UNIVERSITY OF CALIFORNIA

Santa Barbara

Ophionines (Hymenoptera: Ichneumonidae: Ophioninae) of California and the addition of taxa into a phylogenetic reassessment of tribal limits

A thesis submitted in partial satisfaction of the

requirements for the degree Master of Arts

in Ecology, Evolution, and Marine Biology

by

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March 2020

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ABSTRACT

Ophionines (Hymenoptera: Ichneumonidae: Ophioninae) of California and the addition of taxa into a phylogenetic reassessment of tribal limits

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Wasps of the ichneumonid subfamily Ophioninae are mostly large, nocturnal, larval-pupal endoparasitoids of primarily Lepidoptera, with high abundance and diversity, especially in the tropics. Recent genetic studies revealed that this subfamily's level of diversity is far higher than previously thought. Though they are found worldwide, the biodiversity of this subfamily is not known in non-tropical hotspots like California. First, I examined the unrecognized diversity of Ophionines in coastal southern California using a combination of the morphological, geographic, and temporal characteristics of specimens. Second. I added those taxa to a reassessment of the tribes in this subfamily. My findings indicate that the levels of diversity of the Californian Ophionine wasps are far higher than currently realized, with approximately 19 putative new species for the state, exhibiting homoplasy and endemism that calls the Ophioninae tribal designations into question.

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I. General Introduction to Ophionine Diversity in California, with an emphasis on the Coastal Southern Counties

Ophionine wasps (Hymenoptera: Ichneumonidae: Ophioninae) are larval-pupal endoparasitoids of primarily moths (Lepidoptera). Ophioninae occur throughout the world and are mostly nocturnal or crepuscular. They are frequently collected at lights at night and are commonly found in collections. Despite being frequently collected, the ecology, morphology, and classification of many of the genera and species within the Ophioninae remain poorly known.

A. Classification and Phylogeny

Ophioninae is a diverse subfamily composed of 32 known genera with over 1,000 described species distributed worldwide (Yu et al., 2012). Attempts at classification of members of this subfamily focus on morphology, which led to much confusion and ongoing revisions for this morphological variant group.

The Ophionini was the first Ophionine tribe described in Swainson & Shuckard (1840), later revised in Meyer (1937), Cushman (1947), Townes (1971), and Rousse et al. (2016). The tribe Enicospilini was first described in Townes (1971) and revised in Rousse et al. (2016). Thyreodonini is the most recently described Ophionine tribe (Rousse et al., 2016). Anomalonini and Therionini, previously listed in Ophioninae, were placed into Anomaloninae (Short, 1959 and Townes et al., 1965). Ophioninae was broken up into multiple subfamilies in Townes (1969).

Table 1. Description and revision history of the three currently recognized tribes of Ophioninae.

Current Tribes of Ophioninae		
	Description	**Revisions**
Ophionini	Shuckard (1840)	Meyer (1937), Cushman (1947), Townes (1971), Rousse (2016)
Enicospilini	Townes (1971)	Rousse (2016)
Thyreodonini	Rousse (2016)	

A comprehensive morphology-based phylogeny of Ophioninae was proposed in Gauld (1985) using both parsimony and compatibility methods for analyses. Gauld found a high level of homoplasy in morphological characters and concluded that the subfamily was best classified into five major evolutionary lineages: *Ophion* genus-group, *Sicophion* genus-group, *Eremotylus* genus-group, *Thyreodon* genus-group, and *Enicospilus* genus-group.

In 2016, Rousse et al. investigated the relationships among evolutionary lineages within Ophioninae using a combination of morphological and molecular methodologies. Rousse used a morphological dataset of 62 characters along with sequences in the COI region of mitochondrial DNA and the D2-D3 region of 28S ribosomal DNA to construct an updated phylogeny. The combined analysis of Rousse's morphology and molecular data supports the claim that Ophioninae, including the historically problematic genera *Skiapus* and *Hellwigia*, is monophyletic. Rousse's study supports the existence of three tribes including the newly revised tribes Ophionini and Enicospilini, and the new tribe Thyreodonini. These tribes map over and give support to the *Ophion* genus-group, Enicospilus genus-group, and *Thyreodon* genus-group from Gauld's morphological analysis (1985). The other two genus-groups, the *Eremotylus* genus-group and *Sicophion* genus-group, are not supported in Rouse's analysis.

Other integrative taxonomic approaches have been used to classify species in the genus *Ophion* (Schwarzfeld & Sperling, 2014; Schwarzfeld, Broad & Sperling, 2016, Johansson & Cederberg, 2019). Historically, *Ophion* classification has proven problematic due to the genus being notorious for cryptic species and high intraspecific variation, especially when the delineation characters are based on color and size (Linnaeus, 1758, Fabricius, 1798, Gravenhorst, 1829, Ratzeburg, 1848, Thomson, 1888, Kriechbaumer, 1879a, 1879b, 1879c, 1892a, 1892b, and Brauns, 1889). Schwarzfeld & Sperling (2014) used a combination of classic morphology, morphometrics, and DNA analyses (ITS2, COI, and 28S D2-D3) to define the *Ophion scutellaris* species-group. Schwarzfeld et al. (2016) subsequently used morphological and DNA (ITIS2, COI, and 28S) analyses to create the first molecular phylogeny of the entire genus. Following Schwarzfeld's success, Johanssen & Cederberg (2019) used a combination of morphological and DNA(COI) analyses to test Schwarzfeld's phylogeny with the addition of Swedish specimens. They found that the addition of these specimens largely supported the species-groups defined in Schwarzfeld et al. (2016).

The notoriously problematic genus *Hellwigia* was revisited using morphological analysis and rearing in Shaw & Voogd (2019). One of the species "*Hellwigia*" *obscura*, now *Heinrichiella obscura,* was found to not to be an Ophioninae. As the sequence data of this non-ophionine species was used as the representative of *Hellwigia* in previous molecular analyses and phylogeny (Quicke et al., 2009, Rousse et al., 2016), the actual phylogenetic placement of the genus is unknown.

In summary, despite historical and current taxonomic work, phylogenetic relationships among taxa within this subfamily are still lacking and the placement and monophyly of genera within tribes remains unclear.

B. Californian Biodiversity

The subfamily Ophioninae is known for high rates of endemism compared to other ichneumonid subfamilies, with 20 of its 32 genera (62.5%) being restricted to a single geographic region (Gauld, 1985). The Nearctic has the lowest levels of endemicity (1 endemic genus out of 7 = 14%) and the Neotropics have the highest levels of endemicity (50%), although these conclusions may be biased by limited collections and under sampling of the Nearctic (Gauld, 1985). Little, however, is known about the diversity of the Ophioninae in temperate areas, such as California. California encompasses some of the most geographically complicated patterns of genetic diversity of life on Earth and the California Floristic Province is considered one of the world's 25 most biologically rich and endangered terrestrial ecoregions (Myers et al. 2000).

In California, ophionines are abundant, frequently seen at lights at night, and commonly collected in surveys of other nocturnal insects. Five Ophionine genera and 13 species are known to occur in California:

Table 2. Summary of the 13 species of Ophioninae known in California according to Hooker, 1912 and Yu, van Achterberg & Horstmann 2012.

<table>
<tr><th>Genus</th><th>Species</th><th>Notes</th></tr>
<tr><td rowspan="7">Enicospilus</td><td>americanus (Christ, 1791)</td><td rowspan="7">23 described Nearctic species
Far less species rich in temperate region than tropics
Speculated that there is overlap between the South American and North American ranges of Enicospilus species, making it difficult to distinguish the purely North American species (Gauld 1988a).</td></tr>
<tr><td>bifoveolatus (Brullé, 1846)</td></tr>
<tr><td>flavostigma Hooker, 1912</td></tr>
<tr><td>glabratus (Say, 1835)</td></tr>
<tr><td>purgatus (Say, 1835)</td></tr>
<tr><td>sarukhani Gauld, 1988b</td></tr>
<tr><td>texanus (Felt, 1904)</td></tr>
<tr><td rowspan="2">Eremotylus</td><td>abnormus (Felt, 1904)</td><td rowspan="2">Current genus encompasses the former genera Eremotylus Foerster, Chlorophion Townes, Genophion Felt, Chilophion Cushman, Clistorapha Cushman and Boethoneura Cushman (Gauld 1979,1985)
5 described Nearctic species
Speculated to have at least sixteen additional undescribed Nearctic species (Yu et al. 2012; Gauld 1985)</td></tr>
<tr><td>costalis (Cresson, 1879)</td></tr>
<tr><td rowspan="2">Ophion</td><td>magniceps Hooker, 1912</td><td rowspan="2">17 described Nearctic species
estimated that there are approximately 50 Nearctic species based on morphology alone (Gauld, 1985), with recent molecular analyses suggesting many more (Schwarzfeld & Sperling, 2015).</td></tr>
<tr><td>bilineatus Say, 1829</td></tr>
<tr><td>Simophion</td><td>excarinatus Cushman, 1947</td><td>Only 1 described Nearctic species
“several undescribed species” from the Nearctic mentioned by Cushman (1947) and Gauld (1985)
Simophion contains 3 other described species distributed through the Palearctic, Afrotropical, and Neotropical Regions (Yu et al. 2012).</td></tr>
<tr><td>Trophophion</td><td>tenuiceps Cushman, 1947</td><td>A monotypic genus endemic to the Southwestern United States
Rarely collected
Has not been studied since its original description</td></tr>
</table>

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II. Contribution to the Knowledge of Ophionine Diversity in California

A. Depositories of Material Examined

This study is primarily based on the examination of historic specimens that are deposited in the following institutions:

Table 3. Abbreviations and names of the institutions of which specimens were acquired for use in this study.

ASUHIC	Hasbrouck Insect Collection, Arizona State University
CASENT	California Academy of Sciences, San Francisco
EMEC	Essig Museum of Entomology, University of California, Berkeley
SBMNH	Santa Barbara Museum of Natural History, Santa Barbara
SDNHM	The Nat, San Diego Natural History Museum, San Diego
UCBME	Bohart Museum of Entomology, University of California, Davis

UCSBIZC	Vernon and Mary Cheadle Center for Biodiversity and Ecological Restoration, University of California, Santa Barbara

B. Specimens and Sampling

This study is based on the morphological characterization of 2,272 physical Ophioninae specimens. The institutions listed in Table 3 were visited in-person and their Ophioninae, undetermined Ichneumonid, and undetermined insects were scoured for relevant specimens, as almost all of the available specimens of Ophioninae were not identified. The criterion for inclusion in this study was a locality within California with priority on the 7 southern California counties (San Diego, Orange, Ventura, Santa Barbara, Ventura, San Bernardino, and Riverside). A map of the distribution of specimens across California is available in Appendix 2. The specimens had to be in decent enough condition to examine morphology, especially in the wings. Specimens of all 5 known California genera were obtained from these collections. The data of all specimens used in this study is available in the Supplementary Materials.

C. Methods

1. Morphospecies Delimitation

Criterion for Morphospecies Assignment

Morphospecies or operational taxonomic units (OTUs), are taxa distinguished from others based only on morphology. The process for designating morphospecies includes grouping all specimens based on their morphological similarity from a set of published characters. At the start of the study, all specimens were sorted to genera using the New World Ophioninae by David Wahl and Ian Gauld (2002). The morphology of specimens was examined using a set of morphological characters for each genus (Table 4-8) and placed into an OTU. For morphospecies with known sexual dimorphism, they are not separated into different OTUs, despite their different morphologies. The original descriptions of the 13 known Californian species (Ashmead 1890, Brullé 1846, Christ 1791, Cresson 1879, Cushman 1947, Felt 1904, Gauld 1988b, Hooker 1912, Say 1829, Say 1835) were consulted to match to the morphology of my specimens, delineating the first OTUs. If there was any doubt about matching the specimen to a known description, it was assigned to its own OTU. Specimens of putative new species also were left as separate OTUs and will be formally described in future works.

Hierarchy of Character Phylogenetic Value

Although all characters listed below to delineate morphospecies have phylogenetic value, they are not weighted equally. As such, there is an inherent hierarchy of character importance. The first step for morphospecies delineation was investigating wing characters, as these have been key for Ophioninae, especially high-level classification historically (Gauld 1985). If I only relied on a single character type, I would risk overlooking diversity in groups like *Ophion* with cryptic morphology. The next tier of characters for morphospecies delineation were those based on physical structure. These include carina presence/absence, carina length, lengths of body parts, head characters, etc. The reason these characters are not at the highest tier is because these characters have different weight in different genera and they can be subject to variation between specimens of the same morphospecies, whether through natural variation or sexual dimorphism. Non-structural characters, like wing infuscation and body coloration/patterning were considered last as they are historically the most variable.

The morphological terminology used for OTU delineation is a combination of that of American Entomological Institute's Ichneumonid morphology and the Hymenoptera Ontology Portal (Yoder et al. 2010). The diagnostic characters for OTU delineation of each genus and literature evidence of their phylogenetic value are listed below.

Characters for Delineation of Morphospecies Within Genera

Table 4. Morphological characters of phylogenetic value for the genus *Enicospilus*. Evidence and support for each character in the literature is provided in the Source column.

Enicospilus	
Character	**Source**
Width and torsion of mandibles	Gauld (1985) and Gauld (1988a)
Alar sclerite presence/absence and modification	Gauld & Wahl (2002)
Orientation of hairs within the discocubital cell	Gauld (1988a)
Body size and wing infuscation	Gauld (1988a)
R-rs vein of forewing - shape and thickness	Gauld (1985) and Gauld (1988a)

Table 5. Morphological characters of phylogenetic value for the genus *Eremotylus*. Evidence and support for each character in the literature is provided in the Source column.

Eremotylus	
Character	**Source**
Occipital carina complete or interrupted mid-dorsally	Cushman (1947), Gauld (1985), Gauld & Wahl, (2002)
Ocelli size, diameter of ocelli compared to distance between the eyes	Gauld (1985), Leblanc (1989), and Rousse et al. (2016)
Length of malar space	Cushman (1947) and Leblanc (1989)
Width of mandible	Cushman (1947) and Gauld (1985)
Size and shape of clypeus	Cushman (1947), Gauld (1985), and Leblanc (1989)
Antenna length	Cushman (1947), Gauld (1985), and Leblanc (1989)
Epicnemial carina presence/absence and length	Cushman (1947) and Gauld (1985)
Propodeal sculpture	Cushman (1947), Gauld (1985), and Rousse et al. (2016)
R-rs vein of forewing - shape and thickness	Cushman (1947), Gauld (1985), and Gauld & Wahl (2002)
Fore and hindwing infuscation	Cushman (1947)
Length of cu-a where it intersects Cu	Leblanc, (1989) and Gauld & Wahl (2002)

Table 6. Morphological characters of phylogenetic value for the genus *Ophion*. Evidence and support for each character in the literature is provided in the Source column.

Ophion	
Character	**Source**
Pterostigma size and shape	Gauld (1985) and Schwarzfeld & Sperling (2014)
Length of trochantellus	Schwarzfeld & Sperling (2014) and Schwarzfeld et al. (2016)
Ovipositor sheath color	Schwarzfeld & Sperling (2014)
Body coloration and patterning	Schwarzfeld & Sperling (2014) and Schwarzfeld et al. (2016)

Table 7. Morphological characters of phylogenetic value for the genus *Simophion*. Evidence and support for each character in the literature is provided in the Source column.

Simophion	
Character	**Source**
Length of malar space	Cushman (1947)
Ocelli size, diameter of ocelli compared to distance between the eyes	Gauld (1985), Leblanc (1989), and Rousse 2016)
Size and shape of clypeus	Cushman (1947) and Gauld (1985)
-Body and orbit coloration	Cushman (1947)
R-rs vein of forewing - shape and thickness	Cushman (1947), Gauld (1985), and Gauld & Wahl (2002)

Table 8. Morphological characters of phylogenetic value for the genus *Trophophion*. Evidence and support for each character in the literature is provided in the Source column.

Trophophion	
Character	**Source**
Length of malar space	Cushman (1947)
Ocelli size, diameter of ocelli compared to distance between the eyes	Gauld (1985), Leblanc (1989), and Rousse et al. (2016)
Occipital carina complete or interrupted mid-dorsally	Cushman (1947), Gauld (1985), and Gauld & Wahl (2002)
Propodeal sculpture	Cushman (1947), Gauld (1985), and Rousse et al. (2016)
R-rs vein of forewing - shape and thickness	Cushman (1947), Gauld (1985), and Gauld & Wahl (2002)

D. Results

1. **Summary of Findings**

Of the 13 known species in California (Yu et al. 2012), 7 were found during this study, primarily of the well-known genus *Enicospilus*. Eighteen additional morphospecies were delineated, including 11 *Eremotylus*, 5 *Ophion,* 1 *Simophion,* and 1 *Trophophion.* The additional morphospecies of *Eremotylus* and *Trophophion* were likely new, undescribed species. The *Simophion* morphospecies is likely the undescribed male form of *Simophion* *excarinatus.* The *Ophion,* which are known for their cryptic morphology, will need to be re-examined with additional delineation methods, such as those used in Schwarzfeld & Sperling 2014 and Schwarzfeld et al. 2016. Specimens of *Eremotylus subfuliginosus* also were found, thus expanding the species' historic range based on prior literature (Yu et al. 2012). An updated catalog of Californian Ophioninae is provided later in the results, and a catalog including all the morphospecies is available in Appendix 1. Summary tables of the character state of the *Eremotylus* and *Ophion* morphospecies are available in Appendix 3 and 4.

All of the metadata about the specimens used in analyses are located in the Supplementary Materials. All of the photographs used in this study are available for public domain use under the creative commons, CC0. They can be accessed via their catalog number in the Global Biodiversity Information Facility (GBIF) or the Barcode of Life Database (BOLD).

2. **Morphospecies that match descriptions of known species:**

OTU 1 = *Enicospilus americanus* (Christ, 1791)

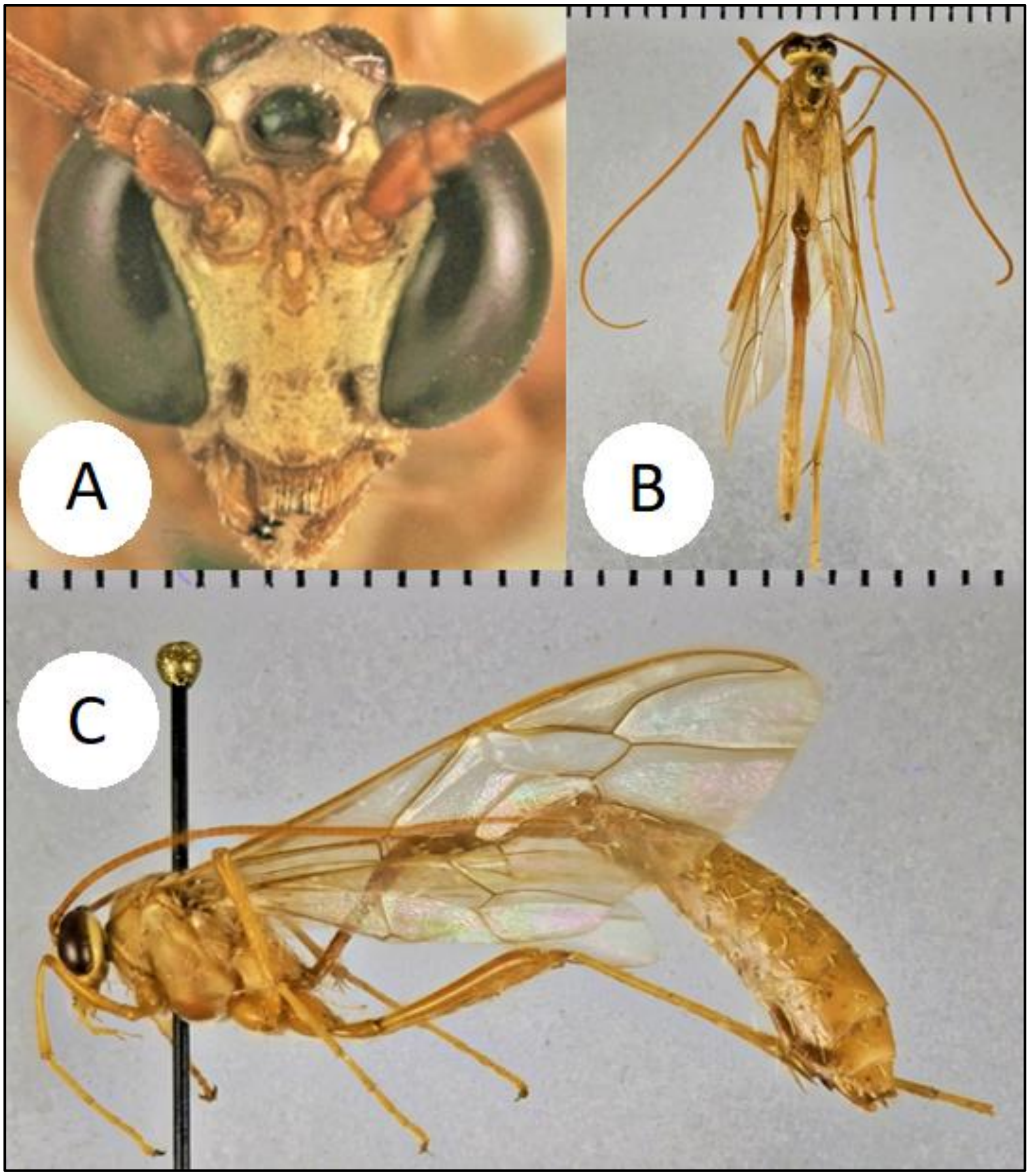

Figure 1. Images of the **A** head, **B** dorsum, and **C** habitus of *Enicospilus americanus*.

Diagnosis

This species represents the largest Ophioninae in California, often with a forewing length of over 21 mm. Compared to other species in the *Enicospilus americanus* complex, this species has short hind tarsal claws, broad central antenna segments, and a forewing often with a yellowish tint and with Rs+2r proximoventrally rounded.

Distribution

This species has been recorded commonly throughout the eastern United States, with a known range extending to California, Southern Canada, and Argentina (Gauld, 1988a). Most of the specimens examined in this study were collected from San Diego County, with some found as far north as Santa Clara County.

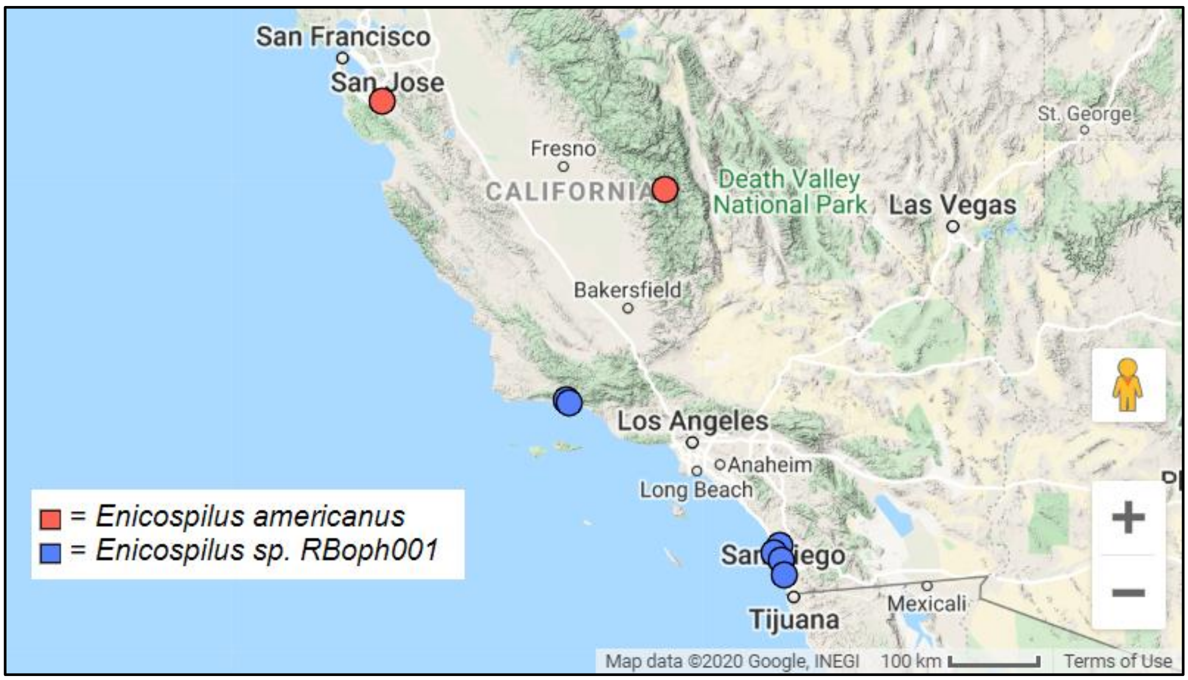

Figure 2. Distribution of *Enicospilus americanus* specimens examined in this study. n=16

Remarks

This species seems to be much less common on the West Coast than in the Eastern U.S. because comparatively fewer specimens (a whole order of magnitude less than in Gauld, 1988a) were found in collections from California.

OTU 2 = *Enicospilus glabratus* (Say, 1835)

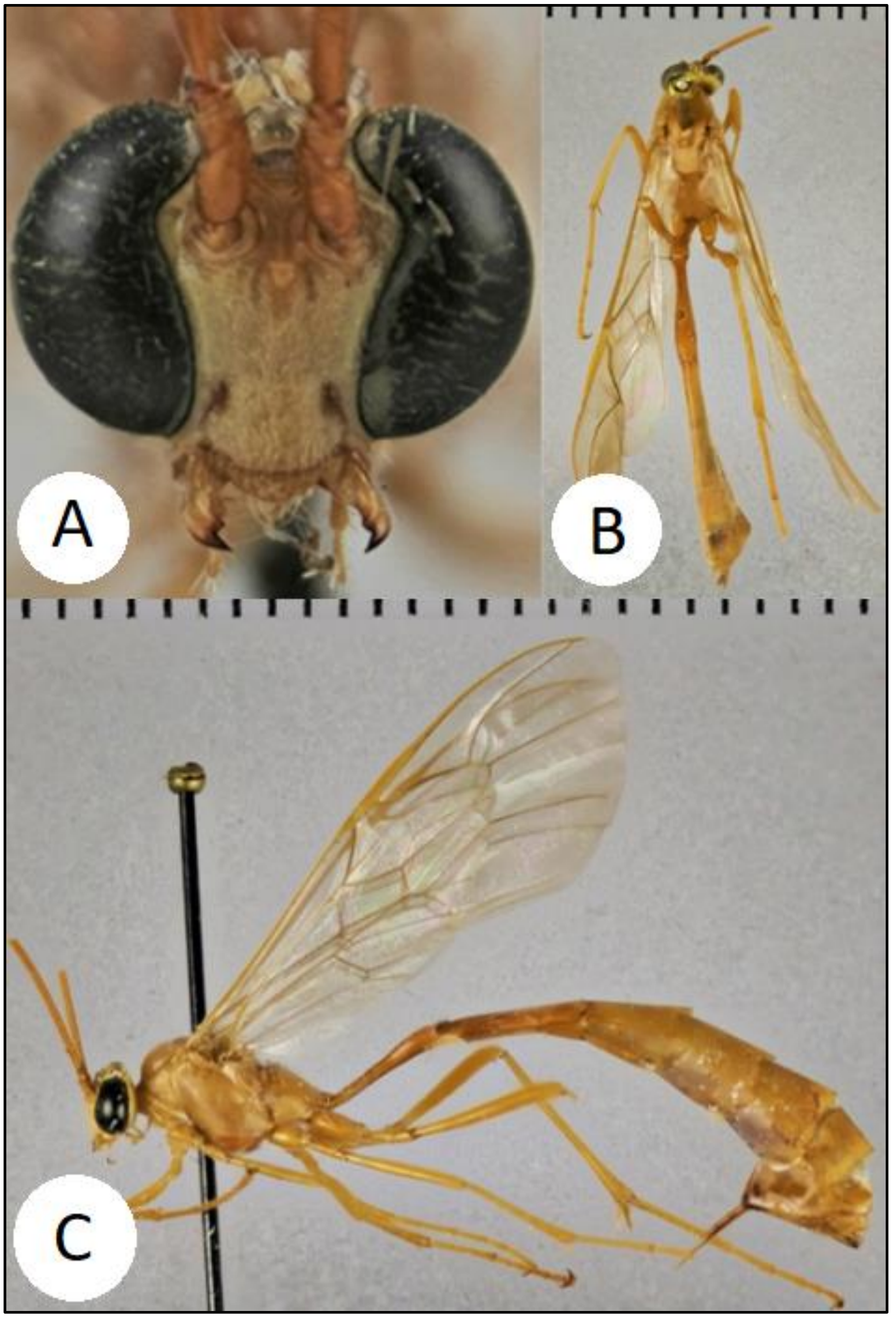

Figure 3. Images of the **A** head, **B** dorsum, and **C** habitus of *Enicospilus glabratus*.

Diagnosis

This is one of the most distinctive species of *Enicospilus* in the United States, being easily recognized by the presence of a clump of closely-packed hairs in the anterior corner of the discosubmarginal cell.

Distribution

This species is one of the most common and widespread *Enicospilus* species in the New World, with a range spanning from the United States south to Argentina, and extending into the Caribbean (Gauld, 1988a). This species has been commonly collected throughout California, especially in the South. In this study, this species was found as far north as Contra Costa County.

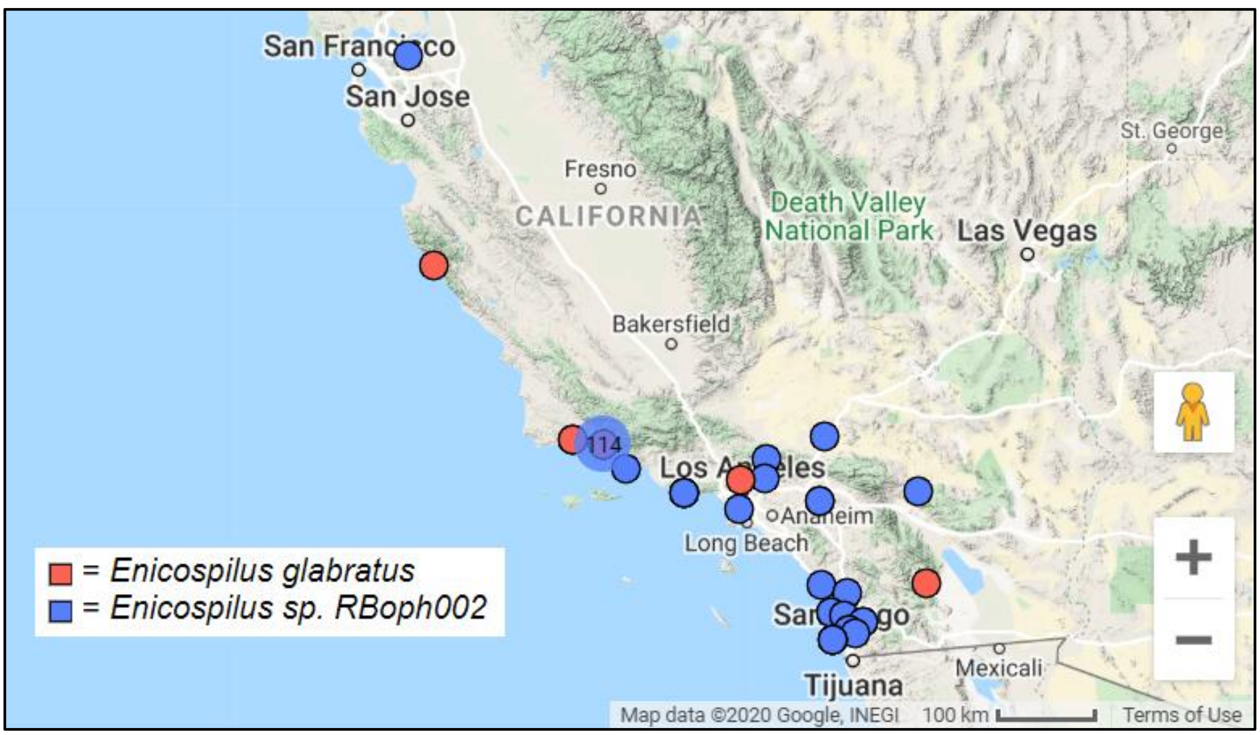

Figure 4. Distribution of *Enicospilus americanus* specimens examined in this study. n=185

Remarks

This species is the most common *Enicospilus* species collected from California over the last 20 years, being most common in late fall. Gauld (1988a) noted that this species was collected in all months of the year in Florida, but that it appeared to be most common in late summer further north.

OTU 6 = *Enicospilus purgatus* (Say, 1835)

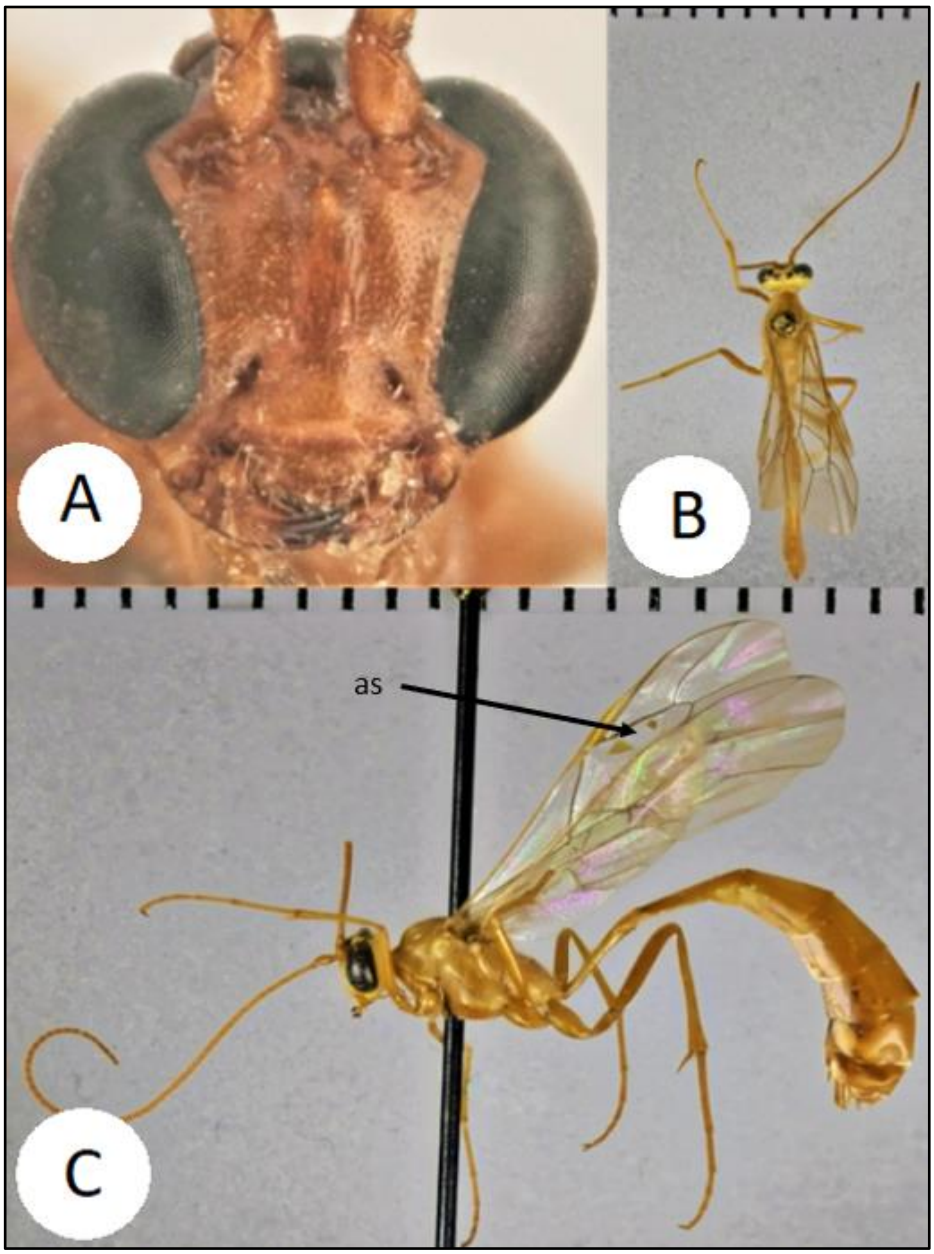

Figure 5. Images of the **A** head, **B** dorsum, and **C** habitus of *Enicospilus purgatus*. The presence of the alar sclerites (as) is labeled.

Diagnosis

Alar sclerites are present within the glabrous fenestra of the forewing's discosubmarginal cell in this species. Unlike other *Enicospilus* species with alar sclerites, the discal sclerite in *E. purgatus* is reduced to a thin crescent, which does not touch the others. Compared to the other Californian *Enicospilus,* including those in the *Enicospilus americanus* complex, this species is much smaller with a forewing length of around 12 mm.

Distribution

Found from Northern Canada to Argentina, throughout habitat types, being quite common in disturbed or agricultural areas (Gaud, 1988a).

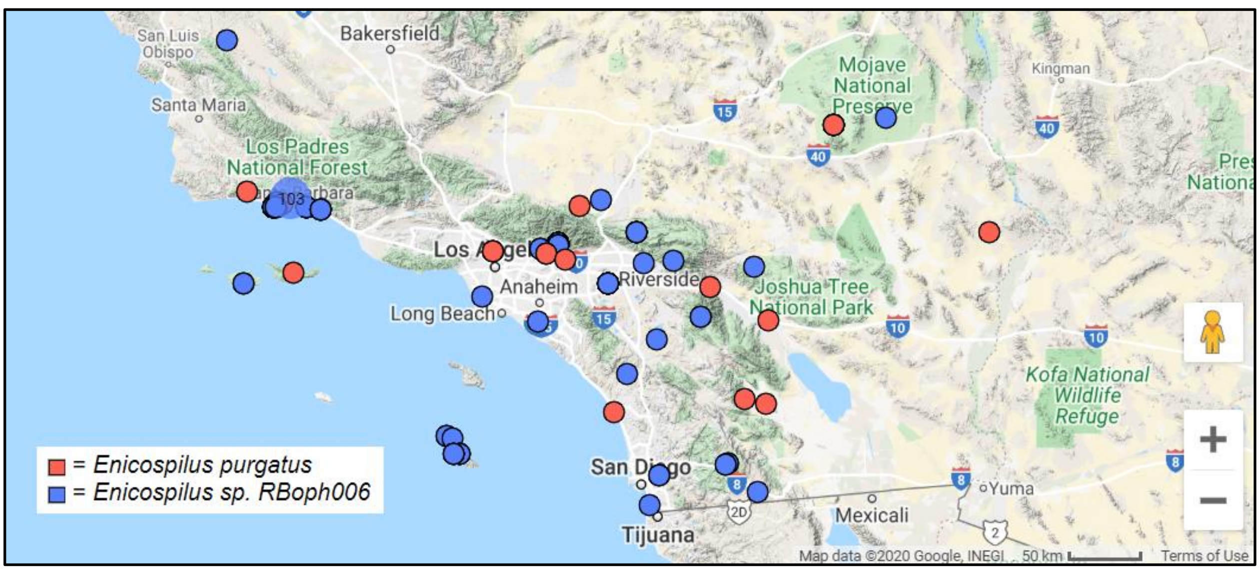

Figure 6. Distribution of *Enicospilus purgatus* specimens examined in this study. n=271

Remarks

An extremely common and ubiquitous species found throughout Southern California, as well as the rest of the United States. Although Gauld (1988a) speculated that several Nearctic species may be confused with this species, our specimens all appeared to be similar and fit the species description.

