First record of a skating crane fly: The unusual ecology, behavior, and morphology of *Phantolabis lacustris* (Alexander, 1938) (Diptera: Limoniidae) with descriptions of the immature stages

R. William Bouchard Jr1,3 and Jon K. Gelhaus2,4

1Minnesota Pollution Control Agency, 520 Lafayette Road, Saint Paul, Minnesota 55155 USA
2The Academy of Natural Sciences of Drexel University, 1900 Ben Franklin Parkway, Philadelphia, Pennsylvania 19103 USA

Abstract: In 2003, large numbers of pupal exuviae and adults of an unusual skating crane fly (Tipuloidea: Limoniidae) were collected from a trout stream in southern Minnesota, USA. The species was identified as *Phantolabis lacustris* (Alexander, 1938), a crane fly with undescribed immature stages and biology. In this paper, we describe the immature stages and adult female along with the ecology and behavior of this unusual crane fly. *Phantolabis lacustris* is the first record of a skating crane fly and has a number of morphological characteristics related to this behavior. These characteristics include expansion of the 3rd tarsus of the meso- and meta-thoracic legs, sub-apical insertion of the tarsal claws, and enlargement of the male hypopygium.

Supercooling points for this fly ranged from −21.3 to −5.2°C, indicating that it is moderately cold tolerant. The skating behavior and cold tolerance of this crane fly is probably related to its emergence in late winter and early spring. A review of *P. lacustris* specimens collected as part of biomonitoring or ecological studies or deposited in museum collections indicates that the species has a broad distribution in the upper Midwest and eastern portions of North America. *Phantolabis lacustris* has probably been overlooked because of its early emergence in March, April, and May and the morphological similarity of its larvae with those of the genus *Hesperoconopa*. The larvae of *P. lacustris* cannot be morphologically separated from *Hesperoconopa* at this time, but their discrete geographic distributions permit the identification of *P. lacustris* and *Hesperoconopa* larvae.

Key words: winter-active, surface mating, surface-floating pupal exuviae, supercooling points, *Hesperoconopa*

The adults of many aquatic insects are active during the winter, even at subzero temperatures (e.g., Young 1969, Kohshima 1984, Ferrington and Saether 1987, Herrmann et al. 1987, Bouchard et al. 2006a, 2009). Aquatic insects are poikilothermic, so buffered water temperatures provide refuge (Moore and Lee 1991) from subzero air temperatures, particularly during the development of immature stages. However, winter-active insects also exhibit a number of physiological, behavioral, and morphological adaptations associated with survival in cold environments, which also allow adults to survive and remain active at low air temperatures (Downes 1965, Danks 1979). For example, some species can survive freezing by inducing controlled extracellular ice formation at relatively-high subzero temperatures (Zachariassen 1985, Lee 1989, Block 1991). A more common cold-hardiness strategy in winter-active insects is to lower the temperature at which their body fluids normally freeze (i.e., supercool) to prevent tissue injury (Sømme 1982, Lee 1989, Zachariassen and Kristiansen 2000, Bouchard et al. 2006b). This strategy permits insects to be active at low temperatures rather than needing to hibernate. In addition to physiological adaptations, many aquatic insects also have behavioral and morphological adaptations associated with activity at low temperatures. Many winter-active aquatic insects do not fly, and instead adult activity takes place on the substrate or water surface. At low temperatures or in marine habitats, the

E-mail addresses: 3will.bouchard@state.mn.us; 4jkg78@drexel.edu

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lack of flight probably minimizes inadvertent dislocation from mating areas or larval habitats (Ferrington and Saether 1987). The loss of flight behaviors often coincides with morphological adaptations including wing reduction or loss, reduced antennae, broadening of the legs, and enlarged hypopygium (Downes 1965, Byers 1969, Ferrington and Saether 1987). Similar morphological adaptations associated with surface mating or skating on the water’s surface have also been observed in many marine Diptera (e.g., Clunio, Telmatetogeton, Pontomyia, Cirrula, Dimecoenia; Neumann 1976, Mathis and Simpson 1981).

The unusual, evolutionary adaptations of insects active at subzero temperatures are interesting, but many winter-active aquatic insect species are also important constituents of their ecosystems (e.g., Bouchard and Ferrington 2009). For example, winter-active insects can be important food sources for trout and other winter-active fish species (e.g., Kelly-Quinn and Bracken 1990, Anderson 2012, French et al. 2014). The ecology and taxonomy of winter-active aquatic insects can also be important when they appear in biomonitoring samples. For these insects to be useful as components of indices of water body biological condition or health, researchers need to be able to accurately identify them and understand their ecological and functional traits (Cranston 1990, Bouchard et al. 2005, Poff et al. 2006).

During late winter 2003, we collected large numbers of crane fly pupal exuviae and adults. The adults were identified as Phantolabis lacustris (Alexander, 1938) (Tipuloidea: Limoniidae), an unusual and rarely-collected species for which the immature stages were unknown. This study documents surface skating behavior in adult P. lacustris, a behavior that is unusual for dipterans and unique in the superfamly Tipuloidea. Additionally, we describe the ecology of P. lacustris, the diagnostic characters for adults and immature stages, and its geographic distribution.

**METHODS**

**Study sites**

Our study of the ecology and behavior of P. lacustris was done largely at Trout Brook (Dakota County, Minnesota, USA; 44.5453°N, 92.8057°W; Fig. 1A), a small cold-water stream with mean daily water temperatures ranging from 1 to 14°C and a drainage area of 46 km². The substrates in this brook are predominantly sand with some areas of gravel, cobble, and soft sediment. We also sampled another small (drainage area = 20 km²) coldwater stream, Valley Creek (Washington County, Minnesota, USA; 44.9188°N, 92.8006°W; Fig. 1B). Valley Creek had measured mean daily temperatures of 2 to 16°C with predominately gravel and cobble substrates and some sand and silt.

