



Afrotropical ants of the ponerine genera *Centromyrmex* Mayr, *Promyopias* Santschi gen. rev. and *Feroponera* gen. n., with a revised key to genera of African Ponerinae (Hymenoptera: Formicidae)

BARRY BOLTON¹ & BRIAN L. FISHER²

c/o Department of Entomology, The Natural History Museum, Cromwell Road, London SW7 5BD, U.K.

Department of Entomology, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118, U.S.A.

Table of contents

Abstract	2
Introduction	2
Measurements and indices	3
Genus <i>Centromyrmex</i>	4
<i>Centromyrmex</i> Mayr	4
Synonymic synopsis of species	7
Key to world species groups of <i>Centromyrmex</i> (workers and queens)	8
I Afrotropical species	8
Key to Afrotropical species (workers)	8
<i>Centromyrmex bequaerti</i> group	10
Species of <i>bequaerti</i> group	11
<i>Centromyrmex bequaerti</i> (Forel)	11
<i>Centromyrmex secutor</i> Bolton & Fisher sp. n.	13
<i>Centromyrmex feae</i> group	14
Afrotropical species of <i>feae</i> group	15
<i>Centromyrmex angolensis</i> Santschi stat. n.	15
<i>Centromyrmex decessor</i> Bolton & Fisher sp. n.	17
<i>Centromyrmex ereptor</i> Bolton & Fisher sp. n.	18
<i>Centromyrmex fugator</i> Bolton & Fisher sp. n.	18
<i>Centromyrmex longiventris</i> Santschi stat. n.	19
<i>Centromyrmex praedator</i> Bolton & Fisher sp. n.	21
<i>Centromyrmex raptor</i> Bolton & Fisher sp. n.	21
<i>Centromyrmex sellaris</i> Mayr	22
II Oriental and Malesian species	25
<i>Centromyrmex hamulatus</i> (Karavaiev)	25
III Neotropical species	25
Genus <i>Feroponera</i>	26
<i>Feroponera</i> Bolton & Fisher gen. n.	26
<i>Feroponera ferox</i> Bolton & Fisher sp. n.	28
Genus <i>Promyopias</i>	28
<i>Promyopias</i> Santschi gen. rev.	28
Synonymic synopsis of species	31
<i>Promyopias silvestrii</i> (Santschi) comb. rev.	31
Appendix 1. Is there a <i>Centromyrmex</i> genus group?	32
Appendix 2. Revised key to genera of Afrotropical Ponerinae (workers)	32

Acknowledgements	35
References	35

Abstract

The ponerine ant genus *Centromyrmex* Mayr is redefined and its Afrotropical species are fully revised. Ten Afrotropical species are recognised of which six are described as new (*decessor*, *ereptor*, *fugator*, *praedator*, *raptor*, *secutor*). Two former infraspecific names are elevated to species rank (*angolensis*, *longiventris*) and four new junior synonyms of *sellaris* (= *arnoldi*, = *congolensis*, = *constanciae*, = *guineensis*) are established. The monotypic genus *Promyopias* Santschi is revived from synonymy and a new monotypic genus, *Feroponera*, type-species *F. ferox* sp. n., is introduced. The possibility of a *Centromyrmex* genus group is discussed and a revised key to Afrotropical genera of Ponerinae is presented.

Key words: Ponerinae, Afrotropical, *Centromyrmex*, *Promyopias*, *Feroponera*, taxonomy

Introduction

The three small genera considered here all fall within the tribe Ponerini of subfamily Ponerinae as defined by Bolton (2003). *Centromyrmex* is a compact and easily recognised genus that contains only 15 species to date, distributed through the world's tropics but with a preponderance of species (10) in the Afrotropical region. As noted below, all of its species appear to be termitophagous and all are superbly adapted to this specialised predatory life style. Indeed, members of the *feae* group are so well adapted that they appear strangely helpless away from their normal habitat. When not in termitaries ants of this fossorial group are usually found singly or in small numbers in the top soil or the root-mat below the leaf litter layer, where their short, powerful, spiny legs facilitate their movement. Weber (1949) described what happened when he found a worker "just beneath the soil surface under a thin cover of dead leaves". The ant was "completely helpless when exposed to the daylight and writhed about when placed on the ground or in my palm. It made no attempt to run away, curling and uncurling without stinging, though it had a long, stout sting". In other words, it seemed unable to walk when removed from its specialised habitat and placed on a surface where it could not use its specialised legs.

Promyopias and *Feroponera* are both rare, monotypic Afrotropical endemics that share a number of interesting characters with *Centromyrmex* but are significantly different and merit generic status. Their relationships and possible affinities are discussed below and a consideration of whether the three together can be regarded as a monophyletic group on morphological grounds is appended. Of the three, only *Centromyrmex* has appeared in recent molecular-based phylogenetic studies, with conflicting results. In the work of Brady *et al.* (2006), *Centromyrmex* appeared as the sister-group of the *Plectroctena* group of genera, as defined by Bolton & Brown (2002), whilst in Moreau *et al.* (2006) *Centromyrmex* appeared to be the sister-group of all the rest of tribe Ponerini.

Members of *Centromyrmex* all seem to be obligate termitophages (*e.g.* Wheeler, 1936; Kempf, 1967; Léviéux, 1983; Delabie, 1995; Dejean & Fénelon, 1996, 1999). This is probably also the case with the other two genera, though both are extremely rare and their biologies remain unknown. In fact, *Promyopias* is represented by less than a dozen specimens in museum collections, and *Feroponera* is known only from its type-series of five workers. The Afrotropical species of *Centromyrmex* are fully revised here for the first time. Until now, the taxonomy of the region's species has been based entirely on inadequate and insufficiently comparative original descriptions of various taxa.

Based on published data and information gleaned from the data labels of material examined it appears that the range of termites preyed upon by *Centromyrmex*, at least in the commoner species, is very broad, but no detailed analysis of the termite prey or prey-specificity of the various species has ever been undertaken. Those termite genera definitely known to be prey are noted under the appropriate *Centromyrmex* species in the revi-

sion below. No *Centromyrmex* species were recorded from Ghanaian leaf litter by Belshaw & Bolton (1994), but specimens may sometimes be found there, as recorded by Watt *et al.* (2002) and as indicated by data on labels of material examined. These ants are, however, quite common in active termitaries (Dejean *et al.* 1996, 1997), as would be expected in termitophagous species.

In addition to the ten Afrotropical species, *Centromyrmex* contains three described Neotropical species, *alfaroi* Emery, *brachycola* (Roger) and *gigas* Forel, revised by Kempf (1967), and two species from the Oriental and Malesian regions, *feae* (Emery) and *hamulatus* (Karavaiev). This genus is absent from the Malagasy and Austral regions. These extralimital forms are treated here more superficially than the Afrotropical species in that their detailed species-rank taxonomy has not been investigated. Even so, major characters of these taxa are included for comparative purposes, to ensure monophyly of the genera, and to indicate relationships of the various species groups.

Recent changes in the subfamily structure of Formicidae (Bolton, 2003; Ward, 2007) and the findings of this investigation have resulted in the need to modify the key to Afrotropical genera of Ponerinae given by Bolton (1994). A revised key is appended to this paper, for testing and comment.

Measurements and indices

Measurements were taken using an optical micrometer, to the nearest 0.01 mm, on a Wild M5 microscope. All measurements are in millimetres. Note that in the discussions and keys below, the term “gaster” refers to the body section that begins with abdomindal segment III.

Total Length (TL). The total outstretched length of the ant from the mandibular apex to the gastral apex.

Head Length (HL). The length of the head capsule excluding the mandibles, measured in full-face view in a straight line from the mid-point of the anterior clypeal margin to the mid-point of the posterior margin. In species where the posterior margin is concave the measurement is taken from the mid-point of a transverse line that spans the apices of the projecting portions.

Head Width (HW). The maximum width of the head, measured in full-face view. (The measurement is usually specified as “behind the eyes”, which applies to queens in this study, but as eyes are completely absent in all workers then HW is taken across the widest point.)

Cephalic Index (CI). HW divided by HL, $\times 100$.

Ocular Index (OI). In queens the maximum diameter of the eye divided by HW, $\times 100$.

Mandible Length (ML). The maximum straight-line length of the fully closed mandibles from apex to mid-point of anterior clypeal margin. Because the mandible is so strongly downcurved in many species the head should be tilted back from full-face view until the maximum length is clearly seen.

Mandibular Index (MI). ML divided by HL, $\times 100$.

Scape Length (SL). The maximum straight-line length of the scape, excluding the basal constriction or neck.

Scape Index (SI). SL divided by HW, $\times 100$.

Pronotal Width (PW). The maximum width of the pronotum in dorsal view.

Weber's Length (WL). The diagonal length of the mesosoma in profile, from the point at which the pronotum meets the cervical shield to the posterior basal angle of the metapleuron.

Abbreviations of depositories

AMNH American Museum of Natural History, New York, U.S.A.

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

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

LACM	Natural History Museum of Los Angeles County, Los Angeles, California, U.S.A.
MCZC	Museum of Comparative Zoology, Cambridge, Massachusetts, U.S.A.
MHNG	Muséum d'Histoire Naturelle, Geneva, Switzerland
MNHN	Muséum National d'Histoire Naturelle, Paris, France
NHMB	Naturhistorisches Museum, Basel, Switzerland
NHRS	Naturhistoriska Riksmuseet, Stockholm, Sweden
SAMC	South African Museum, Cape Town, South Africa
SELN	Station d'Écologie de Lamto, N'Douci, Côte d'Ivoire

Images

Digital color images were created using a JVC KY-F75 digital camera and Syncroscopy Auto-Montage (v 5.0) software.

Genus *Centromyrmex*

Centromyrmex Mayr

Centromyrmex Mayr, 1866: 894. Type-species: *Centromyrmex bohemani* Mayr, 1866: 895, by monotypy. [Junior synonym of *Ponera brachycola* Roger, 1861: 5 (synonymy by Kempf, 1967: 405).]

Spalacomyrmex Emery, 1889: 489. Type-species: *Spalacomyrmex feae* Emery, 1889: 491, by monotypy. [Synonymy with *Centromyrmex* by Emery, 1890b: 40.]

Glyphopone Forel, 1913: 308. Type-species: *Glyphopone bequaerti* Forel, 1913: 308 by monotypy. [Synonymy with *Centromyrmex* by Brown, 1963: 9.]

Leptopone Arnold, 1916: 163 [as subgenus of *Glyphopone*; raised to genus by Wheeler, W.M. 1922: 647; synonymy with *Centromyrmex* by Brown, 1963: 9]. Type-species: *Glyphopone (Leptopone) rufigaster* Arnold, 1916: 163, by original designation [Junior synonym of *Glyphopone bequaerti* Forel, 1913: 308 (synonymy by Brown, 1963: 10)].

Typhloteras Karavaiev, 1925: 128. Type-species: *Typhloteras hamulatum* Karavaiev, 1925: 129, by monotypy. [Synonymy with *Centromyrmex* by Brown, 1953: 8.]

Diagnosis of worker and queen (gyne)

Workers are known for all species; queens are known for *bequaerti*, *decessor*, *fugator*, *sellaris*, *raptor* and *angolensis* of the Afrotropical region, for *alfaroi*, *brachycola* and *gigas* of the Neotropical region, and for *feae* and *hamulatus* of the Oriental and Malesian regions.

1 Mandible triangular (MI 28–38) to elongate-triangular (MI 52–84), with 4–12 teeth; with a distinct basal groove but without a basal pit.

2 Palp formula 4,3.

3 Eyes absent in worker, present in queen.

4 Frontal lobes with their anterior margins considerably posterior to the anterior clypeal margin.

5 Antenna with 12 segments; scape very strongly dorsoventrally flattened in its basal half, the leading edge extremely thin; funiculus gradually incrassate towards the apex but without a differentiated club.

6 Mesotibia, mesobasitarsus and metabasitarsus with strongly sclerotised spiniform or peg-like traction setae.

7 Pretarsal claws small, simple.

8 Metanotal groove absent.

9 Orifice of metapleural gland a small pore or short slit that opens laterally, located well above the ventral margin of the metapleuron and far anterior of the posteroventral angle of the mesosoma.

10 Propodeum unarmed.

11 Helcium located close to mid-height on anterior face of the first gastral segment (abdominal segment III).

12 Prora present but of unusual form and sometimes very weak; see discussion below.

13 Girdling constriction between presclerites and postsclerites of second gastral segment distinct.

14 Stridulitrum absent.

15 Queen only. Eyes and ocelli present. Transverse suture present on the mesopleuron that divides the sclerite into anepisternum and katepisternum. Mesosoma with full complement of flight sclerites. Hind wing with jugal lobe present.

Discussion of female characters

Character 9, in *italics*, is autapomorphic. Some of the other characters may also be apomorphies but have analogues that have apparently developed convergently elsewhere in tribe Ponerini. Characters 1–14 together form an inclusive diagnosis that isolates *Centromyrmex* workers and queens from all other genera in the tribe.

1 In the *bequaerti* group the mandibles are triangular and relatively short, with a small number of strongly defined teeth and a distinctly inflected apical tooth. In all other groups the mandibles are elongate-triangular, pointed apically but without an inflected apical tooth as the latter continues the line of the long axis of the mandible, and with more weakly defined but more numerous teeth on the masticatory margin. The small teeth on the elongate-triangular mandibles are commonly very worn and rounded, leaving the margin with a crenulate or even an almost edentate appearance.

2 The consistent palp formula count of 4,3 has been confirmed in *alfaroi* (worker and queen), *angolensis* (worker and queen), *bequaerti* (worker (all size morphs) and queen), *brachycola* (worker and queen), *decesor* (worker and queen), *ereptor* (worker), *feae* (worker), *fugator* (worker and queen), *hamulatus* (worker), *raptor* (worker and queen) *secutor* (all worker size morphs), *sellaris* (worker and queen). PF 4,3 was earlier recorded for all Neotropical species by Kempf (1967). This consistent count is probably an apomorphy of the genus (the same count also applies in all known males, see below).

3 Loss of eyes in the worker caste but their retention in queens is also characteristic of *Promyopias*: see discussion of potential genus group, below.

5 Extreme flattening of the basal half of the scape allows it to fit tightly against the dorsum of the head when directed laterally or posteriorly. Presumably this is an adaptation that allows the scapes to remain easily mobile in very confined spaces.

6 The apparent cuticular spines on the mesotibia, mesobasitarsus and metabasitarsus are in reality hypertrophied sclerotised setae, with sockets at the base. Their function is to improve traction in the ant's restricted habitat. They also occur in the same locations in *Promyopias* and *Feroponera*: see discussion of potential genus group, below.

8 All species lack any trace of a metanotal groove. Indeed, in all but *alfaroi* there is usually no trace of any suture across the dorsum at the junction of mesonotum and propodeum, so that the line of the posterior termination of the mesonotum is not demarcated in any way. In *alfaroi* a short, unimpressed, weak transverse suture is retained.

9 The unique position of the metapleural gland orifice is given as an unequivocal autapomorphy of *Centromyrmex*; it is a derived state not repeated anywhere else in the Ponerini, where the position of the orifice is always at or very near to the posteroventral corner of the mesosoma, opening laterally or posteriorly.

