

The genus *Calamoncosis* in the Nearctic region (Diptera: Chloropidae)

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Abstract—The Nearctic fauna of the genus *Calamoncosis* Enderlein is reviewed. Five species are present in eastern North America: *C. carncrossi* Nartshuk was recently described from New York; the Palearctic species *C. aprica* (Meigen) and *C. glyceriae* Nartshuk are newly recorded, and two new species, *C. brooksi* and *C. munda*, are described from eastern North America. A sixth species present in the Nearctic Region is represented by one female specimen and is not identifiable. Most Nearctic specimens were collected in peatlands or marshes in Quebec, but there are scattered records from other grass-dominated habitats in Ontario, Manitoba, New York, and Texas. A key to the described species of *Calamoncosis* in the Nearctic Region is given.

Résumé—Nous révisons la faune néarctique du genre *Calamoncosis* Enderlein. Il y a cinq espèces présentes dans l'est de l'Amérique du Nord: *C. carncrossi* Nartshuk récemment décrit de l'état de New York, les espèces paléarctiques *C. aprica* (Meigen) et *C. glyceriae* Nartshuk nouvellement signalées et deux nouvelles espèces, *C. brooksi* et *C. munda*, décrites ici de l'est de l'Amérique du Nord. Une sixième espèce est présente dans la région néarctique, mais le seul spécimen femelle connu n'est pas identifiable. La plupart des spécimens néarctiques ont été récoltés dans des tourbières ou des marécages au Québec, mais il y a récoltes éparpillées provenant d'autres habitats dominés par les herbes en Ontario, au Manitoba, au New York et au Texas. Une clé permet d'identifier les espèces néarctiques connues de *Calamoncosis*.

[Traduit par la Rédaction]

Introduction

Recent research on chloropid diversity in eastern North America has resulted in new Nearctic records for species previously known only from the Palearctic Region. These include *Aphanotrigonum trilineatum* (Meigen) (Beaulieu and Wheeler 2001), *Cetema elongatum* (Meigen) (Savage and Wheeler 1999), *Conioscinella zetterstedti* Andersson (Wheeler 1994), *Dicraeus fennicus* Duda (Beaulieu and Wheeler 2001), *Oscinella angularis* Collin (Nartshuk 2001), and three species of *Lipara* Meigen (Tewksbury *et al.* 2002). In the course of ecological studies on wetland Diptera, we have identified multiple

species of *Calamoncosis* Enderlein from marshes and peatlands in eastern Canada.

The genus *Calamoncosis* includes 27 described species, primarily in the Palearctic Region, but also in the Oriental, Australasian, and Afrotropical regions (Sabrosky 1984²; Cherian 1989; Wendt 1994). There are few published records of described *Calamoncosis* species in the New World; Sabrosky (1965, 1987) included *Calamoncosis* in a catalog and key to the Nearctic genera of Chloropidae, but that was based on one unnamed species from Michigan. Savage *et al.* (2011) and Grégoire Taillefer and Wheeler (2011) recorded an unidentified species of *Calamoncosis* from peatlands in southern Quebec. While the

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²C.W. Sabrosky. 1984. (Draft) Check list of the Chloropidae of the world (Diptera). Unpublished manuscript.

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present paper was in review, Eichiner *et al.* (2011) described a new species of *Calamoncosis* from New York State.

In this paper we review *Calamoncosis* in the Nearctic Region, including the description of two new Nearctic species and notes on two newly recorded species previously known from the Palearctic Region.

Material and methods

Nearctic specimens of *Calamoncosis* are rare in collections. Most specimens examined are deposited in the Lyman Entomological Museum (McGill University, Ste-Anne-de-Bellevue, Quebec) (LEM); additional specimens were examined from the following collections: Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa, Ontario, Canada (CNC); National Museum of Natural History, Smithsonian Institution, Washington, D.C., United States of America (USNM).

