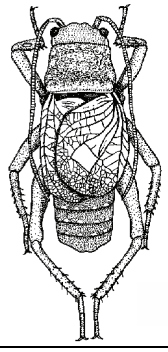

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REVIEW OF THE TRIBE CTENOTILLINI (HYMENOPTERA: MUTILLIDAE) FROM ORIENTAL AND PALAEARCTIC REGIONS

A. S. Lelej

Federal Scientific Center of the East Asia Terrestrial Biodiversity, Far East Branch of the Russian Academy of Sciences, Vladivostok, 690022, Russia. E-mail: lelej@biosoil.ru

Summary. Seven species in the genera *Ctenotilla* Bischoff, 1920, *Cephalotilla* Bischoff, 1920, *Denistilla* **gen. n.** (type species *Mutilla pauli* André, 1898), *Lehritilla* Lelej, 2005, and *Williamstilla* **gen. n.** (type species *Ctenotilla guangdongensis* Lelej, 1992) are reviewed and two new genera are described. New combinations are proposed for *Cephalotilla porcella* (Turner, 1911), **comb. n.**, *Denistilla pauli* (André, 1898), **comb. n.**, *Lehritilla ianthis* (Turner, 1911), **comb. n.**, *L. locascioi* (Lelej, 2005), **comb. n.**, and *Williamstilla guangdongensis* (Lelej, 1992), **comb. n.** The genus *Cephalotilla* is newly recorded from Oriental Region, the genus *Pristomutilla* Ashmead, 1903 is excluded from Oriental fauna. *Denistilla pauli* (André, 1898) is newly recorded from India. Keys to the seven species of one Palaearctic and four Oriental genera are provided.

Key words: Mutillinae, taxonomy, new genera, new combinations, key, Old World.

А. С. Лелей. Обзор трибы Ctenotillini (Hymenoptera: Mutillidae) Ориентальной и Палеарктической областей // Дальневосточный энтомолог. 2023. N 480. С. 1-22.

Резюме. Дан обзор семи видов из родов *Ctenotilla* Bischoff, 1920, *Cephalotilla* Bischoff, 1920, *Denistilla* **gen. n.** (типовой вид *Mutilla pauli* André, 1898), *Lehritilla* Lelej, 2005 и *Williamstilla* **gen. n.** (типовой вид *Ctenotilla guangdongensis* Lelej, 1992) и описаны два новых рода. Предложены новые комбинации для *Cephalotilla porcella* (Turner, 1911), **comb. n.**, *Denistilla pauli* (André, 1898), **comb. n.**, *Lehritilla ianthis* (Turner, 1911), **comb. n.**, *L. locascioi* (Lelej, 2005), **comb. n.** и *Williamstilla guangdongensis* (Lelej, 1992), **comb. n.** Род *Cephalotilla* Bischoff, 1920 указан впервые для Ориентальной области, а род *Pristomutilla* Ashmead, 1903 исключен из Ориентальной фауны. *Denistilla pauli* (André, 1898) впервые указывается из Индии. Даны определительные таблицы 7 видов одного Палеарктического и четырех Ориентальных родов.

INTRODUCTION

According to phylogenetic work based on morphology (Brothers & Lelej, 2017) the tribe Ctenotillini includes ten genera and three subgenera. The Ctenotillini component terminals were usually well grouped (especially males), except that *Pristomutilla* branching off distal to other members (Brothers & Lelej, 2017). In the recent phylogenomic study of Mutillidae using ultraconserved elements (Waldren *et al*., 2023) this tribe was divided in three ones (table 1): Ctenotillini Brothers et Lelej, 2017 with the genera *Arcuatotilla*, *Cephalotilla* (including subgenera *Bidentotilla* and *Taeniotilla*), *Chaetomutilla*, *Ctenotilla*, *Lehritilla* and *Mimecomutilla* (including subgenus *Mimecotilla*); Zeugomutillini Waldren, 2023 with the genera *Montanomutilla*, *Strangulotilla* and *Zeugomutilla*; and Pristomutillini with the genera *Pristomutilla*, *Ceratotilla* and *Viereckia.* Two latter ones were transferred from the subfamily Myrmillinae. Diagnoses and differences between these three tribes which are distributed in the Old World see Waldren *et al.* (2023).

The natural history of the species of tribe Ctenotillini is unknown. Most of the females of this tribe have the granulose or longitudinally striated defined pygidial plate bordered by lateral carina and fore tarsal comb which are used to excavate the soil and the preferred hosts for the species of Ctenotillini maybe bees and wasps which nest in the soil.

The aim of current paper is to review four Oriental and one Palaearctic genera of Ctenotillini (*sensu* Waldren *et al*., 2023) with description of two new genera.

MATERIAL AND METHODS

The following abbreviations are used to denote institutes housing types and specimens examined herein:

BMNH: The Natural History Museum, London, Greater London, United Kingdom.

IBSS: Federal Scientific Center of the East Asia Terrestrial Biodiversity (former Institute of Biology and Soil Science), Vladivostok, Russia.

ISEA–PAN: Institute of Systematics and Evolution of Animals' collection at the Polish Academy of Sciences, Kraków, Poland.

MNHN: Muséum National d'Histoire Naturelle, Paris, France.

MSNF: Museo Zoologica de la «La Specola», sezione del Museo di Storia Naturale, Firenze, Italy.
NMC: National Museum, Colombo, Sri Lanka.
SCAU: South China Agricultural University, Guangzhou, China.
SKYC: Sk. Yamane collection, Kagoshima, Japan.
USNM: National Museum of Natural History, Smithsonian Institution, Washington DC, U.S.A.
ZIN: Zoological Institute, Russian Academy of Sciences, St Petersburg, Russia.

Table 1. Diversity and distribution of the genera/subgenera of the tribes Ctenotillini, Zeugomutillini and Pristomutillini (*sensu* Waldren *et al*., 2023)

Genera	Number of species			
	Total	Pal	Afr	Ori
Tribe Ctenotillini Brothers et Lelej, 2017				
1. *Arcuatotilla* Nonveiller, 1998	1	0	1	0
2. *Cephalotilla* Bischoff, 1920	55	0	54	1
2a. *Bidentotilla* Nonveiller, 1979	1	0	1	0
2b. *Cephalotilla* Bischoff, 1920	53	0	52	1
2c. *Taeniotilla* Nonveiller, 1979	1	0	1	0
3. *Chaetomutilla* Nonveiller, 1979	3	0	3	0
4. *Ctenotilla* Bischoff, 1920	1	1	0	0
5. *Denistilla* **gen. n.**	1	0	0	1
6. *Lehritilla* Lelej, 2005	3	0	0	3
7. *Mimecomutilla* Ashmead, 1903	22	0	22	0
7a. *Mimecomutilla* Ashmead, 1903	2	0	2	0
7b. *Mimecotilla* Nonveiller, 1998	20	0	20	0
8. *Williamstilla* **gen. n.**	1	0	0	1
Subtotal genera/species	**8/87**	**1/1**	**4/80**	**4/6**
Tribe Zeugomutillini Waldren, 2023				
1. *Montanomutilla* Nonveiller, 1979	6	0	6	0
2. *Strangulotilla* Nonveiller, 1979	21	0	19	2
3. *Zeugomutilla* Chen, 1957	9	0	0	9
Subtotal genera/species	**3/36**	**0/0**	**2/25**	**2/11**
Tribe Pristomutillini Waldren, 2023				
1. *Pristomutilla* Ashmead, 1903	65	0	65	0
2. **Ceratotilla* Bischoff, 1920	9	0	9	0
3. **Viereckia* Ashmead, 1903	7	0	7	0
Subtotal genera/species	**3/81**	**0/0**	**3/81**	**0/0**
Total genera/species	**14/204**	**1/1**	**9/186**	**6/17**

Remark: *Pal* – Palaearctic, *Afr* – Afrotropical, *Ori* – Oriental. Data based on Lelej (2007), Pagliano *et al*. (2020) and current data. Two genera from the subfamily Myrmilline sensu Brothers & Lelej, 2017 are asterisked (*).

