

ZOOTAXA

5508

One must imagine Sisyphus happy: Integrative taxonomic characterization of 22 new *Ceroptres* species (Hymenoptera: Cynipidae: Ceroptresini)

LOUIS F. NASTASI¹, CECIL N. SMITH¹, CHARLES K. DAVIS¹, ANNA K.G. WARD², GUERIN BROWN², Y. MILES ZHANG³, SHANNON ROLLINS⁴, CHRIS FRIESEN⁵, CARLY M. TRIBULL⁴, ANDREW A. FORBES² & ANDREW R. DEANS¹

¹Frost Entomological Museum, Department of Entomology, The Pennsylvania State University, University Park, Pennsylvania, USA, 16802.

LFN-email:  lfnastasi@gmail.com,  <https://orcid.org/0000-0001-7825-480X>

CNS-email:  cecilsmith109@gmail.com,  <https://orcid.org/0009-0003-2835-3377>

CKD-email:  ckd5444@psu.edu,  <https://orcid.org/0000-0001-6056-3903>

ARD-email:  ard19@psu.edu,  <https://orcid.org/0000-0002-2119-4663>

²Department of Biology, University of Iowa, Iowa City, Iowa, USA, 52242

AKGW-email:  annakgward@gmail.com,  <https://orcid.org/0000-0003-0251-346X>

GB-email:  guerin-brown@uiowa.edu,  <https://orcid.org/0009-0007-4466-5601>

AAF-email:  andrew-forbes@uiowa.edu,  <https://orcid.org/0000-0001-8332-6652>

³Institute of Evolutionary Biology, University of Edinburgh, Edinburgh, Scotland, United Kingdom.

email:  yuanmeng.zhang@gmail.com,  <https://orcid.org/0000-0003-4801-8624>

⁴Biology Department, Farmingdale State College – State University of New York, Farmingdale, New York, USA, 11735.

email:  srollins1@unm.edu,  <https://orcid.org/0009-0005-7014-9999>

email:  tribulc@farmingdale.edu,  <https://orcid.org/0000-0002-1044-0486>

⁵Manitoba Conservation Data Centre, Winnipeg, Manitoba, Canada.

email:  chris.friesen@gov.mb.ca,  <https://orcid.org/0000-0002-8180-8508>



Magnolia Press
Auckland, New Zealand

LOUIS F. NASTASI, CECIL N. SMITH, CHARLES K. DAVIS, ANNA K.G. WARD, GUERIN BROWN, Y. MILES ZHANG, SHANNON ROLLINS, CHRIS FRIESEN, CARLY M. TRIBULL, ANDREW A. FORBES & ANDREW R. DEANS

One must imagine Sisyphus happy: Integrative taxonomic characterization of 22 new *Ceroptres* species (Hymenoptera: Cynipidae: Ceroptresini)

(*Zootaxa* 5508)

63 pp.; 30 cm.

17 Sept. 2024

ISBN 978-1-77973-153-1 (paperback)

ISBN 978-1-77973-154-8 (Online edition)

FIRST PUBLISHED IN 2024 BY

Magnolia Press

P.O. Box 41-383

Auckland 1041

New Zealand

e-mail: magnolia@mapress.com

<https://www.mapress.com/zt>

© 2024 Magnolia Press

All rights reserved.

No part of this publication may be reproduced, stored, transmitted or disseminated, in any form, or by any means, without prior written permission from the publisher, to whom all requests to reproduce copyright material should be directed in writing.

This authorization does not extend to any other kind of copying, by any means, in any form, and for any purpose other than private research use.

ISSN 1175-5326 (Print edition)

ISSN 1175-5334 (Online edition)

Table of Contents

Abstract	4
Introduction	4
Materials and methods	5
Specimen collection, rearing, and examination	5
Taxonomy	5
Morphological description and examination	6
Specimen imaging	6
Results	6
Key to Females of North American species of <i>Ceroptres</i>	7
New species of <i>Ceroptres</i> Hartig, 1840	11
<i>Ceroptres anansii</i> Nastasi, Smith, & Davis sp. nov.	11
<i>Ceroptres anzui</i> Nastasi, Smith, & Davis sp. nov.	13
<i>Ceroptres bruti</i> Nastasi, Smith, & Davis sp. nov.	14
<i>Ceroptres curupira</i> Nastasi, Smith, & Davis sp. nov.	16
<i>Ceroptres daleki</i> Nastasi, Smith, & Davis sp. nov.	18
<i>Ceroptres dandoi</i> Nastasi, Smith, & Davis sp. nov.	20
<i>Ceroptres demerzelae</i> Nastasi, Smith, & Davis sp. nov.	22
<i>Ceroptres iktomii</i> Nastasi, Smith, & Davis sp. nov.	24
<i>Ceroptres jabbai</i> Nastasi, Smith, & Davis sp. nov.	25
<i>Ceroptres jarethi</i> Nastasi, Smith, & Davis sp. nov.	27
<i>Ceroptres lokii</i> Nastasi, Smith, & Davis sp. nov.	29
<i>Ceroptres lupini</i> Nastasi, Smith, & Davis sp. nov.	32
<i>Ceroptres mallowi</i> Nastasi, Smith, & Davis sp. nov.	34
<i>Ceroptres promethei</i> Nastasi, Smith, & Davis sp. nov.	36
<i>Ceroptres sandiegoae</i> Nastasi, Smith, & Davis sp. nov.	38
<i>Ceroptres selinae</i> Nastasi, Smith, & Davis sp. nov.	40
<i>Ceroptres soloi</i> Nastasi, Smith, & Davis sp. nov.	41
<i>Ceroptres songae</i> Nastasi, Smith, & Davis sp. nov.	43
<i>Ceroptres swiperi</i> Nastasi, Smith, & Davis sp. nov.	45
<i>Ceroptres thrymi</i> Nastasi, Smith, & Davis sp. nov.	46
<i>Ceroptres tikoloshei</i> Nastasi, Smith, & Davis sp. nov.	48
<i>Ceroptres zorroi</i> Nastasi, Smith, & Davis sp. nov.	50
New records of described <i>Ceroptres</i> species	51
<i>Ceroptres cornigera</i> Melika & Buss, 2002 and <i>C. frondosae</i> Ashmead, 1896	51
<i>Ceroptres ensiger</i> (Walsh, 1864)	54
<i>Ceroptres lanigerae</i> Ashmead, 1885	55
<i>Ceroptres pisum</i> (Osten Sacken, 1861)	56
<i>Ceroptres</i> cf. <i>quercusobtusilobae</i> (Karsch, 1880)	56
Discussion	56
<i>Host use in Ceroptres</i>	56
<i>Association of Ceroptres with cecidomyiid midges (Diptera: Nematocera)</i>	57
<i>Species richness of Nearctic Ceroptres</i>	58
<i>Recommendations for future work on Ceroptres</i>	59
Acknowledgments	59
References	61

Abstract

We describe new species in the genus *Ceroptres* Hartig, 1840 (Hymenoptera: Cynipidae: Ceroptresini) represented by voucher material sequenced by Ward *et al.* (2024). We describe 22 new species, all authored by Nastasi, Smith, & Davis: *C. anansii* sp. nov., *C. anzui* sp. nov., *C. bruti* sp. nov., *C. curupira* sp. nov., *C. daleki* sp. nov., *C. dandoi* sp. nov., *C. demerzelae* sp. nov., *C. iktomii* sp. nov., *C. jabbai* sp. nov., *C. jarethi* sp. nov., *C. lokii* sp. nov., *C. lupini* sp. nov., *C. mallowi* sp. nov., *C. promethei* sp. nov., *C. sandiegoae* sp. nov., *C. selinae* sp. nov., *C. soloi* sp. nov., *C. songae* sp. nov., *C. swiperi* sp. nov., *C. thrymi* sp. nov., *C. tikoloshei* sp. nov., and *C. zorroi* sp. nov. After our taxonomic treatment, the genus *Ceroptres* includes 43 species, all but three of which are known from North America. Among our new species are two reared from cecidomyiid midge galls, an association previously recorded but without valid taxonomic association. We provide new records for two additional previously described species; we record *C. ensiger* (Walsh, 1864) from Pennsylvania and confirm characters for the male, and we record *C. lanigerae* Ashmead, 1885 from Texas. We also examined several putative species corresponding to either *C. cornigera* Melika & Buss, 2002 and/or *C. frondosae* Ashmead, 1896, which we regard as a species complex that requires elucidation in future studies. To enable further studies on *Ceroptres*, we provide an updated key to North American females. Overall, we find that species of *Ceroptres* are host specialists associated with a single host gall species or several galls that are phylogenetically or ecologically related. We suggest that there are many North American species of *Ceroptres*, possibly hundreds, still awaiting collection and characterization.

Key words: agastoparasitism, Cecidomyiidae, Cynipini, gall, inquiline

“Sisyphus teaches the higher fidelity that negates the gods and raises rocks. He too concludes that all is well. This universe now without a master seems to him neither sterile nor fertile. Each atom of that stone, each mineral flake of this mountain full of night, alone forms a world. The struggle itself to the heights is enough to fill a man’s heart. One must imagine Sisyphus happy.”

—Albert Camus, *The Myth of Sisyphus*

Introduction

Just as Sisyphus may find fulfillment in eternally rolling a boulder up a mountain, the escapade of describing biodiversity is invigorating to the systematist. Systematists are continually tasked with characterizing the incredible diversity of life on Earth, only to find that there are *always* more taxa to sample and describe. This trend is exemplified by modern strides in systematics of Cynipoidea (Hymenoptera); monographic taxon treatments and user-friendly keys (e.g., van Noort *et al.* 2015, Lobato-Vila & Pujade-Villar 2019, 2021, Buffington *et al.* 2020, van Noort 2024, Nastasi *et al.* 2024a) have greatly bolstered the accessibility of the world fauna and described many new taxa. However, in so doing, these studies have alerted the cynipoid community to a still-enormous diversity of undescribed cynipoid wasps. This is especially true of the inquiline gall wasps, particularly Ceroptresini and Synergini (Hymenoptera: Cynipidae); there were only around 140 described species in these tribes as recently as 2006 (Melika 2006), but around 250 species are currently known (Buffington *et al.* 2020, Lobato-Vila & Pujade-Villar 2019, 2021, Lobato-Vila *et al.* 2022), representing a nearly twofold increase of known species in under two decades. This observation is further underscored by the idea that many cynipoid researchers *still* consider the inquiline gall wasps to be poorly studied (Lobato-Vila & Pujade-Villar 2019, 2021, Buffington *et al.* 2020, Fang *et al.* 2020, Ward *et al.* 2020, 2024, Yang *et al.* 2020).

Because of inquilines’ bizarre life history, which for most species involves developing as obligate residents inside galls induced by other cynipids (Askew 1984, Ronquist 1994), numerous recent studies have aimed to understand their phylogeny and evolution (Ronquist *et al.* 2015, Blaimer *et al.* 2020, Gobbo *et al.* 2020, Ward *et al.* 2020, Lobato-Vila *et al.* 2022, Hearn *et al.* 2023, Ward *et al.* 2024). The most recent of these works, Ward *et al.* (2024), aimed to understand patterns of coevolution between two genera of inquilines (*Ceroptres* Hartig, 1840 and *Synergus* Hartig, 1840) and their gall wasp hosts in North America. The authors attempted to identify their reared specimens of *Ceroptres* but were unable to match their material to named species in the most recently published revision of the group (Lobato-Vila & Pujade-Villar 2019). We find that their difficulties are not due to insufficiencies in this revision but are rather the result of Ward *et al.* sampling almost exclusively undescribed species of *Ceroptres*.

The present study aims to elucidate the species identity of Ward *et al.* (2024)’s voucher material, which is deposited

at PSUC (Frost Entomological Museum, The Pennsylvania State University, University Park, Pennsylvania, USA). We apply an integrative taxonomic approach by considering morphology and ecology of their voucher material in combination with Ward *et al.*'s molecular analyses of DNA barcode and ultraconserved element (UCE) data, finding their vouchers to comprise 22 species new to science which we describe here. While Ward *et al.*'s molecular species delimitation suggested either 36 or 47 species altogether, vouchers were not available for all of their putative species. We also provide novel records of *Ceroptres* from Canada; only one *Ceroptres* species (*C. petiolicola* Osten-Sacken, 1861) has been previously reported from Canada (Nastasi & Deans 2021), but we report here two newly described species from the country as well as members of a putative species complex (see treatment of *cornigera/frondosae* complex).

The present study does not constitute a comprehensive effort to revise *Ceroptres*. Instead, we aim to prepare the genus for a more intensive taxonomic revision by describing species on which data has already been published, synthesizing available knowledge relating to the genus, and by highlighting several outstanding areas that warrant further investigation. To best prepare *Ceroptres* for continuing taxonomic work, we provide an updated key to North American females.

Materials and methods

Specimen collection, rearing, and examination

We primarily studied *Ceroptres* specimens that were reared from galls on oaks (Fagaceae: *Quercus* subgenus *Quercus*) during broader studies of cynipoid biodiversity in North America (Ward *et al.* 2020, 2022a, 2022b, 2024); full information relating to the rearing of these specimens is detailed in the original studies. In short, wasps collected during these efforts were reared by placing field-collected galls in incubators and collecting emerging insects into ethanol at regular intervals. The material we studied here also includes new *Ceroptres* specimens reared during other efforts to collect gall wasps, especially collecting efforts in Centre County, Pennsylvania (USA) and the surrounding region; these specimens were treated similarly but were not placed in incubators. Instead, these individuals were reared from galls stored in a barn with no climate control, to induce environmental conditions as close to natural systems as possible.

Specimens we examined, including all sequence vouchers, are deposited at PSUC (Frost Entomological Museum, Department of Entomology, The Pennsylvania State University, University Park, Pennsylvania, USA) unless otherwise stated. We deposited paratypes of several species at USNM (United States National Museum of Natural History, Washington, DC, USA), which are indicated in the material examined sections. Using Darwin Core biodiversity data standards (Wieczorek *et al.* 2012), we digitized label data of all specimens that we examined. Digitized specimen data for all individuals we examined are available in Supplemental File 1.

Taxonomy

We primarily examined *Ceroptres* specimens from which DNA was extracted for phylogenetic analyses by Ward *et al.* (2024), although we also examined abundant additional *Ceroptres* wasps we reared. We keyed all individuals using Lobato-Vila & Pujade-Villar (2019), carefully checking each character at each couplet to check for possible species identification. For the vast majority of individuals, we found they failed to key to any described species, leading us to conclude that they instead belong to undescribed species. In the few cases where we believed the specimen to represent a known species, we critically evaluated Lobato-Vila & Pujade-Villar's diagnoses, descriptions, figures, and biological data to ensure that we were confident in assigning the material to a known species concept. We discuss cases in which we believed material could belong to a known species but could not definitively confirm their identity in our results under "New records of described *Ceroptres* species" along with records that we definitively matched to known species.

We found several putative new species among Ward *et al.*'s vouchers that were represented only by males. We described new species only for putative species with females, as many diagnostic characters for *Ceroptres* are only applicable to females coupled with the fact that males are known only for seven of the 19 *Ceroptresini* previously

described from North America (Lobato-Vila & Pujade-Villar 2019). In the case of *Ceroptres jabbai* sp. nov., we examined unsequenced females and males that we reared from the same host galls (*Kokkocynips* spp.) that matched Ward *et al.*'s male sequence vouchers, allowing us to describe that species.

Given that *Ceroptres* are believed to be inquilines in other insect galls, we have named our new species after “inquilines” in a broad sense, including fictional, folkloric, and mythological individuals that we consider to be usurpers, thieves, traitors, tricksters, or other similar archetypes.

Morphological description and examination

Our selection of morphological characters is composed of important diagnostic characters treated by Lobato-Vila & Pujade-Villar (2019), who drew many of their characters from Liljeblad & Ronquist (1998) and Melika (2006). We deviate slightly from their terminology, instead referencing the Hymenoptera Anatomy Ontology (Yoder *et al.* 2010) and the Phenotype and Trait Ontology (PATO Curators 2023) in preparing phenotypic descriptions of adult *Ceroptres* wasps. We refer to the cell on the fore wing delimited by the R1 and Rs veins as the marginal cell rather than the radial cell, following some recent conventions in the cynipoid literature (e.g., Buffington *et al.* 2020, Nastasi *et al.* 2024a, 2024b). Terms relating to description of cuticular sculpture follow Harris (1979) and the corresponding treatment by Melika (2006). We use the following abbreviations to refer to the dimensions of the ocellar triangle, including the abbreviation DLO that is absent from the above sources:

- DLO: greatest measurable diameter of either lateral ocellus;
- LOL: distance between the medial ocellus and either lateral ocellus;
- OOL: distance between either lateral ocellus and the corresponding compound eye;
- POL: distance between the two posterior ocelli.

We performed morphological observations and took measurements of mounted specimens using an Olympus SZX16 stereo microscope (Olympus Life Science, Tokyo, Japan) fitted with an optical micrometer. We used a gooseneck illuminator fitted with mylar strips to diffuse light, which was primarily needed for discerning patterns of cuticular sculpture.

We compared material of our new species to additional specimens we reared, Lobato-Vila & Pujade-Villar's (2019) key and descriptions, and available identified material of described *Ceroptres* deposited at USNM.

Given that males aren't known for the majority of *Ceroptres* species, diagnoses in the below taxon treatments refer explicitly to females unless otherwise stated.

Specimen imaging

We took images of point-mounted or card-mounted adult wasps using a Macroscopic Solutions 'Macropod microkit' (Tolland, CT). We stacked images using Zerene Stacker LLC (Richland, WA). We edited images and prepared plates using Adobe Photoshop and Adobe Illustrator (Adobe Inc.). Our figures are also available online at additional higher resolutions (<https://doi.org/10.26207/xxg2-cm48>).

We found the patterns of punctation occurring on the metasomal tergites challenging to photograph effectively. As a result, to ensure clarity of this important diagnostic character, we prepared illustrations of the third metasomal tergite based on holotype females of new species using Adobe Illustrator.

Results

Prior to our study, Ceroptresini included 22 valid species placed in two genera, including 21 species of *Ceroptres* and one species of *Buffingtonella* Lobato-Vila & Pujade-Villar, 2019 (Lobato-Vila & Pujade-Villar 2019). Of the known *Ceroptres* fauna, 18 described species are known from the Nearctic (Lobato-Vila & Pujade-Villar 2019, Nastasi & Deans 2021). We describe 22 new species of *Ceroptres*; after our study, the Nearctic *Ceroptres* fauna now includes 40 species, the global *Ceroptres* fauna now includes 43 species, and the global fauna of the tribe Ceroptresini now includes 44 species. We present an overview of our new species in Table 1 below.

TABLE 1. Overview of Ward *et al.*'s (2024) *Ceroptres* vouchers examined in this study. “Our species” refers to species names designated in the present study; “Ward *et al.* final species assignment” refers to the corresponding species number used in the phylogenetic trees and elsewhere in Ward *et al.* All host galls are those of Cynipini (Hymenoptera: Cynipidae) unless otherwise stated. Species with asterisks (*) represent species that we split relative to hypotheses provided by Ward *et al.* Species with a cross (†) were represented only by unsequenced vouchers from Ward *et al.* but are distinct on the basis of morphological and ecological data; these species also have “N/A” in the “Ward *et al.* final species assignment” column as “final species” numbers were assigned only to species included in their molecular phylogenetic analyses. Hosts reported in the table and our taxonomic treatments refer only to host records from preserved voucher specimens.

Our species	Ward <i>et al.</i> final species assignment	Host(s)
<i>anansii</i> sp. nov.	10	<i>Melikaiella tumifica</i> on <i>Q. rubra</i> and <i>Q. velutina</i>
<i>anzui</i> sp. nov.	COI-K	<i>Melikaiella ostensackeni</i> on <i>Q. palustris</i>
<i>bruti</i> sp. nov.	COI-G	<i>Callirhytis clavula</i> on <i>C. alba</i>
<i>curupira</i> sp. nov.*	3 (in part)	<i>Melikaiella ostensackeni</i> on <i>Q. palustris</i>
<i>daleki</i> sp. nov.	COI-D	<i>Polystepha pilulae</i> (Cecidomyiidae) on <i>Q. imbricaria</i>
<i>dandoi</i> sp. nov.†	N/A	<i>Neuroterus tantulus</i> on <i>Q. alba</i>
<i>demerzelae</i> sp. nov.	7-8-9	<i>Melikaiella ostensackeni</i> on <i>Q. palustris</i> , <i>Q. rubra</i> , and <i>Q. velutina</i>
<i>iktomii</i> sp. nov.	23	<i>Druon ignotum</i> on <i>Q. macrocarpa</i> and <i>Neuroterus saltarius</i> on <i>Q. bicolor</i> and <i>Q. macrocarpa</i>
<i>jabbai</i> sp. nov.	COI-C	<i>Kokkocynips decida</i> , <i>K. imbricariae</i> , and <i>K. rileyi</i> on <i>Q. rubra</i>
<i>jarethi</i> sp. nov.	6b	<i>Callirhytis quercusgemmaria</i> on <i>Q. rubra</i>
<i>lokii</i> sp. nov.	26, 28, and COI-E	<i>Philonix nigra</i> and <i>Acraspis</i> spp. on white oaks
<i>lupini</i> sp. nov.*	3 (in part)	<i>Melikaiella ostensackeni</i> and <i>Zopheroteras sphaerula</i> on <i>Q. rubra</i>
<i>mallowi</i> sp. nov.	15-16	<i>Callirhytis quercusfutilis</i> on <i>Q. alba</i>
<i>promethei</i> sp. nov.*	20 (in part)	<i>Andricus dimorphus</i> on <i>Q. bicolor</i> and <i>Q. macrocarpa</i> and <i>A. nigricens</i> on <i>Q. bicolor</i>
<i>sandiegoae</i> sp. nov.	25	<i>Phylloteras rubinum</i> on <i>Q. alba</i>
<i>selinae</i> sp. nov.	COI-H	<i>Callirhytis quercuspunctata</i> on <i>Q. rubra</i>
<i>soloi</i> sp. nov.	30b	<i>Neuroterus floccosus</i> and <i>N. quercusverrucarum</i> on <i>Q. alba</i> and <i>macrocarpa</i>
<i>songae</i> sp. nov.†	N/A	<i>Polystepha pilulae</i> (Cecidomyiidae) on <i>Q. falcata</i>
<i>swiperi</i> sp. nov.*	20 (in part)	<i>Andricus dimorphus</i> on <i>Q. macrocarpa</i>
<i>thrymi</i> sp. nov.	COI-B	<i>Bassetia flavipes</i> on <i>Q. bicolor</i>
<i>tikoloshei</i> sp. nov.	18-19	<i>Callirhytis quercusfutilis</i> on <i>Q. alba</i> and <i>Q. macrocarpa</i>
<i>zorroi</i> sp. nov.	17	<i>Neuroterus quercusirregularis</i> on <i>Q. stellata</i>
cf. <i>obtusilobae</i>	31	<i>Andricus quercuspetiolicola</i> on <i>Q. stellata</i>
<i>lanigerae</i>	COI-A	<i>Druon quercuslanigerum</i> on <i>Q. fusiformis</i>
<i>cornigera</i> / <i>frondosae</i> complex	Various (see text)	Various (see text)

Key to Females of North American species of *Ceroptres*

Our key is based in part on the taxon treatments and key given by Lobato-Vila & Pujade-Villar (2019) for previously described species. We found the previous key’s reliance on the vertical facial carinae to be rather challenging, especially in the absence of SEM (scanning electron microscope) imaging. Despite this, the utility of the facial carinae in species diagnosis cannot be ignored, and characters relating to the facial carinae are still included in our key where especially useful. Similarly, given that male *Ceroptres* appear somewhat rare, are known only for several species, and (when known) appear somewhat distinct in relation to the morphology of females, we found it much

more practical to provide a key only for females. We have structured our key such that more easily recognizable species key out toward the beginning while species requiring more challenging diagnostic characters (especially fine ratios concerning the malar space, ocellar triangle, antennomeres, and marginal cell) cluster toward the end.

To best determine the applicability of this key to a specimen on hand, one should consult the key to superfamilies in *Hymenoptera of the World* (Goulet & Huber 1993) and then that of Nastasi *et al.* (2024a), who key the North American tribes and genera of Cynipidae *sensu lato*. Alternatively, one could instead reference the key to families and tribes of Cynipoidea in Buffington *et al.* (2020), and then the key to genera provided by Lobato-Vila & Pujade-Villar (2019). To determine whether a *Ceroptres* is a female, one should count the number of antennomeres (12 or 13 in females; 14 or 15 in males where known), and/or examine the metasoma for the presence of the ovipositor and associated structures.

We highly recommend the use of good light diffusion, to best assess characters such as surface sculpture. Additional considerations for observing important morphological characters are given in our Methods. Readers should consult Lobato-Vila & Pujade-Villar's 2019 revision for additional figures of previously described species.

Despite our description of many new species of *Ceroptres* from North America, our observations of additional material and in rearing galls suggest a large fauna of *Ceroptres* is still awaiting description (see Discussion). As a result, some specimens may not route perfectly through the below key to species and may still represent undescribed species. Additionally, we include known biological data throughout the key, although we caution users of this key to consider that their specimens could entirely correspond to species still unknown to science or represent new host associations.

1. Notauli complete, distinctly impressed across more or less entire length of mesoscutum (Fig. 12D). Face with yellowish coloration only around oral fovea (Fig. 12A). Third metasomal tergite with distinct patch of posterodorsal punctures and with at least a narrow band of punctures continuing at least for a short distance along posterior margin (Fig. 12G). Inquilines of *Acraspis* or *Philonix* on white oaks **2**
- Notauli incomplete (e.g., Figs 5E, 13E, 15E); usually with notauli strongly impressed only in posterior half of mesoscutum (Figs 5E, 15E), but occasionally indistinct only in anterior third of mesoscutum (Fig. 13E). Face uniformly colored throughout and never with apparent yellowish coloration (e.g., Fig. 1B). Third metasomal tergite with punctuation variable (e.g., Figs 2G, 4G, 9G, 13G); usually not as described above (other species matching the above punctuation pattern route toward couplet 12). Inquilines of other hosts on various oaks **3**
2. Third metasomal tergite with punctate patch extending laterally for a long distance along posterior margin (Fig. 12G). Apical flagellomere no longer than 3.2× as long as wide. Inquilines of other *Acraspis* or *Philonix* on various white oaks including *Q. alba* **lokii sp. nov.**
- Third metasomal tergite with punctuation continuing for a shorter distance laterally along posterior margin (Fig. 25F). Apical flagellomere 3.7× as long as wide. Inquilines of *Acraspis pezomachoides*² on *Quercus alba*. **pisum (Osten-Sacken, 1861)**
3. Mesopleuron with conspicuous alutaceous sculpture anteriorly and/or ventrally (Fig. 5G). Usually inquilines of Cecidomyiidae (Diptera); one species associated with *Andricus quercuspetiolicola* on *Quercus bicolor* **4**
- Mesopleuron entirely smooth and shining, without any perceptible sculpture (e.g., Figs 1A, 3A). Inquilines of Cynipini only **6**
4. Malar space very short, 0.3× as long as compound eye (Fig. 19B). Mesoscutum finely coriaceous to alutaceous (Fig. 19E). Body very small; holotype 1.5 mm in length (Fig. 19A). Antennae 12-segmented (Fig. 19A). Inquilines in galls of *Polystepha pilulae* on *Quercus falcata* **songae sp. nov.**
- Malar space longer, 0.5× as long as compound eye (Fig. 5B). Mesoscutum more strongly coriaceous (Fig. 5E). Body larger; 2.4–2.5 mm long in known specimens (Fig. 5A). Antennae 12- or 13-segmented. Inquilines in galls of *P. pilulae* on *Quercus imbricaria* or *Andricus quercuspetiolicola* on *Q. bicolor* **5**
5. Antennae 13-segmented (Fig. 5A). OOL longer than LOL. Inquilines in galls of *Polystepha pilulae* on *Quercus imbricaria* **daleki sp. nov.**
- Antennae 12-segmented¹. OOL slightly shorter than LOL. Inquilines in galls of *Andricus quercuspetiolicola* on *Quercus bicolor*. **ensiger (Walsh, 1864)**
6. Pronotum and mesoscutum more or less smooth and unsculptured except for abundant setation and/or setiferous punctuation; at most with mesoscutum faintly alutaceous in large specimens. Known only from Mexico **7**
- Pronotum and mesoscutum always distinctly sculptured over its entire surface; coriaceous to imbricate and never entirely faintly alutaceous (e.g., Fig. 5E). **8**
7. Antennae 13-segmented. Head more or less unsculptured and smooth except for abundant setation (Figs 26F, G). Vertical facial carinae complete, extending from ventral torulus to oral fovea (Fig. 26F) **lenis Lobato-Vila & Pujade-Villar, 2019**

- Antennae 12-segmented. Head with apparent coriaceous sculpture (Figs 26B, C). Vertical facial carinae incomplete, running no more than halfway across lower face and never reaching oral fovea (Fig. 26B). **junquerasi Lobato-Vila & Pujade-Villar, 2019**
- 8. Head and mesosoma more or less entirely rufous in color³ (Figs 15A, 26A) **9**
- Head and mesosoma entirely darker in color, appearing brown to black (e.g., Figs 6A, 8A, 9A). **10**
- 9. Antennae 12-segmented (Fig. 15A). F1 subequal to F2 (Fig. 15D). Inquilines of *Andricus dimorphus* on *Quercus macrocarpa* and *A. nigricens* on *Q. bicolor* **promethei sp. nov.**
- Antennae 13-segmented. F1 shorter than F2 (e.g., Fig. 2D). Inquilines of *Andricus confertus* on *Quercus lobata* **confertus (McCracken & Egbert, 1922)**
- 10. Antennae 13-segmented (e.g., Fig. 10A) **11**
- Antennae 12-segmented (e.g., Fig. 15A) **17**
- 11. Mesoscutellar disc strongly rugose throughout, with interspaces coriaceous (e.g., Figs 9E, 10E) **12**
- Mesoscutellar disc not strongly rugose throughout, with some coriaceous sculpture anteriorly and medially (e.g., Fig. 20E) **15**
- 12. F1 equal to F2 (Figs 9D, 10D). Apical flagellomere shorter, only 2.5–2.7× as long as wide **13**
- F1 shorter than F2 (e.g., Fig. 2D). Apical flagellomere longer, 3.3–3.8× as long as wide **14**
- 13. Third metasomal tergite with large, expansive posterodorsal patch of punctures overtaking entire posterior of tergite (Fig. 9G). Malar space short, 0.3× as long as compound eye (Fig. 9B). Inquilines of *Kokkocynips decidua*, *K. imbricariae*, and *K. rileyi* on *Quercus rubra* **jabbai sp. nov.**
- Third metasomal tergite with a small posterodorsal patch of punctures restricted to a small medial area (Fig. 10G). Malar space longer, 0.5× as long as compound eye (Fig. 10B). Inquilines of *Callirhytis quercusgemmaria* on *Q. rubra* . . . **jarethi sp. nov.**
- 14. Malar space long, 0.7× as long as compound eye. Apical flagellomere shorter, 3.3× as long as wide. Inquilines of *Sphaeroteraps* and *Atrusca* on *Quercus microphylla*. Known only from Aguascalientes (Mexico) **quadratifacies Lobato-Vila & Pujade-Villar, 2019**
- Malar space shorter, 0.5× as long as compound eye. Apical flagellomere longer, 3.8× as long as wide. Inquilines of *Amphibolips quercusostensackeni* on red oaks. Known only from Missouri (USA) **rufiventris Ashmead, 1896**
- 15. Mesoscutellar foveae separated by a wide septum nearly as wide as either fovea. Apical flagellomere short, 2.3× as long as wide. Metasoma rufous, strongly contrasting with coloration of head and mesosoma **catesbaei Ashmead, 1885**
- Mesoscutellar foveae separated by a narrow carina much narrower than either fovea (e.g., Fig. 13E). Apical flagellomere longer, at least 2.7× as long as wide. Metasoma brown or black, not strongly contrasting with coloration of head and mesosoma . . **16**
- 16. Head subcircular in anterior view. OOL equal to LOL. Marginal cell longer, 3.1× as long as wide. Inquilines of *Andricus quercuspetiolicola* on *Quercus michauxii* **petiolicola (Osten-Sacken, 1861)**
- Head strongly subtrapezoidal in anterior view. OOL longer than LOL. Marginal cell shorter, 2.3× as long as wide. Inquilines of *Andricus reniformis* on *Q. vaccinifolia* and *Disholcaspis truckeensis* on *Q. chrysolepis* **montensis Weld, 1957**
- 17. F1 longer than F2 (e.g., Fig. 8D) **18**
- F1 equal to or shorter than F2 (e.g., Figs 9D, 16D) **19**
- 18. Hind leg with coxa, femur, and tibia entirely black (Fig. 26D); hind tarsomeres and other legs at least moderately infuscated. Head and mesosoma black (Fig. 26D). Apical flagellomere shorter, only 2.7× as long as wide. Body larger, 1.8–2.0 mm in length. Inquilines in globular twig galls on red oaks. Known only from Mexico **nigricrus Lobato-Vila & Pujade-Villar, 2019**
- Hind leg at most brownish, never approaching black (Fig. 8A). Head and mesosoma light to dark brown (Fig. 8A). Apical flagellomere longer, 3.8× as long as wide (Fig. 8A). Body extremely small, 0.9–1.1 mm in length (Fig. 8A). Inquilines in galls of *Neuroterus saltarius* and *Druon ignotum*, both on *Quercus macrocarpa*. Known only north of Mexico. . . **iktomii sp. nov.**
- 19. Pedicel and F1 subequal, both only slightly shorter than scape (Fig. 26E). Body very small, 1.0–1.5 mm in length. **minutissimi Ashmead, 1885**
- Pedicel shorter than F1 (e.g., Fig. 6D). Body size variable, typically larger than 1.0 mm but often smaller **20**
- 20. OOL twice DLO (Fig. 26K). Third metasomal tergite entirely without punctation. Marginal cell short, only 2.4× as long as wide. Known only from the State of México (Mexico) **mexicanus Lobato-Vila & Pujade-Villar, 2019**
- OOL never approaching twice as long as DLO. Third metasomal tergite almost always with conspicuous posterodorsal patch of punctures (e.g., Figs 6G, 13G). Marginal cell longer, at least 2.5× as long as wide and usually significantly longer (e.g., Figs 6F, 13F). Known only north of Mexico **21**

21.	Third metasomal tergite with a large, expansive posterodorsal patch of abundant punctures, expanded somewhat anteriorly and/or laterally and usually reaching nearly halfway to second tergite (Figs 2G, 16G, 20G)	22
-	Third metasomal tergite at most with only a small posterodorsal patch of punctures more or less restricted to an area along posterodorsal margin and not reaching more than one third to second tergite (e.g., Fig. 23G)	24
22.	Metasoma distinctly longer than combined length of head and mesosoma (Fig. 2A). Mesoscutellar disc strongly rugose throughout with only interspaces coriaceous (Fig. 2E). F1 0.8× as long as F2 (Fig. 2D)	<i>anzui</i> sp. nov.
-	Metasoma in lateral view subequal to combined length of head and mesosoma (Figs 16A, 20A). Mesoscutellar disc coriaceous anteriorly and medially to rugose toward outer margins (Figs 16E, 20E). F1 0.9× as long as F2 (Figs 16D, 20D)	23
23.	Malar space 0.5× as long as compound eye (Fig. 20B). Apical flagellomere 4.3× as long as wide. POL about twice as long as LOL and OOL (Fig. 20C). Inquilines in galls of <i>Andricus dimorphus</i> on <i>Quercus macrocarpa</i>	<i>swiperi</i> sp. nov.
-	Malar space 0.3× as long as compound eye (Fig. 16B). Apical flagellomere 3.5× as long as wide. POL longer, distinctly more than twice as long as LOL and OOL (Fig. 16C). Inquilines in galls of <i>Phylloteris rubinum</i> on <i>Quercus alba</i>	<i>sandiegoae</i> sp. nov.
24.	F1 0.8–0.9× as long as F2 (e.g., Fig. 13D)	25
-	F1 equal to F2, 1.0× as long (e.g., Fig. 7D)	32
25.	Third metasomal tergite without distinct punctation. LOL equal to or shorter than OOL	26
-	Third metasomal tergite always with a small but distinct posterodorsal patch of punctures (e.g., Fig. 4G). LOL longer than OOL	27
26.	Mesoscutellar disc more or less rugose throughout, with interspaces coriaceous. Mesoscutum alutaceous with weak discontinuous transverse elements. Apical antennomere 3.0× as long as wide. Inquilines in unknown woody stem galls on <i>Quercus stellata</i>	<i>quercusobtusilobae</i> (Karsch, 1880)
-	Mesoscutellar disc anteriorly and medially coriaceous, only weakly rugose toward outer margins. Mesoscutum sculpture coriaceous with setiferous punctation. Apical antennomere longer, 3.2–3.5× as long as wide. Inquilines in galls of <i>Andricus</i> on other <i>Quercus</i> species	<i>snellingi</i> Lyon, 1996
27.	Mesoscutum strongly sculptured, mostly coriaceous-imbricate and usually with some indication of transverse elements laterally (Fig. 24F). Vertical facial carinae rather long, reaching about two thirds across lower face, and delimiting a distinct bulging area (Fig. 24E)	<i>cornigera/frondosae</i> complex ⁴
-	Mesoscutum variable but not as described above. Vertical facial carinae shorter and not strongly bulging between carinae	28
28.	Notauli indistinct only in anterior third of mesoscutum (Figs 13E, 14E). Apical flagellomere 3.2–3.3× as long as wide. Malar space 0.3× as long as compound eye (Figs 13B, 14B)	29
-	Notauli indistinct in anterior half of mesoscutum (e.g., Fig. 4E). Apical flagellomere longer, 3.4–3.7× as long as wide. Malar space 0.3–0.5× as long as compound eye	30
29.	Head subquadrate in anterior view (Fig. 14B). Mesoscutellar disc rugose throughout, with interspaces coriaceous (Fig. 14E). Inquilines in galls of <i>Callirhytis quercusfutilis</i> on <i>Quercus alba</i>	<i>mallowi</i> sp. nov.
-	Head subtrapezoidal in anterior view (Fig. 13B). Mesoscutellar disc coriaceous anteriorly and medially, only strongly rugose posteriorly (Fig. 13E). Inquilines in galls of <i>Melikaiella ostensackeni</i> and <i>Zopheroteris sphaerula</i> on <i>Quercus rubra</i>	<i>lupini</i> sp. nov.
30.	Head round in anterior view (Fig. 4B). Mesoscutellar disc coriaceous anteriorly and medially, only strongly rugose posteriorly (Fig. 4E). Marginal cell longer, 3.1× as long as wide (Fig. 4F). Inquilines in galls of <i>Melikaiella ostensackeni</i> on <i>Quercus palustris</i>	<i>curupira</i> sp. nov.
-	Head subtrapezoidal in anterior view (Figs 3B, 22B). Mesoscutellar disc strongly rugose throughout, with interspaces coriaceous (Figs 3E, 22E). Marginal cell shorter, 2.7× as long as wide (Figs 3F, 22F). Inquilines in galls of <i>Callirhytis</i> on white oaks.	31
31.	Mesoscutum sculpture weakly coriaceous with setiferous punctation throughout (Fig. 22E). Inquilines in galls of <i>Callirhytis quercusfutilis</i> on <i>Quercus alba</i> and <i>Q. macrocarpa</i>	<i>tikoloshai</i> sp. nov.
-	Mesoscutum sculpture strongly coriaceous-imbricate with distinct setiferous punctation throughout (Fig. 3E). Inquilines in galls of <i>Callirhytis clavula</i> on <i>Quercus alba</i>	<i>bruti</i> sp. nov.
32.	Mesoscutellar disc coriaceous anteriorly and medially, only strongly rugose toward outer margins (e.g., Fig. 6E)	33
-	Mesoscutellar disc more or less strongly rugose throughout, with interspaces coriaceous (e.g., Fig. 1E)	36
33.	Mesoscutum weakly coriaceous to alutaceous with distinct setiferous punctation throughout (Fig. 6E). Malar space short, 0.3× as long as compound eye (Fig. 6B). Inquilines in galls of <i>Neuroterus tantulus</i> on <i>Quercus alba</i>	<i>dandoi</i> sp. nov.

