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Phylogenetic placement of the enigmatic longhorned beetle *Vesperoctenus flohri* Bates (Vesperidae) and a first description of its female internal structures

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Abstract

Taxonomic placement of the enigmatic monotypic Mexican longhorned beetle genus *Vesperoctenus* Bates is examined through inclusion in and reanalysis of the dataset of Haddad et al. (2018, *Systematic Entomology* 43: 68–89). We describe and discuss the phylogenetic significance of the internal structures of a recently collected *V. flohri* female from the Sierra de la Laguna mountain range in Mexico, the same specimen from which phylogenomic data was generated. Our phylogenomic analyses (469 genes) recovered *Vesperoctenus* with maximal statistical support within the cerambyciform family Vesperidae, sister to *Vesperus* Dejean (Vesperinae). *Vesperus* + *Vesperoctenus* were recovered sister to Philinae, and collectively form a clade sister to Anoplodermatinae. Thus, we place *V. flohri* within Vesperidae: Vesperinae: Vesperoctenini based on analyses of large-scale phylogenomic data. Finally, we propose that the conservation status of *V. flohri* merits assessment.

Key words

Cerambycidae, distribution, Mexico, morphology, taxonomy, Vesperinae, Vesperoctenini.

1. Introduction

The taxonomic placement of the longhorned beetle *Vesperoctenus flohri* Bates has been highly controversial since its initial description by Bates in 1891. It is the only species within the genus *Vesperoctenus* Bates, is seldom collected, and is only known from Mexico (Baja California Sur, Durango, and Nuevo Leon; Vives 2001).

Table 1. Taxonomic placements of *Vesperoctenus flohri* in major publications since its formal description.

Taxonomic Placement	**Reference**
A longhorned beetle "closely allied" to *Vesperus* Dejean, the name *Vesperoctenus* means "related to *Vesperus* but with comb-like antennae" (of male).	Bates (1891) (original description)
Placed in "Rhipiceridae" near *Callirhipis* Latreille (now Callirhipidae of Byrrhoidea).	Horn (1894)
Reconfirmed in the broad Cerambycidae of that time; Horn's (1894) arguments rejected.	Gahan (1895)
In Cerambycidae: Cerambycinae: Lepturini (in Aurivillius next to *Vesperus* and *Paraphilus* Gahan = *Mantitheus* Fairmaire, now in Philinae).	Aurivillius (1912) Blackwelder (1946)
In Cerambycidae: Lepturinae: Vesperini.	Boppe (1921)
In Vesperinae placed (together with Disteniinae, Oxypeltinae, and Philinae) as a subfamily of Crowson's "Disteniidae" (the family should have been named Vesperidae for priority reasons); This is the first modern exclusion of Vesperinae including *Vesperoctenus* from the family Cerambycidae.	Crowson (1981) (he probably never mentioned *Vesperoctenus* in the book, but Table 14 lists Vesperinae as Palaearctic and C. American)
In Cerambycidae: Lepturinae: Lepturini.	Catalogs and checklists of Cerambycidae *s. l.* of the Western Hemisphere and Neotropics beginning with the original versions (Monné and Giesbert 1994; Monné 1995, 2006) up to the publication of Bousquet et al. (2009)
Incertae sedis within the newly defined Vesperidae (containing the Vesperinae and Philinae of Crowson, 1981, plus the newly added Anoplodermatinae).	Svacha et al. (1997)
In Vesperidae (with the placement of Anoplodermatinae in that family questioned) and closely related to *Vesperus*.	Vives (2001)
In Vesperidae in its own newly erected tribe Vesperoctenini.	Vives (2005)
Vesperoctenini (but not *Vesperus*) moved without explanation to Cerambycidae: Prioninae.	Bousquet et al. (2009)
In Cerambycidae: Prioninae: Vesperoctenini (following Bousquet et al. 2009).	Bouchard et al. (2011) Catalogs and checklists of Cerambycidae *s. l.* of the Western Hemisphere and Neotropics following the publication of Bousquet et al. (2009), from versions dated 2011 till the present: Bezark (2020), Monné (2020) Current versions of online cerambycid databases: Tavakilian and Chevillotte (2020), Nearns et al. (2020)
In Vesperidae: Vesperoctenini as a genus and tribe of uncertain subfamilial position; placement in Prioninae rejected.	Svacha and Lawrence (2014)

The adults are predominantly nocturnal, females are brachypterous, and the larvae, although undescribed, are presumed to be subterranean root feeders (Bates 1891; Vives 2001). The specimens of the type series collected in Durango were reported in Bates (1891) to have been emerging from the ground and attracted to the light of a fire (the type series contained both sexes and thus the females, although flightless, may also be attracted by light). Besides further specimens attracted to UV light, at least one other was obtained by beating branches of *Quercus devia* Goldman in Baja California (Hovore 1988).

Svacha and Lawrence (2014) reviewed the various taxonomic placements of *V. flohri* since its formal description (summarized and updated in Table 1). Recently, *Vesperoctenus* has been classified either within Cerambycidae: Prioninae following Bousquet et al. 2009 (Bouchard et al. 2011; Tavakilian and Chevillotte 2020; Nearns et al. 2020; Monné 2020) or within Vesperidae (Svacha and Lawrence 2014) as a genus and tribe of uncertain subfamilial placement. *Vesperoctenus* has not been included in any molecular phylogenetic studies of Coleoptera to date and all attempts to determine its taxonomic affinities have relied on the incompletely known adult morphology (in particular, the female internal structures remain undescribed). We are not aware of any characters supporting the placement of *Vesperoctenus* in Prioninae. The antennae of both sexes are 12-segmented, unlike any other species in Vesperidae. Further, determining the exact taxonomic placement of *V. flohri* within Vesperidae has been compounded by its adults sharing individual morphological similarities with each of the three vesperid subfamilies – Anoplodermatinae, Philinae, and Vesperinae – making it difficult to conclusively place the species in one of them (see Svacha and Lawrence 2014 for details). Notable examples include the head of both *Vesperus* (Vesperinae) and *Vesperoctenus* constricted posteriorly to form a neck (unlike in Anoplodermatinae and Philinae and in a manner different from the "neck" in Lepturinae), and most Anoplodermatinae and *Vesperoctenus* sharing a 2-2-1 formula of terminal tibial spurs unlike Vesperinae (2-2-2) and Philinae (2-2-2 or 1-2-2); the 2-2-1 formula is also rare in the Cerambycidae. Saito (1990) described a simplified internal female genital tract in *Vesperus* (Vesperinae), *Philus* and *Mantitheus* Fairmaire (Philinae) with an (almost) completely desclerotized, simple, pouch-like spermatheca lacking a spermathecal gland, a situation apparently not known in any other cerambyciform and very probably apomorphic. A similar pouch-like membranous spermatheca has since been described in the philine genus *Heterophilus* (Bi and Lin 2015) where it bears a short

Figure 1. Collecting site of *Vesperoctenus flohri* female in Mexico, Baja California Sur, Sierra de la Laguna (margin of pine-oak forest at the dried lake with two small trees of *Arbutus* in the foreground). Inset: Live female.

spermathecal gland, thus confirming Saito's interpretation of the membranous pouch as a desclerotized spermatheca. Vesperinae and Philinae were also recovered as sister groups in Haddad et al. (2018). However, females of *Vesperoctenus* are particularly rare in collections, have never been dissected, and their internal genitalia remain undescribed. Moreover, *Vesperoctenus* is geographically separated from other Vesperidae – it is the only extant Vesperidae known from North/Central America whereas the Anoplodermatinae are Neotropical, and *Vesperus* and Philinae occur exclusively in the Old World.

