

# Revision of the Rhopalomutillinae (Hymenoptera, Mutillidae): I, generic review with descriptions of three new genera

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## Abstract

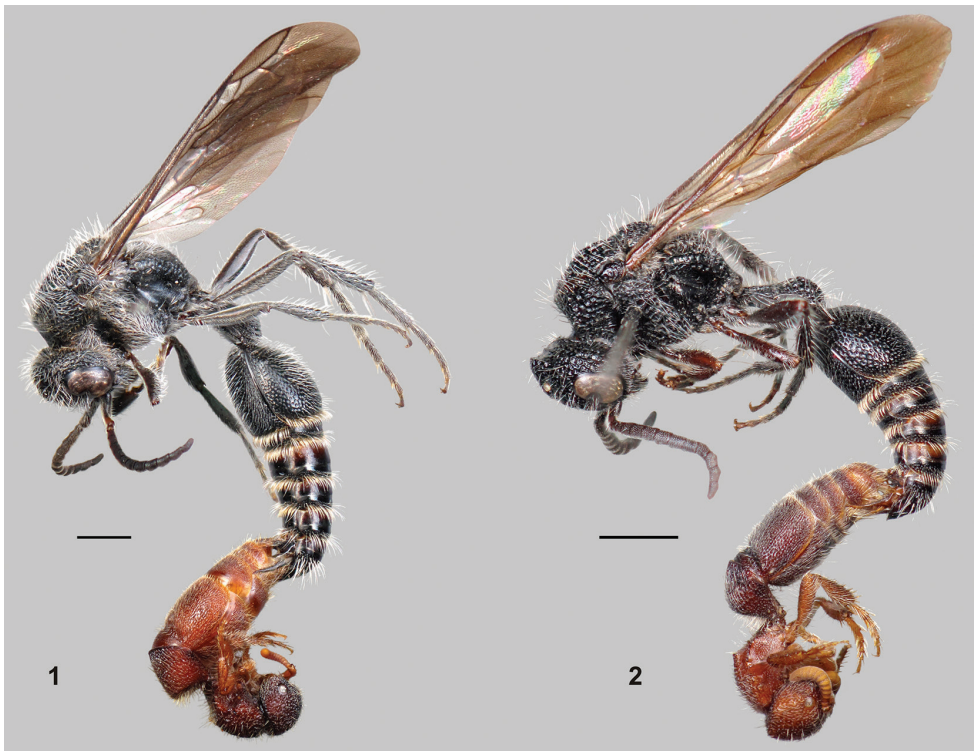
The generic classification of the species of Rhopalomutillinae is reviewed and shown to comprise four distinct genera, three of which are described as new. All genera are known from both sexes and can be distinguished primarily on the basis of differences in the male genitalia and the female mesosomal form. A key is provided to the genera (*Rimulotilla* Brothers, **gen. n.**; *Pherotilla* Brothers, **gen. n.**; *Rhopalomutilla* André, 1901; *Bischoffiella* Brothers & Nonveiller, **gen. n.**) and they are each characterised and discussed. The already-described species are placed in the appropriate genera and the new combinations indicated: *Ri. basalis* (Bischoff, 1920), **stat. n., comb. n.**; *Ri. conifera* (Bischoff, 1920), **comb. n.**; *Ri. tongaana* (Péringuey, 1909), **comb. n.**; *P. japhia* (Cameron, 1902), **comb. n.**; *P. mlanjeana* (Bischoff, 1920), **comb. n.**; *P. oceanica* (Mickel, 1935), **comb. n.**; *P. rufitincta* (Hammer, 1957), **stat. n., comb. n.**; *P. striganovae* (Lelej, 2012), **comb. n.**; *B. cristata* (Bingham, 1912), **comb. n.** In addition, *Rh. javana* Pagden, 1949, **syn. n.**, is synonymized with *P. oceanica* (Mickel, 1935).

## Keywords

Afrotropical, *Bischoffiella*, mutillid wasps, Oriental, *Pherotilla*, *Rhopalomutilla*, *Rimulotilla*

## Introduction

The mutillid subfamily Rhopalomutillinae Schuster, 1949 is a relatively small taxon (about 40 species, including those as yet undescribed) distributed in the Afrotropical and Oriental Regions. Both sexes are very characteristic and unusual morphologically (see below). They exhibit true phoretic copulation, in which the male carries the female in flight while mating (Figs 1, 2) and visiting flowers, the only mutillids to do so apart from a few Myrmosinae (Brothers 1989); as a consequence females and males are collected together and most species are known from both sexes (Brothers in prep.), a highly unusual circumstance for the family. The females have almost never been collected in isolation, and it seems likely that they spend most of their adult life underground; this is supported by their relative scarcity in collections and their morphological similarity to those of species of the Australian genus *Ponerotilla* Brothers, 1994 which have been collected in the underground nests of ants (Brothers 1989, 1994). Although many mutillid species show size differences between the sexes or even within sexes depending on the size of the host, such differences are extreme in the Rhopalomutillinae (Brothers 1989); the maximum and minimum sizes (body lengths in mm) that I have recorded for specimens of *Rhopalomutilla anguliceps* (André, 1897) are 13.7 and 5.9 for males (n=210), and 6.4 and 3.8 for



**Figures 1–2.** Rhopalomutillinae, mating pairs, male above. **1** *Pherotilla rufitincta* (Hammer) **2** *Bischoffiella cristata* (Bingham). Scales = 1 mm.

females ( $n = 18$ ) and I have seen no indication that large males preferentially mate with large females (or vice versa). No information exists about host relationships, but the variability and difference in size of both sexes and the probably subterranean existence of the females, has suggested that they may parasitize ants (Brothers 1989).

A species revision of the *Rhopalomutillinae* as a whole has long been in progress, initially with the collaboration of the late Guido Nonveiller (Zemun, Serbia). It has been delayed by many factors, not the least the initial paucity of specimens in collections, a circumstance which has more recently been remedied by extensive malaise-trap sampling programmes. However, inclusion of a realistic sampling of *rhopalomutilline* diversity in another project, an extensive morphological re-analysis of mutillid higher classification based on exemplars of both sexes for about 100 genera and subgenera in collaboration with Arkady Lelej (Vladivostok, Russia), has required the description of the new genera of *Rhopalomutillinae* at this time. The descriptions which follow include information derived from examination of many as-yet undescribed taxa and undescribed females of known taxa, which will formally be described in subsequent papers.

## Materials and methods

Specimens of *Rhopalomutillinae* were kindly loaned by the curators of many institutions around the world (detailed acknowledgment of the relevant repositories will be done in subsequent papers) and have been examined using standard morphological methods. Photographs were taken with a Canon Powershot G10 digital camera adapted to a Wild M400 photomicroscope using a Clearshot 600 adapter kit (Alexis Scientific) and stacked using CombineZP software (Hadley 2010). Further image processing was done using CorelDRAW X4 and Corel PHOTO-PAINT X4. Drawings were made using a drawing-tube attachment on a Wild M7 stereomicroscope, inked on card or provided with texture using a black wax pencil on a textured board. Abbreviations are: F = flagellomere; S = sternum; T = tergum. In females the maxillo-labial complex is much reduced and the palps are normally concealed; examination of their structure usually necessitated relaxation of specimens and dissection, but the results were sometimes inconclusive because of their extremely small size, so that it is possible that palps may have been lost during dissection and even determination of segmentation was often uncertain.

## Systematics

### *Rhopalomutillinae* Schuster, 1949

*Rhopalomutillinae* Schuster, 1949: 121, 123, 125; Brothers 1975: 623, 1999: 244; Lelej and Nemkov 1997: 12.

**Type genus.** *Rhopalomutilla* André, 1901: 323, male & female.

**Diagnosis.** MALE. Fully winged; black (seldom with the mesosoma partly dark red), without bright pubescent patterns. *Head*: compound eye oval, inner margin deeply emarginate; antennal scrobe with dorsal carina and secretory tubercle (sometimes without both); postmandibular carina forming a simple blunt ridge; oral and mandibular fossae separated by anteriorly unfused depressed bridge; antennal scape without longitudinal carinae; mandible with oblique ventral lamellate expansion basally; maxillary and labial palps six- and four-segmented respectively. *Mesosoma*: pronotum with posterodorsal margin strongly concave; mesoscutum with notaulus present but anteriorly incomplete; parapsidal line/furrow evident but incomplete posteriorly (seldom complete); axilla simply rounded posteriorly; tegula entirely convex (sometimes weakly recurved posteriorly), scarcely elongate and reaching level of trans-scutal articulation; propodeal disc with three large fields delimited by strong longitudinal ridges, lateral margin carinate, disc and declivity abruptly differentiated (seldom distinct but merging); metasternal posterior median process shorter than coxal height, unidentate. *Wings*: fore wing with elongate broad pterostigma completely sclerotized and veins C and SC+R interrupted at its base, marginal cell with acute apex, third abscissa of vein RS without bulla, second submarginal cell broadly sessile anteriorly, crossvein *3r-m* without bulla; hind wing with crossvein *r-m* proximal and complete. *Legs*: each tarsomere 4 with a small oval median pulvillus posteroventrally; tarsal claw with basal lamella separated from acute apex by a deep cleft (lamella rarely highly reduced and apparently absent); fore tibial calcar with linear narrow blade with margin entire; hind coxa with small carinate tubercle dorsally; hind tibia without any apparent preapical secretory structure. *Metasoma*: first segment moderately petiolate, T1 gradually broadened posteriorly and about  $0.5 \times$  as wide and  $> 0.5 \times$  as long as T2 (rarely slightly shorter than this), apically constricted; second metasomal segment without evident felt lines; T2–T6 and S2–S5 (sometimes S6 also) with apical fringes of moderate to strong semi-recumbent setae, but sparser and weaker on sterna and posteriad; T3 with large mediobasal stridulitrum; S7 short and concealed; hypopygium (S8) medially emarginate posteriorly (and usually with prominent process lateroventrally). *Genitalia*: paramere with inner basodorsal margin evenly curved, without parapenial lobe; volsellar digitus absent; penis valve with ventral tooth much reduced to weak rounded swelling distant from rounded apex; well developed eversible endophallus between penis valves.

