

# Revision of the Palaearctic *Gasteruption assectator* aggregate, with special reference to Sweden (Hymenoptera, Gasteruptiidae)

Niklas Johansson<sup>1</sup>, Cornelis van Achterberg<sup>2</sup>

**1** Fredriksberg, Baskarp 566 92 Habo, Sweden **2** Research Associate, Department of Terrestrial Zoology, Naturalis Biodiversity Center, Postbus 9517, 2300 RA Leiden, The Netherlands

Corresponding author: Niklas Johansson ([chrysis32@yahoo.se](mailto:chrysis32@yahoo.se))

---

Academic editor: A. Köhler | Received 15 April 2016 | Accepted 23 August 2016 | Published 7 September 2016

<http://zoobank.org/B15F6CEC-F37D-4BB7-87A8-EBC449652C1F>

---

**Citation:** Johansson N, Achterberg C van (2016) Revision of the Palaearctic *Gasteruption assectator* aggregate, with special reference to Sweden (Hymenoptera, Gasteruptiidae). ZooKeys 615: 73–94. doi: 10.3897/zookeys.615.8857

---

## Abstract

The Palaearctic species of the *Gasteruption assectator* aggregate (Hymenoptera, Gasteruptiidae) are revised and three species are recognised. Two species are re-instated: *Gasteruption boreale* (Thomson, 1883), **stat. n.** and *G. nigritarse* (Thomson, 1883), **stat. n.**, and both are excluded from the synonymy with *G. assectator* (Linnaeus, 1758). The general distribution of both species is given for Europe and in detail for Sweden. A key to the valid Palaearctic species of the *Gasteruption assectator* aggregate is given; key characters and primary types are illustrated. Four new synonyms are listed: *Foenus fumipennis* Thomson, 1883, *Trichofoenus breviterebrae* Watanabe, 1934, and *Gasteruption margotae* Madl, 1987, are synonymized with *Gasteruption boreale* (Thomson, 1883) and *Gasteruption brevicauda* Kieffer, 1904, with *G. undulatum* (Abeille de Perrin, 1879).

## Keywords

Europe, *Gasteruption boreale*, *Gasteruption nigritarse*, key, new records, re-instated species, Sweden, synonyms

## Introduction

The predator inquiline wasp *Gasteruption assectator* (Linnaeus, 1758) (Hymenoptera, Gasteruptiidae) has been considered a very common species with wide intraspecific variation concerning both morphology and colouration (e.g. van Achterberg and Talebi 2014). When working on an updated revision of the Nordic *Gasteruption* species the first author noticed that the specimens from a restricted geographical range could be clustered into three separate morphospecies. The discovery of a couple of hitherto unknown features of the females made it fairly easy to separate the morphospecies involved. Further studies of a larger number of specimens and conclusions drawn from practical field work showed that the three morphospecies have a significant difference in geographical distribution and habitat preference in Sweden. Studies of the type material of the supposed synonyms of *G. assectator* showed that *Foenus borealis* Thomson, 1883, and *F. nigritarsis* Thomson, 1883, are the oldest available names for these valid species. Nearctic synonyms listed by Smith (1996) are not accounted for here because their types need to be studied first. The synonymisation of *Gasteruption brevicauda* Kieffer, 1904, with *G. assectator* made by Madl (1987a) is here rejected and it is considered to be conspecific with *G. undulatum* (Abeille de Perrin, 1879), syn. n.

## Material

The first author studied specimens of the *Gasteruption assectator* aggregate deposited in the Evolutionsmuseet, Uppsala; The Swedish Malaise Trap Project (SMTP); the Biologiska Museet (MZLU), Lund and the Naturhistoriska Riksmuseet (NHRS), Stockholm. In addition the private collections of Anders Nilsson, Johan Abenius, Sven Hellqvist, Bo G. Svensson and Niklas Johansson. The results were checked by the second author with specimens deposited in the Naturalis Biodiversity Center (RMNH), Leiden and the Oberösterreichisches Landesmuseum, Biologiezentrum (BZL), Linz.

## Systematics

### *Gasteruption assectator* (Linnaeus, 1758) *sensu stricto*

Figs 1–3, 25–26, 28

*Ichneumon assectator* Linnaeus, 1758: 566, 1761: 407, 1767: 937; Scopoli 1763: 287; Fabricius 1775: 340, 1781: 435, 1787: 268; Gmelin 1790: 2696; Villers 1789: 174; Rossi 1790: 90; Christ 1791: 375; Petagna 1792: 365; Cederhjelm 1798: 163; Schrank 1802: 263; Hentschius 1804: 112; Illiger 1807: 74; Roman 1932: 2; Hedqvist 1973: 182; Fitton 1978: 376.

*Foenus assectator*; Fabricius 1798: 240; Walckenaer 1802: 75; Latreille 1805: 195; Dahlbom 1831: 77; Curtis 1832: 423; Nees 1834: 308; Stephens 1835: 121;

Labram and Imhoff 1836: 24; Zetterstedt 1840: 408; Westwood 1843: 255; Taschenberg 1866: 93; Tournier 1877: ix (as *affectator*); Thomson 1883: 849.

*Foenus affectator*; Abeille de Perrin 1879: 265, 266, 277.

*Gasteruption assectator*; Schletterer 1885: 276, 316, 1889: 384, 393, 395, 397; Dalla Torre 1902: 1063; Szépligeti 1903: 370 (as *affectator*); Kieffer 1912: 256 (id.); Lindemans 1921: 298 (id.); Roman 1932: 2; Schmiedeknecht 1930: 380, 383 (as *affectator*); Hedicke 1939: 5 (id.); Ferrière 1946: 235, 238, 240 (id.); Leclercq 1948: 75; Hellén 1950: 4; Townes 1950: 123–128; Šedivý 1958: 36, 37; Györfi and Bajári 1962: 48, 51; Schmidt 1969: 293; Hedqvist 1973: 181; Fitton 1978: 376; Dolfuss 1982: 22; Oehlke 1984: 169, 171, 175; Ortega and Baez 1985: 509, 515; Madl 1987a: 401, 1987b: 21, 1988: 37, 1989a: 159, 1989b: 41, 1990a: 127, 1990b: 480; Kozlov 1988: 245, 247; Kofler and Madl 1990: 320; Narolsky and Shcherbal 1991: 23, 24; Wall 1994: 150; Scaramozzino 1995: 3; Smith 1996: 492; Peeters 1996: 134; Neumayer et al. 1999: 220; Pagliano and Scaramozzino 2000: 11, 19; Saure 2001: 29; Yildirim et al. 2004: 1350; Turrisi 2004: 84; Westrich 2008: 7–8; van der Smissen 2010: 372; Zhao et al. 2012: 23–27; van Achterberg 2013: 82; van Achterberg and Talebi 2014: 57–61.