Nearctic specimens were identified using published keys and taxonomic papers on the Palearctic fauna (*e.g.*, Duda 1933; Collin 1946; Nartshuk 1962; Zuska 1968; Nartshuk *et al.* 1970; Wendt 1994) and comparison with identified Palearctic specimens in CNC, LEM, and USNM.

Genitalic preparations were made by removing the abdomen of mounted specimens and heating it in 85% lactic acid in a microwave oven for two periods of 20 s, separated by a cooling period of 1 min. Cleared genitalia were examined in glycerin and subsequently stored in glycerin in a microvial pinned beneath the source specimen.

Results

Calamoncosis Enderlein

Calamoncosis Enderlein, 1911: 235 (type species: *Lipara rufitarsis* Loew, original designation; misidentification, = *Lipara minima* Strobl). *Stizambia* Enderlein, 1936: 187 (*nomen nudum*).

Stizambia Sabrosky, 1941: 767 (type species: *Chlorops aprica* Meigen, original designation). *Rhaphiopyga* Nartshuk, 1971: 292 (as subgenus) (type species: *Calamoncosis glyceriae* Nartshuk, original designation).

Diagnosis

Calamoncosis may be distinguished from other Nearctic genera of oscinelline Chloropidae by a shining frontal triangle with at least one, usually more, rows of setulae on its surface inside the lateral margin; and a shining, punctate scutum and scutellum evenly covered with long dense setulae. The genus is most easily confused with *Siphonella* in the Nearctic Region, but the latter genus has an acute, strongly projecting vibrissal angle and a bare frontal triangle.

Remarks

Sabrosky (1987) included *Calamoncosis* in a key to genera of Nearctic Chloropidae, based on an unnamed species from Michigan. We have not been able to locate specimens in order to verify the identity of that species. Sabrosky's unpublished notes on Chloropidae (now deposited in LEM) make no mention of the specimen(s).

Key to the Nearctic species of *Calamoncosis*

1. Scutellum elongate triangular, with four or five pairs of short strong dark marginal setae arising from distinct tubercles; halter dark brown or black *C. brooksi*
- Scutellum rounded or short triangular, marginal setae short and weak except for apical pair, tubercles small and present only apically or absent; halter yellow or pale brown 2
2. One anterior and one posterior notopleural seta present 3
- One anterior and two posterior notopleural setae present 4

3. Gena as high as width of first flagellomere; frontal triangle 0.8 times length of frons; male cerci with shallow median emargination, hypandrium closed posteriorly *C. carncrossi*
 — Gena and frontal triangle shorter than above; male cerci with V-shaped median emargination, hypandrium open posteriorly *C. aprica*
4. Interfrontal setulae pale; ocellar tubercle microtomentose, contrasting with polished frontal triangle; palpus yellow or yellow brown; female ovipositor not laterally compressed or strongly sclerotized, cerci cylindrical *C. munda*
 — Interfrontal setulae dark; ocellar tubercle bare or lightly microtomentose, not strongly contrasting with frontal triangle; palpus dark brown; female ovipositor sclerotized, laterally compressed, cerci sharply pointed posteriorly *C. glyceriae*

***Calamoncosis aprica* (Meigen)**

Chlorops aprica Meigen, 1830: 158.

Diagnosis

This species can be distinguished from other described species of *Calamoncosis* in the Nearctic Region except *C. carncrossi* by the possession of 1 anterior and 1 posterior notopleural setae (at least 1+2 in other described species). It can be distinguished from *C. carncrossi* by the narrower gena and shorter frontal triangle, as well as characters of the male genitalia.

Material examined

NEARCTIC: **Canada. Ontario:** 10 km S Richmond, sweep fen, 15.vii.1999, S.E. Brooks (1♀, LEM); **Quebec:** Lac St. François National Wildlife Area, Chemin Fraser (45°2.4'N, 74°28.3'W), Malaise trap beside sedge meadow, 18.26.v.1999, S.E. Brooks (1♀, LEM); **United States. Texas:** Val Verde Co., Dolan Falls on Devil's River (29°53'N, 100°59'W), 5–7.v.1995, Malaise trap, J.E. O'Hara (1♀, LEM).

