The ant genus *Tetramorium* Mayr in the Afrotropical region (Hymenoptera, Formicidae, Myrmicinae): synonymisation of *Decamorium* Forel under *Tetramorium*, and taxonomic revision of the *T. decem* species group

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Abstract

In this study we synonymise the genus *Decamorium* Forel under *Tetramorium* Mayr, revise the new *T. decem* species group by providing a diagnosis of the group, an illustrated identification key to species level, and worker-based species descriptions for all five species, which include diagnoses, discussions, images, and distribution maps. The following species are revised in this study: *T. decem* Forel, *comb. r.*, *T. raptor* sp. n., *T. uelense* Santschi, *comb. r.*, *T. ultor* Forel, *comb. r.*, *stat. r. & stat. n.*, and *T. venator* sp. n. In addition, we also designate lectotypes for *T. decem*, *T. uelense*, and *T. ultor*.

Keywords

Afrotropical region, *Decamorium*, taxonomy, Tetramorii, *Tetramorium*, *T. decem* species
Introduction

The genus *Tetramorium* Mayr is globally distributed and with 520 valid species it represents one of the most species-rich ant genera (Bolton 2014). The vast majority of these are found in the tropics of the Old World. In the Afrotropical and Malagasy regions, *Tetramorium* is hyperdiverse by the definitions of Wilson (2003) and Moreau (2008). In Madagascar and the neighbouring islands of the Indian Ocean, recent studies have revealed a highly endemic and astonishingly diverse *Tetramorium* fauna consisting of around 120 species (Bolton 1979; Hita Garcia and Fisher 2011, 2012a, 2012b, unpublished). The known Afrotropical *Tetramorium* fauna was thoroughly revised by Bolton (1976, 1980, 1985), parts of which were recently updated by Hita Garcia et al. (2010) and Hita Garcia and Fisher (2011, 2013), producing a current total of 224 species. In addition, there are at least 100 more undescribed Afrotropical species located in several museum collections awaiting formal description (FHG, unpublished data). Traditionally, what is now considered as *Tetramorium* was divided into the genera *Atopula* Emery, *Macromischoides* Wheeler, *Tetramorium*, and *Xiphomyrmex* Forel until Bolton’s genus-level revision (1976). The name *Tetramorium* was used for a much smaller subset of species with twelve antennal segments. Bolton provided ample evidence for the artificiality of these genera and synonymised them under *Tetramorium*. Particularly noteworthy is the fact that the previous separation of *Xiphomyrmex* (11-segmented antennae) from *Tetramorium* (12-segmented antennae) was based solely on the difference in the antennomere count; Bolton showed this character to be variable in other tetramoriine genera.

Forel (1913a) described *Decamorium* Forel as a subgenus of *Tetramorium* on the basis of the ten-segmented antennae and the very pronounced and deep antennal scrobes. A few years later Arnold (1917) followed Forel and also treated *Decamorium* as a subgenus of *Tetramorium*. He based his decision on the ten-segmented antennae, the well-defined and deep antennal scrobes, the obsolete lateral ridges of the clypeus, and the strongly swollen tibiae and femora in the worker caste. Nevertheless, apart from these two works (Forel 1913a; Arnold 1917), most other authors (and later even Forel himself) have treated *Decamorium* as a genus distinct from *Tetramorium* (Emery 1914, 1924; Forel 1917; Wheeler 1922; Bernard 1953; Bolton 1973, 1976, 1995). In his classification of the Myrmicinae, Emery (1914) was the first to treat *Decamorium* as a “genus” rather than a subgenus, although he did not provide any explanation of his decision. Later, in his “Genera Insectorum”, Emery (1924) continued to list *Decamorium* as a genus. In that work he re-described the genus and separated it from the other then known tetramoriine genera, again on the basis of the ten-segmented antennae of the workers and queens. All subsequent authors listed *Decamorium* as a genus without taxonomic treatment until Bolton’s (1976) revision of the tribe Tetramoriini. As mentioned above, he diagnosed most of the currently valid genera of the tribe and also reviewed *Decamorium*. Bolton (1976) clearly stated that the separation of *Decamorium* from *Tetramorium* on the grounds of the reduced antennal count, reduced clypeal shield, and differences in mandibular dentition was relatively dubious. He doubted
that these characters would persist to diagnose *Decamorium* in the future. However, since then nothing more on the generic limits or alpha taxonomy of *Decamorium* has been published, and all authors continued to list *Decamorium* as a distinct genus (e.g. Hölldobler and Wilson 1990; Bolton 1995, 2003, 2014; Robertson 2000; Hita García et al. 2013).

In this study we propose *Decamorium* as a junior synonym of *Tetramorium* and lower it to the arbitrary rank of a species group. Our decision is based on a critical analysis of the diagnostic characters previously defining *Decamorium*. In addition, we revise the alpha taxonomy of the *T. decem* species group. A diagnosis of the *T. decem* species group is given together with an illustrated identification key to species on the basis of the worker caste. In addition, all members of the species group are described/re-described including diagnoses, discussions, high-quality montage images and distribution maps.

**Abbreviations of depositories**

The collection abbreviations follow Evenhuis (2014). The material upon which this study is based is located and/or was examined at the following institutions:

**BMNH** The Natural History Museum (British Museum, Natural History), London, U.K.

**CASC** California Academy of Sciences, San Francisco, U.S.A.

**LACM** Natural History Museum of Los Angeles County, Los Angeles, U.S.A.

**MCZ** Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A.

**MHNG** Muséum d’Histoire Naturelle de la Ville de Genève, Geneva, Switzerland

**MNHN** Muséum National d’Histoire Naturelle, Paris, France

**MSNG** Museo Civico di Storia Naturale “Giacomo Doria”, Genova, Italy

**NHMB** Naturhistorisches Museum, Basel, Switzerland

**NMK** National Museums of Kenya, Nairobi, Kenya

**ZFMK** Zoological Research Museum Alexander Koenig, Bonn, Germany

**Material and methods**

Most of the material examined in this study is located in the Hymenoptera collections of BMNH, CASC, MCZ, MHNG, and LACM. It includes much historical material collected prior to Bolton’s review of *Decamorium* (1976), but the majority of available material has been collected over the past 20 years in a wide range of Afrotropical countries. All new type material and all imaged specimens can be uniquely identified with specimen-level codes affixed to each pin (e.g. CASENT0103295). In the descriptions presented we list all available specimen-level codes for the type series. It should be noted, however, that the number of stated paratype or syntype workers does not nec-
essarily match the number of listed specimen-level codes because pins can sometimes hold more than one specimen, especially for older species. Digital colour montage images were created using a JVC KY-F75 digital camera and Syncroscopy Auto-Montage software (version 5.0), or a Leica DFC 425 camera in combination with the Leica Application Suite software (version 3.8). All images presented are available online and can be seen on AntWeb (http://www.antweb.org). The distribution maps we provide (Figs 61–66) were generated with the R software (R Core Team 2014). We measured 83 workers with a Leica MZ 12.5 equipped with an orthogonal pair of micrometers at a magnification of 100×. Measurements and indices are presented as minimum and maximum values with arithmetic means in parentheses. In addition, all measurements are expressed in mm to two decimal places. The following measurements and indices used in this study follow Hita Garcia and Fisher (2011, 2012a, 2012b, 2013):

| Code | Description |
|------|-------------|
| **HL** | Head length: maximum distance from the midpoint of the anterior clypeal margin to the midpoint of the posterior margin of head, measured in full-face view. Impressions on the anterior clypeal margin and the posterior head margin reduce head length. |
| **HW** | Head width: width of the head directly behind the eyes measured in full-face view. |
| **SL** | Scape length: maximum scape length excluding basal condyle and neck. |
| **EL** | Eye length: maximum diameter of compound eye measured in oblique lateral view. |
| **PW** | Pronotal width: maximum width of the pronotum measured in dorsal view. |
| **WL** | Weber’s length: diagonal length of the mesosoma in lateral view from the posterovertrventral margin of propodeal lobe to the anterior-most point of pronotal slope, excluding the neck. |
| **PSL** | Propodeal spine length: the tip of the measured spine, its base, and the centre of the propodeal concavity between the spines must all be in focus. Using a dual-axis micrometer the spine length is measured from the tip of the spine to a virtual point at its base where the spine axis meets orthogonally with a line leading to the median point of the concavity. |
| **PTH** | Petiolar node height: maximum height of the petiolar node measured in lateral view from the highest (median) point of the node to the ventral outline. The measuring line is placed at an orthogonal angle to the ventral outline of the node. |
| **PTL** | Petiolar node length: maximum length of the dorsal face of the petiolar node from the anterodorsal to the posterodorsal angle, measured in dorsal view excluding the peduncle. |
| **PTW** | Petiolar node width: maximum width of the dorsal face of the petiolar node measured in dorsal view. |
| **PPH** | Postpetiole height: maximum height of the postpetiole measured in lateral view from the highest (median) point of the node to the ventral outline. The measuring line is placed at an orthogonal angle to the ventral outline of the node. |
| **PPL** | Postpetiole length: maximum length of the postpetiole measured in dorsal view. |
| **PPW** | Postpetiole width: maximum width of the postpetiole measured in dorsal view. |
| **OI** | Ocular index: \( EL / HW \times 100 \) |
Pubescence and pilosity are often of high diagnostic value within the genus *Tetramorium* (e.g. Bolton 1976, 1980, 1985; Hita Garcia et al. 2010; Hita Garcia and Fisher 2012a, 2012b). The varying degree of inclination of pilosity is particularly important for the diagnosis of groups or species. In this context we use the terms “erect”, “suberect”, “subdecumbent”, “decumbent”, and “appressed” following Wilson (1955). The terminology used for the description of surface sculpturing follows Harris (1979) and Bolton (1980).

