



# Molecular phylogeny of lauxaniid flies (Diptera, Cyclorrhapha) confirms non-monophyly of *Sapromyza* Fallén 1810

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## Abstract

Lauxaniids are a species rich group of acalyptrate flies, with most species known from the tropics. Several genera are in suspicion of non-monophyly, but no phylogenetic analysis has been carried out. Three markers (28S rRNA, 16S rRNA and EF 1- $\alpha$ ) were employed to analyze relationships of 66 European lauxaniids, including 9 sequences from GenBank. The data was analysed using the Bayesian and maximum parsimony approach. Genus *Sapromyza* appears in three distinct clades, confirming the expected non-monophyly. New combinations are proposed for the following species: *Homoneura muscaria*, comb. n., *Paralauxania albiceps* comb. n., *Nannomyza basalis* comb. n., *Nannomyza takagii* comb. n. Along with the analysis, *Sapromyza slovaca* sp. n. is described. The type material has been deposited in the Institute of zoology, Slovak Academy of Sciences.

## Keywords

Europe; new species; non-monophyly

# Introduction

Lauxaniidae is one of the most speciose families of acalyptrate flies, currently treated as sister to Sciomyzoidea (Wiegman et al. 2011). They are diverse especially in the tropics and evolved into a range of beautiful forms (Stuckenberg 1971, Papp & Shatalkin 1998, Gaimari & Silva 2010b). Imagos usually rest on the vegetation (Shewell 1987, Papp & Shatalkin 1998) while larvae are known to be saprophagous (Miller & Foote 1975, Miller & Foote 1976, summary information given in Miller 1977). Currently, the family is divided into three subfamilies: Lauxaniinae, Homoneurinae and the recently added Eurychoromyinae (Gaimari & Silva 2010a). Eurychoromyinae is a small group of exclusively Neotropical species. The Homoneurinae were established by Stuckenberg (1971) almost half a century ago. The first person to use the name Lauxaniinae was Shewell (1977).

Homoneurinae are characterised by homoneuriform costa (costal spines reaching vein  $R_{4+5}$ ), the regular presence of ctenidium (row of comb spines on fore femur) (Stuckenberg 1971) and the presence of two or three apical spurs on the mid tibia (McAlpine 1989). Lauxaniinae were characterised by the absence of these characters. Two tribes were proposed, each for one subfamily. Papp (2007) erected the tribe Trigonometopini for 10 Old World Lauxaniinae genera and Sasakawa (1995) proposed Noonamyiini for single genus *Noonamyia* Stuckenberg 1971 within Homoneurinae. Lauxaniinae are considered as paraphyletic by a number of authors (Stuckenberg 1971, Shewell 1987, Papp & Shatalkin 1998, Gaimari & Silva 2010b) although no phylogenetic analysis at the family level has been carried out. The only molecular phylogeny within Lauxaniids is that of Pestano et al. (2003), which focuses on the Madeiran representatives of genus *Sapromyza* Fallén 1820.

The situation at a generic level is not better resolved. One of the most species rich genera within lauxaniids is *Sapromyza*, with about 300 described species worldwide (Gaimari & Silva 2010b). The genus as a whole is largely considered to be a grouping of unrelated taxa (e.g., Shewell 1987, Papp & Shatalkin 1998, Shatalkin 2000, Gaimari & Silva 2010b). Another example of unconvincing relations is the genus *Lauxania* Latreille 1804. Merz (2001) noted that the genus *Lauxania* is morphologically diverse. This is partly due to a replacement of *L. albomaculata* Strobl 1909 from *Calliopum* Strand 1928 to *Lauxania* by Shatalkin (2000). As appropriately noted by Merz (2001), this taxonomical proposal was not based on the rigorous phylogenetic analysis. Pérusse & Wheeler (2000) suspected that, based on the structure of male terminalia, *Lauxania* and *Calliopum* as currently understood may not be reciprocally monophyletic.

During faunistical research of Slovakia, an undescribed species of *Sapromyza* was found. The new species is superficially similar to *S. zetterstedti* Hendel 1908. Both species are described in detail and illustrated. The aim of the present paper is to provide a phylogenetic analysis based on DNA sequences of several European species, including the new species.

## Materials and Methods

The material was collected by sweeping net in 2010–2012 in Slovakia and Austria. Most of the species originated from Slovakia, while 3 were from Austria (*Eusapromyza multipunctata* (Fallén 1820), *Homoneura thalhammeri* Papp 1978 and *Neoparoecus simplicipes* (Yarom 1991)). The specimen of *Sapromyza slovaca* sp. n. used for DNA extraction was not included in the type series (the specimen was unfortunately utilised for DNA extraction—at the time of processing it was not misidentified for *S. zetterstedti*, only the abdomen is preserved: Fig. 10); specimen was caught in the Tematínske kopce hills, Lúka. Freshly caught flies were preserved in 96% alcohol and stored until the isolation of DNA. Isolation and purification were performed using the DNeasy Blood and tissue kit (Qiagen). Three markers were chosen: two nuclear (fragment of 28S rRNA, elongation factor-1a) and one mitochondrial (fragment of 16S rRNA) (Caterino et al. 2000). The primers used for amplification of the sequences are given in

Primer	Sequence
16S-rRNA f	5'-CGCCTGTTTAACAAAAACAT-3'
16S-rRNA r	5'-CCGGTCTGAACTCAGATCACGT-3'
Elongation factor 1-α f	5'-ACAGCVACKGTYTGYCTCATRTC-3'
Elongation factor 1-α r	5'-CAGGAAACAGCTATGACCGCTGAGCGYGARCGTGGTATCAC-3'
28S-rRNA f	5'-AGTTCAGCACTAAGTCACT-3'
28S-rRNA r	5'-CACCATCTTTCGGGTCACAGC-3'

Table 1. Primers used for amplification of the molecular markers.

