

The ant genus *Tetraponera* in the Afrotropical region: synopsis of species groups and revision of the *T. ambigua*-group (Hymenoptera: Formicidae)

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Abstract

The Afrotropical (including Malagasy) species of the ant genus *Tetraponera* F. SMITH, 1862 are evaluated, and five monophyletic species groups are established. A key is provided to these groups and their composition and distribution are summarized. One of these clades, the *T. ambigua*-group, is revised at the species level. Within this group the following new synonymies are proposed (senior synonyms listed first): *T. ambigua* (EMERY, 1895) = *T. erythraea* (EMERY, 1895) = *T. bifoveolata* (MAYR, 1895) = *T. bifoveolata maculifrons* (SANTSCHI, 1912) = *T. ambigua rhodesiana* (FOREL, 1913) = *T. bifoveolata syriaca* (WHEELER & MANN, 1916) = *T. encephala* (SANTSCHI, 1919) = *T. ophthalmica angolensis* SANTSCHI, 1930 = *T. ambigua occidentalis* MENOZZI, 1934; and *T. ophthalmica* (EMERY, 1912) = *T. ophthalmica tenebrosa* SANTSCHI, 1928 = *T. ophthalmica unidens* SANTSCHI, 1928 = *T. nasuta* BERNARD, 1953. This reduces the number of valid species to two, *T. ambigua* and *T. ophthalmica*, both widely distributed on the African continent. Two additional species are described: *T. parops* sp.n., from east Africa and *T. phragmotica* sp.n., from northwestern Madagascar. All four species in the *T. ambigua*-group have a dimorphic worker caste, a trait otherwise unknown in the subfamily Pseudomyrmecinae. The major workers and queens of *T. phragmotica* sp.n. have plug-shaped heads, which are remarkably convergent with those of distantly related ant species in the formicine tribe Campo-nini. The phylogeny and biogeographic history of the *T. ambigua*-group are briefly discussed.

Key words: Formicidae, Pseudomyrmecinae, taxonomy, phylogeny, distribution, convergence, Afrotropics.

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Introduction

Ants are abundant and species-rich in tropical forest canopies (WILSON 1987, TOBIN 1995, BRÜHL & al. 1998, DAVIDSON & al. 2003, FLOREN & LINSEMMAIR 2005). The ant subfamily Pseudomyrmecinae is one of the more distinctive groups inhabiting this environment. The Old World pseudomyrmecines – currently placed in the genus *Tetraponera* F. SMITH, 1862 – are distributed throughout the Paleotropics (WARD 1990, 2001), with particularly high diversity in Madagascar. In this paper the Afrotropical (including Malagasy) fauna is reviewed, and one group is revised at the species level.

Recent molecular phylogenetic studies (WARD & DOWNIE 2005) point to the possibility that *Tetraponera* is paraphyletic relative to the New World pseudomyrmecines (genera *Pseudomyrmex* LUND, 1831 and *Myrcidris* WARD, 1990). Additional evidence is needed to resolve this issue. If paraphyly of *Tetraponera* is confirmed then the species groups recognized here – which are well-defined at both the morphological and molecular level – provide a possible basis for new monophyletic genera.

This paper is dedicated to the memory of Stefan Schödl. Stefan rejuvenated activity in ant taxonomy at the Naturhistorisches Museum (Wien), published exemplary taxonomic papers, and provided generous assistance to those who visited the museum. His early death is a tragic loss to the field of ant systematics.

Methods

In the process of investigating the main lineages of *Tetraponera* most of the known species of the genus were exam-

ined morphologically. The approximate numbers of species studied were: 21 from mainland Africa, 40 from Madagascar, and 33 from the Indo-Australian region (there is no species overlap among these regions). All three castes – workers, queens and males – were available for about half of these species. Revision of the *Tetraponera ambigua*-group involved examination of approximately 625 worker specimens, 14 males, and 55 queens.

In parallel with these morphological studies, I also sequenced six nuclear genes (28S rDNA, wingless, long wavelength rhodopsin, abdominal-A, elongation factor 1-alpha F2 copy, and arginine kinase; total of ~3.4 kb of aligned DNA sequence data) from a representative set of 40 *Tetraponera* species, using methods described in WARD & DOWNIE (2005). Results of the molecular phylogenetic analyses will be published elsewhere, but were helpful here in providing strong support (parsimony bootstraps of 100 %; Bayesian posterior probabilities of 1.00) for monophyly of the five species groups defined by morphology.

Linear measurements and setal counts were taken at 50× with a Wild M5A microscope, as described in WARD (2001). All measurements ranges are given in the order minimum – maximum. Unless otherwise stated, the worker measurements and descriptions exclude major workers (soldiers). The abbreviations used for measurements and indices are given below. The first four measurements are taken with the head in full-face view, such that the posterior margin of the head and the anterolateral corners are in the same plane of view.

HW Maximum head width, including eyes.

- HL Head length, taken along midline, from posterior margin of head to anterior extremity of clypeus.
 EL Eye length, measured in same plane of view as HL.
 MFC Minimum distance between frontal carinae.
 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 anterior peduncle to posterior margin of petiole.
 PH Maximum height of petiole, measured in same view as PL, and excluding protruding teeth or lobes at anteroventral or posteroventral extremities of petiole.
 DPW Maximum width of petiole, 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.
 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 Cepalic setal count: number of standing hairs (those forming an angle of 45° or more with cuticular surface) visible on posterior half of head, as seen in lateral and posterior views.
 MSC Mesosomal setal count: number of standing hairs visible in profile (lateral view) on mesosoma dorsum.
- Specimens of the *Tetraponera ambigua*-group were examined in the following collections:
 AMNH American Museum of Natural History, New York, NY, USA
 ANIC Australian National Insect Collection, CSIRO, Canberra, Australia
 BMNH Natural History Museum, London, U.K.
 CASC California Academy of Sciences, San Francisco, CA, USA
 CUIC Cornell University Insect Collection, Ithaca, NY, USA
 LACM Natural History Museum of Los Angeles County, Los Angeles, CA, USA
 MCSN Museo Civico de Historia Natural "Giacomo Doria", Genoa, Italy
 MCZC Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA
 MHNG Muséum d'Histoire Naturelle, Geneva, Switzerland
 MNHN Muséum National d'Histoire Naturelle, Paris, France
 MRAC Musée Royal de l'Afrique Centrale, Tervuren, Belgium
 NHMB Naturhistorisches Museum, Basel, Switzerland
 NHMV Naturhistorisches Museum, Vienna, Austria
 NMKE National Museums of Kenya, Nairobi, Kenya
 NMWN National Museum of Namibia, Windhoek, Namibia
 PSWC P.S. Ward Collection, University of California at Davis, CA, USA

- SAMC South African Museum, Cape Town, South Africa
 UCDC Bohart Museum of Entomology, University of California at Davis, CA, USA
 UCRC Entomology Research Museum, University of California at Riverside, CA, USA
 USNM National Museum of Natural History, Washington, DC, USA
 ZMAS Zoological Institute, Russian Academy of Science, St. Petersburg, Russia

Species distributions were mapped with the shareware program Versamap (Version 2.07b). The following sources were useful for determining the coordinates of old locality names not found in contemporary atlases and gazetteers: PALMER (1872), BAUM (1903), WHEELER (1922), EMERSON (1928), PEYERIMHOFF (1931), DELACHAUX & THIÉBAUD (1934), MANN (1948), BERNARD (1953b), CHAPIN (1954) and DAVIS & MISONNE (1964).