*Gasteruption affectator*; Semenov 1892: 200.

*Ichneumon annularis* Geoffroy in Fourcroy 1785: 398; Hedicke 1939: 7; Wall 1994: 148 (type lost). Synonymized by with *G. assectator* (Linnaeus) by Olivier (1792).

**Type material.** High resolution photos of the lectotype female of *G. assectator* in the Linnaean collection coll. no 2652- “49 *assector*” (Figs 1–3) designated by van Achterberg and Talebi (2014) was studied. The specimen has an unusually short ovipositor and the pilosity of the sheath is longer than average, but within the variation of the species. The holotype female of *G. brevicauda* (Figs 4–7) from Algeria (Orléansville) was examined and the specimen, with its strongly sculptured mesoscutum, the strong antero-lateral teeth of the pronotum aswell as the orange hind tarsus clearly belongs to *Gasteruption undulatum* (Abeille de Perrin, 1879). The synonymisation with *G. assectator* made by Madl (1987a) is here rejected and *G. brevicauda* Kieffer, 1904, is a new synonym of *G. undulatum* (Abeille de Perrin, 1879) syn. n.

**Additional material.** **Sweden** (**Skåne**: Åhus, **Blekinge**; **Halland**: Breared; **Småland**: Repperda, Bäckebo, Hälleskog, Tvärvskog, Robacken, Iggersdela, Skillingaryd, Södra Vi, Korsberga; **Gotland**: Ardre, Stora Karlsö, Fårö, Mullvalds; **Öland**: Halltorp, Ekerum, Glömminge; **Östergötland**: Simonstorp, Borensberg)

**Diagnosis.** Temples in dorsal view less parallel-sided and usually shorter than of *G. boreale*, head in dorsal view transverse, mostly distinctly wider than long. Occipital carina indistinct and not reflexed. Face mostly slightly narrower than that of *G. boreale*. Hypostomal bridge narrow, at most 0.5 times mandibular base (Fig. 25). Mesoscutum in most cases distinctly reticulate-coriaceous and without satin sheen (Fig. 26), medio-posteriorly in front of scutellum distinctly rugose. Mesosoma and head silvery pilose. Mesosomal surface with a fatty gloss, quite distinct from the more opaque satin sheen in *G. boreale*. Antenna slightly longer than in *G. boreale*, with sixth segment about



**Figures 1–3.** Lectotype of *Gasteruption assectator* (Linnaeus). **1** habitus dorsal **2** habitus lateral **3** labels.

1.8 times longer than wide and subapical segment about 1.5 times longer than wide. Hind coxa dorsally striate-rugose. Hind tibia and basitarsus with white ring which might be interrupted ventrally. Metasoma mainly black with lateral orange patches on tergites 2–4 often merged. Fore and middle tibiae with small, but quite distinct white or yellow patch basally. Ovipositor sheath black or brown, 1.0–1.3 times as long as hind tibia and without prominent bristles but with thinner adpressed pubescence, appearing nearly naked (Fig. 28). The pilosity of equal intensity all over the surface not becoming scarcer towards the tip. In some specimens, especially when the sheath parts



**Figures 4–7.** Lectotype of *Gasteruption brevicauda* (Kieffer). **4** habitus lateral **5** metasoma lateral **6** labels **7** mesoscutum and head dorsal.

are twisted as in the lectotype female, the pilosity might be slightly raised. The species is closely related to *G. boreale* (Thomson, 1883) and *G. nigritarse* (Thomson, 1883), but the female can be distinguished by the slightly longer ovipositor without conspicuous bristles. The male is distinguishable by its slightly shorter head in dorsal view and the often more distinctly reticulate-rugose mesoscutum without satin sheen.

**Distribution.** *G. assectator* is the most widespread and common species of the *assector* aggregate in Europe. Towards its northern distribution limits in northern Scandinavia it seems to be confined to coastal areas with more favorable climate than inland areas.

**Biology.** *Gasteruption assectator* occurs in a wide variety of habitats, varying from agricultural landscapes to deciduous forests and gardens. Most probably *Hylaeus* spp. are used as hosts.

#### ***Gasteruption boreale* (Thomson, 1883), stat. rev.**

Figs 8–18, 27, 29

*Foenus borealis* Thomson, 1883: 849; Hedicke 1939: 7; Hedqvist 1973: 181, 182 (invalid lectotype designation); Wall 1994: 148. Synonymized with *G. assectator* (Linnaeus) by Schletterer (1889) and with *G. minutum* (Tournier) by van Achterberg and Talebi (2014).

*Gasteruption boreale*; Schletterer 1885: 303.

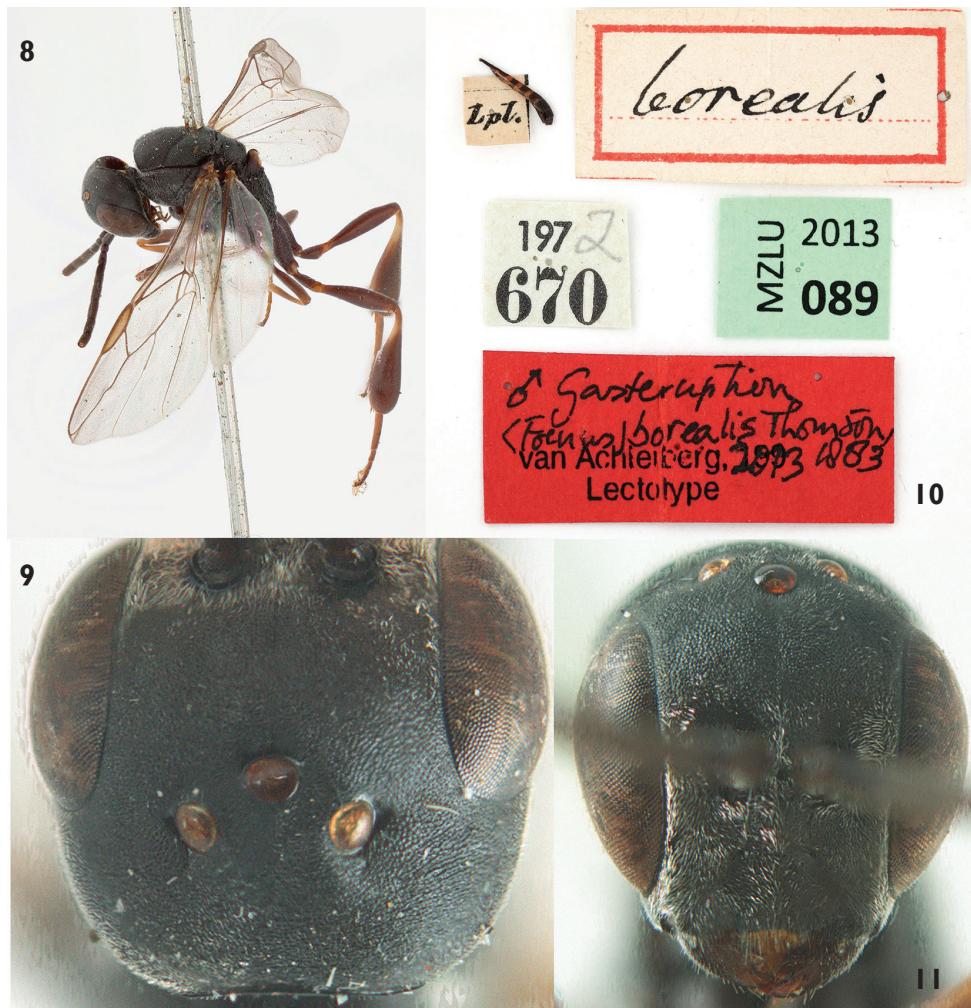
*Foenus fumipennis* Thomson, 1883: 848; Hedicke 1939: 7; Hedqvist 1973: 181, 182 (lectotype designation); Wall 1994: 148. Synonymized with *G. assectator* (Linnaeus) by Schletterer 1885. **Syn. n.**