11 Position of the helcium is similar in *Promyopias* and *Feroponera*: see discussion of potential genus group, below.

12 In the *C. bequaerti* group the prora is a flat transverse plate, slightly indented medially, that traverses the first gastral sternite below the helcium. In all other species groups the prora is represented by a pair of longitudinal ridges on the anterior face of the first gastral sternite, one on each side below the helcium (extremely reduced in *alfaroi* and *raptor*); the space between the ridges is usually shallowly concave. The morphology of

the former can easily be derived from that of the latter by emphasising and elevating the ridges and elevating the cuticle between the ridges. Prorae of this nature are not “normal” for Ponerini, which typically have a cuticular prominence, variously shaped, immediately below the helcium.

Diagnosis of male

Examined for *alfaroi*, *angolensis*, *bequaerti*, *decessor* and *sellaris*; also previously described for *fae* and *hamulatus*.

- 1 Mandible very reduced, almost lobate; edentate or with a small apical tooth.
- 2 Palp formula 4, 3 (*in situ* counts).
- 3 Frontal lobes absent; antennal sockets fully exposed.
- 4 Antenna with 13 segments, filiform.
- 5 Second funicular segment very short, only as long as, or at most $1.10 \times$ longer than, the short scape.
- 6 Eyes large, inner margin shallowly convex to shallowly concave, without a marked concavity or indentation in about the median third; ocelli prominent.
- 7 Notauli variable, see discussion below.
- 8 Parapsidal grooves present.
- 9 Mesonotum with a deep, transverse groove between mesoscutum and mesoscutellum.
- 10 Epimeral lobe present.
- 11 Metapleural gland orifice present.
- 12 Propodeal spiracle with orifice elliptical to slit-shaped.
- 13 Spurs of mesotibia and metatibia as in worker and queen, see below.
- 14 Mesotibiae, mesobasitarsi and metabasitarsi lack the spiniform setae that are so conspicuous in female castes.
- 15 Pretarsal claws simple.
- 16 A membranous arolium present between the pretarsal claws.
- 17 Hindwing with jugal lobe present.
- 18 Prora usually present, its structure as in respective worker and queen but reduced in size; absent in *alfaroi*.
- 19 Gastral segment 2 (= abdominal segment IV) with a distinct girdling constriction between presclerites and postsclerites.
- 20 Pygidium (= abdominal tergite VIII) without a median apical spine.
- 21 Cerci (= pygostyles) present.

Males are known for few Afrotropical species, and very few specimens of each exist. The paucity of material makes it impossible to predict which characters will be of value at species-rank in this sex. For this reason, formal descriptions are not presented in the treatment by species.

Discussion of male characters

None of the characters listed are unequivocally stated as apomorphic at present, but 2 is a strong contender for this status and 5 and 11 are possibilities.

1 A reduced mandible of this form appears apomorphic for the tribe Ponerini as a whole (Bolton, 2003).

2 The 4,3 palp formula of males and the female castes is the same in all *Centromyrmex* where both are known. Elsewhere in Ponerini it is usual for males to have higher palp formula counts than conspecific females (Bolton, 2003), so this equality of PF is most probably an apomorphy of the genus. The plesiomorphic maximum count in Ponerini males is 6,4 (as in Aculeata in general), as opposed to 4,4 in females (Brown, 1963; Bolton, 2003).

5 In Ponerini generally the second funicular segment of males is much longer than the scape (*e.g.* Ogata,

1987; Yoshimura & Fisher, 2007; Bolton & Fisher, 2008). It is not certain whether the very short condition in *Centromyrmex* is plesiomorphic or apomorphic.

6 In many groups of Ponerini the inner margin of the eye is distinctly concave or suddenly indented in approximately its median third (*e.g.* Ogata, 1987; Yoshimura & Fisher, 2007).

7 Notauli are distinctly present in *decessor*, *angolensis* and most *sellaris*. However, in one example of *sellaris* only the anterior portions of the notauli were developed and in another the notauli were present but superficial throughout. Notauli were entirely absent in all *alfaroi* and *bequaerti* males examined.

11 A metapleural gland orifice is visible in all males. Unlike the female castes, males have the orifice in the usual position for Ponerini, close to the posteroventral angle of the metapleuron. The presence of this structure in this sex is uncommon and may be an apomorphy of the genus.

13 In the male of *bequaerti* both the mesotibia and metatibia have two spurs, on each the anterior spur is small and simple, the posterior is large and pectinate. In *alfaroi* the mesotibia has a single small, barbate spur and the metatibia a large pectinate spur. In *angolensis*, *decessor* and *sellaris* the mesotibia lacks spurs and the metatibia has only a single pectinate spur present. These arrangements correspond to those of the female castes of the same species.

16 The arolium is usually white, membranous and very conspicuous.

Comment

The four genus-group names listed in the taxonomic synopsis above as long-standing junior synonyms of *Centromyrmex* are all confirmed here. *Promyopias*, an earlier, fifth junior synonym most recently catalogued in Bolton (2003), is removed from synonymy and reinstated at genus-rank as discussed below.

Synonymic synopsis of species

I Afrotropical species

bequaerti group

- bequaerti* (Forel, 1913)
- = *rufigaster* (Arnold, 1916)
- secutor* Bolton & Fisher **sp. n.**

feae group

- angolensis* Santschi, 1937 **stat. n.**
- decessor* Bolton & Fisher **sp. n.**
- ereptor* Bolton & Fisher **sp. n.**
- fugator* Bolton & Fisher **sp. n.**
- longiventris* Santschi, 1919 **stat. n.**
- praedator* Bolton & Fisher **sp. n.**
- raptor* Bolton & Fisher **sp. n.**
- sellaris* Mayr, 1896
- = *constanciae* Arnold, 1915 **syn. n.**
- = *arnoldi* Santschi, 1919 **syn. n.**
- = *congolensis* Weber, 1949 **syn. n.**
- = *arnoldi* r. *guineensis* Bernard, 1953 **syn. n.**

II Oriental and Malesian species

feae group

- feae* (Emery, 1889)

= *donisthorpei* Menozzi, 1925
feae subsp. *ceylonicus* Forel, 1900
feae subsp. *greeni* Forel, 1901

hamulatus group

hamulatus (Karavaiev, 1925)

III Neotropical species

brachycola group

alfaroi Emery, 1890

brachycola (Roger, 1861)

= *bohemani* Mayr, 1866

= *brachycola* var. *paulina* Forel, 1911

gigas Forel, 1911

Key to world species groups of *Centromyrmex* (workers and queens)

- 1 Mesotibia with 1 or 2 spurs. Procoxa not hypertrophied. Protibia not inflated. Pronotum not marginate anterodorsally2
- Mesotibia without spurs. Procoxa hypertrophied. Protibia inflated. Pronotum marginate anterodorsally. (Afrotropical, Oriental, Malesian)*feae* group
- 2 Mesotibia with 1 spur. Propodeal spiracle not high on side, not very close to dorsal margin of mesosoma. Apical tooth of mandible weakly or not differentiated, not inflected but more or less continuing the line of the long axis of the mandible. Monomorphic species3
- Mesotibia with 2 spurs. Propodeal spiracle high on side, very close to dorsal margin of mesosoma. Apical tooth of mandible strongly differentiated and inflected, not continuing the line of the long axis of the mandible. Polymorphic species. (Afrotropical).....*bequaerti* group
- 3 Ventral process of petiole consisting of two stout teeth. Metasternal process a pair of elongate, narrowly triangular spines. Mesotibial spur pectinate. (Malesian)*hamulatus* group
- Ventral process of petiole consisting of a single keel. Metasternal process a pair of low rounded tumuli or low triangular crests. Mesotibial spur simple to weakly barbate. (Neotropical)..... *brachycola* group

I Afrotropical species

Key to Afrotropical species (workers)

NOTE. The few known queens will also run in this key, except characters relating to shape of mesosoma in workers do not apply to queens.

- 1 Mesotibia with two spurs. Metatibia with two spurs, the anterior spur smaller and simple, the posterior spur larger and pectinate. Propodeal spiracle high on side, close to dorsal outline and at about the midlength of the sclerite. Pronotum not marginate anterodorsally. In profile the propodeal dorsum continues the line of the mesonotal dorsum. Subpetiolar process large, keel-shaped. Metasternal process bispinose. Polymorphic species. (*bequaerti* group)2
- Mesotibia without spurs. Metatibia with a single large pectinate spur only. Propodeal spiracle low on side, far from dorsal outline. Pronotum marginate anterodorsally. In profile the propodeal dorsum slopes steeply down from the line of the mesonotal dorsum. Subpetiolar process a short slender spine or small

- triangular tooth. Metasternal process not bispinose. Monomorphic species. (*feae* group)3
- 2 With mesosoma in profile the bulla of the metapleural gland is short and does not extend to near the base of the propodeal spiracle. Metatibia with spiniform setae such as are seen on the mesotibia. Protibia ventrally with a single stout spiniform seta, similar to those on the mesotibia, located close to the apex on its outer surface, anterior to and opposite the large spur. (Cameroun, Gabon, Central African Republic, Democratic Republic of Congo, Angola, Malawi, Zambia, Zimbabwe) *bequaerti*
- With mesosoma in profile the bulla of the metapleural gland is long and extends to, or even touches, the base of the propodeal spiracle. Metatibia without spiniform setae such as are seen on the mesotibia. Protibia ventrally without a stout spiniform seta that is similar to those on the mesotibia, at most a simple slender seta located close to the apex on its outer surface, anterior to and opposite the large spur. (Gabon) *secutor*
- 3 Petiole node in dorsal view conspicuously broader than long4
- Petiole node in dorsal view at least as long as broad, usually distinctly longer than broad9
- 4 Apical third of metatibia with a total of more than 3 thickly spiniform setae that arise from its anterior surface opposite the pectinate spur; one or more thickly spiniform setae also arise from the dorsal (outer) surface of the metatibia in the apical third of its length5
- Apical third of metatibia with only 1–2 (extremely rarely 3) thickly spiniform setae that arise from the apex of its anterior surface, opposite the pectinate spur; no thickly spiniform setae arise from the dorsal (outer) surface of the metatibia in the apical third of its length6
- 5 Mandible with 5–6 main teeth that are separated by diastemata, the latter are unarmed or have indistinct low crenulations present. With base of gaster in absolute profile the prora is visible as a distinct raised cuticular crest that extends from the base of the helcium onto the anteroventral surface of the first gastral sternite. Smaller species with narrower head and shorter mandibles, HW 1.20–1.34, PW 0.94–1.12, CI 102–105, MI 71–75. (Cameroun, Gabon, Democratic Republic of Congo) *decessor*
- Mandible serially dentate, with 10–12 teeth; all teeth are similar in size and without diastemata separating them. With base of gaster in absolute profile the prora is undeveloped, lacking a raised cuticular crest that extends from the base of the helcium onto the anteroventral surface of the first gastral sternite. Larger species with much broader head and longer mandibles, HW 1.92–2.02, PW 1.50–1.62, CI 119–123, MI 82–84. (Zambia, Zimbabwe) *raptor*
- 6 Anterior apex of metatibia with a single thickly spiniform seta, approximately opposite the pectinate spur. (Liberia, Ivory Coast, Ghana, Cameroun, Gabon, Central African Republic, Democratic Republic of Congo, Angola) *angolensis*
- Anterior apex of metatibia with two thickly spiniform setae, approximately opposite the pectinate spur. 7
- 7 CI 108–118; at low magnification and in full-face view the head capsule appears conspicuously broader than long. Mandibles relatively slightly longer, MI 68–75. Larger species, HW 0.90–1.13. (Guinea, Ivory Coast, Ghana, Nigeria, Cameroun, Gabon, Democratic Republic of Congo, Uganda, Kenya, Zambia, Mozambique, Zimbabwe) *sellaris*
- CI 98–101; at low magnification and in full-face view the head capsule appears slightly longer than broad or about as long as broad. Mandibles relatively slightly shorter, MI 59–64. Smaller species, HW 0.65–0.818
- 8 With mesosoma in profile the slope of the anterior portion of the propodeum is steep and slopes abruptly from the mesonotum. Smaller species, HW 0.65–0.68, WL 1.06–1.14. (Cameroun, Gabon) .. *longiventris*
- With mesosoma in profile the slope of the anterior portion of the propodeum is shallow and slopes only weakly from the mesonotum. Larger species, HW 0.79–0.81, WL 1.31–1.34. (Gabon, Central African Republic, Democratic Republic of Congo) *ereptor*
- 9 Basal margin of mandible, from basal tooth to basalmost curve, shallowly convex; basal margin much shorter than masticatory margin. Larger species, HL 1.06, HW 0.99, PW 0.82. (Democratic Republic of

- Congo)*praedator*
- Basal margin of mandible, from basal tooth to basalmost curve, shallowly concave; basal margin almost equal in length to masticatory margin. Smaller species, HL < 0.90, HW < 0.85, PW < 0.70. (Democratic Republic of Congo, South Africa).....*fugator*

***Centromyrmex bequaerti* group**

Worker and queen (gyne). A small group of two Afrotropical species. Workers are known for both, the queen is known for *bequaerti*. Workers and queens with characters of the genus, listed above, and also the following characters diagnostic of the group, of which apomorphies are in *italics*.

Worker caste polymorphic.

Mandibles short, triangular (MI < 40 in workers) and with 4–7 teeth, the apical tooth differentiated and inflected.

Pronotum without margination either anteriorly or laterally.

Mesosoma in profile with dorsum of propodeum continuing the line of the mesonotum, the former not sloping steeply away from the latter.

Mesonotum behind promesonotal suture not elevated, not transversely marginate.

Metasternal process present as a pair of narrow erect spines that are very closely approximated and nearly parallel; the metasternal pit is between the spines posteriorly.

Propodeum in dorsal view broad, not strongly bilaterally compressed.

Propodeal spiracle in worker very high on the side and at about the midlength of the sclerite; orifice of spiracle long, slit-shaped.

Propodeal lobes low and rounded.

Procoxa not hypertrophied, only slightly larger than mesocoxa and metacoxa.

Mesotibia with two spurs: in all worker sizes the anterior spur is small, simple to barbate. The posterior (main) spur is pectinate in large workers, but the pectination decreases with reduced size until, in the smallest workers, the spur is only barbate.

Metatibia with two spurs: in all worker sizes the anterior spur is small, simple to barbate. The posterior (main) spur is always broadly pectinate.

Petiole without an anterior peduncle; in profile the anterior face of the node rises from directly behind the anterolateral cuticular processes that protect the articulation.

Petiole node in profile becomes longer and lower as body size decreases.

Subpetiolar process large, roughly keel-like.

Prora conspicuous in profile as an elevated, roughly vertical ridge; in anterior view prora forms a transverse plate (slightly indented centrally) across the entire anterior face of the first gastral sternite.

Sculpture extremely reduced, the ants very smooth and shiny.

Standing setae present on all dorsal surfaces of head and body in worker, including dorsal surface of scape. Setae also present on ventral head and gastral sternites.

