

Revision of *Carexomyza* Roháček with descriptions of three new Nearctic species (Diptera: Anthomyzidae)

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Abstract. The formerly monotypic genus *Carexomyza* Roháček, 2009 (Diptera: Anthomyzidae) is revised to include one Palaearctic, viz. *C. caricis* (Roháček, 1999), and three new Nearctic species, viz. *C. lonsdalei* sp.n., *C. marshalli* sp.n. and *C. browni* sp.n., all from Canada and the northern United States of America. *Carexomyza* is re-diagnosed and its phylogenetic position within extant Anthomyzinae discussed. All species are described or diagnosed and illustrated and a hypothesis about their relationships (based both on morphological and molecular data) is presented. The biology of *Carexomyza* species is treated for the first time, with new information about habitat, host-plant association, life history and adult behaviour. The distribution of *Carexomyza* species is summarized.

Key words. Anthomyzidae, *Carexomyza*, new species, taxonomy, molecular phylogeny, biology, distribution, Holarctic.

1. Introduction

A series of taxonomic revisions of the Nearctic Anthomyzidae has appeared over a period of 16 years beginning in 2004. *Fungomyza* Roháček, 1999, *Stiphrosoma* Czerny, 1928, *Quametopia* Roháček & Barber, 2011, *Arganthomyza* Roháček, 2009, *Ischnomyia* Loew, 1863, and *Anthomyza* Fallén, 1810, have been completed (ROHÁČEK & BARBER 2004, 2005, 2011, 2013, 2016). The flies discussed here constitute one of the last genera represented in this regional fauna requiring formal reporting and revision (see ROHÁČEK & BARBER 2016).

The monotypic genus *Carexomyza* was erected by ROHÁČEK (2009) in order to transfer the European species *Paranthomyza caricis* Roháček, 1999, out of *Paranthomyza* Czerny, 1902. This step was taken after molecular evidence (ROHÁČEK et al. 2009) indicated that the original (tentative) placement of this species within *Paranthomyza*, based on morphological analysis (ROHÁČEK 1999), was no longer justified. The suggestion by ROHÁČEK (2009) that congeners of both these monotypic genera might be “discovered either in eastern and central Asia and/or in the Nearctic Region” was partially realized

about two years later when a provisional morphotype from the Nearctic was recognized as representing three species referable to *Carexomyza*. The authors’ knowledge of the presence of *Carexomyza* species in North America led them to include this genus in the new generic key to Nearctic Anthomyzidae (ROHÁČEK & BARBER 2016: 26). Most recently, ROHÁČEK et al. (2019) included two of these unnamed *Carexomyza* species in the dataset of (largely Holarctic) taxa used to study the phylogenetic relationships of Anthomyzidae using molecular methods.

As with the European *Carexomyza caricis* (ROHÁČEK 1999, 2013), known only from five localities in England, Finland and Sweden, the Nearctic species described here are all poorly represented in museum collections. Though many more specimens have been accumulated by concentrating field collections on the sweeping of *Carex* (Cyperaceae) sedges or aspirating these flies directly from the bases of these plants, the total number of collection localities still remains quite small. A largely terricolous diurnal behaviour is thought to make these

flies less accessible with sweep nets than are many other Anthomyzidae and there is some evidence presented of vespertine activity that may increase their accessibility by sweep netting in the evening.

To better clarify all aspects of this poorly known genus, the biology, distribution, morphology and taxonomy of its species are thoroughly elaborated upon here, and their phylogenetic relationships are tested using both molecular and morphological data.

2. Material and methods

2.1. Material

2.1.1. Collecting

Most Nearctic specimens studied here were obtained by KNB while sweeping graminoid communities dominated by *Carex* species. Early collections utilized an aspirator (pooter) during daytime searches until it was determined that sweeping in the evening was much more productive (see section 3.4, Biology and section 3.5, *Collections at Cochrane, Ontario*). It should be emphasized that collection of *Carexomyza* requires repeated sweeping of the same area, sometimes over an extended period of time, and is most productive after the light intensity and perhaps heat of the day moderate in the evening, at least in Ontario. A few specimens from museum collections include reference to collection by Malaise and pan traps, but these traps were not used by the authors. Specimens were either collected directly into ethanol or held alive in screened tubes if near an indoor workspace. Live specimens could then be used for rearing or be freeze-killed and/or transferred to ethanol. Specimens used for molecular work were either killed with ethyl acetate (in the field) or freeze-killed, then pinned and air-dried, or killed and maintained in 95% ethanol.

Intensive collection sites. Two sites were repeatedly sampled over several years for *Carexomyza*, primarily by repetitive sweeping:

1. The “Finn Hill” site is located within the city limits of Sault Ste. Marie, Ontario, and yielded only *C. lonsdalei* sp.n. (see section 3.4, Biology). A mixed graminoid meadow represents a significant part of this public property that is bordered on the east by a ditch-drained roadway (Black Road) and on the west by a wooded slope (see Figs. 34, 36). The sedge-dominated portion of the meadow yields to a mix with grasses or dominant grass to the north and west while scrub willow dominates further to the north. The productive area for *C. lonsdalei* was near the southern boundary of the meadow, a wet site that receives seepage flow from the hillside (to the west) and is immediately bordered to the south by even wetter soil supporting a plant community dominated by *Scirpus microcarpus* J. & C. Presl, and *Typha latifolia* L. *Carex stipata* var. *stipata* Muhl. ex Willd. (referred to from here onwards simply as *Cx. stipata*) (see Figs. 35, 36) is con-

sidered the host plant of *C. lonsdalei* at this site where the density of this plant is the highest encountered by KNB in searches for collection sites, mostly in northern Ontario.

2. The “Cochrane” site is located about 13.5 km S of Cochrane, Ontario and is the only site where all three Nearctic species of *Carexomyza* were collected (see section 3.5, *Collections at Cochrane, Ontario*). The site is a relatively small pocket supporting dominant sedges within a hydroelectric transmission right-of-way running roughly NW–SE and situated between Highway 11 and a small pond (see Figs. 1–3). The soil is saturated (or nearly so) through most, if not all, of the growing season. By far, the dominant plant species is *Carex utriculata* Boott in Hook. (see Figs. 3, 4; collections in western Canada had previously implicated *Cx. utriculata* as a host plant for both *C. marshalli* sp.n. and *C. browni* sp.n.) in the central pocket but this dominance yields to *Typha latifolia* closer to the pond while drier soils on the other margins see strong growths of grasses such as *Calamagrostis canadensis* (Michx.) P. Beauv. A broad strip of *Scirpus microcarpus* borders the primary pocket towards the road while *T. latifolia* also appears next to the road in a relatively shallow primary ditch. Though it is present toward the southeast limit of the sedge pocket, *Cx. stipata* is a very minor component of the vegetation and sweeping did not yield any *Carexomyza* (even the few *C. lonsdalei*) that could be attributed unequivocally to this plant. Various other herbs and graminoids are present. Evening temperatures for 7 July 2018 were estimated using data for station “Timmins A” (GOVERNMENT OF CANADA 2019a), a weather station about 50 km SW of the study site. Sunset was estimated for collection site coordinates using an online calculator (GOVERNMENT OF CANADA 2019b).

2.2. Methods

2.2.1. Rearing

Attempts to rear *Carexomyza* were made only for *C. lonsdalei* from the Finn Hill site (see above). Procedures were generally those previously described for other anthomyzids, particularly for *Quametopia* (ROHÁČEK & BARBER 2011), but instead using *Cx. stipata* as an oviposition substrate and as a larval food material. In summary, short sections of the sedge leaves (collected at Finn Hill and stored in a freezer) were presented on wet white sand in shallow plates in inverted, vented cup cages. Adult flies were collected at Finn Hill on 10 June and 16 June 2012 (~26♂ 34♀) and fed a mixture of ground pollen and sucrose (equal volumes) presented on the screened top of the cup cage. Cages were misted daily and maintained at 22°C, 16L:8D, 60–70% RH. Eggs were removed from the sections of sedge leaves at about 3-day intervals when fresh sedge-leaf sections were added to the cages; this continued over the oviposition period of 14–28 June 2012 (reported on reared adult specimens as ending



Figs. 1–4. Habitat of *Carexomyza* species at the site near Cochrane, Ontario: (Fig. 1, 23 June 2013; Figs. 2, 3, 18 August 2013; Fig. 4, 9 July 2012). **1, 2:** the pocket of dominant *Carex utriculata* (paler green) is situated just in front and to the left of the *Typha latifolia* in the background; **3:** view from within the sedge pocket with the band of *Scirpus microcarpus* evident beyond; **4:** *Carex utriculata* showing fruiting heads and thick build-up of dried thatch. Photos by K.N. Barber.

25 June 2012 as the last period only yielded 10 unembryonated eggs). Eggs were held on moist filter paper in 5-cm diameter covered Falcon petri plates until hatching (lingering embryonated eggs were forcibly “hatched” by rupturing the chorion then carefully applying pressure with a moist artist’s brush). First-instar larvae were presented moist sections of sedge in covered Falcon plates and checked daily when possible. Sedge sections were replaced and larvae transferred when judged necessary. By September, it became obvious that the larvae were not going to pupariate without a cold period so the following transitional and storage conditions were applied: 18.ix.2012, 10°C, 12L:12D; 5.x.2012, 4°C, 0L:24D; 3.iii.2013, 22°C, 16L:8D.

2.2.2. Specimen preparation, label data and genitalia preparation

Critical-point-drying was used to prepare specimens preserved in ethanol. Specimens were either mounted directly on pins or on card points. The presentation of label data is strictly verbatim for the primary types but standardized for all other material examined. A number of specimens each had the entire abdomen detached, placed into a vial

with 10% solution of potassium hydroxide (KOH) in water and boiled for several minutes. KOH was neutralized with glacial acetic acid (CH_3COOH) and the abdomen washed in water and transferred to glycerine. It was examined and further dissected in a drop of glycerine on a slide under a binocular microscope. After examination, all parts of the abdomen were transferred to a small plastic tube (or microvial) containing glycerine, sealed with hot forceps (or closed by stopper) and pinned below the respective specimen; this is indicated by the abbreviation “genit. prep.” in the text.

2.2.3. Drawings, photos and measurements

Larger structures (postabdomen, legs) were drawn on squared paper using a binocular microscope with an ocular screen. Wings were photographed using a compound microscope with a digital camera while images of adult habitus and female head and thorax were obtained using a binocular microscope. Details of the male and female terminalia were drawn by means of Abbe’s drawing apparatus on a compound microscope at larger magnification (130–500×). Five main characteristics of each species were measured: body length (measured from an-

Table 1. List of analysed species of the genus *Carexomyza* with localities (countries) and GenBank sequence accession numbers.

Species	Locality	12S	16S	COIa	COIb	COII	CytB	28S	ITS2
<i>C. lonsdalei</i> sp.n.	Canada (ON)	KJ418449	KJ418471	KJ418563	KJ418609	KJ418637	KJ418656	KJ418515	KJ418696
<i>C. marshalli</i> sp.n.	Canada (ON)	MN238852	MN238853	MN226408	MN218813	MN226409	MN228503	MN238854	MN238855
<i>C. browni</i> sp.n.	Canada (BC)	KJ418450	KJ418472	KJ418564	KJ418610	KJ418638	KJ418657	KJ418516	KJ418697
<i>C. caricis</i> (Roháček, 1999)	UK (England)	EU268521	EU268547	KJ418553	KJ418598	n/a	n/a	KJ418499	KJ418687

terior margin of head to end of cercus, thus excluding the antenna), wing length (from wing base to wing tip), wing width (maximum width), index $Cs_3 : Cs_4$ (= ratio of length of 3rd costal sector : length of 4th costal sector) and index $r-m/dm-cu : dm-cu$ (= ratio of length of section between $r-m$ and $dm-cu$ on cell dm : length of $dm-cu$). Ten males and 10 females (3 smallest, 4 medium and 3 largest examined specimens of each sex) of each species were measured.

2.2.4. Molecular analyses

Taxon sampling. The analysed dataset contains 65 species (62 Anthomyzidae + 3 outgroup taxa). All taxa for which specimens are available for DNA extraction are included in the molecular analysis. Except for one addition (*Carexomyza marshalli* sp.n.), they are listed in full (with names, authors and source localities of analysed specimens) in Roháček et al. (2019, table 1). Because two of the three *Carexomyza* species were treated as unnamed new taxa in the latter paper, all four *Carexomyza* species examined in this study are listed here with complete data (Table 1). We used one specimen per species except for an unnamed species of the *Mumetopia nigrimana* group, of which we processed two specimens. The outgroup included *Geomyza tripunctata* Fallén, 1823 and *Opomyza florum* (Fabricius, 1794) (Opomyzidae, the sister family of the Anthomyzidae, cf. Roháček 1998, 2006), and *Clusia flava* (Meigen, 1830) (Clusiidae, the most generalized family of the Opomyzoidea, cf. McALPINE 1989) was used to root the phylogenetic trees. Of significance in the present study, *Chamaebosca* Speiser, 1903, known from two type specimens, of which only the holotype of *C. microptera* Speiser, 1903 is available for study (see Roháček 1998), is not yet represented in the molecular dataset for lack of material. This leaves the *Chamaebosca* group of genera sensu Roháček & Barber (2009) represented here by only the *Mumetopia–Stiphrosoma* clade.

DNA extraction, PCR and sequencing. The adult flies used for analysis were air-dried or ethanol-preserved. The molecular procedures and protocols are fully documented in Roháček et al. (2019). GenBank accession numbers for the sequences are listed in Roháček et al. (2019: table 1), so only those of the *Carexomyza* species are listed here (Table 1). Remnants of the analysed specimens are deposited at SMOG except for that of *C. caricis* where the entire specimen was crushed for DNA extraction.

Alignment and phylogenetic analyses. Alignment protocols are fully outlined in Roháček et al. (2019). The final dataset consisted of 66 specimens as terminal “taxa” (65

species) and 4580 characters: 12S–349 bp, 16S–361 bp, 28S–615 bp, COI–1248 bp, COII–633 bp, CytB–646 bp, ITS2–728 bp. Both Bayesian inference (BI) and maximum likelihood (RAxML) analyses were performed (see details in Roháček et al. 2019). The node support values are given with the posterior probability (PP) below the nodes (if value > 0.5) and the bootstrap value (BV) appearing above the nodes in the resulting tree depicted in Fig. 91. For the Bayesian analysis the standard deviation of split frequencies was in all cases < 0.002. The mean log-likelihood value for the best-fit BI tree was –42146.66, for the RAxML tree it was –43664.896995.

2.3. Morphological terminology and abbreviations

The adult morphological terminology follows that used by Roháček & Barber (2016) except where “orbit” is replaced here with “orbital plate”. This includes the terms proposed in ZATWERNICKI (1996) for structures of the male genitalia. Some terminological synonyms of the latter (GRIFFITHS 1972; McALPINE 1981; CUMMING & WOOD 2009; 2017) appear below following an equal sign within brackets. Morphological terms of the male postabdomen and genitalia are displayed in Figs. 16–26, 77–82, 84, of the female postabdomen and genitalia in Figs. 27–33, 86–90. **Abbreviations.** **A₁** – anal vein; **ac** – acrostichal (seta); **afa** – aedeagal part of folding apparatus; **ag** – accessory gland; **bm** – basal membrane; **C** – costa; **ce** – cercus; **cp** – caudal process of transandrium; **cs** – connecting sclerite; **Cs₂**, **Cs₃**, **Cs₄** – 2nd, 3rd, 4th costal sector; **CuA₁** – cubitus; **dc** – dorsocentral (seta); **dm** – discal medial cell; **dm-cu** – discal medial-cubital (= posterior, tp) cross-vein; **ea** – ejacapodeme (= ejaculatory apodeme); **ep** – epandrium (= perianthrium); **f** – filum of distiphallus; **f₁**, **f₂**, **f₃** – fore, mid, hind femur; **fc** – fulcrum of phallapodeme; **gs** – gonostylus (= surstylus); **hu** – humeral (= postpronotal) (seta); **hy** – hypandrium; **is** – internal sclerite(s); **M** – media; **ma** – medandrium (= intraperianthrial sclerite, subepandrial sclerite); **npl** – notopleural (seta); **oc** – ocellar (seta); **ors** – orbital (= fronto-orbital) (seta); **pa** – postalar (seta); **pg** – postgonite (= paramere); **pha** – phallapodeme (= aedeagal apodeme); **pp** – phallophore (= basiphallus); **ppl** – propleural (= proepisternal) (seta); **prg** – pregonite; **prs** – presutural (seta); **pvt** – postvertical (seta); **R₁** – 1st branch of radius; **R₂₊₃** – 2nd branch of radius; **R₄₊₅** – 3rd branch of radius; **r-m** – radial-medial (= anterior, ta) cross-vein; **s** – saccus of distiphallus; **S1–S8**, **S10** – abdominal sterna; **sa** – su-

praalar (seta); **sc** – scutellar (seta); **Sc** – subcosta; **sp** – spermatheca; **stpl** – sternopleural (= katepisternal) (seta); **T1–T8, T10** – abdominal terga; **t₁, t₂, t₃** – fore, mid, hind tibia; **ta** – transandrium (= posterior hypandrial bridge); **vi** – vibrissa; **vr** – ventral receptacle; **vte** – outer vertical (seta); **vti** – inner vertical (seta).

2.4. Depository Abbreviations

AMNH – American Museum of Natural History, Division of Invertebrate Zoology, New York, NY, U.S.A.; **BDUC** – Museum of Zoology, Invertebrate Section, Department of Biological Sciences, University of Calgary, Calgary, AB, Canada; **BIOUG** – Biodiversity Institute of Ontario, University of Guelph, Guelph, ON, Canada; **BMNH** – The Natural History Museum (formerly British Museum of Natural History), London, England, U.K.; **CASC** – California Academy of Sciences, Department of Entomology, San Francisco, CA, U.S.A.; **CNCI** – Canadian National Collection of Insects, Arachnids & Nematodes, Ottawa, ON, Canada; **DEBU** – University of Guelph Insect Collection, School of Environmental Sciences, University of Guelph, Guelph, ON, Canada; **INHS** – Illinois Natural History Survey, Insect Collection, Champagne, IL, U.S.A.; **JKH** – Collection of J. Kahanpää, Helsinki, Finland; **LACM** – Natural History Museum of Los Angeles County, Los Angeles, CA, U.S.A.; **LEMQ** – Lyman Entomological Museum, McGill University, Macdonald Campus, Ste-Anne-de-Bellevue, QC, Canada; **MTEC** – Montana Entomology Collection, Montana State University, Bozeman, MT, U.S.A.; **MZLU** – Museum of Zoology, Lund University, Lund, Sweden; **NBMB** – New Brunswick Museum, St. John, NB, Canada; **NHRS** – Naturhistoriska Riksmuseet, Stockholm, Sweden; **OXUM** – Hope Entomological Collections, University Museum of Natural History, Oxford, England, U.K.; **PCM** – Collection of P.J. Chandler, Melksham, England, U.K.; **RBCM** – Royal British Columbia Museum, Natural History Section, Victoria, BC, Canada; **RSME** – National Museum of Scotland, Edinburgh, Scotland, U.K.; **SEMC** – Snow Entomological Museum, University of Kansas, Lawrence, KS, U.S.A.; **SMOC** – Silesian Museum, Opava, Czech Republic; **UAM** – University of Alaska Museum, Department of Entomology, Fairbanks, AK, U.S.A.; **USNM** – National Museum of Natural History, Smithsonian Institution, Department of Entomology, Washington, DC, U.S.A.; **ZSMC** – Zoologische Staatssammlung München, München, Germany.

3. Results and discussion

3.1. Taxonomy

The genus is re-diagnosed following a set of numbered characters used by ROHÁČEK (2006, 2009) and ROHÁČEK & BARBER (2016).

3.2. *Carexomyza* Roháček, 2009

Carexomyza Roháček, 2009: 14 [key to Palaearctic genera], 75–76 [description], 106–108 [relationships]; ROHÁČEK & TÓTHOVÁ 2014: 169, 170, 173 [molecular phylogeny]; ROHÁČEK & BARBER 2016: 28 [key to Nearctic genera].

Type species: *Paranthomyza caricis* Roháček, 1999: 385 (original designation).

Re-diagnosis. (1) **Head** (Figs. 5–11): Slightly higher than long or as long as high. (2) Eye large, rather narrowly subovoid to reniform, covering most of head in profile, with longest diameter oblique. (3) Frons moderately broad despite large eyes; frontal triangle relatively narrow and reaching anterior half to two-fifths of frons, often appearing shiny despite some microtomentum. (4) Orbital plate well-delimited, anterior part silvery-grey or silvery-white microtomentose up to posterior ors, posterior part with microtomentum often matching that of adjacent stripe. (5) Stripe between posterior part of orbital plate and frontal triangle silvery-grey to silvery-blue microtomentose. (6) Frontal lunule reduced but distinct. (7) Antenna geniculate between pedicel and 1st flagellomere, the latter strongly compressed laterally with short white ciliation anteriorly. (8) Arista sparsely short ciliate. (9) Palpus yellow, slender, with 1 longer subapical seta and a few ventral setulae. Cephalic chaetotaxy: (10) pvt short but crossed; (11) vte, vti and oc long; (12) 2 long ors and 1–2 microsetulae in front of anterior ors; (13) a single row of short postocular setulae; (14) 1 long vi and 1 slightly shorter subvibrissa; (15) peristomal setulae small and few in number. (16) **Thorax** (Figs. 5–11): Slightly narrower than head, blackish brown and more or less shiny, despite some microtomentum. Thoracic chaetotaxy: (17) 1 hu, 2 npl (anterior longer); (18) 1 small but distinct prs; (19) 1 short sa, 1 longer pa; (20) 3 postsutural dc becoming shorter anteriorly; (21) ac microsetae in 2 rows (often incomplete) ending at most in front of posterior dc; (22) 2 sc (apical long, laterobasal short); (23) 1 small upcurved ppl; (24) 2 almost equally long stpl. (25) Legs, except for apical tarsomeres, unicolourous, yellow (Fig. 6); (26) f₁ with ctenidial spine; (27) t₂ with distinct but short ventroapical seta; (28) male f₃ with posteroventral row of short thickened setae in distal half (Figs. 6, 83). (29) **Wing**: Narrow and relatively short (Figs. 12–15); (30) wing membrane unicolourous. (31) C with inconspicuous thicker setulae among fine hairs on Cs₂; (32) R₂₊₃ long, running parallel to C, ending farther from wing apex than does M; (33) R₄₊₅ almost straight; (34) cell dm of medium length, extending to or slightly beyond midlength of wing; cross-vein r-m situated near middle or somewhat in front of middle of cell dm and straight to more or less oblique. (35) CuA₁ not reaching wing margin, A₁ ending far from it. (36) Alula relatively small and narrow. **Male abdomen**: (37) T1 distinctly separated from T2, no fusion; (38) T2–T5 large, broad and subequal in length. (39) S1–S5 well-sclerotized but much narrower and somewhat paler than associated terga. **Male postabdomen** (Fig. 16): (40) T6



Figs. 5–8. Habitus of *Carexomyza* species: **5:** *C. lonsdalei* sp.n. (male holotype, body length 1.8 mm); **6:** *C. marshalli* sp.n. (male holotype, body length 1.9 mm); **7:** *C. caricis* (Roháček, 1999) (female, England, body length 2.3 mm); **8:** *C. browni* sp.n. (male holotype, body length 1.8 mm). Photos by M. Deml (7, adapted from Roháček 2009: fig. 173) and K.N. Barber (others).

short, transverse, distinctly sclerotized but medially unpigmented (seemingly divided into two plates). (41) S6 and S7 strongly asymmetrical, partly fused and situated laterally, each with a few small setae. (42) S8 medium-sized, less asymmetrical, more setose and situated dorsally. **Male genitalia:** (43) Epandrium relatively broad

and more or less straight anterodorsally (Figs. 38, 77), with sparse setae subequal or 2 pairs somewhat longer. (44) Medandrium relatively small, slightly wider than anal fissure ventrally; (45) cercus relatively large (Fig. 39), simple in shape. (46) Gonostylus lobate (Fig. 60) to elongately tapering to subacute apex (Fig. 20), sparsely

setose on inner side, micropubescent on outer side. (47) Hypandrium symmetrical (Fig. 80), without dorsally projecting flat lobes anteriorly; (48) transandrium with peculiar, ventrally expanded caudal process (Figs. 21, 22) incorporating sclerotized medial part of basal membrane including spinose armature and ventrally terminated by a pair of distinctive flat sclerites. (49) Pregonite firmly fused to hypandrium, posteriorly dilated (Figs. 21, 43), sometimes with blunt posteroventral process (Figs. 64, 84). (50) Postgonite (attached to a flat basal sclerite, see Fig. 24) simple, relatively long, slender (Fig. 21), with narrow dark-pigmented anterior part carrying 1 anterior seta. (51) Aedeagal part of folding apparatus densely covered by rounded flat (Fig. 26) to tooth-like (Fig. 84) excrescences. (52) Connecting sclerite (Fig. 26) long, slender, partly pilose, spinulose or with fine grain-like tubercles. (53) Basal membrane medially sclerotized (Fig. 22), spinose and fused with caudal process of transandrium, only laterally membranous (Fig. 21). (54) Phallopodeme with short symmetrically forked base (Fig. 23). Aedeagus with (55) short bipartite phallopore (with posteroventral part fused ventrally with basal part of saccus, Figs. 26, 82) and (56) large distiphallus composed of voluminous membranous saccus and slender sclerotized filum. (57) Saccus (Figs. 26, 84) with pair of internal sinuate sclerites, ventrally protruding tooth in middle and numerous pale spines on surface of distal part; (58) filum (Figs. 26, 84) formed by 2 long, dark, band-like sclerites fused basally and apically, with simple lanceolate apex (Fig. 25). (59) Ejacapodeme distinct (Figs. 26, 82), with well-developed digitiform projection. **Female abdomen:** (60) Subshiny (more laterally), with broad transverse terga (T2–T6) and much narrower sterna (S2–S5), all with short setae. (61) **Female postabdomen** (Figs. 27–29, 87–89): Relatively broad and short, telescopically retractable from 7th segment, with both terga and sterna unusually strongly sclerotized and dark. (62) T6 and S6 relatively large. (63) T7 and S7 separate, both dark-pigmented, S7 relatively large and long. (64) T8 plate-shaped, relatively large, broad posteriorly and more or less tapered anteriorly; (65) S8 relatively short, medially longitudinally divided but not invaginated into 8th segment. **Female genitalia:** (66) Female genital chamber (uterus) with anterior part strongly curved dorsally (Figs. 51, 70, 86). (67) Internal sclerites of female genital chamber (Figs. 32, 33, 90) well-developed, consisting of 2 pairs of sclerites (anterior and posterior) and a ventral annular sclerite; (68) annular sclerite elongate, situated under anterior pair of internal sclerites (sometimes posteriorly fused with them). (69) Ventral receptacle (Figs. 30, 86, 90) short, having small, slightly sclerotized and distally rounded cup-like tip. (70) Remnants of accessory gland (Figs. 33, 90) small, of uncertain form, on variously slender to terminally dilated ducts. (71) Spermathecae (1+1) subsphaerical, short pyriform to lemon-shaped (Figs. 31, 49, 71), with dark cervix and carrying dark blunt surface spinulae terminally and basally; (72) spermathecal ducts relatively short (Figs. 70, 90). (73) T10 (Figs. 28, 66, 67) small, short and transverse, dark, with

1 pair of dorsal setae; (74) S10 simple (Figs. 27, 29, 89), pale-pigmented, longer and wider than T10, with reduced micropubescent. (75) Cercus relatively short and broad (Figs. 27, 28), with comparatively sparse and fine setae.

Discussion. The genus *Carexomyza* was established by ROHÁČEK (2009) for *Paranthomyza caricis* Roháček, 1999, which had formerly been tentatively placed in the genus *Paranthomyza* Czerny, 1902 by ROHÁČEK (1999). Transfer of this species to a separate genus was justified not only by great dissimilarities in its postabdominal structures compared to those of *Paranthomyza nitida* (Meigen, 1838), the type species and the only other member of *Paranthomyza* (as shown by ROHÁČEK 2009), but also by subsequent phylogenetic hypotheses based on molecular data analyses of European and/or Holarctic Anthomyzidae (ROHÁČEK et al. 2009, 2019; ROHÁČEK & TÓTHOVÁ 2014).

