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Chalcochares hirsutifemur (Banks) (Hymenoptera: Pompilidae: Pompilinae), a probable obligate parasitoid of *Aptostichus* Simon (Araneae: Mygalomorphae: Euctenizidae) in California

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Chalcochaes hirsutifemur (Banks) (Hymenoptera: Pompilidae: Pompilinae), a probable obligate parasitoid of *Aptostichus* Simon (Araneae: Mygalomorphae: Euctenizidae) in California

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Abstract. Size equivalence, seasonal synchronicity, geospatial sympatry, habitat specificity, and host-searching behavior implicate the spider wasp *Chalcochaes hirsutifemur* (Banks) (Hymenoptera: Pompilidae: Pompilinae) as an obligate parasitoid on species of the wafer-lid spider genus *Aptostichus* Simon (Araneae: Mygalomorphae: Euctenizidae) on coastal sandy back dunes in San Luis Obispo and Santa Barbara counties, CA. This is substantiated by 2010–2022 macrophotographs, videos, and field observations. Such host evidence supports recent unpublished phylogenomic studies that place *Chalcochaes* as a sister genus of the spider wasp tribe Aporini, in which all species are known obligate parasitoids on trapdoor spiders and related Mygalomorphae. *Chalcochaes hirsutifemur* and *C. engleharti* (Banks) are separated based on morphological, geographic, and probable host spider differences. Resource partitioning on the coastal sand dunes between *C. hirsutifemur* and three species of smaller *Aporus* Spinola is proposed.

Key words. *Chalcochaes engleharti*, *Aporus hirsutus*, *Aporus luxus*, *Aptostichus atomarius*, *Aptostichus simus*, resource partitioning.

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Introduction

The genus *Chalcochaes* Banks (Pompilinae: Pompilini) possesses several unique external morphological characteristics (Evans 1950). The hind wings and anal lobe are extraordinarily large. Some external morphological characteristics resemble those of the spider wasp genus *Calopompilus* Ashmead (Pepsinae: Pepsini): rather short legs and antennae; and female metasoma stout with basal segments mildly constricted. The characteristic of female metasoma stout with basal segments mildly constricted is found only in the two species of *Chalcochaes* and *Calopompilus pyrromelas* (Walker) (Evans 1950; Townes 1957). *Chalcochaes* is like the genus *Psorthaspis* Banks (Pompilinae: Aporini) in overall head and thoracic structure and the subgenus *Plectraporus* Bradley of the genus *Aporus* Spinola (Pompilinae: Aporini) in possessing a hairy, bluish body, very broad front and vertex with eyes positioned toward side of head, and rather long, flattened above and straight sided pronotum (Evans 1950, 1966; Wasbauer and Kimsey 1985). Similarity in external morphology of these spider wasp genera is probably the result of likeness in habitat, ecology, host spider type, and host capture. *Calopompilus*, *Psorthaspis*, and *Aporus* are obligate parasitoids on wafer-lid spiders, other trapdoor spiders, and related Mygalomorphae that they capture and entomb in the spiders' own burrows (Williams 1928; Jenks 1938; Kurczewski et al. 2021, 2023).

Chalcochaes contains only two species, *C. engleharti* (Banks) (Fig. 1) and *C. hirsutifemur* (Banks) (Fig. 2–4), in the Nearctic Region, *C. engleharti* ranging from central Texas to southern Mexico and *C. hirsutifemur* from southern New Mexico and California to north-central Mexico (Fig. 5; Evans 1950, 1966; Wasbauer and Kimsey 1985). *Chalcochaes hirsutifemur* females are rather large (12–20 mm long; Evans 1966), hairy, and stout-bodied with bluish or purplish fine pubescence (Fig. 2–4; Abela 2021d, 2021e). The broad wings are fuliginous and strongly violaceous. The gena is enlarged behind the compound eyes. The antenna flagellum is short; flagellomere 1 in the female is only 3.1–3.6 (mean, 3.3; $n=10$) times longer than its width. The forelegs are short. The fore tarsi are rather strongly spinose. The fore tibiae have long, stout, curved spines apicomediaally (Evans 1950, 1966).

Chalcochaes hirsutifemur inhabits arid and semi-arid regions in southern California, Arizona, New Mexico, Texas, and Mexico (Fig. 5); chaparral is the preferred habitat (Wasbauer and Kimsey 1985). This species is uncommon on southern California coastal dunes and hills (Wasbauer and Kimsey 1985). There is a single