Queen only (*bequaerti*). Large eyes and conspicuous ocelli present. Mesosoma with full complement of flight sclerites. Transverse suture present on mesopleuron (absent or vestigial in workers except in largest examples of *bequaerti*, where it is weakly delineated). Propodeal spiracle slit-shaped and close to metanotal-propodeal suture. Jugal lobe present on hindwing. Petiole node in profile much higher than long.

Comment

At first glance the species of the *bequaerti* group appear quite different from those of the *faae* group, and when taken in isolation their differences are arguably of genus-rank significance. However, the Malesian spe-

cies *hamulatus* forms an almost perfect morphological intermediate between the two groups. For distribution of shared and independent characters see under *hamulatus*, below.

Species of *bequaerti* group

Centromyrmex bequaerti (Forel)

(Figs 1–4)

Glyphopone bequaerti Forel, 1913: 308, fig. 1. Holotype queen, DEMOCRATIC REPUBLIC OF CONGO: Kasongo (Pons) (MHNG) [examined]. [Combination in *Centromyrmex* by Brown, 1963: 10.]

Glyphopone (Leptopone) rufigaster Arnold, 1916: 163, figs 10, 10a. Holotype queen, ZIMBABWE: Victoria Falls (*G. Arnold*) (not in BMNH or SAMC) (see note). [Combination in *Leptopone* by Wheeler, W.M. 1922: 766; in *Centromyrmex* and synonymy with *bequaerti* by Brown, 1963: 10.]

NOTE. The holotype of *rufigaster* cannot be found. Comparison of the original description of *rufigaster* with the holotype of *bequaerti* and all of the more recent queen material of the latter has produced no reason to doubt Brown's synonymy.

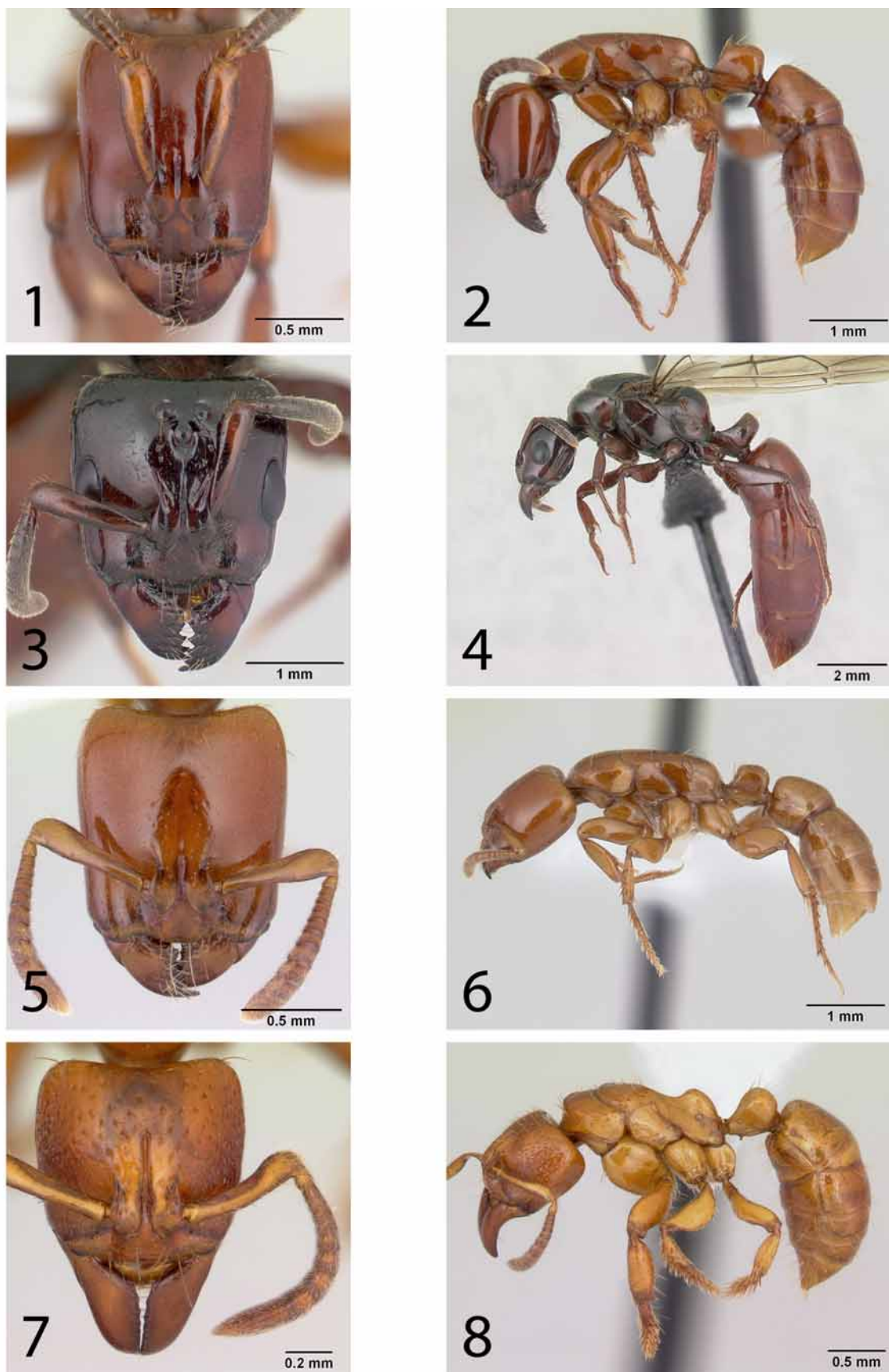
WORKER (not previously described). TL 4.7–10.3, HL 0.99–2.04, HW 0.80–1.86, CI 81–93, ML 0.26–0.70, MI 28–38, SL 0.50–1.08, SI 60–68, PW 0.57–1.28, WL 1.50–2.84 (20 measured).

With characters of the genus and the *bequaerti* group. Mandible smooth, with scattered small pits and 5–7 teeth of which the apical is the largest. Number of teeth on mandible decreases with reduced size, from a maximum of 7 in largest workers to a minimum of 5 in smallest examined; the most common dental count is 5. Entire head, including ventral surface, smooth and shining, with scattered small pits. Bulla of metapleural gland conspicuous, low, its apex widely separated from the base of the propodeal spiracle. Protibia ventrally with a conspicuous single stout spiniform seta, similar to those on the mesotibia, this seta located close to the apex on its outer surface, anterior to and opposite the large spur. Spiniform setae present dorsally on mesotibia, mesobasitarsus, metatibia and metabasitarsus, most sparse on the metatibia. Petiole in largest workers (HW *ca* 1.86) with length of the tergite in profile $0.73 \times$ the height of the tergite at its mid-length; in the smallest workers (HW *ca* 0.80) the length of the tergite in profile is $1.15 \times$ the height of the tergite at its mid-length. In effect, the petiole tergite is higher than long in larger workers, longer than high in smaller workers. Mesosoma, petiole and gaster shiny, unsculptured except for setal pits and, in larger workers, some weak striation on the metapleuron. Pubescence almost absent, extremely sparse, short and inconspicuous except on pronotal collar, propleuron, and sternite of petiole. Colour yellow to deep dull red; smaller workers usually lighter in colour than larger workers.

QUEEN. TL 14.0–15.6, HL 1.96–2.24, HW 1.84–2.24, CI 96–100, OI 29–31, ML 0.74–0.84, MI 34–39, SL 1.14–1.26, SI 55–60, PW 1.85–2.25, WL 3.70–4.70 (5 measured). Somewhat larger than largest workers in associated series. Queens will run out to the correct species using the characters provided in the key to workers except for the position of the slit-shaped propodeal spiracle, which is somewhat lower on the side in queens than in workers.

MALE. Known; see under diagnosis of genus.

This widespread species is worker polymorphic, polygynous and an obligate predator of termites, especially of the subfamilies Termitinae and Macrotermitinae (Dejean & Fénelon, 1996, 1999). These authors also describe the organisation of *bequaerti* colonies within termitaries, saying that each queen of the polygynous colony, accompanied by a number of workers, occupies a separate chamber in the host termitary. From data labels of material examined *bequaerti* has been recorded from termitaries of the following genera: *Amitermes*, *Coactotermes*, *Cubitermes*, *Furculitermes*, *Odontotermes*, *Trinervitermes* and *Tuberculitermes*. Dejean *et al.*,



FIGURES 1–8. Full face and lateral view of body. Figs 1–2: *Centromyrmex bequaerti* worker CASENT0005922; Figs 3–4: *C. bequaerti* queen CASENT006695; Figs 5–6: *C. secutor* paratype worker CASENT0178749; Fig. 7–8: *C. angolensis* worker CASENT0417147.

(1996, 1997) record it as common in nests of *Cubitermes*, but the species was not found in nests of *Proculitermes* (Dejean & Bolton, 1995). It has also been collected from rotten logs and occasionally from samples of leaf litter.

Material examined. **Cameroun:** Ebodjie (A. Dejean); Abong-Mbang (A. Dejean); Pan Pan (A. Dejean); Bakundu (A. Dejean). **Gabon:** La Makandé, Forêt des Abeilles (S. Lewis); CNRS Makokou (W.H. Gotwald); Plateau d'Ipassa (J.A. Barra); Prov. Ogooue-Maritime, Res. Monts Doudou, NW Doussala (B.L. Fisher); Prov. Woleu-Ntem, ESE Minvoul (B.L. Fisher). **Central African Republic:** Pref. Sanghu-Mbaéré, Parc. Nat. Dzanga-Ndoki, Mabéa Bai (B.L. Fisher). **Democratic Republic of Congo:** Keyberg (A.E. Emerson); Yangambi Reserve (Raignier & van Boven); Stanleyville [= Kisangani] (N.A. Weber); NE Labefu (Ross & Leech); Kikwit, Kinzambi (A. Dejean); Kasongo (Pons). **Angola:** Dundo to Chingofu (Kistner & Swift); Capemba, nr Dundo (Kistner & Swift); Dundo, R. Mussungue (Kistner & Swift); R. Mussungue, nr Calondo, Res. de Gado (Kistner & Swift); Mussungue Forest, nr Dundo (Kistner & Swift); Santa Comba to N. Lisboa (D.H. Kistner). **Malawi:** SW shore Lake Nyasa, betwn Fort Johnston and Monkey Bay (S.A. Neave); Kasungu, Mtunthama (J. Feehan). **Zambia:** Lunda, Congo border (H.S. Evans); Lusaka, Leopard Hill (B.L. Fisher); Choma (B.L. Fisher).

Centromyrmex secutor Bolton & Fisher sp. n.

(Figs 5–6)

HOLOTYPE WORKER. TL 6.9, HL 1.38, HW 1.26, CI 91, ML 0.46, MI 33, SL 0.80, SI 63, PW 0.91, WL 2.00.

With characters of the genus and the *bequaerti* group; answering the description of *bequaerti* in all except the following characters:

Bulla of metapleural gland is hypertrophied and extends anterodorsally to the base of the propodeal spiracle, which it just fails to touch (see comments under paratypes).

Protibia ventrally lacks a stout spiniform seta that is similar to those on the mesotibia; at most there is a simple slender seta located close to the apex on its outer surface, anterior to and opposite the large spur.

Spiniform setae are absent from the metatibia.

Pubescence is present on declivity of propodeum, especially near its base; the pubescence is more obvious in smaller than in larger workers.

Dorsum of the mandible with a flattened area just distal of the basal groove and the flattened area has a distinctly crowded patch of minute punctures.

PARATYPE WORKERS. TL 4.5–7.3, HL 0.86–1.45, HW 0.69–1.38, CI 80–95, ML 0.28–0.50, MI 30–34, SL 0.46–0.80, SI 58–67, PW 0.54–0.98, WL 1.36–2.10 (10 measured).

The mandible has 5 teeth in larger workers (including the holotype) but only 4 in the smallest workers. It is not certain that the largest worker morph has been found, so larger workers may have more than 5 teeth. In most paratypes the bulla of the metapleural gland reaches the base of the propodeal spiracle.

QUEEN and MALE: unknown.

Holotype worker. **Gabon:** La Makandé, Forêt des Abeilles, i.–ii.1999 (S. Lewis) (BMNH).

Paratypes. 15 workers with same data as holotype (BMNH, CASC, MCZC).

This species is closely related to *bequaerti* and shows the same polymorphic variations in the worker, but the two species differ consistently in the characters listed above in all worker sizes. As in *bequaerti* the petiole tergite of *secutor* in profile is distinctly higher than long in large workers, and very obviously longer than high in smaller workers.

Centromyrmex feae group

Eight Afrotropical species and the extralimital species *C. feae*, from the Oriental and Malesian regions, form a group of closely related species, the *feae* group, named for its first-described member. Workers and queens with characters of the genus, as listed above, and also with the following characters diagnostic of the group, of which apomorphies are in *italics*.

Worker and queen (gyne)

Mandible elongate-triangular and strongly downcurved (MI 52–84 in workers). Mandible pointed at apex but the point continues the line of the long axis of the mandible; there is no differentiated inflected apical tooth.

Mid-points of frontal lobes in workers separated medially by a narrowly triangular strip of cuticle, the mid-points of the lobes conspicuously not touching.

Frontal groove on mid-dorsum of head is broad and extends far posterior of the terminus of the frontal lobes.

Pronotum marginate anterodorsally; pronotal dorsum forms a plateau behind the anterior margination.

Mesosoma in profile with anterior portion of propodeum sloping down from the mesonotum so that the posterior half of the propodeal dorsum is on a much lower level than the mesonotal dorsum (worker only).

Metanotal groove absent (worker only).

Metasternal process absent. A thickly rounded oblique tumulus of cuticle arises on each side of the fully exposed metasternal pit; the tumuli diverge posteriorly and terminate at the metacoxae.

Propodeum unarmed, in dorsal view bilaterally compressed so that the dorsum is narrow.

Propodeal lobes extremely reduced to vestigial.

Orifice of propodeal spiracle subcircular to elliptical, abutting the bulla of the low metapleural gland.

Petiole with at least a short anterior peduncle.

Subpetiolar process small, in profile a short, slender spine or a small, acutely triangular tooth.

Procoxa hypertrophied, very swollen and much larger than the mesocoxa and metacoxa; in profile procoxa >> mesocoxa > metacoxa.

Protibia swollen and disproportionately large.

Protarsal segments 2–4 very strongly expanded laterally, deeply V-shaped, the apices of the V terminating in a very coarse spiniform seta on each side.

Mesotibia with spurs absent.

Metatibia with a single, large pectinate spur.

Metabasitarsus very short, at most only about half the length of the metatibia.

Prora represented by a pair of weakly divergent ridges on anterior face of first gastral sternite, one on each side below the helcium; space between the ridges shallowly concave (extremely reduced in *raptor*).

Scapes and all dorsal surfaces of head and body with standing setae present except for sloping portion of propodeum, where they are completely absent, and posterior propodeal dorsum, where they are absent or represented by one to a few very short standing setae. Pubescence generally sparse to absent.

Queen only. Transverse suture present on the mesopleuron that divides the sclerite into anepisternum and katepisternum (absent in workers). Mesosoma with full complement of flight sclerites. Hind wing with jugal lobe present.

