

A journal of world insect systematics

INSECTA MUNDI

1013

Pepsis elegans Lepeletier
(Hymenoptera: Pompilidae: Pepsinae)—a secretive spider wasp
and century-long conundrum

Frank E. Kurczewski

1188 Converse Drive NE
Atlanta, GA 30324

Date of issue: October 27, 2023

Center for Systematic Entomology, Inc., Gainesville, FL

Kurczewski FE. 2023. *Pepsis elegans* Lepelletier (Hymenoptera: Pompilidae: Pepsinae)—a secretive spider wasp and century-long conundrum. *Insecta Mundi* 1013: 1–15.

Published on October 27, 2023 by
Center for Systematic Entomology, Inc.
P.O. Box 141874
Gainesville, FL 32614-1874 USA
<http://centerforsystematicentomology.org/>

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Electronic copies (online ISSN 1942-1354) in PDF format

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Pepsis elegans Lepeletier
(Hymenoptera: Pompilidae: Pepsinae)—a secretive spider wasp
and century-long conundrum

Frank E. Kurczewski

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

Abstract. After 105 years of study and 425 recent natural photographs, the host spider and nesting behavior of *Pepsis elegans* Lepeletier (Hymenoptera: Pompilidae: Pepsinae) remain a mystery. *Pepsis elegans* is the only species in the large and impressive genus *Pepsis* Fabricius that lives east of the Mississippi River, mainly in the southern U.S. The other 14 Nearctic *Pepsis* species inhabit the southern U.S. west of the Mississippi River and northern Mexico. They capture and provision their nests with large, hairy, heavy-bodied, stout-legged tarantulas of the genus *Aphonopelma* Pocock (Araneae: Mygalomorphae: Theraphosidae), the only native theraphosid genus in this region. There are no tarantulas east of the Mississippi River, except in East Baton Rouge Parish, LA, and no valid host spider records or nesting biology information for *P. elegans*, the largest spider wasp in the eastern US. Rau and Rau's (1918) questionable field observation of this secretive, dark, violaceous-winged spider wasp yielded no nest, host spider or wasp specimen, and only initiated questions about its identification and nesting biology. The method of host spider transport, as described in Rau and Rau's (1918) observation, is identical with that of *Entypus fulvicornis* (Cresson) (Hymenoptera: Pompilidae: Pepsinae), a species similar in size and color to *P. elegans* and often misidentified as such and vice versa. Potential host spider for *P. elegans* may include cork-lid trapdoor spiders in the genus *Ummidia* Thorell, especially *U. audouini* (Lucas) (Araneae: Mygalomorphae: Halonoproctidae). This spider is abundant, sizeable, and stout enough to provide sufficient food for the developing *P. elegans* larva. The genus *Ummidia* and *P. elegans* have nearly identical geographic location maps and occur in the same habitat. *Pepsis elegans* could conveniently use the spider's burrow as a nest without having to excavate one from the ground surface and be detected by the burrowing activity or lengthy, arduous, and cumbersome host spider transport. *Pepsis elegans* females from various localities had dried mud on the forewings and body inferring they were underground in moist, fine-grained soil as in a burrow. Females were active at night introducing the possibility of cryptic nocturnal nesting, as in some other *Pepsis* species. *Ummidia audouini* is nocturnally accessible in its burrow entrance, holding the trapdoor slightly ajar as it waits in the darkness to ambush unsuspecting prey. Punzo's (2005) study of the closely related, orange-amber-winged, southwestern U. S. and Mexican *P. cerberus* Lucas is questionable based on the spider misidentification, possible wasp misidentification, and incompatible spider wasp-tarantula size difference. The host of *P. cerberus* and *P. novitia* Banks, a possible *P. cerberus* × *P. elegans* hybrid (Hurd 1952), is likely the southwestern wafer-lid spider *Eucteniza relata* (O. P.-Cambridge) (Araneae: Mygalomorphae: Euctenizidae) (Gillaspy 1990) and not *Aphonopelma* as indicated by Punzo (2005).

Key words. *Pepsis cerberus*, *Pepsis novitia*, *Pepsis menechma* species-group, *Calopompilus pyrromelas*, *Ummidia audouini*, *Eucteniza relata*.

ZooBank registration. urn:lsid:zoobank.org:pub:A5795DAA-ABE6-494D-A6A5-1BCA9D84D0C7

Introduction

Species of the large tarantula hawk-wasp genus *Pepsis* Fabricius (Hymenoptera: Pompilidae: Pepsinae) are noticeable inhabitants in the warm arid and tropical regions of the Americas. They occur only in the Western Hemisphere and the vast majority of the ~135 species are Neotropical in distribution (Vardy 2000). Fifteen *Pepsis* species inhabit the Nearctic Region, nearly all in the southwestern U. S. and Mexico (Hurd 1952; Vardy 2000, 2002, 2005). Tarantulas of the genus *Aphonopelma* Pocock (Araneae: Mygalomorphae: Theraphosidae) are their predominant host spiders (Hurd 1952; Williams 1956; Cazier and Mortenson 1964; Punzo 1994, 2005; Vardy 2000), *Aphonopelma* being the only native theraphosid genus in this region (Hamilton et al. 2016). There is a

