) and Succulent Karoo region (11 species). In addition, at least five species are recorded from the extreme dry regions of Namibia.

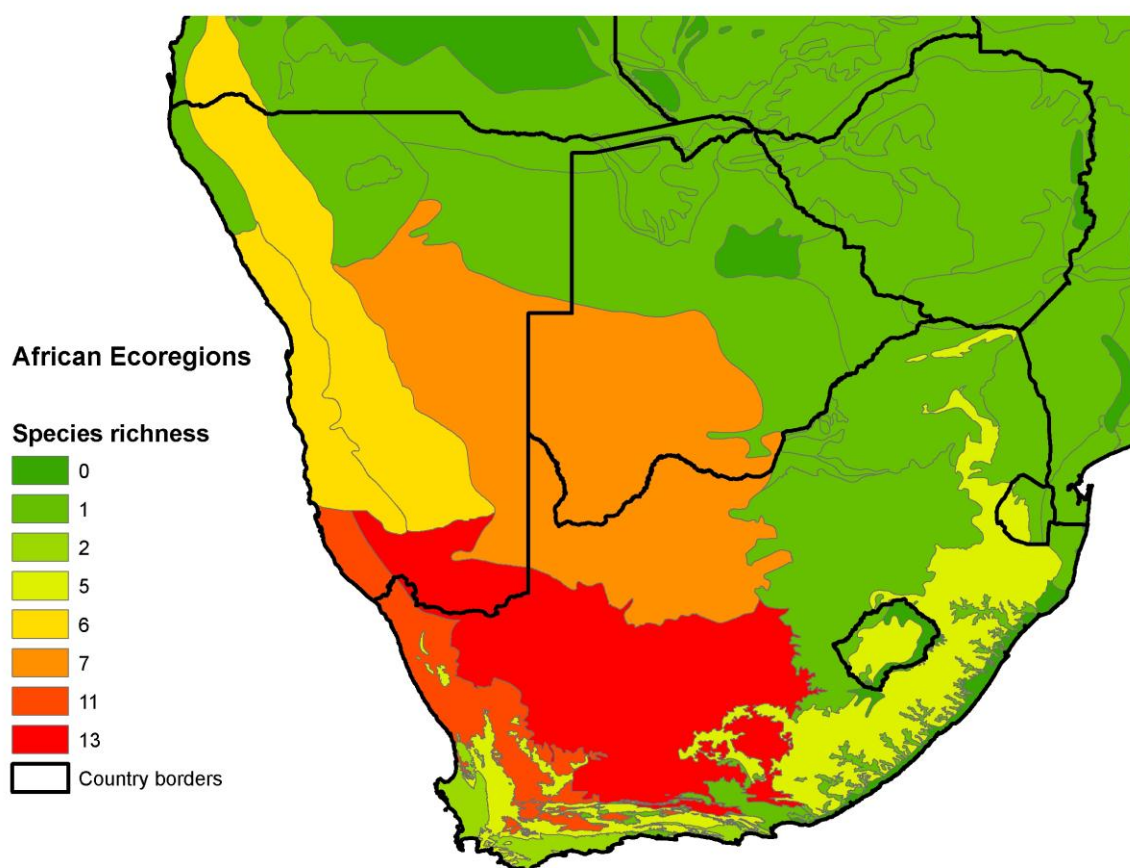


FIGURE 36. Map showing the diversity of *T. solidum*-group species across the different ecoregions of southern Africa. Numbers in the key indicate number of species.

Of the four models that were used for predicting the potential ranges for individual *Tetramorium* taxa, Generalised Additive Models (GAM) and Boosted Regression Trees (BRT) performed the best (Table 1). According to these model predictions, maximum annual precipitation was the most correlated and important variable influencing the current distribution of all *T. solidum*-species group taxa (Fig. 37 - 43).

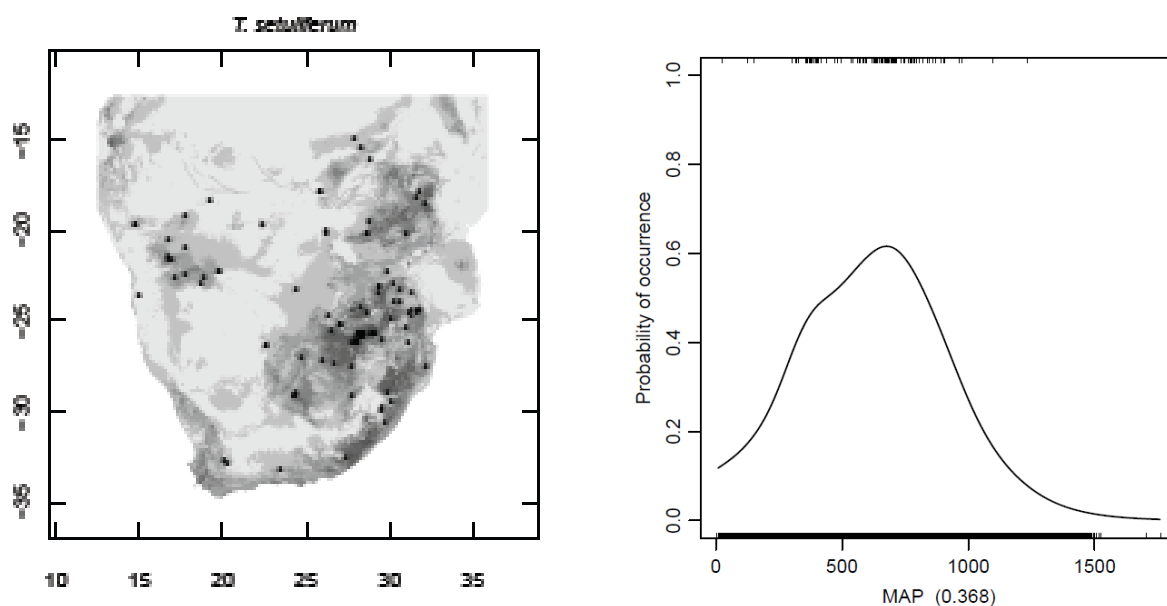


FIGURE 37. Map showing predicted distribution of *T. setuliferum* (left), response curve showing the influence of precipitation on the distribution of *T. setuliferum* (right). Black dots indicate actual occurrence records.

