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Rhyacophila dandaganu, a new caddisfly from the southern Cumberland Plateau (USA) (Trichoptera: Rhyacophilidae)

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Abstract

We describe a new species in the caddisfly genus *Rhyacophila* (Trichoptera: Rhyacophilidae) from the southern Cumberland Plateau of the United States. *Rhyacophila dandaganu* n. sp. is placed in the *Rhyacophila lobifera* Group from North America, the second known species in this group. The new species is distinguished from *Rhyacophila lobifera* Betten, 1934 by the shape and dimensions of several genitalic structures, as well as the absence of parameres accompanying the endotheca and the characteristic shape of the tenth segment and phallicata. We discuss the geographic range of these two species and the questions raised by the curious (apparent) lack of sympatric populations. We discuss some testable hypotheses that might determine how populations of *R. dandaganu* n. sp. and *R. lobifera* could maintain phenotypic distinctiveness, in the absence of obvious geographic barriers to gene flow, including behavioral, chemical or tactile mating cues.

Key words: *Rhyacophila,* Cumberland Plateau, new species, parameres, distribution, Appalachia

Introduction

Species of the genus *Rhyacophila* are typically associated with cool or cold-water habitats, in seeps and small streams and cold rivers across the Northern Hemisphere (Ross 1956). More than 700 species are known worldwide (Holzenthal *et al.* 2007; Morse 2017) and many species groups are known to be endemic to small geographic areas (Ross 1956; Mey 1999; Prather & Morse 2001). Although believed to be an ancient lineage, many extant *Rhyacophila* species are not clearly aligned with known species groups (Ross 1956). Ross (1956) and later Schmid (1970) considered the dilemma posed by the limited available evidence, namely that we cannot distinguish between scenarios predicting differential rates of diversification or extinction among *Rhyacophila* lineages. The extinction of forms could alter the patterns of similarity among the surviving groups or clusters of lineages, causing some species or groups to appear unrelated to others. Alternatively the evolution of new structures or structural novelty could be a force driving the evolution of character differences in these divergent species or monophyletic groups. Deep phylogeny aside, within *Rhyacophila* species groups of eastern North America, interspecific morphological divergence is often a function of changes in the relative dimensions or shape of genitalic characters in a common, base bodyplan, and not the evolution of new structures (Ross 1956; Schmid 1970). However, in the species we describe below, we describe a situation where speciation has putatively been accompanied by the evolutionary loss (or gain) of parameres (the sclerotized spine-tipped membranous arms of the endothecum). We know of no other species groups in *Rhyacophila* from eastern North America where the male genitalia varies on the presence or absence of parameres, within the group.

Rhyacophila lobifera Betten, 1934 was first described from a small tributary of Lake Michigan near North Chicago, Illinois, USA (Betten 1934). Subsequent collections expanded the known geographic range of *R.*

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lobifera to the states of Arkansas, Illinois, Indiana, Kansas, Kentucky, Michigan, Missouri, Ohio, Oklahoma, Pennsylvania, Tennessee, West Virginia and Ontario in Canada (Mosely & Betten, 1940; Ross 1944; Resh 1975; Hamilton *et al.* 1983; Usis & MacLean 1986; Tarter & Floyd 1990; Masteller & Flint 1992; Moulton & Stewart 1996; Etnier *et al.* 1998; Floyd *et al.* 2012; D.C. Houghton pers. comm.). Recent collections in northwestern Georgia and northern Alabama revealed a new species of *Rhyacophila,* described here. We review all previously published specimen records of *R. lobifera* from the region and confirm that all *R. lobifera* recorded from the state of Alabama are *Rhyacophila dandaganu,* n.sp. We discuss biogeographical evidence and some testable hypotheses of putative mechanisms that might explain these species geographic distributions.

Materials and methods

We first identified *Rhyacophila dandaganu* n. sp. adult males hatched from live pupae, collected from DeKalb County, Alabama and reared in the laboratory at the University of Tennessee-Knoxville. The strong resemblance to *R. lobifera* raised the possibility that previously published Alabama records of *R. lobifera* might instead be specimens of the undescribed species. Therefore, we obtained the specimens associated with the records in Harris *et al.* (1991) and Hicks and Haynes (2000) from Harris and the University of Alabama Trichoptera collection. Additionally, we examined all accessioned specimens of *R. lobifera* held in the University of Tennessee Dave A. Etnier Trichoptera Collection and the Illinois Natural History Survey (INHS) collection at the University of Illinois at Urbana-Champaign, including paratypes deposited by Betten at the INHS. Lastly, additional collections made by the authors, students and colleagues, including a number of larvae or pupae reared using the metamorphotype (MMT) method (Wiggins 1996) were invaluable in adding occurrence records.

Specimens were preserved on pins or in varying concentrations of alcohol. For illustration, the abdomens of the insect were detached and cleared with a hot solution of KOH or lactic acid, then rinsed and stored in a genital vial associated with the specimen. We took high-resolution digital microscopic photographs of specimens and then used these images as the base for line drawings with Adobe Illustrator.

We follow the terminology used by Holzenthal *et al.* (2007) for comparisons of the morphology of male genitalia. Abbreviations of morphological structures: VIII= eighth abdominal segment, IX= ninth abdominal segment, X= tenth abdominal segment, a.s. = anal sclerite, b.s.= basal segment of inferior appendage (coxopodite of some authors), d.s.= distal segment of inferior appendage (harpagone of some authors), e= endotheca, pm = parameres, ph = phallicata.

