

Wing Condition and Distribution of a Mesoamerican Montane Genus of Wood-degrading Beetles, *Oileus* Kaup (Coleoptera: Passalidae), with the Description of a New Species

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Distribution areas, in terms of size and shape, are usually related to dispersal capacity, and the latter is partly related to flight capacity in insects. Thus, wing condition (brachypterous or macropterous) is expected to correlate with the area size of the species distribution range. Here, we studied this aspect for the first time in Passalidae, a subsocial group of saproxylophagous beetles. To obtain the geographic distribution of species, we performed species distribution models in the Mesoamerican genus *Oileus*, which has seven species (including one new species from Oaxaca, Mexico) restricted to either side (west or east) of the Isthmus of Tehuantepec (except for *Oileus rimator* which is distributed in both sides of the Isthmus). Species distribution models were used to estimate biogeographic affinities among species and to compare the potential distributional area with respect to the species wing condition (four brachypterous and three macropterous). Additionally, we described the sound-emitting structures (*plectrum*, region located on hind wings) for all *Oileus*, being the first study describing it for all species of the same genus. Macropterous species tend to have larger potential distribution areas (between 149,027–364,107 km²) than brachypterous species (9,063–15,716 km²), and all brachypterous species inhabit montane areas. These results coincide with what would be expected if the loss of flight capacity reduced dispersal capacity. However, because of the limited data, we could not statistically test this relationship. Future analyses should evaluate the relationship between passalid species distributions (total area and elevation) and wing morphology, including species with narrow and wide distributions, both altitudinally and latitudinally.

Key words: Bess beetles, Species distribution models, Macropterism, Braquiapterism, Stridulatory apparatus

BACKGROUND

The family Passalidae, commonly known as bess beetles or wood-degrading beetles, is a group of subsocial saproxylophagous beetles found mainly in forested habitats, and contains approximately

900 extant species (Boucher 2005). Regarding its distribution in America, the family comprises the tribes Passalini and Proculini (Beza-Beza et al. 2020). Passalini is mainly distributed in South America with about 230 described species, and Proculini is mainly distributed in Mesoamerica with about 250 described

species. Most species in Passalidae have a restricted distribution, covering small geographic areas and a few biogeographic provinces; therefore, species are used to delimit endemism areas (Schuster 1992), except for some species that are distributed on a continental scale from Mexico to Argentina.

The causes of the restricted distributions of most passalid species have not been established. Their ecological relationship with forest cover (Kattan et al. 2010) and their limited vagility (Galindo-Cardona et al. 2007; Schuster and Cano 2006) are the main factors considered so far. Dispersal capacity is only known for *Spasalus crenatus* MacLeay and *Odontotaenius disjunctus* Illiger, highlighting low dispersal rates and movement between different types of habitats (Galindo-Cardona et al. 2007; Jackson et al. 2009). Although passalids are not recognized as good fliers, their ability to fly must be related to their dispersal ability. Species restricted to montane habitats tend to have reduced hind wings; thus, species elevational range is a factor in wing morphology (Ariza-Marín and Amat-García 2023). In fact, for Proculini, which originated in the mountains of Mesoamerica (Beza-Beza et al. 2021), around 40% of the described species have reduced hind wings (hemi-brachypterous or brachypterous), all of which are restricted to montane ecosystems. In turn, of the seven genera in Passalini, which is postulated to have originated in South America (Fonseca 1987; Reyes-Castillo and Halfpeter 1978), only *Passalus* contains brachypterous species (18 of 172 species) (Jiménez-Ferbans et al. 2022), all of which inhabit mountain areas. Thus, wing condition is expected to affect dispersal ability and to be related to the size of a species' distribution area. Wing traits such as length, area and wing loading are used to compare dispersal capacity in saproxylic insects (Gibb et al. 2006).

Moreover, wings not only play a dispersion role, but they also have a specific zone located on the radial cell (*plectrum*) which is densely covered with

stridulatory spines (Reyes-Castillo and Jarman 1983). Therefore, all species produce sounds to communicate with conspecifics; in fact, sound-emitting structures can be used to discriminate related species (Ariza-Marín and de Luna 2020). However, to date, no study has described nor compared the stridulatory structures of all species of the same genus.

The Proculini genus *Oileus* has equal numbers of brachypterous (*Oileus bifidus* (Zang), *Oileus heros* (Truqui), and *Oileus nonstriatus* (Dibb)) and macropterous (*Oileus rimator* (Truqui), *Oileus sargi* (Kaup), and *O. gasparilomi* Cano and Schuster) species. Even though the distribution area of *Oileus* has not been studied recently, the genus generally exhibits a Mesoamerican Montane distribution pattern (Reyes-Castillo and Halfpeter 1978), and according to Beza-Beza et al. (2021), it is originated in Nuclear Mesoamerica during the Eocene, and is associated with montane habitats. Consequently, *Oileus* brachypterous species inhabit tropical montane cloud forests and Neotropical montane oak forests, whereas macropterous species inhabit those forests and tropical rainforest (Reyes-Castillo et al. 2006) (except for *O. gasparilomi*, which is restricted to montane forests (Cano and Schuster 2012)). In addition, brachypterous species are distributed to the east side of the Isthmus of Tehuantepec and macropterous species to the west of the Isthmus, except for *O. rimator*, a macropterous species distributed on both sides of the Isthmus (Reyes-Castillo 2003) (Table 1).

Here, we performed species distribution models for *Oileus* species and discussed the possible relationship between the size of their distribution area and wing condition (brachypterous and macropterous). Additionally, we describe a new brachypterous species from the east of the Isthmus of Tehuantepec (Oaxaca, Mexico), describe the stridulatory spines of all species, and provide a key for the identification of the species of the genus.

Table 1. Distribution of *Oileus* species based on literature records (Reyes-Castillo et al. 2006), and specimens deposited in IEXA Collection. States of each country are in parenthesis

Species	Distributions	Elevation (m.a.s.l.)
<i>Oileus bifidus</i> (Zang)	Mexico (Oaxaca)	1840
<i>Oileus gasparilomi</i> Cano & Schuster	Guatemala (Quiché)	1795
<i>Oileus heros</i> (Truqui)	Mexico (Puebla and Veracruz)	1460–2240
<i>Oileus nonstriatus</i> (Dibb)	Mexico (Hidalgo and Puebla)	1280–2060
<i>Oileus rimator</i> (Truqui)	Mexico (Chiapas, Guerrero, Hidalgo, Oaxaca, Puebla and Veracruz)	800–2860
<i>Oileus sargi</i> (Kaup)	Mexico (Chiapas), Guatemala, Honduras, El Salvador, Nicaragua, Costa Rica and Panamá	820–2755

MATERIALS AND METHODS

Distribution of *Oileus* species

We calculated the potential distribution for five of the seven species of *Oileus* using species distribution models (SDM) with an algorithm based on ellipsoids (Osorio-Olvera et al. 2020), which follows the niche definition proposed by Hutchinson (1957) as an n-dimensional space. Methodologically, our SDM process consisted of five steps: (1) obtaining and cleaning of species occurrences, (2) defining the accessible area for each species, (3) selection and preparation of scenopoetic variables, (4) model selection, and (5) model performance and binarization. For the remaining two species, which are only known from the type material (*O. bezai* sp. nov., *O. gasparilomi*), we determined the biogeographic provinces in which the type material is located, using the biogeographic regionalization proposed by Morrone et al. (2022).

To obtain species occurrences, we used open-access databases (GBIF: <https://www.gbif.org/>) and specimens deposited in the following entomological collections: Entomological Collection of the Instituto de Ecología A. C. (IEXA), Universidad del Valle de Guatemala Collection (UVGC), Museo de Historia Natural de Costa Rica (MNCR), and the personal collection of Dr. Alan Gillogly (AGC). We removed GBIF records without coordinates. For occurrences obtained from collections without coordinates, we used the collection information to georeference the occurrences in Google Earth Pro version 7.3.4.8248; this was done only for specimens with geographic information, at least for second-order administrative divisions. To avoid spatial autocorrelation in each species, we removed species occurrences close to each other (1 km radius) using the package “spThin” (Aiello-Lammens et al. 2015).

Then, to define the accessible area for each species (M) (Soberón and Peterson 2005), we selected the polygons that intersected species occurrences with two shapefiles, terrestrial ecoregions (Olson et al. 2001) and biogeographic provinces of the neotropics (Morrone et al. 2022), using the package “sp” (Pebesma et al. 2023). We dissolved the polygons in each shapefile and then merged both shapefiles using the package “rgeos” (Bivand et al. 2023). To build the “M” for each species, we manually edited the merged shapefile using biogeographic barriers and the known distribution for each species, and made a buffer of ten kilometers on the shapefile with the software Qgis 3.22.12 (QGIS.org 2022).