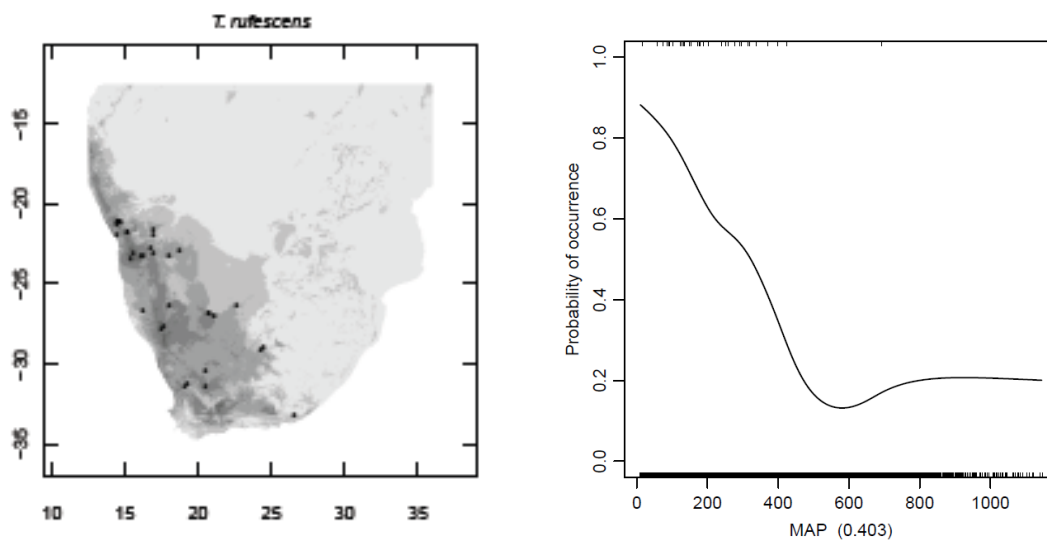


FIGURE 38. Map showing predicted distribution of *T. rufescens* (left), response curve showing the influence of precipitation on the distribution of *T. rufescens* (right). Black dots indicate actual occurrence records.

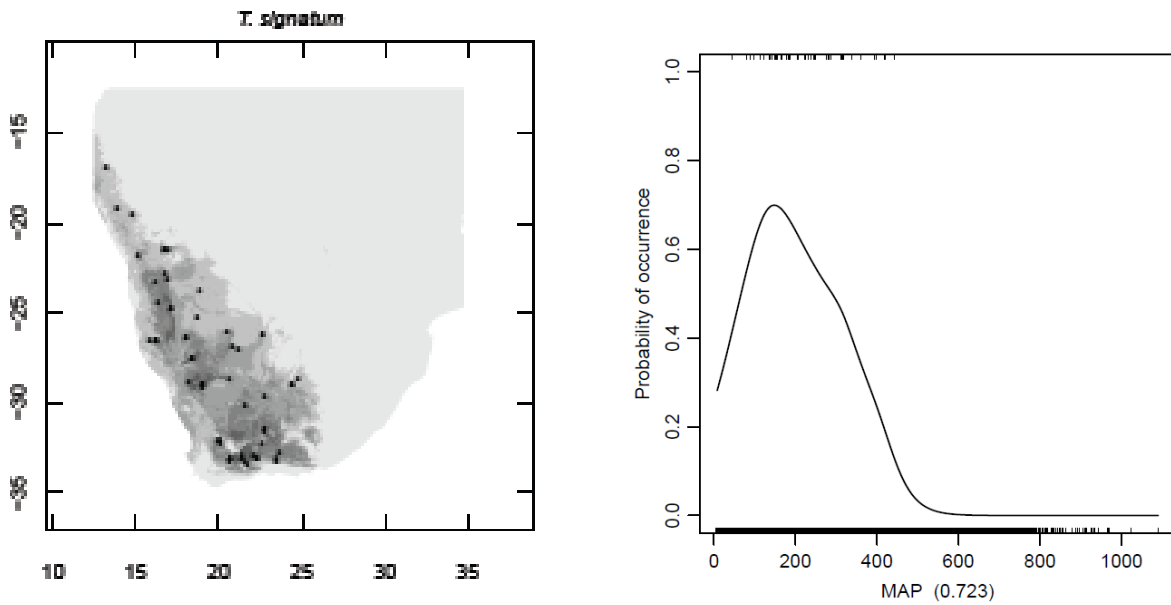


FIGURE 39. Map showing predicted distribution of *T. signatum* (left), response curve showing the influence of precipitation on the distribution of *T. signatum* (right). Black dots indicate actual occurrence records.

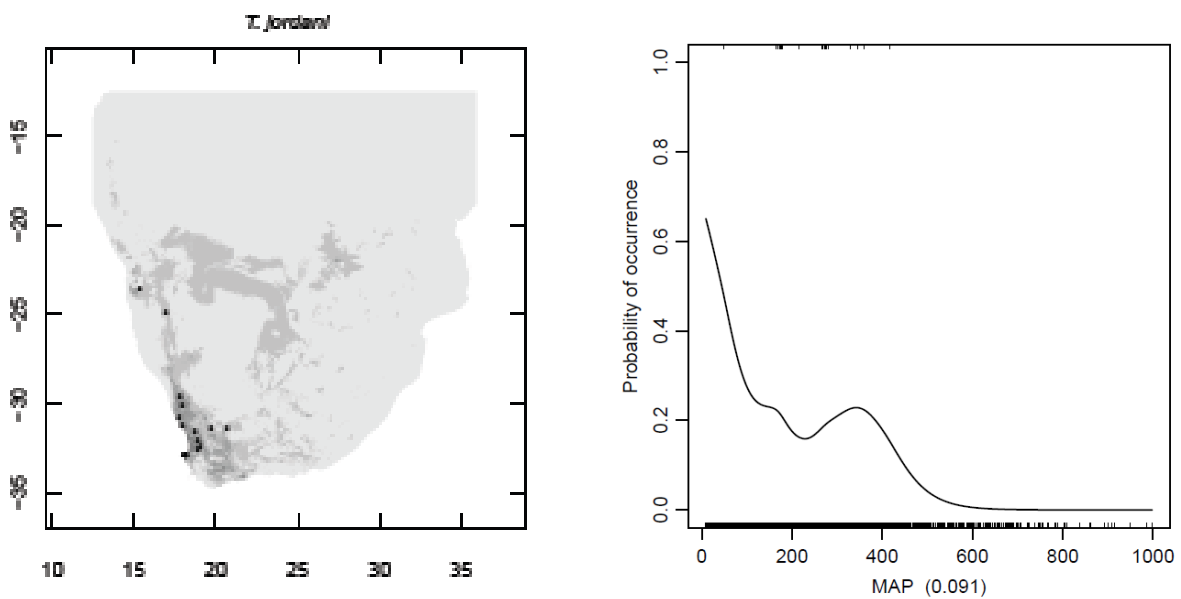


FIGURE 40. Map showing predicted distribution of *T. jordani* (left), response curve showing the influence of precipitation on the distribution of *T. jordani* (right). Black dots indicate actual occurrence records.