PALEARCTIC: **Belgium.** Uitbergen, Kalkense, Meersen Nature Reserve (51°01'N, 03°57'E), sweep, 3.vii.2000, S.E. Brooks (1♂, LEM), **Poland. Pomorze:** nr. Klukowe Legi, nr. Slowinski National Park (54°42.2'N, 17°17.9'E), sweep in field, 19.v.2007, J. Mlynarek (1♂, LEM).

Remarks

Although *C. aprica* is known only from female specimens in North America, the single posterior notopleural seta is characteristic for this species, and the specimen matches Palearctic material in other characters. Examination of male genitalia would be required to confirm whether or not the Nearctic specimens are conspecific with those from the Palearctic Region.

In Europe, *C. aprica* is usually an inquiline in galls of species of *Lipara* on *Phragmites australis* (Cav.) Trin. ex Steud. (Poaceae) (Grochowska 2002). No species of *Lipara* have yet been reported in association with *P. australis* in Quebec, but Grochowska (2002) also reported specimens of *C. aprica* reared from damaged plants of other species, in which they were secondary invaders associated with other herbivorous insects. Specimens of *C. aprica* have been reared from stems of *Tripolium pannonicum* (Jacq.) Dobrocz. (Asteraceae) in Germany (M. von Tschirnhaus, personal communication).

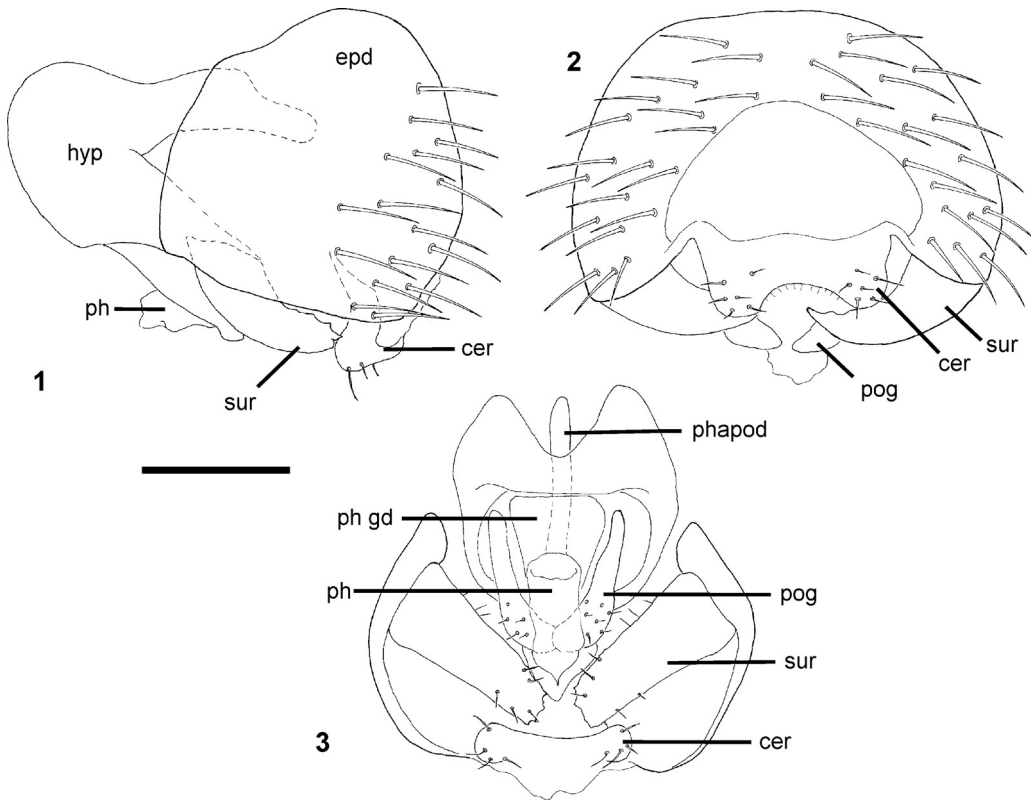
***Calamoncosis brooksi* Grégoire Taillefer and Wheeler, n. sp.**

