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The ant genus *Tetraponera* (Hymenoptera: Formicidae) in the Afrotropical region: taxonomic review and key to species

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Abstract

The arboreal ant genus *Tetraponera* is widely distributed in the Paleotropics. Five species groups were previously recognized in the Afrotropical region (including Madagascar), and two of these were revised. This paper provides a taxonomic treatment of the remaining species. A survey of the *T. allaborans* group on the African mainland leads to the recognition of fourteen species: *T. clypeata* (Emery) (= *T. braunsi* (Forel) **syn. nov.**); *T. continua* (Forel) (= *T. claveaui* (Santschi) **syn. nov.**); *T. cortina* **sp. nov.**; *T. dispar* **sp. nov.**; *T. emeryi* (Forel) (= *T. braunsi durbanensis* (Forel) **syn. nov.**); *T. exactor* **sp. nov.**; *T. furtiva* **sp. nov.**; *T. gerdae* (Stitz); *T. liengmei* (Forel); *T. mayri* (Forel); *T. pedana* **sp. nov.**; *T. penzigi* (Mayr) (= *T. scotti* Donisthorpe **syn. nov.** = *T. zavattarii* (Menozzi) **syn. nov.** = *T. penzigi praestigiatrix* Santschi **syn. nov.**); *T. pumila* **sp. nov.**; and *T. tessmanni* (Stitz). A full revision of the Malagasy species of the *T. allaborans* group is deferred, but the following new synonymy is established: *T. hysterica* (Forel) = *T. hysterica inflata* (Emery) **syn. nov.**; *T. longula* (Emery) = *T. sahlbergii deplanata* (Forel) **syn. nov.**; *T. mandibularis* (Emery) = *T. flexuosa* (Santschi) **syn. nov.**; *T. morondaviensis* (Forel) = *T. arrogans* (Santschi) **syn. nov.** = *T. demens* (Santschi) **syn. nov.** = *T. hysterica dimidiata* (Forel) **syn. nov.**; and *T. sahlbergii* = *T. sahlbergii spuria* (Forel) **syn. nov.** = *T. plicatidens* (Santschi) **syn. nov.** In the *T. ambigua* group the following synonymy is reinstated (**syn. rev.**): *T. ambigua* (Emery) = *T. erythraea* (Emery) = *T. bifoveolata* (Mayr) = *T. angolensis* Santschi; and *T. ophthalmica* (Emery) = *T. unidens* Santschi. A new species is described in the Madagascar-endemic *T. grandidieri* group: *T. elegans* **sp. nov.** Scrutiny of the *T. natalensis* group indicates the occurrence of ten species: *T. andrei* (Mayr), *T. anthracina* (Santschi), *T. caffra* (Santschi), *T. insularis* **sp. nov.**, *T. kosi* **sp. nov.**, *T. mocquerysi* (André), *T. natalensis* (F. Smith), *T. redacta* **sp. nov.**, *T. schulthessi* (Santschi), and *T. setosa* **sp. nov.** *T. insularis* is known only from Madagascar, while the other nine species are confined to the African mainland. The following new synonymy is proposed for the *T. natalensis* group (senior synonym cited first): *T. anthracina* = *T. poultoni* Donisthorpe **syn. nov.** = *T. triangularis* (Stitz) **syn. nov.**; *T. mocquerysi* = *T. mocquerysi biozellata* (Karavaiev) **syn. nov.** = *T. mocquerysi elongata* (Stitz) **syn. nov.** = *T. emacerata* (Santschi) **syn. nov.** = *T. triangularis illota* (Santschi) **syn. nov.** = *T. ledouxi* Terron **syn. nov.** = *T. lemoulti* (Santschi) **syn. nov.** = *T. mocquerysi lepida* Wheeler **syn. nov.** = *T. monardi* (Santschi) **syn. nov.** = *T. emacerata oberbecki* (Forel) **syn. nov.** = *T. emacerata odiosa* (Forel) **syn. nov.**; and *T. natalensis* = *T. angusta* (Arnold) **syn. nov.** = *T. capensis* (F. Smith) **syn. nov.** = *T. natalensis cuitensis* (Forel) **syn. nov.** = *T. mocquerysi lutea* (Stitz) **syn. nov.** = *T. natalensis obscurata* (Emery) **syn. nov.** = *T. prelli* (Forel) **syn. nov.** = *T. natalensis usambarensis* (Forel) **syn. nov.** The extensive synonymy under *T. mocquerysi* and *T. natalensis* reflects the conviction that previous taxonomists underestimated the extent of intraspecific variation in these taxa, but further study and testing of this conclusion is warranted. An illustrated worker- and queen-based key is provided for all species of *Tetraponera* occurring in Africa and Madagascar, except the Malagasy members of the *T. allaborans* group.

Key words: arboreal ants, Pseudomyrmecinae, taxonomy, distribution, phylogeny

Introduction

Tropical arboreal environments are notable for a high diversity and abundance of ants (Davidson *et al.* 2003; Floren *et al.* 2014; Klimes *et al.* 2015; Longino & Colwell 2020; Leponce *et al.* 2021). Progress in understanding the origin, evolution, and functional dynamics of these ant communities is facilitated by improved systematic knowledge. This study is concerned with clarifying the taxonomy of one group of arboreal ants, the genus *Tetraponera* F. Smith, in Africa and Madagascar. A member of the ant subfamily Pseudomyrmecinae, whose species nest almost exclusively above-ground (Ward 1990), *Tetraponera* is widespread in the Indomalayan and Afrotropical regions, typically nesting in dead twigs of trees and shrubs or, less commonly, in the domatia of specialized ant-plants (Janzen 1972; Ward 1991, 2001; Davidson & McKey 1993).

This paper is the third in a series treating the taxonomy of Afrotropical *Tetraponera*. In previous contributions, five species groups were recognized (Ward 2006) and revisions were provided for two of them: the *T. ambigua* group (Ward 2006) and the *T. grandidieri* group (Ward 2009). Here the remaining species, mostly members of the *T. allaborans* and *T. natalensis* groups, are delimited, described, and keyed. An exception is made for the Malagasy members of the *T. allaborans* group, a species-rich and taxonomically challenging assemblage, for which a separate treatment will be necessary.

Prior indications that the genus *Tetraponera* might be paraphyletic, based on genetic studies with modest numbers of nuclear genes (Ward & Downie 2005; Chomicki *et al.* 2015), have not been upheld by recent phylogenomic analyses employing targeted enrichment of ultraconserved elements (UCEs). Utilizing a probe set that targets more than 2,500 UCE loci, these new analyses suggest that *Tetraponera* and the New World pseudomyrmecines (*Pseudomyrmex* Lund + *Myrcidris* Ward) are reciprocally monophyletic (Branstetter *et al.* 2017; Ward, unpublished). The

six species groups of *Tetraponera* previously established on the basis of morphology (Ward 2001, 2006) are also strongly supported as monophyletic with genetic data (Chomicki *et al.* 2015), providing a reliable phylogenetic foundation for the taxonomic work presented here.

Materials and methods

Specimens were examined in the following collections:

AFRC AfriBugs Collection, Pretoria, South Africa
AMNH American Museum of Natural History, New York, NY, USA
ANIC Australian National Insect Collection, CSIRO, Canberra, Australia
ASIC Andreas Schulz Insect Collection, Leichlingen, Germany
BMNH Natural History Museum, London, U.K.
CASC California Academy of Sciences, San Francisco, CA, USA
CMNH Carnegie Museum of Natural History, Pittsburgh, PA, USA
CPDC Jacques Delabie Collection, CEPEC/CEPLAC, Itabuna, Bahia, Brazil
CUIC Cornell University Insect Collection, Ithaca, NY, USA
DZUP Coleção Entomológica Pe. Jesus Santiago Moure, Departamento de Zoologia da Universidade Federal do Paraná, Curitiba, Paraná, Brazil
FHGC Francisco Hita Garcia Collection, Biodiversity and Biocomplexity Unit, Okinawa Institute of Science and Technology, Okinawa Prefecture, Japan
FSCA Florida State Collection of Arthropods, Gainesville, Florida, United States
HZIC Herbert Zettel Collection, Vienna, Austria
IEGG Istituto di Entomologia "Guido Grandi", Università di Bologna, Bologna, Italy
KUBC Faculty of Forestry, Kasetsart University, Bangkok, Thailand
KUEC Institute of Tropical Agriculture, Kyushu University, Fukuoka, Japan
KUES Seiki Yamane Collection, Kagoshima University, Kagoshima, Japan
LACM Natural History Museum of Los Angeles County, Los Angeles, CA, USA
MCZC Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA
MHNC Musée d'Histoire Naturelle, La Chaux-de-Fonds, Switzerland
MHNG Muséum d'Histoire Naturelle, Geneva, Switzerland
MNHN Muséum National d'Histoire Naturelle, Paris, France
MRAC Musée Royal de l'Afrique Centrale, Tervuren, Belgium
MSNG Museo Civico de Historia Natural "Giacomo Doria", Genoa, Italy [=MCSN]
MZLU Museum of Zoology, Lund University, Lund, Sweden
NHMB Naturhistorisches Museum, Basel, Switzerland
NHMW Naturhistorisches Museum, Vienna, Austria
NMKE National Museums of Kenya, Nairobi, Kenya
NMWN National Museum of Namibia, Windhoek, Namibia
OXUM Hope Entomological Collections, University Museum, Oxford, UK
PSWC P.S. Ward Collection, University of California at Davis, CA, USA
SAMC Iziko South African Museum, Cape Town, South Africa
STDC Shawn T. Dash Collection, Hampton University, Hampton, VA, USA
UASK Schmalhausen Institute of Zoology, National Academy of Sciences of Ukraine, Kiev, Ukraine
UCDC Bohart Museum of Entomology, University of California at Davis, CA, USA
UMSC Institute for Tropical Biology and Conservation, Universiti Malaysia Sabah, Kota Kinabalu, Malaysia
USNM National Museum of Natural History, Washington, DC, USA
ZMAS Zoological Institute, Russian Academy of Science, St. Petersburg, Russia
ZMHB Museum für Naturkunde, Berlin, Germany (formerly Zoologisches Museum, Museum für Naturkunde der Humboldt-Universität)
ZMUH Zoologisches Institut und Zoologisches Museum der Universität Hamburg, Hamburg, Germany (referenced but no relevant material found)

The following measurements, indices, and setal counts were employed (for further details, see Ward 2001, 2006). All linear measurements were taken in millimeters, and are given here to two decimal places.

HW Maximum head width, including eyes.

HL Head length, taken along midline, from the posterior margin of the head to the anterior extremity of the clypeus (concavities at either end do not reduce the measurement, i.e., in such cases measurement is taken from the midpoint of a line drawn across the anterior or posterior margin of the head capsule).

EL Eye length, measured in same plane of view as HL.

MFC Minimum distance between the margins of the frontal carinae, posterior to their fusion with, or approximation to, the antennal sclerites.

SL Scape length, excluding radicle.

FL Length of profemur, measured along its long axis in posterior view.

FW Width of profemur, measured in same view as FL and at right angles to it.

PL Length of petiole in lateral view from lateral flanges of the anterior peduncle to the posterior margin of petiole.

PH Maximum height of petiole, measured in lateral view, orthogonal to PL, and excluding protruding teeth or lobes at anteroventral or posteroventral extremities of the petiole.

DPW Maximum width of petiole, measured in dorsal view.

PPW Maximum width of postpetiole, measured in dorsal view.

LHT Length of metatibia, excluding proximomedial condyle (Ward 2001: fig. 5).

CI Cephalic index: HW/HL.

FCI Frontal carina index: MFC/HW.

REL Relative eye length: EL/HL.

REL2 Relative eye length, using HW: EL/HW.

SI Scape index: SL/HW.

SI2 Scape index, using HL: SL/HL.

SI3 Scape index, using EL: SL/EL.

FI Profemur index: FW/FL.

PLI Petiole length index: PH/PL.

PWI Petiole width index: DPW/PL

CSC Cephalic setal count: number of standing hairs (i.e., those forming an angle of 45º or more with cuticular surface) visible on the posterior half of the head, as seen in lateral and posterior views.

MSC Mesosomal setal count: number of standing hairs visible in profile (lateral view) on the mesosoma dorsum.

HTC Metatibial setal count: number of standing hairs visible in outline on the outer (extensor) surface of the metatibia.

MTC Mesotibial setal count: number of standing hairs visible in outline on the outer (extensor) surface of the mesotibia.

Setal counts exclude very short hairs, i.e., those less than about 0.04 mm long. The setal count is necessarily approximate in species, such as *T. mocquerysi* (André) and *T. tessmanni* (Stitz), where there is an insensible gradation between standing pilosity and uplifted (suberect or subdecumbent) pubescence. Terms for inclination of pilosity follow Wilson (1955: 23). Sculptural descriptors are taken from Harris (1979). Assessment of integument sculpture was made under soft (diffuse) illumination.

Species accounts are arranged alphabetically by species group, and then by species. The "synonymy" under each species is divided into two parts. The first part lists all available names that are equivalent to the valid name, citing the original combination, original description, type specimen(s), type locality, collector, location of types, and reference to any previously published synonymy. A statement that type specimens were "examined" means that they were examined physically by the author. Many of the relevant types have also been imaged and placed on AntWeb (https://www.antweb.org), thanks to the efforts of Brian Fisher and collaborators, and when this is the case the imaged specimens are cited by their specimen code (unique specimen identifier). Any unavailable (infrasubspecific) names that pertain to the species under consideration are listed at the end of the first part. The second part of the

synonymy documents the history of subsequent name usage (changes in status, rank or combination), descriptions of additional castes or life stages, and references to biology or phylogeny. In this second section the history of each available name is listed separately, for greater clarity.

The term "Afrotropical region" is here used in the broad sense (Kirk-Spriggs & Sinclair 2017), to include the continent of Africa south of the Sahara Desert, the southern tip of the Arabian Peninsula, and Madagascar and adjacent islands. The expression "DR Congo" is used as shorthand for the Democratic Republic of Congo.

The specimen records under "Material Examined" are a summary of unique locality-by-collector combinations, sorted alphabetically by country, first administrative division, locality name, collector, and (if given) elevation. The abbreviation "c.u." signifies collector unknown. These specimen records are the basis of the distribution maps (Figures 35–46), which were generated with SimpleMappr (https://www.simplemappr.net). Specimen records without coordinates were georeferenced using Google Earth, GEOnet Names Server (https://geonames.nga.mil/gns/html/), and the following literature sources: Arnold (1954), Balogh *et al.* (1965), Baum (1903), Benson *et al.* (1933), Bottego (1895), Bouvier (1922), Chamberlin (1927), Chapin (1954), Davis & Misonne (1964), Delachaux & Thiébaud (1934), Donisthorpe (1945), Dugmore (1910), Eltringham (1918), Evans & Fletcher (1952), Friedmann & Williams (1969), Hocking (1970), Kizungu (2006), Lamotte *et al.* (2003), Loveridge (1957), Martin *et al.* (1909), Mason & Rozkosny (2015), Molyneux (1903), O'Leary (2003), Penzig (1895), Peters (1956), Renaut & Owen (2005), Room (1971), Tessmann (1913), Wheeler (1922b), Wittmer (1970), and Young (1917). Geolocation of some Ed Ross collection sites was made possible by consulting his field notes and annotated maps in the archives of the California Academy of Sciences. Most institutions in which specimens were examined have not yet adopted the use of unique specimen identifiers, so these are not cited in the main text of the paper, except when referencing type material, imaged specimens, or other material of special interest.

Results

List of Afrotropical *Tetraponera*

This list includes valid names (in bold) and synonyms, the known distribution of each species, and the castes examined in this study (w = worker; q =queen; m= male).

***allaborans*-group: African species**

clypeata (Emery 1886: 361); South Africa [w, q, m]
= *braunsi* (Forel 1913: 112) **syn**. **nov**.
= *clypeata braunsi equidentata* (Arnold 1916: 184); unavailable name.
continua (Forel 1907: 138); Ethiopia, Niger, Senegal, The Gambia [w, m]
= *claveaui* (Santschi 1913: 304) **syn**. **nov**.
***cortina* sp. nov.**; Central African Republic, DR Congo, Gabon [w, q, m]
***dispar* sp. nov.**; Republic of Congo [w]
emeryi (Forel 1911a: 367); Eswatini, South Africa, Zimbabwe [w, q, m]
= *braunsi durbanensis* (Forel 1914: 218) **syn**. **nov**.
***exactor* sp. nov.**; South Africa [q]
***furtiva* sp. nov.**; South Africa [w, ergatoid q?]
gerdae (Stitz 1911: 381); Eritrea, Kenya, Tanzania, Zimbabwe [w, q, m]
liengmei (Forel 1894: 88); Mozambique, Namibia, South Africa, Zimbabwe [w, q]
mayri (Forel 1901: 53); Cameroon [q]
***pedana* sp. nov.**; Central African Republic, Kenya, Uganda [w, m]
penzigi (Mayr 1907: 10); Ethiopia, Kenya, Tanzania, Uganda [w, q, m]
= *scotti* Donisthorpe 1931: 498 **syn**. **nov**.
= *penzigi praestigiatrix* Santschi 1937a: 50 **syn**. **nov**.
= *zavattarii* (Menozzi 1939: 99) **syn**. **nov**.
***pumila* sp. nov.**; Ghana to Kenya, south to Zimbabwe [w, q]

tessmanni (Stitz 1910: 131); Ghana to DR Congo [w, q, m]
= *tessmanni castanea* (Wheeler 1922a: 112) (synonymy by Brown 1950: 248)

***allaborans*-group: Malagasy species** (excluding undescribed species to be treated later)

diana (Santschi 1911b: 119); Madagascar [w, q]
exasciata (Forel 1892: 261); Madagascar [w, q, m]
fictrix (Forel 1897: 198); Madagascar [w, q, m]
hysterica (Forel 1892: 258); Madagascar [w, q, m]
= *hysterica inflata* (Emery 1899a: 273) **syn. nov.**
longula (Emery 1895a: 340); Madagascar [w, q, m]
= *sahlbergii deplanata* (Forel 1904: 375) **syn. nov.**
mandibularis (Emery 1895a: 340); Madagascar [w, q, m]
= *flexuosa* (Santschi 1911b: 120) **syn. nov.**
morondaviensis (Forel 1891: 206); Madagascar [w, q, m]
= *hysterica dimidiata* (Forel 1895: 487) **syn. nov.**
= *arrogans* (Santschi 1911b: 117) **syn. nov.**
= *demens* (Santschi 1911d: 282) **syn. nov.**
perlonga Santschi 1928: 60; Madagascar [w, q, m]
rakotonis (Forel 1891: 206); Madagascar [w, q, m]
sahlbergii (Forel 1887: 386); Madagascar [w, q, m]
= *sahlbergii spuria* (Forel 1897: 199) **syn. nov.**
= *plicatidens* (Santschi 1926: 26) **syn. nov.**

***ambigua*-group**

ambigua (Emery 1895b: 23); Senegal to Arabian Peninsula, south to South Africa [w, q, m]
= *erythraea* (Emery 1895b: 23) (synonymy by Ward 2006: 123; here reconfirmed) **syn. rev.**
= *bifoveolata* (Mayr 1895: 146) (synonymy by Ward 2006: 123; here reconfirmed) **syn. rev.**
= *bifoveolata maculifrons* (Santschi 1912: 162) (synonymy by Ward 2006: 123)
= *ambigua rhodesiana* (Forel 1913: 112) (synonymy by Ward 2006: 123)
= *bifoveolata syriaca* (Wheeler & Mann 1916: 167) (synonymy by Ward 2006: 123)
= *encephala* (Santschi 1919: 84) (synonymy by Ward 2006: 123)
= *bifoveolata maculifrons umbrata* (Santschi 1929: 98); unavailable name
= *angolensis* Santschi 1930: 61 (synonymy by Ward 2006: 123; here reconfirmed) **syn. rev.**
= *ambigua occidentalis* Menozzi 1934: 154 (synonymy by Ward 2006: 123)
ophthalmica (Emery 1912: 98); west and central Africa, east to Kenya [w, q, m]
= *unidens* Santschi 1928: 60 (synonymy by Ward 2006: 126; here reconfirmed) **syn. rev.**
= *ophthalmica tenebrosa* Santschi 1928: 61 (synonymy by Ward 2006: 126)
= *nasuta* Bernard 1953: 222 (synonymy by Ward 2006: 126)
parops Ward 2006: 126; Mozambique, Kenya, Somalia, Tanzania, [w, q, m]
phragmotica Ward 2006: 127; Madagascar [w, q]

***grandidieri*-group**

elegans **sp. nov.**; Madagascar [w]
grandidieri (Forel 1891: 203); Madagascar [w, q, m]
= *grandidieri hildebrandti* (Forel 1891: 203) (synonymy by Ward 2009: 287)
hespera Ward 2009: 295; Madagascar [w, q, m]
hirsuta Ward 2009: 296; Madagascar [w]
inermis Ward 2009: 297; Madagascar [w, q, m]
manangotra Ward 2009: 298; Madagascar [w, q, m]

merita Ward 2009: 299; Madagascar [w, q, m]
variegata (Forel 1895: 487); Madagascar [w, q]

***natalensis*-group**

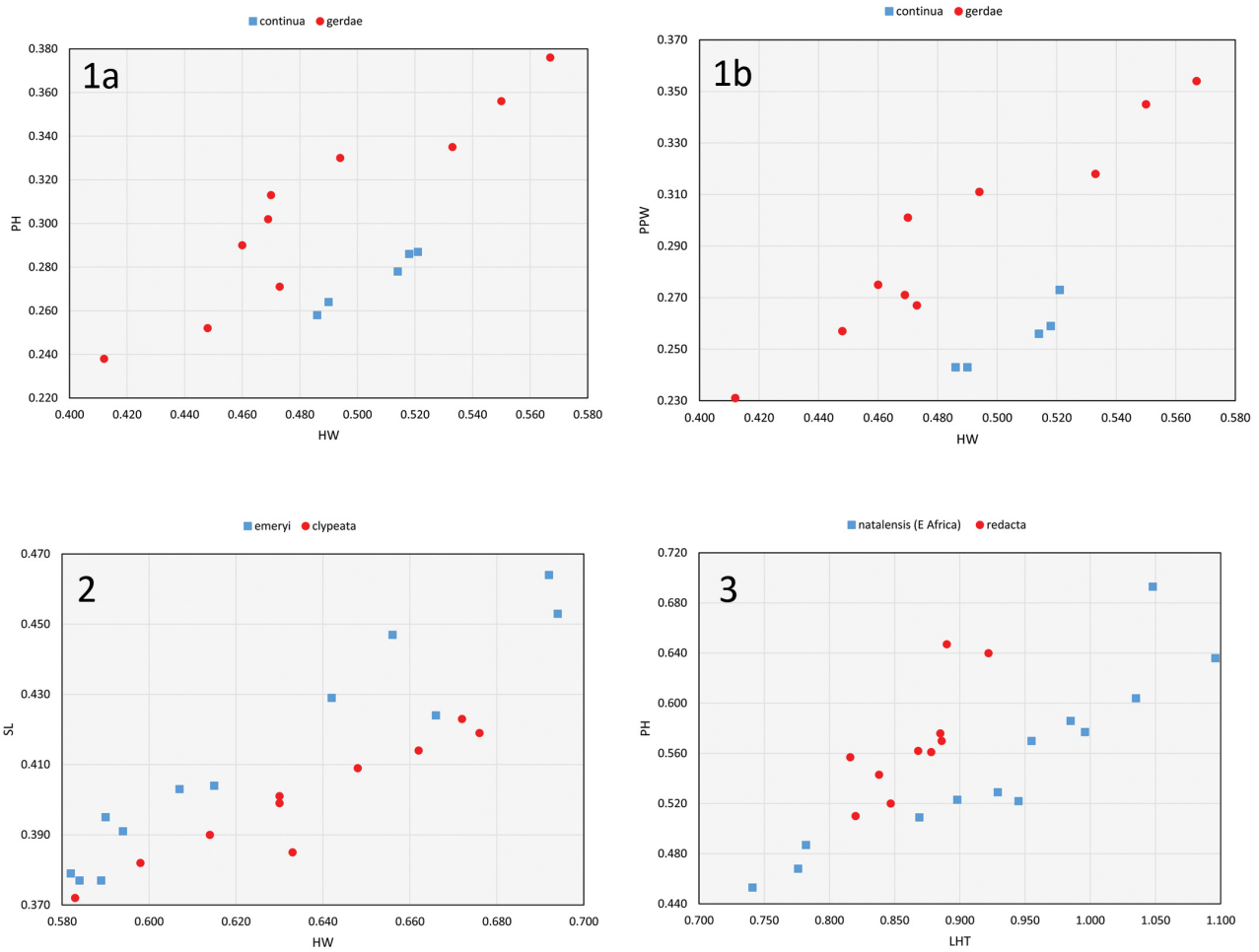
andrei (Mayr 1895: 144); Mozambique, Kenya, Tanzania [w, q, m]
anthracina (Santschi 1910: 355); Cameroon to DR Congo, east to Uganda [w, q, m]
= *triangularis* (Stitz 1910: 131) **syn**. **nov**.
= *poultoni* Donisthorpe 1931: 497 **syn**. **nov**.
caffra (Santschi 1914d: 15); Mozambique, South Africa, Zimbabwe [w, q, m]
insularis **sp. nov.**; Madagascar [w]
kosi **sp. nov.**; South Africa [w, q, m]
mocquerysi (André 1890: 319); The Gambia to Ethiopia, south to Angola and Tanzania [w, q, m]
= *emacerata* (Santschi 1911a: 352) **syn**. **nov**.
= *emacerata oberbecki* (Forel 1911b: 275) **syn**. **nov**.
= *mocquerysi elongata* (Stitz 1911: 378) **syn**. **nov**.
= *triangularis illota* (Santschi 1914c: 334) **syn**. **nov**.
= *emacerata odiosa* (Forel 1916: 403) **syn**. **nov**.
= *lemoulti* (Santschi 1920b: 375) **syn**. **nov**.
= *mocquerysi lepida* Wheeler 1922a: 106 **syn**. **nov**.
= *mocquerysi biozellata* (Karavaiev 1931: 42) **syn**. **nov**.
= *monardi* (Santschi 1937b: 218) **syn**. **nov**.
= *ledouxi* Terron 1969: 629 **syn**. **nov**.
natalensis (F. Smith 1858: 160); Kenya to South Africa, Angola, eastern DR Congo [w, q, m]
= *capensis* (F. Smith 1858: 160) **syn**. **nov**.
= *natalensis obscurata* (Emery 1895b: 22) **syn**. **nov**.
= *mocquerysi lutea* (Stitz 1911: 381) **syn**. **nov.**
= *prelli* (Forel 1911a: 365) **syn**. **nov.**
= *natalensis usambarensis* (Forel 1911a: 367) **syn**. **nov**.
= *natalensis cuitensis* (Forel 1911a: 368) **syn**. **nov**.
= *natalensis cuitensis bulawayana* (Forel 1913: 112); unavailable name
= *natalensis cuitensis quaniama* (Santschi 1937b: 218); unavailable name.
= *angusta* (Arnold 1949: 266) **syn**. **nov**.
redacta **sp. nov.**; Kenya [w, q, m]
schulthessi (Santschi 1915: 249); Kenya to South Africa [w, q, m]
setosa **sp. nov.**; Uganda [w, m]

***rufonigra*-group**

aethiops F. Smith 1877: 71; Nigeria to western Uganda [w, q, m]
= *spininoda* (André 1892: 51) (synonymy by Emery 1912: 97)
latifrons (Emery 1912: 98); Nigeria to DR Congo [w, q, m]

Key to species of Afrotropical *Tetraponera* based on the worker and queen castes

This key is based predominantly on workers, but an attempt has been made to include identifying features of queens as well. Some caution should be exercised, however, because queen sample sizes are smaller than those of workers and the limits of intraspecific variation are less well understood. In addition, queens are unknown for six of the 38 species treated in the key (*T. continua*, *T. dispar*, *T. elegans*, *T. insularis*, *T. pedana*, *T. setosa*).



FIGURES 1–3. Bivariate plots of various metric measurements in *Tetraponera* workers. 1a, petiole height (PH) against head width (HW) in *T. continua* (n = 5) and *T. gerdae* (n = 10); 1b, postpetiole width (PPW) against head width (HW), for the same individuals; 2, scape length (SL) against head width (HW) in *T. emeryi* (n = 12) and *T. clypeata* (n = 10); 3, petiole height (PH) against length of metatibia (LHT) in *T. natalensis* from Kenya and Tanzania (n = 13) and *T. redacta* (coastal Kenya) (n = 10).

1 Worker with well separated frontal carinae (MFC 0.39–0.71, FCI 0.21–0.35), three distinct ocelli, and a prominent, recurved anteroventral tooth on the petiole (Figs 33, 34); large species (worker HW 1.57–2.20, queen HW 2.30–2.50); west and central Africa (*rufonigra*-group) 2

\- Worker with more closely adjacent frontal carinae (MFC 0.06–0.24, FCI 0.08–0.25); worker with 0–2 ocelli and/or lacking prominent anteroventral petiolar tooth (usually both conditions apply); generally smaller species (worker HW 0.42–1.68, queen HW 0.47–1.61); widespread 3

2 Frontal carinae widely separated, their minimum distance greater than one quarter of head width (worker FCI 0.28–0.35, queen FCI 0.36–0.37) (Fig. 34a); standing pilosity relatively common, conspicuous on the pronotum and propodeum (worker MSC 27–45, queen MSC 45–50) (Fig. 34b); mandibles smooth and shiny, with scattered fine punctures; Nigeria to DR Congo . . . . . *latifrons*

\- Frontal carinae less widely separated, their minimum distance equal to about one quarter of head width or less (worker FCI 0.21–0.25, queen FCI 0.25–0.26) (Fig. 33a); standing pilosity less common, sparse on the pronotum and absent from the propodeum (worker MSC 1–7, queen MSC 10–14) (Fig. 33b); mandibles longitudinally rugulose and subopaque; Nigeria to DR Congo and western Uganda . . . . . *aethiops*

3 Worker mesonotum strongly transverse, 2–4× wider than long, with a rounded anterior margin and straight posterior margin, appearing more or less semicircular in dorsal view; pronotum with sharp lateral margination, extending in attenuated form to the lateral borders of the propodeum and petiole; head and mesosoma usually with dense punctulate-coriarious sculpture which imparts a matte appearance (punctulate with shiny interspaces in one Ugandan species); posteroventral margin of petiole with a median notch (*natalensis* group) 4

\- Worker mesonotum about as long as wide and appearing ovoid or sub-rectangular in dorsal view; pronotum, propodeum and petiole usually with soft-edged lateral margins, if sharply marginate (a few Madagascar species) then head and mesosoma shiny, not matte; posteroventral margin of petiole lacking median notch 13

4 Medium-sized species (worker HW 1.27–1.54, queen unknown), blackish brown in color with strongly contrasting luteous

legs, except for brown band on metafemur (Fig. 26b); standing pilosity very sparse (CSC 0–2, MSC 0–2), lacking on petiole; postpetiole and abdominal tergite 4 each with 0–2 standing hairs; endemic to Madagascar . . . . . *insularis*

- Variable in color and size but without the above color pattern; standing pilosity varying from sparse to abundant, but *if* lacking on petiole and very sparse on postpetiole and gaster, *then* body size smaller (worker HW 1.03–1.15, queen HW 1.22–1.26); occurring on African mainland 5

5 Body-dark brownish-black *and* petiole as sharply marginate as the lateral margin of pronotum; standing pilosity sparse (worker CSC 0–2, worker MSC 0–4, queen CSC 2, queen MSC 0–6), the few erect setae relatively long, and distinct from the inconspicuous, short pubescence; worker: eyes large, about one half head length or more (REL 0.49–0.56) 6

- Color variable but *if* dark brownish-black *then* petiole more soft-margined than pronotum, and pilosity common (worker CSC 8–60, worker MSC 20–120, queen CSC 7–16, queen MSC 12–75) and blending into a background of conspicuous suberect and subdecumbent pubescence; worker: eyes generally smaller, usually less than one half head length (REL 0.40–0.52) 7

6 Smaller species (worker HW 1.03–1.15, queen HW 1.22–1.26, worker LHT 0.74–0.85, queen LHT 0.88–0.94); petiole, postpetiole, and abdominal tergite 4 with 0, 0, and 0–2 standing hairs, respectively; Mozambique, Tanzania, Kenya . . . . . *andrei*

- Larger species (worker HW 1.40–1.54, queen HW 1.45–1.49, worker LHT 1.08–1.21, queen LHT 1.14–1.22); petiole, postpetiole, and abdominal tergite 4 with 2–4, 2–6, and approximately 4–20 standing hairs, respectively; central Africa (Cameroon to Uganda) . . . . . *anthracina*

7 Dark brown to brownish-black, with lighter appendages; petiole with weak lateral margination, in dorsal view obovate, with rounded sides (Fig. 27b); worker petiole in profile with similar anterodorsal and posterodorsal slopes, or with less strongly inclined anterodorsal slope (Fig. 27b); standing pilosity conspicuous (worker CSC 8–60, worker MSC 21–120, worker HTC+MTC 0–50; queen CSC 7–16, queen MSC 12–75, queen HTC+MTC 2–42), often grading into an underlying suberect to decumbent pubescence 8

- Color variable, usually yellow- to orange-brown, but *if* medium to dark brown *then* petiole with better defined lateral margination, in dorsal view narrowly obovate to subtrapezoidal, sides more or less straight, and diverging posteriorly (as in Fig. 25b); worker petiole variable in profile, but often with steep anterodorsal face and more shallowly inclined posterodorsal face (Fig. 28b); standing pilosity usually less common (worker CSC 2–18, worker MSC 3–28, worker HTC+MTC 0–10, queen CSC 2–8, queen MSC 8–24, queen HTC+MTC 0–4) and more distinct from underlying pubescence 9

8 Head and mesosoma with scattered punctures, densest on anterior two thirds of head, the interspaces mostly smooth and shiny, or with weak reticulation; anterior clypeal margin lacking denticles, at most feebly crenulate; body very densely pilose (worker CSC ca. 40–60, worker MSC ca. 70–120; queen unknown); Uganda . . . . . *setosa*

- Head and mesosoma densely punctulate-coriarious, imparting a matte appearance to the integument (lacking shiny interspaces); anterior clypeal margin usually with several denticles, sometimes weakly defined; standing pilosity conspicuous but less abundant (worker CSC 8–34, worker MSC 21–100, queen CSC 7–16, queen MSC 12–75); widespread, west Africa to Ethiopia, south to Angola and Tanzania . . . . . *mocquerysi*

9 Scapes short (worker SI 0.45–0.49, queen SI 0.46–0.49) and profemur robust (worker FI 0.45–0.52, queen FI 0.49–0.53; worker FW/PL 0.49-0.56, queen FW/PL 0.44-0.51), such that worker FW/SL 0.68-0.77 and queen FW/SL 0.76-0.84; small species (worker HW 0.98–1.08, queen HW 1.10–1.16) 10

- Scapes longer (worker SI 0.50–0.55, queen SI 0.49–0.54) and profemur more slender (worker FI 0.38–0.47, queen FI 0.43–0.49; worker FW/PL 0.40-0.48, queen FW/PL 0.39-0.43) such that worker FW/SL 0.53-0.66 and queen FW/SL 0.62-0.73; size variable (worker HW 0.92-1.68, queen HW 1.00-1.61) 11

10 Body light orange-brown, with variable infuscation around the ocelli and at the tip of the gaster (Fig. 25); petiole more robust, appearing broader in dorsal view (worker DPW/HW 0.45-0.49, queen DPW/HW 0.53-0.56); South Africa, Mozambique, Zimbabwe . . . . . *caffra*

- Body predominantly medium brown, with lighter yellowish-brown appendages (Fig. 32) and sometimes lighter maculation on the gaster; petiole more slender, appearing slightly narrower in dorsal view (worker DPW/HW 0.39-0.44, queen DPW/HW 0.48-0.51); South Africa . . . . . *kosi*

11 Larger species (worker HW 1.38–1.68, queen HW 1.46–1.61; worker LHT 1.14–1.36, queen LHT 1.24–1.40), with smaller eyes relative to head width (worker REL2 0.43–0.49, queen REL2 0.46–0.49); Kenya to South Africa . . . . . *schulthessi*

- Smaller species (worker HW 0.92–1.29, queen HW 1.00–1.29; worker LHT 0.74–1.10, queen LHT 0.76–1.01), with larger eyes relative to head width (worker REL2 0.48–0.56, queen REL2 0.51–0.58) 12

12 Worker mesonotum essentially indistinguishable from basal face of propodeum, not bounded posteriorly by a distinct transverse impression; worker petiole relatively high and short (PLI 0.67–0.80, PH/HL 0.43–0.50, PH/LHT 0.61–0.73) (Fig. 3); queen petiole short (PL/HW 0.84–0.87); coastal Kenya . . . . . *redacta*

- Worker mesonotum usually distinguishable from basal face of propodeum, and separated from it by a transverse impression, albeit sometimes feeble; worker petiole height and length variable, but in east Africa (Tanzania, Kenya), close to the range of *T. redacta*, petiole tending to be longer and of lower height (PLI 0.64–0.70, PH/HL 0.39–0.45, PH/LHT 0.55–0.66) (Fig. 3); in same region queen petiole tending to be longer (PL/HW 0.85–0.93); Kenya, excluding coastal region, to South Africa, Angola, and eastern DR Congo . . . . . *natalensis*

13 Appendages long and slender: scape length three-quarters or more of head width in workers (SI 0.72–0.90), slightly less in queens (SI 0.67–0.76), and length of metatibia subequal to, or slightly less than, that of head (worker LHT/HL 0.85–1.12, queen LHT/HL 0.83–0.98); worker with three distinct ocelli; endemic to Madagascar (*grandidieri* group) 14

- Appendages shorter and more robust: scape length about two-thirds or less of head width (worker SI 0.40–0.70, queen SI 0.39–0.68) and length of metatibia distinctly less than that of head (worker LHT/HL 0.54–0.82, queen LHT/HL 0.48–0.69); worker with two ocelli or (more commonly) none; found in both Madagascar and mainland Africa 22

14 Basal margin of mandible with a prominent tooth, in addition to four teeth on the masticatory margin (Ward 2009, fig. 1); an-

terior clypeal margin deflected ventrally; eastern and northern Madagascar . . . . . *merita*

- Basal margin of mandible lacking tooth, masticatory margin with four teeth (Ward 2009, fig. 2); anterior clypeal margin directed forward, not deflected ventrally 15

15 Petiole broad (worker PWI 0.61–0.65, worker DPW/HW 0.50–0.53; queen PWI ~0.66, queen DPW/HW ~0.55), subtriangular in dorsal view, and with a relatively short, thick anterior peduncle; workers larger, HW1.48–1.58, LHT 1.64–1.76; eastern Madagascar . . . . . *manangotra*