With regards to other extant genera of the subfamily Anthomyzinae, and those of the *Chamaebosca* group of genera in particular (as defined by ROHÁČEK & BARBER 2009, and including the *Mumetopia*–*Stiphrosoma* clade that is now considered the sister group of *Carexomyza*, see section 3.8, Phylogenetic relationships), the genus *Carexomyza* seems to be largely characterized by plesiomorphic features while its true autapomorphies are rather scarce. These may include (5) frons with distinct silvery-grey to silvery-blue microtomentose stripe between posterior part of orbital plate and frontal triangle; (21) ac microsetae reduced to 2 (often incomplete) rows; (43) epandrium broad and anterodorsally straight (as in *Stiphrosoma* species); (48) transandrium with large caudal process incorporating medial sclerotized part of basal membrane and terminated by a pair of peculiar ventral sclerites (U); (55) phallopore short, bipartite, with posteroventral part fused ventrally with basal part of saccus; (57) saccus with ventrally protruding sclerotized tooth in middle (U); (64) female T8 broad posteriorly and more or less tapered anteriorly; (65) female S8 short, medially longitudinally divided but not invaginated into 8th segment; (66) female genital chamber (uterus) with anterior part strongly curved dorsally (U); (67) internal sclerites of female genital chamber well-developed, complex, consisting of 2 pairs of sclerites (anterior and posterior) and by ventral annular sclerite; (68) annular sclerite elongate, situated under anterior pair of internal sclerites (sometimes posteriorly fused with them); (69) ventral receptacle short, having small, slightly sclerotized and distally rounded cup-like tip. Some of these apomorphies are shared with genera of the *Chamaebosca* group (*Mumetopia*, *Stiphrosoma*, etc.), e.g. 43, 55, 64, 67, 69 but those marked above by “(U)” are considered unique within the whole family (extant taxa). The distinctively silvery-grey to silvery-blue microtomentose stripe between the posterior part of the orbital plate and the frontal triangle (character 5) is not unique to *Carexomyza* because it seems to have evolved in parallel in the unrelated *Arganthomyza* Roháček, 2009 and the *Anthomyza macra* group (see ROHÁČEK & BARBER 2016). Additional diag-

nostic features of *Carexomyza* can also be 37, 40, 52, the construction and armature of the saccus, spermathecae with distinct dark cervix and short cercus, but the polarity of these characters is unknown and/or similar structures/features can also be found (as homoplasies) in some other distantly related genera.

Species included. *Carexomyza lonsdalei* sp.n., *C. marshalli* sp.n., *C. browni* sp.n. (all Nearctic, described below) and *C. caricis* (Roháček, 1999) (Palearctic).

General biology and distributional limits. A particular behaviour of adults, at least for the Nearctic species, is their apparent movement from low in the thatch and duff layers during the day to the more aerial portions of the sedges as the light and heat moderate during the evening (see section 3.4, Biology and especially section 3.5, *Collections at Cochrane, Ontario*). Such terricolous and vespertine behaviours may limit their accessibility by sweep netting during the day and may thus account for the low numbers of specimens and locality records in museum collections. This may well be an adaptive behaviour that is more strongly developed at lower-latitude localities in these flies that may exhibit a lower heat tolerance than do many other anthomyzids. But see the discussion below (sections 3.5 and 3.6, Biology) about the possible limits on the expression of such behaviour.

An obvious common thread in the known botanical associates of *Carexomyza* spp. is their association with *Carex* sedges. Most of this evidence is observational and indirect but includes increasing refinement or restriction of sweep sampling to relatively homogeneous stands. Circumstances surrounding the repeated success of finding these flies in association with *Carex* are compelling for all four species.

Carex paniculata L. seems to be the preferred host plant of *C. caricis* as most of the known specimens (including types) have been collected in this sedge, including those from suction sampling in England (ROHÁČEK 1999, 2006, 2009). Because *Cx. paniculata* is a widespread plant in Europe, it is likely that *C. caricis* is more widespread within the range of *Cx. paniculata* although no records are known south of those from England. However, some records from northern Europe (where *Cx. paniculata* was absent, cf. LANSDOWN 2014; ROHÁČEK 2013) indicate that *C. caricis* can also live in other sedge species, particularly at higher latitudes. Hitherto, we do not have any information about the vespertine and/or nocturnal activity of adults of *C. caricis* but this behaviour can also be expected for this Palearctic species.

For the Nearctic species, the strongest plant associations are with two species of *Carex*. These are *Cx. utriculata* for at least *C. marshalli* and *C. browni*, and *Cx. stipata* for *C. lonsdalei*. A third species, *Cx. pellita* Muhl. ex Willd., may be implicated for *C. lonsdalei*, but is based on a single collection of three females. Single specimens of *C. marshalli* were taken from *Cx. aquatilis* var. *aquatilis* Wahlenb., and from *Cx. stipata*, but *Cx. utriculata* was abundant nearby in both sites. Only for *C.*

lonsdalei do we have a more substantial demonstration that the larvae of this species can mature to adult when presented exclusively with leaf tissue of *Cx. stipata* (see section 3.4, Biology), but larvae have not yet been collected in the field.

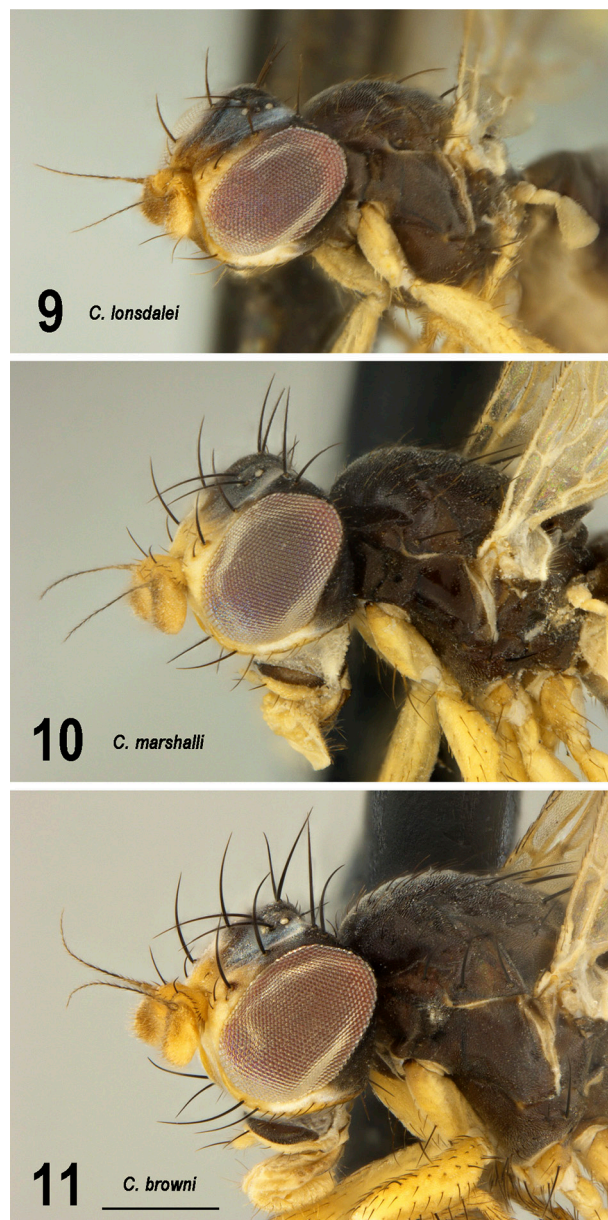
It must be noted here that KNB has made several references to “fen” habitat on specimen labels (sites in Alberta, Ontario, Utah). However, all these sites are not true fens and are better described as sedge meadows (or more generically as graminoid wetlands) as part of the marsh wetland class delineated by the NATIONAL WETLANDS WORKING GROUP (1997). This leaves only a single reference to a fen in Churchill, Manitoba for a single specimen of *C. marshalli* besides the type locality for *C. caricis* as fen habitat. Additionally, emergent stands of *Carex*, such as *Cx. utriculata*, do not support populations of *Carexomyza* although seasonal flooding is possible and may even be necessary.

All four species of *Carex* are extremely widespread in North America with *Cx. utriculata* perhaps having a higher upper latitude limit (BALL et al. 2002). None of these host plants would appear to restrict the distributions for Nearctic *Carexomyza* spp. longitudinally. All three species of *Carexomyza* occur in British Columbia and Ontario, with *C. lonsdalei* recorded east as far as southwestern Québec and both *C. browni* and *C. marshalli* from northwestern New Brunswick, the latter two species being essentially transcontinental. Latitudinal limits may be constrained by the availability of cooler, or at least moderated, microclimates in the thatch and duff layers.

3.3. Identification key to world species of *Carexomyza*

- | | |
|---|---|
| 1 Male | 2 |
| 1' Female | 5 |
| 2 Head bristling generally weaker (Figs. 5, 6; see also lead 6, cf. Figs. 9, 10); S5 with pigmentation deeply emarginated posteriorly (Figs. 17, 45); gonostylus elongate, tapered to narrow apex (Figs. 20, 40); pregonite posteriorly dilated but lacking distinct, blunt posteroventral process (Figs. 21, 43) | |
| 2' Head bristling generally stronger (Fig. 8; see also lead 6', cf. Figs. 7, 11); S5 with pigmentation not emarginated posteriorly; gonostylus lobately spoon-shaped, parallel-sided and blunt-tipped (Figs. 60, 78); pregonite with large, blunt posteroventral process (Figs. 64, 84) | 4 |
| 3 Base colour of stripe between posterior part of orbital plate and frontal triangle typically brown from vertex usually to level of posterior ors, rarely contrasting with ocellar triangle and external margin of orbital plate; oc not reaching to level of anterior ors; vibrissa usually yellow to light brown, rarely black, subvibrissa yellow to light brown but never black; mesopleuron sparsely microtomentose but lacking a dorsal bare area (cf. Fig. 9); caudal process of transandrium | |

- longer (Fig. 22); saccus of distiphallus ventrally with acutely projecting tooth in middle (Fig. 26) [North America] *C. lonsdalei* sp.n.
- 3' Base colour of stripe between posterior part of orbital plate and frontal triangle often entirely yellow or becoming brown posteriorly, often contrasting with darkened ocellar triangle and external margin of orbital plate; oc reaching to or in front of level of anterior ors; vibrissa usually black, rarely brown, never yellow, subvibrissa black or brown, never yellow; mesopleuron very sparsely microtomentose and usually bare dorsally (cf. Fig. 10); caudal process of transandrium shorter (Fig. 41); saccus of distiphallus ventrally with blunt tooth in middle (Fig. 44) [North America] *C. marshalli* sp.n.
- 4 Eye subovoid, with longest diameter about 1.4 times shortest diameter (Fig. 8); epandrium narrower in caudal view, about 1.5 times height (Fig. 58); gonostylus relatively shorter (about 0.70 times epandrial height), with larger micropubescent area covering most of its convex outer side (Fig. 60); pregonite with blunt posteroventral process simple (Fig. 64) [North America] *C. browni* sp.n.
- 4' Eye suboval to reniform, more elongate, with longest diameter at least 1.6 times shortest diameter (cf. Fig. 7); epandrium distinctly wider in caudal view, about 1.8 times height (Fig. 77); gonostylus relatively longer (about 0.75 times epandrial height) and with micropubescent part on outer side reduced (Fig. 78); pregonite with blunt posteroventral process armed with distinct posterobasal rectangular tooth (Fig. 84) [Northwestern Europe] ... *C. caricis* (Roháček, 1999)
- 5 Frons broadly and distinctly darkened brown or paler brown to level of anterior ors or even to anterior margin at least laterally, orbital plate also at least partly pale brown to dark brown anterior to the posterior ors (Fig. 9); face darkened at least medially, inner side of 1st flagellomere entirely darkened or fading near ventral margin (Fig. 9); oc not reaching to level of anterior ors; cerci entirely dark (Fig. 28); anterior pair of internal sclerites (embracing ring sclerite) distant from posterior pair of internal sclerites (Figs. 32, 33); S6 narrower and paler than S7 (Fig. 29); T8 short subtriangular (Fig. 28) [North America] *C. lonsdalei* sp.n.
- 5' Frons seldom distinctly darkened so far anteriorly, orbital plate yellow anterior to the posterior ors (Figs. 10, 11) except sometimes darkened around bases of ors (Fig. 11); face almost always yellow, inner side of 1st flagellomere more narrowly darkened (sometimes obscurely) on no more than anterodorsal half (Figs. 10, 11); oc reaching to or in front of level of anterior ors; cerci pale (Fig. 88) or with only basal third slightly darkened (Fig. 47); both pairs of internal sclerites close together (Figs. 50, 51, 69, 70, 86, 90); S6 wider and almost as dark as S7 (Figs. 48, 68, 89); T8 longer, subtrapezoidal (Figs. 47, 67) or with only triangular pigmentation longer (Fig. 88) 6



Figs. 9–11. Head and thorax of topotypical paratype females of Nearctic *Carexomyza* species. 9: *C. lonsdalei* sp.n.; 10: *C. marshalli* sp.n.; 11: *C. browni* sp.n. — **Scale bar:** 0.3 mm. Photos by K.N. Barber.

- 6 Head bristling generally weaker (Fig. 10), e.g. subvibrissa of similar length and strength to that of seta on pedicel; inner side of 1st flagellomere narrowly darkened anterodorsally (Fig. 10) or with faint darkening on anterodorsal half more obscure, rarely more intensely darkened; mesopleuron very sparsely microtomentose and usually bare dorsally, shiny, contrasting with more densely microtomentose propleuron (when viewed in same plane, Fig. 10); T10 with anterior corners rounded (Fig. 47); genital chamber with posterior pair of sclerites large (Figs. 50, 51) [North America] *C. marshalli* sp.n.
- 6' Head bristling generally stronger (Figs. 7, 11), e.g. subvibrissa longer and stronger than seta on pedicel; inner side of 1st flagellomere clearly darkened on an-

terodorsal half (Fig. 11); mesopleuron more densely microtomentose, similar to density on propleuron (Fig. 11); T10 with anterior corners acutely projecting (Fig. 88) to curved laterally (Figs. 66, 67); genital chamber with posterior pair of sclerites small (Figs. 69, 70, 86, 90) 7

- 7 Eye subovoid, with longest diameter about 1.4 times shortest diameter (Fig. 11); outer side of 1st flagellomere narrowly pale brown anterodorsally (Fig. 11; appears more extensively darkened in some air-dried specimens); S7 about as long as broad, slightly tapered posteriorly, with all corners rounded (Fig. 68); genital chamber with annular sclerite separate, lying below anterior pair of sclerites (Figs. 69, 70); T10 with anterior corners projecting and curved laterally (Figs. 66, 67) [North America] *C. browni* sp.n.
- 7' Eye suboval to reniform, more elongate, with longest diameter at least 1.6 times shortest diameter (Fig. 7); 1st flagellomere darker, anterodorsal third to half of outer side brown; S7 narrower, distinctly longer than broad, tapered and rounded posteriorly (Fig. 89); genital chamber with annular sclerite modified, partly fused posteriorly with adjacent paired sclerites, with anterior part bent ventrally (Figs. 86, 90); T10 with anterior corners acute (Fig. 88) [Northwestern Europe] *C. caricis* (Roháček, 1999)

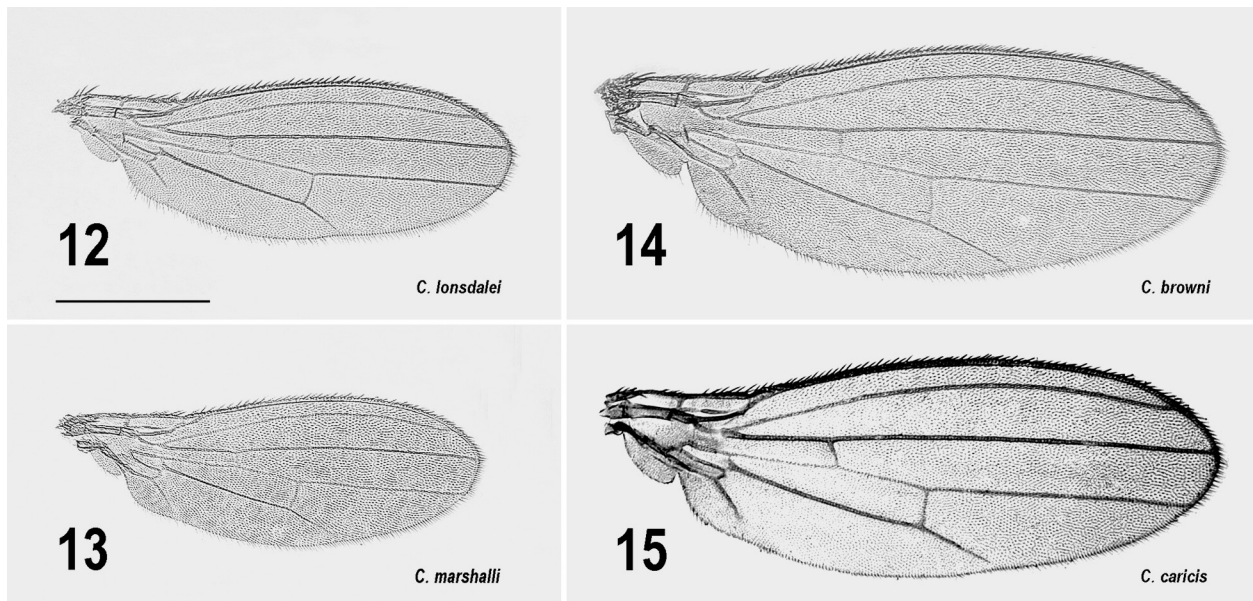
3.4. *Carexomyza lonsdalei* sp.n.

(Figs. 5, 9, 12, 16–33)

Carexomyza sp.n. 1: ROHÁČEK et al. 2019: 753 (fig. 2), 755 (fig. 4) [molecular phylogeny, trees only].

Description. Male (Fig. 5). Total body length 1.51–2.05 mm; general colour blackish brown, only anterior half of head and all legs yellow; thorax (more) and abdomen (less) relatively shiny despite sparse grey to greyish-brown microtomentum. **Head:** About as long as high and slightly wider than thorax in dorsal view; occiput slightly concave dorsally. Frons moderately broad, slightly tapering anteriorly; its anterior part (about two-fifths) yellow, remainder of frons blackish brown (except stripe between posterior part of orbital plate and frontal triangle rarely pale brown). Orbital plate pale yellow and silvery-white microtomentose up to posterior ors, dark brown and silvery-blue microtomentose in posterior part (up to vti) and internally confluent with similarly microtomentose stripe between posterior part of orbital plate and frontal triangle (in frontal view, often appearing shinier on dark part of orbital plate despite microtomentum). Frontal lunule reduced, very short, yellow. Frontal triangle relatively narrow, reaching to anterior two-fifths of frons, blackish brown and sometimes appearing somewhat shinier than dull remainder of frons despite greyish microtomentum. Ocellar triangle concolourous with frontal triangle, often appearing shinier (as in dark part of orbital plate), only slightly protruding. Ocelli small and situated

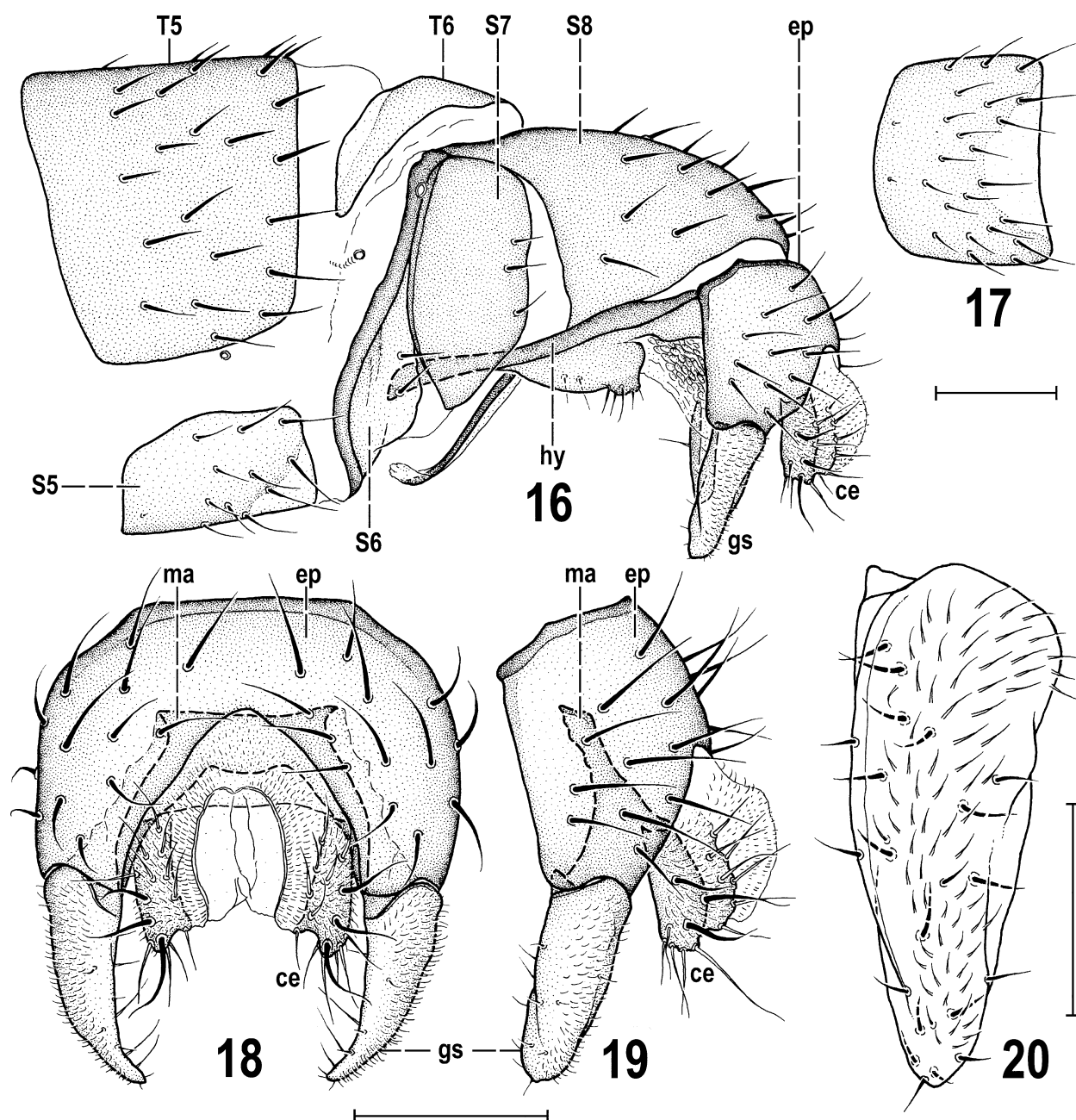
far (more than twice diameter of ocellus) from each other; oc setae arising from margin of ocellar triangle. Stripe between posterior part of orbital plate and frontal triangle dull brown to dark brown (rarely pale brown) and distinctly silvery-blue microtomentose, rarely extending slightly beyond apex of frontal triangle (never to anterior margin of frons) as faint brown stripe. Occiput brownish black, with sparse grey microtomentum. Face (prae-frons) dull yellow, medially concave, laterally with broad golden yellow microtomentose stripe extended (as widened, ochreous-darkened and shiny stripe) along ventral margin of gena. Parafacialia and gena concolourous, whitish yellow and silvery-white microtomentose, but gena ventrally with (relatively broad) ochreous, posteriorly darker-brownish marginal stripe; postgena dark brown like occiput, sharply separated from whitish-yellow gena anteriorly. Cephalic chaetotaxy: all setae distinctly shorter (e.g. oc not reaching level of anterior ors, cf. Fig. 9) than those of *C. browni* and *C. caricis* and less distinctly shorter than those of *C. marshalli*; pvt small with apices crossed; vti usually longest cephalic seta; vte, oc and posterior ors only slightly shorter than vti and subequal in length; 2 long ors (posterior somewhat longer than anterior); usually only 1 (rarely 2) microsetula in front of anterior ors; only 1 pair of very minute microsetulae medially in anterior fourth of frons; 5 or 6 exclinate postocular setulae in single short row at posterodorsal margin of eye (continued by vertical row of similar setulae on postgena); no inclinate setula behind vte; 1 long vi (as long as but finer than anterior ors) and 1 shorter (usually two-thirds of vi) subvibrissa, both usually pale-pigmented (Fig. 5); gena with 3 or 4 weak and pale peristomal setulae; postgena with 2 usual (but short and pale) setae ventrally. Eye elongate-subovoid, strongly convex, longest diameter 1.5–1.6 times shortest diameter. Gena highest of all relatives (Fig. 5), shortest height about 0.22 times shortest eye diameter. Palpus slender, pale yellow, with single dark ventral preapical seta and a few (2 or 3) pale setulae. Mouthparts pale yellow but clypeus blackish brown and prementum pale brown. Antenna geniculate, bright yellow; 1st flagellomere strongly compressed laterally, with very short whitish ciliation. Arista subbasal, about 1.6–1.7 times as long as antenna, sparsely and dark short ciliate; two basal aristomeres thickened and yellowish, terminal attenuated aristomere brown. **Thorax:** Entirely blackish brown (or notopleural area lighter brown), sparsely grey (with bluish tinge) microtomentose (Fig. 5), relatively shiny, particularly on scutum anterodorsally and on mesopleuron. Thoracic chaetotaxy: macrosetae relatively short, weak and (at least partly) pale-pigmented; 1 hu (weaker than npl), 2 npl (anterior markedly longer but pale), 1 small and pale prs, 1 sa (short), 1 pa (longer), 3 usually dark-pigmented postsutural dc becoming shorter anteriorly, foremost dc usually half length of middle dc, posterior dc longest of thoracic setae; 2 or 3 dc microsetae in front of them; ac microsetae reduced, in 2 or 3 incomplete pairs and none behind middle dc; 2 sc, apical sc as long as posterior dc, laterobasal sc weak, only slightly longer than foremost dc; 1 fine and



Figs. 12–15. Wings of *Carexomyza* species (male paratypes): **12:** *C. lonsdalei* sp.n.; **13:** *C. marshalli* sp.n.; **14:** *C. browni* sp.n.; **15:** *C. caricis* (Roháček, 1999). — **Scale bar:** 0.5 mm. Photos by K.N. Barber (12–14) and J. Roháček (15, adapted from Roháček 2006: fig. 496).

pale upcurved ppl; 2 rather long, pale stpl (also anterior relatively long) with 0 or 1 microseta in front of them and 2 or 3 pale setae in ventral corner of sternopleuron. Scutellum medium-long, rounded-triangular, convex dorsally. Subscutellum distinct. **Legs:** Yellow, only distal half to almost entire (usually on mid leg) apical tarso-meres blackish brown. Fine setosity of legs pale-pigmented, only most robust setae darker. Coxae with a few longer setae. f_1 with relatively long ctenidial spine (distinctly longer than maximum width of t_1) and usual rows of posteroventral (with seta in the middle longest) and posterodorsal long setae, some of which can also be pale. f_2 without peculiarities; f_3 with posteroventral row of 4–6 (usually sparsely arranged) short black spine-like setae in distal two-fifths. t_1 without, t_2 with short (not longer than maximum width of t_2), t_3 with very short ventroapical seta, otherwise uniformly setulose. All tarsi simply setulose (setulae slightly longer ventrobasally); pretarsal claws relatively long and dark. **Wing** (Fig. 12): Relatively narrow and short compared to body length (cf. Fig. 5), with pale ochreous-brown veins and membrane. C with thicker (but hardly longer) setulae among fine setosity of Cs_2 . Sc distally connected with R_1 and preapical kink developed. R_{2+3} long, slightly bent in parallel with C, apically straightened to slightly upcurved and terminating distinctly farther from apex of wing than does M. R_{4+5} very slightly bent to straight and ending close to (in front of) apex of wing. M straight, parallel with R_{4+5} . Cell dm of medium length, slightly widened distally; cross-vein r-m usually oblique and situated slightly in front of middle of cell dm. Terminal section of CuA_1 slightly to distinctly longer than dm-cu. CuA_1 almost reaching and A_1 ending far from wing margin. Alula distinct but relatively small and narrow. Wing measurements: length 1.35–1.79 mm, width 0.45–0.62 mm, $Cs_3 : Cs_4 = 0.94–1.47$, $r-m \backslash dm-cu : dm-cu = 2.08–2.78$. Haltere whitish yellow

