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Frank E. Kurczewski

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A journal of world insect systematics

INSECTA MUNDI

0959

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Frank E. Kurczewski

1188 Converse Drive NE
Atlanta, GA 30324

Rick C. West

6365 Willowpark Way
Sooke, BC, Canada V9Z 1L9

Date of issue: October 28, 2022

Center for Systematic Entomology, Inc., Gainesville, FL

Kurczewski FE, West RC. 2022. Host selection and nesting behavior of Nearctic trapdoor spider-hunting spider wasps (Hymenoptera: Pompilidae: Pepsinae, Pompilinae). *Insecta Mundi* 0959: 1–24.

Published on October 28, 2022 by
Center for Systematic Entomology, Inc.
P.O. Box 141874
Gainesville, FL 32614-1874 USA
<http://centerforsystematicentomology.org/>

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Printed copies (ISSN 0749-6737) annually deposited in libraries

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The Natural History Museum, London, UK
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Electronic copies (Online ISSN 1942-1354) in PDF format

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Host selection and nesting behavior of Nearctic trapdoor spider-hunting spider wasps (Hymenoptera: Pompilidae: Pepsinae, Pompilinae)

Frank E. Kurczewski

1188 Converse Drive NE
Atlanta, GA 30324
kurczewskifrank@gmail.com

Rick C. West

6365 Willowpark Way
Sooke, BC, Canada V9Z 1L9
rickcwest3@gmail.com

Abstract. Host records and nesting behavior of the Nearctic trapdoor spider-hunting spider wasps (Hymenoptera: Pompilidae) *Calopompilus* Ashmead and *Priocnemissus* Haupt (Pepsinae: Pepsini) and *Aporus* Spinola and *Psorthaspis* Banks (Pompilinae: Aporini) are reviewed, investigated, compared, and discussed. First time incidental trapdoor spider host records for *Priocnemis* (*Priocnemissus*) *minorata* Banks (Pepsinae: Pepsini), *Anoplius* (*Lophopompilus*) *carolina* (Banks) (Pompilinae: Pompilini), and *Notocyphus dorsalis dorsalis* Cresson (Notocyphinae: Notocyphini) are included, although they are not typical trapdoor spider-hunting spider wasp species. The Palearctic *Aporus* (*Aporus*) *unicolor* Spinola, *A. (Aporus) bicolor* Spinola and *A. (Aporus) planiceps* (Latreille) are referenced for comparison with Nearctic *Aporus* sensu stricto. Early 20th century papers on species of *Aporus* and *Psorthaspis* are revived. New information on nesting behavior of Nearctic trapdoor spider-hunting spider wasps is described and first host trapdoor spider records for *Psorthaspis formosa* (Smith), *P. legata* (Cresson) and *P. mariae* (Cresson) are documented. Potential Pompilidae species in the genera *Calopompilus* and *Aporus* are suggested for host trapdoor spider remains found in burrows with spider wasp eggs, larvae and cocoons (pupae) based on geographic distribution, habitat, spider species, trapdoor and burrow structure, wasp cocoon size, and wasp congeneric host records.

Key words. Aporini, Pepsini, *Calopompilus*, *Priocnemissus*, *Aporus*, *Psorthaspis*, *Anoplius carolina*, *Notocyphus dorsalis*, Antrodiaetidae, Atypidae, Euctenizidae, Nemesiidae, Halonoproctidae.

ZooBank registration. urn:lsid:zoobank.org:pub:A431FD0A-FD44-404B-ADAA-8AFFABB8AF10

Introduction

Nearctic trapdoor spider-hunting spider wasp (Hymenoptera: Pompilidae) taxa comprise *Calopompilus* Ashmead and *Priocnemissus* Haupt (Pepsinae: Pepsini) and *Aporus* Spinola and *Psorthaspis* Banks (Pompilinae: Aporini). Trapdoor spider-hunting spider wasps are atypical in habitat, ecology, host preference and nesting behavior compared to typical fossorial non-trapdoor spider-hunting pompilid species (Evans 1953; Evans and Yoshimoto 1962). Trapdoor spider-hunting spider wasps include only a small percentage of the Nearctic spider wasp fauna (Krombein 1979). Spider wasps that capture and provision nests with trapdoor spiders have been scarcely studied compared to pompilids that prey on araneomorph spiders (Evans and Yoshimoto 1962; Kurczewski and Kurczewski 1968; Krombein 1979; Wasbauer and Kimsey 1985; Kurczewski and Edwards 2012; Kurczewski et al. 2017, 2020b, 2022). Including this paper, trapdoor spider (Araneae: Mygalomorphae) host records are available for only 10 of the 35 (28.6%) Nearctic taxa of trapdoor spider-hunting spider wasps and complete nesting behavior information through oviposition for only three (8.6%) of the species. These spider wasp species remain little studied because their host trapdoor spiders are seldom seen, spend most of their time underground, and the spider's burrow is usually used by the wasp as a nest.

Trapdoor spider is a common name that refers to various mygalomorph spider families that usually excavate a cylindrical silk-lined burrow in the ground with an affixed silk, soil and plant debris-hinged flap or lid under

which the spider waits to ambush prey (Comstock 1912; Gertsch 1979). In Antrodiaetidae there is technically no “lid” but rather a turret or collar that can be pulled over the entrance at the sides by the spider inside (Coyle 1971). Only sparse information is available on the natural history of trapdoor spiders and their daily activities. Females often spend their entire life underground inside their burrows and males wander on the ground surface usually only in search of females, often at night when most spider wasps are inactive. The mygalomorph families of interest in this study are Antrodiaetidae (folding trapdoor spiders), Atypidae (purse-web spiders), Euctenizidae (wafer-lid trapdoor spiders), Halonoproctidae (cork-lid trapdoor spiders), and Nemesiidae (tube trapdoor spiders).

Trapdoor spiders are rarely found by searching the forest floor litter because of their camouflaged burrow entrance and secretive lifestyle (Stevenson and Godwin 2020). Much trapdoor spider-hunting spider wasp activity, therefore, occurs sight unseen in dense woodland beneath clumps of soil, fallen dried leaves, or plant debris as the female wasp searches the forest floor for trapdoor spider burrow entrances. Most eastern U.S. trapdoor spider-hunting spider wasps have a cryptic lifestyle in woodland with dense understory vegetation and thick leaf litter. The wasp often captures the host spider within its burrow or nearby, is seldom seen dragging the large, immobilized prey across the ground surface—a readily visible and time-consuming activity—and uses the spider’s burrow as a nest. There is little or no spider wasp burrow excavation or nest closure at the ground surface, as is frequently seen in fossorial spider wasps.

In this paper we review what little information is available on the host preference and nesting behavior of Nearctic and three Palearctic species of trapdoor spider-hunting spider wasps. We re-examine nearly century-old, forgotten references on Nearctic trapdoor spider-hunting spider wasps. We present heretofore unpublished observations and host records for numerous trapdoor spider-hunting spider wasp species. We unveil literature and document research information for trapdoor spider burrows containing spider remains with unidentified spider wasp eggs, larvae or cocoons (pupae), and speculate on the species of spider wasp parasitoids.

Materials and Methods

The small amount of literature on Nearctic trapdoor spider-hunting spider wasps and trapdoor spiders was searched, reviewed, categorized, and analyzed. Habitat, ecology, host preference and nesting behavior of the various Nearctic species of spider wasps were described, compared and discussed. This information is presented in taxonomic order following the species arrangement of Pompilidae in the Hymenoptera of America North of Mexico, Synoptic Catalog (Krombein 1979). Three Palearctic spider wasp species in the subgenus *Aporus* are included for comparison with their North American congeners. Potential trapdoor spider-hunting spider wasp species are suggested for trapdoor spider burrows with spider remains and spider wasp eggs, larvae and cocoons (pupae). We used the following spider wasp and trapdoor spider criteria in order to reach our conclusions regarding the potential spider wasp species: geographic distribution, habitat, soil type, ecology, spider trapdoor and burrow type, wasp and spider size equivalence, wasp congeneric host preference, and wasp congeneric nesting behavior. This involved reading and gathering information on trapdoor spider-hunting spider wasps and trapdoor spiders in the form of taxonomic revisions, keys to genera and species, genera and species descriptions, ecological characteristics, habitat classification, natural history, nesting behavior, synoptic catalogs, geographic species lists, and species distribution maps. Online photographs and videos of trapdoor spider-hunting spider wasps and trapdoor spiders in their natural surroundings on websites such as iNaturalist.org, BugGuide.net and flickr.com were examined, assessed, and referenced in our nesting behavior descriptions and host records.

Frank Kurczewski identified the various spider wasp species. Rick West and the following people identified the families, genera and species of Mygalomorphae: Jason Bond, University of California–Davis, Davis, CA; Richard Bradley, The Ohio State University, Columbus, OH; Glavis Edwards, Florida State Collection of Arthropods, Gainesville, FL; Rebecca Godwin, Piedmont University, Demorest, GA; Marshal Hedin, San Diego State University; San Diego, CA.

Results

***Calopompilus* Ashmead.** The genus *Calopompilus*, formerly *Chirodamus* Haliday (Townes 1957), currently contains nine species in North America (Waichert et al. 2014). Eight of the species occur in the U.S. and, collectively, range from the Pacific to the Atlantic Coast (Townes 1957). *Calopompilus setaerotundus* Waichert and Pitts is an outlier species endemic to Central America (Roig-Alsina 1989; Waichert et al. 2014). *Calopompilus* is one of the “most primitive” genera in the family Pompilidae as evidenced by broad hind wings and anal lobe, lack of specialization in wing venation, stout “scoliid” body structure, and full complement of leg bristles (Townes 1957). Short and stout legs and antenna segments, bidentate mandibles, short and wide clypeus, long and flat pronotum, and tarsal claws with an erect tooth are seemingly adaptations for hunting trapdoor and, perhaps, other burrowing spiders (Kurczewski, pers. obs.). *Calopompilus heiligbrodtii* (Cresson), *C. maculipennis* (Smith), and *C. pyrromelas* (Walker) have small and distinct teeth or “serrations” on the outer side of the hind tibia, whereas such teeth are faint and obsolete in *C. albopilosus* (Cresson) and *C. fortis* (Cresson) (Townes 1957). Does the lack of distinct teeth on the outer side of the hind tibia of *C. albopilosus* and *C. fortis* imply that these species use the spider’s burrow as a nest instead of excavating their own nest? Many other genera of Pepsini such as *Pepsis*, *Hemipepsis*, *Priocnessus*, *Entypus*, and *Priocnemis* have prominent teeth on the outer side of the hind tibiae that facilitate pushing soil upward during burrow excavation (Kurczewski, pers. obs.).

***Calopompilus albopilosus* (Cresson).** *Calopompilus albopilosus* females are all black with moderately infuscate forewings and paler hindwings (Townes 1957). They are 8.5–13 mm in body length. *Calopompilus albopilosus* inhabits the Appalachian and Piedmont Regions from southern New York to Georgia (Townes 1957). Females occur in “open woods” and “rich moist woods,” especially in West Virginia, Virginia and Maryland (Krombein 1952, 1954, 1963, 1979; Townes 1957). Townes (1957) and Krombein (1963) both believed this species has two generations per year based on specimens collected from May to September. Krombein (1963) found this species on the vegetation of tulip tree (*Liriodendron tulipifera* L.) (Magnoliaceae). There are no host spider records for this wasp species.