- Mesoscutum more strongly and evenly coriaceous with distinct setiferous punctation throughout (e.g., Fig. 7E). Malar space somewhat longer, 0.4× as long as compound eye (e.g., Fig. 7B). Inquilines in galls of various hosts including other *Neuroterus* species on *Quercus alba* 34
- 34. Apical flagellomere shorter, 2.5× as long as wide (Fig. 21A). Head round in anterior view (Fig. 21B). Inquilines in galls of *Bassetia flavipes* on *Quercus bicolor* ***thrymi* sp. nov.**
- Apical flagellomere longer, 3.0–3.3× as long as wide (Figs 7A, 18A). Head round or subtrapezoidal in anterior view (Figs 7B, 18B). Inquilines in other galls 35
- 35. Transfacial line shorter, 0.8× as long as compound eye (Fig. 7B). Head subtrapezoidal in frontal view (Fig. 7B). Apical flagellomere shorter, 3.0× as long as wide (Fig. 7A). Inquilines in galls of *Melikaiella ostensackeni* on red oaks ***demerzelae* sp. nov.**
- Transfacial line longer, 1.0× as long as compound eye (Fig. 18B). Head round in anterior view (Fig. 18B). Apical flagellomere longer, 3.3× as long as wide (Fig. 18A). Inquilines in galls of *Neuroterus floccosus* or *N. quercusverrucarum* on white oaks . . . ***soloi* sp. nov.**
- 36. Head strongly subtriangular in anterior view (Fig. 25C). Mesoscutum sculpture coriaceous. Malar space 0.3× as long as compound eye (Fig 25C). Inquilines of *Druon quercuslanigerum* on red oaks. ***lanigerae* Ashmead, 1885**
- Head subquadrate or subtrapezoidal in anterior view (Figs 1B, 17B, 23B). Mesoscutum sculpture strongly coriaceous-imbricate (Figs 1E, 17E, 23E). Malar space variable, 0.3–0.5× as long as compound eye. Inquilines of other Cynipini galls on various oaks. 37
- 37. Notauli shorter, indistinct in anterior half of mesoscutum (Fig. 1E). Apical flagellomere shorter, 2.9× as long as wide (Fig. 1A). Inquilines in galls of *Melikaiella tumifica* on *Quercus rubra* and *Q. velutina*. ***anansii* sp. nov.**
- Notauli somewhat longer, indistinct only in anterior third of mesoscutum (Figs 17E, 23E). Apical flagellomere longer, 3.6–3.7× as long as wide (Figs 17A, 23A). Inquilines in other galls 38
- 38. Malar space short, 0.3× as long as compound eye (Fig. 17B). Pedicel 1.2× as long as wide (Fig. 17D). Inquilines of *Callirhytis quercuspunctata* on *Quercus rubra* ***selinae* sp. nov.**
- Malar space longer, 0.5× as long as compound eye (Fig. 23B). Pedicel about 1.0× as long as wide (Fig. 23D). Inquilines of *Neuroterus quercusirregularis* on *Quercus stellata* ***zorroi* sp. nov.**

1: According to Lobato-Vila & Pujade-Villar (2019), the type of *C. ensiger* has broken antennae, but the original description says that the antennae are 12-segmented in females.

2: See comments by Osten-Sacken (1865: 369-370) and Lobato-Vila & Pujade-Villar (2019) regarding this host association.

3: The types of *C. quercusobtusilobae* (Karsch, 1880) and *C. rufiventris* Ashmead, 1896 appear rufous in color, but Lobato-Vila and Pujade-Villar (2019) suggest that they are of questionable coloration in relation to their original descriptions, possibly as the result of discoloration. We agree with their interpretation; as a result, *C. quercusobtusilobae* and *C. rufiventris* will not key here and instead key to couplets 29 and 15, respectively.

4: *Ceroptres cornigera* Melika & Buss, 2002 and *C. frondosae* Ashmead, 1896 both key here. Characters included in the key follow Lobato-Vila & Pujade-Villar (2019), who discuss the possibility of these species being synonymous or otherwise unsatisfactorily circumscribed. Our examination suggests there may be additional undescribed species keying here; see remarks for “*Ceroptres cornigera* / *frondosae* complex” under “New records for described *Ceroptres*” for further details.

New species of *Ceroptres* Hartig, 1840

Ceroptres anansii Nastasi, Smith, & Davis sp. nov.

Fig. 1

urn:lsid:zoobank.org:act:6ED95A25-79E1-4D63-8174-AF030A8C8225

Material examined. Holotype ♀—USA • Iowa, Tiffin, FW Kent Park; reared from gall of *Melikaiella tumifica* on *Quercus rubra*; gall collected 25 May 2017; emerged 30 Apr 2018; DNA sequence voucher # 810-043-9B; GenBank Accession # OR372032; PSUC_FEM_255545.

Paratypes (1 ♀)—USA • 1 ♀; Pennsylvania, Ambler, Robbins Park; same host gall and plant as holotype; gall

collected 26 June 2018; emerged 29 Apr 2019; DNA sequence voucher # 1416-043-16A; GenBank Accession # number; PSUC_FEM_OR372078.

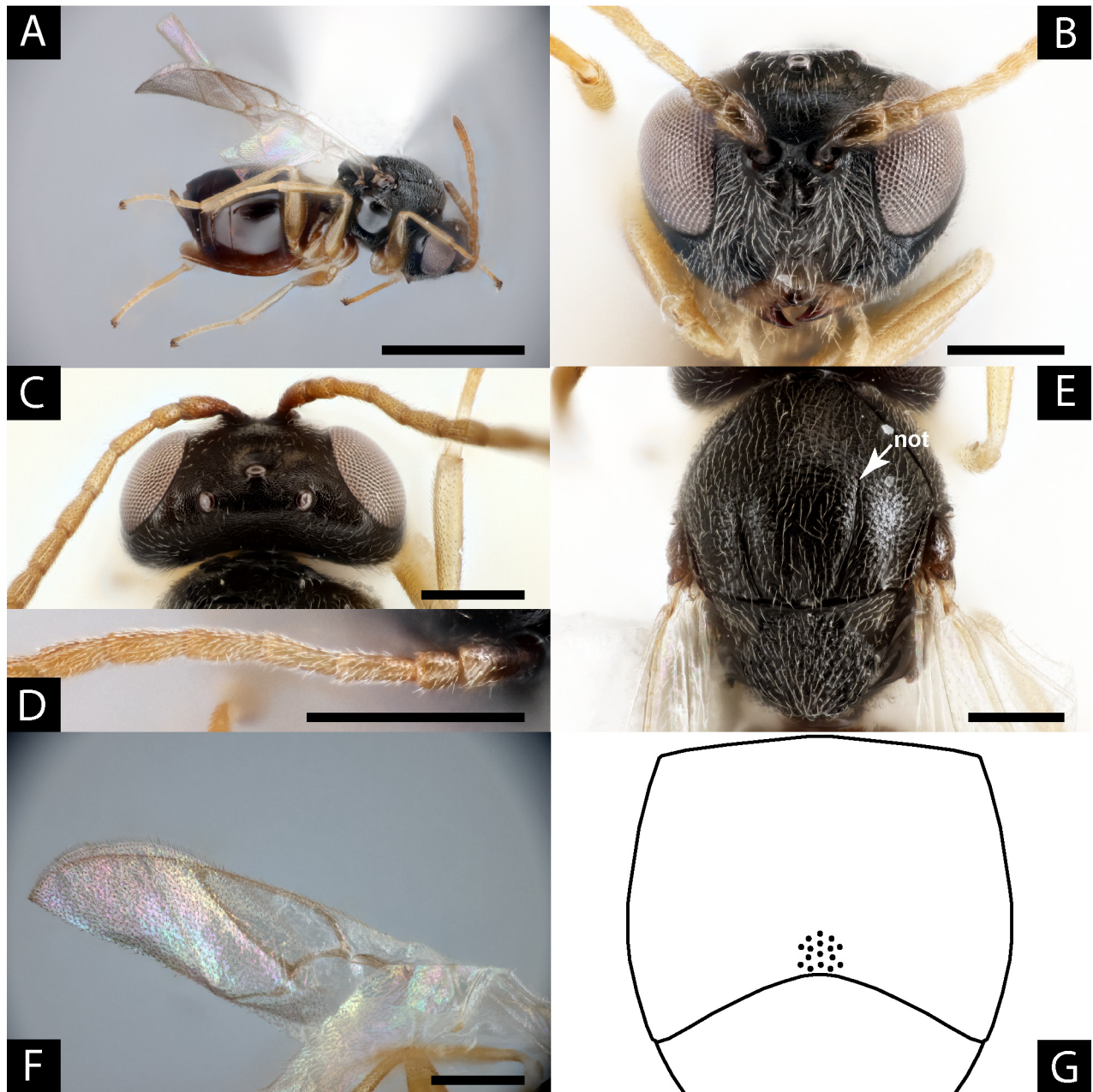


FIGURE 1. Diagnostic characters of *Ceroptres anansii* Nastasi, Smith, & Davis sp. nov. All images show holotype female (PSUC_FEM_255545). Scale bars: A = 1.0 mm; B–F = 0.25 mm. A: Lateral habitus. B: Head in anterior view. C: Head in dorsal view. D: Proximal antenna. E: Mesosoma in dorsal view; not = notaulus, with arrow indicating the end. F: Fore wing in lateral view. G: Punctuation pattern on third metasomal tergite in dorsal view (not to scale).

Etymology. Named for Anansi, a deity originating from folklore among the Akan people of Ghana, Ivory Coast, and Togo. Anansi is frequently portrayed as a spider who employs trickster tendencies, similar to the indigenous American figure Iktomi (see *Ceroptres iktomii*).

Diagnosis. *Ceroptres anansii* is morphologically close to *C. zorroi* and *C. selinae*; these species all have 12-segmented antennae (Fig. 1A), F1 equal to F2 (Fig. 1D), a strongly rugose mesoscutellar disc (Fig. 1E), and incomplete notauli (Fig. 1E). *C. anansii* is best separated from these species by the shorter notauli, which are indistinct in the entire anterior half of the mesoscutum (Fig. 1E), and by the short length of the apical flagellomere ($2.9\times$ as long as wide in *C. anansii* but at least $3.6\times$ as long as wide in *C. zorroi* and *C. selinae*).

Description. Female—Body 2.0 mm in length ($n = 2$). Head and mesosoma entirely black. Metasoma dark brown. Antennae 12-segmented, filiform, about two thirds as long as body. Pedicel $1.5\times$ as long as wide. F1 $1.0\times$ as long as F2. Apical flagellomere $2.9\times$ as long as wide. Head in anterior view subtrapezoidal. Dorsal head sculpture coriaceous; conspicuously sculptured throughout. Frons sculpture excluding facial carinae coriaceous. Facial vertical carinae distinct, reaching about two thirds across lower face. Transfacial line $0.9\times$ as long as compound eye. Malar space $0.4\times$ length of compound eye. POL:LOL:OOL:DLO in holotype 18:9:8:6. POL twice LOL and slightly longer than twice OOL. OOL slightly shorter than LOL, longer than DLO. Lateral pronotum sculpture coriaceous. Mesopleuron smooth and shining, without apparent sculpture. Mesoscutum sculpture coriaceous-imbricate with distinct setiferous punctation throughout. Notauli incomplete, indistinct in about anterior half of mesoscutum. Mesoscutellar disc strongly rugose with interspaces coriaceous. Mesoscutellar foveae distinct, short, and subrectangular, separated by narrow carina. Metapleural sulcus meeting mesopleuron at about three quarters height. Lateral propodeal carinae conspicuous; more or less straight and subparallel. Fore wing marginal cell $2.5\times$ as long as wide. Fore wing marginal setae distinct; short. Legs with coxae brown; remainder of legs yellow except apical tarsomeres infuscated on each leg. Tarsal claws with conspicuous, strong basal tooth. Metasoma excluding ovipositor and sheaths in lateral view subequal to combined length of head and mesosoma. Hypopygial spine not conspicuously projecting. Third metasomal tergite with a small patch of scattered punctures posterodorsally.

Male—Unknown.

Biology. *Ceroptres anansii* was reared from sexual generation galls of *Melikaiella tumifica* (Osten Sacken, 1865) on *Quercus rubra* L.

Distribution. Tiffin, Iowa and Ambler, Pennsylvania (USA).

Remarks. *Ceroptres anansii* corresponds to Ward *et al.*'s (2024) “species 10”.

Ceroptres anzui Nastasi, Smith, & Davis sp. nov.

Fig. 2

urn:lsid:zoobank.org:act:EA710803-D7CE-4BD3-848A-3D795B360A4D

Material examined. Holotype ♀—USA • Kentucky, Walton, Walton Community Park; reared from gall of *Melikaiella ostensackeni* on *Quercus palustris*; gall collected 5 Sep 2016; emerged 9 Sep 2016; DNA sequence voucher # 583-016-4B; GenBank Accession # OR372015; PSUC_FEM_255522.

Etymology. Named for Anzû, a half-man-half-bird creature in Mesopotamian mythology that stole the Tablet of Destinies, an artifact that declared the god Enlil as the supreme ruler of the universe.

Diagnosis. *Ceroptres anzui* is the only known *Ceroptres* in which the metasoma is distinctly longer than the combined length of the head and mesosoma (Fig. 2A). *Ceroptres anzui* is further characterized by the following combination of characters: F1 $0.8\times$ as long as F2 (Fig. 2D). Malar space $0.5\times$ as long as compound eye (Fig. 2B). Mesoscutellar disc strongly rugose throughout, with interspaces coriaceous (Fig. 2E). Third metasomal tergite with a large posterodorsal patch of punctures (Fig. 2G).

Description. Female—Holotype body 1.9 mm in length. Head and mesosoma entirely black. Metasoma brown. Antennae 12-segmented, subclavate, about two thirds as long as body. Pedicel $1.2\times$ as long as wide. F1 $0.8\times$ as long as F2. Apical flagellomere $3.5\times$ as long as wide. Head in anterior view round. Dorsal head sculpture coriaceous; conspicuously sculptured throughout. Frons sculpture excluding facial carinae coriaceous. Facial vertical carinae distinct, reaching about one third across lower face. Transfacial line $0.8\times$ as long as compound eye. Malar space $0.5\times$ length of compound eye. POL:LOL:OOL:DLO in holotype 14:6:5:5. POL slightly longer than twice LOL nearly three times OOL. OOL slightly shorter than LOL, equal to DLO. Lateral pronotum sculpture coriaceous. Mesopleuron smooth and shining, without apparent sculpture. Mesoscutum sculpture coriaceous with distinct setiferous punctation throughout. Notauli incomplete, indistinct in anterior half of mesoscutum. Mesoscutellar disc strongly rugose with interspaces coriaceous. Mesoscutellar foveae distinct, somewhat longer, and somewhat subquadrate, separated by narrow carina. Metapleural sulcus meeting mesopleuron at about four fifths height. Lateral propodeal carinae conspicuous; more or less straight and subparallel. Fore wing marginal cell $2.9\times$ as long as wide. Fore wing marginal setae distinct; long. Legs with coxae, femora, and tibiae brownish and tarsi mostly yellow. Tarsal claws with conspicuous, strong basal tooth. Metasoma excluding ovipositor and sheaths in lateral view distinctly longer than combined length of head and mesosoma. Hypopygial spine only very slightly projecting;

prominent projecting portion about as long as wide. Third metasomal tergite with a large posterodorsal patch of abundant punctures, expanded somewhat anteriorly and/or laterally and reaching nearly halfway across tergite.

Male—Unknown.

Biology. *Ceroptres anzui* was reared from asexual generation galls of *Melikaiella ostensackeni* Pujade-Villar, 2014 on *Quercus palustris* Michx.

Distribution. Walton, Kentucky (USA).

Remarks. *Ceroptres anzui* corresponds to Ward *et al.*'s (2024) “species COI-K”.

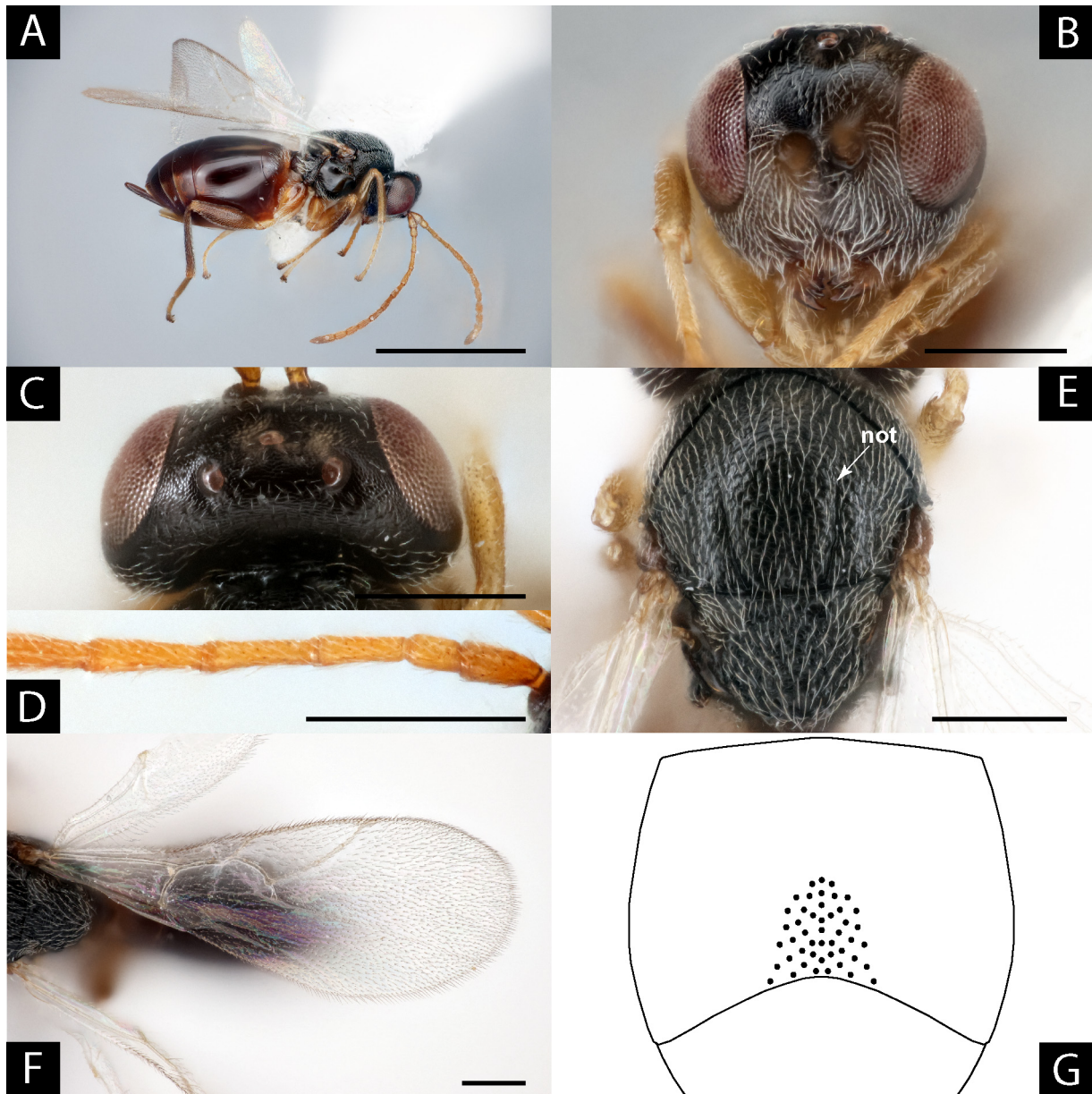


FIGURE 2. Diagnostic characters of *Ceroptres anzui* Nastasi, Smith, & Davis sp. nov. All images show holotype female (PSUC_FEM_255522). Scale bars: A = 1.0 mm; B–F = 0.25 mm. A: Lateral habitus. B: Head in anterior view. C: Head in dorsal view. D: Proximal antenna. E: Mesosoma in dorsal view; not = notaulus, with arrow indicating the end. F: Fore wing in lateral view. G: Punctuation pattern on third metasomal tergite in dorsal view (not to scale).

***Ceroptres bruti* Nastasi, Smith, & Davis sp. nov.**

Fig. 3

urn:lsid:zoobank.org:act:505C036E-F7EA-4BBA-A554-3DD7C6F2345A

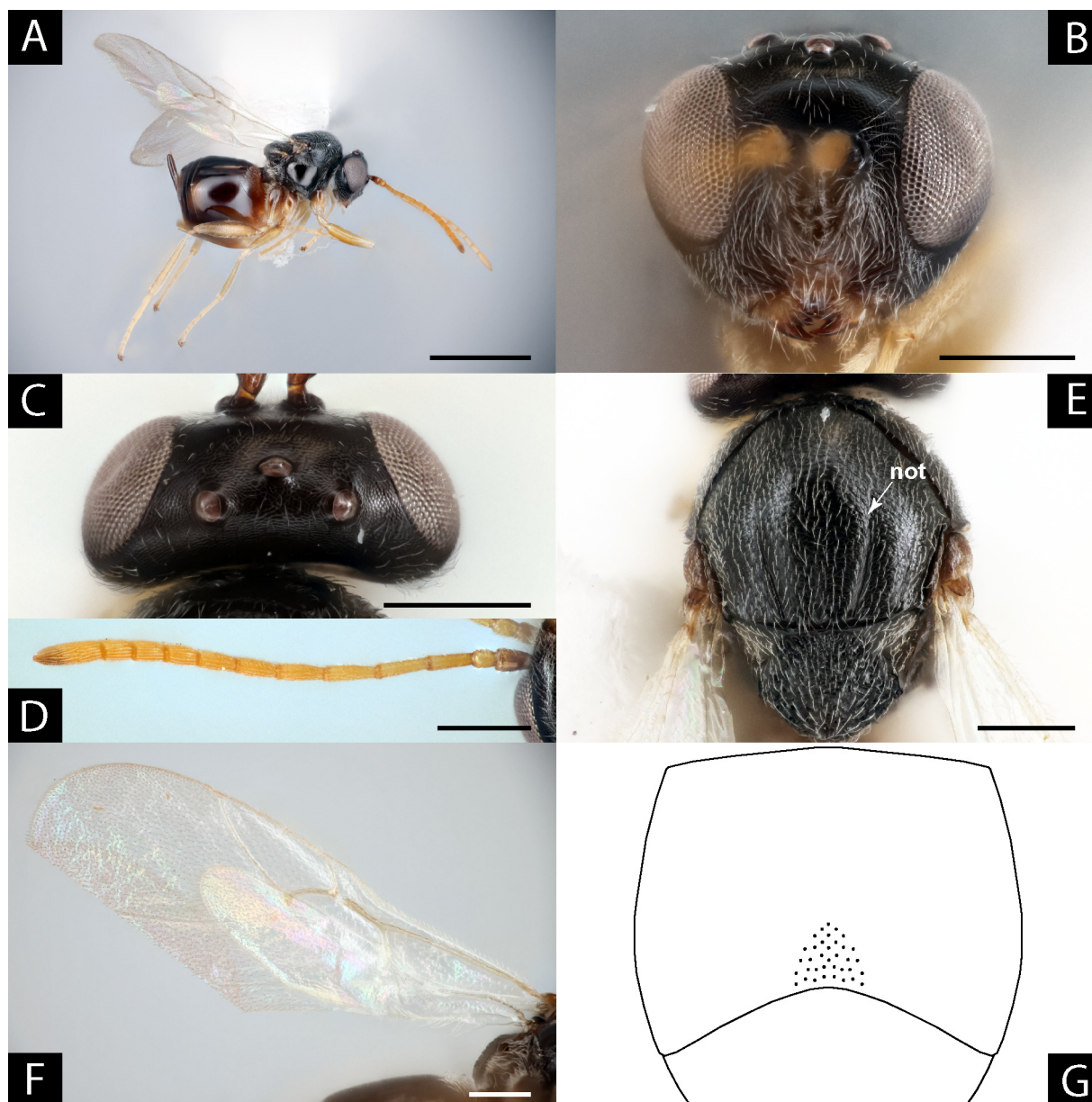


FIGURE 3. Diagnostic characters of *Ceroptres bruti* Nastasi, Smith, & Davis sp. nov. All images show holotype female (PSUC_FEM_255536). Scale bars: A = 1.0 mm; B–F = 0.25 mm. A: Lateral habitus. B: Head in anterior view. C: Head in dorsal view. D: Antenna. E: Mesosoma in dorsal view; not = notaulus, with arrow indicating the end. F: Fore wing in lateral view. G: Punctuation pattern on third metasomal tergite in dorsal view (not to scale).

Material examined. Holotype ♀—USA • Iowa, Iowa City, 340 Ellis Ave; reared from gall of *Callirhytis clavula* on *Quercus alba*; gall collected 22 May 2019; emerged 23 May 2019; DNA sequence voucher # 1608-034-1A; GenBank Accession # OR372098; PSUC_FEM_255536.

Etymology. Named for Marcus Junius Brutus, a Roman politician famous for betraying Julius Caesar in orchestrating his assassination, thereby freeing Rome from Caesar's iron fist. Brutus is also accordingly fictionalized in Shakespeare's *Julius Caesar*.

Diagnosis. *Ceroptres bruti* is close to several species in which F1 is shorter than F2 (Fig. 3D), the third metasomal tergite has a small posterodorsal patch of punctures (Fig. 3G), and the LOL is longer than the OOL (Fig. 3C). *Ceroptres bruti* is closest to *C. tikolostei*; these species are extremely similar morphologically but can be differentiated by the sculpture of the mesoscutum, which is strongly coriaceous-imbricate in *C. bruti* (Fig. 3E) but only weakly coriaceous in *C. tikolostei* (Fig. 22E).

Description. Female—Holotype body 1.8 mm in length. Head and mesosoma entirely black. Metasoma brown.

Antennae 12-segmented, subclavate, about three quarters as long as body. Pedicel 1.3× as long as wide. F1 0.9× as long as F2. Apical flagellomere 3.4× as long as wide. Head in anterior view subtrapezoidal. Dorsal head sculpture weakly coriaceous but conspicuously sculptured throughout. Frons sculpture excluding facial carinae coriaceous. Facial vertical carinae distinct, reaching about halfway across lower face. Transfacial line 0.9× as long as compound eye. Malar space 0.4× length of compound eye. POL:LOL:OOL:DLO in holotype 17:8:7:6. POL slightly longer than twice LOL and nearly three times OOL. OOL slightly shorter than LOL and slightly longer than DLO. Lateral pronotum sculpture coriaceous. Mesopleuron smooth and shining, without apparent sculpture. Mesoscutum sculpture coriaceous-imbricate with distinct setiferous punctation throughout. Notauli incomplete, indistinct in anterior half of mesoscutum. Mesoscutellar disc strongly rugose with interspaces coriaceous. Mesoscutellar foveae distinct, very short, and subrectangular, separated by narrow carina. Metapleural sulcus meeting mesopleuron at about three quarters height. Lateral propodeal carinae conspicuous; more or less straight and subparallel. Fore wing marginal cell 2.7× as long as wide. Fore wing marginal setae distinct; long. Legs coxae brown; remainder of legs yellow except apical tarsomeres infuscated on each leg. Tarsal claws with conspicuous, strong basal tooth. Metasoma excluding ovipositor and sheaths in lateral view slightly shorter than combined length of head and mesosoma. Hypopygial spine only very slightly projecting; prominent projecting portion about as long as wide. Third metasomal tergite with a small patch of scattered punctures posterodorsally.

Male—Unknown.

Biology. *Ceroptres bruti* was reared from galls of *Callirhytis clavula* Osten Sacken, 1865 on *Quercus alba* L.

Distribution. Iowa City, Iowa, USA.

Remarks. *Ceroptres bruti* corresponds to Ward *et al.*'s (2024) "species COI-G". *Ceroptres quercusarbos* (Fitch, 1859) was described from galls of *Callirhytis clavula* (Osten Sacken, 1865), the same host from which *C. bruti* was reared. Lobato-Vila & Pujade-Villar (2019) considered *C. quercusarbos* to be *incertae sedis* on the basis of the type specimen being destroyed, and Fitch's original description (1859) is not sufficient for determining whether *C. bruti* is conspecific with *C. quercusarbos*.

Ceroptres bruti is extremely close morphologically to *C. tikoloshei* Nastasi, Smith, & Davis sp. nov. Ward *et al.*'s (2024) analysis of DNA barcode data placed the two species in separate clades. Additionally, the two species are associated with different species of *Callirhytis* Förster, 1869. As a result, we prefer to treat these as two separate species despite only subtle morphological differences between them.

***Ceroptres curupira* Nastasi, Smith, & Davis sp. nov.**

Fig. 4

urn:lsid:zoobank.org:act:39A01681-061E-415E-97F5-1249E2890C6E

Material examined. Holotype ♀—USA • Iowa, Coralville, North Ridge Pavilion; reared from gall of *Melikaiella ostensackeni* on *Quercus palustris*; gall collected 11 July 2017; emerged 8 Sep 2017; DNA sequence voucher # 993-097-13; GenBank Accession # OR372057; PSUC_FEM_255568.

Etymology. Named for Curupira, a trickster demon derived from Tupi-Guarani mythology; it is usually portrayed as a creature with backward feet, which the creature uses to create footprints that confuse travelers and drive them toward madness.

Diagnosis. *Ceroptres curupira* is close to several species in which F1 is shorter than F2 (Fig. 4D), the third metasomal tergite has a small posterodorsal patch of punctures (Fig. 4G), and the LOL is longer than the OOL (Fig. 4C). *Ceroptres curupira* can be distinguished from the other most similar species (particularly *C. tikoloshei* and *C. bruti*) by the head shape, which is round in anterior view in *C. curupira* (Fig. 4B) but subtrapezoidal in *C. bruti* and *C. tikoloshei* (Figs 3B, 22B), the sculpture of the mesoscutellar disc, which is coriaceous anteriorly and medially in *C. curupira* (Fig. 4D) but strongly rugose throughout in the other species (Figs 3D, 22D), and by the dimensions of the marginal cell, which is 3.1× as long as wide in *C. curupira* (Fig. 4F) but 2.6-2.7× as long as wide in the other species (Figs 3F, 22F).

Ceroptres curupira shares a host gall with *C. lupini*, although the two species are easily distinguished by the following characters in addition to the aforementioned characters and those in the key to species: Apical flagellomere 3.7× as long as wide in *C. curupira* but only 3.2× as long as wide in *C. lupini*. Fore wing marginal cell 3.1× as long as wide in *C. curupira* (Fig. 4F) but only 2.5× as long as wide in *C. lupini* (Fig. 13F). Metasoma brown in *C. curupira* (Fig. 4A) but black in *C. lupini* (Fig. 13A).

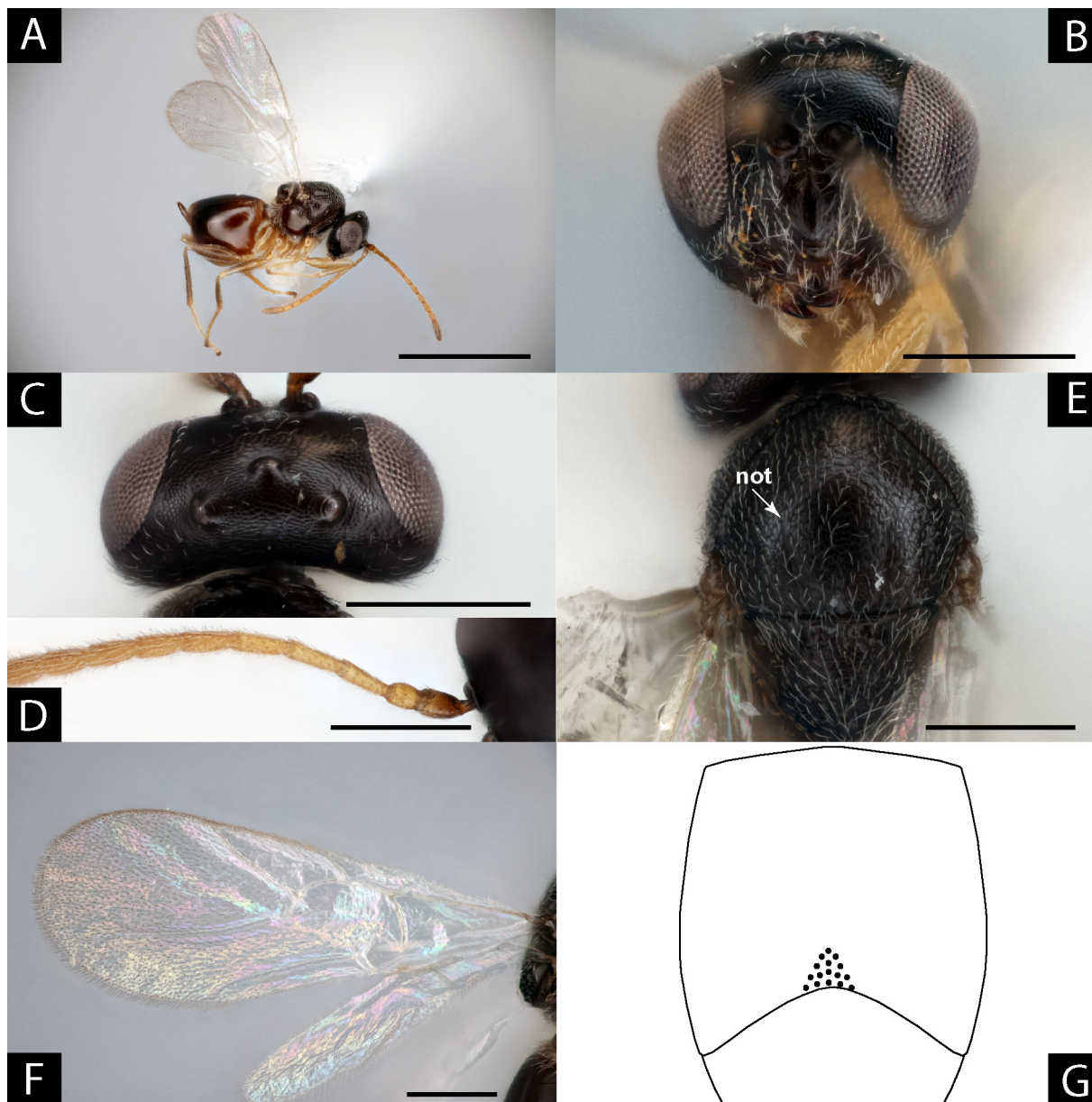


FIGURE 4. Diagnostic characters of *Ceroptres curupira* Nastasi, Smith, & Davis sp. nov. All images show holotype female (PSUC_FEM_255568). Scale bars: A = 1.0 mm; B–F = 0.25 mm. A: Lateral habitus. B: Head in anterior view. C: Head in dorsal view. D: Proximal antenna. E: Mesosoma in dorsal view; not = notaulus, with arrow indicating the end. F: Fore wing in lateral view. G: Punctuation pattern on third metasomal tergite in dorsal view (not to scale).