OTU 8 = *Enicospilus texanus* (Ashmead, 1890)

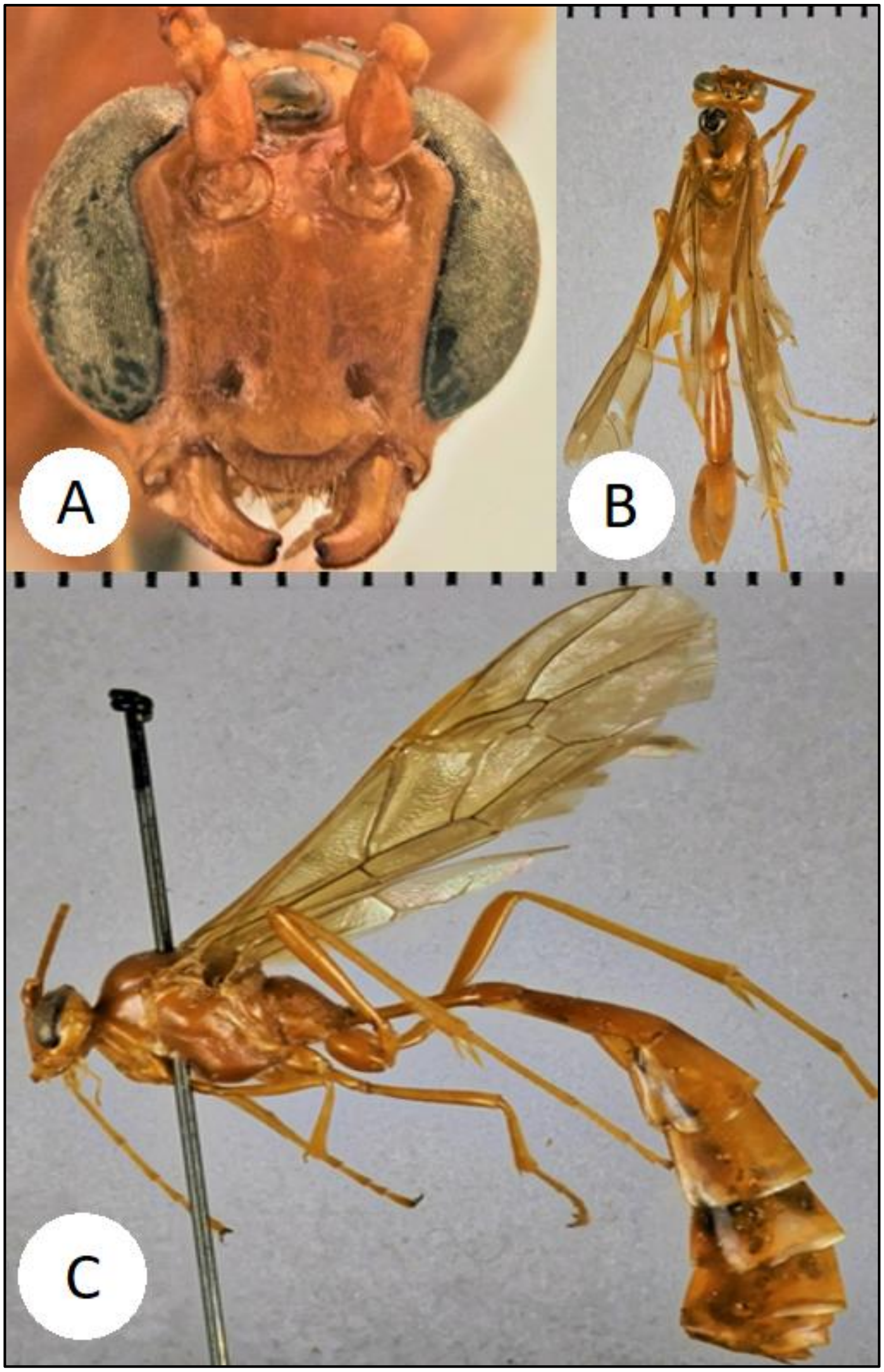

Figure 7. Images of the **A** head, **B** dorsum, and **C** habitus of *Enicospilus texanus*.

Diagnosis

In comparison to the other species of the *Enicospilus americanus* complex this species has long mandibles, lateral longitudinal carina of propodeum absent behind the anterior transverse carina, and dark forewings with a weakly sinuous Rs+2r that is straightened before joining Rs (Gauld, 1988a).

Distribution

This species is widespread throughout the southern states of the United States, ranging in the East from Virginia to Ohio and in the West from Northern Mexico to Washington (Gauld, 1988a).

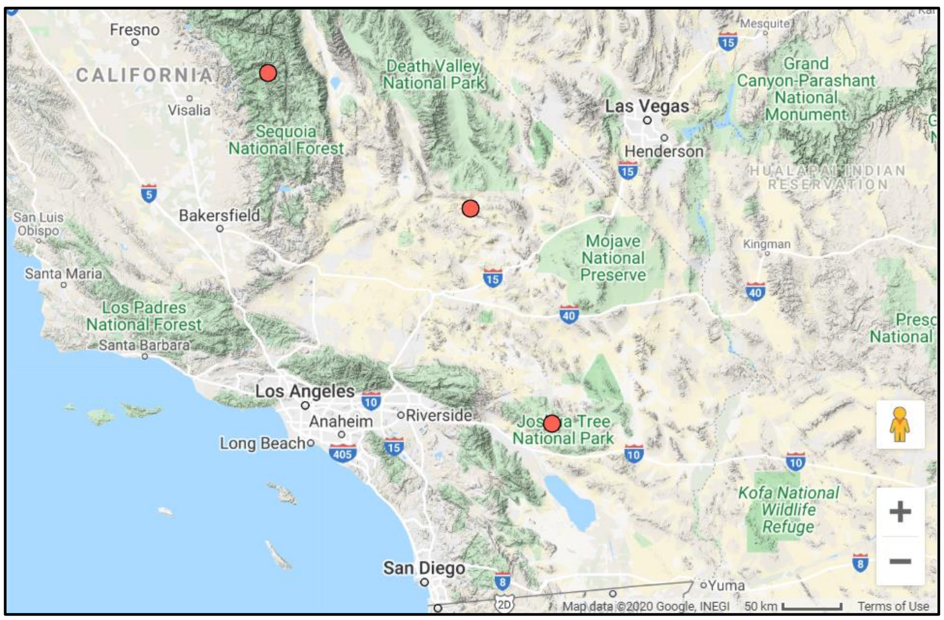

Figure 8. Distribution of *Enicospilus texanus* specimens examined in this study. n=8

Remarks

In California, this species is rare and has been mainly found in the Southern parts of the state.

OTU 10 = *Eremotylus c.f. costalis* (Cresson, 1879)

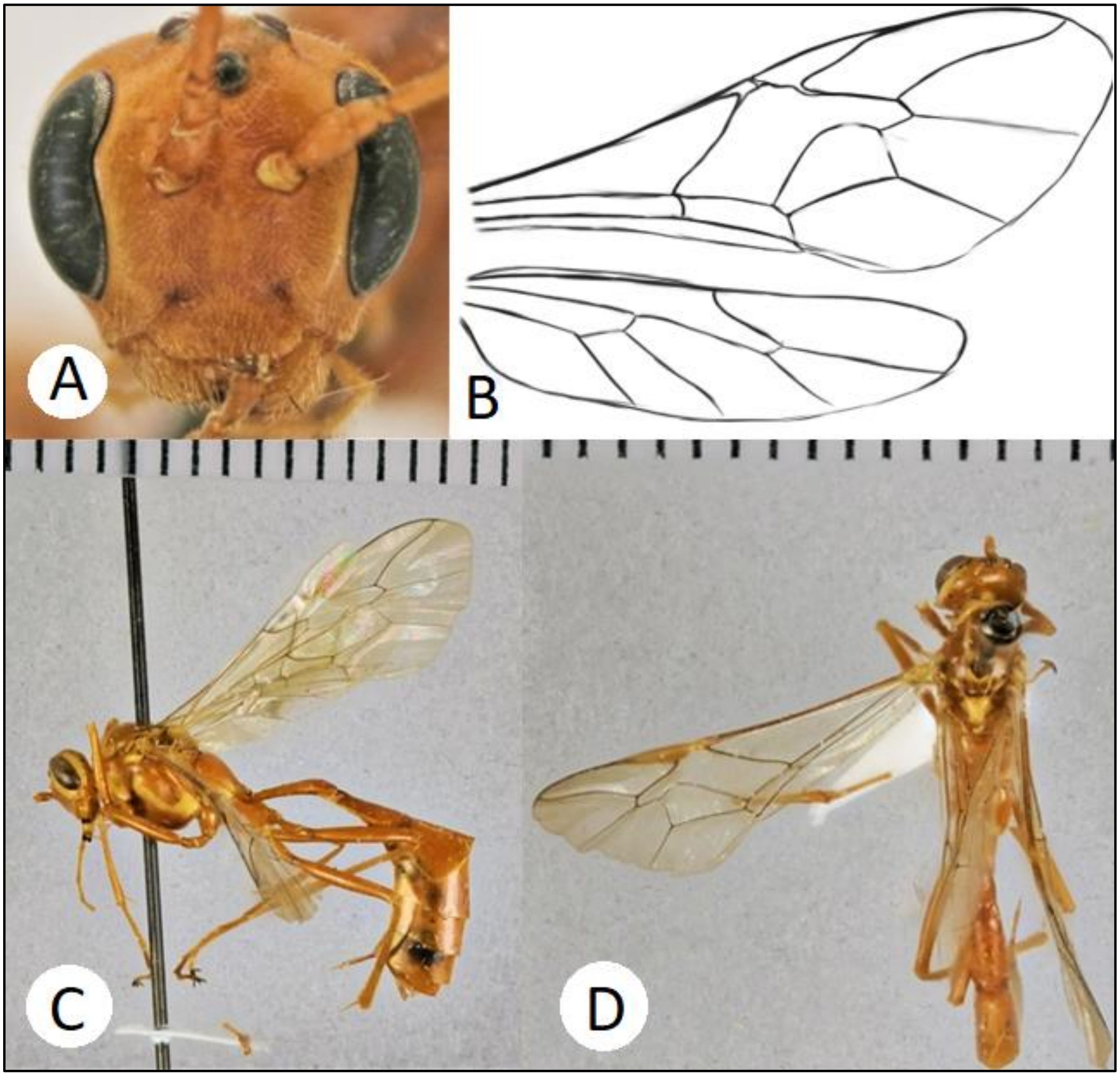

Figure 9. Images of the **A** head, **B** wing venation, **C** habitus, and **D** dorsum of *Eremotylus cf. costalis.*

Diagnosis

Antennae shorter than the length of the forewing. Ocelli small, diameter of ocelli much less than half of the distance between the eyes.

Distribution

This species has been found in the mountainous regions of Colorado, Idaho, Oregon, and California (Leblanc, 1989). Our specimens were found throughout Southern California, although they were rare.

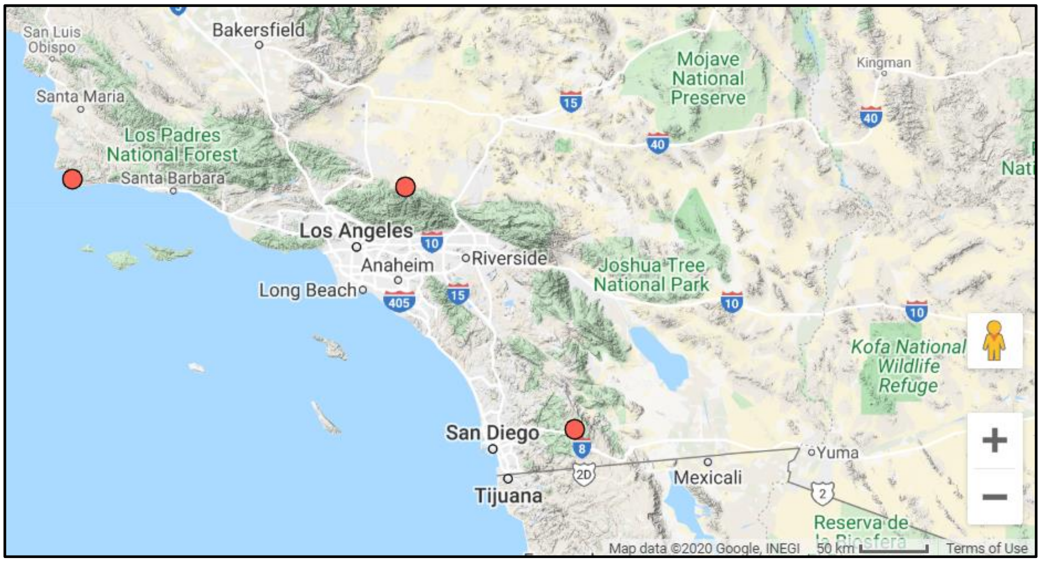

Figure 10. Distribution of *Eremotylus c.f. costalis* specimens examined in this study. n=5

Remarks

This morphospecies is morphologically variable, with some forms being inconsistent with the description of this species, such as the lack of black markings, labrum of varying length, and lack of wing infuscation. However, it does fit within the morphological limits of the *Eremotylus costalis* complex, because of the strongly reduced ocelli (Fig. 5A) and shortened antennae. A longer length clypeus and non-enlarged head separate it from *Eremotylus bulbosus.* Whether these differences are sufficient to signify a distinct species within the complex or just represent intraspecific variation is currently unclear and will have to be explored in future work.

OTU 14= *Simophion excarinatus* Cushman, 1947

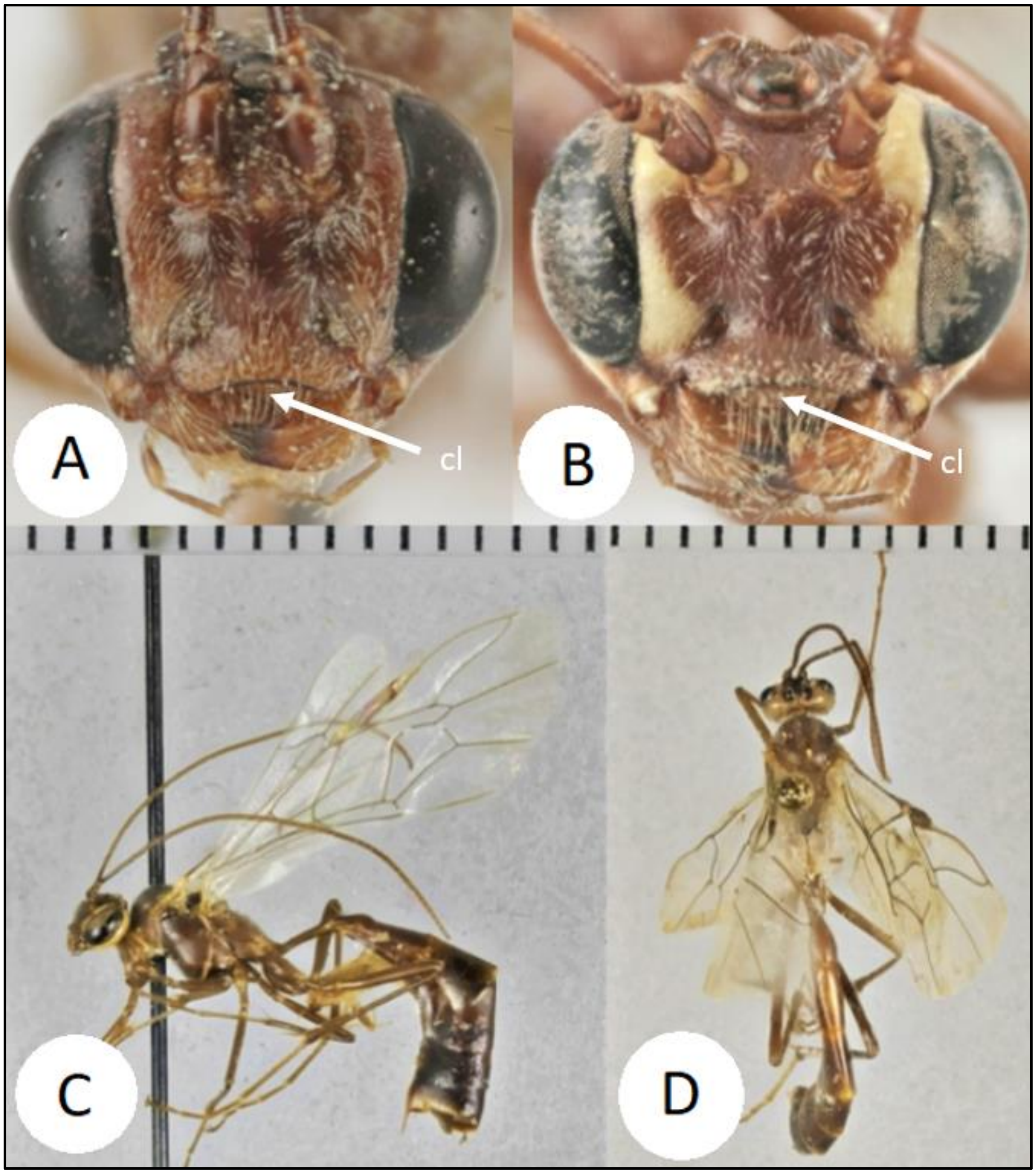

Figure 11. Images of the **A,B** head, **C** dorsum, and **D** habitus of *Simophion excarinatus.* The concavely truncate clypeus (cl) is labeled.

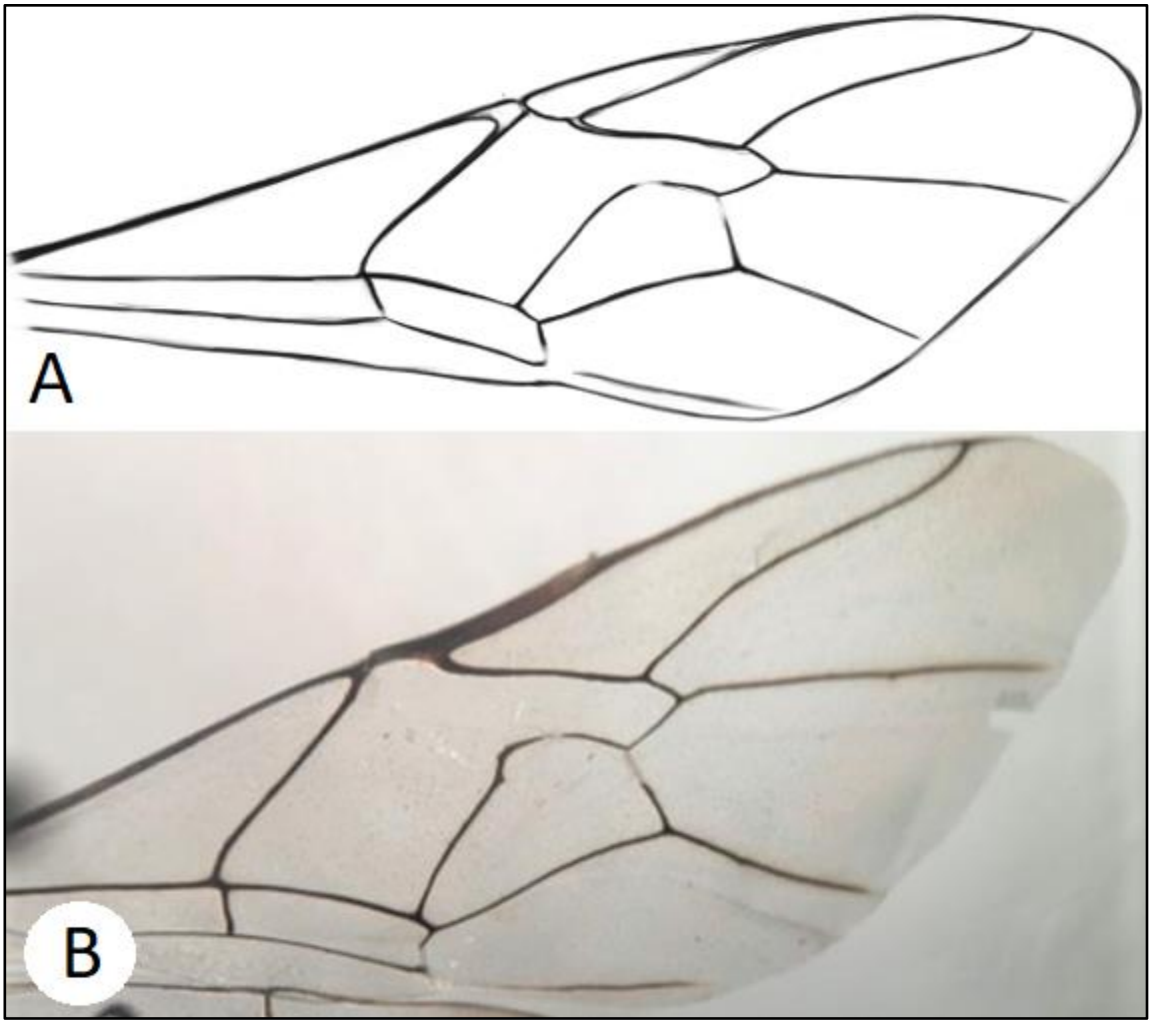

Figure 12. Forewing venation of **A** the typical specimen and **B** a variant specimen of *Simophion excarinatus.*

Diagnosis

Clypeus concavely truncate, more than twice as broad as long, epicnemial carina absent, fore-tibial spur with membranous flange absent, raised base of second tergite absent, and dark ferruginous in color with most having a cream-colored head.

Distribution

This species has been found throughout the arid regions of the Southwestern United States. Specimens from California were also collected from arid habitats in San Bernardino and Riverside Counties. n=44

Remarks

There is some variation among specimens of this species, mainly in face color patterns and small differences in wing venation. Some specimens have the yellowish-white orbit markings that are typical for this species, but others have no markings (Fig. 6). I do not believe this difference is enough to claim a new species, but additional specimens without these markings will need to be examined and sequenced. The forewing venation also has some variation within specimens of this species, consisting of a remnant of what appears to be a ramellus, as well as extra scleratization of other veins (Fig. 7).

OTU 9 = *Trophophion tenuiceps* Cushman, 1947

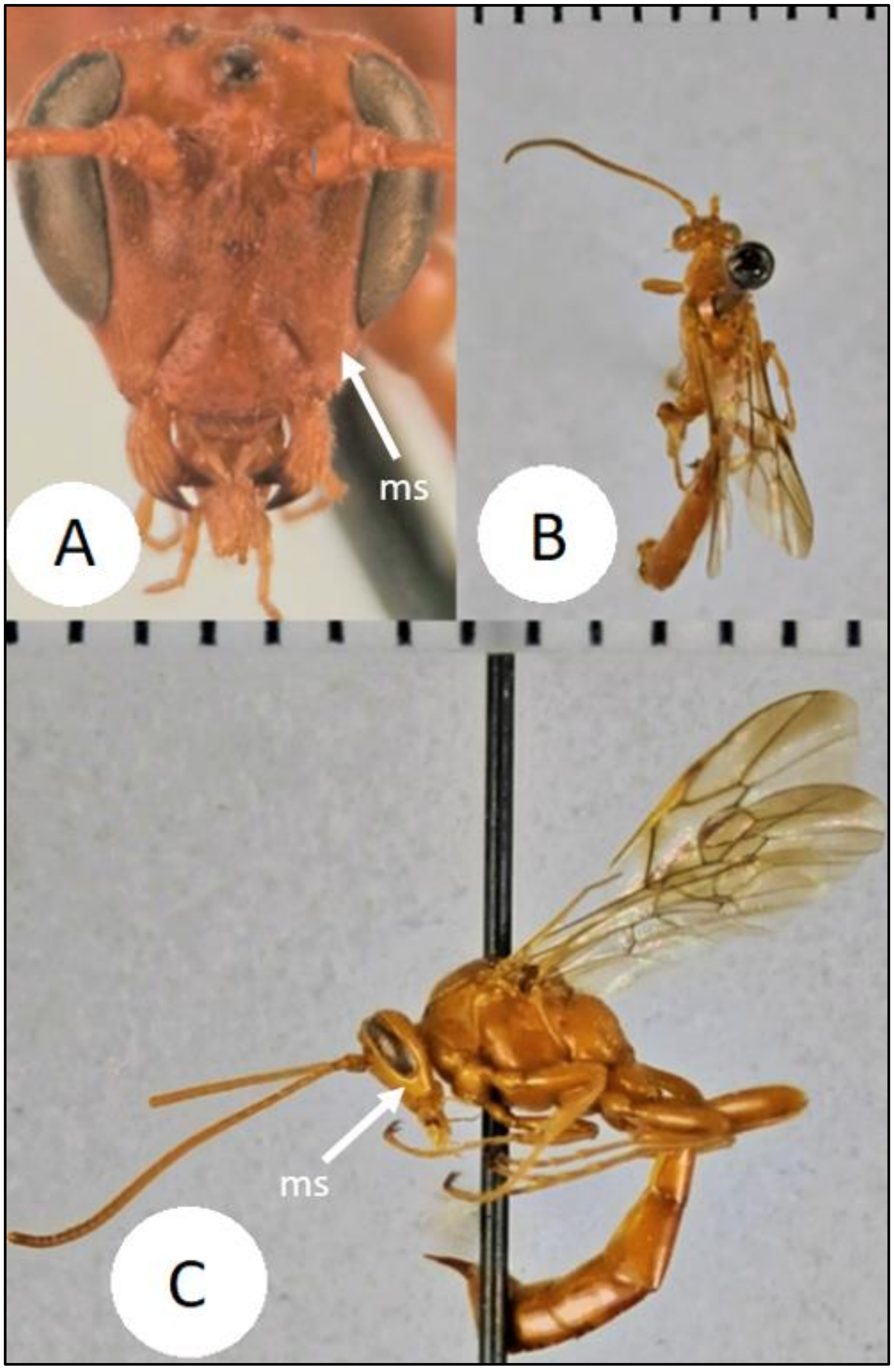

Figure 13. Images of the **A** head, **B** dorsum, and **C** habitus of *Trophophion tenuiceps.* The elongated malar space (ms) is labeled.

Diagnosis

Anthophagous mouthparts, enlarged labrum, long maxillae, and malar space longer than the basal width of the mandible. Antennae subclavate and are shorter than the length of the forewing. Diameter of ocelli much less than half the distance between the eyes.

Distribution

Historically found in the arid habitats of the Southwestern U.S. Desert (Cushman, 1947).

Remarks

A very rare taxon n=4, the most recent specimen in the collections visited was collected in 1963. More specimens are needed to extract more information about this taxon.

3. **Novel Morphospecies**

OTU 11 = *Eremotylus* sp. RBoph011

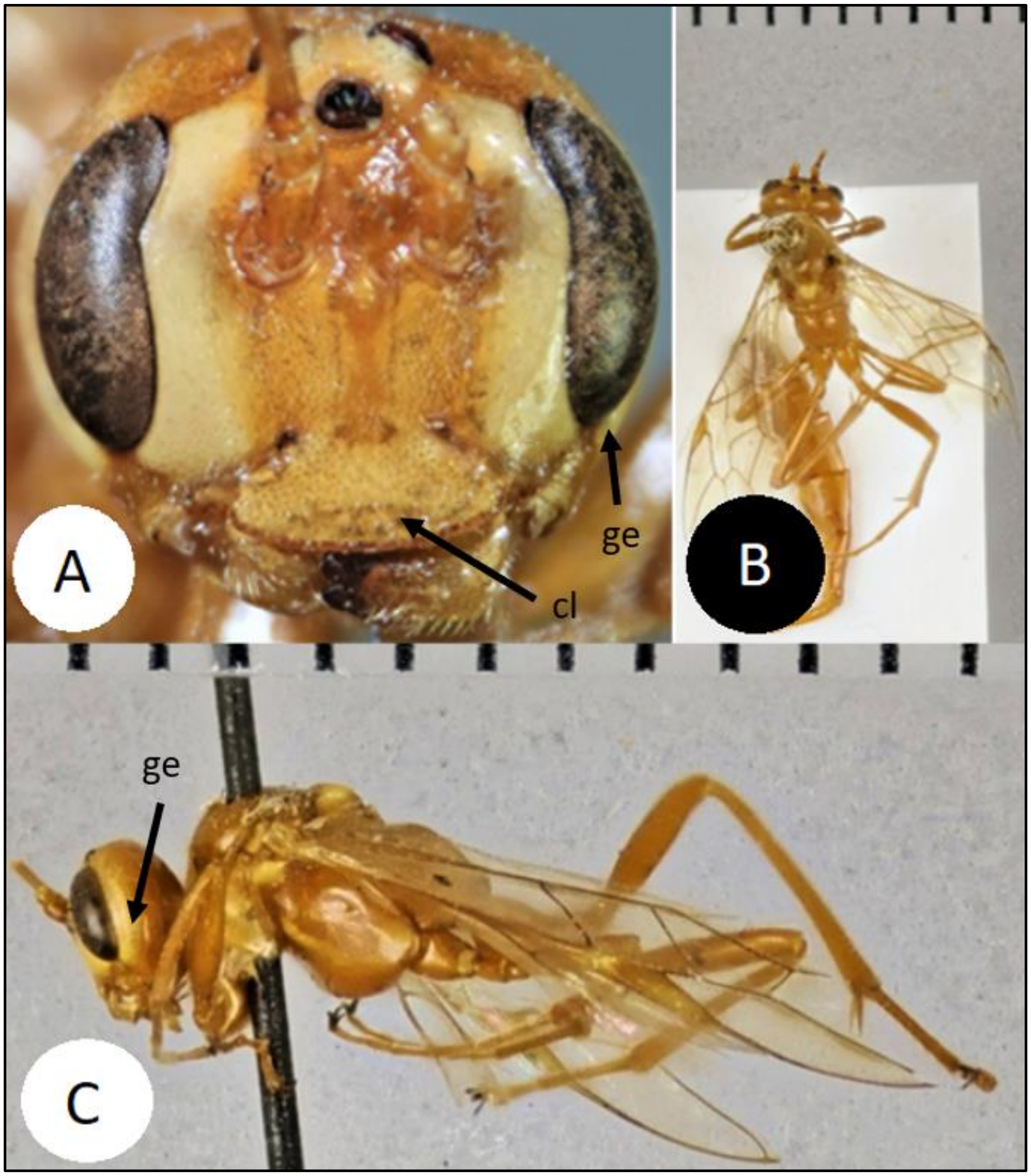

Figure 14. Images of the **A** head, **B** dorsum, and **C** habitus of *Eremotylus* sp. RBoph011. The rounded margin of the clypeus (cl) and enlarged gena (ge) are labeled.

Diagnosis

Antennae shorter than the length of the forewing. Clypeus rounded instead of truncate. Diameter of the ocelli is much smaller than the distance between the eyes. Head round and enlarged. Malar space is longer than the basal width of the mandible. Eyes barely emarginate, enlarged gena that can be seen in profile, and vertex enlarged so that it can be seen over ocelli in profile.

Distribution

Only one specimen of this morphospecies was found at Bluff Camp, Ventura County.

Remarks

This morphospecies has the shortened antennae and small ocelli characteristic of species in the *Eremotylus costalis* complex. However, it does not match the description of either of the described *E. costalis* complex species (Appendix 2), so has been designated a novel morphospecies. Despite possessing the greatly enlarged head characteristic of *Eremotylus bulbosus*, this morphospecies lacks the characters in the description of this species, including its characteristic black markings (Leblanc, 1989). Only 3 specimens of *Eremotylus bulbosus* from Michigan were used in the original description of this species. As such, it is highly unlikely that our single specimen is the same species due to the great physical distance and morphological differences.

OTU 12 = *Eremotylus* sp. RBoph012

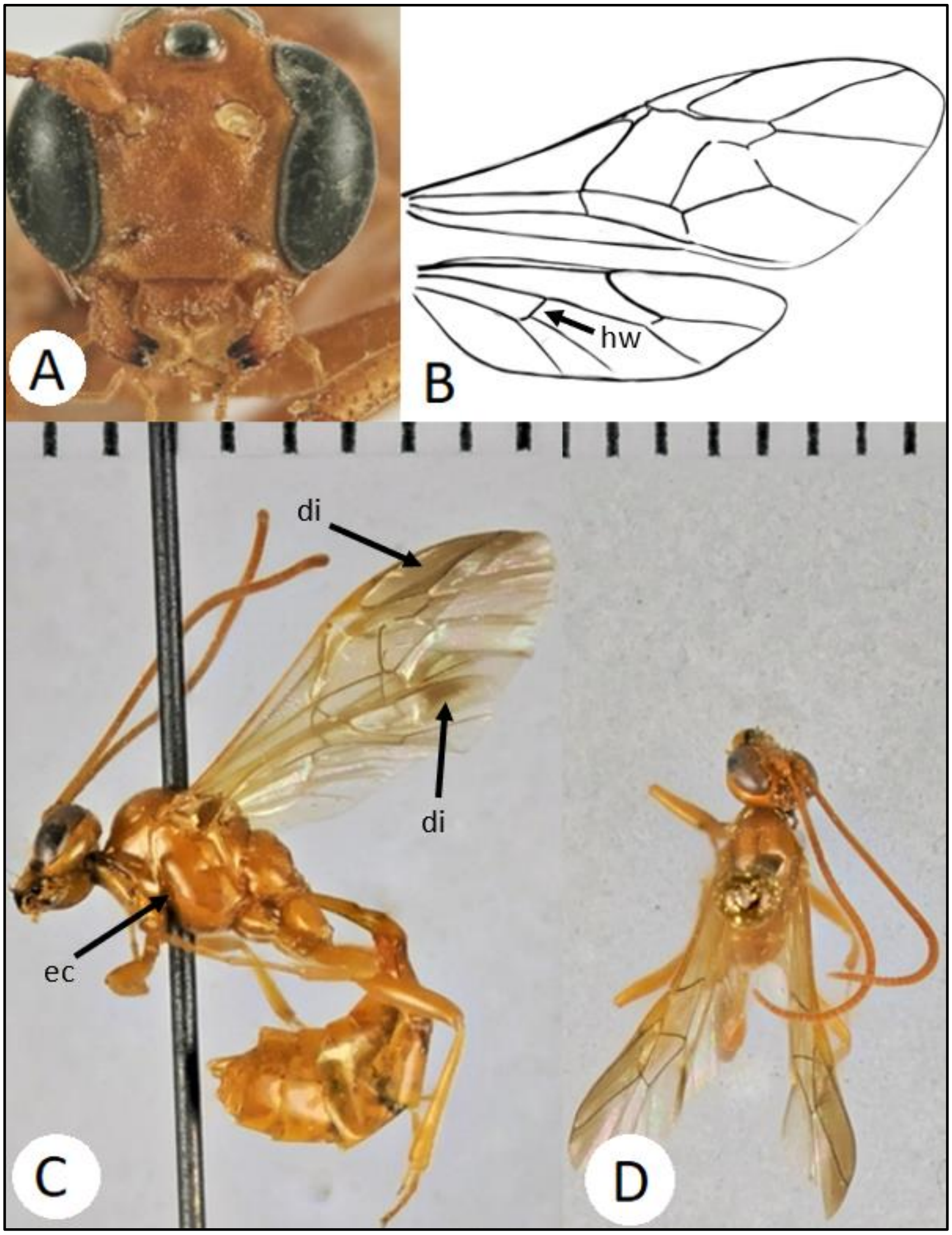

Figure 15. Images of the **A** head, **B** wing venation**, C** habitus, and **D** dorsum of *Eremotylus* sp. RBoph012. The presence of the epicnemial carina (ec), the dark infuscation of the wings (di), and the intersection of the Cu1 vein with CU-a on the hindwing (hw) are labeled.

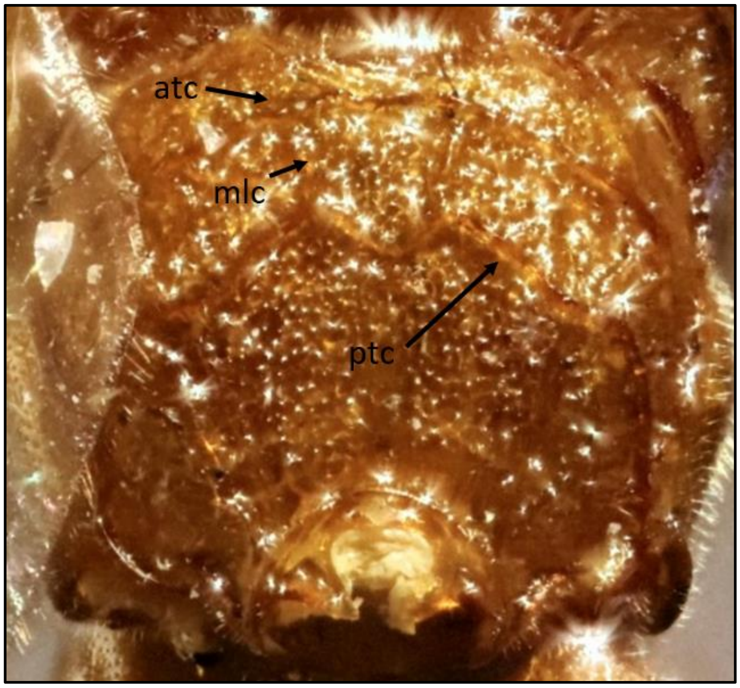

Figure 16. Propodeal sculpture of *Eremotylus* sp. RBoph012, displaying the presence of the anterior transverse carina (atc), mid-longitudinal carina (mlc), and the posterior transverse carina (ptc).

Diagnosis

Occipital carina is not complete, with a large part missing dorsally. Epicnemial carina present and conspicuous, propodeum with the anterior transverse carina, posterior carina, and mid-longitudinal carina present, conspicuous, and complete, respectively, and both hind and forewings with fuscous markings near wing tips. Cu1 vein of hindwing intersects CU-a at around 0.5 x between M and 1A.

Table 9. Summary of the character states possessed by *Eremotylus* sp. RBoph012 for the morphological characters delineating *Eremotylus* morphospecies.

Character	State
Occipital carina	Dorsally interrupted
Size and shape of clypeus	Large, truncated
Epicnemial carina	Present
Propodeal sculpture	Complete
R-rs vein of forewing	Thickened and angled
Fore and hindwing infuscation	Markings on tips of fore and hindwing
Length of cu-a where it intersects Cu	0.5x

Distribution

This morphospecies was found in the desert regions of southern California, from San Diego through San Bernardino and Riverside counties .