Description

***Rhyacophila dandaganu* n. sp.**
Figs 1–2

Diagnosis. This species is very similar to *Rhyacophila lobifera* Betten 1934, but consistently differs in several characters of the male ninth and tenth abdominal segments and genitalia. Males of *R. dandaganu* n. sp. may be easily distinguished by the complete absence of parameres accompanying the endotheca (Figure 1a). On the inferior appendages of *R. dandaganu* n. sp., the basal lobe of the dorsal tip of the distal segment of the inferior appendages is more bulbous and the dorsal segments more narrowed and acutely pointed, than in *R. lobifera*. In lateral view, the dorsal margin of segment IX of *R. dandaganu* n. sp. is broader than *R. lobifera,* where segment IX narrows dorsally to a thin band in lateral profile (Ross 1944, Fig. 120A; Schmid 1970, Plate 14). In *R. dandaganu* n. sp., segment X is (in lateral view) produced as an elongated, slender curved acuminate tip of the posterodorsal projection of X, where *R. lobifera* is closely appressed and not elongated or acuminate and curved. In caudal view, segment X of the new species has a distinctive hourglass emargination (Figure 1b), quite different from the stocky shoulder of X in *R. lobifera* (Figure 1d). When appropriately cleared and extruded, the two species are easily distinguished by the emargination of the distal end of the phallicata. In *R. dandaganu* n. sp., the posteroapical lateral lobes of phallicata are simple, and the phallicata has a small posteromedian knob (Figure 1c). In *R. lobifera*, the posteroapical lateral lobes are bifid, and the phallicata has a prominent, elongate posteromedian lobe that extends nearly half the distance to the apices of the lateral lobes (Figure 1d). In *R. lobifera,* the parameres are long sclerotized spines, produced from paired fleshy lobes extending from the mass of the endotheca and which can be extruded to the length of the phallicata.

Females and larvae are currently indistinguishable from those of *R. lobifera*.