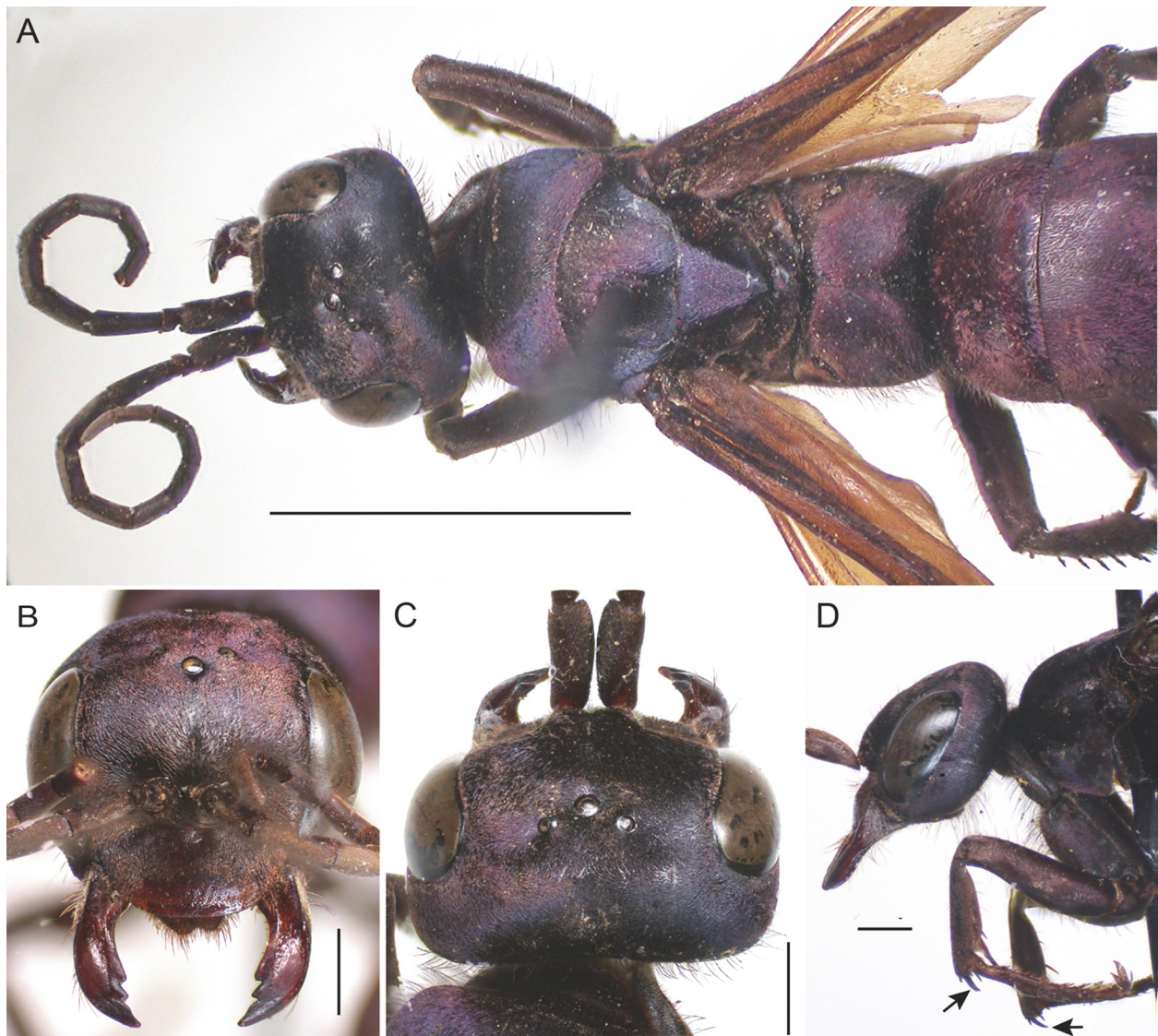


Figure 1. *Chalcochaes engleharti* (Banks), female; Camp Bullis, Bexar County, Texas; 29 May 1952; K. Stockley collector (det. M. Wasbauer 1956). A. Head, mesosoma, and anterior part of metasoma, dorsal view. B. Head, anterior view. C. Head, dorsal view. D. Head, anterior part of mesosoma, and fore legs, lateral view (arrow, apicomediaal spine on fore tibia). Scale bars: 5 mm (A); 1 mm (B–D).

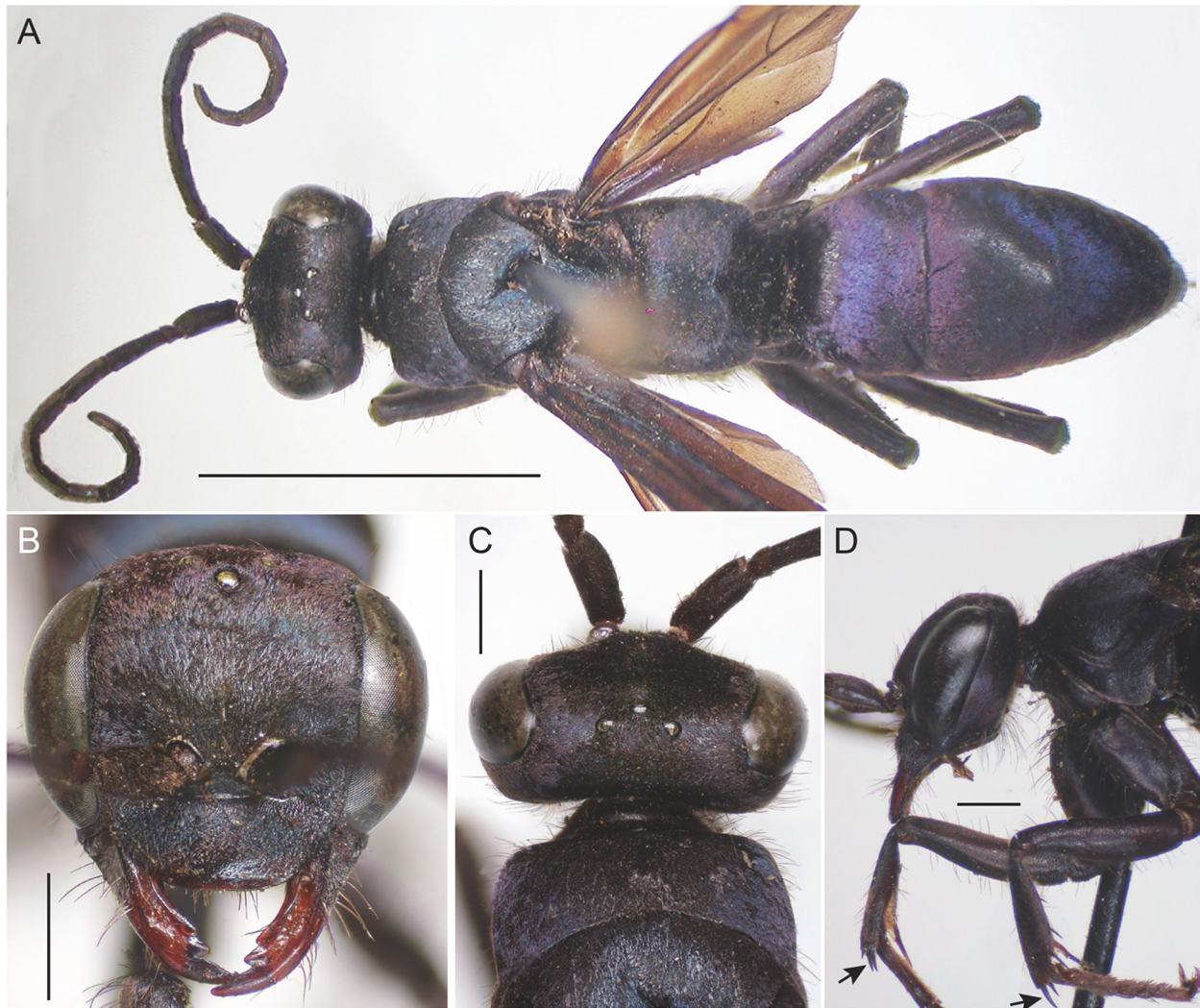


Figure 2. *Chalcochares hirsutifemur* (Banks), female; Anza, Riverside County California; 24 June 195? L. A. Stange collector (det R. Snelling 1963). A. Whole body, dorsal view. B. Head, anterior view. C. Head and anterior part of mesosoma, dorsal view. D. Head, anterior part of mesosoma, and fore legs, lateral view (arrow, apicomeres spine on fore tibia). Scale bars: 5 mm (A); 1 mm (B–D).

generation per year with nearly all collection dates being in June, July, and August (Wasbauer and Kimsey 1985). Nothing is known about the biology of *C. hirsutifemur* except for flower visitation records (Evans 1950; Wasbauer and Kimsey 1985; Abela 2011, 2020, 2021a, 2021b, 2021c, 2021d, 2021e, 2021f; Horner 2019). Females are rarely seen on the ground surface. The absence of host capture and nesting information infers that this species has a secretive lifestyle, perhaps capturing and ovipositing on wafer-lid spiders in or near their burrows.