To define scenopoetic variables for performing

ecological niche models, we used the historical climate data summarized in the 19 bioclimatic variables of WorldClim 2.1 (Fick and Hijmans 2017) with a resolution of 30 arcseconds for the present. To avoid autocorrelation among the variables, we performed a Pearson’s correlation test and selected variables with correlation values lower than 0.7. Then, we cropped the selected variables of each species by its “M”, with the package “raster” (Hijmans et al. 2023).

For model selection, building, and binarization, we used the package “ntbox” (Osorio-Olvera et al. 2020), by uploading the cleaned occurrences and cropped variables one species at a time. We selected the best model using the following steps: 1) dividing the occurrences for training and testing models (75% train and 25% test), allowing all possible combinations of variables (greater than or equal to two); 2) calculating the ellipsoid with the minimum volume that contains 95% of training presences, using 10000 background points, and an omission rate of 0.05; and 3) calculating the partial ROC with 100 replicates. The best model had the lowest omission rate and significant partial ROC. We performed the ellipsoid model with the variable combination of the best model, and binarized the outcome using the 90th percentile of suitability values associated with species occurrences. Finally, using Qgis 3.22.12 (QGIS.org 2022), we intersected the binarized potential distribution with the biogeographic provinces of the neotropics (Morrone et al. 2022), calculated the area of potential distribution belonging to each province, and performed a cluster analysis with the proportion of each biogeographic province per species using the package “cluster” (Rousseeuw et al. 2019).

Specimen revision and preparation

External morphological characters were examined using a LEICA EZ4HD stereomicroscope. Male and female genitalia of specimens of the new species were dissected, and the female genitalia were placed in genitalia vials containing 95% glycerol. The right metathoracic wing was dissected from one specimen by species (paratype in the new species), extended, and pasted in metallic tape with its ventral side upward, covered with gold-palladium for micrographs, and saved in a wing reference of the IEXA collection. Body parts were measured using a digital caliper. The terminology used in the description of external characters corresponds to Reyes-Castillo (1970) and Boucher (2005) for the head and genital characters. Photographs were taken using a Leica Z16APOA stereomicroscope with a camera attached (LEICA DMC 2900) for external characters, whereas for genital characters we used a camera attached to a LEICA

EZ4HD. Micrographs of the plectrum of the allotype were taken using a scanning electron microscope (JEOL JSM-5600 LV) with a working distance (WD) of 23 mm and 4000 amplifications. In each micrograph the spine length, width, and distance to the nearest spine were measured for five randomly selected spines. The spine density was calculated by dividing the number of spines over the area of the micrograph. Spine measurements were performed using the ImageJ2 software (Rueden et al. 2017).

The specimens of the new species were compared with specimens identified by Pedro Reyes-Castillo, of *O. bifidus*, *O. heros*, *O. nonstriatus*, *O. rimator*, and *O. sargi* deposited in the IEXA collection. For *O. gasparilomi*, we compared the new species with a paratype deposited in IEXA and the original description. The type series of *Oileus bezai* sp. nov. will be deposited in the following collections: IEXA: Entomological Collection of the Instituto de Ecología, A.C. (IEXA), Colección Nacional de Insectos of Universidad Nacional Autónoma de México (CNIN), and the Entomological Collection of the Universidad del Magdalena, Colombia (CBU MAG-ENT).

RESULTS

Distribution of *Oileus* species

We generated SDM for *O. sargi*, *O. rimator*, *O. bifidus*, *O. heros*, and *O. nonstriatus* (Fig. 1). *O. sargi* and *O. rimator* are the most widely distributed species, covering seven biogeographic provinces, the first ranging from Chiapas (Mexico) to Costa Rica (Fig. 1e), and the latter from the north of Veracruz to Chiapas (Fig. 1d). Brachypterous species are distributed in fewer provinces located in the east-central region of Mexico (*O. heros* in five, Fig. 1b; *O. bifidus* in four, Fig. 1a; *O. nonstriatus* in three, Fig. 1c). Regarding species only known from the type material, *O. bezai* sp. nov. is distributed in the province of Sierra Madre del Sur and *O. gasparilomi* in the province of the Chiapas Highlands near the border with the Veracruz province (Fig. 1f).

Overall, *Oileus* species tend to be restricted to one side (west or east) of the Isthmus of Tehuantepec (Fig. 1a–c, e), except for *O. rimator*, which has occurrences on both sides of the Isthmus (Fig. 1d). In terms of biogeographic provinces, potential distribution areas for all species intersect with the Veracruz province, from 7% in *O. nonstriatus* to 50% in *O. bifidus* (Fig. 1a–e). The degree of overlap among species was high when comparing *O. rimator* against the brachypterous species; however, the overlap was low (3–9%, Table 2) when

comparing all species against *O. rimator*. In contrast, the degree of overlap for other comparisons is low (under 30%), which implies low sympatry leading to low biogeographic similarity among potential distribution areas (Fig. 2a).

In terms of the total potential distribution area, macropterous species tend to have larger areas (between 149,027 km² [*O. rimator*] and 364,107 km² [*O. sargi*]) than brachypterous species (9,063 km² [*O. nonstriatus*], 13,805 km² [*O. heros*] and 15,716 km² [*O. bifidus*]) (Fig. 2b). In addition, the two biogeographic provinces that covered larger areas exceeded 70% of the total potential distribution area for brachypterous species, whereas in macropterous species this area covers 50% of the potential distribution.

Morphology of stridulatory spines

In general, spines located on the posterior zone (Z3) were the shortest (except in *O. rimator*) and those in the apical zone (Z1) had the highest spine density (except in *O. rimator*), whereas the width and distance between spines showed different patterns for each species. Regardless of the zone, *O. heros* had the longest spines, whereas *O. rimator* had the shortest. Finally, *O. rimator* had a higher density of spines for all zones (Table 3), whereas *O. bezai* sp. nov. had the lowest spine density on the apical (Z1) and posterior zones (Z3).

TAXONOMY

Oileus bezai sp. nov. Ariza-Marín, Jiménez-Ferbans and Reyes-Castillo

(Fig 3)

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Material examined: Eleven specimens.

Type material: HOLOTYPE: (♂), “MEXICO, Oaxaca, 1 km N Mixistlán | 2440 m | Bosque mesófilo de montaña | 29.ii.1988, Reyes, Boucher & Castillo col. | *Oileus* sp.n. Reyes-Castillo Det.1988” (IEXA). PARATYPES: same data as holotype, (2 ♀ ♀ (IEXA), 1 ♀ (CNIN), 2 ♀ (CBU MAG-ENT)). “MEXICO, Oaxaca, 4.4 km N Tlahuitotepec | 2420 m | Bosque de pino-encino | 28.ii.1988, Reyes, Boucher & Castillo col. | *Oileus* sp. nov. Reyes-Castillo Det. 1988”, (1 ♂ (CBU MAG-ENT), 1 ♂ (IEXA), 2 ♂ ♂ (CNIN), 1 ♀ (IEXA), 1 ♀ (CNIN)). “MEXICO, Oaxaca, 3 km S Sn Miguel Metepec. Oaxaca | 2470 m | Bosque mesófilo montaña, Tr. 15 | 29.ii.1988, Reyes, Boucher, Castillo col. | *Oileus* sp. n. Reyes-Castillo Det.1988”, (1 ♂ (CBU MAG-ENT)).

Etymology: Noun in the genitive to honor Dr. Cristian Beza for his valuable contributions to the taxonomy, systematics, and biogeography of passalids, in addition to his support and scientific collaboration

with all authors of this publication.