We found additional larval and adult specimens and information in museums, literature reviews, and biological monitoring reports.

**Phenology and behavior**

**Sampling surface-floating pupal exuviae** We collected samples of surface-floating pupal exuviae (SFPE; Ferrington et al. 1991, Kranzfelder et al. 2015) from Trout Brook every other week from 28 January through 10 March 2008 and

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Figure 1. Phantolabis lacustris habitats in Minnesota, USA. A.—Trout Brook. B.—Valley Creek.
weekly from 10 March through 16 May 2008. Sample collection consisted of a 10-min sampling period within a ∼50 m reach of the stream. We began sample collection at the downstream and worked upstream. We sampled SFPE by scooping them into a pan from areas where they had accumulated (e.g., snags, in vegetation, back eddies). We poured this material through a standard (No. 120), 125-μm sieve before transferring the samples to 118-ml jars and filling the jars with 75% ethanol for preservation. In the laboratory, we transferred the sample material to a 125-μm sieve and rinsed with water to remove the preservative. We placed a small portion of the sample in a picking tray, removed Phan- tolabis pupal exuviae from the subsample under a dissecting microscope (10×), and placed the exuviae into vials with 75% ethanol. After a complete pass of the picking tray, we swirled the sample and scanned it again. This was repeated until 2 successive passes did not recover additional SFPE. We processed material from the sample in this manner until the full sample was sorted. We also removed and preserved adults present in the sample.

We compared emergence patterns to mean daily air temperatures and estimated mean daily water temperatures. In 2003, we deployed a StowAway® TidbiT® temperature logger (Onset, Bourne, Massachusetts) in Trout Brook to measure water temperature every 15 min. We then developed a regression model to predict mean daily water temperatures from mean daily air temperatures recorded at the Midwest Regional Climate Center for River Falls, Wisconsin USA (∼38 km from study stream) during the 2008 sampling period ($R^2 = 0.93$).

**Collection and observation of adults** During site visits to collect SFPE, we also collected adults from the water’s surface and from overhanging vegetation along the margins of the stream with a white, plastic pan (20 × 25 cm). We sampled the overhanging vegetation by pressing the pan gently into the vegetation at the water’s surface to collect specimens on the water and to dislodge specimens clinging to the vegetation such that they fell or were swept into the pan. Adults were then handpicked or aspirated from the pan. Most specimens were fixed in 75% ethanol, but some were collected live. Live insects were collected in the field by scooping them into 3.7-ml snap-top vials with a small amount of stream water and placing the vials into a cooler with stream water and snow to keep them at 0 to 5°C until returning to the laboratory. In the field and laboratory, adults were observed and recorded with photography and video to characterize and document their behavior.

**Collection of immature stages** During site visits to collect SFPE, we collected kick samples to identify the habitats in which larvae and pupae occur. We took kick samples from a variety of habitats including submerged vegetation, cobble/gravel riffles, sand, detritus, soft sediments, and semiaquatic habitat along the edge of the stream. We collected larvae and pupae from Trout Brook with a D-frame dip net with a 500-μm-aperture mesh. We collected larvae with kick nets by placing the net in the stream, disturbing the substrate upstream of the net, and allowing the current to wash material into the net. We placed the kick samples in a white, 20 × 25-cm plastic pan with a small amount of stream water and then picked larvae and pupae from the detritus. We fixed some larvae and pupae in 75% ethanol. We collected other specimens for rearing and placed these in 3.7-ml snap-top vials with a small amount of water and held them in a cooler with snow until returning to the laboratory.

**Rearing** We placed field-collected larvae in 35 × 10-mm petri dishes with sand and water collected from the field site. We held the dishes at 5 to 10°C and added stream water daily as needed. Larvae were checked daily until death and then preserved in 75% ethanol.

Adult specimens in copula that were collected from the field were held in 3.7-ml snap-top vials at 5 to 10°C. We monitored any eggs laid in the vial daily until we observed extensive fungal growth or larvae hatched. Eggs that failed to hatch were preserved in 75% ethanol, as were any dead adults or larvae.

**Cold hardiness**

Adult specimens used for supercooling point (SCP) experiments were collected from Valley Creek on 20 March 2007 with the same methods described in the *Collection and observation of adults* section. These specimens were placed in a growth chamber maintained at 5°C. Surface contact thermometry was used to estimate SCPs following Carrillo et al. (2004). Insects were cooled at a rate of ∼1°C/min, and SCPs were estimated by determining the lowest temperature reached before the release of the latent heat of fusion. We did this test on a total of 8 male and 2 female *P. lacustris*.

**Examination of specimens**

In addition to the specimens collected from Trout Brook and Valley Creek, we also obtained adult, pupal, and larval specimens from other localities through loans and gifts. Type specimens and other adult material were obtained on loan through museums (Smithsonian Institution, University of Michigan, and University of Kansas). In addition to material from museum collections, we examined larval specimens from water quality programs and contractors in the United States and Canada when possible. In some cases, only photos of these larval specimens were examined. We also compiled records from published reports. All records of *P. lacustris* compiled in this study are listed in Appendix S1.

To examine the morphology in more detail, some adults and larvae were cleared and slide mounted in Euparal. The larvae were cleared with 10% KOH, placed in glacial acetic
acid for several minutes, dehydrated with 95% ethanol, and slide mounted under 18-mm square cover glasses. The heads of some of these larval specimens were dissected and slide mounted under a separate 18-mm square cover glass. For adults, wings, 1 set of legs, and antennae were dissected from the head and thorax and each slide mounted under 12-mm circular cover glasses. The head, thorax, and abdomen of adults were cleared with 10% KOH, placed in glacial acetic acid for several minutes, dehydrated with 95% ethanol, and slide mounted individually under 12-mm circular cover glasses. Pupal exuviae and eggs were slide mounted in Euparal without clearing under 18-mm square cover glasses.