*Trichofoenus breviterebrae* Watanabe, 1934: 285; Hedicke 1939: 45. Synonymized with *G. assectator* (Linnaeus) by Pagliano and Scaramozzino (2000). **Syn. n.**

*Gasteruption margotae* Madl, 1987c: 225–227, 1990b: 480; Wall 1994: 149. Synonymized with *G. assectator* (Linnaeus) by Madl (1990b). **Syn. n.**

**Type material.** In Thomsons collection in MZLU four males and one female are placed at the label *Foenus borealis*. Hedqvist (1973) states that the type series by Thomson only consisted of three males and one female but this is probably a simple miscalculation. The female (from Norway) was originally selected as lectotype by Hedqvist (1973) but the selection was declared as invalid (van Achterberg and Talebi 2014) because the listed original locality of the type series (= Lappland) excludes the selection of a lectotype from Norway. One male (Figs 8–11) was designated lectotype by van Achterberg and Talebi (2014) and the species was synonymized with *Gasteruption minutum* (Tournier, 1877). All males and the female in the type series belong to one distinct species (see key below). The wider malar space exhibited by the lectotype is clearly shorter than the mandibular base and fits within the range of this species and is not as long as in *G. minutum*.

The type series of *Gasteruption fumipenne* consists of the lectotype from Gotland. The size, habitus, antennae and smooth sculpture on the mesoscutum of the lectotype



**Figures 8–11.** Lectotype of *Gasteruption boreale* (Thomson). **8** habitus lateral **9** head dorsal **10** labels **11** head anterior.

(Figs 12–13) indicates, despite the lacking metasoma, that it concerns a female of *G. boreale*. This is the only specimen known from the Baltic island Gotland, but the type locality (“Olle hau” = Ulla hau, Fårö, Gotland, Sweden) was at the time of the collection an active sand dune field with old pines. It was quite a different ecosystem than at the mainland of Gotland where *G. assectator* is the most common (and now only?) of the three species. The other specimen under this label is a male of *G. assectator* from Scania (Skåne). The synonymisation with *G. assectator* made by Schletterer (1889) is rejected and *F. fumipennis* is to be regarded as a new synonym of *G. boreale* (Thomson).

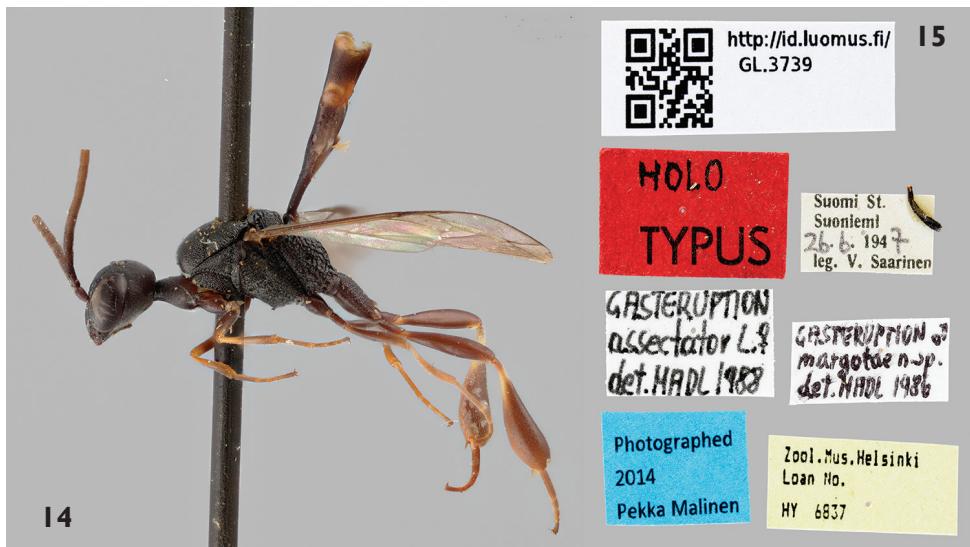
The type series of *G. margotae* consists of the male holotype (Figs 14–15) from Finland (Madl 1987c); the holotype is a typical male of *G. boreale* (Thomson). The study of the holotype shows that the synonymisation with *G. assectator* made by Madl



**Figures 12–13.** Lectotype *Foenus fumipennis* Thomson. **12** habitus lateral **13** labels.

(1990) is unjustified after resolving the *G. assectator* aggregate and that *G. margotae* is clearly a new synonym of *G. boreale* (Thomson).

The examined type series of *G. breviterebrae* (Fig. 16) consists of the holotype female and a paratype male from Sakhalin (Far East Russia). The holotype shows the typical features of *G. boreale* (Thomson), viz., the less sculptured mesoscutum and the bristly ovipositor sheath. The slightly aberrant red marks on the metasoma fall within the geographical variation of *G. boreale*. The synonymisation with *G. assectator* made



**Figures 14–15.** Holotype of *Gasteruption margotae* Madl. **14** habitus lateral **15** labels.

by Pagliano and Scaramozzino (2000) is here rejected and *T. breviterebrae* is a new synonym of *G. boreale* (Thomson).

