

RESEARCH PAPER

Integrative taxonomy of Central European *Planetella* (Diptera: Cecidomyiidae) indicates high species diversity, intraspecific variation and low host specificity

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Abstract. A first attempt is made to revise the European species of the gall midge genus *Planetella* Westwood, 1840 (Diptera: Cecidomyiidae), with a focus on the fauna of the Czech Republic, Slovakia and Denmark. A total of 19 species are recognized based on unique DNA sequences, of which 13 are described as new to science: *Planetella adami* Ševčík & Hippa sp. nov., *P. aestivalis* Ševčík & Hippa sp. nov., *P. antennata* Ševčík & Hippa sp. nov., *P. atrobrunnea* Ševčík & Hippa sp. nov., *P. attilai* Ševčík & Hippa sp. nov., *P. csabai* Ševčík & Hippa sp. nov., *P. davidi* Ševčík & Hippa sp. nov., *P. galiciensis* Ševčík & Hippa sp. nov., *P. hlisnikovskyyi* Ševčík & Hippa sp. nov., *P. muranica* Ševčík & Hippa sp. nov., *P. riparia* Ševčík & Hippa sp. nov., *P. submontana* Ševčík & Hippa sp. nov., and *P. thermophila* Ševčík & Hippa sp. nov. Four previously described species are recognized in the collected material: *Planetella arenariae* (Rübsaamen, 1899b), *P. fasciata* (Meigen, 1818) sp. restit., *P. gallarum* (Rübsaamen, 1899a), and *P. granifex* (Kieffer, 1898). For each of these species, DNA sequences are provided, as well as detailed illustrations of the male terminalia and male flagellomeres. Four additional species are represented only with larva, female or incomplete specimens. The phylogeny of European *Planetella* is tentatively reconstructed based on the combined analysis of three gene markers (28S, 16S, COI), but without providing any new infrageneric classification. The phylogenetic placement of the genus *Planetella* within the subfamily Cecidomyiinae is reconstructed based on four gene markers (18S, 28S, 16S, COI). The monophyly of *Planetella* is well supported, as well as its placement in the supertribe Cecidomyiidi. The genera *Acodiplosis* Kieffer, 1895 and *Putoniella* Kieffer, 1896 appear as the closest relatives of *Planetella*. The delimitation of the tribe Hormomyiini is discussed.

Key words. Diptera, Bibionomorpha, Cecidomyiinae, gall midges, DNA barcoding, new species, molecular markers, phylogenetic analysis, systematics, Central Europe, Palaearctic Region

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Introduction

Species of the genus *Planetella* Westwood, 1840 (Diptera: Cecidomyiidae: Cecidomyiinae) are among the largest gall midges in terms of adult body size, which may exceed 10 mm (GAGNÉ 1989). They can be recognized mainly by the forward-projecting thorax, on the same vertical plane as the head in lateral view, in combination

with large body size, orange-brown body coloration, and association with sedges (Cyperaceae).

A total of 53 species are included in this Holarctic genus (GAGNÉ & JASCHHOF 2021, ŠEVČÍK et al. 2021) in its current broad sense (*sensu* SKUHRAVÁ 1997 and GAGNÉ & JASCHHOF 2021). A possible exclusion from the genus of the Japanese species *Trishormomyia bambusae* Felt, 1932



was discussed by ŠEVČÍK et al. (2021) who described a new *Planetella* species from Taiwan.

All validly described species, except *Planetella taiwanensis* Ševčík, Hippa & Burdíková, 2021, were published before 1930 (GAGNÉ & JASCHHOF 2021). In the late 19th and early 20th century, species descriptions based on galls on host plants (extended phenotype), on larvae and/or females were commonly accepted, i.e. not up to current standards of integrative taxonomy. This makes a reliable interpretation of most validly published and accepted names very challenging and makes the validity of synonyms hitherto proposed uncertain. Moreover, even when adult males or females were included, the type specimens are often poorly preserved or have been completely lost. For example, the type species of the genus, *Planetella extrema* (Walker, 1837), is based on the female holotype, with the wings lost and antennae broken off (EDWARDS 1938). With current knowledge, *Planetella* species should not *a priori* be assumed to be host specific at the level of *Carex* species. Thus, species descriptions based on extended phenotype alone must be considered unreliable. A further taxonomic problem is that often the original descriptions and figures of *Planetella* species are not diagnostic. Sometimes, figures are completely absent or were published in later publications by the same or different authors.

The species now in *Planetella* s. lat. were originally described in several different, mostly monotypic, genera. All of these were synonymized by SKUHRAVÁ (1997) under the oldest available name, *Planetella*. This broad interpretation of the genus was followed by GAGNÉ & JASCHHOF (2021). The infrageneric classification of *Planetella* is, however, beyond the scope of this paper. A revised infrageneric classification can possibly be done when the Nearctic and East Palearctic faunas are better known and carefully revised.

The biology of particular species of *Planetella* is lesser known than in many other genera of gall-forming Cecidomyiidae. All the species, for which the biology has been recorded, are associated with the speciose sedge genus *Carex*, with only one Nearctic species being recorded from *Cyperus* sp. (GAGNÉ & JASCHHOF 2021). However, records of exact associations between a recognizable species of *Planetella* and a reliably identified host plant are rare, and finding the galls is even less common.

This paper represents the first attempt to interpret and properly describe the species of *Planetella* in Central Europe, with focus on the Czech Republic, Slovakia and Denmark. The opportunity is also taken to describe a new species from northern Spain (Galicia). The species concept adopted here is based primarily on the structure of the male terminalia, in combination with DNA sequence data. Female characters are not considered in this study, although they exist, because females of most *Planetella* species are either unknown or they are not reliably associated with conspecific males. The only proper association can be made by molecular methods because more than one species can be reared from a single host plant. Female terminalia in Cecidomyiidae, as well as in the other

families of Sciaroidea, are much less studied than male terminalia and they usually do not provide sufficient details and distinct structures to ensure the identification at the species level, although in some genera of gall midges the female terminalia play an important role for the species identification. This study thus must be considered as preliminary, because many nominal species are not covered by recent sampling, and because females of most species are unknown. The revision of *Planetella* is a long-term task and much more primary natural history and taxonomic investigation is needed.

A second aim of this paper is to present the first phylogenetic hypothesis for the relationships among the European species of *Planetella*, as revealed by multigene analysis, including the position of the genus within the subfamily Cecidomyiinae. The most recent reconstructions of the phylogeny of Cecidomyiidae, based on molecular markers (DORCHIN et al. 2019, SIKORA et al. 2019), did not include representatives of this genus. A separate tribe, Hormomyini, was proposed in the literature (GAGNÉ & JASCHHOF 2021) to comprise *Planetella* sensu lato, but it has not yet been supported by phylogenetic evidence.

Material and methods

Field studies and morphological identification. Specimens for this study were collected in the years 2014–2023 at different localities in the Czech Republic, Slovakia, Denmark, Poland, and Spain. Several collecting methods were used, including Malaise traps, emergence traps, laboratory rearing from field-collected host plants with galls, and sweep netting. All specimens are deposited in the ethanol collection of the Ševčík lab at the University of Ostrava (JSL-UOC), except the holotypes and some paratypes which are prepared on slides and deposited in the National Museum of the Czech Republic, Prague (NMPC) and in the Silesian Museum, Opava, Czech Republic (SMOC).

The morphological terminology adopted here principally follows that by GAGNÉ (2018). For the sorting of specimens and preliminary identification, Olympus SZX7 stereomicroscope and Olympus CX41 compound microscope were used. All the holotypes of the new species, as well as at least one male specimen of the other species, were slide-mounted in Euparal, while most of the paratypes and non-type specimens are kept in ethanol. All the line drawings were made by the second author (H. Hippa) using a drawing tube attached to a Leitz Diaplan or Leitz Laborlux compound microscope. The male terminalia are illustrated for all the species included in this study, as well as the antennal flagellomere 4 and outline of flagellomere 1, with or without associated pedicel.

Molecular methods. The samples used for DNA isolation were stored in 70–96% ethanol. DNA was extracted using NucleoSpin Tissue Kit (MACHEREY-NAGEL), following the manufacturers' protocol. Either the entire specimen or the abdomen were used for DNA extraction, allowing also sufficient tissue maceration for the species identification. The primers used for PCR amplification (total volume 20 µl) of particular gene fragments are shown in Table 2.

The PCR products were purified using the Gel/PCR DNA Fragments Extraction Kit (GENEAID) and were sequenced by Eurofins Genomics (Germany). The sequences were assembled and edited in SeqTrace 0.9.0 (STUCKY 2012). GenBank accession numbers for all the sequences are listed in Table 1.

All the sequences were aligned using MAFFT version 7 (KATO & STANDLEY 2013) on the MAFFT server (<http://mafft.cbrc.jp/alignment/server/>). Resulting alignments were visually inspected and manually refined in BioEdit 7.2.5 (HALL 1999) when necessary. In order to remove all unreliably aligned regions of rRNA genes, the web server based GBLOCKS 0.91b program (CASTRESANA 2000) was used (http://phylogeny.lirmm.fr/phylo.cgi/one_task.cgi?task_type=gblocks), with conditions set as follows: allow smaller blocks, allow gap positions within the final blocks, allow less strict flanking positions and do not allow many contiguous non-conserved positions.

Two phylogenetic analyses were performed. A total of 22 species of *Planetella* were included in the first dataset, focussing on phylogenetic relationships within the genus, plus 13 species of other Cecidomyiidae genera in the outgroup (Tab. 1). For the second dataset, designed to show the position of *Planetella* within Cecidomyiinae, only 4 species of *Planetella* were selected, plus 43 species of Cecidomyiinae in the ingroup. As outgroup taxa for the second dataset we included several representatives of the lower subfamilies of Cecidomyiidae.

The final length of concatenated alignment was 1535 bp in dataset 1, the lengths of individual alignments were the following: 16S = 292 bp, 28S = 585 bp, COI = 658

bp. In dataset 2, the final length of concatenated alignment was 2486 bp, the lengths of individual alignments were the following: 16S = 280 bp, 18S = 993 bp, 28S = 555 bp, COI = 658 bp.

Both the final concatenated datasets were partitioned by gene and codon position and subsequently analysed using maximum likelihood (ML) method. Analyses were conducted using IQtree software (NGUYEN et al. 2015).

Best-fitting substitution models were chosen automatically by the IQ-TREE software. For Dataset 1: COI_1 – TPM2+F+I+G4; COI_2 – TIM2+F+I+G4; COI_3 – HKY+F+I+G4; 16S – GTR+F+G4; 28S – TPM2+F+G4; for Dataset 2: COI_1 – TPM2u+F+G4; COI_2 – GTR+F+I+G4; COI_3 – TN+F+I+G4; 16S – GTR+F+I+G4; 18S – HKY+F+I+G4; 28S – TPM2u+F+I+G4; without free-rate heterogeneity. Branch supports were evaluated using 1000 ultrafast bootstrap (HOANG et al. 2017). All other settings were left as default. The node support values are given in the form of ultrafast bootstrap (= ufboot). The resulting phylogenetic trees (consensus trees) were visualized using Interactive Tree Of Life (iTOL v6; LETUNIC & BORK 2021).

The trees were rooted by *Porricondyla nigripennis* (Meigen, 1830) in the case of dataset 1 (phylogenetic relationships within the genus *Planetella*), and by *Catotricha subobsoleta* (Alexander, 1924) for dataset 2 (phylogenetic position of the genus *Planetella* within the subfamily Cecidomyiinae).

Genetic distances were calculated in MEGA11 (TAMURA et al. 2021) using Kimura 2-parameter model and they are demonstrated in Table 3.

Table 1. List of specimens used for the phylogenetic analysis, with GenBank accession numbers.

Species	Voucher code	Sampling locality and year	16S	28S	18S	COI
<i>Acodiplosis inulae</i> (Loew, 1847)	C30	Slovakia, 2014	MG684520	MG684648	MG684556	MG684804
<i>Ametrodiplosis thalictricola</i> (Rübsaamen, 1895)	C189	Denmark, 2021	N/A	OR656641	OR656618	OR669972
<i>Anthodiplosis rudimentalis</i> (Kieffer, 1901)	C193	Denmark, 2022	N/A	N/A	N/A	OR669974
<i>Asphondylia sarothamni</i> Loew, 1850	OUT18	Czech Republic, 2014	KP288724	KP288807	KP288770	KX453761
<i>Camptodiplosis auriculariae</i> Buxton & Barnes, 1953	C52	Czech Republic, 2014		MG684652	MG684576	
	C157	Czech Republic, 2022	OR677419			OR669999
<i>Catotricha subobsoleta</i> (Alexander, 1924)	OUT42	USA, 2014	KP288738		KP288784	KT316873
	CatSub	USA, 2014		MG554155		
<i>Cecidomyia pini</i> (De Geer, 1776)	cecpin	from GenBank	MN201461	MN201224	N/A	MN191270
<i>Cecidomyia</i> sp. 1	C171	Czech Republic, 2023	OR677421	OR656638	OR656615	OR669969
<i>Cecidomyia</i> sp. 2	C202	Czech Republic, 2023	N/A	N/A	OR656620	OR669975
<i>Contarinia cracca</i> (Loew, 1850)	C145b	Slovakia, 2022	N/A	OR656632		OR669963
	C145c	Slovakia, 2022			OR656609	
<i>Contarinia loti</i> (De Geer, 1776)	C13	Czech Republic, 2014	N/A	MG684649	MG684549	MG684798
<i>Contarinia rumicis</i> (Loew, 1850)	C136	Denmark, 2019	OR677413	OR656630	OR656607	OR669961
<i>Contarinia subulifex</i> Kieffer, 1897	C147b	Slovakia, 2022	OR677416	OR656634	OR656611	OR669965
<i>Clinodiplosis cilicrus</i> (Kieffer, 1889)	clcil	from GenBank	MN201464	MN201227	N/A	MN191273
<i>Dasineura trifolii</i> (F. Löw, 1874)	C6	Slovakia, 2014	MG684508	MG684639	MG684569	MG684795
<i>Dasineura urticae</i> (Perris, 1840)	C104	Slovakia, 2018	OR677411	OR656628	OR656605	OR669959
<i>Dicerura dentata</i> Spungis, 1979	C2	Slovakia, 2012	MG684506	MG684618	MG684545	MG684788

(continues on next page)

Table 1. List of specimens used for the phylogenetic analysis, with GenBank accession numbers (continuation).

Species	Voucher code	Sampling locality and year	16S	28S	18S	COI
<i>Didactylomyia longimana</i> (Felt, 1908)	C72	Slovakia, 2014	MG684518	MG684621	MG684557	MG684807
<i>Herbomyia robusta</i> Mohn, 1955	C133	Denmark, 2019	OR677412	OR656629	OR656606	OR669960
<i>Heteropeza pygmaea</i> Winnertz, 1846	HePy	Slovakia, 2016	MT446561	MT446788	MT446700	MT446887
<i>Janetia cerris</i> (Kollar, 1850)	C146b	Slovakia, 2022	OR677415	OR656633	OR656610	OR669964
<i>Lasioptera rubi</i> (Schränk, 1803)	OUT17	Czech Republic, 2014	KP288723	KP288806	MG684579	KT316860
<i>Lestodiplosis juniperina</i> (Felt, 1907)	C161	Czech Republic, 2022	OR677420	OR656637	OR656614	OR669968
<i>Lestodiplosis polyperi</i> (Loew, 1850)	C27	Czech Republic, 2014	MG684539	MG684653	MG684554	MG684800
<i>Loewiola centaureae</i> (Loew, 1875)	C22	Italy, 2014	MG684517	MG684650	MG684553	MG684834
<i>Lopesia niloticae</i> Gagné, 1993	lopnil	from GenBank	MN201506	MN201275	N/A	MN191318
<i>Mayetiola destructor</i> (Say, 1817)	mayetiola	from GenBank	NC_013066	KC177649	KC177284	NC_013066
<i>Mikiola fagi</i> (Hartig, 1839)	OUT7	Slovakia, 2013	KJ136730	KJ136767	MG684574	MG684809
<i>Mycodiplosis coniophaga</i> (Winnertz, 1853)	myccon	from GenBank	MN201513	MN201284	N/A	MN191325
<i>Mycodiplosis</i> sp.	C151	Denmark, 2020	OR677418	OR656636	OR656613	OR669967
<i>Obolodiplosis robiniae</i> (Haldeman, 1847)	C12	Czech Republic, 2014	MG684516	MG684647	MG684548	MG684821
<i>Odontodiplosis</i> sp. 1	C85	Czech Republic, 2014	OR677410	OR656626	MG684555	MG684802
<i>Odontodiplosis</i> sp. 2	C142	Czech Republic, 2022	OR677414	OR656631	OR656608	OR669962
<i>Oligotrophus juniperinus</i> (Linnaeus, 1758)	C17	Italy, 2014	MG684511	MG684637	MG684571	MG684793
<i>Placochela nigripes</i> (Löw, 1877)	C18	Czech Republic, 2014	MG684533	MG684651	MG684551	MG684803
<i>Planetella adami</i> Ševčík & Hippa sp. nov.	PLA61	Slovakia, 2017	OR677445	OR656664		OR669997
<i>Planetella aestivalis</i> Ševčík & Hippa sp. nov.	PLA27a	Slovakia, 2019	OR677437	OR656656		OR669989
<i>Planetella antennata</i> Ševčík & Hippa sp. nov.	PLA52	Slovakia, 2022	OR677443	OR656662		OR669995
<i>Planetella arenariae</i> (Rübsaamen, 1899)	PLA11b	Slovakia, 2018	OR677431	OR656650		OR669983
<i>Planetella atrobrunnea</i> Ševčík & Hippa sp. nov.	PLA3	Slovakia, 2017	OR677427	OR656646		OR669979
<i>Planetella attilai</i> Ševčík & Hippa sp. nov.	PLA30d	Slovakia, 2020	OR677439	OR656658		OR669991
<i>Planetella csabai</i> Ševčík & Hippa sp. nov.	PLA11	Slovakia, 2018	OR677430	OR656649		OR669982
<i>Planetella davidi</i> Ševčík & Hippa sp. nov.	PLA47	Slovakia, 2022	OR677442	OR656661		OR669994
<i>Planetella fasciata</i> (Meigen, 1818)	PLA33	Czech Republic, 2020	OR677440	OR656659	OR656624	OR669992
<i>Planetella galiciensis</i> Ševčík & Hippa sp. nov.	PLA19	Spain, 2019	OR677435	OR656654		OR669987
<i>Planetella gallarum</i> (Rübsaamen, 1899)	PLA6a	Denmark, 2016	OR677429	OR656648	OR656622	OR669981
<i>Planetella granifex</i> (Kieffer, 1898)	PLA18a	Slovakia, 2019	OR677434	OR656653	OR656623	OR669986
<i>Planetella hlisnikovskyi</i> Ševčík & Hippa sp. nov.	PLA34	Czech Republic, 2021	OR677441	OR656660		OR669993
<i>Planetella muranica</i> Ševčík & Hippa sp. nov.	PLA2	Slovakia, 2016	OR677426	OR656645		OR669978
<i>Planetella riparia</i> Ševčík & Hippa sp. nov.	PLA54b	Slovakia, 2022	OR677444	OR656663		OR669996
<i>Planetella</i> sp. A	PLA20	Denmark, 2019	OR677436	OR656655		OR669988
<i>Planetella</i> sp. B	PLA14c	Slovakia, 2018	OR677432	OR656651		OR669984
<i>Planetella</i> sp. C	PLA63	Slovakia, 2017	N/A	OR656665		OR669998
<i>Planetella</i> sp. D	PLA29	Slovakia, 2017	OR677438	OR656657		OR669990
<i>Planetella submontana</i> Ševčík & Hippa sp. nov.	PLA1	Slovakia, 2016	OR677425	OR656644		OR669977
<i>Planetella taiwanensis</i> Ševčík et al., 2021	PLA5	Taiwan, 2016	OR677428	OR656647	OR656621	OR669980
<i>Planetella thermophila</i> Ševčík & Hippa sp. nov.	PLA15	Slovakia, 2018	OR677433	OR656652		OR669985
<i>Polystepha quercus</i> Kieffer, 1897	C181	Czech Republic, 2022	OR677423	OR656640	OR656617	OR669971
<i>Porricondyla nigripennis</i> (Meigen, 1830)	OUT16	Slovakia, 2014	KP288722	KP288805	KP288768	KT316859
<i>Putoniella pruni</i> (Kaltenbach, 1872)	C20	Czech Republic, 2014	OR677409	OR656625	OR656603	OR669957
<i>Rabdophaga heterobia</i> (Loew, 1850)	OUT22	Slovakia, 2014	MG684509	MG684642	MG684572	MG684796
<i>Rhizomyia</i> sp.	C180	Czech Republic, 2022	OR677422	OR656639	OR656616	OR669970
<i>Rhopalomyia tanaceticola</i> (Karsch, 1879)	C29	Czech Republic, 2014	MG684515	MG684641	MG684568	MG684792
<i>Sitodiplosis moselana</i> (Géhin, 1857)	simo	from GenBank	GAKJ00000000.1	GAKJ00000000.1	GAKJ00000000.1	GAKJ00000000.1
<i>Spanolepis selloanae</i> Gagné, 2021	C102	Spain, 2018	N/A	OR656627	OR656604	OR669958
<i>Stomatosema obscurum</i> (Mamaev, 1967)	C73	Slovakia, 2014	MG684519	MG684622	MG684558	MG684808
<i>Thecodiplosis brachyntera</i> (Schwägrichen, 1835)	C204	Czech Republic, 2023	N/A	OR656643	N/A	OR669976
<i>Wachtliella caricis</i> (Loew, 1850)	C192	Denmark, 2022	OR677424	OR656642	OR656619	OR669973
<i>Xylodiplosis nigratarsis</i> (Zetterstedt, 1850)	C150	Slovakia, 2018	OR677417	OR656635	OR656612	OR669966

Table 2. Primers used for PCR amplification and sequencing of the nuclear 18S and 28S and mitochondrial 16S and COI genes.

Gene fragment	Direction	Primer sequences (5'→3')	Source
COI	F	GGTCAACAAATCATAAAGATATGG	FOLMER et al. (1994)
	R	TAAACTTCAGGGTGACCAAAAAATCA	FOLMER et al. (1994)
18S	F	AACCTGGTTGATCCTGCCAGT	KATANA et al. (2001)
	R	TGATCCTTCTGCAGGTTACACCTACG	KATANA et al. (2001)
	R	GGTTAGAAGTAGGGCGGTATCT	CAMPBELL et al. (1995)
28S	F	ACCCGCTGAATTTAAGCAT	DAYRAT et al. (2001)
	F	AGAGAGAGAGTTCAAGAGTACGTG	BELSHAW & QUICKE (1997)
	R	TAGTTCACCATCTTTCGGGTC	LAURENNE et al. (2006)
16S	F	TAATCCAACATCGAGGTC	ROHÁČEK et al. (2009)
	R	CGAAGGTAGCATAATCAGTAG	ROHÁČEK et al. (2009)
	F	CGCCTGTTTATCAAAAACAT	PALUMBI et al. (1991)
	R	CCGGTCTGAACTCAGATCACGT	PALUMBI et al. (1991)

Table 3. Kimura 2-parameter (K2P) genetic distances among the species of *Planetella* included in this study.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
1 <i>Planetella submontana</i> sp. n.																								
2 <i>Planetella attilai</i> sp. n.	8,0%																							
3 <i>Planetella</i> sp. D	8,2%	11,0%																						
4 <i>Planetella muranica</i> sp. n.	12,7%	13,5%	14,2%																					
5 <i>Planetella thermophila</i> sp. n.	14,4%	14,2%	13,3%	5,2%																				
6 <i>Planetella adami</i> sp. n.	15,3%	13,5%	15,2%	8,2%	8,9%																			
7 <i>Planetella csabai</i> sp. n.	14,7%	14,2%	15,2%	8,6%	10,0%	9,5%																		
8 <i>Planetella hlisnikovskiyi</i> sp. n.	12,2%	12,2%	13,3%	8,5%	9,1%	8,7%	9,3%																	
9 <i>Planetella</i> sp. B	9,6%	11,3%	10,8%	11,7%	13,0%	13,9%	12,7%	10,1%																
10 <i>Planetella riparia</i> sp. n.	9,2%	10,1%	10,8%	11,7%	11,7%	12,9%	12,9%	9,9%	5,4%															
11 <i>Planetella galiciensis</i> sp. n.	9,6%	9,2%	12,0%	10,3%	11,0%	11,3%	11,1%	9,2%	7,0%	6,8%														
12 <i>Planetella fasciata</i>	10,6%	10,8%	11,9%	10,6%	11,3%	12,6%	11,7%	9,6%	7,2%	8,4%	6,2%													
13 <i>Planetella antennata</i> sp. n.	9,9%	11,1%	11,8%	10,8%	11,3%	13,5%	11,5%	10,3%	8,5%	8,4%	7,2%	7,8%												
14 <i>Planetella davidi</i> sp. n.	12,4%	12,7%	12,9%	12,4%	13,3%	14,4%	13,8%	11,9%	10,8%	10,2%	9,7%	10,6%	10,8%											
15 <i>Planetella arenariae</i>	11,5%	12,5%	12,7%	12,0%	11,9%	12,6%	11,3%	11,7%	10,9%	10,8%	10,9%	9,9%	11,3%	11,8%										
16 <i>Planetella gallarum</i>	15,7%	15,7%	15,1%	14,4%	16,3%	16,7%	16,2%	14,8%	12,8%	12,2%	13,5%	12,6%	13,5%	11,0%	15,3%									
17 <i>Planetella</i> sp. A	14,2%	16,1%	16,1%	15,7%	17,2%	18,1%	17,1%	15,0%	15,8%	15,0%	15,2%	15,0%	15,1%	15,4%	15,5%	18,4%								
18 <i>Planetella granifex</i>	12,9%	14,0%	14,2%	11,9%	12,4%	12,8%	13,1%	12,4%	12,0%	11,5%	11,1%	12,2%	11,3%	12,0%	12,2%	15,5%	11,2%							
19 <i>Planetella taiwanensis</i>	16,1%	14,2%	17,2%	14,6%	13,5%	15,7%	15,7%	13,3%	13,1%	12,0%	11,8%	12,7%	11,8%	13,5%	12,6%	16,1%	18,4%	16,2%						
20 <i>Planetella aestivalis</i> sp. n.	14,2%	13,0%	15,6%	18,2%	18,2%	19,6%	19,2%	17,2%	17,4%	16,4%	16,7%	17,4%	16,8%	18,2%	16,8%	20,4%	18,2%	16,7%	17,6%					
21 <i>Planetella atrobrunnea</i> sp. n.	17,4%	15,9%	18,0%	15,7%	15,9%	17,1%	17,2%	14,4%	17,0%	16,6%	15,9%	15,5%	15,1%	16,1%	14,9%	19,8%	20,6%	17,4%	14,9%	18,7%				
22 <i>Planetella</i> sp. C	16,4%	16,6%	17,6%	14,9%	16,8%	16,6%	17,2%	14,7%	15,5%	15,3%	15,1%	14,5%	14,9%	15,5%	16,8%	17,2%	17,8%	16,2%	15,5%	20,7%	17,0%			
23 <i>Planetella</i> sp. near <i>aestivalis</i>	15,0%	13,3%	15,4%	19,6%	18,2%	19,6%	19,4%	18,0%	17,6%	16,6%	16,5%	17,1%	17,4%	18,8%	17,0%	21,4%	18,5%	17,0%	18,4%	3,0%	18,6%	20,9%		
24 <i>Planetella</i> sp. near <i>granifex</i>	12,9%	14,0%	13,8%	12,6%	13,0%	14,3%	14,2%	12,2%	11,9%	11,8%	11,7%	11,8%	11,7%	12,6%	12,4%	16,3%	11,2%	3,3%	17,0%	16,7%	18,0%	16,2%	16,9%	

Results and discussion

The results are presented in several subsections, covering a key to the included species, taxonomy and nomenclature of particular species, and two separate phylogenetic analyses. We consider it premature to present here a detailed diagnosis of the genus because most of the diagnostic characters stated in the literature are not distinctly developed in all the species currently included in the genus (e.g. the forward-projecting thorax) and we also believe that the definitive generic or subgeneric concept will be based mostly on a comprehensive molecular phylogenetic analysis, which will include also non-European taxa.

