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## CONSPECIFIC POLLEN ON INSECTS VISITING FEMALE FLOWERS OF *PHORADENDRON JUNIPERINUM* (VISCACEAE) IN WESTERN ARIZONA

William D. Wiesenborn<sup>1</sup>

**ABSTRACT.**—*Phoradendron juniperinum* (Viscaceae) is a dioecious, parasitic plant of juniper trees (*Juniperus* [Cupressaceae]) that occurs from eastern California to New Mexico and into northern Mexico. The species produces minute, spherical flowers during early summer. Dioecious flowering requires pollinating insects to carry pollen from male to female plants. I investigated the pollination of *P. juniperinum* parasitizing *Juniperus osteosperma* trees in the Cerbat Mountains in western Arizona during June–July 2016. I examined pollen from male flowers, aspirated insects from female flowers, counted conspecific pollen grains on insects, and estimated floral constancy from proportions of conspecific pollen in pollen loads. The tricolpate pollen from *P. juniperinum* was subangular in shape with open furrows in polar view and oval-spherical in shape in equatorial view. Most insects on flowers were small (<3 mm in length). Insects carrying conspecific pollen to female flowers included 6 species of Hymenoptera in 6 families and 6 species of Diptera in 5 genera and 4 families. Conspecific pollen was found on 41% of the insects, with only 18% carrying >1 grain, and numbers of grains on insects did not differ among the species collected. *Phoradendron juniperinum* was most likely pollinated by 2 species of flies in *Hippelates* (Chloropidae) and *Desmometopa* (Milichiidae) and 1 species of parasitic wasp in *Apanteles* (Braconidae). Insects in these genera were widespread and frequently collected, with half of specimens carrying conspecific pollen that comprised most of the pollen load. Other Diptera carrying conspecific pollen included 1 species in *Olcella* (Chloropidae), 2 species in *Mythicomomyia* (Mythicomomyiidae), and 1 species in Scatopsidae. Other Hymenoptera with conspecific pollen included 1 species of bee in *Lasioglossum* (Halictidae), 1 species of wasp in *Parancistrocerus* (Vespidae), and 3 species of parasitic wasps in Chalcidoidea. Minute flies, such as Tephritidae or Chloropidae, are the most common pollinators among *P. juniperinum* and the 2 other examined species of *Phoradendron* (*P. californicum* and *P. coryae*). Pollination of *Phoradendron* likely differs among species due to different host plants, plant communities, and flowering seasons.

**RESUMEN.**—*Phoradendron juniperinum* (Viscaceae) es una planta dioica parasitaria que crece en los juníperos, *Juniperus* (Cupressaceae), y que se encuentra presente desde el este de California hasta Nuevo México y en el norte de México. Estas especies producen flores esféricas diminutas al comienzo del verano. Esta floración dioica necesita de insectos polinizadores que trasladen el polen desde las plantas macho a las hembras. Durante junio–julio del año 2016, investigué la polinización de *P. juniperinum* parasitando en los árboles de *Juniperus osteosperma* en las montañas Cerbat, al oeste de Arizona. Examiné el polen de las flores macho, los insectos aspirados de las flores hembra, contabilicé el polen conspecifico en insectos y estimé la constancia floral a partir de las proporciones del polen conspecifico en los cargamentos de polen. El polen tricollado de *P. juniperinum* presentó forma subangular, con surcos abiertos en dirección al polo y forma oval-esférica en dirección ecuatorial. La mayoría de los insectos en las flores eran pequeños (<3 mm de longitud). Entre los insectos que transportaron polen conspecifico hacia las flores hembra se incluyeron 6 especies de Hymenoptera de 6 familias, y 6 especies de Diptera de 5 géneros y 4 familias. Encontramos polen conspecifico en 41% de los insectos, donde sólo 18% acarreo > 1 grano, y un gran número de granos en los insectos no difirió entre las especies colectadas. La planta *Phoradendron juniperinum* fue, probablemente, polinizada por 2 especies de moscas, *Hippelates* (Chloropidae) y *Desmometopa* (Milichiidae), y por 1 especie de avispas parasitarias, *Apanteles* (Braconidae). Encontramos a estos insectos muy esparcidos y, a menudo, los colectamos junto a la mitad de los especímenes portadores de polen conspecifico que abarcaron la mayor parte del cargamento de polen. Otros Diptera portadores de polen conspecifico incluyeron 1 especie de *Olcella* (Chloropidae), 2 especies de *Mythicomomyia* (Mythicomomyiidae) y 1 especie de Scatopsidae. Otros himenópteros con polen conspecifico incluyeron 1 especie de abejas *Lasioglossum* (Halictidae); 1 especie de avispas, *Parancistrocerus* (Vespidae); y 3 especies de avispas parasitarias, Chalcidoidea. Las moscas diminutas, tales como las Tephritidae o las Chloropidae, son los polinizadores más comunes entre los *P. juniperinum* y entre las otras especies examinadas de *Phoradendron* (*P. californicum* y *P. coryae*). La polinización de *Phoradendron* probablemente difiere de entre las demás especies debido a las diferentes plantas huéspedes, a las comunidades de plantas y a las temporadas de floración.