Photographs were taken with a Canon® EOS 80D (Tokyo, Japan) camera equipped with a Canon EF 100 mm macro lens with image stabilizer. Image stacking was processed with Zerene Stacker (https://zerenesystems .com/cms/home) with some modifications through Adobe® Photoshop®.

RESULTS

Morphological descriptions

The original description of P. lacustris (Alexander 1938) was brief and included only adult males, not the immature stages (egg, larva, and pupa) or the female adult. Alexander (1938) described the adult male of P. lacustris as Erioptera (Psiloconopa) lacustris from specimens collected from the upper peninsula of Michigan. At that time, he noted the distinctiveness of its venation from other regional species, the lack of trichiation on its wing veins, and the single pair of gonostyles in the male and compared it to Erioptera pilipennis Alexander (now Hesperoconopa pilipennis). He did not specifically state which features led him to conclude the 2 species were similar (Alexander 1938).

In 1956, Alexander moved E. lacustris to Cryptolabis and created the monotypic subgenus Phantolabis (Alexander 1956), noting that the species could no longer be retained in Erioptera and seemed closer to Cryptolabis, particularly the subgenus Baeoura. Unfortunately, he did not indicate the morphological features that led to this conclusion, although the single pair of gonostyles (dististyle) in Phantolabis and Cryptolabis could have been a deciding factor since most crane flies have 2 pairs of gonostyles. Yet Alexander also stated that the “structure of the male hypopygium, particularly the phallosome, including the aedeagus” is different than other subgenera of Cryptolabis.

Forty years after description, the monotypic genus Phantolabis was first included in a generic key (Alexander and Byers 1981) albeit without illustrations. Females are first described in that key, although only by stating that the female terminalia is “not as above” in contrast with Cryptolabis females that have “cercus and hypogynial valves of ovipositor short and fleshy.”

We describe all life stages of P. lacustris here and also provide the first illustrations of this species. The morphological terminology and abbreviations used here follow Alexander and Byers (1981) but include some updated terms for adult wing venation and genitalia from Gelhaus (2009).

Phantolabis lacustris (Alexander, 1938)

Additional references: Alexander (1938, pages 76–77) (as Erioptera [Psiloconopa] lacustris). Alexander (1943, page 486; 1956, pages 184–185) (as Cryptolabis [Phantolabis] lacustris). Alexander (1965, page 78) and Alexander and Byers (1981, page 175) (as Phantolabis lacustris).

Adult diagnosis A small Chioneinae crane fly with general coloration dark grayish brown (Fig. 2A, B); wings with a brownish tinge, evenly in male (Fig. 2C), with some lighter areas in female in cells r1, r, and m, and in apical wing cells r3 to m4 (Fig. 2D), wing membrane wrinkled overall; veins almost without macrotrichia; cell r3 long; meron large; prothoracic and metathoracic legs with tarsi 3 with keel-like edge, tarsal claws inserted subapically, tip of tars 5 extended and flattened beyond tarsal claw insertion; male hypopygium with a single flat gonostyle, its margin with peg-like spines; interbase slender, curved, and needle like, parameres absent.

Adult male Material examined: n = 135 (Appendix S1); measured: n = 10. Body length: 2.9 to 4.1 mm (dry), 3.3 to 4.9 mm (ethanol); wing length: 4.6 to 5.6 mm, width 1.4 to 1.7 mm.

Head (Fig. 3A). Spherical, dark brownish gray. Ros- trium short, ≈¼ head length; palps short, ≈½ length of head length, with 5 segments, terminal segment slightly larger than preceding segment with tapered apex. Antenna (Fig. 3B) even

Figure 2. Phantolabis lacustris adult. A.—Male habitus (lateral view). B.—Female habitus (lateral view). C.—Male wing. D.—Female wing.
dark reddish brown, short, 0.8 to 0.9 mm long, length twice that of head; scape and pedicel wedge shaped; 10 flagellomeres (terminal flagellomere 10 incompletely divided), flagellomere 1 and 10 slightly extended, remaining flagellomeres barrel-shaped and similar sized, verticils sparse and minute, length of each scarcely ½ width of flagellomere.

**Thorax.** Mesonotum dark gray (pruinosity), with dark brown central longitudinal stripe, a pair of dark brown lateral areas on poststatural mesonotum. Pleura with sclerites poorly indicated, meron large, as large as metathoracic coxa.