Diagnosis: Brachypterous species, body size 34–39 mm. This is the second brachypterous species of *Oileus* reported from the Mexican state of Oaxaca,

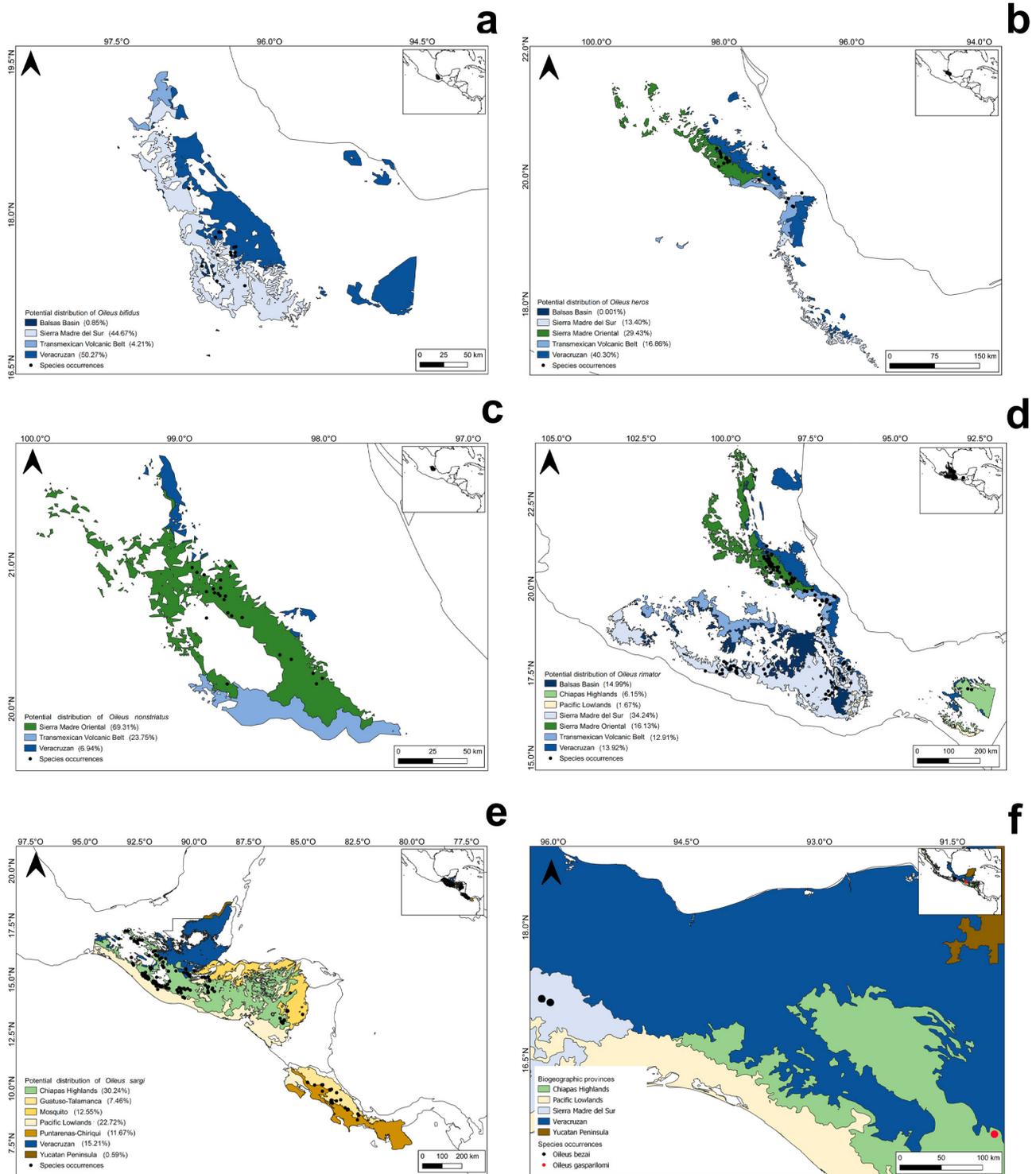


Fig. 1. Species distribution models (SDM) and occurrences for *Oileus* species. a) SDM for *Oileus bifidus*, b) SDM for *Oileus heros*, c) SDM for *Oileus nonstriatus*, d) SDM for *Oileus rimator*, e) SDM for *Oileus sargi*, f) Occurrences for *Oileus gasparilomi* and *Oileus bezai* sp. nov. Polygon color changes with biogeographic provinces. Points correspond to species occurrences.

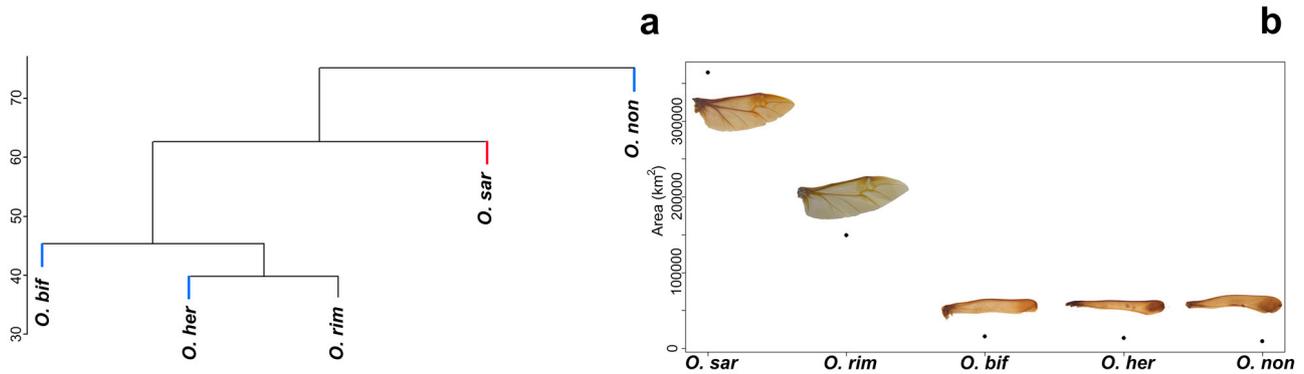


Fig. 2. Biogeographic affinities and distributional areas of *Oileus* species. a) UPGMA cluster analysis performed with proportion of biogeographic provinces of distribution area for each species, b) Size of potential distribution area; wing morphology is illustrated for each species. *O. bifidus* (*O. bif*), *O. heros* (*O. her*), *O. nonstriatus* (*O. non*), *O. rimator* (*O. rim*), *O. sargi* (*O. sar*). Blue lines indicate species restricted to the west of the Tehuantepec Isthmus. Red lines indicates species restricted to the east of the Tehuantepec Isthmus. Black lines indicate species distributed on both sides of the Tehuantepec Isthmus.

Table 2. Geographic overlapping of *Oileus* species. Rows are the percentage of overlap for each species against the other

	<i>O. bifidus</i>	<i>O. heros</i>	<i>O. nonstriatus</i>	<i>O. rimator</i>	<i>O. sargi</i>
<i>O. bifidus</i>	-	16.51	0	49.44	0
<i>O. heros</i>	18.79	-	17.43	93.11	0
<i>O. nonstriatus</i>	0	26.56	-	79.47	0
<i>O. rimator</i>	5.21	8.63	4.83	-	2.97
<i>O. sargi</i>	0	0	0	1.22	-

Table 3. Measurements of *plectum* spines for *Oileus* species. Numerical description of variation of *plectum* spines in three *plectum* zones. Apical zone (Z1), medial zone (Z2), basal zone (Z3). Spine length (SL), Spine width (SW), Distance to nearest spine (DNE), Spine density in 10 μm^2 (SD)

Species: Zone	SL (μm)	SW (μm)	DNE (μm)	SD
<i>O. bezai</i> : Z1	13.042 ± 0.929	4.039 ± 0.291	5.276 ± 0.702	2.125
<i>O. bezai</i> : Z2	13.286 ± 0.680	3.478 ± 0.408	7.292 ± 1.453	1.859
<i>O. bezai</i> : Z3	8.550 ± 1.485	3.021 ± 0.151	7.093 ± 0.861	1.328
<i>O. bifidus</i> : Z1	12.688 ± 1.021	3.311 ± 0.202	6.769 ± 0.704	2.524
<i>O. bifidus</i> : Z2	12.127 ± 0.835	3.460 ± 0.266	7.968 ± 0.593	1.461
<i>O. bifidus</i> : Z3	9.615 ± 0.628	3.654 ± 0.519	5.887 ± 0.969	1.594
<i>O. gasparilomi</i> : Z1	10.869 ± 1.054	2.882 ± 0.243	5.779 ± 0.753	2.524
<i>O. gasparilomi</i> : Z2	10.574 ± 0.873	3.201 ± 0.249	6.110 ± 0.820	1.992
<i>O. gasparilomi</i> : Z3	9.968 ± 0.728	3.755 ± 0.309	6.785 ± 1.637	1.859
<i>O. heros</i> : Z1	13.853 ± 0.836	3.938 ± 0.232	6.739 ± 0.735	2.258
<i>O. heros</i> : Z2	14.710 ± 0.848	3.912 ± 0.299	6.427 ± 0.768	1.859
<i>O. heros</i> : Z3	11.644 ± 0.881	3.002 ± 0.109	6.756 ± 1.132	1.727
<i>O. nonstriatus</i> : Z1	9.189 ± 0.761	3.148 ± 0.191	6.117 ± 0.698	2.391
<i>O. nonstriatus</i> : Z2	11.424 ± 1.082	3.519 ± 0.198	8.354 ± 1.133	1.594
<i>O. nonstriatus</i> : Z3	6.090 ± 1.096	2.471 ± 0.147	6.936 ± 0.818	1.859
<i>O. rimator</i> : Z1	8.946 ± 0.873	3.304 ± 0.309	5.315 ± 0.995	2.656
<i>O. rimator</i> : Z2	8.960 ± 0.909	3.139 ± 0.279	5.616 ± 1.058	2.789
<i>O. rimator</i> : Z3	10.458 ± 0.698	3.577 ± 0.323	5.305 ± 0.758	2.391
<i>O. sargi</i> : Z1	12.826 ± 0.833	2.949 ± 0.279	6.925 ± 0.486	2.524
<i>O. sargi</i> : Z2	10.289 ± 0.418	2.778 ± 0.194	9.265 ± 0.669	1.859
<i>O. sargi</i> : Z3	10.702 ± 0.591	3.600 ± 0.354	5.410 ± 0.676	1.992