Letters f and r refer to forward and reverse.

Table 1. Sequencing was performed externally by german company GATC Biotech. Quality of sequences was checked visually in Bioedit (Hall 1999). In the case of low quality sequences, a new PCR reaction was run.

DNA sequences of the outgroup were downloaded from GenBank. Following sciomyzoid taxa were chosen: *Trypetoptera punctulata* (Scopoli 1763) (Sciomyzidae), *Zodion cinereum* (Fabricius 1794) (Conopidae), *Myopa buccata* (Linnaeus 1758) and *M. vesiculosa* Say 1823 (Conopidae), *Helcomyza ustulata* Curtis 1825 (Helcomyzidae). In the case of the two *Myopa* species, they were combined into one hybrid taxon *Myopa*. Additionally, sequences of two celyphids and 9 another lauxaniid species (*Sapromyza* endemic to Madeira, Pestano et al. 2003) were downloaded (see Table 2).

The alignment of sequences was performed in Guidance 2 (Penn et al. 2010, Sela et al. 2015) using the MAFFT algorithm. The aligned sequences were tested for the best model of molecular evolution by jModeltest (Posada 2008, Darriba et al. 2012, Guindon & Gascuel 2003), implemented via Phylemon 2.0 (Sánchez et al. 2011). The alignments for all three markers were concatenated by SequenceMatrix, v. 1.7.8 (Vaidya et al. 2011), and exported into nexus and TNT format. Two methods were employed to analyse the dataset: Bayesian in MrBayes, v. 3.2 (Ronquist et al. 2011) and maximum parsimony in TNT (Goloboff et al. 2003). Resulting trees were edited in Figtree, v. 1.3.1 (Rambaut 2006–2009) and Photoshop CE.

In using the Bayesian approach, data were partitioned into three blocks according to the markers. Four parameters (Revmat, Statefreq, Shape and Pinvar) were allowed to change independently for each of the partitions. The same dataset was imported into TNT. As the searching algorithm was chosen ratchet and initial level was set to 99, other parameters were left in default. From the resulting trees was constructed strict consensus tree. Bootstrap with 500 replicates was chosen as the branch support value.

The terminology follows McAlpine (1981). Keys of Papp (1979) and Shatalkin (2000) were used for the determination in coordination with its English translation (Schacht et al. 2004). Line arts were redrawn in Photoshop CE from photographs taken by Micrometrics digital camera mounted on Stemi 2000-C ZEISS microscope. The type material has been deposited in the Institute of Zoology, Slovak Academy of Sciences (SAV).

Table 2. Accession numbers of DNA sequences used in the phylogenetic analysis.

