



## Review of the tribe Smicromyrmini Bischoff, 1920 (Hymenoptera: Mutillidae)

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### Abstract

Twenty-six genera and five subgenera of the tribe Smicromyrmini are reviewed. The tribe (528 valid species) is Afrotropical (15 genera /126 species), Palaearctic (13/213) and Oriental (14/204) in distribution. The females are known for 80%, and males for 87%, of the 26 genera and five subgenera. The hitherto unknown female of *Rasnitsynitilla* Lelej in Lelej & van Harten, 2006 is described. New combinations are proposed for *Rasnitsynitilla bartolozzii* (Lo Cascio et Grita, 2014), **comb. nov.** (from the genus *Smicromyrme* Thomson, 1870) and *Skorikovia sanguinicollis* (Klug, 1829), **comb. nov.** (from the genus *Ephutomma* Ashmead, 1899). The genus *Indratilla* Lelej, 1993 is newly recorded from India and the subgenus *Eremotilla* Lelej, 1985 from the Oriental Region. Keys to females and males of these genera and subgenera of Smicromyrmini are provided. Habitus photos of males and/or females are provided for each genus and subgenus.

**Key words:** Aculeata, taxonomy, keys, new combination, Afrotropical, Palaearctic, Oriental, Old World

### Introduction

According to recent phylogenetic work based on morphology (Brothers & Lelej 2017) the subfamily Mutillinae includes four tribes: Ctenotillini Brothers & Lelej, 2017, Mutillini Latreille, 1802 (with subtribes Mutillina Latreille, 1802 and Ephutina Ashmead, 1903), Smicromyrmini Bischoff, 1920, and Trogaspidiini Bischoff, 1920. Waldren *et al.* (2020) announced upcoming changes to Mutillinae classification based on molecular phylogeny of Mutillidae using Ultra-Conserved Elements (Waldren *et al.* in press). In Brothers and Lelej (2017), the Smicromyrmini component terminals were usually grouped, except that *Promecilla* and *Pseudocephalotilla* were often shown branching off sequentially distal to the other members (Brothers & Lelej 2017). In both classifications, composition of the tribe Smicromyrmini is similar, except three genera (*Antennotilla* Bischoff, 1920; *Pseudocephalotilla* Bischoff, 1920; and *Psammotherma* Latreille, 1825) were transferred to a new tribe in the molecular analysis (Waldren *et al.*, in press). Structurally, members of this new tribe apparently differ from the remaining Smicromyrmini only by features of the male genitalia and females are known for only one of these genera. Therefore, there is no consistent mechanism for separating both sexes of these genera from the remaining Smicromyrmini. For these reasons, we included those taxa in this work to aid readers in diagnosing all of these genera. The tribe *sensu lato* (with 528 valid species) is Afrotropical (15 genera/126 species), Palaearctic (13/213) and Oriental (14/204) in distribution (Table 1). The females are known for 80%, and males for 87%, of the 26 genera and five subgenera. The genus *Smicromyrme* Thomson includes more species than any of the other genera, but this is partly due to the age of this name and the tendency for previous authors to include most members of the tribe in this genus (*e.g.* Bischoff 1920). In the Afrotropical region, and to a lesser extent the Oriental region, this is a place-holder for species of Smicromyrmini that do not fit readily into newer genus concepts (Williams *et al.* 2019).

**TABLE 1.** Diversity and distribution of the genera of tribe Smicromyrmini.

| Genera   | Number of species |               |               |               |            |            |            |
|--|-------------------|---------------|---------------|---------------|------------|------------|------------|
|  | Total             | Pal           | Afr           | Ori           | Near       | Neot       | Aust       |
| 1. <i>Andreimyrmex</i> Lelej                         | 20                | 2             | 0             | 20            | 0          | 0          | 0          |
| 2. <i>Antennotilla</i> Bischoff                      | 1                 | 0             | 1             | 0             | 0          | 0          | 0          |
| 3. <i>Corytilla</i> Arnold                           | 4                 | 0             | 4             | 0             | 0          | 0          | 0          |
| 4. <i>Ctenoceraea</i> Nonveiller                     | 1                 | 0             | 1             | 0             | 0          | 0          | 0          |
| 5. <i>Dentilla</i> Lelej in Lelej & Kabakov          | 23                | 17            | 6             | 2             | 0          | 0          | 0          |
| 6. <i>Ephucilla</i> Lelej                            | 16                | 3             | 0             | 16            | 0          | 0          | 0          |
| 7. <i>Ephutomma</i> Ashmead                          | 17                | 15            | 1             | 1             | 0          | 0          | 0          |
| 8. <i>Guineomutilla</i> Suárez                       | 1                 | 0             | 1             | 0             | 0          | 0          | 0          |
| 9. <i>Gynandrotilla</i> Arnold                       | 1                 | 0             | 1             | 0             | 0          | 0          | 0          |
| 10. <i>Indratilla</i> Lelej                          | 1                 | 0             | 0             | 1             | 0          | 0          | 0          |
| 11. <i>Karunaratnea</i> Lelej                        | 4                 | 0             | 0             | 4             | 0          | 0          | 0          |
| 12. <i>Mickelomyrme</i> Lelej                        | 23                | 2             | 0             | 23            | 0          | 0          | 0          |
| 13. <i>Nemka</i> Lelej                               | 18                | 5             | 0             | 16            | 0          | 0          | 0          |
| 14. <i>Nordeniella</i> Lelej                         | 9                 | 0             | 0             | 9             | 0          | 0          | 0          |
| 15. <i>Nuristanilla</i> Lelej in Lelej & Kabakov     | 1                 | 1             | 0             | 0             | 0          | 0          | 0          |
| 16. <i>Paglianotilla</i> Lelej in Lelej & van Harten | 1                 | 0             | 1             | 0             | 0          | 0          | 0          |
| 17. <i>Physetopoda</i> Schuster                      | 47                | 42            | 2             | 5             | 0          | 0          | 0          |
| 18. <i>Promecilla</i> André                          | 27                | 3             | 5             | 20            | 0          | 0          | 0          |
| 19. <i>Psammotherma</i> Latreille                    | 4                 | 0             | 4             | 0             | 0          | 0          | 0          |
| 20. <i>Pseudocephalotilla</i> Bischoff               | 4                 | 0             | 4             | 0             | 0          | 0          | 0          |
| 21. <i>Rasnitsynitilla</i> Lelej                     | 4                 | 1             | 4             | 0             | 0          | 0          | 0          |
| 22. <i>Sinotilla</i> Lelej                           | 20                | 2             | 0             | 19            | 0          | 0          | 0          |
| 23. <i>Skorikovia</i> Ovtchinnikov                   | 7                 | 7             | 0             | 0             | 0          | 0          | 0          |
| 24. <i>Smicromyrme</i> Thomson                       | 272               | 113           | 90            | 70            | 0          | 0          | 0          |
| 24.1. <i>Astomyrme</i> Schwartz                      | 16                | 16            | 0             | 0             | 0          | 0          | 0          |
| 24.2. <i>Eremotilla</i> Lelej                        | 24                | 18            | 0             | 6             | 0          | 0          | 0          |
| 24.3. <i>Erimyrme</i> Lelej                          | 13                | 11            | 1             | 1             | 0          | 0          | 0          |
| 24.4. <i>Rhombotilla</i> Nagy                        | 1                 | 1             | 0             | 0             | 0          | 0          | 0          |
| 24.5. <i>Smicromyrme</i> Thomson                     | 12                | 12            | 0             | 1             | 0          | 0          | 0          |
| 24.6. <i>Smicromyrme incertae sedis</i>              | 206               | 55            | 89            | 62            | 0          | 0          | 0          |
| 25. <i>Sulcotilla</i> Bischoff                       | 1                 | 0             | 1             | 0             | 0          | 0          | 0          |
| 26. <i>Tsunekimyrmex</i> Lelej                       | 1                 | 0             | 0             | 1             | 0          | 0          | 0          |
| Total genera/species                                 | <b>26/528</b>     | <b>13/213</b> | <b>15/126</b> | <b>14/204</b> | <b>0/0</b> | <b>0/0</b> | <b>0/0</b> |

Remark: *Pal*—Palaeartic, *Afr*—Afrotropic, *Ori*—Oriental, *Near*—Nearctic, *Neot*—Neotropic, *Aust*—Australia. Data based on Lelej 2007, Pagliano *et al.* 2020 with updating.

## Material and methods

Terminology mostly follows the Hymenoptera Anatomy Ontology (2013). We use the abbreviations T1, T2, T3, etc., to denote the first, second, third, etc., metasomal terga, while S2, S3, etc., denote the second, third, etc., metasomal sterna, and F1, F2, F3, etc., denote the antennal flagellomeres; OOD is an abbreviation for ocellular distance, the minimal distance between a lateral ocellus and the inner eye margin; POD is an abbreviation for inter-ocellar distance, the minimal distance between the lateral ocelli.

Specimens were examined with various stereomicroscopes in multiple laboratories. Most habitus photographs

were taken using a Leica MC170 HD camera through a Leica M165C stereomicroscope and lit using a ring light under an opaque dome. The remaining photographs were taken with an Olympus SZX16 stereomicroscope and an Olympus DP74 digital camera, then stacked using Helicon Focus software. The final illustrations were post-processed for contrast and brightness using Adobe® Photoshop® software.

Information on the photographed specimens is summarized in Table 2. Acronyms for collections from which specimens were borrowed or are deposited are as follows:

|             |  |
|-------------|--|
| <b>CGNC</b> | Personal collection of Carol Nagy, many specimens now apparently located in The Steinhardt Museum of Natural History and National Research Center, Tel Aviv University, Tel Aviv, Israel (Kimsey & Brothers 2016). |
| <b>CSCA</b> | California State Collection of Arthropods, Sacramento, California, USA.  |
| <b>DEI</b>  | Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany.   |
| <b>DJBC</b> | Collection of Denis J. Brothers, to be deposited in Iziko South African Museum (SAMC), Cape Town, South Africa (Brothers 2022).  |
| <b>FSCA</b> | Florida State Collection of Arthropods, Gainesville, Florida, USA.   |
| <b>IBSS</b> | Federal Scientific Center of the East Asia Terrestrial Biodiversity (formerly Institute of Biology and Soil Science), Vladivostok, Russia.   |
| <b>MNHN</b> | Muséum Nationale d’Histoire Naturelle, Paris, France.  |
| <b>RMNH</b> | Naturalis Biodiversity Center, Leiden, South Holland, the Netherlands.   |
| <b>USNM</b> | United States National Museum of Natural History, Smithsonian Institution, Washington D.C., USA.   |
| <b>ZIN</b>  | Zoological Institute, St. Petersburg, Russia.  |
| <b>ZMMU</b> | Zoological Museum of Moscow University, Russia.  |

## Taxonomic results

### Tribe Smicromyrmini Bischoff, 1920

Smicromyrmini Bischoff, 1920: 23; Invrea 1964: 151 (Smicromyrminae); Brothers 1975: 592 (Smicromyrmina); Lelej 1985: 180; Lelej 1995b: 2; Lelej & Nemkov 1997: 4; Brothers 1999: 245 (Smicromyrmina); Brothers & Lelej 2017: 47; Pagliano *et al.* 2020: 169.

**Diagnosis.** MALE. Eye without setae; inner margin deeply notched. F1 shorter than F2. Scutellum simple, without median carina or postero-lateral denticle. Wing venations not reaching outer wing margin; distance between origin of *RS* on vein *Sc* and base of stigmatic cell nearly 2 × stigmatic cell length; hind wing without anal lobe. Tarsal claws without inner denticles. Metasomal segment 1 narrow; segment 2 with lateral felt line on T2 and sometimes on S2; S8 not reduced, plate-like; genitalia with symmetrical penis valves. FEMALE. Head not enlarged; eye oval, slightly protruding from head capsule, without setae; maxillary palpus six segmented; labial palpus four segmented. Mesosoma widest at pronotum or propodeum; mesopleuron concave; meso-metapleural suture ending at pronotal spiracle; dorsum of propodeum without row of denticles. Claws without inner denticles. T1 much narrower than T2, not petiolate; T2 with one or three, (two lateral transverse in some *Mickelomyrme*, subbasal band in some *Dentilla*, discal spots entirely obliterated in some species of many genera) subbasal spots of pale setae or without any spots.

**Genera included.** 26 genera and 5 subgenera (Brothers & Lelej 2017, Pagliano *et al.* 2020).

**Diversity and distribution.** Widely distributed in the Old World and numbers 26 genera, 528 species: Palaearctic (13/213), Afrotropical (15/126), and Oriental (14/204) Regions (Lelej 2007, Pagliano *et al.* 2020, Thaochan *et al.* 2022). The endemic genera are: *Nuristanilla* Lelej in Lelej & Kabakov, 1980, ♀ and *Skorikovia* Ovtchinnikov, 2002, ♂, ♀ in the Palaearctic Region; *Indratilla* Lelej, 1993, ♂, ♀; *Karunaratnea* Lelej, 2005, ♂, ♀; *Nordeniella* Lelej, 2005, ♂, ♀, and *Tsunekimyrm* Lelej, 1995b, ♂ in the Oriental Region; and *Antennotilla* Bischoff, 1920, ♂; *Corytilla* Arnold, 1956, ♂, ♀; *Ctenoceraea* Nonveiller, 1993, ♂; *Guineomutilla* Suárez, 1977, ♀; *Gynandrotilla* Arnold, 1946, ♂; *Paglianotilla* Lelej in Lelej & van Harten, 2006, ♂; *Psammotherma* Latreille, 1825, ♂; *Pseudocephalotilla* Bischoff, 1920, ♂, ♀; and *Sulcotilla* Bischoff, 1920, ♂, ♀ in the Afrotropical Region.

**TABLE 2.** Overview of photographed specimens.

| Figure    | Taxon                            | Sex | Country              | Museum | Notes  |
|-----------|----------------------------------|-----|----------------------|--------|--|
| 1         | <i>Andreimyrmex long</i>         | ♂   | China                | ZMMU   | Holotype   |
| 2,3,110   | <i>Andreimyrmex rong</i>         | ♀   | Vietnam              | RMNH   | Holotype   |
| 4a        | <i>Antennotilla phoebe</i>       | ♂   | South Africa         | FSCA   | Identified by KAW                                |
| 4b        | <i>Antennotilla phoebe</i>       | ♂   | South Africa         | DJBC   | Identified by Denis Brothers                     |
| 5,6       | <i>Corytilla pallidipes</i>      | ♂   | Botswana             | CSCA   | Identified by KAW                                |
| 7–10      | <i>Ctenoceraea pectinella</i>    | ♂   | Senegal              | MNH    | Illustrations of Holotype from Nonveiller (1993) |
| 11,12     | <i>Denitilla rasmitsyni</i>      | ♂   | United Arab Emirates | RMNH   | Paratype   |
| 13,14,111 | <i>Denitilla curtiventris</i>    | ♀   | Greece               | CSCA   | Identified by Guido Pagliano                     |
| 15,16     | <i>Denitilla curtiventris</i>    | ♂   | Greece               | CSCA   | Identified by Guido Pagliano                     |
| 17,18     | <i>Ephucilla najia</i>           | ♂   | Taiwan               | CSCA   | Identified by KAW                                |
| 19–21,112 | <i>Ephucilla thalia</i>          | ♀   | Taiwan               | DEI    | Holotype   |
| 22,23     | <i>Ephutomma angustata</i>       | ♂   | Uzbekistan           | CSCA   | Identified by KAW                                |
| 24,25,113 | <i>Ephutomma fletcheri</i>       | ♀   | Sri Lanka            | USNM   | Identified by ASL                                |
| 26        | <i>Guineomutilla mateui</i>      | ♀   | Cameroon             | DJBC   | Identified by Guido Nonveiller                   |
| 27        | <i>Gynandrotilla ferruginea</i>  | ♂   | South Africa         | DJBC   | Identified by Denis Brothers                     |
| 28,29     | <i>Indratilla gynandromorpha</i> | ♀,  | Sri Lanka            | USNM   | Identified by Børge Petersen                     |
| 29        | <i>Indratilla gynandromorpha</i> | ♂   | Sri Lanka            | ZIN    | Holotype   |
| 30,31,114 | <i>Karunaratnea palatupanae</i>  | ♀   | Sri Lanka            | IBSS   | Paratype   |
| 32–34     | <i>Karunaratnea palatupanae</i>  | ♂   | Sri Lanka            | USNM   | Holotype   |
| 35–37     | <i>Mutilla alberici</i>          | ♀   | Taiwan               | DEI    | Lectotype  |
| 38–40     | <i>Mutilla hageni</i>            | ♂   | Taiwan               | DEI    | Lectotype  |
| 41,42,115 | <i>Nemka viduata</i>             | ♀   | Italy                | FSCA   | Identified by KAW                                |
| 43,44     | <i>Nemka viduata</i>             | ♂   | Greece               | FSCA   | Identified by KAW                                |
| 45,46     | <i>Nordeniella thermophila</i>   | ♀   | Sri Lanka            | USNM   | Identified by ASL                                |
| 47,48     | <i>Nordeniella thermophila</i>   | ♂   | Sri Lanka            | USNM   | Identified by ASL                                |
| 49        | <i>Nuristanilla kabakovi</i>     | ♀   | Afghanistan          | ZIN    | Holotype   |
| 50        | <i>Paglianotilla hogenesi</i>    | ♂   | Yemen                | IBSS   | Paratype   |
| 51,52     | <i>Paglianotilla hogenesi</i>    | ♂   | Yemen                | RMNH   | Paratype   |
| 53,54     | <i>Physetopoda halensis</i>      | ♀   | Italy                | FSCA   | Identified by Marcelo Romano                     |

.....continued on the next page

TABLE 2. (Continued)

| Figure      | Taxon                                | Sex | Country              | Museum | Notes                                      |
|-------------|--------------------------------------|-----|----------------------|--------|--|
| 55,56       | <i>Physetopoda oratoria</i>          | ♂   | Russia               | USNM   | Identified by ASL                          |
| 57,58       | <i>Promecilla regia</i>              | ♀   | India                | USNM   | Identified by Børge Petersen               |
| 59,60       | <i>Promecilla regia</i>              | ♂   | India                | USNM   | Identified by Børge Petersen               |
| 61          | <i>Psammotherma flabellata</i>       | ♂   | South Africa         | FSCA   | Identified by KAW                          |
| 62          | <i>Psammotherma flabellata</i>       | ♂   | South Africa         | DJBC   | Identified by Denis Brothers               |
| 63,64       | <i>Pseudocephalotilla beira</i>      | ♀   | South Africa         | DJBC   | Identified by Denis Brothers               |
| 65          | <i>Pseudocephalotilla beira</i>      | ♂   | South Africa         | DJBC   | Identified by Denis Brothers               |
| 66          | <i>Pseudocephalotilla tettensis</i>  | ♀   | Zimbabwe             | FSCA   | Identified by KAW                          |
| 67–69       | <i>Rasnitsynitilla schmideggeri</i>  | ♂   | United Arab Emirates | IBSS   | Identified by ASL                          |
| 70–72       | <i>Rasnitsynitilla schmideggeri</i>  | ♀   | United Arab Emirates | IBSS   | Identified by ASL                          |
| 73          | <i>Rasnitsynitilla brachyptera</i>   | ♂   | Yemen                | IBSS   | Paratype                                   |
| 74          | <i>Sinotilla boheana</i>             | ♂   | China                | ZMMU   | Identified by ASL                          |
| 75,76       | <i>Sinotilla belokobylskiji</i>      | ♀   | Thailand             | CSCA   | Identified by KAW                          |
| 77          | <i>Skorikovia elongata</i>           | ♂   | Tajikistan           | FSCA   | Identified by KAW                          |
| 78,79       | <i>Skorikovia elongata</i>           | ♀   | Tajikistan           | FSCA   | Identified by KAW                          |
| 80,81       | <i>Tsunekimyrmec fluctuata</i>       | ♂   | Philippines          | IBSS   | Identified by ASL                          |
| 82,83       | <i>Sulcotilla sulcata</i>            | ♀   | Cameroon             | IBSS   | Identified by Guido Nonveiller             |
| 84,85       | <i>Sulcotilla sulcata</i>            | ♂   | Cameroon             | IBSS   | Identified by Guido Nonveiller             |
| 86,87       | <i>Sm. (Astomyrme) ausonius</i>      | ♀   | Italy                | CASC   | Identified by Guido Pagliano               |
| 88,89       | <i>Sm. (Astomyrme) ausonius</i>      | ♂   | Italy                | FSCA   | Identified by Guido Pagliano               |
| 90,91       | <i>Sm. (Eremotilla) tekensis</i>     | ♀   | Kazakhstan           | USNM   | Identified by ASL                          |
| 92,93       | <i>Sm. (Eremotilla) schwarzi</i>     | ♂   | Turkey               | CASC   | Identified by Børge Petersen               |
| 95,95       | <i>Sm. (Eremotilla) perisii</i>      | ♀   | Italy                | FSCA   | Identified by Marcelo Romano               |
| 96,97       | <i>Sm. (Erimyrme) sicanus</i>        | ♀   | Italy                | FSCA   | Identified by Guido Pagliano               |
| 98,99       | <i>Sm. (Erimyrme) sicanus</i>        | ♂   | Italy                | FSCA   | Identified by Guido Pagliano               |
| 100–103     | <i>Sm. (Rhombotilla) riparius</i>    | ♀   | Romania              | CGNC   | Illustrations of Holotype from Nagy (1966) |
| 104,105,109 | <i>Smicromyrme (s. str.) rufipes</i> | ♀   | Estonia              | FSCA   | Identified by KAW                          |
| 106         | <i>Smicromyrme (s. str.) rufipes</i> | ♂   | Italy                | FSCA   | Identified by Guido Pagliano               |
| 107         | <i>Smicromyrme (s. str.) rufipes</i> | ♂   | Estonia              | FSCA   | Identified by KAW                          |

