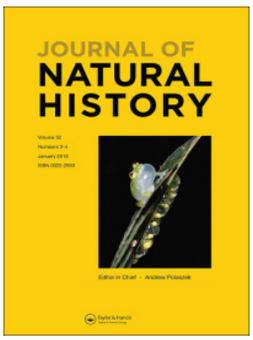

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ABSTRACT

Aximopsis gabrielae Zhang, Gates and Campos sp. nov. is described from southern Mexico in the Yucatan Peninsula, Mexico. This species is a koinobiont gregarious larval-pupal endoparasitoid of the caterpillar of *Quadrus cerialis* (Stoll) (Lepidoptera: Hesperiidae) feeding on the shrub *Piper amalago* L. (Piperaceae) in the semi-evergreen forest. This is the first record of *Aximopsis* parasitoids on Hesperiidae (Lepidoptera). Morphological, biological, ecological and geographical data are integrated to delineate the new species.

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Introduction

Discovery of species and their interactions is essential to develop a deeper understanding of biodiversity (Wilson 2017). Around 75% of described species involve interactions between plants, herbivores and natural enemies (Price 2002). The study of these trophic interactions contributes to understanding natural history, ecology and evolution (Thompson 2014; Travis 2020), specialisation (Dyer et al. 2007; Forister et al. 2012), and species distributions (Giannini et al. 2013).

The pantropical and megadiverse genus *Piper L.* is made up of more than 1300 species in the Neotropics (Quijano-Abril et al. 2006), is abundant and locally diverse (Gentry 1982), and supports complex communities of arthropods (Marquis 1991; Vanin et al. 2008). Recent studies have shown that the chemical diversity of *Piper* can decrease caterpillar host immune responses and increase the recruitment of parasitoids (Richards et al. 2010, 2015; Glassmire et al. 2016; Salazar et al. 2016; Slinn et al. 2018). *Piper amalago* L. is a common species in the American tropics, frequently found on the banks of rivers and secondary roadside formations (Guimarães and Giordano 2004). *Quadrus cerialis* (Stoll, 1782) (Lepidoptera: Hesperiidae), is a *Piper* generalist species distributed throughout the Neotropics (Beccaloni et al. 2008; Warren

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et al. 2012). Long-term rearing programmes in Costa Rica reported *Q. cerialis* feeding on leaves of more than 25 *Piper* species and being parasitised by braconid, ichneumonid, eulophid and bethylid wasps, as well as tachinid flies (Janzen and Hallwachs 2012; Dyer and Gentry 2021). In an extensive survey along the Yucatan Peninsula, Mexico (Campos-Moreno et al. 2021), we found 14 individuals of *Q. cerialis* feeding on *P. amalago*, and one of these caterpillars yielded parasitoids belonging to *Aximopsis* Ashmead (Eurytomidae).

The genus *Aximopsis sensu lato* (Eurytomidae) was recently redefined by Lotfalizadeh et al. (2007) to include *Conoaxima* Brues, *Eurytomaria* Masi, *Mesoeurytoma* Cameron, *Aximogastroma*, and the *nodularis* species group of *Eurytoma* Illiger, based on the morphological character of having superficial or absent posterior tentorial sulci. The 41 described species of *Aximopsis s.l.* are found worldwide except in Australia and Antarctica (Delvare et al. 2019; Noyes 2021), and the genus includes many undescribed species in tropical regions. *Aximopsis* species are parasitoids of endophytic insects, living in branches, stems or leaf mines; most known species are parasitoids of Coleoptera and Hymenoptera (Zerova 1995, 2010; Gates et al. 2006; Gates 2009; Delvare et al. 2019; Naghizadeh et al. 2019; Noyes 2021), but also of caterpillars of several lepidopteran families (e.g. Gates and Delvare 2008; Lotfalizadeh and Hosseini 2014; Tavares et al. 2015).

A new interaction involving *P. amalago* (Piperaceae), *Q. cerialis* (Lepidoptera: Hesperiidae) and a new species of *Aximopsis* is reported and described in this paper.

Materials and methods

We collected a caterpillar of *Q. cerialis* feeding on *P. amalago* (Figure 1(a)) in a patch of semi-evergreen forest in the south-western Yucatan Peninsula (18°36'26.8" N, 90°48'14.4" W) within Campeche State, in a forest reserve of Comisión Nacional Forestal (CONAFOR), established in 1971 (SARH 1981), with an upper canopy dominated by *Spondias mombin* L. (Anacardiaceae), *Pouteria campechiana* (L.) (Sapotaceae) and *Brosimum alicastrum* Sw. (Moraceae). The caterpillar collected was reared in the laboratory at El Colegio de la Frontera Sur (ECOSUR) in a plastic cup covered with mesh, under ambient conditions, until adult parasitoids emerged; the pupal remains from which the parasitoids emerged were preserved in ethanol. The caterpillar was photographed in the laboratory using a Leica DMLB optical stereo microscope with a Nikon D850 digital camera, and identified by Lee Dyer and Carmen Pozo (Figure 1(b)). The caterpillar pupated after 7 days, and 12 days later adults of *Aximopsis* (Eurytomidae) emerged (Figure 2).

Ethanol-preserved specimens were dehydrated using increasing concentrations of ethanol and transferred to hexamethyldisilazane (HMDS) (Heraty and Hawks 1998) before point-mounting. The specimens were identified using a Leica M205C stereomicroscope with 10× oculars and a Leica LED ring light source for point-mounted specimen observation. We took scanning electron microscope (SEM) images with a Hitachi TM3000 (Tungsten source). Body parts of disarticulated specimens were adhered to a 12.7 × 3.2 mm Leica/Cambridge aluminium SEM stub with a carbon adhesive tab (Electron Microscopy Sciences, #77825-12). Stub-mounted specimens were sputter coated with gold-palladium using a Cressington Scientific 108 Auto from multiple angles to ensure complete coverage (~20–30 nm coating). Coloured images were obtained with a Canon 60D DSLR, with a Canon MP-E 65 mm F/2.8 Macro photo lens or a Mitutoyo M Plan Apo 10× objective mounted on to the Canon EF Telephoto 70–200 mm zoom lens, and a Canon MT–24EX Macro Twin Lite Flash (Tokyo,

Figure 1. (a) *Piper amalago* (Piperaceae). Photo by Eric Tepe. (b) Caterpillar of *Quadrus cerialis* (Hesperiidae). Photo by Humberto Bahena-Basave.