*Phoradendron* (Viscaceae), or mistletoe, is a genus of perennial plants that parasitize branches or trunks of a variety of woody plants

(Trelease 1916, Wiens 1964, Kuijt 2003). The genus includes 234 species distributed from the northern United States to northern Argentina

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and from the eastern Pacific islands to the eastern Caribbean (Kuijt 2003). Most *Phoradendron* plants are around 1 m in diameter and consist of a mass of hanging stems that support scale-like or expanded leaves. Mistletoes obtain water and other inorganic nutrients from their host plants by tapping into xylem with their haustoria and produce organic nutrients from photosynthesis in leaves and stems (Kuijt 1969, 2003).

Flowers on *Phoradendron* (Kuijt 2003) are unisexual, typically around 1 mm in diameter, and borne on spike-like inflorescences. Male flowers are spherical with 3 or 4 petals that surround and individually support a minute, sessile anther. Female flowers are similar but contain a short style with an indistinct rounded or faintly bilobed stigma atop an inferior ovary. Both sexes of *Phoradendron* flowers were described by Trelease (1916) as containing a small vestigial nectar gland and “apparently adapted to pollination by such short-tongued insects as flies and small bees.” Kuijt (1969) also described Viscaceae flowers as pollinated primarily by insects, mostly Hymenoptera. *Phoradendron* fruits are eaten by birds that disperse seeds by defecation (Larson 1996, Kuijt 2003).

Dioecious flowering in many *Phoradendron* species enables the study of pollination by examination of conspecific pollen loads on insects visiting flowers on female plants. This approach was used in the only other studies of mistletoe pollination by examining *Phoradendron californicum* Nuttall parasitizing *Acacia greggii* A. Gray (Fabaceae) in southern Nevada and *Phoradendron coryae* Trelease parasitizing *Quercus turbinella* E. Greene (Fagaceae) in western Arizona (Wiesenborn 2016a, 2016b). Female flowers on *P. californicum* during winter were visited by 3 species of bees and wasps in Hymenoptera and 13 species of flies in Diptera that carried conspecific pollen. Flies in Tephritidae and Calliphoridae were most likely to pollinate the plant. Different species of insects carrying conspecific pollen visited female flowers on *P. coryae* during summer. Flower visitors included 2 species of Coleoptera, 1 species of Hymenoptera, and 6 species of Diptera. Plants were most likely pollinated by a species of beetle in Melyridae and 2 species of flies in Chloropidae.

*Phoradendron juniperinum* Engelm ex A. Gray, or juniper mistletoe, is a dioecious

species of mistletoe found mostly on species of *Juniperus* (Cupressaceae) but also on other genera in the family (Kuijt 2003). Juniper mistletoe ranges from southern Oregon southward through eastern California into northern Baja California and eastward into southwestern Colorado, western New Mexico, and northern Mexico (Kuijt 2003, fig. 57). *Phoradendron juniperinum* differs from a second species of mistletoe on juniper, *Phoradendron bolleanum* (Seemann) Eichler, by its scale-like rather than broad leaves. *Phoradendron juniperinum* is the only mistletoe on junipers in western Arizona (Kearney and Peebles 1951, Kuijt 2003). The plant flowers during June and July (Hawksworth and Wiens 2002). Inflorescences produce 5–9 flowers on male plants and 2 flowers on female plants (Hawksworth and Wiens 2002; Kuijt 2003, fig. 144).