Description. Female—Holotype body 1.4 mm in length. Head and mesosoma entirely black. Metasoma brown. Antennae 12-segmented, subclavate, about two thirds as long as body. Pedicel 1.3× as long as wide. F1 0.9× as long as F2. Apical flagellomere 3.7× as long as wide. Head in anterior view round. Dorsal head sculpture coriaceous; conspicuously sculptured throughout. Frons sculpture excluding facial carinae coriaceous. Facial vertical carinae distinct, reaching about halfway across lower face. Transfacial line 0.9× as long as compound eye. Malar space 0.3× length of compound eye. POL:LOL:OOL:DLO in holotype 13:6:5:4. POL slightly longer than twice LOL nearly three times OOL. OOL slightly shorter than LOL, longer than DLO. Lateral pronotum sculpture coriaceous. Mesopleuron smooth and shining, without apparent sculpture. Mesoscutum sculpture coriaceous with distinct setiferous punctation throughout. Notauli incomplete, distinct only in posterior half of mesoscutum. Mesoscutellar disc coriaceous anteriorly and medially, only appearing strongly rugose posteriorly. Mesoscutellar foveae distinct, short, and subrectangular, separated by narrow carina. Metapleural sulcus meeting mesopleuron at about three

quarters height. Lateral propodeal carinae conspicuous; more or less straight and subparallel. Fore wing marginal cell 3.1× as long as wide. Fore wing marginal setae distinct; long. Fore and mid legs uniformly yellow except slight infuscation on coxae; hind legs with coxae, femora, and tibiae brown. Tarsal claws with conspicuous, strong basal tooth. Metasoma excluding ovipositor and sheaths in lateral view subequal to combined length of head and mesosoma. Hypopygial spine strongly projecting, with prominent projecting portion about 1.5x as long as wide. Third metasomal tergite with a small patch of scattered punctures posterodorsally.

Male—Unknown.

Biology. *Ceroptres curupira* was reared from an asexual generation gall of *Melikaiella ostensackeni* Pujade-Villar, 2014 on *Quercus palustris* Münchh.

Distribution. Coralville, Iowa (USA).

Remarks. *Ceroptres curupira* corresponds to Ward *et al.*'s "species 3". Ward *et al.*'s analysis of DNA barcodes suggested that three species were present amongst these individuals, but their UCE analysis suggested only one species. However, only two individuals were sequenced for UCEs, both of which corresponded to sp. 9 in their DNA barcode analysis. Our morphological examination identified three morphologically distinct groups that correspond to three species delimited with their DNA barcode data. Our *C. curupira* corresponds to Ward *et al.*'s sp. 10 in their DNA barcode analysis, our *C. tikoloshei* corresponds to Ward *et al.*'s sp. 18-19, and a single, morphologically distinct male corresponds to their sp. 8; in the latter case, the male is greatly morphologically distinct from the other material we examined, but it is unclear to us whether this individual is simply distinct on the basis of sexual dimorphism or if it may instead comprise an additional undescribed species (see "Unassociatable male specimens" below).

Ceroptres daleki Nastasi, Smith, & Davis sp. nov.

Fig. 5

urn:lsid:zoobank.org:act:A6BC1099-4290-4565-8F4B-D1121CAF7C66

Material examined. Holotype ♀—USA • North Carolina, Asheville, Richmond Hill Park; reared from gall of *Polystepha pilulae* on *Quercus imbricaria*; gall collected 4 Sep 2016; emerged 22 May 2017; DNA sequence voucher # 577-056-2; GenBank Accession # OR372013; PSUC_FEM_255558.

Etymology. Named for the Daleks, a species of aliens from the *Doctor Who* franchise widely regarded as merciless, destructive creatures who are devoted only to usurping all life forms across the universe. Just as the Daleks travel between worlds to overtake new enemies, *C. daleki* has evidently journeyed to a new world in its association with galls of midges rather than those of oak gall wasps.

Diagnosis. *Ceroptres daleki* belongs to a group of species with conspicuous alutaceous sculpture on the mesopleuron (Fig. 5G), most of which, including *C. daleki*, are associated with galls of cecidomyiid midges rather than those induced by Cynipini. Among species with a sculptured mesopleuron, *C. daleki* is closest to *C. ensiger* (Walsh, 1864), but is easily separated by the 13-segmented antennae (Fig. 5A) (12-segmented in *C. ensiger*) and the shape of the mesoscutellar foveae (subtriangular in *C. daleki* as in Fig. 5F, but subrectangular and much wider than long in *C. ensiger*). *Ceroptres daleki* is known in association with galls of *Polystepha* midges on *Quercus falcata* Michx., while *C. ensiger* is known only from galls of *Andricus quercuspetiolicola* (Bassett, 1863) on *Q. bicolor* Michx.

Description. Female—Body of holotype 2.4 mm in length. Head and mesosoma entirely black. Metasoma brown. Antennae 13-segmented, subclavate, about three quarters as long as body. Pedicel 1.0× as long as wide. F1 1.0× as long as F2. Apical flagellomere 3.1× as long as wide. Head in anterior view subtrapezoidal. Dorsal head sculpture coriaceous; conspicuously sculptured throughout. Frons sculpture excluding facial carinae coriaceous. Facial vertical carinae distinct, reaching about one third across lower face. Transfacial line 1.0× as long as compound eye. Malar space 0.5× length of compound eye. POL:LOL:OOL:DLO in holotype 17:7:8:6. POL slightly longer than twice LOL and OOL. OOL slightly longer than LOL, longer than DLO. Lateral pronotum sculpture coriaceous. Mesopleuron with abundant, well-impressed alutaceous sculpture; speculum smooth. Mesoscutum sculpture strongly coriaceous-imbricate, with setiferous punctation throughout. Notauli incomplete, indistinct in anterior third of mesoscutum. Mesoscutellar disc strongly rugose with interspaces coriaceous. Mesoscutellar foveae distinct and subtriangular; inner margins divergent posteriorly, separated by narrow carina. Metapleural sulcus meeting

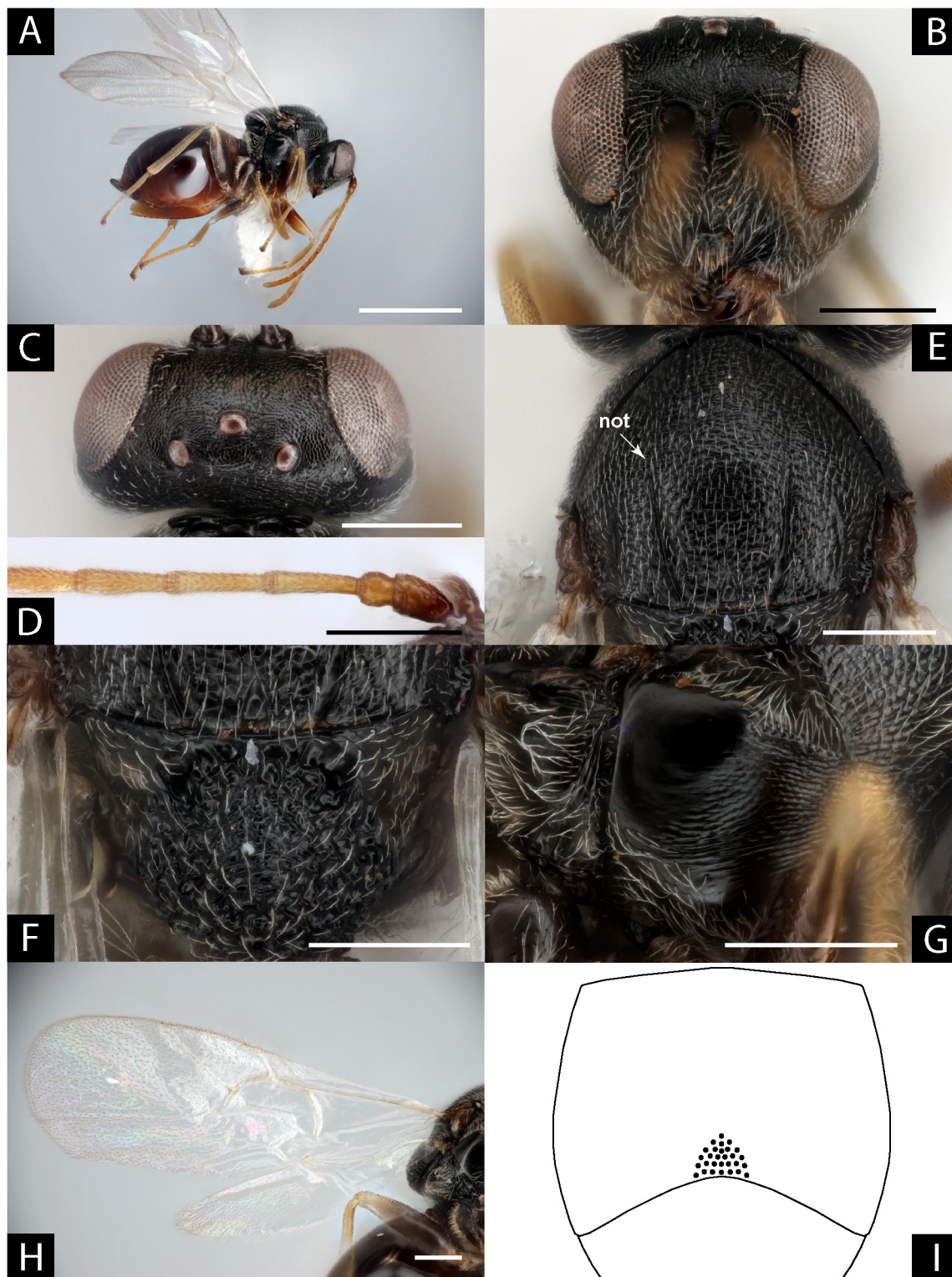


FIGURE 5. Diagnostic characters of *Ceroptres daleki* Nastasi, Smith, & Davis sp. nov. All images show holotype female (PSUC_FEM_255558). Scale bars: A = 1.0 mm; B–H = 0.25 mm. A: Lateral habitus. B: Head in anterior view. C: Head in dorsal view. D: Proximal antenna. E: Mesoscutum in dorsal view; not = notaulus, with arrow indicating the end. F: Scutellum in dorsal view. G: Mesopleuron in lateral view. H: Fore wing in lateral view. I: Punctuation pattern on third metasomal tergite in dorsal view (not to scale).

mesopleuron at about four fifths height. Lateral propodeal carinae conspicuous; more or less straight and subparallel. Fore wing marginal cell $2.5\times$ as long as wide. Fore wing marginal setae distinct; long. Legs yellow except for coxae, trochanters, femora, and apical tarsomeres brown. Tarsal claws with conspicuous, strong basal tooth. Metasoma

excluding ovipositor and sheaths in lateral view subequal to combined length of head and mesosoma. Hypopygial spine only very slightly projecting; prominent projecting portion about as long as wide. Third metasomal tergite with a small patch of scattered punctures posterodorsally.

Male—Unknown.

Biology. Reared from galls of *Polystepha pilulae* (Beutenmüller, 1892) on *Quercus imbricaria* Michx.

Distribution. Asheville, North Carolina (USA).

Remarks. *Ceroptres daleki* corresponds to Ward *et al.*'s "species COI-D". See also remarks for *Ceroptres songae*.

***Ceroptres dandoi* Nastasi, Smith, & Davis sp. nov.**

Fig. 6

urn:lsid:zoobank.org:act:7388A6DA-9A4C-4726-A8B5-C57A9CC3F017

Material examined. Holotype ♀—USA • Pennsylvania, Centre County, Centre Hall, Greens Valley Road; 40.871, -77.700; A Guiguet & LF Nastasi leg.; reared from gall of *Neuroterus tantulus* on a species of white oak - *Quercus* sp.; gall collected 19 July 2020; emerged 19 July 2020; PSUC_FEM_253650.

Paratypes (28 ♀ and 16 ♂)—USA • 7 ♀, 5 ♂; same data as holotype; PSUC_FEM_253559; 253561–253571 (specimen PSUC_FEM_253566 deposited at USNM) • 3 ♀, 5 ♂; same data as holotype but host plant reported as *Quercus alba*, collected by LF Nastasi, and emerged 27 July 2020; PSUC_FEM_253578–253585 (specimen PSUC_FEM_253583 deposited at USNM) • 16 ♀, 6 ♂; same data as holotype but host plant reported as *Quercus* cf. *michauxii* and collected by LF Nastasi; PSUC_FEM_253586–253607 (specimens PSUC_FEM_253591, 253597, and 253600 deposited at USNM) • 1 ♀; Pennsylvania, Iowa City, Waterworks Prairie Park; reared from gall of *Neuroterus tantulus* on *Quercus alba*; gall collected 19 July 2016; emerged 30 Aug 2016; voucher # 409-052-3A; PSUC_FEM_255555 • 1 ♀; Iowa, Tiffin, FW Kent Park; reared from gall of *Neuroterus tantulus* on *Quercus alba*; emerged 15 Nov 2017; voucher # 925-952-11B; PSUC_FEM_255554.

Etymology. Named for Edward Dando, a famed food thief in 19th century Britain who is credited with consuming massive quantities of oysters and refusing to pay for them, declaring that he "refuse[d] to starve in a land of plenty". We find this name to be especially apt for this species, as we reared *C. dandoi* from galls of *Neuroterus tantulus* which superficially resemble the shells of some mollusks, evidently Dando's favorite food.

Diagnosis. *Ceroptres dandoi* is distinct among known *Ceroptres* based on the coriaceous to alutaceous sculpture of the mesoscutum (Fig. 6E) in combination with the short malar space (0.3× as long as compound eye as in Fig. 6B) and the sculpture of the mesoscutellar disc (coriaceous anteriorly and medially rather than strongly rugose throughout as in Fig. 6E).

Description. Female—Body 1.0–1.2 mm in length (n = 10; holotype 1.1 mm). Head and mesosoma entirely black. Metasoma dark brown. Antennae 12-segmented, subclavate, about two thirds as long as body. Pedicel 1.4× as long as wide. F1 1.0× as long as F2. Apical flagellomere 3.3× as long as wide. Head in anterior view round. Dorsal head sculpture coriaceous; conspicuously sculptured throughout. Frons sculpture excluding facial carinae coriaceous. Facial vertical carinae distinct, reaching about halfway across lower face. Transfacial line 1.0× as long as compound eye. Malar space 0.3× length of compound eye. POL:LOL:OOL:DLO in holotype 10:5:4:3. POL twice LOL and slightly longer than twice OOL. OOL slightly shorter than LOL, longer than DLO. Lateral pronotum sculpture coriaceous. Mesopleuron smooth and shining, without apparent sculpture. Mesoscutum sculpture weakly coriaceous to alutaceous with setiferous punctation throughout. Notauli incomplete, indistinct in anterior half of mesoscutum. Mesoscutellar disc coriaceous anteriorly and medially, only appearing strongly rugose posteriorly. Mesoscutellar foveae distinct, somewhat longer, and somewhat subquadrate, separated by narrow carina. Metapleural sulcus meeting mesopleuron at about three quarters height. Lateral propodeal carinae conspicuous; more or less straight and subparallel. Fore wing marginal cell 3.0× as long as wide. Fore wing marginal setae distinct; long. Legs uniformly yellow except metacoxae and apical tarsomeres which are at least partly slightly infuscated. Tarsal claws with conspicuous, strong basal tooth. Metasoma excluding ovipositor and sheaths in lateral view subequal to combined length of head and mesosoma. Hypopygial spine strongly projecting, with prominent projecting portion about 1.7x as long as wide. Third metasomal tergite with a small posterodorsal patch of scattered punctures.

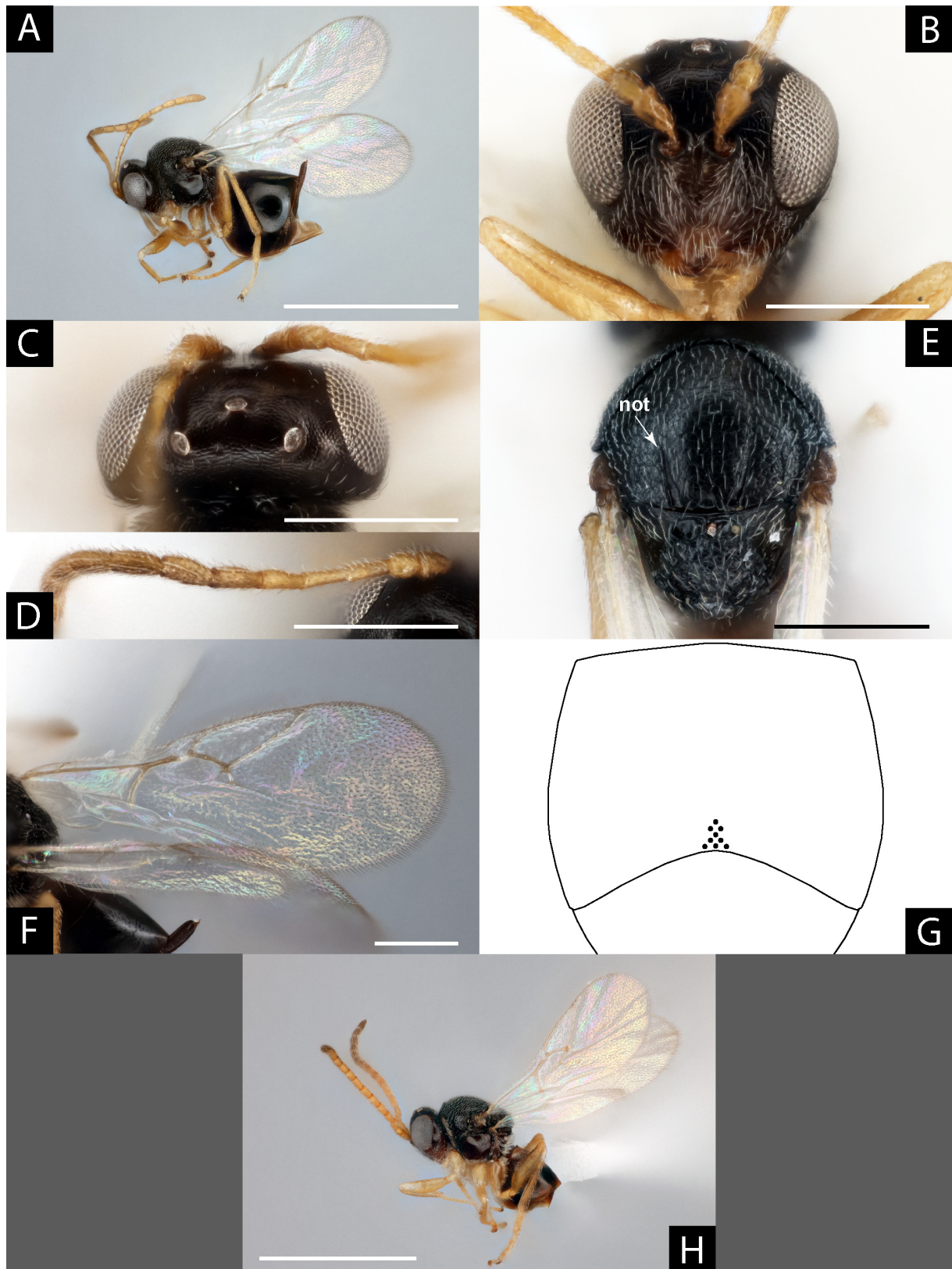


FIGURE 6. *Ceroptres dandoi* Nastasi, Smith, & Davis sp. nov. A–D; F–G: Holotype female (PSUC_FEM_253560); E = Paratype female (PSUC_FEM_253590); H: Paratype male (PSUC_FEM_253600). Scale bars: A & H = 1.0 mm; B–F = 0.5 mm. A: Adult female, lateral habitus. B: Head in anterior view. C: Head in dorsal view. D: Proximal antenna. E: Mesosoma in dorsal view; not = notaulus, with arrow indicating end of distinct portion. F: Fore wing. G: Punctuation pattern on third metasomal tergite in dorsal view (not to scale). H: Adult male, lateral habitus.

Male—Same as female except for the following: Body 0.9–1.2 mm in length ($n = 10$). Head and mesosoma color occasionally lighter brown. Antennae 15-segmented, subequal to body length. Apical flagellomere $2.5\times$ as long as wide. Metasoma smaller than in female.

Biology. *Ceroptres dandoi* was reared from asexual generation galls of *Neuroterus tantulus* Weld, 1952 on *Quercus alba* L. We also examined additional specimens for which the host gall was identified as “*Neuroterus cf tantulus*” or “*Neuroterus sp.*,” evidently resulting from taxonomic issues in the genus *Neuroterus* Hartig, 1840. There were also specimens for which the host plant was identified only as a species of white oak. After examining galls from which these specimens were reared, we find it likely that all known *C. dandoi* were reared from galls of *N. tantulus* on *Q. alba*.

Distribution. Iowa City and Tiffin, Iowa and Centre Hall, Pennsylvania (USA).

Remarks. Specimens of *C. dandoi* were among Ward *et al.*’s (2024) vouchers but were not sequenced.

Ceroptres demerzelae Nastasi, Smith, & Davis sp. nov.

Fig. 7

urn:lsid:zoobank.org:act:8B79B57F-ECA5-42B5-A75B-48291A397828

Material examined. Holotype ♀—USA • Missouri, Hannibal, Riverside Park; reared from gall of *Melikaiella ostensackeni* on *Quercus velutina*; gall collected 3 June 2017; emerged 11 Oct 2017; DNA sequence voucher # 840-016-73; GenBank Accession # OR382033; PSUC_FEM_255528.

Paratypes (6 ♀)—USA • 1 ♀; same locality as holotype; reared from gall of *Melikaiella ostensackeni* on *Quercus rubra*; gall collected 3 June 2017; emerged 15 July 2017; DNA sequence voucher # 843-016-26A; GenBank Accession # OR372034; PSUC_FEM_255521 • 1 ♀, X ♂; Iowa, Iowa City, City Park; reared from gall of *Melikaiella ostensackeni* on *Quercus palustris*; gall collected 7 June 2017; emerged 21 July 2017; DNA sequence voucher # 856-016-20A; GenBank Accession # OR372038; PSUC_FEM_255526 • 1 ♀; Iowa, Iowa City, FW Kent Park; reared from gall of *Melikaiella ostensackeni* on *Quercus rubra*; gall collected 8 June 2017; emerged 5 Aug 2017; DNA sequence voucher # 870-016-41A; GenBank Accession # OR372046; PSUC_FEM_255525 • 1 ♀; Michigan, Traverse City, backyard; reared from gall of *Melikaiella ostensackeni* on *Quercus rubra*; gall collected 12 July 2016; emerged 4 Aug 2016; DNA sequence voucher # 401-016-13A; GenBank Accession # OR372007; PSUC_FEM_255523 • 1 ♀; Michigan, Traverse City, backyard; reared from gall of *Melikaiella ostensackeni* on *Quercus rubra*; gall collected 12 July 2016; emerged 17 Aug 2016; DNA sequence voucher # 400-016-13; GenBank Accession # OR372005; PSUC_FEM_255527 • 1 ♀; Missouri, St. Louis, Creve Coeur Lake; reared from gall of *Melikaiella ostensackeni* on *Quercus palustris*; gall collected 29 June 2017; emerged 19 July 2019; DNA sequence voucher # 933-016-18D; GenBank Accession # OR372052; PSUC_FEM_255524.

Etymology. Named for Demerzel, an android who serves as the loyal aide to the Emperors of the Galaxy in Isaac Asimov’s *Foundation* series as well as the recent television adaptation. In the television series, she fulfills a role similar to that of an inquiline, appearing to act in the best interest of one of the emperors, only to later usurp the emperors’ authority.

Diagnosis. See diagnosis to *C. soloi*.

Description. Female—Body 1.1–1.9 mm in length ($\bar{x} = 1.5$; $n = 6$). Head and mesosoma entirely black. Metasoma dark brown. Antennae 12-segmented, filiform, about two thirds as long as body. Pedicel $1.3\times$ as long as wide. F1 $1.0\times$ as long as F2. Apical flagellomere $3.0\times$ as long as wide. Head in anterior view subtrapezoidal. Dorsal head sculpture coriaceous; conspicuously sculptured throughout. Frons sculpture excluding facial carinae coriaceous. Facial vertical carinae distinct, reaching about halfway across lower face. Transfacial line $0.8\times$ as long as compound eye. Malar space $0.4\times$ length of compound eye. POL:LOL:OOL:DLO in holotype 13:6:6:5. POL slightly longer than twice LOL and OOL. OOL equal to LOL, longer than DLO. Lateral pronotum sculpture coriaceous. Mesopleuron smooth and shining, without apparent sculpture. Mesoscutum sculpture coriaceous with distinct setiferous punctation throughout. Notauli incomplete, indistinct in anterior half of mesoscutum. Mesoscutellar disc coriaceous anteriorly and medially, only appearing strongly rugose posteriorly. Mesoscutellar foveae distinct, short, and subrectangular, separated by narrow carina. Metapleural sulcus meeting mesopleuron at about four fifths height. Lateral propodeal carinae conspicuous; more or less straight and subparallel. Fore wing marginal cell $3.1\times$ as long as wide. Fore wing marginal setae distinct; short. Fore entirely yellow except brownish coxae and infuscated

apical tarsomeres; mid and hind legs with coxae, trochanters, femora, tibiae, and apical tarsomeres brown. Tarsal claws with conspicuous, strong basal tooth. Metasoma excluding ovipositor and sheaths in lateral view subequal to combined length of head and mesosoma. Hypopygial spine only very slightly projecting; prominent projecting portion about as long as wide. Third metasomal tergite with a small patch of scattered punctures posterodorsally.

Male—Unknown.

Biology. *Ceroptres demerzelae* was reared from asexual generation galls of *Melikaiella ostensackeni* Pujade-Villar, 2014 on *Quercus palustris* Münchh, *Q. rubra* L., and *Q. velutina* Lam.

Distribution. Iowa City, Iowa, Traverse City, Michigan, Hannibal and St. Louis, Missouri (USA).

Remarks. *Ceroptres demerzelae* corresponds to Ward *et al.*'s (2024) “species 7-8-9”.

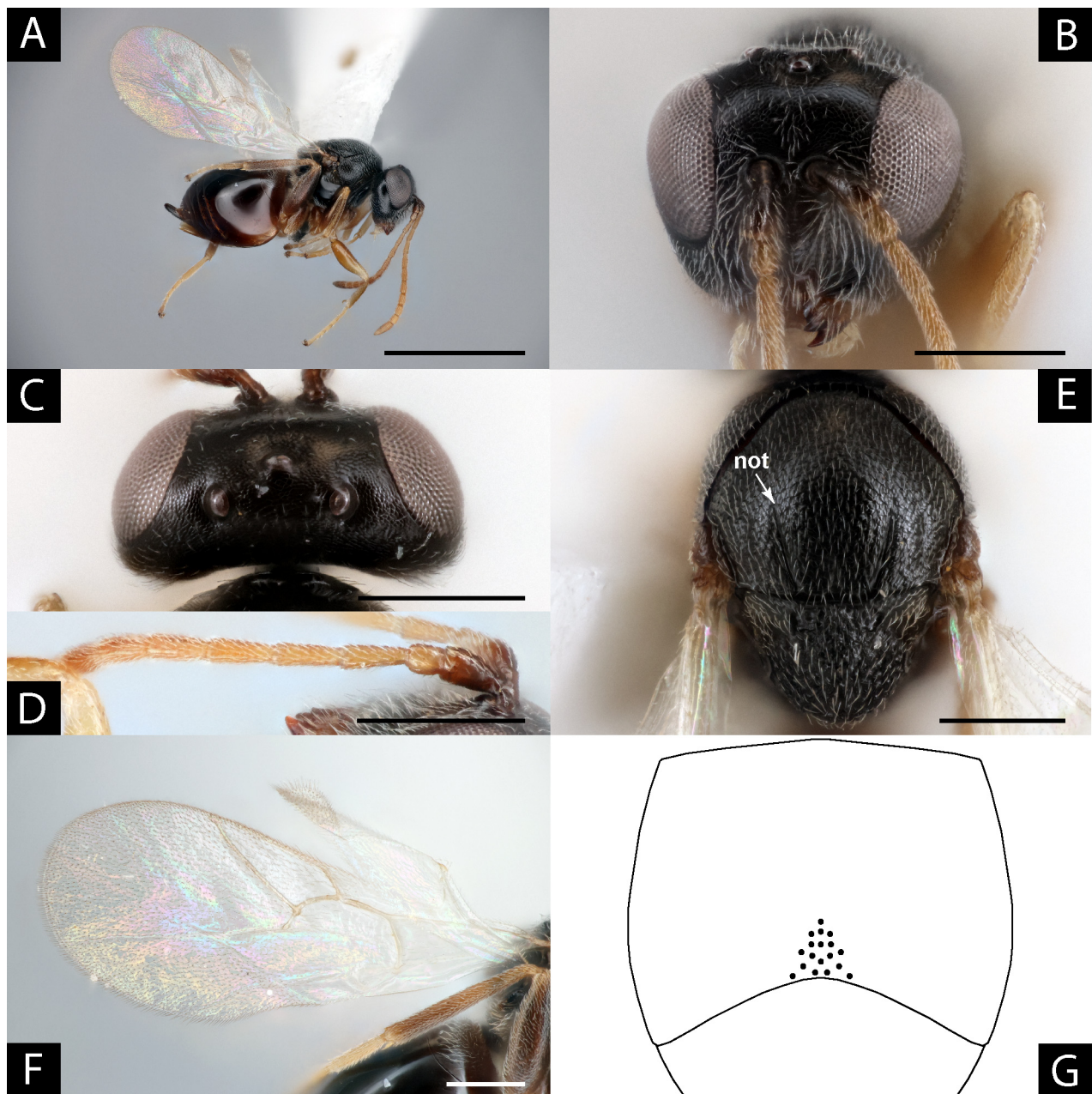


FIGURE 7. Diagnostic characters of *Ceroptres demerzelae* Nastasi, Smith, & Davis sp. nov. All images show holotype female (PSUC_FEM_255528). Scale bars: A = 1.0 mm; B–F = 0.25 mm. A: Lateral habitus. B: Head in anterior view. C: Head in dorsal view. D: Proximal antenna. E: Mesosoma in dorsal view; not = notaulus, with arrow indicating the end. F: Fore wing in lateral view. G: Punctuation pattern on third metasomal tergite in dorsal view (not to scale).

***Ceroptres iktomii* Nastasi, Smith, & Davis sp. nov.**

Fig. 8

urn:lsid:zoobank.org:act:4D358B97-C691-4CF0-869C-06E28ED73C30

Material examined. Holotype ♀—USA • Iowa, Iowa City, Pentacrest; reared from gall of *Neuroterus saltarius* on *Quercus bicolor*; gall collected 27 June 2016; emerged 23 May 2017; DNA sequence voucher # 360-021-82B; GenBank Accession # OR372003; PSUC_FEM_255530.

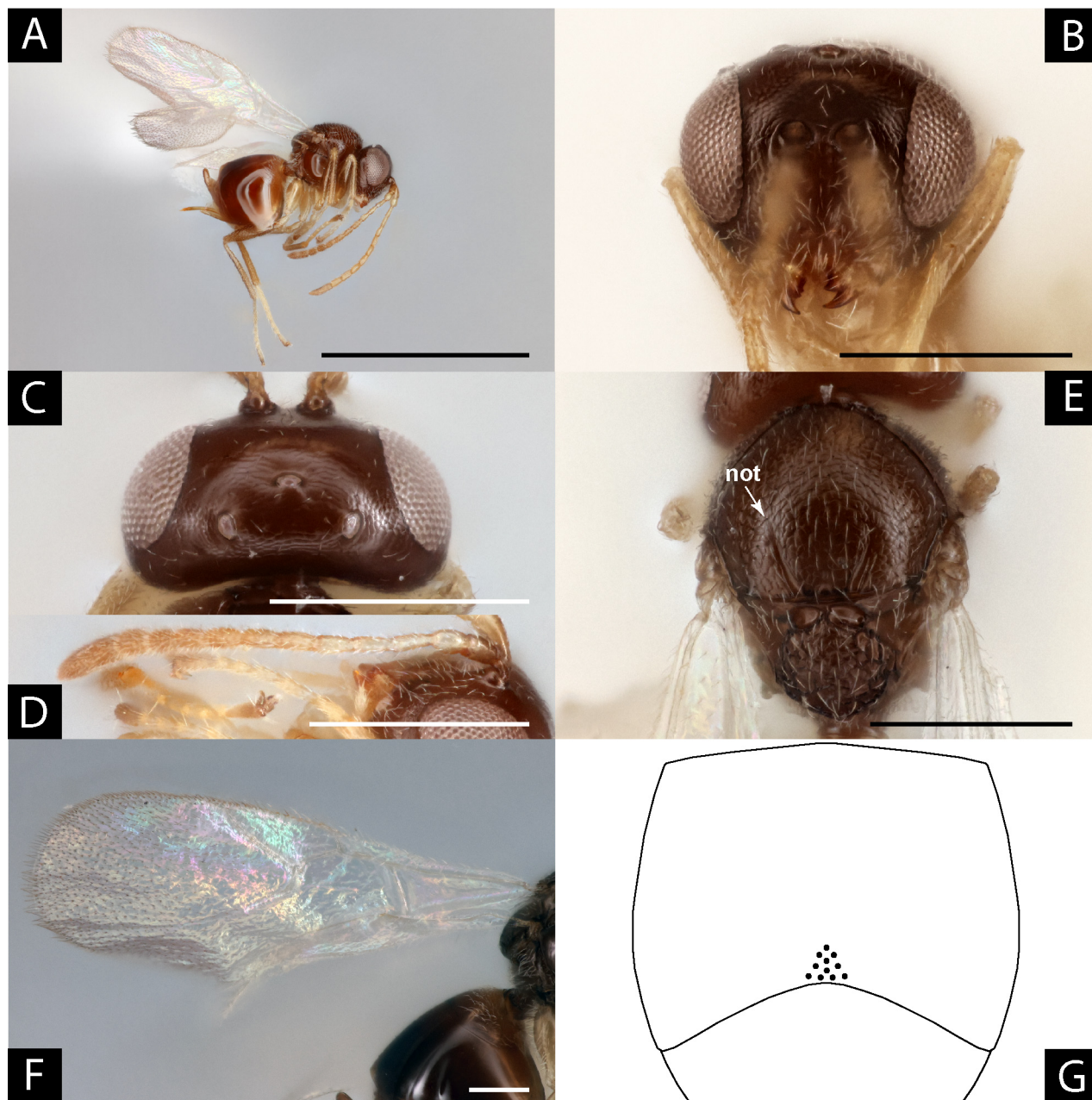


FIGURE 8. Diagnostic characters of *Ceroptres iktomii* Nastasi, Smith, & Davis sp. nov. All images show holotype female (PSUC_FEM_255531). Scale bars: A = 1.0 mm; B–F = 0.25 mm. A: Lateral habitus. B: Head in anterior view. C: Head in dorsal view. D: Proximal antenna. E: Mesosoma in dorsal view; not = notaulus, with arrow indicating the end. F: Fore wing in lateral view. G: Punctuation pattern on third metasomal tergite in dorsal view (not to scale).

Paratypes (5 ♀)—USA • 1 ♀; same locality as holotype; reared from gall of *Neuroterus saltarius* on *Quercus macrocarpa*; gall collected 27 June 2016; emerged 8 Aug 2016; DNA sequence voucher # 358-021-3B; GenBank

Accession # OR372001; PSUC_FEM_255531 • 1 ♀; Iowa, Iowa City, Spirit Lake; reared from gall of *Druon ignotum* on *Quercus macrocarpa*; gall collected 5 Aug 2017; emerged 28 Aug 2017; DNA sequence voucher # 1051-008-11B; GenBank Accession # OR372062; PSUC_FEM_255515 • 1 ♀; Pennsylvania, Centre County, State College, PSU campus near HUB; DC Montelongo leg.; reared from gall of *Neuroterus saltarius* on *Quercus* sp.; gall collected 11 June 2020; emerged 11 June 2020; PSUC_FEM_255659 (deposited at USNM) • 2 ♀; same locality, collector, and host gall as preceding; gall collected 12 June 2020; emerged 12 June 2020; PSUC_FEM_255695; 255696.

Etymology. Named for Iktomi, a trickster spirit derived from folklore of several groups of indigenous Americans, especially the Lakota. Iktomi is frequently portrayed as a spider who uses his cunning and inclination for mischief to provide learning opportunities relating to morality.

Diagnosis. *Ceroptres iktomii* is distinct from nearly all known *Ceroptres* on the basis of the length of F1, which is longer than F2 (Fig. 8D). This character state is shared only by *C. nigriscrus* Lobato-Vila & Pujade-Villar, 2019; these two species are easily differentiated by the color of the hind leg (nearly entirely black in *C. nigriscrus* but brownish in *C. iktomii* [Fig. 8A]) and the dimensions of the apical flagellomere (2.7× as long as wide in *C. nigriscrus* but 3.8× as long as wide in *C. iktomii* [Fig. 8A]).

Description. Female—Body 0.8–1.1 mm in length ($\bar{x}$ = 1.0; n = 6). Head and mesosoma entirely brown. Metasoma brown. Antennae 12-segmented, subclavate, about two thirds as long as body. Pedicel 1.5× as long as wide. F1 1.1× as long as F2. Apical flagellomere 3.8× as long as wide. Head in anterior view subtrapezoidal. Dorsal head sculpture coriaceous; conspicuously sculptured throughout. Frons sculpture excluding facial carinae coriaceous. Facial vertical carinae distinct, reaching about one third across lower face. Transfacial line 0.9× as long as compound eye. Malar space 0.4× length of compound eye. POL:LOL:OOL:DLO in holotype 10:5:4:3. POL twice LOL and slightly longer than twice OOL. OOL slightly shorter than LOL, longer than DLO. Mesopleuron smooth and shining, without apparent sculpture. Lateral pronotum sculpture weakly coriaceous but conspicuously sculptured throughout. Mesoscutum sculpture coriaceous to alutaceous. Notauli incomplete, distinct only in posterior third of mesoscutum. Mesoscutellar disc strongly rugose with interspaces coriaceous. Mesoscutellar foveae distinct, short, and subrectangular, separated by narrow carina. Metapleural sulcus meeting mesopleuron at about four fifths height. Lateral propodeal carinae conspicuous; more or less straight and subparallel. Fore wing marginal cell 2.8× as long as wide. Fore wing marginal setae distinct; very long. Legs with coxae, trochanters, and femora brown, tibiae light brown, and tarsi yellow except apical tarsomere which is brown. Tarsal claws with conspicuous, blunt, rounded basal lobe. Metasoma excluding ovipositor and sheaths in lateral view subequal to combined length of head and mesosoma. Hypopygial spine strongly projecting, with prominent projecting portion about 1.3x as long as wide. Third metasomal tergite with a small patch of scattered punctures posterodorsally.

