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NOTES ON GEOGRAPHIC DISTRIBUTON

The first New World record for *Zoophthora rhagonycharum* (Bałazy) S. Keller (Zoopagomycota, Entomophthorales) infecting *Rhagonycha* spp. (Coleoptera, Cantharidae)

Ann E. Hajek[1], James K. Liebherr[1], Siegfried Keller[2]

1 *Department of Entomology, Cornell University, Ithaca, New York, USA*
2 *Agroscope, Reckenholzstrasse 191, CH-8046 Zurich, Switzerland (retired)*

Corresponding author: *Ann E. Hajek (aeh4@cornell.edu)*

Abstract. The entomophthoralean fungus *Zoophthora rhagonycharum* (Bałazy) S. Keller, previously recorded in Europe from Poland and Switzerland, is now reported in North America from New York State, United States of America. On both continents, this obligate insect pathogen is known only from resting spores found within dead, adult native soldier beetles (Cantharidae) of the genus *Rhagonycha* Eschscholtz, 1830. Resting spores have undulating, light brown episporia. In New York, columnar rhizoids attach cadavers tightly to the undersides of leaves in the understory of hardwood forests in late June and early July.

Key words. Allegheny hardwood forests, entomopathogenic fungus, insect pathogen, geographic distribution

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INTRODUCTION

At least 246 species in the fungal order Entomophthorales (phylum Zoopagomycota, subphylum Entomophthoromycotina, class Entomophthoromycetes) are acute pathogens of arthropods (Sacco and Hajek 2023). In the basic life cycle of entomophthoralean species, two types of spores are usually produced: relatively short-lived conidia, associated with infection during that season, and long-lived resting spores (either azygospores or zygospores) that survive during periods when hosts are not active or present (Keller 2007b). For some fungal species, these two types of spores can be produced from the same infected arthropod, whereas for others only one or the other spore type is produced per cadaver (Hajek et al. 2018). Identification of entomophthoralean species has historically been based principally on morphology, often emphasizing conidial morphology, and host associations. However, conidial stages have not been found for all entomophthoralean species, complicating identifications (Hajek et al. 2018). When only resting spores in or on hosts are found, the form genus *Tarichium* Cohn has been used to describe species. Recently, for the first time, using molecular methods, two species known only from resting spore stages in adult crane flies (Tipulidae) were placed phylogenetically in the genus *Zoophthora* A. Batko (Hajek et al. 2016).

An entomophthoralean pathogen known only from resting spores has been reported from small soldier beetles (Cantharidae, Cantharinae) in Poland (*Rhagonycha lignosa* (O.F. Müller, 1764)) and Switzerland (*Rhagonycha fulva* (Scopoli, 1763)) (Keller 2013). This pathogen was initially named *Tarichium rhagonycharum* Bałazy (Bałazy 1982) because only resting spores had been found in cadavers of these beetles. However, Bałazy (1993) stated that this was undoubtedly a species of *Zoophthora* (family Entomophthoraceae, subfamily Erynioideae), based on rhizoid morphology, but the species remained in *Tarichium* at that time because conidia had not been seen. However, despite conidia not having been observed, this species was subsequently recombined with the genus *Zoophthora*, based on typical characters of the genus, which include hyphal-like hyphal bodies and compound rhizoids (Keller 2007a).

The genus *Zoophthora* was named in 1964 (Batko 1964) and later split into four subgenera (Batko 1966). Each subgenus was subsequently raised to the generic level (Humber 1989). Presently, *Zoophthora* is considered to be the most derived genus in the Erynioideae (Gryganskyi et al. 2013), an entomophthoralean subfamily in which conidiophores are branched and conidia are mononucleate (Keller and Petrini 2005). All species of *Zoophthora* form passively dispersed secondary capilliconidia that are produced on elongated