**Results**

*Tetramorium Mayr*

*Tetramorium* Mayr, 1855: 423. Type species: *Formica caespitum*, by subsequent designation of Girard 1879: 1016.

*Tetrogmus* Roger, 1857: 10. Type species: *Tetrogmus caldarius*, by monotypy. [Tetrogmus junior synonym of Tetramorium: Roger 1862: 297; Bolton 1976: 359; confirmed here.]

*Xiphomyrmex* Forel, 1887: 385 [as subgenus of *Tetramorium*]. Type species: *Tetramorium (Xiphomyrmex) kelleri*, by subsequent designation of Wheeler, W.M. 1911: 175. [Xiphomyrmex junior synonym of Tetramorium: Bingham 1903: 175; Bolton 1976: 359; Bolton 1980: 195; Bolton 1994: 106; Bolton 2014; confirmed here.]

*Triglyphothrix* Forel, 1890: cvi. Type species: *Triglyphothrix walshi*, by monotypy. [Triglyphothrix junior synonym of Tetramorium: Bolton 1985: 247; confirmed here.]

*Atopula* Emery, 1912: 104. Type species: *Atopomyrmex nodifer*, by original designation. [Atopula junior synonym of Tetramorium: Bolton 1976: 359; Bolton 1980: 195; Bolton 1994: 106; confirmed here.]

*Decamorium* Forel, 1913a: 121 [as subgenus of *Tetramorium*]. Type species: *Tetramorium (Decamorium) decem*, by monotypy. [Decamorium raised to genus: Emery 1914: 42; Wheeler W.M. 1922: 664, 906.] Syn. n.
Macromischoides Wheeler, W.M. 1920: 53. Type species: Macromischa aculeata, by original designation. [Macromischoides Santschi, 1924: 206, incorrect subsequent spelling.] [Macromischoides junior synonym of Tetramorium: Bolton 1976: 359; Bolton 1980: 196, confirmed here.]

Lobomyrmex Kratochvíl, 1941: 84 [as subgenus of Tetramorium]. Type species: Tetramorium (Lobomyrmex) ferox silhavyi (junior synonym of Tetramorium ferox), by monotypy. [Lobomyrmex junior synonym of Tetramorium: Bolton 1976: 359; Bolton 1980: 196; confirmed here.]

Sulcomyrmex Kratochvíl, 1941: 84 [as subgenus of Tetramorium]. Unavailable name. Proposed without designation of type species and therefore unavailable. Species included by Kratochvíl (1941) are all referable to Tetramorium: Bolton 1976: 359.

Apomyrmex Calilung, 2000: 66. Type species: Apomyrmex manobo, by original designation. [Apomyrmex junior synonym of Tetramorium: Bolton 2003: 227, 269; confirmed here.]

Decamorium Forel—a junior synonym of Tetramorium Mayr

As outlined in the introduction, in the past various authors expressed very different opinions about the status of Decamorium. After examination of all available material and dissemination of all previous literature, we have come to the conclusion that Decamorium is best treated as a junior synonym of Tetramorium. Our reasons are summarised below:

1. Antennomere count

As outlined above, the antennomere count was the main diagnostic character qualifying Decamorium as a genus (Emery 1924; Bolton 1976). Antennomere count has traditionally been considered a very good diagnostic character for separating closely related genera. Yet over the past few decades it has become apparent that the antennal count can vary within a genus, sometimes significantly. Some examples include the genera Carebara Westwood with eight to eleven segments (Fernandez 2004), Temnothorax Mayr which typically has twelve segments, rarely eleven (Bolton 2003; Radchenko 2004), Cardiocondyla Emery with eleven and twelve segments (Seifert 2003), or Pheidole with nine to twelve (Bolton 2003). Also, in some African species of Carebara the major workers always have one antennal segment more than the minor workers. Furthermore, subgroups of the same genus often have been placed in different genera in the past due to varying antennomere counts. One good example is Myrmelachista Roger outlined in Longino (2006). It was originally described by Roger (1863) as two genera: Decamera Roger (a junior homonym of a beetle genus and replaced by the name Hincksidris Donisthorpe) having ten-segmented antennae, and Myrmelachista having eleven-segmented antennae. This division turned out to be incorrect, and Brown (1973) and Snelling and Hunt (1976) formally synonymised them more than a century later.

In what is now considered to be Tetramorium one can find eleven-segmented and twelve-segmented antennae throughout all biogeographical regions, even though most of
these forms were previously separated into *Xiphomyrmex* (11-segmented antennae) and *Tetramorium* (12-segmented antennae). Bolton (1976) provided evidence based on sting appendage types showing that this separation was an artificial one, and consequently synonymised *Xiphomyrmex* under *Tetramorium*. Based on this intrageneric variation in antennal segmentation, we accept that a small and highly specialised African species group within *Tetramorium* could have an even more reduced count of ten antennal segments.

This is further supported by the presence of a very small species from India that possesses 10-segmented antennae: *T. decamerum* (Forel). This species was treated as *Triglyphothrix* by Bolton (1976), thus not taken into consideration as a *Tetramorium*. The later synonymisation of *Triglyphothrix* under *Tetramorium* Bolton (1985) provided a “genuine” *Tetramorium* with 10-segmented antennae. Consequently, this character is not unique to *Decamorium*, but already present in *Tetramorium*.

2. Clypeal shield

The reduced clypeal shield seen in *Decamorium* (Fig. 1A) is not unique to its species. Within the tropical *Tetramorium* fauna most species have a very well-developed and clearly distinctive clypeal shield (Figs 1F, 1G, 1F, 1I), but there are a number of species, such as *T. nodiferum* (Emery) (Fig. 1B), *T. simulator* Arnold (Fig. 1C), *T. aculeatum* (Mayr) (Fig. 1D), or *T. anodontion* Bolton (Fig. 1E), in which this shield is much less pronounced or almost reduced. The clypeal shield generally varies from species to species in its height and the sharpness of its dorsal edge. When the development of this character

![Figure 1](https://example.com/figure1.png)
across several hundred Tetramorium species is considered, Decamorium emerges as one extreme of a cline that ranges from almost no clypeal shield to a very sharp and high shield, such as in the members of the T. sericeiventre Emery species group (Fig. 11).

3. Mandibular dentition

The mandibular dentition of Decamorium and Tetramorium seemed slightly different back in 1976, but as anticipated by Bolton, it has become clear that there is much more variation within Tetramorium. Currently there is no significant difference in mandibular dentition between Decamorium and Tetramorium. In Decamorium the mandibular count consists of three apical teeth followed by a series of four or five denticles, while in Tetramorium there are two to three apical teeth followed by a series of three to eight denticles (Bolton 2003). Consequently, this character has no diagnostic importance in this group since the values of Decamorium fall well within the range of the larger Tetramorium.

4. Tetramorium simulator Arnold

If one considers the whole tribe Tetramoriini, then it becomes apparent that the specialised habitus of Decamorium is not unique. Several authors have stated that Decamorium are specialised termite hunters, and that their specialised morphology could be an adaptation to such a dangerous lifestyle (Arnold 1917; Bolton 1976; Longhurst et al. 1979). Interestingly, both Arnold (1917) in the original description and later Bolton (1980) noted the similarities in general body shape and diet between members of Decamorium and the species Tetramorium simulator from South Africa. We agree that the similarities in morphology are indeed obvious, especially in profile view (Fig. 2). However, at present it is not clear whether the shared morphology is based on a close phylogenetic relationship between Decamorium and T. simulator or a result of convergent evolution due to a similar lifestyle hunting termites. We believe the latter more likely since the twelve-segmented antennae, the much broader head, and sculptured clypeus of T. simulator suggest a closer relationship to another group with twelve-segmented antennae than to Decamorium. Therefore, we hypothesise that both have evolved from different Tetramorium lineages and acquired the specialised habitus independently from each other. Another remarkable aspect is the lack of a strong and sharp clypeal shield in T. simulator, which seems to have been reduced in a manner almost similar, though less pronounced, to Decamorium.

5. Male morphology

We do not intend to go into details of male morphology here, but so far there is not a single character that would separate the males of Decamorium from the males of
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6. Molecular evidence

In addition to our morphological analysis above, there is also molecular evidence supporting the synonymisation of *Decamorium* under *Tetramorium*. Based on a multi-gene dataset, Ward et al. (in press) show that *Decamorium* is nested within a larger *Tetramorium* clade. However, how *Decamorium* is integrated into *Tetramorium* and to which groups/lineages it is most closely related remains unknown. Further phylogenetic/phylogenomic studies that deal with a greater number of species groups and a good proportion of species are needed to clarify relationships within the hyperdiverse *Tetramorium* and its satellite genera.