Chalcochares hirsutifemur females are probably obligate parasitoids on wafer-lid spiders of the genus *Aptostichus* Simon (Araneae: Mygalomorphae: Euctenizidae) and, possibly, other genera of Euctenizidae. The large genus *Aptostichus* (>40 species) is found mainly in California and is characterized by cryptic psammophilic carapace and abdomen coloration (Fig. 6–7; Bond 2012). *Aptostichus* species have few readily identifiable external morphological characteristics (Bond 2012). *Chalcochares hirsutifemur* females probably capture *Aptostichus atomarius* Simon (San Bernardino Hills trapdoor spider) (Fig. 6; Abela 2014a) and *A. simus* Chamberlin (Southern coastal dune trapdoor spider) (Fig. 7; Abela 2014b) on southern California coastal sandy back dunes from Monterey to San Diego counties based on size equivalence, seasonal synchronicity, geospatial sympatry, habitat specificity, and host-searching behavior. The shallow to moderately deep, silk-lined burrows of *Aptostichus*



Figures 3–4. *Chalcochares hirsutifemur* female taking nectar from flowers of *Eriogonum parvifolium* (Seacliff buckwheat), Sandy coastal back dunes, Vandenberg Air Force Base, Santa Barbara County, CA; 13 August 2021; A. Abela (Abela 2021d, 2021e). **3)** Note hairy head, thorax, and basal metasoma; and spinous legs, especially foretibia and foretarsus. Photograph © Alice Abela. **4)** Note short antenna segments; hairy head, thorax, and femora; wide vertex with rather small eyes situated on side of head; swollen occiput behind compound eyes; enlarged and flattened pronotum with straight sides; and spinous legs, especially foretibia and foretarsus. Photograph © Alice Abela.

species are remarkably similar in structure (Bond 2012; Abela, pers. obs.). The spider is often restricted to living in such a burrow for most of its life. *Aptostichus simus* individuals sit beneath the wafer-lid at night in anticipation of capturing unsuspecting invertebrate prey that wander too close to the entrance. During the heat of the day the spider moves to the cooler end of its burrow, usually in the shade beneath vegetation (Abela, pers. obs.). The burrow entrance is covered by a flimsy, thin, silk and sand wafer-lid, rendering it largely indistinguishable from the surrounding sand surface but relatively easy for wasp entry.

Aptostichus atomarius, *A. stephencolberti* Bond (Stephen Colbert trapdoor spider), *A. miwok* Bond (Miwok trapdoor spider), and *A. simus* are all potential host spider species of *C. hirsutifemur* in central and southern California coastal sand dunes. *Aptostichus stanfordianus* Smith (Stanford Hills Trapdoor Spider) is another possible host spider species of *C. hirsutifemur*. Hawk (2022) photographed *C. hirsutifemur* at Pinnacles National Park, San Benito County, CA where Bond (2012) reported an abundance of *A. stanfordianus*. When mapped, the distribution of *C. hirsutifemur* far exceeds that of species of *Aptostichus*, extending into southwestern Texas and western/central Mexico (Fig. 5; Bond 2012). However, *Aptostichus* likely has a larger distribution than is currently known including additional species from Baja California, southern Arizona, and Sonora (Hedin, pers. comm.). Species of *Eucteniza* Ausserer and *Entychides* Simon should also be considered as potential hosts of *C. hirsutifemur* in Mexico and Arizona based on their size, range, and ecology (Hedin, pers. comm.). A possible impediment for wasp entry into *Eucteniza* and *Entychides* burrows is the thicker cork-like trapdoor (Bond and Opell 2002; Bond and Godwin 2013). However, the mandibles of *C. hirsutifemur* are bidentate and the foretarsi are rather strongly spinose (Evans 1950).

The purpose of this paper is to present actual and circumstantial evidence of an obligate parasitoid-host relationship between *C. hirsutifemur* and *Aptostichus* wafer-lid spiders. We introduce observations on the host-searching, digging, and prospective nesting behavior of the wasp as there is no such information in the literature or on specimen labels in insect collections. Abela's macrophotographs, videos, and field observations of *Chalcochares hirsutifemur*, *Aptostichus atomarius* and *A. simus* provided the catalyst for undertaking such a study.

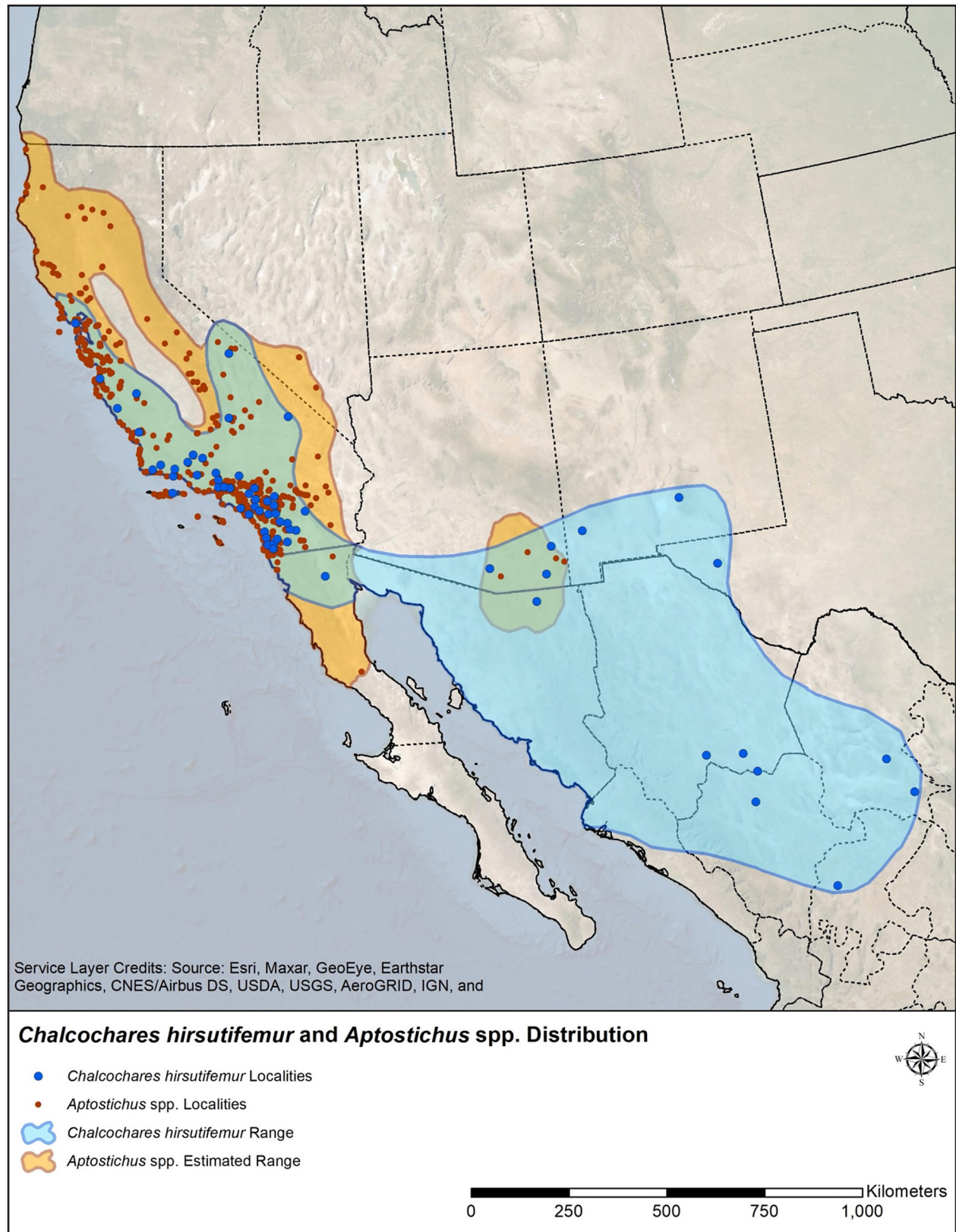


Figure 5. Geographic locality and range map for *Chalcochares hirsutifemur* (from Evans 1966; Wasbauer and Kimsey 1985) and *Aptostichus* species (from Bond 2012).



