

Nomenclature and taxonomy of the genus *Stylops* (Strepsiptera): an annotated preliminary world checklist

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Abstract. Taxonomy and nomenclature of the genus *Stylops* Kirby, 1802 (Strepsiptera) have been understood differently in different parts of world for a long time. Largest differences came from erroneous concept of host specialization of individual species. For this reason, we re-evaluated taxonomy and nomenclature in all *Stylops* species based on distances of DNA barcode sequences (cytochrome c oxidase subunit I). Twenty six species (123 individuals) out of sixty six recognized *Stylops* species from all distribution range were DNA barcoded and their sequences compared. Taxonomy of all West Palaearctic species was restructured to be congruent with results of analysis of the genetic distances. Single European species *Stylops melittae* Kirby, 1802 is divided into thirty species, whose species status is restituted: *S. analis* Perkins, 1918; *S. andrenophilus* Luna de Carvalho, 1974; *S. ater* Reichert, 1914; *S. aterrimus* Newport, 1851; *S. borcherti* Luna de Carvalho, 1974; *S. dalii* Curtis, 1828; *S. deserticola* Medvedev, 1970; *S. dinizi* Luna de Carvalho, 1974; *S. gwynanae* Günther, 1957; *S. hammella* Perkins, 1918; *S. ibericus* Luna de Carvalho, 1969; *S. kinzelbachi* Luna de Carvalho, 1974; *S. liliiputanus* Luna de Carvalho, 1974; *S. lusohispanicus* Luna de Carvalho, 1974; *S. madrilensis* Luna de Carvalho, 1974; *S. maxillaris* Pasteels, 1949; *S. moniliaphagus* Luna de Carvalho, 1974; *S. nevinsoni* Perkins, 1918; *S. obenbergeri* Ogleblin, 1923; *S. obsoletus* Luna de Carvalho, 1974; *S. paracuellus* Luna de Carvalho, 1974; *S. pasteelsi* Luna de Carvalho, 1974; *S. praecocis* Luna de Carvalho, 1974; *S. risleri* Kinzelbach, 1967; *S. rutherenicus* Schkaff, 1925; *S. salamancanus* Luna de Carvalho, 1974; *S. spreta* Perkins, 1918; *S. thwaitesi* Perkins, 1918; *S. ventricosae* Pierce, 1909; and *S. warnckeii* Luna de Carvalho, 1974. *Stylops hartfordensis* Pierce, 1909 is a single species from North America, whose status is restituted from

S. bruneri Pierce, 1909. Names of fifteen West Palaearctic species, fourteen East Palaearctic species and fifteen Nearctic species are supposed to be new junior subjective synonyms: *S. muelleri* Borchert, 1971 = *S. ater*; *S. dominiquei* Pierce, 1909 = *S. bimaculatae* Perkins, 1918 = *S. aterrimus*; *S. nitidiusculae* Poluszyński, 1927 = *S. hammella*; *S. esteponensis* Luna de Carvalho, 1974 = *S. maxillaris*; *S. flavipedis* Hofeneder, 1924 = *S. nitidae* Pasteels, 1954 = *S. giganteus* Luna de Carvalho, 1974 = *S. melittae*; *S. transversa* Pasteels, 1949 = *S. nevinsoni*; *S. duriensis* Luna de Carvalho, 1974 = *S. spreta*; *S. championi* Pierce, 1919 = *S. alfkeni* Hofeneder, 1939 = *S. albofasciatae* Günther, 1957 = *S. borealis* Kifune & Hirashima, 1985 = *S. thwaitesi*; *S. orientis* Kifune & Maeta, 1990 = *S. hirashimai* Kifune & Maeta, 1990 = *S. circularis* Kifune & Hirashima, 1985; *S. truncatus* Kifune & Hirashima, 1985 = *S. oblongulus* Kifune & Hirashima, 1985 = *S. truncatoides* Kifune & Hirashima, 1985 = *S. collinus* Kifune & Maeta, 1990 = *S. aburanae* Kifune & Maeta, 1990 = *S. japonicus* Kifune & Hirashima, 1985; *S. dentatae* Kifune & Maeta, 1990 = *S. aino* Kifune & Maeta, 1990 = *S. izumoensis* Kifune & Maeta, 1990 = *S. nipponicus* Kifune & Maeta, 1990 = *S. subcircularis* Kifune & Maeta, 1990 = *S. fukuiensis* Kifune, 1991 = *S. yamatonis* Kifune & Hirashima, 1985; *S. mandibularis* Pierce, 1911 = *S. moestae* Pierce, 1919 = *S. sinuatus* Pierce, 1919 = *S. advarians* Pierce, 1909; *S. oklahomae* Pierce, 1909 = *S. bipunctatae* Pierce, 1909; *S. neonanae* Pierce, 1919 = *S. duboisi* Bohart, 1937 = *S. bruneri*; *S. vicinae* Pierce, 1909 = *S. childreni* Gray & Westwood, 1832; *S. solidulae* Pierce, 1909 = *S. cornii* Pierce, 1909; *S. swenki* Pierce, 1909 = *S. crawfordi* Pierce, 1909; *S. salicifloris* Pierce, 1909 = *S. hippotes* Pierce, 1909; *S. grandior* Pierce, 1919 = *S. multiplicatae* Pierce, 1909; *S. pacificus* Bohart, 1936 = *S. polemonii* Pierce, 1909; *S. bisalicidis* Pierce, 1919 = *S. medionitans* Pierce, 1919 = *S. subcandidae* Pierce, 1909. Twelve names were recognized as unjustified emendations and these names are new junior objective synonyms: *S. trimmeranae* Kinzelbach, 1978 = *S. trimmerana* Smith, 1857 (= *S. aterrimus*); *S. dalei* Kinzelbach, 1978 = *S. dalii*; *S. gwynanai* Luna de Carvalho, 1974 = *S. gwynanae*; *S. hammelae* Kinzelbach, 1978 = *S. hammella*; *S. nitidiusculai* Luna de Carvalho, 1974 = *S. nitidiusculae* Poluszyński, 1927 (= *S. hammella*); *S. kirbyi* Kinzelbach, 1978 = *S. kirbii* Leach, 1817 (= *S. melittae*); *S. spencei* Kinzelbach, 1971 = *S. spencei* Luna de Carvalho, 1974 = *S. spencii* Pickering, 1836 (= *S. melittae*); *S. melittai* Luna de Carvalho, 1974 = *S. melittae*; *S. spretae* Ulrich, 1930 = *S. spretus* Luna de Carvalho, 1974 = *S. spreta*; *S. thwattei* Luna de Carvalho, 1969 = *S. thwaitesi*. Nine names are recognized as nomina nuda and therefore unavailable in zoological nomenclature. Years of publications of the species names were corrected based on the original literature. Bee hosts are summarized for each species according to the new synonymies.

Key words. Strepsiptera, Stylopidae, integrative taxonomy, DNA barcode, nomenclature, revised status, new synonym, bee parasite, *Andrena*, Andrenidae

Introduction

Genus *Stylops* Kirby, 1802 belongs to the order Strepsiptera, obligate parasites of various insect orders (KATHIRITHAMBY 2009, KINZELBACH 1971). Strepsiptera are well known for complicated life cycles and unusual morphological differences between alate males and wingless neotenic females. The first instars develop inside the female's body and leave her through the front part of body in the case of obligate endoparasitic species. First instars actively find a host and invade its host body. In the species, which parasitise Hymenoptera, the first instar larvae need to be transferred by a vector (KATHIRITHAMBY et al. 2012, LINSLEY & MACSWAIN 1957). When first instars reach the final host individual, they moult into endoparasitic larvae and grow inside the host body. Mature larvae extrude their cephalothoraxes through the host cuticle, males make puparium and pupate, while females become neotenic imago inside puparium. Basal lineages (Mengenillidia) pupate outside the host body, the others (Stylopida) pupate inside the host, but with exposed front part of body (KATHIRITHAMBY 2009, KATHIRITHAMBY et al. 2003). Adult females release sex pheromone and attract short-living males for mating (CVAČKA et al. 2012, LAGOUTTE et al. 2013, TOLASCH et al. 2012). Both sexes are known to manipulate their host's morphology and behaviour, which seems to enhance their mating (STRAKA et al. 2011) and reproductive success (LINSLEY & MACSWAIN 1957).

The genus *Stylops* is the most species rich genus of the Strepsiptera in terms of the described species (KATHIRITHAMBY 2014, KINZELBACH 1971). There are more than 110 available species names; however, the number of species that are really valid is uncertain. The diversity of *Stylops* depends on the species concept used, and the species concepts were previously very variable among taxonomists. Genus *Stylops* and the first single species was first described by KIRBY (1802). At that time, he presented only a single host species, the bee *Andrena nigroaenea* (Kirby, 1802). More than one hundred years later, PIERCE (1909, 1911, 1919) and PERKINS (1918) described approximately 60 species from North America and Europe based on the principle of single host association. This species classification strategy was followed by HOFENEDER (1924a), NOSKIEWICZ & POLUSZYŃSKI (1927), PASTEELS (1949, 1954) in general and for the genus *Stylops*, this strategy was also largely followed by KIFUNE & HIRASHIMA (1985), KIFUNE & MAETA (1990), KIFUNE (1991) and LUNA DE CARVALHO (1969). By contrast, BOHART (1936, 1937, 1941) and also, in part, LUNA DE CARVALHO (1974) took into account existing morphological differences of *Stylops* (males, females and first instars) from different hosts and the similarities of *Stylops* from related hosts that belong to the same host subgenus of *Andrena* (BORCHERT 1963). Bohart's classification method, that species correspond to the subgeneric rank of the host, was adopted in earlier studies published by KINZELBACH (1971), but he decided that the variability of the West Palaearctic species forms a continuum, so all the European species were synonymized under the single name *S. melittae* Kirby, 1802 (KINZELBACH 1978). KINZELBACH (1978), however, proposed to recognise former species that were allied to hosts as subspecies. Since that time, faunistic lists of species from various European countries have contained a single *Stylops* name for specimens from all the hosts (BLEIDORN et al. 2004, KUHLMANN 1998, PEKKARINEN 1997, POHL 2004, POHL & OEHlke 2003, SMIT & SMIT 2005, SOON et al. 2012), unlike lists of Nearctic (KATHIRITHAMBY & TAYLOR 2005) or

East Palaearctic species (KIFUNE et al. 1994). Most authors continue listing all the collected host species, which may help associate them with the correct *Stylops* species in the future, especially when host specialisation seems to be relatively stable in this genus and the number of species is considerably higher than one (JŮZOVÁ et al. 2015).

In this study we aim to make clearer the overview of the published species names of the genus *Stylops* which are available for taxonomic studies, make new suggestions concerning synonymy, remove unavailable names (nomina nuda), check correct spelling and specify correct dates of publication of available names. We use available information from DNA barcode sequences and compare genetic distances among and within species. Recent view of taxonomy is changing from a single *Stylops* species recognized in Europe to many species in this genus (there is a different situation in North America or Asia) and for this reason, formally, but still preliminarily, we sort all known *Stylops* names to species reflecting variability in barcode sequences (JŮZOVÁ et al. 2015), their host specificity and published morphological variability. It is the first conceptual unification of nomenclature and taxonomy in this species rich genus after a hundred years. We also summarize hosts for each published *Stylops* name and discuss possible taxonomic problems for future re-evaluations. We understand this study as a very first step towards modern taxonomy of *Stylops* and better knowledge and easier work on these bee parasites.