Pollination of *P. juniperinum* parasitizing *Juniperus osteosperma* (Torrey) Little in western Arizona was investigated by examining pollen loads on insects visiting female flowers. I considered the following questions: (1) What taxa of insects carry *P. juniperinum* pollen to female flowers? (2) Do individuals of these taxa carry different amounts of *P. juniperinum* pollen? (3) How specific are these insects to *P. juniperinum* flowers based on pollen loads? (4) Which taxa of insects are more likely to pollinate *P. juniperinum*? (5) Are the taxa of insects carrying pollen to female flowers on *P. juniperinum* different from those on *P. californicum* and *P. coryae*?

## METHODS

The study was conducted in the Cerbat Mountains, 33 km northwest of Kingman, Mohave County, Arizona. Insects were collected from *P. juniperinum* plants parasitizing *J. osteosperma* along Big Wash Road, an unpaved road that ascends eastward from U.S. Highway 93. *Juniperus osteosperma* was the dominant juniper in the area and grew between 1165 and 1477 m elevation along the road. *Phoradendron juniperinum* was found between 1213 and 1411 m elevation, where the density of *J. osteosperma* was greatest.

I sampled 7 female *P. juniperinum* plants on different juniper trees for insects. The plant sampled at the lowest elevation (1280 m; 35.457° N, 114.225° W) was 1.0 km west of the plant sampled at the highest elevation (1321 m;

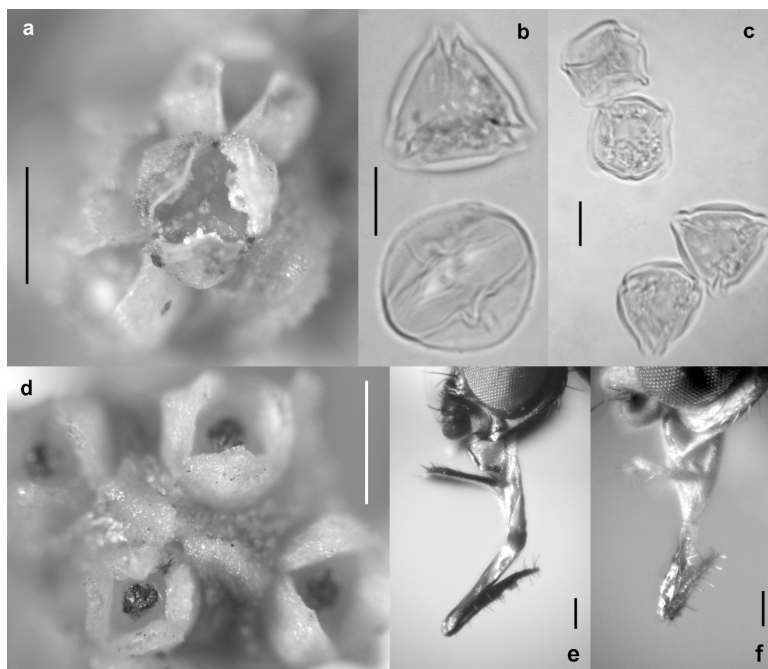


Fig. 1. *Phoradendron juniperinum* parasitizing *Juniperus osteosperma* in the Cerbat Mountains near Kingman, Arizona, during July 2016: a, male flowers; b–c, brightfield photomicrographs of pollen; b, grains in polar (top) and equatorial (bottom) views; c, grains in different aspects; d, female flowers; e–f, lateral views of fly mouthparts; e, *Desmometopa* sp. (Milichiidae); f, *Hippelates* sp. (Chloropidae). Scale bars in panels a and d are 1 mm; scale bars in panels b and c are 10 µm; scale bars in panels e and f are 0.1 mm.

35.461°N, 114.215°W). Abundances of juniper mistletoe varied from rare at the lowest plant to common at the highest plant. Sampled plants were 15–28 cm in diameter and grew 1.5–2.5 m above ground on junipers 3–7 m in height. Trees with sampled plants supported different abundances of male *P. juniperinum*. Two host trees supported >5 male plants, 2 trees supported at least 1 male plant, and on 3 host trees male plants were absent and not apparent on nearby trees. I deposited a pressing (UNLV 64832) of a host *J. osteosperma* tree, a *P. juniperinum* female plant, and a nearby male plant at the Wesley E. Niles Herbarium, University of Nevada, Las Vegas. Sampled plants were within interior chaparral (Pase and Brown 1982) with *J. osteosperma* dominating the overstory and *Pinus monophylla* Torrey & Frémont (Pinaceae) distributed sparsely near the higher plants. Nearby shrubs included scattered *Quercus turbinella* E. Greene, *Acacia greggii* A. Gray (Fabaceae), *Yucca baccata* Torrey (Agavaceae), *Cylindropuntia acanthocarpa* (Engelmann & J.M. Bigelow) F.M. Knuth (Cactaceae), and *Opuntia*