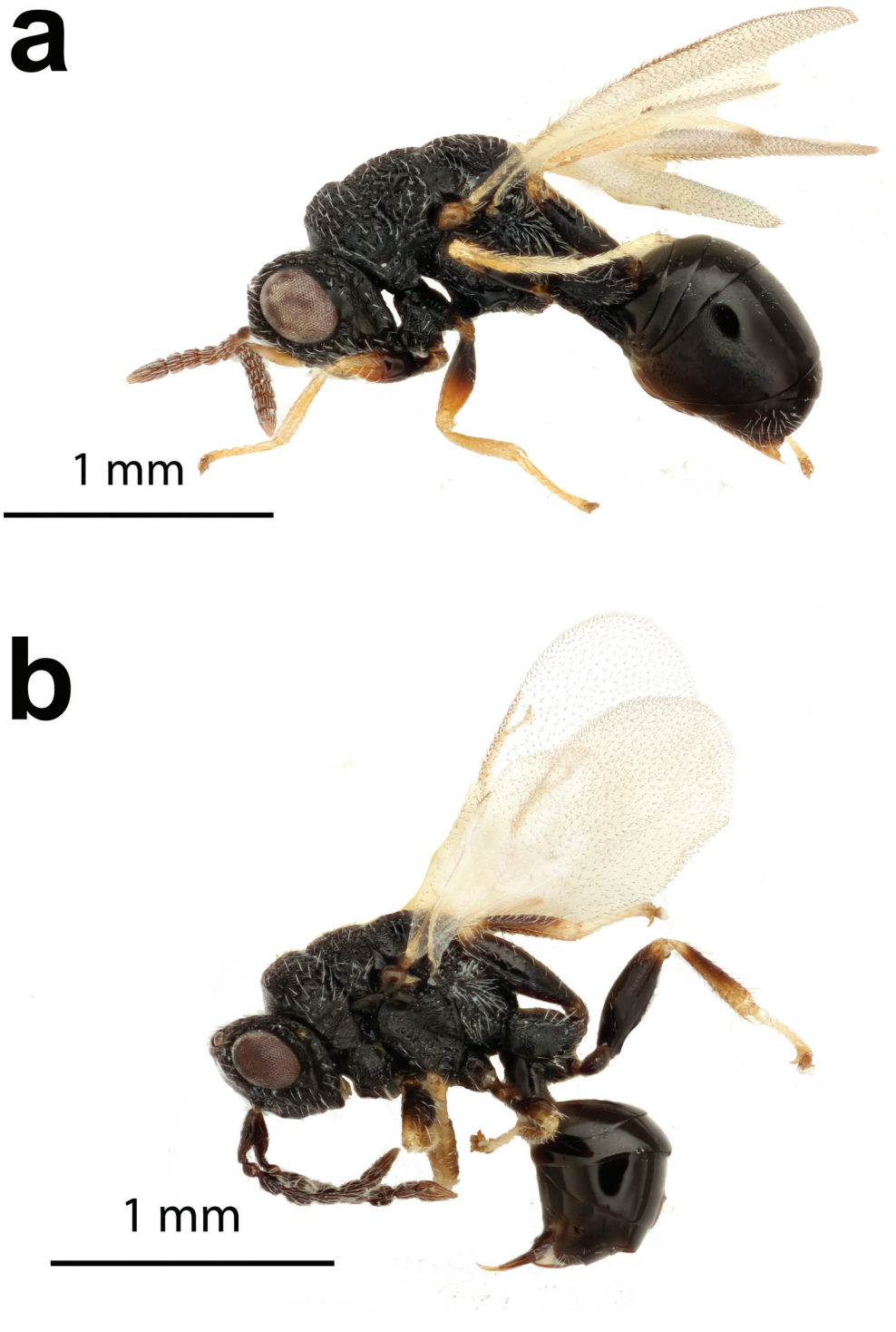

Figure 2. *Aximopsis gabrielae* sp. nov. (a) Female lateral habitus. (b) Male lateral habitus. Photos by Miles Zhang.

Japan) with custom-made diffusers to minimise hot spots. Images were saved as TIF files and focus stacked using Zerene Stacker v. 1.04. Image editing was done in Adobe Photoshop, and plate layout was performed in Inkscape.

Terminologies used for surface sculptures follow Harris (1979), while the morphology follows Gibson (1997), Lotfalizadeh et al. (2007) and Cruaud et al. (2021). The following measurements and abbreviations were used: F1–Fn, the first and the following flagellomeres; POL (post-ocellar distance), the distance between the inner margins of the posterior ocelli; OOL (ocellar–ocular distance), the distance from the outer margin of lateral ocellus to the inner margin of compound eye; LOL (lateral–ocular distance), the distance between lateral and frontal ocelli; St1–Stn, the first and the following gastral sternites; Gt1–Gtn, the first and the following gastral tergites. Voucher specimens were deposited in the ECOSUR Arthropod Collection (ECO-CH-AR) and the National Museum of Natural History (NMNH). Partial mtDNA cytochrome c oxidase subunit 1 (*COI*) for *A. gabrielae* (559 bp) was acquired as a by-product of an ongoing phylogenomic study of Eurytomidae using Ultraconserved Elements (Zhang et al. unpublished data), with GenBank accession number MZ644991.

Results

A caterpillar of *Quadrus cerialis* was collected, and later about 80 adults of an Eurytomidae wasp emerged from the pupae. A study of these wasps revealed that this species belongs to the genus *Aximopsis* and is new to science. Its description is given below.

Taxonomy

Family EURYTOMIDAE **Walker, 1832**

Subfamily EURYTOMINAE **Walker, 1832**

Genus *Aximopsis* Ashmead 1904

Description

Aximopsis gabrielae ***Zhang, Gates and Campos, sp. nov.***

(Figures 2–8)

Female. Holotype body length 2.4 mm.

Diagnosis

Aximopsis gabrielae can be distinguished from other members of *Aximopsis s.l.* by the absence of horns on the vertex and mesodorsal pronotum (Figures 2(a–b), 3(a)), *sensu* Gates et al. (2006), the clypeus ventrally protruding, the protuberant supraclypeal area forming a bump (Figures 3(a), 4(b)) and the very short, cup-like funiculars in the female. The male has four

funiculars very shortly tapering basally and not at all tapering apically, and a two-segmented clava, with a slight division near the tip (Figure 8(a)), while all other known species have strongly tapering F1–F4, giving the appearance of a peduncle for the following segment.

Type material

Holotype ♀. Mexico, Campeche, Escarcega Forestal Reserve CONAFOR, 15 August 2018 18°36'26.8'' N, 90°48'14.4'' W (D.Campos – C.Pozo Leg.) Ex. Pupa *Q. cerialis*. USNMENT01558247. Paratypes: same locality as holotype (8♂, 7♀) (USNMENT01558218, 01558221, 01558290, 01558326, 01558422, 01558427, 01558433, 01558523, 01558547, 01558557, 01558586, 01558603, 01558609, 01558654, 01558659) (6 ♂♂, 50♀♀) (ECO-CH-AR 0596- 0651).

Colour. Black except for the following: flagellomeres, tegula, wing veins brown; scape, pedicel, apices of femora, tibiae, tarsi, ovipositor sheaths testaceous (Figure 2(a)).