## Key to the genera and subgenera of the tribe Smicromyrmini

### Males (unknown in *Guineomutilla*, *Nuristanilla*, and *Smicromyrme* (*Rhombotilla*))

1. Apterous ..... 2
- Alates ..... 3
2. T1 long with distinct dorsal face, with lateral white spots. T2 black with medial subbasal white spot and two postero-lateral white spots. Tegula long, projecting over mesoscuto-scutellar suture.—Volsella short, half gonostylus length, ventrally with dense setae longer than basal gonostylus width (Ori) ..... 10. *Indratilla* Lelej, 1993
- T1 short, without distinct dorsal face and lateral white spots. T2 ferruginous with black posterior third and posterior white fringe. Tegula short, scarcely projecting over mesoscuto-scutellar suture (Afr) ..... 9. *Gynandrotilla* Arnold, 1946
3. S2 with short lateral felt lines, sometimes reduced to a few small punctures ..... 4
- S2 without any trace of lateral felt lines ..... 16
4. Mandible strongly widened apically, preapical inner teeth equal to or larger than apical tooth ..... 5
- Mandible not widened apically, preapical inner teeth distinctly smaller than apical tooth, second preapical tooth sometimes (*Pseudocephalotilla*) larger than apical tooth ..... 6
5. Inner eye margin with deep notch. Stigmatic cell  $0.7 \times$  distance between base of stigmatic cell and origin of RS on vein Sc. T2 width  $1.2 \times$  propodeal width (Ori) ..... 26. *Tsunekimyrm* Lelej, 1995
- Inner eye margin with weak notch. Stigmatic cell  $1.4 \times$  distance between base of stigmatic cell and origin of RS on vein Sc. T2 width  $1.5 \times$  propodeal width (Afr, Ori, Pal) ..... 5. *Dentilla* Lelej in Lelej & Kabakov, 1980
6. Flagellomeres overlapped, F1–5 with row of tyloids or inner part of F1–7(10) with apophyses (Afr) ..... 7
- Flagellomeres not overlapped, F1–5 without row of tyloids and inner part without apophyses ..... 9
7. Flagellomeres overlapped, F1–5 with row of tyloids. T7 with cuticular yellowish spot (Afr) . . . 2. *Antennotilla* Bischoff, 1920
- F1–7(10) with apophyses. T7 black, without cuticular yellowish spot ..... 8
8. Double series of apophyses different: longer one  $\sim 6 \times$  flagellomere diameter, shorter one equal to flagellomere length. Mandible bidentate, with strong subbasal tooth ventrally (Afr) ..... 4. *Ctenoceraea* Nonveiller, 1993
- Double series of apophyses more or less equal in length. Mandible tridentate, with ventral basal carina, without subbasal tooth (Afr) ..... 19. *Psammotherma* Latreille, 1825
9. Genital volsella with basal external lobe and long narrow cuspis; basivolsella with long setae ..... 10
- Genital volsella without basal external lobe or long narrow cuspis; basivolsella with setae short or absent ..... 14
10. Mandible bidentate at apex (Ori, Pal) ..... 12. *Mickelomyrm* Lelej, 1995
- Mandible tridentate at apex ..... 11
11. Mesopleuron beneath with one or two pairs of precoxal denticles or tubercles ..... 12
- Mesopleuron beneath without precoxal denticles or tubercles ..... 13
12. Hypostomal bridge without tooth; eye broadly oval; prementum evenly convex or weakly medio-longitudinally carinate; oblique metapleural suture running anterodorsally from endophragmal pit; mesopleuron beneath with precoxal paired transverse/oblique carinae (may be toothed mesally) (Ori, Pal) ..... 13. *Nemka* Lelej, 1985
- Hypostomal bridge with tooth; eye subcircular; prementum with posteromedian domelike elevation; oblique metapleural suture running horizontally from endophragmal pit; mesopleuron beneath with precoxal paired transverse tubercles and teeth (Afr) . . . . . 25. *Sulcotilla* Bischoff, 1920
13. Mandible beneath with large subventral tooth, distance between subventral tooth and dorsal mandibular carina equal or more than basal mandibular width. Apex of volsellar cuspis curved inside (Pal) ..... 23. *Skorikovia* Ovtchinnikov, 2002
- Mandible beneath with small subventral tooth, distance between subventral tooth and dorsal mandibular carina much less than basal mandibular width. Apex of volsellar cuspis narrowly straight (Afr, Pal) ..... 21. *Rasnitsynitilla* Lelej in Lelej & van Harten, 2006
14. Penis valve shortened, swollen apex curved down and oriented outside (Afr) ..... 20. *Pseudocephalotilla* Bischoff, 1920
- Penis valve not shortened, apex not swollen and not oriented outside ..... 15
15. F1 length equal its maximal width, and  $0.6 \times$  F2. Tegula not projecting or at most scarcely projecting over mesoscuto-scutellar suture (Afr, Ori, Pal) ..... 24. *Smicromyrme* Thomson, 1870
- 15a. Mandible beneath without subventral tooth, if with inconspicuous one then without excision (Pal) ..... 24.1. Subgenus *Astomyrm* Schwartz, 1984
- Mandible beneath with well developed subventral tooth separated by excision ..... 15b
- 15b. Mandible bidentate. Clypeus more or less flattened ..... 15c
- Mandible tridentate. Clypeus concave. (Afr, Ori, Pal) ..... 24.3. Subgenus *Erimyrme* Lelej, 1985
- 15c. Clypeus without preapical teeth (Ori, Pal) ..... 24.2. Subgenus *Eremotilla* Lelej, 1985
- Clypeus with two preapical teeth or tubercles (Pal) ..... 24.5. Subgenus *Smicromyrme* Thomson, 1870
- 15 (-). F1 length  $0.5\text{--}0.6 \times$  its maximal width, and  $0.3\text{--}0.4 \times$  F2. Tegula projecting over mesoscuto-scutellar suture for  $1/5\text{--}1/4$  of its length (Ori, Pal) ..... 22. *Sinotilla* Lelej, 1995
16. Mandible strongly widened apically, preapical inner teeth equal to or larger than apical tooth ..... 17
- Mandible narrowed apically, preapical inner teeth considerably smaller than apical tooth ..... 18
17. Mandible not excised beneath, without tooth or lobe near base. F1 length  $0.7 \times$  maximal width (Fig. 5) (Ori, Pal) ..... 1. *Andreimyrm* Lelej, 1995
- Mandible excised beneath, with large subbasal lobe. F1 length  $1.5\text{--}1.6 \times$  maximal width (Afr, Ori, Pal) ..... 7. *Ephutomma* Ashmead, 1899
18. Mandible beneath without large subbasal tooth or lobe, at most with small projection in basal half ..... 19.

- Mandible beneath with large subbasal lobe or tooth . . . . . 20
- 19. Flagellomeres overlapped. Penis valve shortened, apex curved down and oriented outside. T2 with central spot of pale setae (Afr) . . . . . 16. *Paglianotilla* Lelej in Lelej & van Harten, 2006
- Flagellomeres not overlapped. Penis valve not shortened, apex not oriented outside. T2 without central spot of pale setae (Ori) . . . . . 14. *Nordeniella* Lelej, 2005
- 20. Brachypterous: forewing slightly projecting over T2. Distance between base of stigmatic cell and origin of *RS* on vein *Sc* equal or even less than stigmatic cell length. Propodeum dorsally with two medial sharp teeth (Ori) . . . . . 11. *Karunaratnea* Lelej, 2005
- Wings well developed: forewing touch metasomal apex. Distance between base of stigmatic cell and origin of *RS* on vein *Sc* more than stigmatic cell length. Propodeum dorsally without medial sharp teeth . . . . . 21
- 21. Genital volsella without wide external basal lobe, inner and lower margins of volsella with setae not longer than volsellar cuspis . . . . . 22
- Genital volsella with more or less wide external basal lobe (basivolsella) with setae longer than volsellar cuspis . . . . . 23
- 22. Vertex with raised subtriangular carinated platform (Afr) . . . . . 3. *Corytilla* Arnold, 1956
- Vertex without raised subtriangular carinated platform (Ori, Pal) . . . . . 6. *Ephucilla* Lelej, 1995
- 23. Mandible beneath usually not excised, with rounded subventral lobe. Thickened basivolsellar setae not reaching the apex of gonostylus (Afr, Ori, Pal) . . . . . 18. *Promecilla* André, 1902
- Mandible beneath deeply excised, with large subventral tooth. Thickened basivolsellar setae usually protruding beyond apex of gonostylus (in *scutellaris* species-group not longer than volsellar cuspis) (Afr, Ori, Pal) . . . . . 17. *Physetopoda* Schuster, 1949

**Females** (unknown in *Antennotilla*, *Ctenoceraea*, *Gynandrotilla*, *Paglianotilla*, *Psammotherma*, *Tsunekimyrmex*)

- 1. T6 convex, without distinct pygidial plate, with glabrous shiny area widened posterad . . . . . 2
- T6 with distinct flattened pygidial plate, carinated laterally, longitudinally striate, granulous or with glabrous shiny apical part, or entirely glabrous, shiny . . . . . 8
- 2. Scutellar scale more or less developed . . . . . 3
- Scutellar scale totally lacking . . . . . 6
- 3. Scutellar scale strongly developed. Mesosomal dorsum with parallel sides or slightly widened posterad.—F1 distinctly longer than F2. T6 not carinated even apically (Ori) . . . . . 11. *Karunaratnea* Lelej, 2005
- Scutellar scale weak, but distinct. Mesosomal dorsum often narrowed posterad . . . . . 4
- 4. T6 with glabrous shiny medial part, not carinated laterad, considerably convergent basally with basolateral tufts of dense pale setae (Ori, Pal) . . . . . 22. *Sinotilla* Lelej, 1995
- T6 with elongated shiny glabrous pygidial plate, weakly carinate laterad . . . . . 5
- 5. F1 equals its apical width and length of F2. T1 short, without lateral pale spots (Ori, Pal) . . . . . 6. *Ephucilla* Lelej, 1995
- F1 longer than its apical width and 1.3 × longer than F2. T1 long with distinct dorsal face, with lateral white spots (Ori) . . . . . 10. *Indratilla* Lelej, 1993
- 6. F1 1.6 × its maximum width. Mesosoma elongated, distinctly narrowed posterad . . . . . 7
- F1 1.0–1.1 × its maximum width. Mesosoma not elongated, with more or less parallel sides or widened posterad (Ori) . . . . . 14. *Nordeniella* Lelej, 2005
- 7. T1 with distinct anterior and dorsal surfaces, upper edge of the truncation projecting in the center above. T6 with pygidial plate convex, non sculptured, apical half weakly carinated laterally (Afr) . . . . . 8. *Guineomutilla* Suárez, 1977
- T1 gently sloping without dorsal surface and truncation. T6 with convex pygidial plate non sculptured and not carinated even in apical half (Afr, Ori, Pal) . . . . . 18. *Promecilla* André, 1902
- 8. T2 with central yellowish cuticular spot, without spots of pale setae (Pal) . . . . . 15. *Nuristanilla* Lelej in Lelej & Kabakov, 1980
- T2 without pale cuticular spot, with one or three basal spots of pale setae, rarely (some *Dentilla*) with basal band of pale setae . . . . . 9
- 9. Scutellar scale lacking . . . . . 10
- Scutellar scale more or less developed . . . . . 11
- 10. Mandible wide, tridentate apically (Fig. 7) (Ori, Pal) . . . . . 1. *Andreimyrmex* Lelej, 1995
- Mandible falcate and edentate with acute apex (Afr) . . . . . 3. *Corytilla* Arnold, 1956
- 11. Head widened posterad, posteriorly angulate. Pronotum dorsally with medial longitudinal depression (sulcus) laterally bordered by tubercles (Afr) . . . . . 25. *Sulcotilla* Bischoff, 1920
- Head not widened posterad, posteriorly rounded. Pronotum dorsally without medial longitudinal depression (sulcus) . . . . . 12
- 12. Pygidial plate narrow, usually less than 0.3 × T6 width, narrowed and generally closed dorsally, at least 2 × higher than wide; usually with long setae laterally (Fig. 113) . . . . . 13
- Pygidial plate generally at least 0.5 × T6 width, usually open dorsally, its shape variable: elongate with more or less parallel lateral sides (Fig. 109), broadly ovate (at most 1.7 × higher than wide, Fig. 115), or triangular in shape (widened dorsally, Fig. 111) . . . . . 14
- 13. Eye enlarged, minimal distance between eyes 1.1–1.3 × longitudinal eye diameter. Scutellar scale generally lowly produced (Afr, Ori, Pal) . . . . . 7. *Ephutomma* Ashmead, 1899
- Eye moderate in size, minimal distance between eyes 1.6–1.8 × longitudinal eye diameter. Scutellar scale usually erect, well-developed, nail-like (Afr, Ori, Pal) . . . . . 17. *Physetopoda* Schuster, 1949
- 14. T2 with one or three spots of pale setae disposed in central horizontal line. T1 posterodorsally with small medial spot of pale setae (Afr) . . . . . 20. *Pseudocephalotilla* Bischoff, 1920

|         |   |  |
|---------|---|--|
| -       | T2 with one or three spots of pale setae disposed basally. T1 posterodorsally at most with fringe of pale setae   | 15   |
| 15.     | Pygidial plate short-oval (Ori, Pal)  | 13. <i>Nemka</i> Lelej, 1985                                 |
| -       | Pygidial plate elongated, with parallel sides, or widened basally   | 16   |
| 16.     | T2 with three basal spots of pale setae disposed in horizontal line and with at most median apical patch of pale setae. Scutellar scale more than 2 × as wide as long (Ori, Pal)  | 12. <i>Mickelomyrme</i> Lelej, 1995                          |
| -       | T2 with one basal medial spot of pale setae, if lateral pale spots present, then they are disposed posterior to median patch, and with apical band or fringe of pale setae. Scutellar scale usually only slightly wider than its length | 17   |
| 17.     | Pronotum with protruding humeral part, distinctly wider than propodeum (Afr, Ori, Pal)  | 5. <i>Dentilla</i> Lelej in Lelej & Kabakov, 1980            |
| -       | Pronotum without protruding humeral part, usually narrower or at most scarcely wider than propodeum   | 18   |
| 18 (-). | Basal medial spot of pale setae on T2 not enlarged: distance between spot and band of pale setae of tergum more than spot diameter (Afr, Ori, Pal)  | 24. <i>Smicromyrme</i> Thomson, 1870                         |
| 18a.    | Metasomal segment 1 constricted posterad. Pygidial plate rhomboid with granulated sculpture (Pal)   | 24.4. Subgenus <i>Rhombotilla</i> Nagy, 1966                 |
| -       | Metasomal segment 1 not constricted posterad. Pygidial plate another shape, longitudinally striate with striae reaching posterior margin or apically smooth   | 18b  |
| 18b.    | Pygidial plate triangular, conspicuously widened basally (Ori, Pal)   | 24.2. Subgenus <i>Eremotilla</i> Lelej, 1985                 |
| -       | Pygidial plate elongated, often with more or less parallel sides  | 18c  |
| 18c.    | Pygidial plate with striae reaching posterior margin (Pal)  | 24.5. Subgenus <i>Smicromyrme</i> Thomson, 1870              |
| -       | Pygidial plate with striae not reaching posterior margin, apical portion smooth   | 18d  |
| 18d.    | Mesosoma with well developed anterodorsal and posterodorsal angles, dorsally more or less flattened, in lateral view (Pal)  | 24.1. Subgenus <i>Astomyrme</i> Schwartz, 1984               |
| -       | Mesosoma with rounded anterodorsal and posterodorsal angles, dorsally weakly arcuate, in lateral view (Afr, Ori, Pal)   | 24.3. Subgenus <i>Erimyrme</i> Lelej, 1985                   |
| 18 (-). | Basal medial spot of pale setae on T2 enlarged, distance between spot and band of tergum equal to spot diameter or less than it   | 19   |
| 19.     | Pygidial plate apically distinctly angulate, lateral carina distinctly widened apically. Clypeus without median basal tubercle (Afr, Pal)   | 21. <i>Rasnitsynitilla</i> Lelej in Lelej & van Harten, 2006 |
| -       | Pygidial plate apically rounded, lateral carina not widened apically. Clypeus with median basal tubercle (Pal)  | 23. <i>Skorikovia</i> Ovtchinnikov, 2002                     |

## List of genera and subgenera

### 1. *Andreimyrme* Lelej, 1995

(Figs 1–3, 110)

*Andreimyrme* Lelej, 1995b: 5, ♂, ♀; 1996a: 100, ♀; 2002: 50; 2005: 38; 2007: 88; Lelej *et al.* 2007: 56, ♂; Lelej & Brothers 2008: 7; Lo Cascio 2015: 544; Brothers & Lelej 2017: 95, ♂, ♀; Okayasu *et al.* 2018: 303, ♀; Williams *et al.* 2019: 16, ♀; Pagliano *et al.* 2020: 169; Okayasu 2020: 56, ♂, ♀; Terine *et al.* 2021: 185, ♀; Okayasu *et al.* 2021: 3, ♂, ♀.

**Type species** *Andreimyrme long* Lelej, 1995b, ♂, by original designation.

**Dignosis.** MALE. Clypeus deeply concave. Mandible robust, widened apically, tridentate at apex with additional large inner tooth; ventral margin not emarginate basally. Scape bicarinate ventrally; F1 0.7 × as long as wide. Notaulus complete, reaching anterior margin of mesoscutum; parapsidal signum scarcely visible; mesoscutellum punctate; mesopleuron anteriorly with medial deep glabrous depression, without or with precoxal denticle. S2 without basomedial carina and without lateral felt line (except *A. davidi* (André, 1898) with trace of felt line); S8 (hypopygium) without tubercle or carina; genital volsella wide, without basal external lobe, with long setae on inner and ventral margins. FEMALE. Genal carina distinct, forming sharp hypostomal tooth; clypeus with subventral transverse ridge; mandible slender tridentate, wide tridentate, or broadly expanded; prementum armed with posterior rounded tubercle. Mesosomal lateral margins subparallel or convergent posteriorly; prescutellar scales absent; scutellar scale obliterated; metanotal-propodeal suture obliterated. Protarsus with external comb of long spines. T2 with posterior band of pale setae; pygidial plate subconvex with lateral margins defined by weak carinae, subparallel or slightly convergent anteriorly; surface of pygidial plate smooth or longitudinally rugose.

**Diversity and distribution.** Twenty species (one with two subspecies); 15 from females only, five from males only. Predominantly from the Oriental Region but two species penetrate to the Palearctic part of China and *A. pakistanensis* Lelej & Ullah in Lelej *et al.* 2007 is known from Pakistan (Okayasu *et al.* 2021).

**Remarks.** Females of this genus were recently keyed and reviewed (Okayasu *et al.* 2021); most species (15/20) are known from females only.

## 2. *Antennotilla* Bischoff, 1920

(Figs 4a, 4b)

*Antennotilla* Bischoff, 1920: 24 (key), 1921: 710 (description), ♂; Lelej & Brothers 2008: 7; Brothers & Lelej 2017: 95, ♂; Pagliano *et al.* 2020: 169.

**Type species** *Mutilla phoebe* Péringuey, 1899, ♂, by subsequent designation of Bischoff 1921: 710.

**Diagnosis.** MALE. Head normal shape, rounded dorsoposteriorly. Mandible not widened to apex, with weak subbasal tooth beneath, preapical inner tooth distinctly smaller than apical one, inner subbasal tooth much larger than apical one. F1 significantly shorter than F2. Flagellomeres overlapped, F1–5 with row of tyloids. T2 without medial subbasal spot of white setae. S2 with short lateral felt lines. T7 with cuticular yellowish spot. Penial valves short, their apex curved and oriented outside. FEMALE. Unknown.

**Diversity and distribution.** Only known by the type species (male only), which is recognized from South Africa.

**Remarks.** Based on a recent molecular phylogenetic analysis (Waldren *et al.* in press), this genus belongs in a new tribe.