Male—Unknown.

Biology. *Ceroptres iktomii* was reared from asexual generation galls of *Druon ignotum* (Bassett, 1881) on *Quercus macrocarpa* Michx. and asexual generation galls of *Neuroterus saltarius* Weld, 1926 on *Q. bicolor* Willd. and *Q. macrocarpa*.

Distribution. Iowa City, Iowa and State College, Pennsylvania (USA).

Remarks. *Ceroptres iktomii* corresponds to Ward *et al.*'s (2024) “species 23”.

Ceroptres jabbai Nastasi, Smith, & Davis sp. nov.

Fig. 9

urn:lsid:zoobank.org:act:F691E475-4634-45D0-B073-7BEA1527B8AB

Material examined. Holotype ♀—USA • Pennsylvania, Huntingdon County, State Game Lands 322; A Guiguet leg.; reared from gall of *Kokkocynips rileyi* on *Quercus rubra*; gall collected 6 Sep 2020; emerged 18–21 June 2021; PSUC_FEM_255598.

Paratypes (5 ♀ and 4 ♂)—USA • 1 ♂; Iowa, Effigy Mounds; 43.088, -91.187; reared from gall of *Kokkocynips imbricariae* on *Quercus rubra*; gall collected 6 Oct 2018; emerged 25 Nov 2019; DNA sequence voucher # 1564-59-2; GenBank Accession # OR372088; PSUC_FEM_255560 • 1 ♂; Ohio, Union Township, rest stop on I-70W, 13 miles west of Wheeling, West Virginia; reared from gall of *Kokkocynips rileyi* on *Quercus rubra*; gall collected 10 Sep 2017; emerged 17 Sep 2018; DNA sequence voucher # 1194-093-2C; GenBank Accession # OR372068;

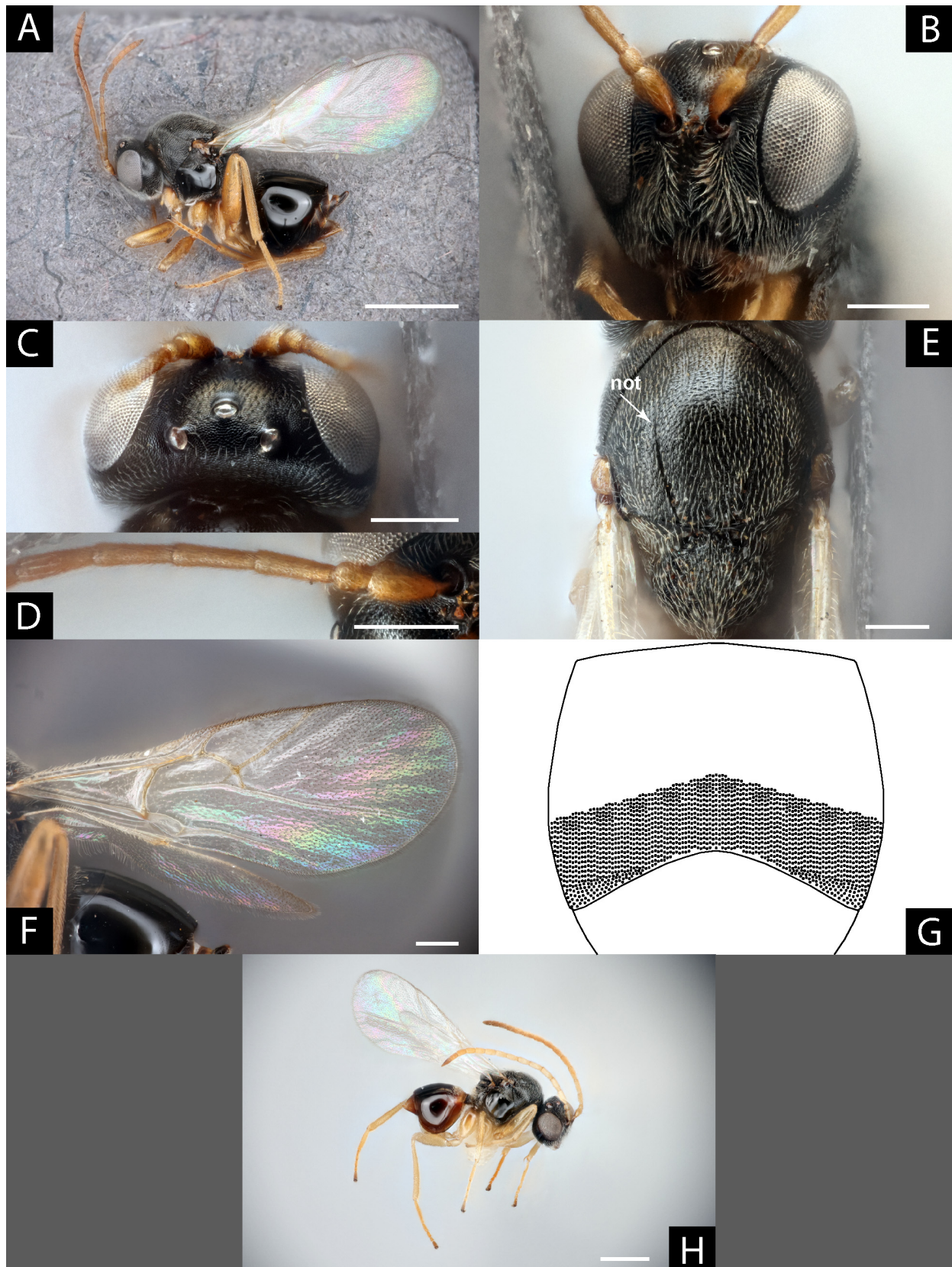


FIGURE 9. *Ceroptres jabbai* Nastasi, Smith, & Davis sp. nov. A–G: Holotype female (PSUC_FEM_255598); H: Paratype male (PSUC_FEM_255566). Scale bars: A & H = 1.0 mm; B–F = 0.5 mm. A: Adult female, lateral habitus. B: Head in anterior view. C: Head in dorsal view. D: Proximal antenna. E: Mesosoma in dorsal view; not = notaulus, with arrow indicating end of distinct portion. F: Fore wing. G: Punctuation pattern on third metasomal tergite in dorsal view (not to scale). H: Adult male, lateral habitus.

PSUC_FEM_255566 • 2 ♀; Pennsylvania, Centre County, State Game Lands 176; A Guiguet leg.; reared from gall of *Kokkocynips decidua* on *Quercus rubra*; gall collected 4 Oct 2020; emerged 23–26 July 2021; PSUC_FEM_255682–255683 (specimen PSUC_FEM_255683 deposited at USNM) • 1 ♂; Pennsylvania, Centre County, Patton Woods; AR Deans leg.; reared from gall of *Kokkocynips decidua* on *Quercus* sp., species of red oak; gall collected 3 Oct 2020; emerged 23–26 July 2021; PSUC_FEM_255618 (deposited at USNM) • 1 ♀; Pennsylvania, Centre County, Pine Grove Mills; AR Deans leg.; reared from gall of *Kokkocynips rileyi* on *Quercus rubra*; gall collected 30 Sep 2020; emerged 23–24 Aug 2021; PSUC_FEM_255604 • 1 ♂; Pennsylvania, Pennsylvania Furnace; DC Montelongo leg.; reared from gall of *Kokkocynips rileyi* on *Quercus rubra*; gall collected 24 Sep 2020; emerged 11–15 June 2021; PSUC_FEM_255592 • 1 ♀; Pennsylvania, Pine Grove Mills; AR Deans leg.; reared from gall of *Kokkocynips rileyi* on *Quercus rubra*; gall collected 29 Sep 2020; emerged 11–15 June 2021; PSUC_FEM_255593 • 1 ♀; Pennsylvania, Pine Grove Mills; AR Deans leg.; reared from gall of *Kokkocynips rileyi* on *Quercus rubra*; gall collected 12 Sep 2020; emerged 12 Sep 2020; PSUC_FEM_255641.

Etymology. Named for Jabba the Hutt, a crimelord from the *Star Wars* franchise. Jabba is known for his indulgence in all senses, which is particularly showcased in the 1983 film *Return of the Jedi*. We apply this name to *C. jabbai* specifically because *C. jabbai* exhibits the most expansive host preferences of known *Ceroptres* species, with three known host gall species, therein displaying overindulgence in an inquiline gall wasp.

Diagnosis. *Ceroptres jabbai* can be distinguished from all other *Ceroptres* by the following combination of characters: Female antennae 13-segmented (Fig. 9A). Third metasomal tergite with distinct patch of posterodorsal punctures overtaking most of the tergite (Fig. 9G). Mesoscutellar disc rugose throughout (Fig. 9E). Malar space short, 0.3× as long as compound eye (Fig. 9B).

Description. Female—Body 1.9–2.6 mm in length ($\bar{x}$ = 2.4; n = 5). Head and mesosoma entirely black. Metasoma dark brown. Antennae 13-segmented, subclavate, about two thirds as long as body. Pedicel 2.0× as long as wide. F1 1.0× as long as F2. Apical flagellomere 2.7× as long as wide. Head in anterior view subtrapezoidal. Dorsal head sculpture coriaceous; conspicuously sculptured throughout. Frons sculpture excluding facial carinae coriaceous. Facial vertical carinae distinct, reaching about halfway across lower face. Transfacial line 0.8× as long as compound eye. Malar space 0.3× length of compound eye. POL:LOL:OOL:DLO in holotype 20:10:10:7. POL twice LOL and OOL. OOL equal to LOL, longer than DLO. Lateral pronotum sculpture coriaceous. Mesopleuron smooth and shining, without apparent sculpture. Mesoscutum sculpture coriaceous-imbricate with setiferous punctation throughout. Notauli incomplete, indistinct in anterior half of mesoscutum. Mesoscutellar disc coriaceous anteriorly and medially, only appearing strongly rugose posteriorly. Mesoscutellar foveae distinct, somewhat longer, and subrectangular, separated by narrow carina. Metapleural sulcus meeting mesopleuron at about four fifths height. Lateral propodeal carinae conspicuous; more or less straight and subparallel. Fore wing marginal cell 2.6× as long as wide. Fore wing marginal setae distinct; long. Legs uniformly yellow except metacoxae and apical tarsomeres which are at least partly slightly infuscated. Tarsal claws with conspicuous, strong basal tooth. Metasoma excluding ovipositor and sheaths in lateral view subequal to combined length of head and mesosoma. Hypopygial spine only very slightly projecting; prominent projecting portion about as long as wide. Third metasomal tergite with a very large posterodorsal patch of scattered punctures overtaking most of the tergite.

Male—Same as female except for the following: Body 1.4–1.9 mm in length ($\bar{x}$ = 1.7; n = 2). Antennae 15-segmented, subequal to body length. Pedicel 1.6× as long as wide. Apical flagellomere 2.9× as long as wide. Metasoma smaller than in female.

Biology. *Ceroptres jabbai* was reared from galls of *Kokkocynips decidua* (Beutenmüller, 1913), *K. imbricariae* (Ashmead, 1896), and *K. rileyi* (Ashmead, 1896), all on *Quercus rubra* L. All host galls were the asexual generation.

Distribution. Effigy Mounds, Iowa, and numerous localities in central Pennsylvania (USA).

Remarks. *Ceroptres jabbai* corresponds to Ward *et al.*'s (2024) “species COI-C”.

Ceroptres jarethi Nastasi, Smith, & Davis sp. nov.

Fig. 10

urn:lsid:zoobank.org:act:0642FA46-2EDF-4BE7-8451-770280CFD16F

Material examined. Holotype ♀—USA • Michigan, Traverse City, backyard; reared from gall of *Callirhytis quercusgemmaria* on *Quercus rubra*; gall collected 13 Aug 2017; emerged 27 June 2018; DNA sequence voucher # 1076-101-18; GenBank Accession # OR372065; PSUC_FEM_255570.

Etymology. Named for Jareth the Goblin King, the primary antagonist portrayed by David Bowie in Jim Henson's *Labyrinth* who is a thief, trickster, and master of disguise.

Diagnosis. Female *Ceroptres jarethi* may be distinguished by all other known *Ceroptres* by the following combination of characters: Antennae 13-segmented (Fig. 10A). F1 equal to F2 (Fig. 10D). Mesoscutellar disc strongly rugose throughout (Fig. 10E). Mesoscutellar foveae separated by a wide septum nearly as wide as either fovea (Fig. 10E). Apical flagellomere short, only 2.5× as long as wide (Fig. 10A).

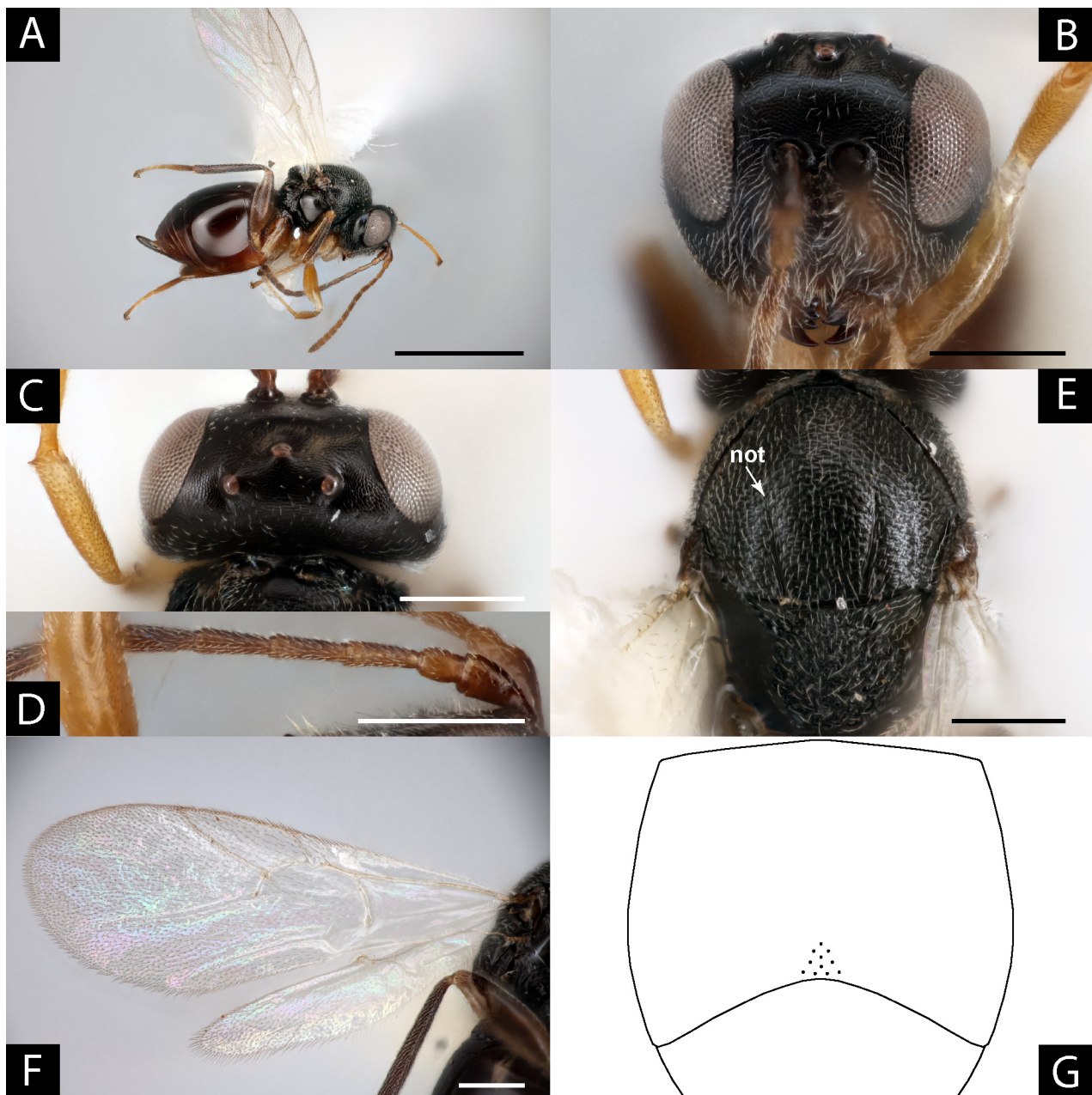


FIGURE 10. Diagnostic characters of *Ceroptres jarethi* Nastasi, Smith, & Davis sp. nov. All images show holotype female (PSUC_FEM_255570). Scale bars: A = 1.0 mm; B–F = 0.25 mm. A: Lateral habitus. B: Head in anterior view. C: Head in dorsal view. D: Proximal antenna. E: Mesosoma in dorsal view; not = notaulus, with arrow indicating the end. F: Fore wing in lateral view. G: Punctuation pattern on third metasomal tergite in dorsal view (not to scale).

Description. Female—Holotype body 1.8 mm in length. Head and mesosoma entirely black. Metasoma brown. Antennae 13-segmented, subclavate, about two thirds as long as body. Pedicel 1.3× as long as wide. F1 1.0× as long as F2. Apical flagellomere 2.5× as long as wide. Head in anterior view subtrapezoidal. Dorsal head sculpture coriaceous; conspicuously sculptured throughout. Frons sculpture excluding facial carinae coriaceous. Facial vertical carinae distinct, reaching about one third across lower face. Transfacial line 0.9× as long as compound eye. Malar space 0.5× length of compound eye. POL:LOL:OOL:DLO in holotype 15:8:7:5. POL slightly less than twice LOL and slightly more than twice OOL. OOL slightly longer than LOL, longer than DLO. Lateral pronotum sculpture coriaceous. Mesopleuron smooth and shining, without apparent sculpture. Mesoscutum sculpture coriaceous with distinct setiferous punctation throughout. Notauli incomplete, indistinct in anterior half of mesoscutum. Mesoscutellar disc strongly rugose with interspaces coriaceous. Mesoscutellar foveae distinct, short, and subrectangular, separated by wide septum. Metapleural sulcus meeting mesopleuron at about three quarters height. Lateral propodeal carinae conspicuous; more or less straight and subparallel. Fore wing marginal cell 3.1× as long as wide. Fore wing marginal setae distinct; short. Fore legs entirely yellow except apical tarsomeres infuscated; mid and hind legs brown except tarsi yellow with infuscated apical tarsomeres. Tarsal claws with conspicuous, strong basal tooth. Metasoma excluding ovipositor and sheaths in lateral view subequal to combined length of head and mesosoma. Hypopygial spine only very slightly projecting; prominent projecting portion about as long as wide. Third metasomal tergite with a small patch of scattered punctures posterodorsally.

Male—Unknown.

Biology. *Ceroptres jarethi* was reared from asexual generation galls of *Callirhytis quercusgemmaria* (Ashmead, 1885) on *Quercus rubra* L.

Distribution. Traverse City, Michigan (USA).

Remarks. *Ceroptres jarethi* corresponds to Ward *et al.*'s (2024) “species 6b”.

Ceroptres lokii Nastasi, Smith, & Davis sp. nov.

Figs. 11–12

urn:lsid:zoobank.org:act:67E838DF-9CE9-4617-B316-D9F4D168E7AF

Material examined. Holotype ♀—USA • Iowa, Iowa City, Hickory Hills Park; reared from gall of *Philonix nigra* on *Quercus alba*; gall collected 18 July 2018; emerged 31 May 2019; DNA sequence voucher # 1443-023-2A; GenBank Accession # OR372081; PSUC_FEM_255534.

Paratypes (6 ♀ and 3 ♂)—CANADA • 1 ♀; Manitoba, Warren, 3.5 E along Hwy 67, PMT at 67; 50.12307, -97.44780; Chris Friesen leg.; reared from gall of *Acraspis quercushirta* on *Quercus macrocarpa*; gall collected 5 Sep 2021; emerged 6–7 June 2022; PSUC_FEM_254600 • 1 ♀; Manitoba, Warren, oak woodland along train tracks; 50.12785, -97.53930; Chris Friesen leg.; reared from gall of *Philonix nigra* on *Quercus macrocarpa*; gall collected 8 Sep 2021; emerged May 2022; PSUC_FEM_254602. USA • 1 ♂; Iowa, Iowa City, Hickory Hills Park; reared from gall of *Acraspis quercushirta* on *Quercus macrocarpa*; gall collected 27 Sep 2016; emerged 23 May 2017; DNA sequence voucher # 646-001-7B; GenBank Accession # OR372020; PSUC_FEM_255504 • 1 ♀; same locality as preceding; reared from gall of *Acraspis macrocarpa* on *Quercus macrocarpa*; gall collected 18 July 2018; emerged 17 Sep 2018; DNA sequence voucher # 1442-001-4; GenBank Accession # OR372080; PSUC_FEM_255505 • 1 ♂; New York, Vestal, Vestal Hills Elementary School; 42.085, -75.945; reared from gall of *Philonix nigra* on *Quercus alba*; gall collected 17 Oct 2018; emerged 16 June 2019; DNA sequence voucher # 1568-023-3A; GenBank Accession # OR372090; PSUC_FEM_255535 • 1 ♂; same locality as preceding; reared from gall of *Acraspis erinacei* on *Quercus alba*; gall collected 17 Oct 2018; emerged 31 May 2019; DNA sequence voucher # 1566-002-3A; GenBank Accession # OR372089; PSUC_FEM_255506 • 2 ♀; Pennsylvania, State College, PSU campus near Theater Building and Stuckerman Building; AR Deans & HM Hines leg.; reared from gall of *Philonix nigra* on *Quercus alba*; gall collected 25 Oct 2019; PSUC_FEM_255594; 255596 • 1 ♀; Pennsylvania, State College, Holmes Foster Park; LF Nastasi leg.; reared from gall of *Acraspis quercushirta* on *Quercus alba*; gall collected 22 Oct 2020; PSUC_FEM_255595.

Etymology. Named for Loki, a trickster god originating in Norse mythology and since appearing in a wide variety of contexts. Additionally, *C. lokii* may comprise multiple species, therein further embodying the infamous trickster tendencies of its namesake.



FIGURE 11. Lateral habitus of *Ceroptres lokii* Nastasi, Smith, & Davis sp. nov. Scale bars = 1.0 mm. A: Holotype female (PSUC_FEM_255534) reared from gall of *Philonix nigra* on *Quercus alba*. B: Paratype female (PSUC_FEM_255505) reared from gall of *Acraspis macrocarpae* on *Quercus macrocarpa*. C: Paratype male (PSUC_FEM_255504) reared from gall of *Acraspis quercushirta* on *Quercus macrocarpa*. D: Paratype male (PSUC_FEM_255506) reared from gall of *Acraspis erinacei* on *Quercus alba*.

Diagnosis. *Ceroptres lokii* is very similar to *C. pisum* (Osten-Sacken, 1861); in both species, the head has a distinct “halo” of yellowish coloration around the oral fovea (Fig. 12A) and metasomal tergite 3 has a prolonged line of punctures continuing for at least a short distance along the posterior margin (e.g., Fig. 12G). However, *C. lokii* is easily distinguished from *C. pisum* by the length of the dimensions of the apical flagellomere (nearly 4.0× as long as wide in *C. pisum* and 2.8–3.2× as long as wide in *C. lokii* [e.g., Fig. 11B]). The punctation patterns on the third metasomal tergite are also diagnostic; the punctation extends further laterally in *C. lokii* (Fig. 12G) and is visible in lateral view continuing along the posterior tergite, but in *C. pisum* is less extended laterally (Fig. 25F) and not distinctly visible in lateral view.

Description. Female—Body 1.6–2.8 mm in length ($\bar{x}$ = 2.5; n = 10). Head and mesosoma entirely black except for lightened area around oral fovea. Metasoma dark brown. Antennae 13-segmented, subclavate, about three quarters as long as body. Pedicel about 1.4× as long as wide. F1 0.7× as long as F2. Apical flagellomere about 2.7–3.2× as long as wide. Head in anterior view subtrapezoidal. Dorsal head sculpture coriaceous; conspicuously sculptured throughout. Frons sculpture excluding facial carinae coriaceous. Facial vertical carinae distinct, reaching about two thirds across lower face. Transfacial line 0.9× as long as compound eye. Malar space 0.4× length of compound eye. POL:LOL:OOL:DLO in holotype 18:7:7:7. POL twice LOL and OOL. OOL equal to LOL, equal to DLO. Lateral pronotum sculpture coriaceous. Mesopleuron smooth and shining, without apparent sculpture. Mesoscutum sculpture coriaceous with distinct setiferous punctation throughout. Notauli complete, moderately well impressed across entire length of mesoscutum. Mesoscutellar disc strongly rugose with interspaces coriaceous. Mesoscutellar foveae distinct, short, and ovate, separated by narrow carina. Metapleural sulcus meeting mesopleuron at about three quarters height. Lateral propodeal carinae conspicuous; more or less straight and subparallel. Fore wing marginal cell 3.0× as long as wide. Fore wing marginal setae distinct; long. Legs uniformly yellow except coxae and apical tarsomeres at least partly infuscated distally. Tarsal claws with conspicuous, strong basal tooth.

Metasoma excluding ovipositor and sheaths in lateral view subequal to combined length of head and mesosoma. Hypopygial spine not conspicuously projecting. Third metasomal tergite with a posterodorsal patch of punctures which continues as a band laterally at least for a short distance along posterior margin.

Male—Same as female except for the following: Body 1.7–2.6 mm in length ($\bar{x}$ = 2.2; n = 3). Antennae 15-segmented. Pedicel 1.1× as long as wide. Head sometimes with yellow coloration more extensive, reaching toruli in anterior view and continuing along genae and postgenae in lateral view.

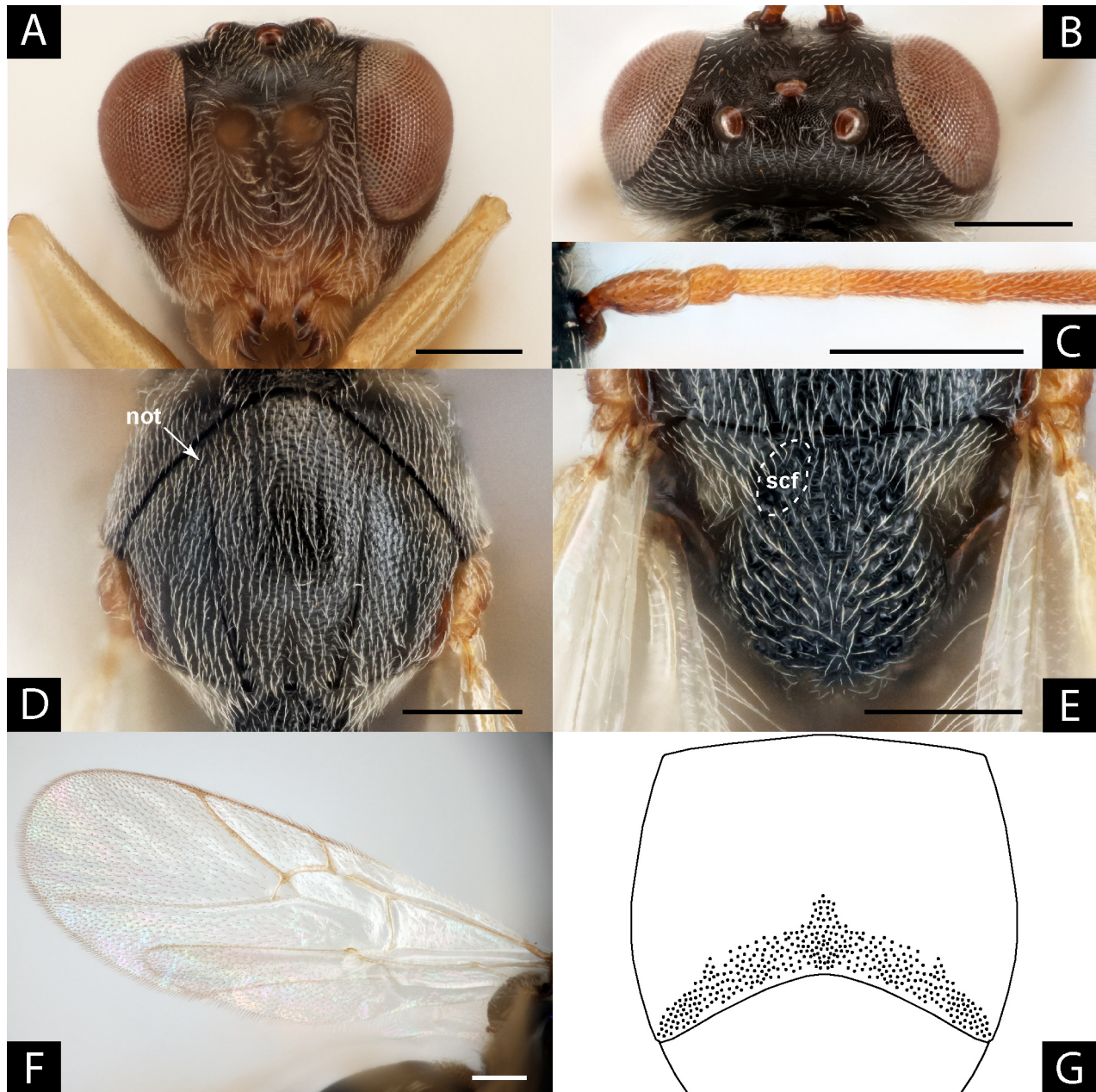


FIGURE 12. Diagnostic characters of *Ceroptres lokii* Nastasi, Smith, & Davis sp. nov. All images show holotype female (PSUC_FEM_255534) reared from gall of *Philonix nigra* on *Quercus alba*. Scale bars = 0.25 mm. A: Head in anterior view. B: Head in dorsal view. C: Proximal antenna. D: Anterior mesoscutum in dorsal view; not = notaulus, with arrow indicating the end. E: Scutellum in dorsal view; scf = mesoscutellar fovea. F: Punctuation pattern on third metasomal tergite in dorsal view (not to scale). G: Line drawing of the third metasomal tergite showing the punctation pattern.

Biology. *Ceroptres lokii* has been reared from galls of *Acraspis erinacei* (Beutenmüller, 1909) on *Quercus alba* L., *A. quercushirta* Bassett, 1864 on *Q. macrocarpa* Michx., and *Philonix nigra* (Gillette, 1889) on both *Q. alba* and *Q. macrocarpa*. Ward *et al.* (2024) also recorded this species from galls of *Acraspis macrocarpae* Bassett, 1890 on

Q. macrocarpa (Ward *et al.* 2024), although *A. macrocarpae* was recently synonymized with *Acraspis quercushirta* (Nicholls *et al.* 2022). All known host galls were the asexual generation.

Distribution. Ward *et al.* (2024) collected galls producing *Ceroptres lokii* from Iowa City, Iowa and Vestal, New York (USA). We examined new material reared from Warren, Manitoba (Canada) and State College, Pennsylvania (USA).

Remarks. Ward *et al.*'s sequences corresponding to *Ceroptres lokii* formed a monophyletic clade that appears sister to other Nearctic *Ceroptres* associated with galls of Cynipini. Their species delimitation analyses suggested the presence of as many as three species: one associated with *Philonix nigra* on *Q. alba* (Ward *et al.*'s "species 28"), a second associated with *Acraspis erinacei* on *Q. alba* ("species COI-E"), and a third associated with galls of *A. quercushirta* and *P. nigra* on *Q. macrocarpa* ("species 26"). Our morphological examination revealed great morphological variability between individuals, especially regarding the dimensions of the apical flagellomere, the extent of punctation of the metasoma, and, to a lesser degree, coloration. Until further revisionary work on *Ceroptres* can be undertaken and more material can be studied, we consider these specimens to represent a single species, as it is currently unclear whether these specimens represent a single highly polymorphic species or a complex of multiple morphologically distinct species.

Ceroptres lupini Nastasi, Smith, & Davis sp. nov.

Fig. 13

urn:lsid:zoobank.org:act:5D6DA236-EB40-4839-A9C3-3B2C36A28561

Material examined. Holotype ♀—USA • Iowa, Tiffin, FW Kent Park; reared from gall of *Zopheroteris sphaerula* on *Quercus rubra*; gall collected 18 Oct 2016; emerged 15 May 2017; DNA sequence voucher #667-062-6; GenBank Accession # OR372024; PSUC_FEM_255561.

Paratypes (11 ♀)—USA • 1 ♀; Iowa, Coralville, North Pavilion Park; reared from gall of *Melikaiella ostensackeni* on *Quercus rubra*; gall collected 6 June 2017; emerged 22 May 2018; DNA sequence voucher # 853-016-23; GenBank Accession # OR372037; PSUC_FEM_255529 • 1 ♀; Iowa, Elkader, Turkey River; 42.843, -91.187; reared from gall of *Zopheroteris sphaerula* on *Quercus rubra*; gall collected 6 Oct 2018; emerged 5 May 2019; DNA sequence voucher # 1563-062-4; GenBank Accession # OR372086; PSUC_FEM_255562 • 1 ♀; Pennsylvania, Centre County, State College, Curtin Rd.; AR Casadei leg.; reared from gall of *Zopheroteris sphaerula* on *Quercus rubra*; gall collected 27 Sep 2021; emerged before 18 Feb 2022; PSUC_FEM_255627 • 2 ♀; Pennsylvania, Centre County, State College, Penn State campus outside Mueller Lab; A Guiguet leg.; reared from gall of *Zopheroteris sphaerula* on *Quercus rubra*; gall collected 13 Oct 2020; emerged 18–19 May 2021; PSUC_FEM_253574–253575 (specimen PSUC_FEM_253574 deposited at USNM) • 5 ♀; Pennsylvania, Centre County, PSU campus near student health center; AR Deans leg.; reared from gall of *Zopheroteris sphaerula* on *Quercus* sp.; gall collected 7 Oct 2021; emerged 17–18 May 2022; PSUC_FEM_255660–255664 • 1 ♀; Pennsylvania, State College, Outside Mueller Lab; A Guiguet leg.; reared from gall of *Zopheroteris sphaerula* on *Quercus* sp.; gall collected 13 Oct 2020; emerged 12 Mar 2021; PSUC_FEM_255591 (deposited at USNM).

Etymology. Named for Arsène Lupin, a fictional thief initially appearing in early-1900s French serials written by Maurice Leblanc.

Diagnosis. See diagnosis to *C. mallowi*. *Ceroptres lupini* shares a host gall with *C. curupira*; characters useful for distinguishing these two species are given in the diagnosis to *C. curupira*.

Description. Female—Body 1.4–2.2 mm in length ($\bar{x}$ = 1.9; n = 12). Head and mesosoma entirely black. Metasoma black. Antennae 12-segmented, subclavate, about two thirds as long as body. Pedicel 1.3× as long as wide. F1 0.9× as long as F2. Apical flagellomere 3.2× as long as wide. Head in anterior view subtrapezoidal. Dorsal head sculpture coriaceous; conspicuously sculptured throughout. Frons sculpture excluding facial carinae coriaceous. Facial vertical carinae distinct, reaching about one third across lower face. Transfacial line 0.8× as long as compound eye. Malar space 0.3× length of compound eye. POL:LOL:OOL:DLO in holotype 18:10:9:6. POL twice OOL and almost twice LOL. OOL equal to LOL, longer than DLO. Lateral pronotum sculpture coriaceous. Mesopleuron smooth and shining, without apparent sculpture. Mesoscutum sculpture coriaceous with distinct setiferous punctation throughout. Notauli incomplete, indistinct only in anterior third of mesoscutum. Mesoscutellar disc coriaceous anteriorly and medially, only appearing strongly rugose posteriorly. Mesoscutellar foveae distinct,

short, and subrectangular, separated by narrow carina. Metapleural sulcus meeting mesopleuron at about three quarters height. Lateral propodeal carinae conspicuous; more or less straight and subparallel. Fore wing marginal cell $2.5\times$ as long as wide. Fore wing marginal setae distinct; short. Legs with coxae, trochanters, femora, tibiae, and apical tarsomere brown; remaining tarsomeres yellow. Tarsal claws with conspicuous, strong basal tooth. Metasoma excluding ovipositor and sheaths in lateral view subequal to combined length of head and mesosoma. Hypopygial spine only very slightly projecting; prominent projecting portion about as long as wide. Third metasomal tergite with a small patch of scattered punctures posterodorsally.

Male—Unknown.

Biology. We reared *C. lupini* from asexual generation galls of *Melikaiella ostensackeni* Pujade-Villar, 2014 and asexual generation galls of *Zopheroteras sphaerula* Weld, 1926, both on *Quercus rubra* L.