*basilaris* Engelmann & J. Bigelow (Cactaceae). Groundcover consisted of *Eriogonum fasciculatum* Benth (Polygonaceae) and *Gutierrezia* sp. (Asteraceae). The area is grazed by cattle at low density. Distributions of *P. juniperinum* and its congeners narrowly overlapped along Big Wash Road. *Phoradendron californicum* on *A. greggii* and *P. juniperinum* both occurred at low density within 1213–1248 m elevation, and *P. coryae* on *Q. turbinella* and *P. juniperinum* both occurred within 1280–1411 m elevation.

Insects were collected from *P. juniperinum* female flowers on 15 dates, starting 21 June 2016 when female flowers began to open and ending 22 July 2016 when plants began to dry out. Female flowers were recognized with a hand lens by their dark red stigmas and typical occurrence in pairs, although some inflorescences produced 4 flowers (Fig. 1d). Male flowers (Fig. 1a) were first seen to open on 11 June 2016. I individually aspirated insects into a 125-mL plastic screw-capped flask containing a 4-dram glass vial with 4 mL of 70% EtOH. All insects landing on or walking onto female flowers were aspirated. Insects were

collected from each plant for 10–60 min on each date for a total of 20.2 h between 07:50 and 11:10 Mountain Standard Time. Air temperature during collections was 24–35 °C, relative humidity was 21%–32%, cloud cover was 0%–60%, and wind speed was <10 km/h. Only one rainfall event during 1 June–22 July 2016 was evident from wet soil on 2 July 2016. Rainfall during this period was not measured at the closest (4 km east) automated gauge (Packsaddle Mountain; MCFCD 2016). *Eriogonum fasciculatum* flowered abundantly early during the study, and *Gutierrezia* sp. flowered sparsely late in the study.

Pollen from *P. juniperinum* was examined after mounting the grains in polyvinyl alcohol (Dafni 1992). I collected male inflorescences into 70% EtOH during 8–15 July 2016 and vortexed pollen from the flowers. Alcohol containing pollen was centrifuged at 3400 revolutions per minute for 5 min, and then the alcohol was drawn off and replaced with 3.5 mL of water. I poured the water and suspended pollen into a 100-mL teflon evaporating dish and added 1 mL of a 12% solution of hydrolyzed polyvinyl alcohol. The mixture was vortexed and dried for 2 h at 45 °C. Pollen grains embedded in the resulting clear plastic film were viewed with brightfield microscopy, measured with an eyepiece reticle at 400×, photographed through a 100× oil-immersion objective lowered onto the film, and described following figure 11.3 in Faegri et al. (1989).

Pollen on insects aspirated from female flowers was also extracted, mounted, and examined. Each collection vial was vortexed for 30 s, and the alcohol and suspended pollen was centrifuged as above. I drew off the alcohol, replaced it with 4 mL of water, centrifuged the pollen suspension a second time, drew off the water, and added 0.6 mL of water. The water and pollen was mixed and transferred with a pipette into a 35-mL porcelain evaporating dish. I added 0.3 mL of the polyvinyl alcohol solution to the dish, and the mixture was vortexed and dried for 1.5 h at 45 °C. This produced a 25-mm-diameter circular film containing pollen from each insect. Insects were mounted on points after drying in hexamethyldisilazane to prevent shrinkage (Brown 1993), except for wasps in Vespidae, which were pinned. I examined the entire area of each circular film for pollen. The film was pressed between 2 microscope

slides and scanned at 100× with a compound microscope by moving the stacked slides with a mechanical stage. I recognized pollen grains by their yellow color and symmetrical shape, categorized grains as *P. juniperinum* or as differing from *P. juniperinum*, and counted grains in each category. Pollen was counted as *P. juniperinum* if it matched the size, shape, furrowing, and mottling of pollen collected from male flowers. Pollen that could not be distinguished as *P. juniperinum* at 100× was viewed at 200×. Numbers of pollen grains in both categories were summed to calculate the total pollen load on each insect. Tricolpate pollen differing from *P. juniperinum* was also described, following Faegri et al. (1989).

