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Morphometric analysis and taxonomic re-evaluation of *Pepsis cerberus* Lucas and *P. elegans* Lepeletier (Hymenoptera: Pompilidae: Pepsinae: Pepsini)

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Abstract. Hurd (1952) separated *Pepsis cerberus* Lucas from *P. elegans* Lepeletier (Hymenoptera: Pompilidae: Pepsinae: Pepsini) based on external morphology and biogeography. Vardy (2005) synonymized the familiar and historically well-documented *P. cerberus* and *P. elegans*, combining these Nearctic taxa with several Neotropical variants in an extremely broad definition of *P. menechma* Lepeletier. In doing so, Vardy (2005) breached the principle of nomenclatural stability. He ignored the prevailing usage and clearly violated articles 23.2, 23.3 and 23.9.1.2 of the ICZN (1999). Morphological differences, ecological divergence, and narrow sympatric geographic distribution of *P. cerberus* and *P. elegans* contradict Vardy (2005) and justify full species status (Kurczewski 2023a). Furthermore, we propose the removal of the two species from the *P. menechma* list of synonyms and recommend full species reinstatement as *Pepsis cerberus*, **restored status** and *Pepsis elegans*, **restored status**. *Pepsis menechma* becomes a senior synonym of *P. elegans*. Morphometric re-examination and statistical analysis of *P. cerberus* and *P. elegans* structural features strongly support their reinstatement. Quantitative measurement of 10 parasitoid-related morphological characteristics of the females revealed the two species differ significantly in frons width/head width, head length/head width, vertex length/head width, vertex length/head length, flagellomere 1 length/flagellomere 1 width, forewing length/mesosoma width, and hind tibial inner spur length/hind basitarsus length. *Pepsis cerberus* and *P. elegans* females are structurally and statistically similar in gena-postgena corner radius, fore femur width/mesosoma width, and number of hind tibial serrations.

Key words. Parasitoid-related morphological characteristics, 2-sample t-test, Mann-Whitley test, restored species status, *Eucteniza relata*, *Ummidia audouini*.

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Introduction

The impressively large and colorful species of the tarantula hawk-wasp genus *Pepsis* Fabricius (Hymenoptera: Pompilidae: Pepsinae: Pepsini) 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). Hurd (1952) separated *P. cerberus* Lucas, 1895 (Fig. 1) and *P. elegans* Lepeletier, 1845 (Fig. 2) females from other Nearctic *Pepsis* females based on the middle [and hind] tibial spurs being acutely

Figures 1–2. Habitus photographs of *Pepsis cerberus* Lucas and *P. elegans* Lepeletier females. **1)** *Pepsis cerberus* female habitus, Portal, Cochise County, Arizona. Photograph © Akira Shimizu. **2)** *Pepsis elegans* Lepeletier female habitus, Atlanta, Fulton County, Georgia. Photograph © Brenna Decker.

curved near their apices (Fig. 3Gj). Hurd (1952) separated *P. cerberus* from *P. elegans* using external morphology and biogeography. However, *P. cerberus* and *P. elegans* became junior synonyms when Vardy (2005) re-introduced *Pepsis menechma* Lepeletier, 1845 after 160 years in obscurity. Vardy (2005) likely chose *P. menechma* over *P. elegans* because the former appeared several pages earlier in Lepeletier's (1845) *Histoire Naturelle des Insectes. Hyménoptères* (page 481 for *P. menechma* and 489 for *P. elegans*). Vardy (2005) ignored the prevailing usage and clearly violated articles 23.2, 23.3 and 23.9.1.2 of the ICZN (1999) by synonymizing *P. cerberus* and *P. elegans* under *P. menechma*. Vardy (2005) admitted that *P. menechma* "conforms with the current interpretation of *P. elegans*." *Pepsis menechma* had been totally absent from the Hymenoptera literature for nearly two centuries while *P. elegans* was cited consistently in multiple documents during that period. Both *P. cerberus* and *P. elegans* are listed as distinct species in Krombein et al.'s (1979) Hymenoptera Catalog whereas there is no mention of *P. menechma*. Vardy's (2005) *Pepsis menechma* extends across ~11,250 km and two continents—an extraordinarily vast range for a ground-nesting spider wasp. Vardy (2005) failed to consider the difference in climate, habitat, ecology, and host spiders of *P. cerberus* and *P. elegans* based on the vast contrast in their Level 1 Ecological Regions of North America (Fig. 4; Commission for Environmental Cooperation Working Group 2006). Hurd (1952), in contrast, believed that *P. cerberus* and *P. elegans* are "sufficiently isolated reproductively" as separate populations that have "attained the...level of species." *Pepsis cerberus* and *P. elegans* occur together in a narrow sympatric zone in south-central Texas but are otherwise geographically, ecologically, morphologically, and potentially host spider distinct (Fig. 4; Hurd 1952; Kurczewski 2023a). In this paper, we present additional morphological and statistical evidence to support the separate species designation of *P. cerberus* and *P. elegans*. Given this new evidence, the two species should be removed from the synonym list of *P. menechma* and reinstated as *Pepsis cerberus*, **restored status** and *Pepsis elegans*, **restored status**. *Pepsis menechma* becomes a senior synonym of *P. elegans*.