Figures 6–7. *Aptostichus* spp. 6) *Aptostichus atomarius* female on sand. Sandy Coastal back dunes, Vandenberg Air Force Base, Santa Barbara County, CA; 3 June 2014; A. Abela (Abela 2014a) Photograph © Alice Abela. 7) *Aptostichus simus* female on sand. Sandy Coastal back dunes, Vandenberg Air Force Base, Santa Barbara County, CA; 11 June 2014; A. Abela (Abela 2014b). Photograph © Alice Abela.

Materials and Methods

This study began in July 2020 when Alice Abela emailed photographs of a rather large, blue, hairy spider wasp to Frank Kurczewski for identification. Kurczewski immediately recognized the species as being *Chalcochaeres hirsutifemur*, an uncommon and unusual genus and species from the southwestern United States and Mexico. He asked Abela to observe and photograph this spider wasp species as nothing was known about its host spider or host-searching, digging, and nesting behavior. Abela was working at the time on nature projects in the area where this species was, surprisingly, rather prevalent. In July–August 2021 Abela made observations, took additional photographs of *C. hirsutifemur*, and posted them on BugGuide.com, flickr.com, and iNaturalist.org. She also made 1 and 4 minute long-videos of two females host-searching and digging for host spiders in 2021 and 2022. Concurrently, Kurczewski reviewed the sparse morphological, taxonomic, ecological, and geographic distribution reports on *C. hirsutifemur* by Evans (1950, 1966), Krombein (1979), and Wasbauer and Kimsey (1985).

Abela's first video of a host-searching female of *C. hirsutifemur* was made 1 July 2021 on sandy coastal back dunes, Vandenberg Air Force Base, Santa Barbara County, CA. Abela made a second video of a *C. hirsutifemur* host-searching in the same location on 11 August 2022 during which the wasp spent several minutes digging before flying away. Her second video revealed the wasp, during excavation, had exposed the silken tubular entrance of an *Aptostichus* burrow. This burrow would have been too small in diameter for the wasp to enter, the silk was severed, and lack of recent occupancy probably caused the wasp to continue searching elsewhere.

Abela's macrophotographs of this species were taken 30 June 2011, 2 July 2020, and 9 July–16 August 2021 at this location and Guadalupe-Nipomo Dunes National Wildlife Refuge, San Luis Obispo County, CA (Fig. 8). She used a Canon 5D Mark III or Mark IV with a Canon EF 100 mm f/2.8 Macro USM, Canon MP-E 65 mm f/2.8 1–5× Macro, or LAOWA 100 mm F2.8 CA Dreamer Macro 2× paired with a Canon Macro Twin Lite MT-24EX or Canon Macro Twin Lite MT-26EX-RT or a Venus Kx 800 Twin Flash. Her photographs were shot from a kneeling, sitting, or prone position. We examined and analyzed 22 photographs of *C. hirsutifemur* for locality, date, plant/flower species, adult male and female external morphology, and wing wear as an indicator of age and longevity. We also examined photographs of *C. hirsutifemur* from nearby Rancho Guadalupe Dunes Preserve in San Luis Obispo, CA by Van Loon and Van Loon (2021) and in Pinnacles National Park, San Benito County, CA by Hawk (2022).

Specimens of *Chalcochaeres engleharti* and *C. hirsutifemur* were photographed by Akira Shimizu using a digital camera (Nikon Coopix 4500 and MDC lens) equipped with a stereo microscope (Leitz TS) and a transmitted light microscope (Leitz Dialux). Photographs were stacked using ZM (Hadley 2008) and the final synthesized photographs were post-processed for contrast and brightness using Adobe Photoshop software.

