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The *Pepsis menechma* Lepeletier  
(Hymenoptera: Pompilidae: Pepsinae) taxonomic  
and nomenclatural problem

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# The *Pepsis menechma* Lepeletier (Hymenoptera: Pompilidae: Pepsinae) taxonomic and nomenclatural problem

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**Abstract.** Hurd (1952), in revising the Nearctic species of *Pepsis* Fabricius, separated *P. cerberus* Lucas from *P. elegans* Lepeletier based on external morphology and geography. Vardy (2005), in his Western Hemisphere *Pepsis* revision, combined these taxa and several Neotropical color and structural variants in a broad definition of *P. menechma* Lepeletier extending across ~11,250 km and two continents. Vardy (2005) synonymized the familiar and well-documented, 160-year-old *P. elegans* under *P. menechma* probably because it appeared several pages later in Lepeletier's (1845) *Histoire Naturelle des Insectes. Hyménoptères*. Vardy's (2005) interpretation of *Pepsis menechma* as a viable species presents a taxonomic and nomenclatural problem. He violated the principle of nomenclatural stability in synonymizing the widely and established species names *P. elegans* and *P. cerberus* under *P. menechma*, a name that had not been used for 160 years. Recent discoveries warrant a re-evaluation of the problematic taxonomy of this species complex. Morphological and ecological divergence of *P. elegans* and its sister taxon, *P. cerberus*, combined with their narrow sympatric distribution justifies species recognition. Hurd's (1952) two species concept for *P. elegans* and *P. cerberus* is more practicable, useful, and nomenclaturally acceptable than Vardy's (2005) *P. menechma*. *Pepsis cerberus* Lucas and *P. elegans* Lepeletier should be reinstated as species and removed from the synonymy of *Pepsis menechma* Lepeletier.

**Key words.** *Pepsis cerberus*, *Pepsis elegans*, *Pepsis novitia*, *Pepsis menechma* species-group, hybridization, introgression.

**ZooBank registration.** urn:lsid:zoobank.org:pub:F59B3131-74DE-4704-9936-337E380BF3E0

## Introduction

Species of the tarantula hawk-wasp genus *Pepsis* Fabricius 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 (Hurd 1952; Vardy 2000). Fifteen *Pepsis* species inhabit the Nearctic Region, nearly all in the southwestern U.S. and Mexico (Hurd 1952; Vardy 2000, 2002, 2005). Salman (1930) and Hurd (1952) separated *P. elegans* Lepeletier and *P. cerberus* Lucas females from other Nearctic *Pepsis* females based on the middle tibial spurs being acutely curved near their apices. *Pepsis elegans* is the only *Pepsis* that lives east of the Mississippi River, mainly in the southern United States (Fig. 1, 10). It is a relatively large, attractive, and historically popular spider wasp (Pompilidae). When Vardy (2005) re-introduced *Pepsis menechma* Lepeletier, a species name that few could spell and fewer could pronounce, *P. elegans* and the closely related *P. cerberus* (Fig. 2) became obsolete junior synonyms. Vardy (2005) likely chose *Pepsis menechma* over *P. elegans* because it appeared several pages earlier in Lepeletier's (1845) *Histoire Naturelle des Insectes. Hyménoptères*. Vardy (2005) ignored the prevailing usage and clearly violated articles 23.2, 23.3 and 23.9.1 of the ICZN (1999) by synonymizing *P. elegans* under *P. menechma*. *Pepsis menechma* had been absent from the literature for 160 years while *P. elegans* was cited consistently in the Hymenoptera literature since 1845 including one large paper on its distinct external morphology (Salman 1929). Both *P. cerberus* and *P. elegans* are listed as separate species in Krombein et al.'s (1979) Hymenoptera catalog. There is no mention of *P. menechma*. *Pepsis elegans* and *P. cerberus* occur together at several localities in a narrow sympatric zone in south-central Texas (Fig. 10), but are otherwise geographically, ecologically, morphologically, and potentially host spider distinct (Kurczewski, In Rev.). Vardy's (2005) *Pepsis menechma* extends across ~11,250 km and two continents—an extraordinarily vast range for a ground-nesting