Recently, phylogenomic studies have greatly improved our understanding of Coleoptera systematics and evolution (e.g., Haddad et al. 2018; Shin et al. 2018; McKenna et al. 2019; Vasilikopoulos et al. 2019). Studies of cerambyciform systematics and evolution have also been gaining momentum (e.g., Haddad and McKenna 2016; Haddad et al. 2018; Lee and Lee 2020; Souza et al. 2020a, b; Nie et al. 2021). In this study, we sought to determine the phylogenetic placement of *Vesperoctenus* using phylogenomic data, since morphology alone has failed to provide a clear answer to this. We specifically chose to do this within the context of the Haddad et al. (2018) data set since it includes representatives of all cerambyciform families (Cerambycidae *sensu stricto*, Disteniidae, Oxypeltidae, and Vesperidae) and subfamilies, along with the families Megalopodidae and Orsodacnidae. A female specimen of *V. flohri* was collected from the Sierra de la Laguna mountain range in Baja California Sur, Mexico. This specimen was used for obtaining phylogenomic data and for morphological study, including the first description of the female genitalia. Our molecular results conclusively establish the placement of this enigmatic genus within the higher-level phylogeny of cerambyciforms. We also argue that the conservation status of *V. flohri* requires consideration given our poor knowledge of its biology, distribution, genetic differentiation across its populations, and the reality of persistent threats to its habitat.

2. Methods

2.1. Specimen collection

N. Gutiérrez and P. Svacha collected a female specimen of *V. flohri* in Mexico, Baja California Sur, Sierra de la Laguna (23°32’60”N, 109°58’53”W, 1743 m) on 22 May 2018 at about 9:30 AM (Fig. 1). Vegetation in the area consists of natural grasslands and pine/oak forest, with a temperate subhumid climate and average annual temperatures of 14.7°C (CONANP 2003a). The female was preserved in clean ethyl alcohol and used for both molecular and morphological study. An extensive search for larvae on roots of various trees and herbs at this and another locality was unsuccessful.

2.2. Geographical distribution of *Vesperoctenus flohri*

Documented localities of *V. flohri* were obtained from online databases, museum collections, and the literature. This information was stored in an Excel spreadsheet and then exported to the R statistical environment (R Core Team 2019). Once in R, data management was performed using dplyr package tools (Wickham et al. 2020), while the map was produced using the packages sf, ggplot2, gridExtra, OpenStreetMap, ggsn, and patchwork (Wickham 2016; Baptiste 2017; Pebesma 2018; Fellows 2019; Pedersen 2019; Santos-Baquero 2019; Ooms 2020).

2.3. Dissection of female internal structures

The legs, prothorax and right part of pterothorax were preserved for DNA and the remaining body was treated in hot 5% KOH to dissolve soft tissues. The cleaned cuticle was opened by microscissors to expose the internal structures – ovipositor, internal genitalia, metathoracic furca (metendosternite), and tentorium.

2.4. DNA extraction, library preparation, enrichment, and sequencing

We used anchored hybrid enrichment (AHE; Lemmon et al. 2012) to generate phylogenomic data for this study. Our previous studies of beetle phylogeny using AHE have produced well-resolved phylogenies with overall strong statistical support for relationships (Haddad et al. 2018; Shin et al. 2018; Johnson et al. 2018). DNA extraction, library preparation, enrichment and sequencing were performed only for the *Vesperoctenus* specimen collected for this study and following the methods outlined in Haddad et al. (2018) and Shin et al. (2018) with a few minor changes: an Arbor Biosciences myBaits target capture kit was used for hybridization-based capture and enrichment. Genomic data was extracted from a single leg of the specimen. Sequencing was performed by Novogene using a HiSeq X Ten (Illumina) sequencer and PE150 reads.

2.5. Read processing, assembly, and orthology assessment

Anchored hybrid enrichment data for *Vesperoctenus* was trimmed with Trimmomatic v 0.36 (Bolger et al. 2014) and then assembled using the program SOAPdenovo2 (Luo et al. 2012). Orthologous genes were identified using Orthograph (Petersen et al. 2017) exactly as in Haddad et al. (2018). Official gene sets (OGS) for three reference taxa in OrthoDB v7 (Waterhouse et al. 2011, 2013) were used: *Danaus plexippus* Linnaeus (Lepidoptera: Danaidae) (Zhan et al. 2011), *Nasonia vitripennis* Walker (Hymenoptera: Pteromalidae) (Werren et al. 2010) and *Tribolium castaneum* (Coleoptera: Tenebrionidae) (Richards et al. 2008). Following the methods in Haddad et al. (2018), 522 COGs (clusters of orthologous groups) were identified based on this pipeline before the filtering stage. We repeated this Orthograph pipeline for all data used in this study. Default parameters were retained in Orthograph throughout this process.

2.6. Multiple sequence alignment (MSA)

A script from Orthograph (Petersen et al. 2017) was used to summarize the fasta files generated from the orthology prediction pipeline for each orthologous gene, and the files were subsequently saved in a folder organized by orthologous gene ID. MSAs were then generated for each orthologous gene using the L-INS-i algorithm in MAFFT v7.130b (Katoh and Standley 2013). FASconCAT v1.0 (Kück and Meusemann 2010) was then used to generate an aligned supermatrix (781,854 NT sites) from the MSAs for the NT data. The resulting supermatrix was partitioned by gene.

2.7. Partitioning and modeling

PartitionFinder v. 2 (Lanfear et al. 2012) identified the best-fit cluster of partitions and models for the nucleotide data (using the rcluster option; Lanfear et al. 2014). The corrected Akaike information criterion (AICc; Hurvich and Tsai 1989) in PartitionFinder was used to determine partition clusters using the following parameters: model_selection = AICC; models = GTR+I+G, GTR+G; branch lengths = linked; search = rcluster, and the options: rate = 1.0, base = 1.0, model = 0.0, alpha = 1.0 with rcluster-percent = 10.0, using the command line script with the –raxml option. This resulted in 274 total partitions (262 with model GTR+I+G and 12 with model GTR+G, so the former model was used for the RAxML run).

2.8. Phylogenetic analyses

We conducted a partitioned maximum likelihood (ML) analysis (1000 rapid bootstrap replicates) for NT data (781,854 bp) in RAxML 8.2.12 (Stamatakis 2014). The analysis was performed on the HPC (high performance computing) cluster at the University of Memphis. Results from the bootstrap analyses were mapped onto the resulting ML tree. We consider nodes with a ML bootstrap support (MLBS) value greater or equal to 95% to be strongly supported.

