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# Analysis of *Pepsis basifusca* Lucas (Hymenoptera: Pompilidae: Pepsinae) taxonomy, morphology, biogeography, and potential host spider

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# Analysis of *Pepsis basifusca* Lucas (Hymenoptera: Pompilidae: Pepsinae) taxonomy, morphology, biogeography, and potential host spider

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**Abstract.** A first-time analysis of taxonomically relevant characters, functional morphology, geographic distribution, ecoregion preference, and hypothetical host spiders of *Pepsis basifusca* Lucas (Hymenoptera: Pompilidae: Pepsinae) is presented. This analysis is compared with other Nearctic species in Vardy's (2005) *Pepsis menechma* species-group, particularly *P. cerberus* Lucas and *P. elegans* Lepeletier which are suspected parasitoids of trapdoor spiders. *Pepsis basifusca* females differ from females of these species in possessing a rounded gena-postgena in dorsal view; straight mid and hind tibial spurs; short hind tibial inner spur; and short, very stout, and backward slanted hind tibial bristles. *Pepsis basifusca* Level III Ecoregions comprise mountains, plateaus, highlands, and tablelands, often at high elevation (~3,000–5,000 feet (914–1,524 meters), from Utah, Colorado, Kansas, and Missouri to Panama. *Pepsis basifusca*, the smallest Nearctic congener, should be expected to capture comparatively small mygalomorph spiders like some other species in Vardy's (2005) *Pepsis menechma* species-group. Based on taxonomic, morphological, biogeographical, and potential host spider criteria, *P. basifusca* should probably be removed from this group and transferred to another species-group.

**Key words.** *Pepsis cerberus*, *Pepsis elegans*, *Pepsis menechma* species-group, Mygalomorphae, Level III Ecoregions of the Continental United States.

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## Introduction

The impressively large and colorful species of the tarantula hawk-wasp genus *Pepsis* Fabricius (Hymenoptera: Pompilidae: Pepsinae) are unrivaled in appearance 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, mainly in the southwestern U. S. and Mexico (Hurd 1952; Vardy 2000, 2002, 2005). Tarantulas (Araneae: Mygalomorphae: *Aphonopelma* Pocock) are the predominant host spiders of the Nearctic *Pepsis* species (Hurd 1952; Williams 1956; Cazier and Mortenson 1964; Punzo 1994, 2005; Vardy 2000; Kurczewski et al. 2020), *Aphonopelma* being the only native theraphosid genus in the region (Hamilton et al. 2016). There is a strong geospatial relationship between the Nearctic *Pepsis* species and their *Aphonopelma* host species (Kurczewski et al. 2020). In the West Indies, southern Mexico, Central America and South America, *Pepsis* species often capture and provision nests with other genera of theraphosids instead of *Aphonopelma* (Kurczewski et al. 2013, 2020, 2022, in press). Not all species of *Pepsis* are "tarantula hawk-wasps." Comparatively small and medium-size (14–32 mm) Neotropical *Pepsis* females capture comparatively 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), bald-legged spiders (Paratropididae), mouse spiders (Actinopodidae), wandering spiders (Ctenidae), and, very rarely, wolf spiders (Lycosidae) (Kurczewski et al. 2020, 2022, in press). There are only two host records for wolf spiders among the 57 species of *Pepsis* that were studied (Sandoval 2023; Timm 2023; Kurczewski et al., in press). *Pepsis* females may avoid wolf spiders because of their small size, visual acuity, maneuverability, speed, ferocity, and alertness (Williams 1956). Host records for comparatively small species in

the *Pepsis menechma* species-group to which *P. basifusca* Lucas was assigned by Vardy (2005) indicate or infer a preference for trapdoor spiders and related Mygalomorphae: *P. amyntas* Mocsáry (Actinopodidae), *P.* ?*chrysoptera* Burmeister (Pycnothelidae), *P. cerberus* Lucas and *P. novitia* Banks (?Euctenizidae), and *P. elegans* Lepeletier (?Halonoproctidae) (Kurczewski 2023b; Kurczewski et al., in press). The sizes of the comparatively small females in the *Pepsis menechma* species-group are at variance with the capture of large tarantulas (Kurczewski 2023b).

## Materials and Methods

This paper consolidates taxonomic, morphological, and distributional information, presents first-time ecoregion and habitat details, and speculates on the potential host spiders of *P. basifusca*. The only reference sources available for this species are Hurd (1952) and Vardy (2005). Hurd's (1952) morphological description and distribution map of this species are published under the name *P. angustimarginata* Viereck, a junior synonym (Vardy 2005). Examination of 34 natural online photographs of males and females on flowers on BugGuide.net, iNaturalist.org, and insectimages.org provided little to no information on ecoregion, habitat, host-searching, or host spider(s) of *P. basifusca*. Recently (2022, 2023), Steve Mlodinow (pers. comm.) sent photographs and vegetation information on *P. basifusca* habitats from three adjacent southeastern Colorado counties. Analysis of host spider selection is based on comparison with other species in Vardy's (2005) *Pepsis menechma* species-group (Kurczewski 2023b; Kurczewski et al., in press). *Pepsis basifusca*, *P. cerberus*, and *P. elegans* identifications are based on specimen determination labels by Paul D. Hurd, Jr., Howard E. Evans, and Colin Vardy.