## 3. *Corytilla* Arnold, 1956

(Figs 5–6)

*Corytilla* Arnold, 1956: 63, figs 12, 12a, 12b, ♂; 1962: 846, figs 2, 2a, ♂, ♀; Lelej & Brothers 2008: 17; Brothers & Lelej 2017: 95, ♂, ♀; Pagliano *et al.* 2020: 169.

**Type species** *Corytilla pallidipes* Arnold, 1956, ♂, by original designation.

**Diagnosis.** MALE. Mandible acuminate apically, beneath with large subbasal tooth. F2 a little shorter than F3. Vertex with raised subtriangular carinated platform between posterior ocelli. Mesonotum posterolaterally with full length notauli and short parapdis, hind angles produced into short blunt teeth. T2 with lateral felt lines, S2 without any traces of lateral felt lines. Forewings with very large radial and three radiomedial cells. FEMALE. Mandibles falcate and edentate with acute apex. F2 1.25 × F1 and equal in length F3. Mesosoma little wider behind than in front, one-fifth longer than wide in front. Scutellar scale lacking. T2 with oblong spot of pale golden setae, apical margin and also that of T3 with narrow fringe of same setae. Pygidial plate marginate, the basal two-thirds closely and longitudinally striate, the apical third smooth.

**Diversity and distribution.** Four species, three based on males only and one from both sexes, are recognized in the Afrotropical Region.

**Remarks.** Each of the four species in this genus is known from males, but only one species is known from the female as well. There are no available keys to separate all the species. The males are relatively abundant in Malaise trap samples from southern Africa (KAW, pers. obs.), but we have never seen a female that fits Arnold's (1962) diagnosis.

## 4. *Ctenoceraea* Nonveiller, 1993

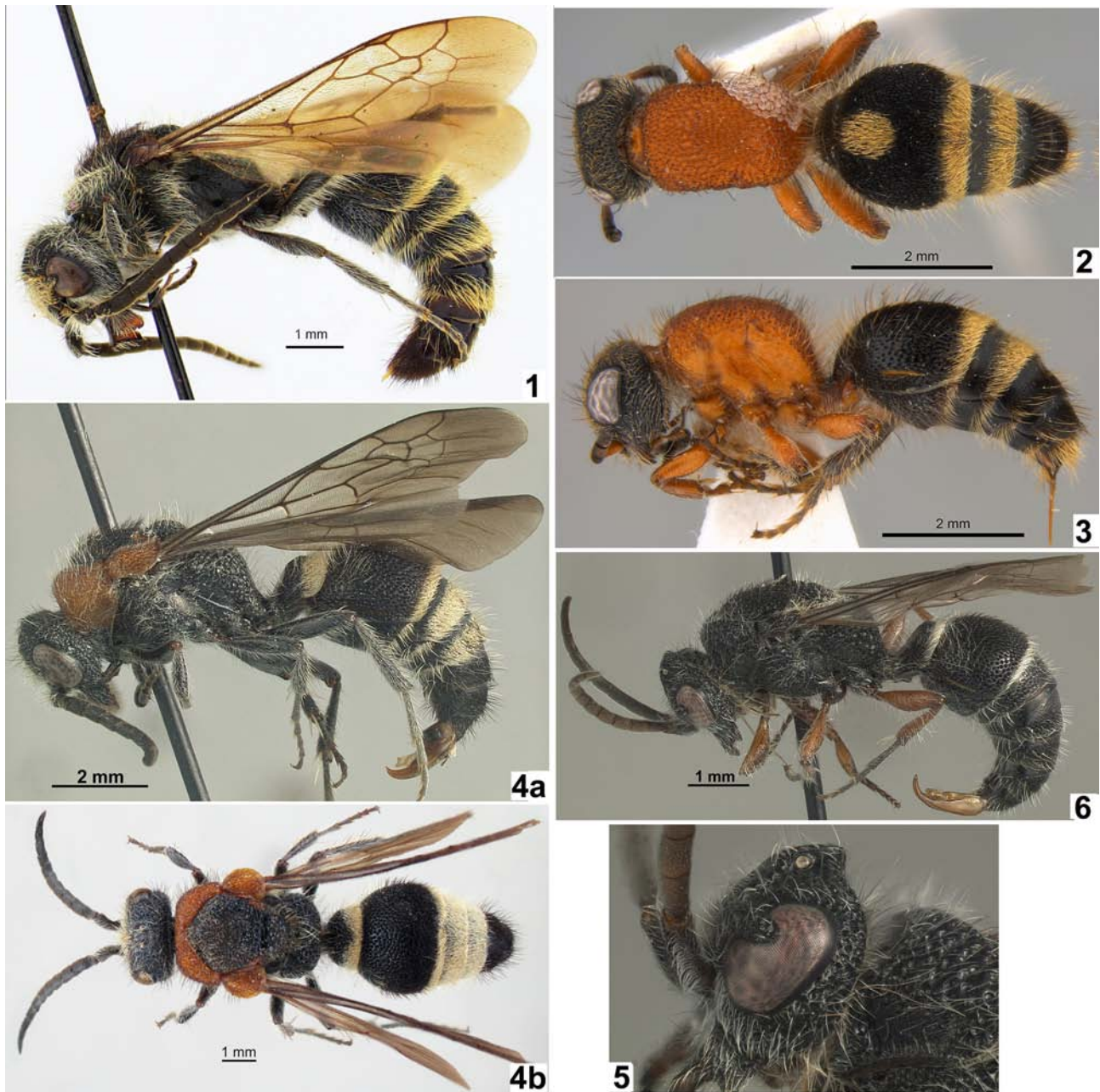
(Figs 7–10)

*Ctenoceraea* Nonveiller, 1993: 17, figs 1–4, ♂; Lelej & Brothers 2008: 17; Brothers & Lelej 2017: 95, ♂; Pagliano *et al.* 2020: 170.

**Type species** *Ctenoceraea pectinella* Nonveiller, 1993, ♂, by monotypy.

**Diagnosis.** MALE. Mandibles beneath with strong subbasal tooth and small preapical inner tooth. Eyes deeply emarginate. F1–8 inside with double series of apophyses: a very long one on the outer side of each article, directed sideways, on F5 nearly 6 × diameter of F5, the other before and after being progressively shorter, and a short one on the inner side, turned forwards. Mesosoma with slightly convex mesoscutellum and very large tegula. Mesopleuron not divided by a transverse impression; sternal part without tubercles. T1 short and narrow, with definite short

dorsal face distinctly separated by carina from declivous anterior slope. T2 with long felt lines, S2 with short felt lines. S8 with subbasal weak transversal swelling. T7 simple. Wings hyaline: Forewings with two radiomedial and one discoidal cell; stigmatic cell nearly completely sclerotized, hyaline only in the middle. Genitalia with long and narrow gonostylus, sharp-pointed and distally strongly curved downwards. Penis valvae short, nearly of equal length. Volsella with a broad cuspis, as long as the valvae, digitus as shown in the Fig. 9. FEMALE (unknown).



**FIGURES 1–6.** 1. *Andreimyrmex long* Lelej, 1995, ♂, holotype, lateral habitus; 2–3. *A. rong* Williams in Okayasu *et al.*, 2021, ♀, holotype, habitus (2. Dorsal view, 3. Lateral view); 4a, 4b. *Antennotilla phoebe* (Péringuey, 1899), ♂: (4a. Lateral view, 4b. Dorsal view); 5–6. *Corytilla pallidipes* Arnold, 1956, ♂ (5. Head, lateral view, 6. Lateral habitus). (Photographs by V. Loktionov (1), D. Brothers (4b), and K. Williams (2, 3, 4a, 5, 6)).

**Diversity and distribution.** One the type species, known only in the male sex, from Senegal is recognized.

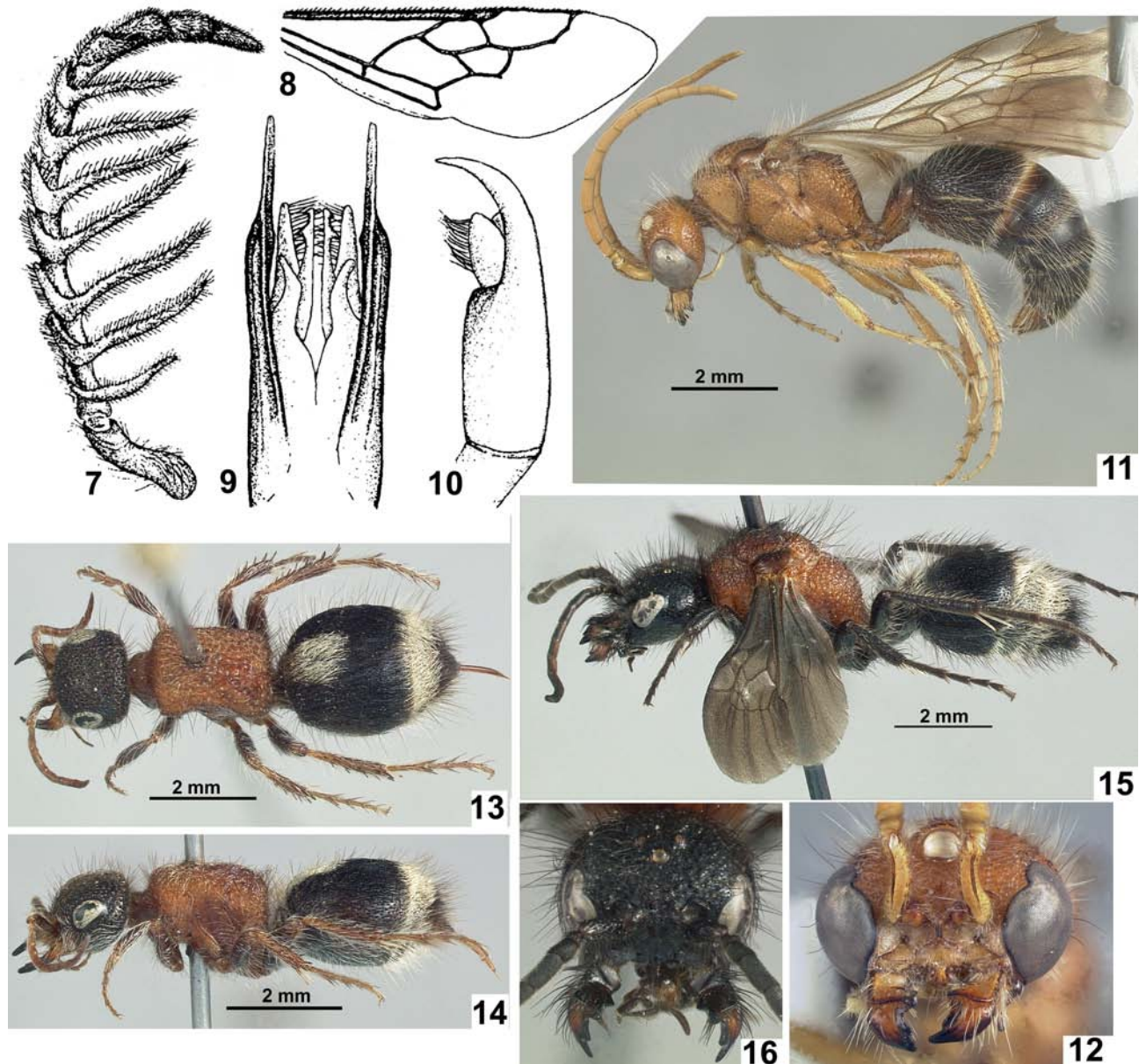
**Remarks.** The male of *Ctenoceraea* has first metasomal segment similar to that of female of *Guineomutilla*, and they possibly belong to the same genus. On the other hand, the slightly convex mesoscutellum and weak transverse subbasal swelling of S8 are similar to males of some genera of Trogaspidiini. The genus is especially rare (apparently known from only one male specimen) and has not been analyzed in a modern phylogenetic context, so its tribal placement here is somewhat tenuous.

5. *Dentilla* Lelej in Lelej & Kabakov, 1980

(Figs 11–16, 111)

*Dentilla* Lelej in Lelej & Kabakov, 1980: 195, ♂, ♀ (as subgenus of *Smicromyrme* Thomson); Lelej 1985: 190, ♂, ♀; Lelej & Brothers 2008: 19; Brothers & Lelej 2017: 95, ♂, ♀; Pagliano *et al.* 2020: 170.

**Type species.** *Mutilla erronea* André, 1900 [1902], ♂, by original designation (junior subjective synonym of *Mutilla curtiventris* André, 1901 according to Pagliano & Strumia (2007: 69), resurrected to valid species by Lelej & Yildirim (2009: 15).



**FIGURES 7–16.** 7–10. *Ctenoceraea pectinella* Nonveiller, 1993, ♂, holotype (7. Antenna, 8. Forewing, 9. Genitalia, dorsal view, 10. Genitalia, lateral view); 11–12. *Dentilla rasnitsyni* Lelej in Lelej & van Harten, 2011, ♂, paratype (11. Lateral habitus, 12. Head, face view); 13–16. *D. curtiventris* (André, 1901): 13. Dorsal habitus, ♀, 14. Lateral habitus, ♀, 15. Lateral habitus, ♂, 16. Head, face view. (Photographs by K. Williams, 7–10 from Nonveiller 1993).

**Diagnosis.** MALE. Inner eye margin with weak notch. Mandible strongly widened apically, quadridentate, rarely tridentate, beneath with large subbasal tooth; preapical inner teeth equal to apical one or larger than it. Clypeus concave, anterior border usually with protruding medial part. Stigmatic cell  $1.4 \times$  distance between base of stigmatic cell and origin of base *RS* on *Sc*. T2 with long lateral felt lines, S2 with short (reduced) lateral felt lines.

FEMALE. Head not widened posterad, posteriorly rounded. Pronotum with protruding humeral part, distinctly wider than propodeum. Scutellar scale more or less developed. T2 with one or three basal spots of pale setae, rarely with basal band of pale setae. Pygidial plate widely triangular, carinated laterally, surface with divergent striae.

**Diversity and distribution.** Twenty-three species (13 based on males only, nine on females only, and one known from both sexes) are recognized predominantly from the Palaearctic Region; there are six Afrotropical species (two of these penetrate from the Palaearctic); and *Dentilla kompantsevi* Lelej, 1995 and *D. malinka* (Nurse, 1903) are Oriental.

**Remarks.** All but three of the species are dull brown in color and apparently nocturnal in their behavior. These nocturnal species are somewhat commonly encountered in arid habitats from North Africa east to India (Lelej 2002, 2005). The more colorful diurnal species occur mainly in the Mediterranean (Lelej, 2002). Lelej's (1985) key includes about half of the currently recognized species.

## 6. *Ephucilla* Lelej, 1995

(Figs 17–21, 112)

*Ephucilla* Lelej, 1995b: 3 (key), 10 (description), ♂, ♀; Lelej & Brothers 2008: 21; Brothers & Lelej 2017: 95, ♂, ♀; Williams *et al.* 2019: 17, ♀; Pagliano *et al.* 2020: 171; Okayasu 2020: 62, ♂, ♀.

**Type species.** *Mutilla naja* Zavattari, 1913 by original designation.

**Diagnosis.** MALE. Head robust, elevated posterad (rounded posterad in *undata* group), frons and vertex longitudinally striate (vertex densely punctate in *undata* group). Mandible tridentate (bidentate in *undata* group), deeply excised beneath with large ventral subbasal tooth (dorsal margin basomedially highly crooked in *undata* group). Clypeus convex (concave in *undata* group) anteriorly with protruding midpart. POD 1.5–2.6 × posterior ocellus diameter. Scape distinctly bicarinate beneath. F1 equal to (in *naja* group) or 1.25 × (in *undata* and *drupa* groups) its maximal width. Tegula slightly protruding beyond scuto-scutellar suture. Mesopleuron beneath with distinct, oblique, precoxal ridges. Metacoxa mesally carinate. Wing hyaline or infuscated, stigmatic cell 0.5–0.6 × distance between base of stigmatic cell and origin of *RS* on vein *Sc*. Metasoma black or with bluish, metallic lustre (in *naja* and *undata* groups) or some basal segments red (in *drupa* group). T1 with distinct dorsum, T2 with lateral felt lines, S2 with strong median basal carina and without any trace of felt lines. T7 usually with longitudinal median impunctate area, widened posterad, S8 simple, without any tubercles or carinae. Genital volsella not widened basally, setae on inner and ventral margin shorter than cuspis length. FEMALE. Genal carina weakly developed; hypostomal tooth absent or angulate to dentiform; clypeus with subapical transverse lamellate carina and basomedial longitudinal tubercle; prementum without dome-like tubercle. Mandible slender. Pronotum without projecting humeral angle; scutellar scale weakly developed. Protarsus without external comb of long spines. T1 without pale setal spots; T2 with apical narrow band of pale setae, slightly widened medially; T3 with wide uniform band of pale setae; T6 lacking distinct flattened pygidium, glabrous, elongate, unsculptured and polished throughout; lateral margins of pygidial plate very weakly carinate apically.

**Diversity and distribution.** Sixteen Oriental species (three also occur in the eastern Palaearctic) are recognized in *Ephucilla*. Three are known from both sexes, nine are known from the male sex only and four are based on females only.

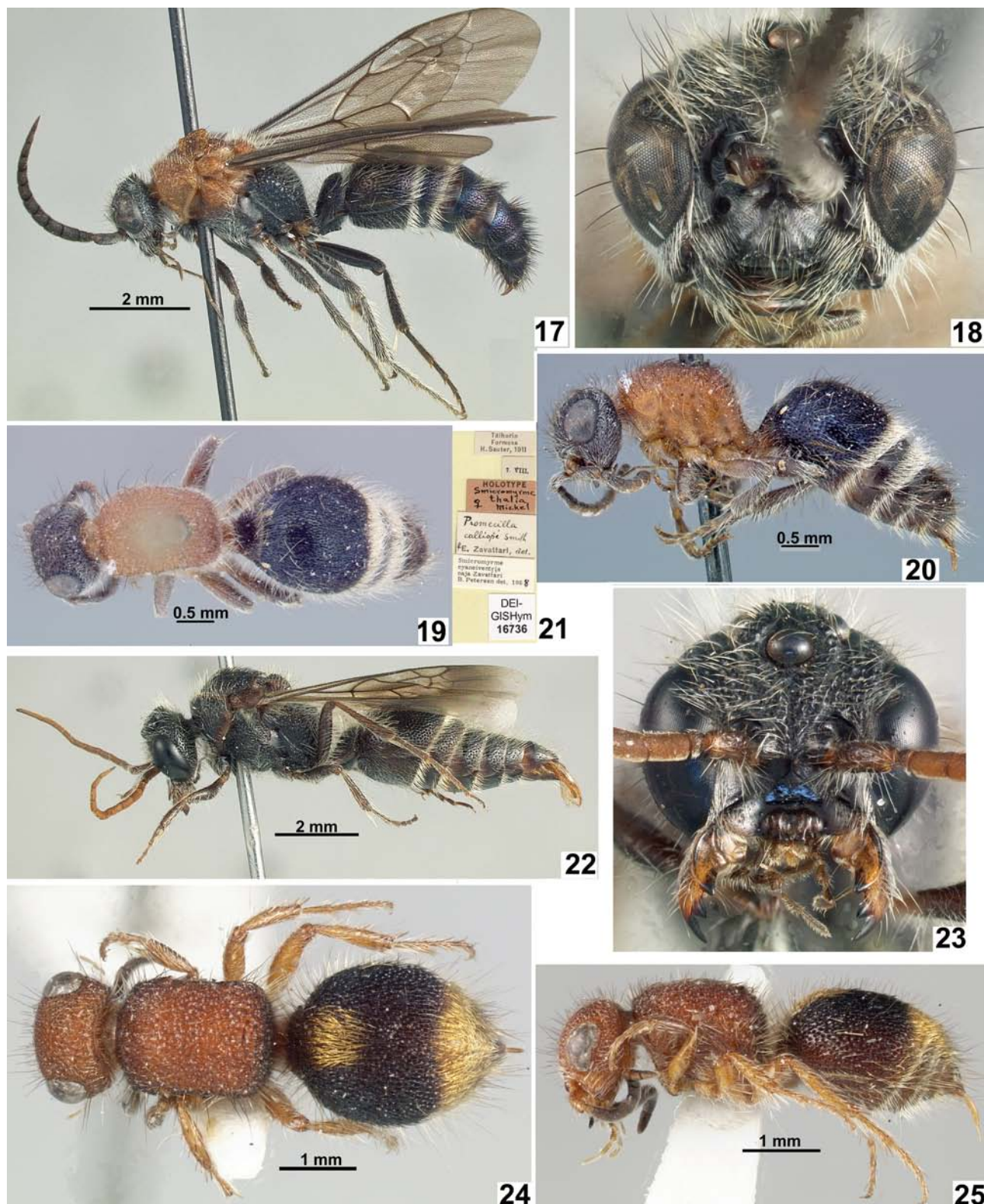
**Remarks.** This genus is easily confused with *Sinotilla* Lelej, 1995, because the lateral pygidial carinae are easily overlooked. In fact, two of the species were initially placed in *Sinotilla* (Lelej 2005). Structurally, females are similar to *Indratilla* Lelej, 1993 from Sri Lanka, but that genus always has T1 and T2 each with two apical whitish setal spots. There are no available keys to separate the species of this genus.