Species of insects with >1 specimen captured on *P. juniperinum* female flowers were identified to the lowest taxonomic rank possible. Parasitic wasps in Chalcidoidea were identified only if they carried *P. juniperinum* pollen. I keyed Coleoptera to family with Borror et al. (1981) and to genus with Jackman and Lu (2002) and Kingsolver (2002). Hymenoptera, except Vespidae, were identified to family or to Chalcidoidea with Triplehorn and Johnson (2005). Braconidae were keyed to subfamily with van Achterberg (1990) and to genus with Mason (1981). Halictidae were identified to genus and subgenus with Michener (2000). Vespidae were keyed to family and subfamily with Borror et al. (1981), to genus with Carpenter (2004), and to species with Bohart (1952). Chalcidoidea were identified to family or genus by Roger Burks. I keyed Diptera to family with McAlpine (1981). Scatopsidae were identified to tribe with Cook (1981), and Mythicomyiidae were identified to genus with Hall (1981) and to species with Melander (1960). I keyed Tachinidae to genus with Wood (1987), Milichiidae to genus with Sabrosky (1987a), and Chloropidae to genus with Sabrosky (1987b). I compared identified specimens with those at the Entomology Research Museum, University of California, Riverside, and deposited vouchers of species carrying pollen at the museum (UCRC-ENT 496370–90). Lengths of insects were measured with an uninstalled ocular reticle. I photographed the mouthparts on 2 species of flies that had been vortexed to remove pollen at different focal planes and overlaid the photographs with Zerene Stacker version 1.04 (Zerene Systems, Richland, WA).

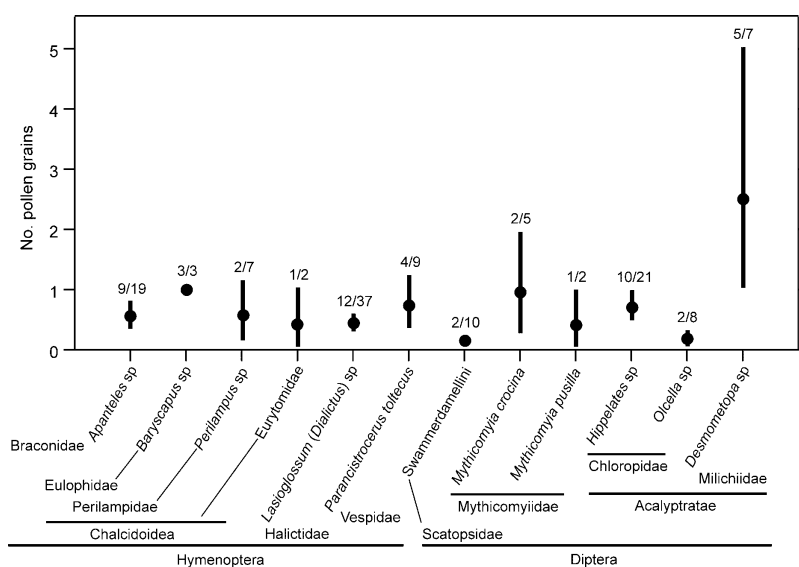


Fig. 2. Numbers of conspecific pollen grains ( $\bar{Y} \pm SE$ ) on insects collected from *Phoradendron juniperinum* female flowers in the Cerbat Mountains during July 2016. Numbers above bars are the number of insects with conspecific pollen over the number of insects collected. Point estimates were back-transformed from data transformed  $\log(Y + 1)$ .

Amounts of *P. juniperinum* pollen on insects were compared among the species collected. Numbers of *P. juniperinum* pollen grains were transformed  $\log(Y + 1)$  and compared among species with a one-way analysis of variance using ANOVA in Systat (version 10.2, Chicago, IL). Normality of the residuals was determined by examining the linearity of the residuals plotted against their expected values under normality (Neter et al. 1996). Floral constancy (Dafni 1992, Willmer 2011), or specificity of insects to *P. juniperinum*, was examined by calculating proportions of conspecific pollen in pollen loads. Proportions of conspecific pollen on insects carrying  $>2$  pollen grains were compared with ANOVA among species with  $>1$  specimen. Proportions were transformed  $2\arcsin(Y^{1/2})$  to normalize residuals, determined as above, and weighted by  $1/s^2$  in each species to balance unequal variances among species due to unequal pollen loads (Neter et al. 1996). I decomposed the variation in proportions among species into independent contrasts (Neter et al. 1996) in an ANOVA that compared Hymenoptera versus Diptera, wasps (Braconidae, Perilampidae, and Vespidae) versus bees (Halictidae), and calyprate flies (Mythicomomyiidae) versus acalyprate (Chloropidae and Milichiidae) flies. Means

of transformed data were back-transformed for reporting.