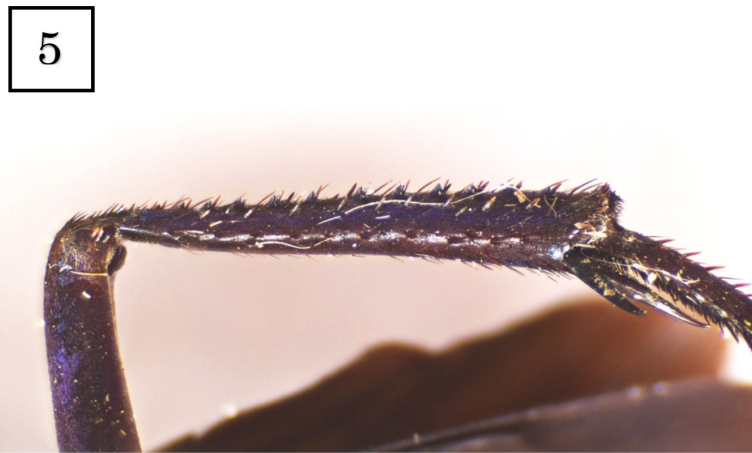
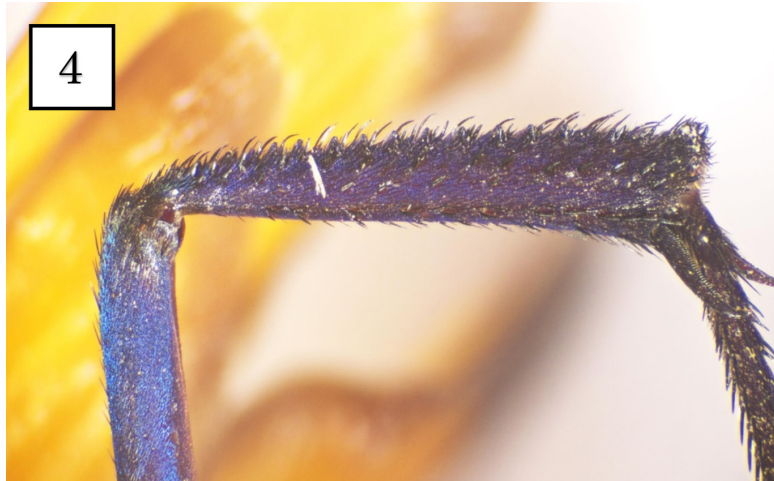
**Figures 1–3.** *Pepsis* spp., female habitus. 1) *Pepsis elegans* female habitus, Atlanta, Fulton County, Georgia. Photograph © Brenna Decker. 2) *Pepsis cerberus* female habitus, Florida Canyon, Pima County, Arizona. Photograph © Chris Grinter. 3) *Pepsis novitia* female habitus, Tampico, Tamaulipas State, Mexico. Photograph © Brittany Kohler.

spider wasp. Vardy (2005) defended his taxonomic interpretation of *P. menechma* stating it “is one of the most structurally variable species in the genus.” Is Vardy (2005) correct in his broad definition of *P. menechma* based on its vast geographic distribution and resultant synonymy of several distinct color and structural variants or are his variants closely related species in a limited species complex? This paper examines, analyzes, discusses, and critiques Vardy’s (2005) taxonomic definition of *Pepsis menechma* and the current synonymic statuses of *P. elegans*, *P. cerberus*, and *P. novitia* Banks. It demarcates the morphological, ecological, distributional, and potential host spider differences of these taxa and describes their previous taxonomic histories.