Key to species of *Planetella* recognized in this study

The following key is based on males only because females have not been reliably associated for most of the species. The number of flagellomeres appears as an important character, especially if it is different than 12. Like in most other Cecidomyiidi, males have distinctly binodose flagellomeres, usually 12-segmented, but superficially looking like 24-segmented (actually with 24 nodes). In all the species included in this paper, where the sexes were associated, males and females have the same number of flagellomeres, while their shape and structure is much simpler in females, and the antennae are also substantially shorter in females. In males, an additional short apical flagellomere of variable shape is usually present but sometimes not counted or overlooked in the past. We have tried to specify this in descriptions and keys. The other useful characters are body coloration, mainly of the thorax and abdomen, the presence or absence of the eye-bridge, and details on the male terminalia, especially the shape of the gonostylus and gonocoxite, the shape of hypoproct, and the shape and size of cerci. In any case, a safe identification of particular species should be based not only on morphological characters but also on DNA sequences, ideally from more than one specimen.

- 1 Antennae with 12 binodose flagellomeres, sometimes with an additional small apical segment, shorter than penultimate one. 2
- Antennae with more than 12 binodose flagellomeres. 11
- 2 Abdominal tergites with broad pale transverse anterior bands, eyes separated, without eye-bridge. *P. fasciata* Meigen, 1818 (Figs 4C,D, 13C)
- Abdominal tergites greyish brown, dark brown or rufous, with only small markings and spots, not reaching the sides of tergites. 3
- 3 Eyes widely separated, body mostly blackish brown, shiny, cerci small, rounded distally, hypoproct pear-shaped, distally broad, gonocoxite narrow, about 3× as long as broad. *P. hlišnikovskyi* Ševčík & Hippa **sp. nov.** (Figs 10C,D, 14E)
- Eye-bridge present, body mostly orange-brown, greyish or brownish, not shiny, terminalia different. 4
- 4 Body slender, scutum not produced above head, eye-bridge broad (with 2–3 ommatidia touching), gono-

- stylus relatively short and narrow, hypoproct narrow and apically excavated, aedeagus long, slightly shorter than gonocoxite, and narrow throughout.
- *P. arenariae* (Rübsaamen, 1899b) (Figs 4A,B)
- Scutum more or less produced above head, eye bridge usually narrow, membranous, terminalia different. 5
 - 5 Gonostylus broad, ovoid, with a small apical tooth, gonocoxite broad, hypoproct relatively long, apically excavated, aedeagus shorter than hypoproct. Female with a prolonged, apically pointed abdomen. Widely distributed species. Galls on several species of *Carex*. *P. granifex* (Kieffer, 1898) (Figs 5C,D, 13A)
 - Gonostylus relatively narrow, apically rounded or pointed, and/or with a row of small closely-set teeth. 6
 - 6 Hypoproct subrectangular in shape, posteriorly straight. 7
 - Hypoproct concave posteriorly, with apical depression. 9
 - 7 Gonostylus relatively short, maximum as long as half of gonocoxite, aedeagus relatively short, broad and apically rounded. *P. gallarum* (Rübsaamen, 1899a) (Figs 5A,B, 13B)
 - Gonostylus longer than half of gonocoxite, aedeagus elongated. 8
 - 8 Hypoproct about as broad as cercus, gonocoxite with a distinct rounded mediobasal lobe. *P. attilai* Ševčík & Hippa **sp. nov.** (Figs 8, 14A,B)
 - Hypoproct small, narrower than cercus, mediobasal lobe of gonocoxite broad and indistinct. *P. riparia* Ševčík & Hippa **sp. nov.** (Figs 11A,B,C, 14G)
 - 9 Apical depression of hypoproct shallow, gonostylus narrow, four times as long as broad. A large species, with a broad eye-bridge (2 to 6 ommatidia broad) and robust females. ... *P. aestivalis* Ševčík & Hippa **sp. nov.** (Figs 6E,F, 13D)
 - Apical depression of hypoproct relatively deep, gonostylus broader, about twice as long as broad, eye-bridge thin, membranous. 10
 - 10 Gonostylus club-shaped, distally distinctly broader than basally, thorax with distinct dark markings. *P. davidi* Ševčík & Hippa **sp. nov.** (Figs 9C–E, 14C)
 - Gonostylus slightly narrowing towards distal end, apically hooked, thorax mostly orange brown. *P. submontana* Ševčík & Hippa **sp. nov.** (Figs 12D,E, 14H)
 - 11 Antennae with 14 or 15 binodose flagellomeres, body mostly dark brown. 12
 - Antennae with more than 20 binodose flagellomeres. 16
 - 12 Antennae with 14 binodose flagellomeres, hypoproct apically excavated. *P. muranica* Ševčík & Hippa **sp. nov.** (Figs 11D–G, 14F)
 - Antennae with 15 binodose flagellomeres, the apical one may be shorter. Thorax mostly dark brown, except for the area around scutum and scutellum. Flagellomeres compact, relatively short. 13
 - 13 Hypoproct narrow, about as broad as aedeagus or cercus, body shiny blackish brown, palpus with 2 pal-

- pomeres, apical one pointed and blackish brown.
 *P. atrobrunnea* Ševčík & Hippa sp. nov. (Figs 7D,E, 13H)
- Hypoproct broad, distinctly broader than aedeagus. ...
 14
 - 14 Hypoproct apically almost straight, about as long as aedeagus, palpus with 2 palpomeres. *P. csabai* Ševčík & Hippa sp. nov. (Figs 9A,B, 13I)
 - Hypoproct apically more or less excavated, slightly shorter than aedeagus, palpus with 3 or 4 palpomeres.
 15
 - 15 Hypoproct apically distinctly excavated, palpus with 4 palpomeres. *P. adami* Ševčík & Hippa sp. nov. (Figs 6A–D, 13E,F)
 - Hypoproct apically rounded or slightly depressed, palpus with 3 palpomeres. *P. thermophila* Ševčík & Hippa sp. nov. (Figs 12A–C, 14I)
 - 16 Antennae with 21 binodose flagellomeres, abdominal tergites 2 to 7 with broad transverse anterior pale band, gonocoxite broad, only twice as long as broad, aedeagus thin, elongated, longer than gonocoxite, gonostylus apically rounded (Slovakia). *P. antennata* Ševčík & Hippa sp. nov. (Figs 7A–C, 13G)
 - Antennae with 22 binodose flagellomeres, abdominal tergites dark, orange-brown, gonocoxite narrow, three times as long as broad, aedeagus longer than gonocoxite, gonostylus narrow, more than half as long as gonocoxite, apically with a pointed tooth (Galicia, Spain). ...
 *P. galiciensis* Ševčík & Hippa sp. nov. (Figs 10A,B, 14D)

Review of species

1. Previously described species recognized in our material

The types of previously described species are mostly in a poor condition, as noted already by EDWARDS (1938). The type specimens of the species described by Johann Wilhelm Meigen are deposited in the Muséum national d'Histoire naturelle (MNHN) and visualised at their web pages (<https://science.mnhn.fr/taxon/genus/planetella>). The original colour drawings by Meigen were published by MORGE (1975). These Meigen's species were all collected as adults, without data on their host plants and without reliable association of sexes.

The specimens from the collection of Ewald Heinrich Rübsaamen are mostly placed in the Museum für Naturkunde Berlin (ZMHB), although they are not explicitly marked as types. They usually represent a series of specimens (males, females, exuviae, larvae) reared from the host plant and stored in alcohol. The first author of this paper visited the Berlin Museum für Naturkunde in October 2022 and studied all the available types of *Planetella*, but without dissecting their terminalia and without designation of lectotypes.

The following species of *Planetella* can be interpreted with high degree of certainty and satisfactorily associated with new material.

Planetella arenariae (Rübsaamen, 1899b)

Homomyia [sic!] *arenariae* Rübsaamen, 1899b: 602. Type locality: Germany.

Dyodiplosis arenariae: RÜBSAAMEN (1910: 287).

Type material. SYNTYPES: ♂♂ and ♀♀ in alcohol, studied (coll. ZMHB, Berlin).

Additional material examined (all in coll. JSL-UOC). **DENMARK:** WJ, Bjerregård, 11.xii.2016, 1 larva (specimen after DNA extraction, No. PLA8b) in gall on *Carex arenaria*, H. H. Bruun leg.; North West Zealand, Ordrup Næs, 1.v.2021, 1 ♀ (specimen after DNA extraction, No. PLA46c) reared from galls on *C. arenaria*, H. H. Bruun leg.; SZ, Bagholt Mose, 2022, 1 larva (specimen after DNA extraction, No. PLA57) in gall on *C. appropinquata*, H. H. Bruun leg. **SLOVAKIA:** Cerová vrchovina Protected Landscape Area, Hájnačka, Buková, *Quercus cerris* forest, 12.ix.–11.x.2018, 2 ♂♂ (specimens after DNA extraction, No. PLA11b, PLA11c), Malaise trap near *Carex michelii*, J. Roháček & J. Ševčík leg.

DNA sequences. DNA sequences (COI barcode region, 28S, 16S) of the specimen No. PLA11b are deposited in GenBank. Their Accession numbers are provided in Table 1.

Diagnosis. This species is well characterized by scutum not produced above the head and details on the male terminalia (relatively long gonocoxite, short and apically rounded gonostylus, narrow and apically excavated hypoproct, aedeagus narrow throughout and slightly shorter than gonocoxite), see Figs 4A,B.

Biology. We report here two new hosts other than *Carex arenaria*, i.e. *C. appropinquata* and *Carex michelii* (the latter is only a potential host), confirming broader host and habitat range for this species. There are also some other hosts mentioned in the older literature, e.g. *Carex hirta* and *C. vulgaris* (= *C. nigra*), see BAYER (1917), the former supposedly being confirmed by rearing of the adults (specimens with unknown depository, not studied by us).

Comments. RÜBSAAMEN (1899d) in his original description mentioned (among others) the following characters: antennae with 2 + 12 segments in both sexes, flagellomeres binodose, four palpomeres. The larvae were found in small galls on leaves and stems of *Carex arenaria*. He considered the species as not being a typical *Planetella*, rather 'a transition between genera *Hormomyia* and *Diplosis*'. In the molecular phylogenetic tree (Fig. 15), this species represents a sister taxon to all the other species of *Planetella* included in this study, see below.

Planetella fasciata (Meigen, 1818) sp. restit.

Cecidomyia fasciata Meigen, 1818: 94. Type locality: Germany.

Type material. HOLOTYPE: ♀, pinned, not studied, but photos available at the web page of MNHN Paris: <https://science.mnhn.fr/taxon/species/planetella/fasciata>.

Additional material examined (all in coll. JSL-UOC). **CZECH REPUBLIC: BOHEMIA:** Doksy, 31.v.–18.vi.2020, 1 ♀ (specimen after DNA extraction, No. PLA33), Malaise trap in *Carex* spp., M. Tkoč leg., Doksy, 15.v.–6.vi.2022, Malaise trap in *Carex* spp., 1 ♀ (specimen after DNA extraction, No. PLA33b), M. Tkoč leg.; Jilové, Pod lesem Nature Reserve, 29.vii.–2.ix.2022, Malaise trap, 1 ♀ (specimen after DNA extraction, No. PLA79), L. Blažej & J. Hejduk leg., Jilové, Pod lesem Nature Reserve, 2.ix.–4.xi.2022, Malaise trap, 1 ♂ (specimen after DNA extraction, No. PLA81), L. Blažej & J. Hejduk leg. **SLOVAKIA:** Muránska planina National Park, Rosiarka Nature Reserve, 920 m, 26.v.–21.vi.2022, 3 ♂♂ (specimens after DNA extraction, No. PLA52c,d,e, one of them figured), 1 ♀ (PLA52b), Malaise trap in *Carex rostrata*, all J. Roháček & J. Ševčík

leg.; Tisovec, Trstie Nature Reserve, 14.vi.–12.vii.2023, 1 ♂ (PLA70), Malaise trap in *Carex rostrata*, J. Roháček & J. Ševčík leg.

Diagnosis. This species is well characterized by the broad pale anterior bands on the abdominal tergites, in combination with 12 binodose flagellomeres. It is also one of the few species of *Planetella* with the eyes completely separated in both sexes, without an eye-bridge. The following combination of characters on the male terminalia is also diagnostic (Figs 4C,D): narrow gonostylus, club-shaped and apically rounded hypoproct, almost as long as gonocoxite, aedeagus narrow throughout and slightly shorter than gonocoxite.

Comments. This species has been considered as a junior synonym of *Planetella grandis* (Meigen, 1804). Although the identity of *P. grandis* has not been clarified yet and its terminalia remain unknown, the only male syntype of *P. grandis* clearly has a dark unbanded abdomen (the first three abdominal segments are still preserved, see <https://science.mnhn.fr/taxon/species/planetella/grandis>), without distinct pale transverse bands, and thus definitely represents a different species than the other three syntypes. The male syntype currently lacks the head, but EDWARDS (1938) mentioned that the male type of *P. fasciata* has well separated eyes and 15 flagellomeres (14 + a small apical segment), although the figure of the dark specimen in MORGE (1976) shows just 12 binodose flagellomeres. EDWARDS (1938) possibly refers in this case to British males, which he considered as conspecific.

In any case, *P. fasciata* is herewith reinstated as a valid species and its male terminalia and flagellomeres are figured for the first time (Figs 4C,D, 14C). We use the right of the first revising author to interpret this species in this way, although it may well be shown in the future that several closely related species with the eyes separated, 12 flagellomeres and banded abdomen exist.

The species figured by KIEFFER (1913) as *P. cornifex* (Kieffer, 1898) may represent a junior synonym of *P. fasciata*, see below (under *P. cornifex*).

Planetella gallarum (Rübsaamen, 1899)

Dichrona gallarum Rübsaamen 1899a: 542. Type locality: Germany.

Type material. SYNTYPES: 1 ♂ 8 ♀♀, in alcohol, Berlin, 30.i.–12.v.1896, (vial No. 380a, coll. ZMHB Berlin), examined.

Additional material examined. DENMARK: East Jutland, Strandkær (Biowide 060; Brunbjerg et al. 2019), 7.vi.2016, 1 ♂ 1 ♀, reared from galls on *Carex nigra* var. *recta*, H. H. Bruun leg., specimens after DNA extraction, prepared on slides, No. PLA6a, PLA6b (coll. JSL-UOC). 1 larva: the same data, specimen after DNA extraction, No. PLA6c (coll. JSL-UOC); 1 larva: West Jutland, Ejstrup (Biowide 031), 9.vi.2016, reared from gall on *Carex nigra* var. *recta*, H. H. Bruun leg., specimen after DNA extraction, prepared on slide, No. PLA10 (coll. JSL-UOC).

Diagnosis. This species can be recognized by the short, apically blunt gonostylus, only about half as long as gonocoxite, hypoproct subrectangular and posteriorly straight, aedeagus broad and apically rounded, reaching to two thirds of gonocoxite, and gonocoxites relatively broad (Figs 5A,B). It belongs to the group with 12 flagellomeres, narrow eye bridge, and mostly light orange-brown coloration, without distinct dark markings.

Discussion. This species is represented in our material

only by specimens from Denmark. It is interesting that we have not found it yet in the Czech Republic or Slovakia. It appears as not restricted to a single species of *Carex*. In the original description by RÜBSAAMEN (1899b), three different *Carex* species are mentioned as hosts, i.e. *Carex stricta* (= *C. elata*), *C. gracilis* (= *C. acuta*), *C. goodenoughii* (= *C. nigra*). All these three *Carex* species are rather closely related, several of them forming hybrids. They are all part of the large *Carex* sect. *Phacocystis*, and even a smaller and tighter group within it. It is thus possible that *Planetella gallarum* may be specific to this group of carices.

Planetella granifex (Kieffer, 1898)

Pseudhormomyia granifex Kieffer 1898: 58. Type locality: France, Moselle.

Type material. SYNTYPES: Lost.

Additional material examined. CZECH REPUBLIC: MORAVIA: Polanka nad Odrou, Přemyslov Nature Reserve, v.–vi.2009, 1 ♂ (specimen after DNA extraction, No. PLA12b, figured in Figs 5C,D), reared from tussock of *Carex acuta*, J. Roháček & J. Ševčík leg.; the same locality and collectors, 5.x.2018, 1 larva (specimen after DNA extraction, No. PLA12) in gall on *Carex acuta*. Podyjí National Park, Lipinská louka, 26.iv.–20.v.2021, 1 ♂ (specimen after DNA extraction, No. PLA35), Malaise trap in *Carex buekii*, J. Roháček & J. Ševčík leg.; the same locality and collectors, 20.v.–25.vi.2021, 1 ♂ (specimen after DNA extraction, No. PLA41); Poodří Protected Landscape Area, Bernartice, 29.v.–24.vi.2022, 2 ♂♂ (specimens after DNA extraction, No. PLA53, PLA53b), emergence trap in *C. buekii*, J. Ševčík leg. BOHEMIA: Doksy, 15.v.–6.vi.2022, 2 ♂♂ (specimens after DNA extraction, No. PLA51, PLA51b), Malaise trap in *Carex* spp., M. Tkoč leg. DENMARK: Madesø, 10.viii.2018, 1 larva (specimen after DNA extraction, No. PLA7) in gall on *C. acutiformis*; Hestetang, 1 ♂ (specimen after DNA extraction, No. PLA50), reared from *C. acutiformis*; Klinteskov, 16.iii.2019, 1 ♂ (specimen after DNA extraction, No. PLA22), reared from *C. acutiformis*; SJ, Pamhule Skov, 22.v.2020, 1 ♀ (specimen after DNA extraction, No. PLA46), reared from *C. acutiformis*; SZ: Purlund, 2022, 1 ♂ (specimen after DNA extraction, No. PLA49), reared from *Carex nigra*, all H. H. Bruun leg. SLOVAKIA: Cerová vrchovina Protected Landscape Area, Salonkáš, 11.x.2018, 2 larvae (specimens after DNA extraction, No. PLA14a, PLA14b) in galls on *C. acuta*, J. Ševčík leg.; the same locality and collector, 3.iv./11.iv.2019, 2 ♀♀ (specimens after DNA extraction, No. PLA14d, PLA14e) reared from galls on *C. acuta*, one of them in Fig. 2; Cerová vrchovina Protected Landscape Area, Tachty, meadow, 21.v.–19.vi.2019, 2 ♂♂ (specimens after DNA extraction, No. PLA18a, PLA18b), Malaise trap in *C. acutiformis*, J. Roháček & J. Ševčík leg.; the same locality and collectors, 28.viii.–25.ix.2019, 1 ♂ (specimen after DNA extraction, No. PLA28a); the same locality and collectors, 12.v.–11.vi.2021, 1 ♂ (specimen after DNA extraction, No. PLA38); the same locality and collectors, 20.viii.–16.ix.2021, 1 ♂ (specimen after DNA extraction, No. PLA44); Muránska planina National Park, Trsteník valley, 10.vi.–13.vii.2021, 1 ♂ 1 ♀ (specimens after DNA extraction, No. PLA42c, PLA42d), 13.vii.–19.viii.2021, 1 ♂ (specimen after DNA extraction, No. PLA42), emergence trap over *C. rostrata*, J. Roháček & J. Ševčík leg.; Tisovec, Trstie Nature Reserve, 12.vii.–16.viii.2023, 1 ♂ (specimen after DNA extraction, No. PLA71), Malaise trap in *C. rostrata*, J. Roháček & J. Ševčík leg. (all specimens in JSL-UOL collection).

Diagnosis. This species can be easily recognized by the shape of gonostylus, which is ovoid, with a small apical tooth, in combination with apically excavated subrectangular hypoproct, aedeagus much shorter than hypoproct, and broad gonocoxite (Figs 5C,D). Female has distinctly prolonged abdomen posteriorly (Fig. 1B). It belongs to the group with 12 flagellomeres, narrow eye bridge, and uniform, mostly light orange-brown coloration.

Variation. According to DNA sequences, two distinct

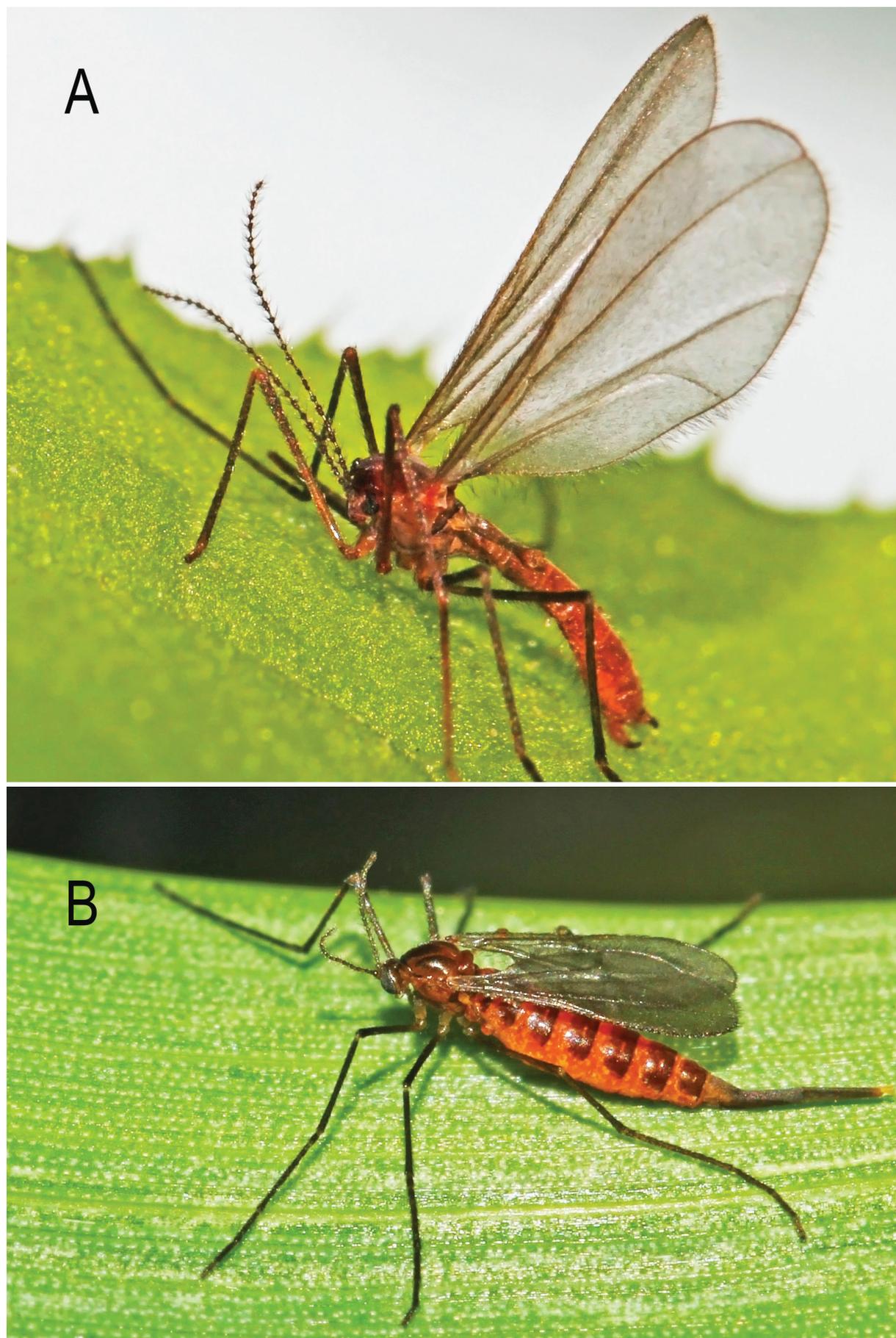


Fig. 1. Adults of *Planetella* species. A – male of *Planetella submontana* Ševčík & Hippa sp. nov. collected when sitting on a Malaise trap (Slovakia, Muránska planina, Trsteník, 16.vi.–14.vii.2016). B – female of *Planetella granifex* (Kieffer, 1898) reared from gall on *Carex acuta* (Slovakia, Cerová vrchovina, Salonkáš, 3.iv.–11.iv.2019). All photos by J. Ševčík.