geospatial connection between certain Nearctic *Pepsis* species and their *Aphonopelma* host species (Kurczewski et al. 2020). In southern Arizona, for example, the abundance of *A. chalcodes* Chamberlin (Hamilton et al. 2016) coincides with it being the prevalent host spider of four *Pepsis* species in the region: *P. chrysothemis* Lucas, *P. thisbe* Lucas, *P. mexicana* Lucas, and *P. grossa* (Fabricius) (Kurczewski et al. 2020). These four wide-ranging *Pepsis* species capture or probably capture *A. hentzi* (Girard) in Texas and Oklahoma, *A. anax* (Chamberlin) in south-central Texas, *A. gabeli* Smith in southwestern Texas, southern Arizona and southern New Mexico, and *A. steindachneri* (Ausserer) in southern California and Baja California Norte (Hamilton et al. 2016; Kurczewski et al. 2020). In the West Indies, southern Mexico, Central America and South America, *Pepsis* species often hunt and capture other genera of theraphosids instead of *Aphonopelma* (Kurczewski et al. 2013, 2020, 2022b, In Prep.). Not all species of *Pepsis* are “tarantula hawk-wasps.” Small and medium-size South American *Pepsis* species capture small and medium-size species of Mygalomorphae and Araneomorphae such as tube trapdoor spiders (Nemesiidae), armored trapdoor spiders (Idiopidae), curtain-web spiders (Dipluridae), funnel-web trapdoor spiders (Pycnothelidae), baldlegged spiders (Paratropidae), mouse spiders (Actinopodidae), wandering spiders (Ctenidae), and, very rarely, wolf spiders (Lycosidae) (Kurczewski et al. 2020, 2022b, In Prep.). There is only a single host record for wolf spiders (Lycosidae) among the 56 species of *Pepsis* that were studied. *Pepsis* species avoid wolf spiders because of their smaller size, visual acuity, maneuverability, speed, ferocity, and alertness (Williams 1956). Wolf spiders are the usual target of the smaller, faster species in the genus *Entypus* Dahlbom (Pompilidae: Pepsinae: Pepsini) (Kurczewski et al. 2020, 2022a, b).

Pepsis elegans Lepeletier and *P. cerberus* Lucas are comparatively small (16–28 mm), North American species in the *Pepsis menechma* species-group (Vardy 2005). Their host preferences are unknown or unsubstantiated. Salman (1930) and Hurd (1952) separated *P. elegans* and *P. cerberus* females from other Nearctic *Pepsis* females based on the middle tibial spurs being acutely curved near their apices. Females of *P. elegans* are black with bluish or violet pubescent reflection, have infusate violaceous wings, and yellowish orange to orange antenna flagellomeres (Fig. 1, 2). Females of *P. cerberus* have a refulgent bluish body, orange-amber dark base and dark-fringed wings, and black antennae. The forewing of *P. cerberus* females from Arizona is ~10–12 % longer than that of *P. elegans* females from the eastern U. S. There are differences in the shape of the male genitalia and subgenital plate of the two species (Salman 1930; Hurd 1952). The upper surface of the hind tibia of *P. cerberus* females is aligned with moderately small conical serrations and numerous, long, stout, posterior-curved, subtending bristles (Salman 1930; Hurd 1952; Vardy 2005). In *P. elegans* females, the upper surface of the hind tibia is aligned with slightly smaller conical serrations and sparser, shorter, thinner, straighter subtending bristles (Salman 1930; Hurd 1952; Vardy 2005). The inner hind tibial spur is longer and straighter in *P. elegans* (Salman 1930; Vardy 2005). *Pepsis elegans* females have a shorter flagellum, much shorter flagellomere 1, and wider flagellomere 1 compared to *P. cerberus* females (Kurczewski 2023). Flagellomere 1 of *P. elegans* females averages ~3.0 times as long as wide. In *P. cerberus* females, flagellomere 1 length divided by its width averages ~4.1, a significant difference. The gena recedes more behind the compound eye in *P. cerberus* than in *P. elegans*, strengthening the argument that these two species are distinct (Shimizu, pers. comm.).

Pepsis elegans is a secretive, albeit attractive, predominantly southeastern U. S. spider wasp that is seldom seen in the field except on flowers and leaves (Fig. 1). Females are rarely photographed host-searching among plant litter in nature preserves, parks, gardens, and overgrown and manicured lawns (Fig. 2). Their natural habitat appears to be mesic open woodland, sometimes near a stream or pond (Fig. 3). Rau and Rau’s (1918) field observation of *P. dubitata* Cresson [= *P. elegans*] produced no nest, wasp specimen or host spider, a sight unseen wasp identification by S. A. Rohwer, and a phantom geographic location record in Hurd (1952). Disregarding Rau and Rau’s (1918) observation and S. A. Rohwer’s questionable identification, females of *P. elegans* have never been reported nesting which implies the host spider is, perhaps, a burrow inhabitant. Dried mud on the forewings and bodies of some wasps infers they were underground in moist, fine-grained soils as in a burrow. The wasp might capture the spider in or near its burrow, conveniently use the burrow as a nest and, sometimes, hunt and subdue the spider at night. Night photographs of *P. elegans* revealed nocturnal activity of females (Webster 2014, 2022), as in some other *Pepsis* species (Hurd 1952; Williams 1956; Cazier and Mortenson 1964; Punzo 2005). Relatively large (BL, ~21–28 mm), potential host spiders found in the wasp’s hunting locale include the cork-lid trapdoor spider genus *Ummidia* Thorell, especially *U. audouini* (Lucas) (Mygalomorphae: Halonoproctidae) and, west of the Mississippi River, juveniles of the tarantula *Aphonopelma hentzi* (Mygalomorphae: Theraphosidae). Host