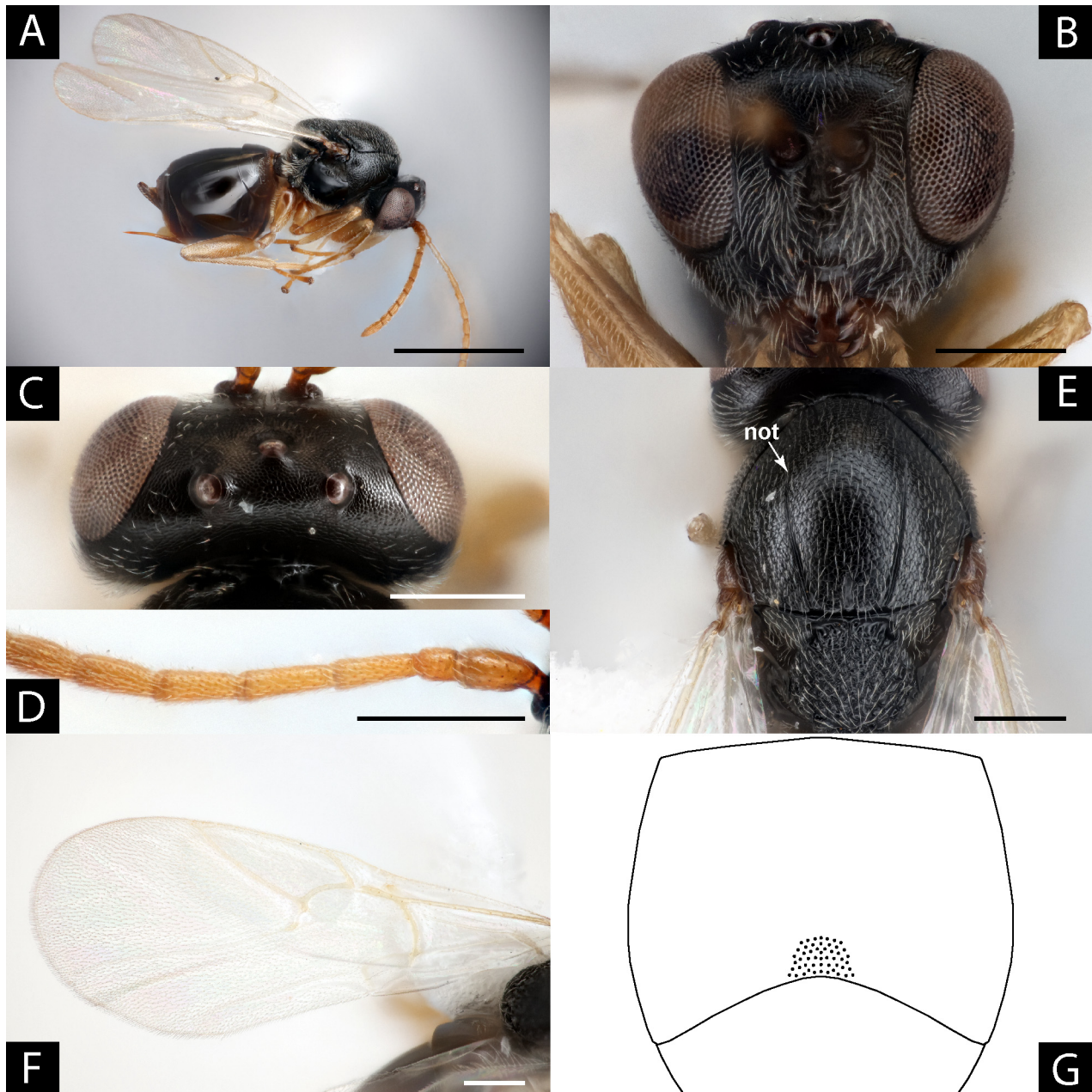


FIGURE 13. *Ceroptres lupini* Nastasi, Smith, & Davis sp. nov. All images show holotype female (PSUC_FEM_255561). Scale bars: A & F = 0.5 mm; B–F = 0.25 mm. A: Lateral habitus. B: Head in anterior view. C: Head in dorsal view. D: Proximal antenna. E: Mesosoma in dorsal view; not = notaulus, with arrow indicating end of distinct portion. F: Fore wing. G: Punctuation pattern on third metasomal tergite in dorsal view (not to scale).

Distribution. Coralville, Elkader, and Tiffin, Iowa, and State College, Pennsylvania (PA).

Remarks. *Ceroptres lupini* corresponds to part of Ward *et al.*'s (2024) "species 3" along with *C. curupira*. As a result of our morphological observations in combination with Ward *et al.*'s sequence data, it is apparent that their species 3 comprises at least two species, and possibly a third. Ward *et al.*'s species delimitation using DNA barcode data suggested the presence of three species, the third of which was represented by only a single male voucher that we are unable to match to either *C. lupini* or *C. curupira*. Ward *et al.*'s analysis of UCEs suggested the presence of only a single species, but their sequences corresponded to only individuals matched as a single species in their DNA barcode dataset.

***Ceroptres mallowi* Nastasi, Smith, & Davis sp. nov.**

Fig. 14

urn:lsid:zoobank.org:act:543DD2C7-D73B-4332-BC76-C217D8FA4B2E

Material examined. Holotype ♀—USA • Pennsylvania, White Oak, White Oak Park; reared from gall of *Callirhytis quercusfutilis* on *Quercus alba*; emerged 13 May 2017; voucher # 118-051-6A; PSUC_FEM_255552.

Paratypes (3 ♀)—USA • 1 ♀; Iowa, Iowa City, Hickory Hills Park; reared from gall of *Callirhytis quercusfutilis* on *Quercus alba*; gall collected 15 June 2017; emerged 2 May 2018; DNA sequence voucher # 899-051-20; GenBank Accession # number; PSUC_FEM_255549 • 2 ♀; Pennsylvania, State College, Musser Gap; collected while ovipositing into gall of *Callirhytis quercusfutilis* [reported on labels as *Andricus quercusfutilis*] on *Quercus alba*; collected 22 May 2021; PSUC_FEM_255619; 255700.

Etymology. Named for Hober Mallow, a character in Isaac Asimov's *Foundation* franchise who is portrayed as a trickster who plays an essential role in orchestrating an uprising against the oppressive Empire.

Diagnosis. *Ceroptres mallowi* is close to several species in which F1 is shorter than F2 (Fig. 14D), the third metasomal tergite has a small posterodorsal patch of punctures (Fig. 14G), and the LOL is longer than the OOL (Fig. 14C). Of these species, *C. mallowi* is closest to *C. lupini*. The two species are easily distinguishable based on the different head shapes (subquadrate in *C. mallowi* as in Fig. 14B and subtrapezoidal in *C. lupini* as in Fig. 13B) and by differences in sculpture of the mesoscutellar disc (rugose throughout with interspaces reticulate in *C. mallowi* as in Fig. 14E but coriaceous anteriorly and medially in *C. lupini* as in Fig. 13E).

Ceroptres mallowi was reared from the same host gall as *C. tikoloshei*. These two species are distinguished by the aforementioned characters, particularly the length of the notauli, which are indistinct only in anterior third in *C. mallowi* (Fig. 14E) but indistinct in anterior half in *C. tikoloshei* (Fig. 22E) and the length of the malar space, which is 0.3× as long as compound eye in *C. mallowi* (Fig. 14B) but 0.5× as long in *C. tikoloshei* (Fig. 22B).

Description. Female—Body 2.0–2.4 mm in length ($\bar{x}$ = 2.1; n = 3). Head and mesosoma entirely black or entirely dark brown. Metasoma dark brown. Antennae 12-segmented, subclavate, about two thirds as long as body. Pedicel 1.4× as long as wide. F1 0.8× as long as F2. Apical flagellomere 3.3× as long as wide. Head in anterior view subquadrate. Dorsal head sculpture coriaceous; conspicuously sculptured throughout. Frons sculpture excluding facial carinae coriaceous. Facial vertical carinae distinct, reaching about one third across lower face. Transfacial line 0.8× as long as compound eye. Malar space 0.3× length of compound eye. POL:LOL:OOL:DLO in holotype 17:8:7:5. POL slightly longer than twice LOL and OOL. OOL slightly shorter than LOL, longer than DLO. Lateral pronotum sculpture coriaceous. Mesopleuron smooth and shining, without apparent sculpture. Mesoscutum sculpture coriaceous with distinct setiferous punctation throughout. Notauli incomplete, indistinct in anterior third of mesoscutum. Mesoscutellar disc strongly rugose with interspaces coriaceous. Mesoscutellar foveae distinct, short, and subrectangular, separated by narrow carina. Metapleural sulcus meeting mesopleuron at about three quarters height. Lateral propodeal carinae conspicuous; more or less straight and subparallel. Fore wing marginal cell 2.6× as long as wide. Fore wing marginal setae distinct; short. Legs uniformly yellow except metacoxae and apical tarsomeres which are at least partly slightly infuscated. Tarsal claws with conspicuous, strong basal tooth. Metasoma excluding ovipositor and sheaths in lateral view subequal to combined length of head and mesosoma. Hypopygial spine only very slightly projecting; prominent projecting portion about as long as wide. Third metasomal tergite with a small patch of scattered punctures posterodorsally.

Male—Unknown.

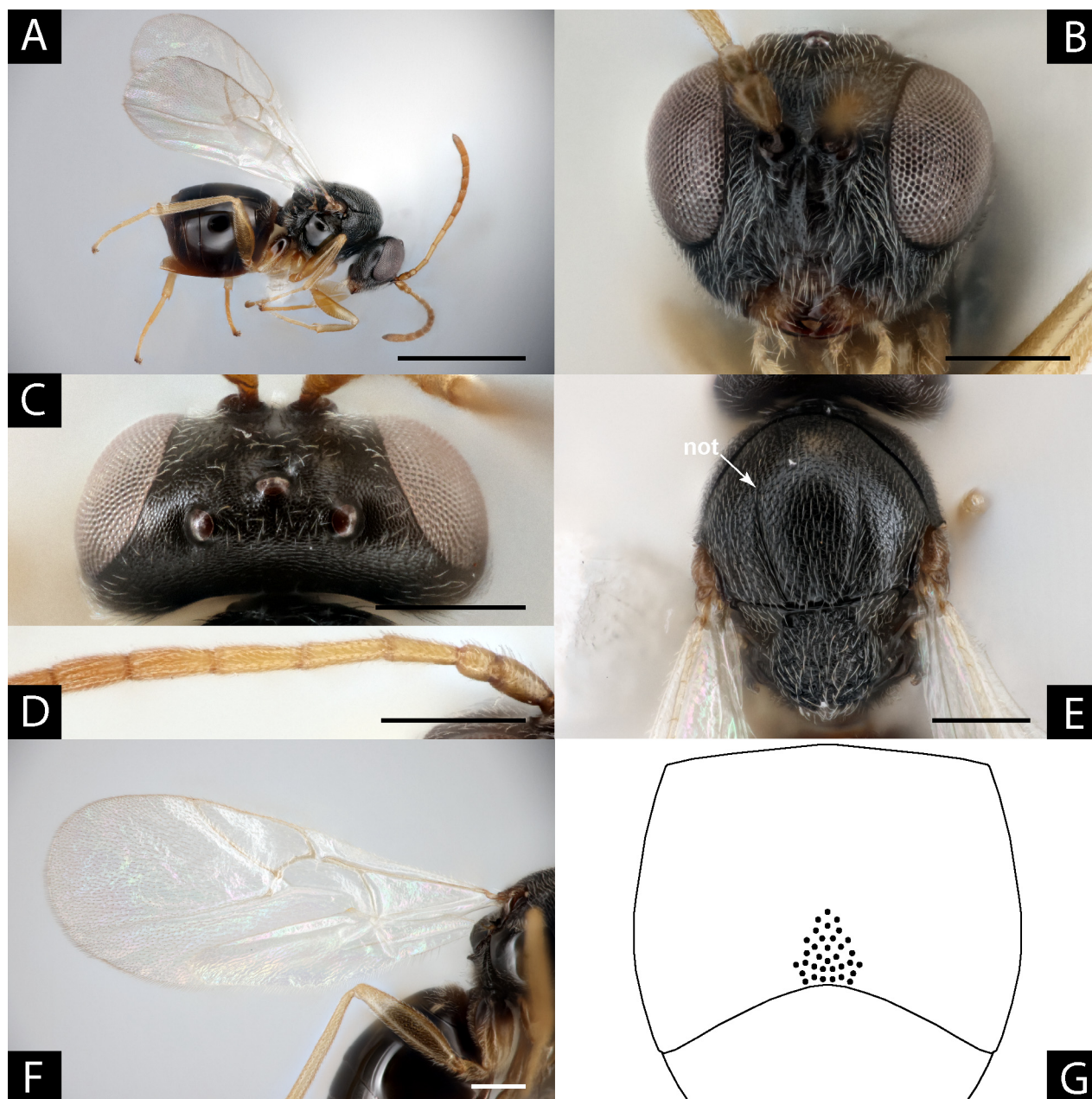


FIGURE 14. *Ceroptres mallowi* Nastasi, Smith, & Davis sp. nov. All images show holotype female (PSUC_FEM_255552). Scale bars: A & F = 0.5 mm; B–F = 0.25 mm. A: Lateral habitus. B: Head in anterior view. C: Head in dorsal view. D: Proximal antenna. E: Mesosoma in dorsal view; not = notaulus, with arrow indicating end of distinct portion. F: Fore wing. G: Punctuation pattern on third metasomal tergite in dorsal view (not to scale).

Biology. *Ceroptres mallowi* has been reared from sexual generation galls of *Callirhytis quercusfutilis* (Osten Sacken, 1861) on *Quercus alba* L. Ward *et al.* (2024) also reared individuals with sequences matching *C. mallowi* from galls of *Neuroterus*, but vouchers from this host were unavailable for morphological examination.

Distribution. Known from two US states: Iowa (Hickory Hills Park and Mormon Hand Cart Trail, both in Iowa City) and Pennsylvania (White Oak Park, White Oak).

Remarks. *Ceroptres mallowi* corresponds to Ward *et al.*'s (2024) “species 15-16”; their analysis of UCEs found *C. mallowi* to comprise two separate, paraphyletic species, although their analysis of DNA barcodes found them to represent a single well-supported species. Our assessment finds that they are all alike in morphology, thus corresponding with the suggestion of their analysis of DNA barcodes.

Ceroptres mallowi is morphologically very similar to *C. bruti* and *C. tikoloshei*, and all three are associated with galls of *Callirhytis* Förster, 1869 on white oaks; both *C. mallowi* and *C. tikoloshei* have been reared from galls

of *Callirhytis quercusfutilis*. In addition to the morphological characters discussed in the diagnosis, their distinction is reiterated by Ward *et al.*'s analysis of DNA barcodes, wherein the three species fall into distant, entirely separate clades.

***Ceroptres promethei* Nastasi, Smith, & Davis sp. nov.**

Fig. 15

urn:lsid:zoobank.org:act:93641685-5D49-4FDA-8256-B1BF149BC550

Material examined. Holotype ♀—USA • Iowa, Iowa City, Horn Elementary School; reared from gall of *Andricus dimorphus* on *Quercus macrocarpa*; gall collected 17 Sep 2017; emerged 19 Sep 2018; DNA sequence voucher # 1218-005-3; GenBank Accession # OR372070; PSUC_FEM_255508.

Paratypes (3 ♂)—USA • 1 ♂; Iowa, Lansing, Mt. Hosmer; 43.385, -91.222; reared from gall of *Andricus dimorphus* on *Quercus macrocarpa*; gall collected 6 Oct 2018; emerged 1 Sep 2019; DNA sequence voucher # 1553-005-14; GenBank Accession # OR372085; PSUC_FEM_255509 • 1 ♂; Iowa, Iowa City, Hickory Hills Park; reared from gall of *Andricus nigricens* on *Quercus bicolor*; gall collected 27 Sep 2016; emerged 14 Sep 2017; DNA sequence voucher # 642-009-31B; GenBank Accession # OR372016; PSUC_FEM_255516 • 1 ♂; same locality as previous; reared from gall of *Andricus dimorphus* on *Quercus macrocarpa*; gall collected 27 Sep 2016; emerged 22 Sep 2017; DNA sequence voucher # 645-005-2; GenBank Accession # OR372017; PSUC_FEM_255507.

Etymology. Named for Prometheus, a titan from Greek mythology who was credited with stealing fire from the Olympian gods and bestowing it upon humanity to aid in their progress as a civilization. We apply this name to *C. promethei* specifically because *C. promethei* is one of the few *Ceroptres* species with reddish body coloration, therein exhibiting the color of fire.

Diagnosis. *Ceroptres promethei* resembles *C. confertus* (McCracken & Egbert, 1922) due to the lighter rufous body coloration of the female. Lobato-Vila & Pujade-Villar (2019) mention two other species (*C. quercusobtusilobae* [Karsch, 1880] and *C. rufiventris* Ashmead 1896) whose types appear rufous, but they suggest that the rufous coloration of these specimens is due to discoloration as Ashmead's original description states that the head and mesosoma of the holotype are black. As a result, we consider only *C. confertus* and *C. promethei* to truly exhibit rufous body coloration. Female *C. promethei* can be distinguished from *C. confertus* by the following combination of characters: Antennae 12-segmented (Fig. 15A) (13-segmented in *C. confertus*). Facial vertical carinae distinct, reaching about two thirds across lower face (Fig. 15B) (carinae apparently entirely absent in *C. confertus*). F1 1.0× as long as F2 (Fig. 15D) (shorter, 0.8× as long as F2 in *C. confertus*).

Ceroptres promethei was reared from galls of *Andricus dimorphus* (Beutenmüller, 1913) on *Quercus macrocarpa* Michx. and *A. nigricens* (Gillette, 1888) on *Q. bicolor* Willd. *C. swiperi* is also associated with *Andricus dimorphus*; however, female *C. promethei* can be easily distinguished from *C. swiperi* by the following characters beyond the coloration of the body: Third metasomal tergite with a small posterodorsal patch of punctures (Fig. 15G) (with a larger posterodorsal patch of punctures in *C. swiperi* as in Fig. 20G). Mesoscutellar disc sculpture strongly rugose throughout (Fig. 15E) (with coriaceous sculpture anteriorly and medially in *C. swiperi* as in Fig. 20E). Apical flagellomere 3.6× as long as wide (Fig. 15A) (4.3× as long as wide in *C. swiperi* as in Fig. 20A).

Male *C. promethei* are generally darker in color than the holotype female; two males we examined have an entirely black head and mesosoma, while a third male has some rufous coloration on the head and mesosoma.

Description. Female—Body of holotype 2.8 mm in length. Head and mesosoma entirely rufous. Metasoma rufous. Antennae 12-segmented, filiform, about two thirds as long as body. Pedicel 1.5× as long as wide. F1 1.0× as long as F2. Apical flagellomere 3.6× as long as wide. Head in anterior view subquadrate. Dorsal head sculpture coriaceous; conspicuously sculptured throughout. Frons sculpture excluding facial carinae coriaceous. Facial vertical carinae distinct, reaching about two thirds across lower face. Transfacial line 0.8× as long as compound eye. Malar space 0.6× length of compound eye. POL:LOL:OOL:DLO in holotype 20:9:9:9. POL slightly longer than twice LOL and OOL. OOL equal to LOL, equal to DLO. Lateral pronotum sculpture coriaceous. Mesoplewuron smooth and shining, without apparent sculpture. Mesoscutum sculpture coriaceous with distinct setiferous punctation throughout. Notauli incomplete, indistinct in anterior half of mesoscutum. Mesoscutellar disc strongly rugose with interspaces coriaceous. Mesoscutellar foveae distinct, somewhat longer, and somewhat subquadrate, separated by narrow carina. Metapleural sulcus meeting mesopleuron at about four fifths height. Lateral propodeal

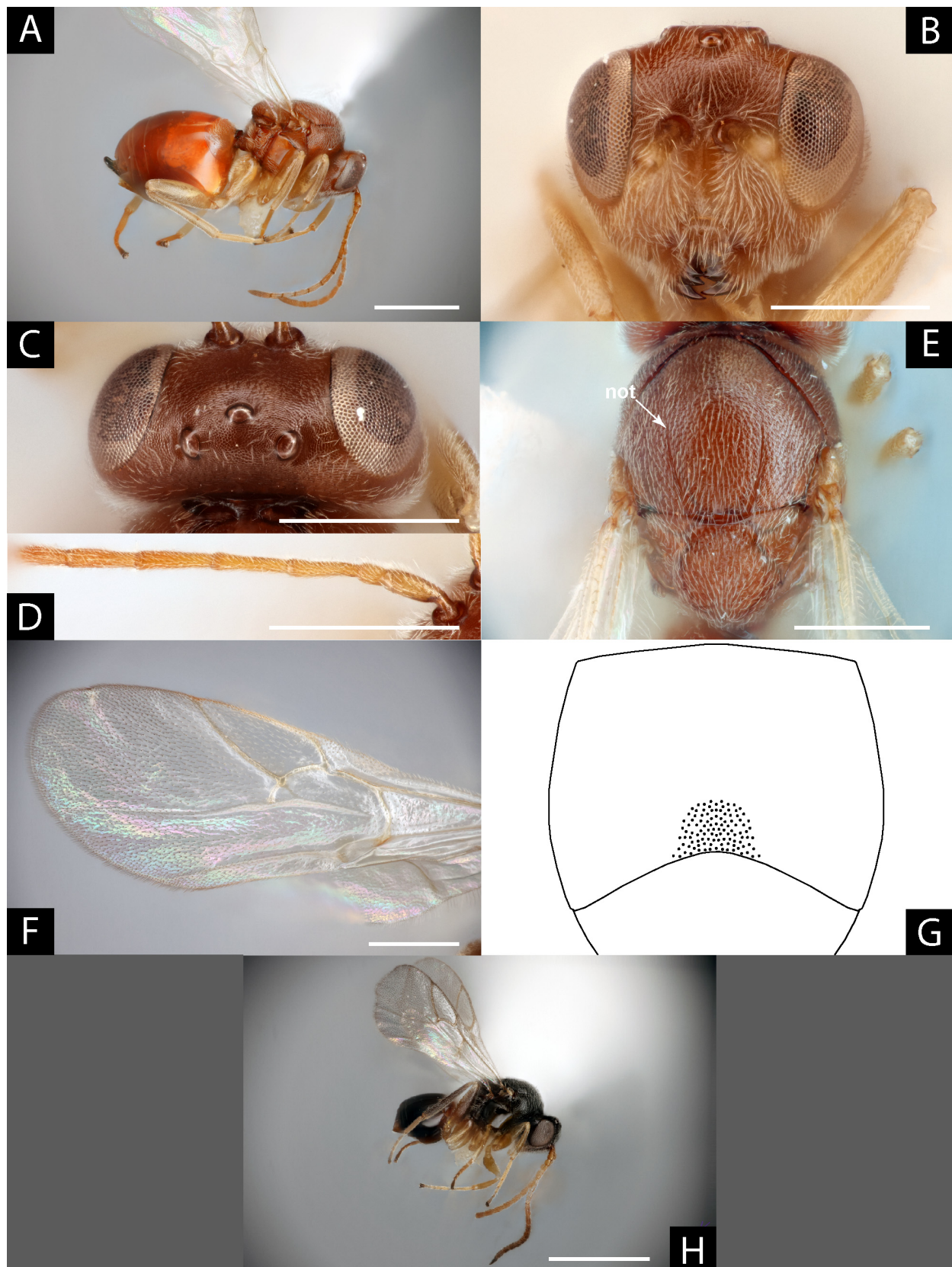


FIGURE 15. *Ceroptres promethei* Nastasi, Smith, & Davis sp. nov. A–G: Holotype female (PSUC_FEM_255508); H: Paratype male (PSUC_FEM_255507). Scale bars: A & H = 1.0 mm; B–F = 0.5 mm. A: Adult female, lateral habitus. B: Head in anterior view. C: Head in dorsal view. D: Proximal antenna. E: Mesosoma in dorsal view; not = notaulus, with arrow indicating end of distinct portion. F: Fore wing. G: Punctuation pattern on third metasomal tergite in dorsal view (not to scale). H: Adult male, lateral habitus.

carinae conspicuous; more or less straight and subparallel. Fore wing marginal cell $2.5\times$ as long as wide. Fore wing marginal setae distinct; short. Legs uniformly yellow except apical tarsomeres which are at least partly infuscated. Tarsal claws with conspicuous, strong basal tooth. Hypopygial spine not conspicuously projecting. Third metasomal tergite with a small patch of scattered punctures posterodorsally.

Male—Same as female except for the following: Body 1.7–2.1 mm in length ($\bar{x}=1.9$; $n=3$). Generally darker in color; mostly brown to black, with more limited rufous coloration relative to female. Antennae 15-segmented. Antennae slightly shorter than body length. Malar space $0.4\times$ length of compound eye. Metasoma smaller than in female.

Biology. *Ceroptres promethei* was reared from asexual generation galls of *Andricus dimorphus* (Beutenmüller, 1913) on *Q. macrocarpa* Michx. and asexual generation galls of *Andricus nigricens* (Gillette, 1888) on *Quercus bicolor* Willd.

Distribution. Iowa City and Lansing, Iowa (USA). An iNaturalist observation (ID #185529688; <https://www.inaturalist.org/observations/185529688>) may depict a female of this species from Ingleside, Illinois, as it shows a rufous *Ceroptres* wasp ovipositing into mature galls of *Andricus dimorphus*, one of the hosts from which the type material was reared.

Remarks. *Ceroptres promethei* represents part of Ward *et al.*'s (2024) “species 20”, along with *C. swiperi*. While their species 20 formed a well-supported monophyletic lineage, we find that their two female voucher specimens are strongly morphologically distinct (see diagnosis). In relation to Ward *et al.*'s DNA barcode analysis, *C. swiperi* is represented by a single sequence that is sister to those comprising *C. promethei*, thus causing *C. promethei* to form a monophyletic group. The clade representing Ward *et al.*'s “species 20” had relatively low support (bootstrap = 84), and sequences corresponding to our *C. promethei* and *C. swiperi* are moderately divergent, with around a 4% average distance. Overall, all data suggest that Ward *et al.*'s species 20 does not constitute a group of conspecific individuals. We have examined additional specimens reared from *Andricus dimorphus* galls that do not clearly resemble *C. promethei* or *C. swiperi*; further rearing of *Andricus dimorphus* galls should be undertaken to best understand the relationships of the associated *Ceroptres* species.

Ceroptres sandiegoae Nastasi, Smith, & Davis sp. nov.

Fig. 16

urn:lsid:zoobank.org:act:6CEA2ABC-0070-4CCA-AA3F-83E7C50B1557

Material examined. Holotype ♀—USA • Iowa, Iowa City, FW Kent Park; reared from gall of *Phylloteris rubium* on *Quercus alba*; gall collected 18 Oct 2016; emerged 10 Oct 2017; DNA sequence voucher # 662-082-1; GenBank Accession # OR372021; PSUC_FEM_255564.

Etymology. Named for Carmen Sandiego, the titular character of a variety of video games, television series, and other media. Sandiego plays the role of an extremely intelligent master thief and detective, among others.

Diagnosis. *Ceroptres sandiegoae* belongs to a group of species that has 12-segmented antennae (Fig. 16A), F1 shorter than F2 (Fig. 16D), and a large patch of punctures on the third metasomal tergite (Fig. 16G). *C. sandiegoae* is best recognized among similar species (*C. anzui* and *C. swiperi*) by combination of the short malar space ($0.3\times$ as long as compound eye as in Fig. 16B), the metasoma being shorter than the combined length of the head and mesosoma (Fig. 16A), and the marginal cell being somewhat long ($3.0\times$ as long as wide as in Fig. 16F).

Description. Female—Body of holotype 2.0 mm in length. Head and mesosoma entirely black. Metasoma dark brown. Antennae 12-segmented, subclavate, about two thirds as long as body. Pedicel $1.4\times$ as long as wide. F1 $0.9\times$ as long as F2. Apical flagellomere $3.5\times$ as long as wide. Head in anterior view subtrapezoidal. Dorsal head sculpture coriaceous; conspicuously sculptured throughout. Frons sculpture excluding facial carinae coriaceous. Facial vertical carinae distinct, reaching about halfway across lower face. Transfacial line $0.8\times$ as long as compound eye. Malar space $0.3\times$ length of compound eye. POL:LOL:OOL:DLO in holotype 16:7:6:6. POL slightly longer than twice LOL nearly three times OOL. OOL slightly shorter than LOL, equal to DLO. Lateral pronotum sculpture coriaceous. Mesopleuron smooth and shining, without apparent sculpture. Mesoscutum sculpture coriaceous. Notauli incomplete, indistinct in anterior third of mesoscutum. Mesoscutellar disc coriaceous anteriorly and medially, only appearing strongly rugose posteriorly. Mesoscutellar foveae distinct, short, and subrectangular, separated by narrow carina. Metapleural sulcus meeting mesopleuron at about four fifths height. Lateral propodeal carinae conspicuous;

more or less straight and subparallel. Fore wing marginal cell $3.0\times$ as long as wide. Fore wing marginal setae distinct; short. Legs uniformly yellow except coxae and apical tarsomeres which are at least partly infuscated. Tarsal claws with conspicuous, strong basal tooth. Metasoma excluding ovipositor and sheaths in lateral view subequal to combined length of head and mesosoma. Hypopygial spine only very slightly projecting. Third metasomal tergite with a large, expansive posterodorsal patch of abundant punctures, expanded anteriorly and reaching nearly halfway to posterior margin of second metasomal tergite.

Male—Unknown.

Biology. The holotype female was reared from asexual generation galls of *Phylloterax rubinum* (Gillette, 1888) on *Quercus alba* L. Ward *et al.* (2024) also sequenced corresponding specimens reared from *Callirhytis quercusfutilis*, but vouchers from this host were not available for study.

Distribution. Known only from FW Kent Park, Johnson, Iowa (USA).

Remarks. *Ceroptres sandiegoae* corresponds to Ward *et al.*'s (2024) “species 25”.

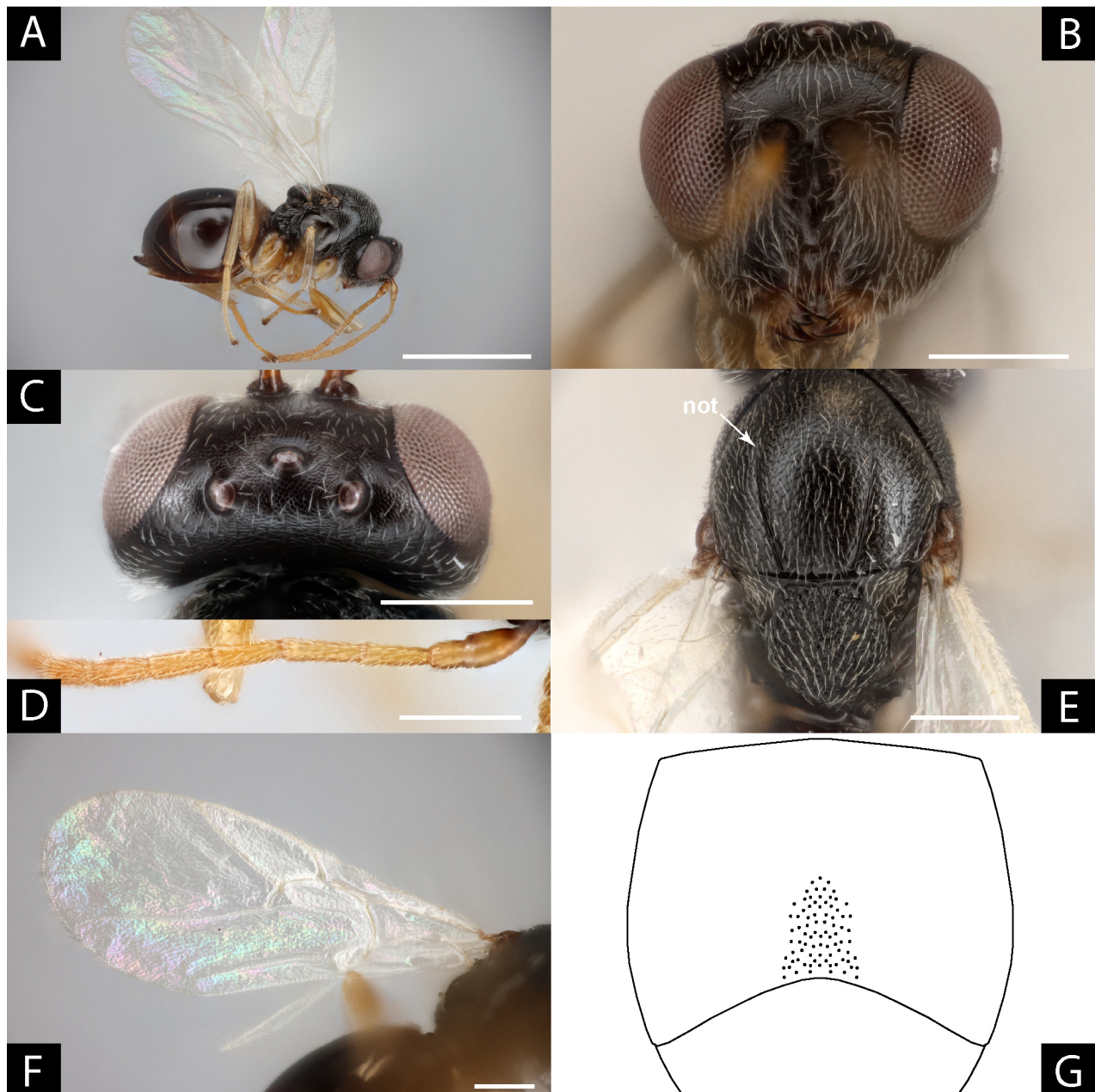


FIGURE 16. *Ceroptres sandiegoae* Nastasi, Smith, & Davis sp. nov. All images show holotype female (PSUC_FEM_255564). Scale bars: A = 1.0 mm; B–F = 0.25 mm. A: Lateral habitus. B: Head in anterior view. C: Head in dorsal view. D: Proximal antenna. E: Mesosoma in dorsal view; not = notaulus, with arrow indicating end of distinct portion. F: Fore wing. G: Punctuation pattern on third metasomal tergite in dorsal view (not to scale).

***Ceroptres selinae* Nastasi, Smith, & Davis sp. nov.**

Fig. 17

urn:lsid:zoobank.org:act:C3F282DC-C3B4-4B77-9776-631DA3F1112E

Material examined. Holotype ♀—USA • Missouri, St. Peters, Rabbit Run Park; reared from gall of *Callirhytis quercuspunctata* on *Quercus rubra*; gall collected 2 Sep 2016; emerged 5 June 2018; DNA sequence voucher # 542-069-37; GenBank Accession # OR372011; PSUC_FEM_255563.

Etymology. Named for Selina Kyle, a character from the DC Comics franchise perhaps more commonly known by the moniker Catwoman. She is famously known as a trickster, especially within the context of her tumultuous relationship with the infamous Batman.

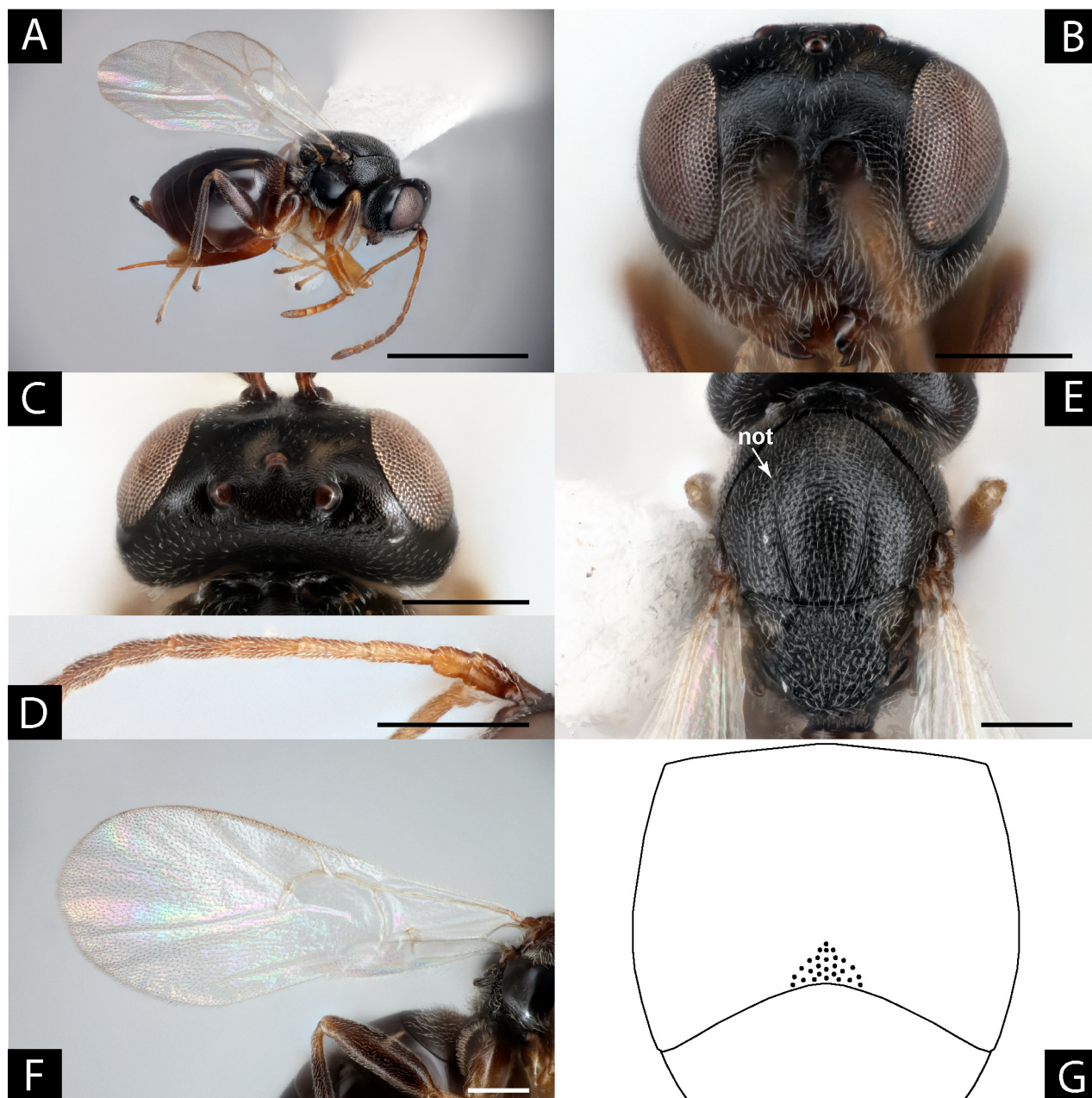


FIGURE 17. *Ceroptres selinae* Nastasi, Smith, & Davis sp. nov. All images show holotype female (PSUC_FEM_255563). Scale bars: A = 1.0 mm; B–F = 0.25 mm. A: Lateral habitus. B: Head in anterior view. C: Head in dorsal view. D: Proximal antenna. E: Mesosoma in dorsal view; not = notaulus, with arrow indicating end of distinct portion. F: Fore wing. G: Punctuation pattern on third metasomal tergite in dorsal view (not to scale).

