

Review of the Strepsiptera fauna of the Nordic countries with the description of two new species of *Stylops* Kirby (Stylopidae)

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Abstract

Twisted-winged parasites (Strepsiptera) is a small insect order with around 610 species worldwide and whose members are obligate parasites of other insects. While recent advances in molecular methods have significantly improved our understanding of the species diversity, there is no review of Strepsiptera diversity from the Nordic countries that fully reflect the current state of taxonomic knowledge. Here we revise the Nordic Strepsiptera fauna, present an updated and annotated checklist of species, including new distribution data and host associations based on new records from museums, private collectors, previous publications, and databases. We describe two new species of *Stylops* (Strepsiptera: Stylopidae) from the Nordic countries, *Stylops sapmiensis* Lähteenaro & Bergsten, **sp. nov.** and *Stylops serotinus* Lähteenaro & Straka, **sp. nov.**, supported by molecular, morphological, and host-use data. A key to genera of Nordic Strepsiptera based on males and to species based on females is provided together with distribution maps of known species.

Key words: Twisted-winged parasites, taxonomy, identification key, Europe, new species

Introduction

Strepsiptera, commonly known as twisted-winged parasites, is a small insect order of about 610 species known for their extraordinary life-cycles and associated morphological characteristics. All species are obligate endoparasites of other insects, and have hosts from seven different orders (Kathirithamby, 2009). Strepsiptera display extreme sexual dimorphism owing to the different lifestyles of the adult sexes (Kathirithamby, 1989; Kinzelbach, 1971). Except for the family Mengenillidae with about 20 species, adult Strepsiptera females remain as endoparasites in their hosts while adult males are free-living for a brief period, which is also reflected in their appearance. Males possess typical adult insect characteristics but with uniquely fan-shaped hindwings and haltere-like forewings inspiring the name of the order (Greek strepsi, “twisted”; pteron, “wing”). In contrast, females remain larviform and are only partly extruded outside the host. Even the larval instars of Strepsiptera differ from each other both in function and form. The tiny host-seeking first instar larva is mobile and free-living until it enters a host and moulds into a legless secondary larva (Kathirithamby, 1989).

Given that Strepsiptera are elusive in nature, difficult to find, tiny and confusing, it is not surprising that they were discovered rather late by naturalists in general (e.g. Kirby, 1802, 1813; Rossi, 1793). The exploration of the fauna in the Nordic countries started even later and proceeded remarkably unevenly. Among the Nordic countries, Strepsiptera was first discovered in Finland in the second half of the 19th century (Mäklin, 1866, 1867). Mäklin (1866) reported *Stylops* on a female *Andrena cineraria* (Linnaeus, 1758) from Sjundeå parish in southern Finland that he had collected in June 1855. This was followed by a report of a styloped female of *Miscus campestris* (now *Ammophila pubescens* Curtis, 1836) collected in June 1866 in Rautus parish (then in Finland, today Russia) which was identified as *Xenos vesparum* v. *sphecidarum* Siebold, 1839 (now *Tuberoxenos sphecidarum* (Siebold, 1839)) (Mäklin, 1967). Towards the end of the 19th century detailed morphological studies on Strepsiptera were carried out by Meinert (1896a, 1896b) who also documented *Stylops* from Denmark, including a male specimen in the Copenhagen collections taken by Christian Drewsen near Strandmøllen north of Copenhagen.

The first mention of a Strepsiptera parasite in the Nordic countries that is not associated with bees or wasps comes from Denmark. At a meeting of the Skandinaviske Naturforskare Society, Hansen (1892) reported a fully developed *Elenchus* male dissected from a pupa *in situ* in a *Liburnia brevipennis* Sahlberg, 1871 female (Delphacidae) (now *Muellerianella brevipennis* (Boheman, 1847)) from Horsens, Jylland. Strepsiptera is notably lacking from the influential works of Carl Gustaf Thomson in Sweden during the second half of the 19th century. Instead, we find the first mentions from Sweden unspecific or uncertain, noting that *Stylops* is a parasite of *Andrena* in Sweden (Aurivillius, 1903), and a dissected male of *Xenos vesparum* from a *Polistes bighumis* (Linnaeus, 1758), possibly with a Swedish origin (Tullgren & Wahlgren, 1920). A small remark by Aurivillius (1903) indicates that a type specimen of *Andrena nigrospina* Thomson, 1872 from Sweden is a styloped individual which has later been confirmed (Baker, 1994; Nilsson, 2010).

In the 1920s and 1930s there was a certain consolidation of faunistic and ecological knowledge, especially in Finland. Strepsiptera were noted in leafhoppers (Lindberg, 1925) and somewhat later identified and studied in great detail with regard to ecology and effects on the host (Kanervo *et al.*, 1957; Kontkanen, 1950; Lindberg, 1936, 1939, 1943, 1949, 1960; Raatikainen, 1966, 1967a, 1967b). Summaries of the Finnish fauna were presented by Hellén (1935a, 1935b, 1936).

Scattered discoveries were made in the other Nordic countries: *Elenchus* in Sweden (Ahlberg, 1925), *Halictoxenos* as the first record of the order in Norway (Ulrich, 1933) and soon also reported from Sweden (Gaunitz, 1938). It continued with *Halictophagus* in Sweden (Heqvist, 1958), more about *Stylops* in Denmark (Jensen, 1971) and Norway (Løken, 1967; Meidell, 1967), *Elenchus* in Norway (Andersen & Fjellberg, 1975) and *Tuberoxenos* in Sweden (Merisuo & Pekkarinen, 1980).

At this time, the somewhat more advanced state of knowledge in Finland allowed the publication of summaries and more synthetic studies (Pekkarinen & Raatikainen, 1973; Raatikainen, 1970, 1972) including the excellent summary by Pekkarinen & Raatikainen (1973). In Sweden, an attempt at synthesizing the knowledge was made in Landin (1971) where it still had to be stated that many genera were not proved to occur in Sweden or did occur but with uncertainly identified species. In Denmark a general résumé and family-level keys to males, females and larvae were presented by Larsson (1966), who also included Mengeidae since representatives of this extinct family have been found in Baltic amber.

In Finland, studies and summaries continued rather uninterruptedly (Lähteenaro, 2019a, 2024; Lähteenaro & Paukkunen, 2019; Pekkarinen, 1984, 1997; Pekkarinen & Valtonen, 2000; Söderman, 2010), and they were resumed in Sweden and later in Denmark (Nielsen *et al.*, 2014; Nielsen & Oyre, 2016), whereas in Norway there are no new publications except online material (Aarvik & Elven, 2014). Strepsiptera interest in Sweden was gaining momentum after the dipterologist Hans Bartsch discovered a sandpit north of Stockholm where swarms of *Stylops ater* could be observed every early spring (Bartsch, 2006; Bergsten, 2007; see also Lind, 2014 for a popular account), turning it into a traditional opening of the field season for some local entomologists. Soon, the phenomenon was also discovered in other localities in the Stockholm-Uppsala region, and later also in southern Sweden. Around the same time, the mass collecting effort of the Swedish Malaise Trap Project (Karlsson *et al.*, 2020) revealed that *Elenchus* males were not so rare but appeared in Malaise-trap catches across much of the country.

More recently, molecular methods have advanced our understanding of species diversity within Strepsiptera which has led to significant taxonomic changes (Benda *et al.*, 2021, 2022; Jůzová *et al.*, 2015; Lähteenaro *et al.*, 2024b; Straka *et al.*, 2015b). For example, the former European species *Stylops melittae*, has been divided into about 30 different species (Straka *et al.*, 2015b) and genomic data have revealed numerous undescribed species

(Lähteenaro *et al.*, 2024b). Currently, there exists no up-to-date information about the distribution of Strepsiptera species in the Nordic countries. Although some Nordic countries have recently published checklists of the order (Lähteenaro, 2019a; Nielsen *et al.*, 2014), these do not fully follow the current taxonomic knowledge. In this paper, we describe two new species of *Stylops* from the Nordic countries supported by molecular evidence. In addition, we present an annotated and updated checklist of Strepsiptera from the Nordic countries, including geographic distribution and known host records.

Materials and methods

The collections of the following museums were examined: Zoological collections of the Finnish Museum of Natural History Luomus (MZH), Zoological collections of Turku University (ZMUT), Zoological Collections of Oulu University (ZMUO), Entomological Collections of the Swedish Museum of Natural History (NHRS), Zoological Museum of the Uppsala University (UUZM), Lund University Biological Museum—Zoological collections (MZLU), and the Gothenburg Museum of Natural History (GNM). For several collection holdings, finding Strepsiptera specimens amounted to screening through the collections of the presumed Hymenoptera and Hemiptera hosts. We also examined all Strepsiptera specimens sorted out from material in the Swedish Malaise Trap Project (SMTP) (Karlsson *et al.*, 2020). Additionally, we are in debt to numerous private collectors who have donated or lent material to the NHRS for examination. Important material from the private collections of Jakub Straka (JSPC), the National Museum of the Czech Republic (NMPC) and from Kansas University Natural History Museum (KUNHM) is also cited.

Henning Bang Madsen has provided information on Strepsiptera in Denmark both in private collections and in the following institutions: Zoological Museum, University of Copenhagen (ZMUC), Natural History Museum, Aarhus (NHMA), and at the Department of Biology, University of Copenhagen (HBM-BIO).

Observation data were collected from the following online databases: laji.fi (Finnish Biodiversity Info Facility), artsdatabanken.no (Norway), slu.se/artdatabanken (SLU Swedish Species Information Centre) and GBIF.org (Global Biodiversity Information Facility). The reliability of each of these observations was assessed individually, and improbable and double observations were excluded. We also provided species level identification for observations when they were not originally specified but could be determined based on host associations. Previously published observations in the literature were gathered from the Nordic countries. Iceland was not included as no Strepsiptera has been reported from the country.

Preparation

Adult females were extracted from their host for morphological examination. For dry specimens, hosts were first relaxed in water vapour before dissecting out the endoparasitic female with forceps. Females were cleared in ATL buffer, proteinase K (Qiagen) and DTT at 56°C for several hours. Cleared specimens were stored in 96% ethanol before they were dried and glued to point cards.

Imaging

Specimens were photographed with a Canon EOS R camera attached to a Novoflex Balpro 1 bellows with a 20x, 10x or 5x Mitutoyo lens and lateral lights with diffusers. A StackShot Macro Rail system (Cognisys Inc.) was used to shoot a stack of photos with different foci, which were processed with Zerene Stacker (Zerene Systems LLC, Richland, WA, USA). SEM images of holotypes were taken for the new species descriptions. The point cards with dried cephalothoraces were mounted on a specimen holder with adhesive carbon tabs. The specimens were not coated to preserve the original colouration. Images were taken with a Quanta FEG 650 SEM (FEI Company, OR, USA) in low vacuum. Images were processed and arranged to plates with Adobe Photoshop® 2025 (Adobe System Incorporated, San Jose, CA, USA). Line drawings were made with Adobe Illustrator® 2025 software.

Measurements and terminology

Measurements for the species descriptions were taken from photographs with the ImageJ program (v. 1.54g). Cephalothorax length was measured from the apex of the clypeal lobe (ventral view) to the constriction of abdominal segment I, whereas the cephalothorax width is the maximum distance between its lateral margins. Length of the head includes lateral extensions. Terminology used in species descriptions of the female cephalothorax was adapted from Benda *et al.* (2022, 2024), Löwe (2016) and Kinzelbach (1971). The cephalothorax is described in morphological orientation, even though their functional orientation in the host's body is inverted.

Results

Checklist of Nordic species and descriptions of new species

In the checklist below, we provide Strepsiptera species recorded from Nordic countries along with their alternative names as found in Nordic literature. Additionally, we present recorded host associations from Nordic countries (**Nordic hosts**), all additional confirmed hosts abroad (**additional hosts**) and distribution of species at fauna province level according to the definitions in the monograph series Fauna Entomologica Scandinavica (Brill) (**distribution**). We also provide information on the preferred habitats of the species based on Nordic observations (**habitat**) as well as on their phenology in Nordic countries (**phenology**). Additional information that is considered relevant is provided in the notes (**notes**). New country records are presented with reference to Nielsen *et al.* (2014) and Nielsen & Oyre (2016) in Denmark, Lähteenaro (2024) in Finland, Løken (1967) and Andersen and Fjellberg (1975) for Norway and Landin (1971) and Merisuo & Pekkarinen (1980) for Sweden, except for *Stylops* spp., which was considered a single species (*Stylops melittae*) until 2015 and therefore all records are new, except in Finland, where the new classification has been accounted for in Lähteenaro (2024).

A summary of the Nordic Strepsiptera species and their hosts in each Nordic country is provided in table 1. An overview of potential future Strepsiptera species in the Nordic countries is provided in table 2. All collected observation data (from collections, online databases and previous publications) are presented in one summary file (supplementary table 1).

TABLE 1. Strepsiptera species in Nordic countries and their host associations. Symbols: *—Publ. Nielsen 2014, no precise location information; **—Publ. Løken 1967 and Meidell 1967, no precise location information; ()—Former Finland.

Strepsiptera Species	Host species	Denmark	Norway	Sweden	Finland
Elenchidae					
<i>Elenchus</i> Curtis, 1831					
<i>Elenchus tenuicornis</i> (Kirby, 1815)		X	X	X	X
	Delphacidae	X	X	X	X
	<i>Achantodelphax spinosa</i> (Fieber, 1866)				X
	<i>Chloriona glaucescens</i> Fieber, 1866				X
	<i>Chloriona smaragdula</i> (Stål, 1853)				X
	<i>Criomoprhus borealis</i> (J. Sahlberg, 1871)				X
	<i>Criomoprhus moestus</i> (Boheman, 1847)				X
	<i>Delphacinus mesomelas</i> (Boheman, 1849)				X
	<i>Delphacodes venosus</i> (Germar, 1830)				X
	<i>Dicranotropis hamata</i> (Boheman, 1847)				X
	<i>Javesella pellucida</i> (Fabricius, 1794)	X*	X		X
	<i>Javesella discolor</i> (Boheman, 1847)				X

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TABLE 1. (Continued)

Strepsiptera Species	Host species	Denmark	Norway	Sweden	Finland
	<i>Javesella dubia</i> (Kirschbaum, 1868)			X	X
	<i>Javesella forcipata</i> (Boheman, 1847)				X
	<i>Javesella obscurella</i> (Boheman, 1847)				X
	<i>Kosswigianella denticauda</i> (Boheman, 1847)				X
	<i>Megadelphax sordidula</i> (Stål, 1853)				X
	<i>Muellerianella brevipennis</i> (Boheman, 1847)	X			
	<i>Megamelus notula</i> (Germar, 1830)				X
	<i>Ribautodelphax albobstriata</i> (Fieber, 1866)				X
	<i>Ribautodelphax collina</i> (Boheman, 1847)				X
	<i>Stiroma affinis</i> Fieber, 1866				X
	<i>Stiroma bicarinata</i> (Herrich-Schäffer, 1835)				X
	<i>Xantodelphax flaveola</i> (Flor, 1861)				X
	<i>Xantodelphax straminea</i> (Stål, 1858)				X
Halictophagidae					
<i>Halictophagus</i> Curtis, 1832					
<i>Halictophagus silwoodensis</i> Waloff, 1981		X	X	X	X
	Ulopidae	X	X	X	X
	<i>Ulopa reticulata</i> (Fabricius, 1794)			X	
<i>Halictophagus curtisi</i> Dale, 1832		X			
	Cicadellidae	X			
Corioxenidae					
<i>Malayaxenos</i> Kifune, 1981					
<i>Malayaxenos trapezonoti</i> Pohl & Melber, 1996				X	
	Rhyparochromidae			X	
Xenidae					
<i>Tuberoxenos</i> Benda, Pohl, Nakase, Beutel & Straka, 2022					
<i>Tuberoxenos sphecidarum</i> (Siebold, 1839)				X	(X)
	<i>Ammophila pubescens</i> Curtis, 1836			X	(X)
	<i>Ammophila sabulosa</i> (Linnaeus, 1758)			X	
	<i>Podalonia luffii</i> (E.Saunders, 1903)			X	
	<i>Podalonia hirsuta</i> (Scopoli, 1763)			X	
Stylopidae					
<i>Stylops</i> Kirby, 1802					
<i>Stylops ater</i> Reichert, 1914		X	X	X	X
	<i>Andrena cineraria</i> (Linnaeus, 1758)	X	X	X	X
	<i>Andrena vaga</i> Panzer, 1799	X	X	X	X
<i>Stylops aterrimus</i> Newport, 1851		X		X	
	<i>Andrena tibialis</i> (Kirby, 1802)	X			

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TABLE 1. (Continued)

Strepsiptera Species	Host species	Denmark	Norway	Sweden	Finland
	<i>Andrena scotica</i> Perkins, 1916	X		X	
	<i>Andrena nigrospina</i> Thomson, 1872	X*		X	
<i>Stylops gwynanae</i> Günther, 1957		X*			
	<i>Andrena bicolor</i> Fabricius, 1775	X*			
<i>Stylops melittae</i> Kirby, 1802		X			
	<i>Andrena nitida</i> (Müller, 1776)	X			
	<i>Andrena flavipes</i> Panzer, 1799	X			
<i>Stylops nevinsoni</i> Perkins, 1918		X	X	X	X
	<i>Andrena fucata</i> Smith, 1847	X	X	X	X
<i>Stylops sapmiensis</i> sp. nov. Lähteenaro & Bergsten			X	X	X
	<i>Andrena lapponica</i> Zetterstedt, 1838		X	X	X
<i>Stylops serotinus</i> sp. nov. Lähteenaro & Straka				X	X
	<i>Andrena fuscipes</i> (Kirby, 1802)			X	X
<i>Stylops spretus</i> Perkins, 1918		X	X	X	X
	<i>Andrena falsifica</i> Perkins, 1915			X	
	<i>Andrena minutula</i> (Kirby, 1802)	X	X**		
	<i>Andrena minutuloides</i> Perkins, 1914			X	X
	<i>Andrena niveata</i> Friese, 1887	X		X	
	<i>Andrena semilaevis</i> Pérez, 1903		X**	X	
	<i>Andrena subopaca</i> Nylander, 1848	X	X	X	X
<i>Stylops thwaitesi</i> Perkins, 1918		X	X	X	X
	<i>Andrena afzeliella</i> (Kirby, 1802)	X		X	
	<i>Andrena gelriae</i> van der Vecht, 1927		X**		X
	<i>Andrena intermedia</i> Thomson, 1870			X	X
	<i>Andrena wilkella</i> (Kirby, 1802)	X	X**	X	X
<i>Halictoxenos</i> Pierce, 1909					
<i>Halictoxenos arnoldi</i> Perkins, 1918				X	
	<i>Lasioglossum xanthopus</i> (Kirby, 1802)			X	
<i>Halictoxenos spencei</i> Nassonov, 1893		X	X	X	X
	<i>Lasioglossum fulvicorne</i> (Kirby, 1802)				X
	<i>Lasioglossum nitidiusculum</i> (Kirby, 1802)			X	
	<i>Lasioglossum punctatissimum</i> (Schenck, 1853)	X		X	
	<i>Lasioglossum calceatum</i> (Scopoli, 1763)	X	X	X	X
	<i>Lasioglossum fratellum</i> (Pérez, 1903)	X			X
<i>Halictoxenos tumulorum</i> Perkins, 1918		X	X	X	X
	<i>Seladonia tumulorum</i> (Linnaeus, 1758)	X	X	X	X
	<i>Halictus rubicundus</i> (Christ, 1791)			X	

Corioxenidae

Malayaxenos trapezonoti Pohl & Melber, 1996 (figure 1)

Nordic hosts unknown.

Additional hosts *Trapezonotus arenarius* (Linnaeus, 1758); *T. desertus* Seidenstucker, 1951 (Heteroptera: Rhyparochromidae) (Pohl & Melber, 1996).

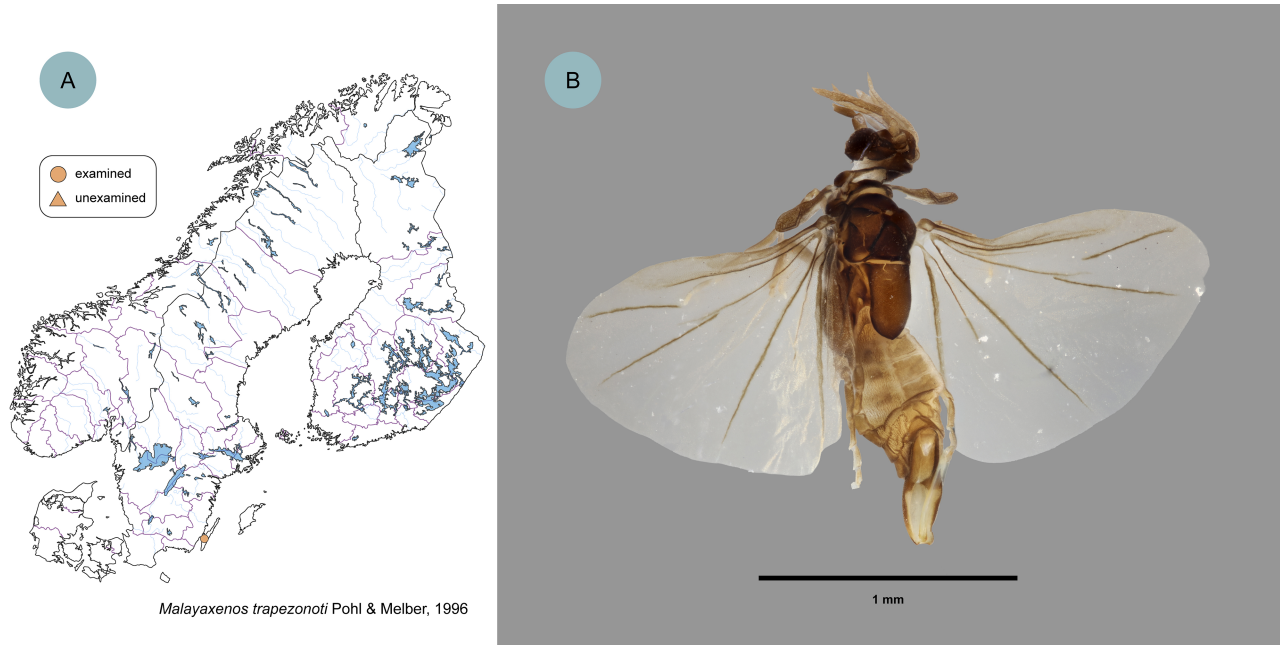


FIGURE 1. Localities of *Malayaxenos trapezonoti* Pohl & Melber, 1996 in Nordic countries (A) and *M. trapezonoti* male (NHRS-MELA000000453) from Öland, Sweden (B).

Distribution

Sweden: Öland. **New to Sweden.**

Habitat The only known Nordic record was collected from a sandy roadside with shrubs in a dry agricultural landscape on limestone.

Phenology The only known Nordic record is from July.

Notes The sole Nordic record from Sweden in 2018 presents also the first known location of the species outside its type locality in Germany (Pohl & Melber, 1996)). As only a single free-living male has been found, no host information from the Nordic countries is available. Both known associated host species occur in all included Nordic countries.

Elenchidae

Elenchus tenuicornis (Kirby, 1815) (figure 2)

Stylops tenuicornis Kirby, 1815.

Elenchus chlorionae Lindberg, 1939.

Elenchus delphacophilus Ahlberg, 1925.

Elenchus walkeri Curtis, 1831.

Pseudelenchus carpathicus Ogloblin, 1925.