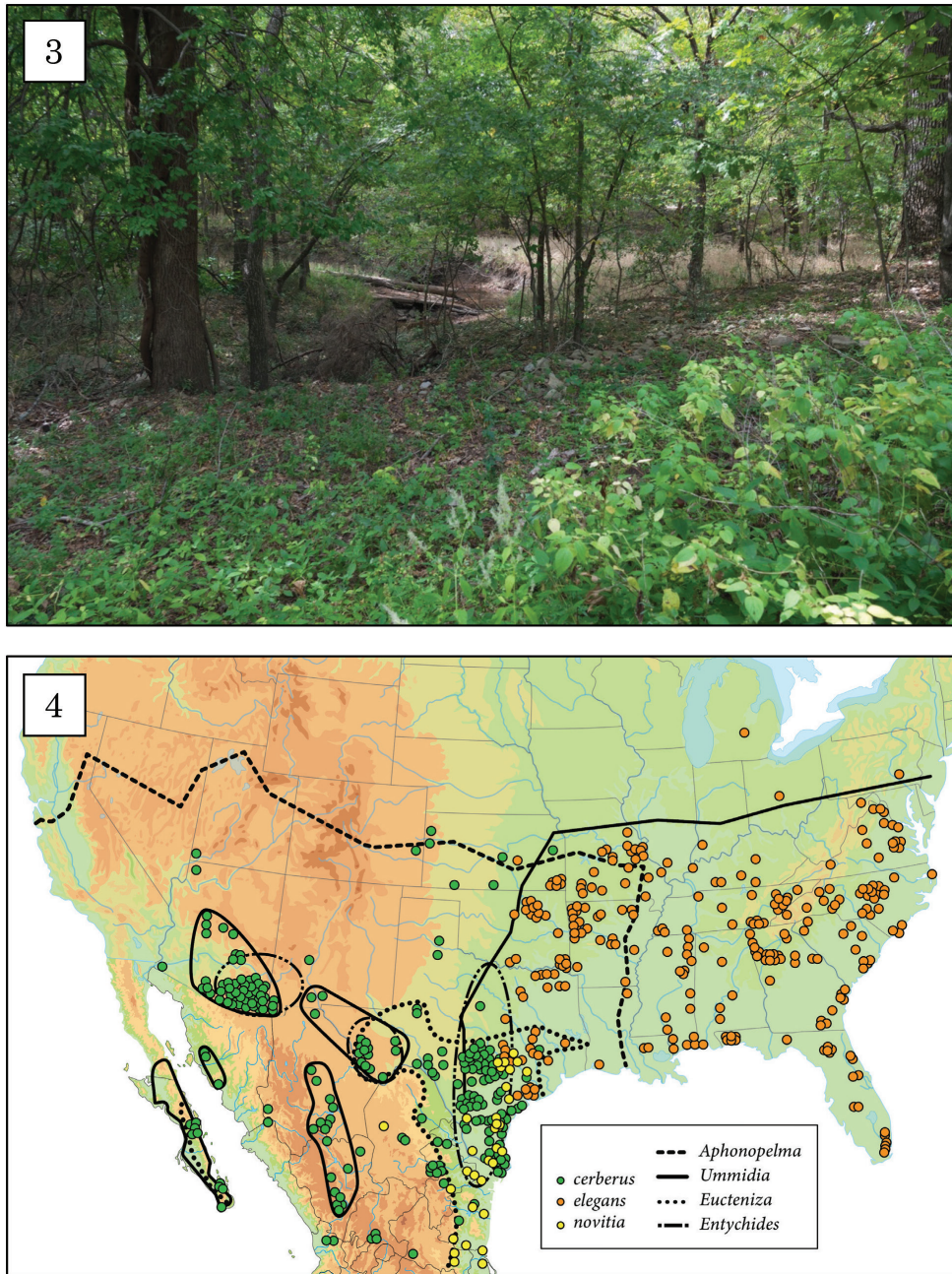
Figures 1–2. *Pepsis elegans*. 1) Female imbibing nectar from *Asclepias incarnata* L. (Apocynaceae), near Skiatook, Tulsa County, Oklahoma. Note dried mud on forewings. Photograph © Thomas Shahan. 2) Female host-searching on foot path, Webster’s Garden, Pryor, Mayes County, Oklahoma. Note dried mud on forewings. Photograph © Robert Webster.

spiders in the *Pepsis menechma* species-group capture trapdoor spider families (Mygalomorphae: Actinopodidae, Pycnothelidae). *Pepsis amyntas* Mocsáry (BL, ~18 mm) in Argentina caught and immobilized an *Actinopus cordobensis* Ríos-Tamayo and Goloboff (Actinopodidae), adult female (BL, ~20 mm), on a lawn near the spider's burrow and used the spider's burrow as a nest (Paoloni 2017; Kurczewski et al. In Prep.). *Pepsis amyntas* also captured and immobilized an *Actinopus ?cochabamba* Ríos-Tamayo, adult or subadult female, in Bolivia (Jiménez 2014; Kurczewski et al. In Prep.). *Pepsis ?chrysoptera* Burmeister captured an adult or subadult female of an unidentified Pycnothelidae in Brazil (Domingues 2017; Kurczewski et al. In Prep.). Equivalence in body length of spider wasp and host spider is important in successful capture of cursorial hunting or burrowing spiders by non-aporine spider wasps, although the host spider may weigh several times the weight of the spider wasp (Kurczewski and Kiernan 2015).

There are no substantiated host records for *P. elegans* or *P. cerberus*, but inferences about their host spiders can be extrapolated from the literature and their geographic distribution (Fig. 4). *Pepsis cerberus* reportedly captures tarantulas (Punzo 2005), although spider misidentification, possible wasp misidentification, and incompatible spider wasp-host spider size difference makes this association questionable. The comparatively small size of *P. cerberus* females is at variance with the capture of large adult and subadult tarantulas (*Aphonopelma*). Gillasp (1990) reported that the southwestern wafer-lid spider, *Eucteniza relata* (O. P.-Cambridge) (Mygalomorphae: Euctenizidae), is likely the host spider of *P. cerberus* and *P. novitia* Banks, a possible hybrid of *P. cerberus* × *P. elegans* (Hurd 1952), in south-central Texas as both spider and spider wasps were seasonally abundant on the same lawns (Fig. 4). Similarly, *P. elegans* may capture and deposit immobilized *Ummidia* sp., especially *U. audouini*, in the spider's burrow as the two species are often photographed at the same localities (Coin 2004, 2005; Hartgerink 2007, 2008, 2012; Raney 2014, 2020; Newton 2016, 2018; Miller 2020a, b; Gallaway 2021, 2022; Wiggins 2019, pers. comm.). *Eucteniza relata* makes a thinner, wafer-lid trapdoor compared to the thicker, more solid trapdoor of *Ummidia audouini* (Hedin, pers. comm.). The thicker cork-lid trapdoor of *Ummidia* coincides with the more quadrate gena-postgena-vertex of *P. elegans* and, likely, more extensive mandibular musculature.