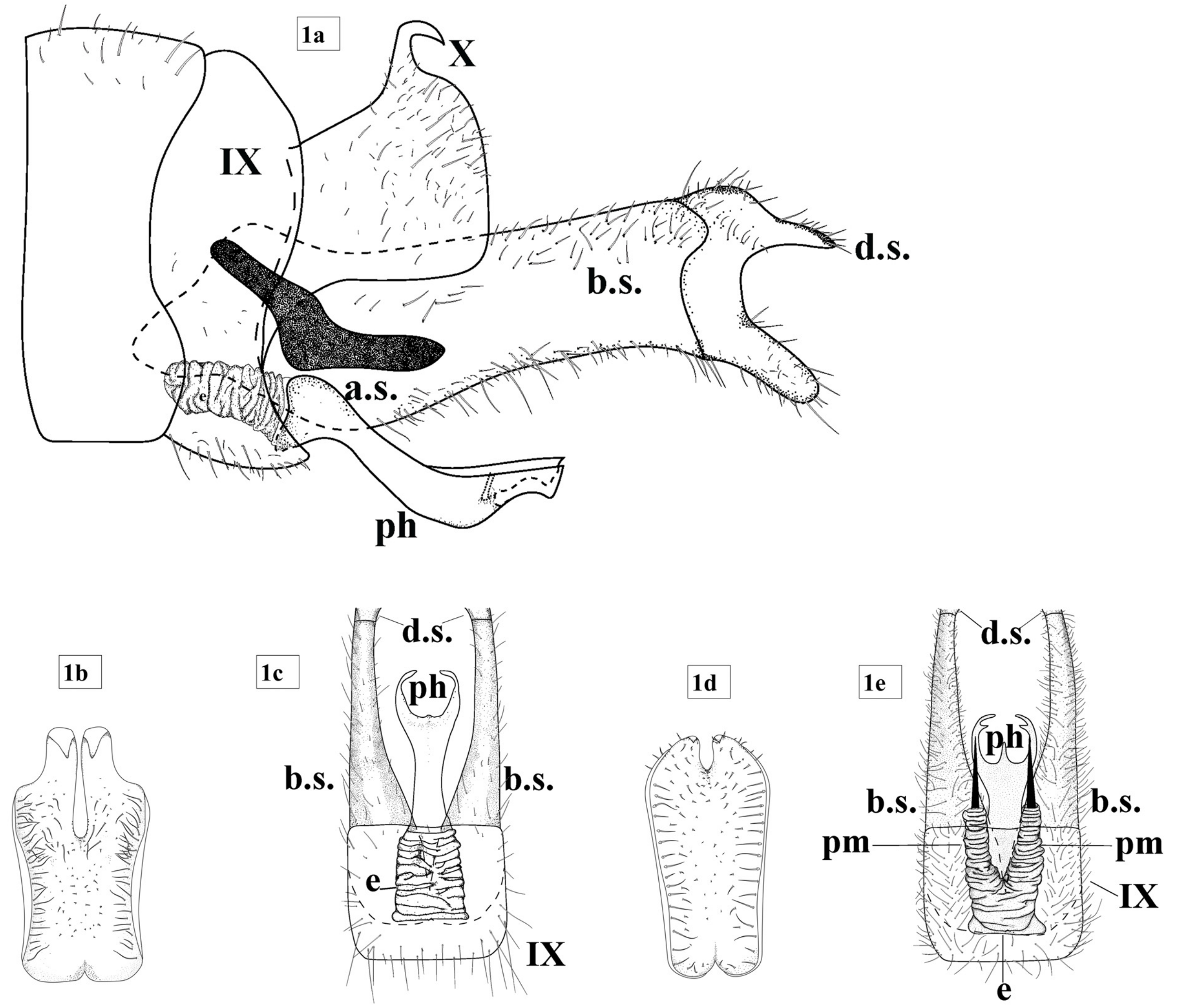

FIGURE 1. 1a. *Rhyacophila dandaganu* new species, male genitalia lateral view. **1b**. Caudal view X segment. **1c**. Male genitalia, ventral view. **1d.** *Rhyacophila lobifera* Betten 1934*,* caudal view X segment. **1e.** Male genitalia, ventral view. IX—ninth segment, X—tenth segment, a.s.—anal sclerite, e—endotheca, ph—phallicata, b.s.—basal segment of inferior appendages, d.s.—distal sgement of inferior appendages, pm—paramere.

Description

Adult. Body length 10–14 mm. Head: 3 ocelli, maxillary palps with five segments, the second rounded and globule-like. Leg spur count 1, 2, 4. Body: yellowish-brown, antennae, palpi brown, wings brown mottled with darker pigments, legs yellowish-brown. *Pinned*.

Male genitalia (Figure 1). Segment IX is a simple, completely sclerotized ring, broadest (in lateral view) at mid height, tapering to 0.5x at the ventral margin (Figure 1a). In lateral view, the dorsum of IX tapers to a width of 0.3x of the maximum width. Segment X is massive, subtriangular in lateral view, with acuminate hook-like tips, separated from the body of the main sclerite by a vertical distance equal to the length of the hook and extending posteriorly at an angle of roughly 90°, slightly bent at tip. In caudal view (Figure 1b), the acuminate hooks of X are produced as pair of dorsally projecting lobes, divided by narrow emargination extending 0.4x the height of X. In lateral view, margins of the dorsum of X as hooked projections, occupying dorsal 0.2x of sclerite (Figure 1a). In caudal view X with hourglass shape (lower 0.3x of sclerite constricted, Figure 1b). Distal terminus of anal sclerite is foot-shaped in lateral view, with a long root (approximately the length of the "foot"). No tergal strap is produced under or along the anal sclerite. The phallus is simple and scoop-like, with the phallotheca produced as a straw-like hollow cylinder, arising from the center of a thinly sclerotized, slightly emarginate shelf that joins the lateral lobes of the "scoop" of the phallus (Figure 1c). The endotheca lacks parameres (Figure 1a, 1c). The inferior appendages ("claspers or harpagones" of some authors) are two segmented. The basal segment of the inferior appendages is slightly constricted mid-length, thicker at the ends, and lightly covered with silky hairs along the length. The distal segment of the inferior appendages has both a dorsal and ventral lobe. The dorsal lobe tapers sharply into a needle-like point, while the ventral lobe is roundly tapered and setose along the entire length, which is slightly longer than the length of the dorsal lobe.