For the geographic location map (Fig. 5), natural relief maps of the U. S. and Mexico were combined into a natural relief base map. Hurd's (1952) geographic location map for *P. angustimarginata* was overlaid on the base map, size adjusted, and the localities copied. Vardy's (2005) map of Mexican *P. basifusca* localities was then overlaid on this map and the localities copied. Localities from Evans (1997), BugGuide.net, flickr.com, iNaturalist.org, gbif.org, and SCAN were added. Specimen locality records from 16 insect collections were copied into the proper locations using translucent state maps size adjusted for accuracy. The potential host spider geographic limit lines copied from Bond and Opell (2002), Bond and Godwin (2013), Hamilton et al. (2016), and Godwin and Bond (2021) were applied individually. The following insect museum curators, collection managers, and their assistants sent geographic locality information for *P. basifusca* and its junior synonym, *P. angustimarginata*: Christy Bills, Natural History Museum of Utah; David Bowles, University of Arkansas; Roberta Brett and Peter Oboyski, Essig Museum of Entomology, University of California–Berkeley; Anthony Cognato, A. J. Cook Arthropod Research Collection, Michigan State University; Crystal Cooke, Gillette Museum of Arthropod Diversity, Colorado State University; Brenna Decker, Utah State University; Brennen Thomas Dyer and Lynn Kimsey, R. M. Bohart Museum, University of California-Davis; Chris Grinter and Denise Montelongo, California Academy of Sciences; Alex Harman, K. C. Emerson Entomology Museum, Oklahoma State University; Sangmi Lee, Arizona State University; Rachel Kathryn Osborn, Snow Entomological Museum, University of Kansas; John Oswald, Texas A&M University Insect Collection; Kristin Simpson and Robert Sites, Enns Entomological Museum, University of Missouri; Helen Vessels, New Mexico State University Arthropod Collection; Alexander Wild, University of Texas Biodiversity Collections; Kevin Williams, California Department of Food & Agriculture; and Douglas Yanega, University of California–Riverside. Kansas State University did not reply to my request for *Pepsis basifusca* locality information. The Level III "Ecoregions of the Continental United States" map by the Commission for Environmental Cooperation Working Group (2006) was edited to show previously unknown and disconnected ecoregions and habitats for *P. basifusca* in the Nearctic Region (Fig. 6).

Macrophotographs of *P. basifusca*, *P. cerberus*, and *P. elegans* females in dorsal view were solicited from several insect museums, examined for relevant taxonomic characteristics, and measured. Measurements of gena-postgena left and right corner radius, median ocellus width/head width, vertex length/head width, flagellomere 1 length/width, and hind tibial inner spur length/basitarsomere length were made (Table 1). Measurement of head structures is based on females of equal head width. Left and right corner radius measurements of females of *P. basifusca*, *P. cerberus*, and *P. elegans* gena-postgena are based on an online formula obtained through google.com (Fig. 2). Flagellomere 1 length measurement was divided by its width measurement at the middle of the segment (Fig. 3). Vertex length was measured from the bottom of the hind ocellus to the occipital carina, as suggested by

**Table 1.** Morphological and ecological characteristics of *Pepsis basifusca* Lucas and *P. cerberus* Lucas (Hurd 1952; Vardy 2005; Kurczewski 2023a, b; Shimizu, pers. comm.).

| Characteristics | *Pepsis basifusca* | *Pepsis cerberus* |
|---|---|---|
| Male 4th sternite hair brush | Broad single row | Double hemispherical row |
| Male subgenital plate | Long, narrow; rounded apex | Short, flat, expanded apex |
| Male genitalia | Digitus thin, bent distad | Digitus apex with obtuse angle |
| Female flagellomere 1 length/width | 4.0–4.1 | 4.0–4.1 |
| Female gena-postgena | Moderately swollen | Strongly swollen |
| Female gena-postgena corner radius | 0.8706–0.9262 | 0.6215–0.6726 |
| Female median ocellus width/head width | 0.057–0.061 | 0.072–0.080 |
| Female vertex length/ head width | 0.247–0.253 | 0.276–0.287 |
| Female mid, hind tibial spurs | Straight throughout | Curved or hooked apically |
| Female hind tibial inner spur length/ basitarsomere length | 0.31–0.40 | 0.34–0.44 |
| Female hind tibial subtending bristles | Short, very stout, slanted backward | Long, moderately stout, curved backward |
| Level III Ecoregions | Mountains, plateaus, highlands, and tablelands, especially at high elevation | Highland and lowland areas, including plains, prairies, and basins. |
| Potential host spider family | ?Small immature tarantulas (Theraphosidae) | ?Wafer-lid trapdoor spiders (Euctenizidae) |

Akira Shimizu (pers. comm.). Hind tibial serrations and subtending bristles of the females were examined, measured, counted, and photographed (Fig. 4; Shimizu, pers. comm.).