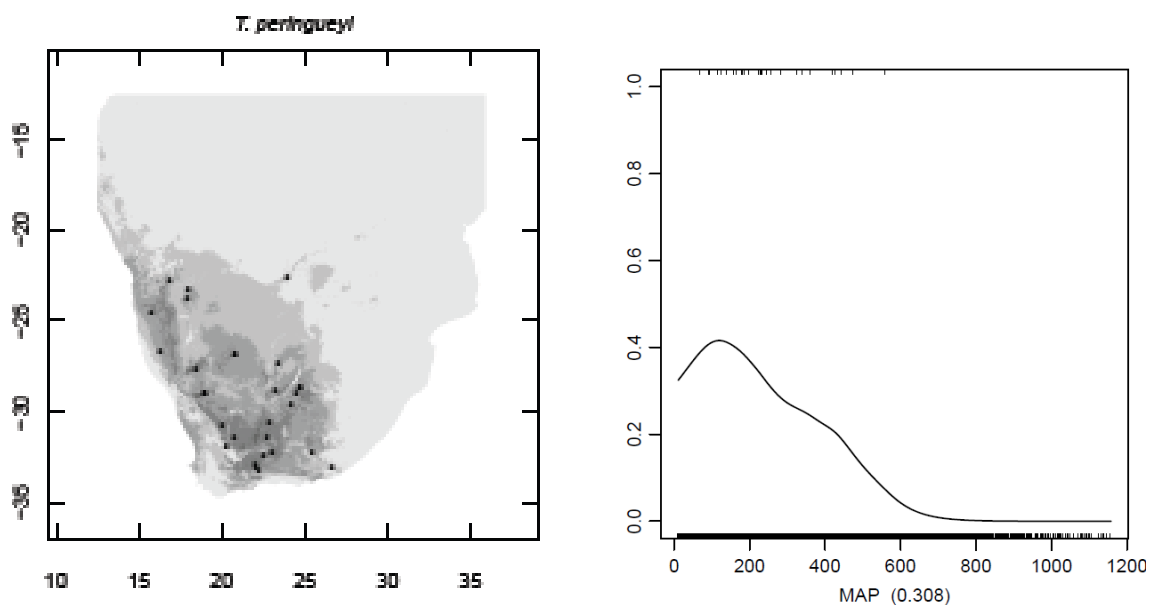


FIGURE 41. Map showing predicted distribution of *T. peringueyi* (left), response curve showing the influence of precipitation on the distribution of *T. peringueyi* (right). Black dots indicate actual occurrence records.

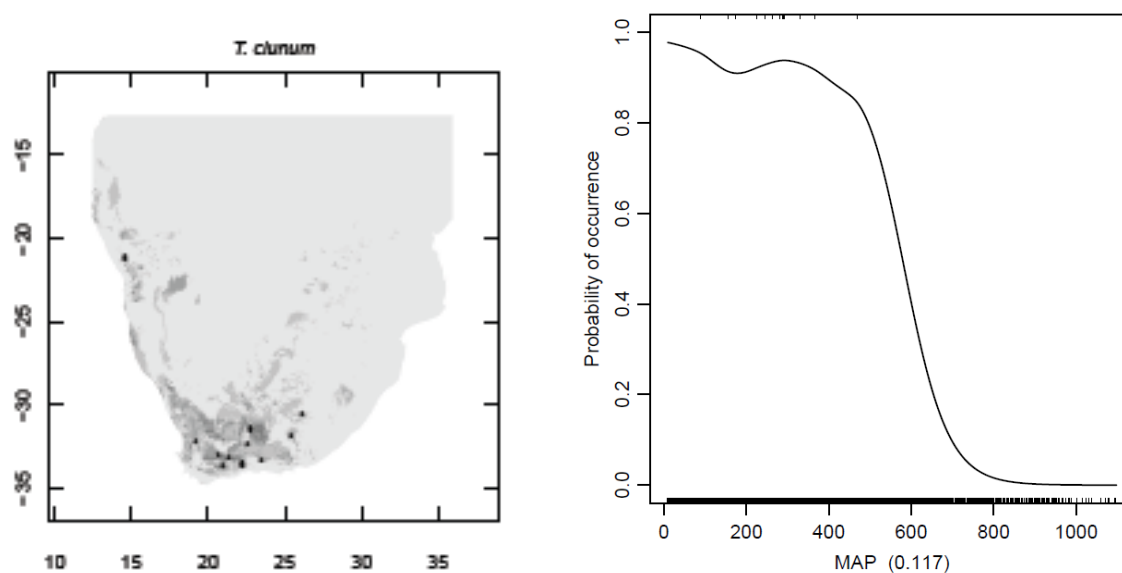


FIGURE 42. Map showing predicted distribution of *T. clunum* (left), response curve showing the influence of precipitation on the distribution of *T. clunum* (right). Black dots indicate actual occurrence records.