Material and methods

We used primary literature for all of the *Stylops* names. We extracted information about the name of author, correct year of publication, original host, and type locality. We prepared list of species with preliminary synonyms. Results of the phylogenetic study by JŮZOVÁ et al. (2015) and the distances between DNA barcode sequences (mitochondrial gene Cytochrome c oxidase subunit I; COI) are used as a leading concept for synonymy here, but we never use it as a rule. Each *Stylops* name was considered a separate case that needs to be examined individually. Names of *Stylops* proposed by authors that used a single host specialisation approach for species definition received the most attention. Species synonymy is always considered, when several *Stylops* names are proposed from host bees of the same subgenus. We follow this affiliation of host subgenus to *Stylops* species as a guideline, except for several cases in which multiple *Stylops* species are likely to be parasites of the hosts belonging to the same subgenus; for example when such *Stylops* species are confirmed by DNA sequence differences or significant morphological differences noted in the literature, or live in distant biogeographic regions. These cases are individually commented on in the notes for each species. No species with unknown host was listed under the synonyms, but as a full species because we cannot decide about synonymy of these species now, except using published evidence. Suggestions of a new name synonymy or a name restoration are presented as ‘supposed new junior subjective synonym’, and ‘status restituted (stat. restit.)’, respectively. All the newly proposed nomenclatural changes are given in bold. Names of host species are listed, but only those directly associated with *Stylops* species name, so the host list is neither complete, nor definitive.

Changes in name spelling of numerous names proposed by LUNA DE CARVALHO (1969, 1974) and KINZELBACH (1978) are considered unjustified emendations, and thus new junior objective synonyms of the original names. Those decisions are based on the Article 33.2.1 (ICZN 1999), because ‘two or more names in the same work [were] treated in a similar way’ and they used the emended spellings systematically throughout their publications.

Each published name is provided with information about the described sex or the first instar (L1); because of the widely used descriptions of morphology of puparia in the Strepsiptera and complicated definition of female, we use ‘F’ for female including female puparium, ‘M’ for male. When holotype was designated and information about it presented in the description, then we present this information for each name.

The names of the *Andrena* host species were obtained according to the updated world bee checklist (ASCHER & PICKERING 2014), and only the current nomenclature of the hosts is used. The subgeneric names of the hosts are used according to GUSENLEITNER & SCHWARZ (2002).

DNA barcode sequences from the published phylogenetic study (JÚZOVÁ et al. 2015) are available from GenBank (<http://www.ncbi.nlm.nih.gov/>). All accession numbers to published sequences are listed in a paragraph under each species in the list. The following list of *Stylops* species is divided for better orientation according to the biogeographic regions – West Palaearctic, East Palaearctic and Nearctic.

List of species of the genus *Stylops*

Stylops Kirby, 1802

Stylops Kirby, 1802: 113. Type species: *Stylops melittae* Kirby, 1802. Designation by monotypy.

= *Katastylops* Pierce, 1919: 454. Synonymized by BOHART (1941: 123).

= *Neostylops* Pierce, 1919: 455. Synonymized by BOHART (1936: 9).

= *Prostylops* Pierce, 1919: 455. Synonymized by BOHART (1941: 123).

Note. Generic name *Stylops* is masculinum (ICZN 1999: 30.1.4.3).

West Palaearctic Region

All the West Palaearctic species of *Stylops* were synonymized with *Stylops melittae* by KINZELBACH (1978: 118), except a few forgotten names, thus the statuses of nearly all species are restituted here in this sense.

Stylops analis Perkins, 1918, stat. restit.

Stylops analis Perkins, 1918: 73, F. Type locality: Great Britain, New Forest.

Host. Not reported in the original description (PERKINS 1918). The host of this species is likely *Andrena (Larandrena) ventralis* Imhoff, 1832, which is supposed to be a junior synonym of *A. analis* Fabricius, 1804. The host is presumed based on the Perkins’s practice to use the host name as the name of parasite. The previously proposed host, *A. (Tarsandrena) tarsata* Nylander, 1848 (KINZELBACH 1971, 1978; ULRICH 1930), is incorrect because its association

with the host name *A. analis* was likely based on an old name association mistake in *Andrena* genus (GUSENLEITNER & SCHWARZ 2002).

Note. No DNA sequence is known for *Stylops* from *A. ventralis*. The species status of *S. analis* needs to be confirmed in the future based on newly collected material.

Stylops andrenaphilus Luna de Carvalho, 1974, stat. restit.

Stylops andrenaphilus Luna de Carvalho, 1974: 331, F. Type locality: Spain, Burgos, Estépar.

Host. *Andrena (Simandrena) propinqua* Schenck, 1853 (LUNA DE CARVALHO 1974).

Note. No DNA sequence is known for *Stylops* from *Andrena propinqua*. The species status of *S. andrenaphilus* needs to be confirmed in the future.

Stylops ater Reichert, 1914, stat. restit.

= *Stylops alterimus*: ANONYMUS (1898a: 509, with reference to plate). Incorrect subsequent spelling of *Stylops aterrimus* Newport, misidentification.

= *Stylops aterrimus*: ANONYMUS (1898b: plate “Zuchtwahl II”, Figs 7a and 7b, not paginated). Incorrect subsequent spelling of *Stylops aterrimus* Newport, misidentification.

Stylops ater Reichert, 1914: 151, M. Type locality: Germany, Merseburg.

? = *Stylops krygeri* Pierce, 1919: 445, F. Type locality: Denmark, Fejø. Status uncertain, see note.

= *Stylops ovinae* Noskiewicz & Poluszyński, 1927: 1098. **Nomen nudum**.

= *Stylops mülleri* Borchert, 1971: 18, M, F. Type locality: Germany, Berlin-Spandau, Weinmeisterhorn. **Supposed new junior subjective synonym.**

Host. *Andrena (Melandrena) vaga* Panzer, 1799 (BORCHERT 1971, REICHERT 1914).

DNA barcode sequences. KF803437, KF803438, KF803490, JN082812, KF803528, KF803529.

Notes. Two names, *Stylops alterimus* and *S. aterrimus* [sic!] appeared in a Lexicon (ANONYMUS 1898a,b). These are not available names, because they obviously refer to *S. aterrimus* Newport and there is no reason to think that new names were intentionally created in a summarizing publication like lexicon, despite the accompanying figure depicting a different species, not *S. aterrimus* Newport.

Stylops ater was subjectively considered an incorrect subsequent spelling (HOFENEDER & FULMEK 1943), or a junior synonym of *S. aterrimus* (ULRICH 1930: 14). However, there is no evidence that the name *S. ater* is merely an incorrect original spelling of *S. aterrimus*, and the name fulfills all the formal conditions for available name proposed before 1931 by method of indication (see ICZN 1999: Articles 12, 12.2.7). Therefore, we consider *Stylops ater* Reichert an available and valid name. The name *S. ater* was used consistently in the REICHERT’s (1914) publication and his reference that he provided the same material for making the figure used in the Lexicon (ANONYMUS 1898a,b) does not affect its availability, as no available species name was proposed in that book (ANONYMUS 1898a,b). The name *S. ater* was not mentioned by KINZELBACH (1978: 118), who listed European species names.

Examination of the type specimen of *S. krygeri* is required. According to KINZELBACH (1978), *S. krygeri* might be the appropriate name for the *Stylops* species from *A. vaga*. However, the

description of the female specimen mentions black basal half of the cephalothorax, which does not match *S. ater*. Such a character is typical for *S. nevinsoni* or *S. thwaitesi*.

Distances between DNA barcode sequences of this species and the other *Stylops* species are 10–20 % and almost invariable within *S. ater* (JÚZOVÁ et al. 2015).

Stylops aterrimus Newport, 1851, stat. restit.

- = *Stylops aterrimus* Newport, 1851: 340, M. Type locality: Great Britain, Hampstead.
- = *Stylops spencii* auct., nec PICKERING (1836).
- = *Stylops Trimmerana* Smith, 1857: 118, M. Type locality: Great Britain. Synonymized with *S. aterrimus* by PIERCE (1908: 77).
- ? = *Stylops dominiquei* Pierce, 1909: 102, M, F. Type locality: France, Nantes. **Supposed new junior subjective synonym.**
- ? = *Stylops bimaculatae* Perkins, 1918: 71, M. Type locality: Great Britain, Berkshire, Crowthorne, Wellington College. **Supposed new junior subjective synonym.**
- = *Neostylops trimmerana*: PIERCE (1919: 456). New generic placement.
- = *Stylops aterrima*: ULRICH (1930: 14). Incorrect gender agreement.
- = *Stylops perkinsi* PASTEELS, 1949: 188, M, F. New substitute name for *S. spencii* Perkins, 1918.
- = *Stylops niger* v. BENEDEN: KINZELBACH (1978: 121). **Nomen nudum.** VAN BENEDEN (1878) used common name ‘*Stylops noir*’ and reproduced description from SMITH (1857).
- = *Stylops trimmeranae* Kinzelbach, 1978: 133. Unjustified emendation. **New junior objective synonym.**

Hosts. *Andrena (Plastandrena) tibialis* (Kirby, 1802) (LUNA DE CARVALHO 1974, PASTEELS 1949, PICKERING 1836), *Andrena (Hoplandrena) trimmerana* (Kirby, 1802) (NEWPORT 1851, SMITH 1857), *Andrena (Agandrena) agilissima* (Scopoli, 1770) (PIERCE 1909).

DNA barcode sequences. KF803429, KF803504, KF803521, KF803522, KP213298, KP213299, KP213300.

Notes. The original tractate written by Newport was published in two parts (called memoirs). Name *S. aterrimus* was published in the second part, which appeared in the year 1851 and not as early as the first part in 1847 (PIERCE 1908).

For differential diagnosis between *S. aterrimus* and *S. nassonowi* and further details about these closely related species see STRAKA et al. (in prep).

Distances between DNA barcode sequence of this species and the other *Stylops* species are 4–20 % (JÚZOVÁ et al. 2015).

Stylops borcherti Luna de Carvalho, 1974, stat. restit.

- Stylops borcherti* Luna de Carvalho, 1974: 349, F. Type locality: Spain, Madrid, Alcalá de Henares.

Host. *Andrena (Melandrena) albopunctata* (Rossi, 1792) (LUNA DE CARVALHO 1974).

Note. This name is possibly a synonym, but it is unclear whether it belongs to *S. melittae* or *S. ater*, both known from the subgenus *Melandrena* in Europe. The latter species was used for comparison to *S. borcherti* by the original author, but we expect rather synonymy with *S. melittae* because *S. melittae* is known to occur in Spain, whereas *S. ater* is not (LUNA DE CARVALHO 1974). No DNA sequence is known for *Stylops* from this host species. The status of this species is restituted for the time being until its status is clarified using integrative taxonomy or from the study of the type material.

***Stylops dalii* Curtis, 1828, stat. restit.**

Stylops dalii Curtis, 1828: plate 226, M, F. Type locality: Great Britain.

= *Stylops dalei* Kinzelbach, 1978: 121. Unjustified emendation. **New junior objective synonym.**

Host. *Andrena (Holandrena) labialis* (Kirby, 1802) (CURTIS 1828).

DNA barcode sequence. KF803473.

Note. Distances between DNA barcode sequence of this species and the other *Stylops* species are 9–18 % (JÚZOVÁ et al. 2015).

***Stylops deserticola* Medvedev, 1970, stat. restit.**

Stylops deserticola Medvedev, 1970: 200, M (holotype), F. Type locality: Kazakhstan, Almaty Province, Kerbulak.

= *Stylops desertorum*: MEDVEDEV (1970: 201). Incorrect original spelling.

Host. *Andrena (Melanapis) fuscosa* Erichson, 1835 (MEDVEDEV 1970).

Note. MEDVEDEV (1970) used two names in his original description. The name *S. desertorum* was used only in a figure and was fixed as incorrect original spelling by KINZELBACH (1978: 120).

This species from south-eastern Kazakhstan is traditionally listed among the West Palaearctic species (KINZELBACH 1978), so we maintain this placement.

No DNA sequence is known for *Stylops* from this host subgenus.

***Stylops dinizi* Luna de Carvalho, 1974, stat. restit.**

Stylops dinizi Luna de Carvalho, 1974: 343, F. Type locality: Spain, Madrid, Vaciamadrid.

Host. *Andrena (Campilogaster) incisa* Eversmann, 1852 (LUNA DE CARVALHO 1974).