The photographs were taken with an Olympus SZX16 stereomicroscope and an Olympus DP74 digital camera, and then stacked using Helicon Focus software. The final illustrations were post-processed for contrast and brightness using Adobe® Photoshop® software. Terminology mostly follows the Hymenoptera Anatomy Consortium (2022) for the general morphology, and Harris (1979) for the integument sculpture. Abbreviations for the collectors in Sri Lanka follow those of Krombein & Pulawski (1994). The following abbreviations are used in the text: F = flagellomere, S = metasomal sternum; T = metasomal tergum.

TAXONOMY

Subfamily Mutillinae Latreille, 1802

Tribe Ctenotillini Brothers et Lelej, 2017

DIAGNOSIS. MALE. At least T4–6 with medial longitudinal carina (except non-carinated T4–6 in *Lehritilla*), prementum tuberculate, mandible apically bidentate, without subapical inner tooth, S7 medially or laterally tuberculate (except unarmed in *Ctenotilla caeca*), gonostylus apically straight or slightly down curved (strongly in *Williamstilla* **gen. n.**), parapenial lobes dorsally elongate with deep emargination separating them. FEMALE. The sculpture of the pygidial plate is presently the most reliable character to separate females of tribes Ctenotillini, Zeugomutillini and Pristomutillini (granulose or microreticulate in Ctenotillini, although striate in *Lehritilla* and some *Cephalotilla* (Nonveiller, 1979); glabrous or weakly longitudinally striate in Zeugomutillini, coarsely longitudinally striate in *Pristomutilla* (with at least one species having it transversely striate-rugose (Nonveiller, 1995). Scutellar scale lacking.

Key to the Oriental genera and species of tribe Ctenotillini

Males (unknown in *Lehritilla ianthis*, *L. locascioi*)

1. T3–7 without medial longitudinal carina. – S8 (hypopygium) with strong medial longitudinal curved carina, S7 with lateral lobe. Mandible with weak subbasal inner tooth. (***Lehritilla*** Lelej, 2005). Gonostylus bilobed: dorsal lobe short strong curved and oriented inwards, ventral lobe narrow long, slightly longer than volsella. 9.0 mm ..... ***L. lanka*** Lelej, 2005
– At least T4–6 with medial longitudinal carina ……..... 2
2. S8 medially with deep concavity bordered by lateral tuft of setae. S7 at most with lateral tubercle …… 3
– S8 medially with highly elevated wide shiny longitudinal part bordered by long setae. S7 with strong lateral process curved inward. (***Williamstilla* gen. n.**). 7.2–10.4 mm ……..... ***W. guangdongensis*** (Lelej, 1992), **comb. n.**
3. S8 apically with deep triangular emargination bordered by carina. (***Denistilla* gen. n.**). 10.0–11.0 mm …….... ***D. pauli*** (André, 1898), **comb. n.**
– S8 apically rounded or straight ……...……..... 4

4. S8 with subbasal lateral tubercle. S7 without lateral tubercle. S2 not invaginated laterally, basally with weak medial longitudinal carina. Mesopleuron beneath strongly punctured, with precoxal tubercle. (***Ctenotilla*** Bischoff, 1920). 9.0–16.0 mm ……. ***C. caeca*** (Radoszkowski, 1879)
– S8 without subbasal lateral tubercle. S7 with lateral tubercle. S2 invaginated sublaterally with distinct lateral longitudinal carina and medial longitudinal carina. Mesopleuron beneath transversally striated, without precoxal tubercle. (***Cephalotilla*** Bischoff, 1920). 8.8–10.4 mm …… ……..…….... ***C. porcella*** (Turner, 1911), **comb. n.**

Females (unknown in *Lehritilla lanka*)

1. Pygidial plate longitudinally striated. (***Lehritilla*** Lelej, 2005) …….……. 2
– Pygidial plate granulose or microreticulate …….……... 3
2. Eyes projecting over head (face view). Mesosoma dorsally rugoso-striate throughout. Pygidial plate longitudinally striate throughout. T2 spots of yellowish setae. 5.2–7.0 mm ……..…... ***L. ianthis*** (Turner, 1911), **comb. n.**
– Eyes not projecting over head (face view). Mesosoma dorsally rugoso-striate in anterior half and strongly tuberculate in posterior half. Pygidial plate longitudinally striate with micropunctate apex. T2 spots of silver setae. 5.2–9.0 mm …….. ***L. locascioi*** (Lelej, 2005), **comb. n.**
3. T2 with two basal white spots disposed transversely. (***Denistilla*** **gen. n.**). 6.0–7.5 mm ……. ***D. pauli*** (André, 1898), **comb. n.**
– T2 without two subbasal white spots disposed transversely ……... 4
4. T2 apically and T3 with medially interrupted band of yellowish setae. (***Williamstilla*** **gen. n.**). 5.5–8.5 mm ……. ***W. guangdongensis*** (Lelej, 1992), **comb. n.**
– T2 apically and T3 with non interrupted band of yellowish or white setae, band on T2 widened medially …….. 5
5. T1 width much less than propodeum width. Postgenal carina anterad with dent. (***Cephalotilla*** Bischoff, 1920). 6.0–7.2 mm ……. ……..…….... ***C. porcella*** (Turner, 1911), **comb. n.**
– T1 width more or less equal propodeum width. Postgenal carina anterad without dent. (***Ctenotilla*** Bischoff, 1920). 5.8–10.0 mm ... ***C. caeca*** (Radoszkowski, 1879)

Genus *Ctenotilla* Bischoff, 1920

Ctenotilla Bischoff, 1920: 28 (in key); 1921, 86A(4): 585 (description), ♂, ♀; Nonveiller, 1979: 71, ♂, ♀; Lelej & Brothers, 2008: 18, ♂, ♀; Brothers & Lelej, 2017: 95, ♂, ♀; Pagliano *et al*., 2020: 161.

Type species: *Mutilla pectinifera* André, 1893, ♀, by subsequent designation of Bischoff, 1921: 585 (junior subjective synonym of *Mutilla caeca* Radoszkowski, 1879, ♂, according to Nonveiller, 1959: 176).

DIAGNOSIS. MALE. At least T4–6 with medial longitudinal carina. S8 with deep concavity bordered by lateral tuft of setae, basally with lateral tubercle, apically

weakly emarginated. S7 without lateral tubercle. S2 not invaginated laterally, basally with weak medial longitudinal carina. Mesopleuron beneath with precoxal tubercle, strongly punctured. FEMALE. Pygidial plate granulose. T2 without two subbasal white spots disposed transversely. T2 apically and T3 with non interrupted band of white setae, band on T2 widened medially. T1 width more or less equal propodeum width. Postgenal carina anterad without dent.

SPECIES INCLUDED. The genus *Ctenotilla* sensu Bischoff (1920–1921) included 31 species and two subspecies divided in three species-groups, but after the revision (Nonveiller, 1979) only type species *Mutilla pectinifera* André, 1893 (=*Mutilla caeca* Radoszkowski, 1879) was retained.

DISTRIBUTION. East Mediterranean.

***Ctenotilla caeca* (Radoszkowski, 1879)**

Figs 1–3, 7–9, 36–37

Mutilla caeca Radoszkowski, 1879: 150, ♂, lectotype, ♂ "Caucasus", designated by Nonveiller, 1979: 73 [ISEA–PAN].

Mutilla pectinifera André, 1893: 295, ♀, lectotype, ♀ "Grèce", coll. E. André designated by Nonveiller, 1989: 79 [MNHN]. Synonymized with *C. caeca* (Radoszkowski, 1879) by Lelej, 1978: 81.

