UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO

POSGRADO EN CIENCIAS BIOLÓGICAS

INSTITUTO DE ECOLOGÍA

SISTEMÁTICA

OGYGES (COLEOPTERA: PASSALIDAE) UN GÉNERO DE LAS MONTAÑAS DE MESOAMÉRICA: REVISIÓN TAXONÓMICA, ANÁLISIS FILOGENÉTICO MOLECULAR Y BIOGEOGRAFÍA EVOLUTIVA

TESIS

QUE PARA OPTAR POR EL GRADO DE:

DOCTOR EN CIENCIAS

PRESENTA:

ENIO BOANERGES CANO DÁVILA

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MÉXICO, D.F. ENERO, 2016.

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Director General de Administración Escolar, UNAM
P r e s e n t e

Me permito informar a usted, que el Subcomité de Biología Experimental y Biomedicina, en su sesión ordinaria del día 26 de octubre de 2015 aprobó el jurado para la presentación de su examen para obtener el grado de **DOCTOR EN CIENCIAS**, del Posgrado en Ciencias Biológicas, del alumno **CANO DÁVILA ENIO BOANERGES** con número de cuenta **511451184** con la tesis titulada **"*Ogyges* (Coleoptera: Passsalidae) un género en las montañas de Mesoamérica: revisión taxonómica, análisis filogenético molecular y biogeografía evolutiva"**, bajo la dirección del **DR. JUAN JOSÉ MORRONE LUPI:**

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Sin otro particular, me es grato enviarle un cordial saludo.

A T E N T A M E N T E
"POR MI RAZA HABLARA EL ESPIRITU"
Cd. Universitaria, D.F. a 07 de enero de 2016

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DRA. MARÍA DEL CORO ARIZMENDI ARRIAGA
COORDINADORA DEL PROGRAMA

AGRADECIMIENTOS

Agradezco al programa de Doctorado en Ciencias Biológicas de la Universidad Nacional Autónoma de México (UNAM), por el establecimiento del programa de doctorado en modalidad a distancia en Guatemala, a través del convenio entre la Universidad de San Carlos de Guatemala (USAC) y la Universidad Nacional Autónoma de México (UNAM).

Agradezco a la Escuela de Biología de la Universidad de San Carlos de Guatemala y al Laboratorio de Entomología Sistemática de la Universidad del Valle de Guatemala, por el apoyo académico durante el transcurso del posgrado.

Los programas PAEP-UNAM y DIGED-USAC proveyeron los fondos para las visitas internacionales a museos y colecciones.

Agradezco especialmente el apoyo que durante años he recibido de mis tutores, Dr. Juan José Morrone, Dr. Santiago Zaragoza, Dr. Jack Schuster y Dr. Juan Fernando Hernández.

AGRADECIMIENTOS PERSONALES

Agradezco a los miembros del jurado, Dr. Pedro Reyes Castillo, Dr. Harry Brailovsky Alperowitz, Dr. Santiago Zaragoza Caballero, Dr. Juan Márquez Luna y Dr. Alfonso Neri García Aldrete.

Agradezco a Pedro Reyes Castillo, Larry Jiménez Ferbans, Stéphane Boucher, Max Barclay, Malcolm Kerley y María Peña, por la hospitalidad y apoyo en la revisión de colecciones.

Por las imágenes de los especímenes agradezco a Michael Branstetter, Katja Neven, Lars Hendrich, Yrea Hastenpflug-Vesmanis, Michael Balke, Lutz Behne, Larry Jiménez y Cristian Beza.

Mucho del material utilizado fue colectado gracias al apoyo de los proyectos "Faunistic Survey of the Dynastinae (Coleoptera: Scarabaeidae) of México, Guatemala, and Belize" de Brett Ratcliffe y Ronald Cave y "Leaf Litter Arthropods of Mesoamerica (LLAMA)" de John Longino y Robert Anderson. Agradezco también a los colectores, Laura Sáenz, Faustino Camposeco, José Monzón, Manuel Acevedo y Alejandro González Madrid.

Adiós, que te vaya bien…

INDICE

RESUMEN

Los objetivos de este trabajo fueron: 1) demostrar la monofilia del género *Ogyges* con base en análisis filogenéticos molecular y morfológico; 2) realizar una síntesis de la historia taxonómica del género *Ogyges*, con base en la revisión de literatura y revisión de los especímenes tipo, especímenes históricos y formas incluidas o relacionadas con el género *Ogyges;* 3) describir nuevas especies, elaborar una clave para las especies y redescribir el género *Ogyges;* y 4) elaborar un análisis filogenético morfológico del género *Ogyges* y tomarlo como base para realizar un análisis biogeográfico del género en América Central Nuclear. Para ello se recolectó material en Chiapas, Guatemala, El Salvador, Honduras y Nicaragua y se revisaron especímenes de diversas colecciones, incluyendo los tipos primarios de 14 especies (13 de *Ogyges* y una de *Veturius*) y una forma infrasubespecífica que fue descrita dentro de *Ogyges*. Para *O. laevissimus, O. crassulus, O. politus* y *Arrox granulipennis* (originalmente incluida dentro de *Ogyges*), se revisaron imágenes de alta resolución y el análisis se complementó con la revisión de paratipos y topotipos. El material tipo fue localizado en las siguientes colecciones: Instituto de Ecología, Xalapa, Veracruz, México (IEXA); Muséum National d'Histoire Naturelle, París, Francia (MNHN); British Museum of Natural History, Londres, Gran Bretaña (BMNH), Senckenberg Research Institute and Natural History Museum, Frankfurt, Alemania (SNM); Zoologische Staatssammlung, Munich, Alemania (ZSM); Senckenberg Deutsches Entomologisches Institut, Eberswalder, Alemania (SDEI), United States Nacional Museum, Washington D.C. (USNM) y Colección de Artrópodos de la Universidad del Valle de Guatemala, Guatemala (UVGC). En total se revisaron l071 especímenes (incluyendo 21 especímenes de los grupos externos), lo que llevó a la elaboración de una clave dicotómica y a la descripción de nueve nuevas especies dentro del género *Ogyges*: *O. handali* Cano y *O. menchuae* Cano de Guatemala; *O. cavei* Cano, *O. laurae* Cano, *O. llama* Cano, *O. mutenroshii* Cano, *O. ratcliffei* Cano y *O. toriyamai* Cano de Honduras; y *O. sandinoi* Cano de Nicaragua, el primer registro objetivo del género para este país. La revisión detallada de la historia taxonómica, así como de especímenes históricos de los museos de Londres (BMNH), París (MNHN) y Munich (ZSM), mostró que los problemas taxonómicos de *Ogyges* provienen del método de clasificación quinario (taxones con únicamente cinco miembros) adoptado por Kaup en 1871, del embrollo introducido por Kuwert en 1896 al confundir el *Proculejus championi* de Bates con el *Proculejus laevior* (=*Veturius laevior*] de Kaup y de que el especímen tipo de *P. laevior* (= *V. laevior*) permaneció inasequible para la mayoría de los autores relevantes en el estudio de *Ogyges*. Como resultado del presente estudio se llegó a la redescripción del género *Ogyges* y se señalaron los caracteres que lo separan de

grupos afines, incluyendo el descubrimiento de una autapomorfía exclusiva en la forma de los dientes suprainternos, la cual apoya la monofilia del género. Se realizó un análisis filogenético molecular con base en el marcador mitocondrial 12S rRNA que incluyó 41 especies americanas, de 18 géneros (2 Passalini, 16 Proculini), a fin de resolver las relaciones filogenéticas dentro de la tribu Proculini, a travéz de inferencia bayesiana. El árbol del gen mostró un soporte moderado para la tribu Proculini y un fuerte soporte para varios géneros, incluyendo *Ogyges*, el cual se resuelve como monofilético. Este análisis, al incluir varios géneros con especies de alas reducidas y alas normales, demostró que la braquiptería (i.e. alas reducidas, élitros ovales y fusionados y ojos reducidos) ha evolucionado varias veces en Passalidae. Para evaluar la monofilia del género se realizó un análisis filogenético morfológico (53 caracteres) utilizando máxima simplicidad y el género mexicano *Proculejus* como grupo externo, recuperando a *Ogyges* como monofilético y con tres clados (aquí reconocidos como grupos de especies) bien soportados: *O.* (superespecie *championi*), *O.* (superespecie *laevissimus*) y *O.* (superespecie *crassulus*). Cada grupo de especies muestra un patrón de distribución diferente y mayormente alopátrico. El grupo de especies de *O. championi*, con 10 especies se distribuye en el bloque Maya, en el sistema de montañas al norte de la zona de sutura de Motozintla-Comaltitlán en Chiapas y al norte de los valles secos de los ríos Cuilco y Motagua en Guatemala. Los dos grupos restantes se distribuyen en el bloque Chortís. El grupo de especies de *O. laevissimus* con siete especies, se distribuye a lo largo de la Cadena Volcánica del Pacífico, desde Guatemala a El Salvador y del suroeste de Honduras hasta el extremo noroeste de Nicaragua. El grupo de especies de *O. crassulus* con 10 especies, está distribuido del noreste de Guatemala al norte de Honduras. Se hipotetiza que las mayores barreras que han afectado la distribución de los escarabajos montanos del género *Ogyges* (y probablemente otros organismos) en América Central Nuclear son: El Istmo de Tehuantepec en México, las zonas de sutura de Motozintla-Comaltitlán en Chiapas y del Motagua-Cuilco en Guatemala, los valles de tierras bajas de los ríos Colón y Comalí entre las fronteras de Honduras y Nicaragua (o quizás, la sutura norte del Terreno Siuna en Nicaragua), el sistema de fallas del río Guayape en Honduras, y el intrincado sistema de valles secos del sistema Ulúa-Chamelecón-Olancho, en el centro de Honduras.

ABSTRACT

The objectives of this study were: 1) to demonstrate the monophyly of *Ogyges* based on molecular and morphological analyses; 2) to synthesize the taxonomic history of *Ogyges* based on literature and revision of the type specimens, historic specimens, and forms previously included within or related to *Ogyges;* 3) to describe new species, to provide a new key to identify species and to redescribe the genus; and 4) to undertake a phylogenetic morphological analysis of *Ogyges* as basis of a biogeographical analysis of Nuclear Central America. Thus, specimens from Chiapas, Guatemala, El Salvador, Honduras and Nicaragua were collected and simultaneously, material from collections was revised, including the primary types of 14 species (13 of *Ogyges*, one of *Veturius*) and an infrasubspecific form originally included within *Ogyges*. For the species *O. laevissimus, O. crassulus, O. politus* and *Arrox granulipennis* (originally included within *Ogyges*), high resolution images of the primary types together with paratypes and topotypes, were studied. The type material was localized in the following collections: Instituto de Ecología, Xalapa, Veracruz, México (IEXA); Muséum National d'Histoire Naturelle, Paris, France (MNHN); British Museum of Natural History, London, Great Britain (BMNH), Senckenberg Research Institute and Natural History Museum, Frankfurt, Germany (SNM); Zoologische Staatssammlung, Munich, Germany (ZSM); Senckenberg Deutsches Entomologisches Institut, Eberswalder, Germany (SDEI), United States Nacional Museum, Washington D.C. (USNM) and Colección de Artrópodos de la Universidad del Valle de Guatemala, Guatemala (UVGC). A total of 1071 specimens (including 21 specimens of outgroups) were examined, which led to the construction and publishing of a dichotomous key to the species of *Ogyges* and the description of nine new species: *O. handali* Cano and *O. menchuae* Cano from Guatemala; *O. cavei* Cano, *O. laurae* Cano, *O. llama* Cano, *O. mutenroshii* Cano, *O. ratcliffei* Cano and *O. toriyamai* Cano from Honduras; and *O. sandinoi* Cano from Nicaragua, the first objective register of the genus for this country. The detailed revision of taxonomic history, together with the revision of historical specimens of the London (BMNH), Paris (MNHN) and Munich (ZSM) museums, show that most of the taxonomic problems of *Ogyges* stem from the quinary method of classification (taxa with only five members) adopted by Kaup in 1871, the noise introduced by Kuwert in 1896 confusing *Proculejus championi* of Bates with *Proculejus laevior* (=*Veturius laevior*) of Kaup, and that the type specimen of *P. laevior* (= *V. laevior*) remained unnoticed by most relevant authors. As a result of this study, the genus *Ogyges* was redescribed and characters separating it from related genera were indicated, and an exclusive autapomorphy, in the form of suprainternal teeth that support the monophyly,

was discovered. A bayesian phylogenetic molecular analysis based on the 12S rRNA mitochondrial marker, for 41 American species of Passalidae of 18 genera (2 Passalini, 16 Proculini), was conducted in order to resolve the relationships within the tribe Proculini. The gene tree moderately supported the tribe Proculini and strongly supported several genera, including *Ogyges*, resolved as monophyletic. This analysis included flightless and flying genera and species, showing that brachyptery (i.e. reducing wings, oval and fused elytra and reduced eyes) has evolved several times in Passalidae. The morphological analysis (53 characters) to test the monophyly of *Ogyges* based on maximum parsimony, with the Mexican genus *Proculejus* as outgroup, recovered *Ogyges* as monophyletic with at least five synapomorphies. It is composed of three well supported clades (here recognized as species groups), named: *O.* (superspecies *championi*), *O.* (superspecies *laevissimus*), and *O.* (superspecies *crassulus*). Each species group shows a distinct, generally allopatric distribution. The *O. championi* species group, with 10 species, is distributed in the Maya block, in the mountainous system north of Motozintla-Comaltitlán suture zone in Chiapas, and north of the dry valleys of the Cuilco and Motagua rivers in Guatemala. The two remaining species groups are distributed in the Chortís block. The *O. laevissimus* species group, including 7 species, runs mostly along the Pacific Volcanic Chain from Guatemala to El Salvador and from southwestern Honduras to the northwestern border in Nicaragua. The *O. crassulus* species group, with 10 species, is distributed from northeastern Guatemala (Merendón) to northern Honduras. The Isthmus of Tehuantepec in México, the Motagua-Cuilco and Motozintla-Comaltitlán suture zones in Guatemala and Chiapas, the lowland valleys of Colón and Comalí rivers between Nicaragua and Honduras (or perhaps, the northern suture of the Siuna Terrane in Nicaragua), the Guayape fault system in Honduras, and the intricate dry valleys of Ulúa-Chamelecón-Olancho in central Honduras, are hypothesized to have acted as barriers that affected the geographical distribution of *Ogyges,* as well as probably other montane organisms.

INTRODUCCIÓN

Ogyges Kaup, 1871, es un género que se distribuye en los bosques nubosos de las montañas entre 800-3000 msnm, desde Chiapas (Reserva "El Triunfo"), México hasta Guatemala, Honduras, El Salvador y Nicaragua. Fue sinonimizado con *Proculejus* por Hincks (1953) y posteriormente revalidado por Reyes-Castillo (1970). Reyes-Castillo & Castillo (1986), Schuster & Reyes-Castillo (1990) y Schuster *et al*. (2005) describieron varias especies para totalizar 16 especies válidas, y con esto ampliaron implícitamente el concepto original del género *Ogyges.* De acuerdo con estos autores, *Ogyges* se caracteriza por la ausencia de sutura frontoclipeal y por la estructura media frontal del tipo "marginatus" (Schuster & Reyes-Castillo 1990). Sin embargo, más recientemente, Boucher (2006: 346) notó que el género, aunque resulta monofilético, no es apoyado por autapomorfías. Todas las especies actualmente asignadas a *Ogyges* son incapaces de volar, presentando alas reducidas, élitros redondeados y fusionados, y ojos reducidos, cuatro caracteres compartidos con otros géneros y especies de Passalidae que habitan en montañas (e.g. *Xylopassaloides* Reyes-Castillo *et al., Proculus* Kaup*, Proculejus* Kaup, *Undulifer* Kaup, *Pseudacanthus* Kaup, *Arrox granulipennis* (Zang), *Veturius* (*Publius*) *talamacaensis* Boucher, *Verres intermedius* Kaup, *Oileus heros* Truqui, *Petrejoides jalapensis* (Bates) y *Cylindrocaulus patalis* (Lewis), entre otros). Reyes-Castillo *et al.* (1987) relacionaron *Ogyges* con *Oileus, Odontotaenius, Heliscus, Pseudoarrox, Pseudacanthus, Undulifer y Xylopassaloides.* De acuerdo con la larva del tercer estadio, Schuster (1992) relacionó *Ogyges* con *Vindex* y *Xylopassaloides*, porque comparten el patrón de setas tipo "*Vindex*". Basado en los caracteres de la región frontoclipeal y la genitalia de ambos sexos, Boucher (2006: 346, 359-361) relacionó *Ogyges* a *Proculejus* y *Proculus* en un clado con cinco sinapormorfías (Boucher 2006: 359). En el transcurso de este trabajo fueron descubiertas y descritas varias nuevas especies de Guatemala, Honduras y el Norte de Nicaragua, lo cual, aunado a la aparición de dos especies no descritas de México y Honduras, pueden complicar tentativamente el panorama del género *Ogyges*. Así, en este trabajo se presenta un compendio taxonómico y una nueva diagnosis del género.

HISTORIA TAXONÓMICA

Kaup (1871: 69-70) describió el género *Ogyges* para acomodar a las especies *Proculejus laevissimus* Kaup, 1868 y *P. laevior* Kaup, 1868, separándolas del género *Proculejus* por las estrías elitrales superficiales y la ausencia de setas en los lados de los élitros ["von *Proculejus* unterscheiden sie sich durch die seichten Flügeldeckenfurchen und Mangel der Haare an den Seiten"]. En la introducción de los géneros de la Subfamilia Proculinae en su monografía, Kaup (1871: 58) usó el nombre *Oxyges* (Figura 1), el cual es un error tipográfico, debido a que en páginas posteriores (69-70, 117-118) él usó únicamente el nombre *Ogyges* para incluir ambas especies bajo el sistema taxonómico quinarista [taxones con cinco miembros (Mac Leay 1819)] que él adoptó (vea Kaup 1871: 3-12), con tres especies "pendientes de ser descubiertas" o añadidas (Figura 1). Wytsman (1884: 337) y Bates (1886: 7) siguieron a Kaup (1871: 69-70) aceptando el género *Ogyges* como válido (ellos usaron *Oxyges*, un error posteriormente corregido por Zang (1903: 419)) para *O. laevissimus* (Figs. 7, 7a, Lámina 2, Tabla 1 en Bates [1886]) y *O. laevior* (= *Veturius laevior*, de acuerdo a Schuster *et al.* 2005). Las dificultades de separación entre *Ogyges* y *Proculejus* han permanecido constantes a lo largo de su historia taxonómica.

I. Oileus.	II. Proculejus.	III. Proculus.	IV. Oxyges.	V. Publius.
1.	*brevis*	. . . . .	*laevissimus*	*crassus*
2. *sagittarius*	*hirtus*	. . . . .	*laevior*	. . . . .
3.	*Truquii*	*Goryi*	. . . . .	. . . . .
4.	*quitensis*	*Mniszechi*	. . . . .	. . . . .
5. *heros*	*Sartorii*	*opacipennis*	. . . . .	. . . . .
		13 Arten.		

Figura 1. Tabla quinarista de géneros y especies, de la publicación de Kaup (1871: 58). Con puntos se indican las especies aún no descubiertas. *Oxyges* = *Ogyges*.

Cuando describió *Proculejus championi*, Bates (1886: 4-6; Figs. 5, 5a y Lámina 2, Tabla 1, de la publicación original) consideró dos secciones en *Proculejus* [de una manera diferente a como lo hizo Kaup, en 1868 (p. 13-19), pero más cercano a Kaup en el trabajo de 1871 (p. 60-65)]: 1, las especies que tienen los intervalos elitrales con setas y punturaciones [1. Marginal interstices of the elytra more or less punctulate and hairy] y, 2, las especies que

tienen los élitros sin setas [2. Elytra entirely glabrous]. En la segunda sección, con élitros y pronoto glabros, Bates (1886: 5-6) incluyó su *Proculejus championi* (actualmente *Ogyges championi*) de Guatemala y, sin haber visto algún espécimen, él admitió cierta semejanza con *Proculejus quitensis* Kaup (=*Passalus quitensis* (Kaup) de Ecuador), siguiendo el mismo criterio de Kaup (1871: 63-64). Posteriormente, Bates (1889: 383) describió *Proculejus nudicostis* de Chilpancingo, Guerrero, México, señalando la similitud [glabrous sides of the elytra and thorax] con *P. championi*.

Kuwert (1891: 192), en su compilación sistemática de Passalidae, listó ambas especies de Kaup bajo *Ogyges* (ambas citadas como de Colombia y midiendo 30 mm), indicando con un obelisco que él no vio especímenes de *O. laevissimus* [Mir fehlende Arten oder solche, welche ich nicht gesehen habe, sind vorn mit einem † angezeichnet.] y, debido a la ausencia de símbolos, sugiriendo que él conocía (o poseía especímenes) de *O. laevior*. También, bajo *Proculejus* él puso al *P. championi* de Bates, indicando con el símbolo de un obelisco, que de las seis especies incluidas, él solo había examinado a *P. brevi*s Truqui, de Mirador [Miradore], México.

Posteriormente, Kuwert (1896: 221, Tabla V, Figuras 9 y 10, como aparecen en la publicación original) en su tratado dicotómico de Passalidae (publicado póstumamente y como serie, por W. Rothschild y K. Jordan, de acuerdo a la nota aclaratoria en Kuwert (1896:209)) arregló su grupo 3, Proculejinae, en tres géneros: 1) *Ogyges* Kaup con el clípeo formado por una fuerte protuberancia (convexo) y con los hombros glabros [Clypeusrandung durch starke Wulstung entstanden. Schulterecken unbehaart], 2) describió *Proculejoides* Kuwert, un género con un claro surco clipeal delimitando con la frente y con hombros glabros [Clypeus mit sicherer Randfurche; Schulterecken unbehaart] y, 3) mantuvo al género *Proculejus* Kaup, con un claro surco clipeal delimitando con la frente y con hombros punturado setosos [Clypeus mit sicherer Randfurche; Schulterecken behaart und punktirt]. En un trabajo posterior [él murió en 1894], Kuwert (1897: 291-292) expandió la descripción de cada género e incluyó una clave para las especies y sus respectivas diagnosis. Para *Ogyges*, tal y como hizo Kaup (1871), Kuwert asignó a *O. laevissimus* y a *O. laevior* (= *Veturius laevior*); para su género *Proculejoides*, él asignó el *Proculejus championi* de Bates [escrito en la publicación como *O. championi*] como la única especie del género; y para *Proculejus* él incluyó a *P. nudicostis* (con hombros y lados de los élitros glabros) y aproximadamente a

las mismas especies que actualmente conocemos para el género (*sensu* Reyes-Castillo (1970: 115-120), *sensu* Boucher (2006: 345)).

Casey (1897: 642-643) adicionó una nueva especie a *Proculejoides* Kuwert: *P. crassulus* de Honduras. Mas tarde, Zang (1905: 229-231) describió *Proculejoides granulipennis* (= *Arrox granulipennis*), una especie con el ápice de la mandíbula tridentada, de Chiapas, México. Siguiendo a Kuwert (1897) y los criterios de Bates (1889), Zang puso a *P. granulipennis* cerca de *Proculejus nudicostis* aunque comentó que "de las tres especies de *Proculejoides*, las cuales, desafortunadamente no he visto, la más similar es *nudicostis* Bates" [Unter den 3 Arten der Gattung *Proculejoides*, von denen mir leider keine einzige vorliegt, am nächsten verwandt mit *nudicostis* Bates]. Aparte de la interpretación de Zang, Kuwert (1897), como se indicó previamente, no incluyó a *P. nudicostis* en su género *Proculejoides* sino que dentro de *Proculejus*.

Arrow (1906: 443) criticó la monografía de Kuwert indicando que "the absence of the types of the older systematists too rendered it impossible to allocate the old names among the forms tabulated by him…". Arrow (1906: 450) también notó un serio problema introducido por Kuwert en relación al género *Proculejoides*: Kuwert confundió sus especímenes de *Proculejoides championi* con la especie *Ogyges laevior* [las etiquetas de un espécimen de la colección Oberthür (ex colección Kuwert) en el MNHN, París (Figura 2), relata esta historia]. Arrow escribió: "M. Oberthür sent me a specimen of it [de "*P. championi",* identificado por Kuwert como *O. laevior*] from the Kuwert collection, which reveals the fact that this species is that figuring in the Monograph [Kuwert 1896: Fig. 9, Lámina V] not as *Proculejoides championi* [como debiera ser] but as *Ogyges laevior*, of Kaup, which is an obviously different insect". Arrow concluyó que Kuwert no vió la serie tipo de Bates, ignorando que era realmente la especie *P. championi*: "the few characters tabulated [en las claves de Kuwert 1896: 221; 1897: 291-292] as distinctive of *Proculejoides championi,* Bates, do not apply to it, and were apparently only derived from what he wrongly assumed it to be from Bates' description". En esas claves Kuwert, como lo estableció Arrow, confundió lo que Kaup llamó *Ogyges laevior*, la cual es la misma especie de Bates (*P. championi*) y homónimo de *O. laevior* Kaup. Adicionalmente, el dibujo de *Ogyges* de Kuwert (1896: Fig. 9, Lámina V), con una sutura frontoclipeal bien marcada y con tubérculos internos distintos, es más reminiscencia de *Proculejus* que de *Ogyges* Kaup (*O. laevissimus* carece de

tubérculos internos y *O. laevior* Kaup carece de sutura frontoclipeal) o de *Proculejoides championi*, y, como dijo Arrow, en *P. championi* "the front of the clypeus forms a broad depressed band, not cut off, as stated [por Kuwert], by a transverse groove". Finalmente, Arrow (1906: 450) propuso retener el nombre *Proculejoides* Kuwert y lo desambiguó al proveer una nueva diagnosis para separarlo de *Ogyges laevissimus* (pero nada dijo acerca del *O. laevior* de Kaup). Kuwert (1896: 221) no designó una especie tipo o hizo referencia a especie alguna cuando describió *Proculejoides*, pero en un trabajo subsecuente de la serie (Kuwert 1897: 292) asignó *P. championi* a este género. De acuerdo al artículo 67.2.2. del Código Internacional de Nomenclatura Zoológica (ICZN 1999) "if a nominal genus or subgenus was established before 1931 without included nominal species, the nominal species that were first subsequently and expressly included in it are deemed to be the only originally included nominal species". Así, Gravely (1918: 47) consideró a *P. championi* como la especie tipo de *Proculejoides*, tal y como fue emendado por Arrow (1906) y establecido por Hincks & Dibb (1935: 33).

Gravely (1918) aceptó la división de géneros hecha por Kuwert (1897: 291-292); sin embargo, no pudo ver especímenes de *Ogyges laevissimus* y *O. laevior* aunque consideró la posibilidad de sinonimizar, basado en los élitros glabros, *Ogyges* con su interpretación de *Pseudacanthus* (vea Gravely 1918: 30), en la subfamilia Pseudacanthinae, dependiendo de la revisión de las mandíbulas cuando fuera posible. Sin embargo, él examinó y mantuvo a *Proculejoides* como un género válido dentro de la subfamilia Passalinae, aunque trató únicamente a *P. championi* (Gravely 1918: 47-48, Fig. II-3) y enlistó a *Proculejoides crassulus* y *Proculejoides granulipennis* (en Gravely 1918: 7) como "forms not referred to either in Kuwert's work or there". Los criterios de Gravely influyeron notablemente para que más tarde Hincks & Dibb (1935) consideraran a *Ogyges laevissimus* y a *O. laevior* como miembros del género *Pseudacanthus* en la subfamilia Pseudacanthinae (Hincks 1953: 29). En el sentido de Gravely (1918: 30) y de Hincks & Dibb (1935: 20-21), *Pseudacanthus* incluye una mezcla de especies actualmente repartidas en varios géneros como *Pseudacanthus*, *Odontotaenius*, *Oileus, Petrejoides, Yumtaax, Proculejus* y *Ogyges*. Más tarde, Hincks (1953: 29-30), después de ver los especímenes de *O. laevissimus,* con el ápice de la mandíbula claramente bidentado, transfirió *Ogyges* (*O. laevissimus* y *O. laevior*, sin haber visto a este último) de *Pseudacanthus* (un género con el ápice de la mandíbula

tridentado) y lo colocó como sinónimo junior de *Proculejus*, para él, un género con el ápice de la mandíbula bidentado. En el mismo trabajo Hincks (1953: 31-32) describió a *Proculejus politus*, muy cercano a *O. laevissimus*, de El Salvador; esos cambios posteriormente fueron compilados en el suplemento del catálogo de Hincks & Dibb (1958: 10). Hincks & Dibb (1935: 34) aceptaron el género *Proculejoides* con tres especies, *P. championi, P. crassulus* y *P. granulipennis*, y pusieron el *Ogyges laevior* de Kuwert (no Kaup) bajo sinonimia de *P. championi*. La especie tipo de *Ogyges*, *O. laevissimus*, fue fijada por Hincks & Dibb (1935: 20).

En el arreglo de los géneros americanos de Passalidae, Reyes-Castillo (1970: 174-177) revivió *Ogyges* (con *Proculejoides* como sinónimo junior) consistiendo de seis especies: *O. laevissimus, O. laevior*, *O. championi*, *O. politus, O. crassulus* y *O. granulipennis*. Una especie de Chiapas, *O. marilucasae*, fue adicionada por Reyes-Castillo & Castillo (1986), hasta que el género fue revisado por Schuster & Reyes-Castillo (1990), en donde, siguiendo a Kuwert (1897:291-292) sinonimizaron a *O. championi* con *O. laevior* Kuwert (no Kaup) y describieron siete especies de Guatemala, Honduras y El Salvador. En la revisión del género, ellos también propusieron cuatro linajes dentro del género, uno de los cuales incluyó una nueva especie de Honduras (*O. adamsi* Schuster & Reyes-Castillo) y los otros tres incluyeron las tres especies descritas en el siglo XIX: *O. laevior* (=*O. championi* de Bates), *O. crassulus* (no el de Casey) y *O. laevissimus*. Schuster *et al.* (2005) localizaron el tipo de *O. laevior* Kaup y demostraron que se trataba del raro y endémico *Veturius laevior* (Kaup), de Costa Rica (también vea Boucher 2004, 2006); además revalidaron a *Ogyges championi* y transfirieron a *O. granulipennis* de Chiapas al complejo *Veturius-Publius*, para posteriormente transferirlo a *Publius* (vea Schuster 1992: 360) y finalmente a *Arrox* (vea Boucher 2006: 391-393).

Figura 2. *Ogyges championi* de la Colección Oberthür (ex Colección Kuwert), revisado por Kuwert y por Arrow. Depositado en el Museo de Historia Natural de París. a. Hábito dorsal. b. Vista lateral. c. Detalle lateral de los élitros. d. Etiquetas.

La larva del tercer estadio de *Ogyges* ha sido descrita para cinco especies (Schuster & Reyes-Castillo 1981: 109, Schuster 1992: 361-362), el cariotipo se conoce únicamente para *O. politus* de El Salvador (Virkki & Reyes-Castillo 1972) y el intestino posterior para *O. laevissimus* (Fonseca *et al*. 2011).

El análisis filogenético morfológico realizado por Boucher (2006) recuperó a *Ogyges* como monofilético y relacionado con *Proculus* y con *Proculejus*, pero sin autapomorfías. El autor notó que la separación de *Proculejus,* basado exclusivamente en la ausencia de sutura frontoclipeal, no es convincente.

Actualmente *Ogyges* incluye 25 especies (Cano 2014), además de dos especies aún no descritas por lo cual, la concepción original del género *sensu* Kaup (1871) para una sola especie (*O. laevissimus*) y el reacomodo de Reyes-Castillo (1970) para "cuatro especies" (excluyendo *A. granulipennis* y *V. laevior*), se ha ampliado y en consecuencia se hace necesaria una nueva diagnosis del género, como sigue:

REDESCRIPCIÓN DEL GÉNERO *OGYGES* KAUP 1871

Referencias

Especie tipo, *Proculejus laevissimus* Kaup 1868, designado por Hincks & Dibb (1935: 20).

Ogyges Kaup 1871: 69-70; Kuwert 1891: 192; Kuwert 1896: 291; Kuwert 1897: 291-292; Arrow 1906: 450; Reyes-Castillo 1970: 174-177; Schuster & Reyes-Castillo 1981: 109; Reyes-Castillo & Castillo 1986: 147-148; Reyes-Castillo, Fonseca & Castillo 1987; Schuster & Reyes-Castillo 1990: 1-49; Schuster 1992: 361-362; Reyes-Castillo 2003: 167-168; Schuster *et al*. 2005: 118-130; Schuster 2006: 388; Boucher 2006: 319, 330, 343, 346, 355, 360-361, 364-365, 368-369; Fonseca *et al*. 2011: 3, 15-16; Cano 2014 (451-484).

Oxyges Wytsman 1884: 337 (ortografía incorrecta, inválida, introducida por Kaup 1871: 58); Bates 1886: 7; Zang 1903: 419, enmienda a Wytsman.

Redescripción. Especies de tamaño moderado hasta grande (18.7 mm – 46 mm). Coloración negro brillante hasta opaco grafito o con reflejos iridiscentes azulados. Todas las especies son incapaces de volar. El cuerpo es robusto y dorsalmente convexo. Borde anterior del labro recto o ligeramente cóncavo. Clípeo grueso o delgado, vertical, inclinado, recto o transversalmente ligeramente convexo; continuo o separado del área mediofrontal por una serie de granulitos, una inflexión, punturaciones o un, claramente marcado, surco frontoclipeal; borde central anterior con o sin una emarginación en forma de "v". Área frontal y vertex glabros, solamente con escasas setas largas entre las áreas laterofrontales y los agujeros lateroclipeales; tegumento liso o con granulaciones, punturaciones o surcos localizados; áreas lateropostfrontales profundas a moderadamente profundas. Ángulos anteriores de la cabeza obtusos a muy obtusos. Cuerno central libre o no libre; tubérculos internos y quillas posterofrontales presentes o ausentes. Estructura mediopostfrontal en vista lateral deprimida a tumosa, extendida hacia adelante, pero en una especie muy tumosa y fusionada a los tubérculos internos hipertélicos. Ojos reducidos; canthus ocular ventralmente cubre al menos la mitad del diámetro de un ojo. Mandíbulas con únicamente dos dientes apicales de ápice agudamente redondeado (incluyendo los tenerales); diente suprainterno en vista dorsal simétrico o casi simétrico para ambas mandíbulas, cada diente ampliamente

dividido en tres tubérculos; el tubérculo superior amplio en su base, agudo en el ápice y ligeramente curveado hacia atrás; el tubérculo inferior más pequeño (menos de la mitad del superior), cónico a piramidal, dividido para formar otro tubérculo similar, bien marcado (Figura 3) hasta obsoleto (en especímenes viejos); en vista ventral el tubérculo superior está dirigido oblicuamente hacia arriba (dirección ventral) y los dos inferiores hacia abajo (dirección dorsal). Lígula ventralmente apicalmente unidentada (raramente bidentada), con una quilla anterior transversal bien marcada a obsoleta, o incluso, ausente (una tumosidad está presente). Mentum con área medial basal convexa; cicatrices basales laterales presentes, opacas o brillantes. Maza antenal muy ancha o casi tan larga como ancha, dorsalmente aplanada o cóncava y cubierta de tomentum; último segmento de curveado a fuertemente curveado. Ángulos anteriores del pronoto redondeados, surco marginal angosto y sin punturas, foseta lateral del pronoto glabra. Metasterno con o sin setas en las esquinas anteriores, setas nunca densas pero cuando están presentes, sin fuertes punturaciones; disco metasternal rodeado o no por fuertes punturaciones; surco marginal del metasterno de muy angosto hasta linear, glabro o a lo más con algunas setas dispersas. Élitros fusionados, ovales, más anchos en la parte media, húmeros expandidos lateralmente; sin setas en las interestrías laterales, los húmeros y la epipleura (excepto algunas setas diminutas y escasas sobre el borde anterior vertical (o declive), entre las interestrías 1-9); estrías elitrales fuertemente a moderadamente marcadas, hasta casi borradas; punturaciones de superficiales y diminutas hasta profundas y bien marcadas, mayormente circulares, nunca cuadradas o rectangulares. Alas con mecanismos de plegamiento reducidos hasta extremadamente reducidos. Surco anterior ventral del profémur presente y bien marcado; raramente, en algunos especímenes pobremente marcado o evanescente.

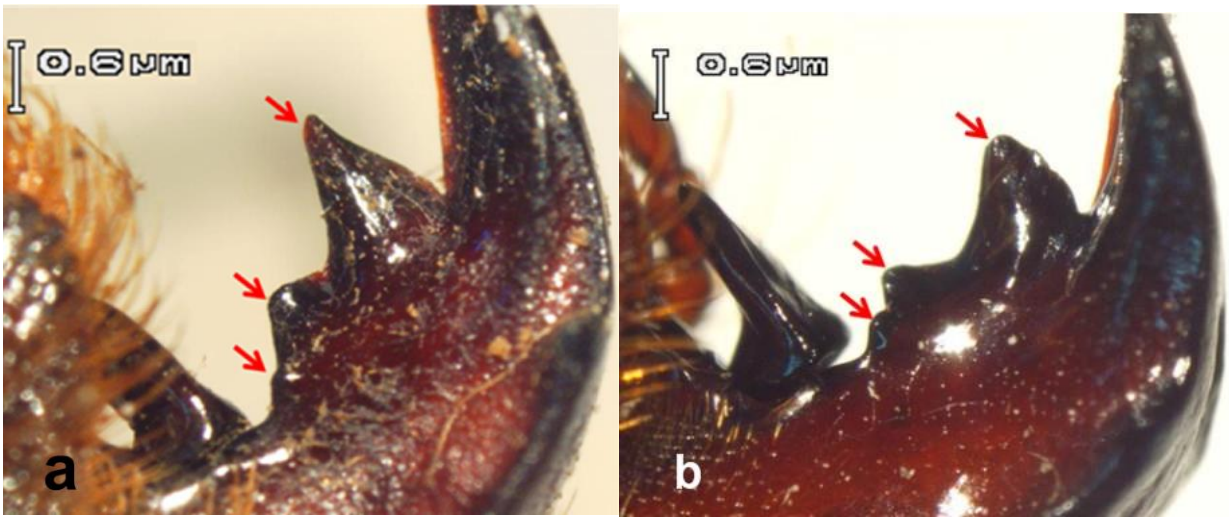

Figura 3. Diente suprainterno tridentado característico del género *Ogyges*. a. *Ogyges laevissimus*, la especie tipo del género. b. *Ogyges championi*, la especie tipo del género sinónimo *Proculejoides*.

Ogyges se puede separar fácilmente de la mayoría de especies de Proculini, excepto de las especies de *Proculus* y *Proculejus*, así como de algunas especies de *Xylopassaloides*, *Veturius* y *Vindex*, por la presencia de dos dientes apicales en la mandíbula (en lugar de tres). Puede ser separado de la mayoría de especies de *Proculejus* por el surco marginal del metasterno angosto, el surco anterior ventral del profémur bien marcado (excepto en especímenes de *O. tzutuhili*), los ángulos anteriores del metasterno glabros o escasamente setosos, la epipleura glabra y la ausencia de setas a lo largo de las interestrías laterales y foseta lateral pronotal (excepto de *P. nudicostis* y *P. obesus* con mandíbulas tridentadas). De *Proculus* se puede separar porque su tamaño es más pequeño (18- 46 mm, comparado con las medidas de *Proculus* de 51- 80 mm) y por los húmeros glabros. Algunas especies de *Ogyges* con estrías elitrales fuertemente marcadas se pueden confundir con *Xylopassaloides*, pero las punturaciones laterales circulares (en lugar de cuadradas), más pequeñas que el ancho de la interestría, lo distinguen de *Xylopassaloides*. De las pocas especies que no pueden volar de *Vindex*, puede ser separado por los tubérculos internos (cuando están presentes) que no llegan al clípeo y por el surco marginal del metasterno angosto. De *Veturius* con el ápice de las mandíbulas bidentado se puede separar fácilmente por la maza antenal ancha.