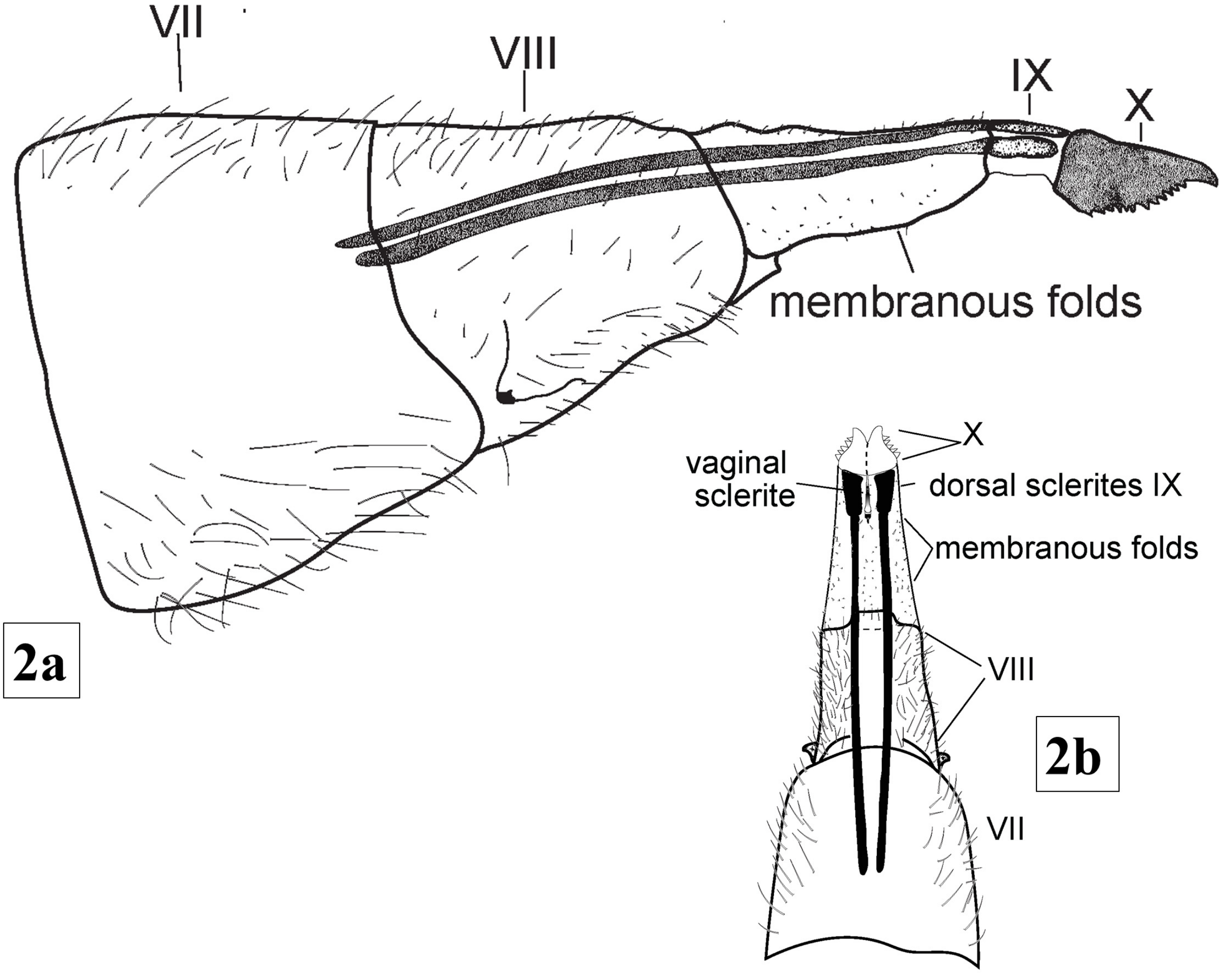

FIGURE 2. 2a. *Rhyacophila dandaganu* new species. female genitalia lateral view. **2b.** female genitalia ventral view. VII—seventh segment, VIII—eighth segment, IX—ninth segment, X—tenth segment. Internal rods are illustrated as if viewing cleared specimen.

Female genitalia (Figure 2). The terminal segment, X, in females of the new species is a pair of rounded, scalloped shaped sclerites with sharp terminal posterior tips. X is margined with tiny dentations or spines, as with *R. lobifera,* produced from the lateral margins of the scalloped-shaped body of X (Figure 2a). The sclerotized portion of segment IX is the terminus of a pair of internal sclerous rods, each rod fused to one of a pair of small dorsal sclerites at the posterior margin of the segment which are in turn fused to X. Each sclerotized rod fused to segment IX also extends headward along the main body axis, often as far as segment VII (Figure 2b). The posteroventral margin of segment VIII has a sclerotized shelf overlapping the anterior margin of segment IX (Figure 2b; see also Figure 129, Ross 1944; Figure 55, Prather & Morse 2001). The anterolateral corners of the integument of segment VIII are produced as thickened, radially sclerotized pits in the integument, remarkably distinct in cleared specimens. The depiction of the vaginal sclerites given in Prather and Morse (2001) and Ross (1944), describes the shape of the vaginal sclerites of females of both *R. lobifera* and *R. dandaganu* n. sp.

Etymology. The epithet of this species is the Cherokee word for Lookout Mountain Town, a lower Cherokee stronghold built after troops led by John Sevier destroyed the permanent Cherokee settlements in the Upper Tennessee River Valley (Mooney 1992). Dandaganu was located approximately 10 km north of the type locality, in the vicinity of Rising Fawn, GA. Translated "where he is looking at him", or "two looking at each other", this name describes the landscape of the opposing mountain ranges along Lookout Mountain and the Chattanooga area (Mooney 1992). From Lookout Mountain near the type locality, mountains within watersheds where specimens of *R. lobifera* have been collected are visible across the Tennessee Valley. Because the type locality of the new species is just above the location of historic Lookout Mountain Town, this name is an appropriate descriptor of the known biogeography of the species as well as the landscape of the Lookout Mountain region.

Material examined (illustrated in Figure 3).

Holotype ♂: USA: Georgia: Dade County, Lookout Mountain, Long Branch at Yankee Road (County Highway 95), 34.67105°N, 85.50462°W, 590 m asl, 27.iv.2011, J. Robinson and D. Etnier. (INHS 797,001). *Pinned*

Paratypes. Same data as holotype, 7♂. 2♀ (INHS). *Pinned*

Material Examined

19♂♂, 30♀♀ (♂INHS 797,011; ♀INHS 797,012), USA: Alabama: Blount County, Blue Springs Creek near Chamblees Mill, 34.0603°N, 86.6350°W, 180 m, 18.iv.1985, blacklight, S. Harris (18♂♂, 29♀♀ deposited Steve Harris's collection, hereafter SCH); Harris *et al.* 1991. *In alcohol*

♂: USA: Alabama: Blount County, Blackburn Fork at County Highway 79, 33.9203°N, 86.6079°W, 134 m, 18.iv.1985, blacklight, S. Harris (SCH; Harris *et al.* 1991). *In alcohol*

8♂♂: USA: Alabama: Cherokee County, Johnnies Creek at County Highway 275 bridge, 34.3069°, 85.6874°W, 275 m, 21.iv.1989, blacklight, K. Frazier (SCH). *In alcohol.* ♂ retained at INHS (INHS 797,013). *In alcohol*