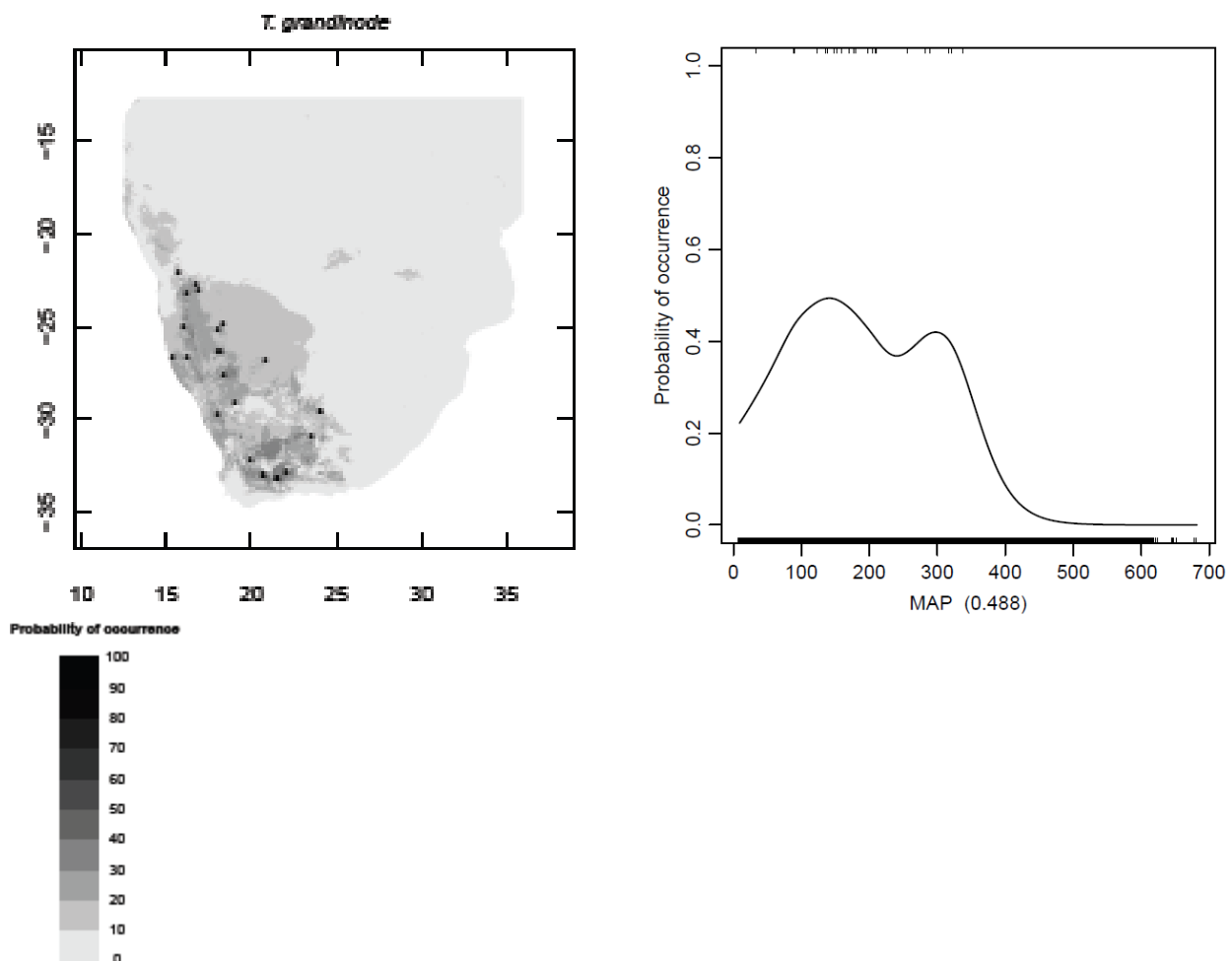


FIGURE 43. Map showing predicted distribution of *T. grandinode* (left), response curve showing the influence of precipitation on the distribution of *T. grandinode* (right). Black dots indicate actual occurrence records.

Species distribution modeling also revealed two distinct bioclimatic affinities within the *T. solidum*-species group. First, *T. setuliferum*, which is the most widespread species in the group, was predicted to be the only species that extends its distribution towards the eastern parts of southern Africa (Fig. 37) even to areas that experience up to 1000 mm rainfall per annum. The distribution of almost all other species in the group was predicted to be restricted to the dry areas towards the western parts of the region that experience less than 600mm rainfall per annum (Figs 38 – 43).

Phylogenetic analysis

A total of 658 bp of the *COI* gene were sequenced for 113 specimens of the *T. solidum*-group. One sequence of *T. rothschildi* was excluded in the analysis because of its low quality. The final alignment, including data obtained from GenBank, contained 154 samples. The analysis in MrBayes v3.1.2 using the TIM2+I+G model of sequence evolution for 3 000 000 generations resulted in a sample of trees with a mean likelihood score of $-\ln L = 11072.7422$. The number of estimated parameters (K) was 346, the base frequencies were estimated as follows: A = 0.3669, C = 0.1718, G = 0.0466 and T = 0.4148, p-inv = 0.4220 for the proportion of invariable sites and gamma shape = 0.4690. The average standard split frequency of the chains after 3 million generations was 0.011. The inferred tree topology showed that taxa in the *T. solidum*- group formed a well-supported monophyletic clade that was well-separated from other *Tetramorium* taxa (Figures 44-47). The *T. solidum*-group was resolved into 15 well-supported lineages, all with strong nodal support (Fig. 44): A (*T. setuliferum*), B (*Tetramorium* sp. nov. 2), C (*T. dichroum*), D (*T. clunum*), E (*T. solidum*), F (*Tetramorium* sp. nov. 1), G (*T. peringueyi*), H (*Tetramorium* sp. nov. 3), I (*Tetramorium* sp. nov. 5), J (*T. grandinode*), K (*Tetramorium* sp. nov. 4), L (*T. glabratum*), M (*T. signatum*), N (*T. jordani*), O (*T. rufescens*). Clade F-G (*T. sp. nov. 1* and *T. peringueyi*) formed a monophyletic group, and H-I (*T. sp. nov. 3* and *T. sp. nov. 5*) also formed a monophyletic group which were both strongly supported. Interestingly, even though these species (*T. sp. nov. 3* and *T. sp. nov. 5*) are phylogenetically very closely related, whereas morphologically they are very distinct (see Chapter 1). The obvious characters separating these two species is the absence of erect hairs on the dorsum of *T. sp. nov. 3* and these hairs are present in abundance in *T. sp. nov. 5* (Chapter 1, Figs 33A-C and 35A-C). Propodeal spines, are long in *T. sp. nov. 3* but reduced to short teeth in *T. sp. nov. 5* (Chapter 1).