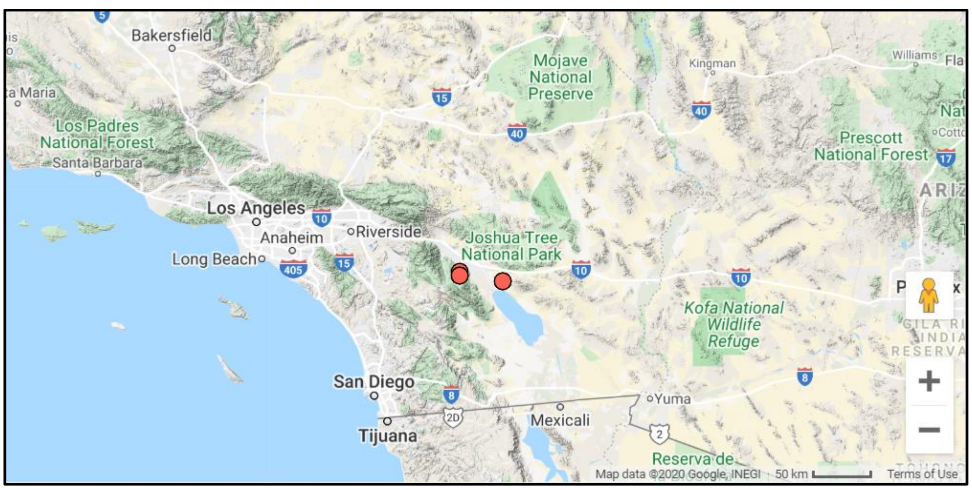

Figure 17. Distribution of *Eremotylus* sp. RBoph012 specimens examined in this study. n=7

Remarks

This is the only morphospecies of California *Eremotylus* that has a large part of the occipital carina missing dorsally. Whether this is a new species or a variant of *Eremotylus* sp.

RBoph019 will need to be ascertained through additional work. For the purposes of this study it will be designated as a separate morphospecies.

OTU 13 = *Eremotylus* sp. RBoph013

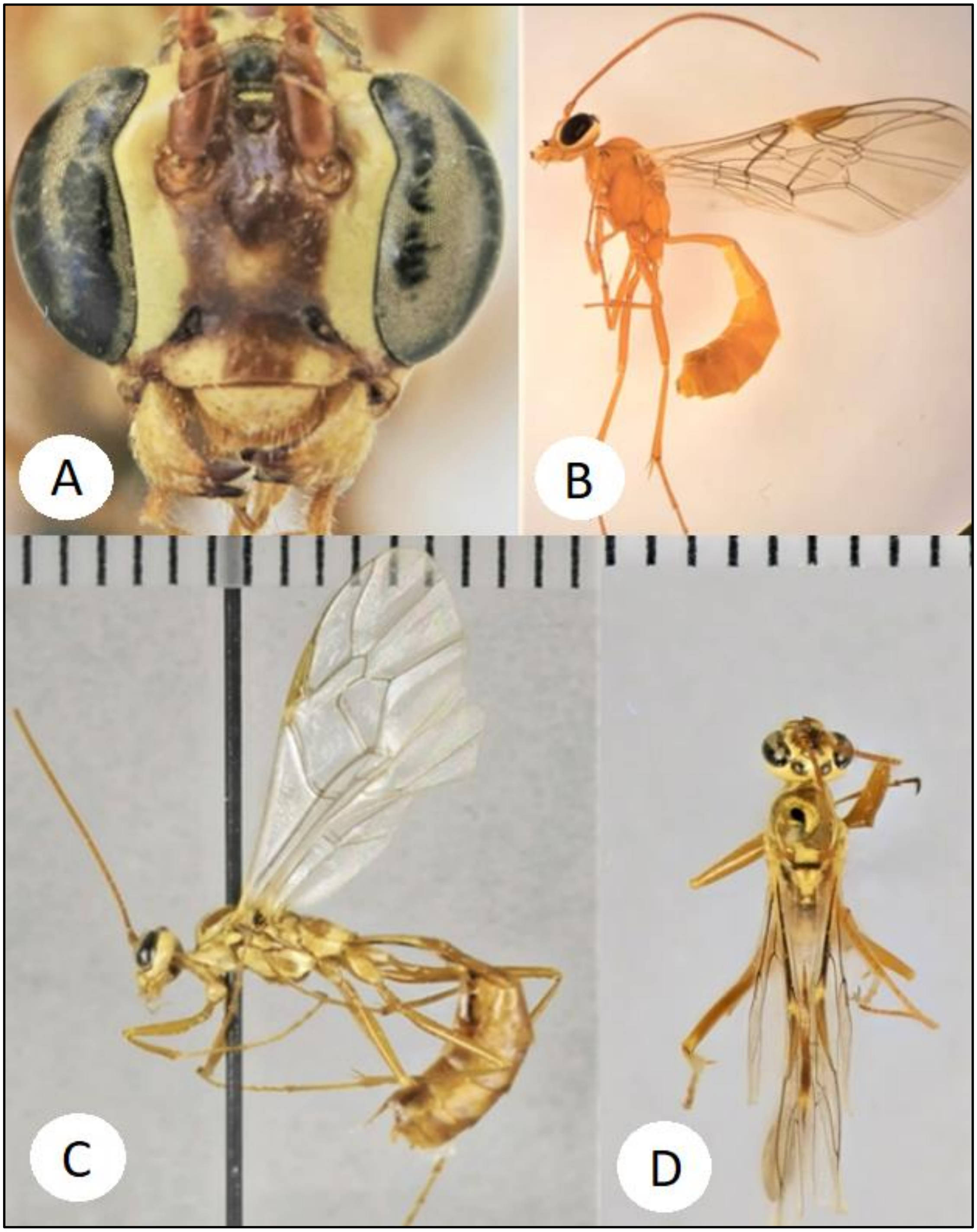

Figure 18. Images of the **A** head, **B,C** habitus, and **D** dorsum of *Eremotylus* sp. RBoph013.

Figure 19. Propodeum of *Eremotylus* sp. RBoph013.

Diagnosis

Occipital carina complete, epicnemial carina not present or conspicuous, propodeum with only vestigial mid-longitudinal carina present, both hind and forewings clear and without markings, and Cu1 vein of hindwing intersects CU-a at around 0.25x between M and 1A.

Table 10. Summary of the character states possessed by *Eremotylus* sp. RBoph013 for the morphological characters delineating *Eremotylus* morphospecies.

Character	State
Occipital carina	Complete
Epicnemial carina	Absent
Propodeal sculpture	Vestigial mid-longitudinal carina
Fore and hindwing infuscation	None
Length of cu-a where it intersects Cu	0.25x

Distribution

This morphospecies was found in the desert regions of San Bernardino and Riverside County.

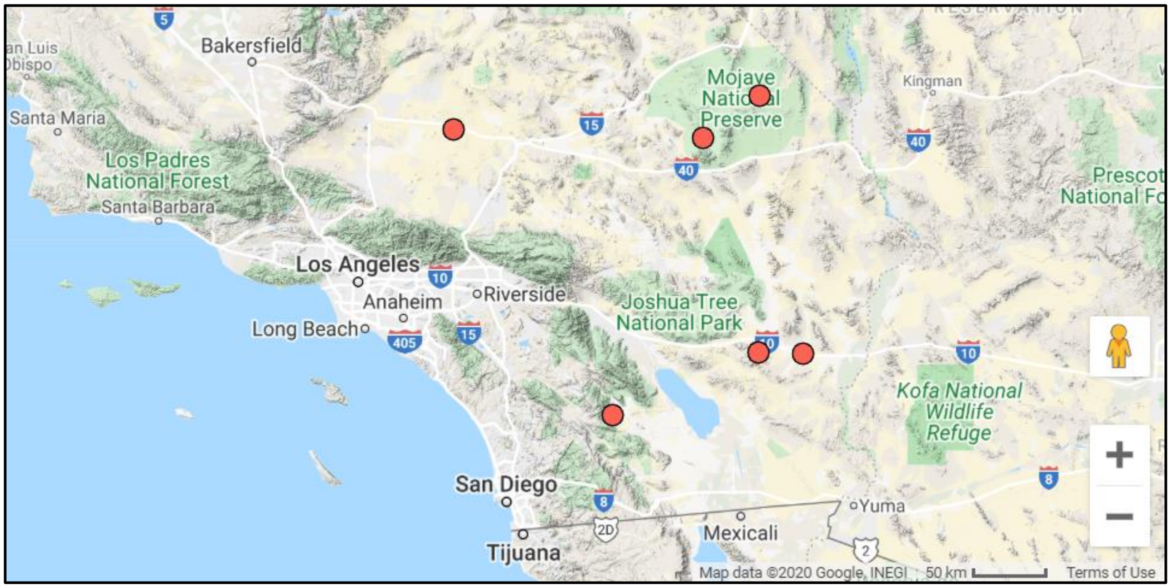

Figure 20. Distribution of *Eremotylus* sp. RBoph013 specimens examined in this study. n=6

Remarks

This was the only *Eremotylus* morphospecies that lacked the epicnemial carina. Although the lack of an epicnemial carina is a main character of the genus *Simophion*, this specimen did key to *Eremotylus.*

OTU 15 = *Eremotylus* sp. RBoph015

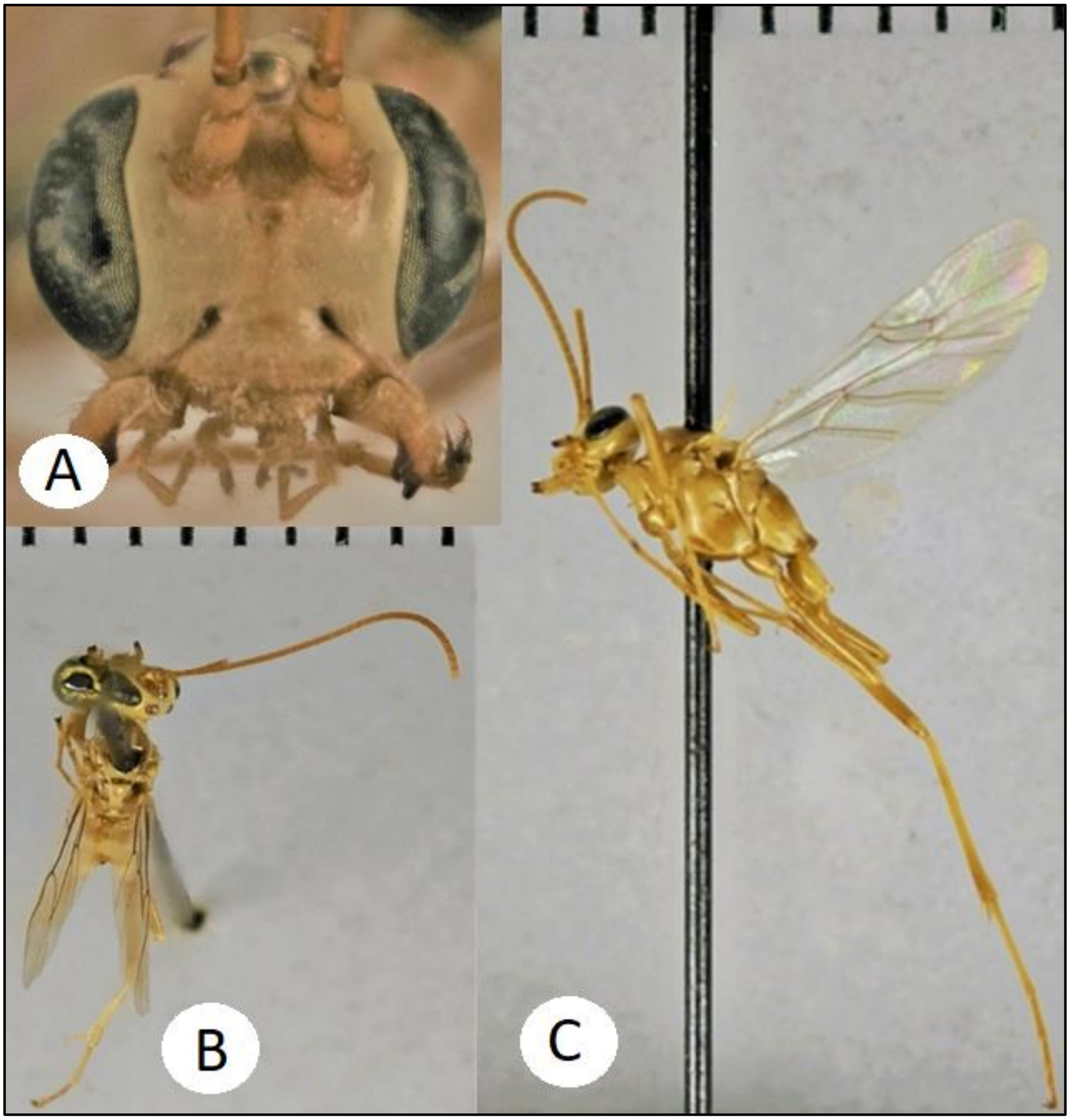

Figure 21. Images of the **A** head, **B** dorsum**,** and **C** habitus of *Eremotylus* sp. RBoph015.

Figure 22. Propodeum of *Eremotylus* sp. RBoph015.

Diagnosis

Occipital carina complete, epicnemial carina present and conspicuous, propodeum only with vestigial mid-longitudinal carina present, and Cu1 vein of hindwing intersects CU-a at around 0.8-0.9x between M and 1A.

Table 11. Summary of the character states possessed by *Eremotylus* sp. RBoph015 for the morphological characters delineating *Eremotylus* morphospecies.

Character	State
Occipital carina	Complete
Ocelli size	Small
Epicnemial carina	Present
Propodeal sculpture	Vestigial mid-longitudinal carina
Length of cu-a where it intersects Cu	0.8-0.9x

Distribution

Only one specimen of this morphospecies was found in Pozo, San Luis Obispo County.

Remarks

Only one damaged specimen was available. The unique combination of characters in the above diagnoses allowed its inclusion as a separate morphospecies in this study, but more specimens are needed for further taxonomic work.

OTU 17 = *Eremotylus* sp. RBoph017

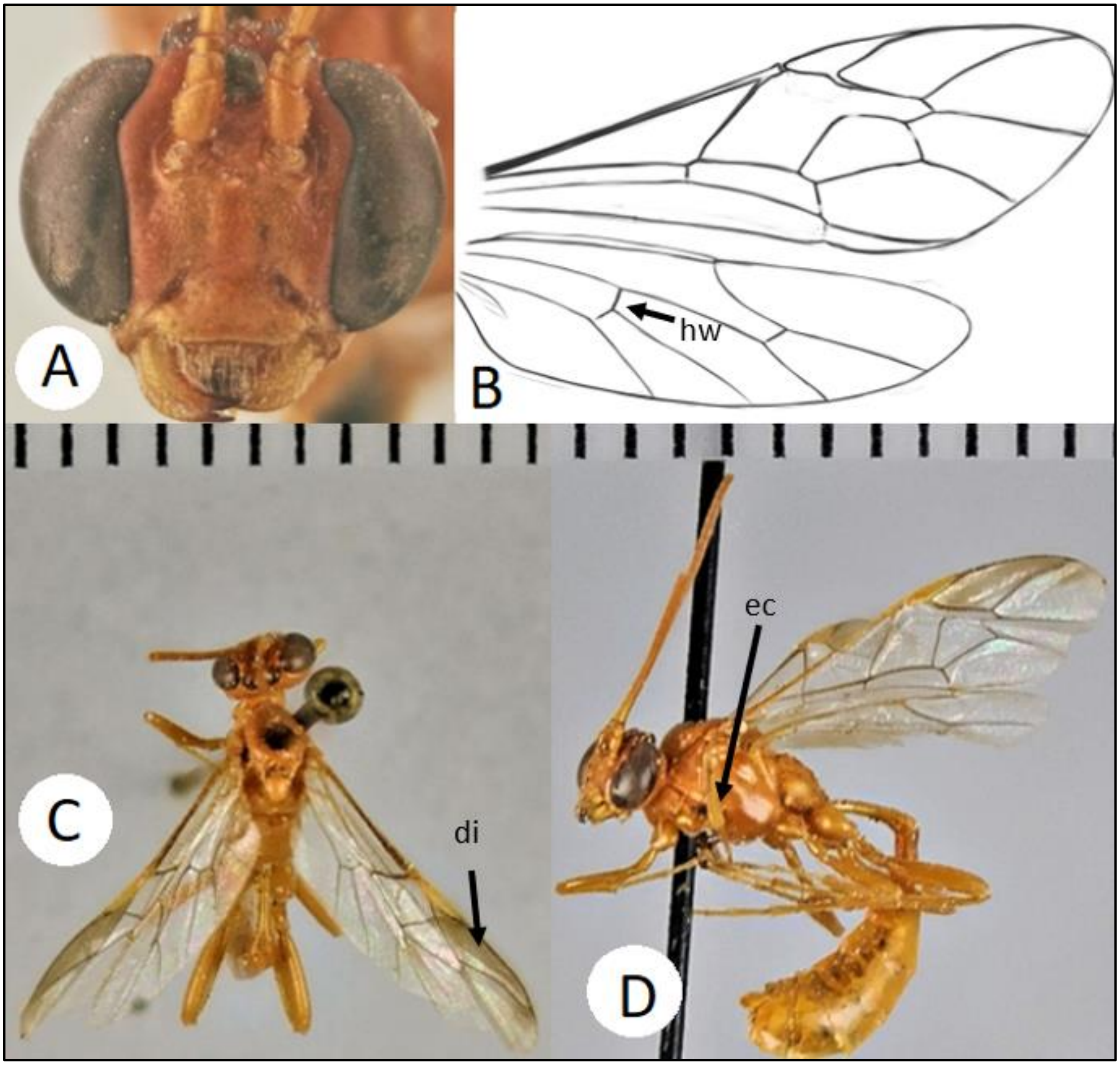

Figure 23. Images of the **A** head, **B** wing venation**, C** dorsum, and **D** habitus of *Eremotylus* sp.RBoph017. The presence of the epicnemial carina (ec), the dark infuscation of the wings (di), and the intersection of the Cu1 vein with CU-a on the hindwing (hw) are labeled.

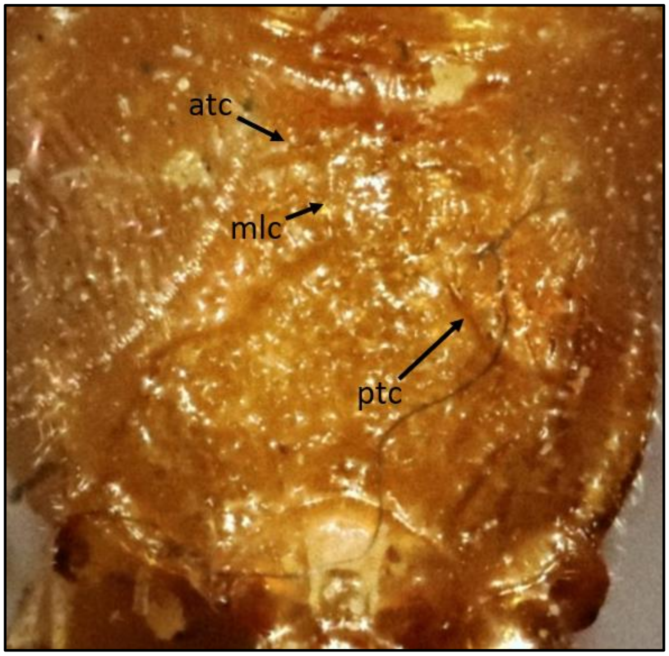

Figure 24. Propodeal sculpture of *Eremotylus* sp.RBoph017 displaying the presence of the anterior transverse carina (atc), mid-longitudinal carina (mlc), and the posterior transverse carina (ptc).

Diagnosis

Occipital carina complete, epicnemial carina present and conspicuous, propodeum with the anterior transverse carina, posterior carina, and mid-longitudinal carina present, conspicuous, and complete, fore wings with dark infuscation near pterostigma, and Cu1 vein of hind wing intersecting CU-a at around 0.6x between M and 1A.

Table 12. Summary of the character states possessed by *Enicospilus* sp. RBoph017 for the morphological characters delineating *Eremotylus* morphospecies.

Character	State
Occipital carina	Complete
Epicnemial carina	Present
Propodeal sculpture	Complete
Fore and hindwing infuscation	Forewing markings near pterostigma
Length of cu-a where it intersects Cu	0.6x

Distribution

Only one specimen of this morphospecies was found in Mecca, Riverside County.

OTU 18 = *Eremotylus* sp. RBoph018

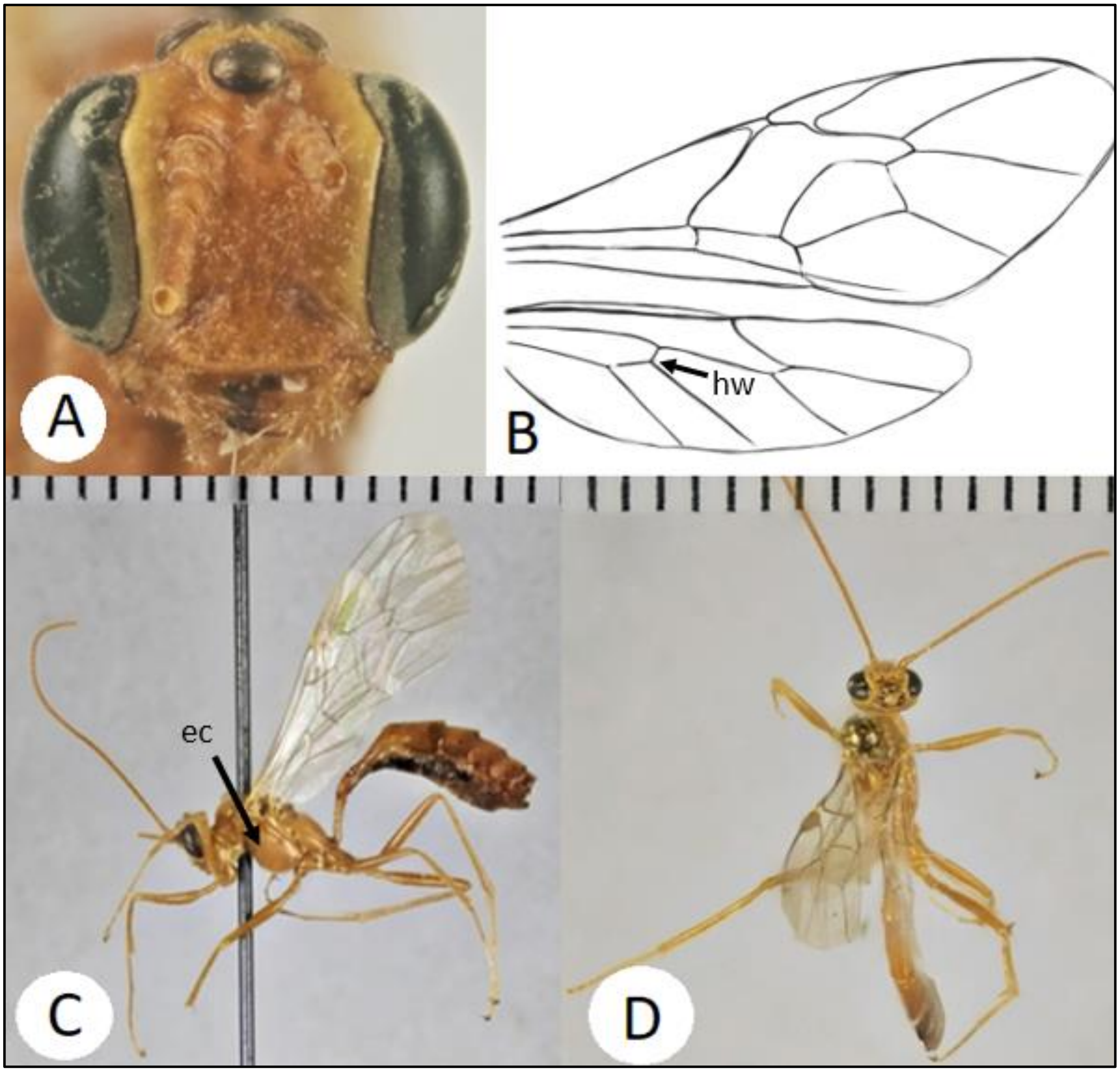

Figure 25. Images of the **A** head, **B** wing venation**, C** habitus, and **D** dorsum of *Eremotylus* sp. RBoph018. The presence of the epicnemial carina (ec) and the intersection of the Cu1 vein with CU-a on the hindwing (hw) are labeled.

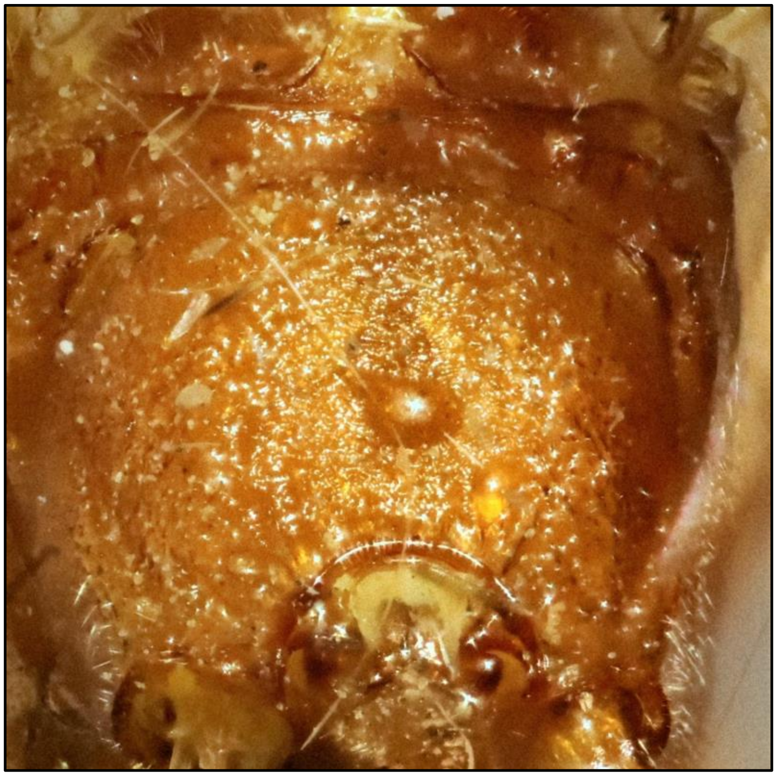

Figure 26. Propodeum of *Eremotylus* sp. RBoph018.

Diagnosis

Occipital carina complete, epicnemial carina present and conspicuous, propodeum only with vestigial mid-longitudinal carina present, both hind and forewings clear and without markings, and Cu1 vein of hindwing intersecting CU-a at around 0.6x between M and 1A.

Table 13. Summary of the character states possessed by *Eremotylus* sp. RBoph018for the morphological characters delineating *Eremotylus* morphospecies.

Character	State
Occipital carina	Complete
Epicnemial carina	Present
Propodeal sculpture	Vestigial mid-longitudinal carina
Fore and hindwing infuscation	None
Length of cu-a where it intersects Cu	0.6x

Distribution

This morphospecies was found in the mountainous regions of San Bernardino and Riverside County.

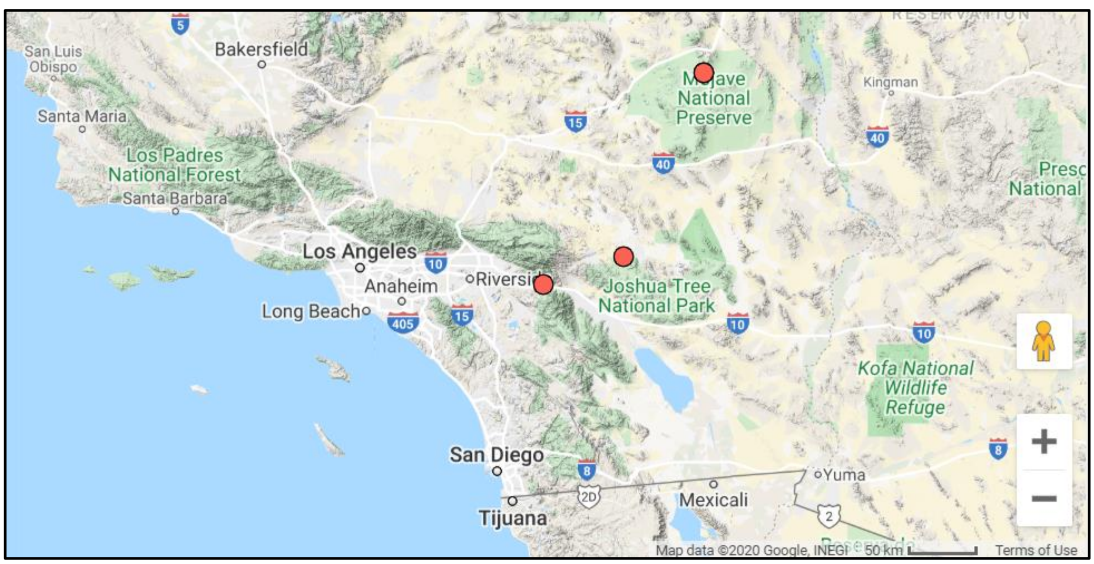

Figure 27. Distribution of *Eremotylus* sp. RBoph018 specimens examined in this study. n=6

OTU 19 = *Eremotylus* sp. RBoph019

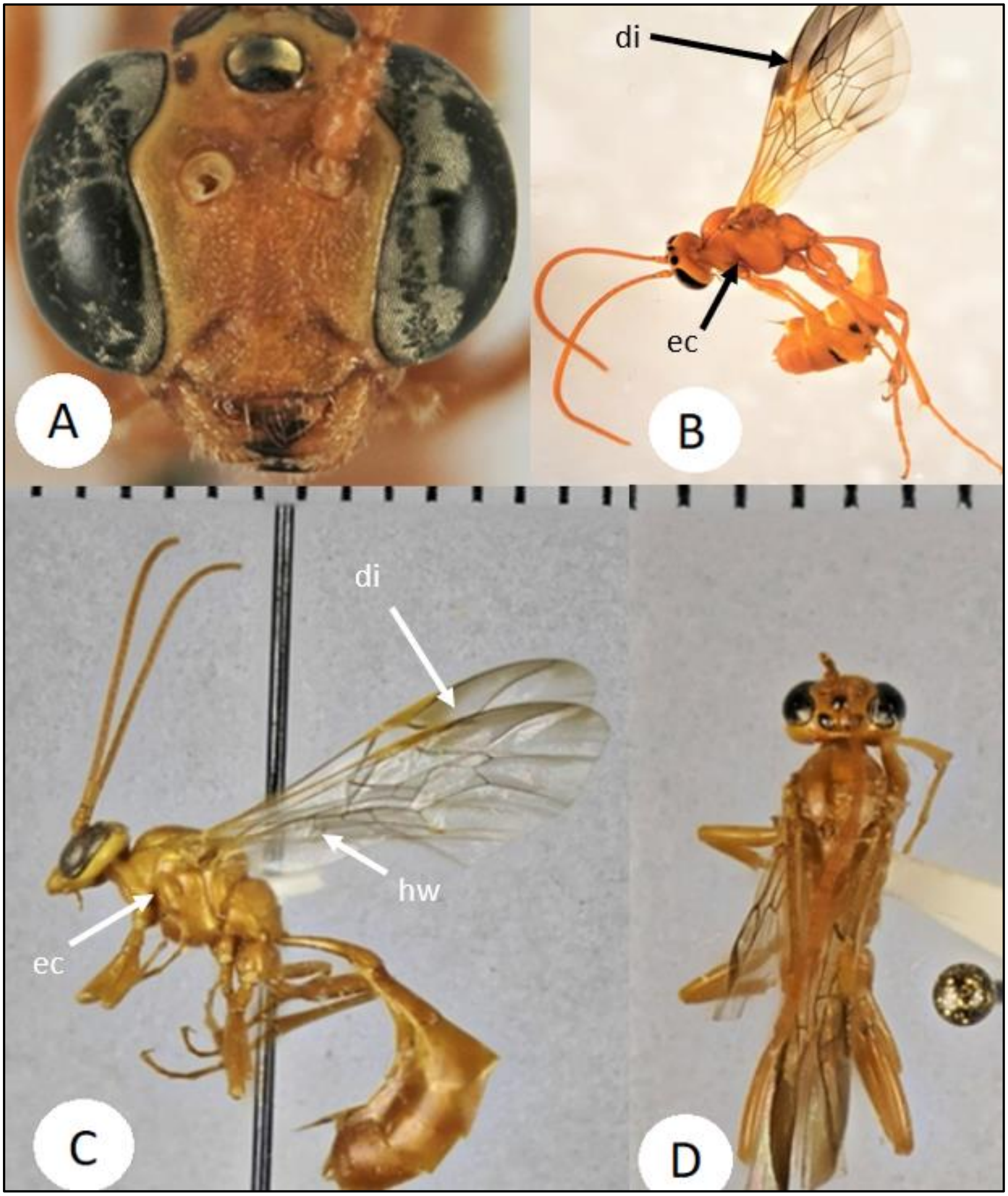

Figure 28. Images of the **A** head, **B** wing venation**, C** habitus, and **D** dorsum of *Eremotylus* sp.RBoph019. The presence of the epicnemial carina (ec), the dark infuscation of the wings (di), and the intersection of the Cu1 vein with CU-a on the hindwing (hw) are labeled.

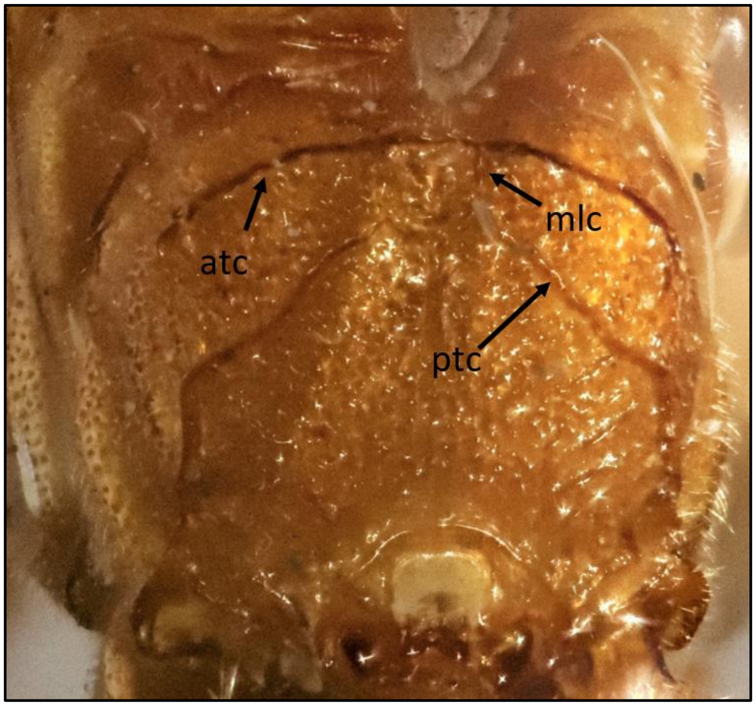

Figure 29. Propodeal sculpture of *Eremotylus* sp. RBoph019 displaying the presence of the anterior transverse carina (atc), mid-longitudinal carina (mlc), and the posterior transverse carina (ptc).

Diagnosis

Occipital carina complete, epicnemial carina present and conspicuous, propodeum with the anterior transverse carina, posterior carina, and mid-longitudinal carina present, conspicuous, and complete, forewing with dark infuscation near pterostigma, and Cu1 vein of hindwing intersecting CU-a at around 0.4x between M and 1A.

Table 14. Summary of the character states possessed by OTU19 for the morphological characters delineating *Eremotylus* morphospecies.

Character	State
Occipital carina	Complete
Epicnemial carina	Present
Propodeal sculpture	Complete
Fore and hindwing infuscation	Forewing markings near pterostigma
Length of cu-a where it intersects Cu	0.4x

Distribution

This morphospecies was found in the desert regions of San Diego, San Bernardino, and Riverside Counties.