Note. No DNA sequence is known for *Stylops* from this host subgenus.

***Stylops gwynanae* Günther, 1957, stat. restit.**

= *Stylops gwynanae* Noskiewicz & Poluszyński, 1927: 1098. **Nomen nudum.**

Stylops gwynanae Günther, 1957 in GÜNTHER & ŠEDIVÝ (1957): 412, F. Type locality not indicated. Implemented in the key for species identification, representing valid description under paragraph 13.1.1. of ICBN (1999).

= *Stylops gwynanai* Luna de Carvalho, 1974: 340. Unjustified emendation. **New junior objective synonym.**

Host. *Andrena (Euandrena) bicolor* Fabricius, 1775 (GÜNTHER & ŠEDIVÝ 1957, LUNA DE CARVALHO 1974).

DNA barcode sequences. KF803430, KF803431.

Note. Distances between DNA barcode sequences of *Stylops* from the subgenus *Euandrena* and the other host subgenera are 13–23 % (JÚZOVÁ et al. 2015). Variability within *Stylops* from *Euandrena* from distant localities in the Palaearctic Region reach up to 6 % in DNA barcode distance, and thus more valid sibling species can be recognized from this host bee subgenus. We propose to call *Stylops* from *Euandrena* hosts *S. gwynanae* *sensu lato*. More comprehensive sampling and detailed study are necessary for evaluation of this taxonomic problem.

***Stylops hammella* Perkins, 1918, stat. restit.**

Stylops hammella Perkins, 1918: 71, F. Type locality: Great Britain, near Oxford.

= *Stylops hammelae* Kinzelbach, 1978: 122. Unjustified emendation. **New junior objective synonym.**

?= *Stylops nitidiusculae* Poluszyński, 1927: 95, M, F. Type locality: Ukraine, near Lviv, ‘Filipkowce’. **Supposed new junior subjective synonym.**

= *Stylops nitidiusculai* Luna de Carvalho, 1974: 327. Unjustified emendation. **New junior objective synonym.**

Hosts. *Andrena (Notandrena) chrysosceles* (Kirby, 1802) (PERKINS 1918), *Andrena (N.) nitidiuscula* Schenck, 1853 (LUNA DE CARVALHO 1974, POLUSZYŃSKI 1927).

DNA barcode sequences. KF803448, KF803449, KP213296, KP213297.

Notes. PERKINS (1918) named this species after the collector Mr. Hamm; however, he used an unusual word form that we interpret as a noun in apposition rather than an adjective.

Distances between DNA barcode sequences of *Stylops* from *Andrena* subgenus *Notandrena* and the hosts from other subgenera are 10–18 % (JÚZOVÁ et al. 2015).

***Stylops ibericus* Luna de Carvalho, 1969, stat. restit.**

Stylops ibericus Luna de Carvalho, 1969: 7, F. Type locality: Portugal, Sagres, Vila do Bispo.

Host. *Andrena (Carandrena) nigroviridula* Dours, 1873 (LUNA DE CARVALHO 1969).

Note. No DNA sequence is known for *Stylops* from this host subgenus.

***Stylops kinzelbachi* Luna de Carvalho, 1974, stat. restit.**

Stylops kinzelbachi Luna de Carvalho, 1974: 327, F. Type locality: Spain, Alicante, Elche.

Host. *Andrena (Rufandrena) orbitalis* Morawitz, 1871 (LUNA DE CARVALHO 1974).

Note. No DNA sequence is known for *Stylops* from this host subgenus.

***Stylops liliputanus* Luna de Carvalho, 1974, stat. restit.**

Stylops liliputanus Luna de Carvalho, 1974: 315, M, F (holotype). Type locality: Spain, Madrid.

Host. *Andrena (Aciandrena) astrella* Warncke, 1975 (holotype) (LUNA DE CARVALHO 1974).

DNA barcode sequences. KF803426, KF803427.

Notes. LUNA DE CARVALHO (1974) also refers to the possible host *A. (Graecandrena) montarco* Warncke, 1975; however, other proposed hosts, such as *A. (Aenandrena) hystrix* Schmiedeknecht, 1883, *Andrena (Micrandrena) bayona* Warncke, 1975, *A. (M.) exigua* Erichson, 1835, and *A. (M.) minutuloides* Perkins, 1914, seem to be unlikely.

Distances between DNA barcode sequences of *Stylops* from the subgenus *Aciandrena* and the other host subgenera are very variable: 1–19 % (JÚZOVÁ et al. 2015). DNA distances among individuals from the host subgenus *Aciandrena* are up to 10 %. They are distinctly consisting of several different species lineages, and for this reason, we use only sequences acquired from specimens collected in Spain for the species *S. liliputanus*. We propose to call *Stylops* from *Aciandrena* hosts *S. liliputanus sensu lato*. More comprehensive sampling and detailed study are necessary for evaluation of this taxonomic problem.

***Stylops lusohispanicus* Luna de Carvalho, 1974, stat. restit.**

Stylops lusohispanicus Luna de Carvalho, 1974: 317, F. Type locality: Portugal: Lisboa.

Host. *Andrena (incertae sedis) verticalis* Pérez, 1895 (LUNA DE CARVALHO 1974). The host of uncertain subgeneric placement.

Note. No DNA sequence is known for *Stylops* from *A. verticalis*.

***Stylops madrilensis* Luna de Carvalho, 1974, stat. restit.**

Stylops madrilensis Luna de Carvalho, 1974: 337, M, F (holotype). Type locality: Spain, Madrid, Arganda.

Host. *Andrena (Ptilandrena) vetula* Lepeletier, 1841 (LUNA DE CARVALHO 1974).

Note. No DNA sequence is known for *Stylops* from this host subgenus in the West Palaearctic Region.

***Stylops maxillaris* Pasteels, 1949, stat. restit.**

Stylops maxillaris Pasteels, 1949: 194, M, F. Type locality: Belgium, Auderghem.

?= *Stylops esteponensis* Luna de Carvalho, 1974: 334, F. Type locality: Spain, Málaga, Estepona. **Supposed new junior subjective synonym.**

Hosts. *Andrena (Chlorandrena) humilis* Imhoff, 1832 (PASTEELS 1949), *Andrena (C.) livens* Pérez, 1895 (LUNA DE CARVALHO 1974).

DNA barcode sequences. KF803466, KF803467, KF803516.

Note. Distances between DNA barcode sequences of *Stylops* from the subgenus *Chlorandrena* and the other host subgenera are 3–18 %, but usually more than 7 % (JÚZOVÁ et al. 2015).

***Stylops melittae* Kirby, 1802**

Stylops melittae Kirby, 1802: 113, M. Type locality not indicated.

= *Stylops Kirbii* Leach, 1817: 135, M. Type locality not indicated. Synonymized with *S. melittae* by PIERCE (1909: 94).

= *Stylops Haworthi* Stephens, 1829: 403. **Nomen nudum.**

= *Stylops spencii* Pickering, 1836: 168, M. Type locality: Great Britain. Synonymized with *S. melittae* by PASTEELS (1949:188).

= *Stylops kirbyi* Kinzelbach, 1978: 125. Unjustified emendation. **New junior objective synonym.**

?= *Stylops flavipedis* Hofeneder, 1924a: 132, M, F. Type locality: Austria, Wien, Kalksburg. **Supposed new junior subjective synonym.**

?= *Stylops nitidae* Pasteels, 1954: 352, F, L1. Type locality: Switzerland, Lausanne, Bois de Helmont. **Supposed new junior subjective synonym.**

= *Stylops spencei* Kinzelbach, 1971: 169. Unjustified emendation. **New junior objective synonym.**

= *Stylops spencei* Luna de Carvalho, 1974: 342. Unjustified emendation. Junior homonym of *S. spencei* Kinzelbach, 1971. **New junior objective synonym.**

= *Stylops melittai* Luna de Carvalho, 1974: 341. Unjustified emendation. **New junior objective synonym.**

?= *Stylops giganteus* Luna de Carvalho, 1974: 352, F. Type locality: Spain, Madrid, Ciempozuelos. **Supposed new junior subjective synonym.**

Hosts. *Andrena (Melandrena) nigroaenea* (Kirby, 1802) (KIRBY 1802), *A. (M.) nitida* (Müller, 1776) (PASTEELS 1954), *A. (Zonandrena) flavipes* Panzer, 1799 (HOFENEDER 1924a), *A. (M.) thoracica* (Fabricius, 1775), *A. (Z.) soror* Dours, 1872 (LUNA DE CARVALHO 1974).

DNA barcode sequences. KF803450, KF803451, KF803452, KF803453, KF803454, KF803455, KF803456, KF803459, KF803460, KF803461, KF803488, KF803489, KF803491, KF803492, KF803493, KF803517, KP213295.

Notes. Distances between DNA barcode sequences of *Stylops* from the subgenera *Melandrena* and *Zonandrena* and the other host subgenera are 8–18 % (JŮZOVÁ et al. 2015). In comparison to other *Stylops* species with known barcode sequences, variability within *Stylops* from *Melandrena* and *Zonandrena* is relatively high, but still at most 2 % in distance (for exception, see below). This fits well with association to a single species from both mentioned subgenera together in the West Palaearctic Region. However, *Melandrena* subgenus hosts also *S. ater* in the West Palearctic Region and rarely the species host pool can overlap in both *Stylops* species. Thus, *A. nigroaenea* can rarely be host of two species of *Stylops* (JŮZOVÁ et al. 2015). To fix the name *S. melittae*, revision of the type will be necessary.

PASTEELS (1949) suggested that the species name *S. spencii*, originally described by (PICKERING 1836) from *A. tibialis*, is a synonym of *S. melittae*, and he proposed a new name for the *Stylops* species that parasitises *A. tibialis*. This problem was first noted by PERKINS (1918), who described the possible irrelevance of Pickering's host identification, and thus, also Pickering's *Stylops* determination. Some uncertainty remains. Examination of the type material or the designation of a neotype is required to fix the nomenclature of the name *S. spencii*.

Stylops moniliaphagus Luna de Carvalho, 1974, stat. restit.

Stylops moniliaphagus Luna de Carvalho, 1974: 332, F. Type locality: Spain, Madrid, Vaciamadrid.

Host. *Andrena (Orandrena) monilia* Warncke, 1967 (LUNA DE CARVALHO 1974).

Note. No DNA sequence is known for *Stylops* from the subgenus *Orandrena*.

Stylops nassonowi Pierce, 1909

Stylops nassonowi Pierce, 1909: 105, F. Type locality: Egypt.

= *Stylops savignyi* Hofeneder, 1924: 254, F. Type locality: Egypt, Aswan, Kitchener's Island. Synonymized with *S. nassonowi* by STRAKA et al. (in prep.).

= *Stylops nassanowi*: LUNA DE CARVALHO (1974: 345). Incorrect subsequent spelling.

Hosts. *Andrena (Plastandrena) pilipes* Fabricius, 1781 (PIERCE 1909), *Andrena (Suandrena) savignyi* Spinola, 1838 (HOFENEDER 1924b).

DNA barcode sequences. KF803433, KF803434, KF803435, KF803436, KF803463, KF803503, KF803518, KF803519, KF803530, KP213301, KP213302, KP213303, KP213304, KP213305, KP213306.

Notes. PIERCE (1909) described *S. nassonowi* from a figure drawing made by NASONOV (1893) from specimens from Germany and Egypt. However, only the specimen from Egypt could be assigned to *S. nassonowi*. Species association of the specimen from Germany is uncertain and may be *S. aterrimus*. For differential diagnosis between *S. aterrimus* and *S. nassonowi*, restitution of status of the latter name and further details about these closely related species see STRAKA et al. (in prep.).

Distances between DNA barcode sequences of this species and the other *Stylops* species are 4–20 % (JŮZOVÁ et al. 2015).

Stylops nevinsoni Perkins, 1918, stat. restit.

Stylops nevinsoni Perkins, 1918: 71, F. Type locality: Great Britain.

