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First host record, nesting behavior, and taxonomic position of the spider wasp genus *Hesperopompilus* Evans and some other Evans genera (Hymenoptera: Pompilidae)

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Abstract. First host record, prey transport, and burrow excavation are described for *Hesperopompilus* sp., an undescribed, rare spider wasp (Hymenoptera: Pompilidae) from Texas. Taxonomic, ecological, and behavioral examination of the genus subsequently led to an investigation of the previously related *Perissopompilus* Evans and *Xerochaes* Evans. Taxonomic, host preference, nesting behavior, and phylogenomic relationships of the three taxa are discussed along with those of *Xenopompilus* Evans. The molecular connection of *Perissopompilus* and *Allochaes* Banks is supported by their common use of host species of Filistatidae.

Key words. *Pompilus*, *Xenopompilus*, *Perissopompilus*, *Xerochaes*, *Ammosphex*, Araneidae, Filistatidae, Thomisidae, Sparassidae.

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Introduction

Evans (1951), in his taxonomic study of the spider wasp tribe Pompilini (Hymenoptera: Pompilidae: Pompilinae), described the comparatively rare subgenera *Xerochaes* and *Perissopompilus* and re-described the comparatively rare genus *Hesperopompilus* Evans (1948), grouping these taxa adjacently in the large worldwide genus *Pompilus* Fabricius. *Pompilus* resembles *Anoplius* Dufour in many structural features but can be distinguished from that genus in the female by the absence of stiff bristles on the apical metasomal tergum and in the male by the toothed tarsal claws (Evans 1951, 1966a; Wasbauer and Kimsey 1985). Evans (1953, 1960, 1968) later described and added the rare subgenus *Xenopompilus* to this group of three subgenera, rearranging them in *Pompilus* in the following phylogenetic order: *Hesperopompilus*, *Xenopompilus*, *Perissopompilus*, and *Xerochaes*. Krombein (1979) and Wasbauer and Kimsey (1985) reaffirmed Evans (1951, 1966a) subgeneric arrangement in *Pompilus* despite the attempts of European workers, notably Day (1981), to elevate the four subgenera to genus status. Evans (1990), in agreement with Krombein (1979) and Wasbauer and Kimsey (1985), referenced *Pompilus silvivagus* Evans. However, Evans (1997) listed the genera *Hesperopompilus* and *Arachnophila* Kincaid, including *Arachnospila* (*Ammosphex*) *silvivaga* (Evans), in his *Spider Wasps of Colorado* following Day's (1981) narrow interpretation of *Pompilus*, with little explanation of their elevated generic status. *Hesperopompilus*, *Xenopompilus*, *Perissopompilus*, and *Xerochaes* were classified thereafter on multiple websites (e.g., BugGuide, Flickr, iNaturalist) as genera, not subgenera. Finally, the four subgenera established by Evans (1948, 1951, 1953) were treated as separate genera by Pitts et al. (2005), Horta-Vega et al. (2009), Wasbauer and Kimsey (2010), Castro-Huertas et al. (2014), Waichert et al. (2015), Rodriguez et al. (2015), and Fernández et al. (2022) based on morphological, host preference, nesting behavior, and, especially, phylogenomic criteria.

Hesperopompilus, *Xenopompilus*, *Perissopompilus*, and *Xerochaes* are restricted to the western Nearctic Region with intrusions into the northern Neotropical Region (Evans 1951, 1966a, 1968; Day 1981; Wasbauer and Kimsey 1985; Castro-Huertas et al. 2014; Fernández et al. 2022). The four taxa are adapted to semi-arid and arid environments including desert scrub, xeric grassland, chaparral, and dry open oak woodland (Evans 1951, 1966a; Wasbauer and Kimsey 1985). Until recently essentially nothing was known of their nesting biology, including host spiders, except for flower visitation records (Evans 1951, 1966a, b; Wasbauer and Kimsey 1985). The advent and expansion of online websites such as BugGuide.net, iNaturalist.org, and flickr.com coupled with existing literature enabled us to investigate the habitat, host preference, and nesting behavior of species in these genera with disparate biological results. Given below in modified taxonomic order following the *Catalog of Hymenoptera North of Mexico* under family Pompilidae (Krombein 1979) is the sparse amount of available literature and online information for *Hesperopompilus* sp. (undescribed), *Perissopompilus phoenix* (Evans), *Ammophila anomalous* (Dreisbach) [previously misidentified as *Perissopompilus phoenix* (Kurczewski et al. 2017)], and *Xerochaes expulsus* (Schultz). The information on *Hesperopompilus* represents the first host record and details of nesting behavior for this genus.

Materials and Methods

Frank Kurczewski, in examining recent photographs on iNaturalist.org, recognized an unusual “Pompilus-type” spider wasp with an especially atypical host spider for this group of Pompilidae. He emailed the link to James Pitts, Utah State University, who identified the spider wasp as an undescribed species of *Hesperopompilus*, a comparatively rare genus in western North America, and for which Pitts has male but no female specimens from Texas. Rick West, Sarah Crews, and Kurczewski separately identified the host spider as belonging to the orb-weaver family Araneidae and arachnologist David Allen Dean, more specifically, as *Eustala anastera* (Walckenaer). Because of the comparative rarity of *Hesperopompilus* and other comparatively rare and rare Evans spider wasp genera, we further investigated the taxonomy, ecology, nesting biology, and phylogenomics of *Hesperopompilus* and the genera once considered to be closely related to this genus. Frank Kurczewski wrote the manuscript. West retouched iNaturalist.org and flickr.com photographs of the spider wasps and host spiders for use as Figures 1–4.