Pepsis cerberus and *P. elegans* are comparatively small Nearctic "tarantula hawk-wasps," the females averaging ~22–25 mm in body length (Punzo 2005; Vardy 2005). Females of *P. cerberus* have a refulgent bluish body, orange-amber dark base and dark-fringed wings, and black antennae (Fig. 1). Females of *P. elegans* are black with pale iridescent bluish or violet reflection, have infuscate violaceous wings, and a yellowish orange to orange flagellum (Fig. 2). The forewing of *P. cerberus* females from the southwestern U.S. and Mexico is significantly longer than that of *P. elegans* females from the southeastern U.S. (Fig. 4; Table 1; Kurczewski 2023a). There are differences in the shape of the male genitalia and subgenital plate of the two taxa (Hurd 1952; Table 1). The hind tibial inner spur is significantly longer and straighter in *P. elegans* (Vardy 2005; Table 1). The upper surface of the hind tibia of *P. cerberus* females is aligned with moderately small conical serrations and interspersed, long, rather stout, posterior-curved, subtending setae (Fig. 3F; Table 1; Kurczewski 2023a). In *P. elegans* females, the upper surface of the hind tibia is aligned with slightly smaller conical serrations and sparser, shorter, thinner, straighter, more slanted subtending setae (Table 1; Kurczewski 2023a). *Pepsis cerberus* females have a longer flagellum and significantly longer [and narrower] flagellomere 1 (Fig. 3Be/f; Table 1; Kurczewski 2023a). Difference in body color; wing color and length; antenna flagellum color, length, and width; female hind tibial armature and inner spur length and shape; male genitalia; and subgenital plate of *P. cerberus* and *P. elegans* is the result of allopatric evolution controlled by climate, habitat, host spider type, and nesting behavior.

The host spiders of *P. cerberus* and *P. novitia* Banks are suspected to be the southwestern trapdoor spider *Eucteniza relata* (O. P.-Cambridge) (Euctenizidae) and related species and genera. Gillaspy (1990) observed females of *Pepsis novitia*, a *P. cerberus* × *P. elegans* hybrid (Hurd 1952) or mesic variant of *P. cerberus* (Kurczewski 2023a), searching on a lawn in Kleberg County, TX for burrows of *E. relata*. He believed this spider species 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; Kurczewski 2023a). Gillaspy (1990) also observed females of typical *P. cerberus* searching similarly on a lawn in Jim Wells County, TX, introducing the likelihood of this species also capturing *E. relata* and depositing the immobilized spider in its own burrow.

Species of *Ummidia*, particularly *U. audouini* (Lucas), are the most likely host spiders of *P. elegans* based on *Pepsis*-Mygalomorphae parasitoid association, size equivalence (BL, ~25–28 mm), geographic and habitat sympatry, seasonal synchrony, abundance, and burrow confinement (Kurczewski 2023b). *Ummidia audouini* is the stoutest and heaviest native spider while *P. elegans* is the largest spider wasp in the southeastern U. S. *Pepsis*