FEMALE. Apterous; medium to dark brown without any bright patterns. *Head*: rounded, with oval to subcircular compound eye very small and flattened; antennal scrobe without any carina above; antennal tubercles with median transverse carina at base; postmandibular carina forming short blunt ridge; oral and mandibular fossae separated by anteriorly unfused depressed bridge; antenna clavate, short and stout, scape somewhat flattened and twisted with apex hooded over base of pedicel, pedicel and flagellomeres much wider than long; maxillary and labial palps each with two segments at most. *Mesosoma*: pronotum about as long as distance between pronotal and propodeal spiracle; metasternum with posterior median process longer than coxal height, acutely unidentate. *Legs*: short with laterally flattened tibiae and ventrally flattened or concave femora; without a pulvillus posteroventrally on any tarsomere; tarsal claws simple,

smoothly concave below; fore tibia with distinct obliquely oval to circular preapical pore on inner (anterior) surface (rarely without), calcar with linear narrow blade; fore basal tarsomere strongly curved, second to fourth tarsomeres short and broadly depressed; hind coxa with small carinate tubercle dorsally; hind tibia smooth and shining on inner (posterior) surface, without any apparent preapical secretory structure. *Metasoma*: no distinct posterior fringes on any segments; anterior and dorsal faces of T1 distinct but merging; T1 more or less parallel-sided posteriorly and almost half length of T2 or longer, almost as wide as T2 (sometimes much narrower); second segment without distinct felt lines; T3 without mediobasal stridulitrum; T6 with differentiated pygidial plate.

**Comments.** In the phylogenetic analyses of Brothers (1975, 1999) and also of Lelej and Nemkov (1997), the subfamily Rhopalomutillinae appears as originating fairly near the base of the mutillid tree, although its relationships with the “higher” subfamilies differ; at that time it had not been realised that several genera should be recognised, and it was effectively treated as monotypic. The current paper provides the basis for recognition of the four component genera and thus enables proper account to be taken of the diversity encountered in the group. A key to the genera is thus provided, for both sexes, and each genus is then characterised and discussed. It should be noted that where both sexes of a described species are indicated below as being known, both have often not yet been described; this will be done in subsequent papers.

### Key to genera of Rhopalomutillinae

- |   |   |  |
|---|---|--|
| 1 | Male; macropterous .....  | 2  |
| – | Female; apterous .....  | 5  |
| 2 | Scutellum strongly protuberant, conical, with a short transverse carina apically; mandible apically bidentate; hypopygium (S8) weakly convex to flat, but with apparent posterior margin deeply incised medially to form a narrow notch; S6 (S7 concealed) with straight posterior margin.....  | <b><i>Rimulotilla</i> Brothers, gen. n.</b>                    |
| – | Scutellum pulvinate, not markedly protuberant, with simple apex; mandible apically tridentate; hypopygium with a prominent ventrally oriented process on each side, posterior margin shallowly excised to form a broad emargination; S6 (S7 concealed) with posterior margin deeply notched on each side, engaging processes of hypopygium..... | 3  |
| 3 | Genital paramere simple, without a cluster of highly differentiated stout setae arising from beneath a dorsal lamelliform lobe, at most a few slender heavier setae present basodorsally (genal carina absent) ...  | <b><i>Pherotilla</i> Brothers, gen. n.</b>                     |
| – | Genital paramere with an obvious cluster of highly differentiated very stout setae arising from beneath a dorsal lamelliform lobe and oriented posteromedially (genal carina present or absent) .....   | 4  |
| 4 | Penis valve with a strong dentate or lamellate projection on outer surface at about midlength .....   | <b><i>Bischoffiella</i> Brothers &amp; Nonveiller, gen. n.</b> |
| – | Penis valve with a smooth outer surface, evenly curved in dorsal view .....   | <b><i>Rhopalomutilla</i> André</b>                             |

- 5 Mesosoma squat with dorsal face about as long as wide, dorsolateral margins posterior to propodeal spiracles often concave, disregarding posterolateral tooth, and usually diverging posteriorly (never converging) .....6
- Mesosoma elongate with dorsal face at least  $1.3 \times$  as long as wide, dorsolateral margins posterior to propodeal spiracles more or less straight, disregarding posterolateral tooth, and usually converging posteriorly (never diverging)...7
- 6 Mesosoma posteriorly with elevated broad sculptured median longitudinal ridge, strongly depressed posteriorly on either side of ridge, depressed areas smoothly merging with propodeal declivity; mesosoma narrower just posterior to propodeal spiracles than just anterior to spiracles .....  
..... ***Bischoffiella* Brothers & Nonveiller, gen. n.**
- Mesosoma more or less evenly convex dorsally, without any median elevated ridge or strong lateral depression posteriorly, propodeal declivity at a distinct angle to dorsal surface; mesosoma narrower just anterior to propodeal spiracles than just posterior to spiracles ..... ***Pherotilla* Brothers, gen. n.**
- 7 Posterodorsal margin of mesosoma with strong transverse scutellar scale; head slightly longer than wide, more or less parallel-sided; pygidium with apical margin deeply emarginate between a pair of strong apical spines.....  
..... ***Rimulotilla* Brothers, gen. n.**
- Posterodorsal margin of mesosoma simple, without any distinct scutellar scale (rarely indicated as a slight acute tubercle); head more or less rounded, about as long as wide; pygidium with simple convex or straight apical margin.....  
..... ***Rhopalomutilla* André**

***Rimulotilla* Brothers, gen. n.**

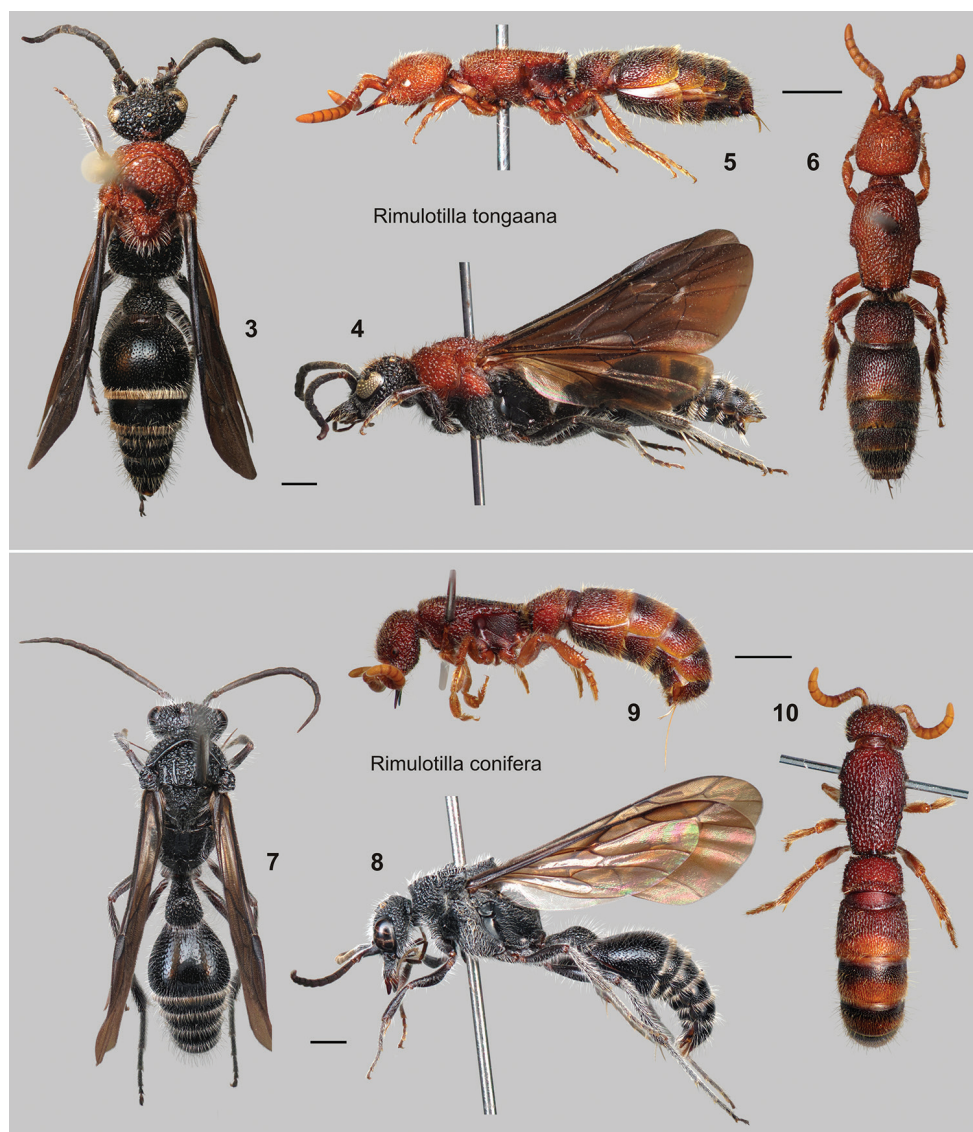
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Figs 3–10, 31–32, 39–40