Nordic hosts *Achantodelphax spinosa* (Fieber, 1866); *Chloriona glaucescens* Fieber, 1866; *C. smaragdula* (Stål, 1853); *Criomorphus borealis* (J. Sahlberg, 1871); *C. moestus* (Boheman, 1847); *Delphacinus mesomelas* (Boheman, 1849); *Delphacodes venosus* (Germar, 1830); *Dicranotropis hamata* (Boheman, 1847); *Javesella discolor* (Boheman,

1847); *J. dubia* (Kirschbaum, 1868); *J. forcipata* (Boheman, 1847); *J. obscurella* (Boheman, 1847); *J. pellucida* (Fabricius, 1794); *Kosswigianella denticauda* (Boheman, 1847); *Megadelphax sordidula* (Stål, 1853); *Megamelus notula* (Germar, 1830); *Muellerianella brevipennis* (Boheman, 1847); *Ribautodelphax albostrata* (Fieber, 1866); *R. collina* (Boheman, 1847); *Stiroma affinis* Fieber, 1866; *S. bicarinata* (Herrich-Schäffer, 1835); *Xantodelphax flaveola* (Flor, 1861); *X. straminea* (Stål, 1858) (Hemiptera: Delphacidae).

Additional hosts Known from numerous species of Delphacidae (Kinzelbach, 1978).

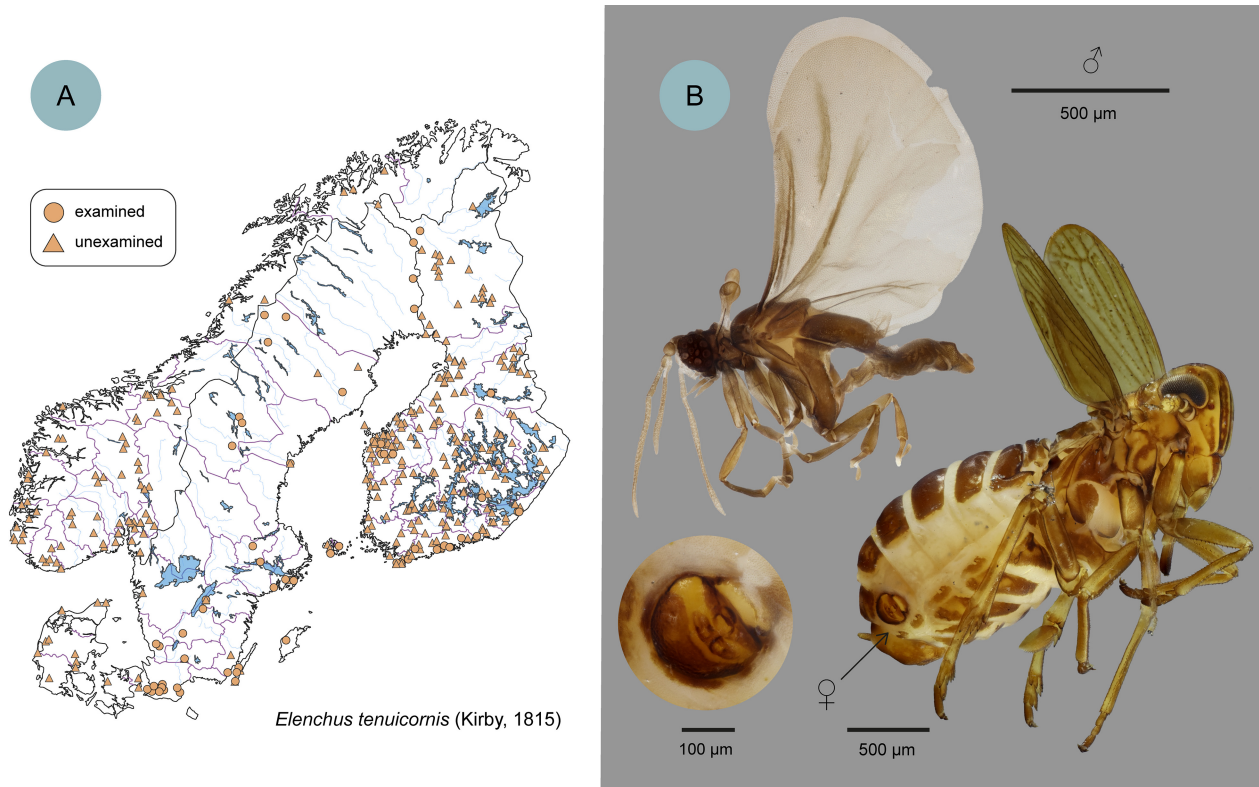


FIGURE 2. Localities of *Elenchus tenuicornis* (Kirby, 1815) in Nordic countries (A) and *E. tenuicornis* male (NHRS-MELA0000000510) and female (NHRS-MELA0000000452) within host (B).

Distribution

Denmark: Nordvestjylland, Nordvestsjælland, Nordøstjylland, Nordøstsjælland, Sønderjylland, Vestjylland, Østjylland.

Finland: Ahvenanmaa, Enontekiön Lappi, Etelä-Häme, Etelä-Karjala, Etelä-Pohjanmaa, Etelä-Savo, Inarin Lappi, Kainuu, Keski-Pohjanmaa, Kittilän Lappi, Perä-Pohjanmaa, Pohjois-Häme, Pohjois-Karjala, Pohjois-Savo, Satakunta, Uusimaa, Varsinais-Suomi.

Norway: Agder, Akershus, Buskerud, Hedmark, Møre og Romsdal, Nordland, Oppland, Oslo, Rogaland, Sør-Trøndelag, Telemark, Troms, Trøndelag, Vestfold, Vestland, Østfold.

Sweden: Bohuslän, Gotland, Halland, Jämtland, Lycksele lappmark, Medelpad, Norrbotten, Skåne, Småland, Södermanland, Torne lappmark, Västerbotten, Västernorrland, Västmanland, Åsele lappmark, Öland, Östergötland.

Habitat Swedish records are from all over the country, and represent a wide range of habitats, though most are open and often grass-dominated (meadows, pastures, marshes, bogs, river edges, mountain heaths, ruderal land, gardens, coastal rocks) and only a few are from woodland sites (both deciduous and coniferous).

Phenology Swedish records are distributed throughout the summer season from May to September with a peak in July. The much larger Finnish material has an earlier peak in June and a relatively small number of late records in August and September. This is the only Nordic Strepsiptera species where both sexes are frequently encountered, and the only species where flying males are documented throughout the season.

Notes The oldest record of *Elenchus tenuicornis* from the Nordic countries is from Denmark in 1868 (Hansen, 1892; Meinert, 1896a). Currently, *E. tenuicornis* is the only recorded *Elenchus* species in Europe.

Halictophagidae

Halictophagus silwoodensis Waloff, 1981 (figure 3)

Halictophagus curtisi sensu auct. (pars).

Nordic hosts *Ulopa reticulata* (Fabricius, 1794) (Hemiptera: Ulopidae).

Additional hosts No additional hosts known.

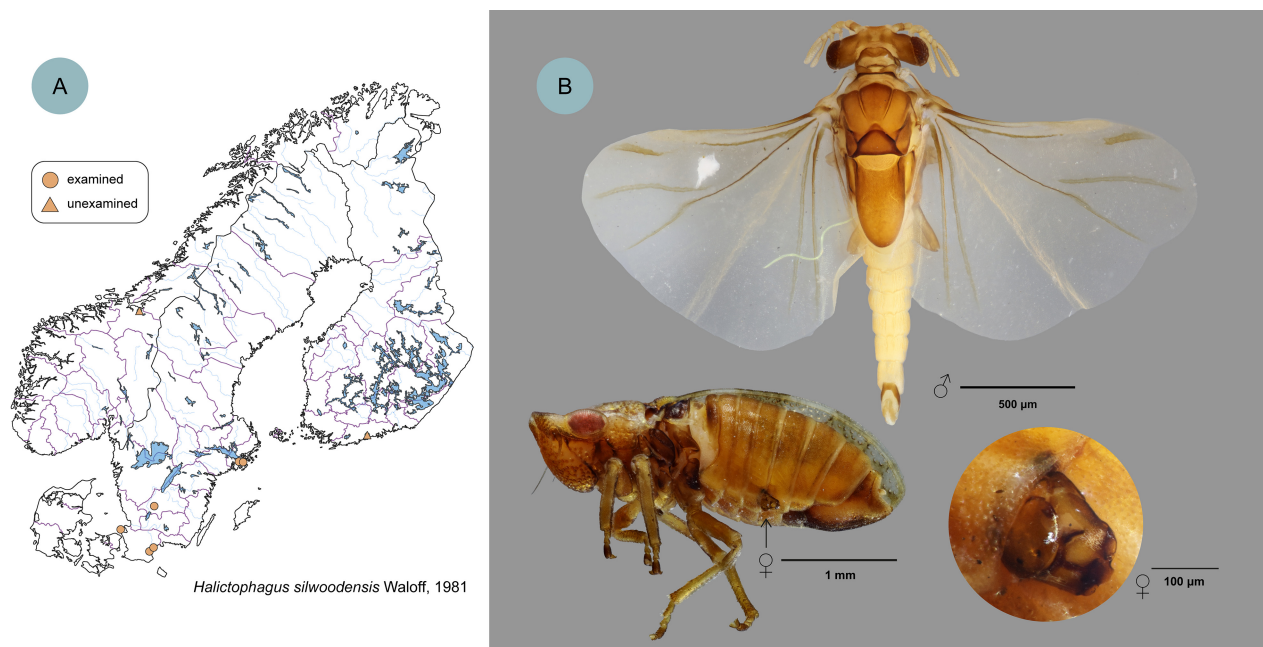


FIGURE 3. Localities of *Halictophagus silwoodensis* Waloff, 1981 in Nordic countries (A) and *H. silwoodensis* male (NHRS-MELA000000454) and female (NHRS-MELA000000460) within host (B).

Distribution

Finland: Uusimaa.

Norway: Trøndelag **New to Norway**.

Sweden: Skåne, Småland, Södermanland.

Habitat Swedish records are from open habitats in the southeast, including sandy pastures as well as bogs in coniferous forests, which makes sense as the host is associated with heather, *Calluna vulgaris*.

Phenology Swedish and Finnish records are from May and June. Free-living males are more commonly encountered than females.

Notes *H. silwoodensis* was first recorded in the Nordic countries from Sweden in 1957 (Heqvist, 1958). At the time, the Swedish specimens were assigned to *Halictophagus curtisi* Dale, 1832 but with remarks of morphological differences between them and of *H. curtisi*. These specimens have been identified as *H. silwoodensis* after the description of the species. Similarly, the first Finnish records from 1963 were first assigned to *H. curtisi* with notes on morphological mismatches and later identified as *H. silwoodensis* (Pekkarinen, 1984; Pekkarinen & Raatikainen, 1973). The new species record for Norway is based on the record in GBIF.

Halictophagus curtisi Dale in Curtis, 1832 (figure 4)

Nordic hosts unknown.

Additional hosts *Eupelix cuspidata* (Fabricius, 1775) (Hemiptera: Cicadellidae).

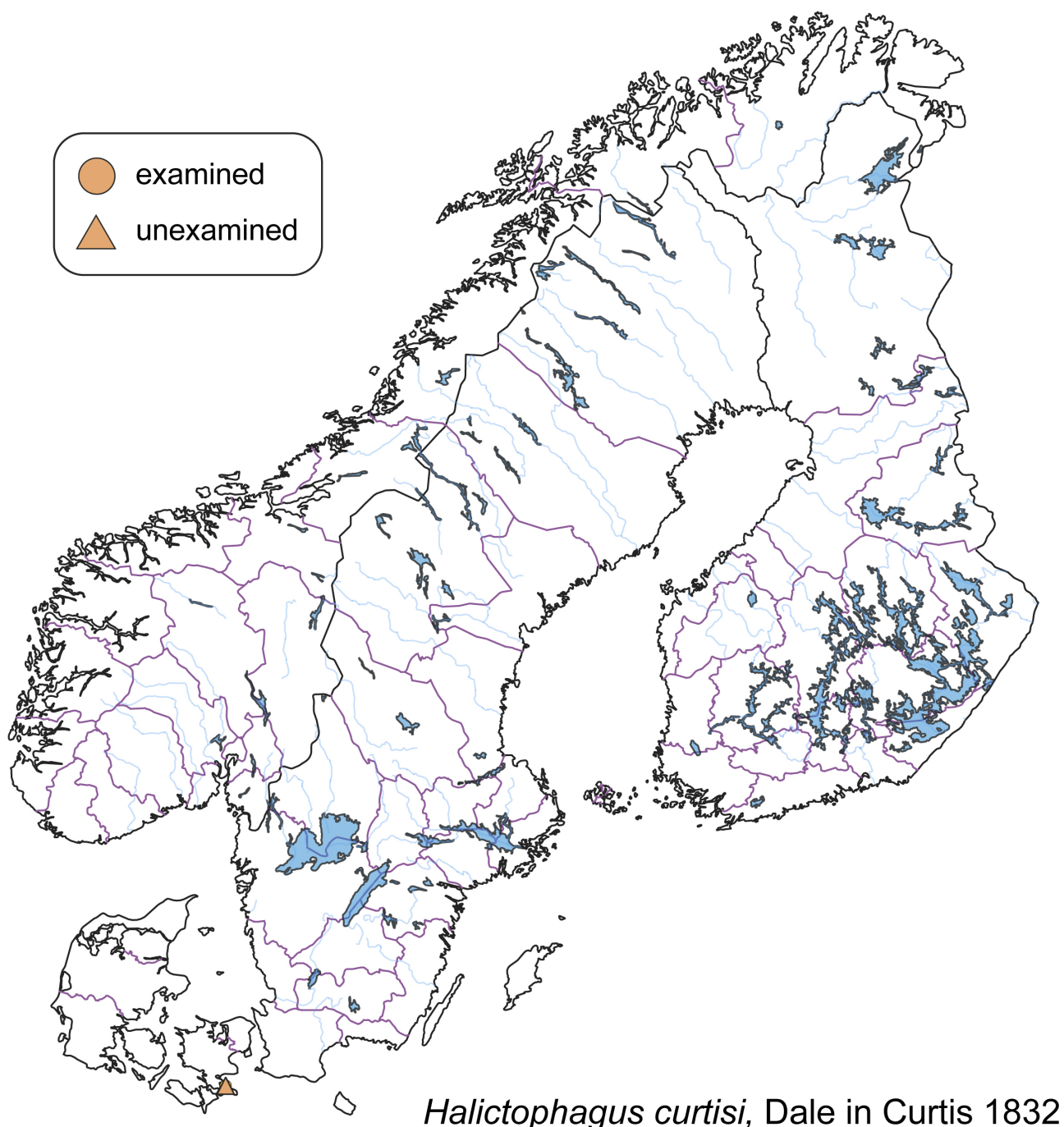


FIGURE 4. Localities of *Halictophagus curtisi* Dale in Curtis, 1832 in Nordic countries.

Distribution

Denmark: Lolland-Falster-Møn.

Habitat -.

Phenology -.

Notes *Halictophagus curtisi* has only been recorded from a single location in Denmark in 2014 (Nielsen & Oyre, 2016). As the only specimen is a male, no host records exist from Nordic countries. The only hypothesized host association of *H. curtisi* is *Eupelix cuspidata* (Fabricius, 1775) (Crowson, 1974) which occurs in all included Nordic countries.

Xenidae

Tuberoxenos spheccidarum (Siebold, 1839) (figure 5)

Xenos spheccidarum Siebold, 1839.

Xenos vesparum var *spheccidarum* Siebold, 1839.

Paraxenos spheccidarum (Siebold, 1839).

Paraxenos sieboldii Saunders 1872.

Pseudoxenos spheccidarum (Siebold, 1839).

Eupathocera spheccidarum (Dufour, 1837).

Nordic hosts *Ammophila pubescens* Curtis, 1836; *A. sabulosa* (Linnaeus, 1758); *Podalonia luffii* (E. Saunders, 1903); *P. hirsuta* (Scopoli, 1763) (Hymenoptera: Sphecidae).

Additional hosts *Ammophila apicalis* Guérin-Méneville, 1835; *A. campestris* Latreille, 1809; *A. dupla* Kohl, 1901; *A. heydeni* Dahlbom, 1845; *A. holosericea* (Fabricius, 1793); *A. nasuta* Lepeletier, 1845; *Podalonia affinis* (Kirby, 1798); *P. dispar* (Taschenberg, 1869); *P. chalybea* (Kohl, 1906); *P. flavida* (Kohl, 1901); *P. ebenina* (Spinola, 1839); *P. nigrohirta* (Kohl, 1888); *P. tydei* (Le Guillou, 1841); *Eremochares dives* (Brullé, 1833); *Prionyx kirbii* (Vander Linden, 1827); *P. viduatus* (Christ, 1791); *P. niveatus* (Dufour, 1854) (Hymenoptera: Sphecidae).

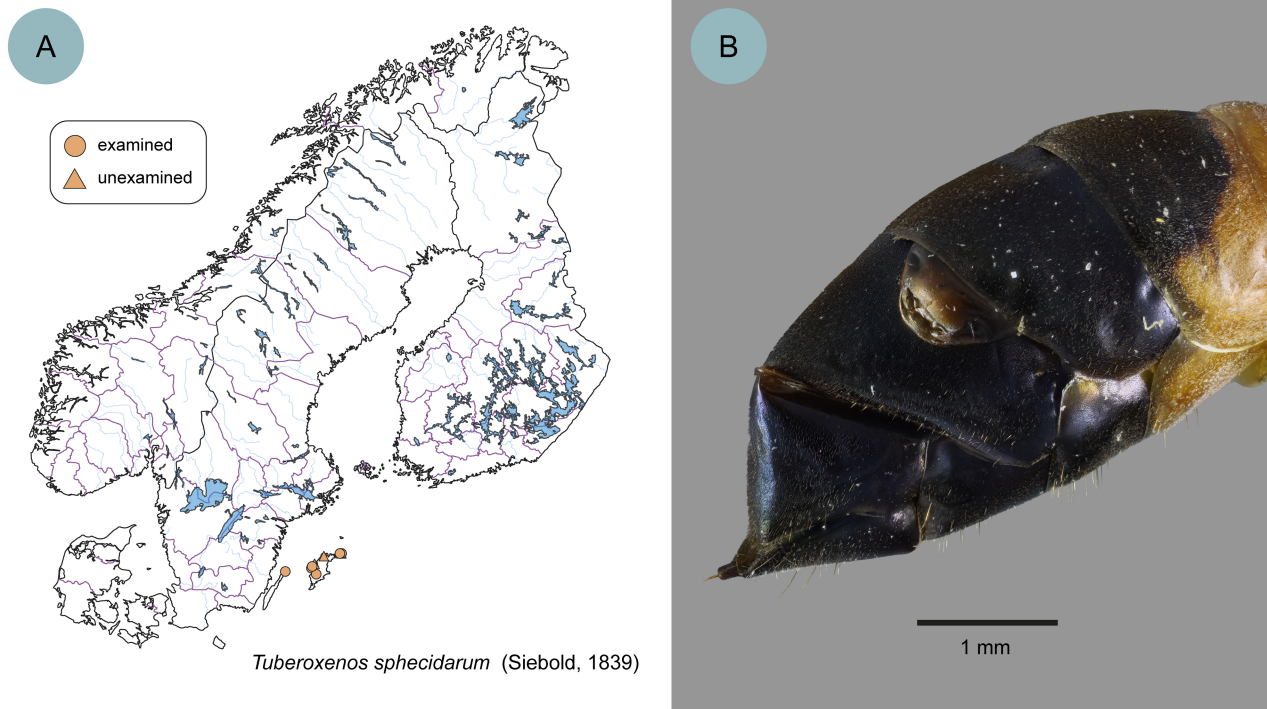


FIGURE 5. Localities of *Tuberoxenos spheccidarum* (Siebold, 1839) in Nordic countries (A) and *T. spheccidarum* female (NHRS-SRAH000009316) extruding between the host tergites (B).

Distribution

Sweden: Gotland, Öland.

Habitat Swedish records are all from very warm sandy areas, sandpits, beaches, and heaths. Considering that large numbers of museum specimens of host species have been scanned for Strepsiptera specimens, it does appear that this is a rare species and its distribution range is limited in Northern Europe despite being associated with common hosts.

Phenology Swedish records are from June to August, mostly July.

Notes The earliest known specimen of *Tuberoxenos spheccidarum* from the current Nordic countries area was recorded in Sweden in 1973. Mäklin (1867) mentions a specimen collected in 1866 in Rautu, which formerly

belonged to Finland but is now in Russian territory. *Tuberoxenos spheccidarum* was moved recently from *Paraxenos* Saunders, 1872 to a new genus *Tuberoxenos* Benda, Pohl, Nakase, Beutel & Straka, 2022 (Benda *et al.*, 2022). Benda *et al.* (2021) proposed at least four distinctive *T. spheccidarum* lineages based on molecular data, possibly representing separate species with different distributions, but refrained from splitting the species due to insufficient sampling. It is not known to which lineage the individuals from Sweden belong, as their dataset did not include specimens from Northern Europe.

Stylopidae

Stylops ater Reichert, 1914 (figures 6, 18B)

Stylops melittae sensu Kinzelbach (pars).

Stylops ovinae Noskiewicz & Poluszynski, 1927 (nomen nudum).

Nordic hosts *Andrena cineraria* (Linnaeus, 1758); *A. vaga* Panzer, 1799 (Hymenoptera: Andrenidae).

Additional hosts Once recorded from *Andrena nigroaenea* (Kirby, 1802) (Jůzová *et al.*, 2015; Straka *et al.*, 2015b) (Hymenoptera: Andrenidae).

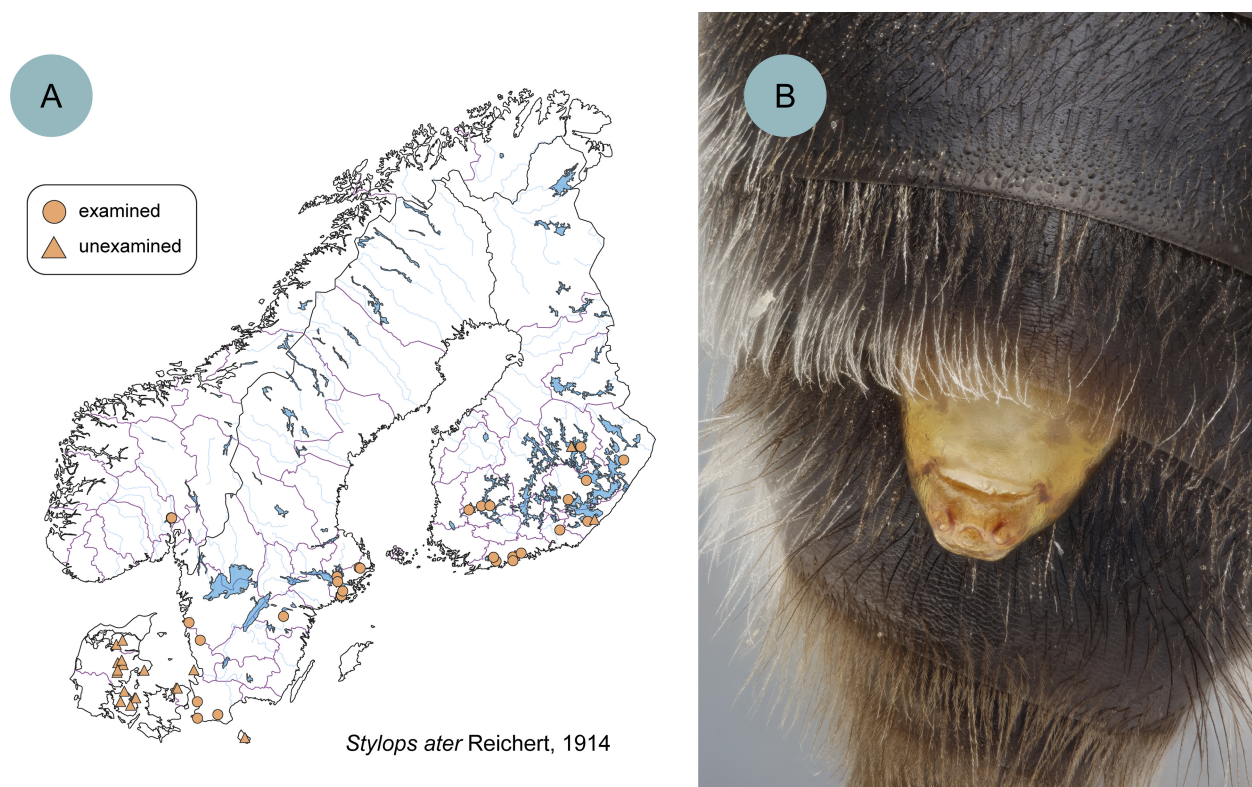


FIGURE 6. Localities of *Stylops ater* Reichert, 1914 in Nordic countries (A) and *S. ater* female (NHRS-MELA000000439) extruding between the host tergites (B).