?= *Stylops transversa* Pasteels, 1949: 191, M, F. Type locality: Belgium, Uccle. **Supposed new junior subjective synonym.**

Hosts. *Andrena* (*Andrena*) *synadelpha* Perkins, 1914 (PERKINS 1918), *Andrena* (*Andrena*) *fulva* (Müller, 1766) (PASTEELS 1949).

DNA barcode sequences. KF803457, KF803458, KF803462, KF803533.

Notes. Distances between DNA barcode sequences of *Stylops* from the subgenus *Andrena* and the other host subgenera are 8–17 % in the West Palaearctic Region (JŮZOVÁ et al. 2015).

Stylops praecocis, which also parasitizes bees of the subgenus *Andrena*, seems to be very closely related and their DNA barcode sequences differ only 1 % in base composition. However, phylogenetic study suggests two distinct *Stylops* clades for early spring and late spring *Andrena* bee hosts (JŮZOVÁ et al. 2015). In addition, significant morphological differences were found in first instars from *A. fulva* (likely *S. nevinsoni*) and *A. praecox* (likely *S. praecocis*) (BORCHERT 1963). For these reasons, we decided to assign both names to valid species; however, more research is needed in this problem.

Stylops obenbergeri Ogloblin, 1923, stat. restit.

Stylops obenbergeri Ogloblin, 1923: 45, M. Type locality: Czech Republic, Prague, Stromovka.

Host. Unknown.

Note. We restore status of this species for the time being, until studies of the type material clarify its synonymization or validity.

Stylops obsoletus Luna de Carvalho, 1974, stat. restit.

Stylops obsoletus Luna de Carvalho, 1974: 324, F. Type locality: Spain, Tarifa?, uncertain location.

Host. *Andrena* (*Distandrena*) *distinguenda* Schenck, 1871 (LUNA DE CARVALHO 1974).

DNA barcode sequence. KF803445.

Note. Distances between DNA barcode sequences of *Stylops* from the subgenus *Distandrena* and the other host subgenera are 8–19 % (JŮZOVÁ et al. 2015).

Stylops paracuellus Luna de Carvalho, 1974, stat. restit.

Stylops paracuellus Luna de Carvalho, 1974: 339, F. Type locality: Spain, Madrid, Paracuellos.

Host. *Andrena* (*Parandrena*) *tunetana* Schmiedeknecht, 1900 (LUNA DE CARVALHO 1974).

Note. No DNA sequence is known for *Stylops* from the host subgenus.

Stylops pasteelsi Luna de Carvalho, 1974, stat. restit.

Stylops pasteelsi Luna de Carvalho, 1974: 326, F. Type locality: Spain, Málaga, Estepona.

Host. Unclear, maybe *Andrena* (*Melittoides*) *ramlehiana* Pérez, 1903.

Notes. There is most likely a mistake either in the identification or in the locality data of the host. The subgenus *Melittoides* has never been collected in Spain, and the species *A. ramlehiana* is known only from the Near East (ASCHER & PICKERING 2014).

No DNA sequence is known for *Stylops* from the subgenus *Melittoides*.

***Stylops praecocis* Luna de Carvalho, 1974, stat. restit.**

- = *Stylops nycthemerae* Noskiewicz & Poluszyński, 1927: 1098. **Nomen nudum.**
- = *Stylops praecocis* Noskiewicz & Poluszyński, 1927: 1098. **Nomen nudum.**
- Stylops praecocis* Luna de Carvalho, 1974: 329, F. Type locality: Spain, Madrid, Vaciamadrid.

Hosts. *Andrena* (*Andrena*) *praecox* (Scopoli, 1763) (LUNA DE CARVALHO 1974), *A. (A.) nycthema* Imhoff, 1868 (NOSKIEWICZ & POLUSZYŃSKI 1927).

DNA barcode sequences. KF803439, KF803484, KF803495, KF803496.

Notes. The name *S. praecocis* Noskiewicz & Poluszyński, 1927 was correctly mentioned as a nomen nudum by PASTEELS (1954); however, he did not provide a description. PASTEELS (1954) provided good figures of the female cephalothoraces with references to the host. However, this does not make his note of the name *S. praecocis* in his main text available for nomenclatural use.

Distances between DNA barcode sequences of *Stylops* from the subgenus *Andrena* and the other host subgenera are 8–17 % in the West Palaearctic Region (JÚZOVÁ et al. 2015). However, see notes under *S. nevinsoni*.

***Stylops risleri* Kinzelbach, 1967, stat. restit.**

Stylops risleri Kinzelbach, 1967: 37, F. Type locality: Spain, Canary Islands, Teneriffe, Las Canadas.

Host. *Andrena* (*Micrandrena*) *lineolata* Warncke, 1968 (KINZELBACH 1967).

DNA barcode sequence. KF803502.

Notes. Distances between DNA barcode sequences of *Stylops* from *A. (M.) lineolata* and the other host species including species from the subgenus *Micrandrena* are 6–17 % (JÚZOVÁ et al. 2015).

The host name published by KINZELBACH (1967) was mentioned before the description of *Stylops* species, so Kinzelbach used the host name as a nomen nudum.

***Stylops ruthenicus* Schkaff, 1925, stat. restit.**

Stylops ruthenicus Schkaff, 1925: 139, M. Type locality: Ukraine, Kharkiv Oblast, Zmiiv.
= *Afrostylops ruthenicus* (Schkaff): Fox & Fox (1964: 756). New generic placement.

Host. Unknown.

Notes. We restore status of this species for the time being until studies of the type material clarify its synonymization or validity.

Fox & Fox (1964) placed *S. ruthenicus* Schkaff, 1925 incorrectly in the genus *Afrostylops* Fox & Fox, 1964; however, the type species of *Afrostylops* belongs to the genus *Myrmecolax* Westwood, 1858, and thus *Afrostylops* is junior synonym of *Myrmecolax* (KINZELBACH 1971).

***Stylops salamancanus* Luna de Carvalho, 1974, stat. restit.**

Stylops salamancanus Luna de Carvalho, 1974: 322, F. Type locality: Spain, Salamanca.

Host. *Andrena* (*Aenandrena*) *hedikae* Jaeger, 1934 (LUNA DE CARVALHO 1974).

DNA barcode sequence. KF803428.

Note. Distances between DNA barcode sequences of *Stylops* from the subgenus *Aenandrena* and the other host subgenera are 9–17 % (JÚZOVÁ et al. 2015).

Stylops spreta Perkins, 1918, stat. restit.

- Stylops spreta* Perkins, 1918: 73, F. Type locality: Great Britain.
 = *Stylops parvulae* Noskiewicz & Poluszyński, 1927: 1098. **Nomen nudum.**
 = *Stylops spretae* Ulrich, 1930: 15. Unjustified emendation. **New junior objective synonym.**
 = *Stylops spretus* Luna de Carvalho, 1974: 322. Unjustified emendation. **New junior objective synonym.**
 ?= *Stylops duriensis* Luna de Carvalho, 1974: 321, F. Type locality: Portugal, Alto Douro. **Supposed new junior subjective synonym.**

Hosts. *Andrena (Micrandrena) minutula* (Kirby, 1802) (NOSKIEWICZ & POLUSZYŃSKI 1927, PERKINS 1918), *A. (M.) tenuistriata* Pérez, 1895 (LUNA DE CARVALHO 1974).

DNA barcode sequences. KF803474, KF803475, KF803476, KF803477, KF803478, KF803479, KF803480, KF803481, KF803497, KF803512, KF803513, KF803514, KF803515, KP213292, KP213293, KP213294.

Notes. Distances between DNA barcode sequences of *Stylops* from the West Palaearctic representatives of the subgenus *Micrandrena* and the other host subgenera are 7–17 % (JŮZOVÁ et al. 2015). Distances between DNA sequences of *Stylops* within the subgenus *Micrandrena* from the West Palaearctic and East Palaearctic Regions are 0–9 % (JŮZOVÁ et al. 2015), which suggests more than one species of *Stylops* parasitizing the subgenus *Micrandrena*. Variability within *Stylops* from *Micrandrena* hosts from distant localities in European continent is only up to 2 % in DNA distance, which suggests only a single species in continental Europe parasitising the bees of the subgenus *Micrandrena*. See also notes under the closely related *Stylops* species, *S. risleri* and *S. kaguyae*.

Stylops thwaitesi Perkins, 1918, stat. restit.

- = *Stylops thwaitesi* Saunders, 1872: 23. **Nomen nudum.**
Stylops thwaitesi Perkins, 1918: 70, M, F. Type locality: Great Britain.
 = *Stylops wilkellae* Perkins, 1918: 70, M, F. Type locality: Great Britain, Surrey, Woking. Synonymized with *S. thwaitesi* by PASTEELS (1954: 349).
 ?= *Stylops championi* Pierce, 1919: 440, M. Type locality: Great Britain, Woking. **Supposed new junior subjective synonym.**
 = *Stylops xanthuriae* Noskiewicz & Poluszyński, 1927: 1098. **Nomen nudum.**
 ?= *Stylops alfskeni* Hofeneder, 1939: 187, M, F. Type locality: Germany, Hannover, Leuchtenberg. **Supposed new junior subjective synonym.**
 = *Stylops twaithei*: PASTEELS (1954: 349). Incorrect subsequent spelling.
 ?= *Stylops albofasciatae* Günther, 1957: 412, M, F. Type locality: Not indicated, probably Czech Republic. **Supposed new junior subjective synonym.**
 = *Stylops thwattesi* Luna de Carvalho, 1969: 8. Unjustified emendation. **New junior objective synonym.**
 ?= *Stylops borealis* Kifune & Hirashima, 1985: 53, M (holotype), F. Type locality: Japan, Hokkaido, Tokachi, Ashoro. **Supposed new junior subjective synonym.**

Hosts. *Andrena (Taeniandrena) ovatula* (Kirby, 1802) (KIFUNE et al. 1994, PERKINS 1918), *A. (T.) similis* Smith, 1849 (HOFENEDER 1939), *A. (T.) albofasciata* Thomson, 1870 (GÜNTHER & ŠEDIVÝ 1957, PASTEELS 1954), *A. (T.) ezoensis* Hirashima, 1965 (KIFUNE & HIRASHIMA 1985, KIFUNE & MAETA 1990), *A. (T.) wilkella* (Kirby, 1802) (GÜNTHER & ŠEDIVÝ 1957, LUNA DE CARVALHO 1974, PASTEELS 1954).

DNA barcode sequences. KF803470, KF803494, KF803544.

Notes. PASTEELS (1949: 186) correctly noted that the name proposed by SAUNDERS (1872) is unavailable, and the author of the name is PERKINS (1918).

We suggest a synonymy of *S. championi* with *S. thwaitesi*, because *S. championi* was described based on the same series of specimens collected by G. C. Champion and described also as *S. wilkellae*. Description of morphological characters presented by PIERCE (1919), especially length of antennal segments, is identical to description provided by PERKINS (1918).

We also suggest synonymization of *S. borealis* with *S. thwaitesi* because of very similar DNA barcode sequences between the West and East Palaearctic individuals. The sequences from the Japanese population differ from the European population of this species by only 1.7–1.9 %. *Stylops thwaitesi* differs from other species in 9–18 % of the DNA barcode sequence base pairs (JŮZOVÁ et al. 2015).

***Stylops ventricosae* Pierce, 1909, stat. restit.**

Stylops ventricosae Pierce, 1909: 109, F. Type locality: Croatia, Fiume [= Rijeka].

Host. *Andrena (Cryptandrena) ventricosa* Dours, 1873.

Note. No DNA sequence is known for *Stylops* from this host subgenus.

***Stylops warnckeii* Luna de Carvalho, 1974, stat. restit.**

Stylops warnckeii Luna de Carvalho, 1974: 325, F. Type locality: Spain, Madrid, Arganda.

Host. *Andrena (Fumandrena) pandosa* Warncke, 1968.