2♂♂: USA: Alabama: Cherokee County, Little River at defunct Canyonland Park chairlift, 34.35185°N, 85.67185°W, 240 m, 21.iv.1989, K.S. Frazer. (University of Alabama Insect Collection 5757). *In alcohol*

6♂♂: USA: Alabama: Cherokee County, Little River at Canyon Mouth Park, 34.28716°N, 85.67971°W, 175 m, 21.iv.1989, K.S. Frazer. (University of Alabama Insect Collection 5756). *In alcohol*

♂MMT: USA: Alabama: DeKalb County, DeSoto State Park, Laurel Creek 300 meters upstream of Lost Falls, 34.4974°N, 85.6223°W, 450 m, 21.iii.2007, hand collected larvae and reared at UTK, J. Robinson, M. Geraghty (National Park Service repository at Mammoth Cave National Park (MACA) LIRI-50569701, INHS 797,014). *In alcohol*

2♂♂MMT: USA: Alabama: DeKalb County, DeSoto State Park, unnamed stream running through DeSoto Lodge grounds, 34.4947°N, 85.6183°W, 460 m, 21.iii.2007, hand collected larvae (emerged 11.iv.2007), J. Robinson, M. Geraghty (MACA LIRI-62880486). *In alcohol*

♀ MMT: USA: Alabama: DeKalb County, DeSoto State Park, unnamed stream running through DeSoto Lodge grounds, 34.4947°N, 85.6183°W, 460 m, 21.iii.2007, hand collected larvae (emerged 20.iv.2007), J. Robinson, M. Geraghty. (INHS 797,015). *In alcohol*

3♂♂: USA: Alabama: Fayette County, Wolf Creek, 33.791°N, 87.525°W, 150 m, 26.iv.1983, blacklight,

S. Harris (SCH). *In alcohol*

3♂♂: USA: Alabama: Tuscaloosa County, Tyro Creek at ford, 33.6099°N, 87.5705°W, 105 m, 28.iv.1982, blacklight, S. Harris (SCH; Harris *et al.* 1991). *In alcohol*

2♂♂: USA: Alabama: Tuscaloosa County, headwaters of Wallace Branch, 33.6262°N, 87.5332°W, 180 m, 26.iv.1983, blacklight, S. Harris, P. O'Neil (SCH; Harris *et al.* 1991). *In alcohol*

♂: USA: Alabama: Tuscaloosa County, Glenn Branch at County Highway 55, 33.55°N, 87.62°W, 120 m, 26.iv.1983, blacklight, P. O'Neil, S. Harris (SCH). *In alcohol*

2♂♂: USA: Alabama: Winston County, Long Branch, 4.4 km N of Nauvoo, 34.02859°N, 87.48431°W, 180 m, 20.iv.1993, M. Hicks, C. Haynes. (UA Insect Collection 4450; Hicks & Haynes 2000). *In alcohol*

♂: USA: Alabama: Winston County, Brushy Creek at Hickory Grove Road, Black Warrior Wildlife Management Area, 7.2 km ESE of Grayson, 8.3 km NW of Addison, 34.25268°N, 87.24707°W, 170 m, 30.iv.1993, M. Hicks. (UA Insect Collection 4451; Hicks & Haynes 2000). *In alcohol*

2♂♂: USA: Alabama: Winston County, Sipsey Fork of the Black Warrior River at Sipsey Fork Recreational Area, 7.3 km W of Grayson, 34.28532°N, 87.39882°W, 160 m, 30.iv.1993, M. Hicks, C. Haynes. (UA Insect Collection 4452; Hicks & Haynes 2000). *In alcohol*