## Materials and Methods

Preparation of this manuscript involved obtaining and interpreting literature on the specific taxa, some documents being over 100 years old; requesting locality, size, color, and geographic distribution information from curators and collection managers of 36 college and university insect collections and museums; and pinpointing and measuring diagnostic external morphological characteristics of the males and, especially, females of the taxa using macrophotographs. Females of three taxa from the *Pepsis menechma* species-group, *P. elegans*, *P. cerberus*, and *P. novitia* were selected for examination of forewing length, flagellomere length and width, and hind tibial armature. The forewings of the three taxa were measured for length. The length of flagellomere 1 was measured and that number was divided by its width measurement at the middle of the segment. The hind tibial serrations and subtending bristles were examined, measured, counted, and photographed.

For construction of the geographic location map (Fig. 10), 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. (2011), Norden (2017), Durand (pers. comm.), BugGuide.net, flickr.com, iNaturalist.org, gbif.org, and SCAN were added. Specimen locality records from 36 insect collections and museums were copied onto their appropriate locations using translucent state maps size adjusted for accuracy. The potential host spider geographic limit lines were traced and applied individually from Bond and Opell (2002), Bond and Godwin (2013), Hamilton et al. (2016), and Godwin and Bond (2021). The following curators, collection managers, and private collectors who provided specimen locality information were 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, Aubière, 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.



**Figures 4–6.** *Pepsis* spp., female upper surface of hind tibia. **4)** *Pepsis cerberus* female upper surface of hind tibia with moderately small conical serrations and numerous, long, stout, posterior-curved bristles, Box Canyon, Pima County, Arizona. Photograph © Brenna Decker. **5)** *Pepsis elegans* female upper surface of hind tibia with small conical serrations and sparser, shorter, thinner, straighter bristles, Biloxi, Harrison County, Mississippi. Photograph © Brenna Decker. **6)** *Pepsis novitia* female upper surface of hind tibia with moderately small conical serrations and numerous long, stout, posterior-curved bristles, Tampico, Tamaulipas State, Mexico. Photograph © Brittany Kohler.

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.

## Results

*Pepsis elegans* and *P. cerberus* are comparatively small Nearctic “tarantula hawk-wasps” with females averaging ~22–25 mm in body length (Punzo 2005; Vardy 2005; Decker pers. comm.). 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 iridescent bluish or violet reflection, have infusate violaceous wings, and yellowish orange to orange flagellomeres (Fig. 1; Table 1). Females of *P. cerberus* have a refulgent bluish body, orange-amber dark base and dark-fringed wings, and black antennae (Fig. 2; Table 1). The forewing of *P. cerberus* females from Arizona is ~10–12 % longer than that of *P. elegans* females from the eastern U. S. (Fig. 1, 2). There are differences in the shape of the male genitalia and subgenital plate of the two taxa (Salman 1930; Hurd 1952). The inner hind tibial spur is longer and straighter in *P. elegans* (Salman 1930; Vardy 2005; Fig. 4, 5; Table 1). The upper surface of the hind tibia of *P. cerberus* females is aligned with moderately small conical serrations and many long, stout, posterior-curved, subtending bristles (Salman 1930; Hurd 1952; Vardy 2005; Fig. 4; Table 1). 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; Fig. 5; Table 1). *Pepsis elegans* females have a shorter flagellum, much shorter flagellomere 1, and wider flagellomere 1 compared to *P. cerberus* females (Fig. 7, 8; Table 1). Flagellomere 1 of *P. elegans* females averages ~3.0 times as long as wide (Fig. 7). In *P. cerberus* females, flagellomere 1 length divided by its width averages ~4.1 (Fig. 8), 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.