3. Results

3.1. Phylogenetic placement of *Vesperoctenus flohri*

Excluding the placement of *Vesperoctenus* which we here report for the first time, the recovered relationships and clades in the partitioned maximum likelihood phylogeny for nucleotide data (Fig. 2) are identical to those of Haddad et al. (2018; their fig. 2), with only minor differences in nodal support; also the original cerambycid subfamilial classification of Haddad et al. (2018) is retained (additional support has been in the meantime obtained for placing Necydalinae and Parandrinae as ingroups of Lepturinae and Prioninae, respectively, e.g. in Nie et al. 2021). *Vesperoctenus flohri*, the focus of our study, is recovered within the cerambyciform family Vesperidae, sister to *Vesperus* (Vesperinae), with maximal nodal

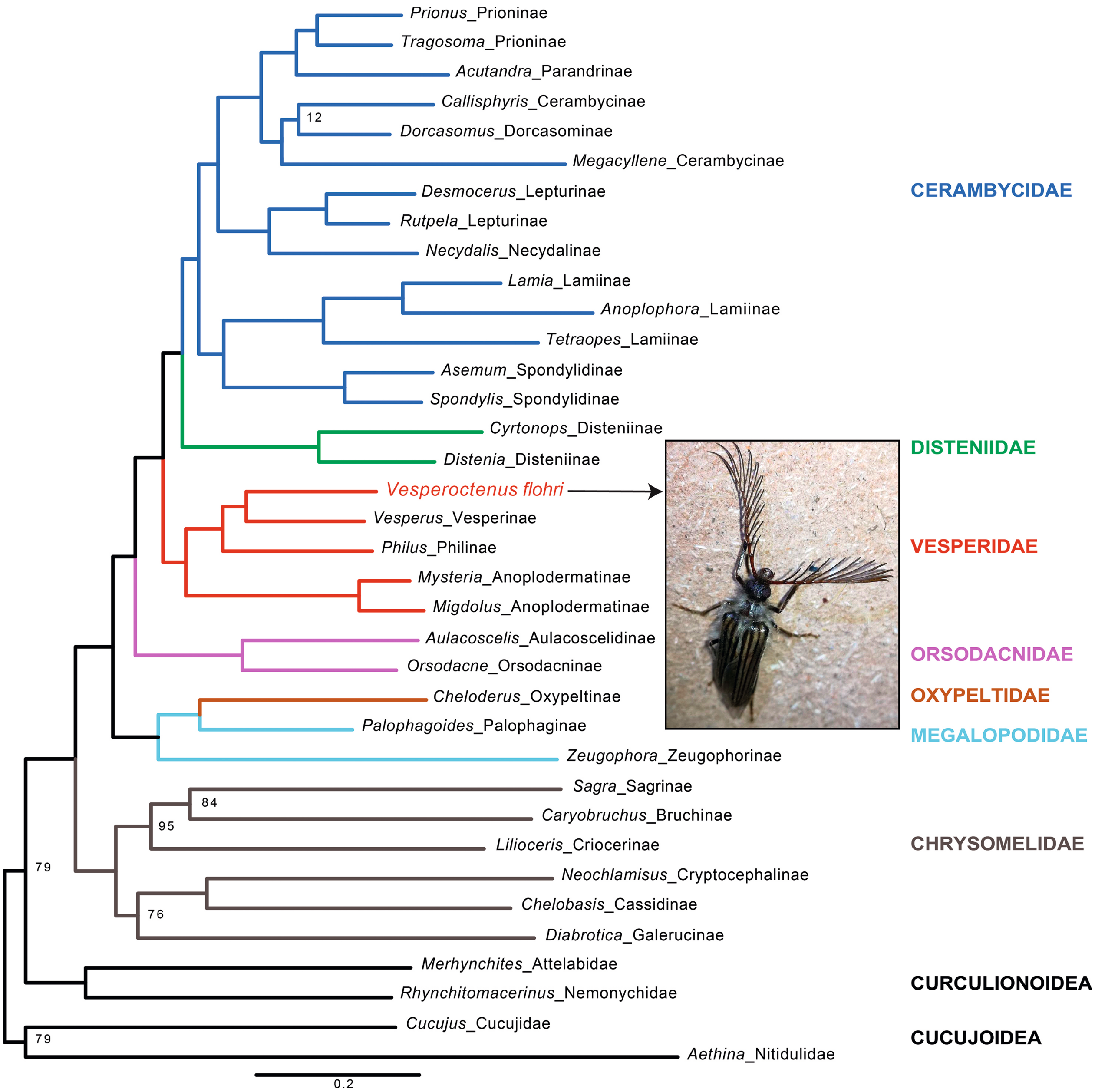


Figure 2. Partitioned maximum likelihood phylogeny for nucleotide data. Maximum likelihood bootstrap support (MLBS) is shown only for nodes with MLBS ≤ 95%. Information regarding the systematics of the sampled exemplars is indicated on the right of the tree. Photograph of male *Vesperoctenus flohri* from Zacatecas (Sierra de Organos) by Juan Carrillo Contreras.

support. *Vesperus* + *Vesperoctenus* are recovered sister to the Philinae (represented by *Philus pallescens* Bates), and these collectively form a clade sister to Anoplodermatinae (represented by *Migdolus fryanus* Westwood and *Mysteria darwini* Lameere), all with maximal support. The monophyly of Vesperidae is likewise maximally supported.

3.2. Female morphology of *Vesperoctenus flohri*

For terminology, see Svacha and Lawrence (2014). *Vesperoctenus flohri* was redescribed by Vives (2001) and the male also by Svacha and Lawrence (2014). Since Vives redescribed the female based on two old dry specimens, we include photographs of our fresh specimen (Fig. 3), the cleared head with open mandibles (Fig. 4a), the cleared pterothorax in lateral view (Fig. 4b), and the right wing (Fig. 4c). As in the male, the anterior margin of the sclerotized postclypeus slightly projects laterally above the membranous anteclypeus (Fig. 4a, arrow), but the paired projections are smaller and less prominent. Fig. 4b shows the unusually broad triangular metanepisternum (broadest of all studied vesperids). *Vesperoctenus flohri* females are brachypterous, but the wing of our specimen (Fig. 4c) is relatively long (its length comprises 90 % of the elytron length), has relatively complete venation with a minute rudiment of the wedge cell, and is more fully developed than that of the female lectotype from Durango depicted in Vives (2001: Fig. 4).

Figure 3. *Vesperoctenus flohri*, female: dorsal, lateral and ventral view (length 21.5 mm).

The tentorium agrees with other Vesperidae (Svacha and Lawrence 2014) in having a broad roof-like tentorial bridge. The metatentorial arms bear long, flat and distally broadened dorsal arms. An extremely narrow connection exists between the pre- and metatentorial arms (it was torn during dissection).

Unlike the male hind coxae which are close together (Fig. 5a), those of the brachypterous flightless female are broadly separate (Figs 3, 6a) and the metendosternite lacks the common basal stalk and both arms abruptly diverge from their origins and run laterodorsally close to the thoracic walls, leaving the central metathoracic space free. The left and right laminae and anterior tendons thus become broadly separate (Fig. 6b).

Female terminalia and internal genitalia. Sternum VIII has a V-shaped sclerotization and long spiculum gastrale (Fig. 7c). The ovipositor (Figs 7a, b) is long, flexible, and without any modifications for digging. The proctiger (the dorsal part between anus and ovipositor base in Fig. 7b) is extremely long, exceeding half of the ovipositor length and bearing two pairs of baculi; the medial pair is long and reaches the ovipositor base while the lateral pair is short and its ends approach the proximal ends of the paraproctal baculi. The valvifer is not distinguished from the coxite, the coxite lobes are long and slender and bear terminal gonostyli. The dorsal baculi are distinctly shorter than the medial pair of proctigeral baculi. The base of the membrane ensheathing the ovipositor is produced into small "intersegmental pouches" (see Discussion). The vagina forms a simple membranous tube, broadened bursa copulatrix is small, without vaginal plates at base, spermathecal duct arising apically (not sidewise as in Anoplodermatinae and most Cerambycidae), short and thin, terminated by a finely sclerotized C-shaped spermatheca with a spermathecal gland at its base (Fig. 7d).