Comments

In most worker specimens the mesonotum appears to have a short elevated face immediately behind the promesonotal suture, and the top of this elevated face is usually equipped with a transverse margination. However, in isolated specimens within series the elevated face is absent. It is suspected that when the pronotum is fully flexed upward, the posterior margin of the pronotum slides up the short elevated anterior section of the

mesonotum until the dorsal surfaces of the two sclerites are on the same level.

The habitus of *fae* group workers is distinctive, the most striking feature being the strange morphology of the legs. The forelegs appear fossorial and the middle and hind legs squat and spiny. All six are short, strong, and powered by the enormously developed coxae, especially the hypertrophied procoxae. Add to this the eyeless head with elongate-triangular, downcurved mandibles, extremely flattened scapes, anteriorly marginate and plateau-like pronotum, strongly sloping anterior portion of propodeum in profile and bilaterally compressed anterior propodeal dorsum, and the result is an appearance that is unlikely to be confused with any other ponerine ant in the region.

Afrotropical species of *fae* group

Centromyrmex angolensis Santschi stat. n.

(Figs 7–10)

Centromyrmex constanciae var. *angolensis* Santschi, 1937: 214. Holotype worker, ANGOLA: Sangévé (A. Monard) (NHMB) [examined]. **Stat. n.**

WORKER. TL 4.3–6.2, HL 0.76–0.98, HW 0.78–1.00, CI 98–103, ML 0.49–0.70, MI 63–71, SL 0.58–0.74, SI 69–76, PW 0.58–0.82, WL 1.26–1.70 (30 measured).

With characters of the genus and the *fae* group. Head capsule in full-face view usually appears slightly longer than broad, sometimes about as long as broad, CI 103 or usually less. Mandibles smooth with scattered small punctures. Masticatory margin of mandible with 7–10 small, low indistinct teeth, reduced to mere crenulations or even more or less smooth in the proximal half when worn. Basal angle of mandible rounded, frequently without trace of a basal tooth but sometimes with a vestigial tooth. Dorsum of head with scattered punctures on smooth cuticle; on sides of head the punctures denser than on dorsum, and also with weak striation within the antennal fossae and on the sides, especially anteriorly. Extent of the striate component is variable. Metatibia with only normal setae dorsally but its anterior surface, at the apex and approximately opposite the pectinate spur, with a single, much stouter and sometimes more darkly coloured spiniform seta. Petiole node in dorsal view broader than long. Pronotal dorsum, and anterior mesonotum, with widely scattered broad, shallow punctures that may be almost effaced. Pronotum dorsally also usually with variable weak oblique or arched faint disorganised sculpture, almost effaced in some specimens. Colour yellow to light brown.

QUEEN. TL 6.0–6.4, HL 0.94–0.96, HW 0.98–1.02, CI 104–106, OI 31–32, ML 0.63–0.65, MI 66–68, SL 0.70–0.74, SI 71–73, PW 0.94–0.96, WL 1.88–1.94 (4 measured). Very similar to the worker but the head averaging slightly broader. The queen will run out successfully in the key to workers. The unique worker character of a single thickly spiniform seta at the anterior apex of metatibia is duplicated in the queen caste.

MALE. Known; see under diagnosis of genus.

Closely related to *sellaris* but worker and queen always with just a single spiniform seta at the inner apex of the metatibia, and always with a narrower head. In addition, the basal dentition of the mandible of *angolensis* can usually be distinguished from that of *sellaris*, as discussed under the latter name.

Recorded on specimen data labels from termitaries of *Apitermes* and *Protermes*, though the range of prey is probably much wider.

Material examined. **Liberia:** Reputa (W.M. Mann). **Ivory Coast:** For. de Teke, Anyama (*T. Diomande*); F.C. Cavally (*K. Yeo*). **Ghana:** Mt Atewa (*R. W. Taylor*). **Cameroun:** Kala (*A. Dejean*); Mbalmayo (*N. Stork*); Prov. Sud, P.N. Campo, ESE Campo (*B.L. Fisher*). **Gabon:** CNRS Makokou (*W.H. Gotwald*); Plateau d'Ipassa (*J.A. Barra*); Prov. Woleu-Ntem, ESE Minvoul (*B.L. Fisher*); Prov. Ogooue-Maritime, Res. Moukalaba, NW Doussala (*B.L. Fisher*). **Central African Republic:** P.N. Dzanga-Ndoki, NE Bayanga (*B.L. Fisher*);



FIGURES 9–16. Full face and lateral view of body. Figs 9–10: *Centromyrmex angolensis* queen CASENT0417149; Figs 11–12: *C. decessor* holotype worker CASENT0178744; Figs 13–14: *C. ereptor* holotype worker CASENT0081171; Figs 15–16, *C. fugator* paratype worker CASENT0178747.

P.N. Dzanga-Ndoki, Lidjombo (*B.L. Fisher*). **Democratic Republic of Congo**: Epulu (*A.E. Emerson*); Epulu (*S.D. Torti*); Epulu (*Ross & Leech*); NW Kolwesi (*Ross & Leech*); Yangambi Reserve (*Raignier & van Boven*). **Angola**: Sangévé (*A. Monard*).

***Centromyrmex decessor* Bolton & Fisher sp. n.**

(Figs 11–12)

HOLOTYPE WORKER. TL 7.9, HL 1.28, HW 1.34, CI 105, ML 0.94, MI 73, SL 0.94, SI 70, PW 1.12, WL 2.32.

With characters of the genus and the *fae* group. Masticatory margin of mandible with 5 low-triangular blunted teeth separated by feebly concave diastemata that are much longer than the teeth are high. Margins of diastemata are unarmed or have reduced denticles or crenulation between the main teeth. Mandibles smooth with scattered small punctures. Head capsule slightly broader than long in full-face view. Dorsum of head with scattered punctures on smooth cuticle, the punctures denser on the sides of the head, especially anteriorly, and also with weak striation or punctate-striation within the antennal fossae. Pronotum more sharply marginate anteriorly, more bluntly laterally. Pronotal dorsum a flat to shallowly convex plateau behind the margination. Mesonotum weakly marginate behind the promesonotal suture. In profile the sloping face of the propodeum behind the mesonotum forms a long, deep concavity and the posterior propodeum is raised into a distinct tumulus. Metatibia with a few darkly coloured spiniform setae near the apex of the dorsum, and with similar but more numerous setae on the apical third of the anterior surface. Orifice of propodeal spiracle higher than wide but elliptical, not slit-shaped. Petiole node in dorsal view broader than long. Subpetiolar process short-spiniform. Petiolar spiracle on the peduncle, at base of anterior face of node. Pronotal dorsum, and anterior mesonotum, with widely scattered broad, shallow punctures that may be almost effaced. Pronotum also with vestiges of some very weak oblique costulae. Colour glossy brownish yellow to light brown, the head and mandibles darkest, the gaster lightest in shade.

PARATYPIC AND NON-PARATYPIC WORKERS. TL 7.0–7.9, HL 1.18–1.30, HW 1.20–1.34, CI 102–105, ML 0.85–0.96, MI 71–75, SL 0.84–0.96, SI 70–75, PW 0.94–1.12, WL 2.04–2.34 (11 measured). As holotype but mandible with 5–6 larger teeth. Sculpture of pronotum and anterior mesonotum dorsally is variable. In some the punctures are more sharply defined than in others, and the weak pronotal costulae may be easily visible to almost effaced. In the most weakly sculptured individuals the punctures are little more than vague depressions in the surface.

QUEEN. TL 9.3–9.80, HL 1.36–1.40, HW 1.42–1.43, CI 102–104, OI 28–29, ML 0.96, MI 69–71, SL 1.35–1.38, SI 70–71, PW 2.84–2.86 (2 measured). The queen will run out in the key to workers. In particular, the unique dentition of the worker is duplicated in the queen caste.

MALE. Known; see under diagnosis of genus.

Holotype worker (top specimen of three on pin), **Gabon**: Prov. Woleu-Ntem, 31.3 km. 108° ESE Minvoul, 2°04.8'N, 12°24.4'E, 600 m., 14.ii. 1998, # 1716-1, ex rotten log, rainforest (*B.L. Fisher*) (CASC).

Paratypes. 4 workers with same data as holotype (2 are middle and bottom specimens on same pin as holotype); 2 workers with same data but # 1699-1; 1 worker with same data but # 1719-1; 1 worker with same data but # 1725-2 (CASC).

The dentition of the mandible is unique among Afrotropical species. The number of thickened spiniform setae on the anterior surface of the metatibia varies from 5 to 7, but 6 appears to be the number most commonly encountered, all located on about the apical third of the length of the metatibia. *C. decessor* is easily separated from the much larger *raptor* by the characters noted in the key.

Non-paratypic material examined. **Cameroun**: Ottotomo (*A. Dejean*); Kala (*A. Dejean*). **Democratic Republic of Congo**: (Zaire (Congo) on data label) Yangambi Reserve (*Raignier & van Boven*); N of Kapona (*Ross & Leech*).

***Centromyrmex ereptor* Bolton & Fisher sp. n.**

(Figs 13–14)

HOLOTYPE WORKER. TL 4.5, HL 0.81, HW 0.79, CI 98, ML 0.52, MI 64, SL 0.57, SI 72, PW 0.62, WL 1.31.

With characters of the genus and the *feae* group. Head capsule in full-face view appears about as long as broad, or slightly longer than broad, CI 98–101 in material examined. Mandibles smooth with scattered minute punctures. Masticatory margin of mandible weakly crenulate. Basal angle of mandible rounded, without a differentiated basal tooth. Dorsum of head with scattered punctures on smooth cuticle; the punctures on sides of head denser than on dorsum, and also with weak striation within the antennal fossae and on the sides, especially anteriorly. Metatibia with only normal setae dorsally but its anterior surface, at the apex and approximately opposite the pectinate spur, with two much stouter spiniform seta with bases close together. With mesosoma in profile the dorsal outline of the propodeum slopes only shallowly downward from the mesonotum; the more or less flat mesonotum passes into the sloping propodeum through a smooth, shallow curve. Petiole node in dorsal view broader than long. Pronotal dorsum with distinct broad, shallow foveolate punctures, the spaces between them with weakly rugulose superficial sculpture. Anterior mesonotum also with a few widely scattered broad, shallow punctures, but these are more sparse and less distinct than on the pronotum. Colour a light brownish yellow.

NON-PARATYPIC WORKERS. TL 4.5–4.6, HL 0.78–0.82, HW 0.79–0.81, CI 99–101, ML 0.48–0.52, MI 59–64, SL 0.57–0.58, SI 72–74, PW 0.62–0.64, WL 1.30–1.34 (3 measured). As holotype.

QUEEN and MALE: unknown.

Holotype worker, **Central African Republic**: Res. Dzanga-Sangha, 12.7 km. 326° NW Bayanga, 3°00'N, 16°12'E, 420 m., 10–17.v.2001, #4083, CASENT 0081171, pitfall trap, rainforest (*B.L. Fisher*) (CASC).

Resembling *longiventris* but larger and with a much more shallowly sloped anterior propodeum; see notes under *longiventris*.

Non-paratypic material examined. **Gabon**: Plateau d'Ipassa (*J.A. Barra*). **Democratic Republic of Congo**: (Zaire on data label) Yangambi Reserve (*Raignier & van Boven*).

***Centromyrmex fugator* Bolton & Fisher sp. n.**

(Figs 15–16)

HOLOTYPE WORKER. TL 4.7, HL 0.78, HW 0.73, CI 94, ML 0.56, MI 72, SL 0.50, SI 68, PW 0.58, WL 1.30.

With characters of the genus and the *feae* group. Head capsule in full-face view longer than broad, the sides extremely shallowly convex, almost straight and feebly converging anteriorly. Mandibles smooth with scattered small punctures. Masticatory margin of mandible with about 10 very small, inconspicuous low, broad teeth, the basal tooth discernible. Proximal of the basal tooth the basal margin is shallowly concave and almost as long as the masticatory margin. Dorsum of head with scattered punctures on smooth cuticle; on sides of head the punctures no denser than on dorsum; there are also some vestigial remnants of punctulate to striolate sculpture within the antennal fossae and anteriorly on the sides. Anterior margination of pronotum blunt, not a sharply defined rim; sides of pronotum not marginate. Dorsal surface of metatibia with 3–4 spiniform setae near the apex, without others located more proximally on the dorsum. Anterior surface of metatibia with 4–5 spiniform setae, all located near the apex. Petiole node in dorsal view longer than broad, the node narrow anteriorly and becoming broader posteriorly. Pronotal dorsum with coarse shallow punctures and low, transversely arched, shallow broad rugulae. Mesonotal dorsum mostly smooth, with a few widely scattered small punctures. Colour yellow to light brownish yellow.

PARATYPE AND NON-PARATYPIC WORKER. TL 4.7–4.8, HL 0.80–0.84, HW 0.77–0.78, CI 93–96, ML 0.58–0.62, MI 73–74, SL 0.52–0.54, SI 68–69, PW 0.60, WL 1.36 (2 measured). Paratype as holotype but the non-paratypic worker with mandibular teeth very reduced, almost effaced, although the small basal tooth remains clearly visible. Sides of head in full-face view are somewhat more convex and converge both anteriorly and posteriorly.

QUEEN. TL 5.1, HL 0.81, HW 0.78, CI 96, OI 22, ML 0.64, MI 79, SL 0.54, SI 69, PW 0.65, WL 1.48. With the characteristic mandibular form of the worker and also with the petiole node distinctly longer than broad in dorsal view. The mesoscutum of the queen is much more coarsely and densely punctate than in the worker.

MALE: unknown.

Holotype worker, **Democratic Republic of Congo** (Zaire on data label): Kinshasa, 4.ii.1985 (*A. Dejean*) (BMNH).

Paratype, 1 worker with same data as holotype (CASC).

Closely resembling *praedator* but smaller and with different mandibular morphology; see the comments under *praedator*. The two collection localities are very far apart and probably have very different ecologies, but there is no doubt that only a single species is represented.

Non-paratypic material examined. **South Africa**: Gauteng Prov., Ezemvelo (*Hawkes & Clark*).

***Centromyrmex longiventris* Santschi stat. n.**

(Figs 17–18)

Centromyrmex sellaris var. *longiventris* Santschi, 1919: 229. Syntype worker, CAMEROUN: Victoria (*Silvestri*) (NHMB) [examined]. **Stat. n.**

WORKER. TL 3.5–3.6, HL 0.65–0.67, HW 0.65–0.68, CI 98–101, ML 0.38–0.40, MI 59–64, SL 0.48–0.50, SI 73–74, PW 0.50–0.56, WL 1.06–1.14 (4 measured).