Head. Rectangular and 1.25× as wide as long in dorsal view, with umbilicate sculpture and bearing filiform, adpressed and sparse setae, those on lower face longer and directed downwards, the others shorter and directed upwards. Lower face strigose, the carinulae converging towards edge of oral fossa and extending above to antennal toruli, clypeus distinctly protruding, its surface forming a bump, mandible weakly tridentate (Figure 3(a)). Malar sulcus absent, malar space 0.62× eye height. Genal carina present, malar sulcus forming a small asetose, imbricate band below eyes. Toruli positioned above lower ocular line, diameter of torulus 1.5× that of the intertorular space. Scrobal depression carinate laterally, with parallel edges, ventromedially carinate. Vertex imbricate, POL:OOL:LOL ratio 2.5:1.4:1. Head posteriorly with postgenal lamina, postgenal groove straight, fading about at level with upper edge of hypostomal carina, and slightly converging ventrally, ending far from genal carina. Subforaminal bridge transversely strigulose and with broad median strip of ornamentation. Posterior tentorial sulci present and deep (Figure 4(a)).

Antenna. Ratio of scape (minus radicle):pedicel:anellus:F1:F2:F3:F4:F5:club 12:4:1:4.2:4:4:3.8:3:8.8; pedicel chalice-shaped; funiculars very short with F2–F4 transverse and cupuliform; funiculars thus bearing a single row of longitudinal sensilla and two whorls of setae, shorter than relevant segment; clava clearly two-segmented (Figure 3(b)).

Fore wing. Ratio of marginal:postmarginal:stigmal veins 1.8:1.2:1. Costal and basal cells and speculum bare except for basal and cubital folds with a line of setae, short setation on the distal parts of the wing (Figure 6(a)).

Mesosoma. Mesosoma 1.33× as long as broad; pro- and mesonotum umbilicate, notauli complete, shallow (Figure 6(b)); lateral prepectus triangular, smooth, sublateral prepectus with deep pit; ventral surface of prepectus with median tooth (Figure 5(b), arrow). Adscrobal area with three long and erect setae. Mesopleuron strigose, epicnemium flat, entirely carinately delimited (Figure 5(a)), anterior projection of ventral shelf elevated, narrowly projecting anteriorly (Figure 5(b)). Ventral part of the femoral depression with a large areola (Figure 5(b)). Metepimeron regularly umbilicate and bearing long, hair-like setae. Postscutellum with inverted V-like raised strip forming a very obtuse angle.

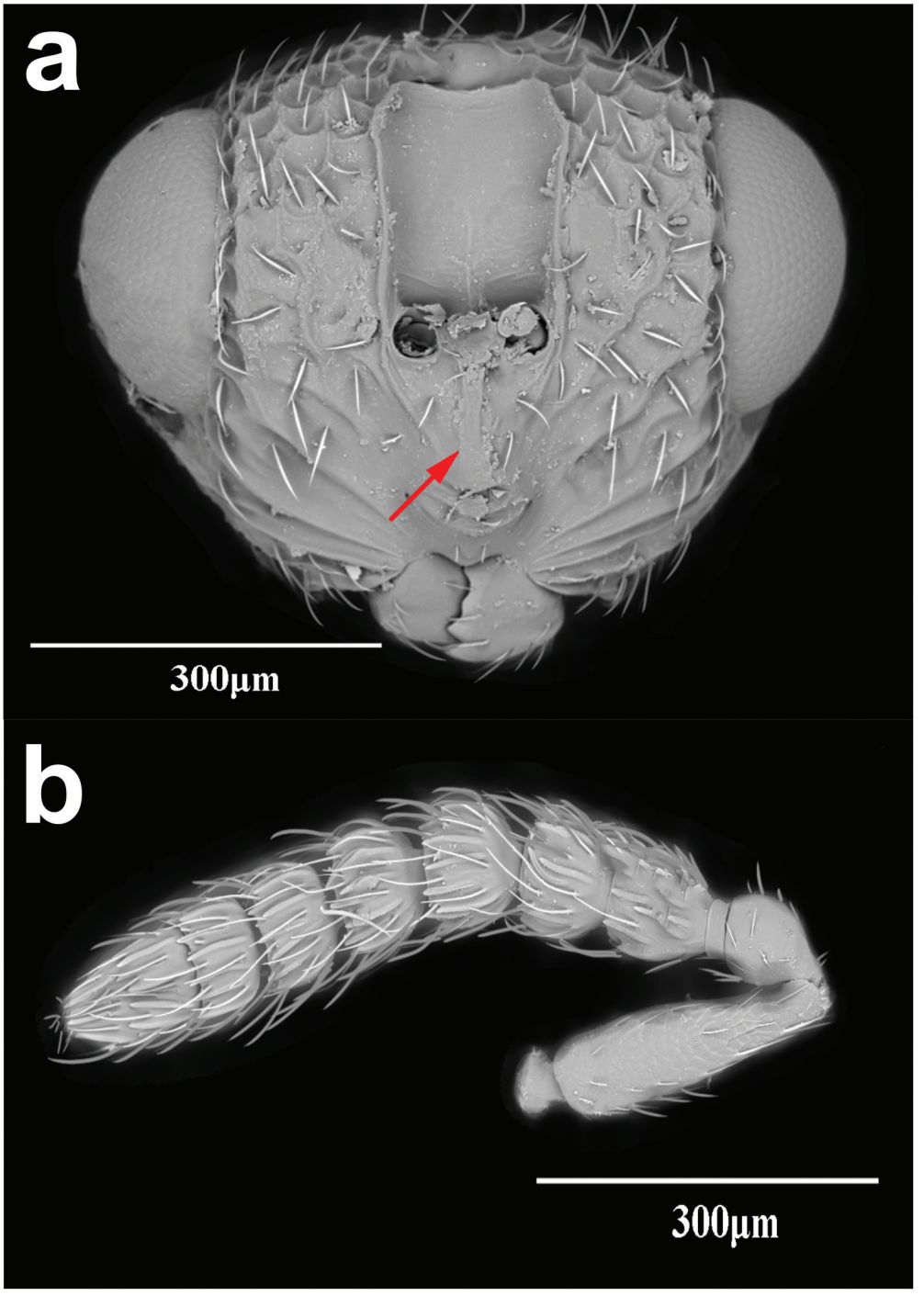

Figure 3. *Aximopsis gabrielae* sp. nov. (a) Head in frontal view, arrow pointing to protuberant supraclypeal area. (b) Female antenna. Photos by Miles Zhang.