4. Discussion

4.1. Molecular phylogeny and systematic placement

The lack of *V. flohri* larvae and molecular data (until now), the scarcity of available adult specimens, and the disjunct distribution of vesperids (not many Old World taxonomists had specimens available for comparison)

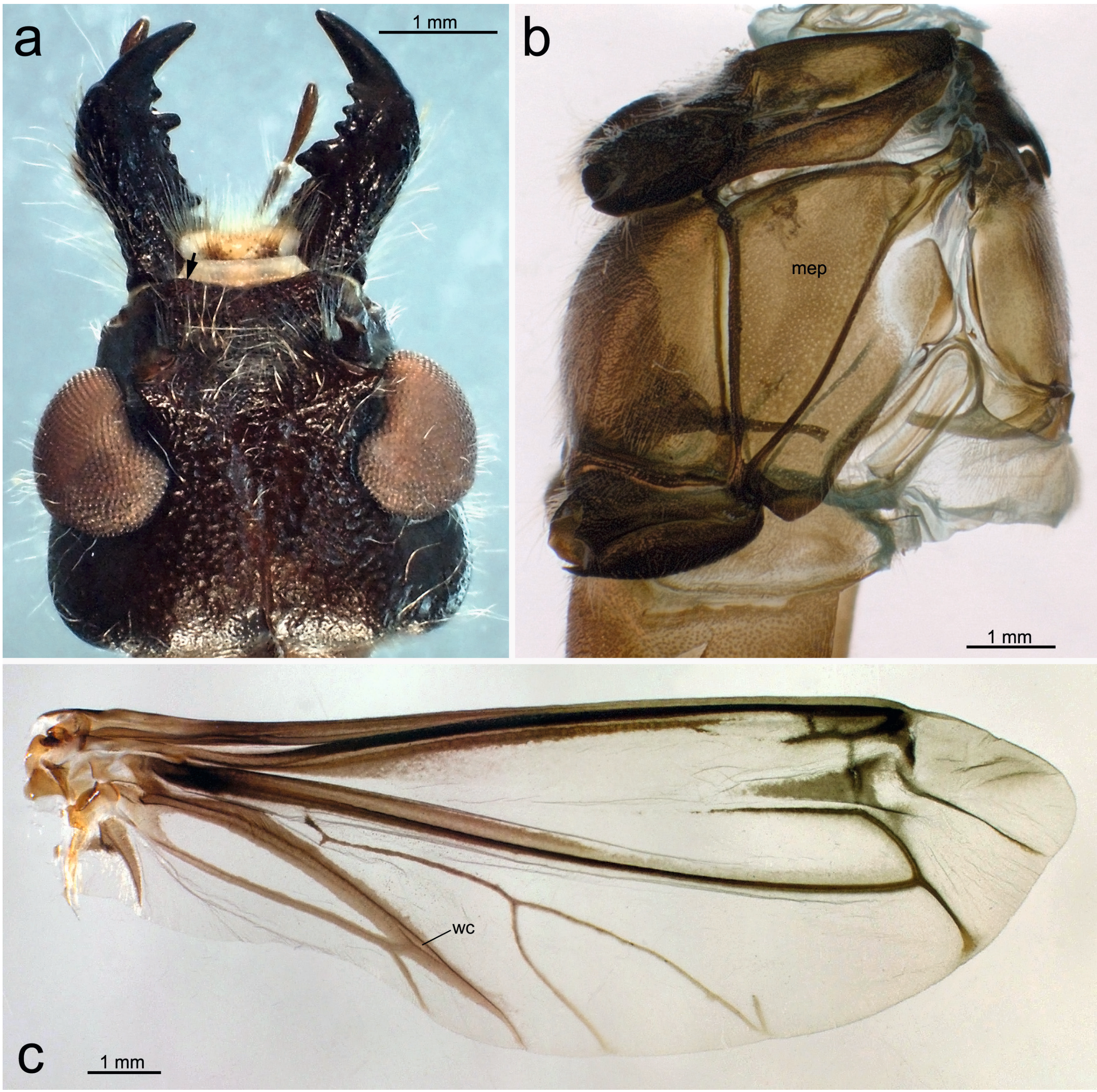


Figure 4. *Vesperoctenus flohri*, female: **(a)** Head, dorsal view (cleared specimen); **(b)** pterothorax, left lateral view (cleared specimen); **(c)** right wing. Lettering: mep – metanepisternum; wc – rudimentary wedge cell; arrow – lateral postclypeal projection.

has rendered the evaluation of the relationships and systematic placement of the genus *Vesperoctenus* difficult and variable (see Introduction and Table 1). Our molecular phylogenetic analysis reconfirms the monophyly of the family Vesperidae in the sense of Svacha et al. (1997) and Haddad et al. (2018) and firmly recovers *Vesperoctenus* within Vesperidae as the sister taxon of *Vesperus*. We therefore place *V. flohri* within Vesperidae: Vesperinae: Vesperoctenini as sister to the Vesperini containing a single genus *Vesperus* with about 20 species (status of some species-level taxa is not fully agreed upon). This phylogenetic placement is interesting, particularly from a biogeographic point of view. *Vesperoctenus* is endemic to Mexico, whereas the monogeneric Vesperini is strictly Mediterranean. Moreover, the Philinae (5 genera, ~19 spp.), which is sister to Vesperinae, is similarly an Old World taxon occurring predominantly in the Oriental Region (one species of *Doesus* reaches subsaharan Africa). Only the Anoplodermatinae is Neotropical in distribution (Svacha and Lawrence 2014). Thus, *V. flohri* is the only extant vesperid in North/Central America and the only non-anoplodermatine vesperid in the New World. Crowson (1981: Table 14 on p. 626) listed Vesperinae (occurring in the Mediterranean region of the Palearctic and in Mexico) among taxa with a relict distribution.

4.2. Morphology

Refer to Svacha and Lawrence (2014) for morphological summaries of individual vesperid subfamilies and for some figures referenced herein. When interpreting morphological characters in light of our obtained molecular