(Figs. 1–3)

Type material

Holotype ♂: **Canada. Quebec:** Lac St. François National Wildlife Area, Chemin Fraser (45°2.4'N, 74°28.3'W), Malaise trap beside sedge meadow, 18–26.v.1999, S.E. Brooks

Figs. 1–3. *Calamoncosis brooksi*, male genitalia: 1, lateral view; 2, posterior view; 3, ventral view (*cer*, cercus; *epd*, epandrium; *hyp*, hypandrium; *ph*, phallus; *ph gd*, phallic guide; *phapod*, phallapodeme; *pog*, postgonite; *sur*, surstylus). Scale bar = 0.1 mm.



(LEM). **Paratypes: Ontario:** Moosonee (51.2 4466°N, 80.67767°W), mesic replicate 2, Malaise trap, 21–24.vi.2010. Northern Biodiversity Program field party (3♂, LEM); **Quebec:** Lanoraie Bog (45°59'N, 73°17'W), Malaise trap, 2.vi.1987, Sanborne, Genier, and Hargreave (1♀, LEM).

Diagnosis

This species can be distinguished from other *Calamoncosis* species in North America by the elongate triangular scutellum with four pairs of distinct tubercles and the dark halter.

Description

Total length 2.0–2.3 mm, wing length 1.7–1.9 mm. Overall colour shining black; head higher than long, frons densely microtomen-

tose, appearing velvety, interfrontal and fronto-orbital setulae sparse, fine, pale; frontal triangle 0.7–0.8 times length of frons, polished including ocellar tubercle, with setulae, as long and strong as interfrontals, in irregular rows on lateral third of triangle; ocellar and inner vertical setae barely differentiated from interfrontals, outer vertical seta and postocellars stronger but pale; eye with sparse ommatrichia, each hair shorter than diameter of 2 ommatidia; gena black, vibrissal angle obtuse, not extending beyond anterior margin of eye, vibrissa black, genal height 0.1 times eye height and approximately 0.5 times height of first flagellomere; face black, with carina weakly developed in dorsal half; antenna with pedicel dark yellow, first flagellomere round, brown, arista short, medium brown, pubescent, with thick base; palpus small, dark brown; proboscis brown, short.

Scutum shining but densely punctate, evenly covered with long pale setulae; thoracic setae: 1 anterior and 2 (rarely 3) posterior notopleural, 1 anterior and 1 posterior postalar, 1 dorsocentral stronger and darker than surrounding setulae; scutellum elongate triangular, slightly longer than wide, punctate and rugose dorsally, apical scutellar setae dark, strong, arising from small but distinct tubercles, three pairs of subapical/lateral setae shorter and weaker, arising from small but distinct tubercles, other scutellar setae as strong as scutal setulae. *Legs*: femora and tibiae dark brown, tarsi yellow; male femoral organ a dense patch of 25–30 small tubercles with minute setulae, tibial organ broad, oval, appearing velvety. *Wing*: hyaline, veins pale brown, ratio of costal sectors C1:C2:C3:C4 = 1:1.1:0.6:0.4; halter dark brown.

Abdomen: slightly paler than thorax, shining.

Male genitalia (Figs. 1–3): epandrium approximately as long as high in lateral view, broad in posterior view, with setae on posterior half; surstylus relatively narrow and slightly recurved, evenly tapering, with dentate apex, with sparse, weak setae; hypandrium robust anteriorly, pregonites, postgonites and phallic guide all well-sclerotized; postgonites with weak setulae posteriorly; basiphallus well-sclerotized, distiphallus longer than basiphallus, membranous; cerci broad, well-sclerotized, rounded ventrally in posterior view and separated by broad U-shaped ventral emargination, with fine setae; subepandrial sclerite not well-developed.