## RESULTS

Pollen grains from *P. juniperinum* were tricolpate. Grains in polar view were sub-angular in shape with flat sides and deep, open furrows (Fig. 1b, top). Furrows in polar view appeared to extend toward the poles as lines. Grains in equatorial view were oval-spherical in shape with broad, sharply edged, distinct furrows (Fig. 1b, bottom). Grains ( $n = 15$ ) averaged  $22 \mu\text{m}$  (range  $19\text{--}23 \mu\text{m}$ ) from corner to opposite side in polar view and  $23$  ( $20\text{--}28$ )  $\mu\text{m}$  long  $\times$   $21$  ( $17\text{--}23$ )  $\mu\text{m}$  wide in equatorial view. Pollen grains in brightfield had a mottled appearance, especially in polar view (Fig. 1b, 1c), suggesting an unevenly sculptured exine.

I aspirated and identified 145 insects from *P. juniperinum* female flowers that included 2 species of Coleoptera in 2 families, 6 species of Hymenoptera in 6 families, and 9 species of Diptera in 8 genera and 5 families. Pollen was found on 12 species (Fig. 2). The most frequently collected species with pollen was a bee in *LasioGLOSSUM* (subgenus *Dialictus*) (Halictidae). This bee was locally abundant, with 62% of specimens aspirated

at the lowest-elevation plant. Most (65%) of the *Lasioglossum* collected were female. A fly species in *Hippelates* (Chloropidae) taken from 6 of the 7 sampled plants was the second most aspirated insect on flowers. Collected *Hippelates* were yellow and brown in coloration and appeared to be the same species as those collected on *P. coryae* (Wiesenborn 2016b). A species of parasitic wasp in *Apanteles* (Braconidae) was the third most aspirated insect, followed by a species of nematoceran fly in Scatopsidae (tribe Swammerdamellini) and the predaceous potter wasp *Parancistrocerus toltecus* Saussure (Vespididae: Eumeninae). Other Hymenoptera that carried pollen (Fig. 2) included 3 species of parasitic wasps in Chalcidoidea: *Baryscapus* sp. (Eulophidae), *Perilampus* sp. (Perilampidae), and a species in Eurytomidae. Other Diptera that carried pollen (Fig. 2) included 2 species in Mythicomyiidae, *Mythicomyia crocina* Melander and *Mythicomyia pusilla* Melander; 1 species of *Desmometopa* (Milichiidae); and a second species of Chloropidae in *Ocella*. Five species of insects from flowers were not carrying pollen. These included 2 species of Coleoptera in *Mordellistena* (Mordellidae) ( $n = 4$ ) and *Zabrotes* (Chrysomelidae: Bruchinae) ( $n = 4$ ), the parasitic flies *Microchaetina* sp. ( $n = 3$ ) and *Erynnia* sp. ( $n = 2$ ) in Tachinidae, and a second species of Milichiidae in *Milichia* ( $n = 2$ ). Most insects with pollen were small, ranging from 1.1 mm in length for the *Baryscapus* to 2.5 mm in length for the *Apanteles*. Exceptions were the *Lasioglossum* bee at 4.4 mm in length and the vespid wasp *P. toltecus* at 8.1 mm in length.

*Phoradendron juniperinum* pollen was found on 53 (41%) of the 130 specimens of species that carried pollen (Fig. 2). Only 23 insects (18%) carried >1 pollen grain, and 11 insects (9%) carried >3 grains. I counted a total of 185 *P. juniperinum* pollen grains on insects. A *Desmometopa* fly carried the most conspecific pollen (58 grains). Numbers of *P. juniperinum* pollen grains on insects did not differ ( $F_{11,118} = 1.36$ ,  $P = 0.20$ ) among the 12 species carrying pollen (Fig. 2). I counted a total of 329 pollen grains differing from *P. juniperinum* on insects. Most of these pollen grains were spherical in shape and without furrows, or tricolpate and semiangular in shape with rounded sides and flat (indistinct) furrows. Pollen of both shapes lacked the mottling

seen on *P. juniperinum* pollen. A *Lasioglossum* bee carried the most pollen (33 grains) from other plants.