De todos las especies de Passalidae, *Ogyges* se puede separar por el diente

suprainterno característico (Figura 3). En el grupo hermano *Proculejus* (Boucher 2006) el diente suprainterno es bidentado, al menos en los especímenes tipo revisados de *P. nudicostis, P. pubicostis* Bates, *P. ganglbaueri* (Kuwert), *P. brevis* (Truqui)*, P. hirtus* (Truqui)*, P. acapulcae* Kuwert y *P. truquii* Kaup. Por otro lado, en el grupo hermano *Proculus* (Boucher 2006) el diente suprainterno presenta un característico largo y ancho dentículo dehiscente (en especímenes viejos), ausente en todos los géneros de Passalidae. En los géneros del Viejo Mundo *Labienus* Kaup y *Pleurarius* Kaup el diente infraterminal del lóbulo incisor puede confundirse con el dentículo superior del diente suprainterno; pero si eso ocurriera, los primeros dos dentículos son más delgados y langos y con la incisión más profunda y las quillas que los conectan son más complejas. Así, considero que la forma del diente suprainterno de *Ogyges* es una autapomorfía exclusiva del género, presente y homóloga en todas las especies conocidas, lo cual apunta hacia la monofilia del género.

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Capítulo 1

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Zootaxa 3889 (4): 451–484
www.mapress.com/zootaxa/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

http://dx.doi.org/10.11646/zootaxa.3889.4.1
http://zoobank.org/urn:lsid:zoobank.org:pub:1F3F076D-A4F1-4B4A-977D-4B99581C6779

Ogyges Kaup, a flightless genus of Passalidae (Coleoptera) from Mesoamerica: nine new species, a key to identify species, and a novel character to support its monophyly

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Table of contents

Abstract

Nine new species of *Ogyges* Kaup (Coleoptera: Passalidae) from the mountainous cloud forests of Mesoamerica are described: *O. handali* **new species** and *O. menchuae* **new species** from Guatemala; *O. cavei* **new species**, *O. laurae* **new species**, *O. llama* **new species**, *O. mutenroshii* **new species**, *O. ratcliffei* **new species**, and *O. toriyamai* **new species** from Honduras; and *O. sandinoi* **new species** from Nicaragua, the first objective record of the genus for this country. A key to the adult *Ogyges* is included. The work also shows that *Ogyges* possesses an exclusive autapomorphy: a trituberculate supraintemal tooth of each mandible (one long and wide apical tubercle and two connected, small, almost conical, basal tubercles). This character state is found in all known *Ogyges* species and is proposed as a synapomorphy that supports the monophyly of the genus.

Key words: Cloud Forest, Guatemala, Chiapas, Honduras, El Salvador, Nicaragua, synapomorphy, autapomorphy, *Proculejus*, *Proculus*

Accepted by A.B.T. Smith: 9 Oct. 2014; published: 3 Dec. 2014

Introduction

Ogyges Kaup (Coleoptera: Passalidae) is a genus distributed in the mountainous cloud forests between 800–3000 m, from Chiapas (El Triunfo Reserve), Mexico to Guatemala, Honduras, El Salvador, and Nicaragua. It was synonymized under *Proculejus* Kaup by Hincks (1953) and later diagnosed and revalidated by Reyes-Castillo (1970); since then, Reyes-Castillo & Castillo (1986), Schuster & Reyes-Castillo (1990), and Schuster *et al.* (2005) described several new species, totaling 16 known valid species. All species of *Ogyges* are flightless, presenting reduced hindwings, rounded and fused elytra, and reduced eyes, four characters shared with other mountain living genera of Passalidae (*e.g.*, *Xylopassaloides* Reyes-Castillo, Fonseca, & Castillo, *Proculus* Kaup, *Proculejus*, *Undulifer* Kaup, and *Pseudacanthus* Kaup). Based on morphological characters, particularly the clypeofrontal region and genitalia of both sexes, Boucher (2006: 346, 359–361) related *Ogyges* to the flightless genera *Proculejus* and *Proculus* in a clade with five synapomorphies (Boucher 2006: 359) and also noted (Boucher 2006: 346) that the genus, although recovered as monophyletic, is not supported by any autapomorphy. Recent field collections in Guatemala, Honduras, and northern Nicaragua provided nine new species of *Ogyges* that potentially can complicate the panorama of this genus; thus, the goals of this paper are to describe the new species with a key to the genus and provide a discussion about a novel diagnostic character that supports their monophyly.

Material and methods

I follow the phylogenetic species concept of Wheeler & Platnick (2000), as the smallest group of populations or lineages diagnosable by a unique combination of character states. For terminology (see Fig. 1) I follow Boucher (2006), because homologies with other passalid taxa (related or unrelated) are well sustained. Nevertheless, instead of the terms central tubercle, orbital canthus, inner tubercles, and hypostomal plate, I use central horn, ocular canthus, internal tubercles, and hypostomal process, respectively. Primary types of most valid species of *Ogyges* were revised, except *O. laevissimus* (Kaup), *O. crassulus* (Casey), and *O. politus* (Hincks), for which pictures were analyzed and complemented with specimens of the species from the type locality (topotypes). Measurements were taken with a digital vernier caliper except for the antennal and ocular measurements, which were taken with an ocular micrometer in a Wild Heerbrugg M3B stereomicroscope. Total length was measured from the tip of the open mandibles to the terminal tip of elytra. All measures are in mm, the mean values ($\bar{x}$) are given in parentheses. Drawings were made with the help of a drawing tube in a Wild Heerbrugg M3B stereomicroscope. Label data of specimens are verbatim. Images of specimens were taken with a Canon Eos Rebel camera with 100 mm macrolens with two flashes, except those of internal teeth of mandible, taken with a camera DP12 adapted to a SZX12 Olympus stereomicroscope. Distribution map for the species was made with the program ArcGis 9.2.

Acronyms of cited collections as follows:

Instituto de Biología, Universidad Nacional Autónoma de México (IBUNAM); Instituto de Ecología, Xalapa, Veracruz, Mexico (IEXA); Muséum National d'Histoire Naturelle, Paris, France (MNHN); Ronald Cave, private collection, Fort Pierce, Florida, United States of America (RC); Senckenberg Research Institute and Natural History Museum, Frankfurt, Germany (SNM); Museo de Historia Natural, Escuela de Biología, Universidad de San Carlos de Guatemala, Guatemala City, Guatemala (USAC); and Arthropod Collection, Universidad del Valle de Guatemala, Guatemala City, Guatemala (UVGC).

Ogyges Kaup 1871

Type species. *Proculejus laevissimus* Kaup, 1868, subsequent designation by Hincks & Dibb (1935: 20).

References. *Ogyges* Kaup, 1871: 69–70; Kuwert 1891: 192; Kuwert 1896: 291; Kuwert 1897: 291–292; Arrow 1906: 450; Reyes-Castillo 1970: 174–177; Schuster & Reyes-Castillo 1981: 109; Reyes-Castillo & Castillo 1986: 147–148; Reyes-Castillo, Fonseca, & Castillo 1987; Schuster & Reyes-Castillo 1990: 1–49; Schuster 1992: 361–362; Reyes-Castillo 2003: 167-168; Schuster *et al.* 2005: 118-130; Schuster 2006: 388; Boucher 2006: 319, 330, 343, 346, 355, 360–361, 364–365, 368–369; Fonseca *et al.* 2011: 3, 15–16.

Oxyges Wytsman 1884: 337 (incorrect subsequent spelling, not valid, introduced by Kaup 1871:58); Bates 1886: 7; Zang 1903: 419.

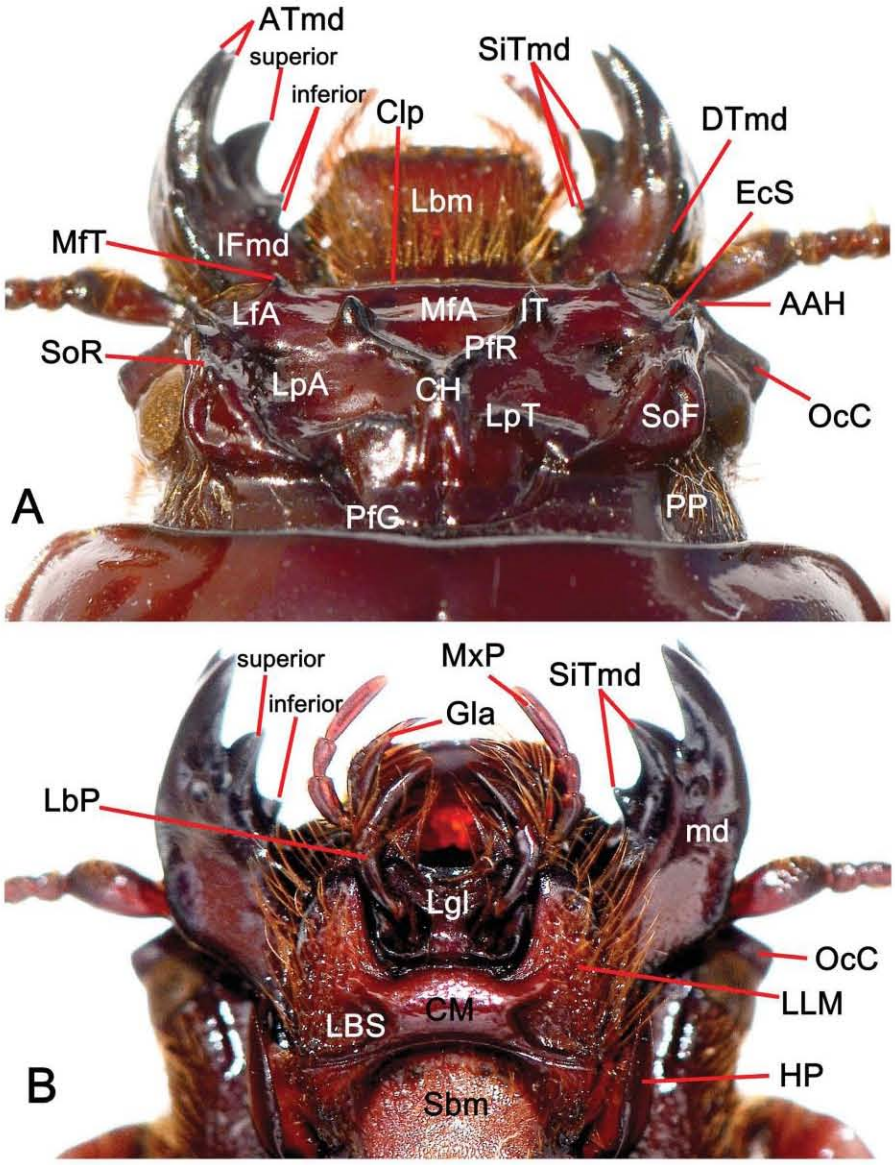

FIGURE 1. Characters of head used in the description of species of Passalidae. A. Dorsal view of head: AAH, anterior angles of head. ATmd, apical teeth of mandible. CH, central horn. Clp, clypeus. DTmd, dorsal teeth of mandible. EcS, epicranial sutures. IFmd, internal face of mandible. IT, internal tubercles. Lbm, labrum. LfA, laterofrontal areas. LpA, lateroposterior areas. LpT, lateroposterior tubercles. MfA, mediofrontal area. MfT, mediofrontal tubercles. OcC, ocular canthus; PfG, postfrontal groove. PfR, posterofrontal ridges. PP, postorbital pits. SiTmd, suprainternal teeth of mandible. SoF, supraorbital fossa. SoR, supraorbital ridge. Superior and inferior refers to suprainternal teeth of mandible. B. Ventral view of head. CM, center mentum. Gla, galea. HP, hypostomal process. LBS, lateral basal scars. LbP, labial palps. Lgl, ligula. LLM, lateral lobes of mentum. md, mandible. MxP, maxilary palps. Sbm, submentum.

Pseudacanthus Kaup, 1869: Hincks & Dibb 1935: 21; Blackwelder 1944: 190. Available genus.

Proculejus Kaup, 1868 (original combination): Harold 1868: 973; Hincks 1953: 30; Hincks & Dibb 1958: 10. Available genus.

Nomenclatural commentary. Rafinesque (1815: 135) placed the name *Ogyges* under the "Classe Helmisia, Les Vers [worms], Sous-Classe Annelidia, Ordre Endobranchia [internal or inconspicuous gills], Famille Chetopodia, Les Chètopodes [=Polychaeta], and S.F. [Subfamily] Euphrisea, Les Euphrysiens [tentacled head]". Since the original publication, the name *Ogyges* Rafinesque has not been applied to any species of Polychaeta. In fact, neither Rafinesque (1815:135) nor any subsequent author made a diagnosis or designated a type species for this genus, failing to fulfill the requirements of availability of the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature 1999). Neave (1940: 398) considered *Ogyges* Kaup, 1871 as a junior homonym of *Ogyges* Rafinesque, 1815:135, but placed the name of Rafinesque as a *nomen nudum* "[*n.n*]". Nonetheless, according to the Code (International Commission on Zoological Nomenclature 1999), *Ogyges* Rafinesque 1815 is unavailable because it lacks description (article 12.1) or indication (article 12.2). Therefore, it does not compete in priority with *Ogyges* Kaup 1871, which is an available and valid name.

Description of newly discovered *Ogyges* species

Ogyges cavei Cano, new species

Figs. 2–3, 21d

Diagnosis. *Ogyges cavei* is a large species that resembles *O. nahuali* Schuster, Cano, & Boucher, by the indistinct elytral punctures and the metasternal disc delimited by strong punctures, but is easily separated by the presence of internal tubercles and the tip of central horn directed upward.

Description. Holotype female, black adult. Total length 40.78, elytral length 22.18, pronotal length 11.12, pronotal width 14.41, humeral width 13.64. Head: anterior border of labrum slightly concave. Clypeus inclined, anterior border straight, with two setae on lateral borders, with a weak platform separating it from the smooth mediofrontal area. Mediofrontal tubercles small and rounded; internal tubercles and posterofrontal ridges present. Laterofrontal areas smooth, with sparse, large setae on lateroclypeal pits. A small, bare, smooth fossa present in front of junction of mediopostfrontal structure and posterofrontal ridges. Lateropostfrontal areas glabrous and smooth. Central horn moderately long, with apex directed upward and slightly forward, without median longitudinal groove posteriorly; lateroposterior tubercles long, rounded, curved backward and almost reaching the supraorbital tumosity and not separated from central horn. Postfrontal groove smooth and shallow, barely deeper at sides. Supraorbital ridge with equal anterior tubercles; supraorbital fossae present and small, posterior 1/2 not bifurcate; external ridge not marked. Ocular canthus with apex slightly swollen, covering more than half of eye. Eyes reduced. Eye width = 0.42 mm. Interocular width = 7.85 mm. Head (measured between tips of canthi) = 9.37 mm; ratio width of both eyes/head = 0.09. Postorbital pits shallow, with minute, punctate setations. Ligula slightly protuberant basally with apical central tooth small with anterior ventral transversal carina present and complete; setose punctures on the median area. Lateral lobes of mentum with abundant setose punctures, except on the moderately protuberant rounded apex; medial basal mentum glabrous; lateral basal scars elongate to sides, punctate-setose and opaque. Hypostomal process elongate, without lateral depression, wide medially and narrow in the apical third. Infraocular ridge present, short and smooth, proximal area declivous and setose, distal area punctate-setose. Mandible with dorsal tooth occupying 1/2 of his length; internal face in dorsal view slightly opaque, not granular. Antennal club (Figs. 2–3) concave with all three antennomeres very wide and subequal; penultimate antennomere slightly wider than the antepenultimate.

Thorax: Lateral fossa of pronotum without punctures except minute, striate punctures ahead and behind, visible at high magnification. Pronotum with marginal groove narrow and smooth, anterior angles rounded, disc brilliant with numerous, minute, opaque punctures visible at moderate magnification. Prosternellum brilliant at center and posteriorly, opaque at anterior 1/3 and sides. Mesosternum with lateral depressions elongate and rugose (shagreened). Mesepisternum with elongate rugose area (shagreened), more marked and oval apically. Metasternum anterior angles with sparse, minute setae; disc delimited by 31–32 well-marked punctures on each side (some partially fused); marginal groove glabrous, narrow, rugose, posteriorly two times wider than medially.

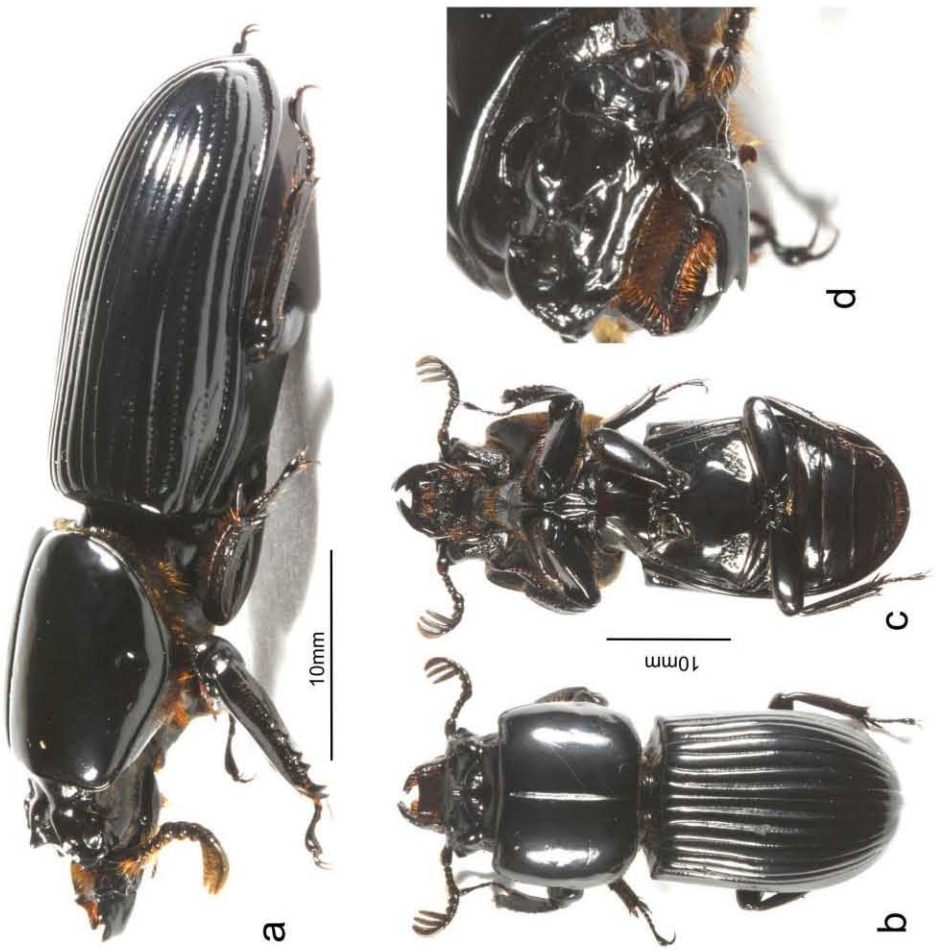

FIGURE 2. Holotype of *Ogyges cavei*: a. lateral view. b. dorsal view. c. ventral view. d. anterolateral view of head.

Elytra: Striations marked; with minute, weakly-defined, superficial punctures, deeper and wider between striae 6–10; junctions of striations 1 and 10 with sparse extra punctures. Anterior border of elytra vertical, with minute setae on interstriae 2 (or 1) to 9.

Legs: Profemur with anterioventral groove marked; metafemur moderately elongate; mesotibia with one spine.

Abdomen: Marginal groove of sternite VII incomplete, occupies 3/5 of sternite.

Variation in paratype: Total length 38.91, elytral length 20.8, pronotal length 10.75, pronotal width 13.64, humeral width 11.63. Disc of metasternum delimited by 35–38 well-marked punctures on each side and with 14–16 small punctures directly on sides of disc.

Material examined. 2 specimens.

Type material. Holotype: HONDURAS: Olancho, La Picucha, 11 km N Catacamas, 14.92740, -85.90983. Bosque nuboso, 1800–2100 m, 8–14 V 2010. L. Sáenz (LSD 451).

Paratype female: HONDURAS: Comayagua, 10 km E Comayagua, 14.45973, -87.54609, Bosque nuboso, 2000 m, 15–19 V 2010. L. Sáenz (LSD 459).

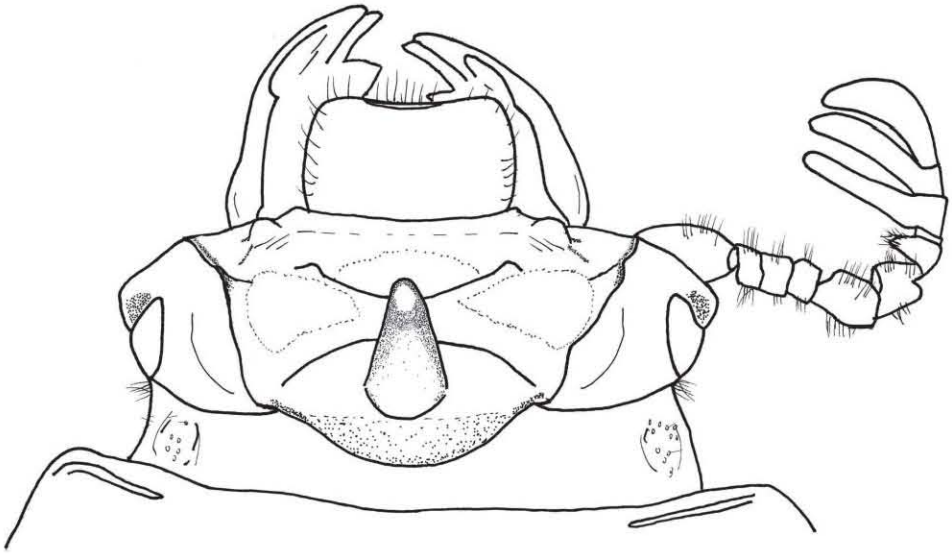

FIGURE 3. Dorsal aspect of head of *Ogyges cavei*.

Holotype and paratype deposited at UVGC.

Etymology. Named after the notable entomologist Ronald D. Cave, in honor of his studies on the entomological diversity of Honduras.

Distribution. The species is known only from two widely separated cloud forests between 1800–2100 m, from Olancho and Comayagua in Honduras (Fig. 4).

Ogyges handali Cano, new species

Figs. 5–6, 21i

Diagnosis. *Ogyges handali* resembles *O. adamsi* Schuster & Reyes-Castillo, by the absence of internal tubercles, the transversal convex clypeus, and the form of the central horn and lateroposterior tubercles. The new species is easily separated of *O. adamsi* by the abundant setae on anterior corners of metasternum (sparse or bare in *O. adamsi*).

Description. Holotype male, black adult: Total length 33.67, elytral length 18.51, pronotal length 8.45, pronotal width 11.16, humeral width 10.31. Head: anterior border of labrum concave. Clypeus thickened, transversely convex, anterior border straight, with a central notch in form of "v"; with rugose sulcus separating from the inclined mediofrontal area. Mediofrontal tubercles small and rounded; internal tubercles absent. Laterofrontal areas roughened. Posterofrontal ridges absent; instead, a transversal ridge (tumose near the central horn) runs between the mediopostfrontal structure and the epicranial sutures, forming the anterior margin of lateropostfrontal areas. Mediofrontal area with several grooves confluent to the clypeus, with a wide, bare, rough fossae present in front of the mediopostfrontal structure. Lateropostfrontal areas glabrous, deep, with several grooves. Central horn long, with apex short and free; posterior 1/3 tumose and clearly differentiated from the lower lateroposterior tubercles and with a deep median longitudinal groove; lateroposterior tubercles lower than central horn, barely marked, separated from central horn and directed forward. Postfrontal groove shallow at middle and laterally deep. Supraorbital ridge brilliant and rugose, with unequal anterior tubercles; posterior 1/2 barely bifurcate but with supraorbital fossae elongate, well marked; external ridge rounded. Ocular canthus with apex slightly swollen, rounded, ventrally extended just to half of eye. Eyes reduced. Eye width = 0.31 mm. Interocular

width = 6.61 mm. Head (measured from tips of canthi) 8.03 mm; ratio width of both eyes/head = 0.08. Postorbital pits punctuate setose. Ligula slightly protuberant basally, with apical central tooth small and anterior transversal carina absent; abundant setose punctures on the median area, basally sparse. Lateral lobes of mentum with moderate setose punctures, more abundant towards the brilliant oval lateral basal scars; medial basal mentum glabrous and smooth. Hypostomal process elongate, without lateral depression, wide medially and narrow in the apical third. Infraocular ridge present, short and smooth, surrounded by setose punctures. Mandible with dorsal tooth occupying 1/2 of the length; internal face of mandible in dorsal view granular. Antennal club (Fig. 5) with all three antennomeres very wide and subequal measuring 1.77 mm long and 2.31 mm wide; antepenultimate antennomere narrower than penultimate.

Thorax: Lateral fossa of pronotum without punctures except sparse, rugose micropunctures ahead and behind, only visible at very great magnification. Pronotum with marginal groove narrow and smooth, anterior angles rounded, disc smooth at moderate magnification. Prosternellum wide and brilliant. Mesosternum bare and shiny, without definite opaque/rugose (shagreened) areas. Mesepisternum brilliant. Metasternum with anterior angles punctate setose; disc not delimited by punctures; marginal groove very narrow and rugose, with disperse setae in the anterior 4/5 of its length, posteriorly four times wider than medially.

Elytra: Brilliant, with well-marked striations; with small, defined, moderately deep punctures; junctions of striations 1 and 10 without extra punctures. Anterior border of elytra vertical, smooth, with minute scattered setae between interstriae 2–8.

Legs: Profemur with anterioventral groove marked; metafemur elongated; mesotibia with one spine.

Abdomen: Marginal groove of sternite VII incomplete, occupies 3/5 of sternite.

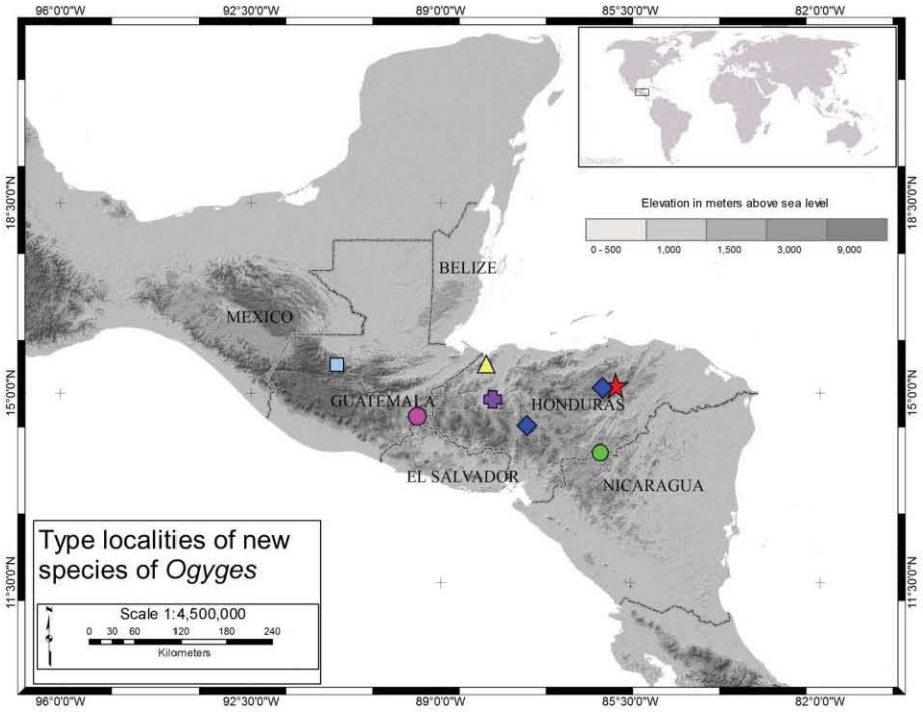

FIGURE 4. Map of northern Central America showing the locality of the new species. Light blue square, *Ogyges menchuae*; rose circle, *O. handali*; blue rhombus, *O. cavei*; yellow triangle, *O. llama*, *O. mutenroshii*; purple cross, *O. toriyamai*; red star, *O. laurae*, *O. ratcliffei*, and light green circle, *O. sandinoi*.

Aedeagus: In ventral view phallus globose; parameres and phallobase partially separated. In dorsal view, ventrodorsal basal sclerotizations of the phallus present (Fig. 6).

Variation in paratypes (n = 19): Total length 30.54–35.58 ($\bar{x}$ = 33.00), elytral length = 16.06–19.17 ($\bar{x}$ = 17.97), pronotal length = 7.5–8.76 ($\bar{x}$ = 8.44), pronotal width = 9.7–11.54 ($\bar{x}$ = 11.03), humeral width = 9.16–11.27 ($\bar{x}$ = 10.36).

Material examined. 49 specimens.

Type material. Holotype male: GUATEMALA: Chiquimula, aldea Santa Rosalía, El Duraznal, cerca del Plan de la Arada, 11 VI 2011, 14°31'30.4"N, 89°22'47.3"W, 1668 m, bosque nuboso, Col. E.B. Cano. Paratypes: Same data as holotype (1 male, 1 female). Same data except 1–4 IV 2011, aprox. 1700 m, Col. C. Suchité (11 males, 14 females). Same data except aldea El Duraznal, cerca de La Mesilla, 1630 m, 20 VIII 1998, Cols. E. Cano & J. Monzón (5). Guatemala: Chiquimula, San José las Minas, camino entre caserío Las Presas y el Plan de la Arada, Bosque nuboso. 1900 m, 24 VI 1998, Col. E. Cano (16).

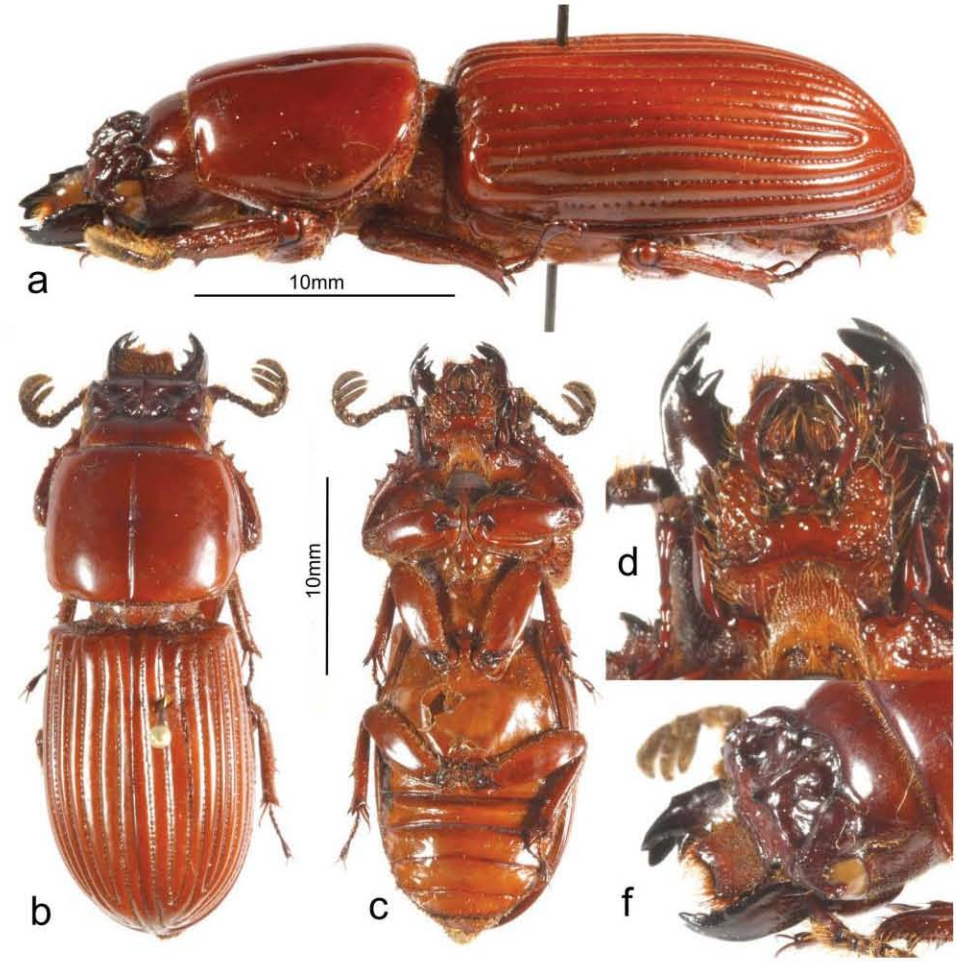

FIGURE 5. Paratype of *Ogyges handali*: a. lateral view. b. dorsal view. c. ventral view. d. ventral view of head and prothorax. e. anterolateral view of head.

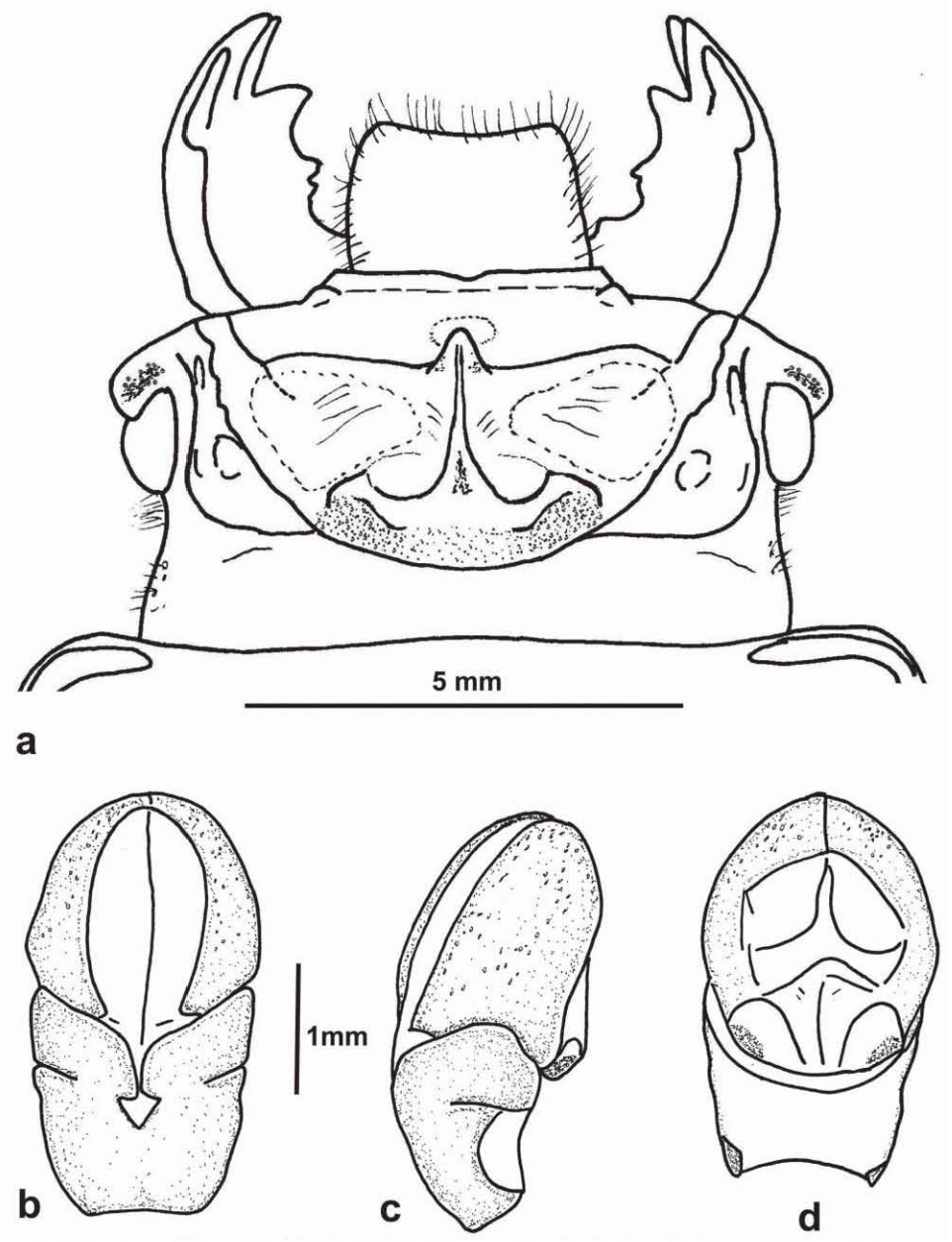

FIGURE 6. *Ogyges handali*: a. dorsal aspect of head. b. ventral view of aedeagus. c. lateral view of aedeagus. d. dorsal view of aedeagus.

Holotype deposited at UVGC, paratypes deposited in UVGC, USAC, IEXA, IBUNAM, SNM, and MNHN.

Etymology. Named in honor of Commander Dr. Schafik Handal, officially recognized as "Hijo Meritísimo de la Ciudad de San Salvador" and "Honor al Mérito Centroamericano", for his efforts in favor of the peace in Central America.

Distribution. The species is known only from the fragmented cloud forests of Cerro Montecristo between 1640–1900 m in Guatemala (Fig. 4). The new species should be present in the protected forest of the El Salvador portion and the bigger forest of the Honduran portion.

***Ogyges laurae* Cano new species**
Figs. 7–8, 21m

Diagnosis. *Ogyges laurae* is the smallest species of the genus *Ogyges*. The elytra with wide and deep dorsal punctures are evidence that this species is closely allied to the "*O. crassulus*" lineage (as suggested by Schuster *et al*. (2005)). It is easily separated from *O. crassulus, O. monzoni* Schuster, Cano, & Boucher and *O. aluxi* Schuster, Cano, & Boucher, by the smaller size, the impunctate (or almost impunctate) medial basal mentum, the scarcely free central horn, and the mesotibia with only one spine.

Description. Holotype male, dark brown teneral, with blue iridescence. Total length 22.91, elytral length 12.53, pronotal length 6.55, pronotal width 8.1, humeral width 7.25. Head: anterior border of labrum slightly concave. Clypeus vertical; anterior border almost straight, with a very small central notch; with an incomplete sulcus formed by striate punctures of granular aspect separating it from the mediofrontal area. Mediofrontal tubercles rounded and defined. Mediofrontal area smooth, with sparse micropunctures; without internal tubercles and posterofrontal ridges. Laterofrontal areas smooth. Lateropostfrontal areas wide, glabrous, smooth, with a few rugosities and frequent micropuntations. Central horn long, basally wide, with apex moderately free and directed forward and slightly upward, without median longitudinal groove posteriorly; lateroposterior tubercles short, laterally rounded, separated from central horn by a sulcus or fossa. Postfrontal groove medially very narrow (constrained by the extended mediopostfrontal structure), gradually enlarged and deeper at sides and almost continuous with the lateropostfrontal areas. Supraorbital ridge with two unequal anterior tubercles; posterior 1/2 bifurcate with supraorbital fossa deep, external ridge well marked. Ocular canthus with apex swollen, almost oblique. Eyes reduced. Eye width = 0.38 mm. Interocular width = 4.61 mm. Head width (between apex of canthus) = 5.07 mm; ratio both eye widths/head = 0.15. Postorbital pits oval, bare, deep and smooth, separated by a keel from an external punctate setose area and located immediately behind the external supraorbital ridge. Ligula slightly protuberant basally, setose punctures present medially, with apical central tooth small and transversal anterior carina absent (a tumosity is present). Lateral lobes of mentum shagreened, with setose punctures; apical area strongly microstriate (except on lateral borders), reaching the anterior borders of center mentum; lateral basal scars oval and opaque; medial basal mentum bare, shiny, without or at most with a few punctures with slender and long setae. Hypostomal process elongate, wide medially and narrow in apical third, without lateral depression. Infraocular ridge present, external and basal area punctate or punctate-setose. Mandible with dorsal tooth occupying 1/2 of his length; internal face in dorsal view smooth. Antennal club (Figs. 7–8) 1.08 mm long, 1.23 mm wide, with last two antennomeres wider than antepenultimate.

Thorax: Lateral fossae of pronotum only on sides with some micropunctures of rugose aspect, visible with great magnification. Pronotum with marginal groove narrow and laterally with abundant micropunctures of rugose aspect (striate); anterior angles rounded; disc smooth, only with sparse micropunctures (visible at great magnification). Prosternellum completely shagreened. Mesosternum glabrous; lateral depressions elongate and rugose (shagreened), widened posteriorly. Mesepisternum with large, rugose (shagreened) area, anteriorly widened and elongate and narrow towards distal portion. Metasternum anterior angles bare or with sparse minute setae; disc delimited by 20–22 well marked punctures on each side; marginal groove bare, very narrow, smooth, posteriorly two times wider than medially.

Elytra: Opaque, with blue iridescence under light; striations marked and with well-defined punctures not connected, slightly deeper and wider between striae 5–10; with micropunctures present on interstria, more abundant and easily visible on 6–10; junctions of striae 1 and 10 with some extra punctures. Anterior border of elytra vertical, with minute setae on interstriae 2 to 7.