Ummidia are medium to comparatively large spiders that construct silk-lined burrows with hinged, cork-like trapdoors (Bond and Coyle 1995). The burrows are often close together, cryptic, and covered with plant litter (Coyle 1981; Bond and Coyle 1995). *Ummidia audouini* is larger and hairier than other congeners in the eastern U. S. and more closely approximates tarantulas in size and appearance (Godwin and Bond 2021). *Ummidia audouini* is a plausible host spider for *P. elegans* because of the *Pepsis*-Mygalomorphae parasitoid relationship, size equivalence (BL, ~25–28 mm), habitat sympatry, seasonal synchrony, abundance, and burrow confinement. *Ummidia audouini* is in the same infraorder as tarantulas. It is the stoutest and heaviest native spider in the southeastern U. S. while *P. elegans* is the largest spider wasp in that region. *Pepsis elegans* and the genus *Ummidia* have nearly identical geographic location maps (Fig. 4; Hurd 1952; Godwin and Bond 2021; Kurczewski 2023). *Pepsis elegans* habitat, mesic open woodland (Fig. 3), resembles *Ummidia* burrowing habitat (Godwin, pers. comm.). Females of *Ummidia* are rarely seen as they often spend their entire lives underground inside their burrows and never wander far from the entrance. They remain just inside their burrow at night, with the trapdoor slightly ajar, waiting to ambush unsuspecting prey. Males of *Ummidia* wander across the ground surface in search of females mainly in June–July when females of *P. elegans* are actively nesting (Kurczewski, pers. obs.). The wasp's host-searching is possibly synchronized with the spiders' mating activities when the males and females are accessible and vulnerable. Females of *Ummidia* exhibit defensive behavior against enemies attempting to enter their burrow. The spider grasps the inner surface of the trapdoor with its chelicerae, pedipalp claws, and first and second pairs of legs while anchoring itself solidly against the burrow walls (Coyle 1981). Some trapdoor spider-hunting spider wasps can chew through the trapdoor using their strong mandibles and seize the spider from within its burrow (Kurczewski and West 2022). *Pepsis elegans* females have “well-developed mandibles” with a “strong...tooth” on the inner margin. The large and “strong” mandibular muscles allow for transverse movement (Salman 1930).

Insofar as purse-web spiders serving as *Pepsis elegans* hosts, *Sphodros niger* (Hentz) and *S. rufipes* (Latreille) (Mygalomorphae: Atypidae) adult females can attain body lengths of 22 and 25 mm, respectively, but their silk, soil and debris tubular retreats extend above ground, often against the side of a tree or other support object (Gertsch and Platnick 1980; Hoffman 2010). Several *P. elegans* females had dried mud plastered on their forewings and body inferring they had been underground in moist, fine-grained soil as in a burrow, not above ground in a silken retreat. Although adult females of the wafer-lid spider genus *Myrmekiaphila* Atkinson (Mygalomorphae:



Figures 3–4. Localities of *Pepsis* spp. 3) *Pepsis elegans*. Females searched for host spiders on the ground, obtained nectar from flowers, and were attracted to artificial light at night near this mesic open woodland, Pryor, Mayes County, Oklahoma. Photograph © Robert Webster. 4) *Pepsis cerberus*, *P. elegans*, *P. novitia*. Geographic location map in Nearctic Region (based on Brimley 1936; Hurd 1952; Krombein 1952; Johnston 2000; Bond and Opell 2002; Vardy 2005; Leavengood et al. 2011; Bond and Godwin 2013; Hamilton et al. 2016; Norden 2017; Godwin and Bond 2021; Durand, pers. comm.; BugGuide.net; flickr.com; iNaturalist.org; gbif.org; SCAN; and specimen records from 36 insect collections as indicated in Materials and Methods). Black lines represent range limits of potential host spider genera. Solid black line represents geographic limit of *Ummidia* (Halonoproctidae) species (Godwin and Bond 2021). Dashed black line represents geographic limit of *Aphonopelma* (Theraphosidae) species (Hamilton et al. 2016). Dotted black line represents geographic limit of *Eucteniza* Ausserer (Euctenizidae) species (Bond and Godwin 2013). Dash-dotted black line represents geographic limit of *Entychides* Simon (Euctenizidae) species (Bond and Opell 2002).

Euctenizidae) are appropriate in size (BL, ~20–24 mm) and excavate tubular, vertical, silk-lined burrows in the ground (Bond and Platnick 2007), their geographic distribution is not sympatric with that of *P. elegans*. *Pepsis elegans* inhabits Kansas, Missouri, southern Illinois, Indiana, Ohio, and Pennsylvania and the southern Atlantic Coastal Plain (Fig. 4; Kurczewski 2023), all areas outside of *Myrmekiaphila* range. In the folding-door spider *Antrodiaetus unicolor* (Hentz) complex (Mygalomorphae: Antrodiaetidae) adult females are 13–22 mm in body length and they excavate tubular, vertical, silk-lined burrows in the ground. Although this complex is partly sympatric with *P. elegans*, its climate and habitat are humid, cool, dense forests of the Appalachian Mountains and Piedmont Region (Coyle 1971), not mesic open woodland.

Materials and Methods

The purpose of this paper is to consolidate, update, and rectify the biological and ecological information for *P. elegans* and *P. cerberus*, demarcate differences in the two species, and investigate reports that females, unlike Nearctic *Pepsis* that provision with tarantulas, capture and provision their nests with trapdoor and related mygalomorph spiders (Ebeling 1975; Gillaspay 1990). This paper describes the prior research on these species that occurred over the past century, emphasizing the shortcomings and potential and manifest errors. It challenges the unsubstantiated host information and introduces new host possibilities. The prospective host information is drawn from a variety of sources. The preparation of this manuscript involved examining 425 recent (2004–2023) natural photographs and associated sparse information from BugGuide.net, iNaturalist.org, flickr.com, gbif.org, and SCAN; questioning individuals who posted online photographs of host-searching females for answers about the habitat and large potential host spiders in the area; and obtaining and interpreting library literature on *P. elegans*, *P. cerberus*, and their potential host spiders, some documents being 105 years old.