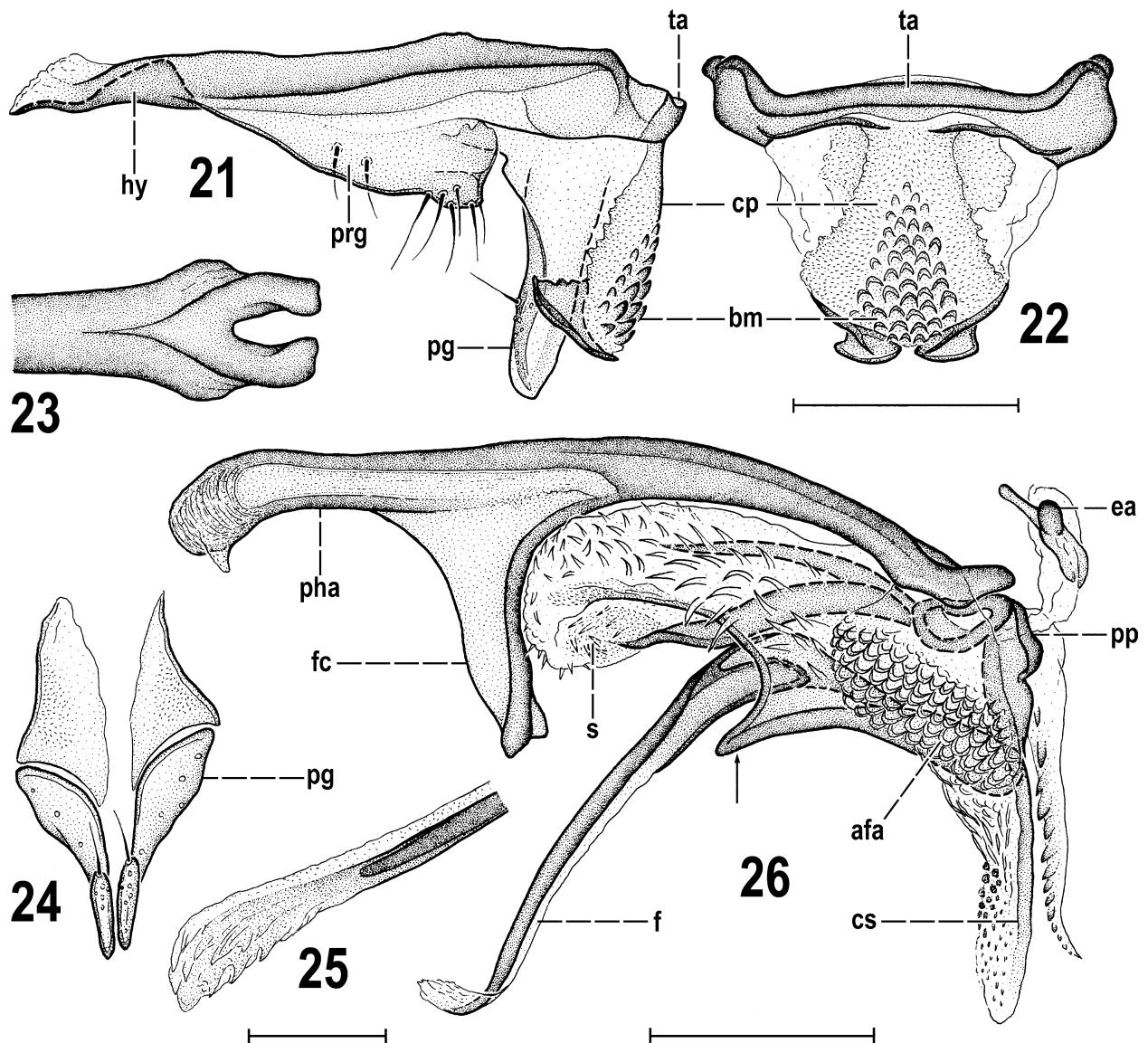
to white, with some ochreous tinge on stem; knob of medium size. **Abdomen:** Slightly lighter than thorax, with terga somewhat darker brown than sterna (Fig. 5), all sclerites with greyish (less bluish than on thorax) microtomentum, subshiny. Preabdominal terga large, extended laterally and bent onto ventral side of abdomen, short setose, with marginal setae longest and thickest; terga dorsally duller due to dense microtomentum, laterally subshiny. T1 distinctly shorter and usually paler than and separated from T2. T2 subequal or slightly shorter than T3, T3 and T4 subequal in length; T5 longer but narrower than T4. Preabdominal sterna relatively narrow, finely and sparsely setulose, only S1 bare, transverse and distinctly wider than S2. S2 as long as broad, not narrower than S3, with anterior dark stripe distinctly separated. S3 and S4 subequal, both distinctly longer than broad; S5 (Fig. 17) markedly wider but not longer than T4, slightly wider than long, with distinctive pattern (dark pigmentation deeply emarginated posteromedially). **Postabdomen** (Fig. 16): Sclerites well-sclerotized and dark-pigmented. T6 well-developed, although transverse and broadly desclerotized and unpigmented medially, seemingly divided into 2 plates (right markedly larger, left small, narrowly triangular). S6 and S7 situated laterally (Fig. 16), both strongly asymmetrical. S6 short, with strong dark anterior ledge-like margin; S7 distinctly (up to twice) longer but with anterior ledge-like margin slender; S6 with 2, S7 with 3 or 4 small setae. S8 situated dorsally (Fig. 16), less asymmetrical, about twice as long as S7, with a number of setae. **Male genitalia:** Most similar to those of *C. marshalli*, see also below. Epandrium (Figs. 16, 18, 19) relatively short (shorter than that of *C. marshalli*), broader than high, with anterodorsal margin somewhat straightened (Fig. 18); epandrial setae of moderate size, none particularly enlarged. Anal fissure (Fig. 18) subtriangular (rather semicircular in *C. mar-*



Figs. 16–20. *Carexomyza lonsdalei* sp.n., male paratype: **16:** postabdomen, left side, laterally; **17:** S5 (pregenital sternum), ventrally; **18:** external genitalia, caudally; **19:** ditto, laterally; **20:** gonostylus, laterocaudally (widest extension). — **Scale bars:** 20 – 0.05 mm; others – 0.1 mm. For abbreviations see p. 72.

shalli); cercus (Figs. 16, 18, 19) relatively large (more than half length of gonostylus), with a few longer setae, of which 3 posterolateral dark-pigmented in contrast to other (usually shorter) pale-pigmented setae. Medandrium somewhat wider than anal fissure ventrally (Fig. 18), with dorsolateral corners slightly projecting laterally. Gonostylus (Fig. 20) yellow (in contrast to dark epandrium), narrow, elongate, with tapered but not acute apex (thus very similar to that of *C. marshalli*) only slightly shorter than epandrial height, rather finely and sparsely setose on concave inner side, with largely (except for anterior marginal area) micropubescent outer side. Hypandrium (Fig. 21) of medium length, simple anteriorly,

without dorsally projecting internal leaf-like lobes. Transandrium most similar to that of *C. marshalli* but dorsally less robust, with longer, ventrally more projecting, caudal process integrating armature of basal membrane, latter formed by long posteromedial group of short spines terminated ventrally by pair of distinctive ventral sclerites (see Figs. 21, 22). Pregonite (Fig. 21) firmly fused anteriorly to hypandrium but somewhat incised posteriorly where it is slightly projecting ventrally (more than in *C. marshalli*) and bearing 5–7 setae; 2 more setae situated in anterior part of pregonite as usual. Postgonite (Fig. 21) simple, elongate, pale but with anterior marginal part darkened, having 1 distinct seta in distal third



Figs. 21–26. *Carexomyza lonsdalei* sp.n., male paratype: **21:** hypandrial complex, laterally; **22:** transandrium, caudally; **23:** basal end of phallapodeme, dorsally; **24:** postgonites with attached basal flat sclerite, anteroventrally; **25:** apex of filum, ventrally (widest extension); **26:** aedeagal complex, laterally (arrow indicating sharp tooth of saccus). — **Scale bars:** 25 – 0.03 mm; others – 0.1 mm. For abbreviations see p. 72.

and rounded apex. Each postgonite attached to basal, relatively pale and flat sclerite (see Fig. 24), as in all congeners. Basal membrane and armature largely sclerotized and incorporated into caudal process of transandrium (Figs. 21, 22). Aedeagal part of folding apparatus (Fig. 26) with outer sides densely covered by flat rounded excrescences (not spines); connecting sclerite long, narrowly pigmented posteriorly, with group of small granulous tubercles (or spines) in anterior membranous part. Phallapodeme (Fig. 26) long and rather slender (yet longer than that of *C. marshalli*), with moderately robust ventral fulcrum, symmetrically bifurcate basal end (Fig. 23); apex with laterally somewhat projecting pale-pigmented corners. Aedeagus (Fig. 26) formed by short phallophore and large bifid distiphallus. Phallophore formed by smaller subannular dorsal part and ventrally projecting posterior part that is ventrally fused with base of dis-

tiphallus. Distiphallus complex, composed of relatively long, densely spinose, and only distally membranous saccus, and slender, heavily sclerotized filum. Saccus with basal part more sclerotized and posteriorly coalesced with phallophore, middle part with long, acutely protruding ventral sclerotized tooth (longest of all known species and distinctly different from rounded condition of *C. marshalli*), with pair of slender sinuous sclerites internally, and distal part largely membranous and spinose (Fig. 26). Filum (Fig. 26) formed by two closely attached and partly fused band-like sclerites; terminal part elongate, lancet-shaped, with apex (Fig. 25) submembranous, with fine indistinct (unpigmented) tooth-like armature. Ejacapodeme (Fig. 26) well-developed, with slender digitiform projection. **Female.** Similar to male except for differences mentioned below. Total body length 1.67–2.42 mm. **Head** (Fig. 9): Frons distinctly darker

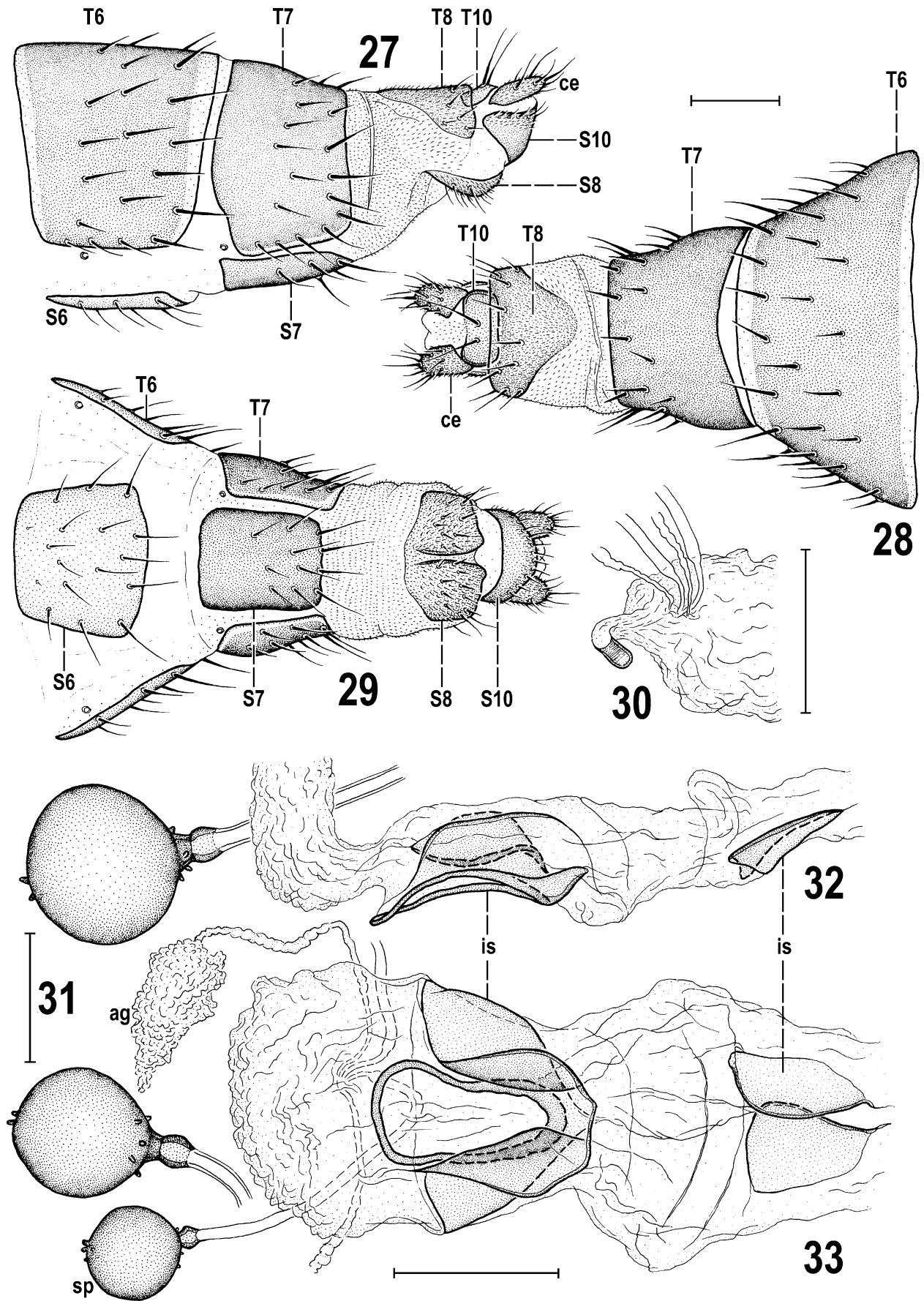
anteriorly, with brown stripe (never pale brown as in a few males) between posterior part of orbital plate and frontal triangle extended anteriorly and typically reaching (usually as paler brown stripe) up to level of anterior ors or even to anterior margin of frons. Orbital plate between anterior and posterior ors at least partly pale brown to dark brown (especially in front of posterior ors), with 1 or 2 microsetulae in front of anterior ors. Vibrissa and subvibrissa usually darker, vi sometimes black, subvibrissa sometimes dark brown. First antennal flagellomere distinctly darker, brownish-darkened anterodorsally on outer side and entirely on inner side; pedicel darker, usually brownish ochreous, particularly dorsally on inner side. Face and gena also darker. Face with ventral half pale brown, and ventral marginal stripe of gena brown to dark brown (posteriorly) and shiny. Gena higher (shortest height up to 0.29 times shortest eye diameter). **Thorax** (Fig. 9): Thoracic setae dark-pigmented. f_3 uniformly finely setulose, without row of thickened spine-like setae. **Wing**: Measurements: length 1.62–2.01 mm, width 0.51–0.68 mm, $Cs_3 : Cs_4 = 0.89–1.27$, $r-m/dm-cu : dm-cu = 1.87–2.92$. **Abdomen**: Preabdominal terga shinier, particularly laterally. T1 hardly paler than T2, latter shorter and narrower than T3. T3 and T4 the widest terga, subequal in length. T5 usually slightly longer than T4 but narrower and tapered posteriorly. All terga wider and more transverse. Preabdominal sterna narrower. Shape of S1 and S2 as in male but S2 longer than broad; S3 and S4 somewhat narrower than S2, elongate-suboblong, longer than broad, S3 in particular. S5 as wide as or slightly wider than S4, more rounded laterally and distinctly tapered anteriorly. **Postabdomen** (Figs. 27–29): T6 broad but tapered posteriorly, dark-pigmented except for narrowly pale anterior and posterior margins, relatively sparsely setose in posterior two-thirds. S6 relatively small but slightly wider than S5 and wider than long, subtrapezoidal, wider posteriorly, distinctly paler than S7, with a few setae. T7 separate from S7, both dark-pigmented. T7 (Fig. 28) much narrower than T6, shallowly emarginate anteromedially, with narrowly pale lateral margins (Figs. 27, 29), mainly setose in posterior half. S7 (Fig. 29) elongate-suboblong, as long as but much narrower and darker than S6, sparsely setose in posterior half. T8 (Fig. 28) wider than long, subtriangular, widest posteriorly (resembling that of *Stiphrosoma* species), with small setae in posterior third. S8 (Fig. 29) relatively short (but somewhat longer than that of *C. marshalli*), medially longitudinally divided, short setulose and micropubescent. **Female genitalia**: Internal sclerotization of female genital chamber (Figs. 32, 33) distinctive: annular sclerite free, elongate, slightly wider anteriorly; pair of adjacent sclerites ventrally fused and partly embracing annular sclerite (Fig. 33), and posterior pair of smaller sclerites (markedly smaller than those of *C. marshalli*) situated very far behind them. Anterior end of genital chamber very strongly bent (at right angle) dorsally and provided with short curved ventral receptacle (Fig. 30) having small, slightly sclerotized, somewhat elongate and distally rounded cup-

like tip. Remains of accessory glands medium-sized, of uncertain shape, situated on slender ducts (Fig. 33). Spermathecae (1+1, one slightly larger than other) subsphaerical to lemon-shaped (Fig. 31), with dark and distinct cervix and a few small spine-like tubercles (2 or 3 on tip, some more basally); stalked globulae on tips of tubercles present but not illustrated; spermathecal ducts relatively short (cf. Fig. 33). T10 (Fig. 28) dark-pigmented (with medial part usually paler), slightly smaller than S10, transversely suboblong, with all corners rounded and usual medial pair of long setae. S10 (Fig. 29) also relatively dark, anteriorly emarginate, posteriorly rounded in ventral view, with setulae and micropubescence at posterolateral margins. Cerci short, dark-pigmented (in contrast to all other congeners), relatively widely separate (Fig. 28), each with a number of short fine setae, 2 or 3 (dorsopreapical, apical and sometimes lateral) longer than others.

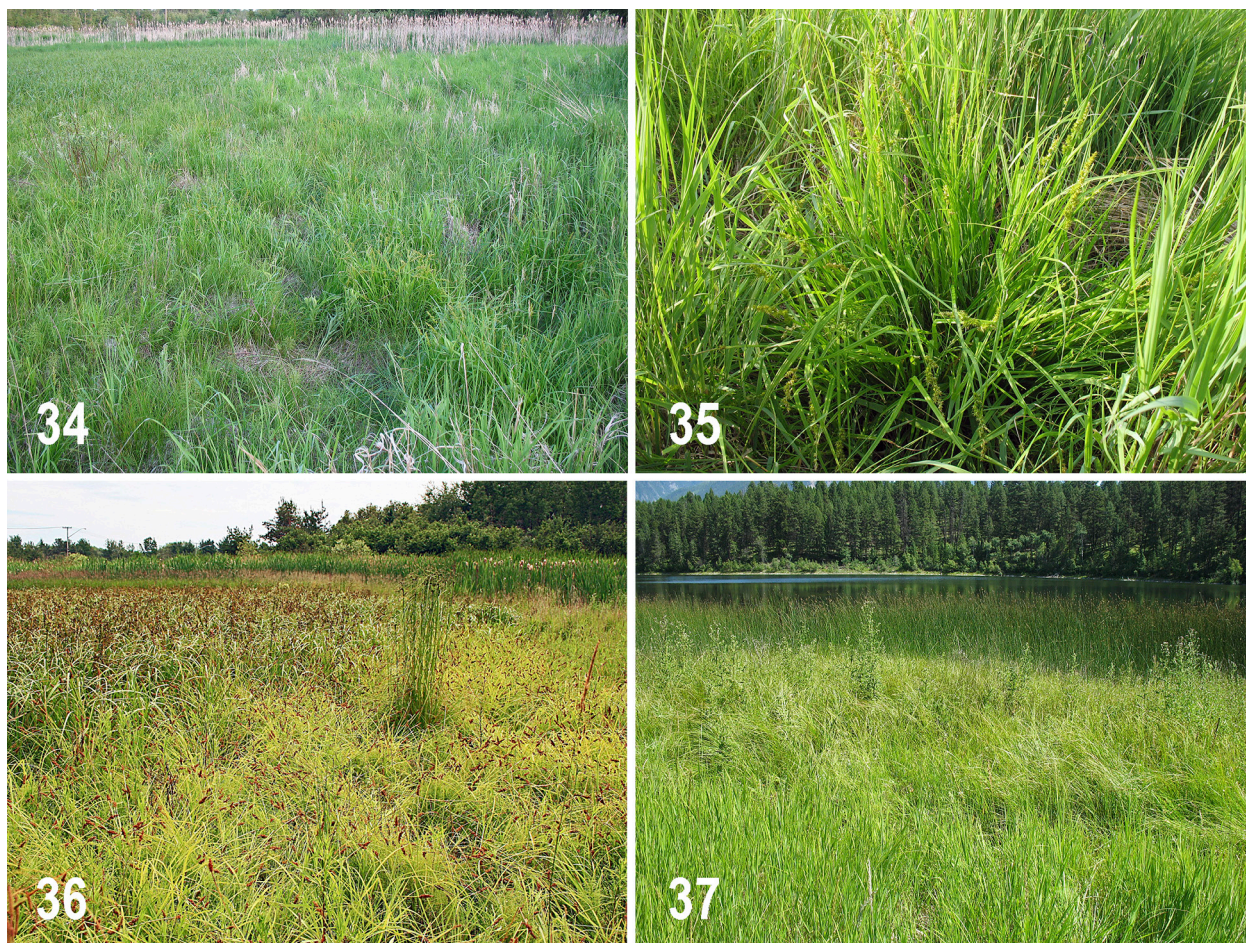
Etymology. This species is named in honour of Dr. Owen Lonsdale, a dipterist and colleague who has provided the authors with exceptional assistance and advice with previous manuscripts.

Discussion. *Carexomyza lonsdalei* sp.n. was included as *Carexomyza* sp.n. 1 in ROHÁČEK et al. (2019: figs. 2, 4) in their phylogenetic analysis but its relationships were not discussed. It most closely resembles another Nearctic congener, *C. marshalli*, including the male and female postabdominal structures. Their sister-species relationship proved to be strongly supported by molecular data (see Fig. 91), but can also be demonstrated by the following synapomorphic characters: inclinate setula behind vte absent; male pregenital sternum (S5) with deeply emarginate pigmentation; male cercus with (3 or 4) longest setae dark-pigmented; apex of filum elongately lanceolate; female S6 narrowed. Moreover, this species pair also shares somewhat reduced ocelli (more so in *C. lonsdalei*) which can also be a synapomorphy. The elongate, distally narrowed gonostylus shared by these species is probably a plesiomorphic character.

The relatively small differences between these two species are given in the above description. *Carexomyza lonsdalei* is (on average) the smallest species of *Carexomyza*. It can also be distinguished from *C. marshalli* by the relatively short cephalic and thoracic setae that are at least partially pale, the reduced yellow colour on the frons and the higher gena (highest of all congeners). The male differs in that the cercus is somewhat shorter, the pregonite is more distinctly separated from the hypandrium posteriorly, the caudal process of the transandrium is longer, and, particularly, the tooth in the middle of the saccus of the distiphallus is very acutely projecting. The female of *C. lonsdalei* differs from that of *C. marshalli* in having the antenna and face distinctly brownish (at least partly), T8 is distinctly triangular and, most distinctly, the cercus is markedly dark and the female genital chamber has the posterior pair of internal sclerites distant from the anterior pair (and the annular sclerite).



Figs. 27–33. *Carexomyza lonsdalei* sp.n., female paratype: 27: postabdomen, laterally; 28: ditto, dorsally; 29: ditto, ventrally; 30: ventral receptacle, sublaterally; 31: spermathecae; 32: internal sclerites of female genital chamber, laterally; 33: ditto, with appendages, ventrally. — Scale bars: 31 – 0.05 mm; others – 0.1 mm. For abbreviations see p. 72.



Figs. 34–37. Habitat of *Carexomyza lonsdalei* sp.n. **34–36:** Sault Ste. Marie–Finn Hill, Ontario site (Figs. 34, 35, 10 June 2012, Fig. 36, 7 July 2010). **34:** view of section of graminoid meadow with high density of *Carex stipata* looking mostly south with *Scirpus microcarpus* and *Typha latifolia* in background; **35:** close-up view of clump of *Cx. stipata*; **36:** maturing *Cx. stipata* next to stand of *S. microcarpus* (similar aspect to that in Fig. 34); **37:** near Fort Steele, British Columbia, pond-side mixed graminoids including a patch dominated by *Carex pellita* (18 July 2011). Photos by J. Roháček (36) and K.N. Barber (others).

Biology. The first encounter of this species (by KNB) at the Finn Hill site (Figs. 34–36) was at dusk in a sweep collection from *Cx. stipata* (19 July 2004, $n=1$), during the third year of sampling this site for anthomyzids. Subsequent collection attempts by sweeping at this site were unsuccessful in 2004, but use of an aspirator (pooter) yielded daytime captures ($n=32$) by targeting the thatch and duff in and around clumps of *Cx. stipata*. In subsequent years, sweeping became the most productive method when effort was concentrated in the early evening (pooter: 2005–2012, $n=9$; sweeps: 2005–2017, $n=248$, besides a few discarded/lost from oviposition trials). The earliest seasonal collection here was 4 June and the latest was 4 August.

Unquantified observations suggest that since 2004, when *C. lonsdalei* was first encountered at the Finn Hill site, the “best spot” to find this species has shifted eastward and the overall predominance of *Cx. stipata* is now less pronounced (much less than appears in Fig. 36 of 2010). This may be the result of changes in drainage, increased prevalence of grasses and herbs, a response to damage caused by trampling of the soil and the bases of plants, or any combination of these factors.

A collection of three females from near Fort Steele, British Columbia, represents the most westerly record for this species, and indicates a possible association with *Cx. pellita* (see Fig. 37). A quick search for the presence of *Cx. stipata* within this site bordering a pond was not successful. Another suggestion of a possible host plant, *Calamagrostis canadensis*, comes from the collection of a single male from the margin of a stream (Manitoulin Island–Perch Creek, Ontario, 1 August 1997). This particular fly specimen was aspirated nearest to the base of a *Ca. canadensis* plant (label reads “sweeps/pooter” for the combined collections at that site), but since the presence of *Carexomyza* in the Nearctic was not recognized at that time, no further inspection of this site was made for the presence of *Cx. stipata* or any other *Carex* species.

At Ignace, Ontario, a site predominated by *Cx. utriculata* and grasses, *C. lonsdalei* was present in small numbers ($n=7$) in 2012, while *C. marshalli* was the species most commonly collected ($n=68$). No *Cx. stipata* was recognized at this roadside, mixed graminoid site (labels mistakenly refer to this as a fen) that might otherwise have been the source of the *C. lonsdalei* specimens. Other available label data refer to “river edge” and

“sedge meadows, floodplain community nr. tamarack bog” in Manitoba, and to “*Carex* meadow” in Québec. An unexpected reference to “tallgrass prairie” (Gardenton, Manitoba) must surely also include moist, possibly riparian, habitat that would contribute a sedge component to the plant community. Besides the Cochrane, Ontario site where all three Nearctic species occurred, and the previously mentioned Ignace site yielding mostly *C. marshalli*, the only other localities at which *C. lonsdalei* co-occurred with another species of *Carexomyza* were Echo Bay, Ontario and Shilo, Manitoba, both times with *C. browni*. As condensed from all specimen labels from all localities, the known flight period of *C. lonsdalei* runs from 25 May (Detroit, Michigan) to 4 August (Sault Ste. Marie, Ontario).

Rearing (Finn Hill site): A total of 75 eggs was collected, of which 41 were not embryonated and 6 (including those damaged) were preserved. The remaining 28 embryonated eggs yielded first-instar larvae, of which 13 were the product of forcible “hatching” on 2 July 2012. These went on to produce 20 mature larvae that were stepped through the cooling period (described above) for overwintering. By 30 December 2012, two larvae were dead while an additional four larvae died and one larva was lost after return to warm conditions on 3 March 2013, leaving a balance of 13 larvae available for pupariation. Subsequently, one died while the others yielded 12 adults (9♂ 3♀). An unplanned absence by KNB meant that seven larvae pupariated on or before 10 March 2013 (ambiguous pupariation periods) leaving only five adults (3♂ 2♀) emerging on a known day, eight days ($n=1$) or nine days ($n=4$) after initial puparium formation (all 12 adults had emerged by 16 March 2013).

Rearing success for this species was moderate to good. Embryonated eggs represented 45.3% ($n=34$) of the total 75 eggs oviposited and suggests inadequate provision of appropriate courtship and mating conditions. Of the 28 hatched eggs that proceeded to further rearing, 20 (71.4%) matured through the larval stages and went into overwintering storage, while the successful emergence of 12 adults represents a 42.9% success rate from egg hatch to adult emergence. The need to forcibly “hatch” 13 of the 28 embryonated eggs is not interpreted to be evidence of an egg diapause. It is likely too early in the season (14–28 June 2012) to be a successful life-history strategy for this species and follows shortly after a presumed overwintering larval diapause; it more likely represents an artefact of the rearing conditions provided. The circumstances surrounding this rearing contrast with the evidence for the egg diapause reported for *Stiphrosoma balteatum* Roháček & Barber, 2005 (ROHÁČEK & BARBER 2005). For *S. balteatum*, all embryonated eggs failed to hatch after several weeks at room temperature while all those of concurrently reared *S. stylatum* Roháček & Barber, 2005 hatched without any delay. For *S. balteatum* and *S. stylatum*, the oviposition periods ran later in the season, from 15 August–26 October 2002 and 4 August–10 October 2002, respectively, compared to that for *C. lonsdalei*.

Distribution. Canada: British Columbia, Manitoba, Ontario, Québec. United States of America: Michigan. Compared to congeners, *C. lonsdalei* has a slightly narrower distribution in Canada (not yet recorded east of Québec), and it is the least frequently encountered Nearctic species (11 localities). This may speak generally to a more cryptic behaviour and habitat, and may explain the absence of records from Alberta and Saskatchewan. It is also the only species known from an eastern U.S.A. state (Michigan: Detroit). Most likely it will yet be found at least further east in Canada despite a concerted but unsuccessful effort by KNB on a particularly promising site in New Brunswick in 2019.