Note. No DNA sequence is known for *Stylops* from this host subgenus.

East Palaearctic Region

***Stylops circularis* Kifune & Hirashima, 1985**

Stylops circularis Kifune & Hirashima, 1985: 50, F. Type locality: Japan, Shikoku, Tokushima, Akui.

?= *Stylops orientis* Kifune & Maeta, 1990: 101, F. Type locality: Japan, Honshu, Tokyo, Nerima-ku, Nakamura-cho.

Supposed new junior subjective synonym.

?= *Stylops hirashimai* Kifune & Maeta, 1990: 102, F. Type locality: Honshu, Matsue, Nagae. Correct original spelling (fixed here). **Supposed new junior subjective synonym.**

= *Stylops hirashinai*: KIFUNE & MAETA (1990: 102). Incorrect original spelling.

Hosts. *Andrena (Melandrena) sasakii* Cockerell, 1913 (KIFUNE & HIRASHIMA 1985), *A. (M.) watasei* Cockerell, 1913, *A. (M.) parathoracica* Hirashima, 1957 (KIFUNE & MAETA 1990).

Notes. In KIFUNE & MAETA (1990), this species name occurred in two different spellings; once in the title as *S. hirashinai* [*lapsus calami*], and correctly as *S. hirashimai* throughout the rest of article. Here we fix *S. hirashimai* as the correct original spelling of the name.

No DNA sequence is known for *Stylops* from this host subgenus from the East Palaearctic Region.

***Stylops japonicus* Kifune & Hirashima, 1985**

Stylops japonicus Kifune & Hirashima, 1985: 46, F. Type locality: Japan, Kyushu, Mt. Hikosan.

?= *Stylops truncatus* Kifune & Hirashima, 1985: 46, F. Type locality: Japan, Hokkaido, Tokachi, Nukabira. **Supposed new junior subjective synonym.**

- ?= *Stylops oblongulus* Kifune & Hirashima, 1985: 47, F. Type locality: Japan, Honshu, Saitama, Hodosan. **Supposed new junior subjective synonym.**
- ?= *Stylops truncatoides* Kifune & Hirashima, 1985: 50, F. Type locality: Japan, Hokkaido, Tokachi, Nukabira. **Supposed new junior subjective synonym.**
- ?= *Stylops collinus* Kifune & Maeta, 1990: 98, F. Type locality: Japan, Honshu, Yamanashi, Masutomi. **Supposed new junior subjective synonym.**
- ?= *Stylops aburanae* Kifune & Maeta, 1990: 98, F. Type locality: Japan, Honshu, Nagano, Ina, Todai. **Supposed new junior subjective synonym.**

Hosts. *Andrena (Andrena) benefica* Tadauchi & Hirashima, 1987, *A. (A.) maukensis* Matsumura, 1911, *A. (A.) longitibialis* Hirashima, 1962, *A. (A.) lapponica shirozui* Hirashima, 1962 (KIFUNE & HIRASHIMA 1985), *A. (A.) nawai* Cockerell, 1913, *A. (A.) aburana* Hirashima, 1962 (KIFUNE & MAETA 1990), *A. (A.) sakagamii* Tadauchi, Hirashima & Matsumura, 1987 (KIFUNE et al. 1994).

DNA barcode sequence. KF803538.

Note. Distances between DNA barcode sequences of *Stylops* from the subgenus *Andrena* from the East- and West Palaearctic Region are 5 % (JÚZOVÁ et al. 2015).

Stylops kaguyae Kifune & Hirashima, 1985

Stylops kaguyae Kifune & Hirashima, 1985: 51, F. Type locality: Japan, Kyushu, Fukuoka.

Hosts. *Andrena (Micrandrena) kaguya* Hirashima, 1965, *Andrena (M.) minutula* (Kirby, 1802) (KIFUNE & HIRASHIMA 1985), *Andrena (M.) hikosana* Hirashima, 1957, *Andrena (M.) komachi* Hirashima, 1965 (KIFUNE & MAETA 1990).

DNA barcode sequences. KF803539, KF803537.

Note. Distances between DNA barcode sequences of *Stylops* from the subgenus *Micrandrena* from the East and West Palaearctic Region are 8–9 % (JÚZOVÁ et al. 2015).

Stylops montanus Kifune & Maeta, 1990

Stylops montanus Kifune & Maeta, 1990: 103, F. Type locality: Japan, Honshu, Nagano, Karuizawa.

Host. *Andrena (Oreomelissa) mitakensis* Hirashima, 1963 (KIFUNE & MAETA 1990).

Note. No DNA sequence is known for *Stylops* from this host subgenus.

Stylops murotai Kifune, 1991

Stylops murotai Kifune, 1991: 157, F. Type locality: Japan, Honshu, Fukui, Izumi-mura, Kebora.

Host. *Andrena (Hoplandrena) takachihoi* Hirashima, 1964 (KIFUNE 1991).

Note. Morphological differences between *Stylops* from *A. takachihoi* and other Japanese *Stylops* from the host subgenus *Hoplandrena* presented in the original description are significant. For this reason, we do not synonymize *S. murotai* with *S. yamatonis* until detailed study of the type material or DNA barcode sequence from *Stylops* from the original host species is performed. No DNA sequence is known for *Stylops* from *A. takachihoi*.

***Stylops pilipedis* Pierce, 1911**

Stylops pilipedis Pierce, 1911: 495, F. Type locality: China, Beijing.

Host. *Andrena (Plastandrena) pilipes* Fabricius, 1781 (PIERCE 1911).

Note. No DNA sequence is known for *Stylops* from this host subgenus in the East Palaearctic Region. Status of this species is uncertain. It might be closely related, or conspecific to *S. nassonowi* or *S. yamatonis*.

***Stylops thwaitesi* Perkins, 1918**

(see above under Western Palaearctic species)

***Stylops valerianae* Kifune & Hirashima, 1985**

Stylops valerianae Kifune & Hirashima, 1985: 55, F. Type locality: Japan, Hokkaido, Tokachi, Ashoromura.

Hosts. *Andrena (Holandrena) valeriana* Hirashima, 1957 (KIFUNE & HIRASHIMA 1985).

Note. No DNA sequence is known for *Stylops* from this host subgenus from the East Palaearctic Region.

***Stylops yamatonis* Kifune & Hirashima, 1985**

Stylops yamatonis Kifune & Hirashima, 1985: 51, F. Type locality: Japan, Kyushu, Kagoshima, Miyanojo.

?= *Stylops dentatae* Kifune & Maeta, 1990: 99, F. Type locality: Japan, Honshu, Nagano, Todai. **Supposed new junior subjective synonym.**

?= *Stylops aino* Kifune & Maeta, 1990: 99, F. Type locality: Japan, Hokkaido, Teshio, Piuka. **Supposed new junior subjective synonym.**

?= *Stylops izumoensis* Kifune & Maeta, 1990: 102, F. Type locality: Japan, Honshu, Shimane Pref., Mt. Makuragi. **Supposed new junior subjective synonym.**

?= *Stylops nipponicus* Kifune & Maeta, 1990: 103, F. Type locality: Japan, Honshu, Yamanashi, Shosenkyo. **Supposed new junior subjective synonym.**

?= *Stylops subcircularis* Kifune & Maeta, 1990: 104, F. Type locality: Japan, Honshu, Nagano, Ina, Habiro. **Supposed new junior subjective synonym.**

?= *Stylops fukuiensis* Kifune, 1991: 155, F. Type locality: Japan, Honshu, Fukui, Ohno, Koike. **Supposed new junior subjective synonym.**

Hosts. *Andrena (Simandrena) yamato* Tadauchi & Hirashima, 1983 (KIFUNE & HIRASHIMA 1985), *A. (Hoplandrena) dentata* Smith, 1879, *A. (H.) rosae* Panzer, 1801, *A. (S.) opacifovea* Hirashima, 1952, *A. (S.) nippon* Tadauchi & Hirashima, 1983, *A. (Plastandrena) japonica* (Smith, 1873), *A. (P.) fukaii* Cockerell, 1914 (KIFUNE & MAETA 1990), *A. (H.) miyamotoi* Hirashima, 1964 (KIFUNE 1991), *A. (S.) kerriae* Hirashima, 1965, *A. (H.) pruniphora* Hirashima, 1964 (KIFUNE et al. 1994).

DNA barcode sequences. KF803536, KF803540, KF803541, KF803543.

Note. This *Stylops* species is closely related to *S. aterrimus* and *S. nassonowi* and can be understood as a member of this species group. On the other hand, DNA barcode distances between sequences from the West-Palaearctic species and *S. yamatonis* are as high as 8 % (JŮZOVÁ et al. 2015).

Nearctic Region

Stylops advarians Pierce, 1909

Stylops advarians Pierce, 1909: 97, F. Type locality: Canada, British Columbia, Vancouver.

?= *Stylops mandibularis* Pierce, 1911: 494, F. Type locality: USA, Illinois, Carlinville. **Supposed new junior subjective synonym.**

?= *Stylops moestae* Pierce, 1919: 443, F. Type locality: USA, Washington, Govan. **Supposed new junior subjective synonym.**

?= *Stylops sinuatus* Pierce, 1919: 450, F. Type locality: USA, Illinois, Carlinville. **Supposed new junior subjective synonym.**

Hosts. *Andrena (Andrena) vicinoides* Viereck, 1904 (PIERCE 1909), *A. (A.) mandibularis* Robertson, 1892 (PIERCE 1911, 1919), *A. (A.) frigida* Smith, 1853 (PIERCE 1919).

DNA barcode sequences. KF803441, KF803485.

Note. Distances between DNA barcode sequences of *Stylops* from the Nearctic representatives of the subgenus *Andrena* and the other host subgenera are 9–18 % (JŮZOVÁ et al. 2015).

Stylops apicalis Bohart, 1937

Stylops apicalis Bohart, 1937: 54, F, L1. Type locality: USA, California, Berkeley.

Host. *Andrena (Andrena) saccata* Viereck, 1904.

Note. This name is not synonymized with the previous species based on the description and the discussion of morphological differences between these species (BOHART 1937, 1941).

No DNA sequence is known for *S. apicalis*.

Stylops bipunctatae Pierce, 1909

Stylops bipunctatae Pierce, 1909: 98, F. Type locality: USA, Indiana.

?= *Stylops oklahoma* Pierce, 1909: 110, F. Type locality: USA, Oklahoma, Ardmore. **Supposed new junior subjective synonym.**

Host. *Andrena (Larandrena) miserabilis* Cresson, 1872 (PIERCE 1909).

Note. No DNA sequence is known for *Stylops* from this host subgenus in the Nearctic Region.

Stylops bruneri Pierce, 1909

Stylops bruneri Pierce, 1909: 98, F. Type locality: USA, Nebraska, Sioux County.

= *Stylops andrenoides* Pierce, 1911: 493, F. Type locality: USA, Illinois, Carlinville. Synonymized with *S. bruneri* by BOHART (1941: 132).

= *Stylops salictariae* Pierce, 1919: 449, F. Type locality: USA, Illinois, Carlinville. Synonymized with *S. bruneri* by BOHART (1941: 132).

?= *Stylops neonanae* Pierce, 1919: 454, F. Type locality: USA, Georgia. **Supposed new junior subjective synonym.**

?= *Stylops duboisi* Bohart, 1937: 52, M (holotype), F. Type locality: USA, California, Davis. **Supposed new junior subjective synonym.**

Hosts. *Andrena (Micrandrena) illinoiensis* Robertson, 1891 (PIERCE 1909), *A. (Parandrena) andrenoides* (Cresson, 1878) (PIERCE 1911), *A. (M.) salictaria* Robertson, 1905, *A. (M.) neonana* Viereck, 1917 (PIERCE 1919), *A. (M.)* sp. (BOHART 1937).

Notes. The name *S. duboisi* is missing in the list of North American species (BOHART 1941). Considering this, Bohart's name is regarded uncertain and thus presented as a synonym according to the host association.