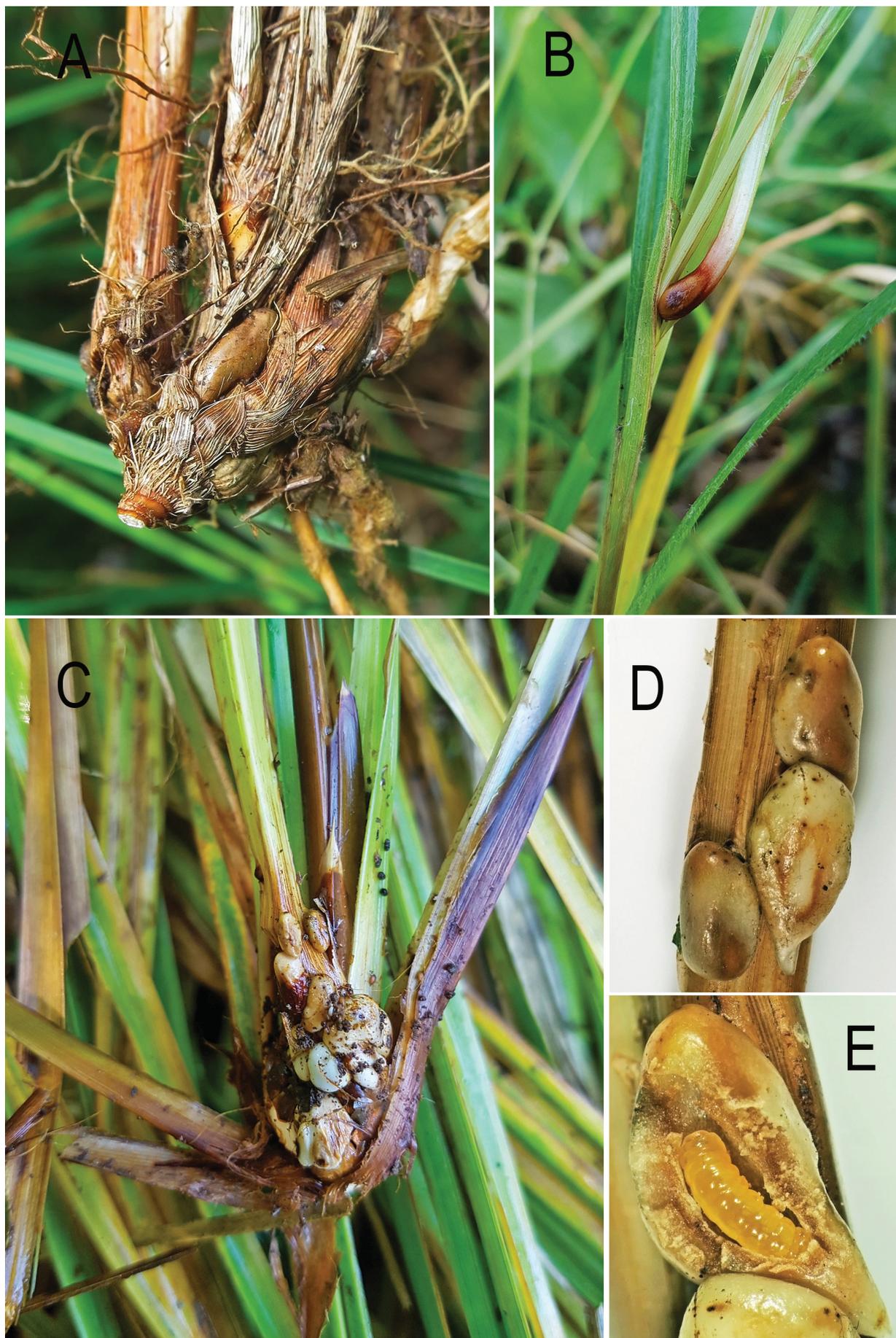


Fig. 2. Galls of *Planetella* species. A – *Planetella gallarum* (Rübsaamen, 1899) on *Carex nigra* var. *recta* (Denmark, Ejstrup, 9.vi.2016, photo by H.-H. Bruun). B – *Planetella* sp. B on *Carex hirta* (Slovakia, Cerová vrchovina, Salonkáš, 11.x.2018, photo by J. Ševčík). C–E – *Planetella granifex* (Kieffer, 1898) on *Carex acuta* (Slovakia, Cerová vrchovina, Salonkáš, 11.x.2018, photos by J. Ševčík).



Fig. 3. Habitats and traps used. A – Malaise trap in a thermophilous *Quercus cerris* forest (Slovakia, Cerová vrchovina, Jestice, Hradisko, 2022), photo by J. Ševčík. B – Malaise trap in a montane peat-bog with *Carex rostrata* (Slovakia, Muránska planina, Rosiarka Nature Reserve, 2022, with Adam Ševčík on the right), photo by J. Ševčík. C – emergence trap over *Carex rostrata* along a submontane stream (Slovakia, Muránska planina, Trsteník, 2021), photo by J. Ševčík. D – Malaise trap in a growth of *Carex acutiformis* near a pond (Slovakia, Cerová vrchovina, Chrámec, 2023, with following dipterists, from left to right: Jindřich Roháček, Michal Tkoč, Kryštof Sopuch, Jan Ševčík), photo by J. Roháček. E – Malaise trap in a forest steppe (Slovakia, Cerová vrchovina, Steblová skala, 2017, with following dipterists, from left to right: Jan Ševčík, Tomáš Sikora, Michal Tkoč), photo by J. Roháček. F – Malaise trap in a forest steppe (Czech Republic, Podyjí National Park, Hardegg, 2020), photo by J. Ševčík.

forms can be distinguished. The more common one, which we consider as true *P. granifex* (specimens listed above), and the second one, differing 3 % in COI barcode sequence, known only from the following three localities:

SLOVAKIA: Muránska planina National park, Rosiarka Nature Reserve, 21.vi.–18.vii.2022, 1 ♂ (No. PLA59, specimen after DNA extraction), J. Roháček & J. Ševčík leg., Malaise trap in *C. rostrata*; the same data except Trstie Nature Reserve, 12.vii.–16.viii.2023, 1 ♀ (PLA72, specimen after DNA extraction); **POLAND:** Białowieża Forest, 23.viii.2018, 1 larva (PLA9, specimen after DNA extraction), H. H. Bruun leg., in gall on *Carex acuta* (all specimens in JSL-UOL collection).

The second form could be considered as a separate species, although we have not found yet any notable difference in the structure of the male terminalia, nor in any other morphological character. If we take into account that *Planetella* populations are very local (due to specific habitats used) and not much mobile (robust females probably only crawl, not fly), thus preventing gene flow and promoting speciation, we prefer to consider such populations as separate cryptic species. The other possibility would be that this is a mere infraspecific variation and gene flow still exists.

In insect molecular studies, species delimitation is usually based on 2 to 4% threshold (difference) in COI barcode sequence, depending on methodology and taxonomic group (e.g. HEBERT et al. 2003a,b, MEIER et al. 2006, RENAUD et al. 2012, KONDO et al 2016, CHAIPHONGPACHARA et al. 2022, KJÆRANDSEN 2022, SRIVATHSAN et al. 2023). YUKAWA et al. (2019) reported for Japanese *Asphondylia* (Cecidomyiidae) only 2% divergence among the species. As stated already by MEIER et al. (2006), threshold value for distinguishing intra- from interspecific distances is largely arbitrary and renders species borders a matter of opinion. In any case, we leave the second form of *granifex* as unnamed until more material is collected.

Discussion. KIEFFER (1898) described this species in the monotypic genus *Pseudhormomyia* Kieffer, 1898, on the basis of several general characters on habitus, including prolonged ovipositor and three palpomeres in female. No figures of this species were provided in the original description. Figures of the male terminalia, female habitus and larva were included in his later work (KIEFFER 1913). Most of Kieffer's types can be considered as almost certainly lost, including this one (GAGNÉ & JASCHHOF 2021). Our interpretation of this species is based on the study of material identified as *P. granifex* in the collection of Rübsaamen in Berlin, as well as on the figures of the male terminalia in KIEFFER (1913) and SKUHRAVÁ (1997).

Based on the original figures in RÜBSAAMEN (1911h), *Planetella caricis* (Rübsaamen, 1911) could be considered conspecific with this species and thus represent a junior synonym of *P. granifex*. However, we have seen several specimens identified as *P. caricis* in the Rübsaamen collection in Berlin, and they most probably represent a different species. Similarity of the galls caused and the range of *Carex* species used as host plants may have caused the confusion.

According to the original description and subsequent figure of the male terminalia in KIEFFER (1913), *P. subterranea* should be a very similar species or even identical with *granifex*.

Biology and distribution. This species currently appears to be the most common and widely distributed *Planetella* in Central Europe, associated mainly with larger sedges (*Carex acuta*, *C. acutiformis*, *C. buekii*, *C. rostrata*), without apparent specificity to a particular host. At the same time, several other species of *Planetella* are associated with *Carex acuta*, *C. acutiformis* and *C. rostrata*. Kieffer (1898) in his original description mentions three host species, *Carex stellulata* (= *C. echinata*), *C. pallescens* and *C. stricta* (= *C. elata*). *P. granifex* also remains one of the few *Planetella* species, where galls (Fig. 1C) are regularly found and well documented.

2. Descriptions of new species

The following species represented in our material are apparently undescribed. We prefer to give them a name, although it is not excluded that some of them will fall into the synonymy in the future, if the type specimens of some previously described species are found or better studied. The species represented only by females or larvae in our material are left undescribed (see below), as well as those species represented by a single damaged specimen (without antennae etc.). Some of them are, however, included in the molecular phylogenetic analysis.

Planetella adami Ševčík & Hippa sp. nov.

(Figs 6A–D, 13E,F)

Type material. HOLOTYPE: ♂, Slovakia, Cerová vrchovina Protected Landscape Area, Steblová skala Nature Reserve, 15.vi.–12.vii.2017, Malaise trap in a forest steppe, leg. J. Roháček & J. Ševčík, specimen after DNA extraction (No. PLA61), prepared on slide (coll. NMPC). PARATYPES: **SLOVAKIA:** 1 ♀ with the same data as holotype, specimen after DNA extraction (No. PLA61b) (coll. SMOC); 2 ♂♂, Cerová vrchovina Protected Landscape Area, Vodokáš, 15.vi.–12.vii.2017, Malaise trap in *Quercus cerris* forest, leg. J. Roháček & J. Ševčík, specimens after DNA extraction (No. PLA64b,c) (coll. JSL-UOC).

Additional material examined. **SLOVAKIA:** 1 ♂, Cerová vrchovina Protected Landscape Area, Steblová skala Nature Reserve, 15.vi.–12.vii.2017, Malaise trap in a forest steppe, leg. J. Roháček & J. Ševčík, specimen after DNA extraction (No. PLA62), prepared on slide (coll. JSL-UOC).

DNA sequences. DNA sequences (COI barcode region, 28S, 16S) taken from the holotype (No. PLA61) are deposited in GenBank. Their Accession numbers are provided in Table 1.

Diagnosis. This species is characterized by 15 flagellomeres (binodose, except the shorter apical one), eyes with an eye-bridge, palpus with 4 short palpomeres, and details of male terminalia (aedeagus reaching to about 2/3 of the length of gonocoxite, hypoproct almost as long as aedeagus, apically slightly excavated, gonostylus narrow, apically rounded, see Figs 6C,D).

Etymology. This species is named after the son of the first author, Adam Ševčík, who was born in 2017 when the type material was collected.

Description. Male. Wing length 7.0 (holotype). Overall body coloration: mostly dark brown, legs and halteres light brown.

Head. Dark brown. Eyes with a distinct eye-bridge, which is membranous, without ommatidia. Antennal

flagellum with 15 flagellomeres, F1–F14 with two nodes and three sets of looped circumfila, the apical flagellomere (F15) shorter (about two thirds as long as F14), uninodal but with three rows of circumfilial loops. Flagellomere 1 (Fig. 13E) about 3.75 times as long as broad, longer and less constricted than the other flagellomeres. Flagellomere 4 (Fig. 13E) 2.9 times as long as broad. Maxillary palpus with 4 palpomeres, P1 to P3 subequal in length, the apical one shorter than the previous ones.

Thorax mostly dark brown, scutum laterally light brown with three dark longitudinal stripes. Scutellum light brown with black lateral lining. Lateral pleura mostly dark brown. Scutum distinctly produced above the head.

Wing elongated, about 2.7 times as long as broad. Veins C, R₁, R₅ and Cu-stem distinct. R₁ joining C in the middle of wing, R₅ reaching C beyond wing apex. Rs indistinct. M₄ indistinct. CuA with dark stem and bent downwards.

Legs with tarsal claws narrow, slightly longer than maximum tarsal diameter, only slightly bent.

Abdomen dark brown, with a light transverse oval spot on each side of the tergite.

Terminalia (Figs 6C,D). Gonocoxite relatively narrow, about 2.4 times as long as broad, mediobasally with a large but relatively narrow microtrichose lobe. Gonostylus narrow, slightly curved, slightly broader in apical half, about 4.4 times as long as broad and 0.6 times as long as gonocoxite, apically with a rounded, transversely grooved dark lobe, pointed medially. Cerci very short, apically bluntly pointed, basally fused. Hypoproct relatively narrow, with a shallow posterior depression, slightly shorter than aedeagus, covered with relatively short setae. Aedeagus elongate, subtriangular, reaching to 3/4 of gonocoxite.

Female (associated with holotype male by COI sequence). Similar to male but darker. Antennae much shorter than in male, about as long as thorax, and thinner. Eyes with a narrow eye-bridge. Antennal flagellum with 15 cylindrical flagellomeres. Abdomen not distinctly pointed, segment 8 relatively broad and of similar size as previous segments. Cercus relatively small, one-segmented.

Variation. We noted remarkable variation in coloration and some morphological characters among the specimens studied. One male has distinctly light, whitish abdomen, bicoloured thorax, more excavated apical part of hypoproct (Figs 6A,B), and cerci apically rounded. We consider this as a mere intraspecific variation because all DNA sequences (COI, 28S, 16S) of this aberrant specimen are 100% identical with the holotype. Alternatively, if we do not accept DNA species concept, the specimen may represent a potentially separate species with the same DNA sequences as the closely related species, which we consider as highly improbable, although several cases of barcode (or BIN) sharing in Sciaroidea were reported in the literature (KJÆRANDSEN 2022), all of them in the family Mycetophilidae.

Biology. Host plant and galls are unknown. All the type specimens were collected at the edge of a thermophilous *Quercus cerris* forest.

Discussion. This species belongs to the group of species with 14 to 15 flagellomeres, eye-bridge present, overall

dark coloration, currently containing five very similar species, *P. adami* sp. nov., *P. atrobrunnea* sp. nov., *P. csabai* sp. nov., *P. muranica* sp. nov., and *P. thermophila* sp. nov., see the key above. They differ only in tiny details on the male terminalia, especially in the shape of hypoproct. Interestingly, K2P distances in COI sequences among these species are relatively high (all more than 5%), see Table 3, allowing their safe identification according to DNA sequences. The closest species to *P. adami* sp. nov., in terms of K2P distance, is *P. muranica* sp. nov., with 8.2% distance (Tab. 3).

Planetella aestivalis Ševčík & Hippa sp. nov.

(Figs 6E, 6F, 13D)

Type material. HOLOTYPE: ♂, Slovakia, Cerová vrchovina Protected Landscape Area, Tachty, 28.viii.–25.ix.2019, Malaise trap in *Carex acutiformis*, leg. J. Roháček & J. Ševčík, specimen after DNA extraction, prepared on slide, No. PLA27a (coll. NMPC). PARATYPES: SLOVAKIA: 1 ♂ 2 ♀♀, the same data as holotype, specimens after DNA extraction, one ♀ prepared on slide (No. PLA27b, PLA28b) (coll. JSL-UOC and SMOC); 1 ♂, the same data as holotype except 20.viii.–16.ix.2021, specimen after DNA extraction (No. PLA43) (coll. JSL-UOC); 8 ♂♂ 25 ♀♀, the same data, in ethanol (coll. JSL-UOC); Cerová vrchovina Protected Landscape Area, Fenek Nature Monument, 19.vii.–17.viii.2022, Malaise trap in *Carex acutiformis*, 1 ♂ 1 ♀ (specimens after DNA extraction, No. PLA55, PLA55b), leg. J. Roháček & J. Ševčík (coll. JSL-UOC).

Additional material examined. CZECH REPUBLIC: Pišť, near pond, 2.viii.–4.ix.2023, emergence trap in *Carex acutiformis*, 3 ♂♂ 1 ♀ (specimens after DNA extraction, No. PLA75, PLA76, PLA76b, PLA77), leg. J. Roháček & J. Ševčík, in ethanol (coll. JSL-UOC).

DNA sequences. DNA sequences (COI barcode region, 28S, 16S) taken from the holotype (No. PLA27a) are deposited in GenBank. Their Accession numbers are provided in Table 1.

Diagnosis. A large, mostly light brown species, with some parts of thorax dark. Antenna with 12 binodose, relatively long flagellomeres, plus a short apical segment. Eyes with a distinct eye-bridge, at least 2 ommatidia broad (see section Variation below). Terminalia (Figs 6E,F) with aedeagus longer than gonocoxite, hypoproct apically almost straight, much shorter than aedeagus, and narrow pointed gonostylus.

Etymology. The name of this species refers to its late occurrence in the season (from the Latin *aestas* = summer); adjective.

Description. Male. Wing length 6.7 mm (paratype in ethanol). Overall body coloration mostly orange brown to greyish brown, with head, antennae, legs, halteres, ventral part of abdomen and gonostyli darker.

Head. Eyes with a broad eye-bridge formed by ommatidia (4–6 ommatidia broad). Antennal flagellum with 12 binodal tricumfilial, relatively long flagellomeres, and apically with a very short (about one third of previous flagellomere) uninodal flagellomere lacking circumfila. Flagellomere 1 (Fig. 13D) 4.2 times as long as broad, of similar shape as the other flagellomeres, flagellomere 4 (Fig. 13D) about 4.7 times as long as broad. Maxillary palpus with 3 palpomeres, P1 and P2 short, P3 almost twice as long as P2.

Thorax mostly light brown. Scutum distinctly produced above the head, with three longitudinal stripes. Posterior

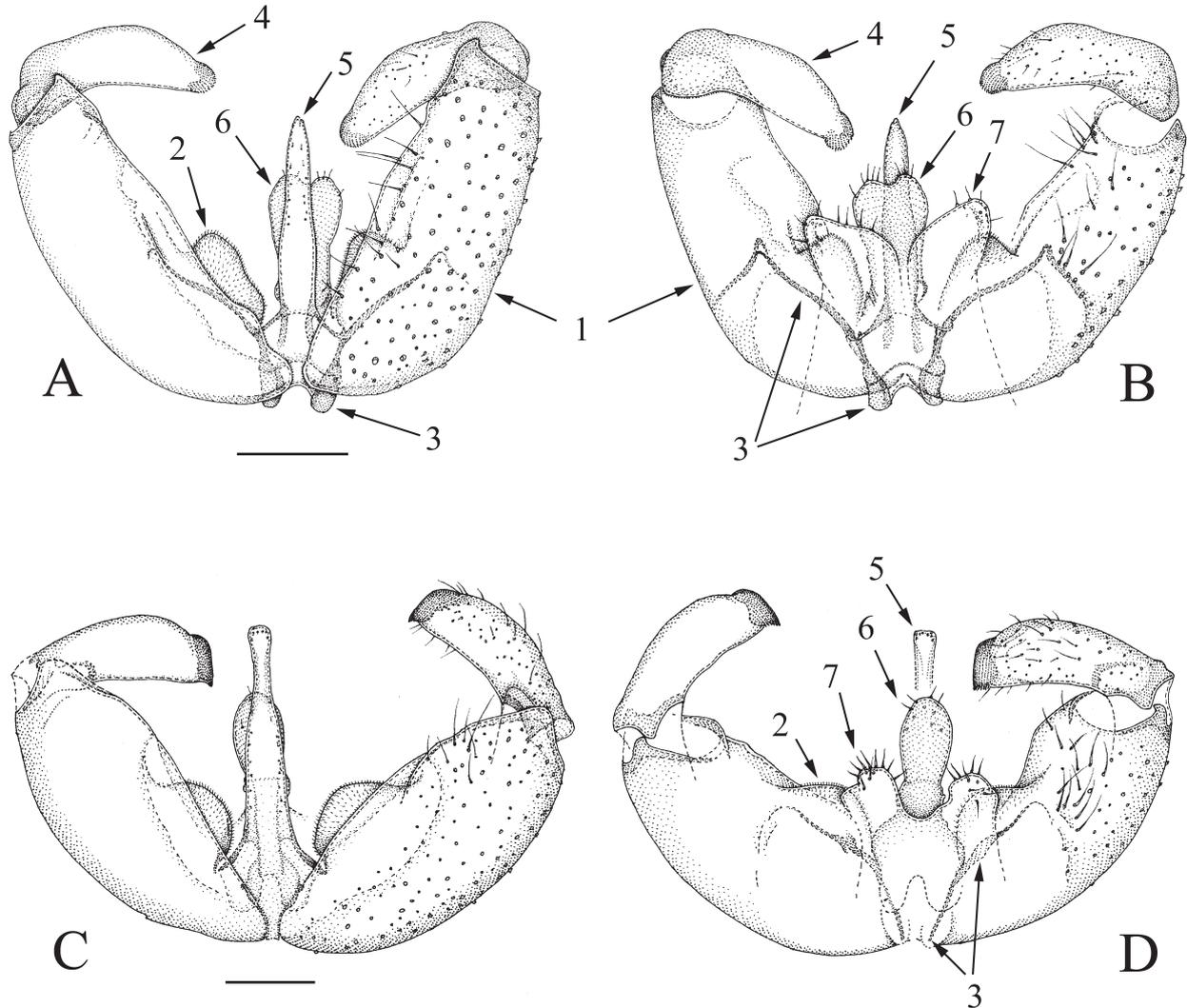


Fig. 4. Male terminalia in ventral (A, C) and dorsal (B, D) view. A, B – *Planetella arenariae* (Rübsaamen, 1899) (Slovakia, specimen PLA11b). C, D – *P. fasciata* (Meigen, 1818) (Slovakia, specimen No. PLA52c). Scale 0.1 mm. 1 = gonocoxite, 2 = basomedial lobe of gonocoxite, 3 = gonocoxal apodeme, 4 = gonostylus, 5 = aedeagus, 6 = hypoproct, 7 = cercus.

half of mediotergite blackish brown. Lateral sclerites mostly greyish brown.

Wing elongated, about 2.6 times as long as broad (paratype in ethanol). Veins C, R₁, R₅ and Cu-stem dark and distinct. R₁ joining C in the middle of wing. R₅ reaching C beyond wing apex. Rs indistinct. M₄ light and indistinct. CuA with dark stem and bent downwards.

Legs with tarsal claws slightly longer than maximum tarsal diameter, only moderately bent, almost straight.

Abdomen mostly light brown, ventrally darker. Tergites 2 to 7 with 2 to 3 light oval spots on each side.

Terminalia (Figs 6E,F). Gonocoxite relatively narrow, about four times as long as broad, mediobasally with a distinct lobe. Gonostylus narrow, slightly curved, 4.5 times as long as broad, shorter than gonocoxite, apically rounded and pointed medially. Cerci relatively small and short, rounded, basally fused. Hypoproct about twice as long as cerci, almost straight apically, only slightly excavated, with several longer marginal setae. Aedeagus narrow, slightly longer than gonocoxite, distinctly longer than hypoproct.