Family	Species	EF 1-α	16S rRNA	28S rRNA
Ingroup				
Lauxaniidae	Aulogastromyia anisodactyla	KU991598	KT956319	KT956373
Lauxaniidae	Calliopum aeneum	_	KT956320	KT956374
Lauxaniidae	Calliopum elisae	KU991599	KT956321	KT956375
Lauxaniidae	Calliopum simillimum	KU991600	KT956322	KT956376
Lauxaniidae	Calliopum splendidum	KU991601	KT956323	KT956377
Lauxaniidae	Homoneura muscaria	KU991602	KT956324	KT956378
Lauxaniidae	Eusapromyza multipunctata	KU991603	KT956325	KT956379
Lauxaniidae	Homoneura biumbrata	KU991604	KT956326	KT956380
Lauxaniidae	Homoneura dilecta	KU991605	KT956327	KT956381
Lauxaniidae	Homoneura interstincta	KU991606	_	KT956382
Lauxaniidae	Homoneura mediospinoza	KU991607	KT956329	KT956383
Lauxaniidae	Homoneura patelliformis	KU991608	KT956330	KT956384
Lauxaniidae	Homoneura remmi	KU991609	KT956331	KT956385
Lauxaniidae	Homoneura thalhammeri	_	KT956328	KT956386
Lauxaniidae	Lauxania cylindricornis	KU991619	KT956342	KT956396
Lauxaniidae	Lauxania minor	KU991620	KT956343	KT956397
Lauxaniidae	Meiosimyza affinis	KU991610	KT956332	KT956387
Lauxaniidae	Meiosimyza conjugata	KU991611	KT956333	KT956388
Lauxaniidae	Meiosimyza decipiens	KU991613	KT956334	KT956389
Lauxaniidae	Meiosimyza decempunctata	KU991612	KT956335	KT956390
Lauxaniidae	Meiosimyza illota	KU991614	KT956336	KT956391
Lauxaniidae	Meiosimyza laeta	KU991615	KT956337	KT956392
Lauxaniidae	Meiosimyza patycephala	KU991616	KT956338	KT956393
Lauxaniidae	Meiosimyza rorida	KU991617	KT956339	KT956394
Lauxaniidae	Meiosimyza subfasciata	KU991618	KT956340	KT956395
Lauxaniidae	Minettia austriaca	KU991621	KT956344	KT956398
Lauxaniidae	Minettia fasciata	KU991622	KT956345	KT956399
Lauxaniidae	Minettia filia	KU991623	KT956346	KT956400
Lauxaniidae	Minettia flaviventris	KU991624	_	KT956401
Lauxaniidae	Minettia longipennis	KU991626	KT956348	KT956402
Lauxaniidae	Minettia lupulina	KU991627	KT956349	KT956403
Lauxaniidae	Minettia loewi	KU991625	KT956347	KT956404
Lauxaniidae	Minettia plumicornis	KU991628	KT956350	KT956405
Lauxaniidae	Minettia tabidiventris	KU991629	KT956351	KT956406
Lauxaniidae	Nannomyza basalis	KU991639	KT956360	KT956417
Lauxaniidae	Neoparoecus simplicipes	KU991630	KT956352	KT956407
Lauxaniidae	Pachycerina pulchra	KU991632	KT956353	KT956409
Lauxaniidae	Pachycerina seticornis	KU991633	KT956354	KT956410
Lauxaniidae	Paralauxania albiceps	KU991637	KT956372	KT956415
Lauxaniidae	Peplomyza discoidea	KU991631	KT956355	KT956411
Lauxaniidae	Peplomyza intermedia	_	KT956356	_
Lauxaniidae	Peplomyza litura	KU991634	KT956357	KT956412
Lauxaniidae	Poecilolycia vittata	KU991635	KT956358	KT956413
Lauxaniidae	Pseudolyciella pallidiventris	KU991636	KT956359	KT956414
Lauxaniidae	Sapromyza apicalis	KU991638	KT956361	KT956416
Lauxaniidae	Sapromyza hyalinata	KU991640	KT956363	KT956420
Lauxaniidae	Sapromyza intonsa	KU991641	KT956364	KT956421

Family	Species	EF 1-α	16S rRNA	28S rRNA
Lauxaniidae	Sapromyza obscuripennis	_	KT956365	KT956418
Lauxaniidae	Sapromyza obsoleta	KU991642	KT956362	_
Lauxaniidae	Sapromyza opaca	KU991643	KT956369	KT956408
Lauxaniidae	Sapromyza palpella	_	_	KT956422
Lauxaniidae	Sapromyza sexpunctata	KU991646	KT956368	KT956419
Lauxaniidae	Sapromyza schnabli	KU991647	KT956370	_
Lauxaniidae	Sapromyza slovaca	KU991648	KT956371	KT956425
Lauxaniidae	Sapromyzosoma quadricincta	KU991644	KT956366	KT956423
Lauxaniidae	Sapromyzosoma quadripunctata	KU991645	KT956367	KT956424
Lauxaniidae	Tricholauxania praeusta	KU991649	KT956341	KT956426
Madeira				
Lauxaniidae	Sapromyza ultima	_	AJ439209.1	_
Lauxaniidae	Sapromyza indigena	_	AJ439213.1	_
Lauxaniidae	Sapromyza hirtiloba	_	AJ439210.1	-
Lauxaniidae	Sapromyza inconspicua	_	AJ439206.1	_
Lauxaniidae	Sapromyza laurisilvae	_	AJ439202.1	_
Lauxaniidae	Sapromyza mauli	_	AJ439198.1	-
Lauxaniidae	Sapromyza biscoitoi	-	AJ439197.1	_
Outgroup				
Sciomyzidae	Trypetoptera punctulata	JN816269.1	JN828251.1	JN837532.1
Conopidae	Zodion cinereum	HM062655.1	_	JN664686.1
Conopidae	Myopa buccata	_	AY573121.1	JN664685.1
Conopidae	Myopa vesiculosa	HM062652.1	_	_
Helcomyzidae	Helcomyza ustulata	JN828427.1	JN828211.1	JN828263.1
Celyphidae	sp.	_	FJ025463.1	FJ025552.1
Celyphidae	Spaniocelyphus umsinduzi	-	-	KC177761.1

Words in italics in the family column specify the sequences; Madeira refers to species endemic to Madeira, sequences of which were downloaded from GenBank, as well as sequences of the outgroup.

# Results

# Phylogenetic analysis

A total of 63 species belonging to 15 out of 19 European genera were included (Merz 2015). Among the few missing genera is *Sciasminettia* Shewell 1971, an extremely rare genus of Europe known only from Spain (Carles-Tolrá 2006). The total length of the alignment was 2229 bp, with 444 bp of 16S rRNA, 823 bp of 28S rRNA and 962 bp of EF-1 $\alpha$ .

The model selected by jModeltest (Posada 2008) based on Akaike information criterion for all three markers was general time reversible model with gamma shaped distribution of rates over sites and with proportion of invariable sites (GTR + I + G).

The search in TNT resulted in 6 trees in length of 3003 steps. A strict consensus tree was constructed (Fig. 1). The strict consensus tree seems to be well resolved. However, almost all deeper nodes, including the monophyly of lauxaniids, were weakly supported (bootstrap value below 75).



