

# Review of the genus *Toxeuma* Walker, 1833 (Hymenoptera, Pteromalidae) from Russia, with a key to Palearctic species

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## Abstract

Species of the genus *Toxeuma* Walker, 1833 from Russia are reviewed. A new species, *Toxeuma leleji* Tselikh, **sp. nov.**, is described from the Russian Far East. *Toxeuma fuscicornis* Walker, 1833 and *T. styliclava* (Hedqvist, 1974) are recorded for the first time from Russia; *Toxeuma acilius* (Walker, 1848) – for the first time for Western and Eastern Siberia and the European part of Russia; *Toxeuma paludum* Graham, 1959 – for the first time for Western and Eastern Siberia; *Toxeuma subtruncatum* Graham, 1959 – for the first time for Primorskii Region. An identification key to females of all Palearctic species of *Toxeuma* is provided.

## Keywords

Fauna, key, new species, parasitoids, Pteromalinae, taxonomy

## Introduction

The pteromalid genus *Toxeuma* Walker, 1833 (type species *Toxeuma fuscicornis* Walker, 1833) belongs to the family Pteromalidae, subfamily Pteromalinae, and is distributed in the Palearctic, Nearctic, and Neotropical regions. Up to now it comprised nineteen species, only six of which (*T. acilius* (Walker, 1848), *T. discretum* Graham,

1984, *T. fuscicorne* Walker, 1833, *T. paludum* Graham, 1959, *T. styliclava* (Hedqvist, 1974), and *T. subtruncatum* Graham, 1959) inhabit the Palaearctic Region (Walker 1833, 1848; Graham 1959, 1969, 1984; Hedqvist 1974; Noyes 2019), with three species (*T. acilius*, *T. paludum*, and *T. subtruncatum*) recorded from Russia (Tselikh 2014, 2019).

Four other species, *T. aciculare* Heydon, 1988, *T. aquilonium* Heydon, 1988, *T. gerra* Heydon, 1988, and *T. inopinum* Heydon, 1988 are distributed in the Nearctic Region (Heydon and Grissell 1988; Noyes 2019).

Nine species, *T. affinis* Ashmead, 1901, *T. aphareus* (Walker, 1839), *T. faceta* Girault, 1913, *T. ferrugineipes* Ashmead, 1901, *T. hawaiiensis* Ashmead, 1901, *T. nigrocyanea* Ashmead, 1901, *T. nubilipennis* Ashmead, 1901, *T. orobia* (Walker, 1842), and *T. tarsata* Ashmead, 1901 are distributed in the Neotropical Region (Walker 1839, 1842; Ashmead 1901; Girault 1913; Noyes 2019).

Including the new species from the eastern Palaearctic Region described in this paper, the genus *Toxeuma* now consists of twenty valid species.

The aim of this work is to describe a new species of *Toxeuma* from Russian Far East and to give new records of two Palaearctic species of *Toxeuma* from Russia. An identification key to all Palaearctic species of *Toxeuma* is also provided.

## Material and methods

The material used in this review is deposited in the Hymenoptera collections of the Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia (**ZISP**), Natural History Museum, London, United Kingdom (**NHMUK**) and Oxford University Museum of Natural History, Oxford, United Kingdom (**OUMNH**).

Morphological terminology, including sculpture and wing venation nomenclature, follows Bouček and Rasplus (1991) and Gibson (1997). The flagellum consists of two anelli, the funiculus (composed of six funicular segments), and the clava of three segments. The following abbreviations are used: **POL** – posterior ocellar line, the minimum distance between the posterior ocelli; **OOL** – ocello-ocular line, the minimum distance between a posterior ocellus and compound eye; **M** – marginal vein; **S** – stigmal vein; **P** – postmarginal vein; **F1–F6** – funicular segments; **Mt2–Mt8** – metasomal tergites (**Mt1** – petiole).

The scape is measured without the radicle; the pedicel is measured in lateral view. The distance between the clypeal margin and the toruli is measured from the lower margins of the toruli. Eye height measured as the maximum diameter, eye length as the minimum diameter. The mesosoma and metasoma are measured in lateral view, the latter including the ovipositor sheaths.

Observations were made using MC-2 ZOOM and Leica MZ16 stereomicroscopes, and images were acquired using a combination of Olympus SZX 10 stereomicroscope and a digital camera EOS 70D, Micromed 3 microscope and a digital camera Toup-Cam UCMOS 5.1MP (ZISP specimens); a Canon 5DsR camera + Mitutoyo 10×

lens or Canon MPE ultra macro lens (65 mm), Canon MT-24ex flash and Cognysis Stachshot, and Helicon remote software (NHMUK specimens); a Leica M165C microscope, Leica 10450028 planapo 1× objective lens and Leica DFC 490 digital camera, and Leica Application Suite v.4.12.0 (OUMNH specimen). The acquired images were then processed with Helicon Focus.