No DNA sequence is known for *Stylops* from *Micrandrena* host subgenus in the Nearctic Region.

Stylops californicus Pierce, 1909

Stylops californica Pierce, 1909: 99, F, L1. Type locality: USA, Southern California.

Host. *Andrena (Tylandrena) subtilis* Smith, 1879 (PIERCE 1909).

Notes. PIERCE (1909) discussed close similarity with *S. subcandidae*. We suggest that these species might be identical. This taxonomic problem should be evaluated using barcode sequences from *Stylops* from *A. subtilis* host.

No DNA sequence is known for *Stylops* from *Tylandrena* host subgenus.

Stylops childreni Gray & Westwood, 1832

Stylops childreni Gray & Westwood, 1832 in GRIFFITH (1832): 684*, plate 59, M. Type locality not indicated.

?= *Stylops vicinae* Pierce, 1909: 110, F. Type locality: USA, New Hampshire; Canada. **Supposed new junior subjective synonym.**

= *Stylops dunningi* Pierce, 1919: 438. Nomen nudum (BOHART 1941).

Host: *Andrena (Melandrena) vicina* Smith, 1853 (PIERCE 1909).

DNA barcode sequence. KF803530.

Notes. There is problematic authorship of the species *S. childreni*. GRIFFITH (1832) is most likely not the only author of the book where the species was described. Species description was prepared based on the work of G. R. Gray, who named the species, and J. O. Westwood, who prepared a figure plate with the name of *Stylops* on the plate and signed the plate, and thus we suggest authorship of the name *S. childreni* to Gray & Westwood equally.

Distances between DNA barcode sequences of *S. childreni* and other related species of *Stylops* from the Nearctic representatives of the subgenus *Melandrena* are 3 % (JŮZOVÁ et al. 2015). For this reason *S. cornii* is not considered to be a synonym of *S. childreni*.

Stylops claytoniae Pierce, 1909

Stylops claytoniae Pierce, 1909: 99, F. Type locality: USA, Georgia, Thomasville.

= *Stylops imitatrix* Pierce, 1909: 104, F. Type locality: USA, Texas, Round Mountain. Synonymized with *S. claytoniae* by PIERCE (1911: 494).

= *Stylops vierecki* Pierce, 1909: 110, F. Type locality: USA, Texas, Fedor. Synonymized with *S. claytoniae* by PIERCE (1911: 494).

Host. *Andrena (Scrapteropsis) imitatrix* Cresson, 1872 (PIERCE 1909).

DNA barcode sequences. KF803471, KF803505.

Notes. The names presented as synonyms were proposed for the hosts *A. claytoniae* Robertson, 1891, *A. imitatrix* and *A. profunda* Viereck, 1917 by PIERCE (1909). *Andrena claytoniae* and *A. profunda* are, however, junior synonyms of *A. imitatrix*. PIERCE (1911, 1919) later

recognised this relationship between the host names and downgraded the name *S. vierecki* as a variety and later both *S. imitatrix* and *S. vierecki* as subspecies of *S. claytoniae*. The host bee name *A. profunda* was presented before the name description (PIERCE 1909), and thus the host name was published as a nomen nudum.

Distances between DNA barcode sequences of *Stylops* from the subgenus *Scapteropsis* and the other host subgenera are 4–20 % (JŮZOVÁ et al. 2015).

Stylops cornii Pierce, 1909

Stylops cornii Pierce, 1909: 100, F, L1. Type locality: USA, Wisconsin, Milwaukee.

= *Stylops graenicheri* Pierce, 1909: 103, F. Type locality: USA, Wisconsin, Milwaukee. Synonymized with *S. cornii* by BOHART (1941: 133).

?= *Stylops solidulae* Pierce, 1909: 107, M, F. Type locality: USA, Washington, Pullman. **Supposed new junior subjective synonym.**

= *Neostylops solidulae*: PIERCE (1919: 457). New generic placement.

Hosts. *Andrena (Melandrena) commoda* Smith, 1879, *A. (M.) nivalis* Smith, 1853 (PIERCE 1909).

DNA barcode sequence. KF803440.

Note. According to the phylogenetic analysis based on DNA sequences, *S. childreni* and *S. cornii* could be different species (distance in DNA barcode sequences between these two related *Stylops* species is 3 %) (JŮZOVÁ et al. 2015), and for this reason these names are not considered to be synonyms here.

Stylops crawfordi Pierce, 1909

Stylops crawfordi Pierce, 1909: 100, M, F. Type locality: USA, Texas, Dallas.

?= *Stylops swenki* Pierce, 1909: 108, F, L1. Type locality: USA, Nebraska, Lincoln. **Supposed new junior subjective synonym.**

= *Stylops asteridis* Pierce, 1911: 494, F. Type locality: USA, Illinois, Carlinville. Synonymized with *S. swenki* by BOHART (1941: 130).

= *Neostylops crawfordi*: PIERCE (1919: 456). New generic placement.

Hosts. *Andrena (Callandrena) crawfordi* Viereck, 1909, *A. (C.) simplex* Smith, 1853 (PIERCE 1909), *A. (C.) asteris* Robertson, 1891 (PIERCE 1911).

DNA barcode sequences. KF803444, KF803472.

Note. Distances between DNA barcode sequences of *Stylops* from *Callandrena* subgenus and the other host subgenera are 13–20 % (JŮZOVÁ et al. 2015).

Stylops cressoni Pierce, 1909

Stylops cressoni Pierce, 1909: 102, F, L1. Type locality: USA, Maine, Waldoboro.

Host. *Andrena (Holandrena) cressonii* Robertson, 1891.

DNA barcode sequences. KF803442, KF803443.

Note. Distances between DNA barcode sequences of *Stylops* from the Nearctic subgenus *Holandrena* and the other host subgenera are 9–20 % (JŮZOVÁ et al. 2015).

Stylops cuneiformis Bohart, 1936

Stylops cuneiformis Bohart, 1936: 16, M. Type locality: USA, California, Coronado.

Host. Unknown.

Note. Validity of this species needs to be studied using morphological methods using the type material as well as the recently collected material preserved for DNA analyses.

Stylops elongatus Bohart, 1937

Stylops elongatus Bohart, 1937: 53, M (holotype), F. Type locality: USA, California, Riverside, Soboba Hot Springs.
= *Stylops elongata*: BOHART (1941: 132). Incorrect gender agreement.

Host. *Andrena (Onagrandrena) oenothera* Timberlake, 1937, *A. (O.) blaisdelli* Cockerell, 1924 (BOHART 1937, 1941).

Note. No DNA sequence is known for *Stylops* from this host subgenus.

Stylops erigeniae Pierce, 1919

Stylops erigeniae Pierce, 1919: 446, F. Type locality: USA, Maryland, Plummers Island.

Hosts. *Andrena (Ptilandrena) erigeniae* Robertson, 1891.

DNA barcode sequences. KF803446, KF803447.

Note. Distances between DNA barcode sequences of *Stylops* from *Ptilandrena* subgenus and the other host subgenera are 6–19 % (JŮZOVÁ et al. 2015).

Stylops hartfordensis Pierce, 1909, stat. restit.

Stylops hartfordensis Pierce, 1909: 103, F. Type locality: USA, Georgia, Thomasville.

= *Stylops nasoni* Pierce, 1909: 104, F. Type locality: USA, Pennsylvania, Ashbourne. Synonymized with *S. bruneri* by BOHART (1941: 132).

Host. *Andrena (Simandrena) nasonii* Robertson, 1895.

DNA barcode sequences. KF803486, KF803487.

Notes. This species was synonymized with *S. bruneri* by BOHART (1941), which seems to be a parasite of *Andrena* subgenus *Micrandrena*. *Stylops hartfordensis*, as a parasite of the Nearctic *Simandrena* species, is tentatively restored from synonymy here because of significant difference in the host subgenera and the size of the hosts.

Distances between DNA barcode sequences of *Stylops* from the Nearctic subgenus *Simandrena* and the other host subgenera are 4–19 % (JŮZOVÁ et al. 2015). However, sequences from the Nearctic *Micrandrena* hosts are not yet known.

Stylops heterocingulatus Bohart, 1937

Stylops heterocingulatus Bohart, 1937: 55, F, L1. Type locality: USA, California, Davis.

= *Stylops heterocingulata*: BOHART (1941: 126). Incorrect gender agreement.

Hosts. *Andrena (Simandrena) pensilis* Timberlake, 1938, *A. (S.) angustitarsata* Viereck, 1904 (BOHART 1937, 1941).

Note. No DNA barcode sequence is known from this species.

Stylops hippotes Pierce, 1909

Stylops hippotes Pierce, 1909: 103, F. Type locality: USA, Ohio, Columbus.

?= *Stylops salicifloris* Pierce, 1909: 106, F. Type locality: USA, Washington, Washington and Seattle. **Supposed new junior subjective synonym.**

= *Stylops centroclarus* Bohart, 1937: 50, M (holotype), F, L1. Type locality: USA, California, Berkeley. Synonymized with *S. salicifloris* by BOHART (1941: 124).

Host. *Andrena (Trachandrena) hippotes* Robertson, 1895, *A. (T.) salicifloris* Cockerell, 1897 (PIERCE 1909), *A. (T.) quintiliformis* Viereck, 1917 (BOHART 1941).

DNA barcode sequences. KF803464, KF803465, KF803506, KF803511.

Note. Distances between DNA barcode sequences of *Stylops* from *Trachandrena* subgenus and the other host subgenera are 5–19 % (JÚZOVÁ et al. 2015). See also note under *S. multiplicatae*.

Stylops leechi Bohart, 1941

Stylops leechi Bohart, 1941: 128, M, F. Type locality: Canada, British Columbia, Vancouver.

Host. *Andrena (Andrena) vicinoides* Viereck, 1904 (BOHART 1941).

Note. No DNA sequence is known from this *Stylops* species.

Stylops multiplicatae Pierce, 1909

Stylops multiplicatae Pierce, 1909: 104, F. Type locality: USA, Wisconsin, Milwaukee.

?= *Stylops grandior* Pierce, 1919: 451, F. Type locality: USA, Montana, Big Fork. **Supposed new junior subjective synonym.**

Host. *Andrena (Trachandrena) miranda* Smith, 1879 (PIERCE 1909, 1919).

DNA barcode sequences. KF803482, KF803483.

Note. We recognise this species name as valid because the DNA barcode sequences indicate significant differences from the related *S. hippotes*. Distance between these two species in DNA sequences is 4 % (JÚZOVÁ et al. 2015). However, both species have closely related hosts placed in the same subgenus and this complicates synonymous list of names described from *Trachandrena* host species. This group should be studied using broader sampling of material from wider distribution range.

Stylops nubeculae Pierce, 1909

Stylops nubeculae Pierce, 1909: 105, F. Type locality: USA, Colorado.

Host. *Andrena (Cnemidandrena) nubecula* Smith, 1853 (PIERCE 1909).

Note. No DNA sequence is known for *Stylops* from this host subgenus.

Stylops nudae Pierce, 1911

Stylops nudae Pierce, 1911: 495, F. Type locality: USA, Illinois, Carlinville.

Host. *Andrena (Trachandrena) nuda* Robertson, 1891 (PIERCE 1911).

Note. There are multiple *Stylops* species within the *Trachandrena* subgenus hosts. Without any DNA barcode sequence of *Stylops* from *A. nuda*, we cannot reliably suggest synonymy of this name.

Stylops packardi Pierce, 1909

Stylops packardi Pierce, 1909: 105, M. Type locality: USA, Massachusetts, Salem.

Host. *Andrena (Leucandrena) barbilabris* (Kirby, 1802) (PIERCE 1909).

Note. No DNA sequence is known for *Stylops* from this host subgenus.

Stylops polemonii Pierce, 1909

Stylops polemonii Pierce, 1909: 106, F, L1. Type locality: USA, Colorado.