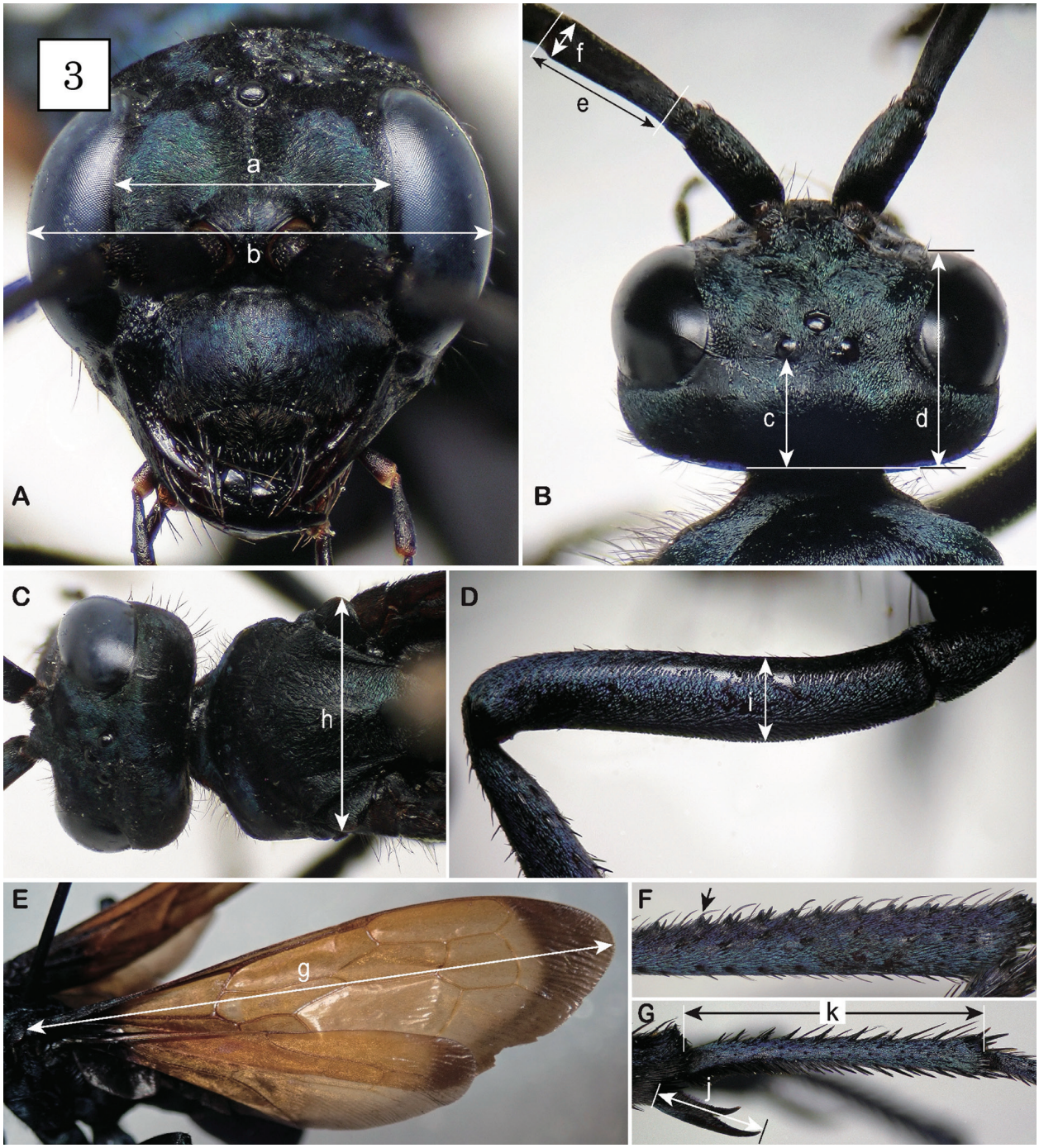

Figure 3. *Pepsis cerberus* Lucas. **A)** Head, anterior view. **B)** Head, dorsal view. **C)** Head and anterior part of mesosoma, dorsal view. **D)** Left fore femur, lateral view. **E)** Left fore and hind wings, lateral view. **F)** Left hind tibia, lateral view (arrow, serration [integumental tooth-like projection]). **G)** Right hind tibia apically and basitarsus, mesial view. Measurement parts: **a)** Frons width (middle interocular distance). **b)** Head width (trans-facial distance). **c)** Vertex length (distance from posterior margin of lateral ocellus to occipital carina). **d)** Head length (distance from anterior margin of compound eye to posterior margin of postgena). **e)** Flagellomere 1 length. **f)** Flagellomere 1 width. **g)** Fore wing length (distance from posterior margin of tegula to wing tip). **h)** Mesosoma width (distance between lateral margins of tegulae). **i)** Fore femur width. **j)** Hind tibial inner spur length. **k)** Hind basitarsus length. Photographs © Akira Shimizu.