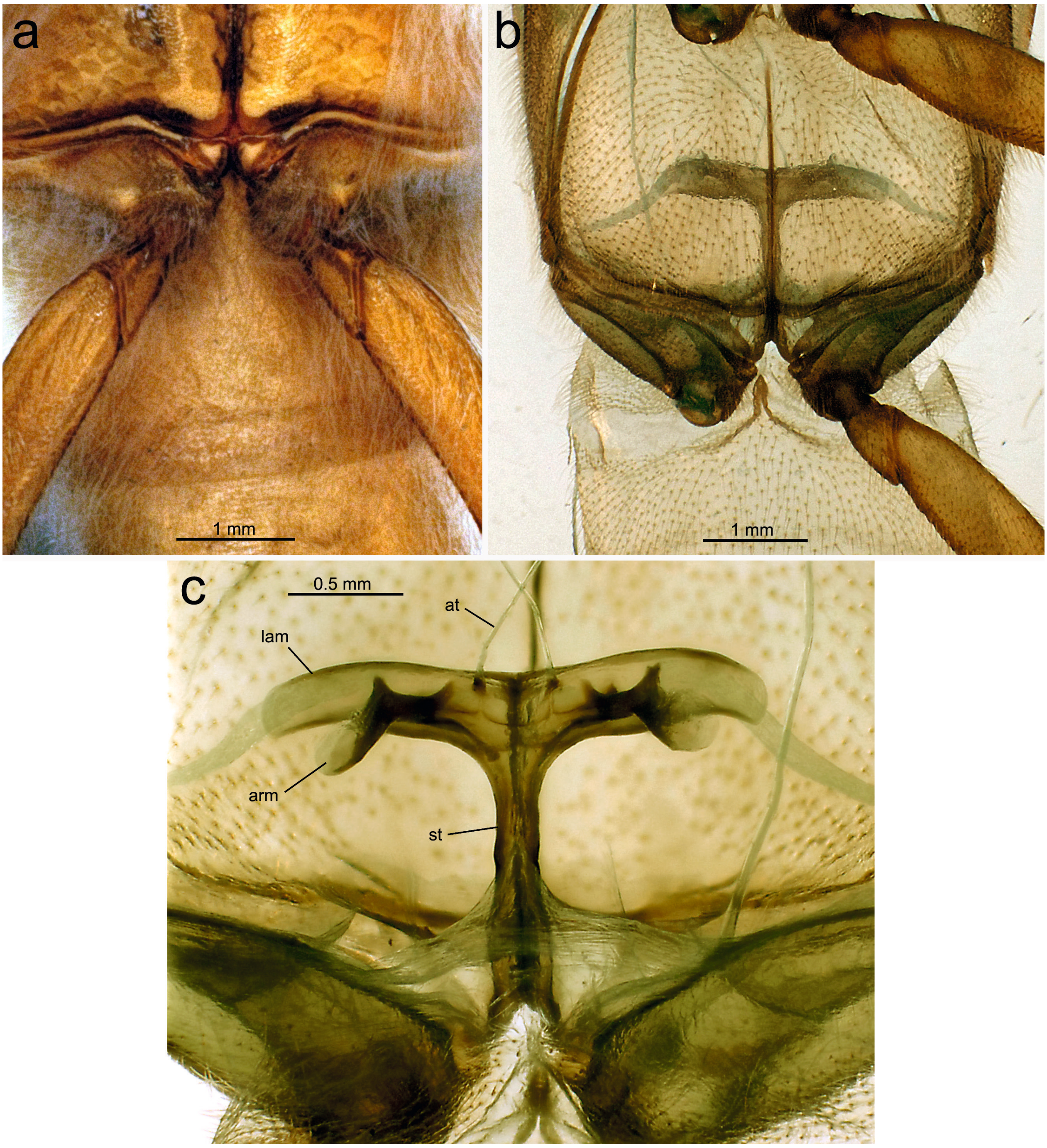


Figure 5. (a) *Vesperoctenus flohri*, male, hind coxae, ventral view (the dense ventral pilosity was largely removed); **(b)** *Vesperus strepens*, male (cleared specimen), dtto; **(c)** *V. strepens*, male (cleared specimen), metendosternite, dorsal view. Lettering: arm – metendosternal arm; at – anterior tendon; lam – metendosternal lamina; st – basal stem.

phylogeny (monophyletic Philinae + (*Vesperus* + *Vesperoctenus*) as a sister group to the Anoplodermatinae), we find that the similarities of the "non-anoplodermatine" vesperid clade are either difficult to polarize or probable symplesiomorphies.

Vesperoctenus (as well as *Vesperus* and the Philinae) does not share most of the probable synapomorphies of the Neotropical Anoplodermatinae: procoxal cavities closed externally (open in other Vesperidae); wing invariably without a wedge cell (wedge cell present in macropterous specimens of Philinae, *Vesperoctenus* and some *Vesperus*) and with MP_{3+4} attached to MP_{1+2} at about half length of the latter (at about one-third length or less in all other Vesperidae and in most other non-chrysomelid chrysomeloids); metendosternite in dissected species (both sexes of *Pathocerus* and *Migdolus*, male of *Hypocephalus*) without laminae (with laminae in males and most females of other dissected Vesperidae including the modified metendosternites of some flightless females, although strongly reduced in females of some species of *Vesperus*, see below and Fig 6); short sclerotized "digging" ovipositor (long flexible non-digging ovipositor with terminal gonostyli in all other Vesperidae, Figs 7a, b and Saito 1990, although the ovipositor is slightly shorter

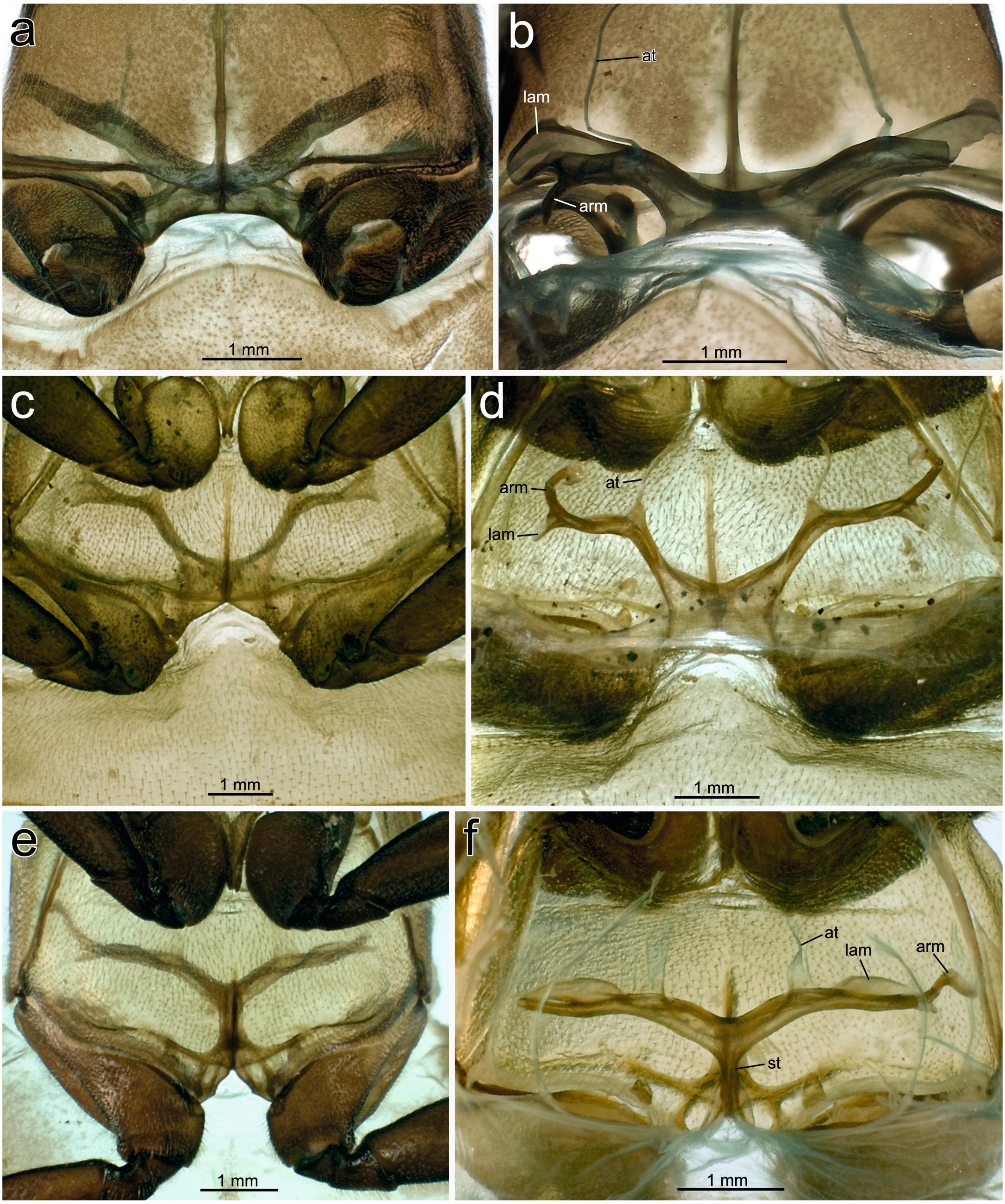


Figure 6. (all cleared specimens). **(a)** *Vesperoctenus flohri*, female, hind coxae, ventral view; **(b)** *V. flohri*, female, metendosternite, dorsal and slightly anterior view (tip of right arm missing); **(c)** *Vesperus strepens*, female, hind coxae, ventral view; **(d)** *V. strepens*, female, metendosternite, dorsal view; **(e)** *Mantitheus pekinensis*, female, hind coxae, ventral view; **(f)** *M. pekinensis*, female, metendosternite, dorsal view (tip of left arm missing). Lettering: arm – metendosternal arm; at – anterior tendon; lam – metendosternal lamina; st – basal stem (missing in females of *Vesperoctenus* and *Vesperus*).

and more robust in females of *Heterophilus* whose oviposition mode is unknown: Bi and Lin 2015).