***Calopompilus fortis* (Cresson).** *Calopompilus fortis* females are all black with infumate wings (Townes 1957). They are 13–19 mm in body length. This species inhabits the Appalachian and Piedmont Regions from southern New York to Georgia (Townes 1957), with an outlier population in Missouri (Kurczewski, pers. obs.). Females inhabit “woods” and “open woods,” especially in Pennsylvania, West Virginia, Virginia and Maryland where they search for host spiders under dead leaves and make short flights to new hunting areas (Krombein 1952, 1954, 1963, 1979; Townes 1957; Kurczewski, pers. obs.). Krombein (1963) believed this species has more than one generation per year based on its occurrence from early summer into early fall in Virginia. Kurczewski (1961) and Kurczewski and Kurczewski (1987) collected four females and 42 males of *C. fortis* at several locations in Crawford County, Pennsylvania feeding on the flowers of *Pastinaca sativa* L. (Wild Parsnip) (Apiaceae) and an unidentified species of Salicaceae (Willow family). There are no host spider records for this wasp species.

Antrodiaetus unicolor (Hentz) complex and *A. robustus* (Simon) (Antrodiaetidae) are the most likely host spiders of *Calopompilus fortis* and *C. albopilosus*. *Antrodiaetus unicolor* complex contains *A. unicolor* (Hentz) and *A. microunicolor* Hendrixson and Bond (Hendrixson and Bond 2005a, b). Adult females of *A. unicolor* are equivalent in body length (13–22 mm) to females of *C. fortis* (13–19 mm), and immatures/juveniles (<13 mm) to females of *C. albopilosus* (8.5–13 mm). Adult female spider body lengths are from Coyle (1971) and Hendrixson and Bond (2005a); wasp body lengths are calculated from Townes (1957). Equivalent body length of wasp and spider is a requirement for successful spider wasp-host spider association in non-aporine spider wasp species (Kurczewski and Kiernan 2015). *Antrodiaetus unicolor* (Hentz) complex is the most abundant mygalomorph spider group throughout much of its range in the eastern U.S. (Coyle 1971). *Antrodiaetus unicolor* complex has approximately the same central and southern Appalachian and Piedmont Regions geographic distribution as *C. albopilosus* and *C. fortis*, occurring from lower Michigan, northern Ohio and Vermont to Georgia and Alabama with peripheral populations in Missouri, Arkansas, Louisiana, and southern Mississippi (Coyle 1971; Hendrixson and Bond 2005a, b; Swanson 2010; R. West, pers. obs.). *Antrodiaetus microunicolor*, in contrast, is limited to the Appalachian Mountains of southeastern Tennessee, southwestern North Carolina, and northern Georgia (Hendrixson and Bond 2005b). *Antrodiaetus robustus* is geographically limited to Indiana, Ohio, Pennsylvania, West

Virginia, Maryland, and northern Virginia (Coyle 1971; West per. obs.). *Antrodiætus* species live in humid, cool, dense forests with sloped loamy soils (Coyle 1971), the same habitat as *C. albopilosus* and *C. fortis*. *Antrodiætus* species construct tubular, quasi-vertical, silk-lined burrows widened just below the entrance and at the bottom (Coyle 1971). The silk lining of the burrow extends above the soil surface forming an inward-collapsed flexible collar composed of silk, excavated soil and plant debris from the surroundings. The spider collapses the collar by pulling inward from inside its burrow, producing a folding in the middle like two half circles. The wasp, using its short, stocky, bristly forelegs, dentate tarsal claws, and bidentate mandibles, might remove or tear open the covering of silk, soil particles and plant debris, enter the open burrow, descend the tunnel to the spider positioned at the bottom or chase it onto the ground surface, sting it in its ventral cephalothorax, drag it into its own burrow, and deposit an egg on its abdomen.

Coyle (1971) found 21 immature, unidentified pompilid wasps in *A. unicolor* complex burrows in Jefferson County, IN; Summers County, WV; Towns County, GA; and Johnson County, AR. There was variation in pompilid cocoon size, suggesting more than one spider wasp species may have been involved (Coyle 1971). However, such variation could also represent sexual difference in cocoon size as female spider wasp cocoons are usually noticeably larger than male cocoons. In each such burrow the paralyzed spider was found at the bottom, dorsal side upward, rhythmically moving its legs, with the wasp's egg or early instar larva affixed centrally to the dorsum of the spider's abdomen. A soil plug, apparently constructed by the wasp, sealed the spider with attached wasp's egg into the bottom of its burrow. Soil for the plug was removed by the wasp from the burrow wall just above the plug. The wasp larva, after feeding on the spider for four days, moved away from the spider remains on its fifth day and spun a silken, parchment-like cocoon near the burrow wall. Cocoon construction took less than 24 hours (Coyle 1971).

***Calopompilus heiligbrodtii* (Cresson).** *Calopompilus heiligbrodtii* females are black with orange wings; the forewing base and apical margin and hind margin of the hindwing are fuscous (Townes 1957). Females are 12–23 mm in body length. All collection records for *C. heiligbrodtii* are from central and southern Texas (Townes 1957). Dates of collection from May to December imply at least two generations per year (Townes 1957). This is a scarce species as we found no online photographs of the wasp in its natural surroundings to associate it with a particular habitat (Kurczewski pers. obs.).

Kurczewski et al. (2020b) presented the first two host records for *C. heiligbrodtii* based on iNaturalist.org online photographs: *Eucteniza relata* (O. P.-Cambridge) (Euctenizidae), adult male [det. R. Godwin], and *Myrmekiaphila comstocki* Bishop and Crosby, adult or subadult female (Euctenizidae) [det. R. Godwin] (Table 1). The male of *Eucteniza relata* was wandering on a pavement surface where it was attacked, stung and immobilized by the wasp. It laid on the surface, dorsal side upward with legs spread outward, while the wasp examined its cephalothorax with her antennae and mouthparts apparently for its state of paralysis. The female of *Myrmekiaphila comstocki*, dorsal side upward, was attacked by the wasp on the ground, possibly near its burrow entrance. The wasp, on her back with wings spread outward, tried to position the end of her abdomen underneath the ventral cephalothorax of the spider in an attempt to re-sting it.

An immobilized juvenile *Eucteniza relata* [det. M. Hedin], 18–19 mm long, was found, dorsal side upward, between two rocks near where a different species of Euctenizidae was found immobilized two days earlier near Wimberley, Hays County, TX (J. Thompson, pers. comm.). Both spiders may have been unused prey of *Calopompilus heiligbrodtii* or *C. maculipennis* (Smith) based on geographic location, habitat and comparative host size.

***Calopompilus maculipennis* (Smith).** *Calopompilus maculipennis* females are black with infumate forewings that have a large central oval or subcircular orange spot (Townes 1957). They are 18–22 mm in body length. *Calopompilus maculipennis* inhabits the southeastern U.S. from southern Kansas to North Carolina, and southward to Texas and Florida (Townes 1957; Leavengood et al. 2011). Dates of collection from April to October in Texas suggest two or more generations per year (Townes 1957). Females have been photographed on and near the ground on live and dried plant leaves, other plant debris and rough soil (Kurczewski pers. obs.). A hunting female was photographed in a loblolly pine, post oak and blackjack oak woodland, “Running along the ground rapidly, opening and closing its wings repeatedly” (Clark 2017). There are no host spider records for this wasp species, although a juvenile *Myrmekiaphila comstocki* was photographed in the same habitat as *C. maculipennis* (Clark

Table 1. Nearctic Pompilidae species and their host trapdoor spider species. Species of Pompilidae are listed in taxonomic order according to Krombein (1979). Species of trapdoor spiders (Mygalomorphae) are listed in taxonomic order according to the World Spider Catalog (2020).

Pompilidae species	Host spider species (Family)	References
Tribe Pepsini		
<i>Calopompilus heiligbrodtii</i>	<i>Eucteniza relata</i> (Euctenizidae)	Kurczewski et al. 2020b
	<i>Myrmekiaphila comstocki</i> (Euctenizidae)	Kurczewski et al. 2020b
<i>Calopompilus pyrrhomelas</i>	<i>Antrodiaetus pacificus</i> (Antrodiaetidae)	Krombein 1958, 1979
	<i>Antrodiaetus ?pacificus</i> (Antrodiaetidae)	Kurczewski et al. 2020b
	<i>Antrodiaetus pugnax</i> (Antrodiaetidae)	Kurczewski et al. 2020b
	<i>Atypoides riversi</i> (Antrodiaetidae)	This study
	<i>Calisoga longitarsis</i> (Nemesiidae)	Kurczewski et al. 2022; this study
	<i>Hemipepsis ustulata ochroptera</i>	<i>Calisoga longitarsis</i> (Nemesiidae)
<i>Priocnemis minorata</i>	<i>Antrodiaetus unicolor</i> or <i>A. robustus</i> (Antrodiaetidae)	This study
<i>Priocnemis nigripes</i>	<i>Myrmekiaphila comstocki</i> (Euctenizidae)	Drake and Drake 2010; this study.
<i>Priocnemis oregona</i>	<i>Aliatypus californicus</i> (Antrodiaetidae)	Kurczewski et al. 2020b; this study
	<i>Aliatypus californicus</i> or <i>A. erebus</i> (Antrodiaetidae)	This study
	<i>Antrodiaetus hageni</i> (Antrodiaetidae)	Kurczewski et al. 2020b
	<i>Antrodiaetus pacificus</i> (Antrodiaetidae)	Kurczewski et al. 2017; this study
	<i>Antrodiaetus pugnax</i> (Antrodiaetidae)	This study
	<i>Antrodiaetus pugnax</i> or <i>A. montanus</i> (Antrodiaetidae)	This study
	<i>Antrodiaetus</i> sp. (Antrodiaetidae)	Kurczewski et al. 2017; this study
	<i>Atypoides riversi</i> (Antrodiaetidae)	Krombein 1979; this study
	<i>Aptostichus atomarius</i> (Euctenizidae)	Wasbauer and Powell 1962
	<i>Calisoga</i> sp. (Nemesiidae)	Hurd and Wasbauer 1956; this study
	<i>Promyrmekiaphila clathrata</i> (Euctenizidae)	This study
Tribe Aporini		
<i>Aporus hirsutus</i>	<i>Aptostichus atomarius</i> (Euctenizidae)	Kurczewski and Edwards 2012
	<i>Aptostichus simus</i> (Euctenizidae)	Kurczewski et al. 2017; this study
	<i>Aptostichus ?simus</i> (Euctenizidae)	Kurczewski et al. 2021
	<i>Aptostichus ?stanfordianus</i> (Euctenizidae)	Williams 1928
	<i>Aptostichus stephencolberti</i> (Euctenizidae)	Luhrs 2020; Kurczewski et al. 2021
	<i>Aptostichus ?stephencolberti</i> (Euctenizidae)	Kurczewski et al. 2021
	<i>?Cryptocteniza kawtak</i> (Euctenizidae)	This study
<i>Aporus luxus</i>	<i>Antrodiaetus ?gertschi</i> (Antrodiaetidae)	Kurczewski et al. 2020b
	<i>Antrodiaetus ?pacificus</i> (Antrodiaetidae)	Kurczewski et al. 2020b
	<i>Antrodiaetus pugnax</i> or <i>A. montanus</i> (Antrodiaetidae)	This study
	<i>Aptostichus ?hesperus</i> (Euctenizidae)	This study
	<i>Aptostichus miwok</i> (Euctenizidae)	Kurczewski et al. 2020b; this study
	<i>Aptostichus</i> sp., <i>?stanfordianus</i> (Euctenizidae)	Wasbauer 1982
<i>Aporus notabilis pulchritarsis</i>	<i>Aliatypus isolatus</i> (Antrodiaetidae)	Coyle and Icenogle 1994

Pompilidae species	Host spider species (Family)	References
<i>Psorthaspis formosa</i>	? <i>Ummidia</i> sp. (Halonoproctidae)	Vanoye-Eligio et al. 2014; this study
<i>Psorthaspis legata</i>	<i>Myrmekiaphila comstocki</i> (Euctenizidae)	This study
	<i>Myrmekiaphila foliata</i> (Euctenizidae)	This study
<i>Psorthaspis mariae</i>	<i>Ummidia audouini</i> (Halonoproctidae)	This study
<i>Psorthaspis planata</i>	<i>Bothriocyrtum californicum</i> (Halonoproctidae)	Davidson 1905; Jenks 1938
Tribe Pompilini		
<i>Anoplius carolina</i>	<i>Antrodiaetus unicolor</i> complex (Antrodiaetidae)	This study
Tribe Notocyphini		
<i>Notocyphus dorsalis dorsalis</i>	<i>Ummidia</i> sp. (Halonoproctidae)	Kurczewski et al. 2020b

2019). It was the only trapdoor spider photograph among 1069 mostly invertebrate photographs taken by E. Clark, 2014–2020.