With characters of the genus and the *faeae* group. Head capsule in full-face view usually appears about as long as broad, CI 101 or less. Mandibles smooth with scattered small punctures. Masticatory margin of mandible with 7–10 small, low indistinct teeth, reduced to mere crenulations or even more or less smooth when worn. Basal angle of mandible rounded, usually with a very small basal tooth visible but sometimes indistinct or vestigial, or with a slightly accentuated basal angle. Dorsum of head with scattered punctures on smooth cuticle; on sides of head the punctures denser than on dorsum, and also with weak striation within the antennal fossae and on the sides, especially anteriorly. Metatibia with only normal setae dorsally but its anterior surface, at the apex and approximately opposite the pectinate spur, with two much stouter and sometimes more darkly coloured spiniform seta whose bases are close together. With mesosoma in profile the dorsal outline of the propodeum is abruptly angled downward from the mesonotum, so that its anterior portion forms a steep slope. Petiole node in dorsal view broader than long. Pronotal dorsum, and anterior mesonotum, with a few widely scattered broad, shallow punctures that may be almost effaced. Pronotum dorsally also usually with variable weak oblique or arched faint disorganised sculpture; almost effaced in some specimens. Colour yellow to light brownish yellow.

QUEEN and MALE: unknown.

C. longiventris is closely related to *ereptor*. Both species superficially resemble small specimens of *angolensis*, but are easily separated as they have two spiniform setae at the anterior apex of the metatibia, where only one is present in *angolensis*. *C. longiventris* and *ereptor* are best distinguished by size and the shape of the anterior propodeum in profile. The former is smaller and the anterior portion of the propodeum forms a steep slope immediately behind the mesonotum, whereas the latter is larger and the anterior propodeum is



FIGURES 17–24. Full face and lateral view of body. Figs 17–18: *Centromyrmex longiventris* worker CASENT0178742; Figs 19–20: *C. praedator* worker CASENT0102928; Figs 21–22: *C. raptor* holotype worker CASENT0066716; Figs 23–24: *C. raptor* paratype queen CASENT0178746.

only shallowly and gradually sloped from the mesonotum. Only four specimens of this small species are known.

The name *longiventris* itself is misleading as the gaster here is proportionately no longer than in any other member of the group, but in the syntype examined the gaster is distended, probably from initial storage in alcohol that was too dilute.

Material examined. **Cameroun:** Victoria (*F. Silvestri*); Res. Dja (*K. Yeo*). **Gabon:** Plateau d'Ipassa (*J.A. Barra*).

***Centromyrmex praedator* Bolton & Fisher sp. n.**

(Figs 19–20)

HOLOTYPE WORKER. TL 6.4, HL 1.06, HW 0.99, CI 93, ML 0.82, MI 77, SL 0.72, SI 73, PW 0.82, WL 1.90.

With characters of the genus and the *feae* group. Head capsule in full-face view longer than broad, the sides almost straight and approximately parallel. Mandibles smooth with scattered small punctures. Masticatory margin of mandible almost smooth, weakly uneven, the teeth almost entirely effaced. Basal margin of mandible shallowly convex, distinctly shorter than the masticatory margin. Dorsum of head with scattered punctures on smooth cuticle; on sides of head the punctures denser than on dorsum, and also with very weak remnants of punctulate to striolate sculpture within the antennal fossae and anteriorly on the sides. Anterior margination of pronotum thick and bluntly rounded; sides of pronotum not marginate. Dorsal surface of metatibia with 4–5 spiniform setae near the apex and with 3–4 others located more proximally; the most proximal is at about the midlength. Anterior surface of metatibia with about a dozen spiniform setae, most located near the apex but some more basal. Petiole node in dorsal view longer than broad, the node narrow anteriorly and becoming much broader posteriorly. Pronotal dorsum with coarse shallow punctures that are linked by low, broad rugulae. Mesonotal dorsum mostly smooth, with a few widely scattered broad, shallow punctures. Colour yellow to light brownish yellow.

QUEEN and MALE: unknown.

Holotype worker, **Democratic Republic of Congo** (Zaire on data label): Bandundu, Kinzambi For., 25.iii.1985 (*A. Dejean*) (BMNH). [Holotype is damaged: left midleg and right hindleg are absent except for their coxae.]

As only a single specimen is known it is impossible to say whether the almost edentate condition of the mandible is normal or if the teeth have been worn down. The closest relative of *praedator* is *fugator*. They share a similar long petiole node that contrasts strongly to the usual transverse, broad short dorsal shape of *feae* group species, and this makes them immediately recognisable. The two are separated by size and the distinctly different form of their mandibles, as noted in the key and descriptions. Apart from this the metatibia of *praedator* appears to have many more spiniform setae than are seen in *fugator*, but as so little material is available the consistency of this character cannot be tested.

***Centromyrmex raptor* Bolton & Fisher sp. n.**

(Figs 21–24)

HOLOTYPE WORKER. TL 9.6, HL 1.60, HW 1.94, CI 121, ML 1.32, MI 83, SL 1.30, SI 67, PW 1.56, WL 2.96.

With characters of the genus and the *feae* group. Masticatory margin of mandible serially dentate, with 11–12 bluntly triangular low teeth that are all about the same size; distal one-fifth of masticatory margin eden-

tate. Mandibles heavily constructed and large, smooth with scattered small punctures. Head capsule very obviously broader than long in full-face view (range of CI 119–123). Dorsum of head with scattered punctures and with striation around the antennal fossae and on the anterior halves of the sides. Anterodorsal margination of pronotum strongly developed; margination extends around the sides almost to the posterior margin of the sclerite. Pronotal dorsum a flat plateau behind the margination. Mesonotum sharply marginate anteriorly, the margination extends along the sides above the mesopleuron. Sloping anterior portion of propodeum forms a shallow concavity basally, the posterior portion of the propodeum is slightly raised and broadly rounded behind it. Metatibia with darkly coloured spiniform setae on the apical third of the anterior surface, and with similar setae on the apical third of the dorsal surface. Orifice of propodeal spiracle much higher than wide, almost slit-shaped. Petiole node in dorsal view broader than long. Subpetiolar process short, acutely triangular. Petiolar spiracle near mid-height of anterior face of node. Prora extremely feeble, represented only by a pair of short, very low cuticular ridges on the anterior face of the first gastral sternite, on each side below the helcium; the prora hardly discernible in profile. Pronotal dorsum, and anterior mesonotum, with widely scattered broad, shallow punctures upon a weakly shagreenate surface. The mesonotum also shows weak traces of longitudinal sculpture within the marginate area. Colour predominantly mottled dull brownish red, most of dorsal mesosoma and parts of sides infuscated to blackish. Gaster more uniformly coloured and slightly lighter.

PARATYPIC AND NON-PARATYPIC WORKERS. TL 9.8–10.0, HL 1.56–1.68, HW 1.92–2.02, CI 119–123, ML 1.30–1.40, MI 82–84, SL 1.30–1.38, SI 66–69, PW 1.50–1.62, WL 2.88–3.08 (5 measured). Paratypes as holotype but the non-paratypic workers are paler in colour, with a dull yellow gaster and somewhat infuscated mesosoma, especially on the dorsum. Sculpture on the pronotal dorsum and on the mesonotum is similar to the type-series but fainter.

PARATYPE QUEENS. TL 10.2, HL 1.60, HW 1.88, CI 118, OI 24, ML 1.33, MI 83, SL 1.24, SI 66, PW 1.78, WL 3.20. One of the queens has two compound eyes but the other has the right eye present, the left eye entirely absent. Overall, the queens are darker in colour than the workers, the mesosoma being mostly black. The transverse mesopleural suture is conspicuous in both queens but absent from the workers. Queens will run out successfully using the key to workers.

MALE: unknown.

Holotype worker (upper specimen of two on pin, lower specimen is a dealate queen), **Zambia**: Lusaka, Leopard Hill, 12°33.29'S, 30°17.74E, 1300 m., 29.xi.–3.xii.2005, Miombo woodland, BLF#, 13554, CASENT 0066716 (*Fisher et al.*) (CASC).

Paratypes, 1 dealate queen with same data as holotype (lower specimen on pin); 1 worker and 1 alate queen with same data but 13555, CASENT 0066882; 1 worker with same data but 13551, CASENT 0066707 (CASC).

This is the largest Afrotropical member of the genus and its mesosoma the most darkly coloured outside the *bequaerti* group. Its dimensions, and the characters noted in the key, make *raptor* easily recognisable.

Non-paratypic material examined. **Zambia**: Lusaka (*M.G. Bingham*). **Zimbabwe** (Rhodesia on data label): Urungwe Matsikite (*M.G. Bingham*).

***Centromyrmex sellaris* Mayr**

(Figs 25–26)

Centromyrmex sellaris Mayr, 1896: 230. Holotype worker, CAMEROUN: no loc. 1891 (*Y. Sjöstedt*) (NHRS) [examined] (see note 1).

Centromyrmex constanciae Arnold, 1915: 38, pl. 2, fig. 14. Syntype workers and queen, ZIMBABWE: Bembesi, 24.iii.1913 (BMNH) [worker examined]. **Syn. n.** [Description of male: Arnold, 1926: 199.]

Centromyrmex arnoldi Santschi, 1919: 229, figs. a–d. Syntype workers and males, MOZAMBIQUE: Amatongas Forest,

ix.1917 (*G. Arnold*) (NHMB) [examined]. [Variety of *constanciae* by Santschi, 1920: 8. Synonymy with *constanciae* by Arnold, 1926: 199 (in text).] **Syn. n.**
Centromyrmex congolensis Weber, 1949: 5, figs. 3, 4. Holotype worker, DEMOCRATIC REPUBLIC OF CONGO: Niangara, 1.iii.1948 (*N.A. Weber*) (not in AMNH or MCZC, presumed lost; see note 2). **Syn. n.**
Centromyrmex arnoldi r. *guineensis* Bernard, 1953: 186, fig. 1d. Holotype worker, GUINEA: Mt Nimba, Nion, St.22, 700 m., 15.iv.1942 (*Lamotte*) (MNHN) [examined]. **Syn. n.** [Subspecies of *constanciae* by Bolton, 1995: 140.]

NOTES.

1 The unique holotype of *sellaris* was discovered by Dr Hege Vårdal in the NHRS collection, still preserved in alcohol after 117 years. The specimen was accompanied by three labels, two of which merely stated “Camerun” and “Sjöstedt” respectively. A larger and more informative label carried the information “Riksmuseets Entomologiska Afdelning. *Centromyrmex sellaris* Mayr n. sp. Typ. Kamerun, 1891. Colleg. Y. Sjöstedt”. The holotype has now been mounted upon a standard card point.

2 Although the holotype of *congolensis* appears to have been lost, it is possible that it may still be present but unrecognised in Weber’s material, either at AMNH or MCZC. Fortunately, the original description and figures are sufficient to allow identification of the taxon. For these reasons, and because the name is a junior synonym, a neotype has not been designated.

WORKER. TL 4.8–6.1, HL 0.84–0.98, HW 0.90–1.13, CI 108–118, ML 0.58–0.72, MI 68–75, SL 0.64–0.76, SI 67–73, PW 0.74–0.92, WL 1.54–1.80 (15 measured).

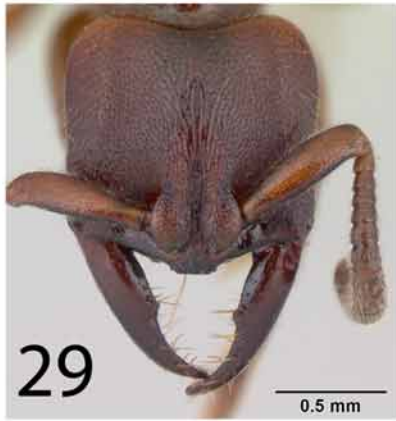
With characters of the genus and the *feae* group. Head capsule in full-face view always appears obviously broader than long, CI 108 or usually more. Mandibles smooth with scattered small punctures. Masticatory margin of mandible with 7–10 small, low blunt teeth that are usually broadly low-triangular but are often reduced to mere crenulations when worn. Basal tooth at basal angle of mandible and usually obvious, only rarely reduced and insignificant. Distal of the basal tooth there is usually a diastema before the next tooth on one or both of the mandibles, but sometimes this is not apparent as a denticle may be present within the diastema on one, or less often both, of the mandibles. Dorsum and sides of head with scattered punctures on smooth cuticle, and also with weak striation within the antennal fossae and on the sides, especially anteriorly. Extent of the striate component is variable. Metatibia with only normal setae dorsally but its anterior surface, at the apex and approximately opposite the pectinate spur, with 2 (3 in a single specimen) much stouter and usually more darkly coloured spiniform setae. Petiole node in dorsal view broader than long. Pronotal dorsum, and anterior mesonotum, with widely scattered broad, shallow punctures that may be almost effaced. Pronotum dorsally also with variable weak oblique or arched faint disorganised sculpture. Colour yellow to light brown.

QUEEN. TL 6.9, HL 1.01, HW 1.12, CI 111, OI 32, ML 0.70, MI 69, SL 0.80, SI 71, PW 1.11, WL 2.00. The queen of this species should run out correctly in the key to workers but care should be taken as the queens of *longiventris* and *ereptor* remain unknown. The form of the mandible described above for the worker is reproduced in the queen caste.

MALE. Known; see under diagnosis of genus.

This species and *angolensis* are the most widely distributed and most commonly encountered species of the *feae* group in Africa. Superficially the two look very similar, but *angolensis* always has a longer, narrower head and only ever has a single stout spiniform seta at the apex of the anterior surface of the metatibia, about opposite the pectinate spur. In addition, the basal mandibular tooth in *angolensis* is generally absent, sometimes vestigially present, but there is never the basal tooth + diastema arrangement that is characteristic of *sellaris*. Care should be taken with this character because of variation in development in *sellaris* but it is usually a good indicator of the species.

The species referred to as *C. sellaris* in Lévieux (1976, 1983) is correctly identified, as indicated by voucher specimens deposited in MCZC.



FIGURES 25–32. Full face and lateral view of body. Figs 25–26: *Centromyrmex sellaris* worker CASENT0066705; Figs 27–28: *Feroponera ferox* paratype worker CASENT0102994; Figs 29–30: *Promyopias silvestrii* worker CASENT0178751; Figs 31–32: *Promyopias silvestrii* queen CASENT0178752.

From data labels on specimens this species has been discovered in termitaries of the genus *Odontotermes*, but the true range of termite prey is undoubtedly much greater.

Material examined. **Guinea:** Mt Nimba, Nion (*Lamotte*). **Ivory Coast:** Lamto, Toumodi (*J. Lévieux*); Lamto (*K. Yeo*); Oumé, nr Goulikao (*S. Katia*); For. de Teke, Anyama (*T. Diomande*). **Ghana:** Tafo (*D. Leston*); Bunso (*D. Leston*); Kwadaso (*J. Plisko*). **Nigeria:** Gambari (*B. Bolton*); Gambari, CRIN (*B. Taylor*). **Cameroun:** no loc. (*Y. Sjöstedt*). **Gabon:** Prov. Woleu-Ntem, ESE Minvoul (*B.L. Fisher*). **Democratic Republic of Congo:** Mulungu (*F.L. Hendricks*); SW Pweto (*Ross & Leech*). **Uganda:** Iganga (*A. Abera*); SW Gulu (*Ross & Leech*); no loc. (*R.H. Le Pelley*). **Kenya:** Western Prov., Kakamega Forest, Shinyalu (*F. Hita Garcia*). **Mozambique:** Amatongas Forest (*G. Arnold*). **Zambia:** Lusaka, Leopard Hill (*B.L. Fisher*). **Zimbabwe:** Bembesi (*G. Arnold*); Bulawayo (*G. Arnold*); Lonely Mines (*H. Swale*).