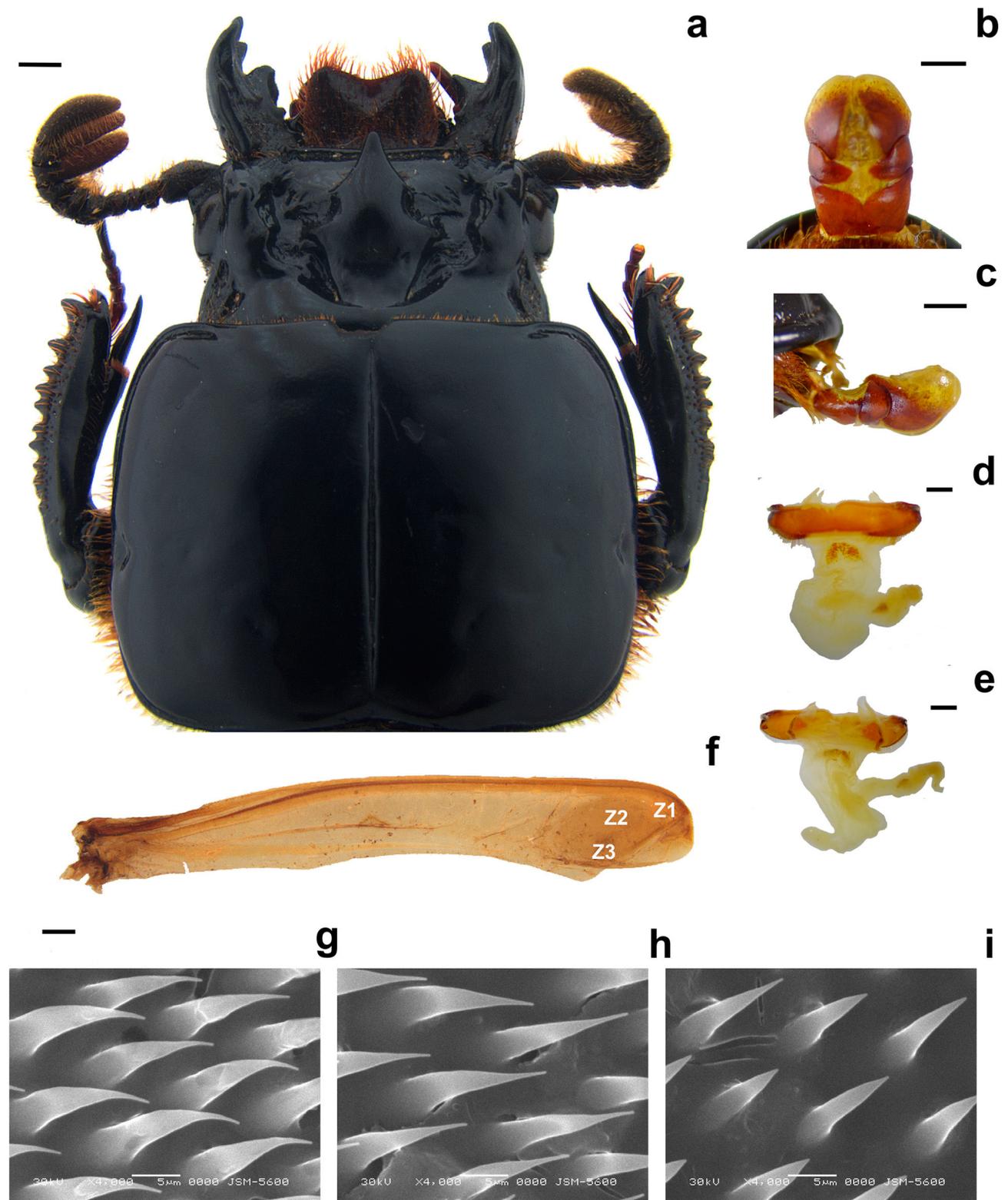


Fig. 3. Morphology of *Oileus bezai* sp. nov. a) head and pronotum, b) aedeagus ventral view, c) aedeagus lateral view, d) female genitalia ventral view, e) female genitalia dorsal view, f) hind wing, g-i: stridulatory spines of *plectrum*, g) apical zone (Z1), h) medial zone (Z2), i) posterior zone (Z3). Scale bar (black lines) 1 mm.

and differs from other brachypterous species by having the following combination of characters: clypeus and frontoclypeal suture straight, ocular canthus with rounded apex, lateral tubercles of mesofrontal structure attached to the base of the cephalic horn, elytral striae marked, mesepimeron glabrous, metasternal groove pubescent, aedeagus in ventral view with medial lobe rounded, and parameres not fused with pallobase.

Description: Habitus: Medium size, measured from mandibles tips to elytral apex, brachypterous, shiny black.

Head: Labrum completely pubescent, central region with less dense pubescence, anterior border concave, anterior angles rounded, and lateral border curved. Frontoclypeus vertical and smooth, anterior border slightly concave at center. Frontoclypeal suture rugose and slightly concave at center. Laterofrontal tubercles rounded, mediofrontal tubercles absent. Frontal area inclined, smooth, glabrous and shiny; frontal ridges absent; internal tubercles absent. Frontal fossae smooth, glabrous, and impunctate. Central tubercle long, basal part attached to the cephalic capsule appearing to have short dorsal ridges, apex free extending beyond frontoclypeal suture with triangular shape in dorsal view, and without a dorsal groove; lateroposterior ridges attached to central tubercle. Supra-orbital ridges bituberculated, posterior tubercle bigger than anterior. Eyes small, ocular canthus rounded, reaching 1/2 of eyes length (in lateral view), apex forming an angle greater than 90°. Postocular sulcus punctuate, setose, and wide (> 5 lines of punctures). Mentum with basal fossae oval, pubescent and shiny, lateral lobes with abundant pubescent, and medio-basal area shiny, without setae. Hypostomal process long and wide. Antennal club trilamellate, with lamellae slightly elongated, width equal to 4–4.5 times the length. Mandibular apex tridentate; internal inferior tooth monocolumnar in right mandible and bifid in left mandible; small basal tubercle on internal surface in both mandibles.

Thorax: Pronotum with anterior angles rounded; anterior border straight to slightly curved; marginal sulcus with tenuous punctures at posterior part; lateral fossae marked without punctations. Pronotum without visible punctations on dorsal view. Prosternellum rhomboidal. Mesosternum completely glabrous, lateral areas opaque. Mesepisternum with large opaque area and glabrous. Mesepimeron glabrous. Metasternum with dense pubescence on anterolateral area (around mesocoxae); metasternal disc delimited by punctures lateroposteriorly; metasternal lateral fossae straight, with scarce setae along its entire extent, and narrower than the width of mesocoxae in the medium region.

Elytra: Shiny, anterior border convex without

pubescence; humeri and epipleura glabrous. All striae marked with rounded punctures.

Hind wings: Brachypterous. The shape and size of *plectrum* spines varies among three anatomical regions: apical, middle and basal (Table 3).

Legs: Anterior ventral border of profemur with marked groove, not reaching apical pubescence. Mesotibiae with dorsal ridge long and heavily setose, and without spines on lateral border, apical spur longer than first tarsomere. Metatibiae without spines, apical spur longer than first tarsomere.

Abdomen: Visible abdominal tergites glabrous; marginal groove incomplete.

Aedeagus: In ventral view, basal peace smaller than medial lobe; phallobase separated from parameres; parameres not fused; medial lobe rounded. In lateral view, medial lobe globose. In dorsal view, parameres as wide as medial lobe. In dorsal view, median lobe with ventrodorsal basal sclerotizations.