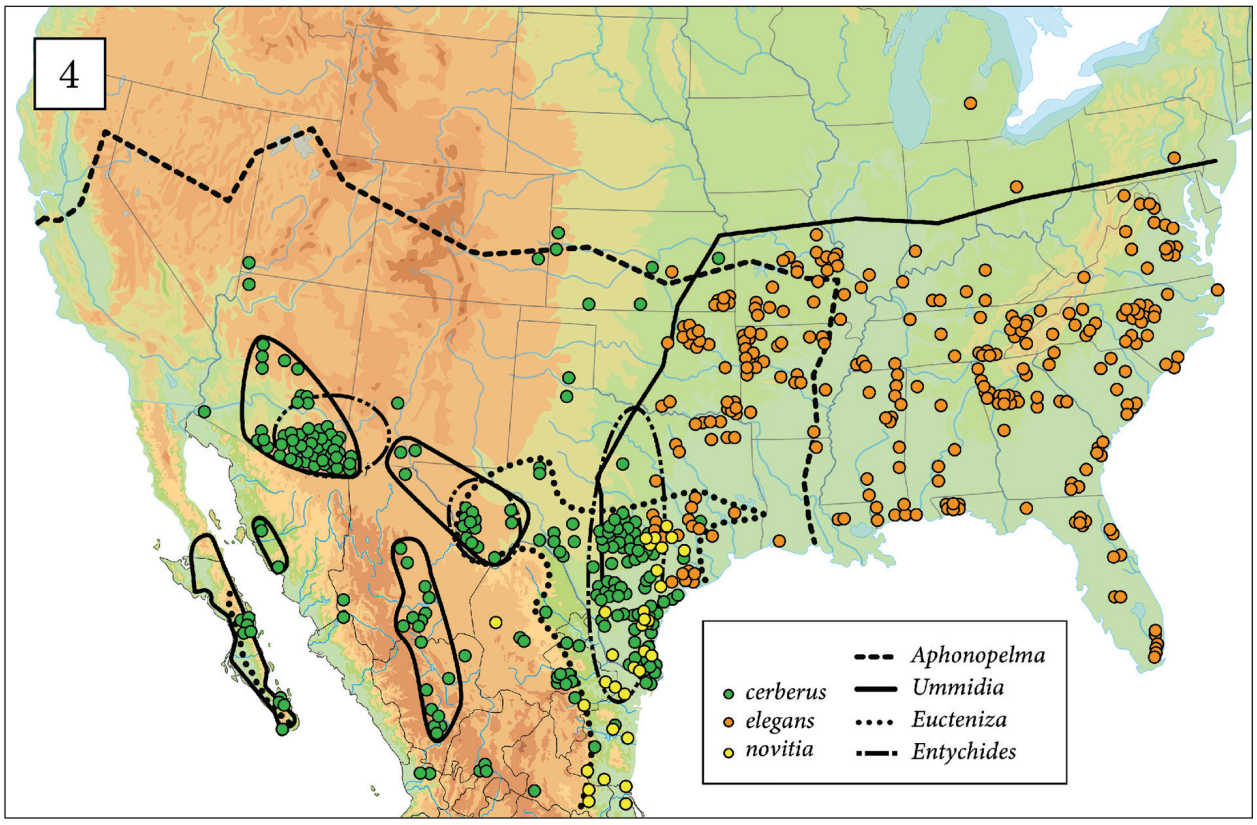

Figure 4. Geographic location map for *Pepsis cerberus* Lucas, *P. elegans* Lepeletier, and *P. novitia* Banks in the Nearctic Region (based on Brimley 1936; Hurd 1952; Krombein 1952; Johnston 2000; Bond and Opell 2002; Vardy 2005; Leavengood et al. 2011; Bond and Godwin 2013; Hamilton et al. 2016; Norden 2017; Godwin and Bond 2021; Durand, pers. comm.; BugGuide.net; flickr.com; iNaturalist.org; gbif.org; SCAN; and specimen records from 36 insect collections). Black lines represent range limits of potential host spider genera. Solid black line represents the geographic limit of *Ummidia* (Halonoproctidae) species (Godwin and Bond 2021). Dashed black line represents the 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 the geographic limit of *Entychides* Simon (Euctenizidae) species (Bond and Opell 2002). Map is adapted from Kurczewski (2023a).

elegans and the genus *Ummidia* have nearly identical geographic location maps (Fig. 4; Godwin and Bond 2021; Kurczewski 2023a, b). *Pepsis elegans* habitat, mesic open woodland (Kurczewski 2023b), resembles *Ummidia* burrowing habitat (Godwin, pers. comm.). *Pepsis elegans* probably uses the spider's burrow as a nest, bypassing the excavation of a separate burrow from the ground surface. *Pepsis elegans* females had dried mud on the forewings and body inferring they were underground in moist fine-grained soil, as in a spider's burrow (Kurczewski 2023b). *Pepsis elegans* females are active at night, introducing the possibility of cryptic nocturnal nesting (Kurczewski 2023b). *Ummidia audouini* is accessible at night in its burrow entrance, holding the trapdoor slightly ajar as it waits in the dark to ambush unsuspecting prey (Coyle 1981; Bond and Coyle 1995).

Materials and Methods

Female specimens of *P. cerberus* and *P. elegans* with intact head, antennae, legs, and wings identified by Howard E. Evans, Paul D. Hurd, Jr., or Colin Vardy were borrowed from the A. J. Cook Arthropod Research Collection, Michigan State University; Enns Entomological Museum, University of Missouri; and Essig Museum, University of California–Berkeley, and sent to Akira Shimizu, Tokyo Metropolitan University, Tokyo, Japan for examination

Table 1. Morphological and ecological characteristics of *Pepsis elegans* Lepeletier and *Pepsis cerberus* Lucas (Hurd 1952; Vardy 2005; Kurczewski 2023a). ** indicates significant difference.