Ctenotilla pectinifera var. *obscura* Nonveiller, 1959: 177, ♂, "Karadagli, Azerbaijan (Kaukasus), 2.VII.28, Bočarnikov" [Qaradağlı, 39°30′45″N 47°04′37″E, 2.VII 1928, O.N. Bocharnikov leg.] [ZIN], examined. Synonymized with *C. caeca* (Radoszkowski, 1879) by Nonveiller, 1979: 73.

MATERIAL EXAMINED. 39♀, 97♂ from **Crimea** (Lelej *et al*., 2016), 3♀, 5♂ from **Azerbaijan** (Lelej *et. al*., 2022), 5♀ from **Greece** including 3♀ identified by G. Nonveiller as *Ctenotilla pectinifera* André (Lelej *et al*., 2003); 1♀, 3♂ from **Turkey** (Lelej, Yildirim, 2009); **Armenia**, near Yerevan, 23–28.VI 1924, 2♂, 1♀ (A. Shelkovnikov) [ZIN]; Jrvezh near Yerevan, 14.VII 1952, 1♂ (M. Ter-Minasyan) [ZIN]; Caucasus, Armenia Geb., 1♀ (Leder, Reitter) [ZIN] [this specimen collected in Nakhchivan near Ordubad – see, Reitter (1890)]; Asni, 28.VI 1961, 1♂ (V. Richter) [ZIN]. **Montenegro**, Bar, 12–24.VII 1955, 2♀ (G. Nonveiller) [ZIN].

DISTRIBUTION. Armenia, Azerbaijan, Bulgaria, Russia (Crimea), Croatia, Greece, Iran, North Macedonia, Montenegro, Romania, Serbia, Syria, Turkey.

Genus *Cephalotilla* Bischoff, 1920

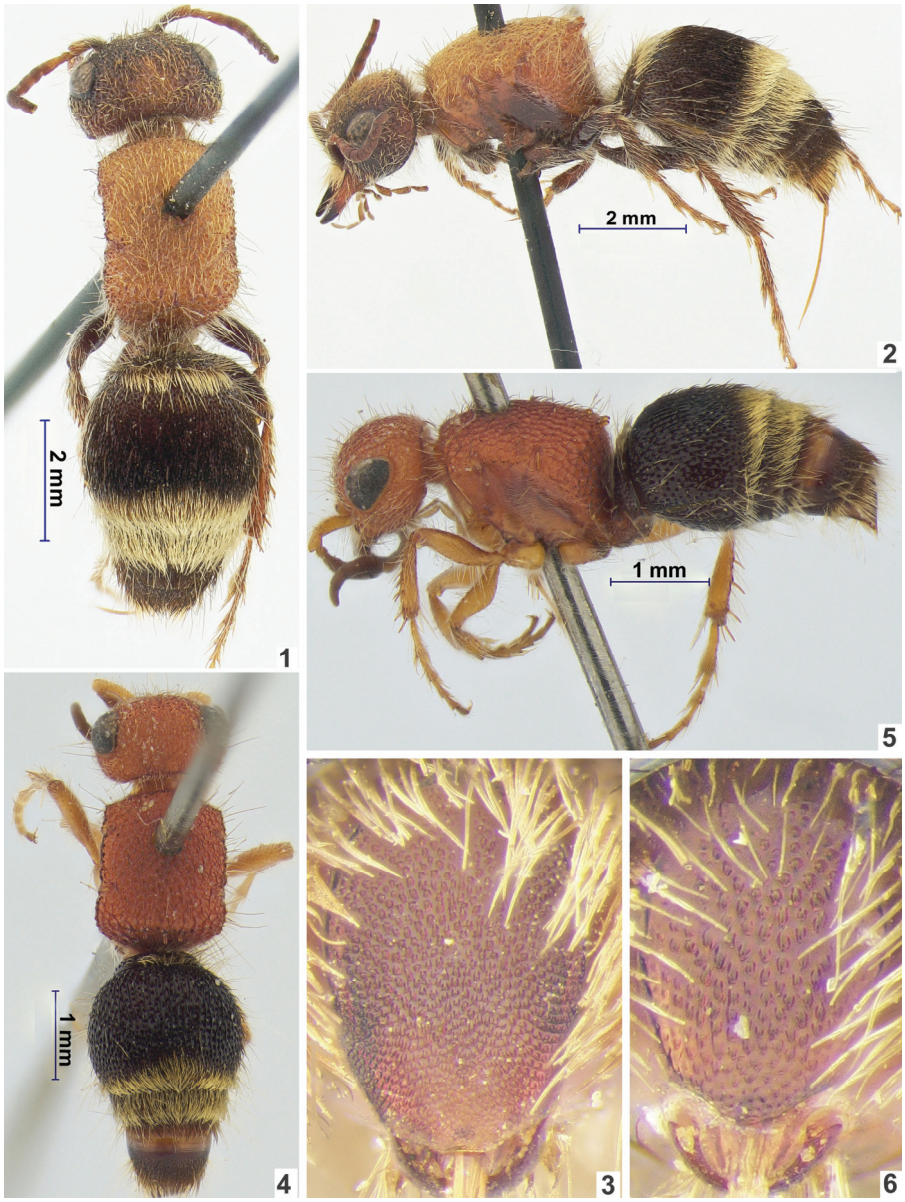
Cephalotilla Bischoff, 1920: 24 (in key); 1921, 86A(4): 509 (description), ♂, ♀; Nonveiller, 1979: 81, ♂, ♀; Lelej & Brothers, 2008: 14, ♂, ♀; Brother & Lelej, 2017: 95, ♂, ♀; Pagliano *et al*., 2020: 157.

Ctenotilla: Brothers, 1975: 592.

Type species: *Cephalotilla kamogana* Bischoff, 1921, ♂, by subsequent designation of Bischoff, 1921: 509 [Afrotropical].

DIAGNOSIS. MALE. T4–6 with medial longitudinal carina. S8 medially with deep concavity bordered by lateral tuft of setae, without subbasal lateral tubercle. S7

with lateral tubercle. S2 invaginated sublaterally with distinct lateral longitudinal carina and medial longitudinal carina. FEMALE. Inner margin of mandible without



Figs 1–6. 1–3 – *Ctenotilla caeca*, ♀; 4–6 – *Cephalotilla porcella*, ♀. 1, 2, 4, 5 – habitus (1, 4 – dorsal view, 2, 5 – lateral view); 3, 6 – T6, pygidial plate.

subbasal denticle. Pygidial plate granulose. T2 without two subbasal white spots disposed transversely. T2 apically and T3 with non interrupted band of yellowish or white setae, band on T2 widened medially. T1 width much less than propodeum width. Postgenal carina anterad with dent.

SPECIES INCLUDED. Oriental *Cephalotilla porcella* (Turner, 1911), **comb. n.** from nominotypical subgenus and undescribed Indian species with reddish-brown head, black legs and narrow pygidial plate. The subgenera *Bidentotilla* Nonveiller, 1979 with one species, *Taeniotilla* Nonveiller, 1979 with one species, and 52 species from nominotypical subgenus are distributed in Afrotropical Region (Nonveiller, 1979).

DISTRIBUTION. Oriental (Sri Lanka, South India) and Afrotropical Regions.

REMARKS. The genus *Cephalotilla* is newly recorded from Oriental Region.

***Cephalotilla* (*Cephalotilla*) *porcella* (Turner, 1911), comb. n.**

Figs 4–6, 10–14, 38–39

Mutilla porcella Turner, 1911: 145, ♀, holotype, ♀, "Hambantota, Ceylon (Fletcher), November" [BMNH].