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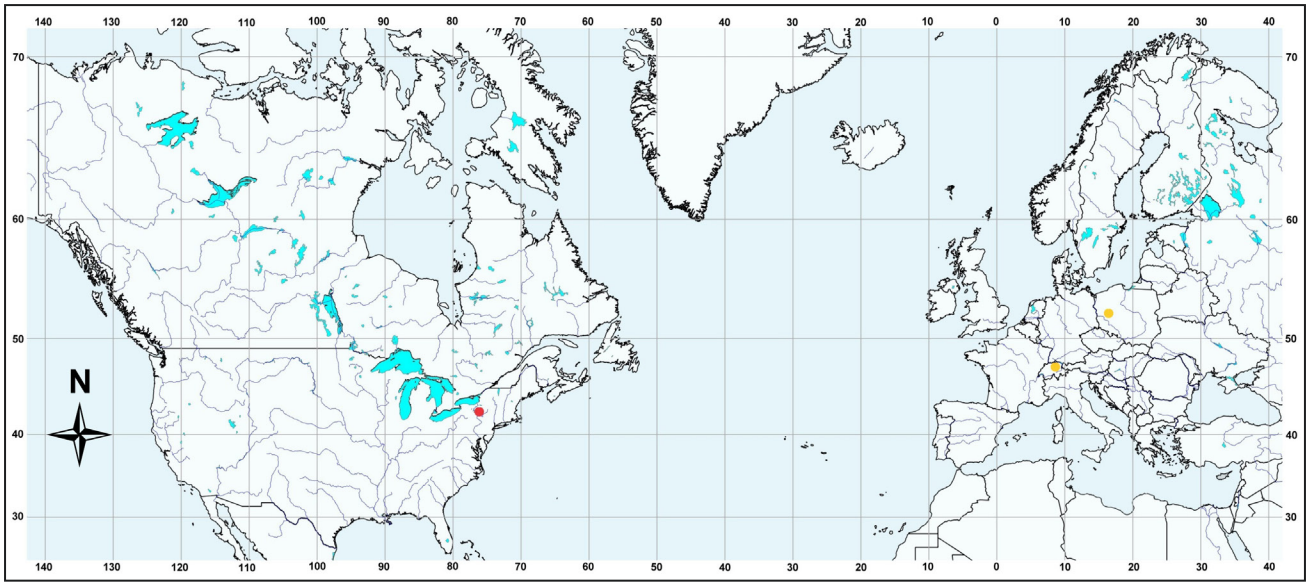

Figure 1. Map showing the collection localities. The red circle denotes the new locality, and the yellow circles are sites listed by Keller (2007a) and Bałazy (1982). Keller (2007a) includes two sites but because they are 10.4 km apart, there is only one circle. This map was created with mapchart.net.

capillary conidiophores, which is unique within this subfamily (Gryganskyi et al. 2013). Most species in this genus produce compound rhizoids (pseudorhizomorphs) with specialized holdfasts that are often accompanied by monohyphal rhizoids; rhizoids function to attach cadavers to substrates.

We collected an entomophthoralean pathogen infecting beetles in the genus *Rhagonycha* in New York State. The fungus had ornamented resting spores and compound rhizoids; conidia were not found. In North America, the only entomophthoralean fungus known to infect *Rhagonycha* or any other species in the soldier beetle subfamily Cantharinae (family Cantharidae) is the generalist *Batkoa major* (Thaxter) Humber (Gryganskyi et al. 2022) but resting spores are not known from *B. major* in North America. Here we report that *Zoophthora rhagonycharum* (Bałazy) S. Keller, identified based on host genus, rhizoids, and resting spores, infects two species of *Rhagonycha* at one site in northeastern North America (Figure 1). This fungal species was previously known only from central Europe (Figure 1).

METHODS

Cadavers of adult *Rhagonycha* spp., filled with resting spores were collected along the Abbott Loop hiking trail in Danby State Forest, Tompkins County, New York State, USA. The majority of cadavers were found on the undersides of leaves in the forest understory. The collection area is an undisturbed natural area in a mixed, second-growth Allegheny hardwood forest. Adult *Rhagonycha* were usually specifically found in areas of Red Oak (*Quercus rubra* L.) and American Beech (*Fagus grandifolia* Ehrh.) trees with undisturbed leaf litter. The specimens were collected under permit #14787 issued by the New York State Department of Environmental Conservation.

For each of four *Rhagonycha* cadavers, diameters for 25–30 resting spores in water were measured at 400× magnification with phase contrast. For scanning electron microscopy, resting spores were sparsely scattered on smooth carbon tape and coated with iridium prior to observation on a Tescan Mira3 FESEM scanning electron microscope at the Cornell Center for Materials Research.