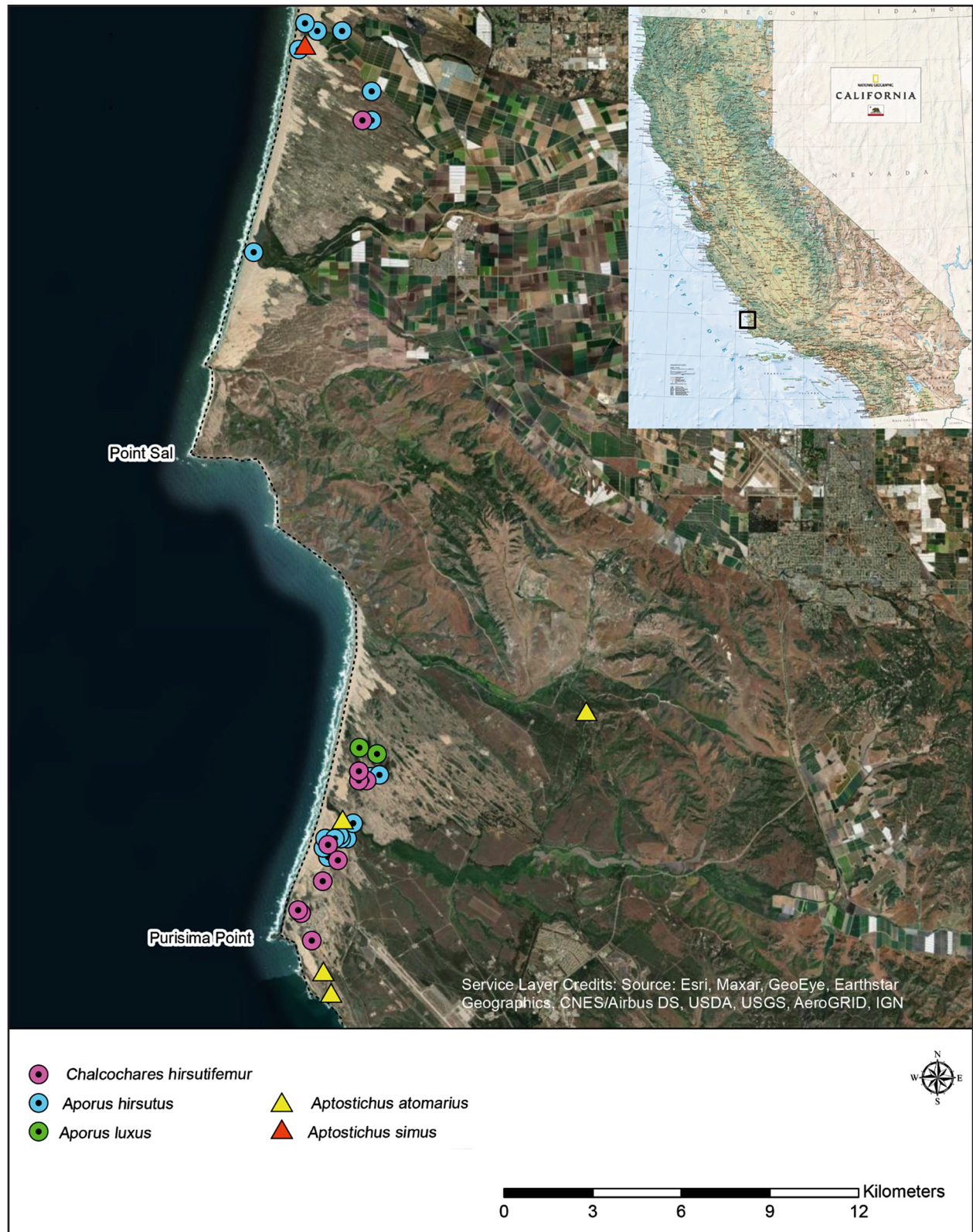


Figure 8. Overhead coastal map of San Luis Obispo and Santa Barbara counties showing research site locations of *Chalcochares hirsutifemur*, *Aporus hirsutus*, *Aporus luxus*, *Aptostichus atomarius*, and *Aptostichus simus*. Rectangular inset on California map in upper right corner indicates area of study.

Abela made observations, excavated burrows, and took 22 photographs of *Aptostichus atomarius* on sandy coastal back dunes, Vandenberg Air Force Base, Santa Barbara County, CA, 21 February 2010–16 August 2021 (Fig. 8). She found no spider wasp larvae, pupae, or cocoons in any of the *A. atomarius* burrows. Abela observed, excavated burrows, and took 83 photographs of *Aptostichus simus* on sandy coastal foredunes and back dunes at Cuesta-by-the-Sea, Guadalupe-Nipomo Dunes National Wildlife Refuge, Montana de Oro State Park, Morro Bay, Morro Strand State Beach, Oso Flaco Lake, and Oso Flaco Dunes Natural Area in San Luis Obispo County, CA; and Ocean Beach Park and Vandenberg Air Force Base [Coastal Dune Scrub, Coastal Live Oak Woodlands, Coastal back dunes, Coastal foredunes, Surf Beach] in Santa Barbara County, CA, 8 June 2014–23 July 2021 (Fig. 8). She found a discarded pompilid cocoon in one *A. simus* burrow as evidence of a parasitoid spider wasp. Abela recorded other locality records and geographic coordinates for *A. atomarius* and *A. simus* in San Luis Obispo and Santa Barbara counties, CA from Bond (2012) (Fig. 5). Additional locality and seasonal records for *A. simus* were examined and added to Fig. 5 from Willems (2018), Hedin (2020), Johnson (2020a), and Noss (2020).

Interpreting the function of external morphological structures of the female wasp involved reading and deciphering Evans' (1950, 1966) keys and description of the genus *Chalcochaes* and, more specifically, females of *C. hirsutifemur* as well as Shimizu et al.'s (2021, 2022) papers on trapdoor spider-hunting spider wasps. Evans' (1966, Fig. 21) map of southwestern United States and Mexican geographic distribution records of *C. hirsutifemur* was used by Abela in formulating her revised geographic distribution map (Fig. 5). Krombein (1979) summarized the taxonomic and distributional information for *C. hirsutifemur*. Wasbauer and Kimsey (1985) highlighted important genus and species taxonomic characteristics, introduced several flower records, and presented a geographic distribution map for *C. hirsutifemur* from which Abela obtained additional California locality records for Fig. 5.

We selected lateral and dorsal photographs of *C. hirsutifemur* females to show diagnostic external morphological structures (Fig. 3–4; Abela 2021d, 2021e). The consolidated information from Abela's photographs, videos, and field observations were analyzed and assessed as to how the external morphological structures of *C. hirsutifemur* might be used in searching for and excavating an *Aptostichus* burrow. Akira Shimizu added detailed macrophotographs of *C. engleharti* and *C. hirsutifemur* to highlight structural features that are probably used in facilitating spider burrow entry and host spider capture (Fig. 1, 2). We chose the largest and sharpest photographs of *Aptostichus atomarius* and *A. simus* females to show significant morphological features against a lighter sand background (Fig. 6–7; Abela 2014a, 2014b). Lynn S. Kimsey, University of California–Davis, Davis, CA provided us with a copy of her joint 1985 paper with Marius Wasbauer that allowed Abela to use California Insect Survey coordinates to produce her revised *C. hirsutifemur* geographic locality and range map (Fig. 5). Kimsey also scanned Evans' (1966) Figure 21 geographic locations for use in this map. Abela's modification of an Esri, Maxar, Geo Eye, Earthstar Geographics map of extreme southern San Luis Obispo and northern Santa Barbara counties enabled pinpointing the exact locations of where wasp and spider species were photographed and observed (Fig. 8). Frank Kurczewski wrote the manuscript based on information provided by the three authors.

Results

Flower visitation records

Chalcochaes hirsutifemur males and females visit a wide variety of flowers for nectar: *Acacia* sp. (Fabaceae), *Asclepias erosa* Torr. and *Asclepias* sp. (Apocynaceae), *Baccharis glutinosa* Pers. (Asteraceae), *Croton californicus* Muell. Arg. (Euphorbiaceae), *Eriogonum fasciculatum* Benth. and *E. parvifolium* Sm. (Polygonaceae) (Fig. 3–4), *Flourensia cernua* DC (Asteraceae), *Foeniculum vulgare* Mill. (Apiaceae), *Helianthus annuus* L. [extra-floral nectaries], *Isocoma hartwegi* (A. Gray) Greene (Asteraceae), *Koeberlinia spinosa* Zucc. (Koeberliniaceae), and *Tamarix gallica* L. (Tamaricaceae) (Evans 1950; Wasbauer and Kimsey 1985; Abela 2011, 2021f, 2021h; Horner 2019; Hawk 2022).

Functional morphology of *Chalcochaes*

In Pompilidae, there are at least two types of morphological adaptations for attacking trapdoor spiders and related Mygalomorphae: *Entomobora*- (Shimizu et al. 2021, fig. 6; 2022, fig. 11) and *Paraclavelia*-morphotypes (Shimizu et al. 2021, fig. 9; Shimizu et al. 2022, fig. 1, 2, 3, 6, 7). The morphological features common to these morphotypes

are frons broader than compound eyes; lower frons deeply depressed or hollowed laterally to antennal sockets; clypeus narrower than lower frons and more or less flattened with basal or basilateral depressions continuous with lower frontal depression(s); and scape curved outward and flattened on lateral face, which fits in lower frontal depression. The features unique to *Entomobora*-morphotype are vertex posterior to ocelli much extended posterodorsally; and pronotal dorsum truncate anteriorly with neck deeply depressed. The feature unique to *Paraclavelia*-morphotype is elongate (longer than mesoscutum at midline), dorsally flattened, low pronotum; and long, stout, curved spine on the fore tibia apicomediaally.