Fig. 1. Bayesian tree. Values above branches are posterior probability values.

The Bayesian analysis was run for 5.87 million generations to reach the convergence (average deviation of split frequencies below 0.01). The tree topology recovered was fairly similar to that of the maximum parsimony tree. As for the maximum parsimony tree, several deeper nodes are weakly supported (e.g., monophyly of *Minettia* or sister group relationships of *S. obsoleta* group to *Calliopum*) but other ones have good



Fig. 2. Maximum parsimony tree. Values above branches are bootstrap values.

support (*Meiosimyza* clade, *Homoneura* + *Cnemcantha* clade). The relative length of branch connecting the Lauxanoidea with outgroup is very high (truncated in Fig. 2) comparing to branches within ingroup.

Monophyly of Lauxanoidea is well supported in both trees. The position of Celyphidae remains unclear: it could be within the lauxaniids as well as sister towards them. In the Bayesian tree, five rather distinct clades can be recognised (Fig. 2). The first one is composed of the genus *Homoneura* and species *Cnemacantha muscaria*. The second clade involves the genera *Pachycerina*, *Sapromyzosoma* and part of the *Sapromyza* species. The third clade involves species of *Calliopum*, *Lauxania*, *Sapromyza* and *Neoparoecus*. The forth clade is composed of species of the genera *Meiosimyza*, *Aulogastromyia*, *Tricholauxania*, *Eusapromyza* Peplomyza and *Pseudolyciella*. Finally, the last one is represented by a single genus, *Minettia*. A few taxa (*Poecilolycia vittata*, *Sapromyza intonsa* group) appear basal to one of these clades and their position will be discussed later.

From these five clades, three were recovered in MP tree, one with slight modification (the *Homonerua* clade includes the celyphids) and the second clade (including *Pachycerina, Sapromyzosoma* and part of *Sapromyza* species) was decomposed into a paraphyletic series of minor clades. Monophyly of genus *Pachycerina* was confirmed, as well as the sister group relationship of *Sapromyzosoma* and *S. sexpunctata* species group.

## Sapromyza slovaca sp. n.

*Type material*. Holotype &: Slovakia: Kremnické vrchy mountains, Ihráč, GPS: N 48° 39' 4.11", E 18° 57' 15.47", 10.–20.VI. 1996, leg. Vidlička & Majzlan, Malaise trap. The specimen is mounted on a paper strip, SAV.

Paratypes: Slovakia: 1♂, 20.–30.V. 1996, other data as holotype; 4♂, 10.–20.VI. 1996, other data as holotype. 1♂, Podunajská nížina lowland, Svätý Jur, GPS: N 48°13' 12.78", E 17° 13' 20.76", 15.VI. 2008, leg. Vidlička & Majzlan, Malaise trap. 1♂, Tematínske kopce hills, Lúka, GPS: N 48° 39' 56.90", E 17° 53' 55.41", 6.–19. VI. 1999, leg. Kozánek & Roller.

*Diagnosis*. Rather small, yellowish body, pair of black spots on 5th and 6th abdominal tergites, the occiput yellowish, convex and narrow frons, oval postpedicel, arista short pubescent, 4 rows of acrostichal setae, 0 + 3 dorsocentral setae, hyaline wings, and simple legs. The genitalia are characteristic, narrow epandrium suppressed by large syntergosternite 7 + 8, surstyli conical and standing apart from the epandrium, aedeagus membranous, postgonites asymmetrical and apically pointing, phallapodeme short, laterally flattened.

*Description*. Body length 2.92–3.35 mm (n = 5, sum of three measurements: head, thorax, abdomen), wing length 4.17 mm (n = 1).

*Coloration.* Body pale yellowish in prepared specimens, orange yellow in living specimens, 5th and 6th abdominal tergites with a pair of black spots (Fig. 3).

*Head* (Figs. 3–5). Frons convex, rather narrow, anterior part also covered with distinct setulae; facial sclerite almost flat, parafacial narrow; gena slightly broader than parafacial; antennae short, situated close to each other, scapus very short, indistinct, postpedicel oval in lateral view; arista short pubescent; ocellar triangle nearly equilateral; compound eyes large, higher than broad; median occipital sclerite of the same colour as whole head; supracervical setae present.



**Figs. 3–10.** *Sapromyza slovaca* sp. n., male, various specimens. (3) Holotype male, lateral view; (4) right wing, paratype; (5–7) head in frontal, lateral and dorsal view, note the absence of occipital patch, paratypes; (8) thorax, dorsal view, paratype, (9,10) abdomen, lateral and ventral view, specimen was stored and photographed in alcohol. This figure is published in colour in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/journals/1876312x.

Chaetotaxy: 2 orbital setae, 1 vertical seta, 1 postvertical seta, postocelar setae strongly convergent, ocelar setae shorter than frons.

*Thorax.* Mesonotum convex (Fig. 8), some specimens a pair of brownish dorsocentral vittae; legs simple; fore femur without ctenidium; all tibiae with well developed dorsal preapical seta; halter pale; wing hyaline, veins yellowish, row of costal setae ending shortly after the adjoining of  $R_{2+3}$  vein (Fig. 4).