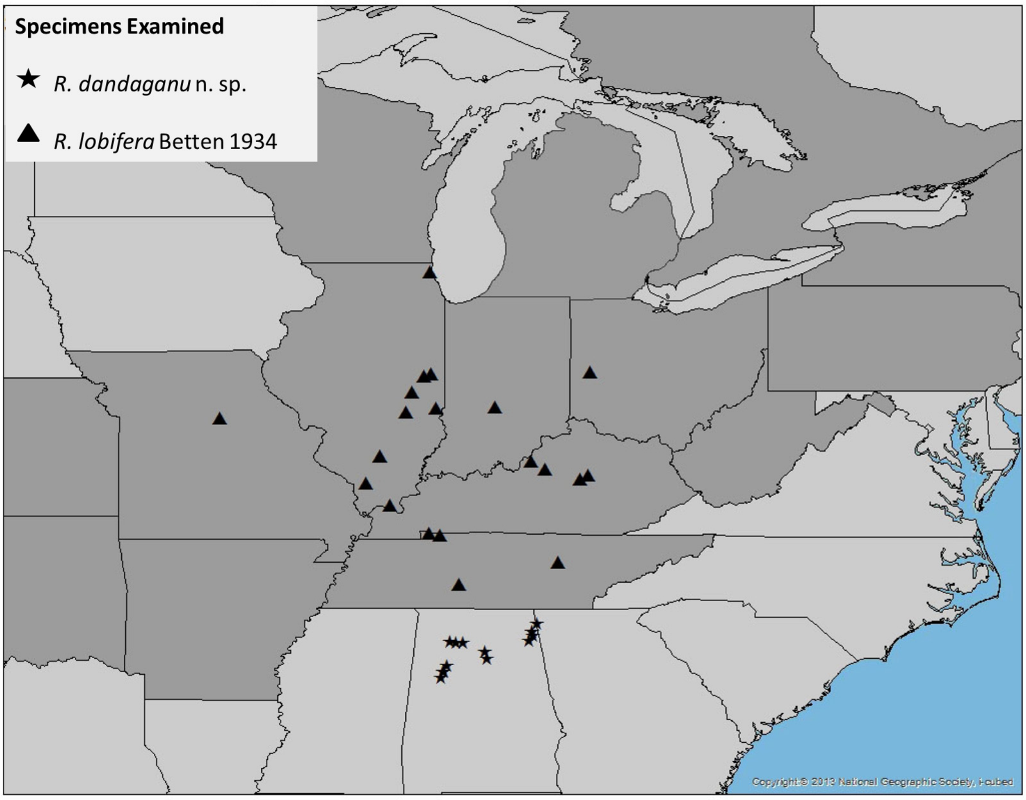

FIGURE 3. Geographic distribution of species in the *Rhyacophila lobifera* species group, including *Rhyacophila dandaganu* new species. States shaded in dark gray have published reports of populations of *R. lobifera*. Map symbols denote specimens of each species we examined for this paper.

Rhyacophila lobifera Betten, 1934

♂. USA: Illinois: Lake County, Pettibone Creek near North Chicago, 42.3093°N, 87.8393°W, 198 m asl. *Paratype* held at INHS. *In alcohol*

1♂. USA: Illinois: Champaign County, Homer, Salt Fork of the Vermilion River, 40.055673°N, 87.958353°W, 206 m, 9.v.1973, blacklight, J. Kingsolver (INHS 56327). *In alcohol*

♂ MMT, 2 P. USA: Illinois: Clark County, East Mill Creek 2.75 km SSW of Marshall, 39.3593°N, 87.7418°W, 158 m, 18.iv.2001, hand collected, H.H. Ross (INHS 3750). *In alcohol*

♂ MMT. USA: Illinois: Cumberland County, Long Point Creek 11 km west of Toledo, 39.2733°N, 88.3557°W, 180 m, 18–19.iv.2001, blacklight trap, H.H. Ross (INHS 3715). *In alcohol*

9♂♂, 4♀♀, 1 ♂ MMT. USA: Illinois: Douglas County, Filson, 39.69137°N, 88.22962°W, 197 m, 1.iv.1938, blacklight and hand collection, H.H. Ross (INHS 56309). *In alcohol*

♂ MMT. USA: Illinois: Jackson County, Carbondale, 37.71°N, 89.23°W, 130 m, blacklight, det. H.H. Ross 1938 (INHS 00310). *In alcohol*

1♂MMT. USA: Illinois: Jefferson County, Mount Vernon, 38.3136°N, 88.9081°W, 146 m, 10.iv.1946, blacklight, H.H. Ross (INHS 56324). *In alcohol*

1♂MMT. USA: Illinois: Jefferson County, Mount Vernon, 38.3136°N, 88.9081°W, 146 m, 10.iv.1946, blacklight, H.H. Ross (INHS 56325). *In alcohol*

2♂♂. USA: Illinois: Lawrence County, 6 km south of Sumner, tributary of Bonpas Creek, 38.63997°N, 87.963982°W, 135 m, 18.iv.2004, blacklight (INHS 76267). *In alcohol*

1♂MMT. USA: Illinois: Massac County, 3km north of Metropolis, Massac Creek, 37.19232°N, 88.70873°W, 107 m, 7.iv.2004, blacklight (INHS 76301). *In alcohol*

10♂♂. USA: Illinois: Vermilion County, Oakwood, Salt Fork of the Vermilion River, 40.08346°N, 87.780433°W, 167 m, 1.v.1935, blacklight, H.H. Ross (INHS 56315). *In alcohol*

1♂. USA: Illinois: Vermilion County, Oakwood, Salt Fork of the Vermilion River, 40.08346°N, 87.780433°W, 167 m, 1.v.1938, blacklight, H.H. Ross (INHS 56318). Record in database says Tompkins County, NY, Ross's labels in jar say Oakwood IL. *In alcohol*

4♂♂. USA: Indiana: Morgan County, 2 miles south of Martinsville, 39.3947°N, 86.4243°W, 183 m, 16.v.1962, blacklight (INHS 55983). *In alcohol*

1 ♂ MMT. USA: Kentucky: Fayette County, Raven Run near Louisville, 37.898664°N, 84.295134°W, 213 m, 6.v.1947, blacklight, H.H. Ross (INHS 56313). *In alcohol*

3 L. USA: Ohio: Guernsey County, Chapman Run at outflow of reservoir at Spring Valley Campground along Interstate 70, 3.iii.2008, T. Jett (nap- 16830981, BOLD specimen 07-17PKS-0748, INHS 797,016). *In alcohol*

3 P. USA: Tennessee: Cumberland County, Crossville, small tributary of Obed River at US 127, 35.996°N, 85.046°W, 519 m, 26.iii.2008, hand collected, J. Robinson and D. Etnier (JLR, nap-46677679, BOLD sequence PKCAD841-08). *In alcohol*

3 P. USA: Tennessee: Cumberland County, Crossville, small tributary of Obed River at US 127, 35.996°N, 85.046°W, 519 m, 28.iii.2008, hand collected, J. Robinson and D. Etnier (JLR, nap-23515129). *In alcohol*