Legs: Profemur with anterioventral groove marked and long; metafemur widened; mesotibia with one spine.

Abdomen: Marginal groove of sternite VII incomplete, occupies 3/5 of sternite.

Aedeagus: In ventral view phallus globose and elongate; paramerers and phallobase separated (Fig. 8).

Variation in paratypes (n = 10): Total length 18.71–22.91 ($\bar{x}$ = 21.34), elytral length 11.53–12.53 ($\bar{x}$ = 11.76), pronotal length 5.51–6.55 ($\bar{x}$ = 5.88), pronotal width 7.24–8.10 ($\bar{x}$ = 7.48), humeral width 6.70–7.47 ($\bar{x}$ = 7.08). Disc of metasternum delimitated by 19–25 well-marked punctures on each side. Elytra slightly brilliant in teneral (light brown) specimens; blue iridescence more easily visible in black specimens.

Material examined. 11 specimens.

Type material. Holotype male. Honduras, Olancho, 11 km N of Catamacas, mountain "La Picucha", 14.92740, -85.90983, 1800–2100 m, 8–14 V 2010. L. Sáenz collector (LSD). Paratypes: Same data as holotype (10).

Holotype deposited in UVGC. Paratypes deposited in UVGC, IEXA, USAC, IBUNAM, SNM, and MNHN.

Etymology. The name of this species is in honor of my friend and myrmecologist Laura Sáenz.

Distribution. Only known from Cerro La Picucha, in Olancho, Honduras (Fig. 4), a mid-altitude cloud forest.

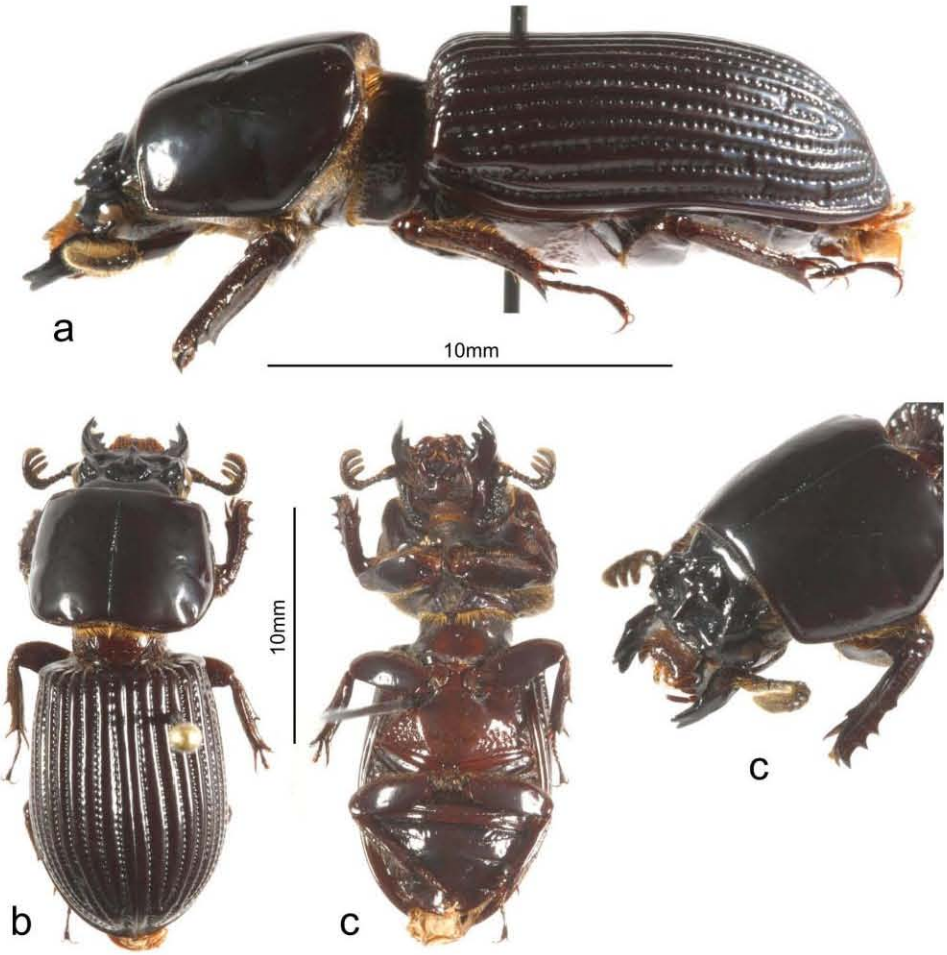

FIGURE 7. Paratype of *Ogyges laurae*: a. lateral view. b. dorsal view. c. ventral view. d. anterolateral view of head and pronotum.

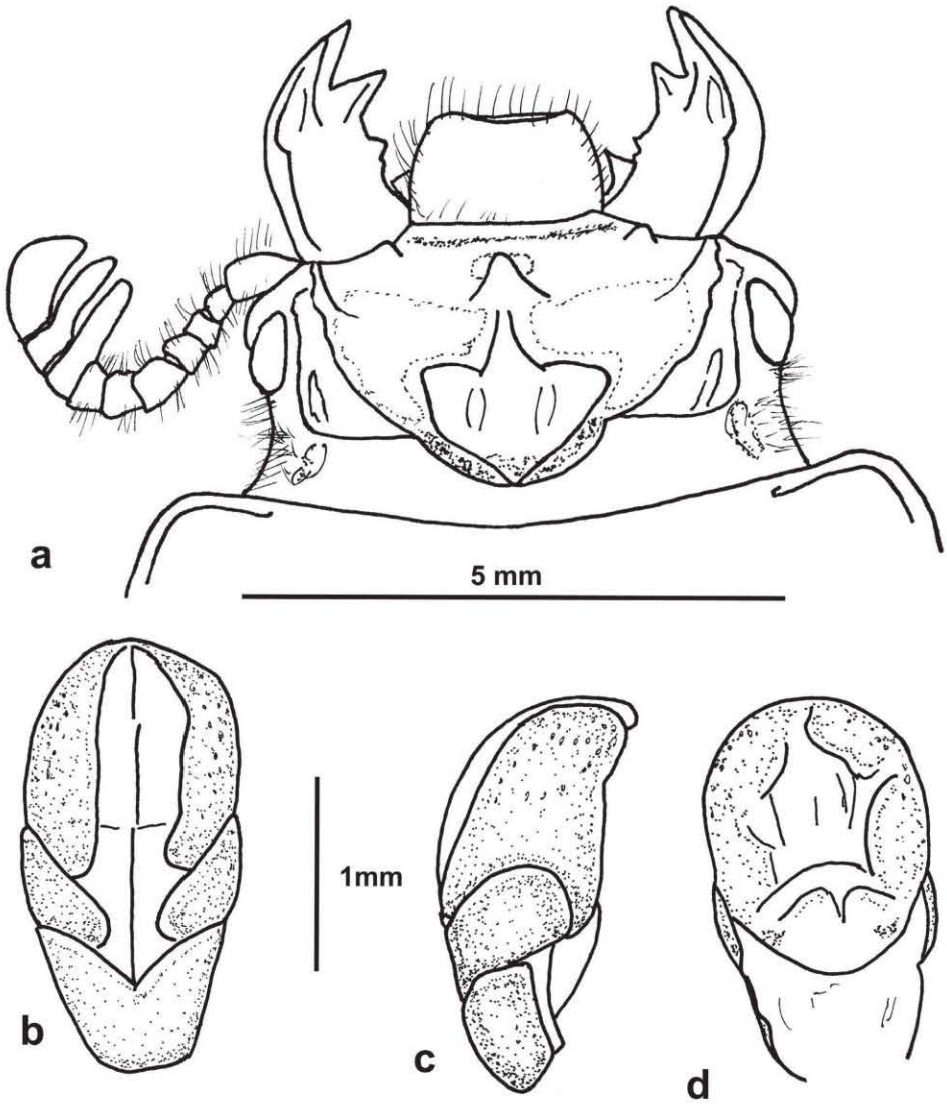

FIGURE 8. *Ogyges laurae*: a. dorsal aspect of head. b. ventral view of aedeagus. c. lateral view of aedeagus. d. dorsal view of aedeagus.

***Ogyges llama* Cano, new species**
Figs. 9–10, 21n

Diagnosis. By the elytra with wide, deep dorsal punctures, *O. llama* is similar to the "*O. crassulus*" lineage (as suggested by Schuster *et al*. (2005)). It is easily separated from *O. monzoni* and O. *aluxi* by the smaller size, the

central horn not free or scarcely free and by the medial central mentum weakly rugopunctate. It can be separated from *O. laurae* by the mesotibia with two spines (instead of one) and the tumose posterior portion of central horn. From the sympatric or almost sympatric *O. crassulus* it is separated by the form of aedeagus, with lateral lobes separated from basal piece, and the widest punctures on posterior striae 6–9.

Description. Holotype male, black (dorsum) to dark brown (venter) teneral, with blue iridescence. Total length 22.61, elytral length 11.85, pronotal length 6.23, pronotal width 8.16, humeral width 7.56. Head: anterior border of labrum slightly concave. Clypeus inclined (> 90°); anterior border straight, lacking a central invagination, with a scabrose (to almost granular) sulcus separating it from the smooth (almost shagreened at great magnification) mediofrontal area. Mediofrontal tubercles rounded and defined; internal tubercles and posterofrontal ridges absent. Laterofrontal areas smooth. Lateropostfrontal areas wide, glabrous, and smooth; a marked or weakly marked keel

FIGURE 9. Paratype of *Ogyges llama*: a. lateral view of head. b. dorsal view. c. ventral view. d. lateral view.

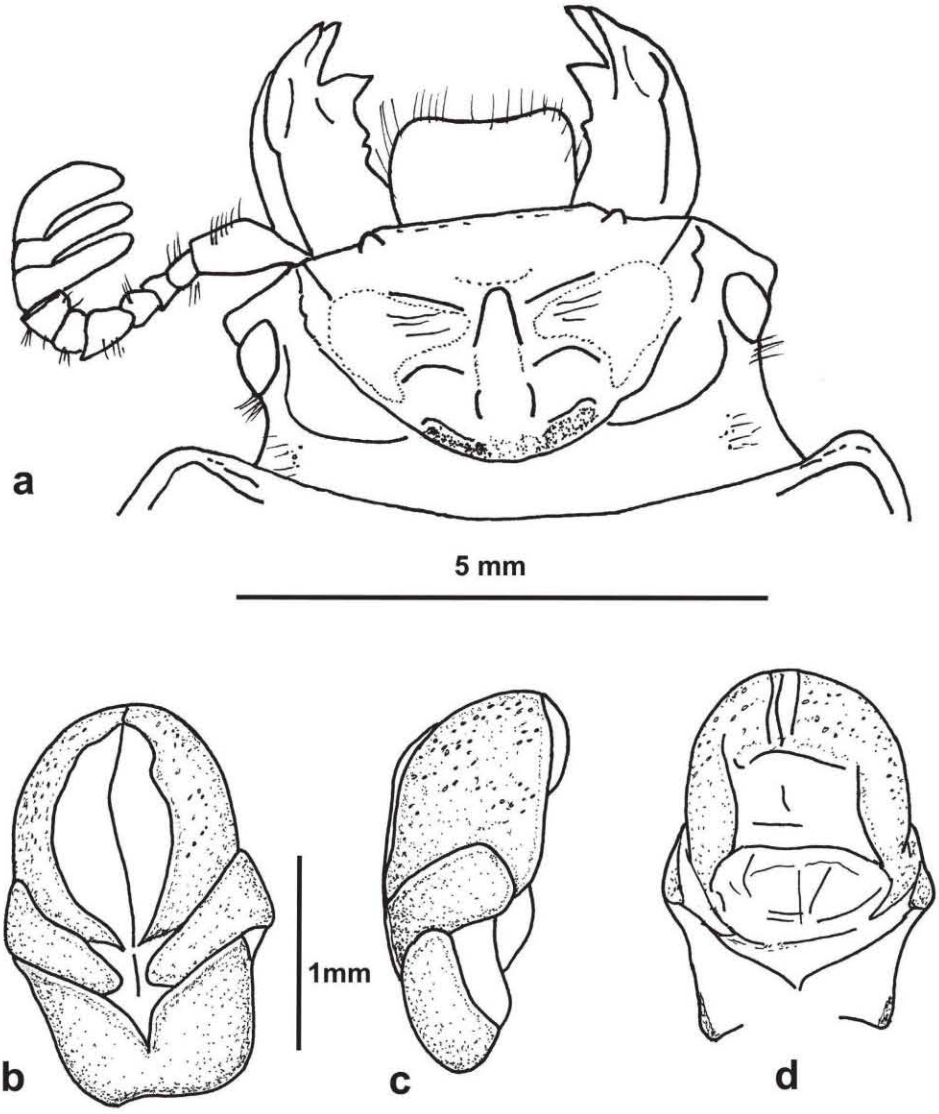

FIGURE 10. *Ogyges llama*: a. dorsal aspect of head. b. ventral view of aedeagus. c. lateral view of aedeagus. d. dorsal view of aedeagus.

runs laterally from the mediopostfrontal structure, forming the anterior border of lateropostfrontal areas. A wide, bare, smooth fossa present in front of the mediopostfrontal structure. Central horn short, narrow, with apex weakly free (or almost not free), directed upward, without median longitudinal groove posteriorly; lateroposterior tubercles not elongate, forming an angle directed forward and sideways, separated from the central horn by a groove. Postfrontal groove shallow, medially very narrow (constrained by the extended mediopostfrontal structure), gradually enlarged at sides and almost continuous with the lateropostfrontal areas. Supraorbital ridge with equal

anterior tubercles; posterior 1/2 bifurcate with the supraorbital fossae deep; external ridge well marked. Ocular canthus with apex straight or slightly swollen, ventrally covering at least the half of eye. Eyes reduced. Eye width = 0.42 mm. Interocular width = 4.61 mm. Head width (measured between tips of ocular canthus) = 5.85 mm; ratio both eye widths/head width = 0.14. Postorbital pits oval, elongate and covered with sparse setae on external border. Ligula slightly protuberant basally, with small central tooth and without a ventral anterior transversal carina (a tumosity is present); medially with setose punctures. Lateral lobes of mentum with moderate setose punctures, lateral basal scars oval and opaque (shagreened); medial basal mentum shiny, with a few scattered small and scabrous setose punctures, setae long and slender. Hypostomal process elongate, without lateral depression, wide medially and narrow in apical third. Infraocular ridge present, short and smooth, surrounded by striate, setose punctures. Mandible with dorsal tooth occupying 1/2 of his length; internal face of mandible in dorsal view smooth, not granular. Antepenultimate antennomere of antennal club subequal in length but less wide than the penultimate (Figs. 9–10); antennal club measures 1.11 mm wide and 1.23 mm long.

Thorax: Lateral fossae and marginal groove of pronotum with abundant striate micropunctures, visible at great magnification; anterior angles rounded; disc smooth except for scattered shallow micropunctures visible at high magnification. Prosternellum opaque, completely shagreened. Mesosternum glabrous; lateral depressions elongate and rugose (shagreened). Mesepisternum with oval, very elongate shagreened area, reaching the posterior border. Metasternum anterior angles glabrous; disc delimited by 12–16 well marked punctures (some partially fused) on each side; marginal groove glabrous, narrow and smooth, posteriorly two times wider than medially.

Elytra: Opaque, with blue iridescence; striations well marked and with defined punctures, slightly deeper and wider between striae 5–10; anterior 1/3 of sixth interstriae of the width of a puncture of striae 6 or 7; junctions of striations 1 and 10 with some extra punctures.

Legs: Profemur with anterioventral groove marked; metafemur moderately widened; mesotibia with two spines.

Abdomen: Marginal groove of sternite VII incomplete, occupies 3/5 of sternite.

Aedeagus: In ventral view phallus globose; parameres and phallobase separated (Fig. 10).

Variation (n = 30): Total length 19.30–24.49 ($\bar{x}$ = 22.95), elytral length 11.7–13.24 ($\bar{x}$ = 12.59), pronotal length 5.60–7.18 ($\bar{x}$ = 6.38); pronotal width 7.55–8.69 ($\bar{x}$ = 8.19); humeral width 6.8–8.26 ($\bar{x}$ = 7.71). Disc of metasternum delimited by 12–24 well marked punctures (some striate or partially fused) on each side.

Material examined. 44 specimens.

Type material. Holotype male. Honduras: Cortés, cerca de San Pedro Sula, 15.512598°, -88.113660° 1580 m, 2 X 2011, Bosque nuboso. Coll. F. Camposeco. Paratypes: Same data as holotype (5 males, 7 females, 30 unknown). Honduras: Cortés Dept. 30 km W of S. Pedro Sula, 1550 m alt., 20-21 III 1987, bosque nuboso, J.C. Schuster, # VI3 female, Type C disturbance sound (1).

Holotype deposited at UVGC. Paratypes deposited in UVGC, IEXA, USAC, RC, SNM, and IBUNAM.

Etymology. Named after colleagues of the National Science Foundation project LLAMA (Leaf Litter Arthropods of Mesoamerica), led by Jack Longino and Bob Anderson. Several new species were collected under the umbrella of this project.

Distribution. This species is known from cloud forests of middle altitude near San Pedro Sula in Honduras (Fig. 4).

Ogyges menchuae Cano, new species

Figs. 11–12, 21p

Diagnosis. *Ogyges menchuae* is most similar to *O. cakchiqueli* Schuster & Reyes-Castillo, *O. championi* (Bates), and *O. kekchii* Schuster & Reyes-Castillo. These species are in the "*O. laevior*" [= *O. championi*] lineage of Schuster & Reyes Castillo (1990). The large internal tubercles separate it from similar species, except from *O. tzutuhili* Schuster & Reyes-Castillo and *O. marilucasae* Reyes-Castillo & Castillo, but is easily separated by the narrow antennal club (very wide in *O. tzutuhili* and *O. marilucasae*), and the smaller size.

Description. Holotype male, black adult. Total length 29.24, elytral length 16.20, pronotal length 8.38, pronotal width 10.61, humeral width 10.03. Head: anterior border of labrum straight, dorsal surface granular. Clypeus vertical, anterior border straight, posteriorly microgranulate, separated from the mediofrontal area by an

inflection; mediofrontal tubercles conical, with apex rounded, moderately enlarged and markedly visible in lateral view. Mediofrontal area slightly microtuberculate, moderately roughened; internal tubercles present and well developed, directed forward and slightly upward, connected to the curved and strongly marked posterofrontal ridges; angle of posterofrontal ridges concave and united to the central horn. Laterofrontal areas roughened, with sparse granulations. Lateropostfrontal areas glabrous, smooth, somewhat roughened and with sparse microtubercles or granulations. Central horn short with apex conical, not free and with median longitudinal (mostly deep) groove dorsally in basal half; lateroposterior tubercles elongate, rounded, directed forward, separated from the central horn by a small groove with sparse or moderate microgranulations. Postfrontal groove deeper at sides and separated from lateropostfrontal areas. Supraorbital ridge with mostly unequal or almost equal anterior tubercles; posterior 1/2 bifurcate, with the supraorbital fossae very deep; external ridge well marked. Ocular canthus with apex swollen, apex forming a right angle. Eyes reduced, width = 0.54 mm (each eye). Interocular width = 6.15 mm. Head width (measured between tips of canthi) = 6.92 mm; ratio both eyes/head = 0.16. Postorbital pits situated immediately behind supraorbital ridges, almost rectangular, shallow and with a few punctures; external borders with setose punctures. Ligula slightly protuberant basally; with a central apical tooth small and with a transversal, well marked anterior ventral ridge; setose punctures present medially. Lateral lobes of mentum with abundant setose punctures; lateral basal scars oval, brilliant and punctate setose, internal border longitudinally striate. Medial basal mentum bare and with sparse micropunctures visible at great magnification. Hypostomal process elongate, wide medially and narrow in apical third, without lateral depression. Infraocular ridge short, external and basal area punctate-pubescent. Dorsal tooth of mandible occupies 1/2 length of the mandible; internal face of mandible in dorsal view, granular. Antennal club (Figs. 11–12) 1.88 mm long, 1.31 mm wide; with last two antennomeres wider than the antepenultimate, this slightly more than twice as wide as long.

Thorax: Lateral fossae of pronotum with micropunctures of rugose aspect, visible with moderate magnification. Pronotum with marginal groove narrow, widened at anterior margin; anterior angles rounded, slightly projected anteriorly immediately behind eyes. Pronotum with dense and shallow micropunctures of rugose aspect, visible at moderate magnification, running from the lateral fossae to the anterior border, internal to marginal groove; disc with sparse micropunctures visible at great magnification. Hypomeron with abundant small shallow punctures. Prosternellum completely shagreened. Mesosternum bare, lateral depressions elongate, rugose (shagreened). Mesepisternum with large and oval rugose (shagreened) area extended to posterior margin. Metasternum with anterior angles bare; disc not delimited by punctures; marginal groove bare and narrow, posterior part 1.5–2.0 times wider than the median part.

Elytra: Striations marked and with small but defined punctures, wider and deeper from 5–10; interstriae 1–7 with sparse micropunctures, more abundant and visible at moderate magnification on interstriae 8–10; junctions of striations 1 and 10 without extra punctures.

Legs: Profemur with anterioventral groove marked, metafemur widened; mesotibia with two (rarely three) spines.

Abdomen: Marginal groove of sternite VII incomplete, occupies 3/5 of sternite.

Aedeagus: In ventral view phallus globose; parameres and phallobase separated; in dorsal view, ventrodorsal basal sclerotizations of the phallus present (Fig. 12).

Variation (n = 20): Total length 29.36–33.15 ($\bar{x}$ = 31.43), elytral length 16.11–18.66 ($\bar{x}$ = 17.29), pronotal length 7.40–9.13 ($\bar{x}$ = 8.56), pronotal width 10.12–11.72 ($\bar{x}$ = 10.93), humeral width 9.46–10.71 ($\bar{x}$ = 10.17). Mediofrontal area more or less smooth to somewhat or moderately roughened, with scarce to barely visible microgranulations. Some specimens present an anterior keel in the concavity of the angle of posterofrontal ridges.

Material examined. 35 specimens.

Type material. Holotype: GUATEMALA: Quiché, Uspantán, aldea Laj Chimel, montaña al norte de la aldea, 2100 m., VII 1998, bosque nuboso. E.B. Cano collector.

Paratypes: GUATEMALA: same data as holotype (1 male, 7 unknown); same data except Norte Laj Chimel, San Pedro, 2100m (1 male, 1 unknown); same data except Aldea Laj Chimel, A.González-Madrid, 30 V 2011 (13); same data except, Aldea Laj Chimel, road to San Pablo, 30 IV 2011, 15°27'30.69"N, 90°46'26.11"W, 2035 m, A. Gónzález-Madrid 30 V 2011 (3 male, 1 unknown); same data except, Aldea Laj Chimel, road to San Pablo, 30 IV 2011, 15°27'30.69"N, 90°46'26.11"W, 2035 m (6); same data except, Montaña El Amay, in logs 15 VI 2012, A. Zamora (2 males).

Holotype deposited in UVGC. Paratypes deposited in UVGC, IEXA, USAC, IBUNAM, SNM, and MNHN.

Etymology. Named in honor of the Nobel Prize winner, Dr. Rigoberta Menchú, who was born in Laj Chimel.

Distribution and ecology. Known only from middle altitude cloud forest at Cerro El Amay, of Laj Chimel, Quiché, Guatemala, 1800–2100 m altitude (Fig. 4).

FIGURE 11. Paratype of *Ogyges menchuae*: a. lateral view of head. b. dorsal view. c. ventral view. d. lateral view.

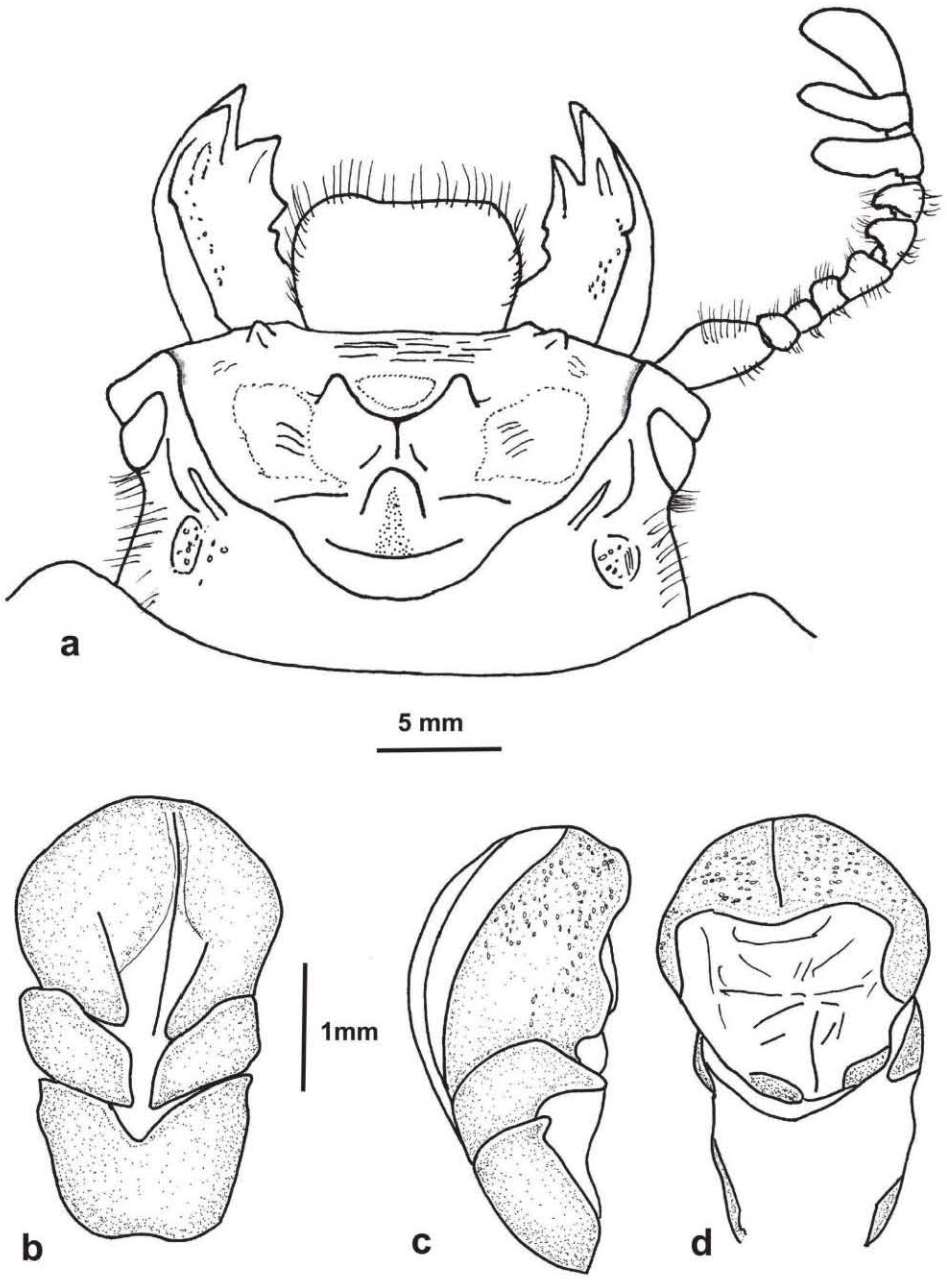

FIGURE 12. *Ogyges menchuae*: a. dorsal aspect of head. b. ventral view of aedeagus. c. lateral view of aedeagus. d. dorsal view of aedeagus.

***Ogyges mutenroshii* Cano, new species**
Figs. 13–14, 21r

Diagnosis. *Ogyges mutenroshii* is most similar to *O. nahuali*, *O. cavei*, and *O. toriyamai* new species, by the small dorsal punctures on elytra and strong punctures on metasternum. Is easily distinguished by the brilliant elytra, the very wide protibia, the form of central horn, the absence of postorbital pits, and the greater reduction in the eye.

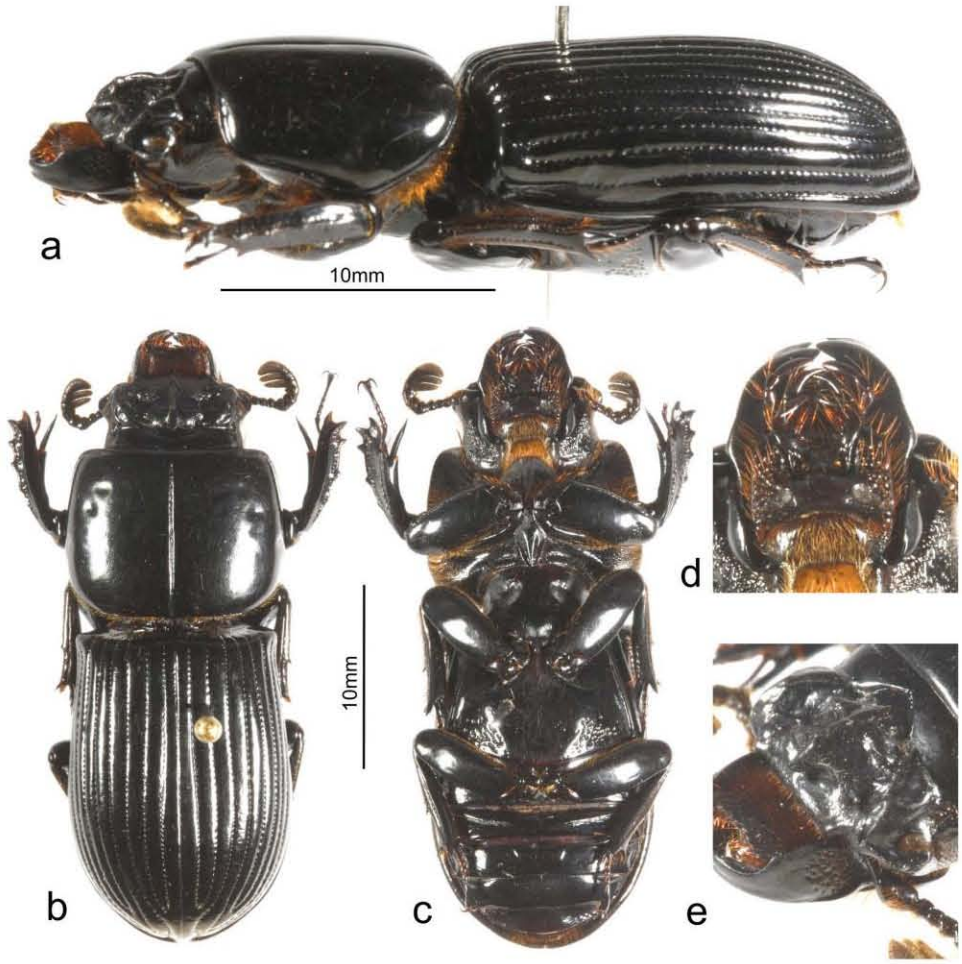

FIGURE 13. Holotype of *Ogyges mutenroshii*: a. lateral view. b. dorsal view. c. ventral view. d. detail of mentum. e. anterolateral view of head.

Description. Holotype, sex unknown, black adult. Total length 34.56, elytral length 18.44, pronotal length 9.24, pronotal width 12.05, humeral width 10.95. Head: anterior border of labrum slightly concave. Clypeus inclined (45°); anterior border straight and thin, with very small, central invagination, without suture separating it from the mediofrontal area (except an indication of slightly rugose area that runs between mediofrontal tubercles). Mediofrontal tubercles rounded and well defined. Mediofrontal area smooth, without internal tubercles and posterofrontal ridges. Laterofrontal areas roughened. Lateropostfrontal areas wide, glabrous and roughened at

sides. Central horn long and very narrow, apical 1/3 declivous in lateral view, dorsally excavated on both sides up to the level of the lateroposterior tubercles, with apex free and slightly directed upward, without median longitudinal groove posteriorly; lateroposterior tubercles somewhat elongate, separated from the posterior keel of the central horn. Postfrontal groove laterally deep. Supraorbital ridge with equal anterior tubercles; posterior 1/2 bifurcate with the supraorbital fossae very deep; external ridge well marked. Ocular canthus with apex swollen, dorsally covering more than 2/3 of eye. Eyes reduced. Eye width = 0.38 mm. Interocular width = 6.92 mm. Head width = 8.46 mm; ratio both eye widths/head width = 0.09. Postorbital pits, immediately behind the external ridge, punctate setose. Ligula almost flat basally, with eroded (also in the paratype) central tooth, with setaceous punctures medially; anterior ventral transversal carina clearly present. Lateral lobes of mentum with abundant setose punctures; lateral basal scars oval, opaque (shagreened), and punctate setose; medial basal mentum bare and shiny, with one-three punctures on each side. Hypostomal process elongate, without lateral depression, wide medially and narrow in apical third. Infraocular ridge present, short and smooth, surrounded by striate, setose punctures. Mandible with dorsal tooth occuppying 1/2 of the length; internal face of mandible in dorsal view, smooth. Antepenultimate antennomere of antennal club slightly longer (or subequal) than penultimate, less wide than the penultimate; antennal lamellae slightly concave dorsally (Figs. 13–14), 1.69 mm wide and 1.92 mm long.

Thorax: Lateral fossae of pronotum only with sparse and very shallow micropunctures, visible at great magnification. Pronotum with marginal groove narrow and smooth, laterally with scattered micropunctures of rugose aspect (striate), visible at great magnification, more abundant in front of lateral fossae; anterior angles rounded; disc smooth. Prosternellum brilliant at center, shagreened at anterior 2/5 and posterior (except on sides) 1/5. Mesosternum glabrous; lateral depressions elongate and rugose (shagreened). Mesepisternum with oval, elongate, shagreened area. Metasternum anterior angles glabrous; disc delimited by 38 and 40 well-marked punctures (some striate) on each side; marginal groove glabrous, narrow and sligthly striate, posteriorly two times wider than medially.

Elytra: Brilliant; striations well marked and with weakly defined punctures between striae 1–3, gradually wider between striae 4–10 and apical 1/3; junctions of striations 1 and 10 with some extra punctures. Vertical anterior border of elytra with sparse, minute setae on interstriae 2–6.

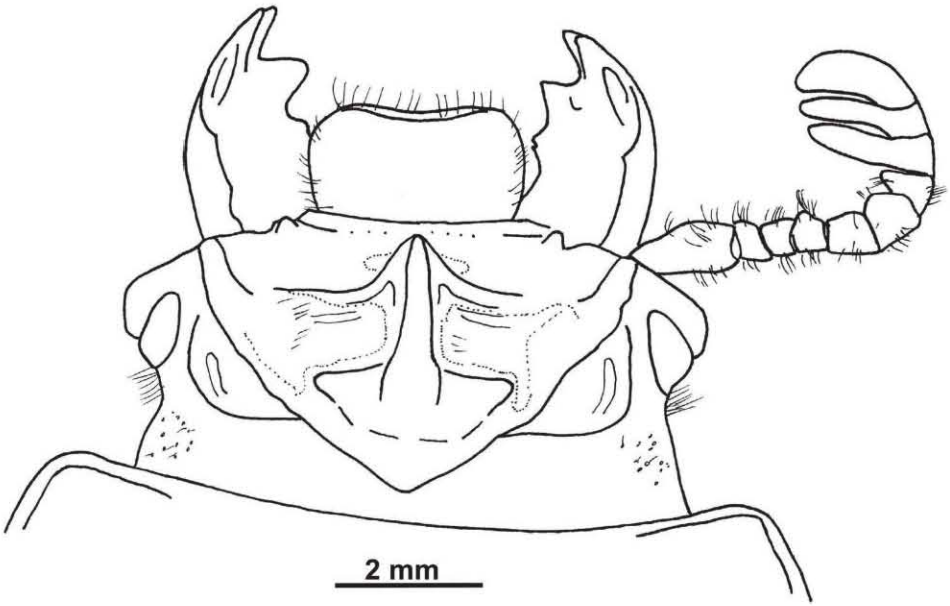

FIGURE 14. Dorsal aspect of head of *Ogyges mutenroshii*.

Legs: Protibia very wide. Profemur with anterioventral groove marked; metafemur elongate; mesotibia with one spine.

Abdomen: Marginal groove of sternite VII incomplete, occupies 3/5 of sternite.

Variation in paratype: Total length 33.19, elytral length 17.74, pronotal length 8.83, pronotal width 11.52, humeral width 10.18. Disc of metasternum delimited by 31 and 45 well-marked punctures (some striate) on each side.

Material examined. 2 specimens.

Type material. Holotype: HONDURAS: Cortés, Parque Nacional Cusuco, 2nd. broadleaved forest. Nr. UTM 16P 369210 1713408. Ca. 1656 m alt., 07–11 VIII 2007. Coll. S. Beynon. Paratype: One specimen, unknown sex, same data as holotype except: UTM 16P 369795 1714017. Alt. aprox. 1550 m. 16–20 VII 2006. Dung baited pitfall trap. Coll. E. Marabuto.

Holotype and paratype deposited at UVGC.

Etymology. Named after Muten Roshi (Master Roshi), a principal character of the Akira Toriyama´s series of manga and anime, "Dragon Ball".

Distribution. This species is known from the middle altitude cloud forest of the Cerro Azul Meambar National Park, in Comayagua Department, Honduras (Fig. 4).

Ogyges ratcliffei Cano new species

Figs. 15–16, 21v

Diagnosis. *Ogyges ratcliffei* seems most similar to *O. nahuali* and *O. cavei*. The smaller size, the noticeable blue reflections on brilliant areas, the narrow and flat lamellae and the shagreened metasternal marginal groove, separate *O. ratcliffei* from *O. cavei*. The lack of punctures surrounding metasternal disc and central horn directed upward, distinguish the new species from *O. nahuali*.

Description. Holotype, female, black adult with blue iridescence. Total length 33.02, elytral length 17.9, pronotal length 8.21, pronotal width 11.95, humeral width 11.12. Head: anterior border of labrum slightly concave. Clypeus slightly inclined, transversaly convex, anterior border straight and thick, with very small central invagination and with external anterior angles acute; separated from the mediofrontal area by a rugose sink running between the conical and moderate mediofrontal tubercles. Mediofrontal area smooth, without internal tubercles and posterofrontal ridges. A small, bare, smooth fossa present in front of the mediopostfrontal structure. Lateropostfrontal areas glabrous and smooth. Central horn moderately long, with apex directed upward and forward, with unclear median longitudinal groove on posterior 1/3; lateroposterior tubercles short, rounded, curved backward and separated from central horn. Postfrontal groove smooth and shallow, deeper at sides. Supraorbital ridge with equal anterior tubercles; posterior 1/2 not bifurcate with supraorbital fossae small; external ridge marked. Ocular canthus with apex straight covering half of one eye. Eyes reduced. Eye width = 0.61 mm. Interocular width = 6.61 mm. Head width (measured between tips of canthi) = 8.06 mm. Ratio width of both eyes/head = 0.15. Postorbital pits located between supraorbital ridge and eye, punctate setose. Ligula slightly protuberant basally, with apical central tooth eroded, anterior ventral carina absent, setose punctures on the median area. Lateral lobes of mentum with abundant setose punctures; medial basal mentum glabrous (except two punctures on one side near the lateral scar); lateral basal scars elongate to external side, punctate-setose and brilliant. Hypostomal process elongate, with poorly marked lateral depression, wide medially and narrow in the apical third. Infraocular ridge present, short and smooth, proximal area declivous and setose, distal area punctate-setose. Mandible with dorsal tooth occupying 1/2 of his length; internal face in dorsal view slightly opaque, not granular. Antennal club not concave, penultimate antennomere wider than the antepenultimate (Figs. 15–16).

Thorax: Lateral fossa of pronotum without punctures except minute striate-punctures ahead and behind, visible at high magnification. Pronotum with marginal groove narrow and smooth, with minute striate-punctures visible at high magnification; anterior angles rounded. Prosternellum opaque on anterior half (or slightly more) and shiny on posterior half. Mesosternum with lateral depressions elongate and rugose (shagreened). Mesepisternum with elongate rugose area (shagreened), more marked and oval apically. Metasternum anterior angles without setae, apical borders shagreened; disc without punctures; marginal groove glabrous, narrow and shagreened throughout, posteriorly two times wider than medially.

Elytra: Shiny, with blue reflections that give a dull appearance. Striations well marked; with minute, superficial punctures on striae 1–4, gradually deeper and wider between 5–10 and well marked from 1–10 on posterior 1/3; junctions of striae 1 and 10 with sparse extra punctures. Anterior border of elytra vertical, with a few minute setae on intrestriae 3–6.

Legs: Profemur with anterior-ventral groove marked; metafemur moderately widened; mesotibia with one spine.