*Pepsis elegans* and *P. cerberus* occupy environments with different climate, habitat, and potential host spiders. *Pepsis elegans* inhabits the moist eastern half of the U. S. where, except in East Baton Rouge Parish, LA (Hamilton et al. 2016), there are no tarantulas (Theraphosidae: *Aphonopelma*) (Fig. 10). The geographic distribution of *P. elegans* coincides with “Eastern Temperate Forests” on a Level I map of the “Ecological Regions of North America,” except where the wasp is absent from the northeastern U. S. (Commission for Environmental Cooperation Working Group 2006). *Pepsis cerberus* occurs in the more arid western half of the U. S. and Mexico where tarantulas abound (Fig. 10). The range in average annual precipitation (inches) for *P. elegans* is 36.3 (Austin, TX)–64.9 (Biloxi, MS), and for *P. cerberus*, 6.7 (LaPaz, MX)–39.5 (Bryan-College Station, TX). The “dividing line” between the moist eastern and more arid western U. S. is between the 97th and 98th W Meridians. *Pepsis elegans* ranges from the 98th W Meridian in Texas, Oklahoma, and Kansas eastward to central Ohio, southern Pennsylvania, and southward to peninsular Florida and the Gulf of Mexico, with an extralimital male specimen from southern Michigan (Hurd 1952; Vardy 2005; Leavengood et al. 2011; Fig. 10; Table 1). *Pepsis cerberus* is found from the 97th W Meridian westward to Arizona and southward through Mexico into Central America (Hurd 1952; Vardy 2005; Fig. 10; Table 1). There are no or few records of *P. cerberus* from southern California, Nevada, Utah, Colorado, Baja California Norte, central-eastern New Mexico, and northcentral Mexico where it is exceptionally hot and arid with little precipitation and sparse vegetation (Fig. 10). These regions are mapped as “North American Deserts” on a Level I map of “Ecological Regions of North America” (Commission for Environmental Cooperation Working Group 2006). The absence of *P. cerberus* from deserts infers that it and its host spiders live in less level, slightly cooler, and wetter climates with more mesic habitat. For example, southeastern Arizona, where *P. cerberus* is abundant (Fig. 10), has highlands that support Sierra Madre fauna and flora consisting of grassland and woodland (Lightfoot, pers. comm.).

A morphologically intermediate form, *P. novitia*, occurs where *P. elegans* and *P. cerberus* overlap in south-central Texas (Hurd 1952; Vardy 2005; Fig. 3, 6, 9, 10). Hurd (1952) believed that *P. novitia* resulted from “zone hybridization” between the two species. *Pepsis novitia* males have 4–5 orange apical flagellomeres and dark infusate to amber dark base and dark-fringed forewings. The females have 2–6 orange apical flagellomeres and orange to amber dark base and dark-fringed forewings (Fig. 3, 9). The orange flagellomeres extend proximally from the antenna apex in both sexes (Vardy 2005; Fig. 9). The forewing length of *P. novitia* females is intermediate between

**Table 1.** Morphological, geographical, ecological, and behavioral characteristics of *Pepsis elegans* Lepeletier and *P. cerberus* Lucas (Hurd 1952; Vardy 2005).