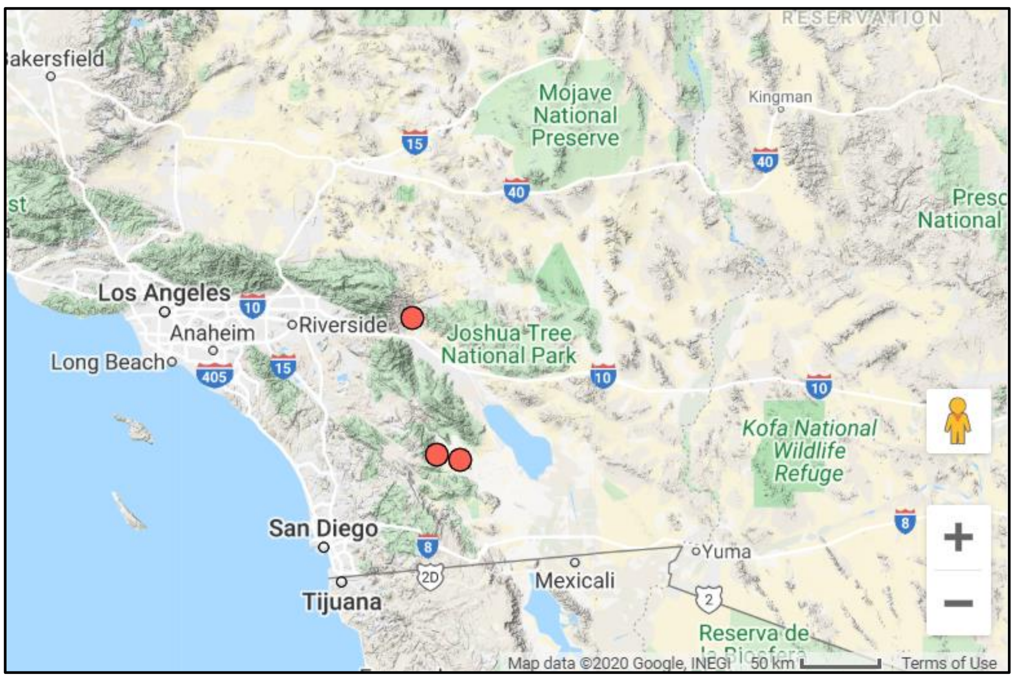

Figure 30. Distribution of *Eremotylus* sp. RBoph019 specimens examined in this study. n=6

OTU 21 = *Eremotylus* sp. RBoph021

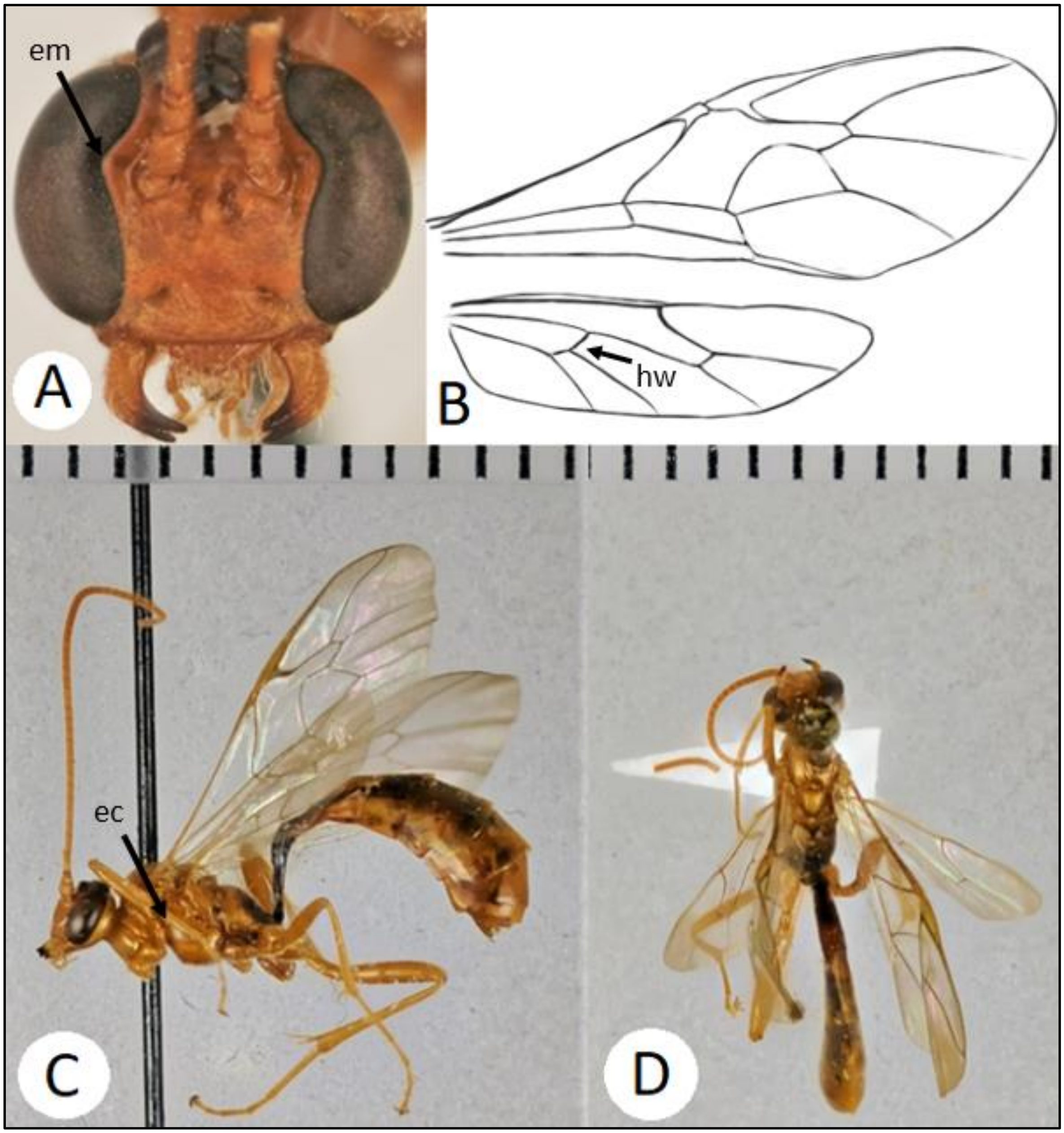

Figure 31. Images of the **A** head, **B** wing venation**, C** habitus, and **D** dorsum of *Eremotylus* sp.RBoph021. The presence of the epicnemial carina (ec) and the intersection of the Cu1 vein with CU-a on the hindwing (hw) are labeled.

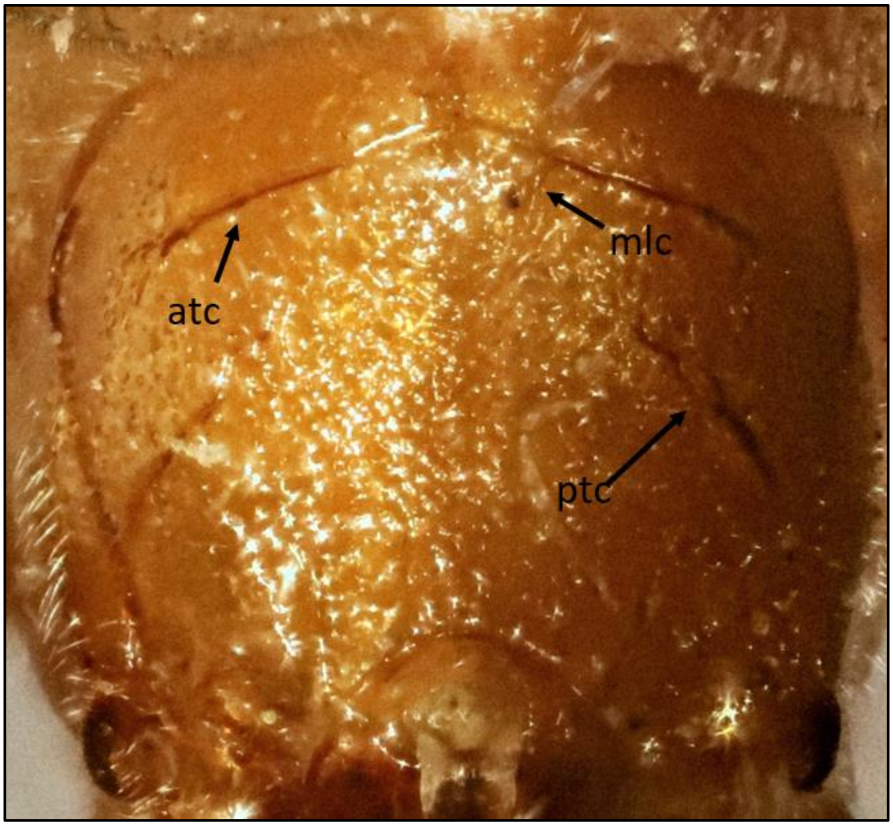

Figure 32. Propodeal sculpture of *Eremotylus* sp.RBoph021 displaying the presence of the anterior transverse carina (atc), mid-longitudinal carina (mlc), and the incomplete posterior transverse carina (ptc).

Diagnosis

Eyes strongly emarginate, occipital carina complete, epicnemial carina present and conspicuous, propodeum with the anterior transverse carina, posterior transverse carina, and mid-longitudinal carina present and conspicuous, but posterior transverse carina not complete. Fore and hind wings clear and without markings or infuscation, and the Cu1 vein of the hindwing intersects CU-a at around 0.5x between M and 1A.

Table 15. Summary of the character states possessed by *Eremotylus* sp. RBoph021for the morphological characters delineating *Eremotylus* morphospecies.

Character	State
Occipital carina	Complete
Epicnemial carina	Present
Propodeal sculpture	Anterior transverse carina, posterior transverse carina, and mid-longitudinal carina present and conspicuous, but posterior transverse carina not complete
Fore and hindwing infuscation	None
Length of cu-a where it intersects Cu	0.5x

Distribution

This morphospecies was found from Imperial County in the south to San Luis Obispo County in the north.

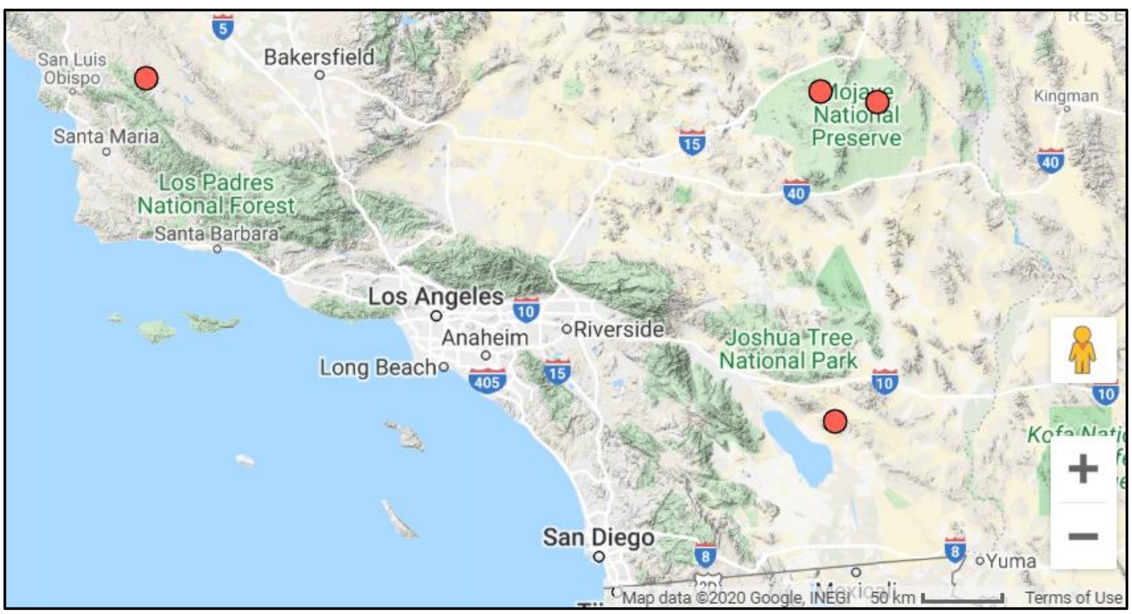

Figure 33. Distribution of *Eremotylus* sp. RBoph021 specimens examined in this study. n=5

OTU 22 = *Eremotylus* sp. RBoph022

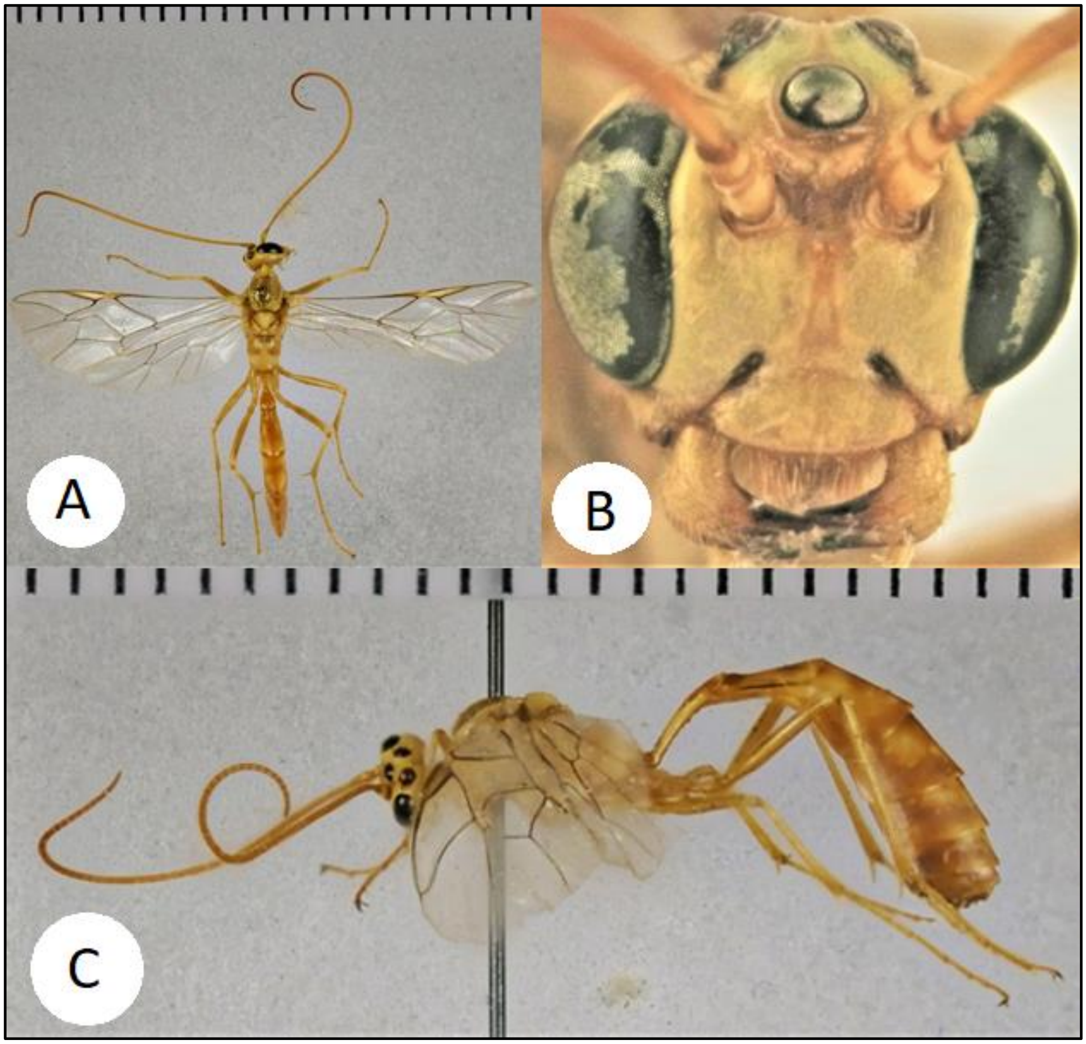

Figure 34. Images of the **A** dorsum, **B** head**,** and **C** habitus of *Eremotylus* sp.RBoph022.

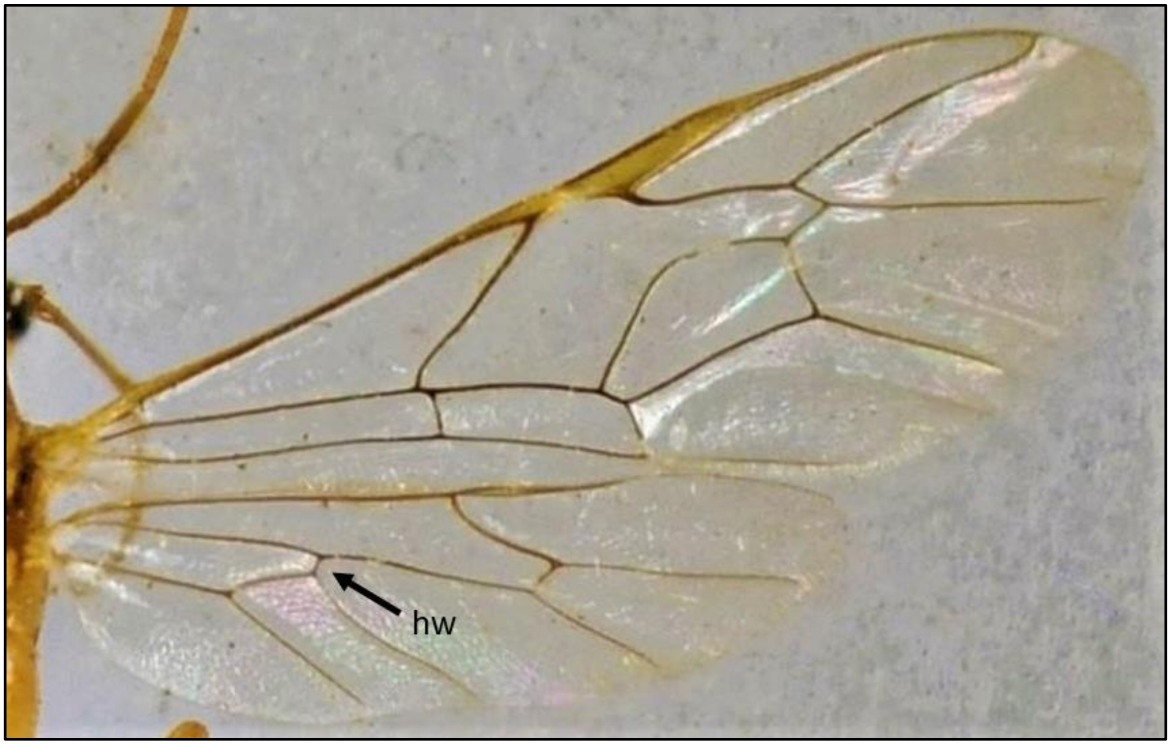

Figure 35. Wing venation and the intersection of the Cu1 vein with CU-a on the hindwing (hw) of *Eremotylus* sp. RBoph022.

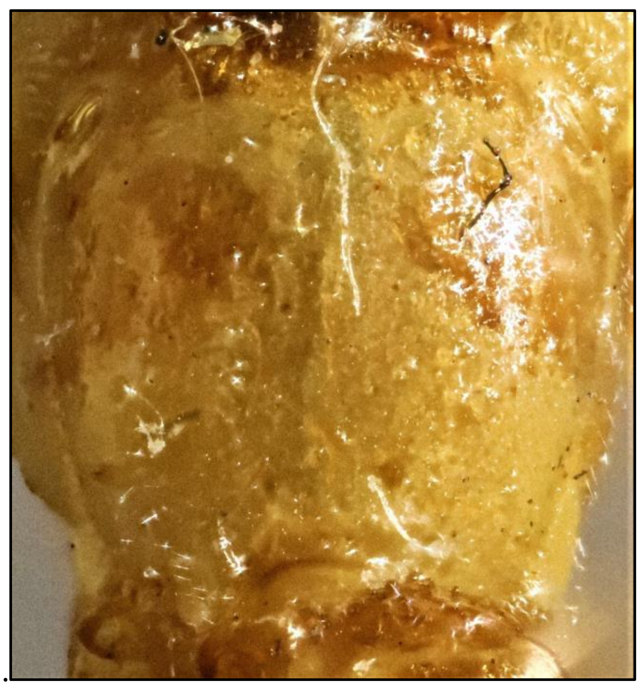

Figure 36. Propodeum of *Eremotylus* sp. RBoph022.

Diagnosis

Eyes weakly emarginate, occipital carina complete, distinct carina between ocellar triangle and eye margin, epicnemial carina present and conspicuous, propodeum only with vestigial mid-longitudinal carina present, fore and hind wings clear and without markings or infuscation, and Cu1 vein of hindwing intersects CU-a at around 0.8x between M and 1A.

Table 16. Summary of the character states possessed by *Eremotylus* sp. RBoph022 for the morphological characters delineating *Eremotylus* morphospecies.

Character	State
Occipital carina	Complete
Epicnemial carina	Present
Propodeal sculpture	Vestigial mid-longitudinal carina
Fore and hindwing infuscation	None
Length of cu-a where it intersects Cu	0.8x

Distribution

This morphospecies was found from San Bernardino County in the south to San Luis Obispo County in the north.

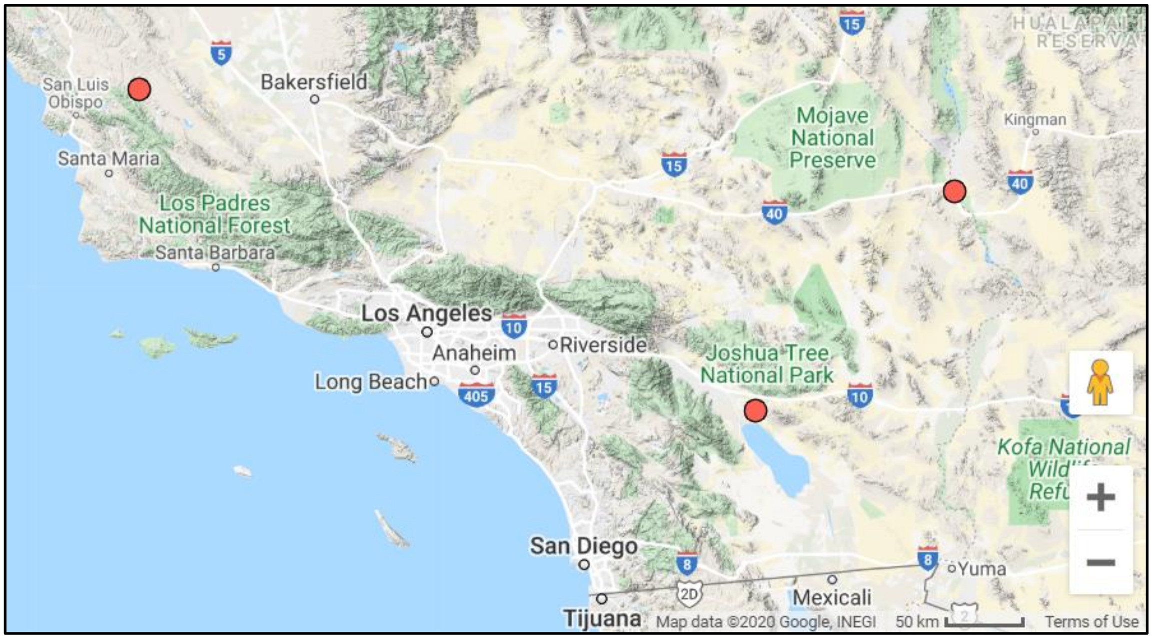

Figure 37. Distribution of *Eremotylus* sp. RBoph022 specimens examined in this study. n=7

OTU 23 = *Eremotylus* sp. RBoph023

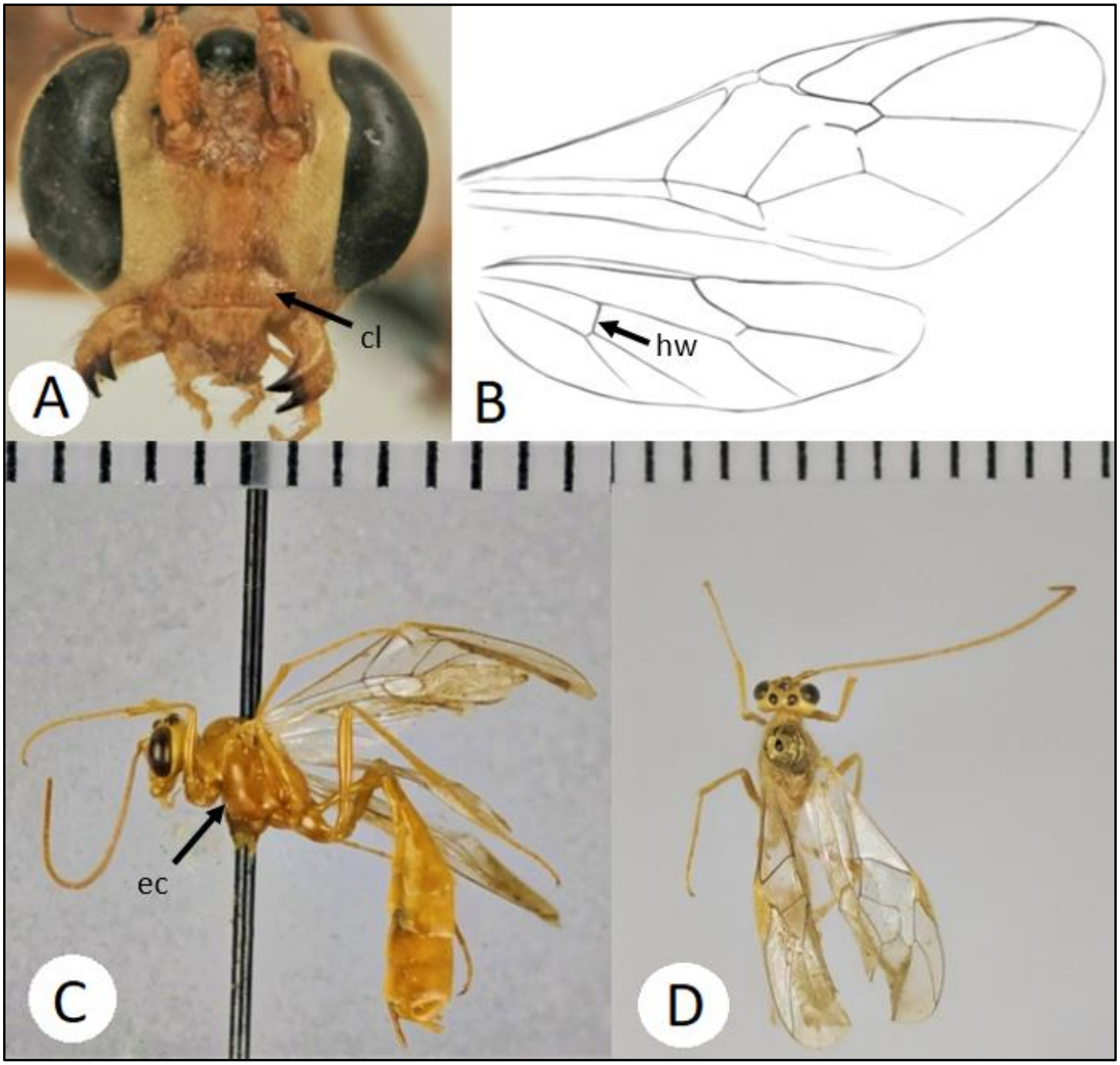

Figure 38. Images of the **A** head, **B** wing venation**, C** habitus, and **D** dorsum of *Eremotylus* sp. RBoph023. The presence of the epicnemial carina (ec), the small clypeus (cl), and the intersection of the Cu1 vein with CU-a on the hindwing (hw) are labeled.

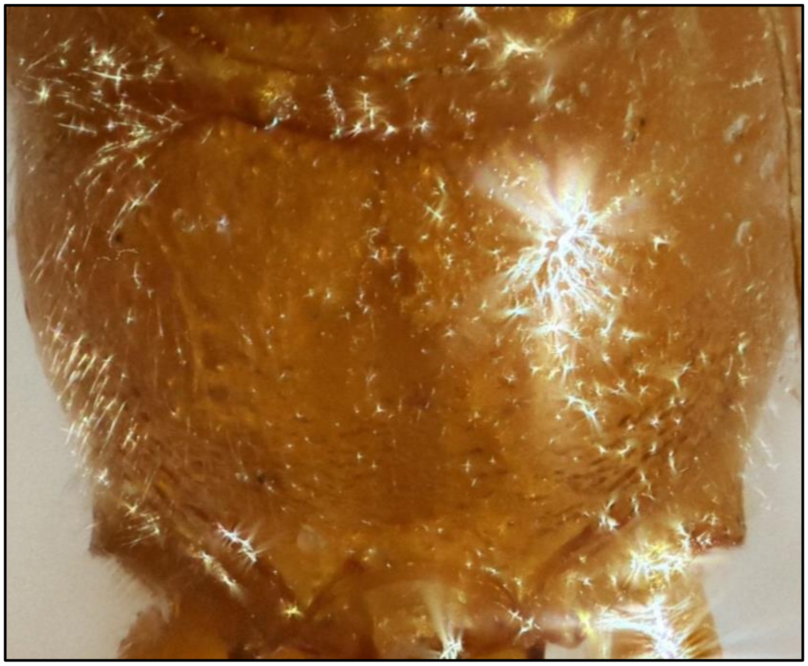

Figure 39. Propodeum of *Eremotylus* sp. RBoph023.

Diagnosis

Clypeus small, occipital carina complete, epicnemial carina present and conspicuous, propodeum only with vestigial mid-longitudinal carina present, fore and hind wings clear and without markings or infuscation, and Cu1 vein of hindwing intersects CU-a at around 0.2x between M and 1A.

Table 17. Summary of the character states possessed by *Eremotylus* sp. RBoph023 for the morphological characters delineating *Eremotylus* morphospecies.

Character	State
Occipital carina	Complete
Size and shape of clypeus	Small, truncated
Epicnemial carina	Present
Propodeal sculpture	Vestigial mid-longitudinal carina
Fore and hindwing infuscation	None
Length of cu-a where it intersects Cu	0.2x

Distribution

This morphospecies was collected in San Diego, San Bernardino, and Riverside Counties.

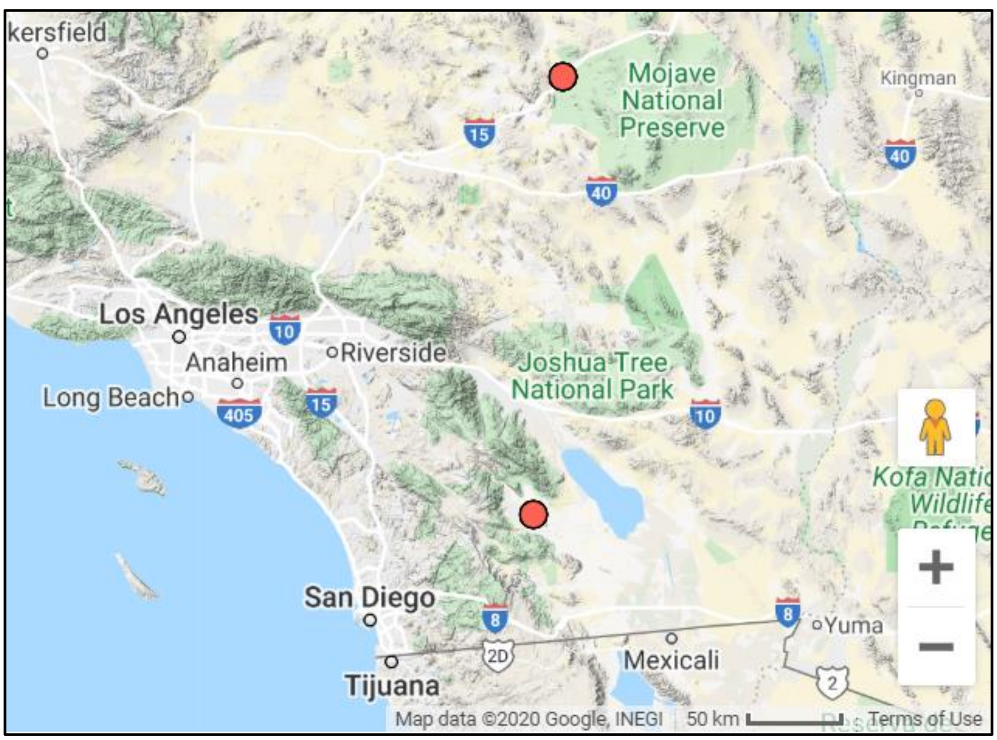

Figure 40. Distribution of *Eremotylus* sp. RBoph023 specimens examined in this study. n=17

OTU 25 = *Eremotylus* sp. RBoph025

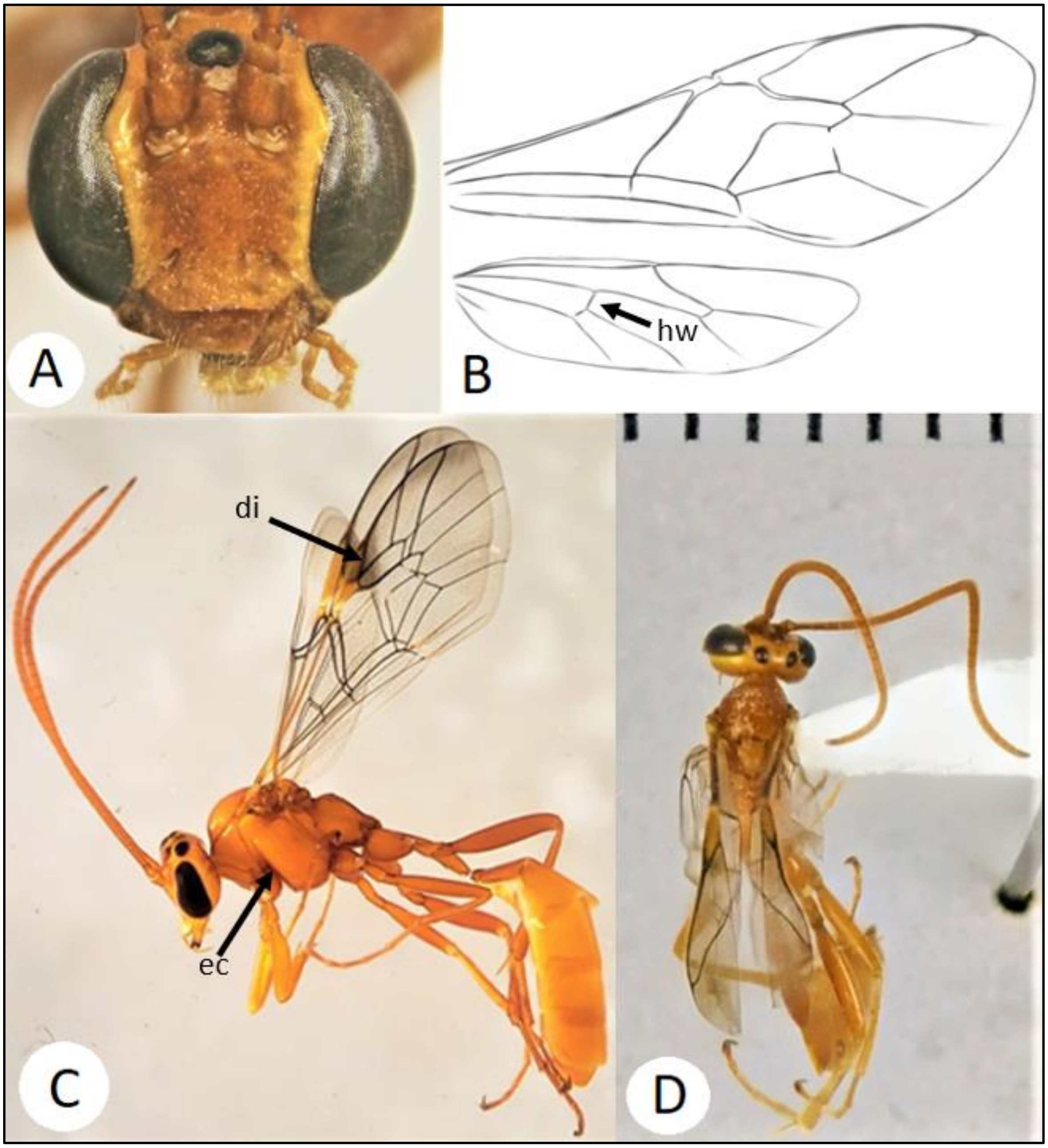

Figure 41. Images of the **A** head, **B** wing venation**, C** habitus, and **D** dorsum of *Eremotylus* sp.RBoph025. The presence of the epicnemial carina (ec), the dark infuscation of the wings (di), and the intersection of the Cu1 vein with CU-a on the hindwing (hw) are labeled.

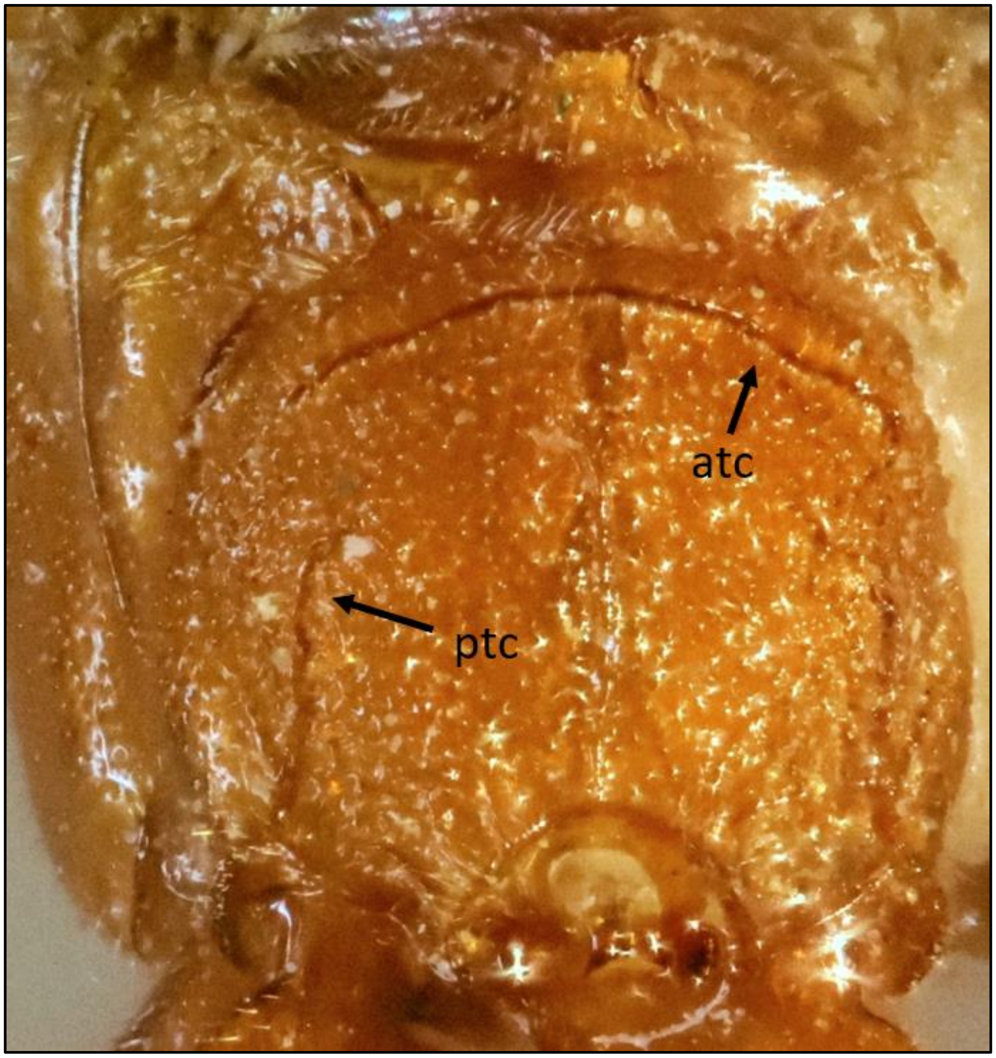

Figure 42. Propodeal sculpture of *Eremotylus* sp.RBoph025 displaying the presence of the anterior transverse carina (atc) and the incomplete posterior transverse carina (ptc).

Diagnosis

Occipital carina complete, epicnemial carina present and conspicuous, propodeum with anterior transverse carina present and complete, posterior transverse carina present but not complete and with a vestigial mid-longitudinal carina, fore wing with infuscation near pterostigma, and Cu1 vein of hindwing intersecting CU-a at around 0.8x between M and 1A.

Table 18. Summary of the character states possessed by *Eremotylus* sp. RBoph025 for the morphological characters delineating *Eremotylus* morphospecies.

Character	State
Occipital carina	Complete
Epicnemial carina	Present
Propodeal sculpture	Anterior transverse carina present, posterior transverse carina present but incomplete, vestigial mid-longitudinal carina
Fore and hindwing infuscation	Forewing marking near pterostigma
Length of cu-a where it intersects Cu	0.8x

Distribution

This morphospecies was collected in the desert regions of Southern California, especially the Anza Borrego Desert in San Diego County.