## Taxonomy

### *Toxeuma* Walker, 1833.

Type species: *Toxeuma fuscicornis* Walker, 1833, by subsequent designation of Westwood (1839: 68).

*Cirdania* Hedqvist, 1974: 145. Type species: *Cirdania styliclava* Hedqvist, 1974, by original designation. Synonymy by Bouček (1991: 205).

**Diagnosis.** Clypeal margin entire, truncate or slightly arched; antennal clava with or without short or long spicula; antennal formula 11263; pronotum with collar margin carinate; notauli complete; prepectus reticulate, without carinae; sculpture of propodeum at least partly irregular, petiole from transverse to slightly elongate; fore wing with slender M, metasoma ovate or lanceolate (Graham 1959; Hedqvist 1974; Heydon and Grissell 1988; Bouček and Rasplus 1991).

**Distribution.** Palaearctic, Nearctic and Neotropics.

**Comments.** Unfortunately, the biology of most *Toxeuma* species is unknown. The only biological records exist for *T. fuscicorne*, which was reared from the primary host *Agromyza schineri* Giraud, 1861 (Diptera, Agromyzidae) (Bouček 1977), and for *T. paludum*, reared from the primary host *Coleophora* sp. (Lepidoptera, Coleophoridae) (Askew 1968).

The genus can be distinguished from other Pteromalidae genera using the keys of Graham (1969) and Bouček and Rasplus (1991).

In this genus, the antennal clava can have three variations: acute (Fig. 24), with a spicula (e.g., Figs 4, 17, 27, 30) or without spicula and rounded apically (e.g., Figs 13, 35). This is an important feature to identify species of this genus. Unfortunately, in the original descriptions of *T. acilius* (Walker, 1848) and *T. paludum* (Graham, 1959) as well as in previously published keys (Graham 1959, 1969) this feature was neither mentioned nor shown on the figures. However, after studying the types and additional material, the presence of a spicula was found in almost all individuals of these species. Interestingly, *T. paludum* Graham is characterized by variation of antennal clava from acute (Fig. 24) to that with very short and straight spicula (e.g., Figs 23, 27).

The discovery of a previously undescribed spicula in some Palaearctic species suggests that some members of *Toxeuma* from Nearctic Region described by Heydon and Grissell (1988) might be synonyms of the Palaearctic species, but additional research is needed to confirm this assumption.

## Key to Palaearctic species of *Toxeuma* Walker based on females

- 1 Antennal clava with spicula (e.g., Figs 4, 17, 27, 30) or distinctly acute apically (Fig. 24) ..... **2**
- Antennal clava without spicula and rounded apically (e.g., Figs 13, 35) ..... **5**
- 2 Antennal clava with long spicula (Fig. 30). Petiole with reticulate sculpture (dorsal view), 1.4–1.8 times as long as broad (Fig. 32) ..... ***T. styliclava* (Hedqvist)**
- Antennal clava acute (Fig. 24) or with short spicula (e.g., Figs 4, 17, 27). Petiole with irregular sculpture (dorsal view), 0.7–1.25 times as long as broad (e.g., Figs 6, 19, 26) ..... **3**
- 3 Mt2 0.85–0.9 times median length of metasoma (Fig. 18). Metasoma 0.4–0.45 times as long as mesosoma and head together (Fig. 15). Sculptured part of petiole 1.17–1.25 times as long as broad (Fig. 19). Propodeum medially as long as scutellum ..... ***T. leleji* sp. nov.**
- Mt2 0.5–0.6 times median length of metasoma (e.g., Figs 25). Metasoma 0.6–0.7 times as long as mesosoma and head together (e.g., Figs 2, 22). Sculptured part of petiole 0.75–1.0 times as long as broad (e.g., Figs 6, 26). Propodeum medially shorter than scutellum ..... **4**
- 4 All legs with femora and tibia metallic blue-green (Fig. 22). Antennal clava acute (Fig. 24) or with very short and straight spicula (e.g., Figs 23, 27). Head and mesosoma metallic blue-green ..... ***T. paludum* Graham**
- All legs with femora and tibia reddish or testaceous (Fig. 2). Spicula of antennal clava longer and curved (e.g., Figs 3, 4, 5). Head and mesosoma bright green ..... ***T. acilius* (Walker)**
- 5 Mt2–Mt8 smooth and shiny (Fig. 37). Metasoma ovate, shorter than mesosoma (Fig. 33). Petiole 1.25–1.55 times as long as broad (Fig. 38) ..... ***T. subtruncatum* Graham**
- Mt2–Mt8 alutaceous (e.g., Figs 7, 11). Metasoma lanceolate, longer than mesosoma (e.g., Figs 9, 10). Petiole 0.5–0.7 times as long as broad (Fig. 12) ..... **6**
- 6 Mt8 1.5–1.7 times as long as broad (Fig. 11). Metasoma 1.05–1.2 times as long as mesosoma and head together (Fig. 10) ..... ***T. fuscicorne* Walker**
- Mt8 up to 1.15 times as long as broad (Fig. 7). Metasoma shorter than mesosoma and head together ..... ***T. discretum* Graham**

