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Tomoxia bucephala A. Costa (Coleoptera: Mordellidae),
a Palearctic tumbling flower beetle established
in North America

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Tomoxia bucephala A. Costa (Coleoptera: Mordellidae),
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Abstract. *Tomoxia bucephala* A. Costa (Coleoptera: Mordellidae), a Palearctic tumbling flower beetle native to Europe, Asia, and northernmost Africa, is now known from North America. The first known occurrences were in 2015 in Essex and Union counties, New Jersey, U.S.A. and in 2019 in Passaic County, New Jersey, all in the New York City metropolitan area. An additional collection documents the species in 2016 from Allegheny County, Pennsylvania, in the Pittsburgh metropolitan area. The multiple occurrences, the large distance between those in New Jersey and Pennsylvania, and multiple detections in natural areas indicate *T. bucephala* is established in North America and apparently invasive. Several morphological features differentiate *T. bucephala* from the two congeners native to North America, *T. inclusa* LeConte and *T. lineella* LeConte, especially coloration patterns of elytral and pronotal vestiture, and coloration of antennae and front legs. This is the first report of a non-native mordellid species established in North America. *Tomoxia bucephala* does not appear to pose a significant direct economic threat in North America since it feeds in decaying trees. However, *T. bucephala* occurrences are within the geographic ranges of *T. inclusa* and *T. lineella*, and the biology of *T. bucephala* is similar to these other *Tomoxia* species. Thus, *T. bucephala* likely will expand its range within North America, with probable ecological impact on communities of native saproxylic beetles, especially *T. lineella* and *T. inclusa*.

Key words. non-native, invasive, saproxylic, New Jersey, Pennsylvania, *Tomoxia lineella*, *Tomoxia inclusa*

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Introduction

The tumbling flower beetle genus *Tomoxia* A. Costa (Coleoptera: Mordellidae: Mordellinae: Mordellini) is relatively small, ca. 8–12 species (Franciscolo 1982; Jackman and Lu 2002; Horák 2020). A precise accounting of its size is not possible at this time because several species originally described in *Tomoxia* have yet to be assessed according to the modern, more restrictive circumscription of the genus (Franciscolo 1982). Based on this circumscription, two species of *Tomoxia* occur in North America: *T. inclusa* LeConte and *T. lineella* LeConte (Jackman and Lu 2002), and five occur in the Palearctic: *T. bucephala* A. Costa, *T. formosana* M. Chûjô, *T. relictæ* Takakuwa, *T. ryukyuanæ* Takakuwa, and *T. similis* Nomura (Horák 2020). Species that appear from their descriptions to fit the modern circumscription of *Tomoxia* also occur in the Neotropics and Australia (Champion 1891; Lea 1917; Ray 1939).

Four morphological characters unequivocally diagnose *Tomoxia* (Franciscolo 1982; Jackman and Lu 2002). The scutellum is wider than long. The hind margin of the scutellum is emarginate. The metatibiae and first metatarsomeres each bear a fine, dorsal, longitudinal ridge. The fourth (penultimate) tarsomeres of front and middle legs are apically truncate.

Tomoxia bucephala is the type species of *Tomoxia* (Horák 2020). In older literature, this species is known as *T. biguttata* (Gyllenhal) [original combination: *Mordella biguttata* Gyllenhal, 1827, which is a junior homonym of *Mordella biguttata* Rossi, 1794] (Selnekovič and Improta 2020).

Tomoxia bucephala is widespread, ranging from England to the Russian Far East, south to Algeria, Azerbaijan, and Kazakhstan (Odnosum 2010; Horák 2020; NBN Atlas 2022). This species is locally common in many parts of its range (Borowiec and Kubisz 1999; Zemoglyadchuk et al. 2020; Zemoglyadchuk and Buialska 2021; UK Beetles 2022).

Life history basics are known for *Tomoxia bucephala*. In Europe, adults are present from May to mid-September, with the peak of activity during June and July (Lameere 1900; Saalas 1923; Zemoglyadchuk et al. 2020). Adults are active on dead, standing and fallen deciduous trees and stumps (Grove 1990; UK Beetles 2022). Their food is primarily fungal spores from Ascomycota and Basidiomycota (Zemoglyadchuk and Buialska 2021). Though adults sometimes visit flowers, particularly species of Apiaceae (Lameere 1900; Alexander 2002), *T. bucephala* apparently does not utilize pollen for food (Zemoglyadchuk and Buialska 2021). Females lay eggs in cracks in bark and in borings previously produced by *Ptilinus pectinicornis* (L.) (Coleoptera: Ptinidae) and other ptinids in these dead trees (Alexander 2002; Leather et al. 2014; Zemoglyadchuk and Buialska 2021). A wide variety of deciduous trees are hosts for larvae of *T. bucephala* (Lentz 1879; Odnosum and Mamaev 1986; Grove 1990; Alexander 2002; Leather et al. 2014; Zemoglyadchuk et al. 2020; Zemoglyadchuk and Buialska 2021), including Norway maple (*Acer platanoides* L., Sapindaceae), birches (*Betula* spp., Betulaceae), European Beech (*Fagus sylvatica* L., Fagaceae), European ash (*Fraxinus excelsior* L., Oleaceae), common walnut (*Juglans regia* L.), Eurasian aspen (*Populus tremula* L., Salicaceae), European oak (*Quercus robur* L., Fagaceae), willows (*Salix* spp., Salicaceae), rowan (*Sorbus aucuparia* L., Rosaceae), littleleaf linden (*Tilia cordata* Mill., Malvaceae), and elms (*Ulmus* spp., Ulmaceae). *Tomoxia bucephala* larvae also develop in conifers, particularly spruces (*Picea* spp., Pinaceae), though apparently less frequently than in deciduous trees (Saalas 1923; Hansen and Larsson 1945). It is likely that certain species of decay fungi present in the wood provide oviposition cues for females (Leather et al. 2014). Larvae develop in fungus-infested wood and take at least two years to reach pupation (Zemoglyadchuk et al. 2020). The overwintering stage is the larva (Zemoglyadchuk et al. 2020).