Chaetotaxy: 0 + 3 dorsocentral setae, becoming progressively longer with the first pair of dorsocentral setae being only half of the third pair, acrostichal setae in 4 rows, medial rows slightly longer than lateral rows, lateral rows quite irregular and sparse; 1 postpronotal seta; 2 notopleural seta; 1 posthumeral seta; 1 supraalar seta; 2 postalar seta; postsutural intra-alar seta missing; 2 pairs of scutellar setae well developed; 1 weak proepisternal seta; katepisternum covered by several small setae and 2 katepisternal setae, anterior katepisternal seta; katepimeron and anepimeron bare.

*Abdomen.* 5th and 6th tergites with a pair of distinct black spots, spot on 6th tergite usually smaller than spot on 5th tergite (Figs. 9 and 10). In detailed inspection, a pair of very small brown patches may be found on 4th tergite. Tergites covered by few irregular rows of setae, row of setae on distal margin elongated. Last two sternites medially divided and with elongated setae.

*Male terminalia* (Figs. 11–15). Syntergosternite 7 + 8 rather large, convex; epandrium, cercus and subepandrium free; epandrium horseshoe-like, narrow; cercus simple; surstylus roughly conical, standing apart from the plane of the epandrium; hypandrium large, trapezoid but weakly sclerotised; postgonites asymmetrical and apically pointed; left postgonite shorter with sclerotised tip turned laterally; right postgonite broader with pointing tip; aedeagus membranous; phallapodeme short and laterally flattened; ejaculatory apodeme slightly irregular, rather large. Female unknown.

*Etymology. slovaca* referring to Slovakia, where the species was first recognised. I dedicate this species to people who are devoted to protection of nature of Slovakia.

*Distribution.* The species is so far known from the western and central part of Slovakia. It was collected on warm open sites, usually on bushes, solitary trees and forest edges.

# Sapromyza zetterstedti Hendel 1908

*Material studied*: Syntypus  $13^{\circ}$ , Thynäs, Norway (Biological museum at Lund University). The specimen is in moderately good condition. The abdomen with last pair of legs is mounted below the specimen. Postpedicels are broken, as well as several setae.

Other specimens studied: 2♂, Slovakia, High Tatra Mountains, Podbanské village, GPS: N 49° 09' 41.34", E 19° 55' 26.88", 1002 m, 30.6.2008, leg. Vidlička & Majzlan, Malaise trap. 3♀, High Tatra Mountains, Podbanské village, GPS: N 49° 10' 40.20", E 19° 55' 02.34", 1052 m, 7.7.2008, 14.7.2008, 4.8.2008, leg. Vidlička & Majzlan, Malaise trap. 3♀, High Tatra Mountains, Zuberec village, GPS: N 49°14' 49.50", E 19° 42' 49.68", 1002 m, 20.6.2011, 11.7.2011, 18.7.2011, leg. Vidlička & Majzlan, Malaise trap.

*Redescription*. Body length 2.90–3.41 mm (n = 5, sum of three measurements: head, thorax, abdomen), wing length 4.21 mm (n = 1).

*Coloration.* Body yellow ochre (Figs. 16 and 17), only the occiput with dark brown rectangular spot (Fig. 22) and 5th and 6th (occasionally also 4th) abdominal tergites with pair of black spots (Fig. 19).



**Figs. 11–15.** *Sapromyza slovaca* sp. n., male terminalia. (11,12) Terminal segment of male terminalia in lateral and posterior view; (13–15) genital complex in lateral, ventral and dorsal view. Abbreviations: ce, cercus; ej ap, ejaculatory apodeme; ep, epandrium; hy, hypandrium; lpa, left postgonite; phap, phalapodeme; rpa, right postgonite; su, surstyly; subep, subepandriuim.

*Head* (Figs. 20–22). Frons almost flat, in anterior part with distinct setae; facial sclerite almost flat, parafacials rather broad; gena slightly broader in comparison to the parafacials; antennae short; facial carina between the antennae present; postpedicel oval in lateral view; arista short pubescent; eyes red, in alcohol preserved specimens with yellowish tinge; median occipital sclerite brown except of the top; supracercvical setae well developed.

*Thorax.* Mesonotum convex (Fig. 23); legs simple; fore femur without ctenidium; all tibiae with well developed dorsal preapical seta; halter pale; wing hyaline (Fig. 18), veins yellowish, row of costal setae ending shortly after the adjoining of  $R_{2+3}$  vein.

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Chaetotaxy: 0 + 3 dorsocentral setae, first pair of dorsocentral setae distinctly weaker and shorter, acrostichals in 4 rows, subequal in length, scutelar setae present; 1 postpronotal seta; 2 notopleural seta; 1 posthumeral (presutural intraalar) seta; 1 supraalar seta; 2 postalar seta; no postsutural intra-alar seta; 2 scutellar setae well developed; 1 weak proepisternal seta; katepisternum covered by several small setae and 2 katepisternal setae, fore katepisternal seta weaker; anepisternum covered with several small setae and 1 strong anepisternal seta; katepimeron and anepimeron bare.