Material examined. Type material: Holotype ♂, ‘CAN:ON: SS-Marie, Finn | Hill, 20.vii.2004, | KNBarber, pooter, | *Carex stipata stipata* | 46°31.63'N 84°17.33'W’, ‘Holotypus ♂ | *Carexomyza* | *lonsdalei* sp.n. | K.N. Barber & J. | Roháček det. 2019’ (red). The specimen is in excellent condition with yellow gonostyli highly visible (CNCL, intact, Fig. 5). Paratypes 155♂ 163♀. **CANADA:** **British Columbia:** ~ 3.5 km NNW Fort Steele, Hwy 95 rest area, 49°38.90'N 115°38.82'W, sweeps, graminoids, mostly *Carex pellita*, 18.vii.2011, K.N. Barber leg., 3♀ (CNCL, 1♀ genit. prep.). **Manitoba:** 20 km E Anola, Brokenhead R., 49°53.1'N 96°22'W, sweep along river edge, 10.vi.1999, T.A. Wheeler leg., 1♀ (LEMQ); 5 km N Gardenton, Tallgrass Prairie Preserve, 49°10.71'N 96°40.76'W, sweep in tallgrass prairie, 17.vi.1999, S. Boucher leg., 1♀, V. Crecoco leg., 1♀ (LEMQ); 5 mi SW Shilo, sedge meadows, floodplain community nr. tamarack bog, 16.vi.1958, J.F. McAlpine leg., 1♀ (CNCL, genit. prep.). **Ontario:** ~ 13.5 km S Cochrane, 48°56.65'N 81°00.18'W, hydro right-of-way, sweeps, mostly *Carex utriculata*, K.N. Barber leg., 12.vii.2013, 1♂ 1♀, 13.vii.2013, 1♀, 28.vii.2017, 1♀ (CNCL); Echo Bay, Echo Bay Marsh, 46°29.62'N 84°04.11'W, sweeps, mostly *Carex utriculata*, 10.vi.2017, K.N. Barber leg., 1♀ (CNCL); ~ 25 km WNW Ignace, 49°29.52'N 92°00.83'W, sweeps, fen, mostly *Carex utriculata* with grasses, K.N. Barber leg., 4.vii.2012, 4♀, 5.vii.2012, 1♂ 1♀, 6.vii.2012, 1♀ (CNCL); Manitoulin Is., ~ 2.2 km N Cold Springs, Perch Ck. at Hwy 540, 45°53.2'N 82°06.3'W, sweeps/pooter, *Calamagrostis canadensis*, 1.viii.1997, K.N. Barber leg., 1♂ (CNCL); S[ault] S[ainte] Marie, Finn Hill, 46°31.63'N 84°17.33'W, pooter, *Juncus effusus*/*Carex stipata stipata*, 23.vii.2004, K.N. Barber leg., 1♀ (CNCL); S.S. Marie, Finn Hill, 46°31.60'N 84°17.30'W, pooter, *Carex stipata stipata*, 23.vii.2004, K.N. Barber leg., 1♀ (CNCL); S.S. Marie, Finn Hill, 46°31.65'N 84°17.34'W, pooter, *Carex stipata stipata*, K.N. Barber leg., 30.vii.2004, 1♂ 2♀ (1♀ head/thorax photo), 4.viii.2004, 2♂ (CNCL); S.S. Marie, Finn Hill, 46°31.65'N 84°17.34'W, sweeps, *Carex stipata stipata*, 2.vii.2016, K.N. Barber leg., 3♂ (CNCL); S.S. Marie, Finn Hill, 46°31.67'N 84°17.30'W, sweeps, mostly *Carex stipata stipata*, 19.vi.2012, K.N. Barber leg., 2♂ 1♀ (CNCL); S.S. Marie, Finn Hill, 46°31.63'N 84°17.33'W, pooter, *Carex stipata stipata*, K.N. Barber leg., 20.vii.2004, 4♂ 1♀ (1♂ genit. prep.), 21.vii.2004, 2♂ 2♀, 22.vii.2004, 3♂ 2♀, 23.vii.2004, 1♂ 3♀ (CNCL), 25.vii.2004, 2♂ 3♀ (CNCL, 1♂ 1♀; SMOC, 1♂ 2♀), 19.vii.2005, 1♀, 6.vii.2008, 2♂ 1♀ (CNCL); S.S. Marie, Finn Hill, 46°31.63'N 84°17.33'W, pooter, mostly *Carex stipata stipata*, 10.vi.2012, K.N. Barber leg., 1♂ 4♀ (CNCL); S.S. Marie, Finn Hill, 46°31.63'N 84°17.33'W, sweeps, *Carex stipata stipata*, K.N. Barber leg., 19.vii.2004, 1♀ (genit. prep.), 6.vii.2008, 1♀ (CNCL), 18.vi.2016, 3♂ 3♀ (AMNH), 29.vi.2016, 1♀ (CNCL); S.S. Marie, Finn Hill, 46°31.63'N 84°17.33'W, sweeps, mostly *Carex stipata stipata*, K.N. Barber leg., 26.vi.2007, 18♂ 16♀ (CNCL, 7♂ 7♀ [1♂ genit. prep., wing photo, left wing in glycerine microvial]; LEMQ, 4♂ 2♀; SMOC, 7♂ 7♀ [2♂ 1♀ genit. prep.]), 8.vii.2010, 2♂ 1♀ (SMOC), 14.vi.2012, 2♂ 6♀, 15.vi.2012, 3♂ 2♀, 16.vi.2012, 4♂ (CNCL), 19.vi.2012, 9♂ 10♀ (CNCL, 3♂ 4♀; BDUC, 3♂ 3♀; CASC, 3♂ 3♀); 26.vi.2012, 2♂ 1♀, 4.vi.2013, 3♂ 3♀ (CNCL), 16.vi.2013, 31♂ 17♀ (CNCL, 17♂ 3♀ [1♂ genit. prep.]; DEBU,

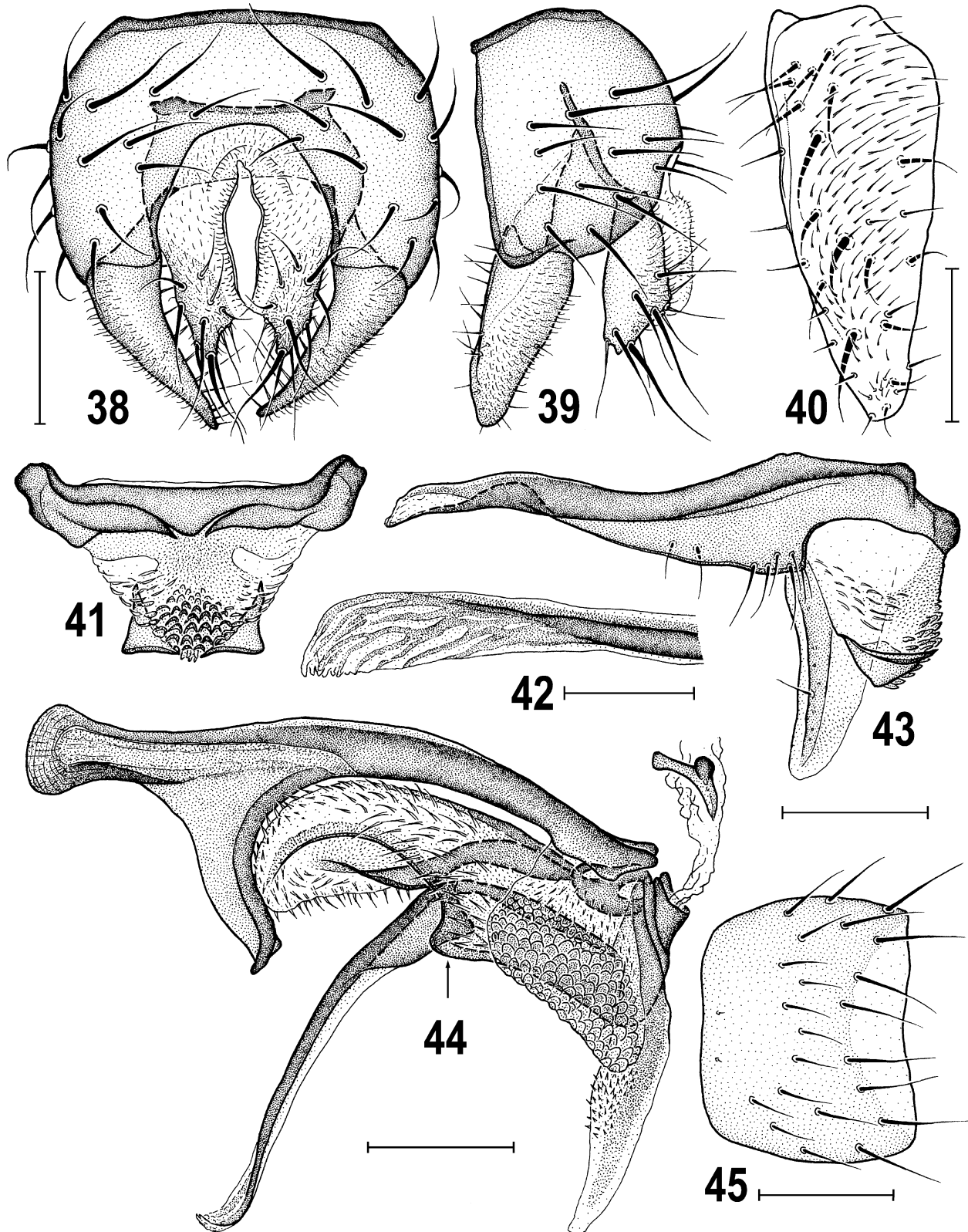
5♂ 5♀; INHS, 3♂ 3♀; LACM, 3♂ 3♀; NBMB, 3♂ 3♀), 8.vi.2014, 2♀, (CNCI), 10.vi.2017, 12♂ 18♀ (CNCI, 7♂ 13♀; USNM, 5♂ 5♀), 12.vi.2017, 4♂ 5♀, 31.vii.2017, 1♂ 2♀ (CNCI); S.S. Marie, Finn Hill, 46°31.63'N 84°17.33'W, used in rearing, sweeps, mostly *Carex stipata stipata*, K.N. Barber leg., 10.vi.2012, 17♂ 14♀, 16.vi.2012, 9♂ 16♀ (1♀ genit. prep.) (CNCI); Lab-reared from ~ 26♂ 34♀ *Carexomyza*, 9A-1, *Carex stipata stipata*, [sourced] S.S. Marie, Finn Hill, 46°31.63'N 84°17.33'W, sweeps, mostly *Carex stipata stipata*, 10 & 16.vi.2012, K.N. Barber leg., oviposition: 14–25.vi.2012 – 22°C, 16L:8D, 60–70% RH, [followed by transitioning cold/dark period] 18.ix.2012 – 10°C, 12L:12D, 5.x.2012 – 4°C, 0L:24D, 3.iii.2013 – 22°C, 16L:8D, [each with the following data and empty puparium in gelatin capsule]: hatch: 26.vi.2012, puparium: ≤ 10.iii.2013, adult: 17.iii.2013, 1♂, hatch: 27.vi.2012, puparium: ≤ 10.iii.2013, adult: 18.iii.2013, 1♀, hatch: 27.vi.2012, puparium: ≤ 10.iii.2013, adult: 17.iii.2013, 1♂, hatch: 29.vi.2012, puparium: ≤ 10.iii.2013, adult: 19.iii.2013, 1♂, forced hatch: 2.vii.2012, puparium: ≤ 10.iii.2013, adult: 17.iii.2013, 1♂, forced hatch: 2.vii.2012, puparium: ≤ 10.iii.2013, adult: 19.iii.2013, 2♂, hatch: 26.vi.2012, puparium: 12.iii.2013, adult: 20.iii.2013, 1♂, forced hatch: 2.vii.2012, puparium: 12.iii.2013, adult: 21.iii.2013, 1♂ 2♀, hatch: 26.vi.2012, puparium: 16.iii.2013, adult: 25.iii.2013, 1♂ (CNCI). **Québec:** Lac St-Francois Nat. Wildlife Area, NW of Aménag. Therrien, close to Ruisseau Th[errien], 45°00.39'N 74°30.99'W, *Carex* meadow, sweeping, T1c, 16.vii.1999, F. Beau-lieu leg., 1♀ (LEMQ 0040279). **UNITED STATES OF AMERICA: Michigan:** Detroit, 25.v.1941, G. Steyskal leg., 1♀ (USNM, with Steyskal 1941 det. as *Anthomyza gracilis* Fallén). — **Other material:** **CANADA: Ontario:** S.S. Marie, Finn Hill, 46°31.65'N 84°17.34'W, pooter, *Carex stipata stipata*, 30.vii.2004, K.N. Barber leg., 1♀ (CNCI, missing antennae); S.S. Marie, Finn Hill, 46°31.63'N 84°17.33'W, sweeps, mostly *Carex stipata stipata*, K.N. Barber leg., 26.vi.2007, 1♂ 1♀ (CNCI, ♂ genit. prep., genitalia damaged, ♀ genit. prep., leg missing, wings tattered), 8.vii.2010, 1♀ (SMOC, used in molecular analysis, in glycerine mount except one wing dry mounted); S.S. Marie, Finn Hill, 46°31.63'N 84°17.33'W, used in rearing, sweeps, mostly *Carex stipata stipata*, 10.vi.2012, K.N. Barber leg., 1♀ (CNCI, genit. prep., left wing not expanded).

3.5. *Carexomyza marshalli* sp.n.

(Figs. 6, 10, 13, 38–51)

Description. Male (Fig. 6). Closely resembling that of *C. lonsdalei* but differing as follows: Total body length 1.74–2.26 mm; general colour blackish brown but anterior two-thirds of head and all legs yellow; thorax and abdomen distinctly shinier than those of all relatives despite some grey or greyish-brown microtomentum. **Head:** Somewhat higher than long. Frons narrower, tapering and largely yellow anteriorly, with yellow colour extended posteriorly along sides of frontal triangle typically to level of anterior ocellus, often up to base of vti, rarely only to level of posterior ors (darkest specimens). Orbital plate pale yellow and silvery-white microtomentose at least up to posterior ors but usually also behind it internally (only a short distance externally), internal silvery-grey microtomentum grading into that of adjacent stripe; posterior part thus usually with narrowed, dark-brown external margin with greyish microtomentum (appearing shinier in frontal view); less frequently posterior part of orbital plate completely dark brown with silvery-grey to silvery-blue microtomentum merging with that of adjacent stripe. Frontal triangle narrow, reaching anterior

two-fifths to third of frons; anterior corner pale brown to ochreous, rest of frontal triangle becoming blackish brown posteriorly and appearing shinier (except in darker specimens) than remainder of frons. Stripe between posterior part of orbital plate and frontal triangle typically yellow or partly (posteriorly) brown and silvery-grey microtomentose (often visible only on darkened margins of frontal triangle and orbital plate), grading into microtomentum of adjacent orbital plate and contrasting with narrow darker part of orbital plate; darker specimens with stripe entirely dark brown and bright silvery-blue microtomentum confluent with that of adjacent orbital plate. Occiput brownish black, with sparse grey microtomentum, shinier than that of *C. lonsdalei*. Cephalic chaetotaxy: setae longer (e.g. oc reaching to or in front of level of anterior ors, cf. Fig. 10) than those of *C. lonsdalei* but somewhat shorter and finer than those of *C. browni* and *C. caricis*; pvt longer and strongly crossed; vti usually longest cephalic seta but vte, oc and/or posterior ors can often be almost as long as vti; 2 (aberrantly 3 on one orbital plate only) long ors (posterior only slightly longer than anterior), and only 1 or 2 (usually 2) microsetulae in front of anterior ors; 1–3 (usually only 1 but rarely up to 4 on one side) pairs of minute microsetulae medially in anterior third of frons; subvibrissa often shorter (only half length of vi); setae on gena and postgena dark-pigmented (Fig. 6). Eye elongate-subovoid; its longest diameter 1.4–1.5 times shortest diameter; gena shorter (Fig. 6), its shortest height only 0.12–0.15 times shortest eye diameter. Palpus usually with more (4 or 5) pale ventral setulae in addition to dark ventral preapical seta. Antenna with 1st flagellomere with longer (longer than that of arista) whitish ciliation on anterior margin; arista 1.5–1.7 times as long as antenna. **Thorax:** Shinier, particularly mesopleuron (usually with large bare and glabrous spot dorsally, cf. Fig. 10) and sternopleuron shinier due to reduced microtomentum. Thoracic chaetotaxy: macrosetae somewhat longer (anterior npl in particular) and almost all dark-pigmented; foremost dc variable, sometimes small but often much longer than is usual in *C. lonsdalei*; exceptionally also 1 presutural dc can be enlarged, thus 1+3 dc present. Two usual stpl, all dark but anterior distinctly shorter than posterior; setae in ventral corner of sternopleuron pale-pigmented. **Legs:** Coloured as in *C. lonsdalei* but setosity generally darker. f_1 with ctenidial spine slightly to distinctly longer than maximum width of t_1 ; f_3 with posteroventral row of 6 or 7 (rarely only 5) usually sparsely arranged short spine-like setae in distal two-fifths to half. **Wing** (Fig. 13): R_{2+3} usually more strongly arched toward C, apically slightly upcurved to it and terminating slightly farther from apex of wing than does M; R_{4+5} ends at wing tip (see Fig. 13). Cell dm with r-m more or less oblique and situated at about middle of cell dm; sometimes dm-cu also oblique. Wing measurements: length 1.50–2.03 mm, width 0.49–0.72 mm, $Cs_3 : Cs_4 = 1.05–1.56$, r-m/dm-cu : dm-cu = 1.93–2.72. **Abdomen:** Somewhat paler than thorax, having all sclerites with greyish (usually without bluish tinge) microtomentum, subshiny. S4 usually somewhat



Figs. 38–45. *Carexomyza marshalli* sp.n., male paratype: **38**: external genitalia, caudally; **39**: ditto, laterally; **40**: gonostylus, ventro-laterocaudally (widest extension); **41**: transandrium, caudally; **42**: apex of filum, ventrally (widest extension); **43**: hypandrial complex, laterally; **44**: aedeagal complex, laterally (arrow indicating blunt tooth of saccus); **45**: S5 (pregenital sternum), ventrally. — **Scale bars**: 42 – 0.03 mm; others – 0.1 mm.

wider than S3 and less elongate (only slightly longer than broad); S5 (Fig. 45) slightly to distinctly wider than long, with dark pigmentation emarginated posteromedially, al-

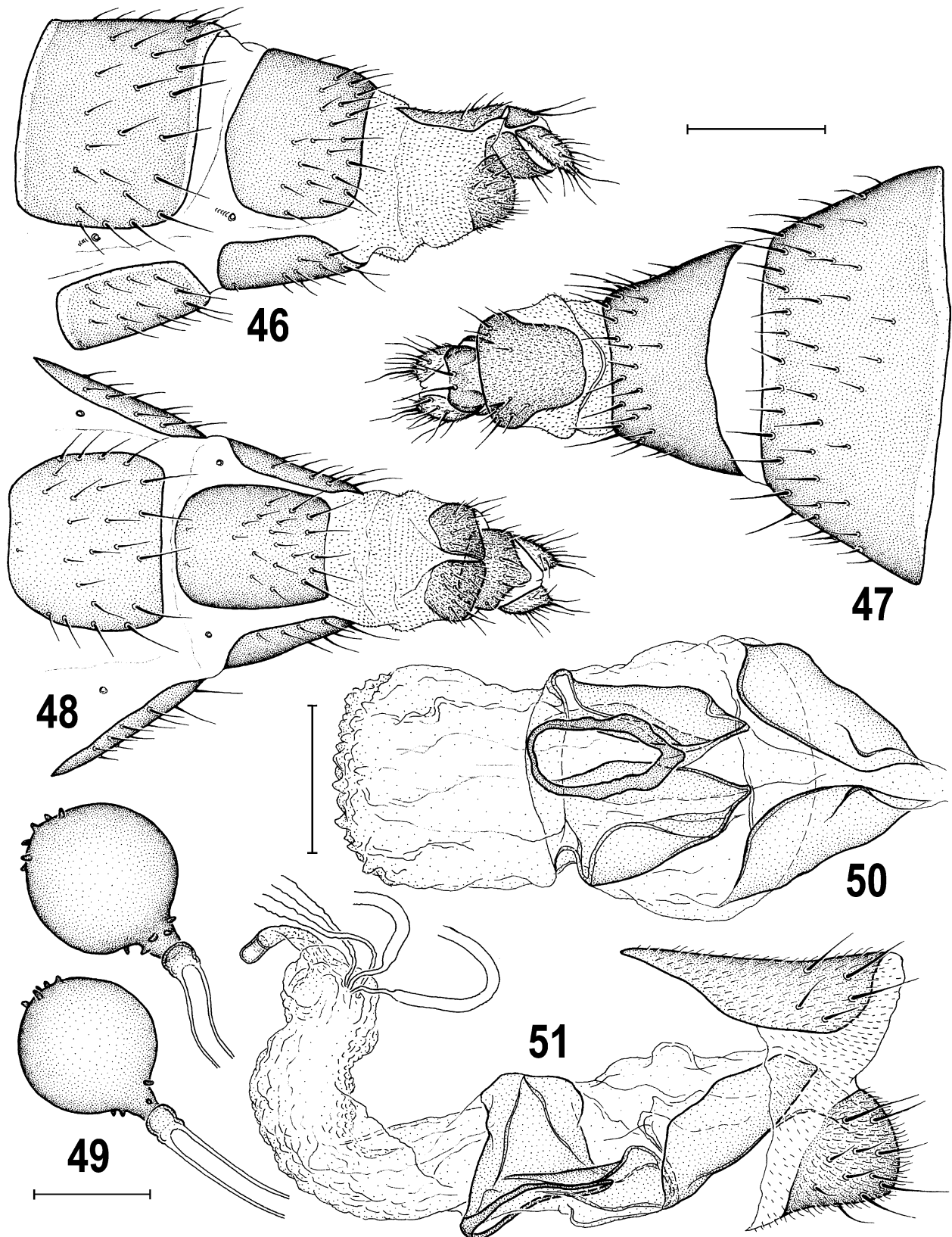
though often less deeply than in *C. lonsdalei*. **Postabdomen**: Sclerites S6–S8 darker and shinier (more sparsely microtomentose) than preabdominal terga. T6 with me-

dial unpigmented part usually smaller and left pigmented plate distinctly shorter but hardly narrower than right plate. S6 with 1 or 2, S7 with 2–4 small setae. **Male genitalia:** Closely resembling those of *C. lonsdalei*. Epan-drium (Figs. 38, 39) longer, with epandrial setae longer and more robust, and anal fissure semicircular, rounded dorsally; cercus (Figs. 38, 39) larger (longer), with apex more acute, with small tooth on apex, but also with some (usually 4) dark-pigmented setae. Medandrium somewhat wider than anal fissure ventrally (Fig. 38), laterally rounded, with dorsolateral corners slightly protruding. Gonostylus (Fig. 40) yellow (to pale brown in some specimens), more gradually narrowed towards apex, inner surface less concave (Fig. 38), with longer and stronger setae on inner side. Hypandrium (Fig. 43) with anterior part as in *C. lonsdalei* but dorsal outline more or less concave. Transandrium (Figs. 41, 43) with dorsal part robust and dark-pigmented, with caudal process distinctly shorter, with spines of (original) basal membrane concentrated more posteroventrally but with similar pair of ventral sclerites (see Figs. 41, 43); membranous lateral parts of basal membrane with additional group of pale spines (Fig. 43) (absent in *C. lonsdalei*). Pregonite (Fig. 43) posteriorly fused (without incision) to hypandrium where it is dilated and not projecting ventrally, bearing 7 or 8 setae; 2 more setae arising on inner side of anterior part of pregonite, not far from posterior group of setae. Postgonite (Fig. 43) with slender, pigmented and distally acute anterior part, having 1 seta in distal third (finer than that of *C. lonsdalei*). Basal membrane posteromedially (including armature) sclerotized and integrated into caudal process of transandrium as given above, only its lateral part membranous (Figs. 43). Aedeagal part of folding apparatus (Fig. 44) with outer sides densely covered by flat rounded excrescences, connecting sclerite with group of small spines in anterior membranous part. Phal-lapodeme (Fig. 44) relatively slender but shorter than that of *C. lonsdalei*, with simply dilated apex without projecting corners. Aedeagus (Fig. 44) generally constructed as in *C. lonsdalei* but saccus of distiphallus more densely and finely spinose, middle part with ventral sclerotized tooth short and rounded (Fig. 44). Filum also very similar including shape of lanceolate apex but latter differing structurally in having multi-branched pigmentation (see Fig. 42). Ejacapodeme (Fig. 44) with digitiform projection somewhat dilated distally. **Female.** Similar to male except differences mentioned below. Total body length 2.06–2.54 mm (up to 2.98 mm when postabdomen expanded). **Head** (Fig. 10): Frons sometimes with indistinct (much less distinct than in *C. lonsdalei*) and anteriorly fading brown extension of stripe between posterior part of orbital plate and frontal triangle; face and gena not distinctly darker than in male in contrast to those of female *C. lonsdalei*; 1st antennal flagellomere darker yellow (or orange yellow), usually only narrowly (sometimes obscurely) pale brownish-darkened anterodorsally (Fig. 10), but very rarely more broadly darkened on inner side (up to anterodorsal half; some air-dried specimens with collapsed flagellomeres darkened on both sides).

Rarely (1 specimen) with 3 oc. Gena higher than in male (shortest height up to 0.22 times shortest eye diameter). **Thorax** (Fig. 10): Pleuron often shinier than in male including dorsal bare area on mesopleuron. **Legs:** f_3 uniformly finely setulose, without thickened spine-like setae. **Wing:** Measurements: length 1.71–2.28 mm, width 0.57–0.82 mm, $Cs_3 : Cs_4 = 0.91–1.39$, $r-m \backslash dm-cu : dm-cu = 1.84–2.82$. **Abdomen:** Preabdominal sterna narrower than in male but relatively wider than those of (female) *C. lonsdalei*; S2–S5 about as long as broad, but some slightly wider than long. **Postabdomen** (Figs. 46–48): T6 somewhat wider and more transverse than that of *C. lonsdalei*, also setosity usually denser but finer. S6 relatively larger (compared to T6), hardly paler than S7, with more setae. T7 (Fig. 47) narrower than T6, more tapered posteriorly, with denser setae, without pale lateral margins but with similar anteromedial emargination to that in *C. lonsdalei*. S7 (Fig. 48) elongate-suboblong but with more rounded sides, somewhat larger, with more setae in posterior half. T8 (Fig. 47) different, about as long as broad, with narrowed anterior part (but not triangular) and widened posterior third, with rounded posterior corners. S8 (Fig. 48) medially longitudinally divided but shorter. **Female genitalia:** Internal sclerotization of female genital chamber (Figs. 50, 51) distinctly different from that of *C. lonsdalei*: annular sclerite free, elongate, but smaller and thicker; anterior pair of sclerites (dorsally adjacent to latter) higher, not fused ventrally (cf. Fig. 51), and posterior pair of sclerites much larger and situated close to annular sclerite (Fig. 50). Anterior end of genital chamber bent at right angle dorsally as in congeners and ventral receptacle (Fig. 51), similar to that of *C. lonsdalei* including cup-like end. Remains of accessory glands of uncertain shape (not illustrated), on relatively slender ducts (Fig. 51). Spermathecae (1+1, one usually only slightly larger than other, occasionally nearly as unequal as in *C. browni*) resembling those of *C. lonsdalei* but with cervix longer (Fig. 49), with small, spine-like tubercles (with stalked globulae on apices not illustrated) usually more numerous (5–7) on tip, and some also on narrowed base of spermatheca. T10 (Fig. 47) similarly shaped but dark-pigmented mainly laterally, with antero-medial part contrastingly paler. S10 (Fig. 48) also dark-pigmented, very slightly wider than T10 but, in contrast to *C. lonsdalei*, subpentagonal, with posteromedial corner somewhat projecting. Cerci short, pale-pigmented, relatively close to each other (Fig. 47).

Etymology. This species is named in honour of the dipterist Dr. Steve Marshall, our friend and colleague and former graduate supervisor of KNB. He has provided access to many of his collections of Anthomyzidae including those of *Carexomyza* besides providing photographs of anthomyzids for inclusion in previous publications.