Female postabdomen: unmodified, segments 8–10 not laterally compressed, cerci cylindrical and setulose.

Etymology

This species is named in honour of our colleague Scott Brooks, one of the new generation of dipterists at the Canadian National Collection. Scott collected the holotypes of this species and *C. munda*, as well as many of the other specimens examined in this study.

Remarks

The unmodified female ovipositor places this species in the subgenus *Calamoncosis* s.s. *Calamoncosis brooksi* is morphologically similar to the Palearctic species *C. aspistylina* Duda, which has longer scutellar tubercles, stouter apical scutellar setae, and a frontal triangle that extends almost to the anterior margin of the frons. Other than its habitat associations with sedge meadows and peatlands, the ecology of *C. brooksi* is unknown. The collecting site in Moosonee, Ontario, was a disturbed area near a wastewater-treatment plant, in contrast to the other collecting localities, which were relatively undisturbed. *Calamoncosis aspistylina* is a herbivore of reed canary grass (*Phalaris arundinacea* L., Poaceae) in the Palearctic Region, and Nartshuk (2001) predicted that it might eventually become established in North America, as did *Oscinella angularis*, which feeds on the same host plant. We have seen no specimens of *C. aspistylina* from North America. Beaulieu and Wheeler (2002) reared seven species of Chloropidae from *P. arundinacea* in southern Quebec, but all were secondary invaders of damaged shoots infested by noctuid moth larvae. No primary feeding damage by Chloropidae was noted in that study.

Calamoncosis carncrossi Nartshuk

Calamoncosis carncrossi Nartshuk in Eichiner *et al.*, 2011: 111.

Remarks

Eichiner *et al.* (2011) described and illustrated the adults and immature stages of this species and provided notes on its biology. It appears to be closely associated with common reed, *Phalaris australis* L. (Poaceae), in eastern North America. *Calamoncosis carncrossi* is most similar to *C. aprica*, but differs from that species in characters of the male genitalia; also, some minor morphometric differences are discussed by Eichiner *et al.* (2011). We examined no specimens of *C. carncrossi* in this study.

***Calamoncosis glyceriae* Nartshuk**

Calamoncosis glyceriae Nartshuk, 1958: 100.
Calamoncosis laminiformis Becker *sensu* Duda
 1933 and Collin 1946 (misidentification).

Diagnosis

Calamoncosis glyceriae can be distinguished from other Nearctic species of *Calamoncosis* by the texture and chaetotaxy of the frons and ocellar tubercle, the colour of the palpus, and, in females, the laterally compressed and sclerotized ovipositor.

Material examined

NEARCTIC: Canada. Quebec: St. Charles Bog (46°44'52.1"N, 70°59'42.0"W), sweeping, restored site T1, 22.vi.2006, A. Grégoire Taillefer (1 ♂, LEM).

PALEARCTIC: Belgium. Uitbergen, Kalkense, Meersen Nature Reserve (51°1'N, 3°57'E), sweep, 3.vii.2000, S.E. Brooks (2 ♂, 2 ♀, LEM); **Flanders:** Wetteren (51°00'N, 3°53'E), sweep ditch beside Schelde River, 3.vii.2000, S.E. Brooks (1 ♂, LEM); **Germany.** Frankfurt (Oder), M.P. Reidel (1 ♀, USNM); **Poland. Pomorze:** Smoldzino (54°39.3'N, 17°13.0'E), sweep meadow, Lupawa River, 20.v.2007, J. Mlynarek (1 ♀, LEM); **Russia.** Kurgan, 16.vii.1951, E.P. Nartshuk (1 ♂ paratype, 1 ♀ paratype, USNM); **United Kingdom. England:** Oxford, 18.vi.1922 (1 ♂, 1 ♀, USNM).

Remarks

We have identified only one specimen of this species in North America, collected in a restored bog previously used for peat extraction (Grégoire Taillefer and Wheeler 2011). The specimen was taken in the same series as some of the types of *C. munda*.