Adult cantharids containing resting spores were identified to insect species using Pelletier and Hébert (2014) and Green (1940).

RESULTS

Family Entomophthoraceae A.B. Frank (1874)
Subfamily Erynioideae S. Keller & O. Petrini (2005)

***Zoophthora rhagonycharum* (Bałazy) S. Keller**, Sydowia 59(1): 110 (2007a)

≡ *Tarichium rhagonycharum* (Bałazy) Bull. Acad. Polon. Sci., Cl. II. Sér. Sci. Biol. 29 (5–6): 223 (1982) [1981]

New record. USA – **New York State** • Tompkins County, Danby State Forest, in an undisturbed Allegheny hardwood forest; 42°18.0′N, 076°29.2′W; 397 m elev.; 19–27.VI.2019, 4–6.VII.2020, 13.VII.2021, 25.VI.2023

(Table 1); A.E. Hajek & J.K. Liebherr; resting spores occurred within dead *Rhagonycha fraxini* (Say, 1823), *Rhagonycha vilis* (LeConte, 1851) and *Rhagonycha* sp. soldier beetle adults (Coleoptera, Cantharidae, Cantharini) attached by rhizoids to the undersides of leaves, often of American Beech in the understory vegetation. Throughout the collection time periods, living adults of the host species were not common and dead beetles filled with resting spore-filled cadavers were rarely found. Voucher specimens of *Z. rhagonycharum* have been deposited in the Cornell University Plant Pathology Herbarium: CUP62801. Specimens of healthy cantharid hosts collected at the same site were deposited in the Cornell University Insect Collection (CUIC): voucher lot #1286.

Identification. Conidia unknown. Resting spores 48.4 ± 1.1 µm (mean ± SE) (min–max: 37.1–60.0 µm), with a double-layered wall, spherical and seldom slightly ovoid. Resting spores individually light brown to hazel (Figure 2A) and *en masse* dark reddish brown (Figure 2B). The existence of resting spores within cadavers was sometimes visible externally through bulging thoracic and abdominal intersegmental membranes

Table 1. Numbers of *Rhagonycha* species infected with *Zoophthora rhagonycharum* collected during June and July between 2019 and 2023.

Year	Date	Host[a]	#
2019	19 June	*R. vilis*	2
2019	27 June	*R. fraxini*	3
2019	27 June	***Rhagonycha*** sp.	1
2020	4 July	*R. vilis*	1
2020	6 July	*R. vilis*	1
2020	6 July	***Rhagonycha*** sp.	1
2021	13 July	***Rhagonycha*** sp.	1
2023	25 June	*R. fraxini*	1

[a] When only portions of the host's body were attached to a leaf (e.g., often the head might be missing), the beetle species could not be identified, and the specimens is indicated as *Rhagonycha* sp.