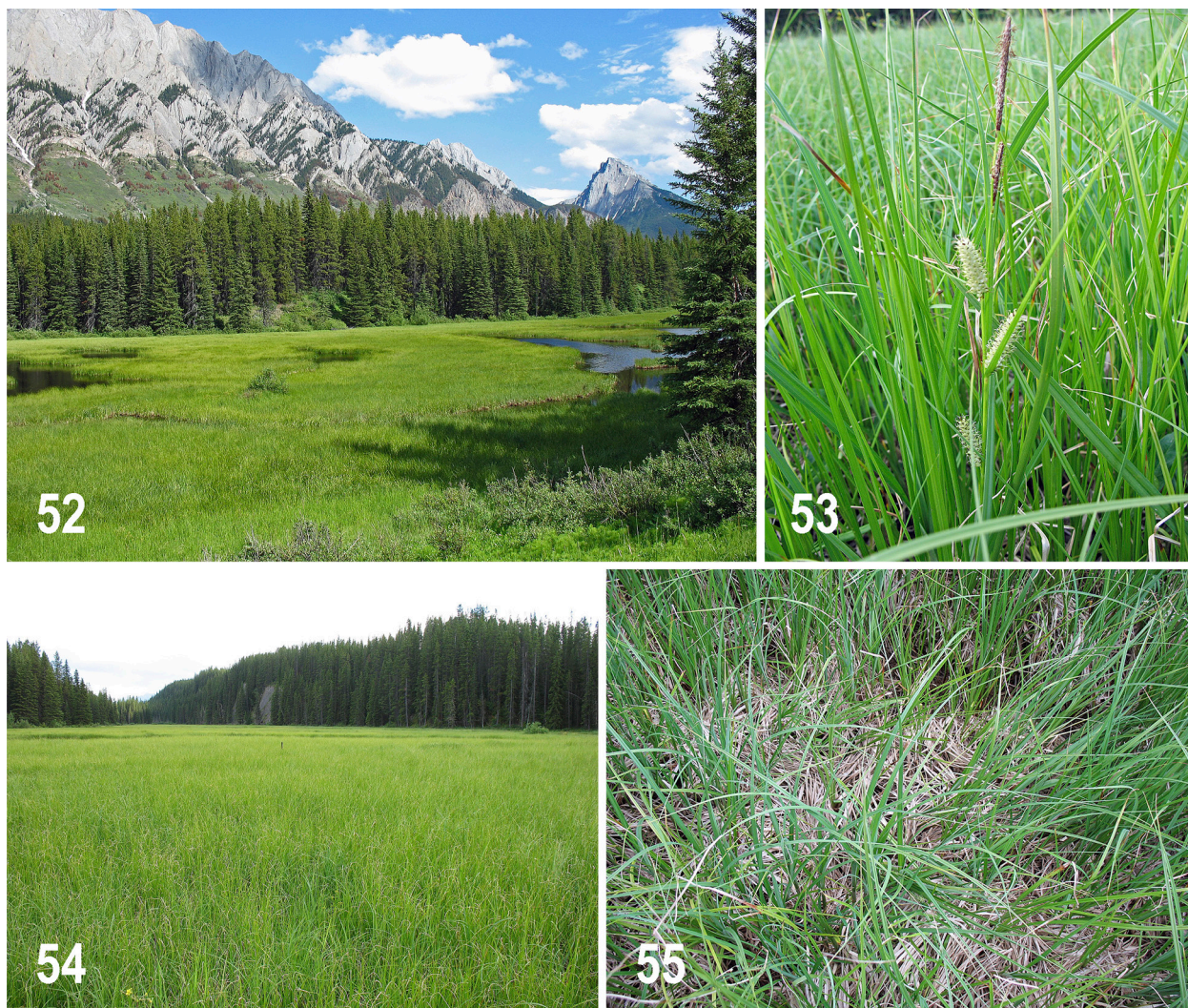
Discussion. *Carexomyza marshalli* sp.n. is the closest relative of *C. lonsdalei*. These two Nearctic species are very similar including the structures of the male and fe-



Figs. 46–51. *Carexomyza marshalli* sp.n., female paratype: 46: postabdomen, laterally; 47: ditto, dorsally; 48: ditto, ventrally; 49: spermathecae; 50: internal sclerites of female genital chamber, ventrally; 51: female genital chamber and 8th abdominal segment, laterally. — Scale bars: 46–48 – 0.2 mm; 49 – 0.05 mm; others – 0.1 mm.

male terminalia and they are also close genetically (see Fig. 91). The external differences between them are relatively subtle and often difficult to use due to variability

(see in the above description); also, male genital structures and postabdominal sclerites are very similar in both species but differ in some detail. *Carexomyza marshalli*



Figs. 52–55. Habitat of *Carexomyza marshalli* sp.n. and *C. browni* sp.n. at Peter Lougheed Provincial Park, Alberta (Fig. 52, 16 July 2011; Figs. 53–55, 13 July 2011). **52, 54:** sedge meadow with dominant *Carex utriculata* leading to open water; **53:** close-up view showing reproductive heads of *Cx. utriculata*; **55:** close-up view of *Cx. utriculata* growth and thick build-up of dried thatch. Photos by K.N. Barber.

has a generally lighter head (yellow area of frons larger) and its thorax (pleural part in particular) is shinier than in *C. lonsdalei*. Other most distinct differences (including those in the male and female terminalia) are given above in the “Discussion” under *C. lonsdalei*.

Biology. The first significant collections of this species (by KNB) were made in Alberta, principally within Peter Lougheed Provincial Park. The most productive site, the type locality, is a sedge meadow (labels mistakenly refer to this as a fen) supporting a dense growth of *Cx. utriculata* (see Figs. 52–55). Subsequent repeated sweep sampling of habitats dominated by *Cx. utriculata* frequently yielded specimens of *C. marshalli* while *C. browni* was often present though usually in lower numbers. However, the most extensive field observations for *C. marshalli* have come from Cochrane, Ontario and are discussed in the following subsection. A record from *Cx. stipata* (~28.5 km E Saint-Quentin, New Brunswick) is misleading as the site supported populations of both *Cx. stipata* and *Cx. utriculata*. The single specimen of *C. marshalli*

was obtained while directing the sweeping at *Cx. stipata* which was often surrounded by *Cx. utriculata*, the presumed nominal host plant for *C. marshalli*. Yet another single female was taken from *Cx. aquatilis* var. *aquatilis* but the source plants were directly across a narrow road from the *Cx. utriculata* that yielded many more specimens (Kananaskis Country, nr. Beehive Natural Area, Alberta). Another reason for questioning the relevance of this latter association is that many collections of anthomyzid flies from *Cx. aquatilis* var. *aquatilis* by KNB in Ontario have never yielded any *Carexomyza*.

Carexomyza marshalli co-occurred with only *C. browni* at eight localities in Alberta (Fish Creek Prov. Pk., S Grande Prairie, Obed, Peter Lougheed Prov. Pk. (2 discrete sites), Spray Valley Prov. Pk., W.A. Switzer Prov. Pk. (2 discrete sites)) and two localities in British Columbia (Ferne, Valemount). The only locality at which these two species co-occurred in Ontario was the Cochrane site where all three species were present. Besides this, a single U.S.A. site yielded both *C. marshalli* and *C. browni* (Nederland, Colorado). Available speci-

Table 2. Captures of *Carexomyza* species near Cochrane, Ontario in 2012 to 2018 (see section 3.5, Biology).

DATE	Total	Captures			Proportions		
		<i>C. lonsdalei</i>	<i>C. browni</i>	<i>C. marshalli</i>	<i>C. lonsdalei</i>	<i>C. browni</i>	<i>C. marshalli</i>
9-Jul-12	16	—	—	16	0.00	0.00	1.00
22-Jun-13	23	—	23	—	0.00	1.00	0.00
12-Jul-13	95	2	21	72	0.02	0.22	0.76
13-Jul-13*	10	1	1	8	0.10	0.10	0.80
18-Aug-13	48	—	—	48	0.00	0.00	1.00
19-Aug-13*	1	—	—	1	0.00	0.00	1.00
7-Jul-14	11	—	—	11	0.00	0.00	1.00
28-Jul-17	95	1	1	93	0.01	0.01	0.98
7-Jul-18	167	—	6	161	0.00	0.04	0.96
	466	4	52	410	0.01	0.11	0.88

* modest collections made the morning following a larger collection the previous day

men label data indicate that a single female has been taken from a fen in Churchill, Manitoba. Other generalized habitat descriptors include “vegetation in badlands” and “*Carex* roots” in Alberta, “forest floor, swamp” in British Columbia, “marshy stream margin” in Colorado, and “overgrown wet shrubby *Sphagnum* bog” in Ontario. The known flight period of *C. marshalli* runs from 17 June (Grande Prairie, Alberta; Valentines Gulch, Utah) to 30 September (Calgary, Alberta).

Collections at Cochrane, Ontario: The collection dates and captures of *Carexomyza* spp. at the Cochrane site are listed in Table 2. Although all three Nearctic species occur there, they were represented at widely disparate rates (~ 1 : 13 : 102 for *C. lonsdalei* : *C. browni* : *C. marshalli*, respectively) out of a total of 466 specimens over all collections and years. The Cochrane site was sampled in five seasons; i.e., 2012–2014, 2017, and 2018, but only in 2013 was there more than one trip made to the site. The two morning collections in 2013 were very limited in both effort and result (13 July, n=10 and 19 August, n=1) so only the late-afternoon and evening collections are plotted in Fig. 56.

It is striking that *C. browni* was the only species captured in the first sample of 22 June (n=23, Fig. 56), the only time a sample at the Cochrane site (through all years, Table 2) was represented by a single species other than *C. marshalli*. The second sample of 12 July yielded all three species with a similar number of *C. browni* (n=21) but clearly outnumbered by *C. marshalli* (n=72). This was the only sample in 2013 in which *C. lonsdalei* was captured (n=2) (other than an additional specimen collected the next morning, 13 July). The third sample of 18 August yielded only *C. marshalli* (n=48) and represents the seasonally latest sample ever taken at the site. This single season of 2013 with three samples suggests that of the two more abundant species, *C. browni* emerges earlier on this site (by 22 June), while *C. marshalli* persists later into the season (at least to 18 August). It should be noted that from all the material studied in this revision, the earliest seasonal record of *C. browni* is 24 May (Echo Bay, Ontario) and that for *C. lonsdalei* is 25 May (Detroit, Michigan), while for *C. marshalli* it is 17 June

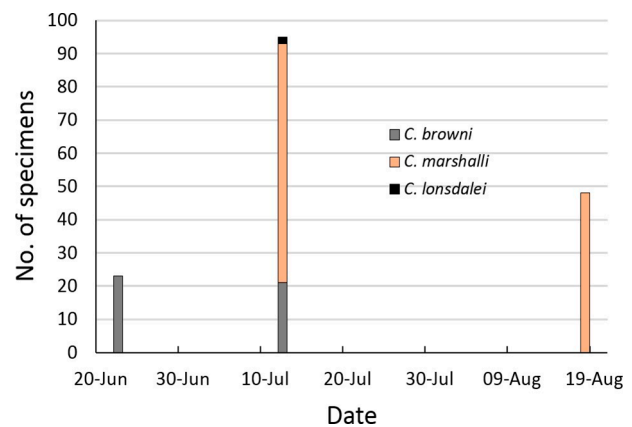


Fig. 56. Evening sweep samples of *Carexomyza* from mostly *Carex utriculata* near Cochrane, Ontario, in the year 2013 (22 June, 12 July, 18 August).

(Grande Prairie, Alberta; Valentines Gulch, Utah). Similarly, the latest record for *C. marshalli* is 30 September (Calgary, Alberta), while that for both *C. lonsdalei* (Finn Hill site) and *C. browni* (Pleasant Valley, Washington) is 4 August.

During the last two samples of 2013, swept specimens were collected into vials in a time series. On 12 July, three serial samples of unrecorded timing or duration yielded *C. browni* at n=5, 5, 11 specimens, respectively, and *C. marshalli* at n=3, 47, 22 specimens, respectively. This result suggests that the earlier sample of 22 June (*C. browni*, n=23) did not overlook *C. marshalli* because of mistiming of the sampling as both species were present over the entire collection period of 12 July. This supports the previous interpretation that *C. browni* becomes active as adults earlier in the season than does at least *C. marshalli* (too few captures of *C. lonsdalei* to assess). Subsequent attempts at collecting time-series samples on 18 August 2013 and 28 July 2017, including the use of a headlamp after sunset, were not very successful. Early samples attempting to minimize repeated sweeping of the same area yielded low numbers on both occasions and the appearance of slugs in the samples curtailed efforts on 28 July 2017.

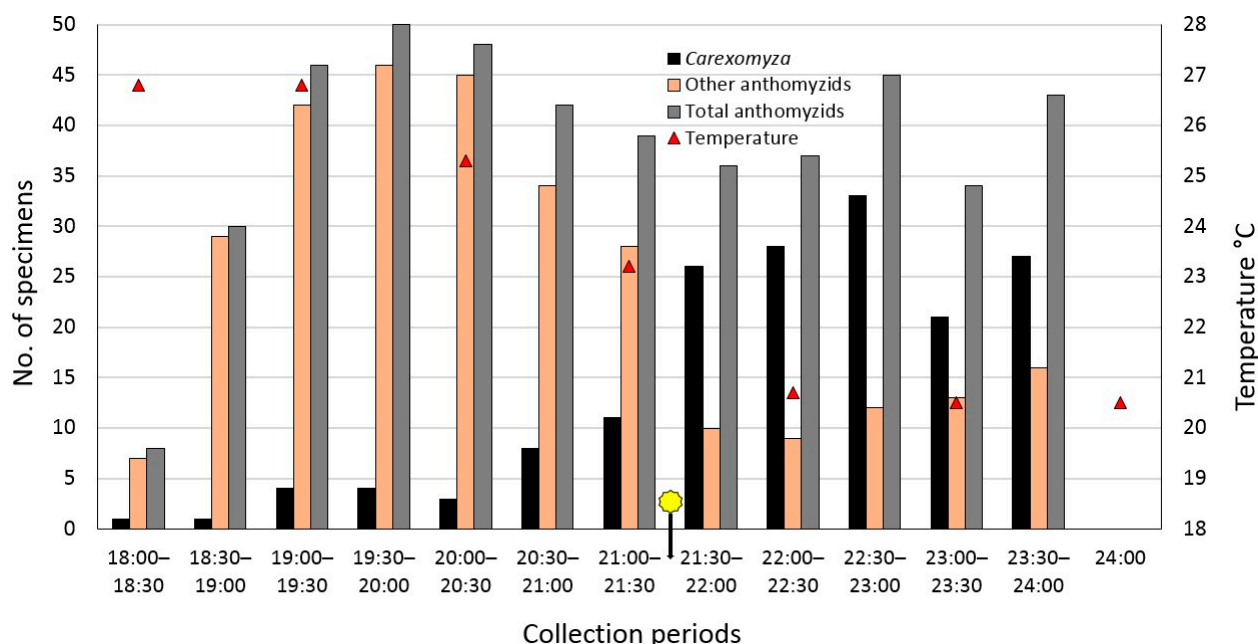


Fig. 57. Evening serial sweep samples of Anthomyzidae from mostly *Carex utriculata* near Cochrane, Ontario, on 7 July 2018. Temperature estimates on the hour. Black arrow indicates sunset at 21:30 EDT.

However, on 7 July 2018, much better success was achieved (although no specimens of *C. lonsdalei* were obtained) with 12 consecutive (nominally) 30-min samples from 18:00–24:00h obtained by sweeping randomly over the entire sample area. The plants remained dry and free of slugs and the headlamp was used beginning at 22:00h (sunset was calculated at 21:30h). Figure 57 provides the results of the 12 samples for all *Carexomyza* spp. combined (*C. marshalli* (n=161), *C. browni* (n=6)), for other anthomyzids (*Anthomyza gilviventris* Roháček & Barber, 2016 (n=166), *A. gibbiger* Roháček & Barber, 2016 (n=111), *A. shewelli* Roháček & Barber, 2016 (n=5), *A. orthogibbus* Roháček & Barber, 2016 (n=4), *A. mcalpinei* Roháček & Barber, 2016 (n=3), *Stiphrosoma balteatum* (n=2)), and for total anthomyzids (n=458).

As the heat of the day began to subside in the early evening, total anthomyzids (including *Carexomyza*) abruptly increased in numbers but were initially dominated by those species that are usually active in higher levels of the plants during the day. These other anthomyzids increased to a peak around 20:00h and then decreased to a low plateau by 22:00h. The *Carexomyza*, on the other hand, increased slowly during the first half of the evening.

As air temperature approached or fell below 22°C and, more importantly, as sunset approached (at 21:30h), the numbers of *Carexomyza* and other anthomyzids reversed positions in relative abundance. This is interpreted to be the result of the diurnally active species moving lower and out of reach with a sweep net (or possibly becoming depleted), while the *Carexomyza* moved up out of the thatch and duff into the aerial parts of the sedges. It is posited here that the decrease in light intensity with the setting of the sun is the more important cue in stimulating this upward movement in *Carexomyza*. The timing of

sunset at 21:30h falls at the time when the largest single increase in captures of *Carexomyza* (n=11 to 26) was obtained and captures remained elevated. These larger samples of *Carexomyza* were obtained after sunset occurred when temperatures dropped no lower than 20.5°C and represent 80.8% (135/167) of captures for the entire 6-hr sampling period. If a temperature threshold alone was sufficient to induce such vertical migration then an increase in captures might have been expected during the sampling of 28 July 2017 when, during the initial period of 19:00–21:00h leading to sunset (21:09hr), the air temperatures fell from 25.1 to 17.6°C yet the captures remained relatively low and steady (n=4, 13, 9, 7). An interaction effect between decreasing light and heat is certainly possible.

This behaviour may be at the root of why *Carexomyza* is not commonly represented in museum collections. Most sampling with a sweep net is conducted during the day and early evening when *Carexomyza* adults are more likely to be out of reach. Locating appropriate prospective habitats with appropriate host plants is still a key prerequisite for success in finding these small, dark anthomyzids. There is no doubt that a single pass through an area with a sweep net does not constitute an adequate sampling effort in the search for *Carexomyza* (a similar experience was encountered at Carter Creek, Utah where specimens were found only during the second of two hours (17:00–19:00hr) of sweeping the same general area). The very first large collection of *Carexomyza* in Peter Lougheed Provincial Park, Alberta (13 July 2011) was an evening collection that yielded n=186 *C. marshalli* and n=38 *C. browni*. A productive evening collection of *C. browni* (Mount Carleton Provincial Park, New Brunswick) is discussed under that species (below) including potential limits to generalizing this vespertine behaviour.

A possible confounding factor in interpreting the behaviour of adult *Carexomyza* is the influence of trampling of the sample area with repetitive sampling. Such a factor is probably impossible to remove given the restricted number of identified sites and the small size of “hotspots” where the densities of the target species are sufficiently high. As would be expected for a species that spends much of the day in the thatch and duff, the combined disturbances of trampling and vigorous sweeping likely contribute a “flushing” effect on these flies.

Distribution. Canada: Alberta, British Columbia, Manitoba, New Brunswick, Ontario, Yukon. United States of America: Colorado, Idaho, Montana, Utah, Wyoming. *Carexomyza marshalli* is widespread across Canada and includes Yukon with a noticeable absence from Saskatchewan in western Canada. It is the only species yet known from Idaho, Utah and Wyoming. Five of the most southerly U.S.A. records are at relatively high elevation (Colorado: Nederland 8500' [2590 m], Florissant 2530 m; Utah: Carter Creek 2215 m, Valentines Gulch 2549 m; Wyoming: Hoback 6500' [1981 m]).

Material examined. Type material: Holotype ♂, ‘CAN: AB: Peter Loughheed | PPK, 13.vii.2011, KNBarber, | sweeps, fen, *Carex utriculata* with cf. *Poa pratensis* | 50°41.82'N 115°06.92'W’, ‘debu | 01503065’, and ‘Holotypus ♂ | *Carexomyza* | *marshalli* sp.n. | K.N. Barber & J. | Roháček det. 2019’ (red). The specimen is in excellent condition with yellow gonostyli highly visible and minor damage to right wing (DEBU, intact, Fig. 6). Paratypes 492♂ 635♀. **CANADA: Alberta:** ~ 22.7 km S Bellevue, Hwy 774, 49°22.62'N 114°22.58'W, sweeps, roadside ditch, mostly *Carex* spp., *Equisetum*, grasses, 17.vii.2011, K.N. Barber leg., 1♀ (CNCI); ~ 18.3 km NW Cadomin, Hwy #40, 53°10.02'N 117°29.72'W, sweeps, edge of roadside pond, K.N. Barber leg., *Carex* spp., 22.vii.2008, 1♂, mostly *Juncus* & non-flowering *Carex*, 24.vii.2011, 2♀ (CNCI); Calgary, Fish Creek Prov. Pk., sweep around pond by 2nd bridge, Shannon Terrace, 9.vii.2010, J.E. Swann leg., 1♀ (BDUC); Calgary, Fish Creek Prov. Pk., 50°55.579'N 114°07.404'W, sweep around pond with sedges near Shannon Terrace, 12.viii.2011, J.E. Swann leg., 2♂ 2♀ (BDUC); Calgary, Fish Creek Prov. Pk., 50°55.600'N 114°07.426'W, sweep, oxbow with sedges, 30.ix.2011, J.E. Swann leg., 2♂ (BDUC); Calgary, Fish Creek Prov. Pk., 50°55.600'N 114°07.427'W, pond near Shannon Terrace, swept from sedges and *Equisetum*, 12.viii.2011, J.E. Swann leg., 8♂ 4♀ (BDUC); Fish Creek Prov. Pk., 50°55.61'N 114°07.43'W, sweeps, mostly *Carex utriculata* and *Equisetum fluviatile*, 12.vii.2011, J.E. Swann & K.N. Barber leg., 2♂ 7♀ (BDUC); ~ 10.7 km N Coleman, Hwy 40, 49°44.15'N 114°28.29'W, sweeps, edge of fen, *Carex utriculata*, 20.vii.2011, K.N. Barber leg., 1♂ 2♀ (CNCI); Elbow-Sheep Wildland Pk., ~ 22.5 km NW Highwood House, 50°31.38'N 114°53.17'W, pooter, *Carex utriculata*, K.N. Barber leg., 14.vii.2011, 1♂ 4♀ (DEBU 01502596–600), 16.vii.2011, 1♂ (DEBU 01503660); Elbow-Sheep Wildland Pk., ~ 22.5 km NW, Highwood House, 50°31.38'N 114°53.17'W, sweeps, *Carex utriculata*, 14.vii.2011, K.N. Barber leg., 1♂ (DEBU 01502584); Elbow-Sheep Wildland Pk., ~ 22.5 km NW Highwood House, 50°31.40'N 114°53.12'W, sweeps, *Carex utriculata*, 14.vii.2011, K.N. Barber leg., 1♂ 6♀ (DEBU 01502662, -64–69); ~ 22.5 km NW Highwood House, ~ 4 km W Mist Creek, 50°31.38'N 114°53.17'W, sweeps, *Carex* sp. (large), 25.vii.2008, K.N. Barber leg., 1♀ (CNCI); ~ 22.5 km NW Highwood House, ~ 4 km W Mist Creek, 50°31.40'N 114°53.12'W, sweeps, *Carex* sp. (small), 25.vii.2008, K.N. Barber leg., 2♀ (CNCI); Hwy 40, S Grande Prairie, *Carex* roots, 17.vi.1987, S.A. Marshall leg., 1♂ (DEBU); Kananaskis, 2 km N Barrier Lake Res. Stn., 51°02.4'N 115°01.7'W, sweep around beaver ponds at trail en-

trance, 29.vii.2003, S. Boucher leg., 1♂ 1♀ (LEMQ 0040431, -32); Kananaskis Country, nr. Beehive Natural Area, 50°05.08'N 114°36.45'W, sweeps, roadside seep, *Carex aquatilis aquatilis*, 17.vii.2011, K.N. Barber leg., 1♀ (CNCI); Kananaskis Country, nr. Beehive Natural Area, 50°05.07'N 114°36.47'W, sweeps, hillside seep, *Carex utriculata*, K.N. Barber leg., 17.vii.2011, 6♂ 10♀ (1♂ genit. prep.), 20.vii.2011, 3♂ 5♀ (CNCI); Kananaskis Country, nr. Beehive Natural Area, 50°05.07'N 114°36.47'W, pooter, hillside seep, *Carex utriculata*, 20.vii.2011, K.N. Barber leg., 2♂ 6♀ (CNCI); Kananaskis Country, nr. Beehive Natural Area, 50°05.08'N 114°36.50'W, sweeps, hillside seep, *Carex utriculata*, K.N. Barber leg., 17.vii.2011, 6♂ 7♀, 20.vii.2011, 3♂ 12♀ (CNCI); Kluskin Hill, 55°15.540'N 118°30.620'W, sweep vegetation in badlands, 21.vii.2003, S. Boucher leg., 1♀ (LEMQ 0040469); 25 mi N Nordegg, *Carex* roots, 20.vii.1987, S.A. Marshall leg., 1♀ (DEBU); ~ 14.4 km E Obed, Range Rd. 213 @ RR crossing, 53°32.19'N 117°01.02'W, sweeps, mostly *Carex utriculata*, 25.vii.2011, K.N. Barber leg., 1♂ 2♀ (CNCI, 1♀ genit. prep.); Peter Loughheed Prov. Pk., 50°41.82'N 115°06.92'W, sweeps, fen, *Carex utriculata* with cf. *Poa pratensis*, K.N. Barber leg., 13.vii.2011, 63♂ 116♀ (DEBU 01503058–064, -066–075, -076 [♂ genit. prep.], -077–084, -085 [♂ genit. prep.], -086–92, -093 [♂ genit. prep.], -094–110, -111 [♂ genit. prep.], -112–118, -119 [♂ genit. prep.], -120 [♂ genit. prep.], -122 [♂ genit. prep., wing photo, left wing in glycerine microvial], -131–39, -141–149, -150 [♀ genit. prep.], -151–154, -155 [♀ genit. prep.], -156–185, -187–196, -198–226, -227 [♀ genit. prep.], -228–232, -234–250, [♀ genit. prep.]), 14.vii.2011, 1♂ 4♀ (DEBU 01503296, -299–302), 15.vii.2011, 6♂ 10♀ (DEBU 0150335–38, -40, -41, 0150343–52), 16.vii.2011, 15♂ 24♀ (DEBU 01503395–409, 01503412–433, -434 [♀ head/thorax photo], -435 [♀ genit. prep.]); Peter Loughheed Prov. Pk., Upper Lake Drive, 50°36.98'N 115°07.13'W, sweeps, edge of fen, *Carex utriculata*, K.N. Barber leg., 14.vii.2011, 3♂ 11♀ (DEBU 01503315–17, -19, -20, -22–24, -26–31), 16.vii.2011, 60♂ 69♀ (DEBU 01503508–579, -581–583, -585–615, -617–639), 21.vii.2011, 1♂ 3♀ (DEBU 01503672–75); Peter Loughheed Prov. Pk., Upper Lake Drive, 50°36.98'N 115°07.13'W, sweeps/pooter, edge of fen, *Carex utriculata*, 15.vii.2011, K.N. Barber leg., 4♂ 8♀ (DEBU 01503366–77); Peter Loughheed Prov. Pk., Upper Lake Drive, 50°36.98'N 115°07.13'W, pooter, edge of fen, *Carex utriculata*, 16.vii.2011, K.N. Barber leg., 3♂ (DEBU 01503640–42); Peter Loughheed Prov. Pk., Upper Lake Drive, 50°36.94'N 115°07.16'W, sweeps, edge of fen, *Carex utriculata*, 16.vii.2011, K.N. Barber leg., 1♂ 1♀ (DEBU 01503653, -54); Spray Valley Prov. Pk., 50°48.95'N 115°09.84'W, sweeps, fen, *Carex utriculata?* and *Poa* sp., 13.vii.2011, K.N. Barber leg., 1♀ (DEBU 01502857); Spray Valley Prov. Pk., Buller Mt. day use, 50°52.02'N 115°21.23'W, sweeps, edge of fen, *Carex utriculata?*, 15.vii.2011, K.N. Barber leg., 1♀ (DEBU 01503380); W.A. Switzer Prov. Pk., Beaver Ranch Trail, 53°29.67'N 117°48.00'W, sweeps, sedge-filled oxbow, *Carex utriculata?*, 22.vii.2011, K.N. Barber leg., 8♂ 2♀ (DEBU 01503778–787); W.A. Switzer Prov. Pk., Beaver Ranch Trail, 53°29.80'N 117°48.02'W, sweeps, edge of Jarvis Ck., *Carex utriculata*, 22.vii.2011, K.N. Barber leg., 15♂ 28♀ (DEBU 01503724–738, -740–767); W.A. Switzer Prov. Pk., off Hay River Rd. W, 53°33.44'N 117°48.43'W, sweeps, mostly *Carex utriculata*, K.N. Barber leg., 22.vii.2011, 4♂ 5♀ (DEBU 01503802–10), 24.vii.2011, 19♂ 15♀ (DEBU 01503877–895, -899–913). **British Columbia:** Fernie, Annex Pk., 49°30'43"N 115°04'07"W, 2.viii.2010, S.M. Paiero leg., 2♂ 2♀ (DEBU 00334415 [♂ genit. prep.], -98, -31, -33); Fernie, Annex Pk., 49°30.72'N 115°04.13'W, sweeps, wet ditch, *Carex utriculata*, K.N. Barber leg., 17.vii.2011, 1♂ 1♀, 18.vii.2011, 1♂ (CNCI); Fernie, Annex Pk., 49°30.66'N 115°04.16'W, sweeps, pond margin, *Carex utriculata*, K.N. Barber leg., 18.vii.2011, 1♂, 19.vii.2011, 1♀ (CNCI); Mt. Robson Prov. Pk., Hwy #16, small road towards Mt. Robson, 53°03'N 119°15'W, forest floor, swamp, (Universität Bielefeld, Ca1519), 6.viii.2002, M. v. Tschirnhaus leg., 1♂ (ZSMC); ~ 27 km N Sparwood, Lower Elk Valley Rd., 49°50.24'N 114°53.29'W, sweeps, edge of creek, *Carex utriculata?*, 20.vii.2011, K.N. Barber leg., 1♂ (CNCI); Sum-