**Additional material.** **Sweden** (*Småland*: Bäckebo, Skillingaryd, Ränneslätt, Jönköping; *Västergötland*: Baskarp; *Södermanland*: Huddinge; *Uppland*: Ross-holm; *Dalarna*: Leksand, Ludvika; *Hälsingland*: Hornslandet; *Västerbotten*: Vindejn, Hällnäs; *Lycksele lappmark*: Gällivare); **Finland** (*Åland*: Hammarland; *Åbo*: Harvaluoto).

**Diagnosis.** Head in dorsal view almost parallel-sided behind eyes, elongate, about as wide as long (Figs 9, 18). Occipital carina indistinct and not reflexed. Frons with satin sheen. Mesoscutum smooth, weakly rugose/shagreened with satin sheen, medio-posteriorly in front of scutellum rugose-reticulate (Figs 17–18, 27). Mesosoma and head silvery pilose. Mesosoma with a satin sheen, quite distinct from the rather matt gloss occurring in *G. assectator*. Whitish pubescence of eye of female mostly distinctly longer and denser than of *G. assectator*. Antenna slightly shorter than in *G. assectator* with sixth segment about 1.5 times longer than wide and subapical segment about 1.2 times longer than wide. Only apical half of hind coxa weakly striate dorsally. Hind tibia and basitarsus with white ring which might be interrupted ventrally. Metasoma mainly black with orange lateral patches on tergites 2–4 which might be partially reduced, especially in northern specimens. Inner sides of tibiae often red brown to orange with white or yellow basal patch indistinct on fore and middle tibiae. Ovipositor sheath black or brown, 0.7–1.0 times as long as hind tibia, its apical half entirely with stout, rather scarce black bristles angled backwards at about 45° (Fig. 29). The species is closely related to *G. assectator* (Linnaeus) but the female can be distinguished by the shorter ovipositor sheath, the less sculptured mesoscutum and the more scarce promi-



**Figure 16.** Lectotype of *Trichofoenus breviterebrae* Watanabe, habitus lateral.

ment bristles on the apical half of the ovipositor sheath. The male is hard to distinguish from *G. assectator* and identification is not always possible with certainty. In most cases the male of *G. boreale* can however be separated from *G. assectator* by its slightly more elongated, parallel-sided head in dorsal view, the more or less enlarged malar space and its less sculptured mesoscutum.

**Description.** Female. Length of body 6–11 mm (fore wing 3.5–5.5 mm)

*Head.* Temples parallel-sided behind eyes in dorsal view. Occipital carina not raised. Frons and vertex with satin sheen. Malar space short, at most about 0.5 times mandibular base. Hypostomal bridge narrow, at most 0.5 times mandibular base. Eyes with dense white pubescence. Antenna short; sixth segment about 1.5 times longer than wide and subapical segment about 1.2 times longer than wide.

*Mesosoma.* Surface largely smooth with satin sheen, mesoscutal sculpture of almost equal intensity as on vertex. Antesternal carina narrow, non-lamelliform. Pronotal sides with very small pointed teeth antero-ventrally, but these are sometimes entirely absent. Upper half of mesopleuron mostly considerably weaker sculptured than its more rugose lower part.

*Legs.* Hind tibia stout as in *G. assectator*. Hind coxa often with weaker rugae apically than on basal half, dissolving amidst rugose background. Hind tibial spurs often brighter than hind tibia.



**Figures 17–18.** *Gasteruption boreale* (Thomson), ♀. **17** habitus lateral **18** habitus dorsal.

**Metasoma.** Ovipositor sheath entirely black or brown, 0.7–1.0 times as long as hind tibia, its apical half entirely with stout, black bristles angled backwards at about 45° (Fig. 29).

**Colour.** Black. Mandible apically, hind tibial spurs and patches laterally on tergites 2–4 reddish brown. Patches rarely intercepted. Fore and middle tibiae mostly with indistinct yellow or ivory basal patch. Inner side of tibiae often orange. Basal ivory ring of hind tibia usually indistinct.

**Distribution.** As Thomson's name implies this species is most common in boreo-alpine areas. In northern Europe it is quite widespread and common at higher latitudes and high altitude sites in the southern part, but becoming scarcer towards the southern lowlands in Sweden. Specimens are examined from Austria, Bulgaria, Finland, Germany, Netherlands (den Dolder, de Bilt, Tilburg, Wageningen, Groesbeek,

Rhenen, Velp, Maastricht, Drimmelen, Rotterdam, Voerendaal), Norway, Russia, Serbia and Sweden.

**Biology.** The species occur in (boreal) landscapes dominated by coniferous forests where it can be locally common. Many of the sites in Scandinavia are at high altitude. *G. boreale* is lacking from more open localities as well as in regions dominated by deciduous forests. It has been observed searching high stumps of *Pinus* trees and it also attends old wooden walls and artificial bee nests in gardens. Probably it is a kleptoparasitoid of *Hylaeus* spp.

***Gasteruption nigritarse* (Thomson, 1883), stat. rev.**

Figs 19–24, 30

*Foenus nigritarsis* Thomson, 1883: 849; Schletterer 1889: 398; Hedicke 1939: 7; Hedqvist 1973: 181, 182 (lectotype designation); Wall 1994: 149. Synonymized with *G. assectator* (Linnaeus) by Schletterer (1889).

*Gasteruption nigritarse*; Schletterer 1885: 310.

**Type material.** Lectotype female (Figs 19–22) from Lund (Scania) selected by Hedqvist (1973). All 12 specimens under *Foenus nigritarsis*, both males and females (including the designated lectotype by Hedqvist) belong to the same distinct species and are well separable from *Gasteruption assectator sensu stricto* (see key below).

**Additional material. Sweden (Småland:** Bäckebo; **Skåne;** **Halland;** **Östergötland:** Svensksund; **Uppland:** Grisslehamn, Svartsjö, Roslagsbro, Skansen; **Öland:** Borgehage, Himmelsberga).

**Diagnosis.** Head dorsally more parallel-sided than in *G. assectator*, elongate and about as wide as long. Occipital carina indistinct and not reflexed. Mesoscutum superficially reticulate and (especially laterally) rugose, medio-posteriorly in front of scutellum more rugose-reticulate. Mesosoma laterally and face with long, thick golden pubescence. Hind tibia and basitarsus darker, often with the basal ring lacking or interrupted. Fore and middle tibiae often with large distinct ivory patch covering about one third of tibia. Metasoma mainly black with well-defined orange lateral patches on tergites 2–5 which might be partially reduced, especially in northern specimens. Ovipositor sheath entirely black or brown, 0.7–1.0 times as long as hind tibia and its apical half dorsally with stout, black bristles angled backwards at about 45°. The bristles are all conspicuously widened and bent apically, reminiscent of “velcro” (Fig. 30). The species is closely related to *G. assectator* (Linnaeus) and *G. boreale* (Thomson), but the female can be distinguished by the stout velcro-like bristles dorsally on the apical half of the ovipositor sheath, its denser pubescence of head and mesosoma and its broader hypostomal bridge. The male is distinguishable by its broader hypostomal bridge as well as the thick golden facial pubescence.