Robert Androw sent loans of undetermined North American mordellids from the Carnegie Museum of Natural History to Robert Naczi for his determination. In these shipments, RN recognized specimens of *Tomoxia bucephala*. In addition, RN found online photos by John Rosenfeld that documented this species from an additional locality in North America. In this paper, we document the first known collections of *T. bucephala* from North America, provide evidence for its establishment in the U.S.A., provide tools for identification of this species, and assess its potential economic and ecological impact.

Materials and Methods

For research on North American mordellid systematics, diversity, and biogeography, we studied 265 *Tomoxia* specimens from the following collections in the United States, by loans and visits.

BBC Brad Barnd collection, Greenfield, Indiana.

BTRC Brian T. Raber collection, Katy, Texas.

BYUC Brigham Young University Arthropod Collection, Provo, Utah.

CMNH Carnegie Museum of Natural History, Pittsburgh, Pennsylvania.

CSUC C.P. Gillette Museum of Arthropod Diversity, Colorado State University, Fort Collins, Colorado.

EGRC Edward G. Riley collection, College Station, Texas.

FMNH Field Museum of Natural History, Chicago, Illinois.

FSCA Florida State Collection of Arthropods, Gainesville, Florida.

JLC James Louderman collection, Chicago, Illinois.

- JMLC** John M. Leavengood, Jr. collection, Tampa, Florida.
KESC Kyle E. Schnepf collection, Gainesville, Florida.
MEM Mississippi Entomological Museum, Mississippi State University, Mississippi State, Mississippi.
NYSM New York State Museum, Albany, New York.
RNC Robert Naczi collection, Brewster, New York.
SERC Smithsonian Environmental Research Center, Edgewater, Maryland.
TAMU Texas A&M University Insect Collection, College Station, Texas.
UKIC University of Kentucky Insect Collection, Lexington, Kentucky.
UTIC University of Texas Insect Collection, Austin, Texas.

Specimens of *T. bucephala* were among specimens of undetermined Mordellidae extracted from Lindgren funnel trap samples submitted to the Carnegie Museum's Biodiversity Services Facility (BSF). The BSF is a for-profit service primarily focused on screening survey trap samples for invasive wood-boring Coleoptera. The majority of its samples are submitted by the United States Department of Agriculture's Animal and Plant Health Inspection Service-Plant Protection and Quarantine program, but a number of state agencies involved in Cooperative Agricultural Pest Survey projects also utilize the service annually (McElrath et. al. 2016; Androw 2021). Lindgren funnel traps are hanging, multi-funnel traps that visually simulate tree trunks, and are run with a variety of chemical lures that target wood-boring Coleoptera. The most commonly used lures are general attractants, such as ethanol for deciduous borers, and alpha-pinene for conifer feeders. However, many highly species- or genus-specific, pheromone-based lures are regularly deployed for narrowly targeted surveys for exotic pests. *Tomoxia bucephala* was collected using an ethanol and alpha-pinene combination lure (BSF samples 61492 and 61268) and a specific lure for the non-native bark beetle *Pityogenes chalcographus* (L.) (Curculionidae: Scolytinae) (BSF sample 91236).

In addition, we searched online sources of *Tomoxia* specimens and photographs for records of *T. bucephala* in North America: BugGuide (BugGuide 2022), GBIF (GBIF 2022), iNaturalist (iNaturalist 2022), and SCAN (SCAN 2022).

We photographed specimens with a Nikon DS-Ri2 camera attached to a Nikon SMZ800N microscope, and used Nikon NIS-Elements BR 5.20.00 software for image stacking.

Results

We found several recent specimens and photographs that document *Tomoxia bucephala* from multiple localities in North America. The specimens are clearly *Tomoxia* because of the transverse, emarginate scutellum (Fig. 1–3), the fine, dorsal, longitudinal ridges on the metatibia and first metatarsomere (Fig. 4A), and the apically truncate penultimate tarsomeres of the front and middle legs (Fig. 4B).

We documented several differences between these recent records of *Tomoxia* and the native *T. inclusa* and *T. lineella*. These differences clearly distinguish the recent records from the native species, and diagnose the recent records as the Palearctic *T. bucephala*.

Elytral vestiture coloration patterns provide one means of distinguishing *Tomoxia bucephala* from *T. inclusa* and *T. lineella*. *Tomoxia bucephala* possesses pale hairs along the elytral suture for nearly the full length of the elytra (Fig. 1–3). Additionally, the elytra of *T. bucephala* lack humeral lunules (Fig. 1–3, 5A–B). In contrast, *T. inclusa* has pale hairs extending continuously from the elytral base to only 30–40% of the length of the elytra, and has a lunule margined by pale hairs in the humeral region of each elytron (Fig. 5C, 6). Similar to *T. bucephala*, *T. lineella* has pale hairs flanking the elytral suture for most of its length (Fig. 7). Also similar to *T. bucephala*, *T. lineella* lacks humeral lunules on the elytra (Fig. 5D, 7). The aspects of elytral vestiture coloration that distinguish *T. bucephala* from *T. lineella* are presence and extent of oblique, pale stripes. The pale coloration on the elytra of *T. bucephala* is usually continuous and unbroken, and stripes are lacking (Fig. 1–2). However, sometimes the pale coloration is present as stripes (e.g., Fig. 3). When stripes are present in *T. bucephala*, they extend from the elytral bases only as far as the medial region. In contrast, *T. lineella* always has at least one stripe that extends to the apical half of each elytron (Fig. 7).



Figure 1. *Tomoxia bucephala*, aspect of living beetle, Allegheny County, Pennsylvania, U.S.A. **A.** Dorsal view. **B.** Dorsolateral view. **C.** Ventral view. Scale bars for all images = 1.0 mm. See text for complete voucher specimen collection data.



Figure 2. *Tomoxia bucephala*, aspect of museum specimen, Essex County, New Jersey, U.S.A. **A.** Dorsal view. **B.** Dorsolateral view. **C.** Lateral view. Scale bars for all images = 1.0 mm. See text for complete voucher specimen collection data.

