

The Strepsiptera of the Netherlands revisited (Insecta)

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KEY WORDS

DNA-barcoding, faunistics, hosts, twisted-wing insects

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The Strepsiptera fauna of the Netherlands is revised. Recent molecular work provided new insights in the taxonomy of the genus *Stylops*, raising the number of species in Europe from one to thirty. With this knowledge all available Strepsiptera material from the Netherlands is re-examined and additional DNA barcode sequences are generated and analyzed for 61 specimens belonging to eleven species. This revealed a third and yet unrecorded parasite for *Andrena nigroaenea*. The total number of Strepsiptera species recorded from the Netherlands is raised from six to 21. The known hosts and distribution of all species is provided.

Introduction

The order Strepsiptera is arguably one of the most intriguing groups of insects. Nearly everything about these endoparasites is different from most other holometabolous insects. Their sexual dimorphism is extreme. Where the females of all but one family never leave the body of their host and retain a larva-like appearance, whereas the males look like normal adult insects and are free-living, albeit only for a couple of hours. Like Diptera the males only have one pair of 'normal' developed wings, the others having been reduced to flaps which are less halter-like than in Diptera (figure 1). The wings are fan-shaped and look quite fragile, they are however suitable for flight (John Smit personal observation). Furthermore, even the visual system of the males is unusual for insects; with aspects from both compound as well as simple eyes (Buschbeck et al. 2003).

Enigmatic as they already are, DNA-barcoding revealed them to be even more intriguing. For recent molecular work (Jůzová et al. 2015) shows that *Stylops* does contain a range of species in the western Palearctic. This disproves the general accepted view of Kinzelbach (1978), who synonymized all earlier described species under the one *S. melittae* Kirby. Up until Kinzelbach's synopsis, every *Stylops* species found in another *Andrena*-host was described as a separate species, with its host as the most prominent and diagnostic character for separating it from the already known species. Kinzelbach (1978) showed that some of the characters previously used to identify females were in fact artifacts on the cephalothorax. Furthermore, he presented drawings of 62 cephalothoraxes showing that the suggested differences in their outline actually form a continuum when looked at a large enough sample size. As for the males, due to their short lifespan they are rarely encountered making it impossible to give an accurate diagnosis for the different species. Therefore Kinzelbach (1978) treated all *Stylops* as one species with a wide spectrum of *Andrena* hosts, as did nearly all subsequent authors. In fact the work by Jůzová et al. (2015) also shows that in the case of *Stylops* ecological traits are a better taxonomic indicator than morphological ones. Currently, the number of known species from

Europe is raised from one to thirty (Straka et al. 2015a).

In this paper, we present a renewed checklist of the Strepsiptera from the Netherlands. The taxonomy of the genus *Stylops* is updated, as well as for the genera *Halictoxenos* and *Pseudoxenos*. In the previous Dutch checklist, all species of the latter two genera were treated as a single species per host genus (Smit & Smit 2005, 2010, Smit 2007). Here we follow the insight obtained for *Stylops*, that ecological traits, especially host relationships are a better taxonomic indicator than morphology. Therefore we tentatively recognize *Halictoxenos* and *Pseudoxenos* species mainly described on basis of host specificity as valid, though their validity still needs to be verified. *Pseudoxenos heydeni* (Saunders) is removed from the checklist, for this appears to be a more southern European species (Batelka & Straka 2005, Kinzelbach 1978). The total number of Strepsiptera species recorded from the Netherlands is increased from six to 21.

Material and methods

All Strepsiptera material previously recorded has been re-examined. Furthermore, all newly collected material, as well as the records from the online database www.waarneming.nl have been examined, assigned to the appropriate species when possible and included in the data presented here.

DNA barcoding

DNA extraction was conducted on single legs for males or the entire body for females, using the NucleoMag 96 Tissue kit by Macherey-Nagel on a Thermo Scientific KingFisher Flex magnetic bead extraction robot, with a final elution volume of 150 µl. The standard COI barcoding fragment (Hebert et al. 2003) was amplified using a cocktail of primers LCO1490 and HCO2198 (Folmer et al. 1994), and LepF1 and LepR1 (Hebert et al. 2004). PCR reactions contained 18.75 µl mQ, 2.5 µl 10x PCR buffer CL, 1.0 µl 10 mM of each primer, 0.5 µl 2.5 mM dNTPs and 0.25 µl 5U Qiagen Taq, with 1.0 µl of template DNA. PCR was performed



1. Male *Stylops ater*. Photo: John Smit
1. Mannetje *Stylops ater*.

using an initial denaturation step of 180 s at 94 °C, followed by 40 cycles of 15 s at 94 °C, 30 s at 50 °C and 40 s at 72 °C, and finishing with an extension of 300 s at 72 °C and pause at 12 °C. Bidirectional sequencing was performed at BaseClear (www.baseclear.com). Sequences were edited manually with Sequencher 4.10.1 (Gene Codes Corporation). For all barcoded specimens, sequences and collection data were uploaded to the Barcode of Life Database (BOLD, www.boldsystems.org). BOLD accession codes are provided for the specimens that produced DNA barcodes.

Results

DNA barcoding

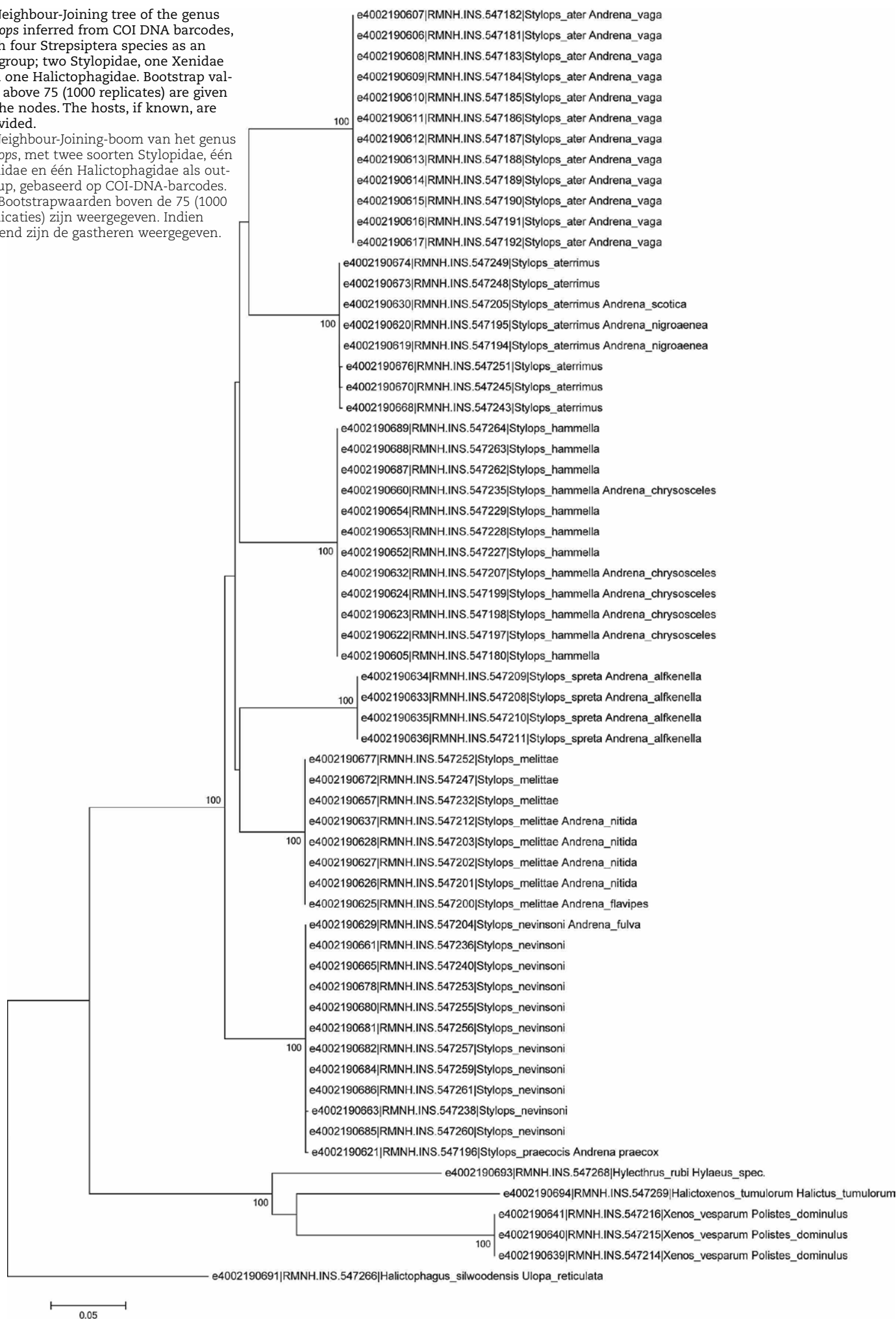
DNA barcodes were obtained for 61 specimens belonging to eleven species. The Neighbour-Joining tree of all analyzed specimens is given in figure 2 and full details of the specimens used for DNA barcoding are provided in table 1. The majority of these barcodes are of *Stylops* species (n=56) belonging to seven species, with an average distance of 12.1% (0.2-15.4%). Most species have a clear and well defined barcoding-gap of over 10%. However, like Jůzová et al. (2015) showed, there are exceptions, for instance *Stylops nevinsoni* Perkins and *S. praecocis* Luna de Carvalho only differ 0.2%. Nevertheless, both are considered valid species because there are distinct morphological differences between the first instars of *Stylops* from *Andrena praecox* (Scopoli) and *A. fulva* (Müller) (Straka et al. 2015a). They also note that *Andrena nigroaenea* (Kirby) can rarely host a second *Stylops* species (Jůzová et al. 2015, Straka et al. 2015a). Therefore, we combined our barcoding sequences with the ones from Jůzová et al. (2015) in order to assure that we use the same species-concept. Additionally, the sequences of Straka et al. (2015b) were added, who not only revealed the differences between *S. aterrimus* Newport and *S. nassonowi* Pierce but also showed that *Andrena scotica* Perkins [= *A. carantonica* Pérez (Else & Edwards 2018)] can host two different parasites as well, like *A. nigroaenea*. Moreover, the

combined molecular data revealed a third *Stylops* and previously unrecorded parasite for *Andrena nigroaenea*. This renders all host-based identifications regarding at least *A. nigroaenea* and *A. scotica* unreliable. Therefore information on the host can be used as an indication of the identification of the *Stylops* species, but should be treated with caution and ideally be checked molecularly. The Neighbour-Joining tree for the combined molecular data is given in figure 5.

Identification

The Strepsiptera names used in the checklist below are derived from the host-parasite information provided by Kinzelbach (1978) and, especially for the genus *Stylops*, by Straka et al. (2015a, 2015b), combined with molecular data. Good diagnostic morphological characters for Strepsiptera are scarce. However, Löwe et al. (2016) provide an extensive description with a large amount of characters revealed with scanning electron microscopy of the female cephalothorax of *Stylops ater* Reichert under its synonymous name *S. ovinae* Noskiewicz & Poluszyński. Furthermore Straka et al. (2015b) provide a description of the female of *S. nassonowi* as well as the first instar. With the recent molecular and biological data of Jůzová et al. (2015), Straka et al. (2015a) and the data presented here as a basis, it would be good to compare these morphological characters for the remainder of the species to see whether or not the females are indeed separable morphologically. As for the males, the amount of available material is so limited that it is difficult to provide any morphological characters, though there seems to be at least some difference in the antenna between some males from different hosts (John Smit personal observation). The growing database of DNA barcodes provides a means to identify the species and link the free living males with the endoparasitic females and thus their hosts. However, even within the molecular data, the COI barcode alone might prove insufficient for species-level identification as shown by Jůzová et al. (2015) and Straka et al. (2015a) with *Stylops praecocis* and *S. nevinsoni*.