# Results

*Pepsis basifusca* is the smallest (males, 11–22 mm; females, 14–27 mm; Vardy 2005) congener in the Nearctic Region. Like *P. cerberus* and many other *Pepsis* species, *P. basifusca* is black with strong bluish or violet pubescent reflection, has black antennae, and orange-amber dark base and dark-fringed forewings (Fig. 1). *Pepsis basifusca* male 4$^{th}$ metasomal sternite has a broad, transverse band of setae (Table 1), the outer ones rather dense, long, slightly curved inwards and backwards and forming a "brush"; shorter, thinner, sparser, and more upright setae towards the center; and 5$^{th}$ sternite with a few scattered setae (Vardy 2005). The head of *P. basifusca* females in dorsal view is "moderately swollen" (Vardy 2005; Fig. 2; Table 1). The gena-postgena of *P. basifusca* females is more rounded and less quadrate than *P. cerberus* and *P. elegans* females as indicated by their corner radius values of 0.8706–0.9262, 0.6215–0.6726, and 0.6146–0.6703 inches, respectively (Fig. 2; Table 1). *Pepsis basifusca* female vertex length/head width in dorsal view is 0.247–0.253, or less than *P. cerberus* (0.276–0.287) and *P. elegans* females (0.260–0.267; Table 1). The median ocellus of *P. basifusca* females is smaller in diameter/head width (0.057–0.061) than *P. cerberus* (0.072–0.080) and *P. elegans* females (0.073–0.083; Table 1). Flagellomere 1 length of *P. basifusca* females is much less than the distance between the compound eyes at the vertex (Fig. 3). Flagellomere 1 in *P. basifusca* females averages 4.0–4.1 times as long as wide and is similar in length to *P. cerberus* females (4.0–4.1; Kurczewski 2023a; Table 1). Female femora, especially hind femora, have long, erect, and recumbent setae (Hurd 1952). Female hind tibial serrations are slightly more numerous (16–21) than *P. cerberus* (15–19) and *P. elegans* (15–17; Shimizu, pers. comm.), moderately small, conical in shape, and point slightly backward (Fig. 4). The subtending hind tibial bristles are abundant, short, very stout, and slant noticeably backward (Fig. 4). The hind tibial inner spur of *P. basifusca* females is 0.31–0.40 the length of the basitarsus and 1.25–1.30 times as long

as the outer spur (Vardy 2005; Shimizu, pers. comm.; Table 1). The hind tibial inner spur of *P. basifusca* is shorter than *P. cerberus* (0.34–0.44) and *P. elegans* (0.40–0.51; Shimizu, pers. comm.).

*Pepsis basifusca* occurs from Utah, Colorado, Kansas, and Missouri southward through Mexico to Panama (Hurd 1952; Vardy 2005) (Fig. 5). It has a disconnected geographic distribution in the southwestern U. S. (Fig. 6). This species does not inhabit the West Coast, Baja California, Central Great Plains, including most of Texas and Oklahoma, and the southeastern U. S. (Hurd 1952). Such a geographic distribution infers that the West Coast, Rocky Mountains, Central Great Plains, and southeastern U. S. forests have unsuitable climate, inappropriate habitat, and absence of potential host spiders. In Mexico and Central America, *P. basifusca* has a distribution pattern like that of *P. cerberus* and its hybrid with *P. elegans*, *P. novitia*, combined. The Level III Ecoregions of the Continental United States for *P. basifusca* include plateaus, highlands, tablelands, and mountains, often at moderately high elevation (Commission for Environmental Cooperation Working Group 2006; Fig. 6). Southwestern U. S. Level III ecoregions not inhabited by *P. basifusca* include very high elevation mountains, lowland plains, prairies, basins, and low elevation deserts (Commission for Environmental Cooperation Working Group 2006; Fig. 6). The "High Plains" of eastern New Mexico and northwestern Texas where *P. basifusca* occurs is a misnomer as it is mainly a flat plateau or tablelands of short grass prairie >3,000–5,000 feet (914–1,524 meters) in elevation. In north-central Mexico and the southwestern U. S., 126 of 137 (92.0%) collection localities are above 3,000 feet (914 meters) in elevation (Fig. 5, 6). *Pepsis basifusca* collection localities in eastern Kansas, Missouri, and Arkansas and along the Gulf of Mexico and Gulf of California are at much lower elevation (Fig. 5). An extensively wide range in average annual precipitation (inches) accompanies *P. basifusca* collection localities: 2.36 (Nombre de Dios, Durango, MX)–118.50 (Monteverde, Puntarenas, Cost Rica).