Female (associated with holotype male by COI sequence). Similar to male but darker, with robust abdomen and legs. Antennae shorter and thinner than in male, about 1.5 times as long as thorax. Flagellum with 12 binodose flagellomeres (plus a short apical segment), similar in shape to male but slightly less constricted. Eyes with a distinct eye-bridge, 3 or 4 ommatidia broad. Abdomen rounded, not distinctly pointed, with light oval spots on tergites 2 to 7. Cercus one-segmented, oval in shape, about twice as long as broad.

Variation. The breadth of the eye-bridge is variable among the specimens studied, spanning from 2 to 6 ommatidia. According to DNA sequences, two distinct forms can be distinguished. The more common one, which is here described as *Planetella aestivalis* sp. nov., and the second one, undescribed, differing 3% in COI barcode sequence, hitherto known only from a single locality in the Czech Republic (listed here as ‘Additional material’). The latter form can be considered as a separate species, although we have not yet found reliable differences in the structure of

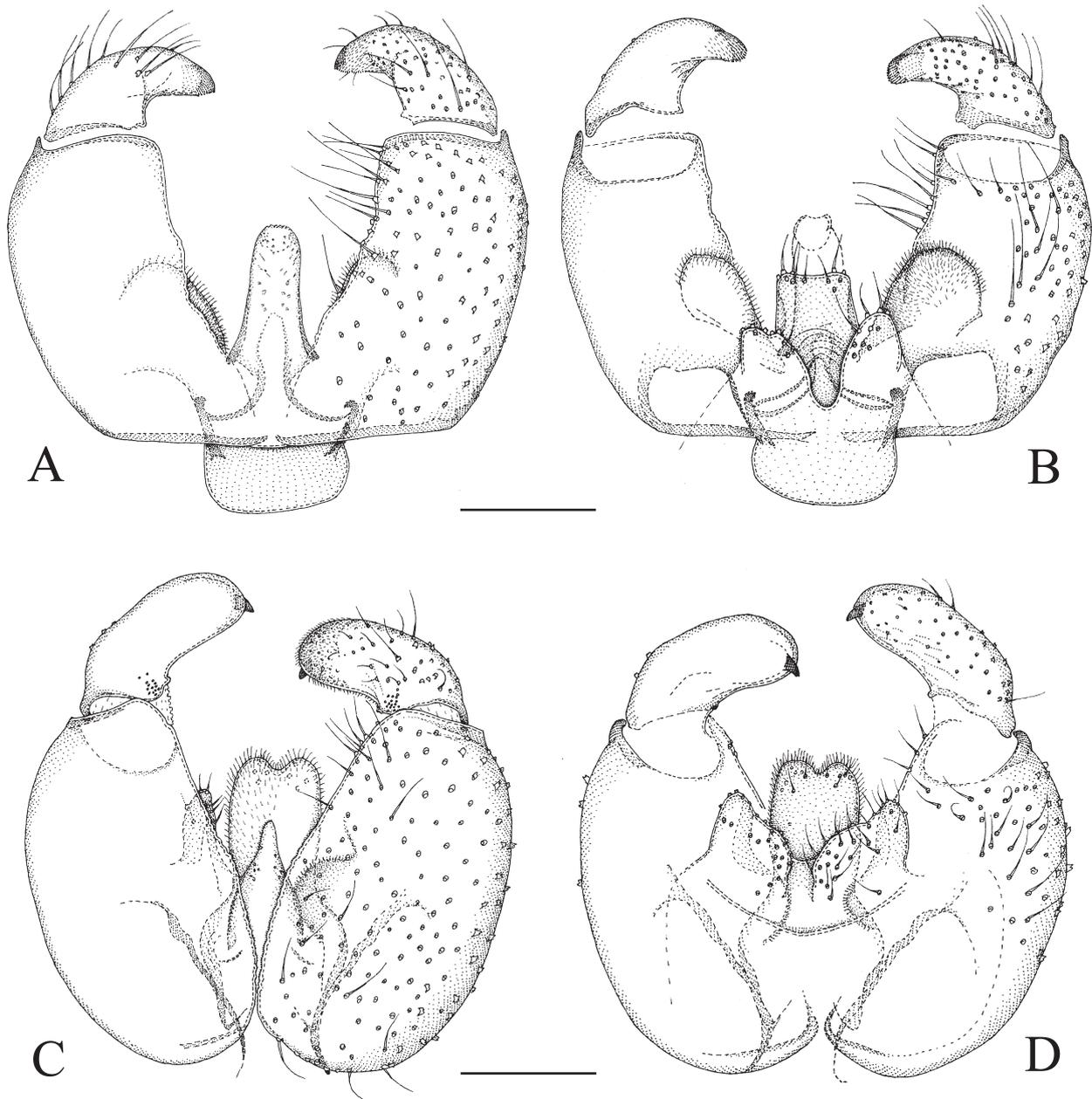


Fig. 5. Male terminalia in ventral (A, C) and dorsal (B, D) view. A, B – *Planetella gallarum* (Rübsaamen, 1899) (Denmark, specimen PLA6a). C, D – *P. granifex* (Kieffer, 1898) (Czech Republic, specimen PLA12b). Scale 0.1 mm.

the male terminalia, except the slightly different shape of hypoproct, which appears as rounded apically, not excavated, and cerci more pointed, rather than rounded.

Biology. This species is associated with *Carex acutiformis*. The galls remain unknown.

Discussion. This species is currently known only from two localities in Slovakia and one in the Czech Republic. The closest species to *P. aestivalis* sp. nov., in terms of K2P distance (Tab. 3), is *P. attilai* sp. nov., with 13.0% distance, and *P. submontana* sp. nov., with 14.2% distance, indicating its relatively high genetic isolation from the other species of the genus. In the phylogenetic tree (Fig. 15), these three species form a monophyletic group with 100% support, together with *Planetella* sp. D, an unrecognized species from Slovakia (see below).

Planetella antennata Ševčík & Hippa sp. nov.

(Figs 7A,B,C, 13G)

Type material. HOLOTYPE: ♂, Slovakia, Muránska planina National Park, Rosiarka Nature Reserve, 16.–21.vi.2022, Malaise trap in *Carex rostrata*, leg. J. Roháček & J. Ševčík, specimen after DNA extraction, prepared on slide, No. PLA52 (coll. NMPC). PARATYPES (3 ♂♂): SLOVAKIA: 1 ♂, Muránska planina National Park, Trsteník valley, 12.v.–16.vi.2016, Malaise trap among *Carex rostrata* and *Carex umbrosa*, leg. J. Roháček & J. Ševčík, specimen after DNA extraction, in ethanol (No. PLA56) (coll. JSL-OUC), 2 ♂♂ (one of them after DNA extraction, No. PLA69): Muránska planina National Park, Trstie Nature Reserve, 14.vi.–13.vii.2023, Malaise trap in *Carex rostrata*, leg. J. Roháček & J. Ševčík (coll. NMPC, SMOC).

DNA sequences. DNA sequences (COI barcode region, 28S, 16S) taken from the holotype (No. PLA52) are deposited in GenBank. Their Accession numbers are provided in Table 1.

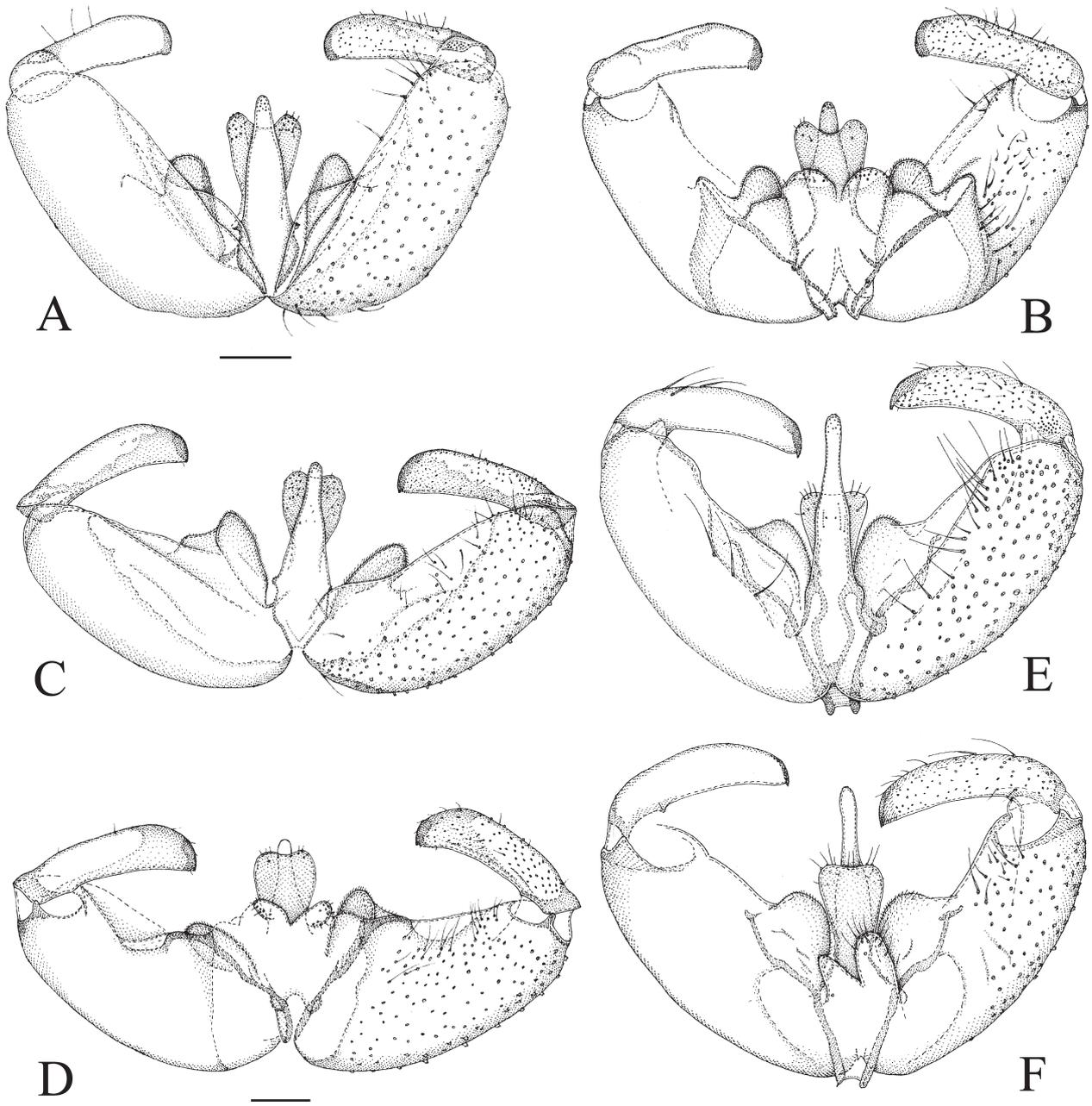


Fig. 6. Male terminalia in ventral (A, C, E) and dorsal (B, D, F) view. A, B (specimen No. PLA62) and C, D (holotype, No. PLA61) – *Planetella adami* Ševčík & Hippa sp. nov. E, F – *P. aestivalis* Ševčík & Hippa sp. nov. (holotype). Scale 0.1 mm.

Diagnosis. This is the only European species of *Planetella* with 21 binodose flagellomeres (the apical one trinodose), eyes broadly separated, and banded abdomen. Male terminalia with gonocoxite broad, twice as long as broad, and aedeagus thin, elongated, longer than gonocoxite.

Etymology. The name refers to the unusual number of antennal flagellomeres; adjective.

Description. Male. Wing length 6.5 (holotype) to 7.3 mm (paratype). Overall body coloration: thorax mostly dark brown, abdomen light, whitish yellow with narrow dark posterior bands, legs and halteres light brown.

Head dark brown. Eyes broadly separated, without eye-bridge. Antennal flagellum with 21 binodal tricircumfilial flagellomeres, except for the apical flagellomere which is

trinodose. Flagellomere 1 (Fig. 13G) about 3.5 times as long as broad, slightly longer and less constricted but of similar shape as the other flagellomeres, flagellomere 4 (Fig. 13G) 2.8 times as long as broad. Maxillary palpus with 3 palpomeres, with the apical palpomere about twice as long as the previous one.

Thorax bicoloured, darker in anterior half, with scutellum light and lateral pleura mostly light brown. Both scutum (anteriorly) and scutellum lined with black lateral stripes. Anepisternum light with dark spot in upper half. Laterotergite mostly light brown with dark band posteriorly. Mediotergite with light anterior band and blackish brown posteriorly. Scutum distinctly produced above the relatively small head.

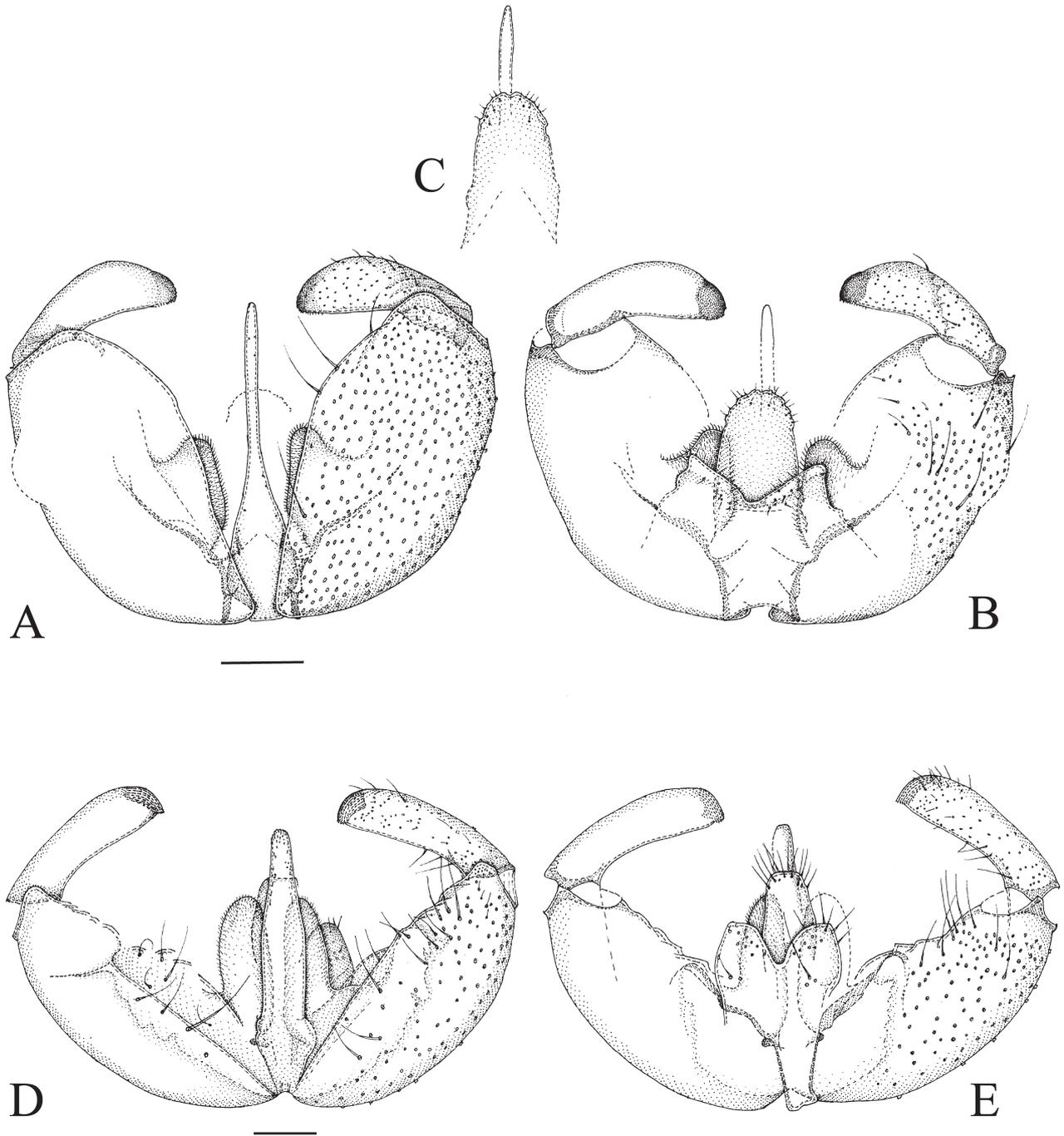


Fig. 7. Male terminalia in ventral (A, D) and dorsal (B, E) view, and hypoproct and apex of aedeagus in ventral view (C). A, B, C – *Planetella antennata* Ševčík & Hippa sp. nov. (holotype). D, E – *P. atrobrunnea* Ševčík & Hippa sp. nov. (holotype). Scale 0.1 mm.

Wing elongated, about 2.7 times as long as broad. Veins C, R_1 , R_3 and Cu-stem distinct. R_1 joining C before the middle of wing. R_5 reaching C beyond wing apex. Rs indistinct. M_4 indistinct. CuA with dark stem and bent downwards.

Legs with tarsal claws narrow, slightly longer than maximum tarsal diameter, proximally straight, bent in apical half.

Abdomen distinctly banded. Tergites 1 to 7 whitish grey anteriorly, with dark transverse band posteriorly. Band on tergite 6 narrower and darker than the others. Tergite 8 and terminalia mostly dark.

Terminalia (Figs 7A,B). Gonocoxite broad, about twice as long as broad, mediobasally with a small but distinct lobe. Gonostylus relatively short and narrow, slightly curved, broader in apical half, about three times as long as broad, half as long as gonocoxite, apically with a rounded, transversely grooved dark lobe. Cerci short, apically pointed, basally fused. Hypoproct broad, evenly rounded apically, distinctly longer than cerci. Aedeagus narrow, elongate, longer than gonocoxites.

Female. Unknown.

Biology. This species is associated with *Carex rostrata*

in montane and submontane habitats, where all the type specimens were collected. The galls are unknown.

Discussion. This species is remarkable by banded abdomen, 21 flagellomeres, eyes broadly separated and details on male terminalia. The only other European species with distinctly banded abdomen (*Planetella fasciata*, see above) has only 12 flagellomeres and different male terminalia (narrow gonocoxites, narrow hypoproct, and cerci apically rounded). In terms of K2P genetic distance (Tab. 3), the closest species to *P. antennata* sp. nov., are *P. galiciensis* sp. nov., with 7.2% distance, and *P. fasciata*, with 7.8% distance.

***Planetella atrobrunnea* Ševčík & Hippa sp. nov.**

(Figs 7D,E, 13H)

Type material. HOLOTYPE: ♂, Slovakia, Nitriansky kraj, Iža, Bokrošské slanisko NR, 106 m, 21.iv.–5.v.2017, Malaise trap, L. Vidlička & O. Majzlan leg., specimen after DNA extraction (No. PLA3), prepared on slide (coll. NMPC). PARATYPES: SLOVAKIA: 1 ♂, Cerová vrchovina Protected Landscape Area, Chrámec, near pond, 13.iv.–11.v.2023, Malaise trap in *Carex acutiformis*, leg. J. Roháček & J. Ševčík, specimen after DNA extraction (No. PLA67), in ethanol (coll. JSL-UOC); 1 ♂, Cerová vrchovina Protected Landscape Area, Chrámec, Vlčia dolina valley, 13.iv.–11.v.2023, Malaise trap in *Quercus cerris* forest, with *Carex michelii* in the undergrowth, leg. J. Roháček & J. Ševčík, specimen after DNA extraction (No. PLA65b), in ethanol (coll. JSL-UOC).

DNA sequences. DNA sequences (COI barcode region, 28S, 16S) taken from the holotype (No. PLA3) are deposited in GenBank. Their Accession numbers are provided in Table 1.

Diagnosis. This species is characterized by 15 binodose flagellomeres, eyes with an eye-bridge, maxillary palpus with 2 palpomeres, apical one longer, blackish brown and apically pointed. It is habitually very similar to *Planetella adami* sp. nov. and *P. csabai* sp. nov. but differs in details on the male terminalia (narrow and apically straight hypoproct) and in DNA sequences.

Etymology. The specific name refers to the blackish dark brown coloration of this species; adjective.

Description. Male. Wing length 7.5 (holotype). Overall body coloration: mostly dark brown, legs and halteres light brown.

Head blackish brown. Eyes with a narrow eye-bridge, which is membranous, without ommatidia. Antennal flagellum with 15 flagellomeres (paratype, antennae broken off in holotype), F1–F14 each with three rows of circumfilial loops. The apical flagellomere (F15) either uninodal, apically pointed (left antenna of paratype), about half as long as the previous one, or binodal, apically blunt (right antenna of paratype) but with distal node shorter, as long as basal node. Flagellomere 1 (Fig. 13H) 3.6 times as long as broad, longer and less constricted than the other flagellomeres. Flagellomere 3 (Fig. 13H) three times as long as broad. Maxillary palpus with 2 palpomeres, apical one longer, blackish brown and apically pointed.

Thorax mostly dark brown, scutum laterally light brown with three dark longitudinal stripes. Scutellum laterally light brown with black spots anterolaterally. Lateral pleura mostly dark brown. Scutum distinctly produced above the head.

Wing elongated, about 3.5 times as long as broad. Veins C, R₁, R₃ and Cu-stem distinct. R₁ joining C slightly before the middle of wing. R₅ reaching C beyond wing apex. Rs

indistinct. M₄ indistinct. CuA with dark stem and bent downwards.

Legs with tarsal claws narrow, slightly longer than maximum tarsal diameter, only slightly bent apically.

Abdomen dark brown, with a light transverse oval spot on each side of the tergite.

Terminalia (Figs 7D,E). Gonocoxite narrow, about 2.5 times as long as broad, mediobasally with a small lobe. Gonostylus narrow, slightly curved, about 4.7 times as long as broad and 0.6 times as long as gonocoxite, apically with a small, rounded, transversely grooved dark lobe, pointed medially. Cerci rather short, apically bluntly pointed, basally fused. Hypoproct relatively narrow, distal margin almost straight, distinctly longer than cerci but slightly shorter than aedeagus. Aedeagus narrow, elongate, subtriangular, shorter than gonocoxites. Gonocoxal apodemes strongly sclerotized, medially fused.

Female. Unknown.

Variation. We noted a variation in the structure of the apical (15th) flagellomere, see above.

Biology. The galls are unknown. The type specimens were collected in three different habitats, in a salt marsh (holotype), at the edge of a pond in *Carex acutiformis* growth (paratype No. PLA67), and at the edge of a thermophilous *Quercus cerris* forest with *Carex michelii* in the undergrowth (paratype No. PLA65b).

Discussion. This species belongs to the group of species with 15 flagellomeres, narrow eye-bridge, dark coloration, currently containing four species (see the key above) differing slightly in the shape of hypoproct and substantially in DNA sequences. According to K2P genetic distances (Tab. 3), the closest species appears to be *P. hlisnikovskiyi* sp. nov., with 14.4% of genetic distance, indicating its high genetic isolation from the other species of the genus.

***Planetella attilai* Ševčík & Hippa sp. nov.**

(Figs 8, 14A,B)

Type material. HOLOTYPE: ♂, Slovakia, Cerová vrchovina Protected Landscape Area, Tachty, 12.v.–11.vi.2021, Malaise trap in *Carex acutiformis*, leg. J. Roháček & J. Ševčík, specimen after DNA extraction, prepared on slide (No. PLA37) (coll. NMPC). PARATYPES: SLOVAKIA: 1 ♂, Cerová vrchovina Protected Landscape Area, Tachty, 28.v.–22.vi.2020, Malaise trap in *Carex acutiformis*, leg. A. Balázs, specimen after DNA extraction, in ethanol, No. PLA30d (coll. JSL-UOC); 1 ♂, Muránska planina National Park, Trsteník valley, 12.v.–16.vi.2016, Malaise trap among *Carex rostrata* and *Carex umbrosa*, leg. J. Roháček & J. Ševčík, specimen after DNA extraction, prepared on slide (No. PLA1b) (coll. JSL-UOC).

DNA sequences. DNA sequences (COI barcode region, 28S, 16S) taken from the paratype (No. PLA30d) are deposited in GenBank. Their Accession numbers are provided in Table 1. The COI sequence of the paratype (No. PLA30d) is identical with that of the holotype (No. PLA37).

Diagnosis. A mostly light brown to orange brown species, with some parts of thorax dark. Antenna with 12 binodose, relatively long flagellomeres, plus a short apical segment. Eyes with a thin, membranous eye-bridge. Terminalia with a subrectangular, distally rounded hypoproct, and relatively narrow gonostylus.

Etymology. This species is named after Dr. Attila Balázs, a

specialist on Odonata, organizing entomological research in Cerová vrchovina Protected Landscape Area, who collected one of the paratypes.

Description. Male. Wing length 5.5 mm (holotype). Overall body coloration mostly orange brown to greyish brown, with head, antennae, legs, halteres, ventral part of abdomen and gonostyli darker.

Head. Eyes with a narrow, membranous eye-bridge, about 1 to 2 ommatidia broad. Antennal flagellum with 12 binodal tricircumfilial, relatively long flagellomeres, and apically with a very short (about one third of previous flagellomere) uninodal flagellomere lacking circumfila. Flagellomere 1 four times as long as broad, of similar shape as the other flagellomeres, flagellomere 4 about 4.5 times as long as broad (Fig. 14A). Maxillary palpus with 3 palpomeres, the apical palpomere (P3) about 1.5 times as long as P2.

Thorax mostly light brown. Scutum distinctly produced above the head, with three longitudinal stripes. Mediotergite blackish brown, except for the anterior margin. Lateral sclerites mostly greyish brown.