Myrmekiaphila comstocki and *Eucteniza relata* are potential hosts of *Calopompilus maculipennis* in Texas as its equivalent-size congener, *C. heiligbrodtii*, captures both spider species there (Kurczewski et al. 2020b). Females of *Myrmekiaphila* spp. and *E. relata* are appropriate size prey for *C. maculipennis*, being ~20 mm in body length. There are 12 potential prey species of *Myrmekiaphila* in the southeastern U.S. The combined geographic distributions of the common *Myrmekiaphila foliata* Atkinson from Ohio and Virginia to Mississippi, Alabama and Georgia in the high elevation Appalachian Region and the equally common *M. comstocki* from low elevation Texas, Oklahoma, Arkansas and Louisiana (Bond and Platnick 2007) are sympatric with that of *C. maculipennis* (Townes 1957). The other 10 *Myrmekiaphila* species are uncommon and have limited geographic distributions in one or a few states. *Eucteniza relata* is the commonest trapdoor spider in central and southern Texas, as indicated by its common name—the southwestern trapdoor spider (Bond and Godwin 2013). *Myrmekiaphila* and *Eucteniza* species construct tubular, silk-lined, quasi-vertical burrows in the ground (Bond and Platnick 2007). The burrow is covered with a cork-like lid composed of silk and soil particles and has a silken hinge. The short stout forelegs, enlarged pronotum, dentate tarsal claws and bidentate mandibles of *C. maculipennis* (Townes 1957) are seemingly adapted for lifting the cork-like lid from the *Myrmekiaphila* and *Eucteniza* burrows or tearing through it to allow the wasp entry. Several *Myrmekiaphila* species, including *M. comstocki* and *M. foliata*, excavate lateral side burrows off the main burrow and seal them with silken cork and soil partitions (Atkinson 1886). Such barriers may prevent or make more difficult entry by potential predators and parasitoids as *C. maculipennis*.

Coyle (1971) reported an unidentified pompilid wasp cocoon at Bennett Springs State Park, Dallas/Laclede Counties, MO in a “medium-sized” *Antrodiaetus stygius* Coyle burrow. “Small pieces of spider exoskeleton were attached to the outside of the cocoon.” Fred Coyle (pers. comm.) indicated the body length of this spider would approximate 13–15 mm. Potential pompilid parasitoids in that area include *Calopompilus maculipennis*, *C. feroculis* (Banks), and *Priocnemis nigripes* (Cresson) based on geographic distribution, habitat, equivalent size of spider wasp and spider and congeneric host records. Three species of larger *Psorthaspis* also inhabit southern Missouri but their host records indicate a specificity for the trapdoor spider genus *Ummidia* (Halonoproctidae).

***Calopompilus pyrrhomelas* (Walker).** Females of *C. pyrrhomelas* are black with orange wings; the basal and apical margins of the forewing are fuscous (Townes 1957). Female body length is 17–28 mm, making this species one of the largest in the genus. *Calopompilus pyrrhomelas* ranges from British Columbia to northern Mexico, especially at higher elevation (Townes 1957). It is noticeably absent from the montane states of Montana, Wyoming and Colorado and the southern California mountains. Females commonly visit the flowers of many species of plants for nectar. There may be only a single generation per year in this species as the dates of collection range from late June to October (Townes 1957). Numerous photographs from BugGuide.net and Naturalista.org show females on dried leaves, presumably at the edge of or inside woodland (Kurczewski pers. obs.).

Krombein (1958) reported *C. pyrrhomelas* capturing *Antrodiaetus pacificus* (Simon) (Antrodiaetidae) in the northwestern U.S. (Table 1). An *A. pugnax* (Chamberlin), adult female, was collected from its burrow in Benton County, OR by Coyle (1971) and labeled “prey of *Dinocnemis*,” a synonym of *Calopompilus* and undoubtedly *C.*

pyrrhomelas, the only species of *Calopompilus* in Oregon (Table 1). Kurczewski et al. (2020b) reported prey capture of *A. ?pacificus* [det. R. C. West] by *C. pyrrhomelas* in Trinity County, CA (Table 1). The wasp, with wings raised dorsally, stung the spider underneath its mouthparts and in its ventral cephalothorax near the leg bases. The spider remained on the ground, dorsal side upward, during the stinging sequence with legs raised upward in an immobilized position (Collier 2018; Fig. 1). Kurczewski et al. (2020b) reported on a photograph taken by T. L. Hammond in Santa Clara County, CA. The wasp stood next to an immobilized *Calisoga longitarsis* (Simon) (Nemesiidae) [det. M. Hedin], adult or subadult female, with abdomen and right rear leg detached and lying on the ground. Nemesiidae (tube-web trapdoor spiders or false tarantulas) is a new host spider family for *C. pyrrhomelas*. This spider might have been mutilated by the wasp for feeding purposes or by two adult female wasps fighting over its possession or by foraging ants that frequently amputate and carry off body parts. This observation does not support successful development of the wasp larva if an egg was to be affixed on the spider's abdomen. Nonetheless, the wasp dragged the mutilated false tarantula minus its abdomen backwards on the ground, dorsal side upward, grasping the middle of its right foreleg with her mandibles. Brookshire (2020) photographed a *C. pyrrhomelas* female in Marin County, CA with an immobilized *Calisoga longitarsis* (Nemesiidae) [det. M. Hedin], adult male. The wasp attempted to re-sting the spider as it laid dorsal side upward on a sidewalk, while grasping the end of its second left leg with her mandibles. De Schrijver (2021) photographed a *C. pyrrhomelas* female with *Calisoga longitarsis* [det. M. Hedin] in Alameda County, CA. *Calopompilus pyrrhomelas* is also a parasitoid of *Atypoides riversi* O. P.-Cambridge (Antrodiaetidae) according to a photograph taken by Thatcher (2022) at the Ring Mountain Preserve, Corte Madera, Marin County, CA. The wasp grasped the immobilized spider, which laid on its right side, by the femur of its left foreleg with her mandibles and dragged it backwards across the ground. Burrows of *A. riversi* are similar in type, length and structure to those of species of *Antrodiaetus* (F. Coyle, pers. comm.).

***Priocnemissus* Haupt.** The subgenus *Priocnemissus* is Holarctic in geographic distribution with three species inhabiting the U.S. (Townes 1957). *Priocnemissus* females lack the weaponry of morphological structures that would enable them to raise the lid of a trapdoor spider's burrow and adopt it as a nest as in the spider wasp tribe Aporini. *Priocnemissus* females excavate their own burrows from the ground surface, using the mandibles to break the soil crust, or modify an underground cavity in the soil and do not use the spider's burrow as a nest (Evans 1997; Kurczewski pers. obs.). The strong suberect lobe-like teeth on the upper edge of the hind tibia facilitate soil removal from the burrow (Yoshimoto 1954; Evans and Yoshimoto 1962; Kurczewski et al. 2017). *Priocnemis minorata* and *P. oregona* nests are used by the wasp over successive days, culminating in a multi-celled design (Yoshimoto 1954; Evans and Yoshimoto 1962; Kurczewski et al. 2017). Using self-excavated burrows often necessitates long distance prey transport and visual exposure of the provisioning wasp on the ground surface.

***Priocnemis (Priocnemissus) minorata* Banks.** Females of *P. minorata* are all black in color with lightly to moderately infusate wings (Townes 1957). They are 8–14 mm long, averaging 11.38 mm (Kurczewski and Kiernan 2015). This species occurs throughout the eastern U.S., except along the Gulf of Mexico and in Florida. There are a few disjunct records from Oregon, Washington, and British Columbia (Townes 1957). *Priocnemis minorata* inhabits moist woodland (Yoshimoto 1954; Townes 1957; Evans and Yoshimoto 1962). The species is highly polyphagous in host spider selection, capturing no less than eight families of araneomorph spiders ranging taxonomically from Dysderidae to Philodromidae (Kurczewski and Kiernan 2015; Kurczewski et al. 2017). All host records of *P. minorata* from the eastern U.S. are from the spring, implying only a single generation per year (Yoshimoto 1954; Townes 1957; Evans and Yoshimoto 1962; Kurczewski and Kiernan 2015).

A recent, highly surprising host association is a female of *P. minorata* from the Todd Natural Reserve, Sarver, Butler County, PA photographed with an immobilized mygalomorph spider, *Antrodiaetus unicolor* or *A. robustus* (Antrodiaetidae), immature male [det. R. Godwin; M. Hedin; R. C. West]. The wasp held the spider upright, grasping the base of its right hindcoxa with her mandibles, and dragged it backwards across the ground (Coulter 2021). Emphasizing the rarity of this host record, *P. minorata* is a well-studied (144 host records, 1953–2014) parasitoid on eight different families of araneomorph spiders (Yoshimoto 1954; Townes 1957; Evans and Yoshimoto 1962; Kurczewski and Kiernan 2015).



Figures 1–8. Trapdoor spider-hunting spider wasps and their hosts. **1)** *Calopompilus pyrrhomelas* female, with wings raised dorsally, stinging an *Antrodiaetus* sp., probably *pacificus* (Antrodiaetidae), adult or subadult female, dorsal side upward, under its mouthparts, Pacific Crest Trail, Klamath Mountains, Trinity County, CA. Photograph © Chris Collier. **2)** *Priocnemis (Priocnemissus) oregona* female resting during prey transport of an immobilized *Antrodiaetus* sp., probably *pacificus*, subadult female, dorsal side upward, just north of Corvallis, Benton County, OR. Photograph © Julia Pearson. **3)** *Aporus (Aporus) luxus* female dragging an immobilized *Antrodiaetus* sp., probably *pacificus*, adult or subadult female, backwards across a gravelly path, dorsal side upward, grasping the tibia of its third left leg with her mandibles. The end of the wasp’s metasoma is bent downward against the ground and used for added leverage, Oregon Caves National Monument, Cave Junction, OR. Photograph © Ivan Yates. **4)** *Aporus (Aporus) luxus* female dragging an immobilized *Aptostichus ?hesperus* (Chamberlin) backwards on the ground, grasping the patella of its second left leg with her mandibles, San Jacinto, Riverside County, CA. Photograph © Richard Seaman. **5)** *Aporus (Plectraporus) hirsutus* female dragging an immobilized *Aptostichus simus* (Euctenizidae), juvenile, dorsal side upward, backwards across sand, grasping the end of its right pedipalp with her mandibles, coastal relict dunes, Vandenberg Air Force Base, Santa Barbara County, CA. Photograph © Alice Abela. **6)** *Psorthaspis planata* female attempting to pry open the silk, soil and debris trapdoor of *Bothriocyrtum californicum* (Halonoproctidae), using her mandibles and forelegs in unison, Santee, San Diego County, CA. Photograph © Gilbert Quintana. **7)** *Psorthaspis mariae* female dragging *Ummidia audouini* (Halonoproctidae), juvenile, backwards across rough soil, grasping its abdomen with her mandibles, Ellijay, Gilmer County, GA. The wasp holds the bent end of her abdomen on the ground for added leverage. The partly open trapdoor flap is seen below the wasp and spider’s abdomen. Photograph © Danielle Burgess. **8)** Early instar larval spider wasp, probably *Psorthaspis mariae*, feeding on the dorsum of the abdomen of *Ummidia audouini*, penultimate female, 6 km S of Lynx, Adams County, OH. Photograph © Laura Hughes.