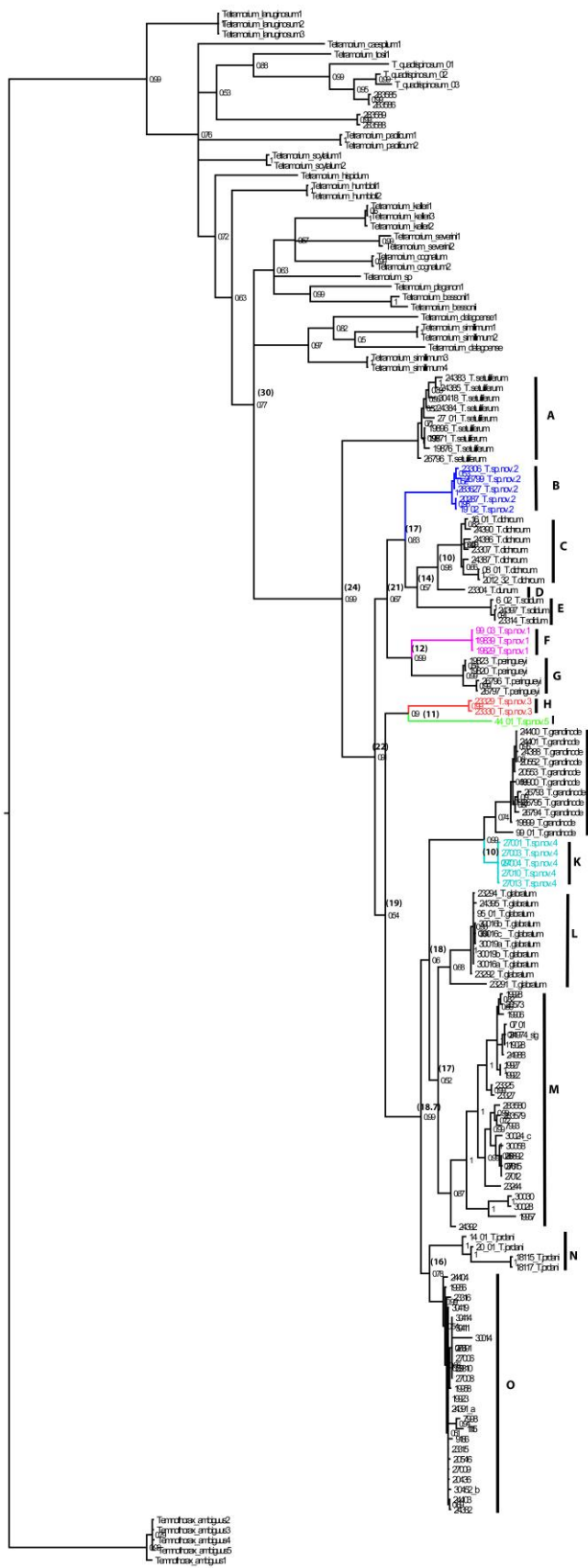


FIGURE 44. Maximum clade probability tree obtained from the fossil-calibrated BEAST analysis (Outgroups at the top and bottom, without bars and letters on the right. Members

of the *Tetramorium solidum*-group are included in clades A-O. Values in brackets indicate divergence estimates (millions of year ago). Nodal support is given as Bayesian posterior probabilities.

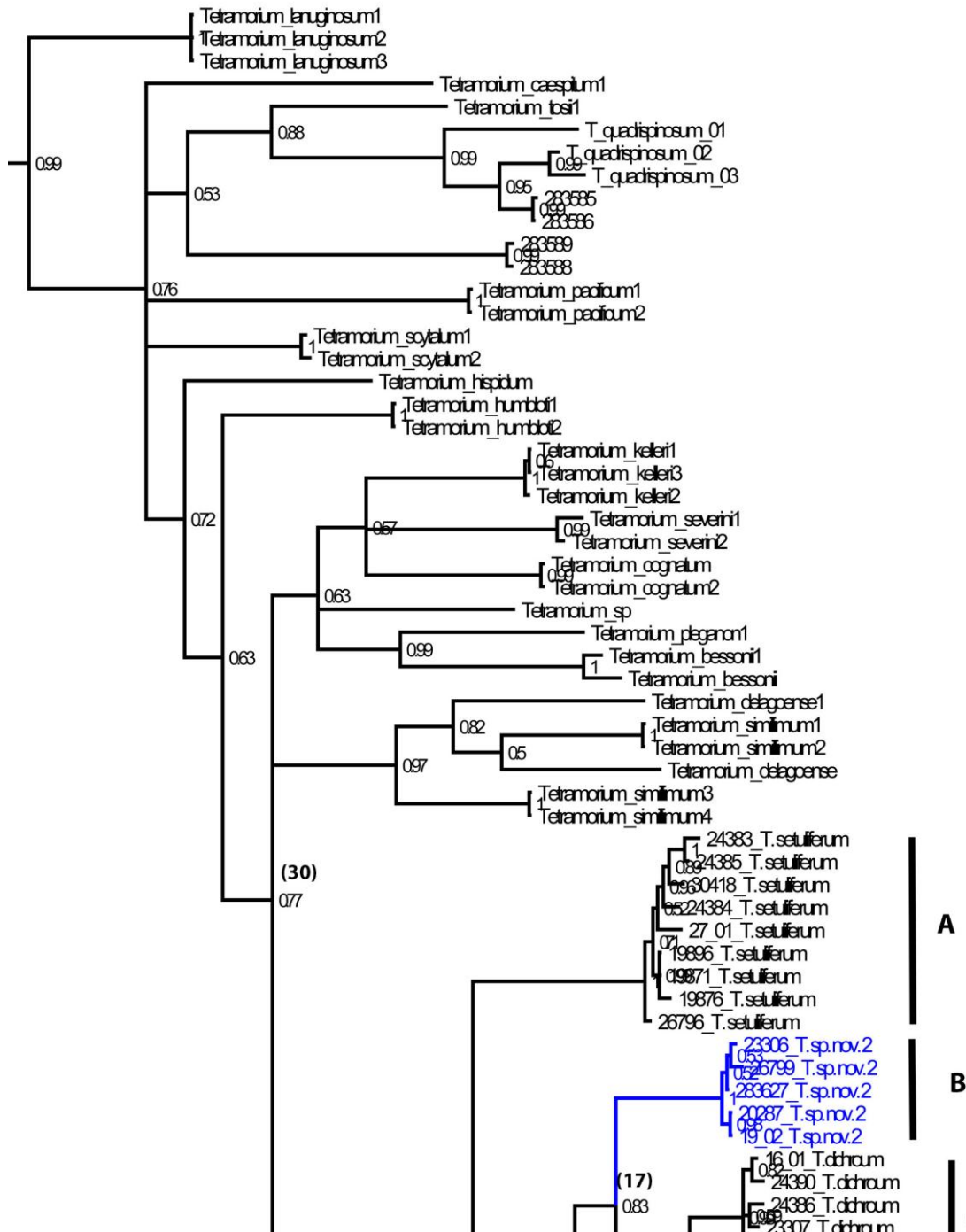


FIGURE 45. Portion of the BEAST tree in Fig. 44, maximum clade probability tree obtained from the fossil-calibrated BEAST analysis, showing a portion of the main tree (outgroup and clades A-B).