Revision of the *Tetramorium decem* species group

Synopsis of the *Tetramorium decem* species group

*Tetramorium decem* Forel, 1913a, **comb. r.**
*Tetramorium raptor* Hita Garcia, **sp. n.**
*Tetramorium uelense* Santschi, 1923, **comb. r.**
*Tetramorium ultor* Forel, 1913b, **comb. r., stat. r. & stat. n.**
*Tetramorium venator* Hita Garcia, **sp. n.**
Diagnosis of *Tetramorium decem* species group

Ten-segmented antennae; antennal scape relatively short (SI 67–76); anterior clypeal margin with distinct but often shallow impression; frontal carinae strongly developed and noticeably raised, forming dorsal margin of very well-developed antennal scrobes, curving down ventrally and anteriorly halfway between posterior eye margin and posterior head margin and forming posterior and usually ventral scrobe margins; antennal scrobes very well developed, deep and usually with clearly defined margins all around, median scrobal carina absent; eyes relatively large (OI 32–40); mesosoma relatively flat, low, and elongated, margination between lateral and dorsal mesosoma moderately developed (LMI 33–38); propodeum armed with short triangular to elongate-triangular teeth (PSLI 9–19); propodeal lobes short, rounded to triangular; tibiae and femorae strongly swollen; petiolar node nodiform with moderately rounded antero- and postero-dorsal margins, petiolar dorsum weakly to strongly convex, node in profile between 1.0 to 1.3 times higher than long (LPeI 77–100), node in dorsal view around 1.1 to 1.3 times longer than wide (DPeI 76–92); postpetiole in profile globular, around 1.1 to 1.4 times higher than long (LPpI 71–88); mandibles and clypeus unsculptured, smooth, and shiny; sculpture on cephalic dorsum between frontal carinae and dorsal mesosoma variable, ranging from unsculptured, smooth, and shiny to longitudinally rugose/rugulose, often punctate or puncticulate; petiole usually weakly sculptured, postpetiole unsculptured to weakly sculptured; gaster unsculptured, smooth, and shiny; pilosity greatly reduced, head with several pairs of standing hairs, mesosoma with one pair, waist segments sometimes with one long pair each, and sometimes first gastral tergite with one pair; sting appendage triangular.

Taxonomic and biogeographic notes on the group

The *T. decem* species group is endemic to the Afrotropical region where it is widely distributed (Fig. 3). *Tetramorium raptor* and *T. uelense* are found in West and Central Africa and *T. venator* occurs through most of the equatorial rainforest belt from Liberia in West Africa to Western Kenya. By contrast, *T. decem* and *T. ultor* are species from eastern and southeastern Africa. Surprisingly, the group seems to be absent from South Africa based on the material available to us, but *T. decem* or *T. ultor* are likely to be found there or in neighbouring Botswana or Namibia. Furthermore, we expect the distribution ranges of *T. decem*, *T. uelense*, and perhaps *T. ultor* to expand with further ant inventory or collecting projects in Afrotropical savannahs, dry forests, and other arid habitats. These were sparsely sampled in sub-Saharan Africa in the past since most modern ant inventories have focused on rainforests (e.g. Belshaw and Bolton 1994; Watt et al. 2002; Fisher 2004; Yanoviak et al. 2007; Hita Garcia et al. 2009), whereas only a few studies have examined ant faunas from drier localities (e.g. Robertson 1999, 2002; Braet and Taylor 2008).

The separation of the *T. decem* species group from all other *Tetramorium* species groups is straightforward and easy. So far, only the members of the *T. decem* group have
ten-segmented antennae, whereas all other Afrotropical Tetramorium have either eleven or twelve. Consequently, the T. decem species group is unlikely to be confused with another Afrotropical group. The morphology of the five species of the group is very uniform, likely due to their strongly specialised lifestyle, which makes the taxonomy of the group challenging at first sight. However, good diagnostic characters separate them fairly well from each other, especially eye size, propodeal spine/teeth length, petiolar node shape, mesosomal sculpture, and body colouration. These characters are remarkably consistent within each species throughout its whole distribution, as are the species-specific habitat preferences.

**Identification key for T. decem species group (workers)**

1  
Dorsum of promesonotum with conspicuous longitudinally rugose/rugulose sculpture (Fig. 4A, B).......................................................................................................................... 2

-  
Dorsum of promesonotum unsculptured, smooth, and usually very shiny (Fig. 4C, D).......................................................................................................................... 3

**Figure 3.** Map of sub-Saharan Africa showing the known distribution ranges of the five members of the T. decem species group: T. decem (filled circle), T. raptor (empty circle), T. uelense (filled square), T. ultor (empty square), and T. venator (star).
Slightly smaller species (WL 0.88–0.93); propodeum armed with shorter, triangular, and acute teeth (PSLI 10–11); dorsum of promesonotum longitudinally rugulose with very little ground sculpture, lateral pronotum mostly unsculptured and shiny, only dorsally longitudinally rugulose; generally of uniform dark brown colour; rainforest species (Fig. 5A, B) [Cameroon, Nigeria] ...... *T. raptor*

– Slightly larger species (WL 0.98–1.06); propodeum armed with longer, triangular to elongate-triangular, and acute teeth (PSLI 16–18); dorsum of promesonotum and lateral pronotum strongly longitudinally rugose with distinct punctate ground sculpture; strongly bicoloured species with dark brown or black gaster contrasting with light brown to reddish brown on remainder of body; savannah species (Fig. 5C, D) [Cameroon, Ghana, Guinea, Nigeria, and Republic of the Congo] .................. *T. uelense*

3 Generally larger species (WL 1.02–1.16); propodeal teeth relatively longer (PSLI 17–19); petiolar node in profile relatively higher, in profile 1.2 to 1.3 times higher than long (LPeI 77–82); strongly bicoloured species with dark brown or black gaster contrasting with light brown to reddish brown remainder of body (Fig. 6A) [Kenya, Tanzania, and Zimbabwe] .............. *T. decem*

– Generally smaller species (WL 0.85–0.98); propodeal teeth relatively shorter (PSLI 9–13); petiolar node relatively lower; in profile around 1.0 to 1.2 times higher than long (LPeI 86–100); usually of uniform brown colour, if bicoloured, then only slightly so and never as well developed as above (Fig. 6B) .............. 4

4 Smaller eyes (OI 33–36); body colouration uniformly light brown to chestnut brown (Fig. 7A, B) [Kenya, Mozambique, Tanzania, Zambia, and Zimbabwe] ................................................................. *T. ultor*

– Larger eyes (OI 37–40); body colouration uniformly dark brown to black, always darker than above (Fig. 7C, D) [Central African Republic, Cameroon, Democratic Republic of Congo, Gabon, Ghana, Kenya, Liberia, Tanzania, Uganda] ................................................................. *T. venator*

*Tetramorium decem* Forel, 1913a, comb. r.
Figs 1A, 2A, 2B, 3, 6A, 8

*Tetramorium* (*Decamorium*) *decem* Forel, 1913a: 121. [Combination in *Decamorium* by Wheeler 1922: 906; senior synonym of *Decamorium ultor* by Bolton 1976: 298.]

Type material. Lectotype [designated here], pinned worker, ZIMBABWE, Redbank, 19.98333 S, 28.37759 E, 7.IV.1912 (G. Arnold) (MHNG: CASENT0909196) [examined]. Paralectotypes [designated here], seven pinned workers with same data as lectotype (BMNH: CASENT0901035; MHNG: CASENT0248316; MSNG: CASENT0904789) [examined].

[Note: the GPS data of the type locality was not provided by the locality label or the original description. The data presented above is based on our own geo-referencing
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**Figure 4.** Mesosoma in dorsal view. **A** *T. raptor* (CASENT0195628) **B** *T. uelense* (CASENT0914084) **C** *T. ultor* (CASENT0235465) **D** *T. venator* (CASENT0401714).

**Figure 5.** Body in profile and mesosoma in dorsal view. **A, B** *T. raptor* (CASENT0280848) **C, D** *T. uelense* (CASENT0914084).

**Figure 6.** Body in profile. **A** *T. decem* (CASENT0914088) **B** *T. venator* (CASENT0195574).
of the town of Redbank located in the Matabeleland North Province. Consequently, the location should be considered as an approximation and not the exact position of the type locality.

**Non-type material.** KENYA: Coastal Province, Malindi District, Arabuko Sokoke Forest, 3.28 S, 39.97 E, 75 m, Brachystegia forest, 26.V.2001 (R.R. Snelling & D.J. Martins); Coastal Province, Malindi District, Arabuko Sokoke Forest, 3.32111 S, 39.92944 E, ca. 50 m, VI.2009 (F. Hita Garcia & G. Fischer); TANZANIA: Mkomazi Game Reserve, Ibaya, 3.96667 S, 37.8 E, in burnt grassland, 19.–20.XI.1994 (A. Russel-Smith).

**Diagnosis.** *Tetramorium decem* can be recognised by the following combination of characters: relatively larger species (HW 0.59–0.62; WL 1.02–1.16); propodeal teeth relatively longer (PSLI 17–19); petiolar node in profile around 1.2 to 1.3 times higher than long (LPeI 77–82); dorsum of promesonotum unsculptured, smooth, and very shiny; strongly bicoloured species with dark brown or black gaster contrasting with light brown to reddish brown remainder of body.