# Discussion

The *Pepsis menechma* species-group is an artificial assemblage of 10 (11) small and medium-size species in which relationships are difficult to assess (Vardy 2005; Kurczewski 2023a). Half of the species in this group, including *P. basifusca*, have relatively little in common morphologically with the other species in the group (Vardy 2005). *Pepsis basifusca* differs from other species in the *P. menechma* species-group in possessing a moderately swollen gena-postgena; mid and hind tibial spurs not curved apically; hind tibial inner spur moderately short; and hind tibial bristles short, very stout, and slanted backward (Table 1). *Pepsis basifusca* resembles *P. cerberus* in comparative small size and coloration but not much else. *Pepsis basifusca* males can be differentiated from those of *P. cerberus* and *P. elegans* in having a broad transverse row of sensory setae on metasomal sternite 4 instead of two oblique rows or patches, different genitalia, and distinct subgenital plate (Hurd 1952; Vardy 2005; Table 1). The head of *P. basifusca* females in dorsal view is "moderately swollen," while that of *P. cerberus* and *P. elegans* females is "strongly swollen" (Vardy 2005; Kurczewski 2023a, b). The gena-postgena of *P. basifusca* females is rounder and less quadrate than *P. cerberus* and *P. elegans* females (Fig. 2; Table 1), inferring less internal head space for mandibular musculature. The individual ocelli of *P. basifusca* females are slightly smaller in diameter than those of *P. cerberus* and *P. elegans* females (Fig. 2; Table 1), inferring that *P. basifusca* may be more diurnal and less nocturnal in its activities than *P. cerberus* and *P. elegans*. Mid and hind tibial spurs of *P. basifusca* females are rather straight and not curved apically as in *P. cerberus* and *P. elegans* (Hurd 1952; Vardy 2005; Table 1), implying they may be used differently. The hind tibial inner spur of *P. cerberus* and *P. elegans* is longer than *P. basifusca* (Table 1). The subtending bristles on the upper surface of the hind tibiae of *P. basifusca* females are short, very stout, and slanted noticeably backward (Fig. 4; Table 1). Those of *P. cerberus* females are long, less stout, and curved apically backward (Kurczewski 2023a).

*Pepsis basifusca* is absent from the West Coast, Rocky Mountains, Central Great Plains, including most of Oklahoma and Texas, and southeastern U. S. (Hurd 1952; Vardy 2005). These areas consist of extremely high mountains, lowland plains, prairies, basins, and low-elevation deserts. The competitive exclusion principle may be operational throughout much of Texas and Oklahoma considering the abundance of *P. cerberus* and *P. elegans*, two species in the *Pepsis menechma* species-group that are suspected of capturing wafer-lid (Euctenizidae) and cork-lid (Halonoproctidae) trapdoor spiders, respectively, (Kurczewski 2023b). The geographic distribution of *P. basifusca* in the southwestern U. S. is coincident with specific Level III Ecoregions, in particular moderately high

mountains, plateaus, highlands, and tablelands (>3,000–5,000 feet; Fig. 5, 6), while *P. cerberus* and *P. elegans* do not follow suit (Kurczewski 2023a, b). The geographic distribution of *P. basifusca* in Mexico and Central America is equivalent to that of *P. cerberus* and *P. novitia* combined (Kurczewski 2023a), except *P. basifusca* inhabits montane areas to 2,500 meters (8,202 feet; Vardy 2005). The contiguous north to south Cold Desert of Nevada and western Utah, Mohave Desert, and Sonoran Desert likely serve as a vast, arid physical barrier to the westward migration of this species and may be responsible for its absence from California and Baja California.

Host records for *P. basifusca* capturing wolf spiders (Lycosidae) of the *Hogna carolinensis* species-group (Kurczewski et al. 2020) are erroneous and pertain to *Entypus* (Hymenoptera: Pompilidae: Pepsinae) species (Kurczewski et al., in press). Females of *P. basifusca*, the smallest Nearctic congener, should be expected to capture and provision nests with comparatively small Mygalomorphae like some other species in the *Pepsis menechma* species-group, if Vardy's (2005) species-group is validly constructed (Kurczewski 2023b; Kurczewski et al., in press). *Pepsis amyntas* used the host spider's burrow for a nest, as is probably the case in other *Pepsis menechma* species-group members that are parasitoids on trapdoor and related mygalomorph spiders. *Pepsis basifusca* does not have the obvious pompilid structural characteristics associated with capturing and entombing trapdoor spiders in their own burrows (see Shimizu et al. 2021, 2022; Kurczewski 2023b). For example, *P. basifusca* female heads in dorsal view are rounded, less quadrate, and not adapted for removing wafer- and cork-lid trapdoors as in the stout genae-postgenae and mildly quadrate heads of *P. cerberus* and *P. elegans* females (Kurczewski 2023a, b). Furthermore, the geographic distribution of *P. basifusca* is largely allopatric with the wafer-lid spider genera *Eucteniza* Ausserer, *Myrmekiaphila* Atkinson, and *Entychides* Simon (Euctenizidae) and the cork-lid spider genus *Ummidia* Thorell (Halonoproctidae) (Fig. 5). *Pepsis basifusca* might capture relatively small tarantulas, as *Aphonopelma* species have the same northern geographic distribution limits and occur in the same habitats (Fig. 5–8). If such is the case, this would argue for removal of *P. basifusca* from the *Pepsis menechma* species-group in which the species appear to capture and provision nests with trapdoor spiders and related Mygalomorphae.