- Petiole more slender (worker PWI 0.38–0.53, worker DPW/HW 0.30–0.46; queen PWI 0.42–0.65, queen DPW/HW 0.37–0.50), obovate in dorsal view, and with a thin, elongate anterior peduncle; workers smaller, HW 0.95–1.44, LHT 1.05–1.59 16

16 Petiole very slender (worker PLI 0.38–0.43; Fig. 22b), petiole length equal to, or exceeding, head width (worker PL/HW 1.01–1.05); legs relatively long (worker LHT/HW 1.22–1.29); queen unknown but expected to have comparably long petiole and legs; eastern Madagascar . . . . . *elegans*

- Petiole less elongate (worker PLI 0.49–0.59, queen PLI 0.52–0.60), petiole length shorter than head width (worker PL/HW 0.70–0.85, queen PL/HW 0.77–0.88); legs shorter (worker LHT/HW 1.02–1.22, queen LHT/HW 1.00–1.13). 17

17 Scape with conspicuous suberect and subdecumbent hairs; body tricolored: metasoma, appendages, and ventral margin of mesosoma orange, most of mesosoma reddish-brown, and head dark brownish black; endemic to Manongarivo Massif, Madagascar . . . . . *hirsuta*

- Most hairs on scape appressed or decumbent, and generally inconspicuous, except those at the apex; body color variable but usually without preceding tricolor pattern; widespread 18

18 Metanotal spiracle of worker not protruding above the profile of the mesosoma, as seen in lateral view (Ward 2009, fig. 5); head broad (worker CI 0.88–0.97, queen CI 0.87–0.89); head and mesosoma reddish-brown, metasoma and appendages paler; eastern Madagascar . . . . . *inermis*

- Metanotal spiracle of worker more or less protruding above the profile of the mesosoma, as seen in lateral view (Ward 2009, fig. 6); head usually more elongate (worker CI 0.77–0.90, queen CI 0.79–0.86); color variable 19

19 Worker: dorsum of propodeum laterally compressed, the propodeum appearing subtriangular in posterior view; body and legs concolorous orange-brown; relatively large (worker HW 1.14–1.36, queen HW ~1.36); Ankarana massif, northern Madagascar . . . . . *hespera* (in part)

- Worker: dorsum of propodeum more broadly rounded, the propodeum appearing domeshaped in posterior view; color and size variable, but *if* body and legs concolorous orange-brown *then* smaller in size (worker HW 1.01–1.12, queen HW 1.01–1.19) 20

20 Legs uniformly light orange-brown, femora lacking conspicuous black banding; body usually bicolored, such that dark head contrasts with lighter orange-brown mesosoma and metasoma, less commonly unicolorous orange; eastern and northern Madagascar . . . . . *grandidieri*

- Legs light orange-brown, with contrasting black bands on the distal portions of the mesofemur and metafemur; body concolorous or bicolored (in latter case both head and gaster are dark brownish-black) 21

21 Body concolorous yellow brown or orange brown; northwestern Madagascar . . . . . *hespera* (in part)

- Body bicolored, head and gaster dark brown and contrasting with the lighter mesosoma; eastern Madagascar . . . . . *variegata*

22 Long axis of compound eye directed anteromedially (e.g., Ward 2006, fig. 4); upper half of mesosternum sparsely pubescent; workers dimorphic, with a discrete soldier subcaste (*ambigua*-group) 23

- Long axis of compound eye directed anteriorly or anterolaterally; mesosternum densely pubescent almost throughout; workers monomorphic (*allaborans*-group) 26

23 Smaller species (worker HW 0.51–0.71, queen HW 0.50–0.69) with elongate head (worker CI 0.66–0.79, queen CI 0.52–0.67); masticatory margin of mandible with four teeth; African mainland and Arabian Peninsula 24

- Larger species (worker HW 0.80–0.92, queen HW 1.03) with broader head (worker CI 0.89–0.92, queen CI 0.74); masticatory margin of mandible with six teeth; endemic to Madagascar . . . . . *phragmotica*

24 Standing pilosity common on mesosoma dorsum (worker MSC 12–44, queen MSC 20–56); larger species (worker HW 0.61–0.71, queen HW 0.62–0.69), with disproportionately smaller eyes (worker REL2 0.54–0.60, queen REL2 0.59–0.64); Senegal to Arabian Peninsula, south to South Africa. . . . . *ambigua*

- Standing pilosity virtually absent from mesosoma dorsum in worker except for one pair of long setae on pronotum (worker MSC 2–3), and relatively sparse in queen (queen MSC 8–13); smaller species (worker HW 0.51–0.59, queen HW 0.50–0.60), with larger eyes (worker REL2 0.63–0.72, queen REL2 0.66–0.73). 25

25 Worker: standing pilosity common on posterior half of head, conspicuous in profile (CSC 12–22); queen: posterolateral corner of head with a linear patch of raised, roughened cuticle, flanking the ocellar triangle; petiole short and robust (worker PLI 0.54–0.61, worker PL/HL 0.46–0.50, queen PLI 0.59–0.64); east Africa (Somalia to Mozambique). . . . . *parops*

- Worker: standing pilosity sparse on posterior half of head (CSC 2–4); queen: posterolateral corner of head without a linear patch of raised, roughened cuticle; petiole usually more elongate (worker PLI 0.47–0.56, worker PL/HL 0.50–0.54, queen PLI 0.46–0.55); west and central Africa, east to Kenya . . . . . *ophthalmica*

26 Occurring on Madagascar and Comoros Islands . . . . . Malagasy *allaborans*-group (treated no further here)

- Occurring on African mainland 27

27 Worker frontal carinae more closely contiguous (worker FCI 0.08–0.14), minimum distance between them less than one quarter of scape length (worker MFC/SL 0.13–0.22); petiole elongate and slender (worker PLI 0.50–0.61, queen PLI 0.49–0.59; worker PWI 0.38–0.48, queen PWI 0.40–0.51); masticatory margin of mandible with 3 teeth; scape generally longer (worker SI 0.56–0.67; queen SI2 0.38–0.47) (Figs 4, 7–10) 28

- Worker frontal carinae more widely separated (worker FCI 0.13–0.24), minimum distance between them varying from one quarter to one half of scape length (worker MFC/SL 0.26–0.54); petiole relatively short and broad (worker PLI 0.72–1.21,

queen PLI 0.73–1.29; worker PWI 0.57–0.97, queen PWI 0.59–1.22); masticatory margin of mandible with 4-5 teeth; scape generally shorter (worker SI 0.41–0.58, queen SI2 0.28–0.37) (Figs 5, 6, 11–16) 32

28 Known only from queen caste and suspected of being a workerless social parasite; conspicuous standing pilosity on mesosoma (MSC 16) and petiole (Fig. 9b); small in size (HW 0.55, LHT 0.43); South Africa . . . . . *exactor*

- Workers and queens; standing pilosity sparse on mesosoma (worker MSC 0–2, queen MSC 0–6) and absent from petiole (Figs 4b, 7b, 8b, 10b); size variable, generally larger 29

29 Small (worker HL 0.66–0.67, worker LHT 0.43–0.44) with broad head (worker CI 0.77–0.78) and relatively large eyes (worker REL 0.35) (Fig. 7a); queen unknown but expected to be similar (HL ~0.75, LHT ~0.48, CI ~0.75, REL ~0.35); light orange-brown; Republic of Congo . . . . . *dispar*

- Larger (worker HL 0.74–0.99, worker LHT 0.48–0.64; queen HL 0.88–1.12, queen LHT 0.54–0.65) with more elongate head (worker CI 0.70–0.76, queen CI 0.67–0.72) and smaller eyes (worker REL 0.28–0.32, queen REL 0.27–0.31) (Figs 4a, 8a, 10a); color varying from yellowish-orange to dark brown; occurring in southern Africa (South Africa, Eswatini, Zimbabwe) 30

30 Worker: scape shorter (SI 0.56–0.62) and petiole shorter and broader (PWI 0.46–0.48, PL/HW 0.72–0.77); medium-brown with variably lighter mesonotum and appendages (Fig. 10); alate/dealate queen unknown, an apparent ergatoid with SI 0.56 and PL/HW 0.83; South Africa . . . . . *furtiva*

- Scape longer (worker SI 0.61–0.68; queen SI 0.57–0.66) and petiole more slender (worker PWI 0.38–0.46, worker PL/HW 0.79–0.94; queen PL/HW 0.92–1.03); uniformly yellowish-orange or dark brown 31

31 Yellowish-orange (Fig. 8); scape longer (worker SI 0.64–0.68; queen SI2 0.43–0.47) (Fig. 2); South Africa, Eswatini, Zimbabwe . . . . . *emeryi*

- Dark brown (Fig. 4); scape tending to be shorter (worker SI 0.61–0.64; queen SI2 0.38–0.42) (Fig. 2); South Africa . *clypeata*

32 Eyes very small (worker REL2 <0.32, queen REL2 ~0.32) and scape very short (worker SI <0.45, queen SI ~0.40); petiole broad (worker PWI ~0.90, queen PWI ~1.00), and furnished with a large, subrectangular subpetiolar process, rounded anteroventrally and posteroventrally (Fig. 16b); orange-brown to reddish-brown 33

- Eyes larger (worker REL2 0.33–0.48, queen REL2 0.35–0.53) and scape longer (worker SI 0.47–0.58, queen SI 0.45–0.60); petiole less broad (worker PWI 0.57–0.86, queen PWI 0.59–0.81), lacking a large subrectangular ventral process; brown to brownish-black 34

33 Queen (based on original description): 6.3 mm long, with elongate head (CI ~0.60) and tridentate median clypeal lobe; worker unknown but expected to be moderately large (HW ~0.75) with a dentate clypeal lobe and elongate head (CI ~0.70); see discussion in text; Cameroon . . . . . *mayri*

- Queen: 4–5 mm long, with broader head (CI 0.71–0.78) and convex, edentate median clypeal lobe; worker: small (HW 0.58–0.66) with moderately broad head (CI 0.76–0.84); median clypeal lobe convex, lacking teeth (Fig. 16a); obligate inhabitant of *Vitex*; Ghana to DR Congo . . . . . *tessmanni*

34 Worker with standing pilosity as follows: one to several pairs of setae on the frontal carinae, and usually one pair on the vertex and pronotum (CSC 0–2, MSC 0–2); worker propodeum and petiole laterally rounded, their dorsal surfaces appearing broadly convex in posterior view; queen of moderate size (HW 0.75–0.87, LHT 0.60–0.68) and with frontal carinae relatively close, the minimum distance between them less than one fifth of head width (queen FCI 0.15–0.18); Mozambique, Namibia, South Africa, Zimbabwe . . . . . *liengmei* (Forel)

- Worker with standing pilosity sparser, lacking on frontal carinae, vertex, and pronotum (CSC 0, MSC 0); worker propodeum and petiole laterally submarginate, and their dorsal surfaces appearing almost flat in posterior view; queen variable in size, usually smaller, but if approaching or exceeding the above size range, then frontal carinae more widely separated, the minimum distance between them more than one fifth of head width (queen FCI >0.20) 35

35 Anterior margin of clypeus with only a single pair of stout setae, directed anteroventrally (Fig. 15a); very small (worker HW 0.42–0.53, queen HW 0.47; worker LHT 0.30–0.38, queen LHT 0.37); Ghana to Kenya, south to Zimbabwe . . . . . *pumila*

- Anterior margin of clypeus with multiple setae, one pair directed anteriorly, and 4–6 setae directed anteroventrally; generally larger (worker HW 0.41–0.83, queen HW 0.47–0.94; worker LHT 0.36–0.72, queen LHT 0.40–0.90) 36

36 Head relatively broad (worker CI 0.78–0.86, queen CI 0.64–0.68) (Figs 13a, 14a); frontal carinae more widely separated relative to eye length, the minimum distance between them equal to, or exceeding, one half of eye length (worker MFC/EL 0.50–0.65, queen MFC/EL 0.55–0.64) 37

- Head more elongate (worker CI 0.61–0.73, queen CI 0.50–0.64) (Figs 5a, 6a, 11a); frontal carinae less widely separated relative to eye length, the minimum distance between them less than one half of eye length (worker MFC/EL 0.30–0.48, queen MFC/EL 0.37–0.44) 38

37 Upper third of head and most of mesosoma dorsum smooth and shiny, with scattered punctures (Fig. 13); legs shorter, worker LHT 0.37–0.47, worker LHT/HW 0.64–0.73 (queen unknown); Central African Republic, Uganda, Kenya . . . . . *pedana*

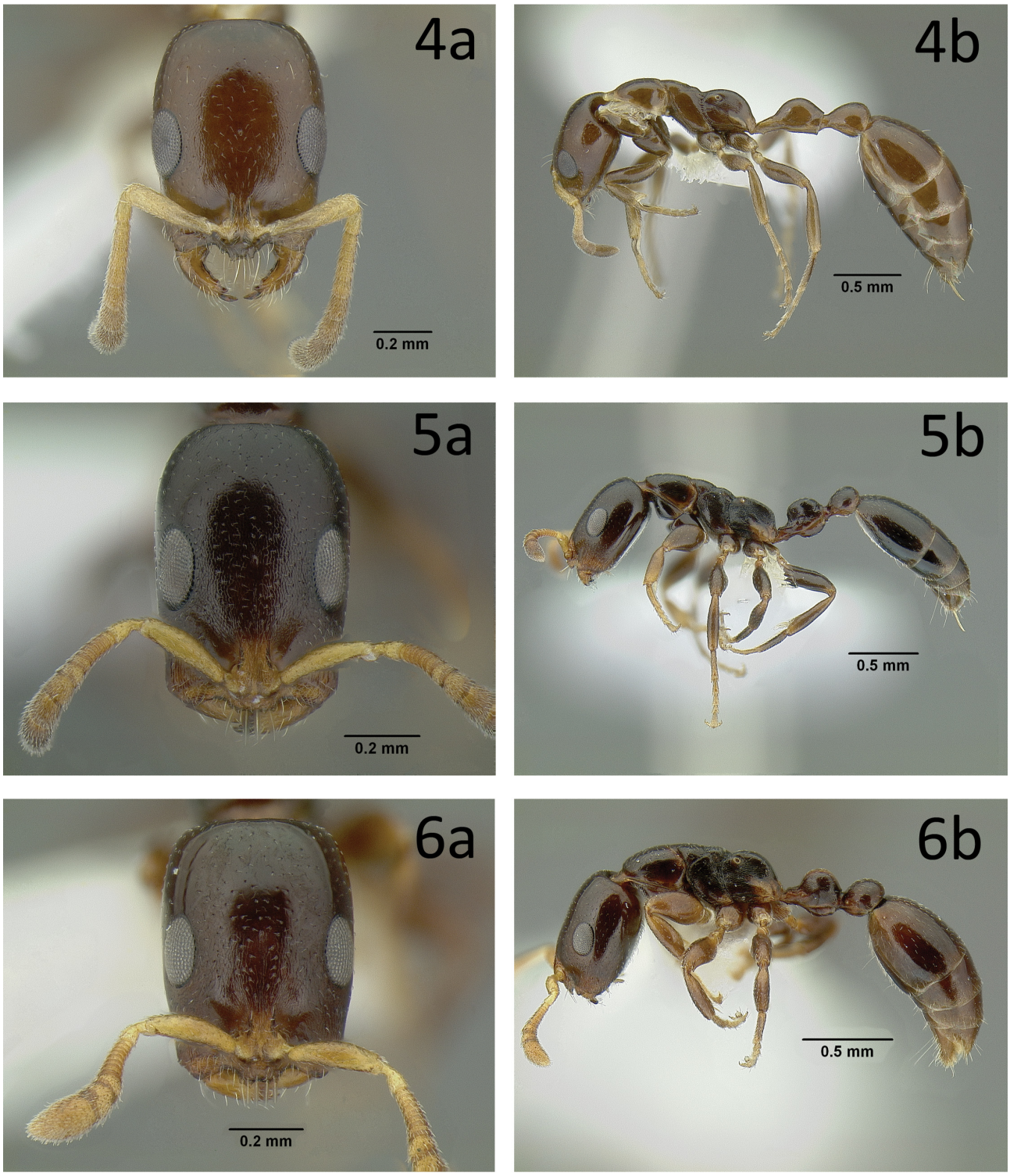
- Dorsum of head and mesosoma predominantly reticulate-coriarious and opaque (Fig. 14); legs longer, worker LHT 0.50–0.72, queen LHT 0.79–0.90; worker LHT/HW 0.77–0.88, queen LHT/HW 0.94–1.01); east Africa (Ethiopia to Tanzania) . . *penzigi* (Mayr) . . . . . .

38 Upper third of head smooth and shiny, with scattered punctures; frontal carinae more closely adjacent (worker FCI 0.12–0.15, queen FCI 0.17) (Fig. 6a); legs shorter (worker LHT/HW 0.73–0.78, queen LHT/HW 0.86); central Africa . . . . . *cortina*

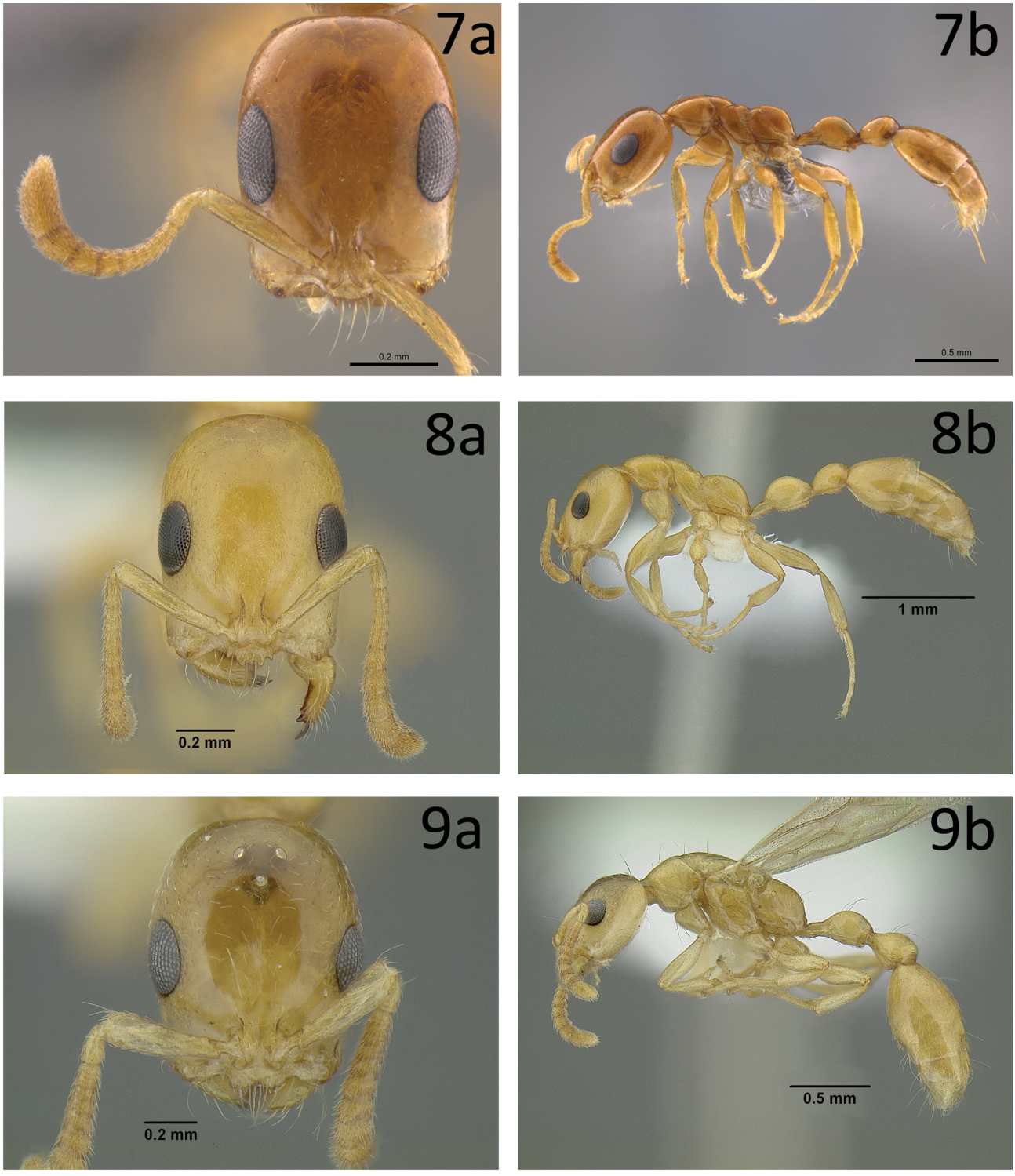
- Head sublucid, with scattered punctures on coriarious background sculpture; frontal carinae more widely separated separated (worker FCI 0.16–0.19, queen FCI 0.22–0.23) (Figs 5a, 11a); legs longer (worker LHT/HW 0.87–1.00, queen LHT/HW 0.99–1.01) 39

39 Petiole short, high and broad (worker PLI 0.82–0.93, queen PLI 0.73–0.78; worker PH/HW 0.56–0.67, queen PH/HW 0.72–0.78; worker DPW/HW 0.43–0.53, queen DPW/HW 0.61–0.64) (Fig. 11b); postpetiole relatively broad (worker PPW/HW 0.56–0.64, queen PPW/HW 0.77–0.81) (Fig. 1); Eritrea to Zimbabwe . . . . . *gerdae* (Stitz)

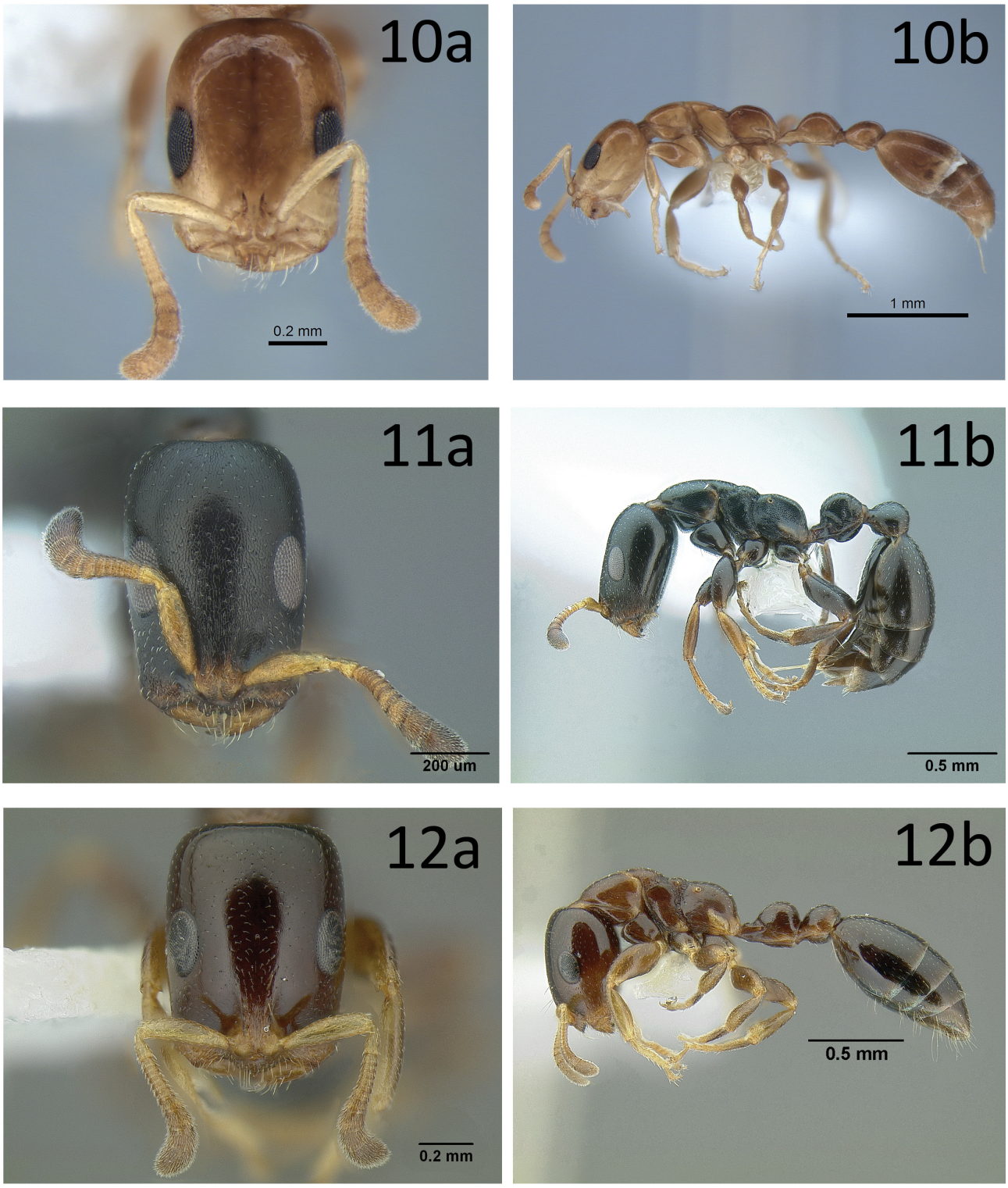
- Petiole slightly more elongate, lower, and narrower (worker PLI 0.72–0.82, PH/HW 0.53–0.55, DPW/HW 0.40–0.43) (Fig. 5b); postpetiole less broad (worker PPW/HW 0.50–0.52) (Fig. 1); queen unknown but expected to have more slender petiole (PLI ~0.70, PH/HW ~0.70, DPW/HW ~0.60) and postpetiole (PPW/HW ~0.75); west Africa to Ethiopia . . . . . *continua* (Forel)



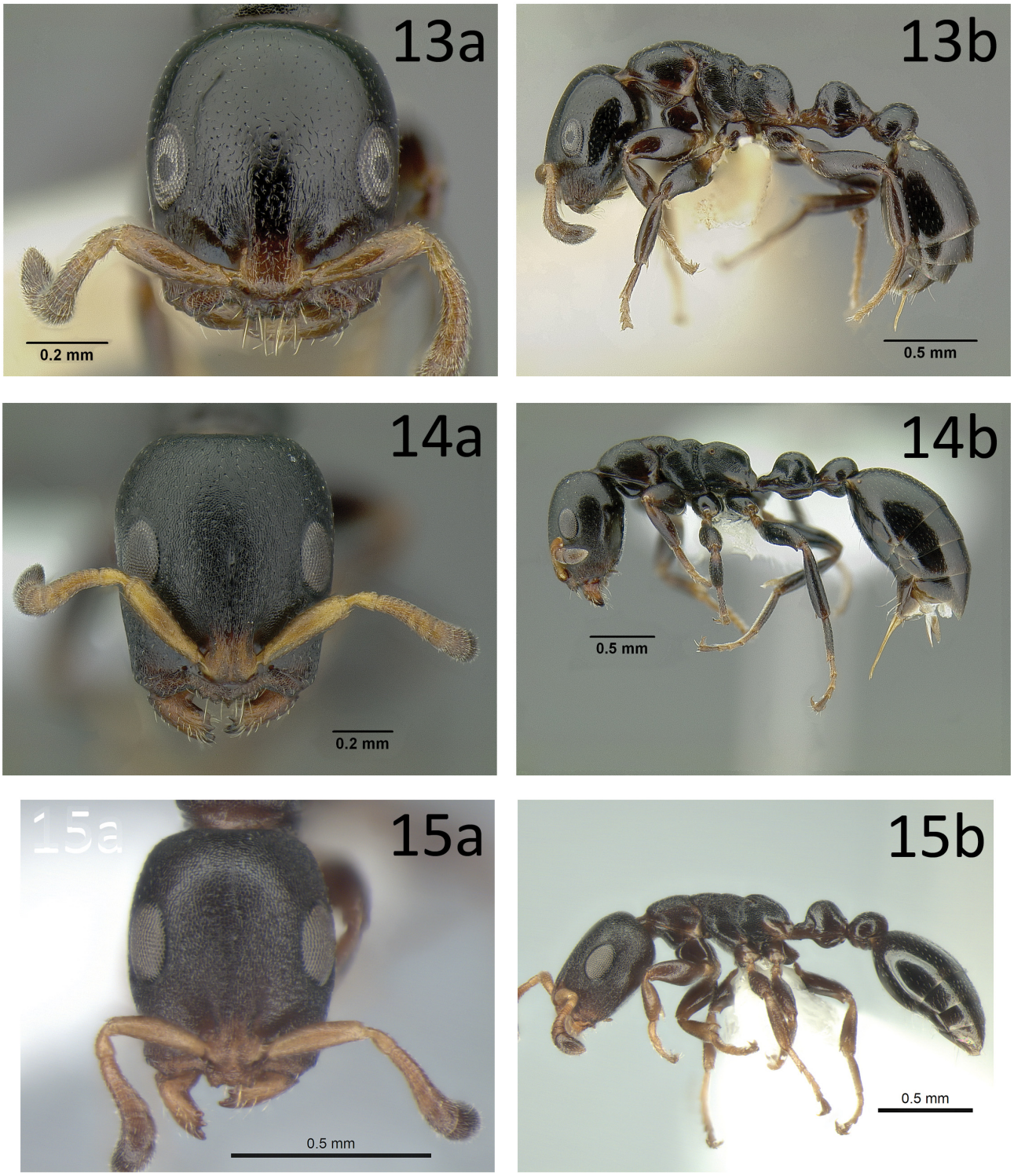
FIGURES 4–6. *Tetraponera allaborans* group, workers, full-face (dorsal) view of head (a) and lateral profile of body (b). 4, *T. clypeata*, South Africa (CASENT0220741); 5, *T. continua*, The Gambia (CASENT0794348); 6, *T. cortina*, holotype, DR Congo (CASENT0794352). Images from AntWeb (www.antweb.org); photographer Matthew Prebus.



FIGURES 7–9. *Tetraponera allaborans* group, full-face (dorsal) view of head (a) and lateral profile of body (b). 7, *T. dispar*, worker, holotype, Republic of Congo (CASENT0888518); 8, *T. emeryi*, worker, South Africa (CASENT0220743); 9, *T. exactor*, alate queen, holotype, South Africa (CASENT0794350). Images from AntWeb (www.antweb.org); photographers Peter Hawkes (7), Matthew Prebus (8, 9).

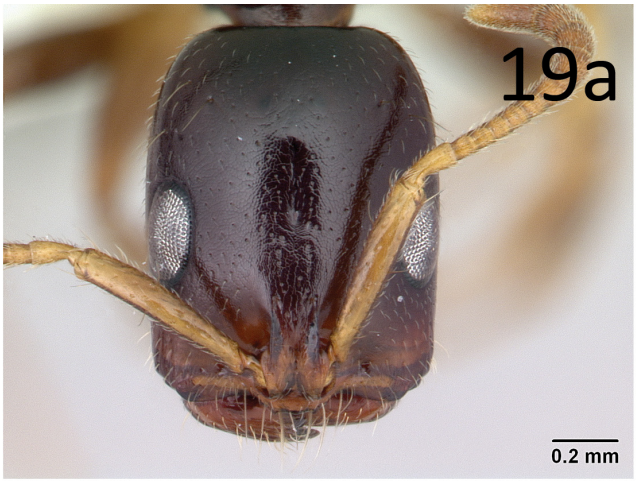


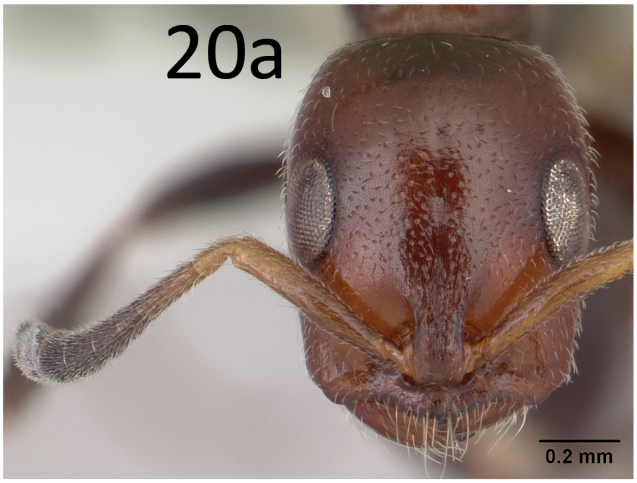
FIGURES 10–12. *Tetraponera allaborans* group, workers, full-face (dorsal) view of head (a) and lateral profile of body (b). 10, *T. furtiva*, holotype, South Africa (CASENT0843646); 11, *T. gerdae*, Kenya (CASENT0842369); 12, *T. liengmei*, South Africa (CASENT0794351). Images from AntWeb (www.antweb.org); photographers Phil Ward (10), Zachary Griebenow (11), Matthew Prebus (12).



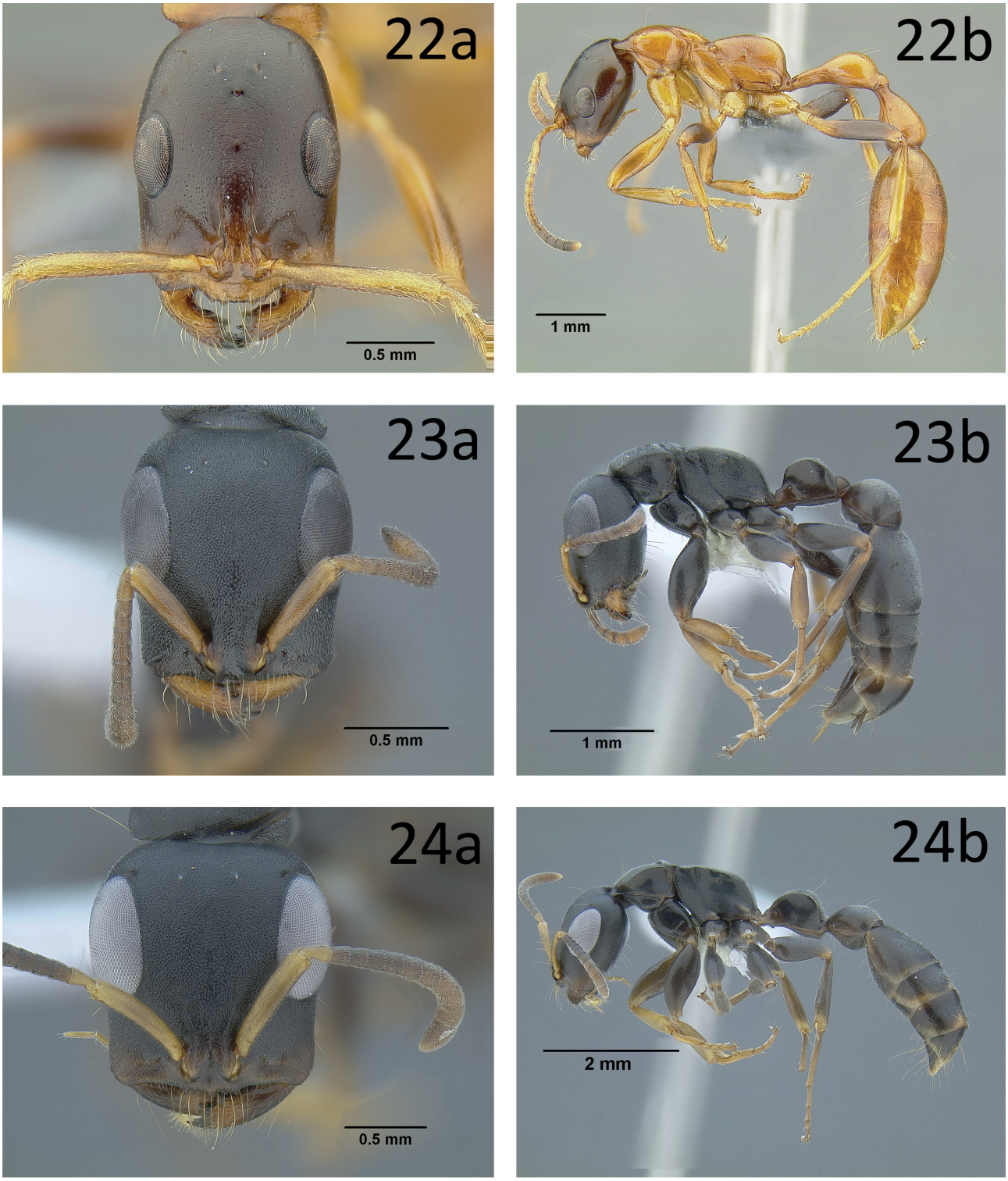
FIGURES 13–15. *Tetraponera allaborans* group, workers, full-face (dorsal) view of head (a) and lateral profile of body (b). 13, *T. pedana*, holotype, Kenya (CASENT0794355); 14, *T. penzigi*, Kenya (CASENT0794353); 15, *T. pumila*, holotype, Burundi (CASENT0863337). Images from AntWeb (www.antweb.org); photographers Matthew Prebus (13, 14), Phil Ward (15).

FIGURES 16–18. *Tetraponera allaborans* group, workers, full-face (dorsal) view of head (a) and lateral profile of body (b). 16, *T. tessmanni*, Cameroon (CASENT0794354); 17, *T. hysterica*, Madagascar (CASENT0012842); 18, *T. longula*, Madagascar (CASENT0012843). Images from AntWeb (www.antweb.org); photographers Matthew Prebus (16), April Nobile (17, 18).