**Type species.** *Mutilla* (*Rhopalomutilla*) *tongaana* Péringuey, 1909: 386, male

**Diagnosis.** MALE. Head strongly transverse with vertex dorsally produced as an angle behind ocelli in anterior view; no genal carina; mandible bidentate; scutellum almost conical with strong transverse apical tubercle; S6 with posterior margin simple; S8 weakly and evenly convex, slightly elevated posteriorly with deep median notch in posterior margin; penis valves symmetrical, each almost triangular with many long setae along posterodorsal margin; paramere without any stronger setae. FEMALE. Head slightly longer than wide in anterodorsal view; mesosoma elongate with abrupt concave narrowing between metathoracic spiracle and propodeal spiracle, lateral margins of propodeum converging posteriorly; disc of propodeum posteriorly with strong transverse median tubercle (scutellar scale) and small tooth at lateral angle; metasoma strongly elongate with T1 broad and long; pygidial plate broad and poorly defined, posterior margin deeply concave between strong apical teeth.





**Figures 3–10.** *Rimulotilla* gen. n. **3–6** *Ri. tongaana* (Péringuey) **3–4** male, dorsal & lateral views **5–6** female, lateral & dorsal views **7–10** *Ri. conifera* (Bischoff) **7–8** male, dorsal & lateral views **9–10** female, lateral & dorsal views. Scales = 1 mm.

**Description.** MALE. Body black (sometimes with mesosoma partly dark red), wings entirely infuscated (sometimes hyaline basally). *Head*: vertex more or less evenly rounded laterally but strongly elevated behind ocelli, posterodorsal margin of head in anterior view more or less straight on each side but forming a marked angle mesally; antennal scrobe above with diagonal transverse carina and secretory tuber-

cle; clypeus with sculptured median area, inner marginal teeth stronger than lateral teeth; genal carina absent (sometimes an irregular slight vertical ridge present), postgena slightly convex; postmandibular carina present, strong to weak; pleurostomal carina forming a ridge from posterior mandibular articulation to margin of oral fossa much anterior to half its length; mandible apically bidentate, subapical tooth smaller than apical tooth, ventral basal lamella scarcely developed. *Mesosoma*: mesoscutum with anteroadmedian lines weakly developed; notaulus incomplete anteriorly; parapsidal line incomplete posteriorly or complete; tegula convex, densely punctate; scutellum strongly convex, tapering posteriorly, with very strong elevated transverse tubercle; metanotal dorsellum with sides irregular but more or less straight, sculpture variable; propodeum with disc and declivity abruptly differentiated; lateral face of pronotum not strongly tapered, anteroventral margin carinate and continuous with anteroventral tooth; mesepisternum with transverse depression well developed and extending diagonally from scrobe towards ventral extremity of pronotum; mesosternum without any distinct projections. *Legs*: pubescence denser on tibiae and tarsi; claws deeply cleft apical to broad lamellate base; fore tibia without any apical secretory structure or with a vertically elongate preapical groove/pore on inner (anterior) surface; mid and hind tibiae with few inconspicuous preapical dorsal spines, and fewer very inconspicuous lateral spines (seldom absent). *Metasoma*: T2 widest posterior to midlength; T2 and S2 without any traces of lateral felt lines; pygidium (T7) with apical margin convex, edges slightly recurved (seldom not); S1 with a median tooth near base; S6 with posterior margin entire, with sparse apical fringe; hypopygium (S8) weakly convex, forming a slightly elevated lamelliform plate with deep median apical notch overlying true posterior margin, without any separate ventrally-projecting lateral lobes. *Genitalia*: basal ring very short; paramere almost straight with fairly broad apex, densely and finely setose on outer surface, without any differentiated strong setae; penis valves symmetrical, short, triangular, with a row of long fairly strong setae along posterodorsal margin.

**FEMALE.** *Head*: slightly elongate in anterodorsal view; sides behind eyes evenly and weakly convex, produced far beyond eye, well differentiated from posterodorsal margin of head; posterodorsal margin convex, without any distinct oblique depression at each side; clypeus with median lamellate tubercle dorsally, a median tubercle above obtusely triangular ventral concavity, a tooth at each side of concavity; gena broad, genal carina weak or absent; postmandibular carina weak and long or strong and short, separated from postgenal carina; pleurostomal carina forming a ridge from posterior mandibular articulation to margin of oral fossa; mandible more or less straight and evenly tapering distally, apically unidentate; maxillary palp unsegmented, cylindrical; labial palp two- or unsegmented, cylindrical; antennal scape with or without a weak blunt tubercle posterolaterally, flattened anteromesal surface not delimited by any carinae; pedicel without any distinct tuft of fine setae. *Mesosoma*: elongate, very distinctly longer than wide; anterodorsal margin distinct with short anterior face; humeral angle blunt; lateral margin fairly even and smooth, anteriorly



gently rounded and weakly convex, very abruptly and strongly converging and concave to base of propodeum then almost straight to posterolateral angle with short tooth; disc of propodeum posteriorly with small tubercles on each side of strong smooth tubercle (scutellar scale) slightly overhanging margin; posterior face of propodeum nearly vertical; lateral face of pronotum with anterior oblique carina absent or scarcely indicated, a straight carina running along anteroventral margin, ventral margin straight, anteroventral extremity blunt; mesepisternum weakly and evenly convex. *Legs*: fore leg with femur flattened below, tibia with prominent preapical oval to arcuate secretory pore on inner (anterior) surface, tibial calcar with blade finely pectinate on margin; mid and hind femora longitudinally concave below, each with a narrow elongate preapical lamella anteroventrally; mid and hind tibiae with preapical dorsal spines strong and fairly easy to distinguish, preapical lateral spines fairly weak and moderately difficult to distinguish. *Metasoma*: slender; T1 with anterior face meeting dorsal face at a rounded right angle, dorsal face long, broad and somewhat transverse, almost as wide as T2, sides weakly convex and weakly diverging from base;  $T2 < 0.75 \times \text{length } T3$ –T6, with broad deep basal depression weakly convex posteriorly, sides beyond basal depression diverging then weakly convex and scarcely converging posteriorly, no trace of felt-line patch, posterior margin weakly concave to straight; T3 with posterior margin straight; T5 without any lateral tuft of long setae; pygidium (T6) with pygidial plate broad, with an irregular lateral bounding ridge basally, apical margin forming a semicircular concavity between two strong acute teeth; S1 with a short simple median carina anterior to a broad flat triangular area elevated anteriorly and becoming somewhat depressed posteriorly; S2–S4 with simple posterior margins; S5 with posterior margin lobed (sometimes tuberculate) on each side, with a posterolateral cluster of denser setae (sometimes without); S6 with apex acute, sides carinate, no flattened strong setae.

**Species included.** *Rimulotilla basalis* (Bischoff, 1920), male & female?, stat. n., comb. n.; *Ri. conifera* (Bischoff, 1920), male & female?, comb. n.; *Ri. tongaana* (Péringuey, 1909), male & female, comb. n.; two undescribed species, one male only, the other male & female.

**Distribution.** Central, eastern and southern Africa (Burundi, Democratic Republic of Congo, Kenya, Malawi, Mozambique, Namibia, South Africa, Tanzania, Zambia, Zimbabwe).

**Etymology.** From the Latin noun *rimula*, a small cleft (referring to the form of S8), combined with *-tilla*, a common suffix derived from the genus *Mutilla*; gender feminine.

**Comments.** Phoretic copulation in this genus probably has a shorter duration than in the other genera of *Rhopalomutillinae* since there are few recorded copulating pairs in collections and the apical sterna of the males are less modified than in the other genera. The only species for which I have seen directly associated male and female specimens (and actually collected a mating pair myself) is *Ri. tongaana*, hence its designation as the type species. Other sex associations have mainly been based on collection of both sexes in malaise traps at similar times and places.