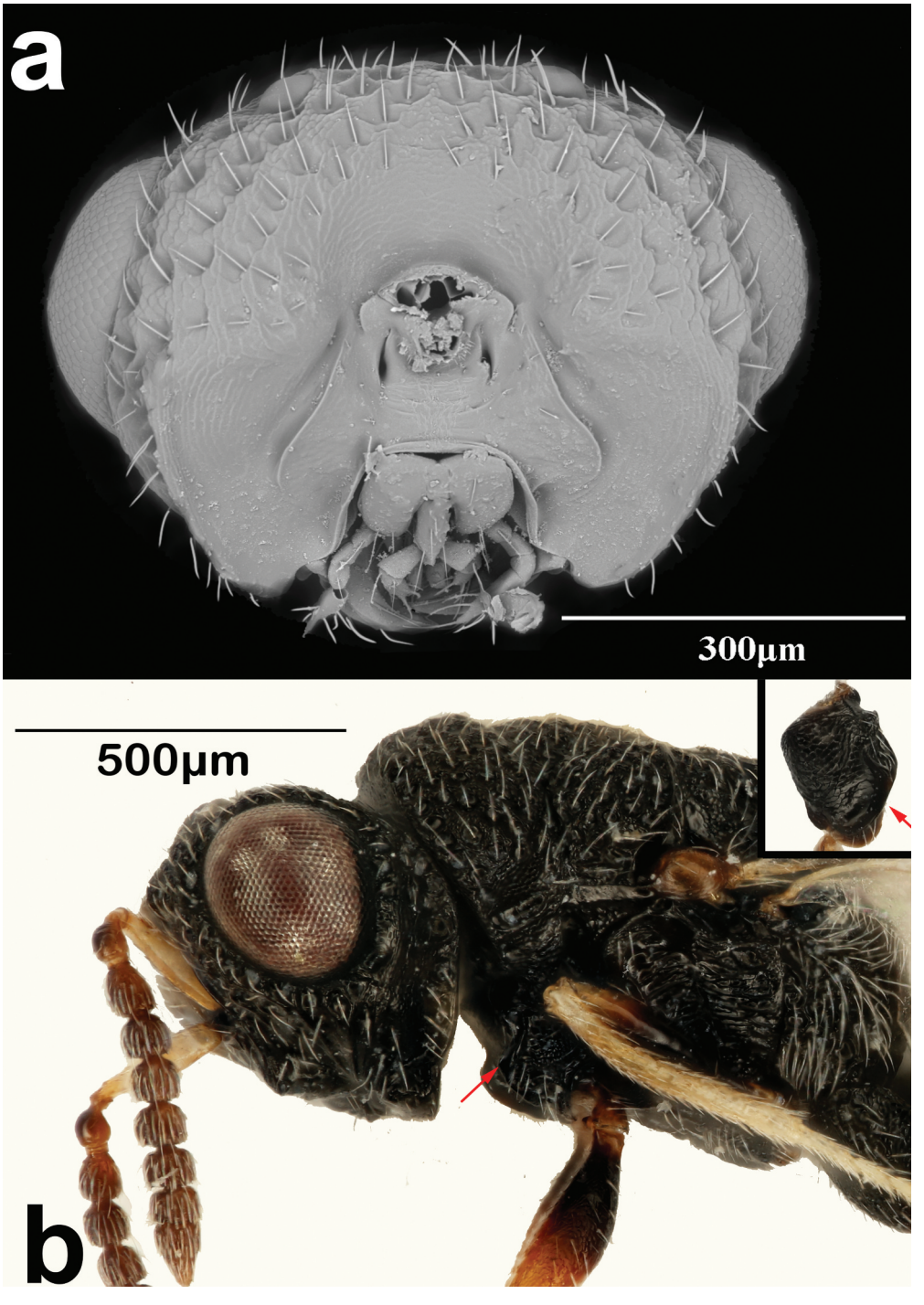

Figure 4. *Aximopsis gabrielae* sp. nov. (a) Head in posterior view. (b) Female, anterolateral view; inset: procoxa in anterior view, arrow pointing to the oblique groove. Photos by Miles Zhang.

Propodeum flattened medially, the relevant surface carinately delimited laterally, reticulate anteriorly and transversely strigulose laterally, followed by subquadrate adpetiolar areola; propodeum coarsely umbilicate laterally and bearing filiform, erect setae (Figure 7(b)).

Leg. Oblique carina on procoxa forming a shelf for reception of lower head (Figure 4(b), arrow), imbricate. Mesocoxa without lamella; metacoxa bare dorsally, metatibia with a row of adpressed setae, subequal to the width of the metatibia.

Metasoma. Petiole longer than metacoxa, cylindrical, rugose to alveolate, 0.4× as long as gaster in lateral view; dorsally with median carina leading to anterior teeth above the 'can-opener' shaped articular area; no ventral transverse carina delimiting petiole from petiolar part of St1. Gaster elliptical in lateral view, narrowly tapering posteriorly (Figure 7(a)), smooth, setose from Gt4. Gt4 much longer than other tergites, emarginate posteriorly in dorsal view.

Male. Length 2.2 mm. Colour largely similar to females, except antennae wholly black, and tibiae dark brown; sculpture as described for females (Figure 2(b)). Antenna with four funiculars longer than wide, cupuliform, funiculars with single row of longitudinal sensilla and two or more rows of filiform, erect setae longer than their bearing segment. Clava two-segmented, tip of clava tapering (Figure 8(a)). Gastral petiole in lateral view 0.65× as long as metasoma, cylindrical, weakly reticulate to smooth. Metasoma triangular in shape (Figure 8 (b)).

Variation. Female body length ranges from 2.2 to 2.5 mm, male from 2 to 2.3 mm.

Biology. A gregarious larval-pupal endoparasitoid of *Quadrus cerialis* (Lepidoptera: Hesperiidae) feeding on *Piper amalago* (Piperaceae). Caterpillars of *Q. cerialis* are abundant in August (unpublished data), the month when *A. gabrielae* parasitised one of the caterpillars collected.

Distribution

Southern Mexico, in the Yucatan Peninsula, in a forest reserve of semi-evergreen tropical forest. This species is probably widespread through the Neotropical Region, where *Q. cerialis* and *P. amalago* are distributed.

Etymology

Aximopsis gabrielae is named in honour of Gabriela Pérez-Lachaud, who has dedicated most of her life to the study of the ecology and behaviour of parasitoids in south-eastern Mexico.

Discussion

This is the first report of *Aximopsis* parasitising larvae of Hesperiidae; our study contributes to the knowledge of a group of species within the genus *Aximopsis* parasitising Lepidoptera. Several species formerly included in *Eurytoma* but that conform to the generic concept of *Aximopsis* of Lotfalizadeh et al. (2007) parasitise pyralid moth larvae. For example, *Aximopsis oryzivora* (Delvare) attacks the stem borer *Sesamia calamistis* Hampson (Noctuidae) (Delvare 1988 cited in Gates and Delvare 2008), and *Aximopsis*