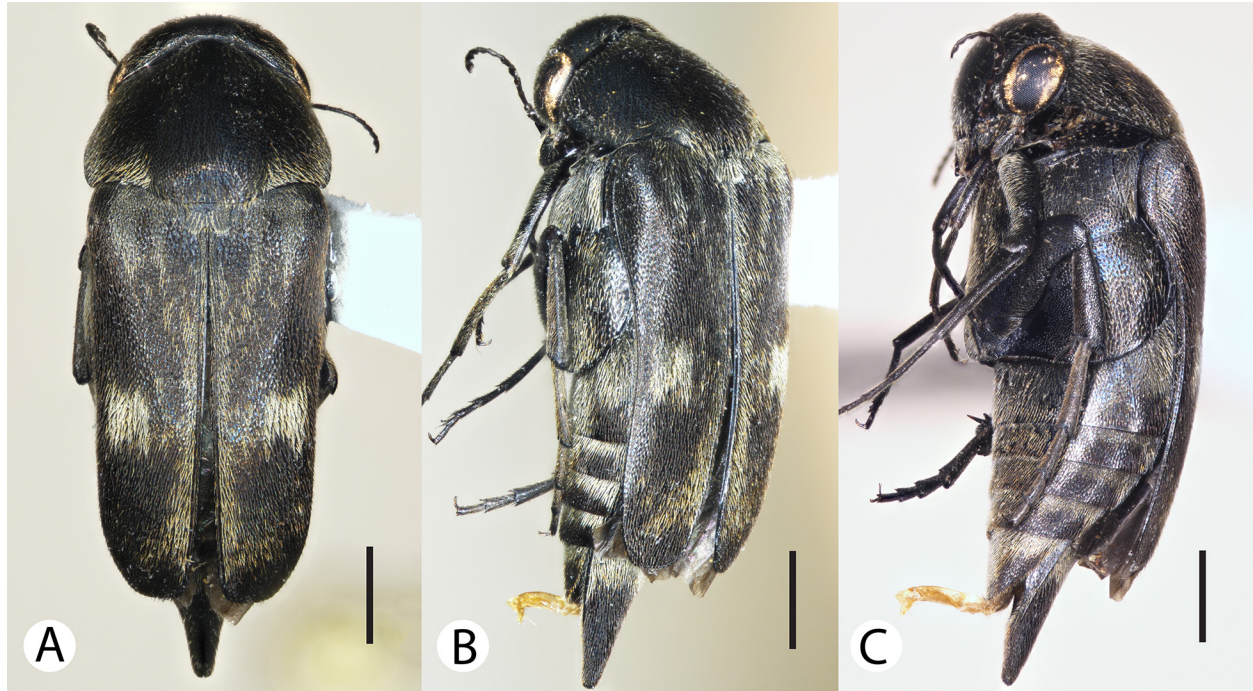


Figure 3. *Tomoxia bucephala*, aspect of museum specimen, Union County, New Jersey, U.S.A. **A.** Dorsal view. **B.** Dorsolateral view. **C.** Lateral view. Scale bars for all images = 1.0 mm. See text for complete voucher specimen collection data.

Another feature that distinguishes *T. bucephala* from *T. inclusa* is coloration of pronotal vestiture. In *T. bucephala*, the pronotum has stripes of pale pubescence along lateral and often basal margins, two longitudinal bands of pale hairs in the medial region (often faint), and no additional bands or spots of pale hairs (Fig. 5A–B). *Tomoxia inclusa* has pale pubescence along the pronotal margins and two longitudinal, medial pale bands. In addition, *T. inclusa* has a pale spot in the anterior half of the pronotum laterad to each longitudinal pale band (Fig. 5C). The pronotum of *T. lineella* has pale stripes and/or spots between the pair of medial stripes and the pale margins (Fig. 5D).

Tomoxia bucephala specimens have antennae and profemora uniformly very dark brown or black (Fig. 1–3, 8A). *Tomoxia inclusa* is variable in antennal and profemoral coloration; the antennae vary from pale brown to dark brown (Fig. 6, 8B), and the profemora from medium brown to black. In contrast to *T. bucephala*, the profemora and the first 3 antennomeres (often more) of *T. lineella* are pale brown or medium brown, sometimes only in part (Fig. 7, 8C).

In order to facilitate identification of *Tomoxia* species, we provide a description of *T. bucephala* and an identification key to the three species of *Tomoxia* now known in North America north of Mexico.

***Tomoxia bucephala* A. Costa, 1854**

Figures 1–4, 5A–B, 8A, 9

Diagnosis. Antenna, legs, and body uniformly very dark brown or black; elytra unstriped or with relatively short stripes that extend from base toward medial region, but do not extend beyond it; pronotum with pale pubescence along the margins and with two pale longitudinal stripes in medial region (often faint) but no additional stripes or spots.

Description. *Length.* Length of beetle in repose (head resting against bases of front legs), from vertex to elytral apices 5.3–6.0 mm, from vertex to apex of pygidium 6.2–7.6 mm. *Ground color.* Uniformly very dark brown or black, including head, antennae, elytra, venter, and legs. *Antenna.* Reaching nearly to base of pronotum when