### ***Toxeuma acilius* (Walker, 1848)**

Figs 1–6

*Lamprotatus acilius* Walker, 1848: 169. Lectotype male, (NHMUK, examined) designated by Graham 1959: 104.

*Toxeuma acilius* (Walker, 1848) new combination in Graham, 1959: 104.

**Material examined.** **Lectotype** male (NHMUK): UNITED KINGDOM: “LECTOTYPE”, “Type”, “England”, “*Lamprotatus Acilius* Walker ♂ / Stood under this name in old B.M.

Coll. C. Waterhouse”, “*Acilius*,” “*Toxeuma ericae* (Delucchi)”, “*Toxeuma acilius* (Walk.) det. M.W.R. de V. Graham”, “B.M. TYPE HYM. 5.1928”, “NHMUK 013456778”.

**Other material:** UNITED KINGDOM: England, 1 female, Berkshire, Wytham Wood, 3.VIII.1954, coll. M.W. Graham. RUSSIA: **Bryansk Prov.**, 2 females, 15 km E Pochep Town, Uruch’e Vill., 52°55.00’N, 33°57.50’E, 20.VIII.2020, coll. O. Kosheleva and E. Tselikh; **Kamchatka Reg.**, 1 female, 80 km S Lazo Vill., Kronotsky Reserve, Ipuin, 19.VII.2013, coll. D. Rachin and E. Tselikh; **Sakhalinskaya Prov.**, 1 female, Kunashir Island, Dubovoe Vill., 22.VII.1973, coll. D. Kasparyan; 1 female, Mendeleevo Vill., 3.VIII.2011, coll. D. Rachin and E. Tselikh; **Smolensk Prov.**, 1 female, Smolensk, 54°49.103’N, 32°5.09’E, 23.VIII.2020, coll. O.V. Kosheleva; **Tyumen’ Prov.**, 1 female, 2 km SW Tyumen’, Bereznayakovsky Vill., 3.VII.2018, coll. Tselikh.

**Distribution.** Czech Republic, Germany, Netherlands, Romania, Russia (Russian Far East; Western and Eastern Siberia, European part of Russia – new records), Sweden, United Kingdom (Walker 1848; Graham 1959; Tselikh 2014, 2019; Noyes 2019).

### *Toxeuma discretum* Graham, 1984

Figs 7–9

*Toxeuma discretum* Graham, 1984: 501. Holotype female (NHMUK, examined).

**Material examined.** *Holotype* female (NHMUK): UNITED KINGDOM: “Holotype”, “England: Oxon Bald Hill, nr. Lewknor, 18.6.1958”, “*Toxeuma discretum* sp.n. HOLOTYPE ♀ M. de V. Graham det. 1983”, “B.M. TYPE HYM 5.3020”, “NHMUK 013456774”.

**Distribution.** Belgium, France, Sweden, United Kingdom (Graham 1984; Noyes 2019).

### *Toxeuma fuscicornis* Walker, 1833

Figs 10–14

*Toxeuma fuscicornis* Walker, 1833: 378; lectotype female (NHMUK, not examined) designated by Graham (1969: 147).