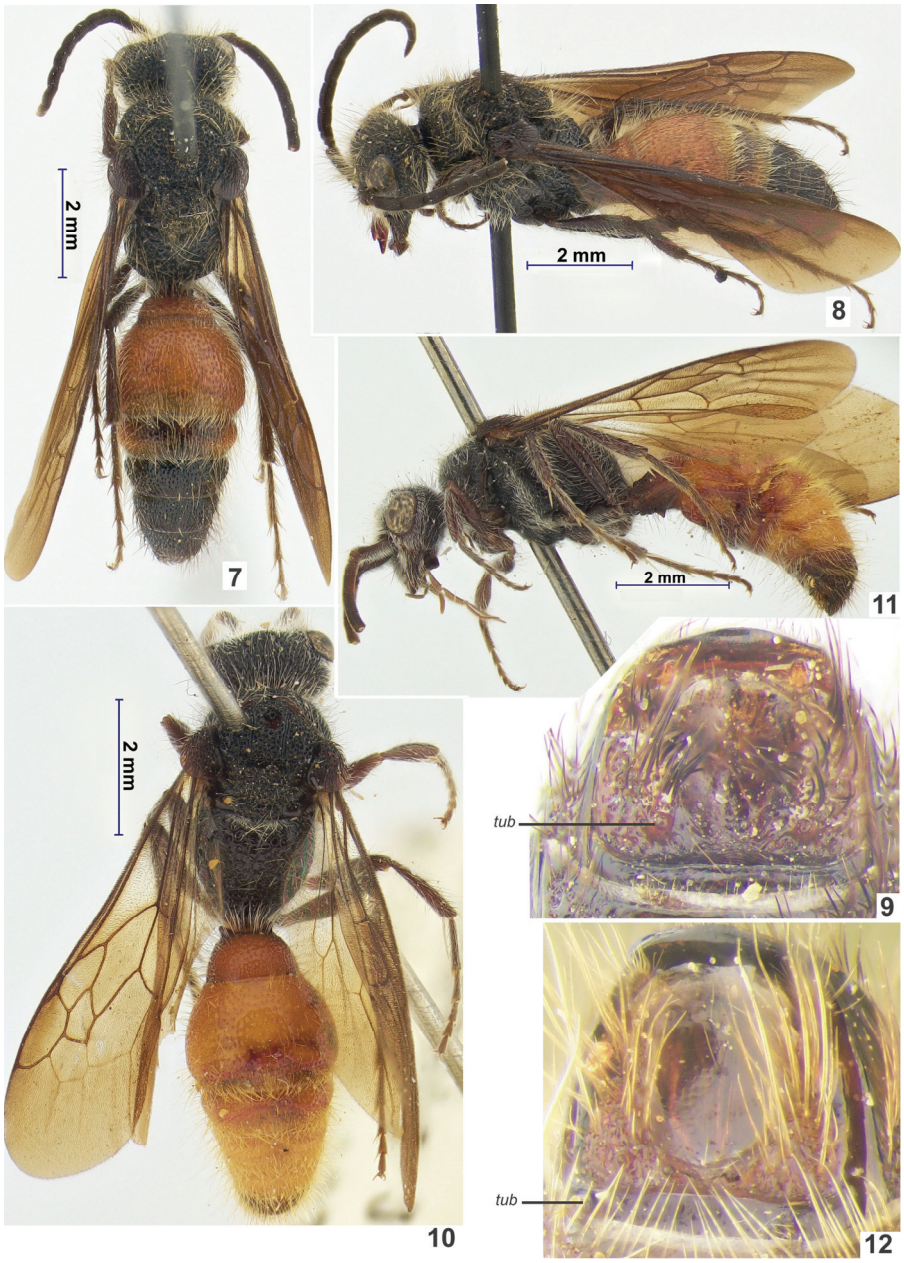
Ctenotilla porcella: Lelej, 1992: 283, ♀; Nonveiller, 1995: 33, ♀; Lelej, 2005: 34.

MATERIAL EXAMINED (24♀, 23♂). **Sri Lanka**. Vareniya, 18.XII 1923, 1♀ [NMC]; Weerawila, 27.XI 1984, 1♀ (L. Bartolozzi) [MSNF]; Mannar District: Kokmotte Bungalow, Wilpattu National Park, 21–25.V 1976, 1♀ (KVK, PBK, SK, DWB) [USNM]; the same place but 22–23.I 1977, 1♀, 1♂ (KVK *et al*.) [USNM]; Anuradhapura District: Padaviya, 13–22.III 1976, MT, 2♂ (PBK, SK, DWB) [IBSS, USNM]; Amparai District: Dehiattekandiya, 23–24.VII 1993, 1♀, 1♂ (KVK, PBK, B.B. Norden) [USNM]; Ekgal Aru, 9–12.VI 1976, 10♀, 5♂ (KVK, PBK, SK) [IBSS, USNM]; the same place but 19–23.II 1977, 3♀ (KVK, PBK, PF, DWB) [IBSS, USNM]; the same place but 11–15.IX 1977, 1♀ [USNM]; Lahugala Sanctuary, 15.VI 1976, 1♀ (KVK, PBK, SR) [USNM]; Matale District, Kibissa, 2.VIII 1978, 1♂, 1♀, *in copula* (KVK, PBK, TW, VK) [USNM]; the same place but 1–3.III 1979, 1♀, 1♂ (KVK, PBK, TW, VK) [USNM]; Sigiriya, 17.VI 1975, 1♂ (Messersmith *et al*.) [USNM]; Kandy District, Hasalaka, 22–25.II 1970, 1♂ [USNM]; Monaragala District: Angunakolapelessa, 17–19.VI 1978, 1♂ (KVK, TW, VK, L. Jayawickrema) [USNM]; the same place but 21–23.I 1979, 4♂ from MT and 3♀ (KVK, PBK, TW, SS, TG) [USNM]; the same place but 27–28.III 1981, MT, 6♂ (KVK, TW, LW) [USNM]; Hambantota District: Palatupana, 3–6.II 1975, 2♀, 1♂ (KVK, PBK, PF, EGD) [USNM]; the same place but 29.III–2.IV 1981, 1♀ (KVK, TW, LW) [USNM].

DISTRIBUTION. Sri Lanka.

NATURAL HISTORY. *Cephalotilla porcella* (Turner, 1911) is distributed in Dry Zone of Sri Lanka, mostly at low elevation (Fig. 13). A seasonal dynamic in Sri Lanka see Fig. 14.

REMARKS. Most of the material from Sri Lanka has been identified by Børge Petersen as *Ctenotilla porcella* (Turner, 1911).



Figs 7–12. 7–9 – *Ctenotilla caeca*, ♂; 10–12 – *Cephalotilla porcella*, ♂. 7, 8, 10, 11 – habitus (7, 10 – dorsal view, 8, 11 – lateral view); 9, 12 – S7–8. *tub* – lateral tubercle.

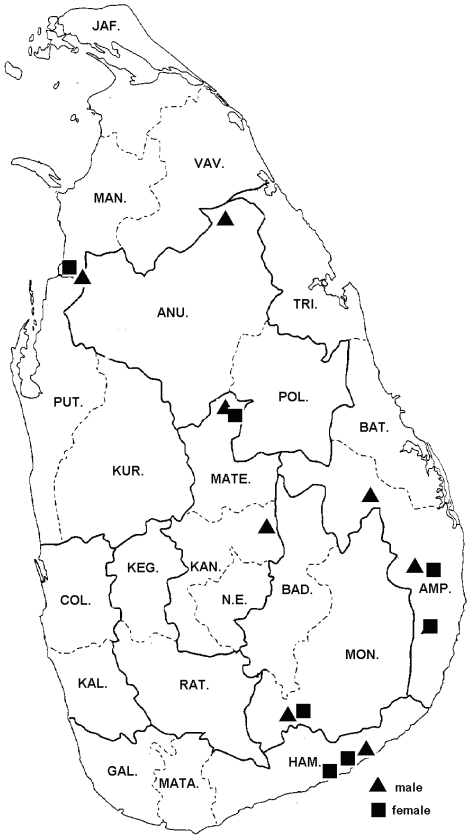


Fig. 13. Map of Sri Lankan Provinces (solid lines), Districts (dashed lines) and the localities, where specimens of *Cephalotilla porcella* have been collected (see material). District abbreviations follow those of Krombein & Pulawski (1994).