**Figs. 16–24.** *Sapromyza zetterstedti* Hendel 1908 (16) Male, lateral view; (17) female, lateral view, (18) wing; (19) detail of female abdomen, lateral view, note the small dark spot on 4th tergit; (20) head in frontal view; (21) head in lateral view; (22) head in dorsal view, note the brown rectangular spot on the vertex; (23) mesonotum, dorsal view, (24) detail of male abdomen, ventral view. This figure is published in colour in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline. com/content/journals/1876312x.

*Abdomen*. 5th and 6th tergites with a pair of black spots; in some specimens, pair of smaller spots is clearly developed also on 4th tergite (Figs. 16, 17 and 19). Tergites covered by 1 to 4 transversal rows of setae, row of setae on distal margin elongated. Sternites weakly sclerotised, posteriorly slightly broader both in males and females (Fig. 24).

*Male terminalia* (Figs. 25–28). Syntergosternite 7 + 8 large, convex and laterally fusing to epandrium; epandrium, cerci and subepandrium fusing; cerci asymmetrical, apically pointing and covered with strong setae; hypandrium weakly developed; postgonites well developed, strongly asymmetrical and apically pointing; left postgonite arched,



**Figs. 25–28.** Male terminalia of *Sapromyza zetterstedti* Hendel 1908 (25) Epandrium in posterior view; (26) male terminalia in anterior view; (27) male terminalia in laterl view; (28) male terminalia in ventral view. Abbreviations: ce, cercus; ej ap, ejaculatory apodeme; ep, epandrium; hy, hypandrium; lpa, left postgonite; pa, postgonites; phap, phalapodeme; rpa, right postgonite; su, surstyly.



**Figs. 29–32.** Female terminalia and last abdominal segments of *Sapromyza zetterstedti* Hendel 1908. (29) Lateral view; (30) dorsal view; (31) posterior view; (32) ventral view. Abbreviations: ce, cercus; Vt–VIIt, 5th to 7th tergit; VIIIs, 8th sternit.

right postgonite with two unequal arms; aedeagus reduced to soft tube; phalapodeme short and laterally flattened; ejaculatory apodeme oval, rather large; cerci simple. *Female terminalia* (Figs. 29–32). Three spermathecae present; 7th tergite narrow, with distinctly developed tergal and sternal part; 8th tergite with ventral part sclerotised only; 8th sternum well developed; last segments fused to single ring sclerite, distally with two long setae; cerci fused.

*Remarks. Sapromyza zetterstedti* is a *nomen novum* established by Hendel (1908). The species was originally described by Zetterstedt (1847) as *Sapromyza quadrinotata*. The description is very brief; Zetterstedt (1847) noticed only that the species has ferruginous eyes, rear end of abdomen with four black dots, subhyaline wings, round antennae and pubescent arista ("seta subnuda"). The species should occur in southern parts of Sweden; adults can be spotted in July (Zetterstedt 1847).

# Key to the Palaearctic species of *Sapromyza* with single pair of black spots on the abdominal tergites

The English version (Shacht et al. 2004) of the key of Shatalkin (2000) is adjusted. The key begins with antithesis 33: "Ocellar bristles located inside ocellar triangle", which leads to couplet 43.

43 Only tergite VI with pair of lateral spots; palpus black in apical half; third antennal segment sometimes apically darkened, surstylus broad, leaf-like (Fig. 156) ... *S. bisigillata* Rondani

- Tergites V–VI with pair of lateral spots; palpus variable, third antennal segment variable, surstylus variable ...44
- 44 Palpus apically black, 2.5 mm ... S. nitida Czerny

- Palpus yellow ... 45

45 Large species: 4.4 mm, genitalia fig. 192, Kuril Islands ... S. paramerata Shatalkin

- Small species: 2.3-3.0 mm ... 46

37 Occiput with brown rectangular spot, antennae clearly separated (Fig. 20) ... *S. zetterstedti* Hendel

- Occiput without spot, antennae almost touching (Fig. 5) ... S. slovaca sp. n.

# Discussion

# Phylogeny

The present phylogeny has a number of limitations, like including taxa from a single geographic region (Europe), a relatively small number of taxa comparing to the world diversity and a relatively small (3) number of markers involved. Although the tree topologies are fairly similar, deeper nodes are mostly weakly supported in both Bayesian and maximum parsimony trees. Therefore, well supported and shallow nodes will be discussed in preference.

One of the main differences among the two trees constructed is the position of *Pachycerina, Sapromyzosoma* and part of *Sapromyza* species. While in the Bayesian tree they form a single clade, in maximum parsimony they are decomposed into a series of minor clades. Because MP is prone to the long branch attraction artefact (LBA, Bergsten 2005), the analysis was repeated without the outgroup. If the LBA was responsible for decomposing of the clade, excluding of the outgroup should result in recovering the clade. This is what really happened (results not shown). Consequently, the different topologies are attributed to the LBA artefact.

One of the well-supported deep nodes is monophyly of Lauxanoidea. The position of celyphids remains uncertain.