Priocnemis (Priocnemissus) nigripes (Cresson). Females of *P. nigripes* are black with the apical half of first, all of second and basal half of third metasomal tergite ferruginous; much of head, mesosoma and coxae are shades of brownish maroon; wings are moderately infusate (Townes 1957). Females are 11.5–15.5 mm in body length. *Priocnemis (Priocnemissus) nigripes* ranges from Nebraska and Kansas southward and eastward to Arkansas, Alabama, and North Carolina (Townes 1957; Trammel 2008). The flight period is early spring (Townes 1957). Several photographs on BugGuide.net and iNaturalist.org show females of *P. (Priocnemissus) nigripes* searching on the ground through dried leaves and other plant litter in woodland (Kurczewski pers. obs.). A photograph from Brown County, KS was taken in an “oak-hickory remnant forest” (Kurczewski pers. obs.).

Priocnemis (Priocnemissus) nigripes is the eastern U.S. equivalence of the western U.S. *P. (Priocnemissus) oregona*. Both species have basically the same external morphology, are approximately the same size, have similar body coloration, occur in woodland, and their period of adult activity is spring. *Priocnemis (Priocnemissus) nigripes* selectively hunts trapdoor spiders based on Trammel’s (2008) observation in Arkansas of a female entering the burrow of a trapdoor spider and remaining inside for “quite a while.” The burrow in question probably belonged to *Myrmekiaphila comstocki* (Euctenizidae) [det. F. A. Coyle], the commonest trapdoor spider in the area. If *P. nigripes* used the spider’s burrow as a nest rather than excavating its own nest, as in *P. minorata* and *P. oregona*, this would expand the range of nesting behavior variation in Nearctic species of *Priocnemissus*. This parasitoid-host spider association was later confirmed [det. M. Hedin] by photographs taken by Drake and Drake (2010).

Priocnemis (Priocnemissus) oregona Banks. Females of *P. oregona* are black with a red metasoma, except for the basal segment which is black. The wings are fuscous (Townes 1957). Females are 10–18 mm in body length. *Priocnemis oregona* ranges from British Columbia to probably Baja California, Mexico, less commonly eastward into the Great Basin (Townes 1957). *Priocnemis oregona* is a common spring-nesting species in the northwestern U.S. (Townes 1957). Elva Paulsen (pers. comm.) described its habitat in Coos County, OR as a sandy cut-bank along a gravel road through “thick coastal forest.” Several observations of *P. oregona* indicate or imply that the wasp excavates her own burrow and does not use the spider’s burrow as a nest. Evans (1997) noted that *P. oregona* nests in preexisting cavities in soil and preys on ground-dwelling spiders. Kevin Hall (pers. comm.) observed a *P. oregona* that “kept trying to crawl under leaves and burrow into the soil.” Gintel (2020), in a series of photographs, showed a *P. oregona* female beginning a burrow excavation in sandy soil in Spokane County, WA, using her mandibles and forelegs. All host records for *P. oregona* are for trapdoor spiders (Table 1).

Townes (1957) noted a female of *P. (Priocnemissus) oregona* collected in California bearing a label, “from nest of ground spider.” The first reported actual host records for *P. oregona* are for *Calisoga* sp. [as *Brachythele* sp.] (Nemesiidae), *Aptostichus atomarius* Simon [as *Actinoxia versicolor* Simon] (Euctenizidae), and *Atypoides riversi* O. P.-Cambridge (Antrodiaetidae), three different trapdoor spider families (Hurd and Wasbauer 1956; Wasbauer and Powell 1962; Krombein 1979). A female of *P. oregona* from Oregon was collected with *Antrodiaetus hageni* (Chamberlin) by Coyle (1971). Vincent (1993) listed *P. oregona* as a probable parasitoid of larger individuals of *Atypoides riversi* on the western slopes of the Sierra Nevada Mountains in El Dorado County, CA. McGarry (2009) photographed a *P. oregona* female after stinging, paralyzing and during prey transport of an *Aliatypus californicus* (Banks) or *A. erebus* Coyle (Antrodiaetidae) [det. M. Hedin], juvenile, in Plumas County, CA. The wasp dragged the immobilized spider backwards on the ground, holding it in a perpendicular position while grasping its left hindcoxa with her mandibles. She dragged it down an open hole in the ground (McGarry 2009), probably the entrance to the wasp’s burrow. A *P. oregona* female from Josephine County, OR was photographed with a female of *Antrodiaetus pacificus* (Brown 2010). Another photograph shows a female of *P. oregona* from Multnomah County, OR examining a recently stung female of *Antrodiaetus pacificus*, ~20 mm long, with her antennae (Notis 2013). Kurczewski et al. (2017) published five host records from Oregon for *P. oregona*, in each case *Antrodiaetus* sp. (Antrodiaetidae) (Pearson 2011; Fig. 2). Most, if not all, of these host records were for *A. pacificus* (West, pers. obs.).

Li (2018), VanDerslice (2021), Cambarellus (2021), Walker (2021), Maughn (2021) and Ueda (2022) photographed *P. oregona* in Santa Clara, Contra Costa, San Mateo and Santa Cruz Counties, CA with immobilized *Promyrmekiaphila clathrata* (Simon) (Euctenizidae), adult or subadult females [det. M. Hedin], the wasps dragging the spiders backwards on the ground while grasping them variously with their mandibles: dorsal side upward, third right femur base and second right patella, coxa of third right leg, on spider’s right side, fourth left

trochanter and fourth left and right coxa-trochanter joint; ventral side upward, left hindcoxa; straddling carapace, facing spider's posterior; and by the pedicel with the spider being in an upright position. A *P. oregona* female from Multnomah County, OR is photographed dragging an *Antrodiaetus* sp., adult female, "considerably" larger than herself backwards on the ground, grasping its abdomen with her mandibles (Coolidge 2019). A photograph from San Mateo County, CA shows a *P. oregona* female examining an immobilized *Atypoides riversi*, subadult female [det. M. Hedin], with her antennae as it laid, ventral side upward, on the ground (Asquith 2019). A photograph from Thurston County, WA shows a female of *P. oregona* with an immobilized *Antrodiaetus* sp., dorsal side upward, walking backwards up the side of a fence, grasping its pedicel with her mandibles (IcebergTitanic 2020). Another *P. oregona* photograph shows the wasp pulling an immobilized *Antrodiaetus pugnax* or *A. montanus* Chamberlin and Ivie [det. R. C. West], ventral side upward, backwards across the ground in Deschutes County, OR, grasping its left rear trochanter with her mandibles (Giraudier 2020). Vail (2020) presented several photographs and a video of a *P. oregona* female resting beside an immobilized *Antrodiaetus pacificus* lying ventral side upward on the ground in Cowlitz County, WA. Melton (2021) video-taped *P. oregona* in Chelan County, WA transporting an immobilized *A. pacificus* backwards on the ground, dorsal side upward, grasping the patella of its right foreleg with her mandibles.

An *A. hageni* from British Columbia was photographed being stung in its ventral cephalothorax by *P. oregona*, with both wasp and spider in the dorsal side upward position on the ground (Kurczewski et al. 2020b). Three photographs from San Mateo County, CA implicate *Atypoides californicus* (Banks) [det. M. Hedin] as host spider of *P. oregona* (Kurczewski et al. 2020b). Two photographs from California show a *P. oregona* female attempting to pull an *Atypoides californicus* [det. M. Hedin] from its burrow entrance, apparently to sting it, grasping its left foreleg with her mandibles (Kurczewski et al. 2020b). The wasp presumably dragged the spider from its burrow before stinging it, according to the description beneath the photograph. The wasp grasped the immobilized spider's third right leg near its end with her mandibles and dragged it backwards across a trail. A recent video and photograph show prey manipulation and ventral side upward prey transport of *Antrodiaetus pacificus* and *A. ?pacificus* in Thurston County, Washington and Union County, Oregon, respectively (Haugh 2021; Lipscomb 2021). The wasp in the video dragged the spider across a patio into leaf litter beneath a shrub (Haugh 2021). Kapranoff (2021) photographed a *P. oregona* female in San Mateo County, CA transporting an immobilized *Aptostichus ?stanfordianus* Smith, subadult female or juvenile, backwards on the ground, ventral side upward, grasping a hindcoxa with her mandibles. She held the spider at times above the ground surface. Hogan (2021) photographed a *P. oregona* female dragging an immobilized *Atypoides riversi*, adult or subadult female, backwards toward "a small hole in the ground" in Marin County CA. Maier (2021) observed a *P. oregona* female pulling an immobilized *Antrodiaetus pugnax*, adult or subadult female, backwards along a sidewalk in Kelowna, BC, Canada.

Dame (2007) excavated a *Promyrmekiaphila clathrata* (Simon) (Euctenizidae) burrow in California and, at a depth of ~25 mm, found a spider wasp cocoon with pupa, 40 × 8 mm. The pupa subsequently died and was never identified. Potential pompilid parasitoids of that spider include *Aporus luxus* and *Priocnemis oregona*, based on geographic distribution, habitat, size equivalence, and congeneric host records.

Aporus Spinola. *Aporus* is a genus in the specialized tribe Aporini in which the species capture only trapdoor spiders and use the spider's burrow as a nest (Krombein 1979). The subgenus *Aporus* Spinola contains nine Nearctic species and subspecies while the subgenus *Plectraporus* Bradley has only a single species, *A. (Plectraporus) hirsutus* (Banks), in the United States and Mexico (Krombein 1979). Seven of the nine *Aporus* s. str. species and subspecies inhabit the western U.S. and Mexico. *Aporus niger* (Cresson) is a common eastern U.S. species and *A. calcaratus* (Fox) occurs sparingly in Florida (Evans 1966; Krombein 1979; Leavengood et al. 2011). The genus *Aporus* is characterized structurally by thin and somewhat flattened head; antennae at or near bottom of eyes; dentate mandibles; short and wide clypeus; large and elongate prothorax, especially pronotum; enlarged forefemur; hind tibia without dorsal serrations; dentate tarsal claws; and reduced wing venation (only two submarginal cells) (Evans 1966; Day 1988). Thin and somewhat flattened head, dentate mandibles, dentate tarsal claws, enlarged pronotum and swollen forefemur work in conjunction to lift the spider's trapdoor lid from the entrance to allow the wasp entry to the spider's burrow.

***Aporus (Aporus) luxus* (Banks).** *Aporus luxus* is widespread in the western coastal states and provinces from British Columbia to Baja California, Mexico (Evans 1966; Krombein 1979; Wasbauer and Kimsey 1985). This

species inhabits open ground, including sandy areas (Krombein 1979), but is absent from the southwestern deserts (Wasbauer and Kimsey 1985). Females are black with strong bluish or violaceous pubescence; forewings are fuscous and violaceous (Evans 1966). Females are 8–14 mm in body length. The back of the head is less concave than in *A. (Plectraporus) hirsutus* but the head profile is nonetheless thin and flattened; vertex crest is not very sharp; pronotum is relatively long; front femur is moderately swollen; and, front tarsal claw has a strong tooth (Evans 1966). The lack of a foretarsal digging rake, moderately enlarged forefemur, and capture of a non-psammophilous host spider family such as Antrodiaetidae indicate that *A. luxus* is less “sand loving” than *A. hirsutus*.