**Legs (Fig. 3C).** Even dark reddish brown. As noted by Alexander (1956), setae on legs short and delicate, not conspicuous. Length of male leg segments (in mm)—prothoracic leg: femur = 2.8 to 3.6; tibia = 2.4 to 3.2; tarsus T1 = 1.4 to 1.9, T2 = 0.5 to 0.6, T3 = 0.2 to 0.3, T4 = 0.2, and T5 = 0.2. Mesothoracic leg: femur = 2.1 to 2.7; tibia = 2.0 to 2.5; tarsus T1 = 0.2 to 0.4; T2 = 0.2; T3 = 0.2; T4 = 0.1; T5 = 0.2. Metathoracic Leg: femur = 2.8 to 3.6; tibia = 2.3 to 3.0; tarsus T1 = 0.7 to 0.9, T2 = 0.3 to 0.4, T3 = 0.2, T4 = 0.1 to 0.2, and T5 = 0.2. Prothoracic leg (Fig. 3C-1) with foretarsus elongated, ½ to ⅓ length of tibia and equal in length to remaining tarsomeres; tarsomere T2 cylindrical; T3 expanded at apex appearing wedge shaped; T4 narrowed at base, venter with spinules; T5 slightly wider before apex, pair of claws inserted subapically, apex extended as flat shelf past insertion of claws. Male mesothoracic leg
Wing (Fig. 3D). Even brown tinge, no indication of a stigma. Membrane dull, not shiny, strongly wrinkled overall. Macrotrichia along costal vein short and hard to see except in microscopic slide mounts (as noted by Alexander 1938). Macrotrichia extend around wing margin but pale and delicate, remaining wing veins bare. Halter with large knob, slightly brown. Vension: Subcosta (Sc) extending close to costal vein in apical half, ending opposite fork of Radial Sector (Rs), crossvein sc-r at end of Sc, sometimes indistinct; Rs relatively long, gently curved after origin; Rs with 3 branches reaching wing margin, dividing into $R_{2+3+4}$ and $R_5$; Rs in rough alignment with $R_{2+3+4}$ or slightly offset (as noted by Alexander 1956 and Alexander and Byers 1981); $R_{2+3+4}$ about 2.5 to 3 × length of basal section of $R_5$; length of $R_2$ and $R_{2+3}$ subequal; cells $r_3$ and $r_4$ elongate, veins $R_3$ and $R_4$ gently curved anteriorly at wing margin, that of $R_5$ comparably curved slightly posteriorly. Discal medial cell (dm) open by absence of m-m crossvein, leaving veins $M_{1+2}$ and separating veins $M_3$ and $M_4$ reaching wing margin (= terminal CuA-1; Gelhaus 2009); crossvein m-cu (= basal section of CuA-1; Gelhaus 2009) at fork of vein M. Vein A-2 straight. Anal angle of wing well developed.

Abdomen. Dark brown, segments 1 through 7 lightly sclerotized with fine pale setae; hypopygium (Fig. 4A) heavily sclerotized, extremely large; segment 8 with tergite narrow, with setae; segment 9 with sternite and tergite 9 fused into a ring (laterally with small point as seen dorsally in slide mounts only); tergite 9 with dorsoposterior margin slightly extended medially, margin straight, without apical lobes. Gonocoxite large, strongly sclerotized medially with single gonostylus at apex, setae overall, strongest along inner surface; a few spinoid setae at inner apex, edges of apex slightly produced dorsally and ventrally, most prominent dorsally. Gonostylus broad, relatively flat, shiny reddish brown on dorsal surface, overall triangular shaped, expanded beyond narrowed base and then narrowing to a rounded apex, a single row of 12 to 17 short flat teeth along dorsal edge. A short, smooth rod with slightly curved apex (possible vestigial outer gonostylus) extending along base of inner gonostylus (Fig. 4B). Interbase a curved needle-like spine, extending along aedeagus. Proctiger overlaying aedeagus, with pair of pale sclerites laterally. Aedeagus long, straight, slender, divided into 3 closely appressed rods starting at midlength, apices separated; a spatulate lobe extending anteriorly from base, lateral sclerites bent forward, apex reaching about midlength of aedeagus. Parameres (gonopophyses) apparently absent.

**Adult Female**

Material examined: $n = 14$ (Appendix S1); measured $n = 5$. Body length: 4.5 to 5.4 mm (dry), wing length: 4.8 to 5.2 mm, wing width: 1.5 to 1.6 mm.

Head. As in male, except: antennal length 0.7 to 0.8 mm.

Thorax. Overall as in male.

Legs. Length of female leg segments (in mm)—prothoracic leg: femur = 1.6 to 1.8; tibia = 1.6 to 1.8; tarsus $T_1 = 1.0$ to 1.1, $T_2 = 0.4$, $T_3 = 0.2$ to 0.3, $T_4 = 0.1$ to 0.2,
and T5 = 0.2. Mesothoracic leg: femur = 1.5 to 1.7; tibia = 1.5 to 1.6; tarsus T1 = 0.4, T2 = 0.2, T3 = 0.1 to 0.2, T4 = 0.1, and T5 = 0.2. Metathoracic Leg: femur = 2.3 to 2.6; tibia = 2.2; tarsus T1 = 0.8 to 1.0, T2 = 0.3 to 0.4, T3 = 0.2, T4 = 0.1 to 0.2, and T5 = 0.2. Prothoracic leg longest of the set of legs—although ⅓ shorter than comparable leg of male—with prothoracic tarsus (T1) elongate, ⅓ to ∼½ length of tibia and equal in length to remaining tarsomeres; T2 cylindrical; T3 slightly widened apically, with ventral aspect of apex slightly lengthened; T4 narrowed at base, venter without noticeable spinules; T5 slightly wider before apex, pair of claws inserted subapically, apex extended slightly as flat shelf past insertion of claws. As in male, mesothoracic leg distinctly shortest, ∼½ length of prothoracic leg, slightly shorter than metathoracic leg. Mesothoracic femur and tibia ∼⅓ shorter than that in male; T1 ∼⅕ length of tibia and ∼½ length of remaining tarsomeres; T2 cylindrical; T3 apex lengthened ventrally, ventral to insertion of following tarsomere; T4 smaller, narrow at base and gradually thickened to truncate apex, few spinoid setae ventrally; T5 with pair of claws inserted near apex, apex truncate. Metathoracic leg slightly longer than prothoracic leg. Metathoracic femur of female shorter than that of male; T1 cylindrical; T2 cylindrical; T3 cylindrical, without spinoid setae, apex truncate; T4 base slightly narrowed, apex truncate; T5 with pair of claws inserted near apex, apex not extended.

Wing. Wing as in male with strong brown tinge, but with lighter areas in cell r1, r, and m, and apical wing cells from r3 to m3. A few macrotrichia along Rr in 1 female. Membrane dull, not shiny, strongly wrinkled overall.