Chalcochares engleharti and *C. hirsutifemur* have a broad frons (Fig. 1B, 2B) and long, stout, curved spine on the fore tibia (Fig. 1D, 2D, arrows). The former is probably employed as a lever in prying open the lid and supporting it (see also Shimizu et al. 2021, figs 7, 8, 11) and the latter may function as a hook when the wasp lifts the trapdoor (Shimizu et al. 2022, p. 126). These species, however, do not have any of the other features listed above. Species of *Chalcochares* are morphologically much less specialized in preying on trapdoor and wafer-lid spiders than species of the *Entomobora*- and *Paraclavelia*-morphotypes. This lack of specialized morphological features is probably why the genus *Chalcochares* was initially placed taxonomically in the subfamily Pompilinae, tribe Pompilini by Evans (1950).

Chalcochares engleharti can be separated morphologically from *C. hirsutifemur* by its vertex elevated strongly above (Fig. 1B vs 2B) and extended behind the compound eyes and very swollen genae (Fig. 1A, C, D vs 2A, C, D) (Evans 1950, 1966), inferring the mandibular muscles of *C. engleharti* are larger and stronger than those of *C. hirsutifemur*. *Chalcochares engleharti* may be adapted to prying open the thicker trapdoors of larger and more powerful spiders such as *Ummidia* Thorell, *Eucteniza*, and *Entychides*, while *C. hirsutifemur* may be limited to opening the much thinner, flimsier wafer-lids of the smaller *Aptostichus*.

Host-searching

A *C. hirsutifemur* female searching for a host spider was videographed for 1 minute by Alice Abela on 1 July 2021 on sandy coastal back dunes, Vandenberg Air Force Base, Santa Barbara County, CA. The wasp ran circuitously across the sand and dried ground vegetation periodically flicking her wings. She paused in one spot and dug downward for half her body length removing the sand backwards, using her forelegs alternately. She backed from the excavation briefly and circled 3 times in 37 seconds. Such behavior infers the wasp was attempting to receive sensory information about the underground location of a potential host spider. She exited the excavation and ran across the ground flicking her wings, avoiding the bare sand, and staying mainly on dried ground vegetation as she continued her search for the remaining 23 seconds of the video.

Another female was observed on the same sandy coastal back dunes on 16 August 2021. She ran across the sand searching for a host spider and periodically dug in bare sand and beneath small shrubs, exhibiting behavior like host-searching females of *Aporus* (*Plectraporus*) *hirsutus* (Banks) and *A. (Aporus) luxus* (Banks) (Kurczewski et al. 2021). Based on her larger size, host-searching behavior, specific location, and sizeable host spiders in the vicinity, this *C. hirsutifemur* female was likely targeting the wafer-lid spider *Aptostichus atomarius* or, less likely, *A. simus* (Fig. 6–7).

Abela videographed a *C. hirsutifemur* female, ~20 mm long, searching for a host spider for 4 minutes at the same location on 11 August 2022. The wasp walked back and forth across the bare sand in a zig-zag manner, flicking her wings, for 30 seconds. She then stopped in two spots, 25–30 cm apart, each with a small amount of plant debris, and dug with her forelegs for 25 seconds and 1+ minute, occasionally flicking her wings. In both spots she circled once or twice and changed her angle of excavation. At the second dig, the wasp's body entered the sand for 2/3 its length. During this excavation she exposed the forked silken entrances of an *Aptostichus* burrow which ran horizontally beneath the sand surface. The silken burrow was severed at a length of 2.5 cm from the entrance. This burrow was probably too small (8–10 mm) for wasp entry, it was severed implying a previous entry, and the silk looked old, causing her to vacate and continue searching not only on the bare sand but on dried plant debris and underneath overhanging vegetation. She resumed her search for another 2 minutes, stopped in one place for 1–2 seconds, dug, searched further, and flew off.

A comparatively large (~25 mm long), paralyzed *A. atomarius* female was found lying dorsal side upward on sandy back dunes at Vandenberg Air Force Base, Santa Barbara County, CA on the evening of 3 May 2013 in an area where *C. hirsutifemur* was prevalent (Fig. 6; Abela 2013). There was no wasp in attendance. The spider

twitched its appendages when touched. It was presumably stung earlier in the day and left abandoned on the sand surface, perhaps because of its large size and potential difficulty in transport back to its burrow.

Discussion

Chalcochares (Pompilinae: Pompilini) resembles *Calopompilus* (Pepsinae: Pepsini) morphologically (Evans 1950, Wasbauer and Kimsey 1985), perhaps the result of the two unrelated genera being obligate parasitoids on wafer-lid and related mygalomorph spiders while displaying convergent ecological and behavioral traits. *Chalcochares* is also structurally like the genera *Psorthaspis* and *Aporus* (Pompilinae: Aporini) for the same reason--a dependence on wafer-lid and related spiders as a source of larval food (Evans 1950, 1966; Wasbauer and Kimsey 1985). Recent unpublished phylogenomic data support *Chalcochares* as a sister genus to the tribe Aporini, especially the genus *Psorthaspis* (J. P. Pitts, pers. comm.). The pompiline genus *Chalcochares* is linked to the tribe Aporini based on molecular, ecological, and probable parasitoid-host relationship.

Chalcochares engleharti is separated morphologically from *C. hirsutifemur* by its strongly extended vertex and very swollen genae (Fig. 1 vs Fig. 2) (Evans 1950, 1966), inferring the mandibular muscles of *C. engleharti* are larger and stronger than those of *C. hirsutifemur*. *Chalcochares engleharti* may be adapted to prying open the thick trapdoors of larger and stronger trapdoor spiders such as *Ummidia*, *Eucteniza*, and *Entychides* while *C. hirsutifemur* is limited to opening the much thinner, flimsier wafer-lids of the smaller *Aptostichus*. There are at least two types of morphological adaptations in spider wasps for attacking trapdoor spiders and related Mygalomorphae: *Entomobora*- and *Paraclavelia*-morphotypes (Shimizu et al. 2021, 2022). In the *Entomobora*-morphotype, the vertex is strongly elevated above the eye tops and extends far behind the eyes (Shimizu et al. 2021, fig. 6; 2022, fig. 11). Although *C. engleharti* is less specialized morphologically than species of *Entomobora* Gistel (Shimizu 2021, fig. 11), it may attack large and powerful spiders living in subterranean burrows with thick trapdoors.

