ISRAEL JOURNAL OF ENTOMOLOGY, Vol. 50 (1), pp. 49–64 (3 August 2020)

A review of species identifications of North American *Aphonopelma* Pocock, 1901 (Araneae: Theraphosidae) in papers noting attacks by *Pepsis* Fabricius, 1804 (Hymenoptera: Pompilidae)

Danniella Sherwood* & Ray Gabriel

Arachnology Research Association, United Kingdom.
**Corresponding author: danni.sherwood@hotmail.com*

ABSTRACT

A literature review of works noting the attack of theraphosid spiders by wasps of the genus *Pepsis* Fabricius, 1804 in the United States is presented. The specific identifications of the host taxa in these papers are revisited and discussion on their probable correct identifications is given.

KEYWORDS: Tarantula spider, tarantula hawk wasp, identification, review, literature, taxonomy, Nearctic, United States.

INTRODUCTION

At present, the only genus of the family Theraphosidae Thorell, 1869 recognised within the United States is *Aphonopelma* Pocock, 1901, although this genus has been highlighted in both molecular and morphological studies to be an unsuitable taxon to house North American material, an issue that will have future implications for the systematics of these charismatic spiders (Hamilton *et al.* 2016; Turner *et al.* 2018; Sherwood 2019). The taxonomy of pompilid wasps in the United States is also fairly current, with two genera *Pepsis* Fabricius, 1804 and *Hemipepsis* Dahlbom, 1844 recorded within its borders, both genera being known to attack and hunt mygalomorph spiders.

The identification of theraphosid spiders in the United States was made significantly easier following the publication of Hamilton *et al.* (2016). Even in the absence of voucher specimens it is possible in many cases (except in overlap areas where two morphologically indistinguishable sister species occur) to narrow down a most suitable candidate taxon based on location, habitat type, time of year and the general habitus of specimens from a photograph.

The first scientific report of theraphosid spiders being hunted by pompilid wasps in the United States was by Lincecum (1867), who detailed observations in the first volume of the *American Naturalist*. Over six decades later, Petrunkevitch (1926) studied in detail the interactions between the wasp *Pepsis marginata* Palisot de Beauvois, 1809 [= *Pepsis reaumuri* Dahlbom, 1845 per Vardy (2002)] and the Puerto Rican theraphosid *Cyrtopholis portoricae* Chamberlin, 1917. Passmore

DOI: 10.5281/zenodo.3970538; ISSN (online) 2224-6304
urn:lsid:zoobank.org:pub:43777772-6211-4525-9116-01E7D7AC022F

(1936) gave detailed photographs—the first of their kind—of his observations of theraphosid attacks by wasps in California. Petrunkevitch (1952) gave a second detailed account of an attack focusing on *C. portoricae* as the host species once again. Earlier, Kellogg (1908) had told of an intense battle between a wasp and a tarantula, resulting in both parties succumbing from their wounds.

During the latter half of the 20th century, more studies were conducted on pompilid wasps and their host interactions. Williams (1956) conducted detailed life studies on pompilids in California and contributed important information to how they incapacitate and manoeuvre theraphosid hosts. Baerg (1958) briefly mentioned being brought dead wasps and spiders by his students whilst teaching at the university campus in Fayetteville, Arkansas. Cazier and Mortenson (1964) added more observational data on wasp-spider interactions. After this period, research appears to have stagnated until Cooke (1985) briefly described and lavishly illustrated his observations from Arizona.

The end of the 1980s marked a prolific period in publications on pompilid-theraphosid interactions. Punzo and Garman (1989) detailed *Pepsis* attacking a theraphosid species in a laboratory setting. This was followed by numerous studies by Fred Punzo in the 1990s and 2000s (Punzo 1994*a*, *b*, 2005*a–c*, 2006, 2007; Punzo & Ludwig 2005), which massively contributed towards current understanding of *Pepsis* behaviour and ecology in the United States. These works were a combination of laboratory and in situ based papers, thus providing datasets for multiple contexts. During this period, Vardy (2000, 2002, 2005) significantly added to the taxonomy of the genus *Pepsis* revising most species recognised at the time and describing numerous new taxa, whilst also summarising all available literature dealing with *Pepsis* wasps hunting theraphosid spiders. Most recently, Kurczewski and Edwards (2012) and Kurczewski *et al.* (2017) published monographs on the life history of pompilid wasps in the United States and provided lists of new records of theraphosids being attacked by *Pepsis* species.

