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Occurrence and biology of *Pseudogonalos hahnii* (Spinola, 1840) (Hymenoptera: Trigonalidae) in Fennoscandia and the Baltic states

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Pseudogonalos hahnii is the only known species of Trigonalidae in Europe. It is a hyperparasitoid of lepidopteran larvae via ichneumonid primary parasitoids. Possibly, it has also been reared from a symphytan larva. We report the species for the first time from Estonia, Lithuania and Russian Fennoscandia, and list all known observations from Finland and Latvia. An overview of the biology of the species is presented with a list of all known host records.

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1. Introduction

Trigonalidae is a moderately small family of parasitic wasps of little over 100 species and about 20 genera (Carmean & Kimsey 1998, Chen *et al.* 2014). They are mainly found in the tropics and subtropics (Carmean & Kimsey 1998). Five species have been described from the Nearctic (Smith & Stocks 2005) and around two dozen species from the Palaearctic (Lelej 2003, Chen *et al.* 2014). Only one species occurs in Europe (Madl 2013). Trigonalidae clearly belong to Parasitica, but morphologically they possess some features that are reminiscent of Aculeata and Symphyta. For example, head shape, mouthparts and tarsal plantulae are shared with Symphyta and general body shape and terminal ovipositor with Aculeata (Weinstein & Austin 1991). The trigonalid ovipositor is reduced and hidden within the abdomen and it is not known if it is used in egg placement (Quicke *et al.* 1999).

In the past, Trigonalidae have been variously placed within or near almost all other apocritan lineages (Carmean & Kimsey 1998) and they have been considered to be phylogenetically close to Evanioidea, Megalyroidea, Ceraphronoidea or Aculeata (Sharkey 2007, Klopfstein *et al.* 2013). Evidence, both morphological and molecular, is mounting that Trigonalidae are closely related to stinging wasps (Aculeata) and Evanioidea (Klopfstein *et al.* 2013, Zimmermann & Vilhelmsen 2016, Branstetter *et al.* 2017, Peters *et al.* 2017). Trigonalidae is also closely related to the extinct Cretaceous family Maimetshidae

(Vilhelmsen *et al.* 2010, Perrichot *et al.* 2011) which is currently also placed in superfamily Trigonaloidea (Aguiar *et al.* 2013). Asymmetrical mandibles (not present in all maimetshids) and female tarsal plantulae unite these two families, but maimetshids differ from Trigonalidae by their exserted ovipositor and missing antennal tyloids (Vilhelmsen *et al.* 2010, Perrichot *et al.* 2011). The oldest fossils of true Trigonalidae are known from French Albian Amber (100 to 113 mya) (Nel *et al*. 2003).

Almost all trigonalid species are hyperparasitoids, attacking Ichneumonidae (Hymenoptera) and Tachninidae (Diptera) (referred in this paper as primary hosts) that parasitize leaf-feeding lepidopteran or symphytan larvae (referred in this paper as secondary hosts). Two Australian species develop as primary parasitoids of sawflies (Weinstein & Austin 1991). One trigonalid species has been reared from a tachinid developing on a detrivorous crane fly (Diptera: Tipulidae) larva (Gelhaus 1987). Trigonalid females are very fecund and oviposit thousands of eggs along or within the margins of plant leaves. The eggs in turn are by chance ingested by lepidopteran or symphytan larvae (Carmean 1991, Weinstein & Austin 1991). The eggs have never been observed to have been purposefully oviposited near host animals (Schnee 2011). Among parasitoids, only some tachinid flies are known to depend on this same method of host ingestion to reach their hosts (Stireman *et al.* 2006). Mechanical and chemical stimuli incite the 1st instar trigonalid larva to hatch and it bores through the secondary host larva's gut wall to search for a primary ichneumonid or tachinid parasitoid larva present within the secondary larva's hemocoel, after which it develops as a hyperparasitoid (Weinstein & Austin 1991). Trigonalid larval development is then delayed until the ichneumonid or tachinid primary host pupates or is near pupation, after which the trigonalid larva consumes the primary host. The first three trigonalid larval instars are endoparasitic while the fourth and fifth instars are ectoparasitic after which pupation takes place. The third instar has a heavily chitinized head and formidable mandibles, suggesting that it uses them to fight and kill other possible parasitoid larvae it encounters within the host. After eclosion, the adult uses its strong mandibles to cut through the host cocoon, pupa or puparium (Weinstein & Austin 1991). Some Trigonalidae species depend on their eggs being brought with phytophagous larvae into nests of social vespids, where they develop as primary parasitoids of vespid larvae (Weinstein & Austin 1991). In addition to Trigonalidae, only a few Hymenoptera groups (Eucharitidae, Perilampidae, Ichneumonidae: Eucerotinae) oviposit their eggs away from hosts but these groups have planidial larvae, i.e. larvae that actively seek and enter the host animal (Heraty & Murray 2013, Shaw 2014). Likewise, some elampine cuckoo wasps (Hymenoptera: Chrysididae) oviposit into free-living aphids and depend on digger wasp (Hymenoptera: Crabronidae) females to prey on and carry these aphids into their nests, wherein the elampine larvae develop as parasitoids on crabronid progeny (Winterhagen 2015).