***Pherotilla* Brothers, gen. n.**

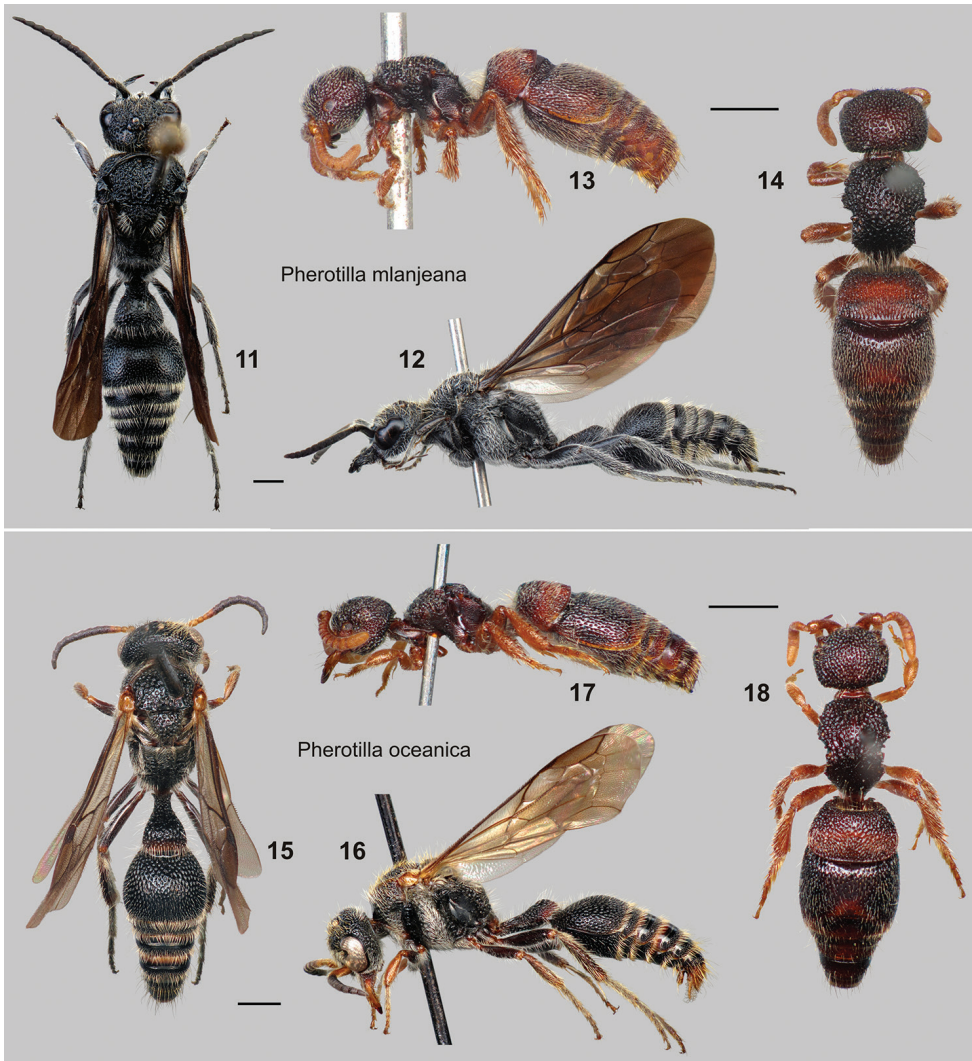
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Figs 1, 11–18, 33–34, 41–42

**Type species.** *Rhopalomutilla mlanjeana* Bischoff, 1920: 180, male & female (name determined under Article 61.4 of the Code (ICZN 1999))

**Diagnosis.** MALE. Head transverse with vertex evenly rounded in anterior view; no genal carina; mandible tridentate; scutellum pulvinate, evenly swollen; S6 with posterior margin deeply notched laterally; S8 strongly sculptured with prominent peg-like process laterally and posterior margin broadly and unevenly emarginate; penis valves asymmetrical with right valve larger than left (sometimes symmetrical), each elongate without any setae along posterodorsal margin, outer surface smoothly convex; paramere without cluster of very strong setae arising under a flange dorsobasally but often with a few slightly stronger long setae near base. FEMALE. Head rounded in anterodorsal view, about as wide as long; mesosoma squat, lateral margin with several teeth or tubercles, strongly convex anteriorly, with gradual concave narrowing between metathoracic spiracle and propodeal spiracle, lateral margins of propodeum diverging posteriorly; disc of propodeum posteriorly indistinct, without any median tubercle and with strong tooth at lateral angle; metasoma slightly elongate with T1 broad; pygidial plate oval, bounded by carina ventrolaterally, surface covered by dense recumbent setae, posterior margin convex between weak apical teeth.

**Description.** MALE. Body black (seldom with tegula and/or legs brown); wings hyaline basally (sometimes almost entirely infuscated). *Head:* transverse with vertex more or less evenly rounded without any elevation behind ocelli, posterodorsal margin of head in anterior view more or less evenly curved; antennal scrobe above with transverse carina separated from secretory tubercle; clypeus with ventral marginal teeth; genal carina completely absent, postgena slightly convex; postmandibular carina weak and short or moderate and long (rarely absent), pleurostomal carina absent (sometimes a ridge from posterior mandibular articulation to margin of proboscidal fossa slightly posterior to half its length); mandible tridentate with middle apical tooth smaller than other two, ventral basal lamella gradually narrowed apicad. *Mesosoma:* mesoscutum anteroadmedian lines separated by a longitudinal ridge; notaulus incomplete anteriorly; parapsidal line very short and incomplete posteriorly; tegula evenly convex or slightly recurved posteriorly; scutellum pulvinate, evenly swollen without any posterior tubercle; metanotal dorsellum variable in form and sculpture; propodeum with disc and declivity very weakly differentiated, evenly merging; lateral face of pronotum fairly strongly tapered, anteroventral margin a weak ridge continuous with undeveloped anteroventral tooth (sometimes tooth moderately developed); mesepisternum with transverse depression moderately developed to imperceptible; mesosternum with a short crenulate transverse carina on each side about halfway between anterior margin and mid coxa or without any distinct projections. *Legs:* pubescence denser on tibiae and tarsi; claws deeply cleft apical to broad lamellate base; fore tibia without any apical secretory structure (sometimes with a vertically elongate preapical groove/pore on inner



**Figures 11–18.** *Pherotilla* gen. n. **11–14** *P. mlanjeana* (Bischoff) **11–12** male, dorsal & lateral views **13–14** female, lateral & dorsal views **15–18** *P. oceanica* (Mickel) **15–16** male, dorsal & lateral views **17–18** female, lateral & dorsal views. Scales = 1 mm.

(anterior) surface); mid and hind tibiae with preapical dorsal and lateral spines few and difficult to distinguish. *Metasoma*: fairly slender; T2 widest beyond midlength; T2 and S2 without any traces or with dispersed traces of lateral felt lines; pygidium (T7) with apical margin convex, edges not recurved (sometimes slightly so, rarely flangelike); S1 without any tooth; S6 with posterior margin deeply notched on each side; hypopygium (S8) strongly sculptured with prominent peg-like process laterally and posterior margin broadly and unevenly emarginate. *Genitalia*: basal ring moderate; paramere curved with narrow apex, without any differentiated very strong setae except some-

times with a few long thicker setae along basodorsal margin; penis valves asymmetrical (sometimes symmetrical) with right valve slightly larger than left, without any setae.