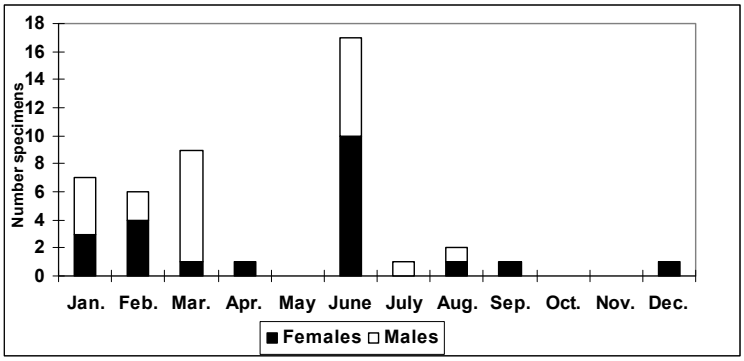


Fig. 14. Seasonal dynamic of *Cephalotilla porcella* in Sri Lanka.

Genus *Denistilla* Lelej, gen. n.

https://zoobank.org/NomenclaturalActs/C7DB47DA-2370-4BF0-BE76-B2515F610CC5

Pristomutilla: Lelej, 2005: 36; Pagliano *et al*., 2020: 166.

Type species: *Mutilla pauli* André, 1898, designated here.

DIAGNOSIS. MALE. T4–7 with medial longitudinal carina. S7 with lateral tubercle. S8 apically with deep triangular emargination bordered by carina. Gonostylus sharply narrowed distally of parapenial lobe apex. Three-four basal metasomal segments ferruginous-red. FEMALE. Prementum tuberculate. Genal carina lacking. Inner margin of mandible without subbasal denticle. Propodeum posterodorsally with complete row of spines, middle spine longest. T2 with two basal spots of white setae disposed transversely and two narrow apical spots of white setae. Pygidial plate granulose and carinated laterally.

DESCRIPTION. MALE. Head not rounded posterad, dorsally with well-defined preoccipital carina. Eyes weakly notched inside. Prementum strongly tuberculate. Mandible with obtuse preapical tooth on inner border, well-defined dorsal curved carina and large triangle acuminated lobe beneath. Scape curved with upper defined carina, space below carina punctured setose. Ocelli small. Antennal tubercle large, carinated, transverse carina between torulus and eye defined. Tegula large, projecting over mesoscuto-scutellar suture. Pterostigma large closed, not sclerotized. Radial cell slightly shorter than first radio-medial cell. Mesopleuron beneath swollen without tooth. T2 with long lateral felt line, S2 without any lateral felt line. S7 with lateral tubercle. S8 apically with deep triangular emargination bordered by carina. Gonostylus sharply narrowed distally of parapenial lobe apex.

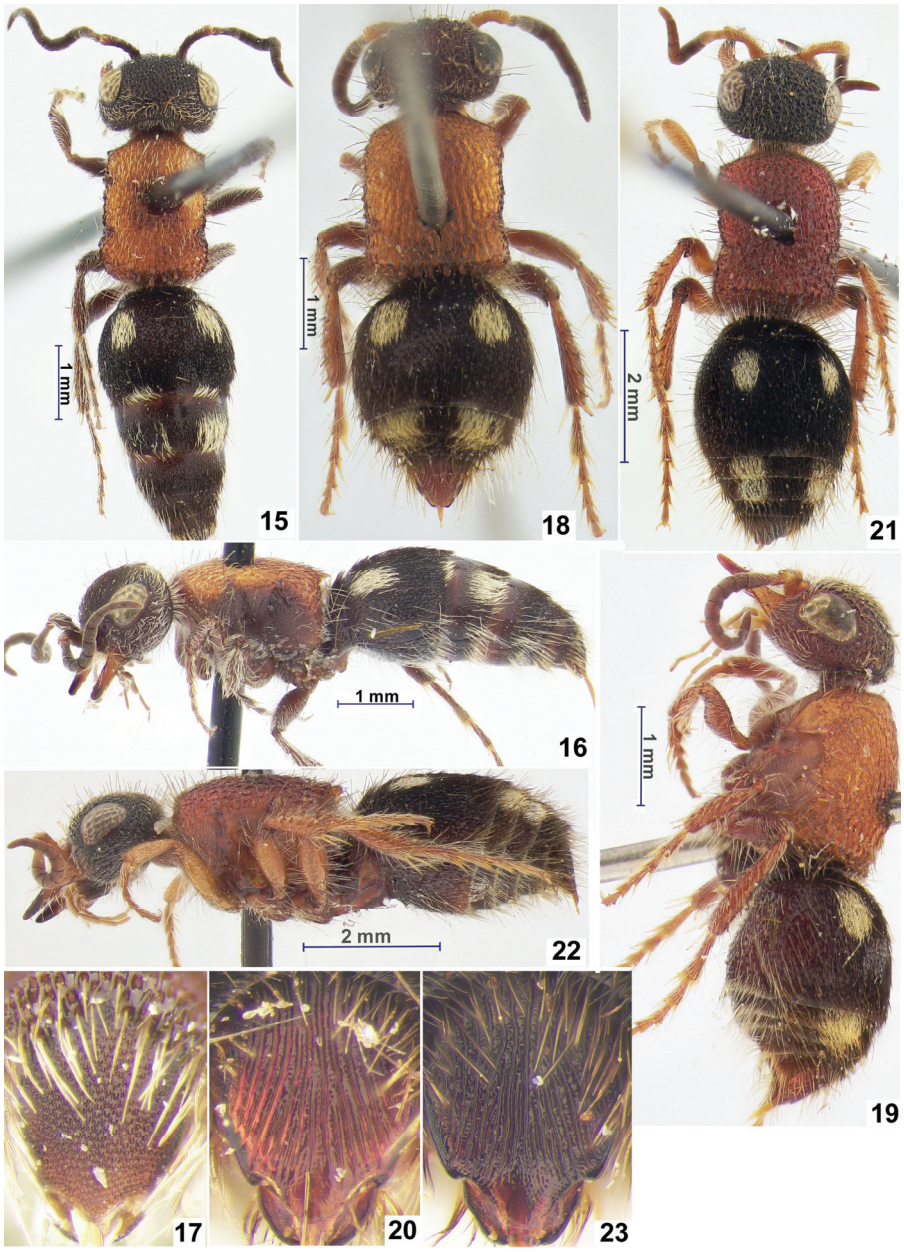
FEMALE. Prementum tuberculate. Hypostomal carina tuberculate. Genal carina lacking. Clypeus with basomedial tooth. F1 slightly flattened, almost twice as long as F2. Pronotum with well-defined humeral carina. Propodeum posterodorsally with complete row of spines, middle spine longest. T1 much narrower than propodeum, dorsally without pale spots. T2 with two basal spots of white setae disposed transversely and two narrow apical spots of white setae. T2 with lateral long felt line. T3 with widely interrupted band of white setae. Pygidial plate rater wide, granulose and carinated laterally.

SPECIES INCLUDED. Type species *Denistilla pauli* (André, 1898), **comb. n.** and undescribed species (female) from South India with very narrow granulose pygidial plate and short propodeal spines.

DISTRIBUTION. Pakistan, India: Rajasthan, Uttar Pradesh.

REMARKS. The male of *Denistilla* **gen. n.** belongs to the group with medial carina on T4–6 but differs by having S8 with deep triangle apical emargination bordered by carina (S8 apically rounded or straight in other genera). The female of new genus belong to the group with granulose pygidial plate, but differs by having T2 with two basal spots of white setae disposed transversely (T2 without two spots of white setae disposed transversely in other genera).