Pseudogonalos Schulz, 1906 is a palaearctic genus that includes three valid species: *Pseudogonalos hahnii* (Spinola, 1840), *P. harmandi* Schulz, 1906 and *P. angusta* Chen, van Achterberg, He & Xu, 2014 (Carmean & Kimsey 1998, Chen *et al.* 2014). Only a single and now lost *P. harmandi* specimen is known from Darjeeling, North-Eastern India (Carmean & Kimsey 1998). Recently, Chen *et al.* (2014) described a third *Pseudogonalos* species from China (Inner Mongolia), *P. angusta* Chen, van Achterberg, He & Xu, 2014. *Pseudogonalos hahnii* is a widespread but rare palaearctic species, and it is the only European species of the family (Lelej 2003, Schnee 2011).

Pseudogonalos hahnii is a black species with dark spotted fore wings. The habitus (Fig. 1) is reminiscent of some aculeate wasps, e.g. a pemphredine sphecid. It can be separated from the other hymenopterans in the region by the combination of various characters: characteristic fore wing venation with 10 developed cells and well-developed costal cell, hind wing with 2 cells, raised crests near the point of antennal insertions on the middle of the face, antennae with 26–27 segments, mandibles with 3–5 large teeth, presence of tarsal plantar lobes on tarsal segments and cleft tarsal claws (Gauld & Bolton 1988, Chen *et al.* 2014).

In this article, we review the biology and distribution of the only European trigonalid spe-

Fig. 1. Habitus of *Pseudogonalos hahnii*. Specimen collected from Parikkala, Finland. Photo: Pekka Malinen.

cies *P. hahnii* in Fennoscandia and the Baltic states.

2. Materials and methods

We compiled all published records of *Pseudogonalos hahnii* from the study region and gathered data from the following public and private collections:

Institute of Agricultural and Environmental Sciences, Estonian University of Life Sciences [former Institute of Zoology and Botany], Tartu, Estonia (IZBE)
Entomological collection of the Nature Research Centre, Vilnius, Lithuania (NRC)
Finnish Museum of Natural History, University of Helsinki, Finland (MZH)
Natural History Museum, University of Tartu, Estonia (TUZ)
Private collection of Ali Karhu (Coll. Karhu)
Private collection of Juha Pöyry (Coll. Pöyry)
Private collection of Martti Koponen (Coll. Koponen)
Private collection of Mikk Heidemaa (Coll. Heidemaa)
Private collection of Reima Leinonen and Guy Söderman (Coll. Leinonen & Söderman)
Private collection of Veli Vikberg (Coll. Vikberg)

Two Finnish specimens were DNA barcoded by the Canadian Centre for DNA barcoding (CCDB) and their DNA barcode sequences were deposited in the BOLD systems database. They are available from GenBank through the accession numbers MF040884 and MF04088 (Digital Object Identifier (DOI): dx.doi.org/10.5883/DS-PSEHAH)

There has been some dispute about the correct spelling of the family (“Trigonalidae” vs. “Trigonalyidae”) and superfamily (“Trigonaloidea” vs. “Trigonalyoidea”) names. We follow Carmean and Kimsey (1998) and use Trigonalidae as done recently by Aguiar *et al.* (2013), Madl (2013) and Broad (2016). For differing opinions, see Lelej (2003) and Chen *et al.* (2014). For nomenclature of host species, we follow Fauna Europaea (de Jong *et al.* 2014).