Proportions of *P. juniperinum* pollen in pollen loads differed ( $F_{6,22} = 5.38$ ,  $P = 0.001$ ) among the 7 species of insects with specimens carrying >2 grains (Fig. 3). Proportions of conspecific pollen did not differ ( $F_{1,22} = 0.30$ ,  $P = 0.59$ ) between Hymenoptera ( $\bar{x} = 24\%$ ) and Diptera (43%). A weak and nonsignificant difference ( $F_{1,22} = 3.38$ ,  $P = 0.080$ ) in proportions of conspecific pollen was observed between bees in Halictidae and wasps in Braconidae, Perilampidae, and Vespididae. Slightly higher proportions of conspecific pollen were observed on wasps (38%) than on bees (12%). Among wasps, the braconid *Apanteles* carried the highest proportion (68%) of conspecific pollen. Proportions of *P. juniperinum* pollen on Diptera differed ( $F_{1,22} = 6.73$ ,  $P = 0.017$ ) between calyptrate (Mythicomyiidae) and acalyprate (Chloropidae and Milichiidae) flies. Proportions of conspecific pollen were higher on chloropids and milichiids (63%) compared with mythicomyiids (10%).

## DISCUSSION

Flies in *Hippelates* and *Desmometopa* and parasitic wasps in *Apanteles* appeared to be most likely to pollinate *P. juniperinum* among the diverse insects that carried pollen to female flowers. Insects in these genera were frequently aspirated and widely distributed across plants, with 51% of specimens carrying conspecific pollen that comprised most of the pollen load, suggesting high floral constancy to the plant. These flies and wasps are too large (2.0–2.5 mm in length) to enter the corollas of *P. juniperinum* (0.5–1.0 mm between petals, Fig. 1a, 1d), requiring pollen to be transferred on mouthparts. The relatively long, seta-covered mouthparts on *Desmometopa* and *Hippelates* flies (Fig. 1e, 1f) appear capable of carrying pollen and reaching the stigmas inside flowers. Although *Lasioglossum* bees were most frequently collected, they were not widely dispersed and carried low proportions of *P. juniperinum* pollen, indicating low floral constancy. Only pollen carried by *Lasioglossum* bees on their short mouthparts and not on their hind legs, as is typical in bees, would likely be transferred to stigmas of *P. juniperinum*.

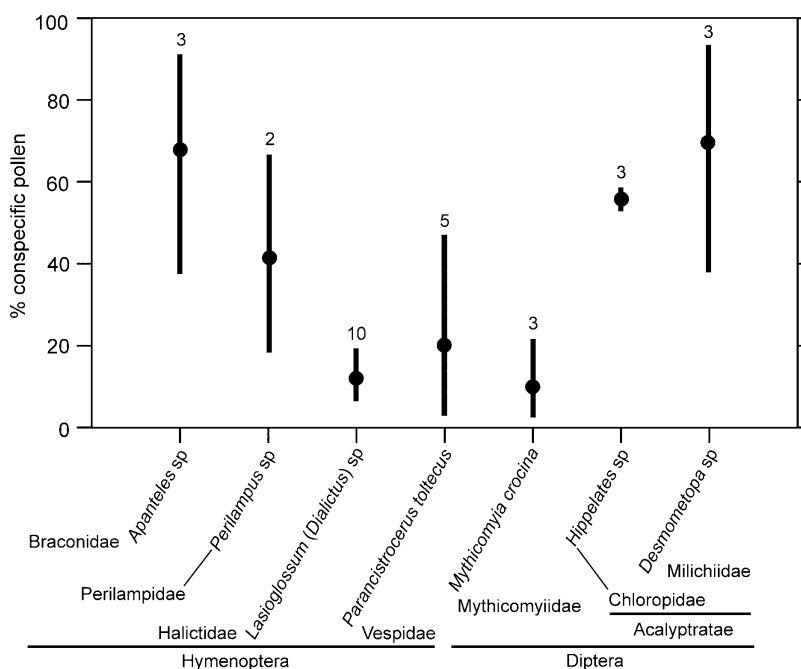


Fig. 3. Percentages of pollen load ( $\bar{y} \pm SE$ ) comprised of *P. juniperinum* pollen. Numbers of insects are above the bars. Point estimates were back-transformed from data transformed  $2 \arcsin(Y^{1/2})$ .

The availability of insects that pollinate *P. juniperinum* depends on each species' food requirements as larvae. Chloropid fly larvae in Oscinellinae, including *Hippelates*, mostly consume living or decomposing herbaceous plants, although immature insects, decomposing wood, and fungi may also be eaten (Nartshuk 2014). Larvae of Milichiidae in *Desmometopa* consume decomposing plant or animal tissue or excreta (Sabrosky 1983). Larvae of wasps in *Apanteles* develop by parasitizing the larvae of small moths (Mason 1981).