In this work, we examine literature noting the hunting and attack of theraphosid spiders by pompilid wasps of the genus *Pepsis* in the United States (Table 1). Many of these works utilised old (now synonymised or invalid) binomial names or simply misidentified host species. Herein, we discuss and suggest their possible modern and valid equivalents in an attempt to better place these studies in a modern context.

MATERIALS AND METHODS

Literature noting theraphosid spiders in the United States as hosts of *Pepsis* were reviewed and descriptive text and figures (if applicable) compared against descriptions and figures in Hamilton *et al.* (2016) and against our own notes and data collected from *Aphonopelma* (*sensu lato*) examined in museum collections (e.g. Sherwood 2019).

Table 1. Summary of original identifications of theraphosid spiders in literature noting their hunting by *Pepsis* wasps with herein proposed modern identifications and notes.

Original reference(s)	Identification(s) in original work	Suggested modern identification(s)	Notes
Lincecum (1867)	*Aphonopelma hentzi*	*Aphonopelma hentzi*	Original identification is congruent with modern taxonomic hypotheses.
Kellogg (1908)	*Eurypelma* [*sic*]	*Aphonopelma iodius*	Only theraphosid species in the vicinity of Stanford University (per Hamilton *et al.*, 2016).
Passmore (1936)	*Aphonopelma steindachneri*	*Aphonopelma steindachneri* and also possibly *Aphonopelma eutylenum* [one figure only]	Original identification is congruent with modern taxonomic hypotheses but one figure may also illustrate the additional sympatric species. This would be the first time it were recorded in the published literature if so.
Williams (1956)	*Aphonopelma* sp.	*Aphonopelma iodius*	Only theraphosid species on Mount Diablo (per Hamilton *et al.*, 2016).
Baerg (1958)	*Dugesiella hentzi*	*Aphonopelma hentzi*	Only theraphosid species in Arkansas (per Hamilton *et al.*, 2016), species-level identification in initial work entirely correct, only generic nomen outdated.
Cazier & Mortensen (1964)	*Aphonopelma chalcodes*	*Aphonopelma chalcodes*	Original identification is congruent with modern taxonomic hypotheses.
Cooke (1985)	*Aphonopelma* sp.	*Aphonopelma chalcodes* and possibly other sympatric *Aphonopelma* spp. [= *A. gabeli* and/or *A. chiricahua*]	Only one photo demonstrates a readily identifiable specimen based on colour of carapace pubescence. Other photos could illustrate other sympatric species.
Punzo & Garman (1989)	*Rhestochia echina* [*sic*]	*Aphonopelma hentzi*	We provide a presumptive identification, based on locality and previous name applied by original work which is a junior synonym of *A. hentzi*.

Table 1. Summary of original identifications of theraphosid spiders in literature noting their hunting by *Pepsis* wasps with herein proposed modern identifications and notes. *(continued)*

Original reference(s)	Identification(s) in original work	Suggested modern identification(s)	Notes
Punzo (1994*a, b*)	*Aphonopelma echina*	*Aphonopelma hentzi*	We provide a presumptive identification, based on locality and previous name applied by original work which is a junior synonym of *A. hentzi*.
Punzo (2005*a–c*)	*Aphonopelma steindachneri*	*Aphonopelma gabeli*	We provide a presumptive identification, the spider cannot be *A. steindachneri* as this species does not occur in Texas. *A. gabeli* has a somewhat similar habitus to that of *A. steindachneri* and does occur in BBNP.
Punzo & Ludwig (2005)	*Aphonopelma moderatum* and *Aphonopelma texense*	*Aphonopelma moderatum* and *Aphonopelma anax*	*A. texense* no longer a valid taxon and the spider under this name in this work is very likely to be *A. anax*.
Punzo (2006)	*Aphonopelma harlingenum* and *Aphonopelma heterops*	*Aphonopelma anax* and *Aphonopelma moderatum*	*A. anax* and *A. moderatum* are the only species known to occur in this area. The paratype of *A. harlingenum* was a misidentified specimen of *A. anax* whilst *A. heterops* is a junior synonym of *A. moderatum*.
Punzo (2007)	*Aphonopelma steindachneri*	*Aphonopelma gabeli*	See above comments for Punzo (2005*a–c*).
Kurczewski & Edwards (2012)	*Aphonopelma anax*	*Aphonopelma anax*	Original identification is congruent with modern taxonomic hypotheses and photographs are consistent with habitus of *A. anax*.
Kurczewski *et al.* (2017)	*Aphonopelma* cf. *anax*, *Aphonopelma chalcodes*, *Aphonopelma hentzi*, *Aphonopelma* cf. *harlingenum* and *Aphonopelma steindachneri*	*Aphonopelma anax*, *Aphonopelma chalcodes*, *Aphonopelma hentzi*, *Aphonopelma anax* and *Aphonopelma steindachneri*	Original identifications (with exception of *A*. cf. *harlingenum*) are congruent with modern taxonomic hypotheses. Specimens identified as *A.* cf. *harlingenum* likely to be *A. anax* given location.