Diagnosis. See diagnosis to *Ceroptres zorroi*.

Description. Female—Holotype body 2.0 mm in length. Head and mesosoma entirely black. Metasoma dark brown. Antennae 12-segmented, subclavate, about two thirds as long as body. Pedicel 1.2× as long as wide. F1 1.0× as long as F2. Apical flagellomere 3.6× as long as wide. Head in anterior view subquadrate. Dorsal head sculpture coriaceous; conspicuously sculptured throughout. Frons sculpture excluding facial carinae coriaceous. Facial vertical carinae distinct, reaching about halfway across lower face. Transfacial line 0.9× as long as compound eye. Malar space 0.3× length of compound eye. POL:LOL:OOL:DLO in holotype 15:7:8:6. POL slightly longer than twice LOL and slightly shorter than twice OOL. OOL slightly longer than LOL, longer than DLO. Lateral pronotum sculpture coriaceous-imbricate. Mesopleuron smooth and shining, without apparent sculpture. Mesoscutum sculpture strongly coriaceous-imbricate, with setiferous punctation throughout. Notauli incomplete, indistinct in anterior third of mesoscutum. Mesoscutellar disc strongly rugose with interspaces coriaceous. Mesoscutellar foveae somewhat indistinct, short, and subrectangular, separated by narrow carina. Metapleural sulcus meeting mesopleuron at about three quarters height. Lateral propodeal carinae conspicuous; more or less straight and subparallel. Fore wing marginal cell 2.7× as long as wide. Fore wing marginal setae distinct; long. Fore legs entirely yellow except apical tarsomeres infuscated; mid and hind legs brown except tarsi yellow with infuscated apical tarsomeres. Tarsal claws with conspicuous, strong basal tooth. Metasoma excluding ovipositor and sheaths in lateral view subequal to combined length of head and mesosoma. Hypopygial spine not conspicuously projecting. Third metasomal tergite with a small patch of scattered punctures posterodorsally.

Male—Unknown.

Biology. *Ceroptres selinae* was reared from asexual generation galls of *Callirhytis quercuspunctata* (Bassett, 1863) on *Quercus rubra* L.

Distribution. St. Peters, Missouri (USA).

Remarks. *Ceroptres selinae* corresponds to Ward *et al.*'s (2024) “species COI-H”.

Ceroptres soloi Nastasi, Smith, & Davis sp. nov.

Fig. 18

urn:lsid:zoobank.org:act:F196A306-B05F-4ADA-9A30-781ADBBA2DC1

Material examined. Holotype ♀—USA • Iowa, Iowa City, lower commuter lot; reared from gall of *Neuroterus quercusverrucarum* on *Quercus alba*; gall collected 14 July 2017; emerged 9 Aug 2017; DNA sequence voucher # 1014-055-1; GenBank Accession # OR372059; PSUC_FEM_255556.

Paratypes (8 ♀)—USA • 1 ♀; USA • Illinois, Urbana, Crystal Lake Park; reared from gall of *Neuroterus floccosus* on *Quercus macrocarpa*; gall collected 11 Sep 2017; emerged 5 Feb 2018; DNA sequence voucher # 1210-022-13; GenBank Accession # OR372069; PSUC_FEM_255533 • 1 ♀; Ohio, Englewood; reared from gall of *Neuroterus floccosus* on *Quercus macrocarpa*; gall collected 7 Sep 2017; emerged 15 Nov 2017; DNA sequence voucher # 1168-022-5A; GenBank Accession # OR372066; PSUC_FEM_255532 • 6 ♀; Pennsylvania, Centre County, Bellefonte, Green Valley Rd; A Guiguet leg.; reared from gall of *Neuroterus quercusverrucarum* on *Quercus montana*; gall collected 15 Oct 2020; emerged 20-24 May 2021; DNA sequence voucher # number; GenBank Accession # number; PSUC_FEM_255622; 255644; 255645; 255697–255699 (specimens PSUC_FEM_255644 and 255645 deposited at USNM).

Etymology. Named for Han Solo, a character from the *Star Wars* franchise portrayed by Harrison Ford. Solo is portrayed as a smuggler, thief, and jack-of-all-trades that was instrumental in implementing the destruction of the Death Star.

Diagnosis. *Ceroptres soloi* is very similar to *C. demerzelae*. These two species are best distinguished by the length of the transfacial line (1.0× as long as compound eye in *C. soloi* as in Fig. 18B but 0.8× as long as compound eye in *C. demerzelae* as in Fig. 7B), and the shape of the head in anterior view (subtrapezoidal in *C. demerzelae* as in Fig. 7B but round in *C. soloi* as in Fig. 18B). The two species are also associated with different hosts; *C. soloi* is associated with galls of *Neuroterus* Hartig, 1840 on white oaks, while *C. demerzelae* is associated with galls of *Melikaella* Pujade-Villar, 2014 on red oaks.

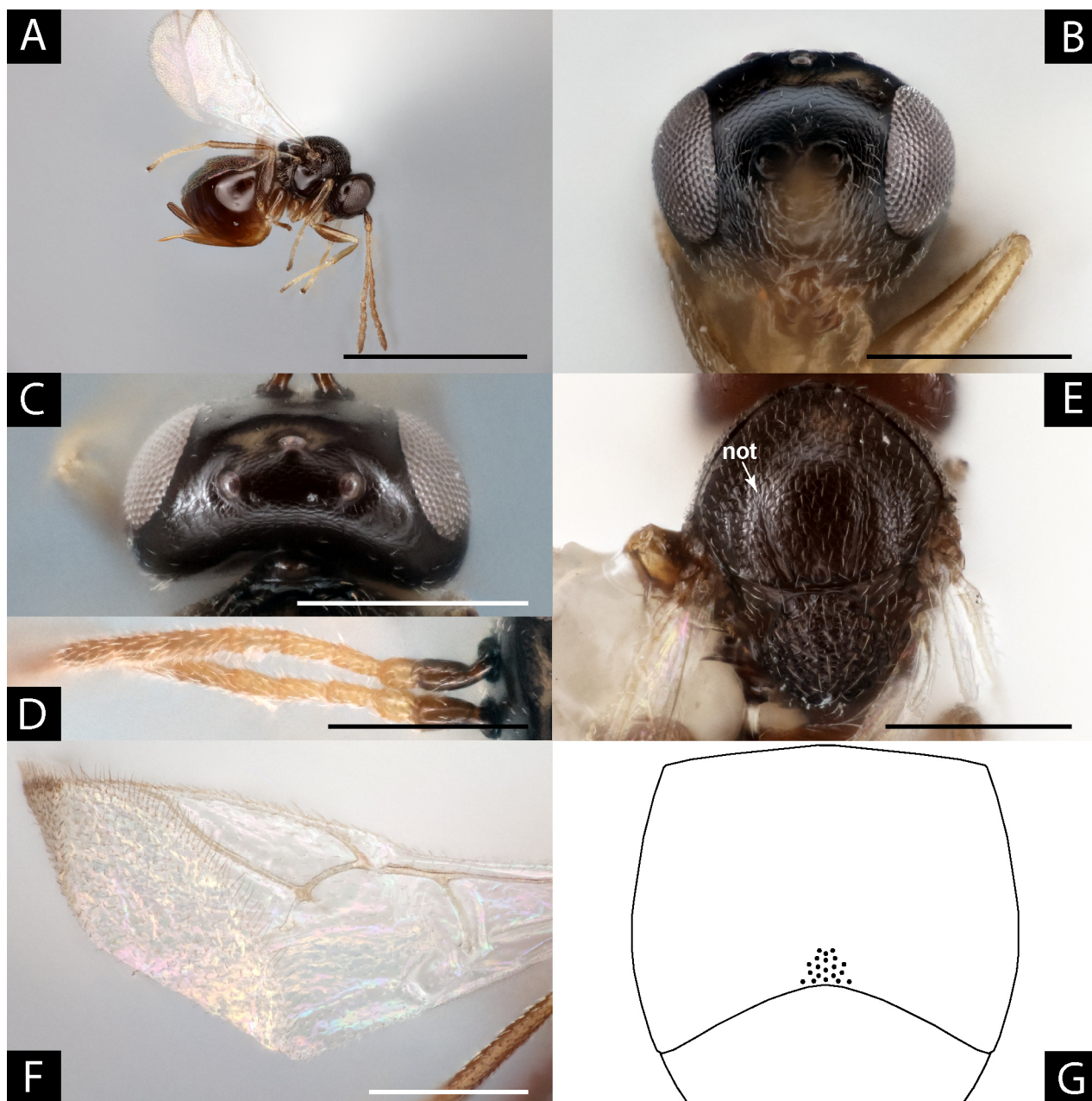


FIGURE 18. *Ceroptres soloi* Nastasi, Smith, & Davis sp. nov. All images show holotype female (PSUC_FEM_255556). Scale bars: A = 1.0 mm; B–F = 0.25 mm. A: Lateral habitus. B: Head in anterior view. C: Head in dorsal view. D: Proximal antenna. E: Mesosoma in dorsal view; not = notaulus, with arrow indicating end of distinct portion. F: Fore wing. G: Punctuation pattern on third metasomal tergite in dorsal view (not to scale).

Description. Female—Body 0.9–1.7 mm in length ($\bar{x}$ = 1.2; n = 9). Head and mesosoma entirely dark brown. Metasoma dark brown. Antennae 12-segmented, subclavate, about three quarters as long as body. Pedicel 1.4× as long as wide. F1 1.0× as long as F2. Apical flagellomere 3.3× as long as wide. Head round in anterior view. Dorsal head sculpture coriaceous; conspicuously sculptured throughout. Frons sculpture excluding facial carinae coriaceous. Facial vertical carinae distinct, reaching about one third across lower face. Transfacial line 1.0× as long as compound eye. Malar space 0.4× length of compound eye. POL:LOL:OOL:DLO in holotype 10:5:5:3. POL twice LOL and OOL. OOL equal to LOL, longer than DLO. Lateral pronotum sculpture coriaceous to alutaceous. Mesopleuron smooth and shining, without apparent sculpture. Mesoscutum sculpture coriaceous with distinct setiferous punctation throughout. Notauli incomplete, indistinct in anterior half of mesoscutum. Mesoscutellar disc coriaceous anteriorly and medially, only appearing strongly rugose posteriorly. Mesoscutellar foveae distinct, short, and subrectangular, separated by narrow carina. Metapleural sulcus meeting mesopleuron at about four fifths height.

Lateral propodeal carinae conspicuous; more or less straight and subparallel. Fore wing marginal cell $2.8\times$ as long as wide. Fore wing marginal setae distinct; very long. Legs with coxae, femora, and tibiae brownish and tarsi mostly yellow. Tarsal claws with conspicuous, blunt, rounded basal lobe. Metasoma excluding ovipositor and sheaths in lateral view subequal to combined length of head and mesosoma. Hypopygial spine strongly projecting, with prominent projecting portion about $2.0\times$ as long as wide. Third metasomal tergite with a small patch of scattered punctures posterodorsally.

Male—Unknown.

Biology. *Ceroptres soloi* was reared from asexual generation galls of *Neuroterus floccosus* (Bassett, 1881) on *Quercus macrocarpa* Michx. and asexual generation galls of *N. quercusverrucarum* (Osten Sacken, 1861) on *Q. alba* L. and *Q. montana* Willd.

Distribution. Urbana, Illinois, Iowa City, Iowa, Englewood, Ohio, and Bellefonte, Pennsylvania (USA).

Remarks. *Ceroptres soloi* corresponds to Ward *et al.*'s (2024) "species 30b".

Ceroptres songae Nastasi, Smith, & Davis sp. nov.

Fig. 19

urn:lsid:zoobank.org:act:CB432152-0B41-4432-9D7D-83C3D06A8C76

Material examined. Holotype ♀—USA • North Carolina, Asheville, Richmond Hill Park; reared from gall of *Polystepha pilulae* on *Quercus falcata*; gall collected 4 Sep 2016; emerged 13 Nov 2016; voucher # 628-056-1; PSUC_FEM_255557.

Etymology. Named for River Song, a character from the *Doctor Who* franchise portrayed by Alex Kingston. Song is a noted trickster and thief who encounters the titular Doctor numerous times throughout their interplanetary adventures. She is also the focus of a major plot twist in the show's sixth series, therein overturning audiences' expectations and providing another layer to Song's association with subversion, and therefore inquiline gall wasps.

Diagnosis. *Ceroptres songae* belongs to a group of species with conspicuous alutaceous sculpture on the mesopleuron; most of these species, including *C. songae*, are associated with galls of cecidomyiid midges rather than those induced by Cynipini. *Ceroptres songae* is easily distinguished from other species with a sculptured mesopleuron by the 12-segmented antennae (Fig. 19A), short malar space ($0.3\times$ as long as compound eye as in Fig. 19B), and the very small body size (holotype only 1.2 mm in length as in Fig. 19A).

Description. Female—Body of holotype 1.5 mm in length. Head and mesosoma dark brown. Metasoma brown. Antennae 12-segmented, subclavate, about three quarters as long as body. Pedicel $1.3\times$ as long as wide. F1 $1.0\times$ as long as F2. Apical flagellomere $3.3\times$ as long as wide. Head in anterior view round. Dorsal head sculpture coriaceous; conspicuously sculptured throughout. Frons sculpture excluding facial carinae coriaceous. Facial vertical carinae distinct, reaching about one third across lower face. Transfacial line $0.9\times$ as long as compound eye. Malar space $0.3\times$ length of compound eye. POL:LOL:OOL:DLO in holotype 13:6:6:4. POL slightly longer than twice LOL and OOL. OOL equal to LOL, longer than DLO. Lateral pronotum sculpture coriaceous. Mesopleuron with small area of distinct alutaceous sculpture anteroventrally. Mesoscutum sculpture somewhat coriaceous-imbricate with distinct setiferous punctation throughout. Notauli incomplete, indistinct in anterior half of mesoscutum. Mesoscutellar disc coriaceous anteriorly and medially; posteriorly strongly rugose with interspaces unsculptured to alutaceous. Mesoscutellar foveae distinct, somewhat longer, somewhat subtriangular with inner margins moderately divergent posteriorly, separated by narrow carina. Metapleural sulcus meeting mesopleuron at about four fifths height. Lateral propodeal carinae conspicuous; more or less straight and subparallel. Fore wing marginal cell $2.4\times$ as long as wide. Fore wing marginal setae distinct; long. Legs with coxae, trochanters, and femora brown, tibiae light brown, and tarsi yellow except apical tarsomere brown. Tarsal claws with conspicuous, strong basal tooth. Metasoma excluding ovipositor and sheaths in lateral view subequal to combined length of head and mesosoma. Hypopygial spine strongly projecting but prominent projecting portion about as long as wide. Third metasomal tergite with a small patch of scattered punctures posterodorsally.

Male—Unknown.

Biology. Ward *et al.* (2024) reared *Ceroptres songae* from galls of *Polystepha pilulae* (Beutenmüller, 1892) on *Quercus falcata* Michx.

Distribution. Asheville, North Carolina (USA).

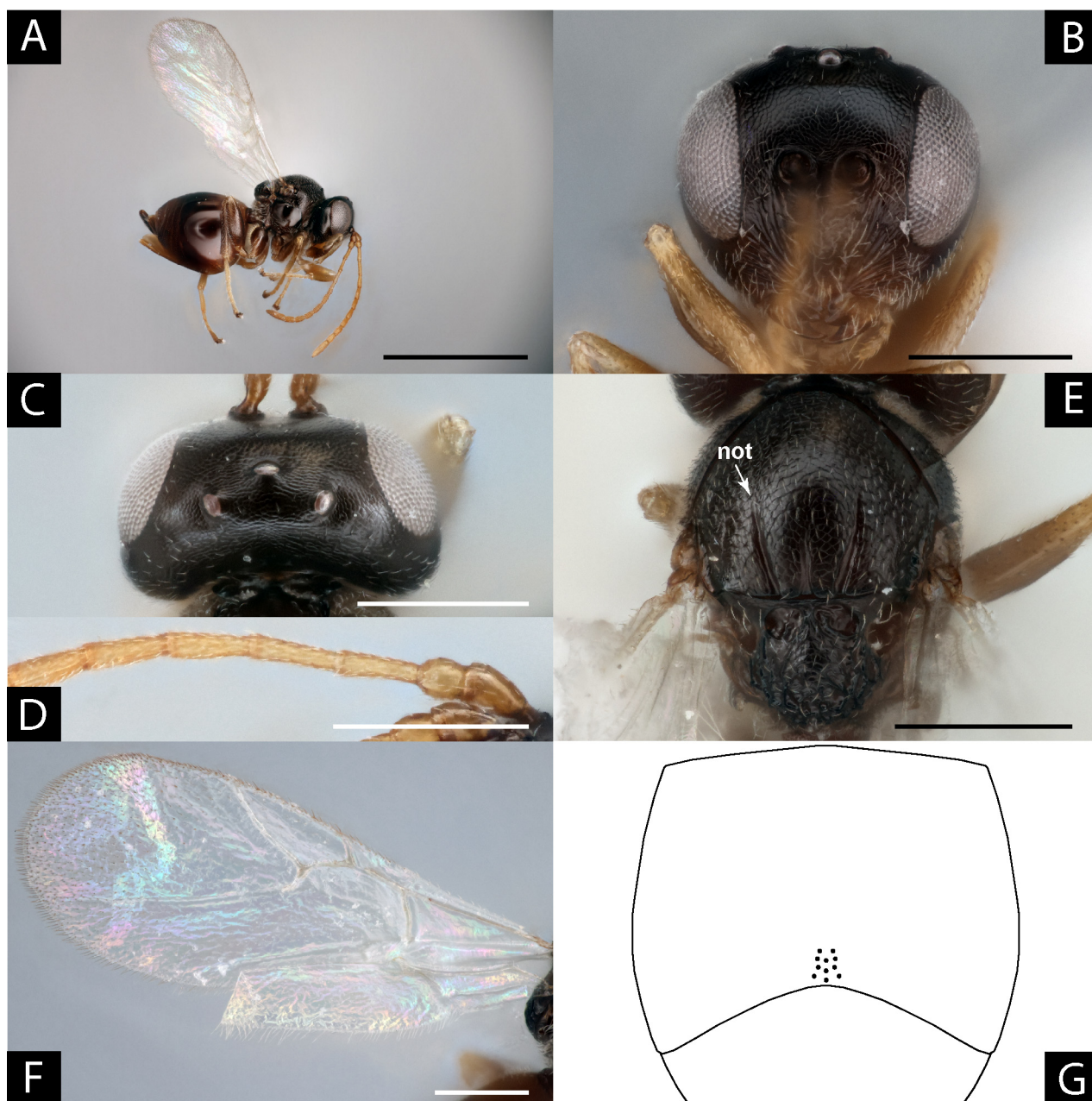


FIGURE 19. *Ceroptres songae* Nastasi, Smith, & Davis sp. nov. All images show holotype female (PSUC_FEM_255557). Scale bars: A = 1.0 mm; B–F = 0.25 mm. A: Lateral habitus. B: Head in anterior view. C: Head in dorsal view. D: Proximal antenna. E: Mesosoma in dorsal view; not = notaulus, with arrow indicating end of distinct portion. F: Fore wing. G: Punctuation pattern on third metasomal tergite in dorsal view (not to scale).

Remarks. The holotype of *C. songae* was not sequenced by Ward *et al.* (2024), but was included among their voucher material deposited at PSUC. *Ceroptres songae* and *C. daleki* were reared from the same host gall but on different host plants. The holotype females for the two species emerged in different seasons, late autumn for *C. songae* but late spring for *C. daleki*. Previous studies of inquiline gall wasps (e.g., Ward *et al.* 2020) suggest that temporal isolation may contribute to speciation in inquilines of the same gall, although the difference in host plant could also be a relevant factor. Continued collecting and rearing of *Polystepha* gall inquilines might allow for further study of these hypotheses. We provide additional commentary on the association of *Ceroptres* with galls of cecidomyiid midges in the Discussion.

***Ceroptres swiperi* Nastasi, Smith, & Davis sp. nov.**

Fig. 20

urn:lsid:zoobank.org:act:16E878FB-2FFF-4E7C-A473-83909D45ED8A

Material examined. Holotype ♀—USA • Iowa, Iowa City, City Park; 41.667, -91.549; reared from gall of *Andricus dimorphus* on *Quercus macrocarpa*; gall collected 3 Oct 2018; emerged 17 Sep 2019; DNA sequence voucher # 1551-005-9A; GenBank Accession # OR372084; PSUC_FEM_255510.

Etymology. Named for Swiper the Fox, the primary antagonist in the Nickelodeon animated series *Dora the Explorer*. Swiper's main role in the series is to attempt to steal crucial objects acquired by Dora and her colleagues during their adventures, just as inquiline gall wasps apparently take advantage of nutritive gall tissues intended for gall inducers' progeny.

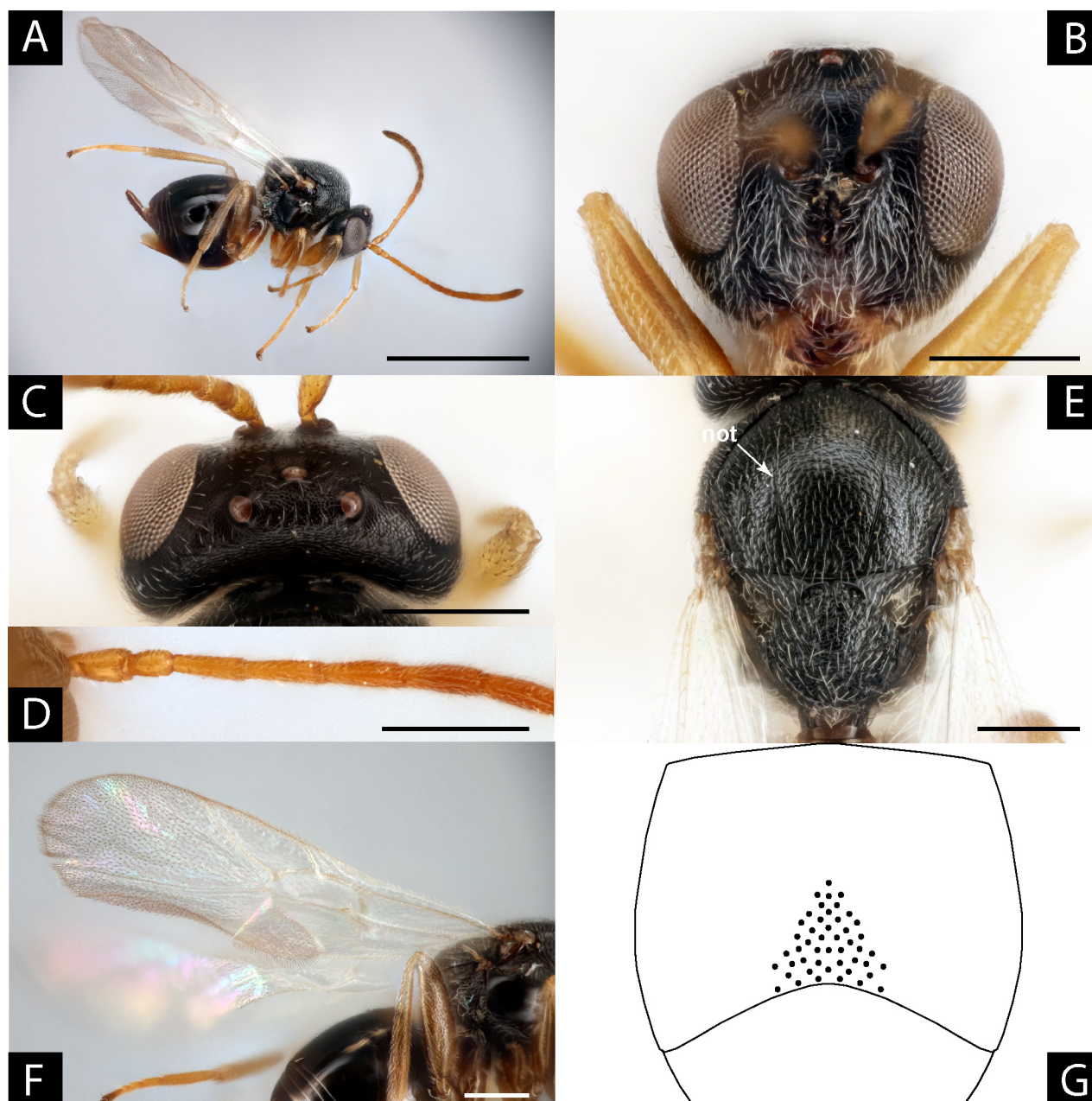


FIGURE 20. *Ceroptres swiperi* Nastasi, Smith, & Davis sp. nov. All images show holotype female (PSUC_FEM_255510). Scale bars: A = 1.0 mm; B–F = 0.25 mm. A: Lateral habitus. B: Head in anterior view. C: Head in dorsal view. D: Proximal antenna. E: Mesosoma in dorsal view; not = notaulus, with arrow indicating end of distinct portion. F: Fore wing. G: Punctuation pattern on third metasomal tergite in dorsal view (not to scale).

Diagnosis. *Ceroptres swiperi* belongs to a group of species with 12-segmented antennae (Fig. 20A), F1 shorter than F2 (Fig. 20D), and a large patch of punctures on the third metasomal tergite (Fig. 20G). *Ceroptres swiperi* is best separated from other similar species (*C. anzui* and *C. sandiegoae*) by the combination of the long malar space ($0.5\times$ as long as compound eye as in Fig. 20B) and the metasoma being shorter than the combined length of the head and mesosoma (Fig. 20A).

Ceroptres swiperi shares its host gall with *Ceroptres promethei*, but the two are easily distinguished by the characters noted in the diagnosis for *C. promethei*.

Description. Female—Body of holotype 1.6 mm in length. Head and mesosoma entirely black. Metasoma dark brown. Antennae 12-segmented, filiform, about three quarters as long as body. Pedicel $1.9\times$ as long as wide. F1 $0.9\times$ as long as F2. Apical flagellomere $4.3\times$ as long as wide. Head in anterior view subtrapezoidal. Dorsal head sculpture coriaceous; conspicuously sculptured throughout. Frons sculpture excluding facial carinae coriaceous. Facial vertical carinae distinct, reaching about halfway across lower face. Transfacial line $0.9\times$ as long as compound eye. Malar space $0.5\times$ length of compound eye. POL:LOL:OOL:DLO in holotype 14:7:7:5. POL twice LOL and OOL. OOL equal to LOL, longer than DLO. Lateral pronotum sculpture coriaceous. Mesopleuron smooth and shining, without apparent sculpture. Mesoscutum sculpture coriaceous with distinct setiferous punctation throughout. Notauli incomplete, indistinct in about anterior half of mesoscutum. Mesoscutellar disc coriaceous anteriorly and medially, only appearing strongly rugose posteriorly. Mesoscutellar foveae distinct, short, and somewhat ovate, separated by narrow carina. Metapleural sulcus meeting mesopleuron at about three quarters height. Lateral propodeal carinae conspicuous; more or less straight and subparallel. Fore wing marginal cell $3.1\times$ as long as wide. Fore wing marginal setae distinct; short. Legs uniformly yellow except coxae and apical tarsomeres at least partly infuscated. Tarsal claws with conspicuous, blunt, rounded basal lobe. Metasoma excluding ovipositor and sheaths in lateral view subequal to combined length of head and mesosoma. Hypopygial spine only very slightly projecting; prominent projecting portion about as long as wide. Third metasomal tergite with a large posterodorsal patch of abundant punctures, expanded somewhat anteriorly and/or laterally and reaching nearly halfway across tergite.

Male—Unknown.

Biology. Ward *et al.* (2024) reared *Ceroptres swiperi* from asexual generation galls of *Andricus dimorphus* (Beutenmüller, 1913) on *Q. macrocarpa* Michx.

Distribution. Iowa City, Iowa (USA).

Remarks. *Ceroptres swiperi* corresponds to part of Ward *et al.*'s (2024) "species 20"; see remarks for *C. promethei*.

Ceroptres thrymi Nastasi, Smith, & Davis sp. nov.

Fig. 21

urn:lsid:zoobank.org:act:DE3C078B-94C6-4567-BA0C-438107E5ED2B

Material examined. Holotype ♀—USA • Iowa, Iowa City, City Park; reared from gall of *Bassettia flavipes* on *Quercus bicolor*; gall collected 7 June 2017; emerged 12 Feb 2018; DNA sequence voucher # 852-013-27; GenBank Accession # OR372042; PSUC_FEM_255520.

Paratypes (4 ♀ and 1 ♂)—USA • 1 ♀; Iowa, Iowa City, City Park; reared from gall of *Bassettia flavipes* on *Quercus bicolor*; emerged 15 Aug 2017; voucher # 974-013-1ALT; PSUC_FEM_255519 • 3 ♀, 1 ♂; Pennsylvania, State College, 218 College Ave.; 40.797, -77.860; DC Montelongo leg.; reared from gall of *Bassettia flavipes* [reported on labels as *Callirhytis flavipes*] on *Quercus* sp.; gall collected 11 June 2020; PSUC_FEM_253548–253551 (specimen PSUC_FEM_253548 deposited at USNM).

Etymology. Named for Thrym, a supernatural being originating in Norse mythology. In the Eddic poem *Brymskviða*, Thrym steals Thor's famous hammer Mjöltnir, but is unable to outsmart Thor and his associates.

Diagnosis. *Ceroptres thrymi* belongs to a group of species with 12-segmented antennae (Fig. 21A), F1 equal to F2 (Fig. 21D), a small posterodorsal patch of punctures on the third metasomal tergite (Fig. 21G), and coriaceous sculpture anteriorly and medially on the mesoscutellar disc (Fig. 21D), along with *C. dandoi*, *C. demerzelae*, *C. lanigerae*, and *C. soloi*. Among these species, *C. thrymi* is distinguished by the dimensions of the apical flagellomere, which is only $2.5\times$ as long as wide (Fig. 21A) (at least $3.0\times$ as long as wide in other species) in combination with the round head (Fig. 21B). *Ceroptres thrymi* also has the shortest marginal cell among these species ($2.6\times$ as long as wide as in Fig. 21F; $2.8\text{--}3.1\times$ as long as wide in other species).

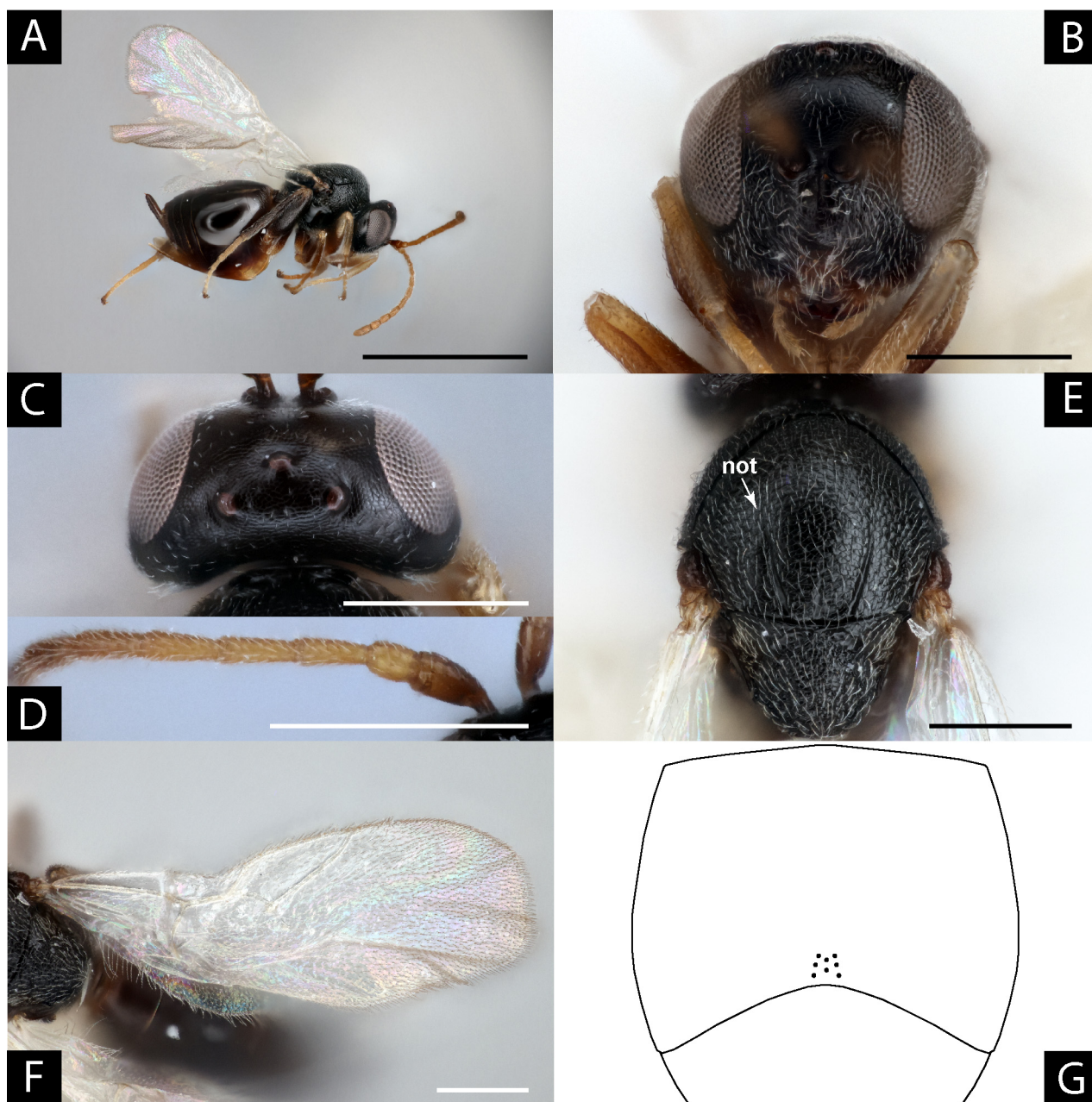


FIGURE 21. *Ceroptres thrymi* Nastasi, Smith, & Davis sp. nov. All images show holotype female (PSUC_FEM_255520). Scale bars: A = 1.0 mm; B–F = 0.25 mm. A: Lateral habitus. B: Head in anterior view. C: Head in dorsal view. D: Proximal antenna. E: Mesosoma in dorsal view; not = notaulus, with arrow indicating end of distinct portion. F: Fore wing. G: Punctuation pattern on third metasomal tergite in dorsal view (not to scale).

Description. Female—Body 1.1–1.6 mm in length ($\bar{x}$ = 1.3; n = 5). Head and mesosoma entirely black. Metasoma brown. Antennae 12-segmented, subclavate, about half as long as body. Pedicel 1.5× as long as wide. F1 1.0× as long as F2. Apical flagellomere 2.5× as long as wide. Head round in anterior view. Dorsal head sculpture coriaceous; conspicuously sculptured throughout. Frons sculpture excluding facial carinae coriaceous. Facial vertical carinae distinct, reaching about one third across lower face. Transfacial line 0.9× as long as compound eye. Malar space 0.4× length of compound eye. POL:LOL:OOL:DLO in holotype 11:6:5:4. POL slightly less than twice LOL and slightly more than twice OOL. OOL slightly shorter than LOL, longer than DLO. Lateral pronotum sculpture coriaceous. Mesopleuron smooth and shining, without apparent sculpture. Mesoscutum sculpture coriaceous with distinct setiferous punctation throughout. Notauli incomplete, indistinct in anterior half of mesoscutum. Mesoscutellar disc coriaceous anteriorly and medially, only appearing strongly rugose posteriorly. Mesoscutellar foveae somewhat indistinct, short, and subrectangular, separated by narrow carina. Metapleural sulcus meeting mesopleuron at about

four fifths height. Lateral propodeal carinae conspicuous; more or less straight and subparallel. Fore wing marginal cell 2.6× as long as wide. Fore wing marginal setae distinct; long. Legs with coxae, trochanters, femora, tibiae, and apical tarsomere brown; remaining tarsomeres yellow. Tarsal claws with conspicuous, strong basal tooth. Metasoma excluding ovipositor and sheaths in lateral view subequal to combined length of head and mesosoma. Hypopygial spine strongly projecting, with prominent projecting portion about 1.8x as long as wide. Third metasomal tergite with a small patch of scattered punctures posterodorsally.

Male—Same as female except for the following: Body 1.3 mm in length (n=1). Antennae 15-segmented. Antennae slightly shorter than body length. Pedicel 1.0× as long as wide. Apical flagellomere 2.5× as long as wide.

Biology. *Ceroptres thrymi* was reared from sexual generation galls of *Bassettia flavipes* (Gillette, 1890) on *Quercus bicolor* Willd.

Distribution. Iowa City, Iowa and State College, Pennsylvania (USA).

Remarks. *Ceroptres thrymi* corresponds to Ward *et al.*'s "species COI-B".

Ceroptres tikoloshei Nastasi, Smith, & Davis sp. nov.