**Description.** Female. Length of body 8–11 mm (fore wing 4.0–5.5 mm)

**Head.** Temples parallel-sided behind eyes in dorsal view. Occipital carina not raised.

Frons and vertex with satin sheen. Malar space short, at most about 0.5 times mandibular



**Figures 19–22.** Lectotype of *Gasteruption nigritarse* (Thomson). **19** habitus lateral **20** labels **21** head anterior **22** head ventral.

base. Hypostomal bridge at least 0.7 times width of mandibular base, medio-laterally often with distinct transverse striae. Face covered with dense golden pubescence.

*Mesosoma.* Surface vaguely reticulate and strongly shagreened. Antesternal carina narrow and non-lamelliform. Pronotal sides with very small pointed teeth antero-ventrally, but these are sometimes entirely absent.



**Figure 23.** *Gasteruption nigritarse* (Thomson), ♀, habitus dorso-lateral.

**Legs.** Hind tibia rather stout as in *G. assectator*. Hind tibial spurs and hind tibia mostly similarly coloured.

**Metasoma.** Ovipositor sheath entirely black or brown, 0.7–1.0 times as long as hind tibia, its apical half dorsally with stout, black bristles angled backwards at about 45° and conspicuously widened and bent backwards apically.

**Colour.** Black. Mandible apically orange. Sometimes small patch on hind tibia baso-ventrally white or ivory. Northern specimens of both sexes often with entirely black hind tibia. Fore and middle tibiae often with large distinct ivory patch covering about one third of tibia. Fore, middle and hind tarsus black. Patches laterally on tergites 2–5 reddish brown. Last sternite apically often extensively orange. Colour of hind tibial spurs variable, mostly black or dark brown.

**Distribution.** *Gasteruption nigritarse* is a rather rare locally but widespread species in Europe. Specimens examined from Austria, Germany, Czech Republic, Netherlands (Breda, Waalwijk, Putten (GE), Maastricht, Wageningen, Rhenen, Arnhem), Serbia, Sweden and Turkey.

**Biology.** The species primarily occur in small-scale agricultural landscapes where it is to be found especially on walls of log barns (Fig. 23). An association with the bees *Hylaeus difformis* and/or *Hylaeus pictipes* is highly probable, at least in Scandinavia and is based on observed behaviour of the wasps. *Gasteruption nigritarse* seems to have diminished dramatically in Scandinavia during the last century, probably due to the loss of habitat and is only known from a couple of localities.

### Key to Palaearctic species of the *Gasteruption assectator* aggregate

- 1 Females (ovipositor present) ..... 2
- Males (ovipositor absent) ..... 4
- 2 Hypostomal bridge 0.7–0.8 times as wide as mandibular base and weakly striate medio-laterally (Figs 22, 24). Occipital carina conspicuously bent inwards medio-ventrally, resulting in parallel running lower parts (Figs 22, 24). Hind tibia in northern populations often with reduced white markings. In lateral view apical half of ovipositor sheath with hooked bristles (“velcro-type”; Fig. 30). Facial pubescence thick and golden ..... *G. nigritarse* (Thomson, 1883), stat. rev.
- Hypostomal bridge narrow, at most 0.5 times as wide as mandibular base and without striation medio-laterally (Fig. 25). Occipital carina evenly diverging medio-ventrally (Fig. 25). Hind tibia mostly with distinct white ring basally. Ovipositor sheath without “velcro”-type of bristles (Figs 28–29). Facial pubescence thin and silvery ..... 3
- 3 Mesoscutum and coxae more opaque, less rugose, smoother and with satin sheen (Figs 17–18, 27). Sculpture of mesoscutum and head similar, shagreened (Fig. 27). Ovipositor sheath 0.7–1.0 times as long as hind tibia, in dorsal view its apical half with more scarce distinct straight bristles, angled backwards at about 45° (Fig. 29) ..... *G. boreale* (Thomson, 1883), stat. rev.
- Mesoscutum and coxae more shiny and rugose, with a “fatty” gloss (Fig. 26). Sculpture of mesoscutum distinctly rougher than that of head, reticulate-coriaceous (Fig. 26). Ovipositor sheath 1.0–1.3 times as long as hind tibia, in dorsal view normally only with dense bright adpressed pubescence, thus appearing naked in lower magnifications (Fig. 28) ..... *G. assectator* (Linnaeus, 1758)