Results

Hesperopompilus sp. (undescribed) [det. J. P. Pitts] was photographed at Martinez, Bexar County, Texas by Yukioz (2022). His two photographs illustrate the mechanics of prey transport and nest excavation. In Figure 1 the wasp grasped an immobilized *Eustala anastera* (Walckenaer) (Araneidae), adult or subadult female [det. D. A. Dean], by its left second coxa with her mandibles and dragged the spider backwards across an exposed tree rootlet. The spider was held slightly above the substrate in a cephalothorax upright position. Figure 2 shows the wasp in front of her nest entrance excavating a burrow in sandy soil using her forelegs alternately. She held her apical antenna segments against the floor of the opening and wings flat on the dorsum.

Evans (1966b) reported a *Perissopompilus phoenix* with a paralyzed *Filistata* sp. [= *Kukulcania* sp. (Filistatidae)], juvenile [det. H. W. Levi], from 7 miles NE of Desert Center, Riverside County, California collected by Paul D. Hurd, Jr. The wasp dragged the crevice weaver spider backwards across sparsely vegetated soil and through *Larrea* bushes.

Jackson (1994, 2002) presented a second host association for *Perissopompilus phoenix*. On Islas Flecha and Cerraja in the Gulf of California off the coast of Bahía de Los Ángeles, Baja California Norte, México, *P. phoenix* [det. C. T. Jackson], presumably the commonest spider wasp on the islands, was reportedly the major parasitoid on *Metepeira arizonica* Chamberlin and Ivie (Araneidae), adult and subadult female [det. G. A. Polis], the most abundant spider on the islands [Jackson, unpublished MS (1994) and PhD (2002) theses]. The spiders dropped from their webs to the ground and disappeared beneath cholla cacti detritus when the wasps were flying in the vicinity (Jackson, pers. comm.). The wasps disappeared under rocks and cacti detritus and were later seen dragging paralyzed spiders backwards across the ground (Jackson, pers. comm.).



Figures 1–2. *Hesperopompilus* sp. (undescribed). **1)** Female dragging a *Eustala anastera* (Araneidae), adult or subadult female, backwards across an exposed tree rootlet, grasping the immobilized orb-weaver spider by its left second coxa with her mandibles. The spider was held slightly above the substrate in a cephalothorax upright position. **2)** Female in front of her nest entrance excavating a burrow in sandy soil using her forelegs alternately. She held her apical antenna segments against the floor of the opening and wings flat on her dorsum. Photographs © Yukioz.



Figures 3–4. Pompilid spp. and their hosts. **3)** *Ammosphex anomalus*, identified initially as *Perissopompilus phoenix*, female dragging a *Xysticus* sp. (Thomisidae), adult female, backwards across stony ground, grasping the femur of its right hind leg with her mandibles. Photograph © Alice Abela. **4)** *Xerochaeres expulsus* female dragging an *Olios giganteus* (Sparassidae), immature male, backwards across the ground, grasping the trochanter of its left foreleg with her mandibles. Photograph © Kelly Harrington.

Ammosphex anomalus [det. F. E. Kurczewski, J. P. Pitts], misidentified initially as *Perissopompilus phoenix* in Kurczewski et al. (2017), was photographed on Mount Pinos, Los Padres National Forest, Ventura County, California by Alice Abela (2016). The wasp, 8.8 mm long, grasped an immobilized *Xysticus* sp. (Thomisidae), adult female [det. G. B. Edwards], 6.2 mm long, by its left or right hind leg with her mandibles and dragged it rapidly backwards across stony and gravelly ground (Fig. 3), pausing periodically to examine the spider with her antennae and mouthparts.

Xerochares expulsus [det. F. E. Kurczewski] was photographed by Marco Alejandro Sanzón (2021) at Angostura, Angostura Municipality, Sinaloa State, México straddling an immobilized *Curicaberis ?culiacan* Rheims (Sparassidae), adult female [det. C. A. Rheims]. The wasp, atop the huntsman spider, which was dorsal side upward, grasped its left pedipalp with her mandibles as she rested with the spider on a dried leaf (Kurczewski et al. 2022).

Kelly Harrington (2022) photographed and videographed a *Xerochares expulsus* [det. F. E. Kurczewski] with an immobilized *Olios giganteus* Keyserling (Sparassidae), immature male [det. R. C. West], at the Boyce Thompson Arboretum, Superior, Pinal County, Arizona. The wasp, with raised wings, stood beside the immobilized huntsman spider and examined it with her mouthparts as it lay on the ground in a cephalothorax upright position. She, then, pulled the spider slowly and jerkily backwards across the ground, grasping the trochanter of its left foreleg with her mandibles (Fig. 4; Kurczewski et al. 2022).