Wing elongated, about 2.7 times as long as broad. Veins C, R₁, R₅ and Cu-stem dark and distinct. R₁ joining C in the middle of wing. R₅ reaching C beyond wing apex. Rs indistinct. M₄ light and indistinct. CuA with dark stem and bent downwards.

Legs with tarsal claws slightly longer than maximum tarsal diameter, gradually bent.

Abdomen mostly light brown, ventrally darker. Tergites with 2 to 3 light oval spots on each side.

Terminalia (Fig. 6). Gonocoxite about three times as long as broad, mediobasally with a broad rounded lobe. Gonostylus relatively narrow, slightly curved, 3.3 times as long as broad, shorter than gonocoxite, apically rounded and pointed medially. Cerci short, pointed or rounded, basally fused. Hypoproct longer than cerci, subrectangular, apically rounded or slightly excavated, with several marginal setae. Aedeagus narrow, subtriangular, as long as gonocoxites, longer than hypoproct. Gonocoxal apodemes strongly sclerotized, medially fused.

Female. Unknown.

Variation. The paratype from Trsteník (No. PLA1b) differs slightly from the holotype and the other paratypes in details of the male terminalia (Figs 8A,B versus 8C,D), mainly in the shape of hypoproct, shape of cerci and in the small mediobasal lobe on the gonocoxite. The difference in COI barcode sequence between this paratype and the holotype is only 6 nucleotides (less than 1%), indicating that they belong to the same species.

Biology. This species is associated with *Carex acutiformis*, *Carex rostrata* and *Carex umbrosa*. The galls remain unknown.

Discussion. This species is characterized by its smaller size, 12 flagellomeres, the eyes with a thin eye-bridge, narrow gonostylus and rectangular, apically rounded or only slightly excavated hypoproct. It is currently known only from two localities in Slovakia. According to K2P genetic distances (Tab. 3), the closest species appears to be *P. submontana* sp. nov., with only 8.0% of genetic distance.

Planetella csabai Ševčík & Hippa sp. nov.

(Figs 9A,B, 13I)

Type material. HOLOTYPE: ♂, Slovakia, Cerová vrchovina Protected Landscape Area, Hajnáčka, Buková (Zaboda), 8.viii.–12.ix.2018, Malaise trap in *Quercus cerris* forest, leg. J. Roháček & J. Ševčík, specimen after DNA extraction (No. PLA11), prepared on slide (coll. NMPC). PARATYPE: SLOVAKIA: 1 ♂, Cerová vrchovina Protected Landscape Area, Jestice, Hradisko, 17.viii.–13.ix.2022, Malaise trap in *Quercus cerris* forest, leg. J. Roháček & J. Ševčík, specimen after DNA extraction (No. PLA58), in ethanol (coll. JSL-UOC).

DNA sequences. DNA sequences (COI barcode region, 28S, 16S) taken from the holotype (No. PLA11) are deposited in GenBank. Their Accession numbers are provided in Table 1.

Diagnosis. This species is characterized by 15 binodose flagellomeres, eyes with an eye-bridge, palpus with 3 palpomeres. It is very similar to *Planetella adami* sp. nov. but differs in details on the male terminalia (hypoproct as long as aedeagus, apically only slightly excavated, Figs 9A,B) and in DNA sequences.

Etymology. This species is named after Csaba Balázs, a zoologist at the Administration of Cerová vrchovina Protected Landscape Area in Rimavská Sobota (Slovakia), who organized dipterological research in the area and helped us to select the best habitats there, including the localities of this new species.

Description. Male. Wing length 6.3 (paratype). Overall body coloration: mostly dark brown, legs and halteres light brown.

Head dark brown. Eyes with a distinct eye-bridge, which is membranous, without ommatidia. Antennal flagellum with 15 flagellomeres, each with three rows of circumfilial loops (except the apical one in holotype). The apical flagellomere (F15) either uninodal (holotype), about half as long as the previous one, or binodal (paratype) but with distal node shorter, as long as basal node. Flagellomere 1 (Fig. 13I) about 4 times as long as broad, longer and less constricted than the other flagellomeres. Flagellomere 4 (Fig. 13I) 3.3 times as long as broad. Maxillary palpus with 3 palpomeres, subequal in length.

Thorax mostly dark brown, scutum laterally light brown with three dark longitudinal stripes. Scutellum laterally light brown with black spots anterolaterally. Lateral pleura mostly dark brown. Scutum distinctly produced above the head.

Wing elongated, about 3 times as long as broad. Veins C, R₁, R₅ and Cu-stem distinct. R₁ joining C slightly before the middle of wing. R₅ reaching C beyond wing apex. Rs indistinct. M₄ indistinct. CuA with dark stem and bent downwards.

Legs with tarsal claws narrow, slightly longer than maximum tarsal diameter, only slightly bent apically.

Abdomen dark brown, with a light transverse oval spot on each side of the tergite.

Terminalia (Figs 9A,B). Gonocoxite narrow, about 2.5 times as long as broad, mediobasally with a small lobe. Gonostylus narrow, slightly curved, about 4.7 times as long as broad and 0.6 times as long as gonocoxite, apically with a small, rounded, transversely grooved dark lobe, pointed medially. Cerci rather short, apically bluntly pointed, basal-

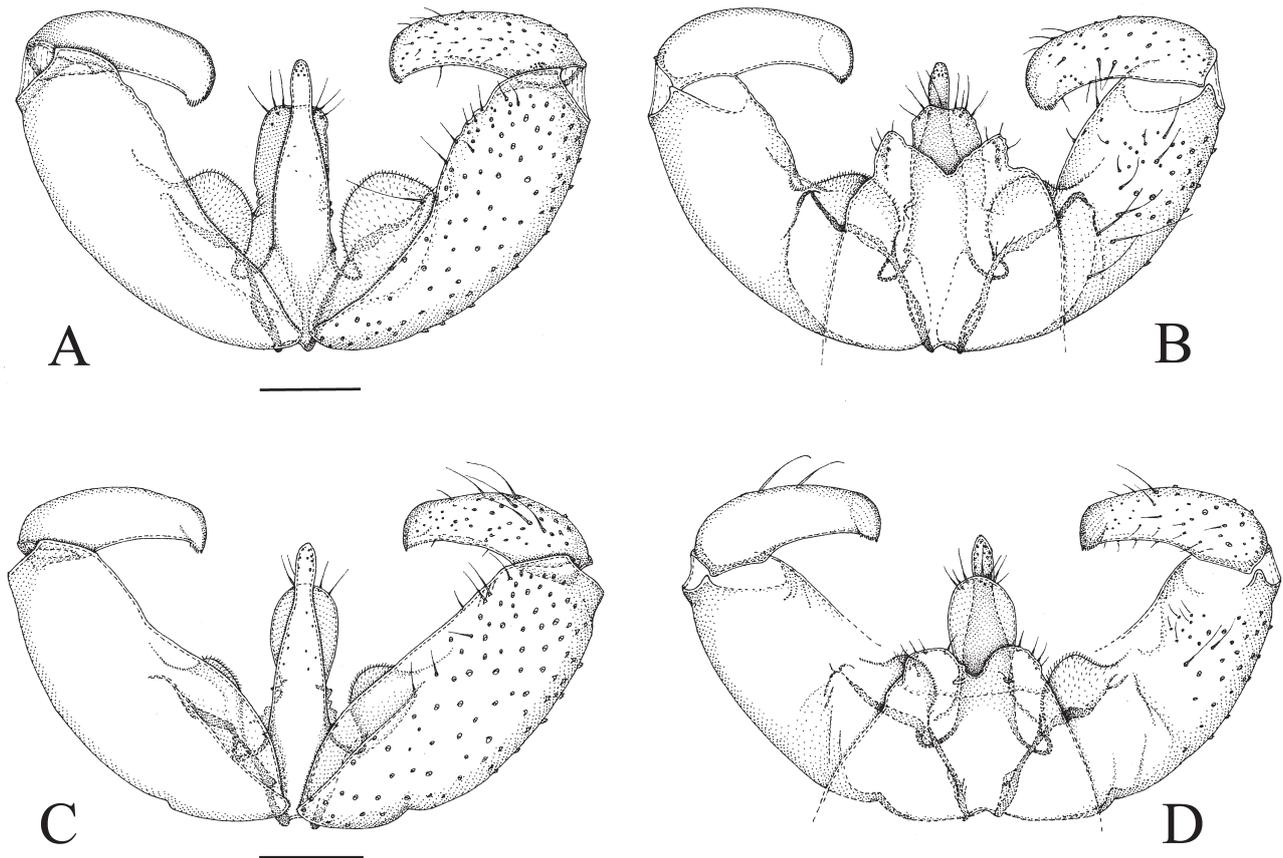


Fig. 8. *Planetella attilai* Ševčík & Hippa sp. nov. (A, B – holotype, C, D – paratype No. PLA1b). Male terminalia in ventral (A, C) and dorsal (B, D) view. Scale 0.1 mm.

ly fused. Hypoproct relatively narrow, distal margin almost straight, distinctly longer than cerci but slightly shorter than aedeagus. Aedeagus narrow, elongate, subtriangular, shorter than gonocoxites. Gonocoxal apodemes strongly sclerotized, medially fused.

Female. Unknown.

Biology. The galls are unknown. Both the type specimens were collected at the edge of a thermophilous *Quercus cerris* forest and, unlike in other species, rather late during the season, from mid-August to mid-September. The most probable host plants are *Carex michelii* (holotype) and *Carex humilis* (paratype). These *Carex* species were found near the Malaise traps.

Variation. We noted a variation in the structure of the apical (15th) flagellomere, see above.

Discussion. This species is known only from two localities in Cerová vrchovina Protected Landscape Area (southern Slovakia) and it belongs to the group of species with 14 or 15 flagellomeres, eye-bridge present and dark coloration, currently containing five very similar species, see the discussion under *Planetella adami* sp. nov. (above). They differ in small details on the male terminalia, especially in the shape of hypoproct, but considerably in DNA sequences. The closest relative to *P. csabai* sp. nov., in terms of K2P distance, is *P. muranica* sp. nov., with 8.6% distance (Tab. 3). The other species differ in more than 9%.

Planetella davidi Ševčík & Hippa sp. nov.

(Figs 9C,D,E, 14C)

Type material. HOLOTYPE: ♂, Slovakia, Cerová vrchovina Protected Landscape Area, Jestice, Hradisko, 4.v.–25.v.2022, Malaise trap in *Quercus cerris* forest, leg. J. Roháček & J. Ševčík, specimen after DNA extraction, prepared on slide, No. PLA47 (coll. NMPC). PARATYPE: the same data as holotype, specimen after DNA extraction (No. PLA47b) (coll. JSL-OUC).

DNA sequences. DNA sequences (COI barcode region, 28S, 16S) taken from the holotype (No. PLA47) are deposited in GenBank. Their Accession numbers are provided in Table 1.

Diagnosis. A mostly light brown species, with dark mediotergite and other dark spots on several places on thorax. Antenna with 12 binodose flagellomeres, plus a short apical segment. Eyes with a narrow, membranous eye-bridge. Terminalia with a narrow, apically excavated hypoproct, and a club-shaped, distally distinctly broadened gonostylus (Figs 9C,D,E).

Etymology. This species is named after David Ševčík (a younger son of the first author), who was born in the same year when this species was collected.

Description. Male. Wing length 5.5 mm. Overall body coloration mostly light brown, with legs and halteres brownish.

Head. Eyes with a narrow, membranous eye-bridge, ommatidia not touching. Antennal flagellum with 12 binodal trircumfilial flagellomeres, and apically with a short

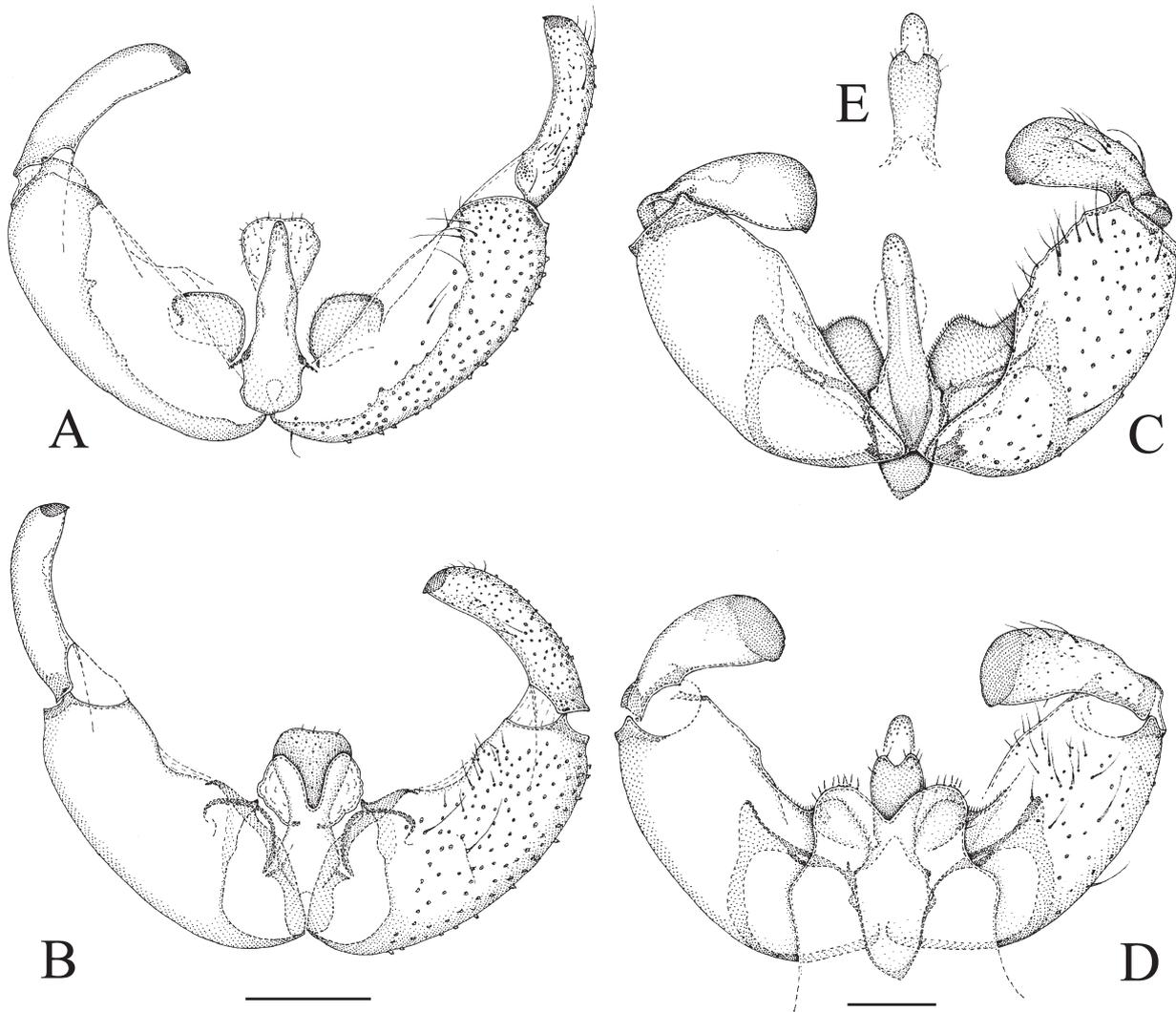


Fig. 9. Male terminalia in ventral (A, C) and dorsal (B, D) view, and hypoproct and apex of aedeagus in ventral view (E). A, B – *Planetetella csabai* Ševčík & Hippa sp. nov. (holotype). C, D, E – *P. davidi* Ševčík & Hippa sp. nov. (holotype). Scale 0.1 mm.

uninodal flagellomere lacking circumfila. Flagellomere 1 (Fig. 14C) about 4.6 times as long as broad, slightly longer but of similar shape as the other flagellomeres, flagellomere 4 (Fig. 14C) about 3.8 times as long as broad. Maxillary palpus with 2 palpomeres, with the apical palpomere about twice as long as the previous one.

Thorax mostly light orange brown. Scutum distinctly produced above the head. Blackish marks on both sides of scutum anteriorly and on both sides of scutellum. Lateral sclerites mostly brownish, except anterior one, which is dark. Mediotergite blackish brown, except anterior margin.

Wing elongated, about 2.8 times as long as broad. Veins C, R₁, R₅ and Cu-stem dark and distinct. R₁ joining C in the middle of wing. R₅ reaching C beyond wing apex. Rs missing. M₄ light and indistinct. CuA with dark stem and bent downwards.

Legs with tarsal claws about as long as maximum tarsal diameter, gradually bent, as long as empodium.

Abdomen light brown, with a light oval spot on each side of the tergite.

Terminalia (Figs 9C,D,E). Gonocoxite relatively broad, about twice as long as broad, mediobasally with a small

lobe. Gonostylus distinctly broadened posteriorly, slightly curved, twice as long as broad, shorter than gonocoxite, apically with a broad, rounded, transversely grooved dark lobe. Cerci relatively broad, rounded, basally fused. Hypoproct narrow, only slightly broader than aedeagus, apically excavated, distinctly longer than cerci. Aedeagus narrow, elongate, longer than hypoproct. Gonocoxal apodemes strongly sclerotized, medially fused.

Female. Unknown.

Biology. This species is probably associated with *Carex humilis*, growing in the thermophilous forest (with *Quercus cerris*) around the Malaise trap where both the type specimens were collected. The galls remain unknown.

Discussion. This species is characterized by its coloration, 12 flagellomeres, eyes with thin eye-bridge, typical shape of gonostylus, and narrow hypoproct. It is known only from the type locality in southern Slovakia. Its sister species in the phylogenetic tree (Fig. 15) is *Planetetella gallarum* but its closest relative in terms of K2P genetic distance is *P. galiciensis* sp. nov., with 9.7% distance (Tab. 3), nested in different part of the tree.

***Planetella galiciensis* Ševčík & Hippa sp. nov.**

(Figs 10A,B, 14D)

Type material. HOLOTYPE: ♂, Spain, Galicia, Fragas do Eume Natural Park, 150 m, 16.–30.v.2019, Malaise trap 2, leg. María J. Servia & J. Ševčík, specimen after DNA extraction, prepared on slide, No. PLA19 (coll. NMPC).

DNA sequences. DNA sequences (COI barcode region, 28S, 16S) taken from the holotype (No. PLA19) are deposited in GenBank. Their Accession numbers are provided in Table 1.

Diagnosis. This is the only European species of *Planetella* with 22 flagellomeres and uniform orange brown coloration. Male terminalia (Figs 10A,B) with gonocoxite three times as long as broad, aedeagus longer than gonocoxite, gonostylus narrow, more than half as long as gonocoxite, apically with a pointed tooth.

Etymology. This species is named after Galicia, northern Spain, where the holotype was collected; adjective.

Description. Male. Wing length 6.8 mm. Overall body coloration mostly reddish brown, with legs and halteres lighter.

Head. Eyes narrowly connected with eye-bridge. Antennal flagellum with 22 binodal tricircumfilial flagellomeres, the apical one with a short uninodal appendage lacking circumfila. Flagellomere 1 (Fig. 14D) 3.2 times as long as broad, slightly longer and less constricted but of similar shape as the other flagellomeres, flagellomere 4 (Fig. 14D) 2.9 times as long as broad. Left flagellomere 2 in holotype with an aberrant medial projection. Maxillary palpus short, with 3 palpomeres, the apical palpomere about twice as long as the previous one.

Thorax mostly reddish brown. Scutum with three longitudinal darker stripes. Scutellum dark brown. Laterotergite darker in upper part. Both scutum (anteriorly) and scutellum lined with black curved lateral stripes. Scutum distinctly produced above the head.

Wing elongated, about 3 times as long as broad. Veins C, R₁, R₅ and Cu-stem dark and distinct. R₁ joining C almost in the middle of wing. R₅ reaching C beyond wing apex. Rs indistinct. M₄ light. CuA with dark stem and distally bent downwards.

Legs with tarsal claws about 1.5 times as long as maximum tarsal diameter, gradually bent.

Abdomen brownish, with a light oval spot on each side of the tergite.

Terminalia (Figs 10A,B). Gonocoxite relatively narrow, about three times as long as broad, mediobasally with a broad lobe. Gonostylus very narrow, only slightly curved, evenly broad throughout, 4.7 times as long as broad, shorter than gonocoxite, apically with a pointed, transversely grooved dark lobe. Cerci short, apically rounded, basally fused. Hypoproct relatively broad, subrectangular, basally broader, distinctly longer than cerci. Aedeagus narrow, elongate, apically pointed, as long as gonocoxites. Gonocoxal apodemes strongly sclerotized, medially fused.

Female. Unknown.

Biology. Unknown. The holotype was collected in the Atlantic coastal forest, along a small forest brook joining the river Eume.

Discussion. This is the only European species of *Planetella*

with 22 flagellomeres. The second highest number of flagellomeres (21) can be found in *P. antennata* sp. nov., which has, however, eyes separated and banded abdomen (see above). Its sister species in the phylogenetic tree (Fig. 15) is *P. antennata* sp. nov. but its closest relative in terms of K2P genetic distance is *P. fasciata*, with 6.2% distance (Tab. 3).

***Planetella hlisnikovskyi* Ševčík & Hippa sp. nov.**

(Figs 10C,D, 14E)

Type material. HOLOTYPE: ♂, Czech Republic, Němčičky, 31.v.2021, sweeping over *Carex montana* in a thermophilous oak forest, J. Ševčík leg., specimen after DNA extraction, prepared on slide, No. PLA34 (NMPC).

DNA sequences. DNA sequences (COI barcode region, 28S, 16S) taken from the holotype (No. PLA34) are deposited in GenBank. Their Accession numbers are provided in Table 1.

Diagnosis. A large, dark, blackish brown species. Antenna with 12 binodose flagellomeres. Eyes widely separated. Terminalia with a broad, pear-shaped hypoproct.

Etymology. This species is named after David Hlisnikovský, a Czech botanist who identified the host species.

Description. Male. Wing length 6.0 mm. Overall body coloration mostly glossy dark brown, with legs and halteres brownish.

Head. Eyes broadly separated, without eye-bridge. Antennal flagellum with 12 binodal tricircumfilial flagellomeres, and apically with a short uninodal flagellomere lacking circumfila. Flagellomere 1 (Fig. 14E) about 3.6 times as long as broad, slightly longer but of similar shape as the other flagellomeres, flagellomere 4 (Fig. 14E) about 3.5 times as long as broad. Maxillary palpus with 3 palpomeres, with the apical palpomere about twice as long as the previous one.

Thorax uniformly blackish brown. Scutum distinctly produced above the head.

Wing elongated, about 3.2 times as long as broad. Veins C, R₁, R₅ and Cu-stem dark and distinct. R₁ joining C almost in the middle of wing. R₅ reaching C beyond wing apex. Rs missing. M₄ light and indistinct. CuA with dark stem and bent downwards.

Legs with tarsal claws almost twice as long as maximum tarsal diameter, gradually bent.

Abdomen dark brown, with a light oval spot on each side of the tergite.

Terminalia (Figs 10C,D). Gonocoxite relatively narrow, about three times as long as broad, mediobasally with a small lobe. Gonostylus narrow, slightly curved, evenly broad throughout, three times as long as broad, shorter than gonocoxite, apically with a rounded, transversely grooved dark lobe. Cerci short, rounded, basally fused. Hypoproct broad, pear-shaped, distinctly longer than cerci. Aedeagus narrow, elongate, subtriangular, longer than hypoproct.

Female. Unknown.

Biology. This species is most probably associated with *Carex montana*, on which the holotype was collected. The galls remain unknown.

Discussion. This is a remarkable species, characterized by the dark coloration, 12 flagellomeres, eyes broadly

separated and details on male terminalia. The other dark *Planetella* species have more flagellomeres and different male terminalia. Its closest relatives in terms of K2P genetic distance (Tab. 3) are *P. muranica* sp. nov., with 8.5% distance, and *P. adami* sp. nov., with 8.7% distance, both with the eye bridge present, altogether (with other two species) forming a well-supported clade (Fig. 15).

***Planetella muranica* Ševčík & Hippa sp. nov.**

(Figs 11D,E,F,G, 14F)

Type material. HOLOTYPE: ♂, Slovakia, Muránska planina National Park, Červená skala env., Trsteník valley, 16.vi.–14.vii.2016, Malaise trap over *Carex rostrata* and *Carex umbrosa*, leg. J. Roháček & J. Ševčík, specimen after DNA extraction, prepared on slide, No. PLA2 (coll. NMPC). PARATYPES: 4 ♂♂ (two of them after DNA extraction, No. PLA2b, prepared on slide, PLA2c in ethanol), the same locality and Malaise trap, 12.v.–16.vi.2016 (coll. SMOC, JSL-OUC); 1 ♂ in ethanol (after DNA extraction, No. PLA40), the same locality, 10.vi.–13.vii.2021, emergence trap 3 over *Carex umbrosa* (coll. JSL-OUC); 1 ♀ in ethanol (after DNA extraction, No. PLA45), the same locality, 10.vi.–13.vii.2021, emergence trap 2 over *Carex rostrata* (coll. JSL-OUC).

DNA sequences. DNA sequences (COI barcode region, 28S, 16S) taken from the holotype (No. PLA2) are deposited in GenBank. Their Accession numbers are provided in Table 1.

Diagnosis. A large, dark brown species. Antenna with 14 binodose flagellomeres. Eyes with narrow eye-bridge. Terminalia with a broad, pear-shaped hypoproct, and gonostylus relatively long, as long as gonocoxite.