RESULTS AND DISCUSSION

Lincecum (1867) discussed the species *Aphonopelma hentzi* (Girard, 1853) being hunted by pompilids in Texas. This species was the first to be formally described from the United States (Girard 1853; Smith 1995, 2015), as *Mygale hentzii* Girard, 1853. The distinctive colouration of female *A. hentzi*, consisting of sooty black leg pubescence, beige/gold carapace pubescence and long, bright red hairs on the legs and opisthosoma (Fig. 1), meant it was likely readily recognisable to many across its large range. The taxonomic identity of *A. hentzi* was not revisited until the latter half of the 20th century when Smith (1995), upon finding the type material to be lost, designated a neotype from Oklahoma. However, in the same paper he split many populations formally considered as *A. hentzi* into new species based on select morphological characteristics. This approach, based on small sample sizes, was to be challenged by Prentice (1997, 2005) and an integrative morphological and molecular analysis by Hamilton *et al.* (2016) found many of the *hentzi* species-group taxa described by Smith (1995) and yet others described earlier by Chamberlin (1940) to be synonymous with *A. hentzi*.

Kellogg (1908) noted a "*Eurypelma*" (a generic name now invalid) in California attacked by a wasp, the end result being the spider and the wasp both dying from injuries inflicted from each other. This observation was made near the campus of Stanford University where Kellogg worked, and the only theraphosid species in this area is (per Hamilton *et al.* 2016) *Aphonopelma iodius* (Chamberlin & Ivie, 1939), and this can thus confidently be proposed as the modern identification for the host taxon.

Passmore (1936) photographed and documented *Aphonopelma steindachneri* (Ausserer, 1875) around San Diego as a host of *Pepsis grossa* (Fabricius, 1798) [cited as *Pepsis formosa* (Say, 1823)]. One figure (Passmore 1936: 156, fig. 2) shows what appears to be a mature female specimen with black leg pubescence. The other figures predominately show an attack on an adult male of *A. steindachneri*, a further specimen of indeterminable sex in the burrow of a wasp and interestingly a more hirsute male (Passmore 1936: 156, fig. 1), which could be the sympatric *Aphonopelma eutylenum* Chamberlin, 1940. In the latter species, males typically possess long setae densely covering the legs and the dorsal opisthosoma (Fig. 2), in contrast with the less hirsute males of *A. steindachneri* (Fig. 3). Thus, it is possible that Passmore (1936) actually records two species in his work, which would suggest he could also have been the first author to record the hunting of two theraphosid species by the same *Pepsis* species within a single work.

Williams (1956) refers to the theraphosids in his work simply as *Aphonopelma* sp., although he notes that he did not attempt to identify the spiders to the species level. The theraphosid material used in his work was collected on Mount Diablo (Williams 1956: 450) and he provides photographs of a specimen being attacked by a wasp. Given the location and the fact that the carapace and leg pubescence can be seen to be light (despite the fact the photographs are in black and white),

Figs 1, 2: (1) *Aphonopelma hentzi* (Girard, 1853), adult female habitus; (2) *Aphonopelma eutylenum* Chamberlin, 1940, adult male habitus. (Photos: C.A. Hamilton, University of Idaho, US.)