3. Results

Synonymy and records of *Pseudogonalos hahnii* from Fennoscandia and the Baltic states are presented below. The records are listed in chronological order within countries, and the acronyms in parentheses refer to specimen depositories. Coordinates are given in the WGS84 system. The symbol ~ indicates that the coordinates were estimated from the locality name.

Pseudogonalos hahnii (Spinola, 1840)
Trigonalys hahnii Spinola, 1840
Trigonalis anglicana Shuckard, 1841
Trigonalis macquartii Guérin, 1842
Trigonalis nigra Westwood, 1843
Trigonalis aterrima Eversmann, 1849
Trigonalis nigra var. *solitaria* Jacobs, 1878
Trigonalis hahni var. *phaeognatha* Enderlein, 1905
Trigonalis hahni var. *enslini* Torka, 1936
Trigonalis prudnicensis Torka, 1936

Estonia: 1 ♂, Uderna (~58.183N, 26.400E), 24.VII.1988, leg. Kalle Remm (IZBE, id:

IZBE0722218); 1 ♀, Elva (~58.225N, 26.416E), 3.VII.1992, leg. Kalle Remm (IZBE, id: IZBE0722219); 1 ♀, Sirgala (~59.283N, 27.717E), 15.VII.2004, leg. Villu Soon (TUZ, id: TUZ055034); 1 ♀, Luunja park (~58.356N, 26.883E), 21.VII.2005, leg. Kaupo Elberg (IZBE, id: IZBE0722220); 1 ♀, Järvselja (~58.269N, 27.309E), 2.VIII.2005, leg. Villu Soon (TUZ, id: TUZ055031); 1 ♀, Tartu, Tüki (58.409N, 26.530E), margin of mixed forest (near flooded area), Malaise trap, 4.–12.VII.2007, leg. Mikk Heidemaa (Coll. Heidemaa); 1 ♀ and 3 ♂♂, Vehendi (58.231N, 26.155E), Malaise trap, 3.–9.VII.2010, leg. Villu Soon (TUZ, ids: TUZ055029, TUZ055030, TUZ055033, TUZ055038); 1 ♀, Vehendi (58.231N, 26.155E), Malaise trap, 16.–24.VII.2010, leg. Villu Soon (TUZ, id: TUZ055032); 1 ♀, Sõõru 1 km NW (58.651N, 26.892E), Malaise trap, 25.VI–4.VII.2011, leg. Villu Soon (TUZ, id: TUZ055035); 2 ♀♀, Sõõru 1 km NW (58.651N, 26.892E), Malaise trap, 4.–21.VII.2011, leg. Villu Soon (TUZ, ids: TUZ055036, TUZ055037); ; 1 ♂, Tartu, Ihaste (58.349N, 26.771E) 23.IX.2017, leg. Villu Soon (TUZ, id: TUZ108320). Total 10 females and 5 males.

Finland: 1 ♀, Helsinki, Fredriksberg (= Pasila) (~60.197N, 24.931E), on a leaf of *Salix caprea*, 28.VII.1943, leg. Adolf Nordman (MZH); 1 ♀, Finby (= Särkisalo), Vedudden (~60.112N, 22.953E), 9.VII.1948, leg. Rabbe Elfving (MZH); 1 ♀, Vanaja (~60.978N, 24.503E), 10.VII.1949, leg. Erkki Valkeila (MZH); 1 ♀, Lohja (~60.251N, 24.066E), on a leaf of *Ribes*, 26.VII.1954, leg. Erkki Rantalainen (MZH); 1 ♂, Helsinki, Haaga (~60.221N, 24.896E), 23.VII.1969, leg. Jonny Perkiömäki (Coll. Vikberg); 1 ♀, Lohja, Vappula, Jusola (60.215N, 23.984E), rocky meadow, 2.VII.2004, leg. Juha Pöyry (Coll. Pöyry); 1 ♀, Lohja, Hiitti (60.275N, 24.032E), dry meadow, 20.VII.2004, leg. Juho Paukkunen (MZH, http://id.luomus.fi/GP. 70893); 1 ♀, Mikkeli, Otava (61.626N, 27.066E), house yard or road verge, 5.VII.2005, leg. Martti Koponen (Coll. Koponen); 1 ♀, Parikkala, Melkoniemi, Peltola (61.529N, 29.377E), meadow, 7.VII.2007, leg. Pekka Malinen & Tomi Salin (MZH); 1 ♀, Nastola, Lemo (61.062N, 25.836E), 24.VII.2008, leg. Tomi Salin (MZH, http://id.luomus.fi/ GP.71215); 1 ♀, Liperi, Käsämä (62.634N, 29.330E), bog, Malaise trap, 30.VI–4.VII.2012, leg. Ali Karhu (Coll. Karhu, http://id.luomus.fi/ GP.96316); 1 ♂, Janakkala, Kalpalinna, Turistirinne (60.928N, 24.592E), 24.VIII.2012, leg. Veli Vikberg (Coll. Vikberg); 1 ♂, Janakkala, Kalpalinna, Turistirinne (60.927N, 24.594E), 12.VII.2013, leg. Veli Vikberg (Coll. Vikberg); 1 ♀, Tohmajärvi, Jalajanvaara (62.207N, 30.316E), meadow, 19.VII.2013, leg. H. Hokkanen, G. Söderman & R. Leinonen (Coll. Leinonen & Söderman); 1 ♀, Janakkala, Kalpalinna, Turistirinne (60.929N, 24.593E), 25.VII.2016, Veli Vikberg (visual observation). Total 12 females and 3 males.