Etymology. The species name is derived from the Muránska planina National Park in Slovakia, where all the type specimens were collected; adjective.

Description. Male. Wing length 6.8 mm (paratype PLA2c). Overall body coloration mostly glossy dark brown, with legs and halteres brownish.

Head. Eyes with a narrow, membranous eye-bridge, ommatidia not touching. Antennal flagellum with 14 binodal tricircumfilial flagellomeres, the apical flagellomere (F14) only slightly shorter and less constricted than F13. Flagellomere 1 (Fig. 14F) about 3.6 times as long as broad, slightly longer and more cylindrical than the other flagellomeres, flagellomere 4 (Fig. 14F) about 3.3 times as long as broad. Maxillary palpus with 3 palpomeres, subequal in length.

Thorax uniformly brown to blackish brown. Scutum distinctly produced above the head, without distinct longitudinal stripes. Scutum anteriorly and scutellum laterally with black lining.

Wing elongated, about 2.4 times as long as broad (paratype PLA2c). Veins C, R₁, R₅ and Cu-stem dark and distinct. R₁ joining C in the middle of wing. R₅ reaching C beyond wing apex. Rs missing. M₄ light and indistinct. CuA with dark stem and bent downwards.

Legs with tarsal claws slightly longer than maximum tarsal diameter, gradually bent. Empodia reaching to about half the length of claw.

Abdomen dark brown, with a light oval transverse spot on each side of the tergite (T2 to T7).

Terminalia (Figs 11D,E). Gonocoxite about 2.5 times as long as broad, mediobasally with a distinct rounded lobe.

Gonostylus relatively long and narrow, slightly broader subapically, 4.2 times as long as broad, almost as long as gonocoxite, apically with a rounded, transversely grooved dark lobe, pointed medially. Cerci short, rounded, basally fused. Hypoproct broad, pear-shaped, distally convex, with a shallow depression. Aedeagus narrow, elongate, subtriangular, slightly longer than hypoproct. Gonocoxal apodemes strongly sclerotized, medially fused.

Female (associated with holotype male by COI sequence). Similar to male, with slightly more robust abdomen. Antennae shorter and thinner than in male, about 1.5 times as long as thorax. Eyes with a narrow, membranous eye-bridge, without any ommatidia connected. Abdomen dark brown, with light narrow oval spot on each side of tergites 2 to 7. Cercus one-segmented, pointed apically, suboval in shape, about twice as long as broad.

Variation. The paratype No. PLA2b differs slightly from the holotype and the other paratypes in the narrower shape of hypoproct (Figs 11D,E (holotype) versus F,G (paratype)). The COI barcode sequence of this paratype and the holotype are 100% identical, confirming that they belong to the same species.

Biology. This species is associated with *Carex rostrata* and *Carex umbrosa*, on which the type material was collected. The galls remain unknown.

Discussion. This is a remarkable species, characterized by the dark coloration, 14 flagellomeres, eyes with a narrow eye-bridge and details on the male terminalia. Its closest relative in terms of K2P genetic distance (Tab. 3), as well as in the phylogenetic tree (Fig. 15), is *P. thermophila* sp. nov., with 5.2% distance, while all the other *Planetella* species are more than 8% distant.

***Planetella riparia* Ševčík & Hippa sp. nov.**

(Figs 11A,B,C, 14G)

Type material. HOLOTYPE: ♂, Slovakia, Cerová vrchovina Protected Landscape Area, Hostice, near pond, 25.v.–22.vi.2022, emergence trap over *Carex riparia*, leg. J. Roháček & J. Ševčík, specimen after DNA extraction, in ethanol, (No. PLA54) (coll. NMPC). PARATYPES: 1 ♂, the same data but 22.vi.–19.vii.2022, specimen after DNA extraction, in ethanol, No. PLA54c (coll. SMOC); 1 ♀, the same data as holotype, specimen after DNA extraction, in ethanol (No. PLA54b) (coll. JSL-UOC); 5 ♂♂ 2 ♀♀, the same data as holotype, in ethanol (coll. JSL-UOC).

DNA sequences. DNA sequences (COI barcode region, 28S, 16S) taken from the female paratype (No. PLA54b) are deposited in GenBank. Their Accession numbers are provided in Table 1. The COI sequence of this paratype is identical to that of the holotype.

Diagnosis. A mostly orange brown species, with some body parts dark brown. Antenna with 12 binodose, relatively long flagellomeres, plus a short apical segment. Eyes with a thin, membranous eye-bridge. Terminalia with a narrow, rectangular hypoproct, cerci apically rounded, and relatively narrow and long gonostylus.

Etymology. This species is named after its host plant, *Carex riparia*; adjective.

Description. Male. Wing length 5.4 mm (holotype). Overall body coloration mostly orange brown to greyish brown, with head, antennae, some parts of thorax, legs, halteres, ventral part of abdomen and gonostyli darker.

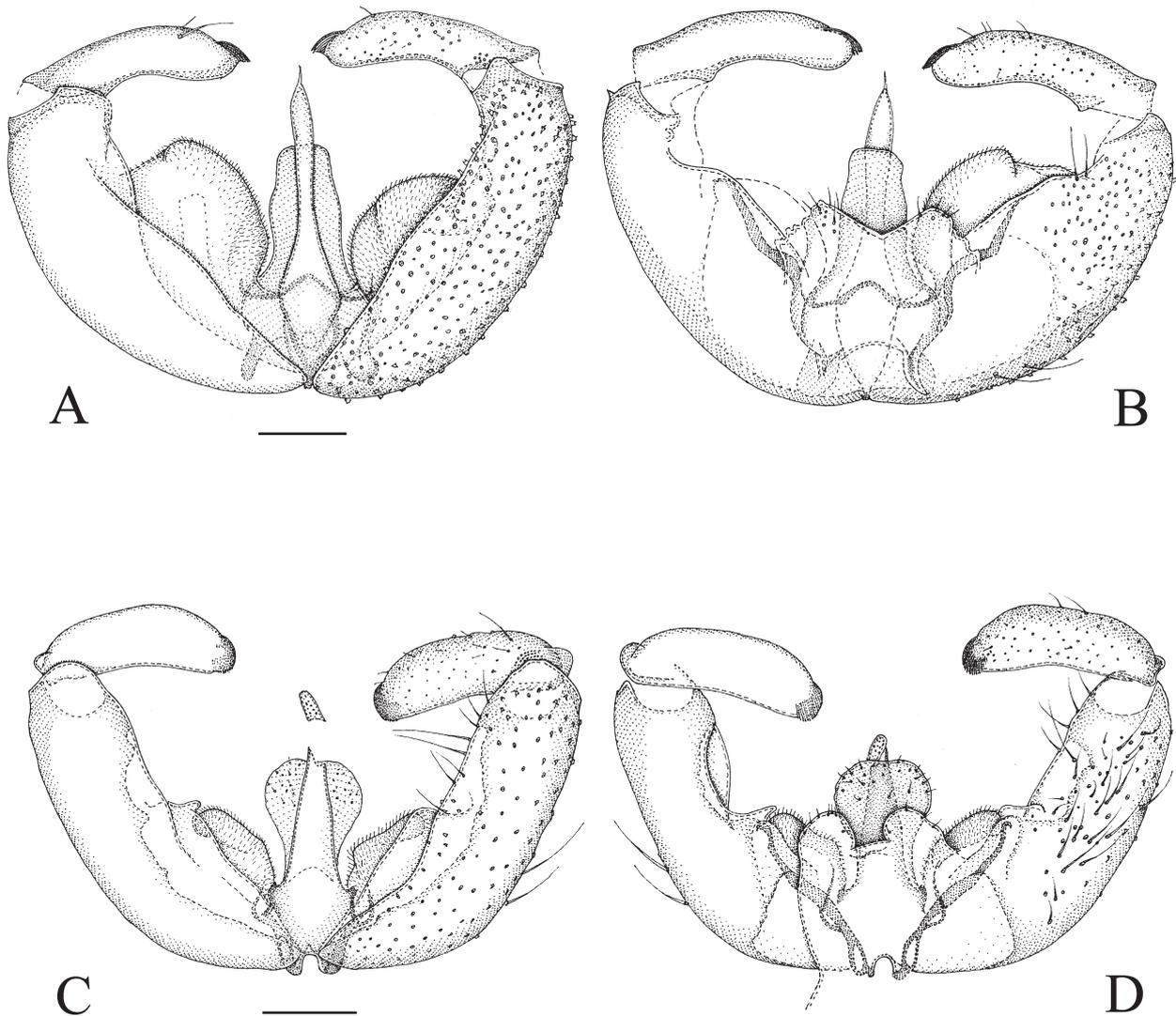


Fig. 10. Male terminalia in ventral (A, D) and dorsal (B, E) view, and hypoproct and apex of aedeagus in ventral view. A, B – *Planetella galiciensis* Ševčík & Hippa sp. nov. (holotype). C, D – *P. hlisnikovskyyi* Ševčík & Hippa sp. nov. (holotype). Scale 0.1 mm.

Head. Eyes with a narrow, membranous eye-bridge, about 1 to 2 ommatidia broad but ommatidia not touching. Antennal flagellum with 12 binodal tricircumfilial, relatively long flagellomeres, and apically with a very short (about one third of previous flagellomere) uninodal flagellomere lacking circumfila. Flagellomere 1 (Fig. 14G) about 4 times as long as broad, of similar shape as the other flagellomeres but less constricted, flagellomere 4 (Fig. 14G) about 4.7 times as long as broad. Maxillary palpus with 3 palpomeres, the basal one (P1) short, P2 about 1.5 times as long as P1, P3 about as twice long as P2.

Thorax mostly light orange brown, with scutum, scutellum and lateral sclerites darker or bicoloured, light brown and dark brown. Scutum produced above the head, with three dark longitudinal stripes. Mediotergite medially brown, its anterior and lateral margins light.

Wing elongated, about 2.7 times as long as broad. Veins C, R₁, R₅ and Cu-stem dark and distinct. R₁ joining C in the middle of wing. R₅ reaching C beyond wing apex. Rs

present. M₄ light and indistinct. CuA with dark stem and bent downwards.

Legs with tarsal claws slightly longer than maximum tarsal diameter, gradually bent.

Abdomen mostly light greyish to orange brown, ventrally darker. Tergites (T2 to T7) with 3 to 4 light oval spots on each side.

Terminalia (Figs 11A,B,C). Gonocoxite broad, about twice as long as broad, mediobasally with a broad, shallow emargination, not a distinct lobe. Gonostylus relatively narrow, slightly curved, three times as long as broad, almost as long as gonocoxite, apically rounded and pointed medially. Cerci rounded, basally fused. Hypoproct slightly longer than cerci, relatively small, subrectangular, apically straight or slightly rounded (depending on view). Aedeagus narrow, subtriangular, as long as gonocoxites, not much longer than hypoproct.

Female (associated with holotype male by COI sequence). Similar to male in most characters. Eyes with

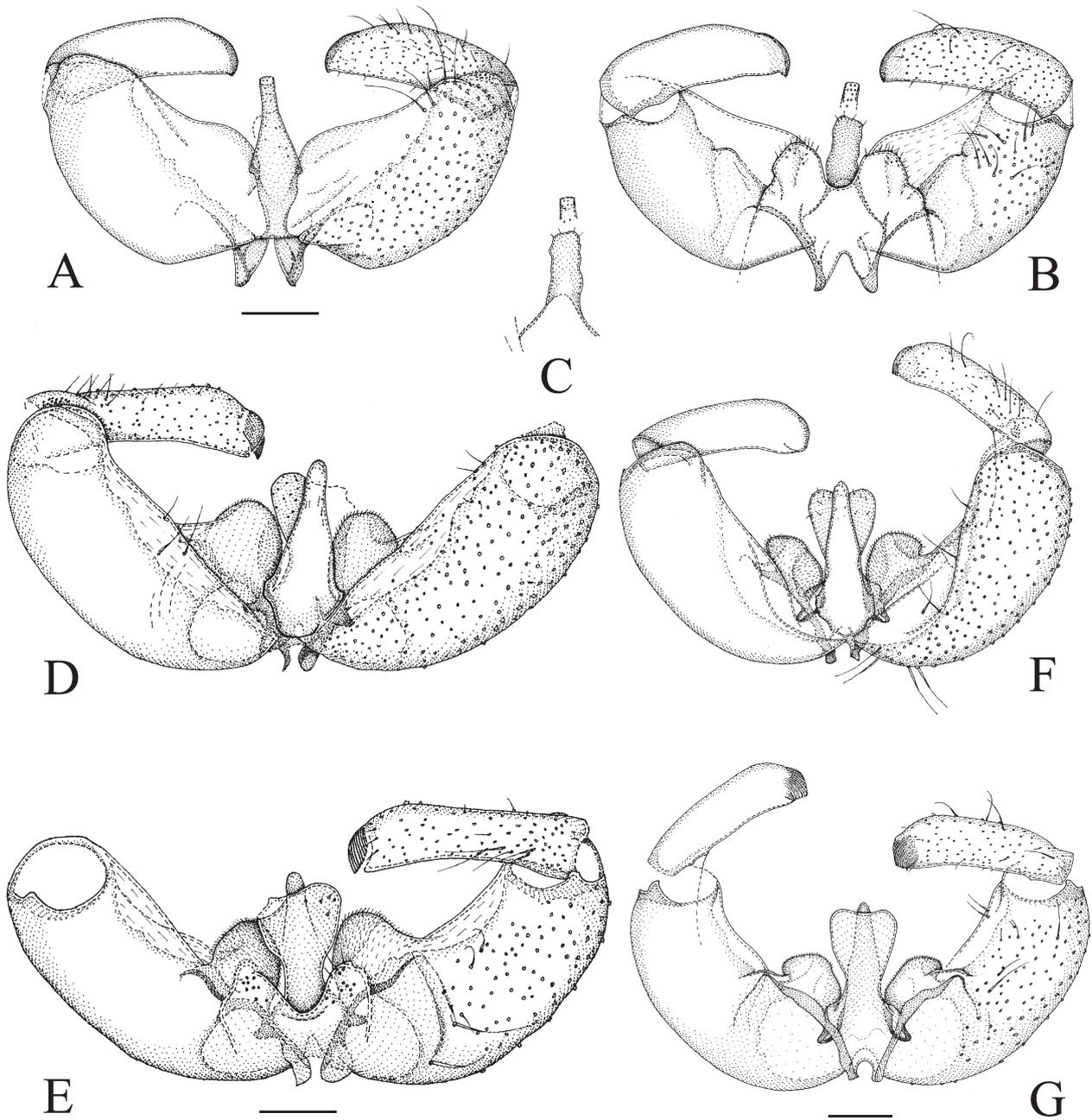


Fig. 11. Male terminalia in ventral (A, D, F) and dorsal (B, E, G) view, and hypoproct and apex of aedeagus in ventral view (C). A, B, C – *Planetella riparia* Ševčík & Hippa sp. nov. (holotype). D, E (holotype) and F, G (paratype) – *P. muranica* Ševčík & Hippa sp. nov. Scale 0.1 mm.

a narrow eye-bridge. Flagellomeres less constricted and shorter than in male. Abdomen vividly brownish orange, each tergite with 3 small light oval spots on each side. Abdomen broad, not distinctly pointed. Cercus small, globular, one-segmented.

Biology. This species is associated with *Carex riparia*, from which it has been reared. The galls remain unknown.

Discussion. This species is characterized by its smaller size, 12 flagellomeres, eyes with a thin eye-bridge, narrow gonostylus and a small, narrow, rectangular, apically straight hypoproct. It is currently known only from the type locality in Slovakia. This species is, however, very similar, or possibly identical, to some of the type specimens of

Planetella tuberifica and *P. tumorifica*, see below (chapter 3). We prefer to give a new name to this species, apparently rare and local, because of small differences in the male terminalia found between our material and the type specimens of both *P. tuberifica* and *P. tumorifica*, although these may be caused by the fact that the type specimens have not been cleared and softened. In this group of species, characterized by 12 flagellomeres and narrow eye-bridge, with at least 5 very similar species, differing only in tiny details on the male terminalia, it is advisable to confirm morphological identification with molecular data, which is impossible in older type material.

***Planetella submontana* Ševčík & Hippa sp. nov.**

(Figure 12D,E, 14H)

Type material. HOLOTYPE: ♂, Slovakia, Trsteník, 8.–29.vi.2018, reared from tussock of *Carex umbrosa*, leg. J. Roháček & J. Ševčík, specimen after DNA extraction, prepared on slide, No. PLA4 (coll. NMPC). PARATYPE: ♂, the same locality as holotype but 16.vi.–14.vii.2016, Malaise trap among *Carex rostrata* and *Carex umbrosa*, leg. J. Roháček & J. Ševčík, specimen after DNA extraction (No. PLA1), prepared on slide (coll. SMOC).

DNA sequences. DNA sequences (COI barcode region, 28S, and 16S) taken from the paratype (No. PLA1) are deposited in GenBank. Their Accession numbers are provided in Table 1.

Diagnosis. A mostly light brown to orange species (Fig. 1A), with some parts of thorax dark. Antenna with 12 binodose, relatively long flagellomeres, plus a short apical segment. Eyes with a narrow membranous eye-bridge. Terminalia with a relatively narrow, apically excavated hypoproct, and broadly pointed gonostylus.

Etymology. The name of this species refers to the submontane type locality; adjective.

Description. Male. Wing length 5.1 mm. Overall body coloration mostly orange brown, with head, antennae, legs, halteres and gonostyli darker.

Head. Eyes with a narrow, membranous eye-bridge, ommatidia not touching. Antennal flagellum with 12 binodal tricircumfilial, relatively long flagellomeres, and apically with a very short (about one third of previous flagellomere) uninodal flagellomere lacking circumfila. Flagellomere 1 (Fig. 14H) 4.4 times as long as broad, slightly longer but of similar shape as the other flagellomeres, flagellomere 4 (Fig. 14H) about 4.6 times as long as broad. Maxillary palpus with 3 palpomeres, subequal in length.

Thorax mostly light orange brown. Scutum distinctly produced above the head, with three longitudinal stripes. Anterior margin of scutum darker, as well as mediotergite.

Wing elongated, about 2.6 times as long as broad. Veins C, R₁, R₅ and Cu-stem dark and distinct. R₁ joining C almost in the middle of wing. R₅ reaching C beyond wing apex. Rs present. M₄ light and indistinct. CuA with dark stem and bent downwards.

Legs with tarsal claws slightly longer than maximum tarsal diameter, only moderately bent.

Abdomen basally orange brown, distally orange, gonostyli blackish.

Terminalia (Figs 12D,E). Gonocoxite relatively broad, about twice as long as broad, mediobasally with a long and broad lobe. Gonostylus narrowing to the apex, slightly curved, three times as long as broad, shorter than gonocoxite, apically with a rounded tooth directed medially. Cerci relatively short, subtriangular, basally fused. Hypoproct relatively long, almost twice as long as cerci, subrectangular, posteriorly excavated, with several marginal setae. Aedeagus subtriangular, almost as long as gonocoxites, longer than hypoproct. Gonocoxal apodemes strongly sclerotized, medially fused.

Female. Unknown.

Biology. This species is associated with *Carex umbrosa*, from which it was reared. The galls remain unknown.

Discussion. This species is characterized by its orange

coloration, 12 flagellomeres, eyes with a thin eye-bridge, and the shape of gonostylus and hypoproct. It is known only from the type locality in central Slovakia. Its closest relatives in terms of K2P genetic distance (Tab. 3), as well as in the phylogenetic tree (Fig. 15), are *P. attilai* sp. nov., with 8.0% distance, and *Planetella* sp. D with 8.2% distance.

***Planetella thermophila* Ševčík & Hippa sp. nov.**

(Figure 12A,B,C, 14I)

Type material. HOLOTYPE: ♂, Slovakia, Cerová vrchovina Protected Landscape Area, Hajnáčka, Buková, 26.iv.–7.vi.2018, Malaise trap in *Quercus cerris* forest, leg. J. Roháček & J. Ševčík, specimen after DNA extraction, prepared on slide No. PLA15 (coll. NMPC). PARATYPES: SLOVAKIA: 1 ♂ in ethanol, Cerová vrchovina Protected Landscape Area, Chrámeč, Vlčia dolina, 13.iv.–11.v.2023, Malaise trap in *Quercus cerris* forest with *Carex michelii* in undergrowth, leg. J. Roháček & J. Ševčík, specimen after DNA extraction, prepared on slide, No. PLA65 (coll. JSL-OUC); 1 ♀ in ethanol (after DNA extraction, No. PLA15b), the same data as holotype (coll. JSL-OUC); 1 ♀ in ethanol (after DNA extraction, No. PLA31) (coll. JSL-OUC). CZECH REPUBLIC: Podyjí National Park, Hardegg, 14.v.–12.vi.2020, Malaise trap in a forest steppe (coll. JSL-OUC).

DNA sequences. DNA sequences (COI barcode region, 28S, 18S, 16S) taken from the holotype (No. PLA15) are deposited in GenBank. Their Accession numbers are provided in Table 1.

Diagnosis. A large, dark brown species. Antenna with 15 binodose flagellomeres, the apical one is shorter and variable in shape. Eyes with a narrow eye-bridge. Terminalia with a broad, pear-shaped hypoproct, posteriorly rounded.

Etymology. The name of the new species means ‘warm-loving’ and refers to the thermophilous habitats where all the type specimens were collected; adjective.

Description. Male. Wing length 7.8 mm (holotype). Overall body coloration mostly glossy dark brown, with legs and halteres brownish.

Head. Eyes with a narrow, membranous eye-bridge, ommatidia not touching. Antennal flagellum with 14 binodal tricircumfilial flagellomeres, plus apically with a short uninodal flagellomere lacking circumfila. Flagellomere 1 (Fig. 14I) about 3.6 times as long as broad, slightly longer and more cylindrical than the other flagellomeres, flagellomere 4 (Fig. 14I) about 3.3 times as long as broad. Maxillary palpus with 3 palpomeres, the apical one the longest, almost as long as the first and second together.

Thorax mostly blackish brown. Scutum distinctly produced above the head, brown, with three dark longitudinal stripes.

Wing elongated, about 2.7 times as long as broad. Veins C, R₁, R₅ and Cu-stem dark and distinct. R₁ joining C almost in the middle of wing. R₅ reaching C beyond wing apex. Rs missing. M₄ light and indistinct. CuA with dark stem and bent downwards.

Legs with tarsal claws slightly longer than maximum tarsal diameter, gradually bent. Empodia reaching to about half the length of claw.

Abdomen dark brown, with a light oval spot on each side of the tergite.

Terminalia (Figs 12A,B). Gonocoxite about 2.5 times as long as broad, mediobasally with a distinct rounded lobe.

Gonostylus relatively long and narrow, slightly broader subapically, 4.2 times as long as broad, almost as long as gonocoxite, apically with a rounded, transversely grooved dark lobe, pointed medially. Cerci short, rounded, basally fused. Hypoproct broad, pear-shaped, distally convex, with a shallow depression. Aedeagus narrow, elongate, subtriangular, slightly longer than hypoproct. Gonocoxal apodemes strongly sclerotized, medially fused.

Female (associated with holotype male by COI sequence). Similar to male, with robust abdomen. Antennae shorter and thinner than in male, about 1.5 times as long as thorax. Flagellomeres cylindrical, relatively short, not distinctly binodose. Eyes with a narrow, membranous eye-bridge, without any ommatidia connected. Abdomen dark brown, with light narrow oval spot on each side of tergites 2 to 7. Cercus one-segmented, pointed apically, suboval in shape, about twice as long as broad.

Biology. This species is probably associated with *Carex michelii* and *Carex umbrosa*, on which the type material was collected. The galls remain unknown.

Discussion. This species is characterized by the dark coloration, 14 flagellomeres, eyes with a narrow eye-bridge and details on the male terminalia, especially the broad pear-shaped hypoproct. It is known from the two localities in southern Slovakia and one in the Czech Republic (close to the border with Austria). Its closest relative in terms of K2P genetic distance (Tab. 3), as well as in the phylogenetic tree (Fig. 15), is *P. muranica* sp. nov., with 5.2% distance.

3. Unrecognized described species

The following named Palearctic species remain unrecognized, and/or we have not seen any recent material.

Planetella billoti (Kieffer, 1909)

Hormomyia billoti Kieffer, 1909: 5. Type locality: France, Strasbourg.

Type material. Lost. Most of the types of J.-J. Kieffer are considered as lost (GAGNÉ & JASCHHOF 2021).

Comments. In the original publication by KIEFFER (1909), the species is listed and described in the paragraph starting with the host name *Carex davalliana*. The description consists of one long paragraph, without figures, based only on larva and gall. The gall is reported as 7×2 mm large, pointed at both ends. The galls are at the base of the stem, single or several together. The larva is white, residing in a large cavity. Galls were found in *Flora galliae et germaniae exsiccata* from 1906, collected by Billot in Citadelle de Strasbourg, according to the label. Unrecognized species.

Planetella breinii (Kieffer, 1898)

Hormomyia breinii Kieffer, 1898: 25. Type locality: Switzerland.

Type material. HOLOTYPE: ♀, Switzerland (probably in coll. Entomologisches Institut, Eidgenössische Technische Hochschule, Zurich, Switzerland), not studied.

Comments. This species is difficult to interpret. KIEFFER (1898) just stated that this species is based on *P. fasciata* (Meigen) of BREMI (1847), without any figure or description. BREMI (1847) provided a brief description of the female of *P. fasciata*, which is not diagnostic. Unrecognized species.