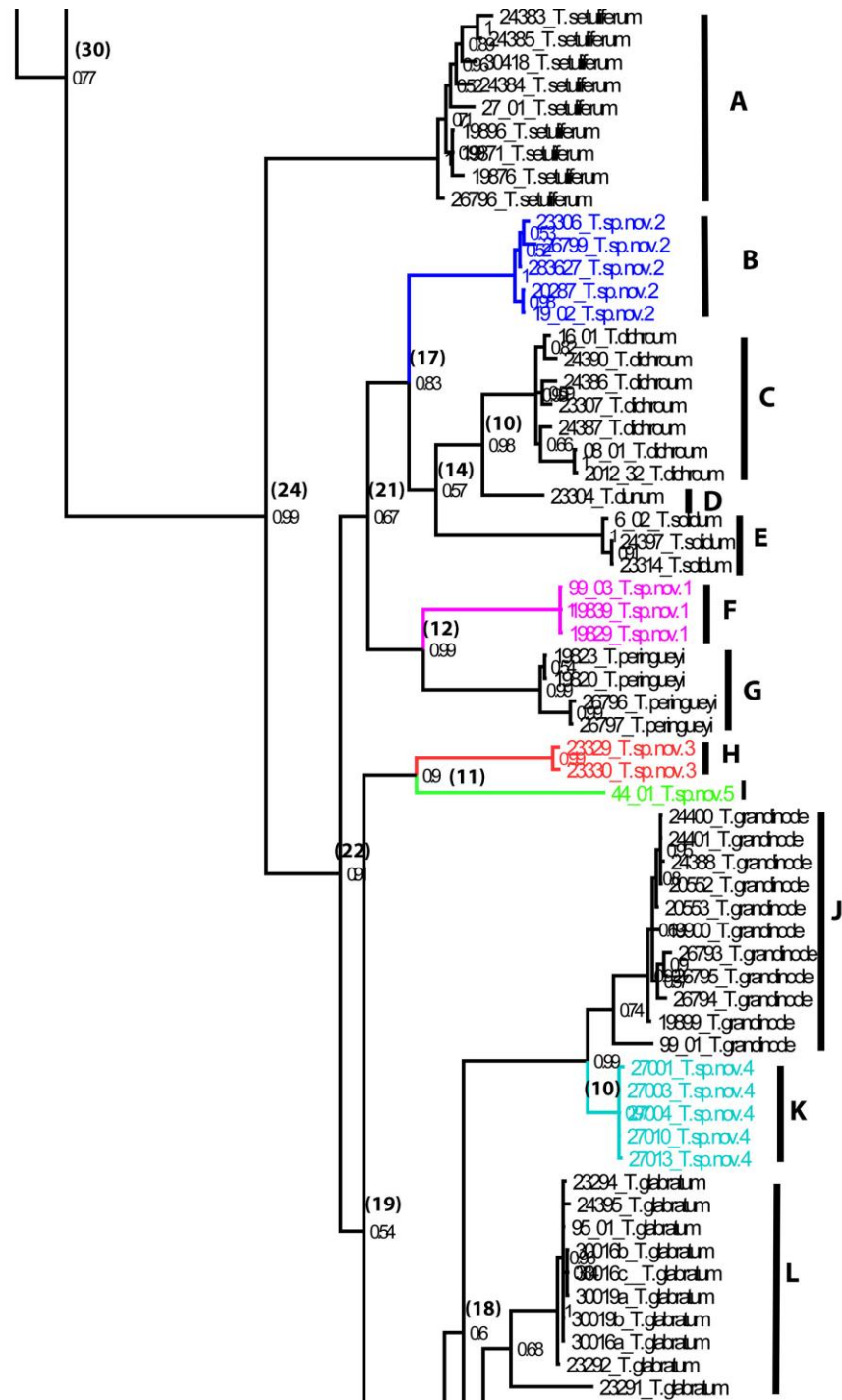


FIGURE 46. Portion of the BEAST tree in Fig. 44, maximum clade probability tree obtained from the fossil-calibrated BEAST analysis, showing some of the clades that belong to *T. solidum*-group (clades A-L).

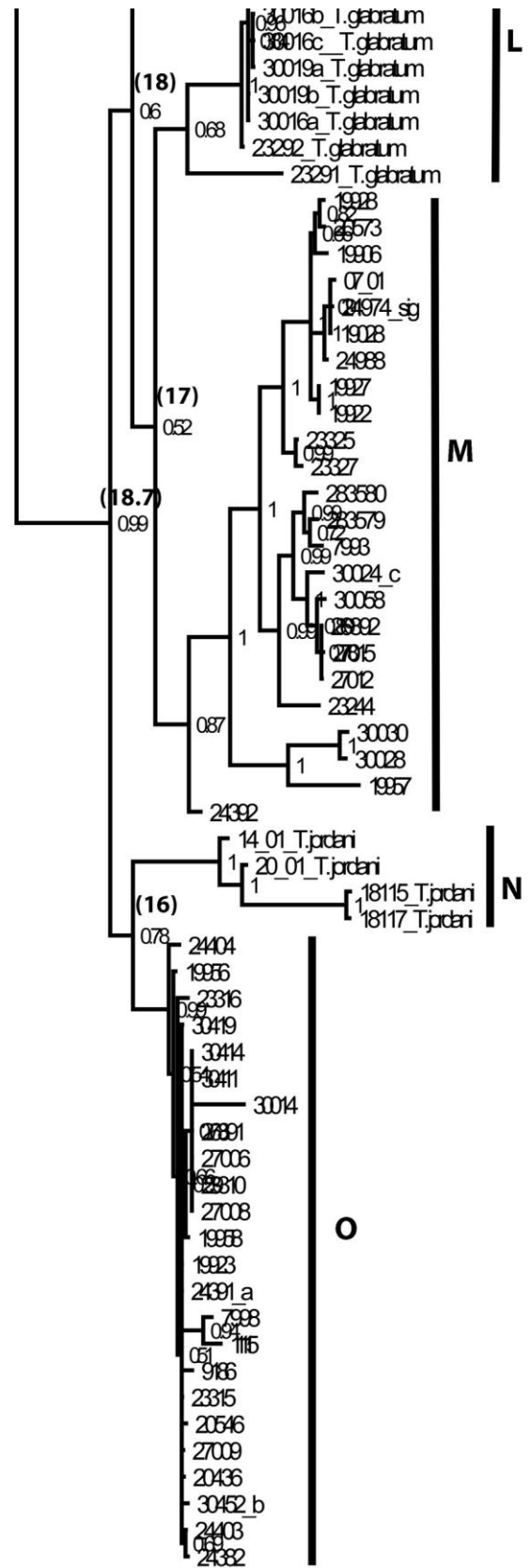


FIGURE 47. Portion of the BEAST tree in Fig. 44, maximum clade probability tree obtained from the fossil-calibrated BEAST analysis, showing some of the clades that belong to *T. solidum*-group (clades L-O).