Sergio Escutia Zúñiga (2022) photographed a *Xerochares expulsus* [det. F. E. Kurczewski] using her mandibles and forelegs to excavate in moist crumbly soil at Concordia, Sinaloa, México.

Discussion

Hesperopompilus and *Xenopompilus* are allied to each other and to the Tribe Aporini, including *Psorthaspis* Banks and *Aporus* Spinola, while *Perissopompilus* is allied to *Evagetes* Lepageletier, *Arachnospila*, *Anoplochares* Banks, *Ammosphex* Wilcke, *Xerochares*, and *Allochares* Banks based mainly on phylogenomic studies (Rodríguez et al. 2015; Waichert et al. 2015). *Hesperopompilus* and *Xenopompilus* are not closely allied to *Perissopompilus* and *Xerochares* based on molecular evidence in contrast to their 1950s close connection based on morphological similarities (Rodríguez et al. 2015; Waichert et al. 2015). *Perissopompilus* and *Allochares* are not only linked phylogenomically but the two genera capture the same host filistatid genus: *Kukulcania* sp. for *Perissopompilus phoenix* (Evans 1966b); and *Kukulcania hibernalis* (Hentz) for *Allochares azureus* (Cresson) (Deyrup et al. 1988). Filistatidae is an extremely rare host family for Pompilidae—only two records are known worldwide. *Kukulcania hibernalis*, the southern house spider, makes flat tangled webs in crevices under tree bark, in root hollows, and, commonly, in corners inside outbuildings and under bridges (Edwards, pers. comm.). The wasp attacks the spider by chasing it from its web through the back opening and onto the ground (Deyrup et al. 1988). In *A. azureus* females, the legs are very smooth with few minute spines and the body is devoid of erect hairs (Evans 1951; Deyrup et al. 1988). *Perissopompilus phoenix* females have unusually weakly spinose legs and smooth body without erect hairs (Evans 1951; Deyrup et al. 1988). Such morphological features in these disparate species probably enable the wasps to maneuver through the flat tangled web in search of potential host spiders without getting entangled.

There are several inconsistencies in Jackson's (1994, 2002) two unpublished theses on the parasitoids of *Metepeira arizonica*. He made no mention of *Perissopompilus phoenix* in his M. S. thesis (1994) despite this species purportedly being the major spider wasp parasitoid of *M. arizonica*. Jackson (pers. comm.) did not see the wasps capture the spiders nor observe them nesting. There are no specimens of *P. phoenix* in the Vanderbilt University or University of Georgia insect collections from which Jackson received his M. S. and Ph. D. degrees, respectively. Jackson (pers. comm.) identified *P. phoenix* from specimens collected in Malaise traps, using Wasbauer and Kimsey's (1985) key, and this identification was reportedly confirmed by Marius Wasbauer (Jackson, pers. comm.). Yet there are no Jackson specimens of *P. phoenix* in the Marius S. Wasbauer Pompilidae Collection at the University of California–Davis (Kimsey, pers. comm.). Jackson (pers. comm.) claims to have the specimens of *P. phoenix* from his study site, but he has not produced any examples despite several requests for them from us. Given these issues, as well as the differences in behavioral repertoire necessary to hunt these two divergent

families of spiders (Filistatidae, Araneidae), we believe his association is likely erroneous and is most likely a misidentification of *Agenioideus humilis* (Cresson) or a species of *Episyron*, which hunt only orb-weaver spiders, are the same size and color as *P. phoenix*, and have an overlapping geographic distribution.

Eustala anastera (Araneidae), the humpbacked orbweaver, is a surprising first host record for the heretofore biologically unstudied genus *Hesperopompilus*. Araneidae is associated in the Nearctic Region as the exclusive host spider family of *Agenioideus humilis*, *Caliadurgus fasciatellus* (Spinola), and species of *Episyron* Schiødte and *Poecilopompilus* Howard. *Eustala anastera* is probably attacked by *Hesperopompilus* on or near its web, forcing the spider to drop to the ground whereupon it is caught, stung, and immobilized.

Crab spiders (Thomisidae) are not web-makers and exhibit a different method of predation. Species of *Xysticus* C. L. Koch live under loose bark, leaves, and shrubs on the ground, and on low plants where they capture unsuspecting prey by ambush (Kaston 1948). Our record of *Xysticus* sp. for *Ammosphex anomalus* supports the initial host record of *X. cunctator* Thorell for this spider wasp species by Wasbauer and Powell (1962).

The two recent host records for *Xerochares expulsus* from Arizona, USA and Sinaloa, México reveal specificity for huntsman spiders (Sparassidae) (Kurczewski et al. 2022). Based on these records, huntsman spiders may be the exclusive or preferred host spider family for *X. expulsus*. Huntsman spiders are large, nocturnal, fast-moving cursorial hunters. *Xerochares expulsus* females are significantly larger (11.5–17.0 mm, Evans 1966a) than those of species of the other Evans genera (4.5–12.0 mm, Evans 1966a) and, consequently, capture significantly larger spiders.

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