Female genitalia: In ventral view, vagina with two proximal ventral lobes sclerotized and one dorsal proximal lobe directed to the right side.

Variation: Medio-basal area of mentum with few setae in allotype and four paratypes. Lateral border of mesotibiae with a small spine in two paratypes.

Dimensions: Total length 34.24–38.92 mm; body height at the metacoxa 7.44–9.15 mm; body height at mesothorax center 5.40–6.40 mm; elytral length at midline 18.51–20.94 mm; pronotal length at midline 8.59–9.64 mm; cephalic width at middle of eyes 7.33–8.44 mm; pronotal width at lateral fossae 10.88–12.50 mm; elytral width at metacoxal 11.66–13.57 mm.

Geographic distribution

Oileus bezai sp. nov is distributed on the Sierra Mixe located at the east of the Sierra Norte Region of the Mexican state of Oaxaca (Fig. 1f, black points).

Taxonomic key to the species of *Oileus* Kaup, 1869 (modified from Cano and Schuster 2012)

1. Eyes normal, globose, less than half covered by ocular canthus; elytra rectangular; humeri pubescent; metasternum pubescent in lateral sides and metasternal fossa posteriorly widening; Macropterous wings 2
- 1' Eyes reduced, kidney-shaped, at least half covered by ocular canthus; elytra oval; humeri glabrous; metasternum glabrous or pubescence restricted to coxae, and metasternal fossa straight; Brachypterous wings 4
2. Lateral margin of mesosternum with abundant setae; body length 30–42 mm 3
- 2' Lateral margin of mesosternum glabrous; body length 26–33 mm; (Fig. 4); Chiapas (Mexico) to Colombia *Oileus sargi* (Kaup)
3. Anterior border of clypeus widely notched at center; mentum

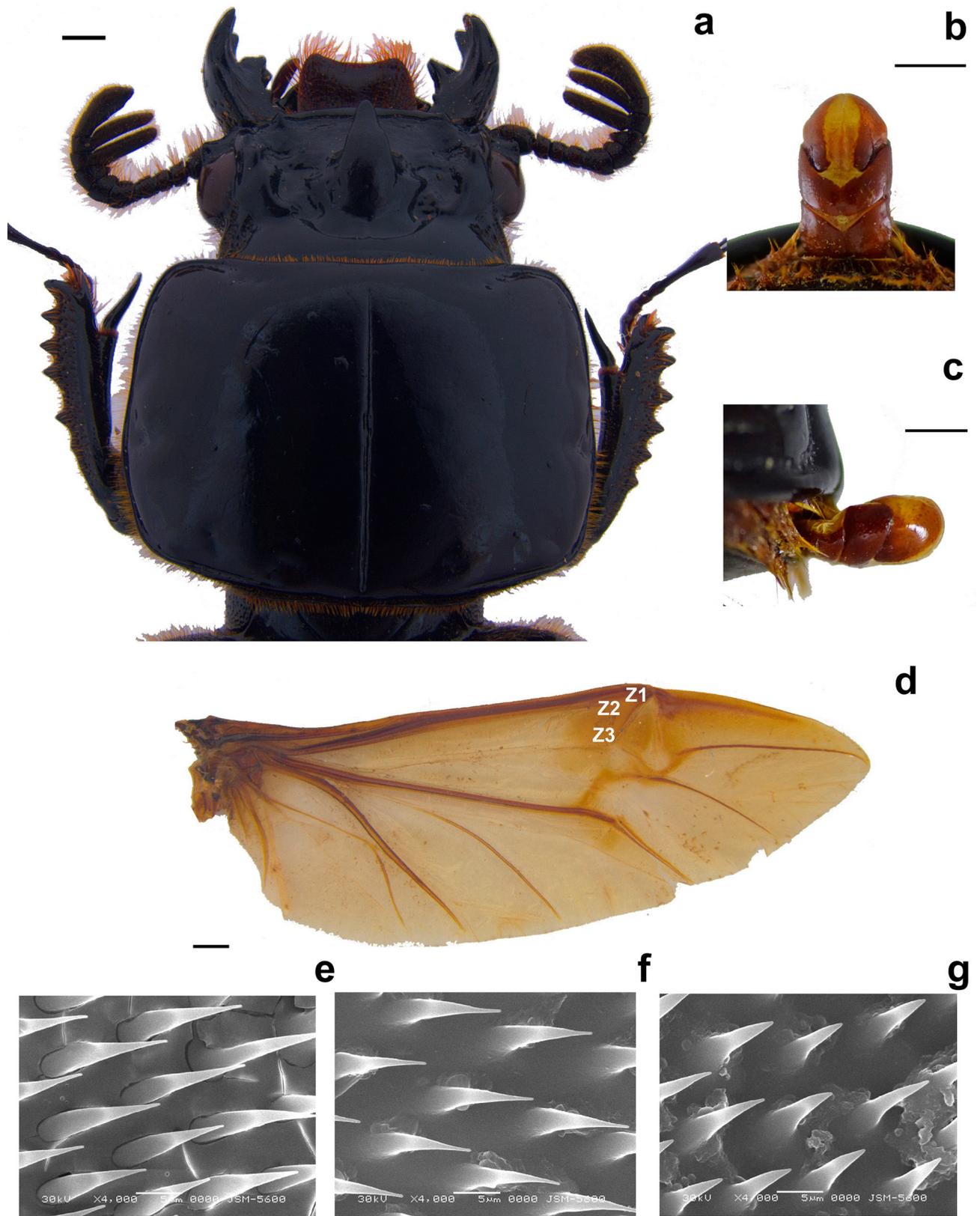


Fig. 4. Morphology of *Oileus sargi* (Kaup). a) head and pronotum, b) aedeagus ventral view, c) aedeagus lateral view, d) hind wing, e–g: stridulatory spines of *pectrum*, e) apical zone (Z1), f) medial zone (Z2), g) posterior zone (Z3). Scale bar (black lines) 1 mm.

- with setigerous punctures outside of lateral scars; body length 30–40 mm; (Fig. 5); Sierra Madre Oriental, Sierra Madre del Sur, Oaxaca mountains and Macizo Central de Chiapas (Mexico) *Oileus rimator* (Truqui)
- 3' Anterior border of clypeus straight; mentum with setigerous punctures restricted to lateral scars; body length 36–42 mm; (Fig. 6); Quiché (Guatemala) *Oileus gasparilomi* Cano and Schuster
4. Elytral striae indistinct or with feebly visible punctuations; cephalic horn with dorsal longitudinal groove, extending more than one half the length of the horn; ocular canthus acute-angled; mesepimeron pubescent 5
- 4' Elytral striae marked with more or less developed but always distinct punctuations; cephalic horn with dorsal longitudinal groove extending one third of the length of the horn, or absent; canthus with rounded apex greater than 90 degrees; mesepimeron glabrous 6
5. Frontoclypeal suture slightly concave at center; central tubercle conic in dorsal view; dorsal surface of mandibles smooth; all elytral striae barely marked; third abdominal sternum pubescent at lateral and medial sides, fourth and fifth abdominal sterna pubescent at lateral sides; aedeagus in lateral side with rounded median lobe and parameres smaller than pallobase; body length 42–47 mm; (Fig. 7); Sierra Madre Oriental (Mexico) *Oileus heros* (Truqui)
- 5' Frontoclypeal suture straight; central tubercle triangular in dorsal view; dorsal surface of mandibles with small punctations; elytral striae 1–2 poorly marked, 3–6 indistinct at least in anterior and posterior third; abdominal sterna glabrous, or with few setae on the middle side of the third sterna; aedeagus in lateral side with flattened median lobe and parameres bigger than pallobase; body length 36–42 mm; (Fig. 8); Sierra Madre Oriental (Mexico) *Oileus nonstriatus* (Dibb)
6. Frontoclypeus and frontoclypeal suture biconvex; central tubercle conic with dorsal longitudinal groove extending one third of the length of the horn, or absent; lateral tubercles of MFS separated from the base of the cephalic horn; metasternal fossa glabrous; aedeagus in ventral view with medial lobe ovate, parameres touching each other at the center; body length 31–44 mm; (Fig. 9); Sierra de Juárez (Mexico) *Oileus bifidus* (Zang)
- 6' Frontoclypeus and frontoclypeal suture straight; central tubercle triangular without dorsal longitudinal groove; lateral tubercles of MFS attached to the base of the cephalic horn; metasternal fossa pubescent; aedeagus in ventral view with medial lobe rounded, parameres separated from each other; body length 34–39 mm; (Fig. 3); Sierra Mixe (Mexico) *Oileus bezai* sp. nov. Ariza-Marín, Jiménez-Ferbans and Reyes-Castillo

DISCUSSION

The brachypterous species of *Oileus* have distribution areas that tend to be smaller than those of macropterous species, which is in agreement with the general idea that flight ability is one of the aspects that has shaped species distributions (Lester et al. 2007). The huge potential distribution reported for *O. rimator* and *O. sargi* are not exceptional; Whitaker et al. (2021) collected specimens of *Odontotaenius disjunctus* (macropterous species) along the east coast of United States from Louisiana to New Hampshire and found a genetic flow among populations, leading

to reconsideration of the idea that passalids are not good flyers. In addition, these species have potential distributional areas divided by biogeographic barriers (Tehuantepec Isthmus: *O. rimator*; Nicaraguan fault: *O. sargi*), therefore, phylogeographic studies are necessary to determine if there are single species or a species complex. Another possibility is to evaluate possible expansion of their geographic distribution in the past, *i.e.*, if the potential area was not partitioned in the last glacial maximum, gene flow possibly existed and the current “allopatric” populations belong to the same species. However, even if we split the potential distribution area of both species by its respective geographic barrier, the potential area of the four macropterous populations is bigger than the potential area of the brachypterous species.