2. Neighbour-Joining-boom van het genus *Stylops*, met twee soorten *Stylopidae*, één *Xenidae* en één *Halictophagidae* als out-group, gebaseerd op COI-DNA-barcodes. De Bootstrapwaarden boven de 75 (1000 replicaties) zijn weergegeven. Indien bekend zijn de gastheren weergegeven.



Checklist of Dutch Strepsiptera

In the checklist provided below, all known hosts from the Netherlands are provided as well as additional hosts known from abroad that occur in the Netherlands as well. An overview of the known Dutch host-parasite associations is provided in table 2. Per species the distribution is provided, ordered alphabetically per province, as well as a full bibliography of Dutch records.

Elenchidae

Elenchus tenuicornis (Kirby, 1815)

Hosts *Xanthodelphax stramineus* (Stål, 1858) (Hemiptera: Delphacidae).

Additional hosts known from several species of Delphacidae, amongst others *Javesella dubia* (Kirschbaum, 1868) (Kathirithamby et al. 1990).

Distribution known from six localities: Province of Gelderland: Wageningen, Oranje Nassau's Oord (1955). Province of Noord-Brabant: Tilburg, De Kaaistoep (2008), Udenhout, De Brand (1990). Province of Noord-Holland: Kennemerduinen (2015). Province of Zeeland: Retranchement, Zwinpolder, 't vinkennest (1998). Province of Zuid-Holland: Linschoten (1922) (figure 3).

Previous records Cobben (1965), De Meijere (1923), Smit (2001), Smit & Smit (2005, 2010) and Van Zuijlen et al. (1996).



3. Localities of *Elenchus tenuicornis* in the Netherlands.
3. Vindplaatsen van *Elenchus tenuicornis* in Nederland.

Halictophagidae

Halictophagus silwoodensis Waloff, 1981

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

DNA barcodes NLSIM293-15

Additional hosts no additional hosts are known.

Distribution first encountered in 2007 in Elst (province of Utrecht), during a specific survey for that species, and not found elsewhere until 2016 when 3 males were collected with a malaise-trap at the Planken Wambuis (province of Gelderland) (figure 4).

Previous records Smit (2007), Smit & Smit (2010).



4. Localities of *Halictophagus silwoodensis* in the Netherlands.
4. Vindplaatsen van *Halictophagus silwoodensis* in Nederland.

Stylopidae

Halictoxenos spencei Nasonov, 1893 (figure 6)

Hosts *Lasioglossum morio* (Fabricius, 1793), *L. parvulum* (Schenk, 1853), *L. punctatissimum* (Schenk, 1853) (Hymenoptera: Halictidae).

Additional hosts *Lasioglossum nitidiusculum* (Kirby, 1802), *L. pygmaeum* (Schenck, 1853), *L. sabulosum* (Warncke, 1986), *L. sexstrigatum* (Schenck, 1869) and *L. villulosum* (Kirby, 1802).

Distribution known from eight localities: Province of Friesland: Ameland (2016). Province of Gelderland: Buurserzand (1990). Province of Limburg: Gerendal (1996), Itteren, Holstraat (2015), Maastricht, St. Pietersberg (2005), Thorn, Koningssteen (1999). Province of Noord-Holland: Noordhollands Duinreservaat (2014), Zuid Kennemerland (2000) (figure 7).

Previous records Oudemans (1900, as *Halictophagus*), Smit & Smit (2005).

Halictoxenos tumulorum Perkins, 1918 (figure 8)

Hosts *Halictus confusus* Smith, 1853, *H. tumulorum* (Linnaeus, 1758) (Hymenoptera: Halictidae).

Additional hosts no additional hosts are known.

DNA barcodes NLSIM294-15

Distribution known from 15 localities, mainly in the southeast, but also in the province of Zuid-Holland, Texel and the province of Drenthe (figure 9).

Previous records Smit (2001), Smit & Smit (2005, 2010)

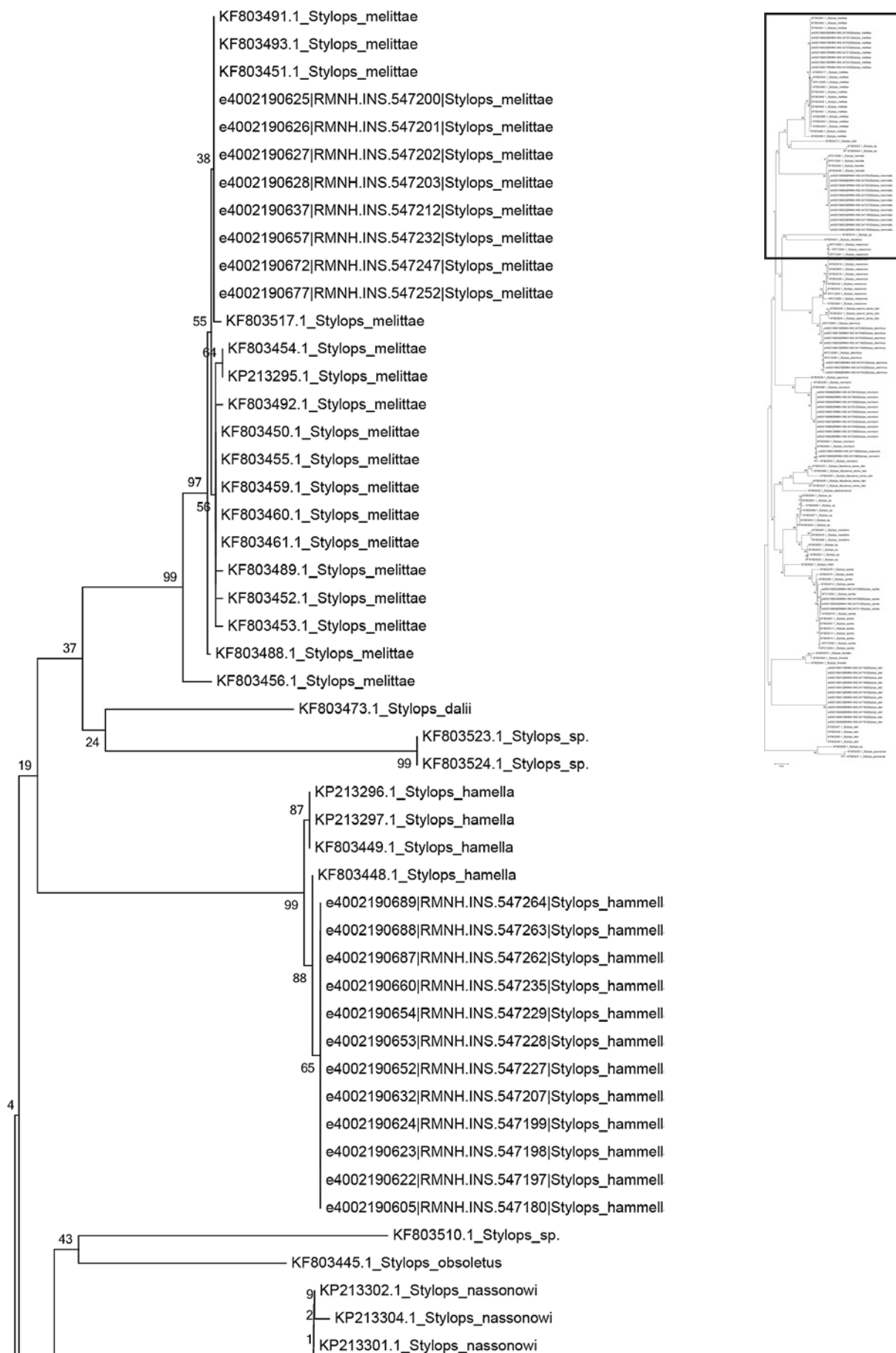
Table 1. Collection data of the specimens used for molecular analyses in this study.
Tabel 1. Gegevens van de exemplaren die voor deze moleculaire analyse zijn gebruikt.