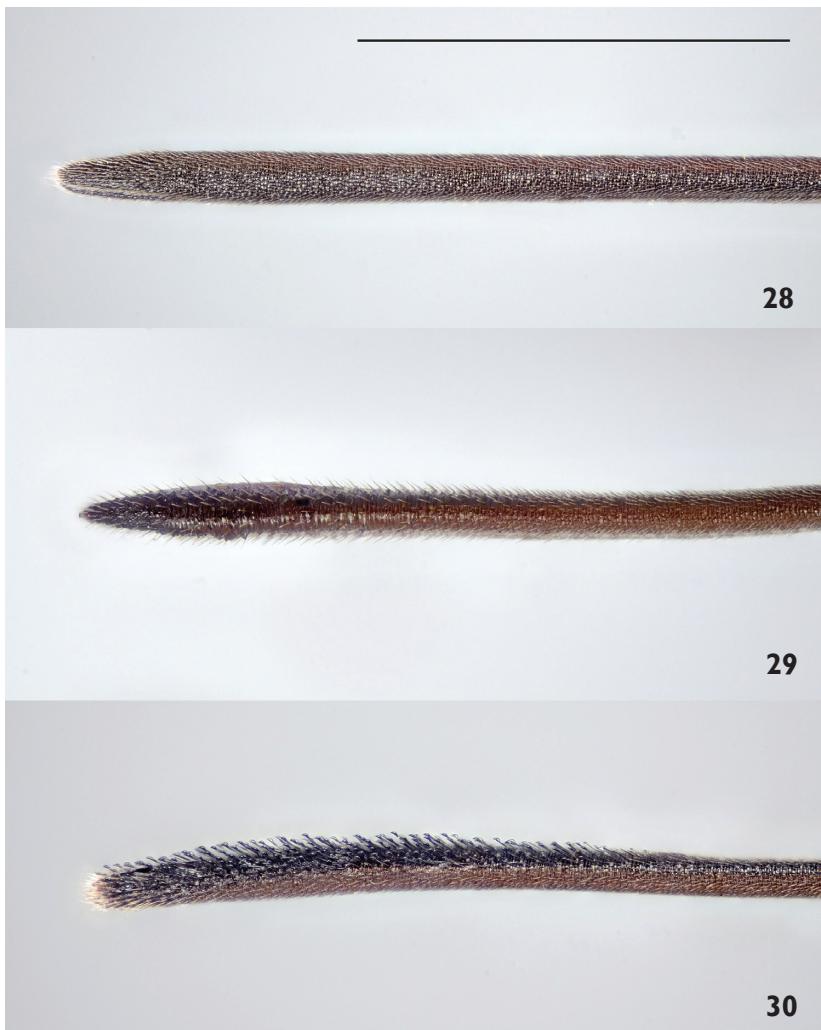


**Figures 24–25.** Hypostomal bridge of *Gasteruption nigritarse* (Thomson) (24) and *G. assectator* (Linnaeus) (25).



**Figures 26–27.** Mesoscutum of *Gasteruption assectator* (Linnaeus) (26) and *G. boreale* (Thomson) (27).

- 4 Hypostomal bridge 0.7–0.8 times as wide as width of mandibular base and weakly striate medio-laterally (Figs 22, 24). Occipital carina conspicuously bent inwards medio-ventrally, resulting in parallel running lower parts (Figs 22, 24). Hind tibia in northern populations often with reduced white markings. Facial pubescence thick and golden .....  
..... *G. nigritarse* (Thomson, 1883), stat. rev.
- Hypostomal bridge narrow, at most 0.5 times width of mandibular base and without striation medio-laterally (Fig. 25). Occipital carina medio-ventrally evenly diverging. Hind tibia mostly with distinct white ring basally. Facial pubescence thin and silvery ..... 5
- 5 Mesoscutum and upper half of mesopleuron rather smooth with small puncture-like grooves and with satin sheen almost of the same intensity as vertex



**Figures 28–30.** Ovipositor sheath of *Gasteruption assectator* (Linnaeus (28), *G. boreale* (29) and *G. nigritarse* (Thomson) (30). Scale bar 1mm.

(Figs 17–18, 27). Head, mesosoma and coxae more opaque and with satin sheen. Sculpture of mesoscutum similar to that of head (Fig. 27). Head in dorsal view more elongated and its temples more parallel-sided behind eyes (Fig. 10)..... *G. boreale* (Thomson 1883), stat. rev.  
— Mesoscutum more roughly reticulate-coriaceus, especially near the sides of mesoscutum, visible even at lower magnifications (Fig. 26); mesoscutal sculpture distinctly different from the less rugose surface of vertex. Head, mesosoma and coxae with “fatty” gloss. Head in dorsal view less elongated and clearly wider than long, generally more converging behind eyes.....  
..... *G. assectator* (Linnaeus, 1758)

## Acknowledgements

We are grateful for the contributions of the following persons: Agnièle Touret-Alby (MNHN, Paris), Gavin Broad (BMNH, London), Hege Vårdal (NHRM, Stockholm), Juho Paukkunen (FMNH, Helsinki), Frode Ødegaard, Johan Abenius, Christer Hansson (MZLU, Lund), Sven Hellqvist, Anders Nilsson and Bo G. Svensson (Evolutionary Museum, Uppsala), Masahiro Ohara (Entomology Collection, Hokkaido University, Sapporo), Magnus Persson, Patrik Ekgfeldt and Christoffer Fägerström. Photos were taken by the Linnean Society (1–3), Hege Vårdal (4–7), Christoffer Fägerström (8–9, 12–13, 19–21), Cornelis van Achterberg (10–11, 16), Pekka Malinen (14–15), Patrik Ekgfeldt (17–18), Christer Hansson (22), Niklas Johansson (23) and Magnus Persson (24–30).

## References

- Achterberg C van (2013) De Nederlandse hongerwespen (Hymenoptera: Evanioidea: Gasteruptiidae). Nederlandse Faunistische Mededelingen 39: 55–87.
- Achterberg C van, Talebi A (2014) Review of Gasteruption Latreille (Hymenoptera, Gasteruptiidae) from Iran and Turkey, with the description of 15 new species. ZooKeys 458: 1–187. doi: 10.3897/zookeys.458.8531
- Abeille de Perrin EEA (1879) Essai de classification des espèces françaises du genre *Faenus* Fabricius. Bulletin de la Société d' Histoire Naturelle de Toulouse 13: 260–279.
- Cederhjelm I (1798) Faunae Ingricæ. Prodromus Exibens Methodicam Descriptionem. Insectorum Agri Petropolensis. Praemissa Mammalium, Avium, Amphibiorum, et Piscium Enumerationes, Lipsiae, 1–348.
- Christ JL (1791) Naturgeschichte, Klassification und Nomenclatur der Insekten vom Bienen, Wespen und Ameisengeschlecht, Frankfurt, 1–535.
- Curtis J (1826–1833) British Entomology, 3–5. Hymenoptera. London.
- Dahlbom AG (1831) Exercitationes hymenopterologicae quas, ad illustrandam faunam Svecicam, venia ampliss. Lund, 1–79.
- Dalla Torre CG de [= KW von] (1902) 2. Subfam. Gasteruptionidae: 1063–1075. In: Catalogus Hymenopterorum hucusque descriptorum systematicus et synonymicus 3: 1–1141.
- Dolfuss H (1982) Die Gasteruptioniden des Bezirkes Scheibbs (Niederösterreich) (Insecta: Hymenoptera, Evanioidea, Gasteruptionidae). Entomofauna 3(2): 21–25.
- Fabricius JC (1775) Systema *Entomologiae*, sistens insectorum classes, ordines, genera, species, adiectis synonymis locis, descriptionibus, observationibus. Flensburgi et Lipisae, 832 pp.
- Fabricius JC (1781) Species insectorum exhibentes eorum differentias specificas, synonyma autorum 1. Hamburgi et Kilonii, 552 pp.
- Fabricius JC (1787) Mantissa *insectorum* sistens eorum species nuper detectas adiectis characteribus, genericis, differentiis, specificis, emendationibus, Hafniae, 348 pp.
- Fabricius JC (1798) Supplementum Entomologiae systematicae. Hafniae, 1–572.