Genus *Tetraponera* F. SMITH, 1862

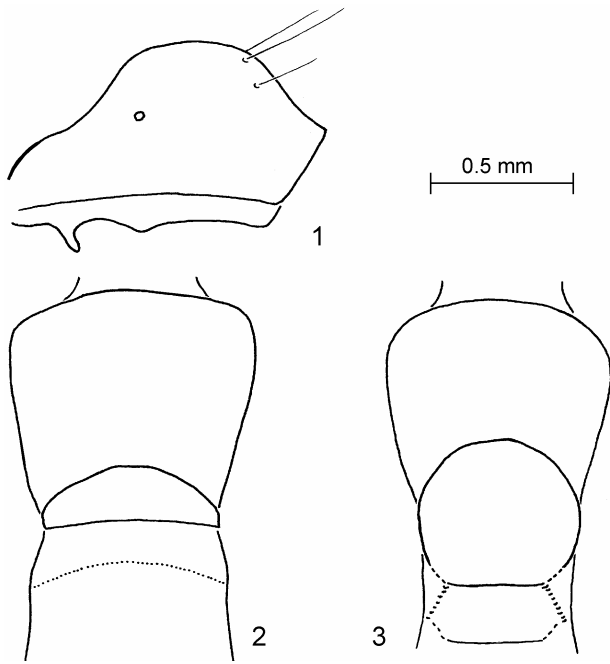
Worker diagnosis. Pseudomyrmecine ants with short mandibles, usually with 3 - 4 (rarely 5 - 6) teeth on masticatory margin and 0 - 2 denticles on basal margin; basal margin lacking proximal tooth; anterodorsal surface of median portion of clypeus continuous, non-truncate, its anterior margin with a line of clypeal setae; median lobe of torulus expanded laterally and covering most of basal condyle of antenna when head is observed in full-face (dorsal) view; frontal carinae relatively well separated (compared to *Pseudomyrmex*), minimum distance between carinae greater than basal scape width; compound eye large and oval (not elongate as in *Pseudomyrmex*), width two-thirds or more of length; metabasitarsal sulcus usually present. For a more detailed description of the genus see WARD (1990, 2001).

The Afrotropical (including Malagasy) species of *Tetraponera*

Morphological scrutiny of a large series of Old World *Tetraponera*, carried out in conjunction with ongoing molecular phylogenetic analyses (P.S. Ward unpubl.), reveals six distinctive, mutually exclusive clades, here treated as species-groups. One of these, the *T. nigra*-group, is confined to the Indo-Australian region, and was previously diagnosed and revised (WARD 2001). A synopsis of the remaining five groups is provided below. The lists of currently valid names in each group give an indication of their relative species richness but some of these names will prove to be junior synonyms. There are also additional undescribed species in the *T. allaborans*-group, *T. grandidieri*-group and *T. natalensis*-group.

Key to species groups of Afrotropical *Tetraponera* based on the worker caste

- 1 Large species (HW > 1.70, MFC > 0.35); head with three distinct ocelli; petiole with prominent, recurved anteroventral tooth (Fig. 1).
 *T. rufonigra*-group
- Smaller species (HW < 1.70, MFC < 0.25); either head with 0 - 2 ocelli or anteroventral tooth of petiole small and simple or (usually) both. 2



Figs. 1 - 3: *Tetraponera* workers, lateral view of petiole (1), dorsal view of anterior two thirds of mesosoma (2, 3). (1) *T. aethiops* (Cameroon); (2) *T. natalensis* (South Africa); (3) *T. rakotonis* (Madagascar).

- 2 Pronotum with sharp lateral margination, extending in attenuated form to the lateral borders of the propodeum and petiole; integument sculpture imparting a matte appearance to most of body; mesonotum strongly transverse, 2 - 3× wider than long, and semicircular in dorsal view with a straight posterior margin (Fig. 2); posteroventral margin of petiole with a median notch (ventral view). *T. natalensis*-group
- Pronotum, propodeum and petiole usually with soft-edged lateral margins; if sharply marginate, then integument shiny; mesonotum about as long as wide and appearing ovoid or subrectangular in dorsal view (Fig. 3); posteroventral margin of petiole lacking median notch (ventral view). 3
- 3 Larger species (HW 0.95 - 1.59), with long and slender appendages: scape length three-quarters or more of head width (SI 0.74 - 0.85) and length of metatibia subequal to that of head (LHT / HL 0.94 - 1.12); head with three distinct ocelli. *T. grandidieri*-group
- Smaller species (HW 0.44 - 1.15), with shorter and more robust appendages: scape length about two-thirds or less of head width (SI 0.40 - 0.70) and length of metatibia distinctly less than that of head (LHT / HL 0.58 - 0.82); head with two ocelli or (more commonly) none..... 4
- 4 Long axis of compound eye directed anteromedially (e.g., Fig. 4); upper half of mesosternum sparsely pubescent; workers dimorphic, with a discrete soldier subcaste. ... *T. ambigua*-group

- Long axis of compound eye directed anteriorly or anterolaterally; mesosternum densely pubescent; workers monomorphic. *T. allaborans*-group

***Tetraponera allaborans*-group**

Worker diagnosis. Small to medium-sized species (HW 0.44 - 1.15); masticatory margin of mandible usually with four (rarely five) teeth, basal margin edentate and shorter than masticatory margin; in a subset of species (the *T. allaborans* 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 - 0.22); scape length about two thirds of head width or less (SI 0.40 - 0.70); compound eyes directed anteriorly; head capsule 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 (Fig. 3); mesopropodeal impression usually containing a raised transverse metanotal (or mesoscutellar?) 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. This is a more inclusive concept of the *T. allaborans*-group than that adopted in WARD (2001). The posterior end of the petiole has a distinctive structure in the *T. allaborans*-group and in two other species groups of *Tetraponera*: the semicircular posterior margin of the sternite, against which the helcial sternite articulates, has retreated dorsomesially, and a new posteroventral margin protrudes below this. As a result the postpetiolar insertion has shifted upward, and the posteroventral margin of the petiole is well separated from it. The workers of the *T. allaborans*-group share this feature with the *T. ambigua*-group (from which they are distinguished by the orientation of the eyes and by differences in mesosomal structure) and with the *T. natalensis*-group (in which the workers lack the mesosternal pilosity seen in the *T. allaborans*-group and also have a differently shaped mesosoma).

Distribution. Africa, Madagascar; India to China, south to northern Australia.

Currently valid names. *T. allaborans* (WALKER, 1859); *T. amargina* XU & CHAI, 2004; *T. apiculata* WARD, 2001; *T. arrogans* (SANTSCHI, 1911); *T. avia* WARD, 2001; *T. bita* WARD, 2001; *T. braunsi* (FOREL, 1913); *T. braunsi durbanensis* (FOREL, 1914); *T. brevis* WARD, 2001; *T. claveaui* (SANTSCHI, 1913); *T. clypeata* (EMERY, 1886); *T. conica* WARD, 2001; *T. connectens* WARD, 2001; *T. continua* (FOREL, 1908); *T. convexa* XU & CHAI, 2004; *T. crassiuscula* (EMERY, 1901); *T. demens* (SANTSCHI, 1911); *T. diana* (SANTSCHI, 1911); *T. emeryi* (FOREL, 1911); *T. exasciata* (FOREL, 1892); *T. extenuata* WARD, 2001; *T. fictrix* (FOREL, 1897); *T. flexuosa* (SANTSCHI, 1911); *T. furcata* XU & CHAI, 2004; *T. gerdae* (STITZ, 1911); *T. hysterica* (FOREL, 1892); *T. hysterica dimidiata* (FOREL, 1895); *T. hysterica inflata* (EMERY, 1900); *T. liengmei* (FOREL, 1894); *T. mandibularis* (EMERY, 1895); *T. mayri* (FOREL, 1901); *T. microcarpa* WU & WANG, 1990; *T. modesta* (F. SMITH, 1860); *T. morondaviensis* (FOREL, 1891); *T. penzigi* (MAYR, 1907); *T. penzigi praestigiatrix* SANT-

SCHI, 1937; *T. perlonga* SANTSCHI, 1928; *T. plicatidens* (SANTSCHI, 1926); *T. protensa* XU & CHAI, 2004; *T. rako-tonis* (FOREL, 1891); *T. sahlbergii* (FOREL, 1887); *T. sahlbergii deplanata* (FOREL, 1904); *T. sahlbergii longula* (EMERY, 1895); *T. sahlbergii spuria* (FOREL, 1897); *T. scotti* DONISTHORPE, 1931; *T. tessmanni* (STITZ, 1910); *T. zavattarii* (MENOZZI, 1939).