Svacha (in Svacha et al. 1997) established the family Vesperidae in the present extent and included *Vesperoctenus* as a genus *incertae sedis*, pointing out some potential synapomorphies with the Neotropical Anoplodermatinae. In light of the present results, the shared and undoubtedly apomorphic 2-2-1 pattern of tibial spurs in *Vesperoctenus* and the anoplodermatine groundplan, and the extreme hairiness of males of *Vesperoctenus* and of some genera of Anoplodermatinae (*Sypilus* Guérin-Méneville, *Cherrocrius* Berg) should be considered parallelisms. The

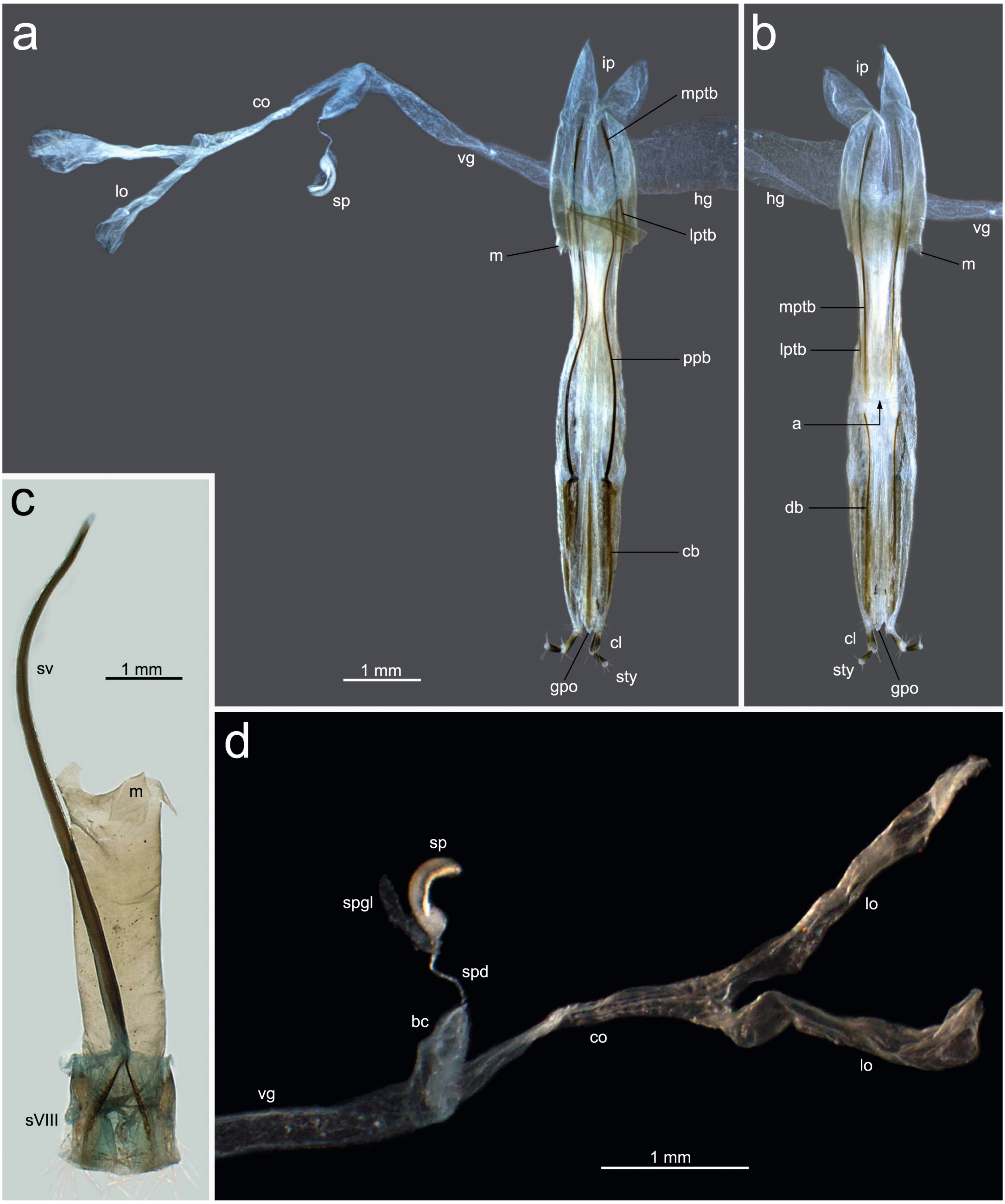
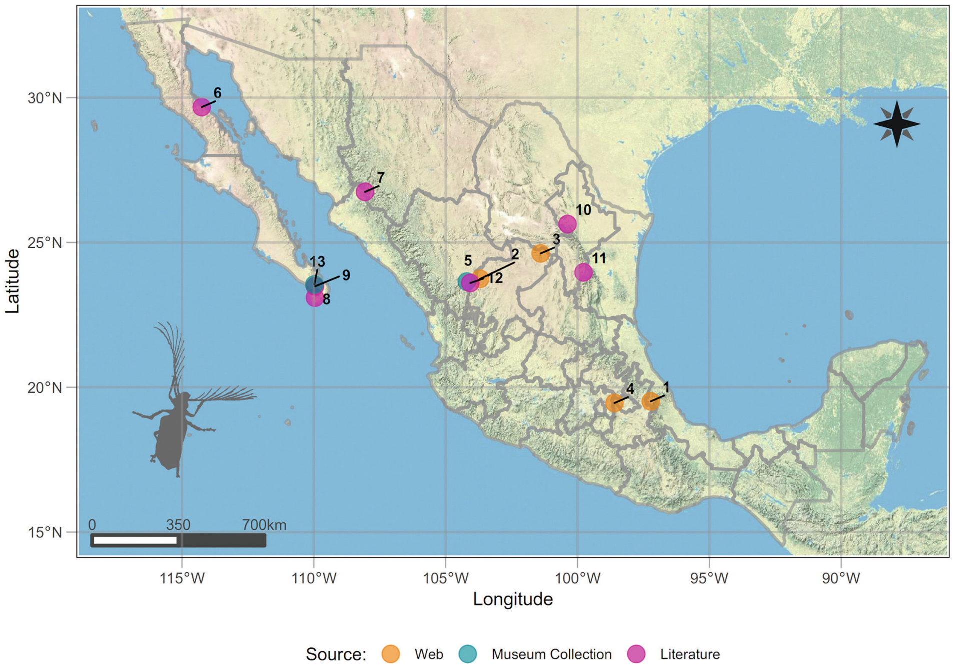


Figure 7. *Vesperoctenus flohri*, female genitalia and sternum VIII. **(a)** Ovipositor and internal genital tract, ventral view; **(b)** ovipositor, dorsal view; **(c)** abdominal sternum VIII and membranous tube ensheathing the ovipositor, ventral view; **(d)** detail of internal genital tract. Lettering: a – anus; bc – bursa copulatrix; cb – coxital baculum; cl – coxite lobe; co – common oviduct; db – dorsal baculum; gpo – gonopore; hg – hindgut; ip – intersegmental pouches; lo – lateral oviduct; lptb – lateral proctigeral baculum; m – membranous tube ensheathing ovipositor; mptb – medial proctigeral baculum; ppb – paraproctal baculum; sp – spermatheca; spd – spermathecal duct; spgl – spermathecal gland; sty – stylus; sv – spiculum ventrale (apodeme of sVIII); sVIII – sternum VIII; vg – vagina.

mandibles of both sexes of *Vesperoctenus* with asymmetrically dentate incisor edges and an outer tubercle (present Fig. 4a for female, fig. 2.1.4 C in Svacha and Lawrence 2014 for male) resemble some Anoplodermatinae and differ from *Vesperus* and Philinae with more or less simple incisor edges and no distinct outer tubercle, but polarity of these characters is uncertain.