For the geographic location map (Fig. 4), natural relief maps of the U. S. and Mexico were combined into a natural relief base map. Hurd's (1952) distribution map for *P. cerberus* and *P. elegans* was overlaid on the base map, size adjusted, and the localities copied. Vardy's (2005) distribution map of Mexican localities was then overlaid on that map and the localities copied. Localities from Brimley (1936), Krombein (1952), Johnston (2000), Leavengood et al. (201), Norden (2017), Durand (pers. comm.), BugGuide.net, flickr.com, iNaturalist.org, gbif.org, and SCAN were added. Specimen records from 36 insect collections and museums were traced into the appropriate locations using translucent state maps size adjusted for accuracy. The potential host spider geographic limit lines were copied from Bond and Opell (2002), Bond and Godwin (2013), Hamilton et al. (2016), and Godwin and Bond (2021) and added individually in layers. The following curators, collection managers, and private collectors provided specimen locality information: Jaz Anderson, Cornell University; Victoria Moseley Bayless and Nathan Lord, Louisiana State University; Christy Bills, Natural History Museum of Utah; David Bowles, University of Arkansas; Sean Brady, Smithsonian Institution; Shawn Clark, Brigham Young University; Anthony Cognato, Michigan State University; Vicki Condo, West Virginia University; Crystal Cooke, Gillette Museum of Arthropod Diversity, Colorado State University; Brenna Decker, Utah State University; Frédéric Durand, Aubièrre, France; Mike Ferro, Clemson University Arthropod Collection; Chris Grinter and Rachel Diaz-Bastin, California Academy of Sciences; Eric Grissell, United States Department of Agriculture at the National Museum of Natural History; Gene Hall, University of Arizona; Alex Harman and Phil Mulder, K. C. Emerson Entomology Museum, Oklahoma State University; Rick Hoebeke, University of Georgia; Brittany Kohler and Lynn Kimsey, R. M. Bohart Museum of Entomology, University of California–Davis; Megan King, Rutgers University Entomological Museum; Lacey Knowles and Taro Eldredge, University of Michigan; Sangmi Lee, Arizona State University; Paul Marek, Virginia Tech University; Luciana Musetti, The Ohio State University; Peter Oboyski, Essig Museum of Entomology, University of California–Berkeley; Rachel Kathryn Osborn, Snow Entomological Museum, University of Kansas; John Oswald and River Martinez, Texas A&M University Insect Collection; Laura Porturas, The Frost Entomological Museum, Pennsylvania State University; Terry Schiefer, Mississippi Entomological Museum, Mississippi State University; Virginia Scott, University of Colorado Museum of Natural History; Kristin Simpson, Enns Entomological Museum, University of Missouri; Elijah Talamas and Natalie McGathey, Florida Department of Agriculture and Consumer Services; Helen Vessels, New Mexico State University Arthropod Collection; Alexander Wild, Larry Clay and Abby Jones, University of Texas Biodiversity

Collections; Kevin Williams, California Department of Food & Agriculture; Douglas Yanega, University of California–Riverside; Vicky Zhuang, University of Texas at El Paso; and Greg Zolnerowich, Kansas State University. The Carnegie Museum and Illinois Natural History Survey did not reply to my request for *Pepsis menechma*, *P. cerberus*, *P. elegans*, and *P. novitia* locality information.

Field Results

Pepsis elegans females were observed host-searching on the ground from 11:43 AM to 6:00 PM EDT and 8:11 AM to 5:56 PM CDT. Females, ~22–25 mm long, searched for spiders on non-manicured, suburban lawns in Durham, Durham County, NC (Coin 2005, 2020, 2022, pers. comm.). Females flew rapidly zigzag, low to the ground, occasionally landed, disappeared briefly in the dense high grasses, resurfaced, and continued searching. “Wandering male trapdoor spiders” [*Ummidia audouini* or *U. carabivora* (Atkinson)] were found in the area (Coin 2004, pers. comm.). In Raleigh, Wake County, NC, females of *P. elegans* flew slowly and sinuously, 30–45 cm above a lawn, landed, and searched through the grasses (Wiggins 2019, pers. comm.). Females near Springfield, Greene County, MO searched through grasses so quickly they were difficult to photograph (Caruthers 2020). Fred A. Coyle (pers. comm.) found 18 *Ummidia* burrows in his lawn which is mowed regularly during the non-winter months and two other burrows at the “edge” of his lawn in Cullowhee, Jackson County, NC. *Pepsis elegans* females were photographed host-searching in plant litter consisting mainly of dried leaves, bark, and twigs that had fallen to the ground (Raney 2014, pers. comm.; Hernandez 2020, pers. comm.; Jackson 2020; Musgnug 2020, pers. comm.; Sommer 2020; Baran 2022; Johnson 2023). Their antennae were held almost straight and angled slightly outward and downward, the tips touching the substrate. The wings laid flat on the dorsum. Females of *P. elegans* at Pryor, Mayes County, OK searched for spiders on the ground in late afternoon in a large garden and adjoining open woodland (Fig. 2, 3; Webster 2015, pers. comm.) and were attracted to artificial light in the evening (11:01 PM–12:26 AM CDT) (Fig. 5; Webster 2014, 2022, pers. comm.). One female at artificial light at night had dried mud from moist, fine-grained soil of an annual flood plain plastered on her pronotum, mesonotum, mesoscutellum, propodeum, tegulae, forewings, mid-femora, mid- and hind tibiae, especially hind tibial teeth, and hind tarsi (Fig. 5; Webster 2014). Other recently emerged (2 June–16 July) females and males with non-frayed wings and older wasps (August) from various locations had dried mud from moist, fine-grained soils on their forewings and body (Anderson 2019; Dunn 2020; Hernandez 2020; King 2020; Belden 2021; Shahan 2022, 2023). Several *Ummidia ?audouini* females on BugGuide.net had moist soil adhering to their abdomen, carapace, and/or legs. Most *Ummidia* burrows are moist to some degree at/near the bottom (Hedin, pers. comm.).

Functional Morphology

An assumption perpetuated online is that *P. elegans* “likely” preys on trapdoor spiders because there are no tarantulas in the eastern U. S. (Ebeling 1975). *Pepsis elegans* has few morphological characteristics typically associated with capturing trapdoor spiders such as thin, flattened, triangular-shaped head; rather sharp vertex crest; enlarged and straight-sided pronotum; short stout forelegs; and swollen fore femora. Morphological characteristics of *P. elegans* females that are relevant in host-searching, capture, and immobilization of the host spider are head “strongly developed” with “thickening” of the “head surface” (Salman 1930); “temple...strongly swollen” (Vardy 2005); and gena and postgenae “strongly rounded” (Salman 1930), thereby increasing the internal area of the head for enlarged mandibular musculature. The large and powerful mandibles are “well developed” with a “strong blunt tooth” and “strong” mandibular muscles, especially the large flexor muscle (Salman 1930). The mandibular articulations are “well developed,” (Salman 1930). Each mandible contains four groups of long sensory setae (Salman 1930).