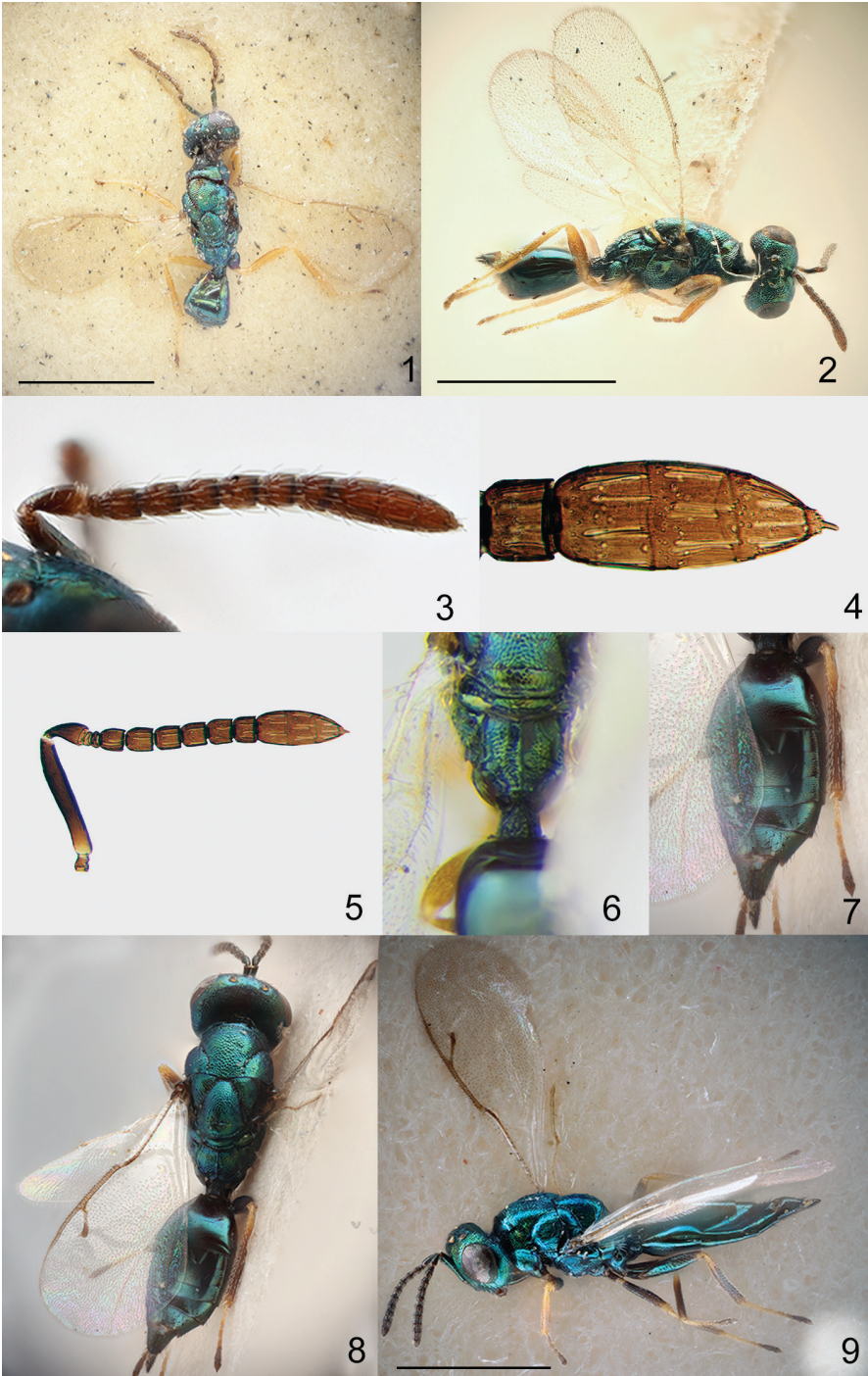
*Miscogaster lugubris* Walker, 1833: 462. Type specimens possibly lost (Graham 1969: 147). Synonymy by Walker (1846: 28) under *Toxeuma ericae* Walker, 1833.

*Toxeuma ericae* Walker, 1833: 379; lectotype female (NHMUK, not examined) designated by Graham (1969: 147). Synonymy by Graham (1959: 101).

*Gastrancistrus accia* Walker, 1848: 156; lectotype female, (NHMUK, not examined) designated by Graham (1969: 147). Synonymy by Graham (1959: 101).

**Material examined. Other material:** RUSSIA: **Belgorod Prov.**, 12 females, 3 males, Borisovka Vill., “Belogor’e” Reserve, “Les na Vorskle”, 11.VI.2018, coll. Tselikh.





**Figures 1–9.** *Toxeuma acilius* holotype male (1) non-type female (2–6) 1 body, dorsal view 2 body, dorso-lateral view 3 antenna (dry material) 4 F6 and antennal clava (slide) 5 antenna (slide) 6 propodeum and petiole, dorsal view *Toxeuma discretum* holotype female (7–9) 7 metasoma, dorsal view 8 body, dorsal view 9 body, lateral view Scale bars: 1.0 mm.

**Distribution.** Belgium, Croatia, Czech Republic, France, Germany, Hungary, Iran, Netherlands, Romania, Russia (new record), Spain, Sweden, Switzerland, United Kingdom (Walker 1833; Graham 1959, 1969; Noyes 2019).