Latvia: 1 ♀, Riga district, Salaspils (~56.861N, 24.349E), 7.VII.1981, leg. Z. Spuris (Abenius & Spuņģis 2001); 1 ♀, Lubāns lake area, (~56.818N, 26.907E), 14.VII.2017, photographed by Uģis Piterāns. Total 2 females.

Lithuania: 1 ♀, Vilnius, Jeruzalė (~54.742N, 25.283E), 1.VIII.1967, leg. Algimantas Jakimavičius (NRC); 2 ♂, Vilnius, Vingis park (~54.684N, 25.229E), 4.VII.1970, leg. Algimantas Jakimavičius (NRC); 1 ♀, Vilnius, Sapieginė (~54.706N, 25.339E), 1.V.1973, leg. Algimantas Jakimavičius (NRC); 1 ♂, Vilnius, Žemieji Paneriai (~54.642N, 25.195E), 21.VI.1974, leg. Algimantas Jakimavičius (NRC); 1 ♀, Vilnius, Jeruzalė (~54.742N, 25.283E), 8.VIII.1974, leg. Algimantas Jakimavičius (NRC); 1 ♂, Vilnius, Jeruzalė (~54.742N, 25.283E), 12.VI.1975, leg. Algimantas Jakimavičius (NRC); 1 ♂, Vilnius (~54.680N, 25.320E), 12.VI.1975, leg. Algimantas Jakimavičius (NRC); 1 ♂, Vilnius, Jeruzalė (~54.742N, 25.283E), 5.IX.1975, leg. Algimantas Jakimavičius (NRC); 1 ♀, Vilnius, Pilaitė (~54.700N, 25.190E), 11.VIII.1976, leg. Vytautas Jonaitis (NRC); 1 ♂, Žiežmariai (~54.820N, 24.450E), 15.VI.1977, leg. Aldona Stanionytė (NRC); 1 ♂, Žiežmariai (~54.820N, 24.450E), 20.VI.1978, leg. Algimantas Jakimavičius (NRC); 1 ♀, Pasmalvės (~55.617N, 26.417E), 29.VI.1988 leg. Eduardas Budrys (NRC); 1 ♀, Smukučių šilelis forest (~55.089N,