**Worker measurements (N=15).**

| Measurement | Lower Limit | Upper Limit | Mean |
|-------------|-------------|-------------|------|
| HL          | 0.71–0.74   | 0.72        | 0.72 |
| HW          | 0.59–0.62   | 0.60        | 0.60 |
| SL          | 0.42–0.45   | 0.43        | 0.43 |
| EL          | 0.19–0.21   | 0.20        | 0.20 |
| PH          | 0.33–0.37   | 0.35        | 0.35 |
| PW          | 0.47–0.50   | 0.50        | 0.49 |
| WL          | 1.02–1.16   | 1.06        | 1.06 |
| PSL         | 0.12–0.14   | 0.13        | 0.13 |
| PTL         | 0.25–0.27   | 0.26        | 0.26 |
| PTH         | 0.31–0.34   | 0.33        | 0.33 |
| PTW         | 0.22–0.24   | 0.23        | 0.23 |
| PPL         | 0.24–0.27   | 0.25        | 0.25 |
| PPH         | 0.32–0.36   | 0.34        | 0.34 |
| PPW         | 0.32–0.36   | 0.34        | 0.34 |
| CI          | 83–85       | 84          | 84   |
| SI          | 70–76       | 72          | 72   |
| OI          | 32–34       | 33          | 33   |
| DMI         | 41–47       | 45          | 45   |
| LMI         | 32–34       | 33          | 33   |
| PSLI        | 17–19       | 18          | 18   |
| PeNI        | 46–51       | 48          | 48   |
| LPeI        | 77–82       | 80          | 80   |
| DPeI        | 85–92       | 88          | 88   |
| PpNI        | 67–76       | 70          | 70   |
| LPpI        | 71–77       | 75          | 75   |
| DPpI        | 128–138     | 133         | 133  |
| PPI         | 143–149     | 147         | 147  |
**Worker description.** Head much longer than wide (CI 83–85); posterior head margin weakly concave. Anterior clypeal margin with distinct, but often shallow median impression. Frontal carinae strongly developed and noticeably raised forming dorsal margin of very well-developed antennal scrobes, curving down ventrally and anteriorly halfway between posterior eye margin and posterior head margin and forming posterior and parts of ventral scrobe margins; antennal scrobes very well developed, deep and with clearly defined margins, but ventral margin less strongly developed, median scrobal carina absent. Antennal scapes short, not reaching posterior head margin (SI 70–76). Eyes very large (OI 32–34). Mesosomal outline in profile flat to weakly convex, relatively low and elongate (LMI 32–34), moderately to strongly marginate from lateral to dorsal mesosoma; promesonotal suture absent; metanotal groove present, distinct, and clearly impressed. Propodeal spines short, elongate-triangular, and moderately acute (PSLI 17–19), propodeal lobes short, triangular, and usually blunt, always significantly shorter than propodeal spines. Tibiae and femorae strongly swollen. Petiolar node nodiform with moderately rounded antero- and postero-dorsal margins, around 1.2 to 1.3 times higher than long (LPeI 77–82), anterior and posterior faces approximately parallel, anterodorsal and postero-dorsal margins situated at about the same height, petiolar dorsum clearly convex; node in dorsal view between 1.1 to 1.2 times longer than wide (DPeI 85–92), in dorsal view pronotum around 2.0 to 2.2 times wider than petiolar node (PeNI 46–51). Postpetiole in profile globular to subglobular, approximately 1.3 to 1.4 times higher than long (LPpI 71–77); in dorsal view around 1.3 to 1.4 times wider than long (DPpI 128–138), pronotum between 1.3 to 1.5 times wider than postpetiole (PpNI 67–76). Postpetiole in profile usually appearing less voluminous than petiolar node, postpetiole in dorsal view around 1.4 to 1.5 times wider than petiolar node (PPI 143–149). Mandibles and clypeus usually fully unsculptured, smooth, and shining, mandibles sometimes with few traces of rugulae apically; cephalic dorsum between frontal carinae mostly unsculptured and shiny, median ruga present and distinct, cephalic dorsum also puncticate to punctate throughout its length, posteriorly close to posterior head margin especially pronounced; scrobal area partly unsculptured, smooth and shiny and partly merging with surrounding rugose sculpture on sides of head. Ground sculpture on head usually weak to absent. Dorsum of mesosoma mostly unsculptured, smooth and shiny with scattered punctures, rarely with few traces of rugulae; lateral mesosoma longitudinally rugose and very conspicuously reticulate-punctate except for mostly unsculptured lateral pronotum and katepisternum. Forecoxae unsculptured, smooth, and shining. Petiolar node and postpetiole superficially longitudinally rugulose or irregularly rugulose superimposed on conspicuous but relatively weak reticulate-punctate ground sculpture. Mesosoma and waist segments appearing mostly matt. First gastral tergite unsculptured, smooth, and shiny. Pilosity and pubescence greatly reduced: head with few pairs of moderately long, standing hairs, anterior pronotum with one long pair, waist segments sometimes with one long pair each, and sometimes first gastral tergite with one long pair; appressed pubescence present everywhere on body, but noticeable only on antennae, cephalic dorsum, legs, and first gastral
Figure 8. *T. decem* non-type worker (CASENT0914088). A Body in profile B Body in dorsal view C Head in full-face view.
tergite. Anterior edges of antennal scapes and dorsal (outer) surfaces of hind tibiae with appressed hairs. Body strongly bicoloured with dark brown to black gaster contrasting with light brown to reddish brown remainder.

**Distribution and biology.** The distribution range of *T. decem* is far smaller than previously thought (Fig. 3). Indeed, most of the material listed in the literature as *T. decem* or labelled as such in museum collections turned out to be either *T. ultor* or *T. venator*, while only a few collections proved to be genuine *T. decem*. Based on the re-defined species definition, *T. decem* is only known from the type locality in Zimbabwe and two additional localities in East Africa: Arabuko Sokoke in Kenya and Mkomazi in Tanzania. Nevertheless, if more extensive sampling efforts are undertaken in East Africa, *T. decem* is likely to be found in more localities in Kenya, Tanzania, and Zimbabwe. Like *T. uelense* and *T. ultor*, *T. decem* prefers arid habitats, such as savannah and woodland. Based on Arnold (1917) and the collection label from some material from Arabuko Sokoke, *T. decem* nests in sandy soil. The diet consists of termites, as with most other members of the species group.

**Discussion.** *Tetramorium decem* is the core species of the group, and was the type species for the description of the subgenus *Decamorium* by Forel (1913a). It is perhaps the most conspicuous species of the group. Its bicolouration, larger size, lack of sculpture on the mesosomal dorsum, and a higher petiolar node render it immediately recognisable. The mostly unsculptured, smooth and shiny mesosomal dorsum distinguishes *T. decem* from *T. raptor* and *T. uelense*, in which the dorsum of the mesosoma is clearly longitudinally rugose/rugulose. *Tetramorium ultor* and *T. venator* both share the lack of sculpture on the mesosomal dorsum with *T. decem*, but can still be easily separated from the latter. *Tetramorium decem* is generally larger in size (WL 1.02–1.16), has longer propodeal spines (PSLI 17–19) and is also conspicuously bicoloured, whereas *T. ultor* and *T. venator* are smaller species (WL 0.85–0.98) with significantly shorter propodeal teeth (PSLI 9–13) and a more uniform brown to black body colouration. In addition, *T. decem* also has a higher petiolar node, in profile around 1.2 to 1.3 times higher than long (LPeI 77–82), compared to the other two, in which the node in profile is only around 1.0 to 1.2 times higher than long (LPeI 86–100). The species that appears to be morphologically closest to *T. decem* is *T. uelense*. Both species share the large body, bicolouration, and preference for arid habitats. However, in addition to the sculpture on the mesosoma, *T. uelense* also has a lower petiolar node, in profile around 1.1 times higher than long (LPeI 88–93). Another character that is shared between *T. decem* and *T. uelense* but absent in the other species of the group is the development of the ventral margin of the antennal scrobe. In *T. raptor*, *T. ultor*, and *T. venator* the margin is clearly and well defined, while in *T. decem* and *T. uelense* it is less so and merges more with the surrounding rugose sculpture.

**Variation.** Based on the available material we did not observe any significant form of intraspecific variation in *T. decem*. 
Tetramorium raptor Hita Garcia, sp. n.
http://zoobank.org/6A9F212B-8460-41C0-9F8C-792D9A4780C4
http://species-id.net/wiki/Tetramorium_raptor
Figs 3, 4A, 5, 9

Type material. Holotype, pinned worker, CAMEROON, Sud-Ouest, Bakundu, 4.49222 N, 9.375 E, collection code ANTC27989, 8.XI.1990 (A. Dejean) (BMNH: CASENT0195628). Paratypes, 14 pinned workers with same data as holotype (BMNH: CASENT0195581; CASENT0195630; CASENT0195631; CASC: CASENT0195633; CASENT0195634; LACM: LACM_ENT_323500; MCZ: CASENT0195628; ZFMK: CASENT0195632).

[Note: the GPS data of the type locality was not provided by the locality label. The data presented above is based on our own geo-referencing of the Bakundu Forest located in the province Sud-Ouest. Consequently, it should be considered an approximation and not the exact position of the type locality.]

Non-type material. CAMEROON: Sud-Ouest, Bakundu, 4.49222 N, 9.375 E, 8.XI.1990 (A. Dejean); NIGERIA: Gambari, 10.VI.1969 (B. Bolton); Gambari, C.R.I.N., 17.VI.1975 (B. Taylor).

Diagnosis. Tetramorium raptor is easily recognisable within the group on the basis of the following combination of characters: relatively smaller species (WL 0.88–0.93); very large eyes (OI 35); propodeum armed with very short triangular teeth (PSLI 10–11); petiolar node in profile around 1.1 times higher than long (LPeI 89–93); dorsum of mesosoma with longitudinally rugulose sculpture; body uniformly dark brown, appendages of lighter brown.