**Biology.** Primary parasitoid of *Agromyza schineri* Giraud, 1861 (Diptera, Agromyzidae) – Bouček (1977).

***Toxeuma leleji* Tselikh, sp. nov.**

<http://zoobank.org/220F64CB-8C8C-4AD4-AFC7-F8FA07081ECF>

Figs 15–21

**Comparison.** *Toxeuma leleji* is similar to *T. acilius* (Walker) and *T. paludum* Graham; the differences between these species are given in the key.

Females of *Toxeuma leleji* are also similar to those of the Nearctic species *Toxeuma inopinum* Heydon because they have an antennal clava with needle-like spicula, F1–F4 elongate, fore wing with pilose basal vein, but *Toxeuma leleji* females have the gena not distinctly hollowed at mouth corner, petiole longer than wide, Mt2 0.85–0.9 times median length of metasoma.

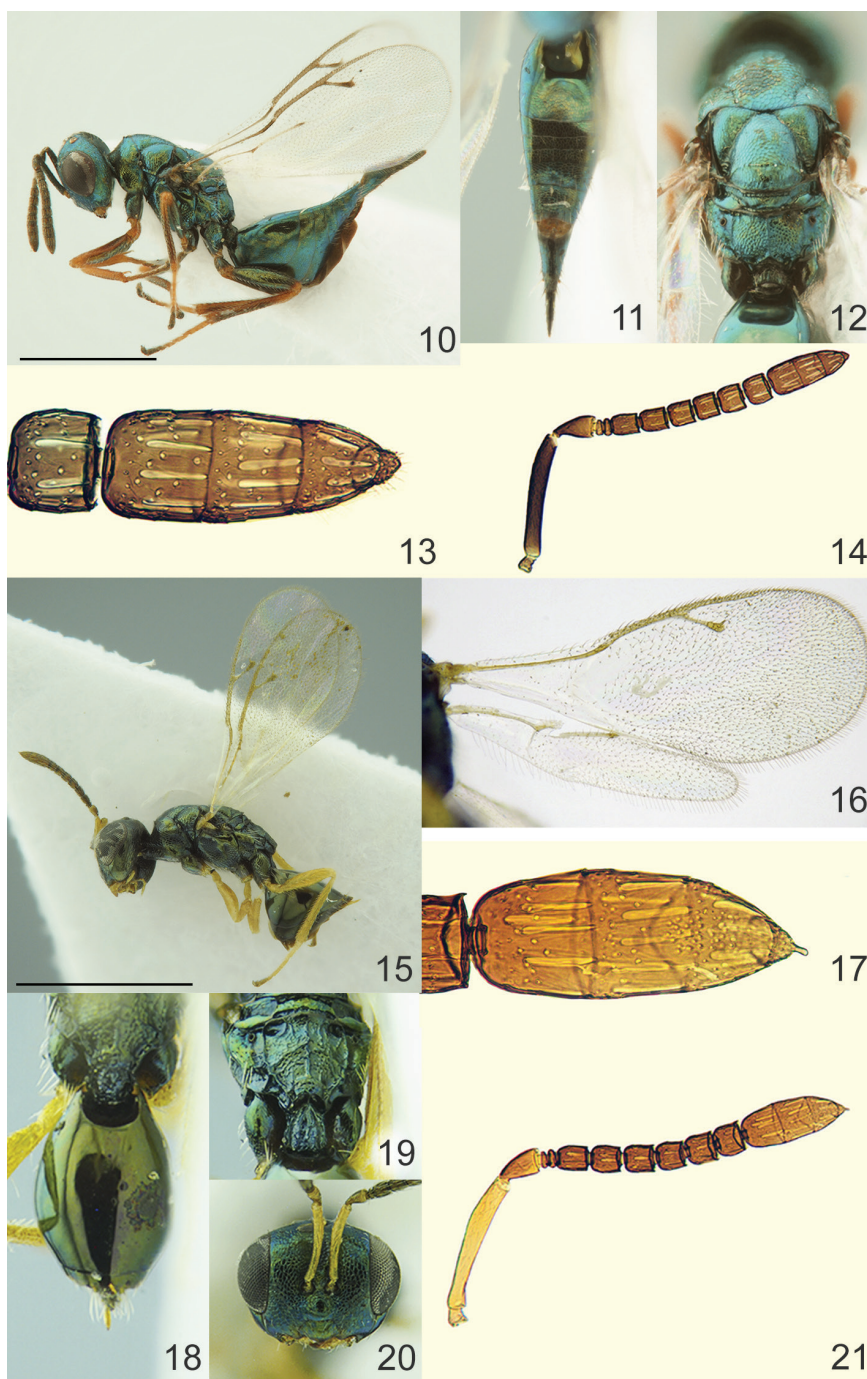
**Description. Female.** Body length 1.5 mm. Fore wing length 1.5 mm.

