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NEW SPECIES OF *PHASSUS* WALKER GHOST MOTH FROM NORTHEASTERN MEXICO AND NOTES ON ITS BIOGEOGRAPHIC SIGNIFICANCE (LEPIDOPTERA: HEPIALIDAE)

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New species of *Phassus* Walker ghost moth from northeastern Mexico and notes on its biogeographic significance (Lepidoptera: Hepialidae)

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Abstract

A new species of *Phassus* Walker, *Phassus zapalinamensis* **sp. n.,** is described from northeastern Mexico based on a single male and female from the Parque Ecoturístico El Chorro (Coahuila) and the Área Natural Protegida Estatal "Cerro La Mota"(Nuevo León), with supplementary geographic records from photos posted at inaturalist.org. Conspecificity of the specimens is supported by a 100% bootstrap in the COI gene. Adults, male and female genitalia and external appearance are illustrated. The forewing pattern is most similar to *P. huebneri* (Geyer, [1838]), a species known only from illustration of the female moth which probably represents several cryptic species in Mexico and Central America. A syntype female specimen of *Phassus marcius* Druce, 1892 and a syntype female of *Phassus argentiferus* Walker, 1856 are **designated here as respective lectotypes**. The new species extends the previously documented range of *Phassus* between Central America and the trans-Mexican Volcanic belt, to almost the Mexico-United States border. This is currently the northernmost limit known for any genus of Hepialidae with Central or South American affinities. We discuss the potential evolutionary significance of the distributional boundary with respect to the possible role of the Jurassic-Cretaceous Mojave-Sonora Megashear fault system and earlier magmatic arcs in northern Mexico.

Keywords

Biogeography, conservation, evolution, morphology, taxonomy, tectonics

Introduction

Phassus Walker, 1856 is a genus of ghost moths most often collected or recorded between Central Mexico and Central America south to Panama (Mielke & Grehan 2017). Larvae are callus feeding stem borers (Grehan *et al.* 2021b), and the larvae of some species are a traditional food source for rural people in Mexico and Central America (Gómez *et al.* 2016). Most species are represented by large, to very large, moths that frequently attract the attention of collectors. This visibility is offset by the paucity of moths attracted to light. The taxonomy and distribution of most *Phassus* species is poorly documented. Recent taxonomic works include the description of *P. violetteae* C. Mielke & Grehan, 2016 (Fig. 14f; Mielke & Grehan 2016), a re-description of *P. aurigenus* Pfitzner, 1914 (Fig. 14j; Grehan *et al.* 2018) in Costa Rica, and the transfer of two species to *Schausiana* Viette, 1950 (Mielke *et al.* 2020). Of the currently eleven valid species, six are recorded from Mexico, four are endemic to Guatemala and Costa Rica, and one (*Phassus exclamationis* Pfitzner, 1938) is of unknown appearance and provenience (Mielke & Grehan 2016, Grehan *et al.* 2018).

In 2018, several photos of a *Phassus* species from northeastern Mexico were posted on iNaturalist, an online social network for sharing biodiversity information through photographic records (https://www.inaturalist.org/). Subsequent efforts to collect specimens were successful, with a male obtained by Arturo Cruz and a female obtained by Carlos Velazco. The internal and external features of these specimens were considered sufficiently distinctive to justify describing them as a new species. We examine the spatial relationships of *Phassus* distribution with some geological and tectonic structures in Mexico, including the Mojave-Sonora Megashear, across northern Mexico.

Materials & Methods

Specimens were dissected by removing the abdomen that was then treated in a cold solution of 5% KOH solution for more than 12 hours. The abdomen was opened by a right lateral cut from the tergosternal bar to the genitalia which was removed, stained with methylene blue, and preserved in glycerol along with the abdominal integument. Terminology for genitalia and wing venation follows Mielke & Casagrande (2013) and Grehan *et al.* (2021a). Wing venation diagrams were drawn over photographic images using InkScape® software. Description of the female only refers to those features that are different from the male. Labels of primary types are given verbatim.

A single leg from each specimen was used to provide a partial COI mitochondrial gene sequence amplified for the standard DNA animal 'barcode' (Hebert *et al.* 2003) at the Canadian Centre for DNA Barcoding (CCDB), following routine protocols as described in Decaëns *et al.* (2021). Sequence data are stored in the Barcode of Life Data Systems (BOLD – www.boldsystems.org; Ratnasingham & Hebert 2007). The standardized 658 bp fragment of the mitochondrial cytochrome C oxidase subunit I gene (COI) of the new species was compared with nine other *Phassus* species and a single species of *Cibyra* Walker ('outgroup') using the Neighbor-Joining method of Saitou & Nei (1987). The percentage of replicate trees in which the associated taxa clustered together in the bootstrap test (1000 replicates) are shown next to the branches (Felsenstein 1985). The similarity distances were computed using the Kimura 2-parameter method (Kimura 1980) and tree was constructed using MEGA X (Kumar *et al.* 2018).

Abbreviations

CGCM (Collection Carlos G. C. Mielke, Curitiba, Paraná, Brazil)
CNIN (Colección Nacional de Insectos, Universidad Nacional Autónoma de México, Ciudad de México, México)
FW (forewing), HW (hindwing)
NHMUK (The Natural History Museum, London, United Kingdom)

Taxonomic section

Phassus zapalinamensis Grehan, C. Mielke & Garzón-Orduña, **sp. n.**

Figs 1a-b, 2a-c, 4a-b, 5a-b, 6, 7a-b, 8a-d, 9a-b, 10a-b, 11a-e, 12a-d, 13a-c, 14a-b, 17a-c.

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Holotype: ♂: Parque Ecoturístico El Chorro: 25.382839, -100.78788, 1904 MASL Arteaga, Coahuila, México. 19 July 2021, 23:50 h. Coll. Alejandro Durán Romero; LEP190310CNIN; (CNIN).

Paratype: 1♀**,** Área natural protegida estatal "Cerro La Mota". García, Nuevo León, México. Leg: Mauricio López Zorrilla y Carlos Gerardo Velazco Macias. 7 September, 2021. Lat: 25.708825 Long: -100.614317 [25° 42' 31.77" 100° 36' 51.5406"], Altitude: 1,045msnm. Hábitat: matorral desértico. [Desertic shrubs]; LEP190301CNIN; (CNIN).

Additional photographic records

July 4, 2018. Arteaga, Coahuila, México. Photo by Arturo Cruz (Fig. 17b). https://www.inaturalist.org/observations/14118610

July 7, 2018. Paseo de Los Osos 3, Lomas de Lourdes, 25090 Saltillo, Coahuila, México. Photo by Emily Villarreal (Fig. 17c). https://www.inaturalist.org/observations/14156592

August 24, 2018. A Chipinque 123, Zona de La Sierra Madre, 66250 San Pedro Garza García, Nuevo León, México. Photo by Ana Epigmenio (Fig. 17a).

https://www.inaturalist.org/observations/16330699

Etymology

Named for the Sierra de Zapalinamé where the holotype originated. The name is an adjective in the nominative singular.

Diagnosis

In comparison with other *Phassus* species, the FW pattern of *P. zapalinamensis* **sp. n.** is distinct from the faintly marbled FW of the Mexican *P. marcius* Druce, 1892 (Fig. 14i), the bright golden-orange shading of the Costa Rican *P. aurigenus* (Fig. 14j), the sinuate shaded bar of the Mexican *P. chrysodidyma* Dyar, 1915 (Fig. 14k), and the pale orange-brown and faint sinuate markings of Central American *P. championi* Druce, 1887 (Fig. 14e). The FW pattern of *P. zapalinamensis* **sp. n.** is similar to four species that share a diffuse, V-shaped dark greyish-brown patch over much of the discal cells, central-anterior cubital cell, and extending to the central post discal transverse band, hereafter referred to as the discal-cubital patch (Fig. 14a-h). The male *P. zapalinamensis* **sp. n.** is distinguished from all *Phassus* species by the presence of an extensive network of fine, strongly marked and irregularly shaped transverse lines over much of the forewing surface, in contrast to similar but faint makings in the other species.