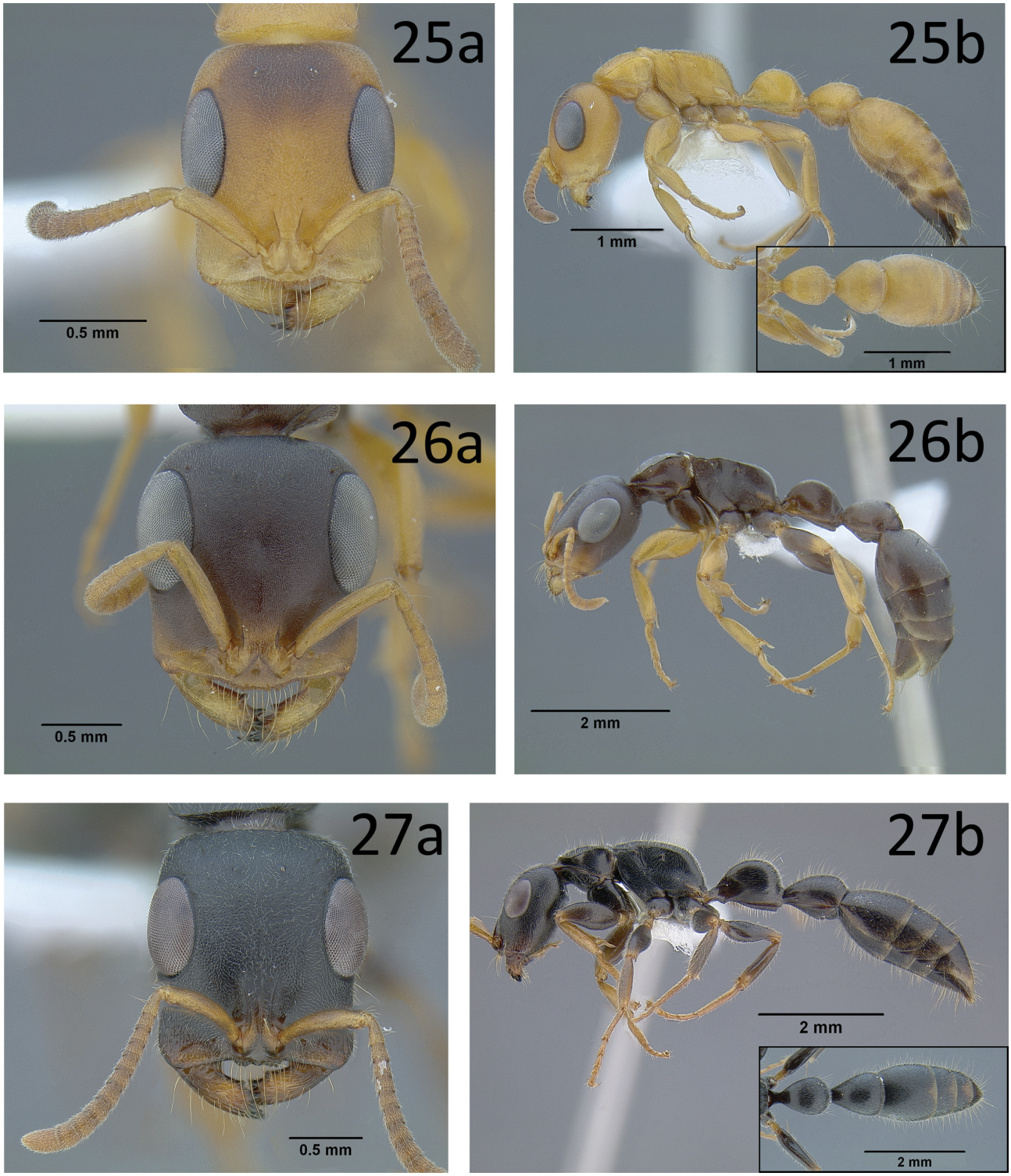




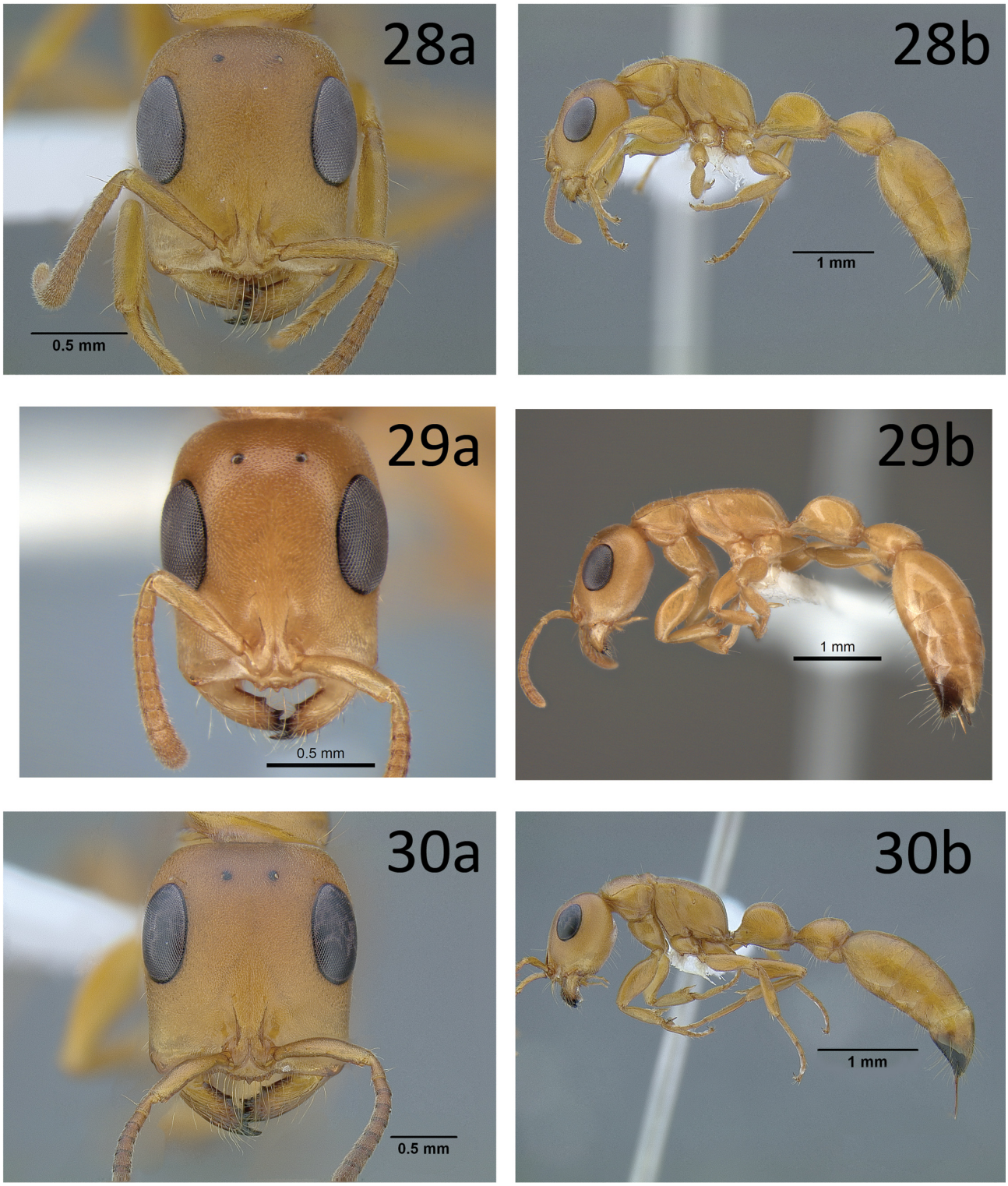
FIGURES 19–21. *Tetraponera allaborans* group, workers, full-face (dorsal) view of head (a) and lateral profile of body (b). 19, *T. mandibularis*, Madagascar (CASENT0012845); 20, *T. morondaviensis*, Madagascar (CASENT0012835); 21, *T. sahlbergii*, Madagascar (CASENT0012851). Images from AntWeb (www.antweb.org); photographer April Nobile.



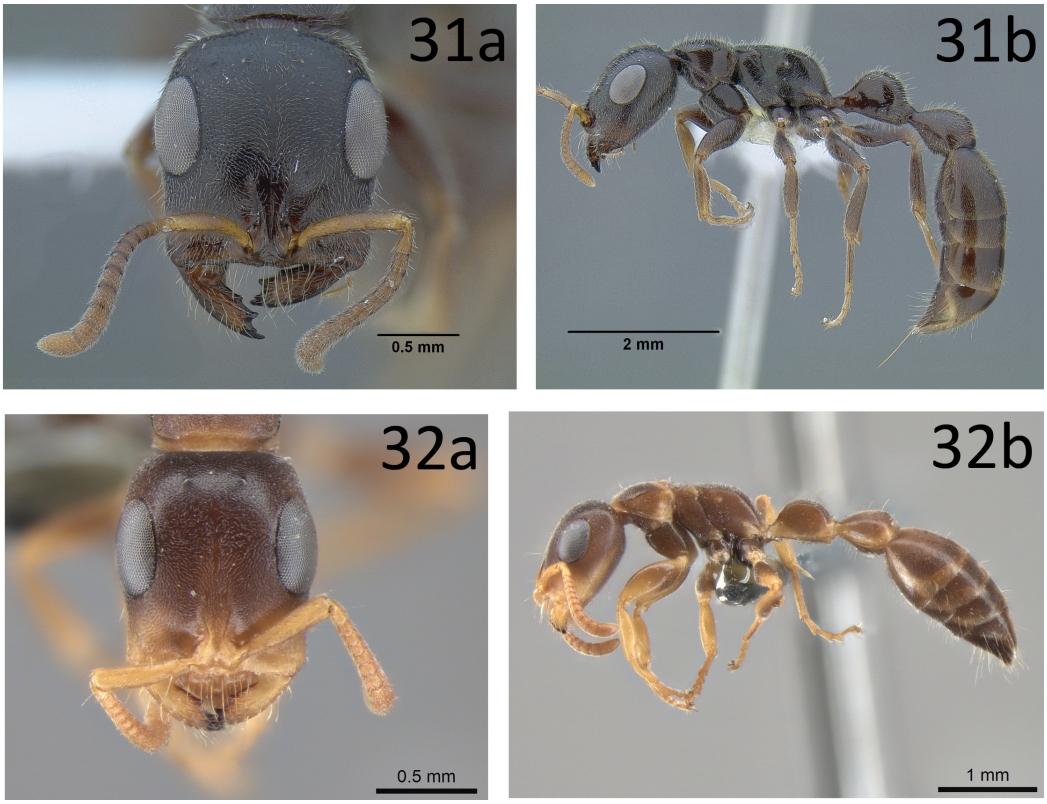
FIGURES 22–24. *Tetraponera grandidieri* group (22) and *T. natalensis* group (23, 24), workers, full-face (dorsal) view of head (a) and lateral profile of body (b). 22, *T. elegans*, Madagascar (CASENT0300734); 23, *T. andrei*, Mozambique (CASENT0794345); 24, *T. anthracina*, Uganda (CASENT0794191). Images from AntWeb (www.antweb.org); photographer Matthew Prebus.



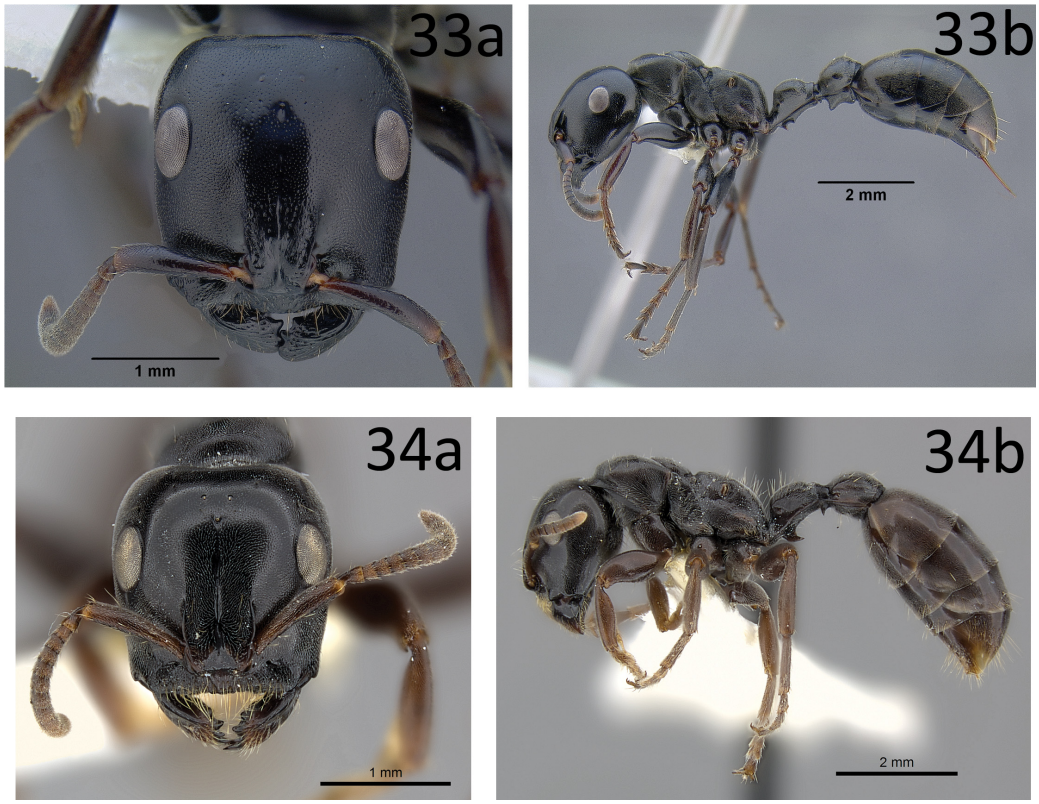
FIGURES 25–27. *Tetraponera natalensis* group, workers, full-face (dorsal) view of head (a) and lateral profile of body (b), with inset in Figs 25b and 27b showing dorsal view of petiole, postpetiole and gaster. 25, *T. caffra*, South Africa (CASENT0220752); 26, *T. insularis*, Madagascar (CASENT0409790); 27, *T. mocquerysi*, Uganda (CASENT0794203). Images from AntWeb (www.antweb.org); photographer Matthew Prebus.



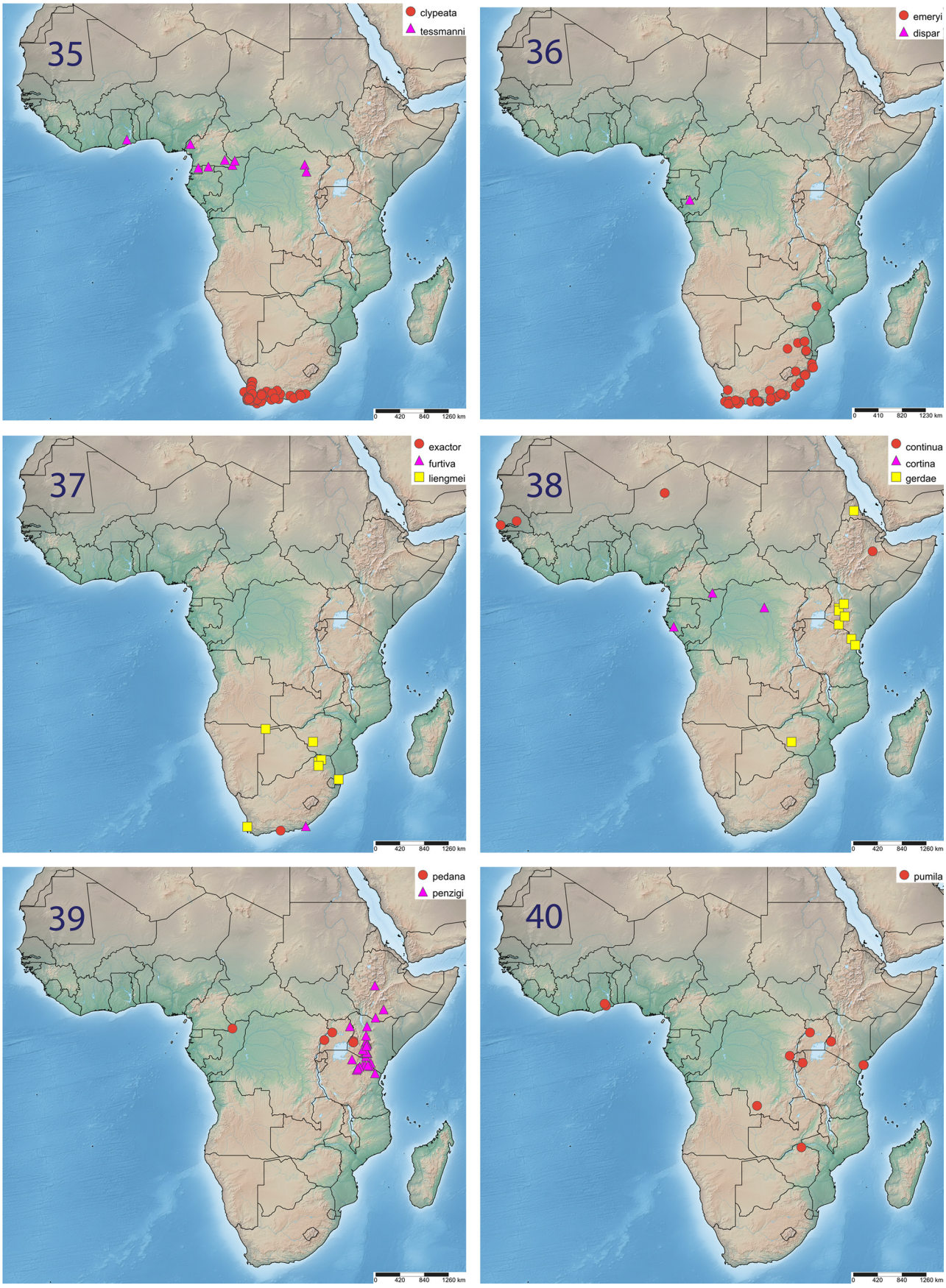
FIGURES 28–30. *Tetraponera natalensis* group, workers, full-face (dorsal) view of head (a) and lateral profile of body (b). 28, *T. natalensis*, Mozambique (CASENT0794194); 29, *T. redacta*, holotype, Kenya (CASENT0863363); 30, *T. schulthessi*, South Africa (CASENT0794193). Images from AntWeb (www.antweb.org); photographers Matthew Prebus (28, 30), Phil Ward (29).



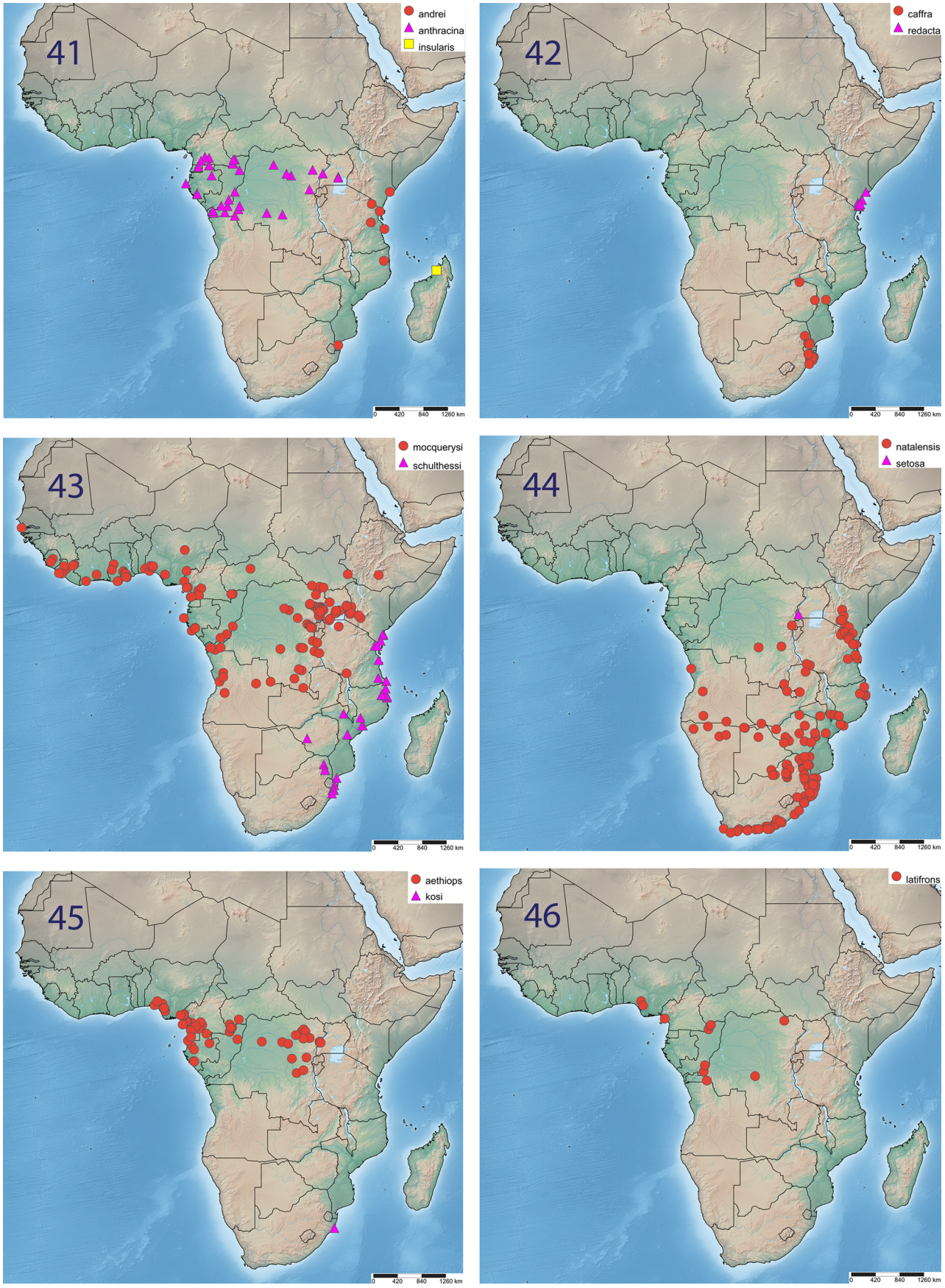
FIGURES 31–32. *Tetraponera natalensis* group workers, full-face (dorsal) view of head (a) and lateral profile of body (b). 31, *T. setosa*, holotype, Uganda (CASENT0794346); 32, *T. kosi*, holotype, South Africa (CASENT0815472). Images from AntWeb (www.antweb.org); photographers Matthew Prebus (31), Jill Oberski (32).



FIGURES 33–34. *Tetraponera rufonigra* group workers, full-face (dorsal) view of head (a) and lateral profile of body (b). 33, *T. aethiops*, Uganda (CASENT0794322); 34, *T. latifrons*, DR Congo (CASENT0217593). Images from AntWeb (www.antweb.org); photographers Matthew Prebus (33), Estella Ortega (34).



FIGURES 35–40. Distribution maps for Afrotropical *Tetraponera*. 35, *T. clypeata* (circles), *T. tessmanni* (triangles); 36, *T. emeryi* (circles), *T. dispar* (triangle); 37, *T. exactor* (circle), *T. furtiva* (triangle), *T. liengmei* (squares); 38, *T. continua* (circles), *T. cortina* (triangles), *T. gerdae* (squares); 39, *T. pedana* (circles), *T. penzigi* (triangles); 40, *T. pumila* (circles).



FIGURES 41–46. Distribution maps for Afrotropical *Tetraponera*. 41, *T. andrei* (circles), *T. anthracina* (triangles), *T. insularis* (square); 42, *T. caffra* (circles), *T. redacta* (triangles); 43, *T. mocquerysi* (circles), *T. schulthessi* (triangles); 44, *T. natalensis* (circles), *T. setosa* (triangle); 45, *T. aethiops* (circles), *T. kosi* (triangle); 46, *T. latifrons* (circles).

Taxonomic treatment by species group

Tetraponera allaborans-group

Worker diagnosis (modified from Ward 2006). Small to medium-sized species (HW 0.41–1.15); masticatory margin of mandible usually with four (rarely five) teeth, the basal margin edentate and shorter than masticatory margin; in a subset of species (the Asian *T. allaborans* complex and the southern African *T. clypeata* complex) masticatory margin with three teeth, basal margin with 1–2 small teeth and longer than masticatory margin; labrum without prominent teeth or tubercles or with a median tubercle near the proximal margin, widely flanked by a lateral pair; anteromedial margin of clypeus variable (crenulate, toothed or entire); frontal carinal distance variable (FCI 0.08–0.25); scape length about two thirds of head width or less (SI 0.41–0.71); compound eyes directed anteriorly; head capsule usually lacking ocelli, rarely with a weak lateral pair; pronotum with weak to moderate lateral margination; mesonotum about as long as wide, ovoid or subrectangular in dorsal view; mesopropodeal impression usually containing a raised transverse metanotal plate, but this reduced or lost in some species; posteroventral margin of petiole well separated from the helcium venter; metabasitarsal sulcus present; mesosternum densely pubescent.

Comments. The *T. allaborans*-group ranges widely in the Afrotropical region (including Madagascar), southeast Asia, and Australasia. Among the six species groups of *Tetraponera* currently recognized (Ward 2006), it is the most species-rich, both globally and regionally.

Tetraponera allaborans-group: African species

Tetraponera clypeata (Emery)

(Figs 2, 4, 35)

Sima clypeata Emery 1886: 361. Syntypes, 3 dealate queens, Cape of Good Hope ["Cap B. Sp."], South Africa (Peringuey) (MSNG, NHMV, SAMC) [examined]. 1 syntype queen in NHMV imaged on AntWeb: CASENT0915850.
Sima Braunsi Forel 1913: 112. Syntypes, 4 workers, 3 dealate queens, Willowmore, South Africa (H. Brauns) (MHNG) [examined]. 1 syntype worker imaged on AntWeb: CASENT0907470. **Syn**. **nov**.
Sima (*Tetraponera*) *clypeata* race *braunsi* var. *equidentata* Arnold 1916: 184. 5 workers, Cape Town, South Africa (Arnold) (BMNH) [examined]. Unavailable name.

Sima clypeata Emery; Emery 1895b: 24. Description of worker.
Sima (*Tetraponera*) *clypeata* Emery; Arnold 1916: 182. Combination in *Sima* (*Tetraponera*).
Tetraponera clypeata (Emery); Wheeler 1922b: 797. Combination in *Tetraponera*.
Tetraponera clypeata (Emery); Chomicki *et al.* 2015: figure S1. Placement in molecular phylogeny.

Sima (*Tetraponera*) *clypeata* race *Braunsi* Forel; Arnold 1916: 182. Combination in *Sima* (*Tetraponera*); subspecies of *S. clypeata*.
Tetraponera clypeata subsp. *braunsi* (Forel); Wheeler 1922b: 797. Combination in *Tetraponera*.
Tetraponera braunsi (Forel); Ward 1990: 488. Raised to species.

Worker measurements (n = 10). HW 0.58–0.68, HL 0.78–0.94, LHT 0.48–0.58, CI 0.71–0.76, FCI 0.10–0.14, REL 0.28–0.31, REL2 0.39–0.44, SI 0.61–0.64, SI3 1.46–1.62, FI 0.40–0.45, PLI 0.50–0.60, PWI 0.39–0.46, LHT/HW 0.83–0.90, CSC 0–2, MSC 0.

Worker diagnosis. Small species; masticatory margin of mandible with three teeth; minimum distance between frontal carinae slightly exceeding basal scape width (FCI 0.10–0.14, MFC/SL 0.16–0.22); scape moderately long, greater than one-half head width (SI 0.61–0.64, SI2 0.45–0.48); median lobe of clypeus produced anteriorly, usually with two pairs of lateral teeth separated by a small concavity, flanked by a weaker pair of outer lateral teeth (Fig. 4a); profemur moderately robust (FI 0.40–0.45), legs moderately short (LHT/HL 0.61–0.65); mesopropodeal impression with irregular longitudinal rugulae, preceded by a short, raised metanotal plate (Fig. 4b); dorsal face of propodeum subequal in length to declivitous face and rounding insensibly into the latter; petiole elongate and slender (see PLI and PWI values), with a well marked anterior peduncle and weak anteroventral tooth; postpetiole longer than broad. Integument predominantly smooth and shiny, with scattered fine punctures and weak reticulation. Standing pilosity inconspicuous, present on frontal carinae and as a single supraocular pair of setae on the vertex, absent from dorsum

of mesosoma, petiole and postpetiole, sparse on succeeding abdominal segments 4–8. Dark brown, appendages lighter.

Comments. *Tetraponera clypeata* belongs to a cluster of closely related species—here termed the *T. clypeata* complex—that also includes *T. dispar*, *T. emeryi*, *T. exactor*, and *T. furtiva*. The workers of this complex can be distinguished from other African members of the *allaborans* group by their reduced mandibular dentition (masticatory margin with 3 teeth), closely adjacent frontal carinae (FCI 0.08-0.14), relatively long scapes (SI 0.56–0.67), and elongate petiole (PLI 0.50–0.61). *T. dispar* differs from *T. clypeata* by its smaller size (worker HW 0.51-0.52), larger eyes (worker REL 0.35), and orange-brown coloration. Workers of *T. emeryi* are light yellowish-orange but otherwise quite similar in structure to those of *T. clypeata* (see further discussion under *T. emeryi*). Workers of *T. furtiva* are medium-brown in color, and with a shorter petiole than *T. clypeata* (PL/HW 0.72–0.77 in *T. furtiva*, versus 0.79–0.88 in *T. clypeata*).

Distribution and biology. Known only from southwestern South Africa (Western Cape, Northern Cape and Eastern Cape provinces), *T. clypeata* nests in dead twigs, stems, and thorns of various plants. Specific nest site records include *Vachellia karroo* thorns, dead stem of *Osteospermum*, dead stem of Restionaceae, "stalks tenanted by *Allodape* bees", "dead branch", and "hollow twigs". Recorded habitats include valley bushveld, coastal scrub forest, fynbos, fenosterbos, renosterveld, "S. Coast Strandveld", spiny forest/thicket, and roadside.

Material examined (ANIC, ASIC, BMNH, CASC, CUIC, HZIC, KUBC, KUEC, MCZC, MHNG, MNHN, MSNG, MZLU, NHMB, NHMW, PSWC, SAMC, UASK, UCDC, USNM, UTIC, ZMAS). **South Africa**: *Eastern Cape*: Faraway Farm, nr. Grahamstown (Rashbrook, V.); Februarie Farm, 39.9 km 268° W Kirkwood (Robertson, H. G.; Tourle, R.); Februarie Farm, 39.9 km 268° W Kirkwood (van Noort, S.); Grahamstown (Weatherill, L.); Hamburg, 10 m (Wild, A. L.); Kranshoek (c.u.); Port Elizabeth (Brauns); Port Elizabeth (c.u.); Port Elizabeth (Krauss, N. L. H.); Southwell (Hepburn); Willowmore (Brauns, H.); *Northern Cape*: Fynbos 2 Site, 6.41 km 295° WNW Nieuwoudtville (van Noort, S.); Glen Lyon farm, 4.98 km 127° SE Nieuwoudtville (van Noort, S.); *province unknown*: Cape Colony [as "Le Cap"] (c.u.); Capland (c.u.); *Western Cape*: 14 km ENE Montagu, 600 m (Ward, P. S.); 2 km NNW Vrede, Anysberg Nature Reserve, 750 m (Ward, P. S.); 3 km E Ashton, 220 m (Ward, P. S.); 3 km S Scarborough (O'Brien, C. W.; O'Brien, L. B.; Marshall, G. B.); Brandfontein Reserve (Robertson, H. G.); Cape of Good Hope [as "Cap B. Sp."] (Péringuey); Cape of Good Hope [as "Cap B. Sza"] (Péringuey, L.); Cape of Good Hope [as "Cape de B. E."] (Brauns); Cape Peninsula, Hout Bay, Little Lions Head (Brinck; Rudebeck); Cape Peninsula, Kirstenbosch (Brinck; Rudebeck); Cape Town (Arnold); Cape Town (Bridwell, J. C.); Cape Town (c.u.); Cape Town (Foly, F.); Cape Town (Phillips, E. P.); Cape Town (Simon, E.); Cape Town above Tokai Forest, Constantiaberge, above Donkerboskloof, 460 m (van Noort, S.); Cecelia Reservaat, Nuwelande (Geertsema, H.); Clanwilliam (Malkin, B.); Constantia [as "Constan"] (c.u.); De Hoop Nature Reserve, 100 m (Danielsson, R.); De Hoop Nature Reserve, Potberg (Smulian, T.); Dikbome, Merweville Koup (Zinn, H.); Grootvadersbosch (c.u.); Hermanus, Fernkloof Nature Reserve, Mt. Cyclopia, 380 m (van Noort, S.); Jacobsbaai (Robertson, H. G.); Kluitjieskraal Forestry Station, Dist. Wolseley (Boonzaaier, A. A.); Koeberg (Robertson, H. G.); Koppie Alleen, De Hoop Nature Reserve (Robertson, H. G.); Lorraine Farm (Robertson, H. G.; Picker, M.); Matjesfontein (Simon, E.); Montagu [as "Montague"] (c.u.); Montagu Pass (Penther); Mosselbay (Penther); Muizenberg, Cape Prov. (Malkin, B.); Olifantsbos, Cape of Good Hope Nature Reserve (Robertson, H. G.); Oudebos River, Kogelberg Nature Reserve, 140 m (Ward, P. S.); Oudebos River, Kogelberg Nature Reserve, 280 m (Ward, P. S.); Piekenierskloof, 15 km S Citrusdal, 370 m (Danielsson, R.); Plant Research Institute, Rosebank, Cape Town (Cillie, J. J.); Retreat (Malkin, B.); Riviersonderend [as "R. Sonder End"], Oudebosch, 455 m (Barnard, K. H.); Seaforth, 5 m (Ward, P. S.); Stellenbosch (Kovalev, O.); Table Mountain (c.u.); Tierberg, nr. Prince Albert (Dean, W. R. J.); Tulbagh (Lightfoot); Tygerberg Nature Reserve, Cape Town, 324 m (Braschler, B.); Vrede, Anysberg Nature Res., 750 m (Ward, P. S.); Wilderness Natl. Park, 17 km SE George (Danielsson, R.); Wolfgat Nature Reserve (van Noort, S.).

***Tetraponera continua* (Forel)**

(Figs 1, 5, 38)

Sima Penzigi subsp. *continua* Forel 1907: 138. Syntype, worker, Gotta, Ethiopia (M. de Rothschild) (MNHN) [examined]. Imaged on AntWeb: CASENT0913722.

Sima Claveaui Santschi 1913: 304. Holotype (by monotypy), worker, Senegal (Claveau) (NHMB) [examined]. Imaged on AntWeb: CASENT0915527. **Syn**. **nov**.

Sima (*Tetraponera*) *penzigi* subsp. *continua* Forel; Emery 1921: 28. Combination in *Sima* (*Tetraponera*).
Tetraponera penzigi subsp. *continua* (Forel); Wheeler 1922b: 800. Combination in *Tetraponera*.
Tetraponera continua (Forel); Chomicki *et al.* 2015: figure S1. Raised to species; placement in molecular phylogeny.

Sima (*Tetraponera*) *claveaui* Santschi; Emery 1921: 27. Combination in *Sima* (*Tetraponera*).
Tetraponera claveaui (Santschi); Wheeler 1922b: 797. Combination in *Tetraponera*.

Worker measurements (n = 5). HW 0.49–0.52, HL 0.71–0.77, LHT 0.42–0.45, CI 0.66–0.70, FCI 0.16–0.20, REL 0.29–0.32, REL2 0.42–0.47, SI 0.50–0.56, SI3 1.07–1.23, FI 0.46–0.53, PLI 0.72–0.82, PWI 0.57–0.63, LHT/HW 0.81–0.89, CSC 0, MSC 0.

Worker diagnosis. Small species, with elongate head (CI 0.66–0.70); frontal carinae well separated, the distance between them exceeding basal scape width (FCI 0.16–0.20, MFC/SL 0.31–0.40); scape short, about one-half head width (SI 0.50–0.56) and one-third of head length (SI2 0.34–0.37); anterior clypeal margin with a crenulate medial protrusion (Fig. 5a); profemur robust (FI 0.46–0.53), legs relatively short (LHT/HL 0.57–0.62); metanotal plate conspicuous, about four-fifths the length of the mesonotum, and bounded anteriorly and posteriorly by transverse impressions that are longitudinally rugulose; dorsal face of propodeum flattened, laterally submarginate, greater in length than the declivitous face and rounding insensibly into the latter; petiole relatively short, high and rounded (see PLI and PWI values), with a distinct anterior peduncle and without well differentiated anterior, dorsal and posterior faces (Fig. 5b); in profile, petiole height equal to, or less than, height of propodeum and slightly exceeding one-half head width (PH/HW 0.53–0.55); in dorsal view, petiole about two-fifths of head width (DPW/HW 0.40–0.43); postpetiole broader than long (PPW/HW 0.50–0.52). Integument sublucid, with scattered fine punctures and weak reticulate-coriarious sculpture, the latter most strongly developed on the metanotum and propodeum. Standing pilosity very sparse, absent from the dorsum of head, mesosoma, petiole, postpetiole, and abdominal tergites 4–6. Dark brown, appendages lighter.

Comments. Characteristic features of the worker of *T. continua* are its small size, elongate head, well separated frontal carinae, laterally submarginate propodeum, relatively robust petiole, very sparse standing pilosity, and dark color. This species is quite similar to *T. gerdae*, but the head is slightly broader, on average, and the petiole and postpetiole are more slender, such that worker PH/HW 0.53–0.55 (versus 0.56–0.67 in *T. gerdae*), worker DPW/HW 0.40–0.43 (versus 0.43–0.53 in *T. gerdae*) and worker PPW/HW 0.50–0.52 (versus 0.56–0.64 in *T. gerdae*) (Fig. 1). For further discussion see under *T. gerdae*.

Distribution and biology. This species is known only from several arid locations between The Gambia and Ethiopia (Fig. 38). A nest series of *T. continua* from The Gambia was taken in an acacia pod.

Material examined (MNHN, NHMB, PSWC, UCDC). **Ethiopia**: *Somali*: Gotta (de Rothschild, M.); **Niger**: *Agadez*: Tin Telloust, Aïr Massif (Matteson, P. C.); **Senegal**: "Senegal" (Claveau); **The Gambia**: *North Bank*: Madiyana Camp, Jinack Island, Nuimi Natl. Park, 0 m (Lush, M. J.).

Tetraponera cortina sp. nov.

(Figs 6, 38)

Type material. *Holotype worker*: DR Congo, Tshopo, Yangambi Reserve, 1949, A. Raignier & J. van Boven (CASENT0794352) (MCZC). *Paratypes*: series of 9 workers, same data as holotype (MCZC, UCDC). The workers have code numbers as follows: "C. 1943" (2 paratype workers), "C. 1944" (2 paratype workers), "C. 1945" (2 paratype workers), "C. 1961" (1 holotype worker, 1 paratype worker), and "C. 1962" (2 paratype workers). The significance of these code numbers is unclear; they might represent different collections or colony series. An inquiry to the Musée Royal de l'Afrique Centrale (Tervuren) about Raignier and van Boven collection numbers yielded no information.

Worker measurements (n = 5). HW 0.49–0.52, HL 0.69–0.71, LHT 0.37–0.40, CI 0.70–0.73, FCI 0.12–0.15, REL 0.27–0.30, REL2 0.38–0.43, SI 0.46–0.52, SI3 1.17–1.37, FI 0.46–0.49, PLI 0.82–0.91, PWI 0.69–0.76, LHT/HW 0.73–0.78, CSC 0, MSC 0.

Worker diagnosis. Small species (HW 0.49–0.52), with moderately elongate head (CI 0.70–0.73); frontal carinae separated by no more than 0.15× head width (FCI 0.12–0.15, MFC/SL 0.26–0.31); scape short, about one-half head width (SI 0.46–0.52) and one-third of head length (SI2 0.33–0.37); anterior clypeal margin with a short, crenu-

late medial protrusion (Fig. 6a); profemur robust (FI 0.46–0.49), legs short (LHT/HL 0.53–0.57); metanotal plate conspicuous, about four-fifths the length of the mesonotum, and bounded anteriorly and posteriorly by transverse impressions with longitudinal rugulae; dorsal face of propodeum flattened, laterally submarginate, shorter than the declivitous face, and rounding insensibly into the latter; petiole short, high and rounded (see PLI and PWI values), with a distinct anterior peduncle and without well differentiated anterior, dorsal and posterior faces (Fig. 6b); in profile, petiole height subequal to height of propodeum and about one-half head width (PH/HW 0.48–0.57); in dorsal view, petiole slightly more than two-fifths of head width (DPW/HW 0.41–0.46), and notably less broad than postpetiole (DPW/PPW 0.72–0.79); postpetiole broader than long and more than one-half head width (PPW/HW 0.53–0.63). Head and mesosoma predominantly smooth and shiny with scattered punctures and faint reticulation, the latter better developed on the side of the mesosoma; petiole, postpetiole and gaster mostly smooth and shiny. Standing pilosity very sparse, absent from the dorsum of head, mesosoma, petiole, postpetiole, and abdominal tergites 4–6. Medium to dark brown, appendages lighter.