70 ♂♂, 20 ♀♀. USA: Tennessee: Maury County, Mount Pleasant, Sugar Creek at railroad trestle, 35.5192°N, 87.2061°W, 215 m, 14–15.iv.2010, blacklight trap, B. Bauer (UT 1.1198). ♂♀ retained at INHS (INHS 797,017). *In alcohol*

11♂♂, 1♀. USA: Tennessee: Montgomery County, Fort Campbell, Piney Fork at Jordan Springs Rd, 36.59584°N, 87.62914°W, 170 m, 14–15.iv.2004, blacklight trap, B. Bauer and D. Etnier (UT 1.935). ♂♀ cleared, retained at INHS (INHS 797,018). *In alcohol*

65♂♂, 3♀. USA: Tennessee: Montgomery County, Fort Campbell, Piney Fork at Jordan Springs Rd, 36.59584°N, 87.62914°W, 170 m, 14–15.iv.2004, blacklight trap, B. Bauer and D. Etnier (UT 1.935). *In alcohol*

2 MMT♂♂, 1MMT♀, 1 L. USA: Tennessee: Montgomery County, Fort Campbell, Piney Fork at Rendesvoux Rd, 36.58786°N, 87.66521°W, 170 m, 31.iii.2004, hand collected, B. Bauer (UT 1.920). *In alcohol*

Remarks on *R. lobifera*

In the original illustration and description of this species (Betten 1934), very little detail is given on the shape, dimensions and secondary characters of the male genitalia, only that the male genitalia are "quite unlike those of the eastern species". Similarly, the illustrations accompanying that description are not very detailed and the illustrated view of the phallicata does not clearly resolve whether or not the endotheca of that individual is accompanied by parameres. However, the illustration of the lateral view is clearly that of *R. lobifera*, as evidenced by the angle of the segment X and the dimensions of the inferior appendages. All other Illinois specimens we have observed have parameres accompanying the phallicata and fit *R. lobifera* as discussed by Ross (1944, 1956), Schmid (1970), Moulton and Stewart (1996), Prather and Morse (2001), including a specimen labeled as “paratype” taken from the type locality by Betten and later donated to Ross in the INHS collection. There are no intermediate forms of these morphological characters among any of these specimens; males are very easily diagnosable by the shape of segment X, the contour of the phallicata and the absence of parameres produced from the endotheca.

Discussion

Morphological similarity to *R. lobifera*

Separation of these species is currently not possible for females or larvae. When properly cleared and prepared, females of *R. dandaganu* are presently not separable from *R. lobifera* and are identical in all characters known to separate females of other species of *Rhyacophila* (e.g. Ross 1944; Schmid 1981; Prather & Morse 1991; Moulton & Stewart 1996). Flint (1962) and Moulton and Stewart (1996) illustrated the larval head and ventral proleg of *R. lobifera*; once again we can find no differences in these characters in *R. dandaganu.* In each species, the basoventral hook is thickened and darkened, and the two teeth along the claw of the proleg are similarly placed. The straw-colored head and dark brown muscle scar spotted patterns of the head are so distinctive that it is possible to distinguish larvae in this species group from other *Rhyacophila* species, in the field. Both species have similar habitat preferences and early spring emergence phenology, with a latitudinal gradient in the emergence of *R. lobifera* from TN to northern IL (Ross 1944). Larvae of *R. dandaganu* are fourth or fifth instar (~20 mm) by early March in sites near the type locality, emerging in the laboratory at the end of March or first of April. We have collected each species in streams or habitats that are later dry during the season, as described by Ross (1944). At present, geography is the best potential identifier of larval specimens from this group.

Biogeography of *Rhyacophila* species groups in southeastern U.S.

Ross (1956, 1965, 1967) discussed global patterns of endemism and phylogenetic diversity within *Rhyacophila*, including eastern North America. The major lineages proposed by Ross (1956) and Schmid (1970) are generally congruent, and Ross’s hypothetical reconstructions (1956, 1965) of early continental transfers of these lineages across the Northern Hemisphere before and after glacial episodes form the basis of our current understanding of the evolution of regional *Rhyacophila* fauna (Hamilton & Morse 1990; Prather & Morse 2001; Armitage 2008; Etnier 2010). Local geographic clustering of cryptic morphological and ecological variation within the *carolina, nigrita* and *invaria* groups of *Rhyacophila* has long fascinated Trichoptera systematists, and (within the eastern N American fauna alone) a number of regionally endemic species of *Rhyacophila* have been identified or formally described (Ross 1944; Flint 1972; Parker 1986; Harris 1989; Harris 1991; Etnier *et al.* 2004; Etnier *et al.* 2010; Zhou *et al.* 2011).

Several *Rhyacophila* species groups in North America have species with similar distributions of range sizes and geographic occurrences. Within these groups there are often species with very small geographic ranges and narrow habitat preferences, as well as widespread species found in many habitats across broad regions (Ross 1956; Flint 1962; Harris *et al.* 1991, Moulton & Stewart 1996). For many groups of animals, including *Rhyacophila* and other Trichoptera species, regions where the ranges of widespread species overlap with the range of narrowly distributed endemics (e.g. the southern Appalachian mountains) have higher species richness than regions on the periphery (Harris *et al.* 1991; Lenat *et al.* 2010; Etnier *et al.* 2010). Ross (1956) suggested that glacial advance and retreat could drive speciation by creating multiple refugia and facilitate demographic exchange during recolonization episodes, potentially generating new reproductively isolated populations and consequently affecting the composition of regional species pools. Evidence for these processes in aquatic systems across eastern North America has been presented for stream fishes (April *et al.* 2013). However, very little is known about rates of gene flow across landscapes, or which landscape-scale factors can limit dispersal of caddisflies, especially during interglacial periods.