ID	Source	Observer	Year	Status	State	Locality	Longitude	Latitude
1	Facebook	Santiago Jaume-Schinkel	2017	Exact	Veracruz	5km away from Tenextepec	-97.22442	19.51319
2	iNaturalist	Juan Carrillo	2018	Exact	Zacatecas	Parque Nacional Sierra de Organos	-103.69858	23.74135
3	iNaturalist	Ben Hurt	2018	Exact	Zacatecas	Concepcion del Oro	-101.39985	24.61960
4	iNaturalist	Francisco Acosta	2018	Exact	Tlaxcala	Nanacamilpa	-98.60014	19.45641
5	AMNH	NA	1985	Approximate	Durango	Reserva de la Biosfera "La Michilía"	-104.20000	23.65000
6	Horn, 1894	NA	1894	Approximate	Baja California	San Francisquito in the Cape Region	-114.25380	29.67319
7	Bates, 1891	NA	1891	Approximate	Durango	Sierra Madre of Durango	-108.05786	26.74572
8	Hovore, 1988	NA	1988	Exact	Baja California	Santa Victoria, La Laguna 1950 m	-109.95846	23.09320
9	Hovore, 1988	NA	1988	Exact	Baja California	17.3 air miles ENE Todos Santos	-109.95821	23.48500
10	Vives, 2001	NA	2001	Approximate	Nuevo Leon	Sierra Nevada	-100.37949	25.63509
11	Vives, 2001	NA	2001	Approximate	Nuevo Leon	Zaragoza	-99.77282	23.96574
12	Terron, 1991	NA	1991	Approximate	Durango	Reserva de la Biosfera "La Michilía"	-104.06700	23.60000
13	Svacha and Gutiérrez	NA	2018	Exact	Baja California	Sierra de la Laguna	-109.98139	23.55000

Figure 8. Documented localities of *Vesperoctenus flohri* based on data from online databases, museum collections, and the literature. Tlaxcala, Veracruz, and Zacatecas are new state records; they originate from observations of *V. flohri* available online.

No reliable synapomorphies could be found for the Philinae + Vesperinae clade because some adults of Philinae are morphologically very generalized cerambyciforms or even chrysomeloids and all similarities are probably plesiomorphic or at least difficult to interpret. The interpretation of larval characters is also difficult (Svacha and Lawrence 2014: 35), particularly in light of the molecular results (Haddad et al. 2018), and since the larvae of *Vesperoctenus* are unknown. Saito (1990) described the female ovipositor and internal genital tract in one *Vesperus* and two Philinae (*Philus* and *Mantitheus*) and found them unique and very probably apomorphic in several characters: the ovipositor has an extremely long proctiger with two pairs of proctigeral baculi instead of one, the bursa copulatrix is small or absent and the spermathecal duct arises apically instead of sidewise as in many other cerambyciforms, the vaginal plates are virtually absent, and the spermatheca is very lightly sclerotized in *Vesperus strepens* (Fabricius) ("fairly stiff": Saito 1990: 250; confirmed by us on another dissected specimen) or membranous in the two philines (and also in *Vesperus luridus* Rossi dissected by us). In all those taxa, the spermatheca lacks a spermathecal gland. The ovipositor of *Vesperoctenus* (Figs 7a, b) is very similar to that of *Vesperus* and the two Philinae in Saito (1990), including the extremely long proctiger bearing two pairs of baculi, but the short sclerotized "digging" ovipositor of the Anoplodermatinae (Svacha and Lawrence 2014: fig. 2.1.5 K) is so derived that it would be difficult to make speculations regarding ovipositor morphology in a vesperid ancestor and claim the ovipositor synapomorphic for Vesperinae + Philinae. The intersegmental pouches (Figs 7a, b) also occur in *Vesperus* and Philinae and have no clear homologues in the derived anoplodermatine ovipositors (Svacha and Lawrence 2014), but they are relatively widespread in various cerambycoids and thus cannot be labelled as a synapomorphy of the non-anoplodermatine vesperid clade. In some Cerambycidae, they serve for storing yeast-like larval gut symbionts which are transferred onto the egg at oviposition. However, Schomann (1937) did not find any such symbionts in those pouches in *Vesperus* and their function in vesperids remains unknown. Also, the desclerotized spermatheca lacking a gland can no longer be considered a synapomorphy of the non-anoplodermatine clade. The spermatheca of another philine (*Heterophilus*), though also membranous, has a small spermathecal gland (Bi and Lin 2015), and *Vesperoctenus* possesses a relatively typical C-shaped moderately sclerotized spermatheca with a distinct gland (Fig. 7d). The reduced bursa copulatrix with missing vaginal plates and with the spermathecal duct arising apically is not entirely unique in the cerambyciforms, but it is worth noting that the only two dissected females of Anoplodermatinae (*Pathocerus* and *Migdolus*) have a large sac-like bursa copulatrix with the spermathecal duct arising sidewise near to its base (Svacha and Lawrence 2014).

Vesperoctenus, *Vesperus,* and known Philinae share the large thin flattened dorsal tentorial arms; in dissected Anoplodermatinae these arms are present but are short and tapering or rod-like, not broad and flattened. Large dorsal arms should be plesiomorphic and although the broad flat almost foliar dorsal ends are unusual, we cannot decide whether such dorsal arms were present in the vesperid ancestor and reduced in the Anoplodermatinae, or whether the broad flat dorsal ends may represent a synapomorphy of the Philinae and Vesperinae.

It would be difficult to list any synapomorphies of the Philinae because of the above mentioned generalized plesiomorphic morphology of some philine taxa. However, Philinae were represented by three relatively different genera (*Philus*, *Spiniphilus* Lin & Bi and *Mantitheus*, the latter with brachelytrous micropterous females resembling females of some *Vesperus*) in the mitochondrial phylogeny of Nie et al. (2021) and formed a strongly supported monophyletic clade sister to *Vesperus*. Potential synapomorphies of the Vesperinae (*Vesperoctenus* and *Vesperus*) include several characters:

1. Head with large inflated occipital region and then abruptly constricted into a narrow neck not including posterior gular region and metatentorial slits. This head type (similar to, but in details, different from that of some lepturine or lepturine-like Cerambycidae in which the neck does include metatentorial slits) is virtually unknown in other groups of the non-chrysomelid Chrysomeloidea.