Comments. Workers of this small species are similar to those of *T. continua* and *T. gerdae*, but can be recognized by their shinier head, more closely adjacent frontal carinae, and shorter legs (see measurements cited in the key). In addition, the petiole tends to be narrower relative to the postpetiole in *T. cortina*, such that DPW/PPW 0.72–0.79, as opposed to 0.75–0.94 in *T. continua* and *T. gerdae*. Workers of *T. pedana* also have a shiny integument and short legs, but they can be distinguished from those of *T. cortina* by their broader head (CI 0.82–0.86 versus 0.70–0.73 in *T. cortina*) and more widely separated frontal carinae (FCI 0.19–0.21 versus 0.12–0.15 in *T. cortina*). A small alate queen (HW 0.47, LHT 0.40) from Gabon, with shiny vertex, moderately elongate head (CI 0.64) and closely adjacent frontal carinae (FCI 0.17), and a small male (HW 0.45, LHT 0.39) with shiny head from Central African Republic, are considered likely to be conspecific with the *T. cortina* workers from DR Congo.

Distribution and biology. *Tetraponera cortina* is known only from the type series collected in central DR Congo and probable alates from Gabon and Central African Republic (see above). The collections come from lowland rainforest, but nothing further is known about the biology.

Material examined. Type series cited above, plus the following specimens provisionally identified as *T. cortina*: **Central African Republic**: *Sangha-Mbaéré*: Parc National Dzanga-Ndoki, Mabéa Bai, 21.4 km 53° NE Bayanga, 510 m (van Noort, S.) (1 male, sweeping, rainforest, marsh clearing) (CASENT0092903) (CASC); **Gabon**: *Ogooué-Maritime*: Réserve des Monts Doudou, 25.2 km 304° NW Doussala, 660 m (van Noort, S.) (1 alate queen, swept from low canopy in coastal lowland rainforest) (CASENT0170712) (CASC).

Tetraponera dispar sp. nov.

(Figs 7, 36)

Type material. *Holotype worker*: Republic of Congo, Niari, Tsingidi, Afog27, 803 m, -2.47106 12.96037, 16 Nov 2013, tall mature forest, canopy fogging, L. Niemand & C. Ngoulou LN-RC1-Afog27 (CASENT0888518) (SAMC). *Paratype*: 1 worker, same data as holotype (CASENT0888519) (CASC).

Worker measurements (n = 2). HW 0.51–0.52, HL 0.66–0.67, LHT 0.43–0.44, CI 0.77–0.78, FCI 0.10, REL 0.35, REL2 0.45, SI 0.62–0.63, SI3 1.39–1.40, FI 0.38–0.39, PLI 0.59–0.60, PWI 0.44–0.48, LHT/HW 0.83–0.86, CSC 2, MSC 1–2.

Worker diagnosis. A member of the *T. clypeata* complex (see characterization under *T. clypeata*), with the following more specific features: very small (HL <0.70), with relatively broad head (CI 0.77–0.78) and large eyes (REL 0.35, EL/LHT 0.52–0.54); mesopropodeal impression simple, lacking longitudinal rugulae; profemur rather slender (FI 0.38–0.39); petiole relatively short (for this complex), such that PLI 0.59–0.60, PL/HW 0.71, and PL/SL 1.13–1.14. Integument predominantly smooth and shiny, with scattered fine punctures. Standing pilosity sparse, present on frontal carinae, vertex (one supraocular pair), and pronotum (one anterolateral pair), absent from remainder of mesosoma and from the petiole and postpetiole. Body light orange-brown.

Comments. *Tetraponera dispar* is a diminutive, orange-brown species in the *T. clypeata* complex. It can be distinguished from other species in that complex by its small size, broad head, and large eyes. In addition, the petiole is relatively short: PL/HW 0.71 and PL/SL 1.13–1.14, compared with PL/HW 0.72–0.94 and PL/SL 1.21–1.43 in other species (these measurements refer to workers only). Finally, the worker of *T. dispar* has an anterolateral pair of setae on the pronotum, whereas these setae are lacking in workers of other species in the *T. clypeata* complex.

Distribution and biology. *Tetraponera dispar* is known only from two workers taken by canopy fogging in primary rainforest in the Republic of Congo. The habitat is illustrated in Janák & Bordoni (2015: 91). The four other species in the *T. clypeata* complex are confined to southern Africa, so *T. dispar* is a striking geographical outlier.

Material examined. Known only from the type series.

Tetraponera emeryi (Forel)

(Figs 2, 8, 36)

Sima Emeryi Forel 1911a: 367. Syntypes, 2 workers, Pretoria, South Africa (Simon) (MSNG) [examined]. Name given by Forel (1911a: 367) for Emery's (1895b: 23) description of workers of "*Sima capensis*" (nec F. Smith) from Pretoria.

Sima Braunsi var. *durbanensis* Forel 1914: 218. Syntype, 1 worker, Durban, South Africa (Arnold) (MHNG) [examined]. Imaged on AntWeb: CASENT0907471. **Syn**. **nov**.

Sima (*Tetraponera*) *Emeryi* Forel; Arnold 1916: 187. Combination in *Sima* (*Tetraponera*).

Tetraponera emeryi (Forel); Wheeler 1922b: 797. Combination in *Tetraponera*.

Tetraponera emeryi (Forel); Chomicki *et al.* 2015: figure S1. Placement in molecular phylogeny.

Sima (*Tetraponera*) *clypeata* race *Braunsi* var. *durbanensis* Forel; Arnold 1916: 184. Combination in *Sima* (*Tetraponera*), as infrasubspecific name.

Tetraponera clypeata subsp. *braunsi* var. *durbanensis* (Forel); Wheeler 1922b: 797. Combination in *Tetraponera*, as infrasubspecific name.

Tetraponera braunsi durbanensis (Forel); Ward 1990: 488. Combination in *Tetraponera*.

Worker measurements (n = 12). HW 0.58–0.69, HL 0.77–0.99, LHT 0.49–0.64, CI 0.70–0.76, FCI 0.08–0.12, REL 0.28–0.32, REL2 0.39–0.44, SI 0.64–0.68, SI3 1.54–1.69, FI 0.36–0.42, PLI 0.51–0.56, PWI 0.38–0.45, LHT/HW 0.84–0.92, CSC 2, MSC 0.

Worker diagnosis. Similar to *Tetraponera clypeata* (see above) except as follows: scapes tending to be longer (SI 0.64–0.68) (Fig. 2), frontal carinae more closely adjacent (FCI 0.08–0.12) and profemur more slender (FI 0.36–0.42); mesopropodeal impression lacking conspicuous longitudinal rugulae; light yellowish-orange in color (Figs 7, 8).

Comments. Workers of *T. emeryi* are most readily distinguished from those of their close relative, *T. clypeata*, on the basis of color: light yellowish-orange as opposed to dark brown in *T. clypeata*. The two species are broadly sympatric in southwestern South Africa. *T. emeryi* workers also tend to have longer appendages and more closely adjacent frontal carinae than *T. clypeata*, but the relevant metrics overlap. Differences in the male terminalia, including a more dorsally deflected posteromedial margin of sternite IX (hypopygium) in *T. emeryi*, support their treatment as different species. For distinctions between *T. emeryi* and *T. furtiva* see under the latter species.

Distribution and biology. *T. emeryi* occurs from the Western Cape of South Africa east to KwaZulu-Natal and Eswatini (Swaziland), and north as far as the Vumba Mountains in eastern Zimbabwe. Nests site records include *Vachellia karroo* thorns, and dead twigs of *Podalyria*, *Buddleja*, *Dombeya*, *Vachellia caffra*, "thorny vine", and unidentified woody plants. Habitats range from from Afromontane forest and forest edge to tropical dry forest, "garden" and "riverine".

Material examined (ANIC, ASIC, CASC, CUIC, KUES, MCZC, MHNG, MSNG, MZLU, NHMB, NHMW, PSWC, SAMC, UASK, UCDC, USNM). **Eswatini**: *Hhohho*: 5 km NE Forbes Reef, 1520 m (Ward, P. S.); Majolomba Gorge, Malolotja Nature Reserve, 1150 m (Ward, P. S.); Malolotja Nature Reserve, E bdy, 3 km N Nkomati R., 800 m (Ward, P. S.); **South Africa**: *Eastern Cape*: Andries Vosloo Kudu Reserve, 12.8 km NNE Fort Brown (Lubertazzi, D.); East London (Fowles, E.); Glenthorpe Farm, nr. Grahamstown (Zachariades, C.); Grahamstown (Brown, W. L.); Grahamstown (Silberbauer, L. X.; Bennett, L.); Grahamstown (Weatherill, L.); King Williams Town (Capener, A.); Mountain Zebra N.P., Cradock (U. Cape Town Ecol. Survey); Pirie Forest (Capener, A.); Port Elizabeth (Brauns); Port Elizabeth (c.u.); Port St. Johns (Bradley, J. C.); Sundays River Valley (c.u.); Tsitsikama N.P. (Kimsey, R. B.); Tsitsikamma Nat. Park (Allen, J.); *Gauteng*: Pretoria (Simon); *KwaZulu-Natal*: 17 km NE Empangeni, Nseleni River (Danielsson, R.); Durban (Arnold); Durban (c.u.); Durban (Cooper, C. B.); Giants Castle, 1750 m (Ward, P. S.); Hilltop Camp, Hluhluwe Game Reserve, 450 m (Ward, P. S.); N of Richards Bay (de Kock, A.; Majer, J. D.); Natal, Umtamvuna Nature Reserve, 160 m (van Noort, S.); Natal, Umtamvuna Nature Reserve,

220 m (van Noort, S.); Nature's Valley, Pinetown (Caldwell, P.); Pinetown (Marley, B.); Sydenham (Marley, H. B.); Umgeni Lagoon (Arnold); Umhlanga Rocks [as "Umhlanga"] (c.u.); Umkumbaan, Durban (Caldwell, P.); *Limpopo*: Tweefontein 14 km NE Warmbaths (Kimsey, R. B.); *Mpumalanga*: Mariepskop [as "Marieps"] (Faure, J. C.); Mariepskop, 1250 m (Fisher, B. L.; *et al*.); Mariepskop, 1250 m (Alpert, G. D.); Salique (Faure, J. C.); *province unknown*: Cape Colony [as "Cap Col."] (Brauns); *Western Cape*: 1 km NE Nature's Valley, 10 m (Ward, P. S.); 9 km ESE George, Kaaimansrivier (Danielsson, R.); Bloukrans-Pass, by Vargrivier (Danielsson, R.); Cape Peninsula, St. Michael's Road, Claremont (Matilya, G. J.); Clanwilliam (Malkin, B.); Claremont, 22 Livingstone Road (Robertson, D. A.; Robertson, H. G.); Claremont, 22 Livingstone Road (Robertson, H. G.); Fernkloof Nature Reserve (Robertson, H. G.); foot of Duivelsbos, Marloth Nature Reserve, 275 m (Robertson, H. G.); Franschhoek Bosreserve, Upper Berg River (Brinck; Rudebeck); Grootvadersbos (c.u. [ex A. J. Prins Collection]); Malgas, 40 m (Danielsson, R.); Mjinga, The Crags (Robertson, D. A.; Robertson, H. G.); Montagu [as "Montague"] (c.u.); Nature's Valley, 10 m (van Noort, S.); Nature's Valley, at Groot Rivier (Danielsson, R.); Oudebos River, Kogelberg Nature Reserve, 180 m (Ward, P. S.); Oudebos River, Kogelberg Nature Reserve, 280 m (Ward, P. S.); **Zimbabwe**: *Manicaland*: Vumba Mts. (c.u.).

***Tetraponera exactor* sp. nov.**
(Figs 9, 37)

Type material. *Holotype queen*: South Africa, Western Cape, Nature's Valley at Groot Rivier, 33°58′S 23°33′E, 15–17 Oct 1994, R. Danielsson, loc. 21 (CASENT0794350) (SAMC).

Queen measurements (n = 1). HW 0.55, HL 0.70, LHT 0.43, CI 0.79, FCI 0.19, REL 0.29, REL2 0.37, SI 0.56, SI3 1.50, FI 0.37, PLI 0.53, PWI 0.46, LHT/HW 0.79, CSC 4, MSC16.

Queen diagnosis. Relatively small species (HW 0.55); head moderately elongate, with broadly rounded sides; median clypeal lobe bluntly bidentate; frontal carinae well separated, the distance between them much greater than basal scape width (FCI 0.19); scape short (SI 0.56), somewhat expanded apically; profemur slender (FI 0.37); dorsal face of propodeum rounding gently into declivitous face, both of similar length; petiole elongate (PLI 0.53), with differentiated anterior peduncle and weak anteroventral tooth (Fig. 9b); postpetiole longer than broad, lacking anteroventral process. Integument smooth and shiny, with scattered fine punctures. Standing pilosity present on frontal carinae and as two long posterolateral pairs (0.14–0.17 mm long) on upper half of head; scattered standing pilosity also present on pronotum (10 setae), mesoscutum (5), propodeum (1), petiole (4), postpetiole (4), and succeeding abdominal segments. Light yellowish-brown.

Comments. This species is evidently closely related to *Tetraponera clypeata* and *T. emeryi*. The queen of *T. exactor* differs from those of *T. clypeata* and *T. emeryi* by its smaller size (HW 0.55, versus 0.63–0.80 [n = 12] in queens of the other species), more broadly rounded head (CI 0.79, versus 0.67–0.72), more widely separated frontal carinae (FCI 0.19, versus 0.11–0.17), shorter but apically expanded scape (SI 0.56, versus 0.57–0.66), smoother integument, and more abundant standing pilosity. In *T. exactor* standing hairs are conspicuous on the mesosoma, petiole and postpetiole (MSC 16; Fig. 9b) whereas in queens of *T. clypeata* and *T. emeryi* standing hairs are very sparse to absent on these structures (MSC 0–6).

Distribution and biology. This species is known only from a single alate queen collected in Nature's Valley, Western Cape, South Africa. No workers have been found that could be attributed to this species, suggesting that it might be a workerless social parasite. Traits indicative of social parasitism include the small size, shiny integument, and increased amounts of standing pilosity compared to related congeners. *T. emeryi* is sympatric with *T. exactor* at Nature's Valley and is a potential host species.

Material examined. Known only from the holotype.

***Tetraponera furtiva* sp. nov.**
(Figs 10, 37)

Type material. *Holotype worker*: South Africa, Eastern Cape, Hamburg, 10 m, 33°17′S 27°28′E, 19 Jan 2003, coastal scrub forest edge, ex *Acacia* thorn, A. L. Wild AW1830 (CASENT0843646) (SAMC). *Paratypes*: 4 work-

ers, same data as holotype (CASENT0796647, CASENT0843643, CASENT0843644, CASENT0843645) (UCDC, SAMC). 1 wingless female, apparent ergatoid queen, same locality, date, coastal scrub forest edge, singleton forager, A. L. Wild AW1834 (CASENT0794420) (UCDC).

Worker measurements (n = 5). HW 0.56–0.61, HL 0.74–0.81, LHT 0.48–0.51, CI 0.73–0.76, FCI 0.11–0.12, REL 0.30–0.32, REL2 0.41–0.42, SI 0.56–0.62, SI3 1.36–1.49, FI 0.42–0.45, PLI 0.56–0.61, PWI 0.46–0.48, LHT/HW 0.84–0.87, CSC 2, MSC 0.

Worker diagnosis. Similar in size and form to *Tetraponera clypeata* and *T. emeryi*, i.e., a small species (HW 0.56–0.61) with relatively elongate head, closely contiguous frontal carinae (FCI 0.11–0.12), a slender petiole (PLI 0.56–0.61), and sparse standing pilosity (CSC 2, MSC 0). Differing from the other two species as follows: head broader, on average (CI 0.73–0.76), and scape short (SI 0.56–0.62); petiole slightly more robust, i.e., shorter and wider, such that PWI 0.46–0.48, PL/HW 0.72–0.77, and FW/PL 0.40–0.45. Body medium-brown in color, the mesonotum, anterior portion of head, and antennae variably lighter (Fig. 10).

Comments. At first glance *Tetraponera furtiva* appears to be a dusky version of *T. emeryi*, being intermediate in coloration between that species and *T. clypeata*. This suggests the possibility that it represents a hybrid population derived from those two species: it occurs within the range of *T. emeryi* and just beyond the known eastern limit of *T. clypeata*, where conceivably reproductive isolating mechanisms are weaker. Nevertheless *T. furtiva* workers do have some distinctive features of their own, most notably shorter scapes than *T. emeryi* (SI 0.56–0.62 versus 0.64–0.68 in *T. emeryi*) and a shorter, broader petiole than both *T. clypeata* and *T. emeryi* (PL/HW 0.72–0.77 and FW/PL 0.40–0.45, versus PL/HW 0.79–0.94 and FW/PL 0.33–0.39 in the other two species). The wingless female (AW1834), here interpreted as an ergatoid queen, is larger than the *T. furtiva* workers (HW 0.67), with well developed ocelli (absent in the workers), a more robust mesosoma with one pair of standing hairs on the posterior margin of the pronotum (standing pilosity absent from the mesosoma dorsum in workers), and a larger gaster.

Distribution and biology. This species is known only from two collections taken at the same site in Eastern Cape Province, South Africa, with precise coordinates of 33.28792°S 27.46790°E (A. L. Wild, pers. comm.). The type workers were collected from a nest or nest fragment in an acacia (*Vachellia*) thorn, at the edge of low, scrubby coastal forest along an estuary.

Material examined. Known only from the type series.

Tetraponera gerdae (Stitz)

(Figs 1, 11, 38)

Sima gerdae Stitz 1911: 381. Holotype (by monotypy) dealate queen, Amani, Tanzania (Vosseler) (ZMHB) [examined]. Imaged on AntWeb: FOCOL1171.

Sima (*Tetraponera*) *gerdae* Stitz; Emery 1921: 27. Combination in *Sima* (*Tetraponera*).
Tetraponera gerdae (Stitz); Wheeler 1922b: 797. Combination in *Tetraponera*.

Worker measurements (n = 10). HW 0.41–0.57, HL 0.62–0.87, LHT 0.36–0.56, CI 0.61–0.68, FCI 0.17–0.20, REL 0.27–0.32, REL2 0.43–0.48, SI 0.48–0.58, SI3 1.02–1.26, FI 0.46–0.57, PLI 0.82–0.93, PWI 0.62–0.76, LHT/HW 0.85–1.00, CSC 0, MSC 0.

Worker diagnosis. Very similar to *T. continua* (see above) but head more elongate, on average (CI 0.61–0.68); petiole less slender (PLI 0.82–0.93), the petiolar node higher (PH/HW 0.56–0.67) (Fig. 11b) and broader (DPW/HW 0.43–0.53), and postpetiole broader (PPW/HW 0.56–0.64) (Fig. 1).

Comments. The holotype queen of *T. gerdae*, notable for its elongate head, closely matches a worker-associated queen from Kora, Kenya. The series of workers from Kora compare well with similar workers from Zimbabwe, Tanzania, Kenya and Eritrea. This species is closely similar to *T. continua*. An argument could be made for treating the two as conspecific, with the slight differences between them being attributable to geographical variation: *continua*-like workers (with a broader head and a more slender petiole and postpetiole) come from arid locations in northern Africa, and most *gerdae*-like samples (with a more elongate head and a more robust petiole and postpetiole) originate from east Africa. The distinctions are maintained, however, between the type worker of *T. continua* from Gotta, Ethiopia and an old series of *T. gerdae*-like workers collected by Penzig (1895) farther north, at Mount Lalamba, in what is now Eritrea (Fig. 38). Thus a simple picture of geographically differentiated populations does

not seem to apply. For now these two taxa are accorded status as separate species but it should be emphasized that sample sizes are limited and additional collections might erase the distinctions.

Distribution and biology. *T. gerdae* is known from scattered localities in mostly arid or semi-arid regions of east Africa (Fig. 38). The series from Kora, Kenya is labeled "ex *Acacia tortilis*", and the workers from Eritrea were in "*Stereospermum dentatum*". This latter collection was made by Penzig, who described the ants (misidentified as *T. penzigi*) occupying live terminal branches of the *Stereospermum* tree, with brood and coccids, and behaving aggressively towards intruders (Penzig 1895). Penzig considered *Stereospermum dentatum* (now a junior synonym of *Stereospermum kunthianum*) to be a true myrmecophyte, but subsequent commentators have expressed doubt (Bequaert 1922, Jolivet 1996), and *T. gerdae* is evidently not restricted to that plant. By contrast the related species, *T. penzigi*, nests only in the swollen stipular thorns of *Vachellia drepanolobium*.

Material examined (BMNH, FHGC, LACM, MHNG, MNHN, MSNG, NHMW, PSWC, SAMC, UCDC, USNM, ZMHB). **Eritrea**: *Semçnawî K'eyih Bahrî*: Mount Lalamba, near Keren (Penzig) [locality from Penzig (1895: 467); given on labels as "Abessinien", "Abissinia" and "Abyssinie"]; **Kenya**: *Baringo*: Lake Baringo (Sibley, G.); Lake Bogoria, geyser (Peters, M.); *Kajiado*: Nguruman, nr. Sampu R., 723 m (Copeland, R.); *Murang'a*: Kora (West, C.); *Samburu*: Barsaloi lugga (Dewhurst, C. F.); **Tanzania**: *Kilimanjaro*: Mkomazi Game Reserve, Kikolo plot (van Noort, S.); *Tanga*: Amani (Vosseler); **Zimbabwe**: *Bulawayo*: Bulawayo (ZBC Radio Mast) (Gardiner, A. J.).

Tetraponera liengmei (Forel)

(Figs 12, 37)

Sima Liengmei Forel 1894: 88. Syntypes, 33 workers, Delagoa, Mozambique (Liengme) (BMNH, MSNG, MCZC, MHNG, NHMB, NHMV) [examined]. 1 syntype worker from BMNH imaged on AntWeb: CASENT0902817. 1 syntype worker from MHNG imaged on AntWeb: CASENT0907472.

Sima (*Tetraponera*) *Liengmei* Forel; Arnold 1916: 181. Combination in *Sima* (*Tetraponera*).
Tetraponera liengmei (Forel); Wheeler 1922b: 798. Combination in *Tetraponera*.

Worker measurements (n = 7). HW 0.53–0.68, HL 0.69–0.95, LHT 0.41–0.57, CI 0.70–0.77, FCI 0.14–0.17, REL 0.27–0.30, REL2 0.36–0.42, SI 0.47–0.52, SI3 1.18–1.41, FI 0.46–0.50, PLI 0.84–0.88, PWI 0.61–0.70, LHT/HW 0.76–0.86, CSC 0–2, MSC 0–2.

Worker diagnosis. Small species; frontal carinae well separated, the distance between them exceeding basal scape width (FCI 0.14–0.17); scape short, about one-half head width (SI 0.47–0.52, SI2 0.35–0.39); anterior clypeal margin broadly convex, crenulate (Fig. 12a); profemur robust (FI 0.46–0.50), legs relatively short (LHT/HL 0.58–0.62); raised metanotal plate between mesonotum and propodeum, bounded anteriorly and posteriorly by distinct transverse impressions that are longitudinally rugulose; dorsal face of propodeum rounded laterally, subequal in length to declivitous face and rounding insensibly into the latter; petiole short, high and rounded (see PLI and PWI values), with a short anterior peduncle and without well differentiated anterior, dorsal and posterior faces; postpetiole broader than long. Integument predominantly smooth and shiny, with scattered fine punctures and weak reticulation. Standing pilosity inconspicuous, present on frontal carinae and usually also as a pair of setae on the vertex and on the pronotal humeri (but the last two pairs sometimes abraded or absent); absent from rest of mesosoma dorsum, petiole and postpetiole, sparse on succeeding abdominal segments 4–8. Dark brown, appendages lighter (Fig. 12).

Comments. *Tetraponera liengmei* belongs to a group of species whose workers have short scapes (SI 0.46–0.58), short broad petioles (PLI 0.72–1.01), well separated frontal carinae (MFC one quarter to one half of scape length), and dark blackish-brown coloration. *T. liengmei* is distinguished from the six other species in this group (*T. continua*, *T. cortina*, *T. gerdae*, *T. pedana*, *T. penzigi*, *T. pumila*) by the presence of standing pilosity on the frontal carinae (also on the vertex of the head and on the pronotal humeri—although these appear to be prone to abrasion) and by the laterally rounded propodeum and petiole, whose dorsal surfaces thus appear broadly convex in posterior view.

Distribution and biology. This species has been recorded from a limited number of sites in Mozambique, Zimbabwe, South Africa, and Namibia. Little is known about its biology. An old collection from Bulawayo, Zimbabwe was taken "in live hollow stems of bush"; more recent series from South Africa were collected "on *Maytenus sen-*

egalensis" [= *Gymnosporia senegalensis*] and "ex *Maytenus* infested with *Gascardia*". These meagre data suggest that the species inhabits live plant stems and possibly has an association with scale insects.

Material examined (ANIC, BMNH, MCZC, MHNG, MSNG, MZLU, NHMB, NHMW, NMWN, PSWC, SAMC, UCDC). **Mozambique**: *Maputo*: Delagoa (c.u.); Delagoa (Liengme); **Namibia**: *Kavango East*: West Caprivi Nature Reserve at 18°09'S 21°13'E (Pusch, M.; Marais, E.); **South Africa**: *Limpopo*: Amsterdam Farm, Louis Trichard district (Cillie, C. J.); Little Leigh Farm, Soutpansberg (Willis, C. K.); Pietersburg (Snowball, G.); *Western Cape*: 2 km NW Darling, 170 m (Danielsson, R.); **Zimbabwe**: *Bulawayo*: Bulawayo (Arnold); Bulawayo (c.u. [probably Arnold]).

Tetraponera mayri (Forel)

Sima Mayri Forel 1901: 53. Syntype(s), queen(s), "Kamerun" (Brauns) [not examined] [type(s) not in ZMUH, probably destroyed in World War II; R. Abraham, pers. comm., 1987]

Sima Mayri Forel; Santschi 1919: 84. Comparison with queen of *S. tessmanni*.
Sima (*Tetraponera*) *mayri* Forel; Emery 1921: 27. Combination in *Sima* (*Tetraponera*).
Tetraponera mayri (Forel); Wheeler 1922b: 798. Combination in *Tetraponera*.

Original description (translated from German): "*Sima Mayri* nov. sp. ♀. L. 6,3 mm. Head rectangular, 1 and 2/3 times as long as wide. The scape is much shorter than the distance from its posterior end to the occipital margin. Funicular segments much broader than long (usually more than twice as broad as long). Eyes in the middle. Median protrusion of clypeus three-toothed. Thorax arched from front to back, without edges or corners. Metanotum rounded. First node of pedicel somewhat longer than wide, margined anteriorly, wider posteriorly than anteriorly, short stalked. Its stalk is hollowed out above, bordered by two edges. Below the node stands a perpendicular, large longitudinal lobe, rounded anteriorly and posteriorly, which gives this species a very particular appearance. Second node wider than the first, wider than long, rounded, not much smaller than the first abdominal segment. Abdomen elongate. Legs fairly short. Smooth, shiny, diffuse punctures. On the thorax, especially on the metanotum, the punctures are strong and abundant. Very diffuse hairs; only ventrally on the abdomen a few more and longer, yellow hairs. Reddish-brown, with more reddish suture margins of all body parts. Mandibles, antennae, and legs dirty red-yellow; middle of femur brownish. Cameroon (Dr. Brauns). Through the lobe of the first petiolar segment distinctly characterized."

Comments. It is probable that the original description is based on a single individual, since no size range or other variation is mentioned. No surviving types or any other specimens of *T. mayri* are known. As noted by Santschi (1919: 84), this species and *T. tessmanni* appear to be closely related. Features in common between the queens of the two species include the conspicuous rectangular subpetiolar lobe, which is rounded anteriorly and posteriorly; very short scape; compressed funicular segments; petiole which is wider posteriorly than anteriorly; broad postpetiole; and reddish-brown color. Apparent differences between *T. mayri* and *T. tessmanni* include size (*T. tessmanni* queens 4–5 mm long, versus 6.3 mm in *T. mayri*), head shape (queen CI 0.71–0.78 in *T. tessmanni*, versus ~0.60 in *T. mayri*), configuration of the median clypeal lobe (anterior margin convex in *T. tessmanni*, tridentate in *T. mayri*), and petiole shape (*T. tessmanni*: wider than long and rounded anteriorly; *T. mayri*: somewhat longer than wide, and margined anteriorly).

Based on the above, workers of *T. mayri* are predicted to be similar to those of *T. tessmanni* but larger in size with a more elongate head and petiole, and a dentate clypeal lobe. Such predictions are incorporated into the worker-based key to Afrotropical *Tetraponera*.

Distribution and biology. This species was collected in German-occupied Cameroon by Dr. Johannes (Hans) Brauns, probably when he visited the region in 1894 (Anonymous, 2014). Nothing is known about the biology of *T. mayri* although, given its similarity to *T. tessmanni*, it is possibly a myrmecophyte-inhabiting specialist. Future surveys of the Cameroon ant fauna should be on the lookout for this species.

Material examined. None.

Tetraponera pedana sp. nov.

(Figs 13, 39)

Tetraponera psw104. Chomicki *et al.* 2015: figure S1. Placement in molecular phylogeny.

Type material. *Holotype worker*: Kenya, Kakamega, Kakamega Forest, Colubus, 1622 m, 0.362 34.589, Jan 2003, rainforest, canopy fogging ex *Teclea nobilis*, W. Freund, T.n. #101 (CASENT0794355) (NMKE). *Paratypes*: 12 workers, same data as holotype (CASENT0863343 to CASENT0863354) (CASC, FHGC, SAMC, UCDC).

Worker measurements (n = 10). HW 0.58–0.67, HL 0.67–0.79, LHT 0.37–0.47, CI 0.82–0.86, FCI 0.18–0.21, REL 0.28–0.31, REL2 0.33–0.37, SI 0.48–0.53, SI3 1.29–1.48, FI 0.46–0.52, PLI 0.92–0.99, PWI 0.70–0.86, LHT/HW 0.64–0.73, CSC 0, MSC 0.

Worker diagnosis. Small species, with broad head (CI 0.82–0.86); frontal carinae well separated, the minimum distance between them about one-fifth of head width (FCI 0.18–0.21, MFC/EL 0.50–0.61, MFC/SL 0.35–0.43); scape short, about one-half head width (SI 0.48–0.53) and two-fifths of head length (SI2 0.40–0.44); anterior clypeal margin with a denticulate medial protrusion (Fig. 13a); profemur robust (FI 0.46–0.52), legs short (LHT/HL 0.55–0.61); metanotal plate conspicuous, oval in shape, about four-fifths the length of the mesonotum, and bounded anteriorly and posteriorly by transverse impressions that are longitudinally rugulose; dorsal face of propodeum flattened, laterally submarginate, shorter in length than the declivitous face and rounding insensibly into the latter; petiole relatively short, high and rounded, about as high as long (see PLI and PWI values), with a distinct anterior peduncle, a steeply ascending anterior face and more gently descending posterior face (Fig. 13b) (posterior face equally steep in some individuals); in dorsal view, petiole one-third to two-fifths of head width (DPW/HW 0.32–0.43); postpetiole broader than long (PPW/HW 0.47–0.56). Dorsum of head, mesosoma, petiole, postpetiole and gaster largely smooth and shiny, with scattered fine punctures, becoming reticulate-coriarious to reticulate-striolate and subopaque on anterior portion of head, side of mesosoma, side of petiole, and (sometimes) dorsal face of propodeum. Standing pilosity very sparse, absent from the dorsum of head, mesosoma, petiole, postpetiole, and abdominal tergites 4–6. Dark brown, appendages lighter.

Comments. A combination of broad head (CI 0.82–0.86), well separated frontal carinae, shiny integument, short legs, and a short, high petiole characterizes the workers of this species. Workers of *T. penzigi* have a similarly broad head and distanced frontal carinae, but the head and mesosoma are more heavily sculptured and opaque, and the legs are longer (LHT/HW 0.77–0.88 in *T. penzigi*, versus 0.64–0.73 in *T. pedana*). Other related species (*T. gerdae*, *T. continua, T. cortina*) differ from *T. pedana* by their more elongate heads (worker CI 0.61–0.73) and more narrowly separated frontal carinae relative to eye length (worker MFC/EL 0.30–0.48).

Distribution and biology. *T. pedana* is known from the Central African Republic, Uganda, and Kenya, from collections made in rainforest and rainforest edge. Foraging workers have been taken in sweep samples, canopy fogging samples, and even pitfall traps. There is no information about the nesting biology of this species, and queens have not yet been found.

Material examined (ASIC, CASC, FHGC, LACM, NMKE, PSWC, UCDC). **Central African Republic**: *Sangha-Mbaéré*: P.N. Dzanga-Ndoki, 38.6 km 173° S Lidjombo, 350 m (van Noort, S.); **Kenya**: *Kakamega*: Kakamega Forest, 1600 m (Wagner, T.); Kakamega Forest, Busumbuli, 1553 m (Wagner, T.); Kakamega Forest, Colobus, 1622 m (Freund, W.); Kakamega Forest, Ivakale, 1585 m (Hita Garcia, F.); Kakamega Forest, Yala, 1527 m (Freund, W.); **Uganda**: *Kabarole*: Kibale NP, Kanyawara Biological Station, 1500 m (van Noort, S.); *Masindi*: Budongo Forest, vic. Sonso, 1050 m (Wagner, T.).

Tetraponera penzigi (Mayr)

(Figs 14, 39)

Sima Penzigi Mayr 1907: 10. Syntypes, 9 workers, 2 alate queens, 2 males, Usambara, Tanzania (Sjöstedt) (NHMV), 2 workers, Kahe, Kilimanjaro, Tanzania [as "Kilim."] (Sjöstedt) (NHMV), 1 worker, Kahe, Kilimanjaro [as "Kilimand."], Tanzania (Sjöstedt) (MHNG) [examined]. 1 worker syntype from NHMV imaged on AntWeb: CASENT0915851. Syntypes, 3 workers, Usambara, Tanzania (Sjöstedt) (ZMHB) [not examined]; imaged on AntWeb: FOCOL1155, FOCOL1156, FOCOL1157.

Tetraponera scotti Donisthorpe 1931: 498. Syntypes, 1 worker (head only), 1 dealate queen, Dyem-Dyem Forest, 8000–9000 ft., Ethiopia (H. Scott) (BMNH) [examined]. Imaged on AntWeb: CASENT0902911, CASENT0902818. **Syn**. **nov**.

Tetraponera penzigi v. *praestigiatrix* Santschi 1937a: 50. Syntype, 1 dealate queen, Dongabesh [as "Dongerbeach"], Mbulu Dist., 5500 ft., Tanzania (B. D. Butt) (NHMB) [examined]. Imaged on AntWeb: CASENT0915538. **Syn**. **nov**.
Sima (*Tetraponera*) *zavattarii* Menozzi 1939: 99. Syntypes, 3 workers, Mega, Ethiopia (E. Zavattari), 1 worker, Neghelli, Ethiopia (E. Zavattari) (IEGG) [examined]. **Syn**. **nov**.

Sima (*Tetraponera*) *Penzigi* Mayr; Arnold 1916: 180. Combination in *Sima* (*Tetraponera*).
Tetraponera penzigi (Mayr); Wheeler 1922b: 800. Combination in *Tetraponera*.
Tetraponera penzigi (Mayr); Chomicki *et al.* 2015: figure S1. Placement in molecular phylogeny.

Tetraponera penzigi praestigiatrix Santschi; Ward 1990: 489. Subspecies of *penzigi*.

Tetraponera zavattarii (Menozzi); Ward 1990: 489. Combination in *Tetraponera*.

Worker measurements (n = 12). HW 0.62–0.83, HL 0.78–1.05, LHT 0.50–0.72, CI 0.78–0.82, FCI 0.20–0.25, REL 0.29–0.33, REL2 0.36–0.43, SI 0.47–0.53, SI3 1.22–1.35, FI 0.40–0.46, PLI 0.80–0.95, PWI 0.69–0.84, LHT/HW 0.77–0.88, CSC 0, MSC 0.

Worker diagnosis. Small to medium in size, with broad head (CI 0.78–0.82); frontal carinae well separated, the minimum distance between them one-fifth to one quarter of head width (FCI 0.20–0.25, MFC/EL 0.50–0.65, MFC/SL 0.40–0.52); scape short, about one-half head width (SI 0.47–0.53) and two-fifths of head length (SI2 0.38–0.41); anterior clypeal margin with a broadly convex, crenulate medial protrusion (Fig. 14a); profemur relatively slender (FI 0.40–0.46), legs relatively long (LHT/HW 0.77–0.88, LHT/HL 0.61–0.72); metanotal plate conspicuous, about one-half to two-thirds the length of the mesonotum, and bounded anteriorly and posteriorly by transverse impressions that are longitudinally rugulose; dorsal face of propodeum flattened, laterally submarginate, as long as or longer than the declivitous face, and weakly differentiated from the latter; petiole relatively short, high and rounded (see PLI and PWI values), with a distinct anterior peduncle and without well differentiated anterior, dorsal and posterior faces (Fig. 14b); in profile, petiole not quite as high as long; in dorsal view, petiole two-fifths to one-half of head width (DPW/HW 0.40–0.50); postpetiole broader than long (PPW/HW 0.48–0.57). Dorsum of head and mesosoma predominantly reticulate-coriarious and opaque, becoming more weakly sculptured and sublucid laterally, and on petiole, postpetiole, and gaster. Standing pilosity very sparse, absent from the dorsum of head, mesosoma, petiole, postpetiole, and abdominal tergites 4–6. Dark brown to brownish-black, antennae and mandibles lighter.

Comments. This species can be recognized by its broad head (worker CI 0.78–0.82, queen CI 0.64–0.68), well separated frontal carinae, relatively long legs (worker LHT/HW 0.77–0.88, queen LHT/HW 0.94–1.01), and distinctive sculpture: dorsum of head and mesosoma finely but densely reticulate-coriarious and opaque. Related species have a shinier integument, and either a more elongate head and more closely adjacent frontal carinae (*T. continua*, *T. cortina*, *T. gerdae*), or shorter legs (*T. pedana*). *T. penzigi* also has larger workers, on average, than these other species.

Distribution and biology. *Tetraponera penzigi* occurs from southern Ethiopia to Tanzania, and lives only in the swollen stipular thorns of *Vachellia drepanolobium*. It interacts in a distinctive manner with its hostplant, differing in colonization ability, spatial distribution, competitive ability, and herbivore deterrence from two species of *Crematogaster* that are also obligate residents of *V. drepanolobium* (Hocking 1970; Young *et al*. 1997; Stanton *et al*. 2002; Baker *et al*. 2017; Boyle *et al*. 2019). The record of *T. penzigi* nesting in *Stereospermum dentatum* (Bignoniaceae) (Penzig 1895) refers to the closely related species, *T. gerdae*.