Abdomen. Brown, segments 1 through 7 lightly sclerotized, with no setae (few on sternite 7). Ovipositor (Fig. 3E) typical for tipuloids, overall strongly sclerotized; tergite 8 broad, setae in grouping laterally, ventrolateral edge narrowed to point; 8th sternite with deep emargination along lateral margin just beyond base; opposite 8th tergite point, hypogynial valves straight, gradually narrowed to rounded apices. Ninth tergite with setae along posterior margin and laterally; 10th tergite with longer setae dorsally, cerci broad, elongated, and gently curved upward just beyond midlength. Three spermathecae, dark brown (Fig. 3F).

Pupa (male and female). Material examined: n = 13 (Appendix S1), measured n = 2 pupae, 2 exuviae. Full pupa length: 8.3 mm (male), 8.8 mm (female), width at midlength 0.8 mm (Fig. 5A, B).

Head, thorax, and terminal genitalic sections. Reddish brown, remainder of abdomen whitish. Respiratory horn absent. Antennal sheath curved evenly, reaching near base of prothoracic leg sheath, with reddish tubercles evenly spaced along ⅜ length; ∼10 tubercles total, largest anteriorly; 2nd and 3rd antennal tubercles paired; paired tubercules also present between antennal sheaths, no tubercles present on ocular field (Fig. 5C). Labial palpus sheath short, truncated apex. Dorsum of thorax with paired short series of 7 to 10 close-set tubercles on either side of midline, a pale seta laterally, a group of 3 pale setae posterolaterally. Wing sheath with reddish tubercle at base, wing venation evident on surface cuticle. Leg sheaths with prothoracic leg longest, closely appressed and reaching to venter of abdominal segment 3; metathoracic leg sheaths distinctly shorter, reaching end of abdominal segment 2. Mesothoracic leg cordate (heart-shaped) tarsi with slightly-swollen sheath. Abdominal surface with series of transverse fine striations, lacking tubercles or spines; ventral setal pattern as shown (Fig. 5A); setal pattern on dorsum of abdominal segments similar to ventral; pleuron with a single seta on anterior and posterior of each segment; terminal segment with pale digitiform appendage dorsally, strongly bent posteriorly beyond base (as in Hesperoconopa).
male genitalic sheath with a pair of upright short spines medially and at apex terminating in a pair of longer, posteriorly-directed spines (Fig. 5E); female cerci sheath with a pair of downturned small spines at apex (Fig. 5D).

**Fourth instar larva** Material examined: $n = 48$ (Appendix S1); measured $n = 8$. Body length 15 mm, width at mid-length 0.5 mm, width of penultimate segment 0.7 mm, apparent terminal segment ~1.0 to 1.3 mm (measured from anal papillae to apex).

**Head.** Head capsule structure typical of higher Chioneinae with head posteriorly consisting of narrow rods (Fig. 6A). Genae consisting of 3 pairs of rods. Ventral pair of rods (ventral externolateralia) elongate, slender, posterior end slightly expanded and curved medially; anterior end (hypostoma) bifurcated, lateral extension with long seta, medial extension at right angle to rod, teeth absent; rods connected medially by pale cuticle extending across the anterior ends. Dorsal 2 pairs of rods split posteriorly at darkest sclerotization, with the divided rods strongly divergent posteriorly; outer pair (dorsal externolateralia) slightly expanded at posterior apex and curved ventrally; inner pair (internolateralia) convergent posteromedially, connected medially with thin pale cuticle, a dark triangular sclerite connecting the apices of the two inner rods. Mandible with 5 teeth: 3 nearly subequal prominent teeth along apex, 2 smaller teeth nearer base. A large patch of hairs near base of mandible. Maxillary palpi broad, pale with nearly truncated apex, covered with dense golden hairs; palpus about twice as long as width at base. Antennae % length of palpi: 1st segment cylindrical, length about 3 x width at base, with circular sensory structure at % length; terminal segment oval, ~½ length of basal segment, with curved seta and a minute papilla at base. Hypopharynx with multiple rows of scales forming semicircular comb, ~20 scales with toothed apices (in 1st row). Epipharynx narrow, with abundant golden hairs directed ventrally.

**Body.** As in *Hesperoconopa*, slender, with penultimate segment of abdomen often slightly to greatly expanded (inflated); terminal segment narrowed and elongate, ending in narrow, knobby apex (apex slightly divided, but this is only clear on slide mounted specimens; Fig. 6B). Thoracic segments covered with short fine appressed golden hairs; most of abdomen, excluding the last segment, not distinctly haired (hair distinguishable only on slide mounts) but with scattered pale setae; terminal abdominal segment with short, golden hairs on posterior %, with a ring of longer pale setae encircling at % from the apex, and another ring of pale setae encircling at apex. Four pale anal papillae, twice as long as width at base, often not visible because of retraction.

**First-instar larva** Material examined: $n = 2$ (Appendix S1). Body length 1.4 to 1.7 mm (Fig. 6C). Head with rod-like sclerites as in older instars. Maxillary palpi as in older instar. Mandible slender, curved, appearing to have a single apical tooth. Body covered in distinct light brown hairs, 4 minute anal papillae surrounding anus, body narrowing and extended past anus (~7% of total body length; Fig. 6D), apex with long setae set on 2 close-set papillae (Fig. 6D).

**Egg** Material examined: $n = 1$ (Appendix S1). Egg oblong, length 0.35 to 0.40 mm, pale brown, surface sculpture with minute bumps (Fig. 6E).