Abdomen: Marginal groove of sternite VII incomplete, occupies 3/5 of sternite.

Material examined. 1 specimen.

FIGURE 15. Holotype of *Ogyges ratcliffei*: a. lateral view of head. b. dorsal view. c. ventral view. d. lateral view.

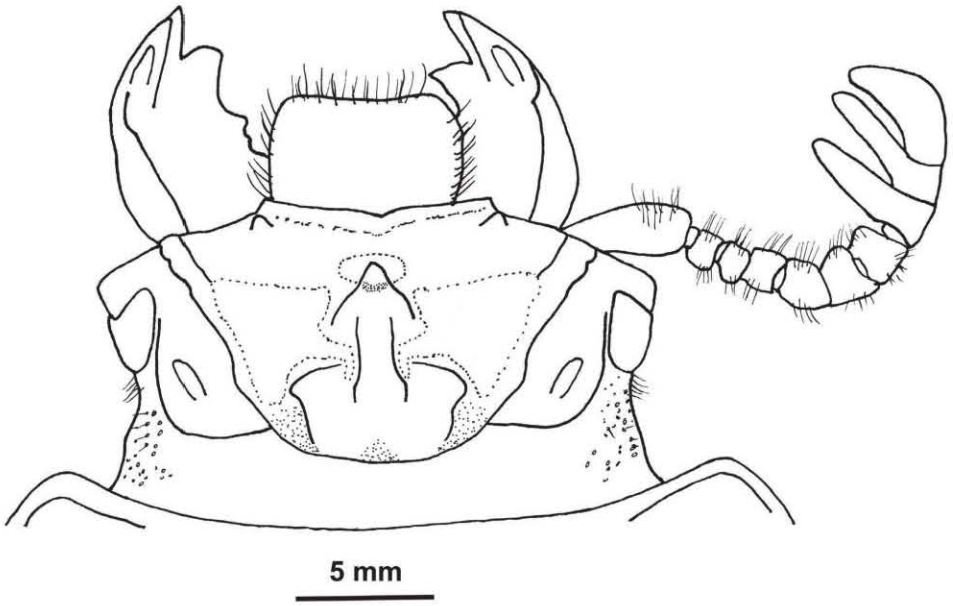

FIGURE 16. Dorsal aspect of head of *Ogyges ratcliffei*.

Type material. Holotype deposited at UVGC: HONDURAS: Olancho, La Picucha, 11 km N Catacamas, 14.92740, -85.90983. Bosque nuboso, 1800–2100 m, 8–14 V 2010. L. Sáenz (LSD 451).

Etymology. Named after the Team Scarab leader, Brett C. Ratcliffe, honoring his studies on the dynastine beetles of the world.

Distribution. The species is known only from the holotype collected in cloud forest between 1800–2100 m, in Olancho, Reserva La Picucha, Honduras (Fig. 4).

Ogyges sandinoi Cano new species

Figs. 17–18, 21w

Diagnosis. Based on the form of clypeus, the central horn, and the mediopostfrontal structure, and the presence of setae on anterior corners of metasternum (sparse in *O. adamsi*), *O. sandinoi* seems closely allied to *O. adamsi* and *O. handali*. This new species is easily distinguished by the smaller size (29–32 mm) and the presence of internal tubercles.

Description. Holotype male, black adult with dark-brown areas in venter. Total length 29.68, elytral length 16.00, pronotal length 8.26, pronotal width 10.27, humeral width 9.81. Head: anterior border of labrum concave or slightly concave. Clypeus thickened, convex, anterior border straight or slightly inclined laterally, with a small central indentation in form of "v"; with a moderately defined punctate sulcus separating it from the mediofrontal area. Mediofrontal tubercles rounded and well defined, with a well or barely defined anterofrontal ridges directed but not connected with the internal tubercles. Mediofrontal area smooth, with conical internal tubercles connected to the short and slightly curved posterofrontal ridges. A wide, bare, hemicircular smooth fossa present in front of the mediopostfrontal structure. Lateropostfrontal areas glabrous and slightly rugose towards lateral sides. Central horn very narrow and long, with apex not free, declivous towards the posterofrontal ridges, with dorsal micropuntations; without median longitudinal dorsal groove; lateroposterior tubercles short, not clearly delineated, rounded, directed slightly posteriorly, not separated from the central horn by a groove. Postfrontal groove shallow,

deeper at sides. Supraorbital ridge with unequal anterior tubercles; posterior half not bifurcate with supraorbital fossa small; external ridge poorly marked; supraorbital fossa shallow and short. Ocular canthus with apex straight or slightly swollen, ventrally covering 3/4 of eye. Eyes reduced. Eye width = 0.38 mm. Interocular width = 5.77 mm. Head width = 7.38 mm; ratio both eye widths/head width (measured between tips of canthi) = 0.10. Postorbital pits located immediately behind supraocular ridge and eye, punctate setose. Ligula almost flat basally, with small central apical tooth, ventral transversal anterior carina absent, with setaceous punctures medially. Lateral lobes of mentum setose punctate; lateral basal scars oval and brilliant; medial basal mentum bare and shiny. Hypostomal process elongate, with shallow lateral depression and with one or two minute setae, wide medially and narrow in apical third. Infraocular ridge present, short and smooth, surrounded by striate, setose punctures. Dorsal tooth of mandible occupies 1/2 length; internal dorsal face of mandible granular. Antennal club concave, measures 1.92 mm long and 2.15 mm wide; antepenultimate antennomere of antennal club less wide than penultimate (Figs. 17–18).

Thorax: Lateral fossae of pronotum without punctures but, together with the marginal grooves, with sparse micropuntations of rugose aspect, visible with great magnification. Pronotum with marginal groove narrow and smooth; disc smooth, slightly opaque; anterior angles rounded; with a small, but present, posterior medial notch. Prosternellum shagreened on anterior half and brilliant posteriorly, except slightly opaque on sides. Mesosternum glabrous; lateral depressions wide, elongate and rugose (shagreened). Mesepisternum with oval, elongate, shagreened area. Metasternum anterior angles with moderate setae; disc not delimited by punctures; marginal groove with setose punctures anteriorly; narrow and smooth, posteriorly two times wider than medially.

Elytra: Brilliant, striations marked, with small, defined, moderately deep punctures; junctions of striations 1 and 10 without extra punctures. Vertical anterior area smooth, with minute to small, scattered setae between portion of interstriae 1–8.

Legs: Profemur with anterioventral groove poorly marked, but present; metafemur elongate; mesotibia with one spine.

Abdomen: Marginal groove of sternite VII incomplete, occupies 3/5 of sternite.

Aedeagus: In ventral view phallus globose; parameres and phallobase scarcely separated laterally; ventrodorsal basal sclerotizations of the phallus present (Fig. 18).

Variation in paratypes (n = 4): Total length 30.02–31.63 ($\bar{x}$ = 30.68), elytral length 15.62–17.62 ($\bar{x}$ = 16.60), pronotal length 7.76–8.91 ($\bar{x}$ = 8.20), pronotal width 10.23–11.19 ($\bar{x}$ = 10.58), humeral width 9.53–10.31 ($\bar{x}$ = 9.80). One specimen with the antennomeres of the left antennal club fused (a teratology).

Material examined. 5 specimens.

Type material. Holotype: NICARAGUA, Nueva Segovia, nr Jalapa, Cerro Jesús. 13.98079, -86.17922. 28–31 May 2011, L. Sáenz collector (LSD). Paratypes (4): Same data as holotype.

Holotype deposited in UVGC. Paratypes deposited in UVGC, IEXA, and USAC.

Etymology. The name of this species is in honor of Augusto César Sandino, a Nicaraguan hero, born in the Segovia Mountains.

Distribution. Only known from Cerro Jesús, at the Nicaraguan-Honduran border (Fig. 4), at mid-altitude cloud forest (1600 m).

Comments. This is the first objective record of the genus *Ogyges* from Nicaragua. Previously, two species, *Ogyges laevissimus* and *O. championi* [as *O. laevior*] have been cited from that country (summarized in Schuster & Reyes-Castillo 1990: 19, 32–33). Because these citations are ambiguous, and following Schuster & Reyes-Castillo (1990) who restricted the species to Guatemala (*O. laevissimus*) and Guatemala and Mexico (*O. championi*), I consider these or any other citation of *O. laevissimus* and *O. championi* from Nicaragua as erroneous. As evidence of this ambiguity, the records of *O. laevissimus* from Nicaragua (Kuwert 1897: 291, Hincks & Dibb 1935: 21, Reyes-Castillo 1970: 177) apparently were based on one specimen at the MNHN, identified by Kuwert (Schuster & Reyes-Castillo 1990: 20 attribute the handwritten label to Kaup), with the locality data (in the same label) indicating Guatem.[ala]/Nicaragua. The specimen of *O. championi* from the MNHN, with the label "Nicaragua", cited by Schuster & Reyes-Castillo (1990), by the barely marked lateral punctures on elytra, apparently belongs to the population of Alta and Baja Verapaz in Guatemala.

FIGURE 17. Holotype of *Ogyges sandinoi*: a. lateral view of head. b. dorsal view. c. ventral view. d. lateral view.

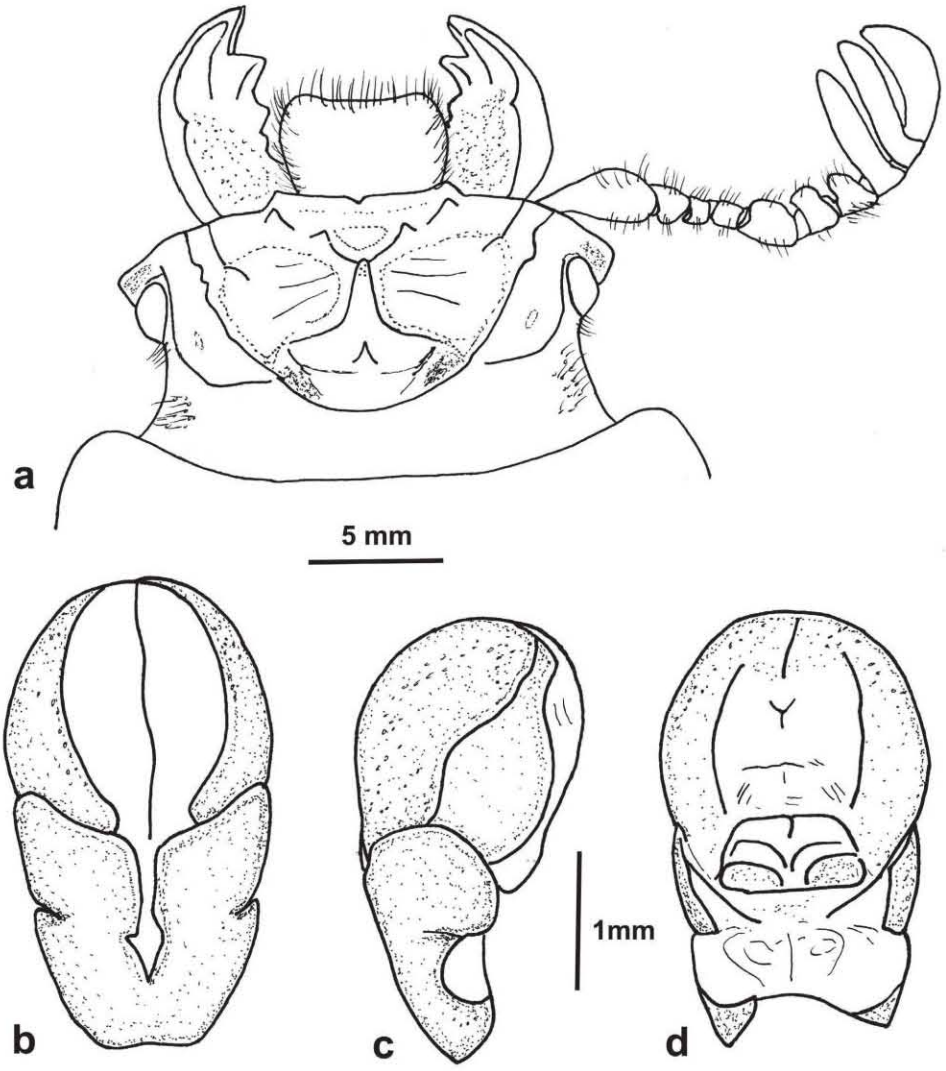

FIGURE 18. *Ogyges sandinoi*: a. dorsal aspect of head. b. ventral view of aedeagus. c. lateral view of aedeagus. d. dorsal view of aedeagus.

***Ogyges toriyamai* Cano new species**
Figs. 19–20, 21x

Diagnosis. *Ogyges toriyamai* seems closely related to *O. mutenroshii* from Cusuco National Park, by the size, the elytral and metasternal punctures and the medially constrained central horn. Is distantly similar to *O. nahuali* and *O. cavei* by the small and shallow elytral punctures, and by the strong punctures surrounding the metasternal disc. The new species is easily distinguished by the opaque aspect of elytra.

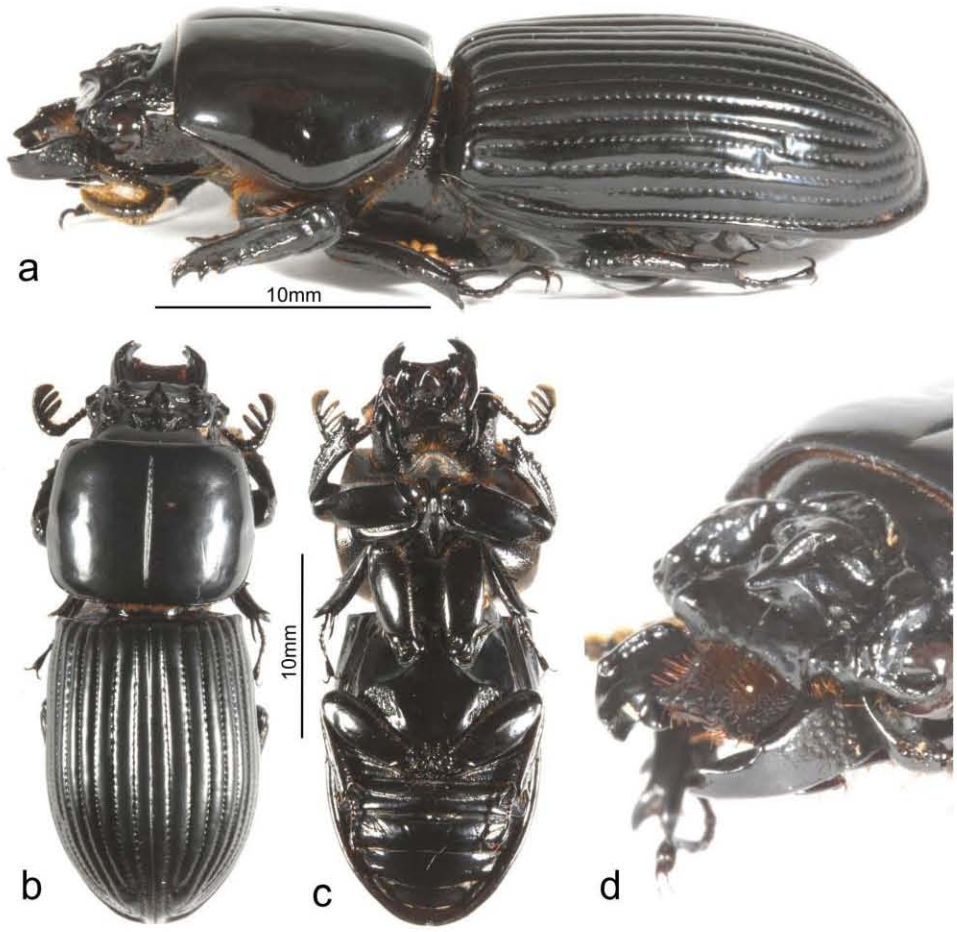

FIGURE 19. Holotype of *Ogyges toriyamai*: a. lateral view. b. dorsal view. c. ventral view. d. anterolateral view of head.

Description. Holotype male, black adult with blue iridescence. Total length 32.45, elytral length 17.26, pronotal length 9.05, pronotal width 11.58, humeral width 11.36. Head: anterior border of labrum slightly concave. Clypeus inclined; anterior border straight, with very small central invagination, without suture separating it from the mediofrontal area. Mediofrontal tubercles conical and well defined. Mediofrontal area smooth, without internal tubercles and posterofrontal ridges. A wide, bare, smooth fossa present in front of the mediopostfrontal structure. Lateropostfrontal areas wide, glabrous and coarsely rugose, anterior border strongly keeled with keel connected to mediopostfrontal structure. Central horn long, narrow, dorsally excavated on both sides to the level of the lateroposterior tubercles, with apex free and slightly directed upward, without median longitudinal groove posteriorly; lateroposterior tubercles somewhat elongate, joined at center to the posterior keel of the central horn. Postfrontal groove deep laterally. Supraorbital ridge with equal anterior tubercles; posterior 1/2 bifurcate with supraorbital fossa deep; external ridge well marked. Ocular canthus with apex straight or slightly swollen, ventrally covering the half of eye. Eyes reduced. Eye width = 0.5 mm. Interocular width = 6.31 mm. Head width = 8.0 mm; ratio both eye widths/head width = 0.12. Postorbital pits located immediately behind the external ridge oval and punctate. Ligula slightly protuberant basally, with small apical central tooth (eroded in old specimens), without

anterior ventral transversal carina and with setaceous punctures medially. Lateral lobes of mentum with abundant setose punctures; basal lateral scars oval, punctate setose and shagreened except on apical border; medial basal mentum bare and shiny, slightly rugose laterally. Hypostomal process elongate, without lateral depression, wide medially and narrow in apical third. Infraocular ridge present, short and smooth, surrounded by striate, setose punctures. Dorsal tooth of mandible occupies 1/2 length; internal dorsal face of mandible smooth. Antepenultimate antennomere of antennal club slightly longer (or subequal) than penultimate, less wide than the penultimate; antennal lamellae slightly concave dorsally (Figs. 19–20), 1.77 mm wide and 1.73 mm long.

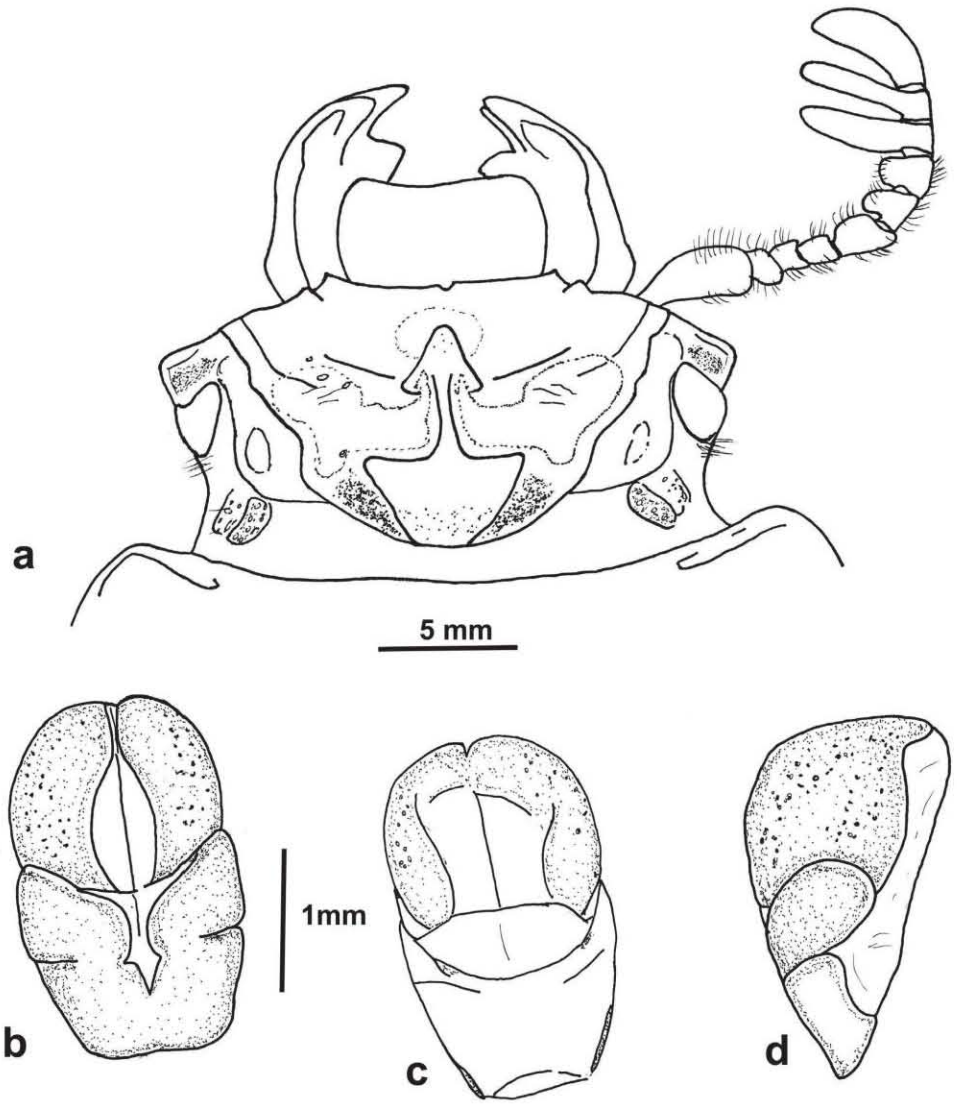

FIGURE 20. *Ogyges toriyamai*: a. dorsal aspect of head. b. ventral view of aedeagus. c. lateral view of aedeagus. d. dorsal view of aedeagus.

FIGURE 21. Details of suprainternal teeth of right mandibles (left in *O. cavei*) of the 25 known species of *Ogyges*: a. *O. adamsi*. b. *O. aluxi*. c. *O. cakchiqueli*. d. *O. cavei*. e. *O. championi*. f. *O. coxchicopi*. g. *O. crassulus*. h. *O. furcillatus*. i. *O. handali*. j. *O. hondurensis*. k. *O. kekchii*. l. *O. laevissimus*. m. *O. laurae*. n. *O. llama*. o. *O. marilucasae*. p. *O. menchuae*. q. *O. monzoni*. r. *O. mutenroshii*. s. *O. nahuali*. t. *O. politus*. u. *O. quichensis*. v. *O. ratcliffei*. w. *O. sandinoi*. x. *O. toriyamai*. y. *O. tzutuhili*.

Thorax: Lateral fossae of pronotum only with some micropunctures of rugose aspect, visible at great magnification. Pronotum with marginal groove narrow and smooth, laterally with abundant micropunctures of rugose aspect (striate), visible at great magnification; anterior angles rounded; disc smooth. Prosternellum brilliant at center, shagreened at anterior 2/5 and posterior 1/5. Mesosternum glabrous; lateral depressions elongate and rugose (shagreened). Mesepisternum with oval, elongate, shagreened area. Metasternum anterior angles glabrous; disc delimited by 38–40 well-marked punctures (some partially fused) on each side; marginal groove glabrous, narrow and slightly striate, posteriorly two times wider than medially.

Elytra: Opaque, with sparse blue iridiscence under direct light; striations marked and with defined punctures, markedly deeper and wider between striae 5–10; junctions of striations 1 and 10 with some extra punctures. Interstriae with abundant brown micropunctures visible at great magnification, particularly on interstriae 7–10. Scarcely minute setae on interstriae 2–6 on vertical anterior border of elytra.

Legs: Profemur with anterioventral groove marked; metafemur moderately widened; mesotibia with one or, occasionally, two spines (the second smaller).

Abdomen: Marginal groove of sternite VII incomplete, occupies 3/5 of sternite.

Aedeagus: In ventral view phallus globose; parameres and phallobase partially separated (Fig. 20).

Variation in paratypes (n = 3): Total length 28.29–31.06 ($\bar{x}$=30.00), elytral length 15.65–17.46 ($\bar{x}$ = 16.74), pronotal length 7.67–8.69 ($\bar{x}$ = 8.24), pronotal width 9.69–11.21 ($\bar{x}$ = 10.68), humeral width 9.26–10.48 ($\bar{x}$ = 10.09). Disc of metasternum delimited by 15–40 well-marked punctures (some partially fused and/or striated) on each side.

Material examined. 4 specimens.

Type material. Holotype: HONDURAS: Comayagua, Parque Nacional Cerro Azul Meambar, 14.87140, -87.90036, bosque nuboso, 800–1120 msnm. 20-24 V 2010. L. Sáenz. LSD 471. Paratypes: Same data as holotype (2 females); one specimen of unknown sex with the following data: Depto: Comayagua, Parque Azul Meambar, Agosto 30, 1996. Col. Marco Mendoza.

Holotype and paratypes deposited at UVGC.

Etymology. Named after Akira Toriyama, the Japanese artist creator of the manga and anime series "Dragon Ball".

Distribution. This species is known from the middle altitude cloud forest of the Cerro Azul Meambar National Park, in Comayagua Department, Honduras (Fig. 4).

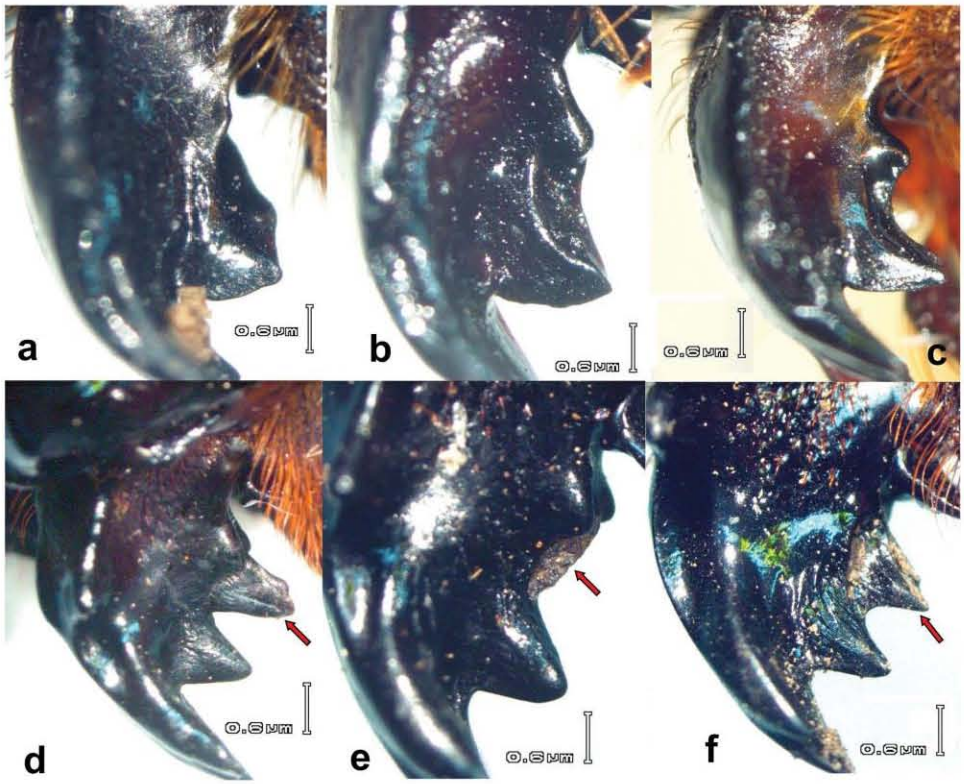

FIGURE 22. Details of suprainternal teeth of right mandibles of *Proculejus* and *Proculus*: a. *Proculejus nudicostis*. b. *Proculejus pubicostis*. c. *Proculejus sartorii* Kaup. d. *Proculus mniszechi* Kaup, teneral. e. *Proculus mniszechi*, old specimen. f. *Proculus opacipennis* (Thompson), teneral. Small arrows indicate the position or absence of dehicent (worn) tubercle in *Proculus*.

Key to species of adult *Ogyges* Kaup

The following modification to the key of Schuster *et al.* (2005) includes the 25 known species of the genus. For terminology see Fig. 1.

1 Internal tubercles noticeably large and united to the mediopostfrontal structure forming a bifid horn. Sierra de las Minas, Guatemala ..... ***O. furcillatus* Schuster & Reyes-Castillo**

\- Internal tubercles normal or absent, if larger than normal then not united forming a bifid horn 2

2 Dorsal elytral stria 1, or 1 and 2, deep; the remaining striae barely visible; anterior corners of metasternum with abundant to moderate setae, disc not delimited by punctures 3

\- All dorsal elytral striae marked, deep, or shallow but of equal depth; anterior corners of metasternum glabrous, with a few or with abundant setae, disc delimited or not by punctures 5

3 Internal tubercles absent; second elytral stria partially erased in anterior half; body length 33–39 mm. Volcanic chain in southwestern Guatemala ..... ***O. laevissimus* (Kaup)**

\- Internal tubercles present; second elytral stria not partially erased in anterior half; body length 30–43 mm. Southeastern Guatemala, El Salvador, and southwestern Honduras 4

4 Clypeus vertical; mesepisternum with distinct rugose (shagreened) area; metasternal marginal groove with abundant setae in anterior half; body length 37–43 mm ..... ***O. politus* (Hincks)**

\- Clypeus inclined (vertical in the only specimen from Volcán San Salvador); mesepisternum without rugose (shagreened) area; metasternal marginal groove glabrous or with 13 setae in anterior half; body length 30–38 mm ..... ***O. hondurensis* Schuster & Reyes-Castillo**

5 Internal tubercles present and well marked 6

\- Internal tubercles absent or obsolete 14

6 Antennal club notably wider than long, concave in dorsal view; wide of last antennomere at least three times its maximum length 7

\- Antennal club slightly longer than wide or equal, plane in dorsal view; wide of the last antennomere at most 2.5 times its maximum length 10

7 Anterior corners of metasternum with scattered long setae; body size 29–32 mm. Northwestern Nicaragua ..... ***O. sandinoi* Cano**

\- Anterior corners of metasternum bare or at most with a few minute setae; body size > 36 mm 8

8 Internal tubercles long, tips free for 1 mm; dorsal elytral striae without defined punctures; body length 36–37 mm. Mountains of northern Guatemala ..... ***O. tzutuhili* Schuster & Reyes-Castillo**

\- Internal tubercles short, free for at most 0.6 mm; dorsal elytral striae with clear punctures, body length 39–48 mm. Chiapas, Mexico and Honduras 9

9 Central horn very short, not projected; mediofrontal tubercles rounded by granulations; metasternal disc impunctate. Chiapas, Mexico ..... ***O. marilucasae* Reyes-Castillo & Castillo**

\- Central horn long and projected upward and forward; mediofrontal area smooth, without granulations; metasternal disc surrounded by strong punctures. Olancho and Comayagua, Honduras ..... ***O. cavei* Cano**

10 Clypeus vertical, with a marked change in the angle between the clypeus and the mediofrontal area; dorsal elytral striae with light punctures, frequently not clearly distinct, body length 24–34 mm 11

\- Clypeus inclined approximately 45°, without much difference in angle between clypeus and mediofrontal area; dorsal elytral striae with distinct punctures; body length 32–35 mm. Cuchumatanes range and Cuilco Mountain, Guatemala ..... ***O. cakchiqueli* Schuster & Reyes-Castillo**

11 Pronotum strongly punctate, rugose anteriorly and posteriorly near marginal groove; lateroposterior tubercles directed posteriorly; aedeagus with phallobase and parameres partially separated; body length 28–32 mm. Sierra de las Minas, Guatemala ..... ***O. coxchicopi* Schuster, Cano, & Boucher**

\- Pronotum with fine and very dispersed micropunctures; lateroposterior tubercles directed to the sides; aedeagus with phallobase and parameres completely separated; body length 22–34 mm 12

12 Elytral punctures not distinct or distinct only in striae 8–10; body length 26–34 mm. Chiapas, Mexico and Guatemala ..... ***O. championi* (Bates)**

\- Elytral punctures distinct, or at least distinct in striae 7–10 13

13 Internal tubercles small, less than 0.2 mm; internal tubercles nearer to respective mediofrontal tubercles than distance between them, body short (22–28 mm) or medium (to 34 mm), metasternal marginal groove slightly widened at distal portion, Alta Verapaz and Baja Verapaz, Guatemala ..... ***O. kekchii* Schuster & Reyes-Castillo**

\- Internal tubercles well developed but not surpassing 0.4 mm in length; internal tubercles separated by the same length between an internal tubercle and the respective mediofrontal tubercle; metasternal marginal groove narrow throughout its length. Quiché Deptment, in Guatemala ..... ***O. menchuae* Cano**

14 Metasternal disc delimited by strong punctures 18

\- Metasternal disc not delimited by punctures 15

15 With moderate long setae on anterior corners of metasternum, central horn with apex short and free. Cerro Montecristo in the junction of the Guatemalan-Honduras-El Salvador border ..... ***O. handali* Cano**

\- Without setae on anterior corners of metasternum (if present then minute and sparse near the coxal margin, and the central horn not free); central horn with apex free or not free. Chiapas, Mexico, northern Guatemala, and Honduras 16

16 Central horn largely free with base wide; lateropostfrontal areas with granulations; antennal lamellae almost as wide as long. Chiapas, Mexico and northern Guatemala ..... ***O. quichensis* Schuster & Reyes-Castillo**

\- Central horn not free or scarcely free; lateropostfrontal areas smooth; antennal lamellae very wide or a little wider than long. Honduras 17

17 Central horn scarcely free, directed upward; body with abundant blue reflections; antennal lamellae narrow and flat; metasternal marginal groove shagreened (opaque); body length 33 mm ..... ***O. ratcliffei* Cano**

\- Central horn not free; body without or with sparse blue reflections; antennal lamellae very wide and concave; metasternal marginal groove absent or poorly marked, smooth and shiny; body length 34–43 mm ..... ***O. adamsi* Schuster & Reyes-Castillo**

18 Dorsal elytra with indistinct to distinct but very shallow punctures, separated by at least 3 times their diameter; medial basal mentum impunctate 19

\- Dorsal elytra with strong and deep punctures, separated by at most one diameter; medial basal mentum with or without punctures 21

19 Elytra smooth and shiny, without blue reflections; prosternellum shiny on posterior half ..... ***O. mutenroshii* Cano**

\- Elytra opaque, with blue reflections; prosternellum opaque (shagreened) 20

20 Central horn dorsally wide at base. Eastern Honduras ..... ***O. nahuali* Schuster, Cano, & Boucher**

\- Central horn dorsally with sides constrained at middle. Western Honduras ..... ***O. toriyamai* Cano**

21 Large species, body length 32–37 mm; center mentum impunctate; central horn with apex free ..... ***O. aluxi* Schuster, Cano, & Boucher**

\- Medium to small species, body length 18–30 mm; center mentum with or without punctures, if impunctate, then body length less than 24 mm; central horn with apex free or not free 22

22 Mesotibia with one spine, posterior portion of central horn evanescent between lateroposterior tubercles, body length 18–23 mm. Eastern Honduras ..... ***Ogyges laurae* Cano**

\- Mesotibia with two spines, posterior portion of central horn tumose, body length 19–30 mm. Western Honduras 23

23 Central horn with apex clearly free; aedeagus with parameres and phallobase separated ..... ***O. monzoni* Schuster, Cano, & Boucher**

\- Central horn with apex not free or barely free; aedeagus with parameres and phallobase fused or separated 24

24 Posterior half of elytra with interstriae 7–8 measuring more than 2 diameters of one adjacent puncture; body length 24–30 mm; lateroposterior tubercles directed sideways ..... ***O. crassulus* (Casey)**

\- Posterior half of elytra with interstriae 7–8 measuring 1.0–1.5 diameters of one adjacent puncture; lateroposterior tubercles slightly directed forward ..... ***O. llama* Cano**

A novel diagnostic character that supports the monophyly of *Ogyges*

Kaup (1871: 69–70) described *Ogyges* to accommodate the species *Proculejus laevissimus* Kaup and *P. laevior* Kaup (=*Veturius laevior* (Kaup), according to Schuster *et al.* 2005), separating these from *Proculejus* by the shallow elytral striae and absence of setae on elytral sides ["von *Proculejus* unterscheiden sie sich durch die seichten Flügeldeckenfurchen und Mangel der Haare an den Seiten"]. Later, Kuwert (1896: 221) diagnosed *Ogyges* as a genus with clypeal margin formed by a strong bulge and humeri bare ["Clypeusrandung durch starke Wulstung entstanden. Schulterecken unbehaart"], separating it from *Proculejus* and *Proculejoides* Kuwert. In the rearrangement of New World genera of Passalidae, Reyes-Castillo (1970: 174-177) resurrected *Ogyges* (with *Proculejoides* as its junior synonym) and broadened and redefined the original scope of the genus (elytra bare, poorly marked striae, and convex clypeus) emphasizing in the lack of clypeofrontal groove, the form of the mediofrontal structure of "*marginatus*" type (central horn carinated, lateroposterior tubercles angular and adjacent to each side of horn) and the bidentate apex of mandible. These were the prevalent criteria to diagnose *Ogyges* that now are inapplicable due to the amount of species discovered in the past four decades (from six nominal species at 1970 to 25 valid species at present work). Moreover, Boucher (2006: 346) considered that the distinction from *Proculejus,* based only on the absence of clypeofrontal groove (the key character), is unconvincing.

Nevertheless, all the known species of *Ogyges*, including the new ones described herein, share an exclusive character state that was never considered in previous works: the symmetrical (same form present in both mandibles) and tridentate suprainternal teeth (Fig. 21). Each suprainternal tooth is widely divided into three tubercles: the superior is wider at base, acute at apex and slightly curved backward, while the inferior is smaller (less than half of superior), of conical to pyramidal shape and clearly divided to form another similar small, dorsal, well marked to obsolete (in old specimens) tubercle (Fig. 21). In ventral view the superior tubercle is slightly directed obliquely upward and the two inferior directed downward. In the sister group *Proculejus* the suprainternal teeth are bidentate (Fig. 22a–c), at least in the examined type specimens of *P. nudicostis* Bates, *P. obesus* Bates, *P. pubicostis* Bates, *P. ganglbaueri* (Kuwert), *P. brevis* (Truqui), *P. hirtus* (Truqui), *P. acapulcae* Kuwert, and *P. truquii* Kaup. On the other hand, in the sister group *Proculus* the suprainternal teeth present a characteristic

dehiscent or worn (in old specimens) (Gravely 1918: 10, Schuster *et al.* 2003: 284, Boucher 2006: 346) long and wide denticle (Fig. 22d–e), absent in all genera of passalids. I consider the form of suprainternal teeth of *Ogyges* an character state exclusive of the genus, found in all known species. Additionally, because this character state is well marked (except in old specimens), it can help to separate *Ogyges* from all other passalid genera in the New World.

Ogyges can be separated from most genera of the Proculini tribe except *Proculus* and *Proculejus*, and some species of *Xylopassaloides*, *Veturius* Kaup, and *Vindex* Kaup, by the presence of two apical teeth on mandible (instead of three). It can be separated from most species of *Proculejus* by the narrow metasternal marginal groove, the well marked profemoral ventral groove (except in some specimens of *O. tzutuhili*), the bare or scarcely setose anterior angles of metasternum, the bare epipleura and the absence of punctate setae along the lateral interstriae and pronotal lateral fossae (except from *P. nudicostis* and *P. obesus*, both species with tridentate mandible). From *Proculus*, it can be separated by its smaller size (18–46 mm, compared with *Proculus* 51–80 mm) and glabrous humeri. Some species of *Ogyges* with well-marked elytral striae can be confused with *Xylopassaloides*, but the circular (instead of squared) lateral punctures, smaller than the width of interstriae, distinguish it from *Xylopassaloides*. From the few flightless species of *Vindex*, it can be separated by the internal tubercles (when present) that do not reach the clypeus and the narrow metasternal lateral groove. From *Veturius* with bidentate apex of mandibles, it can be easily separated by the wider antennal club.

Acknowledgments

I thank the project "Faunistic Survey of the Dynastinae (Coleoptera: Scarabaeidae) of México, Guatemala, and Belize", led by Brett Ratcliffe and Ronald Cave, for support of Parataxonomists collecting scarabs (including Passalidae) in Guatemala. Also, I thank the project LLAMA, led by John Longino and Robert Anderson, for help in collecting material in Honduras and Nicaragua. I thank Laura Sáenz, Faustino Camposeco, José Monzón, and Alejandro González Madrid for specimens collected. I thank José Monzón for images of *Ogyges championi* of Fig. 1. For their help and hospitality when reviewing type material I specially thank Stéphane Boucher, MNHN, Paris; Pedro Reyes Castillo and Larry Jiménez Ferbans, IEXA, Xalapa, Veracruz; and Max Barclay, Malcolm Kerley, and María Peña, BMNH, London. The PAEP-UNAM and DIGED-USAC programs provided the funds for international visits to collections and museums. Financial support was partially provided by Consejo Nacional de Ciencia y Tecnología de Guatemala (CONCYT) under project 065-2006. For academic support I especially thank the Programa de Doctorado en Ciencias Biológicas of the Universidad Nacional Autónoma de México (UNAM), Escuela de Biología of Universidad de San Carlos de Guatemala (USAC), and Universidad del Valle de Guatemala (UVG). I thank Juan Morrone, Jack Schuster, Christoph Neumann, and two anonymous reviewers for comments on the manuscript. This work forms part of the doctoral thesis of Enio B. Cano.