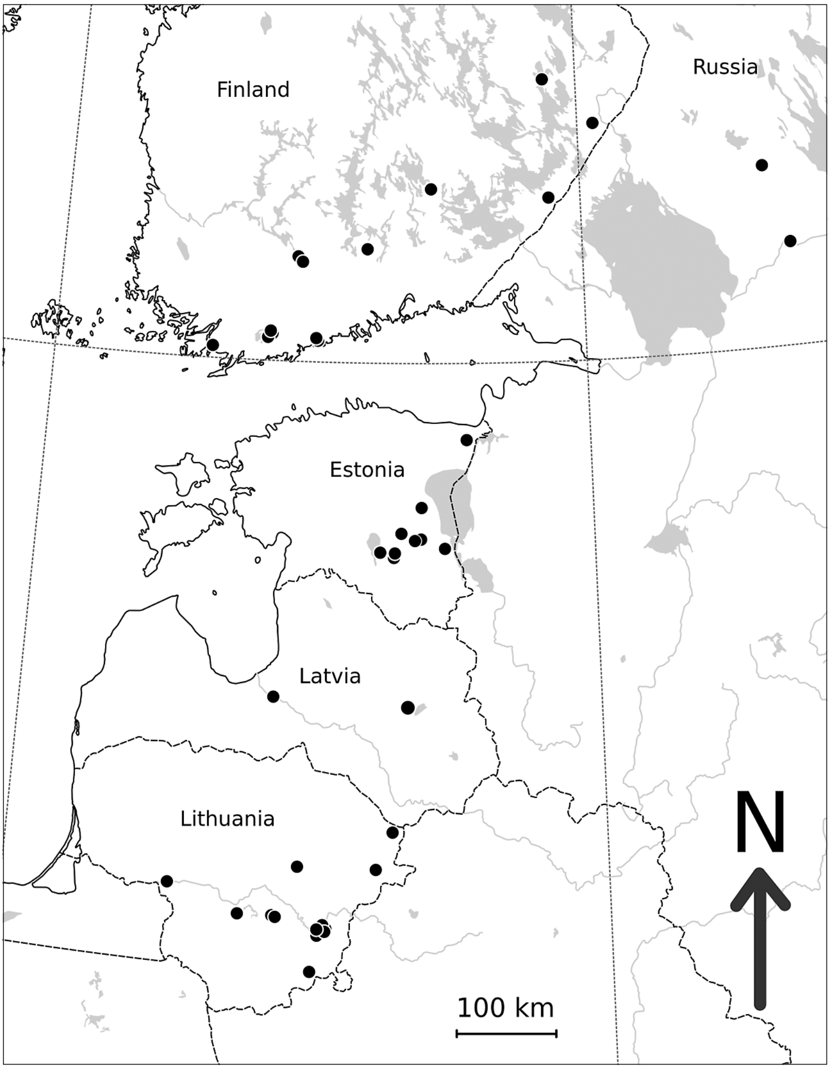

Fig. 2. Distribution of *Pseudogonalos hahnii* in Fennoscandia and the Baltic countries.

22.721E), 9.VII.1998 leg. Vytautas Jonaitis (NRC); 1 ♂, Strošiūnai reserve (~54.806N, 24.508E), 15.VII.1998 leg. Vytautas Jonaitis (NRC); 1 ♂, Akmeniškiai (~55.267N, 26.145E), 08.VII.1999 leg. Vytautas Jonaitis (NRC); 2 ♀, Papiškės (~54.302N, 25.092E), 9.VII.1999 leg. Vytautas Jonaitis (NRC); 1 ♀, Garliava (~54.825N, 23.890E), 28.VII.1999 leg. Vytautas Jonaitis (NRC); 1 ♂, Dukstyna reserve (~55.281N, 24.846E), 19.VII.2000 leg. Vytautas Jonaitis (NRC). Total 9 females and 11 males.

Russian Fennoscandia: 1 ♀, Vazhiny, Svir, (~60.961N, 34.021E), 8.VII.1942, leg. Viljo J. Karvonen (MZH); 1 ♀, Pryazha, (~61.692N, 33.622E), 1943, leg. Paavo Kontkanen (MZH). Total 2 females.

A total of 54 *P. hahnii* specimens are known from the study region. Of these 35 are females and 19 males. The species is here reported from Estonia, Lithuania and Russian Fennoscandia for the first time. The only known Latvian record until 2017 was from 1981 (Abenius & Spuņģis 2001). The species was originally reported from Finland in a short meeting report, which did not include detailed information of collecting sites (Anonymous 1950).

The DNA barcode sequences of the two Finnish specimens were identical. No other DNA barcodes of *P. hahnii* have been deposited in the

Fig. 3. Habitat of *Pseudogonalos hahnii* in Finland (Parikkala, Melkoniemi). Photo: Juho Paukkunen.

BOLD database or GenBank, so comparison with other specimens was not possible.