***Calamoncosis munda* Grégoire Taillefer and Wheeler, n. sp.**

(Figs. 4–6)

Type material

Holotype ♂: **Canada. Quebec:** Lac St. Francois National Wildlife Area, Chemin Fraser, (45°2.4'N, 74°28.3'W), Malaise trap

beside sedge meadow, 18–26.v.1999, S.E. Brooks (LEM). **Paratypes:** same data as holotype (2 ♂, 3 ♀, LEM); **Canada. Quebec:** Bois-des-Bel Bog (45°57'59.1"N 69°25'49.9"W), Malaise trap, restored site, 9–13.vi.2006, A. Grégoire Taillefer (1 ♂, LEM); St-Charles Bog (46°44'52.1"N 70°59'42.0"W), Malaise trap, restored site, 14–16.vi.2006, A. Grégoire Taillefer (3 ♀, LEM); same except 7–9.vii.2006 (1 ♀, LEM); same except 27–29.vii.2006 (1 ♀, LEM); same except sweeping, 22.vi.2006 (1 ♀, LEM); Lanoraie Bog (45°59'N, 73°17'W), Malaise trap, 2.vi.1987, Sanborne, Genier, and Hargreave (1 ♀, LEM); Johnville Bog and Forest Park (45°20.7'N, 71°44.5'W), Malaise trap, 28.vii.1.viii.2005, J. Savage and J. Kuchta (1 ♀, LEM); same except 12–15.viii.2005 (1 ♀, LEM); Ogden, Marlinton Bog (45°2.4'N, 72°10.4'W), Malaise trap, 4–11.vii.2006, A. Moores (1 ♀, LEM); Réserve écologique des Tourbières-de-Lanoraie (45°59.8'N, 73°18.0'W), Malaise trap, 26.vi.3.vii.2006, A. Moores (1 ♀, LEM).