Host records for *Aporus luxus* constitute several species and two families of trapdoor spiders: *Antrodiaetus ?pacificus*, *Antrodiaetus ?gertschi* (Coyle), *Antrodiaetus pugnax* or *Antrodiaetus montanus* (Antrodiaetidae), *Aptostichus ?hesperus* (Chamberlin) [det. J. E. Bond], *Aptostichus ?stanfordianus* Smith, and *Aptostichus miwok* Bond (Euctenizidae) (Wasbauer 1982; Pickart 2013; Seaman 2013; Yates 2018; Celis 2020; Kurczewski et al. 2020b; Table 1, Fig. 3). Two photographs show an *Aporus luxus* female grasping an immobilized spider by the patella of its second left leg with her mandibles and dragging it backwards on the ground (Fig. 4), then dragging it into its burrow, ventral side upward, grasping its spinnerets with her mandibles (Seaman 2013). The wasp captured the spider on the ground surface (R. Seaman, pers. comm.). Schrott (2017) photographed an *Aporus luxus* female on coastal dunes of Del Norte County, CA running across the sand, pausing and digging in search of *Aptostichus miwok* Bond. The wasp excavated a wide depression in the sand, but she did not disappear beneath the surface nor was she perpendicular to the soil surface as in burrowing females of *Aporus hirsutus*. Another photograph shows *Aporus luxus* on coastal dunes of Sonoma County, CA examining an immobilized *Aptostichus miwok*, subadult female, with her antennae and mouthparts as it laid on the sand surface, ventral side upward, with all legs extended laterally (Celis 2020).

***Aporus (Aporus) niger* (Cresson).** Females of *A. niger* are all black with moderately light infusate wings (Evans 1966). Kurczewski and Kurczewski (1987) collected 12 females from “sunlit openings” in deciduous woodland in Erie County, PA that averaged 9.3 mm (6.5–11.0) in body length (Kurczewski 1999). Six females of *A. niger* in the FDACS insect collection averaged 9.98 mm (8.4–10.9) in body length (E. Talamas, pers. comm.). The external morphological characteristics of *A. niger* for capturing trapdoor spiders are much less modified than those of *A. luxus* and, especially, *A. hirsutus*. The back of the head is not noticeably concave; head profile is relatively broad and round; inferior margin of mandible not dentate; pronotum is elongate but noticeably shorter than in *A. luxus* and *A. hirsutus*; forefemur is weakly swollen; and tarsal claw is dentate (Kurczewski, pers. obs.). Unlike the psammophilous *A. hirsutus* and open ground *A. luxus*, *A. (Aporus) niger* is a woodland species found mainly on loamy soils in deciduous-coniferous forests (Kurczewski 1999). Females have been collected from “ravine with woods” and “pine & oak forest” (E. Talamas, pers. comm.). *Aporus niger* ranges from Massachusetts, southern Ontario, lower Michigan, and Wisconsin to Texas and Florida (Krombein 1979; S. Paiero, pers. comm.). There are no host records available for this species (Krombein 1979).

Prospective hosts for *Aporus niger* in the eastern U.S. are purse-web spiders of the genus *Sphodros* (Atypidae), especially *S. niger* (Hentz) and *S. rufipes* (Latreille) and, less so, *S. abboti* Walckenaer and *S. atlanticus* Gertsch and Platnick. *Sphodros niger* occurs from southern Ontario, Michigan and Wisconsin to Kansas, Tennessee, Alabama and Georgia, while *S. rufipes* ranges from Massachusetts, Rhode Island and Illinois to Texas and Florida (Gertsch and Platnick 1980; Hoffman 2010; Swanson 2010; Moler et al. 2020; S. Paiero, pers. comm.). The geographic range of the *Sphodros* species combined is sympatric with the geographic range of *Aporus niger* (Krombein 1979; Hoffman 2010). *Sphodros niger* is the only mygalomorph spider in Wisconsin, lower Michigan, and southern Ontario, except for *Antrodiaetus unicolor* complex (Antrodiaetidae) in the University of Michigan Arboretum, Ann Arbor (Swanson 2010; S. Paiero, pers. comm.). *Aporus niger* is the only aporine wasp in Wisconsin, lower Michigan and southern Ontario (Krombein 1979; S. Paiero, pers. comm.). Wasps in the tribe Aporini capture only mygalomorph spiders (Evans 1966; Krombein 1979). *Sphodros niger* must, therefore, be the host spider species of *Aporus niger* in Wisconsin, lower Michigan and southern Ontario (Kurczewski pers. obs.). Muma and Muma (1945) found one *S. rufipes* silken tube in Maryland with a “hymenopterous parasite” cocoon, possibly that of *A. niger*.

Aporus (Aporus) unicolor Spinola is the European morphological equivalence of *Aporus niger*. This species captures purse-web spiders of the genus *Atypus* Latreille (Atypidae) in England (Else 1975; Day 1988) and

Germany (Gerth et al. 2012). *Aporus niger* and *Aporus unicolor* are equivalent in size and adult external morphology and both species probably capture Atypidae despite living on different continents. Both species are less modified structurally compared to other *Aporus*: rounded head, smaller prothorax, weakly swollen forefemur, and no foretarsal digging rake (Evans 1966; Day 1988; Wahis and Durand 2012). *Aporus unicolor* cuts open the silken purse of *Atypus* with its mandibles and widens the tear with its foretarsal claws in order to gain access to the spider (Early 2013). *Sphodros* females build sturdy silk and sand tubular retreats into the soil at the base of a tree and extend the tubes vertically 30 cm or more up the side of the tree trunk (Gertsch and Platnick 1980). *Sphodros niger* often builds the above-ground portion of its silken tube flat on or near the ground as in the European species of *Atypus* Latreille (Beatty 1986). *Sphodros niger* and *S. rufipes* females can be as large as 22 and 25 mm, respectively, in body length (Gertsch and Platnick 1980; Hoffman 2010), or more than twice the size of *Aporus niger*. If *Aporus niger* is to be successful it probably captures the smaller and more manageable *Sphodros* juveniles.

***Aporus (Aporus) notabilis pulchritarsis* (Cameron).** *Aporus (Aporus) notabilis pulchritarsis* females are black with bluish or violaceous pubescence and fuscous and violaceous wings (Evans 1966). Females are 14–15 mm long. This subspecies occurs from southern Arizona to Oaxaca and Yucatan, Mexico (Krombein 1979). The vertex crest is rather sharp, front femur strongly incrassate, and pronotum moderately long (Evans 1966). *Aporus notabilis pulchritarsis* has the extensive weaponry of morphological structures for unearthing and capturing trapdoor spiders, except it lacks the foretarsal digging “rake” of *A. (Plectraporus) hirsutus* and, therefore, is probably less psammophilous in habitat (Kurczewski pers. obs.). Coyle and Icenogle (1994) reported several burrows of *Aliatypus* Smith (Antrodiaetidae), *A. erebus* Coyle, *A. gulosus* Coyle, *A. isolatus* Coyle, and *A. plutonis* Coyle, with a pompilid wasp larva or cocoon in California and Arizona. One of the spider wasp-trapdoor spider associations resulted in emergence of an adult *Aporus notabilis pulchritarsis* reared from *Aliatypus isolatus* in southern Arizona (Coyle and Icenogle 1994) (Table 1).

***Aporus (Plectraporus) hirsutus* (Banks).** *Aporus hirsutus* females are black, their body, legs and forewings rendered a brilliant bluish, or, less often, greenish or violaceous color (Evans 1966). *Aporus hirsutus* has the ultimate weaponry of structural characteristics consistent with preying on species of *Aptostichus* (Euctenizidae) in loose sand of active and relict sand dunes and deserts in the western U.S. coastal states (Williams 1928; Wasbauer and Kimsey 1985; Kurczewski and Edwards 2012; Kurczewski et al. 2017, 2021). The back of the head is concave and fits snugly against the front of the convex prothorax presenting a streamlined look. The head shape in frontal view is roughly triangular. The head profile is thin and flattened. The pronotum is very long and wide. The front femur is strongly swollen and foretibiae is enlarged. The foretarsus has a series of short, rather wide comb spines forming a digging “rake,” the spines at the apices of segments 1–3 being especially strong (Evans 1966). Females of *Aporus hirsutus* are 6.5–12.5 mm long (Evans 1966). *Aporus hirsutus* ranges from Oregon and western Idaho to Baja California and Sonora, Mexico (Wasbauer and Kimsey 1985).

Williams (1928) observed females of *Aporus hirsutus* searching on the San Francisco, CA sand dunes until one wasp found the limp door-flap to an *Aptostichus* sp., probably *Aptostichus stanfordianus* [det. N. Banks] silk-lined burrow. She slightly pried open the flap, using her mandibles and forelegs, entered part-way in an inverted position and backed out several times in succession interspersed with buzzing her wings. This activity evidently attracted the attention of the trapdoor spider inside. The wasp then walked across the sand ~ 4 cm and dug downward in the sand underneath the spider until she induced it to leave its burrow. The wasp chased the spider across the sand surface, caught it, and stung it in its ventral cephalothorax thereby immobilizing it. She dragged her heavy burden back to its burrow and pulled it inside, using her mandibles, rearranging the spider’s legs to allow entry. The flap closed behind. Upon Williams (1928) excavation of the burrow, the paralyzed spider was found at the bottom, dorsal side upward, with the wasp’s egg affixed dorso-laterally to its abdomen. Following oviposition, the wasp emerged from the sand a short distance from the spider’s closed burrow at a point in the sand where she had previously dug in to oust the spider from its lair. Williams (1928) had observed the same behavior at this location a week earlier.

Alice Abela (pers. comm.) photographed the feeding and hunting activities of *Aporus hirsutus* on active and relict sand dunes in Santa Barbara and San Luis Obispo Counties, CA (Kurczewski et al. 2021). In Santa Barbara County, CA, a female hunting for prey ran across bare sand and stopped periodically to sample the sand with her mandibles and other mouthparts. In certain spots she dug into the sand using her mandibles and foretarsal

digging rake, almost disappearing completely from view, then backed out quickly and repeated this process in another spot. At Vandenberg Air Force Base, a female of *Aporus hirsutus* captured a small immature *Aptostichus* sp., probably *Aptostichus simus* [det. A. Abela], about half her size, and examined it with her antennae and mouthparts. She apparently used this spider solely for adult feeding (Kurczewski et al. 2021). Another female, ~13 mm long, with an immobilized *Aptostichus simus*, juvenile [det. A. Abela], 14.8 mm long, dragged the much heavier spider backwards across the sand, grasping the base of its left or right pedipalp or femur of its second left leg with her mandibles (Abela 2015; Kurczewski et al. 2017, 2021) (Fig. 5). There is no visible evidence of a “trapdoor” on the sand surface for *Aptostichus simus* burrows. However, when carefully exposed, there is a thin flap of sand and silk covering the burrow entrance. *Aporus hirsutus* may locate the spider’s burrow via minute silken strands radiating from the burrow entrance (Kurczewski et al. 2021; R. West, pers. obs.).

Kurczewski and Edwards (2012) observed *Aporus hirsutus* females searching for *Aptostichus* at Sweet Springs Nature Preserve and El Moro Elfin Forest, Baywood-Los Osos, San Luis Obispo County, CA and reported an immobilized *Aptostichus atomarius* [?*Aptostichus simus*] [det. G. B. Edwards] as host spider. The wasps walked slowly or ran across the sand, depending on the sand surface temperature, flicking their wings and tapped their antennal tips on the ground in areas of plant debris. No wasp attempted to fly during their search. Gong (2019) observed hunting females of *A. hirsutus* at Montana de Oro State Park, San Luis Obispo County, CA. She photographed a female walking across the sand, head downward, apparently searching for *Aptostichus* burrows, pausing at spots, and digging with her mandibles and forelegs. In one place the wasp dug downward into the sand for half her body length. Another photograph shows the female on the surface, evidently in an excited state, with raised wings. Five females of *Aporus hirsutus* were observed over two days on sparsely vegetated sand at Marina State Beach, Monterey County, CA hunting for individuals of *Aptostichus simus*, *Aptostichus atomarius* or, possibly, the recently described *Cryptocteniza kawtak* Bond and Hamilton (Euctenizidae) [det. M. Hedin] (Bond et al. 2020; Kurczewski et al. 2021; C. Van Loon and T. Van Loon, pers. comm.).