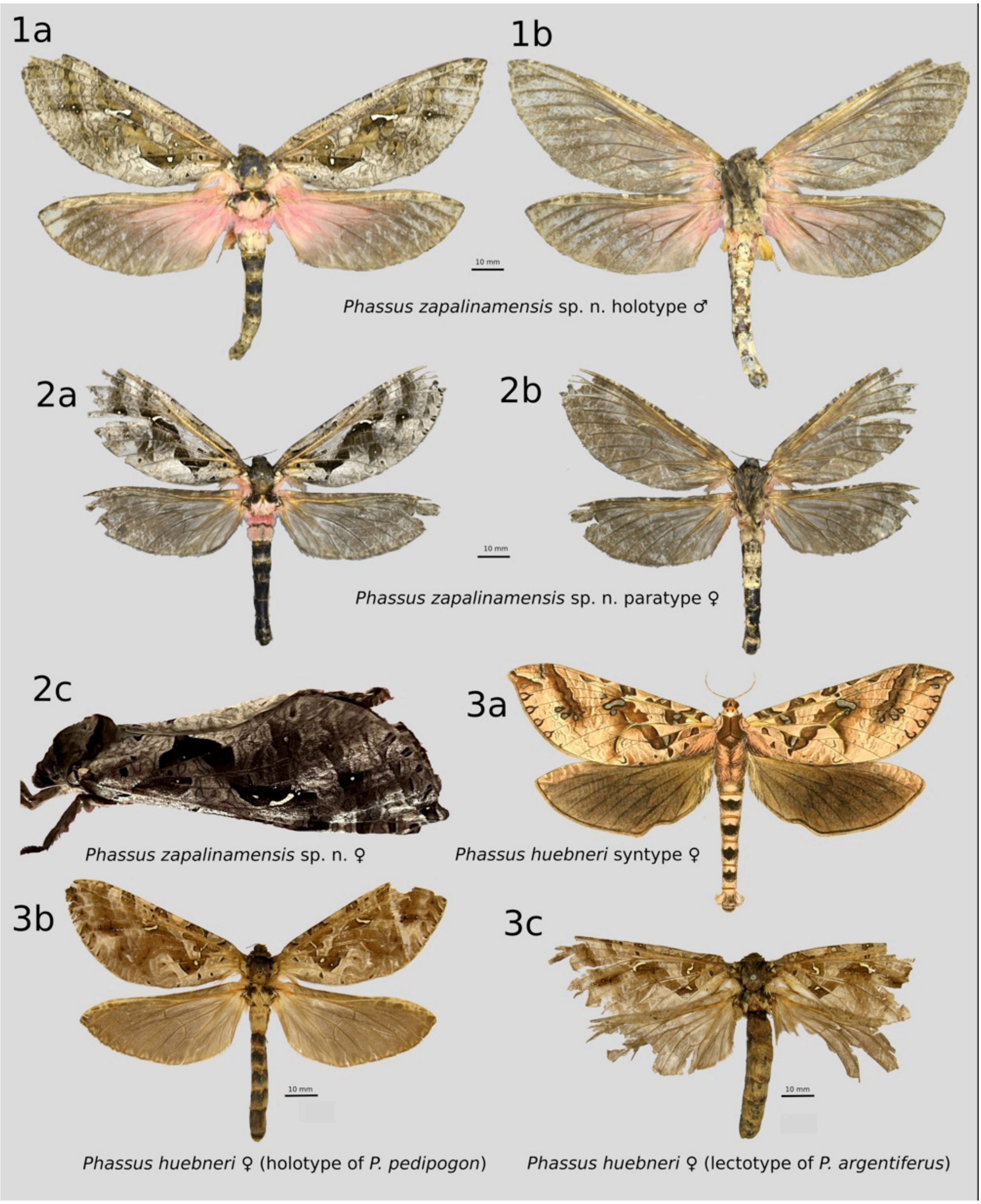
Description

Holotype ♂ (Figs. 1a-b, 14a). Wingspan ~ 150 mm, FW length: 75 mm, width: 30 mm; HW length: 60 mm, width: 26 mm.

Head: Covered with dense greyish, piliform scales. Antenna not intact. Labium with three palpomeres, basal two segments subequal; distal segment length less than half, apically pointed with deep Von Rath's organ (Fig. 5a).

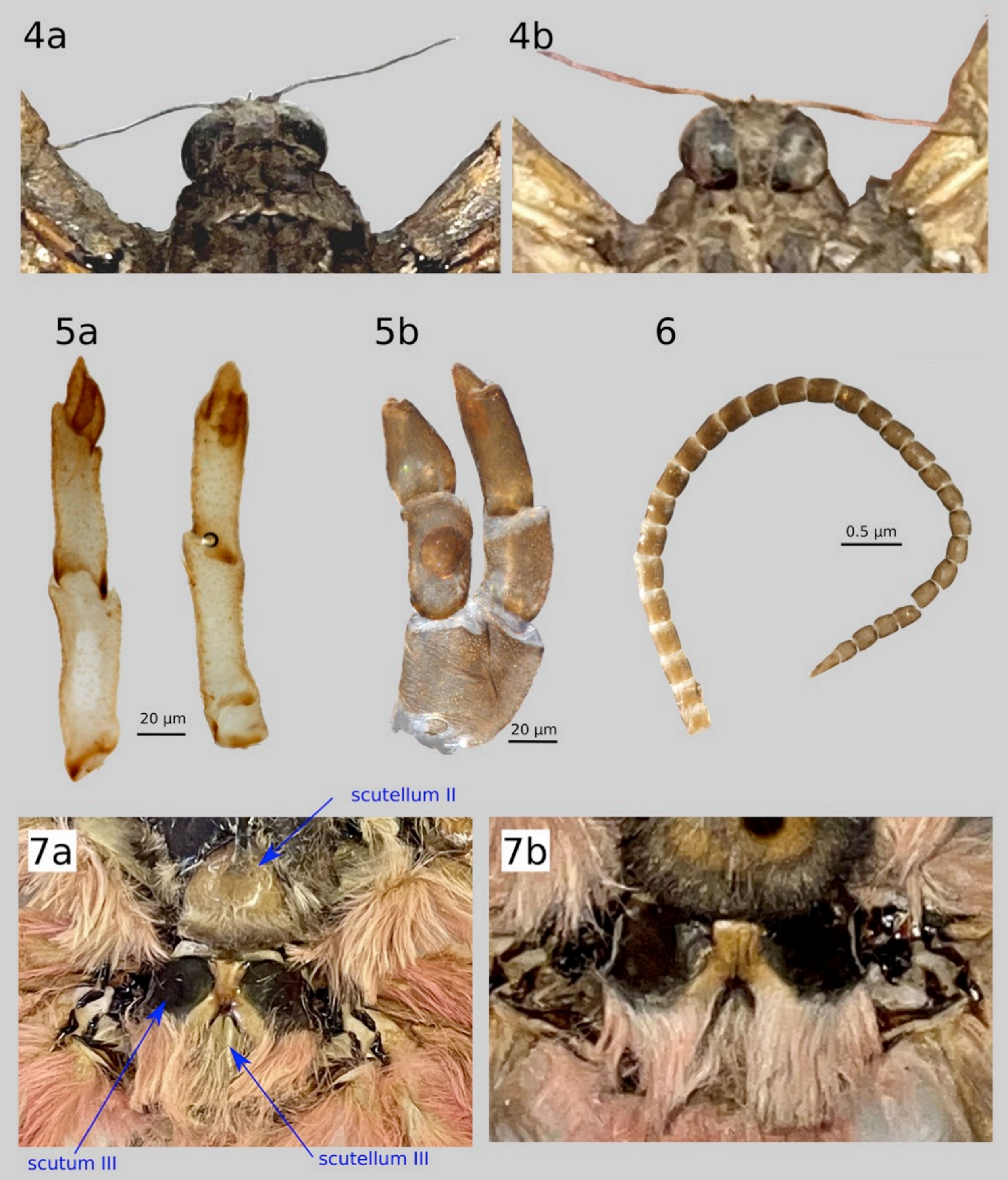
Thorax: Prothorax dorsally covered with dense, dark brown piliform scales, dorsal meso and metathorax with pale orange to yellowish brown scales, except for unscaled dark brown surface of scutellum III (Fig. 7a). Wings mostly covered by lamellar scales. Wing venation (Fig. 8a): branching of Rs1+ Rs2 near apex, Rs3 strongly curved. FW: CuP distally curved; HW: single A. FW ground color pale yellowish to greyish brown with dark shading over most of discal cell (other than antero-central region), basal portion of M cells, and most of premarginal transverse band. Shading to dark blackish brown in cubital triangle, basal and distal sides of stigma, and premarginal band along M1 (Fig. 8c). Remainder of FW covered with fine greyish irregular transverse ovoid or triangular lines with black spots in anal cell and basal cubital cell anterior to CuP. White stigma extends between junction of r-m vein and outer anterior discal cell, near common stalk of Rs veins, central posterior edge concave, bordering dark brown shading extending to M2. Several small scattered spots, particularly central cubital triangle, basal posterior medial discal cell, central M3-CuA1 cell, and adjacent to central M1 within the premarginal band (Fig. 8c). Elongate black patches either side of veins along the outer margin (probably from CuA2 to apex). HW reddish pink basally, merging into greyish brown distally. Ventral surface of FW and HW reddish pink basally, maculation along costal region to apex. Fore and mid legs covered with pale greyish brown scales, hindlegs with yellowish brown scales, reddish-brown tibial androconia (Fig. 10a). Epiphysis present (Fig. 9a), arolium absent.