Characteristics	*Pepsis elegans*	*Pepsis cerberus*
Male 4th sternite hairbrush	Two oblique rows of posteriorly directed setae	Double hemispherical row
Male subgenital plate	Short, flat, truncate to emarginate apex	Short, flat, hemispherical apex
Male genitalia	Digitus apex with obtuse angle	Digitus apex with rounded corners
Female flagellomere 1 length/width**	2.8692 (2.7 – 3.1)	3.4684 (3.0 – 3.7)
Female frons width/head width**	0.60077 (0.57 – 0.61)	0.61263 (0.59 – 0.63)
Female head length/head width**	0.49462 (0.46 – 0.52)	0.52105 (0.48 – 0.56)
Female vertex length/head width**	0.25923 (0.24 – 0.27)	0.30158 (0.28 – 0.33)
Female vertex length/head length**	0.52538 (0.47 – 0.58)	0.57947 (0.52 – 0.64)
Female gena-postgena	Strongly swollen	Strongly swollen
Female gena-postgena corner radius	0.6146 – 0.6703	0.6215 – 0.6726
Female median ocellus width/head width	0.073 – 0.083	0.072 – 0.080
Female mid, hind tibial spurs	Curved or hooked apically	Curved or hooked apically
Female hind tibial spur length/basitarsus length**	0.46231 (0.40 – 0.51)	0.39053 (0.34 – 0.44)
Female hindtibial subtending setae	Short, thin, straight, sparse, more angled backward	Long, moderately stout, strongly curved backward
Female forewing length/mesosoma width**	4.3583 (4.0 – 4.8)	4.6687 (4.3 – 5.1)
Female fore femur width/mesosoma width	0.20462 (0.18 – 0.25)	0.19789 (0.18 – 0.24)
Female number of hind tibial serrations	16.077 (15 – 17)	16.895 (15 – 19)
Level 1 Ecoregions	Eastern U.S. mesic open woodland	Western U.S. semi-arid, sparse woodland, scrubland, grassland
Potential host spider	?*Ummidia* spp., especially *U. audouini* (Halonoproctidae)	?*Eucteniza relata*, related species and genera (Euctenizidae)

and measurement of parasitoid-related morphological structures (Table 2). Similarly, female specimens of the two species were examined and measured on site at Utah State University, Logan, UT by Akira Shimizu (Table 2). Macrophotographs of parasitoid-related morphological structures of females of both species were sent from the same insect museums and the California Academy of Sciences to Frank E. Kurczewski for examination and measurement. Measurement of gena-postgena corner radius was made on females of *P. cerberus* and *P. elegans* by Lukas Friedrich and Frank E. Kurczewski using an online formula from google.com (Table 1; Kurczewski 2024). Nine parasitoid-related morphological characteristics of females of the two species important in facilitating wasp entry into the spider's burrow and/or subsequent host spider capture and immobilization were measured by Akira Shimizu under a stereo microscope (Leitz TS) plus online measurement of the gena-postgena corner radius, as measured by Lukas Friedrich and Frank E. Kurczewski, are defined as follows (Fig. 3A–G):

Frons width – mesial distance between inner edges of compound eyes/head width in anterior view.
Head length – anterior margin of compound eye to postgena hind margin/head width in dorsal view.
Vertex length – posterior edge of lateral ocellus to occipital carina/head width in dorsal view.
Vertex length – posterior edge of lateral ocellus to occipital carina/head length in dorsal view.

Table 2. Measurement of female specimens of *Pepsis elegans* Lepeletier and *Pepsis cerberus* Lucas. Both species are assumed to be parasitoids of trapdoor-spiders and use the host spider's burrow.