?= *Stylops pacificus* Bohart, 1936: 15, M, F, L1. Type locality: USA, California, Berkeley. **Supposed new junior subjective synonym.**

= *Stylops pacifica*: BOHART (1941: 128). Incorrect gender agreement.

Hosts. *Andrena (Euandrena) polemonii* Robertson, 1891 (PIERCE 1909), *Andrena (E.) caerulea* Smith, 1879 (BOHART 1936, 1941), *Andrena (E.) suavis* Timberlake, 1938 (BOHART 1941).

Notes. BOHART (1941) omitted the name *S. polemonii* from his North American species review.

According to the host association, this name is supposed to be a senior subjective synonym of *S. pacificus*.

No DNA sequence is known for *Stylops* from this host subgenus from the Nearctic Region.

Stylops shannoni (Pierce, 1919)

Neostylops shannoni Pierce, 1919: 457, M. Type locality: USA, Maryland, Plummers Island.

= *Stylops shannoni*: BOHART (1941: 125). New generic placement.

Host. Unknown.

Note. Name of *S. shannoni* was associated with findings of stylopized *A. hippotes* by KENER (2002). However, he did not provide a description of the male or any other reliable species indication in the publication. If such an association is correct, *S. shannoni* will be a synonym of *S. hippotes*. The species status, which was described from a free living male, remains uncertain.

Stylops sparsipilosae Pierce, 1909

Stylops sparsipilosae Pierce, 1909: 108, F. Type locality: USA, Maine, Waldoboro.

Host. Unknown.

Note. Host name ‘*A. sparsipilosa* Viereck’ presented by PIERCE (1909) as host association is a nomen nudum (KROMBEIN et al. 1979). Status of this *Stylops* species should be resolved using its type material.

Stylops subcandidae Pierce, 1909

Stylops subcandidae Pierce, 1909: 108, F, L1. Type locality: USA, Southern California.

?= *Stylops bisalicidis* Pierce, 1919: 446, F. Type locality: USA, Alabama. **Supposed new junior subjective synonym.**

?= *Stylops medionitans* Pierce, 1919: 450, F. Type locality: USA, Colorado, Florissant. **Supposed new junior subjective synonym.**

= *Stylops diabola* Pierce, 1919: 454, F. Type locality: USA, North Dakota, Devils Lake. Synonymized with *S. bisalicidis* by BOHART (1941: 131).

Hosts. *Andrena (Thysandrena) candida* Smith, 1879 (PIERCE 1909), *A. (T.) bisalicis* Viereck, 1908 (PIERCE 1919), *A. (T.) medionitens* Cockerell, 1902 (BOHART 1936, PIERCE 1919), *A. (Scaphandrena) scurra* Viereck, 1904 (BOHART 1941).

DNA barcode sequences. KF803432, KF803509.

Notes. PIERCE (1919) used the name *S. medionitans* for this species because he used incorrect spelling for the host species, *Andrena medionitans*. For this reason the *Stylops* name with ‘a’ is the correct original spelling of the name.

Distances between DNA barcode sequences of *S. subcandidae* and the other *Stylops* species are 12–21 % (JÚZOVÁ et al. 2015).

Stylops timberlakei Bohart, 1936

Stylops timberlakei Bohart, 1936: 14, M (holotype), F. Type locality: USA, California, Riverside.

Host. *Andrena (Oligandrena) macrocephala* Cockerell, 1906 (BOHART 1936).

Note. No DNA sequence is known for *Stylops* from this host subgenus.

Stylops vandykei Bohart, 1936

Stylops vandykei Bohart, 1936: 11, M (holotype), F, L1. Type locality: USA, California, Berkeley.

Hosts. *Andrena (Melandrena) perimelas* Cockerell, 1905, *Andrena (M.) pertristis carliniformis* Viereck & Cockerell, 1914 (BOHART 1936).

Note. No DNA sequence is known from this *Stylops* species.

Discussion

The diversity of the order Strepsiptera is poorly known, not only because of insufficient interest in the alpha taxonomy of the order Strepsiptera, but especially because of different species concepts that have been applied simultaneously to this insect group. In case of the genus *Stylops*, we did not know whether the genus included a single (KINZELBACH 1978, POHL 2004) or a hundred (KATHIRITHAMBY 2014) of species in Europe for a long time. Recent molecular analysis (JÚZOVÁ et al. 2015) shows that there are numerous species in Europe, but certainly not hundred. Morphological characters of *Stylops*, which correspond to their host associations (BOHART 1941, BORCHERT 1963), also correspond to their DNA sequences. For this reason, we prepared a preliminary nomenclatoric list of all *Stylops* species as a new starting point for future taxonomic studies. As a result we found 32 West Palaearctic, 9 East Palaearctic and 27 Nearctic species names, which must be considered valid, in total 67 (one overlaps between the West and East Palaearctic Regions) valid species names of *Stylops* in the world. These numbers include also names of species with uncertain validity, especially those described based on free living males collected without knowledge of their host species. A few other uncertain names concern females from the host lineage (subgenus) known to be a host for multiple *Stylops* species, as well as names associated with rarely collected *Andrena* bees, which might only represent other rare hosts of common species, or rare host switches (JÚZOVÁ et al. 2015).

DNA distance analysis of COI barcode sequences of *Stylops* species show that the DNA based approach is applicable for this taxonomic group. However, neither strict species delimitation, nor universally definable distance between species can be postulated. Every species and every lineage need to be considered individually with biological rationality. In most cases, we can recognize ‘clusters’ of closely related individuals with low variability (<2 %) in DNA distances and relatively high (4–12 %) minimal DNA distance from any other individual. We consider a single ‘cluster’ to be a population of a single species. In a very few cases, the variability within the tentative species is slightly larger than 2 % (*S. nassonowi*, *S. spreta*). Such species are distributed over large geographic areas and distant populations probably represent original old populations. There are also several cases of possible different species, which differ in only 3 % or even in less than 1 % in DNA barcode sequence (e.g., *S. praecocis* vs. *S. nevinsoni*). These populations occur sympatrically, but differ in morphology (BORCHERT 1963) and seem to be genetically separated (JŮZOVÁ et al. 2015), and for these reasons the species are considered valid for the time being.

All the hypotheses about species delimitation that were proposed in our study should be tested in detail based on broader population genetic tools and/or morphological methods. The comprehensive morphological revision of the genus *Stylops* with definitions of the type material would be especially helpful for the future nomenclatorial stability. We recommend to continue in barcoding and sequencing other genes and using an integrative taxonomic approach (GIBBS 2009) to maintain certainty in the taxonomy of this peculiar group.

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References

- ANONYMUS 1898a: Brockhaus' Konversations-Lexicon. Vierzehnte vollständig neubearbeitete Auflage. Revidierte Jubiläums-Ausgabe. Sechster Band. F. A. Brockhaus, Leipzig, Berlin, Vienna, 1018 pp., 59 plates, 12 maps.
- ANONYMUS 1898b: Brockhaus' Konversations-Lexicon. Vierzehnte vollständig neubearbeitete Auflage. Revidierte Jubiläums-Ausgabe. Sechzehente band. F. A. Brockhaus, Leipzig, Berlin, Vienna, 1068 pp., 85 plates, 22 maps.
- ASCHER J. S. & PICKERING J. 2014: Discover Life bee species guide and world checklist (Hymenoptera: Apoidea: Anthophila). Available from: http://www.discoverlife.org/mp/20q?guide=Apoidea_species (September 30, 2014).
- BENEDEK P.-J. VAN 1878: Les Commensaux et les Parasites dans le règne animal. Deuxième édition. Librairie Gérard Bailliére, Paris, 239 pp.
- BLEIDORN C., FEITZ F., SCHNEIDER N. & VENNE C. 2004: Zum Vorkommen von *Stylops melittae* Kirby, 1802 (Insecta, Strepsiptera) in Luxemburg. *Bulletin de la Société des Naturalistes Luxembourgeois* **105**: 137–142.
- BOHART R. M. 1936: A preliminary study of the genus *Stylops* in California (part I) (Strepsiptera, Stylopidae). *Pan-Pacific Entomologist* **12**: 9–18.

- BOHART R. M. 1937: A preliminary study of the genus *Stylops* in California (part II) (Strepsiptera, Stylopidae). *Pan-Pacific Entomologist* **13**: 49–57.
- BOHART R. M. 1941: A revision of the Strepsiptera with special reference to the species of North America. *University of California Publications in Entomology* **7**: 91–160.
- BORCHERT H.-M. 1963: Vergleichend morphologische Untersuchungen an Berliner *Stylops-L1* (Strepsipt.) zwecks Entscheidung der beiden Spezifitätsfragen: 1. gibt es an unseren Frühjahrs-Andrenen (Hymenopt., Apidae) mehrere *Stylops*-Arten und 2. gibt es Wirtsspezifitäten? *Zoologische Beiträge* **8**: 331–445.
- BORCHERT H.-M. 1971: Benennung unseres Berliner *Stylops* aus der Sandbiene *Andrena vaga* Pz. *Stylops muelieri* sp. n. (Insecta, Strepsiptera). *Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin, Neue Folge* **10**: 18–27.
- CURTIS J. 1828: *Stylops Dalii*. In: *British Entomology. Vol. V*. Printed for the author, London, pp. 226–227, plate 226.
- CVAČKA J., JIROŠ P., KALINOVÁ B., STRAKA J., ČERNÁ K., ŠEBESTA P., TOMČALA A., VAŠÍČKOVÁ S., JAHN U. & ŠOBOTNÍK J. 2012: *Stylopsal*: The first identified female-produced sex pheromone of Strepsiptera. *Journal of Chemical Ecology* **38**: 1483–1491.
- FOX J. W. & FOX R. M. 1964: A new genus and species of Stylopidae (Strepsiptera) from Liberia, West Africa. *Annals of the Entomological Society of America* **57**: 754–756.
- GIBBS J. 2009: Integrative taxonomy identifies new (and old) species in the *Lasioglossum* (*Dialictus*) *tegulare* (Robertson) species group (Hymenoptera, Halictidae). *Zootaxa* **2032**: 1–38.
- GRIFFITH E. 1832: *The Animal kingdom arranged in conformity with its organization by the Baron Cuvier. Volume XV. Part 2*. Whittaker, Treacher, and Co., London, 796 pp.
- GÜNTHER V. & ŠEDIVÝ J. 1957: *Řád Řasníkřídli – Strepsiptera*. Pp. 407–417. In: KRATOCHVÍL J. (ed.): *Klíč zvířeny ČSR. Díl II. [Key to the fauna of Czechoslovakia]*. ČSAV, Praha, 746 pp.
- GUSENLEITNER F. & SCHWARZ M. 2002: Weltweite Checkliste der Bienengattung *Andrena*: mit Bemerkungen und Ergänzungen zu paläarktischen Arten (Hymenoptera, Apidae, Andreninae, *Andrena*). *Entomofauna* **12(suppl.)**: 1–1280.
- HOFENEDER K. 1924a: *Stylops in copula*. *Verhandlungen der Zoologisch-Botanischen Gesellschaft in Wien* **73**: 128–134.
- HOFENEDER K. 1924b: Wissenschaftliche Ergebnisse der 2. Expedition nach dem Anglo-ägyptischen Sudan 1914. XVI. Hymenoptera. I. Anhang: Strepsiptera. *Denkschriften – Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse* **99**: 254.
- HOFENEDER K. 1939: Über zwei neue Strepsipteren aus *Andrena similis* F. Smith und *Halictus malachurus* Kirby. *Veröffentlichungen aus dem Deutschen Kolonial- und Übersee-Museum in Bremen* **2**: 181–200.
- HOFENEDER K. & FULMEK L. 1943: Verzeichnis der Strepsipteren und ihrer Wirte. *Arbeiten über Physiologische und Angewandte Entomologie aus Berlin-Dahlem* **10**: 139–169.
- ICZN 1999: *International Code of Zoological Nomenclature. Fourth Edition*. International Trust for Zoological Nomenclature, London, XXIX + 306 pp.
- JŮZOVÁ K., NAKASE Y. & STRAKA J. 2015: Host specialisation and species diversity in the genus *Stylops* (Strepsiptera: Stylopidae) revealed by molecular phylogenetic analysis. *Zoological Journal of the Linnean Society*. Early view, 16 pp (doi: 10.1111/zoj.12233).
- KATHIRITHAMBY J. 2009: Host-parasitoid associations in Strepsiptera. *Annual Review of Entomology* **54**: 227–249.
- KATHIRITHAMBY J. 2014: *Strepsiptera. Strepsiptera database*. Available from: <http://rameau.snv.jussieu.fr/cgi-bin/strepsiptera.pl?lang=en> (Last accessed: October 1, 2014).
- KATHIRITHAMBY J., LECHNER G. K., McMAHON D. P., BRYSON A. L. & JOHNSTON J. S. 2012: A free ride and lunch: Stylopization in the solitary hunting wasp, *Ammophila fernaldi* Murray and *A. pictipennis* (Walsh) (Hymenoptera: Sphecidae) by *Paraxenos lugubris* Pierce (Strepsiptera). *Proceedings of the Entomological Society of Washington* **114**: 464–475.
- KATHIRITHAMBY J., ROSS L. D. & JOHNSTON J. S. 2003: Masquerading as self? Endoparasitic Strepsiptera (Insecta) enclose themselves in host-derived epidermal bag. *Proceedings of the National Academy of Sciences* **100**: 7655–7659.
- KATHIRITHAMBY J. & TAYLOR S. J. 2005: A new species of *Halictophagus* (Insecta: Strepsiptera: Halictophagidae) from Texas, and a checklist of Strepsiptera from the United States and Canada. *Zootaxa* **1056**: 1–18.