Aporus hirsutus reportedly captures *Aptostichus atomarius*, *Aptostichus simus* Chamberlin, *Aptostichus stephencolberti* Bond, and *Aptostichus* sp., probably *Aptostichus stanfordianus* (Williams 1928; Krombein 1979; Kurczewski and Edwards 2012; Kurczewski et al. 2017, 2021; Willems 2018; Luhrs 2020) (Table 1). Based on Bond’s (2012) revision of the genus *Aptostichus*, *Aptostichus atomarius*, reported by Kurczewski and Edwards (2012), and *Aptostichus* sp., probably *Aptostichus stanfordianus*, reported by Williams (1928), were possibly misidentified. *Aptostichus atomarius* may be *Aptostichus simus*, and *Aptostichus* cf. *stanfordianus* is *Aptostichus stephencolberti* Bond based on their specific location and habitat. Willems (2018) photographed a female of *Aporus hirsutus* at Oceano Dunes State Vehicular Recreation Area, San Luis Obispo County, CA dragging a relatively small *Aptostichus simus* [det. A. Abela] backwards on the sand, ventral side upward, grasping the base of its third right leg with her mandibles. Johnson (2020a, b) photographed a female of *Aporus hirsutus* at the same site excavating in sand with her mandibles and forelegs and an immobilized *Aptostichus simus* juvenile [det. A. Abela] lying on the sand surface, dorsal side upward, but made no mention of a parasitoid-host spider association. Luhrs (2020) photographed a female dragging an immobilized *Aptostichus stephencolberti* [det. A. Abela] backwards on the ground, dorsal side upward, at Ford Ord Dunes State Park, Monterey County, CA, grasping the back of its abdomen with her mandibles. *Aporus hirsutus* females are usually smaller and much lighter in weight than their host *Aptostichus*. Five *Aporus hirsutus* females collected in San Luis Obispo and Santa Barbara Counties, CA averaged only 10.8 mm (8.1–~13.0) in body length, whereas two host *Aptostichus* specimens (one either *Aptostichus atomarius* or *Aptostichus simus*, and the other *Aptostichus simus*) were 14.5 and 14.8 mm long, respectively (Kurczewski and Edwards 2012; Kurczewski et al. 2017, 2021).

***Aporus (Aporus) unicolor* Spinola.** *Aporus unicolor* is found in continental Europe excluding Scandinavia (Wahis and Durand 2012). It is one of the least modified species in the genus (Day 1988; Wahis and Durand 2012). Its external morphology resembles that of the Nearctic *Aporus (Aporus) niger* in being less developed to open the lid of a trapdoor spider burrow and enter its silk-lined burrow (Day 1988). The head profile of *Aporus unicolor* is relatively broad and round; pronotum is elongate but noticeably shorter than in *Aporus luxus* or *Aporus hirsutus* and with rounded edge; forefemur is weakly swollen; and tarsal claw is dentate (Day 1988; Wahis and Durand 2012). Such a reduction in external morphological characteristics correlates with capturing the purse-web spiders *Atypus affinis* Eichwald (Atypidae) in England (Else 1975; Day 1988; Early 2013) and *Atypus piceus* (Sulzer)

in Germany (Gerth et al. 2012). Using its mandibles to cut and forelegs to widen the tear, *A. unicolor* forces its way into and enters the spider's purse-web where it stings, immobilizes and oviposits on the dorsum of the paralyzed spider's abdomen (Clark 1969; Else 1975; Early 2013). The claim by Gertsch and Platnick (1980) that the tough silken tube made by species of Atypidae makes purse-web spiders "largely immune to attack by pompilid wasps" is, therefore, untenable (Kurczewski pers. obs.). Females of *Aporus unicolor* in England are 6.5–11.0 mm long (Day 1988), while the significantly larger and heavier *Atypus affinis* females are 10–15 mm in body length (Schwendinger 1990). Females of *Atypus piceus* are the same body length as *Atypus affinis* with a maximum of 15 mm.

***Aporus (Aporus) bicolor* Spinola.** *Aporus bicolor* occurs in southern Europe and northern Africa (Wahis and Durand 2012). This species is morphologically dissimilar to *A. unicolor*: head in frontal view is slightly triangular; mandible bidentate; pronotum long and wide; and forefemur moderately swollen (Wahis and Durand 2012; I. Cross, pers. comm.). Cross has photographed females of *A. bicolor* searching for *Nemesia fagei* Frade and Bacelar (Nemesiidae) in Portugal and observed them attempting to enter their burrows. The burrows of *N. fagei* are often blocked with an obelisk-like structure consisting of silk, saliva and sand made by the spider that effectively acts as a deterrent to entry by parasitoids and predators (Bacelar 1937). Cross observed and photographed females of *A. bicolor* trying unsuccessfully to enter the spider's blocked burrow entrance, being thwarted, and moving on to the next entrance only to be thwarted again. In Spain, *A. bicolor* has been reported capturing *Nemesia* sp. (Gros 1983; Gros and Durand 2013). Gros (1983) observed a female of *A. bicolor* enter the burrow of *Nemesia* sp. through the trapdoor, remain inside for 5 minutes, and exit via the trapdoor. In excavating this burrow Gros (1983) found an unresponsive *Nemesia* sp. at the bottom with the wasp's egg attached to its abdomen. Bell (2014) photographed an *A. bicolor* female in Spain standing beside the left rear leg of an immobilized *Iberesia* sp., possibly *I. machadoi* Decae and Cardoso (Nemesiidae). The spider's trapdoor was dislodged and separated from the entrance by the wasp in her capture of the spider. The hinge of the trapdoor appeared to be frayed and possibly chewed by the wasp to gain access. Seconds later, both wasp and spider vanished and were evidently inside the spider's burrow (Bell 2014).

***Aporus (Aporus) planiceps* (Latreille).** *Aporus planiceps* inhabits Spain, southern France and northern Africa (Wahis and Durand 2012). It is one of the most highly modified of the Palearctic species: head flattened in profile and rather triangular in frontal view; face narrow; antennae set very low, at bottom of compound eyes; temple does not rise above eye level; long sharp tooth on mandible; sharp edged, elongate pronotum; and highly swollen forefemur (Wahis and Durand 2012; I. Cross, pers. comm.). Soyer (1945) observed capture of the trapdoor spider *Nemesia carminans* (Latreille) (Nemesiidae) by *A. planiceps* in France. The wasp lifted the trapdoor lid, probably using its mandibles and forelegs, unhesitatingly entered the silk-lined burrow, stung the spider inside, and laid an egg, 1.2 mm long, on the immobilized prey's abdomen in a dorsal-posterior position. Soyer (1945) then captured the wasp as it escaped from the burrow and placed it with a second *N. carminans* in a glass tube wider than the spider in order to observe the interaction between wasp and spider. The wasp grasped a foreleg of the spider, pulled itself atop it to a position perpendicular to its cephalothorax, curved its abdomen underneath, and stung it in its ventral cephalothorax between the second and third coxal cavities. She then stung the spider a second time between the first and second coxal cavities. Finally, the wasp imbibed regurgitated fluid from the spider's mouth—a common after effect following its paralysis.

***Psorthaspis* Banks.** Females of *Psorthaspis* are black with highly contrasting white, yellow, orange or red markings or deep blue or violet pubescence; their wings are totally fuliginous or have dark bands on a hyaline background. They have a thin, flattened, and broad head, strong clypeo-frontal bridge, and the vertex crest is somewhat sharp. The head is attached high on the prothorax. The compound eyes are toward the side of head. The pronotum is rather elongate; forefemur is not incrassate; tarsal claws have an acute, sometimes very strong tooth; and forewing with three submarginal cells (Evans 1954, 1966). Four of the 13 Nearctic species, *P. brimleyi* (Malloch), *P. legata* (Cresson), *P. mariae* (Cresson), and *P. sanguinea* (Smith), are common in the SE U.S., with *P. mariae* (Cresson) ranging as far north as Illinois and New Jersey (Krombein 1979) and southern Ohio (Kurczewski, pers. obs.). The four eastern species occur mainly in woods (Krombein 1979). However, *P. legata* (Cresson) and *P. sanguinea* (Smith) also occur in xeric sandhill habitats which are mostly open-canopied (D. Stevenson, pers.

comm.). Online photographs and observations indicate common hunting behavior among the species. Females run rapidly on the ground flicking their wings or holding them flat on the dorsum, explore holes in the soil, and disappear underneath dried leaves and other plant debris. They make periodic low, short, brief flights between hunting forays. In certain spots females pause, sometimes circle, hold their mouthparts and antennae on or near the ground with the end of their abdomen angled slightly upward, and wings flat on the dorsum (Kurczewski, pers. obs.).

***Psorthaspis formosa* (Smith).** Females are characterized by front, vertex, upper temples, pronotum, mesoscutum, and metasomal tergites 3 and 4 with orange pubescence; face, clypeus, legs, lower pleura, propodeal apex, apex of abdominal tergum 1 and base of tergum 2, and abdominal sterna 1–4 silvery pubescent; remainder of body black; forewing base and two sizeable bands on forewing infuscate (Evans 1966). Females are 13–17 mm in body length. This species ranges from southern Arizona to Costa Rica (Evans 1966; C. Melton, pers. comm.).

Vanoye-Eligio et al. (2014) listed Migidae (tree trapdoor spiders) as the host spider family for a *P. formosa* from Yucatan, Mexico. However, the family Migidae does not occur in North America, the nearest records for this family being from Chile and Argentina in South America (World Spider Catalog 2020). The most likely genus for this parasitoid-host spider association is *Ummidia* sp. (Halonoproctidae), as this genus is common in Yucatan and is the usual host of other larger eastern North American *Psorthaspis* species.

***Psorthaspis legata* (Cresson).** Females have a reddish-orange head, thorax, anterior metasoma and, sometimes, tibiae. The last half of the metasoma is black with tergites 3 and 4 having cream-colored markings. The legs and antennae are largely black. The forewings are hyaline with a pair of dark bands. Females are 5–12 mm in body length, their size dependent on the size of the host spider on which they fed as a larva. *Psorthaspis legata* inhabits woods from Kansas and Texas to Maryland and Florida (Krombein 1979; Kurczewski pers. obs.) and open xeric sandhill habitats (D. Stevenson, pers. comm.).

A female of *P. legata* (Atlanta, Fulton County, GA; 26 April 2021), ~10 mm long, was observed hunting for host trapdoor spiders on a sloped hillside of loamy soil covered in dried oak and sweet gum leaves, sparse pine needles and other plant debris. The wasp, in constant motion, walked rapidly over the dried leaves, head and antennae held downward with wings flat on the dorsum. She went beneath the leaves to explore holes in the ground. Every so often she appeared back on the surface and continued searching through the dried leaves or flew briefly, 10–15 cm, to a new area. Her flights were less than 1 cm above the ground. Her movements on the ground were very ant-like (Kurczewski, pers. obs.). Two days earlier torrential rains had flushed five males of *Myrmekiaphila foliata* Atkinson (Euctenizidae) from this habitat onto a front porch and into a basement (Kurczewski, pers. obs.). The largest males (preserved in alcohol) are 17 and 19 mm long. Adult females of this species are 23 mm long (West, pers. obs.). Considering the much smaller size of the wasp it was probably hunting juvenile spiders (Kurczewski, pers. obs.).

Bringhurst (2021a) provided the first photographic host record for *P. legata*, *Myrmekiaphila comstocki* Bishop and Crosby (Euctenizidae) [det. R. Godwin], adult or subadult female, from the University of Texas at Tyler, Smith County, TX. The wasp, standing atop a dried leaf on the ground surface, grasped the immobilized wafer-lid trapdoor spider with her mandibles during transport, ventral side upward, by its left foretibia and, dorsal side upward, at various places on the side and dorsum of its abdomen. The immobilized spider was released temporarily by the wasp, dorsal side upward, on a dead leaf near the ground (Bringhurst 2021b).