ETYMOLOGY. I am delighted to name this new genus in honor of Denis J. Brothers, world authority on Mutillidae and Aculeate classification and evolution and my best colleague with a common suffix for mutillid genera. Gender feminine.



Figs 15–23. 15–17 – *Denistilla pauli*, ♀; 18–20 – *Lehritilla ianthis*, ♀; 21–23 – *L. locascioi*, ♀, paratype. 15, 16, 18, 19, 21, 22 – habitus (15, 18, 21 – dorsal view, 16, 19, 22 – lateral view); 17, 20, 23 – T6, pygidial plate.

Denistilla pauli (André, 1898), **comb. n.**
Figs 15–17, 27–29, 40–41

Mutilla pauli André, 1898: 23, ♂, ♀, syntypes "Karachi", Pakistan [MNHN].
Pristomutilla pauli: Lelej, 2005: 36; Pagliano *et al*., 2020: 166.

MATERIAL EXAMINED. **India.** Rajasthan, 40 km S Jodhpur, 15.VIII 2004, on Tephrosia purpurea (Fabaceae) and Aerva javanica (Amaranthaceae), 1♂ (T. Osten) [IBSS]; Uttar Pradesh, Gazipur, 15.VIII 1985, 1♀ (M. Yano) [SKYC].

DISTRIBUTION. Pakistan, India: Rajasthan, Uttar Pradesh.

REMARK. André (1898) noted that one of the two males was attached to the same pin as one of the females that means that they have been collected *in copula*. This species is newly recorded from India.

Genus *Lehritilla* Lelej, 2005

Lehritilla Lelej, 2005: 138 (in key); 172 (description), ♂; Lelej & Brothers, 2008: 32, ♂, Brother & Lelej, 2017: 95, ♂; Pagliano *et al*., 2020: 161; Waldren *et al*., 2023: 12.

Type species: *Lehritilla lanka* Lelej, 2005, ♂, by original designation.

DIAGNOSIS. MALE. T3–7 without medial longitudinal carina. Prementum basally tuberculate. Mandible with weak subbasal tooth on inner border, with well-defined dorsal curved carina and large triangle lobe beneath. T2 with long lateral felt line and sharp tubercle between line and lateral tergal border. S2 without any lateral felt line, with short weak basal longitudinal carina. S7 with lateral lobe. S8 with strong medial longitudinal curved carina, Tegula large, projecting over meso-scuto-scutellar suture. Gonostylus with strong short dorsal process and slender long ventral one. FEMALE. Inner margin of mandible without subbasal denticle. T2 with two basal small spots of pale setae disposed transversely. T3–4 with lateral spot of pale setae. Pygidial plate longitudinally striated throughout or apically micropunctate, laterally carinated, apical fifth bordered by wide sternal lateral carina.

DESCRIPTION. FEMALE (hitherto unknown). Mandible with preapical tooth. Prementum basally tuberculate. Hypostomal carina with tooth. Genal carina weak. Clypeus concave with basomedial tubercle, anterior border with two tubercles. F1 1.5 times as long as F2. Pronotum with well defined humeral carina. Procoxa anterad with small shiny tubercle. Propodeum posterodorsally with complete row of short teeth. T1 slightly narrower than propodeum posterad. T2 with two basal spots of pale setae disposed transversely. T3–4 with lateral spot of pale setae. Pygidial plate longitudinally striate throughout or apically micropunctate, laterally carinated, apical fifth bordered by wide sternal lateral carina.

SPECIES INCLUDED. *Lehritilla lanka* Lelej, 2005, ♂; *L. ianthis* (Turner, 1911), ♀, **comb. n.**; *L. locascioi* (Lelej, 2005), ♀, **comb. n.**

DISTRIBUTION. Oriental Region (South India, Sri Lanka).

REMARK. The male of *Lehritilla* has some unique characters within subfamily Mutillinae: bilobed gonostylus, weakly notched eye, and mandible with large triangle

lobe beneath. Waldren *et al.* (2023) was not included this genus in their study because of the lacking material. I confirm here the position of *Lehritilla* in the tribe Ctenotillini sensu Waldren *et al*. (2023). Hitherto unknown females of *Lehritilla* were transferred from the genus *Pristomutilla* (*ianthis* and *locascioi*). *Pristomutilla pauli* (André, 1898) transferred here to the *Denistilla* **gen. n.** (see above). Two retain *Pristomutilla* species (*pectinospinata* Magretti, 1892 and *spinulosa* André, 1898) are transferred or will be transferred to the *Zeugomutilla* Chen, 1957. As a result the distribution of the genus *Pristomutilla* Ashmead, 1903 is limited by Afrotropical Region.

***Lehritilla lanka* Lelej, 2005**
Figs 24–26, 42–43

Lehritilla lanka Lelej, 2005: 173, figs. 93–98, ♂, holotype, **Sri Lanka**, *Mannar District*: Kokmotte Bungalow, 5 mi NE Wilpattu National Park, 21–25.V 1976 (K. Krombein, P. Karunaratne, S. Karunaratne, D. Balasooriya) [USNM], examined; Pagliano *et al*., 2020: 161, ♂.

MATERIAL EXAMINED. Paratypes of *L. lanka*: **Sri Lanka**, 1♂ with the same data as holotype [IBSS]; Anuradhapura District: Hunuwilagama in Wilpattu National Park, 10–19.III 1970, 1♂ (D. Davis, W. Rowe) [USNM]. **India**, South Malabar [Kerala], 1000 ft, VIII 1956, 1♂ (P. Nathan) [USNM].

DISTRIBUTION. Sri Lanka (dry zone), South India: Kerala.

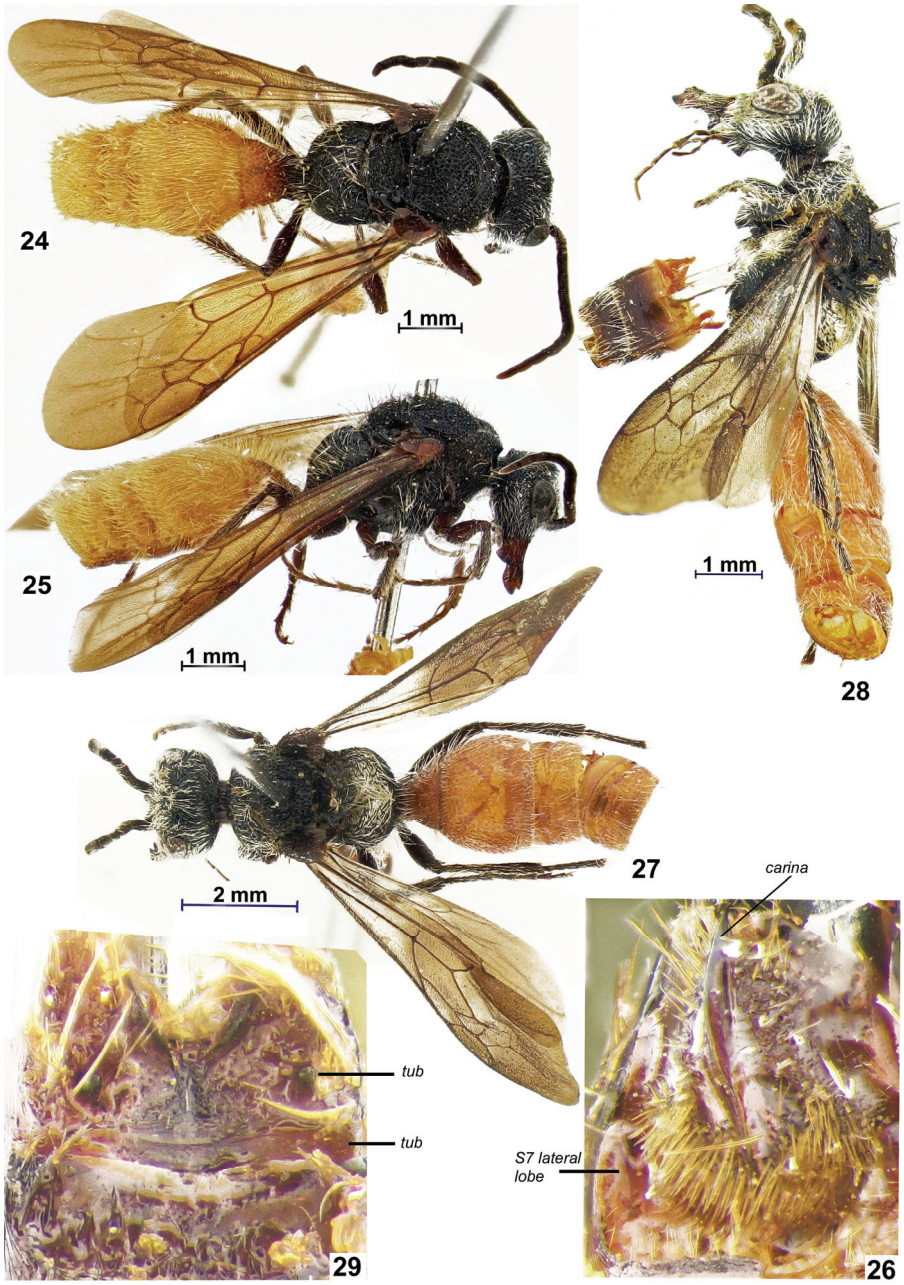
REMARKS. The female of this species might eventually be recognized to be *L. ianthis,* **comb. n.**, based on their co-occurrence in both Sri Lanka and South India. Furthermore in Sri Lanka, Mannar District: 0.8 km NE of Kokmotte Bungalow, 50–100 ft [15–30 m], 21–25.V 1976 both species were collected in one place by the same collectors.