Distribution

Denmark: Bornholm, Fyn, Nordøstjylland, Nordøstsjælland, Østjylland.

Finland: Etelä-Häme, Etelä-Savo, Pohjois-Karjala, Pohjois-Savo, Satakunta, Uusimaa, Varsinais-Suomi.

Norway: Buskerud.

Sweden: Skåne, Småland, Södermanland, Uppland, Västergötland, Östergötland.

Habitat Swedish records are all from sandy, south-facing slopes, both sandpits, roadsides and patches of bare soil in pastures, where the host species typically have their colonies.

Phenology Swedish records are from spring, ranging from early March to late April (and an outlier in mid-May). Flying males are from a short time period at the beginning of that season, mid to late March depending on latitude, local climate, and the particular year's weather. In frequently visited localities it is often very notable that the male's swarming is limited to a few days.

Notes First recorded from Finland in 1855 (Mäklin, 1866). *Stylops ater* has once been found from *Andrena nigroaenea*, which belongs to the same subgenus *Melandrena* as the primary hosts of *S. ater*. As this species is also a host of *S. melittae* and possibly *S. aterrimus*, the female morphology is used for species identification in addition to host association. These three species can be distinguished from each other (Fig. 18). *Stylops ater* has typically a dark basal band which covers the entire cephalothoracic portion of the first abdominal segment, whereas in the other two species the band is more diffuse (*S. aterrimus*) or narrower and shorter (*S. melittae*). *Stylops aterrimus* has a more compact cephalothorax than the other two species and usually a colour pattern that extends to the mesothorax. *Stylops melittae* typically has darkly pigmented spots on both sides of the birth opening, while on the other species the colouring is not as contrasting against the surrounding areas.

Stylops aterrimus Newport, 1851 (figures 7, 18D)

Stylops melittae sensu Kinzelbach (pars).

Nordic hosts *Andrena tibialis* (Kirby, 1802); *A. scotica* Perkins, 1916, *A. nigrospina* Thomson, 1872 (Hymenoptera: Andrenidae).

Additional hosts *A. trimmerana* (Kirby, 1802); *A. agilissima* (Scopoli, 1770); 6; *A. bimaculata* (Kirby, 1802); *A. bucephala* Stephens, 1846; *A. nigroaenea* (Kirby, 1802) (Hymenoptera: Andrenidae).

Distribution

Denmark: Fyn, Lolland-Falster-Møn, Nordvestsjælland, Nordøstsjælland, Sydsjælland, Sønderjylland, Vestjylland, Østjylland.

Sweden: Skåne.

Notes The oldest known record is Swedish, namely the lectotype of *Andrena nigrospina* Thomson, 1872 (Baker, 1994; Nilsson, 2010). *Andrena nigrospina* is a new host association for *S. aterrimus*, based on the female morphology and molecular evidence (unpublished). *Stylops aterrimus* was described as a parasite of *A. nigroaenea* (Smit *et al.*, 2020). However, as *A. nigroaenea* belongs to a different subgenus than the other hosts of *S. aterrimus*, it is possible that the host has been misidentified. Morphological changes caused by stylopisation can make determination of the host species difficult. *Andrena nigroaenea* is also a host of *S. melittae* and sometimes *S. ater*. See notes under *S. ater*.

Stylops gwynanae Günther, 1957 (figure 18I)

Stylops melittae sensu Kinzelbach (pars).

Nordic hosts *Andrena bicolor* Fabricius, 1775.

Additional hosts *Andrena symphyti* Schmiedeknecht, 1883; *A. granulosa* Pérez, 1902 (Hymenoptera: Andrenidae).

Distribution

Denmark: Precise location unknown.

Notes The earliest known specimen of this species from the Nordic countries was recorded in Denmark in 1924 (Nielsen *et al.*, 2014).

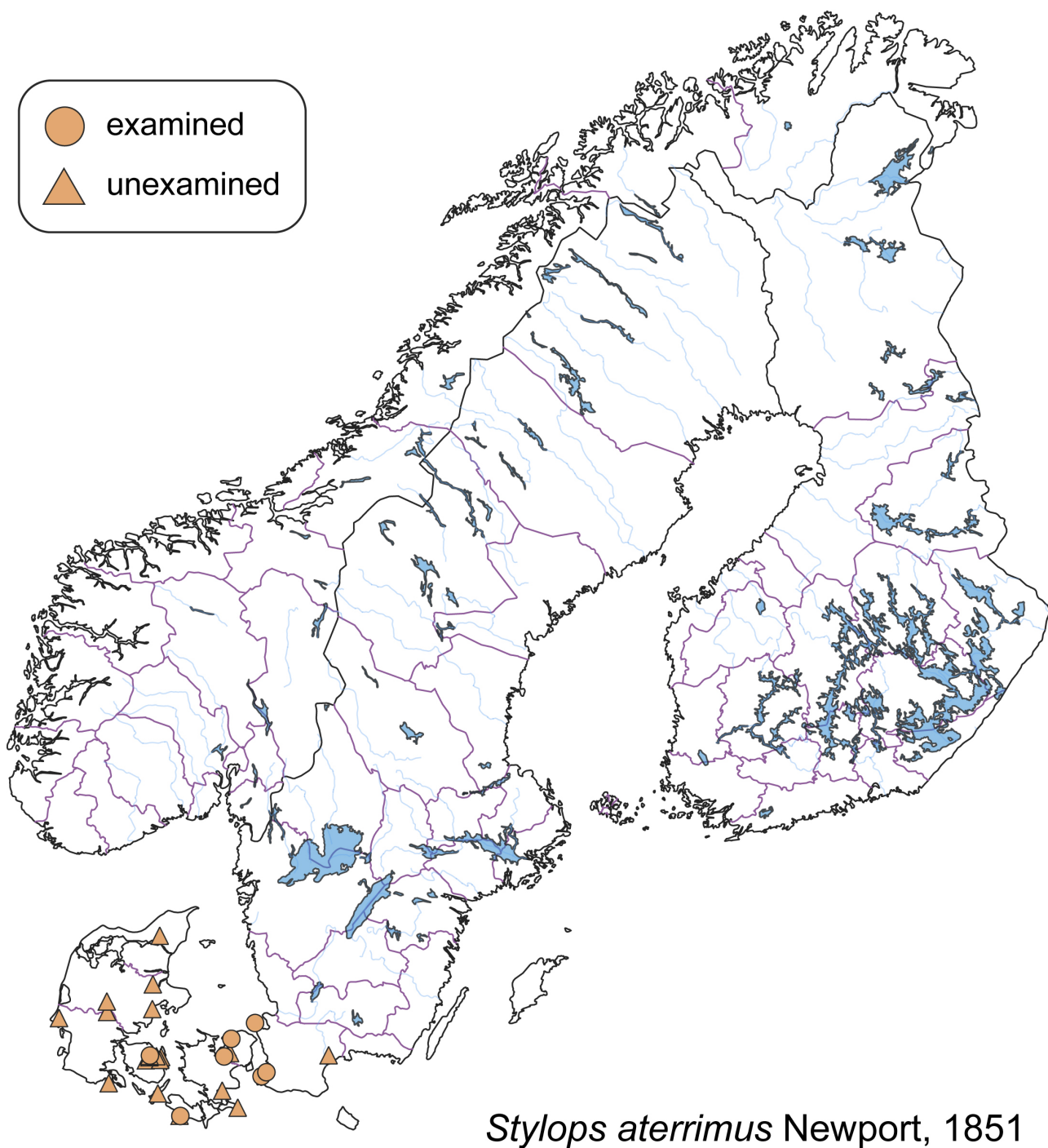


FIGURE 7. Localities of *Stylops aterrimus* Newport, 1851 in Nordic countries.

Stylops melittae Kirby, 1802 (figures 8, 18A)

Nordic hosts *Andrena nitida* (Müller, 1776); *A. flavipes* Panzer, 1799 (Hymenoptera: Andrenidae).

Additional hosts *Andrena soror* (Dours, 1872); *A. thoracica* (Fabricius, 1775); *A. nigroaenea* (Kirby, 1802); *A. gravida* Imhoff, 1832; *A. florentina* Magretti, 1883 (Hymenoptera: Andrenidae).

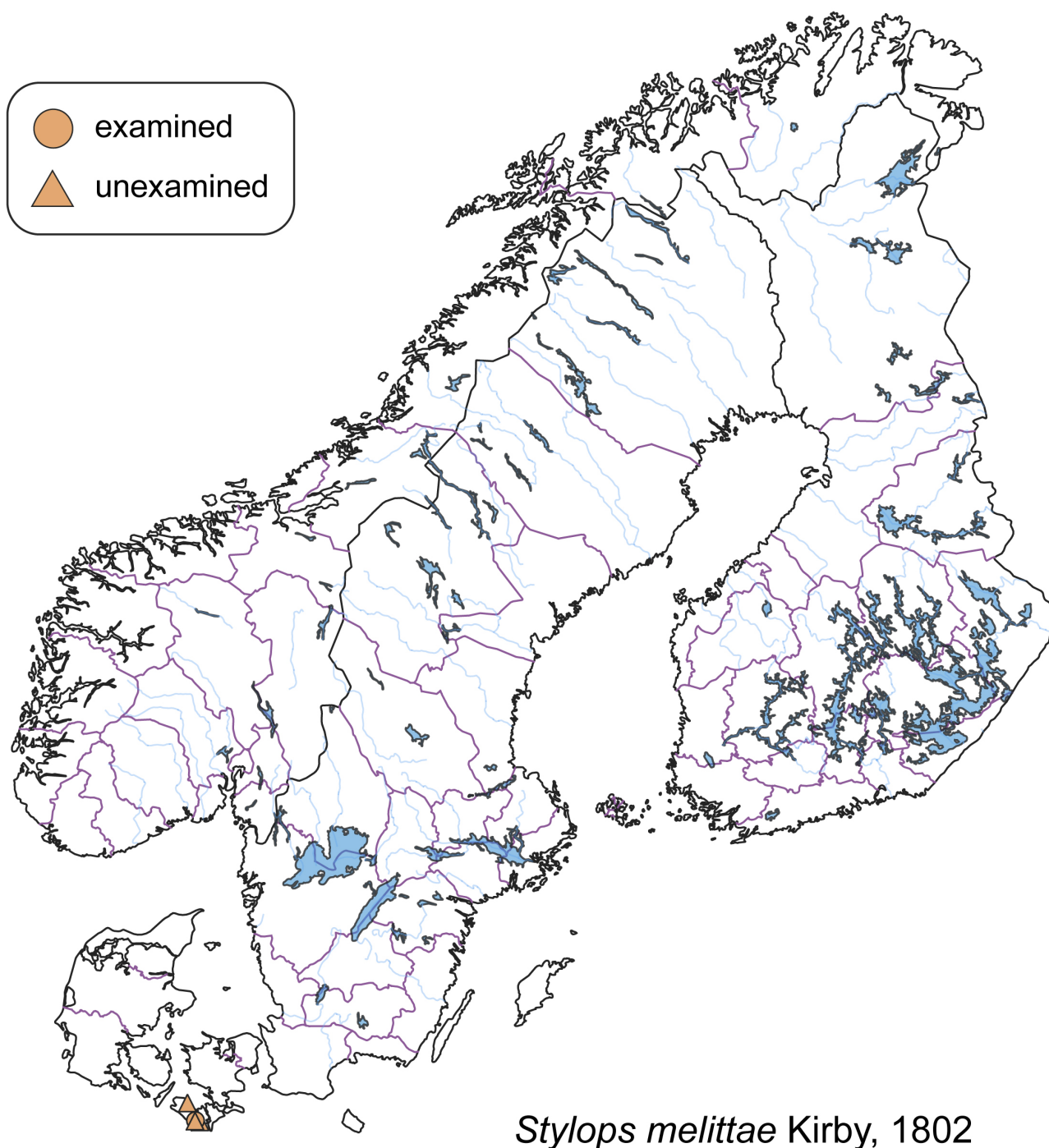


FIGURE 8. Localities of *Stylops melittae* Kirby, 1802 in Nordic countries.

Distribution

Denmark: Lolland-Falster-Møn.

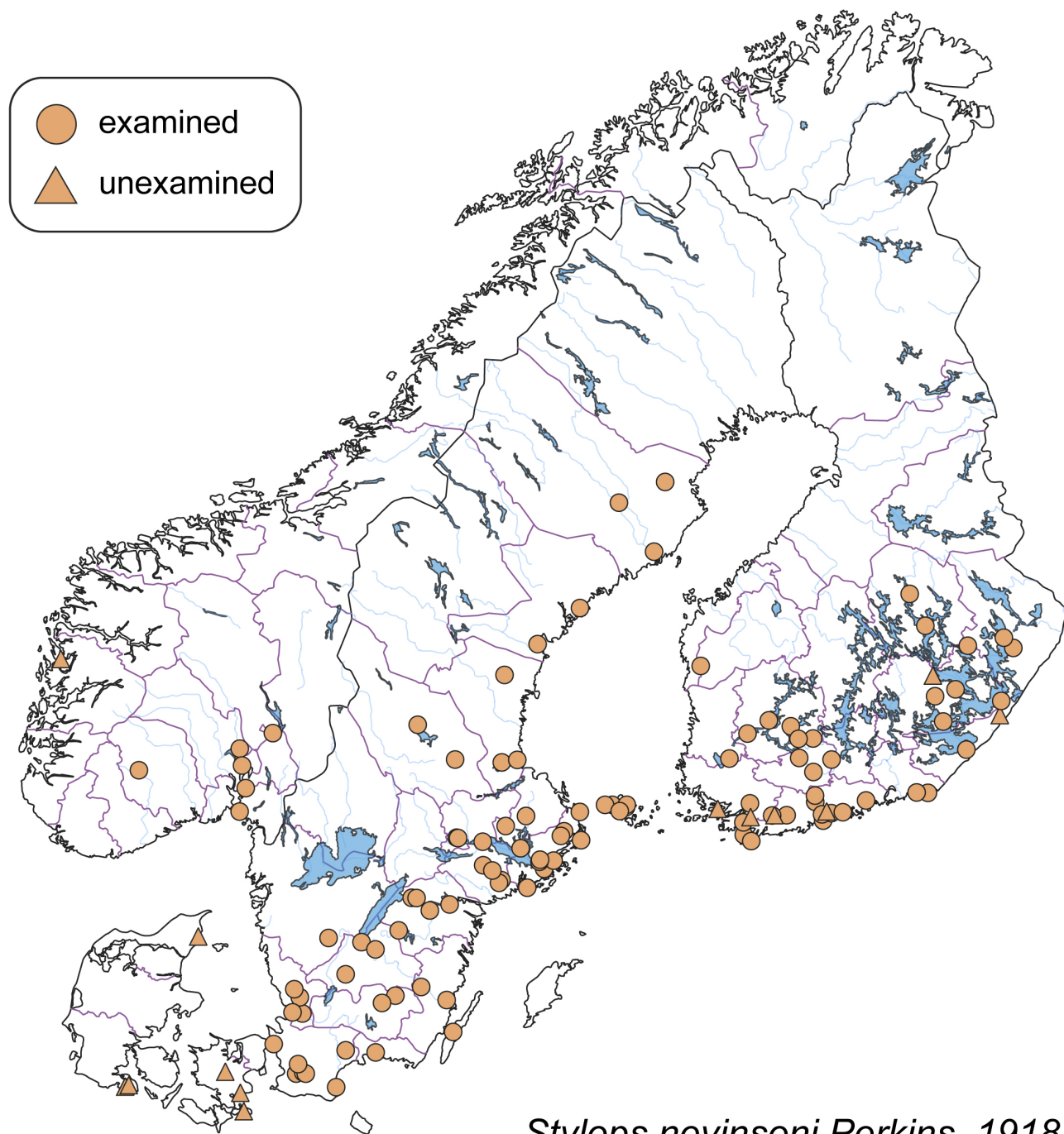
Notes Currently only known from Denmark and the earliest record was collected in 2017. Since all European *Stylops* species were synonymized with *S. melittae* in 1978 (Kinzelbach, 1978), all *Stylops* records from the Nordic countries were assigned to this species until around 2015. *Stylops melittae* possibly shares the host *A. nigroaenea* with *S. aterrimus* and sometimes with *S. ater*. See notes under *S. ater* and *S. aterrimus*.

***Stylops nevinsoni* Perkins, 1918 (figures 9, 18C)**

Stylops melittae sensu Kinzelbach (pars).

Nordic hosts *Andrena fucata* Smith, 1847 (Hymenoptera: Andrenidae).

Additional hosts *Andrena synadelpha* Perkins, 1914; *A. fulva* (Müller, 1766); *A. varians* (Kirby, 1802); *A. helvola* (Linnaeus, 1758) (Hymenoptera: Andrenidae).



***Stylops nevinsoni* Perkins, 1918**

FIGURE 9. Localities of *Stylops nevinsoni* Perkins, 1918 in Nordic countries.

Distribution

Denmark: Lolland-Falster-Møn, Nordøstjylland, Nordøstsjælland, Sydsjælland, Sønderjylland.

Finland: Ahvenanmaa, Etelä-Häme, Etelä-Karjala, Etelä-Pohjanmaa, Etelä-Savo, Keski-Pohjanmaa, Laatokan Karjala, Pohjois-Karjala, Pohjois-Savo, Satakunta, Uusimaa, Varsinais-Suomi.

Norway: Akershus, Buskerud, Hordaland, Telemark, Østfold.

Sweden: Blekinge, Dalarna, Gästrikland, Halland, Hälsingland, Medelpad, Skåne, Småland, Södermanland, Uppland, Västerbotten, Västergötland, Västmanland, Ångermanland, Östergötland.

Habitat Swedish records are from a variety of localities, including gardens, pastures, meadows and semi-open forest, reflecting the broad ecological range of the host species.

Phenology Swedish records are from late May to mid-July. A single male was collected in early June.

Notes The oldest known specimen from the Nordic countries is from Finland, dated to 1866.

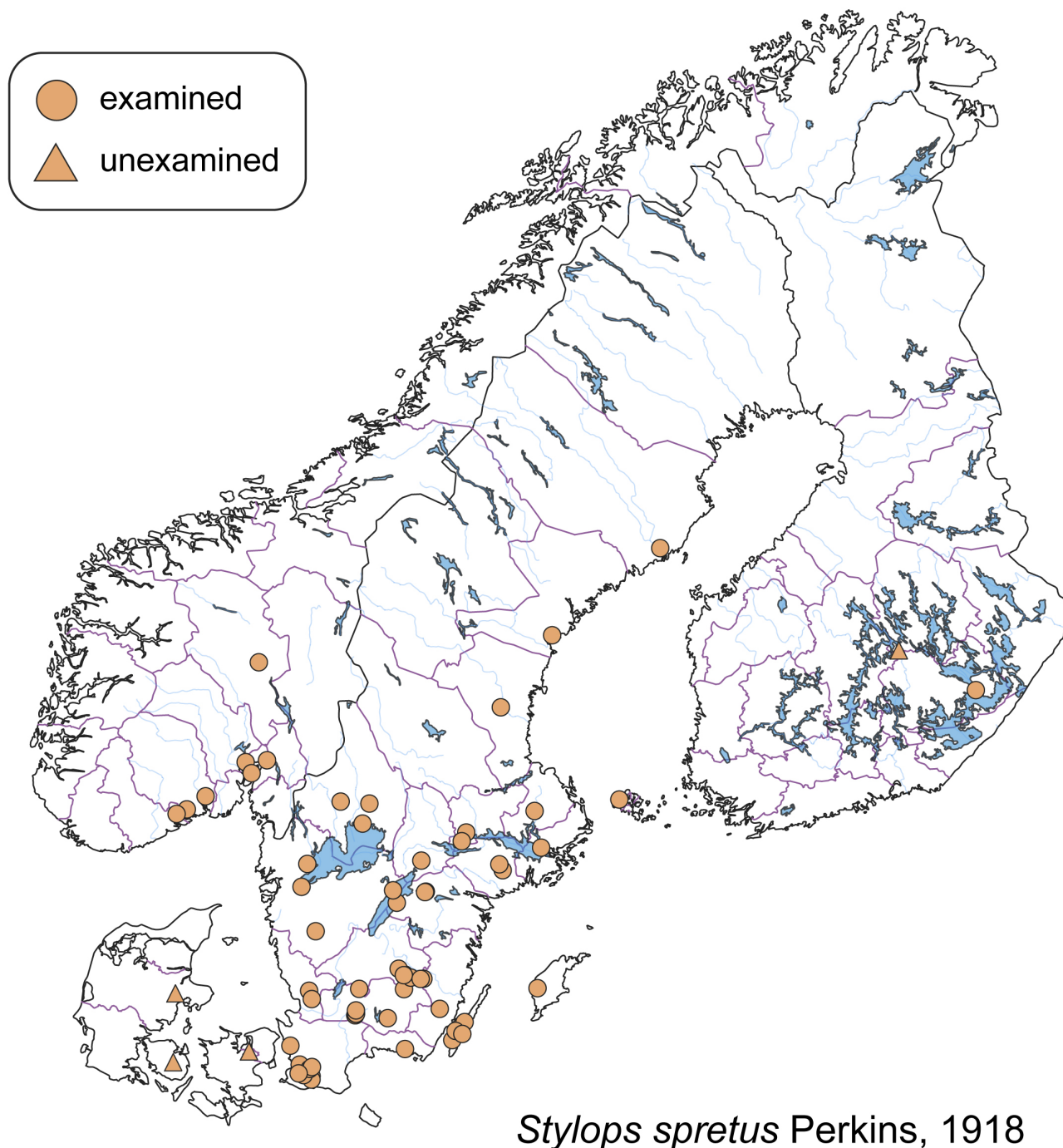


FIGURE 10. Localities of *Stylops spretus* Perkins, 1918 in Nordic countries.

***Stylops spretus* Perkins, 1918 (figures 10, 18G)**

Stylops spreta Perkins, 1918.

Stylops melittae sensu Kinzelbach (pars).

Nordic hosts *Andrena falsifica* Perkins, 1915; *A. minutula* (Kirby, 1802); *A. minutuloides* Perkins, 1914; *A. niveata* Friese, 1887; *A. semilaevis* Pérez, 1903; *A. subopaca* Nylander, 1848 (Hymenoptera: Andrenidae).

Additional hosts *Andrena tenuistriata* Pérez, 1895; *A. strohmella* E. Stöckert, 1928; *A. simontornyella* Noskiewicz, 1939, *A. pusilla* Pérez, 1903 (Hymenoptera: Andrenidae).

Distribution

Denmark: Fyn, Nordøstsjælland, Østjylland.

Finland: Ahvenanmaa, Etelä-Savo, Pohjois-Häme.

Norway: Agder, Akershus, Innlandet, Oslo, Telemark.

Sweden: Blekinge, Dalsland, Gotland, Halland, Hälsingland, Närke, Medelpad, Skåne, Småland, Södermanland, Uppland, Värmland, Västerbotten, Västergötland, Västmanland, Öland, Östergötland.

Habitat Swedish records are from a range of habitats, but frequently open and sandy areas.

Phenology Swedish records are from early May to early July. One male was collected in late May.

Notes The oldest known specimen is from Sweden, collected in 1922. The name of this species has variously been cited as *Stylops spreta* and *S. spretus*, and in the recent checklist of Straka *et al.* (2015) *spretus* was explicitly considered an unjustified emendation without further discussion. It is sometimes a delicate question to decide which words are adjectives, which need gender agreement with the genus name, and which words should preferably be considered as nouns in apposition and thus indeclinable. Here, the name is an adjective, but it would seem that Perkins did not consider it a description of this species but an unusual way of referring to the name of an *Andrena* species, but he failed to mention this explicitly. In that case, §26 of the zoological code (ICZN 1999) applies, what looks like a normal latin adjective should be treated as one.