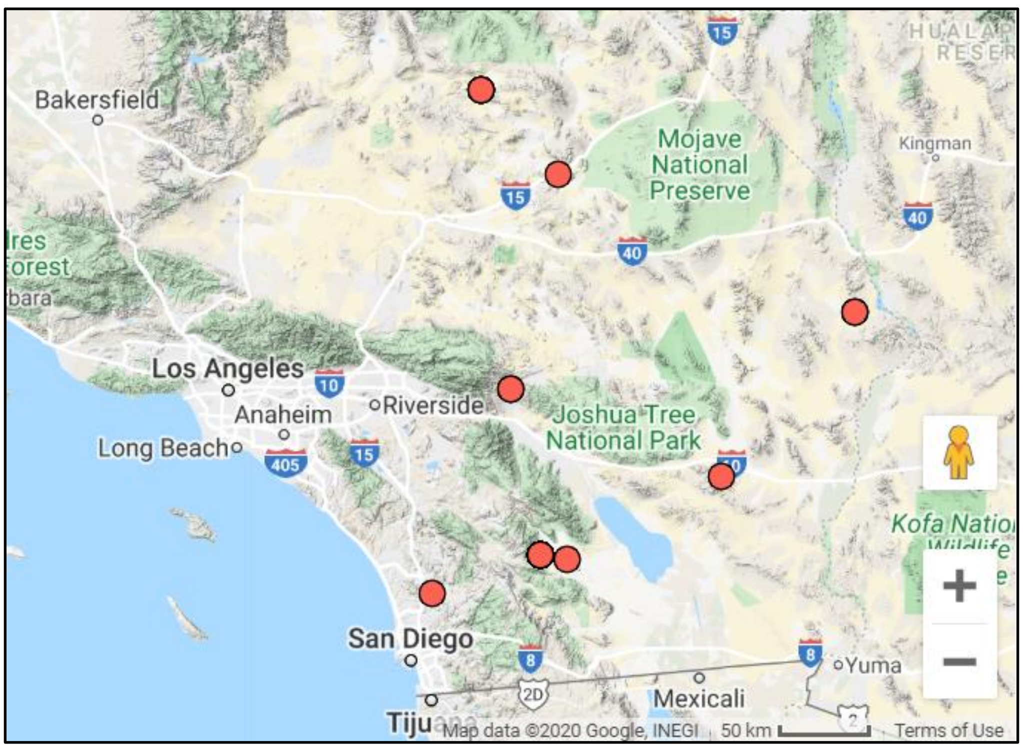

Figure 43. Distribution of *Eremotylus* sp. RBoph025 specimens examined in this study. n=46

Remarks

The most abundant morphospecies of *Eremotylus* found in this study. This morphospecies matches the description of *Eremotylus subfuliginosus*, but the type specimen of *E. subfuliginosus* will need to be examined to confirm as the species designation, because *Eremotylus* has undergone extensive revision since the original description of this species.

OTU 26 = *Eremotylus* sp. RBoph026

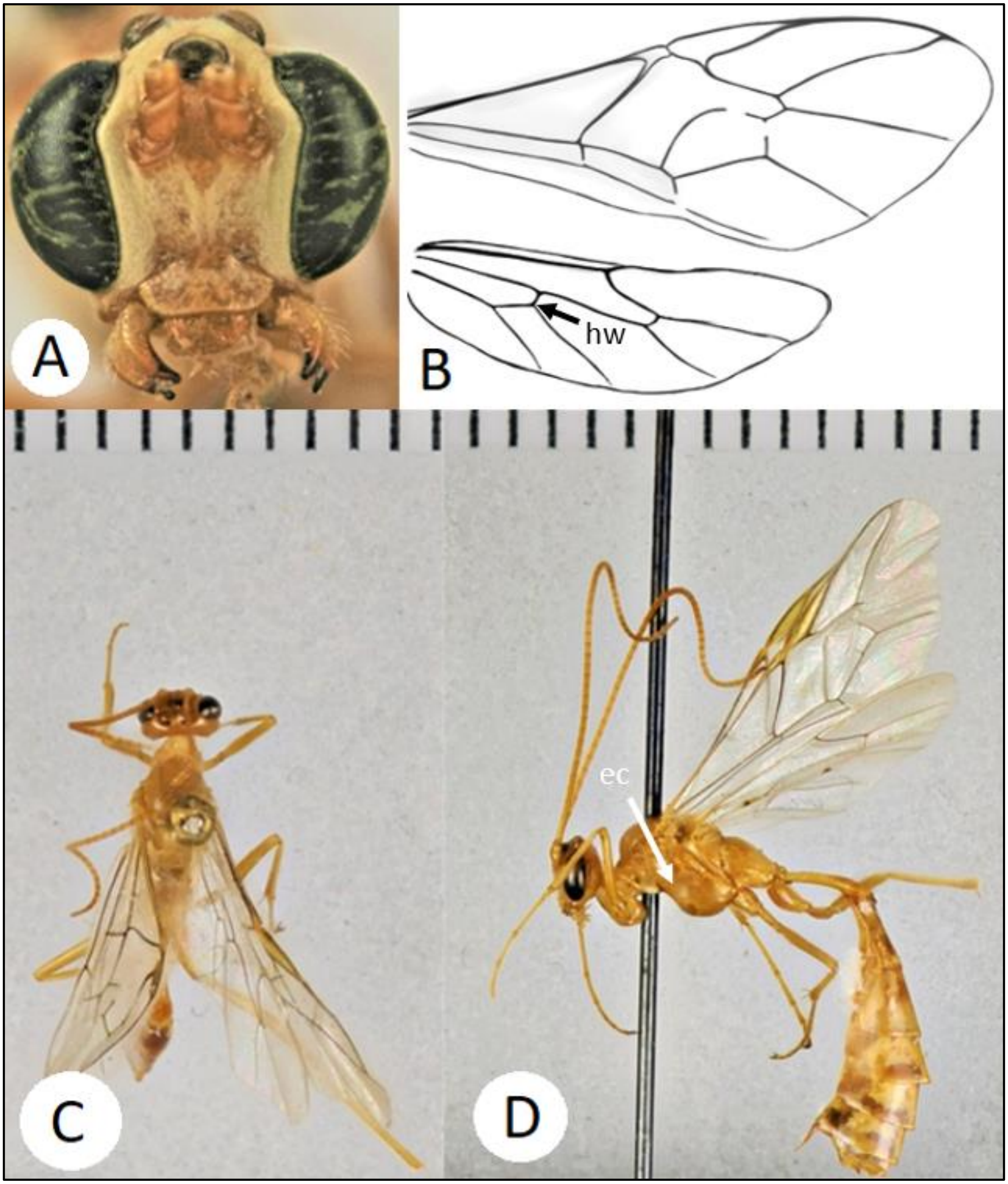

Figure 44. Images of the **A** head, **B** wing venation**, C** habitus, and **D** dorsum of *Eremotylus* sp.RBoph026. The presence of the epicnemial carina (ec) and the intersection of the Cu1 vein with CU-a on the hindwing (hw) are labeled.

Figure 45. Propodeum of *Eremotylus* sp.RBoph026.

Diagnosis

Occipital carina complete, epicnemial carina present and conspicuous, propodeum only with vestigial mid-longitudinal carina present, and Cu1 vein of hindwing intersecting CU-a at around 0.66x between M and 1A.

Table 19. Summary of the character states possessed by *Eremotylus* sp. RBoph026 for the morphological characters delineating *Eremotylus* morphospecies.

Character	State
Occipital carina	Complete
Epicnemial carina	Present
Propodeal sculpture	Vestigial mid-longitudinal carina
Length of cu-a where it intersects Cu	0.66x

Distribution

Found in the desert regions of Southern California.

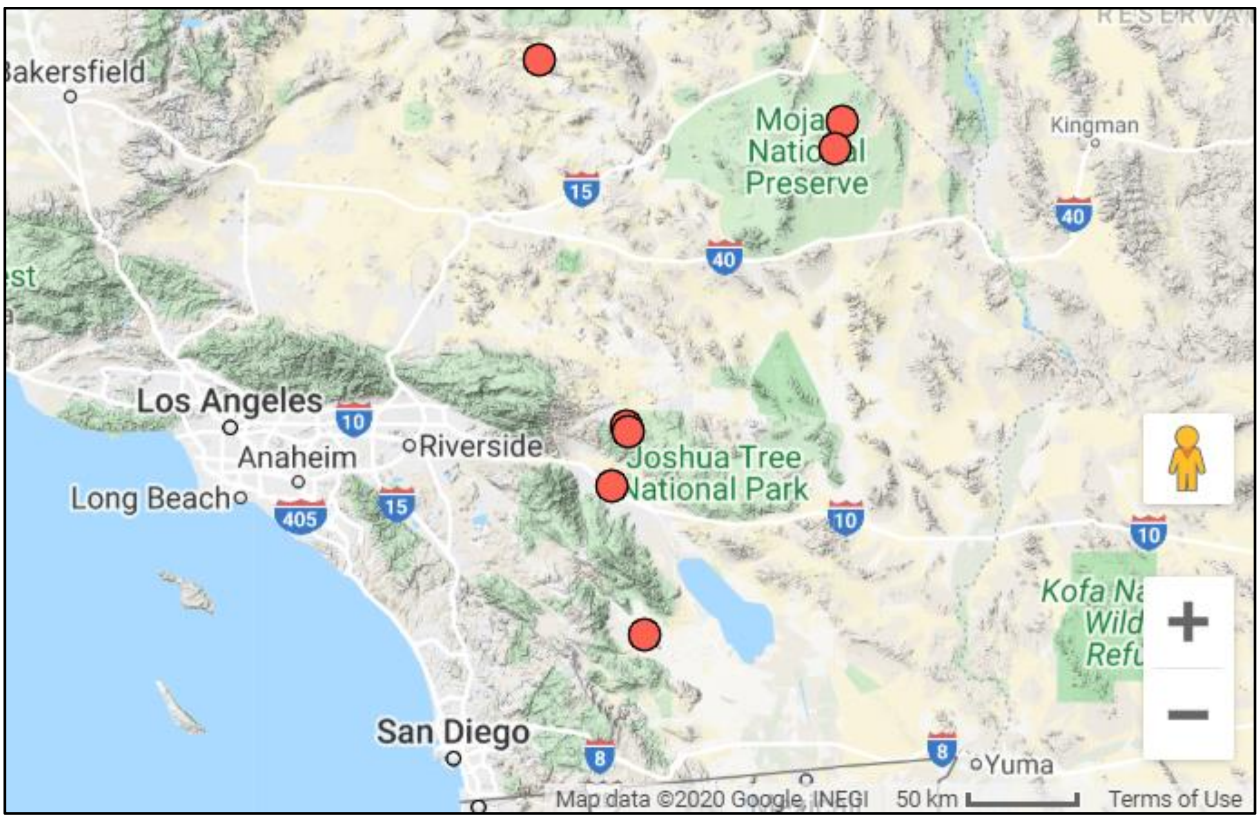

Figure 46. Distribution of *Eremotylus* sp. RBoph026 specimens examined in this study. n=8

OTU 3 = *Ophion* sp. RBoph003

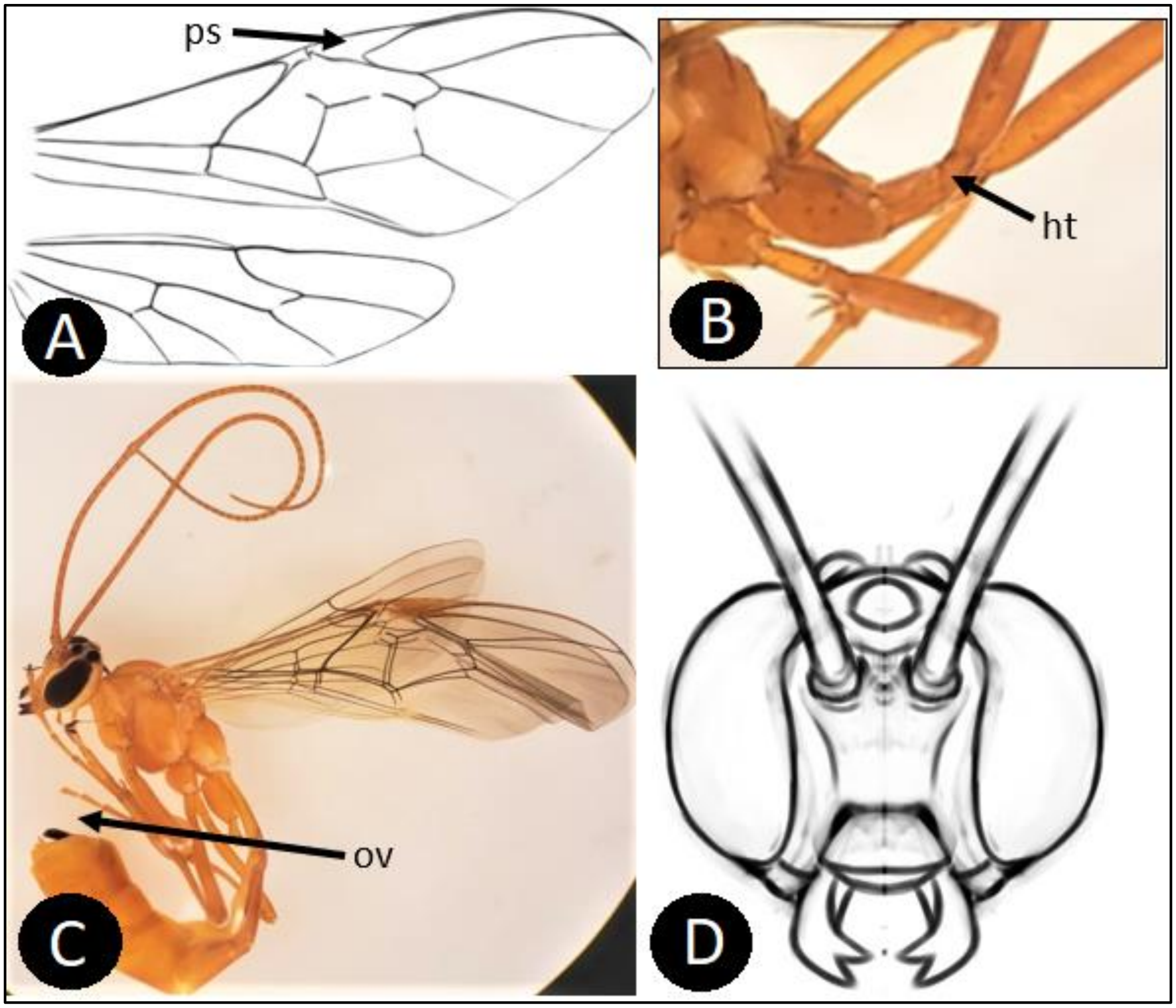

Figure 47. Images of the **A** wing venation, **B** hind trochanter, **C** habitus, and **D** head of *Ophion* sp. RBoph003. The pterostigma (ps), the hind trochantelli (ht), and the ovipositor (ov) are labeled.

Diagnosis

Ovipositor sheath distinctly black, overall body coloration matte fulvous, pterostigma large and triangular.

Table 20. Summary of the character states possessed by *Ophion* sp. RBoph003 for the morphological characters delineating *Ophion* morphospecies.

Character	State
Pterostigma size and shape	Triangular
Length of trochantellus	Long hind trochantellus
Ovipositor sheath color	Black
Body coloration and patterning	Matte fulvous

Distribution

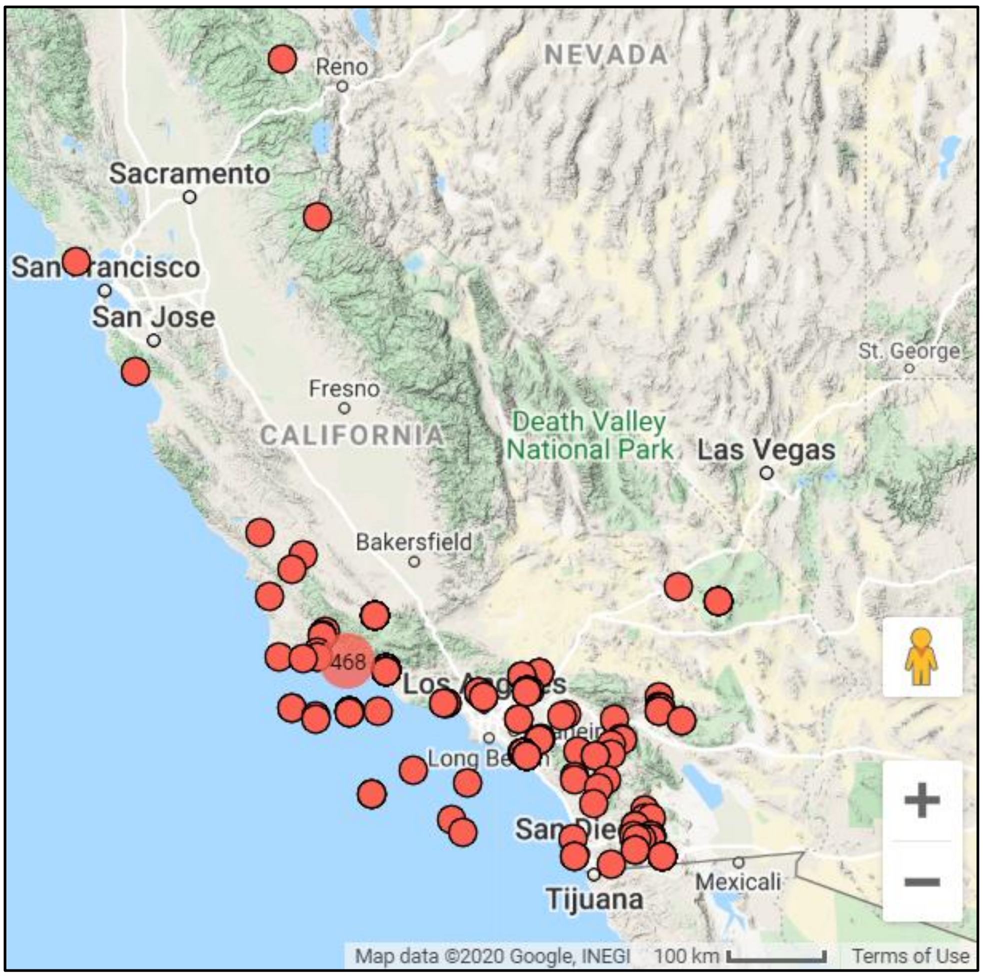

Figure 48. Distribution of *Ophion* sp. RBoph003 specimens examined in this study. n=755

Remarks

The most abundant morphospecies of *Ophion*, and Ophioninae in general, found in this study. Whether this is one widespread, common species or many species that look physically similar will need to be explored in future work. Because this genus is infamous for containing cryptic species, the latter is probably more likely, but I will lump them together as one morphospecies in this analysis.

OTU 4 = *Ophion* sp. RBoph004

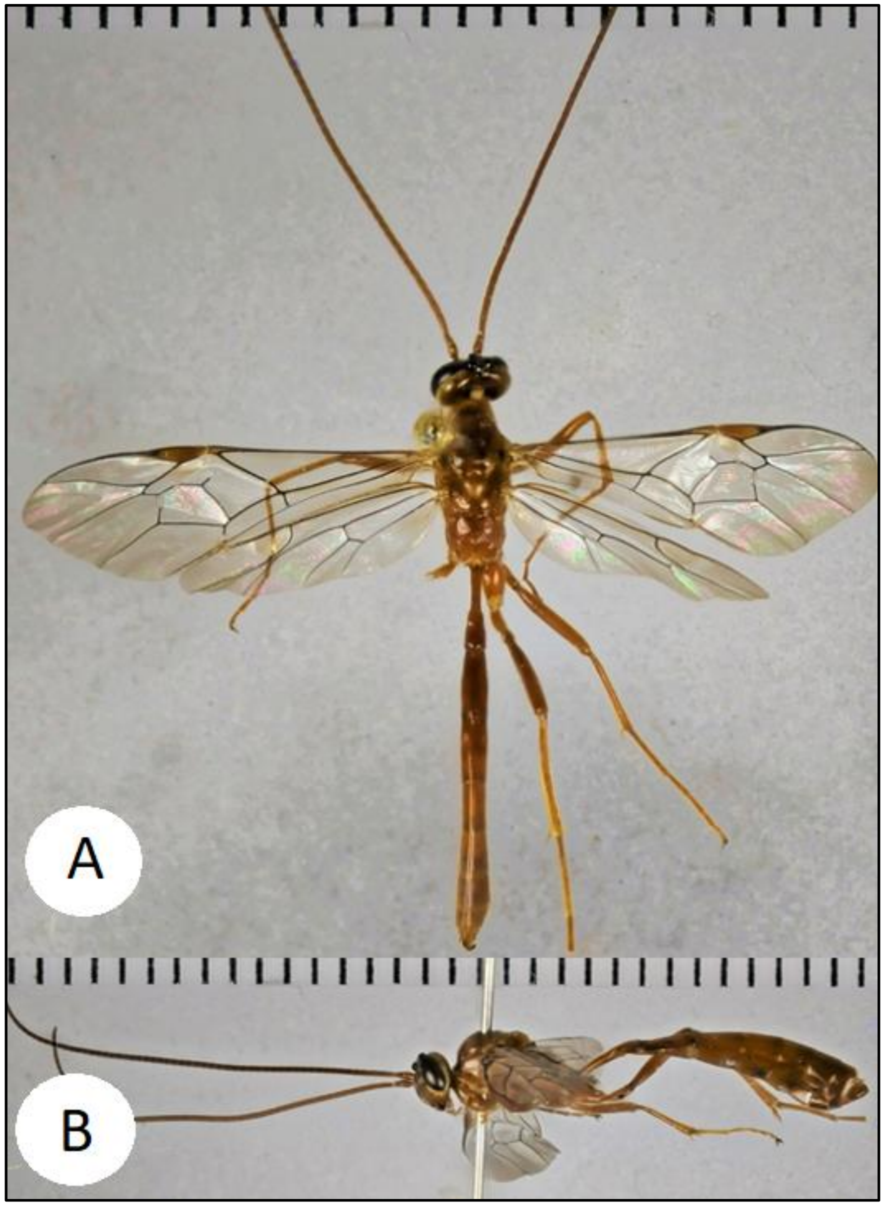

Figure 49. Images of the **A** dorsum and **B** habitus of *Ophion* sp.RBoph004.

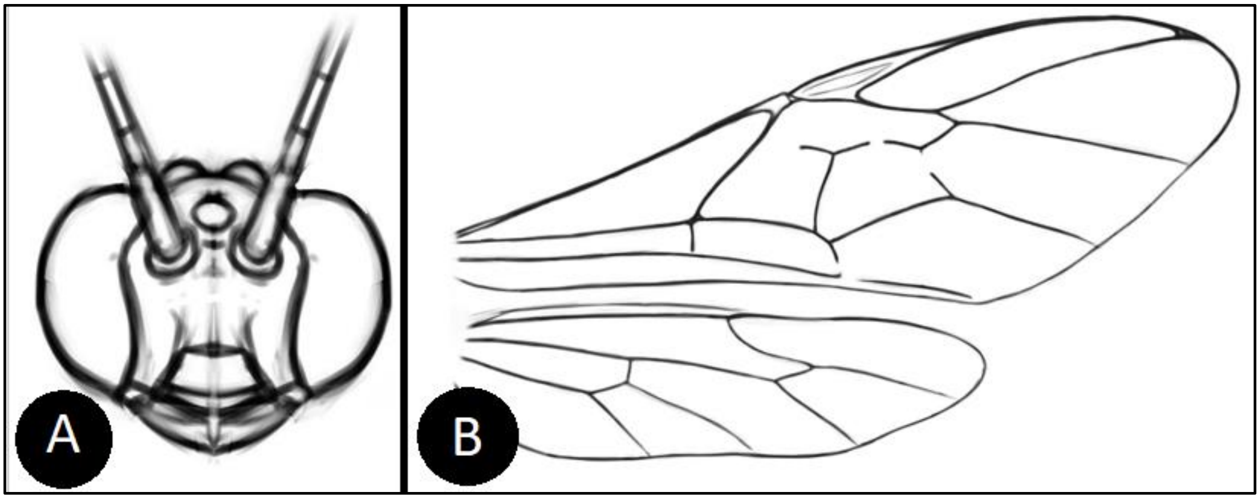

Figure 50. Images of the **A** head and **B** wing venation of *Ophion* sp.RBoph004.

Diagnosis

Infuscated wings, darker ferruginous color rather than matte fulvous.

Table 21. Summary of the character states possessed by *Eremotylus* sp. RBoph004 for the morphological characters delineating *Ophion* morphospecies.

Character	State
Pterostigma size and shape	Narrow
Ovipositor sheath color	Brown
Body coloration and patterning	Matte fulvous

Distribution

A rarer taxon found from San Diego County to Santa Barbara County.

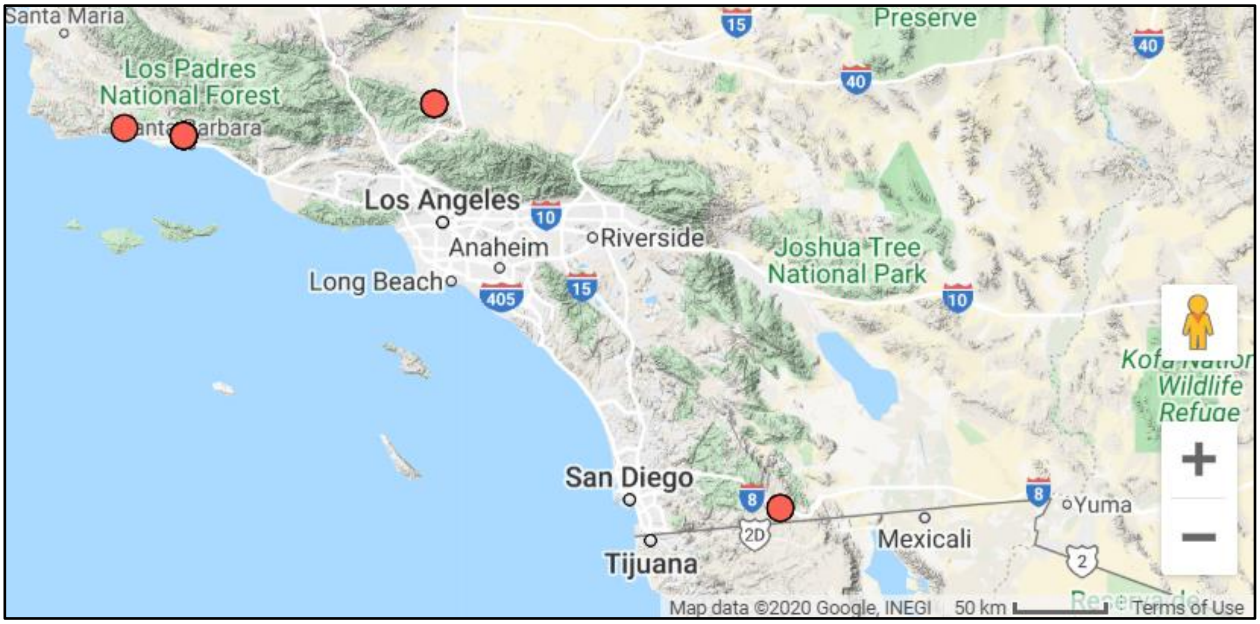

Figure 51. Distribution of *Ophion* sp. RBoph004 specimens examined in this study. n=13

Remarks

The least common morphospecies of *Ophion* found in this study. This morphospecies may represent intraspecific variation within an already known species or may constitute another morphospecies. For the purposes of this study, individuals with these characteristics will be treated as a separate morphospecies.

OTU 5 = *Ophion* sp. RBoph005

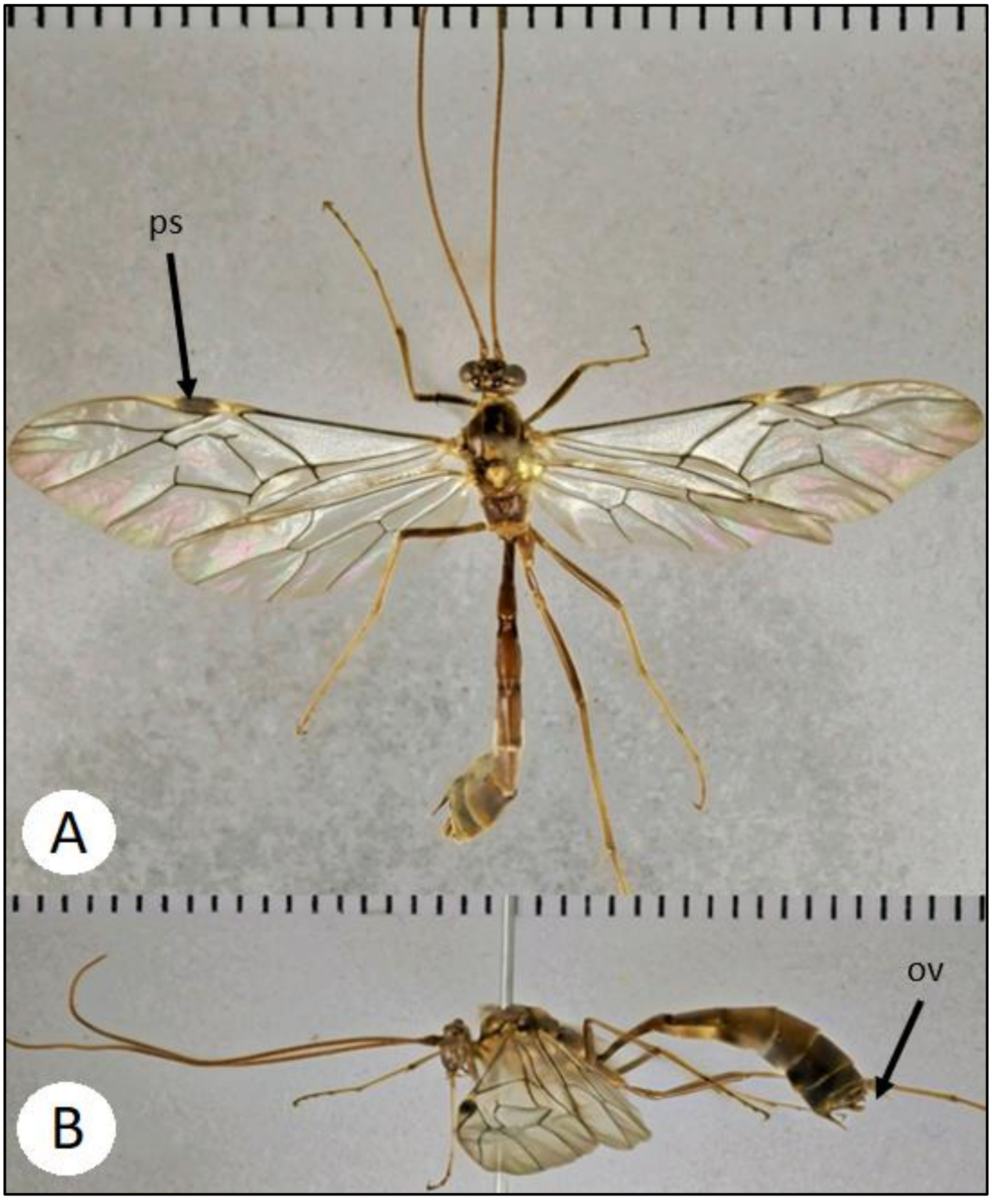

Figure 52. Images of the **A** dorsum and **B** habitus of *Ophion* sp. RBoph005. The pterostigma (pt) and the ovipositor (ov) are labeled.

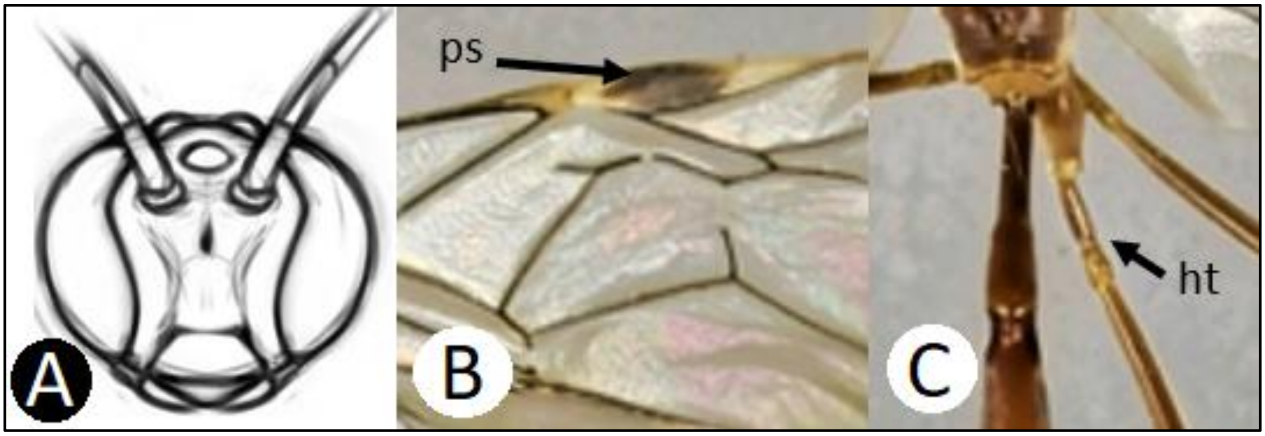

Figure 53. Images of the **A** head, **B** wing venation, and **C** abdomen and hindleg of *Ophion* sp. RBoph005. The pterostigma (pt) and the hind trochantelli (ht) are labeled.

Diagnosis

Dark ferruginous body with flavous/pale markings. Pterostigma dark centrally but with distinct pale borders.

Table 22. Summary of the character states possessed by *Ophion* sp. RBoph005 for the morphological characters delineating *Ophion* morphospecies.

Character	State
Pterostigma size and shape	Narrow, anterior and posterior ends pale
Length of trochantellus	Long hind trochantellus
Ovipositor sheath color	Brown
Body coloration and patterning	Ferruginous with pale pattering

Distribution

Coastal and mountainous areas of Southern California.

Figure 54. Distribution of *Ophion* sp. RBoph005 specimens examined in this study. n=198

Remarks

One of the most striking and recognizable morphospecies of *Ophion* found in California, owing to its bicolored pterostigma.

OTU 7 = *Ophion* sp. RBoph007

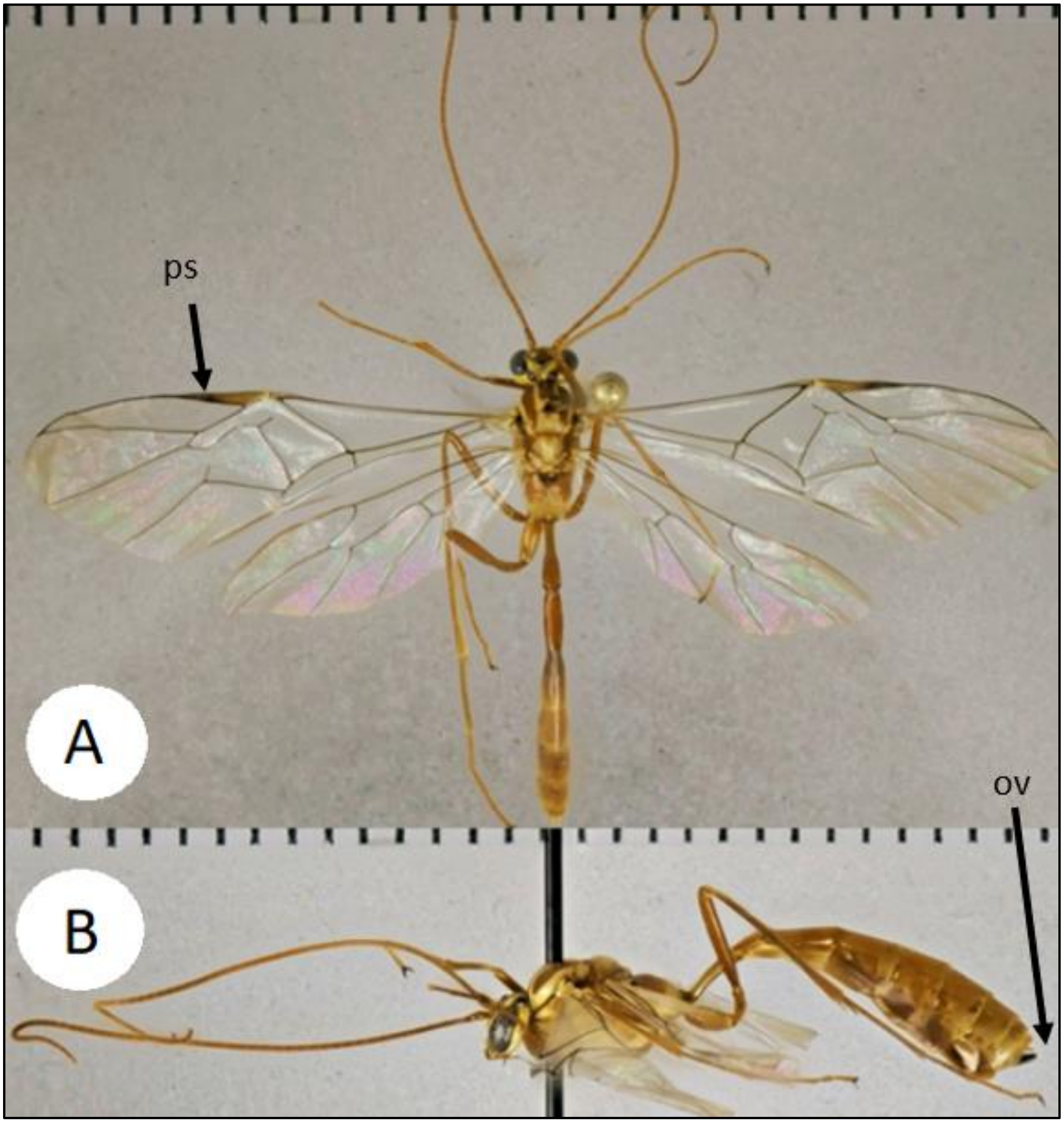

Figure 55. Images of the **A** dorsum and **B** habitus of *Ophion* sp. RBoph007. The pterostigma (ps) and ovipositor (ov) are labeled.