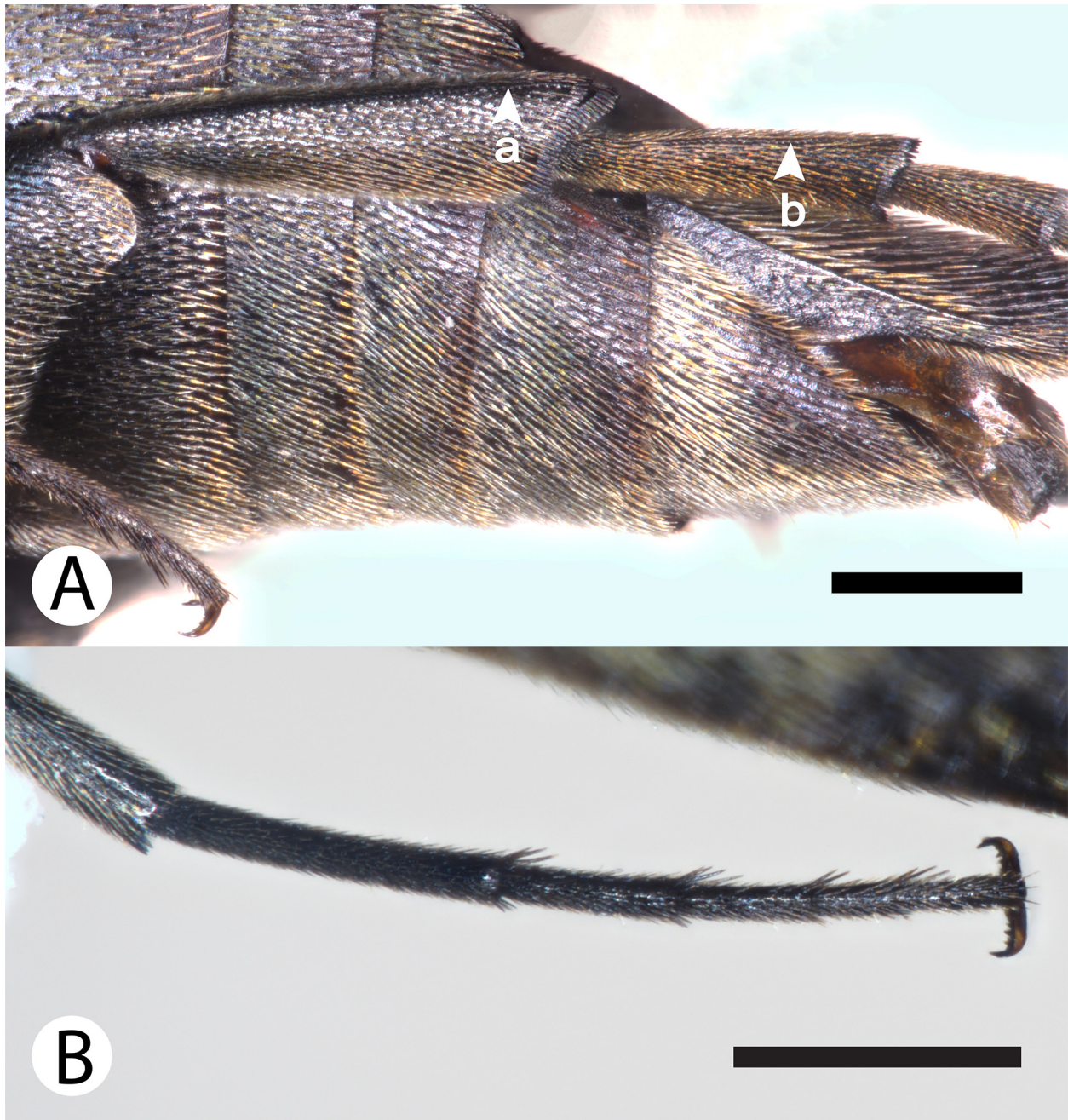


Figure 4. *Tomoxia bucephala* details of museum specimen, Essex County, New Jersey, U.S.A. **A.** Lateral view of portion of hind leg, with “a” indicating dorsal tibial ridge and “b” indicating dorsal ridge on first tarsomere. **B.** Dorsal view of distal portion of mesotibia and mesotarsus. Scale bars for all images = 0.5 mm. See text for complete voucher specimen collection data.

extended posteriorly in repose; antennomeres I–IV comprising narrowly cylindrical portion of antenna, antennomere I cylindrical, about 2× as long as wide, 1.25× as long as II; antennomere II subcylindrical, only slightly longer than wide, the shortest antennomere; antennomeres III–IV cylindrical, each 3–4× as long as wide, III about as long as IV, each nearly 2× as long as antennomere II; antennomeres V–X comprising serrate portion of antenna, each antennomere subtriangular with distal portion the widest, antennomere V about 0.75–1× as