## 7. *Ephutomma* Ashmead, 1899

(Figs 22–25, 113)

*Ephutomma* Ashmead, 1899: 52, 53, ♂, ♀; Lelej 1985: 183, ♂, ♀; Lelej & Brothers 2008: 22; Brothers & Lelej 2017: 95, ♂, ♀; Pagliano *et al.* 2020: 172. Junior subjective synonym of *Pseudophotopsis* André, 1896 according to Brothers 1975: 590. Resurrected as distinct genus and senior objective synonym of *Eremomyrme* Suárez, 1965 by Lelej & Kabakov 1980: 192.

*Eremomyrme* Suárez, 1965. Type species *Mutilla turcestanica* Dalla Torre, 1897, ♂, by automatic designation. Junior objective synonym of *Ephutomma* Ashmead, 1899 (unnecessary replacement name) according to Lelej & Kabakov 1980: 192.



**FIGURES 17–25.** 17–18. *Ephucilla naja* (Zavattari, 1913), ♂: 17. Lateral habitus, 18. Head, face view; 19–21. *E. thalia* (Mickel, 1933), ♀, holotype: 19. Dorsal habitus, 20. Lateral habitus, 21. Labels; 22–23. *Ephutomma angustata* (Skorikov, 1935), ♂: 22. Lateral habitus, 23. Head, face view; 24–25. *E. fletcheri* (Turner, 1911), ♀: 24. Dorsal habitus, 25. Lateral habitus. (Photographs by K. Williams, 19–21 from Integrated insect types database of Taiwanese species <http://twinsectype.nmns.edu.tw/specimen/?id=NMNS-SDEI-01389>).

**Type species.** *Mutilla turcestanica* Dalla Torre, 1897, ♂ (replacement name for *Mutilla incerta* Radoszkowski, 1877, ♂, not Spinola, 1841), by original designation.

**Diagnosis.** MALE. Mandible wide, tridentate, dorsal margin with heighly curved carina, beneath with large subbasal lobe. Clypeus concave, anterior border with medial projection with two teeth or tubercles. Forewing with three radiomedial and two discoidal cells. Stigmatic cell more or less sclerotized. Vosella lamellate, long narrow. FEMALE. Eyes elliptical, approximate, minimal distance between them  $1.1\text{--}1.3 \times$  longitudinal diameter. Clypeus with medial basal tubercle and curved down apical part. Mesosoma narrow and head somewhat wider than pronotum. T2 with large basal spot of pale setae and posterior band widened medially of same setae; T3 with pale band of pale setae. Pygidial plate elongated, sculptured with smooth apical part.

**Diversity and distribution.** Seventeen species are recognized in the genus; 10 based on males only, six based on females only, and one known from both sexes. Fifteen species are Palaearctic, *E. fletcheri* (Turner, 1911) is Oriental, and *E. somalica* (Magretti, 1892) is Afrotropical.

**Remarks.** Like *Dentilla*, most species of *Ephutomma* are apparently nocturnal in behavior, but their body color is generally mostly black. Lelej's (1985) key includes about half of the currently recognized species.

## 8. *Guineomutilla* Suárez, 1977

(Fig. 26)

*Guineomutilla* Suárez, 1977: 219, figs 6, 7, ♀; Lelej & Brothers 2008: 25; Brothers & Lelej 2017: 95, ♀; Pagliano *et al.* 2020: 173.

*Phalacromyrme* Nonveiller in FAO, 1975, nom. nud. Unavailable name (Article 13 of the Code), replaced by *Guineomutilla* Suárez, 1977 in Nonveiller, 1980: 63.

**Type species:** *Guineomutilla mateui* Suárez, 1977, by original designation.

**Diagnosis.** MALE. Unknown. FEMALE. Head transverse, subtrapezoidal-rounded in dorsal view, slightly convex in front and vertex, somewhat narrowed behind eyes and wider than mesosoma. Eyes large, occupying most of the sides of the head, convex, oval. Mesosoma elongated and sub-rectangular, with sub-rectilinear anterior and lateral borders, anterior slightly arched and lateral ones converging backwards, with some unremarkable sinuosity, humeral angles well pronounced at slightly acute angle. Longitudinal profile of mesosoma arched with moderate propodeal slope. Scutellar scale lacking. Metasoma with first segment much narrower than next, but joining it without true constriction; T1 with distinct anterior and dorsal surfaces, upper edge of the truncation projecting in the center above. T2 without any pale design, T3 with band of whitish setae. T6 with pygidial plate convex non sculptured, in apical half weakly carinated laterally.

**Diversity and distribution.** The genus is Afrotropical and known from females only. Only one species is formally described, but four species from Cameroon were named by Nonveiller (1980; Nonveiller in FAO 1975), but never described (*nomina nuda*).

**Remarks.** This genus very similar to and must be closely related to *Promecilla*; it differs in the shape of T1, which has distinct anterior and dorsal surfaces (gently sloping in *Promecilla*).

## 9. *Gynandrotilla* Arnold, 1946

(Fig. 27)

*Gynandrotilla* Arnold, 1946: 50, figs 1, 2, ♂; Lelej & Brothers 2008: 26; Brothers & Lelej 2017: 95, ♂; Pagliano *et al.* 2020: 174;.

**Type species.** *Gynandrotilla ferruginea* Arnold, 1946, ♂, by original designation.

**Diagnosis.** MALE. Apterous. Mandibles acute apically, with preapical tooth, beneath deeply excised. Clypeus raised in the middle, concave transversely on each side of the middle, the apical margin angularly emarginate in the middle and arcuate on each side. Head wider than mesosoma, vertex long. Eyes with small sinus on inner margin, not reniform. Antennae 13-jointed; flagellum elongate and filiform, F1 short, other ones longer than wide, apical flagellomere transversely compressed. Ocelli well developed. Mesosoma not constricted at sutures, all of which

clearly defined; pronotum marginate in front and at the sides, the hind margin angular; tegula fairly large, hirsute; hind margin of the mesonotum transverse, not extending beyond tegula, its posterior corners produced into oblique teeth truncated at the apex. Lateral margins of the nearly flattened scutellum raised; metanotum short but distinct. Propodeum unarmed. T1 not transverse, widened gradually caudad, joining T2 on its cephalic aspect, the anterior angles at its base dilated and directed a little outwards. T7 fairly flattened, wider than long, the apical margin transverse. S1 with a median carina ending caudad in a tooth. S8 (hypopygium) marginate at the sides, feebly concave, its apical margin transverse. Claws unarmed. FEMALE. Unknown.

**Diversity and distribution.** Only the type species, based on the male sex only, is known from Zimbabwe, Botswana and South Africa.

**Remarks.** In southern Africa, this is apparently the only wingless male mutillid with ovate and deeply emarginate compound eyes and a strong ventral mandibular tooth.

## 10. *Indratilla* Lelej, 1993

(Figs 28–29)

*Indratilla* Lelej, 1993: 233, ♂ non ♀; 2005: 42, 179, ♂, ♀; Lelej & Brothers 2008: 28; Brothers & Lelej 2017: 95, ♂, ♀; Pagliano *et al.* 2020: 174.

**Type species.** *Indratilla gynandromorpha* Lelej, 1993, ♂, by original designation.

**Diagnosis.** MALE. Apterous. Head  $1.3 \times$  wider than pronotum. Mandible with well developed preapical tooth on inner border and obtuse basal lobe outside beneath. Ocelli small, ratio POD:OOD 0.6. Clypeus weakly modified, with weakly elevated medial part and slightly emarginated anterior margin. Genal carina developed and ends anterad by obtuse tubercle, ratio of eye height to gena height (head in lateral aspect)  $0.75 \times$ . Eyes weakly sinuate within, not reniform. Preoccipital carina dorsally well developed. Antenna unmodified, two apical flagellomeres dorsoventrally compressed, ratio F1–3 2.4:2.4:2.3. Mesosoma elongated with rounded humeral angle,  $2.5 \times$  longer than minimal width. Tegula large, not touching propodeal spiracle. Scuto-scutellar suture visible, posterolateral scutal angle produced into small tooth, metanotum well visible, mesopleuron weakly convex. Metacoxa mesally carinate. T1 with well developed dorsal and anterior surfaces. T2 with slightly flattened disc and lateral felt lines. S1 with well-developed carina; S2 with basal weak medial, longitudinal carina, without any lateral felt lines. T7 slightly convex. S8 (hypopygium) semitransparent apically, with weakly rounded posterior margin. Genitalia with curved down gonostylus and short broad volsella, penial valves symmetrical, gonostylus ventro-basally with long setae, volsella with dense setae. FEMALE. Head width slightly larger than pronotal width. Eyes moderately large. Genal carina developed and joint with hypostomal carina, latter widened at this point. Prementum not tuberculate. F1  $1.5 \times$  F2. Mandible acuminate with two very weak preapical teeth, without inner subbasal tooth. Mesosoma elongated,  $1.5 \times$  longer than width between propodeal spiracles. Scutellar scale distinct. T1 short with distinct dorsal surface. Disc of T2 flattened even weakly invaginated, with lateral felt line. T6 with pygidial plate glabrous shiny, widened posterad and weakly carinated laterally in apical half and microsculptured in basal half.

**Diversity and distribution.** Only type species, known from both sexes, from the dry zone of Sri Lanka (Lelej 2005) and South India (Tamil Nadu, new record) is recognized.

**Remarks.** The female *Indratilla ceylonica* Lelej, 1993, which was originally assigned to this genus was subsequently transferred to the trogaspidiine genus *Radoszkowskitilla* Lelej, 2005 by Lelej (2005).

## 11. *Karunaratnea* Lelej, 2005

(Figs 30–34, 114)

*Karunaratnea* Lelej, 2005: 145, 148 (key), 181 (description), ♂, ♀; Lelej & Brothers 2008: 30; Brothers & Lelej 2017: 95, ♂, ♀; Pagliano *et al.* 2020: 174.

**Type species:** *Karunaratnea palatupanae* Lelej, 2005, ♂, ♀ (holotype is male), by original designation.

**Diagnosis.** MALE. Head angulate behind the eyes. Mandible tridentate, deeply excised beneath with large subbasal tooth. Clypeus rather flattened with projecting midpart of anterior margin. Ocelli small, POD much less

than OOD. Scape distinctly bicarinate beneath, flagellomeres not shortened, F1  $1.5 \times$  longer its width and slightly shorter than F2. Pronotum angulate. Notauli and parapsids developed in posterior half. Tegula slightly projected over mesoscuto-scutellar suture. Parascutal carina weak. Mesoscutellum simple. Mesopleuron beneath without precoxal ridge. Propodeum shortened, dorsum with two medial sharp tubercles bordered medial elongate cell. Metacoxa carinate inside. Wing shortened, slightly infuscated, stigmatic cell approximately equal to distance between base of stigmatic cell and origin of *RS* on vein *Sc*. T2 with long lateral felt lines, S2 without any trace of felt lines. T7 and S8 punctured throughout. Volsella slightly longer than penial valve, cuspis with tuft of short setae inside and ventral basal setae no longer than cuspis length. FEMALE. Fore tarsus without external comb of spines. Mandible slender bidentate. Clypeus with transverse lamellate carina and small medial basal tubercle. Genal carina weak and forming tubercle on hypostomal carina. F1  $1.25 \times$  longer than its maximum width. Mesosoma slightly divergent posterad, shortened, length equal its maximum width. Posterior propodeal slope abrupt. Scutellar scale well developed. Mid and hind tibia with two row of spines. T6 with shiny smooth medial part not carinated laterally but bordered by pale setae. T2 with posterior narrow fringe of pale setae widened medially, basally with or without medial patch of pale setae. T3 with band of pale setae.

**Diversity and distribution.** Four species (one based on females only, two based on males only, and one known from both sexes) are recognized from Oriental region.

**Remarks.** Lelej (2005) suggested that many undescribed species occur in India and Sri Lanka, so no keys have been produced for separating the members of *Karunaratnea*.

## 12. *Mickelomyrme* Lelej, 1995

(Figs 35–40)

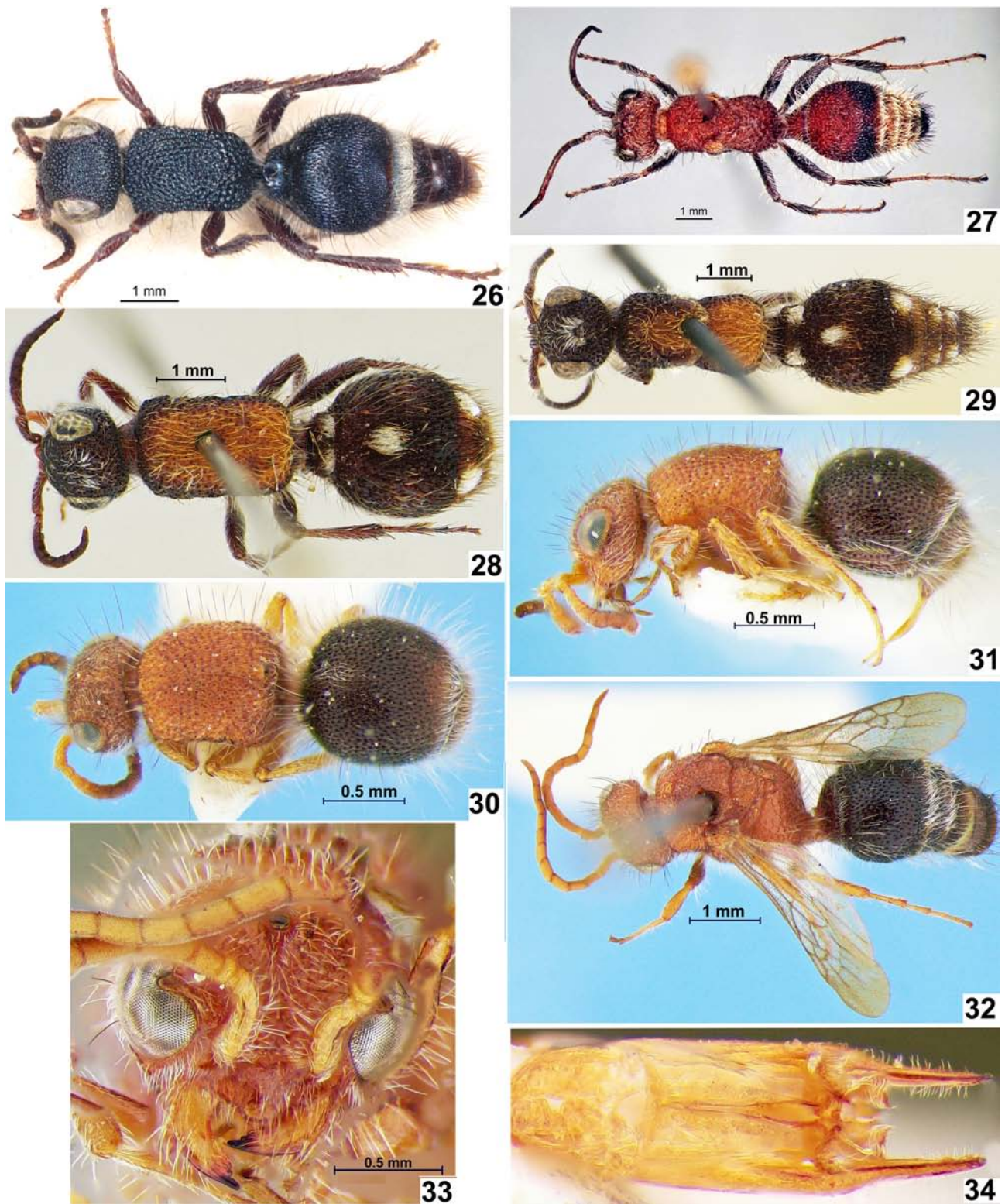
*Mickelomyrme* Lelej, 1995a: 17, ♂, ♀; Lelej & Brothers 2008: 34; Brothers & Lelej 2017: 95, ♂, ♀; Williams *et al.* 2019: 18, ♀; Pagliano *et al.* 2020: 174; Okayasu 2020: 42, ♂, ♀; Thaochan *et al.*, 2022: 155, ♀.

**Type species.** *Mutilla hageni* Zavattari, 1913, ♂, by original designation.

**Diagnosis.** MALE. Head robust, elevated posterad, frons and vertex longitudinally striate. Mandibles bidentate at apex, deeply excised beneath with large subbasal tooth. Clypeus weakly convex with protruding midpart of anterior margin. Ocelli not enlarged. Scape distinctly bicarinate beneath. Tegula protruding behind scuto-scutellar suture  $\frac{1}{4}$ – $\frac{1}{3}$  its length. Parascutal carinae weak. Mesoscutellum simple. Mesopleuron beneath without precoxal tubercles. Metacoxa mesally carinate. Wing dark fuscous, stigmatic cell almost  $2 \times$  shorter than distance between base of stigmatic cell and origin of *RS* on vein *Sc*. Metasoma black or some basal segments yellowish-red. T1 long,  $\frac{2}{3}$  or even more than T2. S2 with short lateral felt lines, T2 with long lateral felt lines. T7 usually with longitudinal median impunctate line, S8 (hypopygium) simple, without any tubercles or carinae. Volsella of genitalia with long narrow cuspis with long setae, basivolsella with rounded lobe outside, external margin of basivolsella with extremely long curved setae. FEMALE. Minimum distance between eyes more than  $1.4 \times$  eye height; genal carina and hypostomal tooth absent; clypeus with subapical transverse ridge; prementum without dome-like tubercle. Mandible slender. Pronotum without projecting humeral angle; scutellar scale distinct, more than twice wider than long. Protarsus with external comb of long spines. T1 without pale setal spots; T2 with three basal spots of pale setae disposed in straight transverse line; T2 at most with apico-medial small patch of pale setae; T3 with wide uniform band of pale setae; T4 sometimes with entire or medially interrupted band of pale setae; pygidial plate elongate, distinctly carinate laterally; surface of pygidial plate longitudinally striate, usually smooth on apical  $\frac{1}{4}$ – $\frac{1}{5}$ .

**Diversity and distribution.** Twenty-three species (one subdivided into two subspecies) are recognized from the Oriental Region, two of these penetrate to the Palaearctic part of China (Pagliano *et al.* 2020). Seven are known from both sexes, nine are based on males only, and seven are based on females only.

**Remarks.** Most females have the disc of T2 marked with three setal spots disposed transversely, but *M. chinensis* (Smith, 1855) has a single spot, *M. athalia* (Pagden, 1949) often has the mesal spot obliterated, and *M. zebina* (Smith, 1860) has the lateral spots disposed posterior to the middle spot. Lelej's (1996b) key includes about half of the currently known species.



**FIGURES 26–34.** 26. *Guineomutilla mateui* Suárez, 1977, ♀, dorsal habitus; 27. *Gynandrotilla ferruginea* Arnold, 1946, ♂, dorsal habitus; 28–29. *Indratilla gynandromorpha* Lelej, 1993: 28. ♀, dorsal habitus, 29. ♂, holotype, dorsal habitus; 30–34. *Karunaratnea palatupanae* Lelej, 2005: 30–31. Paratype, ♀ (30. Dorsal habitus, 31. Lateral habitus); 32–34. Holotype, ♂: 32. Dorsal habitus, 33. Head, face view, 34. Genitalia, ventral view. (Photographs by D. Brothers (26, 27), V. Loktionov (28, 29), and A. Lelej (30–34)).

### 13. *Nemka* Lelej, 1985

(Figs 41–44, 115)

*Nemka* Lelej, 1985: 240, ♂, ♀ (as subgenus of *Smicromyrme* Thomson); 1995a: 2; Lelej & Brothers 2008: 39; Brothers & Lelej 2017: 95, ♂, ♀; Williams *et al.* 2019: 22, ♀; Pagliano *et al.* 2020: 169; 176; Okayasu 2020: 24, ♂, ♀.  
*Horaia* Tsuneki, 1993: 43 (as subgenus of *Smicromyrme* Thomson). Type species *Smicromyrme (Horaia) chihpenchius* Tsuneki, 1993, ♂, by original designation. Junior homonym of *Horaia* Tonnoir, 1930 (Diptera). Junior subjective synonym of *Nemka* Lelej, 1985 according to Lelej, 1995a: 2.