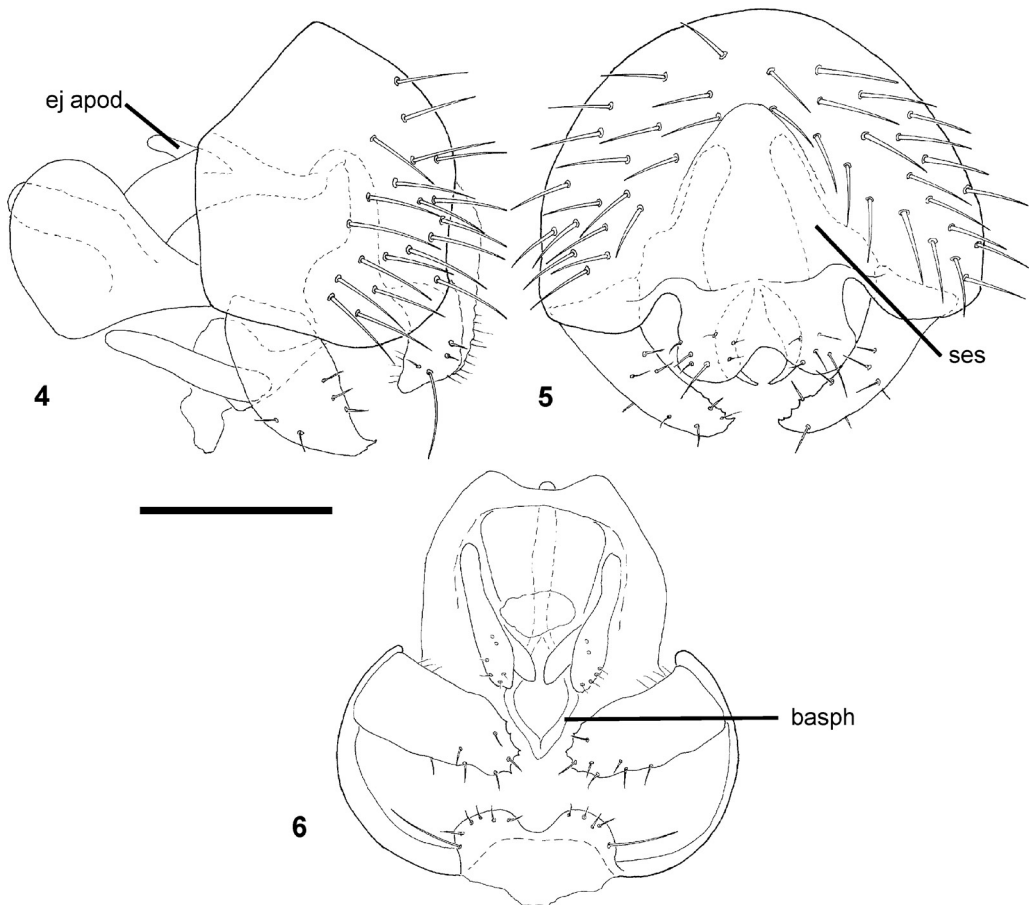
Diagnosis

Calamoncosis munda may be distinguished from other Nearctic *Calamoncosis* species by the dense pale interfrontal setulae, microtomentose ocellar tubercle, and yellow palpus.

Description

Total length 2.1–3.2 mm, wing length 1.9–2.5 mm. Overall colour shining dark brown; head slightly higher than long, frons densely microtomentose, appearing almost pubescent, interfrontal and fronto-orbital setulae dense, fine, pale; frontal triangle 0.5–0.6 times length of frons, polished except for densely microtomentose ocellar tubercle, with two rows of setulae near margin as long and strong as interfrontals; ocellar and inner vertical setae barely differentiated from interfrontals, outer vertical seta and postocellars stronger but pale; eye with dense ommatrichia, each hair as long as diameter of 2 ommatidia; gena densely yellow–gray microtomentose with shining black ventral margin, vibrissal angle acute but not extending beyond anterior margin of eye, vibrissa pale, genal height 0.1 times eye height and approximately 0.5 times

Figs. 4–6. *Calamoncosis munda*, male genitalia: 4, lateral view; 5, posterior view; 6, ventral view (*basph*, basiphallus; *ej apod*, ejaculatory apodeme; *ses*, subepandrial sclerite). Scale bar = 0.1 mm.



height of first flagellomere; face dark, with yellow–gray lunule, narrow carina extending to ventral margin of face; antenna with first flagellomere round, yellow with brown distal margin, arista short, medium brown, pubescent, with thick base; palpus yellow; proboscis yellow–brown, sclerotized, and geniculate, as long as or slightly longer than ventral margin of head.

Scutum shining but densely punctate, evenly covered with long pale setulae; thoracic setae: 1 anterior and 2 posterior notopleural, 1 anterior and 1 posterior postalar, 1 dorsocentral stronger and darker than surrounding setulae; scutellum broadly triangular, as long as wide, punctate and rugose dorsally, apical scutellar setae dark, strong, arising from small

but distinct tubercles, subapical and lateral setae shorter and weaker, arising from barely discernible tubercles, other scutellar setae as strong as scutal setulae. *Legs*: femora dark brown with apex narrowly dark yellow, tibiae dark brown with basal and apical 20%–25% dark yellow, tarsi pale yellow; male femoral organ a dense patch of 30–35 small tubercles with minute setulae, tibial organ broad, oval, appearing velvety. *Wing*: hyaline, veins brown, ratio of costal sectors C1:C2:C3:C4 = 1:1.1:0.6:0.4; halter yellow.

Abdomen: slightly paler than thorax, shining.

Male genitalia (Figs. 4–6): epandrium approximately as long as high in lateral view, broad in posterior view, with setae on poster-

ior half; surstylus relatively narrow and straight, evenly tapering, slightly dentate distally and apically, with sparse weak setae; hypandrium robust anteriorly, pregonites, postgonites, and phallic guide all well-sclerotized; postgonites with several weak setulae posteriorly; basiphallus large, well-sclerotized, distiphallus small, membranous; cerci broad, well-sclerotized, rounded ventrally in posterior view, and separated by narrow U-shaped ventral emargination, with fine setae; subepandrial sclerite well-developed.