Worker measurements (N=12). HL 0.64–0.68 (0.67); HW 0.53–0.56 (0.54); SL 0.37–0.41 (0.39); EL 0.19–0.20 (0.XX); PH 0.31—0.34 (0.33); PW 0.40–0.43 (0.41); WL 0.88–0.93 (0.91); PSL 0.07–0.08 (0.07); PTL 0.23–0.25 (0.24); PTH 0.26–0.28 (0.27); PTW 0.19–0.21 (0.20); PPL 0.21–0.24 (0.22); PPH 0.25–0.28 (0.27); PPW 0.26–0.30 (0.28); CI 80–83 (82); SI 70–73 (72); OI 35; DMI 44–47 (45); LMI 35–37 (36); PSLI 10–11 (11); PeNI 47–51 (48); LPeI 89–93 (90); DPeI 80–85 (82); PpNI 64–70 (68); LPpI 81–88 (85); DPpI 123–130 (125); PPI 137–150 (142).

Worker description. Head much longer than wide (CI 80–83); posterior head margin weakly concave. Anterior clypeal margin with distinct but often shallow median impression. Frontal carinae strongly developed and noticeably raised forming dorsal margin of very well-developed antennal scrobes, curving down ventrally and anteriorly halfway between posterior eye margin and posterior head margin and forming posterior and ventral scrobe margins; antennal scrobes very well developed, deep and with clearly defined margins all around, median scrobal carina absent. Antennal scapes short, far from reaching posterior head margin (SI 70–73). Eyes relatively large (OI 35). Mesosomal outline in profile relatively flat, elongate and low (LMI 35–37), moderately to strongly marginate from lateral to dorsal mesosoma; promesonal suture absent; metanotal groove present and conspicuous, but relatively shallow. Propodeum armed with short, triangular, and usually acute teeth (PSLI 10–11), propodeal lobes short, well round-
ed, and usually larger than propodeal teeth. Petiolar node nodiform with moderately rounded antero- and posterodorsal margins, in profile around 1.1 times higher than long (LPeI 89–93), anterior and posterior faces approximately parallel, anterodorsal and posterodorsal margins situated at about same height and equally angled, petiolar dorsum weakly convex; node in dorsal view around 1.2 to 1.3 times longer than wide (DPeI 80–85), in dorsal view pronotum around 2.0 to 2.2 times wider than petiolar node (PeNI 47–51). Postpetiole in profile globular, approximately 1.1 to 1.2 times higher than long (LPpI 81–88); in dorsal view around 1.2 and 1.3 times wider than long (DPpI 123–130), pronotum around 1.4 to 1.6 times wider than postpetiole (PpNI 64–70). Postpetiole in profile appearing less voluminous than petiolar node, postpetiole in dorsal view around 1.4 to 1.5 times wider than petiolar node (PPI 137–150). Mandibles and clypeus unsculptured, smooth, and shining; cephalic dorsum between frontal carinae with fine irregularly longitudinally rugulose sculpture, rugulae running from posterior clypeal margin to posterior head margin, often interrupted or meandering, rarely with cross-meshes, cephalic dorsum also puncticulate to punctate throughout its length, otherwise without ground sculptured; scrobal area partly unsculptured, smooth and shiny and partly strongly reticulate-punctate; lateral head mainly reticulate-rugose with weak to moderately well developed punctate ground sculpture. Dorsum of mesosoma densely longitudinally rugulose, anteriorly without much ground sculpture, posteriorly on top of strong reticulate-punctate ground sculpture; lateral pronotum and katepisternum mostly unsculptured, smooth, and shiny, remainder of lateral mesosoma irregularly rugose and very conspicuously reticulate-punctate. Forecoxae unsculptured, smooth, and shining. Petiolar node laterally reticulate-punctate, dorsum of node mostly unsculptured, smooth, and shiny; postpetiole mostly unsculptured, smooth, and shiny with scattered punctures. First gastral tergite unsculptured, smooth, and shiny. Pilosity and pubescence greatly reduced: head with few pairs of moderately long, standing hairs, anterior pronotum with one long pair, waist segments sometimes with one long pair each, and sometimes first gastral tergite with one long pair; appressed pubescence present everywhere on body, but noticeable only on antennae, cephalic dorsum, legs, and first gastral tergite. Anterior edges of antennal scapes and dorsal (outer) surfaces of hind tibiae with appressed hairs. Body uniformly dark brown to black, appendages of lighter brown.

**Etymology.** The name of the new species is Latin and means “thief, robber, or plunderer”. It refers to the predaceous lifestyle of *T. raptor*. The species epithet is a nominative noun, and thus invariant.

**Distribution and biology.** *Tetramorium raptor* is currently only known from the type locality Bakundu in the southeast of Cameroon and from Gambari in southwestern Nigeria (Fig. 3). Based on the minimal collection label data, *T. raptor* lives in rainforest litter.

**Discussion.** *Tetramorium raptor* is an easily distinguishable member of the *T. decem* group, but was not recognised until this study. Indeed, all known material was collected in 1969 and 1990, but labelled as *T. uelense* on the basis of the distinctive sculpture on the mesosomal dorsum. The presence of conspicuous, longitudinally rugulose sculpture on the dorsum of the promesonotum distinguishes it from *T. decem*, *T.
ultor, or T. venator, since the latter three all lack sculpture on the promesonotal dorsum. Tetramorium uelense, however, shares the presence of sculpture on the mesosomal dorsum with T. raptor, which led to the abovementioned misidentifications. Nevertheless, careful examination of all material previously listed as T. uelense revealed the presence
Revision of *Tetramorium* species group of two morphologically and ecologically different species. The most obvious differences are body size and colour. *Tetramorium uelense* is strongly bicoloured and larger (WL 0.98–1.06) than the smaller and uniformly-coloured *T. raptor* (WL 0.88–0.93). The latter also has shorter propodeal teeth (PSLI 10–11) than *T. uelense* (PSLI 16–18). Furthermore, *T. raptor* possesses a longitudinally rugulose promesonotal dorsum with very little ground sculpture and a mostly unsculptured and shiny lateral pronotum, whereas *T. uelense* has a promesonotal dorsum that is longitudinally rugose with distinct punctate ground sculpture and a lateral pronotum that is conspicuously rugose with prominent ground sculpture. In addition, both species also differ in habitat choice, as *Tetramorium uelense* seems to prefer savannah while *T. raptor* lives in rainforest.

**Variation.** Based on material from the two known localities, there is no intraspecific variation in *T. raptor*.

*Tetramorium uelense* Santschi, 1923, comb. r.
Figs 3, 4B, 5C, 5D, 10

_Tetramorium* (Decamorium) _decem uelense_ Santschi, 1923: 285. [Combination in *Decamorium* and raised to species by Bolton 1976: 298.]

_Decamorium decem nimba_ Bernard, 1953: 250. [Junior synonym of _T. uelense_ by Bolton 1976: 298; here confirmed.]

**Type material.** Of _uelense_: **lectotype**, pinned worker, D. R. CONGO (Congo belge), Uelé, Vankerhovenville, 3.0 N, 29.5 E (Degreef (NHMB: CASENT0906826) [examined]. **Paralectotype**, pinned queen with same data as lectotype (MRAC) [not examined].

Of _nimba_: **holotype**, pinned worker, GUINEA, Kéoulenta, 7.714053 N, 8.331786 W, St. 1 Savane, (MNHN: CASENT0914084) [examined].

[Note: GPS data for neither of the type localities was included on the locality labels or the original descriptions. The data presented above is based on our own georeferencing of Vankerhovenville located in Province Orientale and Kéoulenta located in the Nzérékoré Region. Consequently, they should be considered approximations and not the exact positions of the type localities.]

**Non-type material.** GHANA: Greater Accra Region, Accra Metropolis District, Legon, 23.VIII.1972 (*D. Leston*); NIGERIA: 16 km N. of Mokwa, 16.X.1976 (*C. Longhurst*).

**Diagnosis.** The following character combination separates *T. uelense* from the other species of the _T. decem_ species group: relatively larger species (WL 0.98–1.06); propodeum armed with short triangular to elongate-triangular teeth (PSLI 16–18); petiolar node in profile around 1.1 times higher than long (LPeI 88–93); dorsum of mesosoma conspicuously longitudinally rugose with distinctive reticulate-punctate ground sculpture; strongly bicoloured with dark brown to black gaster contrasting with light brown to reddish brown remainder of body.