Fig. 22

urn:lsid:zoobank.org:act:93D023AF-194B-4E06-8B8C-770B7F11680E

Material examined. Holotype ♀—USA • Iowa, Iowa City, Mormon Handcart Park; reared from gall of *Callirhytis quercusfutilis* on *Quercus macrocarpa*; gall collected 4 July 2017; emerged 21 Sep 2017; DNA sequence voucher # 963-051-13B; GenBank Accession # OR372054; PSUC_FEM_255551.

Paratypes (4 ♀ and 1 ♂)—Canada • 1 ♀; Manitoba, Warren, Warren Cemetery oak woodland; 50.13659, -97.5519; Chris Friesen leg.; reared from gall of *Callirhytis quercusfutilis* on *Quercus macrocarpa*; gall collected 20 July 2021; emerged 25–28 Aug 2021; PSUC_FEM_254608 (deposited at USNM) • 2 ♀; Manitoba, Warren, narrow oak woodland near Morton Drive; 50.13304 -97.54000; Chris Friesen leg.; reared from gall of *Callirhytis quercusfutilis* on *Quercus macrocarpa*; gall collected 23 June 2020; emerged 21 Aug 2020; PSUC_FEM_254609; 254624.

USA • 1 ♀; Wisconsin, Governor Dodge State Park; reared from gall of *Callirhytis quercusfutilis* on *Quercus alba*; emerged 31 Aug 2017; voucher # 1450-051-9; PSUC_FEM_255553 • 1 ♂; Iowa, Iowa City, Hickory Hills Park; reared from gall of *Callirhytis quercusfutilis* on *Quercus alba*; gall collected 15 June 2017; emerged 19 Oct 2017; DNA sequence voucher # 899-051-18; GenBank Accession # OR372050; PSUC_FEM_255550.

Etymology. Named for the Tikoloshe, a variety of malevolent trickster spirit originating in Nguni folklore.

Diagnosis. See diagnosis to *Ceroptres bruti*.

Description. Female—Body 1.3–1.8 mm in length ($\bar{x}$ = 1.5; n = 5). Head and mesosoma entirely black. Metasoma dark brown. Antennae 12-segmented, subclavate, about two thirds as long as body. Pedicel 1.4× as long as wide. F1 0.8× as long as F2. Apical flagellomere 3.5× as long as wide. Head in anterior view subtrapezoidal. Dorsal head sculpture coriaceous; conspicuously sculptured throughout. Frons sculpture excluding facial carinae coriaceous. Facial vertical carinae distinct, reaching about one third across lower face. Transfacial line 0.9× as long as compound eye. Malar space 0.4× length of compound eye. POL:LOL:OOL:DLO in holotype 13:6:5:4. POL slightly longer than twice LOL and nearly three times OOL. OOL slightly shorter than LOL, longer than DLO. Lateral pronotum sculpture coriaceous. Mesopleuron smooth and shining, without apparent sculpture. Mesoscutum sculpture weakly coriaceous with distinct setiferous punctation throughout. Notauli incomplete, indistinct in anterior half of mesoscutum. Mesoscutellar disc strongly rugose with interspaces coriaceous. Mesoscutellar foveae distinct, short, and subrectangular, separated by narrow carina. Metapleural sulcus meeting mesopleuron at about four fifths height. Lateral propodeal carinae conspicuous; more or less straight and subparallel. Fore wing marginal cell 2.7× as long as wide. Fore wing marginal setae distinct; long. Legs with coxae, trochanters, and femora brown, tibiae light brown, and tarsi yellow except apical tarsomere which is brown. Tarsal claws with conspicuous, strong basal tooth. Metasoma excluding ovipositor and sheaths in lateral view subequal to combined length of head and mesosoma. Hypopygial spine only very slightly projecting; prominent projecting portion about as long as wide. Third metasomal tergite with a small patch of scattered punctures posterodorsally.

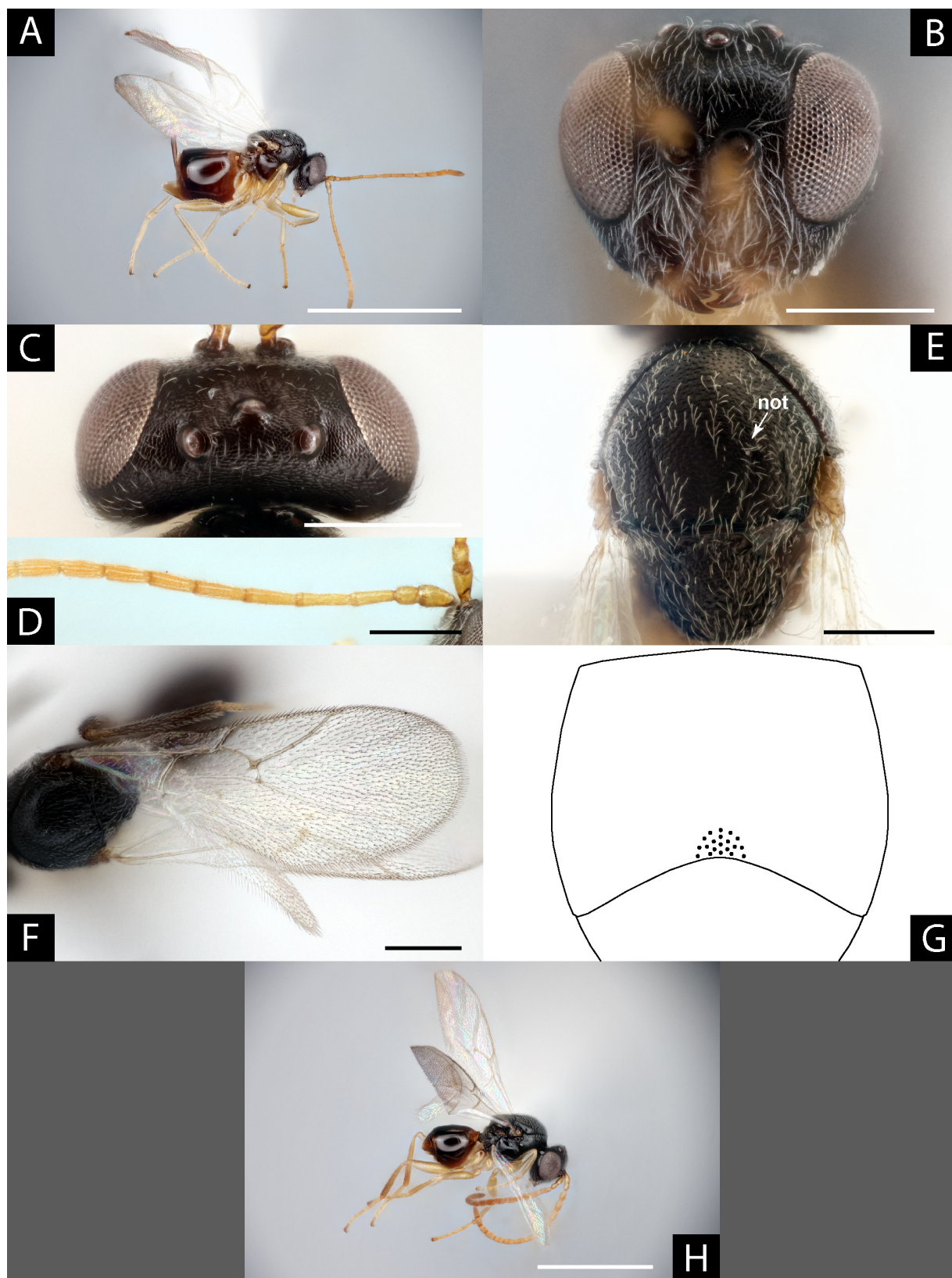


FIGURE 22. *Ceroptres tikoloshei* Nastasi, Smith, & Davis sp. nov. A–E; G: Holotype female (PSUC_FEM_255551); F: Paratype female (PSUC_FEM_255553); H: Paratype male (PSUC_FEM_255550). Scale bars: A & H = 1.0 mm; B–F = 0.5 mm. A: Adult female, lateral habitus. B: Head in anterior view. C: Head in dorsal view. D: Proximal antenna. E: Mesosoma in dorsal view; not = notaulus, with arrow indicating end of distinct portion. F: Fore wing. G: Punctuation pattern on third metasomal tergite in dorsal view (not to scale). H: Adult male, lateral habitus.

Male—Same as female except for the following: Body 1.2 mm in length ($n = 1$). Antennae 15-segmented. Antennae subequal to body length. Pedicel $1.0\times$ as long as wide. Apical flagellomere $2.5\times$ as long as wide. Metasoma smaller than in female.

Biology. *Ceroptres tikoloshei* was reared from sexual generation galls of *Callirhytis quercusfutilis* (Osten Sacken, 1861) on leaves of *Q. alba* L. and *Q. macrocarpa* Michx.

Distribution. Warren, Manitoba (Canada); Iowa City, Iowa; Governor Dodge State Park, Wisconsin (USA).

Remarks. *Ceroptres tikoloshei* corresponds to Ward *et al.*'s (2024) "species 18-19".

Ceroptres zorroi Nastasi, Smith, & Davis sp. nov.

Fig. 23

urn:lsid:zoobank.org:act:E4DB1BE6-2FF5-4141-A8B6-3DA5C2E1F86A

Material examined. Holotype ♀—USA • Texas, Austin; reared from gall of *Neuroterus quercusirregularis* on *Quercus stellata*; gall collected 12 April 2018; emerged 27 Apr 2019; DNA sequence voucher # 1245-118-3; GenBank Accession # OR372076; PSUC_FEM_255574.

Paratypes (2 ♀)—USA • 1 ♀; same collecting event and host as holotype; emerged 10 May 2019; DNA sequence voucher # 1239-118-8A; GenBank Accession # OR372073; PSUC_FEM_255573 • 1 ♀; same collecting event and host as holotype; emerged 21 Apr 2019; DNA sequence voucher # 1259-118-5; GenBank Accession # OR372077; PSUC_FEM_255575.

Etymology. Named for Zorro, a fictional character originating in early-1900s pulp fiction novels. Zorro is portrayed as a thief, trickster, and master of disguise. The application of this name to *C. zorroi* is especially apt given that Zorro's characteristic black garb and mask is resembled by the black coloration of the head and mesosoma of *C. zorroi*.

Diagnosis. *Ceroptres zorroi* is extremely close to *C. selinae*, both of which have 12-segmented antennae (Fig. 23A), F1 equal to F2 (Fig. 23D), a strongly rugose mesoscutellar disc (Fig. 23E), and somewhat long notauli (indistinct only in anterior third of mesoscutum as in Fig. 23E), among other characters. The two species are best separated by the length of the malar space, which is $0.5\times$ as long as compound eye in *C. zorroi* (Fig. 23B) but $0.3\times$ as long in *C. selinae* (Fig. 17B). The pedicel is also slightly longer in *C. selinae* (about $1.0\times$ as long as wide in *C. zorroi* as in Fig. 23D but only $1.2\times$ as long as wide in *C. selinae* as in Fig. 17D).

Description. Female—Body 1.5–1.6 mm in length ($\bar{x} = 1.5$; $n = 3$). Head and mesosoma entirely black. Metasoma brown. Antennae 12-segmented, subclavate, about two thirds as long as body. Pedicel $1.0\times$ as long as wide. F1 $1.0\times$ as long as F2. Apical flagellomere $3.7\times$ as long as wide. Head in anterior view subquadrate. Dorsal head sculpture coriaceous; conspicuously sculptured throughout. Frons sculpture excluding facial carinae coriaceous. Facial vertical carinae distinct, reaching about two thirds across lower face. Transfacial line $0.9\times$ as long as compound eye. Malar space $0.5\times$ length of compound eye. POL:LOL:OOL:DLO in holotype 15:6:6:5. POL $2.5\times$ as long as LOL and OOL. OOL equal to LOL, longer than DLO. Lateral pronotum sculpture coriaceous-imbricate. Mesopleuron smooth and shining, without apparent sculpture. Mesoscutum sculpture coriaceous-imbricate with distinct setiferous punctation throughout. Notauli incomplete, indistinct in anterior third of mesoscutum. Mesoscutellar disc strongly rugose with interspaces coriaceous. Mesoscutellar foveae distinct, very short, and subrectangular, separated by narrow carina. Metapleural sulcus meeting mesopleuron at about three quarters height. Lateral propodeal carinae conspicuous; more or less straight and subparallel. Fore wing marginal cell $2.9\times$ as long as wide. Fore wing marginal setae distinct; long. Legs with coxae, trochanters, femora, tibiae, and apical tarsomere brown; remaining tarsomeres yellow. Tarsal claws with conspicuous, strong basal tooth. Metasoma excluding ovipositor and sheaths in lateral view slightly shorter than combined length of head and mesosoma. Hypopygial spine only very slightly projecting; prominent projecting portion about as long as wide. Third metasomal tergite with a small patch of scattered punctures posterodorsally.

Male—Unknown.

Biology. *Ceroptres zorroi* was reared from sexual generation galls of *Neuroterus quercusirregularis* (Osten Sacken, 1861) on *Quercus stellata* Wangenh.

Distribution. Austin, Texas (USA).

Remarks. *Ceroptres zorroi* corresponds to Ward *et al.*'s (2024) *Ceroptres* "species 17".

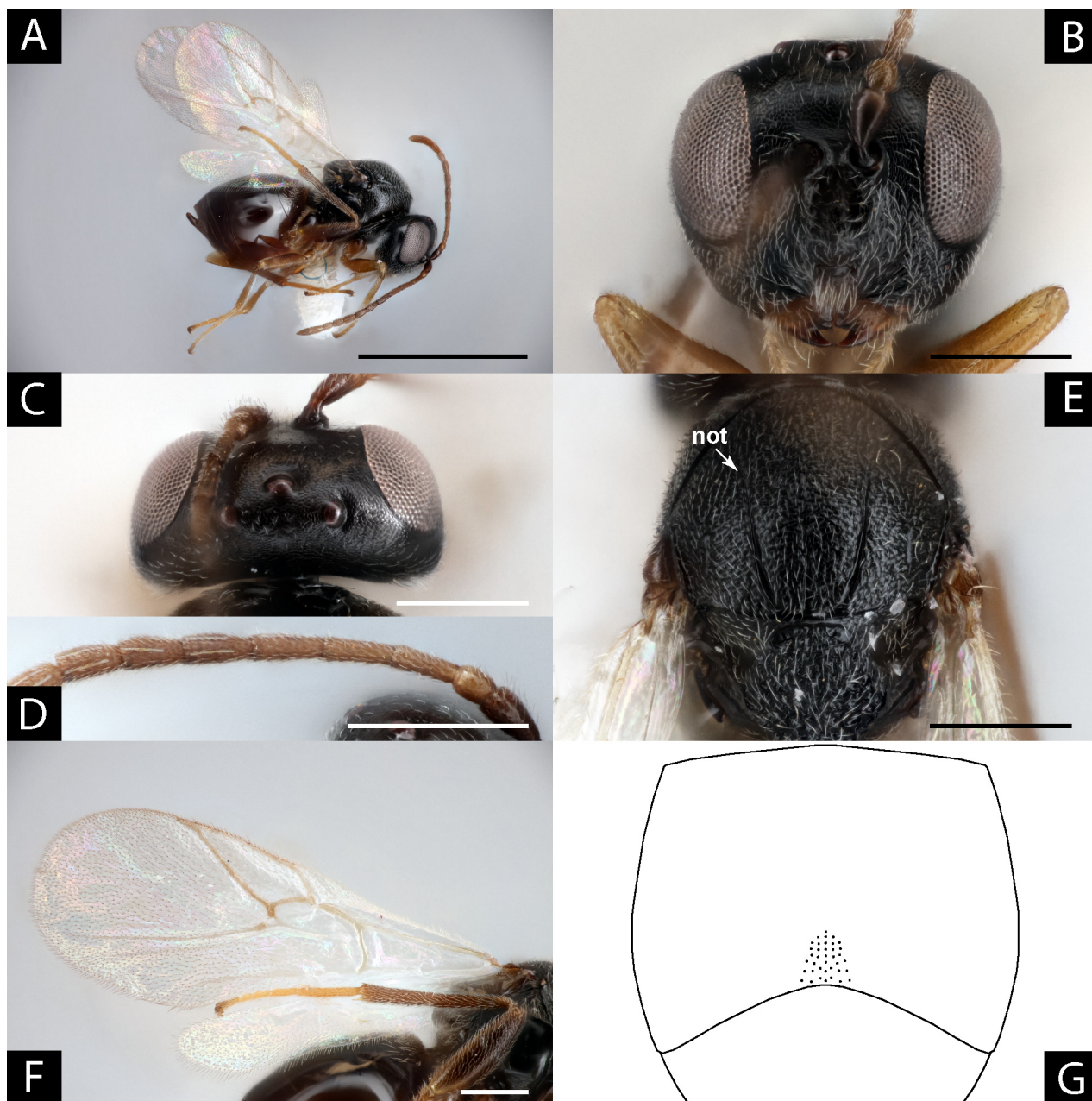


FIGURE 23. *Ceroptres zorroi* Nastasi, Smith, & Davis sp. nov. All images show paratype female (PSUC_FEM_255573) except G which was illustrated from the holotype female (PSUC_FEM_255574). Scale bars: A = 1.0 mm; B–F = 0.25 mm. A: Lateral habitus. B: Head in anterior view. C: Head in dorsal view. D: Proximal antenna. E: Mesosoma in dorsal view; not = notaulus, with arrow indicating end of distinct portion. F: Fore wing. G: Punctuation pattern on third metasomal tergite in dorsal view (not to scale).

New records of described *Ceroptres* species

Ceroptres cornigera Melika & Buss, 2002 and *C. frondosae* Ashmead, 1896

Fig. 24

Material examined. 32 ♀ and 7 ♂—CANADA • 1 ♀; Manitoba, Warren, 3.5 miles east, Prime Meridian Trail; 50.12327, -97.44804; Chris Friesen leg.; reared from gall of *Andricus quercusfrondosus* on *Quercus macrocarpa*; gall collected 21 Sep 2020; emerged 1 Apr 2021; PSUC_FEM_254607 • 1 ♀; Manitoba, Warren, 3.5 miles east, Prime Meridian Trail at Highway 67 South; 50.12224, -97.44804; Chris Friesen leg.; same host as previous; gall

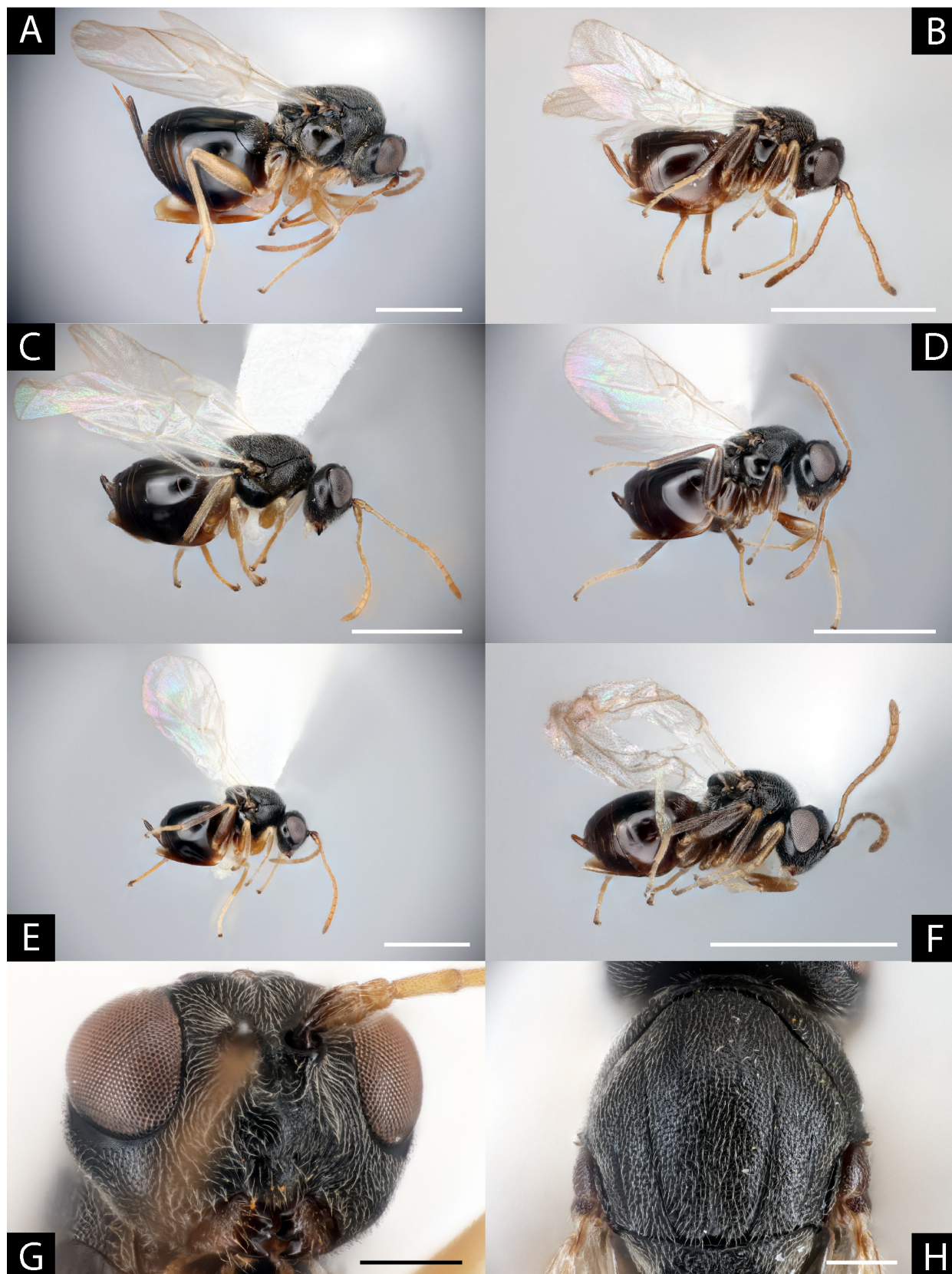


FIGURE 24. *Ceroptres cornigera/frondosae* species complex. Scale bars: A–F = 1.0 mm; G–H = 0.25 mm. A: Female lateral habitus (PSUC_FEM_255511). B: Female lateral habitus (PSUC_FEM_255546). C: Female lateral habitus (PSUC_FEM_255565). D: Female lateral habitus (PSUC_FEM_255538). E: Female lateral habitus (PSUC_FEM_255571). F: Female lateral habitus (PSUC_FEM_255514). G: Female head in anterior view (PSUC_FEM_255511). H: Female dorsal mesoscutum (PSUC_FEM_255511).

collected 16 Jan 2022; PSUC_FEM_254606 • 1 ♀; same locality as previous; Chris Friesen leg.; reared from cryptic twig gall on *Quercus macrocarpa*; gall collected 16 Jan 2022; emerged 13 May 2022; PSUC_FEM_254605 • 3 ♀; Manitoba, Warren, 4 miles east, Prime Meridian Trail; 50.130901, -97.44811; Chris Friesen leg.; reared from gall of *Andricus quercuspetiolicola* on *Quercus macrocarpa*; gall collected 16 Apr 2021; emerged 1 May 2021; PSUC_FEM_254597–254599 • 11 ♀ and 4 ♂; Manitoba, Warren, oak woodland along train tracks; 50.12714, -97.53827; Chris Friesen leg.; same host as previous; gall collected 26 Mar 2021; emerged Mar–May 2021; PSUC_FEM_253572; 245610–254621; 254623; 254625. USA • 1 ♀; Illinois, Urbana, Crystal Lake Park; reared from unidentified gall in twig of *Quercus macrocarpa*; gall collected 9 Mar 2017; emerged 15 May 2017; DNA sequence voucher # 671-083-3B; GenBank Accession # OR372027; PSUC_FEM_254625 • 1 ♀; Iowa, Coralville, North Pavilion Park; reared from gall of *Andricus quercuspetiolicola* on *Quercus bicolor*; gall collected 6 June 2017; emerged 5 Aug 2017; DNA sequence voucher # 852-042-43; GenBank Accession # OR372035; PSUC_FEM_255539 • 1 ♀; Iowa, Iowa city, City Park; reared from gall of *Andricus quercusfoliaformis* on *Quercus macrocarpa*; gall collected 24 June 2016; emerged 30 Oct 2016; DNA sequence voucher # 336-007-2A; GenBank Accession # OR371999; PSUC_FEM_255513 • 1 ♂; same locality and host as previous; gall collected 7 June 2017; emerged 18 Jan 2018; DNA sequence voucher # 860-007-31; GenBank Accession # OR372041; PSUC_FEM_255514 • 1 ♀; same locality as previous; reared from gall of *Andricus quercusfrondosus* on *Quercus bicolor*; gall collected 12 Apr 2017; emerged 8 May 2017; DNA sequence voucher # 700-006-4; GenBank Accession # OR372029; PSUC_FEM_255511 • 1 ♀; same locality as previous; reared from gall of *Andricus quercuspetiolicola* on *Quercus bicolor*; emerged 5 Aug 2017; DNA sequence voucher # 470-042-10A; PSUC_FEM_255543 • 1 ♂; Iowa, Iowa City, Mormon Handcart Trail; reared from gall of *Andricus quercusfrondosus* on *Quercus bicolor*; gall collected 14 July 2017; emerged 21 Sep 2017; DNA sequence voucher # 1016-006-2; GenBank Accession # OR372061; PSUC_FEM_255512 • 1 ♀; Iowa, Iowa City, Pentacrest; reared from gall of *Andricus quercuspetiolicola* on *Quercus alba*; gall collected 6 June 2016; emerged 7 Aug 2016; DNA sequence voucher # 296-010-15; GenBank Accession # OR371996; PSUC_FEM_255517 • 1 ♀; same locality as previous; reared from gall of *Callirhytis scitula* on *Quercus imbricaria*; gall collected 9 May 2017; emerged 9 May 2017; DNA sequence voucher # 294-049-37B; GenBank Accession # OR371995; PSUC_FEM_255547 • 1 ♀; Iowa, Iowa city, University of Iowa Campus; reared from gall of *Callirhytis scitula* on *Quercus palustris*; gall collected 9 June 2017; emerged 13 May 2018; DNA sequence voucher # 886-049-19B; GenBank Accession # OR372048; PSUC_FEM_255548 • 1 ♀; Iowa, Iowa City, University of Iowa Memorial Union; reared from gall of *Andricus quercuspetiolicola* on *Quercus bicolor*; gall collected 20 July 2016; emerged 13 May 2017; DNA sequence voucher # 419-042-26A; GenBank Accession # OR372008; PSUC_FEM_255542 • 1 ♀; Iowa, Tiffin, FW Kent/Evergreen; reared from gall of *Loxaulus quercusmammula* on *Quercus alba*; emerged 15 May 2019; DNA sequence voucher # 996-035-1; PSUC_FEM_255538 • 1 ♀; same locality as previous; reared from gall of *Andricus quercuspetiolicola* on *Quercus bicolor*; gall collected 17 June 2016; emerged 16 May 2017; DNA sequence voucher # 319-042-70A; GenBank Accession # OR371998; PSUC_FEM_255540 • 1 ♀; same locality as previous; same host as previous; gall collected 25 May 2017; emerged 6 July 2017; DNA sequence voucher # 807-042-25; GenBank Accession # OR372030; PSUC_FEM_255541 • 1 ♂; Missouri, St. Peters, Rabbit Run Park; reared from gall of *Callirhytis scitula* on *Quercus velutina*; gall collected 2 Sep 2016; emerged 22 May 2018; DNA sequence voucher # 528-049-5; GenBank Accession # OR372010; PSUC_FEM_255546 • 1 ♀; New York, Vestal, Zoo; reared from gall of *Callirhytis pigra* on *Quercus velutina*; gall collected 17 Oct 2018; emerged 29 May 2019; DNA sequence voucher # 1574-104-14; GenBank Accession # OR372092; PSUC_FEM_255571 • 2 ♀; Pennsylvania, State College, Penn State University, near HUB; DC Montelongo leg.; reared from gall of *Andricus quercuspetiolicola* on *Quercus bicolor*; gall collected 15 June 2020; PSUC_FEM_253546; 253547.

Remarks. We found numerous individuals corresponding to *Ceroptres cornigera* or *C. frondosae* among specimens we examined (Fig. 25A–F), which all shared the following combination of morphological characters: female antennae 12-segmented (Fig. 25A–F); vertical facial carinae long, extending about two thirds across lower face and delimiting a strongly bulging area (Fig. 25G); mesoscutum sculpture mostly coriaceous, usually with apparent raised transverse elements especially laterally (Fig. 24H). We examined specimens reared from the following galls: sexual generation of *Andricus foliaformis* Weld, 1926 on *Quercus macrocarpa* Michx.; sexual generation of *A. quercusfrondosus* on *Quercus bicolor* Willd. and *Q. macrocarpa*; sexual generation of *A. quercuspetiolicola* on *Q. alba* L., *Q. bicolor*, and *Q. macrocarpa*; sexual generation of *Callirhytis pigra* (Bassett, 1881) on *Q. velutina* Lam.; sexual generation of *Callirhytis scitula* Bassett, 1864 on *Q. palustris* Münchh.; sexual generation of *Loxaulus quercusmammula* (Bassett, 1881) on *Q. alba*; one female reared from an unidentified gall on *Q. macrocarpa*; one

female reared from an unidentified cryptic gall in twigs of *Q. macrocarpa*. Only a subset are from the known hosts for *C. cornigera* or *C. frondosae*; *C. frondosae* Ashmead, 1896 is a known associate only of *Andricus quercusfrondosa* Bassett, 1864 (reported by Lobato-Vila & Pujade-Villar [2019] as *Cynips? quercusfrondosa* and evidently carried forth in Nastasi & Deans [2021]) on *Quercus prinoides* Willd., while *C. cornigera* is known from *Callirhytis quercuscornigera* (Osten-Sacken, 1862) on red oaks (Lobato-Vila & Pujade-Villar 2019).

Lobato-Vila & Pujade-Villar (2019) suggest that characters concerning the dimensions of the ocellar triangle are the only diagnostic criteria for separating *C. cornigera* and *C. frondosae*, and the two species might prove synonymous given further study. However, our specimens do not perfectly match Lobato-Vila & Pujade-Villar's (2019) descriptions of either species well. The characters given in their key were variable in our material, and we found no specimens that routed correctly to *C. cornigera* or *C. frondosae*, keying in neither direction but clearly corresponding to that group. It is clear that our specimens represent multiple species, and whether they correspond to *C. cornigera*, *C. frondosae*, or some combination therein requires further study. Some of our material was reared from the same host gall from which *C. frondosae* has been reported (*A. quercusfrondosus*), but given that our material doesn't completely match the characters provided for *C. frondosae*, we are hesitant to suggest that the other hosts from which we reared material are new host records for *C. frondosae* or for *C. cornigera*. Further complicating this is Ward *et al.*'s (2024) molecular data for the material we examined; we found specimens corresponding to their species 1-32-33-34, 5b, 11-12, 14, and COI-F all belong here on the basis of morphological data (Fig. 24A–F).

As a result of these factors, we consider the species identity of the material we examined to be uncertain. Further revisionary work should aim to better resolve the placement of individuals comprising these species, and determine the true number of species belonging here. We consider that *C. cornigera* and *C. frondosae* might comprise a complex of cryptic or functionally cryptic species, and further studies should consider extensive sampling of morphological and molecular data for this group of species in particular. To best address these concerns, we do not separate *C. cornigera* and *C. frondosae* in our key to species, instead preferring to treat them therein as the *cornigera/frondosae* complex. Given the disjunct placement of Ward *et al.*'s putative species that match this complex morphologically, the traits defining the *cornigera/frondosae* complex may best be explained by morphological convergence due to use of similar host galls, although further research will be necessary to truly understand the composition of this species complex.

***Ceroptres ensiger* (Walsh, 1864)**

Fig. 25A

Material examined. ♂—USA • Pennsylvania, State College, Penn State University campus near HUB; DC Montelongo leg.; reared from gall of *Andricus quercuspetiolicola* on *Quercus bicolor*; gall collected 15 June 2020; PSUC_FEM_253545.

Remarks. *Ceroptres ensiger* is one of only a few species of *Ceroptres* in which the mesopleuron is sculptured. We examined a single male matching Lobato-Vila & Pujade-Villar's (2019) redescription that was reared from the same host, *Andricus quercuspetiolicola* (Bassett, 1863) on *Quercus bicolor* Willd., although Lobato-Vila & Pujade-Villar note that the male specimens mentioned in Walsh's description had since been lost; we verify the morphological characters given in their revision for males. Our material represents a new record from Pennsylvania; *C. ensiger* has only been previously reported from Illinois.

Ceroptres ensiger exhibits distinct alutaceous sculpture on the mesopleuron, a character rarely observed in *Ceroptres*. Other described North American species exhibiting this morphology are those associated with cecidomyiid galls (*C. songae* and *C. daleki*), and cecidomyiid midges are frequently reared from galls of *A. quercuspetiolicola* (Ward *et al.* 2022b, supplementary table S1; Nastasi, pers. obs.). Based on morphological resemblance between *C. ensiger* and midge-associated *Ceroptres*, it is possible that *C. ensiger* may be an inquiline of midges developing within galls of *A. quercuspetiolicola*, although careful rearing and gall dissection will be necessary to investigate this possibility. See treatment of *C. daleki* for additional commentary on the morphology of this species.

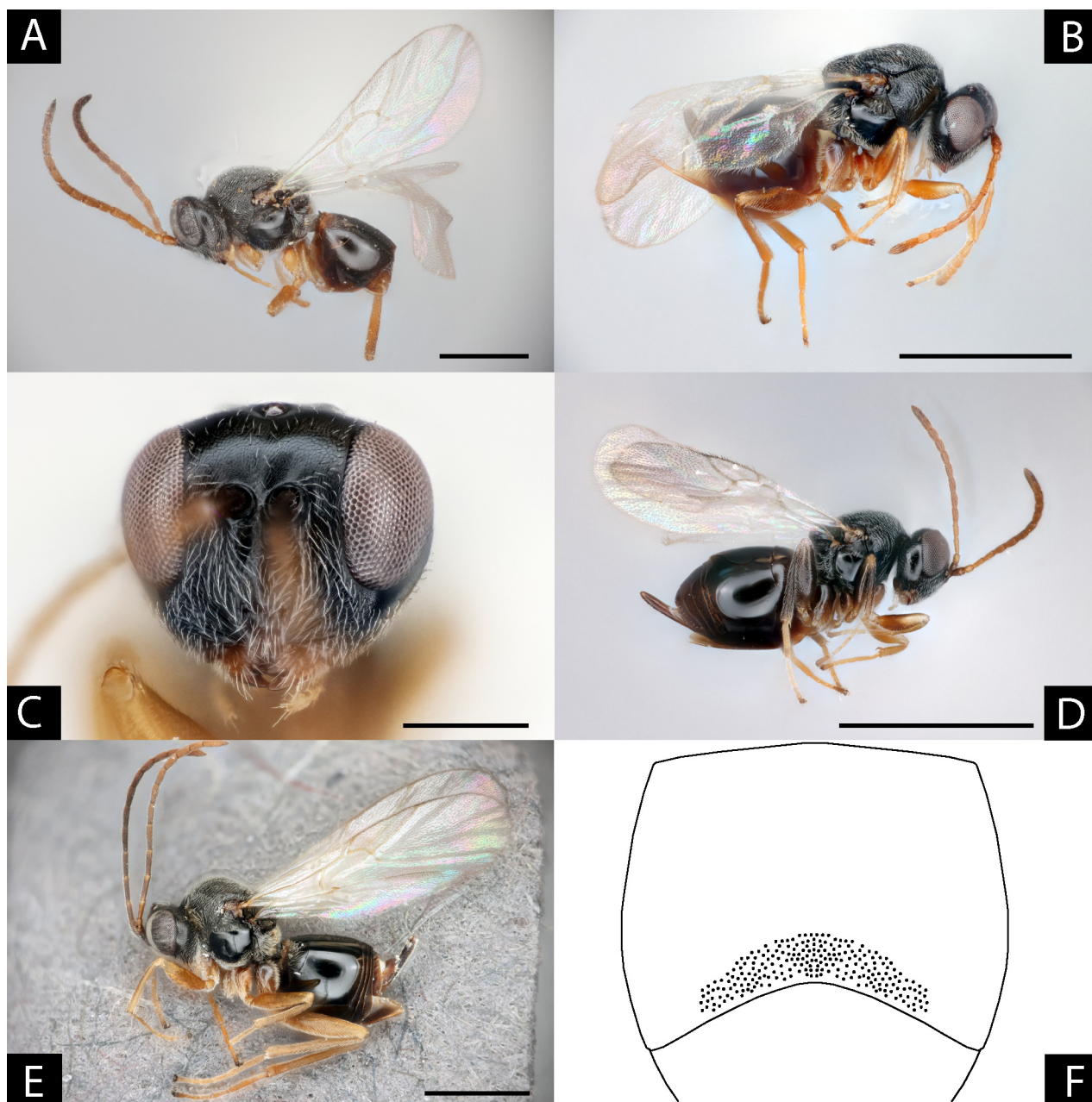


FIGURE 25. Vouchers of previously described *Ceroptres* species. Scale bars: A–B, D–E = 1.0 mm; C = 0.25 mm. A: *Ceroptres ensiger* male, lateral habitus (PSUC_FEM_253545). B: *C. lanigerae* female, lateral habitus (PSUC_FEM_255578). C: *C. lanigerae* female (PSUC_FEM_255578), head in anterior view. D: *C. cf. quercusobtusilobae* female, lateral habitus (PSUC_FEM_255572). E: *C. pisum* female, lateral habitus (PSUC_FEM_255629). F: *C. pisum* female, punctation of third metasomal tergite.