Figs 3, 4: (3) *Aphonopelma steindachneri* (Ausserer, 1875), adult male habitus; (4) *Aphonopelma iodius* (Chamberlin & Ivie, 1939), adult female habitus. (Photos: (3) C.A. Hamilton, University of Idaho, US; (4) D. Sherwood.)

the theraphosid material used in his work can now be confidently identified as *A. iodius*. This species (Fig. 4) is the only theraphosid taxon known to occur in Contra Costa, California (per Hamilton *et al.* 2016). Baerg (1958) mentions being brought dead wasps and spiders (cited as *Dugesiella hentzi*) by his students in Arkansas, who presumably would see them in battle, there is only one theraphosid species in the area (per Hamilton *et al.* 2016), *A. hentzi*, and thus Baerg's species-level identification was entirely correct. Eight years later, Cazier and Mortensen (1964) observed the hunting of *Aphonopelma chalcodes* Chamberlin, 1940 in Arizona and correctly identified this species in their work. Later, Cooke (1985) depicted a number of specimens of *Aphonopelma* being hunted by *Pepsis* in the Chiricahua Mountains of Arizona. At least one of the specimens is *A. chalcodes* (Cooke 1985: 65, fig. 3) evident from the beige/blond leg pubescence and dark colouration of the tarsi and the basal half of the metatarsi. However, the male specimen depicted cannot be identified to the species level as the carapace pubescence is not easily viewable and several species occur in the Chiricahua Mountains. The colour of the carapace pubescence is useful for diagnosing adult males of *A. chalcodes* (Fig. 5) from sympatric species in the Chiricahuas [= *Aphonopelma gabeli* Smith, 1995 and *Aphonopelma chiricahua* Hamilton *et al.*, 2016, which have black carapace pubescence upon maturity, fading to dark brown in aged specimens] providing a dorsal view of the carapace can be seen clearly.

Punzo and Garman (1989) reference the theraphosid species in their work as "*Rhestochia echina* (Simon)" [*sic*], but in actuality the species in question was originally described by Chamberlin (1940) as *Dugesiella echina* Chamberlin, 1940 and was not mentioned in any publication by Eugène Simon. Later encompassed into *Aphonopelma* as the result of the generic synonymies of Raven (1985), this species was treated as a junior synonym of *A. hentzi* by Hamilton *et al.* (2016). Punzo (1994*a*, *b*) later referred to the spider as *A. echina*. In all three works, research was focused around the Trans Pecos and as such, in conjunction with the historical name applied to the spider in these papers, we deduce *A. hentzi* is indeed the most likely candidate for the host taxon.

Punzo (2005*a*) considers the host species of his studies in Big Bend National Park (BBNP), Texas, to be *A. steindachneri* but this species is restricted to California and Northern Baja California (iNaturalist 2020) and does not occur in Texas (Hamilton *et al.* 2016). It is likely that most erroneous historical records of this species in Texas, in both taxonomic and ecological works, could actually relate to specimens of the Texan species *Aphonopelma armada* Chamberlin, 1940, with which *A. steindachneri* shares a prominent dorsoposterior black spot on the opisthosoma (Smith 1995; Hamilton *et al.* 2016), but *A. armada* does not occur in BBNP. Two species are commonly encountered in BBNP: *A. hentzi* and *A. gabeli* evidenced by both distributional data in Hamilton *et al.* (2016), and numerous photographic records viewed by the first author on the website *iNaturalist*. A third species, *Aphonopelma moellendorfi* Hamilton, 2016 is also recorded but is enigmatic and

all currently known details of this species stem from its original description (Chris Hamilton pers. comm.). Whilst females of *A. hentzi* have beige coloured carapace pubescence with sooty black leg pubescence, females of *A. gabeli* have blond/beige leg pubescence (Fig. 6). Adult males of *A. gabeli* have almost completely black

5

6

Figs 5, 6: (5) *Aphonopelma chalcodes* Chamberlin, 1940, adult male habitus; (6) *Aphonopelma gabeli* Smith, 1995, adult female habitus. (Photos: D. Sherwood.)

Fig. 7: *Aphonopelma gabeli* Smith, 1995, adult male habitus. (Photo: R. Gabriel.)

carapace pubescence with black leg pubescence (Fig. 7), the colour of the carapace pubescence fades to a more dull brown as specimens age. Thus, both sexes can easily be distinguished visually from the sympatric species *A. hentzi*. The Californian species *A. steindachneri* also has dark carapace pubescence in both sexes and it is possible that the specimens identified in Punzo (2005*a*) actually correspond to *A. gabeli*. This said, as specimens are not illustrated in their works it is not possible to be entirely certain of the specific identity, but *A. steindachneri* can easily be ruled out as a viable candidate given its divergent biogeographical range. Punzo (2005*b*, *c*) also lists *A. steindachneri* as the theraphosid host species in his other works but again, these identifications are erroneous.