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Capítulo 2

Los tipos primarios de *Ogyges* Kaup
(Coleoptera: Passalidae).

Los tipos primarios de *Ogyges* Kaup (Coleoptera: Passalidae)

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Resumen. Se presentan las imágenes, los datos registrados en las etiquetas, las coordenadas geográficas, mediciones, comentarios taxonómicos y las instituciones depositarias de 19 tipos primarios que fueron descritos o que están incluidos dentro del género *Ogyges* Kaup, 1871.

Palabras clave. *Veturius laevior, Arrox granulipennis*, holotipos, lectotipos, Guatemala, México, Honduras, El Salvador, bosque nuboso.

Abstract. Images, data registered in labels, geographic coordinates, measurements, taxonomic comments, and repository institutions of 19 primary types previously described or included within the genus *Ogyges* Kaup, 1871, are provided.

Key words. *Veturius laevior, Arrox granulipennis*, holotypes, lectotypes, Guatemala, México, Honduras, El Salvador, cloud forest.

Introducción

Ogyges Kaup, 1871, es un género monofilético de Passalidae que se distribuye en las montañas de Mesoamérica, desde Chiapas hasta el norte de Nicaragua. Fue revisado por Schuster y Reyes-Castillo (1990) y varias especies fueron adicionadas posteriormente por Schuster et al. (2005) y Cano (2014). Cuando me encontraba describiendo varias especies de *Ogyges* (Cano, 2014) y para clarificar su validez, tuve la necesidad de revisar los tipos primarios de las especies previamente descritas, así como de otros tres especímenes tipo que

originalmente habían sido descritos dentro de lo que ahora se considera *Ogyges*. Algunos especímenes fueron difíciles de localizar, particularmente porque en la revisión (Schuster y Reyes-Castillo, 1990), no se indicó el lugar de depósito del material. Por otro lado, cuando Cano (2014) describió nueve especies de *Ogyges*, incluyó imágenes de alta resolución y coordenadas precisas de las localidades tipo, con detalles que son potencialmente útiles para separarlas de las especies descritas. Así, los objetivos de este trabajo son proveer imágenes de alta resolución de los tipos primarios, que previo a Cano (2014), continúan o fueron incluidos en algún momento dentro del género *Ogyges*, junto con los datos de las etiquetas y las letras manuscritas de los autores, las coordenadas geográficas, las medidas y los nombres de las instituciones de depósito.

Materiales y métodos

Se revisaron los tipos primarios de las especies conocidas o incluidas previamente a Cano (2014) en *Ogyges*, excepto los de *O. laevissimus, O. crassulus, O. politus* y *Arrox granulipennis*, para lo cual se obtuvieron imágenes y datos por parte de los curadores; sin embargo, se revisó un paratipo de *O. politus*. Las medidas fueron tomadas con un vernier digital. La longitud total se midió desde el ápice de las mandíbulas abiertas, hasta la punta de los élitros. Todas las medidas están dadas en milímetros (excepto cuando se indica). Las coordenadas geográficas están dadas en grados decimales y las altitudes se presentan en metros sobre el nivel del mar. Las imágenes de los especímenes y las etiquetas fueron tomadas con una cámara Canon Eos Rebel con un macro de 100 mm y dos flashes, una cámara Nikon D5100 con un macro manual de 55 mm, sin flash, o con un sistema de automontaje. Los acrónimos de las colecciones citadas son los siguientes: Instituto de Ecología, Xalapa, Veracruz, México (IEXA); Muséum National d'Histoire Naturelle, París (MNHN); British Museum of Natural History, Londres (BMNH), Senckenberg Research Institute and Natural History Museum, Frankfurt, Alemania (SNM); Zoologische Staatssammlung, Munich, Alemania (ZSM); Senckenberg Deutsches Entomologisches Institut, Eberswalder, Alemania (SDEI), United States National Museum, Washington D.C. (USNM); Arthropod Collection, Universidad del Valle de Guatemala, Guatemala (UVGC).

Resultados

Se presentan las imágenes y comentarios de 14 holotipos (además de tres paratipos) y dos lectotipos (además de un paralectotipo) de 16 especies válidas de *Ogyges*. También se incluye el holotipo ("tipo") de una forma infrasubespecífica, no válida, de *Ogyges*, el lectotipo de una especie válida de *Veturius* originalmente descrita dentro de *Ogyges* y el lectotipo de una especie de *Arrox* Zang descrita bajo el género *Proculejoides* Kuwert (sinónimo de *Ogyges*). Los 19 tipos primarios aquí listados se encuentran depositados en IEXA (5), UVGC (6), USNM (1), SDEI (1), SNM (1), ZSM (2) y MNHN (3).

Recuento de los tipos primarios

***Ogyges adamsi* Schuster y Reyes-Castillo, 1990**

Holotipo, Figura 1

Ogyges adamsi Schuster y Reyes-Castillo, 1990: 10-12, 15; Schuster y Cano, 2005: 258-259, 2006: 67; Schuster, 2006: 383, 386; Schuster y Schuster, 1997: 264-265; Cano, 2014: 456, 473, 479, 482.

El holotipo proviene de un bosque nuboso en la Montaña Santa Bárbara, Santa Bárbara, Honduras (aproximadamente 14.899032, -88.13669, 2000 mnsm), colectado por P. Adams el 9 de Julio de 1968 (1968-12), y está depositado en IEXA. Las medidas son 39.95 (longitud total), 21.31 (longitud elitral), 13.35 (ancho humeral), 11.10 (largo del pronoto) y 14.29 (ancho del pronoto).

***Ogyges aluxi* Schuster, Cano y Boucher, 2005**

Holotipo, Figura 2

Ogyges aluxi Schuster, Cano y Boucher, 2005: 125-127; Schuster y Cano, 2006: 67; Schuster, 2006: 382, 386, 390; Cano, 2014: 460, 462, 479, 482.

Ogyges crassulus Schuster y Reyes-Castillo, 1990: 12-15 (*non* Casey); Schuster y Schuster, 1997: 263, 265 (*non* Casey).

Schuster y Reyes-Castillo (1990) confundieron esta especie grande (31-36 mm), con la pequeña (24-25 mm) *Proculejoides crassulus* de Casey (1897). Más tarde, Schuster et al. (2005) describieron esta especie como nueva. El holotipo, ligeramente teneral (café rojizo),

proviene de cerca de San Pedro Sula en Honduras (aproximadamente 15.583235, -88.091243, 1550 m), y se encuentra depositado en la UVGC. Las medidas del holotipo son: 34.55 (longitud total), 17.66 (longitud elitral), 10.90 (ancho humeral), 8.63 (largo del pronoto) y 11.53 (ancho del pronoto).

***Ogyges cakchiqueli* Schuster y Reyes-Castillo, 1990**

Holotipo, Figura 3

Ogyges cakchiqueli Schuster y Reyes-Castillo, 1990: 22-25, 30; Schuster, 1992: 361-362; Schuster et al., 2000: 200, 2005: 118; Schuster y Cano, 2005: 258-259, 262, 265, 2006: 62, 67; Schuster, 2006: 383, 389; Cano, 2014: 465, 479, 481.

Holotipo macho de Huehuetenango en la Sierra de los Cuchumatanes, Guatemala (aproximadamente 15.830617, -91.45027, 2575 m), se encuentra depositado en la UVGC. El espécimen se encontró sin la etiqueta de holotipo, sin embargo el número FT3 en la etiqueta (Figura 3e) hace referencia a que se trata de un espécimen único en esa colecta (J.C. Schuster, com. pers.), por lo cual se procedió a etiquetarlo correctamente, en concordancia con los datos de la descripción original. Las medidas del holotipo son: 34.5 (longitud total), 18.58 (longitud elitral), 10.84 (ancho humeral), 5.8 (largo del pronoto) y 11.2 (ancho del pronoto).

***Ogyges championi* (Bates, 1886)**

Lectotipo y Paralectotipo, Figuras 4-5

Proculejus championi Bates, 1886: 5-6; Kuwert, 1891: 192; Blackwelder, 1944: 190.

Proculejoides championi (Bates); Kuwert, 1897: 292; Arrow, 1906: 450; Gravely, 1918: 10, 47-48; Hincks y Dibb, 1935: 34; Blackwelder, 1944: 191 (también listado como *Proculejus*, p. 190).

Ogyges laevior Kuwert, 1897: 292 (*non* Kaup, 1868); Reyes-Castillo, 1970: 176; Schuster y Reyes-Castillo, 1990: 29-33; Schuster, 1992: 362; Schuster, 1993: 119; Reyes-Castillo, 2003: 167-168; Reyes-Castillo et al., 2006: 250.

Ogyges championi (Bates); Reyes-Castillo, 1970: 176-177; Schuster y Schuster, 1997: 263; Schuster et al., 2000: 200, 2005: 118; Schuster y Cano, 2005: 258-259, 2006: 62, 67; Schuster, 2006: 382, 389; Reyes-Castillo et al., 2006: 257, 261, 269; Chamé-Vázquez et al., 2010: 39; Gutiérrez-Velázquez et al., 2013: 290;

Cano, 2014: 465, 474, 479, 481.

Lectotipo (Figura 4), depositado en el MNHN, París, designado por Schuster et al. (2005). Dos paralectotipos de Purulhá colectados por Champion (1907), con la etiqueta circular de la *Biologia Centrali-Americana* en el MNHN de París, y otros tres especímenes en el BMNH, de Londres. Seis especímenes identificados por Bates, con los siguientes datos: Coban/ Vera Paz/ Conradt/ H.W. Bates [MNHN]/ Biol. Centr. Amer [MNHN]; BCA Coll., II (2) [BMNH]/, se encuentran en MNHN (1) y BMNH (5), pero no fueron incluidos en la publicación original por Bates (1886: 6), ni fueron mencionados en el "Supplement" (Bates, 1889). El paralectotipo de la Figura 5, designado por Schuster et al. (2005), es el "Species Figured" de Bates (1886 [como Figuras 5 y 5a]), colectado por Champion (1907) en Purulhá, Baja Verapaz, Guatemala (aproximadamente 15.215351, -90.219533, 1600 m), la misma localidad del Lectotipo del MNHN; la etiqueta de identificación original tiene la letra manuscrita de Bates y la etiqueta con el nombre *Proculejoides championi* corresponde a la letra manuscrita de Arrow.

***Ogyges coxchicopi* Schuster, Cano y Boucher, 2005**

Holotipo, Figura 6

Ogyges coxchicopi Schuster, Cano y Boucher, 2005: 121-123; Schuster y Cano, 2006: 62, 67; Schuster, 2006: 382, 389; Cano, 2014: 479, 481.

Holotipo macho de la Sierra de las Minas, Guatemala (aproximadamente 15.208838, -89.386491, 1500 m), depositado en la UVGC. Las medidas del holotipo son: 33.20 (longitud total), 17.49 (longitud elitral), 10.53 (ancho humeral), 8.56 (largo del pronoto) y 11.05 (ancho del pronoto).

***Ogyges crassulus* (Casey, 1897)**

Holotipo, Figura 7

Proculejoides crassulus Casey, 1897: 642-643; Gravely, 1918: 7; Hincks y Dibb, 1935.

Proculejoides crassula (Casey); Blackwelder, 1944: 191.

Ogyges crassulus (Casey); Reyes-Castillo, 1970: 176; Schuster et al., 2005: 119-121; Schuster y Cano, 2006: 67; Schuster, 2006: 382, 390; Cano, 2014: 479, 482.

El tipo, de sexo desconocido, fue colectado por Erich Wittkugel en la vecindad de San Pedro

Sula, Honduras (Casey, 1897: 640) y está depositado en el USNM. La colección privada de Casey fue heredada al USNM y trasladada muy poco tiempo después de su muerte, en 1925 (Buchanan 1935: 6), como lo indica la pequeña etiqueta escrita a máquina: CASEY/bequest/1925 (Figura 7e). Se sabe muy bien que Casey no etiquetaba los tipos de su colección; sin embargo, Casey indicó verbalmente que el espécimen que portara la etiqueta con el nombre de la especie, es el que debía ser considerado como el verdadero tipo (Buchanan, 1935: 7). Las medidas del tipo USNM 49202 (Figura 7) son similares a las publicadas por Casey (1897): 25.0 (longitud total), 13.5 (longitud elitral), 8.3 (ancho humeral), 6.7 (largo del pronoto), y 8.8 (ancho del pronoto). Como el individuo 49202 USNM es el único espécimen de *Proculejoides crassulus* que porta la etiqueta con el nombre "*crassulus*", es, por tanto, el holotipo. El holotipo es un espécimen teneral (café rojizo) con dos dientes apicales en la mandíbula (no tres, como dice Casey (1897: 642)). El nombre "Cropulus crassulus Cas.", de la etiqueta manuscrita del holotipo (Figura 7e), nunca fue publicado; por tanto, el probable nombre genérico "Cropulus" para el linaje "*crassulus*" de *Ogyges*, no está disponible (artículo 9.6, ICZN (1999)).

***Ogyges furcillatus* Schuster y Reyes-Castillo, 1990**

Holotipo, Figura 8

Ogyges furcillatus Schuster y Reyes-Castillo, 1990: 26-27, 30; Schuster, 1992: 361; Schuster y Schuster, 1997: 264-265; Schuster et al., 2000: 200; Schuster y Cano, 2005: 258-259, 2006: 62, 67; Schuster, 1993: 119, 2006: 382, 389; Cano, 2014: 479, 481.

Holotipo almacenado en etanol junto con dos larvas (una de primero y otra del tercer instar) y un isópodo, en la UVGC. Fue descrito de San Lorenzo en la Sierra de las Minas, Guatemala (aproximadamente 15.14932, -89.638422, 2200 m). Las medidas del holotipo son: 29.90 (longitud total), 16.23 (longitud elitral), 9.64 (ancho humeral), 7.21 (largo del pronoto) y 9.87 (ancho del pronoto).

***Ogyges hondurensis* Schuster y Reyes-Castillo, 1990**

Holotipo y Paratipo, Figuras 9-10

Ogyges hondurensis Schuster y Reyes-Castillo, 1990: 16-17, 24; Schuster, 1992: 362; Schuster y Schuster, 1997: 264; Schuster et al., 2000: 200, 2005: 119; Schuster y

Cano, 2005: 258-259, 263, 2006: 63, 67; Schuster, 2006: 383, 386, 389; Cano, 2014: 479, 481.

Holotipo (Figura 9) depositado en el IEXA. La Figura 10 es la imagen de un paratipo depositado en la UVGC, colectado en la montaña El Portillo, Departamento de Ocotepeque, Honduras (aproximadamente 14.465578, -89.075784, 1900 m), y que comparte los mismos datos de colecta con el holotipo. Las medidas del holotipo son: 35.54 (longitud total), 18.59 (longitud elitral), 11.08 (ancho humeral), 9.44 (largo del pronoto) y 12.2 (ancho del pronoto).

***Ogyges kekchii* Schuster y Reyes-Castillo, 1990**

Holotipo, Figura 11

Ogyges kekchii Schuster y Reyes-Castillo, 1990: 27-29, 40; Schuster et al., 2000: 200; Schuster y Cano, 2005: 258-259, 2006: 62, 67; Schuster, 2006: 382, 389; Cano, 2014: 465, 479, 481.

El holotipo macho está parcialmente fragmentado (lo que sugiere que fue colectado en piezas). Fue colectado en Purulhá, Alta Verapaz, Guatemala (aproximadamente 15.215351, -90.219533, 1570 m), y está depositado en el IEXA. Las medidas son: 24.35 (longitud total), 13.15 (longitud elitral), 8.54 (ancho humeral), 6.53 (largo del pronoto) y 8.47 (ancho del pronoto).

***Ogyges laevissimus* (Kaup, 1868)**

Lectotipo, Figura 12

Proculejus laevissimus Kaup, 1868: 15; Harold, 1868: 973; Hincks, 1953: 30-31; Hincks y Dibb, 1958: 10.

Ogyges laevissimus (Kaup); Kaup, 1871: 69-70; Kuwert, 1891: 192, 1897: 291; Arrow, 1906: 450; Reyes-Castillo, 1970: 174, 176; Schuster y Reyes-Castillo, 1981: 109; MacVean y Schuster, 1981; Schuster y Reyes-Castillo, 1990; Schuster et al., 2000: 200, 2003: 302; Boucher, 2004: 108, 2006: 346; Schuster y Cano, 2005: 258-259, 262-263, 2006: 63, 67; Schuster, 2006: 383, 389; Villegas-Guzmán et al., 2009: 3; Fonseca et al., 2011: 9; Cano, 2014: 452, 474, 479, 481, 482.

Oxyges laevissimus Wytsman, 1884: 337 (ortografía incorrecta, inválida, introducida por Kaup, 1871:58); Bates, 1886: 7; Zang, 1903: 419, enmienda a Wytsman.

Pseudacanthus laevissimus (Kaup); Hincks y Dibb, 1935: 21; Blackwelder, 1944: 190.

Ogyges laevissimus (Kaup) es la especie tipo del género *Ogyges*, de acuerdo a la designación de Hincks y Dibb (1935:20). Fue descrito por Kaup (1868) como de "Guatemala" basado probablemente en un único espécimen, considerando que en la actualidad solo se conoce un ejemplar tipo y que Kaup proveyó medidas exactas para ¿ese? espécimen: longitud total 16 líneas (33.87mm), protórax 4 líneas (8.47mm) y élitros 9 líneas (19.05mm) [Länge 16´´´, Oberbrust 4´´´, Oberflügel 9´´´]. Sin embargo, Boucher (2004) indica "an unstated number of specimens". El lectotipo (Figura 12) depositado en el ZSM, fue colectado por Moritz Wagner (Figura 12c), y designado por Boucher (2004). De acuerdo con Scherzer (en Wagner y Scherzer (1974: 17)), Moritz Wagner estudió los volcanes en El Salvador y experimentó el terremoto del 16 de abril de 1854, después de lo cual viajó a Guatemala y permaneció en Antigua Guatemala, desde donde visitó los volcanes vecinos [Volcán de Agua y Volcán de Acatenango). Es posible que el único espécimen tipo conocido fue colectado en uno de esos dos volcanes, donde la especie es muy común entre los 2300-3000 m (MacVean y Schuster, 1981). Por ejemplo, 10 especímenes del IEXA colectados el 8 de junio de 1974 por J. Hendrichs, entre los 2600 y 3000 m en el Volcán de Agua, fueron encontrados caminando. La especie fue descrita por Kaup (1868: 15) como *Proculejus laevissimus* (dice *Proc. laevissimus*, en la etiqueta manuscrita de la Figura 12c), indicando que fue depositada en el Museo de Munich [Münchener Sammlung].

***Ogyges marilucasae* Reyes-Castillo y Castillo, 1986**

Holotipo, Figura 13

Ogyges marilucasae Reyes-Castillo y Castillo, 1986: 147-148, 153; Luna-Zendejas et al., 1988: 309; Schuster y Reyes-Castillo, 1990: 30, 34-35; Schuster y Cano, 2006: 67; Schuster, 1993: 119, 2006; Reyes-Castillo, 2003: 168; Reyes-Castillo et al., 2006: 257, 261, 269; Chamé-Vázquez et al., 2010: 39; Cano, 2014: 465, 479, 481.

El holotipo macho proviene de la Reserva El Triunfo, Chiapas, México (aproximadamente 15.583465, -92.712404) y está depositado en el IEXA. Las medidas del holotipo son: 24.35 (longitud total), 13.15 (longitud elitral), 8.54 (ancho humeral), 6.53 (largo del pronoto) y 8.47 (ancho del pronoto).

***Ogyges monzoni* Schuster, Cano y Boucher, 2005**

Holotipo, Figura 14

Ogyges monzoni Schuster, Cano y Boucher, 2005: 123-125; Schuster y Cano, 2006: 67; Schuster, 2006: 382, 390; Cano, 2014: 479, 482.

El holotipo macho es un teneral café rojizo del Cerro Nylon, Morales, Izabal, Guatemala (aproximadamente 15.207997, -88.898599, 1250 m) y está depositado en la UVGC. Basado en observaciones personales los especímenes negros viejos de esta especie y otras del linaje "crassulus" (Schuster et al., 2005) frecuentemente presentan desgaste en los cuernos centrales, pero los cuernos son un carácter muy importante en la taxonomía de Passalidae. Así, la designación de especímenes tenerales, aunque son muy frágiles, provee un mejor apoyo para una clara definición de la especie. Las medidas del holotipo son: 27.73 (longitud total), 14.14 (longitud elitral), 9.34 (ancho humeral), 7.29 (largo del pronoto) y 9.64 (ancho del pronoto).

***Ogyges nahuali* Schuster, Cano y Boucher, 2005**

Lectotipo y Paratipo, Figuras 15-16

Ogyges nahuali Schuster, Cano y Boucher, 2005: 127-129; Schuster, 2006: 382; Cano, 2014: 469, 471, 476, 479, 482.

El holotipo macho (Figura 15) fue colectado a 16 kms del Parque Nacional "La Muralla", Departamento de Olancho en Honduras (aproximadamente 16.0981, -86.74038) y está depositado en el MNHN, París. Las medidas del holotipo son las siguientes: 33.96 (longitud total), 18.52 (longitud elitral), 11.11 (ancho humeral), 9.22 (largo del pronoto) y 11.97 (ancho del pronoto). La porción dorsal distal del cuerno central está gastada. Imágenes de un paratipo almacenado en la UVGC, en la figura 16.

***Ogyges politus* (Hincks, 1953)**

Holotipo y Paratipo, Figuras 17-18

Proculejus politus Hincks, 1953: 29, 31-32.

Ogyges politus (Hincks); Reyes-Castillo, 1970: 176; Virkki y Reyes-Castillo, 1972: 52, 55; Schuster, 1989: 695, 2006: 382, 387, 389; Schuster y Reyes-Castillo, 1990: 20-22, 24; Schuster et al., 2000: 200, 2005: 119; Schuster y Cano, 2005: 258-259, 263, 2006:

63, 67; Boucher, 2006: 298, 346, 308, 357; Cano, 2014: 479, 481.

La serie tipo proviene de un bosque nuboso en la Hacienda Montecristo (aproximadamente 14.415829, -89.357869, 2200 m), en el Cerro Montecristo, El Salvador, cerca de la frontera entre Guatemala, Honduras y El Salvador ("Trifinio"). El holotipo (Figura 17) con la palabra manuscrita "HOLO-" seguida de la tipografía "Typus", está depositado en el SNM, Frankfurt. El paratipo de la Figura 18 está depositado en la UVGC, con la tipografía "Para-typoid". Las medidas del paratipo de la UVGC son: 38.63 (longitud total), 21.19 (longitud elitral), 12.09 (ancho humeral), 10.31 (largo del pronoto) y 13.11 (ancho del pronoto).

***Ogyges quichensis* Schuster y Reyes-Castillo, 1990**

Holotipo, Figura 19

Ogyges quichensis Schuster y Reyes-Castillo, 1990: 15, 36-38; Schuster et al., 2000: 200, 2005: 119; Schuster y Cano, 2005: 258-259, 2006: 67; Schuster, 2006: 382, 389; Reyes-Castillo, 2003: 168; Reyes-Castillo et al., 2006: 257, 261, 269; Chamé-Vázquez et al., 2010: 39; Cano, 2014: 479, 482.

Holotipo hembra de Nebaj, Quiché, Guatemala (aproximadamente 15.374775, -91.712404, 2400 m), almacenado en etanol en la UVGC. Las medidas del holotipo son: 34.83 (longitud total), 18.83 (longitud elitral), 11.32 (ancho humeral), 8.76 (largo del pronoto) y 12.05 (ancho del pronoto).

***Ogyges tzutuhili* Schuster y Reyes-Castillo, 1990**

Holotipo, Figura 20

Ogyges tzutuhili Schuster y Reyes-Castillo, 1990: 37-40; Schuster et al., 2000: 200, 2005: 118-119; Schuster y Cano, 2005: 258-259, 2006: 62, 67; Boucher, 2006: 291; Schuster, 2006: 383, 389; Cano, 2014: 465, 479, 481, 483.

El holotipo proviene de Salamilá, Alta Verapaz, Guatemala (aproximadamente 15.393766, -90.067518, 2400 m) y está depositado en la IEXA. Las medidas del holotipo son: 37.05 (longitud total), 20.64 (longitud elitral), 11.74 (ancho humeral), 9.58 (largo del pronoto) y 12.57 (ancho del pronoto).

El tipo primario de una forma de *Ogyges*

***Ogyges laevior* ab. *vinculotaenia* Kuwert, 1897**

Tipo, Figura 21

Ogyges laevior ab. *vinculotaenia* Kuwert, 1897: 292.

Proculejoides championi ab. *vinculotaenia* (Kuwert); Hincks y Dibb, 1935: 34; Blackwelder, 1944: 191.

Ogyges championi (Bates); Reyes-Castillo, 1970: 176 (como *vinculotaenius*)

Ogyges laevior Schuster y Reyes-Castillo, 1990: 29, 32 (*non* Kaup, 1868).

Proculejus laevior ab. *vinculotaenia;* Boucher, 2006: 562.

La forma *vinculotaenia* fue descrita por Kuwert (1897: 292) basado en un material de San Salvador, El Salvador y subsecuentemente ha sido considerado como sinónimo de *Ogyges championi* (Bates) (vea Hincks y Dibb (1935: 34); Reyes-Castillo (1970: 176)), y miembro del clado *Proculejus*-*Ogyges* (Boucher, 2006: 562). La distribución geográfica de *O. championi* no coincide con la presencia de la forma *vinculotaenia* en San Salvador (la localidad probablemente se refiere al Volcán San Salvador, con bosque nuboso a 1800 m, actualmente llamado "Reserva El Boquerón", aproximadamente a 13.724248, -89.286862), donde sí se conoce otra especie de *Ogyges*, *O. hondurensis*. Así, el tipo de *vinculotaenia* corresponde a un espécimen mal etiquetado de *O. championi*, a una forma de *O. hondurensis* o talvéz a una forma del género mexicano *Proculejus*. Vi el espécimen tipo depositado en la Colección Oberthür del MNHN, en París (Figura 21), y concluyo, como ha sido indicado por autores previos, que es un miembro de la especie *O. championi* [probablemente de la población de Purulhá, Baja Verapaz, debido a que las estrías elitrales laterales son casi indistintas], lo cual apoya la hipótesis de que los datos de la localidad son erróneos. Las medidas del espécimen tipo (con la etiqueta de identificación manuscrita de Kuwert) son las siguientes: 34.38 (longitud total), 18.58 (longitud elitral), 11.65 (ancho humeral), 9.43 (largo del pronoto) y 11.86 (ancho del pronoto). De cualquier manera, el nombre *Ogyges laevior* ab. *vinculotaenia*, no está disponible, de acuerdo al artículo 45.6.2 del Código Internacional de Nomenclatura Zoológica (ICZN, 1999), debido a que "it is deemed to be infrasubspecific if its author used one of the terms "aberration", "ab." or "morph"", y, porque (artículo 45.5 y glosario en el Código) "a name which explicitly refers to an aberration unequivocally treated as an infrasubspecific entity, is unavailable".

Los tipos primarios de dos especies anteriormente incluidas en *Ogyges*

***Arrox granulipennis* (Zang, 1905)**

Lectotipo, Figura 22

Proculejoides granulipennis Zang, 1905: 229-231; Arrow, 1906: 450; Gravely, 1918: 7; Hincks y Dibb, 1935: 34; Blackwelder, 1944: 191.

Ogyges granulipennis (Zang)*;* Reyes-Castillo, 1970: 176.

Publius granulipennis (Zang)*;* Schuster, 1992: 360.

Arrox granulipennis (Zang); Boucher, 2006: 391-393.

Esta especie fue descrita originalmente por Zang (1905) como un *Proculejoides*, basado en dos especímenes de Tumbalá, Chiapas, México (aproximadamente 17.277075, -92.319330, 1500 m) y otro espécimen de una localidad no indicada de Chiapas. Reyes-Castillo (1970) sinonimizó *Proculejoides* con *Ogyges*, e incluyó *granulipennis* como una especie de *Ogyges.* Sin embargo, Schuster y Reyes-Castillo (1990: 5) excluyeron a *O. granulipennis* de *Ogyges*, sin argumentarlo y sin una reasignación formal (aunque lo consideraron dentro del complejo *Publius-Arrox-Veturius*). Posteriormente, Schuster (1992), cuando describió la larva, asignó *granulipennis* a *Publius* "because the specie conforms well to the larval description of the genus by Schuster y Reyes-Castillo (1981)". Recientemente, Boucher (2006), basado en un análisis filogenético morfológico y caracteres genitales, revalidó el género *Arrox* y transfirió *Publius granulipennis* a este género. Zang (1905: 231) indicó que él solo había visto un espécimen de Tumbalá en su colección, además de dos especímenes del Real Museo de Historia Natural de Berlin (uno de Tumbalá y otro más grande de otra localidad [Ein einzelnes Exemplar in meiner Sammlung. Im Kgl. Museum für Naturkunde, dem ich auch mein Stück zu verdanken habe, sah ich zwei weitere, von denen eins durch bedeutendere Gröfse und breiteres Stirnfeld abweicht und auch von einer yern Lokalität stammt.]. Aparte del espécimen de la Colección Zang, Boucher (2006: 391), revisó seis especímenes más de el Museum für Naturkunde de Berlin, y consideró a todos los especímenes como sintipos; el designó el espécimen de la Colección Zang del SDEI (Figura 22) como el lectotipo.

***Veturius laevior* (Kaup, 1868)**

Lectotipo, Figura 23

Proculejus laevior Kaup, 1868: 15-16; Harold, 1868: 973; Hincks, 1953: 30; Hincks y Dibb,

1958: 10.

Ogyges laevior (Kaup); Kaup, 1871: 70.

Pseudacanthus laevior (Kaup); Hincks y Dibb, 1935: 21; Blackwelder, 1944: 190.

Veturius laevior (Kaup); Boucher, 2004: 108; Schuster et al., 2005: 116-118; Boucher, 2006: 561-563; Cano, 2014: 482.

Veturius lineatosulcatus Luederwaldt; Schuster et al., 2005: 117-118 (sinónimo junior); Boucher, 2006: 561.

El nombre *Ogyges laevior* fue usado durante muchos años en el estudio de los escarabajos pasálidos de México y Guatemala. Schuster et al. (2005) demostraron que el epíteto específico *laevior* corresponde a una especie de *Veturius*, un género no relacionado (de acuerdo a Boucher (2006: 359, Fig. 240a)). Kaup en su "Prodromus" (1868: 15) describió esta especie bajo *Proculejus*, género que incluía ocho especies. En un trabajo posterior, cuando reorganizó los taxones para su monografía final, Kaup (1871) adoptó el sistema taxonómico quinario de Macleay (1821). En ese momento, el género *Veturius* consistía de cinco especies y estaba completo (vea Kaup 1871: 105), pero los otros géneros sin sutura frontoclipeal, *Proculus*, *Publius* y *Ogyges* estaban aún incompletos (vea Kaup, 1871: 58). Kaup puso a *P. laevior* en *Ogyge*s, probablemente basado en la presencia de estrías elitrales superficiales [puncturaciones indistintas] y la ausencia de setas en los lados de los élitros, caracteres que el usó para definir *Ogyges*. El género *Proculus* incluye especies gigantes y con humeros setosos; el género *Publius* en ese momento consistía de una sola especie en la tabla de Kaup, *P. crassus* (actualmente, *Veturius crassus*), que presenta las estrías elitrales bien marcadas. Aparte del hecho de colocar a *Veturius laevior* en un taxón no relacionado, derivado del pensamiento quinarista (también vea Boucher, 2006: 562), la rareza de la especie en las colecciones, los ambiguos datos de localidad [aus Guatemala oder Columbien] y la descripción poco detallada que hizo Kaup, pudo haber causado la confusión de los autores posteriores (particularmente Kuwert, 1896: 221, 1897: 292) con el nombre *laevior*, lo cual fue seguido por autores posteriores (excepto Hincks y Dibb, 1935, 1958 y Hincks, 1953). Detalles del lectotipo, depositado en el ZSM, fueron indicados por Schuster et al. (2005) y Boucher (2004, 2006). La especie solo ha sido colectada nuevamente en el Volcán Cacao, en Costa Rica (Schuster et al., 2005).

AGRADECIMIENTOS

Agradezco a Michael Branstetter por las imágenes del holotipo of *Ogyges crassulus*, a Katja Neven, Lars Hendrich y Michael Balke por las imágenes de los holotipos de *Ogyges laevissimus* y *Veturius laevior*, a Lutz Behne por las imágenes del holotipo de *Arrox granulipennis*, a Larry Jiménez por la imágen del holotipo de *Ogyges hondurensis*, a Cristian Beza por la imágen del paralectotipo de *Ogyges championi* y a Yrea Hastenpflug-Vesmanis por las fotografías del holotipo de *Ogyges politus*. Por su apoyo en la revision del material de colecciones agradezco a Stéphane Boucher, MNHN, París; a Pedro Reyes Castillo y Larry Jiménez Ferbans, IEXA, Xalapa, Veracruz; y a Max Barclay, Malcolm Kerley y María Peña, BMNH, Londres. Los programas PAEP-UNAM y DIGED-USAC proveyeron los fondos para las visitas internacionales a museos y colecciones. Por el apoyo académico agradezco especialmente al Programa de Doctorado en Ciencias Biológicas de la Universidad Nacional Autónoma de México (UNAM), a la Escuela de Biología de la Universidad de San Carlos de Guatemala (USAC) y a la Universidad del Valle de Guatemala (UVG). Agradezco a Juan J. Morrone, Jack C. Schuster, Christoph Neumann, Juan Márquez y Pedro Reyes Castillo por la revisión crítica del manuscrito original. Este trabajo forma parte de la Tesis Doctoral de Enio B. Cano.

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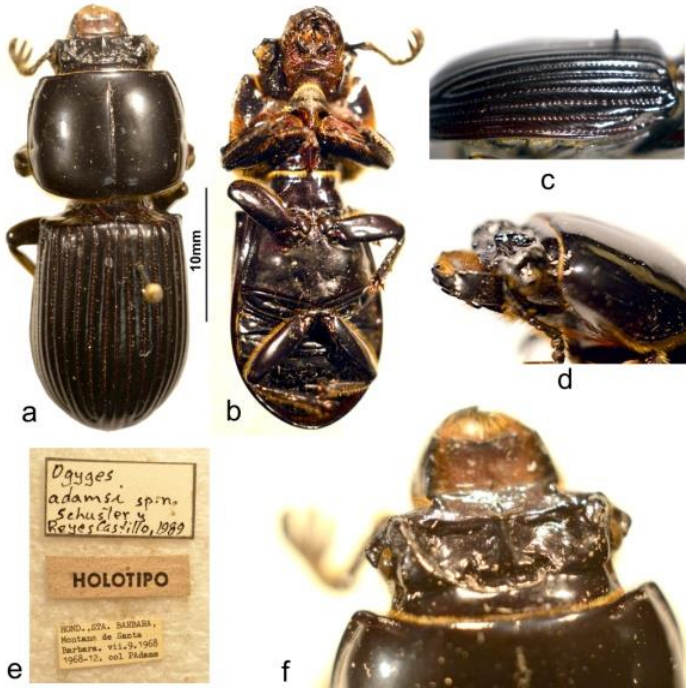

Figura 1. Holotipo de *Ogyges adamsi*. a. Hábito dorsal. b. Hábito ventral. c. Detalle lateral de los élitros. d. Vista anterolateral de la cabeza. e. Etiquetas. f. Vista dorsal de la cabeza.

Figura 2. Holotipo de *Ogyges aluxi.* a. Vista lateral. b. Hábito dorsal. c. Hábito ventral. c. Etiquetas. d. Vista ventral de la cabeza y el protórax.

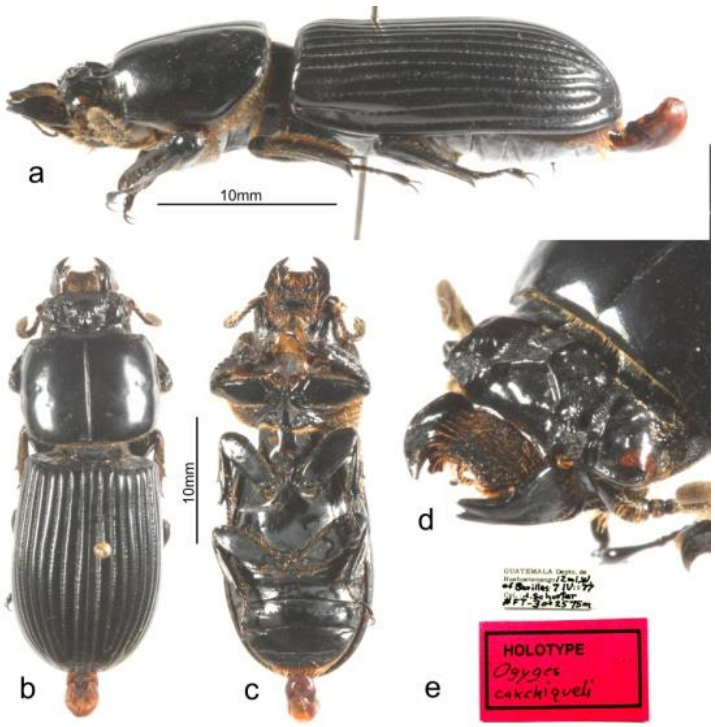

Figura 3. Holotipo de *Ogyges cakchiqueli*. a. Vista lateral. b. Hábito dorsal. c. Hábito ventral. d. Vista anterolateral de la cara. e. Etiquetas.

Figura 4. Lectotipo de *Ogyges championi*. a. Hábito dorsal. b. Vista lateral. c. Lado del élitro y estrías. d. Etiquetas.

Figura 5. Paralectotipo de *Ogyges championi*. a. Etiquetas. b. Vista lateral de los élitros. c. Vista dorsal de la cabeza. d. Vista ventral de la cabeza.

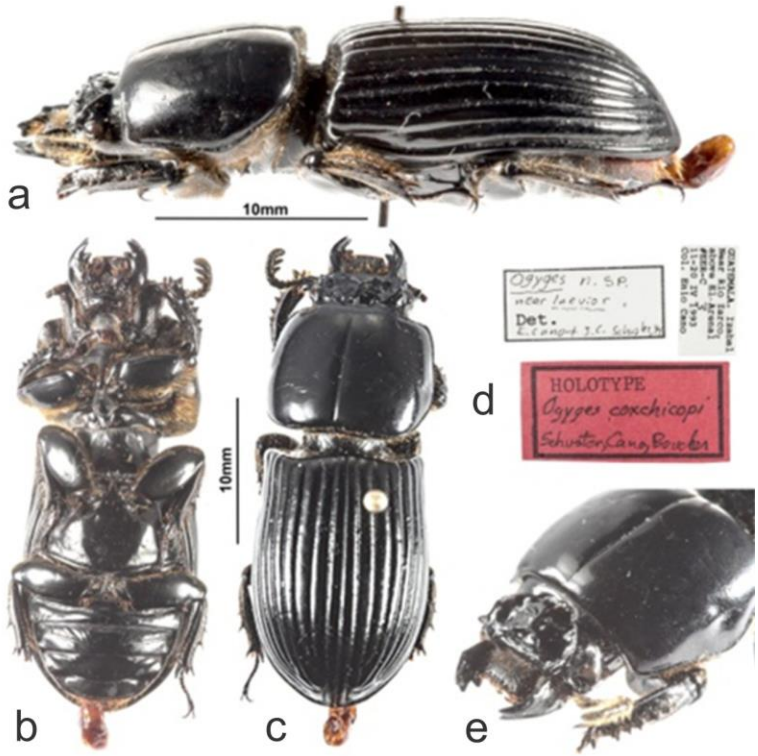

Figura 6. Holotipo de *Ogyges coxchicopi*. a. Vista lateral. b. Hábito ventral. c. Hábito dorsal. d. Etiquetas. e. Vista anterolateral de la cabeza.