mit Lake, mi. 392 Alaska Hwy, 4200', 21.vii.1959, R.E. Leech leg., 1♀ (CNCI); ~ 8.0 km SE Valemount, edge of Kinbasket Lake, 52°46.65'N 119°10.38'W, sweeps, mostly *Carex utriculata*, 23.vii.2011, K.N. Barber leg., 2♂ 2♀ (CNCI); ~ 9.6 km SE Valemount, edge of Kinbasket Lake, 52°45.74'N 119°09.68'W, sweeps, mostly *Carex* spp., 23.vii.2011, K.N. Barber leg., 1♀ (CNCI). **Manitoba:** 12 km ESE Churchill, Launch Rd., 58.7541°N -93.9973°W, 10 m a.s.l., fen, 19.vii.2010, J. Wang leg., 1♀ (BIOUG, Barcode of Life, Sample ID# 10PROBE-16715, in ethanol). **New Brunswick:** ~ 28.5 km E Saint-Quentin, Pat Brook jct. with East Branch, 47°29.46'N 67°00.76'W, sedge meadow, afternoon ~ 13:30–16:00 sweeps, mostly *Carex stipata*, 30.vi.2019, K.N. Barber leg., 1♀ (CNCI). **Ontario:** ~ 13.5 km S Cochrane, 48°56.65'N 81°00.18'W, hydro right-of-way, sweeps, mostly *Carex utriculata*, K.N. Barber leg., 9.vii.2012, 8♂ 7♀ (CNCI), 12.vii.2013, 41♂ 31♀ (CNCI, 22♂ 12♀; AMNH, 5♂ 5♀; CASC, 5♂ 5♀; INHS, 5♂ 5♀; SMOC, 4♂ 4♀), 13.vii.2013, 8♂, 18.viii.2013, 8♂ 7♀ (1♀ genit. prep.), 19.viii.2013, 1♀, 7.vii.2014, 6♂ 5♀ (1♀ genit. prep.) (CNCI), 28.vii.2017, 24♂ 35♀ (CNCI, 13♂ 24♀ [2♀ genit. prep.]; SMOC, 3♂ 3♀; USNM, 8♂ 8♀), 7.vii.2018, 28♂ 21♀ (CNCI, 18♂ 11♀ [1♀ genit. prep.]; LACM, 5♂ 5♀; LEMQ, 5♂ 5♀); ~ 13.5 km S Cochrane, 48°56.65'N 81°00.18'W, hydro right-of-way, “headlamp” sweeps, mostly *Carex utriculata*, K.N. Barber leg., 18.viii.2013, 13♂ 19♀ (1♀ genit. prep.), 28.vii.2017, 14♂ 16♀ (CNCI), 7.vii.2018, 42♂ 59♀ (CNCI, 17♂ 25♀ [3♀ genit. prep.]; MTEC, 4♂ 6♀; NMBM, 4♂ 6♀; RBCM, 4♂ 6♀; SEMC, 4♂ 6♀; SMOC, 9♂ 10♀); ~ 25 km WNW Ignace, 49°29.52'N 92°00.83'W, sweeps, fen, mostly *Carex utriculata* with grasses, K.N. Barber leg., 4.vii.2012, 18♂ 10♀ (CNCI, 14♂ 7♀; SMOC, 4♂ 3♀), 5.vii.2012, 6♂ 4♀ (2♀ genit. prep.), 6.vii.2012, 7♂ 16♀ (CNCI); ~ 25 km WNW Ignace, 49°29.58'N 92°00.97'W, sweeps, fen, graminoids incl. *Carex utriculata*, 5.vii.2012, K.N. Barber leg., 3♂ 2♀ (CNCI); ~ 25 km WNW Ignace, 49°29.48'N 92°00.75'W, sweeps, fen, mostly *Carex utriculata* with grasses, 30.vii.2011, K.N. Barber leg., 2♂ 1♀ (CNCI, 1♂ genit. prep.); Iroquois Falls, overgrown wet shrubby *Sphagnum* bog, 30.vi.1987, J.R. Vockeroth leg., 1♂ (CNCI); Moosonee, 51°16.17'N 80°39.10'W, sweeps, mostly *Carex utriculata*, *Scirpus*, in wet hydro cut, 10.vii.2014, K.N. Barber leg., 1♂ (CNCI); Moosonee, 51°16.54'N 80°39.00'W, sweeps, *Equisetum*, *Rubus*, *Cornus*, graminoids, edge of wet forest trail, 10.vii.2014, K.N. Barber leg., 1♀ (CNCI); Otter Rapids, 50°10.80'N 81°38.59'W, sweeps, *Carex* spp., 19.vii.2009, K.N. Barber leg., 1♀ (CNCI). **Yukon:** 58 mi E Dawson, Gravel Lk., 2050', 10.viii.1962, R.E. Leech leg., 1♀ (CNCI); Klondike Hwy, 8.8 km S Twin Lakes, Conglomerate Mt., 61°37.9'N 135°53.1'W, sweep along Klusha Creek, T.A. Wheeler leg., 15.vii.1998, 1♀, 25.vii.1998, 1♂ (LEMQ). **UNITED STATES OF AMERICA: Colorado:** 3 mi N Nederland, 8500', marshy stream margin, 2.vii.1961, J.G. Chillcott leg., 1♀ (CNCI); Teller Co., Florissant, Petrified Forest Area, 2530 m, 11.viii.1973, P.H. Arnaud Jr. leg., 1♀ (CASC). **Idaho:** Caribou Co., Kendall Cr., 25.vi–3.vii.1981, W.J. Hanson leg., 1♀ (LACM, genit. prep.). **Montana:** 4 mi E Polson, Biol. Note No. 6825, 19.vii.1981 [ambiguous date], T.J. Rogers leg., 1♀ (CNCI). **Utah:** Cache Co., W. Hodges Canyon, Hanson & Knowlton leg., 4–8.viii.1978, 1♂, 28–31.vii.1978, 1♀ (LACM); Cache Co., Tony Grove Jct., Malaise, trap, 19–27.vii.1983, [no collector], 1♀ (LACM); Daggett Co., Ashley Nat. For., ~ 12.8 km S Manila, Hwy 44 @ Carter Creek, 2215 m, 40°52.33'N 109°41.49'W, sweeps (after 19:00), mostly *Carex utriculata*, 18.vi.2018, K.N. Barber leg., 1♂ 5♀ (CNCI); Emery Co., Manti-La Sal Nat. For., Valentines Gulch, ~ 35.9 km NW Huntington, 2549 m, 39°35.61'N 111°12.30'W, mini fen above Huntington Ck., sweeps, mostly *Carex utriculata*, 17.vi.2018, K.N. Barber leg., 2♂ (CNCI); Uintah Co., Whiterocks Canyon, 31.vii.1972, W.J. Hanson leg., 1♂ (LACM). **Wyoming:** Teton Co., Hoback, 6500', 24.vii.1953, R.R. Dreisbach leg., 1♂ (USNM, genit. prep.). — **Other material:** **CANADA: Alberta:** Calgary, Fish Creek Prov. Pk., sweep around pond by 2nd bridge, Shannon Terrace, 9.vii.2010, J.E. Swann leg., 1♀ (BDUC, fractured thorax); Calgary, Fish Creek Prov. Pk., 50°55.600'N 114°07.427'W, pond near Shannon Terrace, swept from sedges and *Equisetum*, 12.viii.2011, J.E. Swann leg.,

1♀ (BDUC, abdomen ruptured); Elbow-Sheep Wildland Pk., ~ 22.5 km NW, Highwood House, 50°31.40'N 114°53.12'W, sweeps, *Carex utriculata*, 14.vii.2011, K.N. Barber leg., 1♂ (DEBU 01502663, genit. prep., left wing missing); Elbow-Sheep Wildland Pk., ~ 22.5 km NW, Highwood House, 50°31.38'N 114°53.17'W, pooter, *Carex utriculata*, 14.vii.2011, K.N. Barber leg., 1♂ (DEBU 01502595, left wing and head lost); Kananaskis Country, nr. Beehive Natural Area, 50°05.07'N 114°36.47'W, pooter, hillside seep, *Carex utriculata*, 20.vii.2011, K.N. Barber leg., 1♀ (CNCI, abdomen lost); Kananaskis Country, nr. Beehive Natural Area, 50°05.08'N 114°36.50'W, sweeps, hillside seep, *Carex utriculata*, 20.vii.2011, K.N. Barber leg., 1♀ (CNCI, genit. prep., thorax damaged, leg missing); Peter Lougheed Prov. Pk., 50°41.82'N 115°06.92'W, sweeps, fen, *Carex utriculata* with cf. *Poa pratensis*, K.N. Barber leg., 13.vii.2011, 2♂ 4♀ (DEBU 01503057, -121 [♂ genit. prep.], -140, -186, -197, -233, various damage of body and/or wings), 14.vii.2011, 1♀ (DEBU 01503298, abdomen ruptured), 15.vii.2011, 2♂ (DEBU 01503339, -53, abdomens ruptured, wings torn in latter); Peter Lougheed Prov. Pk., Upper Lake Drive, 50°36.98'N 115°07.13'W, sweeps, edge of fen, *Carex utriculata*, K.N. Barber leg., 14.vii.2011, 1♂ 2♀ (DEBU 01503318 [1♂ genit. prep. but genitalia missing possibly resulting from a torn apart mating], -321, -325 [2♀ abdomen ruptured]), 16.vii.2011, 3♀ (DEBU 01503580, -584, -616, wing and/or body damage); Peter Lougheed Prov. Pk., Upper Lake Drive, 50°36.98'N 115°07.13'W, sweeps/pooter, edge of fen, *Carex utriculata*, 15.vii.2011, K.N. Barber leg., 1♂ 1♀ (DEBU 01503365, -78, wing and thorax damage, respectively); W.A. Switzer Prov. Pk., Beaver Ranch Trail, 53°29.80'N 117°48.02'W, sweeps, edge of Jarvis Ck., *Carex utriculata*, 22.vii.2011, K.N. Barber leg., 1♂ 1♀ (DEBU 01503723, -69, both headless); W.A. Switzer Prov. Pk., off Hay River Rd. W, 53°33.44'N 117°48.43'W, sweeps, mostly *Carex utriculata*, 24.vii.2011, K.N. Barber leg., 1♂ (DEBU 01503876, headless). **Ontario:** ~ 13.5 km S Cochrane, 48°56.65'N 81°00.18'W, hydro right-of-way, sweeps, mostly *Carex utriculata*, K.N. Barber leg., 9.vii.2012, 1♀ (CNCI, crushed thorax), 28.vii.2017, 1♂ 1♀ (CNCI, ♂ crushed head, genit. prep., ♀ ruptured abdomen), 7.vii.2018, 2♂ 3♀ (CNCI, 1♀, head glued to thorax; SMOC, 2♂ 2♀, in ethanol with 1♂ DNA extraction but no analysis); ~ 13.5 km S Cochrane, 48°56.65'N 81°00.18'W, hydro right-of-way, “headlamp” sweeps, mostly *Carex utriculata*, K.N. Barber leg., 18.viii.2013, 1♀ (CNCI, ruptured abdomen), 28.vii.2017, 2♀ (CNCI, 1♀ genit. prep., with damaged wings, 1♀ missing antennae), 7.vii.2018, 2♂ 4♀ (CNCI, 2♂ 1♀ [1♀ head fractured, missing antennae, 2♂ missing antennae or thorax fractured]; SMOC, 3♀ [1♀ used in molecular analysis in glycerine mount, 2♀ in ethanol with head or abdomen damaged]); ~ 25 km WNW Ignace, 49°29.52'N 92°00.83'W, sweeps, fen, mostly *Carex utriculata* with grasses, K.N. Barber leg., 4.vii.2012, 1♂ 3♀ (CNCI, 1♀, with deformed T5, T6; SMOC, 1♂ 2♀, degraded in ethanol), 5.vii.2012, 1♂ (CNCI, missing antennae), 6.vii.2012, 1♂ (CNCI, ruptured abdomen). **UNITED STATES OF AMERICA: Colorado:** New Castle, 15.vii.1966, W. Boyle & R. Lalonde leg., 1♀ (LEMQ, missing antennae). **Utah:** Cache Co., W. Hodges Canyon, 14–18.vii.1978, Hanson & Knowlton leg., 1♂ (LACM, abdomen lost).

3.6. *Carexomyza browni* sp.n.

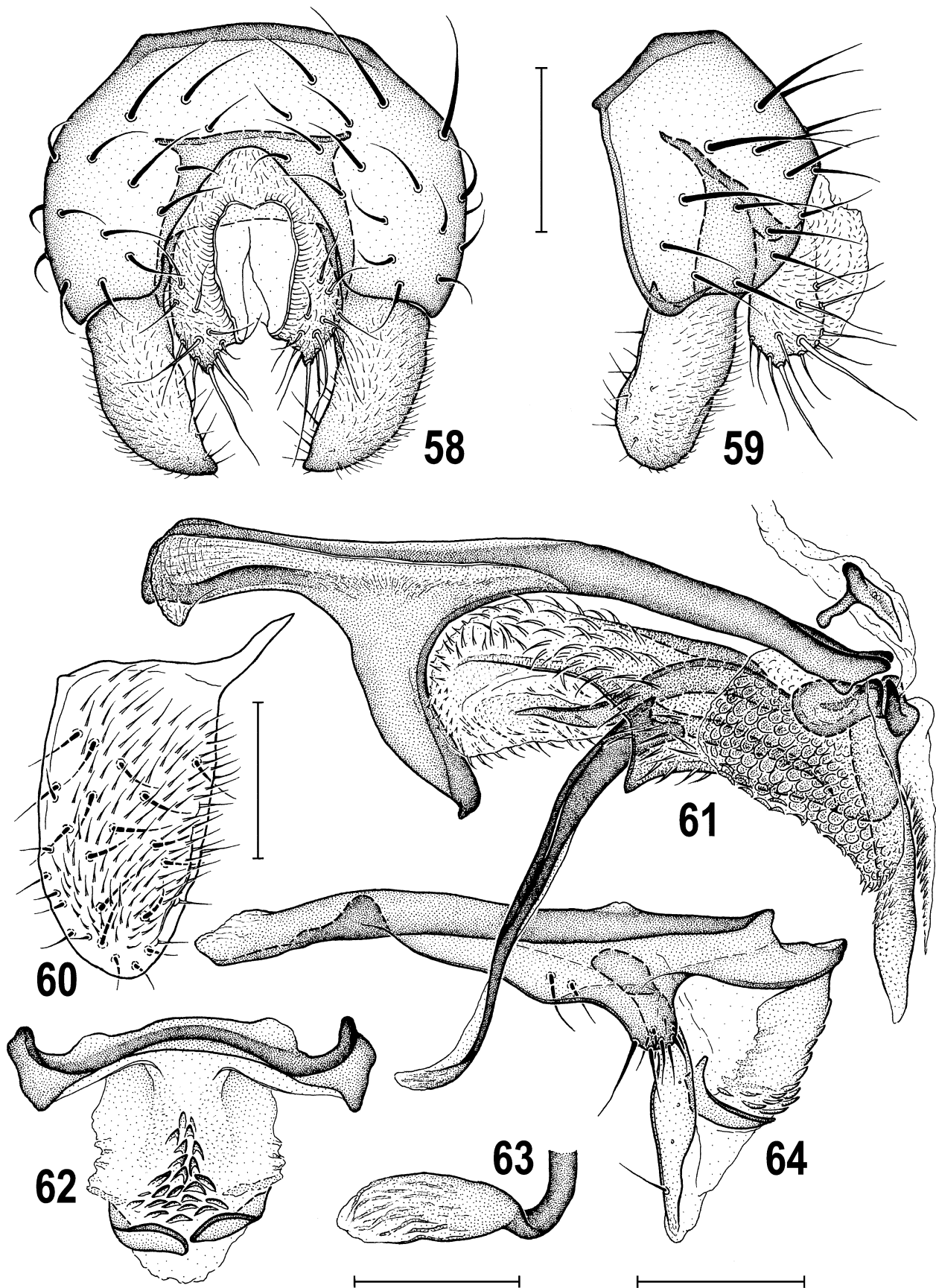
(Figs. 8, 11, 14, 58–72)

Carexomyza sp.n. 3: ROHÁČEK et al. 2019: 753 (fig. 2), 755 (fig. 4) [molecular phylogeny, trees only].

Description. Male (Fig. 8). Total body length 1.67–2.34 mm; general colour blackish brown, only head anteriorly and legs yellow; thorax (more) and abdomen (less) relatively shiny despite sparse greyish-brown microtomentum. **Head:** Slightly higher than long and/or as

long as high, and somewhat wider than thorax in dorsal view; dorsal part of occiput very slightly concave. Frons moderately broad but tapered anteriorly; anterior part (two-fifths to half) yellow, though sometimes pale brown surrounding apex of frontal triangle (anterior extension of stripe), remainder of frons usually brown to blackish brown, rarely with yellow extending posteriorly along margin of frontal triangle to level of posterior ors then pale brown up to vti. Orbital plate yellow and silvery-white microtomentose up to posterior ors (but usually brownish-darkened around bases of both ors), posterior part dark brown and silvery-grey microtomentose up to vti though often appearing shiny externally (in frontal view). Frontal lunule reduced, very small, yellow. Frontal triangle relatively short and narrow, reaching anterior two-fifths to half of frons, blackish brown and sometimes appearing shiny (in contrast to remainder of frons dull) despite microtomentum. Ocellar triangle concolourous with frontal triangle, often appearing shiny (in frontal view, similar to external dark part of orbital plate) and contrasting with adjacent stripe, slightly but distinctly protruding. Ocelli medium-sized and situated close (1.5 times or less diameter of ocellus) to each other; oc setae arising on margin of ocellar triangle. Stripe between posterior part of orbital plate and frontal triangle typically dull brown (rarely pale brown) and silvery-grey to silvery-blue microtomentose, particularly posteriorly, blending into adjacent silvery-grey microtomentum of orbital plate. Occiput brownish black, with sparse dark-grey microtomentum. Face yellow, dull, medially less sclerotized and concave, laterally with golden-yellow stripe extended (but darkened) along ventral margin of gena. Parafacialia whitish yellow and silvery-white microtomentose. Gena largely whitish yellow and silvery-white microtomentose but ventrally with subshiny ochreous marginal stripe terminated with small, elongate dark spot posteroventrally; postgena dark brown. Cephalic chaetotaxy: all setae relatively long and strong (cf. Figs. 8, 11) as in *C. caricis*; pvt short but more or less crossed; vti, vte and posterior (longest) ors strong and subequal in length; oc (longest cephalic seta) usually slightly longer than vti; 2 long ors (posterior somewhat longer than anterior) and 2 (rarely only 1) microsetulae (anterior much shorter than posterior) in front of anterior ors; 1–3 pairs of microsetulae medially, in anterior third of frons; a few (5 or 6) postocular setulae in single short row at postero-dorsal margin of eye and 1 inclinate setula behind vte; 1 long vi and 1 shorter subvibrissa (usually two-thirds to three-fourths, very rarely less than half of vi); gena with a few (4 or 5) weak peristomal setulae; postgena with 2 usual (relatively short) setae. Eye subovoid, strongly convex, longest diameter about 1.4 times shortest diameter. Gena short, shortest height about 0.15 times shortest eye diameter. Palpus slender, pale yellow, with single dark ventral preapical seta. Mouthparts whitish yellow but clypeus almost black and prementum brownish. Antenna strongly geniculate, bright yellow; 1st flagellomere strongly compressed laterally, with short whitish ciliation. Arista subbasal, about 1.6 times as long as antenna,

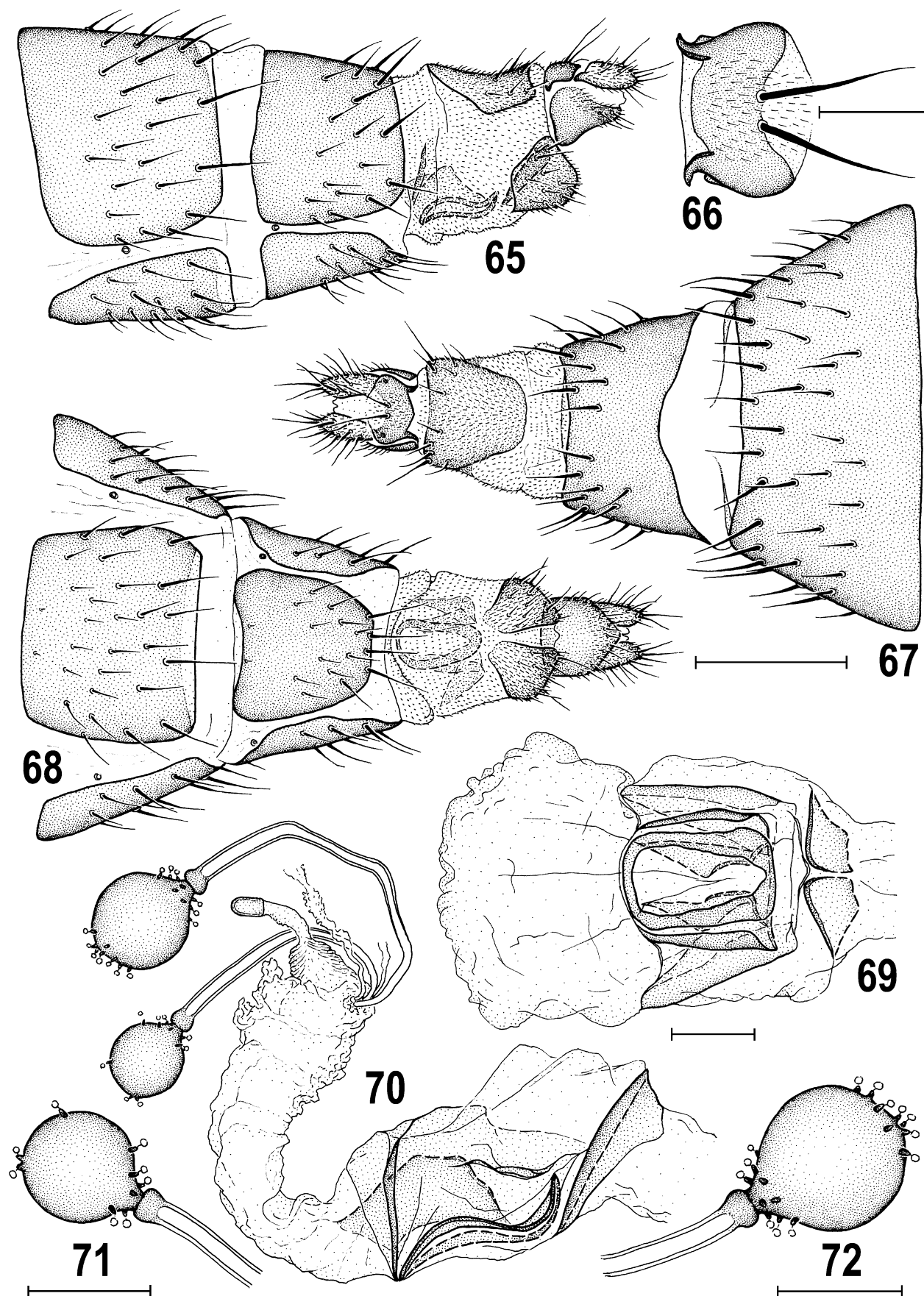
sparsely short ciliate, two basal aristomeres thickened and ochreous, otherwise blackish brown. **Thorax:** Entirely blackish brown, sparsely brownish-grey microtomentose, relatively shiny, most distinctly on scutum anterodorsally, pleural parts duller with no dorsal bare area on mesopleuron. Thoracic chaetotaxy: 1 hu (weaker than npl), 2 npl (anterior longer), 1 small prs, 1 sa (shorter), 1 pa (longer), 3 (2 if anterior dc reduced) postsutural dc becoming shorter anteriorly, foremost dc usually only one-third of middle dc; 3–5 dc microsetae in front of them; only 2 rows of ac microsetae ending in front of posterior dc (i.e., no ac in prescutellar position); 2 sc, apical sc (longest thoracic seta) somewhat longer than posterior dc, laterobasal sc weak but longer than foremost dc; 1 minute (often hardly discernible) upcurved ppl; 2 rather robust stpl (anterior relatively long) with 1 microseta in front of them and 2 or 3 hair-like setae in ventral corner of sternopleuron (all dark-pigmented). Scutellum comparatively long, rounded-triangular, convex dorsally. Subscutellum well-developed. **Legs:** Yellow, only distal half of apical tarsomeres blackish brown. All coxae with a few longer setae. f_1 with relatively short ctenidial spine (about as long as maximum width of t_1) and usual rows of posteroventral (with seta in middle longest) and postero-dorsal long setae. f_2 without peculiarities; f_3 with posteroventral row of 7–10 short black spine-like setae in distal third or two-fifths. t_1 without, t_2 with short (not longer than maximum width of t_2), t_3 with very small ventroapical seta, otherwise uniformly setulose. All tarsi simply setulose (with ventrobasal setulae usually longer); pretarsal claws relatively long. **Wing** (Fig. 14): Relatively narrow but generally wider and larger than in *C. lonsdalei* and *C. marshalli*, with pale ochreous-brown veins and membrane. C with longer and thicker setulae among fine setosity of Cs_2 . Sc distally connected with R_1 , forming preapical kink. R_{2+3} long, bent parallel with C, apically upcurved to it and terminating farther from apex of wing than does M. R_{4+5} very slightly bent to straight and ending near (in front of) apex of wing. M almost parallel with R_{4+5} . Cell dm of medium length, distinctly widened distally; r-m usually oblique and situated at about middle of cell dm. Terminal section of CuA_1 variable but always longer than dm-cu. Both CuA_1 and A_1 not reaching wing margin. Alula relatively narrow. Wing measurements: length 1.63–2.46 mm, width 0.57–0.81 mm, $Cs_3 : Cs_4 = 0.90–1.36$, $r-m/dm-cu : dm-cu = 1.83–2.62$. Haltere yellow or base of stem darker ochreous; knob relatively large. **Abdomen:** Somewhat lighter than thorax, with terga darker brown than sterna, all sclerites with sparse greyish-brown microtomentum, subshiny. Preabdominal terga large, extended laterally and bent onto ventral side of abdomen, blackish short setose, with marginal setae longest and thickest. T1 shorter than and distinctly separated from T2. T2 shorter than T3, T3–T5 subequal in length or T5 slightly longer. Preabdominal sterna relatively narrow, finely and sparsely setulose, only S1 bare, transverse and wider than S2 but (in contrast to *C. caricis*) without posterior emargination. S2 somewhat shorter and narrower than S3, with anterior dark stripe distinctly



Figs. 58–64. *Carexomyza browni* sp.n., male paratype: **58:** external genitalia, caudally; **59:** ditto, laterally; **60:** gonostylus, ventrolaterocaudally (widest extension); **61:** aedeagal complex, laterally; **62:** transandrium, caudally; **63:** apex of filum, ventrally (widest extension); **64:** hypandrial complex, laterally. — **Scale bars:** 63 – 0.05 mm; others – 0.1 mm.

separated. S3–S5 all as long as broad but becoming somewhat larger posteriorly (S5 widest and longest). **Postabdomen:** Sclerites well-sclerotized and dark-pigmented, T6 distinct, though transverse and medially divided into 2 plates (right distinctly larger). S6 short and strongly asymmetrical, as is larger S7, both with dark anterior ledge-like margin (that of S6 thicker); S6 with 2 or 3, S7 with 2 setae or setulae. S8 less asymmetrical, distinctly longer than S7, situated dorsally, with a number of setae. **Male genitalia:** Most similar to those of *C. caricis*. Epandrium (Figs. 58, 59) medium-long, somewhat broader than high but distinctly narrower than that of *C. caricis* and anterodorsally less straight; also epandrial setae stronger. Anal fissure subtriangular; cercus (Figs. 58, 59) large (more than half length of gonostylus), with 2 longer (apical and subapical) and several shorter pale-pigmented setae. Medandrium slightly wider than anal fissure ventrally (Fig. 58) and, in contrast to *C. caricis*, with dorsolateral corners projecting laterally. Gonostylus (Fig. 60) usually ochreous yellow (sometimes brown), more or less contrasting with dark epandrium, lobately spoon-shaped, shorter than height of epandrium, broadly rounded apically as in *C. caricis* but generally wider and more densely setose on concave inner side, with larger micropubescent area covering most of convex outer side. Hypandrium (Fig. 64) more elongate than that of *C. caricis*, anteriorly simple, without dorsally projecting internal leaf-like lobes. Transandrium closely resembling that of *C. caricis* including large, ventrally projecting, caudal process posteromedially armed with group of short spines terminated ventrally by pair of large sclerotized bent plates (Fig. 62). Pregonite (Fig. 64) firmly fused to hypandrium, posterior part markedly projecting posteroventrally and forming blunt process with 8–10 setae; 2 more setae situated in anterior part of pregonite. In contrast to *C. caricis*, posteroventral process of pregonite lacks posterobasal rectangular tooth. Postgonite (Fig. 64) simple, pale, long and relatively slender, with 1 distinct preapical seta (longer than in *C. caricis*) and subacute apex. Basal membrane and armature more or less sclerotized; armature incorporated into caudal process of transandrium as in *C. caricis*. Aedeagal part of folding apparatus (Fig. 61) with external sides densely covered by flat rounded excrescences (not spines), with long, slender and partly spinulose connecting sclerite. Phallopodeme (Fig. 61) relatively long, with robust ventral fulcrum, symmetrically bifurcate basal end and laterally somewhat projecting apex. Aedeagus (Fig. 61) with short phallopore formed by two parts (dorsal and posteroventral), with large, more complex, bifid distiphallus. Distiphallus composed of elongate, densely spinose, and only distally membranous saccus, with slender, heavily sclerotized filum. Saccus of genus-characteristic construction: basal part more sclerotized and coalesced with phallopore, middle part ventrally projecting into acute-angled sclerotized tooth (Fig. 61) and internally reinforced by pair of sinuous sclerites, distal part largely membranous and spinose. Filum formed by two band-like sclerites, basally and apically connected; apex (Fig.