An excellent video taken by Robert Clark on 16 August 2021, 1505 EDT near Warner Robins, Houston County, GA details host capture and burrow entry in *P. legata* (Clark 2021). As the wasp walked across rough ground and dried fallen leaves, a *Myrmekiaphila foliata* [det. R. Godwin], subadult male or juvenile, emerged rapidly from its entrance through the trapdoor and grasped the wasp with its legs. After several seconds of grappling, the spider apparently tried to run away with the wasp clinging underneath. After more grappling, the wasp clung to the right side of the spider's cephalothorax with the end of her abdomen positioned underneath as she stung it more than once near the bases of its right second and third legs. The spider gradually acquiesced and its movements became increasingly slower. The wasp dismounted, walked, and entered the spider's burrow with the trapdoor in the raised position. Seconds later, the wasp exited headfirst through the entrance, walked to the immobilized spider in a dorsal side upward position, and examined it with her antennae. She walked back toward the entrance, stopped, curled her abdomen under her body, and cleaned her sting with her mandibles. She then

entered and exited the spider's burrow, cleaned her mouthparts and antennae with her front legs, walked, and examined the spider with her antennae. The wasp grasped the spider's right hind metatarsus with her mandibles and pulled it backwards on the ground to near the entrance. She released the spider, dorsal side upward, just outside the opening, entered the burrow headfirst, came out seconds later, and pulled the spider inside by grasping the venter of its pedicel with her mandibles. As the spider was pulled slowly inside by the wasp, the trapdoor gradually closed behind (R. Clark, pers. comm.; D. Stevenson, pers. comm.).

***Psorthaspis mariae* (Cresson).** Females have a reddish-orange thorax, black head, legs, antennae, and metasomal tergites 1 and 4, or reddish orange metasomal tergites 1–4. Metasomal tergites 5 and 6 are silvery pubescent. The forewings are hyaline with a pair of dark bands. Females are 12–25 mm in body length, their size dependent on the size of the host spider on which they fed as a larva. This species occurs in woods from Illinois, West Virginia, southern Ohio and southern New Jersey to Florida, Arkansas and Missouri (Krombein 1979; Kurczewski, pers. obs.).

An excellent video taken at Ellijay, Gilmer County, GA by D. D. Burgess (2019) shows an immobilized *Ummidia audouini* (Lucas) (Halonoproctidae), juvenile [det. R. Godwin], lying ventral side upward on the ground with a much smaller female of *P. mariae* attempting to pull it across rough soil by grasping the flexible exoskeleton of its abdomen with her mandibles (Table 1, Fig. 7). After several attempts, the wasp turned the large and much heavier spider dorsal side upward but still struggled to pull it backwards. The wasp even used the end of her abdomen for added leverage, bending the last three segments noticeably downward while implanting the apex in the soil. The spider was only partly paralyzed and moved its legs rhythmically. Twice the wasp released her grasp of the spider, walked to the nearby burrow entrance, slid beneath the overhanging trapdoor flap, and entered the spider's burrow headfirst and dorsal side upward. She exited quickly, walked to the spider, and eventually pulled it to an area of soil beside the trapdoor. She released her grasp of the prey and, this time, squeezed beneath the trapdoor flap upside down, came quickly out, and, using her mandibles, pulled the spider by its abdomen to just under the flap. From inside she pulled the spider slowly down the burrow, coming partly out several times to rearrange the spider's legs to facilitate getting it all the way inside. The flap closed gradually as the spider disappeared. A separate photo taken at the same site shows another *U. audouini* juvenile [det. R. Godwin], dorsal side upward, lying motionless on a stony path, probably an abandoned prey of *P. mariae* (D. D. Burgess, pers. comm.).

Two photographs taken by L. S. Hughes (2019), 6 km S of Lynx, Adams County, in extreme southern Ohio, show an early instar larval spider wasp feeding on the dorsum of the abdomen of a penultimate female of *Ummidia audouini* [det. R. A. Bradley] (Fig. 8; L. S. Hughes, pers. comm.). *Psorthaspis mariae* is the probable spider wasp species based on its northerly geographic distribution, habitat, large size, position of larval wasp attachment, and affinity of the larger *Psorthaspis* species for host Halonoproctidae (Kurczewski, pers. obs.).

***Psorthaspis planata* (Fox).** Females of *P. planata* are all black with bluish or violaceous pubescence and fuscous, violaceous wings (Evans 1966). Females vary widely in body length, 9–22 mm, depending on the size of the spider on which the larval wasp fed. This species occurs from central California and Utah southward to Baja California, Arizona, and other areas of Mexico (Evans 1966; Krombein 1979). *Psorthaspis planata* is common in the California coastal hills and mountains, Channel Islands, recreational parks and trails, and southwestern deserts of Arizona and California (Krombein 1979; Wasbauer and Kimsey 1985; Ramirez 2000).

Early 20th century host records and a nesting behavior study of *P. planata* represent the first natural history reports on species of *Psorthaspis* and their host trapdoor spiders (Davidson 1905; Jenks 1938). Davidson's (1905) note is the first evidence of a parasitoid-trapdoor spider association between *P. planata* and *Bothriocyrtum californicum* (Table 1). Jenks (1938) confirmed this association with a detailed study of the wasp capturing and ovipositing on a host spider in captivity under confined artificial conditions. Jenks (1938) photographic study showed the female of *P. planata* [as *Pedinaspis planatus* (Fox)] using her strong foretarsal claws to raise the flap of the trapdoor and support it on her enlarged and flat prothorax as she slipped through the opening. If the wasp was unable to raise the flap, she chewed a hole through it using her powerful mandibles. The wasp then descended the silk-lined burrow where, at the bottom, she encountered the much larger trapdoor spider. In the ensuing "rough and tumble," the wasp repeatedly stung the spider in its ventral cephalothorax as the spider's chelicera bites glanced harmlessly off the wasp's smooth exoskeleton. After the spider was immobilized from the wasp's venom, the wasp pulled the spider to the bottom of its burrow and laid an egg on the dorsum of its abdomen. The

spider was about twice the body length of the wasp and weighed perhaps 10 times as much. The wasp egg hatched to a larva in a couple of days, the larva fed on the spider for 7–10 days, and eventually spun a cocoon in which the wasp pupated. The spider may remain alive for six months or longer as the wasp larva feeds and develops on its abdomen (Jenks 1938).

Ramirez (2000) reported on the “parasites” of the trapdoor spider *Bothriocyrtum californicum* on the California Channel Islands, Santa Cruz and Santa Catalina, and in San Diego County, CA. He presented several photographs of the spider, its burrow, trapdoor and entrance, wasp cocoons and wasp emergence holes, but, unfortunately, no photographs of the adult wasp. In addition to rearing the all-black with bluish pubescence *Psorthaspis planata* from *B. californicum* he also reared green and blue trapdoor spider-hunting wasps from this spider species, perhaps *Aporus luxus* (Banks) on the Channel Islands and *A. luxus* or *A. concolor* (Smith) in San Diego County. Unfortunately, the reared adult specimens were lost during the identification process (M. Ramirez, pers. comm.). An excellent photograph illustrates how a *P. planata* female uses her mandibles and forelegs in unison to pry open the trapdoor of *Bothriocyrtum californicum* (Fig. 6; G. Quintana, pers. comm.).

***Anoplius (Lophopompilus) carolina* (Banks).** *Anoplius carolina* is black, the second metasomal tergite with a pair of orange spots sometimes confluent in the middle (Evans 1951). The wings are lightly infusate. Females are 9–13 mm in body length. *Anoplius carolina* exhibits no structural characteristics that could be associated with capturing trapdoor spiders. This species is restricted to the Appalachian and Piedmont Regions of the eastern U.S., ranging from southern Quebec to northern Georgia (Evans 1951). Its flight period is midsummer in sunny spots in open woodland (Evans 1951). *Anoplius carolina* nests in mammal burrows or holes in loamy soil in deciduous woodland (Evans and Yoshimoto 1962; Kurczewski and Kiernan 2015).

Nine reported host records for this species are for species of Amaurobiidae: *Callobius bennetti* (Blackwall), *Coras* sp., *Wadotes* sp., and *Wadotes hybridus* (Emerton) (Evans and Yoshimoto 1962; Krombein 1979; Kurczewski and Kiernan 2015; Kurczewski et al. 2017). Our record of the mygalomorph *Antrodiaetus unicolor* complex (Antrodiaetidae), subadult male [det. R. C. West], is highly unusual. This atypical host record is based on photographs of an *A. carolina* female examining the mouthparts of the immobilized trapdoor spider with her own mouthparts in Groton, Middlesex County, MA. The spider laid ventral side upward on the ground in the three photographs sent to us (Murray 2020; T. Murray, pers. comm.).

***Notocyphus dorsalis* Cresson.** *Notocyphus dorsalis* is a polytypic species with three subspecies ranging from central Missouri to Guatemala (Townes 1957; Kurczewski et al. 2020b). Females of *Notocyphus* are strikingly noticeable in the field being black with bright orange head and mesosoma. They possess no structural characteristics that could be associated with capturing trapdoor spiders. They do, however, have atypical pompilid morphological features that are probably associated with their unusual method of attacking juvenile tarantulas wandering on the ground surface, away from their burrows: middle and hind femora and hind tibiae with spine-like bristles, subgenital plate compressed laterally with a median longitudinal ridge, and decurved sting (Townes 1957). The last two structures are used in brief temporary paralysis of the host spider and subsequent oviposition on its abdominal dorsum. The spider revives from the temporary paralysis and continues to perform its daily activities.

Notocyphus dorsalis is mentioned in this paper based on a single trapdoor spider host record—*Ummidia* sp. [det. R. C. West] for *N. d. dorsalis* Cresson from Warsaw, Benton County, Missouri (Table 1; B. Eldridge, pers. comm.), a significant range extension for the wasp (Kurczewski et al. 2020b) and just beyond the northernmost extent in Missouri of the tarantula genus *Aphonopelma* [*hentzi* (Girard)] (Theraphosidae) (Hamilton et al. 2016), its natural host. All other host records for this species, as *N. dorsalis arizonicus* Townes, are for *Aphonopelma chalcodes* Chamberlin juveniles (Minch 1979; Simons 1989; Byrne 2016; Kurczewski et al. 2020b). In such examples, the wasp oviposited on the anterior dorsum of the spider’s abdomen after stinging it in the underside of its cephalothorax. The spider soon recovered from the temporary paralysis and resumed normal activity until the wasp larva fed destructively on its internal organs. Eventually the host tarantula succumbed, the wasp larva pupated *in situ*, and an adult wasp emerged from the spider’s carcass 48 days–15 months later (Minch 1979; Simons 1989; Byrne 2016; Kurczewski et al. 2020b; H. G. Byrne, pers. comm.; M. Dame, pers. comm.).

Discussion

The genus *Calopompilus* and subgenus *Priocnemissus* (tribe Pepsini) and tribe Aporini comprise the Nearctic trapdoor spider-hunting spider wasps (Krombein 1979). *Calopompilus* and *Priocnemissus* do not have the conspicuous structural features for hunting trapdoor spiders possessed by species of Aporini, especially *Aporus*: flattened and thin head, highly enlarged pronotum and swollen forefemur (Evans 1966; Day 1988). *Calopompilus*, instead, is characterized by short wide antenna segments, dentate mandibles, short bristly legs, large pronotum, and “scoliid habitus” (Townes 1957). *Calopompilus* species have not been observed nesting or excavating a burrow, but they selectively capture trapdoor spiders (Kurczewski et al. 2020b). This is not an absolute statement because the smaller *Calopompilus* species from the eastern U.S. have yet to be studied. The reduced, almost obsolete teeth on the hind tibia imply that some, if not all, *Calopompilus* do not excavate their own burrow in the soil for use as a nest. The female wasp may simply lift or bite/tear through the silk, soil and plant debris flap of their host folding trapdoor spider (Antrodiaetidae) or wafer-lid trapdoor spider (Euctenizidae), using her mandibles and forelegs, enter the burrow, sting the spider, lay an egg on its abdomen, partly close the burrow with soil, and leave. But such a scenario does not coincide with photographs of *Calopompilus heiligbrodtii* and *C. pyrromelas* with immobilized trapdoor spiders being captured and immobilized on the ground surface (Kurczewski et al. 2020b). These wasps may somehow lure the spider from its burrow onto the ground surface where odds favor them being successful in capturing and paralyzing the host. The wasp must then drag the immobilized spider back into its burrow to complete the oviposition process.