Regarding wing condition, in passalids wing type is analyzed as a discrete variable with two options: well-developed (macropterism) or reduced (hemibrachyperism and brachypterism); however, both categories could have modified conditions. In particular, the dispersal ability of flying animals (macropterous) could be related to wing length, with a greater wing length implying larger areas of distribution (McCulloch et al. 2016). This pattern possibly applies to the macropterous species of *Oileus*, as the hind wings of *O. rimator* are close to 1.76 times greater than the pronotal width, whereas in *O. sargi* this ratio is 1.87 (estimation obtained from Figs. 4–5). Additionally, wing area and loading could have a positive relationship with elevation (Lozier et al. 2021; Luo et al. 2019), and both variables should differ between *O. rimator* and *O. sargi*; visually, *O. rimator* has slender wings (Figs. 4–5) and a potential distribution restricted to mountains (Fig. 1d), whereas *O. sargi* has rounded wings and wider altitudinal distribution (Fig. 1e). Similarly, brachyptery in Passalidae is apparently related to the habit of living in mountains (Ariza-Marín and Amat-García 2023; Jiménez-Ferbans et al. 2022; Reyes-Castillo 1970). Future work should evaluate the relationship between passalid distribution (total area and elevation) and wing morphology.

From a phylogenetic perspective, reduced wings have been considered as a homoplastic character within passalid genera, except for *Proculus*, *Proculejus* and *Ogyges*, which only have brachypterous species (Cano 2014; Reyes-Castillo 1970; Schuster et al. 2003). However, in *Oileus* this condition could be homologous, judging by the coincident geographic distribution (only the eastern part of the Isthmus) and the morphological similarity among brachypterous species. One line of evidence in favor of this seems to emerge from the phylogeny by Beza-Beza et al. (2020), in which the three macropterous species (*O. gasparilomi*, *O. rimator*,

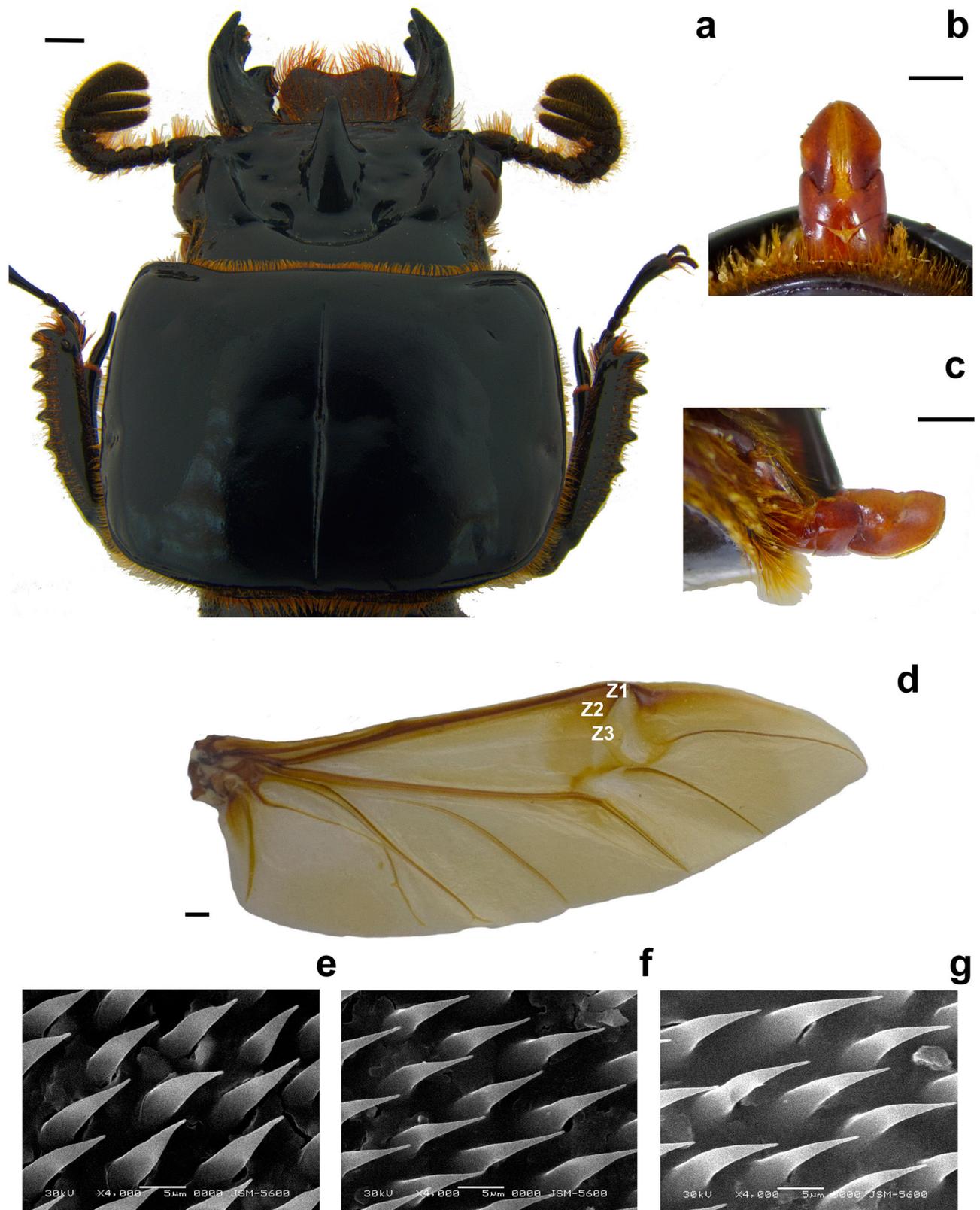


Fig. 5. Morphology of *Oileus rimator* (Truqui). a) head and pronotum, b) aedeagus ventral view, c) aedeagus lateral view, d) hind wing, e–g: stridulatory spines of *pectrum*, e) apical zone (Z1), f) medial zone (Z2), g) posterior zone (Z3). Scale bar (black lines) 1 mm.