**FEMALE.** *Head:* rounded in anterodorsal view; sides produced far behind eye, poorly to fairly well differentiated from posterodorsal margin of head; posterodorsal margin convex, without any distinct depression at each side; clypeus with a median tooth above small triangular area, a broad smooth ventral concavity, an acute lamellate tooth at each side of concavity; gena broad, without or with a weak posterior ridge; postmandibular carina irregular running from mandibular base to level posterior to posterior margin of oral fossa then obsolete; pleurostomal carina forming a ridge from posterior mandibular articulation to margin of oral fossa; mandible evenly curved, with inner margin expanded into an obtuse triangular lamella about one-third length from base, apically weakly bidentate; maxillary palp two- or unsegmented, weakly fusiform; labial palp two- or unsegmented, slightly broadened apically; antennal scape with a lamellate rounded tooth posterolaterally, flat anteromesal surface delimited dorsally by a weak carina basally or not at all; pedicel sometimes with ventral tuft of fine setae. *Mesosoma:* squat, no longer than wide or only slightly so; anterodorsal margin indistinct with fairly short anterior face at an obtuse angle to dorsal face and merging with it; humeral angle dentate or tuberculate; lateral margin uneven and tuberculate, anteriorly strongly convex, gradually converging to notch at base of propodeum then diverging to posterolateral angle with strong tooth; disc of propodeum posteriorly poorly discernible, fairly smooth and without any median tubercle; posterior face of propodeum strongly oblique; lateral face of pronotum flattened with no (or a weak) anterior oblique carina, a curved low ridge running along anteroventral margin, ventral margin fairly straight, anteroventral extremity obtuse; mesepisternum strongly convex, with or without a vertical ridge above or anterodorsal to mid coxa. *Legs:* fore leg with femur flattened below, tibia with preapical elongate to oval secretory pore on inner (anterior) surface, tibial calcar with blade smooth on margin; mid and hind femora flat to weakly longitudinally concave below, each with a basally broad preapical lamella anteroventrally; mid and hind tibiae with preapical dorsal spines very strong and easy to distinguish, preapical lateral spines strong and fairly easy to distinguish. *Metasoma:* fairly slender; T1 with anterior face meeting dorsal face at a rounded right angle, dorsal face long, very broad and transverse, almost as wide as T2, sides broadly convex anteriorly then convex and somewhat diverging posteriorly; T2 about as long as T3–T6, broad deep basal depression strongly convex posteriorly, sides beyond basal depression diverging then convex and converging, small indefinite felt-line patch anterolaterally (sometimes absent), posterior margin straight to weakly concave; T3 with posterior margin straight (sometimes very weakly concave medially); T5 without (seldom with) a tuft of fine setae at posterolateral angle; pygidium (T6) with pygidial plate oval, with a strong lateral bounding carina ventrally, sculpture concealed by dense setae, apical margin convex between two blunt teeth; S1 with a short median carina anterior to a broad flattened triangular area bounded by ridges and elevated anteriorly, narrow lateral marginal depression on each side posteriorly; S4 with posterolateral angle simple (seldom produced); S5 with posterolateral angle not (seldom scarcely) produced,

without (sometimes with) a tuft of setae posterolaterally; S6 entirely slightly convex, apex acute, sides weakly angled to carinate, no flattened strong setae.

**Species included.** *Pherotilla japhia* (Cameron, 1902), male, comb. n.; *P. mlanjeana* (Bischoff, 1920), male & female, comb. n.; *P. oceanica* (Mickel, 1935), male & female, comb. n.; *P. rufitincta* (Hammer, 1957), male & female, stat. n., comb. n.; *P. striganovae* (Lelej, 2012), male & female, comb. n.; five undescribed species, four male only, one male & female.

**Distribution.** Southern to eastern Africa (Kenya, Malawi, Mozambique, Namibia, Tanzania), southern to southeastern Asia (India, Indonesia, Laos, Malaysia, Myanmar, Nepal, Sri Lanka, Thailand, Vietnam).

**Etymology.** From the Greek verb φέρω (*phero*), to carry (referring to their phoretic copulation), combined with *-tilla*, a common suffix derived from the genus *Mutilla*; gender feminine.

**Comments.** Both sexes have already been described for only one of the Afrotropical species (*P. mlanjeana*); although only a single female specimen is known to me, I have designated this as the type species since the male is more typical for the genus than the most commonly collected Afrotropical species (*P. rufitincta*, for which several specimens of both sexes are known). This is the only genus of *Rhopalomutillinae* which is found outside the Afrotropical Region, occurring also in the Oriental Region, for which there is no evident explanation since we know nothing about their ecology. Although two species have been described from far south-east Asia (*Rh. oceanica* Mickel, 1935 from Borneo and *Rh. javana* Pagden, 1949 from Java), these differ only in coloration and I have seen several specimens from neighbouring islands with intermediate colour patterns but essentially identical morphology (including the male genitalia), so have concluded that only one variably coloured species is involved, and *Rh. javana* **syn. n.** should be synonymized with *Rh. oceanica*; a detailed justification will be provided in a subsequent paper.

### *Rhopalomutilla* André, 1901

Figs 19–26, 35–37, 43–45

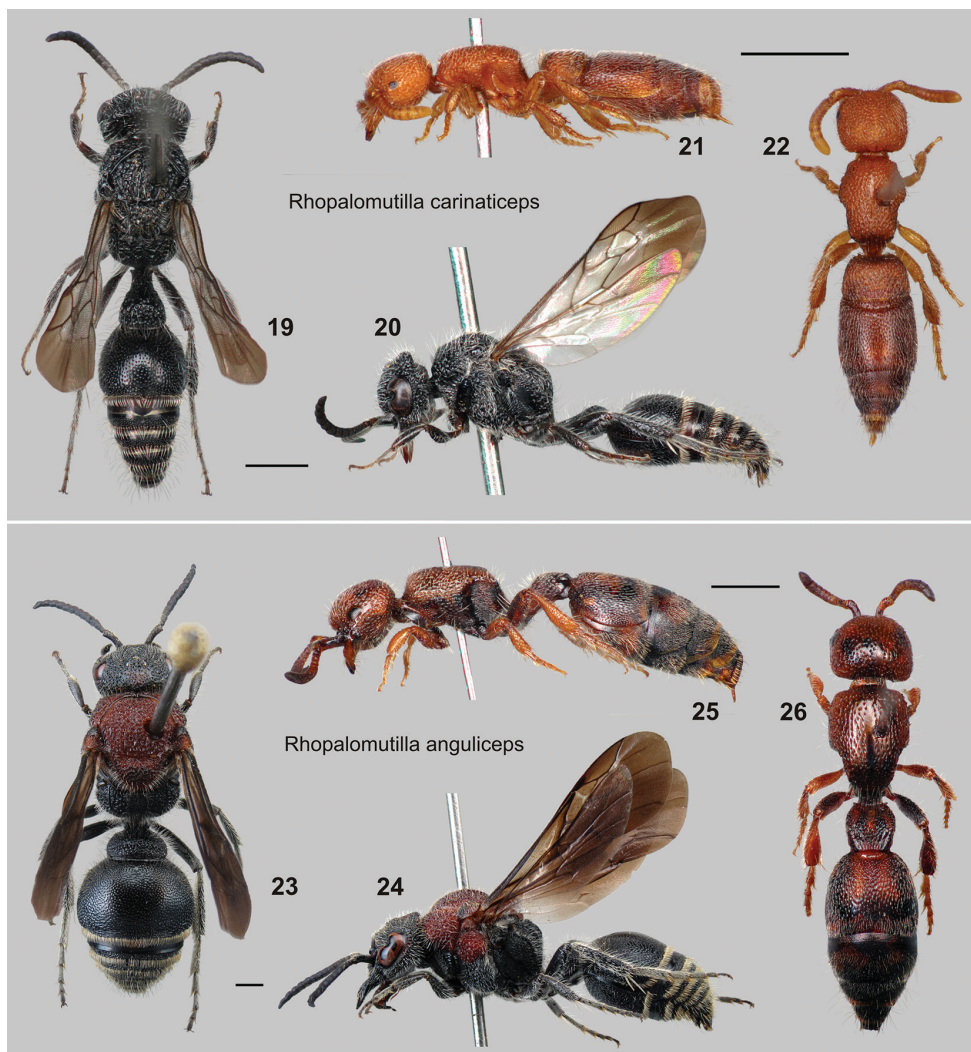
*Mutilla* (*Rhopalomutilla*) André, 1901: 323.

*Rhopalomutilla*; André 1902: 23; Bischoff 1920: 176; Bradley and Bequaert 1928: 76; Lelej and Brothers 2008: 53.

**Type species.** *Mutilla* (*Rhopalomutilla*) *clavicornis* André, 1901: 323, male & female (monotypy).

**Diagnosis.** MALE. Head transverse with vertex straight, curved or angled in anterior view; genal carina present or absent; mandible tridentate; scutellum pulvinate, evenly swollen; S6 with posterior margin deeply notched laterally; S8 strongly sculptured with prominent peg-like process laterally and posterior margin broadly and unevenly emarginate; penis valves asymmetrical with right valve larger than left,





**Figures 19–26.** *Rhopalomutilla* André. **19–22** *Rh. carinataiceps* Bischoff **19–20** male, dorsal & lateral views **21–22** female, lateral & dorsal views **23–26** *Rh. anguliceps* André **23–24** male, dorsal & lateral views **25–26** female, lateral & dorsal views. Scales = 1 mm.

each elongate without any setae along posterodorsal margin, outer surface smoothly convex; paramere with cluster of very strong setae arising under a flange dorsobasally. FEMALE. Head rounded in anterodorsal view, about as wide as long; mesosoma elongate, lateral margin smooth, convex anteriorly, with concave narrowing between metathoracic spiracle and propodeal spiracle, lateral margins of propodeum parallel or converging posteriorly; disc of propodeum posteriorly without any median tubercle (rarely with very small acute median tooth) and with small tooth at lateral angle; metasoma slightly elongate with T1 broad or narrow; pygidial plate narrowly oval, bounded



by lateral carina along entire height (sometimes not reaching dorsal extremity), surface mostly smooth and shining (sometimes with a few longitudinal carinae and/or micro-punctate and finely pubescent dorsally), posterior margin convex between weak apical teeth (sometimes without teeth).