Females of *P. elegans* have short, wide antenna flagellomeres like trapdoor spider-hunting females of *Calopompilus* Ashmead (Pompilidae: Pepsinae: Pepsini) (Townes 1957; Kurczewski et al. 2023). In *P. elegans* females, flagellomere 1 averages ~3.0 times as long as wide (Kurczewski 2023). In *P. cerberus* females, flagellomere 1 length divided by its width averages ~4.1, a significant difference. In males of *P. elegans*, flagellomere 1 is only ~2.0–2.1 times as long as wide. In *P. cerberus* males, it is ~2.8–3.0 times as long as wide, a significant difference. Could the



Figures 5–6. Habitus photos of *Pepsis elegans* and host. 5) *Pepsis elegans*. Female with dried mud plastered on her pronotum, mesonotum, mesoscutellum, propodeum, tegulae, forewings, mid-femora, mid- and hind tibiae, especially hind tibial teeth, and hind tarsi, Pryor, Mayes County, Oklahoma. Photograph © Robert Webster. 6) *Ummidia audouini*. Adult female immobilized by sting of “big black wasp,” lying dorsal side up on Mississippi River delta soil in Bolivar County, Mississippi. © Blake Layton, Jr.

short, wide flagellomeres of *P. elegans* females, like those of *Calopompilus* females, denote an undiscovered but suspected parasitoid-host relationship between this spider wasp and comparably sized trapdoor spiders such as *Ummidia*? Are the short flagellomeres an adaptation designed to locate the spider's trapdoor underneath plant litter where the burrows are close together and area of searching is minimized? Is the short, stout flagellum a structural adaptation to facilitate host capture in a confined space as in a subterranean burrow (Shimizu, pers. comm.)?

The forewing of *P. elegans* from the eastern US. is ~10–12 % shorter than that of *P. cerberus* from Arizona (Kurczewski 2023). The shorter forewings and hindwings of *P. elegans* may enhance maneuverability inside the spider's narrow burrow. *Pepsis elegans* females had dried mud on their forewings and body, inferring they had been underground in a confined space such as in a burrow. The longer forewings and hindwings of *P. cerberus* may serve an increased aposematic function if such is the purpose of the orange-amber color in an open environment.

The fore tibiae of *P. elegans* are “somewhat enlarged” apically (Salman 1930). The tibiae bear “numerous sagitta-shaped spines” and the tarsi, “long sharp spines” (Salman 1930). There are two “long, curved movable spurs” on the apical inner margins of the middle and hind tibia (Salman 1930). The middle tibial spurs of females are acutely curved near their apices; those of the hind tibia are less curved (Salman 1930; Hurd 1952; Vardy 2005). Are the apically enlarged fore tibiae, numerous tibial and tarsal spines, and apically curved middle and hind tibial spurs used in prey capture and/or, with the aid of the mandibles and head, used to lift and hold the spider's trapdoor open if trapdoor spiders are the host?

The hind tibial teeth of *P. elegans* are small with subtending, sparse, rather straight, posterior angled, thin, short bristles (Hurd 1952; Vardy 2005). In *P. cerberus* females, the hind tibial serrations are slightly larger than those of *P. elegans* females (Kurczewski 2023). The subtending bristles of *P. cerberus* that align the upper surface of the hind tibia are more numerous, longer, stouter, and more posterior-curved than those of *P. elegans*. Hind tibial serrations in species of *Pepsis* and other ancestral Pepsini work in conjunction with the forelegs to remove soil from the burrow during excavation and pack soil in the burrow during closure (Williams 1956; Evans and Yoshimoto 1962; Shimizu and Wahis 2004; Kurczewski and West 2022). *Calopompilus pyrrhomelas* (Walker) has small hind tibial serrations and uses the host mygalomorph spider's burrow as a nest (Kurczewski and West 2022; Kurczewski et al. 2023), implying an evolutionary reduction in serration size in connection with limited usage. Could the slightly smaller hind tibial serrations and sparser, shorter, thinner, straighter subtending bristles in *P. elegans* imply similar reduced usage, e. g., appropriating the burrow of a cork-lid trapdoor spider for use as a nest instead of having to excavate a burrow from the ground surface? Such elimination or reduction in burrow excavation might explain the secretive habits of *P. elegans* and the absence of host spider and nesting behavior information.

Discussion

Rau and Rau (1918) reported *P. elegans* [as *P. dubitata*; det. S. A. Rohwer] dragging backwards a “huge spider,” “probably five times as heavy as herself,” by its “head” across sticks, stones, vegetation, and logs for more than “100 yards” in St. Louis County, MO, taking longer than an hour before the wasp with spider in tow disappeared into a “rodent hole.” Such a lengthy and time-consuming prey transport, traveling from a “rodent...tunnel” where the wasp captured the spider to a “rodent hole” “more than 100 yards” away (Rau and Rau 1918), would seem to rule out trapdoor spider as host because trapdoor spider-hunting spider wasps usually use the spider's burrow as a nest (Kurczewski and West 2022; Kurczewski et al. 2023). Rau and Rau's (1918) description of prey transport is identical to prey transport reports for *Entypus fulvicornis* presented by Kurczewski and Edwards (2012), Kurczewski et al. (2017, 2020), Adams (2020), and Van Valkenburgh (pers. comm.). Females of *E. fulvicornis* grasp the host spider with their mandibles by a pedipalp or, less often, chelicera and drag it backwards across the ground, dorsal side upward, for some distance. *Entypus fulvicornis* was misidentified many times as *Pepsis elegans* and vice versa on iNaturalist.org and BugGuide.net due to similarity in size and color. *Entypus fulvicornis* females are approximately the same size (BL, 15–27 mm; Kurczewski, pers. obs.) as females of *P. elegans* (BL, 16–28 mm; Vardy 2005). Both species are black with dark infusate wings and yellowish orange to orange flagellomeres (Townes 1957; Kurczewski and West 2023). Sandoval (2019) erroneously identified a *Pepsis mildei* (dark-winged variant) female with an immobilized large burrowing tarantula, *Tliltocatl vagans* (Ausserer) (Theraphosidae),

from Campeche State, Mexico, as being *P. menechma* [= *P. elegans*] (Kurczewski et al. 2020). *Pepsis mildei* (dark-winged variant), although similar in body, wing, and antenna color, is significantly larger (BL, 23–43 mm; Vardy 2005) than *P. elegans* and has noticeably longer flagellomeres.