Tetraponera ambigua-group

Worker diagnosis. 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 (Fig. 5) or separated from it by a weakly differentiated area (metanotum or mesoscutellum) (Figs. 7, 10, 12); 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. Workers of the *T. ambigua*-group can be distinguished by the orientation of their compound eyes: the long axis is directed anteromedially towards the midline of the front of the head. In all other *Tetraponera* species the eyes are directed anteriorly or anterolaterally. The group is also unique among pseudomyrmecines in having a discrete subcaste of major workers. Small size (minor worker HW < 0.95) separates workers of the *T. ambigua*-group from those of all other species groups except the *T. allaborans*-group.

Distribution. Africa, Arabian Peninsula, Madagascar.

Currently valid names (see species-level revision below). *T. ambigua* (EMERY, 1895); *T. ophthalmica* (EMERY, 1912); *T. parops* sp.n.; *T. phragmotica* sp.n.

Tetraponera grandidieri-group

Worker diagnosis. Medium to large species (HW 0.95 - 1.59); masticatory margin of mandible with four teeth; basal margin lacking teeth and subequal in length to masticatory margin; labrum with a pair of tubercles closely flanking the midline near proximal margin (no median tubercle); anteromedial margin of clypeus crenulate or emarginate; distance between frontal carinae slightly exceeding basal scape width (FCI 0.11 - 0.17), scape length three-quarters or more of head width (SI 0.74 - 0.85); head capsule with three distinct ocelli; pronotum laterally marginate; posteroventral margin of petiole lying adjacent to helcium venter; metabasitarsal sulcus present; legs long and slender (FI 0.28 - 0.32, LHT / HL 0.94 - 1.12); appressed pubescence sparse on abdominal tergite 4. Orange to reddish-brown, head concolorous or darker.

Comments. This is a small homogeneous group, endemic to Madagascar. The relatively large size, slender appendages, presence of three ocelli, and orange-brown body coloration set this group apart from other *Tetraponera* species on the island.

Distribution. Madagascar.

Currently valid names. *T. grandidieri* (FOREL, 1891); *T. grandidieri hildebrandti* (FOREL, 1891); *T. grandidieri variegata* (FOREL, 1895).

Tetraponera natalensis-group

Worker diagnosis. Medium to large species (HW 0.99 - 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 0.10 - 0.18), scape length subequal to head width (SI 0.45 - 0.56); 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 - 3 times wider than long, and semicircular in dorsal view with a straight posterior margin (Fig. 2); dorsal face of propodeum long and flat, sometimes with a weakly differentiated metanotal (or mesoscutellar?) 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. Integument densely punctulate to punctulate-coriarius, the sculpture giving a subopaque (matte) appearance to most of body.

Comments. This is a distinctive group of species, easily recognized in the worker and queen by the sharp margination on the pronotum (extending to the propodeum and petiole) combined with a subopaque and densely punctulate-coriarius integument. The worker has a characteristic form of the mesonotum: semicircular in dorsal view, much wider than long, and with a straight posterior margin (Fig. 2). The median notch on the posteroventral margin of the petiole is also unique to the group.

Distribution. Africa, northwestern Madagascar.

Currently valid names. *T. andrei* (MAYR, 1895); *T. angusta* (ARNOLD, 1949); *T. anthracina* (SANTSCHI, 1910); *T. caffra* (SANTSCHI, 1914); *T. capensis* (F. SMITH, 1858); *T. emacerata* (SANTSCHI, 1910); *T. emacerata oberbecki* (FOREL, 1911); *T. emacerata odiosa* (FOREL, 1916); *T. ledouxi* TERRON, 1969; *T. lemoulti* (SANTSCHI, 1920); *T. mocquerysi* (ANDRÉ, 1890); *T. mocquerysi biozellata* (KARAVAIEV, 1931); *T. mocquerysi elongata* (STITZ, 1911); *T. mocquerysi lepida* WHEELER, 1922; *T. mocquerysi lutea* (STITZ, 1911); *T. monardi* (SANTSCHI, 1937); *T. natalensis* (F. SMITH, 1858); *T. natalensis cuitensis* (FOREL, 1911); *T. natalensis obscurata* (EMERY, 1895); *T. natalensis usambarensis* (FOREL, 1911); *T. poultoni* DONISTHORPE, 1931; *T. prelli* (FOREL, 1911); *T. schulthessi* (SANTSCHI, 1915); *T. triangularis* (STITZ, 1910); *T. triangularis illota* (SANTSCHI, 1914).

Tetraponera rufonigra-group

Worker diagnosis. Large species with broad head (CI > 0.85); masticatory margin of mandible usually with four teeth, preceded by a single tooth on basal margin (in one 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 > 0.18), less so in Asian species (FCI 0.09 - 0.16); scape length one half or more of head width (SI 0.50 - 0.63); head capsule with three prominent ocelli; pronotal humeri subangulate in dorsal view; metanotal plate lacking; mesosternum not densely pubescent; petiole with prominent anteroventral tooth, generally directed posteroventrally (Fig. 1); 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 is a more inclusive concept of the *T. rufonigra*-group than that employed in WARD (2001). Salient features of the worker caste are the large size, broad head, well developed ocelli, angulate pronotal humeri and prominent anteroventral petiolar tooth. Although difficult to discern without removing the mandibles the transverse carina on the ventral surface of the clypeus is apparently unique to the group.

Distribution. West and central Africa; Indian subcontinent to southeast Asia. The two African species (*T. aethiops* F. SMITH, 1877, *T. latifrons* (EMERY, 1912)) are both specialist inhabitants of the antplant *Barteria fistulosa* MASTERS, 1871 (JANZEN 1972).

Currently valid names. *T. aethiops* F. SMITH; *T. concava* XU & CHAI, 2004; *T. latifrons* (EMERY); *T. pilosa* (F. SMITH, 1858); *T. rufonigra* (JERDON, 1851).

Revision of the *Tetraponera ambigua*-group

Synonymic list of species

T. ambigua (EMERY 1895: 23): Saudi Arabia to South Africa, west to Senegal.

= *T. ambigua occidentalis* MENOZZI 1934: 154, **syn.n.**

= *T. ambigua rhodesiana* (FOREL 1913: 112), **syn.n.**

= *T. bifoveolata* (MAYR 1895: 146), **syn.n.**

= *T. bifoveolata maculifrons* (SANTSCHI 1912: 162), **syn.n.**

= *T. bifoveolata syriaca* (WHEELER & MANN 1916: 167), **syn.n.**

= *T. encephala* (SANTSCHI 1919: 84), **syn.n.**

= *T. erythraea* (EMERY 1895: 23), **syn.n.**

= *T. ophthalmica angolensis* SANTSCHI 1930: 61, **syn.n.**

T. ophthalmica (EMERY 1912: 98): West and central Africa, east to Kenya.

= *T. nasuta* BERNARD 1953a: 222, **syn.n.**

= *T. ophthalmica tenebrosa* SANTSCHI 1928: 61, **syn.n.**

= *T. ophthalmica unidens* SANTSCHI 1928: 60, **syn.n.**

T. parops sp.n.: Kenya, Somalia, Tanzania.

T. phragmotica sp.n.: Madagascar.

Key to species based on the worker caste

1 Smaller species (HW 0.51 - 0.71) with elongate head (CI 0.66 - 0.79) (Figs. 4, 6, 8); masticato-

ry margin of mandibles with four teeth; African mainland and Arabian Peninsula. 2

– Larger species (HW 0.80 - 0.92) with broader head (CI 0.89 - 0.92) (Fig. 11); masticatory margin of mandibles with six teeth; endemic to Madagascar. *T. phragmotica* sp.n.