***Stylops thwaitesi* Perkins, 1918 (figures 11, 18E)**

Stylops melittae sensu Kinzelbach (pars).

Stylops wilkellae Perkins, 1918.

Nordic hosts *Andrena afzeliella* (Kirby, 1802); *A. gelriae* van der Vecht, 1927; *A. intermedia* Thomson, 1870; *A. wilkella* (Kirby, 1802); *A. ovatula* (Kirby, 1802). (Hymenoptera: Andrenidae).

Additional hosts *A. russula* Lepeletier, 1841 (Hymenoptera: Andrenidae).

Distribution

Denmark: Nordvestjylland, Sønderjylland, Vestjylland.

Finland: Etelä-Häme, Etelä-Savo, Pohjois-Karjala, Uusimaa, Varsinais-Suomi.

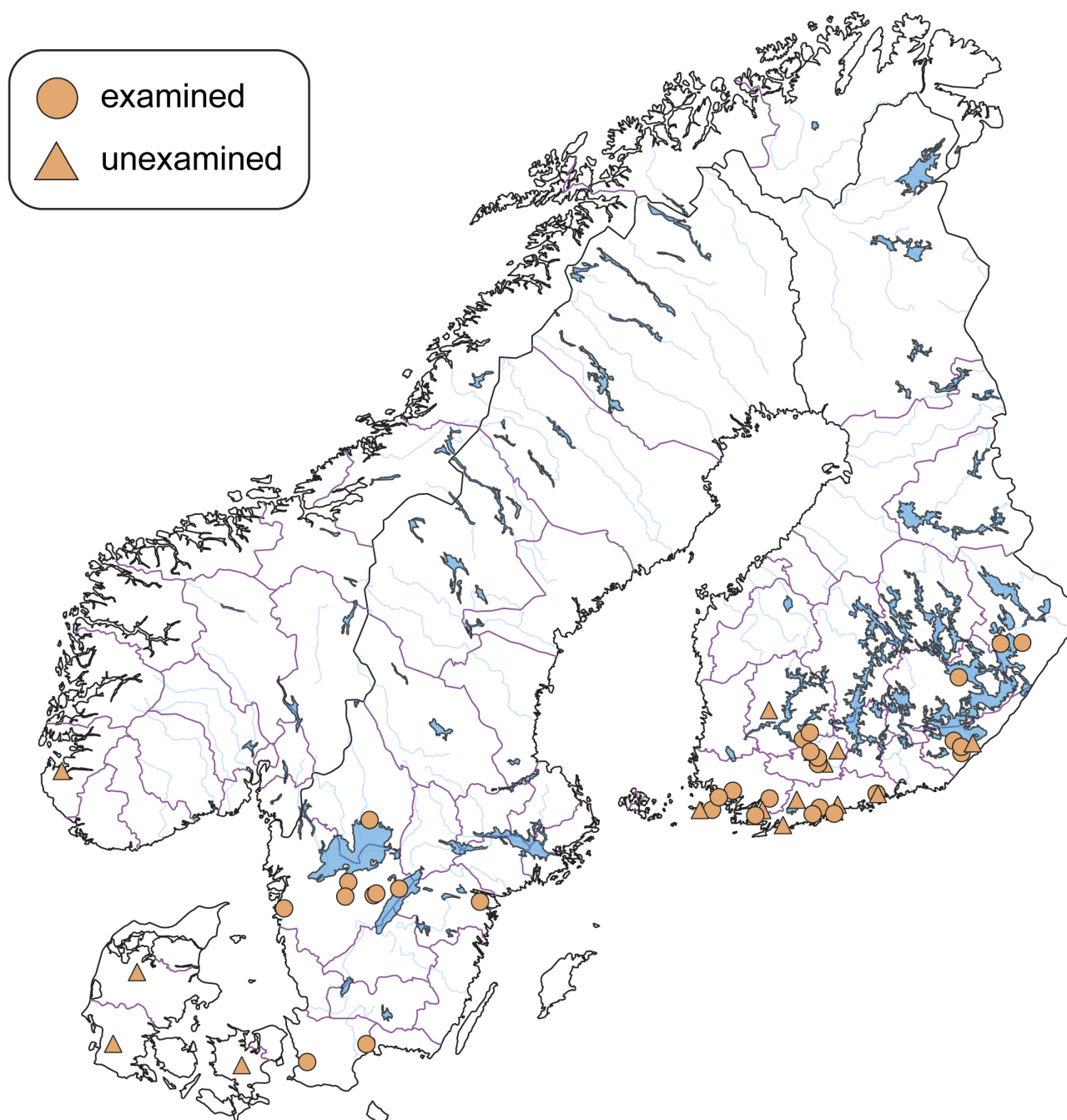
Norway: Rogaland.

Sweden: Bohuslän, Skåne, Värmland, Västergötland.

Habitat Swedish records are from warm, sandy open areas, reflecting the habitat preferences of the host species.

Phenology Swedish records are from late May to mid-June. One male was collected in late May.

Notes The oldest known specimen was collected in Finland in 1914. It can be noted that there are two specimens in MZLU on bee hosts collected by E. Munck af Rosenschöld in Lund, Sweden, without detailed locality information but before 1840 (probably early 1830s). Together with a specimen of *Stylops sapmiensis* **sp. nov.** on a bee collected by Boheman probably in 1836, these are the oldest preserved Nordic Strepsiptera specimens currently known—but they were all undetected until now.



Stylops thwaitesi Perkins, 1918

FIGURE 11. Localities of *Stylops thwaitesi* Perkins, 1918 in Nordic countries.

Stylops sapmiensis sp. nov. Lähteenaro & Bergsten (figures 12, 13, 14, 18F)

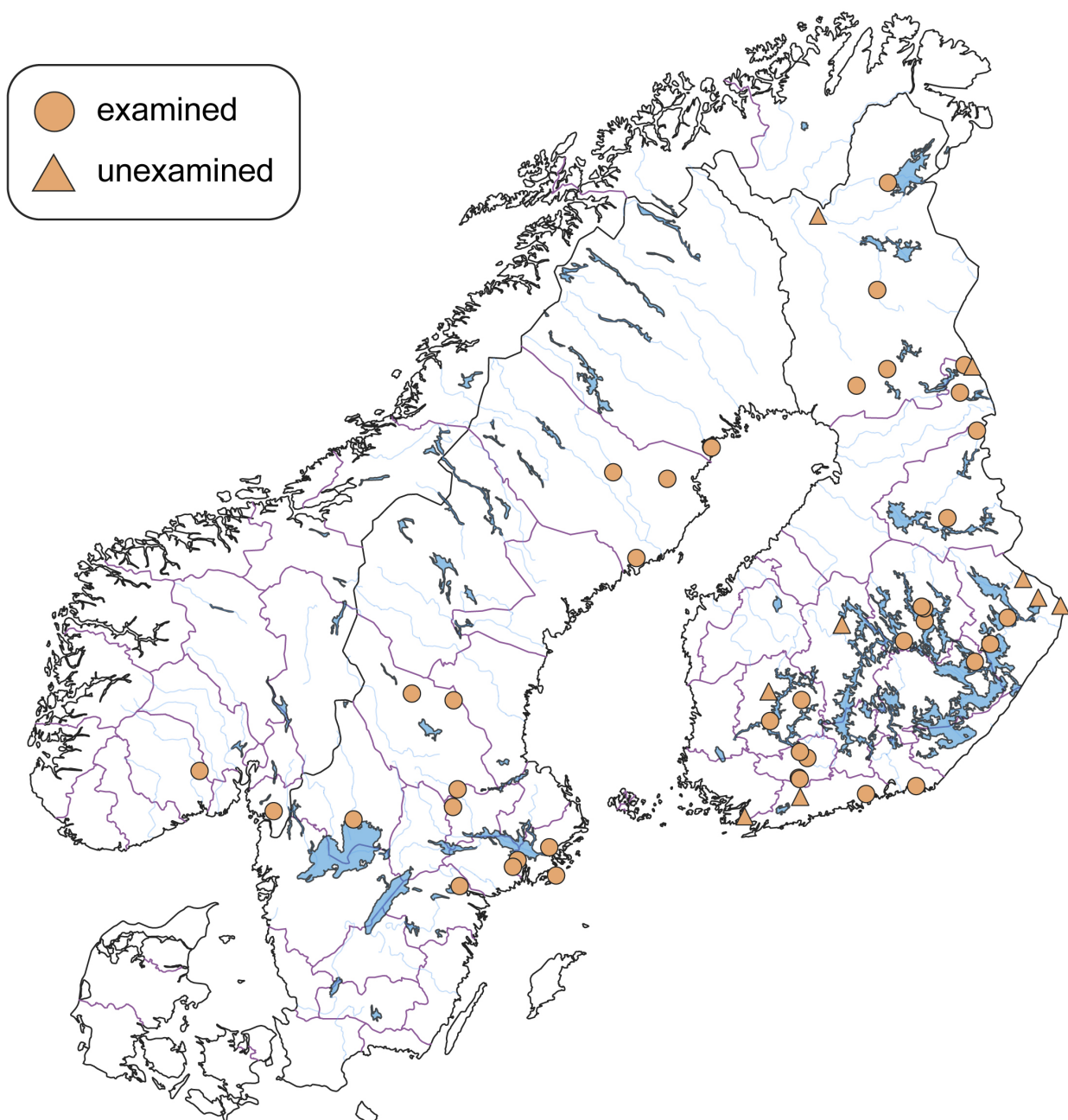
Nordic hosts *Andrena lapponica* Zetterstedt, 1838 (Hymenoptera: Andrenidae).

Additional hosts No additional hosts known.

Distribution

Norway: Østfold, Telemark.

Finland: Enontekiön Lappi, Etelä-Häme, Etelä-Karjala, Inarin Lappi, Kainuu, Koillismaa, Perä-Pohjanmaa, Pohjois-Häme, Pohjois-Karjala, Pohjois-Savo, Sompion Lappi, Uusimaa, Varsinais-Suomi.



Stylops sapmiensis sp. nov. Lähteenaro & Bergsten

FIGURE 12. Localities of *Stylops sapmiensis* Lähteenaro & Bergsten sp. nov. in Nordic countries.

Sweden: Dalarna, Lycksele lappmark, Norrbotten, Södermanland, Uppland, Värmland, Västerbotten, Västmanland, Ångermanland.

Distribution outside Nordic countries Estonia, Poland, Germany, Czechia.

Habitat Swedish records are from forest sites, reflecting the habitat preferences of the host.

Phenology Swedish records are from mid-April to early July.

Notes It has been unclear whether European *Andrena lapponica* is parasitized by the same species (*Stylops japonicus* Kifune & Hirashima, 1985) as the Eastern Palearctic subspecies *Andrena lapponica shirozui* Hirashima, 1962. However, phylogenomic methods (Lähteenaro *et al.*, 2024b) and morphological examinations have confirmed that while the European species is closely related to *S. japonicus* (Lähteenaro *et al.*, 2024a), it differs enough from it to constitute its own separate species. The first confirmed stylopization of *Andrena lapponica* in Nordic countries

is from Finland in 1910 (Hellén, 1935a). However, a specimen from Sweden lacking the collection date probably predates this based on other collecting event information (likely from 1836).

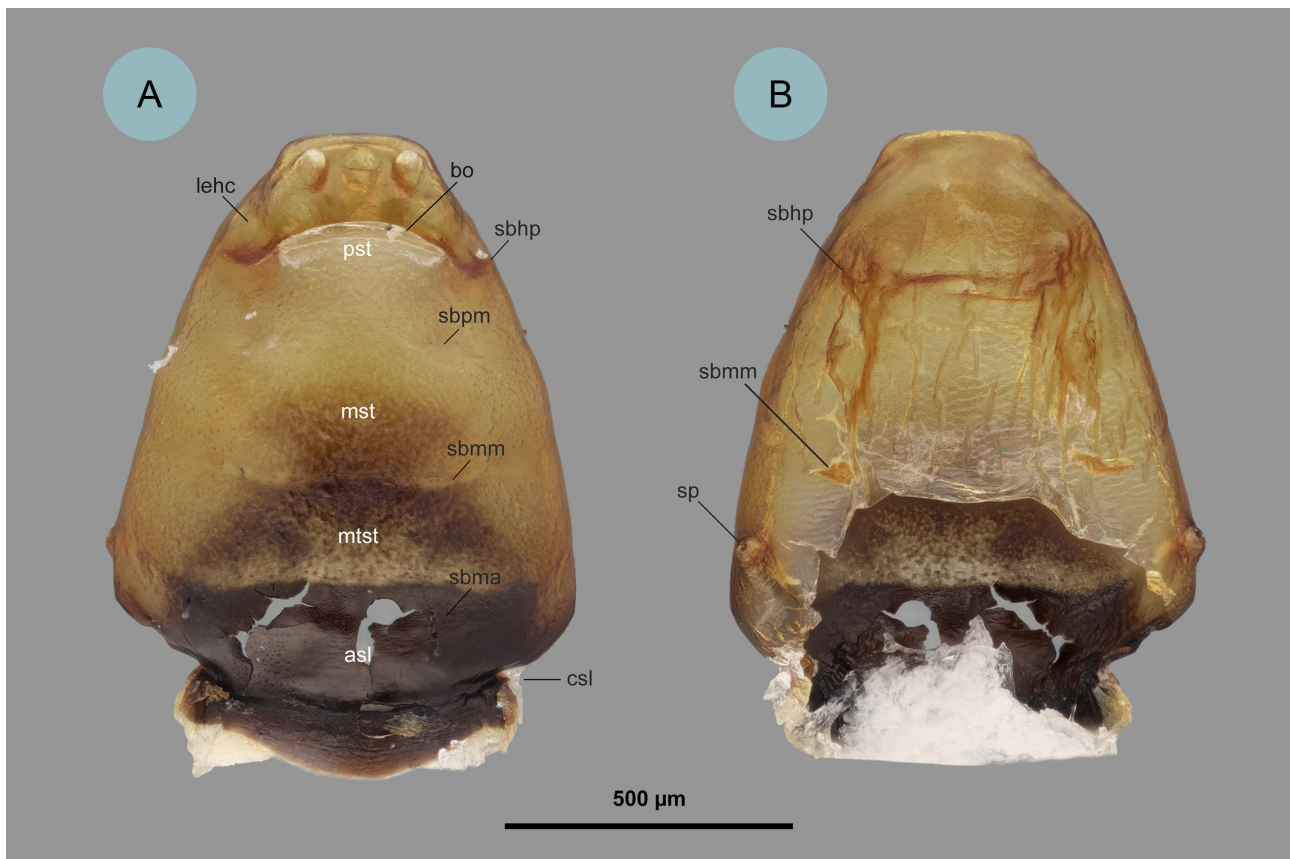


FIGURE 13. Holotype of *Stylops sapmiensis* Lähteenaro & Bergsten **sp. nov.** NHRS (NHRS-SVHE000102811), female cephalothorax. A. Ventral side of cephalothorax; B. Dorsal side of cephalothorax. Abbreviations: asl—abdominal segment I, bo—birth opening, csl—constriction of abdominal segment I, lehc—lateral extension of head capsule, mst—mesosternum, mtst—metasternum, pst—prosternum, sbhp—segmental border between head and prothorax, sbmm—segmental border between mesothorax and metathorax, sbpm—segmental border between prothorax and mesothorax, sbma—segmental border between metathorax and abdomen, sp—spiracle.

Type material

Holotype: 1 ♀ (NHRS-SVHE000102811, NHRS, mounted cephalothorax, abdomen not preserved): Sweden, Ångermanland; Votmyrbäcken, Hallen, Nordmaling/ 11–14.vi.2005/ leg. A. Nilsson. Host: *Andrena lapponica* Zetterstedt, 1838.

Paratypes: 2 ♀♀ (SLp47, JSPC, mounted cephalothorax, abdomen not preserved): Poland; Gozdnica /12–16.iv.2015/ leg. K. Kodejš & J. Straka. 1 ♀ (SLp2, JSPC, mounted cephalothorax, abdomen not preserved): Germany, Wildenthal; Sachsen/ 09.vi.2004 / leg. F. Burger. 1 ♀ (SLp27, JSPC, mounted cephalothorax, abdomen not preserved): Poland; Gozdnica/ 12.–16.iv.2015 / leg. K. Kodejš & J. Straka. 1 ♀ (SLp28, JSPC, mounted cephalothorax, abdomen not preserved): Poland; Gozdnica / 12.–16.iv.2015 / leg. K. Kodejš & J. Straka. 1 ♀ (SLp30, JSPC, mounted cephalothorax, abdomen not preserved): Poland; Gozdnica ; / 12.–16.iv.2015 / leg. K. Kodejš & J. Straka. 27 ♀♀ (SLp31, SLp32, SLp46, JSPC, NMPC): Poland; Gozdnica / 12.–16.iv.2015 / leg. K. Kodejš & J. Straka. 1 ♀ (GNM-HYME000016495b, GNM): Sweden, Södermanland; Ornö/ 22.v.1946 / leg. J. Skovgaard. 1 ♀ (NHRS-MELA000000002, NHRS): Sweden, Västerbotten; Fjnnforsfallet/ 7.vii. 2006/ leg. S. Hellqvist. 1 ♀ (NHRS-MELA000000003, NHRS): Sweden, Uppland; Östra Ryd/ 16.iv.1952 / leg. S. Erlandsson. 1 ♀ (NHRS-MELA000000084, MZLU, mounted cephalothorax, abdomen not preserved): Sweden, Lycksele Lappmark; Ruskträsk, Lycksele/ 7.vi.1996 / leg. M. Sörensson. 1 ♀ (NHRS-MELA000000464, NHRS): Sweden, Värmland; Sörmons grusgrop, Karlstad/ 15.v.2022/ leg. J. Persson. 1 ♂ (NHRS-SRAH000009294, NHRS):

Sweden, Västerbotten; Finnforsfallet/ 7.vii.2006 / leg. S. Hellqvist. 1 ♀ (NHRS-SRAH000009323, NHRS, mounted cephalothorax, abdomen not preserved): Sweden, Västmanland; Halvarsenbenning/ 14.vi.1990/ leg. J. Abenius. 1 ♀ (NHRS-SRAH000009486, NHRS): Sweden, Södermanland; Ekorrtorp/ 8.vi.1989 / leg. L. Norén. 1 ♀ (NHRS-SRAH000009488, NHRS): Sweden, Södermanland; Nysätter/ 1.v.1993 / leg. L. Norén. 1 ♀ (NHRS-SRAH000009490, NHRS): Sweden, Dalarna; [No precise locality information available] / leg. C. H Boheman. 1 ♀ (NHRS-SRAH000009492, NHRS): Sweden, Västmanland; Skinnskatteberg/ vi.1959 / leg. C. B. Gaunitz. 1 ♀ (NHRS-SRAH000009494, NHRS): Sweden, Uppland; Östra Ryd/ 16.iv.1952 / leg. S. Erlandsson. 1 ♀ (NHRS-SRAH000009570, NRM, mounted cephalothorax, abdomen not preserved): Sweden, Norrbotten; Pitholmsheden/ 21.vii.2015 / leg. S. Andersson. 1 ♀ (NHRS-SRAH000009572, NHRS, mounted cephalothorax, abdomen not preserved): Sweden, Norrbotten; Pitholmsheden / 10.vii.2018 / leg. D. Evander. 1 ♀ (NHRS-SVHE000102809, NHRS): Sweden, Dalarna; Trollmosseskogen/ leg. L.-O. Wikars. 1 ♂ (NHRS-SVHE000102810, NHRS): Sweden, Dalarna; Trollmosseskogen/ vi.2005–vii.2005 / leg. L.-O. Wikars. 1 ♀ (KZ.6, MZH): Finland, Pohjois-Savo; Savonranta /21.v–18.vi.1996 / leg. P. Martikainen. 1 ♀ (KZ.113, MZH): Finland, Etelä-Häme; Pirkkala/ 8.vi.1910 / leg. T. Grönbloom. 1 ♀ (KZ.78, MZH): Finland, Perä-Pohjanmaa; Rovaniemen mlk. / 3.vii.1935 / leg. E. Kangas. 1 ♂ (KZ.12, MZH): Finland, Inarin Lappi; Inari/ 7.vi.1947 / leg. W. Hellén. 2 ♀♀ (KZ.114, MZH): Finland, Pohjois-Savo; Kuopio/ 23.vi.1948 / leg. R. Elfving. 2 ♀♂ (KZ.5, MZH): Finland, Etelä-Häme; Hattula/ 5.vi.1953/ leg. E. Valkeila. 3 ♀♀ (KZ.8, MZH): Finland, Etelä-Häme; Vanaja/ 28.v.1954 / leg. E. Valkeila. 1 ♀ (KZ.117, MZH): Finland, Pohjois-Savo; Siilinjärvi/ 14.vii.1954 / leg. R. Elfving. 1 ♀ (KZ.116, MZH): Finland, Pohjois-Karjala; Liperi/ 21.vi.1958 / leg. R. Elfving. 1 ♀ (KZ.3, MZH): Finland, Etelä-Häme; Hattula/ 10.v.1959 / leg. E. Valkeila. 2 ♀ (KZ.115, MZH): Finland, Pohjois-Savo; Suonenjoki/ 9.vi.1963/ leg. R. Elfving. 1 ♀ (KZ.4, MZH): Finland, Etelä-Häme; Hattula/ 28.v.1964 / leg. E. Valkeila. 1 ♀ (KZ.1, MZH): Finland, Etelä-Karjala; Vehkalahti/ 16.vi.1966 / leg. L. Fagerström & B. Fagerström. 2 ♀ (KZ.77, MZH): Finland, Koillismaa; Kuusamo/ 19.vii.1982/ leg. J. Viramo. 1 ♀ (KZ.6, MZH): Finland, Pohjois-Savo; Savonranta/ 21.v–18.vii.1996 / leg. P. Martikainen. 1 ♀ (KZ.7, MZH): Finland, Perä-Pohjanmaa; Tervola/ 28.v.–24.vi.1996 / leg. P. Martikainen. 1 ♀ (KZ.9, MZH): Finland, Perä-Pohjanmaa; Tervola/ 28.v.–24.vi.1996 leg. P. Martikainen. 1 ♀ (KZ.204, MZH): Finland, Kainuu; Sotkamo/ 16.v.–23.v.2001 / leg. R. Leinonen & G. Söderman. 1 ♀ (KZ.11, MZH): Finland, Etelä-Häme; Loppi/ 1.–15.vi.2005 / leg. S. Karjalainen & J. Salminen. 1 ♀ (KZ.13a, MZH): Finland, Etelä-Häme; Loppi/ 1.–15.vi.2005 / leg. S. Karjalainen & J. Salminen. 1 ♀ (KZ.13b, MZH): Finland, Etelä-Häme; Loppi/ 1.–15.vi.2005 / leg. S. Karjalainen & J. Salminen. 1 ♀ (KZ.13c, MZH): Finland, Etelä-Häme; Loppi/ 1.–15.vi.2005 / leg. S. Karjalainen & J. Salminen. 1 ♀ (KZ.2, MZH): Finland, Etelä-Häme; Juupajoki/ 25.vi.2015 / leg. I. Terä. 1 ♀ (KZ.169, MZH): Finland, Kainuu; Kontiolahti/ 14.vi.2016 / leg. M. Pajari. 1 ♀ (KZ.170, MZH): Finland, Kainuu; Suomussalmi/ 14.vi.2017/ leg. R. Leinonen.

All hosts: *Andrena lapponica* Zetterstedt, 1838.