4. Discussion

4.1. Distribution and abundance

Pseudogonalos hahnii is widely distributed in the Baltic states, southern Finland and Russian Karelia (Fig. 2). The northernmost record is from Liperi in Pohjois-Karjala province of eastern Finland. The species is not known from other Nordic countries. It is rare in Finland, and is always found in low numbers. It seems to be scarce also in the Baltic region, but in Estonia, several specimens have been collected in a few localities by Malaise traps. Specimens caught with Malaise traps have also been reported in England and Germany (Shaw 1990, Schnee 2011). 25 of the observations in the study region were made relatively recently, and 29 specimens were collected before 2000. The first specimen was collected in Russian Karelia in 1942, and soon after this the species was found from Finland (1943). In the Baltic states, the species was found notably later (Lithuania 1967, Latvia 1981, Estonia 1988,). Despite the clear increase of the records from 2004 onwards, the species was classified as vulnerable in the latest Red List of Finnish species (Söderman *et al.* 2010).

Within Europe, *P. hahnii* has been found from Belgium, Czech Republic, Estonia, Finland, France, Germany, Greece, Italy, Latvia, Lithuania, the Netherlands, Poland, Russia, Slovakia, Switzerland, Ukraine and the United Kingdom. It has also been recorded from China, Kazakhstan, Mongolia and Siberia (Lelej 2003, Madl 2013, Broad 2016).

4.2. Habitat, egg-laying, phenology and sex ratios

All published habitat information (Schnee 2011) and collection records make it clear that *P. hahnii* is a eurytopic species that is found in a variety of different environments. However, Finnish records are almost solely from herb-rich meadows (Fig. 3). One Finnish specimen has been caught from a leaf of *Salix caprea* and an another from a leaf of *Ribes*.

Pseudogonalos hahnii female lays eggs on the surface foliage of herbaceous and wooden plants (Carmean & Kimsey 1998, Schnee 2011). The female is extremely fecund with its ovarioles containing more than 10,000 eggs and it can be induced to lay well over a thousand eggs per day in experimental conditions (Bischoff 1936). Eggs are microtypic and 0.1–0.15 mm in length and 0.05–0.07 in width (Weinstein & Austin 1991). Eggs also stay viable for a long time (Schnee 2011). Ovipositing has been observed on such di-

Table 1. Published host records of *Pseudogonalos hahnii* in chronological order. "Host plant" refers to the observed or inferred oviposition site of *P. hahnii* female.

Host plant	Secondary host (species and family)	Primary host (species and subfamily)	Reference
Poaceae	*Epipsilia latens* (Hübner, 1809) Noctuidae	*Ophion luteus* (Linnaeus, 1758) Ophioninae	Reichert (1911)
Not known	*Smerinthus ocellatus* (Linnaeus, 1758) Sphingidae	*Callajoppa cirrogaster* (Schrank, 1781) Ichneumoninae	Puhlmann (1916)
Not known	*Papilio machaon* Linnaeus, 1758 Papilionidae	Not known	Berland & Bernard (1938)
Pinus	*Panolis flammea* (Denis & Schiffermüller, 1775) Noctuidae	*Enicospilus merdarius* (Gravenhorst, 1829) Ophioninae	Gauss (1962)
Vaccinium myrtillus	*Ectropis crepuscularia* (Denis & Schiffermüller, 1775) Geometridae	*Aphanistes bellicosus*? (Wesmael, 1849) Anomaloninae	Haeselbarth (1979), Schnee (2015)
Pinus	*Diprion similis* (Hartig, 1836), Diprionidae	Not known	Carmean & Kimsey (1998)
Pteridium aquilinum	*Ceramica pisi* (Linnaeus, 1758) Noctuidae	*Enicospilus ramidulus* (Linnaeus, 1758) Ophioninae	Schnee (2011)
Rubus idaeus, *R. fructicosus*	*Polia nebulosa* (Hufnagel, 1766) Noctuidae	*Erigorgus procerus* (Gravenhorst, 1829) Anomaloninae	Schnee (2011)
Not known	*Xestia triangulum* (Hufnagel, 1766) Noctuidae	*Erigorgus melanops* (Forster, 1855) Anomaloninae	Schnee (2011)
Not known	*Callimorpha dominula* (Linnaeus, 1758) Erebidae	*Heteropelma* amictum (Fabricius, 1775) Anomaloninae	Schnee (2011)
Prenanthes purpurea	*Cucullia lactucae* (Denis & Schiffermüller, 1775) Noctuidae	*Exetastes fornicator* Fabricius 1781) Banchinae	Schnee (2015)