2. Modified female metendosternite. Unlike the metendosternites in the flying males of the Anoplodermatinae which have the common basal stem but lack the laminae, those of the Philinae + Vesperinae clade are "hylecoetoid" (*sensu* Crowson 1938) in males (all are capable of flight), with a long basal stem and large laminae. Fig. 5c shows the male metendosternite of *Vesperus strepens*, that of male *Vesperoctenus* could not be studied in detail but should be similar because the males share the closely adjacent hind coxae (Fig. 5a) and the laminae are preserved even in the modified female metendosternite (see below). This hylecoetoid type also occurs in macropterous females (*Philus* dissected), though the basal stem may be shorter, and is plesiomorphic beyond doubt. Metendosternites of the brachy- or micropterous and (when bearing full egg load) often more or less physogastric females of some genera (*Vesperoctenus* and *Vesperus* of Vesperinae and *Mantitheus* and *Heterophilus* of Philinae) have apparently never been studied. Svacha and Lawrence (2014: 22) noted that the hind coxae are "widely separated in some flightless females" and depicted that character in *Vesperus* (their fig. 2.1.3 A), but none of these females were dissected. Females of *Vesperus* (*V. strepens*, *V. luridus* and *V. conicicollis* Fairmaire and Coquerel dissected) and *Vesperoctenus* have very broadly separated hind coxae and their metendosternite is strongly different from that of the males: The basal stem is completely missing and the arms abruptly diverge from the very base, making the anterior tendons broadly separate; the laminae may be preserved (they are strongly reduced in *Vesperus luridus* and *V. conicicollis*), but likewise widely apart (Figs 6b, d). However, this modification is obviously strongly adaptive and may develop parallelly. While in the female of *Mantitheus* a short basal stem is retained (Fig. 6f), in *Heterophilus* it is extremely reduced, approaching the situation in *Vesperus strepens* (Meiying Lin, pers. comm.). All females of Anoplodermatinae are flightless and the dissected females of *Pathocerus* and *Migdolus* also lack the basal stem and the arms abruptly diverge from the very base (but they lack the laminae like the males). This modification opens the space between abdomen and metathorax and enables protrusion of the egg mass into the posterior part of the metathoracic cavity (confirmed in the dissected female of *Mantitheus* which was collected from its soil pupal chamber with full egg load).

3. Wing, even in macropterous specimens, with at most, a narrow reduced wedge cell (missing in some *Vesperus*); that cell is always large in macropterous Philinae (figures in Lin and Bi 2011, or Svacha and Lawrence 2014). The invariable absence of that cell in all Anoplodermatinae should be a parallel reduction independent from that in some species of *Vesperus*.

4. *Vesperus* and *Vesperoctenus* share the prominent procoxae and reduced narrow intercoxal process. In Philinae the intercoxal process is high and broad and the procoxae, although relatively prominent, are inserted under the process and articulating on it, occasionally by a distinct tubercle (Svacha and Lawrence 2014: fig. 2.1.5 H). With the exception of the extremely derived *Hypocephalus*, the situation is virtually identical in the Anoplodermatinae including the occasional presence of the articulating tubercle (e.g., in *Anoploderma*). Thus, the free prominent coxae of *Vesperus* and *Vesperoctenus* could be synapomorphic.

Autapomorphies of *Vesperoctenus* include: the 12-segmented antennae (the terminal flagellomere may be appendiculate but never completely divided in the other Vesperidae), possibly the very broad (high) metanepisternum (Fig. 4b, narrower in all other studied vesperids), and the extremely long and dense male pilosity if we consider the similarly hairy males in a few Anoplodermatinae a parallel development (see above). The more or less projecting lateral postclypeus should also be autapomorphic because various postclypeal modifications in some Anoplodermatinae are different in details.

No reliable synapomorphies could be found for the sister genus *Vesperus*. Females often have shortened elytra, but in some species, they are about as well developed as in females of *Vesperoctenus* and in *Vesperus macropterus* Sama even the female wings are fully developed and can be used (together with the well-developed elytra) for parachuting from the tall dry herbs whose inflorescences the females oviposit in (Sechi 2011). The desclerotized spermatheca lacking the spermathecal gland (which can no longer be considered synapomorphic for the Philinae + Vesperinae clade) would be a synapomorphy of *Vesperus* if its presence is universal within the genus, but so far it can be confirmed for only two species (*V. strepens* and *V. luridus*).

Other characters occasionally employed in the classification of this group are not helpful in evaluating the relationships and taxonomic position of *Vesperoctenus*. The lateral pronotal margin or carina is present in the Anoplodermatinae and virtually absent in Vesperinae, but it may be present or absent with various transitions in Philinae. The most complete pronotal margin occurs in the flightless females of *Heterophilus* (Lin and Bi 2011; Bi and Lin 2015) which are almost certainly far from the philine groundplan. The mesoscutal stridulatory file is absent in Anoplodermatinae and *Vesperoctenus*, but present to absent in Philinae, and distinct rudiments were also found in a species of *Vesperus* (Svacha and Lawrence 2014: fig. 2.1.4 G).

4.3. Distribution and conservation status

Vesperoctenus flohri has rarely been collected and historically appears to have a very narrow geographic distribution which raises concerns about its conservation status. Few specimens of *V. flohri* are available in museum collections and only a handful of collection records exist in the published literature which have so far limited the distribution of this species to only three Mexican states (Baja California Sur, Durango, and Nuevo Leon). Interestingly, we found a few online observations of the species (on Facebook and iNaturalist) that expand its known geographic distribution to include the Mexican states of Tlaxcala, Veracruz, and Zacatecas (Fig. 8). The new state records in Veracruz and Tlaxcala confirm the presence of *V. flohri* in the Trans-Mexican Volcanic Belt, whereas the ones in Zacatecas might be a possible connection between previous records of the species in Nuevo Leon and Durango. These new records also expand the known habitat of *V. flohri* which is oak/pine forests and grasslands in northern Mexico. The locality in Veracruz (at 2520 m) is the highest altitude where *Vesperoctenus* has been recorded (considering only those records with altitude data), is characterized by dry desert scrub with *Opuntia* cacti and *Yucca*, and its annual temperature varies between 6°C and 11°C (Santiago Jaume-Schinkel, pers. comm.; Lara-Lagunes et al. 2017). On the other hand, vegetation in Nanacamilpa, Tlaxcala is composed of coniferous and latifoliate forest, with subhumid climate and average annual temperature between 12°C and 18°C (INEGI 2009). Finally, *V. flohri* recorded in Sierra de Organos, Zacatecas were attracted to light from a cabin surrounded by grassland and *Pinus*-*Quercus* forests, with a temperate subhumid climate and an average annual temperature between 12°C and 18°C (Juan Carrillo, pers. comm.; CONANP 2003b).

Sixty percent of *Vesperoctenus* records are located in or near national and state protected natural areas with high biological diversity (CONANP 2020). These areas also host countless other endemic species and have historically been under critical threat of mismanagement due to various political and socioeconomic factors (Valdez et al. 2006). For example, the Sierra de la Laguna (the collection site of this study's *V. flohri* specimen) is an isolated mountain range at the southern end of the Mexican State of Baja California Sur. It was declared a Biosphere Reserve by a Mexican presidential decree on June 6, 1994 (DOF 1994), and subsequently by UNESCO (United Nations Educational, Scientific, and Cultural Organization) in 2003 (UNESCO 2011). This geographically isolated mountain complex is comprised of tropical dry deciduous forest and semi-desert ecosystems with high levels of diversity and endemism and is home to several endangered species and species new to science (e.g., Riemann and Ezcurra 2005; León de la Luz and Breceda 2006; Vandeplank et al. 2016). This protected natural area has recently been threatened by an open-pit gold mining project that would negatively impact habitat and water quality in addition to having numerous other harmful outcomes that would impact the reserve (Vandeplank et al. 2016). Mining could cause irrevocable detrimental effects to the diverse species inhabiting the mountain range, including *V. flohri*. Moreover, morphological differences such as that between the female wings of the specimens from Baja California Sur and Durango (see above) may indicate a substantial degree of genetic differentiation between populations. Thus, we argue that the conservation status of *V. flohri* necessitates assessment considering how little we know of its biology and ecology, our growing knowledge of its distribution and habitat, and given the persistent threats to known populations posed by human-induced habitat loss and degradation.

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