***Lehritilla ianthis* (Turner, 1911), comb. n.**
Figs 18–20

Mutilla ianthis Turner, 1911: 142, 144, ♀, syntypes, "Hambantota, Ceylon (*Fletcher*), November" [BMNH].

Pristomutilla ianthis: Nonveiller, 1995: 33, 115, ♀; Lelej, 2005: 36, 176, ♀; Pagliano *et al*., 2020: 165.

MATERIAL EXAMINED (12♀). **Sri Lanka**: Jaffna District: 16 km S of Pooneryn, 24–25.I 1977, 1♀ (KVK, PF, DWB, VG) [USNM]; Mannar District: Ma Villu, 17–21.II 1979, 1♀ (KVK, TW, SS, TG) [USNM]; 0.8 km NE of Kokmotte Bungalow, 50–100 ft [15–30 m], 21–25.V 1976, 1♀ (KVK, PBK, SK, DWB) [USNM]; the same locality but 22–23.I 1977, 1♀ (KVK *et al*.) /*Prisromutilla ianthis* (Turner), B. Petersen det., 1984 [IBSS]; Amparai District, Lahugala Sanctuary, 13–15.VI 1976, 2♀ [USNM]; Monaragala District: Angunakolapelessa, 27–28.III 1981, 1♀ (KVK, TW, LW [USNM]; Hambantota Disrict: Hambantota, 28, 29.XI 1908 (T.B. Fletcher), 2♀ [NMC]; same locality, 29.III–2.IV 1981, 1♀ (KVK, TW, LW) [USNM]; N 374 [probably Hambantota], 1♀ [NMC]. **South India**, Karnataka, 15 km N Bangalore, KT, 25.VII 1996, 1♀ (K. Werner, L. Lorenz) [MSNF].



Figs 24–29. 24–26 – *Lehritilla lanka*, holotype, ♂; 27–29 – *Denistilla pauli*, ♂. 24, 25, 27, 28 – habitus (24, 27 – dorsal view, 25, 28 – lateral view); 26, 29 – S7–8 (26 – lateroventral view, 29 – ventral view. tub – lateral tubercle. (Photographs by V. Loktionov –24, 25).

DISTRIBUTION. Sri Lanka, India: Karnataka.

REMARKS. Probably the females collected by T. Bainbrigge Fletcher in Hambantota in 1908 [NMC] are the syntypes.

***Lehritilla locascioi* (Lelej, 2005), comb. n.**

Figs 21–23

Pristomutilla locascioi Lelej, 2005: 174, fig. 86, ♀, **South India**, Karnataka, 15 km N Bangalore, KT, 23–24.VII 1996 (K. Werner, L. Lorenz) [MSNF], examined; Pagliano *et al*., 2020: 165.

MATERIAL EXAMINED. Paratypes of *P. locascioi* Lelej: **India**, 1♀ with the same label as holotype; same place, 25.VII 1996, 2♀ (K. Werner, L. Lorenz); *Tamil Nadu*: 10 km NE Dindigul, 21.X 1997, 1♀ (A. Sforzi, L. Bartalozzi); Pudukkottai, 20.X 1997, 1♀ (A. Sforzi, L. Bartalozzi); 29 km N Pudukkottai, 20.X 1997, 1♀ (A. Sforzi, L. Bartalozzi); boscaglia c/o confine N della Peryar National Reserve, 23.X 1997, 1♀ (A. Sforzi, L. Bartalozzi) [MSNF; IBSS]; *Karnataka*, Bangalore, Allalsandra, 900 m altitude, 26–29.X 1977, 1♀ (Zool. Mus. Copenhagen Exp.) / *Pristomutilla ianthis* (Turner), B. Petersen det., 1980 [IBSS].

DISTRIBUTION. South India: Karnataka, Tamil Nadu.

REMARKS. The female of *L. locascioi* is most similar to female of *L. ianthis* but has the another shape of head with unprojecting eyes (projecting in *L. ianthis*), mesosoma dorsally rugoso-striate in anterior half and strongly tuberculate in posterior half (rugoso-striate throughout in *L. ianthis*).

Genus *Williamstilla* Lelej, gen. n.

https://zoobank.org/NomenclaturalActs/A27D4891-3152-4CA1-AB82-A285AC584781

Ctenotilla: Lelej, 1992: 282, ♀; 2005, 34. part.; Williams *et al*., 2019: 15, ♀; Pagliano *et al.*, 2020: 161, part.

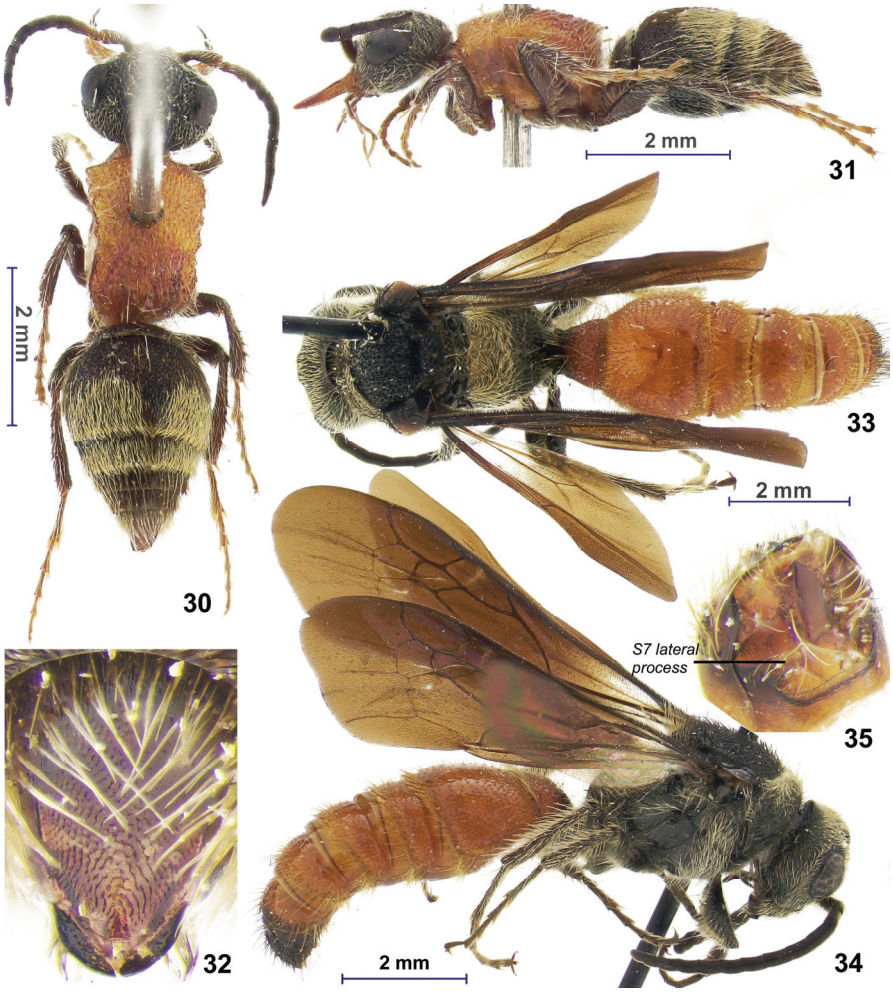
Type species: *Ctenotilla guangdongensis* Lelej, 1992, designated here.