**Worker measurements (N=6).** HL 0.67–0.72 (0.70); HW 0.54–0.59 (0.57); SL 0.39–0.42 (0.41); EL 0.19–0.20 (0.20); PH 0.36–0.38 (0.37); PW 0.43–0.47 (0.45);
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Worker description. Head much longer than wide (CI 80–83); posterior head margin weakly concave. Anterior clypeal margin with distinct, but often shallow median impression. Frontal carinae strongly developed and noticeably raised forming dorsal margin of very well-developed antennal scrobes, curving down ventrally and anteriorly halfway between posterior eye margin and posterior head margin and forming posterior and ventral scrobe margins; antennal scrobes very well developed, deep and with clearly defined margins, but ventral margin less strongly developed, median scrobal carina absent. Antennal scapes short, far from reaching posterior head margin (SI 69–74). Eyes relatively large (OI 34–35). Mesosomal outline in profile relatively flat, elongate and low (LMI 35–37), moderately to strongly marginate from lateral to dorsal mesosoma; promesonotal suture absent; metanotal groove present, distinct, but relatively shallow. Propodeum armed with short, triangular to elongate-triangular, and acute teeth (PSLI 16–18), propodeal lobes reduced, short, and well rounded, usually shorter than propodeal teeth. Tibiae and femora strongly swollen. Petiolar node nodiform with moderately rounded antero- and posterodorsal margins, in profile around 1.1 times higher than long (LPel 88–93), anterior and posterior faces approximately parallel, anterodorsal and posterodorsal margins situated at about same height and equally angled, petiolar dorsum clearly convex; node in dorsal view around 1.2 to 1.3 times longer than wide (DPeI 77–81), in dorsal view pronotum between 2.0 and 2.1 times wider than petiolar node (PeNI 48–49). Postpetiole in profile globular, approximately 1.2 to 1.3 times higher than long (LPpI 75–86); in dorsal view between 1.2 and 1.3 times wider than long (DPpI 122–125), pronotum around 1.4 times wider than postpetiole (PpNI 69–70). Postpetiole in profile more or less of same volume as petiolar node, postpetiole in dorsal view around 1.4 times wider than petiolar node (PPI 141–145). Mandibles and clypeus unsculptured, smooth, and shining; cephalic dorsum between frontal carinae with fine irregularly longitudinally rugulose/rugose sculpture, rugulae/rugae often interrupted, meandering, or with cross-meshes, cephalic dorsum also puncticulate to punctate throughout its length; scrobal area strongly reticulate-punctate; lateral head mainly reticulate-rugose with weak to moderately well developed punctate ground sculpture. Ground sculpture on head usually weak, except scrobal area (see above). Dorsum of mesosoma densely longitudinally rugose on top of strong punctate ground sculpture; lateral mesosoma longitudinally rugose and very conspicuously reticulate-punctate. Forecoxae unsculptured, smooth, and shining. Petiolar node and postpetiole superficially longitudinally rugulose or irregularly rugulose superimposed on conspicuous but relatively weak reticulate-punctate ground sculpture. Mesosoma and waist segments appearing matt. First gastral tergite unsculptured, smooth, and shiny. Pilosity and pubescence greatly reduced: head with few pairs of moderately long, standing hairs, anterior pronotum with one long pair, waist segments sometimes with one long pair each, and sometimes first gastral tergite with one long pair; appressed pu-
bescence present everywhere on body, but noticeable only on antennae, cephalic dorsum, legs, and first gastric tergite. Anterior edges of antennal scapes and dorsal (outer) surfaces of hind tibiae with appressed hairs. Body strongly bicoloured with dark brown to black gaster contrasting with light brown to reddish brown remainder.
Distribution and biology. So far, *T. uelense* is known from a few collections in savannah habitats throughout a relatively wide geographical range from West to Central Africa (Fig. 3). The known distribution spans Guinea through Ghana and Nigeria to the northeast of the D. R. Congo close to South Sudan and Uganda. Compared to most other Afrotropical *Tetramorium* species, there is a wealth of information about the natural history of *T. uelense* (Longhurst, 1979). Longhurst et al. (1979) provided important observation data about nests, foraging, recruitment, and predation on termites. *Tetramorium uelense* live in subterranean nests difficult to locate without observing foraging workers. At least in the area observed by Longhurst et al. (1979), the main prey of *T. uelense* consisted of various species of *Microtermes* Wasmann, and *T. uelense* exerted great predation pressure on these small termites. Scouting is performed by solitary workers that search the leaf litter, fallen grass stems or pieces of wood for prey. After locating termites the scouts return to the colony for recruitment of groups between 10 to 30 workers. These groups locate, immobilise, and retrieve the prey. For more details refer to Longhurst et al. (1979).

Discussion. *Tetramorium uelense* can be easily distinguished from the remainder of the *T. decem* species group. The presence of longitudinally rugose sculpture on the dorsum of the mesosoma separates *T. uelense* immediately from *T. decem*, *T. ultor*, and *T. venator*. In the latter three the mesosomal dorsum is completely unsculptured, smooth, and very shiny. The only other species with sculpture on the dorsum of the mesosoma, which could be confused with *T. uelense*, is *T. raptor*. Nevertheless, both are well separable in morphology and ecology. Most obviously, *T. uelense* is a larger species (WL 0.98–1.06) with distinct bicolouration while *T. raptor* (WL 0.88–0.93) is smaller and a uniform dark brown colour. In addition, *T. uelense* has longer and better developed propodeal teeth (PSLI 16–18) compared to *T. raptor* (PSLI 10–11), even though this might be difficult to see and may require measurements to confirm. Another, more visible character is the sculpture on the mesosomal dorsum, which is strongly longitudinally rugose with distinct punctate ground sculpture in *T. uelense* versus longitudinally rugulose with very little ground sculpture in *T. raptor*. Also, the lateral pronotum of the latter is mostly unsculptured, smooth, and shiny while in *T. uelense* the lateral pronotum is strongly rugose with conspicuous ground sculpture.

Variation. Despite the broad distribution range, we did not observe any significant intraspecific variation in *T. uelense*.
Revision of Tetramorium decem species group

Paralectotypes, seven pinned workers with same data as lectotype (BMNH: CASENT0901036; MHNG: CASENT0195688) [examined].

[Note: the GPS data of the type locality was not provided by the locality label or the original description. The data presented above is based on our own geo-referencing of the Shiloh locality located in Matabeleland North province. Consequently, it should be considered an approximation and not the exact position of the type locality.]

Non-type material. MOZAMBIQUE: Sofala Province, Gorongosa National Park, Limestone Gorge, 18°57'13"S, 34°10'37.6"E, 81 m, 15.V.2012 (G.D. Alpert & E.O. Wilson); Sofala Province, Gorongosa National Park, 5 km S Chitango, 18°59'28.8"S, 34°21'10"E, 10 m, secondary forest, 1.VI.2012 (G.D. Alpert); Sofala Province, Gorongosa National Park, Centracao Outpost (Piva-Joao), 18°30'20"S, 34°29'7"E, small forest along river, 11.VI.2012 (D. Muala & T. Torcida); Sofala Province, Gorongosa National Park, WP092, 18°56.1'3.1"S, 34°23'36.7"E, 51 m, open area, 26.VI.2012 (G.D. Alpert); KENYA: Kwale District, Shimba Hills, Longomangandi National Reserve, 4.23 S, 39.43 E, primary hardwood forest, 2.VI.2001 (R.R. Snelling); TANZANIA: Pwani, Rufiji District, Kichi Hills Forest Reserve, 8.23889 S, 38.65023 E, 499 m, primary forest, 5.–7.III.2008 (P. Hawkess, Y. Mlacha, & F. Ninga); ZAMBIA: Southern Province, 16.79533 S, 26.93833 E, 1330 m, Choma, Gwembe Lodge, miombo woodland, 3.XII.2005 (B.L. Fisher); ZIMBABWE: Ballaballa, 20.45 S, 29.03 E, 1.IV.1945; Umtali, II.1917 (G. Arnold).

Diagnosis. Tetramorium ultor can be recognised by the following combination of characters: relatively smaller species (WL 0.85–0.96); very large eyes (OI 33–36); propodeum armed with short teeth (PSLI 10–13); petiolar node in profile around 1.1 to 1.2 times higher than long (LPeI 86–92); dorsum of promesonotum unsculptured, smooth, and very shiny; body of uniform light to chestnut brown, appendages often lighter.

Worker measurements (N=25). HL 0.62–0.70 (0.66); HW 0.48–0.58 (0.53); SL 0.35–0.42 (0.37); EL 0.16–0.20 (0.19); PH 0.29–0.33 (0.30); PW 0.37–0.45 (0.41); WL 0.85–0.96 (0.89); PSL 0.07–0.09 (0.08); PTL 0.22–0.25 (0.24); PTH 0.25–0.29 (0.27); PTW 0.19–0.22 (0.20); PPL 0.19–0.23 (0.21); PPH 0.25–0.30 (0.27); PPT 0.24–0.30 (0.27); CI 77–82 (80); SI 67–73 (70); IO 33–36 (35); DMI 44–48 (46); LMI 32–35 (34); PSLI 10–13 (12); PeNI 46–50 (48); LPel 86–92 (88); DPel 79–86 (84); PpNI 60–71 (67); LpNI 73–81 (78); DpNI 126–132 (130); PPI 130–145 (139).