Diagnosis

Two other sympatric *Stylops* species parasitize the same nominotypical subgenus *Andrena* as *S. sapmiensis*: *Stylops nevinsoni* and *Stylops praecocis* Noskiewicz & Poluszynski, 1928. *Stylops sapmiensis* can be distinguished from them by a combination of its colouration pattern and typical shape of the cephalothorax (Fig. 13). Typically, the cephalothorax of *S. sapmiensis* is slightly more elongated than those of *S. nevinsoni* and *S. praecocis* and its head capsule narrows apically more in relation to the rest of the cephalothorax (not so prominent in the holotype specimen). The dark basal band of *Stylops nevinsoni* is more angular than the semicircular pattern observed in *S. sapmiensis* and, unlike that of *S. sapmiensis*, does not extend to mesothorax (Fig. 18C). In *S. praecocis*, the diffused dark brown colouration extends ventrally to the lateral margins but does not typically reach the mesothorax. *Stylops sapmiensis* lacks clearly constricted meso-metathoracic and meso-prothoracic segmental borders laterally, which are typically present in *S. praecocis* and sometimes in *S. nevinsoni*. *Stylops sapmiensis* can be distinguished from the Eastern Palaearctic *Stylops japonicus* parasitizing species from subgenus *Andrena* by its more semicircular pattern of colouration in the meso-metathoracic region and less elliptical ventral field of labrum.

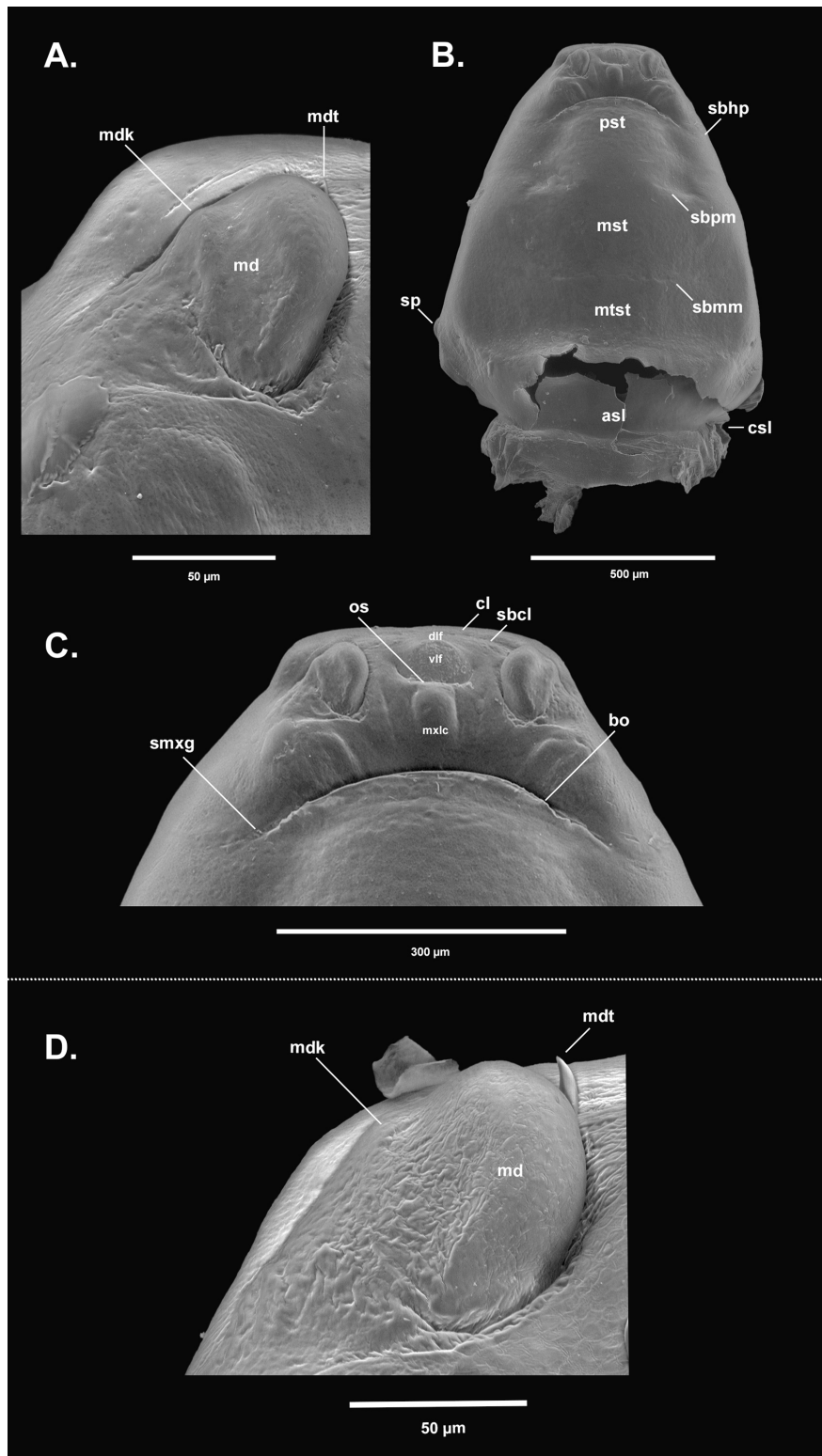


FIGURE 14. Holotype of *Stylops sapmiensis* Lähdenaro & Bergsten **sp. nov.** NHRS (NHRS-SVHE000102811) female (A–C) and paratype JSPC SLp47 female (D), SEM micrographs of cephalothorax. A. Mandible, ventral side; B. Cephalothorax, ventral side; C. Mouthparts, ventral side; D. Mandible of the paratype with better view of the mandible tooth. Abbreviations: bo—birth opening, csl—constriction of abdominal segment I, cl—clypeus, dlf—dorsal labral field, vlf—ventral labral field, md—mandible, mdt—mandibular tooth, mdk—mandible knob, mst—mesosternum, mtst—metasternum, mxlc—maxillolabial complex, os—mouth opening, pst—prosternum, sbhp—segmental border between head and prothorax, sbmm—segmental border between mesothorax and metathorax, sbpm—segmental border between prothorax and mesothorax, sbcl—segmental border between clypeus and labrum, sp—spiracle, smxg—submaxillary groove.

Description

Based on female cephalothorax.

Shape and colouration

Shape of the cephalothorax elongated, longer than wide [length of holotype 0.99 mm (all examined material 0.96–1.13 mm), width 0.78 mm (0.78–1.04)]. Thorax widening posteriorly, head typically clearly narrowing apically, creating subtriangular shape (less prominent in the holotype, variable). Meso-metathoracic and meso-prothoracic segmental borders slightly constricted laterally (sbpm, sbmm, Fig. 13A). Abdominal segment I very slightly protruding laterally. Colouration of the ventral side of the cephalothorax varies from dark brown to golden yellow (Fig. 13A). Basal band clear, angular, not extending to the lateral margins, extending to metathorax. Pigmentation pattern in metathorax semicircular, dark brown marginally, pale centrally with dark spots. Mesothorax with light brown colouration medially.

Head

Head width 0.48 mm (0.48–0.59 mm), length including the lateral extensions 0.22 mm (0.21–0.32 mm), about 1/4 of the entire cephalothorax length. Often narrowing notably apically until the mandibular area. Colouration of the ventral side largely golden yellow, darker pigmentations laterally around segmental border between head and prothorax. Clypeus clearly limited from labral area by a groove, numerous clypeal sensilla present, surface shiny (sbcl, cl, Fig. 14C). Apical margin of clypeal area varies from blunt (holotype) to slightly arcuate. Lateral extensions elongated. Segmental border between head and prothorax limited ventrally by birth opening medially and by sutures laterally. On the dorsal side delimited by a pigmented suture (sbhp, Fig. 13A,B).

Antenna

Absent. Vestige not investigated.

Labrum

Ventral field of labrum semi-elliptic in holotype, but variable, sometimes almost rounded, slightly raised, smooth (vlf, Fig. 14C). Dorsal slightly wrinkled (dlf, Fig. 14C).

Mandible

Anteromedially directed at an angle of 50° (md, Fig. 14A,D). Cuticle slightly rugose at the base, distally smooth. Mandibular knob distinctly raised, often pigmented (mdk, Fig. 14A,D). Mandibular tooth sharp, long and curved, base in the dorsal surface of the mandible, often partially obscured in ventral view (mdt, Fig. 14A,D).

Mouth opening

Mouth opening (OS, Fig. 14C) arcuate laterally, straight medially.

Maxillo-labial complex

Maxilla fused with labial area, establishing a maxillo-labial complex (mxlc, Fig. 14C). Maxilla slightly raised, with vertical ridges. Submaxillary groove inconspicuous, fused with the border between head and prothorax. Labial area raised, slightly protruding towards apex, delimited anteriorly by mouth opening, posteriorly by birth opening.

Birth opening

Birth opening slightly arcuate (bo, Figs. 13A, 14C), prothoracic extension produced forward, lateral head extensions elongated (lech, Fig. 13A).

Thorax

Pro-mesothoracic and meso-metathoracic borders somewhat distinct ventrally, indicated by mesal furrows (sbpm, sbmm, Fig. 13A). Dorsally meso-metathoracic border distinct and indicated by pigmented furrows, pro-mesothoracic mesal furrows more or less indistinct (sbpm, sbmm, Fig. 13B). Cuticle of the thorax reticulate and punctured ventrally. In dorsal view shiny, with deep parallel pigmented wrinkles.

Abdominal segment I and spiracles

Cephalothoracic part of sclerotized abdominal segment I dark brown medially, laterally golden yellow. Differs from metathorax by more rugose cuticular structure. Dorsally pale, limited from metathorax by furrow. Spiracles elevated with latero-dorsal or lateral orientation (sp, Figs. 13A, 14B).

Molecular data

Whole-genome sequencing raw data for the holotype available at Sequence Read Archive (accession number SRR33345357, <https://www.ncbi.nlm.nih.gov/sra>) and mitochondrial COI at BOLD database (Process ID: NOSTR002-25, <https://boldsystems.org/>).

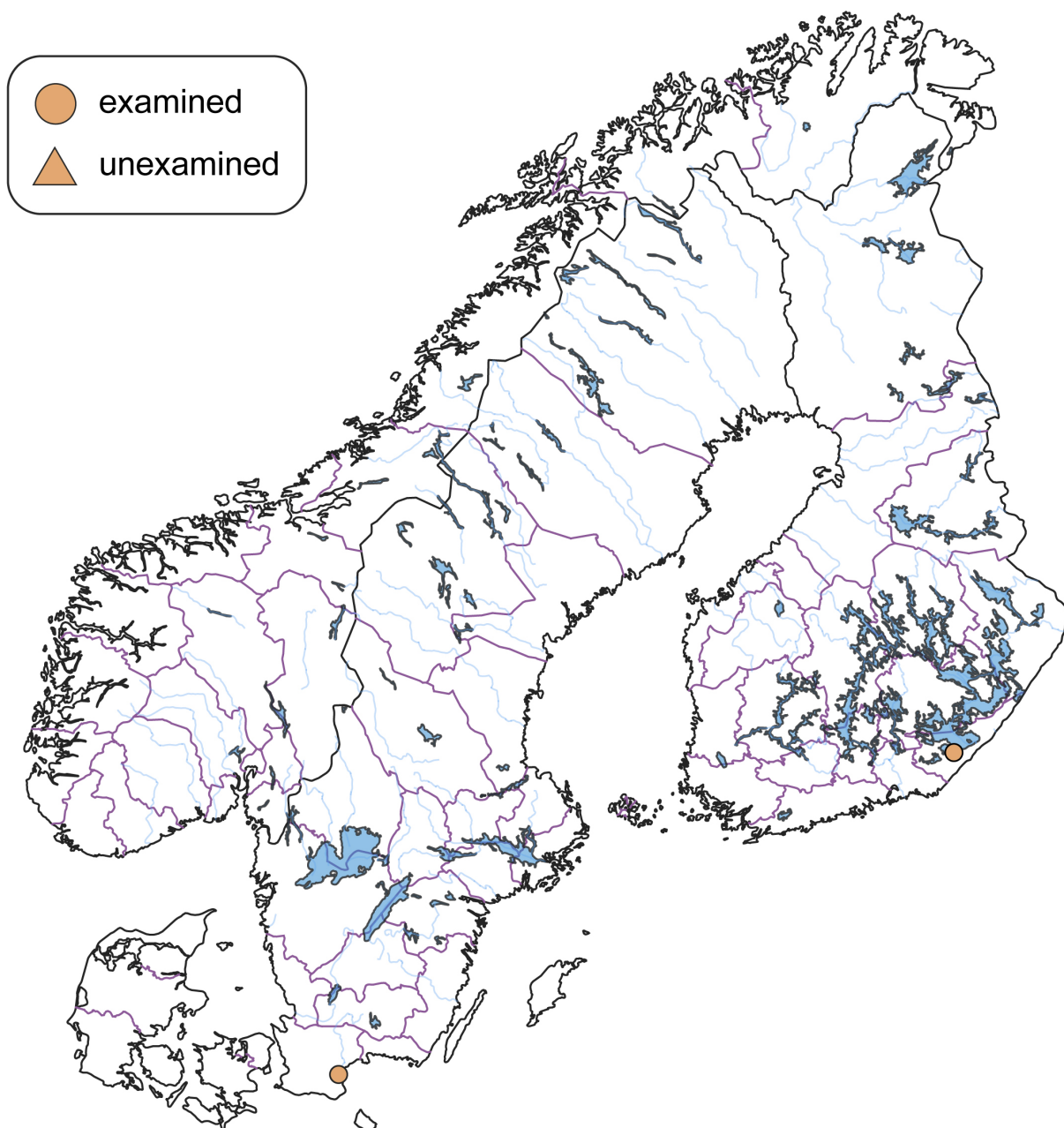
Etymology

Refers to Sápmi Land, area in northern Fennoscandia inhabited by the Sámi people (Sámi, Sápmi) which is the preferred local name of the same area referred to as Lapponia in the name of the host species. The area represents the northernmost known distribution of the species. Adjective.

Stylops serotinus sp. nov Lähteenaro & Straka (figures 15, 16, 17, 18H)

Nordic hosts *Andrena fuscipes* (Kirby, 1802) (Hymenoptera: Andrenidae).

Additional hosts. None known, but possibly *Andrena denticulata* (Kirby, 1802) from the same subgenus (*Cnemiantrena*), which has been reported to be stylopized (Kinzelbach, 1978; Zettel, 2018). Kinzelbach (1978) also included a drawing of the female cephalothorax which is close to the morphology of *Stylops serotinus*. However, further research is needed to confirm the association, as the two bee species have different diets and slightly divergent phenologies.



Stylops serotinus sp. nov. Lähteenaro & Straka

FIGURE 15. Localities of *Stylops serotinus* Lähteenaro & Straka **sp. nov.** in Nordic countries.

Distribution

Finland: Etelä-Savo.

Sweden: Skåne.

Distribution outside Nordic countries Austria, Russia.

Notes Phylogenomic species delimitation methods unambiguously support *Stylops* parasitizing *A. fuscipes* as being an undescribed species (Lähteenaro *et al.*, 2024b). The oldest specimen from the Nordic countries is from Sweden, collected in 1930.

Type material

Holotype

1 ♀ (KZ.163, MZH, mounted cephalothorax, abdomen not preserved): Finland, Etelä-Savo; Lappeenranta, Lauritsila/16.vii.1964/ leg. R. Elfving. Host: *Andrena fuscipes* (Kirby, 1802) (Hymenoptera: Andrenidae).

Paratypes

1 ♀ (NHRS-MELA000000146, MZLU, mounted cephalothorax, abdomen not preserved): Sweden, Skåne: Maglehem / 13.viii.1930 / leg. D. Gaunitz. 2 ♀♀ (KZ.192, ZMUT): Russia, Kivennapa / leg. J. Lounaanmaa. 1 ♀ (SFp1, KUNHM971799): Austria; Moosburg / 14.viii.1955/ leg. D. Baker & M. Baker. 1 ♀ (SFp2, KUNHM971805): Austria; Moosburg / 05.ix.1955/ leg. D. Baker & M. Baker.

Hosts: *Andrena fuscipes* (Kirby, 1802) (Hymenoptera: Andrenidae).

Diagnosis

The species is distinguishable from other members of *Stylops* by the ratio of cephalothorax length and width (wider than long), by irregularly rugose structure (best visible in SEM images) and pale colouration of the anterior intermandibular space (Figs. 16, 17). *Stylops serotinus* can be distinguished from sometimes similarly compact *Stylops aterrimus* by lack of brown colouration outside 1st abdominal segment (basal band) and by a blunt mandibular tooth. *Stylops aterrimus* usually has conspicuous colouration pattern in mesothorax and metathorax and a sharp mandibular tooth (Fig. 18D). *Stylops serotinus* is also a smaller species (cephalothorax length 0.68–0.85) than *S. aterrimus* ($\bar{x}$ = 1.2 mm in Straka *et al.*, 2015a). *Stylops serotinus* can be distinguished from the Nearctic species *Stylops nubeculae*, which parasitizes hosts from the same subgenus *Cnemiandrena*, by blunter mandibular tooth and colouration. *Stylops nubeculae* also have a more sharply defined, laterally angular basal band.

Description

Based on female cephalothorax.

Shape and colouration

Shape of cephalothorax compressed and subtriangular, clearly wider than long, length of the holotype cephalothorax 0.68 mm (all examined material 0.68–0.85 mm), width 0.8 mm (0.8–1.06 mm) (Figs. 16, 17B). Thorax widening posteriorly, with the widest point at the level of spiracles. Anterior head margin protruding very slightly from the remaining head capsule, blunt. Meso-metathoracic and meso-prothoracic segmental borders slightly constricted laterally (sbpm, sbmm, Fig. 16A). Abdominal segment I very slightly protruding laterally (asI, Fig. 16A). Ventral side of cephalothorax mostly golden and pale yellow, slightly darker laterally. Basal band light brown, limited to abdominal segment I and diffuses towards the apex of it, reaches lateral margins. Paler colouration in the labral area in relation to the rest of the head.

Head

Head width 0.49 (all examined material 0.49–0.63), length including the lateral extensions 0.19 mm (0.19–0.23 mm), roughly 1/4 of the entire cephalothorax length. Colouration mostly golden yellow, distinctively paler in labral area, slightly darker pigmentation in area along the segmental border between head and prothorax. Clypeus clearly

delimited from labral area by colour and texture, but without an inconspicuous groove in the border, numerous clypeal sensilla present, surface shiny (cl, Fig. 17C). Apical margin of head capsule blunt. Segmental border between head and prothorax limited ventrally by birth opening medially and sutures laterally (sbhp, Fig. 16A). On dorsal side, delimited by a suture (sbhp, Fig. 16B).

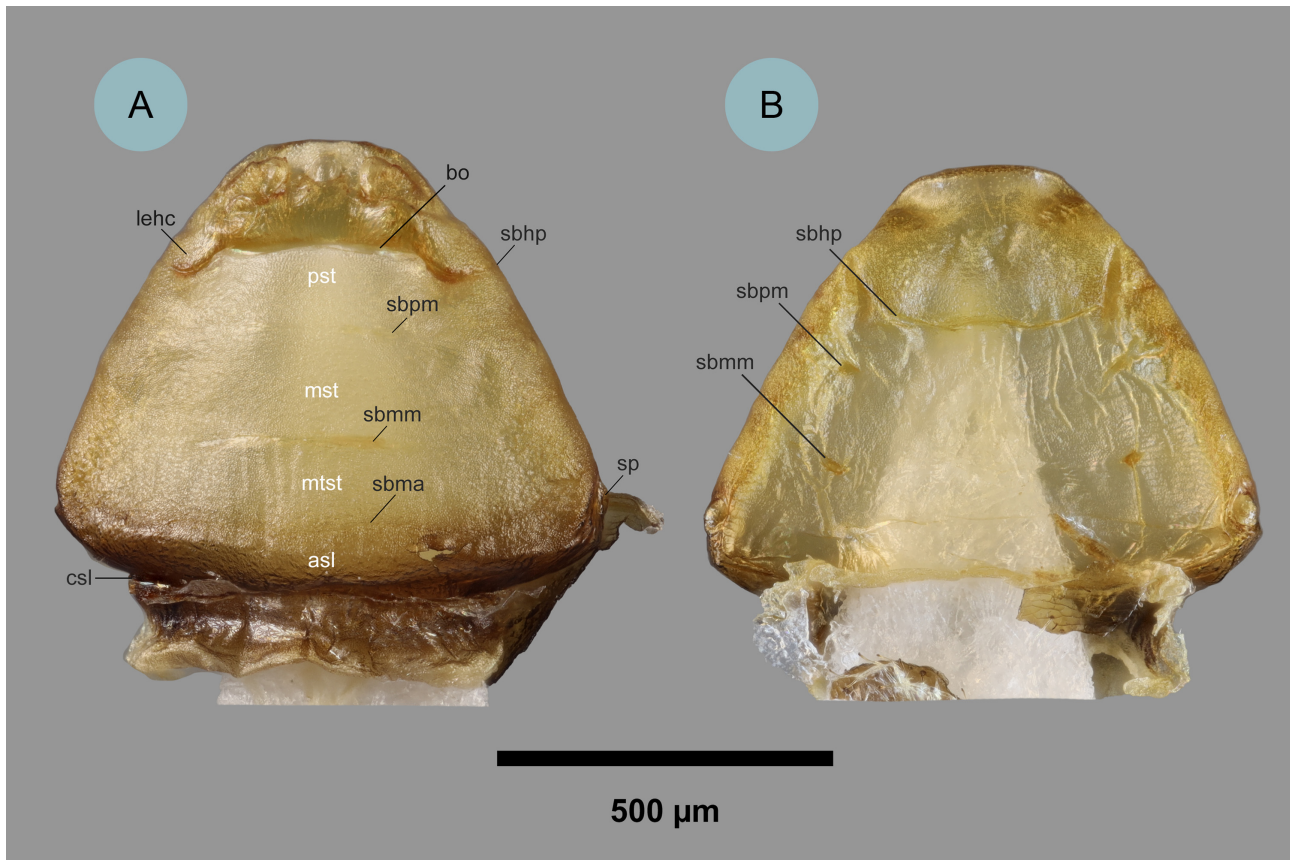


FIGURE 16. Holotype of *Stylops serotinus*. Lähteenaro & Straka **sp. nov.** MZH (KZ.163) female cephalothorax. A. Ventral side of cephalothorax; B. Dorsal side of cephalothorax. Abbreviations: asI—abdominal segment I, bo—birth opening, csl—constriction of abdominal segment I, lehc—lateral extension of head capsule, mst—mesosternum, mtst—metasternum, pst—prosternum, sbhp—segmental border between head and prothorax, sbmm—segmental border between mesothorax and metathorax, sbpm—segmental border between prothorax and mesothorax, sbma—segmental border between metathorax and abdomen, sp—spiracle.

Antenna

Absent. Vestige not investigated.

Labrum

Ventral field elliptic and protruding, raised medially, smooth (vfl, Fig. 17C). Dorsal field corrugated, surrounded by irregularly rugose sculptured intermandibular space (dlf, Fig. 17C).

Mandible

Anteromedially directed at an angle of about 35° (md, Fig. 17A). Cuticle irregularly rugose at the base, distally smooth. Mandibular knob more or less distinctly raised (mdk, Fig. 17A). Mandibular tooth directed apically, widened, slightly blunt, gently curved (mdt, Fig. 17A).