# Homoneura van der Wulp 1891

*Cnemacantha muscaria* Fallén 1823 appears rather surprisingly within the genus *Homoneura. Cnemacantha* Macquart 1835 is exclusively an European monotypic genus and traditionally was treated as a member of Lauxaniinae (Stuckenberg 1971, Collin 1948). The species represents a unique mixture of characters: it is completely dull black, costa is sapromyziform and ctenidium is missing (lauxaniinae features), but has developed two dorsal preapical seta (homoneurinae feature). On the other hand, some undisputable *Homoneura* species (like *H. interstincta* Fallén 1820) lack homoneuriform costa as well (Merz 2003). Importantly, the male terminalia of *C. muscaria* are very similar to its sister species *H. thalhammeri* Papp 1978 (personal observation). The presence of inflated Malpighi tubes in larva and tendency to create a pupal chamber (Semelbauer & Kozánek 2014a) and small body size is also in compliance with this finding. *C. muscaria* is therefore replaced from genus *Cnemacantha* to *Homoneura*.

# Minettia Robineau-Desvoidy 1830

This genus appears to have no close relatives. The current subgeneric division (Shatalkin 2000, 2008) is not in compliance with our results, as two of the subgenera (*Plesiominettia* and *Minettia* s. str.) are not monophyletic. However, this result is in conflict with the apparently uniform structure of male terminalia of *Minettia* s. str. (Shatalkin 2000). The other two subgenera (*Frendelia* and *Scotominettia*) are represented by single species only and appear as sister taxa. The taxon sampling is unfortunately too sparse to carry out more general conclusions. Subgeneric classification of *Minettia* therefore deserves further attention.

# Meiosimyza Hendel 1925 and relatives

This clade is the poorest resolved. The close relatedness among the species of *Meiosimyza*, *Aulogastromyia* Hendel 1925, *Eusapromyza* Malloch 1923 and *Tricholauxania* Hendel 1925 has been already proposed by Shatalkin (2000). The occurrence of *Peplomyza* Haliday 1837 within this clade is less expected, thought it shares with the mentioned genera number of characters, like acrostichal setae organized in two rows, the presence of hairs on radial veins, (present in *Eusapromyza, Tricholauxania* and *P. litura*), brown longitudinal stripes on frons and thorax (indicated in *Eusapromyza*), patterned wings (*Eusapromyza*, some *Meisosimyza*) and some larval characters (shining body, elongated cephaloskeleton, hairs on inner side of labial lobe, held in common in *Meiosimyza, Tricholauxania* and *Aulogastromyia*, Semelbauer & Kozánek 2014b). The Bayesian tree suggests sister position of *Peplomyza* to all other taxa within this clade. Further, *Aulogastromyia* appears well within *M. affinis* Zetterstedt 1847 + *M. laeta* Zetterstedt 1838 clade, as sister species to *M. laeta*. If true, *Aulogastromyia* is a synonym of *Meiosimyza*. However, the structure of the male terminalia of *M. laeta* and *M. affinis* 

seriously differs from that of *A. anisodactyla*. More effort is required to elucidate the relationships within this clade.

# Sapromyza and relatives

The genus *Sapromyza* is clearly not monophyletic and the members of this genus appear in three distinct clades. Rather isolated are members of the *Sapromyza intonsa* group (*S. intonsa* Loew 1847 + *S. palpella* Rondani 1868). The isolated position is also suggested by some larval characters of *S. intonsa*, like unique structure of the ventral organ and cephaloskeleton in the first instar larva (Semelbauer & Kozánek 2014a). However, the support of their position within lauxaniids is particularly weak and is considered as unresolved here.

Part of the Sapromyza species clusters with Calliopum, Lauxania and Neoparoecus Özdikmen & Merz 2006. Morphological coherence of this group is supported by some adult (greenish stripes on composed eyes, personal observation) as well as larval characters (robust cephaloskeleton, sclerotised basal parts of mouth hooks in first instar, hairs on inner surface of labial lobe etc., Semelbauer & Kozánek 2014a). Within this group also falls the Sapromyza obsoleta Fallén 1820, a type species of Sapromyza. Rather surprisingly, Neoparoecus falls well within the closest relatives of S. obsoleta. According to Shatalkin (2000), some species of Sapromyza have slightly thickened arista, which complicates separation of Sapromyza and Neoparoecus. Results of this study suggest that species close to S. obsoleta are also closely related to Neoparoecus. This relationship is supported also by several morphological characters, like the weak dorsal preapical seta on hind tibiae (virtually absent in S. obsoleta, but still clearly present in close relatives, e.g., S. vilosulla Merz 2009) (Merz 2009), the presence of brush on hind legs (in Neoparoecus only several species) (Shatalkin 2000), the position and length of orbital setae and possibly the structure of male terminalia (personal observation). Paraphyly of Sapromyza towards Neoparoecus remains to be confirmed by more inclusive analysis.

Calliopum appears to be monophyletic and sister to S. obsoleta + Neoparoecus clade.

Lauxania appears to be non-monophyletic with Lauxania (Callixania) minor Martinek 1974 in basal position. The subgenus Callixania (only two Palearctic species) markedly differs from Lauxania s. str. by the protraction of facial part of the head, short scapus and structure of the male terminalia (Papp 1979, Merz 2001, Shatalkin 2000). Interestingly, two Nearctic species (L. albiseta Coquilet 1898, L. kafarista Pérusse & Wheeler 2000) treated currently as Lauxania s. str. have structure of aedeagus very similar to L. minor (Pérusse & Wheeler 2000), suggesting that the Callixania is not monophyletic. The phylogenetic analysis suggests that Callixania should be elevated to generic level. Before doing so, Lauxania needs thorough revision as Callixania might be more inclusive than we thought.