Head, mesosoma and metasoma, metallic bluish-green with diffuse coppery lustre; antenna with scape yellow, pedicel yellowish-brown, flagellum brown; all coxae metallic bluish-green with diffuse coppery lustre; all femora, tibiae and tarsi yellow except last segment yellowish-brown; fore wing hyaline, venation yellowish-brown; ovipositor sheath black.

Head in dorsal view 1.93–2.07 times as broad as long and 1.36–1.38 times as broad as mesoscutum; in frontal view 1.28–1.3 times broader than high. POL 1.46–1.57 times OOL. Eye height 1.21–1.26 times eye length and 2.90–2.92 times as long as malar space. Distance between antennal toruli and lower margin of clypeus 0.75 times distance between antennal toruli and median ocellus. Clypeus alutaceous, its lower margin slightly arched. Antenna with scape 0.92–0.96 times as long as eye height and 1.12–1.22 times as long as eye length; pedicel 1.61–1.66 times as long as broad and 1.40–1.42 times as long as F1; combined length of pedicel and flagellum 1.10–1.14 times breadth of head; flagellum almost filiform; F1–F3 longer than broad, F4–F5 subquadrate, F6 transverse (on dry material) and F1 longer than broad, F2–F3 subquadrate, F4–F6 transverse (on slide); clava 2.83–2.86 times as long as broad (on dry material) and 2.58 times (on slide).

Mesosoma 2.20–2.45 times as long as broad. Scutellum finely reticulate, 1.0–1.1 times as long as broad. Propodeum medially as long as scutellum; median carina and plicae present; sculpture reticulate with irregular rugae; nucha short and weakly reticulate. Sculptured part of petiole 1.17–1.25 times as long as broad, with irregular sculpture. Fore wing 2.34–2.89 times as long as maximum width; basal cell bare; basal vein pilose; speculum partly open; M 1.16–1.22 times as long as P and 1.95–2.00 times as long as S.

Metasoma ovate, 1.50–1.64 times as long as broad and 0.40–0.45 times as long as mesosoma and head together; Mt2 0.85–0.90 times median length of metasoma. Ovipositor sheath projecting slightly beyond apex of metasoma.



**Figures 10–21.** *Toxeuma fuscicorne* non-type female (10–14) 10 body, lateral view 11 metasoma, dorsal view 12 scutellum, propodeum and petiole, dorsal view 13 F6 and antennal clava (slide) 14 antenna (slide) *Toxeuma leleji* sp. nov. holotype female (15, 16, 18–20) paratype female (17, 21) 15 body, lateral view 16 fore and hind wings 17 antennal clava (slide) 18 metasoma, dorsal view 19 propodeum and petiole, dorsal view 20 head, frontal view 21 antenna (slide) Scale bars: 1.0 mm.



**Etymology.** The species is named in honour of the prominent entomologist, an expert on Mutillidae (Hymenoptera), Prof. Arkady S. Lelej.

**Material examined.** *Holotype* female (ZISP): RUSSIA: **Sakhalin Prov.**, Kunashir Island, Golovnina Volcano, 27.VII.1981, coll. E. Sugonyaev.

*Paratype* female (ZISP): same data as holotype.

**Distribution.** Russian Far East (Sakhalinskaya Prov.).

### *Toxeuma paludum* Graham, 1959

Figs 22–27

*Toxeuma paludum* Graham, 1959: 102. Holotype female (OUMNH, examined), paratypes (NHMUK, examined).

**Material examined.** *Holotype* female (OUMNH): “Otmoor OX. MWG. (1) 6.7.1956”, “*Toxeuma paludum* TYPE ♀”, “*Toxeuma paludum* sp.n. M. de V. Graham det. 1957 HOLOTYPE [female symbol]”, “TYPE HYM: 1219 *Toxeuma paludum* GRAHAM HOPE DEPT. OXFORD”. Paratype female (NHMUK): UNITED KINGDOM: “PARATYPE”, “OXON. Otmoor. (3) 10.7.1956 M. de V. Graham”, “*Toxeuma paludum* Paratype sp.n. M. de V. Graham”, “NHMUK 013456775”. **Other material:** RUSSIA: **Irkutsk Prov.**, 6 females, 3 males, Sludyanka Vill., “Shamansky Cape”, 05.VIII.2019, coll. E. Tselikh; **Kamchatka Terr.**, 6 females, 3 males, 80 km S Lazo Vill, Kronotsky Reserve, Ipuin, 55°06.969'N, 159°57.952'E, 18.VII.2013, coll. D. Rachin and E. Tselikh; **Sakhalinskaya Prov.**, 1 female, Iturup Island, Goryachie Kluchi Vill., 30.VII.2002, coll. A. Lelej; 1 female, Kunashir Island, Mendeleevo Vill., 3.VIII.2011, coll. D. Rachin and E. Tselikh; 4 females, 3 males, Dubovoe Vill., 49°46.479'N, 145°29.721'E, 21.VII.2011, coll. D. Rachin and E. Tselikh; 8 females, 3 males, Sakhalin Island, Sokol Vill., 4.VIII.2011, coll. D. Rachin and E. Tselikh; 1 female, Shikotan Island, Gorobets Bay, 18.VIII.1998, coll. A. Lelej; **Tyumen' Prov.**, 2 females, 5 males, 35 km NW Tyumen' Sity, Salairka Vill., 5.VII.2018, coll. Tselikh; 5 km N Tyumen' Sity, Lipovoe Lake, 7.VII.2018, coll. Tselikh.