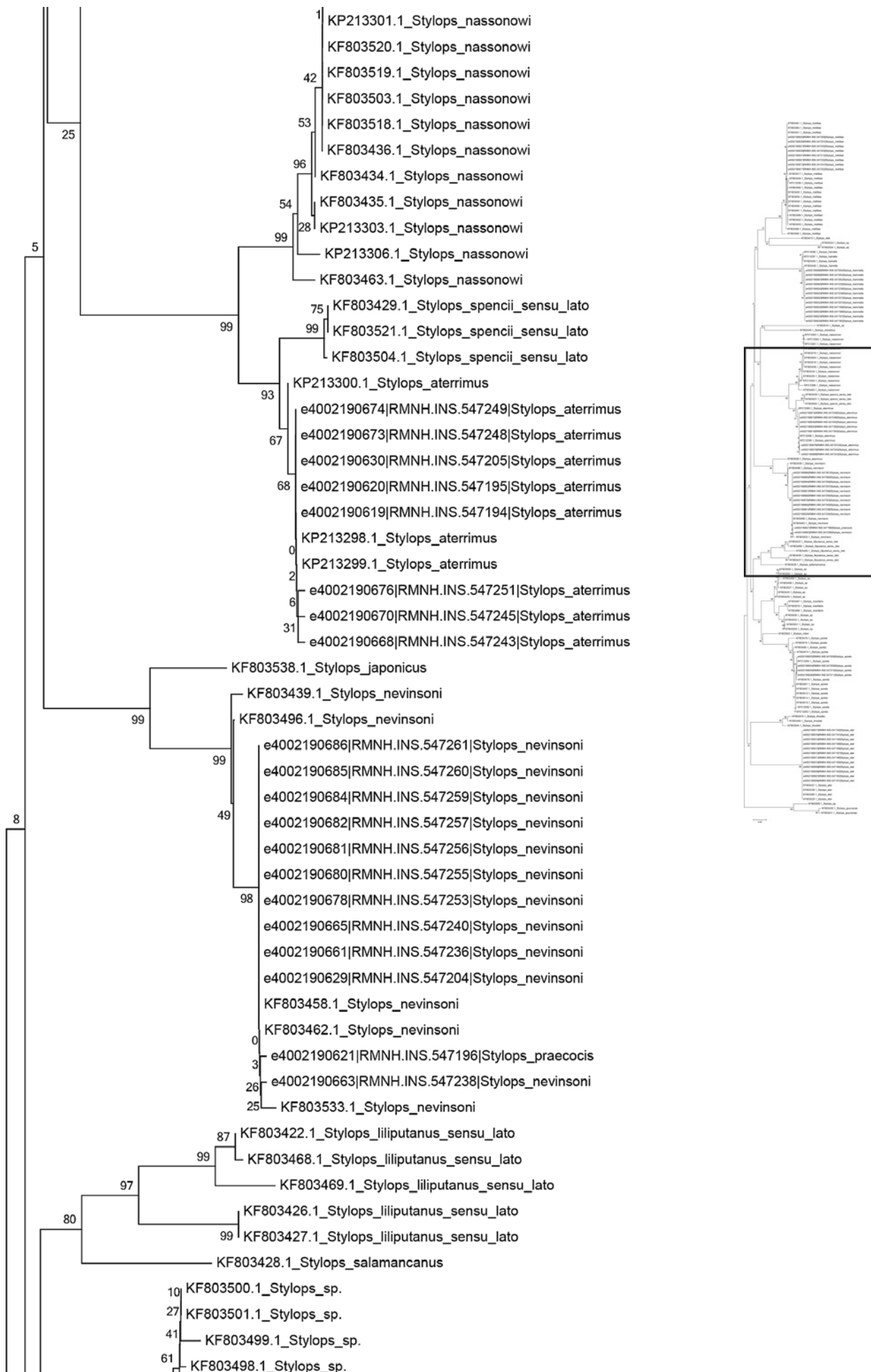
Collection number	Family	Species	Seks	Country	Location
RMNH.INS.547266	Halictophagidae	<i>Halictophagus silwoodensis</i>	female	The Netherlands	Elst, Plantage Willem III
RMNH.INS.547269	Stylopidae	<i>Halictoxenos tumulorum</i>	female	The Netherlands	Lobith, Geuzenwaard
RMNH.INS.547268	Stylopidae	<i>Hylecthrus rubi</i>	female	Spain	Cataluna, Bellprat, Castelo
RMNH.INS.547190	Stylopidae	<i>Stylops ater</i>	female	The Netherlands	Hilversum
RMNH.INS.547191	Stylopidae	<i>Stylops ater</i>	female	The Netherlands	Hilversum
RMNH.INS.547181	Stylopidae	<i>Stylops ater</i>	female	The Netherlands	Soest, de Stompert
RMNH.INS.547182	Stylopidae	<i>Stylops ater</i>	female	The Netherlands	Soest, de Stompert
RMNH.INS.547183	Stylopidae	<i>Stylops ater</i>	female	The Netherlands	Soest, de Stompert
RMNH.INS.547184	Stylopidae	<i>Stylops ater</i>	female	The Netherlands	Soest, de Stompert
RMNH.INS.547185	Stylopidae	<i>Stylops ater</i>	female	The Netherlands	Soest, de Stompert
RMNH.INS.547186	Stylopidae	<i>Stylops ater</i>	female	The Netherlands	Soest, de Stompert
RMNH.INS.547187	Stylopidae	<i>Stylops ater</i>	female	The Netherlands	Soest, de Stompert
RMNH.INS.547188	Stylopidae	<i>Stylops ater</i>	female	The Netherlands	Soest, de Stompert
RMNH.INS.547189	Stylopidae	<i>Stylops ater</i>	female	The Netherlands	Soest, de Stompert
RMNH.INS.547192	Stylopidae	<i>Stylops ater</i>	female	The Netherlands	Maashorst
RMNH.INS.547205	Stylopidae	<i>Stylops aterrimus</i>	female	The Netherlands	Maastricht
RMNH.INS.547243	Stylopidae	<i>Stylops aterrimus</i>	female	The Netherlands	Walem, De Kluis
RMNH.INS.547245	Stylopidae	<i>Stylops aterrimus</i>	female	The Netherlands	Walem, Walem 35
RMNH.INS.547248	Stylopidae	<i>Stylops aterrimus</i>	female	The Netherlands	Walem, Walem 35
RMNH.INS.547249	Stylopidae	<i>Stylops aterrimus</i>	female	The Netherlands	Walem, Walem 35
RMNH.INS.547251	Stylopidae	<i>Stylops aterrimus</i>	female	The Netherlands	Walem, Walem 35
RMNH.INS.547194	Stylopidae	<i>Stylops aterrimus</i>	female	The Netherlands	Deventer, Rijsterborgherpark
RMNH.INS.547195	Stylopidae	<i>Stylops aterrimus</i>	female	The Netherlands	Deventer, Rijsterborgherpark
RMNH.INS.547197	Stylopidae	<i>Stylops hammella</i>	female	The Netherlands	Savelsbos, Zure Dries
RMNH.INS.547198	Stylopidae	<i>Stylops hammella</i>	female	The Netherlands	Savelsbos, Zure Dries
RMNH.INS.547199	Stylopidae	<i>Stylops hammella</i>	female	The Netherlands	Savelsbos, Zure Dries
RMNH.INS.547207	Stylopidae	<i>Stylops hammella</i>	female	The Netherlands	Savelsbos
RMNH.INS.547227	Stylopidae	<i>Stylops hammella</i>	female	The Netherlands	Gronsveld, Savelsbos
RMNH.INS.547228	Stylopidae	<i>Stylops hammella</i>	female	The Netherlands	Gronsveld, Savelsbos
RMNH.INS.547229	Stylopidae	<i>Stylops hammella</i>	male	The Netherlands	Gronsveld, Savelsbos
RMNH.INS.547262	Stylopidae	<i>Stylops hammella</i>	female	The Netherlands	Gronsveld, Savelsbos
RMNH.INS.547263	Stylopidae	<i>Stylops hammella</i>	female	The Netherlands	Gronsveld, Savelsbos
RMNH.INS.547264	Stylopidae	<i>Stylops hammella</i>	male	The Netherlands	Gronsveld, Savelsbos
RMNH.INS.547235	Stylopidae	<i>Stylops hammella</i>	female	The Netherlands	Walem, Schaesberg
RMNH.INS.547201	Stylopidae	<i>Stylops melittae</i>	female	The Netherlands	Eijsden, Caestert beemden
RMNH.INS.547202	Stylopidae	<i>Stylops melittae</i>	female	The Netherlands	Eijsden, Caestert beemden
RMNH.INS.547203	Stylopidae	<i>Stylops melittae</i>	female	The Netherlands	Eijsden, Caestert beemden
RMNH.INS.547212	Stylopidae	<i>Stylops melittae</i>	female	The Netherlands	Eijsden, 't Tiende vrij
RMNH.INS.547200	Stylopidae	<i>Stylops melittae</i>	female	The Netherlands	Riesenbergh
RMNH.INS.547232	Stylopidae	<i>Stylops melittae</i>	female	The Netherlands	Walem, Schaesberg
RMNH.INS.547247	Stylopidae	<i>Stylops melittae</i>	female	The Netherlands	Walem, Walem 35
RMNH.INS.547252	Stylopidae	<i>Stylops melittae</i>	male	The Netherlands	Walem, De Kluis
RMNH.INS.547260	Stylopidae	<i>Stylops nevinsoni</i>	female	The Netherlands	Middelburg, Ter Hooge
RMNH.INS.547259	Stylopidae	<i>Stylops nevinsoni</i>	female	The Netherlands	Heinkenszand, Landlust
RMNH.INS.547255	Stylopidae	<i>Stylops nevinsoni</i>	female	The Netherlands	Goes, Poelbos
RMNH.INS.547256	Stylopidae	<i>Stylops nevinsoni</i>	female	The Netherlands	Goes, Poelbos
RMNH.INS.547257	Stylopidae	<i>Stylops nevinsoni</i>	female	The Netherlands	Goes, Poelbos
RMNH.INS.547261	Stylopidae	<i>Stylops nevinsoni</i>	female	The Netherlands	Maastricht, Sint Pietersberg
RMNH.INS.547204	Stylopidae	<i>Stylops nevinsoni</i>	female	The Netherlands	Gronsveld
RMNH.INS.547236	Stylopidae	<i>Stylops nevinsoni</i>	female	The Netherlands	Walem, Doalkesberg
RMNH.INS.547238	Stylopidae	<i>Stylops nevinsoni</i>	female	The Netherlands	Walem, Doalkesberg
RMNH.INS.547240	Stylopidae	<i>Stylops nevinsoni</i>	female	The Netherlands	Walem, De Kluis
RMNH.INS.547253	Stylopidae	<i>Stylops nevinsoni</i>	female	The Netherlands	Walem, De Kluis
RMNH.INS.547196	Stylopidae	<i>Stylops praecocis</i>	female	The Netherlands	Deventer, Rijsterborgherpark
RMNH.INS.547208	Stylopidae	<i>Stylops spreta</i>	female	France	France, Cap Leucate
RMNH.INS.547209	Stylopidae	<i>Stylops spreta</i>	female	France	France, Cap Leucate
RMNH.INS.547210	Stylopidae	<i>Stylops spreta</i>	female	France	France, Cap Leucate
RMNH.INS.547211	Stylopidae	<i>Stylops spreta</i>	female	France	France, Cap Leucate
RMNH.INS.547214	Xenidae	<i>Xenos vesparum</i>	female	The Netherlands	Cotessen
RMNH.INS.547215	Xenidae	<i>Xenos vesparum</i>	female	The Netherlands	Cotessen
RMNH.INS.547216	Xenidae	<i>Xenos vesparum</i>	female	The Netherlands	Cotessen