Species	Specimen	Frons W/Head W (a/b)	Head L/Head W (d/b)	Vertex L/Head W (c/b)	Vertex L/Head L (c/d)	Flagellomere 1 L/W (e/f)	Forewing L/ Mesosoma W (g/h)	Fore femur W/ Mesosoma W (i/h)	No. hind tibial serrations	Hind tibial spur L/hind basitarsus L (j/k)	Label information
Pepsis elegans Lepeletier	1	0.60	0.50	0.27	0.54	2.7	4.1	0.19	16	0.40	GA: Cartersville, 29.vi.6.1963, J.R.Monroe
	2	0.59	0.48	0.27	0.56	2.8	—	0.25	17	0.46	FL: Gainesville, Bill Platt, 2.viii.1958
	3	0.59	0.48	0.26	0.54	2.9	4.4	0.21	16	0.44	GA: Atlanta, 7-9-1935, P.W.Fattig
	4	0.60	0.49	0.26	0.52	2.9	4.2	0.20	17	0.41	GA: Clarke Co., Athens, 10.v.1972, R.White
	5	0.61	0.46	0.27	0.58	3.0	4.4	0.18	15	0.51	GA: Ogle.Co., 10.vi.1963, D.A.Fry
	6	0.61	0.47	0.27	0.57	2.8	4.2	0.20	15	0.49	NC: Wake Co., 24.viii.1949, H.Townes
	7	0.61	0.50	0.25	0.51	2.9	4.4	0.21	17	0.48	FL: Alachua Co., Gainesville, vi.2005, D.B.Wahl
	8	0.61	0.50	0.26	0.53	2.8	4.4	0.20	16	0.49	MO: Ranken, St. Louis Co., viii.30.1958, E. P. Meiners
	9	0.60	0.50	0.26	0.51	2.8	4.8	0.21	16	0.48	N/A
	10	0.60	0.51	0.25	0.49	2.8	4.6	0.21	16	0.48	MO: Ranken, St. Louis Co., viii.22.1937, E. P. Meiners
	11	0.61	0.52	0.26	0.50	2.9	4.3	0.19	16	0.43	GA: Atlanta, 26.vi.1910
	12	0.61	0.50	0.25	0.51	3.1	4.5	0.20	16	0.45	GA: Billy's Is., Okefenokee Swamp, vi.1912
	13	0.57	0.52	0.24	0.47	2.9	4.0	0.21	16	0.49	TX: Brazos Co., 23.vi.1921, R. K. F.
Pepsis cerberus Lucas	1	0.61	0.56	0.29	0.52	3.0	5.0	0.21	15	0.44	MEXICO: Zacatecas, Jalpa 10m S, 17.ix.1970, G. E. & R. M.Bohart
	2	0.62	0.48	0.31	0.64	3.5	5.1	0.21	15	0.41	AZ: Yavapai, Congress 5mE, 22.vi.1971, G.Bohart & P.Torchio
	3	0.61	0.51	0.28	0.55	3.5	4.4	0.19	18	0.40	AZ: 6mi. W. Douglas, Cochise Co., 28.vii.1948, H. E. Evans
	4	0.62	0.51	0.30	0.59	3.3	4.5	0.19	19	0.39	AZ: 6 mi. W. Douglas, Cochise Co., 2.vii.1948, H. E. Evans
	5	0.61	0.53	0.30	0.56	3.6	4.5	0.19	17	0.37	AZ: 6 mi. W. Douglas, Cochise Co., 28.vii.1948, H. E. Evans
	6	0.60	0.54	0.32	0.59	3.6	4.4	0.19	15	0.38	MEXICO: Vallecillo, N. L., 2–5.vi.1951, P. D. Hurd
	7	0.62	0.52	0.30	0.57	3.6	4.6	0.19	16	0.34	AZ: 6mi. W. Douglas, Cochise Co., 28.vii.1948, H. E. Evans
	8	0.61	0.54	0.33	0.62	3.6	4.5	0.20	17	0.42	TX: Camp Bullis, Bexar Co., 27.v.1952, M. Wasbauer
	9	0.60	0.51	0.29	0.57	3.5	—	0.19	18	0.42	AZ: 6 mi. W. Douglas, Cochise Co., 2.vii.1948, H. E. Evans
	10	0.62	0.53	0.31	0.60	3.4	4.3	0.18	18	0.39	TX: Lung, Gonzales Co., 17.v.1953, M. Wasbauer
	11	0.62	0.51	0.31	0.61	3.4	—	0.20	18	0.39	TX: Leon Creek, Bexar Co., 19.x.1952, B. J. Adelson
	12	0.62	0.52	0.30	0.57	3.5		0.24	17	0.42	AZ: Portal, 5000', 5.viii.1955, R. R. Dreisbach

Species	Specimen	Frons W/Head W (a/b)	Head L/Head W (d/b)	Vertex L/Head W (c/b)	Vertex L/Head L (c/d)	Flagellomere 1 L/W (e/f)	Forewing L/ Mesosoma W (g/h)	Fore femur W/ Mesosoma W (i/h)	No. hind tibial serrations	Hind tibial spur L/hind basitar-sus L (j/k)	Label information
Pepsis cerberus Lucas	13	0.60	0.53	0.29	0.55	3.4	4.7	0.19	18	0.37	AZ: Apache, Cochise Co., 5000', 4.viii.1955, R. R. Dreisbach
	14	0.63	0.52	0.30	0.58	3.5	5.1	0.20	17	0.39	AZ: Portal, 5000', 5.viii.1955, R. R. Dreisbach
	15	0.62	0.52	0.29	0.55	3.4	4.8	0.19	16	0.36	AZ: Apache, Cochise Co., 5000', 4.viii.1955, R. R. Dreisbach
	16	0.60	0.52	0.30	0.58	3.5	4.8	0.19	15	0.38	AZ: Apache, Cochise Co., 5000', 4.viii.1955, R. R. Dreisbach
	17	0.59	0.51	0.29	0.57	3.6	4.5	0.23	18	0.35	AZ: Apache, Cochise Co., 5000', 4.viii.1955, R. R. Dreisbach
	18	0.63	0.51	0.30	0.58	3.7	5.0	0.19	16	0.40	AZ: Portal, 5000', 5.viii.1955, R. R. Dreisbach
	19	0.61	0.53	0.32	0.61	3.3	4.5	0.19	18	0.40	TX: Port Isabel, Cameron Co., 20–23.vi.1948, H. E. Evans