Only a single photographic report shows a Nearctic trapdoor spider-hunting spider wasp, *Psorthaspis planata* (Aporini), sting the trapdoor spider inside its burrow and oviposit thereon (Jenks 1938). This staged activity took place in captivity under confined conditions with the wasp being introduced artificially into the spider’s burrow and sealed inside. Gros (1983), in Spain, observed a female of *Aporus bicolor* enter the burrow of *Nemesia* sp. (Nemesiidae) through its trapdoor, remain inside for five minutes to evidently sting and oviposit on the host spider, and, then, exit through the trapdoor. Observations of other species of Aporini reveal the wasp enticing the spider from its burrow following a series of brief entries and exits in order to lure the spider to its entrance. Once the spider exits its burrow onto the ground surface, it is stung one or more times by the much quicker, more maneuverable spider wasp, e.g., *Aporus hirsutus*, *A. luxus*, *Psorthaspis legata*, *P. mariae* (Williams 1928; Kurczewski et al. 2020b; this study). Species of *Aporus* and *Psorthaspis* have strong mandibles, powerful forelegs, and enlarged pronotum containing extensive musculature for the front legs. Photographs or descriptions show females of *Aporus hirsutus* or *A. luxus*, *Psorthaspis mariae*, or *P. planata* lifting or tearing a hole through the flap of an *Aptostichus* (Euctenizidae), *Ummidia* (Halonoproctidae), or *Bothriocyrtum* (Halonoproctidae) trapdoor, respectively, in order to induce the spider onto the ground surface or gain entry to its burrow (Williams 1928; Kurczewski et al. 2020b).

Despite conspicuous differences in female wasp external morphology, it is difficult to associate *Aporus* species capture of specific trapdoor spider families, genera or species or correlate with their burrow architecture except for *Aporus hirsutus* and the European *Aporus unicolor*. *Aporus (Plectraporus) hirsutus* has an extensive weaponry of morphological structures to access wafer-lid trapdoor spiders in their burrows: tactile hairs over the body and legs; thin and flattened, somewhat triangular head; concave vertex to fit the contours of the prothorax; very long and wide, parallel-sided pronotum; strongly incrassate forefemur; and a “rake” of short, wide comb-spines (Evans 1966; Kurczewski et al. 2021). This species unearths wafer-lid trapdoor *Aptostichus* species in sand dunes and deserts (Williams 1928; Kurczewski et al. 2017, 2020b, 2021). *Aporus (Aporus) luxus* inhabits open ground, including sand, but, unlike *Aporus hirsutus*, is less psammophilous, does not inhabit deserts (Wasbauer and Kimsey 1985), and lacks a hairy body and legs and foretarsal digging rake (Evans 1966). Its pronotum is relatively long and wide and its forefemur is moderately incrassate (Evans 1966). Despite less developed morphological structures designed for attacking trapdoor spiders than *Aporus hirsutus*, *Aporus luxus* successfully attacks species of Antrodiaetidae and Euctenizidae in a variety of habitats (Wasbauer 1982; Kurczewski et al. 2020b). The European *Aporus (Aporus) unicolor* is structurally one of the least modified congeners (Day 1988; Wahis and Durand 2012). Its morphological characteristics are less developed to lift and open the flap of a trapdoor spider burrow: broad and round head, shorter pronotum, and weakly incrassate forefemur (Day 1988). Consequently, *Aporus unicolor* does not attack typical trapdoor spiders with a flap or lid on their burrow. Rather, it preys on

purse-web spiders of the genus *Atypus* (Atypidae) in Europe in their silken, tubular purse-like webs (Else 1975; Day 1988; Gerth et al. 2012).

Four species of *Psorthaspis* captured trapdoor spiders in this study. Based on the structural specializations of the head and prothorax of the females it is likely that all conspecifics prey on trapdoor spiders or some type of burrowing spider (Evans 1954). The geographic distribution of this genus from the Mid-Atlantic Region of the U.S. to the Greater Antilles and South America corresponds closely with that of several trapdoor spider families and areas of trapdoor spider abundance are usually places of *Psorthaspis* species relative abundance (Evans 1954). There is a spider wasp-host spider size equivalence relationship among *Psorthaspis* species. Medium-size species such as *P. mariae* (12–25 mm) and *P. planata* (9–22 mm) capture larger Halonoproctidae (cork-lid trapdoor spiders) and small species like *P. legata* (5–12 mm) capture smaller Euctenizidae (wafer-lid trapdoor spiders). In either case the spider is usually larger and much heavier than the wasp. Most of the observed prey captures in *Psorthaspis* occur near the spider's trapdoor/entrance as the wasp searches for its host on the ground through dried leaves and other plant debris (Kurczewski, pers. obs.).

Calopompilus pyrromelas (17–28 mm) and *Priocnemis oregona* (10–18 mm) are two of the largest spider wasps in the northwestern U.S. and British Columbia (Townes 1957). They prey on the same kind of trapdoor spiders, especially species of *Antrodiaetus* (Kurczewski et al. 2017, 2020b). The two species nest at different times of the year. *Priocnemis oregona* nests only during spring (March to June), whereas *C. pyrromelas* is active in the summer and early fall (July through October) (Townes 1957). *Calopompilus* is one of the most primitive genera in the family Pompilidae (Townes 1957) and its use of primitive trapdoor spiders probably has a long evolutionary association. *Priocnemis oregona* belongs to a presumably more recently evolved genus and this species may have acquired a preference for trapdoor spiders because there is a scarcity of large cursorial araneomorph species in the northwestern U.S. and British Columbia (Kurczewski et al. 2020a). Despite several host records, details of the nesting behavior of *C. pyrromelas* remain unknown. It is not known whether *C. pyrromelas* adopts the spider's burrow for use as a nest. *Priocnemis oregona*, on the other hand, excavates its own multi-celled nest using its mandibles and legs, especially hindlegs (Kurczewski et al. 2017; Kurczewski, pers. obs.). Disadvantages of excavating its own nest include long distance prey transport, more exposure time on the ground surface for enemy surveillance, and, possibly, completion of fewer cells per day.

The capture of incidental trapdoor spiders by three non-trapdoor spider-hunting pompilid species is noteworthy. *Priocnemis (Priocnemissus) minorata* is a polyphagous parasitoid on at least eight families of araneomorph spiders (Kurczewski and Kiernan 2015), but this species captured the folding trapdoor spider genus *Antrodiaetus* (Antrodiaetidae) in this study. This spider wasp species is in the same subgenus as *P. (P.) nigripes* and *P. (P.) oregona*, of which both are host specific on trapdoor species of Mygalomorphae (Kurczewski et al. 2017, 2020b; this study). The capture of *Ummidia* sp. (Halonoproctidae) by *Notocyphus d. dorsalis* in Missouri is easily explained. Its usual host genus *Aphonopelma* (Mygalomorphae: Theraphosidae) does not occur as far north geographically as the wasp (Hamilton et al. 2016; Kurczewski et al. 2020b). In this case, the wasp attacked a trapdoor, instead of cursorial species of Mygalomorphae, and used it as a substitute host. The highly atypical capture of another trapdoor species, *Antrodiaetus unicolor* complex (Mygalomorphae: Antrodiaetidae), by *Anoplius carolina*, which is host specific on species of Amaurobiidae (hacklemesh weavers) (Kurczewski and Kiernan 2015), is difficult to explain. The spider was probably in the wrong place at the wrong time! The *Antrodiaetus unicolor* complex subadult male is approximately the same size and color as its ordinary host hacklemesh weaver spiders, was in the same habitat, and, perhaps, displayed similar escape behavior as the typical Amaurobiidae captured by *Anoplius carolina*.

Acknowledgments

We thank Rebecca Godwin, Piedmont University, Demorest, GA and Dirk Stevenson, Altamaha Environmental Consulting, LLC, for reviewing the manuscript and suggesting changes for improvement. Jason Bond, University of California–Davis, Davis, CA; Richard Bradley, The Ohio State University, Columbus, OH; Glavis Edwards, Florida State Collection of Arthropods, Gainesville, FL; Rebecca Godwin, Piedmont University, Demorest, GA; and, Marshal Hedin, San Diego State University; San Diego, CA aided in the identification of families, genera and

species of trapdoor spiders. Ian Cross, Dorchester, UK; Edgard Gros, Chierry, FR; and Dirk Stevenson, Altamaha Environmental Consulting, Hinesville, GA provided information on some spider wasps and their host trapdoor spiders. Edgard Gros sent us detailed valuable information on trapdoor hunting European genera of spider wasps. Tom Murray, Groton, MA sent us photographs of *Anoplius carolina* with a subadult male of *Antrodiaetus unicolor* complex. Richard Seaman, San Jacinto, CA, sent us photographs of a provisioning female of *Aporus luxus* with its prey *Aptostichus hesperus*. Fred Coyle, Eastern Carolina University, Greenville, NC and Mike Dame, Tucson, AZ sent us information about unidentified pompilid larva in trapdoor spider burrows. Daniel Johnson, Atascadero, CA sent us information about his photographs of *Aporus hirsutus* and *Aptostichus simus*. Martina Ramirez, Loyola Marymount University, Los Angeles, CA, sent us photographs of *Bothriocyrtum californicum* burrows with wasp cocoons but, unfortunately, none of the cocoons reared identifiable spider wasp species. Bogar Celis, Cloverdale, CA, sent us photos of *Aporus luxus* with an immobilized *Aptostichus miwok*. Marshal Hedin sent information on the burrow structure of *A. simus*. Daniel Johnson, Atascadero, CA and Joshua S. Willems, California Polytechnic State University, San Luis Obispo, CA sent us information about wasp behavior associated with their photographs of *A. hirsutus*. Lorri Gong, Port Reyes Station, CA sent us information about *A. hirsutus* searching and digging in sand for burrows of *Aptostichus*. Chloe and Trevor Van Loon, San Jose, CA sent us information about potential *A. hirsutus* host spiders at Moss Landing State Beach, Monterey County, CA. Elijah Talamas, FDACS, Gainesville, FL sent us photographs and ecological information on *Aporus niger* from Florida. Steve Paiero, University of Guelph, Guelph, Ontario, sent us *Aporus niger* and Mygalomorphae locality records from southern Ontario. Alice Abela, Kristian Bell, Danielle Burgess, Cara Coulter, Howard G. Byrne III, Edith Clark, Robert Clark, Mike Dame, Brenda Eldridge, Kevin Hall, T. L. Hammond, Alan Hogan, Laura Hughes, Kelly E. Maier, Charles W. Melton, Elva Paulsen, Gilbert Quintana, Jennifer Thompson, Torrie Vail, Margery VanDerslice and J. S. Willems sent us photographs and videos of spider wasp and trapdoor spider interactions. Abela send us several emails describing the activities of the wasp species as they searched, dug, fed and transported their *Aptostichus* prey. We thank the following persons for use of their spider wasp and host trapdoor spider copyright photographs: Alice Abela, Kristian Bell, Danielle Burgess, Chris Collier, Cara Coulter, Laura Hughes, Shipeng Li, Julia Pearson, Gilbert Quintana, Richard Seaman, and Ivan Yates.

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Received May 17, 2022; accepted September 24, 2022.

Review editor David Plotkin.