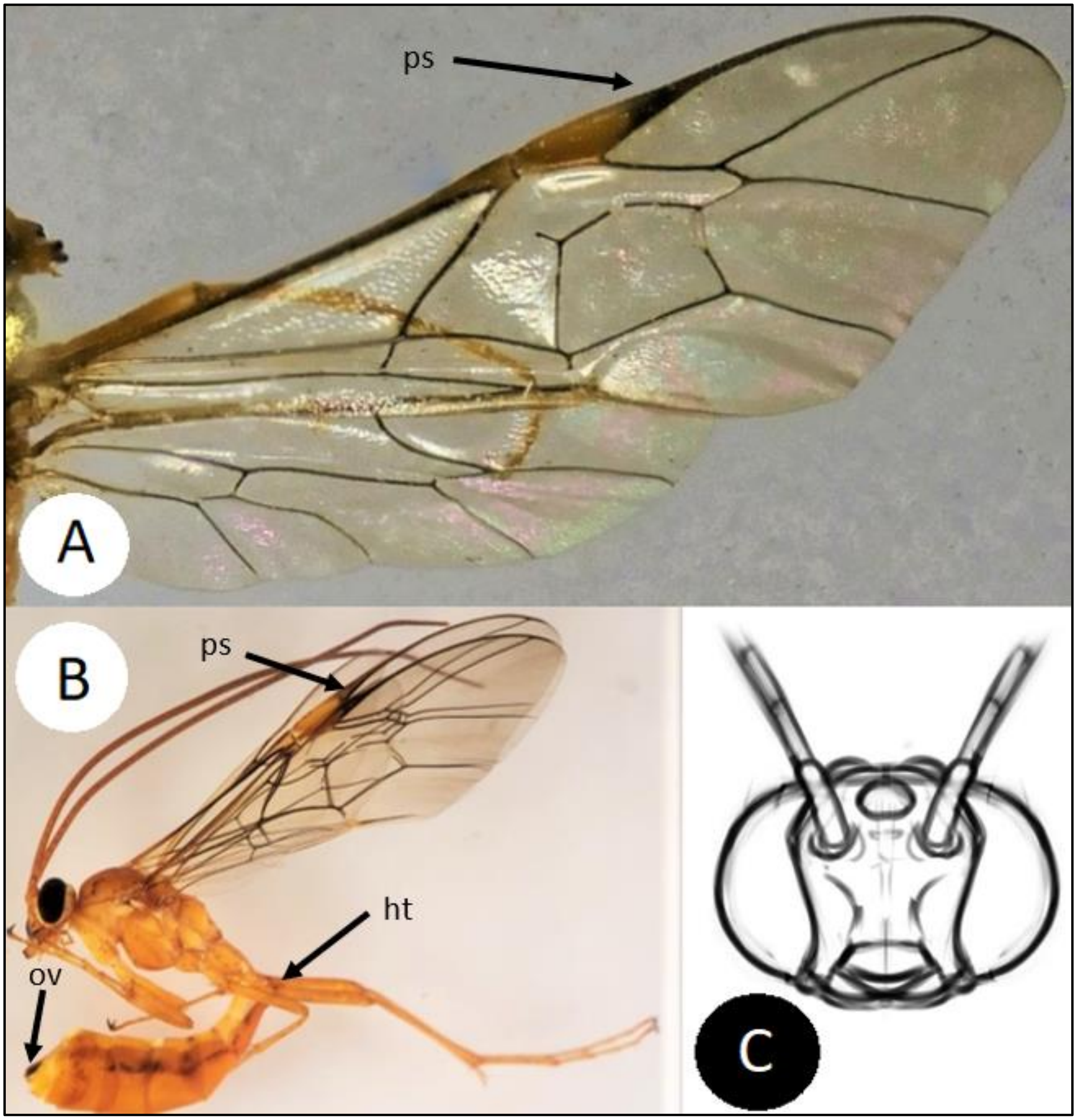

Figure 56. Images of the **A** wing venation, **B** habitus, and **C** head of *Ophion* sp. RBoph007.

Diagnosis

Body coloration overall matte fulvous with flavous patterning. Distal end of stigma and costal vein dark black. The pterostigma (ps), hind trochantelli (ht), and ovipositor are labeled.

Table 23. Summary of the character states possessed by *Ophion* sp, RBoph007 for the morphological characters delineating *Ophion* morphospecies.

Character	State
Pterostigma size and shape	Triangular, apical portion and costal vein black
Length of trochantellus	Long hind trochantellus
Ovipositor sheath color	Black
Body coloration and patterning	Fulvous with flavous patterning

Distribution

Only found in Santa Barbara County.

Figure 57. Distribution of *Ophion* sp. RBoph007 specimens examined in this study. n=20

Remarks

Although this morphospecies is quite recognizable when freshly collected due to its black markings, the lack of specimens in collections may be the result of the stigma pigmentation fading over time.

OTU 27 = *Ophion* sp. RBoph027

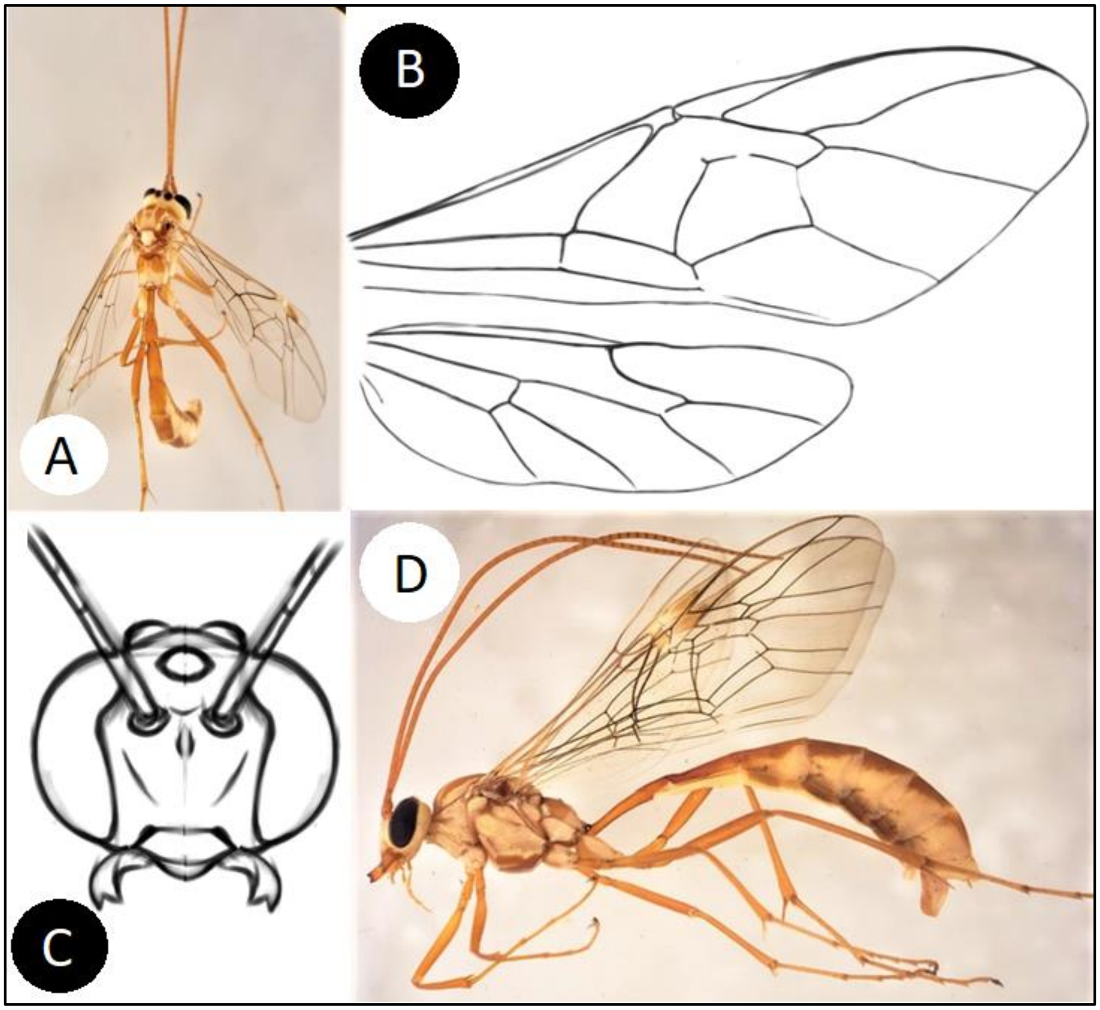

Figure 58. Images of the **A** dorsum, **B** wing venation, **C** head, and **D** habitus of *Ophion* sp.RBoph027.

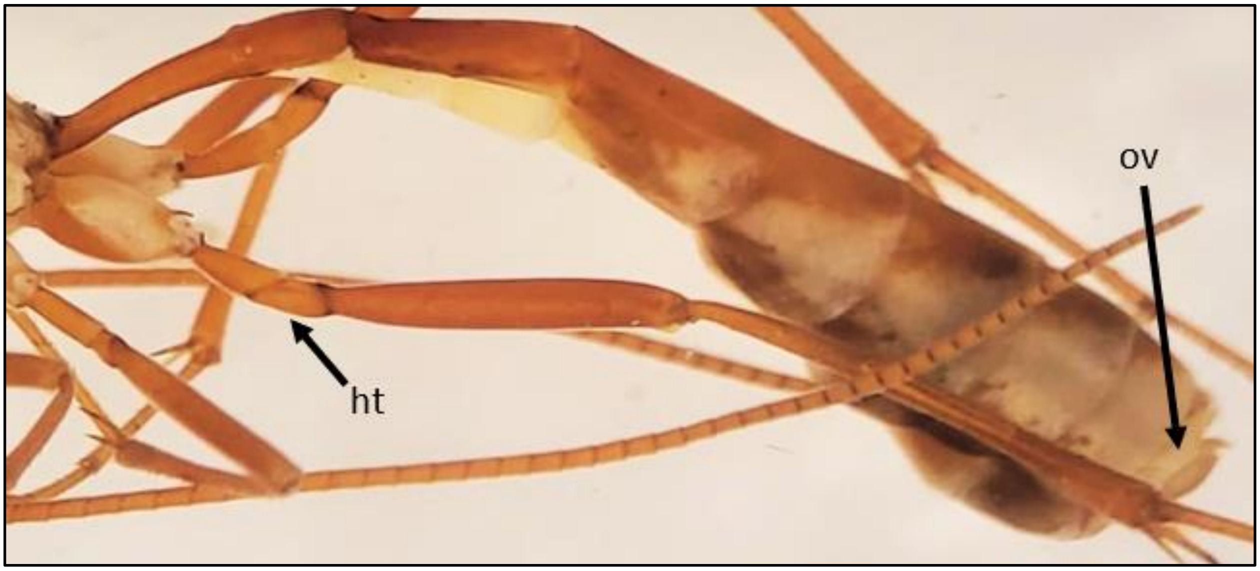

Figure 59. Image of the abdomen and hindleg of *Ophion* sp. RBoph027. The hind trochantelli (ht) and the brown ovipositor (ov) are labeled.

Diagnosis

Ovipositor sheath brown, body base fulvous but with light markings, and overall silver pubescence.

Table 24. Summary of the character states possessed by *Eremotylus* sp. RBoph027 for the morphological characters delineating *Ophion* morphospecies.

Character	State
Pterostigma size and shape	Narrow
Length of trochantellus	Long hind trochantellus
Ovipositor sheath color	Brown
Body coloration and patterning	Fulvous with flavous patterning

Distribution

Widespread and common throughout Southern California.

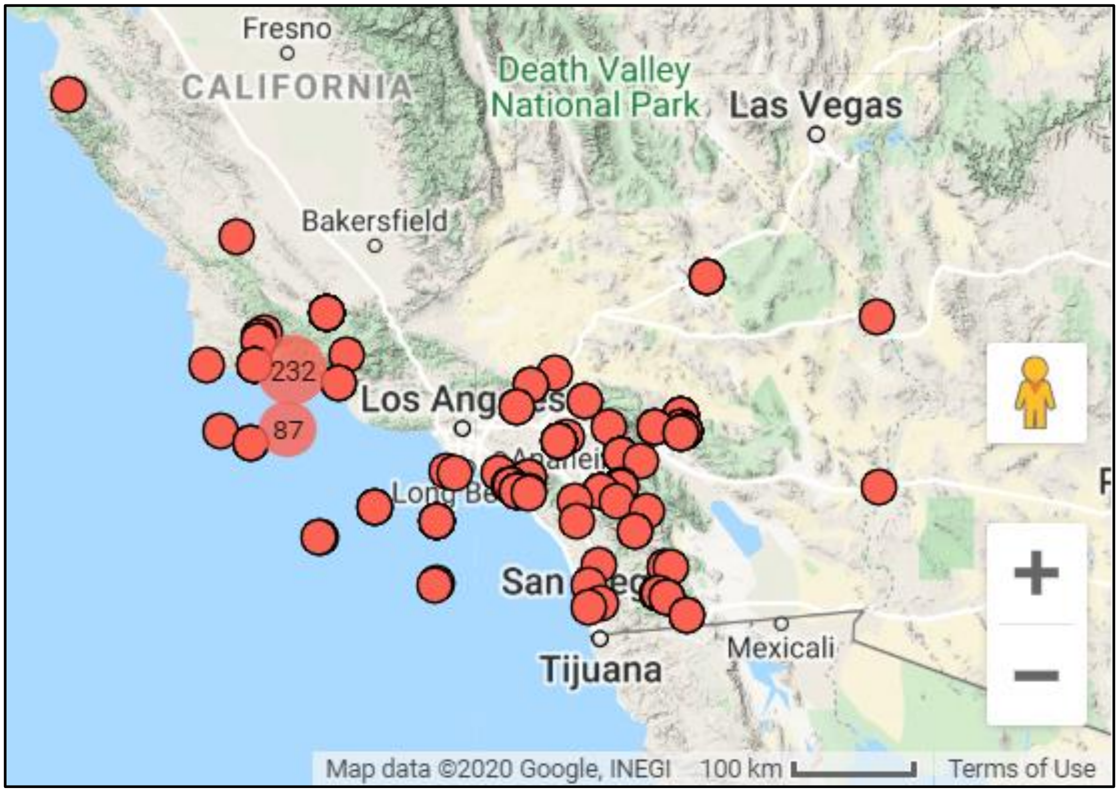

Figure 60. Distribution of *Ophion* sp. RBoph027 specimens examined in this study. n=570

Remarks

The second most common morphospecies of *Ophion*, specifically, and Ophioninae, in general, found in this study.

OTU 29 = *Simophion* sp. RBoph029

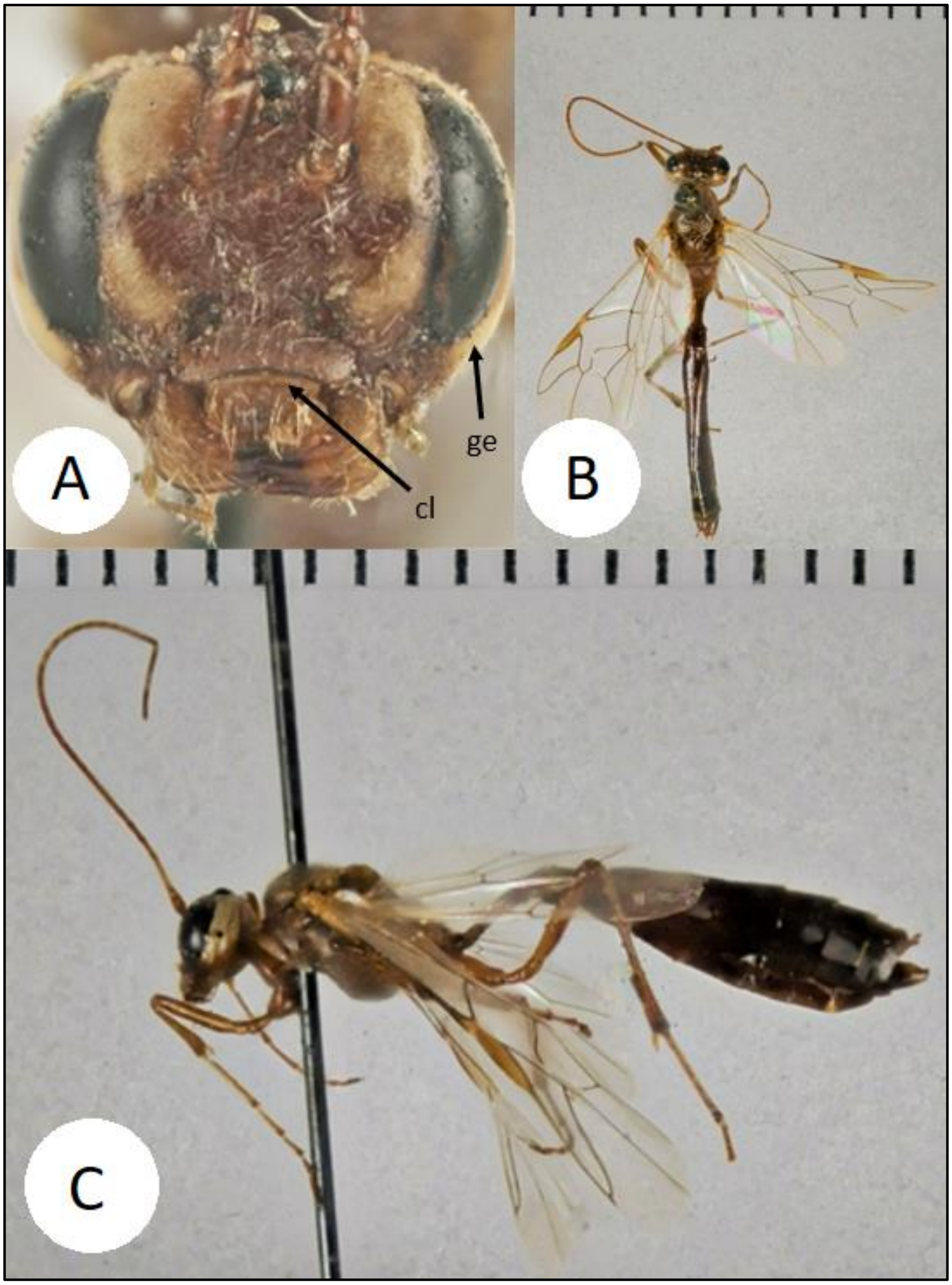

Figure 61. Images of the **A** head, **B** dorsum, and **C** habitus of *Simophion* sp. RBoph029. The concave clypeus (cl) and enlarged gena (ge) are labeled.

Diagnosis

Clypeus concavely truncate and more than twice as broad as long, enlarged gena similar to *Eremotylus* sp. RBoph011, and dark ferruginous coloration with a cream-colored head.

Distribution

Found in the desert regions of San Diego, Riverside, Los Angeles, and San Bernardino counties. n=6

Remarks

I only collected males of this morphospecies, which generally matches the characters described for *Simophion excarinatus*, but these specimens had head characteristics which did not match the *Simophion excarinatus* description; however, only females were used by Cushman in describing this species. This morphospecies, then, is probably the undescribed male form of this species, rather than a new species.

OTU 30 = *Trophophion* sp. RBoph030

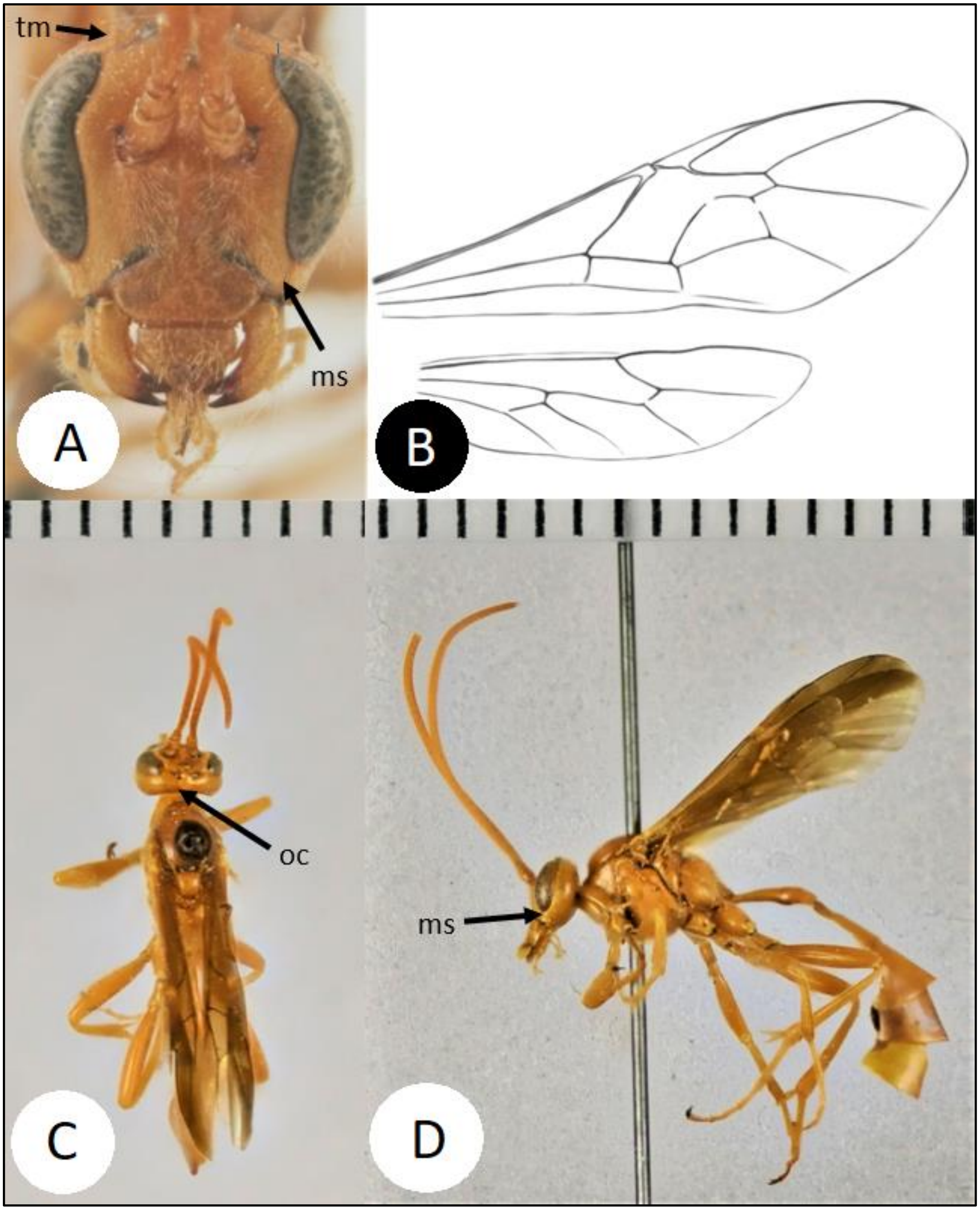

Figure 62. Images of the **A** head, **B** wing venation, **C** dorsum, and **D** habitus of *Trophophion* sp.RBoph030. The occiput (oc), extended temples (tm), and malar space (ms) are labeled.

Diagnosis

Occiput not concave and temple extending beyond eye. Mandibles thinner, malar space shorter, and antennae longer than *Trophophion tenuiceps.*

Distribution

Only one specimen from Tuolumne County was obtained in this study,

Remarks

This specimen was collected far north of the described range of *Trophophion tenuiceps,* but was found in a mountainous desert habitat similar to that where *T. tenuiceps* has been collected. The morphology of this specimen does not entirely match the description of *T. tenuiceps,* especially in its head shape, so is most likely an undescribed *Trophophion* species.

4. **Determined Specimens**

Identified specimens received on loan from the aforementioned institutions were used as references for morphological comparisons, because the type specimens were unavailable for this project. Only identifications determined by the Ophionine experts Dr. Ian Gauld, Dr. David Wahl, or Dr. Henry Townes were used to cross-reference specimens. Identified specimens included:

Table 25. Specimens determined by taxonomic experts to cross-reference to the California morphospecies.

Taxon	**Determiner**	**Catalog Number**	**Depository**	**Collection Date**	**Sex**	**State**	**County**
Enicospilus americanus (Christ,1791)	Ian Gauld 1985	CASENT8423039	CASENT	1925-11-?	Female	California	Alameda
Enicospilus flavostigma (Hooker, 1912)	Henry Townes 1952	UCBMEP0272800	UCBME	1947-09-26	Female	California	Yolo

Enicospilus guatamalensis (Cameron, 1886)	David Wahl 2009	UCBMEP0272867	UCBME	1976-11-25	Female	Florida	Alachua
Enicospilus peigleri (Gauld, 1988a)	David Wahl 2009	UCBMEP0272876	UCBME	1978-07-26	Female	Maryland	Montgomery
Enicospilus texanus (Ashmead, 1890)	Ian Gauld 1985	CASENT8423041	CASENT	1929-06-19	Female	California	Tulare
Enicospilus texanus (Ashmead, 1890)	Ian Gauld 1985	CASENT8423042	CASENT	1937-04-10	Female	Arizona	Pima
Eremotylus subfuliginosus (Ashmead, 1894)	Henry Townes 1952	UCBMEP0272839	UCBME	1951-04-22	Female	California	San Diego
Eremotylus subfuliginosus (Ashmead, 1894)	Henry Townes 1952	UCBMEP0272843	UCBME	1951-04-23	Female	California	San Diego
Eremotylus subfuliginosus (Ashmead, 1894)	Henry Townes 1952	UCBMEP0272842	UCBME	1951-04-23	Female	California	San Diego
Eremotylus subfuliginosus (Ashmead, 1894)	Henry Townes 1952	UCBMEP0272841	UCBME	1951-04-23	Female	California	San Diego
Eremotylus subfuliginosus (Ashmead, 1894)	Henry Townes 1952	UCBMEP0272840	UCBME	1951-04-23	Female	California	San Diego
Enicospilus purgatus (Say,1835)	David Wahl 2009	UCBMEP0272824	UCBME	1971-03-23	Female	California	Riverside
Enicospilus purgatus (Say,1835)	David Wahl 2009	UCBMEP0272826	UCBME	1982-06-?	Female	California	Riverside
Enicospilus purgatus (Say,1835)	David Wahl 2007	UCBMEP0272866	UCBME	1967-03-21	Male	California	Riverside
Enicospilus glabratus (Say,1835)	David Wahl 2009	UCBMEP0272860	UCBME	1959-11-23	Female	California	San Diego
Enicospilus glabratus (Say,1835)	David Wahl 2009	UCBMEP0272861	UCBME	1965-06-18	Female	California	Santa Barbara
Trophophion tenuiceps Cushman, 1947	David Wahl 2008	UCBMEP0272858	UCBME	1963-04-09	Female	California	San Diego
Trophophion tenuiceps Cushman, 1947	Henry Townes 1948	UCBMEP0272857	UCBME	1938-04-16	Male	California	Riverside

5. **Range Expansions/Updated Catalog of Californian Ophioninae**

Eremotylus subfuliginosus was previously recorded from Egypt, Korea, and the United States (New Mexico and Virginia). Confirmed *Eremotylus subfuliginosus* specimens in this California study were all collected in Anza Borrego State Park in San Diego County, California, by E. I. Schlinger in 1951. My morphospecies *Eremotylus* sp. RBoph025 (see diagnoses) matches the description for *Eremotylus subfuliginosus*, but the type specimen of *E. subfuliginosus* will need to be examined to confirm the identification of the California specimens. If these specimens do indeed belong to *Eremotylus subfuliginosus*, this will represent an additional range extension for this species.

Table 26. List of the 14 currently described Ophionine species of California.

Catalog of Californian Ophioninae

Enicospilus Stephens 1835	*americanus* (Christ, 1791)
	bifoveolatus (Brullé, 1846)
	flavostigma Hooker, 1912
	glabratus (Say, 1835)
	purgatus (Say, 1835)
	sarukhani Gauld, 1988b
	texanus (Ashmead, 1890)
Eremotylus Forster, 1869	*abnormus* (Felt, 1904)
	costalis (Cresson, 1879)
	subfuliginosus (Ashmead, 1894)
Ophion Fabricius, 1798	*magniceps* Hooker, 1912
	bilineatus Say, 1829
Simophion Cushman, 1947	*excarinatus* Cushman, 1947
Trophophion Cushman, 1947	*tenuiceps* Cushman, 1947

E. Discussion

1. **Future Directions**

Of the 13 species previously described from California, I did not find 6 in my study, including *Enicospilus bifoveolatus* (Brullé, 1846); *Enicospilus flavostigma* Hooker, 1912; *Enicospilus sarukhani* Gauld, 1988b; *Eremotylus abnormus* (Felt, 1904); *Ophion magniceps* Hooker, 1912; and *Ophion bilineatus* Say, 1829. Additional work will need to be done to confirm whether or not these species still occur in California. It will be important to compare the 18 additional morphospecies described in this study with the type specimens of the 6 missing species to see if there is overlap.

Enicospilus and *Ophion* are speciose and commonly-studied genera, accounting for 80% of described Ophioninae's species (Yu et al., 2012). As previously discussed, the number of Nearctic *Ophion* species are likely much higher than previously realized and cannot be distinguished based on morphology alone. As a consequence, it is no surprise that the 5 *Ophion* morphospecies could not be assigned to known species or confirmed as new species. In contrast, *Enicospilus* species of the United States are much better known and are not as difficult to delineate morphologically as *Ophion.* The lack of the three *Enicospilus* species, *E. bifoveolatus* (Brullé, 1846), *E. flavostigma* Hooker, 1912, and *E. sarukhani* Gauld, 1988b, from California specimens used in the study does not mean they are no longer in California.

The 11 additional *Eremotylus* morphospecies that I found were the most surprising result of this study. It is known that *Eremotylus* prefer arid habitats, such as those present in Southern California (Cushman, 1947, Gauld, 1985), but the potential diversity of this genus both in California, and in general, was greatly underestimated. The high *Eremotylus* diversity compared to the diversity of other taxa is especially surprising because specimens of this genus are much rarer than those of *Ophion* and *Enicospilus*. The diversity of *Eremotylus* in the United States is poorly known and hasn't been examined since the description of *E. bulbosus* from Michigan by Leblanc (1989). If all 11 *Eremotylus* morphospecies from this southern California study are new to science, then the number of species in the Nearctic would more than double. As a consequence, these morphospecies need to be re-examined and formally described. In addition, more extensive surveys need to be conducted to learn more about the distribution and diversity of this genus.

Although a new morphospecies of *Simophion* was found in this study, it does not appear to be one of the hitherto undescribed species of *Simophion* in the United States (Cushman, 1947 and Gauld, 1985). Instead, the new *Simophion* morphospecies I encountered is likely to be the undescribed male form of the described species, *Simophion excarinatus.* The holotype for both the genus *Simophion* and the species *Simophion excarinatus* are female, because no males were available (Cushman, 1947). Besides the strange head, the new male *Simophion* morphospecies matches the characteristics and geographic range of *S. excarinatus*. The type specimen for *S. excarinatus* should be compared to this morphospecies to confirm the matching characteristics. Also, the “several undescribed species” from the Nearctic mentioned by Cushman (1947) and Gauld (1985) need to be located and formally described.

I also discovered a new undescribed species of the very rare, formerly-monotypic genus *Trophophion*. This genus has not been studied since its description (Cushman 1947). Only one specimen of this new species was found for this study and none were collected more recently than the 1960’s. This new morphospecies was collected much farther North than any *Trophophion* has been previously recorded, and its morphology is distinctly different from the description and specimens of *T. tenuiceps* available. Unfortunately, only one, damaged specimen of this morphospecies was found for this study, collected over 80 years ago. This new species will need to be formally described and fresh specimens of *Trophophion* are needed to learn more about this group.

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Appendix 1

Table 27. Summary of the Ophionine taxa of California from this survey. An X represents a lack of placement.

Tribe	Complex/Group	Genus	Species
Enicospilini	*E. americanus* complex	*Enicospilus*	*americanus* (Christ, 1791)
Enicospilini	*E. americanus* complex	*Enicospilus*	*glabratus* (Say, 1835)
Enicospilini	*E. americanus* complex	*Enicospilus*	*texanus* (Ashmead, 1890)
Enicospilini	*E. purgatus* complex	*Enicospilus*	*purgatus* (Say, 1835)
X	*E. costalis* complex	*Eremotylus*	*costalis* (Cresson, 1879)
X	*E. costlalis* complex	*Eremotylus*	sp. RBoph011
X	X	*Eremotylus*	*subfuliginosus* (Ashmead, 1894)
X	X	*Eremotylus*	sp. RBoph012
X	X	*Eremotylus*	sp. RBoph013
X	X	*Eremotylus*	sp. RBoph015
X	X	*Eremotylus*	sp. RBoph017
X	X	*Eremotylus*	sp. RBoph018
X	X	*Eremotylus*	sp. RBoph019
X	X	*Eremotylus*	sp. RBoph021
X	X	*Eremotylus*	sp. RBoph023
X	X	Eremotylus	sp. RBoph025

X	X	Eremotylus	sp. RBoph026
Ophionini	*O. luteus* species group	*Ophion*	sp. RBoph003
Ophionini	X	*Ophion*	sp. RBoph004
Ophionini	*O. luteus* species group	*Ophion*	sp. RBoph005
Ophionini	*O. luteus* species group	*Ophion*	sp. RBoph007
Ophionini	*O. luteus* species group	*Ophion*	sp. RBoph027
X	X	*Simophion*	*excarinatus* Cushman 1947
X	X	*Simophion*	sp. RBoph029
X	X	*Trophophion*	*tenuiceps* Cushman 1947
X	X	*Trophophion*	sp. RBoph030

Appendix 2

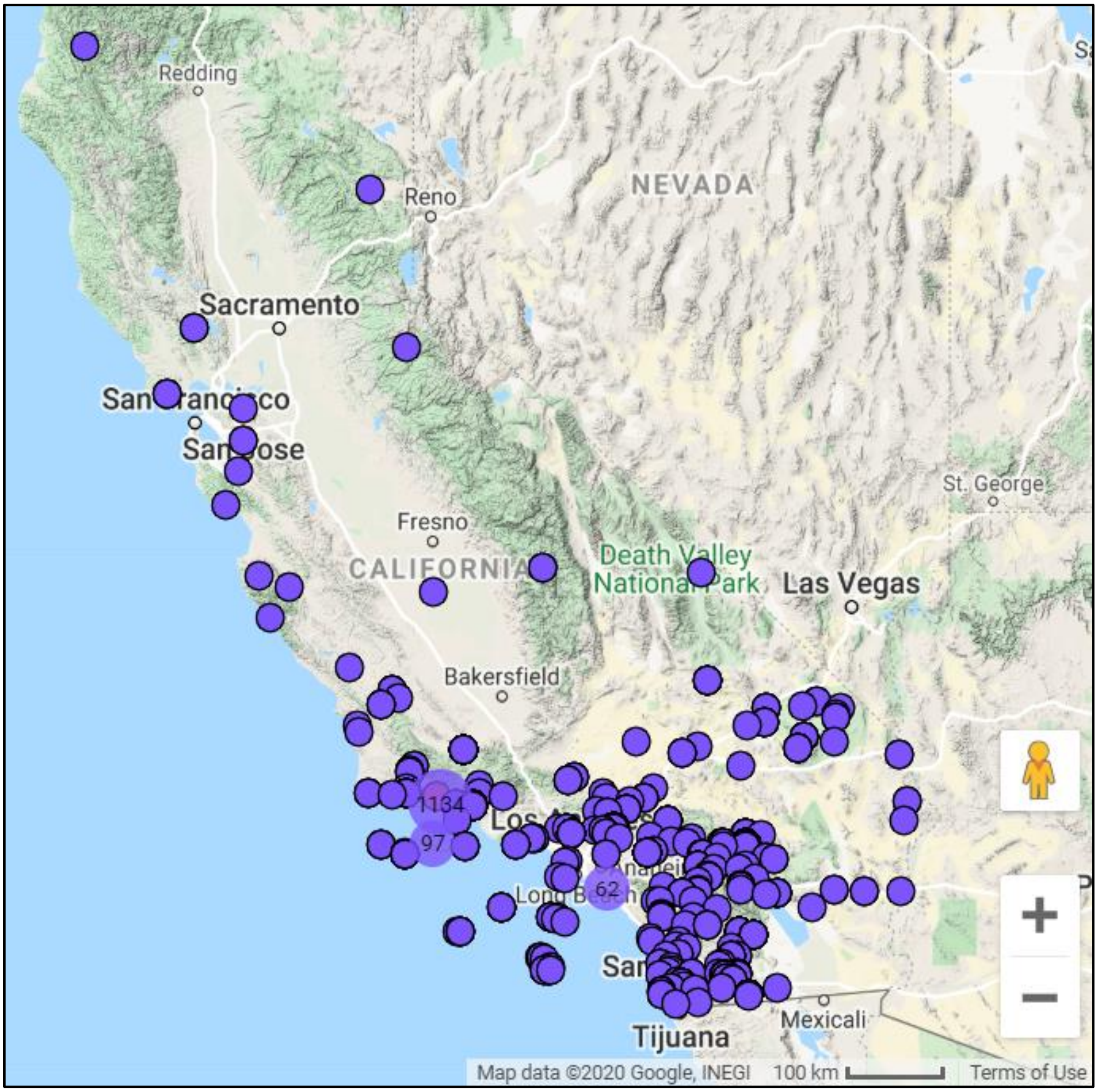

Figure 63. Map of observations of all specimens used in this study from California. n=2272

Appendix 3

Table 28. Summary matrix of the character states of the *Eremotylus* morphospecies. *Eremotylus* sp. RBoph10 and *Eremotylus* sp. RBoph011 are excluded due to their placement in the *E. costalis* complex. X indicates the presence of the character, blank represents the absence, and ? represents the inability to determine the character.

	OTU12	OTU13	OTU15	OTU17	OTU18	OTU19	OTU21	OTU22	OTU23	OTU25	OTU26
Occipital carina complete		X	X	X	X	X	X	X	X	X	X
Epicnemial carina present	X		X	X	X	X	X	X	X	X	X
Anterior transverse carina present	X			X		X	X			X	
Mid-longitudinal complete	X			X		X	X				
Posterior transverse carina present	X			X		X	X			X	
Wing infuscation	X		?	X		X				X	
Length of cu-a where it intersects Cu	0.5x	0.25x	0.8-0.9x	0.6x	0.6x	0.4x	0.5x	0.8x	0.2x	0.8x	0.66x

Appendix 4

Table 29. Summary matrix of the character states of the *Ophion* morphospecies. X indicates the presence of the character, blank represents the absence, and ? represents the inability to determine the character.

	OTU3	OTU4	OTU5	OTU7	OTU27
Pterostigma narrow		X	X		X
Hind trochantellus long	X	?	X	X	X
Ovipositor sheath black in color	X			X	
Body coloration matte fulvous	X	X			

III. Testing the tribal limits of Ophioninae (Hymenoptera, Ichneumonidae) with the addition of Coastal Southern California taxa

A. Abstract

Members of the ichneumonid subfamily Ophioninae have been historically difficult to classify. Tribal classification for this subfamily is defined currently by morphology, however, the high rates of endemism and homoplasy common in this subfamily have made tribal delineation questionable. This study tests the current tribal definitions through the addition of California taxa, because California is known for its high rates of endemism and species diversity and the knowledge of this subfamily in California is limited. I found that California taxa do not possess the tribal synapomorphies defined for Ophionini and Enicospilini. Given that the phylogenetic tribal resolution is dependent on those characters, I call for a re-examination of the higher-level classification of the Ophioninae.

B. Keywords

California, homoplasy, classification, tribal limits

C. Introduction

The subfamily Ophioninae consists of large-bodied, larval-pupal endoparasitoids of primarily Lepidoptera. This subfamily is composed of 32 genera with over 1,000 described species distributed worldwide (Yu et al., 2012). The Ophionini was the first Ophionine tribe described in Swainson & Shuckard (1840), later revised in Meyer (1937), Cushman (1947), Townes (1971), and Rousse et al. (2016). The tribe Enicospilini was first described in Townes (1971) and revised in Rousse et al. (2016). Thyreodonini is the most recently described Ophionine tribe (Rousse et al., 2016). Anomalonini and Therionini, previously listed in Ophioninae, were placed into Anomaloninae (Short, 1959 and Townes et al., 1965). A summary of the current tribal classification in Ophioninae is available in Table 1.