Gena-postgena corner radius – posterior margin of compound eye to occipital carina in dorsal view.
Flagellomere 1 length – flagellomere 1 length/flagellomere 1 width at apex in dorsal view.
Forewing length – wing tip to posterior margin of tegula/mesosoma width in lateral view.
Fore femur width – fore femur mesial width/mesosoma width in lateral view.
Number of hind tibial serrations – Number of hind tibial serrations on upper surface.
Hind tibial inner spur length – Hind tibial inner spur length/hind basitarsus length.

Specimens of *P. cerberus* (Fig. 1, 3A–G) were photographed by Akira Shimizu using a digital camera (Nikon Coopix 4500 and MDC lens) equipped with a stereo microscope (Leitz TS) and a transmitted light microscope (Leitz Dialux). Photographs were stacked using Combine ZM (Hadley 2008) and the final synthesized photographs were post-processed for contrast and brightness using Adobe Photoshop software. Brenna Decker, Utah State University, and Chris Grinter, California Academy of Sciences, sent macrophotographs of specific morphological structures of *P. cerberus* and *P. elegans* to Frank E. Kurczewski. Figure 2 (*P. elegans*) was photographed by Brenna Decker, Utah State University. Figure 4 was adapted from Kurczewski (2023a).

Differences in mean measurements of the nine parasitoid-related structural characteristics made by Akira Shimizu and one structural characteristic made by Frank E. Kurczewski and Lukas Friedrich were analyzed and tested by Diane H. Kiernan using a 2-sample t-test when normality was confirmed and a Mann-Whitney test for the remaining comparisons. A 5% level of significance was used for all tests.

The original idea for this study to validate the separate species designation for *P. cerberus* and *P. elegans* and rectify Vardy's (2005) misinterpretation of *P. menechma* came from Frank E. Kurczewski. The manuscript was written by him in consultation with Akira Shimizu and Diane H. Kiernan. The functional morphology relationships expressed in the Discussion are solely those of Frank E. Kurczewski.

Results

Based on 2-sample t-test results for comparisons 2, 3, 4, 6, 9, and 10 and a Mann-Whitley test for comparisons 1, 5, 7, and 8, *P. cerberus* and *P. elegans* were found to be significantly different (**) in seven and non-significant in only three parasitoid-related structural characteristics:

1) ***Frons width/Head width* – *Pepsis cerberus* has a significantly (Mann-Whitney p=0.010) wider frons/head width (0.61263, n = 19) than *P. elegans* (0.60077, n =13).
2) ***Head length/Head width* – *Pepsis cerberus* has a significantly (p<0.001) longer head/head width (0.52105, n = 19) than *P. elegans* (0.49462, n = 13).
3) ***Vertex length/Head width* – *Pepsis cerberus* has a significantly (p<0.001) longer vertex/head width (0.30158, n = 19) than *P. elegans* (0.25923, n = 13).
4) ***Vertex length/Head length* – *Pepsis cerberus* has a significantly (p<0.001) longer vertex/head length (0.57947, n = 19) than *P. elegans* (0.52538, n = 13).
5) ***Flagellomere 1 length/Flagellomere 1 width* – *Pepsis elegans* has a significantly (Mann-Whitney p<0.001) shorter flagellomere 1 length/flagellomere 1 width (2.8692, n = 13) than *P. cerberus* (3.4684, n = 19).
6) ***Forewing length/Mesosoma width* – *Pepsis cerberus* has a significantly (p=0.002) longer forewing/mesosoma width (4.6687, n = 16) than *P. elegans* (4.3583, n = 12).
7) *Fore femur width/Mesosoma width* – *Pepsis elegans* has a slightly wider fore femur/mesosoma width (0.20462, n= 13) than *P. cerberus* (0.19789, n = 19) but the difference is non-significant (Mann-Whitney p=0.088).
8) *Number of hind tibial serrations* – *Pepsis elegans* has fewer hind tibial serrations (16.077, n = 13) than *P. cerberus* (16.895, n = 19) but the difference is slightly non-significant (Mann-Whitney p=0.057).
9) ***Hind tibial inner spur length/Hind basitarsus length* – Hind tibial inner spur length/hind basitarsus length of *P. elegans* (0.46231, n = 13) is significantly (p<0.001) longer than *P. cerberus* (0.39053, n = 19).
10) *Gena-postgena corner radius* – Gena-postgena corner radius of *P. cerberus* (0.6390, n = 6) and *P. elegans* (0.6408, n = 5) are not significant (p=0.898).