- Ferrière C (1946) Les *Gasteruption* de la Suisse (Hym. Evaniiidae). Mitteilungen der Schweizerischen Entomologischen Gesellschaft Bern 20: 232–248.
- Fitton MG (1978) The species of “*Ichneumon*” (Hymenoptera) described by Linnaeus. Biological Journal of the Linnean Society London 10: 361–383. doi: 10.1111/j.1095-8312.1978.tb00022.x
- Fourcroy AF de (1785) *Entomologia Parisiensis; sive catalogus insectorum quæ in agro Parisiensi reperiuntur; secundam methodam Geoffreanam in sectiones, genera & species distributus: cui addita sunt nomina trivialia & fere trecentæ novæ species 1.* Parisiis, 231 pp.
- Gmelin JF (1790) *Caroli a Linné, sistema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Editio decima tertia, aucta, reformata. Tomus I (V), Lipsiae, 2225–3020.*
- Györfi J, Bajári EN (1962) 9. család: Gasteruptionidae-Dárdahordozó fúrkészek: 41–51. In: 15. Fúrkészdaráz-Alkatúák 12. Ichneumonoidea 12. Hymenoptera 11 (1). Fauna Hungariae 61: 1–53.
- Hedicke H (1939) *Hymenopterorum Catalogus 11, Gasteruptiidae. s’-Gravenhage, 1–54.*
- Hedqvist K-J (1973) Notes on the superfamily Evanioidea in Sweden with keys to families, genera and species (Hym., Apocrita). Entomologisk Tidskrift 94(3–4): 177–187.
- Hellén W (1950) Die Evaniiiden Finnlands (Hym.). Notulae Entomologicae 30: 1–5.
- Hentschius GF (1804) *Epitome Entomologiæ Systematicæ Secundum Fabricium, Continens Genera et Species Insectorum Europæorum.* Lipsiae, 1–224.
- Illiger K (1807) IV. Vergleichung der Gattungen der Hautflügler Piezata Fabr. Hymenoptera Linn. Jur. Magazin für Insektenkunde 6: 189–199.
- Kieffer JJ (1904) *Gasteruption.* In: André E (Ed.) *Species Hyménoptères d’Europe & d’Algérie 7–2, Cynipidae II, Evaniiidae, Stephaniiidae, Suppl. Cynipidae,* Paris, 748 pp.
- Kieffer JJ (1912) Evaniiidae. Das Tierreich 30: 1–431.
- Kofler A, Madl M (1990) Über Evanioidea von Osttirol (Hymenoptera, Evaniiidae, Gasteruptiidae, Aulacidae). Linzer Biologische Beiträge 22(2): 319–324.
- Kozlov MA (1988) Fam. Gasteruptiidae: 244–247. In: Skarlatto OA (Ed.) *Keys to the fauna of the USSR 158, 3. Hymenoptera 3:* 1–268. [In Russian] [Translation 1994: 404–410]
- Labram JD, Imhoff L (1836) Insekten der Schweiz, die vorzüglichsten Gattungen je durch eine Art bildlich dargestellt. Vol. 1: Pl. 24.
- Latreille PA (1805) *Histoire naturelle générale et particulière des crustacés et des insectes.* Paris, 13, 1–432.
- Leclercq J (1948) Evaniiides et Gastéruptionides de Belgique. Labillionea 48(9–10): 74–77.
- Lindemans J (1921) *Gasteruption pedemontanum* Tourn, faun. nov. spec. Entomologische Berichten Amsterdam 5: 297–298.
- Linnaeus C von (1758) *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decimal, reformata.* Holmiae, 824 pp.
- Linnaeus C von (1761) *Fauna Svecica. Editio altera,* Holmiae, 578 pp.
- Linnaeus C von (1767) *Systema naturae. Tom. I. Pars II (12th edition),* Holmiae, 533–1328.
- Madl M (1987a) Über Gasteruptiidae aus Oberösterreich (Hymenoptera, Evanioidea). Linzer Biologische Beiträge 19(2): 401–405.

- Madl M (1987b) Über Gasteruptiidae aus Niederösterreich (Hymenoptera, Evanioidea). Faunistische Abhandlungen Staatliches Museum für Tierkunde Dresden 15(4): 21–25.
- Madl M (1987c) Eine neue *Gasteruption*-Art aus Finnland (Hymenoptera, Gasteruptiidae). Entomofauna 8: 225–228.
- Madl M (1988) Die Gasteruptiidae des Bundeslandes Salzburg (Hymenoptera, Evanioidea). Verhandlungen der Zoologisch-Botanischen Gesellschaft in Österreich 125: 37–40.
- Madl M (1989a) Über Gasteruptiidae aus Tirol und Vorarlberg (Hymenoptera, Evanioidea). Berichte des naturwissenschaftlich-medizinischen Vereins in Innsbruck 76: 159–163.
- Madl M (1989b) Über Gasteruptiidae aus Jugoslawien (Hymenoptera, Evanioidea). Nachrichtenblatt der Bayerischen Entomologen 38: 40–45.
- Madl M (1990a) Beitrag zur Kenntnis des Gasteruptiidae Griechenlands (Insecta, Hymenoptera, Evanioidea). Faunistische Abhandlungen Staatliches Museum für Tierkunde Dresden 17(14): 127–130.
- Madl M (1990b) Über Gasteruptiidae aus Kärnten und Steiermark (Hymenoptera, Evanioidea). Carinthia II 180(100): 479–484.
- Narolsky NB, Shcherbal IS (1991) New data on Gasteruptiidae (Hymenoptera, Evanioidea) - cleptoparasites of the leaf-cutter bee, *Megachile rotundata*. Vestnik Zoologii 1: 22–24. [In Russian with English summary]
- Nees von Esenbeck CG (1834) Hymenopterorum Ichneumonibus affinium monographiae, genera Europaea et species illustrantes 1. Stuttgartiae & Tubingae, 320 pp.
- Neumayer J, Schwarz M, Bregant E (1999) Vorläufiges Verzeichnis ausgewählter Hautflügler Kärtents (Hymenoptera ohne Formicidae und Apidae). In: Holzinger WE, Mildner P, Rottenburg T, Wieser C (Eds) Rote Listen gefährdeter Tiere Kärtents Naturschutz in Kärtents 15. Klagenfurt, 213–231.
- Oehlke J (1984) Beiträge zur Insektenfauna der DDR: Hymenoptera-Evanioidea, Stephanoidea, Trigonalyoidea. Faunistische Abhandlungen der staatliche Museum für Tierkunde, Dresden 11: 161–190.
- Olivier M (1792) *Ichneumon*. Encyclopédie méthodique, Histoire naturelle. Insectes 7: 133–224.
- Ortega G, Baez M (1985) Aulacidae y Gasteruptiidae, das nuevas familias para la fauna del Archipielago Canario (Ins., Hymenoptera). Actas do II Congresso Iberico de Entomologica. Boletim da Sociedade Portuguesa de Entomologia, Supl. 1(2): 507–516.
- Pagliano G, Scaramozzino PL (2000) Gasteruptiidae italiani (Hymenoptera: Evanioidea). Bollettino del Museo di Zoologia dell'Università di Torino 17: 5–38.
- Peeters TMJ (1996) Gasteruptiidae: 134. In: Zuijlen JW van et al. (Eds) Brand-stof. Een inventarisatie van de entomofauna van het natuurreervaat “De Brand” in 1990. Insektenwerkgroep KNNV-afdeling Tilburg, 228 pp.
- Petagna V (1792) Institutiones entomologicae 1. Neapoli, 718 pp.
- Roman A (1932) The Linnean types of ichneumon flies. Entomologisk Tidskrift 53: 1–16.
- Rossi [= Rossius] P (1790) Fauna Etrusca sistens insecta quae in provinciis Florentina et Pisana 2. Liburni, 366 pp.
- Saure C (2001) Trigonalyoidea, Evanioidea, Stephanoidea: 29–30. In: Dathe HH, Taeger A, Blank SM (Eds) Verzeichnis der Hautflügler Deutschlands (Entomofauna Germanica 4). Entomologische Nachrichten und Berichte, Dresden. Beiheft 7: 1–178.