Table 30. Summary of tribal relations in Ophioninae, adapted from Rousse et al. (2016). Remaining genera have unknown placement. An expanded figure with information about each genus is available in Rousse et al. (2016).

Tribe	Synapomorphies	Genera Included	Distribution
Ophionini	1. Ramellus present 2. 1 m-cu angled; 3. Mesopleural furrow extended 4. Thyridia close to the margin of tergite 2	Ophion Xylophion Afrophion Rhopalophion Alophophion Sclerophion	Worldwide
Thyreodonini	5. Laterotergite 2 pendant 6. Propodeum with anterior transverse carina absent	Thyreodon Rhynchophion Dictyonotus	Mostly Neotropical
Enicospilini	7. Spiracular sclerite partially to totally occluded	Dicamptus Enicospilus Laticoleus Hellwigiella	Worldwide, mostly Pantropical

A comprehensive morphology-based phylogeny of Ophioninae was proposed in Gauld (1985) using both parsimony and compatibility methods for analyses. Gauld found a high level of homoplasy in morphological characters and concluded that the subfamily was best classified into five major evolutionary lineages: *Ophion* genus-group, *Sicophion* genus-group, *Eremotylus* genus-group, *Thyreodon* genus-group, and *Enicospilus* genus-group.

In 2016, Rousse et al. investigated the relationships among evolutionary lineages within Ophioninae using a combination of morphological and molecular methodologies. Rousse used a morphological dataset of 62 characters (Table 31-36) along with sequences in the COI region of mitochondrial DNA and the D2-D3 region of 28S ribosomal DNA to construct an updated phylogeny. The overlap and differences between the morphological characters used by Gauld and Rousse are discussed later in this paper. The combined analysis of Rousse's morphology and molecular data supports the claim that Ophioninae, including the historically problematic genera *Skiapus* and *Hellwigia,* is monophyletic. Rousse's study supports classification into three tribes including the newly revised tribes Ophionini and Enicospilini, and the new tribe Thyreodonini. These tribes map over and give support to the *Ophion* genus-group, *Enicospilus* genus-group, and *Thyreodon* genus-group from Gauld's morphological analysis (1985). The other two genus-groups, the *Eremotylus* genus-group and *Sicophion* genus-group, are not supported by Rouse's analysis. Despite the recognition of Thyreodonini, Rousse et al. (2016) was unable to place 20 out of the currently described 32 genera of Ophioninae into distinct tribes, owing to long branch lengths, incomplete or failed CO1 sequences, discrepancies between morphological and molecular results, and a lack of physical specimens.

Although Rousse included specimens and taxa from broad geographic areas (Nearctic, Neotropic, Afrotropic, Palearctic, Indomalay, Australasian, and Oceanian) there were still large gaps in geographic coverage. The aim of this study is to test the currently accepted morphological tribal characterizations for Ophioninae with the addition of specimens from California, especially those in the unplaced genera *Eremotylus, Simophion*, and the monotypic *Trophophion*. This study concentrates on California because it is a biodiversity hotspot with many endemic species (Myers et al., 2000), and Ophioninae are abundantly collected at night in this state. Further, the hypothesized high level of Ophioninae biodiversity in California provides an opportunity to test the robustness of the tribal classification of this subfamily using new taxa. For the purposes of this study, the Southern Coastal Counties of California will be investigated.

D. Materials and Methods

1. **Depositories of Examined Material**

This study is primarily based on the morphological characterization of Ophioninae specimens. I identified specimens for this study by contacting all major entomological collections in California (listed below) in addition to ASUHIC. Because the subfamily is largely undescribed and often unidentified in collections, both pinned specimens and those in alcohol from bycatch were examined. The two criteria for inclusion in this study were a collection locality within the 7 coastal southern California counties (San Diego, Orange, Ventura, Santa Barbara, Ventura, San Bernardino, and Riverside) and in decent enough condition to examine morphology, especially the wings. Some specimens used in this analysis are from outside this range (Appendix 1), being used as morphological controls as they were identified by trusted experts of this taxon (Behm, 2020, unpublished thesis). Ultimately, I was able to identify 190 specimens that met our criteria at the following institutions: Hasbrouck Insect Collection, Arizona State University (**ASUHIC**), the California Academy of Sciences in San Francisco (**CASENT**), the Essig Museum of Entomology, University of California, Berkeley (**EMEC**), the Santa Barbara Museum of Natural History (**SBMNH**), the Nat, San Diego Natural History Museum, San Diego (**SDNHM**), the Bohart Museum of Entomology, University of California, Davis (**UCBME**), and the UCSB Natural History Collections at the Vernon and Mary Cheadle Center for Biodiversity and Ecological Restoration, University of California, Santa Barbara (**UCSBIZC**).

2. **Specimens and Sampling**

The 190 specimens were assigned to 6 genera using the New World Ophioninae by David Wahl and Ian Gauld (2002). From there, 31 operational taxonomic units (OTUs) of Ophioninae were delineated based on morphological characters for each genus using known useful characters based on past literature (Cushman, 1947, Gauld, 1985, Gauld, 1988, Leblanc, 1989, Gauld & Wahl 2002, Schwarzfeld & Sperling, 2014, Schwarzfeld et al., 2016, and Rousse et al. 2016). These characters, and the delineation and diagnoses of each OTU, are discussed in detail in Behm et al. (2020, unpublished thesis). The 8 outgroup specimens of related ichneumonid subfamilies are the same as those in Rousse et al. (2016), including 1 Anomaloninae, 3 Banchinae, 4 Campopleginae, and 1 Cremastinae. The localities, dates of collection, and accession numbers of all material examined are summarized in Appendix 1.

In this study, 62 out of 87 of Rousse's taxa were examined. Taxa without both morphological and molecular data were excluded as they were not analyzed further in Rousse's study or included in his updated phylogeny. In addition, I excluded some of Rousse's taxa that did not have a physical specimen and were only analyzed using sequences available on GenBank.

3. **Creation of Phylogenetic Matrix**

Three morphological matrices were created for this study including: (1) taxa examined by Rousse (2016); (2) California taxa alone; and (3) a combination of both Rousse's and the California taxa. The morphological matrices were created using Mesquite 2.75 (Maddison et al., 2011). The matrices were exported as a nexus file to Notepad++ 7.8.4 (Ho, 2003) for editing and formatting.

The 62 morphological characters used to construct these matrices are the same as those from Rousse et al. (2016) and include 22 head, 15 mesosoma, 6 metasoma, 11 forewing, 3 hindwing, and 5 leg characters. Each of the morphological characters (Table 2-8) were investigated for all 248 individuals; 62 by Rousse and 189 from this study. Definitions for the characters and character states were not provided in Rousse et al. (2016). Because there was some overlap between the morphological characters used by both Rousse et al. (2016) and Gauld (1985) (see discussion), Gauld (1985)'s definitions were used for those characters. The rest of the characters were inferred using definitions from the Hymenoptera Ontology Portal (Yoder et al., 2010).

Table 31. Head characters used for both analyses, summarized from Rousse et al. (2016). ◆ indicates characters that are also represented in Gauld (1985).

Head Characters	States
Labial palp segmentation	• Four-segmented • Three-segmented
Maxillary palp segmentation ◆	• Five-segmented • Four-segmented
Shape of central segments of maxillary palps ◆	• Slender • Enlarged, Globose
Width of mandibles ◆	• Apically at least 0.5x as wide as basally • Apically 0.4–0.5x as wide as basally • Apically less than 0.4x as wide as basally
Torsion of mandibles ◆	• Teeth in a plane less than 5° from the main mandible plane • Teeth in a plane between 5–25° from the main mandible plane • Teeth in a plane between 25–50° from the main mandible plane • Teeth in a plane more than 50° from the main mandible plane
Presence of ventral mandible flange	• Absent • Present
Presence of basal swelling on mandible ◆	• Absent • Present
Presence of mid-longitudinal groove on mandible outer surface	• Absent • Present
Length of mandible upper tooth	• 1-1.5x longer than lower tooth • More than 1.5x longer than lower tooth • Shorter than lower tooth • Mandible unidentate
Bending of mandibular teeth	• Not bent • Strongly bent, teeth axis nearly perpendicular to main mandible axis
Malar space length	• Less than 0.4x basal width of mandible • At least 0.4x basal width of mandible

Shape of clypeus in profile	• Flat • Convex
Shape of ventral margin of clypeus	• In-turned/not differentiated • Impressed/outturned
Presence of median tooth on ventral margin of clypeus	• Absent • Present
Presence of clypeal groove	• Present • Absent
Presence of mid-longitudinal carina on frons	• Absent • Present
Length of antennae	• Shorter than forewing • Greater than or equal to forewing length
Relative length of first and second flagellomeres	• First is less than 1.6x the second • First is greater than or equal to 1.6x the second
Elongation of 20th flagellomere	• Less than 1.6x longer than wide • 1.6-2x longer than wide • Greater than 2x longer than wide
Ocelli size	• Median ocellus diameter less than 0.5x inter-ocular distance through median ocellus • Median ocellus diameter between 0.5-0.7x inter-ocular distance through median ocellus • Median ocellus diameter greater than 0.7x inter-ocular distance through median ocellus
Presence of strong depression between posterior ocelli and occipital carina	• Absent • Present
Completeness of occipital carina	• Complete • Shortly interrupted mid-dorsally • Totally absent dorsally, laterally absent or vestigial

Table 32. Mesosoma characters used for both analyses, summarized from Rousse et al. (2016). ● indicates a tribal synapomorphy defined by Rousse et al. (2016). ◆ indicates characters that are also represented in Gauld (1985).

Mesosoma Characters	**States**
Presence of latero-ventral projecting flange of propleuron	• Absent • Present
Occlusion of mesopleural spiracle ●◆	• Exposed • Partly to totally occluded
Presence/length of epicnemial carina	• Present, reaching above ventral corner of pronotum • Shortened or absent above ventral corner of pronotum
Presence of postero-ventral tubercle on mesopleuron	• Absent • Present
Presence and structure of mesopleural fovea ●◆	• Absent to distinct as an isolated pit • Present and extended into a longitudinal furrow
Completeness of postpectal carina ◆	• Complete • Partially to totally absent ventrally
Broadness of submetapleural carina	• Not distinctly broad • Enlarged into a broad flange anteriorly
Presence of notauli ◆	• Indistinct/vestigial • Distinct
Length of scutellum	• Less than 1.6x longer than basally wide • At least 1.6x longer than basally wide
Shape of hind margin of metanotum ◆	• Unspecialized • Swollen backwards
Swelling of propodeum	• Not swollen • Swollen
Elongation of propodeal spiracle ◆	• Less than 4x longer than wide • At least 4x longer than wide
Presence of anterior transverse carina of propodeum ●◆	• Complete • Partially absent • Totally absent

Presence of posterior transverse carina of propodeum ◆	• Complete • Partially absent • Totally absent
Presence of mid-longitudinal carina on propodeum ◆	• Present • Absent

Table 33. Metasoma characters used for both analyses, summarized from Rousse et al. (2016). ● indicates a tribal synapomorphy defined by Rousse et al. (2016). ◆ indicates characters that are also represented in Gauld (1985).

Metasoma Characters	States
Position of the spiracle of the first tergite ◆	• At or anterior to middle • Distinctly posterior to middle
Presence of the laterotergite of the first tergite ◆	• Present • Absent/Vestigial
Elongation of second tergite ◆	• Less than 3x longer than apically high • More than 3x longer than apically high
Presence of convex median area on anterior margin of the second tergite ◆	• Present • Absent
Presence/position of the thyridia on second tergite ●◆	• Close to anterior margin • Remote by more than their own length • Absent
Presence of the laterotergite of the second tergite ●◆	• Indistinct/folded inside • Pendant

Table 34. Forewing characters used for both analyses, summarized from Rousse et al. (2016). ● indicates a tribal synapomorphy defined by Rousse et al. (2016). ◆ indicates characters that are also represented in Gauld (1985).

Forewing Characters	States
Presence of adventitious vein	• Absent • Present
Position of 2 m-cu vein	• Distal/opposite to rs-m • Basal to rs-m
Presence and length of the glabrous area in the discoido-submarginal cell ◆	• Absent • Present but reduced, not reaching beyond anterior third of Rs+2m • Present, extending beyond anterior third of Rs+2m
Presence of proximal sclerite ◆	• Absent • Present
Presence of central sclerite ◆	• Absent • Present
Shape of 1 m-cu ●◆	• Angled • Curved or without sharp angle
Presence of the ramellus ●◆	• Absent • Present
Shape and length of pterostigma ◆	• Triangular, apically abruptly narrowed • Elongate/narrow, evenly tapered toward apex • Linear
Shape of Rs+2r near pterostigma ◆	• Straight or curved • Distinctly angled
Thickness of Rs+2r near pterostigma ◆	• Not thickened • Rs+2r at least 2x thicker anteriorly than centrally
Central shape of Rs+2r ◆	• Straight • Slightly sinuate • Strongly sinuate or bowed

Table 35. Hindwing characters used for both analyses, summarized from Rousse et al. (2016). ◆ indicates characters that are also represented in Gauld (1985).

Hindwing Characters	States
Shape of vein Rs ◆	• Straight/barely curved • Distinctly curved
Number of distal hamuli ◆	• 5 or less • 6 to 9 • 10 or greater
Interception of Cu and cu-a ◆	• At or above middle • Below middle

Table 36. Leg characters used for both analyses, summarized from Rousse et al. (2016). ◆ indicates characters that are also represented in Gauld (1985).

Leg Characters	States
Presence and length of the membranous flange on the fore tibial spur ◆	• Present, at least 0.3x length of spur • Present, less than 0.3x length of spur • Absent
Specialization of the apical edge of the hind and mid trochantelli ◆	• Unspecialized • Expanded into broad flange or sharp tooth
Shape of the cross section of the hind tibial spurs ◆	• Flattened • Cylindrical
Shape of the hind tarsal claws ◆	• Evenly curved/not elongate • Straight/elongate
Pectination of female outer claw	• Greater than 10 pectinae • At most 10 pectinae • Not pectinate

4. **Bayesian Analysis**

Bayesian analyses of three morphological matrices were completed using MrBayes 3.2.7a (Huelsenbeck and Ronquist, 2001) via CIPRES Science Gateway V 3.3 (Miller et al., 2010). The parameters were almost identical to those used in Rousse et al. (2016), however, I partitioned the matrices into three partitions based on the number of character states per character (2, 3, or 4), whereas Rousse had them undivided. The resulting phylogenetic trees (.tre files) and posterior probability values (pp) from the Bayesian analysis were then exported to FigTree 1.4.4 (Rambaut, 2006) and TreeGraph 2.15.0-887 beta (Stöver and Müller 2010). These programs were used to root to the defined outgroup, ladderize, collapse nodes to support values, and aesthetically edit the trees. All resulting trees are available in the Supplementary Materials.

Table 37. Parameters used for analysis of the three matrices (adaptation of Rousse, California taxa, and combined taxa) in Mr.Bayes.

Parameter Name	Used
Partitions	Two Character States Three Character States Four Character States
Model	Markov k model
Rate/ Range of distribution	gamma, Γ-shaped
Number of generations	100,000,000 generations
Sampling frequency	Every 1,000 generations
Cutoff value to stop (stopval)	0.005 average standard deviation
Number of runs	2
Fraction of samples to discard as burnin	0.25

E. Results

The resulting cladograms from the analyses discussed above were simplified further to collapse the taxa to the generic level for clarity, and they are displayed and discussed below. Because there is no consensus as to which support value represents the best tree hypothesis, the results from trees with nodes collapsed to 0.9 and 0.7 are both discussed. Cladograms for 0.7pp are available in the Supplementary Materials.

The outgroup specimens for all trees are the non-Ophionine taxa used in Rousse et. al (2016). The cladogram of combined taxa exhibits lower phylogenetic resolution than the separate Rousse and California cladograms, and most genera from California do not fit within Rousse's tribal clades. California *Enicospilini*, which previously formed a monophyletic clade, became part of a large polytomy, or unresolved clade, in the combined analysis.

1. **Morphology for only Rousse et al. (2016) taxa**

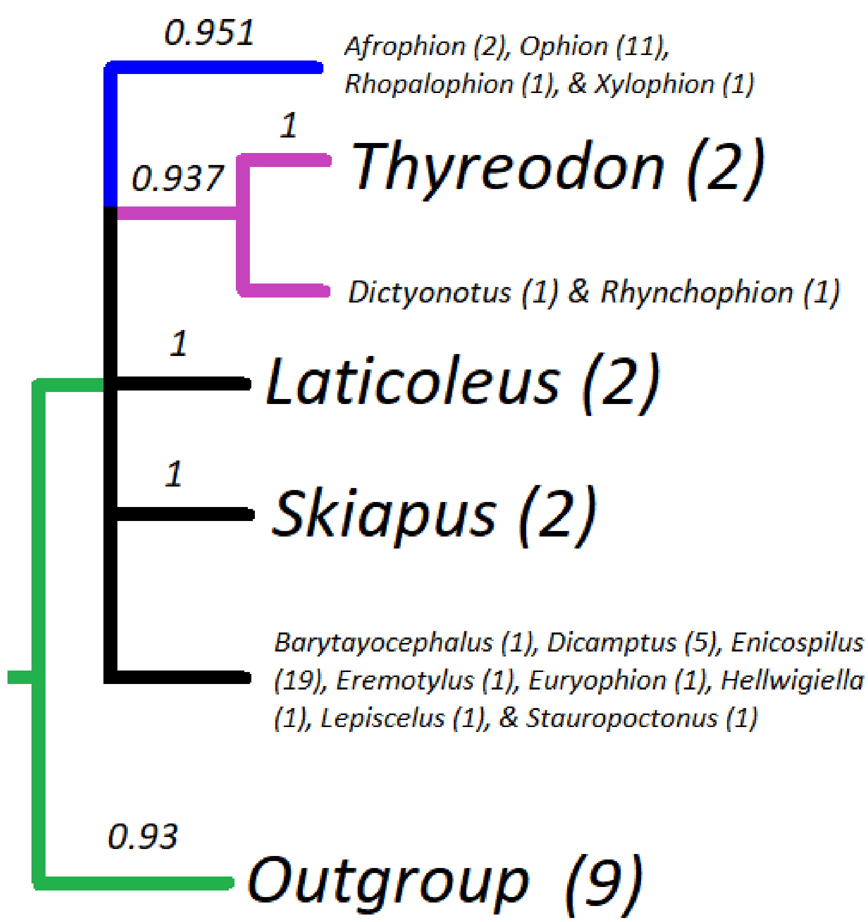

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Figure 64. Simplified cladogram resulting from analysis of morphological characters in Rousse et al. (2016) collapsed to 0.9 pp. Posterior probability values for the individual nodes are listed at the bases of branches. Number of taxa within each clade is listed in parentheses to the right of the name. Green branches represent the outgroup, purple represents Thyreodonini, blue represents Ophionini, and black represents genera without tribal placement. Complete cladograms are available in the Supplementary Materials.

Ophioninae, including *Skiapus*, is monophyletic at all support values. When the cladogram nodes are collapsed to 0.9 pp (Fig. 1), *Thyreodon* (1 pp), *Skiapus* (1 pp), and *Laticoleus* (1 pp) are the only monophyletic genera. Rousse's Ophionini clade is supported as monophyletic (0.951 pp). Thyreodonini also resolves as a monophyletic clade (0.931 pp), but Enicospilini does not resolve into a monophyletic clade. All of the genera not listed above lack tribal resolution and remain unplaced.

When the cladogram nodes are collapsed to the lower support value 0.7 pp (Supplementary Materials), the same genera as at 0.9 pp are monophyletic. *Eremotylus* becomes a sister group to the Ophionini (0.864 pp), *Euryophion* becomes a sister group to Thyreodonini (0.725 pp), and *Hellwigiella* forms a sister group to Thyreodonini + *Euryophion* (0.707 pp). Enicospilini still lacks support as a distinct clade.

2. **Cladogram Based on Morphological Analysis of California Plus Control Taxa**

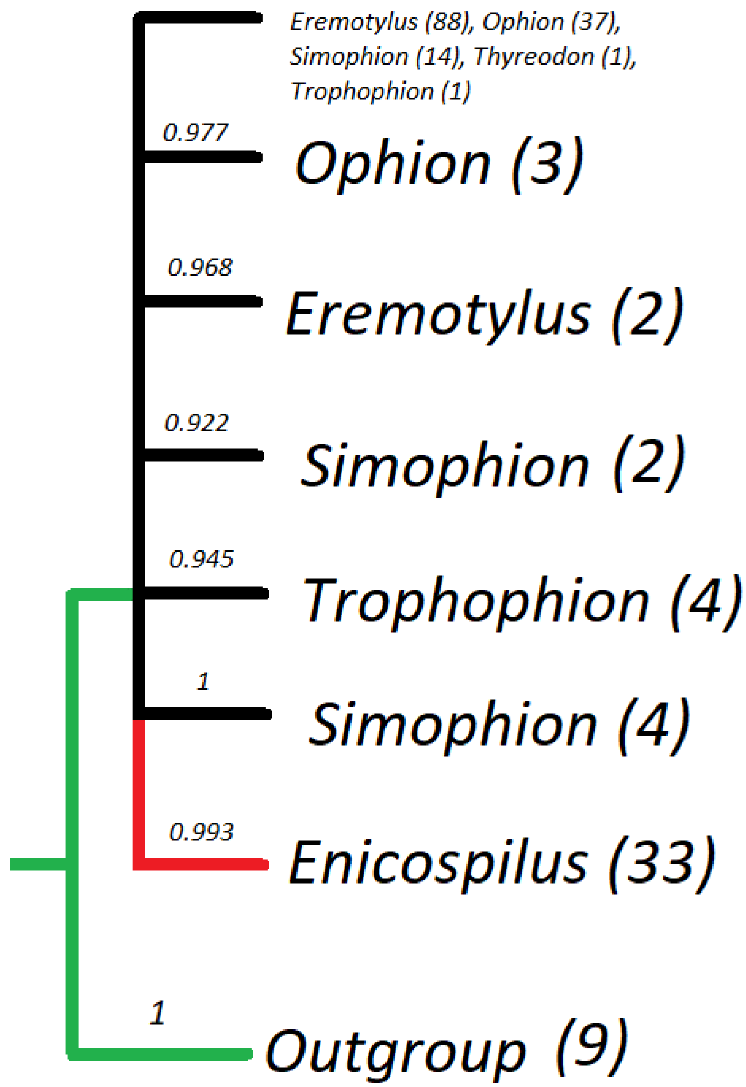

Figure 65. Simplified cladogram of the California taxa, collapsed to 0.9 pp. Support values for the nodes are listed at the bases of their branches. Number of taxa within a clade is listed in parentheses to the right of the name. Green branches represent the outgroup, red represents Enicospilini, and black represents genera without tribal placement. Complete cladograms are available in the Supplementary Materials.

Ophioninae, including *Skiapus*, is monophyletic at all support values. When the cladogram nodes are collapsed to 0.9 pp (Fig. 2), our representatives of Ophionini (*Ophion*) are not recovered as a distinct clade. Only Enicospilini (0.993 pp), represented by *Enicospilus*, is supported as a distinct clade. When the cladogram nodes are collapsed to the lower support value of 0.7 (Supplementary Materials) both our Ophionini (0.881 pp) and

Enicospilini are supported as distinct, monophyletic clades. The other genera remain unplaceable into clades.

3. **Combined Morphology**

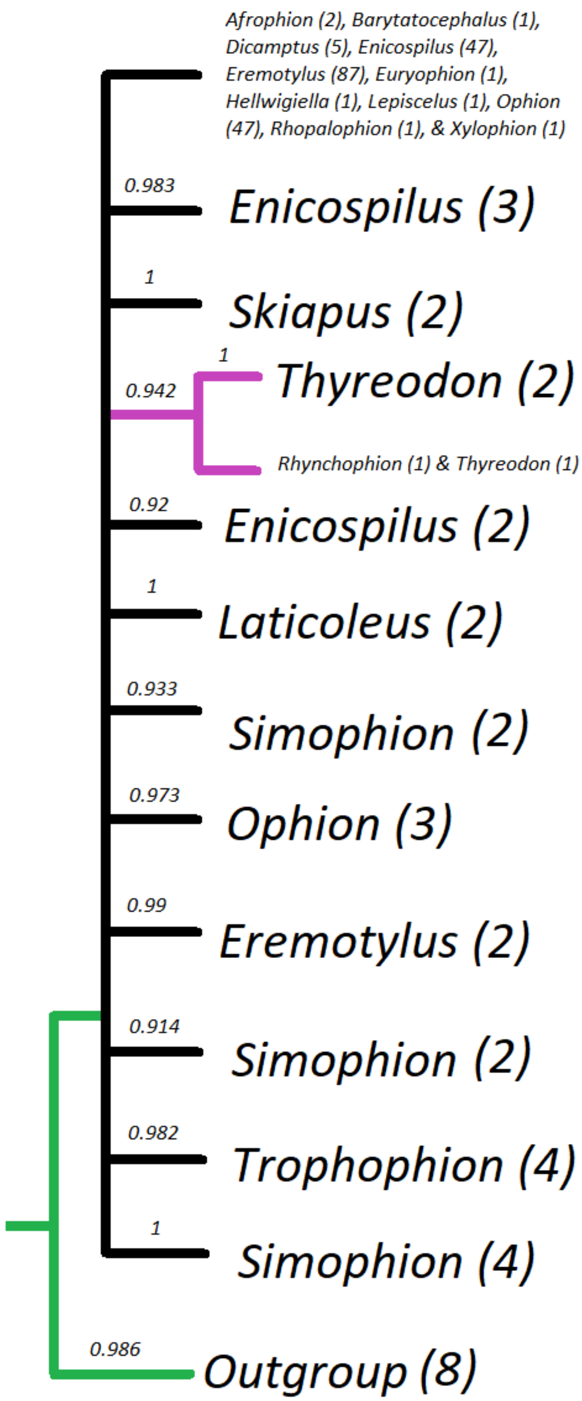

Figure 66. Simplified cladogram of the taxa included in this study and Rousse et al. (2016), collapsed to 0.9 pp. Support values for nodes are listed at the bases of branches. Number of taxa within each clade is listed in parentheses to the right of the name. Green branches represent the outgroup, purple represents Thyreodonini, and black represents genera without tribal placement. Complete cladograms are available in the Supplementary Materials.

Ophioninae, including *Skiapus*, is monophyletic at all support values. When the cladogram nodes are collapsed to 0.9 pp (Fig. 3) and 0.7 pp (Supplementary Materials), the only monophyletic genera are *Laticoleus* (1 pp) and *Skiapus* (1pp). Although Thyreodonini comes out as monophyletic (0.942 pp), the genus *Thyreodon* is now polyphyletic, coming out additionally with *Ryhnchophion.* Ophionini and Enicospilini do not resolve into monophyletic clades.

4. **Morphological Synapomorphies**

Of the 62 characters in the morphological dataset of Rousse et al. (2016), 7 are highlighted by Rousse as the synapomorphies that delineate genera into the three tribes. For Ophionini these are: the presence of a ramellus, shape of the 1-mcu vein, mesopleural furrow presence, and basal position of thyridia. For Thyreodonini these are: shape of the laterotergite of second tergite and the lack of an anterior transverse carina on the propodeum. Enicospilini is only delineated by the occlusion of the spiracular sclerite by the corner of the pronotum. A summary of the tribes, genera, and their geographic distribution is available in Table 30. The examination of these 7 characters in California taxa is discussed below and a summary of each California genus is provided in Table 38.

Synapomorphies of Ophionini:

1. **Presence of Ramellus.** All specimens of *Ophion* collected thus far from California have a ramellus, although its length, orientation, and shape can vary across specimens within morphospecies. However, New World specimens of *Eremotylus* also are recorded to possess a ramellus reduced to a small protuberance (Gauld & Wahl 2002), and a reduced ramellus is found in some of the California *Simophion.*

2. **Vein 1 m-cu.** This character is difficult to distinguish for California specimens because there is no clear definition or angle for the two states. Some *Ophion* possess a clearly angled 1 m-cu (Fig. 4 A-B), but most specimens have an intermediate form that is not as clearly angled or curved (Fig. 4 C-D), California *Enicospilus* (Fig. 4 E-F) clearly and consistently have a curved 1m-cu. *Eremotylus, Simophion,* and *Trophophion* are quite variable, primarily possessing intermediate forms of the 1 m-cu. Because there is not a code for an intermediate state for that character in Rousse's character matrix, specimens with intermediate states were coded as if they were curved.

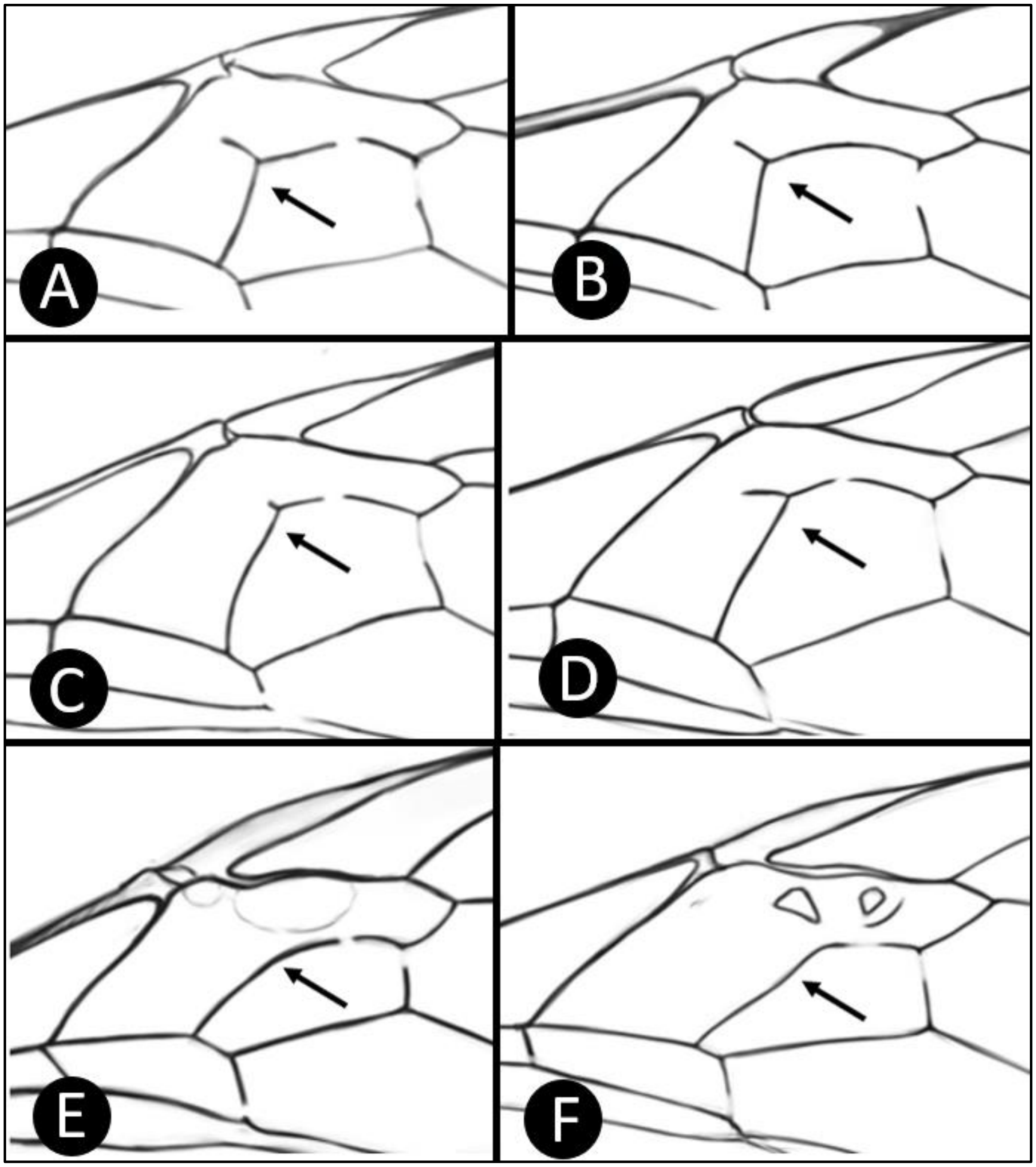

Figure 67. Two morphospecies of *Ophion* from California, **A** *Ophion* sp.RBoph0003 and **B** *Ophion* sp.RBoph007, that possess an angled 1 m-cu. Two morphospecies of *Ophion* from California, **C** *Ophion* sp.RBoph005 and **D** *Ophion* sp.RBoph027, that possess an intermediate form between an angled and curved 1 m-cu. Two species of California *Enicospilus*, **E** *Enicospilus texanus* and **F** *Enicospilus purgatus*, that possess a curved 1 m-cu.

3. **Mesoplueral Fovea as Furrow.** Although this character is found in some California *Ophion* (Fig. 5A), it is faint to undetectable in others (Fig. 5B). Many California specimens of *Eremotylus* and some specimens of

Simophion also possess this character (Fig. 5C), although it is usually faint (Fig. 5D).

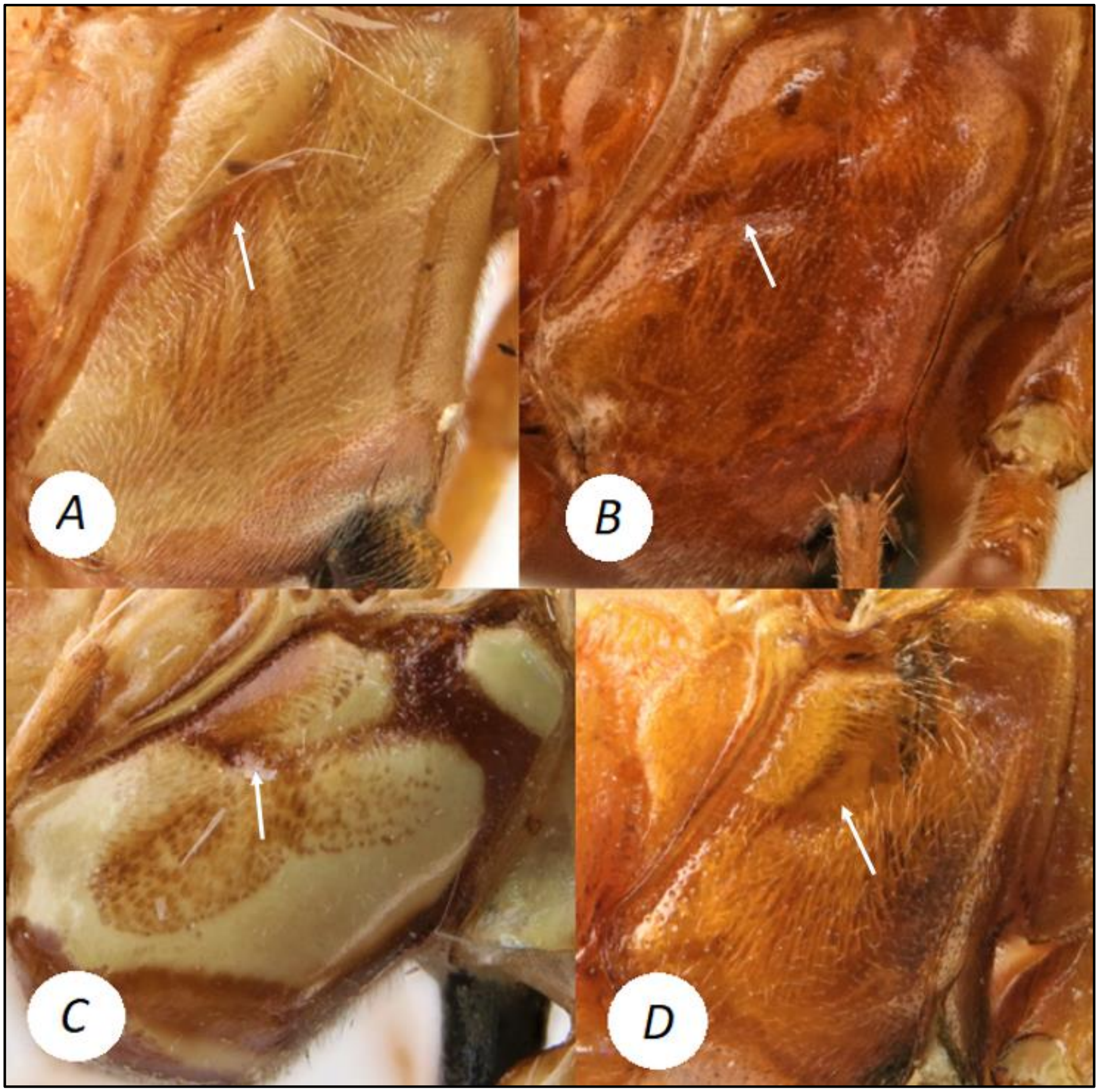

Figure 68. Distinct mesopleural furrow of **A** *Ophion* sp. RBoph027and **C** *Eremotylus* sp. RBoph013. Faint mesoplueral furrow of **B** *Ophion* sp. RBoph004 and **D** *Eremotylus* sp. RBoph025.

4. **Thyridia Close to the Base of the Second Tergite.** This character is present in all California *Ophion* collected to date and is also found within all specimens of *Eremotylus* (Fig. 6C), *Trophophion*, and *Simophion* (Fig.

8B). California *Enicospilus'* thyridium is separated from the base of the second tergite by more than its own length (Fig. 8A), consistent with the characteristics of this genus.

Synapomorphies of Thyreodonini:

5. **Laterotergite 2 pendant.** This character is found in some specimens of the genera *Eremotylus* (Fig. 6C), *Simophion* (Fig. 6B), and *Enicospilus* (Fig. 6A) from California.