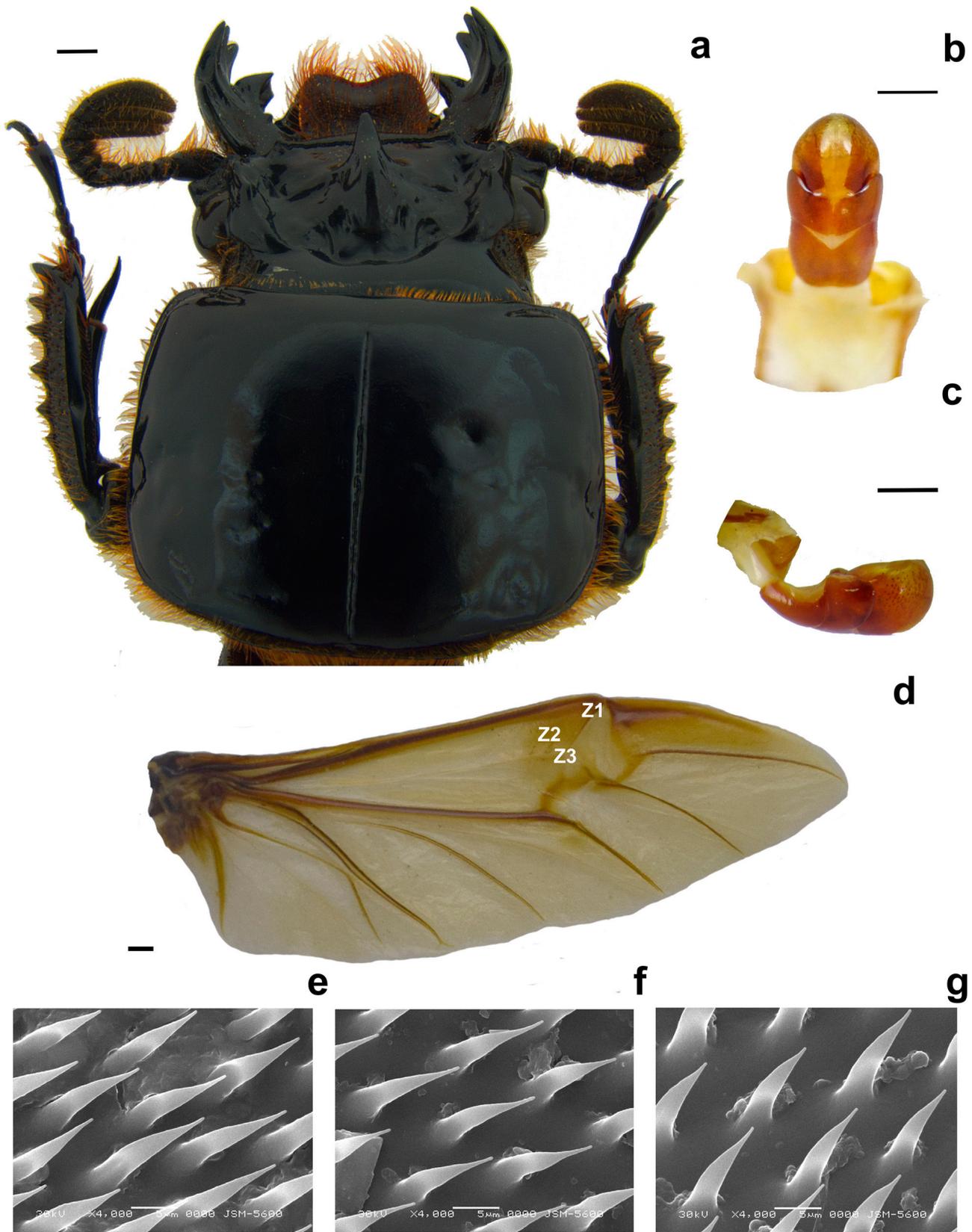


Fig. 6. Morphology of *Oileus gasparilomi* Cano & Schuster. a) head and pronotum, b) aedeagus ventral view, c) aedeagus lateral view, d) hind wing, e–g: stridulatory spines of *plectrum*, e) apical zone (Z1), f) medial zone (Z2), g) posterior zone (Z3). Scale bar (black lines) 1 mm.

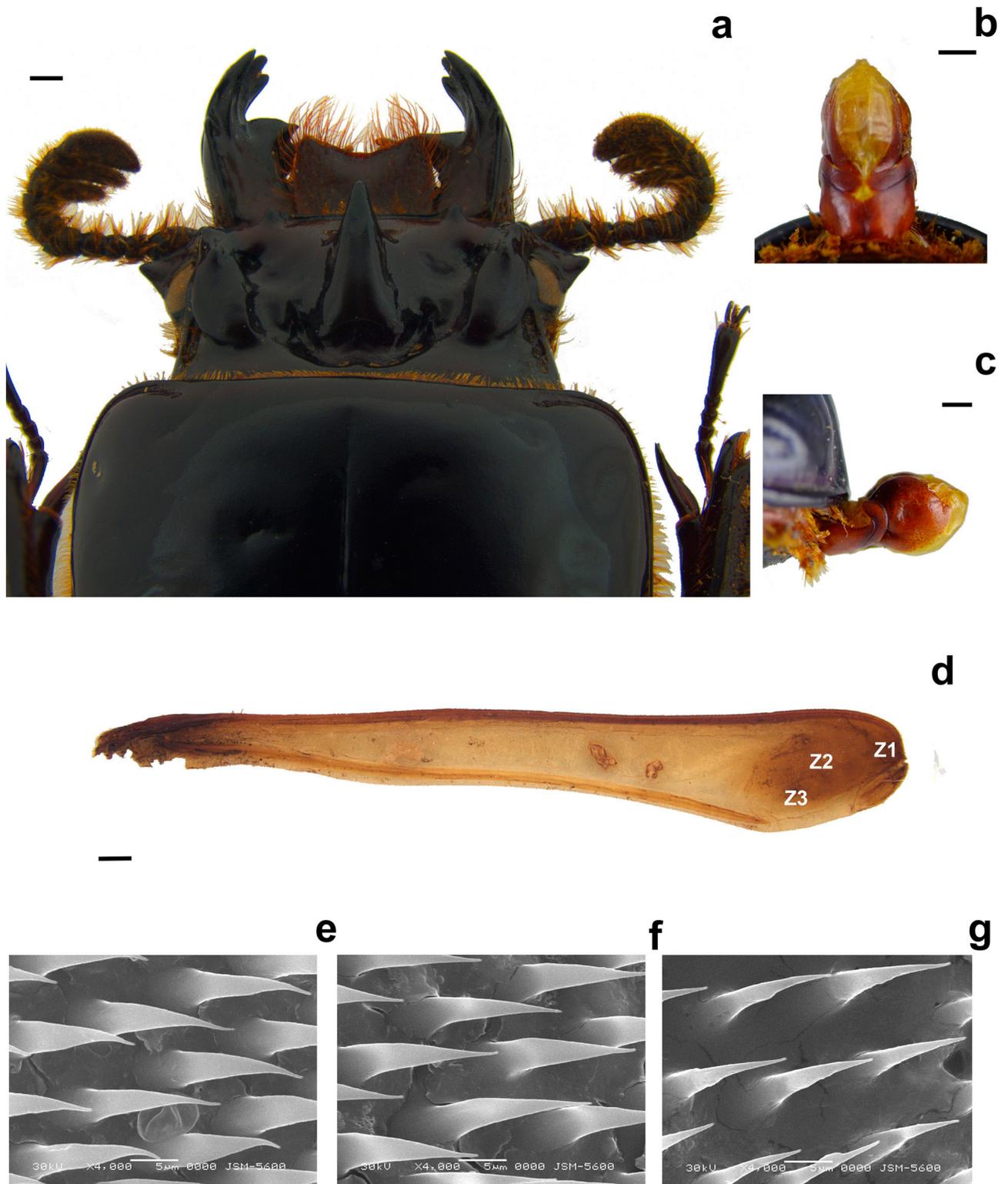


Fig. 7. Morphology of *Oileus heros* (Truqui). a) head and pronotum, b) aedeagus ventral view, c) aedeagus lateral view, d) hind wing, e–g: stridulatory spines of *pectrum*, e) apical zone (Z1), f) medial zone (Z2), g) posterior zone (Z3). Scale bar (black lines) 1 mm.