2 Standing pilosity common on mesosoma dorsum (MSC 12 - 44) (Fig. 5); larger species (HW 0.61 - 0.71), with smaller eyes (REL2 0.54 - 0.60). *T. ambigua*

– Standing pilosity virtually absent from mesosoma dorsum, except for one pair of long setae on pronotum (MSC 2 - 3) (Figs. 7, 10); smaller species (HW 0.51 - 0.59), with disproportionately larger eyes (REL2 0.63 - 0.72). 3

3 Standing pilosity common on posterior half of head, conspicuous in profile (Fig. 9) (CSC 12 - 22); petiole short and robust (PLI 0.54 - 0.61, PL / HL 0.46 - 0.50). *T. parops* sp.n.

– Standing pilosity sparse on posterior half of head (CSC 2 - 4); petiole usually more elongate (PLI 0.47 - 0.56; PL / HL 0.50 - 0.54).
..... *T. ophthalmica*

Species Accounts

Tetraponera ambigua (EMERY, 1895) (Figs. 4, 5, 15)

Sima ambigua EMERY 1895: 23. Syntypes, 1 worker, Hammans Kraal, South Africa (leg. Simon), 1 dealate queen, Makapan, South Africa (leg. Simon) (MCSN) [examined].

Sima ambigua subsp. *erythraea* EMERY 1895: 23. Syntypes, 3 workers, Aden, Yemen (leg. Simon) (MCSN, MHNG) [examined]. **Syn.n.**

Sima bifoveolata MAYR 1895: 146. Syntypes, 21 workers, Delagoa, Mozambique (leg. Brauns) (BMNH, MCSN, MHNG, NHMV), 1 worker, Zanzibar [as "Sansibar"], Tanzania (leg. Brauns) (NHMV) [examined]. **Syn.n.**

Sima bifoveolata [misspelled as "*foveolata*"] st. *maculifrons* SANTSCHI 1912: 162. Syntypes, 4 workers, Obcock, Djibouti (leg. Maindron) (MNHN, NHMB) [examined]. **Syn.n.**

Sima ambigua r. *Rhodesiana* FOREL 1913: 112. Syntype, 1 worker, Plumtree, Zimbabwe (leg. Arnold) (MHNG) [examined]. **Syn.n.**

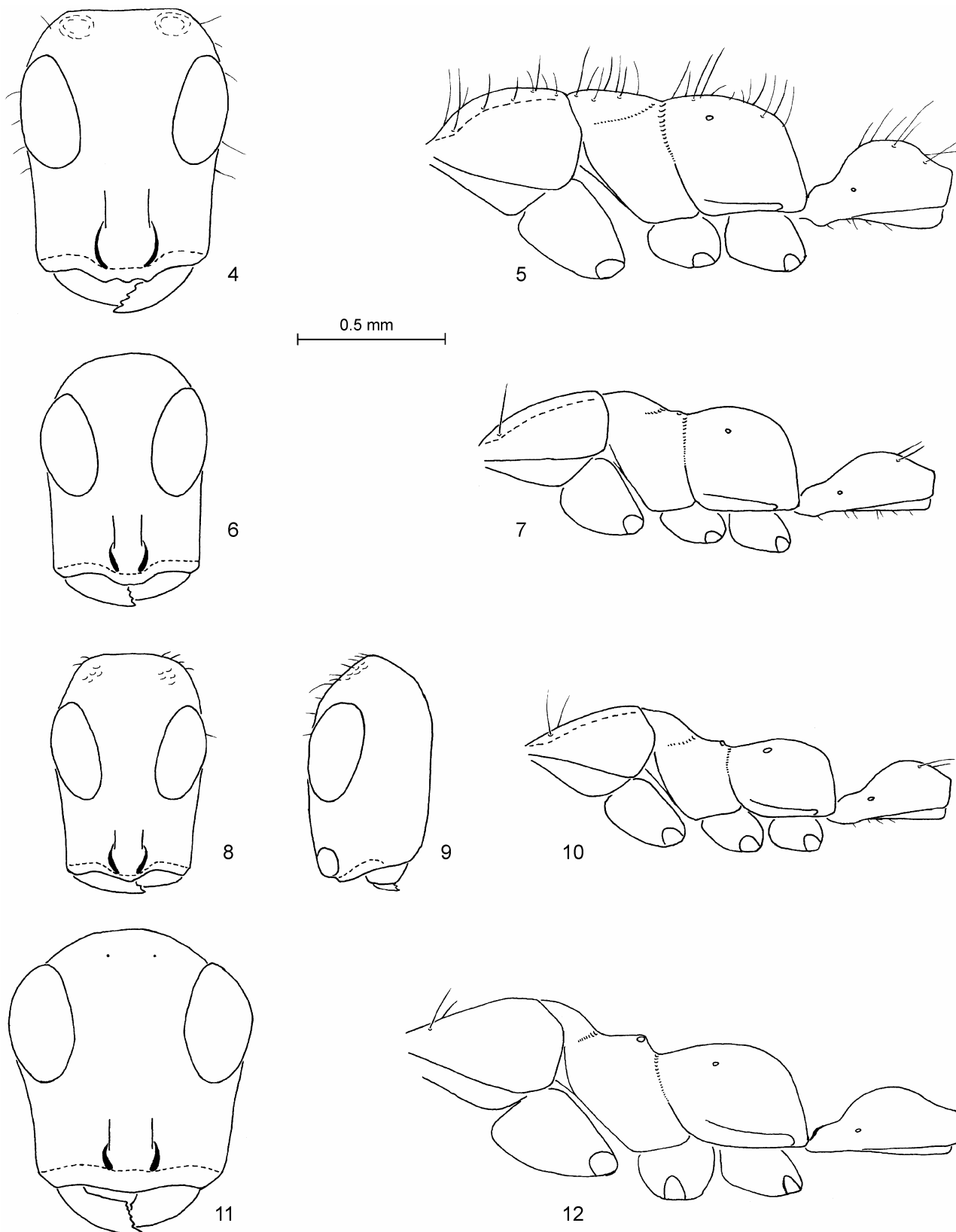
Sima bifoveolata var. *syriaca* WHEELER & MANN 1916: 167. Syntypes, 22 workers, Wadi Gazelle, Sinai, Egypt (leg. W.M. Mann) (MCZC, USNM) [examined]. **Syn.n.**

Sima encephala SANTSCHI 1919: 84. Syntype, 1 dealate queen, Senegal (leg. Claveau) (NHMB) [examined]. **Syn.n.**

Sima ambigua r. *erythraea* v. *occidentalis* STITZ 1917: 336. [Unavailable name.]

Tetraponera ambigua var. *occidentalis* MENOZZI 1934: 154. [First available use of *occidentalis*.] Syntypes, 2 workers, Gara Djenoun, Algeria (leg. Geyr) (probably in ZMHB) [not examined]. **Syn.n.**

Tetraponera ophthalmica st. *angolensis* SANTSCHI 1930: 61. Syntypes, 4 workers, Chimporo, Angola (leg. Monard) (NHMB) [examined]. **Syn.n.**



Figs. 4 - 12: *Tetraponera ambigua*-group, workers, dorsal views of head (4, 6, 8, 11), lateral view of head (9) and lateral views of mesosoma and petiole (5, 7, 10, 12). (4 - 5) *T. ambigua* (South Africa); (6 - 7) *T. ophthalmica* (Cameroon); (8 - 10) *T. parops* sp.n. (paratype worker, Kenya); (11 - 12) *T. phragmotica* sp.n. (paratype worker, Madagascar).