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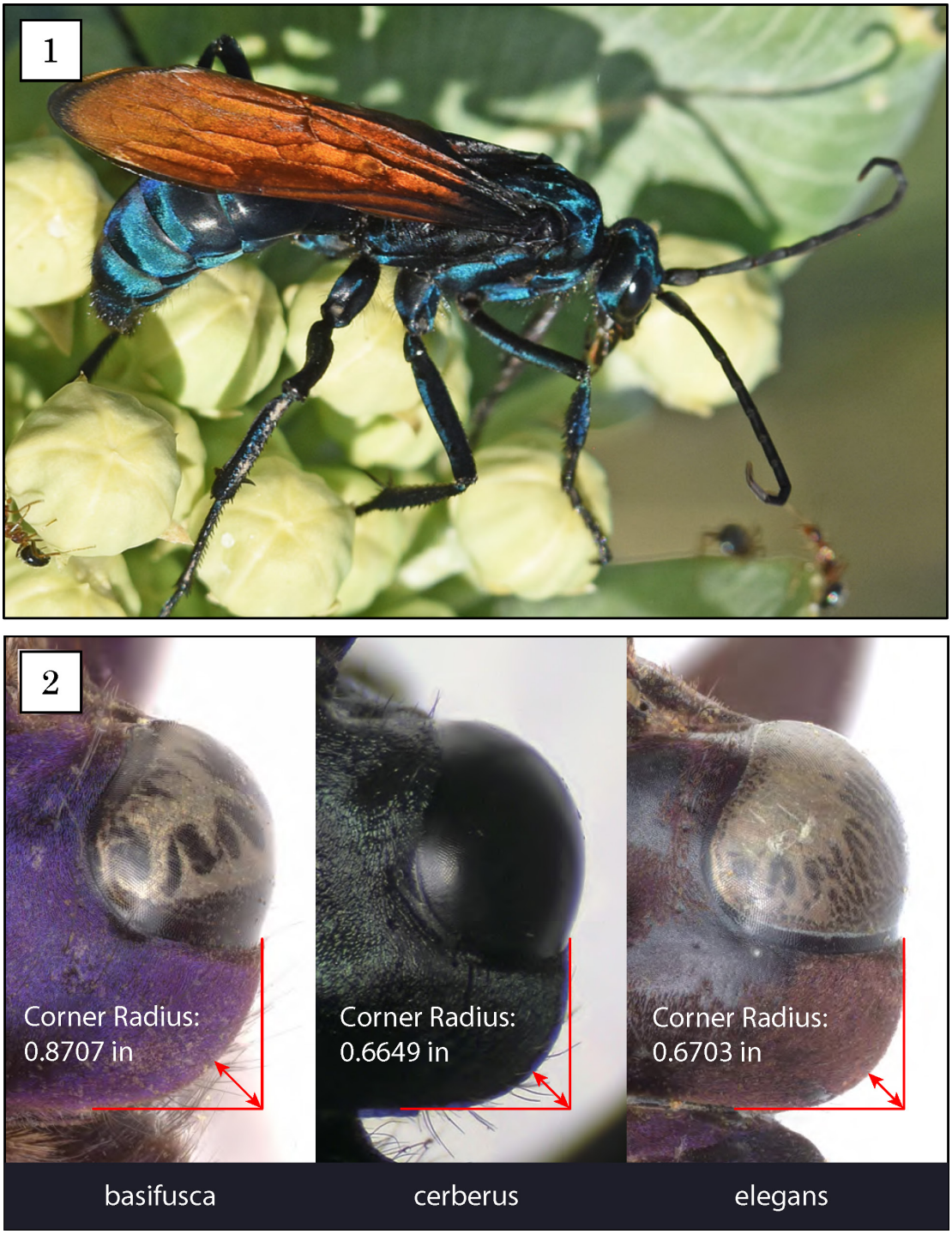
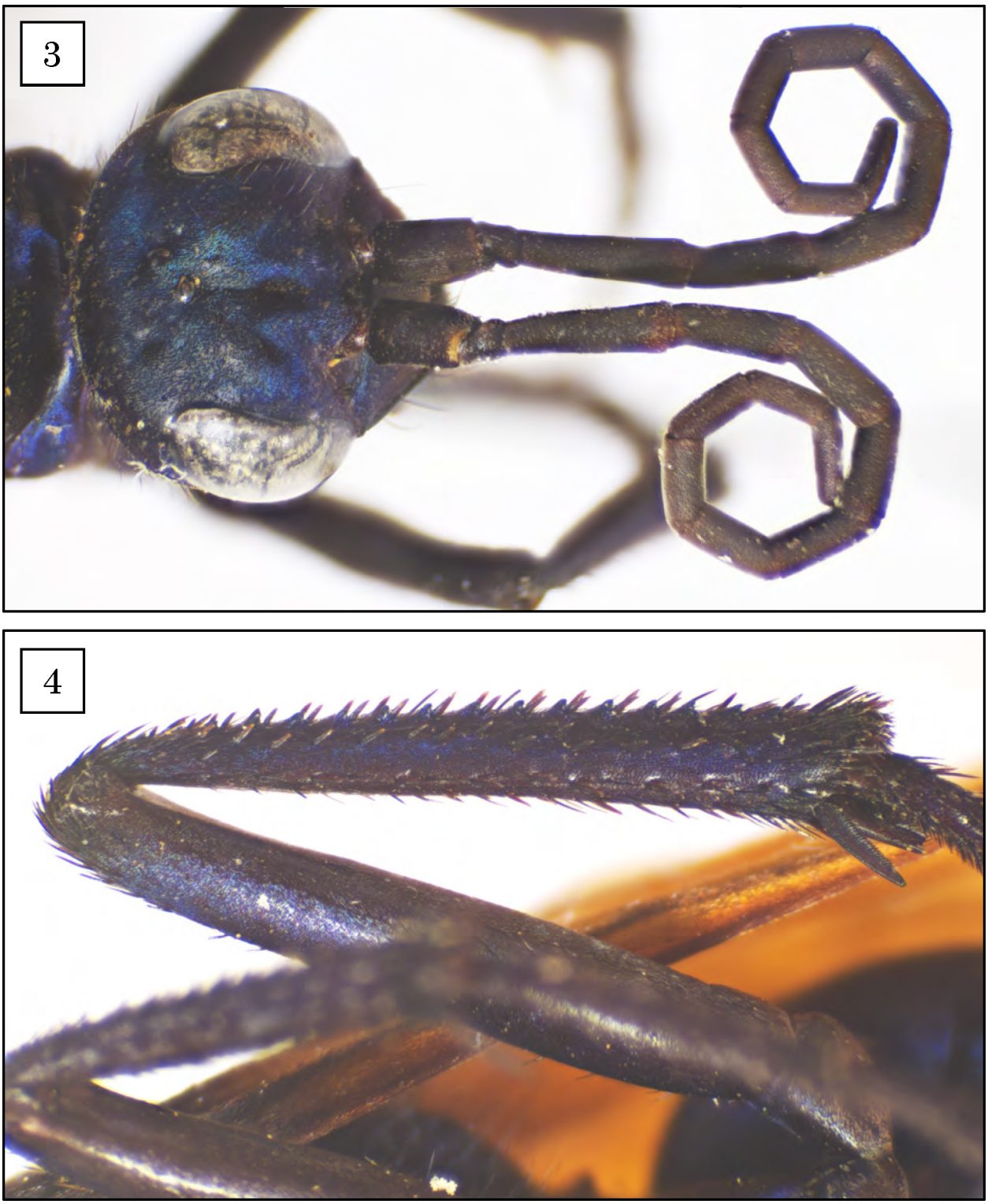