Planetella brunnea (Rübsaamen, 1892)

Hormomyia brunnea Rübsaamen, 1892: 396. Type locality: Switzerland: Bergün.

Type material. HOLOTYPE: ♂, Switzerland: Bergün, H. Loew leg. (no other data, in coll. ZMHB Berlin, number 435), examined.

Comments. The original description contains 3 paragraphs, with figures of the wing, palpus and apical part of antenna. The antennae are reported as having 2 + 24 binodose flagellomeres, the apical one with a small appendage. The number 24 almost certainly refers to nodes, not flagellomeres. Male terminalia are figured by RÜBSAAMEN (1892) in Table XVII, figure 19 (not 14 as mentioned at page 396). The gonocoxite is relatively long and narrow, gonostylus short, pointed, about half as long as gonocoxite. Hypoproct relatively long, subrectangular, with a shallow posterior depression. The type specimen (male) has 12 binodose flagellomeres. The terminalia resemble those of *P. attilai* sp. nov. and *P. galiciensis* sp. nov. but we do not think that these three species are identical.

Planetella caricis (Rübsaamen, 1911)

Amaurosiphon caricis Rübsaamen, 1911: 391. Type locality: Germany, Berlin.

Type material. SYNTYPES: 4 ♂♂ 3 ♀♀, Berlin, 14.iii.–18.iv.1896, (coll. ZMHB Berlin, vial No. 3), examined.

Comments. Figures of female habitus and male terminalia in the original description by RÜBSAAMEN (1911h) correspond to those of *Planetella granifex*. However, as we mentioned above (under *P. granifex*), the specimens identified as *P. caricis* in the Rübsaamen collection in Berlin appear to belong to a different species. The true identity of *P. caricis* is thus unclear to us, but could be potentially solved in the future, when male terminalia of the type specimens are cleared and studied in more detail, or if any other type specimen, better corresponding to the original figures, is found.

Planetella cornifex (Kieffer, 1898)

Hormomyia cornifex Kieffer, 1898: 60. Type locality: France, Moselle.

Type material. Lost (see GAGNÉ & JASCHHOF 2021).

Comments. The original description contains just one paragraph, without figures. Antennae are reported as having 2 + 12 segments in both sexes, all of them binodose (in male), size 6.5–7.0 mm. Larva found in *Carex pallescens* and *C. elata*, galls near the ground, pointed. Figure of the male terminalia is in KIEFFER (1913) and in SKUHRAVÁ (1997). They resemble those of *P. fasciata*, except in the shape of cerci. KIEFFER (1901) in his key states that *P. cornifex* has the eyes widely separated, which would further confirm its synonymy with *P. fasciata*.

Planetella cornuta (Bremi, 1847)

Cecidomyia cornuta Bremi, 1847: 48. Type locality: Switzerland.

Type material. SYNTYPES: ♀♀ (probably in coll. Entomologisches Institut, Eidgenössische Technische Hochschule, Zurich, Switzerland), not studied.

Comments. The original description contains just one paragraph, including figure of female head and thorax

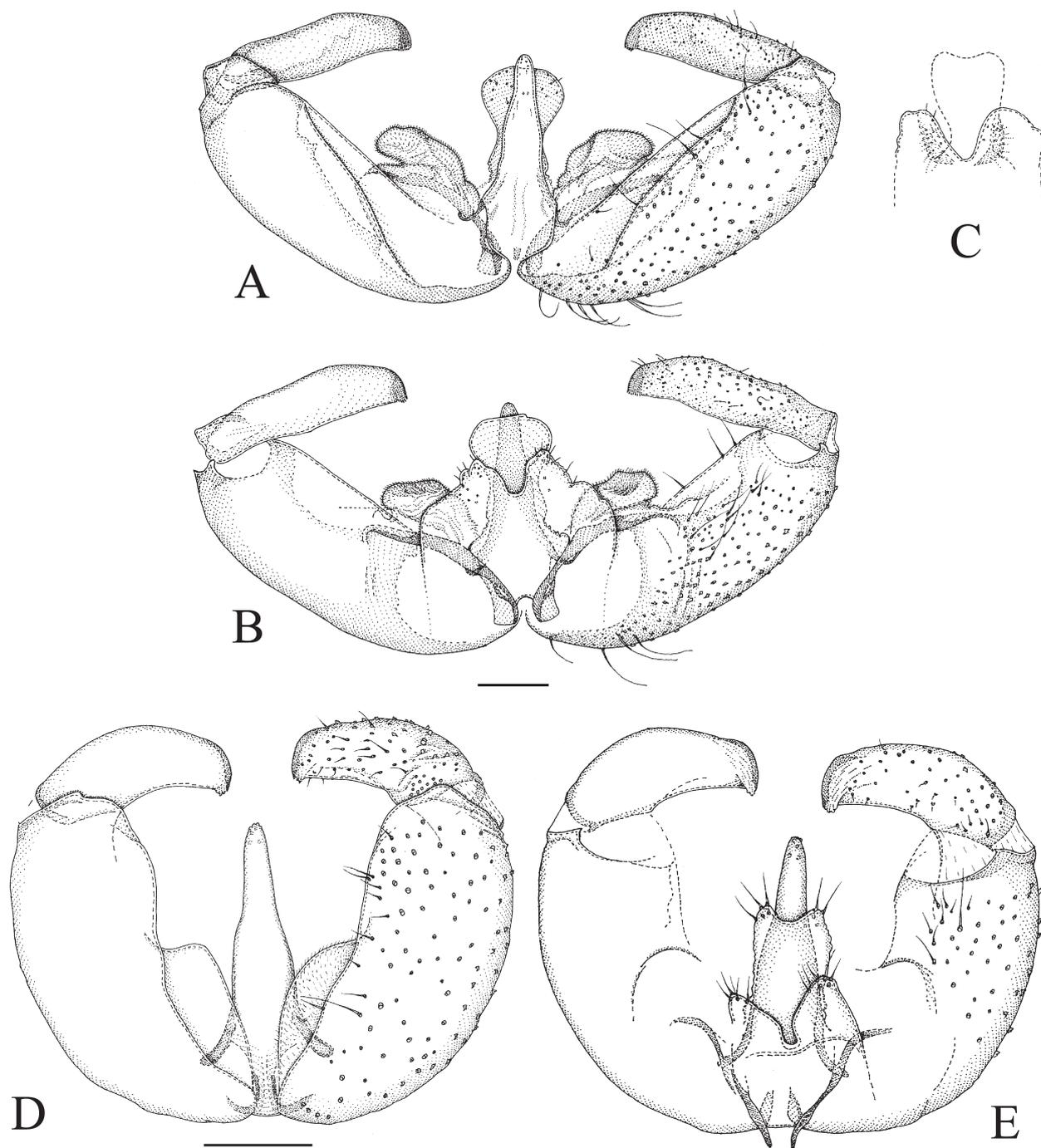


Fig. 12. Male terminalia in ventral (A, D) and dorsal (B, E) view, and cerci and hypoproct in dorsal view (E). A, B, C – *Planetella thermophila* Ševčík & Hippa sp. nov. (holotype). D, E – *P. submontana* Ševčík & Hippa sp. nov. (holotype). Scales: 0.1 mm.

from lateral view, plus detail of antenna. Antenna with only 9 flagellomeres figured, apical flagellomeres probably broken-off. Unrecognized species.

***Planetella cucullata* (Meigen, 1818)**

Cecidomyia cucullata Meigen, 1818: 96. Type locality: Germany.

Type material. HOLOTYPE: sex?, Germany (coll. MNHN Paris, No. MNHN-ED-ED844), not studied.

Comments. The original description is very short and uninformative. The high-resolution photographs of the holotype are available at the web pages of MNHN Paris

(<https://science.mnhn.fr/taxon/species/planetella/cucullata>). The holotype male (No. MNHN-ED-ED849) lacks antennae and wings, and the apical part of the abdomen is broken-off. Unrecognized species.

***Planetella extrema* (Walker, 1837)**

Planetes extremus Walker, 1837: 179.. Type locality: Great Britain, England, near London.

Type material. HOLOTYPE: ♀, England, wings lost and antennae broken-off (coll. BMNH London). Not studied, described by EDWARDS (1938).

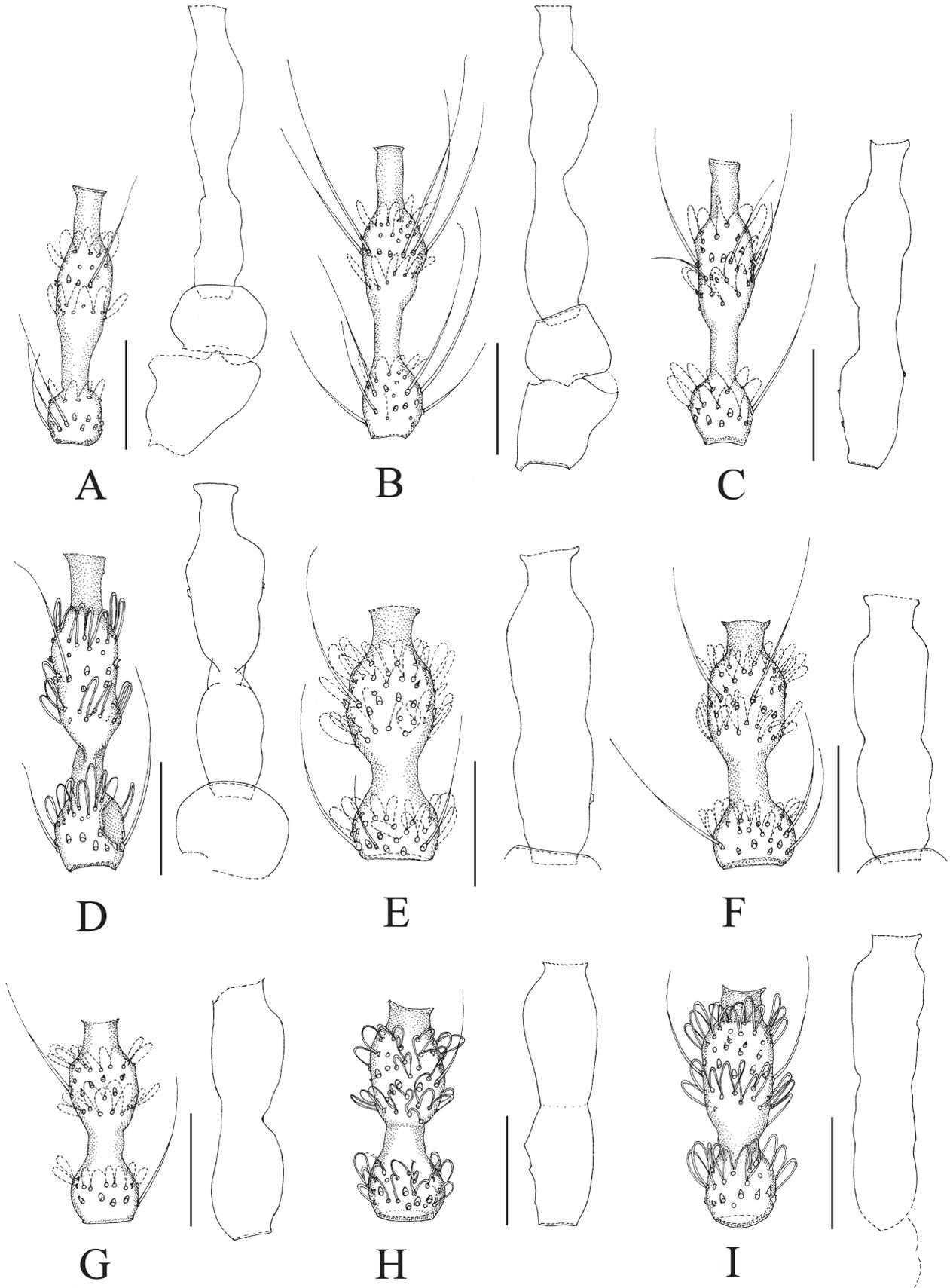


Fig. 13. Antennal flagellomere 4 (except flagellomere 3 in H) and outline of flagellomere 1 with or without associated pedicellus and scapus. A – *Planetella granifex* (Kieffer, 1898), B – *P. gallarum* (Rübsaamen, 1899), C – *P. fasciata* (Meigen, 1818), D – *P. aestivalis* Ševčík & Hippa sp. nov. (holotype), E, F – *P. adami* Ševčík & Hippa sp. nov. (holotype), G – *P. antennata* Ševčík & Hippa sp. nov. (holotype); H – *P. atrobrunnea* Ševčík & Hippa sp. nov. (holotype); I – *P. csabai* Ševčík & Hippa sp. nov. (holotype). Scales: 0.1 mm.

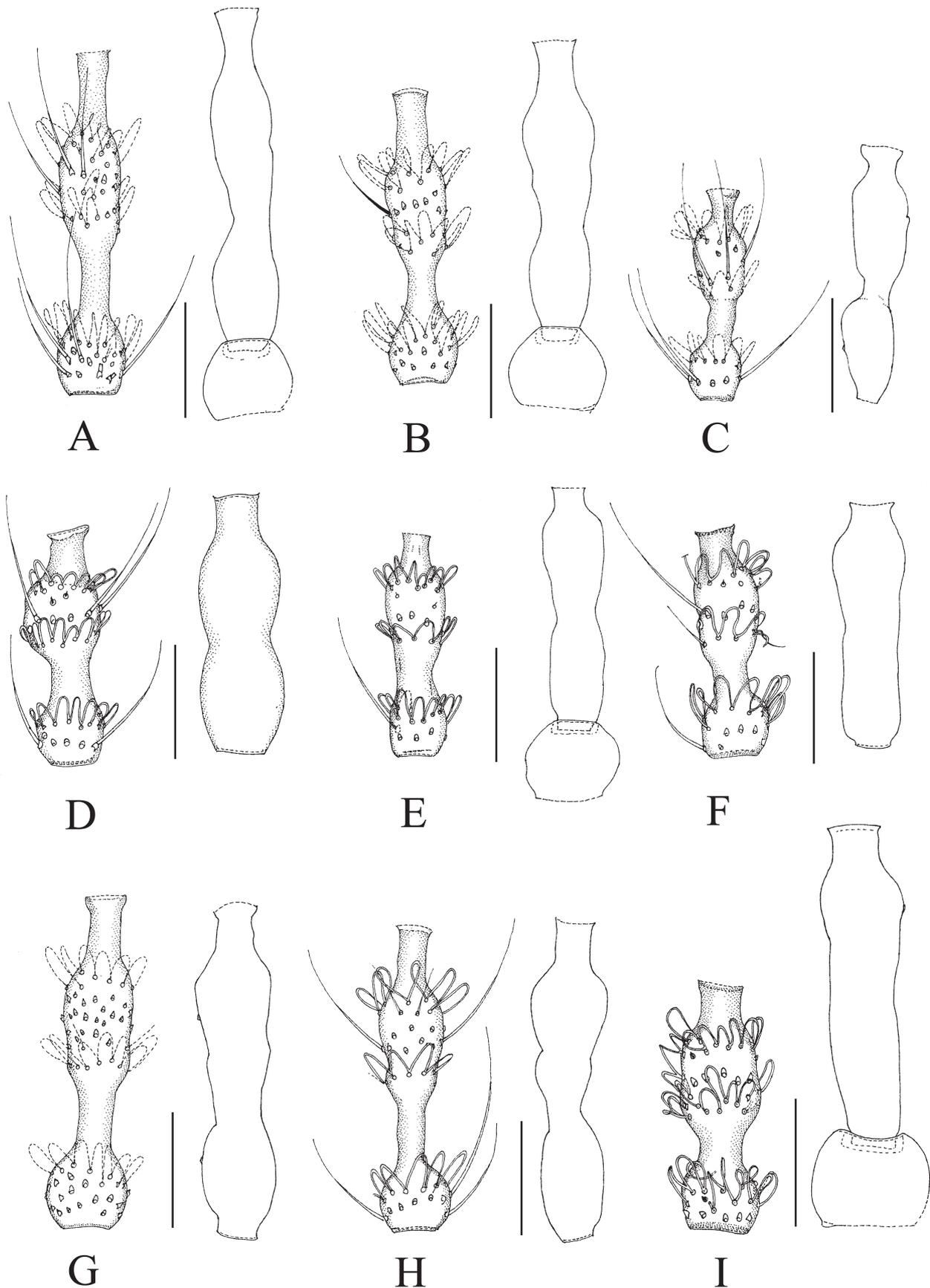


Fig. 14. Antennal flagellomere 4 and outline of flagellomere 1 with or without associated pedicellus. A (holotype), B (paratype) – *Planetella attilai* Ševčík & Hippa sp. nov. (holotype), C – *P. davidi* Ševčík & Hippa sp. nov. (holotype), D – *P. galiciensis* Ševčík & Hippa sp. nov. (holotype), E – *P. hlišnikovskyyi* Ševčík & Hippa sp. nov. (holotype), F – *P. muranica* Ševčík & Hippa sp. nov. (holotype), G – *P. riparia* Ševčík & Hippa sp. nov. (holotype), H – *P. submontana* Ševčík & Hippa sp. nov. (holotype), I – *P. thermophila* Ševčík & Hippa sp. nov. (holotype). Scales: 0.1 mm.

Comments. This is the type species of the genus. The original description is very short. Female type is reported as having ‘25 joints’ which most probably means just 25 nodes, i.e. 12–13 flagellomeres. Unrecognized species.

***Planetella fischeri* (Frauenfeld, 1867)**

Hormomyia fischeri Frauenfeld, 1867: 781. Type locality: Austria, Vienna, Prater.

Type material. HOLOTYPE: Austria: Prater (?coll. NHMW Vienna), not examined.

Comments. It is stated in the original description by FRAUENFELD (1867) that type material was reared from *Carex pilosa* collected by L. Fischer in Prater (Vienna), Austria. The gall was in the form of swellings at the base of leaves. The larva and pupa were described in detail but not illustrated. The adult is described as very dark, scutum produced above the head, with three lateral stripes, abdomen dark brown, head blackish brown, and antennae with 2 + 20 segments, flagellomeres binodose.

The number of flagellomeres would possibly be diagnostic for this species because no other European species of *Planetella* is known to have 20 flagellomeres. The closest in this respect is *P. antennata* with 21 binodose flagellomeres but having distinctly banded abdomen. The holotype should be deposited in Vienna, pending further study.

***Planetella frireni* (Kieffer, 1909)**

Hormomyia frireni Kieffer 1909: 5. Type locality: France, near Bitche.

Type material. Lost (see GAGNÉ & JASCHHOF 2021).

Comments. In the original publication, the species is listed and described in the paragraph starting with the host names *Carex pallescens* and *C. elata*. The description includes one paragraph, without figures, based only on the larva. Galls were found at the base of the leaves, one-sided, located underground. Larva white, 5 mm long, spatula brown. Unrecognized species.

***Planetella gibba* (Zetterstedt, 1850)**

Cecidomyza gibba Zetterstedt, 1850: 3694. Type locality: Sweden, Scania.

Type material. HOLOTYPE: ♀, Sweden, Scania (probably in coll. Museum of Zoology – Entomology, Lund University). Not studied.

Comments. The original description in ZETTERSTEDT (1850) is in Latin. Scutum is described as produced above the head, light brown, with three longitudinal stripes, tips of antennae broken-off. Unrecognized species.

***Planetella gibbosa* (Rondani, 1860)**

Angelina gibbosa Rondani, 1860: 290. Type locality: Italy: Parma.

Type material. HOLOTYPE: ♂, Italy, Parma (coll. Museo Zoologico ‘La Specola’, Florence). Not studied.

Comments. The original description by RONDANI (1860) is very short, uninformative. Unrecognized species.

***Planetella grandis* (Meigen, 1804)**

Cecidomyia grandis Meigen, 1804: 39. Type locality: Germany.

Type material. SYNTYPES: 1 ♂ 3 ♀♀ (coll. MNHN Paris).

Comments. The original description consists of a short

paragraph, stating that this is the largest species known to Meigen, with thorax dark greyish-brown, abdomen blackish brown, lighter on margins of tergites, reddish brown legs, and dark brown halteres. The only male was collected in May in a forest. Later, MEIGEN (1818) mentioned that he caught females in large quantities on a moist forest meadow in May. The size of the male specimen is given as ‘3 Linien’. Linien is 1/12 of inch, which means body length $(2.54/12) \times 3 = 0.64 \text{ cm} = 6.4 \text{ mm}$.

The high-resolution photographs of the type specimens are available at the web pages of MNHN Paris (<https://science.mnhn.fr/taxon/species/planetella/grandis>). The male type (No. MNHN-ED-ED849) is without head and without the apical half of the abdomen. MORGE (1975) provided colour plates of the types of Meigen and *P. grandis* is figured as a large dark brown species with 12 binodose flagellomeres. This could possibly be in concordance with *P. hlisnikovskiyi* sp. nov. described above, but the coloration of the scutum is different, more dark and glossy blackish brown in *P. hlisnikovskiyi* while principally yellowish brown with three distinct longitudinal stripes in *P. grandis*, according to the photo of the type. The eyes of *P. hlisnikovskiyi* are broadly separated while this character state is unclear for *P. grandis*.

***Planetella kneuckeri* (Kieffer, 1909)**

Hormomyia kneuckeri Kieffer, 1909: 6. Type locality: France.

Type material. Gall (lost).

Comments. In the original publication, the species is listed under the host name *Carex stellulata* (= *Carex echinata*). Description contains just a short paragraph, without figures, reporting the galls being at the base of the leaves, located at the level of ground. Unrecognized species.

***Planetella lambertoni* (Kieffer, 1901)**

Hormomyia lambertoni Kieffer, 1901: 25. Type locality: France, Lorraine, Bitche.

Type material. Lost (see GAGNÉ & JASCHHOF 2021).

Comments. The original description is without figures and the types are lost. The adult male is described as 4 mm long, having orange thorax, scutum with three lateral stripes, abdomen with brown dorsal stripes, eyes partially fused, palpi with 3 segments, plus one short basal segment. Antennae with 2 + 12 segments, the first two are not fused, flagellomeres binodose. Last flagellomere is not finished by neck but a short apical segment. Legs with simple long claws. Terminalia with cerci short, hypoproct tongue-shaped, rounded, longer than aedeagus. Collected on a window pane in Bitche, Lorraine, France. Unrecognized species.

***Planetella producta* (Meigen, 1830)**

Cecidomyia producta Meigen, 1830: 267. Type locality: Germany.

Type material. HOLOTYPE: ♂, without antennae and abdomen (coll. MNHN Paris), not studied.

Comments. In the original description, the adult male is described as similar to *P. cucullata* but rather different and substantially larger. Antennae stated to have 24 seg-

ments, most probably meant just nodes. The specimen was collected at the end of June in a forest. The figure in MORGE (1975) shows brownish orange coloration, scutum produced over the head, unicolorous abdomen, antennae with 2 + 12 segments, flagellomeres binodose.

The high-resolution photographs of the holotype are available at the web pages of MNHN Paris (<https://science.mnhn.fr/taxon/species/planetella/producta>). The male type (No. MNHN-ED-ED867) is without antennae and without the abdomen. The thorax is light orange brown, scutum with three longitudinal stripes and strongly produced above the head. MORGE (1975) provided colour plates of the types of Meigen and *P. producta* is figured as a light brown to orange species with 12 binodose flagellomeres. As this combination of characters is found in many species of *Planetella*, this species remains unrecognized.

Planetella rosenhaueri (Rübsaamen, 1892)

Hormomyia rosenhaueri Rübsaamen, 1892d: 394. Type locality: Germany, Berlin.

Type material. HOLOTYPE: ♀, Berlin, 28.iii.1896 (coll. ZMHB Berlin, No. 642), examined.

Comments. The original description includes the information that the gall was found on *Carex acuta* in the collection of Rosenhauer, somewhat similar to that of *Planetella fischeri* (as *Hormomyia fischeri*). Very similar galls are said to be induced on different host plant species by related species. It is also stated there that there are similar galls on *Carex arenaria* and *C. rostrata* in the herbarium of prof. P. Magnus. The larvae taken from the galls are reported as quite different. The adult female is described as having antennae with 2 + 20 segments. Unrecognized species.

RÜBSAAMEN (1917) created a separate genus for this species, *Paurosphondylus*, stating that it has all the flagellomeres uninodal. Most probably, he meant only the females, because no male specimen is present in the type series.

Planetella strobli (Kieffer, 1901)

Hormomyia strobli Kieffer, 1901c: 26. Type locality: Austria: Styria.

Type material. Lost (see CHVÁLA 2008).

Comments. In the original description (without figures), male is described as reddish brown, abdomen with anterior margin light, with lateral spots. The eyes are fused. Palpi with 3 segments, the apical one the longest. Antennae with 2 + 12 segments, described in detail. Wing described in detail. Length 4 mm. Collected by Strobl. The holotype male probably exists somewhere but it has not been located by us. This may be a potentially recognizable species, if the holotype is well preserved. However, according to the monograph by CHVÁLA (2008), the type of *P. strobli* is not present in the Strobl collection in Admont. The figure of male terminalia in KIEFFER (1913) is not detailed enough to recognize this species.

Planetella subterranea (Kieffer & Trotter, 1904)

Pseudohormomyia subterranea Kieffer & Trotter, 1904: 65. Type locality: Italy, Avellino.

Type material. Lost (see GAGNÉ & JASCHHOF 2021).