Divergence dates

Our dating analysis using a fossil-calibrated phylogeny suggests that the *Tetramorium solidum*-group diverged from other species in the genus ca. 30 MYA (Oligocene) (Fig. 46). Diversification of taxa within this group ranges between 24 MYA (clades A) and 10 MYA (clades C and E, and J and K) (Figures 46-47). These estimates date back to the Miocene epoch. Further, our phylogenetic reconstruction suggests that *T. setuliferum* as the basal species in the group (Fig. 46) and that it diverged around 24 MYA from the rest of the taxa within the *T. solidum*-group. The following clades are the youngest species in the group (*T. grandinode* and *T. sp. nov. 5*) and (*T. dichroum* and *T. clunum*), estimated to be 10 MY old.

Taxonomy and phylogeny of *Tetramorium solidum*-group

Bolton, 1980 grouped the species of *Tetramorium solidum*-group into three complexes based on the form of pilosity. The first complex comprises *T. peringueyi*, *T. rothschildi* and *T. dichroum*. These three species are characterized by presence of abundant erect hairs on the dorsal surfaces of the head and body. *Tetramorium rothschildi* is distinguished from the other two species by the presence of branched hairs on the dorsal surfaces of head and body, whereas the other two species have simple hairs. The second complex comprises *T. clunum*, *T. galoasanum* and *T. setuliferum*. These three species lack erect hairs on the dorsal surface of mesosoma, pedicels, petiole, postpetiole and first gastral tergite. They have bizarre pilosity, which consists of short, broad, blunted, much flattened and strongly appressed glittering silvery hairs. The third complex consists of *T. barbigerum*, *T. glabratum*, *T. grandinode*, *T. jordani*, *T. pogonion*, *T. rufescens*, *T. signatum*, and *T. solidum*, in which the body is hairless or nearly so. Only *T. solidum* has a few hairs on the mesosoma (Bolton 1980). My study reveals that the species complexes

identified by Bolton (1980) do not stand up to phylogenetic analysis, illustrating the flux of many morphological characters like hair pattern. The erect pilosity was lost and gained many times and the flattened pilosity was the result of multiple evolutionary events. For example in the first complex, *T. dichroum* and *T. peringueyi* are placed far from one another and likewise in the second complex, *T. clunum* and *T. setuliferum* are widely separated. The third complex is monophyletic, except for *T. solidum*, which is embedded in the first two complexes.

Discussion

Contemporary species richness, abundance and distributions often reflect historical processes that influenced the evolutionary trajectories of regional biotas. Members of the *Tetramorium solidum*-group appear to be arid-adapted and their distribution closely reflects current rainfall patterns in south western Africa. It is therefore conceivable that historical events should have selected for arid-adapted traits in this group. Our genetic analyses suggest that the diversification of ants within *Tetramorium solidum*-group occurred during an era when the species current distributional ranges experienced aridification.

Paleontological history

It is suggested that the south-western parts of Africa became more arid during Miocene (ca. 23 MYA) in response to upwelling of cold subsurface water subsurface which was associated with Benguela Currents (Tankard and Rogers, 1978). It is further suggested that the subtropical and anticyclones over south of Atlantic and Indian Oceans have contributed to the aridity in western parts of South Africa (Schulze, 1965). Major

climatic changes are known from the Miocene epoch, which included the climatic optimum during the Mid-Miocene (about 16-14 MYA) (Hewitt, 2011). These oscillating climatic conditions had severe environmental impacts, which influenced ecosystems and the distribution of many species within them (Linder 2003, 2005). During this period grasslands became a major ecosystem component as they replaced forests with the progression of aridity (Bobe, 2006). In Africa the replacement of forests by open grasslands due to increased and ongoing aridification during the early Miocene (Kürschner *et al.*, 2008) has led to the rapid diversification of many arid-adapted fauna (Jansson and Dynesius, 2002). As for many other taxa, the diversification of grasslands likely drove the diversification and endemism of the *Tetramorium solidum*-group in the western parts of southern Africa. It is suggested that South Africa had wetter climate than today (van Zinderen Bakker and Mercer, 1986). The development of cold Benguela Currents (Tankard and Rogers 1978) and the tectonic uplift which resulted to the changes in topography (Sepulchre *et al.*, 2006) contributed to greater rainfall seasonality in this region. The aridity in southern Africa caused by unstable conditions during Miocene resulted in the radiation of many taxa, including southern African sand lizards (*Pedioplanis* spp., Makokha *et al.*, 2007). The divergence between the two major groups contained within *Pedioplanis*, a South African and a Namibian/southern Angolan lineage, is suggested to have occurred during mid-Miocene in response to the aridity in the region (Makokha *et al.*, 2007). On the other hand, the divergence in some species was not triggered by vegetation change but by vicariance events, for example the formation of Cape Fold Mountains are believed to be the physical barrier between the western and the southern groups of angulate tortoise, *Chersina angulata*, Daniels *et al.*, 2007. These groups are suggested to have separated in the late Miocene, between 10 and 8 MYA (Daniels *et al.*, 2007). It is therefore evident that not all regional taxa respond similarly to historical processes.

According to our phylogeny, the *Tetramorium solidum*-group possibly originated from the eastern parts of southern Africa before diversifying in the south western dry regions. *Tetramorium setuliferum*, which is the basal species, is the only species in *solidum*-group that is able to exist in relatively moist habitats. Ant species differ in their tolerance to desiccation (Hood & Tschinkel, 1990). A possible explanation for *T. setuliferum* being able to prosper in the wet conditions could be due to the species' ability to nest deep underground (H.G. Robertson, personal observations), and by doing so is able to keep the seeds dry for long periods of time, thus halting germination.

Species diversity in dry regions

Seeds are a diverse and abundant resource in arid areas and therefore a preferred energy source of many arid-adapted ants (Buckley, 1982). Changes in vegetation from forests to grasslands during the Miocene may therefore have driven diversification in seed-harvester ants like the *Tetramorium solidum* - group (Bolton, 1980). In southern Africa, the diversification of many other taxa appears to have been influenced similarly during Miocene as a result of dramatic changes in vegetation cover in this region; these include the diversification of dwarf chameleons (*Bradypodion* spp., Tolley *et al.*, 2006) and the Angulate tortoise (*Chersina angulata*, Daniels *et al.*, 2007).