Female postabdomen: unmodified, segments 8–10 not laterally compressed, cerci cylindrical and setulose.

Etymology

The species name is from the Latin *mundus* (“world”), referring to the first described New World species of this genus; in addition, the consonants MND are a widely used acronym for the *Manual of Nearctic Diptera*, a monumental contribution that made the working lives of Dipterists more pleasant.

Remarks

The unmodified female ovipositor places this species in the subgenus *Calamoncosis* s.s. The type specimens were collected in bogs or wet sedge meadows in southern Quebec, including seven specimens from a restored bog previously mined for horticultural peat. Almost all specimens were collected in Malaise traps despite the fact that extensive collecting using sweep nets and yellow pan traps was carried out at all of the collecting localities (Beaulieu and Wheeler 2001; Grégoire Taillefer and Wheeler 2011; Savage *et al.* 2011). Grégoire Taillefer and Wheeler (2011) listed this species as *Calamoncosis* n. sp. A; Savage *et al.* (2011) listed it as *Calamoncosis* sp.

***Calamoncosis* sp. LEM 1**

Material examined

NEARCTIC: **Canada. Manitoba:** Winnipeg, St. Charles Rifle Range (49°54.6'N, 97°20.5'W), Malaise trap at poplar forest/

tallgrass prairie edge, 3–10.vii.1998, Pollock and Roughley (1♀, LEM).

Remarks

This unnamed species is represented by a single female specimen. The ovipositor is unmodified, placing it in the subgenus *Calamoncosis* s.s. The specimen is similar to the Palearctic species *C. minima* (Strobl) but the frontal triangle is distinctly shorter. Although it is unidentified, we are confident that it is not conspecific with the other Nearctic species. This specimen also represents one of the few Nearctic records of the genus outside Quebec and Ontario. An additional female from Lafayette, Indiana (14.v.1918, J.M. Aldrich, USNM), may belong to the same species but the specimen is damaged (head missing, colour faded).

Discussion

Most of the Nearctic specimens examined were collected in peatlands or marshes, and more species may be expected with additional sampling in other habitats, given the breadth of host plants and habitat types exploited by *Calamoncosis* species in the Palearctic Region. For example, multiple species in addition to *C. aprica* are found asinquilines of *Lipara* galls on *Phragmites australis* (Grochowska 2002) and with the likely range expansion of several species of *Lipara* in eastern North America, some of these inquilines may be found here in the future.

Although relatively few specimens of *Calamoncosis* have been collected to date in North America, most of the species occur sympatrically in the same localities and habitats in Quebec. Many species were collected during the same collecting events: *C. aprica*, *C. brooksi*, and *C. munda* were collected in the same Malaise trap at Lac St. François; *C. brooksi* and *C. munda* in the same Malaise trap at Lanoraie Bog; and *C. glyceriae* and *C. munda* in the same sweep sample at St. Charles Bog.

Acknowledgements

The second author's interest in Chloropidae was developed during a Postdoctoral Fellowship in Ottawa from 1991 to 1993, where I had the good fortune to talk Diptera with, among others, Dick Vockeroth, Monty Wood, and Guy Shewell. During that time, and in the years since, I learned from Monty that students come first, and from Dick that good natural history and enthusiasm for the field beat bureaucracy and technology every time. Thanks are extended to Anna Solecki, who spotted the Moosonee specimens of *C. brooksi* in a Malaise-trap sample filled with tabanids, and to Jeff Cumming (CNC) and Lucrecia Rodriguez (USNM) for loans of material. Irina Brake and Michael von Tschirnhaus provided helpful comments on the manuscript. Funding was provided by the Natural Sciences and Engineering Research Council of Canada.

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