Material examined (AMNH, BMNH, CASC, LACM, MCSN, MCZC, MHNG, MNHN, NHMB, NHMV, NMKE, NMWN, PSWC, SAMC, UCDC, UCRC, USNM, ZMAS):

Algeria: Illizi: Tassili n'Ajjer, St. 68, leg. F. Bernard; Tamanghasset: In. Amdjel, Bas Hoggar, leg. P. de Peyerimhoff; Tehi n'Beidiguen, Tifedest, leg. P. de Peyerimhoff. **Angola:** Cuando Cubango: Cubango Cuito, leg. Baum; Cunene: 10 mi NW Cahama, 1200 m, leg. E.S. Ross & R.E. Leech; Chimporo, leg. Monard. **Botswana:** Central: Serowe, leg. P. Forchhammer; Southern: Kokong, leg. Schultze. **Cameroon:** Sud: Réserve de Campo, 40 m, leg. D.M. Olson; Sud-Ouest: Matute, Tiko Plantation, leg. B. Malkin. **Democratic Republic of Congo:** 69 mi S Sampwe, leg. E.S. Ross & R.E. Leech; Mbulula [as "Mbalula"], leg. W.H. Whitcomb; Yangambi Reserve, leg. A. Raignier & J. van Boven. **Djibouti:** Obock, leg. M. Maindron. **Egypt:** Wadi Gazelle, Sinai, leg. W.M. Mann; Wadi Hebran, Sinai, leg. W. Wittmer. **Ethiopia:** Kaccin Uha [as "Katchinoa"], leg. M. de Rothschild. **Gabon:** Ogooue-Maritime: Réserve de la Moukalaba-Dougoua, 12.2 km 305° NW Doussala, 110 m, leg. S. van Noort. **Kenya:** Central: Kora, leg. C. West; Rift Valley: Ewaso Ng'iro River, nr. Mpala Research Centre, 1600 m, leg. R.R. Snelling; Guaso Nyiro, leg. G.M. Allen & G. Brooks; Mpala Research Centre, 1650 m, leg. R.R. Snelling; Olelgasaloi, leg. Meneghetti. **Libya:** Al Jufrah: Wadi Agheib, leg. E. Moltoni; Awbārī: Awbārī [as "Oubari"], collector unknown. **Mozambique:** Maputo: Delagoa Bay, leg. Brauns; Inhaca Island, 1 m, leg. G.D. Alpert; Inhaca Island, 1 m, leg. S. Blackthorn; Maputo, 1 m, leg. G.D. Alpert; Zambézia: 30 km E Quelimane, 1 m, leg. G.D. Alpert; 37 km N Quelimane, 70 m, leg. G.D. Alpert; 52 km N Quelimane, 70 m, leg. G.D. Alpert; 57 km N Quelimane, 70 m, leg. G.D. Alpert. **Namibia:** Gobabeb, leg. M. Nel; Churutabis 108, Bethanien Distr., leg. Huns Exp. '92; Namib desert, FE2, E. Dune Field, leg. A.C. Marsh. **Saudi Arabia:** Abha - Gizan km 28, Wadi Ad Dilla, 700 m, leg. Wittmer & Büttiker. **Senegal:** "Senegal", leg. Claveau. **Somalia:** Mudug: Obbia, leg. Bricchetti. **South Africa:** E. Cape: "Concordia", Rietbron, leg. U. Cape Town Ecol. Survey; Gauteng: Roodeplaat PPRI grounds, nr. Pretoria, leg. F. Grobbelaar & al.; Wonderboom, b. Pretoria, leg. Lingnau; KwaZulu Natal: 10 km NNW Mpila, Umfolozi Game Res., 120 m, leg. P.S. Ward; 2.5 km W Candover, leg. F. Grobbelaar & I.M. Millar; 22 mi ex Mkuzi to Mtubatuba, leg. J.H. Grobler; 4.5 km SW Golela, leg. F. Grobbelaar & I.M. Millar; Dugandlovu Camp, False Bay Park, 10 m, leg. P.S. Ward; Hlabisa, leg. J.H. Grobler; Kuleni Farm, near Hluhluwe, leg. F. Grobbelaar & I.M. Millar; Mkuze Game Reserve, leg. H.G. Robertson; Mkuze Game Reserve, below Mantuma, leg. M. Zini; Munywana & Mzinene confluence, nr. Hluhluwe, leg. F. Grobbelaar & I.M. Millar; Ndumo, Ubombo, leg. D.J. Fletcher; Ndumu Game Res., NRC Camp, leg. H.G. Robertson; Umfolozi Game Reserve, leg. R.M. Crewe; Mpumalanga: 15 mi N Ondersabie ["15 myl vanaf Ondersabie ... noord"], leg. A.J. Prins; Blyderivierspoort Nat. Res., Swadene, leg. R.B. Kimsey; Dendron, leg. Karny; Hans Merensky Nat. Res., leg. R.B. Kimsey; Hotbouschrand, Kruger National Park, leg. L. Braack; Lapalala Nat. Res., leg. R.B. Kimsey; Lower Sabie, Kruger Natl. Pk., 180 m, leg. P.S. Ward; Nylsvley, leg. H.G. Robertson; Pongola, collector unknown; Northern: Olifants Camp,

Kruger Nat. Park, leg. O. Kovalev; Northwest: Hamans Kraal, Transvaal, leg. Simon; Makapan, Transvaal, leg. Simon; Sun City, 1120 m, leg. P.S. Ward; province unknown: Kruger N.P. [as "KNP"], leg. J.J. Cillie; W. Cape: Anysberg Nature Res., 750 m, leg. P.S. Ward; Vrede, Anysberg Nature Reserve, 750 m, leg. P.S. Ward. **Sudan:** 15 mi N Khartoum, leg. R. van den Bosch; Ad Duwaym [as "El Duein, White Nile"], leg. N.A. Weber; Er Renk, Nile R., above Khartoum, leg. N.A. Weber; Kaka, leg. Trägårdh; Malakal, White Nile, leg. N.A. Weber; Port Sudan, leg. N.A. Weber. **Tanzania:** Arusha: Mkomazi Game Reserve, Ibaya, leg. H.G. Robertson; Mkomazi Game Reserve, Simba, leg. H.G. Robertson; Dar Es Salaam: Mbudya I., 18 km NNW Dar Es Salaam, < 5 m, leg. P.S. Ward; Mbudya Island, leg. M. Musgrave; Pwani: 14 km NW Kisiju, 20 m, leg. P.S. Ward; Kisiju, < 5 m, leg. P.S. Ward; Mafia Island, leg. Vesey-Fitzgerald; Tanga: Kange, near Tanga, 50 m, leg. P.S. Ward; region unknown: Zanzibar [as "Sansibar"], leg. Brauns. **Yemen:** Aden, leg. Simon. **Zimbabwe:** Bembesi, leg. G. Arnold; Matopos, leg. G. Arnold; Plumtree, leg. G. Arnold; Sawmills, leg. G. Arnold; Victoria Falls, leg. G. Arnold; Zambesi Valley, 7 km SE Angwa Bridge, leg. J. Weyrich.

Worker measurements (n = 14). HW 0.61 - 0.71, HL 0.86 - 0.99, LHT 0.55 - 0.63, CI 0.69 - 0.79, FCI 0.19 - 0.25, REL 0.41 - 0.45, REL2 0.54 - 0.60, SI 0.52 - 0.60, SI3 0.89 - 1.07, FI 0.43 - 0.51, PLI 0.56 - 0.76, PWI 0.47 - 0.59, LHT / HW 0.84 - 0.94, CSC 18 - 40, MSC 12 - 44.