Pregenital abdomen: Tergosternal sclerite (Fig. 11a) with shallow curve between lateral and dorsal brace with shallow depression parallel to the intermediate zone, tergosternal bar ventrally narrowing to a sharp point, weaker sclerotization along anterior edge at junction with lateral brace. Dorsal brace overlapping, but not fused with anterior ridge of TII. Abdominal sclerites (Fig. 11b, d) with greater sclerotization for sternites and tergum II; tergum II rectangular, anterior ridge fused across median, lateral ridge robust, almost straight, posterior ridge thin; sternum II with elongate anterolateral arms; lateral edge concave near posterior; sclerotization strongest antero-laterally for sternites III-VI; tergum VII subsquare, sternum VII rectangular, narrowing posteriorly; tergum VIII sclerotization T-shaped, expanding latero-posteriorly; sternum VIII sclerite triangular, expanding posteriorly.

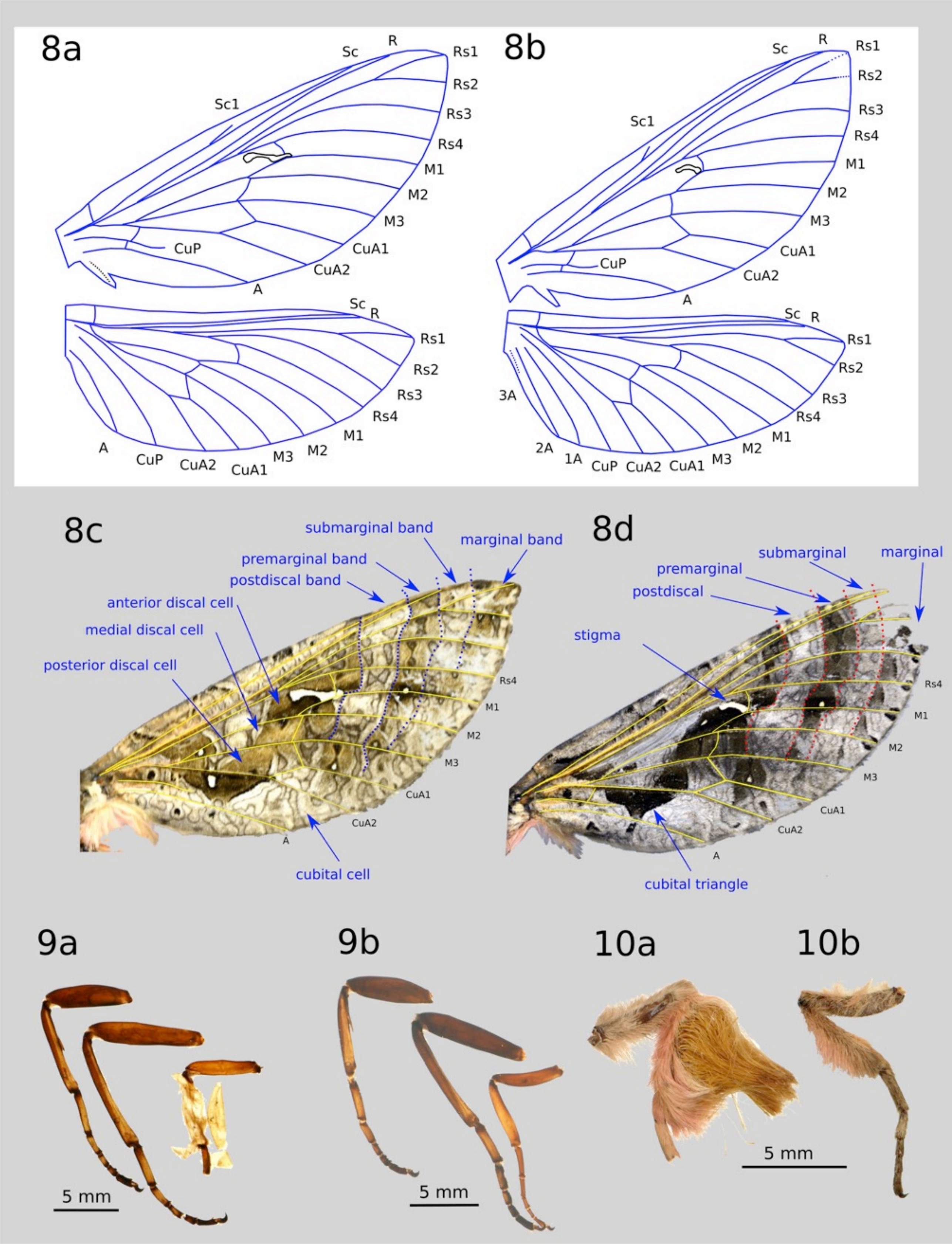


Figs. 1-3. Adults of *Phassus* spp. Figs. 1-2. *Phassus zapalinamensis,* **sp. n.**: holotype male dorsal (Fig. 1a), ventral (Fig. 1b); paratype female dorsal (Fig. 2a), ventral (Fig. 2b); female *in situ* (Fig. 2c, unscaled). Fig. 3. *Phassus huebneri*: syntype female (Fig. 3a, Geyer's (1838) illustration, unscaled); female (Fig. 3b, holotype of *P. pedipogon* – Costa Rica; NHMUK); female (Fig. 3c, lectotype of *Phassus argentiferus* – Mexico; NHMUK).

Genitalia (Fig. 12a-d): Tegumen elongate, not fused with pseudotegumen. Saccus V-shaped, with broad curved anterior margin; posterior margin forming a medially curved, shallow ridge. Tergal lobes absent or membranous. Pseudotegumen dorsally fused by narrow isthmus across median, bordered dorsally by shallow pointed ridge either side of median; anogenital field drop-shaped, tapering to point at the apex of the short, pointed pseudoteguminal arms, fused ventrally, anogenital margin of pseudoteguminal arms strongly sclerotized and curved laterally. Valva elbowed, distal blade anterior margin curving to broad, rounded apex; base of valva narrowing to junction with subrectangular sacculus. Fultura inferior rectangular; fultura superior rectangular, medially divided dorsally.



Figs. 4-7. *Phassus zapalinamensis,* **sp. n.** Head and thoracic morphology: dorsal and ventral view of female paratype head (Fig. 4a-b, unscaled), labial palps of male holotype (Fig. 5a) and female paratype (Fig. 5b), female antenna (Fig. 6), dorsal metathorax of male holotype (Fig. 7a), and female paratype (Fig. 7b, unscaled).



Figs. 8-10. *Phassus zapalinamensis,* **sp. n.** thoracic appendages: wing venation of male (Fig. 8a) and female (Fig. 8b), forewing pattern of male (Fig. 8c) and female (Fig. 8d), legs of male with metatibia burst during preparation (Fig. 9a) and female (Fig. 9b), hind legs showing metatibial androconia in male (Fig. 10a) and its absence in female (Fig. 10b).