Flowers on other plant species have been observed being pollinated or visited by the taxa of insects that carried *P. juniperinum* pollen to female flowers. Flies in Chloropidae and Milichiidae are known pollinators of several plant species (Larson et al. 2001, Heiduk et al. 2010, Bower et al. 2015). Flies in both families, including *Ocella* and *Desmometopa*, have been found trapped together and covered with pollen inside pistillate flowers on tropical *Aristolochia* (Wolda and Sabrosky 1986). Mythicomyiidae visit flowers on desert plants and carry conspecific pollen (Wiesenborn 2003, 2015). Scatopsidae visit flowers (Armstrong 1979) but have not been previously identified

as pollinators. Wasps are common flower visitors that consume nectar (Willmer 2011). Pollen has been found on Braconidae visiting orchids in California (Ackerman and Mesler 1979) and on Vespidae visiting milkweed flowers in Brazil (Vieira and Shepherd 1999) and aster flowerheads in Canada (Horsburgh et al. 2011). Bees in Halictidae are common pollinators of short-corolla flowers, whereas parasitic wasps in Chalcidoidea may feed at flowers but are not generally known as pollinators (Willmer 2011). The orchids and *Aristolochia* flowers visited by braconids, chloropids, and milichiids produce pungent odors (Ackerman and Mesler 1979, Wolda and Sabrosky 1986), suggesting insects may be attracted to *P. juniperinum* by floral volatiles. Olfactory attraction of adult flies to flowers is also suggested by the decomposing matter inhabited by larvae.

Insects visiting female flowers on *P. juniperinum* carried less conspecific pollen than the insects visiting female flowers on other *Phoradendron*. Conspecific pollen was found on 82% of the insects aspirated from *P. californicum*. Median pollen loads were 36.5 grains on Hymenoptera, excluding honeybees, *Apis mellifera* L. (Apidae), and 4.5 grains



on Diptera (Wiesenborn 2016a). On *P. coryae*, 67% of the aspirated insects carried conspecific pollen, with median pollen loads of 1.0 grain on Coleoptera and 2.0 grains on Diptera (Wiesenborn 2016b). The highest load of *P. coryae* pollen (265 grains) was carried by a chloropid fly in *Lihippелates*. Smaller loads of *P. juniperinum* pollen on insects may have been due to the plant occurring at an overall lower density than observed for *P. californicum* and *P. coryae*. Conversely, the low density of *P. juniperinum* may have resulted from low rates of pollination due to low numbers of insects carrying pollen and relatively low conspecific pollen loads. Fruits were sparse on female plants, in contrast to the profuse fruiting of *P. californicum* and *P. coryae* (Wiesenborn 2016b, fig. 1a). The flowering period of *P. juniperinum* in western Arizona may reduce nectar production by flowers and availabilities of pollinating insects. Flowering during June and July occurs after winter rainfall and spring plant growth, and before peak summer rainfall in August and late summer plant growth. June is the driest month at Kingman and received an average 1.5% of annual precipitation during 1901–1967 (DRI 2016).

Species of *Phoradendron* examined are pollinated by different taxa of insects. Only one genus of insect, *Lasioglossum*, was found on both *P. californicum* (Wiesenborn 2016a) and *P. juniperinum*, although the species appeared to differ between the 2 plants. Three genera of insects were shared by *P. coryae* (Wiesenborn 2016b) and *P. juniperinum*: *Hippelates* and *Ocella* carried conspecific pollen to both plant species, and *Microchaetina*, although visiting *P. juniperinum*, carried conspecific pollen only to *P. coryae*. Species of *Ocella* but not *Hippelates* or *Microchaetina* appeared to differ between the 2 plants. The greatest commonality between the 3 *Phoradendron* species is pollination by minute flies, Tephritidae on *P. californicum* and Chloropidae on *P. coryae* and *P. juniperinum*. *Phoradendron coryae* was most distinct due to pollination by the beetle *Attalus futilis* Fall (Melyridae). Beetles were not found on *P. californicum*, and those on *P. juniperinum* did not carry pollen. Different flowering seasons and unrelated host plants that only narrowly overlap likely combine to isolate pollination and reproduction among species of *Phoradendron*.

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