In the same year, Punzo and Ludwig (2005) conducted field work in Zapata County, Texas, where they noted the theraphosid host species to be *Aphonopelma moderatum* (Chamberlin & Ivie, 1939) and *Aphonopelma texense* (Simon, 1891). *Aphonopelma moderatum* is a common species in this area with unmistakeable female habitus (Fig. 8), but *A. texense* is a taxon with a complicated history and the holotype male likely was not collected in the United States at all (Smith 1995; Hamilton *et al.* 2016). It is possible that the specimens referred to as *A. texense* in Punzo and Ludwig (2005) are in actuality *Aphonopelma anax* Chamberlin, 1940 (Fig. 9) the only other species known to occur in sympatry with *A. moderatum* in Zapata County (per Hamilton *et al.* 2016).

A year later, Punzo (2006) published yet more valuable data on *Pepsis* behaviour, detailing in situ observations in Hidalgo County, Texas, citing *Aphonopelma*

Figs 8, 9: Adult female habitus: (8) *Aphonopelma moderatum* (Chamberlin & Ivie, 1939); (9) *Aphonopelma anax* (Chamberlin, 1940). (Photos: C.A. Hamilton, University of Idaho, US).

harlingenum Chamberlin, 1940 and *Aphonopelma heterops* (Chamberlin & Ivie, 1939) as the host theraphosid species. The holotype of *A. harlingenum* was treated as synonymous with *A. hentzi* by Hamilton *et al.* (2016), but they considered the paratype to be conspecific with *A. anax*. We have so far, only seen viable records of *A. anax* from Hidalgo County (iNaturalist 2020) and consider that the material assigned to *A. harlingenum* by Punzo (2006) likely corresponds to *A. anax*. *Aphonopelma heterops* was later synonymised with *A. moderatum* by Hamilton *et al.* (2016) and this distinctive species was likely the second one observed in Punzo (2006). *Aphonopelma moderatum* can be found sympatrically with *A. anax* in southernmost Texas and in Northern Mexico (Hamilton *et al.* 2016; iNaturalist 2020), but can be easily distinguished by the striking colouration of the leg pubescence, consisting of alternate black and gold bands.

Punzo (2007) conducted another field study in BBNP, referring to the theraphosid species as *A. steindachneri*. As discussed above, this species does not occur in Texas and it is probable that the species in question was in fact *A. gabeli*, a common sympatric species in which the males have black carapace pubescence. Kurczewski and Edwards (2012: 4) depict a photograph of a specimen of *A. anax* being attacked by *Pepsis* sp. and the photograph clearly shows features (namely the robust femora) in conjunction with locality data satisfactory to identify the specimen as this species. Five years later, Kurczewski *et al.* (2017) noted the following *Aphonopelma* species in their monographic work on pompilid wasps: *A.* cf. *anax*, *A. chalcodes*, *A. hentzi*, *A.* cf. *harlingenum* and *A. steindachneri* mostly based on photographs published online by various individuals. Of these five listed species, four remain as valid species, but as discussed above *A. harligenum* is not presently a valid taxon. Given the locality data and examination of the online photographic records, we believe the other four species level identifications to be correct and suggest, based on biogeography and examination of the photo of Crispin (2007), which shows a spider with robust femora with short, dark coloured and sparsely distributed, setae on the lateral faces, that the theraphosid host referred to as *A.* cf. *harlingenum* conforms to *A. anax*.

CONCLUSIONS

Overall, most studies featuring North American *Aphonopelma* (*sensu lato*) being hunted and attacked by *Pepsis* wasps focus on species in the *hentzi*, *iodius* and *moderatum* species-groups (*sensu* Hamilton *et al.* 2016). These species groups represent the most widely distributed taxa in terms of North American theraphosid biogeography and thus it is unsurprising that they have, as a result, become the focus of many insightful and significant studies on their fates following attacks by wasps of the genus *Pepsis*. The previously unstable and perplexing state of North American theraphosid systematics undoubtedly contributed to the wide range of species names utilised in these studies to correspond to theraphosid hosts. Whilst examination of physical specimens to determine morphological and molecular data is the ideal situation for species identification, the comprehensive data of Hamilton

et al. (2016) can enable some identifications based on biogeography in combination with secondary features such as colouration and other characteristics of the habitus. As such, some of the outdated identifications presented in ecological and behavioural works presented above can be confidently resolved. Others represent areas of apprehension, but reasonable candidates can be proposed tentatively.