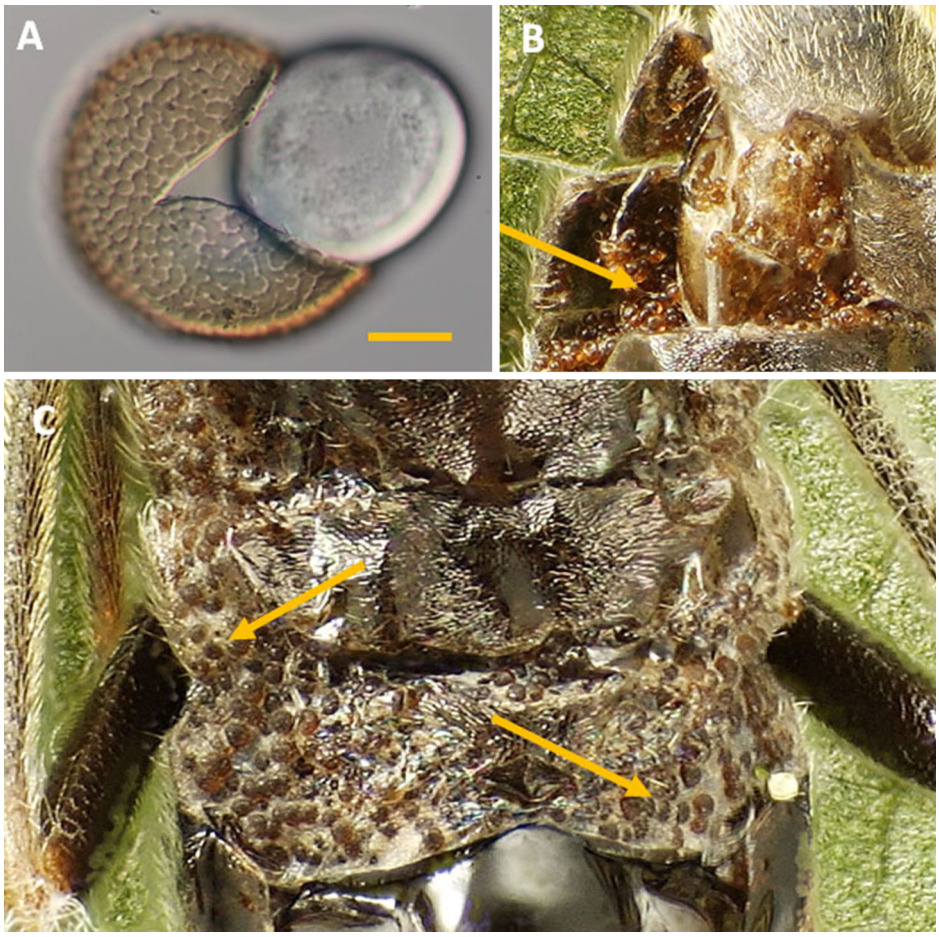

Figure 2. *Zoophthora rhagonycharum*. **A.** Resting spore with light brown undulating episporium broken and releasing the multinucleate epispore within). **B.** Resting spores outside of the beetle's body are *en masse* reddish-brown (see arrow). **C.** Round shapes of resting spores within the abdomen of *R. vilis* adult, seen through the intersegmental membranes (see arrows). Scale bar: A = 20 µm.

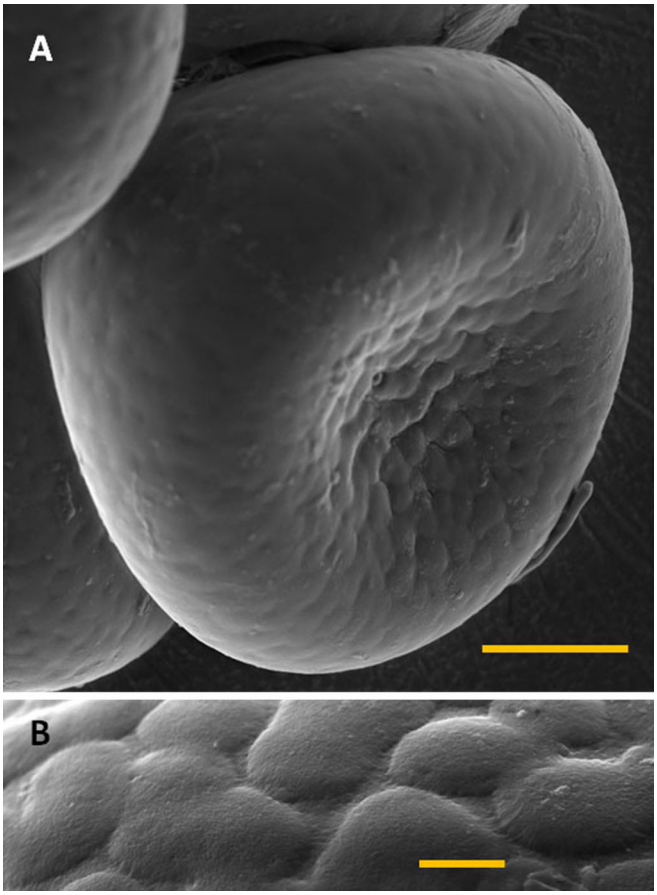

Figure 3. *Zoophthora rhagonycharum* **A.** Scanning electron micrograph of *Z. rhagonycharum* resting spore from within *Rhagonycha fraxini*. **B.** Surface of resting spore within *R. fraxini*. Scale bars: A = 10 µm; B = 2 µm.