**Description.** MALE. Body black (seldom with mesosoma partly dark red); wings basally hyaline and apically infuscated (sometimes entirely hyaline or entirely infuscated). *Head*: transverse with vertex flattened, rounded or medially produced behind ocelli, posterodorsal margin of head in anterior view straight, curved or angled; antennal scrobe above with transverse carina separated from conical secretory tubercle (seldom continuous with it, or carina or tubercle absent); clypeus with median tubercle (seldom without), 4 marginal teeth; genal carina strongly carinate, ridgelike or absent, postgena concave to convex; postmandibular carina varied from strong and extending from mandibular base to occipital foramen to weak and extending from mandibular base to a point slightly anterior to posterior extremity of oral fossa (carina rarely absent); pleurostomal carina forming a curved ridge from posterior mandibular articulation to margin of proboscidal fossa at about half its length (carina seldom barely distinguishable); mandible tridentate, middle apical tooth smaller than other two, ventral basal lamella well developed (sometimes weak, rarely absent), gradually or abruptly narrowed apicad. *Mesosoma*: with mesoscutum anteroadmedian lines distinct (seldom indistinct), forming two smooth longitudinal lines/depressions on either side of a slight ridge; notaulus deep and broad on posterior half or less, absent anteriorly; parapsidal line a short longitudinal scar distant from posterior border; tegula evenly convex (sometimes with posterior margin weakly recurved); scutellum pulvinate, evenly swollen without any posterior tubercle; metanotal dorsellum variable in form and sculpture; propodeum with disc and declivity abruptly differentiated; lateral face of pronotum tapered, anteroventral margin blunt (seldom ventrally carinate) and continuous with anteroventral tooth; mesepisternum with transverse depression weak (seldom well developed); mesosternum without any distinct projections (sometimes with a weak short transverse carina on each side about halfway between anterior margin and mid coxa). *Legs*: tarsal claws with basal lamella separated from acute apex by a deep cleft (sometimes lamella much reduced and apparently absent); fore tibia with an elongate or oval preapical groove/pore on inner (anterior) surface (seldom no discernible secretory structure); mid and hind tibiae with few inconspicuous preapical dorsal and lateral spines (sometimes absent on hind leg). *Metasoma*: fairly slender; T2 widest on posterior half (rarely at about midlength); T2 and S2 without any traces of lateral felt lines; pygidium (T7) with apical margin convex (seldom straight mesally), edges slightly recurved (rarely not recurved); S1 without any tooth; S6 with posterior margin deeply notched on each side; hypopygium (S8) strongly sculptured with prominent peg-like process laterally and posterior margin broadly and unevenly emarginate. *Genitalia*: basal ring moderate; paramere weakly curved to almost straight, with narrow apex, with cluster of differentiated very strong setae obliquely oriented and arising below flange on inner basodorsal margin; penis valves asymmetrical with right valve slightly larger than left, without any setae.

FEMALE. *Head*: rounded in anterodorsal view; sides produced far behind eye, poorly (seldom well) differentiated from posterodorsal margin of head; posterodorsal margin entirely moderately convex (seldom with a slight depression on each side); clypeus with strong median tooth dorsally, a tooth at each side of triangular ventral area; gena broad, no genal carina (seldom distinguishable but weak); postmandibular carina weak and irregular running from mandibular base more or less parallel to oral fossa to level slightly posterior to posterior margin of oral fossa; pleurostomal carina forming a weak fairly straight ridge from posterior mandibular articulation to margin of oral fossa at about half (seldom one-third) its length; mandible evenly curved, inner margin expanded into a weak obtuse long triangular lamella about one-third length from base, apically weakly bidentate; maxillary palp two- or unsegmented, apically narrowed; labial palp two- or unsegmented, curved and more or less cylindrical to clavate (rarely apparently absent); antennal scape with lamellate rounded tooth posterolaterally, anteromesal surface delimited dorsally by a weak carina basally (seldom a weak additional ventral carina or no carinae); pedicel without any distinct tuft of fine setae. *Mesosoma*: elongate; anterodorsal margin indistinct with fairly long anterior face; humeral angle bluntly rounded to weakly carinate; lateral margin fairly even and smooth to tuberculate, anteriorly weakly convex, then strongly converging and concave to base of propodeum, then almost straight and weakly converging to posterolateral angle with strong (seldom small) acute tooth; disc of propodeum posteriorly rounded, fairly smooth, without any median tubercle (rarely with very small acute median tooth); posterior face of propodeum moderately oblique; lateral face of pronotum flattened with no (or a weak) anterior oblique carina, anteroventral margin not carinate, ventral margin almost straight, anteroventral extremity obtuse to rectangular; mesepisternum strongly convex, with or without a vertical ridge above or anterodorsal to mid coxa. *Legs*: fore leg with femur flattened below, tibia with preapical oval to circular secretory pore (rarely absent) on inner (anterior) surface, calcar with blade smooth on margin; mid and hind femora longitudinally concave or flattened below, each with an elongate preapical lamella anteroventrally; mid and hind tibiae preapically with a few strong dorsal spines easy to distinguish, a few weak lateral spines fairly difficult to distinguish. *Metasoma*: fairly slender; T1 with anterior face meeting dorsal face at a rounded right to obtuse angle, dorsal face long and broad or fairly short and narrow but somewhat transverse, almost as wide as T2 or much narrower, sides weakly convex and slightly diverging from base or almost straight and slightly converging from base; T2 about as long as T3–T6, with broad deep basal depression weakly convex posteriorly, sides beyond basal depression diverging then weakly or strongly convex and scarcely converging posteriorly; a small indefinite felt-line patch anterolaterally (sometimes absent), posterior margin strongly concave to straight; T3 with posterior margin strongly concave to straight; T5 with a strong diagonal tuft of long fine setae (rarely without such setae) at posterolateral angle; pygidium (T6) with pygidial plate oval, with a strong lateral bounding carina (sometimes only ventrally), smooth (rarely with a few longitudinal ridges) and shining, but sometimes sparsely micropunctate and setose dorsolaterally or almost entirely, apical margin convex between two small teeth; S1 with a short median

carina (rarely scarcely developed) anterior to a flattened triangular area slightly (rarely not at all) elevated anteriorly; S4 with posterolateral angle produced, often with a tuft of setae; S5 with posterolateral angle produced, often with a small tuft of strong setae; S6 convex but often weakly depressed on each side, apex acute, sides carinate, rarely with a few long flattened setae posterolaterally.

**Species included.** *Rhopalomutilla anguliceps* (André, 1897), male & female; *Rh. carinaticeps* Bischoff, 1920, male & female; *Rh. clavicornis* (André, 1901), male & female; *Rh. punctinoda* (Cameron, 1910), male only; 18 undescribed species, 11 male & female, 7 male only.

**Distribution.** Sub-Saharan Africa (Angola, Botswana, Burkina Faso, Burundi, Cameroon, Chad, Côte d'Ivoire, Democratic Republic of Congo, Gabon, Guinea, Kenya, Malawi, Mozambique, Namibia, Nigeria, Senegal, South Africa, Tanzania, The Gambia, Zambia, Zimbabwe).

**Etymology.** Not stated by André (1901), but undoubtedly from the Greek noun *ῥόπαλος* (*rhopalos*), a club or cudgel (with reference to the clavate antenna of the female), combined with *Mutilla*; gender feminine.

**Comments.** The only species for which both sexes have as yet been described is the type species (*Rh. clavicornis*). This is the largest genus in the subfamily, with the broadest African distribution, species being found in most of the sub-Saharan region except for the densely forested areas and the southernmost parts. It includes two groups based on females, with T1 either about as broad as T2 or much narrower, and also two groups based on males, with the penis valves either simple ventrally or with variably produced lobes; unfortunately, these groups have different members so that a simple subdivision of the genus is not feasible.