The ecology and behaviour of theraphosid spiders is of great research importance and have direct impacts on understanding other areas of their study such as biogeography, conservation, and reproductive biology. By attempting to link historical names, or at least demonstrate viable candidate species, in these papers to currently accepted binomial names we hope to increase the significance of older studies in a modern context. Collective information on *Aphonopelma* (*sensu lato*) in North America, both in taxonomical and ecological contexts, is increasing (e.g. Hamilton *et al.* 2016; Turner *et al.* 2017; Steinman & Sherwood 2018; Hendrixson 2019; Sherwood 2019). Furthermore, it is hoped that the present endeavour will stimulate further research in wasp-spider interactions.

ACKNOWLEDGEMENTS

Lou Sorkin (American Museum of Natural History), Julian Jensen – grandson of Lee Passmore – (Idaho, US), and Andrew Smith (United Kingdom) are warmly thanked for helping provide literature. Chris Hamilton (University of Idaho) gave invaluable comments on an early draft of the manuscript and allowed use of some of his photographs. The first author also thanks Daniel Waysman (Israel) for invaluable assistance with Hebrew translations. Two reviewers who supplied many useful comments, improving the layout and contents are also thanked.

REFERENCES

Ausserer, A. 1875. Zweiter Beitrag zur Kenntniss der Arachniden-Familie der Territelariae Thorell (Mygalidae Autor). *Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien* **25**: 125–206.
https://www.biodiversitylibrary.org/page/16420158#page/229

Baerg, W.J. 1958. *The Tarantula*. University of Kansas Press, Lawrence, Kansas, 88 pp.

Cazier, M.A. & Mortenson, M. 1964. Bionomical observations on tarantula-hawks and their prey (Hymenopteras: Pompilidae: *Pepsis*). *Annals of the Entomological Society of America* **57** (5): 533–541.
https://doi.org/10.1093/aesa/57.5.533

Chamberlin, R.V. 1917. New spiders of the family Avicularíidae. *Bulletin of the Museum of Comparative Zoology* **61** (3): 25–75.
https://www.biodiversitylibrary.org/page/4311043#page/49

———1940. New American tarantulas of the family Avicularíidae. *Bulletin of the University of Utah* **30** (13): 1–39.
https://core.ac.uk/reader/276282374

Chamberlin, R.V. & Ivie, W. 1939. New tarantulas from the southwestern states. *Bulletin of the University of Utah* **29** (11): 1–17.
https://core.ac.uk/download/pdf/276282369.pdf

Cooke, J.A.L. 1985. Of sting and fang. *Science 85* **6** (1): 64–69.

Crispin, P. 2007. Wasp with Tarantula – *Pepsis*. http://bugguide.net/node/view/156506 (accessed 30/07/2020).

Dahlbom, A.G. 1843–1845. *Hymenoptera europaea praecipue borealia... per familias, genera, species et varietates disposita atque descripta*. [Vol. 1]. Officina Lundbergiana, Lund. 528 pp.
https://www.europeana.eu/en/item/9200520/ark__12148_bpt6k99155j

Fabricius, J.C. 1798. *Supplementum entomologiae systematicae*. Proft et Storch, Hafniae. 572 pp. https://www.biodiversitylibrary.org/item/219022#page/5

———1804. *Systema Piezatorum*. Carolum Reichard, Brunsvigae. 439 pp. https://www.biodiversitylibrary.org/item/41385#page/5

Girard, C. 1853. Arachnidians. *In*: Marcy, R. (Ed.), *Natural History of the Red River of Louisiana*. Washington, 32nd Congress, 2nd Session, Senate Appendix F (Zoology), pp. 262–271.

Hamilton, C.A., Hendrixson, B.E. & Bond, J.E. 2016. Taxonomic revision of the tarantula genus *Aphonopelma* Pocock, 1901 (Araneae, Mygalomorphae, Theraphosidae) within the United States. *ZooKeys* **560**: 1–340. https://doi:10.3897/zookeys.560.6264

Hendrixson, B.E. 2019. A new species of *Aphonopelma* (Araneae: Mygalomorphae: Theraphosidae) from the Madrean pine-oak woodlands of northeastern Sonora, Mexico. *Zootaxa* **4688** (4): 519–534. https://doi.org/10.11646/zootaxa.4688.4.4

iNaturalist. 2020. *iNaturalist*. http://inaturalist.org (accessed 30/07/2020).