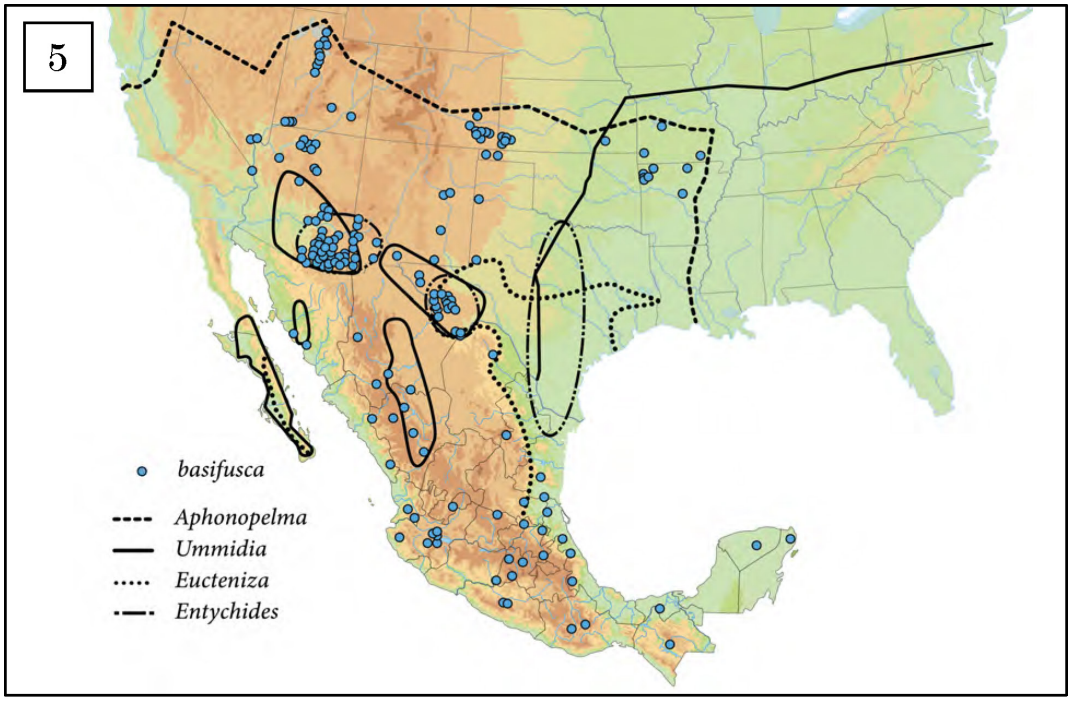
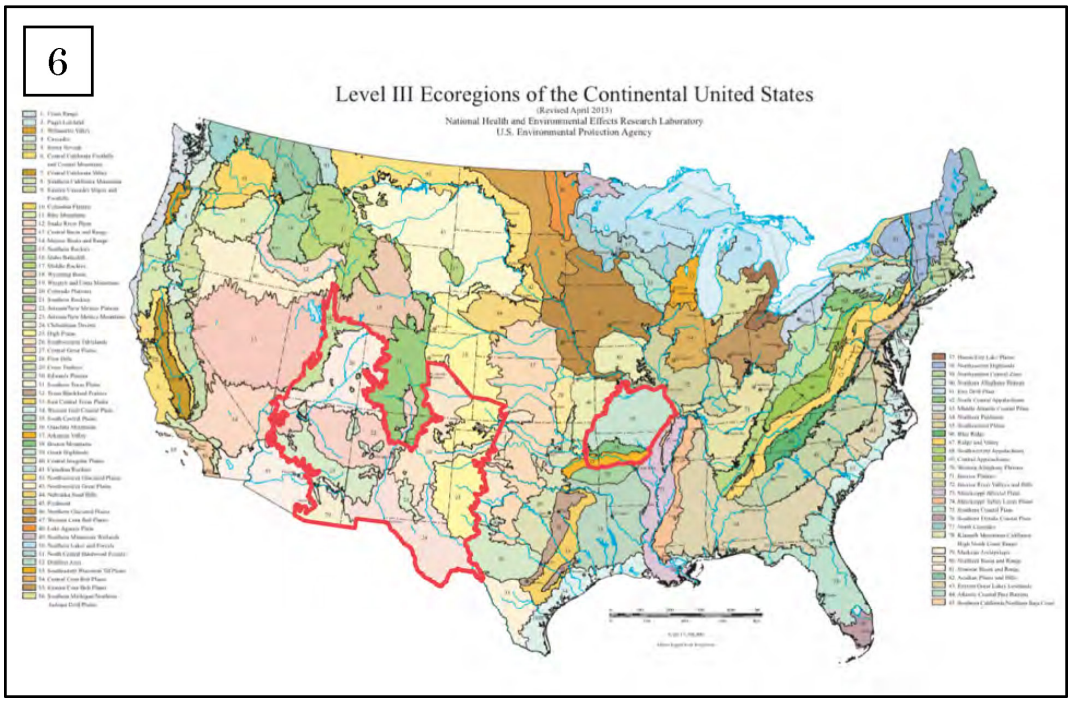