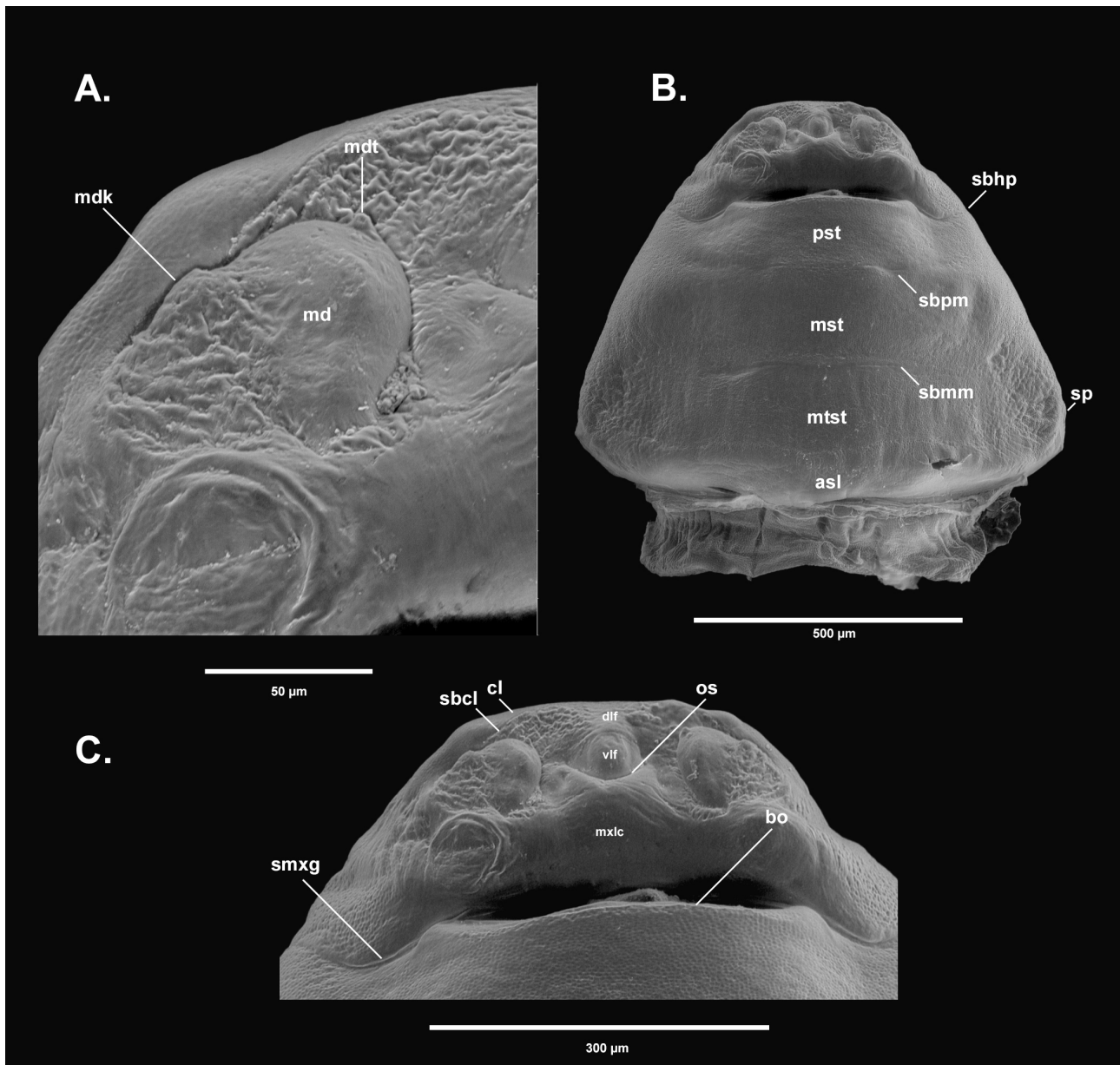


FIGURE 17. Holotype of *Stylops serotinus* Lähteenaro & Straka **sp. nov.**, MZH (KZ.163) female, SEM micrographs of cephalothorax. Abbreviations: bo—birth opening, csl—constriction of abdominal segment I, cl—clypeus, dlf—dorsal labral field, vlf—ventral labral field, md—mandible, mdt—mandibular tooth, mdk—mandible knob, mst—mesosternum, mtst—metasternum, mxlc—maxillo-labial complex, os—mouth opening, pst—prosternum, sbhp—segmental border between head and prothorax, sbmm—segmental border between mesothorax and metathorax, sbpm—segmental border between prothorax and mesothorax, sbcl—segmental border between clypeus and labrum, sp—spiracle, smxg—submaxillary groove.

Mouth opening

Mouth opening (os, Fig. 17C) arcuate.

Maxillo-labial complex

Maxilla slightly raised, rounded (mxlc, Fig. 17C). Submaxillary groove quite distinctly produced anterolaterally, adjacent to border between head and prothorax (smxg, Fig. 17C). Labial area fairly indistinct between maxillae, delimited anteriorly by mouth opening, posteriorly by birth opening. Slightly protruding towards apex, corrugated.

Birth opening

Birth opening truncate (bo, Figs. 16A, 17C), both lateral head extensions and prothoracic extensions short.

Thorax

Pro-mesothoracic and meso-metathoracic borders distinct, indicated ventrally and dorsally by mesal furrows (sbpm, sbmm, Figs. 16A, 17B). Ventral mesal furrows shiny, in segmental border between prothorax and mesothorax forming two separate furrows, in segmental border between mesothorax and metathorax one uniform furrow or two separated narrowly, sometimes slightly pigmented. Dorsal mesal furrows short, with darker pigmentation than thoracic segments. Cuticle of thorax reticulate in ventral view, in dorsal view with deep parallel wrinkles.

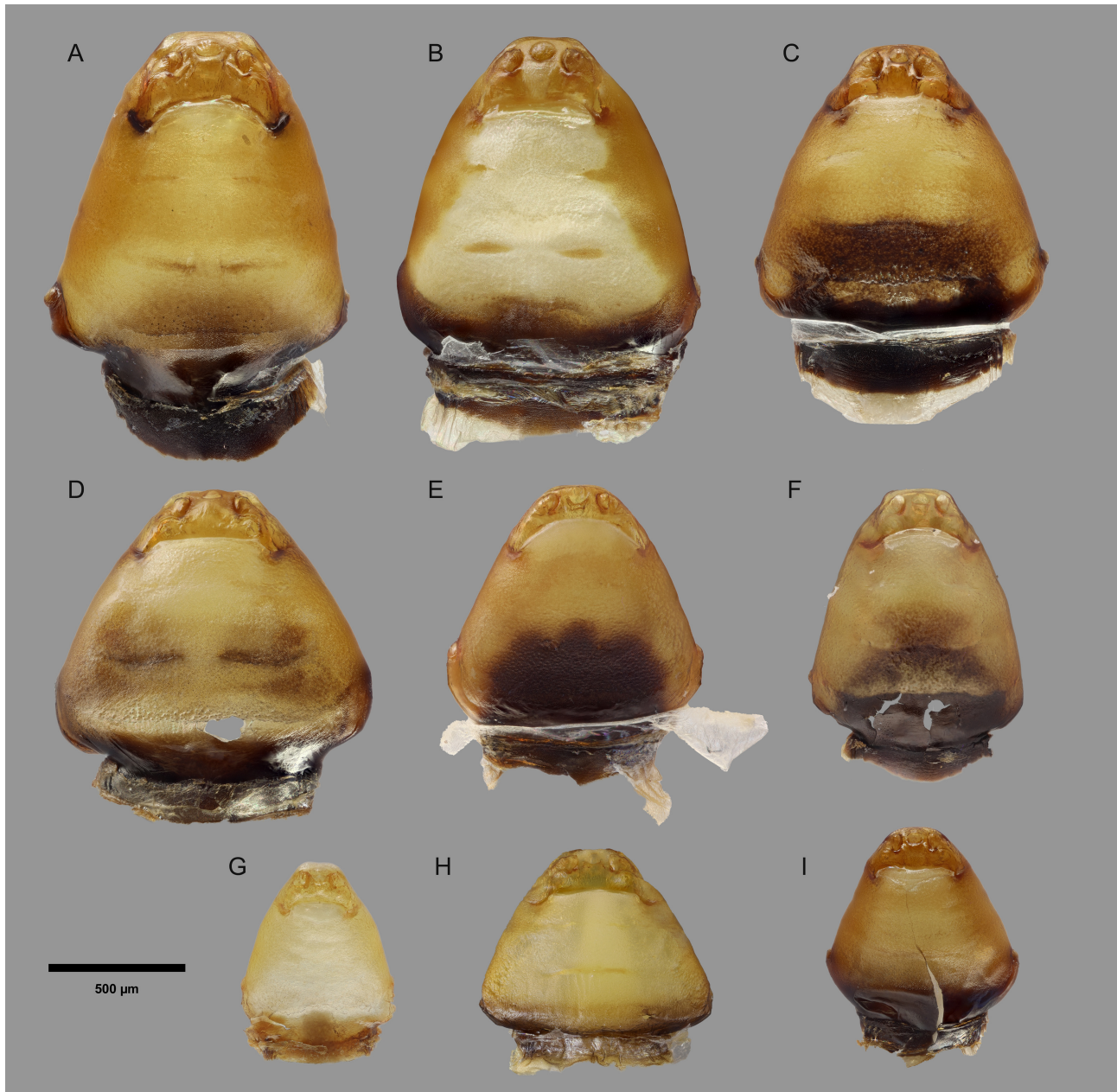


FIGURE 18. Cephalothoraces of female *Stylops* in Nordic countries. A. *Stylops melittae* Kirby, 1802 (SGr97); B. *Stylops ater* Reichert, 1914 (NHRS-SRAH000009527); C. *Stylops nevinsoni* Perkins, 1918 (NHRS-SRAH000009436); D. *Stylops aterrimus* Newport, 1851 (NHRS-MELA000000278); E. *Stylops thwaitesi* Perkins, 1918 (KZ.54); F. *Stylops sapmiensis* Lähteenaro & Bergsten **sp. nov.** (NHRS-SVHE000102811); G. *Stylops spretus* Perkins, 1918 (NHRS-MELA000000178); H. *Stylops serotinus* Lähteenaro & Straka **sp. nov.** (KZ.163); I. *Stylops gwynanae* Günther, 1957 (SSvG1).

Abdominal segment I and spiracles

Cephalothoracic part of sclerotized abdominal segment I light brown ventrally contrasting to paler metathorax (asI, Fig. 16A). Differs from metathorax by more rugose cuticular structure. Dorsally pale, limited from metathorax by furrow. Spiracles slightly elevated with latero-dorsal orientation (sp, Figs. 16A, 17B).

Molecular data

Whole-genome sequencing raw data for the holotype available at Sequence Read Archive (accession number SRR33345358, <https://www.ncbi.nlm.nih.gov/sra>) and CO1 at BOLD database (Process ID: NOSTR001-25, <https://boldsystems.org>).

Etymology

From Latin *serotinus* (= late coming). Refers to the late phenology of the species compared to other species in the genus. Adjective.

Stylops sp. ex *Andrena barbilabris* (Kirby, 1802)

In addition to the known species or species described here, multiple stylopized *A. barbilabris* has been recorded from Denmark and from Sweden. Most of the records from Denmark lack precise location information, but one of them was collected from Nordvestjylland in 1969. All Swedish records are from Skåne. This mining bee species is the host of a North American species, *Stylops packardi* Pierce, 1909. Whether the bee species is parasitized by the same *Stylops* species in Europe is not known.

Halictoxenos arnoldi Perkins, 1918 (Figure 19)

Nordic hosts *Lasioglossum xanthopus* (Kirby, 1802) (Hymenoptera: Halictidae).

Additional hosts

Lasioglossum costulatum (Kriechbaumer, 1873); *L. leucozonium* (Schrank, 1781); *L. quadrinotatum* (Kirby, 1802) (Hymenoptera: Halictidae).

Distribution

Sweden: Skåne **New to Sweden.**

Habitat The Swedish record is from warm coastal clay slopes in the southwest.

Phenology The Swedish record is from August.

Notes The only confirmed record was collected from Sweden in 2003. The main host of *Halictoxenos arnoldi* seems to be *L. xanthopus* (Saure, 2003; Straka *et al.*, 2008) but it has been associated with other host species from the same subgenus *Lasioglossum* as well (Kinzelbach, 1978; Straka *et al.*, 2008). Nielsen *et al.* (2014) identified *Halictoxenos* from *Lasioglossum* (*Sphecodogastra*) *fratellum* and *L. (Sphecodogastra) calceatum* based on the morphology to be *H. arnoldi*. However, subgenus *Sphecodogastra* is parasitized by *Halictoxenos spencei* and even though host sharing is present within Strepsiptera, it is unlikely that one *Halictoxenos* species could utilize so distantly related host species. *Lasioglossum* has been divided into “*Lasioglossum* series”, which includes subgenus *Lasioglossum*, and “*Hemihalictus* series”, which includes subgenera associated with *H. spencei* (Michener, 2007)

and this division is supported by molecular data (Danforth *et al.*, 2003; Zhang *et al.*, 2022). Traditionally, size and location of the pale spots in the female cephalothorax corresponding to the openings of Nassanov's pheromone glands have been used to identify European *Halictoxenos* species (Kinzelbach, 1978; Perkins, 1918). The location of the spots is the same between *H. arnoldi* and *H. spencei*, but the spots tend to be smaller and less visible (or not visible at all) in the former compared with the latter. However, it has not been tested how individually variable the sizes of the spots are and how different treatments of the specimen affect their visibility, so the host subgenus should be taken into account in species determination.

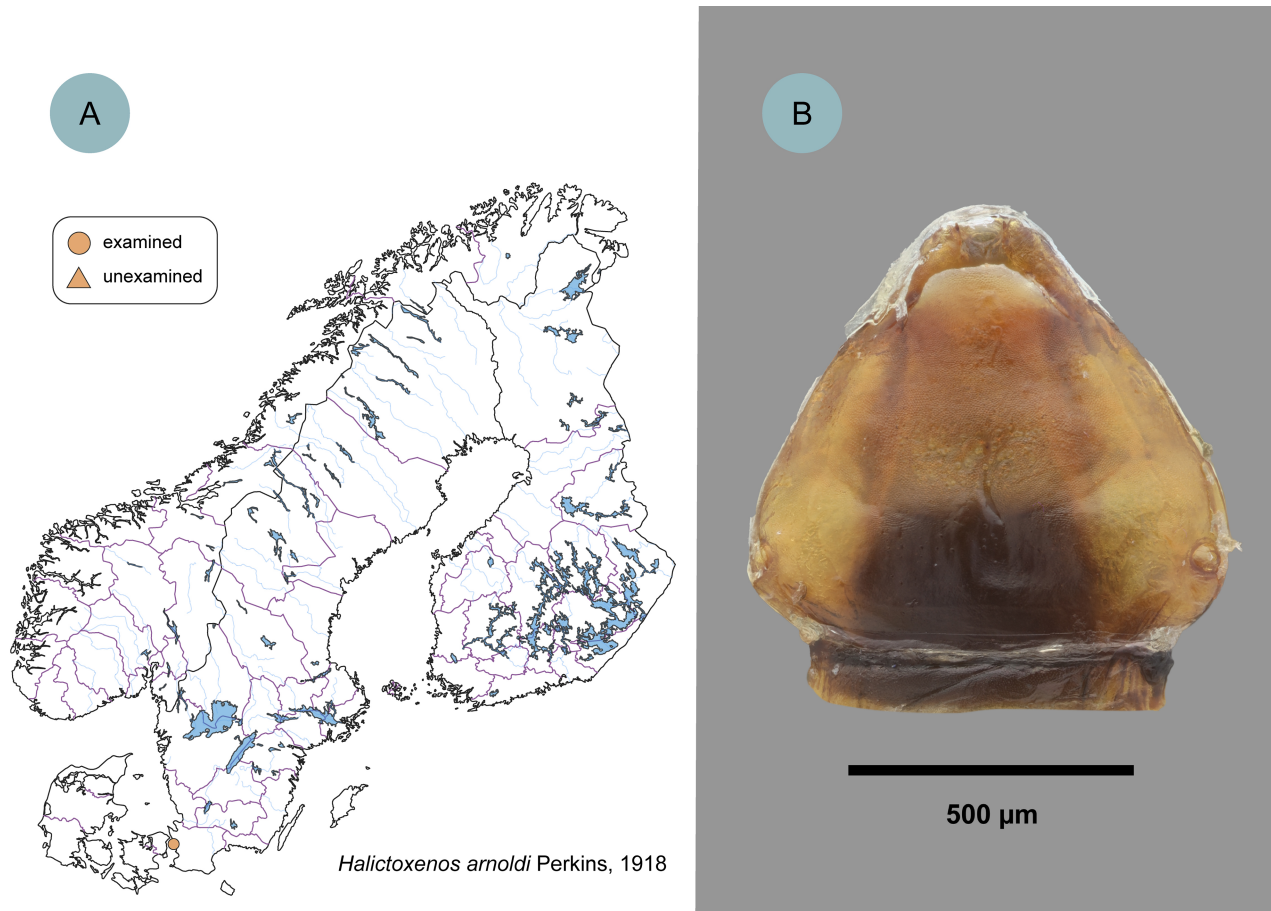


FIGURE 19. Localities of *Halictoxenos arnoldi* Perkins, 1918 in Nordic countries (A) and *H. arnoldi* female (MZLU-2020-129b) cephalothorax (B).

Halictoxenos spencei Nassanov, 1893 (Figure 20)

Halictoxenos calceati Noskiewicz & Poluszynski, 1924.

Halictoxenos cylindrici Perkins, 1918.

Halictoxenos nitidiusculus Ogloblin, 1925.

Nordic hosts *Lasioglossum fulvicorne* (Kirby, 1802); *L. fratellum* (Pérez, 1903); *L. nitidiusculum* (Kirby, 1802); *L. punctatissimum* (Schenck, 1853); *L. calceatum* (Scopoli, 1763); (Hymenoptera: Halictidae).

Additional hosts *Lasioglossum morio* (Fabricius, 1793); *L. parvulum* (Schenck, 1853); *L. pygmaeum* (Schenck, 1853); *L. sabulosum* (Warncke, 1986); *L. sexstrigatum* (Schenck, 1869); *L. villosulum* (Kirby, 1802) (Hymenoptera: Halictidae). Kinzelbach (1978) lists multiple additional confirmed and proposed host species.

Distribution

Denmark: Nordøstjylland, Nordvestjylland, Nordøstsjælland, Østjylland.

Finland: Ahvenanmaa, Uusimaa, Varsinais-Suomi.

Norway: Rogaland.

Sweden: Gotland, Skåne, Södermanland, Öland, Östergötland.

Habitat Swedish records are from open and very warm sandy slopes.

Phenology Swedish records are from May and June.

Notes First recorded from Denmark in 1924 (Nielsen, 2014). *Halictoxenos spencei* is associated with hosts from *Lasioglossum* subgenera *Sphecodogastra* and *Hemihalictus* in the Nordic countries but has been recorded from other subgenera as well from the *Hemihalictus* series in other parts of Europe (Kinzelbach, 1978; Smit *et al.*, 2020). See also notes under *H. arnoldi*.

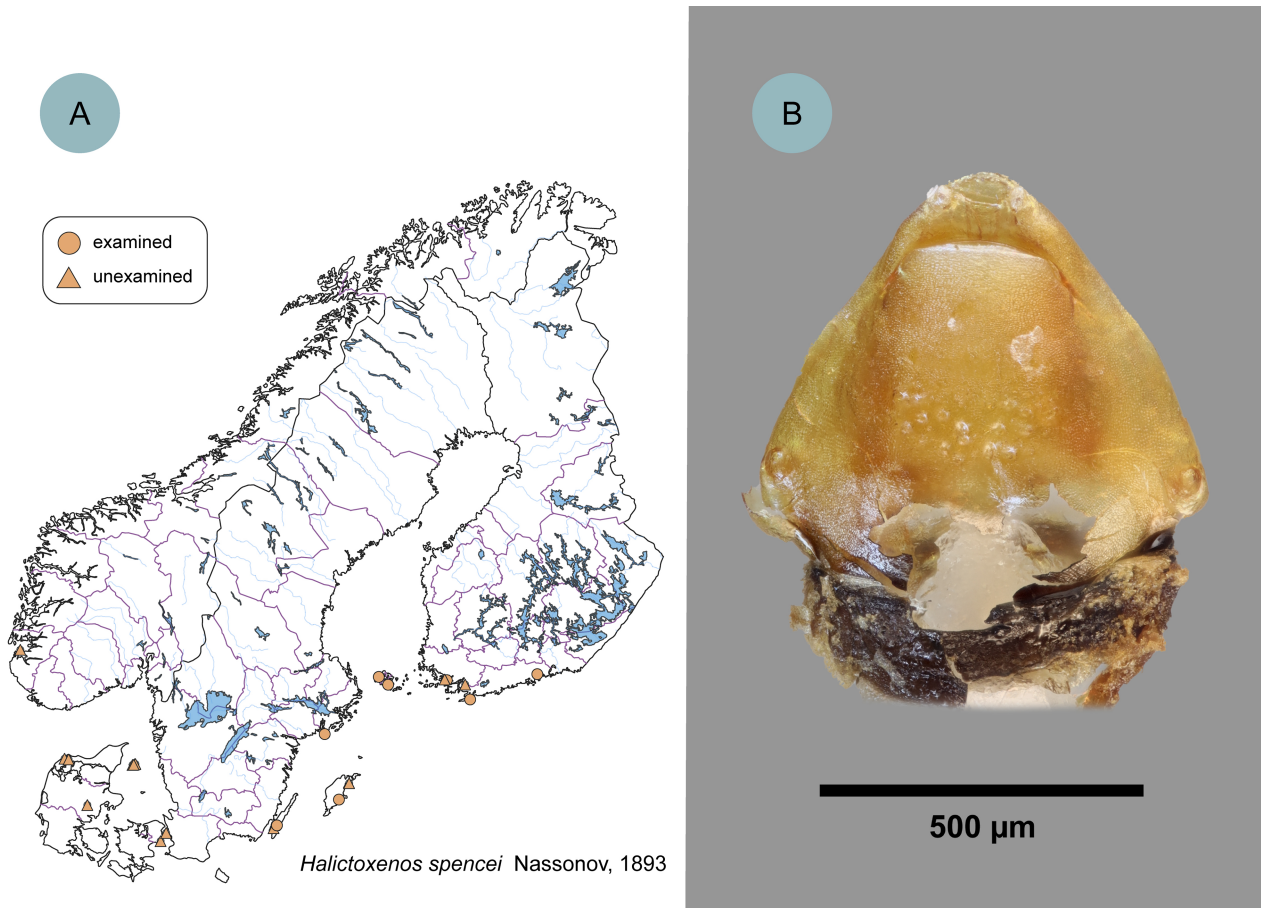


FIGURE 20. Localities of *Halictoxenos spencei* Nasonov, 1893 and female *H. spencei* (NHRS-SRAH000009521) cephalothorax with characteristic spots visible medially (B).

Halictoxenos tumulorum Perkins, 1918 (Figure 21)

Halictoxenos ulrichi Hofeneder, 1939.

Nordic hosts *Seladonia tumulorum* (Linnaeus, 1758); *Halictus rubicundus* (Christ, 1791) (Hymenoptera: Halictidae).

Additional hosts *Halictus confusus* Smith, 1853; *H. kessleri* Bramson, 1879; *H. simplex* Blüthgen, 1923 (Hymenoptera: Halictidae). Kinzelbach (1978) lists multiple additional confirmed and proposed host species.

Distribution

Denmark: Nordøstsjælland, Nordvestsjælland, Østjylland.

Finland: Etelä-Savo, Pohjois-Savo, Uusimaa, Varsinais-Suomi.

Norway: Buskerud, Oslo, Telemark, Vestfold.

Sweden: Bohuslän, Dalarna, Gotland, Halland, Uppland, Värmland, Ångermanland, Öland, Östergötland.

Habitat Swedish records are from a variety of habitats, most frequently from open and sandy habitats.

Phenology Swedish records range from April to September, most in spring and late summer.

Notes The oldest known specimen was collected from Finland in 1891.