Material examined (BMNH, CASC, CUIC, FHGC, HZIC, IEGG, LACM, MHNG, NHMB, NHMW, NMKE, PSWC, SAMC, STDC, UCDC, USNM). **Ethiopia**: *Oromia*: Dyem-Dyem Forest, 2590 m (Scott, H.); Mega (Zavattari, E.); Neghelli (Zavattari, E.); **Kenya**: *Kajiado*: 26 mi SW Nairobi, 1615 m (Irwin, M. E.; Ross, E. S.); 60 mi S Nairobi, on Nmanga Rd. (DeMasi, V.); Oloitokitok [as "N Loitokitok (= Oloit.)"], 1800 m (Zettel, H.); *Laikipia*: 30 km S Mpala Res. Centre, 1650 m (Warui, C.; Abonyo, E.); 4 km SNW [sic] Mpala Research Centre, 1750 m (Snelling, R. R.); Mpala, 1800 m (Palmer, T.); Mpala Farm, 1800 m (Stanton, M. L.); Mpala Research Centre, 1650 m (Snelling, R. R.); vic. Mpala Farm, 1800 m (Isbell, L.); *Machakos*: Hopcrofts Game Ranch, Athi River (Stapley, L.); *Marsabit*: Mt. Kulal, 885 m (Stager, K. E.); *Nairobi City*: Kitengela (Martins, D. J.); Nairobi, 2 mi S airport (Janzen, D. H.); *Nakuru*: Hell's Gate Nat. Park (Zdárková, E.); *Nyeri*: Burguret (Strobele); Mweiga (Hogue, C. L.); *Samburu*: Segera Ranch, Laikipia Plateau (Pruetz, J.); **Tanzania**: *Arusha*: Ardai (Hocking, B.); Arusha (Mann, W. M.); *Kilimanjaro*: Kahe, Kilimanjaro [as "Kilim."] (Sjöstedt); Kahe, Kilimanjaro [as "Kilimand."] (c.u.); Sanya (Hocking, B.); *Manyara*: Dongabesh [as "Dongerbeach"], 1675 m (Butt, B. D.); Lake Manyara (Sibley, G.); Umbulu (Mann,

W. M.); *Mara*: Serengeti Visitor Center (Dash, S. T.); *Tanga*: Usambara [as "Usumbara"] (c.u.); Usambara [as "Usumbara"] (Sjöstedt); **Uganda**: *district unknown*: Karamodja [= Karamoja Province] (Hamann).

***Tetraponera pumila* sp. nov.**
(Figs 15, 40)

Type material. *Holotype worker*: Burundi, Muyinga, Ruvubu National Park, 1382 m, -2.98144 30.45531, 20 Jan 2010–4 Feb 2010, edge of forest, near Ruvubu R., Malaise trap, R. Copeland (CASENT0863337) (USNM). *Paratypes*: 4 workers, same data as holotype (CASENT0796550, CASENT0863335, CASENT0863336, CASENT0863338) (CASC, UCDC, USNM).

Worker measurements (n = 10). HW 0.42–0.53, HL 0.54–0.66, LHT 0.30–0.38, CI 0.70–0.83, FCI 0.17–0.22, REL 0.29–0.34, REL2 0.39–0.44, SI 0.46–0.54, SI3 1.12–1.40, FI 0.42–0.49, PLI 0.85–1.01, PWI 0.64–0.85, LHT/HW 0.67–0.75, CSC 0, MSC 0.

Worker diagnosis. Very small species (HW 0.42–0.53), with moderately elongate head (CI 0.70–0.83); frontal carinae widely separated, the distance between them about twice basal scape width or more (FCI 0.17–0.22, MFC/SL 0.33–0.44); scape short, about one-half head width (SI 0.46–0.54) and slightly more than one-third of head length (SI2 0.34–0.42); anterior clypeal margin with short, truncate median protrusion, furnished with three blunt denticles (Fig. 15a); profemur moderately robust (FI 0.42–0.49), legs short (LHT/HL 0.49–0.59); metanotal plate conspicuous, about 0.7× the length of the mesonotum, bounded anteriorly by a weak transverse impression and posteriorly by a better developed impression with longitudinal rugulae; dorsal face of propodeum somewhat flattened, rather short, and rounding insensibly into the declivitous face; petiole short, high and rounded (see PLI and PWI values), with a distinct anterior peduncle, a steeply ascending anterior face and more gently descending posterior face (Fig. 15b); in profile, petiole as high as or higher than long; in dorsal view, petiole one-third to two-fifths of head width (DPW/HW 0.34–0.43); postpetiole broader than long (PPW/HW 0.50–0.54). Dorsum of head, mesosoma and petiole with dense reticulate-coriarious sculpture, subopaque; sculpture weakened laterally (sometimes also medially on the frons) and on postpetiole; gaster with weak reticulate-coriarious sculpture, sublucid. Median tooth of clypeal lobe flanked by a distinctive pair of blunt setae, about 0.07 mm long and directed anteroventrally; otherwise standing pilosity very sparse, absent from the dorsum of head (including frontal carinae), mesosoma, petiole, postpetiole, and abdominal tergites 4–6. Dark brown, appendages lighter (Fig. 15).

Comments. This species can be recognized by its small size (worker HW 0.42–0.53); unique clypeal pilosity, consisting of pair of stout setae on the clypeal margin, directed anteroventrally, and no others; short, high petiole; and rather dense sculpture on the dorsum of the head and mesosoma. A single worker from vic. Irangi, Sud-Kuvi, DR Congo, has the upper half of the head more extensively shiny, with scattered punctures, but is otherwise structurally similar to the remaining material. The only other members of the *Tetraponera allaborans* group in continental Africa that are this small—*Tetraponera continua*, *T. cortina*, *T. dispar*, and *T. gerdae*—have more extensive clypeal pilosity and a shinier integument.

Distribution and biology. *T. pumila* is widely distributed, from Ghana to Kenya, south to Zimbabawe, but infrequently collected. Collection sites include evergreen and semideciduous forest. No nest series have been collected.

Material examined (ASIC, BMNH, CASC, FHGC, LACM, SAMC, UCDC, USNM). **Burundi**: *Muyinga*: Ruvubu National Park, 1382 m (Copeland, R.); **DR Congo**: *Haut-Katanga*: 38 mi E Sandoa, 960 m (Ross, E. S.; Leech, R. E.); *Sud-Kivu*: vic. Irangi, 900 m (Wagner, T.); **Ghana**: *Eastern*: Mampong (Room, P.); Tafo (Collingwood, C. A. [as "C. A. C."]); **Kenya**: *Kakamega*: Kakamega Forest, 1600 m (Wagner, T.); Kakamega Forest, Busumbuli, 1553 m (Wagner, T.); *Kilifi*: 20 km WSW Malindi, 20 m (Ward, P. S.); Arabuko Sokoke Forest, 45 m (Hita Garcia, F.; Fischer, G.); **Uganda**: *Masindi*: Budongo Forest, vic. Sonso, 1050 m (Wagner, T.); **Zimbabwe**: *Mashonaland Central*: Zambesi Valley, 7 km SE Angwa Bridge (Weyrich, J.).

Tetraponera tessmanni (Stitz)

(Figs 16, 35)

Sima tessmanni Stitz 1910: 131. Syntypes, 2 workers, Alen, Equatorial Guinea (Tessmann) (MHNG, NHMB) [examined]. 1 syntype worker from MHNG imaged on AntWeb: CASENT0907476. Syntypes, 1 dealate queen, 2 workers, Alen, Equatorial Guinea (Tessmann) (ZMHB) [not examined]; imaged on AntWeb: FOCOL1166, FOCOL1167, FOCOL1168.

Viticicola tessmanni var. *castanea* Wheeler 1922a: 112. Syntypes, 17 workers, 3 dealate queens, 1 ergatoid queen, Avakubi, Democratic Republic of Congo (H. O. Lang) (AMNH, LACM, MSNG, MCZC, NHMB, USNM) [examined]. 1 syntype worker from NHMB imaged on AntWeb: CASENT0915540. Synonymy by Brown 1950: 248.

Tetraponera tessmanni (Stitz); Wheeler 1918: 304. Description of larva. Combination in *Tetraponera*.
Sima Tessmannii Stitz; Santschi 1919: 84. Description of queen.
Viticola tessmanni (Stitz); Wheeler 1919: 130. Combination in *Viticicola.*
Sima (*Tetraponera*) *tessmanni* Stitz; Emery 1921: 28. Combination in *Sima* (*Tetraponera*).
Viticola tessmanni (Stitz); Wheeler 1922a: 109. Combination in *Viticicola.*
Viticola tessmanni (Stitz); Wheeler 1922a: 111. Description of male.
Viticola tessmanni (Stitz); Wheeler & Wheeler 1956: 391. Description of larva.
Tetraponera tessmanni (Stitz); Ward 1990: 489. Combination in *Tetraponera*.
Tetraponera tessmanni (Stitz); Chomicki *et al.* 2015: figure S1. Placement in molecular phylogeny.

Tetraponera castanea (Wheeler); Ward 1990: 489. Combination in *Tetraponera*, as junior synonym of *T. tessmanni.*

Worker measurements (n = 10). HW 0.58–0.66, HL 0.73–0.80, LHT 0.42–0.47, CI 0.76–0.84, FCI 0.20–0.24, REL 0.20–0.24, REL2 0.24–0.31, SI 0.41–0.44, SI3 1.42–1.73, FI 0.45–0.50, PLI 1.06–1.21, PWI 0.84–0.98, LHT/HW 0.69–0.73, CSC 2–7, MSC 5–8.

Worker diagnosis. Small species (HW 0.58–0.66, LHT 0.42–0.47); head broad, with rounded sides (Fig. 16a), and small flattened eyes (REL 0.20–0.24); palp formula 4p3,3 or 3,3; frontal carinae widely separated, the minimum distance between them about one-half scape length; scape very short, less than one-half head width (SI 0.41–0.44, SI2 0.32–0.37); anterior clypeal margin broadly convex, straight or weakly immarginate medially, edentate; profemur short and robust (FL/HW 0.67–0.70, FI 0.45–0.50), hind legs short (LHT/HL 0.56–0.59); mesopropodeal groove long and deeply impressed (Fig. 16b); dorsal face of propodeum strongly convex in profile, and rounding insensibly into the longer declivitous face; petiole short, high, and broad (see petiolar indices), rounded in profile and with a prominent ventral process, becoming thin and lamellate anteroventrally (Fig. 16b); postpetiole broader than long. Integument smooth and shiny, with scattered fine punctures, becoming weakly reticulate on the lower half of the mesopleuron and metapleuron; mesopropodeal groove irregularly rugulose. Standing pilosity present as scattered long hairs on the head (CSC 2–7), mesosoma (MSC 5–8), petiole, postpetiole, and gaster, accompanied on most of body by a dense underlying subdecumbent pubescence that grades into short suberect pilosity. Varying in color from light yellowish- or orange-brown to medium brown.

Comments. Among African *Tetraponera* the worker of this species is easily recognized by its diminutive size, very small eyes (REL 0.20–0.24), short scapes and legs, deep mesopropodeal impression, and short, broad petiole with prominent ventral extension. For a discussion of the relationship to *T. mayri* see under that species.

Distribution and biology. Known from Ghana to DR Congo, *T. tessmanni* is an obligate inhabitant of the myrmecophytic liana *Vitex thyrsiflora* (Bequaert 1922; Wheeler 1922a; Schnell & Grout de Beaufort 1966). The colonies of *T. tessmanni* inhabit live stems of the vine, and the aggressive stinging workers actively patrol the foliage of the plant, providing an effective deterrent to herbivory (Djiéto-Lordon *et al.* 2005). The ants are thought to derive all or most of their nutrition from the plant itself, by feeding on callus tissue which develops in ant-excavated cavities in the internal wall of the vine (Bailey 1922). Examining pellets from the trophothylax (food-pouch) of *T. tessmanni* larvae, Wheeler & Bailey (1920) found plant tissue, spores, hyphae, and remains of other larvae. Colonies of *T. tessmanni* are polygynous, and there is considerable variation in queen size, including ergatoid and subapterous forms, as well as normal dealate queens (Wheeler 1922a: 108).

Material examined (AMNH, CASC, CPDC, CUIC, DZUP, LACM, MCZC, MHNG, MSNG, NHMB, PSWC, SAMC, UCDC, USNM). **Cameroon**: *Est*: Masea (McKey, D.); *Sud-Ouest*: Nta Ali Forest Reserve, Mbio, sul de Mamfé (Blatrix, R.); **Central African Republic**: *Sangha-Mbaéré*: P.N. Dzanga-Ndoki, 21.4 km 53° NE Bayanga, 510 m (van Noort, S.); P.N. Dzanga-Ndoki, 38.6 km 173° S Lidjombo, 350 m (van Noort, S.); P.N. Dzanga-Ndoki, Mabéa Bai, 21.4 km 53° NE Bayanga, 510 m (Fisher, B. L.); **DR Congo**: *Haut-Uélé*: Medje (Lang, H. O.); Medje

(c.u.); *province unknown*: "Congo Belge" (c.u.); *Tshopo*: Avakubi (Lang, H. O.); **Equatorial Guinea**: *Wele-Nzas*: Alen (Tessman, G.); **Gabon**: *Woleu-Ntem*: 20.5 km 110° ESE Minvoul, 600 m (Fisher, B. L.); **Ghana**: *Eastern*: Pimpimso (Box, H. E.).

Tetraponera allaborans-group: new synonymy of Malagasy species

The *T. allaborans*-group is represented in the Malagasy region by about 30 species (10 described), which form a single clade (Chomicki *et al.* 2015; Ward, unpubl.). This group will receive treatment in a forthcoming revision. Here synonymy is documented for five of the described species (*T. hysterica*, *T. longula*, *T. mandibularis*, *T. morondaviensis*, and *T. sahlbergii*). With these synonymies established, the remaining valid names (*T. diana*, *T. exasciata*, *T. fictrix*, *T. perlonga*, and *T. rakotonis*) are believed to represent bona fide species.

Tetraponera hysterica (Forel)

(Fig. 17)

Sima hysterica Forel 1892: 258. Syntypes, 3 workers, Village de Nosibé, Imerina, Madagascar (Sikora) (MSNG, MHNG) [examined]. 2 syntype workers from MHNG imaged on AntWeb: CASENT0101635, CASENT0101941. 1 syntype worker from MSNG imaged on AntWeb: CASENT0102034.

Sima Sahlbergi var. *inflata* Emery 1899a: 273. Syntypes, 4 workers, Baie d'Antongil, Madagascar (Mocquerys) (MSNG, MHNG) [examined]. 1 syntype worker from MHNG imaged on AntWeb: CASENT0101575. **Syn. nov.**

Sima (*Tetraponera*) *hysterica* Forel; Emery 1921: 27. Combination in *Sima* (*Tetraponera*).
Tetraponera hysterica (Forel); Wheeler 1922c: 1015. Combination in *Tetraponera*.
Tetraponera hysterica (Forel); Chomicki *et al.* 2015: figure S1. Placement in molecular phylogeny.

Sima hysterica var. *inflata* Emery; Forel 1904: 376. Variety of *S. hysterica*.
Sima (*Tetraponera*) *hysterica* var. *inflata* Emery; Emery 1921: 27. Combination in *Sima* (*Tetraponera*).
Tetraponera hysterica var. *inflata* (Emery); Wheeler 1922c: 1015. Combination in *Tetraponera*.
Tetraponera hysterica inflata (Emery); Ward 1990: 488. Subspecies of *T. hysterica.*

Worker measurements (n = 9). HW 0.73–0.89, HL 0.96–1.22, LHT 0.77–0.92, CI 0.71–0.76, FCI 0.14–0.17, REL 0.25–0.29, REL2 0.34–0.38, SI 0.60–0.67, SI3 1.63–1.93, FI 0.39–0.44, PLI 0.63–0.69, PWI 0.48–0.56, LHT/HW 0.96–1.06, CSC 0–4, MSC 7–14.

Worker diagnosis. Moderate-sized species, with somewhat elongate head and small eyes (see ocular indices); minimum distance between frontal carinae exceeding basal scape width (FCI 0.14–0.17); scape moderately long, notably more than one-half head width and about one-half head length (SI 0.61–0.64, SI2 0.45–0.51); median clypeal lobe crenulate, with a weak (or absent) median tooth, two slightly larger but blunt lateral teeth, and outer lateral teeth reduced to slight protrusions or absent (Fig. 17a); profemur moderately robust (FI 0.39–0.44); mesosoma with a differentiated, transverse metanotal plate, about one third the length of the mesonotum; metanotal plate with a weak median groove; dorsal face of propodeum laterally submarginate, longer than declivitous face and rounding insensibly into the latter; petiole moderately robust (see PLI and PWI values), with a differentiated anterior peduncle and anteroventral tooth, the node with steep anterodorsal face and shallower posterodorsal face (Fig. 17b); postpetiole longer than broad. Integument shiny to sublucid, with weak reticulation and scattered punctures, the punctures moderately coarse on the head, finer elsewhere. Standing pilosity sparse on head, with 0–2 (usually 1) supraocular pair of setae, more common on mesosoma (MSC 7–14) but absent from dorsal face of propodeum. Dark brownish-black, antennae and mandibles lighter.

Comments. The key features of *Tetraponera hysterica* workers are the relatively small eyes and elongate head (such that REL2 0.34–0.38 and CI 0.71–0.76), crenulate (as opposed to conspicuously toothed) median clypeal lobe, short metanotal plate with median furrow, and dark brownish-black coloration. *Tetraponera hysterica* is superficially similar to *T. longula*, another dark-colored rainforest species, but *T. longula* workers have conspicuous clypeal teeth, more closely contiguous frontal carinae (FCI 0.09–0.12) and a more slender petiole (PLI 0.46–0.57) without a well developed anteroventral tooth. *T. hysterica* is actually more closely related to a group of dry forest

species that includes *T. morondaviensis* and *T. perlonga* (Chomicki *et al.* 2015), differing from them by its darker coloration, submarginate propodeum, medially furrowed metanotal plate, and details of pilosity, head shape and clypeal dentition.

Distribution and biology. *T. hysterica* is a rather uncommon rainforest species, known from scattered locations along the east coast of Madagascar, from 14°S to 25°S. It appears to be a generalist inhabitant of dead twigs.

Tetraponera longula (Emery)

(Fig. 18)

Sima Sahlbergi var. longula Emery 1895a: 340. Syntypes, 2 workers, Diego-Suarez, Madagascar (C. Alluaud) (MSNG, MNHN) [examined]. 1 syntype worker from MSNG imaged on AntWeb: CASENT0102031; 1 syntype worker from MNHN imaged on AntWeb: CASENT0101395.

Sima sahlbergi r. *deplanata* Forel 1904: 375. Holotype worker (by monotypy), Fort Dauphin (Sikora) (ZMAS) [examined]. **Syn. nov.**

Sima (*Tetraponera*) *sahlbergi* var. *longula* Emery; Emery 1921: 28. Combination in *Sima* (*Tetraponera*).
Tetraponera sahlbergi var. *longula* (Emery); Wheeler 1922c: 1016. Combination in *Tetraponera*.
Tetraponera sahlbergi longula (Emery); Ward 1990: 488. Subspecies of *T. sahlbergii*.
Tetraponera longula (Emery); Chomicki *et al.* 2015: figure S1. Raised to species; placement in molecular phylogeny.

Sima (*Tetraponera*) *sahlbergi* subsp. *deplanata* Forel; Emery 1921: 28. Combination in *Sima* (*Tetraponera*).
Tetraponera sahlbergi subsp. *deplanata* (Forel); Wheeler 1922c: 1016. Combination in *Tetraponera*.

Worker measurements (n=12). HW 0.67–0.81, HL 0.85–1.04, LHT 0.62–0.74, CI 0.73–0.80, FCI 0.09–0.12, REL 0.28–0.31, REL2 0.37–0.40, SI 0.58–0.62, SI3 1.43–1.69, FI 0.40–0.47, PLI 0.46–0.57, PWI 0.40–0.48, LHT/HW 0.89–0.96, CSC 2, MSC 2–7.

Worker diagnosis. Small- to medium-sized species, with somewhat elongate head, and eyes of moderate size (see ocular indices); minimum distance between frontal carinae slightly exceeding basal scape width (FCI 0.09–0.12); scape moderately long, greater than one-half head width and less than one-half head length (SI 0.58–0.62, SI2 0.42–0.49); median clypeal lobe with prominent median tooth and paired lateral teeth, 0.02–0.05 mm long; flanking this are paired, outer lateral teeth that are usually smaller, and often reduced to slight protrusions (Fig. 18a); profemur moderately robust (FI 0.40–0.47); mesosoma with a differentiated, transverse metanotal plate, about one third the length of the mesonotum; dorsal face of propodeum laterally submarginate, notably longer than declivitous face and rounding into the latter; petiole slender (PLI 0.46–0.57, PWI 0.40–0.48), with a well differentiated anterior peduncle, the node with relatively shallow and similar anterodorsal and posterodorsal faces, as seen in profile (Fig. 18b); postpetiole longer than broad. Integument shiny to sublucid, with weak reticulation and scattered punctures, the punctures rather fine on all surfaces. Standing pilosity sparse on head, with 1 pair of supraocular setae (CSC = 2); mesosoma typically with one pair of rather long standing hairs on the pronotal corners, and a pair of standing hairs on the mesonotum, but occasionally more or fewer (MSC 2–7); standing pilosity absent from dorsal face of propodeum. Dark brownish-black, antennae and distal portions of legs lighter.

Comments. This worker of this species can be recognized by a combination of its small to medium size, dark color, well developed clypeal teeth, raised metanotal plate (lateral view), and slender petiole (PLI 0.46–0.57). *T. longula* is most closely related to a similar, undescribed sister species with a more robust petiole (PLI 0.58–0.67), referred to as "*Tetraponera longula*_cf" in Chomicki *et al.* (2015). *Tetraponera longula* differs from *T. sahlbergii*, the species with which is has been associated nomenclaturally, by its prominent clypeal teeth, shinier integument, and elongate propodeum with submarginate basal face.

Distribution and biology. *T. longula* has a distribution that spans the length of the island of Madagascar. It is confined to rainforest and rainforest edge, where it nests in dead twigs. The type locality is "Diego Suarez" but presumably these specimens, collected by Alluaud, were taken in a nearby rainforest location such as Montagne d'Ambre.

Tetraponera mandibularis (Emery)

(Fig. 19)

Sima mandibularis Emery 1895a: 340. Holotype dealate queen (by monotypy), Diego-Suarez, Madagascar (C. Alluaud) (MSNG) [examined]. Imaged on AntWeb: CASENT0102030.

Sima flexuosa Santschi 1911b: 120. Syntypes, 3 workers, "Madagasc." (MHNG, NHMB) [examined]. 2 syntype workers from NHMB imaged on AntWeb: CASENT0101154, CASENT0101155. 1 syntype worker from MHNG imaged on AntWeb: CASENT0101979. **Syn. nov.**

Sima (*Tetraponera*) *mandibularis* Emery; Emery 1921: 27. Combination in *Sima* (*Tetraponera*).
Tetraponera mandibularis (Emery); Wheeler 1922c: 1015. Combination in *Tetraponera*.
Tetraponera mandibularis (Emery); Chomicki *et al.* 2015: figure S1. Placement in molecular phylogeny.

Sima (*Tetraponera*) *flexuosa* Santschi; Emery 1921: 27. Combination in *Sima* (*Tetraponera*).
Tetraponera flexuosa (Santschi); Wheeler 1922c: 1014. Combination in *Tetraponera*.

Worker measurements (n=8). HW 0.74–0.93, HL 0.95–1.23, LHT 0.70–0.91, CI 0.76–0.80, FCI 0.12–0.16, REL 0.28–0.31, REL2 0.37–0.40, SI 0.62–0.71, SI3 1.58–1.84, FI 0.40–0.43, PLI 0.51–0.57, PWI 0.41–0.45, LHT/HW 0.91–0.97, CSC 4–10, MSC 8–17.

Worker diagnosis. Moderate-sized species, with somewhat elongate head, and eyes of moderate size (see ocular indices); minimum distance between frontal carinae exceeding basal scape width; scape relatively long, about two-thirds of head width and about one-half head length (SI 0.62–0.71, SI2 0.49–0.55); median clypeal lobe protruding only slightly, weakly crenulate; profemur moderately robust (FI 0.40–0.43); mesosoma with a differentiated, transverse metanotal plate, about one third the length of the mesonotum, flanked anteriorly and posteriorly by relatively weak transverse grooves; dorsal face of propodeum subequal in length to declivitous face, and rounding insensibly into the latter; petiole relatively slender (see PLI and PWI values), with a well differentiated anterior peduncle and weak to absent anteroventral tooth, the node with relatively shallow and similar anterodorsal and posterodorsal faces, as seen in profile (Fig. 19b); postpetiole longer than broad. Integument shiny to sublucid, with weak reticulation and scattered punctures. Standing pilosity relatively common on head (CSC 4–10) and mesosoma (MSC 8–17), occasionally present as one to several hairs on dorsal face of propodeum. Dark brown, with antennae, mandibles, clypeus, and legs variably lighter.

Comments. Distinguishing features of the worker of *T. mandibularis* are its dark brown (not black) color, weakly protruding and crenulate clypeal margin, relatively long scapes (SI 0.62–0.71), moderate levels of standing pilosity, and relatively slender petiole (PLI 0.51–0.57). The queen is similar but the clypeal margin is furnished with a robust median tooth, flanked by two blunt lateral teeth. Phylogenetic analysis (Chomicki *et al.* 2015) demonstrates that *T. mandibularis* is closely related to *T. fictrix*, differing primarily by its darker color (*T. fictrix* is reddish-orange). There are a few collections of *T. mandibularis* workers that are lighter in color, suggesting the possibility of occasional introgression with *T. fictrix*.

Distribution and biology. This is a generalist inhabitant of dead twigs that occurs in both rainforest and tropical dry forest, from northern Madagascar south to about 23°S.

Tetraponera morondaviensis (Forel)

(Fig. 20)

Sima Sahlbergii race *morondaviensis* Forel 1891: 206. Syntype, 1 worker, Morondava, Madagascar (Grevé) (MHNG) [examined]. Imaged on AntWeb: CASENT0101715.

Sima hysterica r. *dimidiata* Forel 1895: 487. Syntypes, 4 workers, Central Madagascar (Sikora) (MSNG, MHNG) [examined]. 1 syntype worker from MSNG imaged on AntWeb: CASENT0102035. 3 syntype workers from MHNG imaged on AntWeb: CASENT0101049, CASENT0101050, CASENT0101051. **Syn. nov.**

Sima arrogans Santschi 1911b: 117. Holotype queen (by monotypy), partially dealate, Morondava, Madagascar (G. Grandidier) (MNHN) [examined]. Imaged on AntWeb: CASENT0101397. **Syn. nov.**

Sima demens Santschi 1911d: 282. Holotype worker (by monotypy), Andriolana, Baie d'Ampasindava, Madagascar (Joly) (MNHN) [examined]. Imaged on AntWeb: CASENT0101396. **Syn. nov.**

Sima morondaviensis Forel; Dalla Torre 1893: 54. Raised to species.

Sima (*Tetraponera*) *sahlbergi* subsp. *morondaviensis* Emery; Emery 1921: 28. Combination in *Sima* (*Tetraponera*); subspecies of *S. sahlbergii*.
Tetraponera sahlbergi subsp. *morondaviensis* (Emery); Wheeler 1922c: 1016. Combination in *Tetraponera*.
Tetraponera morondaviensis (Forel); Ward 1991: 338, 346. Raised to species.
Tetraponera morondaviensis (Forel); Chomicki *et al.* 2015: figure S1. Placement in molecular phylogeny.

Sima (*Tetraponera*) *hysterica* subsp. *dimidiata* Forel; Emery 1921: 27. Combination in *Sima* (*Tetraponera*).
Tetraponera hysterica subsp. *dimidiata* (Forel); Wheeler 1922c: 1015. Combination in *Tetraponera*.

Sima (*Tetraponera*) *arrogans* Santschi; Emery 1921: 27. Combination in *Sima* (*Tetraponera*).
Tetraponera arrogans (Santschi); Wheeler 1922c: 1014. Combination in *Tetraponera*.

Sima (*Tetraponera*) *demens* Santschi; Emery 1921: 27. Combination in *Sima* (*Tetraponera*).
Tetraponera demens (Santschi); Wheeler 1922c: 1014. Combination in *Tetraponera*.

Worker measurements (n =10). HW 0.69–0.97, HL 0.89–1.29, LHT 0.67–0.97, CI 0.75–0.78, FCI 0.13–0.16, REL 0.28–0.31, REL2 0.36–0.41, SI 0.63–0.70, SI3 1.59–1.91, FI 0.36–0.43, PLI 0.65–0.73, PWI 0.49–0.56, LHT/HW 0.96–1.05, CSC 2–8, MSC 13–22.

Worker diagnosis. Small to medium-sized species, with relatively broad head (CI 0.75–0.78) and eyes of moderate size (see ocular indices); minimum distance between frontal carinae exceeding basal scape width (FCI 0.13–0.16); scape relatively long, about two-thirds of head width and about one-half head length (SI 0.63–0.70, SI2 0.48–0.53); median clypeal lobe crenulate, broadly convex (Fig. 20a); profemur moderately robust (FI 0.36–0.43); mesosoma with a differentiated, transverse metanotal plate, about one-half the length of the mesonotum; dorsal face of propodeum weakly convex (posterior view), in profile as long as or longer than declivitous face and rounding insensibly into the latter; petiole moderately robust (see PLI and PWI values), with a differentiated anterior peduncle and anteroventral tooth; petiolar node rounded in profile, the anterodorsal face usually steeper than the posterodorsal face (Fig. 20b); postpetiole longer than broad. Head finely reticulate-punctate, sublucid, the punctures dense and relatively coarse (0.01 mm in diameter), and associated with conspicuous, appressed to subdecumbent pubescence (Fig. 20a); mesosoma, petiole, postpetiole and gaster with weaker reticulate sculpture and scattered punctures, sublucid. Standing pilosity moderately common on head (CSC 2–8), more so on mesosoma dorsum (MSC 13–22), but absent from propodeum. Medium reddish-brown to dark-brown, mandibles, antennae, and anterior third of head tending to be lighter (Fig. 20).

Comments. This species can be recognized in the worker caste by the crenulate median clypeal lobe, relatively broad and rather densely punctate head (CI 0.75–0.78), well developed metanotal plate, conspicuous standing pilosity on the promesonotum (absent from the propodeum), robust petiole (PLI 0.65–0.73, PWI 0.49–0.56), and brown to red-brown coloration. Related species, such as *T. perlonga*, tend to be smaller in size and darker in color, and they have a more elongate head (CI 0.64–0.74) and/or finer cephalic sculpture. The *T. morondaviensis* queen can be recognized by its large size (HW 1.08–1.30), massively expanded masticatory margin of the mandible, and ligulate clypeal lobe with medial notch.

Distribution and biology. *T. morondaviensis* is widespread in dry forest of Madagascar, nesting in dead twigs and branches of many kinds of plants. This species forms large polydomous colonies and the workers can be quite aggressive.

Tetraponera sahlbergii (Forel)

(Fig. 21)

Sima Sahlbergii Forel 1887: 386. Holotype worker (by monotypy), Bois d'Ivondro pr. Tamatave, Madagascar (C. Keller) (MHNG) [examined]. Imaged on AntWeb: CASENT0101052.
Sima sahlbergi r. *spuria* Forel 1897: 199. Syntypes, 18 workers, 1 male, Nosy Be [as "Nosibé" and "Nossibé"], Madagascar (Völtzkow) (MSNG, MHNG, NMHV) [examined]. 6 syntype workers, 1 syntype male from MHNG imaged on AntWeb: CASENT0101055, CASENT0101056, CASENT0101057, CASENT0101058, CASENT0101059, CASENT0101060, CASENT0101063. 1 syntype worker from MSNG imaged on AntWeb: CASENT0102036. **Syn. nov.**
Sima (Tetraponera) plicatidens Santschi 1926: 26. Syntypes, 2 alate queens, 2 males, Ankaratra, 2000m, Madagascar (Descarpentries) (NHMB) [examined]. 1 syntype queen, 2 syntype males imaged on AntWeb: CASENT0101149, CASENT0101150, CASENT0101151. **Syn. nov.**

Sima Sahlbergi Forel; Forel 1892: 260. Description of queen.
Sima (*Tetraponera*) *sahlbergi* Forel; Emery 1921: 28. Combination in *Sima* (*Tetraponera*).
Tetraponera sahlbergi (Forel); Wheeler 1922c: 1015. Combination in *Tetraponera*.
Tetraponera sahlbergii (Forel); Chomicki *et al.* 2015: figure S1. Placement in molecular phylogeny.

Sima (*Tetraponera*) *sahlbergi* subsp. *spuria* Forel; Emery 1921: 28. Combination in *Sima* (*Tetraponera*).
Tetraponera sahlbergi subsp. *spuria* (Forel); Wheeler 1922c: 1016. Combination in *Tetraponera*.

Tetraponera plicatidens (Santschi); Ward 1990: 489. Combination in *Tetraponera*.

Worker measurements (n = 17). HW 0.49–0.77, HL 0.69–1.01, LHT 0.48–0.70, CI 0.69–0.76, FCI 0.08–0.14, REL 0.29–0.34, REL2 0.38–0.47, SI 0.55–0.65, SI3 1.31–1.56, FI 0.40–0.45, PLI 0.46–0.62, PWI 0.34–0.52, LHT/HW 0.84–1.02, CSC 2–3, MSC 2–6.

Worker diagnosis. Relatively small species, with somewhat elongate head (CI 0.69–0.76), and eyes of moderate size (see ocular indices); minimum distance between frontal carinae only slightly exceeding basal scape width (FCI 0.08–0.14); scape moderately long, greater than one-half head width and less than one-half head length (SI 0.55–0.65, SI2 0.41–0.45); median clypeal lobe broadly convex, denticulate, furnished with a small median tooth and flanked by one or two pairs of weak lateral teeth, sometimes reduced to crenulations (Fig. 21a); profemur moderately robust (FI 0.40–0.45); mesosoma with a differentiated, transverse metanotal plate, about one third the length of the mesonotum; dorsal face of propodeum flat to weakly convex (posterior view), about as long as declivitous face and rounding into the latter; petiole slender (PLI 0.46–0.62, PWI 0.34–0.52), with a well differentiated anterior peduncle, the node with relatively shallow and similar anterodorsal and posterodorsal faces, as seen in profile (Fig. 21b); postpetiole longer than broad. Head and mesosoma sublucid, with fine reticulate-coriarious sculpture and scattered small punctures. Standing pilosity relatively sparse; head usually with 1 pair of supraocular setae (CSC 2–3); mesosoma with 1–2 pairs of standing hairs on the pronotum and 0–1 pair on the mesonotum (MSC 2–6); standing pilosity absent from dorsal face of propodeum. Dark brownish-black, antennae, mandibles and distal portions of legs lighter.

Comments. This is a widespread and somewhat variable species, recognizable in the worker caste by the combination of (1) relatively small size, (2) a moderately elongate head (CI 0.69–0.76), (3) a broadly convex anterior clypeal margin, that is crenulate or denticulate but lacks prominent teeth, (4) a slender petiole, and (5) sparse standing pilosity. In western populations the sheen of the integument is somewhat dulled by the fine reticulate-coriarious sculpture, compared to similar congeners. *T. sahlbergii* workers from mesic localities in eastern Madagascar tend to have a shinier head and more robust petiole than those from drier habitats on the western half of the island, but intermediate phenotypes occur, and the variation is here treated as intraspecific.

Distribution and biology. This is a common species that occurs in spiny forest, tropical dry forest and disturbed open habitats almost throughout the island of Madagascar. It is a generalist inhabitant of dead twigs or stems of woody plants.

Tetraponera ambigua-group

Worker diagnosis (from Ward 2006). Small to medium-sized species (HW 0.51–0.91); masticatory margin of mandible with four (in one species six) teeth; basal margin lacking distinct teeth (small denticle may be present near apicobasal tooth) and shorter than masticatory margin; labrum without prominent teeth or tubercles; anteromedial margin of clypeus crenulate or entire; distance between frontal carinae notably exceeding basal scape width (FCI 0.15–0.25); scape length one half to two thirds of head width (SI 0.52–0.65); compound eyes directed anteromedially; head capsule without ocelli or with a lateral pair only (if present usually weakly developed), median ocellus lacking; pronotum with soft lateral margination; mesonotum either extending to propodeum or separated from it by a weakly differentiated metanotum; posteroventral margin of petiole well separated from helcium venter; metabasitarsal sulcus generally absent (present in one species); upper half of mesosternum sparsely pubescent; appressed pubescence dense on abdominal tergite 4. Worker caste dimorphic, with a discrete soldier (major worker) subcaste.

Comments. This group of four species was revised by Ward (2006) which should be consulted for more information. Note that the key to workers in Ward (2006) has been expanded here to include the queen caste. No new taxa or major range extensions have been discovered since the earlier treatment. The distribution of *T. parops* is now known to include Mozambique.

In a paper on the ants of Pongara National Park in Gabon, Braet & Taylor (2018) resurrected two junior synonyms in the *Tetraponera ambigua*-group, *T. ophthalmica angolensis* Santschi (previously synonymized under *T. ambigua* by Ward (2006: 123)) and *Tetraponera ophthalmica unidens* Santschi (previously synonymized under *T. ophthalmica* by Ward (2006: 126)), and raised them to species. These actions are considered unjustified and are here reversed, based on the following reasoning.

There are four syntype workers of *Tetraponera ophthalmica angolensis* in NHMB (one imaged on AntWeb: CASENT0915536). Direct examination and measurement of these specimens reveals that their size (HW ~0.65), relative eye size (REL ~0.43), frontal carinal configuration (FCI ~0.19), petiole shape (PLI ~0.60), pilosity, and maculation fall within the range of variation encompassed by *T. ambigua* (see Ward 2006: 125). The syntype dealate queen of *Tetraponera ophthalmica unidens* in MRAC (RMCAENT000017747) was also directly examined and shown to differ in no substantial way from worker-associated queens of *T. ophthalmica* from Cameroon, Central African Republic and Uganda. While there may be additional, cryptic species in the *T. ambigua*-group, no compelling evidence was presented by Braet & Taylor (2018) for resurrection of the names *T. angolensis* and *T. unidens*, and they are here returned to the status of junior synonyms (**syn. rev.**).

Braet & Taylor (2018) instituted other poorly justified taxonomic changes in their paper on the ants of Pongara National Park. They used an outdated subfamily classification, and they ignored or contradicted the results of recent taxonomic studies on the genera *Carebara*, *Crematogaster* and *Nylanderia*. Such actions retard progress in ant systematics and should have been moderated by a more rigorous peer review process.