DIAGNOSIS. MALE. T4–6 with medial longitudinal carina. S7 with strong lateral process curved inward. S8 medially with highly elevated wide shiny longitudinal part bordered by long setae. Apical part of gonostylus sharply down curved. Five-six basal metasomal segments ferruginous-red. FEMALE. Inner margin of mandible without subbasal denticle. Pygidial plate microreticulate and carinated laterally. T2 without two subbasal white spots disposed transversely, T2 apically and T3 with medially interrupted band of yellowish setae.

DESCRIPTION. MALE. Head not rounded posterad, dorsally with well-defined preoccipital carina. Eyes weakly notched inside. Prementum strongly tuberculate. Mandible with preapical tooth on inner border, well-defined dorsal curved carina and large triangle lobe beneath. Scape curved with upper defined carina, space below carina punctured, setose. Ocelli small. Antennal tubercle large, carinated, transverse carina between torulus and eye defined. Tegula large, projecting over mesoscutoscutellar suture. Pterostigma large closed, not sclerotized. Radial cell slightly longer

than first radio-medial cell. Mesopleuron beneath swollen, without tooth. T2 with long lateral felt line, S2 without any lateral felt line. S7 with strong lateral process curved inward. S8 medially with highly elevated wide shiny longitudinal part bordered by long setae. Gonostylus inside preapically with triangle widening. Apical part of gonostylus sharply down curved. Parapenial lode ventrally dentate.

FEMALE. Prementum with weak distinct basal tubercle. Hypostomal carina with tooth closer to mandibular base. Genal carina weak, not tuberculate posterad. Clypeus



Figs 30–35. *Wiiliamstilla guangdongensis*. 30–32 – ♀, paratype; 33–34, ♂. 30, 31, 33, 34 – habitus (30, 33 – dorsal view, 31, 34 – lateral view); 32 – T6, pygidial plate; 35 – S7–8, posterolateroventral view.

more or less gently sloping with small basomedial tubercle, anterior margin weakly rounded, not tuberculate. F1 1.4 times as long as F2, F2–4 weakly emarginated beneath. Pronotum with well-defined humeral carina. Propodeum posterodorsally with complete row of spines, middle spine longest. Ratio width of T1/propodeum = 0.8. T1 apicodorsally with fringe of yellowish setae. T2 without two subbasal white spots disposed transversely, T2 apically and T3 with medially interrupted band of yellowish setae. Pygidial plate elongated, microreticulate, apically rounded, carinated laterally and apically.

SPECIES INCLUDED. Type species only, *Williamstilla guangdongensis* (Lelej, 1992), **comb. n.**

DISTRIBUTION. China: Guangdong, Thailand, Laos, Vietnam.

REMARKS. The male of *Williamstilla* **gen. n.** belongs to the group with medial carina on T4–6 but differs by having S7 with strong lateral process curved inward (S7 at most with lateral tubercle in other genera), by S8 medially with highly elevated wide shiny longitudinal part (S8 medially invaginated in other genera), by apical part of gonostylus sharply down curved (gonostylus gently down curved in other genera). The female of new genus belong to the group with granulose pygidial plate, but differs by having T2 without two subbasal white spots disposed transversely (T2 with two basal white spots disposed transversely in *Denistilla*) and by T2 apically and T3 with medially interrupted band of pale setae (T2 apically and T3 with non interrupted band of pale setae in *Cephalotilla* and *Ctenotilla*). The female of *Williamstilla* **gen. n.** is similar to the female of Afrotropical genus *Chaetomutilla* Nonveiller, 1979, especially *Ch. fornasinii* (Gribodo, 1894), but differs by wider T1.

ETYMOLOGY. I am delighted to name this new genus in honor of Kevin A. Williams, world authority on Mutillidae and my best colleague with a common suffix for mutillid genera. Gender feminine.

Williamstilla guangdongensis (Lelej, 1992), **comb. n.**
Figs 30–35, 44–46

Ctenotilla guangdongensis Lelej, 1992: 282, ♀, holotype, ♀, China: Prov. Guangdong, Ding Hu Shan, 9.VIII 1956, Mo Monyi [SCAU]; 2005: 34, ♀; Williams *et al*., 2019: 15, ♀; Pagliano *et al*., 2020: 161.

DESCRIPTION. MALE (hitherto unknown). The same as for the genus (see above).

MATERIAL EXAMINED. Paratype of C. *guangdongensis* Lelej: **China**, Guangdong, Cebaling, open loess area near river, 21.VI 1990, ♀ (A. Lelej) [IBSS]. Additional material. **China**, Yunnan, 17–20.VII 2010, 1♂; 18.VII 2010, 1♂ (SCAU). **Laos**, Ban Houaykong, 18–30.IV 1999, 1♂ (O. Šauša) [IBSS].

DISTRIBUTION. Cambodia, China (Guangdong, Yunnan), Thailand (Chiang Mai, Kanchanaburi, Loei, Phetchaburi), Vietnam, and Laos (Williams *et al*., 2019).

Figs 36–46. Genitalia of males. 36–37 – *Ctenotilla caeca*; 38–39 – *Cephalotilla porcella*; 40–41 – *Denistilla pauli*; 42–43 – *Lehritilla lanka*, paratype; 44–46 – *Wiiliamstilla guangdongensis.* 36, 38, 40, 42, 44 – dorsal view; 37, 39, 41, 43, 45 –ventral view; 46 – lateral view.

DISCUSSION

In the Old World, the Afrotropical Region has more than twice as many Mutillidae species or subspecies (~1500) as each of the other three Regions (Palaearctic, ~600 spp.; Oriental, ~700 spp.; Australasian, ~300 spp.). In the tribes Ctenotillini, Zeugomutillini and Pristomutillini this trend is much increase, 185 species of 204 are distributed in the Afrotropical Region (Table 1) and the distribution of the Pristomutillini is limited by the Afrotropical Region. The tribe Ctenotillini represents in the Palaearctic by one genus with one species only. Among seven tribes of the subfamily Mutillinae the plesiomorphic Pristomutillini is basal (Waldren *et al*., 2023) while Zeugomutillini and Ctenotillini are close to the apomorphic Smicromyrmini. The male of the genus *Lehritilla* (tribe Ctenotillini) has gonostylus with strong short dorsal process and slender long ventral one. Such shape of gonostylus remind the bilobed gonostylus of the Neotropical genus *Horcomutilla* Casal, 1962 (Sphaeropthalminae: Pseudomethocini) (Cambra *et al*., 2022). The bifurcation and reduction of the gonostylus are known in the spider wasps *Priocnemis hyalinata* species-group (Pompilidae: Pepsinae) (Loktionov & Lelej, 2017).

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