Figura 7. Holotipo de *Ogyges crassulus*. a. Hábito dorsal. b. vista lateroventral. c. Vista ventrolateral. d. Vista dorsal de la cabeza. e. Etiquetas.

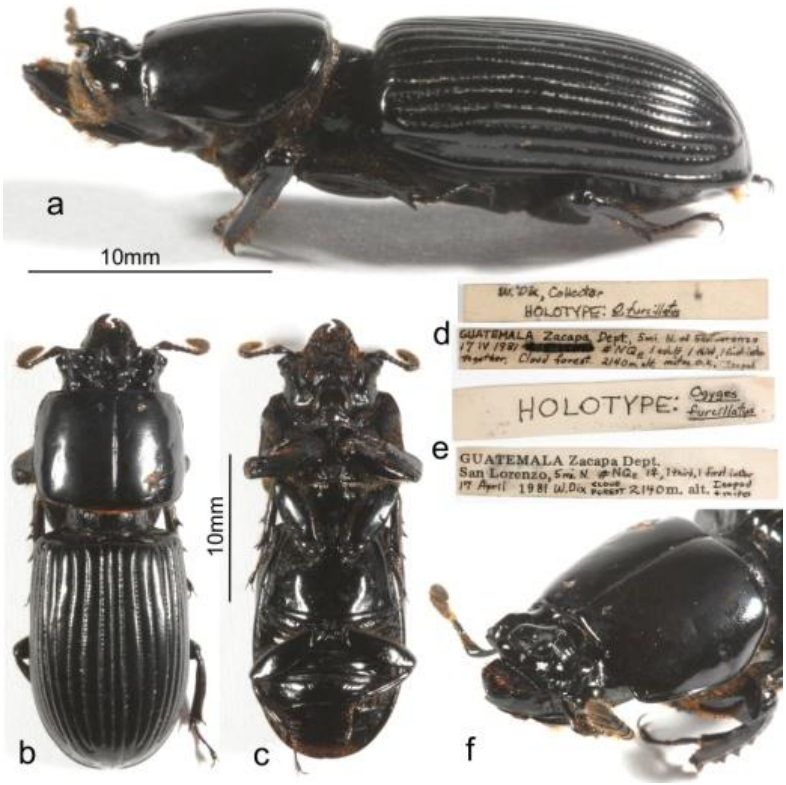

Figura 8. Holotipo de *Ogyges furcillatus*. a. Vista lateral. b. Hábito dorsal. c. Hábito ventral. d. Primera etiqueta con sus dos lados. e. Segunda etiqueta con sus dos lados.

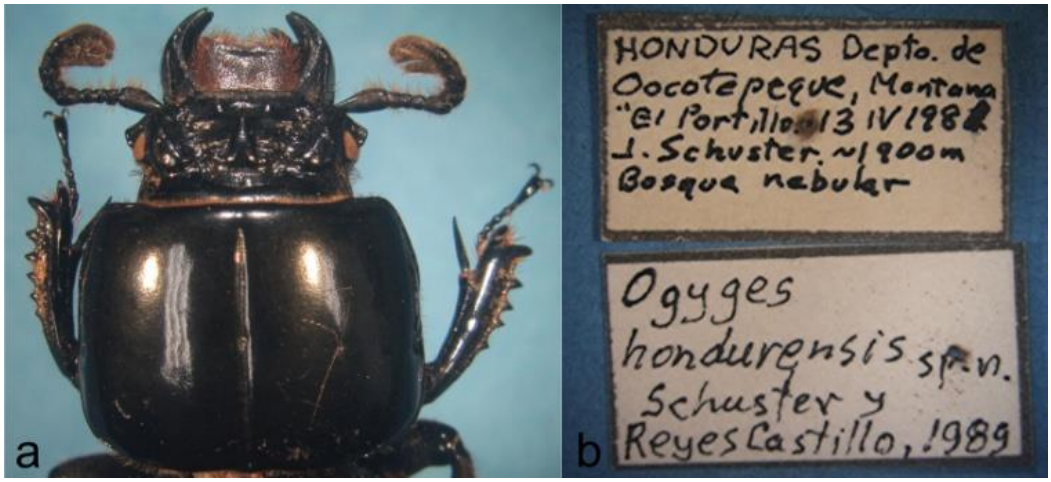

Figura 9. Holotipo de *Ogyges hondurensis*. a. Vista dorsal de la cabeza y protorax. b. Etiquetas.

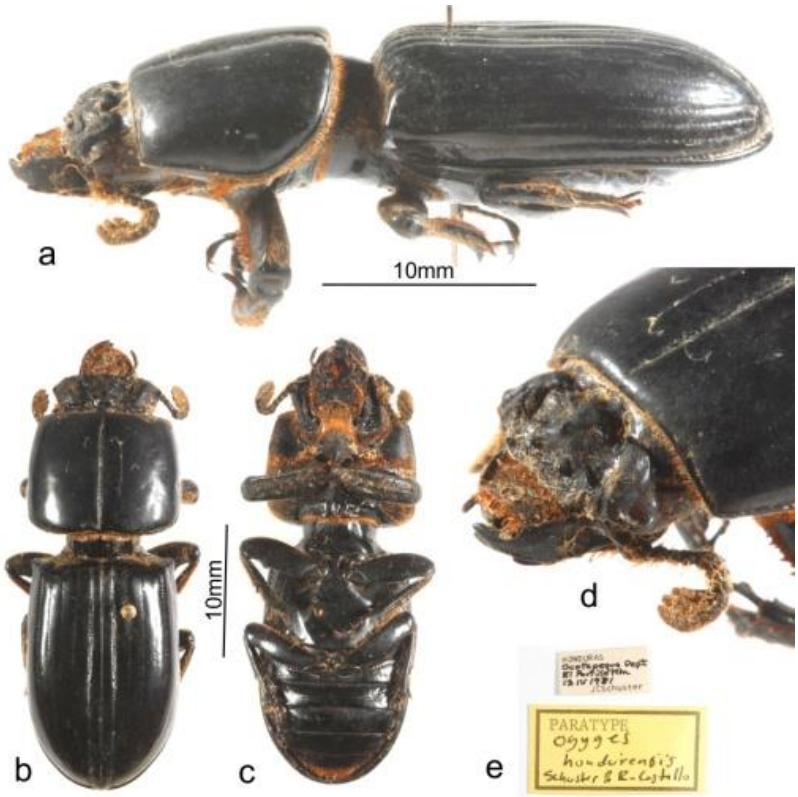

Figura 10. Paratipo de *Ogyges hondurensis*. a. Vista lateral. b. Hábito dorsal. c. Hábito ventral. d. Vista anterolateral de la cabeza. e. Etiquetas.

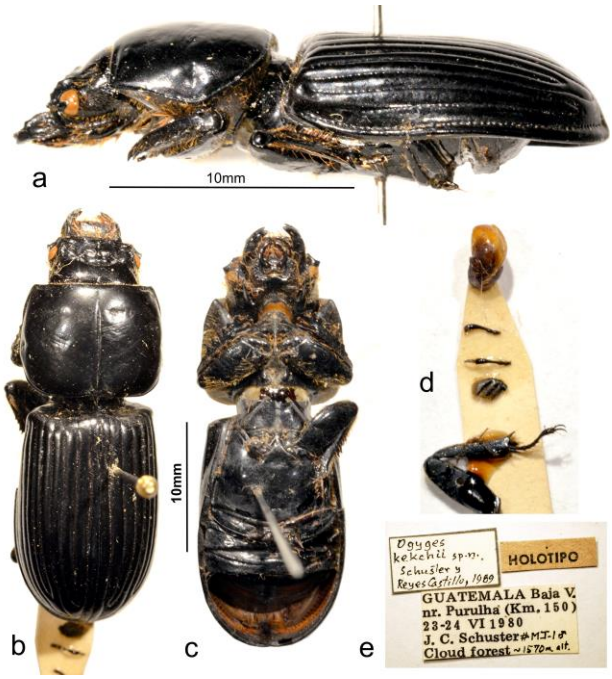

Figura 11. Holotipo de *Ogyges kekchii*. a. Vista lateral. b. Hábito dorsal. c. Hábito ventral. d. Detalle de fragmentos, incluyendo el edeago. e. Etiquetas.

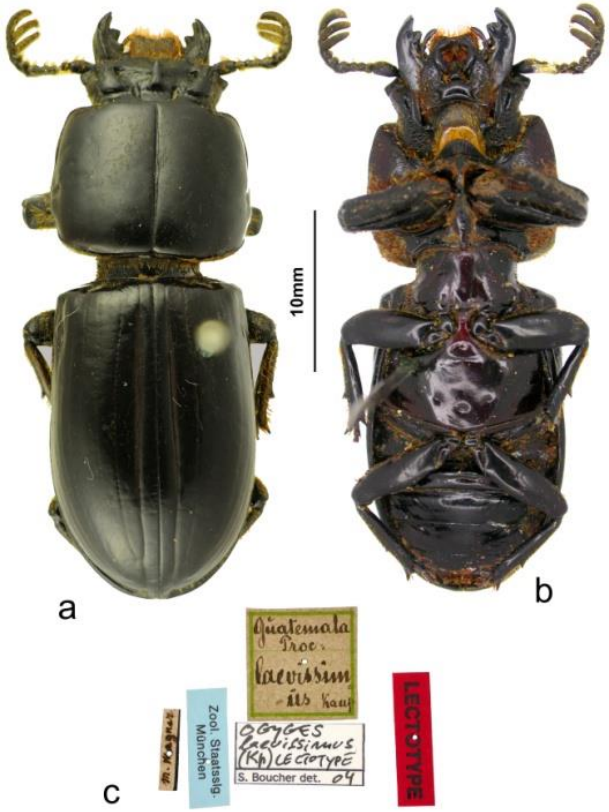

Figura 12. Lectotipo de *Ogyges laevissimus*. a. Hábito dorsal. b. Hábito ventral. c. Etiquetas.

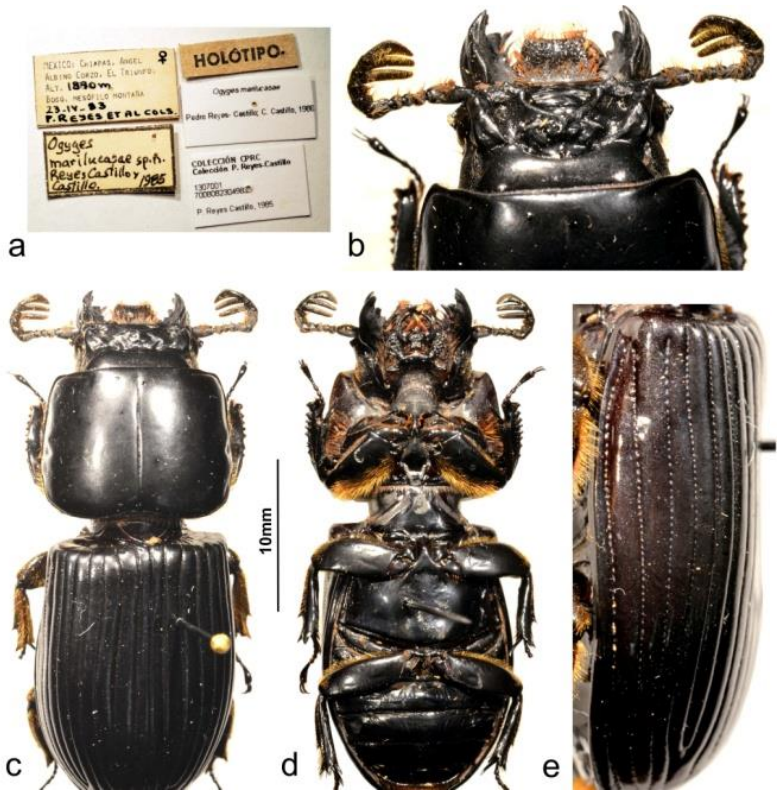

Figura 13. Holotipo de *Ogyges marilucasae*. a. Etiquetas. b. Vista dorsal de la cabeza. c. Hábito dorsal. d. Hábito ventral. e. Vista lateral de los élitros.

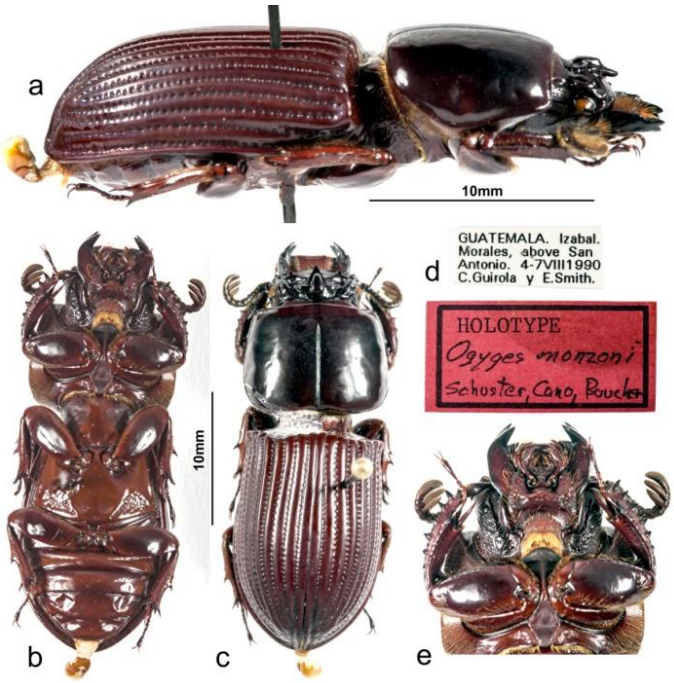

Figura 14. Holotipo de *Ogyges monzoni*. a. Vista lateral. b. Hábito ventral. c. Hábito dorsal. d. Etiquetas. e. Vista ventral de la cabeza y protorax.

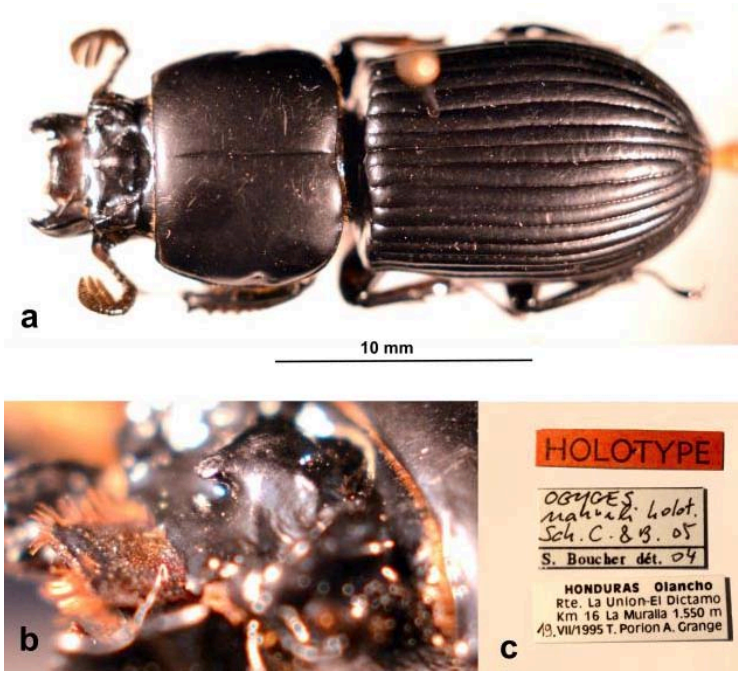

Figura 15. Holotipo de *Ogyges nahuali*. a. Vista dorsal. b. Vista anterolateral del cuerno central. c. Etiquetas.

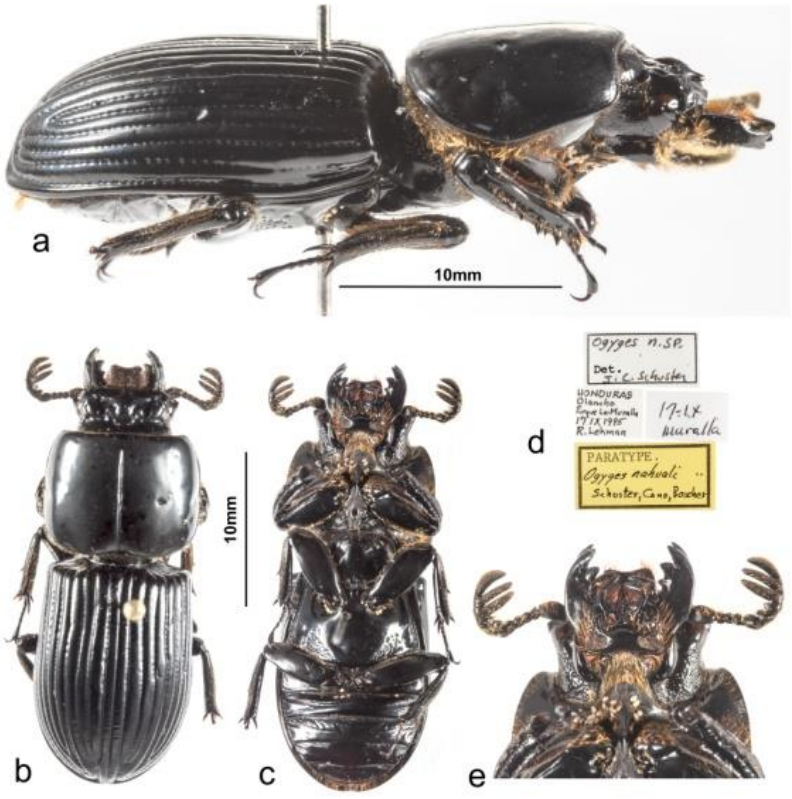

Figura 16. Paratipo de *Ogyges nahuali*. a. Vista lateral. b. Hábito dorsal. c. Hábito ventral. c. Etiquetas. d. Vista ventral de la cabeza y protorax.

Figura 17. Holotipo de *Ogyges politus*. a. Vista dorsal de la cabeza. b. Vista ventral del mentum. c. Vista lateral de la cabeza y mandíbulas. d. Etiquetas.

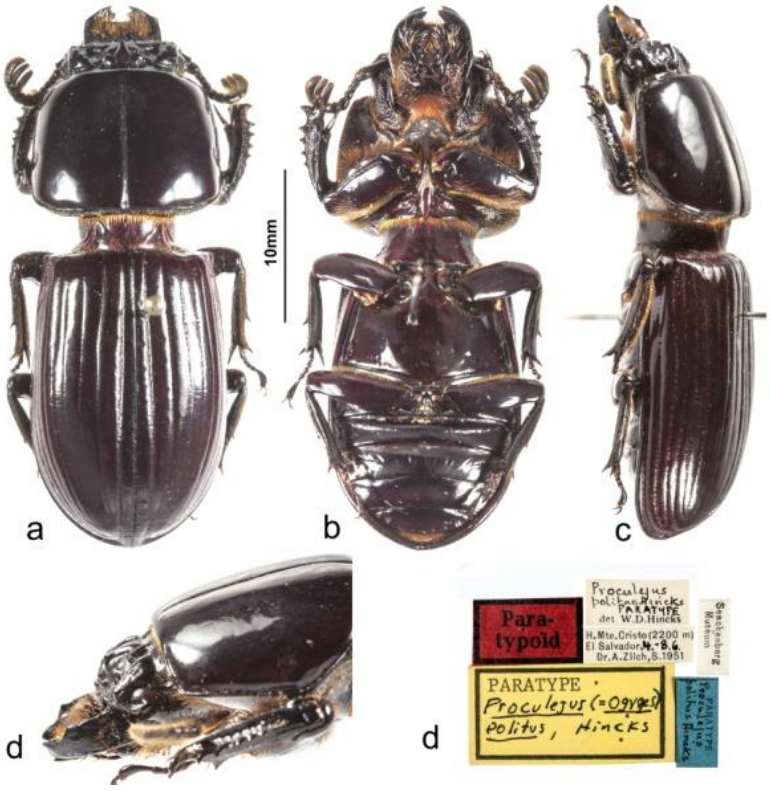

Figura 18. Paratipo de *Ogyges politus*. a. Hábito dorsal. b. Hábito ventral. c. Vista lateral. d. Vista lateral de la cabeza y protorax. e. Etiquetas.

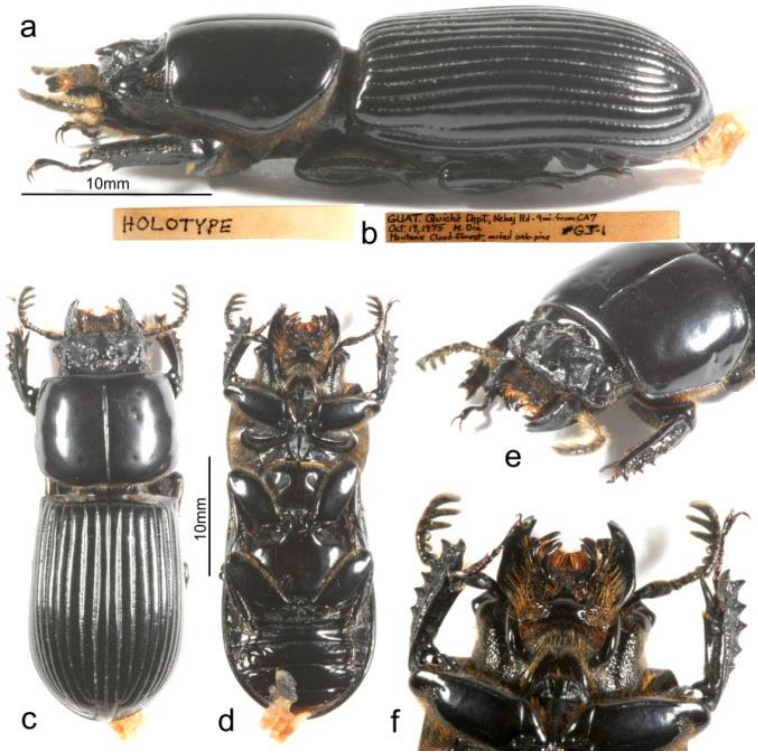

Figura 19. Holotipo de *Ogyges quichensis*. a. Vista lateral. b. Etiquetas. c. Hábito dorsal. d. Hábito ventral. e. Vista anterolateral de la cabeza. f. Vista ventral de la cabeza y protorax.

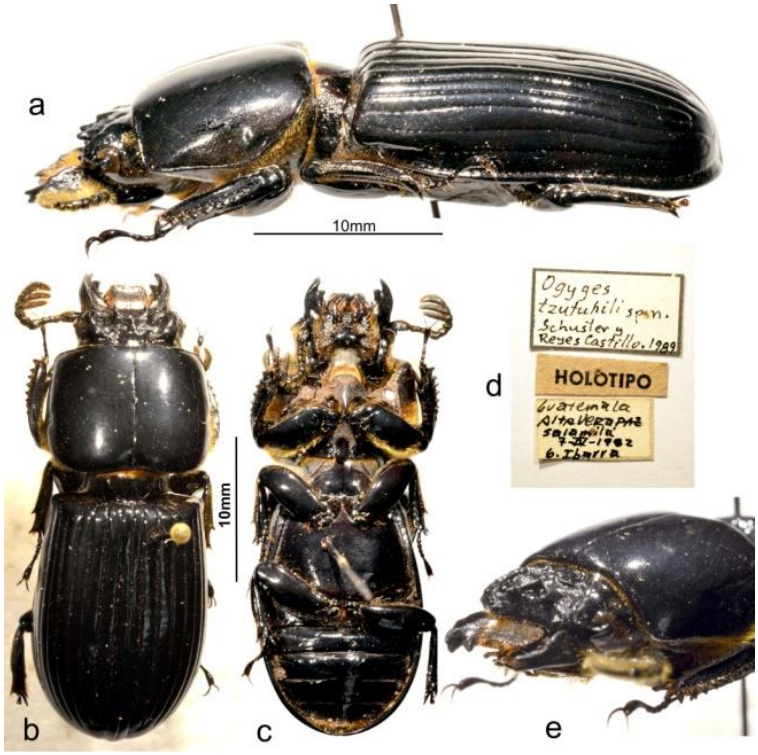

Figura 20. Holotipo de *Ogyges tzutuhili*. a. Vista lateral. b. Hábito dorsal. c. Hábito ventral. d. Etiquetas. e. Vista anterolateral de la cabeza.

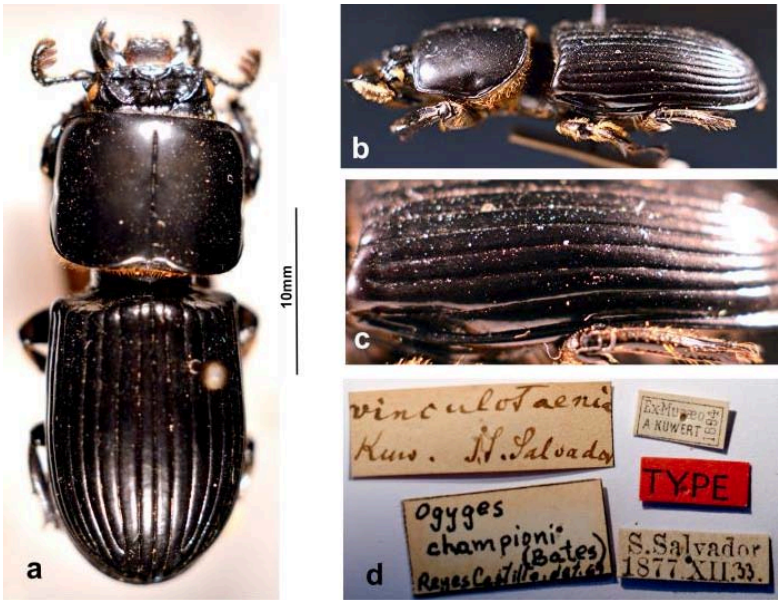

Figura 21. Tipo de *Ogyges laevior* ab. *vinculotaenia*. a. Hábito dorsal. b. Vista lateral. c. Detalle lateral de élitros y estrías. d. Etiquetas.

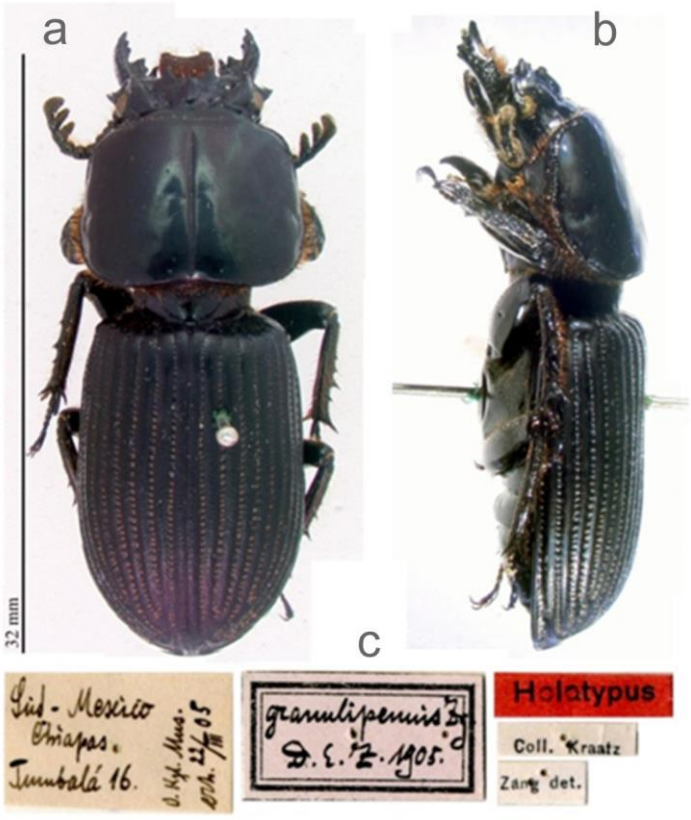

Figura 22. Holotipo de *Arrox granulipennis*. a. Hábito dorsal. b. Vista lateral. c. Etiquetas.

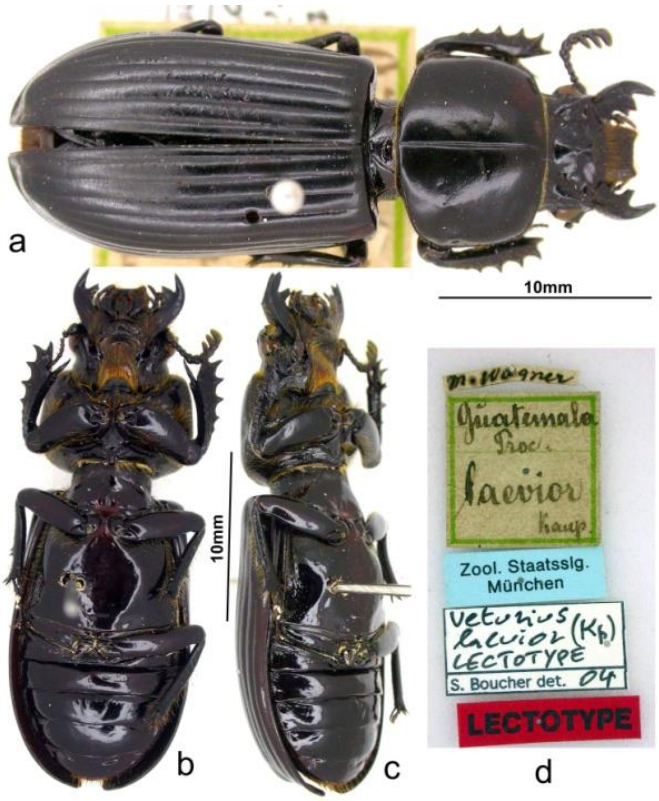

Figura 23. Lectotipo de *Veturius laevior*. a. Hábito dorsal. b. Hábito ventral. c. Vista ventrolateral. d. Etiquetas.

Capítulo 3

PHYLOGENETICS OF *OGYGES* KAUP (COLEOPTERA: PASSALIDAE) AND THE BIOGEOGRAPHY OF NUCLEAR CENTRAL AMERICA

PHYLOGENETICS OF *OGYGES* KAUP (COLEOPTERA: PASSALIDAE) AND THE BIOGEOGRAPHY OF NUCLEAR CENTRAL AMERICA

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ABSTRACT

We undertook a phylogenetic morphological analysis of the genus *Ogyges* Kaup, distributed in Nuclear Central America, from Chiapas, Mexico, to northwestern Nicaragua. *Proculejus* Kaup, distributed north of the Isthmus of Tehuantepec in Mexico, was selected as outgroup. *Ogyges* was recovered as monophyletic with three species groups: *O.* (*championi*), *O.* (*laevissimus*) and *O.* (*crassulus*). Each species group shows a distinct, generally allopatric distribution. The *O. championi* species group, with 10 species, is distributed in the Maya block, more specifically in the mountainous system north of Motozintla-Comaltitlán fault in Chiapas, and north of the dry valleys of the Cuilco and Motagua rivers in Guatemala. The two remaining species groups are distributed in the Chortís block. The *O. laevissimus* species group, including 7 species, runs mostly along the Pacific Volcanic Chain from Guatemala to El Salvador, and from southeastern Honduras to the northwestern border in Nicaragua. The *O. crassulus* species group, with 10 species, is distributed from northeastern Guatemala (Merendón) to northern Honduras. The Isthmus of Tehuantepec in Mexico, the Motagua-Cuilco and Motozintla-Comaltitlán sutures zones in Chiapas and Guatemala, the lowland valleys of Colón and Comalí rivers between Nicaragua and Honduras (or perhaps, the northern suture of the Siuna Terrane in Nicaragua), the Guayape fault system in Honduras, and the intricate dry valleys of Ulúa-Chamelecón-Olancho in Honduras, are hypothesized to have acted as barriers that affected the geographical distribution of *Ogyges,* as well as

probably other montane organisms.

INTRODUCTION

Nuclear Central America (Schuchert, 1935), the mountainous region comprising Chiapas (México), Guatemala, Belize, El Salvador, Honduras and northern Nicaragua, is characterized by several large and high mountain and volcanic ranges reaching 4222 m altitude, separated by deep and dry valleys, with the consequent isolation and independent evolution of populations. With few exceptions (*e.g.,* Wake and Lynch, 1976; Johnson, 1989; Campbell and Frost, 1993; Townsend, 2014; Pérez-Consuegra and Vásquez-Domínguez, 2015), its biotic relevance has been overlooked by biogeographers, and phylogenetic analyses of taxa endemic to this area are scarce. The area has been treated as the Chiapas Highlands biogeographic province (Morrone, 2014), which is part of the Mexican transition zone (Halffter, 1987; Morrone, 2015). Its transitional nature, with a "mixture" of Nearctic and Neotropical biotic elements, has somewhat obscured the analysis of the diversification of particularly speciose taxa, such as plethodontid salamanders (Campbell *et al*. 2010; Townsend 2014; Rovito *et al*. 2015), cricetid mice (Conroy *et al*., 2001; Gutiérrez-García and Vásquez-Domínguez, 2012, 2013; Ordóñez-Garza *et al*., 2014; Pérez-Consuegra and Vásquez-Domínguez 2015), squamates (Campbell and Frost, 1993; CampbelI and Brodie, 1999; Castoe *et al*., 2003; Hasbún *et al*., 2005) and beetles (Schuster, 1993; Micó *et al*., 2006; Cano, 2014; Sokolov and Kavanaugh, 2014).

Ogyges Kaup, a flightless genus of the saproxylophagous family Passalidae, consists of 25 described species restricted to the cloud forests of Chiapas to northern Nicaragua (Cano, 2014). A phylogenetic morphological analysis recovered *Ogyges* as monophyletic and closely related to the also flightless genera *Proculus* and *Proculejus* (Boucher, 2006). Cano (2014) showed that the shape of the suprainternal mandibular tooth represents a synapomorphy for the species of *Ogyges*. *Proculus* includes some gigantic species with many autapomorphies, distributed in Nuclear Central America from the Chimalapas region, Oaxaca (Delgado and Mora-Aguilar, 2014), to northern Honduras, being also probably distributed in the Chocó area in Colombia (Schuster *et al*., 2003). *Proculejus* is distributed in Mexico north of the Isthmus of Tehuantepec (Reyes-Castillo, 1970; Boucher, 2006) and is rather similar to *Ogyges*, except for the presence of a frontoclypeal suture and a different form of suprainternal

mandibular tooth. (The recent discovery of a new Honduran species with a clearly marked suture on the frontoclypeus makes it difficult to place it in either genus.)

We undertook a phylogenetic morphological analysis to test the monophyly of *Ogyges*, including the new Honduran species, using five species of *Proculejus* as an outgroup. Based on the resulting cladogram, we conducted a biogeographical analysis to describe and analyze the barriers and areas of distribution, applying the results in an analysis of the biogeography of Nuclear Central America in an evolutionary framework.

MATERIAL AND METHODS

We studied 1071 adult specimens (see Appendix), belonging to 32 species, deposited in the following collections:

BMNH	The Natural History Museum, London, Great Britain.
IBUNAM	Instituto de Biología, Universidad Nacional Autónoma de México, México, D.F., México.
INECOL	Instituto de Ecología, Xalapa, Veracruz, México.
JYC	Jiichiro Yoshimoto, private collection, Guatemala city, Guatemala.
MNHN	Muséum National d'Histoire Naturelle, Paris, France.
RC	Ronald D. Cave, private collection, Fort Pierce, Florida, USA.
USAC	Universidad de San Carlos de Guatemala, Guatemala City, Guatemala.
UVGC	Universidad del Valle de Guatemala, Guatemala City, Guatemala.

For terminology we follow Boucher (2006), which is based on well-sustained homologies (see Cano, 2014: 452-453). Total length was measured from the tip of open mandibles to the terminal tip of elytra, taken with a digital vernier caliper. Drawings were made using a drawing tube in a Wild Heerbrugg M3B stereomicroscope. Images were taken with a Nikon D5100 camera with macro lens and processed with the Microsoft Digital Image Pro software.

Outgroup selection

We performed a preliminary phylogenetic morphological analysis (Maximum Parsimony) using the flightless genera *Proculejus* and *Proculus* as outgroups, as signaled by Boucher (2006: 359). *Ogyges*, *Proculus* and *Proculejus* were recovered as monophyletic, and related.

A complementary preliminary phylogenetic molecular analysis (12S rRNA) (Cano *et al*. unpublished) also recovered *Proculus* as monophyletic, but unrelated to *Ogyges*. *Proculus* has several synapomorphies and is easily distinguished from both *Ogyges* and *Proculejus*; but, confusion over the boundaries between *Ogyges* and *Proculejus* have remained constant along their taxonomic history. For this reason, and because of the homoplasy involved in flightlessness, we used five species of *Proculejus* as an outgroup in our analysis and selected the flying species *Oileus sargi* Kaup, to root the cladograms.

Character analysis

A total of 53 morphological characters were taken from external structures (48) and male genitalia (5). The distribution of character states is shown in Table 1. Multistate characters (1, 2, 7, 8, 14, 17, 19, 22, 26, 30, 32, 33, 34, 36, 39, 40, 45, and 52) were treated as non-additive, and characters 7, 22, 33, and 45 were treated as additive. Inapplicable characters, those that describe variation with respect to the shape of some feature that is entirely absent in some taxon (Harris *et al*., 2003: 249), were avoided, except for characters 1, 9 and 46.

Alar reduction is widely present in several unrelated genera and species of Passalidae. Brachypterism, together with the associated morphological modifications, shared by all species of *Ogyges*, is a potential synapomorphy of this taxon. Nevertheless, in order to clarify the relationships with *Proculejus*, also brachypterous, we only considered the humeral callus of elytra (character 43) to separate from the outgroup species *Oileus sargi* and *Proculejus nudicostis*. The bluish iridescence (character 45), when present, is distributed on many areas of the body; thus, to avoid overweighting this character, we considered it only once in the analysis.

List of selected characters

0. Frontoclypeal suture: (0) clearly present and deep; (1) absent.

1. Clypeus: (0) delimitated from frons by a complete strong transversal impression; (1) with a shallow incomplete or insinuated delimitation with some granulations; (2) flat, without any indication of separation (although an inflexion is present in the species with vertical clypeus). Non-additive.

2. Clypeus: (0) very thick; (1) thin; (2) thick. Non-additive.

3. Clypeus: (0) inclined; (1) vertical.

4. Small (not minute) punctures on frons: (0) absent; (1) present.

5. Internal tubercles: (0) present (Fig. 1 b); (1) absent. The hyperthelic internal tubercles in *O. furcillatus* are fused to the, also hyperthelic, posterofrontal ridges (character 8).

6. Lateroposterior tubercles (Fig. 1b): (0) well marked; (1) barely marked.

7. Lateropostfrontal areas (frontal fossae) (Fig. 1b) with granulations: (0) absent; (1) present, scarce (almost smooth); (2) present, densely abundant. Additive. When present, granulations are distributed on areas of frons and vertex, particularly around epicranial sutures (Boucher, 2006). We assume covariation in this character and, in order to avoid double weight we only considered granulations on the frons, except those clearly different of the epicranial sutures (character 10).

8. Posterofrontal ridges (Fig. 1b): (0) absent; (1) present, posterior position in origin ("angle"), not surpassing the position of eyes ("championi" type) (Fig. 3a); (2) present, defined or diffused, anterior position in origin ("angle"), at level or surpassing the position of eyes ("laevissimus" type) (Fig. 3b). Non-additive. Although in the original description Schuster and Reyes-Castillo (1990) indicate that *O. furcillatus* lacks posterofrontal ridges, the assumption of presence of internal tubercles by the authors suggest a fusion of both characters. We assume the presence (as hyperthelic) in *O. furcillatus*. In *O. quichensis,* the development of the posteriorly massive center horn, at the level where the junction of lateroposterior tubercles ("angle") should be, obscures the presence of the character; nevertheless, most specimens present a ridge very posterior to the level of the eyes and we consider that, although not lineal (due to a modification in the center horn, of a kind of the *O. furcillatus*), the posterofrontal ridge corresponds to the "championi" type. In *P. pubicostis*, *P. nudicostis* and *O. cavei* the ridge is anterior.

9. Posterofrontal ridges: (0) linear, clearly marked alongside; (1) tumose anteriorly at sides of horn, and then conforming a clear (or diffuse) keel marking the anterior margin of lateropostfrontal areas (frontal fossae). State 1 has not been considered by Cano (2014) and Schuster and Reyes-Castillo (1990) as presence of the posterofrontal ridges ("quillas frontales" or frontal ridges). After a careful examination of tenerals and specimens cleared with KOH we conclude that state 1 of this character is homologous but distinct from character state 0 of the typical *O. championi*.