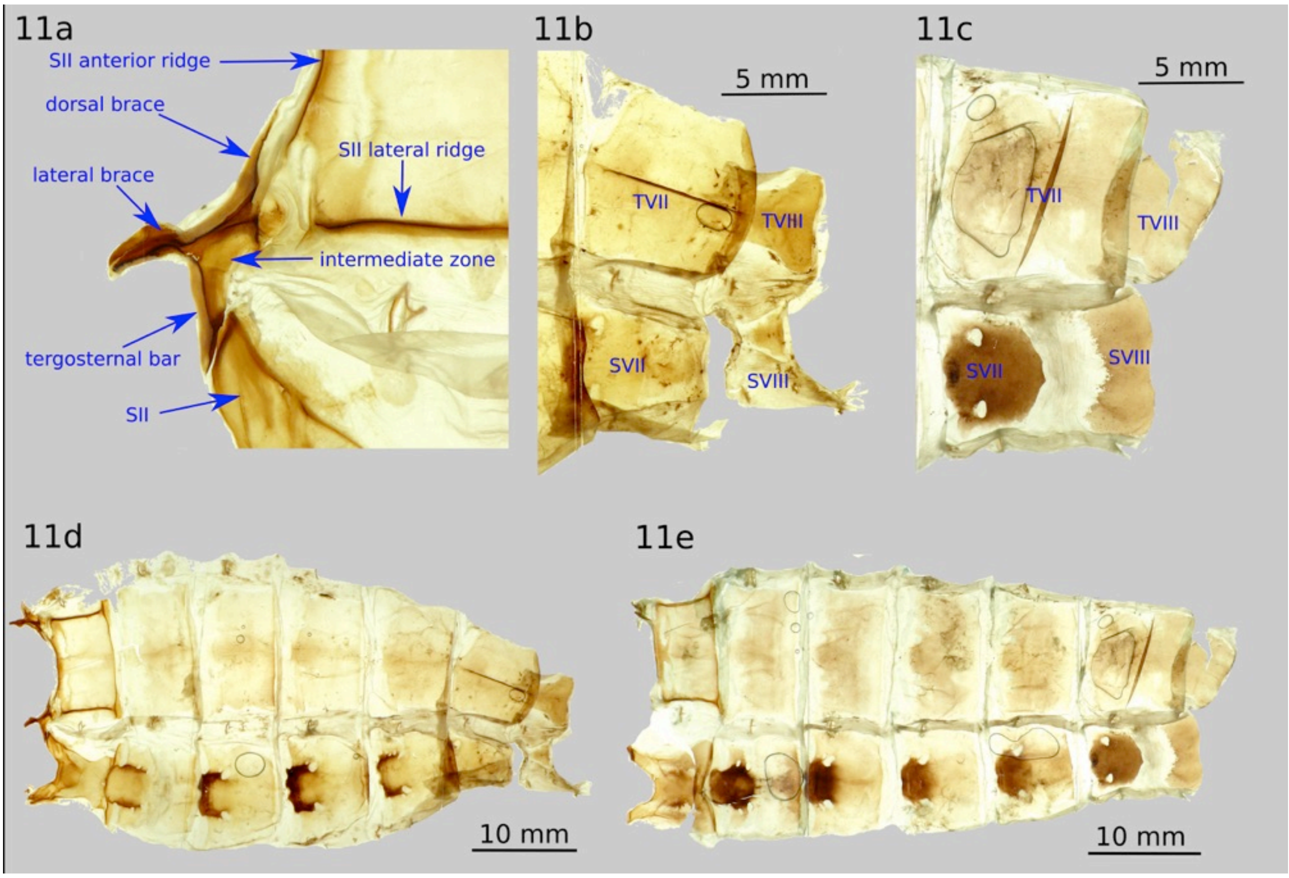


Fig. 11. *Phassus zapalinamensis,* **sp. n.** abdominal sclerites: (a) tergosternal sclerite of male holotype (unscaled), (b) posterior sclerites of male holotype and (c) female paratype, (d) abdomen of male holotype and (e) female paratype.

Paratype ♀ (Figs. 2a, 2b, 2c, 14b). Wingspan ~114 mm, FW length: ~60 mm [apex damaged], width: 24 mm; HW length: 52 mm, width: 22 mm.

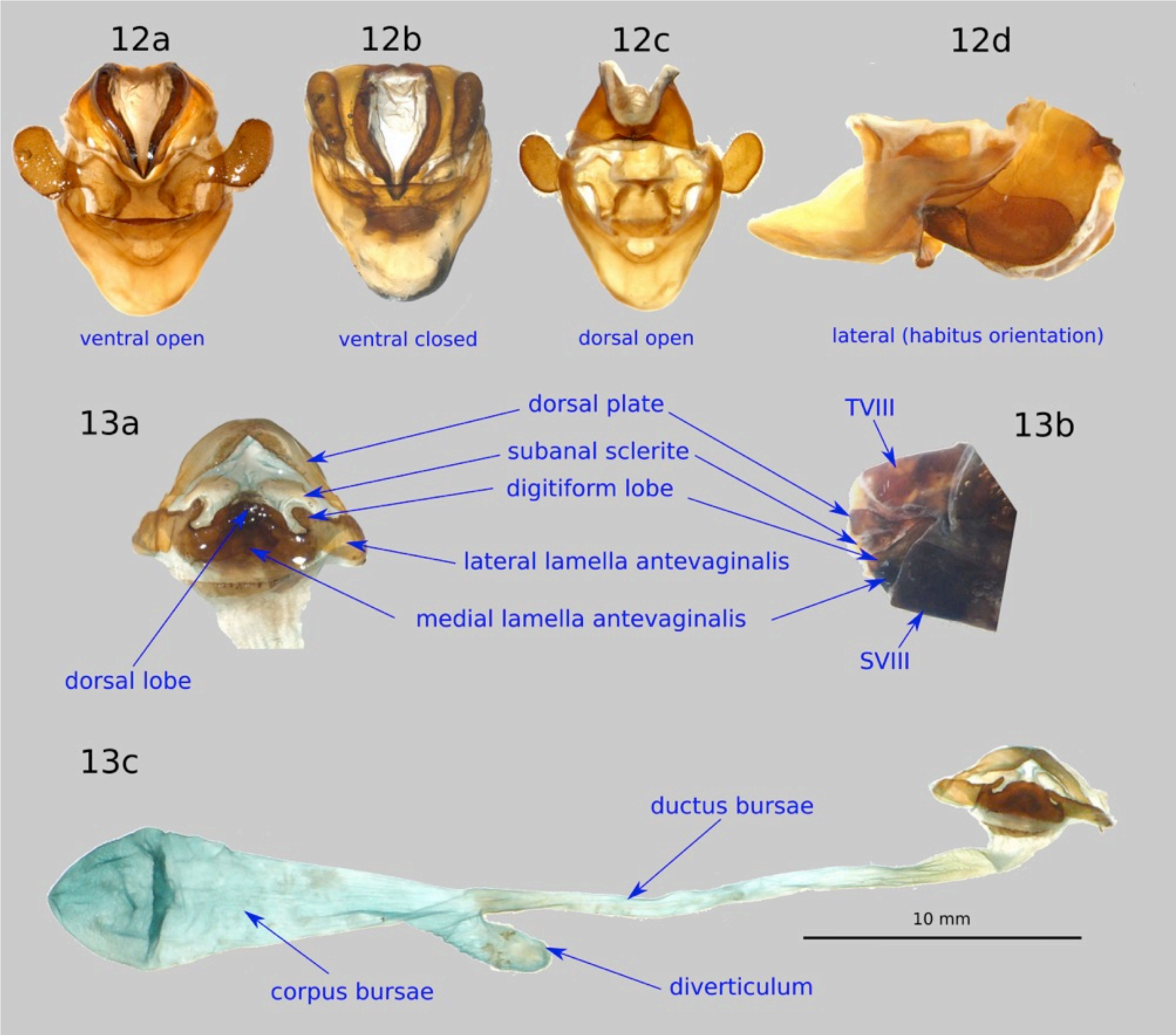
Head (Figs. 4a-b, 5b, 6) and thorax: Labial palps (Fig. 5b) proportionally wider than male. Dorso-medial region between each scutellum III (Fig. 7b) broad. Wings with short, third anal vein 3A (Fig. 8b). FW shaded regions dark brownish-black, stigma a shallow c-shaped curve, extending to common stalk of Rs3+4, cubital triangle sharply narrowed towards CuA and lacking central white spot (Fig. 8d); HW distally blackish grey. Hindlegs without metatibial androconia (Figs. 9b, 10b).

Pregenital abdomen: Tergosternal sclerite not removed intact. Sternum II (Fig. 11e) wider than male, lateral margins evenly concave from antero-lateral arms to posterior. Anterior sclerotization of sternites III-VI more extensive, and particularly for sternum VII forming a subrectangular oval, and sternum VIII forming rectangular sclerite that is wider than long and with a concave posterior margin. Tergum VIII broad rectangle (Fig. 11c).

Genitalia (Fig. 13a-c): External genitalia strongly sclerotized, dorsal plate broadly fused across median, laterally forming a narrow, curved bar hinging with lamella antevaginalis. Anal papillae shallow, setose. Subanal sclerites trapezoidal, narrowly acute point ventro-medially. Lamella antevaginalis with broad, setose medial dorsal lobe, and a digitiform lateral dorsal lobe projecting medially (Fig. 13a). Ductus bursae longer than corpus bursae, latter expanding, sub-ovoid, diverticulum about one quarter of the length of corpus bursae.

Habitat and phenology

The current records of *P. zapalinamensis* **sp. n.** are located in northern margin of a series of sub-parallel east-west oriented mountains south of Saltillo and Monterrey (Fig. 18). This region is at the northeastern limit of dry winter, warm summer, temperate forests of the Sierra Madre oriental (Fig. 19). The holotype male was found in close proximity to mesic habitats (Fig. 16a-b), and this specimen along with one photographic record, is located close to the boundaries of the Sierra de Zapalinamé protected area comprising 11 different plant communities, including xerophytic and mesophytic habitats (Encina-Domínguez *et al*. 2016, 2019). The paratype female was collected from the Área natural protegida estatal "Cerro La Mota" where the vegetation comprises xerophytic shrubs (Carlos Velazco pers. obs.), but there is a mixed temperate oak-coniferous forest about 5 km south at El Jonuco.



Figs. 12-13. *Phassus zapalinamensis,* **sp. n.** Genitalia: male holotype (Fig. 12a-d), female paratype (13a-c).