Chalcochares hirsutifemur compares favorably to *Aporus* (*Plectraporus*) *hirsutus* not only in specific name, bluish coloration, hairy body and legs, narrow eyes positioned toward side of head, short and spinous foretarsi, and enlarged and flattened pronotum, but also in potential host type, host searching and digging behavior, and, presumably, entombment of immobilized spider in its own burrow (Kurczewski et al. 2021). Females of both species search for a host spider by running across the sand, occasionally flicking their wings. They pause periodically, dig in the sand with their mandibles and forelegs for a few seconds to depths of a few mm, back out, then run to the next trial digging site and repeat this behavior. Wasps that constantly move from site to site apparently do not receive appropriate sensory information about the underground presence of a potential host spider. In certain spots, wasps dig deeper, often to half their body length, or they disappear completely in the sand spending several minutes underground. Such wasps may be receiving appropriate sensory information about the presence of a potential subterranean host spider.

Resource partitioning, where two or more species divide resources such as food and space in order to coexist, is seemingly operational in the sandy coastal dunes of San Luis Obispo and Santa Barbara counties, CA. Four species of coastal dune inhabiting blue spider wasps, *Chalcochares hirsutifemur*, *Aporus* (*Aporus*) *concolor* (Smith), *A. (A.) luxus*, and *A. (Plectraporus) hirsutus* are or are suspected of being obligate parasitoids on *Aptostichus* wafer-lid spiders. *Aporus concolor* is the rarest of the four species in this area (Wasbauer and Kimsey 1985; Abela 2014c, 2021g). *Aporus luxus* is scarce to common on the coastal back dunes of Santa Barbara County (Wasbauer and Kimsey 1985; Abela pers. obs.) (Fig. 8). It has been observed searching and digging for host spiders in this area (Kurczewski et al. 2021; Abela pers. obs.). *Aporus luxus* has been reported or photographed with immobilized individuals of *Aptostichus ?hesperus* (Chamberlin) (Kurczewski and West 2022), *A. miwok* (Kurczewski et al. 2020), and *A. ?stanfordianus* Smith (Wasbauer 1982) in central and southern California. The host record of *A. ?stanfordianus* probably pertains to *A. stephencolberti* (Kurczewski et al. 2021). *Aporus hirsutus* is commoner than *A. luxus* on the sandy coastal fore- and back dunes of San Luis Obispo and Santa Barbara counties (Fig. 8; Wasbauer and Kimsey 1985; Abela pers. obs.). *Aporus hirsutus* reportedly captures *A. atomarius* (Kurczewski and Edwards 2012), *A. simus* (Abela 2015; Kurczewski et al. 2017, 2021; Willems 2018; Johnson 2020a, b), *A. stephencolberti* Bond (Luhrs 2020), and *A. sp.*, probably *A. stanfordianus* (Williams 1928; Krombein 1979; Wasbauer and Kimsey 1985). The host record for *A. atomarius* may pertain to *A. simus*, and that for *A. sp.*, probably

A. stanfordianus, is likely *A. stephencolberti* (Kurczewski et al. 2021). An immobilized *A. atomarius* female, ~25 mm long, was found on the sand surface of coastal back dunes in Santa Barbara County, CA in an area where *C. hirsutifemur* females were rather common (Fig. 8; Abela 2013). Because of its large size, this immobilized spider was probably the discarded prey of *C. hirsutifemur* and not that of the much smaller *A. luxus* or *A. hirsutus*.

Aporus hirsutus females are the smallest (6.5–12.5 mm, Evans 1966) of the four coastal dune inhabiting spider wasps. This species inhabits foredunes as well as back dunes and preys mainly on *Aptostichus simus* juveniles (~13–15 mm) (Kurczewski et al. 2021; Abela per. obs.). [An *A. simus* adult female extracted from its burrow was 18 mm long, including chelicerae (Abela pers. obs.)]. *Aporus luxus* females are slightly larger (8–14 mm, Evans 1966) than *A. hirsutus*, inhabit the back dunes, and are probably obligate parasitoids on both *A. simus* and *A. atomarius* juveniles (~15 mm) as they prey on *A. miwok* and *A. stephencolberti*, two species with similar burrowing habits (Kurczewski et al. 2021). Although there are no host records for *Aporus concolor*, it is slightly larger than *A. luxus* (~13–15 mm, Evans 1966; Kurczewski pers. obs.) and inhabits the back dunes. This species probably has the same host requirements as *A. luxus*, capturing juveniles of *Aptostichus* as it and *A. luxus* are similar in appearance, ecology, and external morphology (Evans 1966; Wasbauer and Kimsey 1985). *Chalcochares hirsutifemur* females are, by far, the largest (12–20 mm) of the four coastal dune blue spider wasp species and were more common in July and August than any of the *Aporus* species in an area of back dunes (Fig. 8). Females of *C. hirsutifemur* may capture and entomb in their own burrows equivalent size *A. atomarius* adult and subadult females (~18–25 mm) and *A. simus* adult and subadult females, the two dominant species of *Aptostichus* in this localized area.

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Literature Cited

- Abela A. 2011.** *Chalcochares hirsutifemur*. Available at <https://www.flickr.com/photos/44150996@N06/5890139366>. (Last accessed 21 January 2022).
- Abela A. 2013.** San Bernardino Hills Trapdoor Spider (*Aptostichus atomarius*). Available at <https://www.flickr.com/photos/44150996@N06/8703323325>. (Last accessed 22 January 2022).
- Abela A. 2014a.** San Bernardino Hills Trapdoor Spider (*Aptostichus atomarius*). Available at <https://www.flickr.com/photos/44150996@N06/14342393595>. (Last accessed 21 January 2022).
- Abela A. 2014b.** *Aptostichus simus*. Available at <https://www.flickr.com/photos/44150996@N06/14401326214>. (Last accessed 21 January 2022).
- Abela A. 2014c.** *Aporus concolor*. Available at <https://www.inaturalist.org/observations/106415244>. (Last accessed 17 February 2022).
- Abela A. 2015.** *Aporus hirsutus* with *Aptostichus simus*–*Aporus hirsutus*–female. Available at <https://bugguide.net/node/view/1104818/bgimage>. (Last accessed 29 January 2022).
- Abela A. 2020.** Wasp – *Chalcochares hirsutifemur* – male. Available at <https://bugguide.net/node/view/1909432/bgimage>. (Last accessed 18 January 2022).