verse plants as *Pteridium aquilinum* (Dennstaedtiaceae), pine needles (Pinaceae), grasses (Poaceae), *Phragmites communi*s (Poaceae), *Vaccinium myrtillus*, *Rubus idaeus*, *R. fruticosus* (Rosaceae), Brassicaceae, *Prenanthes purpurea* (Asteraceae) and *Epilobium angustifolium* (Onagraceae) (Shaw 1990, Weinstein & Austin 1991, Schnee 2011, 2015) (Table 1). There are no direct records of oviposition from the study area. During summer 2017, a female was observed flying between and searching on nettles (*Urtica dioica*) and mugworts (*Artemisia vulgaris*) in Latvia (U. Piterāns, pers. comm.).

Like in other investigated trigonalid species, the life span of adult *Pseudogonalos hahnii* is very short, at most 8 days, according to the scant available evidence (Bischoff 1936, Carmean 1991). Trigonalid species of temperate regions normally emerge in spring or summer (Weinstein & Austin 1991). About 75% of the specimens caught in Northern Europe are from July (Fig. 4). Keeping in mind the short adult life span and temporal distribution of the records, *Pseudogonalos hahnii*'s actual flight period may very well center around July in North Europe. Most specimens (total 18) from Germany published by Schnee

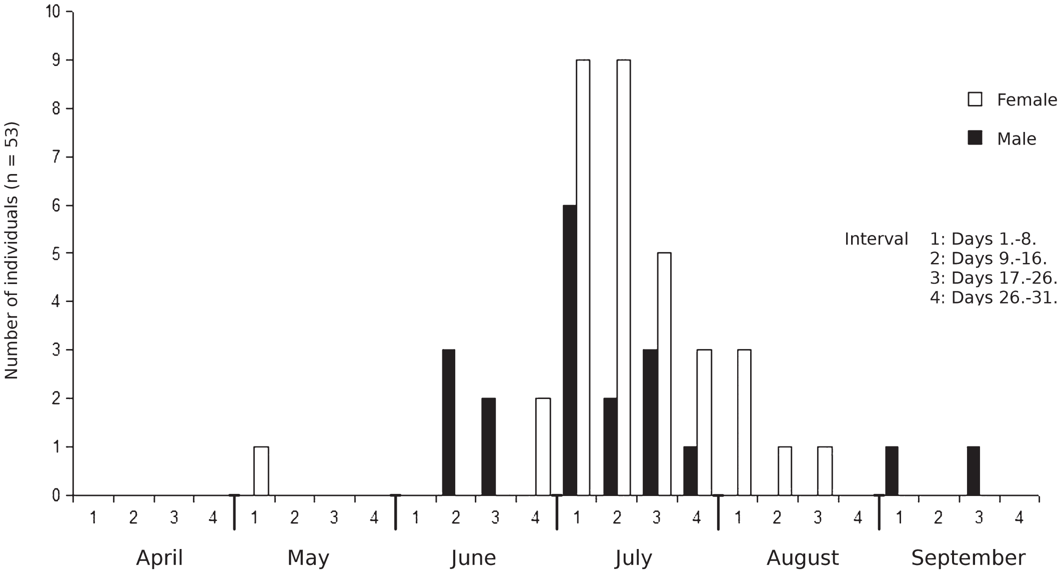

Fig. 4. Phenological distribution of the records of *Pseudogonalos hahnii* in Fennoscandia and the Baltic countries.

(2011, 2015) were also sampled in July. According to Shaw (1982, 1990), many specimens have been caught during August in England. *Pseudogonalos hahnii* seems to be a protandrous species as the peak of the caught males is earlier in the season than that of the females. The above holds true except for three phenological outliers from Lithuania and Estonia (2 males from September and 1 female from early May).

The sex ratio of collected *P. hahnii* is female-biased (1.84 females for each male). The pooled sex ratio of field caught specimens reported by Schnee (2011, 2015) is about the same (2 females for each male). It is not clear why the sex ratios of collected specimens are female biased.

4.3. Host records

There are no rearing or host records of *P. hahnii* from the study area. All reported host records are from Germany, United Kingdom, Russia and Poland (Schnee 2011, 2015, D. Carmean, pers. comm., V. Bryukhov, pers. comm.) (Table 1).