(Figure 2C). Coloration of resting spores was due to an episporium covering the epispore. Episporia could be broken with pressure, revealing an uncolored epispore within (Figure 2A); surfaces of episporia shallowly undulating or ruffled (Figures 2A, 3A, B). Rhizoids pseudorhizomorph, principally emerging as 2–4 broad, white columns from the center of the ventral side of the abdomen but also with individual pseudorhizoids, all of which tightly attach the cadaver very closely to the leaf (Figure 4A). Endings of pseudorhizomorph columns either not specialized or with disc-like holdfasts with uneven edges. Rhizoids and resting spores from *R. vilis* and *R. fraxini* did not differ. For cantharid identification, voucher specimens were compared with CUIC specimens previously identified by J.W. Green.

Remarks. Among all species of Entomophthorales in North America, no species have similar characters to those described, while infecting hosts of this genus (Hutchison 1963; Bałazy 1993; ARSEF 2021). Based on lack of conidia, resting spore size, color, and surface pattern, rhizoids, and genera of infected hosts, this fungal pathogen is consistent with *Z. rhagonycharum*, previously known only from Poland and Switzerland (Keller 2013). Pseudorhizomorphs of *Z. rhagonycharum* in Switzerland emerge from the center of the ventral abdomen, similar to specimens from New York (Figure 4B). In New York, resting spores from *Z. rhagonycharum* were the same size as globose resting spores from European hosts *Rhagonycha lignosa* (Poland: 43–55 µm) (Bałazy 1982) and *R. fulva* (Switzerland: 45.4–48.8 µm; range 33–62 um) (Keller 2007a). However, in Poland, some resting spores were "slightly ovoidal" (61–68 × 45–56 µm); resting spores of these dimensions were not seen in New York (A.E. Hajek unpublished data) and ovoid resting spores were not mentioned for Switzerland, but Bałazy's (1982: figure 6) photo of a specimen from Poland does not show that a high percentage of resting spores were ovoidal.

Most species of Entomophthorales infect hosts within the same arthropod family (Sacco and Hajek 2023). Therefore, we compared our specimens with other fungal species known from resting spores and pseudorhizomorphs that infect cantharids. *Zoophthora crassitunicata* Keller was reported from a minute adult cantharid, "probably *Malthodes* sp." in Switzerland (Keller 2013). However, conidia were produced by *Z. crassitunicata*, as well as resting spores and resting spores of *Z. crassitunicata*, are slightly smaller than those of *Z. rhagonycharum*. *Pandora lipai* (Bałazy, Eilenberg & Papierok) Keller infects four species of cantharids in Poland and Denmark, including *R. lignosa*, but produces conidia from cadavers, and the resting spores, only known from cultures, are much smaller than those of *Z. rhagonycharum* (Keller 2013). *Tarichium coleopterorum* (Petch) Bałazy, described in 1932 in England and not reported elsewhere, produces only resting spores, and rhizoids are pseudorhizomorphs, which makes it similar to our collections, but the resting spores are dark brown and the beetle hosts are unidentified Coleoptera (Keller 2013).