**Type species:** *Mutilla viduata* Pallas, 1773, ♂, by original designation.

**Diagnosis.** MALE. Head not elevated posterad, frons and vertex usually punctate, not longitudinally striate. Mandibles robust apically tridentate, deeply excised beneath with large subbasal tooth. Hypostomal bridge without tooth. Ocelli not enlarged. Scape obscurely bicarinate beneath. Mesopleuron with one or two precoxal denticles or tubercles beneath. Tegula rounded posterad, not or slightly protruding behind mesoscuto-scutellar suture. Wing dark fuscous, stigmatic cell slightly less than distance between base of stigmatic cell and origin of *RS* on vein *Sc*. Metasoma usually with some segments red or yellowish-red. T1 shorter than half of T2. T2 with longer lateral felt lines, S2 with short lateral felt lines. Volsellar cuspis long and narrow with long setae, volsella with basal external lobe and long setae; setae on inner and ventral margin of external lobe extremely long and curved. FEMALE. Unlike the other Oriental and Palaearctic *Smicromyrmini*, *Nemka* females have the pygidium well-defined and short oval in shape. Other useful characters include the presence of a distinct scutellar scale, a single medial setal spot on the T2 disc, and the posterior setal band of T2 variably expanded. Minimum distance between eyes more than  $1.4 \times$  eye height; genal carina and hypostomal tooth absent; clypeus with subapical transverse ridge; prementum without dome-like tubercle. Mandible slender. Pronotum without projecting humeral angle; scutellar scale distinct. Protarsus with external comb of long spines. T1 without pale setal spots; T2 with basomedial spot and apical spot or narrow band of pale setae, the latter slightly widened medially; T3 with wide uniform band of pale setae; pygidial plate short oval, distinctly carinate laterally; surface of pygidial plate longitudinally rugoso-striate throughout or unsculptured apically.

**Diversity and distribution.** Eighteen species are recognized: *Nemka viduata* (Pallas, 1773) with five subspecies and *N. aurantiaca* (Skorikov, 1935) are distributed in Palaearctic, and 16 species occur in Oriental Region, three of these penetrate to the Palaearctic parts of China and Iran. Seven species are known from both sexes, three are known from males only, and eight are known from females only.

**Remarks.** More than half of the known species are included in Lelej's (1995a) key.

### 14. *Nordeniella* Lelej, 2005

(Figs 45–48)

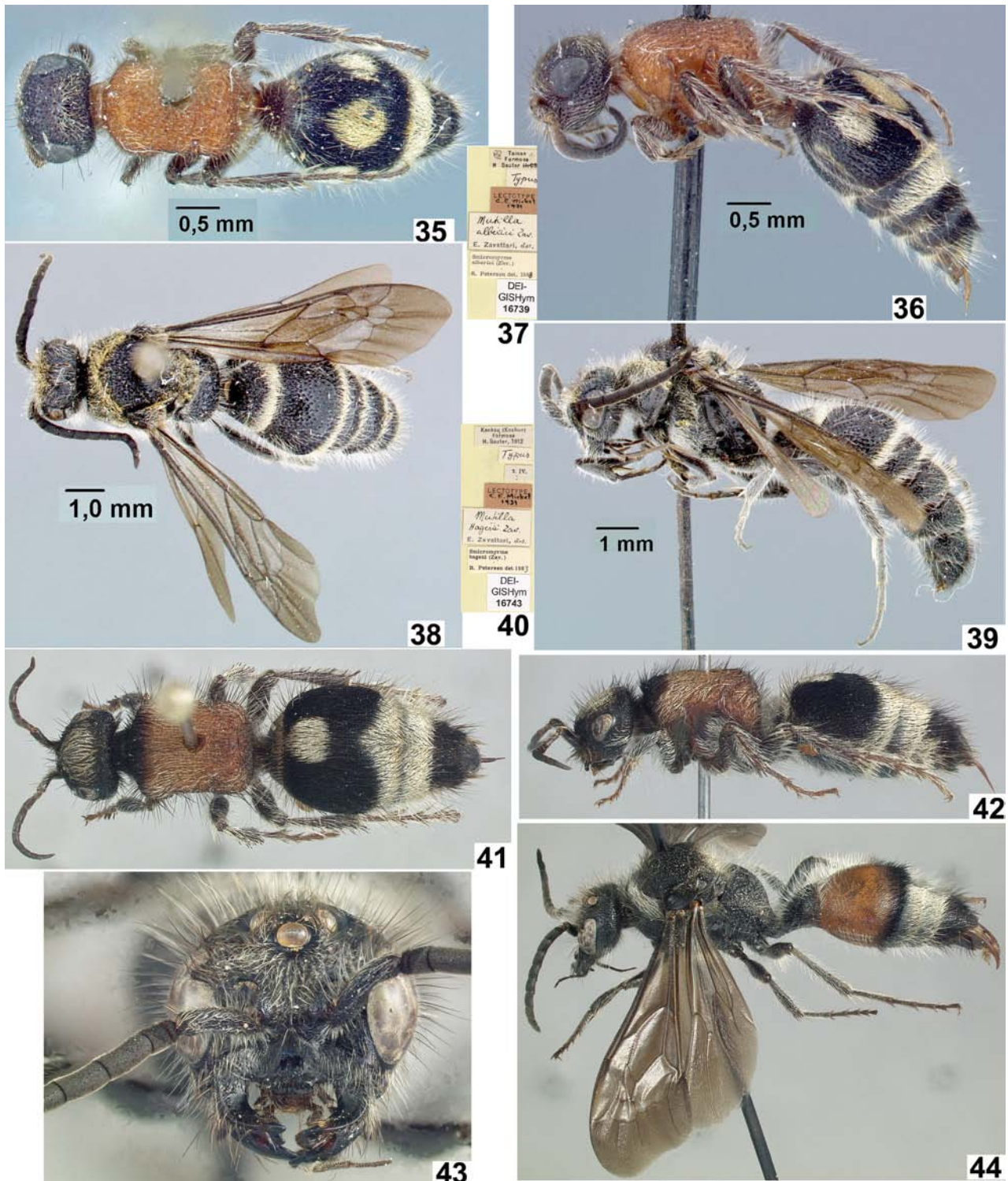
*Nordeniella* Lelej, 2005: 48, 145, 149, 185, ♂, ♀; Lelej & Brothers 2008: 40; Brothers & Lelej 2017: 95, ♂, ♀; Williams *et al.* 2019: 22, ♀; Pagliano *et al.* 2020: 177; Okayasu 2022: 57, ♀; Thaochan *et al.* 2022: 158, ♀.

**Type species.** *Mutilla thermophila* Turner, 1911, by original designation.

**Diagnosis.** MALE. Head angulate behind the eyes. Mandible tridentate, without subbasal tooth beneath. Clypeus rather flattened, anterior border with two medial tubercles. Ocelli small, POD less than OOD. Scape distinctly bicarinate beneath, F1 equal or slightly longer its width and evidently shorter than F2. Pronotum angulate. Notauli and parapsids developed in posterior half. Tegula slightly projected over mesoscuto-scutellar suture. Parascutal carina weak. Scutellum simple. Mesopleuron without precoxal ridge. Propodeum not shortened. Metacoxa mesally carinate. Wing well developed or shortened (in type species), slightly infuscated, stigmatic cell approximately equal to distance between base of stigmatic cell and origin of *RS* on vein *Sc*. T2 with long lateral felt lines, S2 without any trace of felt lines. T7 and S8 punctured throughout. Volsella slightly longer than penial valves, ventrally with tuft of basal setae, which no longer than cuspis. FEMALE. The female of this genus is separated from the other *Smicromyrmini* by F1 subequal F2. The female is similar to that of *Ephucilla*, *Promecilla*, and *Sinotilla* by having the mandible slender and the pygidial plate convex and smooth, but differs by the mesosomal lateral margins subparallel or divergent posterad (convergent in *Ephucilla* and *Promecilla*), the scutellar scale obliterated (present in *Ephucilla* and *Sinotilla*), and the lateral margins of pygidial plate convergent anterad and not carinate throughout (subparallel and with weak carinae posteriorly in *Ephucilla*).

**Diversity and distribution.** Nine species (one known from both sexes, one based on males only, and seven based on females only) are recognized from India, Sri Lanka, Thailand, and Indonesia (Lelej 2005; Williams *et al.* 2019; Okayasu 2022).

**Remarks.** There are no available keys to separate the species in this genus.



**FIGURES 35–44.** 35–40. *Mickelomyrme hageni* (Zavattari, 1913): 35–37. *M. hageni*, ♀ (= *Mutilla alberici* Zavattari, 1913, ♀, lectotype); 38–40. *M. hageni*, ♂ (*Mutilla hageni* Zavattari, 1913, ♂, lectotype). 41–44. *Nemka viduata* (Pallas, 1773), ♀ (41, 42), ♂ (43, 44). 35, 38, 41. Dorsal habitus; 36, 39, 42, 44. Lateral habitus; 37, 40. Labels; 43. Head, face view. (Photographs 35–37 from Integrated insect types database of Taiwanese species <http://twinsecttype.nmns.edu.tw/specimen/?id=NMNS-SDEI-01376>; 38–40 <http://twinsecttype.nmns.edu.tw/specimen/?id=NMNS-SDEI-01380>) and by K. Williams (41–44)).

## 15. *Nuristanilla* Lelej in Lelej & Kabakov, 1980

(Fig. 49)

*Nuristanilla* Lelej in Lelej & Kabakov, 1980: 193, ♀; Lelej & Brothers 2008: 40; Brothers & Lelej 2017: 96, ♀; Pagliano *et al.* 2020: 178.

**Type species.** *Nuristanilla kabakovi* Lelej in Lelej & Kabakov, 1980, ♀, by original designation.

**Diagnosis.** MALE. Unknown. FEMALE. Head slightly narrower its height, but distinctly wider than pronotum. Clypeus with median basal process. Ratio of pedicel and F1–3 0.4:0.9:0.7:0.9. Mesosoma generally widened posterad, scutellar scale developed. Pygidial plate elongated, parallelsided, carinated laterally, with divergent striae, apically smooth. T2 with rounded cuticular (not setal!) yellowish spot, T3–5 with sparse whitish setae.

**Diversity and distribution.** One species, based on the female sex only, is recognized. Only the holotype collected by O.N. Kabakov in Eastern Afghanistan is known for this species.

**Remarks.** The genus is closest to *Ephutomma* by the antennal ratio of F1–3 and by the width of the head and pronotum, but differs by having a yellowish cuticular spot on T2. The same character distinguishes *Nuristanilla* from *Smicromyrme*.

## 16. *Paglianotilla* Lelej in Lelej & van Harten, 2006

(Figs 50–52)

*Paglianotilla* Lelej in Lelej & van Harten, 2006: 24, ♂; Lelej & Brothers 2008: 42; Brothers & Lelej 2017: 96, ♂; Pagliano *et al.* 2020: 178.

**Type species.** *Paglianotilla hogenesi* Lelej in Lelej & van Harten, 2006, by original designation.

**Diagnosis.** MALE. Head rounded behind the eyes. Mandible tridentate, not excised beneath, second preapical tooth enlarge. Clypeus rather flattened. Ocelli small, POD much less than OOD. Scape strongly bicarinate beneath, space between carinae punctate. Flagellomeres shortened, each flagellomere above has apical projection overlapping base of next flagellomere, F1 at least 2.0 × shorter than F2. Pronotum posteriorly angulate medially. Notauli and parapsids well developed. Tegula slightly projecting over mesoscuto-scutellar suture. Parascutal carina weak. Scutellum simple. Mesopleuron without precoxal ridge. Propodeum not shortened. Metacoxa mesally carinate. Wing well developed with three radio-medial and two discoidal cells, more or less infuscated, stigmatic cell much less than distance between base of stigmatic cell and origin of *RS* on vein *Sc*. T2 with long lateral felt lines, S2 without any trace of felt lines. T7 punctured throughout. Hypopygium (S8) posteriorly weakly biemarginated. Volsellar cuspis wide with narrow curved apical part. Penial valves short, their apex curved back and oriented outside. FEMALE. Unknown.

**Diversity and distribution.** One species, based on the male sex only, is recognized from Yemen, but an undescribed species has been examined from South Africa (Lelej & van Harten, 2006).

**Remarks.** The antennal flagellomeres are superficially similar to those of *Antennotilla*, but the genitalia and other features are not similar. *Paglianotilla* and *Indratilla* are apparently the only *Smicromyrmini* to have a distinct mesal white setal patch on T2 in the male sex (Fig. 50).

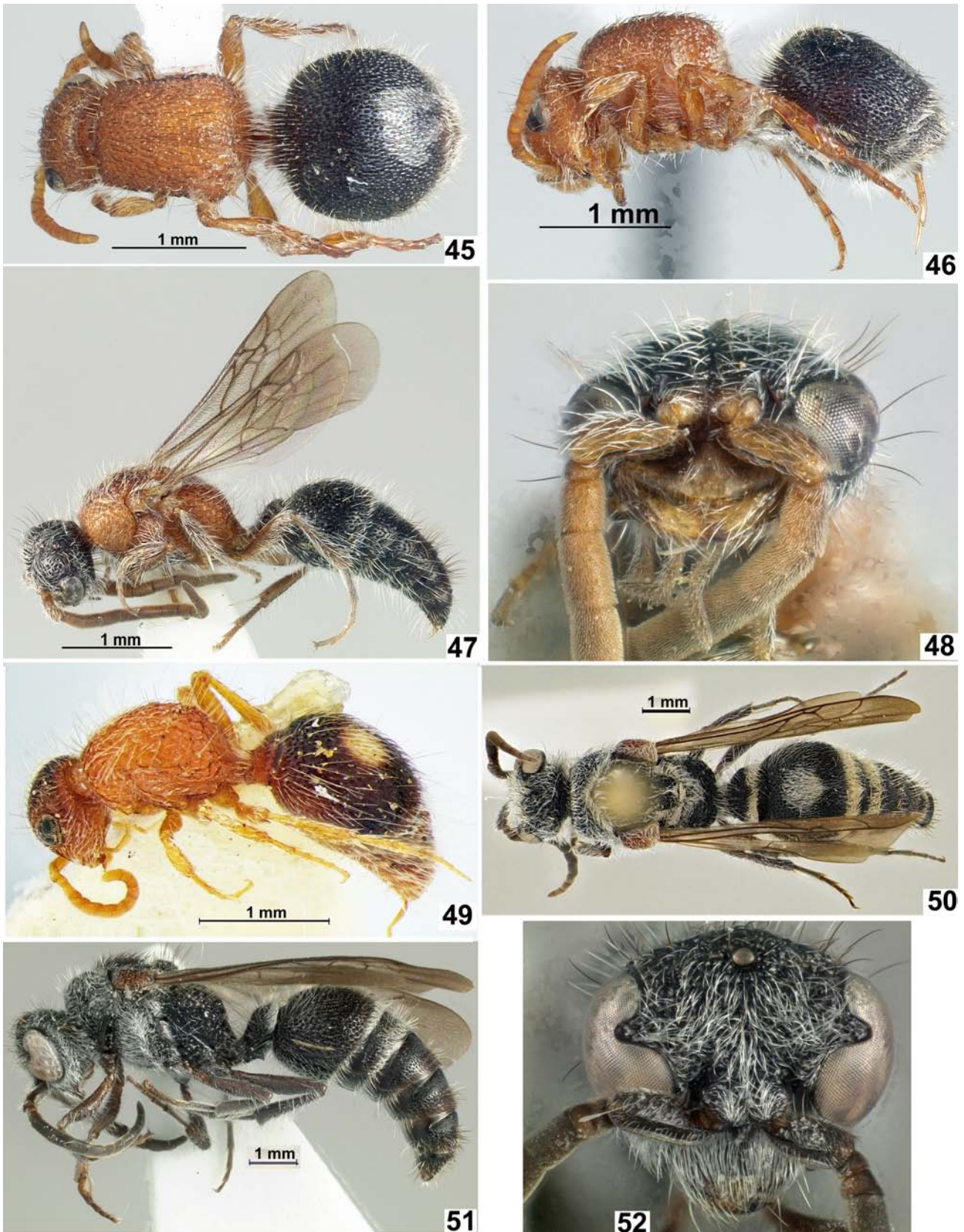
## 17. *Physetopoda* Schuster, 1949

(Figs 53–56)

*Physetopoda* Schuster, 1949: 112, ♂, ♀; Lelej 1985: 197, ♂, ♀; Lelej & Brothers 2008: 46; Brothers & Lelej 2017: 96, ♂, ♀; Williams *et al.* 2019: 23, ♀; Pagliano *et al.* 2020: 178.

*Paramyrme* Lelej, 1977: 531, ♂, ♀ (as subgenus of *Smicromyrme* Thomson); Lelej 1984: 101. Type species *Mutilla montana* Panzer, 1805, ♀, by original designation (junior synonym of *Mutilla halensis* Fabricius, 1787, ♀, according to Panzer, 1806: 212). Junior subjective synonym of *Physetopoda* Schuster, 1949 according to Brothers, 1983: 441.

**Type species** *Physetopoda insularis* Schuster, 1949, ♂ by original designation (junior subjective synonym of *Mutilla rubrocincta* Lucas, 1848, ♂ according to Brothers 1983: 444).



**FIGURES 45–52.** 45–48. *Nordeniella thermophila* (Turner, 1911): 45. ♀, dorsal habitus, 46. ♀, lateral habitus, 47. ♂, lateral habitus, 48. ♂, head, face view. 49. *Nuristanilla kabakovi* Lelej in Lelej et Kabakov, 1980, ♀, holotype, lateral habitus. 50–52. *Paglianotilla hogenesi* Lelej in Lelej et van Harten, 2006, ♂, paratype, dorsal habitus (50), lateral habitus (51), head, face view (52). (Photographs by K. Williams and V. Loktionov (49, 50)).

**Diagnosis.** MALE. Mandible tridentate, rarely bidentate, deeply excised beneath with large subbasal tooth. Clypeus usually with transverse smooth band and two preapical tubercles. Stigmatic cell usually narrow, well- or not sclerotized with thicker posterior abscissa. T2 with lateral felt lines, S2 without any felt lines. Basivolsellar setae long, touch gonostylus apex, rarely (*scutellaris* group) not elongated. FEMALE. This genus is recognized by having a distinct scutellar scale and having the pygidium sides narrowed basally. In other features, this widespread and diverse genus shows considerable variation. Clypeus with curved down apical border and well visible transverse carina and medial basal tubercle. Mandible with two small preapical denticles. Scutellar scale well developed, nail-like. Pygidial plate weak narrowed basally, with lateral tuft of pale (rarely black) setae. T2 with medial basal and apical spots of pale setae, rarely with apical band of pale setae, often with lateral subbasal semicircular spots of pale setae. T3 with band of pale setae.

**Diversity and distribution.** Forty-seven species are known (six are subdivided into multiple subspecies), mostly from the Palaearctic, though many of the Afrotropical members of *Smicromyrme* will likely be transferred to *Physetopoda* in the future and five species are known from the Oriental Region. Four are known from both sexes, 13 are based on females only, and 30 are based on males only.

**Remarks.** Many Palaearctic species are included in regional keys (*e.g.* Lelej 1985, Pagliano & Strumia 2007), but no available keys treat all, or even half, of the species.

### 18. *Promecilla* André, 1902

(Figs 57–60)

*Promecilla* André, 1902: 14 (key), 30 (description), ♀; Cameron 1902: 271, fig. 8, 9, ♀ ♂; Lelej & Brothers 2008: 48; Brothers & Lelej 2017: 96, ♂, ♀; Pagliano *et al.* 2020: 182.

**Type species.** *Mutilla regia* Smith, 1855, ♀, by original designation.

**Diagnosis.** MALE. Clypeus with transverse preapical carina. F1 evidently shorter than F2. Mandible tridentate, with large subbasal lobe beneath. Wings more or less fuscous. Stigmatic cell not sclerotized. T2 with lateral felt lines, S2 without any trace of felt lines. Hypopygium (S8) without any carina or processes. Head, mesosoma, antennae and legs usually black, metasomal segments 2–5(6) yellowish-orange. FEMALE. Clypeus with medial basal tubercle, with strongly bent down apical round and forming sharp transverse carina. Inner eye border weakly sinuous. F1 around 2 × shorter than F2, the latter slightly shorter than F3. Mesosoma elongated, evidently narrowed posterad, propodeum posterad gently sloping. Mesopleuron weakly convex with vertical row of large punctures. Scutellar scale lacking. T6 with pygidial plate convex not sculptured, non carinated even in apical half. Pronotum, and often propodeum dorsally with spot of pale setae. Metasoma often metallic blue.

**Diversity and distribution.** There are twenty-seven recognized species (Bischoff 1920; Lelej 2002, 2005; Pagliano *et al.*, 2020), mostly from the Oriental Region. Three species occur in the Palaearctic and five in the Afrotropical Region. Four species are known from both sexes, three are known from males only, and 20 are known from females only.

**Remarks.** There are no keys that treat all, or even half, of the known *Promecilla* species. This genus commonly has metallic blue or purple body color.