Discussion

The male and female moths of *P. zapalinamensis* **sp. n.** have similar, but not identical, wing patterns. They could not be assumed to be conspecific as they were found at different locations (separated by 40 km), and different dates (July and September respectively). The female wing pattern is most similar to the female of *P. huebneri* illustrated (drawing) by Geyer (1838) without specified locality. The primary type of *P. huebneri* has not been located and this makes the identification of similar undescribed species problematic. In addition, there are two junior synonyms (Mielke & Grehan 2012): *P. argentiferus* Walker, 1856 (Fig. 3c) from Mexico (Walker 1856), and *P. pedipogon* Strand, 1916 (Fig. 3b) from Costa Rica (Strand 1916), neither of which have been dissected.

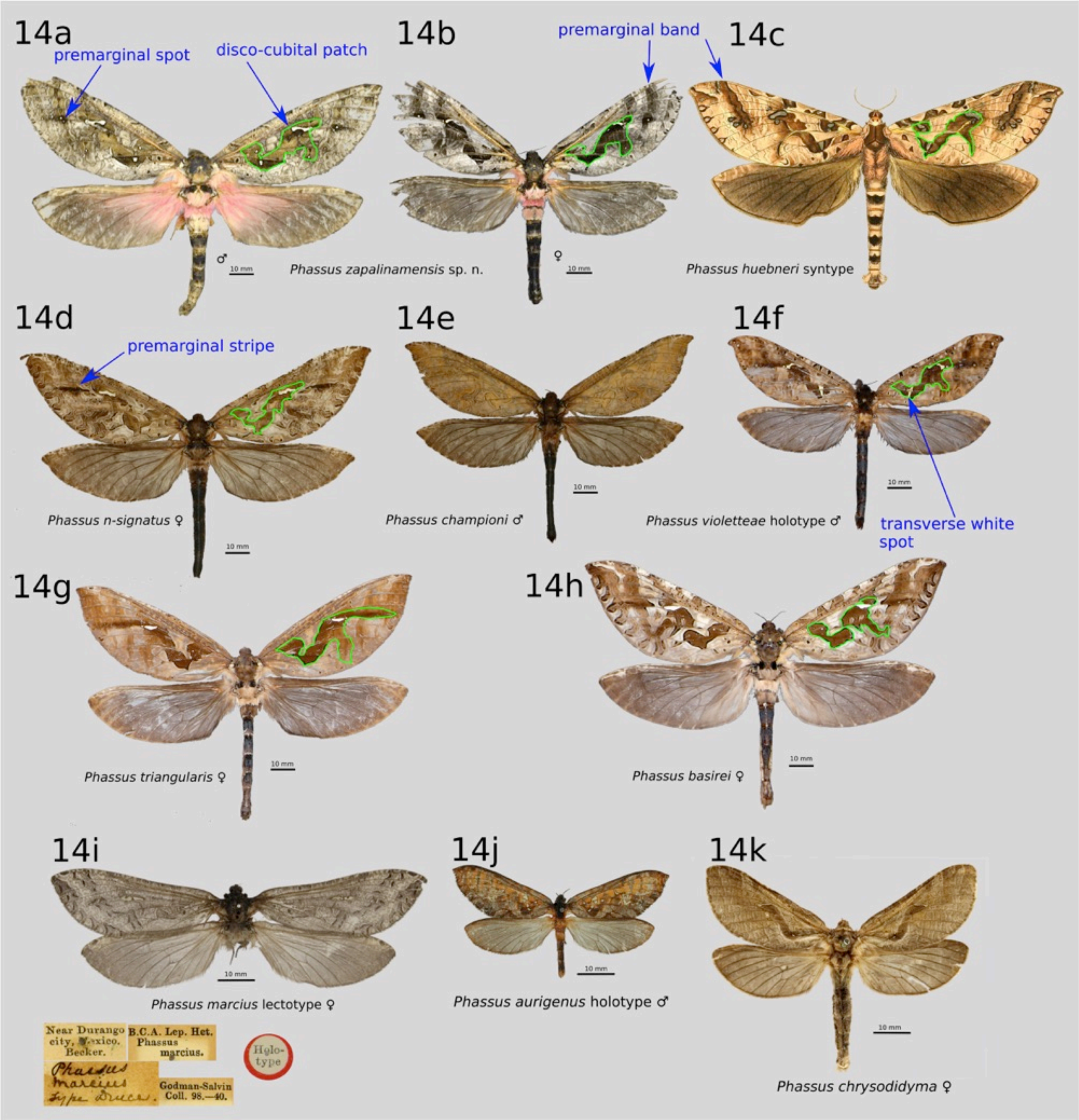


Fig. 14. Comparison of external appearance of *Phassus* species. *Phassus zapalinamensis,* **sp. n.**, holotype male (Fig. 14a), paratype female (Fig. 14b). *Phassus huebneri*, syntype female (Fig. 14c, Geyer's (1838) illustration; no locality, unscaled). *Phassus n-signatus*, female (Fig. 14d; Guatemala, Zacapa; CGCM 24.307; CGCM). *Phassus championi*, male (Fig. 14e; Guatemala, Zacapa; CGCM 24.115; CGCM). *Phassus violetteae,* holotype male (Fig. 14f; Costa Rica). *Phassus triangularis*, female (Fig. 14g; Guatemala, Huehuetenango; CGCM 21.180; CGCM). *Phassus basirei,* female (Fig. 14h; Mexico, Veracruz; CGCM 32.282; CGCM). *Phassus marcius*, lectotype female (Fig. 14i; Mexico, Durango). *Phassus aurigenus*, holotype male (Fig. 14j; Costa Rica) (Photos by Carlos Mielke). *Phassus chrysodidyma*, female (Fig. 14k; Mexico, Arcos; American Museum of Natural History, New York) (Photo by Jane Hyland). Figs 14i-k slightly enlarged.

The *P. huebneri* specimen illustrated (drawing) in lateral view by Geyer (1838) lacks metatibial androconial scales which indicates that it is a female. The female of *P. zapalinamensis* **sp. n.** is similar to Geyer's (1838) illustration of *P. huebneri* (Fig. 3a, 14c) with respect to shading on the discal and cubital cells, and areas and dark markings either side of the veins along the outer FW margin. But Geyer's (1838) specimen has a transverse white band in the cubital portion of the discal-cubital patch between CuA and A that is absent in the female paratype of *P. zapalinamensis*

sp. n. and the two habitus photos of presumptive female moths (Fig. 17b, c).

The holotype male does have the transverse white band cubital portion, as does the holotype female of *P. huebneri* syn. *pedipogon* (Fig. 3b) and the lectotype female of *P. huebneri* syn. *argentiferus* (Fig. 3c). The triangular cubital portion of the discal-cubital patch in the holotype male of *P. zapalinamensis* **sp. n.** has a wide, obtuse, angle at the apex adjacent to the anal vein, whereas in Geyer's (1938) illustration, and the types of the two junior synonyms, the apex is more nearly a right angle. In the female the apex at the anal vein forms a narrow neck or prominence, and in this respect does not correspond to any of the other named specimens.

Illustrations of the male and female genitalia for species of *Phassus* are too limited to provide diagnostic criteria for *P. zapalinamensis.* **sp. n.** The wing pattern of *P. zapalinamensis* **sp. n.** can be confused only with *P. huebneri*, which remains a problematic taxon pending further sampling and locating the primary type/s. The male genitalia of *P. zapalinamensis.* **sp. n.** is similar in overall shape and proportion to that of *P. aurigenus* of Costa Rica, but lacks a bifurcated fultura superior (Grehan *et al*. 2018: fig. 11). It is also similar to a *P.* '*huebneri*' specimen from Choix in northwestern Mexico (Grehan *et al*. 2018: fig. 26), but differs with respect to absence of a bifircated fultura superior and a small spine near pseudotegumen apex. The Choix specimen and *P. zapalinamensis.* **sp. n.** both lack the medial postero-dorsal spine present in the male genitalia of *P. violetteae* from Costa Rica (Grehan *et al* 2018: fig. 27) and *P. triangularis* Edwards, 1885 from Guatemala (Grehan *et al*. 2018: fig. 28). The only published illustration of *Phassus* female genitalia is that of *P. violetteae* (Mielke & Grehan 2016) which has a dorsally prominent medial dorsal lobe, and lacks the lateral digitiform lobe present in *P. zapalinamensis.* **sp. n.**

Given the morphological uncertainties of identification, we applied an alternative measure of similarity in the base-pair composition of the COI sample of the male and female *P. zapalinamensis* **sp. n.** and nine other *Phassus* species (Table 1). The sequences of the two *P. zapalinamensi*s **sp. n.** specimens grouped together with a 100% bootstrap support (Fig. 15). According to the Neighbor-Joining tree, the COI sample for *P. zapalinamensi*s **sp. n.** is most similar to a '*P. huebneri*' specimen from central-western Mexico, but the bootstrap value is too low (43%) to provide strong support for a close relationship. The COI sequence did give strong bootstrap support (99%) for grouping *P. basirei* Schaus, 1890 (Fig. 14h), *P. championi* Druce, 1887 (Fig. 14e), *P. n-signatus* Weymer, 1907 (Fig. 14d), and *P. triangularis* (Fig. 14g), but their relationship with other *Phassus* species is unresolved. The lack of strong bootstrap support linking *P. zapalinamensi*s **sp. n.** with the central-western Mexico *P. huebneri* sample is supportive of our treating *P. zapalinamensi*s **sp. n.** as a distinct species.