Discussion

Pepsis cerberus and *P. elegans* are separate species based on external morphological characteristics, biogeography, ecology, and potential host spiders despite Vardy's (2005) current synonymy of these species under *P. menechma* (Hurd 1952; Kurczewski 2023a). The species name *P. menechma* is being used and cited continuously and incorrectly with the common name "elegant tarantula-hawk wasp," which is based on the long-standing traditional species name *Pepsis elegans*, on online websites such as iNaturalist.org, BugGuide.net, flickr.com, and gbif.org. Kurczewski (2023a) described consistent structural and quantifiable differences between females of *P. cerberus* and *P. elegans* in body color; flagellomere 1 color, length, and width; forewing color and length; hind tibial inner spur length and shape; hind tibial serration size and number; and hind tibial subtending setae density, size, and shape. In our re-evaluation of females of these two species we found significant morphometric differences in frons width/head width, head length/head width, vertex length/head width, vertex length/head length, flagellomere 1 length/flagellomere 1 width, forewing length/mesosoma width, and hind tibial inner spur length/hind basitarsus length. Such significant differences strongly support separate species designation for *P. cerberus*, **restored status** and *P. elegans*, **restored status** and their removal from the incorrect and unwarranted synonymy of *P. menechma. Pepsis menechma* becomes a senior synonym of *P. elegans*.

Pepsis cerberus and *P. elegans* have few morphological characteristics typically associated with capturing trapdoor spiders. Morphological characteristics of *P. cerberus* and *P. elegans* females relevant in host-searching, capture, and immobilization of the host spider include strongly swollen gena-postgena (Vardy 2005; Kurczewski 2024), probably increasing the internal head area for enlarged mandibular musculature attachment. The large mandibles have a strong blunt tooth and strong mandibular muscles (Salman 1930). Significant difference in frons width, head length, and vertex length of *P. cerberus* and *P. elegans* are likely adaptations to enable successful opening and entry of the distinct trapdoors of *Eucteniza relata* (Euctenizidae), related species and genera [*P. cerberus*] and *Ummidia* spp. (Halonoproctidae) [*P. elegans*] burrows, if they are the host spiders. Despite Euctenizidae being called wafer-lid trapdoor spiders and Halonoproctidae cork-lid trapdoor spiders, the thickness and strength of the doors vary among the different genera of both families (Bond and Godwin 2013; Godwin and Bond 2021). *Eucteniza relata* trapdoors are "much thicker" than the "thin and flimsy" trapdoors of Nearctic *Ummidia* species (M. Hedin, pers. comm.). Although *Ummidia* ?*audouni* trapdoors are "definitely" wafer-like, they are "stiff enough" to not collapse inward when the spider occupant underneath inserts its chelicerae and pulls the door tight against the lip of the opening (F.A. Coyle, pers. comm.).

Females of *P. elegans* have significantly shorter antenna flagellomeres than *P. cerberus* (Kurczewski 2023a), possibly to facilitate host capture in a confined subterranean burrow. The forewing of *P. elegans* is significantly shorter than that of *P. cerberus*, similarly enhancing maneuverability inside the spider's narrow burrow (Kurczewski 2023b). The longer orange-amber forewings of *P. cerberus* may serve an increased aposematic function in its more open environment. The middle and hind tibial spurs of females of *P. cerberus* and *P. elegans* are curved apically (Salman 1930; Hurd 1952; Vardy 2005), and possibly used in prey capture and/or, with the aid of the mandibles and head, to lift and hold the spider's trapdoor. Hind tibial inner spurs are significantly shorter and more curved in *P. cerberus* than in *P. elegans* (Table 1; Vardy 2005). The hind tibial teeth of *P. elegans* females are small with sparse, thin, short, rather straight, slanted, subtending setae (Kurczewski 2023a). In *P. cerberus* females, the hind tibial serrations are slightly larger with more numerous, longer, stouter, more posterior-curved subtending setae (Kurczewski 2023a). Hind tibial serrations function in removing soil from the burrow during excavation and assist in packing soil in the burrow during closure (Williams 1956; Evans and Yoshimoto 1962; Shimizu and Wahis 2004; Kurczewski and West 2022). Small hind tibial serrations reduce the capacity of removed soil and favor use of the spider's own burrow as a nest instead of excavating a separate burrow from the ground surface (Kurczewski 2023b).

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