Kellogg, V.L. 1908. *Insect Stories*. George Bell & Sons, London. 298 pp.

Kurczewski, F.E. & Edwards, G.B. 2012. Hosts, nesting behavior, and ecology of some North American spider wasps (Hymenoptera: Pompilidae). *Southeastern Naturalist* **11** (m4): 1–71. https://doi.org/10.1656/058.011.m401

Kurczewski, F.E., Edwards, G.B. & Pitts, J. P. 2017. Hosts, nesting behavior, and ecology of some North American spider wasps (Hymenoptera: Pompilidae), II. *Southeastern Naturalist* **16** (m9): 1–82. https://doi.org/10.1656/058.016.m901

Lincecum, G. 1867. The tarantula killers of Texas. *American Naturalist* **1**: 137–141. https://doi.org/10.1086/270037

Palisot de Beauvois, A.M.F.J. 1805–1821. *Insectes recueillis en Afrique et en Amérique dans les royaumes d'Oware et de Benin, á Saint-Domingue et dans les États Unis, pendant les années 1786-1797*. Fain et compagnie, Paris. 267 pp.

Passmore, L. 1936. Tarantula and tarantula hawk. *Nature Magazine* **27** (3): 155–159.

Petrunkevitch, A. 1926. Tarantula versus tarantula hawk wasp: A study in instinct. *Journal of Experimental Biology* **45** (2): 367–394. https://doi.org/10.1002/jez.1400450202

———1952. The spider and the wasp. *Scientific American* **187**: 20–24. https://doi.org/10.1038/scientificamerican0952-20

Pocock, R.I. 1901. Some new and old genera of S.-American Avicularidae. *Annals and Magazine of Natural History* (7) **8** (48): 540–555. https://doi.org/10.1080/03745480109443359

Punzo, F. 1994*a*. The biology of the spider wasp *Pepsis thisbe* (Hymenoptera: Pompilidae) from Trans Pecos Texas. I. Adult morphometrics, larval development and the ontogeny of larval feeding. *Psyche* **101**: 229–241. https://doi.org/10.1155/1994/70378

———1994*b*. The biology of the spider wasp *Pepsis thisbe* (Hymenoptera: Pompilidae) from Trans Pecos Texas. II. Temporal patterns of activity and hunting behavior, with special reference to the effects of experience. *Psyche* **101**: 243–256. https://doi.org/10.1155/1994/27564

———2005*a*. Studies on the natural history, ecology and behavior of *Pepsis cerberus* and *Pepsis mexicana* (Hymenoptera: Pompilidae) from Big Bend National Park, Texas. *Journal of the New York Entomological Society* **113** (1): 84–95. https://doi.org/10.1664/0028-7199(2005)113[0084:SOTNHE]2.0.CO;2

———2005*b*. Experience affects hunting behavior of the wasp, *Pepsis mildei* Stål (Hymenoptera: Pompilidae). *Journal of the New York Entomological Society* **113** (3): 222–229. https://doi.org/10.1664/0028-7199(2005)113[0222:EAHBOT]2.0.CO;2

———2005*c*. The effect of encounter experience on hunting behavior in the spider wasp, *Pepsis cerberus* Lucas (Hymenoptera: Pompilidae). *Texas Journal of Science* **57** (2): 165–174. https://www.biodiversitylibrary.org/item/248727#page/175

———2006. Effect of host odor cues on behavioral responses of the spider wasp, *Pepsis formosa* (Hymenoptera: Pompilidae). *Texas Journal of Science* **58** (1): 45–54.
https://www.biodiversitylibrary.org/item/249810#page/51

———2007. Interspecific variation in hunting behavior of *Pepsis grossa* (Fabricius) and *Pepsis thisbe* Lucas (Hymenoptera: Pompilidae): a field study. *Journal of Hymenoptera Research* **16** (2): 297–310.
https://www.biodiversitylibrary.org/page/2658703#page/89

Punzo, F. & Garman, B. 1989. Effects of encounter experience on hunting behavior of the spider wasp, *Pepsis formosa* (Say) (Hymenoptera: Pompilidae). *Southwestern Naturalist* **34** (4): 513–518.
https://doi.org/10.2307/3671510