**Distribution.** RUSSIA (Russian Far East; Western and Eastern Siberia – new records), Sweden, United Kingdom (Graham 1959; Tselikh 2014, 2019; Noyes 2019).

**Biology.** Primary parasitoid of *Coleophora* sp. (Lepidoptera, Coleophoridae) (Askew 1968).

### *Toxeuma styliclava* (Hedqvist, 1974)

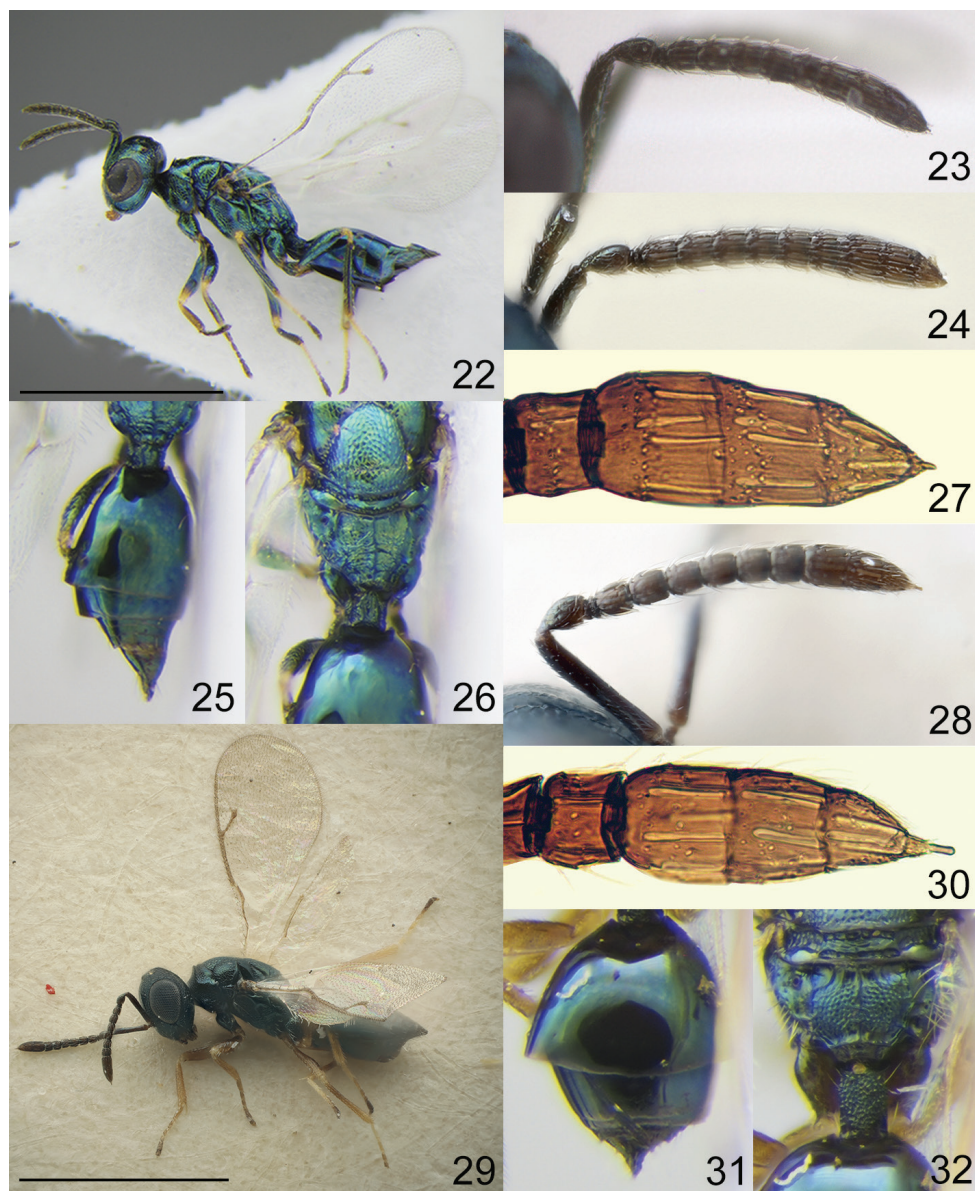
Figs 28–32

*Cirdania styliclava* Hedqvist, 1974: 145–146. Holotype female (NHRS, not examined).