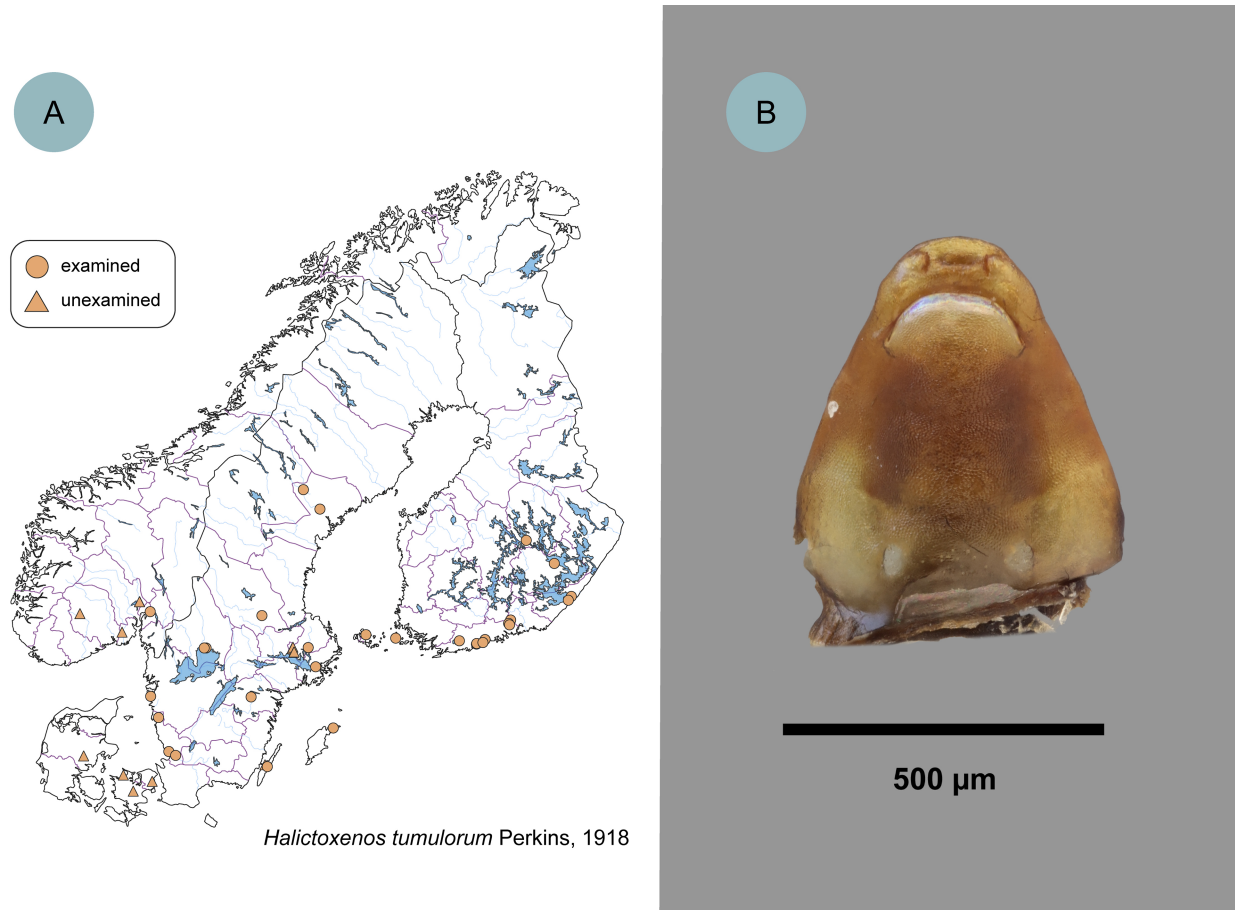


FIGURE 21. Localities of *Halictoxenos tumulorum* Perkins, 1918 in Nordic countries (A) and *H. tumulorum* female (NHRS-MELA000000280) cephalothorax (B).

Doubtfully reported species

Xenos vesparum Rossi, 1793 has repeatedly been cited as a species documented in Sweden (Landin, 1971; Soon *et al.*, 2012; Pekkarinen & Raatikainen, 1973; Hequist, 1958). The origin seems to be Tullgren & Wahlgren (1920) where the authors cite a male *Xenos vesparum* dissected from *Polistes biglumis*. However, the authors are not certain about the geographic origin of this *Polistes* specimen but state that it has “probably Swedish origin” (in Swedish. “troligen svenskt ursprung” 1920: 318). We have been unable to find the specimen in question in any of the Swedish collection holdings, and even if it does still exist it is likely its origin is not deducible from any associated metadata, given how Tullgren and Wahlgren (1920) formulated the ambiguity. *Polistes biglumis* is today a very rare species in Sweden which in modern times have been documented with nests from northeasternmost Sweden (Norrbotten). However, it was seemingly more common and occurred in central Sweden during the 19th century and most specimens in museum holdings were collected at this time (SLU Artdatabanken, 2024). The occurrence of *X. vesparum* in Sweden was therefore probably more likely during the 1800s than later, but until properly documented based on new or historical findings, we find the evidence insufficient. We therefore consider *X. vesparum* not yet documented from Sweden or any of the Nordic countries certainly.

Key to Nordic Strepsiptera

Key to males

A key to genera and, except for *Stylops*, *Halictophagus* and *Halictoxenos*, to species for males. Species that are not yet known but could potentially be found in the region of the Nordic countries (Tab. 2) are included in the key (name within parenthesis), except for *Eurystylops oenipontana* males of which are unknown.

- 1. Tarsi 2- or 3-segmented (Fig. 22A,B) 2
- Tarsi 4-segmented (Fig. 22C) 4

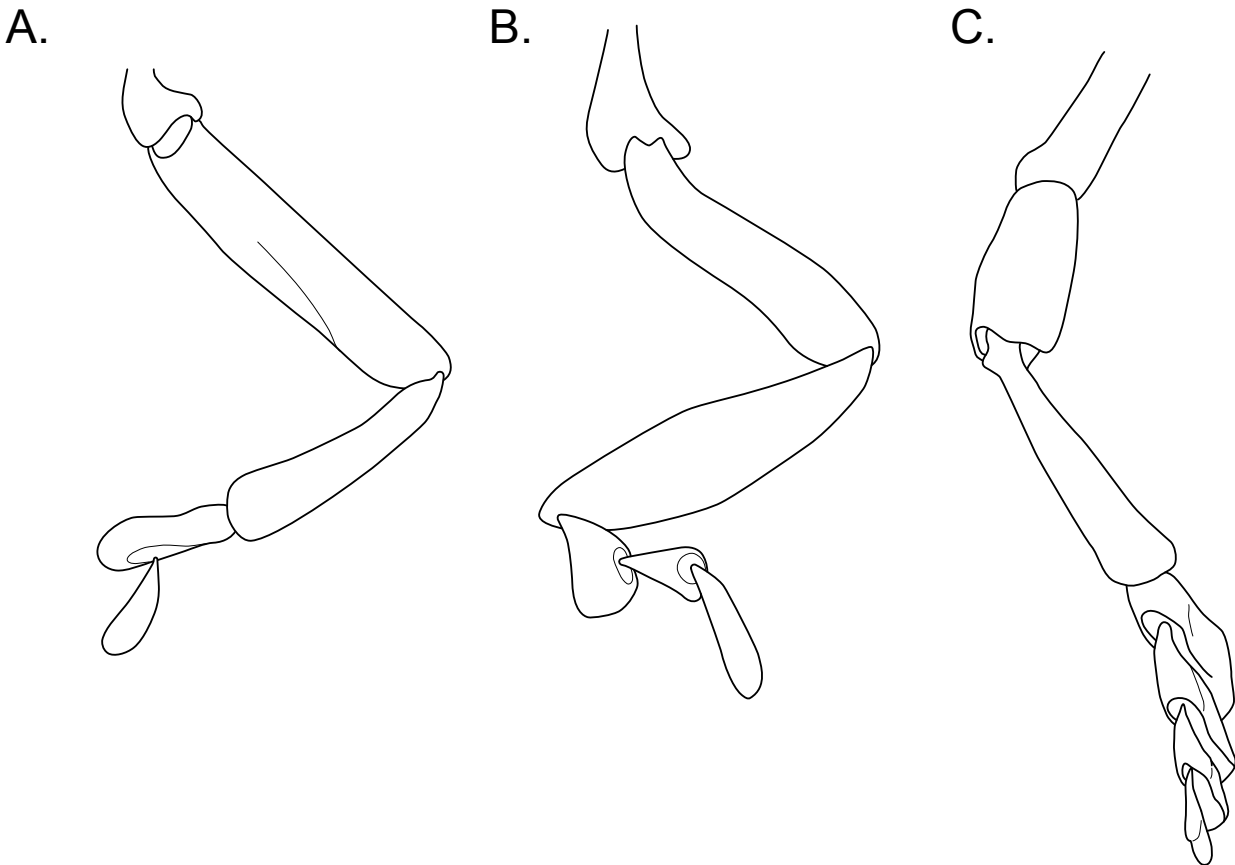


FIGURE 22. Male tarsi. A. *Elenchus*; B. *Halictophagus*; C. *Stylops*.

- 2. Tarsi 2-segmented; antenna 5-segmented (Fig. 23A) *Elenchus tenuicornis*
- Tarsi 3-segmented; antennae 7-segmented (Fig. 23B,C) 3
- 3. Antennomeres with distinct elongate lateral projections on segments 3–6 (Fig. 23B) *Halictophagus* (3 spp.)
- Antennomeres with 2 distinct elongate lateral projections on segments 3–4 (Fig. 23C).
..... (*Stenocranophilus anomalocerus*)
- 4. Antennae 6-segmented (Fig. 23D,E) 5
- Antennae 4- or 5-segmented (Fig. 23F–I) 6
- 5. Body length 2 mm; antennomeres with elongate lateral projections on segments 3–4 (Fig. 23D)
..... *Malayaxenos trapezonoti*
- Body length 3.5–6 mm; antennomere with elongate lateral projection only on segment 3 (Fig. 23E) ... *Stylops* (ca.10 spp)
- 6. Antennae 5-segmented; antennomere 4 very short (Fig. 23F) (*Hylecthrus rubi*)
- Antennae 4-segmented; antennomere 4 at least twice as long as broad (Fig. 23G–I) 7

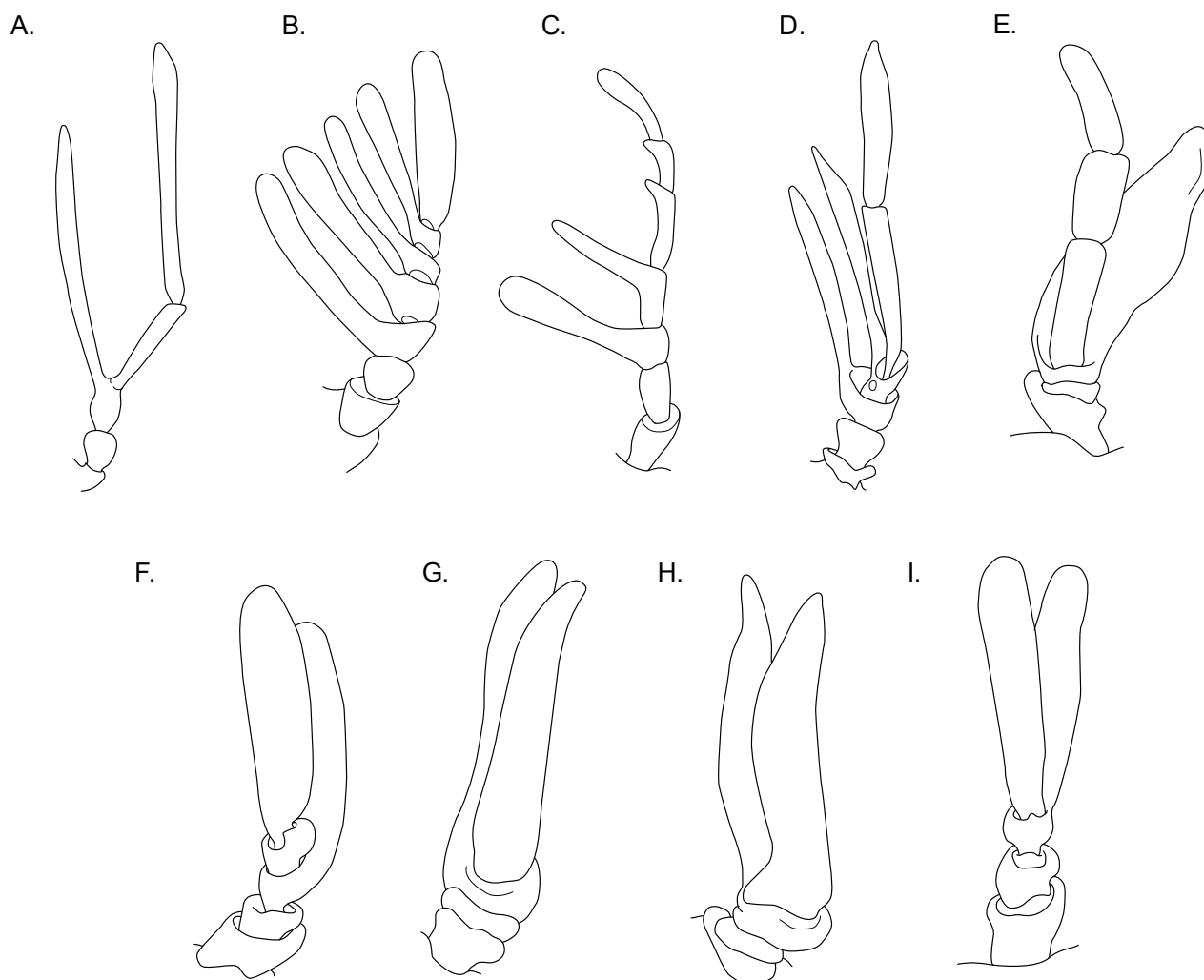


FIGURE 23. Male antennae. A. *Elenchus*; B. *Halictophagus*; C. *Stenocranophilus*; D. *Malayaxenos*; E. *Stylops*; F. *Hylecthrus*; G. *Paraxenos*; H. *Tuberoxenos*; I. *Halictoxenos*. Drawings based on Kinzelbach, 1978 (C & H), Kinzelbach, 1971 (F & I), Pohl & Melber, 1996 (D) and Székessy, 1955 (G).

7. Scutellum anteriorly not pointed; postlumbium at least half as long as wide (Fig. 24A) *Halictoxenos* (3 spp.)
- Scutellum anteriorly pointed; postlumbium much shorter than wide (Fig. 24B) 8
8. Dorsal part of head capsule not divided in two plates 9
- Dorsal part of head capsule divided in two plates (Fig. 24C, “Vertexplatten” sensu Kinzelbach, 1971) 10
9. Lateral projection of antennomere 3 reaches past antennomere 4 with $\frac{1}{2}$ –1 antennomere width; distal parts of antennomeres 3–4 pointed (Fig. 23H) *Tuberoxenos sphecedarum*
- Lateral projection of antennomere 3 reaches past antennomere 4 with max $\frac{1}{2}$ antennomere width; distal parts of both antennomeres 3–4 rounded (Fig. 23G) (*Paraxenos hungaricus*)
10. Body length 4.4–5 mm; Hind wings with vein CuP (Fig. 24D) (*Xenos vesparum*)
- Body length 2–3.5 mm; Hind wings lack vein CuP. (*Pseudoxenos heydenii*)

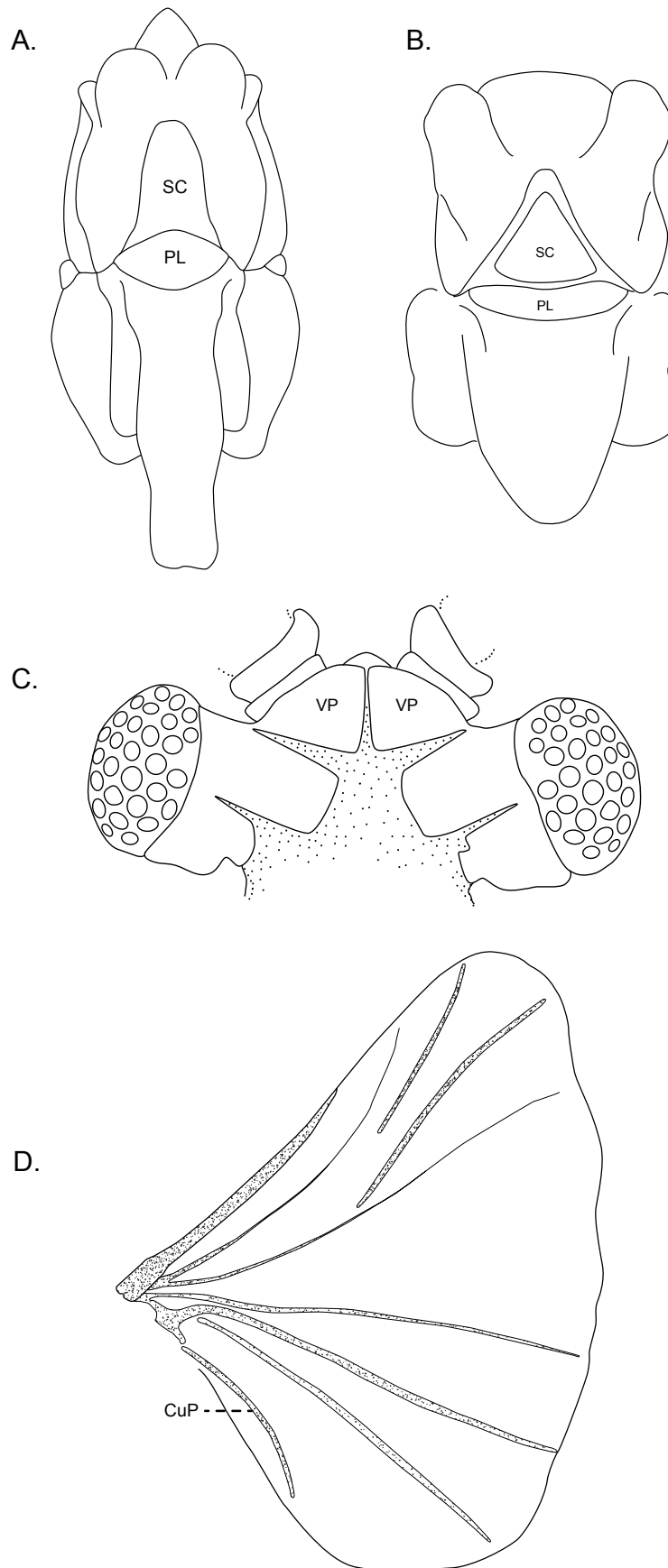


FIGURE 24. Male characteristics. A. Thorax of *Halictoxenos*; B. Thorax of *Tuberoxenos*; C. Head of *Xenos* with “Vertexplatten” (vp); D. Wing of *Xenos* with CuP vein. Abbreviations: sc—scutellum; pl—postlumbium. Drawings based on Kinzelbach, 1978 (A, B, C) and Kinzelbach, 1971 (D).

TABLE 2. An overview of potential future Strepsiptera species for the Nordic countries based on occurrence in neighbouring countries and host presence. Symbols: *—as *Stenocranophilus quadratus* Pierce, 1914.

Species	Family	Host	Near occurrence: reference
<i>Stenocranophilus anomalocerus</i> (Pierce, 1918)	Halictophagidae	Delphacidae	Germany: Oehlke (2011)*; Latvia: Soon <i>et al.</i> (2012)
<i>Halictophagus agalliae</i> Abdul-Nour, 1970	Halictophagidae	Cicadellidae: Agallinae	Germany: Oehlke (2011); Poland: Huflejt & Liana (2004)
<i>Xenos vesparum</i> Rossius, 1793	Xenidae	Vespidae: <i>Polistes</i>	Germany: Oehlke (2011); Poland GBIF (2023)
<i>Pseudoxenos heydenii</i> (Saunders, 1854)	Xenidae	Vespidae: Eumeninae	Germany: Oehlke (2011); Poland: Huflejt & Liana (2004)
<i>Paraxenos hungaricus</i> (Székessy, 1955)	Xenidae	Crabronidae: <i>Bembix</i>	Germany: Oehlke (2011)
<i>Hylecthrus rubi</i> Saunders, 1850	Stylopidae	Colletidae: <i>Hylaeus</i>	Germany: Oehlke (2011)
<i>Eurystylops oenipontana</i> Hofeneder, 1949	Stylopidae	Halictidae: <i>Dufourea</i>	Germany: Oehlke (2011)
<i>Stylops praecocis</i> Luna de Carvalho, 1974	Stylopidae	<i>Andrena</i> (<i>Andrena</i>) (e.g. <i>A. praecox</i> , <i>A. clarkella</i> , <i>A. batava</i> , <i>A. apicata</i> , <i>A. nycthemera</i>)	Germany and Poland Läähteenaro <i>et al.</i> (2024)

Key to females

A key to species for females. Potential but not yet known species from the Nordic countries are not included. In the key, females are viewed from the ventral side (functional dorsal side). To use the key, females need to be either extracted from the host or the host's tergite or sternite covering the cephalothorax must be opened from one side and lifted to reveal the entire cephalothorax. The cephalothorax length is to be measured from the apex of the clypeal lobe to the constriction of abdominal segment I (Fig. 25). The cephalothorax width is the maximum distance between its lateral margins. Note that the size of the cephalothorax varies depending on the size of the host (Kathirithamby, 1989), so the measurements given here are indicative. Given the paucity of samples and the reliance on secondary sources, steps 1–7 involve a degree of uncertainty stemming from limited knowledge of intraspecific variation. The key does not include *Halictophagus curtisi* due to limited knowledge of the female morphology.

1. Cephalothorax without birth-opening, pleural area of prothorax membranous (Fig. 26A); Host: Heteroptera, *Trapezonotus arenarius* & *T. desertus* *Malayaxenos trapezonoti*
- Cephalothorax with birth-opening (Figs. 26B–D & 27–29) 2
2. Birth-opening approximately in the middle of the cephalothorax (Fig. 26B,C); parasites of Auchenorrhyncha (plant hoppers or leaf hoppers) 3
- Birth-opening in the anterior third of cephalothorax; parasites of Hymenoptera (thread-waisted wasps or bees) (Figs. 26D & 27–29) 4
3. Birth-opening wide, cephalothorax round (Fig. 26B); host: Delphacidae spp. *Elenchus tenuicornis*
- Birth-opening narrow, cephalothorax elongated (Fig. 26C); host: *Ulopa reticulata*. *Halictophagus silwoodensis*
4. Spiracles in the anterior $\frac{2}{3}$ of cephalothorax (Fig. 26D); overall colour of cephalothorax dark brown; Nordic hosts: *Ammophila* spp., *Podalonia* spp. *Tuberoxenos sphecidarum*
- Spiracles in the posterior $\frac{1}{3}$ of cephalothorax (Figs. 27–29); cephalothorax mostly pale yellow or light brown; parasites of bees. 5
5. More or less visible pale or clear spots in places of Nasonov's pheromone glands openings, either behind spiracles (Fig. 27A) or medially (Fig. 27B,C), not always visible for *Halictoxenos arnoldi*; if spots not visible, then outline of the cephalothorax with distinct constriction at the posterior edge of the head, creating a sharp triangular overall shape for the cephalothorax; parasites of Halictidae bees. (Genus *Halictoxenos*) 6
- No such pale spots; parasites of *Andrena* bees (Figs. 28–29) (Genus *Stylops*) 8

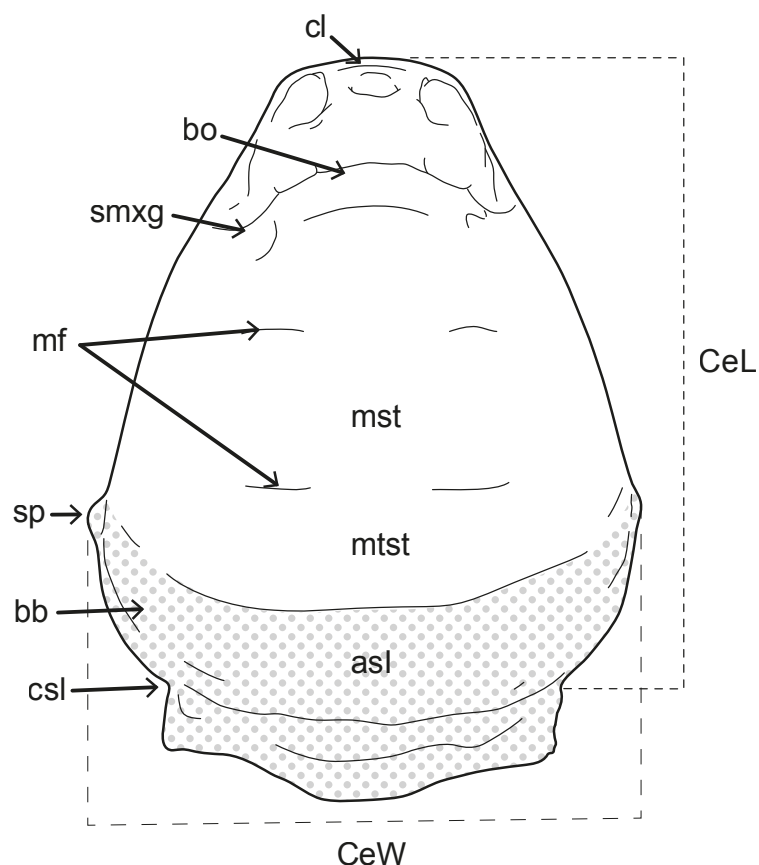


FIGURE 25. General schema of the cephalothorax. Abbreviations: CeL—cephalothorax length, CeW—Cephalothorax width, cl—clypeus, bo—birth opening, smxg—submaxillary groove, mf—mesal furrows, sp—spiracle, bb—basal band, csi—constriction of the abdominal segment 1, asl—abdominal segment 1, mtst—metasternum, mst—mesosternum.