Biogeography

The biogeography of *Phassus* concerns the spatial and temporal origin of the genus and its species with respect to the Earth's tectonic history. Absence of a resolved phylogeny, either for species relationships within *Phassus* or between *Phassus* and other Hepialidae, precludes detailed analysis at this time. The geographic range of *Phassus* is also poorly documented as indicated by the extensive distributional gaps (see Fig. 20a) where over half the current records known to us are from photographic sightings only (inaturalst.org). The distribution range of *Phassus* is not ecologically bounded. There is extensive suitable forest habitat in the south between Panama and South America, but the southern limit of *Phassus* appears to be within Panama (C. Mielke, pers. comm.). The region along the Mexico-United States border is characterized by extensive desert or xerophytic environments, but innumerable other mesic animal and plant taxa have distributions that traverse this region. It is possible that *Phassus* exists further north in western Mexico on one or more of the fragmented mountain habitats ('sky islands') that extend across the Sonora of Mexico and the southeastern United States.

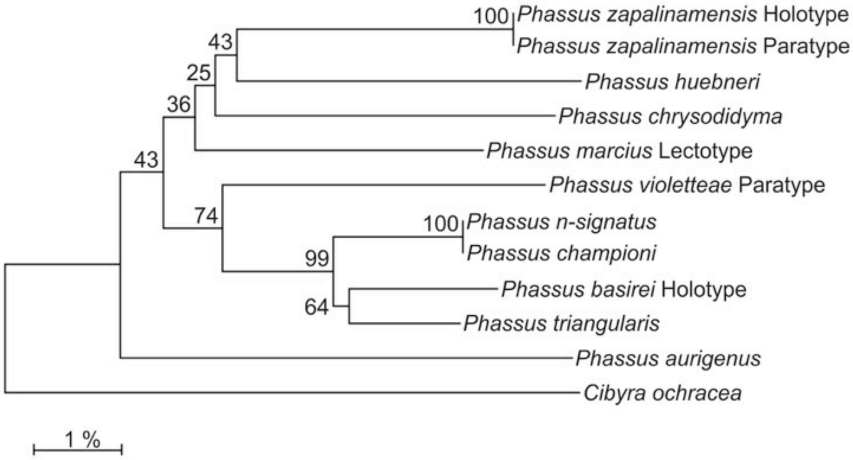


Fig. 15. Neighbor-Joining tree of COI sequences for *Phassus* spp. in comparison with *Cibyra ochracea* C. Mielke ('outgroup').

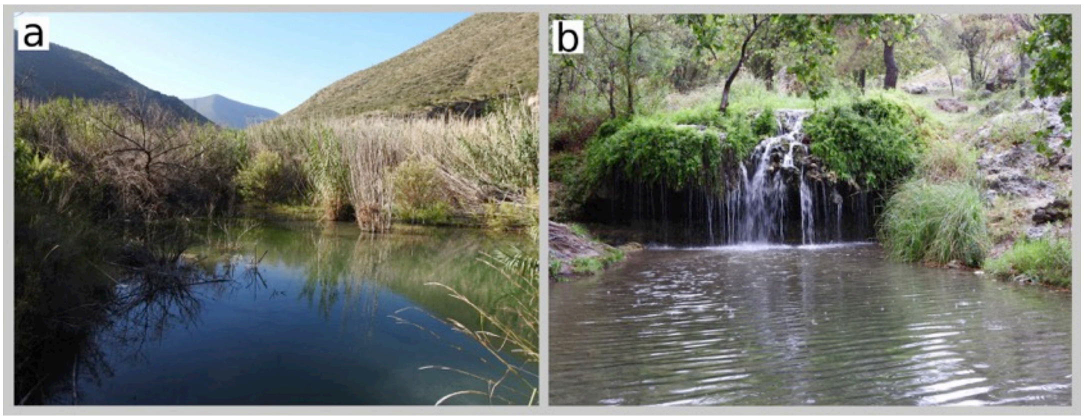


Fig. 16. Examples of habitat near the collection location of the male holotype of *Phassus zapalinamensis,* **sp. n.**: (a) Los Chorros stream, next to Highway 57. Vegetation dominated by *Arundo donax* and some *Schinus molle* and *Salix nigra* trees; (b) Waterfall in the Los Chorros Ecotourism Park (where the male specimen was found). Vegetation dominated by *Typha dominguensis* and *Adiantum capillus-veneris* in the riverbed; *Salix nigra* is present in the forested habitat, although dominated by introduced tree species such as *Platanus* sp. and *Populus alba* that were planted to provide shade for park visitors. Photos by Arturo Cruz.

Fig. 17. Habitus of *Phassus zapalinamensis,* **sp. n.** from inaturalist.org lacking voucher specimens: (a) San Pedro Garza García (photo by Ana Epigmenio), (b) Arteaga [IN1 in Fig. 18] (photo by Arturo Cruz), (c) Saltillo [see Fig. 18] (photo by Emily Villarreal).

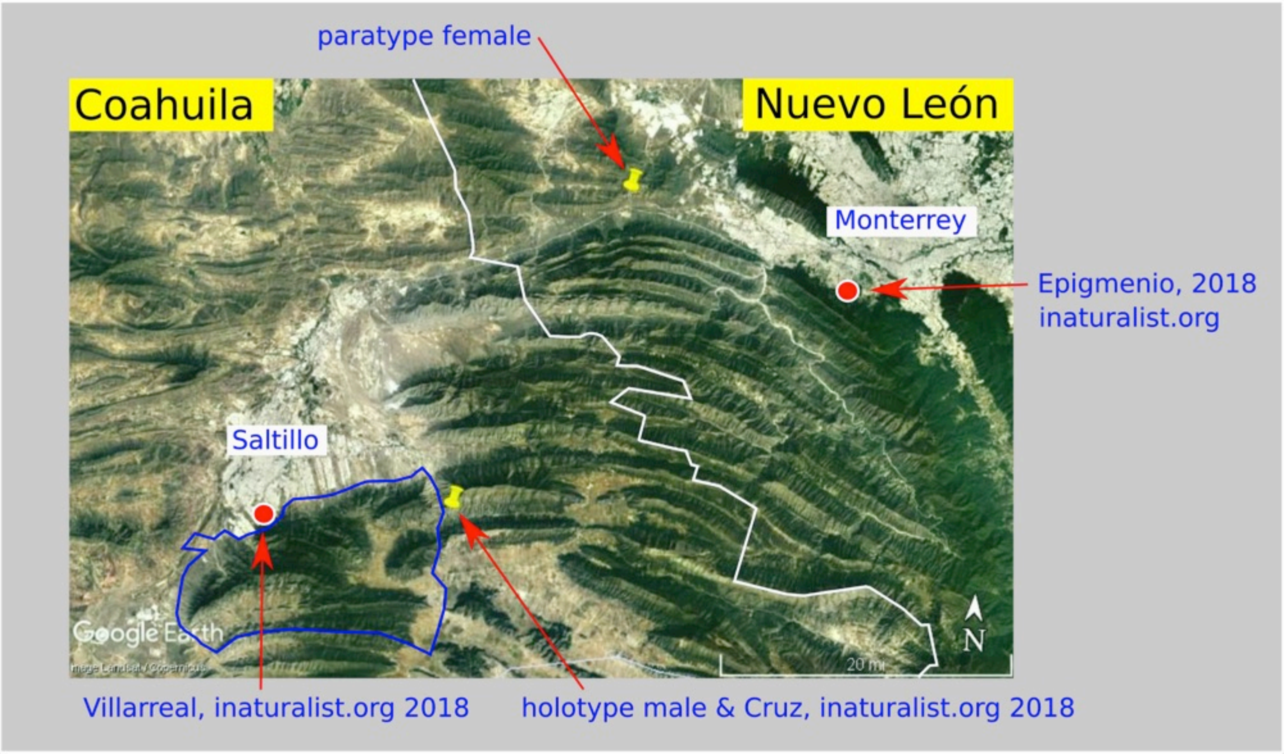


Fig. 18. *Phassus zapalinamensis,* **sp. n.** Specimen and photographic records (latter from inaturalist.org). Blue outline - Reserva Natural Estatal Sierra de Zapalinamé.