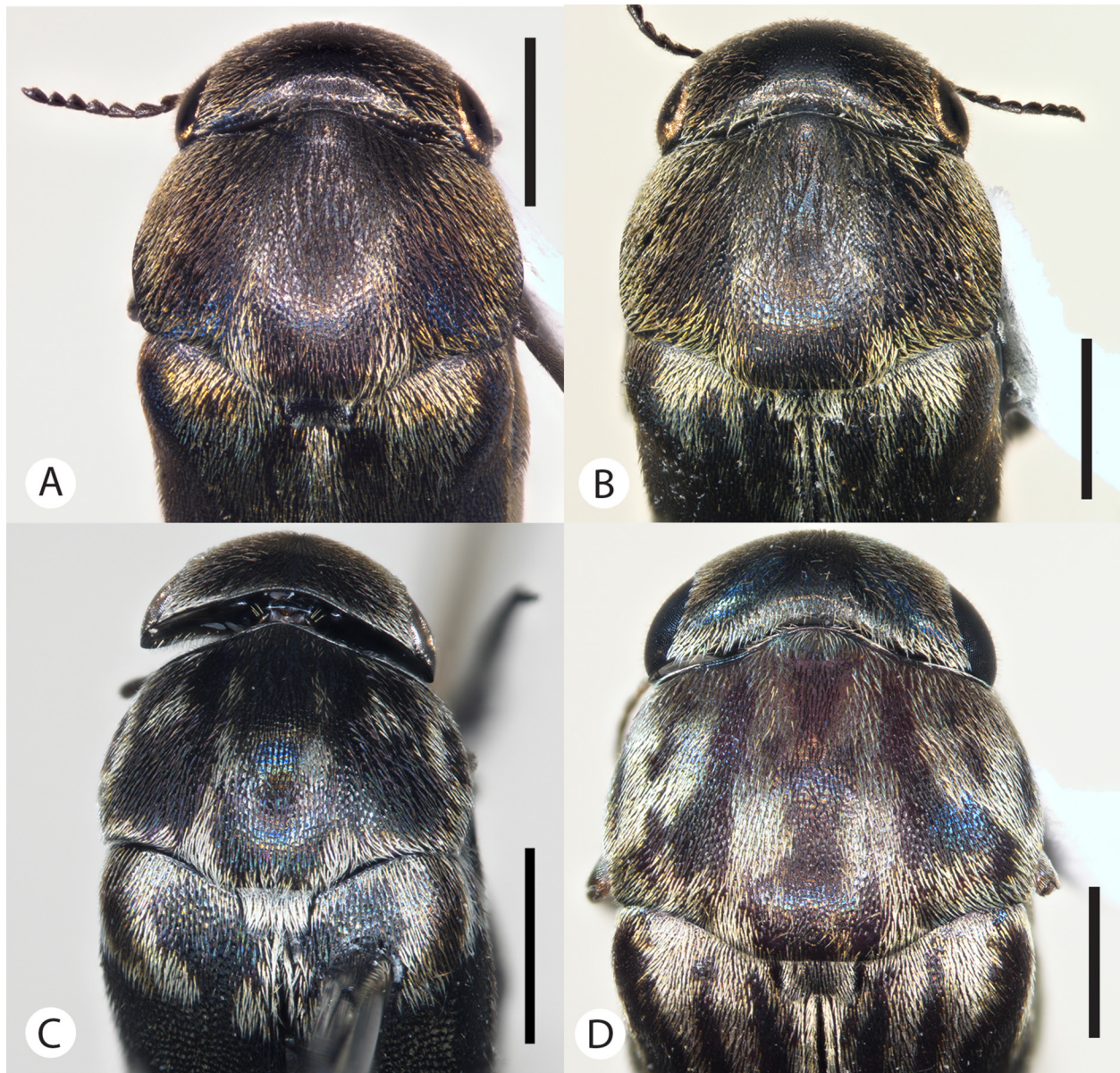


Figure 5. Pronota and adjacent portions of heads and elytra of *Tomoxia* species. **A.** *T. bucephala*, Essex County, New Jersey. **B.** *T. bucephala*, Union County, New Jersey. **C.** *T. inclusa*, Lamar County, Texas. **D.** *T. lineella*, Rockbridge County, Virginia. Scale bars for all images = 1.0 mm. Voucher specimen collection data: A—see text; B—see text; C—Texas. Lamar Co.: Camp Maxey National Guard, Powderly, 3.5 km S, 16–20 Jun 2009, J.C. Abbott (UTIC); D—Virginia. Rockbridge Co.: 0.7 km N of Fairfield, 21 Jun–14 Jul 2017, D. Heltzel, BSF# 74567 (CMNH).

long as IV, antennomere VI as long as V, antennomeres VI–X successively and gradually diminishing in length and width; antennomere XI 2.2× as long as wide, about as long as antennomere IV, antennomere body narrowly triangular, one margin projecting distally as finger-like lobe with obtuse apex, lobe about 0.25× as long as antennomere XI. *Eye*. Reaching posteriolateral margin of head, finely hairy, hairs moderately dense. *Pronotum*. Transverse, wider than elytra, widest at about middle; lateral margins evenly and gradually curved from base to apex, basal angles obtuse, basal margin with truncate lobe occupying central third, basal margin gradually anteriorly curved laterad to basal lobe; lateral margins covered with pale, golden or gray hairs; with median pair of golden or gray stripes running from base to apex, stripes often faint, space between stripes covered by dark brown

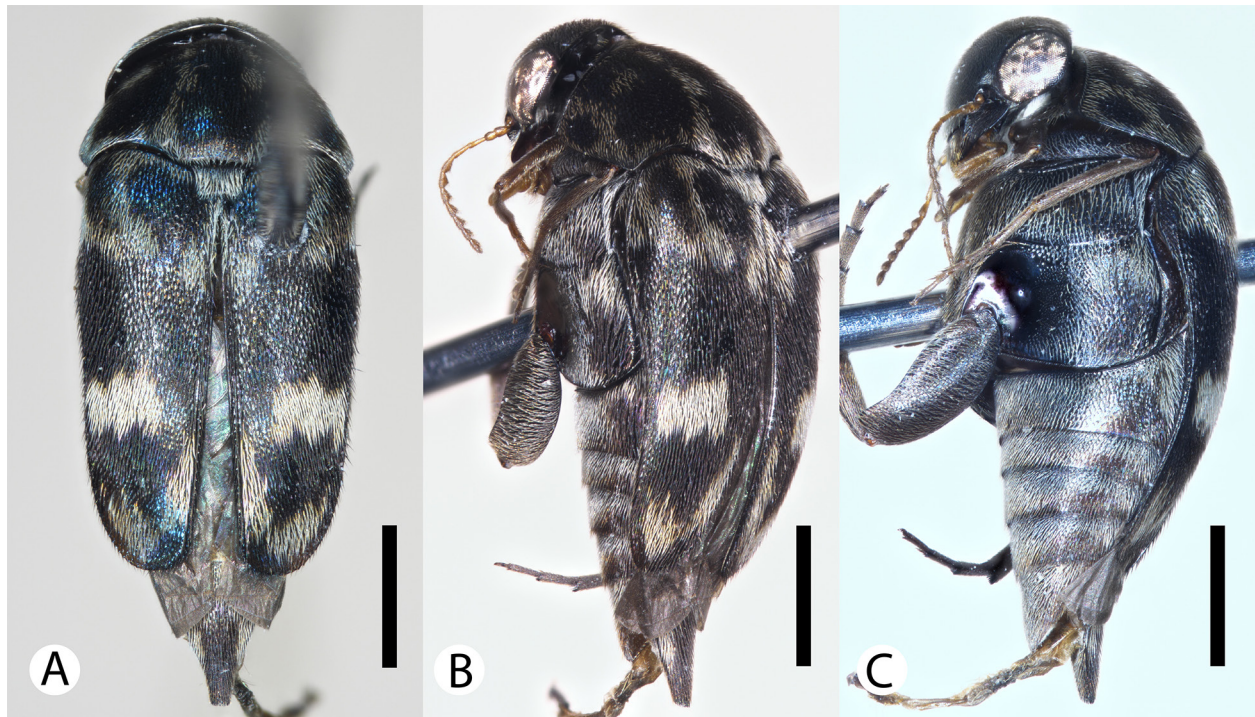


Figure 6. *Tomoxia inclusa*, aspect of museum specimen, Lamar County, Texas, U.S.A. A. Dorsal view. B. Dorso-lateral view. C. Lateral view. Scale bars for all images = 1.0 mm. Voucher specimen collection data as for Fig. 5C.



Figure 7. *Tomoxia lineella*, aspect of museum specimen, Rockbridge County, Virginia, U.S.A. A. Dorsal view. B. Dorsolateral view. C. Lateral view. Scale bars for all images = 1.0 mm. Voucher specimen collection data as for Fig. 5D.