6. Two large pale spots behind spiracles (Fig. 27A); birth opening strongly curved, arcuate; Nordic hosts: *Seladonia tumulorum* & *Halictus rubicundus* *Halictoxenos tumulorum*
- Multiple pale spots medially anterior to an imaginary line between spiracles (Fig. 27B,C) or no visible pale marks 7
7. Medial pale spots larger and easily visible (Fig. 27B); hosts *Lasioglossum* (*Hemihalictus*) & *L. (Sphecodogastra)* spp. *Halictoxenos spencei*
- Medial spots either absent or smaller and less clear (Fig. 27C); hosts *Lasioglossum* (*Lasioglossum*) spp. *Halictoxenos arnoldi*
8. Cephalothorax wider than long, truncate (Fig. 28A,B) 9
- Cephalothorax longer than wide, elongate (Figs. 28C,D & 29) 10
9. Pigmentation pattern in cephalothorax as in Fig. 28A in varying intensity, sometimes only faint lateral spots visible; bigger species, cephalothorax length >0.95 mm; Nordic hosts *Andrena* (*Hoplandrena*) & *A. (Plastandrena)* spp. *Stylops aterrimus*
- No pigmentation in metasternum or mesosternum, dark basal band in abdominal segment 1 diffused (Fig. 28B); smaller species, cephalothorax length <0.90 mm; host *Andrena fuscipes* *Stylops serotinus*
10. Smaller species (cephalothorax length 0.6–0.8 mm) and often no clear pigmentation pattern in metasternum or mesosternum (Fig. 28C,D). 11
- Larger species (cephalothorax length >0.8 mm), pigmentation or no pigmentation in metasternum and/or mesosternum (Fig. 29) 12

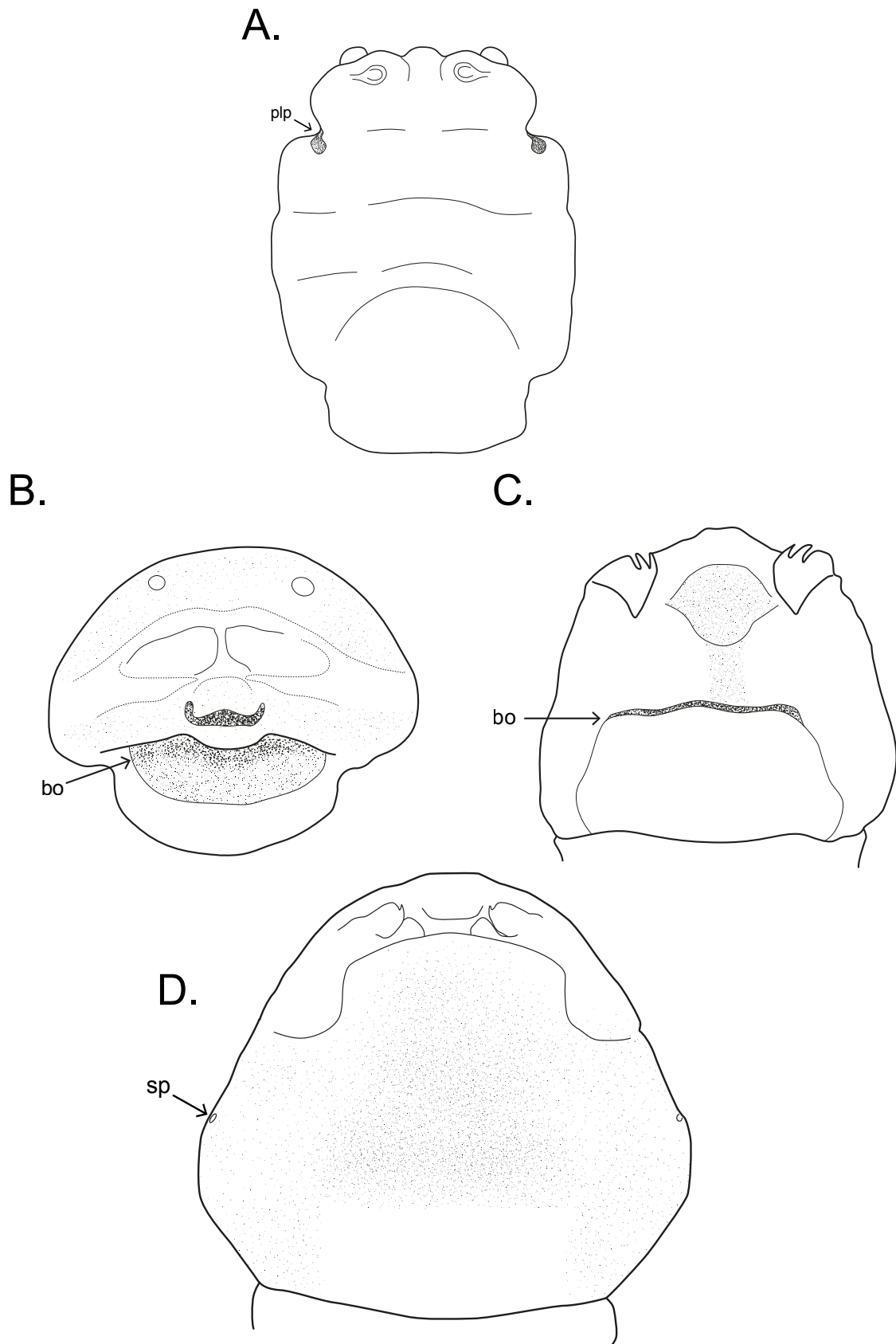


FIGURE 26. Cephalothoraces of A. *Malayaxenos trapezonoti* B. *Elenchus tenuicornis*; C. *Halictophagus silwoodensis*; D. *Tuberoxenos spheccidarum*. Abbreviations: bo—birth opening, plp—pleural area of prothorax, sp—spiracle. Drawings based on Pohl & Albert, 1996, Pohl & Beutel, 2005 and Jandausch *et al.*, 2023 (A), Benda *et al.*, 2022 (D) and partly based on Kinzelbach, 1971 (B) and Waloff, 1981 (C).

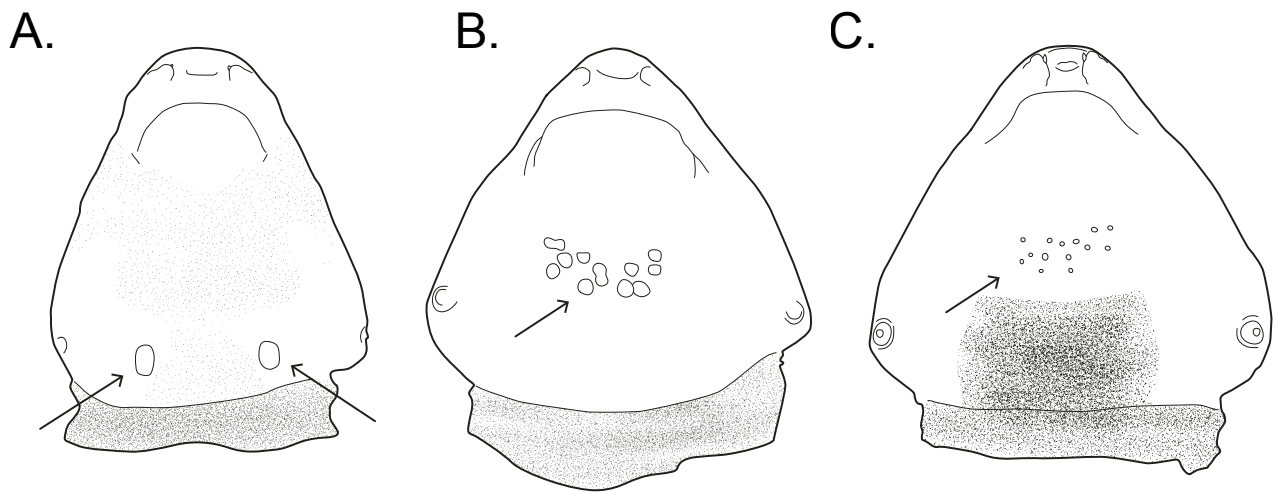


FIGURE 27. Cephalothoraces of A. *Halictoxenos tumulorum*; B. *Halictoxenos spencei*; C. *Halictoxenos arnoldi*.

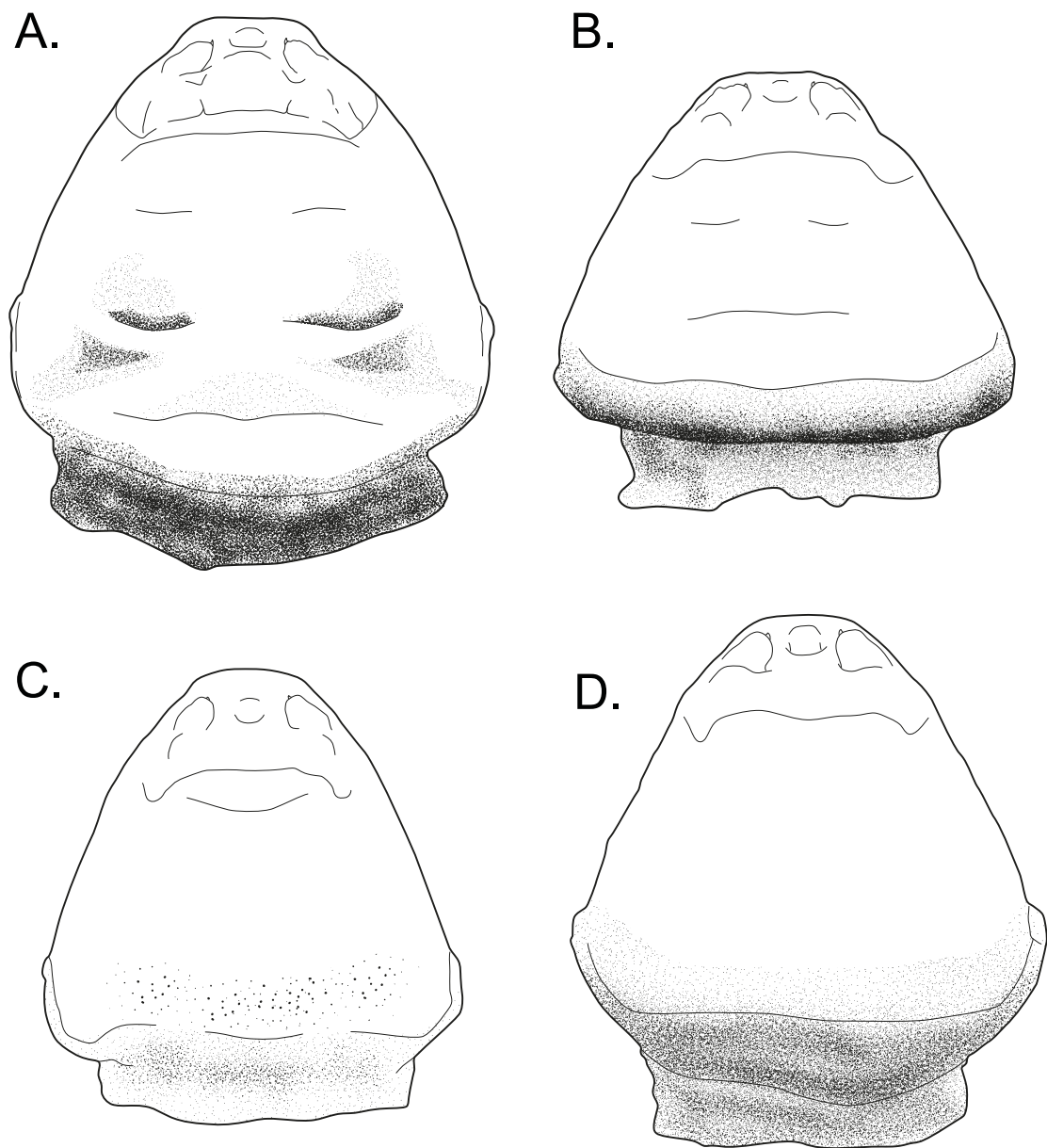


FIGURE 28. Cephalothoraces of A. *Stylops aterrimus*; B. *Stylops serotinus* sp. nov.; C. *Stylops spretus*; D. *Stylops gwynanae*.

11. Colouration of the cephalothorax pale yellow; sometimes darker brown pigmentation in the cephalothoracic part of abdominal segment 1 and metasternum, not extending to lateral margins (Fig. 28C); smaller species, cephalothorax length <0.7 mm; Nordic hosts *Andrena (Micrandrena)* spp. *Stylops spretus*
- Colouration of the cephalothorax light brown, frequently with dark brown pigmentation in the cephalothoracic part of abdominal segment 1, which may extend to the lateral margins (Fig. 28D); larger species, cephalothorax length ≥0.7 mm; Nordic host *Andrena bicolor* *Stylops gwynanae*
12. Submaxillary groove regions darkly pigmented, almost black and edges of the pigmentation distinct (Fig. 29A); basal band does not extend to the lateral margins of the cephalothoracic part of abdominal segment 1, sometimes diffused darker pigmentation in metasternum and mesosternum; Nordic hosts *Andrena nitida* and *A. flavipes* *Stylops melittae*
- Submaxillary groove regions without dark, sharply defined pigmentation; if pigmented, colour lighter brown and diffuse. 13
13. Pigmentation in metasternum and mesosternum almost absent, at most darkened areas around mesal furrows between them (Figs. 28D, 29B). 14
- Pigmentation in metasternum and/or mesosternum (Figs. 28A, 29C–E) 15
14. Species small, cephalothorax length <1 mm; mesal furrows not pigmented (Fig. 28D); Nordic host *Andrena bicolor*. *Stylops gwynanae*
- Species large, cephalothorax length >1 mm; mesal furrows often pigmented and basal band in the cephalothoracic part of abdominal segment 1 dark and extends to the lateral margins (Fig. 29B). Nordic hosts *Andrena vaga* and *A. cineraria* *Stylops ater*

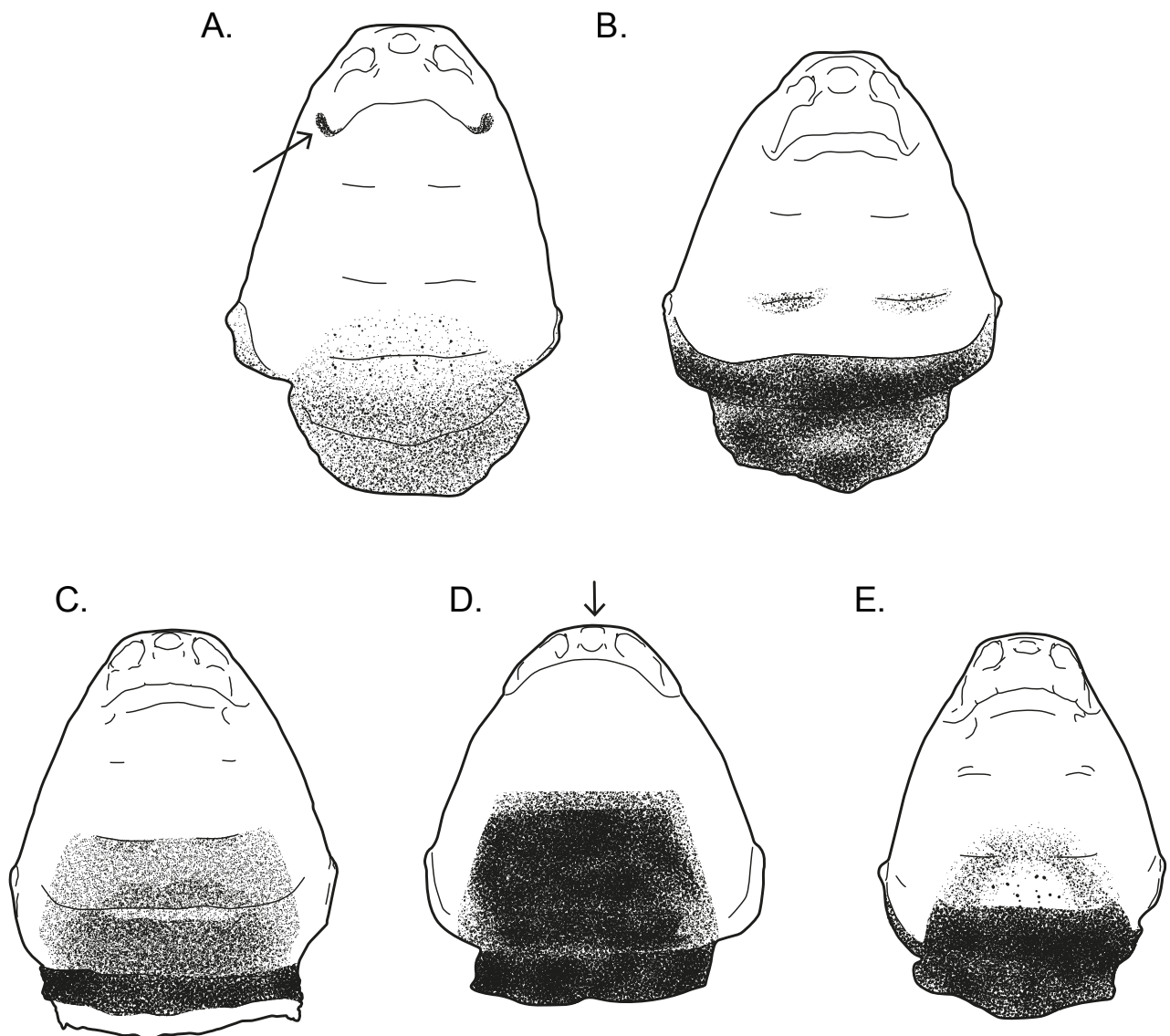


FIGURE 29. Cephalothoraces of A. *Stylops melittae*; B. *Stylops ater*; C. *Stylops nevinsoni*; D. *Stylops thwaitesi*; F. *Stylops sapmiensis* sp. nov.

15.	Pigmentation pattern in metasternum quadrate, can extend to mesosternum (Fig. 29C,D)	16
-	Pigmentation pattern in metasternum and/or mesosternum irregular or semicircular (Figs. 28A, 29E).....	17
16.	Clypeus and birth opening angular (Fig. 29C); Nordic host <i>Andrena fucata</i>	<i>Stylops nevinsoni</i>
-	Clypeus and birth opening rounded, semicircular (Fig. 29D); pigmentation pattern typically very dark; Nordic hosts <i>Andrena (Taeniandrena)</i> spp.....	<i>Stylops thwaitesi</i>
17.	Semicircular pigmentation in the medial metasternum, sometimes extends to mesosternum (Fig. 29E); host <i>Andrena lapponica</i>	<i>Stylops sapmiensis</i>
-	Pigmentation pattern in lateral margins of metasternum, pattern as in Fig. 28A present in varying degrees of intensity; Nordic hosts <i>Andrena (Hoplendrena)</i> & <i>A. (Plastandrena)</i> spp.....	<i>Stylops aterrimus</i>

Discussion

The Nordic countries have a long history of research and records of the order Strepsiptera. However, the research is not evenly distributed across time and the Nordic countries, leading to gaps in knowledge and an imbalance in records. Here we have summarised the accumulated records and knowledge over time from all the Nordic countries collectively, while providing a large number of new records.

Strepsiptera are infamous for their elusiveness. Screening museum collections of hosts, especially hymenopteran hosts, seems to be one of the best ways to acquire Strepsiptera samples (e.g. Lähteenaro, 2019b; Nielsen *et al.*, 2014; Reeves, 2024). However, this method is limited to adult females and male puparia and Strepsiptera that parasitize Hemiptera, are easily overlooked, as the females or male puparium are often hidden by the wings of the host. Overall, in Strepsiptera species that parasitize Hymenoptera, females are encountered more frequently than males. This could be partly due to the fact that males have a short lifespan (Kifune & Maeta, 1975; Linsley & MacSwain, 1957; Pierce, 1909), flying short distances for a very limited time, and are mainly encountered in close vicinity of females during swarming. Furthermore, while females can be collected using pan traps (or more precisely with their hosts), males are rarely encountered in any type of traps, including malaise traps.

In contrast, in leafhopper parasites, males are found more frequently than females. Apparently, they (or at least some of them) have a longer lifespan, might be bivoltine, are more mobile, and have a longer season, than males in Hymenoptera parasite families. This makes them more suitable to be collected with traps (James & Strong, 2018; Raatikainen, 1967a; Raatikainen & Heikinheimo, 1974; Soon *et al.*, 2011). For example, a notable number of adult male Strepsiptera specimens parasitizing Hemiptera has been produced by the Swedish Malaise Trap Project (SMTP) and consecutive malaise trapping schemas. The SMTP project that started wide scale sampling of insects with Malaise traps across Sweden, funded by the Swedish Taxonomy Initiative and owned by Station Linné, collected material with 73 traps at 55 locations from 2003 to 2006 (Karlsson *et al.*, 2020). The material collected by this and ensuing projects included a new Strepsiptera species for the Nordic countries, *Malayaxenos trapezonoti*, several records of *Halictophagus silwoodensis*, previously known from only a single specimen in Sweden (Heqvist, 1958) and considerably expanded the known distribution of *Elenchus tenuicornis*. This speaks in favour of the usefulness of this type of long-term trapping project for gaining information on the biodiversity of lesser-known animal groups. The extensive records of *E. tenuicornis* from Finland in turn were largely collected with sweep netting as well as using a netting apparatus designed for catching insects transported by wind with funnels at differing heights (Raatikainen, 1967a; Raatikainen & Heikinheimo, 1974).

During recent years, molecular methods have been employed to investigate the diversity of *Stylops* (Stylopidae) (Jůzová *et al.*, 2015; Lähteenaro *et al.*, 2024a) and Xenidae (Benda *et al.*, 2021). These studies have led to taxonomic revisions (Benda *et al.*, 2022; Straka *et al.*, 2015b; this study) and have significantly increased our knowledge of the prevalence of cryptic species and host utilization within Strepsiptera. Delimitation and host utilization studies within *Halictoxenos* using molecular data is needed, as determinations are ambiguous and based on rather vague characters of the females, which has led to overlapping host records. The use of female characters in species identification despite their reduced morphology stems from males of *Halictoxenos* being extremely rare, possibly due to facultative parthenogenesis as a reproductive strategy (Kinzelbach, 1978). In fact, for *Halictoxenos arnoldi* the male is still undescribed. Furthermore, the host specificity within *Halictoxenos* is uncertain. While *H. arnoldi* seems to be limited to a single host subgenus, *H. spencei* has been recorded from numerous host subgenera and *H. tumulorum* from two host genera. It is possible that the more generalist species entail cryptic species, but this remains to be tested with molecular data.

Another compelling candidate for genetic investigation is *Elenchus tenuicornis*, as DNA barcode data suggest that it may consist of several species (unpublished). The Nordic Strepsiptera fauna therefore still remains insufficiently known even after this review. Several species are also knocking on the door to the region of the Nordic countries from the south with a warming climate (Tab. 2).

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Supplementary Materials. The following supporting information can be downloaded at the DOI landing page of this paper.

TABLE S1. Strepsiptera records from Nordic countries.