### 19. *Psammotherma* Latreille, 1825

(Figs 61–62)

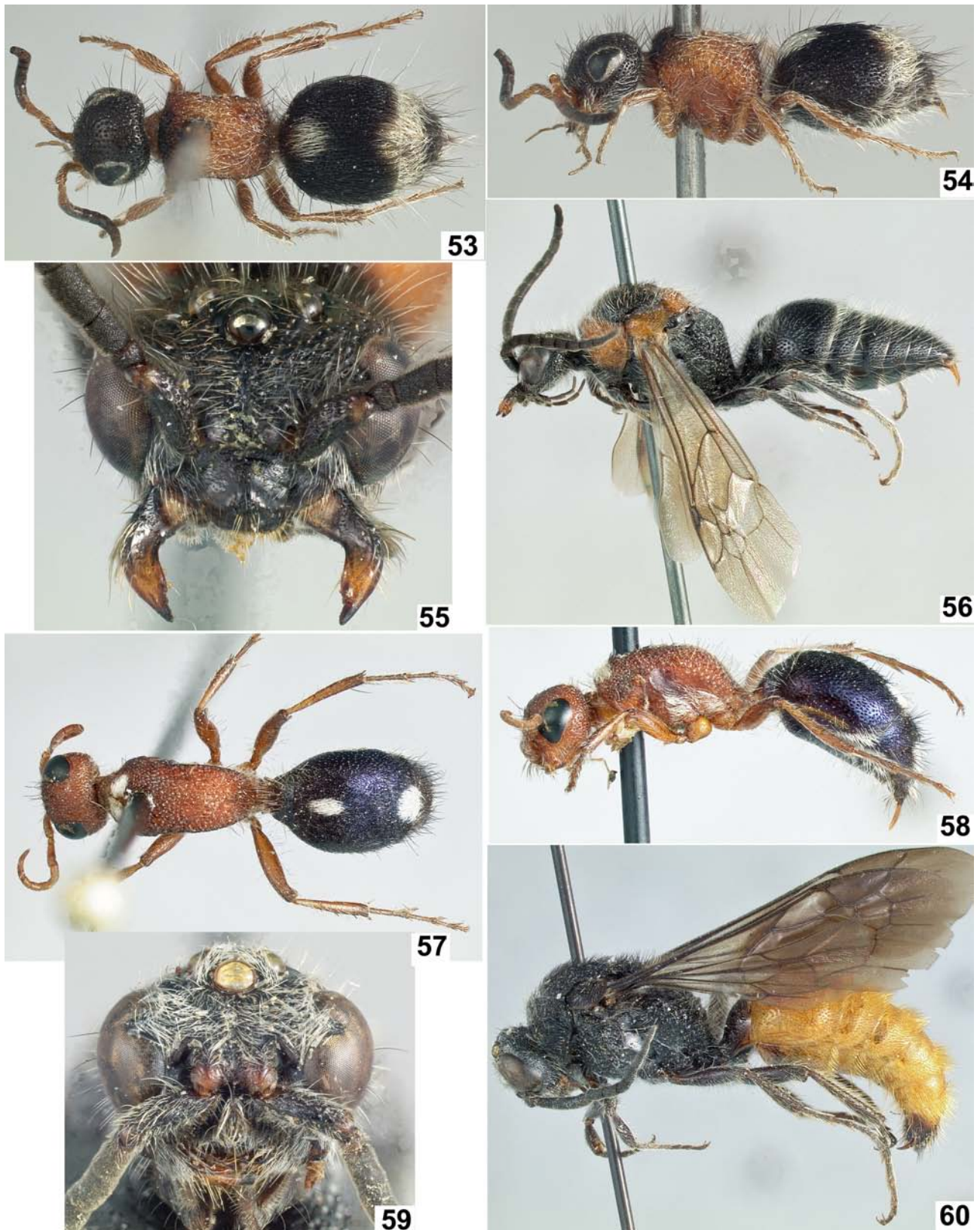
*Psammotherma* Latreille, 1825: 453, ♂; Lelej & Brothers 2008: 48; Brothers & Lelej 2017: 96, ♂; Pagliano *et al.* 2020: 184.

**Type species.** *Mutilla flabellata* Fabricius, 1804, ♂, by subsequent monotypy of Latreille, 1829: 315.

**Diagnosis.** MALE. Head slightly narrower than thorax. Clypeus longitudinally convex, roof-like. Mandible tridentate, not widened apically, preapical inner teeth distinctly smaller than apical one, beneath with basal carina, without subbasal tooth. Ocelli small, POD much less than OOD. Flagellomeres overlapped, F1–7(10) with apophyses, double series of apophyses more or less equal in length. T2 with long lateral felt line, S2 with short lateral felt line. T7 black, without cuticular yellowish spot. FEMALE. Unknown.

**Diversity and distribution.** Four species, all known from males only, are recognized from South Africa.

**Remarks.** Based on a recent molecular phylogenetic analysis (Waldren *et al.* in press), this genus belongs in a new tribe. There are no published keys that treat the species of *Psammotherma*.



**FIGURES 53–60.** 53–54. *Physetopoda halensis* (Fabricius, 1787), ♀: 53. Dorsal habitus, 54. Lateral habitus; 55–56. *Ph. oratoria* (Chen, 1957), ♂: 55. Head, face view, 56. Lateral habitus. 57–60. *Promecilla regia* (Smith, 1855): 57. ♀, dorsal habitus, 58. ♀, lateral habitus 59. ♂, head, face view, 60. ♂, lateral habitus. (Photographs by K. Williams).

## 20. *Pseudocephalotilla* Bischoff, 1920

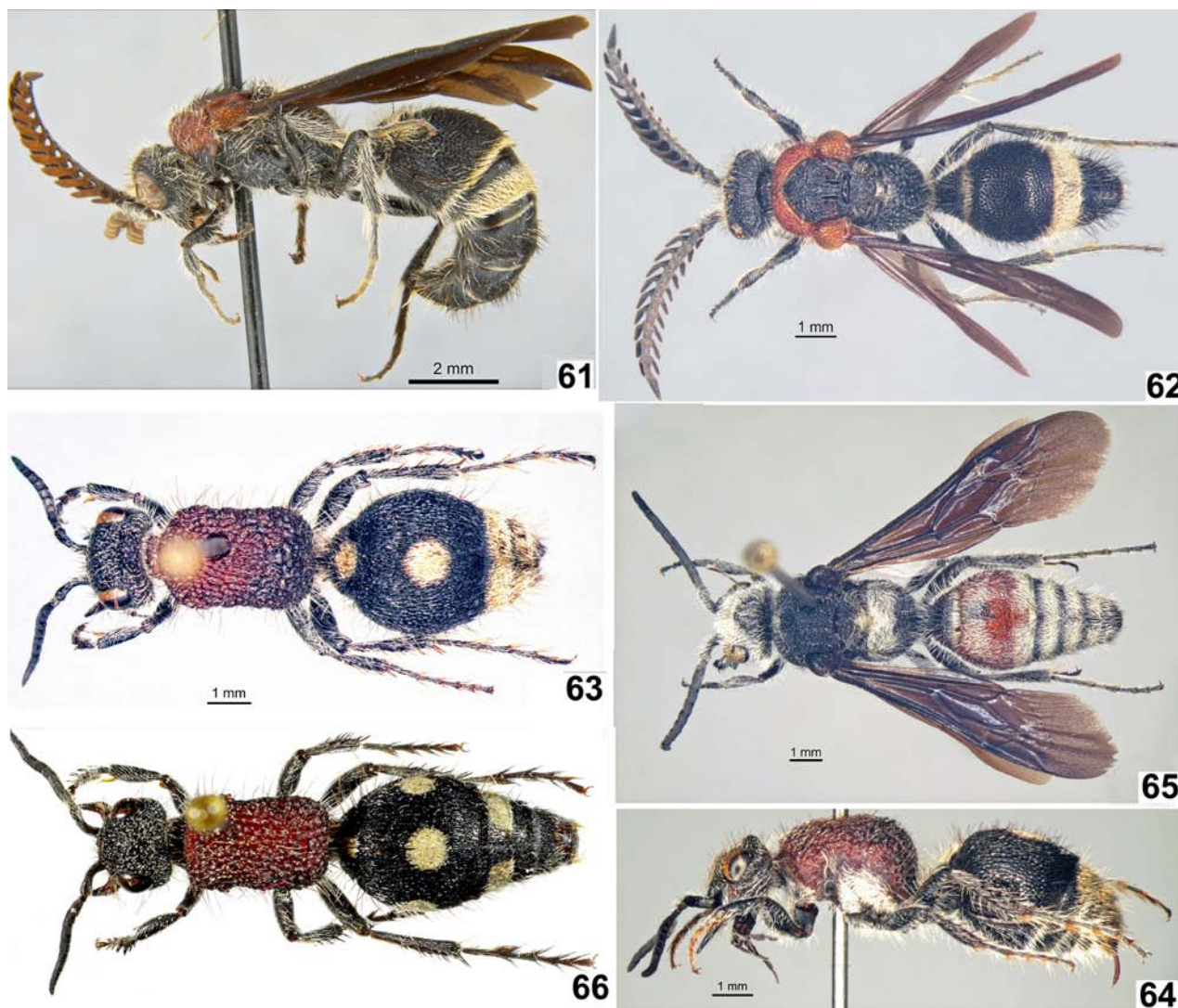
(Figs 63–66)

*Pseudocephalotilla* Bischoff, 1920: 24 (key), 1921: 514 (description), ♂; Nonveiller 1979: 15, ♂, ♀; Lelej & Brothers 2008: 49; Brothers & Lelej 2017: 96, ♂, ♀; Pagliano *et al.* 2020: 185.

**Type species.** *Pseudocephalotilla beirana* Bischoff, 1921, ♂, by subsequent designation of Bischoff 1921: 514.

**Diagnosis.** MALE. Flagellomeres not overlapped. Mandible not widened apically, beneath with large subbasal tooth, first preapical inner tooth distinctly smaller, second preapical tooth larger than apical one. Pronotum anteriorly pulled forward with weak carina. T2 with long lateral felt lines, S2 with short lateral felt lines. Volsella without basal external lobe, with wide acuminate cuspis; basivolsella without short setae. Penis valve shortened, swollen apex curved down and oriented outside. FEMALE. Head not widened posterad, posteriorly rounded. Minimal distance between eyes 1.6–1.8 × longitudinal eye diameter. Pronotum without protruding humeral part, at most scarcely wider than propodeum. Scutellar scale more or less developed. T2 with one or three spots of pale setae disposed in central horizontal line. T1 posterodorsally with small medial spot of pale setae. Pygidial plate elongated, widened basally, longitudinally striated.

**Diversity and distribution.** Four species [two of them: *P. atropos* (Smith, 1855) with eleven subspecies and *P. tettensis* (Gerstaecker in Peters, 1858) with eight subspecies] are recognized from the Afrotropical Region (Pagliano *et al.* 2020).



**FIGURES 61–66.** 61–62. *Psammotherma flabellata* (Fabricius, 1804), ♂: 61. Lateral habitus, 62. Dorsal habitus; 63–65. *Pseudocephalotilla beira* (Péringuey, 1914): 63. ♀, dorsal habitus, 64. ♀, lateral habitus, 65. ♂, lateral habitus; 66. *Pseudocephalotilla tettensis* (Gerstaecker in Peters, 1858), ♀, dorsal habitus. (Photographs by K. Williams, and D. Brothers (62–65)).

**Remarks.** Based on a recent molecular phylogenetic analysis (Waldren *et al.* in press), this genus belongs in a new tribe. Most of the species known in this genus are included in Bischoff's (1921) key to *Smicromyrme*.

## 21. *Rasnitsynitilla* Lelej in Lelej & van Harten, 2006

(Figs 67–73)

*Rasnitsynitilla* Lelej in Lelej & van Harten, 2006: 127, ♂; Lelej & Brothers 2008: 52; Brothers & Lelej 2017: 96, ♂; Pagliano *et al.* 2020: 185.

**Type species.** *Rasnitsynitilla brachyptera* Lelej in Lelej & van Harten, 2006, ♂, by original designation.

**Diagnosis.** MALE. In the tribe Smicromyrmini it is related to *Sulcotilla* Bischoff 1920, *Nemka* Lelej 1985, and *Skorikovia* Ovchinnikov 2002 by having the mandible tridentate and by very long narrow volsellar cuspis. The male of *Rasnitsynitilla* differs from all of them by having shortened wings with very small sclerotized stigmatic cell, by much longer lateral felt line on S2. The male of *Rasnitsynitilla* differs from that of genera *Sulcotilla* and *Nemka* by having the mesopleuron without precoxal tubercle or carina. FEMALE is related to that of *Skorikovia* but differs by having pygidial plate distinctly angulate apically with lateral carina widened apically also, by clypeus without median basal tubercle.

**Description.** FEMALE (hitherto unknown). Head not widened posterad. Clypeus without median basal tubercle. Minimal distance between eyes 1.6–1.8 × longitudinal eye diameter. Pronotum without protruding humeral part, usually narrower or at most scarcely wider than propodeum. Scutellar scale usually slightly wider than its length. T1 posterodorsally at most with fringe of pale setae. T2 with one basal medial spot of pale setae and apical band or fringe of pale setae. Basal medial spot of pale setae on T2 enlarged, distance between spot and band of tergum equal to spot diameter or less than it. Pygidial plate basally widened, apically distinctly angulate, lateral carina distinctly widened apically.

**Diversity and distribution.** Four species: three are recognized from Yemen, Oman, and United Arab Emirates and one from Israel, *Rasnitsynitilla bartolozzii* (Lo Cascio & Grita, 2014), **comb. nov.** (from *Smicromyrme*). One is known from both sexes, two are known from males only, and one is known from females only.

**Remarks.** The hitherto unknown female of *Rasnitsynitilla* is combined with the males based on a long series of *R. schmideggeri* Lelej in Lelej & van Harten, 2006 from United Arab Emirates: 97 ♂, 14 ♀, including several cases when the both sexes were collected in water traps at the same time. The mentioned undescribed male species of *Rasnitsynitilla* from Hazeva, Southern Israel (Lelej & van Harten 2006) possibly belongs to *R. bartolozzii* (Lo Cascio et Grita, 2014) described from Eilat, Israel.

## 22. *Sinotilla* Lelej, 1995

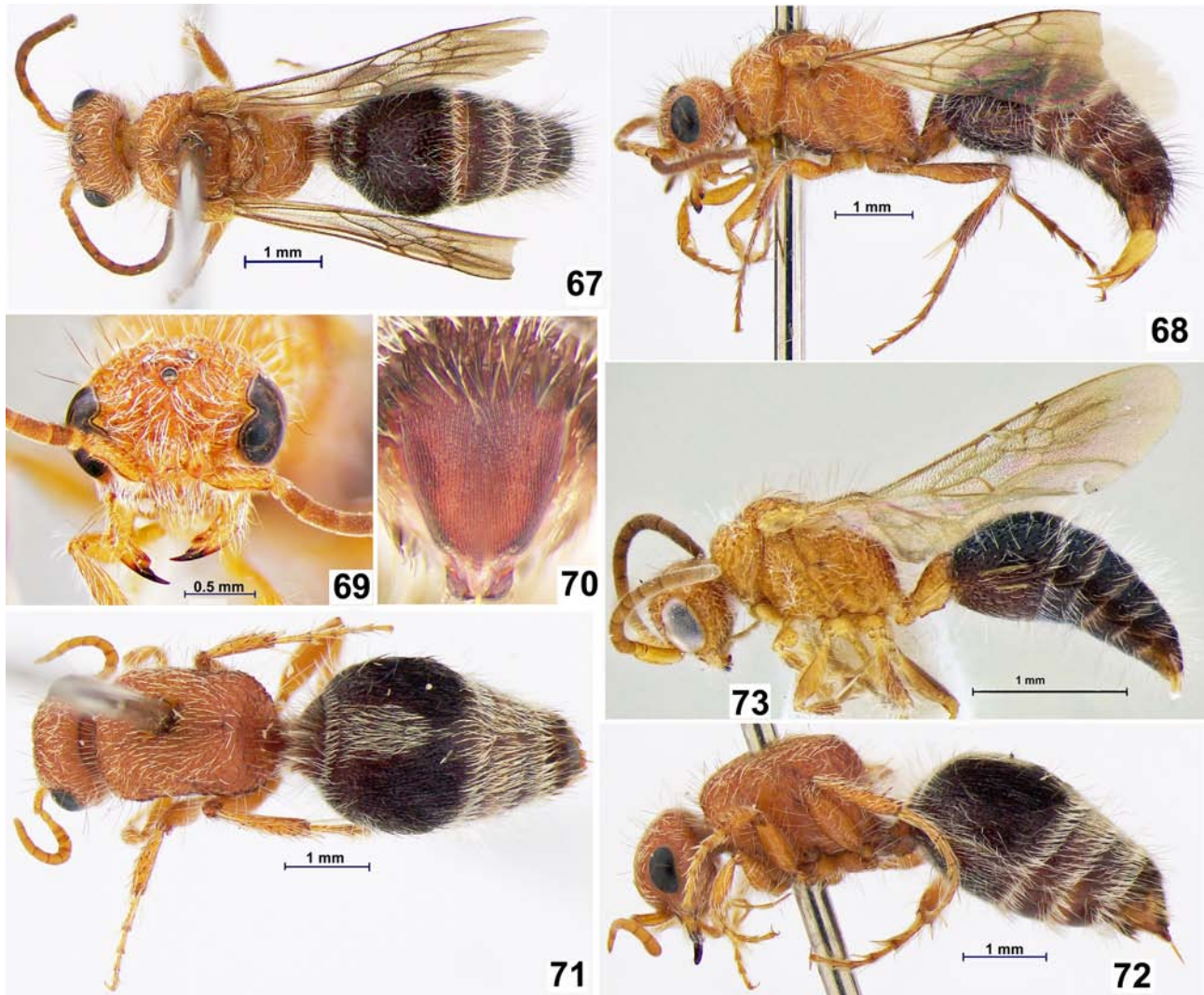
(Figs 74–76)

*Sinotilla* Lelej, 1995b: 3, 4 (key), 18 (description), ♂, ♀; Lelej & Brothers 2008: 55; Brothers & Lelej 2017: 96, ♂, ♀; Okayasu 2017: 152, ♀; 2018: 486, ♀, ♂; Okayasu *et al.* 2018: 313, ♀; Williams *et al.* 2019: 25, ♀; Pagliano *et al.* 2020: 186; Okayasu 2020: 87, ♂, ♀.

**Type species** *Smicromyrme boheana* Chen, 1957, ♂, by original designation.

**Diagnosis.** MALE. Head robust, elevated posterad, frons and vertex longitudinally striate. Mandible bidentate at apex, deeply excised beneath, with large subbasal tooth. Clypeus weakly convex or weakly concave, with protruding midpart of anterior margin. Ocelli small, POD (in type species) 4.3 × posterior ocellus diameter; each ocellus posterad with longitudinal carina, running to occiput. Scape distinctly bicarinate beneath, emargination between carinae with setae. F1 (in type species) half its maximal width and 0.3 × F2. Tegula protruding beyond scuto-scutellar suture for 1/5–1/4 of its length. Parascutal carinae absent. Notauli not visible (in type species) or invisible in anterior one-third (in *S. hong* Lelej, 1995). Parapsidal furrow short. Scutellum simple. Mesopleuron beneath with longitudinal, glabrous, precoxal line. Metacoxa mesally carinate. Wings infuscated; stigmatic cell is less than 0.6 × distance between base of stigmatic cell and origin of *RS* on vein *Sc*. T1 with distinct dorsum, T2 with lateral felt lines, S2 with shorter ones (in type species few small punctures only). T7 densely punctate (in type species) or with

indefinite median impunctate area (in *S. hong*). S8 without tubercles or carinae, densely punctate. Volsella without basal external lobe; volsellar cuspis short and oval, apically and its inner margin with setae not longer than cuspis. FEMALE. Mandible slender. Clypeus with protruding transverse lamellate carina and median basal tubercle. Fore tarsus without external comb of spines. Genal carina developed, with tubercle on hypostomal carina. F1 0.8–1.2 × its maximal width, 1.4–1.6 × pedicel, 1.0–1.5 × F2, latter slightly longer or shorter than F3. Mesosoma convergent posterad (not convergent posterad in *S. belokobylskiji* Lelej, 1995). Scutellar scale weak, but distinct. T2 apically with band of pale setae, slightly widened medially. T3 with wide pale band of pale setae. T6 with glabrous shiny medial part, not carinated laterad even apically, considerably convergent basally with basolateral tufts of dense pale setae.



**FIGURES 67–73.** 67–72. *Rasnitsynitilla schmideggeri* Lelej in Lelej et van Harten, 2006: 67. ♂, dorsal habitus; 68. ♂, lateral habitus; 69. ♂, head, face view; 70. ♀, T6 (pygidial plate); 71. ♀, dorsal habitus; 72. ♀, lateral habitus; 73. *R. brachyptera* Lelej in Lelej et van Harten, 2006, ♂, paratype, lateral habitus. (Photographs by A. Lelej and V. Loktionov (73)).

**Diversity and distribution.** Twenty species (two subdivided into subspecies) are recognized from the Oriental Region, *S. pekiniana* (André, 1905) penetrates to the Palearctic part of China (Pagliano *et al.* 2020), and *S. jambar* Okayasu 2020 is described from Okinawa (Japan) (Okayasu 2020). One is known from both sexes, nine are based on males only, and 10 are based on females only.