Rau and Rau (1918) never found the immobilized spider when they excavated the “rodent hole” down which the wasp with spider in tow disappeared. If the wasp was *Entypus fulvicornis*, the spider may have been a large wolf spider such as *Hogna carolinensis* (Walckenaer), *H. baltimoriana* (Keyserling), *Tigrosa aspersa* (Hentz), or *T. georgicola* (Walckenaer), the largest lycosids in the region. These wolf spiders live underground in soil cavities or excavate and inhabit burrows as deep as 20–30 cm, often with a turret around the entrance that consists of twigs, grasses, pebbles, and mud (Kaston 1948, 1978; Kurczewski, pers. obs.). Rau and Rau (1918) certainly would have mentioned the spider as being an easily recognizable tarantula if it had been one. Tarantulas do not occur as far north as St. Louis County, MO (Hamilton et al. 2016). If the wasp was *Pepsis elegans*, several trapdoor-type spider families and genera of wasp size can be eliminated as potential host spiders because they do not occur in the region: Antrodiaetidae (Coyle 1971); *Eucteniza* Ausserer (Euctenizidae) (Bond and Godwin 2013); and *Myrmekiaphila* Atkinson (Euctenizidae) (Bond and Platnick 2007). The only potential host trapdoor spider of suitable size (BL, ~25–28 mm) and ecology in the St. Louis County, MO area is *Ummidia audouini* (Godwin and Bond 2021; Godwin, pers. comm.). As indicated above, *P. elegans* females may be able to chew through the trapdoor with their stout mandibles and seize or entice the spider from its burrow entrance, as in some other spider wasp species (Kurczewski and West 2022).

Although Rau and Rau (1918) searched at length underground, they were unable to find the wasp or her nest-cell after she entered the “rodent hole” with her host spider. Yet Hurd (1952), in his *Revision of the Nearctic species of the pompilid genus Pepsis*, placed a St. Louis County, MO locality dot on his *P. elegans* distribution map and cited Rau and Rau’s (1918) observation of this species. Sievert Allen Rohwer, Agricultural Research Service, U. S. Department of Agriculture, Washington, DC evidently identified “*Pepsis dubitata*” sight unseen in which case the wasp could have been *P. elegans* or *Entypus fulvicornis*, a species similar in size and color and for which the description of its host spider transport is identical to Rau and Rau’s (1918) description. There are early 1900s specimens of *E. fulvicornis* from St. Louis County, MO in the Smithsonian Institution insect collection (Townes 1957). Karl V. Krombein, who worked with Rohwer in the Hymenoptera Section at the U. S. National Museum, intimated to me (1962, pers. comm.) that Rohwer sometimes made mistakes in identification that he (Krombein) would correct. Since Rohwer’s collection is at the Smithsonian Institution, I emailed their Curator of Hymenoptera, Sean Brady, regarding Rau and Rau’s (1918) wasp. Brady (pers. comm.) informed me that there is no specimen of *P. menechma*, *P. elegans* or *P. dubitata* from St. Louis County, MO in the Smithsonian insect collection, confirming Rau and Rau’s (1918) admission that they never recovered the wasp and keeping its identity questionable.

Layton (2021, pers. comm.) described an unidentified, big black wasp capturing and immobilizing a large black spider on Mississippi River delta soil in Bolivar County, MS. After the spider stopped struggling, the wasp grasped its “fangs” with her mandibles and dragged it backwards a short distance into its “silk-lined” burrow. The immobile spider was unearthed from the burrow the next day and identified as *Ummidia audouini*, adult female (Fig. 6). There are few large (BL, 25–28 mm), predominantly black spider wasps with dark wings in Mississippi that are sizeable and stout enough to capture and immobilize *U. audouini*, *P. elegans* being the largest and most likely one. Other comparatively large, predominantly black pompilid species in the area are highly selective of their host spider, capturing large Lycosidae (wolf spiders), Pisauridae (fishing spiders), or Araneidae (orb-weaving spiders) (Townes 1957; Kurczewski and Edwards 2012; Kurczewski et al. 2017, 2020, 2022a, b), but not cork-lid trapdoor spiders (Halonoproctidae).

Punzo (2005) studied the “natural history, ecology, and behavior of *P. cerberus*...” in Big Bend National Park, Brewster County, southwestern Texas. Punzo evidently identified the wasp himself as he did not mention a hymenopterist in the paper. There are four comparatively small, bluish-bodied, orange-amber-black-fringed-winged *Pepsis* species females with black antennae in Brewster County, TX: *P. cerberus* (BL, 16–28 mm; Vardy 2005); *P. basifusca* (BL, 14–27 mm; Vardy 2005); *P. chrysothemis* (BL, 20–30 mm; Vardy 2000); and *P. pallidolimbata* Lucas (BL, 17–31 mm; Vardy 2000). Their likeness in size and color would make species identification extremely difficult for a non-hymenopterist such as Punzo. Punzo’s (1999–2003) study was completed before the publication of Vardy’s (2005) *Pepsis menechma* species-group, so he would not have had access to Vardy’s updated description and key to species. Punzo (2005) identified the host tarantula as being *Aphonopelma steindachneri*