II Oriental and Malesian species

Centromyrmex feae (Emery)

Spalacomyrmex feae Emery, 1889: 491 (worker). [Combination in *Centromyrmex* by Emery, 1890b: 40 (footnote).

Description of queen and male: Forel, 1900: 303; further description of male: Wheeler, 1936: 207. Senior synonym of *Centromyrmex donisthorpei* Menozzi, 1925: 443 (queen): synonymy by Brown, 1955: 103.]

Centromyrmex feae subsp. *ceylonicus* Forel, 1900: 303 (worker and male).

Centromyrmex feae subsp. *greeni* Forel, 1901: 325 (worker). [Originally described as *C. greeni*; reduced to subspecies of *feae* by Emery, 1911: 58.]

This is the nominal species of the mostly Afrotropical *C. feae* group, the diagnosis and discussion of which is given above. It is suspected that a close analysis of *feae* and its subspecies will reveal more than one real species concealed under this name.

Centromyrmex hamulatus (Karavaiev)

Typhloteras hamulatum Karavaiev, 1925: 129 (worker). [Combination in *Centromyrmex* by Brown, 1953: 8. Description of queen and male: Karavaiev, 1926: 419.]

This is currently the sole member of the *C. hamulatus* group and is quite widespread in the Malesian region. In morphological terms *hamulatus* forms a striking intermediary between the Old World species of the *bequaerti* group and the *feae* group, but it also has several apomorphies of its own.

i. Characters shared between workers of *hamulatus* and *bequaerti* group: shape of head capsule; close proximity of frontal lobes medially; non-swollen protibiae; lack of hypertrophy of procoxae; lack of pronotal margination; elongate slit-like orifice of propodeal spiracle; presence of spiniform metasternal process.

ii. Characters shared between workers of *hamulatus* and *feae* group: structure of mandible; dorsal outline shape of mesonotum and propodeum; position of propodeal spiracle; bilaterally compressed propodeal dorsum; petiole anteriorly pedunculate; form of prora; distribution of setae; monomorphic worker caste.

iii. Characters of *hamulatus* workers not shared by *bequaerti* or *feae* groups: mesotibia with 1 spur; metatibia with 1 spur; subpetiolar process a pair of stout teeth; mesopleuron with a weak transverse sulcus; constriction of second gastral segment strong and conspicuously cross-ribbed.

III Neotropical species

Centromyrmex alfaroi Emery, 1890b: 40 (worker). [Description of queen: Emery, 1906: 115.]

Centromyrmex brachycola (Roger)

Ponera brachycola Roger, 1861: 5 (queen). [Combination in *Centromyrmex* by Emery, 1890a: 74. Description of worker: Emery, 1906: 114. Senior synonym of *Centromyrmex bohemanni* Mayr, 1866: 895 (worker) and of *Centromyrmex brachycola* var. *paulina* Forel, 1911: 287 (worker): synonymies by Kempf, 1967: 405.]

Centromyrmex gigas Forel, 1911: 287 (worker). [Description of queen: Borgmeier, 1937: 223.]

The Neotropical fauna of *Centromyrmex* was last revised by Kempf (1967), who recognised the three species listed. It seems likely that more species now await description in the main collections of South American ants. The three species are currently regarded as a single group, weakly defined by the characters noted in the key to world groups, above, but further work may modify this arrangement.

In general the Neotropical species have mandibles shaped as in the *feae* and *hamulatus* groups, without a strongly developed, inflected apical tooth. An acute metasternal process is absent in *alfaroi*, where the structure of that part of the ventral mesosoma closely resembles that of the *feae* group: a pair of low, divergent tumuli. In *brachycola* the metasternal process is represented by a pair of widely separated, posteriorly divergent short crests that are low and triangular. Neither has the spiniform structure seen in the *hamulatus* and *bequaerti* groups. *C. alfaroi*, like *bequaerti* of the Afrotropical region, is known to be polygynous (Delabie, 1995).

Genus *Feroponera*

Feroponera Bolton & Fisher gen. n.

Type-species: *Feroponera ferox* sp. n., by present designation.

DIAGNOSIS OF WORKER

A monotypic Afrotropical genus.

1 Mandible with a basal groove but no basal pit; *cuticle of dorsum with a marked pale patch that is much lighter in colour, adjacent to teeth 4 + 5.*

2 Mandible subtriangular, short and stout (MI 37–38), with 5 teeth: *apical tooth the largest by far, curved and acute, strongly crossing over the opposing mandible at full closure; also at full closure a space is present between the masticatory margins posterior to tooth 3; preapical tooth reduced; third tooth triangular, the largest after the apical; fourth tooth triangular, smaller than third; fifth tooth smaller still; proximal of the fifth tooth the basal angle is abruptly but bluntly rounded.*

3 Palp formula 2,3; apical labial palpomere globular.

4 *Anterior clypeal margin on each side with a broadly triangular tooth that projects anteriorly over the basal margins of the closed mandibles.*

5 Frontal lobes confluent medially; in full-face view their anterior margins overhang the anterior clypeal margin except medially, where a small toothlike clypeal prominence is visible.

6 Mid-dorsal groove of head does not extend posterior of the terminus of the frontal lobes.

7 Eyes absent.

8 Antenna with 12 segments, *with a conspicuous 4-segmented club that is longer than SL.*

9 Pronotum marginate anteriorly, more bluntly so laterally.

10 Metanotal groove absent.

11 Orifice of metapleural gland posterior, near the posteroventral corner of the mesosoma.

12 Metasternal process a pair of separated elongate triangular teeth; metasternal pit located between them.

13 Propodeum unarmed, bilaterally compressed in dorsal view so that the dorsum is much narrower than the mesonotum.

- 14 Propodeal spiracle elliptical, low on the side, almost touching the dorsal margin of the metapleural gland bulla.
- 15 Propodeal lobes extremely reduced, rounded.
- 16 Procoxa much larger than mesocoxa and metacoxa.
- 17 Mesotibia, mesobasitarsus and metabasitarsus with stout spiniform traction setae (none on metatibia).
- 18 Mesotibia with 2 spurs, both simple.
- 19 Metatibia with 2 spurs: the anterior simple, the posterior large and broadly pectinate.
- 20 *Metatibial posterior surface with a slightly depressed broadly oval area of pale, very finely granular, cuticle that extends proximally from the base of the spur and appears to be glandular.*
- 21 Petiole sessile, without an anterior peduncle; subpetiolar process deep but blunt.
- 22 Helcium arises just below mid-height of anterior face of first gastral segment.
- 23 Prora a pair of insignificant ridges that arise on each side of the helcium base and extend weakly around the anteroventral corner of the first gastral sternite; anterior face of sternite between the ridges very feebly concave.
- 24 Constriction of second gastral segment conspicuous, weakly cross-ribbed.
- 25 Stridulitrum absent.

Discussion of worker characters

Apomorphic characters, in *italics* above, include 1 (pale mandibular patch), 2 (dentition), 4, 8 (antennal club) and 20. In some respects *Feroponera* workers are superficially similar to *Promyopias* workers but, as well as the different apomorphic characters of the two, *Feroponera* also differs markedly in characters 3, 5, 6, 15, 18 (mesotibial spurs) and 23. Characters 1–25 together form an inclusive diagnosis that isolates *Feroponera* workers from all other genera in the tribe.

1 A mandibular pale patch is very obvious in all workers. This patch of translucent cuticle on the mandible dorsally covers a much paler internal structure. The colour may be the result of a cavity within the mandible that is lined with paler tissue, or it may be made entirely of lighter internal tissue. The structure may be glandular, but this cannot be determined by light microscopy. The structure appears unique to *Feroponera*, but it should be mentioned that *Centromyrmex secutor* has a flattened area with a distinctly crowded patch of minute punctures in approximately the same position.

2 The form of the mandible and its dentition is unique. When the mandibles are fully closed the section that overlaps the opposite mandible extends to tooth 3. The overall impression is that of a shorter, stouter, much less extreme version of the mandibles exhibited by *Emeryopone*.

3 PF was obtained by dissection of one of the paratypes; the strangely reduced count is almost certainly apomorphic.

4 A similar pair of large clypeal teeth can be seen in the unrelated Neotropical genus *Dinoponera*. In the Afrotropical region *Streblognathus* and *Asphinctopone* have angular or dentate lateral corners to an extensive median clypeal lobe, but these do not correspond to the situation in *Feroponera* where no such lobe is developed.

5 The three genera *Centromyrmex*, *Promyopias* and *Feroponera* form a sequence in which the median clypeus reduces in length and the frontal lobes become progressively closer to the anterior margin.

8 The 4-segmented club is conspicuously much longer than the preceding 7 funicular segments together, and is much longer than the scape.

17 The presence and distribution of spiniform setae is duplicated in *Centromyrmex* and *Promyopias*: see discussion of potential genus group, below.

20 The position and shape of this depressed and apparently glandular area corresponds to that seen in the workers of *Diacamma* and in at least 25 Old World species of *Pachycondyla* (*sensu lato*; the feature does not appear in any New World species that we are aware of), but it is by no means universal even in Old World spe-

cies. We suspect that it is an independent development of this genus.

22 Position of the helcium is similar in *Centromyrmex* and *Promyopias*: see discussion of potential genus group, below.

23 Structure of the prora is basically the same as that seen in the *Centromyrmex feae* group.

***Feraponera ferox* Bolton & Fisher sp. n.**

(Figs 27–28)

HOLOTYPE WORKER. TL 3.7, HL 0.71, HW 0.63, CI 89, ML 0.27, MI 38, SL 0.38, SI 60, PW 0.43, WL 1.09.

With characters of the genus, and the following. Mandibles smooth with scattered small pits. Frontal lobes divided medially only by a line. The 4 segments of the antennal club are relatively long, together about 0.50 mm., twice as long as funicular segments 1–7 together and distinctly longer than SL. Dorsum of head densely but shallowly irregularly reticulate-rugulose to punctate-rugulose. Dorsal surface of scape with suberect pubescence that is quite dense, but without long, stout setae; leading edge of scape with sparse subdecumbent pubescence only. Dorsum of head with dense pubescence, without standing setae. Pronotal dorsum with shallow poorly defined punctures and also with arched-transverse low rugular sculpture that is best defined at the midline. Sculpture of mesonotal dorsum much reduced from that of pronotum, the propodeal dorsum smooth. PW 1.95 × the maximum width of the bilaterally compressed propodeal dorsum. Side of mesosoma with superficial fine shagreenate-striolate sculpture, densest on the pronotum; only the katapisternum smooth. Dorsal surface of metatibia without spiniform setae. Petiole node in profile narrowing dorsally, the dorsum extremely feebly convex and the posterodorsal angle more rounded than the anterodorsal. Subpetiolar process an obtusely triangular point. Anterior face of first gastral tergite vertical in profile, forming a distinct angle with the dorsal surface. Gasteral tergites 1–2 densely punctate, the sculpture fading out on tergites 3–4. Dorsum of pronotum and mesonotum with pubescence; dorsum of propodeum with pubescence reduced but with a few short slender setae present; dorsum of petiole with a few slender setae of varying lengths; gasteral tergites with pubescence and also a few longer setae, especially on tergites 4–5.

PARATYPE WORKERS. TL 3.5–3.8, HL 0.67–0.70, HW 0.59–0.62, CI 87–90, ML 0.25–0.27, MI 37–38, SL 0.36–0.39, SI 61–63, PW 0.43–0.46, WL 1.04–1.10 (4 measured). As holotype.

Holotype worker, **Cameroun**: Ndupe, 25.xi.1990, *Cubitermes* survey (A. Dejean) (BMNH).

Paratypes. 4 workers (one dissected) with same data as holotype (BMNH, CASC).

QUEEN and MALE: unknown.

The type-series was recovered from an abandoned termitary of *Cubitermes* and was recorded in Dejean, Durand & Bolton (1996) as “n. sp. (near *silvestrii*)”. The termitary was not occupied, and provides no evidence that the species is termitophagous, but the modified condition of the mandibles and clypeus implies that its diet is carnivorous and specialised.

Genus *Promyopias*

***Promyopias Santschi* gen. rev.**

Promyopias Santschi, 1914: 323 [as subgenus of *Myopias* by Forel, 1917: 238; as subgenus of *Pseudoponera* by Wheeler, W.M. 1922: 649. Raised to genus by Emery, 1915: 26; Santschi, 1924: 158. Provisional synonymy with *Centromyrmex* by Brown, 1973: 184; synonymy with *Centromyrmex* by Bolton, 1994: 164.] Type-species: *Myopias (Promyopias) silvestrii* Santschi, 1914: 324, by monotypy. **Gen. rev.**

DIAGNOSIS OF WORKER AND QUEEN (gyne)

A monotypic Afrotropical genus.

1 Mandible elongate and narrow (MI 55–60 in worker). Apex of mandible armed with a short vertical series of 3–4 small teeth (may be worn and indistinct). Apical half of inner margin of mandible concave. Basal angle of mandible at about the midlength of the inner margin (where a small tooth is present) and proximal of this the long basal margin is shallowly convex. A weak basal groove present but without a dorsal longitudinal groove and without a basal pit.

2 Palp formula 4,4.

3 Median portion of clypeus projects slightly anteriorly, its anterior margin transverse.

4 Frontal lobes with their anterior margin close to, but not overhanging, the anterior clypeal margin; in full-face view the distance from the most anterior point of a frontal lobe to the anterior clypeal margin is about equal to the basal width of the scape.

5 Eyes absent in worker, present in queen.

6 Antenna with 12 segments; scape somewhat dorsoventrally flattened; funiculus gradually incrassate towards the apex but without a strongly differentiated club.

7 Frontal groove on mid-dorsum of head extends far posterior of the terminus of the frontal lobes.

8 Pronotum bluntly and obtusely marginate anteriorly and laterally.

9 Mesopleuron without a transverse suture that divides the sclerite into anepisternum and katepisternum.

10 Metanotal groove (worker only) vestigial to moderately developed in dorsal view; in profile the propodeum continues the line of the mesonotum.

11 Orifice of metapleural gland a posteriorly directed curved slit that is shielded from lateral view by a small lobe of cuticle, the orifice about level with the upper portion of the propodeal lobe.

12 Metasternal process present as a pair of distinctly separated triangular long teeth that are slightly divergent and slightly curved posteriorly; metasternal pit is between the teeth.

13 Propodeum unarmed, weakly bilaterally compressed in dorsal view so that propodeal dorsum is narrower than mesonotum.

14 Propodeal spiracle broadly elliptical, almost round, low on the side and at about the midlength of the sclerite, abutting the metapleural gland bulla.

15 Propodeal lobes bluntly triangular and prominent.

16 Procoxa not hypertrophied but larger than the mesocoxa and metacoxa.

17 Mesotibia, mesobasitarsus and metabasitarsus with strongly sclerotised spiniform traction setae; such setae absent from metatibia.