In a more recent paper Taylor & McGavin (2020) promulgated further unwarranted taxonomic changes in the *Tetraponera ambigua* group. Their study was concerned with ants inhabiting *Vachellia* and other trees in Mkomazi Game Reserve, Tanzania. Based on questionable evidence Taylor & McGavin (2020) resurrected two additional synonyms of *Tetraponera ambigua*: *T. bifoveolata* (Mayr) and *T. erythraea* (Emery). *T. bifoveolata* was said to be distinguished from *T. ambigua* by the presence of a major worker (soldier) caste, while *T. erythraea* was claimed to have more abundant mesosomal pilosity and an "alitrunk [sic] profile in three shallow convexities". These arguments have little merit. Major workers are found in all species of the *T. ambigua* group (Ward 1996), and *T. ambigua* workers show modest (and continuous) variation in mesosomal pilosity, with MSC values ranging from 12 to 44. The syntype workers of *T. ambigua*, *T. bifoveolata* and *T. erythraea* fall within this range of variation (types directly examined). The difference in mesosomal profile between *T. ambigua* and *T. erythraea* is also of dubious value. *T. ambigua* workers from more northern locations, including Yemen (the type locality of *T. erythraea*), tend to have a better developed metanotal impression, which enhances the convexity of the mesonotum and the dorsal face of the propodeum when viewed in profile, but this character is quite variable and has not been shown to have diagnostic value. The synonymy of *T. bifoveolata* and *T. erythraea* under *T. ambigua* is here reconfirmed (**syn. rev.**).

If the treatment of *Tetraponera* is indicative, then other taxonomic changes proposed in Taylor & McGavin (2020), involving the genera *Camponotus*, *Crematogaster*, *Nesomyrmex*, and *Polyrhachis*, require critical reexamination.

Tetraponera grandidieri-group

Worker diagnosis (modified from Ward 2009). Medium to large species (HW 0.95–1.59, HL 1.05–2.01, LHT 1.05–1.83); masticatory margin of with four teeth; basal margin with 0–1 teeth and subequal in length to masticatory margin; labrum with a pair of tubercles closely flanking the midline near the proximal margin but lacking a median tubercle; palp formula 6,4; anteromedial margin of clypeus crenulate or emarginate; distance between frontal carinae exceeding basal scape width (FCI 0.11–0.18), scape length three-quarters or more of head width (SI 0.72–0.90); eye length about one-third of head length (REL 0.28–0.36); head capsule with three distinct ocelli; pronotum laterally marginate, but not strongly so; mesopropodeal impression well developed; petiole relatively long (PLI 0.38–0.59, PWI 0.37–0.65); posteroventral margin of petiole lying adjacent to helcium venter; metabasitarsal sulcus present; legs long and slender (FI 0.27–0.36, LHT/HL 0.85–1.12); appressed pubescence sparse on abdominal tergite 4; standing pilosity uncommon (CSC 2–3, MSC 1–6), absent from mesonotum, propodeum, and extensor surfaces of the tibiae. Orange to reddish-brown, head concolorous or darker; gaster and portions of femora may also be infuscated.

Comments. This group, which is endemic to the island of Madagascar, was previously revised (Ward 2009)

and seven species were recognized. Recent collections by Brian Fisher and colleagues have turned up one additional species.

Tetraponera elegans sp. nov.

(Fig. 22)

Type material. *Holotype worker*: Madagascar, Toamasina: CFAM, Tsaravoniana, 1018 m, -18.75737 48.42302 ±100 m, 8–9 Dec 2012, rainforest, ex dead twig above ground, B. L. Fisher *et al*. BLF30230 (CASENT0300734) (CASC). *Paratypes*, 4 workers: same data as holotype (CASC, UCDC); 6 workers: same data as holotype except 9 Dec 2012, ex dead bamboo above ground, B. L. Fisher *et al*. BLF30248 (CASC, UCDC).

Worker measurements (n = 8). HW 1.03–1.19, HL 1.36–1.64, LHT 1.32–1.54, CI 0.73–0.78, FCI 0.12–0.15, REL 0.30–0.32, REL2 0.40–0.42, SI 0.84–0.90, SI3 2.04–2.18, FI 0.27–0.31, PLI 0.39–0.43, PWI 0.37–0.45, LHT/HW 1.22–1.29, CSC 2–3, MSC 1–2.

Worker diagnosis. With characteristics of the *T. grandidieri* group and the following more specific features: basal margin of mandible edentate; anterior clypeal margin broadly convex and crenulate, directed forward, not anteroventrally; head elongate (CI 0.73–0.78); metanotal spiracle not protruding in lateral view of mesosoma; dorsal face of propodeum broadly convex in lateral and posterior views; petiole long and slender, anterior peduncle weakly inflected; petiole length equal to, or exceeding, head width; standing pilosity sparse on head and mesosoma (CSC 2–3, MSC 1–2), usually 1–2 pairs of setae on dorsum of petiole and postpetiole; short appressed to subdecumbent hairs absent or inconspicuous on most of body; integument mostly sublucid, with fine coriarious/puncticulate sculpture; body orange brown, with contrasting dark brown head; appendages light orange-brown, the distal portions of antennae and femora contrastingly dark brown.

Comments. The worker of this species is readily distinguished from other members of the *T. grandidieri* group by its long and slender petiole, whose length equals or exceeds head width (PL/HW 1.01–1.05). In all other species in the *T. grandidieri* group petiole length is considerably less than head width (PL/HW 0.70–0.85). The legs and head of *T. elegans* are also notably elongate, and the body coloration is distinctive, especially the distal infuscation of the antennae. Molecular data suggest that *T. elegans* is the sister species of *T. manangotra* (Ward, unpubl.), from which it can be separated by the foregoing characteristics as well as the much smaller size (HW 1.03–1.19, compared with HW 1.48–1.58 in *T. manangotra*).

Distribution and biology. This species is known only from two adjacent rainforest localities in the Corridor Forestier Analamay-Mantadiafour in eastern Madagascar. Three nest series were collected, one from a dead twig (BLF30230), and two from dead bamboo (BLF30194, BLF30248). A fourth collection consists of a single worker taken on low vegetation.

Material examined (CASC, PSWC, UCDC). **Madagascar**: *Toamasina*: CFAM, Tsaravoniana, 1018 m (Fisher, B. L.; *et al*.); CFAM, Tsaravoniana, 1036 m (Fisher, B. L.; *et al*.); CFAM, Ambatoharanana, 1016 m (Fisher, B. L.; *et al*.).

Tetraponera natalensis-group

Worker diagnosis. Medium to large species (HW 0.92–1.68); masticatory margin of mandible with three teeth, preceded by a single tooth on basal margin; basal margin notably longer than masticatory margin; labrum with a pair of widely flanking lateral tubercles near proximal margin and a median tubercle on distal third of labrum near cleft; anteromedial margin of clypeus usually crenulate or toothed, rarely emarginate; distance between frontal carinae equaling or exceeding basal scape width (FCI 0.08–0.19), scape length about half of head width and subequal to eye length (SI 0.45–0.57, SI3 0.81–1.23); head capsule typically with two ocelli, median ocellus lacking or weakly developed; pronotum with sharp lateral margination, extending (sometimes weakened) to lateral borders of propodeum and petiole; mesonotum 2–4 times wider than long, with a semicircular or broadly arched anterior margin and a straight to weakly arched posterior margin, the posterior margin occasionally weakly defined; dorsal face of propodeum long and flat, sometimes with a weakly differentiated area (metanotal plate?) interpolated between propodeum and mesonotum; posteroventral margin of petiole notched medially, as seen in ventral view, and well

separated from helcium venter, as seen in lateral view; metabasitarsal sulcus present; appressed pubescence dense on abdominal tergite 4. Head and mesosoma usually densely punctulate to punctulate-coriarious, the sculpture imparting a subopaque (matte) appearance, but punctulate with shiny interspaces in one species. Sculpture weaker on petiole, postpetiole, and gaster, which are correspondingly sublucid.

Comments. Members of this group can be distinguished from other Afrotropical *Tetraponera* by the laterally marginate mesosoma and petiole, short and broadly transverse mesonotum, and medially notched posteroventral margin of the petiole. All species, except *T. setosa* **sp. nov.**, also have characteristic punctulate-coriarious sculpture that imparts a matte appearance to the head and mesosoma. One of the ten species in the *T. natalensis* group, *T. insularis* **sp. nov.**, is endemic to Madagascar; the remainder are restricted to the African mainland.

Tetraponera andrei (Mayr)

(Figs 23, 41)

Sima Andrei Mayr 1895: 144. Holotype worker (by monotypy), Delagoa Bay, Mozambique (Brauns) (NHMV) [examined]. Imaged on AntWeb: CASENT0915848.

Sima (*Sima*) *andrei* Mayr; Arnold 1916: 179. Combination in *Sima* (*Sima*).
Tetraponera andrei (Mayr); Wheeler 1922b: 796. Combination in *Tetraponera*.
Tetraponera andrei (Mayr); Chomicki *et al.* 2015: figure S1. Placement in molecular phylogeny.

Worker measurements (n = 8). HW 1.03–1.15, HL 1.14–1.30, LHT 0.74–0.85, CI 0.89–0.95, FCI 0.17–0.19, REL 0.50–0.56, REL2 0.53–0.59, SI 0.46–0.50, SI3 0.81–0.91, FI 0.45–0.50, PLI 0.75–0.86, PWI 0.69–0.81, LHT/HW 0.71–0.74, CSC 0–2, MSC 0–3.

Worker diagnosis. Moderate-sized species, with broad head (CI 0.89–0.95) and large eyes (REL 0.50–0.56); posterior margin of eye attaining the level of the lateral ocelli; frontal carinae widely separated, the minimum distance between them almost one-fifth of head width (FCI 0.17–0.19) and more than one-third of scape length (MFC/SL 0.35–0.40); scapes relatively short (SI 0.46–50), less than eye length (SI3 0.81–0.91); anterior clypeal margin almost straight (slightly emarginate medially) and weakly crenulate (Fig. 23a); profemur robust (FI 0.45–0.50); mesonotum bounded posteriorly by a well marked, longitudinally rugulose impression; metanotal plate lacking; dorsal face of propodeum flattened, laterally submarginate, longer than declivitous face and rounding insensibly into the latter; petiole relatively short and high (see PLI and PWI values), dorsolaterally marginate, and with an anteroventral tooth; in profile, petiolar node with steep anterodorsal and posterodorsal faces, rounding insensibly into one another (Fig. 23b); postpetiole broader than long. Head and mesosoma densely punctulate-coriarious, matte. Standing pilosity very sparse (CSC 0–2, MSC 0–3), absent from petiole and postpetiole, the few erect setae relatively long, and distinct from the inconspicuous, short pubescence. Dark brownish-black, the mandibles, antennae, tibiae and tarsi lighter.

Comments. Within the *T. natalensis* group this species is easily recognized by its small worker size (HW 1.03–1.15), large eyes, short and strongly marginate petiole (PL/HW 0.50–0.55), dark color, and sparse standing pilosity. Workers of the most closely similar species, *T. anthracina*, are larger (worker HW 1.40–1.54), have more closely adjacent frontal carinae (FCI 0.14–0.16), lack a rugulose transverse impression at the posterior margin of the mesonotum, and have standing pilosity on the petiole and postpetiole (2–4 and 2–6 standing hairs, respectively).

Distribution and biology. *Tetraponera andrei* is an East African species of rather limited distribution, being known only from Mozambique, Tanzania, and Kenya. Workers have been collected foraging on foliage and tree trunks, in semi-dry habitats. One nest collection is known, from a dead twig (BLF37780).

Material examined (CASC, MCZC, NHMW, PSWC, SAMC, UCDC). **Kenya**: *Lamu*: Waboniland (c.u.); **Mozambique**: *Cabo Delgado*: P.N. Quirimbas, Taratibu, 505 m (Fisher, B. L.; *et al*.); *Maputo*: Delagoa Bay (Brauns); **Tanzania**: *Kilimanjaro*: Mkomazi Game Reserve, Dindera Dam (van Noort, S.); *Morogoro*: Morogoro (Loveridge, A.); *Pwani*: Mafia Is. (Vesey-Fitzgerald); *Tanga*: Kange, near Tanga, 50 m (Ward, P. S.).

Tetraponera anthracina (Santschi)

(Figs 24, 41)

Sima anthracina Santschi 1910: 355. Syntypes, 5 workers, Combra-Tora, Brazzaville, Congo-Brazzaville (Weiss) (MHNG, NMHB) [examined]. 1 syntype worker from NHMB imaged on AntWeb: CASENT0915524.

Sima triangularis Stitz 1910: 131. Holotype worker (by monotypy), Alen, Equatorial Guinea (Tessmann) (ZMHB) [examined]. Imaged on AntWeb: FOCOL1154. **Syn**. **nov**.

Tetraponera poultoni Donisthorpe 1931: 497. Holotype worker (by monotypy), Uganda (J. E. M. Mellor) (OXUM) [examined]. **Syn**. **nov**.

Tetraponera anthracina (Santschi); Wheeler 1922a: 106. Combination in *Tetraponera*.
Sima anthracina Santschi; Santschi 1928: 58. Combination in *Sima*.
Tetraponera anthracina (Santschi); Menozzi 1942: 166. Combination in *Tetraponera*.
Tetraponera anthracina (Santschi); Terron 1968: 339. Description of queen, male.
Tetraponera anthracina (Santschi); Terron 1977: 115. Colony development.
Tetraponera anthracina (Santschi); Chomicki *et al*. 2015: figure S1. Placement in molecular phylogeny.

Tetraponera triangularis (Stitz); Wheeler 1922b: 800. Combination in *Tetraponera*.

Note: publication dates for *Sima anthracina* Santschi (1910) and *Sima triangularis* Stitz (1910) are 23 February 1910 and August 1910, respectively.

Worker measurements (n = 11). HW 1.40–1.54, HL 1.47–1.67, LHT 1.08–1.21, CI 0.92–0.99, FCI 0.14–0.16, REL 0.49–0.53, REL2 0.52–0.56, SI 0.49–0.52, SI3 0.90–0.99, FI 0.44–0.46, PLI 0.72–0.79, PWI 0.78–0.85, LHT/HW 0.76–0.8, CSC 2, MSC 4.

Worker diagnosis. Large species, with broad head (CI 0.92–0.99) and large eyes (REL 0.49–0.53); posterior margin of eye attaining the level of the lateral ocelli; frontal carinae well separated, the minimum distance between them about 0.15× head width (FCI 0.14–0.16) and more than one-quarter of scape length (MFC/SL 0.27–0.31); scapes of moderate length (SI 0.49–52), slightly less than eye length (SI3 0.90–0.99); anterior clypeal margin broadly and weakly convex, with a short median denticle, usually flanked by 2–3 smaller denticles on each side (Fig. 24a); profemur moderately robust (FI 0.44–0.46); mesonotum bounded posteriorly by a well marked but simple impression, lacking longitudinal rugulae; distinct metanotal plate not present, although anterior extremity of propodeum with a weakly differentiated arched-transverse area in some individuals; dorsal face of propodeum flattened, laterally marginate, longer than declivitous face and rounding insensibly into the latter; petiole relatively short and high (see PLI and PWI values), dorsolaterally marginate, and with an anteroventral tooth; in profile, petiolar node with gently rounded anterodorsal face and steeper posterodorsal face (Fig. 24b); postpetiole about as broad as long. Head and mesosoma densely punctulate-coriarious, matte. Standing pilosity sparse; upper half of head with a single pair of supraocular setae, pronotum with two pairs of setae, situated on the anterolateral and posterolateral corners (CSC 2, MSC 4); propodeum, petiole, postpetiole, and abdominal tergite 4 with 0, 2–4, 2–6, and 4–20 standing hairs, respectively; standing pilosity distinct from the inconspicuous, short pubescence. Dark brownish-black, the mandibles, antennae, tibiae and tarsi lighter, especially the scapes, second antennal segment, protibia and protarsus.

Comments. The key distinguishing features of *T. anthracina* workers are their broad head (CI 0.92–0.99), large eyes (REL 0.49–0.53), sharp lateral margination of the mesosoma and petiole, dark color, and sparse standing pilosity (CSC 2, MSC 4). The superficially similar and sympatric species, *T. mocquerysi*, has a more elongate head (CI 0.80–0.90), softer lateral margination on the mesosoma and petiole, and more extensive standing pilosity (CSC 8–34, MSC 21–100). For differences between *T. anthracina* and *T. andrei*, see under the latter species.

Distribution and biology. *T. anthracina* is found in wet forested regions of West and Central Africa, from Nigeria to western Uganda. It is a generalist inhabitant of dead twigs. Terron (1977) gave a detailed account of colony development and caste production in this species, based on observations of laboratory colonies.

Material examined (AMNH, ANIC, BMNH, CASC, LACM, MCZC, MHNG, MSNG, NHMB, NHMW, OXUM, PSWC, SAMC, UCDC, USNM, ZMHB). **Cameroon**: *Centre*: Metet (Good, A. I.); *region unknown*: "Cameroon" (Terron, G.); "Kamerun" (Conradt, L.); *Sud*: Ebolowa, Nkoemvon (Jackson, D.); Ekok, 24 mi E Tekmo, 650 m (Ross, E. S.; Lorenzen, K.); Nkoemvon (Jackson, D.); **Central African Republic**: *Sangha-Mbaéré*: P.N. Dzanga-Ndoki, 21.4 km 53° NE Bayanga, 510 m (van Noort, S.); P.N. Dzanga-Ndoki, 37.9 km 169° S Lidjombo, 360 m

(Fisher, B. L.); P.N. Dzanga-Ndoki, 38.6 km 173° S Lidjombo, 350 m (Fisher, B. L.); P.N. Dzanga-Ndoki, 38.6 km 173° S Lidjombo, 350 m (van Noort, S.); P.N. Dzanga-Ndoki, Mabéa Bai, 21.4 km 53° NE Bayanga, 510 m (Fisher, B. L.); Res. Dzanga-Sangha, 12.7 km 326° NW Bayanga, 420 m (Fisher, B. L.); Res. Dzanga-Sangha, 12.7 km 326° NW Bayanga, 420 m (van Noort, S.); Res. Dzanga-Sangha, 12.7 km 326° NW Bayanga, 470 m (Fisher, B. L.); **DR Congo**: *Équateur*: Bumba (c.u.); *Ituri*: Epulu, 950 m (Ross, E. S.; Leech, R. E.); *Kasaï*: Luebo (Schouteden, H.); *Kasaï Oriental*: Vill. Malela (Chief Kasende) (Bequaert, J.); *Kongo Central*: 50 km S Tshela (Ross, E. S.; Leech, R. E.); 6 mi E Tshela (Ross, E. S.; Leech, R. E.); Thysville (c.u.); *Kwango*: 21 mi W Popokabaka (Ross, E. S.; Leech, R. E.); 3 mi E Kenge (Ross, E. S.; Leech, R. E.); *Kwilu*: Wamba, Kikongo Mission (Chapman, T.); *Mai-Ndombe*: Mongende (Schouteden, H.); *Nord-Kivu*: 39 km S Walikale, 700 m (Ross, E. S.; Leech, R. E.); *province unknown*: "Congo" (Kohl); *Tshopo*: Kisangani [as "Stanleyville"] (Kohl, H.); Kisangani [as "Stanleyville"] (Lang, H. O.); Yangambi Reserve (Raignier, A.; van Boven, J.); **Equatorial Guinea**: *Centro Sur*: Uelleburg (Tessman, G.); *Wele-Nzas*: Alen [as "Alcu"] (Tessman, G.); **Gabon**: *Ogooué-Ivindo*: CNRS, Makokou (Gotwald, W. H.); *Ogooué-Maritime*: Port Gentil (Ross, E. S.; Leech, R. E.); Res. Moukalaba, 10.8 km 214° SW Doussala, 110 m (Fisher, B. L.); Res. Moukalaba, 12.2 km 305° NW Doussala, 110 m (Fisher, B. L.); Réserve de la Moukalaba-Dougoua, 7 km NW Doussala, 110 m (van Noort, S.); *province unknown*: "Gabon" (Faure, F.); *Woleu-Ntem*: 27.6 km 108° ESE Minvoul, 600 m (Fisher, B. L.); 31.3 km 108° ESE Minvoul, 600 m (Fisher, B. L.); **Republic of Congo**: *Brazzaville*: Brazzaville (Weiss, A.); *Likouala*: 55 km NW Boha, Lac Telle (Alpert, G. D.); *Pool*: Comba [as "Combra-Tora"] (Weiss); Lesio-Loun Park, 330 m (Braet; Sharkey); **Uganda**: *Bundibugyo*: Sempaya, Semliki Natl. Park, 700 m (Ward, P. S.); *district unknown*: "Uganda" (Mellor, J. E. M.); *Kampala*: Kampala (c.u.); Kampala (Gedye, A. F. J.); *Wakiso*: Dedewe Forest, pr. Kampala (c.u.).

Tetraponera caffra (Santschi)

(Figs 25, 42)

Sima natalensis st. *caffra* Santschi 1914d: 15. Syntypes, 8 workers, 3 dealate queens, 1 male, Dukudu, Zululand, South Africa (Tragardh) (MHNG, NHMB) [examined]. 1 syntype worker from NHMB imaged on AntWeb: CASENT0915532.

Sima natalensis obscurata var. *caffra* (Santschi); Arnold 1916: 178.
Tetraponera natalensis caffra (Santschi); Wheeler 1922b: 799. Combination in *Tetraponera*.
Tetraponera caffra (Santschi); Ward & Downie 2005: 326. Raised to species.
Tetraponera caffra (Santschi); Chomicki *et al.* 2015: figure S1. Placement in molecular phylogeny.

Worker measurements (n = 9). HW 0.98–1.06, HL 1.08–1.29, LHT 0.73–0.84, CI 0.82–0.92, FCI 0.10–0.13, REL 0.43–0.47, REL2 0.51–0.56, SI 0.45–0.48, SI3 0.84–0.92, FI 0.45–0.49, PLI 0.69–0.80, PWI 0.68–0.76, LHT/HW 0.74–0.8, CSC 2–7, MSC 3–8.

Worker diagnosis. Relatively small species, with head longer than broad (CI 0.82–0.92) and eyes of moderate size (REL 0.43–0.47); posterior margin of eye not attaining the level of the lateral ocelli; frontal carinae separated by about basal scape width (FCI 0.10–0.13, MFC/SL 0.21–0.28); scapes short (SI 0.45–0.48), markedly less than eye length (SI3 0.84–0.92); anterior clypeal margin slightly produced medially, furnished with a small median denticle, flanked by a lateral pair of denticles (denticles sometimes obsolete, so that clypeal margin appears crenulate rather than denticulate) (Fig. 25a); profemur relatively robust (FI 0.45–0.49, FW/PL 0.49-0.54); mesonotum bounded posteriorly by a weak transverse impression, often quite faint; metanotal plate not present; dorsal face of propodeum flattened, laterally submarginate, longer than declivitous face and rounding insensibly into the latter; petiole relatively short and high (see PLI and PWI values), dorsolaterally submarginate, and with an anteroventral tooth; in profile, petiolar node with steep anterodorsal and posterodorsal faces, rounding insensibly into one another; in dorsal view, petiole narrowly obovate to subtrapezoidal, the sides diverging posteriorly (Fig. 25b); postpetiole slightly broader than long. Head and mesosoma densely punctulate-coriarious, matte. Standing pilosity relatively sparse (CSC 2–7, MSC 3–8), absent from mesonotum, propodeum and extensor faces of tibiae (HTC 0, MTC 0); body with a rather dense cover of fine pubescence, partly decumbent and suberect. Light orange-brown, the upper third of head around ocelli and the tip of gaster variably infuscated.

Comments. This is a small, light orange-brown species whose workers have short scapes (SI 0.45–0.48) and a robust profemur (FI 0.45–0.49, FW/SL 0.69-0.76). There is usually also a conspicuous dark patch on the upper third

of the head, surrounding the ocelli (Fig. 25a), although this is weakly developed in some individuals. The other three species in the *T. natalensis* group with similar orange-brown coloration, *T. natalensis*, *T. redacta*, and *T. schulthessi*, have longer scapes (SI 0.50–0.55) and a more slender profemur (FI 0.38–0.46, FW/SL 0.53-0.66), and they lack infuscation on the upper third of the head. Workers of *T. schulthessi* are also notably larger in size (HW 1.38–1.68, versus 0.98–1.06 in *T. caffra*). See under *T. kosi* for comparison with that darker-colored species.

Distribution and biology. *Tetraponera caffra* is known from South Africa, Zimbabwe and Mozambique. All nest-site records are from hollow thorns of *Vachellia* species, including *V.* cf. *karroo*, *V. nilotica*, *V. tortilis* and *V. xanthophloea*. Although apparently a nest-site specialist, *T. caffra* inhabits dead thorns and the workers are rather timid in their behavior. There is no evidence of a mutually beneficial relationship between the ants and the plants, although the association deserves greater study.

Material examined (CASC, MHNG, MSNG, NHMB, PSWC, SAMC, UCDC, USNM). **Mozambique**: *Sofala*: 10 km NNE Chitengo, Gorongosa Natl. Park, 25 m (Ward, P. S.); **South Africa**: *KwaZulu-Natal*: "Zululand" (c.u.); "Zululand" (Trägårdh); 10 km NNW Mpila, Umfolozi Game Res., 120 m (Ward, P. S.); 2.5 km W Candover (Grobbelaar, F.; Millar, I. M.); 4.5 km SW Golela (Grobbelaar, F.; Millar, I. M.); Abu Madi Game Ranch, 200 m (Ward, P. S.); Cloete Farm, near Hluhluwe (Millar, I. M.; Grobbelaar, E.); Dugandlovu Camp, False Bay Park, 10 m (Ward, P. S.); Dukudu, Zululand (Trägårdh); Hilltop Camp, Hluhluwe Game Res., 450 m (Ward, P. S.); Kuleni Farm, near Hluhluwe (Grobbelaar, F.; Millar, I. M.); Mlalazi N.R., 11 m (Taylor, R.); Pongola (c.u.); *Limpopo*: Guernsey, near Klaserie (Grobbelaar, F.; Millar, I. M.); *Mpumalanga*: Mwewe, E of Mhlosana (Millar, I. M.; Stals, R.); near Bosfontein (Millar, I. M.; Stals, R.); near Driekoppies (Millar, I. M.; Stals, R.); near Sibayeni (Millar, I. M.; Stals, R.); nr. Masibekela, 8 km NE Mananga (Millar, I. M.; Stals, R.); **Zimbabwe**: *Manicaland*: Umtali (Arnold, G.); *Mashonaland Central*: Zambesi Valley, 7 km SE Angwa Bridge (Weyrich, J.).

Tetraponera insularis sp. nov.

(Figs 26, 41)

Tetraponera psw112. Chomicki *et al.* 2015: figure S1. Placement in molecular phylogeny.

Type material. *Holotype worker*: Madagascar, Mahajanga, Forêt Anabohazo, 21.6 km 247° WSW Maromandia, 120 m, 14°19′S 47°55′E, 11–16 Mar. 2001, ex dead twig above ground, tropical dry forest, Fisher *et al*. BLF03360 (CASENT0409790) (CASC). Note: specimen label gives Adm1 as "Antsiranana". *Paratypes*: Two workers, same data as holotype (CASENT0409791, CASENT0409792) (CASC).

Worker measurements (n=6). HW 1.27–1.54, HL 1.47–1.61, LHT 0.98–1.17, CI 0.86–0.96, FCI 0.14–0.18, REL 0.40–0.50, REL2 0.46–0.52, SI 0.50–0.55, SI3 0.98–1.20, FI 0.43–0.46, PLI 0.75–0.90, PWI 0.68–0.84, LHT/HW 0.75–0.79, CSC 0–2, MSC 0–2.

Worker diagnosis. Large species, with relatively broad head (CI 0.86–0.96) and moderately large eyes (REL 0.40–0.50); posterior margin of eye attaining, or nearly so, the level of the lateral ocelli; frontal carinae well separated, the minimum distance between them about 0.16× head width (FCI 0.14–0.18) and more than one-quarter of scape length (MFC/SL 0.28–0.33); scapes of moderate length (SI 0.50–55), equal to or exceeding eye length (SI3 0.98–1.20); anterior clypeal margin broadly and weakly convex, with a short median denticle, flanked by 3–4 denticles on each side, sometimes ill-defined (Fig. 26a); profemur moderately robust (FI 0.43–0.46); mesonotum bounded posteriorly by a well marked but simple impression, lacking longitudinal rugulae; distinct metanotal plate not present, although anterior extremity of propodeum with a very weakly differentiated arched-transverse area; dorsal face of propodeum flattened, laterally marginate, longer than declivitous face and rounding insensibly into the latter; petiole relatively short and high (see PLI and PWI values), dorsolaterally marginate, and with an anteroventral tooth; in profile, petiolar node with steep anterodorsal and posterodorsal faces, rounding insensibly into one another; postpetiole broader than long. Head and mesosoma densely punctulate-coriarious, matte. Standing pilosity very sparse, one or no pairs of setae on upper half of head and pronotum (CSC 0–2, MSC 0–2), lacking on mesonotum, propodeum, and petiole; postpetiole and abdominal tergite 4 each with 0–2 standing hairs; standing pilosity distinct from the inconspicuous, short pubescence. Dark brownish-black, with contrasting luteous mandibles, antennae, and legs, except for brown band on metafemur; this lighter coloration also variably developed on the anterior half of the head capsule.

Comments. This species can be differentiated from other members of the *T. natalensis* group by the combination of large worker size (HW 1.27–1.54), very sparse standing pilosity (CSC 0–2, MSC 0–2), and distinctive coloration: dark-brown body with contrastingly pale-yellow appendages and a dark brown patch on the metafemur.

Distribution and biology. *Tetraponera insularis* is the only representative of the *T. natalensis* group found in Madagascar. It is known from just two collections (BLF03360, BLF40198), both from the Sahamalaza Peninsula on the northwest coast of the island, and taken from dead twigs in disturbed tropical dry forest.

Material examined (CASC, PSWC, UCDC). **Madagascar**: *Mahajanga*: Forêt Anabohazo, 21.6 km 247° WSW Maromandia, 120 m (Fisher, B. L.; *et al*.); Parc Sahamalaza, Forêt Anabohazo, 141 m (Fisher, B. L.; *et al*.).

Tetraponera kosi sp. nov.

(Figs 32, 45)

Type material. *Holotype worker*: South Africa, KwaZulu-Natal, St. Lucia, nr Main Beach, 9 m, -28.36359 32.43065, 9 Apr 2010, nest in *Vachellia kosiensis* thorn, forest fringe (Northern Coastal Forest), P. G. Hawkes SL-MB-wp08-N (CASENT0815472) (SAMC). Paratypes: 17 workers, 5 queens, and 3 males, same data as holotype, except collection codes SL-MB-wp08-NT-2, SL-MB-wp08-NT-3, and SL-MB-wp08-NT-4 (CASENT0886898 to CASENT0886922) (AFRC, CASC, MCZC, PSWC, SAMC, UCDC).

Worker measurements (n=9). HW 0.98-1.08, HL 1.11-1.31, LHT 0.75-0.85, CI 0.82-0.88, FCI 0.10-0.13, REL 0.43-0.46, REL2 0.50-0.56, SI 0.46-0.49, SI3 0.85-0.97, FI 0.45-0.51, PLI 0.68-0.74, PWI 0.61-0.72, LHT/HW 0.76-0.79, CSC 3-6, MSC 4-5.

Worker diagnosis. Similar to *T. caffra* (see above) with regard to head size, eye size, configuration of frontal carinae, and shape of anterior clypeal margin; scapes similarly short (SI 0.46-0.49) and profemur robust (FI 0.45-0.51, FW/PL 0.52-0.56); mesonotum bounded posteriorly by a very weak transverse impression; metanotal plate not differentiated from dorsal face of propodeum; petiole relatively short and narrow (PLI 0.68-0.74, PWI 0.61-0.72, FW/PH 0.72-0.76); in profile, petiolar node with steep anterodorsal face rounding into a more gently sloping posterodorsal face; in dorsal view, petiole narrowly obovate (DPW/HW 0.39-0.44). Standing pilosity relatively sparse (CSC 3-6, MSC 4-5). Medium brown, the mandibles, antennae, anterior margin of head, tibiae, and tarsi light yellowish-brown; in some workers, luteous coloration extending to parts of the pronotum, postpetiole and gaster, producing a banded pattern on the latter.

Comments. Like *T. caffra*, the worker of this species has rather short scapes and a robust profemur such that FW/SL 0.68-0.77 (0.69-0.76 in *T. caffra*), as opposed to FW/SL 0.53-0.66 in other orange-brown and medium brown species in the *T. natalensis* group. Workers of *T. kosi* are distinguished from those of *T. caffra* by their predominantly darker (medium brown) coloration and a slightly less robust petiole (DPW/HW 0.39-0.44, FW/PH 0.72-0.76, as opposed to DPW/HW 0.45-0.49, FW/PH 0.64-0.71 in *T. caffra*). Although samples sizes are small, similar differences seem to apply to the queens: those of *T. kosi* are predominantly medium to dark brown in color, with a more slender petiole (DPW/HW 0.48-0.51; n=4), while the queens of *T. caffra* are light orange-brown, with a slightly broader petiole (DPW/HW 0.53-0.56; n=2). A possible distinguishing feature of *T. kosi* males is longer metatibiae (LHT/HW 1.09-1.13; n=3) compared to *T. caffra* (LHT/HW 1.07; n=1) but this requires confirmation. At a coarse geographical scale, the known population of *T. kosi* is contained within the range of *T. caffra* (Figs 43, 46), and hence the phenotypic differences between them can be interpreted as indicating that they are not conspecific. Further studies are needed, however, on the relationship between the two taxa.

Distribution and biology. *T. kosi* is known only from one coastal forest site in KwaZulu-Natal, South Africa, where four nest series were collected in thorns of *Vachellia kosiensis*, each from a different tree. The ants were found to keep scale insects in the thorns (Peter Hawkes, pers. comm., 14 January 2022), in apparent contrast to *T. caffra*.

Material examined. Known only from type material.

Tetraponera mocquerysi (André)

(Figs 27, 43)

Sima Mocquerysi André 1890: 319. Syntypes, 12 workers, Sierra Leone (Mocquerys) (MSNG, MHNG, MNHN, NHMB, NHMV) [examined]. 3 syntype workers imaged on AntWeb: CASENT0904032 (MSNG), CASENT0913719 (MNHN),

CASENT0915531 (NHMB).

Sima Mocquerysi st. *emacerata* Santschi 1911a: 352. Holotype (by monotypy), worker, Nakuro, Rift Valley, Kenya (C. Alluaud) (MNHN) [examined]. Imaged on AntWeb: CASENT0913720. **Syn**. **nov**.

Sima Oberbecki Forel 1911b: 275. Holotype (by monotypy), worker, Congo da Lemba, Democratic Republic of Congo (Mayné) (MRAC) [examined]. **Syn**. **nov.**

Sima mocquerysi v. *elongata* Stitz 1911: 378. Syntype, 1 worker, Budduwald, Tanzania (A. Friedrichs) (ZHMB) [examined]. Imaged on AntWeb: FOCOL1161. **Syn**. **nov**.

Sima triangularis st. *illota* Santschi 1914c: 334. Syntypes, 1 dealate queen, 1 worker, Olokemej, Nigeria (MHNG, NHMB) [examined]. 1 syntype worker from NHMB imaged on AntWeb: CASENT0915541. **Syn**. **nov.**

Sima Prelli var. *odiosa* Forel 1916: 403. Syntype, 1 worker, "Congo" (Kohl) (MHNG) [examined]. Imaged on AntWeb: CASENT0907475. **Syn**. **nov.**

Sima Le Moulti Santschi 1920b: 375. Holotype (by monotypy), dealate queen, Fort-Crampel, Central African Republic (LeMoult) (NHMB) [examined]. Imaged on AntWeb: CASENT0915530. **Syn**. **nov.**

Tetraponera mocquerysi var. *lepida* Wheeler 1922a: 106. Syntype, 1 worker, Faradje, Democratic Republic of Congo (Lang & Chapin) (MCZC) [examined]. **Syn**. **nov.**

Sima (*Sima*) *mocquerysi* var. *biozellata* Karavaiev 1931: 42. Syntypes, 1 worker, Naivasha, Kenya (Dogiel), 1 worker, 1 alate queen, Mabira, Kenya (Dogiel & Sokolow) (UASK) [examined]. Imaged on AntWeb: CASENT0916865, **Syn**. **nov.**

Sima monardi Santschi 1937b: 218. Holotype (by monotypy), worker, Tyihumbwe, Angola (D. Monard) (MHNC) [examined]. **Syn**. **nov.**

Tetraponera ledouxi Terron 1969: 629. Syntypes, workers, queens, males, "région de Yaoundé", Cameroun [no explicitly labeled types found, but material collected by Terron in Cameroon (ANIC) examined]. **Syn**. **nov.**

Tetraponera mocquerysi (André); Wheeler 1922a: 106. Combination in *Tetraponera*.

Tetraponera mocquerysi (André); Chomicki *et al*. 2015: figure S1. Placement in molecular phylogeny.

Sima Mocquerysi st. *emacerata* Santschi; Santschi 1914a: 70. Description of queen.

Sima emacerata Santschi; Santschi 1920a: 9. Raised to species.

Tetraponera mocquerysi subsp. *emacerata* (Santschi); Wheeler 1922a: 107. Combination in *Tetraponera*; subspecies of *T. mocquerysi*.

Sima emacerata Santschi; Santschi 1928: 57. Raised to species.

Sima mocquerysi st. *emacerata* Santschi; Santschi 1933: 100. Subspecies of *S. mocquerysi*.

Sima emacerata Santschi; Bernard 1953: 221. Raised to species.

Tetraponera emacerata (Santschi); Ward 1990: 488. Combination in *Tetraponera*.

Sima Oberbecki Forel; Forel 1916: 403. Description of queen.

Sima (*Tetraponera*) *oberbecki* Forel; Emery 1921: 28. Combination in *Sima* (*Tetraponera*).

Tetraponera oberbecki (Forel); Wheeler 1922b: 800. Combination in *Tetraponera*.

Sima emacerata v. *oberbecki* Forel; Santschi 1928: 58. Variety of *S. emacerata*.

Tetraponera emacerata oberbecki (Forel); Ward 1990: 489. Combination in *Tetraponera*; subspecies of *T. emacerata*.

Tetraponera mocquerysi var. *elongata* (Stitz); Wheeler 1922b: 798. Combination in *Tetraponera*.

Tetraponera mocquerysi elongata (Stitz); Ward 1990: 488. Subspecies of *T. mocquerysi.*

Tetraponera triangularis subsp. *illota* (Santschi); Wheeler 1922b: 801. Combination in *Tetraponera*.

Sima (*Tetraponera*) *prelli* var. *odiosa* Forel; Emery 1921: 28. Combination in *Sima* (*Tetraponera*).

Tetraponera prelli var. *odiosa* (Forel); Wheeler 1922b: 800. Combination in *Tetraponera*.