Corrections to previously published species occurrences of *R. dandaganu* n. sp. as *R. lobifera* Betten, 1934

All records of *Rhyacophila lobifera*, reported in Harris *et al.* (1991) and Hicks and Haynes (2000), are confirmed as *Rhyacophila dandaganu* n. sp. (see material examined, Figure 3). We know of no confirmed records, published or unpublished, of *Rhyacophila lobifera* from the states of Alabama, Georgia or North Carolina, and no such occurrences were reported by Prather and Morse (2001). The occurrence of *R. lobifera* is common in small-stream habitats along the Ridge and Valley and Cumberland Plateau regions, extending into OH, PA, WV and KY, and across the Midwestern prairie states (Ross 1944; Moulton & Stewart 1996). Previous records and literature mentions of *R. lobifera* in eastern North Carolina are, in fact, records of an undescribed *Rhyacophila* species that is difficult to distinguish from *R. lobifera* in larval stages (Jim Glover, SCDNR, pers. comm.; John Morse pers. Comm.; Lenat *et al.* 2010).

Geographic features associated with known range of *Rhyacophila dandaganu*, n. sp.

The known geographic range of *Rhyacophila dandaganu* n. sp.is limited to the Cumberland Plateau and Ridge and Valley ecoregions of northern Alabama and northwest Georgia, south of the Tennessee River. The type locality is on Lookout Mountain, where the species is common and abundant in small perennial and seasonal streams along the extent of the mountain to the south, and throughout Alabama to the west. No populations east or north of the base of Lookout Mountain have yet been located. One larva, presumably *R. dandaganu* n. sp., has been collected from a small seepage in Chickamauga National Battlefield but no adults were taken there during the course of a 3 year intensive survey of aquatic insects (Robinson and Parker unpublished data, Robinson *et al.* 2016). No Tennessee specimens or populations of *R. dandaganu* are yet known, but should be expected on Lookout Mountain or the nearby vicinity. From the specimen records we have reviewed, the minimum distance between known populations of these species appears to be around 130 km. Despite multiple intentional collecting efforts targeted in the area between known populations of these species, we cannot refine our conception of the distribution of these species to sufficiently exclude the hypothesis that the Tennessee River is a dispersal barrier isolating these two species.

However, we remain skeptical of any mechanistic significance to this observation of the northern boundary of the geographic range of this species. It is difficult for us to accept that a river would serve as a geographic barrier for an aquatic insect species with such a broad tolerance of larval habitats. We have collected *R. lobifera* beneath streamside stones along the edges of larger rivers, and the ephemeral larval habitat is seasonally abundant. Adults of both species have a distinct early emergence period, egg diapause until late fall, a very fast larval growth period throughout winter, with pupal enclosure and eclosion in early spring. During our collections during the adult flight period, ambient evening air temperatures during the flight period of this species have often dipped below 50 F, which could potentially limit the distance travelled by individuals. However, we have collected adults of both species in flight during daylight hours. None of these observations reasonably support the idea that the Tennessee River could be a barrier to adult dispersal, and further collections should elucidate the real boundaries.

Is there a hybrid zone?

The geography of species occurrences, alone, cannot provide evidence for any particular mechanism of speciation (Barraclough & Vogler 2000). We have no specimens from the region where individuals of these two species are most likely to co-occur, despite a number of intensive collection efforts. If reproductive contact between these species does occur, it seems most likely to occur north of the Tennessee River in Alabama or Tennessee. The most geographically proximal records of these species are approximately 130 km apart: the intervening Tennessee Valley may have populations of either or both, but no specimens or records are yet known. To the west, Mississippi is particularly poor habitat for “mountain caddisflies” (Etnier 2010) and is a candidate barrier to contact between *R. dandaganu* and populations of *R. lobifera* further west in Arkansas and Missouri. However, the distribution of *R. lobifera* in middle and west Tennessee is not well documented (Etnier *et al.* 1998).

The factors driving speciation, or shaping the geographic distribution of species, are complex and varied. Many authors agree that habitat-filtering and dispersal limitation mechanisms can work at multiple spatial and temporal gradients and scales. For example, factors promoting adult dispersal could differentially affect the fitness of larval and adult life history stages (Martin 1985; Lavandier & Cereghino 1995; Taira & Tanida 2011). Classic allopatric theory emphasizes the demographic effects of these factors during speciation, where the distribution of populations across the landscape can potentially lead to reproductive isolation by limiting reproductive contact *a priori*. Alternatively, other mechanisms could drive reproductive isolation by skewing mate choice preference by pre-zygotic exclusion mechanisms (e.g. pairwise divergence in pheromone composition or other tactile communication, or changes affecting the mechanical coupling of disparate genitalic structures). Because we know of no co-occurring populations of these species, we cannot now test these hypotheses on the mechanisms driving any reproductive isolation accompanying this morphological divergence. However, it seems likely that *some* isolation mechanism is (or has recently) been at work to maintain this morphological divergence, and further study may elucidate these processes. However, we cannot yet rule out the hypothesis that the new species is restricted by the Tennessee River.

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