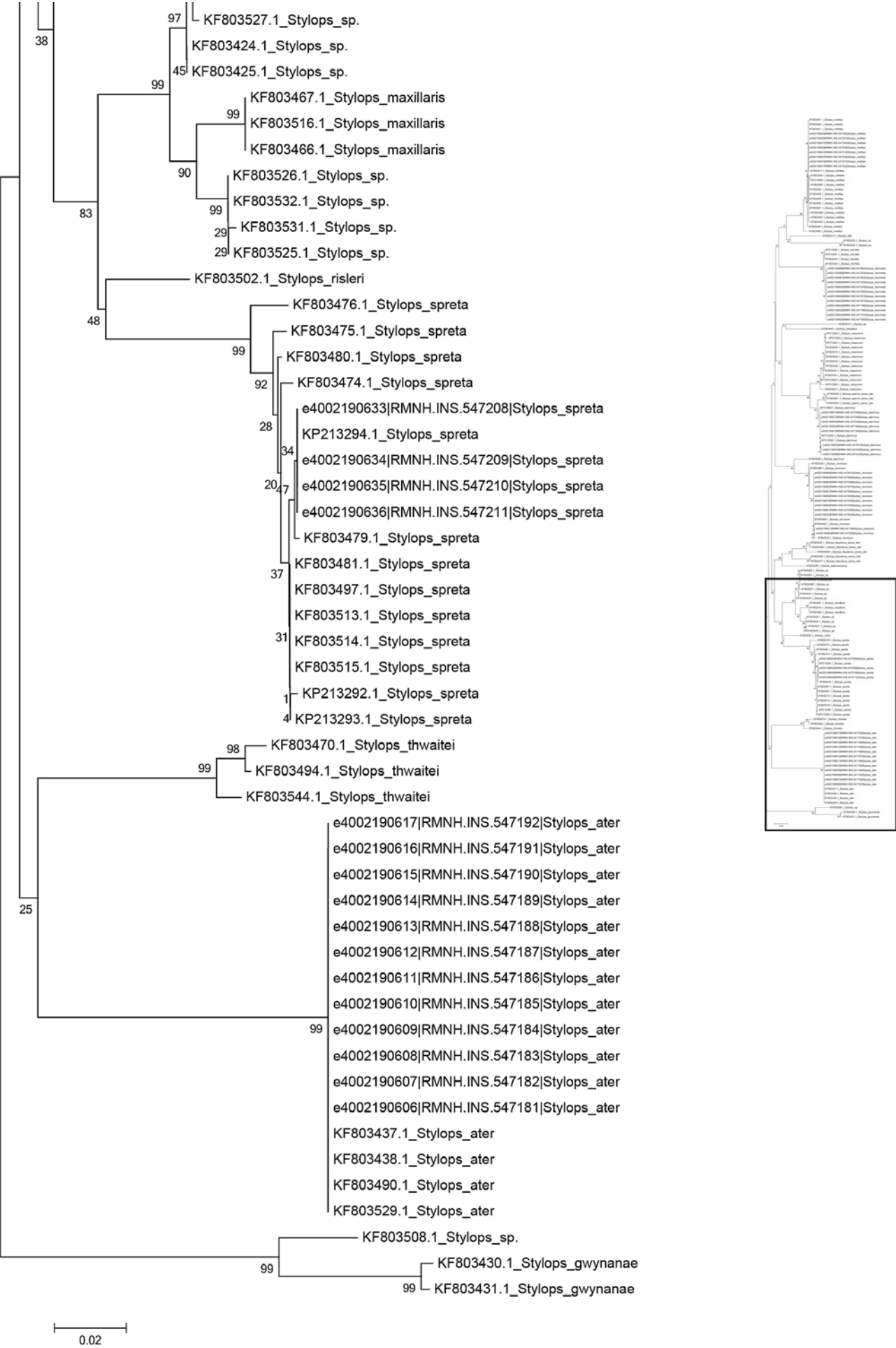
	Latitude	Longitude	Date	Legator	Host
	51,98792	5,52551	27/04/2012	J.T. Smit	<i>Ulopa reticulata</i>
	51,85632	6,11299	26/07/2012	J. Smit	<i>Halictus tumulorum</i>
	41,5125	1,45861	13/08/2009	J. Smit	<i>Hylaeus spec.</i>
	52,22692	5,19694	11/03/2012	M. Reemer	<i>Andrena vaga</i>
	52,22692	5,19694	11/03/2012	M. Reemer	<i>Andrena vaga</i>
	52,13977	5,30131	11/03/2012	J.T. Smit	<i>Andrena vaga</i>
	52,13977	5,30131	11/03/2012	J.T. Smit	<i>Andrena vaga</i>
	52,13977	5,30131	11/03/2012	J.T. Smit	<i>Andrena vaga</i>
	52,13977	5,30131	11/03/2012	J.T. Smit	<i>Andrena vaga</i>
	52,13977	5,30131	11/03/2012	J.T. Smit	<i>Andrena vaga</i>
	52,13977	5,30131	11/03/2012	J.T. Smit	<i>Andrena vaga</i>
	52,13977	5,30131	11/03/2012	J.T. Smit	<i>Andrena vaga</i>
	52,13977	5,30131	11/03/2012	J.T. Smit	<i>Andrena vaga</i>
	52,13977	5,30131	11/03/2012	J.T. Smit	<i>Andrena vaga</i>
	51,69472	5,63309	20/03/2012	P. van Breugel	<i>Andrena vaga</i>
	50,81542	5,71354	15/03/2012	I. Raemakers	<i>Andrena scotica</i>
	50,85988	5,85588	06/04/2012	E. de Bree	
	50,85988	5,85588	08/04/2012	E. de Bree	
	50,85988	5,85588	08/04/2012	E. de Bree	
	50,85988	5,85588	08/04/2012	E. de Bree	
	50,85988	5,85588	08/04/2012	E. de Bree	
	52,25168	6,13407	24/03/2012	J. Smit	<i>Andrena nigroaenea</i>
	52,25168	6,13407	24/03/2012	J. Smit	<i>Andrena nigroaenea</i>
	50,79736	5,74178	03/04/2012	I. Raemakers	<i>Andrena chrysosceles</i>
	50,79736	5,74178	03/04/2012	I. Raemakers	<i>Andrena chrysosceles</i>
	50,79736	5,74178	03/04/2012	I. Raemakers	<i>Andrena chrysosceles</i>
	50,79736	5,74178	15/03/2012	I. Raemakers	<i>Andrena chrysosceles</i>
	50,79736	5,74178	25/03/2012	E. de Bree	
	50,79736	5,74178	25/03/2012	E. de Bree	
	50,79736	5,74178	25/03/2012	E. de Bree	
	50,79736	5,74178	28/04/2012	E. de Bree	
	50,79736	5,74178	28/04/2012	E. de Bree	
	50,79736	5,74178	28/04/2012	E. de Bree	
	50,85988	5,85588	06/04/2012	E. de Bree	<i>Andrena chrysosceles</i>
	50,76157	5,68482	16/03/2012	I. Raemakers	<i>Andrena nitida</i>
	50,76157	5,68482	16/03/2012	I. Raemakers	<i>Andrena nitida</i>
	50,76157	5,68482	16/03/2012	I. Raemakers	<i>Andrena nitida</i>
	50,76149	5,71316	29/05/2012	I. Raemakers	<i>Andrena nitida</i>
	50,80639	5,72766	20/03/2012	I. Raemakers	<i>Andrena flavipes</i>
	50,85988	5,85588	06/04/2012	E. de Bree	
	50,85988	5,85588	08/04/2012	E. de Bree	
	50,85988	5,85588	08/04/2012	E. de Bree	
	51,48516	3,58746	10/04/2012	E. de Bree	
	51,46133	3,80428	10/04/2012	E. de Bree	
	51,48886	3,84653	10/04/2012	E. de Bree	
	51,48886	3,84653	10/04/2012	E. de Bree	
	51,48886	3,84653	10/04/2012	E. de Bree	
	50,81553	5,67097	29/04/2012	E. de Bree	
	50,80639	5,72766	01/04/2012	I. Raemakers	<i>Andrena fulva</i>
	50,85988	5,85588	06/04/2012	E. de Bree	
	50,85988	5,85588	06/04/2012	E. de Bree	
	50,85988	5,85588	06/04/2012	E. de Bree	
	50,85988	5,85588	08/04/2012	E. de Bree	
	52,25168	6,13407	24/03/2012	J. Smit	<i>Andrena praecox</i>
	42,08333	3,08333	04/05/2012	I. Raemakers	<i>Andrena alfkenella</i>
	42,08333	3,08333	04/05/2012	I. Raemakers	<i>Andrena alfkenella</i>
	42,08333	3,08333	04/05/2012	I. Raemakers	<i>Andrena alfkenella</i>
	42,08333	3,08333	04/05/2012	I. Raemakers	<i>Andrena alfkenella</i>
	50,75831	5,93903	09/09/2012	J.T. Smit	<i>Polistes dominulus</i>
	50,75831	5,93903	09/09/2012	J.T. Smit	<i>Polistes dominulus</i>
	50,75831	5,93903	09/09/2012	J.T. Smit	<i>Polistes dominulus</i>

5. The combined Neighbour-Joining tree of the genus *Stylops* inferred from the COI DNA sequences of the material analyzed in this study as well as the ones from Jůzová et al. (2015) and Straka et al. (2015b). Bootstrap values above 75 (1000 replicates) are given at the nodes.

5. Gecombineerde Neighbour-Joining-boom van het genus *Stylops* van de sequenties uit deze studie en die van Jůzová et al. (2015) en Straka et al. (2015b), gebaseerd op COI-DNA-barcodes. De Bootstrapwaarden boven de 75 (1000 replicaties) zijn weergegeven.









6. Male *Lasioglossum punctatissimum* with a female *Halictoxenos spencei* protruding from its abdomen, between the fifth and sixth tergite.
Photo: Tim Faasen

6. Mannetje *Lasioglossum punctatissimum* met een vrouwtje *Halictoxenos spencei* uitstekend tussen tergiet 5 en 6.



7. Localities of *Halictoxenos spencei* in the Netherlands.

7. Vindplaatsen van *Halictoxenos spencei* in Nederland.



8. Female *Halictus tumulorum* with a female *Halictoxenos tumulorum* protruding from its abdomen, between the fifth and sixth tergite.
Photo: Albert Jacobs

8. Mannetje *Halictus tumulorum* met een vrouwtje *Halictoxenos tumulorum* uitstekend tussen tergiet 5 en 6.



9. Localities of *Halictoxenos tumulorum* in the Netherlands.

9. Vindplaatsen van *Halictoxenos tumulorum* in Nederland.

Stylops analis Perkins, 1918

Hosts *Andrena ventralis* Imhoff, 1832 (Hymenoptera: Andrenidae).

Additional hosts no additional hosts are known.

Distribution known from only one locality: Heeze (2018) (province of Noord-Brabant) (figure 10).

Previous records none.

Stylops andrenaphilus Luna de Carvalho, 1974

Host *Andrena dorsata* Kirby, 1802 (Hymenoptera: Andrenidae).

Additional hosts *Andrena propinqua* Schenk, 1853 is recorded as host for *S. andrenaphilus* (Straka et al. 2015), which is generally regarded a synonym of *A. dorsata*, a concept we follow in this paper. However, the taxonomical status of these two species is still subject to discussion, and if both prove to be valid species both are likely to be hosts for *S. andrenaphilus*.

Distribution known from two localities: Province of Gelderland: Lobith, Geuzenwaard (2014, 2018) and Millingerwaard (2014, 2017) (figure 11).

Previous records none.

Stylops ater Reichert, 1914 (figure 12)

Host *Andrena vaga* Panzer, 1799 (Hymenoptera: Andrenidae).

Note Found once as a parasite of *Andrena nigroaenea* (Júzová et al. 2015, Straka et al. 2015a), making all host-based identifications unreliable.

Additional hosts *Andrena cineraria* (Linnaeus, 1758).

DNA barcodes NLSIM223-15, NLSIM224-15, NLSIM225-15, NLSIM226-15, NLSIM227-15, NLSIM228-15, NLSIM229-15, NLSIM230-15, NLSIM231-15, NLSIM232-15, NLSIM233-15, NLSIM234-15.

Distribution widely distributed in the east and the south, especially on sandy soil (figure 13).

Previous records Nieuwenhuijsen (2017), Smit et al. (2012).

Stylops aterrimus Newport, 1851

Hosts *Andrena bimaculata* (Kirby, 1802), *A. nigroaenea* (Kirby, 1802) and *A. scotica* Perkins, 1916 [= *A. carantonica* Pérez, 1902 (Else & Edwards 2018)] (Hymenoptera: Andrenidae).

Note one female *A. nigroaenea* was found in Deventer (province of Overijssel) in 2012 with two female *S. aterrimus*, which represents the third *Stylops* species found in this particular host. Furthermore one female *A. scotica* was found in Maastricht (province of Limburg) in 2012, with one female *S. aterrimus*. All other records of both hosts are plotted separately (figures 32, 34) for they can host two or even three different *Stylops* species, rendering all host-based identifications unreliable.

Additional hosts *Andrena agilissima* (Scopoli, 1770).

DNA barcodes NLSIM236-15, NLSIM237-15, NLSIM247-15, NLSIM271-15, NLSIM273-15, NLSIM276-15, NLSIM277-15, NLSIM279-15.

Distribution is poorly known for it is solely based on the rather rare host *A. bimaculata* and a few molecularly identified specimens. Known from six localities: Province of Gelderland: Beek (Ubbergen) (2017). Province of Limburg: Maastricht (2012), Reijmerstok, Vosberg-grub (2004), Walem (2012). Province of Overijssel: Deventer (2012). Province of Utrecht: Utrecht, Grift-park (2017, 2018) (figure 14).