Figure 8. Antennae of *Tomoxia* species. **A.** *T. bucephala*, Essex County, New Jersey. **B.** *T. inclusa*, Lamar County, Texas. **C.** *T. lineella*, Bronx County, New York. Scale bars for all images = 0.5 mm. Voucher specimen collection data: A—see text; B—as for Fig. 5C; C. New York. Bronx Co.: New York Botanical Garden Forest, 16–25 July 2012, E. Rivera and R. Naczi (RNC).

hairs, portions laterad to each stripe covered with golden or gray hairs to a varying extent and a dark brown patch of varying size and shape, sometimes pale hairs nearly fill this area and sometimes dark brown hairs fill all but the pale stripes at margins. *Scutellum*. Transverse, 1.5–1.8× as wide as long, posterior margin shallowly and broadly emarginate, entire surface covered with golden and/or gray hairs. *Elytra*. Each 3.9–4.4 × 0.9–1.2 mm, both elytra 2.0–2.5 mm wide at base; covered with dark brown hairs, except for the following areas covered with pale brown or pale gray or whitish hairs: along suture from base to a point 85–95% of elytral length, most of area in distal 15–20% of elytra, one suborbicular spot in medial region of each elytron between suture and lateral margin that often merges with pale hairs along suture, within an area at base just mesad to humeri that extends mesally to suture and extends obliquely from base toward suture in medial area of elytra, this basal pale area sometimes with 1–2 dark brown oblique stripes within it that parallel the oblique margin of the pale basal area; apices evenly and widely rounded from margins to suture. *Pygidium*. Widely conical, dorsally covered with golden or gray hairs in basal 35–40%, remaining portion covered with very dark brown hairs; apically truncate, microctenidiate at apical margin; 1.8–2.5× as long as hypopygium. *Venter*. Uniformly covered with golden or grayish hairs. *Mouthparts*. Terminal maxillary palpomere triangular, scalene, lateral side the longest, mesal side the shortest, apical side with sulcus spanning its length. *Legs*. Pro-, meso-, and metatibiae 0.9× as long as corresponding pro-, meso-, and metafemora; protibia 1.1–1.3× as long as protarsus, mesotibia 0.8–0.9× as long as mesotarsus, metatibia 0.6–0.7× as long as metatarsus; first metatarsomere 0.7–0.8× as long as metatibia; metatibia with apical ctenidium spanning tibial width and closely adjacent subapical ctenidium spanning about 0.25 of tibial width, metatibia with fine dorsal ridge spanning nearly entire tibial length, first metatarsomere with apical ctenidium spanning its width, first metatarsomere with fine dorsal ridge spanning nearly its entire length; metatibial apical spurs very dark brown, outer 0.5× as long as inner; claws toothed, with 3–4 teeth per claw, each tooth 0.3–0.5× as long as adjacent untoothed portion of claw at base of teeth.

Identification Key to *Tomoxia* Species Occurring in North America North of Mexico

1. Elytra with pale hairs extending along suture continuously from scutellum to 30–40% of elytral length; each elytron bearing a pale-margined lunule curving from humerus toward suture *T. inclusa* LeConte
- Elytra with pale hairs extending along suture continuously from scutellum almost to apices; elytra without humeral lunules **2**
2. Each elytron unstriped or with oblique pale stripes extending from base toward medial region but not beyond; pronotum with pair of longitudinal pale stripes in medial region (often faint) but no additional stripes or spots between medial stripes and pale pubescence along margins; profemora and first 3 antennomeres blackish or very dark brown *T. bucephala* A. Costa
- Each elytron with at least two oblique pale stripes, with at least one stripe extending from base to apical half; pronotum with pale stripes and/or spots between pair of medial stripes and pale pubescence along margins; profemora and first 3 antennomeres pale brown or medium brown, at least in part *T. lineella* LeConte

Specimens and photographs document *Tomoxia bucephala* from four North American localities (Fig. 9). The first known occurrence of *T. bucephala* is one specimen collected in a Lindgren funnel trap in Union County, New Jersey during 20 May–4 June 2015 (Fig. 3). Also in 2015, two specimens were collected in a Lindgren funnel trap in Essex County, New Jersey during 3–18 June (Fig. 2). In 2019, two specimens were collected in a Lindgren funnel trap in Passaic County, New Jersey, during 5–26 June.

All of these New Jersey occurrences are in the northeastern portion of the state, in the New York City metropolitan region. The greatest distance between any two of these occurrences, the ones in Passaic and Union counties, is 31 km (19 mi). The closest two of these occurrences, the ones in Essex and Passaic counties, are 16 km (10 mi) apart. The Essex and Union counties occurrences are 18 km (11 mi) apart.

Photographs document *Tomoxia bucephala* from southwestern Pennsylvania on 10 June 2016 (Rosenfeld 2016; Fig. 1). This occurrence is in the Pittsburgh metropolitan area, and is 480 km (300 mi) from the nearest New Jersey occurrence. John Rosenfeld submitted these photos on 10 June 2016 as unidentified. On 15 June 2016, a BugGuide community member identified them as *T. lineella*, an identification that has remained since then.

Despite the fact all known records of *Tomoxia bucephala* are from metropolitan regions, all but one of them were collected in or adjacent to wooded natural areas. The exception is the Union County, New Jersey location, which is in an industrial area, though only 0.5 km from a wooded natural area.

***Tomoxia bucephala* specimens and photographs examined. USA. NEW JERSEY: Essex Co.,** 5.1 km SW West Orange, 3–18 Jun 2015, LFT [Lindgren funnel trap], A. MacDonald and C. Miles, BSF# 61492 (CMNH-2 females). **Passaic Co.,** 5.4 km NW of Passaic, 5–26 Jun 2019, LFT, S. Limbachia, BSF# 91236 (CMNH-2 females). **Union Co.,** 1.4 km S Linden, 20 May–4 Jun 2015, LFT, K. Moore and P. Milicia, BSF# 61268 (CMNH-1 female). **PENNSYLVANIA: Allegheny Co.,** Allison Park, 10 Jun 2016, J. Rosenfeld, (BBC-1 female), photographs of this specimen when it was alive: BugGuide #1236790, 1236791, 1236792 (Rosenfeld 2016: <https://bugguide.net/node/view/1236790/bgimage>, <https://bugguide.net/node/view/1236791/bgimage>, <https://bugguide.net/node/view/1236792/bgimage>).