18 Mesotibia and metatibia each with two spurs, the anterior small and simple, the posterior larger and pectinate.

19 Pretarsal claws small, simple.

20 Petiole in profile without an anterior peduncle.

21 Subpetiolar process low, anterior and roughly broadly triangular.

22 Helcium located close to mid-height on anterior face of the first gastral segment (abdominal segment III).

23 Prora a longitudinal, thick, bluntly convex crest that extends from just below the helcium almost to the apex of the first gastral sternite.

24 Girdling constriction between presclerites and postsclerites of second gastral segment present but shallow.

25 Stridulitrum absent.

26 Queen only (dealate). Moderately large eyes and conspicuous ocelli present. Mesosoma with full complement of flight sclerites. Transverse suture absent from mesopleuron (as in worker).

Discussion of female characters

Apomorphic characters, in *italics* above, include 1, 4 and 23. Characters 1–25 together form an inclusive diagnosis that isolates *Promyopias* workers and queens from all other genera in the tribe.

1 Elongate narrow mandibles that are linear to curvilinear have evolved independently several times in Ponerini. Often the narrowed mandible is universal in a genus (*e.g.* *Harpegnathos*, *Odontomachus*, *Anoche-tus*, *Plectroctena*, *Myopias*, *Boloponera*) but sometimes it is developed in some species groups of a genus but not others (*e.g.* *Leptogenys stuhlmanni* group and *L. maxillosa* group, *Pachycondyla agilis* group). In each case the detailed mandibular morphology, while consistent within a group, differs from that of other groups, which strongly suggests separate evolutions. The structure in *Promyopias* shows equally elongate but discernible basal and apical sections that are still quite distinct as the inner margin of the apical section is concave while the basal section is convex; the detailed structure here is unique.

2 PF 4,4 is the plesiomorphic maximum count for workers and queens in tribe Ponerini (Brown, 1963; Bolton, 2003).

4 In the sequence *Centromyrmex*–*Promyopias*–*FerAPONERA* the anterior margins of the frontal lobes draw closer to the anterior clypeal margin. In the first the anterior margins of the frontal lobes are plesiomorphically well posterior of the anterior clypeal margin, in the second quite close and in the third slightly overhanging the clypeal margin.

5 The loss of eyes in the worker caste but not in queens is also characteristic of *Centromyrmex*: see discussion of potential genus group, below.

6 The scape is broad in dorsal view and somewhat dorsoventrally flattened, but by no means as strongly flattened in its basal half as in *Centromyrmex*.

10 A discernible metanotal groove, that runs uninterruptedly across the entire dorsum of the mesosoma in workers, is variably developed. In two specimens the groove was vestigial, in three moderate and in one quite distinct.

11 Orifice of the metapleural gland is located normally here, close to the posteroventral corner of the mesosoma.

12 A bidentate to bispinose metasternal process is usual in Ponerini.

17 The presence and distribution of spiniform setae is duplicated in *Centromyrmex* and *FerAPONERA*: see discussion of potential genus group, below.

18 This distribution of tibial spurs is certainly plesiomorphic in Ponerini as a whole; it is the basal condition from which all tibial spur modifications within the tribe have been derived.

22 Position of the helcium is similar in *Centromyrmex* and *FerAPONERA*: see discussion of potential genus group, below.

23 The development of the prora in *Promyopias* appears unique in Ponerini.

Comment

Santschi (1914) initially associated *Promyopias* with *Myopias*, the latter a moderately sized genus (34 described species) widespread in the Oriental, Malesian and Austral regions, because of supposed overall similarities in the form of the mandible and clypeus. It now seems certain that these similarities are the result of convergence through the development of similar predatory behaviours and life styles in the two genera. Major characters of *Myopias* that differentiate it from *Promyopias* include: eyes usually present in worker (absent in one species); scape not flattened; mesonotum sharply defined; spiniform setae entirely absent from middle and hind tibiae and basitarsi; helcium located at base of first gastral segment; posterodorsal margin of helcium with a median emargination; prora an anteroventral tooth; stridulitrum present.

During its history *Promyopias* has been regarded as a separate genus or as a subgenus of two other ponerine genera. The provisional synonymy of *Promyopias* with *Centromyrmex* proposed by Brown (1973) and accepted by Bolton (1994, 2003) was based on the presence and distribution of spiniform setae on the legs. It

is now apparent that this decision was incorrect and *Promyopias* is formally reinstated at genus-rank here.

Synonymic synopsis of species

silvestrii (Santschi, 1914) **comb. rev.**
= *asili* (Crawley, 1916)

***Promyopias silvestrii* (Santschi) comb. rev.**
(Figs 29–32)

Myopias (*Promyopias*) *silvestrii* Santschi, 1914: 324, fig. 10. Syntype workers, GUINEA: Mamou, 24.viii.1913 (*F. Silvestri*) (NHMB) [examined]. [Combination in *Promyopias* by Emery, 1915: 26; in *Pseudoponera* (*Promyopias*) by Wheeler, W.M. 1922: 779; in *Promyopias* by Brown, 1963: 10; in *Centromyrmex* by Bolton, 1995: 140.] **Comb. rev.** *Promyopias asili* Crawley, 1916: 30, fig. Holotype queen, MALAWI: Mlanje, 15.xi.1913 (*S.A. Neave*) (BMNH) [examined]. [Combination in *Pseudoponera* (*Promyopias*) by Wheeler, W.M. 1922: 779. Synonymy with *silvestrii* by Brown, 1963: 10.]

WORKER. TL 6.0–6.3, HL 1.05–1.16, HW 1.00–1.12, CI 95–99, ML 0.62–0.68, MI 55–61, SL 0.62–0.64, SI 57–62, PW 0.74–0.86, WL 1.78–1.90 (5 measured).

With characters of the genus and the following. Dorsum of head densely punctulate-costulate, the sculpture stops near the posterior margin so that the occipital surface is mostly smooth and shining. Ventral surface of head longitudinally striolate and with scattered small punctures. Head capsule deep, in profile the maximum depth about $0.75 \times$ HL. Scapes and cephalic dorsum with dense long pubescence that may be elevated, but without long setae such as are present on the clypeus and inner mandibular margins. Pronotum bluntly and obtusely marginate anteriorly and laterally. Metanotal groove vestigial to distinct across the dorsum, not impressed in profile. Pronotal dorsum broadly and densely punctate except for the median strip, which is smooth. Punctate sculpture on mesonotum weaker and more widely spaced than on pronotum; on propodeal dorsum the punctures weaker still, very sparse and almost effaced posteriorly. Sides of mesosoma finely striolate everywhere, or at most with posterior portion of mesopleuron smooth. PW about $1.85 \times$ the maximum width of the propodeal dorsum. Gastral tergites with scattered small punctures. Dorsal surfaces of body with conspicuous pubescence or very short standing hairs everywhere. Occasionally one or two longer setae may occur on the petiole and gastral tergites 1–3, but long conspicuous setae are mostly confined to the apical gastral segment and the gastral sternites.

QUEEN. TL 7.6, HL 1.14, HW 1.17, CI 103, OI 21, ML 0.72, MI 63, SL 0.68, SI 58, PW 0.97, WL 2.32. All main morphological characters of the worker are duplicated in the queen caste; see under diagnosis of the genus.

MALE: unknown.

An uncommon but widely distributed species. Its diet, presumably termites but not actually demonstrated, may be more restricted or specialised than in *Centromyrmex*. The morphology of the mandible is unique and immediately identifies *silvestrii*.

Material examined. **Guinea:** Mamou (*F. Silvestri*). **Ivory Coast:** For. de Teke, Anyama (*T. Diomande*); Lamto, Toumodi (*J. Lévieux*); Goudi (*J. Lévieux*). **Cameroun:** Prov. Sud-Ouest, Bimbia Forest, ESE Limbe (*B.L. Fisher*). **Angola:** S. Rob't Williams (*Ross & Lorenzen*). **Malawi:** Mlanje (*S.A. Neave*)

Appendix 1. Is there a *Centromyrmex* genus group?

The three characters discussed below may diagnose a *Centromyrmex* genus group within tribe Ponerini (*sensu*

Bolton, 2003), which contains the three genera *Centromyrmex*, *Promyopias* and *Feraponera*. At present none of these characters have been proven to be synapomorphies or independently evolved, but they are universal in these genera. The status of the characters must await a more comprehensive survey of the entire tribe.

1 Presence of strongly sclerotised, stoutly spiniform traction setae on the metabasitarsus in workers and queens.

Only these three genera in Ponerini have stout spiniform traction setae on the metabasitarsus in the female castes. Similar setae, usually more strongly developed, are also universal on the mesotibia and mesobasitarsus of all three genera. Elsewhere in the tribe such setae also occur on the mesotibia, and sometimes also the mesobasitarsus in *Cryptopone*, though they are never as strongly developed; and on the mesotibia of a single species of the *Plectroctena* genus group, *Psalidomyrmex foveolatus*. However, none of these exhibit such setae on the metabasitarsus.

Ps. foveolatus acquired mesotibial spiniform setae independently, as the *Plectroctena* genus group (*Plectroctena* (16 species), *Loboponera* (9 species) and *Psalidomyrmex* (6 species)) has a unique set of apomorphies (Bolton & Brown, 2002) not exhibited by the *Centromyrmex* group. No other member of the *Plectroctena* group has spiniform traction setae on any of the legs.

In *Cryptopone* (22 species) the traction setae are more feebly developed, are restricted to the mid-leg (usually just to the mesotibia), and are always absent from the metabasitarsus. In addition, *Cryptopone* species differ from the genera treated here as all have a basal mandibular pit present and a palp formula of 2,2 at maximum (Brown, 1963). It therefore seems reasonable to assume that spiniform traction setae evolved independently in *Cryptopone*.

2 Helcium projects from near midheight of anterior face of first gastral segment in workers and queens.

In Ponerini the helcium is usually attached very low on the anterior face of the first gastral segment, and the first gastral tergite forms a relatively long vertical face above it. Exceptions to this, in addition to the *Centromyrmex* group, where the helcium is relatively high and the anterior face of the first gastral tergite is shortened, occur in *Harpegnathos*, various *Cryptopone* species and the monotypic genera *Dolioponera* and *Boloponera*. Fisher (2006) speculates that the last two together may constitute the sister-group of the *Plectroctena* group of genera. *Harpegnathos*, based on its unique morphology, cannot be considered as close to *Centromyrmex* and its allies. *Cryptopone*, despite its differences from the potential group under discussion here, may be related but the possibility awaits investigation.

3 Eyes absent in worker caste.

The absence of eyes in the worker caste may be a synapomorphy of the group. In most genera of Ponerini eyes are usually present, even if often very reduced, but there are some where eyes are absent in some species but present in others (e.g. *Hypoconera*, *Plectroctena*, *Cryptopone*, *Pachycondyla*, *Myopias*), and in *Dolioponera* larger workers have eyes while smaller ones are eyeless (Fisher, 2006). Loss of eyes may therefore be apomorphic within species, in individual species in a genus, or in a group of species within a genus, but it is worth noting that universal loss appears only to have happened in the three genera revised here.

Appendix 2. Revised key to genera of Afrotropical Ponerinae (workers)

This key is based on that of Bolton (1994). It includes genera newly described since that date but excludes former genera of Ponerinae that have more recently been dispersed to different subfamilies (Bolton, 2003; Ward, 2007).

- 1 Mandible long and linear, in full-face view inserted in the middle of the anterior margin of the head2
- Mandible linear to triangular, in full-face view inserted at the anterolateral corner of the head.....3
- 2 Nuchal carina (separating dorsal from posterior surfaces of head) converging in a V at the midline, and

- also receiving a pair of prominent dark posterior apophyseal lines that converge to form the sharp median-dorsal groove of the vertex. Dorsalmost tooth of apical mandibular series truncated *Odontomachus*
- Nuchal carina forming a broad, uninterrupted curve across the posterodorsal extremity of the head; posterior surface without paired dark apophyseal lines; on vertex the median groove absent or ill-defined and shallow. Dorsalmost tooth of apical mandibular series acute. *Anochetus*
 - 3 Dorsal (outer) surface of mesobasitarsus and metabasitarsus equipped with strongly sclerotised spiniform or peg-like setae; slender ordinary setae usually also present4
 - Dorsal (outer) surface of mesobasitarsus and metabasitarsus without setae or only with slender ordinary setae, without strongly sclerotised spiniform or peg-like setae6
 - 4 Mandible elongate and narrow, subfalcate. Apex of mandible armed with a short vertical series of 3 - 4 small teeth. Apical half of inner margin of mandible concave; elongate basal margin shallowly convex. Prora a longitudinal, thick, bluntly convex crest that extends from just below the helcium almost to the apex of the first gastral sternite. Labial palp with 4 segments..... *Promyopias*
 - Mandible triangular to elongate-triangular; apex of mandible without a short vertical series of 3 - 4 small teeth. Prora a transverse plate or a pair of weak longitudinal ridges on anterior face of first gastral sternite. Labial palp with 3 segments5
 - 5 Antennal funiculus gradually incrassate but without a distinct apical club. Anterior clypeal margin without teeth that overhang the base of the mandible. Maxillary palp with 4 segments. Orifice of metapleural gland lateral and relatively high on side, inconspicuous. Posterior surface of metatibia without a depressed area of pale cuticle above the spur..... *Centromyrmex*
 - Antennal funiculus with a distinct 4-segmented apical club. Anterior clypeal margin with a strong triangular tooth on each side that projects over the base of the mandible. Maxillary palp with 2 segments. Orifice of metapleural gland near posteroventral corner of mesosoma. Posterior surface of metatibia with a depressed area of pale cuticle above the spur.....*Feroponera*
 - 6 Ventral apex of metatibia, when viewed from in front with the metafemur at right-angles to the body, with a single large pectinate spur; without a second smaller spur in front of the pectinate main spur in the direction of observation7
 - Ventral apex of metatibia, when viewed from in front with the metafemur at right-angles to the body, with two spurs, consisting of a large pectinate spur and a second smaller spur which is in front of the pectinate main spur in the direction of observation15
 - 7 Mandible elongate, linear and weakly curved, the inner margin with 0-2 blunt teeth8
 - Mandible triangular to elongate-triangular, the apical (masticatory) margin sometimes edentate but usually with several to many teeth9
 - 8 Mandibular articulation associated with a marked semicircular excavation of the dorsal anterior margin of the head. Mandible with a longitudinal groove on the inner half of the dorsal surface *Plectroctena*
 - Mandibular articulation not associated with a semicircular excavation of the dorsal anterior margin of the head. Mandible without a longitudinal groove on the inner half of the dorsal surface*Boloponera*
 - 9 Basal portion of mandible with a distinct circular or near-circular pit or fovea dorsolaterally..*Cryptopone*
 - Basal portion of mandible without a dorsolateral pit or fovea10
 - 10 Gaster in profile and in dorsal view with a distinct impression between the presclerites and postsclerites of the second segment that appears as a girdling constriction of the gaster 11
 - Gaster in profile and in dorsal view without an impression between the presclerites and postsclerites of the second segment; gaster without a girdling constriction.....*Asphinctopone*
 - 11 Mandible elongate-falcate, with an extremely long apical tooth so that the tips cross over at rest. Apical (masticatory) margin edentate or crenulate. Labrum prominent, in dorsal view projecting beyond the anterior clypeal margin as a striated lobe. Palp formula 3,4 *Psalidomyrmex*
 - Mandible short and triangular, lacking an extremely long apical tooth. Apical (masticatory) margin multi-