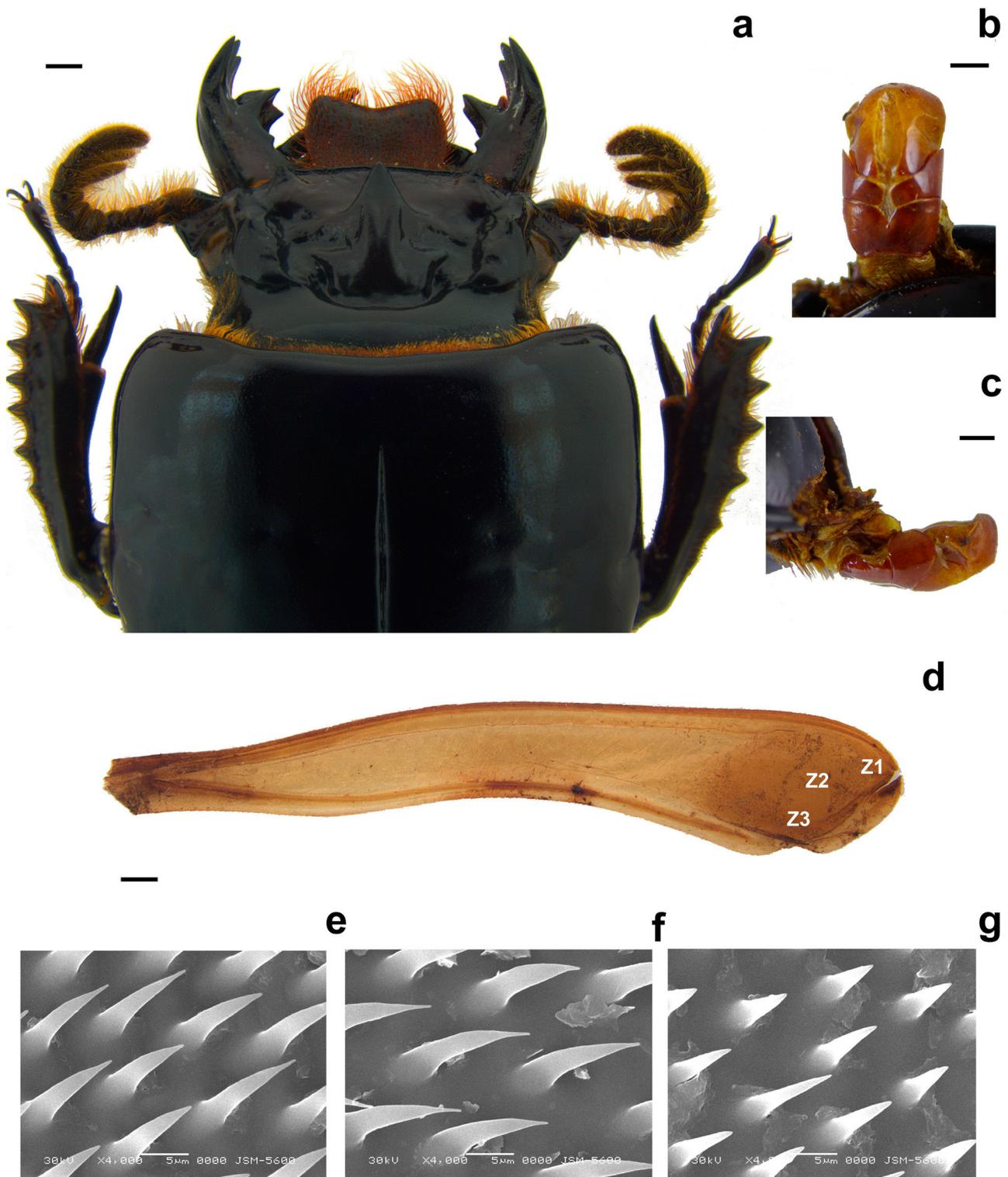


Fig. 8. Morphology of *Oileus nonstriatus* (Dibb). a) head and pronotum, b) aedeagus ventral view, c) aedeagus lateral view, d) hind wing, e–g: stridulatory spines of *pectrum*, e) apical zone (Z1), f) medial zone (Z2), g) posterior zone (Z3). Scale bar (black lines) 1 mm.

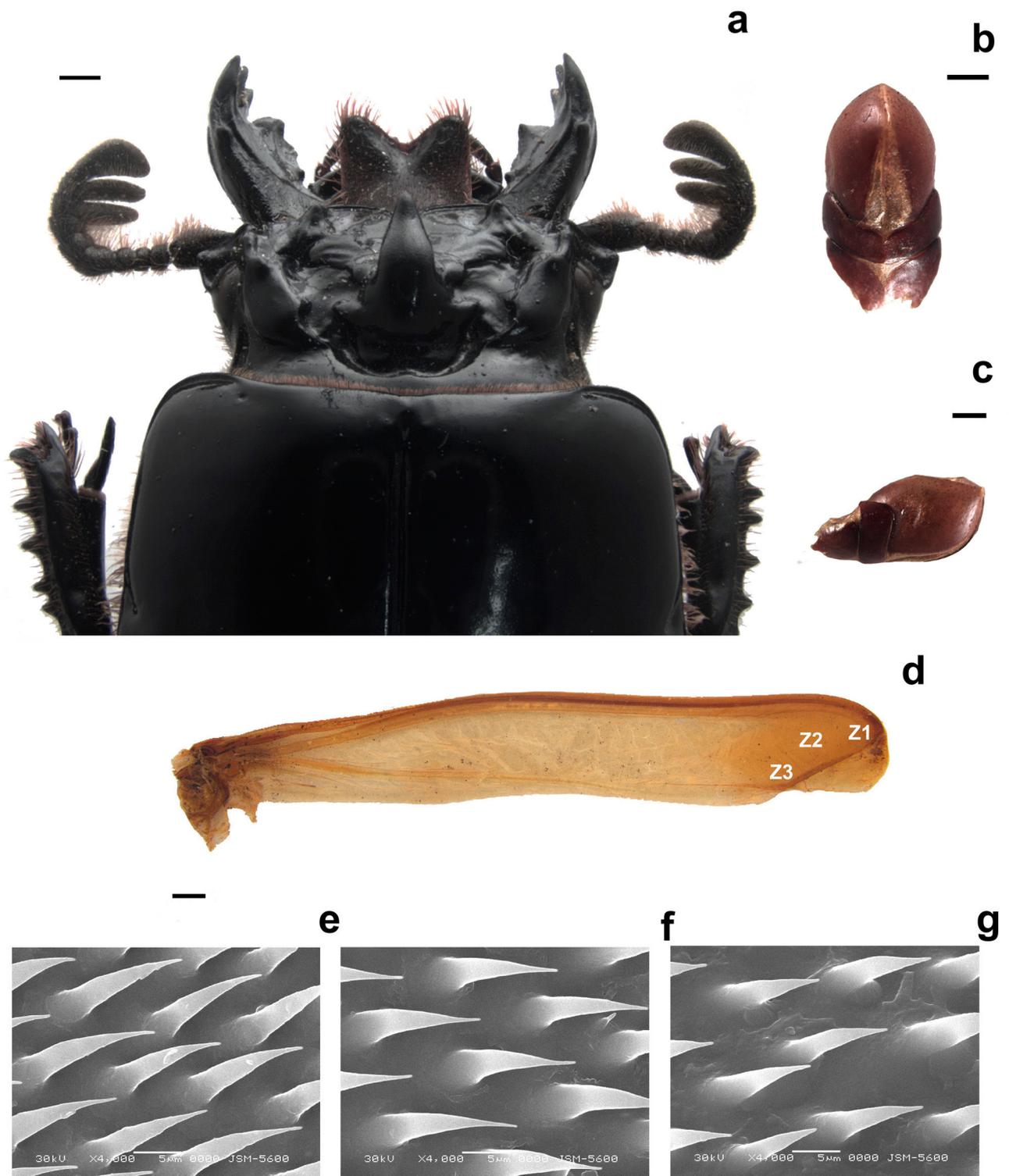


Fig. 9. Morphology of *Oileus bifidus* (Zang). a) head and pronotum, b) aedeagus ventral view, c) aedeagus lateral view, d) hind wing, e–g: stridulatory spines of *pectrum*, e) apical zone (Z1), f) medial zone (Z2), g) posterior zone (Z3). Scale bar (black lines) 1 mm.

and *O. sargi*) are the sister clade of *Oileus bifidus* (brachypterous). However, further phylogenetic studies should include more brachypterous species in order to test the hypothesis that brachypterism originated only once within *Oileus*.

In relation to the biogeographic affinities of *Oileus* species, the potential distribution areas for all species intersect with the Veracruz province. Butler et al. (2023) show that the Veracruz province is a climate stable area, with constant rainfall and low precipitation seasonality, promoting high humidity, a key factor for the distribution of passalid beetles (Jiménez-Ferbans et al. 2010), specially for montane species (such as *Oileus* species), which are less tolerant to low humidity conditions (Beza-Beza et al. 2023).

Finally, this is the first study to illustrate and compare stridulatory spines of all species of a passalid genus. Ariza-Marín and de Luna (2020) showed that this structure has interspecific variation between closely related species after comparing 14 females per species, which is to be expected, considering that passalid sounds play a crucial role in conspecific interactions within their societies (Schuster 1983). Thus, we recommend that these somatic characters be described in future taxonomic descriptions to prove their species specificity and further the understanding of their variation within passalids. Having a more complete database describing stridulatory structures would permit us to compare the morphology between the described and undescribed species and determine if this trait changes among genera.

CONCLUSIONS

Wing condition in *Oileus* species seems to be related to the range of potential areas of distribution. However, this relationship must be tested in a formal comparison, including wing morphology traits like size, shape, area, and wing loading. Finally, another aspect that must be analyzed is the role of historical biogeographic processes as drivers of *Oileus* species distribution and diversification; for instance, even when all species are potentially distributed in the Veracruz province, there is low geographic overlap among them. Performing SDM projected to the past would permit testing the presence of Pleistocene refugia and allopatric distribution in the Veracruz province and, consequently, to propose the main factors in shaping the diversity of Passalidae in this region.

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