Previous records Smit & Smit (2005).



10. Locality of *Stylops analis* in the Netherlands.

10. Vindplaats van *Stylops analis* in Nederland.

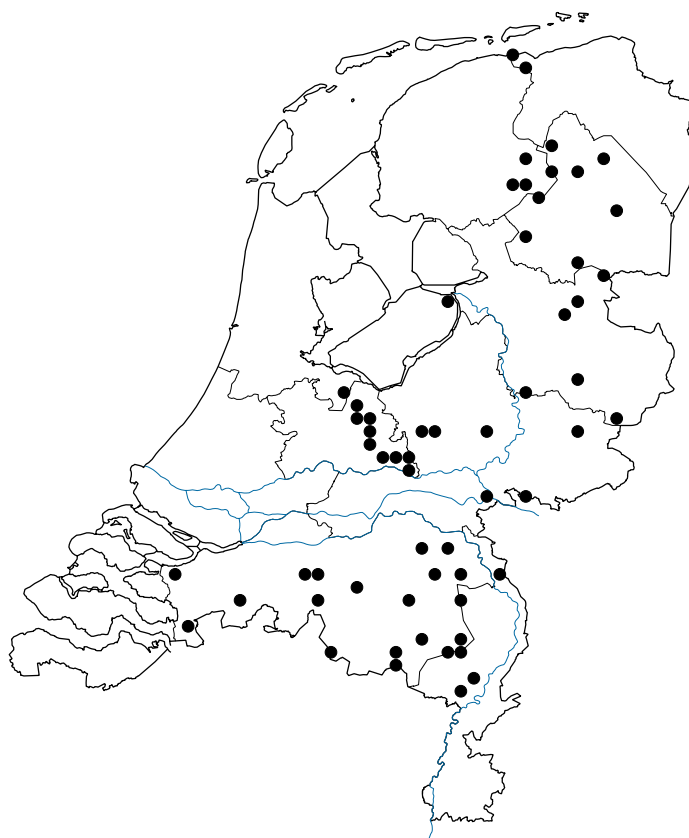


11. Localities of *Stylops andrenaphilus* in the Netherlands.

11. Vindplaatsen van *Stylops andrenaphilus* in Nederland.



12. Female *Adrena vaga* with a male *Stylops ater* on its abdomen.
Photo: John Smit
12. Vrouwtje *Adrena vaga* met een mannetje *Stylops ater* op het achterlijf.



13. Localities of *Stylops ater* in the Netherlands.
13. Vindplaatsen van *Stylops ater* in Nederland.



14. Localities of *Stylops aterrimus* in the Netherlands.
14. Vindplaatsen van *Stylops aterrimus* in Nederland.



15. Localities of *Stylops gwynanae* in the Netherlands.
15. Vindplaatsen van *Stylops gwynanae* in Nederland.

Table 2. Known host-parasite associations from the Netherlands.
Tabel 2. De bekende gastheerrelaties van Strepsiptera uit Nederland.

Orde	Familie	Gastheer	Strepsiptera
Hemiptera	Delphacidae	<i>Xanthodelphax stramineus</i> (Stål, 1858)	<i>Elenchus tenuicornis</i> (Kirby, 1815)
	Ulopidae	<i>Ulopa reticulata</i> (Fabricius, 1794)	<i>Halictophagus silwoodensis</i> Waloff, 1981
Hymenoptera	Halictidae	<i>Lasioglossum morio</i> (Fabricius, 1793)	<i>Halictoxenos spencei</i> Nasonov, 1893
		<i>Lasioglossum parvulum</i> (Schenk, 1853)	<i>Halictoxenos spencei</i> Nasonov, 1893
		<i>Lasioglossum punctatissimum</i> (Schenk, 1853)	<i>Halictoxenos spencei</i> Nasonov, 1893
		<i>Halictus confusus</i> Smith, 1853	<i>Halictoxenos tumulorum</i> Perkins, 1918
		<i>Halictus tumulorum</i> (Linnaeus, 1758)	<i>Halictoxenos tumulorum</i> Perkins, 1918
	Andrenidae	<i>Andrena apicata</i> Smith, 1847	<i>Stylops nevinsoni</i> Perkins, 1918
		<i>Andrena barbilabris</i> (Kirby, 1802)	<i>Stylops cf. packardi</i> Pierce, 1909
		<i>Andrena bicolor</i> Fabricius, 1775	<i>Stylops gwynanae</i> Günther, 1957
		<i>Andrena bimaculata</i> (Kirby, 1802)	<i>Stylops aterrimus</i> Newport, 1851
		<i>Andrena chrysosceles</i> (Kirby, 1802)	<i>Stylops hammella</i> Perkins, 1918
		<i>Andrena clarkella</i> (Kirby, 1802)	<i>Stylops nevinsoni</i> Perkins, 1918
		<i>Andrena dorsata</i> Kirby, 1802	<i>Stylops andrenaphilus</i> Luna de Carvalho, 1974
		<i>Andrena flavipes</i> Panzer, 1799	<i>Stylops melittae</i> Kirby, 1802
		<i>Andrena florea</i> Fabricius, 1793	<i>Stylops spec.</i>
		<i>Andrena fucata</i> Smith, 1847	<i>Stylops nevinsoni</i> Perkins, 1918
		<i>Andrena fulva</i> (Müller, 1766)	<i>Stylops nevinsoni</i> Perkins, 1918
		<i>Andrena gravida</i> Imhoff, 1832	<i>Stylops melittae</i> Kirby, 1802
		<i>Andrena haemorrhoa</i> (Fabricius, 1781),	<i>Stylops spec.</i>
		<i>Andrena helvola</i> (Linnaeus, 1758)	<i>Stylops nevinsoni</i> Perkins, 1918
		<i>Andrena minutula</i> (Kirby, 1802)	<i>Stylops spreta</i> Perkins, 1918
		<i>Andrena nigroaenea</i> (Kirby, 1802)	? <i>Stylops ater</i> Reichert, 1914
		<i>Andrena nigroaenea</i> (Kirby, 1802)	<i>Stylops aterrimus</i> Newport, 1851
		<i>Andrena nigroaenea</i> (Kirby, 1802)	? <i>Stylops melittae</i> Kirby, 1802
		<i>Andrena nitida</i> (Müller, 1776)	<i>Stylops melittae</i> Kirby, 1802
		<i>Andrena praecox</i> (Scopoli, 1763)	<i>Stylops praecocis</i> Luna de Carvalho, 1974
		<i>Andrena scotica</i> Perkins, 1916	<i>Stylops aterrimus</i> Newport, 1851
		<i>Andrena scotica</i> Perkins, 1916	? <i>Stylops nassanowi</i> Pierce, 1909
		<i>Andrena subopaca</i> Nylander, 1848	<i>Stylops spreta</i> Perkins, 1918
		<i>Andrena synadelpha</i> Perkins, 1914	<i>Stylops nevinsoni</i> Perkins, 1918
		<i>Andrena tibialis</i> (Kirby, 1802)	<i>Stylops nassanowi</i> Pierce, 1909
		<i>Andrena vaga</i> Panzer, 1799	<i>Stylops ater</i> Reichert, 1914
		<i>Andrena varians</i> (Kirby, 1802)	<i>Stylops nevinsoni</i> Perkins, 1918
		<i>Andrena ventralis</i> Imhoff, 1832	<i>Stylops analis</i> Perkins, 1918
		<i>Andrena wilkella</i> (Kirby, 1802)	<i>Stylops thwaiti</i> Saunders, 1872
	Vespididae: Eumeninae	<i>Ancistrocerus claripennis</i> Thompson, 1874	<i>Pseudoxenos cf. schaumii</i> Saunders, 1872
		<i>Ancistrocerus gazella</i> (Panzer, 1798)	<i>Pseudoxenos cf. schaumii</i> Saunders, 1872
		<i>Ancistrocerus parietum</i> (Linnaeus, 1758)	<i>Pseudoxenos schaumii</i> Saunders, 1872
		<i>Ancistrocerus trifasciatus</i> (Müller, 1776)	<i>Pseudoxenos andradei</i> Luna de Carvalho, 1953
		<i>Stenodynerus xanthomelas</i> (Herrich-Schäffer, 1839)	<i>Pseudoxenos klugi</i> (Saunders, 1852)
	Vespididae: Polistinae	<i>Polistes dominula</i> (Christ, 1791)	<i>Xenos vesparum</i> Rossius, 1793

Stylops gwynanae Günther, 1957

Host *Andrena bicolor* Fabricius, 1775 (Hymenoptera: Andrenidae).
Additional hosts no additional hosts are known.
Distribution known from two localities: Lobith, Geuzenwaard (2013) and Westervoort (2006) (province of Gelderland) (figure 15).
Previous records none.

Stylops hammella Perkins, 1918

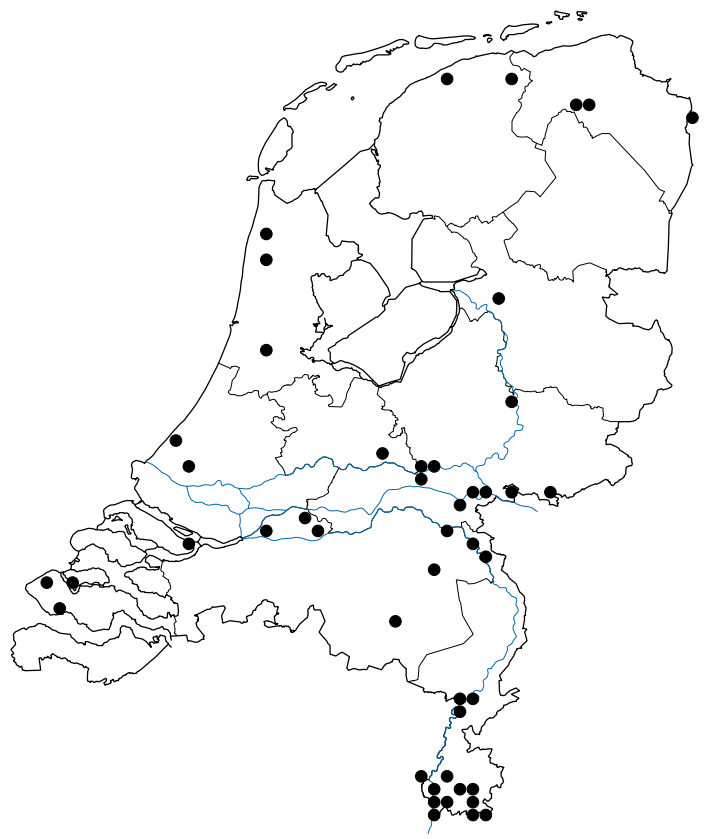
Host *Andrena chrysosceles* (Kirby, 1802) (Hymenoptera: Andrenidae).
Additional hosts *Andrena nitidiuscula* Schenck, 1853.
DNA barcodes NLSIM239-15, NLSIM240-15, NLSIM241-15, NLSIM249-15, NLSIM255-15, NLSIM256-15, NLSIM257-15, NLSIM263-15, NLSIM290-15, NLSIM291-15, NLSIM292-15.
Distribution primarily found in the province of Limburg and along the major rivers (figure 16), which seems more restricted than the distribution of its host (Peeters et al. 2012).
Previous records Smit & Smit (2005).