Worker diagnosis. Masticatory margin of mandible with four teeth; anterior margin of median clypeal lobe varying from convex and crenulate to obtusely tridentate (Fig. 4); median lobes of antennal sclerites expanded laterally and covering most of the antennal insertions; ocelli absent or represented by a pair of weak lateral ocelli; pronotum laterally submarginate; mesosoma dorsum more or less flat in profile, mesosonotum weakly convex and not separated from anterior margin of propodeum by prominently raised metanotal spiracles (Fig. 5); dorsal face of propodeum subequal in length to declivitous face, the two surfaces better differentiated than in other *T. ambigua*-group species; petiole relatively robust, less than twice as long as high; metabasitarsal sulcus absent. Integument coriaceous/punctulate and sublucid; a pair of more coarsely sculptured patches of cuticle variably developed on posterolateral corners of head; side of propodeum with varying amounts of weak irregular longitudinal carinulae, extending onto adjacent mesopleuron. Standing pilosity common (see CSC and MSC values), present on mesonotum and propodeum; scattered appressed pubescence on most of body, moderately dense on abdominal tergite 4 (hairs separated by less than their lengths). Pale yellowish-orange to orange-brown.

Comments. Within the *T. ambigua*-group the worker of this species is characterized by its intermediate size, relatively small eyes (REL2 0.54 - 0.60), relatively flat profile of the mesosoma dorsum, and abundant standing pilosity. There is some variability in the configuration of the median clypeal lobe, shape of the petiole and details of sculpture – as might be expected in a widespread species – but the variation appears to be continuous and is consistent with the hypothesis of a single polytypic species. Of course, a more detailed genetic and phenotypic analysis might reverse this judgment.

Distribution and biology. *Tetraponera ambigua* is widely distributed in the Afrotropical region (Fig. 15) from the Arabian Peninsula and the Sahara to South Africa. This species is a generalist inhabitant of dead twigs, and appears to be more common in semi-arid environments than in rainforest.

***Tetraponera ophthalmica* (EMERY, 1912)** (Figs. 6, 7, 16)

Sima ophthalmica EMERY 1912: 98. Holotype (by monotypy), worker, "Kamerun" (leg. Conradt) (MCSN) [examined].

Tetraponera ophthalmica st. *unidens* SANTSCHI 1928: 60. Syntype, dealate queen, Mongende, Democratic Republic of Congo (leg. H. Schouteden) (MRAC) [examined]. **Syn.n.**

Tetraponera ophthalmica v. *tenebrosa* SANTSCHI 1928: 61. Syntype, worker, Lukula, Democratic Republic of Congo (leg. H. Schouteden) (MRAC) [examined]. **Syn.n.**

Tetraponera nasuta BERNARD 1953a: 222. Holotype, dealate queen, Zouépo, 1215 m, Guinea (leg. Lamotte) (MNHN) [examined]. **Syn.n.**

Material examined (ANIC, CASC, CUIC, LACM, MCSN, MHNG, MNHN, MRAC, NHMB, NHMV, PSWC, SAMC, UCDC):

Cameroon: Sud: 7 mi S Ebolowa, 580 m, leg. E.S. Ross & K. Lorenzen; Nkoemvon, leg. D. Jackson; Réserve de Campo, 40 m, leg. D.M. Olson; Sud-Ouest: Lac Barombi Mbo, Kumba, 400 m, leg. E.S. Ross & K. Lorenzen; Myuka, Victoria Div., leg. B. Malkin; province unknown: "Cameroon", leg. G. Terron; "Kamerun", leg. L. Conradt. **Central African Republic:** P.N. Dzanka-Ndoki, 21.4 km 53° NE Bayanga, 510 m, leg. S. van Noort; P.N. Dzanka-Ndoki, 38.6 km 173° S Lidjombo, 350 m, leg. S. van Noort; Res. Dzanga-Sangha, 12.7 km 326° NW Bayanga, 420 m, leg. S. van Noort. **Democratic Republic of Congo:** "Congo", leg. Kohl; Kisangani [as "Stanleyville"], leg. H. Kohl; Lukula, leg. H. Schouteden; Mongende, leg. H. Schouteden; Thysville, collector unknown; Uvira, leg. J.C. Bradley; vic. Irangi, 900 m, leg. T. Wagner. **Gabon:** Ogooue-Maritime: Réserve de la Moukalaba-Dougoua, 12.2 km 305° NW Doussala, 110 m, leg. S. van Noort. **Guinea:** Zouépo, 1215 m, leg. Lamotte. **Kenya:** Kakamega: Isecheno, Isecheno Forest Reserve, 1600 m, leg. R.R. Snelling; Rift Valley: Masai-Mara, 1580 m, leg. D.M. Olson & L. Farley. **Uganda:** Budongo Forest, vic. Sonso, 1050 m, leg. T. Wagner; Buwalasi, Mt. Elgon, 5000 ft., leg. J.C. Bradley; Maragambo For., Q.E. Park, 1000 m, leg. E.S. Ross & R.E. Leech.

Worker measurements (n = 11). HW 0.52 - 0.59, HL 0.71 - 0.88, LHT 0.46 - 0.56, CI 0.67 - 0.73, FCI 0.15 - 0.19, REL 0.45 - 0.50, REL2 0.64 - 0.71, SI 0.60 - 0.65, SI3 0.85 - 0.96, FI 0.42 - 0.47, PLI 0.47 - 0.56, PWI 0.35 - 0.46, LHT / HW 0.89 - 0.99, CSC 2 - 4, MSC 0 - 2.

Worker diagnosis. Relatively small species with elongate head and large eyes; masticatory margin of mandible with four teeth; clypeus narrow and protruding anteromedially (Fig. 6); median lobes of antennal sclerites expanded laterally and covering most of the antennal insertions; ocelli absent (represented at most by small flecks of dark pigment below the cuticle); profemur moderately slender; pronotum laterally submarginate; mesonotum flat to weakly convex in profile, metanotal spiracles not conspicuously raised; dorsal face of propodeum rounding in-

sensibly into declivitous face; petiole slender, about twice as long as high; metabasitarsal sulcus absent. Integument finely coriarius/punctulate and sublucid. Standing pilosity sparse (see CSC and MSC values), absent from the mesonotum and propodeum; typically one pair of long setae on pronotum and petiole, and one or two pairs of shorter setae on postpetiole; scattered appressed pubescence on most of body, moderately dense on abdominal tergite 4 (hairs separated by less than their lengths). Usually pale yellow to yellowish-brown, occasionally much darker (blackish-brown).

Comments. This species can be readily distinguished from *T. ambigua* by its smaller size, disproportionately larger eyes, and much sparser standing pilosity. The anterior clypeal margin of queens and soldiers is adorned with a single median tooth, especially stout in soldiers (anterior clypeal margin usually crenulate or bluntly tridentate in queens and soldiers of *T. ambigua*). For differences between *T. ophthalmica* and *T. parops* sp.n. see under the latter species.

Distribution and biology. *Tetraponera ophthalmica* occurs in west Africa and central Africa in areas of higher rainfall (Fig. 16). It is apparently a generalist inhabitant of dead twigs.

***Tetraponera parops* sp.n.** (Figs. 8, 9, 10, 16)

Holotype worker. Kenya: 4 km NW Watamu, < 5 m (3° 20' S, 39° 59' E), 15.XII.1990, ex dead twig of *Rhizophora*, mangrove, leg. P.S. Ward, #11154, specimen code CASENT 0106133 (CASC).