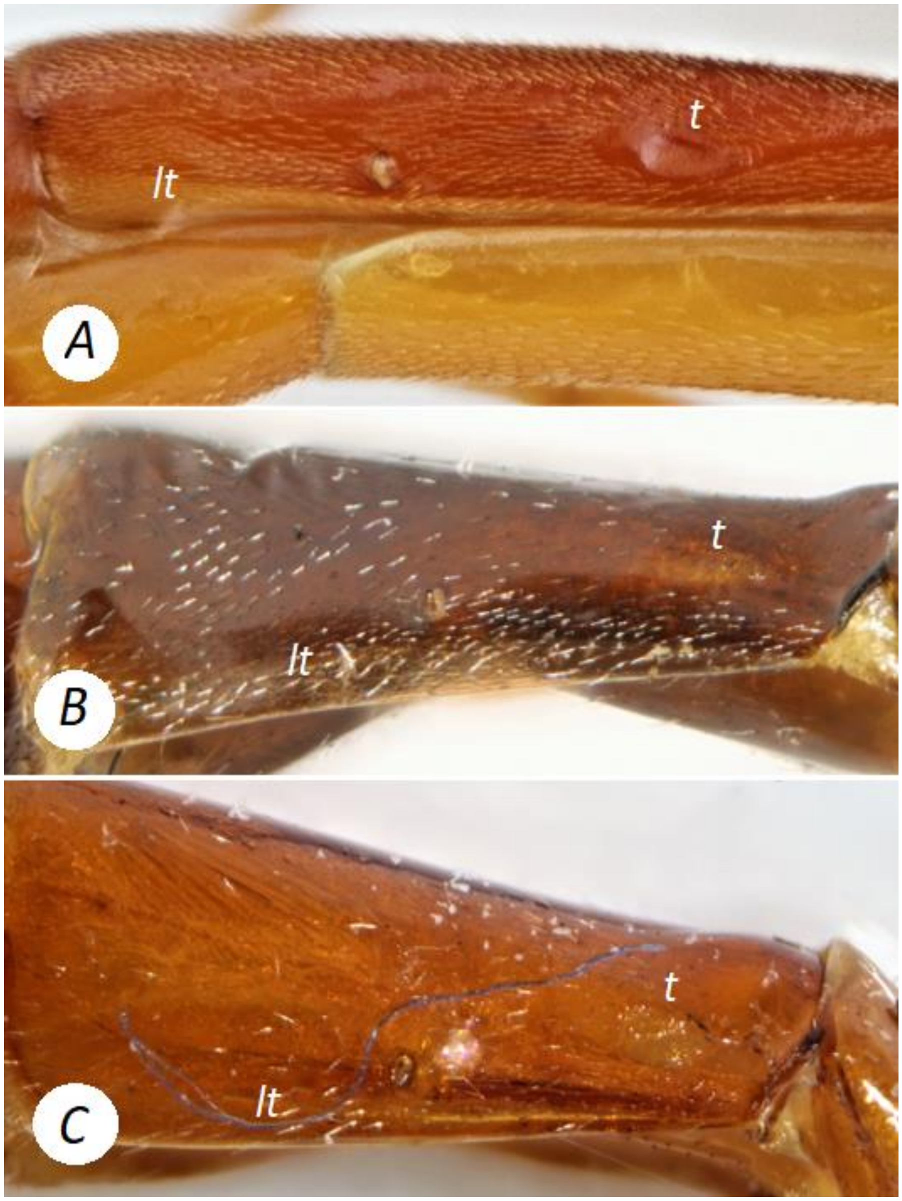

Figure 69. Second tergite of **A** *Enicospilus texanus*, ***B*** *Simophion excarinatus*, and **C** *Eremotylus* sp.RBoph011, showing a pendant laterotergite (lt). The thyridia (t) is close to the base in *Simophion* and *Eremotylus* but farther than its own length in *Enicospilus.*

6. **Propodeum with anterior transverse carina absent.** This character is found in specimens of all California genera except *Enicospilus* (Figs 7-8).

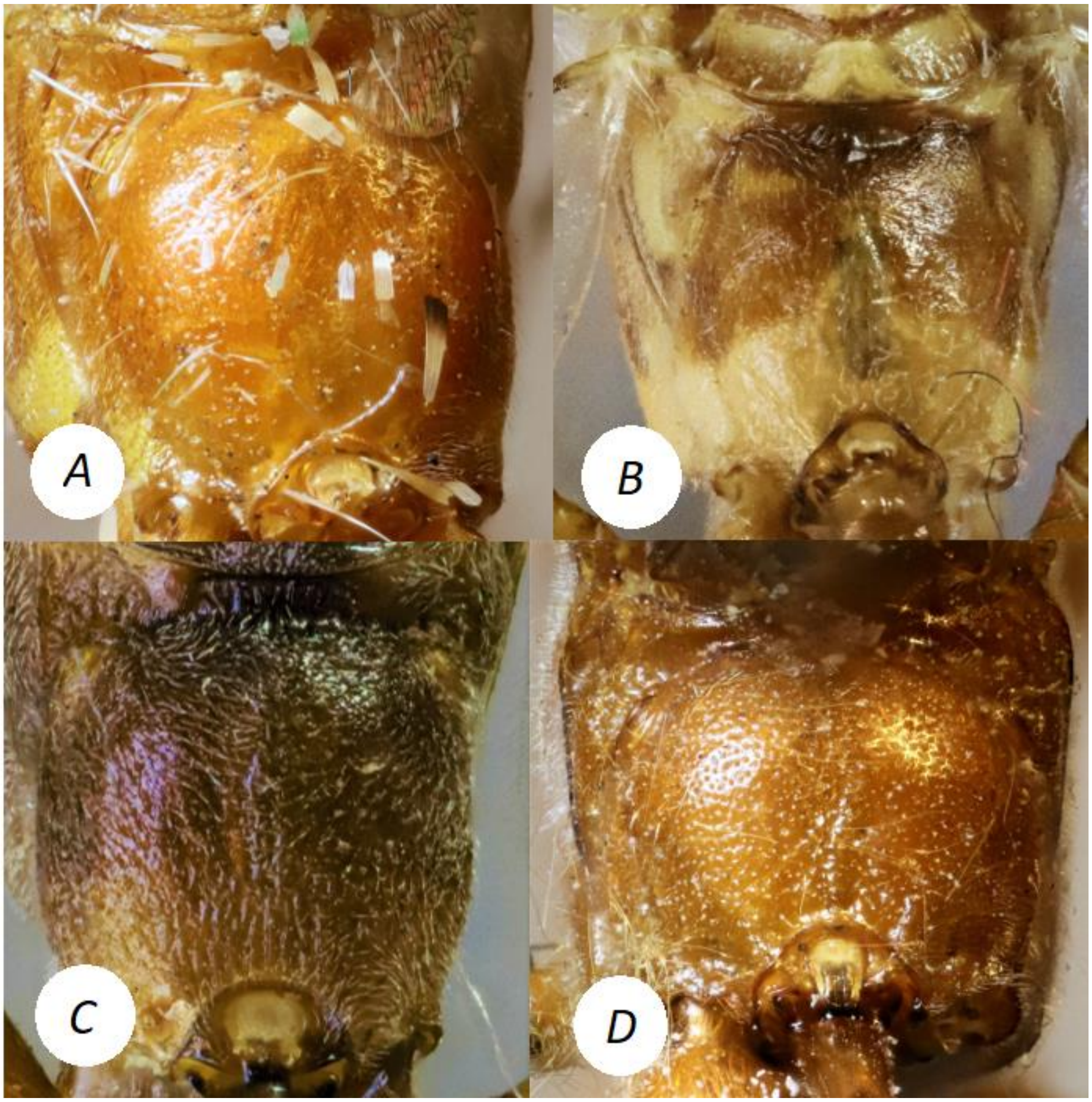

Figure 70. Propodeal sculpture of California specimens **A** *Eremotylus,* **B** *Ophion*, **C** *Simophion*, and **D** *Trophophion***,** demonstrating the lack of an anterior transverse carina.

Figure 71. Propodeal sculpture of *Ophion* sp.RBoph005 demonstrating the presence of an anterior transverse carina.

Synapomorphy of Enicospilini:

7**. Spiracular Sclerite of Mesopleuron is Partially to Totally Occluded by the Expansion of the Upper Corner of the Pronotum.** Although this character is defined as the single synapomorphy of Enicospilini, it is present in almost every Ophioninae specimen from California, regardless of genus (Fig. 9).

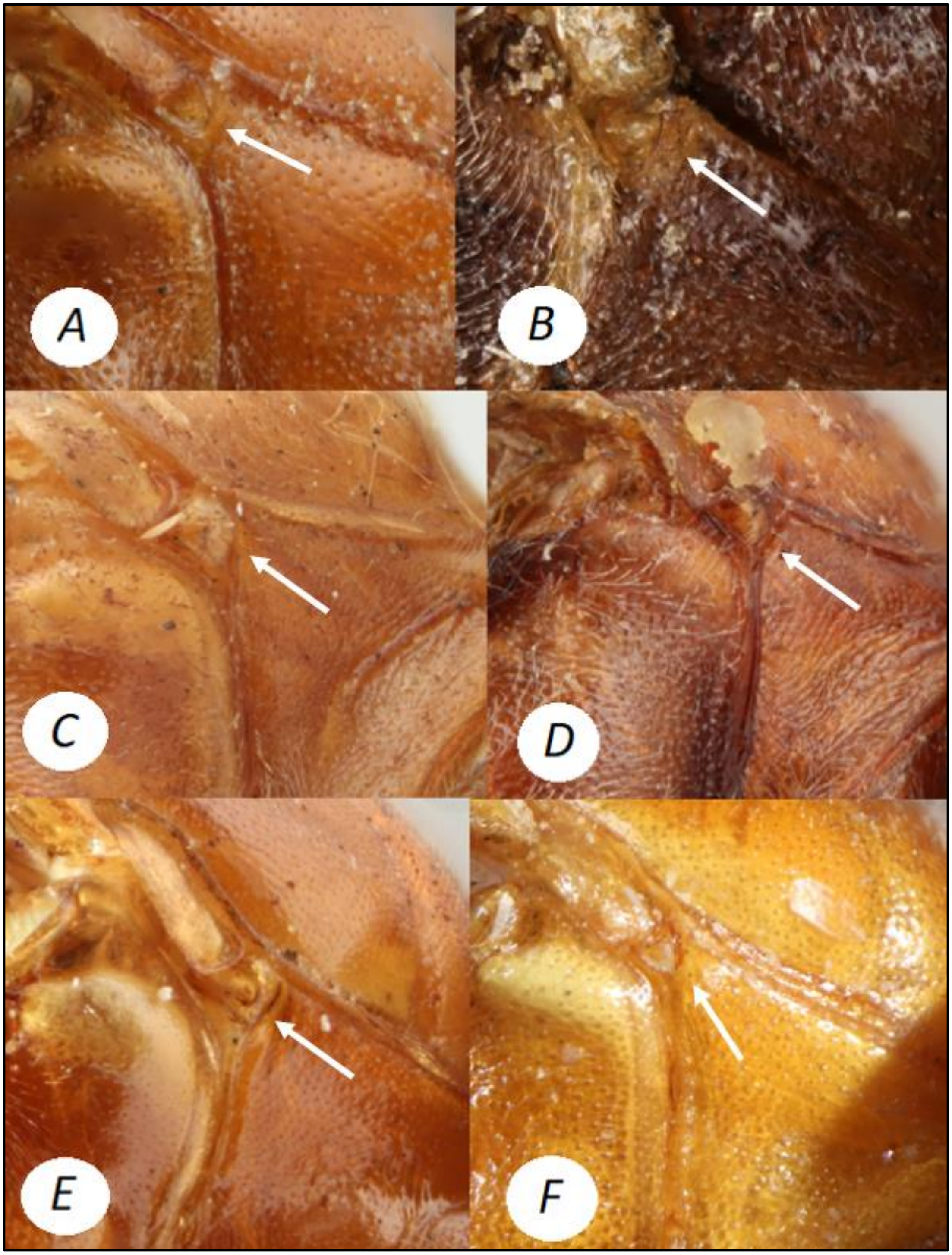

Figure 72. Spiracle of mesopleuron partly to totally occluded by the expansion of the upper corner of the pronotum in **A** *Trophophion,tenuiceps*, **B** *Simophion excarinatus*, **C** *Enicospilus americanus*, **D** *Enicospilus texanus*, **E** *Ophion* sp. RBoph004, and **F** *Eremotylus* sp. RBoph019.

Table 38. Summary of the states of the tribal synapomorphies, as defined in Rousse et al. (2016), for California genera. X represents the presence of the character and blank represents the absence.

Synapomorphy	Rousse (2016)	CA Enicospilus	CA Eremotylus	CA Ophion	CA Simophion	CA Trophophion
Ramellus present	Ophionini		X	X	X	
Always clearly angled 1 m-cu						
Mesopleural furrow			X	X	X	
Thyridia close to base			X	X	X	X
Pendant laterotergite	Thyreodonini	X	X		X	
Anterior transverse carina absent			X	X	X	X
Sclerite occluded	Enicospilini	X	X	X	X	X

F. Discussion

1. **Overview**

As more species of Ophioninae are discovered, homoplasy and morphological variation will make it increasingly difficult to classify members of this subfamily using morphology. Higher level classification, such as genus-groups and tribes, is especially problematic. In the case of California, the morphological variation invalidates the current tribal definitions of Rousse et al. (2016). Not only did California taxa not possess the proposed synapomorphies, but also many genera had synapomorphies for tribes they did not belong to.

2. **Weight of Morphology on Ophionine Tribal Limits**

Until recently, the classification of Ophioninae was based on entirely morphological analyses. The current tribal definitions are solely defined by morphology, although they have been revised since their creation to account for additional variation. Despite this, the morphological synapomorphies are not congruent with the variation observed within this subfamily. Even with the addition of molecular data, Rousse et al. (2016) found that only the delineation of the Ophionini was strengthened by morphological data. Rousse (2016) believed that Thyreodonini's morphological characters may not be sufficient for tribal assignment because of widespread homoplasy. He also suspected that morphological characters may not have helped delineate the Enicospilini because of the aberrant morphology of taxa like *Skiapus*.

3. **Morphological Characters**

Most (⅔) of the morphological characters used by Rousse et al. (2016) were those used by Gauld (1985) for genus-group delineations. Gauld suggested that morphological characters alone would be insufficient in delineating Ophionine groups, especially in regions with high endemism with potentially extensive homoplasy. These two studies, however, used somewhat different characters in their analysis. Of the characters used by Gauld (1985), 21 were not used in Rousse et al. (2016), but 19 additional characters were included in Rousse et al. (2016). The characters that Gauld used to delineate his genus-groups were analyzed using parsimony methods to judge their phylogenetic value and effectiveness in delineation. Gauld removed four of his characters and four character-states that he deemed to have little phylogenetic value. Rousse et al. (2016) re-incorporated two characters that were excluded by Gauld (shape of hindwing Rs vein, mandible tooth length where the upper tooth is reduced). Although those two characters do not necessarily apply to California taxa, parsimony analysis on the 19 characters added by Rousse et al. (2016) would have helped establish the value and effectiveness of these additional characters in phylogeny construction.

4. **Inadequacy in the Delineation of Tribes with the Addition of California Taxa**

The phylogeny constructed with the taxa from Rousse (2016) (Fig. 1) did not resolve genera in Ophioninae, except for *Thyreodon*, *Laticoleus,* and *Skiapus*. Despite this lack of generic resolution, Ophionini and Thyreodonini, but not the Enicospilini, were supported as monophyletic clades at all support values. Morphology alone was inadequate for phylogenetic reconstructions of California taxa (Fig. 2). The *Ophionini* and *Enicospilini* were resolved as monophyletic clades, but the genera *Eremotylus, Simophion,* and *Trophophion* were not. Because Rousse used one specimen of *Eremotylus* and no specimens of the latter two genera in his analyses, it is not currently possible to compare their phylogenetic placement between the two studies.

With the addition of data on California taxa to Rousse's dataset, the combined tree loses resolution into clear groups (Fig. 3). The only genera that are still monophyletic are *Skiapus* and *Laticoleus*, and the genera of Ophionini and Enicospilini are now parts of a large polytomy. The tribes Ophionini and Enicospilini, although revised in Rousse et al. (2016), do not cleanly map onto identified groups when California Ophioninae are added. Genera in the tribe Thyreodonini are not found in California therefore Thyreodonini is unchanged by the addition of California taxa.

As discussed above, California specimens do not fit previously proposed tribal synapomorphies. Although Enicospilini's single tribal synapomorphy is the occluded mesopleural sclerite, nearly all California specimens regardless of genus possessed this character (Fig. 9). The two tribal synapomorphies for Thyreodonini are also found in several California genera despite the absence of this tribe in this region (Fig. 6-8). The synapomorphies identified previously for Ophionini do not hold for California specimens, because they are found in several other genera and specimens, which sometimes exhibit intermediate forms (Figures 4-6). The disconnect between Rousse's synapomorphies and my analyses is not surprising because Gauld (1985) warned that homoplasy is a common feature in the Ophioninae. He suggests that a strict phylogenetic classification for this group is not possible based on morphology alone, unless all genera are lumped together or a multiplicity of new genera are erected.

5. **Future Directions**

The delineation of tribes in Ophioninae based on synapomorphies should be abandoned at the present time. I recommend a re-examination of Ophionine tribes, prioritizing molecular methods and worldwide collections. If morphology is to be used for classification, the characters should be analyzed to support their phylogenetic value using parsimony methods. Until then, the higher-level classification of Ophioninae should be based on Gauld's (1985) genus-group concepts rather than on a tribal classification system.

Acknowledgements

I would like to thank the curators of the collections listed above for giving me the opportunity to study their specimens. I especially thank Dr. Pascal Rousse for providing the sequence data and nexus files from his 2016 paper. I thank Paul and Sandy Russell, Ken Schneider, Elaine Tan, Dr. Matthew Gimmel, and Zach Brown for collecting fresh California Ophioninae. I thank our undergraduate interns Lina Solomon, Christina Zhu, and Madison Clarke for their hard work taking photographs and archiving data from the specimens analyzed in this study. I also thank Madison Clarke for the wing illustrations used in this paper. I thank Jessica Gillung for her help and instruction in using Mr.Bayes. I thank Dr. Hillary Young, Dr. Katja Seltmann, and Dr. Scott Cooper for their guidance and for reviewing and making suggestions for this manuscript. Funding for this project was provided, in part, by the Institute of Museum and Library Services (MA-30-16-0387-16) and the UC Santa Barbara Associated Student Coastal Fund Program.

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Appendix 1

Catalog Number	**Genus**	**Species**	**Sex**	**Collection Date** (dd-mmm-yyyy)	**State**	**Region**
UCBMEP0272858	*Trophophion*	*tenuiceps*	female	09-004-1963	CA	San Diego County
EMEC1215760	*Trophophion*	sp.RBoph009	female	13-004-1958	CA	San Bernardino County
UCBMEP0272857	*Trophophion*	*tenuiceps*	male	16--004-1938	CA	Riverside County
EMEC1215762	*Trophophion*	sp.RBoph009	male	13-004-1958	CA	San Bernardino County
UCSB-IZC00032707	*Trophophion*	sp.RBoph030		09-006-1938	CA	Tuolumne County
UCSB-IZC00025354	*Eremotylus*	sp.RBoph010	female	13-006-1964	CA	Los Angeles County
EMEC1215666	*Eremotylus*	sp.RBoph010	female	23-004-1966	CA	Santa Barbara County
CASENT8423001	*Eremotylus*	sp.RBoph010	female	17-006-1928	CA	San Bernardino County
SDNHM098277	*Eremotylus*	sp.RBoph010	female	04-006-1928	CA	San Diego County

UCRCENT509724	*Eremotylus*	sp.RBoph010	female	13-007-1950	CA	Upper Santa Ana River
SBMNHENT0113753	*Eremotylus*	sp.RBoph011	male	08-007-1977	CA	Santa Barbara County
CASENT8423009	*Eremotylus*	sp.RBoph013	female	00-004-1959	CA	San Bernardino County
EMEC1215675	*Eremotylus*	sp.RBoph013	female	28-005-1956	CA	San Bernardino County
EMEC1215766	*Eremotylus*	sp.RBoph013	female	01-005-1956	CA	San Bernardino County
EMEC1215772	*Eremotylus*	sp.RBoph013	female	16-004-1958	CA	Riverside County
EMEC1215660	*Eremotylus*	sp.RBoph017	male	25-004-1952	CA	Riverside County
UCRCENT509664	*Eremotylus*	sp.RBoph018	female	20-004-1968	CA	Riverside County
UCRCENT509660	*Eremotylus*	sp.RBoph018	female	27-004-1968	CA	San Bernardino County
CASENT8423005	*Eremotylus*	sp.RBoph018	female	11-002-1961	CA	San Bernardino County
UCRCENT509665	*Eremotylus*	sp.RBoph018	female	27-004-1968	CA	San Bernardino County
UCSB-IZC00033989	*Eremotylus*	sp.RBoph018	female	14-004-1985	CA	San Bernardino County
UCSB-IZC00034009	*Eremotylus*	sp.RBoph018	female	14-004-1985	CA	San Bernardino County
UCRCENT509662	*Eremotylus*	sp.RBoph019	female	27-002-1968	CA	San Bernardino

						County
UCRCENT509673	*Eremotylus*	sp.RBoph019	female	23-004-1985	CA	Riverside County
UCBMEP0272851	*Eremotylus*	sp.RBoph019	female	18-004-1957	CA	San Diego County
UCBMEP0272847	*Eremotylus*	sp.RBoph019	female	24-004-1963	CA	Riverside County
EMEC1215680	*Eremotylus*	sp.RBoph021	female	10-011-1955	CA	San Bernardino County
EMEC1215747	*Eremotylus*	sp.RBoph021	female	11-011-1955	CA	San Bernardino County
UCRCENT509677	*Simophion*	sp.RBoph029	male	16-011-1963	CA	Riverside County
UCSB-IZC00034006	*Eremotylus*	sp.RBoph022	female	20-003-1975	CA	San Bernardino County
UCBMEP0272839	*Eremotylus*	*subfuliginosus*	female	22-004-1951	CA	San Diego County
UCBMEP0272843	*Eremotylus*	*subfuliginosus*	female	23-004-1951	CA	San Diego County
UCBMEP0272842	*Eremotylus*	*subfuliginosus*	female	23-004-1951	CA	San Diego County
UCBMEP0272841	*Eremotylus*	*subfuliginosus*	female	23-004-1951	CA	San Diego County
UCBMEP0272840	*Eremotylus*	*subfuliginosus*	female	23-004-1951	CA	San Diego County
UCRCENT509534	*Simophion*	sp.RBoph029	male	12-004-1974	CA	Los Angeles County
UCRCENT509678	*Simophion*	sp.RBoph029	male	27-002-1972	CA	San Bernardino County

CASENT8423039	*Enicospilus*	*americanus*	female	00-011-1925	CA	Alameda County
CASENT8423041	*Enicospilus*	*texanus*	female	19-006-1929	CA	Tulare County
CASENT8423042	*Enicospilus*	*texanus*	female	10-004-1937	AZ	Pima County
UCBMEP0272800	*Enicospilus*	*flavostigma*	female	26-009-1947	CA	Yolo County
SDNHM098255	*Enicospilus*	*texanus*	male	19-005-1939	CA	San Diego County
CASENT8423044	*Enicospilus*	*texanus*	female	04-005-1968	CA	San Bernardino County
CASENT8423045	*Enicospilus*	*texanus*	male	05-005-1987	CA	San Bernardino County
UCRCENT509669	*Eremotylus*	*sp.RBoph012*	female	27-005-1968	CA	San Bernardino County
UCRCENT509668	*Eremotylus*	sp.RBoph012	female	11-004-1969	CA	Riverside County
UCSB-IZC00033985	*Eremotylus*	sp.RBoph012	female	13-005-1978	CA	San Diego County
CASENT8423013	*Eremotylus*	sp.RBoph012	female	29-003-2001	CA	Riverside County
CASENT8423012	*Eremotylus*	sp.RBoph012	female	29-003-2001	CA	Riverside County
EMEC1215670	*Eremotylus*	sp.RBoph026	female	30-003-1958	CA	Riverside County
EMEC1215770	*Eremotylus*	sp.RBoph026	female	01-005-1956	CA	San Bernardino County
EMEC1215692	*Eremotylus*	sp.RBoph026	male	01-005-1968	CA	Los Angeles County

CASENT8423004	*Eremotylus*	sp.RBoph026	female	04-005-1974	CA	San Bernardino County
UCRCENT509620	*Eremotylus*	sp.RBoph025	female	16-005-2003	CA	San Bernardino County
UCRCENT509619	*Eremotylus*	sp.RBoph025	female	16-005-2003	CA	San Bernardino County
EMEC1215732	*Eremotylus*	sp.RBoph025	female	29-004-1956	CA	San Bernardino County
UCRCENT509666	*Eremotylus*	sp.RBoph025	female	07-004-1989	CA	Riverside County
SDNHM098269	*Eremotylus*	sp.RBoph023	male	12-006-1978	CA	San Diego County
UCBMEP0272850	*Eremotylus*	sp.RBoph023	female	24-004-1978	CA	San Bernardino County
UCBMEP0272844	*Eremotylus*	sp.RBoph023	female	24-004-1978	CA	San Bernardino County
SDNHM098259	*Eremotylus*	sp.RBoph023	male	12-006-1978	CA	San Diego County
SDNHM098239	*Enicospilus*	*glabratus*	male	18-008-1976	CA	San Diego County
SDNHM098256	*Enicospilus*	*americanus*	male	10-005-1996	CA	San Diego County
SDNHM098218	*Enicospilus*	*americanus*	female	29-005-1994	CA	San Diego County
UCBMEP0272860	*Enicospilus*	*glabratus*	female	23-011-1959	CA	San Diego County
UCBMEP0272861	*Enicospilus*	*glabratus*	female	18-006-1965	CA	Santa Barbara County

CASENT8423047	*Simophion*	*excarinatus*	female	18-003-1978	CA	San Bernardino County
UCRCENT509535	*Simophion*	*excarinatus*	female	09-003-1979	CA	Riverside County
UCSB-IZC00031163	*Simophion*	sp.RBoph029	male	02-006-1962	AZ	Maricopa County
CASENT8423048	*Simophion*	*excarinatus*	female	18-003-1978	CA	San Bernardino County
UCSB-IZC00031102	*Simophion*	sp.RBoph029	male	04-008-1966	CA	
UCRCENT509676	*Simophion*	*excarinatus*	female	23-002-1964	CA	Riverside County
CASENT8423008	*Simophion*	*excarinatus*	female	18-003-1978	CA	San Bernardino County
EMEC1215751	*Simophion*	*excarinatus*	female	25-003-1966	CA	San Bernardino County
UCSB-IZC00033142	*Simophion*	sp.RBoph029	male	22-002-1963	CA	San Bernardino County
UCRCENT509533	*Simophion*	*excarinatus*	female	09-003-1964	CA	Riverside County
UCRCENT509670	*Eremotylus*	sp.RBoph025	female	26-004-1968	CA	San Bernardino County
UCRCENT509672	*Eremotylus*	sp.RBoph025	female	27-004-1968	CA	San Bernardino County
UCBMEP0272848	*Eremotylus*	sp.RBoph023	female	24-004-1978	CA	San Bernardino County
UCBMEP0272856	*Eremotylus*	sp.RBoph023	male	06-004-1964	CA	San Diego County

UCRCENT509659	*Eremotylus*	sp.RBoph026	female	27-004-1968	CA	San Bernardino County
UCRCENT509762	*Eremotylus*	sp.RBoph012	male	02-004-1990	CA	Riverside County
UCSB-IZC00033702	*Eremotylus*	sp.RBoph012	female	13-005-1978	CA	San Diego County
UCBMEP0272824	*Enicospilus*	*purgatus*	female	23-003-1971	CA	Riverside County
UCBMEP0272826	*Enicospilus*	*purgatus*	female	00-006-1982	CA	Riverside County
UCBMEP0272866	*Enicospilus*	*purgatus*	male	21-003-1967	CA	Riverside County
CASENT8423036	*Ophion*	*bilineatus*	male	22-002-1981	CA	Alameda County
EMEC1215664	*Eremotylus*	sp.RBoph015	female	27-004-1962	CA	San Luis Obispo County
SDNHM098262	*Eremotylus*	sp. RBoph024	female	27-004-1982	CA	Imperial County
EMEC1215668	*Eremotylus*	sp.RBoph022	female	02-005-1962	CA	San Luis Obispo County
UCSB-IZC00032359	*Eremotylus*	sp.RBoph022	female	22-003-1969	AZ	Maricopa County
UCSB-IZC00025720	*Eremotylus*	sp.RBoph022	female	12-004-1964	AZ	Pinal County
UCBMEP0272867	*Enicospilus*	*guatamalensis*	female	25-011-1976	FL	Alachua County
UCBMEP0272876	*Enicospilus*	*peigleri*	female	26-007-1978	MD	Montgomery County
UCSB-IZC00029909	*Eremotylus*	sp.RBoph022	female	22-002-1926	AZ	Maricopa County
UCSB-IZC00032711	*Eremotylus*	sp.RBoph013	female	04-007-2019	CA	Riverside County

UCSB-IZC00032405	*Eremotylus*	sp.RBoph025	female	04-006-2019	CA	Riverside County
UCSB-IZC00032555	*Simophion*	*excarinatus*	female	03-019-2019	CA	San Bernardino County
UCSB-IZC00003508	*Simophion*	*excarinatus*	female	03-019-2019	CA	San Bernardino County
UCSB-IZC00025321	*Simophion*	*excarinatus*	female	03-019-2019	CA	San Bernardino County
UCSB-IZC00025217	*Eremotylus*	sp.RBoph025	female	04-023-2019	CA	San Diego County
UCSB-IZC00016052	*Eremotylus*	sp.RBoph025	female	04-022-2019	CA	San Diego County
UCSB-IZC00025125	*Enicospilus*	*purgatus*	male	04-023-2019	CA	San Diego County
UCSB-IZC00032617	*Eremotylus*	sp.RBoph025	female	04-025-2019	CA	San Diego County
UCSB-IZC00025172	*Eremotylus*	sp.RBoph025	female	04-024-2019	CA	San Diego County
UCSB-IZC00032381	*Eremotylus*	sp.RBoph025	female	04-024-2019	CA	San Diego County
UCSB-IZC00032872	*Eremotylus*	sp.RBoph025	female	04-024-2019	CA	San Diego County
UCSB-IZC00025552	*Eremotylus*	sp.RBoph025	female	04-024-2019	CA	San Diego County
UCSB-IZC00025206	*Eremotylus*	sp.RBoph025	female	04-024-2019	CA	San Diego County
UCSB-IZC00032511	*Eremotylus*	sp.RBoph013	female	04-024-2019	CA	San Diego County
UCSB-IZC00025273	*Eremotylus*	sp.RBoph025	female	04-023-2019	CA	San Diego County
UCSB-IZC00024975	*Eremotylus*	sp.RBoph025	female	04-023-2019	CA	San Diego County

UCSB-IZC00025301	*Eremotylus*	sp.RBoph019	female	04-023-2019	CA	San Diego County
UCSB-IZC00025152	*Eremotylus*	sp.RBoph025	female	04-022-2019	CA	San Diego County
UCSB-IZC00025086	*Eremotylus*	sp.RBoph025	female	04-022-2019	CA	San Diego County
UCSB-IZC00020017	*Eremotylus*	sp.RBoph025	female	04-022-2019	CA	San Diego County
UCSB-IZC00001660	*Eremotylus*	sp.RBoph025	female	04-022-2019	CA	San Diego County
UCSB-IZC00032423	*Eremotylus*	sp.RBoph025	female	04-022-2019	CA	San Diego County
UCSB-IZC00025275	*Eremotylus*	sp.RBoph025	female	04-023-2019	CA	San Diego County
UCSB-IZC00025141	*Eremotylus*	sp.RBoph025	female	04-023-2019	CA	San Diego County
UCSB-IZC00027163	*Eremotylus*	sp.RBoph025	female	04-023-2019	CA	San Diego County
UCSB-IZC00025311	*Eremotylus*	sp.RBoph025	female	04-023-2019	CA	San Diego County
UCSB-IZC00025110	*Eremotylus*	sp.RBoph025	female	04-023-2019	CA	San Diego County
UCSB-IZC00025188	*Eremotylus*	sp.RBoph025	male	04-023-2019	CA	San Diego County
UCSB-IZC00025065	*Eremotylus*	sp.RBoph025	male	04-023-2019	CA	San Diego County
UCSB-IZC00024987	*Eremotylus*	sp.RBoph025	female	04-023-2019	CA	San Diego County
UCSB-IZC00025274	*Eremotylus*	sp.RBoph025	female	04-023-2019	CA	San Diego County
UCSB-IZC00027216	*Ophion*	sp.RBoph027	male	04-021-2019	CA	Santa Barbara County

UCSB-IZC00025276	*Enicospilus*	sp.RBoph006	female	04-009-2019	CA	Santa Barbara County
UCSB-IZC00027310	*Ophion*	sp.RBoph003	female	04-027-2019	CA	Santa Barbara County
UCSB-IZC00035693	*Ophion*	sp.RBoph003	male	04-017-2019	CA	Santa Barbara County
UCSB-IZC00035691	*Ophion*	sp.RBoph027	male	04-020-2019	CA	Santa Barbara County
UCSB-IZC00035690	*Enicospilus*	sp.RBoph006	female	04-001-2019	CA	Santa Barbara County
UCSB-IZC00027281	*Ophion*	sp.RBoph007	female	03-024-2019	CA	Santa Barbara County
UCSB-IZC00024972	*Ophion*	sp.RBoph007	female	04-012-2019	CA	Santa Barbara County
UCSB-IZC00035269	*Ophion*	sp.RBoph007	female	04-012-2019	CA	Santa Barbara County
UCSB-IZC00034784	*Enicospilus*	*glabratus*	female	05-023-2019	CA	Santa Barbara County
UCSB-IZC00027222	*Eremotylus*	sp.RBoph025	female	04-023-2019	CA	San Diego County
UCSB-IZC00034877	*Enicospilus*	*glabratus*	female	11-001-2015	CA	Los Angeles County
UCRCENT509669	*Eremotylus*	sp.RBoph022	female	03-008-2018	CA	Riverside County
UCSB-IZC00031326	*Eremotylus*	sp.RBoph025	female	08-016-2019	AZ	Cochise County

UCSB-IZC00031181	*Enicospilus*	*texanus*	male	08-017-2019	AZ	Santa Cruz County
UCSB-IZC00034848	*Enicospilus*	*purgatus*	female	05-001-2017	CA	Los Angeles County
UCSB-IZC00035436	*Enicospilus*	*purgatus*	female	03-028-2019	CA	Los Angeles County
UCSB-IZC00034932	*Ophion*	sp.RBoph027	female	02-002-2019	CA	Los Angeles County
UCSB-IZC00034898	*Enicospilus*	*glabratus*	female	07-001-2016	CA	Los Angeles County
UCSB-IZC00033859	*Ophion*	sp.RBoph003	female	07-007-2019	CA	Santa Barbara County
UCSB-IZC00009691	*Ophion*	sp.RBoph004	male	02-028-2018	CA	Santa Barbara County
UCSB-IZC00009717	*Ophion*	sp.RBoph004	male	02-015-2018	CA	Santa Barbara County
UCSB-IZC00009680	*Ophion*	sp.RBoph004	female	03-010-2018	CA	Santa Barbara County
UCSB-IZC00009702	*Ophion*	sp.RBoph004	female	03-008-2018	CA	Santa Barbara County
UCSB-IZC00009073	*Ophion*	sp.RBoph004	female	03-007-2018	CA	Santa Barbara County
UCSB-IZC00011030	*Ophion*	sp.RBoph004	female	05-011-2018	CA	Santa Barbara County
UCSB-IZC00014586	*Ophion*	sp.RBoph004	male	05-011-2017	CA	Santa Barbara County

UCSB-IZC00009661	*Ophion*	sp.RBoph005	female	01-031-2018	CA	Santa Barbara County
UCSB-IZC00010276	*Ophion*	sp.RBoph005	female	03-008-2018	CA	Santa Barbara County
UCSB-IZC00009122	*Ophion*	sp.RBoph005	female	03-015-2018	CA	Santa Barbara County
UCSB-IZC00009706	*Ophion*	sp.RBoph005	female	02-016-2018	CA	Santa Barbara County
UCSB-IZC00033494	*Ophion*	sp.RBoph005	female	01-019-2019	CA	Santa Barbara County
UCSB-IZC00009161	*Ophion*	sp.RBoph007	female	03-008-2018	CA	Santa Barbara County
UCSB-IZC00011207	*Ophion*	sp.RBoph007	female	04-014-2018	CA	Santa Barbara County
UCSB-IZC00004794	*Ophion*	sp.RBoph007	male	03-027-2018	CA	Santa Barbara County
UCSB-IZC00010080	*Ophion*	sp.RBoph007	female	04-005-2018	CA	Santa Barbara County
UCSB-IZC00010278	*Enicospilus*	*glabratus*	female	05-009-2015	CA	San Diego County
UCSB-IZC00007710	*Enicospilus*	*glabratus*	male	08-020-2017	CA	Santa Barbara County
UCSB-IZC00015950	*Enicospilus*	*purgatus*	female	04-014-2016	CA	Santa Barbara County
UCSB-IZC00010722	*Enicospilus*	*purgatus*	female	05-020-2018	CA	Santa Barbara County

UCSB-IZC00035013	*Enicospilus*	*purgatus*	female	05-023-2019	CA	Santa Barbara County
UCSB-IZC00031580	*Enicospilus*	*glabratus*	male	06-005-2019	CA	Santa Barbara County
UCSB-IZC00035736	*Ophion*	sp.RBoph003		05-026-2019	CA	Santa Barbara County
UCSB-IZC00032074	*Enicospilus*	*glabratus*	male	08-018-2019	CA	Santa Barbara County
UCSB-IZC00025436	*Ophion*	sp.RBoph003	male	03-022-2019	CA	Santa Barbara County
UCSB-IZC00025511	*Ophion*	sp.RBoph003	male	03-023-2019	CA	Santa Barbara County
UCSB-IZC00035716	*Ophion*	sp.RBoph027	male	05-010-2019	CA	Santa Barbara County
UCSB-IZC00027294	*Ophion*	sp.RBoph027	female	04-001-2019	CA	Santa Barbara County
UCSB-IZC00035737	*Ophion*	sp.RBoph007	female	04-026-2019	CA	Santa Barbara County
UCSB-IZC00035694	*Ophion*	sp.RBoph027	male	04-030-2019	CA	Santa Barbara County
UCSB-IZC00031823	*Ophion*	sp.RBoph027	male	06-002-2019	CA	Santa Barbara County
UCSB-IZC00035708	*Ophion*	sp.RBoph003	female	04-028-2019	CA	Santa Barbara County
UCSB-IZC00034823	*Enicospilus*	*purgatus*	female	05-009-2019	CA	Santa Barbara

						County
UCSB-IZC00035727	*Ophion*	sp.RBoph003	female	04-019-2019	CA	Santa Barbara County
UCSB-IZC00033084	*Ophion*	sp.RBoph005	female	04-019-2019	CA	Santa Barbara County
UCSB-IZC00009151	*Ophion*	sp.RBoph005	female	02-002-2018	CA	Santa Barbara County
UCSB-IZC00009707	*Ophion*	sp.RBoph005	female	03-006-2018	CA	Santa Barbara County
UCSB-IZC00032072	*Eremotylus*	sp.RBoph021	female	08-016-2013	AZ	Cochise County
UCSB-IZC00033085	*Thyreodon*	*atricolor*	female	08-007-2014	AZ	Cochise County
UCSB-IZC00009077	*Simophion*	*excarinatus*	female	03-008-2018	CA	Riverside County
UCSB-IZC00009198	*Simophion*	*excarinatus*	female	03-008-2018	CA	Riverside County
UCSB-IZC00010280	*Simophion*	*excarinatus*	female	03-008-2018	CA	Riverside County
UCRCENT509531	*Simophion*	*excarinatus*	female	12-003-2005	CA	Riverside County