The highest diversity of the species in the *T. solidum*-group is concentrated in the Nama-Karoo region, with 13 species recorded from this region (Fig. 36). This semi-arid to arid region is about 400, 000 km² and has shallow soils that are rich in plant nutrients (Ellis and Lambrechts, 1986). It experiences an annual rainfall of about 100 mm to nearly 500 mm per annum (Venter *et al.*, 1986). Eleven species were recorded from Succulent Karoo region, which is considered to be a major biodiversity hotspot (Myers *et al.*, 2000).

Identification of the areas with high endemism and species rarity is important for conservation priorities. Anthropogenic activities such as pollution, habitat fragmentation,

introduction of invasive species, etc., have negatively influenced ecosystems and caused a great decline in biodiversity (Burlakova *et al.*, 2011). The present climate conditions in the region which are more arid to the west are still favourable for the ants in the *T. solidum*-group but future climate changes might negatively impact the diversity of this group. Work on similar taxa will help to understand other factors that have shaped the distribution of species diversity in the region and can help to identify more areas that need conservation priority. Although a number of studies have focused on the influence of relatively recent Plio-Pleistocene divergences in shaping the South African biota, the current study adds to a list of studies highlighting the importance of potentially older, Miocene processes in driving the diversification of arid adapted taxa.

One matter that was not fully resolved in this study was the species *T. rufescens* and *T. signatum*. The confusion between these species arises from discrepancies between the mitochondrial gene tree, and the taxonomic classification based on morphology. I therefore concluded that the processes that shape morphology are dissimilar to those that influence evolution of the gene tree and I suspect the tree is influenced by introgression as a result of hybridization. I ruled out the possibility of nuclear pseudogenes as there were no symptoms of nuclear mitochondrial pseudogene contamination, which include PCR ghost bands or sequence ambiguities (Bensasson *et al.*, 2001). The discrepancies between morphology and phylogeny data of *T. rufescens* and *T. signatum* suggest that taxonomic work is still needed on these two species. Specifically, future work should include biparentally inherited nuclear genetic markers to resolve the causes of these discrepancies.

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Chapter 3

Conclusion

A holistic approach that integrates classical taxonomy, the evolutionary history of species and a biogeographical analysis of current distribution patterns is useful in understanding the patterns of biodiversity we see today. Insects are by far the most diverse taxon on the planet with an estimated 1 million described species (Chapman, 2009). Although estimates vary, the true number of insect species is likely about five times higher (Chapman, 2009), and under current rates of habitat destruction and climate change, indicate that millions of species will become extinct long before they have been described.

To date, most studies on African ant systematics have focused on taxonomy only (Robertson, 2000 and references therein; Bolton, 2000, 2007; Bolton & Brown, 2002; Bolton & Fisher, 2008, 2011, 2012; Fisher, 2006; Hita Garcia *et al.*, 2010; LaPolla *et al.*, 2011; Robertson, 2002; Schöning *et al.*, 2008; Seifert, 2003; Snelling, 2007), very few on phylogeny (Kronauer *et al.*, 2007 ; LaPolla, 2004), and none on the factors and processes that are responsible for shaping the current distribution patterns. This latter approach formed the basis of this thesis but before assessing these processes, I evaluated the taxonomy of *T. solidum*-group since its last revision more than 30 years ago. The fresh material from various ant surveys and field trips my colleagues and I have conducted, has given an opportunity to revise the taxonomy of the group and to identify five new species (Chapter 1). The phylogenetic relationships of species in the *T. solidum*-group were explored for the first time (Chapter 2). The molecular analysis provided support for recognition of the morphologically distinguishable species in this group, except in *T. rufescens* and *T. signatum*, where uncertainties remain regarding the delimitations of these two species, due possibly to hybridization influencing the phylogenetic tree.

Overall this study has yielded a number of useful insights on the *T. solidum* – group. I have found that its origin dates back to the early Miocene (24 MYA) and that the group likely originated in the grasslands in the south-eastern African region. The dated phylogeny has confirmed that the diversification of this group in the western dry parts of southern Africa coincided with the aridification process which resulted to open grassland in southern Africa. Bioclimatic modelling identified seasonal rainfall as the most important factor that influences the distribution of species in this group in southern Africa, as these ants are mainly restricted to the west parts of southern Africa, which experience winter rainfall.

An understanding of the potential causes that led to the diversity and endemism of a group in a particular area can help to come up with conservation and management strategies. Modelling methods have been used to provide useful predictions of impacts that can be caused by future climates and that could give insights for conservation and management planning (Midgley *et al.*, 2003). For example, Midgley (2003) used bioclimatic modelling to assess and identify the impacts of potential climate change on the future distribution of Proteaceae in the Cape Floristic Region. This region is known for its high endemism, which is suggested to have resulted partly from past climatic changes (Cowling *et al.*, 1989, Midgley and Roberts, 2001).

The high species diversity and endemism of ants in arid regions of southern Africa make it a useful group for understanding the evolutionary processes that influenced the distribution of fauna in these regions. Although a number of studies have focused on the influence of relatively recent, Plio-Pleistocene divergences in shaping the South African biota, the current study adds to a list of studies highlighting the importance of potentially older, Miocene processes in driving the diversification of arid adapted taxa. An understanding of past processes that shaped the distribution of biota can help to predict the species that may be at risk of future rapid shift in global climate that has been forecast

for the planet. The phylogenetic relationships and dated phylogenies can be used to examine the evolution of novel traits, for example, the overhanging tergo-sternal suture in *T. setuliferum* (Fig. 4B) might be the ancestral character in the *solidum*-group as this is the distinguishing character for the basal species. Ants occurring in similar conditions as *T. solidum*-group can offer great potential in identifying priority areas for conservation and for further testing historical biogeographic processes that shaped the distribution of species in arid regions of southern Africa.

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Supplementary material

Table 1: Values for the area under the curve of the four models developed for the species of *Tetramorium solidum*-group.

ANN*	GAM*	BRT*	RF*
0.631	0.7475	0.761	0.7805
0.708	0.6395	0.649	0.698
0.682	0.6975	0.8095	0.693
0.6465	0.616	0.6245	0.6805
0.7795	0.782	0.8285	0.833
0.6825	0.8075	0.799	0.784
0.6885	0.7205	0.7825	0.6915
0.8045	0.818	0.869	0.857
0.7785	0.802	0.852	0.7715
0.8325	0.888	0.9075	0.8215
0.621	0.8435	0.6	0.591

* AUC range (Thuiller et al. 2006) : <0.8 = poor; $0.8-0.9$ = fair; $0.9-0.95$ = good; $0.9-1$ = very good.