- dentate. Labrum does not project beyond clypeus as a striated lobe in dorsal view. Palp formula 2,2 or less12
- 12 Metafemur mid-dorsally with a longitudinal groove on the basal half. Second gastral segment with dorsum vaulted, strongly arched and downcurved posteriorly. Sternite of second gastral segment much reduced and with a bluntly U-shaped outline in profile, much smaller than the tergite..... *Loboponera*
- Metafemur mid-dorsally without a longitudinal groove on the basal half. Second gastral segment with dorsum not vaulted, not arched and strongly downcurved posteriorly. Sternite of second gastral segment longitudinal, without a bluntly U-shaped outline in profile, only slightly smaller than the tergite.....13
- 13 Petiole in profile subcylindrical, long and low, without an erect scale or node. Prora absent from first gastral sternite below helcium. Postsclerites of second gastral segment (posterior to gastral constriction) cylindrical, in profile very much longer than high and much longer than the first segment.... *Dolioponera*
- Petiole in profile with an erect scale or node. Prora present on first gastral sternite below helcium. Postsclerites of second gastral segment (posterior to gastral constriction) not cylindrical, in profile as high as long or nearly so and at most only slightly longer than the first segment.....14
- 14 Subpetiolar process in profile with an acute angle posteroventrally and with a fenestra or thin spot anteriorly which is translucent.....*Ponera*
- Subpetiolar process in profile a simple lobe, without an acute posteroventral angle and lacking an anterior fenestra or thin spot*Hypoponera*
- 15 Pretarsal claws of middle and hind legs armed on the inner curvature with a tooth, either close to the midlength or near the base, or the entire inner curvature dentate to pectinate16
- Pretarsal claws of middle and hind legs simple, the inner curvature without a tooth medially or near the base, never dentate or pectinate18
- 16 Pretarsal claws of middle and hind legs pectinate or with 1-3 small teeth behind the apex. If only one preapical tooth present on claw, then mandible with only 1-3 teeth and clypeus with a sharp median longitudinal carina *Leptogenys* (part)
- Pretarsal claws of middle and hind legs never pectinate, the claws always with only a single preapical tooth. Mandible usually with more than three teeth but may be edentate, in which case the clypeus lacks a median longitudinal carina17
- 17 Helcium located approximately at midheight on the front of the first gastral segment so that the first gastral segment does not have a long vertical anterior face in profile. Mesotibia and metatibia each with two pectinate spurs. Sculpture of fine, dense shagreening universal, with associated larger punctures. Eyes never positioned well behind the midlength of the sides of the head..... *Platythrea*
- Helcium located very low on the front of the first gastral segment so that the first gastral segment has a long vertical anterior face in profile. Mesotibia and metatibia each with one large pectinate spur and one small, simple spur. Sculpture usually not of universal fine dense shagreening with associated larger punctures, but if present then the eyes are positioned a considerable distance behind the midlength of the sides of the head..... *Pachycondyla* (part)
- 18 Petiole dorsally with a comb of five long spines which curve backwards over the base of the first gastral segment. Propodeum with a pair of stout spines *Phrynoponera*
- Petiole dorsally without a comb of five spines. Propodeum unarmed or at most with a pair of short teeth19
- 19 Sides of petiole converge dorsally into a sharp crest that runs the length of the segment. Posterolateral margins of petiole also sharply angulate in the dorsal half, these sharp angles meeting the dorsal crest at its posterior end. Anterior clypeal margin broadly concave, the concavity terminating at each side in a prominent angle or tooth-like projection. Prora of first gastral sternite vestigial to absent in profile
.....*Streblognathus*
- Petiole scale like to nodiform but lacking a sharp crest that runs the length of the dorsum. Clypeus usually

- prominent but if shallowly concave medially, then the concavity does not terminate in prominent angles or teeth. Prora of first gastral sternite conspicuous in profile20
- 20 Mandible armed with only 1–3 teeth (usually 2)..... *Leptogenys* (part)
- Mandible armed with 5 or more teeth *Pachycondyla* (part)

Acknowledgements

Our sincere thanks to the following people who loaned types and other material, or who answered our enquiries regarding individual specimens. Dr Daniel Burckhardt (NHMB); Dr James Carpenter (AMNH); Mr Stefan Cover (MCZC); Dr Bernhard Merz (MHNG); Dr Hamish Robertson and Ms Margie Cochrane (SAMC); Mr Roy R. Snelling (LACM); Ms Christine Taylor and Mr Conrad Gillett (BMNH); Dr Hege Vårdal (NHRS); Dr Claire Villemant (MNHN); Dr Kolo Yéo (SELN). Ms April Nobile kindly took the images for the figures. We also thank Dr Steven O. Shattuck and Dr Philip S. Ward for reviewing the manuscript. Field work for this study was supported in part by NSF grant EF-0431330.

References

- Arnold, G. (1915) A monograph of the Formicidae of South Africa. Part 1. (Ponerinae; Dorylinae.) *Annals of the South African Museum*, 14, 1–159.
- Arnold, G. (1916) A monograph of the Formicidae of South Africa. Part 2. (Ponerinae; Dorylinae.) *Annals of the South African Museum*, 14, 159–270.
- Arnold, G. (1926) A monograph of the Formicidae of South Africa. Appendix. *Annals of the South African Museum*, 23, 191–295.
- Belshaw, R. & Bolton, B. (1994) A survey of the leaf litter ant fauna in Ghana, West Africa. *Journal of Hymenoptera Research*, 3, 5–16.
- Bernard, F. (1953) La réserve naturelle intégrale du Mt Nimba. 11. Hyménoptères Formicidae. *Mémoires de l'Institut Français d'Afrique Noire*, 19 (1952), 165–270.
- Bolton, B. (1994) *Identification Guide to the Ant Genera of the World*, 222 pp. Cambridge, Mass.
- Bolton, B. (1995) *A New General Catalogue of the Ants of the World*, 504 pp. Cambridge, Mass.
- Bolton, B. (2003) Synopsis and classification of Formicidae. *Memoirs of the American Entomological Institute*, 71, 1–370.
- Bolton, B. & Brown, W.L., Jr. (2002) *Loboponera* gen. n. and a review of the Afrotropical *Plectroctena* genus group. *Bulletin of The Natural History Museum (Entomology Series)*, 71, 1–18.
- Bolton, B. & Fisher, B.L. (2008) The Afrotropical ponerine ant genus *Phrynoponera* Wheeler. *Zootaxa*, 1892, 35–52
- Borgmeier, T. (1937) Formigas novas ou pouco conhecidas da America do Sul e Central, principalmente do Brasil. *Archivos do Instituto de Biologia Vegetal*, 3, 217–255.
- Brady, S.G., Schultz, T.R., Fisher, B.L. & Ward, P.S. (2006) Evaluating alternative hypotheses for the early evolution and diversification of ants. *Proceedings of the National Academy of Sciences U.S.A.*, 103, 18172–18177.
- Brown, W.L., Jr. (1953) Characters and synonymies among the genera of ants. Part 1. *Breviora*, 11, 1–13.
- Brown, W.L., Jr. (1955) The ant *Centromyrmex donisthorpei* Menozzi, a synonym. *Psyche*, 62, 103.
- Brown, W.L., Jr. (1963) Characters and synonymies among the genera of ants. Part 3. Some members of the tribe Ponerini. *Breviora*, 190, 1–10.
- Brown, W.L., Jr. (1973) A comparison of the Hylean and Congo-West African rain forest ant faunas. In Meggers, B.J., Ayensu, E.S. & Duckworth, W.D. (eds.). *Tropical Forest Ecosystems in Africa and South America: a Comparative Review*, 161–185.
- Crawley, W.C. (1916) A new species of ponerine ant captured by an *Asilus*. *Entomologist*, 49, 30–31.
- Dejean, A. & Bolton, B. (1995) Fauna sheltered by *Procupitermes niapuenis* termitaries of the African rainforest. *Journal of African Zoology*, 109, 481–487.
- Dejean, A., Bolton, B. & Durand, J.L. (1997) *Cubitermes subarquatus* termitaries as shelters for soil fauna in African rainforests. *Journal of Natural History*, 31, 1289–1302.
- Dejean, A., Durand, J.L. & Bolton, B. (1996) Ants inhabiting *Cubitermes* termitaries in African rain forest. *Biotropica*, 28, 701–713.

- Dejean, A. & Féneron, R. (1996) Polymorphism and oligogyny in the ponerine ant *Centromyrmex bequaerti*. *Insectes Sociaux*, 43, 87–99.
- Dejean, A. & Féneron, R. (1999) Predatory behaviour in the ponerine ant *Centromyrmex bequaerti*: a case of termitolesty. *Behavioural Processes*, 47, 125–133.
- Delabie, J.H.C. (1995) Inquilinismo simultaneo de duas especies de *Centromyrmex* em cupinzeiros de *Syntermes* sp. *Revista Brasileira de Entomologia*, 39, 605–609.
- Emery, C. (1889) Viaggio di Leonardo Fea in Birmania e regioni vicine. 20. Formiche di Birmania e del Tenasserim raccolte da Leonardo Fea (1885–87). *Annali del Museo Civico di Storia Naturale di Genova*, (2) 7 [27], 485–520.
- Emery, C. (1890a) Voyage de M.E. Simon au Venezuela (Décembre 1887–Avril 1888). *Annales de la Société Entomologique de France*, (6) 10, 55–76.
- Emery, C. (1890b) Studii sulle formiche della fauna neotropica. *Bullettino della Società Entomologica Italiana*, 22, 38–80.
- Emery, C. 1906. Studi sulle formiche della fauna Neotropica. *Bullettino della Società Entomologica Italiana*, 37 (1905), 107–194.
- Emery, C. (1911) In Wytsman, P. *Genera Insectorum*. Hymenoptera, Fam. Formicidae, subfam. Ponerinae. Fasc. 118, 124 pp. Bruxelles.
- Emery, C. (1915) Formiche raccolte nell'Eritrea dal Prof. F. Silvestri. *Bollettino del Laboratorio di Zoologia generale e agraria della R. Scuola superiore d'Agricoltura in Portici*, 10, 3–26.
- Fisher, B.L. (2006) *Boloponera vicans* gen. n. and sp. n. and two new species of the *Plectroctena* genus group. *Myrmecologische Nachrichten*, 8, 111–118.
- Forel, A. (1900) Les formicides de l'Empire des Indes et de Ceylan. Part 7. *Journal of the Bombay Natural History Society*, 13, 303–332.
- Forel, A. (1901) Nouvelles espèces de Ponerinae. (Avec un nouveau sous-genre et une espèce nouvelle d'*Eciton*.) *Revue Suisse de Zoologie*, 9, 325–353.
- Forel, A. (1911) Ameisen des Herrn Prof. v. Ihering aus Brasilien (Sao Paulo usw.) nebst einigen anderen aus Südamerika und Afrika. *Deutsche Entomologische Zeitschrift*, 1911, 285–312.
- Forel, A. (1913) Formicides du Congo Belge. Récoltés par MM. Bequaert, Luja, etc. *Revue Zoologique Africaine*, 2, 306–351.
- Forel, A. (1917) Cadre synoptique actuel de la faune universelle des fourmis. *Bulletin de la Société Vaudoise des Sciences Naturelles*, 51, 229–253.
- Karavaiev, V. (1925) Ponerinen aus dem Indo-Australischen Gebiet (Fortsetzung). *Konowia*, 4, 115–131.
- Karavaiev, V. (1926) Ameisen aus dem Indo-Australischen Gebiet. *Treubia*, 8, 413–445.
- Kempf, W.W. (1967) A synopsis of the Neotropical ants of the genus *Centromyrmex* Mayr. *Studia Entomologica* (N.S.), 9 (1966), 401–410.
- Lévieux, J. (1976) Etude de la structure du nid de quelques espèces terrioles de fourmis tropicales. *Annales de l'Université d'Abidjan, ser. C*, 12, 23–33.
- Lévieux, J. (1983) The soil fauna of tropical savannas. IV: The ants. In Boulière, F. (ed.). *Tropical savannas*, 525–540. Elsevier, Amsterdam.
- Mayr, G. (1866) Diagnosen neuer und wenig gekannter Formiciden. *Verhandlungen der k.k. Zoologisch-Botanischen Gesellschaft in Wien*, 16, 885–908.
- Mayr, G. (1896) Beiträge zur Kenntniss der Insektenfauna von Kamerun. 5. Formiciden gesammelt von Herrn Yngve Sjöstedt. *Entomologisk Tidskrift*, 17, 225–252.
- Menozi, C. (1925) Nouvelles fourmis des Philippines. *Philippine Journal of Science*, 28, 439–449.
- Moreau, C.S., Bell, C.D., Vila, R., Archibald, S.B. & Pierce, N. (2006) Phylogeny of the ants: diversification in the age of angiosperms. *Science*, 312, 101–104.
- Ogata, K. (1987) A generic synopsis of the poneroid complex of the family Formicidae in Japan. *Esakia*, 25, 97–132.
- Roger, J. (1861) Die *Ponera*-artigen Ameisen. (Schluss.) *Berliner Entomologische Zeitschrift*, 5, 1–54.
- Santschi, F. (1914) Formicides de l'Afrique occidentale et australe du voyage de Mr. le Professeur F. Silvestri. *Bollettino del Laboratorio di Zoologia generale e agraria della R. Scuola superiore d'Agricoltura in Portici*, 8, 309–385.
- Santschi, F. (1919) Fourmis nouvelles éthiopiennes. *Revue Zoologique Africaine*, 6, 229–240.
- Santschi, F. (1920) Formicides nouveaux du Gabon, du Congo, de la Rhodesia et du Natal. *Annales de la Société Entomologique de Belgique*, 60, 6–17.
- Santschi, F. (1924) Revue du genre *Plectroctena* F.Smith. *Revue Suisse de Zoologie*, 31, 155–173.
- Santschi, F. (1937) Fourmis angolaises. Résultats de la Mission scientifique suisse en Angola (2me voyage) 1932–1933. *Revue Suisse de Zoologie*, 44, 211–250.
- Ward, P.S. (2007) Phylogeny, classification and species-level taxonomy of ants. *Zootaxa*, 1668, 549–563.
- Watt, A.D., Stork, N.E. & Bolton, B. (2002) The diversity and abundance of ants in relation to forest disturbance and plantation establishment in southern Cameroon. *Journal of Applied Ecology*, 39, 18–30.
- Weber, N.A. (1949) New ponerine ants from Equatorial Africa. *American Museum Novitates*, 1398, 1–9.

- Wheeler, W.M. (1922) The ants of the Belgian Congo. *Bulletin of the American Museum of Natural History*, 45, 1–1139.
- Wheeler, W.M. (1936) Ecological relations of ponerine and other ants to termites. *Proceedings of the American Academy of Arts and Sciences*, 71, 159–243.
- Yoshimura, M. & Fisher, B.L. (2007) A revision of male ants of the Malagasy region: Key to subfamilies and treatment of the genera of Ponerinae. *Zootaxa*, 1654, 21–40.