63) relatively simple, spoon- to lancet-shaped, membranous, more elongate than that of *C. caricis*. Ejacapodeme (Fig. 61) well-developed, with long digitiform projection. **Female.** Similar to male unless mentioned otherwise. Total body length 1.75–2.62 mm. **Head** (Fig. 11): Frons more broadly brown-darkened to level of anterior ors or (rarely) even to anterior margin as fading extension of stripe between posterior part of orbital plate and frontal triangle (as in *C. lonsdalei*). First antennal flagellomere darker, pale brownish-darkened anterodorsally (on both inner and outer sides, as in Fig. 11) up to anterodorsal half on inner side (anterodorsal half on outer side only in some air-dried specimens); whitish ciliation of anterior margin longer than in male. **Thorax** (Fig. 11): Mesopleuron without bare area dorsally (as in male). **Legs:** f_3 finely short setulose, lacking row of spine-like setae. **Wing:** Measurements: length 1.75–2.78 mm, width 0.59–0.99 mm, $Cs_3 : Cs_4 = 0.84–1.11$, $r-m/dm-cu : dm-cu = 1.90–2.92$. **Abdomen:** Preabdominal terga shinier, particularly laterally. T2–T4 subequal in length, wider and more transverse, becoming wider posteriorly or T3 as wide as T4. T5 hardly shorter than T4 but distinctly narrower and tapered posteriorly. Sterna slightly narrower. S3 not wider than S2, S2 and S5 about as long as wide, but S3 and S4 often slightly longer than wide. **Postabdomen** (Figs. 65, 67, 68): T6 broad, tapered posteriorly, dark-pigmented, setose in posterior two-thirds. S6 large and dark, slightly wider than long (less transverse than that of *C. caricis*), with posterior margin pale. 7th segment with separate T7 and S7 (Figs. 65, 68), both dark-pigmented. T7 (Fig. 67) much narrower than T6, shallowly emarginate anteromedially. S7 (Fig. 68) smaller than S6 but larger than that of *C. caricis*, about as long as broad, slightly tapered posteriorly, with all corners rounded. T8 (Fig. 67) about as long as broad, widest posteriorly and anteriorly narrowed, with small setae in posterior fourth only. S8 (Fig. 68) short (shorter than that of *C. caricis*) medially longitudinally divided, darker posteriorly, short setulose. **Female genitalia:** Internal sclerotization of female genital chamber (Figs. 69, 70) composed of distinct free (suboblong in ventral view) annular sclerite, pair of complex crooked (partly fused) sclerites dorsal to former and pair of narrower subvertical sclerites situated closely behind them. Anterior end of genital chamber strongly bent (at right angle) dorsally and provided with short ventral receptacle (Fig. 70), with small, more sclerotized and rounded cup-like tip, longer than that of *C. caricis*. Accessory glands (more precisely their remains) small, of uncertain shape, situated on terminally slightly dilated ducts. Spermathecae (1+1, one distinctly larger than other, in contrast to those of *C. marshalli* where usually only slightly unequal) subsphaerical to short pyriform (Figs. 70–72), with dark-pigmented short (shorter than in *C. caricis*) cervix and variable number of small spine-like tubercles (both terminally and basally on body of spermatheca) with usual stalked globulae on tips; spermathecal ducts relatively short (Fig. 70). T10 (Figs. 66, 67) smaller than S10, with usual medial pair of long setae, having anterior dark-pigmented part similar (al-



Figs. 65–72. *Carexomyza browni* sp.n., female paratype: **65:** postabdomen, laterally; **66:** T10, enlarged, dorsally; **67:** postabdomen, dorsally; **68:** ditto, ventrally; **69:** internal sclerites of female genital chamber, ventrally; **70:** female genital chamber with appendages, laterally; **71:** smaller spermatheca; **72:** larger spermatheca. — **Scale bars:** 65, 67, 68 – 0.2 mm; others – 0.05 mm.

though longer) to that of *C. caricis* but differing in having anterior corners strikingly projecting and curved laterally (Fig. 66). S10 (Fig. 68) somewhat wider than T10, rounded-pentagonal in ventral view, darker than in *C. caricis*, with setulae and micropubescence only at posterolateral margins. Cerci relatively short, pale-pigmented, not widely separate (Fig. 67), each with a number of short setae, 2 (dorsopreapical and subapical) longer than others.

Etymology. This species is named in honour of Dr. Brian Brown, an accomplished dipterist, a friend and former schoolmate of KNB.

Discussion. *Carexomyza browni* sp.n. is very similar and most closely allied to the only European representative of the genus, *C. caricis*. The latter species and *C. browni* (as *Carexomyza* sp.n. 3) were recently included in the molecular analysis of Anthomyzidae by ROHÁČEK et al. (2019: figs. 2, 4). This Nearctic–Palearctic sister pair is strongly supported by molecular data (cf. Fig. 91 and also trees in ROHÁČEK et al., l.c.) and can also be characterised by the broad, lobately spoon-shaped gonostylus, the pregonite with a large, blunt posteroventral process and the modified female T10 with more or less acutely projecting anterior corners.

The differences between these species are relatively subtle and are all stressed in the above description as well as in the diagnosis of *C. caricis* below. *Carexomyza browni* can be most dependably distinguished from *C. caricis* in having the epandrium (see caudal view) narrower and more strongly setose, the gonostylus broader and more densely setose on the inner side and more extensively micropubescent on the outer side, the blunt posteroventral process of the pregonite without a posterobasal rectangular tooth, and the female postabdomen with a broad S7, the peculiarly projecting anterior corners of the T10 and the separate annular sclerite in the genital chamber.

Biology. The important collections and observations from Cochrane, Ontario (repeated collections over several years) are discussed under *C. marshalli*. This discussion includes the suggestion that adults of *C. browni* emerge earlier in the season than do those of *C. marshalli* (at least at that site) and perhaps die off earlier in the season as well. Collections from western Canada, i.e., British Columbia and particularly Alberta, indicate frequent co-occurrence with *C. marshalli* in association with *Cx. utriculata*, as already mentioned under *C. marshalli*, while such co-occurrence was rare in Ontario (only at the Cochrane site where all three Nearctic species co-occur). A singular U.S.A. site (Nederland, Colorado) also yielded these two species. As mentioned previously, *C. browni* and *C. lonsdalei* co-occurred at Echo Bay, Ontario.

The most significant collection of this species is from Parson, British Columbia, the type locality, where only *C. browni* was captured. This site was a roadside strip

(see Figs. 73, 74) bordering an extensive marsh and supporting a rather sparse population of *Cx. utriculata* mixed with *Equisetum palustre* L. & *E. ×litorale* Kühlew. ex Rupr. The primary collection of 18 July 2011 was made shortly after an intense afternoon rain event that likely saturated the road allowance and effectively “flooded” the flies out of the thatch and duff making them very easy to capture by sweeping from about 17:00–19:00h. This was the most productive collection of this species at any time or place (38♂ 70♀, including specimens from the following morning) and is remarkable for the absence of *C. marshalli*. This collection is essentially contemporaneous with those from Peter Lougheed Provincial Park, Alberta (13–16 July 2011), where *C. marshalli* (n=250) outnumbered *C. browni* (n=45) by more than five times. Clearly, these contrasting differences in relative abundance are not seasonal differences (as suggested for the Cochrane, Ontario site and discussed under *C. marshalli*), since the Parson site is a relatively warmer site at about 789 m a.s.l., while the Peter Lougheed Prov. Pk. site is a cooler site at about 1620 m a.s.l. Rather, this comparison demonstrates that *C. browni* may occur in association with *Cx. utriculata* in the absence of *C. marshalli*.

Further to this point, the most recent collections made by KNB were in Mount Carleton Provincial Park, New Brunswick, 24 & 25 June 2019. The site (Figs. 75, 76) represented a broad sedge meadow surrounding the course of Caribou Brook and the patches of *Cx. utriculata* were rather sparse and no *Cx. stipata* were observed. All 27 specimens collected here were of *C. browni* on calendar dates similar to the earliest collection of 22 June 2013 at the Cochrane, Ontario site; the only collection event there in which the only species represented was *C. browni* (see section 3.5, Biology). The Caribou Brook site was not investigated further into the season for the possible presence of other species of *Carexomyza*. However, a single specimen of *C. marshalli* was collected a few days later (30 June) on a nearby site (~ 28.5 km E Saint-Quentin) supporting both *Cx. utriculata* and *Cx. stipata* (as discussed under *C. marshalli*). The 27 specimens of *C. browni* from Caribou Brook were collected mainly from two foci with n=2 taken in the evening of 24 June (19:00–21:45h), n=3 in the afternoon of 25 June and n=22 that evening (18:00–20:00h). Though not rigorously comparable, these results did reflect that specimens of *C. browni* were more readily obtained in the evening with a sweep net. However, though not quantified (not all anthomyzids were collected), the abundance of other diurnally active species of anthomyzids did not appear to decrease through the short periods of evening collections (as observed in Cochrane, Ontario) either evening. The evening of 24 June had clear skies and the temperature dropped noticeably as did the insect activity generally as judged (by eye) from the sweep net catches when only n=2 *C. browni* were captured. In contrast, the evening of 25 June was overcast and air temperatures remained more moderate yielding n=22 *C. browni* over a shorter period of time. Though the evening of 24 June was clear, the



Figs. 73–76. Habitat of *Carexomyza browni* sp.n. **73, 74:** Parson, British Columbia (18 July 2011); **73:** roadside growth of *Carex utriculata* mixed with *Equisetum palustre* & *E. x-litorale*; **74:** close-up view of sparse *Cx. utriculata* growth and build-up of dried thatch; **75, 76:** Caribou Brook, Mount Carleton Provincial Park, New Brunswick; **75:** graminoid meadow surrounding Caribou Brook (one focal collection area to the immediate right); **76:** close-up view of thick build-up of dried thatch and rather sparse growth of *Cx. utriculata*. Photos by K.N. Barber.

collection foci were in the shadow of surrounding forest by 20:45h and the overcast of the following evening confounded the onset of sunset (collections were terminated by 20:00h that evening, well before sunset of 21:28h). As such, these observations further suggest that those made at Cochrane, Ontario (especially those depicted in Fig. 57) may not necessarily occur broadly nor frequently and may require particular combinations of light, temperature, and humidity.

Two other particular sites in British Columbia yielded moderate numbers of both *C. browni* and *C. marshalli* with *C. browni* dominating: $n=15$ to 4 (Fernie, 17–19 July 2011) and $n=30$ to 5 (Valemount, 23 July 2011) specimens of *C. browni* to *C. marshalli*, respectively. There may well be regional differences in relative proportions of sympatric populations of these two species where *C. browni* dominates mixed collections in British Columbia, while *C. marshalli* dominates those in Alberta and perhaps eastward to Ontario (the Caribou Brook, New Brunswick site the possible exception). The number of known locality records are equal for these two species in British Columbia ($n=6$). In Alberta, there are more localities recorded for *C. marshalli* than for *C. browni* ($n=$

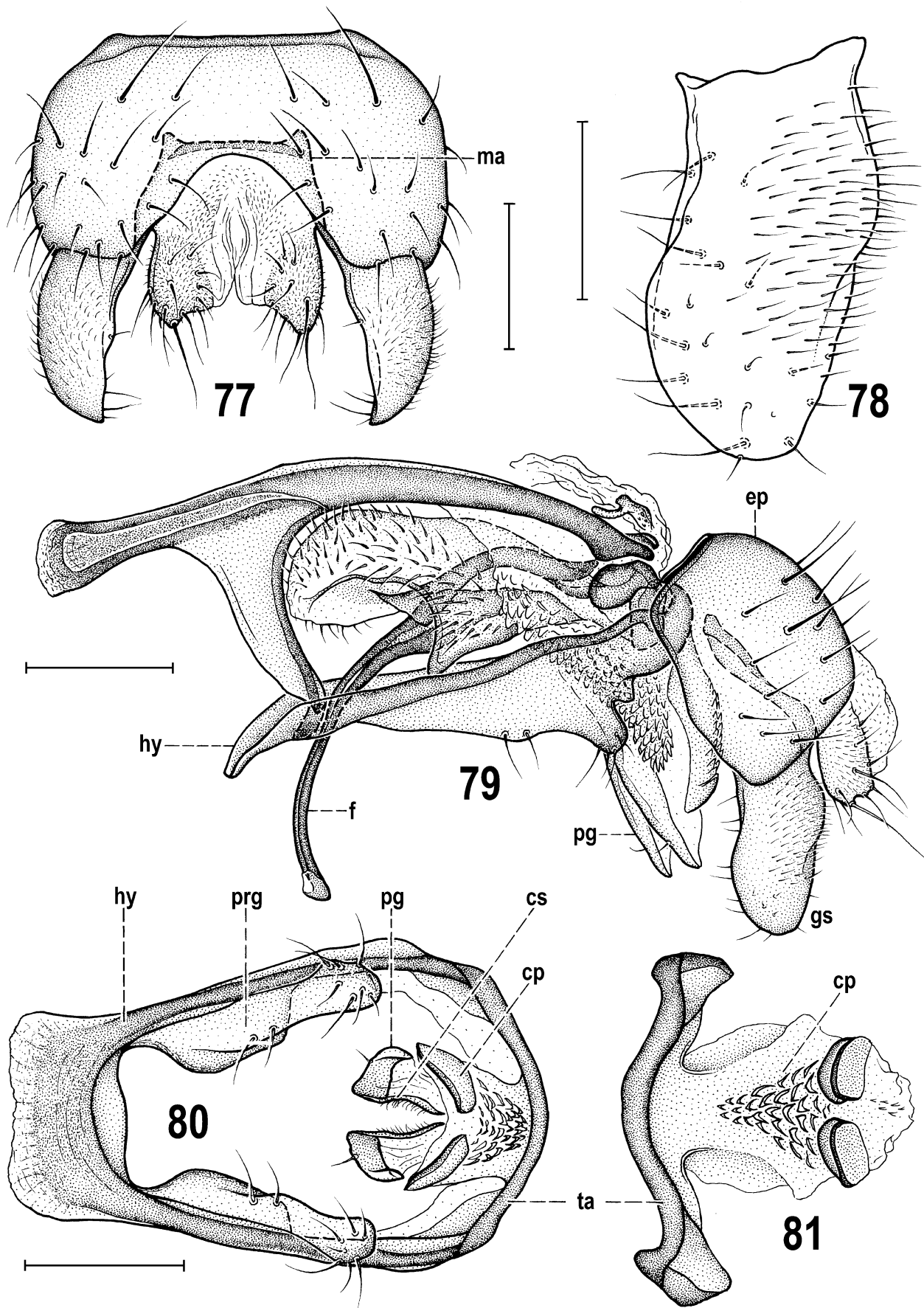
17 vs. 8), while in Ontario there are more localities known for *C. browni* ($n=10$ vs. 6). One exceptional record of a single female taken from a mix of *Equisetum arvense* L. & *E. laevigatum* A. Braun (Fernie, British Columbia) is misleading, as these plants were growing immediately adjacent to a thick growth of *Cx. utriculata* that yielded more specimens of *C. browni* and of *C. marshalli*. Additional habitat descriptors from label data include “*Carex* roots” in Alberta, “sedge meadows, floodplain community nr. tamarack bog” in Manitoba, “grass/sedges along river margin” in Yukon, and “marshy stream margin” in Colorado. The minimum flight period for *C. browni* runs from 24 May (Echo Bay, Ontario) to 4 August (Pleasant Valley, Washington).

Distribution. Canada: Alberta, British Columbia, Manitoba, New Brunswick, Ontario, Saskatchewan, Yukon. United States of America: Alaska, Colorado, Minnesota, Montana, Washington. *Carexomyza browni* is also widely distributed in Canada in the same jurisdictions as is *C. marshalli* but, additionally, with the only record for Saskatchewan. The southern record for *C. browni* is also at a relatively high elevation (Colorado: Nederland 8500’

[2590 m]) and this is the only species of *Carexomyza* yet known from Alaska, Minnesota and Washington.

Material examined. Type material: Holotype ♂, 'CAN: BC: Parson, Crest- | brook Rd, 18.vii.2011, KN | Barber, sweeps, wet ditch, | *Carex utriculata* with *Equis- | etum palustre* & *E. ×litorale* | 51°03.68'N 116°39.06'W' and 'Holotypus ♂ | *Carexomyza | browni* sp.n. | K.N. Barber & J. | Roháček det. 2019' (red). The specimen is in excellent condition with brown gonostyli highly visible (CNCI, intact, Fig. 8). Paratypes 152♂ 190♀. **CANADA: Alberta:** Fish Creek Prov. Pk., 50°55.61'N 114°07.43'W, sweeps, mostly *Carex utriculata* and *Equisetum fluviatile*, 12.vii.2011, J.E. Swann & K.N. Barber leg., 1♂ (BDUC, genit. prep.); Hwy 40, S Grande Prairie, *Carex* roots, 17.vi.1987, S.A. Marshall leg., 1♂ (DEBU); ~ 14.4 km E Obed, Range Rd. 213 @ RR crossing, 53°32.19'N 117°01.02'W, sweeps, mostly *Carex utriculata*, 25.vii.2011, K.N. Barber leg., 1♂ (CNCI); Peter Lougheed Prov. Pk., 50°41.82'N 115°06.92'W, sweeps, fen, *Carex utriculata* with cf. *Poa pratensis*, K.N. Barber leg., 13.vii.2011, 8♂ 30♀ (DEBU 01503123 [♂ genit. prep.], -124 [♂ genit. prep.], -125–130, -251–280), 14.vii.2011, 1♂ (DEBU 01503297), 15.vii.2011, 1♂ 2♀ (DEBU 01503342, -54, -55), 16.vii.2011, 2♂ 1♀ (DEBU 01503410, -11, -36); Peter Lougheed Prov. Pk., Upper Lake Drive, 50°36.94'N 115°07.16'W, sweeps, edge of fen, *Carex utriculata*, 16.vii.2011, K.N. Barber leg., 1♂ (DEBU 01503652); Spray Valley Prov. Pk., 50°48.95'N 115°09.84'W, sweeps, fen, *Carex utriculata*? and *Poa* sp., 13.vii.2011, K.N. Barber leg., 1♀ (DEBU 01502858); W.A. Switzer Prov. Pk., Beaver Ranch Trail, 53°29.80'N 117°48.02'W, sweeps, edge of Jarvis Ck., *Carex utriculata*, 22.vii.2011, K.N. Barber leg., 1♂ 3♀ (DEBU 01503739, -770–772); W.A. Switzer Prov. Pk., off Hay River Rd. W, 53°33.44'N 117°48.43'W, sweeps, mostly *Carex utriculata*, K.N. Barber leg., 22.vii.2011, 1♀ (DEBU 01503811), 24.vii.2011, 3♂ 1♀ (DEBU 01503896–898, -914). **British Columbia:** Fernie, Annex Pk., 49°30.72'N 115°04.13'W, sweeps, wet ditch, mostly *Equisetum arvense* & *E. laevigatum*, 17.vii.2011, K.N. Barber leg., 1♀ (CNCI); Fernie, Annex Pk., 49°30.72'N 115°04.13'W, sweeps, wet ditch, *Carex utriculata*, K.N. Barber leg., 17.vii.2011, 3♂ 3♀, 18.vii.2011, 4♀, 19.vii.2011, 1♀ (CNCI); Fernie, Annex Pk., 49°30.66'N 115°04.16'W, sweeps, pond margin, *Carex utriculata*, 18.vii.2011, K.N. Barber leg., 3♀ (CNCI); Hatzic Lake, 24.vii.1953, W.R.M. Mason leg., 1♂ (CNCI, genit. prep.); Kinbasket Lake, BC Hydro drawdown study, pan trap, 12.vi.2010, Cooper Beuchesne & Assoc. Ltd. leg., (08PTRT15), 1♂, (02PCOT01), 1♀ (RBCM); Parson, Crestbrook Rd., 51°03.68'N 116°39.06'W, sweeps, wet ditch, *Carex utriculata* with *Equisetum palustre* & *E. ×litorale*, K.N. Barber leg., 18.vii.2011, 30♂ 59♀ (CNCI, 15♂ 35♀ [1♀ genit. prep., 1♀ head/thorax photo]; AMNH, 2♂ 4♀; CASC, 2♂ 4♀; SMOC, 7♂ 10♀ [3♂ 2♀ genit. prep.]; USNM, 4♂ 6♀), 19.vii.2011, 4♂ 6♀ (CNCI, 1♂ wing photo, left wing in glycerine microvial); ~ 8.0 km SE Valemount, edge of Kinbasket Lake, 52°46.65'N 119°10.38'W, sweeps, mostly *Carex utriculata*, 23.vii.2011, K.N. Barber leg., 17♂ 13♀ (CNCI, 11♂ 7♀ [1♂ with left wing in glycerine microvial, 1♀ genit. prep.]; BDUC, 3♂ 3♀; RBCM, 3♂ 3♀). **Manitoba:** 5 mi SW Shilo, sedge meadows, floodplain community nr. tamarack bog, 16.vi.1958, J.F. McAlpine leg., 1♀ (CNCI). **New Brunswick:** Mt. Carleton Prov. Pk., Caribou Brook, 47°24.26'N 66°49.63'W, sedge meadow, mostly *Carex utriculata*, K.N. Barber leg., evening ~ 19:00–21:30 sweeps, 24.vi.2019, 1♀, afternoon sweeps, 25.vi.2019, 1♂ 1♀ (CNCI), evening ~ 19:00–20:00 sweeps, 25.vi.2019, 7♂ 3♀ (CNCI, 4♂ 1♀; NBMB, 3♂ 2♀); Mt. Carleton Prov. Pk., Caribou Brook, 47°24.26'N 66°49.68'W, sedge meadow, mostly *Carex utriculata*, evening ~ 21:30–21:45 sweeps, 24.vi.2019, 1♂, K.N. Barber leg. (CNCI); Mt. Carleton Prov. Pk., Caribou Brook, 47°24.25'N 66°49.75'W, sedge meadow, mostly *Carex utriculata*, K.N. Barber leg., afternoon sweeps, 25.vi.2019, 1♂ (CNCI), evening ~ 18:00–19:00 sweeps, 25.vi.2019, 8♂ 4♀ (CNCI, 5♂ 2♀ [1♂ 1♀ genit. prep.]; NBMB, 3♂ 2♀). **Ontario:** ~ 40 km NE Chapleau, 47°59.76'N 82°55.04'W, wet roadside sweeps, mostly *Carex utriculata*, 23.vi.2013, K.N. Barber leg., 3♂ 7♀ (CNCI); ~ 13.9 km W Chapleau, 47°49.20'N 83°35.42'W, hydro right-of-way, sweeps, mostly *Carex utriculata*, grasses, 13.vii.2013, K.N. Barber leg., 1♂

(CNCI); ~ 13.5 km S Cochrane, 48°56.65'N 81°00.18'W, hydro right-of-way, sweeps, mostly *Carex utriculata*, K.N. Barber leg., 22.vi.2013, 12♂ 10♀ (CNCI, 6♂ 4♀ [1♂ 1♀ genit. prep.]; INHS, 3♂ 3♀; LEMQ, 3♂ 3♀), 12.vii.2013, 13♂ 7♀ (CNCI, 6♂ 2♀; LACM, 4♂ 2♀; SMOC, 3♂ 3♀), 13.vii.2013, 1♂, 28.vii.2017, 1♂, 7.vii.2018, 2♂ 2♀ (CNCI); ~ 13.5 km S Cochrane, 48°56.65'N 81°00.18'W, hydro right-of-way, "headlamp" sweeps, mostly *Carex utriculata*, 7.vii.2018, K.N. Barber leg., 2♀ (CNCI); ~ 3.8 km ENE Dugwal, 48°35.33'N 80°57.90'W, sweeps, wet ditch, *Carex utriculata*, *Equisetum fluviatile*, *Scirpus*, 23.vi.2013, K.N. Barber leg., 2♂ 2♀ (CNCI); Echo Bay, Echo Bay Marsh, 46°29.71'N 84°04.04'W, sweeps, mostly *Carex* spp. nr. lookout, 24.v.2007, K.N. Barber leg., 1♀ (CNCI); Echo Bay, Echo Bay Marsh, 46°29.66'N 84°04.12'W, near lookout, sweeps, mostly *Carex utriculata*, K.N. Barber leg., 8.vi.2013, 3♂ 4♀, 15.vi.2013, 2♂ 2♀ (CNCI); ~ 7.0 km E Foleyet, 48°14.34'N 82°20.75'W, hydro right-of-way, sweeps, mostly *Carex utriculata*, 23.vi.2013, K.N. Barber leg., 5♂ 1♀ (CNCI); ~ 2.0 km W Hallebourg, 49°40.36'N 83°32.11'W, sweeps, wet ditch, mostly *Carex utriculata*, K.N. Barber leg., 22.vi.2013, 1♂ 1♀, 12.vii.2013, 1♂ (CNCI); ~ 43 km W Hearst, 49°44.07'N 84°14.74'W, hydro right-of-way opposite Forde Lk., sweeps, mostly *Carex utriculata*, 21.vi.2013, K.N. Barber leg., 2♀ (CNCI); Lake Superior Prov. Pk., Hwy 17 near jct. Agawa Rock, 47°22.31'N 84°41.23'W, sweeps, mostly *Carex utriculata*, 12.vii.2014, K.N. Barber leg., 1♂ 1♀ (DEBU 01503929, -30); Hwy 101 at Prairie Bee River (west side bridge), 47°51.81'N 83°54.33'W, sweeps, mostly *Carex utriculata*, 14.vii.2013, K.N. Barber leg., 2♂ (CNCI); Smooth Rock Falls, 49°16.04'N 81°36.08'W, sweeps, *Carex utriculata*, K.N. Barber leg., 8.vii.2012, 1♂ 1♀ (1♂ genit. prep.), 22.vi.2013, 3♂ (CNCI). **Yukon:** Alaska Hwy at Yukon River crossing, 60°34'N 134°40'W, sweep grass/sedges along river margin, 2.vii.1997, T.A. Wheeler leg., 1♂ 1♀ (LEMQ); Atlin Road, Snafu Creek Government Campground, sweep sedges along creek, 25.vi.1997, T.A. Wheeler leg., 1♂ (LEMQ). **UNITED STATES OF AMERICA: Alaska:** Kenai National Wildlife Refuge, Long Term Ecological Monitoring Program, E edge of Chickaloon Flats between Little Indian Ck. and Big Indian Ck. near winter trail, section 35, LTEMP site 6691, sweep net sample, 7.vi.2004, S. Grimes leg., 1♂ (UAM, ID:3105, BOLD ID:DKNWR044-11); Kenai, Ninilchik, 60°03'N 151°40.2'W, beach, 2.vii.2006, D. & W.N. Mathis leg., 1♀ (USNM). **Colorado:** 3 mi N Nederland, 8500', marshy stream margin, 2.vii.1961, J.G. Chillecott leg., 1♂ (CNCI, genit. prep.). **Minnesota:** Clearwater Co., Itasca State Pk., Cat. No. 127.2, 25.v.1960, F.J. Rohlf leg., 1♀ (SEMC). **Montana:** Gallatin Co., Gallatin R., 2 mi N Gallatin Gtwy [Gateway], 4100', 23.vi.2001, J.B. Runyon leg., 1♀ (MTEC). **Washington:** Pierce Co., Clover Creek, T.L. Whitworth leg., 9.vi.1979, 1♀, 20.vi.1980, 1♀ (LACM); Pierce Co., Pleasant Valley, 4.viii.1978, T.L. Whitworth leg., 1♀ (LACM). — **Other material:** **CANADA: Alberta:** Hwy 40 S Grande Prairie, *Carex* roots, 17.vi.1987, S.A. Marshall leg., 1♀ (DEBU, genit. prep., legs mostly missing, terminalia damaged). **British Columbia:** Hatzic, 30.vii.1953, W.R.M. Mason leg., 1♀ (CNCI, genit. prep., damage to antenna, wing, thoracic setae, mid leg absent); Kinbasket Lake, BC Hydro drawdown study, Malaise trap, Cooper Beuchesne & Assoc. Ltd. leg., (34MTRT15), 22–23.vii.2009, 1♂ (genit. prep., badly shriveled), (02MCOT01), 12.vi.2010, 1♂ (genit. prep., body crushed) (RBCM); Parson, Crestbrook Rd., 51°03.68'N 116°39.06'W, sweeps, wet ditch, *Carex utriculata* with *Equisetum palustre* & *E. ×litorale*, K.N. Barber leg., 18.vii.2011, 4♂ 3♀ (CNCI, 3♂ 3♀ [1♂ headless, 1♂ abdomen lost, 1♂ 3♀ dirty or damaged, 1♀ genit. prep.]; SMOC, 1♂, used in molecular analysis, dry mounted with abdomen in glycerine mount), 19.vii.2011, 1♀ (CNCI, genit. prep., dirty with thorax partly crushed). **Ontario:** ~ 13.5 km S Cochrane, 48°56.65'N 81°00.18'W, hydro right-of-way, sweeps, mostly *Carex utriculata*, K.N. Barber leg., 22.vi.2013, 1♂ (thorax fractured), 12.vii.2013, 1♂ (missing antennae) (CNCI). **Saskatchewan:** Uranium City, 18.vi.1962, J.G. Chillecott leg., 1♀ (CNCI, missing antennae). **UNITED STATES OF AMERICA: Washington:** Pierce Co., Clover Creek, 20.vi.1980, T.L. Whitworth leg., 1♀ (LACM, missing antennae); Pierce Co., Pleasant Valley, 4.vi.1978, T.L. Whitworth leg., 1♂ 1♀ (LACM, both missing antennae).



Figs. 77–81. *Carexomyza caricis* (Roháček, 1999), male holotype (Figs. 77–80) and paratype (Fig. 81): 77: external genitalia, caudally; 78: gonostylus, sublaterally (widest extension); 79: genitalia, laterally; 80: hypandrial complex, ventrally; 81: transandrium, caudally. — **Scale bars:** 78 – 0.05 mm; others – 0.1 mm. For abbreviations see p. 72. Adapted from Roháček (1999: figs. 17–21).