*Toxeuma styliclava* (Hedqvist, 1974) new combination in Bouček (1991: 205).

*Toxeuma mucronatum* Graham, 1984: 501–502. Holotype female (NHMUK, not examined). Synonymy by Bouček, 1991: 205.

**Material examined.** *Paratype* female (NHMUK): SWEDEN: “Sk. Sandhammaren 24/7 1973 leg. K. J. Hedqvist”, “PARATYPUS *Cirdania* gen.n. *styliclava* sp.n. ♀ K-J Hedqvist det. 1973”, “Hedqvist coll. BMNH(E) 2011-27”, “NHMUK 013456781”. **Other material:** RUSSIA: **Primorskii Reg.**, 1 female, Lazovsky Reserve, “Korpad”, 10–14.VIII.2010,



**Figures 22–32.** *Toxeuma paludum* holotype female (23) paratype female (24) non-type female (22, 25, 26) 22 body, lateral view 23 antenna (dry material) 24 antenna (dry material) 25 metasoma, dorsal view 26 scutellum, propodeum and petiole, dorsal view 27 F6 and antennal clava (slide) *Toxeuma styliclava* paratype female (28, 29) non-type female (30–32) 28 antenna (dry material) 29 body, lateral view 30 F6 and antennal clava (slide) 31 metasoma, dorsal view 32 propodeum and petiole, dorsal view Scale bars: 1.0 mm.

coll. D. Rachin and E. Tselikh; 1 female, Ussuriysky Reserve, 3.VIII.1961, coll. V. Trjapitzin; **Sakhalinskaya Prov.**, 1 female, Kunashir Island, Stolbchaty Cape, 3.VIII.2011, coll. D. Rachin and E. Tselikh; 1 female, Sernovodsk Vill., 22.VII.1981, coll. E. Sugonyaev; 1 female, Tret'yakovo Vill., 29–30.VII.2011, coll. D. Rachin and E. Tselikh; 1 female, Sakhalin Island, Sokol Vill., 4.VIII.2011, coll. D. Rachin and E. Tselikh.

**Distribution.** Belgium, France, Russia (Russian Far East – new record), Sweden (Hedqvist 1974; Noyes 2019).

***Toxeuma subtruncatum* Graham, 1959**

Figs 33–38

*Toxeuma subtruncatum* Graham, 1959: 105. Holotype male (OUMNH, not examined).

**Material examined.** *Paratype* female (NHMUK): UNITED KINGDOM: “ENGLAND: Warw Ufton Wood 15.vi.1957”, “M.W.R. de V. Graham coll. BMNH(E) 1995-489”, “*Toxeuma subtruncatum* Paratype ♀”, “PARATYPE”, “NHMUK 013456776”; *paratype* male (NHMUK): “Wytham Wood BERKS. (2) 16.5.1951 M.W. Graham”, “*Toxeuma subtruncatum* M. de V. G. sp.n”, “NHMUK 010749000”. **Other material:**



**Figures 33–38.** *Toxeuma subtruncatum* paratype female (33, 34) paratype male (36) non-type female (35, 37, 38) 33 body, lateral view 34 antenna (dry material) 35 antennal clava (slide) 36 body, lateral view 37 metasoma, dorsal view 38 propodeum and petiole, dorsal view Scale bars: 1.0 mm.

UNITED KINGDOM: “Wytham Wood BERKS 11.6.1951 M.W. Graham”, “*Toxeuma subtruncatum* Graham”, “NHMUK 013456773”; RUSSIA: **Primorskii Reg.**, 1 female, Ussuriysky Reserve, 30.VII.1975, coll. N. Storozheva; **Sakhalinskaya Prov.**, 1 female, Kunashir Island, Dubovoe Vill., 31.VIII.1973, coll. D. Kasparyan.

**Distribution.** Belgium, Czech Republic, Netherlands, Russia (Russian Far East; including Primorskii Reg. – new record), Sweden, United Kingdom (Graham 1959; Tselikh 2014, 2019; Noyes 2019).

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