- Scaramozzino PL (1995) Hymenoptera Trigonalyoidea, Evanioidea, Stephanoidea. In: Minelli A, Ruffo S, Posta S (Eds) Checklist delle specie della fauna italiana 94: 1–4.
- Schlitterer A (1885) Die Hymenopteren-Gattung *Gasteruption* Latr. (*Foenus* aut.). Verhandlungen der Zoologisch-Botanischen Gesellschaft in Wien 35: 267–326.
- Schlitterer A (1889) Die Hymenopteren-Gruppe der Evaniiiden. Annalen des Kaiserlich-Königliches Naturhistorischen Hofmuseums 4: 373–546.
- Schmidt K (1969) Beiträge zur Kenntnis der Hymenopterenfauna des Mittelrheingebietes, insbesondere des mainzer Sandes. Mainzer Naturwissenschaftliches Archiv 8: 292–302.
- Schmiedeknecht O (1930) Die Hymenopteren Nord- und Mitteleuropas mit Einschluss von England, Südschweiz, Südtirol und Ungarn nach ihren Gattungen und zum grossen Teil auch nach ihren Arten analytisch bearbeitet, 2<sup>nd</sup> ed, Jena, 1062 pp.
- Schrank F von Paula (1802) Fauna Boica. Durchgedachte Geschichte der in Baiern einheimischen und zahmen Tiere 2. Nürnberg, 412 pp.
- Scopoli JA (1763) Entomologia carniolica. Vindobonae, 420 pp.
- Šedivý J (1958) Die tschechoslowakische Arten der Gasteruptioniden (Hym.). Acta Societas Entomologicae Cechosloveniae, Praha (= Časopis Československé Společnosti Entomologické) 55: 34–43.
- Semenov A (1892) Revisio Hymenopterorum Musei Zoologici Academiae Caesareae Scientiarum Petropolitanae. III Familia Evaniiidae. Bulletin de l'Académie Impériale des Sciences de St.-Pétersbourg, Nouvelle Serie 3, 35: 197–218.
- Smissen J van der (2010) Teil IV. Beitrag zur Stechimmen-fauna Südfrankreichs (Ardèche, Drôme, Gard, Vaucluse) Hymenoptera Aculeata: Apidae, Chrysidae, Scoliidae, Vespiidae, Pompilidae, Sphecidae). Verhandlungen des Vereins für Naturwissenschaftliche Heimatforschung zu Hamburg e.V. 43: 355–415.
- Smith DR (1996) Review of the Gasteruptiidae (Hymenoptera) of Eastern North America. Proceedings of the Entomological Society of Washington 98(3): 491–499.
- Stephens JF (1835) Illustrations of British Entomology. Mandibulata 7: 1–306.
- Szépligeti V (1903) Neue Evaniiiden aus der Sammlung des Ungarischen National-Museums. Annales Musei Nationalis Hungarici 1: 364–395.
- Taschenberg EL (1866) Die Hymenopteren Deutschlands nach ihren Gattungen und theilweise nach ihren Arten als Wegweiser für angehende Hymenopterologen und gleichzeitig als Verzeichniss der Halle'schen Hymenopterenfauna. Leipzig, 277 pp.
- Thomson CG (1883) XXX. Öfversigt av de I Sverige funna arter av Hymenoptera-slägget *Foenus*. Opuscula Entomologica 9: 843–850.
- Tournier H (1877) Tableau synoptique des especes europeennes de genre *Foenus* Fabr. (Hymenopteres). Annales de Société entomologique de Belgique 20: 6–10.
- Townes HK (1950) The Nearctic species of Gasteruptiidae (Hymenoptera). Proceedings of the United States National Museum 100: 85–145. doi: 10.5479/si.00963801.100-3259.85
- Turrisi GF (2004) The Evanioidea of the Campadelli Collection (Hymenoptera). (Systematic catalogue of the Campadelli Collection. II). Annali del Museo Civico di Storia Naturale di Ferrara 7: 81–86.
- Villers C de (1789) Caroli Linnæi entomologia, Faunae Suecicae descriptionibus 3. Lugduni, 657 pp.

- Walckenaer CA (1802) Faune Parisienne, Insectes ou Histoire abrégée des insectes des environs de Paris: classés d'après le système de Fabricius. Précédée d'un discours sur les insectes en général, pour servir d'introduction à l'étude de l'entomologie 2. Paris, 438 pp.
- Wall I (1994) Seltene Hymenopteren aus Mittel-, West- und Südeuropa (Hymenoptera Apocrita: Stephanoidea, Evanioidea, Trigonalyoidea). Entomofauna 15(14): 137–184.
- Watanabe C (1934) On Evaniiidae and Gasteruptionidae from Japan (Hymenoptera). Transactions of the Sapporo Natural History Society 13: 280–286.
- Westrich P (2008) Zur Überflutungstoleranz von Hymenopteren in Gallen von *Lipara lucens* (Diptera: Chloropidae). Eucera 1: 1–16.
- Westwood JO (1843) On *Evania* and some allied genera of hymenopterous insects. Transactions of the Royal Entomological Society of London 3(4): 237–278.
- Yildirim E, Çoruh S, Kolarov J, Madl M (2004) The *Gasteruption* (Hymenoptera: Gasteruptiidae) of Turkey. Linzer Biologische Beiträge 36(2): 1349–1352.
- Zetterstedt JW (1838–40) Insecta Lapponica descripta. Lipsiae, 1139 pp.
- Zhao K-X, Achterberg C van, Xu Z-F (2012) A revision of the Chinese Gasteruptiidae (Hymenoptera, Evanioidea). ZooKeys 237: 1–123. doi: 10.3897/zookeys.237.3956