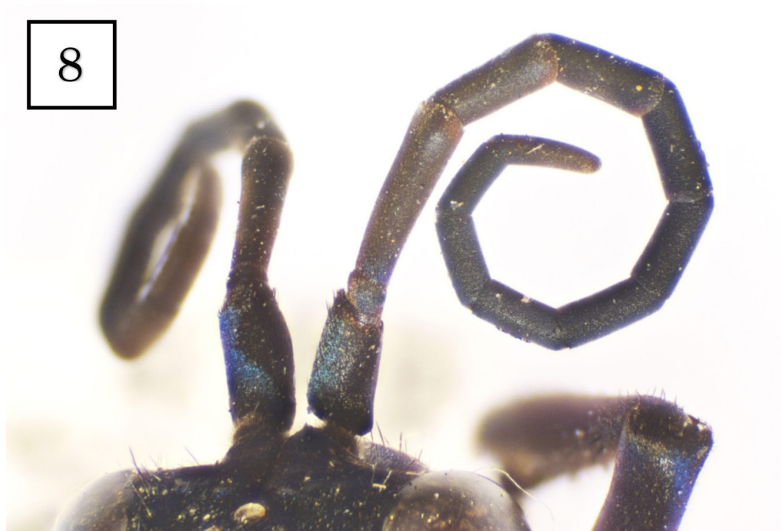
Characteristic	<i>Pepsis elegans</i>	<i>Pepsis cerberus</i>
Wasp color	Black body, orange flagellomeres, dark violaceous wings	Bright blue body, black antennae, orange wings
Antenna dimensions	Shorter, wider flagellomeres	Longer, narrower flagellar segments
Hind tibial armature	Small conical serrations	Moderately small conical serrations
Hind tibial setation	Sparser, shorter, thinner, straighter bristles	More numerous, longer, stouter, posterior-curved bristles
Hind tibial spurs	Longer and straighter but slightly curved apically	Slightly shorter and more curved apically
Genitalic volsella	Angular terminus with subapical projection	Hemispherical terminus
Geographic distribution	SE U.S. E of 98th W Meridian	SW U.S. W of 97th W Meridian to Central America
Habitat	Mesic open woodland	Semi-arid, sparse scrubland/grassland/woodland
Host spider	?cork-lid trapdoor spider ( <i>Ummidia</i> )	?wafer-lid trapdoor spider ( <i>Eucteniza</i> )

those of *P. cerberus* and *P. elegans* females and is ~2–7% longer than the forewing length of *P. elegans* females (Fig. 1, 3). Antenna flagellomere 1 length divided by its width in males and females of *P. novitia* is intermediate between *P. elegans* and *P. cerberus* averaging ~2.5–2.6 and ~3.5–3.8, respectively (Fig. 9). Flagellomeres are slightly shorter in *P. novitia* than in *P. cerberus* (Fig. 8, 9). *Pepsis novitia* female hind tibial serrations are moderately small as in *P. cerberus* (Fig. 4, 6). The subtending bristles are numerous, long, stout, and strongly posterior-curved as in *P. cerberus* (Fig. 4, 6). The male genitalia and subgenital plate of *P. novitia* are intermediate between those of *P. cerberus* and *P. elegans* (Hurd 1952). *Pepsis novitia* resembles *P. cerberus* in size and color (Fig. 2, 3) and may differ slightly because of the more easterly, moister environment in which it occurs (Fig. 10). The range in average annual precipitation (inches) for *P. novitia* is 21.2 (Roma, TX)–44.7 (Tampico, MX) with localities situated in more mesic habitat. Gillaspay (1990) found *P. novitia* seasonally abundant on “well-watered lawns” in residential areas of south-central Texas and in “moist woods” of coastal Veracruz, Mexico, whereas he observed *P. cerberus* commonly on “dry lawns” farther west in south-central Texas. He categorized *P. novitia* as a “lawn” inhabitant and *P. cerberus* as a “country” inhabitant. *Pepsis novitia* and *P. cerberus* range southward into Mexico minus *P. elegans* (Fig. 10). Of 172 specimens from southern Texas and Mexico in the University of Texas Biodiversity Collections labelled “*Pepsis menechma*,” 86 (50.0%) have orange apical flagellomeres (*P. novitia*) and 86 (50.0%) have black antennae (*P. cerberus*). Ninety-seven of the specimens (56.4%) are from Kingsville, Kleberg County, TX (Latitude 27.51 N; Longitude 97.86 W) and represent biannual spring and fall emergence.