Worker description. Head much longer than wide (CI 77–82); posterior head margin weakly concave. Anterior clypeal margin with distinct, but often shallow median impression. Frontal carinae strongly developed and noticeably raised forming dorsal margin of very well-developed antennal scrobes, curving down ventrally and anteriorly halfway between posterior eye margin and posterior head margin and forming posterior and ventral scrobe margins; antennal scrobes very well developed, deep and with clearly defined margins all around, median scrobal carina absent. Antennal scapes short, not reaching posterior head margin (SI 67–73). Eyes very large (OI 33–36). Mesosomal outline in profile relatively flat, long and low (LMI 32–35), moderately marginate from lateral to dorsal mesosoma; promesonal suture absent; metanotal groove present and distinct, but relatively shallow. Propodeum armed with short, tri-
angular, and mostly blunt teeth (PSLI 10–13), propodeal lobes short, triangular, and usually blunt, in profile usually longer and more voluminous than propodeal spines. Tibiae and femora strongly swollen. Petiolar node nodiform with moderately rounded antero- and posterodorsal margins, in profile around 1.1 to 1.2 times higher than long (LPeI 86–92), anterior and posterior faces approximately parallel, anterodorsal and posterodorsal margins situated at about same height and equally angled, petiolar dorsum weakly convex; node in dorsal view around 1.1 to 1.2 times longer than wide (DPeI 79–86), in dorsal view pronotum between 2.0 to 2.2 times wider than petiolar node (PeNI 46–50). Postpetiole in profile globular, approximately 1.2 to 1.4 times higher than long (LPpI 73–81); in dorsal view around 1.3 times wider than long (DPpI 126–132), pronotum approximately 1.4 to 1.5 times wider than postpetiole (PpNI 60–71). Postpetiole in profile appearing less voluminous than petiolar node, postpetiole in dorsal view between 1.3 to 1.5 times wider than petiolar node (PPI 130–145). Mandibles and clypeus usually fully unsculptured, smooth, and shining; cephalic dorsum between frontal carinae mostly unsculptured and shiny, median ruga present and distinct, cephalic dorsum also puncticulate to punctate throughout its length, close to posterior head margin especially pronounced; scrobal area unsculptured, smooth, and very shiny; lateral head ventral of antennal scrobe mainly reticulate-rugose; ground sculpture on head usually weak to absent. Dorsum of mesosoma mostly unsculptured, smooth, and shiny with scattered punctures, rarely with few traces of rugulae; lateral mesosoma mostly unsculptured and shiny, posteriorly irregularly rugose and conspicuously reticulate-punctate. Petiolar node and postpetiole only weakly sculptured, laterally usually superficially rugulose and punctate on lower half and more unsculptured on upper half, node dorsally mostly smooth; postpetiole mostly unsculptured, smooth, and shiny with scattered punctures. First gastral tergite unsculptured, smooth, and shiny. Pilosity and pubescence greatly reduced: head with few pairs of moderately long, standing hairs, anterior pronotum with one long pair, waist segments sometimes with one long pair each, and sometimes first gastral tergite with one long pair; appressed pubescence present everywhere on body, but noticeable only on antennae, cephalic dorsum, legs, and first gastral tergite. Anterior edges of antennal scapes and dorsal (outer) surfaces of hind tibiae with appressed hairs. Body uniformly brown, appendages often lighter.

**Distribution and biology.** *Tetramorium ultor* is widespread in eastern and southern Africa (Fig. 3). It is distributed from Kenya south to Mozambique, and also found in Zambia and Zimbabwe. Most localities are tropical dry forest habitats or miombo woodland. Also, *T. ultor* seems to be a ground-active species nesting in or under rotten logs and is likely termitophagous like the other group members.

**Discussion.** Since Bolton (1976) synonymised *T. ultor* under *T. decem*, almost all of the material of *T. ultor* examined here was identified and/or labelled as *T. decem* prior to this study. However, after careful examination of all the available material, we have come to the conclusion that *T. ultor* is distinctive enough to merit species status. *Tetramorium ultor* is smaller (WL 0.85–0.96), has shorter propodeal teeth (PSLI 10–13), a lower petiolar node, around 1.1 to 1.2 times higher than long (LPeI 86–92),
Figure 11. *T. ultor* paralectotype worker (CASENT0901036). A Body in profile B Body in dorsal view C Head in full-face view.

and is of uniform light brown to chestnut brown body colouration. By contrast, *T. decem* is larger (WL 1.02–1.16), has longer propodeal spines (PSLI 17–19), a higher petiolar node, in profile around 1.2 to 1.3 times higher than long (LPeI 77–82), and is conspicuously bicoloured. In addition, both species share most of their distribution range without any intermediate forms. Furthermore, *T. ultor* is unlikely to be confused with *T. raptor* and *T. uelense* since the latter two have a conspicuously rugose/rugulose promesonotum, which is completely unsculptured, smooth and shiny in *T. ultor*. The last species of the group, *T. venator*, is the one most similar to *T. ultor*, and
both species are allopatric. However, both species can be separated by eye size, colour, and a different habitat choice. *Tetramorium venator* has larger eyes (OI 37–40) and is of a much darker brown than *T. ultor*, which has smaller eyes (OI 33–36) and is of a lighter brown. In addition, the latter species is more arid-adapted, occurring in woodlands and dry forests while *T. venator* seems to be a forest specialist found in primary, secondary, or disturbed rainforests. We consider the above arguments as sufficient to justify the heterospecificity of both species. Further arguments are provided below in the description of *T. venator*.

**Variation.** Based on the available material, we did not observe any intraspecific variation in *T. ultor*.

_Tetramorium venator_ Hita Garcia, sp. n.
http://zoobank.org/02C5E77F-FFD9-4204-843C-1E541B84972A
http://species-id.net/wiki/Tetramorium_venator
Figs 3, 4D, 6B, 7C, 7D, 12

**Type material.** Holotype, pinned worker, KENYA, Western Kenya, Kakamega Forest, Bunyala Forest Fragment, 0.37889 N, 34.69917 E, 1448 m, disturbed primary forest, Kakamega 2008 survey, leaf litter, pitfall trap, Transect 35, position 10 m, 1.VIII.2008 (G. Fischer) (CASC: CASENT0195574). Paratypes, six pinned workers with same data as holotype (BMNH: CASENT0195625; CASC: CASENT0217165; BMNH: CASENT0195625; LACM: CASENT0195627; MCZ: CASENT0195624; NMK: CASENT0195626; ZFMK: CASENT0195623).

**Non-type material.** CAMEROON: Centre, Mbalmayo, 1.XI.1993 (N. Stork); Centre, Ottotomo, 24.IV.1986 (A. Dejean); Est, Abong Mbang, 28.VI.1988 (A. Dejean); Sud, Bondé Forest, N’kolo village, 27.5 km 155°SE Elogbatindi, 3.22167 N, 10.24667 E, 40 m, rainforest, 12.IV.2000 (B.L. Fisher); Sud, Res. de Faune de Campo, Massif des Mamelles, 15.1 km 84°É Ébodjé, 2.59417 N, 9.9595 E, 180 m, rainforest, 4.IV.2000 (B.L. Fisher); Sud, Res. de Faune de Campo, 2.16 km 106°ESE Ébodjé, 2.56783 N, 9.84433 E, 10 m, littoral rainforest, 9.IV.2000 (B.L. Fisher); Sud, P. N. Campo, 43.3 km 108°ESE Campo, 2.2825 N, 10.20617 E, 290 m, rainforest, 7.IV.2000 (B.L. Fisher); Sud-Ouest, Bimbía Forest, 7.4 km 119°ESE Limbe, 3.98183 N, 9.2625 E, 40 m, 14.IV.2000 (B.L. Fisher); Sud-Ouest, Korup N. P., 6.9 km 317°NW Mundemba, 5.016 N, 8.864 E, 110 m, rainforest, 19.IV.2000 (B.L. Fisher); CENTRAL AFRICAN REPUBLIC: Prefecture Sangha-Mbaéré, Parc National Dzanga-Ndoki, Mabéya Bai, 21.4 km 53°NE Bayanga, 3.03333 N, 16.41 E, 510 m, rainforest, 1.–7.V.2001 (B.L. Fisher); DEMOCRATIC REPUBLIC OF CONGO: Epulu, 750 m, 1.38333 N, 28.58333 E, rainforest, 1.XI.1995 (S.D. Torti); Kikwit, Kinzambi, 27.III.1984 (A. Dejean); 44 miles E. of Kileba, 1110 m, 16.1.1958 (E.S. Ross & R.E. Leech); GABON: La Makandé Forêt des Abeilles, 1.1.–1.II.1999 (S. Lewis); Ogooué-Ivindo, Makokou, C.N.R.S., 10.VII.1974 (W. Gotwald); Ogooue-Maritime, Réserve des Monts Doudou; 24.3km 307°NW Doussala, 2.2225 S, 10.40583 E, 370 m, coastal lowland rainforest,
Revision of *Tetramorium decem* species group

5.–12.III.2000 (*S. van Noort*); Ogooue-Maritime, Aire d’Exploit. Rationnelle de Faune des Monts Doudou, 24.3 km 30°NW Doussala, 2.22639 S, 10.49717 E, 375 m, rainforest, 6.III.2000 (*B.L. Fisher*); Ogooue-Maritime, Reserve de la Moukalaba-Dougaoua, 12.2 km 30°NW Doussala, 2.28333 S, 10.54533 E, 110 m, coastal lowland rainforest, sited within forest, 24.II.–3.III.2000 (*S. van Noort*); Ogooue-Maritime, Reserve de Faune de la Moukalaba-Dougaoua, 10.8 km 214°SW Doussala, 2.42267 S, 10.54533 E, 110 m, rainforest, 29.II.2000 (*B.L. Fisher*); Ogooue-Maritime, Reserve de Faune de la Moukalaba-Dougaoua, 12.2 km 30°NW Doussala, 2.31667 N, 10.53333 E, 110 m, rainforest, 1.III.2000 (*B.L. Fisher*); Woleu-Ntem, 31.3 km 108°ESE Minvoul, 2.08 N, 12.40667 E, 600 m, rainforest, 7.–15.II.1998 (*B.L. Fisher*); GHANA: Akwapim, Tafo, 19.1.1970 (*B. Bolton*); Ashanti, Poano, cocoa, 9.IX.1992 (*R. Belshaw*); Atewa Forest Reserve, near Kibi, primary forest, 24.III.1992 (*R. Belshaw*); Eastern, Kade, 1.I.1992 (*R. Belshaw*); Enchi, 17.V.1969 (*D. Leston*); Esunkawkaw Forest Reserve, primary forest, 27.X.1992 (*R. Belshaw*); Nkwanda near Nkwawk, secondary forest, 12.XII.1991 (*R. Belshaw*); Portrase, 1.III.1992 (*R. Belshaw*); KENYA: Western Kenya, Kakamega Forest, Bunyala Forest Fragment, 0.37889 N, 34.69917 E, 1448 m, disturbed primary forest, 1.VIII.2008 (*G. Fischer*); LIBERIA: Monrovia, 5.VII.1957 (*E.S. Ross & R.E. Leech*); TANZANIA: Kigoma Region, Gombe Stream National Park, 4.7 S, 29.616667 E, 915–1012 m, 29.XII.2009–12.I.2010 (*R. O’Malley*); UGANDA: Semuliki NP, 00.83556, 30.15542 ± 200 m, 676 m, rainforest, 30.–31.VII.2012 (*B.L. Fisher et al.*); Semuliki NP, 00.84483, 30.15052 ± 200 m, 680 m, rainforest, 2.VIII.2012 (*B.L. Fisher et al.*).