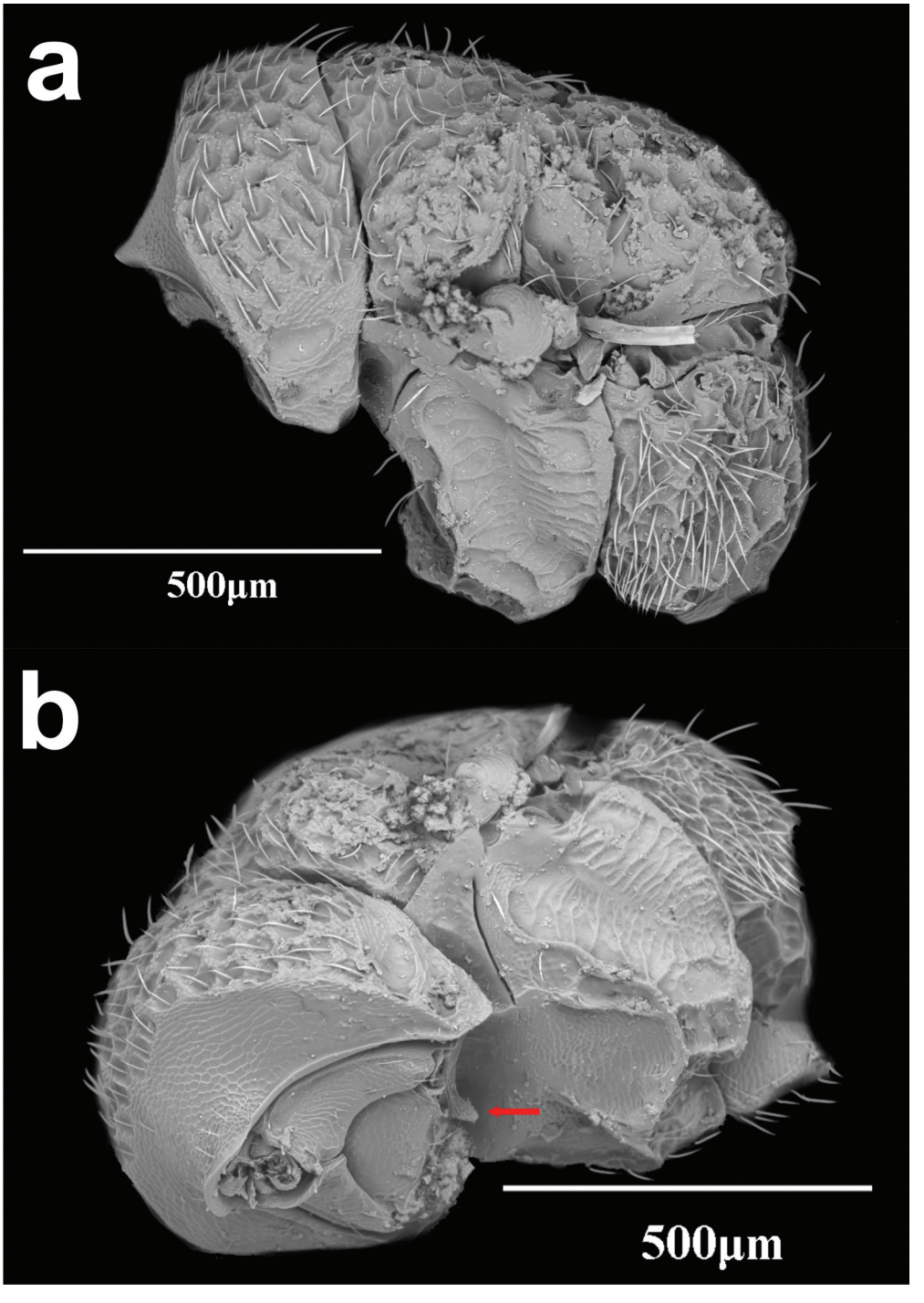

Figure 5. *Aximopsis gabrielae* sp. nov. (a) Mesosoma in lateral view. (b) Mesosoma in lateroventral view, arrow pointing to median tooth on prepectus. Photos by Miles Zhang.

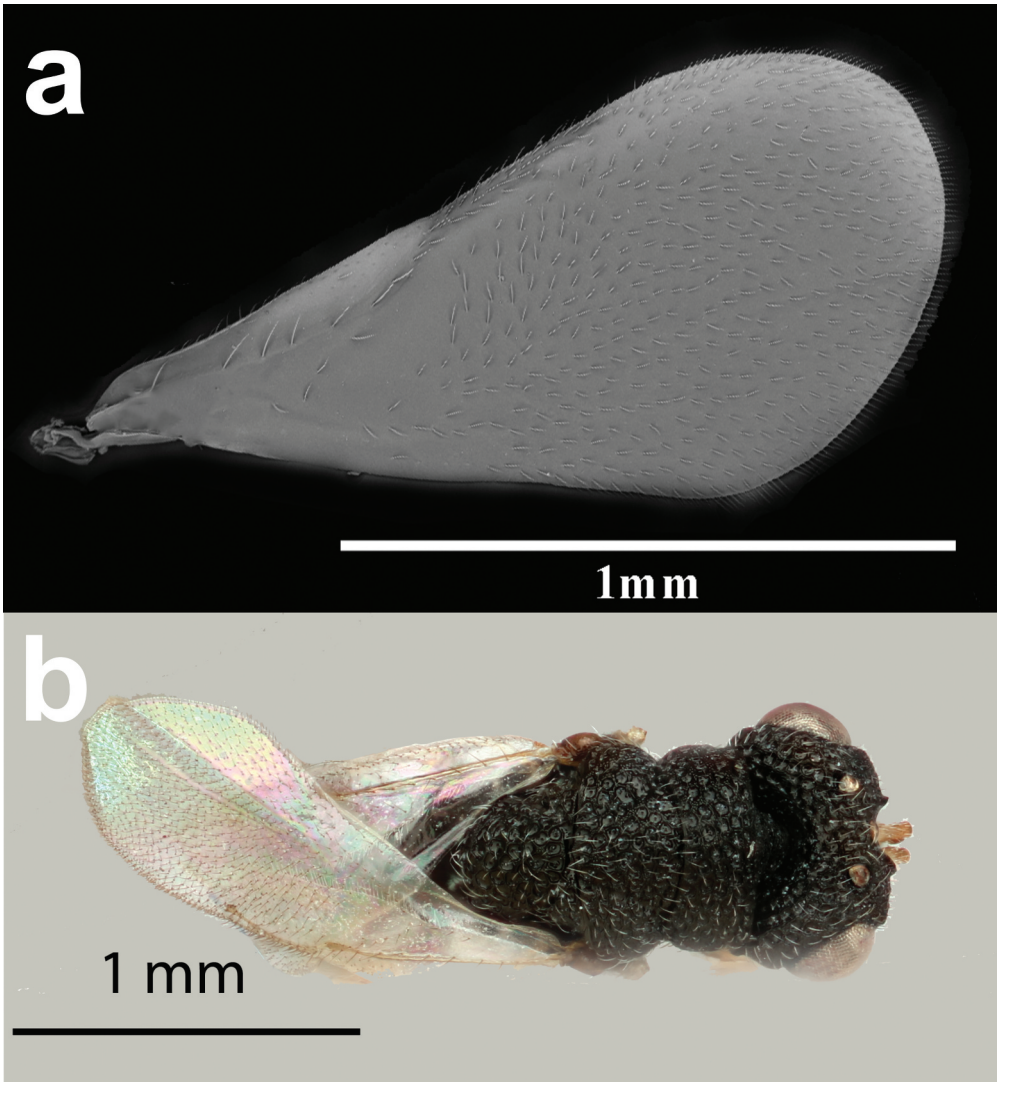

Figure 6. *Aximopsis gabrielae* sp. nov., female. (a) Fore wing. (b) Dorsal habitus. Photos by Miles Zhang.

augasmae (Zerova) and *Aximopsis* sp. near *ghazvini* (Zerova) parasitise *Etiella zinckenella* (Treitschke) (Pyralidae) (Lotfalizadeh and Hosseini 2014). Another undescribed *Aximopsis* species was reared from the pupae of *Thyrinteina arnobia* Stoll (Geometridae) and *Thagona tibialis* Walker (Erebidae) (Tavares et al. 2015).