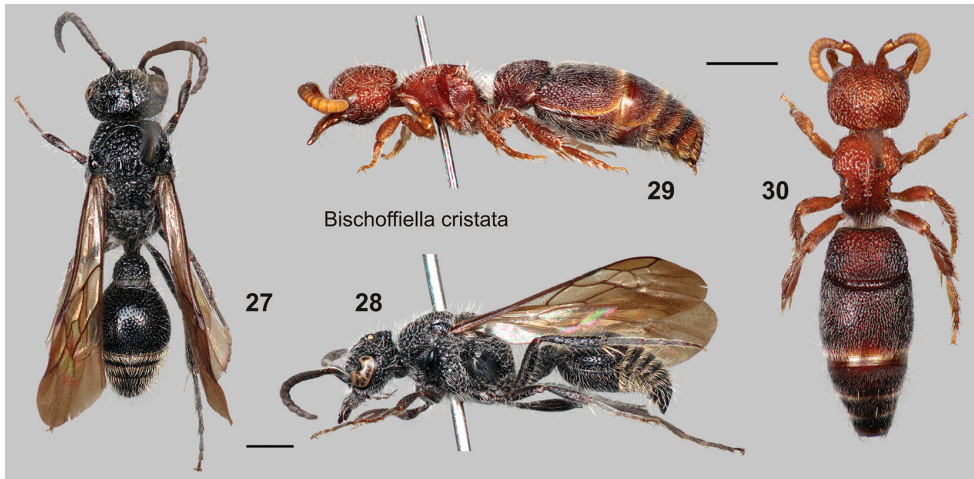
### ***Bischoffiella* Brothers & Nonveiller, gen. n.**

<http://zoobank.org/B42AEC7C-B2B2-4AA4-99C9-7174F20446EE>

Figs 2, 27–30, 38, 46

**Type species.** *Mutilla cristata* Bingham, 1912: 536, male.

**Diagnosis.** MALE. Entirely black. Head transverse with vertex curved or medially protuberant in anterior view; genal carina present or absent; mandible tridentate; scutellum pulvinate, evenly swollen; S6 with posterior margin deeply notched laterally; S8 strongly sculptured with prominent rounded peg-like process laterally and posterior margin broadly and unevenly emarginate or weakly produced; penis valves symmetrical (rarely weakly asymmetrical with right valve scarcely larger than left), each elongate without any setae along posterodorsal margin, outer surface with dentate to lamellate protuberance; paramere with cluster of very strong setae arising under a flange dorsobasally. FEMALE. Head rounded in anterodorsal view, about as wide as long; mesosoma squat, lateral margin fairly smooth, strongly convex anteriorly, with strong concave narrowing between metathoracic spiracle and propodeal spiracle, lateral margins of propodeum weakly diverging posteriorly; disc of propodeum posteriorly



**Figures 27–30.** *Bischoffiella cristata* (Bingham). **27–28** male, dorsal & lateral views **29–30** female, lateral & dorsal views **29–32**. Scales = 1 mm.

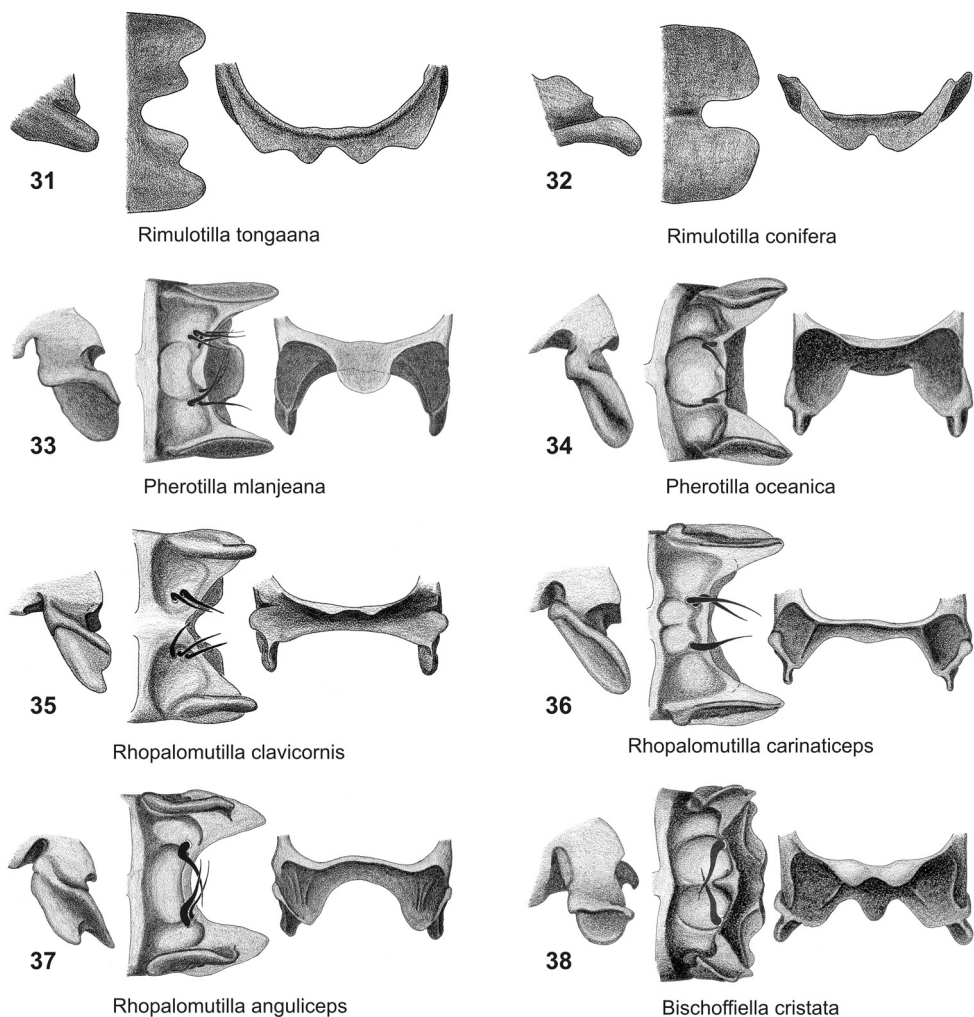
indistinct, with a very strong median longitudinal ridge elevated and broadened posteriorly and ending abruptly in a vertical face (appearing as an enlarged but narrow scutellar scale) and with a very strong tooth at lateral angle; metasoma slightly elongate with T1 broad; pygidial plate oval, longitudinally sculptured, bounded by carina laterally, surface covered by dense semirecumbent setae, posterior margin convex between rounded extremities of lateral carinae.

**Description.** MALE. Body black; wings moderately infuscated but hyaline on about basal third. *Head*: vertex ending abruptly posteriorly, posterodorsal margin of head in anterior view evenly rounded or medially protuberant; antennal scrobe with irregular convex dorsal carina more or less continuous with weak lateral secretory tubercle; clypeus with median area flattened, sometimes with dorsal tubercle; genal carina absent or strong, postgena convex to concave; postmandibular carina evident only laterally; pleurostomal carina distinct; mandible apically tridentate, with middle apical tooth smaller than other two, ventral basal lamella poorly developed. *Mesosoma*: mesoscutum with anteroadmedian lines shallow, separated by a longitudinal ridge; notaulus deep and broad on posterior half, absent anteriorly; parapsidal line a broad short longitudinal scar distant from posterior border; tegula evenly convex, more or less evenly and finely punctate, punctures coarser anteriorly than posteriorly with a restricted smooth area anteromedially; scutellum with reticulate punctation finer than that on scutum; metanotal dorsellum rectangular to trapezoidal; propodeum with disc and declivity abruptly differentiated; lateral face of pronotum tapered, anteroventral margin blunt, continuous with anteroventral tooth (sometimes tooth absent); mesepisternum with transverse depression almost indistinguishable; mesosternum with a short crenulate transverse carina on each side about halfway between anterior margin and mid coxa. *Legs*: tarsal claws with basal lamella separated from acute apex by a deep

cleft; fore tibia with an obliquely oval preapical pore on inner (anterior) surface; mid and hind tibiae with preapical dorsolateral spines difficult to distinguish. *Metasoma*: fairly slender; T2 widest posterior to midpoint; T2 and S2 with inconspicuous dispersed traces of linear felt lines; pygidium (T7) with apical margin weakly convex, edges scarcely recurved (sometimes not recurved); S1 with a distinct paired longitudinal carina diverging posteriorly; S6 with posterior margin deeply notched on each side and posteriorly expanded medially; hypopygium (S8) strongly sculptured with prominent apically broadly rounded peg-like process laterally and posterior margin broadly and unevenly emarginate to medially produced. *Genitalia*: basal ring moderate; paramere curved with narrow apex, with cluster of differentiated very strong setae obliquely oriented and arising below flange on inner basodorsal margin; penis valves symmetrical (rarely weakly asymmetrical with right valve scarcely larger than left), without any setae, with rounded tooth or lamellate lobe on outer surface.