Sima emacerata v. *odiosa* Forel; Santschi 1928: 57. Variety of *S. emacerata*.

Tetraponera emacerata odiosa (Forel); Ward 1990: 489. Combination in *Tetraponera*; subspecies of *T. emacerata*.

Tetraponera le moulti [sic] (Santschi); Wheeler 1922b: 798. Combination in *Tetraponera*.

Tetraponera lemoulti (Santschi); Ward 1990: 488.

Tetraponera mocquerysi lepida Wheeler; Ward 1990: 488. Subspecies of *T. mocquerysi.*

Tetraponera mocquerysi biozellata (Karavaiev); Ward 1990: 488. Combination in *Tetraponera*; subspecies of *T. mocquerysi.*

Tetraponera monardi (Santschi); Ward 1990: 488. Combination in *Tetraponera*.

Tetraponera ledouxi Terron; Terron 1970: 113. Evidence of temporary social parasitism.

Worker measurements (n = 12). HW 1.04–1.58, HL 1.21–1.77, LHT 0.85–1.34, CI 0.80–0.90, FCI 0.09–0.14, REL 0.41–0.52, REL2 0.48–0.6, SI 0.53–0.57, SI3 0.90–1.14, FI 0.39–0.47, PLI 0.67–0.78, PWI 0.61–0.78, LHT/HW 0.79–0.86, CSC 8–34, MSC 21–100.

Worker diagnosis. Medium to large species, with somewhat elongate head (CI 0.80–0.90) and moderately large eyes (REL 0.41–0.52); posterior margin of eye not attaining the level of the lateral ocelli; frontal carinae moderately separated, the minimum distance between them less than 0.15× head width (FCI 0.09–0.14) and usually less than one-quarter of scape length (MFC/SL 0.16–0.26); scapes of moderate length (SI 0.53–0.57, SI2 0.44–0.48), subequal to eye length (SI3 0.90–1.14); anterior clypeal margin broadly and weakly convex, with a short median denticle, usually flanked by 2–3 smaller denticles on each side, sometimes ill-defined (Fig. 27a); profemur slender to moderately robust (FI 0.39–0.47); mesonotum bounded posteriorly by a well marked but simple impression, lacking longitudinal rugulae; distinct metanotal plate not present, although anterior extremity of propodeum with a weakly differentiated arched-transverse area in some individuals; dorsal face of propodeum flattened, laterally submarginate, longer than declivitous face and rounding insensibly into the latter; petiole of moderate length and height (PL/HW 0.62–0.77; see also PLI and PWI values), with rather weak dorsolaterally margination, and with an anteroventral tooth; in profile, petiolar node with similar anterodorsal and posterodorsal faces, rounding insensibly into one another, or with less less strongly inclined anterodorsal face; in dorsal view petiole obovate, with rounded sides (Fig. 27b); postpetiole longer than broad. Head and mesosoma densely punctulate-coriarious, matte. Standing pilosity common to abundant (CSC 8–34, MSC 21–100, HTC+MTC 0–50), conspicuous on dorsum of head, mesosoma, petiole, postpetiole and gaster, and tending to grade into short, suberect pubescence, especially on mesosoma and petiole. Dark brownish-black, the mandibles, clypeus, antennae, tibiae and tarsi variably lighter (brown to luteous).

Comments. Four other species in the *Tetraponera natalensis* group have predominantly dark (brownish-black) coloration. Workers of *Tetraponera mocquerysi* can be distinguished from those of *T. andrei*, *T. anthracina*, and *T. insularis* by their soft-margined and longer petiole (PL/HW 0.62–0.77), more closely adjacent frontal carinae (FCI 0.09–0.14), and more abundant standing pilosity. *T. mocquerysi* differs from the fourth species, *T. setosa*, by its more elongate head (CI 0.80–0.90), denticulate clypeal margin, matte integument, and less abundant standing pilosity than *T. setosa*. In a few populations of *T. natalensis* the workers assume a medium to dark brown color, making them superficially similar to those of *T. mocquerysi*, but workers of the latter can be disinguished by having (1) a petiole that is obovate in dorsal view, with weak lateral margination, (2) a petiolar profile in which the posterodorsal face is as steep or steeper than the anterodorsal face (usually the opposite in *T. natalensis*), and (3) greater amouts of standing pilosity, on average (CSC 8–34 and MSC 21–100, versus CSC 4–18 and MSC 3–25 in *T. natalensis*).

T. mocquerysi is here interpreted as a widespread and rather variable species. As shown by the measurements and diagnostic features cited above, this includes variation in head shape, eye size, scape length, anterior propodeal configuration, and petiole shape. When large enough samples are examined, however, the variation appears to be continuous—there is no evidence of phenotypic gaps. *T. mocquerysi* does show notable among-colony variation in worker body size (and that of cohabiting queens and males), even within single localities. It is possible that there is some size-assortative mating in this species—or that the size differences reflect cryptic species—but this remains to be investigated. The size variation of this species is reminiscent of a similar situation in Australian populations of *Tetraponera punctulata* (Ward, 2001).

Distribution and biology. *T. mocquerysi* is found in rainforest and similar mesic habitats, from The Gambia in west Africa, east to Ethiopia, and south to Angola and western Tanzania. It is a generalist inhabitant of dead twigs or branches, with specific nest site records from *Erigeron bonariensis*, *Erythrina*, *Ficus*, *Maesa lanceolata*, *Manihot esculenta*, *Senna*, *Triumfetta cordifolia*, and various unidentified woody plants. Under the name *Tetraponera ledouxi*, Terron (1969, 1970) reported *T. mocquerysi* to be a temporary social parasite of *T. anthracina*, but this behavior must be facultative because *T. mocquerysi* has a much wider distribution than *T. anthracina* (Figs 41, 43).

Material examined (AMNH, ANIC, ASIC, BMNH, CASC, CPDC, CUIC, FHGC, KUES, LACM, MCZC, MHNC, MHNG, MNHN, MRAC, MSNG, MZLU, NHMB, NHMB, NHMW, NMKE, PSWC, SAMC, UASK, UCDC, USNM, ZMHB). **Angola**: *Cuanza Norte*: Vila Salazar (Malkin, B.); *Cuanza Sul*: 4 mi SW Quilenda, 900 m (Ross, E. S.; Leech, R. E.); *Huambo*: Mont. Moko, 1890 m (Fisher, B. L.); *Lunda Sul*: Tyihumbwe (Monard, D.); *Malanje*: Malanje [as "Melange"] (Malkin, B.); **Benin**: *Ouémé*: Pobé, 57 km NNE Pto. Novo, 150 m (Lattke, J.); **Cameroon**: *Centre*: Makak, 90 km SW Yaoundé, 650 m (Ross, E. S.; Lorenzen, K.); Mt. Fébé, Yaoundé, 1050 m (Ross, E. S.; Lorenzen, K.); *region unknown*: "Cameroon" (Terron, G.); "Kamerun" (Conradt, L.); *Sud*: Ebodjé

(Blatrix, R.); Ebolowa, Nkoemvon (Jackson, D.); Nkoemvon (Jackson, D.); Réserve de Campo, 40 m (Olson, D. M.); *Sud-Ouest*: Matute, Tiko Plantation (Malkin, B.); Rengo Camp, Korup National Park (Blatrix, R.); Victoria (Malkin, B.); **Central African Republic**: *Nana-Grébizi*: Fort Crampel (Le Moult); *Sangha-Mbaéré*: P.N. Dzanga-Ndoki, 21.4 km 53° NE Bayanga, 510 m (van Noort, S.); P.N. Dzanga-Ndoki, Mabéa Bai, 21.4 km 53° NE Bayanga, 510 m (Fisher, B. L.); Res. Dzanga-Sangha, 12.7 km 326° NW Bayanga, 420 m (Fisher, B. L.); Res. Dzanga-Sangha, 12.7 km 326° NW Bayanga, 420 m (van Noort, S.); Res. Dzanga-Sangha, 12.7 km 326° NW Bayanga, 470 m (Fisher, B. L.); **Côte d'Ivoire**: *Bas-Sassandra*: 35 km N San Pedro (Pulawski, W. J.); *Lagunes*: 3.5 km S Sangrobo, S-P de Tiassale (Brown, W. L.; Brown, D. E.); **DR Congo**: *Haut-Katanga*: Biano (Ogilvie, J.); Dilolo (Ogilvie, J.); Kalemie [as "Albertville"] (Augustine); Kalemie [as "Albertville"] (Cockerell,, J. D. A.); Kongolo (Whitcomb, W. H.); Lubumbashi (Bequaert, M.); Lubumbashi [as "Elisabethville"] ("Miss. Agric."); Lusinga, Park Upemba, 1800 m (Ross, E. S.; Leech, R. E.); Mbulula [as "Mbalula"] (Whitcomb, W. H.); Munowe, Park Upemba, 1450 m (Ross, E. S.; Leech, R. E.); *Haut-Uélé*: Faradje (c.u.); Garamba (Lang; Chapin); Moto (Burgeon, L.); Yakuluku (Lang; Chapin); *Ituri*: 24 mi S Mambasa, 950 m (Ross, E. S.; Leech, R. E.); Ituri F., Beni-Irumu (Weber, N. A.); Ituri Forest, vic. Epulu (Gregg, T.); Ituri, Congo-Belge (c.u.); Kasonsero, Semliki (Bequaert, J.); *Kasaï Oriental*: Kasende (Bequaert, J.); *Kongo Central*: Congo da Lemba (Mayné, R.); Kidada (Kitobola) (Schouteden, H.); Lukula (Daniel); Lukula [as "Lukulu"] (Bequaert, J.); *Mai-Ndombe*: Mongende (Schouteden, H.); *Maniema*: Lubutu (c.u.); *Nord-Kivu*: 39 km S Walikale, 700 m (Ross, E. S.; Leech, R. E.); Mwenda, Mt. Ruwenzori, 1455 m (Bradley, J. C.); *province unknown*: "Congo" (Kohl); *Sud-Kivu*: Fizi (c.u.); Irangi, Luhoho R., 900 m (Ross, E. S.; Leech, R. E.); Luhoho Riv., Bunyakiri, 1100 m (Ross, E. S.; Leech, R. E.); Lwiro R., 47 km N Bukavu, 1650 m (Ross, E. S.; Leech, R. E.); S. slope Mt. Kahuzi, 1900 m (Ross, E. S.; Leech, R. E.); *Tshopo*: Kisangani [as "Stanleyville"] (c.u.); Kisangani [as "Stanleyville"] (Kohl, H.); Kisangani [as "Stanleyville"] (Lang, H. O.); Yangambi Reserve (Raignier, A.; van Boven, J.); **Ethiopia**: *Oromia*: Arussi Galla, Ganale Gudda (Bottego, V.); **Gabon**: *Ogooué-Maritime*: Gamba, 50 m (Yanoviak, S. P.); Port Gentil (Ross, E. S.; Leech, R. E.); Res. Moukalaba, 12.2 km 305° NW Doussala, 110 m (Fisher, B. L.); Réserve de la Moukalaba-Dougoua, 12.2 km 305° NW Doussala, 110 m (van Noort, S.); Réserve de la Moukalaba-Dougoua, 7 km NW Doussala, 110 m (van Noort, S.); **Ghana**: *Brong-Ahafo*: Baudua (Leston, D.); Goaso (Leston, D.); *Central*: 30 mi E Tahoradi (Richards, O. W.); *Eastern*: Aburi (Room, P.); Adeigo (Leston, D.); Adeigo (Room, P.); Bunso (Leston, D.); Kakurantumi (Leston, D.); Mpraeso, 500 m (Ross, E. S.; Lorenzen, K.); Nkawkaw, 80 km NW Koforidua (Pulawski, W. J.); Osiam (Leston, D.); Sajumasi (Leston, D.); Tafo (Gibbs, D. G.); Tafo (Bolton, B.); Tafo (Leston, D.); Tafo Cocoa Plantn. (Leston, D.); *Greater Accra*: Legon (Leston, D.); Pokoase (Krauss, N. L. H.); *Western*: Chama (Brauns); **Guinea**: *N'Zérékoré*: Camp 1, Mt. To (Lamotte); Nimba, Camp 4, 1000 m (Lamotte, M.); **Kenya**: *Kakamega*: Kakamega Forest, 1500 m (Olson, D. M.; Farley, L.); Kakamega Forest, 1600 m (Wagner, T.); Kakamega Forest, 1650 m (Fischer, G.); Kakamega Forest (Stubbs, A. E.); Kakamega Forest, Colobus road, 1650 m (Fischer, G.); Kakamega Forest, Isiuku Falls, 1650 m (Fischer, G.); Kakamega Forest, Udo's camp, 1650 m (Hita Garcia, F.); Kakamega Forest, Isecheno, 1800 m (Snelling, R. R.); *Kisumu*: Kisumu, Kyanza [sic] (Bohart, R. M.); *Nakuru*: Naivasha (Dogiel); Nakuro (Rift-Valley) (Alluaud, C.); *Trans Nzoia*: Kitale, Uasin Gishu, 2100 m (Arambourg, C.; Chappuis, P. A.; Jeannel, R.); *Vihiga*: Kaimosi Mission, 27 mi NE Kisumu, 1650 m (Ross, E. S.; Leech, R. E.); **Liberia**: *Bong*: Cuttington Col., Up. Bong Co. (Carroll, R.); Gibi (Mann, W. M.); *Lofa*: Belleyella (Mann, W. M.); *Margibi*: Du River, Camp No. 3 (c.u.); Harbel, Firestone Plantation (Ross, E. S.; Lorenzen, K.); Robts Fld (Krauss, N. L. H.); *Montserrado*: Monrovia (Cook, O. F.); *Nimba*: Mt. Nimba airstrip, Nimba Co. (Carroll, R.); **Nigeria**: *Cross River*: Obudu CR, SE State (Medler, J. T.); *Edo*: Sapoba Forest Reserve, 20 km S Benin City (Janzen, D. H.); *Ogun*: Lagos Colony, Isheri (Malkin, B.); Olokemej (c.u.); Olokemeji, Ibadan (Bridwell); Olokemenji (c.u.); *Oyo*: CRIN (Taylor, B.); Gambari (Bolton, B.); Ibadan (Noyes, J.); *Plateau*: Jos (Meyer, R. W.); *state unknown*: Araromi (c.u.); **Republic of Congo**: *Pool*: Lesio-Loun Park, 330 m (Braet; Sharkey); Lesio-Loun Park, 330 m (Sharkey; Braet); Kindamba, Meya, Bangu-Forst (Balogh & Zicsi); **Sierra Leone**: *province unknown*: "Sierra Leone" (Brauns); "Sierra Leone" (Mocquerys); *Southern*: Njala (Hargreaves, E.); Periwahun [as "Parmbog"] (Hargreaves, E.); **South Sudan**: *Central Equatoria*: Kagelu (Myers); *Jonglei*: S of Nelichu, Boma Plateau (Myers, J. G.); **Tanzania**: *Kagera*: Budduwald (Friedrichs, A.); *Kigoma*: Mahale Mountains N.P., 950 m (Kiyono, M.); Mahale Mts., 780 m (Uehara, S.); Mwamgongo (Meneghetti); *Mara*: Ukerewe I. (Conrads); *Njombe*: Tandala (c.u.); **The Gambia**: *Western*: Kombo St. Mary, Abuko (Söderlund, M.); **Uganda**: *Buikwe*: 10 mi W Jinja, 1200 m (Ross, E. S.; Leech, R. E.); Mabira (Dogiel); *Bundibugyo*: 1 km ENE Sempaya, 870 m (Ward, P. S.); Kirumia River Trail, Semliki Natl. Park, 720 m (Ward, P. S.); Ruwenzori Range, Bundibugyo, 1050 m (Fletcher, D. S.); Ruwenzori Range, Semliki Forest, 870 m (Fletcher, D. S.); Rwakasenyi,

Semliki Natl. Park, 685 m (Blaimer, B. B.); Semliki River, Semliki Natl. Park, 660 m (Ward, P. S.); Sempaya, Semliki Natl. Park, 680 m (Ward, P. S.); Semuliki National Park, 676 m (Fisher, B. L.; *et al*.); Semuliki National Park, 680 m (Fisher, B. L.; *et al*.); Semuliki National Park, 685 m (Fisher, B. L.; *et al*.); Semuliki National Park, 690 m (Fisher, B. L.; *et al*.); Semuliki National Park, 701 m (Fisher, B. L.; *et al*.); Semuliki National Park, Kirumia River, 710 m (Fisher, B. L.; *et al*.); Bushenyi: Kalinzu Forest, 1450 m (Yamane, S.); *district unknown*: "Ouganda Central" (Alluaud, C.); Kibale Forest, 0°31'–0°41'N, 30°19'–30°32'E (Chapman, L.); Lake Edward [as "Eduard See"] (Hamann); Lake George [as "Georg See"] (Hamann); Lake Victoria [as "Viktoria See"] (Hamann); *Jinja*: Jinja (c.u.); *Kabarole*: Fort Portal (Daly, H. V.); Kanyawara (Roth, V.); Kanyawara, Kibale Natl. Park, 1490 m (Ward, P. S.); Kanyawara, Kibale Natl. Park, 1500 m (Ward, P. S.); Kanyawara, Kibale Natl. Park, 1510 m (Suarez, A. V.); Kanyawara, Kibale Natl. Park, 1510 m (Ward, P. S.); Kanyawara, Kibale Natl. Park, 1520 m (Ward, P. S.); Kanyawara, Kibale Natl. Park, 1600 m (Ward, P. S.); Kanyawara, Kibale NP, 1465 m (van Noort, S.); Kanyawara, Kibale NP, 1484 m (van Noort, S.); Kanyawara, Kibale NP, 1491 m (van Noort, S.); Kanyawara, Kibale NP, 1494 m (van Noort, S.); Kanyawara, Kibale NP, 1495 m (van Noort, S.); Kanyawara, Kibale NP, 1498 m (van Noort, S.); Kanyawara, Kibale NP, 1505 m (van Noort, S.); Kanyawara, Kibale NP, 1506 m (van Noort, S.); Kanyawara, Kibale NP, 1587 m (van Noort, S.); Kanyawara, Kibale NP, 1510 m (Hawkes, P. G.); Kibale Forest (Chapman, L.); Kibale Forest Res. (Orr, M. R.); Kibale National Park, Kanyawara Biological Station, 1504 m (Fisher, B. L.; *et al*.); Kibale National Park, Kanyawara Biological Station, 1510 m (Fisher, B. L.; *et al*.); Kibale National Park, Kanyawara Biological Station, 1520 m (Fisher, B. L.; *et al*.); Kibale National Park, Kanyawara Biological Station, 1540 m (Fisher, B. L.; *et al*.); Kibale National Park, Kanyawara Biological Station, 1552 m (Fisher, B. L.; *et al*.); Kibale NP, Kanyawara Biol. Stn., 1500 m (Fischer, G.); *Kampala*: Kampala (Gedye, A. F. J.); Makerere (Nyerere); *Kasese*: Ruwenzori Range, Bugoye, 1370 m (Fletcher, D. S.); *Masindi*: Budongo Forest, vic. Sonso, 1050 m (Wagner, T.); *Rakai*: W. shores of Vic. Nyanza, Buddu, 1130 m (Neave, S. A.); *Sironko*: 13 mi NE Mbale, 1300 m (Ross, E. S.; Leech, R. E.); Buwalasi, Mt. Elgon, 1525 m (Bradley, J. C.); *Wakiso*: Entebbe (c.u.); Entebbe (Fisher, B. L.; *et al*.); Entebbe (Hamann); Entebbe (Messersmith, D. H.); Entebbe Botanical Gardens, 1160 m (Ward, P. S.); Kawanda Res. Station, N. Kampala (Daly, H. V.).

Tetraponera natalensis (F. Smith)

(Figs 3, 28, 44)

Pseudomyrma natalensis F. Smith 1858: 160. Syntype, 1 dealate queen, "Pt. Natal", South Africa (BMNH) [examined]. Imaged on AntWeb: CASENT0902819.

Pseudomyrma capensis F. Smith 1858: 160. Syntype(s), worker(s), Cape of Good Hope, South Africa (types apparently lost, not in BMNH) [not examined]. **Syn**. **nov.**

Sima natalensis var. *obscurata* Emery 1895b: 22. Syntypes, 2 workers, Cape of Good Hope [as "Capo di Buena Esp."] (MSNG) [examined]. 1 syntype worker imaged on AntWeb: CASENT0904031. **Syn**. **nov.**

Sima mocquerysi v. *lutea* Stitz 1911: 381. Syntypes, 1 dealate queen, 1 worker, Ins. Kwidschwi, Kiwusee, Democratic Republic of Congo (A. Friedrichs) (ZMHB) [examined]. Imaged on AntWeb: FOCOL1160, FOCOL1158. **Syn**. **nov.**

Sima Prelli Forel 1911a: 365. Syntype, 1 worker, Monga, Tanzania (Prell) (MHNG) [examined]. Imaged on AntWeb: CASENT0907474. **Syn**. **nov.**

Sima natalensis var. *usumbarensis* Forel 1911a: 367. Syntype, 1 worker, Monga, Tanzania (Prell) (MHNG) [examined]. Imaged on AntWeb: CASENT0907452. **Syn**. **nov.**

Sima natalensis subsp. *cuitensis* Forel 1911a: 368. Syntype, 1 worker, Cubango-Cuito, Angola (Baum) (MHNG) [examined]. Imaged on AntWeb: CASENT0907453. **Syn**. **nov.**

Sima angusta Arnold 1949: 266. Syntypes, 2 workers, Bulawayo, Zimbabwe (SAMC) [examined]. **Syn**. **nov.**

Sima natalensis r. *cuitensis* v. *Bulawayana* Forel 1913: 112. 5 workers, Bulawayo, Zimbabwe (Arnold) (MHNG) [examined]. Unavailable name.

Sima natalensis st. *cuitensis* v. *quaniama* Santschi 1937b: 218. 1 worker, Kamba, Angola (D. Monard) (NHMB) [examined]. Unavailable name.

Tetraponera natalensis (F. Smith); F. Smith 1877: 69. Combination in *Tetraponera*; revived from synonymy.

Sima natalensis (F. Smith); Emery 1892: 237. Combination in *Sima*.

Sima natalensis (F. Smith); Emery 1895b: 22. Description of worker.

Sima natalensis (F. Smith); Emery 1899b: 6. Description of larva.

Tetraponera natalensis (F. Smith); Wheeler 1922b: 798. Combination in *Tetraponera*.

Tetraponera natalensis (F. Smith); Wheeler & Wheeler 1973: 208. Description of larva.
Tetraponera natalensis (F. Smith); Chomicki *et al.* 2015: figure S1. Placement in molecular phylogeny.

Sima capensis (F. Smith); Mayr 1866: 906. Combination in *Sima*.
Pseudomyrma capensis F. Smith; Gerstäcker 1871: 355. Senior synonym of *P. natalensis*.
Tetraponera capensis (F. Smith); Wheeler 1922b: 797. Combination in *Tetraponera*.

Sima natalensis race *obscurata* Emery; Arnold 1916: 177. Description of queen, male.
Tetraponera natalensis var. *obscurata* (Emery); Wheeler 1922b: 799. Combination in *Tetraponera*.
Tetraponera natalensis obscurata (Emery); Ward 1990: 489. Subspecies of *T. natalensis.*

Tetraponera mocquerysi var. *lutea* (Stitz); Wheeler 1922b: 798. Combination in *Tetraponera*.
Tetraponera mocquerysi lutea (Stitz); Ward 1990: 488. Subspecies of *T. mocquerysi.*

Sima (*Tetraponera*) *prelli* Forel; Emery 1921: 28. Combination in *Sima* (*Tetraponera*).
Tetraponera prelli (Forel); Wheeler 1922b: 800. Combination in *Tetraponera*.

Sima natalensis var. *usumbarensis* Forel; Santschi 1914a: 70. Description of queen.
Tetraponera natalensis var. *usumbarensis* (Forel); Wheeler 1922b: 799. Combination in *Tetraponera*.
Tetraponera natalensis usumbarensis (Forel); Ward 1990: 489. Subspecies of *T. natalensis.*

Tetraponera natalensis subsp. *cuitensis* (Forel); Wheeler 1922b: 799. Combination in *Tetraponera*.

Tetraponera angusta (Arnold); Ward 1990: 487. Combination in *Tetraponera*.

Worker measurements (n = 23). HW 0.92–1.29, HL 1.07–1.55, LHT 0.74–1.10, CI 0.77–0.91, FCI 0.09–0.12, REL 0.41–0.45, REL2 0.48–0.56, SI 0.51–0.55, SI3 0.95–1.11, FI 0.42–0.46, PLI 0.64–0.80, PWI 0.50–0.75, LHT/HW 0.78–0.89, CSC 3–18, MSC 3–25.

Worker diagnosis. Small to medium-sized species, with somewhat elongate head (CI 0.77–0.91) and moderately large eyes (REL 0.41–0.45, REL2 0.48–0.56); posterior margin of eye not attaining the level of the lateral ocelli; frontal carinae relatively closely adjacent, the minimum distance between them about 0.10× head width (FCI 0.09–0.12) and about one-fifth of scape length (MFC/SL 0.18–0.23); scapes of moderate length (SI 0.51–0.55, SI2 0.42–0.47), subequal to eye length (SI3 0.95–1.11); anterior clypeal margin broadly and weakly convex, with a short median denticle, flanked by 2–3 smaller denticles on each side, sometimes ill-defined (Fig. 28a); profemur relatively slender (FI 0.42–0.46); mesonotum bounded posteriorly by a simple transverse impression, often quite faint; distinct metanotal plate not present, although anterior extremity of propodeum with a weakly differentiated arched-transverse area in some individuals; dorsal face of propodeum flattened, laterally submarginate, longer than declivitous face and rounding insensibly into the latter; petiole of moderate length and height (PL/HW 0.64–0.80; see also PLI and PWI values), dorsolaterally submarginate, and with an anteroventral tooth; in profile, petiolar node typically with relatively steep anterodorsal face, followed by a somewhat flattened dorsum, sloping gradually downward posteriorly at a gentler incline than the anterodorsal face (Fig. 28b), but anterodorsal face more gently sloping in some workers; in dorsal view, petiole narrowly obovate to subtrapezoidal, with more or less straight sides (as in Fig. 25b); postpetiole longer than broad. Head and mesosoma densely punctulate-coriarious, matte; vertex sometimes more weakly sculptured, sublucid. Standing pilosity sparse to moderately common (CSC 3–18, MSC 3–25, HTC+MTC 0–5); fine but dense pubescence covering most of body, with a tendency to be come uplifted (suberect to subdecumbent) on the mesosoma and petiole, and in some populations (e.g., Usambara Mountains, Tanzania) grading into short standing pilosity. Typically yellow- to orange-brown, with tip of gaster infuscated, but body of darker complexion (medium to dark brown) in some populations.

Comments. *T. natalensis* workers can be characterized by their small to medium size (HW 0.92–1.29, LHT 0.74–1.10), scapes and eyes of moderate length (SI 0.51–0.55, REL 0.41–0.45), relatively slender profemur (FI 0.42–0.46), and a petiolar profile typically consisting of a steep anterodorsal face followed a more gently sloping posterodorsal face (Fig. 28b), although deviations from this pattern occur. Individuals are usually yellow- to orange-brown in color, with relatively sparse standing pilosity. There are three other yellowish to orange species in the *T. natalensis* group. Two of these can be readily distinguished from *T. natalensis*: *T. schulthessi* by its larger size, and *T. caffra* by its shorter scapes and more robust profemur. The third species, *T. redacta*, is closely similar to *T. natalensis*, differing primarily by the lack of a differentiated mesonotum in the worker and by a petiole that

is shorter and higher than that of *T. natalensis* workers and queens in nearby populations (see further discussion under *T. redacta*). Some workers of *T. natalensis* are duskier in color—corresponding to the forms described as *T. natalensis obscurata* and *T. prelli*—and these could be confused with those of *T. mocquersyi*; the latter, however, differ in petiole shape and pilosity (see key). Such darker morphs of *T. natalensis* have been recorded from Angola, Namibia, South Africa, and Tanzania.

Distribution and biology. Ranging from Kenya (excluding the coastal region) to Mozambique and South Africa, thence west to DR Congo, Angola and Namibia (Fig. 44), *T. natalensis* has been recorded from a diversity of (mostly drier) habitats including savanna woodlands, shrublands, bushveld/grassland, semideciduous forest, coastal thicket, riparian forest, tropical moist forest and rainforest. It is a generalist dead-twig inhabitant, and has been recorded nesting in dead twigs or branches of a wide variety of woody plants, including *Cedrela odorata*, *Dombeya*, *Ficus sycomorus*, *Maesopsis eminii*, *Rubus*, *Senna didymobotrya*, *Terminalia*, *Vachellia tortilis*, *Vachellia karroo* (thorn), and unidentified vines and trees.

Material examined (AMNH, ANIC, BMNH, CASC, CUIC, FHGC, FSCA, HZIC, KUBC, KUEC, KUES, LACM, MCZC, MHNG, MNHN, MSNG, MZLU, NHMB, NHMW, NMKE, NMWN, PSWC, SAMC, UCDC, UMSC, USNM, ZMAS, ZMHB). **Angola**: *Cunene*: Kamba (Monard, D.); *Huambo*: Mont. Moko, 1970 m (Fisher, B. L.); *Kuando Kubango*: Cubango-Cuito (Baum); *Luanda*: Luanda to Catete, km. 13, T-512 (Kistner, D. H.; Swift, R. J.); **Botswana**: *North West*: Okavango Delta, Smiti (Russell-Smith, A.); Smiti (Russell-Smith, A.); *South East*: Kgale Hill, 3 km SW Gaborone, 1300 m (Ward; Stronkhorst); **DR Congo**: *Haut-Katanga*: 37 mi NE Elisabethville, 1225 m (Ross, E. S.; Leech, R. E.); Mbulula [as "Mbalula"] (Whitcomb, W. H.); *Kasaï Oriental*: Kasende (Bequaert, J.); *Sud-Kivu*: Ile Idjwi [as "Ins. Kwidschwi"] (Friedrichs, A.); **Eswatini**: *Manzini*: Mlilwane Wildlife Sanct., 750 m (Ward, P. S.); **Kenya**: *Kajiado*: Emali Range, 1650 m (Hamud, S.); Ngong, 2440 m (van Someren, G.); Oloitokitok [as "Loitokitok (= Oloitok.)"], 1800 m (Zettel, H.); *Laikipia*: Ewaso Ng'iro River, nr. Mpala Research Centre, 1600 m (Snelling, R. R.); Mpala RC, Ewaso Ng'iro, 1600 m (Snelling, R. R.); Mpala Research Centre, 1650 m (Snelling, R. R.); *Makueni*: Kibwezi (Clifton, M. P.); *Murang'a*: Tana River (Clark, J. L.); *Nairobi City*: Nairobi, 1600 m (Ward, P. S.); Nairobi (Meneghetti); Nairobi (Patrizi, S.); *Taita Taveta*: Voï, 600 m (Alluaud; Jeannel); **Malawi**: *Thyolo*: Thyolo [as "Cholo"] (Wood, R. C.); **Mozambique**: *Cabo Delgado*: 15.4 km 47° from Pemba, 40 m (Fisher, B. L.; *et al*.); 24.5 km 346° from Pemba, 20 m (Fisher, B. L.; *et al*.); 9.5 km 297° from Pemba, 20 m (Fisher, B. L.; *et al*.); P.N. Quirimbas, 325 m (Fisher, B. L.; *et al*.); P.N. Quirimbas, Mareja Res., 125 m (Fisher, B. L.; *et al*.); P.N. Quirimbas, Mareja Res., 240 m (Fisher, B. L.; *et al*.); P.N. Quirimbas, Taratibu, 300 m (Fisher, B. L.; *et al*.); P.N. Quirimbas, Taratibu, 325 m (Fisher, B. L.; *et al*.); P.N. Quirimbas, Taratibu, 360 m (Fisher, B. L.; *et al*.); P.N. Quirimbas, Taratibu, 505 m (Fisher, B. L.; *et al*.); Quiterajo forest, 100 m (Fisher, B. L.; *et al*.); *Gaza*: Nuanetsi R. [as "Wanetsi R."] (Marley, H. B.); *Maputo*: Delagoa (Staudinger); Inhaca Island, 1 m (Alpert, G. D.); Umbelusi (c.u.); *Sofala*: 1 km S Chitengo, Gorongosa Natl. Park, 40 m (Ward, P. S.); 3.5 km SE Chitengo, Gorongosa Natl. Park, 40 m (Ward, P. S.); Gorongosa Park, Chitengo, 30 m (Hauser, M.); *Tete*: 30 km NW Tete, 500 m (Alpert, G. D.); Chiuta Dist., Ruoni North, 324 m (Hawkes, P.; Fisher, J.); *Zambézia*: 30 km E Quelimane, 1 m (Alpert, G. D.); 52 km N Quelimane, 70 m (Alpert, G. D.); 57 km N Quelimane, 70 m (Alpert, G. D.); Milange (Alpert, G. D.); Mt. Mabu, 1200 m (Fisher, B. L.; *et al*.); Mt. Mabu, 1400 m (Fisher, B. L.; *et al*.); Mt. Mabu, 1600 m (Fisher, B. L.; *et al*.); Mt. Mabu, 375 m (Fisher, B. L.; *et al*.); Mt. Mabu, 825 m (Fisher, B. L.; *et al*.); Mt. Mabu, 960 m (Fisher, B. L.; *et al*.); **Namibia**: *Kavango East*: Mahango Game Reserve (O'Brien, C. W.; O'Brien, L. B.; Marshall, G. B.); Poppa Valle Rest Camp (O'Brien, C. W.; O'Brien, L. B.; Marshall, G. B.); *Kunene*: Kaoko Otavi (c.u.); *Oshana*: Ondongua (Barnard, K. H.); *Oshikoto*: 40 km WNW Grootfontein, Gaub Farm No. 47 (Hogue, C. L.); *Otjozondjupa*: Nurugas [as "Nuragas"] (c.u.); *Zambezi*: 2 km W Hippo Island, East Caprivi (Marais, E.; Pusch, M.); **South Africa**: *Eastern Cape*: 2 mi ESE Grahamstown (Daly, H. V.; Farquharson, F.); Albany, Thursford Farm (Robertson, H. G.); Algoa Bay, Capland (Brauns); Algoa Bay, Capland (c.u.); Algoa-Bay (Brauns, H.); Andries Vosloo Kudu Reserve, 12.8 km NNE Fort Brown (Lubertazzi, D.); Februarie Farm, 40.2 km 267° W Kirkwood (van Noort, S.); Fort Beaufort (Samways, M.); Grahamstown (Brown, W. L.); Grahamstown (Weatherill, L.); Katburg, E. Cape Prov., 1220 m (Turner, R. E.); King Williams Town (Capener, A.); Mount Coke, King Williams Town (Capener, A.); picnic site near Februarie Farm (Robertson, H. G.); Pirie Forest (Capener, A.); Port Elizabeth (Brauns); Port Elizabeth (c.u.); Port St. John, Pondoland (Turner, R. E.); Tsitsikama N.P., Stormsrivier Pass (Danielsson, R.); Umgazi R. Mth. (Bohart, R. M.); Van Stadens Mouth (c.u.); *Gauteng*: Lemon Tree Tea Garden, Cullinan, 1440 m (Hawkes, P. G.); Pretoria (Grobler, J. H. [as "J. H. G."]); Pretoria, Garsfontein (Craninx, A.); Pretoria, Lynnwood (Danielsson, R.); *KwaZulu-Natal*: "Natal" (c.u.); "Pt. Natal" (c.u.); 17 km NE Empangeni, Nseleni River (Danielsson, R.); 2 km

S Umfolozi (Brown, W. L.; Brown, D. E.); 30 km N Mtubatuba (O'Brien, C. W.; O'Brien, L. B.; Marshall, G. B.); Abu Madi Game Ranch, 200 m (Ward, P. S.); Berea (Marley, H. W. B.); Dugandlovu Camp, False Bay Park, 10 m (Ward, P. S.); Durban (Barley, H. B.); Durban (c.u.); Durban (Cooper, C. B.); Durban (Marley, H. B.); Durban (Peckham, G. W.); Estcourt (c.u.); Fannes I., St. Lucia (Fletcher, D. J. C.; Crewe, R.); Hilltop Camp, Hluhluwe Game Res., 450 m (Ward, P. S.); Hluhluwe Game Reserve (Brinck; Rudebeck); iSimangaliso Wetland Park World Heritage Site, Sodwana Bay Section, Mgobezeleni catchment (Armstrong, A. J.; Gomez, A.; Ngcamu, L.); Lake Subaya (McDonald, E.); Malvern (Barker); Maputa (Marley, H. B.); Mposa, Lower Umfolozi Dist. (Bradley, J. C.; Leigh, J. R.); Mtunzini (Villet, M.); N of Richards Bay (de Kock, A.; Majer, J. D.); Natal, Umtamvuna Nature Reserve, 160 m (van Noort, S.); Ndumo Game Reserve [as "Indumu Game Park"] (Daly, H. V.); Pongola (c.u.); Pongola (Prins, A. J.); Richards Bay (Danielsson, R.); Richards Bay (Faure, J. C.); Slievyre, Natal (Haviland); Sodwana Bay, 10 m (Ward, P. S.); Sodwana Bay (Car, C.); Sodwana Bay (Nel, J. J.); Sodwana Bay [as "Sordwana"] (c.u.); Sodwana Bay [as "Sordwana"] (Faure, J. C.); St. Lucia (Faure, J. C. [as "J. C. F."]); Tembe Elephant Reserve, Inspection Headquarters (van Noort, S.; Huntly, P. M.); Umfolozi Game Res. (Crewe, R. M.); Umfolozi R., Umfolozi Game Ref. (Crewe, R. M.); Umkumbaan, Durban (Caldwell, P.); *Limpopo*: Entabeni (Capener, A.); Entabeni Nature Reserve, 1375 m (Irwin, M. E.; Parker, F. D.; Hauser, M.); Hans Merensky Nat. Res. (Kimsey, R. B.); Kruger National Park, Punda Maria [as "Punda Malia"] (Capener, A.); Lapalala {as "Lapellala"] (Villet, M.); Lapalala {as "Lapellala"] (Weisenbacher, B.); Lephalale, 987 m (Hawkes, P.; Fisher, J.); Olifants Camp, Kruger Nat. Park (Kovalev, O.); Two Rivers Platinum SOC2, 937 m (Hawkes, P.; Fisher, J.); Warmbaths (Capener, A.); *Mpumalanga*: Blyderivierspoort Nat. Res., Swadene (Kimsey, R. B.); Crocodile R.E., Transvaal (Lang, H.); Dunstable Farm (Robertson, H.); Lapalala Nat. Res. (Kimsey, R. B.); Mariepskop, 1250 m (Fisher, B. L.; *et al*.); Mariepskop, 700 m (Kingman, A.); Mariepskop (Faure, J. C.); Mariepskop, Sybrand Van Niekerk Resort, 700 m (Alpert, G. D.); near Mariepskop (Robertson, H.); Nelspruit (Duvenhage, G.); Nylsvley (Robertson, H. G.); Songimvelo Nature Reserve, Kromdraai Camp cabin area, 800 m (Ubick, D.; Ubick, S.); *North West*: Hammans Kraal, Transvaal (Simon); Makapan, Transvaal (Simon); Marico-Bosveld, 1080 m (Pedersen, J.); Marico-Bosveld Ontspanningsklub, 1080 m (Ward, P. S.); Zeerust (Stange, L.; Miller, R.); *province unknown*: "Kereu" (c.u.); Kruger N. Park (Prins, A. J.); *Western Cape*: Cape of Good Hope [as "Capo di Buena Esp."] (c.u.); Groot Brak Valley (Macpherson, M. A.; Roux, A.); Grootvadersbos (Prins, A. J.; Prins, A.); Grootvadersbosch (c.u.); Grootvadersbosch (Prins, A. J.); Keurbooms River, Knysna (Barnard, K. H.); Keurboomstrand (de Weerdt, A.); Malgas, 40 m (Danielsson, R.); Mossel Bay (Turner, R. E.); Stinkhoutbos, Flower Valley, 210 m (Slingsby, P.); Storms River Pass, Knysna District (Balfour-Browne, J.); **Tanzania**: *Arusha*: Arusha Nat. Park, Momela Lk (Daly, H. V.); Muruangoin, 1080 m (Lamborn, W. A.); *Kilimanjaro*: above Kisiwani, on Nakombo River (Robertson, H. G.); Kilimandjaro, Kiboscho (Alluaud, C.); Mkomazi Game Reserve, above Ibaya (Robertson, H. G.); Mkomazi Game Reserve, Ibaya (Russell-Smith, A.); Mkomazi Game Reserve, Ibaya Camp (van Noort, S.); Mkomazi Game Reserve, Ibaya Forest (Robertson, H. G.); Mkomazi Game Reserve, Ibaya Hill (van Noort, S.); Mkomazi Game Reserve, Kinondo forest (Robertson, H. G.); Mkomazi Game Reserve, Kisima Hill (van Noort, S.); Mkomazi Game Reserve, Kisima pitfall site (McGavin, G.); Mkomazi Game Reserve, Kisima Plot (van Noort, S.); Nakombo River (Robertson, H. G.); *Morogoro*: Dutumi [as "Duthumi"] (Loveridge, A.); Kanga Forest Reserve, 820 m (Hawkes, P.; Makwati, J.; Mtana, R.); *Pwani*: 14 km NW Kisiju, 20 m (Ward, P. S.); 33 km W Dar Es Salaam, 120 m (Ward, P. S.); *Rukwa*: 39 mi SE Sumbawanga, 1530 m (Ross, E. S.; Leech, R. E.); Kalambo (Gérard); *Tanga*: 3 km E Amani, 410 m (Ward, P. S.); Amani, 950 m (Ward, P. S.); Amani (c.u.); Amani (Kirby, H.); Amani Hills (Quick, D.); Kange, near Tanga, 50 m (Ward, P. S.); Monga (Prell); **Zambia**: *Central*: Lusaka, Leopard Hill, Kapuka Farm, 1300 m (Fisher, B. L.; *et al*.); *Northern*: 5.3 km 247° Senga Hill, 1650 m (Fisher, B. L.; *et al*.); **Zimbabwe**: *Bulawayo*: Bulawayo (Arnold, G.); Bulawayo (c.u.); Bulawayo (Stevenson, R. H. R.); Bulawayo [as "Bulawaya"] (Arnold, G.); Bulawayo, 12 Kent Street (Stange, L. A.); Helenvale (c.u. [probably Arnold]); Hillside, Bulawayo (Arnold, G.); *Copperbelt*: Makabo (Silvester Evans, H.); *Harare*: Highlands, Harare (Cumming, M.); Salisbury (Watshaw, A.); *Manicaland*: Cashel (c.u.); Penkridge, Melsetter District (Stevenson, R. H. R.); Umtali (Arnold, G.); *Mashonaland Central*: Zambesi Valley, 7 km SE Angwa Bridge (Weyrich, J.); *Masvingo*: Kyle Dam Wall area (Crewe, R. M.; Fletcher, D. J.); Sabi Valley (c.u.); *Matabeleland North*: Lukosi Mission, 15 km S Hwange (Miller, R.; Stange, L.); Sawmills (Arnold, G.); *Matabeleland South*: Plumtree (Arnold, G.); *Midlands*: Sebakwe (c.u.).