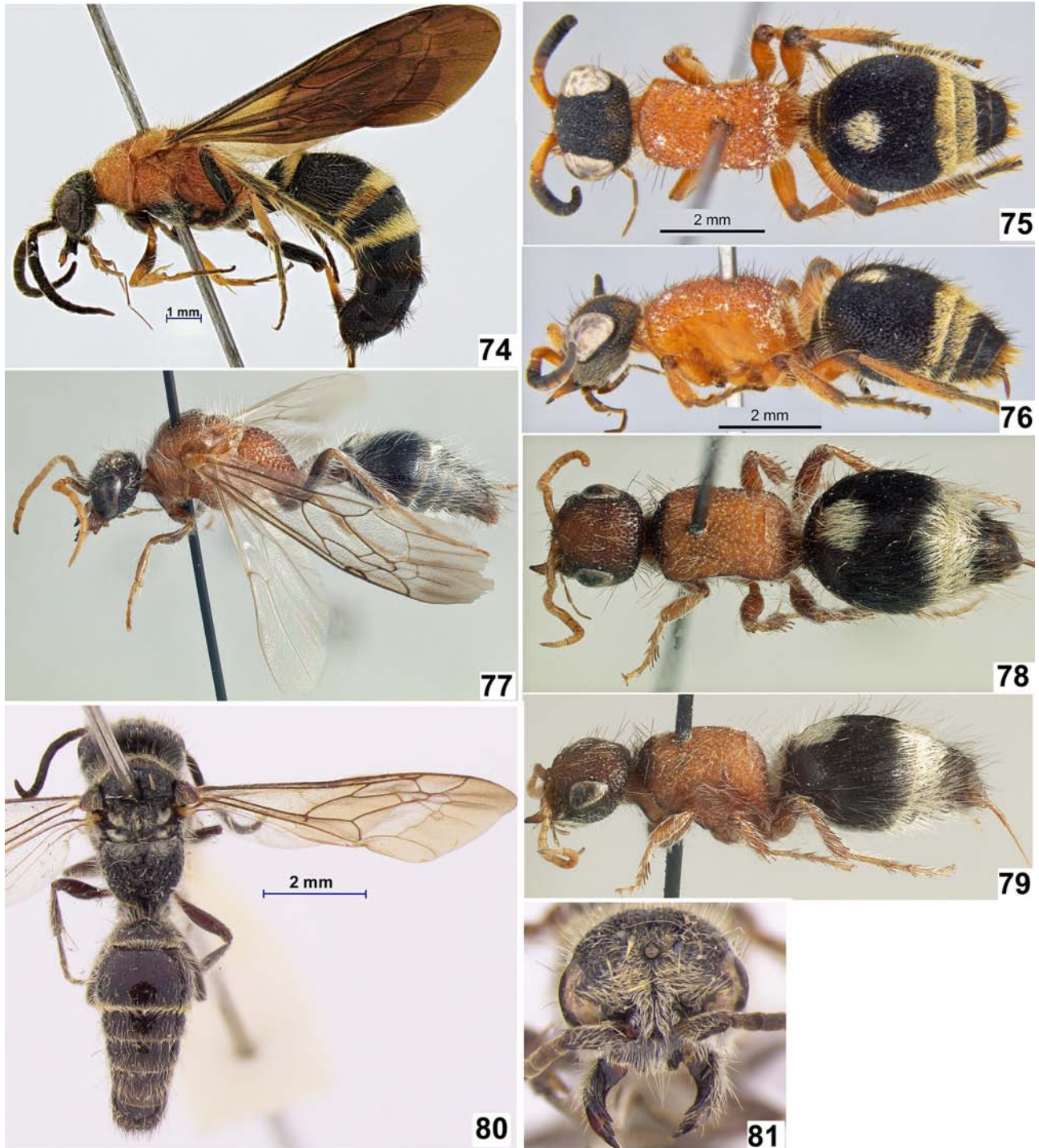
**Remarks.** Females of the genus were reviewed by Okayasu (2017), but many additional species have been treated or described subsequently (*e.g.* Okayasu *et al.* 2018, Okayasu 2020).

23. *Skorikovia* Ovtchinnikov, 2002

(Figs 77–79)

*Skorikovia* Ovtchinnikov, 2002: 94, ♂, ♀; Lelej 2002: 63; Lelej & Osten 2004: 257; Pagliano & Strumia 2007: 83; Lelej & Brothers 2008: 56; Lelej & Yildirim 2009: 17; Muskovits & György 2011: 106; Brothers & Lelej 2017: 96, ♂, ♀; Pagliano *et al.* 2020: 187.

**Type species.** *Mutilla elongata* Radoszkowski 1885, ♂, by original designation.



**FIGURES 74–81.** 74. *Sinotilla boheana* (Chen, 1957), ♂, lateral habitus; 75–76. *S. belokobylskiji* Lelej, 1995, ♀: 75. Dorsal habitus, 76. Lateral habitus. 77–79. *Skorikovia elongata* (Radoszkowski, 1885): 77. ♂, lateral habitus; 78. ♀, dorsal habitus; 79. ♀, lateral habitus; 80–81. *Tsunekimyrmec fluctuata* (Smith, 1865), ♂: 80. Lateral habitus, 81. Head, face view. (Photographs by K. Williams and A. Lelej (74, 80, 81)).

**Diagnosis.** MALE. Mandible usually tridentate with large subbasal tooth beneath (*S. turanica* (Morawitz, 1893) with bidentate mandible and without large subbasal tooth currently is placed in *Smicromyrme incertae sedis* AL). Volsella with long cusps apically often curved inside, basivolsella with large external lobe curved upward. Volsella apically and basivolsella with long suberect setae. Clypeus basally with longitudinal median carina-like elevation which flattened anterad and widened triangularly forming plate with obscure border. Mesopleuron ventrally without precoxal tooth. Metasomal bands of pale setae weaker than in *Nemka*. FEMALE. Pygidial plate triangularly-elongated, basally weakly curved and widened, lateral carina weakly widened apically; densely longitudinally striate, striae slightly divergent from median line. Clypeus basally with median wide tubercle compressed dorso-ventrally and curved up. T2 with medial large basal spot of pale setae and apical band of such setae medially widened triangularly or not widened. T3 with band of pale setae, T4 with lateral spot or large band of pale setae.

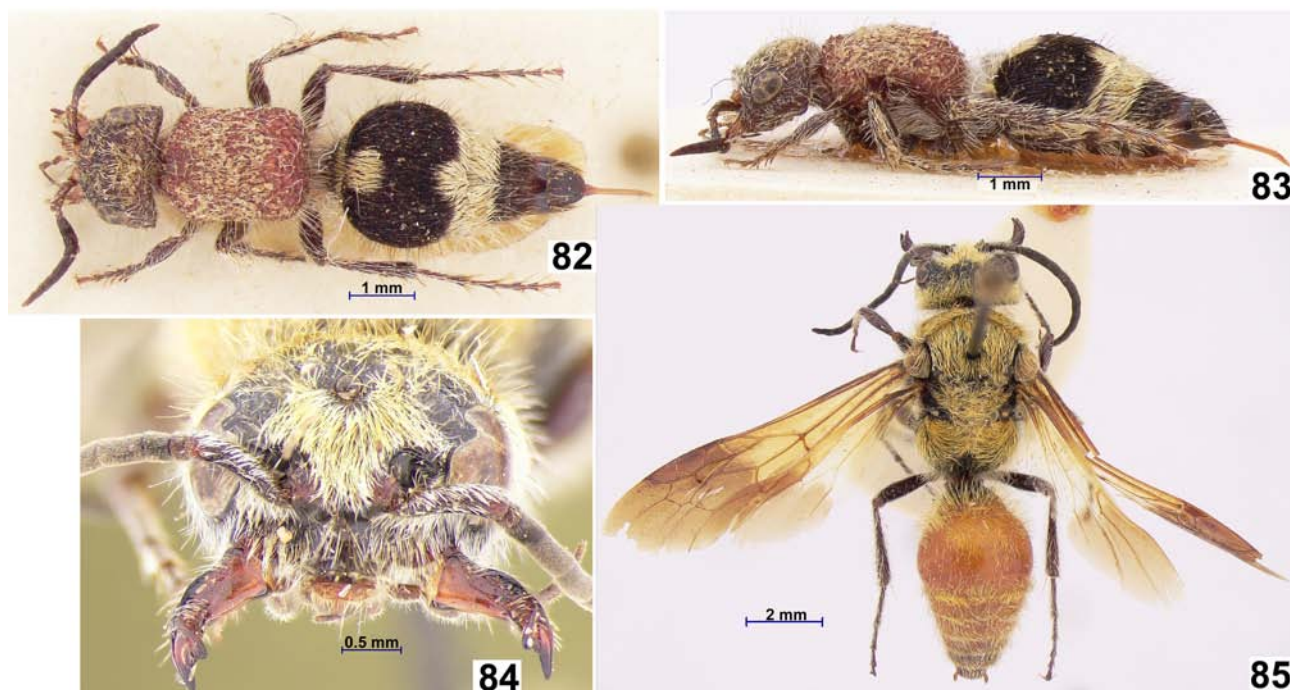
**Diversity and distribution.** Seven species are recognized from the Palaearctic, including *S. sanguinicollis* (Klug, 1829), **comb. nov.** (from the genus *Ephutomma*), but additional species will be likely discovered in Africa among *Smicromyrme* species.

**Remarks.** Although many of these species are nocturnal, they generally have coloration more typical of diurnal *Smicromyrmini*. A key to the Palaearctic males was provided by Lelej and Yildirim (2009).

## 24. *Smicromyrme* Thomson, 1870

*Smicromyrme* Thomson, 1870: 208, ♂, ♀; Lelej & Brothers 2008: 56; Brothers & Lelej 2017: 96, ♂, ♀; Okayasu 2018: 480, ♀, ♂; Williams *et al.* 2019: 26, ♀; Pagliano *et al.* 2020: 187; Okayasu 2020: 8, ♂, ♀; Thaochan *et al.* 2022: 160, ♀.

**Type species.** *Mutilla rufipes* Fabricius, 1787, ♀, by monotypy.



**FIGURES 82–85.** *Sulcotilla sulcata* (Magretti, 1884): 82. ♀, dorsal habitus, 83. ♀, lateral habitus, 84. ♂, head, face view, 85. ♂, dorsal habitus. (Photographs by A. Lelej).

**Diagnosis.** MALE. Head not enlarged; vertex elevated posteriorly; frons and vertex punctate; clypeus flattened or concave; prementum without dome-like tubercle. Mandible narrowed to apex, bidentate or tridentate; subapical inner denticle smaller than apical; ventral margin excised into large subbasal tooth or not excised at most with small subbasal tooth. F1 as long as wide. Mesopleuron without precoxal denticles or tubercles; propodeum without a pair of dorsal median teeth. Wings fully developed. Metasomal segment 2 with lateral felt line on T2 and shorter on S2; S8 without tubercles or carinae; volsella without basal external lobe; gonostylus with small inner protuberance. FEMALE. Minimum distance between eyes more than  $1.4 \times$  eye height; distance between posterior angle of eye

and posterior margin of head 1.5–2.0 × eye height; genal carina and hypostomal tooth absent; clypeus with subapical transverse ridge; prementum without dome-like tubercle. Mandible slender. Pronotum without projecting humeral angle; scutellar scale distinct, slightly wider than long. T1 without pale setal spots; T2 with one or three subbasal spots and apical band of pale setae; if T2 with three spots, then lateral ones disposed behind the median one; distance between median spot and apical band of T2 larger than spot diameter; pygidial plate elongate, distinctly carinate laterally, surface usually striated or with smooth apical part.

**Diversity and distribution.** Two hundred seventy-two species are recognized from the Palaearctic (113), Afrotropical (90), and Oriental (70) Regions (Bischoff 1920–1921; Lelej 2002, 2005; Pagliano *et al.* 2020; Thaochan *et al.* 2022).

**Remarks.** Five subgenera are in use for the Palaearctic species: nominotypical (10 species), *Astomyrme* Schwartz, 1984 (16), *Eremotilla* Lelej, 1985 (24), *Erimyrme* Lelej, 1985 (13), and *Rhombotilla* Nagy, 1966 (1), but 206 species are still retained in *Smicromyrme incertae sedis* (Pagliano *et al.* 2020). In the Afrotropical region, and to a lesser extent the Oriental region, this is a placeholder for species of Smicromyrmini that do not fit readily into newer genus concepts. Even in the Palaearctic region, nearly half of the *Smicromyrme* species fit this *incertae sedis* status, in that they are not placed into one of the subgenera below, but they are real members of the genus *Smicromyrme*.

#### 24.1. Subgenus *Astomyrme* Schwartz, 1984

(Figs 86–89)

*Astomyrme* Schwartz, 1984:22, ♂, ♀; Lelej, 1985: 219 (as subgenus of *Smicromyrme* Thomson); Lelej & Brothers 2008: 9 (as subgenus of *Smicromyrme* Thomson); Brothers & Lelej 2017: 95; Pagliano *et al.* 2020: 187 (as subgenus of *Smicromyrme* Thomson).

**Type species.** *Smicromyrme ausonius* Invrea, 1950, ♂, by original designation.

**Diagnosis.** MALE. Mandible tridentate without subventral tooth, if with inconspicuous one then without excision (*S. morawitzi* Lelej, 1979). Clypeus flattened or concave. F1 0.5 × F2. Second abscissa of *R* often thickened. Length of first metasomal segment less than its maximal width. Volsellar cuspis long and projecting over gonostylus inner protuberance. Head and metasoma black. Mesosoma totally or partly ferruginous-red. FEMALE. Pygidial plate elongated with glabrous apical part or widened basally with divergent from middle striae. Head and metasoma black. T2 with one or three basal spots of pale setae and apical band of pale setae widened medially. T3 with band of pale setae.

**Diversity and distribution.** The subgenus *S. (Astomyrme)* includes 16 Palaearctic species. Eleven species are based on males only, one is known from females only, and four are known from both sexes.

**Remarks.** There are at least three species-groups: *ausonius* group (male with small ocelli), *massageta* group (male with large ocelli), and *morawitzi* group (mandible with inconspicuous subventral tooth).

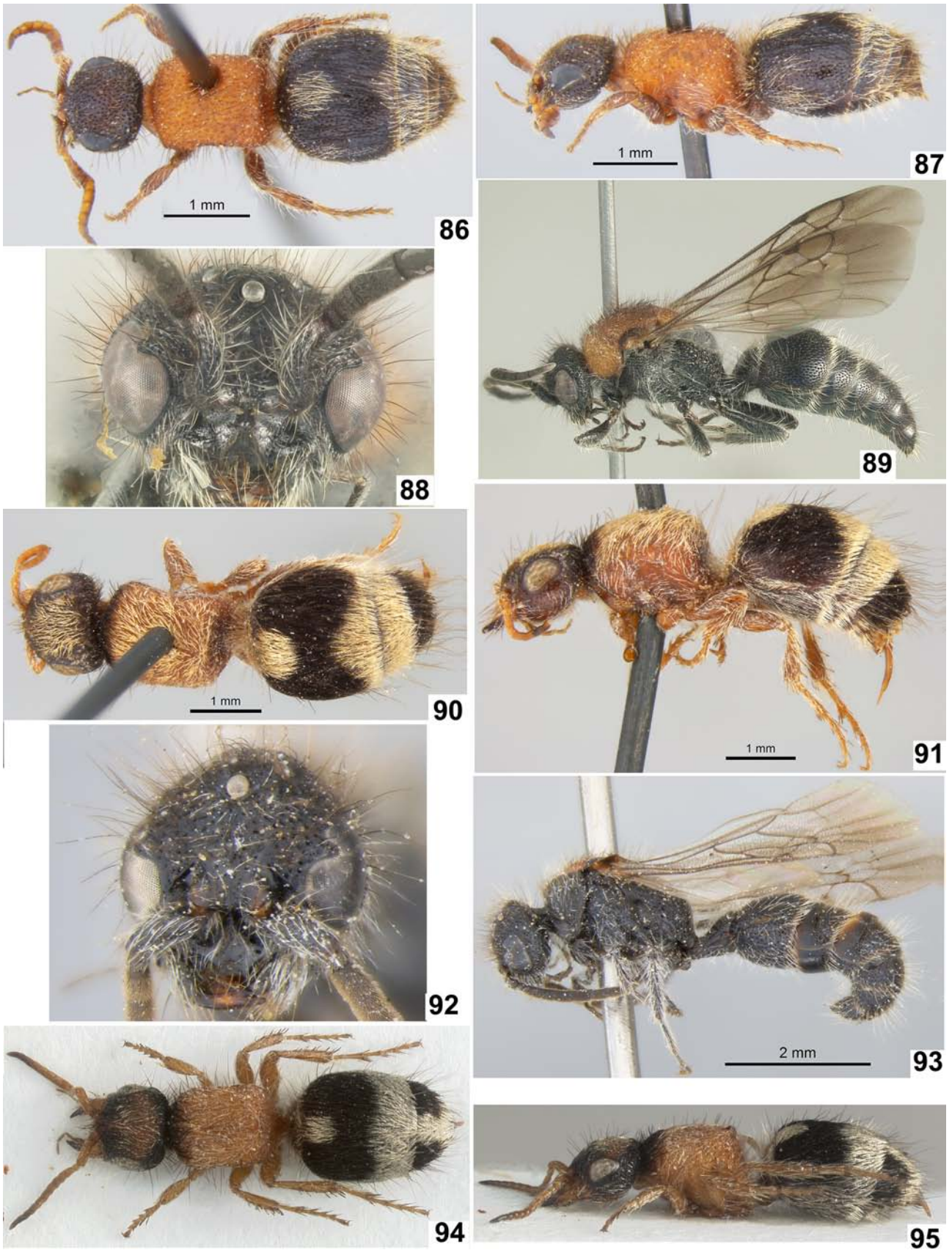
#### 24.2. Subgenus *Eremotilla* Lelej, 1985

(Figs 90–95)

*Eremotilla* Lelej, 1985: 223, ♂, ♀ (as subgenus of *Smicromyrme* Thomson); Lelej & Brothers 2008: 23 (as subgenus of *Smicromyrme* Thomson); Brothers & Lelej 2017: 95; Pagliano *et al.* 2020: 188 (as subgenus of *Smicromyrme* Thomson).

**Type species.** *Smicromyrme tekensis* Skorikov, 1935, ♀, by original designation.

**Diagnosis.** MALE. Mandible bidentate with large subventral tooth. Clypeus more or less flattened with elevated triangle medial part and anterior border with two teeth or tubercles. Volsella without basal external lobe, cuspis touch or projecting over gonostylus inner protuberance. Head and metasoma black. FEMALE. Pygidial plate widened basally with divergent striae from middle. T2 with one or three basal spots of pale setae and apical band of pale setae widened medially. T3 usually with band of pale setae, T4–5 with black setae, rarely T3–4 with medial spot of pale setae and T5 with band of pale setae (*S. nigriceps* Nonveiller, 1959, *S. perisii* (Sichel et Radoszkowski, 1869) and *coromandelica* species-group).



**FIGURES 86–95.** 86–89. *Smicromyrme (Astomyrme) ausonius* Invrea, 1950: 86. ♀, dorsal habitus, 87. ♀, lateral habitus, 88. ♂, head, face view, 89. ♂, lateral habitus. 90–91. *S. (Eremotilla) tekensis* Skorikov, 1935: 90. ♀, dorsal habitus, 91. ♀, lateral habitus; 92–93. *S. (Eremotilla) schwarzi* Suárez, 1975: 92. ♂, head, face view, 93. ♂, lateral habitus; 94–95. *S. (Eremotilla) perisii* (Sichel et Radoszkowski, 1869): 94. ♀, dorsal habitus, 95. ♀, lateral habitus. (Photographs by K. Williams).

**Diversity and distribution.** The subgenus *S. (Eremotilla)* includes 18 Palearctic and six (*coromandelica* species-group) Oriental species (Lelej 2005: 187). Fourteen species are based on females only, seven are based on males only, and three are known from both sexes.

**Remarks.** The Oriental females were keyed by Lelej (2005), most of the Palearctic species are included in Lelej's (1985) key.

### 24.3. Subgenus *Erimyrme* Lelej, 1985

(Figs 96–99)

*Erimyrme* Lelej, 1985: 236, ♂, ♀ (as subgenus of *Smicromyme* Thomson); Lelej & Brothers 2008: 24 (as subgenus of *Smicromyme* Thomson); Brothers & Lelej 2017: 95; Pagliano *et al.* 2020: 190 (as subgenus of *Smicromyme* Thomson).

**Type species.** *Smicromyrme septentrionalis* Hoffer, 1936, ♀, by original designation (junior subjective synonym of *Mutilla sicana* De Stefani, 1887, ♂ according to Petersen, 1988: 194).