10. Area between laterofrontal tubercles and epicranial suture: (0) not shagreened; (1) shagreened.

11. Dorsal groove of center horn: (0) absent or unclear; (1) present, clearly marked (Fig. 1b).

12. Length of center horn (base to tip): (0) short; (1) long.

13. Sides of postfrontal groove: (0) shallow; (1) deep.

14. Supraocular fossae: (0) absent; (1) present, shallow; (2) present, deep; (3) present, very deep (Fig. 1b). Non-additive.

15. Postoorbital pits (Fig. 1b): (0) shallow; (1) deep.

16. Apex of ocular canthus: (0) acute; (1) rounded.

17. Antennal club size: (0) normal, almost as long as wide; (1) wider than long, wide of last antennomere at most 2.5 times its maximum length; (2) very wide, wide of last antennomere at least tree times its maximum length. Non-additive.

18. Antennal club in dorsal view: (0) flat; (1) concave.

19. Dorsal mandibular area facing dorsal tooth: (0) smooth; (1) granular; (2) granular punctate-striate (or abundantly granular). Non-additive.

20. Number of teeth of mandibular apex: (0) three, same size (Fig. 2a); (1) two, almost same size (Fig. 2b).

21. Suprainternal teeth: (0) asymmetrical (Figs 2c, 2d); (1) symmetrical.

22. Left suprainternal teeth: (0) superior large and bifurcate, with distant, extra basal, very small, denticle (Fig. 2d); (1) superior large, connected to one small inferior tooth (Fig. 2e); (2) superior large, connected to one small and divided into two, inferior teeth (Fig. 2f). Additive. Dentition of *Ogyges* and *Proculejus* seems to be very specialized and different from other Passalidae (with the probable exception of *Passipassalus*, an unrelated South American genus). The divided inferior portion of suprainternal teeth is here interpreted as an evolutionary novelty in *Ogyges* evolved from a common ancestor with *Proculejus*.

23. Medial basal mentum: (0) glabrous; (1) punctate setose.

24. Lateral fossae of mentum: (0) brilliant; (1) opaque.

25. Anterior ventral carina of ligula: (0) absent (central area tumose) (Fig. 4d); (1) present, complete, forming a plate (Fig. 4c).

26. Pronotal habitus: (0) quadrate; (1) rectangular, transverse, almost flat in dorsal view; (2) rounded, almost rectangular and very convex, with posterior sides angulose. Non-additive.

27. Lateral margin of pronotum: (0) with strong punctations (Fig. 4 e); (1) impunctate (Fig. 4f).

28. Lateral fossae of pronotum: (0) punctate setose; (1) glabrous.

29. Rugose micropunctations (at moderate magnification) on external border of lateral fossae of pronotum: (0) absent (Fig. 4e); (1) present (Fig. 4f).

30. Prosternellum: (0) brilliant (only the apical small portion chagreened); (1) brilliant at center (chagreened on sides); (2) opaque (completely chagreened). Non-additive.

31. Prepimeron: (0) smooth (Fig. 1c); (1) chagreened, almost greasy (Fig. 1d).

32. Mesosternal lateral scar: (0) longitudinal; (1) circular, apical; (2) absent. Non-additive.

33. Anterior corners of metasternum: (0) with abundant setae; (1) with scattered long setae (Fig. 1d); (2) glabrous (Fig. 1c). Additive. As some specimens of *Ogyges* with glabrous metasternum (e.g. *O. championi, O. marilucasae, O. quichensis, O. tzutuhili, O. nahuali* and *O. laurae*) present 1-2 minute scattered setae when tenerals, we consider this character as additive.

34. Metasternal disc posteriorly: (0) smooth; (1) with patch of strong punctations without setae (Fig. 1c); (2) with patch of small setose puntations. Non-additive.

35. Anterior profemoral groove: (0) present (Fig. 1a); (1) absent (Fig. 1d).

36. Metafemur: (0) elongate, tree longer than wider; (1) widened, at most 2.4 times longer than wider; (2) intermediate, between 2.5-2.8 longer than wider. Non-additive.

37. Posterior border of metatrochanter: (0) without grooves; (1) with small longitudinal groove (Fig. 4h).

38. Posterior border of metatrochanter: (0) glabrous; (1) with row of setae (Fig. 4g).

39. Elytral dorsal striae: (0) all shallow, marked (Fig. 3a); (1) all deep, well-marked (Fig. 3b); (2) elytral striae 1, or 1 and 2 deep, rest barely visible or erased (Fig. 3c). Non-additive.

40. Dorsal elytral punctures: (0) almost superficial; (1) superficial; (2) indistinct; (3) deep. Non-additive.

41. Elytral tegument: (0) shiny; (1) opaque.

42. Bluish reflections: (0) absent; (1) present.

43. Humeri between intervals 7-9: (0) without a distinct tumosity, elytra parallel; (1) with tumosity notably expanded laterally (“humeral callus”), elytra not parallel.

44. Humeri setation (humeral callus): (0) setose; (1) glabrous.

45. Sides of elytra: (0) glabrous; (1) setose; (2) secondarily glabrous. Additive. The presence of micropunctations (visible only at great magnification) on glabrous elytra of *Ogyges* and *Oileus sargi*, suggest a secondary loss of setae in these taxa.

46. Sides of elytra: (0) setose on intervals 7-10 and all intervals on posterior declivity; (1) setose on intervals 8-10.

47. Parameres and phallobase: (0) separated (Fig. 4i); (1) fused (or separation barely indicated) only at sides (Figs. 4j, 4k).

48. Parameres: (0) separated at middle (Figs. 4i); (1) fused at middle (Fig. 4k).

49. Median lobe ventrally: (0) globose; (1) elongate.

50. Median lobe apically (ventral): (0) glabrous; (1) with minute setae.

51. Median lobe ventrally: (0) with longitudinal membrane; (1) sclerotized.

52. Total length of body: (0) medium-sized (24-34 mm); (1) big (35-46 mm); (2) small (18-24 mm). Non-additive.

The cladograms were constructed using software TNT (Goloboff *et al*., 2008). A first analysis was conducted treating all characters under equal weights. Then, we tested the effect of homoplasy on the results by conducting different implied weights analyses (Goloboff, 1993), with constants of concavity (k) set to different integer values of 1–12, where 1 is weighted most severely against homoplastic characters. Implied weights analyses were conducted using the heuristic "traditional search" algorithm of TNT, with 1000 replications and tree-bisection-reconnection branch-swapping (TBR), holding 1000 trees during each replication.

Figure 1. **a**. *Ogyges crassulus*, ventral view. The anterior profemoral groove indicated with red arrows. **b**. *O. championi*, dorsal view. IT= internal tubercles; PfR= posterofrontal ridges; LpA= lateroposterior areas; LpT= lateroposterior tubercles; SoF= supraocular fossa; PP= postorbital pits. **c**. Sternum of *O. crassulus*. The white arrow indicates the smooth prepimeron and the bare anterior corners of metasternum; the black arrow indicates the patch of strong punctations posterior to the metasternal disc. **d**. Sternum of *Proculejus brevis*. The red arrows are signaling the absence of anterior profemoral groove. The white arrow indicates the chagreened ("greasy") prepimeron and the slightly setose anterior corners of metasternum.

Biogeographical analysis

We plotted the distribution of individuals of all species of *Ogyges* on a map, using ArcGis 9.2. After the phylogenetic analysis, each well-supported clade was colored. Barriers were hypothesized in relation to the dry (to moist) lowland valleys (principally < 1000m) and

major fault systems separating mountainous/volcanic ranges, and were analyzed and delineated.

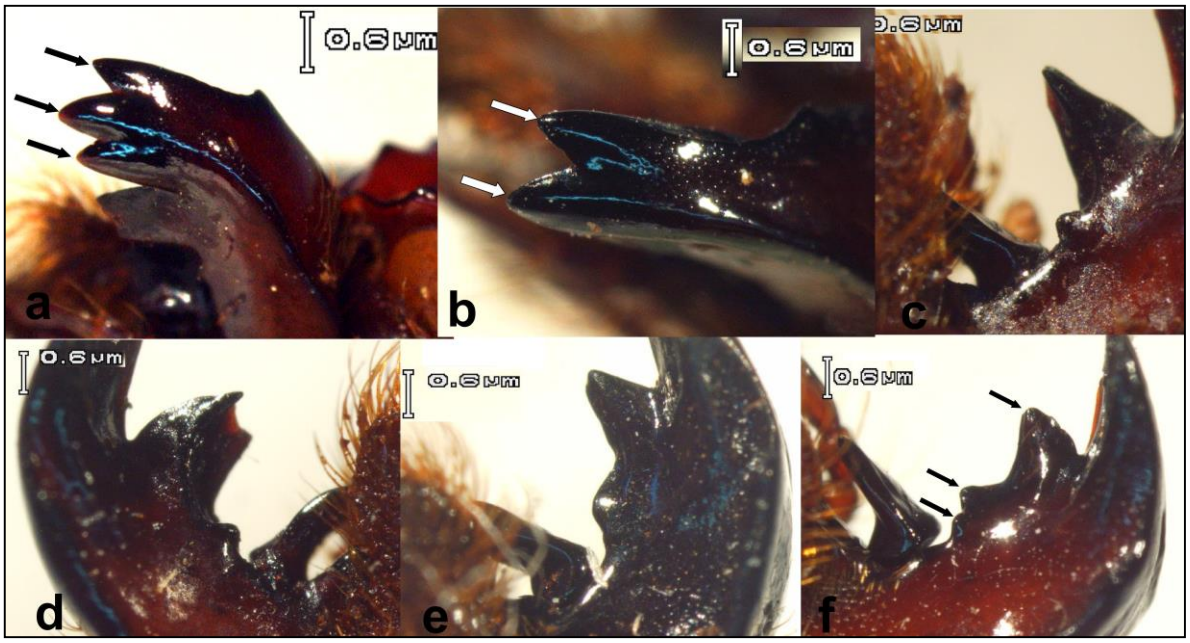

Figure 2. Mandibular teeth of Passalidae. **a**. Tridentate mandibular apex of *Oileus sargi*. **b**. Bidentate mandibular apex of *Ogyges championi*. **c**. Right suprainternal tooth of *O. sargi*. **d**. Left suprainternal tooth of *O. sargi*. **e**. Right (= left, because are symmetrical) suprainternal tooth of *Proculejus sartorii*. **f**. Right (= left) suprainternal tooth of *O. championi*.

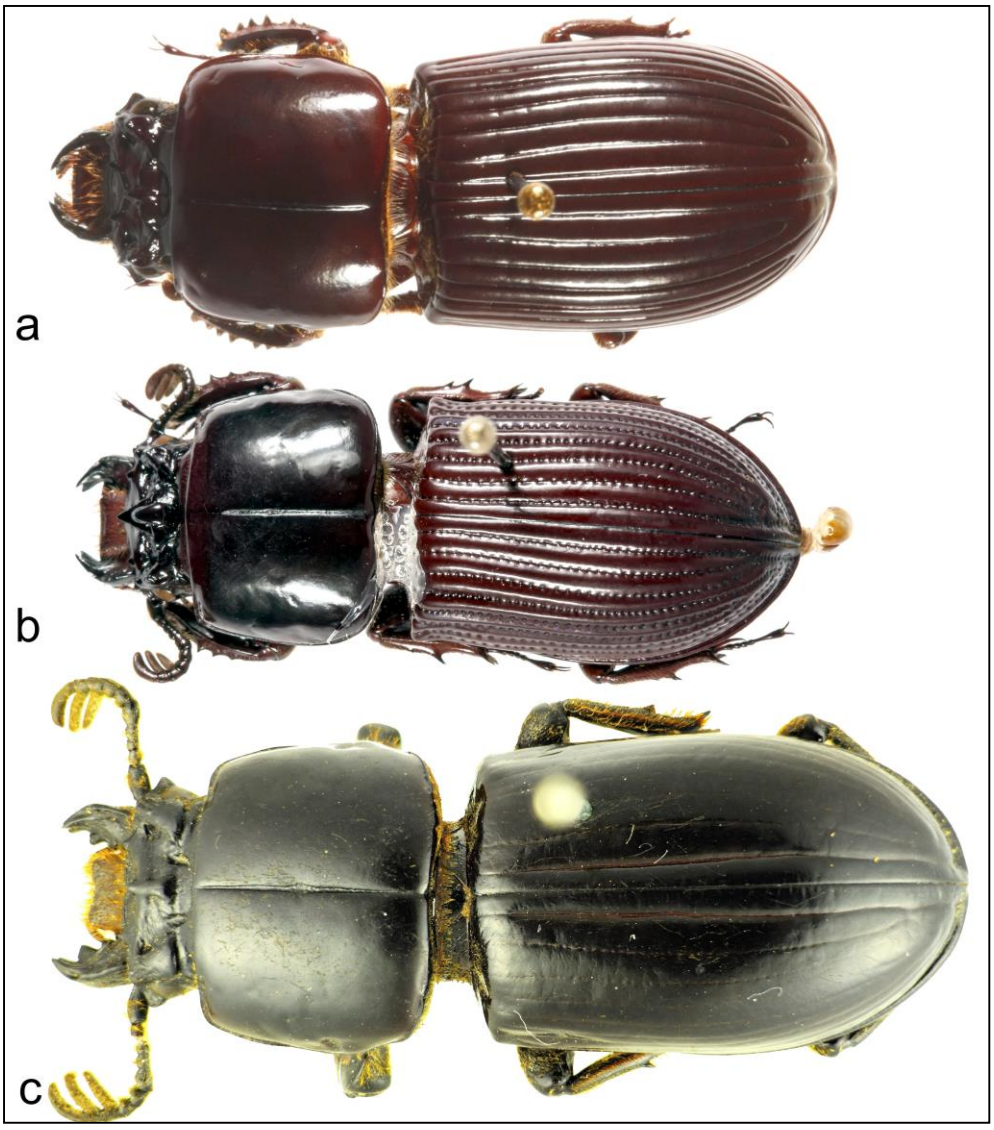

Figure 3. Dorsal habitus. **a**. *Ogyges championi*. **b**. *O. monzoni*. **c**. *O. laevissimus*.

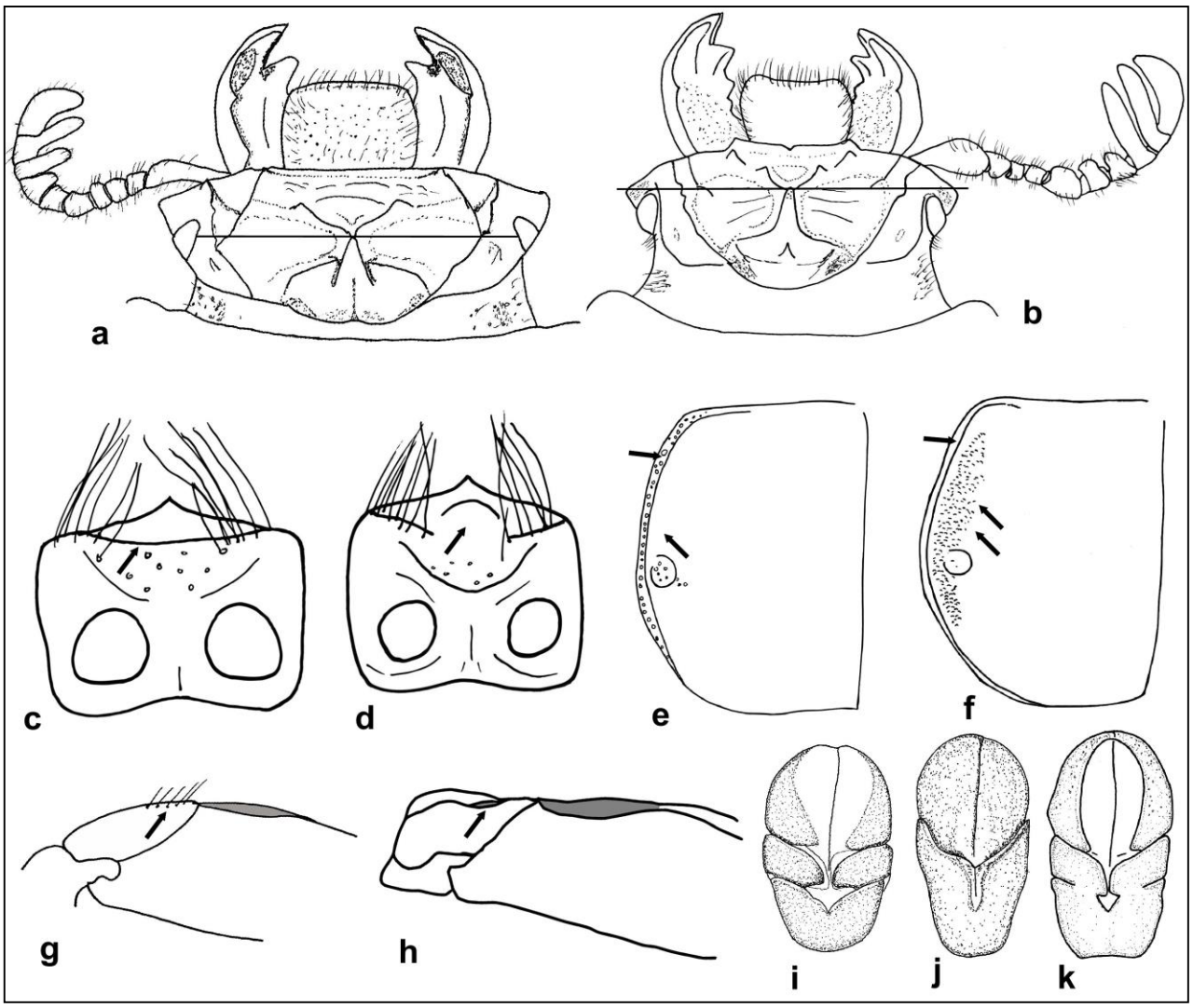

Figure 4. a. *Ogyges coxchicopi* Schuster et al., head. Transversal line indicates the origin of posterofrontal ridges. Arrows indicates the character states. **b**. *O. sandinoi* Cano, head. Transversal line indicates the origin of posterofrontal ridges. Arrows indicates the character states. **c**. Anterior ventral carina of ligula of *O. championi* (Bates) **d**. Anterior ventral carina of ligula of *O. crassulus* (Casey). **e**. Laterodorsal view of pronotum of *Proculejus nudicostis* Bates. **f**. Laterodorsal view of pronotum of *O. championi*. **g**. Posterior border of metatrochanter of *O. crassulus*. **h**. Posterior border of metatrochanter of *P. sartorii* Kaup. **i**. Ventral view of aedeagus of *O. monzoni* Schuster et al. **j**. Ventral view of aedeagus of *O. crassulus*. **k**. Ventral view of aedeagus of *O. handali* Cano.

RESULTS

Phylogenetic analysis

The analysis of the data matrix (Table 1) under equal weights and with concavity K= 3 led to three cladograms, but with K= 6 led to only one tree with 183 steps, a CI 0.399 and RI

0.754 (Fig. 5). In all the analyses, the 27 species of *Ogyges* were recovered as a monophyletic group, as generally occurred with the five species of the outgroup *Proculejus*. We recognize three main clades within *Ogyges,* named *O.* (*championi*) species group, *O.* (*laevissimus*) species group and *O.* (*crassulus*) species group (Fig. 5).

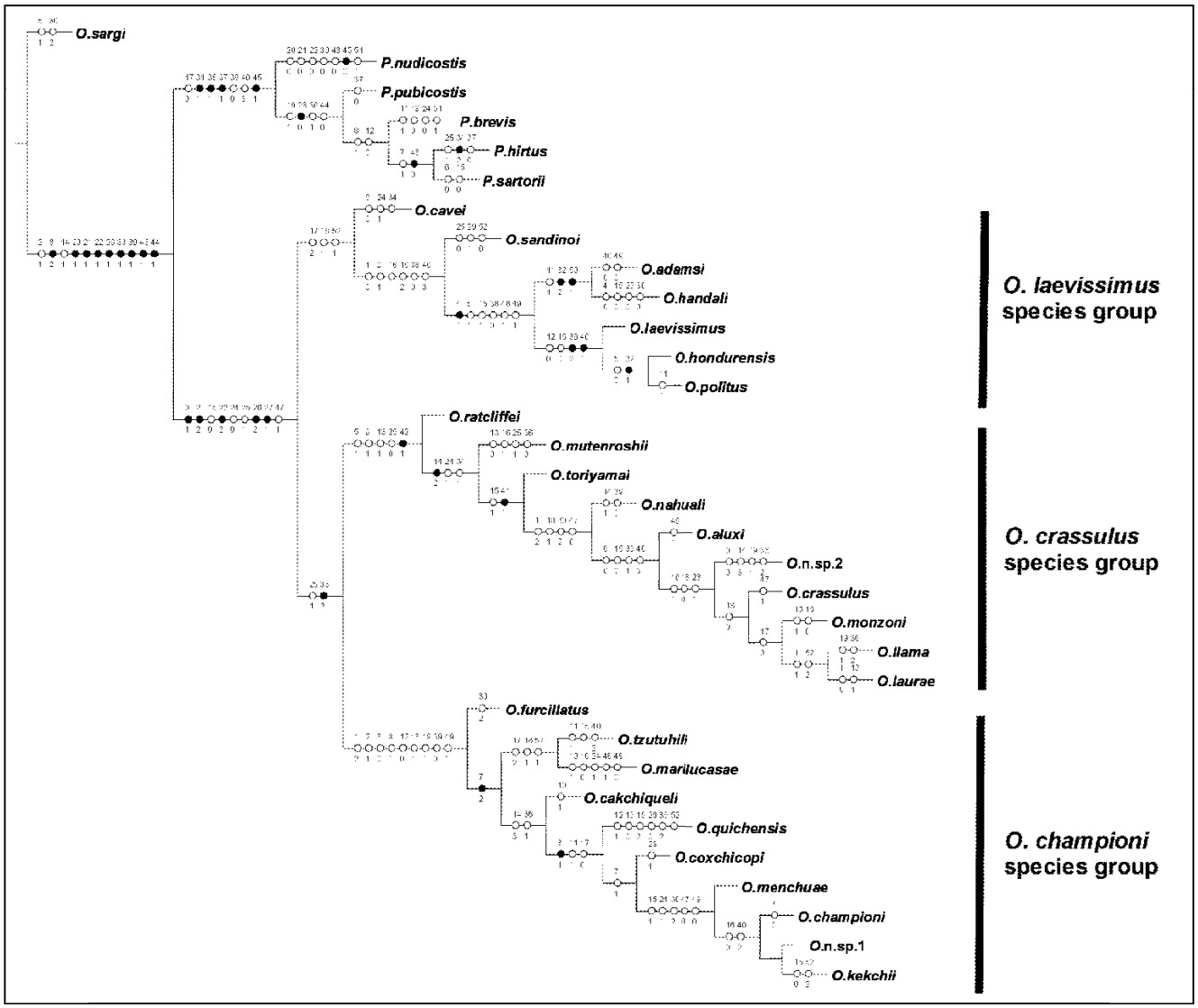

Figure 5. Cladogram of *Ogyges* obtained with concavity K=6, with character state changes indicated. The tree major clades were named as aggregates of species (species groups). The 53 characters are named from 0-52.

The synapomorphies that support the monophyly of *Ogyges* are the frontoclypeal suture absent (a reversal in *Ogyges* n.sp.2) (character 0[1]), the left suprainternal mandibular teeth with the large tooth connected to a smaller tooth divided in two (character 22[2]), the

very convex pronotal habitus (character 26[2]), the lateral margin of pronotum without punctures (character 27[1]), and the parameres and phallobase fused (partially separated) (character 47[1]) with two independent reversals within the *O. crassulus* and *O. championi* species groups.

The *O. laevissimus* species group, with 7 species, is supported by three character states: antennal club very wide (character 17[2]) and concave in dorsal view (character 18[1]), and total length big (35-46 mm) (character 52[1]). These three states were resolved as parallelisms with the subclade *O. tzutuhili* + *O. marilucasae* of the *O. championi* species group. It is the sister taxon to the two remaining groups within *Ogyges*.

The clade "*crassulus*" + "*championi*" is supported by only two character states, presence of rugose micropunctuations (at moderate magnification) on external border of lateral fossae of pronotum (character 29[1]; a reversion (absence) in *O. quichensis*; a parallelism (presence) with *O. sandinoi*), and anterior corners of metasternum glabrous (probably, secondarily glabrous) (character 33[2]).

The *O. crassulus* species group, with 10 species, is supported by four character states: internal tubercles absent (character 5[1]), posterofrontal ridges tumose anteriorly at sides of horn conforming a keel running at the anterior margin of frontal fossae (character 9[1]), sides of postfrontal groove deep (character 13[1]) (a reversal in *O. mutenroshii* and the clade of *O. crassulus*, *O. monzoni*, *O. llama* and *O. laurae*) and bluish reflections present in all species (character 42[1]). The characteristic patch of strong punctations on metasternum (character 34[1]) is absent in the basal species *O.* (*crassulus*) *ratcliffei*, but is a convergence in *O.* (*laevissimus*) *cavei*. The deep punctures on elytra (character 40[3]) are present only in the subclade of *O. aluxi*, *Ogyges* n.sp.2, *O. crassulus*, *O. monzoni*, *O. llama* and *O. laurae*, but apparently is a convergence with the species of the genus *Proculejus*.

The *O. championi* species group, with 10 species, is supported by five character states: clypeus flat (character 1[2]) and thin (character 2[1]), posterofrontral ridges present and posterior in position (character 8[1]), apex of ocular canthus rounded (character 16[1]) and internal face of mandible granular (character 19[1]). The median lobe of aedeagus elongated (character 49[1]) was resolved as a paralellism in a subclade of *O. laevissimus* species group and as reversals (median lobe globose (49[0]) in *O. marilucasae* and the subclade *O. menchuae* + *O. championi* + *Ogyges* n.sp.1 + *O. kekchii*). The *O. championi*

species group shares with some species of *Proculejus* the particular conformation of the mediofrontal structure (*sensu* Reyes-Castillo, 1970), as observed by the character state 8 [1] (posterofrontal ridges of the "championi" type) and the symplesiomorphic state 12 [0] (center horn short).

Biogeographical analysis

Based on the cladogram (Fig. 5), *Ogyges* and its three internal clades show clear distributional patterns (Fig. 6). *Ogyges* is separated from the species of *Proculejus* by the dry valley of the Isthmus of Tehuantepec. The *O. championi* species group (Fig. 6), with 10 species, is distributed in Chiapas, Mexico, in the northern mountain system from San Cristóbal de las Casas to Lagunas de Montebello and in the southern system of mountains in the Reserve "El Triunfo", and also in Guatemala, in the Sierra de los Cuchumatanes, Montaña Cuilco, Sierra de las Minas and Sierra de Santa Cruz. The distribution of this species group corresponds to the Maya block (Gutiérrez-García and Vásquez-Domínguez, 2012), whereas the remaining species groups are endemic to the Chortís block (Townsend, 2014). Apparently dryness (now and in past geological times) of the Motagua-Cuilco and Motozintla-Comaltitlán suture zones is the barrier separating it from the *O. crassulus* and *O. laevissimus* species groups, and corresponds (partially) to the subhumid corridor delineated by Stuart (1954).

The distribution of the *O. laevissimus* species group (Fig. 6) runs mostly along the Pacific Volcanic Chain from Guatemala to El Salvador, and to the north in Guatemala (Zacapa department) and then to southeastern Honduras and northern Nicaragua, where distribution corresponds approximately to the Southern Cordillera of the Honduran Chortis highlands delimitated by Weyl (1980: 93-94) and highlighted by Townsend (2014: 214). It is separated from the majority of species of the *O. crassulus* species group, by a series of intrincate lowland (~300-700m) dry forests between the Central and Southern Cordilleras, perhaps related to the Ulúa-Chamelecón-Olancho system. Nevertheless, two species are sympatric with species of the *O. crassulus* species group, making the limits unclear: *O.* (*laevissimus*) *cavei* at Sierra de Agalta (Cerro La Picucha), and *O.* (*laevissimus*) *adamsi* at Montaña Santa Bárbara. The eastern limit of its distribution (and also of the genus *Ogyges*) is represented by the lowland moist to dry valleys of the Colón river in Nicaragua (0-700m)

and his tributary, the Comalí river in Honduras (730-950m) (or perhaps, the northern suture of the Siuna Terrane in Nicaragua) (Fig. 6). Otherwise, the moist (Atlantic) to dry (Central and Pacific) lowland (0-800m) Guayape fault system (Fig. 6) could be considered as a major barrier.

The *O. crassulus* species group, with 10 species, presents a distribution almost exclusive to northern Honduras, slightly extending to Guatemala at the Sierra del Merendón (Fig. 6). It corresponds well with the Northern and Central Cordilleras of the Honduran Chortís highlands (Weyl, 1980: 92-94; Townsend 2014: 214). The Guayape fault system (Fig. 6) represents the eastern distributional limit of this species group.

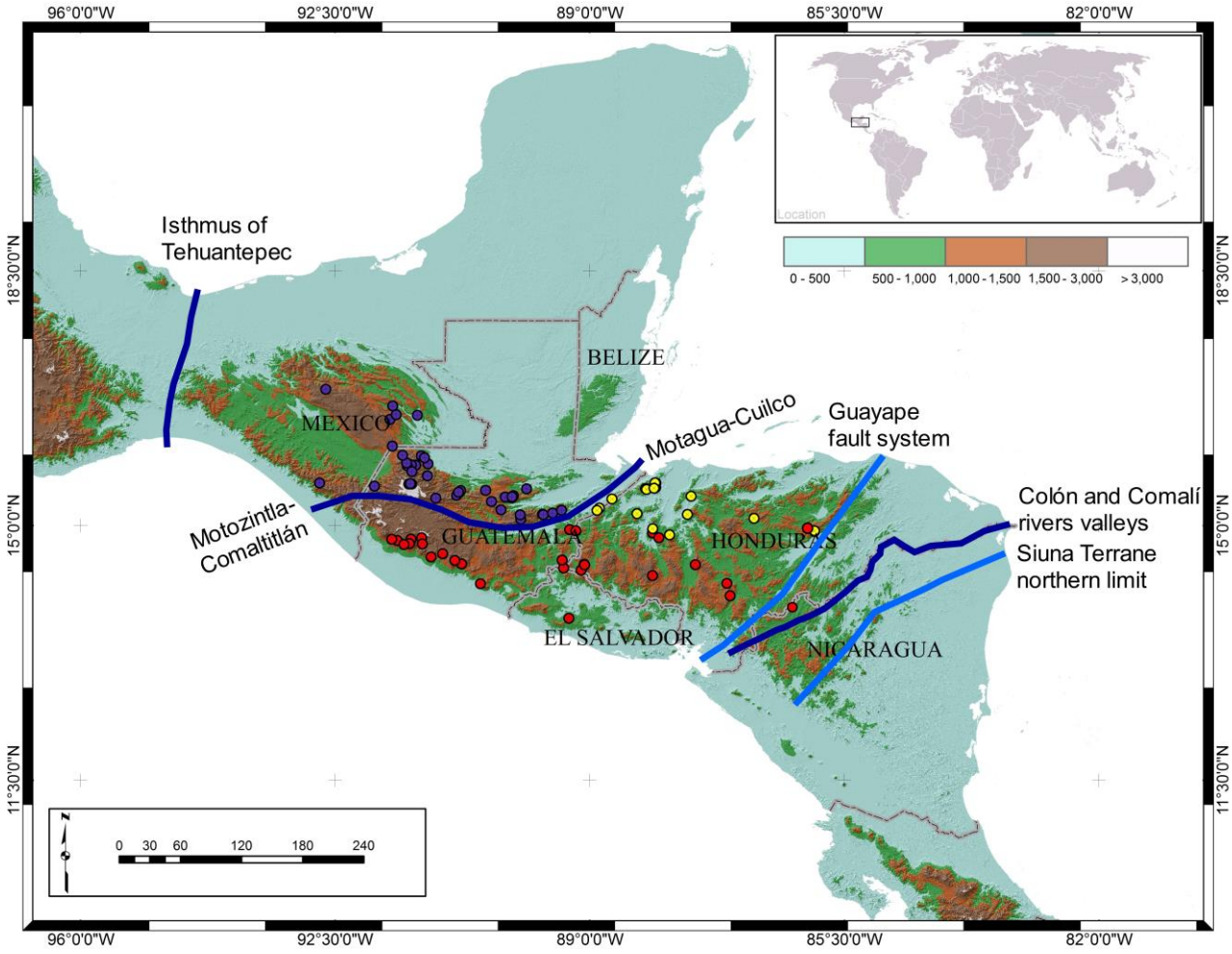

Figure 6. Distribution of the three clades of *Ogyges* in Nuclear Central America. Purple circles = *O. championi* species group; red circles = *O. laevissimus* species group; yellow circles = *O. crassulus* species group. Major barriers indicated with blue. Minor, or inconclusive barriers indicated with light blue.

DISCUSSION

Phylogeny

The high homoplasy levels (CI= 0.399) could be explained by the covariation of characters associated with flightlessness in taxa of Passalidae (reduced eyes, very narrow wings, and oval and fused elytra), but also because they have similar ecological niches (interior of rotten logs in humid forests). Flightlessness seems to have evolved several times in montane passalids, as seen in unrelated genera (e.g., *Passalus, Chondrocephalus, Veturius, Arrox*, etc.) and the body shape of passalids living in sapwood/heartwood tends to be convex (Johki and Kon, 1987; Lobo and Castillo, 1997; Kon *et al*., 2002).

When we consider the characters used traditionally to separate *Ogyges* from *Proculejus*, the frontoclypeal suture, the shape of the internal teeth of the mandibles, the punctuate border of pronotum, the sculpture of prepimeron, and the lateral setation of elytra are the most relevant. Of these, until now, only the internal teeth have proven to be stable and autapomorphic in *Ogyges* (also see Cano 2014). Nevertheless, a clearly marked frontoclypeal suture appeared only once in a terminal species (a reversal) of the *O. crassulus* species group, suggesting that the character is homoplasic in Passalidae.

The genus *Proculejus* urgently needs to be revised. At least two species, *P. nudicostis* Bates and *P. obesus* (Bates), do not share the bidentate apex of mandible, the setose lateral elytra and the form of internal teeth. Additionally, in one phylogenetic analysis (concavity K= 3, strict consensus), *P. nudicostis* was recovered as basal and excluded from *Proculejus*.

Based on the phylogeny and distributions of more than twice as many species as Schuster and Reyes-Castillo (1990: 40-45), we reject some of their -non based on phylogeny- groupings of *Ogyges* and suggest others that appear more natural (Fig. 5).

Biogeography

Ogyges belongs to the Mesoamerican Montane cenocron. According to Halffter (1987), taxa belonging to it evolved in Nuclear Central America and then dispersed northwest and southeast of it. They have ancient South American affinities and are distributed mainly in mountain and cloud forests, although they penetrate occasionally in pine-oak forests. In the Oligocene–Miocene they dispersed from Central America northward (Morrone, 2015).

Regarding the vicariance between *Proculejus* and *Ogyges*, the Isthmus of

Tehuantepec has been considered as a biogeographic break for several taxa (Marshall and Liebherr, 2000; Morrone and Márquez, 2001). A vicariant event during the Pliocene has been suggested as responsible for the divergence of several taxa, although an earlier vicariance at the end of the Miocene may have also occurred (Daza *et al*., 2010).

The Motagua-Polochic-Jocotán fault has been invoked as a sharp biogeographic break for vertebrate taxa (Castoe *et al*. 2009, Daza *et al*., 2010). Actually, for flightless passalids, we suspect that, although low altitude areas may be barriers, they are more effective if they are dry, at least at present. The Polochic suture zone valley, parallel to the north of the Motagua suture valley, is moister than the Motagua valley and does not separate species of passalids as well as does the Motagua; for example, three species of the *O. championi* species group are found on both sides of the Polochic suture zone (*O.* (*championi*) *tzutuhili*, *O.* (*championi*) *kekchii*, and *O.* (*championi*) *championi*). Here we recognize the Motagua-Cuilco (0-2000m) dry valleys system and the Motozintla-Comaltitlán suture zones (0-1900m), as the major biogeographic barrier involved in the vicariance between the *O. championi* species group of the Maya block and the rest of the genus distributed in the Chortis block. The Motagua suture zone (together with the Polochic suture zone) apparently acted as a barrier for several lowland and highland vertebrates from ~3-8 (Daza *et al*., 2010: 351), or from ~4-5.5 (Castoe *et al*. 2009: 95) million years ago.

The distributional limits between the *O. crassulus* and *O. laevissimus* species groups are unclear. Species of the *O. laevissimus* species group are distributed in the Quaternary Volcanic Chain and the, of Tertiary volcanic origin, Southern Cordillera of the Chortis highlands in Honduras. But, again, the lowland dry valleys, such as the labyrinthic systems between the Ulua and Chamelecon rivers and the Olancho Department in Central Honduras, merge as barriers. As to the timing of taxa divergence, Townsend (2014) suggests that most of the biota of Honduras could not have survived the mid-Miocene volcanic eruptions; over 5,000 km^3 of ignimbrites up to 2,000 m thick were deposited on top of the low-relief surface of the southern and western Chortís Block, and tens of thousands of square kilometers were covered repeatedly in thick layers of ash (Townsend 2014). Thus, supposedly Honduran *Ogyges* would have to have originated after this event.

The southern limit of distribution of *Ogyges* falls on the Segovias range in Northwestern Nicaragua, where mountains exceed 1500 m elevation. We (EBC, JCS) have

collected passalids extensivelly in the further south cloud forests between 1200-1500m, in the mountains sourrounding Jinotega and Matagalpa (Selva Negra, El Quetzal, Peñas Blancas, La Dalia and Datanlí-El Diablo,) and in Granada at Mombacho volcano (1300m), without trace of *Ogyges*.

We suspect that further detailed study of other taxa will confirm the vicariance hypothesis suggested by *Ogyges.* Other taxa for further study with similar distributions include; *Proculus* (Passalidae) (Schuster *et al*., 2003), *Xylopassaloides* (Passalidae) (Reyes-Castillo *et al*., 1987; Schuster, 1993), Y*aaxkumukia* (Scarabaeidae) (Micó *et al*., 2006), and the *integripenis* species group of *Geocharidius* (Carabidae) (Sokolov and Kavanaugh, 2014).

ACKNOWLEDGMENTS

We thank Facultad de Ciencias, Universidad Nacional Autónoma de México (UNAM), Universidad del Valle de Guatemala, and Museo de Historia Natural of Escuela de Biología of Universidad de San Carlos de Guatemala, for academic support. For help when reviewing type material we thank Stéphane Boucher, MNHN, Paris; Pedro Reyes Castillo and Larry Jiménez Ferbans, IEXA, Xalapa, Veracruz; and Max Barclay, Malcolm Kerley, and María Peña, BMNH, London. E.B. Cano thanks the programs PAEP-UNAM and DIGED-USAC who provided the funds for international visits to collections and museums and the Programa de Doctorado en Ciencias Biológicas of the Universidad Nacional Autónoma de México (UNAM), for support. This work forms part of the doctoral thesis of Enio B. Cano.

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Table 1. Data matrix analyzed. Character states of polymorphic taxa are indicated between square brackets; inapplicable characters are indicated by a dash (-), and missing characters by a question mark (?). All characters are coded from 0 to 52.