As already stated, *Aximopsis* species are parasitoids of endophytic insects. Interestingly, this is the first time a member of *Aximopsis* is recorded attacking caterpillars that build shelters. *Quadrus* is a concealed feeder, and according to Gentry and Dyer (2002), concealed feeders experience very high levels of parasitism. *Quadrus cerialis* has been recorded as host to *Apanteles* Förster (Braconidae), *Goniozus* Förster (Bethylidae), *Hyposoter* Förster (Ichneumonidae) and *Siphosturmia* Coquillett (Tachinidae) (Janzen

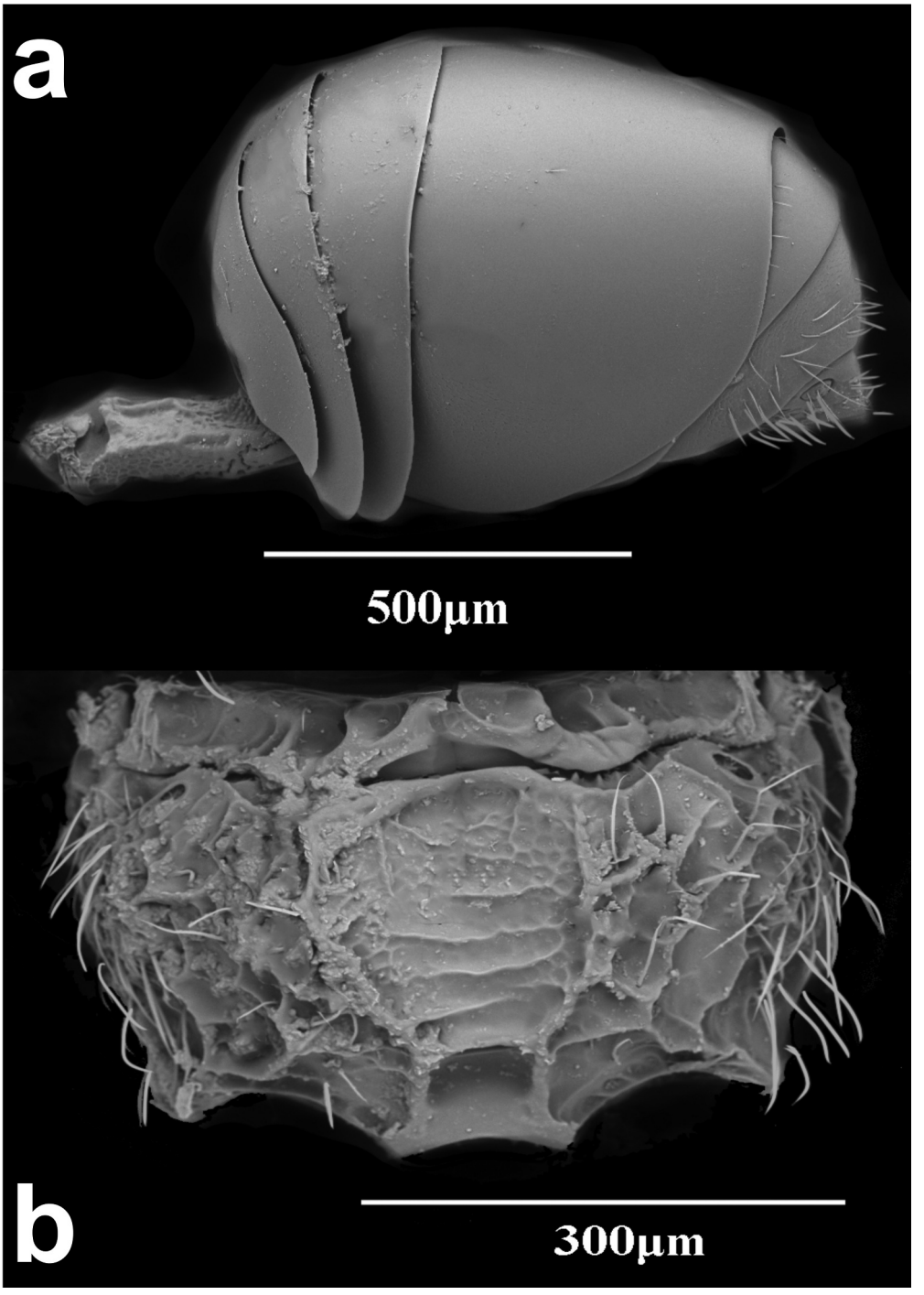

Figure 7. *Aximopsis gabrielae* sp. nov., female. (a) Metasoma in lateral view. (b) Propodeum in dorsal view. Photos by Miles Zhang.

and Hallwachs 2012; Dyer and Gentry 2021). Our finding of a new species of eurytomid