Comments. The original description is without figures. Female is compared in table with *P. granifex*. In *P. subterranea*, the empodium is stated as longer than half of the claw (shorter in *P. granifex*); 3rd palpomere as narrowing in basal half, then the same to the end; flagellomere with two whorls of setae. In all other respects, as KIEFFER & TROTTER (1904) stated, these two species are identical, except in the shape of spatula. Galls were found on *Carex divulsa*, subterranean, similar to *P. granifex*. Collected in Avellino (Italy). Subsequent figure of the male terminalia in KIEFFER (1913) indicates that this species is very similar or perhaps identical with *P. granifex*. Considering the possible existence of several cryptic species related to *P. granifex*, this species is left here as unrecognized.

Planetella tarda (Rübsaamen, 1914)

Jaapiola tarda Rübsaamen, 1914: 95. Type locality: Germany, Triglitz.

Type material. SYNTYPES: 1 ♂ (No. 481a) and 1 ♀ (No. 481b, coll. ZMHB Berlin), both examined.

Comments. The original description in RÜBSAAMEN (1914) contains only text without figures. Characters given to describe the genus: Scutum not much produced over the head, antennae binodose, in females less conspicuously. Three palpomeres, palpomere 1 longer and broader. Claws simple, almost as long as empodium. Gonostylus broadened. Both ‘lamellae’ in the same position, apically with a notch. Last abdominal segment stretchable, with two upper and one lower lamella. Description of the species: Length 10 mm. Eyes black, broadly converging on the top of the head. The face, neck and back of the head are dark chestnut brown, yellow-brown; Basal segments not lighter, but more reddish, 2 + 19 segmented, all segments without white markings, black hairy. Thorax mostly blackish brown, described in detail. Abdomen described. Wing described.

Larvae whitish, similar to *Planetella gallarum* (*‘Dichrona gallarum’*), in galls on *Carex vesicaria*. Spatula sternalis with two teeth in *P. tarda*, but only one tooth in *P. gallarum*. The gall received from Mr. Otto Jaap, who collected them near Triglitz in der Priegnitz.

Both apparently complete antennae have 14 binodose flagellomeres, plus an apical shorter segment, not 19 as stated in the description. The species thus belongs to the group of several species with 14 flagellomeres (plus the apical short one), which differ in tiny details of the male terminalia and DNA sequences are necessary to safely distinguish particular species in this group. We thus leave this species as unrecognized.

Planetella tuberifica (Rübsaamen, 1899)

Hormomyia tuberifica Rübsaamen, 1899a: 546, fig.7. Type locality: Germany, Berlin.

Type material. SYNTYPES: 3 ♂♂ 4 ♀♀ 3 exuviae, Berlin, 24.iii.–12.v.1896, *Carex stricta* (vial No. 681, coll. ZMHB Berlin), examined.

Comments. In RÜBSAAMEN (1899a), only habitus figure of female is included, showing striped scutum produced over the head, and striped abdomen. The number of flagellomeres is indistinct from the figure.

In the next work by RÜBSAAMEN (1899b), only text without figures is included. Female is reported as having

the abdomen reddish with posterior margin of each segment with glossy black stripes in about one third, ‘lamelles’ of short ovipositor blackish, scutum honey brown, produced over the head, with three stripes. Head and antennae blackish. Male of similar colour as female but abdomen lighter. Antennae similar to those of *P. arenariae* (described in the same paper), described in detail but the number of flagellomeres is not stated. Aedeagus reported as very long, longer than gonocoxites. Larvae in galls at base of stems and leaf sheaths of *Carex elata*.

Male terminalia studied (but not cleared in KOH) by the first author of this paper. The three males included represent two different species, one of them with terminalia different from any species treated here, the second similar to (or identical with) *P. tumorifica*, see below.

Planetella tumorifica (Rübsaamen, 1899)

Hormomyia tumorifica Rübsaamen, 1899b: 603. Type locality: Germany, Berlin.

Type material. SYNTYPES: 4 ♂♂ 2 ♀♀ 2 exuviae, Berlin, 14.iii.–29. iv.1896, *Carex pseudobrivoidea*, leg. Thureau (vial No. 384a, coll. ZMHB Berlin), examined.

Comments. The description in RÜBSAAMEN (1899d, the same paper where *P. tuberifica* is also described) contains a text without figures, stating that abdomen is reddish with strip-like black spots dorsally, thorax dull red, scutum glossy black, male antennae with 2 + 12 flagellomeres. It is also said that lobes of ‘lamelles’ are not rounded like in *Hormomyia tuberifica* and long lamella (hypoproct?) is not laterally excavated. The aedeagus is reported as very long. Larvae were found in similar galls as *P. tuberifica*, but on leaves of *Carex pseudocyperus*.

Male terminalia studied (but not cleared in KOH) and photographed by us. They are very similar to *Planetella riparia* Ševčík & Hippa sp. nov., except in the shape of hypoproct, which is more rectangular apically in *P. riparia*, and the shape of cerci which appear more pointed in *P. tumorifica*. Considering these differences and a large number of *Planetella* species with 12 flagellomeres, including *Planetella* sp. B (see below), the closest relative of *P. riparia* sp. nov. (Fig. 15), we prefer to treat all these species as distinct.

Planetella westermanni (Meigen, 1830)

Cecidomyia westermanni Meigen, 1830: 269. Type locality: Germany: near Kiel.

Type material. HOLOTYPE: ♂ (lost).

Comments. The original description is very short, without figures, and this species is not figured in MORGE (1975). It is stated that it was collected near Kiel, into the collection of Mr. Westermann. Unrecognized species.

Planetella winnertzi (Kieffer, 1898)

Hormomyia winnertzi Kieffer, 1898: 26. Type locality: Germany.

Type material. Lost (see GAGNÉ & JASCHHOF 2021).

Comments. In the original publication, only short remarks are included, without proper description. For example, ‘*H. ampla* and *H. funesta* remain dubious like almost all the species described by Walker and it is not possible to recognize them’. In the same paper, also *Planetella*

granifex (as *Pseudhormomyia granifex*) and *P. cornifex* (as *Hormomyia cornifex*) were described. This species was included in the key by RÜBSAAMEN (1917) among the species with uninodal flagellomeres. Apparently, he referred to females only, as in the case of *P. rosenhaueri* (see above), because no species of *Planetella* currently known has uninodal flagellomeres in the males. Unrecognized species.

4. Species left unnamed

The following four species are included in the molecular analysis but they are left unnamed because of the absence of adult males or the male specimens are in poor condition. We included them here just to illustrate the enormous species diversity of *Planetella* in Central Europe.

Planetella sp. A

Material examined. DENMARK: Havrehede, 1.v.2019, 1 ♀ (specimen after DNA extraction, No. PLA20), reared from galls on *Carex acutiformis*, H. H. Bruun leg.; the same locality, date and collector, 1 ♀ (specimen after DNA extraction, No. PLA21), reared from galls on *Carex elata*; Denmark, Toggerup Enghave, 30.iii.2019, 1 larva (specimen after DNA extraction, No. PLA25) in galls on *Carex cespitosa*, H. H. Bruun leg. (all in coll. JSL-UOC).

Comments. This material was tentatively identified by H. H. Bruun and M. Skuhrová as *P. tarda* Rübsaamen 1914, according to the shape and position of the galls. However, both the female specimens studied have the antennae broken-off, so we cannot confirm their conspecificity with the specimens of *P. tarda* with 15 flagellomeres in Berlin museum. According to the position in the phylogenetic tree (Fig. 15), its closest relative is *Planetella granifex*, so most probably this species has 12 flagellomeres and other characters typical of *P. granifex*.

Planetella sp. B

Material examined. SLOVAKIA: Cerová vrchovina Protected Landscape Area, Salonkáš, 11.x.2018, larva in gall on *Carex hirta*, specimen after DNA extraction, No. PLA14c, J. Ševčík leg. (coll. JSL-UOC).

Comments. Only larva of this species was found. The gall was unusually placed in the middle of the stem of *Carex hirta* (Fig. 2B). The adult specimens remain unknown. According to the position in the phylogenetic tree (Fig. 15), its closest relative is *Planetella riparia* sp. nov.

Planetella sp. C

Material examined. SLOVAKIA: Cerová vrchovina Protected Landscape Area, Steblová skala, 16.iv.–16.vi.2017, 1 ♂ without antennae (specimen in ethanol, after DNA extraction, No. PLA63), Malaise trap in a forest steppe, leg. J. Roháček & J. Ševčík leg. (coll. JSL-UOC).

Comments. This is the only specimen of this species available to us. It is partially damaged, so we prefer not to describe it in this contribution. It belongs to the group of dark brown species with the eyes separated and its closest relative is *Planetella taiwanensis* Ševčík, Hippa & Burdík, 2021, according to the phylogenetic tree in Fig. 15, or *P. fasciata*, according to K2P genetic distance (Tab. 3). Both the latter species have the eyes separated, without the eye bridge, although they nested in different clades (Fig. 15).

Planetella sp. D

Material examined. SLOVAKIA: Nitriansky kraj, Iža, Bokrošské slanisko NR, 106 m, 5.–26.v.2017, ♂ specimen after DNA extraction (No. PLA29), Malaise trap, L. Vidlička & O. Majzlan leg. (coll. JSL-UOC).

Comments. This is also the only specimen of this species available to us and it is not in a condition allowing description (the head is missing), so we prefer to wait until more specimens are collected. According to the tree in Fig. 15, it belongs to the *Planetella aestivalis* sp. nov. group (see above).

Relationships within the genus *Planetella*

Figure 15 shows relationships among the species of *Planetella* included in this study. All the *Planetella* species form a monophyletic group with relatively strong support (ufboot = 97), and with *Putoniella pruni* (Kaltenbach, 1872) as a sister group, altogether also forming a highly supported clade (ufboot = 99). Within the monophyletic genus *Planetella*, *P. arenaria* represents a sister branch to all the other species of the genus, and may thus possibly represent a separate monobasic genus or subgenus, with the oldest available name *Dyodiplosis* Rübssaamen, 1912. Already RÜBSAAMEN (1899d) in his original description of *P. arenariae* stated that this species is not a typical *Planetella* but ‘forms a transition between the genera *Hormomyia* and *Diplosis*’. In any case, infrageneric classification of *Planetella* is beyond the scope of this first study, pending more revisionary work, mainly in the Nearctic and in lesser known parts of the Palearctic Region. Some of the characters used to separate genera (or subgenera) in the past, like the existence of the eye bridge or number of flagellomeres, are irregularly distributed across the tree (Fig. 15), so they apparently evolved parallelly in different clades.

The clade containing all the other *Planetella* species is only moderately supported (ufboot = 71). The clade containing *P. granifex* and an unidentified related species (known as larvae and female only, possibly *P. tarda*) form a well-supported branch (ufboot = 100), as well as the clade containing *P. gallarum* and *P. davidi* sp. nov (ufboot = 97). The next clade is well supported (ufboot = 98) and includes the remaining 17 species. This broad clade branches into two subclades, each well-supported (ufboot = 96 and ufboot = 93, respectively). The relationships within these subclades are mostly well resolved, defining several smaller clades, including the group of 4 species with 14 binodose flagellomeres (plus 15th shorter one), forming together with *P. hlisnikovskiyi* sp. nov. a maximum supported clade (ufboot = 100). Since *P. hlisnikovskiyi* sp. nov. is one of the few species with the eyes broadly separated, as well as *P. fasciata* and *P. taiwanensis* which nested in different parts of the tree, this character appears to develop parallelly and should not be used to separate possible subgenera and genera, as proposed by EDWARDS (1938). Maximum support (ufboot = 100) is also in the clade *P. riparia* sp. nov. + *P. sp. B* in *Carex hirta* and in the clade containing *P. attilai* sp. nov., *P. submontana* and *P. aestivalis* sp. nov.

The Kimura 2-parameter (K2P) genetic distances for COI marker among the 24 species of *Planetella* are presented in Tab. 3. The interspecific differences ranged from 3% (between two cryptic species *P. aestivalis* sp. nov. and *P. sp. near aestivalis*) to 21.4% (between *Planetella gallarum* and *P. sp. near aestivalis*), with the mean interspecific distance being 13.7%.

Phylogenetic position of *Planetella* within Cecidomyiinae

The phylogenetic position of *Planetella* within the family Cecidomyiidae is shown in Fig. 15. The four species of *Planetella* included in this dataset form a monophyletic and well-supported group (ufboot = 98), as well as the clades containing also *Putoniella pruni* (ufboot = 96) and *Acodiplosis inulae* (ufboot = 97). A separate tribe, Hormomyiini, currently comprising the genus *Planetella* only (see GAGNÉ & JASCHHOF 2021), may thus well include also the genera *Putoniella* Kieffer, 1896 and *Acodiplosis* Kieffer, 1895, and constitute a well-supported monophyletic group. Both the latter genera are currently unplaced to tribe (DORCHIN et al. 2019, GAGNÉ & JASCHHOF 2021) and *Putoniella* has not yet been included in any molecular phylogenetic study of Cecidomyiidae. The concept of the tribe Hormomyiini clearly requires further study, as well as the concept of tribes in the supertribe Cecidomyiidi in general. Considering the high number of genera of Cecidomyiidi unplaced to tribe (144 genera, according to GAGNÉ & JASCHHOF 2021), not counting undescribed genera, this may be a long-term and difficult task.

The supertribe Cecidomyiidi is well-recovered in this study (Fig. 16), with maximum support (ufboot = 100), as well as the supertribe Lasipteridi (ufboot = 100). Representatives of the supertribes Brachineuridi and Stomatosematidi grouped together in a moderately supported clade (ufboot = 88), which is sister to the clade (Lasipteridi + Cecidomyiidi). The entire subfamily Cecidomyiinae is recovered as monophyletic, with maximum support (ufboot = 100).

Within Cecidomyiidi, relationships of particular genera and possible tribes remain more obscure. In concordance with DORCHIN et al. (2019), *Loewiola centaureae* Loew, 1875 appears as sister to *Cecidomyia* Meigen, 1803 with high support (ufboot = 98). Their sister relationship with *Xylodiplosis nigratarsis* (Zetterstedt, 1850) is less supported (ufboot = 78). These three genera could constitute the tribe Cecidomyiini in the strictest sense. The giant genus *Contarinia* appears as paraphyletic, with respect to the genera *Anthodiplosis* Kieffer, 1912 and *Thecodiplosis* Kieffer, 1895. The position of the former genus is surprising because genus *Anthodiplosis* is currently placed in the tribe Clinodiplosini (see DORCHIN et al. 2019, GAGNÉ & JASCHHOF 2021).

The tribe Clinodiplosini, excluding *Anthodiplosis*, is recovered with good support (ufboot = 95). The genera *Lestodiplosis* Kieffer, 1894 and *Odontodiplosis* Felt, 1908 grouped together with maximum support (ufboot = 100), representing the tribe Lestodiplosini. Three genera of

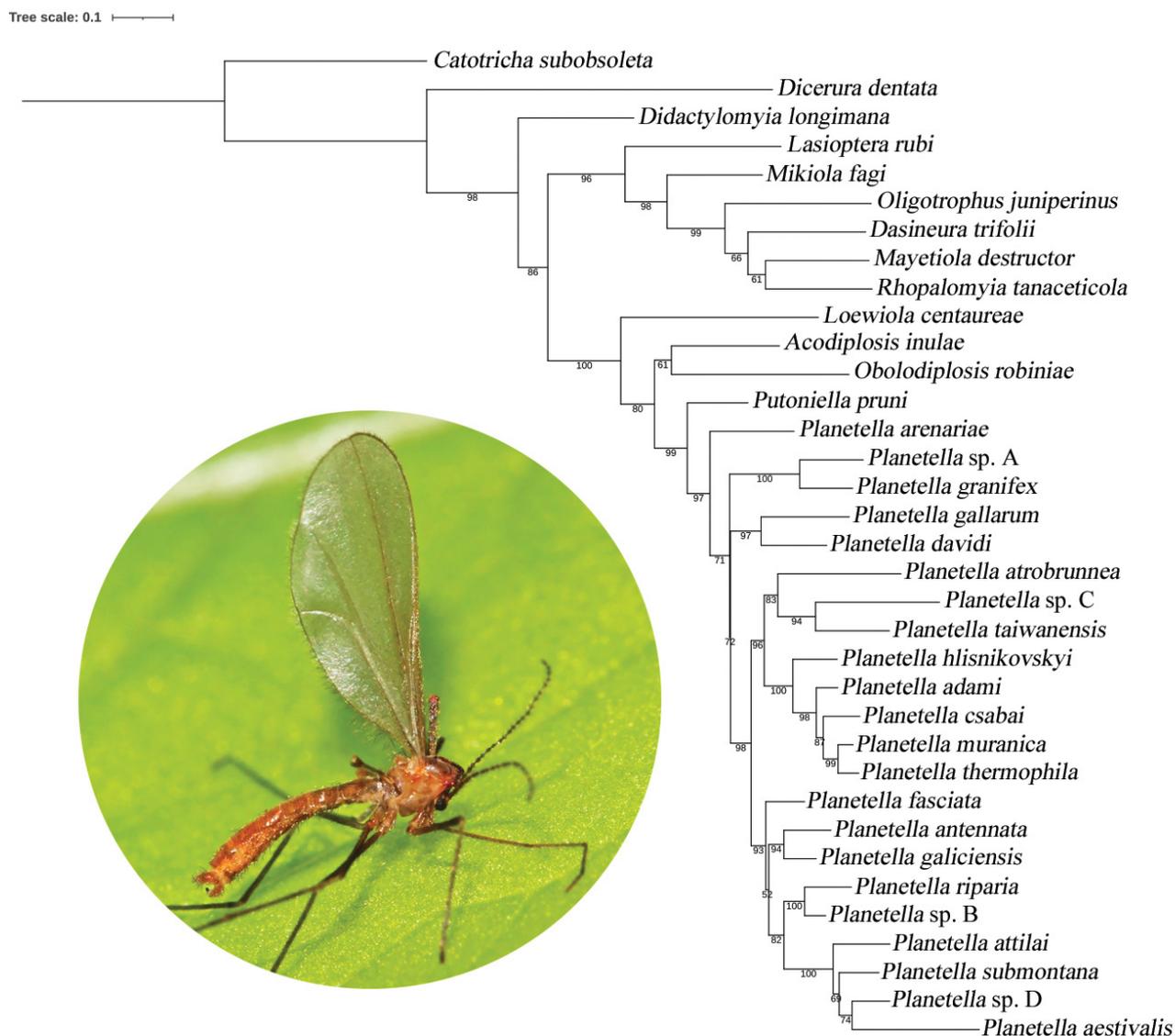


Fig. 15. Maximum likelihood hypothesis (IQtree) for relationships among the species of *Planetella* Westwood, 1840 (Diptera: Cecidomyiidae) based on DNA sequence data (28S, 16S, and COI), 1535 characters. Support numbers refer to ultrafast bootstrap values (ufboot) over 50.

Asphondyliini grouped together with moderate support (ufboot = 89) but with maximum support (ufboot = 100) for the sister relationship between *Asphondylia* Loew, 1850 and *Placochela* Rübsaamen, 1916. The mycophagous species *Camptodiplosis auriculariae* Buxton & Barnes, 1953 appears as an isolated branch but not far from the genus *Mycodiplosis* Rübsaamen, 1895. Taxonomy and phylogenetic relationships of the mycophagous genera of Cecidomyiidae are still very little studied and represent a challenge for the future. The mainly tropical tribe Lopesiini is represented in our dataset only by two genera, *Lopesia* Rübsaamen 1908 and *Obolodiplosis* Felt, 1908, and they both are nested close to *Planetella*, but as two separate branches, not a single clade.

Within Lasiopteridi, *Dasineura* Rondani, 1840 appears as a paraphyletic or polyphyletic genus, similarly to results of previous molecular studies (DORCHIN et al. 2019, SIKORA et al. 2019). Two genera of Dasineurini, *Mikiola* Kieffer, 1896 and *Janetia* Kieffer, 1896, grouped

together in a separate, well-supported clade (ufboot = 96), which is sister to the well-supported clade (ufboot = 99) containing the rest of the genera of Lasiopteridi included in this dataset, including *Herbomyia robusta* Möhn, 1955, hitherto unplaced to tribe.

In any case, the phylogenetic tree for Cecidomyiidae presented in this paper is still based on a very limited taxon sampling, as well as on a limited gene sampling, and further studies are required to elucidate complicated relationships in this speciose family of Diptera.

Conclusions

The genus *Planetella* in a broad sense represents a complex taxonomic case, with many different problems involved. These problems include the absence of the types (or types being in a poor state), very short and uninformative original descriptions (often without figures), relatively small morphological differences between species, intraspecific variation, insufficient knowledge

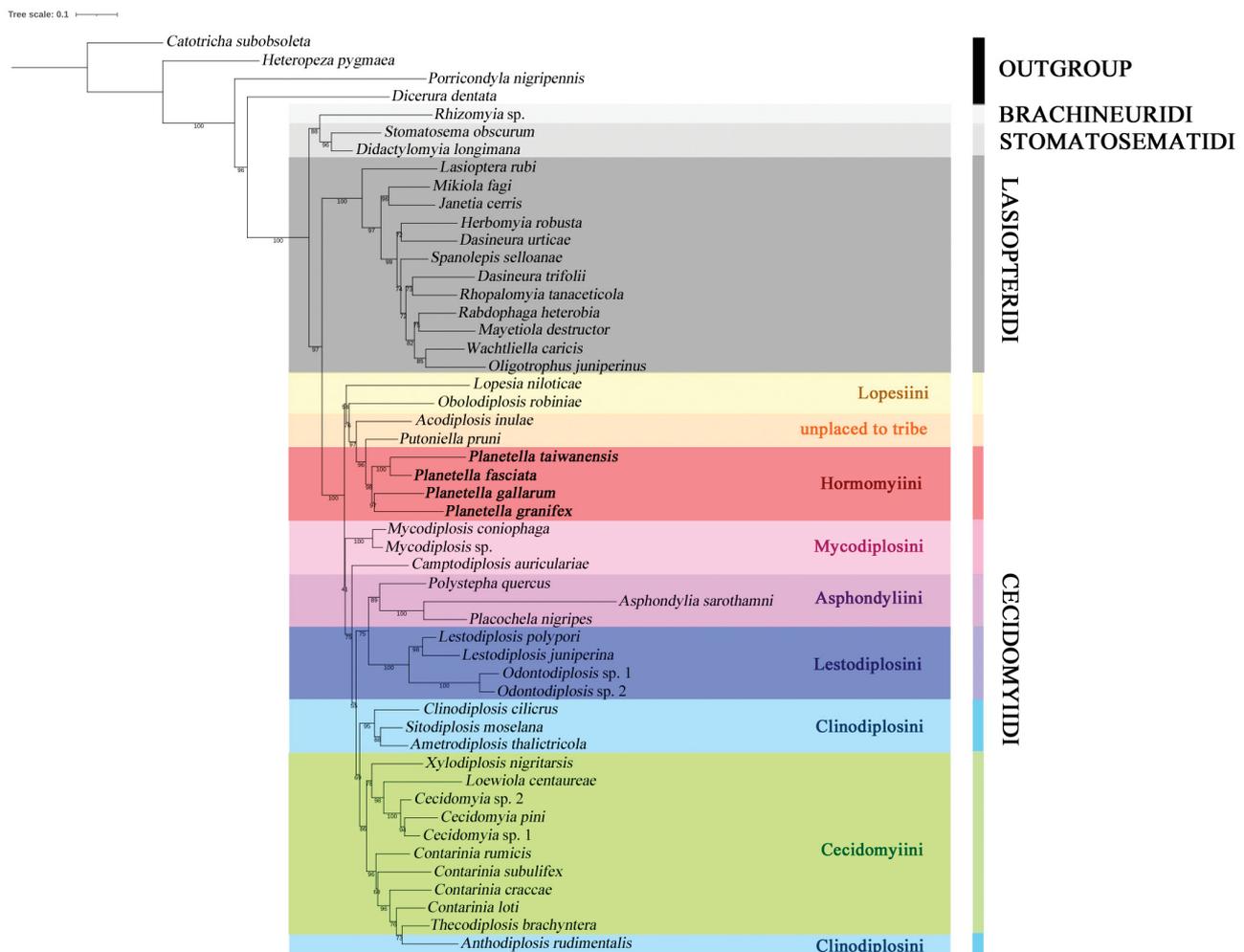


Fig. 16. Maximum likelihood hypothesis (IQtree) for relationships among the genera of Cecidomyiidae (Diptera) based on DNA sequence data (28S, 18S, 16S, and COI), 2486 characters. Support numbers refer to ultrafast bootstrap values (ufboot) over 50.

of the larval stages, females and host plants, and limited knowledge of the distribution and ecology of particular species. Additionally, most of the species treated here appear to be range restricted and several also locally rare, surviving as isolated populations in just a few localities, potentially as remnants of formerly coherent distributions. Such a fragmentary distribution may prevent gene flow and promote further speciation, but at the same time it may lead to extinction of local populations as wetlands and natural forests represent habitats vulnerable to human exploitation. Such a fragmentary distribution may also explain the relatively high degree of intraspecific variation in some morphological characters which we noted in this study.

We decided to adopt here an integrative approach, based on combination of morphological and molecular data and a DNA barcoding species concept. This approach enabled us to recognize 24 different species in the material under study, some of them known only as larva and/or female. We thus recommend following this concept also in future studies which should be based on a more comprehensive taxon sampling than was possible here.

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