Stylops melittae Kirby, 1802

Hosts *Andrena flavipes* Panzer, 1799, *A. gravida* Imhoff, 1832, *A. nigroaenea* (Kirby, 1802) and *A. nitida* (Müller, 1776) (Hymenoptera: Andrenidae).
Note the only two sequenced Dutch *Stylops* specimens from *A. nigroaenea* from Deventer (2012) belong to *S. aterrimus*, a previously unrecorded parasite of this host. Nevertheless, the other *Stylops* specimens of this host may belong to *S. melittae*, which is stated to be the primary parasite of *A. nigroaenea* (Straka et al. 2015a). However, since host-based identification of this parasite is unreliable, the records are plotted separately (figure 32).
Additional hosts *A. thoracica* (Fabricius, 1775).
DNA barcodes NLSIM242-15, NLSIM243-15, NLSIM244-15, NLSIM245-15, NLSIM250-15, NLSIM260-15, NLSIM275-15, NLSIM280-15.
Distribution Widely distributed in the Netherlands, not known from the Frisian Islands (figure 17).
Previous records Nieuwenhuijsen (2017), Smit (1994, 2001), Smit & Smit (2005, 2010).



16. Localities of *Stylops hammella* in the Netherlands.
16. Vindplaatsen van *Stylops hammella* in Nederland.



17. Localities of *Stylops melittae* in the Netherlands.
17. Vindplaatsen van *Stylops melittae* in Nederland.



18. Localities of *Stylops nassonowi* in the Netherlands.
18. Vindplaatsen van *Stylops nassonowi* in Nederland.



19. Female *Andrena varians* with a female *Stylops nevinsoni* protruding from its abdomen, between the fifth and sixth tergite. Photo: Tim Faasen

19. Vrouwtje *Andrena varians* met een vrouwtje *Stylops nevinsoni* uitstekend tussen tergiet 5 en 6.

Stylops nassonowi Pierce, 1909

Host *Andrena scotica* Perkins, 1916 [= *A. carantonica* Pérez, 1902 (Else & Edwards 2018)] and *A. tibialis* (Kirby, 1802) (Hymenoptera: Andrenidae).

Note the only sequenced Dutch *Stylops* specimen from *A. scotica* from Maastricht (2012) belongs to *S. aterrimus*, one of two known parasites from this host. According to the data of Jůzová et al. (2015) and Straka et al. (2015b) *S. nassonowi* is more commonly found as a parasite of *A. scotica* (figure 5). However, since host-based identification of this parasite is unreliable, the records are plotted separately (figure 34).

Additional hosts *Andrena trimmerana* (Kirby, 1802).

Distribution is poorly known for the distribution is solely based on one host: *A. tibialis*: known from four localities: Province of Gelderland: Arnhem (1986), Panterden (2017) and Wageningen (1997). Province of Limburg: Maastricht (2017) (figure 18).

Previous records Slikboer (2018), Smit (1994, 2001), Smit & Smit (2005).

Stylops nevinsoni Perkins, 1918 (figure 19, 20)

Hosts *Andrena fulva* (Müller, 1766) and *A. synadelpha* Perkins, 1914 (Hymenoptera: Andrenidae).

Note This species is treated as a valid species separate from *Stylops praecocis*, despite the fact that the distance between the DNA barcodes are rather small (Jůzová et al. 2015, figures 2, 3), see under *S. praecocis*. This makes it difficult to assign the hosts to either one of the *Stylops* species.

Possible hosts see also *Stylops praecocis*: *Andrena apicata* Smith, 1847, *A. clarkella* (Kirby, 1802), *A. fucata* Smith, 1847, *A. helvola* (Linnaeus, 1758) and *A. varians* (Kirby, 1802).

Possible Additional hosts *Andrena lapponica* Zetterstedt, 1838 and *A. mitis* Schmiedeknecht, 1883.

DNA barcodes NLSIM246-15, NLSIM264-15, NLSIM266-15, NLSIM268-15, NLSIM281-15, NLSIM283-15, NLSIM284-15, NLSIM285-15, NLSIM287-15, NLSIM288-15, NLSIM289-15.

Distribution a common species and widely distributed in the Netherlands, except for the northwestern part and the Frisian islands (figure 21).

Previous records Piet (1942), Smit (1994, 2001), Smit & Smit (2005).

Stylops cf. *packardi* Pierce, 1909

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

Note This species was described from north America, where its host *Andrena barbilabris* also occurs (Peeters et al. 2012, Straka et al. 2015a). Whether or not the *Stylops* species parasitizing the European *A. barbilabris* is the same as the one in America needs to be verified, unfortunately no DNA barcodes are available for *Stylops packardi* nor for the European parasite of *A. barbilabris*.

Additional hosts no additional hosts are known.

Distribution known from four localities: Province of Gelderland: Arnhem (2005), Millingerwaard (1995), Rheden, Stikke Trui (1992) and Stokkum (2003) (figure 22).

Previous records Smit (2001), Smit & Smit (2005).

Stylops praecocis Luna de Carvalho, 1974 (figure 23)

Host *A. praecox* (Scopoli, 1763).

Note Despite the fact that the distance between the DNA barcodes of *Stylops praecocis* and *S. nevinsoni* are rather small (Jůzová et al. 2015, figure 2, 3) it is treated as a valid species separate from *S. nevinsoni* by Straka et al. (2015a) because the

phylogenetic study of Jůzová et al. (2015) indicate that the early spring and late spring hosts form two distinct *Stylops* clades. Furthermore Straka et al. (2015a) found morphological differences in the first instars taken from *A. fulva* (*S. nevinsoni*) and *A. praecox* (*S. praecocis*). Therefore it is treated as a separate species here as well.

Possible hosts see also *Stylops nevinsoni*: *Andrena apicata* Smith, 1847, *A. clarkella* (Kirby, 1802), *A. fucata* Smith, 1847, *A. helvola* (Linnaeus, 1758) *A. lapponica* Zetterstedt, 1838 *A. mitis* Schmiedeknecht, 1883 *A. nycthemera* Imhoff, 1866 and *A. varians* (Kirby, 1802).

DNA barcodes NLSIM238-15.

Distribution known from seven localities: Province of Drenthe: Leggelderveld (2018). Province of Flevoland: Lelystad (2013). Province of Gelderland: Arnhem (1994), Rheden, Stikke Trui (1992, 1993), Westervoort (1989). Province of Noord-Brabant: Tongelaar (2013). Province of Overijssel: Deventer (2012). (figure 24).

Previous records Smit (1994, 2001), Smit & Smit (2005).

Stylops sprete Perkins, 1918

Host *Andrena minutula* (Kirby, 1802) and *A. subopaca* Nylander, 1848 (Hymenoptera: Andrenidae).

Additional hosts *Andrena alfenella* Perkins, 1914, *A. falsifica* Perkins, 1915, *A. minutuloides* Perkins, 1914, *A. niveata* Friese, 1887, *A. proxima* Kirby, 1802, *A. saundersella* Perkins, 1914 and *A. stroh-mella* Stoeckhert, 1928.

Distribution only known from three localities: Province of Gelderland: Westervoort (1995). Province of Limburg: Cottessen (1991). Province of Utrecht: Langbroek (2006) (figure 25)

Previous records Oudemans (1900), Slikboer (2018), Smit & Smit (2005).

Stylops thwaitesi Perkins, 1918

Host *Andrena wilkella* (Kirby, 1802) (Hymenoptera: Andrenidae).

Additional hosts *Andrena intermedia* Thomson, 1870, *A. lathyri* Alfken, 1899, *A. ovatula* (Kirby, 1802) and *A. similis* Smith, 1849.

Distribution only known from one very old record: Leiden (1800) (province of Zuid-Holland) (figure 26).

Previous records Oudemans (1900).

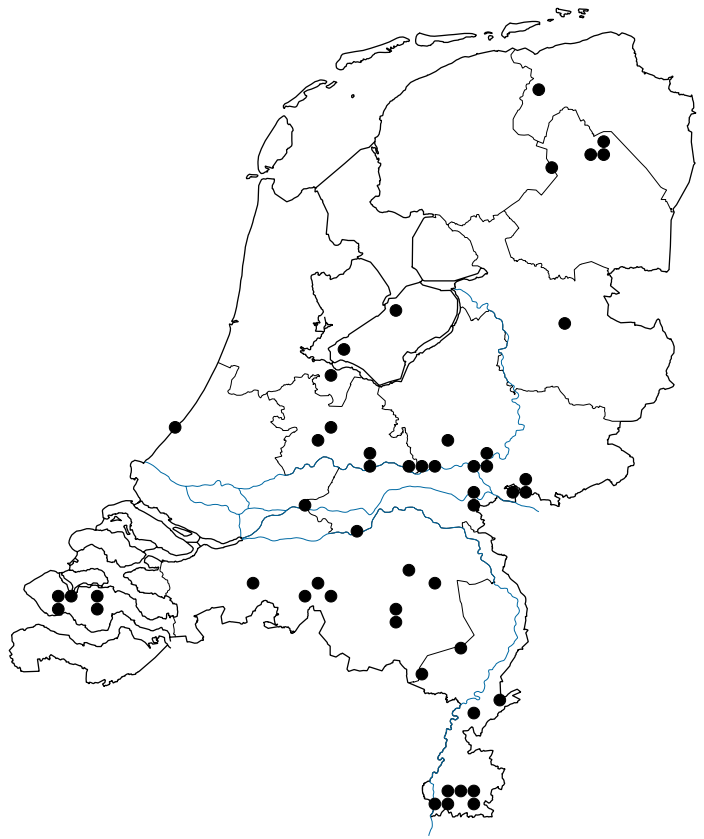
Stylops spec.

There are quite a number of parasitized *Andrena* specimens that could not be assigned to either one of the *Stylops* species given above, for there are no barcodes available of the parasites and the hosts could not be identified reliably. It is known that *Stylops* parasites alter the morphology of their *Andrena* hosts, increasingly with increasing numbers of parasites per host (Askew 1971, Smit 1994, Smit & Smit 2005). Males tend to become more feminine in morphology and vice versa, making their identification a challenge sometimes. These data are plotted in figure 27.

Apart from the *Stylops* species not associated with an identified *Andrena* host, four additional distribution maps are provided for the *Stylops* specimens associated with *Andrena florea* (figure 28) and *A. haemorrhoea* (Fabricius) (figures 29, 30), for their identity remains unresolved, as well as for *A. nigroaeneae* (figures 31, 32) and *A. scotica* (figures 33-34) which are not identified molecularly, for both can host more than one *Stylops* species.



20. Female *Andrena fulva* with a male *Stylops nevinsoni* on its abdomen. Photo: Engelbert Luitsz
20. Vrouwtje *Andrena fulva* met een mannetje *Stylops nevinsoni* op het achterlijf.



21. Localities of *Stylops nevinsoni* in the Netherlands.
21. Vindplaatsen van *Stylops nevinsoni* in Nederland.



22. Localities of *Stylops cf. packardi* in the Netherlands.
22. Vindplaatsen van *Stylops cf. packardi* in Nederland.



23. Female *Andrena praecox* with a female *Stylops praecocis* protruding from its abdomen, between the fifth and sixth tergite. Photo: Antoine van der Heijden
23. Vrouwtje *Andrena praecox* met een vrouwtje *Stylops praecocis* uitstekend tussen tergiet 5 en 6.