3.7. *Carexomyza caricis* (Roháček, 1999)

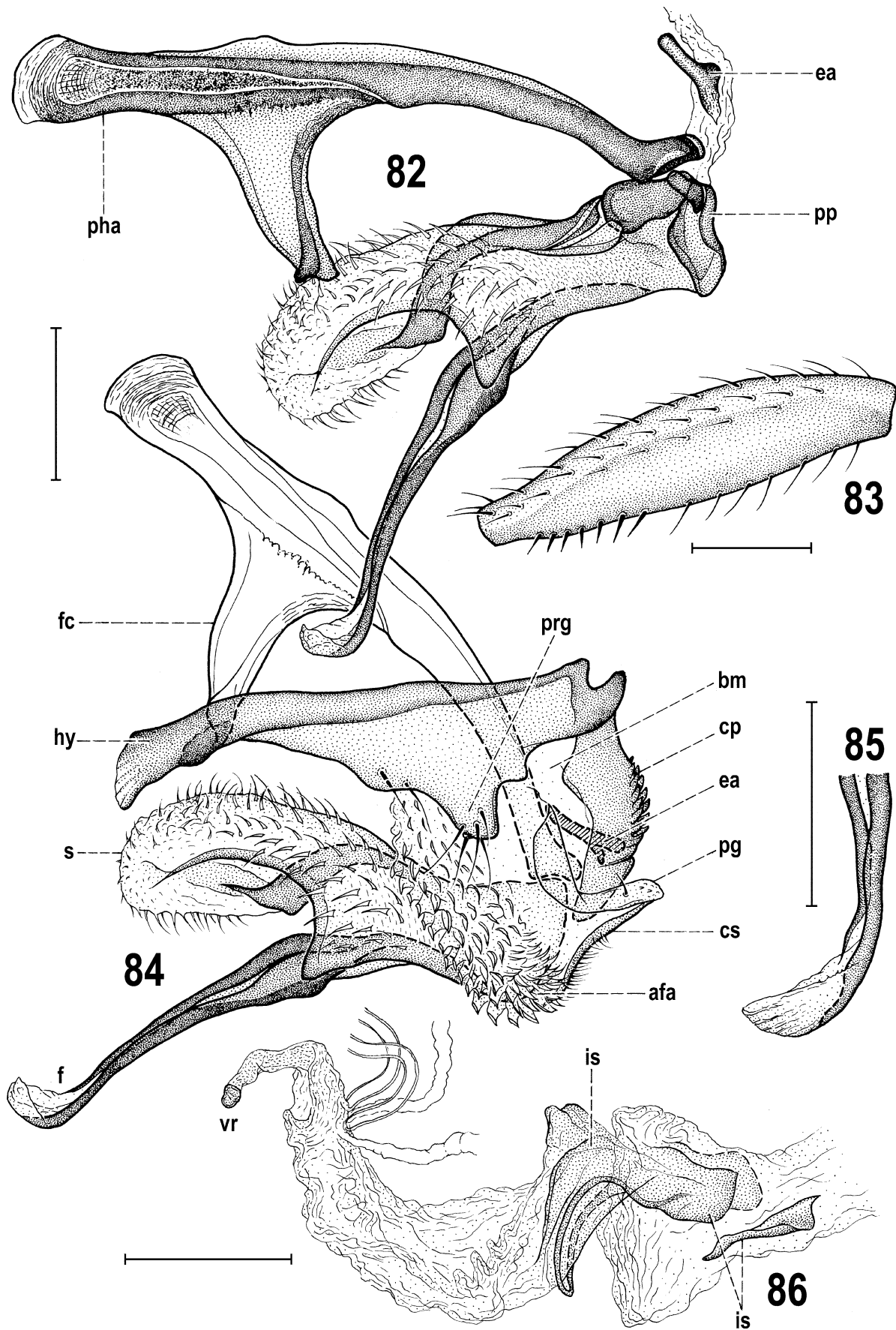
(Figs. 7, 15, 77–90)

Paranthomyza caricis Roháček, 1999: 385–391 [description]; ROHÁČEK 2006: 235–241 [redescription, biology, distribution]; ROHÁČEK et al. 2009: 54, 56 [molecular phylogeny].
Carexomyza caricis: ROHÁČEK 2009: 77 [generic combination, distribution], 107 [phylogeny], 132 [host-plant association]; ROHÁČEK 2013: 35 [biology, distribution]; ROHÁČEK & TÓTHOVÁ 2014: 170; ROHÁČEK et al. 2019: 753, 755 [molecular phylogeny].

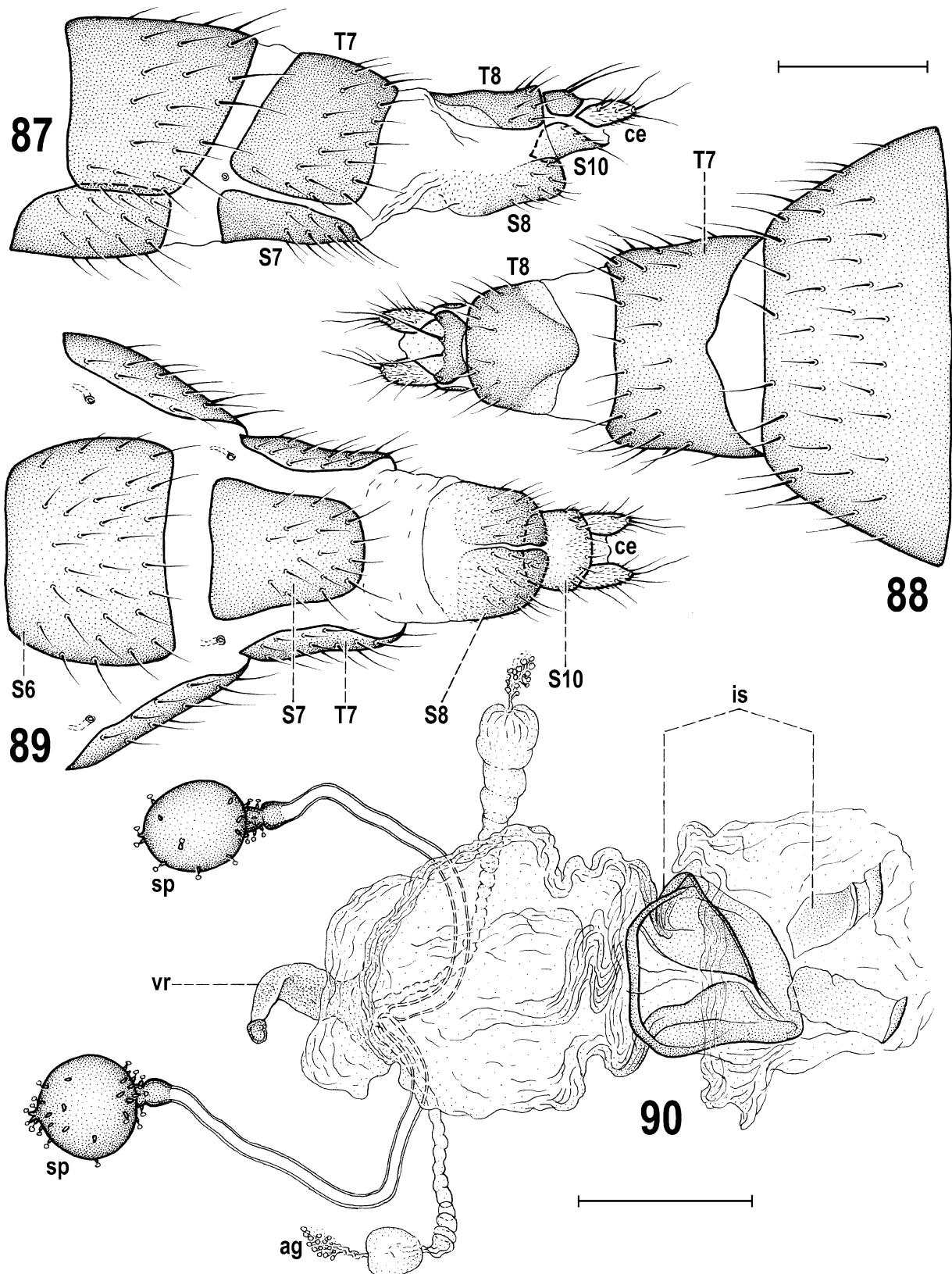
Diagnosis. Full descriptions of *C. caricis* are given by ROHÁČEK (1999, 2006, as *Paranthomyza*). Therefore the species is only diagnosed here with some additional characters obtained during comparison with its closest relative, *C. browni*. *Carexomyza caricis* differs from the latter species as follows: **Male.** Total body length 1.79–2.08 mm. **Head:** oc setae inserted slightly outside margin of ocellar triangle. Stripe between orbital plate and frontal triangle dull brown and reaching up to anterior corner of latter and silvery-grey microtomentose (with bluish hue only suggested) behind posterior ors, this microtomentose area expanded and confluent with that of adjacent orbital plate. Ventral marginal stripe of gena brownish. Eye suboval to reniform and more elongate, with longest diameter about 1.6–1.7 times shortest diameter. **Thorax:** As in *C. browni*. **Legs:** Most of apical tarsomeres brown, f_1 with ctenidial spine somewhat shorter than maximum width of t_1 and f_3 with posteroventral row of 6–8 short black spine-like setae in distal third (Fig. 83). **Wing** (Fig. 15): Relatively long. Wing measurements: length 1.79–2.03 mm, width 0.61–0.68 mm, $Cs_3 : Cs_4 = 0.90–1.17$, $r-m \backslash dm-cu : dm-cu = 2.35–3.08$. **Abdomen:** T2 usually as long as T3, S1 with posterior emargination, S3 and S4 of same width. **Male genitalia:** Epandrium (Figs. 77, 79) distinctly wider in caudal view and anterodorsal margin straighter (see Fig. 77), with setae finer but with two pairs of them somewhat longer than others. Cercus (Figs. 77, 79) with 1 longer subapical and several shorter pale setae. Gonostylus lobately spoon-shaped (Fig. 78), but somewhat more elongate, with fewer setae on concave inner side. Hypandrium (Figs. 79, 80, 84) similarly formed but somewhat shorter. Transandrium also similar but armature of basal membrane terminated by shorter ventral sclerites (Figs. 81, 84). Pregonite (Figs. 79, 84) with posterior part projecting posteroventrally and forming blunt process with distinct posterobasal rectangular tooth and bearing 6–8 setae; 2 more setae situated in anterior part of pregonite. Postgonite (Figs. 79, 84) simple, pale, bearing 1 preapical setula (smaller than that of *C. browni*) and non-acute apex (cf. Fig. 84, with postgonite curved in consequence of erect position of genitalia). Aedeagal part of folding apparatus (Fig. 84) with external sides densely covered by small teeth and spines, with very slender and finely pilose connecting sclerite. Phallapodeme (Fig. 82) shorter, with relatively strong ventral fulcrum; apex dilated but not projecting laterally. Aedeagal complex (Figs.

82, 84): Saccus with shorter and more sinuous internal sclerites, filum shorter and more basally dilated, with spoon-shaped apex (Fig. 85) less elongate. Ejacapodeme (Fig. 82) with shorter base and longer digitiform projection. **Female** (Fig. 7). Total body length 2.03–2.60 mm. **Head:** 1st antennal flagellomere distinctly darker than in male and more so than in *C. browni* female, with anterodorsal third to half of both inner and outer sides brownish. **Wing:** Measurements: length 1.99–2.42 mm, width 0.65–0.83 mm, $Cs_3 : Cs_4 = 0.96–1.14$, $r-m \backslash dm-cu : dm-cu = 1.84–2.73$. **Abdomen:** T3 slightly shorter than T4. **Postabdomen** (Figs. 87–89): Constructed as in *C. browni* but differing as follows: Most sclerites with finer setosity. T7 less tapered posteriorly (Fig. 88). S7 (Fig. 89) narrower (particularly posteriorly), distinctly longer than broad, tapered and rounded posteriorly. T8 (Fig. 88) about as long as broad, with anteriorly narrowed pigmentation (more so than in *C. browni*). S8 (Fig. 89) longer. **Female genitalia:** Internal sclerites of female genital chamber (Figs. 86, 90) with annular sclerite modified, thin anteriorly and dilated and partly fused posteriorly with adjacent flat anterior pair of sclerites, with pair of small posterior sclerites differently formed (Fig. 90). Anterior end of genital chamber less strongly bent dorsally (Fig. 86), ventral receptacle (Figs. 86, 87) with sclerotized cup-like tip shorter. Accessory glands (or their remains) small but with terminally strongly dilated ducts (Fig. 90). Spermathecae (1+1) subsphaerical to lemon-shaped (Fig. 90), one only slightly larger than other, with longer, dark-pigmented cervix and more numerous spine-like tubercles. T10 (Fig. 88) short, transverse, dark-pigmented, tapered anteriorly and its anterior corners acute. S10 (Fig. 89) only slightly wider than long, suboblong and paler. Cerci pale-pigmented, widely separate (Fig. 88), each with 3 longer and several shorter setae.

Discussion. The close relationship of *C. caricis* to *C. browni* is discussed above under the latter species. Because *C. browni* was included (but not specifically discussed) in the time-calibrated molecular analysis by ROHÁČEK et al. (2019: fig. 4, as *Carexomyza* sp.n. 3), it is possible to treat the time divergence of these sister species here. Based on the latter hypothesis, the Palaeartic *C. caricis* diverged from the Nearctic *C. browni* about 0.71 (0.37–1.15) MYA (see ROHÁČEK et al. 2019, table S1, as *Carexomyza* sp.n. 3). This time of separation closely approximates that of two Nearctic–Palaeartic divergences in the genus *Anthomyza*, particularly that of the *A. dissors* (Palaeartic) + *A. mcalpinei* (Nearctic) pair which also split in the Pleistocene, 0.69 (0.35–1.12) MYA. It was suggested (ROHÁČEK et al. 2019) that these disjunctions of Nearctic and Palaeartic relatives have been caused by the fragmentation of the original Holarctic populations as the result of climatic oscillations (cooling in particular) that occurred several times during the Pleistocene. If so, we can anticipate that *C. caricis* is also present in the northeastern Palaeartic (as are the Palaeartic members of *Anthomyza* discussed



Figs. 82–86. *Carexomyza caricis* (Roháček, 1999), male and female paratypes: **82:** aedeagal complex (without aedeagal part of folding apparatus), laterally; **83:** male left hind femur, posteriorly; **84:** male internal genitalia (in erect position), laterally; **85:** apex of filum, ventrally; **86:** female genital chamber, laterally. — **Scale bars:** 83 – 0.2 mm; others – 0.1 mm. For abbreviations see p. 72. Adapted from Roháček (1999: figs. 22–26).



Figs. 87–90. *Carexomyza caricis* (Roháček, 1999), female paratype: **87**: postabdomen, laterally; **88**: ditto, dorsally; **89**: ditto, ventrally; **90**: female genital chamber with appendages, ventrally. — **Scale bars**: 90 – 0.1 mm; others – 0.2 mm. For abbreviations see p. 72. Adapted from Roháček (1999: figs. 27–30).

above) because ancestors of these pairs were spreading into the Palaearctic across the Bering Strait (ROHÁČEK et al. 2019).

Biology. The limited biological information available for this species comes entirely from two localities in England. Most specimens were taken from tussocks

of *Cx. paniculata*. These collections were made either by sweeping (P.J. Chandler, pers. comm. to JR, 1997, Hampshire: Greywell Fen, 1990–1991) or by suction sampler (J.W. Ismay and B. Schulten, pers. comm. to JR, 2006, Wiltshire: Jones's Mill, 2004). However, the record from northern Sweden suggests another host plant is involved there, where *Cx. paniculata* is not yet recorded (LANSDOWN 2014). ROHÁČEK (2013) reports an additional record from each of southern Sweden and southwestern Finland. The record from Sweden is likely outside the known range of *Cx. paniculata* and the habitat described as a “sandy railway embankment through pasture-land” does not carry any information about sedge components. The collection site in Finland may be within the range of *Cx. paniculata*, but it has been confirmed by the collector that *Cx. paniculata* was not present there (J. Kahanpää, pers. comm., to JR, 2013). Other *Carex* species that form tussocks or develop sufficient thatch and duff layers of decomposing material might serve as hosts for *C. caricis*. It is interesting to speculate about the possibility that *Cx. utriculata* can also serve as a host since this sedge is also known from Europe, particularly Finland and Sweden (GBIF SECRETARIAT 2019). The limited number of specimens of *C. caricis*, few known localities and distinct collections suggest that the behaviour of this species is similar to that of the Nearctic species, viz. adults may also limit their diurnal activity to the lower layers of the thatch and duff making them difficult to intercept with a sweep net. The minimum flight period derived from the few existing records runs from 31 May to 18 July.

Distribution. United Kingdom (England), Finland, Sweden. This species is known only from a single locality in Finland and two localities in each of England and Sweden. This paucity of collections is almost certainly an artefact of inadequate sampling and the fly's cryptic diurnal behaviour. However, it is notable that *C. caricis* has not yet been recorded by the long-term studies of Anthomyzidae associated with sedges (*Carex* and *Scirpus* spp., including *Cx. paniculata*, see Roháček 2009) in Central Europe and might well be restricted to more northern latitudes in the (western or entire) Palaearctic Region.

Material examined. Type material: Holotype ♂, [UNITED KINGDOM: England:] ‘HANTS | Greywell Fen | wooded fen | 3.VII.1991 | P.J. Chandler’, and ‘Holo- | typus [typewritten within black frame] | Paranthomyza | caricis sp. n. ♂ | J. Roháček det. 1998 [handwritten]’ (red). The specimen is in good condition, double-mounted on minuten pin (BMNH, intact, examined). Allotype ♀ (BMNH) and paratype ♀ (PCM), same data but collected in “tussock area”, with red ‘Allo- | typus’ and ‘Para- | typus’ labels, respectively. Other paratypes 2♂ 4♀. **UNITED KINGDOM:** same locality as for holotype, open streambank, 3.vii.1991, 1♂ (headless, genit. prep.) 1♀; same locality, without further data, 15.vii.1990, 1♂ 1♀, 20.vi.1991, 1♀ (genit. prep.), all P.J. Chandler leg. (RSME, 1♂ 1♀; SMOC, 1♂ 1♀; PCM, 1♀); **SWEDEN:** To. Abisko Vitmyt, S Marmobrottet, [no.] 2479, 15–18.vii.1983, H. Andersson leg., 1♀ (MZLU). — **Other material** (see also ROHÁČEK 2006, 2013): **FINLAND:** St. Kankaanpää, Kyynärjärvi, coordinates 686888:35244, 13.vi.2004, J. Kahanpää leg., 1♂ (id jka-06-03373) (JKH). **UNITED KINGDOM: England:** Wilts. Jones's Mill, 31.v.2004, J.W. Ismay & B. Schulten leg., 11♂ 11♀ (OXUM, 9♂ 9♀; SMOC, 2♂ 2♀, 1♂ used for molecular

work, 1♂ genit. prep.). **SWEDEN:** Vr. Munkfors kommun, Ransäter, Rudstorp, 59°46'22.64"N, 13°28'25.37"E, sandy railway embankment through pasture-land, MT, SMTP leg., 18–25.vi.2005, 2♂ (1♂ genit. prep.), 7–15.vii.2005, 1♂ (NHRS, 2♂; SMOC, 1♂).

3.8. Phylogenetic relationships

The dataset of anthomyzid species analysed here differs from that of ROHÁČEK et al. (2019) only by the addition of a single species, *C. marshalli*. This addition proved to have a negligible impact on the general tree topology despite removing two previous trichotomies (cf. ROHÁČEK et al. 2019: fig. 2a versus Fig. 91), because the newly resolved clades remain poorly supported (PP=0.66, 0.55). *Typhamyza* is now depicted as a sister to the *Amygdalops*–*Cercagnota* pair but this node is weakly supported (PP=0.70). There is also a novel trichotomy introduced in the current study within the *Mumetopia*–*Stiphrosoma* clade indicating that the previously poorly supported (PP=0.70) positioning of the *Mumetopia nigrimana* group among *Stiphrosoma* species is no longer recognized. This group could still be a sister group of *Stiphrosoma* as recognized by the result of the RAxML analysis (BV=88%; ROHÁČEK et al. 2019: fig. 2b) and also by the previous morphological analysis (ROHÁČEK & BARBER 2009: figs. 36–38).

The molecular study by ROHÁČEK et al. (2019) was devoted to a discussion of the phylogeny of the *Anthomyza* group of genera so that the relationships of *Carexomyza* are discussed here for the first time. It should also be noted that in previous morphological hypotheses, the genus *Cercagnota* Roháček & Freidberg, 1993 was considered the probable sister group of the *Chamaebosca* group of genera (represented by the *Mumetopia*–*Stiphrosoma* clade in molecular analyses), see ROHÁČEK & BARBER (2009: figs. 36–38) and ROHÁČEK (2009: fig. 137). This presumption was rejected by ROHÁČEK & TÓTHOVÁ (2014) because this and all subsequent molecular analyses (see ROHÁČEK et al. 2019 and that presented in Fig. 91) definitely exclude *Cercagnota* (more precisely its only known species *C. collini* (Czerny, 1928)) from this alliance and, besides, the morphological support of this previous relationship was always poor (ROHÁČEK & BARBER 2009).

Whereas previous morphological (ROHÁČEK 2009) and molecular (ROHÁČEK et al. 2009; ROHÁČEK & TÓTHOVÁ 2014) analyses only revealed that *Carexomyza caricis* is not distinctly allied to *Paranthomyza nitida* nor to any of the other analysed species (its sister group had not been recognized), the most recent molecular hypothesis by ROHÁČEK et al. (2019: figs. 2a, 2b, 4 with three *Carexomyza* species included) found the genus to represent a distinctive, strongly supported monophyletic lineage, forming a sister group of the *Mumetopia*–*Stiphrosoma* clade. This sister-group relationship has been confirmed and conserved here with the addition of the fourth species, *C. marshalli*, to the dataset (see Fig. 91). The molecularly well-supported relationship of *Carexomyza* with the *Mumetopia*–*Stiphrosoma* clade (a subset

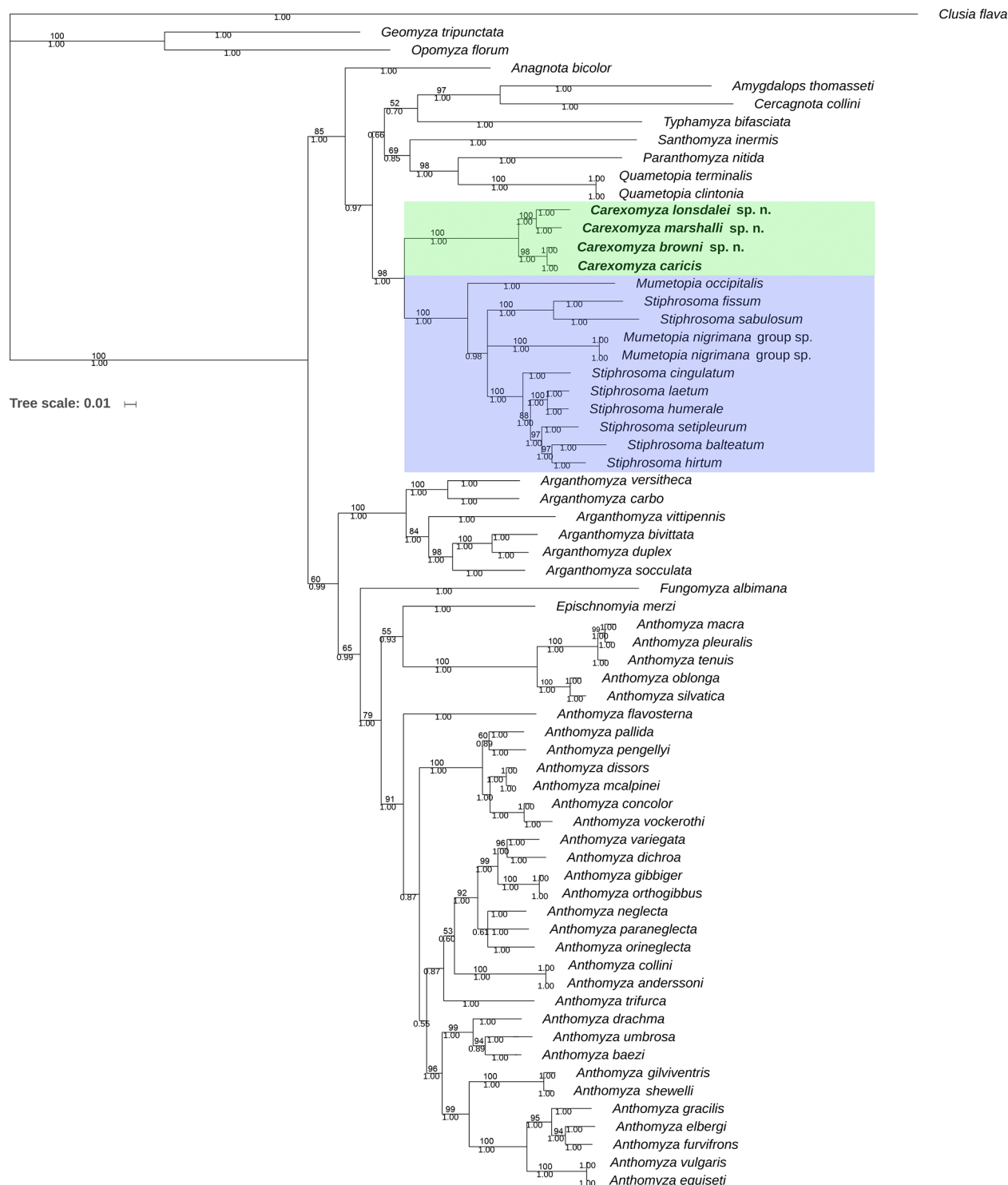


Fig. 91. Bayesian hypothesis for relationships of 62 species of Anthomyzidae based on DNA sequence data (12S, 16S, 28S, COI, COII, CytB, ITS2) representing 4580 characters. Numbers below nodes = posterior probability (PP) values if > 0.5, and above nodes = bootstrap support values (BV) for RAxML. The taxa discussed in the text are in the green box (*Carexomyza* species) and the blue box (members of the *Mumetopia*–*Stiphrosoma* clade).

of the *Chamaebosca* group of genera) indicates that this affinity could also be supported by morphological synapomorphies.

Morphological comparison of *Carexomyza* with all members of the *Chamaebosca* group of genera (including those unnamed, see ROHÁČEK & BARBER 2009) revealed several characters in the male and, particularly, female

postabdominal structures which could be considered synapomorphic of the cluster containing all these groups. These include (numbering of characters is the same as in the above generic diagnosis): (43) epandrium relatively broad and anterodorsally more or less straight; (55) phallopore short and bipartite (with posteroventral part fused ventrally with basal part of saccus); (64) female T8

plate-shaped, relatively large, broad posteriorly and more or less tapered anteriorly; (67) internal sclerites of female genital chamber well-developed, composed of two pairs of sclerites (anterior and posterior) and a ventral annular sclerite (but the latter is modified to a slender transverse loop-like structure, apomorphic for the *Chamaebosca* group, see ROHÁČEK & BARBER 2005, 2009); (69) ventral receptacle short, having a small, slightly sclerotized and distally rounded cup-like tip. In this context, a surprisingly similar microhabitat and behaviour of (most) representatives of these groups can also be mentioned, i.e., their association with clumps and tufts of various graminoids where adults live close to the ground and this habit seems to be reflected in shortening of their wings (often being shorter than body length and sometimes reduced to brachyptery, see ROHÁČEK & BARBER 2009).

The present molecular hypothesis (Fig. 91) has resolved the relationships of species within the genus *Carexomyza*. Two distinct sister pairs have been recognized, viz. *C. lonsdalei*–*C. marshalli* and *C. browni*–*C. caricis*, both strongly supported in both BI and RAxML analyses. While the former pair is purely Nearctic, the latter contains Nearctic (*C. browni*) and Palearctic (*C. caricis*) relatives. The morphological synapomorphies of both these sister pairs are discussed above under *C. lonsdalei* and *C. browni*, respectively.

Following the time-calibrated molecular hypothesis by ROHÁČEK et al. (2019: fig. 4, table S1), the *Carexomyza* lineage diverged from that of the *Mumetopia*–*Stiphrosoma* clade (representing the *Chamaebosca* group of genera) relatively long ago, in the lower Miocene, about 17.28 (14.12–21.03) MYA. The hypothetical common ancestor of these groups was of New World origin because the majority of their species (including the most ancestral species) occur in the Americas while only a few (and most advanced) representatives of *Stiphrosoma* and *Carexomyza* inhabit the Palearctic Region. Based on this study, the ancestor of the previously discussed sister pairs of *Carexomyza* split much later, in the Pliocene, ca 3.78 (2.75–4.97) MYA. Because only three species of *Carexomyza* were included in the time-calibrated hypothesis by ROHÁČEK et al. (2019) (*C. marshalli* was absent), the time of divergence of *C. lonsdalei* from *C. marshalli* remains unknown but it can be presumed that they split sooner than did the *C. browni*–*C. caricis* pair inasmuch as they are more dissimilar genetically (cf. Fig. 91). The splitting of the *C. browni*–*C. caricis* pair (*C. browni* treated as *Carexomyza* sp.n. 3 in ROHÁČEK et al. 2019: fig. 4) occurred relatively recently, in the Pleistocene, ca 0.71 (0.37–1.15) MYA, as discussed above under *C. caricis*.

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