Punzo, F. & Ludwig, L. 2005. Behavioral responses of *Pepsis thisbe* (Hymenoptera: Pompilidae) to chemosensory cues associated with host spiders. *Journal of Insect Behaviour* **18** (6): 757–766.
https://doi.org/10.1007/s10905-005-8738-0

Prentice, T.R. 1997. Theraphosidae of the Mojave Desert west and north of the Colorado River (Araneae, Mygalomorphae, Theraphosidae). *Journal of Arachnology* **25**: 137–176.
https://www.biodiversitylibrary.org/page/52992333#page/147

———2005. Theraphosidae. *In*: Ubick, D., Paquin, P., Cushing, P.E. & Duperre, N. (Eds.), *Spiders of North America: An identification manual*. American Arachnological Society, New Hampshire. 377 pp.

Raven, R.J. 1985. The spider infraorder Mygalomorphae (Araneae): Cladistics and systematics. *Bulletin of the American Museum of Natural History* **182**: 1–180.
http://hdl.handle.net/2246/955

Say, T. 1823. Descriptions of some new species of hymenopterous insects collected during the expedition to the Rocky Mountains under the command of Major Long 1819–20. *Western Quarterly Reporter of Medical, Surgical and Natural Science* **2**: 71–82.

Sherwood, D. 2019. *Aphonopelma braunshausenii* Tesmoingt, 1996 is a *nomen dubium*, with review of some historic morphological characters ineffective at species delineation (Araneae: Theraphosidae). *Zootaxa* **4657** (3): 573–580.
https://doi.org/10.11646/zootaxa.4657.3.9

Simon, E. 1891. Liste des espéces de la famille des Avicolariidae qui habitent le Mexique et l'Amérique du Nord. *Actes de la Société Linnéenne de Bordeaux* **44**: 307–326.
https://www.biodiversitylibrary.org/item/87652#page/315

Smith, A.M. 1995. *Tarantula Spiders: Tarantulas of the U.S.A. and Mexico*. Fitzgerald Publishing, London, 196 pp.

———2015. *Aphonopelma hentzi* – named after a very spiritual spider man, also additional notes on the historical type material and the locality where the type specimen was collected in June (not May) 1852. *Journal of the British Tarantula Society* **30** (1): 12–18.

Steinman, M. & Sherwood, D. 2018. Some notes and observations on a predation of *Anaxyrus boreas halophilus* (Baird & Girard, 1853) by *Aphonopelma steindachneri* (Ausserer, 1875) (Araneae: Theraphosidae). *Newsletter of the British Arachnological Society* **143**: 14–16.

Thorell, T. 1869. On European spiders. *Nova Acta Regiae Societatis Scientiarum Upsaliensis, Ser.* 3 **7**: 1–108.
https://www.biodiversitylibrary.org/page/15372575#page/159

Turner, S.P., Longhorn, S.J., Hamilton, C.A., Gabriel, R., Pérez-Miles, F. & Vogler, A.P. 2018. Re-evaluating conservation priorities of New World tarantulas (Araneae: Theraphosidae) in a molecular framework indicates non-monophyly of the genera, *Aphonopelma* and *Brachypelma*. *Systematics and Biodiversity* **16** (1): 89–107.
https://doi.org/10.1080/14772000.2017.1346719

Vardy, C.R. 2000. The New World tarantula-hawk wasp genus *Pepsis* Fabricius (Hymenoptera: Pompilidae). Part 1. Introduction and the *P. rubra* species-group. *Zoologische Verhandelingen* **332**: 1–86.
https://repository.naturalis.nl/document/46285

———2002. The New World tarantula-hawk wasp genus *Pepsis* Fabricius (Hymenoptera: Pompilidae). Part 2. The *P. grossa* to *P. deaurata* groups. *Zoologische Verhandelingen* **337**: 1–134.
https://repository.naturalis.nl/document/46718

———2005. The New World tarantula-hawk wasp genus *Pepsis* Fabricius (Hymenoptera: Pompilidae). Part 3. The *P. inclyta* to *P. auriguttata* groups. *Zoologische Mededelingen* **79** (5): 1–305. http://repository.naturalis.nl/document/42157

Williams, F.X. 1956. Life history studies of *Pepsis* and *Hemipepsis* wasps in California (Hymenoptera: Pompilidae). *Annals of the Entomological Society of America* **49** (5): 447–466. https://doi.org/10.1093/aesa/49.5.447