***Ceroptres lanigerae* Ashmead, 1885**

Figs 25B–C

Material examined. 2 ♀—USA • 1 ♀; Texas, Kyle, Lake Kyle; 29.986, -97.862; reared from gall of *Druon quercuslanigerum* on *Quercus fusiformis*; gall collected 1 Nov 2018; emerged 28 May 2019; DNA sequence voucher # 1589-160-34A; GenBank Accession # OR372096; PSUC_FEM_255577 • 1 ♀; same data as previous except the following: emerged 3 June 2019; DNA sequence voucher # 1589-160-35; GenBank Accession # OR372097; PSUC_FEM_255578.

Remarks. *Ceroptres lanigerae* was originally described from material collected in Florida (USA) (Ashmead

1885; Lobato-Vila & Pujade-Villar 2019). We examined two females reared from the known host, galls of the asexual generation of *Druon quercuslanigerum* (Ashmead, 1881), collected in Kyle, Texas (USA), which represent a new state record.

Ward *et al.* (2024) included a sequence from BOLD identified as *C. lanigerae* (MN935928.1) that did not match those from vouchers we identified as *C. lanigerae*. When this sequence is viewed on the BOLD database website (accessible here), it is specifically identified as “*Ceroptres cf lanigerae*”, suggesting that there was some doubt about the identification of the wasp. Our examination confirms that this sequence is not a proper representative of *C. lanigerae* as Ward *et al.*’s material instead corresponds to true *C. lanigerae*, as our material is morphologically identical to the description of *C. lanigerae* given by Lobato-Vila & Pujade-Villar (2019) and was reared from the known host gall.

***Ceroptres pisum* (Osten Sacken, 1861)**

Figs 25E–F

Material examined. 1 ♀—USA • Pennsylvania, Centre County, State Game Lands 176; A Guiguet coll.; reared from gall of *Acraspis pezomachoides* on *Quercus alba*; gall collected 8 Oct 2020; emerged 11–15 June 2021; PSUC_FEM_255629.

Remarks. *Ceroptres pisum* was previously reported only from Washington, D.C. We reared one female perfectly matching Lobato-Vila & Pujade-Villar’s (2019) description of *C. pisum* from asexual generation galls of *Acraspis pezomachoides* (Osten Sacken, 1862), the host allegedly associated with the type specimen (Lobato-Vila & Pujade-Villar 2019). Our specimen was collected in Pennsylvania and represents a new state record for *C. pisum*.

***Ceroptres cf quercusobtusilobae* (Karsch, 1880)**

Fig. 25D

Material examined. ♀—USA • Texas, Austin; reared from gall of *Andricus quercuspetiolicola* on *Quercus stellata*; gall collected 12 Apr 2018; emerged 23 Aug 2018; DNA sequence voucher # 1243-117-30; GenBank Accession # OR372075; PSUC_FEM_255572.

Remarks. We examined a single female representing Ward *et al.*’s (2024) sp. 31, which we keyed to couplet 20 in Lobato-Vila & Pujade-Villar (2019). This individual generally matches the characters provided for *Ceroptres quercusobtusilobae* (Karsch, 1880), and was reared from a gall of *Andricus quercuspetiolicola* (Bassett, 1863) on *Quercus stellata* Wangenh. This record corresponds to the known host plant, but the identity of the gall from which the type of *C. quercusobtusilobae* was reared is unknown. We hesitate to consider this a confirmation of the host gall species, as there are some differences between the specimen we examined and Lobato-Vila & Pujade-Villar’s redescription. As such, we cannot rule out the possibility of this specimen corresponding to a separate, undescribed species. Our individual does not clearly exhibit transverse elements on the mesoscutum and has a longer apical flagellomere (nearly 4.0× as long as wide in our specimen; apparently about 3.0× in *C. quercusobtusilobae*), among other differences. As a result, we are hesitant to consider our specimen a true exemplar of *C. quercusobtusilobae* at this time; our specimen could instead represent a separate, undescribed species.

Discussion

Host use in Ceroptres

Patterns of host use in *Ceroptres* are further elucidated by our observations. After our study, *Ceroptres* species are now associated with over 40 named host gall species in the Cynipidae and Cecidomyiidae (Supplemental Files 2–3). The majority of known North American *Ceroptres* species (27 of 40 species; Supplemental File 2) are evidently specialists known from only a single host gall species. Nearly all remaining *Ceroptres* species are associated with two or three host gall species and seem to attack host galls that are phylogenetically related in the same genus, or

ecologically related in their occurrence on the same or closely related oak species. The remaining two species, *C. junquerasi* Lobato-Vila & Pujade-Villar, 2019 and *C. snellingi* Lyon, 1996, are associated with nine and seven host gall species, respectively. Only morphological data were used to associate these two species with their respective host galls and given the typical number of host gall associations for a given species, it seems likely that these two species in particular could be found to comprise species complexes. Lobato-Vila & Pujade-Villar (2019) state that both of these species exhibit morphological variability, further supporting this possibility. We find that the characters listed by Lobato-Vila & Pujade-Villar as variable for these species, particularly the F1/F2 ratio and ocellar triangle ratios, are very consistent across conspecific individuals in the species we examined. While Lobato-Vila & Pujade-Villar do not state whether these morphological differences correspond with different host galls or host plants, it is likely that further study will reveal numerous host-specific lineages amongst *C. junquerasi* and *C. snellingi*. Similar trends are probably true amongst the several described Palearctic *Ceroptres* species, which are each known from many host galls and exhibit some degree of intraspecific morphological variation (Pujade-Villar & Nieves-Aldrey 1993, Melika 2006, Lobato-Vila & Pujade-Villar 2019), therein likely comprising overly lumped species concepts.

When considering how many North American *Ceroptres* species are associated with a single host gall species, six galls (five species of Cynipini and the midge *Polystepha pilulae*) are associated with more than one *Ceroptres* species. Of these, five host gall species are each associated with two *Ceroptres* species, while *Melikaiella ostensackeni* Pujade-Villar, 2014 is associated with four *Ceroptres* species (Supplemental File 3). In each case, the associated *Ceroptres* species vary to some degree with the host plant on which the gall is induced (Table 1), further implying that host preference for *Ceroptres* may incorporate both plant- and gall-related cues.

It is possible that our observations regarding host associations are impacted by incomplete knowledge of host use for a given *Ceroptres* species. Further study is necessary to elucidate any further host records for our new species as well as those previously described. Additionally, in the case of oak gall wasp hosts themselves, we cannot rule out the possible impact of cryptic species, as preliminary data from ongoing studies suggest that this may be the case for some oak galls with multiple associated *Ceroptres*, particularly *Andricus quercuspetiolicola* (Bassett, 1863) (Forbes *et al.*, in litt.).

Overall, our observations favor the idea that *Ceroptres* are specialists either on a single host gall species or several closely related gall species. Records of highly polyphagous species probably correspond to multiple host-specific lineages, and we suggest that the majority of *Ceroptres*-gall wasp associations constitute species-specific relationships, especially given the possibility of further cryptic species amongst oak gall wasps.

Whether there are discrete phylogenetic patterns of host use in *Ceroptres* still requires further study. When referencing our species designations along with Ward *et al.*'s phylogenetic analyses, it is evident that Nearctic species associated with cecidomyiid galls are sister to Nearctic species associated with Cynipini; this agrees with preliminary UCE data from an ongoing study of cynipoid phylogenetics (Nastasi *et al.*, in prep.). This suggests that there may have been a single transition from preference for Cynipini galls to those induced by cecidomyiid midges given that Palearctic *Ceroptres* are probably sister to all Nearctic species (Ward *et al.* 2024). Ward *et al.* also found *C. lokii* to be sister to the remaining Nearctic Cynipini associates. Beyond this, it is difficult to determine whether any additional clades have phylogenetically defined host preferences above the species level. A major component of this dilemma is an unresolved generic taxonomy for Nearctic Cynipini, with many genera in need of revision; taxonomic issues are especially prevalent in the genera *Andricus* Hartig, 1840, *Callirhytis* Förster, 1869, *Dryocosmus* Giraud, 1859, and *Neuroterus* Hartig, 1840 (Cuesta-Porta *et al.* 2020, Brandão-Dias *et al.* 2022, Melika *et al.* 2021), taxa with which many species of *Ceroptres* are now associated. After these large, polyphyletic genera are revised, it may be possible to determine more discrete relationships between *Ceroptres* and host gall clades. Similarly, it is evident that many additional undescribed species of *Ceroptres* exist; collecting, describing, and sequencing these species would undoubtedly allow for a more developed understanding of factors related to host use in the genus.

Association of Ceroptres with cecidomyiid midges (Diptera: Nematocera)

The association of *Ceroptres* with galls induced by cecidomyiid midges was first suggested by the description of *Ceroptres inermis* (Walsh, 1864). This species was recently considered a *nomen dubium* by Lobato-Vila & Pujade-Villar (2019), leaving no valid *Ceroptres* species associated with midge galls. We here describe two new species from midge galls: *Ceroptres songae* from galls of *Polystepha pilulae* (Beutenmüller, 1892) on *Quercus falcata*

Michx., and *Ceroptres daleki* from galls of *P. pilulae* on *Q. imbricaria* Michx. We have examined material of an additional undescribed *Ceroptres* species that was reared from galls of another midge, *Polystepha symmetrica* (Osten Sacken, 1862), on *Quercus falcata* Michx. We refrain from describing this additional species here as the two known specimens, both adult females, are damaged and would not allow for sufficient characterization of the species. We also have DNA barcodes of an additional species dissected from an additional midge gall (see “Species richness of Nearctic *Ceroptres*” below) and have reviewed an iNaturalist observation (<https://www.inaturalist.org/observations/95795533>) depicting specimens reared from galls of *Polystepha pustuloides* (Beutenmüller, 1907) on *Quercus ilicifolia*. It is possible that one of these species corresponds to Walsh’s *Ceroptres inermis*, but substantiating this would require locating the type material which is presumably lost (Lobato-Vila & Pujade-Villar 2019).

These cecidomyiid-associated species may form a clade sister to those associated with Nearctic Cynipini, as *C. daleki* was found to be the sister of all other Nearctic species in Ward *et al.*’s (2024) analysis of DNA barcode data. We also have preliminary analyses suggesting that midge-associated *Ceroptres* could be the sister to all other Ceroptresini (Nastasi *et al.*, unpublished data). It is highly likely that additional cecidomyiid galls on oaks act as hosts for *Ceroptres*; further work on *Ceroptres* should involve substantial rearing of midge galls to further investigate the extent of this association.

Other inquiline cynipids in the tribe Synergini have been recorded in association with cecidomyiid midges. Species in the synergine genera *Synergus* and *Saphonecrus* have been reared from galls of *Dryomyia* and *Janetia* (Askew 1999, Ebrahim *et al.* 2006). An additional synergine species, *Rhoophilus loewi* Mayr, 1881, is an inquiline of galls induced by moths (van Noort *et al.* 2007), representing an additional association of an inquiline cynipid with an additional gall-inducing host lineage. Considering these observations, it is possible that cynipoid wasps will continue to be found in association with other lineages of gall inducers, especially those that also induce galls on major cynipid host plants such as oaks.

Species richness of Nearctic Ceroptres

Our study confirmed Ward *et al.*’s (2024) assertion that *Ceroptres* is a species-rich genus. Based on our observations, it is evident that several key factors have obscured the true richness of *Ceroptres* species. The genus has only recently been revised for the first time (Lobato-Vila & Pujade-Villar 2019), and this revision focused primarily on examining type material for previously described species. Additionally, *Ceroptres* are rare compared to *Synergus*, the other ubiquitous genus of oak gall inquilines in North America; *Synergus* are far more commonly reared from their host galls than *Ceroptres* (pers. obs.) despite the association of both genera with a wide diversity of host gall species (Ward *et al.* 2024). This latter factor is especially detrimental to progressing knowledge of *Ceroptres* diversity, as rearing many oak galls might yield only one or several *Ceroptres* wasps, hence our descriptions of many species from only one female specimen. Male *Ceroptres* are also somewhat rare relative to females and are known for only 15 of the 40 described species, although several males are unknown on the basis of lost type material (Lobato-Vila & Pujade-Villar 2019). It is unclear whether the lack of knowledge of males is the result of the general rarity of *Ceroptres*, or perhaps instead due to parthenogenesis as is widespread in other gall wasps (Stone *et al.* 2002).

Despite these challenges, *Ceroptres* appears to be a highly diverse genus, and our observations relating to host use suggest that there are many species awaiting discovery. Ward *et al.* (2024) studied *Ceroptres* from fewer than 50 host gall species, while there are around 680 species of Cynipini known from North America (Melika *et al.* 2021, Nastasi *et al.* 2024a). Confirmation of the association of *Ceroptres* with midge galls further expands possible diversity on the basis of host associations. Ward *et al.* (2024) do suggest that *Ceroptres* species exhibit some degree of host preference relating to gall phenotype, relative to other inquilines. However, even considering that only a subset of North American Cynipini may host *Ceroptres*, there could be hundreds of additional unknown *Ceroptres* species awaiting discovery, especially given the probable diversity of still-undescribed Cynipini and Cecidomyiidae in the region. The apparent rarity of *Ceroptres* in terms of prevalence in gall rearing also means that commonly-reared galls could host obscure *Ceroptres* species.

In line with this idea, we are already aware of nearly 50 additional putative undescribed *Ceroptres* species. Among these are several species represented only by male vouchers from Ward *et al.*’s (2024) sequencing study, species that were destructively sampled by Ward *et al.* for sequencing UCEs, and additional specimens we’ve collected during other studies. We provide a tentative list of putative undescribed species including known

host associations in Supplemental File 4; preserved specimens of most of these species are deposited at PSUC (Supplemental File 1).

Recommendations for future work on Ceroptres

Overall, we recommend an integrative taxonomic approach consisting of morphological, ecological, and genetic data in further investigating *Ceroptres* wasps. Our findings suggest that molecular data alone are likely insufficient for delimiting species of *Ceroptres*. In most cases, *Ceroptres* species were sufficiently delimited by Ward *et al.* (2024), but in two cases, we found that a single, well-supported clade recognized as a single species by molecular data truly comprised two reciprocally monophyletic species that were elucidated on the basis of morphological data. We also found several additional complications relating to morphological data, especially in our treatments of *C. lokii* and the *C. cornigera/frodosae* complex.

Our study revealed high utility in characters in the antennae for species diagnosis. As a result, many species diagnoses require measurement of antenna segment dimensions or counts of antennomeres. Given the relative ease with which antennae are damaged or broken, locating additional character systems should be a priority, as specimens with even one antennomere missing may not be identifiable via our key to species. Through our examination, we identified several character systems that could benefit from clarification in future studies. While still a character of the antennae, we found that the ratios of the length and width of the first two antennomeres could be quite variable between different species. These dimensions appear to be consistent within species in other gall wasp taxa (e.g., Nastasi *et al.* 2024b), and the proximal antennomeres are likely less prone to damage than the distal. The dimensions and shape of the mesoscutum also appeared to vary, especially with regard to the shape of the anterior margin. The distinction and size of the areolet may also be useful. We did not include these characters here given that these characters were not included or emphasized in the last revision of *Ceroptres* (Lobato-Vila & Pujade-Villar 2019), and we were not able to examine all described species in order to collect this data for them. More generally, studies of internal structures, particularly genitalia, are sorely lacking in Cynipoidea. While microhymenopteran genitalia are somewhat uncommonly examined in the context of taxonomy, genitalia morphology has great importance to species recognition in Ceraphronoidea (Trietsch *et al.* 2020). Recent studies (Dal Pos *et al.* 2023, Griebenow *et al.* 2023) have also improved accessibility of terminology relating to hymenopteran genitalia.

Future works may also benefit from providing a clear comparative distinction allowing for recognition of subclavate and subfiliform antenna shapes. While these designations are usually straightforward on the basis of general observation of antenna shape, there were several cases where antenna shape initially appeared intermediate to either type, although we were ultimately able to assign all species' antenna forms to either category.

Lastly, published studies have not yet examined the large amounts of unidentified *Ceroptres* deposited in major North American collections such as USNM. *Ceroptres* specimens identified only to genus make up more than seven drawers at AMNH (C. Lebeau pers. comm.), while USNM has two tightly packed drawers, consisting of no fewer than 1,500 specimens (L. Nastasi, pers. obs.). The most recent revision of *Ceroptres* (Lobato-Vila & Pujade-Villar 2019) examined only type material and newly collected specimens and given that we did not aim to provide a comprehensive review or revision of *Ceroptres*, we also refrained from intimately perusing unsorted material here. Unsorted material of all kinds is well known as a valuable resource in understanding taxonomy and often forms the foundation of revisionary studies. A future revision of *Ceroptres* should aim to accumulate as much material as possible in order to provide the most comprehensive treatment of the genus. Given our observations, it would be wholly unsurprising to find dozens, if not hundreds, of undescribed *Ceroptres* species amongst unsorted museum material.

Acknowledgments

We thank Antonio Casadei, Antoine Guiguet, Denise Montelongo, Sofia Sheikh, Joseph Verry, and Caleb Wilson for collecting many of the specimens we examined; Christian Weinrich for suggesting the species name *Ceroptres dandoi*; Laura Porturas (PSUC) for assisting in uploading digitized specimen data; Heather Hines, John Tooker, and Laura Porturas (PSU) for their assistance and encouragement in our studies of gall wasp biodiversity; Christine

Lebeau (AMNH) and Matt Buffington (USNM) for providing information about *Ceroptres* in their respective collections; Irene Lobato-Vila for allowing us to replicate images from the 2019 revision of *Ceroptres* (Figure 26).

This material is based upon work supported by the National Science Foundation under Grant No. DEB-1856626. Any opinions, findings, and conclusions or recommendations expressed in this material are those of the authors and do not necessarily reflect the views of the National Science Foundation. LFN was supported by two awards from the Society of Systematic Biologists: Mini-ARTS and the Graduate Student Research Award. CNS was supported by the Erickson Discovery Grant (The Pennsylvania State University). Funding for some collections was provided to AAF by the University of Iowa and to AKGW by the Center for Global and Regional Environmental Research.

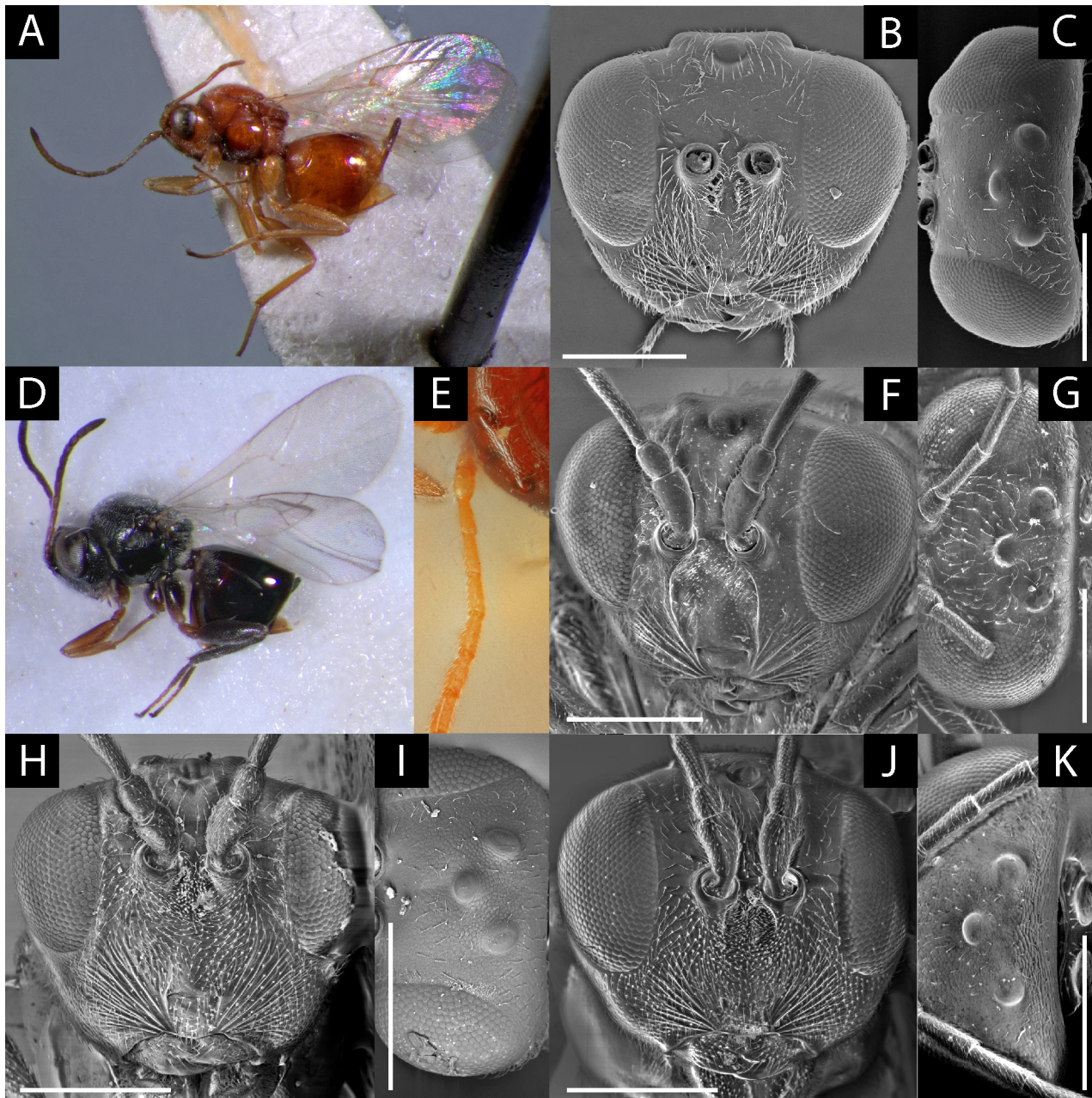


FIGURE 26. Previously described *Ceroptres* species. Scale bars: 0.25 mm. A: *Ceroptres confertus* female, lateral habitus. B: *C. junquerasi* female, head in anterior view. C: *C. junquerasi* female, ocellar triangle in dorsal view. D: *C. nigriscrus* female, lateral habitus. E: *C. minutissimi* female, antenna. F: *C. lenis* female, head in anterior view. G: *C. lenis* female, ocellar triangle in dorsal view. H: *C. quadratifacies* female, head in anterior view. I: *C. quadratifacies* female, ocellar triangle in dorsal view. J: *C. mexicanus* female, head in anterior view. K: *C. mexicanus* female, ocellar triangle in dorsal view. Images for Figure 26 were generously provided to us by Irene Lobato-Vila from the 2019 revision of *Ceroptres* (Lobato-Vila & Pujade-Villar 2019).

References

- Ashmead, W.H. (1885) A bibliographical and synonymical catalogue of the North American Cynipidae, with description of new species. *Transactions of the American Entomological Society*, 12 (3–4), 291–304.
<https://doi.org/10.2307/25076460>
- Ashmead, W.H. (1896) Descriptions of new parasitic Hymenoptera. *Transactions of the American Entomological Society*, 23 (2), 179–234.
- Askew, R.R. (1984) n.k. In: *The biology of gall wasps. Biology of Gall Insects*. Edward Arnold, London, pp. 223–271.
- Askew, R.R. (1999) Confirmation of an association of *Synergus* Hartig and *Saphonecрус* Dalla Torre and Kieffer (Hym., Cynipidae) with oak galls of Cecidomyiidae (Dipt.). *Entomologist's Monthly Magazine*, 135, 89–90.
- Blaimer, B.B., Gotzek, D., Brady, S.G. & Buffington, M.L. (2020) Comprehensive phylogenomic analyses re-write the evolution of parasitism within cynipoid wasps. *BMC Evolutionary Biology*, 20, 155.
<https://doi.org/10.1186/s12862-020-01716-2>
- Brandão-Dias, P.F.P., Zhang, Y.M., Pirro, S., Vinson, C.C., Weinersmith, K.L., Ward, A.K.G., Forbes, A.A. & Egan, S.P. (2022) Describing biodiversity in the genomics era: A new species of Nearctic Cynipidae gall wasp and its genome. *Systematic Entomology*, 47 (1), 94–112.
<https://doi.org/10.1111/syen.12521>
- Buffington, M.L., Forshage, M., Liljeblad, J., Tang, C.T. & van Noort, S. (2020) World Cynipoidea (Hymenoptera): a key to higher-level groups. *Insect Systematics and Diversity*, 4 (4), 1.
<https://doi.org/10.1093/isd/ixaa003>
- Cuesta-Porta, V., Arnedo, M.A., Cibrián-Tovar, D., Barrera-Ruiz, U.M., García-Martíñón, R.D., Equihua-Martínez, A., Estrada-Venegas, E.G., Clark-Tapia, R., Romero-Rangel, S. & Pujade-Villar, J. (2020) A New Genus of Oak Gall Wasp, *Striatoandricus* Pujade-Villar (Hymenoptera: Cynipidae: Cynipini) from America with Descriptions of Two New Mexican Species. *Zoological Studies*, 59, e8.
<https://doi.org/10.6620%2FZS.2020.59-08>
- Dal Pos, D., Mikó, I., Talamas, E.J., Vilhelmsen, L. & Sharanowski, B.J. (2023) A revised terminology for male genitalia in Hymenoptera (Insecta), with a special emphasis on Ichneumonidea. *PeerJ*, 11, e15874.
<https://doi.org/10.7717/peerj.15874>
- Fang, Z., Tang, C.T., Zhu, Y., Xiong, T., Sinclair, F., Hearn, J., Mikolajczak, K.M., Melika, G., Stone, G.N. & Fang, S. (2020) *Lithosaphonecрус edurus* Fang, Melika, and Tang, a New Cynipid Inquiline Species (Hymenoptera: Cynipidae: Synergini) from Sichuan, China. *Proceedings of the Entomological Society of Washington*, 122 (4), 805–820.
<https://doi.org/10.4289/0013-8797.122.4.805>
- Fitch, A.M.D. (1859) Fifth report on the noxious and other insects of the state of New York. Insects infesting deciduous forest trees. *Annual Reports of the New York State Agricultural Society*, 18, 781–829.
- Gobbo, E., Lartillot, N., Hearn, J., Stone, G.N., Abe, Y., Wheat, C.W., Ide, T. & Ronquist, F. (2020) From inquilines to gall inducers: genomic signature of a life-style transition in *Synergus* gall wasps. *Genome Biology and Evolution*, 12 (11), 2060–2073.
<https://doi.org/10.1093/gbe/evaa204>
- Goulet, H. & Huber, J. (Eds.) (1993) *Hymenoptera of the world: an identification guide to families*. Centre for Land and Biological Resources Research, Research Branch, Agriculture Canada, Ottawa, 668 pp.
- Griebenow, Z.H., Richter, A., van de Kamp, T., Economo, E.P. & Lieberman, Z.E. (2023) Comparative morphology of male genitalia skeletomusculature in the Leptanillinae (Hymenoptera: Formicidae), with a standardized muscular terminology for the male genitalia of Hymenoptera. *Arthropod Systematics & Phylogeny*, 81, 935–1018.
<https://doi.org/10.3897/asp.81.e104810>
- Harris, R.A. (1979) A glossary of surface sculpturing. State of California Department of Food and Agriculture, *Occasional Papers in Entomology*, 28, 1–31
- Hartig, T. (1840) Ueber die Familie der Gallwespen. *Zeitschrift für Entomologie*, 2, 176–210.
- Hearn, J., Gobbo, E., Nieves-Aldrey, J.L., Branca, A., Nicholls, J.A., Koutsovoulos, G., Lartillot, N., Stone, G.N. & Ronquist, F. (2023) Phylogenomic analysis of protein-coding genes resolves complex gall wasp relationships. *Systematic Entomology*, 49 (1), 1–28.
<https://doi.org/10.1111/syen.12611>
- Karsch, F. (1880) Neue Zooecidien und Cecidozoën. *Zeitschrift für die Gesamten Naturwissenschaften*, 53, 286–309.
- Liljeblad, J. & Ronquist, F. (1998) A phylogenetic analysis of higher-level gall wasp relationships (Hymenoptera: Cynipidae). *Systematic Entomology*, 23 (3), 229–252.
<https://doi.org/10.1046/j.1365-3113.1998.00053.x>
- Lobato-Vila, I. & Pujade-Villar, J. (2019) Revision of world Ceroptresini (Hymenoptera: Cynipidae) with the description of a new genus and five new species. *Zootaxa*, 4685 (1), 1–67.
<https://doi.org/10.11646/zootaxa.4685.1.1>
- Lobato-Vila, I. & Pujade-Villar, J. (2021) The genus *Synergus* Hartig (Hymenoptera: Cynipidae: Synergini) in the New World: a complete taxonomic revision with a key to species. *Zootaxa*, 4906 (1), 1–121.
<https://doi.org/10.11646/zootaxa.4906.1.1>

- Lobato-Vila, I., Bae, J., Roca-Cusachs, M., Kang, M., Jung, S., Melika, G., Péntzes, Z. & Pujade-Villar, J. (2022) Global phylogeny of the inquiline gall wasp tribe Synergini (Hymenoptera: Cynipoidea: Cynipidae): first insights and establishment of a new cynipid tribe. *Zoological Journal of the Linnean Society*, 195, 1338–1354.
<https://doi.org/10.1093/zoolinnean/zlab085>
- Lyon, R.J. (1996) New cynipid wasps from the southwestern United States (Hymenoptera: Cynipidae). *Pan-Pacific Entomologist*, 72 (4), 181–192.
- McCracken, I. & Egbert, D. (1922) California gall-making Cynipidae with descriptions of new species. *Stanford University Publications, Biological Sciences*, 3 (1), 1–76.
- Melika, G. (2006) *Gall wasps of Ukraine. Vol. 1*. Vestnik zoologii, The Schmalhausen Institute of Zoology, National Academy of Sciences of Ukraine, Kiev, 300 pp.
- Melika, G., Pujade-Villar, J., Nicholls, J.A., Cuesta-Porta, V., Cooke-McEwen, C. & Stone, G.N. (2021) Three new Nearctic genera of oak cynipid gall wasps (Hymenoptera: Cynipidae: Cynipini): *Burnettweldia* Pujade-Villar, Melika & Nicholls, *Nicholtsiella* Melika, Pujade-Villar & Stone, *Disholandricus* Melika, Pujade-Villar & Nicholls; and re-establishment of the genus *Paracraspis* Weld. *Zootaxa*, 4993 (1), 1–81.
<https://doi.org/10.11646/zootaxa.4993.1.1>
- Nastasi, L.F. & Deans, A.R. (2021) Catalogue of Rose Gall, Herb Gall, and Inquiline Gall Wasps (Hymenoptera: Cynipidae) of the United States, Canada and Mexico. *Biodiversity Data Journal*, 9.
<https://doi.org/10.3897/BDJ.9.e68558>
- Nastasi, L.F., Buffington, M.L., Davis, C.K. & Deans, A.R. (2024a) Key to the North American tribes and genera of herb, rose, bramble, and inquiline gall wasps (Hymenoptera, Cynipoidea, Cynipidae *sensu lato*). *ZooKeys*, 1196, 177–207.
<https://doi.org/10.3897/zookeys.1196.118460>
- Nastasi, L.F., Tooker, J.F., Davis, C.K., Smith, C.N., Frey, T.S., Hatfield, M.J., Presnall, T.M., Hines, H.M. & Deans, A.R. (2024b) Cryptic or underworked? Taxonomic revision of the *Antistrophus rufus* species complex (Cynipoidea, Aulacideini). *Journal of Hymenoptera Research*, 97, 399–439.
<https://doi.org/10.3897/jhr.97.121918>
- Nicholls, J.A., Melika, G., Digweed, S.C. & Stone, G.N. (2022) Pairing of sexual and asexual generations of Nearctic oak gallwasps, with new synonyms and new species names (Hymenoptera: Cynipidae, Cynipini). *Zootaxa*, 5145 (1), 1–79.
<https://doi.org/10.11646/zootaxa.5145.1.1>
- Osten-Sacken, C.R. von (1861) On the Cynipidae of the North American oaks and their galls. *Proceedings of the Entomological Society of Philadelphia*, 1 (3), 47–72.
- Osten-Sacken, C.R. von (1865) Contributions to the natural history of the Cynipidae of the United States and of their galls. *Proceedings of the Entomological Society of Philadelphia*, 4 (3), 331–380.
- PATO curators (2023) Phenotype and Trait Ontology. Available from: <https://github.com/pato-ontology/pato/> (accessed 29 March 2024)
- Pujade-Villar, J. & Nieves-Aldrey, J.L. (1993) Revisión de las especies europeas del género *Ceroptres* Htg., 1840 (Hymenoptera: Cynipidae). *Boletín de la Asociación Española de Entomología*, 17 (2), 49–63.
- Ronquist, F. (1994) Evolution of parasitism among closely related species: phylogenetic relationships and the origin of inquilinism in gall wasps (Hymenoptera, Cynipidae). *Evolution*, 48, 241–266.
<https://doi.org/10.2307/2410091>
- Ronquist, F., Nieves-Aldrey, J.L., Buffington, M.L., Liu, Z., Liljeblad, J. & Nylander, J.A. (2015) Phylogeny, evolution and classification of gall wasps: the plot thickens. *PLoS One*, 10 (5), e0123301.
<https://doi.org/10.1371/journal.pone.0123301>
- Stone, G.N., Schönrogge, K., Atkinson, R.G., Bellido, D. & Pujade-Villar, J. (2002) The Population Biology of Oak Gall Wasps (Hymenoptera: Cynipidae). *Annual Review of Entomology*, 47, 633–668.
<https://doi.org/10.1146/annurev.ento.47.091201.145247>
- Trietsch, C., Mikó, I., Ezray, B. & Deans, A.R. (2020) A Taxonomic Revision of Nearctic *Conostigmus* (Hymenoptera: Ceraphronoidea: Megaspilidae). *Zootaxa*, 4792 (1), 1–155.
<https://doi.org/10.11646/zootaxa.4792.1.1>
- van Noort, S. (2024) WaspWeb: Hymenoptera of the World. Available from: <https://www.waspweb.org> (accessed 20 August 2024)
- van Noort, S., Buffington, M.L. & Forshage, M. (2015) Afrotropical Cynipoidea (Hymenoptera). *ZooKeys*, 493, 1–176.
<https://doi.org/10.3897/zookeys.493.6353>
- van Noort, S., Stone, G.N., Whitehead, V.B. & Nieves-Aldrey, J.L. (2007) Biology of *Rhoophilus loewi* (Hymenoptera: Cynipoidea: Cynipidae), with implications for the evolution of inquilinism in gall wasps. *Biological Journal of the Linnean Society*, 90, 153–172.
<https://doi.org/10.1111/j.1095-8312.2007.00719.x>
- Walsh, B.D. (1864) On dimorphism in the hymenopterous genus *Cynips*; with an appendix, containing hints for a new classification of Cynipidae and a list of Cynipidae, including descriptions of several new species, inhabiting the oak-galls of Illinois. *Proceedings of the Entomological Society of Philadelphia*, 2, 443–500.
- Ward, A.K.G., Sheikh, S.I. & Forbes, A.A. (2020) Diversity, host ranges, and potential drivers of speciation among the inquiline enemies of oak gall wasps (Hymenoptera: Cynipidae). *Insect Systematics and Diversity*, 4 (6), 3.

<https://doi.org/10.1093/isd/ixaa017>

- Ward, A.K., Bagley, R.K., Egan, S.P., Hood, G.R., Ott, J.R., Prior, K.M., Shiekh, S.I., Weinersmith, K.L., Zhang, L., Zhang, Y.M. & Forbes, A.A. (2022a) Speciation in Nearctic oak gall wasps is frequently correlated with changes in host plant, host organ, or both. *Evolution*, 76 (8), 1849–1867.
<https://doi.org/10.1111/evo.14562>
- Ward, A.K., Busbee, R.W., Chen, R.A., Davis, C.K., Driscove, A.L., Egan, S.P., Goldberg, B.A.R., Hood, G.R., Jones, D.G., Kranz, A.J., Meadely-Dunphy, S.A., Milks, A.K., Ott, J.R., Prior, K.M., Sheikh, S.I., Shzu, S., Weinersmith, K.L., Zhang, L., Zhang, Y.M. & Forbes, A.A. (2022b) The arthropod associates of 155 North American cynipid oak galls. *Zoological Studies*, 61, e57.
<https://doi.org/10.1101/2022.04.26.489445>
- Ward, A.K.G., Zhang, Y.M., Brown, G.E., Hippie, A.C., Prior, K.M., Rollins, S., Sierra, N., Sheikh, S.I., Tribull, C.M. & Forbes, A.A. (2024) Speciation in kleptoparasites of oak gall wasps often correlates with shifts into new tree habitats, tree organs, or gall morphospace. *Evolution*, 78 (1), 174–187.
<https://doi.org/10.1093/evolut/qpaa202>
- Weld, L.H. (1957) New American cynipid wasps from oak galls. *Proceedings of the United States National Museum*, 107 (3384), 107–122.
<https://doi.org/10.5479/si.00963801.107-3384.107>
- Yang, X.H., Liu, Z., Pang, Y., Su, C.Y. & Zhu, D.Y. (2020) Three new species of Synergini wasps from same galls on *Lithocarpus glaber* (Thunb.) in Hunan, China (Hymenoptera, Cynipidae). *Insect Systematics & Evolution*, 51 (4), 551–583.
<https://doi.org/10.1163/1876312X-00002304>
- Yoder, M.J., Mikó, I., Seltmann, K.C., Bertone, M.A. & Deans, A.R. (2010) A gross anatomy ontology for Hymenoptera. *PloS one*, 5 (12), e15991.
<https://doi.org/10.1371/journal.pone.0015991>

Supplementary Materials. The following supporting information can be downloaded at the DOI landing page of this paper:

Supplemental File 1. Material examined - digitized specimen data presented as a DarwinCore archive.