*Sapromyza (Schumannimyia) hyalinata* (Meigen 1826) appears as sister species to 7 species of *Sapromyza* from Madeira (Báez 2001, Pestano et al. 2003). This clade appears

well outside of the *S. obsoleta* clade suggesting that it deserves generic level. Madeiran *Sapromyza* can be treated possibly as *Schumannimyia*. This solution seems likely as *S. hirtiloba*, *S. mauli*, *S. laurisilvae*, *S. inconspicua* and *S. ultima* remind *S. hyalinata* with several characters, like black or dark brown body, yellowish anterior part of frons and yellow halter.

The rest of the Sapromyza species clusters with Pachycerina Macquart 1835 and Sapromyzosoma Lioy 1864. Interestingly, most species of Sapromyza from this clade bear dots on the abdominal tergites. The only exception is S. (Nannomyza) basalis Zetterstedt 1847. S. slovaca sp. n. is sister to S. opaca Becker 1895 + S. sexpunctata Meigen 1826, and they together form a sister group to Sapromyzosoma. This relationship seems likely as it is supported also by the larval morphology (Semelbauer & Kozánek 2014a). It is feasible that all species of "Sapromyza" within this clade deserve their own genus. S. albiceps Fallén 1820 is a peculiar and easy recognisable species with long legs, giving it spider-like appearance. It has a unique sexual dimorphism: the female is yellowish with two pairs of brown spots on fifth and sixth abdominal tergite, while male has the fifth and sixth abdominal tergites without markings and has strikingly white head with single pair of orbital seta. Furthermore, the male genitalia are very simple, slightly reminding those of Pachycerina (surstyly fused to epandrium, phalapodeme slightly laterally flattened). On the other hand, S. obsoleta is typical in having free surstyly with strong inner teeth and stick-like phallapodeme. Hendel (1908) erected Paralauxania for this species and it is resurrected here. Nannomyza Frey 1941 is elevated to a generic level, as already proposed by Papp & Shatalkin (1998). It is not clear whether all species with dots on abdominal tergites like S. zetterstedti, S. bisigillata Rondani 1868, S. obscuripennis Loew 1847 and other Holarctic species should be included into one or several genera. For example, close relatives of S. sexpunctata are morphologically uniform, but S. obscuripennis has a very peculiar structure of male terminalia. S. zetterstedti shares some characters with S. obscuripennis (occipital spot, flat frons and separated antennae), but male terminalia resemble more those of Sapromyzosoma. To resolve this taxonomic uncertainty, all species of interest (with a pair of black dots on abdominal tergites) should be carefully analysed.

Two species will be discussed separately: *Poecilolycia vittata* (Walker 1849) and *Pseudolyciella pallidiventris* (Fallén 1820). Morphology of larvae suggests that both species are close to each other and at the same time related to *S. sexpunctata* and *Sapromyzosoma* (Semelbauer & Kozánek 2014a). However, the phylogenetic analysis did not recover this relationship. This apparent conflict could be resolved by a more extensive taxon sampling and adding more molecular and morphological characters.

## Sapromyza slovaca sp. n.

Phylogenetic analysis suggests that *S. slovaca* is sister to *S. sexpunctata* + *S. opaca* clade. This result is largely intuitive, as *S. slovaca* is very similar to both species. Within the Palaearctic region, several other species are likely members of this clade, but were not included in the analysis. These are *S. zetterstedti*, *S. bisigillata*, *S. nitida* Czerny 1932 (western Palaearct), *S. paramerata* Shatalkin 1993 and *S. pseudopaca* Shatalkin 1993

(eastern Palearct). Within this group, the new species can be easily recognised by the following combination of characters: yellowish coloration, occiput without brown spot, two pairs of black dots on the abdominal tergites and small body size. Complications may arise, when third pair of abdominal dots is recognised. In this case, the small body size and the shape of the male terminalia can still safely separate the species.

# Conclusions

This study presents the first attempt at the phylogenetic analysis of the representatives of the Lauxaniidae family. The results suggest that within European species there are at least five major clades. One of them is represented by Homoneurinae genera (*Homoneura* and *Cnemacantha*), while four clades are represented by Lauxaniinae genera.

Cnemacantha muscaria is replaced to the genus Homoneura, Sapromyza albiceps is recovered as Paralauxania albiceps, and Nannomyza is elevated to a generic level.

A number of taxonomic changes were indicated by phylogenetic analysis, but a more thorough analysis is needed. Several species of *Sapromyza* with dots on abdominal tergites and possibly *S. intonsa* species group deserves reclassifying in separate genera; the subgenus *Callixania* possibly deserves generic level; species close to *S. obsoleta* might be paraphyletic to *Neoparoecus;* Madeiran *Sapromyza* species can be possibly replaced in *Schumannimyia* and together deserve generic level, the relationships of *Meiosimyza* and related genera remain largely unresolved, although the results suggest that *Aulogastromyia* and possibly *Tricholauxania* are synonyms of *Meiosimyza*.

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