Paratypes. Series of workers, queens and one male, same locality and date as holotype, leg. P.S. Ward, # 11151, 11154, 11159, 11160-1 (BMNH, CASC, MCZC, NMKE, PSWC, SAMC, UCDC).

Material examined (BMNH, CASC, MCZC, NMKE, PSWC, SAMC, UCDC):

Kenya: Central: Kora, leg. C. West; Coast: 4 km NW Watamu, < 5 m, leg. P.S. Ward; Shimba Hills, leg. B. Hölldobler. **Somalia:** Chisimaio: Ola Vager, "leg. SBS". **Tanzania:** Arusha: Mkomazi Game Reserve, Ibaya, leg. H.G. Robertson; Pwani: Kisiju, < 5 m, leg. P.S. Ward.

Worker measurements (n = 10). HW 0.51 - 0.56, HL 0.73 - 0.84, LHT 0.46 - 0.51, CI 0.66 - 0.71, FCI 0.16 - 0.22, REL 0.42 - 0.47, REL2 0.63 - 0.68, SI 0.59 - 0.62, SI3 0.91 - 0.95, FI 0.44 - 0.52, PLI 0.54 - 0.61, PWI 0.42 - 0.47, LHT / HW 0.89 - 0.95, CSC 12 - 22, MSC 2 - 3.

Worker diagnosis. Small species with elongate head; masticatory margin of mandible with four teeth; clypeus narrow and somewhat protruding anteromedially (Fig. 8); median lobes of antennal sclerites expanded laterally and covering most of the antennal insertions; ocelli absent; profemur robust; pronotum laterally marginate but not strongly so; profile of mesosoma dorsum interrupted by raised metanotal spiracles; dorsal face of propodeum rounding insensibly into declivitous face; petiole as in Fig. 10; metabasitarsal sulcus absent. Integument finely coriarius/punctulate and sublucid, with roughened patches at posterolateral corners of head. Short standing pilosity common on head, especially at the posterolateral patches of coarser sculpture, elsewhere rather sparse; pronotum typically with a single pair of long setae, and one or two pairs of standing hairs present on petiole and postpetiole; scattered appressed pubescence on most of body, moderately

dense on abdominal tergite 4 (hairs separated by less than their lengths). Pale yellow to yellowish-brown.

Comments. Workers of *T. parops* sp.n. are similar to those of *T. ophthalmica*, but differ by the presence of abundant standing pilosity on the upper half of the head (CSC 12 - 22, compared with 2 - 4 in *T. ophthalmica*). The pilosity is particularly well developed at two roughened patches of cuticle on either side of the head near the posterior margin. These cuticular patches are absent in *T. ophthalmica*. The petiole of *T. parops* tends to be shorter, the eyes smaller, and the profemur more robust, compared with *T. ophthalmica*. In these respects *T. parops* workers are somewhat intermediate in morphology between *T. ophthalmica* and *T. ambigua*, although they are not likely to be confused with *T. ambigua* because workers of the latter species are larger and possess much more abundant mesosomal pilosity. The queens of *T. parops* can be distinguished from those of *T. ophthalmica* by the presence of a longitudinal line of roughened, punctate integument on the posterolateral corner of the head, flanking the ocellar triangle. *Tetraponera parops* queens also appear to have more robust petioles (PLI 0.59 - 0.64; n = 4) than those of *T. ophthalmica* (PLI 0.46 - 0.55; n = 5) but larger sample sizes might erase this distinction.

Because *T. parops* is allopatric to *T. ophthalmica* I was initially hesitant to treat it as a separate species. Nevertheless, the westernmost samples of *T. parops* from Kora, Kenya, close to the eastern limits of *T. ophthalmica*, do not appear to grade towards the latter. In addition, based on a small sample of males (1 male of *T. parops*, 2 males from Cameroon tentatively identified as *T. ophthalmica* – but unassociated with workers) there appear to be marked differences in the male genitalia of the two forms, of a magnitude not expected to occur within species. The species referred to as "*Tetraponera ophthalmica*" in WARD & DOWNIE (2005: 326) is actually *T. parops*.

Distribution and biology. *Tetraponera parops* is known only from arid and semi-arid regions of east Africa (Kenya, Tanzania, Somalia). Colonies have been collected in dead twigs.

Tetraponera phragmotica sp.n. (Figs. 11, 12, 13, 14, 16)

Holotype worker. Madagascar: Nosy Be, 2 km ENE Andoany (= Hellville), < 5 m (13° 24' S, 48° 18' E), 4.V.1989, ex dead twig of *Albizia*, roadside, leg. P.S. Ward, #10492, specimen code CASENT 0106134 (CASC).

Paratypes. Series of five workers (two soldiers) and two dealate queens, same locality and date as holotype, leg. P.S. Ward, #10492, 10493, 10494 (BMNH, SAMC, PSWC); 1 worker, Madagascar: Nosy Be airport (13° 19' S, 48° 19' E), 21.II.1991, leg. G.D. Alpert (MCZC).

Material examined. Known only from the type series.

Worker diagnosis. Relatively large species (for the *T. ambigua*-group) with broad head and protruding eyes (Fig. 11); masticatory margin of mandible with six teeth; anterior margin of clypeus broadly convex and edentate; frontal carinae separated by more than twice basal scape width; lateral ocelli present, but very small, median ocellus absent; profemur slender (FI 0.40 - 0.43); lateral pronotal margins weakly developed; profile of mesosoma dorsum as in Fig. 12, interrupted by prominently raised metanotal spiracles; dorsal face of propodeum rounding insensibly into declivitous face; petiole slender, with short an-

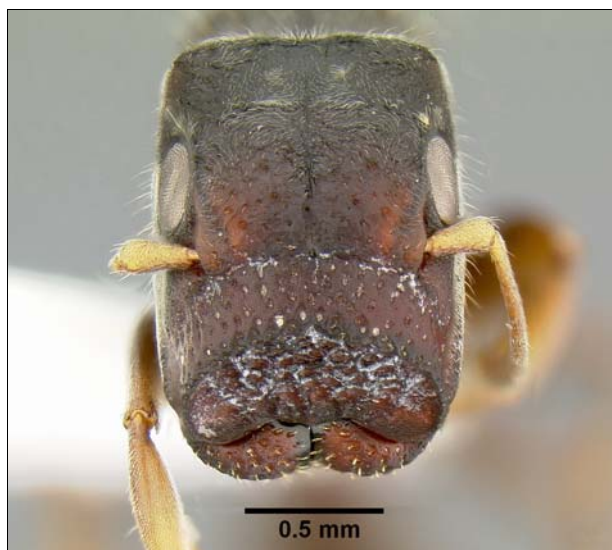


Fig. 13: *Tetraponera phragmotica* sp.n., soldier, dorsal view of head.



Fig. 14: *Tetraponera phragmotica* sp.n., soldier, lateral view of body.

terior peduncle preceding an elongate node; metabasitarsal sulcus present as a weakly impressed line on the upper half of basitarsus. Integument largely smooth and shining, with a faint overlay of coriariouly / punctulate sculpture, most notably on dorsum of head and sides of mesosoma. Standing pilosity sparse (see CSC and MSC values), absent from mesonotum, propodeum and petiole; scattered appressed pubescence on most of body, moderately dense on abdominal tergite 4 (hairs separated by less than their lengths). Black to brownish-black, mandibles, scapes, tarsi, parts of tibiae, and distal extremities of femora lighter yellowish-brown.