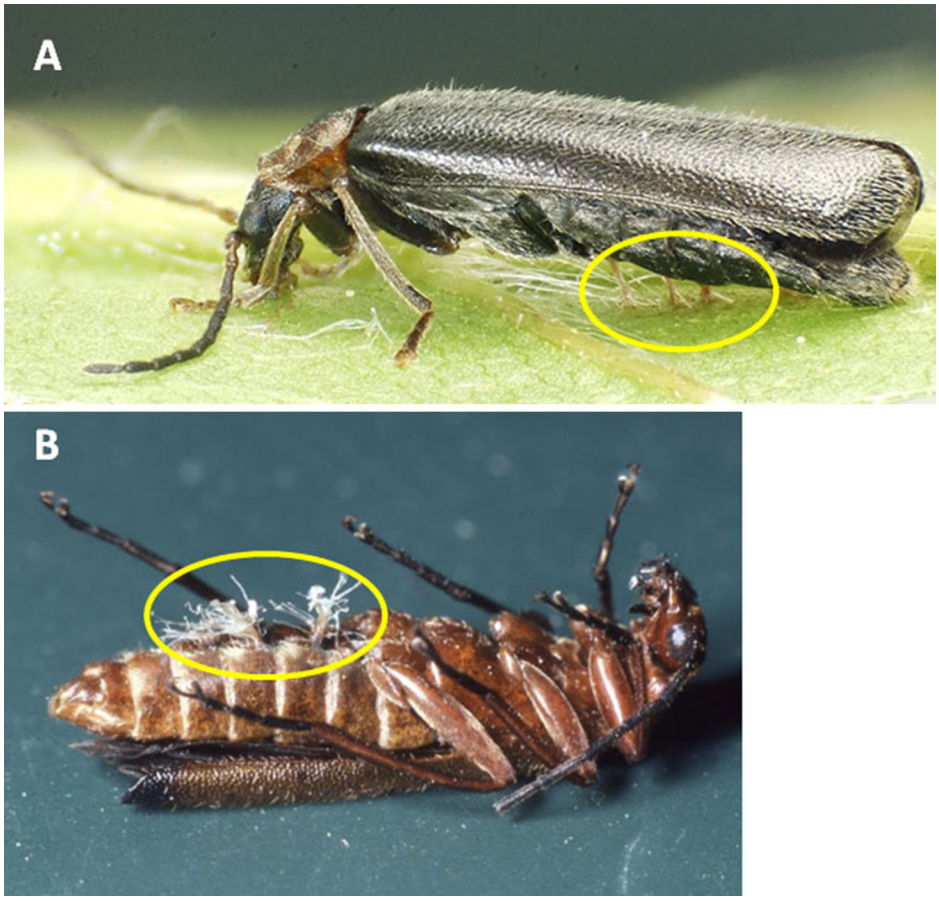

Figure 4. A. Lateral view showing rhizoid columns extending ventrally from the abdomen of *Rhagonycha vilis* to the leaf (3 columns seen within the circle). Hind leg of beetle was removed. **B.** For comparison, rhizoid columns extending ventrally from the abdomen of *Rhagonycha fulva* collected in Switzerland (circled). Beetle was flipped over and is laying on its dorsum so rhizoids are extending upward.

DISCUSSION

Zoophthora rhagonycharum has never before been reported from any continent except Europe, where it is known from Poland and Switzerland (Keller 2013). The epispores of the New York specimens were light brown to hazel, which is consistent with European collections: hazel brown (Poland) or brown (Switzerland). In Poland, episporia were reported as being smooth (Bałazy 1982), whereas in Switzerland episporia were described as having minute knobs (Keller 1991). However, in both cases, compound microscopes were used for examination, and it can be difficult to see clearly the surfaces of episporia that are not sculptured more deeply. These descriptions fit the very low ruffling of the surfaces of epispores from New York specimens.

Rhizoids of specimens from Europe and New York were comparable (Figure 4), erupting through intersegmental membranes in the centers of ventral sides of the abdomen of adult beetles. Unfortunately, there are no DNA sequences for *Z. rhagonycharum* from Europe or North America, but, based on the size and appearance of resting spores, rhizoids, and the host genus, our collections are highly consistent with descriptions for the species *Z. rhagonycharum* in Europe. Among Entomophthorales, the same species occur on different continents, for example, *Pandora neoaphidis* (Remaud. & Hennebert) Humber, and *Zoophthora radicans* (Bref.) A. Batko (Bałazy 1993; USDA ARSEF 2021), and therefore so could *Z. rhagonycharum*. Given that in New York (1) this pathogen infects small, innocuous, native, forest-dwelling beetles (3.4–6.3 mm body length; Pelletier and Hébert 2014), and (2) the ephemeral cadavers are evident only from mid-June to mid-July, it is completely understandable that this fungus in North America has been overlooked until recently. As the larval stages of Cantharidae live within humus and leaf litter near the soil surface, where they prey upon small arthropods during summer and overwinter as mature larvae (LeSage 1991), the immature stages were not encountered during our surveys for adult beetles and cadavers containing resting spores.

Zoophthora rhagonycharum was collected in association with *R. lignosa* in late June and July from the undersides of leaves within forests in Poland, conditions and phenology similar to those of our New York collections. Conversely, Swiss collections of the fungus in association with *R. fulva* were made in early August within grasslands, and the adult beetles were positioned head downward, attached to grass blades (Keller 1991). This seasonality is consistent with the phenology of *R. fulva* in North America, where adventive adult beetles are observed from the last week of July through August (Pelletier and Hébert 2014). Therefore, we hypothesize that the timing and locations of occurrence of *Z. rhagonycharum* (forest in late June/early July vs. grassland in late July/August) could differ at least in part due to the timing and locations of beetle hosts.