**Diagnosis.** MALE. Mandible tridentate with large subventral tooth. Clypeus concave, smooth glabrous, anterior border with two teeth or narrow medial emargination, rarely with additional preapical medial tubercle. Stigmatic cell elongated, non sclerotized. Volsella with external weak basal lobe, cuspis touch or projecting over gonostylus inner protuberance. Head, metasoma and legs black. Antenna black or reddish-brown beneath. Mesosoma usually with some sclerites ferruginous-red, rarely totally black. FEMALE. Pygidial plate narrow, longitudinally striate, glabrous apically. T2 with three subbasal spots of pale setae and apical band of pale setae or rarely with apical medial spot of pale setae. T3 with band of pale setae. Head and metasoma black.

**Diversity and distribution.** The subgenus *S. (Erimyrme)* includes 11 Palearctic species, the Oriental *S. triguttatus* (Mickel, 1933), and the Afrotropical *S. andreinii* (Magretti, 1906). Most of the species (8/11) are based on males only, one is based on females only, and two are known from both sexes.

**Remarks.** About half of the species are included in Lelej's (1985) key.

### 24.4. Subgenus *Rhombotilla* Nagy, 1966

(Figs 100–103)

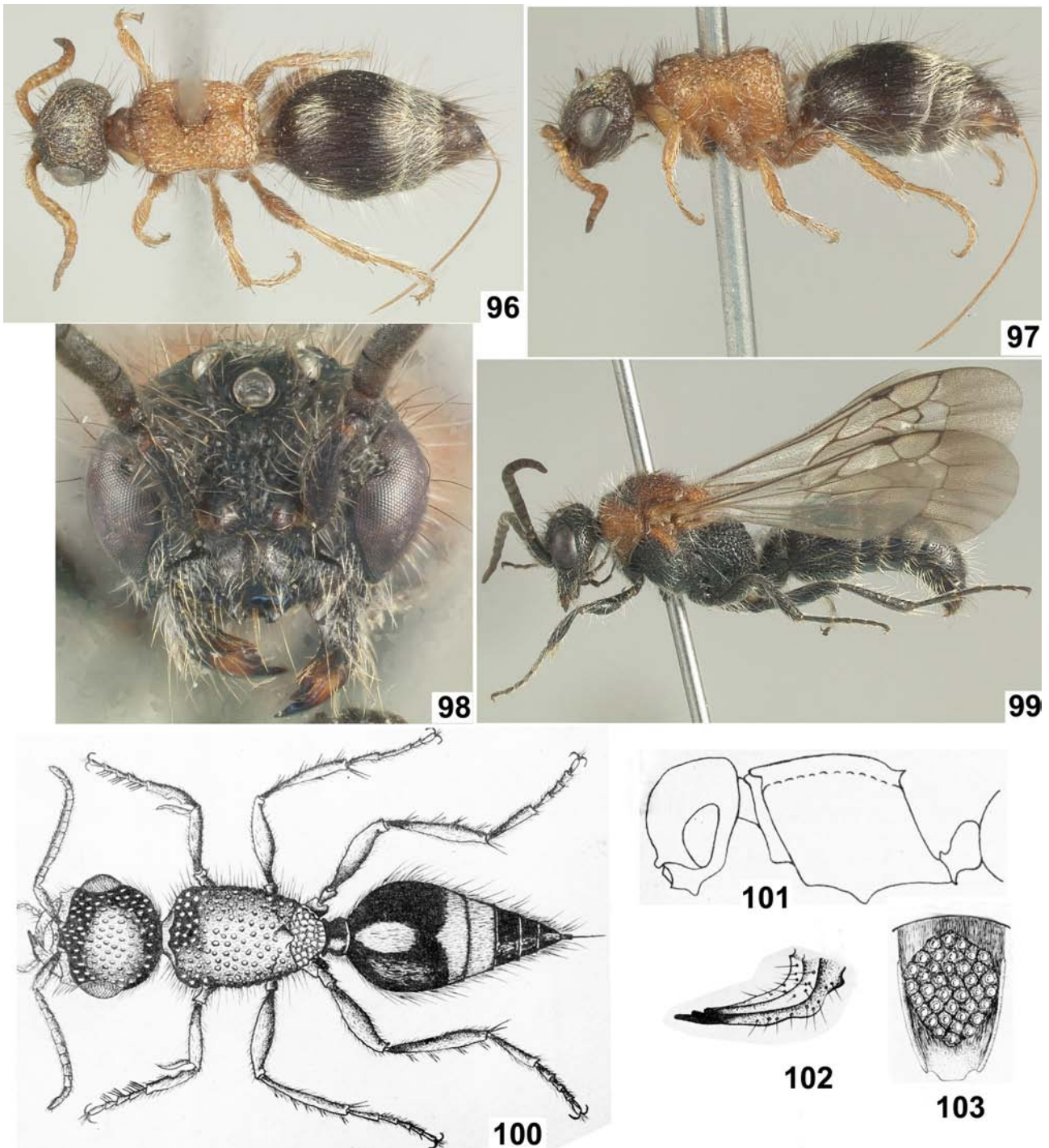
*Rhombotilla* Nagy, 1966: 113, ♀ (as subgenus of *Smicromyme* Thomson); Lelej 1985: 216, ♀; Lelej & Brothers 2008: 52 (as subgenus of *Smicromyme* Thomson); Brothers & Lelej 2017: 96; Pagliano *et al.* 2020: 191 (as subgenus of *Smicromyme* Thomson).

**Type species.** *Smicromyrme (Rhombotilla) riparius* Nagy, 1966, ♀, by original designation (misspelled as *riparia*).

**Diagnosis.** MALE. Unknown. FEMALE. Distinguishable from *Smicromyrme* s. str. by the shape of the mesosoma, which in the dorsal view is almost parallel-sided and only very slightly convergent posterad; mesosoma dorsally arched. First metasomal segment with almost parallel sides; not wider than long. The well-defined pygidial plate is granularly sculptured, the sides marginated, in the center rhombus-shaped fields with coarse, regular punctures.

**Diversity and distribution.** The subgenus *S. (Rhombotilla)* includes one Palearctic species. Only the female holotype, collected by C. Nagy in Agigea (Romania), is known for this species.

**Remarks.** This is a remarkably rare taxon, apparently based on one female specimen only. The slender first metasomal segment (Fig. 100) is unique among Palearctic *Smicromyrmini*, but is somewhat similar to that of *Indratilla* (Fig. 28). *Smicromyrme (Rhombotilla) vinuta*, male, described from Afghanistan (Nagy 1972) belongs to the genus *Promecilla* André, 1902 (Lelej & Kabakov 1980).



**FIGURES 96–103.** 96–99. *Smicromyrme (Erimyrme) sicanus* (De Stefani, 1887): (96. ♀, dorsal habitus, 97. ♀, lateral habitus, 98. ♂, head, face view, 99. ♂, lateral habitus; 100–103. *S. (Rhombotilla) riparius* Nagy, 1966, ♀: 100. Dorsal habitus, 101. Head, mesosoma and basal metasoma, lateral view, 102. Mandible, 103. Pygidial plate. (Photographs by K. Williams; 100–103 from Nagy 1966).

**24.5. Subgenus *Smicromyrme* Thomson, 1870**  
(Figs 104–109)

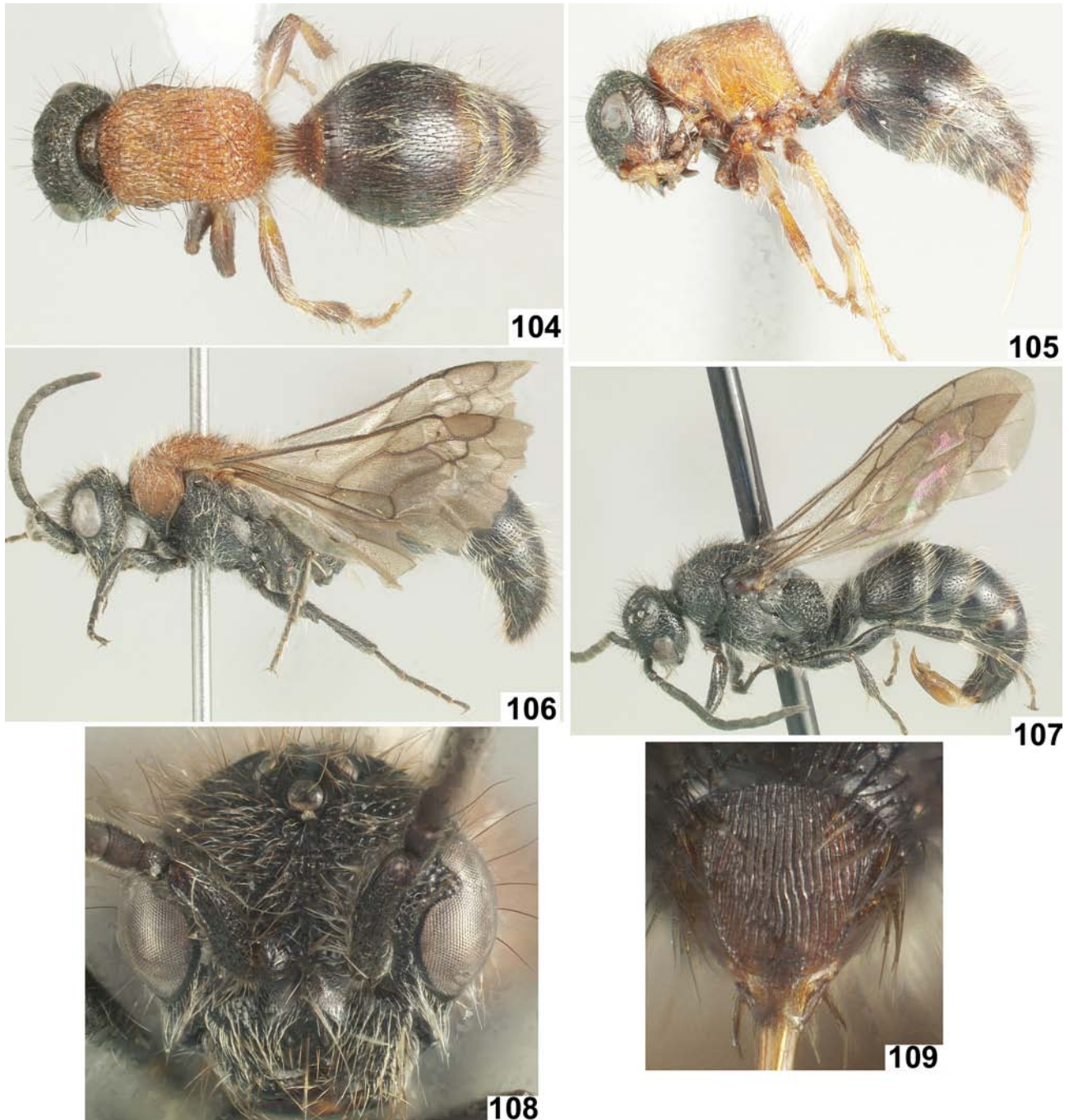
*Smicromyrme* Thomson, 1870: 208, ♂, ♀; Lelej 1985: 231, ♂, ♀ (as nominotypical subgenus); 1995b: 26 (as nominotypical subgenus); 2002: 69 (as nominotypical subgenus); Pagliano *et al.* 2020: 191 (as nominotypical subgenus).

**Type species.** *Mutilla rufipes* Fabricius, 1787, ♀, by monotypy.

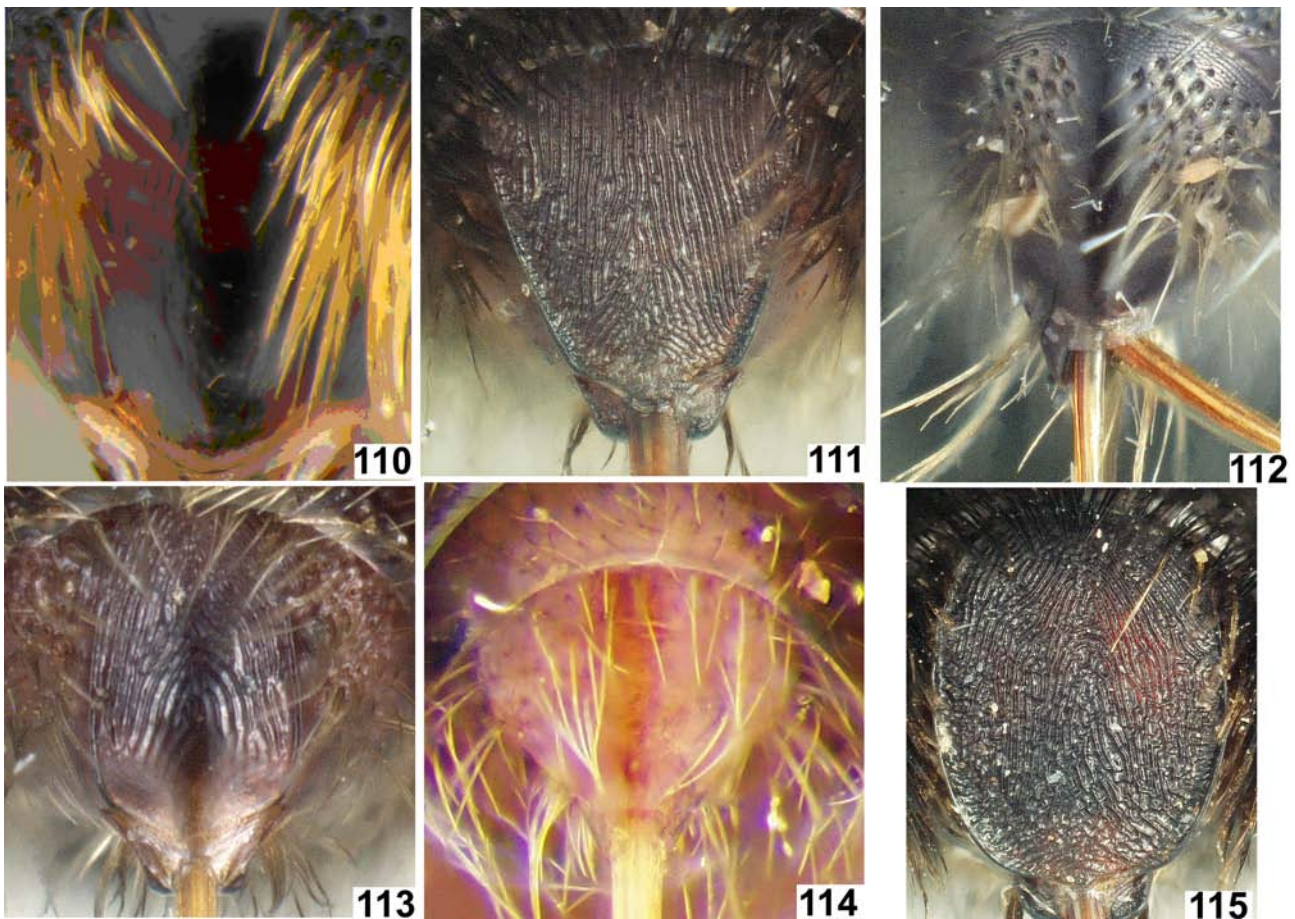
**Diagnosis.** MALE. Mandible bidentate with large subventral tooth. Clypeus more or less flattened with two preapical tubercles. Volsella without external basal lobe, cuspis usually short, at most touch protuberance of gonostylus. Head and metasoma black. Metasoma without band of pale setae at most posterior border of terga with fringe with of pale setae. FEMALE. Pygidial plate narrow with more or less parallel sides, longitudinally striated, rarely with glabrous apex. T3 with band of pale setae.

**Diversity and distribution.** The subgenus *S.* (*Smicromyrme*) includes 12 Palearctic species, two of them are subdivided into subspecies and *S.* (*S.*) *strandii* (Zavattari, 1913) penetrates to Oriental part of China. Four species are based on females only, four are based on males only, and four are known from both sexes.

**Remarks.** Most of the species are included in Lelej's (1985) key. The type species, *S. rufipes*, is amongst the most widespread species of *Smicromyrme*, but there are concerns about misidentifications and the species was recently recognized to comprise a complex of at least three different species (Schmid-Egger & Schmidt 2021).



**FIGURES 104–109.** *Smicromyrme* (*s. str.*) *rufipes* (Fabricius, 1787): 104. ♀, dorsal habitus, 105. ♀, lateral habitus, 106. ♂, lateral habitus, 107. ♂, *f. nigra*, lateral habitus, 108. ♂, head, face view, 109. ♀, pygidial plate. (Photographs by K. Williams).



**FIGURES 110–115.** Smicromyrmini, ♀, pygidial plate (T6). 110. *Andreimyrmex rong* Williams in Okayasu *et al.*, 2021, holotype; 111. *Dentilla curtiventris* (André, 1901); 112. *Ephucilla thalia* (Mickel, 1933); 113. *Ephutomma fletcheri* (Turner, 1911); 114. *Karunaratnea palatupanae* Lelej, 2005, paratype; 115. *Nemka viduata* (Pallas, 1773). (Photographs by K. Williams and A. Lelej (114)).

## 25. *Sulcotilla* Bischoff, 1920

(Figs 82–85)

*Sulcotilla* Bischoff, 1920: 28 (key), 1921: 555 (description), ♀; Brothers 1975: 592, ♀, ♂; Lelej & Brothers 2008: 60; Brothers & Lelej 2017: 96, ♂, ♀; Pagliano *et al.* 2020: 204.

**Type species.** *Mutilla sulcata* Magretti, 1884, ♀, by subsequent designation of Bischoff 1921: 555.

**Diagnosis.** MALE. Hypostomal bridge with tooth. Eye subcircular. Mandible tridentate, slightly widened apically, excided beneath with outside large subbasal tooth. Prementum with posteromedian domelike elevation. Oblique metapleural suture running horizontally from endophragmal pit. Mesopleuron beneath with transverse precoxal one proximal pair of tubercles and one distal pair of teeth. T2 with long, S2 with short lateral felt line. Genital volsella with basal external lobe and long narrow cuspis; basivolsella with very long setae. FEMALE. Head widened posterad, posteriorly angulate. Pronotum dorsally with medial longitudinal depression (sulcus), laterally bordered by tubercles. Scutellar scale developed. Head and mesosoma ferruginous; antennae, legs and metasoma black. T1 with fringe of white setae; T2 basally with medial spot of white setae and apically with medial smaller spot and fringe of white setae. T3 with band of white setae. T4–5 laterally with sparse white setae. Pygidial plate oval carinated, with irregular and wavy longitudinally wrinkled sculpture.

**Diversity and distribution.** One species, known from both sexes, is recognized from the Afrotropical Region.

**Remarks.** The male has been recognized for nearly 50 years (Brothers 1975), but it hasn't been described or illustrated in the published literature.

## 26. *Tsunekimyrmex* Lelej, 1995

(Figs 80–81)

*Tsunekimyrmex* Lelej, 1995b: 3 (key), 16 (description), ♂; 64; Lelej & Brothers 2008: 64; Brothers & Lelej 2017: 96, ♂; Pagliano *et al.* 2020: 204.

**Type species** *Mutilla fluctuata* Smith, 1865, by original designation.

**Diagnosis.** MALE. Head robust, rounded posterad, frons longitudinally striate, vertex densely punctate. Mandible robust, tridentate apically, deeply excised beneath, forming large subbasal, dorsal margin medially elevated. Clypeus convex, with median longitudinal carina, anterior margin protruding and shallowly emarginated. Ocelli small, POD  $3.7 \times$  posterior ocellus diameter, ocellar area slightly elevated. Scape distinctly bicarinate beneath. F1 equal its maximal width. Tegula not protruding beyond axillae. Parascutal carinae well developed and highly elevated. Notauli full, parapsidal furrow short. Scutellum simple. Mesopleuron without precoxal tubercles. Metacoxa mesally carinate. Wings subhyaline, stigmatic cell  $0.7 \times$  distance between base of stigmatic cell and origin of *RS* on vein *Sc*. T2 with long, S2 with short lateral felt line. T7 without median impunctate area. S8 densely punctate. Genital volsella widened basally, with long narrow cuspis; basivolsella with external, extremely long, strong setae; volsella with long, parallel setae on inner margin and a few longer ones on apex. FEMALE. Unknown.

**Diversity and distribution.** One species, based on males only, is recognized from the Philippines.

**Remarks.** This species is similar in appearance to many other Oriental genera, like *Mickelomyrmex* (Fig. 38), but has large, dilated mandibles like *Dentilla* (Figs 12, 16) and *Ephutomma* (Fig. 23).

## Discussion

In the Old World, the Afrotropical Realm has more than twice as many Mutillidae species or subspecies (~1500) as each of the other three Realms (Palearctic, ~600 spp.; Oriental, ~700 spp.; Australasian, ~300 spp.). Within most tribes and subfamilies, such as the subfamily Dasylabrinae or mutilline tribe Trogaspidiini, this trend is consistent (Pagliano *et al.* 2020). Of the higher Mutillidae, Smicromyrmini is the only tribal lineage with more Palearctic species than Afrotropical or Oriental species. It is not clear, however, whether this indicates truly higher diversity in this Realm. The Smicromyrmini are typically small-bodied and, as seen even in the key to genera, this group relies on microscopic differences, especially in male genitalia, to separate the taxa. It seems likely that many more Oriental and Afrotropical species will eventually be discovered.

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