Comments. Within the *T. ambigua*-group the (minor) worker of this species is easily recognized by its relatively large size (HW > 0.80, LHT > 0.70), broad head, dark shiny integument, and the presence of a metabasitarsal sulcus. The soldier subcaste is also very distinctive: the pronotum and head are much enlarged and the anterior portion of the head has an expanded and abruptly truncate clypeus (Figs. 13 - 14). The truncate portion is semicir-

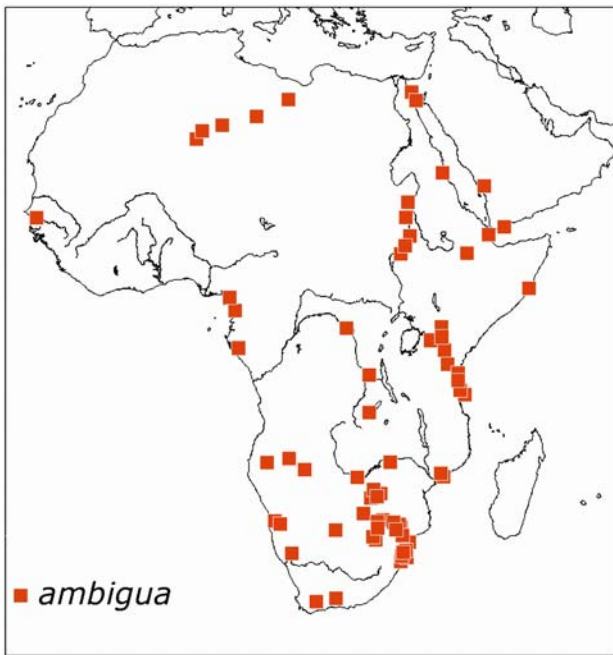


Fig. 15: Distribution of species in the *Tetraponera ambigua*-group: *T. ambigua*.

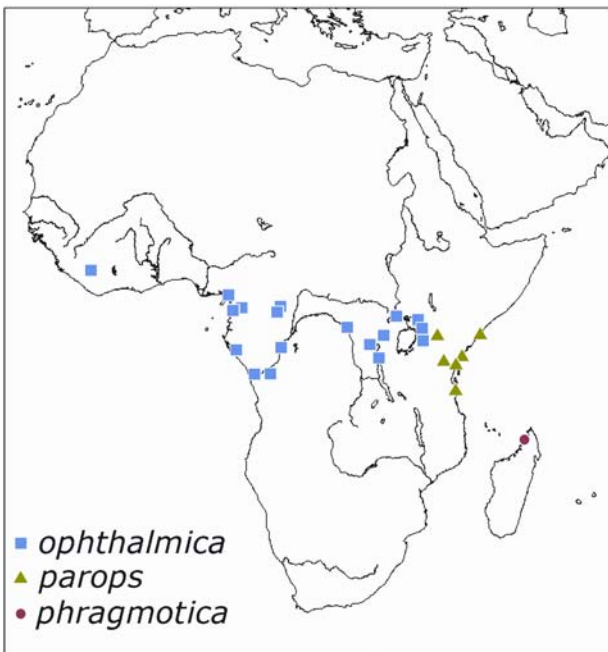


Fig. 16: Distributions of species in the *Tetraponera ambigua*-group: *T. ophthalmica*, *T. parops*, and *T. phragmotica*.

cular in anterior view, with a raised outer rim and a coarsely pitted rugulose interior. The mandibles complete the truncation anteroventrally and have coarse setigerous pits. The portion of the clypeus posterior to the truncation has smaller scattered foveate pits, about 0.05 mm in diameter. The head of the queen is similarly phragmotoc but also possesses distinct ocelli, which are essentially absent in the soldier.

Distribution and biology. *Tetraponera phragmotica* is known only from the island of Nosy Be in northwestern Madagascar. The collections from 2 km ENE Andoany were taken in dead twigs of two adjacent *Albizia* trees (one recently felled, one standing) along a roadside next to mangroves.

Discussion

The *Tetraponera ambigua*-group is a compact and distinctive assemblage of species, whose monophyly is supported by both morphological and molecular evidence. One of the more notable features of the group is the presence of a discrete soldier (major worker) subcaste, a phenomenon not recorded in any other species of Pseudomyrmecinae. In the three African species the soldier shows a modest amount of modification: the head and pronotum are enlarged and the clypeus and mandibles have become more robust and heavily sclerotized. But in the Malagasy species, *T. phragmotica* sp.n., the head of the soldier is hypertrophied and strongly truncate (Figs. 13-14), with the mandibles and anterior portion of the clypeus transformed into a plug, well suited for blocking the nest entrance of these twig-dwelling ants. The form of the plug – including the pitted surface of the clypeus – is uncannily similar to that seen in species of *Camponotus* MAYR, 1861 belonging to the subgenus *Colobopsis* MAYR, 1861 (FOREL 1892, WHEELER 1904, 1910). Cases of phragmosis are known in a few other ants (HÖLDOBLER & WILSON 1990) but the convergence with *Colobopsis* is especially striking in this Malagasy *Tetraponera*.

In preliminary molecular phylogenetic analyses *T. phragmotica* sp.n. is sister to the three African species of the *T. ambigua*-group (P.S. Ward, unpubl.). The timing and significance of this divergence is unclear, in part because the closest relatives of the *T. ambigua*-group have not been clearly identified. Mid-Tertiary dispersal of a *T. ambigua*-group ancestor from the African mainland to Madagascar seems to be the most likely explanation. A similar situation occurs in the *T. natalensis*-group. Here there are about eight species, all confined to the African continent except for one undescribed species in northwestern Madagascar. Improved species-level taxonomy and more detailed phylogenetic analyses are needed to elucidate the history of these and other *Tetraponera* ants in the Afrotropical region.

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Zusammenfassung

Die afrotropischen (einschließlich die madegassischen) Arten der Ameisengattung *Tetraponera* F. SMITH, 1862 werden beurteilt und fünf monophyletische Artengruppen werden errichtet. Diese Gruppen werden mittels eines Bestimmungsschlüssels zugänglich gemacht; ihre Zusammensetzung und Verbreitung werden zusammengefasst. Eine dieser Gruppen, die *T. ambigua*-Gruppe, wird auf Art-niveau revidiert. Innerhalb dieser Gruppe werden die folgenden neuen Synonymien vorgeschlagen (ältere Synonyme jeweils vorangestellt): *T. ambigua* (EMERY, 1895) = *T. erythraea* (EMERY, 1895) = *T. bifoveolata* (MAYR, 1895) = *T. bifoveolata maculifrons* (SANTSCHI, 1912) = *T. ambigua rhodesiana* (FOREL, 1913) = *T. bifoveolata syriaca* (WHEELER & MANN, 1916) = *T. encephala* (SANTSCHI, 1919) = *T. ophthalmica angolensis* SANTSCHI, 1930 = *T. ambigua occidentalis* MENOZZI, 1934; sowie *T. ophthalmica* (EMERY, 1912) = *T. ophthalmica tenebrosa* SANTSCHI, 1928 = *T. ophthalmica unidens* SANTSCHI, 1928 = *T. nasuta* BERNARD, 1953. Die Zahl der gültigen Arten wird somit auf zwei reduziert, *T. ambigua* und *T. ophthalmica*, beide am afrikanischen Kontinent weit verbreitet. Zwei weitere Arten werden hier neu beschrieben: *T. parops* sp.n. aus Ostafrika und *T. phragmotica* sp.n. aus Nordwestmadagaskar. Alle vier Arten der *T. ambigua*-Gruppe haben dimorphe Arbeiterinnen, ein Merkmal, das sonst aus der Unterfamilie Pseudomyrmecinae unbekannt ist. Die Major-Arbeiterinnen und Gynen von *T. phragmotica* haben stöpselförmige Köpfe, eine bemerkenswerte Konvergenz zu jenen der entfernt verwandten Ameisenarten aus der Formicinen-Tribus Camponotini. Die Phylogenie und die biogeographische Geschichte der *T. ambigua*-Gruppe werden kurz diskutiert.

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