- KENNER R. D. 2002: Stylops shannoni (Stylopidae: Strepsiptera): a new species for Canada, with comments on *Xenos pecki*. *Journal of the Entomological Society of British Columbia* **99**: 99–102.
- KIFUNE T. 1991: Two new species of the genus Stylops (Strepsiptera, Stylopidae) with stylopized records of the Andrenid bees in Japan. (Studies on the Japanese Strepsiptera XIV.) *Japanese Journal of Entomology* **59**: 155–163.
- KIFUNE T. & HIRASHIMA Y. 1985: Nine new species of the genus Stylops (Strepsiptera: Stylopidae) parasitic on the genus *Andrena* (Hymenoptera: Andrenidae) of Japan (Studies on the Japanese Strepsiptera X). *Esakia* **23**: 45–57.
- KIFUNE T. & MAETA Y. 1990: Ten new species of the genus Stylops (Strepsiptera, Stylopidae) parasitic on the genus *Andrena* (Hymenoptera, Andrenidae) of Japan (Studies on the Japanese Strepsiptera XIII). *Esakia* **29**: 97–110.
- KIFUNE T., TADAUCHI O. & LEE C. E. 1994: Records of the Strepsiptera parasitic on the Korean Apoidea (Notulæ Strepsipterologicae-XXIII). *Esakia* **34**: 209–214.
- KINZELBACH R. K. 1967: Stylops risleri n.sp. von Teneriffa (Stylopidae, Strepsiptera). *Notulae Entomologicae* **47**: 37–43.
- KINZELBACH R. K. 1971: *Morphologische Befunde an Fächerflüglern und ihre phylogenetische Bedeutung (Insecta: Strepsiptera)*. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart, 256 pp.
- KINZELBACH R. K. 1978: Fächerflügler (Strepsiptera). Pp. 1–166. In: SENGLAUB K., HANNEMANN H.-J. & SCHUMANN H. (eds): *Die Tierwelt Deutschlands*, 65. Teil. Gustav Fischer, Jena, 166 pp.
- KIRBY W. 1802: *Monographia Apum Angliae; or, an attempt to divide into their natural genera and families, such species of the Linnean genus Apis as have been discovered in England: with descriptions and observations. To which are prefixed some introductory remarks upon the class Hymenoptera, and a synoptical table of the nomenclature of the external parts of these Insects*. J. Raw, Ipswich, London, 258 pp.
- KROMBEIN K. V., HURD P. D., SMITH D. R. & BURKS B. D. 1979: *Catalog of Hymenoptera in America north of Mexico, Volumes 1–3*. Smithsonian Institution Press, Washington, D.C., 2735 pp.
- KUHLMANN M. 1998: Nachweise mit Bienen und Wespen (Hymenoptera Aculeata) assoziierter Milben (Acari) und Fächerflügler (Strepsiptera). *Linzer Biologische Beiträge* **30**: 69–80.
- LAGOUTTE R., ŠEBESTA P., JIROŠ P., KALINOVÁ B., JIROŠOVÁ A., STRAKA J., ČERNÁ K., ŠOBOTNÍK J., CVAČKA J. & JAHN U. 2013: Total synthesis, proof of absolute configuration, and biosynthetic origin of stylopsal, the first isolated sex pheromone of Strepsiptera. *Chemistry – A European Journal* **19**: 8515–8524.
- LEACH W. E. 1817: On the Rhipiptera of Latreille, an order of insects named by Kirby Strepsiptera. Pp. 133–136. In: LEACH W. E. & NODDER R. P.: *The zoological miscellany; descriptions of new and interesting animals. Volume 3*. R. and A. Taylor, London, 151 pp.
- LINSLEY E. G. & MACSWAIN J. W. 1957: Observations on the habits of *Stylops pacifica* Bohart. *University of California Publications in Entomology* **11**: 395–430.
- LUNA DE CARVALHO E. 1969: Contribuição para o conhecimento dos Estrepsípteros de Portugal (V Nota). *Memórias e Estudos do Museo Zoológico da Universidade de Coimbra* **1969**: 5–12 + I–V.
- LUNA DE CARVALHO E. 1974: Contribuição para o estudo dos Stylops da Península Ibérica (Streps. Stylopidae). *Eos: Revista Española de Entomología* **48**: 301–365.
- MEDVEDEV L. N. 1970: Novoe dlya fauny SSSR semeystvo i novye vidy veerokrylykh (Strepsiptera) iz Yugo-Vostochnogo Kazakhstana. (A family of Strepsiptera previously unknown from the USSR and new species from South-East Kazakhstan). *Entomologicheskoe Obozrenie* **49**: 199–202 (in Russian, English summary).
- NASONOV N. 1893: K' morfologiï Stylops melittae. [On the morphology of *Stylops melittae*]. *Warsaw University News* **1893**: 1–24, 27–30.
- NEWPORT G. 1851: The natural history, anatomy and development of *Meloe* (continued). Second memoir. The history and general anatomy of *Meloe*, and its affinities, compared with those of the Strepsiptera and Anoplura, with reference to the connection which exists between structure, function, and instinct. *Transactions of the Linnean Society of London* **20**: 321–357.
- NOSKIEWICZ J. & POLUSZYŃSKI G. 1927: Embryologische Untersuchungen an Strepsipteren. 1. Teil. Embryogenese der Gattung *Stylops* Kirby. *Bulletin International de l'Académie Polonaise des Sciences et des Lettres, B, Sciences Naturelles* **6**: 1093–1227, pl. 98–101.
- PASTEELS J. 1949: Enquêtes sur les Strepsiptères (1re série). *Bulletin et Annales de la Société Entomologique Belgique* **85**: 185–196.
- PASTEELS J. 1954: Enquêtes sur les Strepsiptères (4e série). – Strepsiptères du Musée zoologique de Lausanne. *Bulletin et Annales de la Société Entomologique de Belgique* **90**: 349–355.

- PEKKARINEN A. 1997: Parasitism of *Stylops* (Strepsiptera, Stylopidae) in poly- and oligolectic *Andrena* hosts (Hymenoptera, Apoidea). *Entomologica Fennica* **8**: 109–111.
- PERKINS R. C. L. 1918: Synopsis of British Strepsiptera of the genera *Stylops* and *Halictoxenus*. *Entomologist's Monthly Magazine* **54**: 67–76, plate 1.
- PICKERING W. B. 1836: Observations on the economy of the Strepsiptera, with the description of *Stylops spencii*, a new British species recently discovered. *Transactions of the Entomological Society of London* **1**: 163–168.
- PIERCE W. D. 1908: A preliminary review of the classification of the order Strepsiptera. *Proceedings of the Entomological Society of Washington* **9**: 75–85.
- PIERCE W. D. 1909: A monographic revision of the twisted winged insects comprising the order Strepsiptera Kirby. *Bulletin of the United States National Museum* **66**: I–XII, 1–232, pl. 1–15.
- PIERCE W. D. 1911: Notes on insects of the order Strepsiptera, with descriptions of new species. *Proceedings of the United States National Museum* **40**: 487–511.
- PIERCE W. D. 1919: The comparative morphology of the order Strepsiptera: together with records and descriptions of insects. *Proceedings of the United States National Museum* **54** (1918): 391–501.
- POHL H. 2004: Fauna Europaea: *Stylops*. *Fauna Europaea version 2.5*. Available from: <http://www.faunaeur.org> (December 26, 2012).
- POHL H. & OEHlke J. 2003: Verzeichnis der Fächerflügler (Strepsiptera) Deutschlands. *Entomologische Nachrichten und Berichte* **8**: 273–275.
- POLUSZYŃSKI G. 1927: *Stylops nitidiusculae* n. sp. *Polskie Pismo Entomologiczne* **6**: 92–99.
- REICHERT A. 1914: Aus der Wochenstube einer Strepsipteren-Mutter. *Entomologisches Jahrbuch* **23**: 148–152.
- SAUNDERS S. S. 1872: Stylopitarum, ordinem Strepsipterorum Kirbii constituentium, mihi tamen potius Coleopterorum Familiae, Rhipiophoridis Meloidisque propinquae, Monographia. *Transactions of the Entomological Society of London* **20**: 1–49, lxxvi, plate VII.
- SCHKAFF B. 1925: Description d'une nouvelle espèce de *Stylops* [Strepsipt.]. *Bulletin de la Société Entomologique de France* **8**: 139–140.
- SMIT J. T. & SMIT J. 2005: De waaiervleugeligen (Strepsiptera) van Nederland. [Strepsiptera of the Netherlands]. *Entomologische Berichten* (Amsterdam) **65**: 43–51 (in Dutch).
- SMITH F. 1857: Observations on the difficulties attending the discrimination of the species of the genus *Stylops*. *Transactions of the Entomological Society of London, New Series* **4**: 115–118, plate 24.
- SOON V., KESKÜLAT T. & KURINA O. 2012: Strepsiptera species in Estonia. *Entomologica Fennica* **22**: 213–218.
- STEPHEN'S J. F. 1829: Ordo VII. Strepsiptera, Kirby. P. 403. In: *A systematic catalogue of British insects. Part I.* Baldwin and Cradock, London, 403 pp.
- STRAKA J., ALQARNI A. S., JŮZOVÁ K., HANNAN M. A., HINOJOSA-DÍAZ I. A. & ENGEL M. S. (in prep.): Rediscovered parasitism of *Andrena savignyi* Spinola (Hymenoptera: Andrenidae) by *Stylops* (Strepsiptera: Stylopidae) and revised taxonomic status of the parasite.
- STRAKA J., REZKOVÁ K., BATELKOVÁ J. & KRATOCHVÍL L. 2011: Early nest emergence of females parasitised by Strepsiptera in protandrous bees (Hymenoptera Andrenidae). *Ethology, Ecology & Evolution* **23**: 97–109.
- TOLASCH T., KEHL S. & DÖTTERL S. 2012: First sex pheromone of the order Strepsiptera: (3R,5R,9R)-3,5,9-Tri-methyldodecanal in *Stylops melittae* Kirby, 1802. *Journal of Chemical Ecology* **38**: 1493–1503.
- ULRICH W. 1930: *Ordnung: Fächerflügler. Strepsiptera Kirby (1813)*. Die Tierwelt Mitteleuropas. Queller und Meyer, Leipzig, 26 pp.