Searches of online specimens and photographs have revealed no additional records of *Tomoxia bucephala* for North America (BugGuide 2022; GBIF 2022; iNaturalist 2022; SCAN 2022).

Tomoxia lineella was collected in the same collecting event as the *T. bucephala* specimens from Essex County, New Jersey (*T. lineella* voucher specimen: NEW JERSEY: Essex Co., 5.1 km SW West Orange, 3–18 Jun 2015, LFT, A. MacDonald and C. Miles, BSF# 61492, CMNH-1 female). No other mordellids were collected with *T. bucephala*.

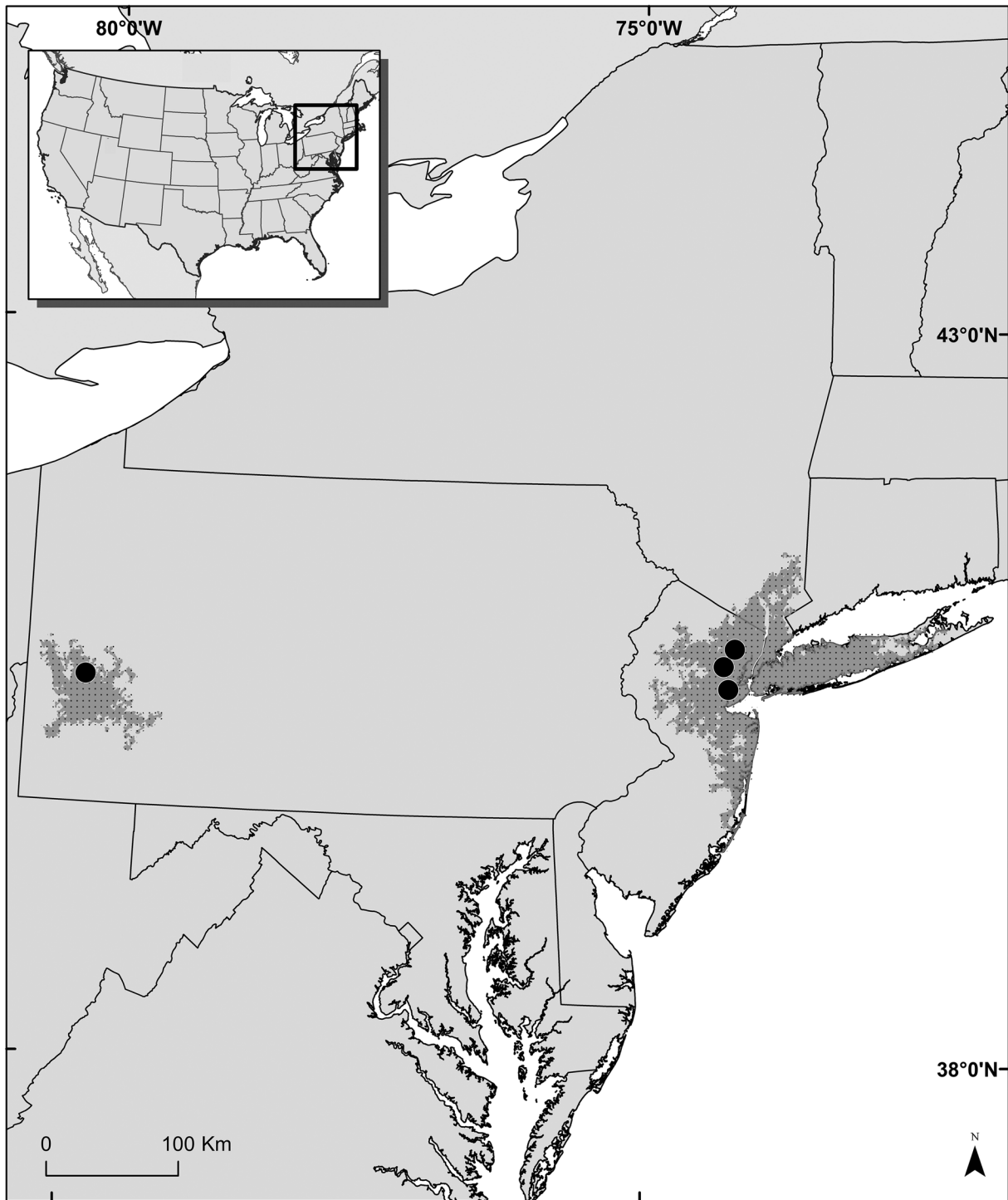


Figure 9. Map of known occurrences of *Tomoxia bucephala* in North America. Areas of heavier shading indicate metropolitan regions of New York City and Pittsburgh.

Discussion

Apparently, our reports are the first records from North America of *Tomoxia bucephala*, a tumbling flower beetle native to the Eastern Hemisphere. This is also the first report of any non-native mordellid introduced in North America (Bright 1986; Bousquet et al. 2013).

Evidence indicates that the Palearctic *Tomoxia bucephala* is now established in North America. Collections from four localities are known, all from outdoor settings. In addition, the species is documented from two separate regions: northeastern New Jersey and southwestern Pennsylvania. From this evidence, we conclude that *T. bucephala* is now established in the U.S.A. Since *T. bucephala* is non-native, appears to have established itself, and appears to be spreading in natural areas, we also consider it an invasive species. However, the degree of invasiveness (mild, moderate, or severe) of *T. bucephala* is unknown.

Is the introduction and invasion of the non-native *Tomoxia bucephala* likely to have a significant economic and ecological impact in North America? Since *T. bucephala* feeds on dead trees that have decayed sufficiently to host wood-decaying fungi, it is unlikely that this species will have an appreciable economic impact in North America. In order to answer the question about ecological impact, it is necessary to consider its potential for invasion and its potential for interactions with native insect species, especially its congeners in North America, *T. inclusa* and *T. lineella*.