All lepidopteran secondary hosts of *P. hahnii* recorded so far are from the families Noctuidae (six species), Erebidae (one species), Geometridae (one species), Sphingidae (one species) and Papilionidae (one species) (Table 1) (Schnee 2011, 2015). In Kirov region, western central Russia, *P. hahnii* was photographed emerging from a pupa of *Papilio machaon* Linnaeus (Papilionidae) on 13 June 2015 (V. Bryukhov, pers. comm.) (Fig. 5). The Canadian National Collection has a specimen of *P. hahnii* from Poland labelled "Host: *Diprion similis* (Htg.)" (Carmean & Kimsey 1998, D. Carmean & J. Huber, pers. comm.). In Germany, thousands of hibernating *Diprion* (Diprionidae) cocoons have been investigated for decades by forestry protection in pine forests and no *P. hahnii* has ever been reared, and therefore the record of the sawfly *D. similis* as a host of *P. hahnii* could be regarded as unconfirmed (H. Schnee, pers. comm.). However, as all Trigonalidae rearing records are always very rare occurrences, we see no reason for discounting the *D. similis* host record. It is not known, whether *P. hahnii* developed as a primary parasitoid of *D. similis* or parasitized an unknown primary parasitoid of *D. similis*.

Primary hosts of *P. hahnii* recorded so far are all from the family Ichneumonidae: Ophioninae (three species), Ichneumoninae (one species), Banchinae (one species) and Anomaloninae (three species plus one likely additional species) (Haeselbarth 1979, Schnee 2011, 2015) (Table

Fig. 5. *Pseudogonalos hahnii* emerging from *Papilio machaon* pupa. 13 June 2015. Kirov region, Russia. Photo: Vladimir Bryukhov.

1). All these four subfamilies are koinobiont endoparasitoids (Gauld & Bolton 1988). Species that parasitize lepidopteran caterpillars from the endoparasitic koinobiont subfamilies Campopleginae and Metopiinae are other possible primary hosts. On the contrary, species from ectoparasitic or idiobiont ichneumonid subfamilies parasitizing Lepidoptera are not likely to act as primary hosts (Schnee 2011). Ctenopelmatine ichneumonids could serve as possible primary hosts via sawfly larva as the members of the subfamily are larval koinobiont endoparasitoids of sawflies (Gauld & Bolton 1988, Schnee 2011). Another possible primary host group for *P. hahnii* are tachinid flies that attack lepidopteran (or even symphytan) larvae (Weinstein & Austin 1991, Schnee 2011) as several trigonalid wasp species have indeed been reared from tachinid puparia (Li *et al.* 2012, Smith *et al.* 2012). There are some erroneous or at least highly dubious old records that *P. hahnii* could parasitize vespine wasps (Vespidae) or their parasitoids. There is also one report of *P. hahnii* parasitizing the neotropical paper wasp *Polistes lanio* (Fabricius) that Carmean and Kimsey (1998) consider clearly improbable.

If host records of *P. hahnii* can be considered scanty, even less is known about the host relationships of the two other *Pseudogonalos* species. There are no host records for *P. angusta* or *P. harmandi*. Weinstein and Austin (1991) cite Popov's (1945) rearing records of *P. harmandi* from *Trogus* sp. (Ichneumoninae) and *Ophion* sp. (Ophioninae), but these records are erronoeus (Carmean & Kimsey 1998).

Pseudogonalos hahnii is rarely collected, probably because as a hyperparasitoid with a remarkable strategy, it needs a herbivorous host to be parasitized by a primary parasitoid (the primary host) before it can complete its development. The trigonalid larva will develop to adulthood regardless whether the herbivorous secondary host was parasitized by the ichneumonid primary parasitoid before or after it ingested the trigonalid eggs. The trigonalid larva can stay viable within the herbivorous secondary host for several months and wait for the ichneumonid parasitoid female to oviposit into the same secondary host (Schnee 2011). High fecundity of the female and wide host spectrum make it more likely that at least some of the *P. hahnii* progeny will reach adulthood every year. Future collection efforts, rearings and laboratory studies will surely widen considerably the known primary and secondary host spectrum and other aspects of the biology of *P. hahnii*.

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