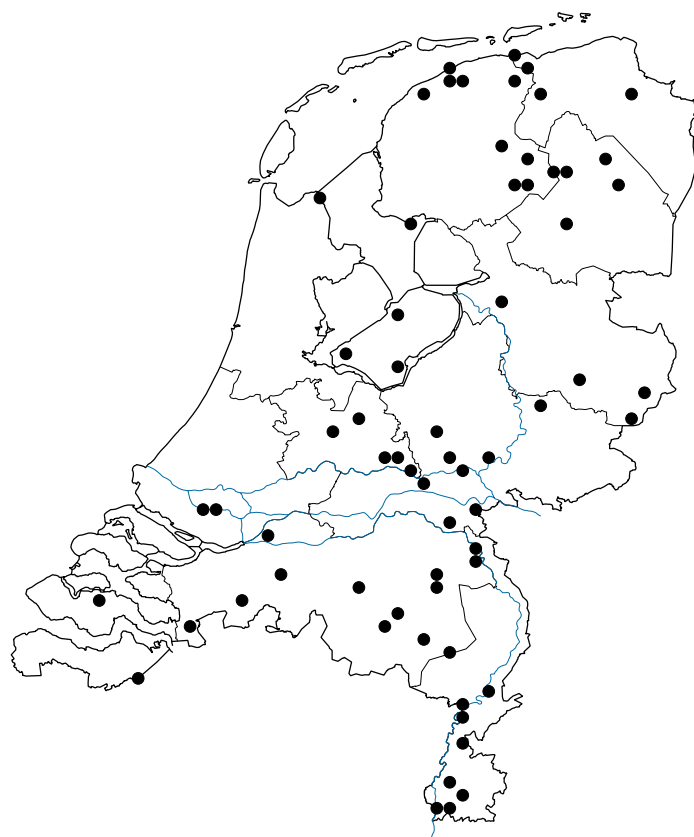
24. Localities of *Stylops praecocis* in the Netherlands.
24. Vindplaatsen van *Stylops praecocis* in Nederland.



25. Localities of *Stylops spreta* in the Netherlands.
25. Vindplaatsen van *Stylops spreta* in Nederland.



26. Locality of *Stylops thwaitesi* in the Netherlands.
26. Vindplaats van *Stylops thwaitesi* in Nederland.



27. Localities of *Stylops* specimens that are not associated with a host species, in the Netherlands.
27. Vindplaatsen van *Stylops*-individueen die niet geassocieerd zijn met een gastheer in Nederland.



28. Male *Andrena florea* with a female *Stylops* spec. protruding from its abdomen, between the fourth and fifth tergite. Photo: Annemiek van Dijk

28. Mannetje *Andrena florea* met een vrouwtje *Stylops* spec. uitstekend tussen tergiet 4 en 5.



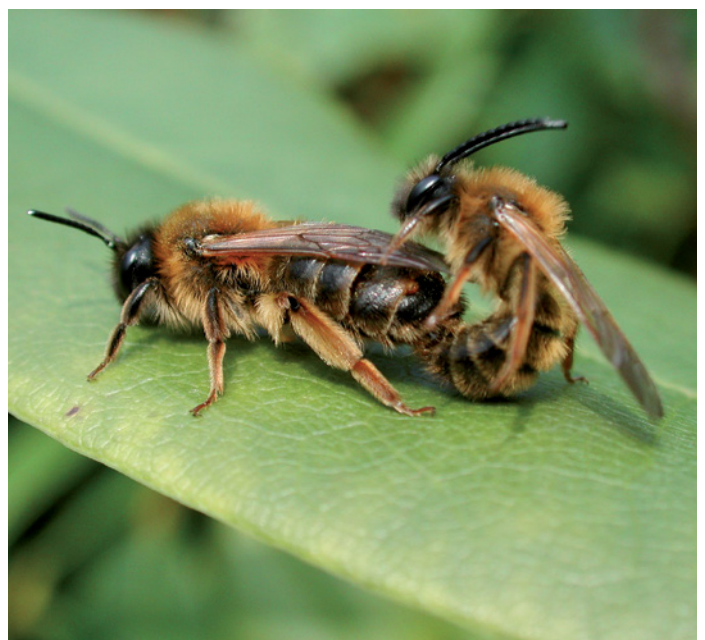
29. Localities of *Stylops* specimens associated with *Andrena florea*, in the Netherlands.

29. Vindplaatsen van *Stylops* individuen geassocieerd met *Andrena florea* in Nederland.



30. Localities of *Stylops* specimens associated with *Andrena haemorrhoa*, in the Netherlands.

30. Vindplaatsen van *Stylops* individuen geassocieerd met *Andrena haemorrhoa* in Nederland.



31. Copula of *Andrena nigroaenea* with a female *Stylops* spec. protruding from the abdomen of the female, between the fourth and fifth tergite. Photo: Hans Arentsen

31. Koppel *Andrena nigroaenea* met een vrouwtje *Stylops* spec. uitstekend uit het achterlijf van het vrouwtje, tussen tergiet 4 en 5.



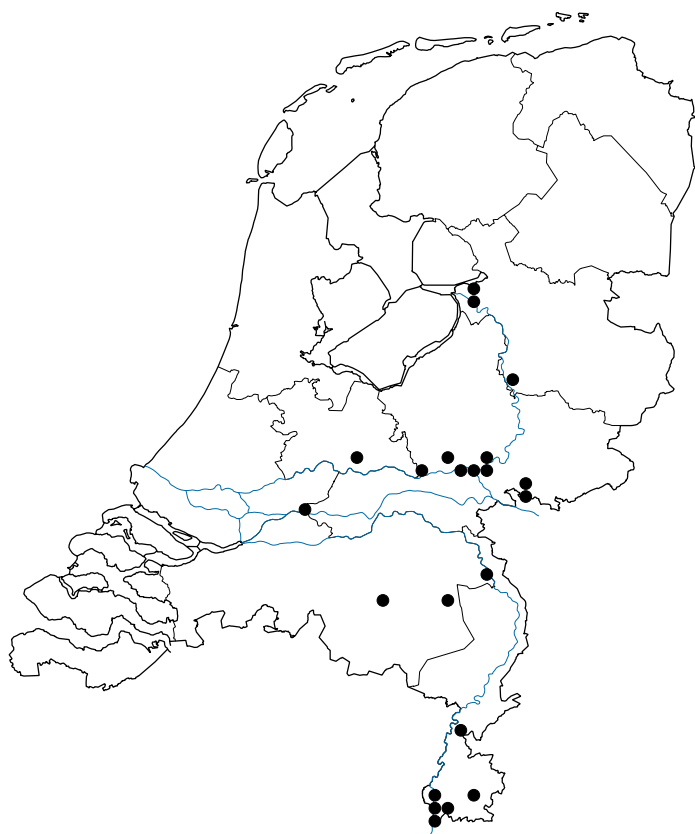
32. Localities of *Stylops* specimens associated with *Andrena nigroaenea*, in the Netherlands.

32. Vindplaatsen van *Stylops* individuen geassocieerd met *Andrena nigroaenea* in Nederland.



33. Female *Andrena scotica* with a male *Stylops* spec. on its abdomen. Photo: Cor Zonneveld

33. Vrouwtje *Andrena scotica* met een man *Stylops* spec. op het achterlijf.



34. Localities of *Stylops* specimens associated with *Andrena scotica*, in the Netherlands.

34. Vindplaatsen van *Stylops* individuen geassocieerd met *Andrena scotica* in Nederland.



35. Localities of *Pseudoxenos andradei* in the Netherlands.

35. Vindplaatsen van *Pseudoxenos andradei* in Nederland.

Xenidae

Pseudoxenos andradei Luna de Carvalho, 1953

Host *Ancistrocerus trifasciatus* (Müller, 1776) (Hymenoptera: Vespidae).

Additional hosts no additional hosts known.

Distribution known from five localities: Province of Gelderland: Arnhem, Meinerswijk (1997), Rheden Stikke Trui (1997). Province of Limburg: Swartbroek, de Krang (2016), Thorn, Koningssteen (1996). Province of Noord-Brabant: Strijbeek, Langven (1997) (figure 35).

Previous records Smit (2001), Smit & Smit (2005).

Pseudoxenos klugi (Saunders, 1852)

Host *Stenodynerus xanthomelas* (Herrich-Schäffer, 1839) (Hymenoptera: Vespidae).

Additional hosts no additional hosts are known.

Distribution only one record from the Netherlands: Tilburg, De Kaaistoep (1998) (province of Noord-Brabant) (figure 36).

Previous records Smit & Smit (2005, 2010).

Pseudoxenos schauumi Saunders, 1872

Host *Ancistrocerus parietum* (Linnaeus, 1758) (Hymenoptera: Vespidae).

Additional hosts no additional hosts are known, but it is possible that the hosts mentioned under *Pseudoxenos* cf. *schaumi* belong to this species as well. However, molecular studies are needed in order to ascertain the correct species delimitations.

Distribution known from two localities: Bergerhei (1992) and Thorn, Abdijcomplex (1995) (province of Limburg) (figure 37).

Previous records Smit & Smit (2005).

Pseudoxenos cf. *schaumi* Saunders, 1872

The hosts given below have never been linked to a certain *Pseudoxenos* species, it is possible that all belong to *P. schauumi*, however, given the recent insight in the species delimitations within the genus *Stylops* it is possible that more species of *Pseudoxenos* are involved. Additional molecular studies are needed to clarify the situation.

Hosts *Ancistrocerus claripennis* Thompson, 1874 and *A. gazella* (Panzer, 1798) (Hymenoptera: Vespidae).

Additional hosts no additional hosts are known.

Distribution known from nine localities: province of Gelderland: Millingerwaard (2000), Pannerden, dijk (2000), Westervoort, emplacement (1996, 1997). Province of Limburg: Maastricht, emplacement (1995), Nuth, Vaesrade (2017), Roermond (1966). Province of Noord-Brabant: Bavel (2016), Tilburg Grollegat (1993), Veghel, de Donken (2016) (figure 38).

Previous records Sanders (1966), Smit & Smit (2005).

Xenos vesparum Rossius, 1793 (figure 39, 40)

Host *Polistes dominula* (Christ, 1791) (Hymenoptera: Vespidae).

Additional hosts several species of the subgenus *Polistes*: *P. atrimaculatus* Zimmerman, 1930, *P. biglumis* (Linnaeus, 1758), *P. nimpha* (Christ, 1791) and *P. semenowi* Morawitz, 1889 (Hymenoptera: Vespidae).

Note a second *Xenos* species has been described, *X. minor* Kinzelbach, 1971, which is associated with the (former) subgenus *Leptopolistes* (Batelka & Straka 2005, Kinzelbach 1971, 1978, Neumayer et al. 2011, Smit & Smit 2014).

DNA barcodes NLSIM251-15, NLSIM252-15, NLSIM253-15.