- Abela A. 2021a.** *Chalcochares hirsutifemur* – male. Available at <https://bugguide.net/node/view/2026646/bgimage>. (Last accessed 18 January 2022).
- Abela A. 2021b.** *Chalcochares hirsutifemur* – female. Available at <https://bugguide.net/node/view/2026651/bgimage>. (Last accessed 18 January 2022).
- Abela A. 2021c.** *Chalcochares hirsutifemur* – male. Available at <https://bugguide.net/node/view/2026657/bgimage>. (Last accessed 18 January 2022).
- Abela A. 2021d.** *Chalcochares hirsutifemur* – female. Available at <https://www.flickr.com/photos/44150996@N06/51381199366/>. (Last accessed 23 January 2022).
- Abela A. 2021e.** *Chalcochares hirsutifemur* – female. Available at <https://www.flickr.com/photos/44150996@N06/51382207490>. (Last accessed 30 January 2022).
- Abela A. 2021f.** *Chalcochares hirsutifemur* – female. Available at <https://inaturalist.ca/observations/91711119>. (Last accessed 18 January 2022).
- Abela A. 2021g.** Possible *Aporus concolor*. Available at <https://www.flickr.com/photos/44150996@N06/51321585734>. (Last accessed 24 January 2022).
- Abela A. 2021h.** *Chalcochares hirsutifemur* – female. Available at <https://bugguide.net/node/view/2026640/bgpage>. (Last accessed 24 February 2022).
- Bond JE. 2012.** Phylogenetic treatment and taxonomic revision of the trapdoor spider genus *Aptostichus* Simon (Araneae, Mygalomorphae, Euctenizidae). *ZooKeys* 252: 1–209.
- Bond JE, Godwin RL. 2013.** Taxonomic revision of the trapdoor spider genus *Eucteniza* Ausserer (Araneae, Mygalomorphae, Euctenizidae). *ZooKeys* 356: 31–67.
- Bond JE, Opell BD. 2002.** Phylogeny and taxonomy of the genera of south-western North American Euctenizinae trapdoor spiders and their relatives (Araneae: Mygalomorphae, Cyrtaucheniidae). *Zoological Journal of the Linnean Society* 136: 487–534.
- Evans HE. 1950.** A taxonomic study of the Nearctic spider wasps belonging to the tribe Pompilini (Hymenoptera: Pompilidae). Part I. *Transactions of the American Entomological Society* 75: 133–270.
- Evans HE. 1966.** A revision of the Mexican and Central American spider wasps of the subfamily Pompilinae (Hymenoptera: Pompilidae). *Memoirs of the American Entomological Society* 20: 1–422.
- Hadley A. 2008.** Combine ZM. Available from URL: Combine ZM – Download (lo4d.com). (Last accessed 4 June 2023).
- Hawk M. 2022.** Spider Wasps (Family Pompilidae). Available at <https://www.inaturalist.org/observations/120882119>. (Last accessed 10 June 2022).
- Hedin M. 2020.** Southern Coastal Dune Trapdoor Spider. Available at <https://www.inaturalist.org/observations/52851332>. (Last accessed 23 January 2022).
- Horner DK. 2019.** Pompilidae? – *Chalcochares* – male. Available at <https://bugguide.net/node/view/1697404/bgimage>. (Last accessed 28 January 2022).
- Jenks GE. 1938.** Marvels of metamorphosis. A scientific “G-man” pursues rare trapdoor spider parasites for three years with a spade and a candid camera. *The National Geographic Magazine* 74: 807–828.
- Johnson D. 2020a.** Southern Coastal Dune Trapdoor Spider. Available at <https://www.inaturalist.org/observations/58093062>. (Last accessed 24 January 2022).
- Johnson D. 2020b.** *Aporus hirsutus*. Available at <https://ecuador.inaturalist.org/observations/56888065>. (Last accessed 24 January 2022).
- Krombein KV. 1979.** Family Pompilidae. P. 1523–1570. In: Krombein KV, Hurd PD, Jr., Smith DR, Burks BD (eds.). *Catalog of Hymenoptera in America north of Mexico. Volume 2, Apocrita (Aculeata)*. Smithsonian Institution Press; Washington, DC. 2209 p.
- Kurczewski FE, Abela AJ, West RC. 2021.** Nesting behavior, ecology, and functional morphology of the trapdoor spider-hunting spider wasp *Aporus (Plectraporus) hirsutus* (Banks) (Hymenoptera: Pompilidae). *Insecta Mundi* 0902: 1–23.
- Kurczewski FE, Edwards GB. 2012.** Hosts, nesting behavior, and ecology of some North American spider wasps (Hymenoptera: Pompilidae). *Southeastern Naturalist* 11 (Monograph 4): 1–71.
- Kurczewski FE, Edwards GB, Pitts JP. 2017.** Hosts, nesting behavior, and ecology of some North American spider wasps (Hymenoptera: Pompilidae), II. *Southeastern Naturalist* 16 (Monograph 9): 1–82.
- Kurczewski FE, Hedin M, West RC. 2023.** Nesting behavior of the spider wasp *Calopompilus pyrrhomelas* (Walker) (Hymenoptera: Pompilidae). *Insecta Mundi* 0980: 1–7.
- Kurczewski FE, West RC. 2022.** Host selection and nesting behavior of Nearctic trapdoor spider-hunting spider wasps (Hymenoptera: Pompilidae: Pepsini, Aporini). *Insecta Mundi* 0959: 1–24.
- Kurczewski FE, West RC, Waichert C, Kissane KC, Ubick D, Pitts JP. 2020.** New and unusual host records for some North American and South American spider wasps (Hymenoptera: Pompilidae). *Zootaxa* 4891: 1–112.

- Luhrs C. 2020.** *Aporus hirsutus*. Available at <https://www.inaturalist.org/observations/61356505>. (Last accessed 27 January 2022).
- Noss C. 2020.** Southern Coastal Dune Trapdoor Spider. Available at <https://www.inaturalist.org/observations/64829527>. (Last accessed 23 January 2022).
- Shimizu A, Broad G, Yoshimura J, Pitts JP. 2022.** First records of the spider wasps *Ctenocerus* Dahlbom and *Paraclavelia* Haupt from Asia, with discussions on the systematics of Ctenocerinae (Hymenoptera: Pompilidae). *European Journal of Taxonomy* 845: 101–131. <https://doi.org/10.5852/ejt.2022.845.1957>.
- Shimizu A, Pitts JP, Rodriguez J, Wahis R, Yoshimura J. 2021.** Systematics and convergent evolution in three Australian genera of Pepsinae spider wasps (Hymenoptera: Pompilidae). *Austral Entomology* 60: 301–316. <https://doi.org/10.1111/aen.12530>
- Van Loon C, Van Loon T. 2021.** *Chalcochares hirsutifemur*. Available at <https://www.inaturalist.org/observations/96979600>. (Last accessed 28 January 2022).
- Wasbauer MS. 1982.** Prey records for some North American spider wasps (Hymenoptera: Pompilidae). *Pacific Entomologist* 58: 223–230.
- Wasbauer MS, Kimsey LS. 1985.** California spider wasps of the subfamily Pompilinae (Hymenoptera: Pompilidae). *Bulletin of the California Insect Survey* 26: 1–130.
- Willems JS. 2018.** Southern Coastal Dune Trapdoor Spider. Available at <https://www.inaturalist.org/observations/12967309>. (Last accessed 23 January 2022).
- Williams FX. 1928.** Studies in tropical wasps—their hosts and associates (with descriptions of new species). *Bulletin of the Experiment Station of the Hawaiian Sugar Planter's Association (Entomology)* 19: 1–179.

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