We propose two hypotheses regarding the occurrence of *Z. rhagonycharum* in North America. *Rhagonycha* is a very diverse Holarctic genus, with at least 46 species in the Nearctic (Ramsdale 2002) and 258 species in the Palearctic (Löbl and Smetana 2007). Some species have broad geographic ranges; for example, *R. fraxini* occurs from the eastern coast of North America to Alaska (Green 1940). It is plausible that *Z. rhagonycharum* naturally has a Holarctic distribution but had not been detected in North America until now. This fungus infects four species of *Rhagonycha* across its aggregate Holarctic range, with any possible fungal-host relationships in Asia and western North America yet to be discovered.

Conversely, fungi are well known for invading new areas (Fisher 2012) and, as a second hypothesis, perhaps *Z. rhagomycharum* was accidentally introduced from Europe to North America in the more recent past. This would likely have occurred due to transport of resting spores in living or dead *R. fulva*, or in associated soil or plant debris. Resting spores of the entomophthoralean fungus *Entomophaga maimaiga* Humber, Shimazu & R.S. Soper have been purposefully used to spread this fungus within the northern Midwest of the United States (Hajek et al. 2021). This fungus also travelled a long distance when it was accidentally introduced from Japan to northeastern North America after 1971 (Weseloh 1998; Nielsen et al. 2005); we assume that transport was due to human activity. In addition, resting spores of *E. maimaiga* survive in the soil for numerous years (Hajek et al. 2018), allowing this fungus to await future availability of its hosts. *Rhagonycha fulva*, one of the two host species of *Z. rhagonycharum* in Europe, has adventively colonized North America, being first documented in North America in British Columbia in 1948 (Brown 1950), and subsequently in Quebec in 1975 (Chantal 1981) and Wisconsin in 2004 (Young and Dorshorst 2008). The earliest record for *R. fulva* in New York State is from Jefferson County, near Cape Vincent, 24 July 1996 (CUIC, 4 specimens). The distribution of *R. fulva*, as reported by Pelletier and Hébert (2014), extends from the Canadian maritime provinces of New Brunswick and Nova Scotia, westward along the St. Lawrence River to the Great Lakes, including northwestern New York State. This, coupled with its presence in the Vancouver area of British Columbia, is consistent with adventive introductions via maritime shipping (Lindroth 1957). We have not collected *R. fulva* during our survey for *Z. rhagonycharum*, although in North America the species is "Common in shrubby fields, forb fields and forest edges" (Pelletier and Hébert 2014: 141), a type of habitat absent at our collecting site. Moreover, *R. fulva* is distributed along the riparian and lacustrine margins associated with the St. Lawrence River and Lakes Ontario and Erie, all approximately 200 km from our sampling locality in New York (GBIF 2023). Once introduced to North America, however, *R. fulva* might have vectored the fungus, leading to establishment of *Z. rhagonycharum* in populations of the native woodland inhabitants, *R. fraxini* and *R. vilis*.

Preliminary data suggest that *Z. rhagomycharum* can persist within populations of different *Rhagonycha* species exhibiting somewhat different phenologies and habitat preferences. Continued study of the occurrence of this fungus in North America, where the adventive European *R. fulva* is spreading, as well as among populations of native North American *Rhagonycha*, would elucidate variation of fungal phenology and possible discovery of *Z. rhagonycharum* in additional host species and habitats during different seasons.

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ADDITIONAL INFORMATION

Conflict of interest
The authors declare that no competing interests exist.

Ethical statement
No ethical statement is reported.

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Author Contributions
Conceptualization: AEH. Data curation: AEH, JKL. Formal analysis: AEH, JKL, SK. Investigation: AEH, JKL, SK. Methodology: AEH, SK. Project administration: AEH. Resources: AEH, JKL. Validation: SK. Visualization: AEH, JKL, SK. Writing – original draft: AEH. Writing – review and editing: AEH, JKL, SK.

Author ORCID iDs
Ann E. Hajek https://orcid.org/0000-0001-5740-4717
James K. Liebherr https://orcid.org/0000-0001-9831-884X
Siegfried Keller https://orcid.org/0009-0005-7052-7865

Data availability
All data that support the findings of this study are available in the main text.

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