The larvae of *Tomoxia inclusa* and *T. lineella* develop in dead deciduous trees, like *T. bucephala* larvae. Brimley (1951) reported seeing *T. inclusa* emerging from dead basswood (*Tilia americana* L., Malvaceae), and Downie and Arnett (1996) reported *T. inclusa* beat from dead hardwood limbs. Authors have reported *T. lineella* from several genera and families of dead trees: *Acer saccharum* Marshall, Sapindaceae; *Carya* sp., Juglandaceae; *Fagus grandifolia* Ehrh., Fagaceae; *Fraxinus* sp., Oleaceae; *Tilia americana*; *Ulmus* sp., Ulmaceae (Dury 1893; Frost 1913; Liljeblad 1945; Brimley 1951; Downie and Arnett 1996). Lisberg and Young (2003) collected and reared for identification larvae of *T. lineella* from *Populus grandidentata* Michx. (Salicaceae).

From what is known about the biology of native *Tomoxia* species, it is evident that *T. lineella* is a generalist in its larval stage, completing its larval development in a great diversity of dead, decaying deciduous trees. In these aspects of their ecologies, *T. bucephala* and *T. lineella* are similar. Probably due to its relative rarity, too little is known about the biology of *T. inclusa* to reach the same conclusion, except its larvae also develop in dead deciduous trees.

Tomoxia lineella and *T. inclusa* have large geographic ranges. *Tomoxia lineella* is known from Nova Scotia west to Saskatchewan, south to Florida and Iowa (Dozier 1918; Liljeblad 1945; Bright 1986; Downie and Arnett 1996; Majka and Jackman 2006; Bousquet et al. 2013). The known range of *T. inclusa* is New Brunswick west to Ontario, south to Florida and Texas (Liljeblad 1945; Bright 1986; Downie and Arnett 1996; Webster et al. 2012; Bousquet et al. 2013).

Since *Tomoxia bucephala* and *T. lineella* are wide-ranging ecological generalists with very similar niches, it is reasonable to expect that *T. bucephala* will continue its invasion of North America. Possibly, *T. bucephala* will expand its geographic range to occupy much of the range of *T. lineella*. It is also possible that *T. bucephala* will compete with *T. lineella* and other saproxylic insects with similar biologies. Collection of *T. bucephala* and *T. lineella* from the same locality in Essex County, New Jersey and during the same time period indicate that interaction between these two species is probably already underway. What effect *T. bucephala* will have on communities of native saproxylic insects is unknown but will be worth studying, especially the prospect of competition between *T. bucephala* and *T. lineella* and *T. inclusa*.

The year of earliest known collection of *Tomoxia bucephala* in North America, 2015, suggests a recent introduction. However, the under-collected nature of mordellids particularly and of small beetles generally makes it quite likely that this species has been present in North America longer than we realize.

The relatively great distance (480 km/300 mi) between the two regions of known occurrences, the New York City and Pittsburgh metropolitan areas, raises the possibility that separate introductions of *Tomoxia bucephala* have occurred. Alternatively, it is possible that detection of *T. bucephala* has lagged sufficiently behind its introduction and spread, and that it occurs in intervening areas between New York City and Pittsburgh. Surveys in intervening areas that target *T. bucephala* would be helpful in addressing these questions.

The mode of introduction of *Tomoxia bucephala* to the U.S.A. is uncertain. The fact all known localities are in the metropolitan areas of major cities suggests the introduction may have been related to international trade or horticulture, both of which are frequent means of introduction of non-native insects (Meurisse et al. 2019). The polyphagous nature of *T. bucephala* larvae probably served as an advantage in its establishment in North America, and polyphagy has been recognized as an apparent advantage in establishment of non-native insects generally (Aukema et al. 2010). However, no information is available at this time to implicate a pathway of introduction for *T. bucephala*.

Two programs are noteworthy for their essential roles in the detection of *Tomoxia bucephala* in North America: the Biodiversity Services Facility of the Carnegie Museum of Natural History (BSF) and BugGuide. The BSF retains, processes, labels, and makes available for study numerous beetle specimens that are bycatch of pest-monitoring traps throughout eastern U.S.A. (McElrath et al. 2016; Androw 2021). During a typical season, RAA receives on average 8,000 raw Lindgren funnel trap samples to screen for exotic pest species. During the screening process, a wide variety of bycatch taxa are extracted for preparation, identification, and eventual deposition in the CMNH collection. In many cases, these non-target specimens would be discarded by other screening agencies. These specimens are primarily native taxa from nearly all North American coleopteran families, as well as many other orders. Though choosing which specimens will be prepared for deposition is a subjective process, a routine has developed. Specimens of lineages of personal interest to staff members are routinely selected. Taxa representing lineages that are poorly represented in the CMNH collection are chosen to expand those holdings. Species known to be uncommon or rare are always extracted.

One of the most important opportunities for the BSF is to gain access to a specialist for identification of a group for which no expertise exists within the Carnegie staff—and this is often the motivation to review a taxon more exhaustively, as is the case of Mordellidae. Prior to 2018, mordellids were selected somewhat casually, but once access to the expertise of RN was gained, Mordellidae was declared a “target” taxon and nearly all specimens were extracted, prepared, and sent for identification. It is within these mixes of undetermined bycatch specimens from the BSF program that new records emerge, as in the present case, by which the BSF program brought to light the first specimens of *Tomoxia bucephala* known to have been collected from the wild in North America.

BugGuide is an online repository for a growing number of photographs of arthropods submitted by community scientists and experts (BugGuide 2022). Most of the photographs are of species in the field or collected from the field for photography. BugGuide provides major advantages for discovering introductions of non-native species, range extensions of natives, and undescribed species because of ease of access to a large collection of photographs of the majority of beetle species from throughout the U.S.A. and Canada. In the present example, photos on BugGuide document the presence of a living specimen of *Tomoxia bucephala* from a region distant from the BSF specimens, and thus provide evidence for the establishment of the species in North America.

Both BSF and BugGuide have previously enabled detection of non-native beetle species in North America (e.g., Moyer 2010; McElrath et al. 2016; Androw 2021). With such past examples and the present one of *Tomoxia bucephala*, both BSF and BugGuide clearly manifest much potential to continue enabling important discoveries in the North American beetle fauna.

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