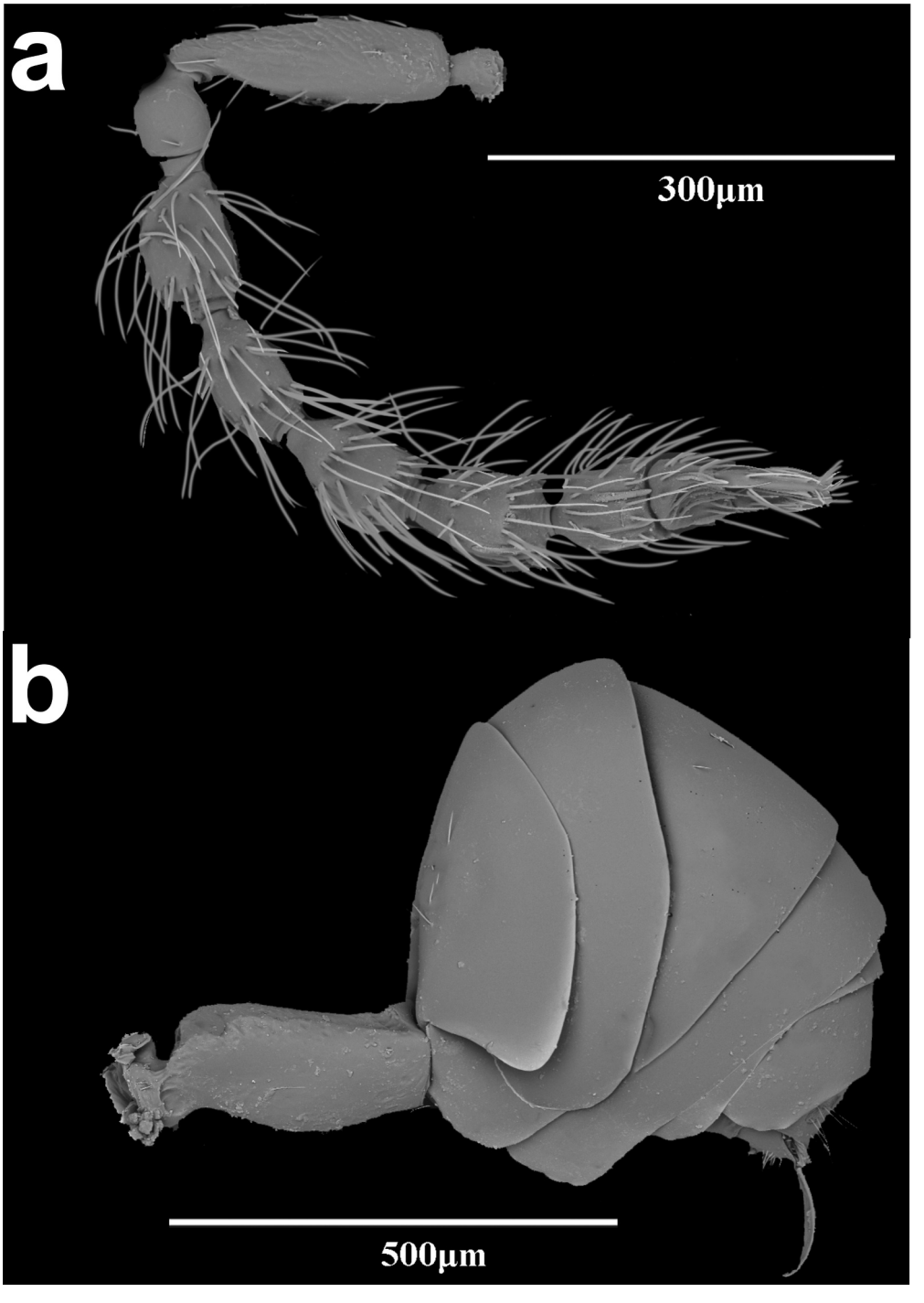

Figure 8. *Aximopsis gabrielae* sp. nov., male. (a) Antenna. (b) Metasoma in lateral view. Photos by Miles Zhang.

attacking *Q. cerialis* adds to the diversity of parasitoids of this species. Baer and Marquis

(2020), studying a community of caterpillars that build shelters, found a negative correlation between parasitism and predation of the herbivore, which was modulated by shelter traits. Their results provide support for the parasitoid enemy-free space hypothesis (Murphy et al. 2014), which proposes that parasitoids prefer hosts that are less likely to be killed by predators.

In addition to the ecological differences, *A. gabrielae* differs from other known *Aximopsis s.l.* morphologically in the presence of deep posterior tentorial sulci, which are absent or superficial in other species. Other notable characters include the protruding clypeus, very short funiculars in females, and the segmentation of the flagellum in the males. Based on preliminary phylogenomic data (Zhang et al. unpublished data), *A. gabrielae* groups with other Neotropical *Aximopsis* species, but the genus itself is paraphyletic.

Given the Neotropical region's undescribed diversity, additional taxonomic, ecological and phylogenetic studies of *Aximopsis* are needed to fully understand its host range and generic limits. Nevertheless, knowing the interaction with *Q. cerialis/P.amalago* species gives us some idea about the potential distribution of *A. gabrielae* and expands our knowledge of the biology of the genus *Aximopsis*.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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References

Baer CS, Marquis RJ. 2020. Between predators and parasitoids: complex interactions among shelter traits, predation and parasitism in a shelter-building caterpillar community. Funct Ecol. 34:2186–2198. doi:10.1111/1365-2435.13641.

Beccaloni GW, Viloria AL, Hall SK, Robinson GS. 2008. Catalogue of the host plants of the Neotropical butterflies. Zaragoza (Spain): Sociedad Entomológica Aragonesa.

Campos-Moreno DF, Dyer LA, Salcido D, Massad TJ, Pérez-Lachaud IG, Tepe E, Whitfield JB, Pozo C. 2021. Importance of Interaction rewiring in determining spatial and temporal turnover of tritrophic (*Piper*-caterpillar-parasitoid) interactions in the Yucatan Peninsula, Mexico. Biotropica. 53:1071–1081. doi:10.1111/btp.12946.

Cruaud A, Delvare G, Nidelet S, Sauné L, Ratnasingham S, Chartois M, Blaimer BB, Gates M, Brady SG, Faure S, et al. 2021. Ultra-conserved elements and morphology reciprocally illuminate conflicting phylogenetic hypotheses in Chalcididae (Hymenoptera, Chalcidoidea). Cladistics. 37:1–35. doi:10.1111/cla.12416.

Delvare G. 1988. Revision of the *Eurytoma* (Hym.: Eurytomidae) of West Africa described by Risbec. Ann Soc Entomol Fr. 24(2):117–149.

Delvare G, Stojanova AM, Benoit L, Lecomte J, Askew RR. 2019. Exploring insect biodiversity: the parasitic Hymenoptera, chiefly Chalcidoidea, associated with seeds of asphodels (Xanthorrhoeaceae), with the description of nine new species belonging to Eurytomidae and Torymidae. Zootaxa. 4597:1–90. doi:10.11646/zootaxa.4597.1.1.

Dyer LA, Gentry GL. 2021. Caterpillars and parasitoids of La Selva Costa Rica; [accessed 2021 Jan 12]. http://www.caterpillars.org .

Dyer LA, Singer MS, Lill JT, Stireman JO III, Gentry GL, Marquis RJ, Ricklefs RE, Greeney HF, Wagner DL, Morais HC, et al. 2007. Host specificity of Lepidoptera in tropical and temperate forests. Nature. 448:696–699. doi:10.1038/nature05884.

Forister ML, Dyer LA, Singer MS, Stireman JO III, Lill JT. 2012. Revisiting the evolution of ecological specialization, with emphasis on insect–plant interactions. Ecology. 93:981–991. doi:10.1890/11-0650.1.

Gates MW. 2009. A new species of *Aximopsis sensu lato* Ashmead (Hymenoptera, Chalcidoidea, Eurytomidae) parasitic on *Euglossa* spp. (Hymenoptera, Apidae). ZooKeys. 20:165–174. doi:10.3897/zookeys.20.137.

Gates M, Delvare G. 2008. A new species of *Eurytoma* (Hymenoptera: Eurytomidae) attacking *Quadrastichus* spp. (Hymenoptera: Eulophidae) galling *Erythrina* spp. (Fabaceae), with a summary of African *Eurytoma* biology and species checklist. Zootaxa. 1751:1–24. doi:10.11646/zootaxa.1751.1.1.

Gates MW, Metz MA, Schauff ME. 2006. The circumscription of the generic concept of *Aximopsis* Ashmead (Hymenoptera: Chalcidoidea: Eurytomidae) with the description of seven new species. Zootaxa. 1273:9–54. doi:10.11646/zootaxa.1273.1.2.