Distribution first record from 2005, however, rapidly following the



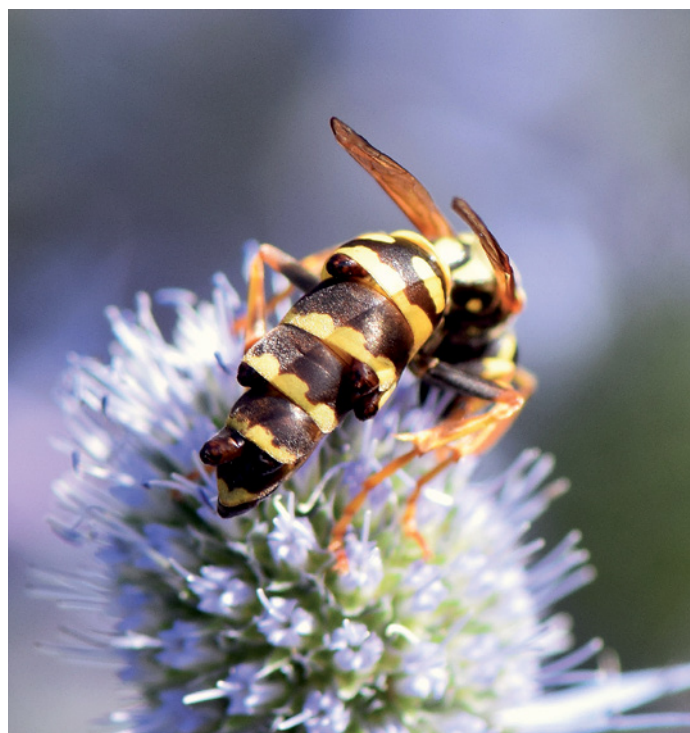
36. Localities of *Pseudoxenos klugi* in the Netherlands.
36. Vindplaatsen van *Pseudoxenos klugi* in Nederland.



37. Localities of *Pseudoxenos schauumi* in the Netherlands.
37. Vindplaatsen van *Pseudoxenos schauumi* in Nederland.



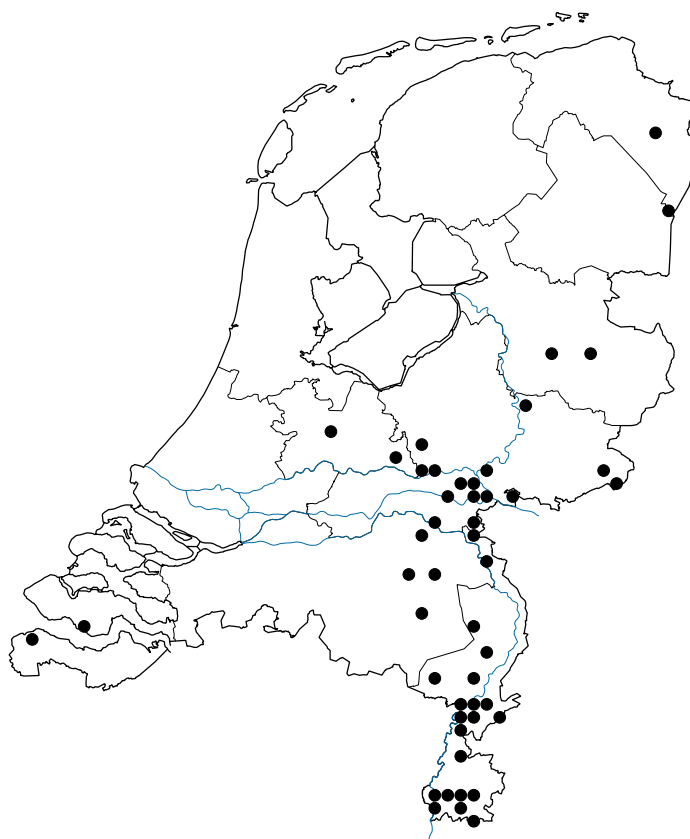
38. Localities of *Pseudoxenos* cf. *schaumi* in the Netherlands.
38. Vindplaatsen van *Pseudoxenos* cf. *schaumi* in Nederland.



39. Female *Polistes dominulus* with six male pupae of *Xenos vesparum* protruding from its abdomen, between several tergites (no 5 & 6 protrude from between the fifth and sixth tergite). Photo: Arno van Stipdonk
39. Vrouwtje *Polistes dominulus* met zes mannelijke puparia van *Xenos vesparum* die tussen verschillende tergieten uitsteken (no 5 & 6 steken tussen tergiet 5 en 6 uit).



40. Male *Xenos vesparum*. Photo: Pieter van Breugel
40. Mannetje *Xenos vesparum*.



41. Localities of *Xenos vesparum* in the Netherlands.
41. Vindplaatsen van *Xenos vesparum* in Nederland.

Table 3. An overview of the Strepsiptera species, including their hosts, expected to turn up in the Netherlands.
Tabel 3. Een overzicht van de nog te verwachten Strepsiptera soorten in Nederland, inclusief de bekende gastheren.

Strepsiptera	Host
Stylopidae	
<i>Halictoxenos arnoldi</i> Perkins, 1918	<i>Lasioglossum xanthopus</i> (Kirby, 1802) (Hymenoptera: Halictidae)
	<i>Lasioglossum costulatum</i> (Kriechbaumer, 1873) (Hymenoptera: Halictidae)
	<i>Lasioglossum leucozonium</i> (Schrank, 1781) (Hymenoptera: Halictidae)
	<i>Lasioglossum quadrinotatum</i> (Kirby, 1802) (Hymenoptera: Halictidae)
<i>Stylops dalii</i> Curtis, 1828	<i>Andrena labialis</i> (Kirby, 1802) (Hymenoptera: Andrenidae)
<i>S. maxillaris</i> Pasteels, 1949	<i>Andrena humilis</i> Imhoff, 1832 (Hymenoptera: Andrenidae)
<i>S. obsoletus</i> Luna de Carvalho, 1974	<i>Andrena distinguenda</i> Schenck, 1871 (Hymenoptera: Andrenidae)
Halictophagidae	
<i>Halictophagus agalliae</i> Abdul-Nour, 1970	<i>Agallia laevis</i> Ribaut, 1935 (Hemiptera: Cicadellidae)
	<i>Agallia consobrina</i> Curtis, 1833 (Hemiptera: Cicadellidae)
<i>Halictophagus curtisi</i> Dale, 1832	<i>Eupelix cuspidate</i> (Fabricius, 1775) (Hemiptera: Cicadellidae)
Corioxenidae	
<i>Malayaxenos trapezonoti</i> Pohl & Melber, 1996	<i>Trapezonotus arenarius</i> (Linnaeus, 1758) (Heteroptera: Lygeidae)
	<i>Trapezonotus desertus</i> Seidenstucker, 1951 (Heteroptera: Lygeidae)

expanding distribution of its host (Smit 2003, Smit & Smit 2008). Now occurring mainly in the south and east of the Netherlands (figure 41).

Previous records Smit & Smit (2005, 2008, 2010).

Discussion

It is quite obvious that the taxonomy of Strepsiptera is far from resolved. In both genera *Pseudoxenos* and in *Stylops* additional name-changes are expected. In order to resolve the exact species delimitations additional molecular analyses are needed. There are still several species for which no DNA barcodes are available. Especially intriguing is the parasite of *Andrena haemorrhoa*. This host species belongs to the subgenus *Trachandrena*, for which three *Stylops* species have been described, all from the United States. Only for *S. hippotes* Pierce there are DNA barcodes available (Júzová *et al.* 2015), therefore the validity of the other species cannot be verified (Straka *et al.* 2015a), nor can the identity of the *Stylops* from the Palearctic *A. haemorrhoa* be verified. The same accounts for *S. cf. packardi* from *Andrena barbilabris*. Furthermore, the identity of the parasite of *A. florea* remains unresolved, no DNA barcodes are available, and it has not previously been recorded as a host of a *Stylops* species.

Another intriguing challenge is to find a way to identify the parasites from *Andrena* species that host multiple *Stylops* species, for the host-association cannot be used for that purpose. This is at least the case for *Andrena nigroaenea* and *A. scotica*, but can perhaps occur in other species as well.

Apart from the taxonomical uncertainties there are also a few species that are still expected to turn up in the Netherlands because their hosts do occur here and are sometimes even quite common. An overview is given in table 3.

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Samenvatting

Hernieuwd overzicht van de Nederlandse Strepsiptera (Insecta)

Recent moleculair werk heeft nieuwe inzichten opgeleverd in de taxonomie van het genus *Stylops*, waarbij het aantal soorten in Europa van één naar 30 is opgeschroefd. Met deze nieuwe inzichten is al het materiaal in Nederland opnieuw onderzocht. Tevens zijn van 61 individuen een DNA-barcodesequentie gegenereerd, verdeeld over elf soorten. Deze sequenties zijn samengevoegd met die uit beide recente Tsjechische studies teneinde er zeker van te zijn dat hetzelfde soortconcept wordt gehanteerd. Uit die studies bleek dat zowel *Andrena nigroaenea* als *A. scotica* twee verschillende parasieten kan bevatten. Uit de gezamenlijke data blijkt dat *A. nigroaenea* nog een derde soort *Stylops* kan herbergen: *S. aterrimus*. Dit heeft tot gevolg dat in ieder geval voor de gastheren *A. nigroaenea* en *A. scotica* de *Stylops*-soorten niet op basis van de gastheren vastgesteld kan worden, mogelijk geldt dit voor meer gastheren. Over het algemeen geldt dat de gastheer een goede eerste indicatie is van de identiteit van de *Stylops*-soort, maar voorzichtigheid is geboden en idealiter wordt deze gecontroleerd aan de hand van hun DNA-sequentie. Ondanks de groeiende database van DNA-sequenties zijn er nog verschillende soorten waarvan de identiteit nog niet vaststaat, dit geldt bijvoorbeeld voor de parasiet van *Andrena barbilabris* (Kirby), waarvan alleen een *Stylops* is beschreven uit Noord-Amerika die mogelijk verschilt van de Europese soort. Ook van *Andrena haemorrhoa* (Fabricius) is het nog onduidelijk welke *Stylops* daarop parasiteert. Deze soort behoort tot het subgenus *Trachandrena*, waarvan drie soorten *Stylops* zijn beschreven, allemaal uit Noord-Amerika. Alleen van *S. hippotes* Pierce zijn DNA-barcodes beschikbaar, waardoor de validiteit van de andere twee soorten niet geverifieerd kan worden, noch voor de *Stylops* van de Europese gastheer. Ook voor *Andrena florea* geldt dat de identiteit van de parasiet nog niet duidelijk is, de soort is niet eerder als gastheer van *Stylops* gemeld en er zijn nog geen DNA-sequenties beschikbaar. In dit artikel wordt een nieuwe checklist gepresenteerd van de Strepsiptera van Nederland. Hierbij is niet alleen de taxonomie van het genus *Stylops* geüpdate, maar ook die van de genera *Halictoxenos* en *Pseudoxenos*. In de vorige Nederlandse checklist werden alle soorten van beide genera geschaard onder één soort per genus. In navolging van de recente inzichten bij het genus *Stylops*, waarbij de gastheerrelaties een betere indicatie van de taxonomie lijken te geven dan morfologie, worden hier de verschillende soorten voorlopig als valide soorten opgevoerd, hoewel hun validiteit nog vastgesteld dient te worden. *Pseudoxenos heydeni* komt daarmee te vervallen voor de Nederlandse lijst, dit lijkt meer een Zuid-Europese soort te zijn. Het aantal soorten Strepsiptera in Nederland wordt hierbij verhoogd van 6 naar 21 soorten.