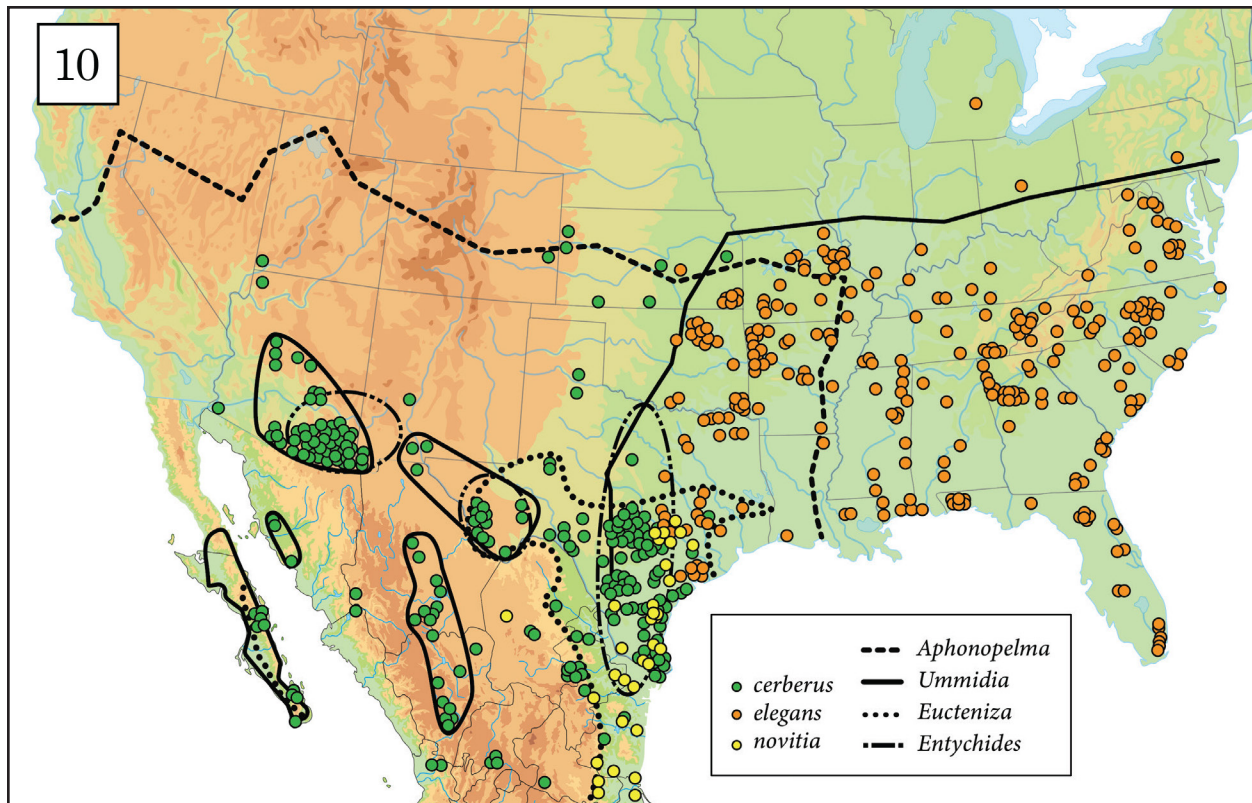
## Discussion

Hurd (1952) believed that *P. elegans* and *P. cerberus* are “sufficiently isolated reproductively” as separate populations that have “attained the...level of species.” Their “divarication” is well founded in external morphology, body and wing color, geographic distribution, habitat, and potential host spider (Fig. 1, 2, 10; Table 1). *Pepsis elegans* and *P. cerberus* occur together at several localities in a narrow sympatric zone in south-central Texas (Fig. 10), but are otherwise geographically, ecologically, morphologically, and potentially host spider distinct (Kurczewski, In





**Figures 7–9.** *Pepsis* spp., female antennae. 7) *Pepsis elegans* female antennae with short, wide, yellowish orange flagellomeres, Biloxi, Harrison County, Mississippi. Photograph © Brenna Decker. 8) *Pepsis cerberus* female antennae with longer, narrower, black flagellomeres, Box Canyon, Pima County, Arizona. Photograph © Brenna Decker. 9) *Pepsis novitia* female antennae with intermediate length, orange apical and brown proximal flagellomeres, Tampico, Tamaulipas State, Mexico. Photograph © Brittany Kohler.