**Figures 1–2.** *Pepsis* spp. **1)** *Pepsis basifusca***.** Female on *Asclepias latifolia* (Torr.) Raf. (Apocynaceae), Withers Canyon, Otero Canyon, Colorado. Note dried mud on right hind tibia and basitarsus and forewing. Photograph © Steven Mlodinow. Species identifications by iNaturalist.org. and Matthias Buck, respectively. **2)** *Pepsis basifusca*, *P. cerberus*, and *P. elegans* female dorsal view of gena-postgena: *P. basifusca*, 5 miles W Portal, Cochise County, Arizona, elevation 5,400 feet. Photograph © Denise Montelongo; *P. cerberus*, 5 miles E Congress, Yavapai County, Arizona. Photograph © Akira Shimizu; *P. elegans*, Eureka Springs, Carroll County, Arkansas. Photograph © Denise Montelongo. Areas in red angles with arrows show genae-postgenae of *P. basifusca*, *P. cerberus*, and *P. elegans*. Length of red arrows indicates gena-postgena of *P. basifusca* is rounder (corner radius: 0.8707) and less quadrate than *P. cerberus* (corner radius: 0.6649) and *P. elegans* (corner radius: 0.6703).

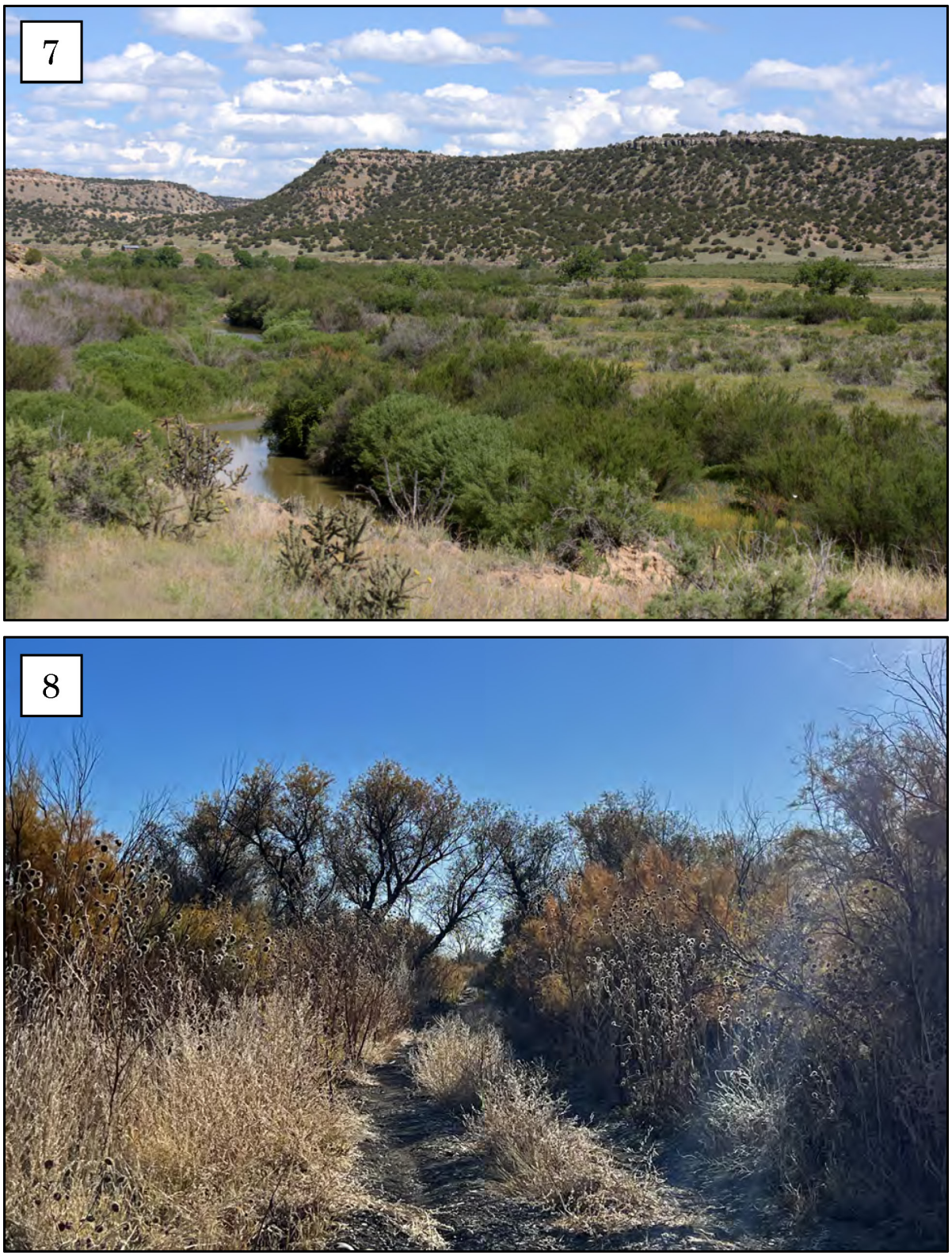



**Figures 3–4.** *Pepsis basifusca*. **3)** Female head and antennae showing moderately short flagellomeres, Box Canyon, Santa Rita Mountains, 6 miles NW Greaterville, Pima County, Arizona. Photograph © Brenna Decker. **4)** Female upper surface of hind tibia with numerous, moderately small, conical, backward-directed serrations; many subtending, short, moderately thick, backward-slanted bristles; and inner and outer spurs, Box Canyon, Santa Rita Mountains, 6 miles NW Greaterville, Pima County, Arizona. Photograph © Brenna Decker.




**Figures 5–6.** Distribution of *Pepsis basifusca*. **5)** Geographic location map for the Nearctic Region (based on Hurd 1952; Evans 1997; Bond and Opell 2002; Vardy 2005; Bond and Godwin 2013; Hamilton et al. 2016; Godwin and Bond 2021; BugGuide.net; flickr.com; iNaturalist.org; gbif.org; SCAN; and specimen records from 16 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* (Euctenizidae) species (Bond and Opell 2002). **6)** Level III Ecoregions in the United States showing areas of occurrence in red outline. Photograph © Commission for Environmental Cooperation Working Group (2006).




**Figures 7–8.** *Pepsis basifusca* habitat. **7)** Picketwire Canyonlands, Otero County, Colorado: red rock with junipers, tall grass, milkweed, and other flowering plants. Photograph © Steven Mlodinow. **8)** Fort Lyon, Bent County, Colorado: weed patch opening among tamarisk near Arkansas River. Photograph © Steven Mlodinow.