**Habitat**

*Phantolabis lacustris* specimens were not common in museum collections, possibly due to the emergence of adults in late winter. The type locality was described as “on the shores of Lake Superior” (Alexander 1938). However, when the subgenus *Phantolabis* was described in Alexander (1956) this locality was described as “not far from Lake Superior”. A letter dated 25 May 1935 from Alan Stone to Alexander indicated that the flies were collected from Lake Superior (Smithsonian Archives, RU7298, box 50, folder 8). Lake Superior is an unusual habitat for *P. lacustris* because all other
records of this species are from lotic habitats. However, other typically-lotic taxa, such as *Diamesa nivioriana* (Fitch) (Diptera:Chironomidae) and *Allocapnia* (Plecoptera:Capniidae), can emerge along the shores of Lake Superior in late winter (RWB, personal observation). Alexander (1956) discussed additional material from J. S. Rogers from “small clear streams” in the southern peninsula of Michigan. The description of these Michigan streams are similar to contemporary collections of this species compiled in this study which are generally ground-water influenced (i.e., coldwater) streams. The most studied streams from which *P. lacustris* was collected (Trout Brook and Valley Creek, Minnesota, this study) are heavily influenced by ground water. The temperatures in these streams are greatly moderated by these inputs and either do not or rarely freeze during the winter in Minnesota. *Phantolabis lacustris* therefore appears to be an inhabitant of coldwater and coolwater streams. However, more work is needed to determine the thermal preferences and requirements of the larvae of this species.

Habitat data from collections, when specified, indicated that the larvae and pupae were collected from sand and sand/gravel substrates, and this is what we found in our 2 studied streams. In Trout Brook, *P. lacustris* larvae were collected from sand and sand/gravel substrates only. No larvae were collected from cobble riffles, soft sediments in slack water areas, or semiaquatic habitats along the margins of the stream despite efforts to locate the species in these habitats.

**Phenology**

We collected larvae from Trout Brook on 28 January and 12 February 2008. After 12 February, 2 collection efforts on 24 February and 10 March 2008 did not produce any larvae or pupae, despite extensive searching in multiple habitats including sand, fine sediment, cobble, and semi-aquatic habitats. Material from other localities in eastern North America (Appendix S1) included larval specimens collected from August through February of multiple years. We collected pupae from the larval habitat on 17, 24, and 30 March and 29 April 2008. The single pupa collected on 29 April 2008 was 2 wk after the last adult or pupal exuvia was collected or observed. No larvae or pupae were collected 7, 15, 22 April or 8 and 16 May 2008.

We collected pupal exuviae in the Trout Brook samples from 10 March through 15 April 2008 (Fig. 7). Adult *P. lacustris* were also first identified in Trout Brook SFPE samples on 10 March 2008. Large numbers of skating adults were observed on 14 March 2008. Males emerged slightly before females based on examination of the pupal exuviae samples (Fig. 7). During numerous observations of adult activity in the field and laboratory, these insects were never observed flying.

Emergence of *P. lacustris* adults in Trout Brook appeared to correspond to an increase in air and water temperatures (Fig. 8). In 2008, this trend of increasing water temperatures was also associated with a short period of higher flow and cooler water temperatures resulting from snow melt, so we cannot rule out spring spates as cues for pupation and emergence. The last SFPE was collected on 15 April 2008, and the last adults were observed skating on 7 April 2008, indicating that the observed activity of adults generally corresponded to collections of SFPE. Predicted daily water temperatures during the observed emergence of *P. lacustris* in Trout Brook were 7.3°C on average (range: 4.0–11.3°C) and daily air temperatures were 3.8°C on average (range: −8.3–16.9°C). All other adult *P. lacustris* examined in this study (Appendix S1) were collected in March, April, and May in other streams in Minnesota, Michigan, and Georgia, but no water temperature data were associated with these specimens. We estimated that the mean SCP (±SE) for 10 adults from Valley Creek was −13.2°C (±1.8) with a range of −21.3 to −5.2°C. These SCPs are on average lower than mean daily air temperatures, but at least some individuals could be exposed to minimum daily temperatures below their SCP.

**Behavior**

During visits to Trout Brook, we observed and documented the emergence and mating behavior of *P. lacustris* because winter-active insects often have unusual behaviors associated with emergence at low temperatures. These crane flies emerged in a manner similar to many Chironomidae. Adults emerged from pupal exuviae at the water’s surface in the middle of the stream or from undercut banks and overhanging vegetation. Early in the emergence period adults, which were mostly males, remained close to the edge of the stream, often in vegetation or undercut banks. During the peak of emergence and activity, males swarmed on the water’s surface in various locations in the stream, including
areas of slack water and riffles (Video S1). When males encountered a female they immediately attempted to copulate with her. Females were often grasped by 2 to 4 males as they emerged in the middle of the stream (Fig. 9A). After females emerged completely from their pupal exuviae, they quickly coupled with 1 of the males. Coupling began with a face-to-back position with dorsal flexion of the male’s abdomen (see Neumann 1976). Once coupled, the position changed to end to end with 180° torsion of the male’s abdomen. This mating position is observed in some surface-mating chironomids (Neumann 1976, Ferrington and Saether 1987). After coupling, males were observed pulling females to the shore, sometimes several meters from the stream margin. This behavior is somewhat unusual because in most surface-mating Diptera in which females have fully developed legs, the female drags the male (e.g., Oliveridia hugginsi: Ferrington and Saether 1987).

We did not observe oviposition behavior. However, based on the short ovipositor of the female, eggs are likely deposited shallowly in substrates. Eggs deposited in the lab were not enclosed in a gelatinous matrix, indicating that the eggs are deposited singly.

Although _P. lacustris_ has macropterous wings, numerous observations of this crane fly in the field and laboratory indicated that this species does not fly. Flight was not observed even at temperatures >10°C or when the adults were placed in a pan with water. Instead their wings are used across the surface of the water as in many Chironomidae (e.g., Clunio, Corynocera, Pontomyia, Fleuria, Oliveridia hugginsi). However, many chironomids have wing reductions or modifications because less wing surface area is needed for skating than for flying. _Phantolabis lacustris_ wings do not appear to be greatly modified, but this species has other adaptations for skating and surface mating. The 3rd tarsi on the meso- and meta-thoracic legs are expanded. The tarsal claws are also subapically inserted, as they are in 2 unrelated families of surface skating Hemiptera: Gerridae and Veliidae. In gerrids and veliids, this morphological adaption reduces the likelihood of breaking the water film (Caponigro and Erikssen 1976), and probably has the same function in _P. lacustris_. The meso- and meta-thoracic legs are also shorter than typical of tipuloids. The morphological adaptations to the
tarsi associated with surface skating behavior in *P. lacustris* are unique among the Tipuloidea. The male hypopygium is also enlarged, which is similar to other surface mating flies (Ferrington and Saether 1987).