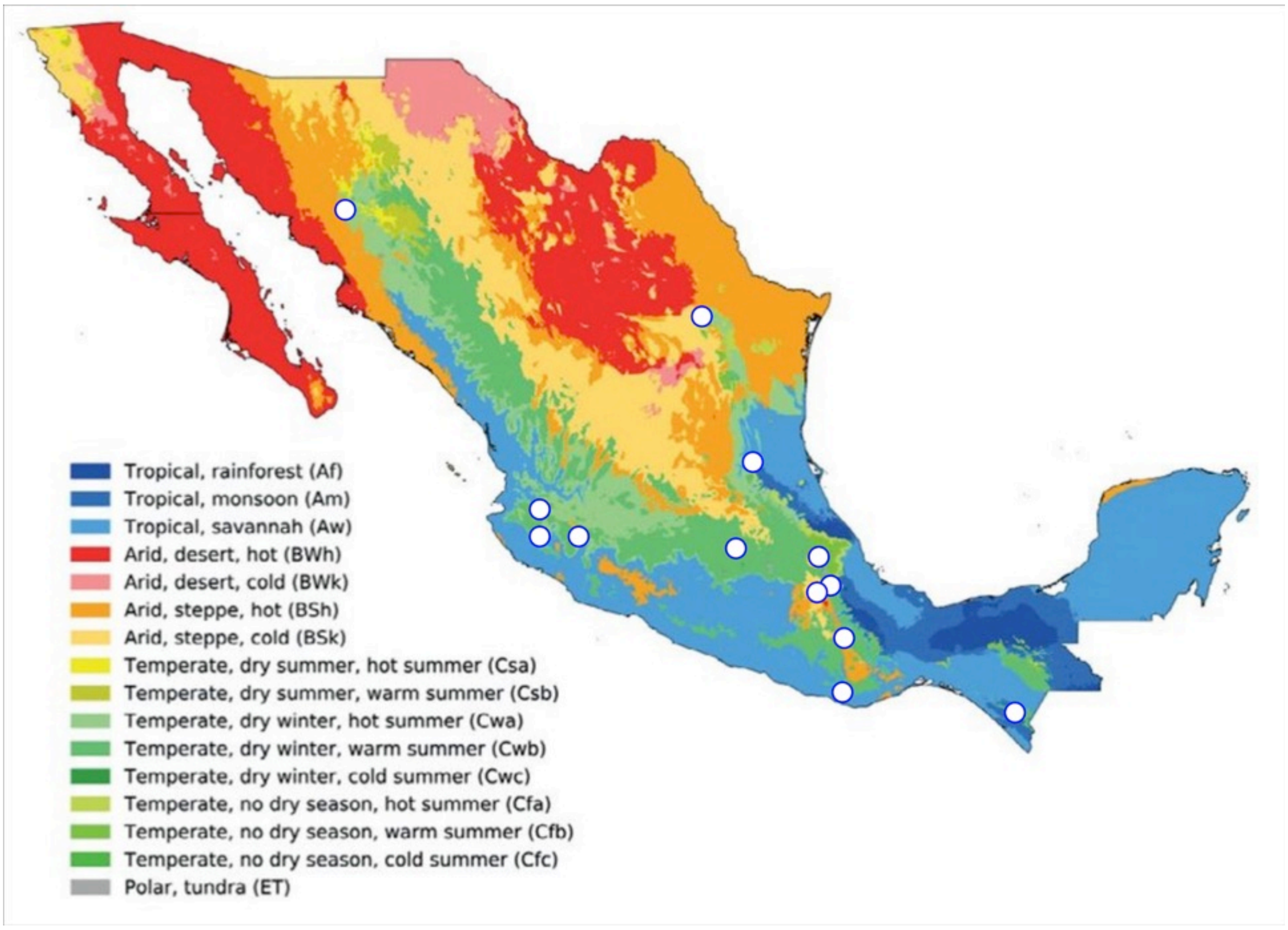


Fig. 19. Distribution records of *Phassus* spp. in Mexico with respect to general climatic zones (modified from Martínez-Austria (2020)).

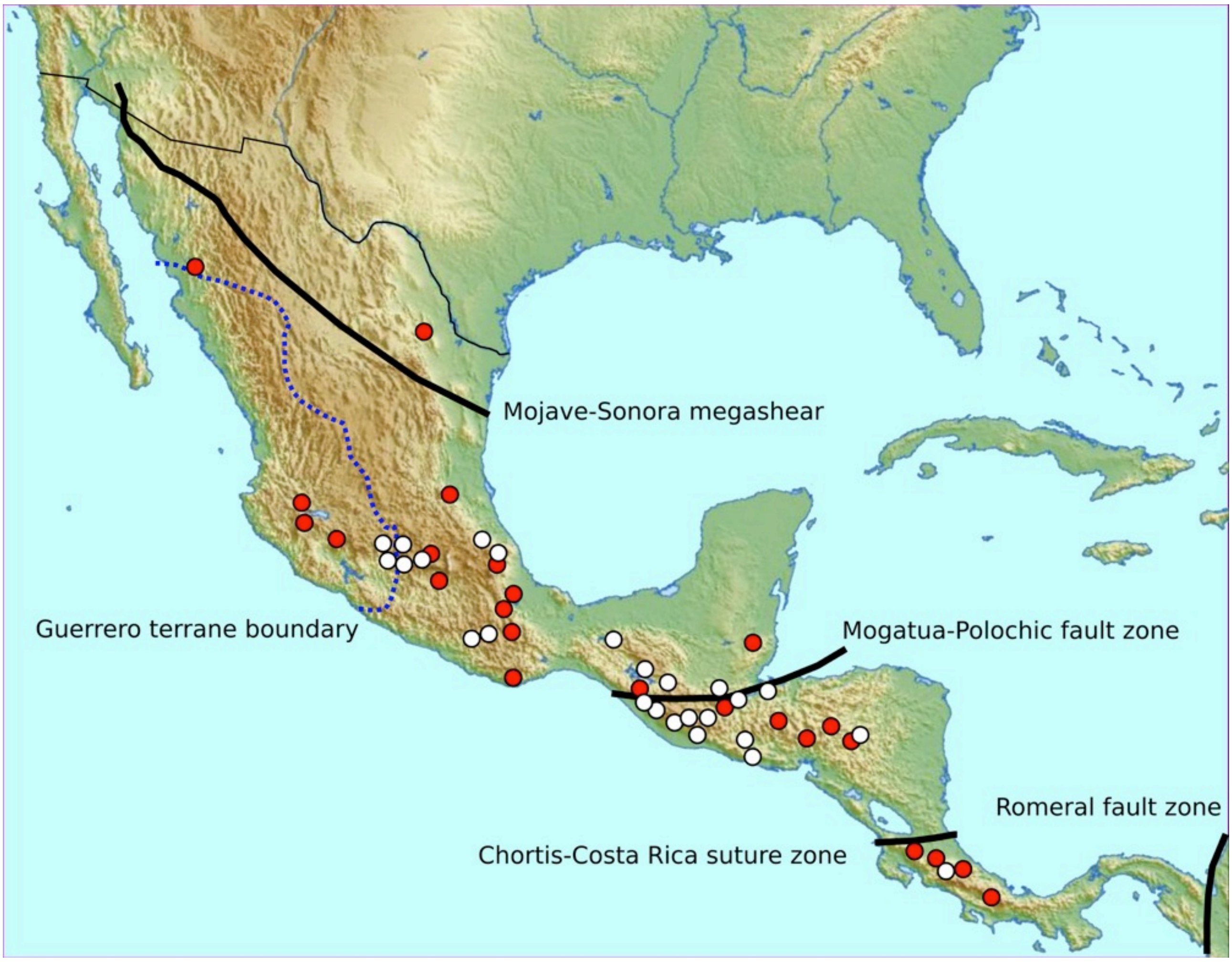


Fig. 20. Distribution records of *Phassus* (red circles) and *Schusiana* (white circles). Major regional tectonic structures as black lines.

The northern and southern boundaries of *Phassus* lie within or near two major tectonic structures.The southern boundary lies to the west of the Romeral fault zone which represents the southeastern tectonic boundary of the Caribbean plate as it became inserted between North and South America beginning about 58 Ma. This tectonic structure is known to be correlated with the distributional limits of many animal and plant taxa (Heads 2016). Whether the range of *Phassus* extends to the Romeral fault zone will require targeted investigation. Over the last century there have been no records of *Phassus* from Barro Colorado Island in Panama by the Smithsonian Tropical Research Institute (no specimens at the Smithsonian collections, or from any other collection so far reviewed or examined by JRG and CGCM).