(Ausserer) (Theraphosidae), but this species is restricted to California and Baja California Norte and does not occur in Texas (Hamilton et al. 2016; Sherwood and Gabriel 2020). The host tarantulas in Punzo's (2005) study were probably *A. gabeli* (Adult BL, ~44–64 mm) and/or *A. hentzi* (Adult BL, ~39–67 mm) (Hamilton et al. 2016; Sherwood and Gabriel 2020), both large species. Punzo (2005) stated that *P. cerberus* did not selectively capture large tarantulas, yet he reported host tarantula carapace widths of 14–20 mm (17–24 mm in carapace length minus the chelicerae) for this species which translates to 42–60 mm in BL (West, pers. comm.). *Pepsis cerberus* females, if correctly identified, were as small as “14.98 mm” and averaged only “21.9 mm” in body length (Punzo 2005), making it highly improbable that such comparatively small wasps attacked tarantulas twice or more their body length and 10 or more times their weight. Small *Pepsis* species are “unwilling, if not unable” to attack large tarantulas (Williams 1956). *Pepsis* fatalities frequently occurred when smaller wasps attempted to subdue larger tarantulas (Williams 1956). *Pepsis mexicana* (BL, 16–34 mm; Vardy 2000), *P. pallidolimbata*, *P. chrysothemis*, and *P. ruficornis* (BL, 17–34 mm; Vardy 2005), all comparatively small species of *Pepsis*, when hunting, showed “little interest” in tarantulas that were larger than themselves (Williams 1956; Kurczewski et al. 2013, 2020). After analyzing Punzo's (2005) data, it is apparent that he misidentified the host spider, possibly misidentified the spider wasp, and incompatibly associated the spider wasp-host spider size difference. Punzo (2005) did not provide any photographs or diagrams or describe the capture of the host spider.

Gillaspy (1990) observed *Pepsis novitia* females “searching actively over well-watered lawns” in Kingsville, Kleberg County, TX. The objective of their search “appeared to be” the southwestern wafer-lid spider *Eucteniza relata* (Bond and Godwin 2013), common in residential lawns in southern Texas. Gillasp (1990) believed this spider was being captured by *P. novitia* and “entombed” in their own burrows. The geographic location maps of *P. novitia* and *E. relata* are sympatric in southern Texas and northeastern Mexico (Fig. 4; Bond and Godwin 2013). Gillasp (1990) observed females of *P. cerberus* similarly searching for spiders on dry lawns in Alice, Jim Wells County, TX, introducing the likelihood of this species also selectively capturing *E. relata* and depositing the immobilized spider in its own burrow. *Eucteniza relata* females have body lengths of up to 27.5 mm and would provide sufficient food for the developing larva of either wasp taxon. The burrow of *E. relata* is an unbranched vertical tube in the ground, 7–25 cm deep, lined with silk (Bond and Opell 2002). It has a hinged, silk and soil, solid wafer-lid (Bond and Godwin 2013). If this spider wasp-host spider parasitoid relationship is correct, then Punzo's (2005) paper on comparatively small *P. cerberus* provisioning with much larger tarantulas is probably fabricated! Observations of species in the *Pepsis menechma* species-group in Argentina, Bolivia, and Brazil reveal females selectively capturing and depositing immobilized trapdoor spiders in their own burrows (Jiménez 2014; Domingues 2017; Paoloni 2017; Kurczewski et al. In Prep.).

Acknowledgments

Matthias Buck, Royal Alberta Museum, Edmonton, AB, Canada; Sarah C. Crews, California Academy of Sciences, San Francisco, CA; Akira Shimizu, Tokyo Metropolitan University, Tokyo, Japan; and Chris Starr, University of West Indies, St. Augustine, Trinidad and Tobago reviewed early- and late-stage versions of the manuscript. Buck found several records of *Pepsis elegans* misidentified as *Entypus fulvicornis* on iNaturalist.org. Chris A. Hamilton, University of Idaho, and Danniella Sherwood, Arachnology Research Association, sent information about the species of *Aphonopelma* in Brewster County, TX and corrected Punzo's misidentification of *A. steindachneri*. Rick C. West, Sooke, BC, Canada, calculated *Aphonopelma* body lengths from carapace widths and lengths. Patrick Coin, Durham Technical Community College; LeRoy Elliott, Columbia, MO; John Hartgerink, Baton Rouge, LA; Blake Layton, Jr., Mississippi State University; Kristin Ann Musgnug, University of Arkansas; Donald Newton, North Little Rock, AR; Herschel Raney, Conway, AR; Robert Webster, Pryor, OK; and Aubrey Wiggins, North Carolina Department of Natural and Cultural Resources, sent photographs and/or answered questions about host-searching females of *P. elegans* and potential host spiders at their respective localities. Jose Hernandez, Tulsa, OK sent 24 unposted photographs of *P. elegans* females hunting in ground litter in Tulsa County, OK and Harris County, TX. Cody Van Valkenburgh forwarded his video of *Entypus fulvicornis* dragging backwards an immobilized *Rabidosa rabida* (Walckenaer). Akira Shimizu answered questions about trapdoor spider hunting spider wasp antenna flagellum sensory receptors, flagellum size, and head morphology. Rebecca L. Godwin, Piedmont

University; Richard Bradley, The Ohio State University; Fred A. Coyle, Western Carolina University; Marshal Hedin, San Diego State University; William A. Shear, Hampden-Sydney College; and Dirk J. Stevenson, Altamaha Environmental Consulting, LLC, Hinesville, GA answered questions about *Ummidia* habitat and burrows. James P. Pitts, Utah State University, sent email copies of Hurd (1952) and Williams (1956). Brenna Decker, Utah State University, forwarded macrophotographs of female *Pepsis elegans* and *P. cerberus*. Brittany Kohler, University of California–Davis, sent macrophotographs of male and female *P. novitia*. Thomas Shahan, Tulsa, OK, provided his photograph of *P. elegans* as Figure 1. Robert Webster’s photographs of *P. elegans* females and habitat from Pryor, Mayes County, OK are Figures 2, 3, and 5. Webster furnished valuable information about the wasp’s habitat. Frank Kurczewski and Lukas Friedrich, Atlanta, GA designed Figure 4. Blake Layton, Jr.’s photograph of an immobilized *Ummidia audouini* is Figure 6.

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Received April 27, 2023; accepted September 20, 2023.

Review editor Davide Dal Pos.