Photographs of skating males revealed that, when skating, the prothoracic legs are held to the side and slightly forward (Fig. 9B, C). The shorter mesothoracic legs are held forward with the tarsi curled under the leg and back toward the body (Fig. 9C). The metathoracic legs are held behind the body. The meso- and meta-thoracic legs appear to support the fly on the water’s surface, whereas the prothoracic legs seem to function as sensory structures. In an aquarium in the laboratory the flies used their prothoracic legs to explore obstacles they encountered.

**DISCUSSION**

**Morphology**

The adults of *P. lacustris* are morphologically distinct from other crane fly genera. *Phanotolabis* has an obviously massive single gonostylus, and we also note a previously-unreported small, rod-like lobe at the base of the gonostyle. The function and homology of this rod are unclear, but its position on the gonocoxite could indicate that it is a reduced remnant of a 2nd gonostyle, since most crane fly groups have 2 pairs of gonostyles. Similar reduced gonostyles occur in unrelated crane fly groups, such as the vestigial outer gonostyle in some *Tipula* (e.g., *T. atreia* Petersen and Gelhaus and *T. triton* Alexander; Petersen et al. 2004) and reduced dorsal gonostyle in some *Dicranomyia* (e.g., *D. jirissana* Podenas and related species; Podenas et al. 2019). The enlargement of the hypopygium in *P. lacustris* may be related to its surface mating behavior as it is in other Diptera (Ferrington and Saether 1987). *Phanotolabis lacustris* also has other morphological adaptations unique in the Tipuloidea that are likely associated with skating behavior including an expansion of the 3rd tarsus of the meso- and meta-thoracic legs and subapical insertion of the tarsal claws.

Pupae of *Hesperoconopa* and *Phanotolabis* are morphologically very similar. Pupae of both genera possess a membranous lobe on the dorsum of the genital sheath, which is a unique feature among Tipuloidea (Hynes 1968). *Phanotolabis* and *Hesperoconopa* pupae both have pigmented tubercles on the dorsum of the thorax. However, in *Phanotolabis* these tubercles are arranged in a series along the ec dysial margin, whereas in *Hesperoconopa* their distribution is scattered (see Fig. 2 in Hynes 1968). Additionally, in *Hesperoconopa* (see Fig. 2 in Hynes 1968) these tubercles are smaller. Both genera also have pigmented tubercles on ∼½ of the antennal sheath length. In the specimens of *Hesperoconopa* we examined, pigmented tubercles were present on the ocular field. These tubercles are absent in *Phanotolabis*. We examined a small number of *Hesperoconopa* pupae and pupal exuviae (*n = 4*), so more comparative work is needed to determine how these genera can be distinguished in the pupal stage and if these differences are consistent for all *Hesperoconopa* species.

*Hesperoconopa* and *Phanotolabis* larvae are exceedingly similar and have a single lobed abdominal extension unique to the 2 genera, instead of the more typical spiracular disk. We were unable to identify morphological characters that could be used to separate mature larval specimens of these genera.

We elect to keep the *Phanotolabis* and *Hesperoconopa* genera separate based on differences in the adult wing, legs, and particularly the male hypopygium, even though their larvae are nearly identical morphologically and are absolutely distinct from known larvae of other crane fly genera (Table 1). The single pair of gonostyles with spinules along the margin and the massive gonocoxites in *Phanotolabis* differ from the more typical 2 pair of gonostyles and smaller gonocoxites found in *Hesperoconopa* and most other crane flies. Both genera have interbases, but *Phanotolabis* lacks the parameres seen in *Hesperoconopa*. These genera also differ in some non-genitalic features. The wings of *Phanotolabis* have a similar venation to those of *Hesperoconopa*, but *Phanotolabis* lacks the setae on their wing veins and the macrotrichia on their wing. In addition, the wing of *Phanotolabis* is broad with a strongly developed anal angle, whereas the shape of the *Hesperoconopa* wing is more slender without a developed anal angle. However, it is possible that, even with these differences, *Phanotolabis* and *Hesperoconopa* are congeneric and that *P. lacustris* is a highly-derived species that has atypical morphologies associated with winter activity and skating behavior.

**Winter activity**

To our knowledge this is the first detailed description of skating behavior in the superfamily Tipuloidea, which has >15,000 species (Oosterbroek 2018). Many crane fly species have lost the ability to fly, but these species have morphological modifications to the wings including the reduction or complete loss of wings (Byers 1969). Tokunaga (1940) described the behavior of the crane fly *Dicranomyia (Idioglochina) kotoshoensis* Alexander as “swarming on the surface of sea water,” which indicates this species was skimming on the water’s surface, but *D. kotoshoensis* also has the ability to fly.

The apparent loss of flight in *P. lacustris* may be related to the low temperatures at which this species emerges or to reduced predation during the winter. Flight loss is common in high altitude and winter-emerging taxa in temperate zones (Downes 1965, Danks 1979, Young and Yang 2002), which may be because of the difficulty for poikilothermic organisms to attain body temperatures sufficient for flying at low temperatures (Byers 1969). In addition, the probability of dislocation from the larval habitat is also lower for flightless organisms, which is more important in winter when suitable habitats (i.e., open, unfrozen water bodies)
are uncommon. Winter activity of *P. lacustris* may also be associated with reduced predation (Stark et al. 1998, Bouchard et al. 2009) because fewer invertebrate predators (e.g., Gerridae and Gyrinidae) are present on the surface of the water and trout feed less at the surface during the winter months.