Gentry AH. 1982. Neotropical floristic diversity: phytogeographical connections between Central and South America, Pleistocene climatic fluctuations, or an accident on the Andean orogeny? Ann Mo Bot Gard. 69:557–593. doi:10.2307/2399084.

Gentry GL, Dyer LA. 2002. On the conditional nature of neotropical caterpillar defenses against their natural enemies. Ecology. 83:3108–3119. doi:10.1890/0012-9658(2002)083[3108:OTCNON]2.0.CO;2.

Giannini TC, Chapman DS, Saraiva AM, Alves-dos-santos I, Biesmeijer JC. 2013. Improving species distribution models using biotic interactions: a case study of parasites, pollinators and plants. Ecography. 36:649–656. doi:10.1111/j.1600-0587.2012.07191.x.

Gibson GA. 1997. Morphology and Terminology. In: Gibson GA, Huber JT, Woolley JB, editors. Annotated keys to the genera of Nearctic Chalcidoidea (Hymenoptera). Ottawa (ON, Canada): NRC Research Press; p. 16–44.

Glassmire AE, Jeffrey CS, Forister ML, Parchman TL, Nice CC, Jahner JP, Wilson JS, Walla TR, Richards LA, Smilanich AM, et al. 2016. Intraspecific phytochemical variation shapes community and population structure for specialist caterpillars. New Phytol. 212:208–219. doi:10.1111/nph.14038.

Guimarães EF, Giordano LCDS. 2004. Piperaceae do Nordeste brasileiro I: estado do Ceará. Rodriguésia. 55:21–46. doi:10.1590/2175-78602004558402.

Harris RA. 1979. Glossary of surface sculpturing. Occas Papers Entomol. 28:1–31.

Heraty J, Hawks D. 1998. Hexamethyldisilazane: a chemical alternative for drying insects. Entomol News. 109:369–374.

Janzen DH, and Hallwachs W. 2012. Philosophy, navigation and use of a dynamic database ("ACG Caterpillars SRNP") for an inventory of the macrocaterpillar fauna, its food plants and parasitoids, of the Area de Conservación Guanacaste (ACG), northwestern Costa Rica. [accessed 2018 May 8]. http://janzen.sas.upenn.edu .

Lotfalizadeh H, Delvare G, Rasplus JY. 2007. Phylogenetic analysis of Eurytominae (Chalcidoidea: Eurytomidae) based on morphological characters. Zool J Linn Soc. 151:441–510. doi:10.1111/j.1096-3642.2007.00308.x.

Lotfalizadeh H, Hosseini F. 2014. Chalcidoid parasitoids (Hymenoptera) of *Etiella zinckenella* (Treitschke) (Lep.: Pyralidae) on *Sophora alopecuroides* L., in Iran. North West J Zool. 10:251–258.

Marquis RJ. 1991. Herbivore fauna of *Piper* in a Costa Rican wet forest: diversity, specificity and impact. In: Price PW, Lewinsohn TM, Fernandes GW, Benson WW, editors. Plant-animal interactions: evolutionary ecology in tropical and temperate regions. New York: John Wiley and Sons; p. 179–205.

Murphy SM, Lill JT, Bowers MD, Singer MS. 2014. Enemy-free space for parasitoids. Environ Entomol. 43:1465–1474. doi:10.1603/EN13201.

Naghizadeh A, Lotfalizadeh H, Nikdel M. 2019. *Aximopsis trypeticola* (Zerova, 1978) n. comb.(Hym.: Eurytomidae) a parasitoid of *Bruchidius virgatus* (Fahraeus, 1839) in Iran. Biharean Biol. 13:47–48.

Noyes JS 2021. Universal Chalcidoidea Database. World Wide Web electronic publication; [accessed 2021 Jan 12]. http://www.nhm.ac.uk/chalcidoids .

Price PW. 2002. Resource-driven terrestrial interaction webs. Ecol Res. 17:241–247. doi:10.1046/j.1440-1703.2002.00483.x.

Quijano-Abril M, Callejas-Posada R, Miranda-Esquivel D. 2006. Areas of endemism and distribution patterns for Neotropical *Piper* species (Piperaceae). J Biogeogr. 33:1266–1278. doi:10.1111/j.1365-2699.2006.01501.x.

Richards LA, Dyer LA, Forister ML, Smilanich AM, Dodson CD, Leonard MD, Jeffrey CS. 2015. Phytochemical diversity drives plant–insect community diversity. Proc Natl Acad Sci. 112:10973–10978.

Richards LA, Dyer LA, Smilanich AM, Dodson CD. 2010. Synergistic effects of amides from two *Piper* species on generalist and specialist herbivores. J Chem Ecol. 36:1105–1113. doi:10.1007/s10886-010-9852-9.

Salazar D, Jaramillo A, Marquis RJ. 2016. The impact of plant chemical diversity on plant herbivore interactions at the community level. Oecologia. 181:1199–1208.

Secretaria de Agricultura y Recursos Hidráulicos SARH. 1981. Ciencia Forestal. In: Revista de la Secretaria de Agricultura y Recursos Hidráulicos. Vol. 1. México (DF): Subsecretaría Forestal y de Fauna Silvestre; p. 141.

Slinn HL, Richards LA, Dyer LA, Hurtado PJ, Smilanich AM. 2018. Across multiple species, phytochemical diversity and herbivore diet breadth have cascading effects on herbivore immunity and parasitism in a tropical model system. Front Plant Sci. 9:656.

Tavares W de S, Wilcken CF, de Sousa Ramalho F, Soares MA, Fernandes FL, Serrão JE, Zanuncio JC. 2015. Discovery of the first *Aximopsis* (Hymenoptera: Eurytomidae) parasitoid of Lepidoptera in Brazil and notes on its biology. Fla Entomol. 98:1077–1080. doi:10.1653/024.098.0411.

Thompson J. 2014. Interaction and coevolution. Chicago: University of Chicago Press.

Travis J. 2020. Where is natural history in ecological, evolutionary, and behavioral science? Am Nat. 196:1–8. doi:10.1086/708765.

Vanin S, Ramos C, Guimaraes E, Kato MJ. 2008. Insect feeding preferences on Piperaceae species observed in Sao Paulo city, Brazil. Rev Bras Entomol. 52:72–77.

Warren AD, Davis KJ, Grishin Nv, Pelham JP, Stangeland EM 2012. Interactive listing of American butterflies; [accessed 2021 Jan 14]. http://www.butterfliesofamerica.com/ .

Wilson EO. 2017. Biodiversity research requires more boots on the ground. Nat Ecol Evol. 1:1590. doi:10.1038/s41559-017-0360-y.

Zerova MD. 1995. Parasitic Hymenoptera-Eurytominae and Eudecatominae of Palaearctics. Kiev: National Academy of Sciences of Ukraine.

Zerova MD. 2010. Palaearctic species of the genus *Eurytoma* (Hymenoptera, Chalcidoidea, Eurytomidae): morphological and biological peculiarities, trophical associations and key to determination. Vestn Zool. 24:1–204.