**Figure 10.** Geographic location map for *Pepsis cerberus*, *P. elegans*, and *P. novitia* in the 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 listed 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* (Euctenizidae) species (Bond and Godwin 2013). Dash-dotted black line represents geographic limit of *Entychides* Simon (Euctenizidae) species (Bond and Opell 2002).

Rev.). *Pepsis novitia*, a possible hybrid taxon, and *P. cerberus* range southward into Mexico while *P. elegans* does not. Until an intergrading series is demonstrated between *P. elegans* and *P. cerberus*, it is best to regard them as separate species (Hurd 1952). Vardy (2005) disagreed with Hurd's (1952) assessment and synonymized *P. elegans*, *P. cerberus*, *P. novitia*, and several other Neotropical color and structural variants under *P. menechma*. Some of the variants are probably the result of hybridization with repeated backcrossing and introgression while others may be closely related species in a species complex. Vardy (2005) did not find "constant specific differences" in structure or color in his broad interpretation of intraspecific variation that extended across ~11,250 km and two continents, although *P. elegans* is distinct morphologically, geographically, ecologically, and in potential host specificity (Kurczewski, In Rev.). Vardy (2005) failed to consider the potential difference in *P. cerberus* and *P. elegans* host spiders and ecology based on the vast contrast in their Level I Ecoregions (Commission for Environmental Cooperation Working Group 2006).

*Pepsis menechma*, as a species name, laid dormant in the scientific literature for 160 years. It was resurrected for use by Vardy (2005) probably because it appeared as a specific name several pages before *Pepsis elegans* in Lepeletier's (1845) *Histoire Naturelle des Insectes. Hyménoptères*. Vardy (2005) admitted that the identity of *P. menechma* "conforms with the current interpretation of *P. elegans*," a long-standing, well-known, and well-documented species. *Pepsis elegans* was the familiar name cited and referenced routinely from 1845 to 2005 in

catalogs, monographs, revisions, periodicals, faunal lists, and theses. *Pepsis elegans* was the species selected for the first detailed morphological examination of a Nearctic spider wasp (Pompilidae) because of its size, availability, and suitability (Salman 1929, 1930). Both *P. cerberus* and *P. elegans* are listed as distinct species in Krombein et al's (1979) Hymenoptera Catalog. Vardy (2005) totally ignored the prevailing usage and clearly violated articles 23.2, 23.3 and 23.9.1 of the ICZN (1999) by synonymizing *P. elegans* and *P. cerberus* under *P. menechma*.

Hurd's (1952) two species concept for *P. elegans* and *P. cerberus* is more practicable and useful than Vardy's (2005) highly variable, single species (*P. menechma*) interpretation. Difference in body color, wing color and size, antenna flagellum color, length and width, female hind tibial armature, and male genitalia and subgenital plate of *P. elegans* and *P. cerberus* is the result of allopatric evolution driven in part by climate, habitat, host spider type, and nesting behavior (Table 1). Several Nearctic species of *Pepsis*, *Hemipepsis* Dahlbom, *Entypus* Dahlbom, and *Cryptocheilus* Panzer demonstrate geographic variation in wing color from West to East in the U. S. (Hurd 1952; Townes 1957; Vardy 2000, 2002, 2005), but these species do not show analogous variation trans-country in other morphological structures such as hind tibial armature and flagellum color and size. Difference in male genitalia, subgenital plate, wing size, antenna flagellomere length and width, and female hind tibial armature as a combination in *P. elegans* and *P. cerberus* infers that their lineages separated earlier than those of Pepsini species that demonstrate only geographic variation in wing color. Given this new evidence, *Pepsis cerberus* Lucas and *P. elegans* Lepeletier should be reinstated as species and removed from the synonymy of *Pepsis menechma* Lepeletier. *Pepsis novitia* Banks may be a mesic variant of *P. cerberus* with *P. elegans* introgressive morphological characteristics in southern Texas, Mexico, and Central America, far south of the *P. elegans* southeastern U. S. geographic range.

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