The mean SCP for adult *P. lacustris* (−13.2°C) was not as low as another common dipteran found in Trout Brook and Valley Creek during the same period, *Diamesa mendotae* Muttkowski (Chironomidae), which had a mean SCP of −21.5°C (Bouchard et al. 2006a). The stonefly *Allocapnia pygmaea* (Burmeister 1839) (Plecoptera:Capniidae) also occurs in Trout Brook and had a mean SCP (±SE) of −10.24°C (±0.47°C) and −11.95°C (±0.47°C) for males and females, respectively (Bouchard et al. 2009). Like *P. lacustris*, *A. pygmaea* emerges in late winter and early spring, although this species usually emerges before *P. lacustris*. In contrast, *D. mendotae* adults can be observed throughout the winter, which could be related to its ability to survive lower air temperatures. These results are not definitive, but *P. lacustris* appears to be moderately cold hardy, which may limit it to emergence in late winter or early spring in Minnesota. It is possible that adults of *P. lacustris* are exposed to air temperatures below SCPs which could be lethal. However, the habitat of this crane fly (i.e., thermally-buffered streams) may also provide additional protection from low temperatures and increase the likelihood of survival and mating.

Available collections of larvae indicate that *P. lacustris* undergoes larval development from late winter through midwinter of the following year. Larvae may aestivate during summer months since we found no larval records during these months. However, these larvae could instead be missed by conventional sampling techniques because of their small size during the summer or because they use buried substrates that are difficult to sample. Larvae pupate in mid to late winter and pupation lasts ~1 mo. During this period, we did not find pupae in the larval habitat in Trout Brook, which may indicate that pupae move deeper into sand substrates. Pupae may move up through the substrate before emergence because some crane fly pupae are mobile (Pritchard 1983). The movement of *P. lacustris* pupae deeper into sand substrates may be a mechanism to avoid displacement in an unstable substrate during higher flows caused by snowmelt. Adult emergence and activity of *P. lacustris* occurs from March through May.

**Distribution**

Larvae of *P. lacustris* have been collected on numerous occasions, but because of morphological similarities with the genus *Hesperoconopa*, their identity remained unknown or confused with *Hesperoconopa* until this study associated the *Phantolabis* larval stage with the adult. With this association, we determined that larvae apparently belonging to this species have also been collected in Alabama, Indiana, New Jersey, New York, Pennsylvania, South Carolina, Vermont, and Wisconsin in the United States and Ontario in Canada (Appendix S1). In some cases, only photos of these
larval specimens were examined. We also used records based only on published reports (Appendix S1). The genus *Hesperoconopa* has only been confirmed from western North America, so we located these additional *Phantolabis* records with a literature search for *Hesperoconopa* in studies east of the Rocky Mountains in the United States and Canada. This was effective because the larvae of *Hesperoconopa* and *Phantolabis* are morphologically distinct from other crane fly larvae and the 2 genera are geographically distinct.

The association of the larva and a comprehensive review of available *P. lacustris* specimens permitted better delineation of the range of this species. This study greatly expands the known distribution of *P. lacustris* from a handful of localities in Michigan to across the northern United States, southern Canada, along the Appalachian Mountains, and the eastern Coastal Plain (Fig. 10). Adult *P. lacustris* have been collected from Michigan, Minnesota, and Georgia, and pupae have been collected from Minnesota (Appendix S1). Without the association of the larva of *P. lacustris*, its known range was inaccurate because the winter activity of this species makes adult collections difficult.

Observations of *P. lacustris* indicate that the adult does not fly and should have limited dispersal capabilities, but it has a wide distribution and occurs in ground-water fed streams with sandy substrates across eastern and central North America. In some streams, *P. lacustris* was abundant and potentially an important component of the invertebrate communities in these streams. For example, Entrekin et al. (2009) determined that *P. lacustris* (as *Hesperoconopa*) was the primary collector–gatherer in 1 stream reach (82.2 mg ash-free dry mass m$^{-2}$ y$^{-1}$). Further, this species occurred in streams that harbor trout, so it could be an important food source for trout in these streams.

The nearly identical morphology of *P. lacustris* and *Hesperoconopa* larvae has resulted in the misidentification of *P. lacustris* larvae. The larvae of *P. lacustris* will key out as *Hesperoconopa* in McAlpine et al. (1981), Hilsenhoff (1995), and Byers and Gelhaus (2008) and to *Phantolabis/Hesperoconopa* in Gelhaus and Podeniene (2019). Based on the known distribution of *Hesperoconopa* and our delineation of the distribution of *Phantolabis*, we consider all larval specimens identified as *Hesperoconopa* from central and eastern North America to be *Phantolabis*. At present, the best routine distinction between the larval stages of these genera appears to be their geographic distribution as the 2 groups are not sympatric. *Hesperoconopa* is found in western North America from Colorado to the Pacific Coast, and *Phantolabis* is found in eastern and central North America. Regardless, we urge caution in assigning larval identifications to either genus in areas between these regions, such as the Northern Great Plains, without having associated larvae or adults.

In addition to providing a means to separate *P. lacustris* and *Hesperoconopa* larvae, this study also describes the phenology and ecology of *P. lacustris*. Hilsenhoff (1987) gives *Hesperoconopa* (most likely *P. lacustris*) in Wisconsin a tolerance value of 1 (0–10 scale where 0 is most intolerant of organic pollution). This assignment is probably accurate because *P. lacustris* seems limited primarily to high quality streams, although a more systematic analysis of the pollution tolerance of this species is needed. Most of the known larval records of *P. lacustris* were collected as part of biological monitoring efforts which demonstrate that documenting this unusual species' water body type and habitat preferences and phenology will make collections of this unusual species more useful in biological monitoring.

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