The northern boundary of *Phassus* is close to the Mojave-Sonora Megashear (or suture zone), a tectonic structure extending across northern Mexico from southern California to the Gulf of Mexico. The precise structural significance of the Mojave Sonora Megashear is debated among geologists (Amato *et al.* 2009, Price *et al.* 2019). It may represent a Late Jurassic fault initiated during expansion of the Gulf of Mexico (Aranda-Gómez *et al*. 2005), and possibly extended to South America at 160 Ma before southward displacement of the Maya block (Keppie 2004). The megashear cuts across a region of extensive subduction related volcanic magmatic activity followed by episodes of rifting and basin development (Campbell & Anderson 2003, Anderson & Nourse 2005, Stern & Dickinson 2010). Examples of other taxa with a northern Mexico distributional boundary include the angiosperm groups Gesnerioideae (Heads 2014, fig. 3.15), Crossosomataceae (Heads 2014, fig. 3.1), Turneraceae – Series Microphyllae (Arbo & Espert 2009), and the Troidini butterflies (Heads 2014, fig. 3.22). The northern Mexico region presents a phylogenetic break in the Laurales between Calycanthaceae in the southern United States (and eastern Asia and Australia), and Siparun in Central America and South America (Heads 2014, fig. 3.7). This break may be comparable to that between the meso-central American *Phassus*, and the North American hepialid fauna north of Mexico that have immediate affinities that are Old World (*Gazoryctra* Hübner, *Phymatopus* Wallengren, *Korscheltellus* Börner) or unresolved (*Sthenopis* Packard) (see Grehan & Mielke 2018).

Determination	Type	bp	GenBank	BOLD	Collection data	Depository
Phassus zapalinamensis	Holotype	658	---	barcode SNB 6947	Mexico, Coahuila, Arteaga	UNAM
Phassus zapalinamensis	Paratype	658	---	barcode SNB 6948	Mexico, Nuevo León, García	UNAM
Phassus huebneri	---	658	JX215837	BC-CGCM-15.774	Mexico, Colima, Comala	CGCM
Phassus chrysodidyma	---	658	GU661558	BC-CGCM 23.890	Mexico, Michoacán, Cerro El Laurel	CGCM
Phassus marcius	Lectotype	658	---	---	Mexico, Durango, near Durango City	NHMUK
Phassus violetteae	Paratype	658	GU661567	BC-CGCM 23.473	Costa Rica, Cartago, Tapantí	INBIO
Phassus n-signatus	---	658	HQ972133	BC-CGCM 23.940	Guatemala, Quetzaltenango, Zunil	CGCM
Phassus championi	---	658	GU661528	BC-CGCM 23.684	Guatemala, São Marcos, Bogomal	CGCM
Phassus basirei	Holotype	658	---	---	Mexico, Coatepec	USNM
Phassus triangularis	---	658	JX215839	BC-CGCM-1.964	Mexico, Veracruz, Soteapan	CGCM
Phassus aurigenus	---	658	JX215852	BC-CGCM-14.005	Costa Rica, Cartago, Tapantí	CGCM
Cibyra ochracea	---	658	JX215598	BC-CGCM-13.615	Brazil, Santa Catarina, São Bento do Sul	CGCM

marcius	AACTTTATACTTTATTTTCGGTATTTGAGCTGGTATAGTTGGTACATCTTTAAGATTATTAATCCGGACAGAATTAGGAAATCCTGGATCTTTAATTGGGGATGATCAAATTTATAATGTAATTGTAACAGCTCATGCTTTTATTATAATTTTTTTCATAGTAATACCTATTATAATTGGAGGATTTGGAAATTGATTAGTTCCTTTAATACTTGGAGCCCCTGATATAGCATTTCCACGAATAAATAATATAAGATTTTGATTATTACCACCATCATTAATATTATTAATTTCTAGAAGAATTGTAGAAAATGGGGCAGGAACAGGTTGAACTGTTTATCCACCTTTATCTGCAAATATTGCTCATGCAGGAAGTTCTGTAGACTTAGCTATTTTTTCTTTACATTTAGCTGGAATTTCTTCTATTTTAGGGGCCGTAAATTTTATTACTACTGTAATTAATATGCGATCAAATGGAATATCTTTTGATCGCATACCTTTATTTGTTTGAAGAGTTGCAATTACTGCTTTATTATTACTACTTTCATTACCTGTTTTAGCAGGTGCTATTACTATATTATTAACAGACCGAAATTTAAATACTTCATTTTTTGATCCTGCTGGGGGTGGTGACCCTATTTTATATCAACATTTATTC
basirei	AACTTTATATTTTATTTTTGGTATTTGAGCTGGTATAATTGGTACATCTTTAAGATTACTAATTCGAACAGAATTGGGGAACCCTGGATCTCTAATTGGAGATGATCAAATTTATAATGTAATTGTTACAGCCCATGCTTTTATTATAATTTTTTTTATAGTTATACCTATTATGATTGGGGGCTTTGGAAATTGATTAATTCCTTTAATATTAGGTGCTCCTGATATAGCATTTCCCCGAATAAATAATATAAGATTTTGATTATTACCACCCTCATTAATATTATTAATTTCTAGAAGAATTGTAGAAAATGGGGCAGGAACAGGATGAACTGTTTATCCACCATTATCTTCAAATATTGCACATGCTGGAAGATCTGTAGATTTAGCTATTTTTTCCTTACATTTAGCTGGAATTTCATCTATTTTAGGAGCTGTAAATTTTATTACTACTGTAATTAATATACGATCAAATGGTATGTCATTTGATCGTATACCTTTATTTGTTTGAAGAGTTGCAATTACTGCTTTATTATTATTACTTTCTTTACCTGTTTTAGCAGGAGCTATTACTATACTATTAACAGATCGAAATTTAAATACTTCATTTTTTGATCCTGCTGGGGGGGGGGATCCTATTTTATATCAACATTTATTT
INBIO	Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica

Table 1. Data for the sequences from the different species of the *Phassus* and the outgroup (*Cibyra ochracea*). BOLD – voucher at The Barcode of Life Data System; bp – base pairs. Sequences for *P. marcius* and *P. basirei* provided by Nick Grishin.

In southern Mexico the distribution of *Phassus* extends into the Guerrero super terrane (Fig. 20b) that is made up of former island arcs of Pacific origin that fused with the original western coast of Mexico about 100 million years ago (Clennett *et al.* 2020). The absence of extensive collection records for northern Mexico precludes any inference about the presence or absence of *Phassus* across the Guerrero terrane.

While there is no comprehensive phylogeny for *Phassus* and its putative relatives, there is some morphological evidence supporting a close affinity with the genus *Schausiana*. The male genitalia are similar in overall shape and proportions, particularly in the relative size and shape of the pseudotegumen (see Mielke *et al.* 2020). The valva of both genera is distally lobate, and the anogenital boundary is ovoid. The genera share the callus feeding and stem boring larval habit, although this is also applicable to all meso and south American Hepialidae beyond the southern Andes (Grehan *et al.* 2021b). *Phassus* and *Schausiana* also share the presence of a metatibial androconial brush in the male. While that feature distinguishes *Phassus* and *Schausiana* from all other Hepialidae in meso-America, it does not necessarily predict a close relationship as the structure is also present in more distantly related genera in South America, Asia, and Australasia (Grehan & Mielke 2020).

The distribution of *Schausiana* is encompassed within the distribution range of *Phassus*, but the geographic overlap is only across the southern range of *Phassus*. The northern boundary of *Schausiana* overlaps with the eastern part of the trans-Mexican volcanic belt, extending west only to the south easternmost Guerrero terrain (Fig. 20b). The trans-Mexican volcanic belt formed in early Miocene time, about 19 Ma (Ferrari *et al.* 2012). This magmatic activity occurred over an earlier strike slip fault between western and eastern Mexico – the Trans-Mexican volcanic belt lineament, a sinistral strike slip fault in the Jurassic and displacing southern Mexico to the southeast (Alaniz-Alvarez *et al.* 1996). It is possible that all three tectonic and geological processes affected differentiation of *Phassus* and *Schausiana*, but much more extensive geographic sampling and systematic resolution of both genera will be essential to address these possibilities. The possibility of a broader affinity involving *Pallas* Mielke & Grehan, 2016 in Guatemala (Mielke & Grehan 2016) and *Phthius* Mielke & Grehan, 2017 in southeastern Brazil (Mielke & Grehan 2017) also needs to be further investigated. Future surveys of *Phassus* across the central northern regions of Mexico are highly desirable, including sampling of mesic forests on the southern tip of Baja California.

Primary type designations

Phassus argentiferus Walker, 1856
Fig. 3c
Walker (1856) described *Phassus argentiferus* based on an uncertain number of specimens. A syntype ♀, deposited in NHMUK, bears the label "type". This specimen is **here designated as lectotype**. It has the following labels: /Type/ Mexico/ 1. *Phassus argentiferus*/ argentiferus, Sz/.

Phassus marcius Druce, 1892
Fig. 14i
Druce (1892) described *Phassus marcius* based on an uncertain number of specimens. A syntype ♀, deposited in NHMUK, bears the label "type". This specimen is **here designated as lectotype**. It has the following labels: /*Phassus marcius* type Druce/ Near Durango city, Mexico. Becker/ Godman-Salvin Coll. 98.—40./ B.C.A. Lep. Het. *Phassus marcius*/ Holotype/.

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