**FEMALE.** *Head*: rounded in anterodorsal view but vertex slightly longitudinally raised in the middle posteriorly, sides behind eyes weakly convex and somewhat converging posteriorly, produced more than twice length of eye, well differentiated from posterodorsal margin of head; posterodorsal margin convex medially; clypeus with very strong acute median tooth above small acute tooth flanked by a small acute tooth on each side at dorsomedial extremity of fairly strong dorsolateral bounding carina of smooth obtusely triangular depressed area, a strong acute lamellate tooth at ventrolateral extremity of carina; gena broad, without any genal carina; postmandibular carina moderate and fairly regular running from mandibular base to level somewhat posterior to posterior margin of oral fossa; pleurostomal carina forming a fairly distinct straight ridge from posterior mandibular articulation to margin of oral fossa at about one-third its length; mandible apically very weakly bidentate, inner margin expanded into a weak very obtuse long triangular lamella about one-third length from base; maxillary palpus two-segmented, basal segment elongate and weakly broadened apically, apical segment much narrower and cylindrical; labial palpus two-segmented, basal segment short and cylindrical; antennal scape with a lamellate narrowly rounded tooth posterolaterally, flattened anteromesal surface delimited dorsally by a weak carina over about basal third; pedicel without any ventral tuft of fine setae. *Mesosoma*: weakly elongate; anterodorsal margin extremely indistinct with long anterior face smoothly merging at a very obtuse angle with dorsal face; humeral angle rounded; lateral margin uneven but fairly smooth, anteriorly rounded, diverging from humeral angle to rounded protuberance just anterior to prothoracic spiracle then angled and convex, then converging and margin angled and strongly concave and converging to base of propodeum, lateral margin of propodeum concave and converging then diverging to posterolateral angle with a very strong acute flattened tooth; propodeal disc fairly long, with a very strong median longitudinal ridge elevated and broadened posteriorly and ending abruptly in a vertical face (appearing as an enlarged but narrow scutellar scale); posterior face of propodeum strongly oblique; lateral face of pronotum without any anterior oblique carina, anteroventral extremity narrowly rounded; mesepisternum strongly convex with a weak short vertical ridge immediately anterodorsal to mid coxa. *Legs*: fore leg

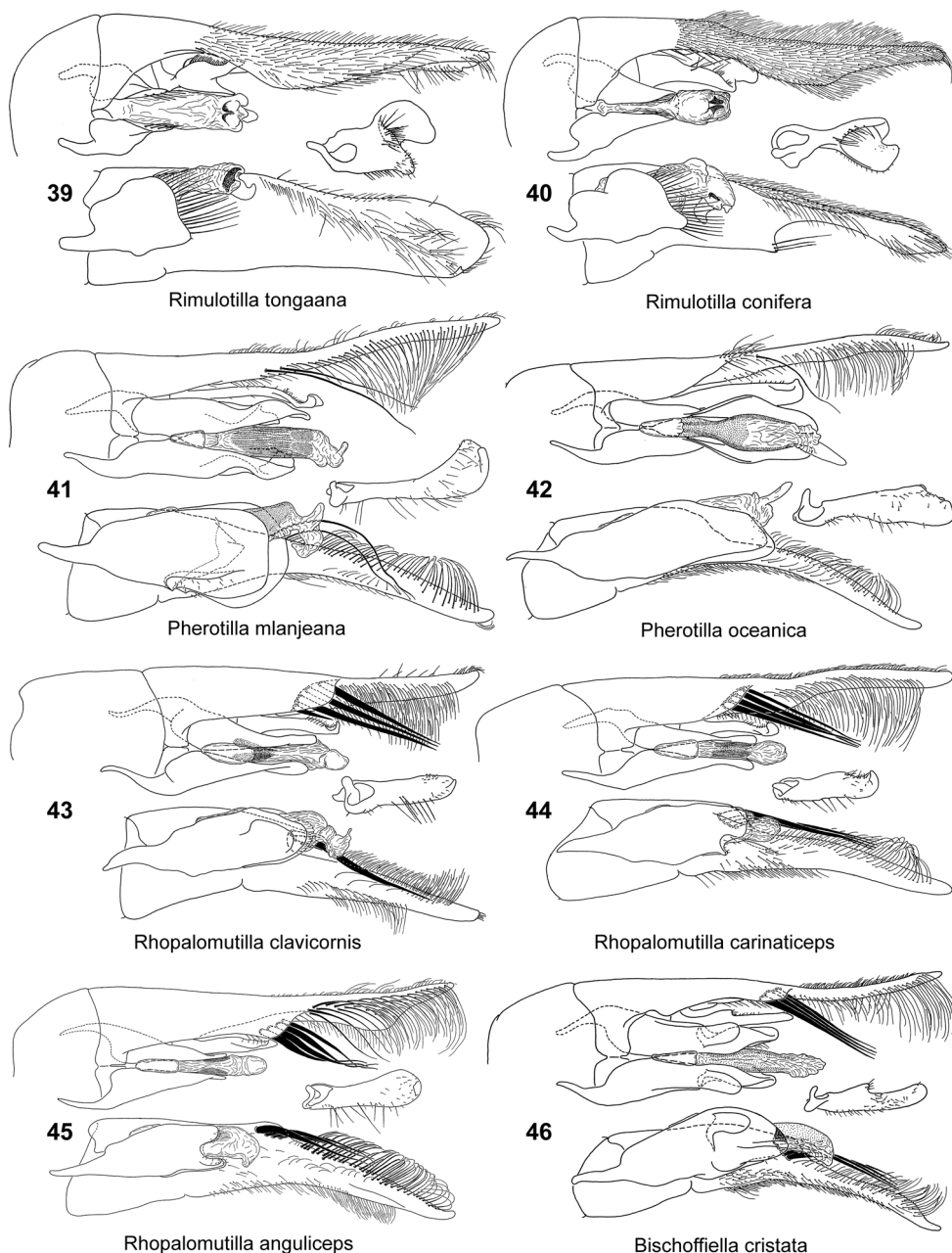




**Figures 31–38.** Rhopalomutillinae, hypopygium (S8): left = lateral view, anterior to left; centre = ventral view, anterior to left; right = posterior view. **31–32** *Rimulotilla* gen. n. **31** *Ri. tongaana* (Péringuey) **32** *Ri. conifera* (Bischoff) **33–34** *Pherotilla* gen. n. **33** *P. mlanjeana* (Bischoff) **34** *P. oceanica* (Mickel) **35–37** *Rhopalomutilla* André **35** *Rh. clavicornis* (André) **36** *Rh. carinaticeps* Bischoff **37** *Rh. anguliceps* André **38** *Bischoffiella cristata* (Bingham).

with femur flattened below, tibia with preapical oval secretory pore on inner (anterior) surface, calcar with blade smooth on margin; mid and hind femora distinctly longitudinally concave below, each with a very broad preapical lamella anteroventrally; mid and hind tibiae preapically with a few strong dorsal spines easy to distinguish, a few (several on mid tibia) lateral spines fairly easy to distinguish. *Metasoma*: fairly slender; T1 with anterior face weakly concave, meeting dorsal face at a fairly narrowly rounded





**Figures 39–46.** *Rhopalomutillinae*, male genitalia: upper = dorsal view; middle = left volsella, extrolateral view; bottom = sagittal view, penis valves and right paramere (right volsella not shown). **39–40** *Rimulotilla* gen. n. **39** *Ri. tongaana* (Péringuey) **40** *Ri. conifera* (Bischoff) **41–42** *Pherotilla* gen. n. **41** *P. mlanjeana* (Bischoff) **42** *P. oceanica* (Mickel) **43–45** *Rhopalomutilla* André **43** *Rh. clavicornis* (André) **44** *Rh. carinataceps* Bischoff **45** *Rh. anguliceps* André **46** *Bischoffiella cristata* (Bingham).

angle, dorsal face very broad and transverse, more than half as long as wide, almost as wide and more than half as long as T2, sides convex and diverging posteriorly; T2 about as long as T3–T6, with broad deep basal depression strongly convex posteriorly, sides beyond basal depression somewhat diverging then converging, small indefinite felt-line patch anterolaterally; T3 with posterior margin very weakly concave medially; T5 without any tuft of setae at posterolateral angle; pygidium (T6) with pygidial plate broadly oval, with a strong lateral bounding carina along most of ventral height, sculpture somewhat concealed by dense semirecumbent setae, apical margin strongly convex between rounded extremities of lateral carinae; S1 with a short simple median elevation anterior to a broad flattened pentagonal area bounded by moderate irregular ridges and elevated anteriorly, narrow lateral marginal depression on each side over posterior half; S4 with a very weak tuft (sometimes absent) of fine setae at posterolateral angle which is very slightly produced; S5 with posterolateral angle produced and with a tuft of bent setae laterally; S6 slightly convex but with a longitudinal median ridge posteriorly, apex acute, sides carinate, no flattened strong setae.

**Species included.** *Bischoffiella cristata* (Bingham, 1912), male & female, comb. n.; two undescribed species, both male & female.

**Distribution.** Eastern and southern Africa (Angola, Botswana, Kenya, Malawi, Mozambique, Namibia, South Africa, Tanzania, Zambia, Zimbabwe).

**Etymology.** Named, at the suggestion of the late Guido Nonveiller, in recognition of the fundamental contributions of Hans Bischoff (Berlin) to the study of African Mutillidae, and validating this name which was found attached to a female specimen (misidentified as *Rh. clavicornis* by Bischoff) in the Royal Museum for Central Africa, Tervuren, Belgium by J. Chester Bradley who had recognized that it represented a different genus (see Bradley and Bequaert 1923: 216–7).

**Comments.** The type species is the only one yet described, from the male only; both sexes are known for all three included species, however.

## Acknowledgments

The many curators and colleagues who made specimens available for this protracted study are thanked for their assistance and patience; the persons and institutions involved will be fully acknowledged in the papers dealing with the species. Information shared and generous collaboration provided by the late Guido Nonveiller (Zemun, Serbia) are gratefully acknowledged. Funding was provided by the University of KwaZulu-Natal Research Office.

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