**Diagnosis.** *Tetramorium venator* can be recognised by the following combination of characters: relatively smaller species (WL 0.87–0.98); very large eyes, largest in the group (OI 37–40); propodeum armed with very short, triangular, and moderately acute (PSLI 9–12); petiolar node in profile between 1.0 to 1.2 times higher than long (LPeI 90–100); dorsum of promesonotum unsulptured, smooth, and very shiny; head, mesosoma, waist segments, and gaster uniformly very dark brown to black, appendages of lighter brown.

**Worker measurements** (**N=25**). HL 0.64–0.71 (0.67); HW 0.51–0.59 (0.54); SL 0.38–0.43 (0.40); EL 0.19–0.22 (0.21); PH 0.30–0.36 (0.32); PW 0.39–0.45 (0.41); WL 0.87–0.98 (0.92); PSL 0.06–0.09 (0.07); PTL 0.23–0.26 (0.25); PTH 0.25–0.29 (0.26); PTW 0.18–0.22 (0.20); PPL 0.21–0.25 (0.22); PPH 0.25–0.30 (0.26); PPW 0.25–0.30 (0.26); CI 79–83 (81); SI 70–75 (74); OI 37–40 (38); DMI 43–46 (44); LMI 33–37 (35); PSLI 9–12 (10); PeNI 45–51 (48); LPel 90–100 (93); DPeI 76–85 (80); PpNI 63–67 (65); LPpl 80–86 (84); DPpl 115–124 (119); PPI 130–144 (135).

**Worker description.** Head much longer than wide (CI 79–83); posterior head margin weakly concave. Anterior clypeal margin with distinct, but often shallow median impression. Frontal carinae strongly developed and noticeably raised forming dorsal margin of very well-developed antennal scrobes, curving down ventrally and anteriorly halfway between posterior eye margin and posterior head margin and forming posterior and ventral scrobe margins; antennal scrobes very well developed, deep and with clearly defined margins all around, median scrobal carina absent. Antennal scapes short, not reaching posterior head margin (SI 70–75). Eyes very large (37–40).
Mesosomal outline in profile relatively flat, long and low (LMI 33–37), moderately marginate from lateral to dorsal mesosoma; promesonotal suture absent; metanotal groove present and distinct, but relatively shallow. Propodeum armed with very short, triangular, and moderately acute teeth (PSLI 9–12), propodeal lobes short, triangular to rounded, and usually blunt, in profile more or less of same length as propodeal teeth and appearing more voluminous than propodeal spines. Tibiae and femorae strongly swollen. Petiolar node nodiform with moderately rounded antero- and posterodorsal margins, in profile between 1.0 to 1.2 times higher than long (LPel 90–100), anterior and posterior faces approximately parallel, anterodorsal and posterodorsal margins situated at about same height and equally angled, petiolar dorsum usually conspicuously convex, sometimes only weakly so; node in dorsal view around 1.2 to 1.3 times longer than wide (DPeI 76–85), in dorsal view pronotum between 2.0 to 2.2 times wider than petiolar node (PeNI 45–51). Postpetiole in profile globular, approximately 1.2 times higher than long (LPpI 80–86); in dorsal view around 1.2 times wider than long (DPpI 115–124), pronotum approximately 1.5 to 1.6 times wider than postpetiole (PpNI 63–67). Postpetiole in profile appearing less voluminous than petiolar node, postpetiole in dorsal view between 1.3 to 1.5 times wider than petiolar node (PPI 130–144). Mandibles and clypeus usually fully unsculptured, smooth, and shining; cephalic dorsum between frontal carinae mostly unsculptured and shiny, median ruga present and distinct, cephalic dorsum also puncticulate to punctate across its length, close to posterior head margin especially pronounced; scrobal area unsculptured, smooth and very shiny; lateral head ventral of antennal scrobe mainly reticulate-rugose; ground sculpture on head usually weak to absent. Dorsum of mesosoma mostly unsculptured, smooth and shiny with scattered punctures, rarely with few traces of rugulae; lateral mesosoma mostly unsculptured and shiny, posteriorly irregularly rugose and conspicuously reticulate-punctate. Petiolar node and postpetiole only weakly sculptured, laterally usually superficially rugulose and punctate on lower half and more unsculptured on upper half, node dorsally mostly smooth; postpetiole mostly unsculptured, smooth and shiny with scattered punctures. First gastral tergite unsculptured, smooth, and shiny. Pilosity and pubescence greatly reduced: head with few pairs of moderately long, standing hairs, anterior pronotum with one long pair, waist segments sometimes with one long pair each, and sometimes first gastral tergite with one long pair; appressed pubescence present everywhere on body, but noticeable only on antennae, cephalic dorsum, legs, and first gastral tergite. Anterior edges of antennal scapes and dorsal (outer) surfaces of hind tibiae with appressed hairs. Head, mesosoma, waist segments, and gaster uniformly very dark brown to black, appendages of lighter brown.

**Etymology.** The name of the new species is Latin and means “hunter” referring to the predatory lifestyle of *T. venator*. The species epithet is a nominative noun, and thus invariant.

**Distribution and biology.** *Tetramorium venator* is the most widespread and abundant species of the group. It is found throughout much of the equatorial forest belt from Liberia in the west to Kenya in the east (Fig. 3). Even though there was no material from Benin, Togo, Nigeria, Equatorial Guinea or South Sudan available for this study, we
expect that *T. venator* will be found in most or all of these countries. Based on the available data, this species lives in the leaf litter stratum of primary, secondary, or disturbed rainforests. Additionally, *T. venator* seems to be found at lower elevations in West and Central Africa, but also occurs at mid elevations further east in the eastern D.R. Congo, Tanzania, and Kenya, where it reaches its highest known elevation at the type locality at 1448 m. Based on unpublished stable isotope data from the type series, *T. venator* is a predatory species, and we assume that it feeds on termites. This is supported by some series from Cameroon that were collected while foraging in the nests of *Cubitermes* Wasmann.

**Discussion.** Despite being common and collected fairly often prior to this study, most of the material of *T. venator* was identified and labelled as *T. decem*. Indeed, more than 90% of all the material listed as the latter species at the beginning of our revision turned out to be *T. venator*. Nevertheless, our revision shows that they are clearly not conspecific. *Tetramorium venator* is smaller in size (WL 0.87–0.98), has larger eyes (OI 37–40), shorter propodeal teeth (PSLI 9–12), a lower petiolar node (LPeI 90–100), and has a uniform body colouration. By contrast, *T. decem* is larger (WL 1.02–1.16), has smaller eyes (OI 32–34), longer propodeal spines (PSLI 17–19), a higher petiolar node (LPeI 77–82), and is distinctly bicoloured. Also, *T. venator* is a rainforest species while *T. decem* lives in savannah or woodland.

The abovementioned very large eyes of *T. venator* separate it also from *T. ultor*, which has smaller eyes (OI 33–36). In addition, *T. ultor* is also of a much lighter colour, usually light brown to chestnut brown, and prefers dry forest or woodland habitats. It should be noted, however, that *T. ultor* and *T. venator* are morphologically very close to each other and differ significantly only in eye size, colour and habitat preference. They could represent different ecotypes of the same species, one adapted to more shaded and humid forest versus one specialised to more arid savannah, woodland, and dry forest. Nevertheless, if this was true, then we would see some intermediate forms in transitional habitats, and there are none at present. As a matter of fact, *T. venator* is also found in secondary and disturbed rainforests. The type series was collected in a highly disturbed rainforest fragment in Kenya and the material from Gombe in Tanzania is from a rainforest-woodland mosaic. Both species are also separated by the Great Rift Valley, which separates different faunistic sub-regions of the Afrotropical region. We consider *T. venator* as a faunal element of the Guineo-Congolian forest zone, while we believe *T. ultor* is a species of the arid corridor running from East to Southern Africa. Based on the available material and African biogeography in general, we conclude that our two species hypothesis is more likely.

Furthermore, *T. venator* cannot be misidentified with either *T. uelense* or *T. raptor* since both possess strongly developed rugulose/rugose sculpture on the promesonotal dorsum that is absent in *T. venator*. At present, *T. venator* overlaps in its distribution with *T. uelense* and *T. raptor* in West and Central Africa. We think it might also overlap with *T. decem* and *T. ultor* in East Africa, even though it currently seems as if they are widely separated geographically. However, since the sampling is very patchy, especially in East Africa, much more *T. decem* and *T. ultor* material is likely to be collected with further inventories, and these two species will be found in close proximity to *T. venator*. Never-
Figure 12. *T. venator* holotype worker (CASENT0195574). A Body in profile  B Body in dorsal view  C Head in full-face view.
Revision of *Tetramorium decem* species group

Intriguingly, even though *T. venator* is very broadly distributed in Equatorial Africa, there seems to be no significant intraspecific variation.

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