***Tetraponera redacta* sp. nov.**
(Figs 3, 29, 42)

Type material. *Holotype worker*: Kenya, Kilifi: Gedi Natl. Monument, 5 m, 3°19′S 40°01′E, 17 Dec 1990, P. S. Ward PSW11180, ex dead twig of thorny vine, semideciduous forest (CASENT0863363) (NMKE). *Paratypes*: Six workers, 1 male, same data as holotype (CASENT0795283, CASENT0886923 to CASENT0886927) (CASC, PSWC, SAMC, UCDC).

Worker measurements (n = 10). HW 0.97–1.16, HL 1.13–1.34, LHT 0.82–0.92, CI 0.80–0.91, FCI 0.08–0.11, REL 0.43–0.46, REL2 0.50–0.55, SI 0.50–0.53, SI3 0.94–1.05, FI 0.43–0.46, PLI 0.67–0.80, PWI 0.57–0.7, LHT/HW 0.80–0.84, CSC 3–7, MSC 4–9.

Worker diagnosis. Relatively small species, with somewhat elongate head (CI 0.80–0.91) and moderately large eyes (REL 0.43–0.46, REL2 0.50–0.55); posterior margin of eye not attaining the level of the lateral ocelli; frontal carinae relatively closely adjacent, the minimum distance between them about 0.10× head width (FCI 0.08–0.11) and about one-fifth of scape length (MFC/SL 0.16–0.22); scapes of moderate length (SI 0.50–0.53, SI2 0.41–0.48), subequal to eye length (SI3 0.94–1.05); anterior clypeal margin broadly and weakly convex, with a short median denticle, flanked by 2–3 smaller denticles on each side, rather ill-defined (Fig. 29a); profemur relatively slender (FI 0.43–0.46); mesonotum essentially indistinguishable from dorsal face of propodeum, not bounded posteriorly by a distinct transverse impression; dorsal face of propodeum flattened, laterally submarginate, longer than declivitous face and rounding insensibly into the latter; petiole relatively short and high (PLI 0.67–0.80; PH/HL 0.43–0.50, PH/LHT 0.62–0.73) (Fig. 3), dorsolaterally submarginate, and with an anteroventral tooth; in profile, dorsum of petiolar node more or less semicircular and with similar anterodorsal and posterodorsal faces (Fig. 29b); in dorsal view, petiole narrowly obovate to subtrapezoidal; postpetiole longer than broad. Head and mesosoma densely punctulate-coriarious, matte; vertex sometimes more weakly sculptured, sublucid. Standing pilosity sparse (CSC 3–7, MSC 4–9, HTC+MTC 0); fine but dense pubescence covering most of body. Yellow- to orange-brown, with tip of gaster infuscated.

Comments. This species is difficult to distinguish from *T. natalensis*. In *T. redacta* workers the mesonotum is more or less fused with the dorsal face of the propodeum, and lies in the same plane as the latter, whereas in most workers of *T. natalensis* the mesonotum is separated from the propodeum by a distinct transverse impression and, in profile, it has a slight upward tilt anteriorly. This feature is variable in *T. natalensis*, however, and some workers approach the condition seen in *T. redacta*. *T. redacta* workers and queens have a relatively short and high petiole. Over its entire geographical range, *T. natalensis* shows sufficient variability in petiole shape to overlap that of *T. redacta*. When considering only *T. natalensis* workers from Kenya and Tanzania, adjacent to the range of *T. redacta*, differences are more pronounced and almost diagnostic (Fig. 3). As far as known, the distributions of the two species do not overlap: *T. redacta* is restricted to coastal Kenya, while *T. natalensis* is found farther inland and farther south (Figs 42, 44). One would be tempted, therefore, to interpret *T. redacta* as representing nothing more than an allopatric variant of *T. natalensis*, hardly deserving recognition as a distinct species. Phylogenomic (ultra-conserved element) data show, however, that *T. redacta* is more closely related to *T. caffra* than to *T. natalensis* (Ward, unpubl.). *T. caffra* occurs in southern Africa, and can be easily distinguished from both *T. redacta* and *T. natalensis* by its shorter scape and broader profemur (see key). *T. redacta* is thus genetically distinct from *T. natalensis*, despite a close similarity that is presumably attributable to either convergence or shared ancestral features.

Distribution and biology. *T. redacta* is known only from coastal Kenya, in littoral vegetation and semideciduous forest, where it has been found nesting in dead twigs of vines, a rutaceous (?) shrub, a scandent shrub, and other unidentified woody plants. In the residue vial of one collection (PSW11183) John Heraty discovered planidial larvae of a eucharitine wasp. Further study is needed of the distribution of *T. natalensis* and *T. redacta* in Kenya to determine if their ranges overlap. Currently the closest known populations are about 100 km apart.

Material examined (BMNH, CASC, CUIC, MCZC, MNHN, NHMW, PSWC, UCDC, USNM). **Kenya**: *Kilifi*: 16 km WSW Malindi, 20 m (Ward, P. S.); 4 km NW Watamu, 5 m (Ward, P. S.); Gedi Natl. Monument, 5 m (Ward, P. S.); Gedi, near Malindi (Daly, H.); *Kwale*: Diani Beach [as "Diana Beach"] (Krauss, N. L. H.); Kwale, 450 m (Ross, E. S.; Leech, R. E.); Kwali Forest, 20 mi W Mombasa (Steele); Maji-Chumvi (Wa-Nyika) (Alluaud, C.); Shimba Hills (Hölldobler, B.); Simu Beach, Kwale (Ross, E. S.; Leech, R. E.); *Lamu*: Waboniland (c.u.); *Mombasa*: nr. Mombasa, Shanzu (Brown, L. F.).

***Tetraponera schulthessi* (Santschi)**
(Figs 30, 43)

Sima Schulthessi Santschi 1915: 249. Syntype, 1 alate queen, Rikatla, Delagoa, Mozambique (Junod) (NHMB) [examined]. Imaged on AntWeb: CASENT0915539.

Tetraponera schulthessi (Santschi); Wheeler 1922b: 800. Combination in *Tetraponera*.
Sima schulthessi Santschi; Santschi 1928: 58. Description of worker.
Tetraponera schulthessi (Santschi); Ward 1990: 489. Combination in *Tetraponera*.
Tetraponera schulthessi (Santschi); Chomicki *et al.* 2015: figure S1. Placement in molecular phylogeny.

Worker measurements (n = 11). HW 1.38–1.68, HL 1.49–1.87, LHT 1.14–1.36, CI 0.87–0.93, FCI 0.09–0.14, REL 0.40–0.44, REL2 0.43–0.49, SI 0.50–0.54, SI3 1.02–1.23, FI 0.38–0.45, PLI 0.61–0.80, PWI 0.61–0.80, LHT/HW 0.79–0.85, CSC 3–13, MSC 3–28.

Worker diagnosis. Large species, with moderately broad head (CI 0.87–0.93) and relatively small eyes (REL 0.40–0.44, REL2 0.43–0.49); posterior margin of eye not attaining the level of the lateral ocelli; frontal carinae variably adjacent, the minimum distance between them about 0.10× head width or more (FCI 0.09–0.14) and about one-fifth to one-quarter of scape length (MFC/SL 0.16–0.28); scapes of moderate length (SI 0.50–0.54, SI2 0.44–0.50), equal to or greater than eye length (SI3 1.02–1.23); anterior clypeal margin broadly and weakly convex, with a short median denticle, flanked by 2–3 smaller denticles on each side, sometimes ill-defined (Fig. 30a); profemur relatively slender (FI 0.38–0.45); mesonotum bounded posteriorly by a transverse impression, often quite weak; distinct metanotal plate not present, although anterior extremity of propodeum with a weakly differentiated arched-transverse area in some individuals; dorsal face of propodeum flattened, laterally submarginate, longer than declivitous face and rounding insensibly into the latter; petiole of moderate length and height (PL/HW 0.67–0.77; see also PLI and PWI values), dorsolaterally submarginate, and with an anteroventral tooth; in profile, petiolar node with steep anterodorsal face and more gently sloping posterodorsal face (Fig. 30b); postpetiole about as long as broad. Head and mesosoma densely punctulate-coriarious, matte. Standing pilosity sparse to moderately common (CSC 3–13, MSC 3–28, HTC+MTC 0–10); fine but dense pubescence covering most of body. Yellow- to orange-brown, with tip of gaster infuscated.

Comments. Workers of *Tetraponera schulthessi* can be distinguished from other yellow- or orange-brown species in the *T. natalensis* group (*T. caffra*, *T. natalensis, T. redacta*) by their large size (HW 1.38–1.68, LHT 1.14–1.36) and small eyes relative to head width (REL2 0.43–0.49).

Distribution and biology. This is a common east African species, occurring from Kenya to South Africa, in savanna woodlands, semideciduous forest, rainforest, coastal thicket, and mangroves. It is broadly sympatric with the closely related *T. natalensis*, yet remains distinct from it. *Tetraponera schulthessi* is a generalist dead-twig inhabitant, with nest records from *Afaelia quanzensis*, *Allophyllus*, *Ficus*, *Sclerocarya birrea*, "thorny shrub", "vine", and unidentified woody plants.

Material examined (CASC, FHGC, KUES, LACM, MCZC, NHMB, PSWC, SAMC, UCDC, USNM). **Kenya**: *Kilifi*: 20 km WSW Malindi, 20 m (Ward, P. S.); Arabuko Sokoke Forest, 50 m (Hita Garcia, F.; Fischer, G.); Gedi Natl. Monument, 5 m (Ward, P. S.); Karacha Forest, 16 mi N Kilifi (Irwin, M. E.; Ross, E. S.); Sokoke Forest (Hogue, C.; Williams, J.); *Kwale*: Diani Beach [as "Diana Beach"] (Krauss, N. L. H.); **Mozambique**: *Cabo Delgado*: 24.5 km 346° from Pemba, 20 m (Fisher, B. L.; *et al*.); 26.7 km 353° from Pemba, 120 m (Fisher, B. L.; *et al*.); 9.5 km 297° from Pemba, 20 m (Fisher, B. L.; *et al*.); Namoto forest, 35 m (Fisher, B. L.; *et al*.); Namoto forest, 40 m (Fisher, B. L.; *et al*.); P.N. Quirimbas, Mareja Res., 125 m (Fisher, B. L.; *et al*.); P.N. Quirimbas, Mareja Res., 180 m (Fisher, B. L.; *et al*.); P.N. Quirimbas, Taratibu, 300 m (Fisher, B. L.; *et al*.); P.N. Quirimbas, Taratibu, 325 m (Fisher, B. L.; *et al*.); P.N. Quirimbas, Taratibu, 505 m (Fisher, B. L.; *et al*.); Quiterajo forest, 100 m (Fisher, B. L.; *et al*.); *Maputo*: Rikatla, Delagoa (Junod); *Sofala*: 3.5 km SE Chitengo, Gorongosa Natl. Park, 40 m (Ward, P. S.); Chitengo, Gorongosa Natl. Park, 40 m (Ward, P. S.); *Tete*: Chiuta Dist., Ruoni North, 324 m (Hawkes, P.; Fisher, J.); *Zambézia*: 37 km N Quelimane, 70 m (Alpert, G. D.); 57 km N Quelimane, 70 m (Alpert, G. D.); Mt. Mabu, 375 m (Fisher, B. L.; *et al*.); **South Africa**: *KwaZulu-Natal*: Abu Madi Game Ranch, 200 m (Ward, P. S.); Mkuze Game Reserve (Robertson, H. G.); Mkuze Game Reserve, at rest camp (Robertson, H. G.); Mkuze Game Reserve, Mantuma Rest Camp (Robertson, H. G.); Mkuze Game Reserve, near Malibali Hide (Robertson, H. G.); Umfolozi Game Res. (Crewe, R. M.); Umfolozi Game Res. (Crewe, R. M.); *Limpopo*: Hans Merensky Nat. Res. (Kimsey,

R. B.); *Mpumalanga*: Blyderivierspoort Nat. Res., Swadene (Kimsey, R. B.); Mariepskop, 705 m (Alpert, G. D.); **Tanzania**: *Lindi*: Rondo Forest Reserve, 870 m (Hawkes, P.; Mlacha, Y.; Ninga, F.); *Pwani*: 14 km NW Kisiju, 20 m (Ward, P. S.); *Tanga*: Amani (Williams, F. X.); Amani, 950 m (Ward, P. S.); Kange, near Tanga, 50 m (Ward, P. S.); **Zimbabwe**: *Matabeleland North*: Sawmills (c.u. [probably Arnold]).

Tetraponera setosa sp. nov.

(Figs 31, 44)

Tetraponera psw113. Chomicki *et al.* 2015: figure S1. Placement in molecular phylogeny.

Type material. *Holotype worker*: Uganda, Bushenyi, Kalinzu Forest, 1450m, 0°25′S 30°05′E, 27 Sep 2006, S. Yamane UG06-SKY-101 (CASENT0794346) (CASC). *Paratypes*: 6 workers, same data as holotype (CASENT0795232 to CASENT0795235 (KUES, PSWC, UCDC).

Worker measurements (n= 5). HW 1.37–1.43, HL 1.46–1.55, LHT 1.05–1.14, CI 0.90–0.94, FCI 0.09–0.11, REL 0.43–0.45, REL2 0.47–0.50, SI 0.51–0.54, SI3 1.05–1.14, FI 0.38–0.40, PLI 0.68–0.73, PWI 0.63–0.65, LHT/HW 0.77–0.80, CSC ca. 40–60, MSC ca. 70–120.

Worker diagnosis. Relatively large species, with broad head (CI 0.90–0.94) and eyes of moderate size (REL 0.43–0.45); posterior margin of eye not attaining the level of the lateral ocelli; frontal carinae moderately separated, the minimum distance between them 0.10× head width (FCI 0.09–0.11) and about one-fifth of scape length (MFC/SL 0.18–0.20); scapes of moderate length (SI 0.51–0.54, SI2 0.47–0.50), exceeding eye length (SI3 1.05–1.14); anterior clypeal margin very weakly convex, with a slight median emargination, lacking distinct denticles, at most feebly crenulate (Fig. 31a); profemur slender (FI 0.38–0.40); mesonotum bounded posteriorly by a well marked but simple impression, lacking longitudinal rugulae; distinct metanotal plate not present, although anterior extremity of propodeum with a weakly differentiated arched-transverse area; dorsal face of propodeum flattened, laterally submarginate, longer than declivitous face and rounding insensibly into the latter; petiole of moderate length and height (PL/HW 0.66–0.70; see also PLI and PWI values), with a short anterior peduncle, weak dorsolateral margination, and a modest anteroventral tooth; in profile, petiolar node with anterodorsal and posterodorsal faces rounding insensibly into one another, the anterodorsal face slightly less steeply inclined than the posterodorsal face (Fig. 31b); postpetiole longer than broad. Head and mesosoma with scattered punctures, densest on anterior two thirds of head, the interspaces smooth and shiny to weakly reticulate; petiole, postpetiole and gaster smooth and shiny, with fine punctures. Standing pilosity abundant (CSC ca. 40–60, MSC ca. 70–120, HTC+MTC 9–22), relatively short, grading into the pubescence, which varies from suberect to appressed, and covers most of the body. Dark brownish-black, the mandibles, antennae, tibiae and tarsi variably lighter.

Comments. The workers of this species are relatively large (HW 1.37–1.43, LHT 1.05–1.14) and dark-colored, with distinctive sculpture: the head and mesosoma have scattered punctures on a smooth to weakly reticulate, shiny background. This is in contrast to all other members of the *T. natalensis* group in which the head and mesosoma are densely punctulate-coriarious, and the integument has a matte appearance. *T. setosa* also has an exceptionally dense cover of fine, short standing pilosity over the entire body, that grades into suberect pubescence. It is most similar to *T. mocquerysi*, differing by the sculptural and pilosity differences mentioned above, as well as the broader head (CI 0.90–0.94, versus 0.80–0.90 in *T. mocquerysi* workers), absence of denticles on the anterior clypeal margin, and a more slender profemur (FI 0.38–0.40 and FW/HW 0.28–0.29, versus FI 0.39–0.47 and FW/HW 0.30–0.35 in *T. mocquerysi* workers).

Distribution and biology. *Tetraponera setosa* is known only from one collection series at the type locality, a moist evergreen forest at medium altitude, in western Uganda.

Material examined. Known only from type material.

Tetraponera rufonigra-group

Worker diagnosis. Large species with broad head (CI 0.86–0.99); masticatory margin of mandible usually with four teeth, preceded by a single tooth on basal margin (in one Asian species masticatory margin with five teeth and

basal margin without teeth); basal margin subequal in length to masticatory margin; labrum either lacking prominent tubercles (Asian species) or with a single median tubercle near proximal margin; ventral surface of clypeus with a transverse carina, anterior to posteroventral border, weakened medially in African species; frontal carinae well separated in African species (FCI 0.21–0.35), less so in Asian species (FCI 0.09–0.16); scape length one half or more of head width (SI 0.49–0.63); head capsule with three prominent ocelli; pronotal humeri subangulate in dorsal view; metanotal plate lacking; mesosterum not densely pubescent; petiole with prominent anteroventral tooth, generally directed posteroventrally; posteroventral margin of petiole closely associated with helcium venter, lacking a ventrally extended hood; metabasitarsal sulcus present; appressed pubescence dense on abdominal tergite 4.

Comments. This group comprises four Asian species that are apparently generalists, nesting in dead (and sometimes live) twigs and branches of a wide variety of plants, and two West African species that are specialist inhabitants of the antplant *Barteria* (Janzen 1972; Ward 2001 2006; Bharti & Akbar 2014).

Tetraponera aethiops F. Smith

(Figs 33, 45)

Tetraponera Aethiops F. Smith 1877: 71. Syntype, 1 worker, "S. Africa" (BMNH) [examined]. Imaged on AntWeb: CASENT0902813.

Sima spininoda André, 1892: 51. Syntypes, 10 workers, 3 alate queens, Gabon (Mocquerys) (MHNG, MNHN, NHMV) [examined]. 1 syntype worker from MNHN imaged on AntWeb: CASENT0913718. Synonymy by Emery 1912:97.

Sima aethiops (F. Smith); Dalla Torre 1893: 53. Combination in *Sima*.

Sima aethiops (F. Smith); Santschi 1911c: 207. Description of male.

Sima (*Pachysima*) *aethiops* (F. Smith); Emery 1912: 97, 98. Combination in *Sima* (*Pachysima*); description of larva; description of queen.

Pachysima aethiops (F. Smith); Wheeler 1918: 305. Combination in *Pachysima*; description of larva.

Tetraponera aethiops (F. Smith); Ward 1990: 487. Combination in *Tetraponera*.

Tetraponera aethiops (F. Smith); Chomicki *et al.* 2015: figure S1. Placement in molecular phylogeny.

Sima (*Pachysima*) *spininoda* André; Stitz 1916: 374. Combination in *Sima* (*Pachysima*).

Pachysima spininoda (André); Wheeler 1922b: 801. Combination in *Pachysima* (implied), as junior synonym of *P. aethiops*.

Tetraponera spininoda (André); Ward 1990: 487. Combination in *Tetraponera*, as junior synonym of *T. aethiops*.

Worker measurements (n = 10). HW 1.70–2.17, HL 1.72–2.35, LHT 1.50–2.08, CI 0.92–0.99, FCI 0.21–0.25, REL 0.27–0.30, REL2 0.28–0.32, SI 0.49–0.53, SI3 1.60–1.86, FI 0.32–0.36, PLI 0.62–0.74, PWI 0.79–0.88, LHT/HW 0.86–0.97, CSC 6–12, MSC 1–7.

Worker diagnosis. Large, robust species; frontal carinae separated by a distance equal to one quarter of head width or less; clypeus not produced as a median lobe, its anterior margin straight, very weakly convex, or slightly concave (Fig. 33a); profemur slender (FI 0.32–0.36), legs moderately long (LHT/HL 0.84–0.91); mesopropodeal impression well marked in profile; dorsal face of propodeum broad and flat, rounding gradually into declivitous face; petiole short and broad, with a short anterior peduncle; postpetiole broader than long; anteroventral petiolar tooth usually spiniform and relatively slender (sometimes triangular), typically followed by a second weaker tooth behind; venter of postpetiole with small, spiniform tooth at anterior margin and, posterior to this, a more prominent rounded boss, directed anteroventrally (Fig. 33b). Mandibles longitudinally rugulose and opaque. Most of body covered with fine, dense punctures (and associated pubescence) and subopaque, such sculpture being more weakly developed on the upper part of the head, which is correspondingly shinier. Standing pilosity sparse (MSC 1–7), absent from propodeum, and from extensor surfaces of tibiae. Dark brownish-black, appendages dark to medium brown.

Comments. Workers of *T. aethiops* are readily distinguished from those of their sister species, *T. latifrons*, by their rugulose mandibles, less widely separated frontal carinae, sparse pilosity, and longer legs. In *T. latifrons* the mandibles are smooth and shiny, the frontal carinae are more widely separated (FCI 0.28–0.35 versus 0.21–0.25 in *T. aethiops*), standing pilosity is conspicuous on the mesosoma dorsum (MSC 27–45 versus 1–7 in *T. aethiops*), and the legs are shorter (LHT/HW 0.76–0.81 versus 0.86–0.97 in *T. aethiops*). In addition, in *T. latifrons* the anteroventral teeth of both the petiole and postpetiole are better developed, yet unaccompanied by additional teeth or protuberances in a more posterior position on each segment, as seen in *T. aethiops*.

Distribution and biology. In the original description the type locality is stated to be "S. Africa" (Smith 1858) but this is almost certainly an error. *Tetraponera aethiops* occurs in wet tropical forest from Nigeria to DR Congo and western Uganda, and is an obligate inhabitant of two myrmecophytic species of *Barteria* (Passifloraceae) (Bequaert 1922; Kokolo *et al.* 2019) that do not occur in South Africa. *T. aethiops* has also been recorded (Stitz 1910) nesting in live stems of *Heinsia myrmoecia* (Rubiaceae), but Davidson & McKey (1993) cast doubt on this report, noting that the internodal swellings of that plant are too small to support a large ant species such as *T. aethiops*. As a result of their painful sting, aggressive behavior, and habit of pruning encroaching vegetation, *T. aethiops* workers provide effective protection of *Barteria* against herbivores and competing plants (Janzen 1972; McKey 1974; Dejean *et al.* 2008), although the pruning behavior may have the primary effect of reducing competition with other ants (Yumoto & Maruhashi 1999). Recent studies of this system have included examination of population structure in the ant and its hostplant (Blatrix *et al.* 2017), and confirmation that fungal "gardens" in the plant domatia provide additional nutritional benefits to the ants beyond those obtained from cohabiting scale insects (Blatrix *et al.* 2012; Kokolo *et al.* 2016).

Material examined (AMNH, BMNH, CASC, CMNH, CPDC, CUIC, LACM, MCZC, MHNG, MNHN, MSNG, NHMB, NHMW, PSWC, SAMC, UCDC, USNM). **Cameroon**: *Centre*: Metet (Good, A. I.); Metet (Schwab, G.); Yaounde (Van Zwaluwenburg; McGough); Yaoundé (c.u.); *Littoral*: Edéa [as "Edia"] (Schwab, G.); *region unknown*: "Cameroun" (c.u.); "Kamerun" (Conradt, L.); *Sud*: Ebolowa, Nkoemvon (Jackson, D.); Efulen (Grissett, F.); Kribi (Johnson, S. E.); Lolodorf (Good, A. I.); Nkoem-Vone (Collingwood); Réserve de Campo, 40 m (Olson, D. M.); *Sud-Ouest*: Bakingili, 10 m (DiGiulio, J. A.); Iriba Inene, Korup National Park (Blatrix, R.); Korup Natl. Park, 320 m (Koch, G.); Korup, K11 (Jackson, D.); Limbe [as "Victoria"] (Buchholz); Mabete, Victoria Div. (Malkin, B.); Matute, Tiko Plantation (Malkin, B.); Moliwe [as "Molive"] (c.u.); Mundemba (McKey, D.); Rengo Camp, Korup National Park (Blatrix, R.); **Central African Republic**: *Lobaye*: Boda (Charleuf, P.); *Sangha-Mbaéré*: Nola (Le Moult); P.N. Dzanga-Ndoki, 21.4 km 53° NE Bayanga, 510 m (van Noort, S.); P.N. Dzanga-Ndoki, 38.6 km 173° S Lidjombo, 350 m (Fisher, B. L.); P.N. Dzanga-Ndoki, 38.6 km 173° S Lidjombo, 350 m (van Noort, S.); P.N. Dzanga-Ndoki, 5.9 km 72° ENE Bayanga, 410 m (Fisher, B. L.); P.N. Dzanga-Ndoki, Mabéa Bai, 21.4 km 53° NE Bayanga, 510 m (Fisher, B. L.); Res. Dzanga-Sangha, 12.7 km 326° NW Bayanga, 420 m (Fisher, B. L.); Res. Dzanga-Sangha, 12.7 km 326° NW Bayanga, 420 m (van Noort, S.); **DR Congo**: *Équateur*: Lingunda (Mairesse, L.); *Haut-Uélé*: Ambelokudi (Lang, H. O.); Ambelokundi (Lang, H. O.); Bafwaboka (Lang, H. O.); Medje (Lang, H. O.); Medje (Lang; Chapin); Paulis (c.u.); Uélé, Tuku (van den Plas, P.); *Ituri*: Epulu (Bradley, J. C.); Epulu, 950 m (Ross, E. S.; Leech, R. E.); *Maniema*: 62 mi E Kibombo (Ross, E. S.; Leech, R. E.); *Nord-Kivu*: 39 km S Walikale (Ross, E. S.; Leech, R. E.); *province unknown*: "Congo" (Kohl); Nyangme à Stanleyville (Fauconnet); *Sud-Kivu*: 45 mi E Kama, 750 m (Ross, E. S.; Leech, R. E.); *Tshopo*: Avakubi (c.u.); Avakubi (Lang, H. O.); Isangi (Lang, H. O.); Kisangani [as "Stanleyville"] (c.u.); Kisangani [as "Stanleyville"] (Kohl, H.); Kisangani [as "Stanleyville"] (Lang, H. O.); Panga (Lang, H. O.); **Equatorial Guinea**: *Litoral*: Eloby (Brauns); Eloby (c.u.); Eloby [as "Elaby"] (Brauns); *province unknown*: Bioko [as "Fernando Po"] (c.u.); Bioko [as "Fernando Poo"] (Conradt); Riv. San Benito (Guiral); **Gabon**: *Estuaire*: Kouame, E. of Libreville (Ross, E. S.); *Moyen-Ogooué*: Sam Kita (Faure, F.); *Ogooué-Ivindo*: M'Passa, near Makokou (Fisher, B. L.); *Ogooué-Maritime*: Res. Monts Doudou, 24.3 km 307° NW Doussala, 375 m (Fisher, B. L.); Res. Moukalaba, 12.2 km 305° NW Doussala, 110 m (Fisher, B. L.); *province unknown*: "Gabon" (c.u.); "Gabon" (Mocquerys); "Gabun" (Staudinger); *Woleu-Ntem*: 27.6 km 108° ESE Minvoul, 600 m (Fisher, B. L.); 31.3 km 108° ESE Minvoul, 600 m (Fisher, B. L.); **Nigeria**: *Cross River*: Calabar (Usua, E. J.); *Delta*: Ofore (Carnes, M. A.); *Edo*: Ogbesse Benin (Box, H. E.); Sapoba For. Reserve, 20 km S Benin City (Janzen, D. H.); *Ogun*: Alo, 70 mi E Lagos (Lamborn, W. A.); *Ondo*: Ifon (Simpson, J. J.); *Osun*: Ifetedo (Biues, D. J.); **Republic of Congo**: *Likouala*: 25 km NW Boha, 30 km SE Lac Telle (Alpert, G. D.); **Uganda**: *Bundibugyo*: Kirumia River Trail, Semliki Natl. Park, 720 m (Ward, P. S.); Sempaya, Semliki Natl. Park, 680 m (Ward, P. S.); Semuliki National Park, 676 m (Fisher, B. L.; *et al.*); *Kabarole*: Fort Portal (Osmaston, H. A.); **unknown**: "S. Africa" (c.u).

Tetraponera latifrons (Emery)

(Figs 34, 46)

Sima (*Pachysima*) *latifrons* Emery, 1912: 98. Holotype (by monotypy), alate queen, Gabon (Staudinger) (MSNG) [examined]. Imaged on AntWeb: CASENT0904042.

Sima (*Pachysima*) *latifrons* Emery; Santschi 1914b: 288. Description of worker, male.
Pachysima latifrons (Emery); Wheeler 1918: 305, 308. Combination in *Pachysima*; description of larva.
Tetraponera latifrons (Emery); Ward 1990: 488. Combination in *Tetraponera*.
Tetraponera latifrons (Emery); Chomicki *et al*. 2015: figure S1. Placement in molecular phylogeny.

Worker measurements (n = 8). HW 1.57–2.20, HL 1.68–2.45, LHT 1.21–1.75, CI 0.90–0.97, FCI 0.28–0.35, REL 0.27–0.30, REL2 0.29–0.32, SI 0.50–0.52, SI3 1.61–1.74, FI 0.39–0.41, PLI 0.62–0.79, PWI 0.77–0.85, LHT/HW 0.76–0.81, CSC 1–6, MSC 27–45.

Worker diagnosis. Similar to *T. aethiops* except as follows: frontal carinae separated by a distance greater than one quarter of head width (FCI 0.28–0.35); profemur more robust (FI 0.39–0.41), legs shorter (LHT/HL 0.71–0.75); anteroventral petiolar tooth robust and prominent, directed posteroventrally, not followed by a second, more posterior tooth; anteroventral tooth of postpetiole well developed, spiniform, not followed posteriorly by a prominent protrusion (Fig. 34b). Mandibles smooth and shiny with scattered fine punctures. Standing pilosity more common (MSC 27–45), notably in the form of a dense brush of forwardly-directed hairs on the clypeus and by conspicuous hairs on the pronotum, propodeum, petiole and postpetiole.

Comments. *T. latifrons* is more setose, shorter-legged, and smaller (on average) than *T. aethiops*. See under the latter species for further discussion of the differences between the two.

Distribution and biology. Another obligate *Barteria* inhabitant, *T. latifrons* is broadly sympatric with *T. aethiops*, but evidently less common. At a study site in Sapoba Forest, Nigeria, Janzen (1972) reported that both species had similar biology, but that the colonies occurred in a ratio of about 1:100. More recent work in Gabon has shown that the two species have differing hostplant preferences and protective behavior, with *T. latifrons* occurring more frequently in *Barteria dewevrei*, and *T. aethiops* being preferentially associated with *Barteria fistulosa* and showing a stronger reaction to leaf disturbance (Kokolo *et al.* 2019). Given differences in morphology of the workers and larvae (Wheeler 1918; Wheeler & Wheeler 1956) it seems probable that there are additional biological differences between the two species yet to be discovered.

Material examined (AMNH, BMNH, CASC, CUIC, LACM, MCZC, MHNG, MNHN, MSNG, NHMW, PSWC, SAMC, USNM). **Cameroon**: *Sud-Ouest*: Victoria (Malkin, B.); **Central African Republic**: *Sangha-Mbaéré*: P.N. Dzanga-Ndoki, 38.6 km 173° S Lidjombo, 350 m (van Noort, S.); P.N. Dzanga-Ndoki, 5.9 km 72° ENE Bayanga, 410 m (Fisher, B. L.); P.N. Dzanga-Ndoki, Mabéa Bai, 21.4 km 53° NE Bayanga, 510 m (Fisher, B. L.); **DR Congo**: *Haut-Uélé*: Niangara (c.u.); Niangara (Lang, H. O.); Niangara (Lang; Chapin); *Kasaï Oriental*: Kondué (Luja); *Kongo Central*: 75 mi W Popokabaka (Ross, E. S.; Leech, R. E.); **Gabon**: *province unknown*: "Gabon" (Staudinger); "Gabun" (c.u.); **Nigeria**: *Edo*: Ogbesse Benin (Box, H. E.); Sapoba For. Reserve, 20 km S Benin City (Janzen, D. H.); **Republic of Congo**: *Brazzaville*: Brazzaville [as "de Brazza"] (c.u.); *Pool*: Lesio-Loun Park, 330 m (Braet; Sharkey); Lesio-Loun Park, 330 m (Sharkey; Braet).

Concluding remarks

As with other ant genera centered in tropical latitudes, such as *Crematogaster* and *Camponotus*, the species-level taxonomy of *Tetraponera* has been burdened by a plethora of named but poorly characterized taxa. Although the current study has uncovered new species, it has also highlighted a considerable amount of "taxonomic inflation" due to the profligate naming of species, subspecies, and varieties by Forel, Santschi, and other workers in the late nineteenth and early twentieth centuries. These individuals focused on slight morphological differences, worked with small sample sizes, and had inchoate views about the nature of species. The taxonomic hypotheses in this paper are based on adherence to the biological species concept (Mayr 1942; Coyne & Orr 2004) and on a recognition that species can encompass significant genetic variation and population structure. The conclusions about species boundaries should be considered provisional, however, and subject to refinement with further evidence. A key point is that when two closely similar forms show (1) overlapping geographical distributions, and (2) no diminution of their differences in sympatry, this is a compelling argument for treating them as separate species (Tobias *et al.* 2010; Galtier 2019). Conversely, allopatric variants present a more difficult situation, and require careful assessment before being treated as heterospecific. Are such allopatric forms connected by intermediate populations—or likely to be so, under more comprehensive geographic sampling? Do they show a degree of difference comparable to that of closely related sympatric species (Tobias *et al*. 2010)? Such joint scrutiny of phenotypic variation and geographical

distribution is a critical component of the methodology employed here. In addition, published phylogenetic studies of Pseudomyrmecinae (Ward & Downie 2005; Chomicki *et al.* 2015) and ongoing phylogenomic (UCE) work (Ward, in prep.) have provided useful insights.

Based on current understanding, the ant genus *Tetraponera* is represented in the Afrotropical region by 28 species in mainland Africa, and approximately 40 species in Madagascar. Given the relatively high frequency of rare taxa—five of the eleven newly described species are known from just a single locality, for example—it seems almost certain that additional species await discovery. Nevertheless, the contrast between continental Africa and Madagascar is likely to remain, pointing to opportunities for diversification on the island that are not present on the mainland.

This study has also improved the delimitation of specialized, myrmecophyte-inhabiting species of *Tetraponera* and their relatives. This lays the foundation for detailed comparative studies that could provide insight into the evolution of specialized ant-plant associations. Particular attention should be paid to the *T. allaborans* group in Africa: it includes several poorly known species, related to the well-studied *T. penzigi*, that appear to have a propensity to inhabit live stems and associate with Coccoidea. Studies of their ecology and behavior should prove enlightening.

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