O. sargi	0	-	0	0	0	1	1	0	0	-	0	0
	1	0	0	1	0	1	0	0	0	0	0	0
	1	0	0	0	1	0	2	0	0	0	0	0
	2	0	1	0	0	0	0	0	0	2	-	0
	0	0	0	0	0							
P. nudicostis	0	-	1	0	0	0	1	0	2	0	0	
	0	1	0	1	1	0	0	0	0	0	0	0
	0	1	0	1	0	1	0	0	1	0	1	0
	1	2	1	0	1	3	0	0	0	1	0	-
	0	0	0	0	1	0						
P. pubicostis	0	-	1	0	0	0	1	0	2	0	0	
	0	1	0	1	1	0	0	0	1	1	1	1
	0	1	0	1	0	0	0	1	1	0	1	0
	1	1	0	0	1	3	0	0	1	0	1	1
	0	0	0	0	0	0						
P. hirtus	0	-	1	0	0	0	1	1	1	0	0	0
	0	0	1	1	0	0	0	1	1	1	1	0
	1	1	1	0	0	0	1	1	0	1	2	1
	1	0	0	1	3	0	0	1	0	1	0	0
	0	0	0	0	0							
P. brevis	0	-	1	0	0	0	1	0	1	0	0	1
	0	0	1	1	0	0	0	0	1	1	1	0
	0	0	1	0	0	0	1	1	0	1	0	1
	1	1	0	1	3	0	0	1	0	1	1	0
	0	0	0	1	0							
P. sartorii	0	-	1	0	0	0	0	1	1	0	0	0
	0	0	1	0	0	0	0	1	1	1	1	0
	1	0	1	0	0	0	1	1	0	1	0	1
	1	1	0	1	3	0	0	1	0	1	0	0
	0	0	0	0	0							
O. laevissimus	1	0	2	0	1	1	1	0	2	1	0	
	0	0	0	1	1	0	2	1	2	1	1	2
	0	0	1	2	1	1	0	1	0	0	1	0
	0	0	0	0	2	1	0	0	1	1	2	-
	1	1	1	0	0	1						
O. hondurensis	1	0	2	0	1	0	1	0	2	1	0	
	0	0	0	1	1	0	2	1	2	1	1	2
	0	0	1	2	1	1	0	1	0	1	1	0
	0	0	0	0	2	1	0	0	1	1	2	-
	1	1	1	0	0	1						
O. politus	1	0	2	0	1	0	1	0	2	1	0	1
	0	0	1	1	0	2	1	2	1	1	2	0
	0	1	2	1	1	0	1	0	1	1	0	0
	0	0	0	2	1	0	0	1	1	2	-	1
	1	1	0	0	1							
O. championi	1	2	1	1	0	0	0	0	1	0	0	
	1	0	0	3	1	0	0	0	1	1	1	2
	0	1	1	2	1	1	1	2	0	0	2	0
	0	1	0	1	0	2	0	0	1	1	2	-
	0	0	0	0	0	0						
O. n.sp.1	2	1	1	0	0	0	1	1	0	0	1	0
	0	3	1	0	0	0	1	1	1	2	0	1

	1	2	1	1	1	2	0	0	2	0	0	1
	0	1	0	2	0	0	1	1	2	-	0	0
	0	0	0	0								
O. kekchii	1	2	1	1	0	0	0	1	1	0	0	1
	0	0	3	0	0	0	0	1	1	1	2	0
	1	1	2	1	1	1	2	0	0	2	0	0
	1	0	1	0	2	0	0	1	1	2	-	0
	0	0	0	0	2							
O. furcillatus	1	2	1	0	0	0	0	0	1	0	0	
	0	0	0	1	0	1	1	0	1	1	1	2
	0	0	1	2	1	1	1	2	0	0	2	0
	0	2	0	1	0	0	0	0	1	1	2	-
	1	0	1	0	0	0						
O. cakchiqueli	1	2	1	0	0	0	0	2	1	0	1	
	0	0	0	3	0	1	1	0	1	1	1	2
	0	0	1	2	1	1	1	1	0	0	2	0
	0	1	0	1	0	0	0	0	1	1	2	-
	1	0	1	0	0	0						
O. coxchicopi	1	2	1	1	0	0	0	1	1	0	0	
	1	0	0	[23]	0	1	0	0	1	1	1	2
	1	0	1	2	1	1	1	1	0	0	2	0
	0	1	0	1	0	0	0	0	1	1	2	-
	1	0	1	0	0	0						
O. quichensis	1	2	1	1	0	[01]	0	2	1	0	[01]	
	1	1	0	3	0	0	0	0	2	1	1	2
	0	0	1	2	1	1	0	1	0	0	2	0
	0	2	0	1	0	0	0	0	1	1	2	-
	1	0	1	0	0	1						
O. tzutuhili	1	2	1	0	0	0	0	2	1	0	0	
	1	0	0	1	1	1	2	1	1	1	1	2
	0	0	1	2	1	1	1	1	0	0	2	0
	0	2	0	1	0	2	0	0	1	1	2	-
	1	0	1	0	0	1						
O. marilucasae	1	2	1	0	0	0	0	2	1	0	1	
	0	0	0	1	0	0	2	1	1	1	1	2
	0	1	1	2	1	1	1	1	0	0	2	0
	0	2	0	1	0	0	0	0	1	1	2	-
	1	1	0	0	0	1						
O. menchuae	1	2	1	1	0	0	0	1	1	0	0	
	1	0	0	3	1	1	0	0	1	1	1	2
	0	1	1	2	1	1	1	2	0	0	2	0
	0	1	0	1	0	0	0	0	1	1	2	-
	0	0	0	0	0	0						
O. crassulus	1	2	2	0	0	1	0	0	2	1	0	
	0	1	0	2	0	1	1	0	0	1	1	2
	1	1	0	2	1	1	1	2	0	0	2	1
	0	1	0	1	1	3	1	1	1	1	2	-
	1	0	0	0	0	0						
O. aluxi	1	2	2	0	0	1	0	0	2	1	0	0
	1	1	2	0	0	1	1	0	1	1	2	0
	1	0	2	1	1	1	2	0	0	2	1	0
	1	0	1	1	3	1	1	1	1	2	-	0
	0	1	0	0	0							
O. monzoni	1	2	2	0	0	1	0	0	2	1	0	
	0	1	0	2	1	0	0	0	0	1	1	2
	1	1	0	2	1	1	1	2	0	0	2	1
	0	1	0	1	1	3	1	1	1	1	2	-
	0	0	0	0	0	0						

O. llama	1	1	2	0	0	1	0	0	2	1	0	0
	1	0	2	0	1	0	0	1	1	1	2	1
	1	0	2	1	1	1	2	0	0	2	1	0
	2	0	1	1	3	1	1	1	1	2	-	0
	0	0	0	0	2							
O. laurae	1	0	2	0	0	1	0	0	2	1	0	0
	1	1	2	0	1	0	0	0	1	1	2	1
	1	0	2	1	1	1	2	0	0	2	1	0
	1	0	1	1	3	1	1	1	1	2	-	0
	0	0	0	0	2							
O. n.sp.2	0	-	2	0	0	1	0	0	2	1	0	0
	1	1	3	0	1	1	0	1	1	1	2	1
	1	0	2	1	1	1	2	0	0	2	1	0
	2	0	1	1	3	1	1	1	1	2	-	0
	0	0	0	0	0							
O. adamsi		1	0	2	0	1	1	1	0	2	1	0
	1	1	0	1	1	1	2	1	2	1	1	2
	0	0	1	2	1	1	0	1	0	2	1	0
	0	0	0	[01]	1	0	0	0	1	1	2	-
	1	1	0	1	0	1						
O. handali		1	0	2	0	0	1	1	0	2	1	0
	1	1	0	1	0	1	2	1	2	1	1	2
	0	0	0	2	1	1	0	0	0	2	1	0
	0	0	0	0	1	3	0	0	1	1	2	-
	1	1	1	1	0	1						
O. sandinoi		1	0	2	0	0	0	1	0	2	1	0
	0	1	0	1	0	1	2	1	2	1	1	2
	0	0	0	2	1	1	1	1	0	0	1	0
	0	0	0	1	1	3	0	0	1	1	2	-
	1	0	0	0	0	0						
O.nahuali		1	2	2	0	0	1	1	0	2	1	0
	0	1	1	1	1	0	1	1	0	1	1	2
	0	1	0	2	1	1	1	2	0	0	2	1
	0	2	0	1	0	0	1	1	1	1	2	-
	0	0	0	0	0	0						
O. cavei	1	1	2	0	0	0	0	0	2	0	0	0
	1	0	1	0	0	2	1	0	1	1	2	0
	1	1	2	1	1	0	1	0	0	1	1	0
	2	0	1	1	0	0	0	1	1	2	-	?
	?	?	?	0	1							
O. ratcliffei		1	1	2	0	0	1	1	0	2	1	0
	0	1	1	1	0	0	1	0	0	1	1	2
	0	0	0	2	1	1	1	1	0	0	2	0
	0	2	0	1	1	0	0	1	1	1	2	-
	?	?	?	?	0	0						
O. toriyamai		1	1	2	0	0	1	1	0	2	1	0
	0	1	1	2	1	0	1	0	0	1	1	2
	0	1	0	2	1	1	1	1	0	0	2	1
	0	2	0	1	1	0	1	1	1	1	2	-
	1	0	0	0	0	0						
O. mutenroshii		1	1	2	0	0	1	1	0	2	1	0
	0	1	0	2	0	1	1	0	0	1	1	2
	0	1	1	2	1	1	1	1	0	0	2	1
	0	0	0	1	1	0	0	1	1	1	2	-
	?	?	?	?	0	0						

APPENDIX. Material examined.

***Oileus sargi* (Kaup)** (6 specimens). MEXICO: Chiapas, 30 mi N of Huixtla, #PST-1, 17 IV 1983, J.C. Schuster (1, UVGC). GUATEMALA: Chiquimula, Plan de la Arada, 1600m, 19 VII 1999, José Monzón, col. (1, UVGC); Escuintla, Fca. El Rosario, Volcán de Agua, 13-17 IX 1998, Alt. 1720m, #VNh-3, J.C. Schuster (1, UVGC); Quetzaltenango, Colomba, Costa Cuca, Volcán Lacandón, aldea Santa Anita 14° 47′26”N, 91° 43′ 30.6”W, 16 VI 2005, Cafetal, 1544m, E.B. Cano (1, UVGC); Zacapa, La Unión, 4-IV-1988, V. Gaitan (1, UVGC). HONDURAS: Ocotepeque Dept., El Portillo, VI 1992, 1900m, J.C. Schuster (1, UVGC).

***Proculejus nudicostis* Bates** (3). MEXICO: Omiltemi, Guerrero, 26-VII-65, G y V Halffter (1, INECOL); idem but 11-IV-63, G. Halffter, A, Barrera, A. Martinez, leg. (1, INECOL); Guerrero, 5 miles southwest Filo de Caballo, July 17, 1984, Carroll, Schaffner, Fruidlander (1, UVGC).

***P. pubicostis* Bates** (1). MEXICO: km 50 Teotitlán - Huautla, Oaxaca, 9-XI-68, P. Reyes, M. Cabrera, col., Alt 2400, bosque nebular. En tronco podrido muy húmedo (1, INECOL).

***P. hirtus* (Truqui)** (1). MEXICO: H[idal]go, La Mojonera, 28.X.1992., leg J. Pál. (1, UVGC).

***P. sartorii* Kaup** (7). MEXICO: Hidalgo, Tlanchinol, a 4 km del pueblo, bosque nuboso, 28 VII 2010, S. Orellana (1, UVGC); Hgo., Hwy. 105, 2.4 mi N Tlanchinol, 5000′, 8 May 1983, C.W. & L. O′Brien & GB Marshall (5, UVGC); Hidalgo, Tlanchinol, 26 V 78, madera de *Quercus* (1, UVGC).

***P. brevis* (Truqui)** (3). MEXICO: Oaxaca, carretera Llano de las Flores - Cerro Pelón, km 129, 17° 26′ 38” N, 96° 31′ 11” W, 2855m, 20 IX 1998, E.N. Smith, CONENS 9938 (1, UVGC); 10.9 km NE Cerro Pelón, Oaxaca, 26-II-84, alt. 2170m, bosque pino-encino, P. Reyes col. (2, INECOL).

***Ogyges adamsi* Schuster and Reyes-Castillo** (14). HONDURAS: Santa Bárbara, Montaña Santa Bárbara, VII.9.1968, 1968-12. Col. P. Adams (1 holotype, 1 paratype, INECOL); Teguc[igalpa], 28 XII 1980, in rotting tree, J.V. Mankins (1 paratype, INECOL); idem but 22-12-1980, in rotting trees, J.V. Mankins (2 paratypes, UVGC); 6-10-77, L. Yojoa, Hond., J.V. Mankins Collector, dibujo E. Aranda (1 paratype, INECOL); Francisco Morazán, arriba de El Rosario, Fca. La Tigra, 1700m, 20 VII 1991, J.C. Schuster, bosque nuboso, en tronco podrido (2 males, 2 females, UVGC); Rosario, San Juancito Mts., Honduras, Elev. 5120 feet,

VII,[space],1930, Honduras exped, *O. yohoaensis* [unpublished name] (1 paratype, UVGC); III-2-1979, Mt. Ayuca, Honduras, Dept de F.M [Francisco Morazán], Coll. H.J. Marcus (2 paratypes, UVGC); San Juancito 7 mi SW, Francisco Morazán, Honduras, 16-VI-67, Coll. R.W. McDiarmid (1 UVGC).

***O. aluxi* Schuster, Cano and Boucher** (26). HONDURAS: Cortés, Dept. + 30km W of Sn Pedro Sula, 1550m, 20-21 III 1987, J.C. Schuster (2, UVGC+ 11 UVGC paratypes); Cortés, N San Pedro Sula, 1650m, 2 X 2011, F. Camposeco, 15.586585N, -88.100232W (1, UVGC); Cortés, N of Cofradía, Cusuco, 1420-40m, 26 III 1991, J.C. Schuster (7 paratypes, UVGC); San Pedro Sula, Norte de Cofradía, P.N. El Cuzuco, 1900m, junio 1999, Monzón & Bailey (2, UVGC); Yoro, 10km, NO Morazán, 24 III 1991, 780m, J.C. Schuster (2, UVGC); Yoro, Sinaí, N15º26', W87º22', 1410m, Jun 2002, R.D. Cave (1, RC).

***O. cakchiqueli* Schuster and Reyes-Castillo** (36). GUATEMALA: Huehuetenango, San Juan Ixcoy, 7 mi S de San Juan Ixcoy, 5 IV 1977, 2850m, J.C. Schuster col., bosque nebular de encinos #FF2 (1 paratype, INECOL); idem but S of San Juan Ixcoy, 8 VII 1977, 2280 m, J.C.S. col. (4 paratypes, INECOL); Huehuetenango, mountain above San Mateo Ixtatán, in log, 7 Feb. 1965, D.E. Breedlove, Collection of the CAS, San Francisco, Calif. (1 paratype, INECOL); Huehuetenango, San Mateo Ixtatán, 2975m, 2.6 miles of S. Mateo, 24 VII 1990, Brodie, Campbell (1, UVGC); Huehuetenango, Todos Santos, Villa Alicia, 2450m, 9-10 V 2002, A. Bailey (10, UVGC); Huehuetenango, Todos Santos, montaña sur de aldea Max, octubre 2001, bosque nuboso, J. Monzón (3, UVGC); Huehuetenango, Todos Santos, camino a Max, Rio Ocho, 2850m, 15.505477, -91.643826, J. Monzón, R. Anderson (2, UVGC); Huehuetenango, Santa Eulalia, 1kkm NW of Sta. Eulalia, 2750m, 15° 45′ 49"N, 91° 30′ 25"W, 2 III 1991, F.G. Thompson, S.P. Christman (1, UVGC); Huehuetenango, Fca. San Luis, 8km NE de Sta. Eulalia, 2490m, VII 1994, J.C. Schuster (pieces) (1, UVGC); Huehuetenango, Montaña de Cuilco, 2000m, bosque nuboso, 1996, M. Acevedo (4, UVGC); Huehuetenango, Cuilco Mt., above El Paraiso, 2100m, 9 III 1996, cloud forest, E.B. Cano (5, UVGC); Huehuetenango, Cuilco, arriba de Peña Roja, 2200m, 20 julio 1998, E.B. Cano, J. Monzón (3, UVGC).

***O. cavei* Cano** (2). HONDURAS: Olancho, La Picucha, 11 km N Catacamas, 14.92740, -85.90983, bosque nuboso, 1800–2100 m, 8–14 V 2010. L. Sáenz (LSD 451) (holotype, UVGC); Comayagua, 10 km E Comayagua, 14.45973, -87.54609, Bosque nuboso, 2000 m,

15–19 V 2010. L. Sáenz (LSD 459) (paratype, UVGC).

***O. championi* (Bates)** (151). GUATEMALA: Baja Verapaz, Purulhá, 25 XII 1975, P. Reyes C. col. (4, INECOL); Idem but dibujo Aranda (1, INECOL); idem but 4-VI-93, alt. 1600m, bosque nebular, P. Reyes-Castillo, col. (3, INECOL); Baja Verapaz, Purulhá, Ranchitos del Quetzal, 2100m, 7 IX 2013, Centeno D. (1, UVGC); Baja Verapaz, Purulhá, Biotopo del Quetzal, Cerro Quisis, 9 IX 2001, bosque nuboso, 2000-2200m, tronco podrido, V. Ríos, R. Ávila y L. Benítez (4, UVGC; 2, USAC); idem but 16 IX 2001, 1700-1900m, L. Benítez (3, UVG); idem but 10 IX 2001 (3, UVGC; 1 USAC); idem but 16 IX 2001 (1, UVGC); Baja Verapaz, Purulhá, Biotopo del Quetzal, 19 IV 1998, E. Cano (7, UVGC), idem but 15 XI 1988 (1, USAC); idem but 26 V 1987 (1, USAC); idem but 15 XI 1988, M. Barrios (1, USAC); idem but 11 V 2000, A. Higueros (1, USAC); idem but agosto 2000, A. Higueros (1, USAC); idem but 1700m, 12 VI 2000, A. Higueros (1, USAC); idem but 6 V 2000 (1, USAC); Baja Verapaz, Purulhá, 9-10 III 1996, L. Rivera (1, UVGC); Baja Verapaz, Purulhá, nr. Biotopo, 1 XI 1989, J. Schuster (2, UVGC); Baja Verapaz, nr. Purulhá, 9 V 1976, 1640m, J. Schuster (2, UVGC); idem but 6 VII 1984 (3, UVGC); idem but 23 VI 1980 (1, UVGC); Baja Verapaz, Purulhá, VII 1984, J. Schuster (1, UVGC); idem but 5-6 IX 1992 (1, UVGC); Baja Verapaz, Purulhá, marzo 1996, F. Rivera (1, UVGC); Baja Verapaz, Purulhá, 1570m, 24 VI 1980, Col. J. Schuster (1, UVGC); Baja Verapaz, km 156, Purulhá, 13 IX 1981, C. Porter (1, UVGC); Baja Verapaz, Purulá, 5km E Purulhá, 1530-1650m, 22/24 julio 1977, E. Fisher, P. Sullivan (1, UVGC); Baja Verapaz, Purulhá, km 156-160, 12-13/III/1994, C. Cardona (2, UVGC); Baja Verapaz, 5 mi E Purulhá, 11 VII 1991 (6, UVGC); Baja Verapaz, Purulhá, VII 1984, J. Schuster (1, UVGC); idem but 1570m, 24 VI 1980 (1, UVGC); Baja Verapaz, Purulhá, km 163.5, 15 III 1986, A. López (1, UVGC); Baja Verapaz, Purulhá, 9-10 III 1996, E. Kepfer (4 , UVGC); Baja Verapaz, Purulhá, Biotopín, 1500m, junio-julio 1998, 15.799002E, 16838959N, C. Bailey, J. Monzón (6, UVGC); Baja Verapaz, 5 mi E. Purulhá, 11 VII 1991, P. Hubbell (2, UVGC); Baja Verapaz, Purulhá, Hotel del Biotopo [posada Montaña del Quetzal], 5 VIII 1988, R. Pérez (2, UVGC); idem but 8 VIII 1988, J. Schuster (1, UVGC); Baja Verapaz, Purulhá, Biotopo del Quetzal, 1-18 VII 1997 (1, UVGC); Baja Verapaz, Purulhá, 4 III 1988, R. Mora (1, UVGC); Baja Verapaz, Cerro Verde, 1700m, 16 VI 2000, A. Higueros (1, UVGC); idem but 13 VI 2000, 1900m (1, USAC); idem but 1800m (5, USAC); idem but 8 VI 2000, 1800m (1 USAC); idem but La Unión Barrios, Cerro Verde,

1800m, VII 2000, A. Higueros (1, UVGC); idem but VIII 2000 (1, UVGC); Baja Verapaz, Purulhá, Cerro Verde, 30 IX 2001, b. nuboso, 2000-2200m, tronco podrido, transecto 3, L. Benitez (1, UVGC); Baja Verapaz, Unión Barrios, Cerro Verde, 11 XI 1978, M. Dix (2, UVGC); Baja Verapaz, "Cobán", Purulhá, 9 V 1991, M. Centeno (1, UVGC); Baja Verapaz, 4 km SW Purulhá, 1900m, 3 XII 1991, leg. R. Baranowski (1, UVGC); Baja Verapaz, 5 mi E Purulhá, upper tropical, 11 VII 1991, P. Hubbell (1, UVGC); Baja Verapaz, Chilascó, VI 1998, bosque nuboso (1, UVGC); idem but VI 1996 (1, UVGC); Baja Verapaz, 7km al S de Sta. Elena 3 XI 1979, M. Monzón (1, UVGC); idem but, F. Asturias (1, UVGC); Baja Verapaz, Unión Barrios, IX-1975, alt. 1440m, E.C. Welling col. (2, INECOL); Baja Verapaz, Finca las Nubes [Sierra de las Minas], 2400m, 22 VI 1993, M.C. Paiz (1, UVGC); Alta Verapaz, Tactic, a más de 1400m, VI-76, E.C. Wellig col. (7, INECOL); Alta Verapaz, Senahú, 1350m, Fca. El Volcán, 21 VI 1984, J. Schuster, hembra [15.504484, -89.866665](2, UVGC); Alta Verapaz, Senahú, Finca El Volcán, 25 III 1997, C. Estrada, E. Curley, R. Mejía (3, UVGC); idem but 12 XI 1984, C. MacVean, 1500m (2, UVGC); Alta Verapaz, 21 km San Cristobal Mexabaj, 1570msnm, 4 III 1989, J. Schuster (4, UVGC); idem but 3 III 1989 (2, UVGC); Alta Verapaz, Chelemhá, VI 1989, F. Herrera (2, UVGC); Alta Verapaz, Cobán, 10 XII 1993, Arturo Godoy (2, UVGC); Alta Verapaz, municipio de San Juan Chamelco, campamento Ecoquetzal, aprox. 1 hora en carro y 3 horas a pie de S.J. Chamelco, VI 1996, J.C. Schuster (2, UVGC); Alta Verapaz, 7-10/V/2010, A. Monterroso (1, UVGC); Alta Verapaz, Col. G. Kramer, 1976 (1, UVGC); Zacapa, Sierra de las Minas, 17 XI 1994, E. Curley (1, UVGC); idem but 1800m, 18 VII 1994 (2, UVGC); Zacapa, San Lorenzo, Sierra de las Minas, Cerro del Mono, 9 VI 1993, 2200m, J. Monzón (2, UVGC); Zacapa, Sierra de las Minas, 1800m, 20 III 1997, A. Pinelo (1, UVGC); Zacapa, San Lorenzo, VII 1986, D. Hernández (1, UVGC); idem but 10 XI 1986 (1, UVGC); Zacapa, San Lorenzo, 8 IV 1982, J. Schuster (2, UVGC); Zacapa, Sierra de las Minas, 2200m, III 2007, Col. R. Gramajo (1, UVGC); Zacapa, San Lorenzo, Sierra de las Minas, 17 IV 1994, X. Segovia (1, UVGC); Zacapa, Sierra de las Minas, 23 IV 1995, H. Pezzarosi (1, UVGC); Zacapa, Sierra de las Minas, San Lorenzo, 4 X 1987, bosque húmedo encino-pino, 1900m (1, UVGC); Zacapa, 12-19 III 2001, A. Monterroso (1, UVGC); Zacapa, Sierra de las Minas, zona núcleo, IV 2007, M.J. Larrave (1, UVGC); Zacapa, 4 mi N of San Lorenzo 18 IV 1981, 2110m, J. Schuster (1, UVGC); idem but 8 IV 1982, 2165m (1, UVGC); idem but 2150m (1, UVGC);

El Progreso, Cerro Pinalón, arriba de los Albores, 5 V 1990 (1, UVGC).

***O. coxchicopi* Schuster, Cano and Boucher** (18). GUATEMALA: Izabal, nr. Rio Zarco, above El Arenal, #EER-C, 11-20 IV 1993, Col. Enio Cano (holotype, UVGC); same data (13 paratypes, UVGC); Zacapa, rd. to Jones, Fca. Monte Morán, 8 IV 1983, S. Ubico, 1600m. alt, #PNO-5 (4, UVGC).

***O. crassulus* (Casey)** (74). GUATEMALA: Izabal, Morales, above San Antonio, 4-7 VIII 1994, C. Guirola, E. Smith (7, UVGC); Izabal, Los Amates, Cerro Nylon, 8-11 IV 1990, J.C. Schuster #WIe-2, 1120m, alt. (11, UVGC); idem but 8-IV 1990 (1, UVGC); idem but 11 IV 1990 (2, UVGC); idem but 8-11 IV 1990, 1240m (1, UVGC); Izabal, Morales, Sierra de Caral, finca Firmeza, 450m [?], J. Monzón (1, UVGC); idem but Caral, 1150m, 7-14 VIII 1994 (1, UVG) ; idem but, Caral, Negro Norte, V 1995, J.Monzón, 1200m (2, UVGC); idem but 1200m, abril 1997 (6, UVGC); idem but, 27 Junio 1998, 1150m, E.B. Cano, J.Monzón (6, UVGC); idem but Sierra Caral, 1150m, 15°22.67N, 88°41.68W, 1150m, 30 VIII 1997, J. Monzón (13, UVGC); Idem but 25 III 1997, J.Monzón, A.C. Bailey (4, UVGC); Izabal, Morales, Negro Norte, Finca Firmeza, 27 VI 1998, 1150m, E.B. Cano (6, UVGC); Izabal, Morales, S de Caral, aldea Negro Norte, cerro del Aguacate, 23-27 VI 1991 (9, UVGC); Izabal, Morales, Sierra Caral, quebrada La Firmeza, 1-2 IV 1992, Col. C. Guirola (1, UVGC); Izabal, 30km SSE of Morales, N 15°21.368´, 88°40.726´, 1240m, under wood, 21 July 2007, R.S.Zack Coll. (1, UVGC). HONDURAS: Cortés, Merendón, 15°30´12”N, 88°11´54”W, 7 June 2003, R.Turnbow (1, UVGC); Cortés, P.N. Cusuco, UTM 16P377265 1713975, ALT 1235M, 25-29 VI 2006, dung baited pitfall trap, col. K. Draysob (1, UVGC).

***O. furcillatus* Schuster and Reyes-Castillo** (47). GUATEMALA: Zacapa, 5 mi N S. Lorenzo, 17 VI 1981, W. Dix (holotype, UVGC); Zacapa, San Lorenzo, 2100m alt. 18 IV 1981, J.Schuster, bosque nebular #NR-1, dibujo F. Aranda (1 paratype, INECOL); Zacapa, above San Lorenzo, 1-15 IV 1993, # EERB, Enio Cano, col. (1, INECOL); Zacapa, Sierra de las Minas, Fca. Santa Clara, Cerro Pinalón, 2500m, B. nuboso, 23-24 VIII 1998, E. Cano (2, UVGC); El Progreso, arriba Albores, Cerro Pinalón, 1-7 marzo 1993, Col. E. Cano, #EER89 (1, INECOL; 8, UVGC); idem but 24-27 Feb. 1993, #EER (7, INECOL; 6, UVGC); El Progreso, Cerro Pinalón, arriba de Los Albores, 25 II 1990, J. Monzón, C. Granizo (6, UVGC); idem but 28 III, 1992, #WN, J.C. Schuster (2, UVGC); idem but 2450m, 6-9 VIII 1991, without collector (2, UVGC); idem but 7 VII 1990, A. Joachim, trampa pitfall (2,

UVGC); idem but 7 VIII 1990, I. Flores, T. pitfall (1, UVGC); Progreso, above Los Albores, Fca. Las Nubes, 2 VII 1993, 2500m, M.C. Paiz (6, UVGC); "Guatemala", Aug 77, M. Mogollón, col., 11364 (1 paratype, INECOL).

***O. handali* Cano** (49). GUATEMALA: Chiquimula, aldea Santa Rosalía, El Duraznal, cerca del Plan de la Arada, 11 VI 2011, 14°31'30.4"N, 89°22'47.3"W, 1668 m, bosque nuboso, Col. E.B. Cano (holotype, UVGC); same data (2 paratypes, UVGC); same data except 1–4 IV 2011, aprox. 1700 m, Col. C. Suchité (11 males, 14 females, paratypes, UVGC); same data except aldea El Duraznal, cerca de La Mesilla, 1630 m, 20 VIII 1998, Cols. E. Cano & J. Monzón (5 paratypes, UVGC); Chiquimula, San José las Minas, camino entre caserío Las Presas y el Plan de la Arada, Bosque nuboso. 1900 m, 24 VI 1998, Col. E. Cano (16 paratypes, UVGC).

***O. hondurensis* Schuster and Reyes-Castillo** (9). HONDURAS: Dept. Ocotepeque, Montaña "El Portillo", 13 IV 1988, J.Schuster, 1900m, bosque nebular, dibujo E. Aranda (holotype, INECOL); Ocotepeque Dept., El Portillo Mtn., 2 VII 1985, 1900m, J.C. Schuster (1 paratype, UVGC); idem but 13 IV 1981 (1 paratype, UVGC); idem but 19 VII 1981 (1 paratype, UVGC); idem but 27 VII 1981 (1 paratype, UVGC); idem but 13 IV 1981 (1, UVGC); Intibuca Dept., 7 mi E. La Esperanza, 1740m, 7 IV 1977, #L.V., J.C. Schuster, Col. (2 paratypes, INECOL); F. Feb 79, L. Volcán S.S., Consuelo J.M. (1 paratype, INECOL).

***O. kekchii* Schuster and Reyes-Castillo** (38). GUATEMALA: Baja Verapaz, Purulhá, 13-24 VI 1980, J.C.S. #MI-1 male, cloud forest, 1570m alt. (holotype, INECOL); Baja Verapaz, nr. Purulhá, 27 X 1985, P. Mayorga (1 paratype, UVGC); Baja Verapaz, Purulhá (km 150), 23-24 VI 1980, J.C. Schuster, cloud forest, 1570m alt. (3 paratypes, UVGC); Baja Verapaz, Purulhá, Biotopo del Quetzal, 15 XI 1988, Col. M. Barrios (4, USAC), idem but 25 VII 1987, 2100m (2, USAC); idem but Agosto 2000, A. Higueros (2, USAC); idem but, Cerro Quisis, 2200m, 28 VII 2001, V. Ríos, R. Ávila y L. Benítez (5, USAC; 3 UVGC); idem but 2000-2200m, 30 IX 2001 (2, USAC; 2, UVGC); idem but 9 IX 2001 (2, USAC; 3 UVGC); Baja Verapaz, Purulhá, Posada del Quetzal 15 IV 1988, E. Cano (1, UVGC); Baja Verapaz, Purulhá, en tronco podrido 4 VI 1993, E. Padilla (1, UVGC); Baja Verapaz, Purulhá, Biotopo del Quetzal 1-18 VII 1997 (2, UVGC); Baja Verapaz, Guaxabajá, RBSM (Sierra de las Minas), junio 2002, 2640m, 15°08´42"N, 89°57´20"W, Col. A. Higueros (1, USAC); Alta Verapaz, Tactic, VI 1976, 1400m, E.C. Wellig col. (1 paratype, INECOL); Alta Verapaz,

Mpio. Tucurú, Chelem Há, 2200-2300, Mt. Yalijux, bosque nebular, 7 V 1989, G. Ibarra (1, UVGC); idem but 22 III 1989 (1, UVGC); Alta Verapaz, Chelem Há, 22 III 1989, José Monzón (1, UVGC); Alta Verapaz, Senahú, aldea Secampana, Las puertas, montaña Yalijux, 15°24´34"N, 90°02´50"W, 23 V 1999, 1880m, S. Pérez (1, UVGC); Alta Verapaz, San Juan Chamelco, campamento Ecoquetzal, VI 1998, 2300m, J.C. Schuster (1, UVGC).

***O. laevissimus* (Kaup)** (50). GUATEMALA: Volcán de Agua, Departamento Antigua, 8-VI-74, J. Hendrichs col., altitud 2600-3000m, caminando (10, INECOL); V[olcán] Atitlán, Depto. Sololá, 29 I 1977, C. MacVean col. 2500m (1, INECOL); Sololá, Nahualá, VIII-75, a más de 2350m alt., E.C. Welling col. (5, INECOL); Quetzaltenango, Cantel, VIII 1978, más de 2200m, E.C. Welling (1, INECOL); idem but VIII-1975 (12, INECOL); Quetzaltenango, VIII 1975, a más de 2200m, E.C. Welling (3, INECOL); idem but VI 1976, alt 2200m (1, INECOL); Quetzaltenango, Zunil, 2000m, VII 76, E.C. Welling (17, INECOL).

***O. laurae* Cano** (11). HONDURAS: Olancho, 11 km N of Catamacas, mountain "La Picucha", 14.92740, -85.90983, 1800–2100 m, 8–14 V 2010. L. Sáenz collector (LSD) (holotype, UVGC); idem (10 paratypes, UVGC).

***O. llama* Cano** (44). HONDURAS: Cortés, cerca de San Pedro Sula, 15.512598°, -88.113660° 1580 m, 2 X 2011, bosque nuboso. Coll. F. Camposeco (holotype, UVGC); idem (42 paratypes, UVGC); Cortés Dept. 30 km W of S. Pedro Sula, 1550 m alt., 20-21 III 1987, bosque nuboso, J.C. Schuster, # VI3 female, Type C disturbance sound (1 paratype, UVGC).

***O. marilucasae* Reyes-Castillo and Castillo** (27). MEXICO: Chiapas, El Triunfo, 12-V-85, M. Vertiz (2, IBUNAM); idem but 24-I-85, F. Arias (3 paratypes, IBUNAM); idem but 23-I-85, F. Arias (4 paratypes, IBUNAM); idem but Reserva El Triunfo, 9 julio 1993, S. Zaragoza (11, IBUNAM); idem but 24-I-85, M. Vertiz (1 paratype, IBUNAM); idem but 23-I-85, H. Velazco (1 paratype, IBUNAM); idem but 23-I-85, M. Vertiz (1 paratype, IBUNAM); Reserva "El Triunfo", campamento "El Triunfo", 23-VIII-96, B. Gómez y Gómez (3, INECOL); Mpio. Jaltenango, Reserva El Triunfo, 29 IV 1992, B. Gómez Col. (1 INECOL);

***O. menchuae* Cano** (36). GUATEMALA: Quiché, Uspantán, aldea Laj Chimel, montaña al norte de la aldea, 2100 m., VII 1998, bosque nuboso. E.B. Cano (holotype, UVGC); idem (8 paratypes, UVGC); idem, except Norte Laj Chimel, San Pedro, 2100m (2 paratypes, UVGC);

idem but aldea Laj Chimel, A.González-Madrid, 30 V 2011 (13 paratypes, UVGC); idem but, Aldea Laj Chimel, road to San Pablo, 30 IV 2011, 15°27'30.69"N, 90o46'26.11"W, 2035 m, A. Gónzález-Madrid 30 V 2011 (4 paratypes, UVGC); same data except, Aldea Laj Chimel, road to San Pablo, 30 IV 2011, 15°27'30.69"N, 90°46'26.11"W, 2035 m (6 paratypes, UVGC); same data except, Montaña El Amay, in logs 15 VI 2012, A. Zamora (2 paratypes, UVGC).

***O. monzoni* Schuster, Cano and Boucher** (14). GUATEMALA: Izabal, Morales, above San Antonio, 4-7 VIII 1990, C. Guirola, E. Smith (2 specimenes, including holotype, UVGC); same data (10 paratypes, UVGC); Izabal, Los Amates, Cerro Nylon, above San Antonio, 1295m alt., 11 IV 1990, #WI-2, J.C. Schuster (1, UVGC); idem but, 1250m, 8-11 1990, J.C. Schuster (1). HONDURAS: Cortés, Parq. Nac. Cusuco, 5 km W Bs Aires, 26-27 agosto 1994, R.D. Cave (1).

O. mutenroshii Cano (2). HONDURAS: Cortés, Parque Nacional Cusuco, 2nd. broadleaved forest. nr. UTM 16P 369210 1713408. Ca. 1656 m alt., 07–11 VIII 2007. Coll. S. Beynon (holotype, UVGC); idem except UTM 16P 369795 1714017 alt. aprox. 1550 m. 16–20 VII 2006, dung baited pitfall trap, Coll. E. Marabuto (1 paratype, UVGC).

***O. nahuali* Schuster, Cano and Boucher** (5). HONDURAS: Olancho, route La Unión – El Dictamo, 16 km La Muralla, 1550 m, VII 1995, T. Porion & A. Grange (holotype, MNHN); Olancho, Parque Nacional La Muralla, 17 IX 1995, R. Lehman (1 paratype, UVGC); Olancho, Parque Nacional la Muralla, Sendero Pizote, 10 VI 2003, R. Turnbow (1 paratype, UVGC); P.N. La Muralla, 15.07N, 86.45W, 16 Jul 1998, col R. Cave (1, RC); Olancho, La Picucha, 11 km N Catacamas, 14.92740, -85.90983, bosque nuboso, 1800–2100 m, 8–14 V 2010, L. Sáenz (1, UVGC).

***O. politus* (Hincks)** (18). EL SALVADOR: H. Mte. Cristo, 2200m, Dr. A. Zilch, S. 1951 (Paratype, UVGC); Trifinio, 22-VII-70, Virkki, citogenética (1, INECOL); Idem but 27/7-60 (1, INECOL); idem but S. Ana, Trifinio, 8.III.1960. Réc.: J. Bechyné (2, one also with label: dibujo E. Aranda, INECOL); Hacienda Montecristo, Metapán, 13 mayo 1973 (1, UVGC); Chalatenango, 18-III-99 (1, UVGC); GUATEMALA: Chiquimula, camino entre San José Las Minas y al Plan de la Arada, 24 VI 1998, 1640-1910m (5, UVGC); Chiquimula, aldea Santa Rosalía, 14.49027N, -89.368611W, 1700m, 1-IV 2011, C. Suchité (4, UVGC); Santa Rosa, Pueblo Nuevo Viñas, Cerro Miramundo, finca Miramundo, 27-28 V 1999, E.B.

Cano, bosque encino casi nuboso (algunos pinos) (3, UVGC).

O. quichensis **Schuster and Reyes-Castillo** (20). MEXICO: Chiapas, Municipio de Ocosingo, second ridge NE of Las Margaritas, above La Soledad, 1828m, 1 VII 1981, D.E. & P.N. Breedlove (1 paratype, INECOL). GUATEMALA: Quiché, 9 mi ruta CA 7 hacia Nebaj, 19-X-1975, M. Dix (holotype, UVGC); Quiché, Uspantán, aldea Laj Chimel, 4 V 2006, 2300m, J. Rivas (3, UVGC); idem but norte Laj Chimel, San Pedro 2100m, VIII 1998, E. Cano & J. Monzón (1 UVGC), idem but aldea Laguna Danta 1 VI 1998, E. Cano (5 UVGC), idem but 2200m, 15 septiembre 2008, Monzón & Anderson (3 UVGC); Huehuetenango Dept., 9 mi Oeste de Barillas, 7 IV 1977, alt. 2250m #FK, J. Schuster, col. (1 paratype, INECOL); Huehuetenango, Todos Santos, Villa Alicia, 2450m, 9-10 V 2002, Col. A. Bailey (2, UVGC); Huehuetenango, Nentón, Yalambojoch, Reserva Ixcansán, 15.68176N, -91.23022W, 1800m, 14 VI 2013, M.Acevedo (2, UVGC); Huehuetenango, Soloma, Cerro Cruz Maltín, aldea Crinolina, 1900m, 18 V 2002, J.Monzón (1, UVGC).

O. ratcliffei **Cano** (1). HONDURAS: Olancho, La Picucha, 11 km N Catacamas, 14.92740, -85.90983, bosque nuboso, 1800–2100 m, 8–14 V 2010, L. Sáenz (LSD 451) (holotype, UVGC).

O. sandinoi **Cano** (5). NICARAGUA: Nueva Segovia, nr Jalapa, Cerro Jesús, 13.98079, -86.17922, 28–31 May 2011, L. Sáenz collector (LSD) (holotype, UVGC); 4 paratypes with the same data (3, UVGC; 1, USAC).

O. toriyamai **Cano** (8). HONDURAS: Comayagua, Parque Nacional Cerro Azul Meambar, 14.87140, - 87.90036, bosque nuboso, 800–1120 m, 20-24 V 2010, L. Sáenz. LSD 471 (holotype, UVGC); 2 paratypes with the same data, UVGC; Comayagua, Parque Azul Meambar, Agosto 30, 1996, Col. Marco Mendoza (1 paratype, UVGC); Santa Bárbara, Parque Nacional Santa Bárbara, 18 IV 2014, Yoshimoto leg (1, JYC); same data but 16 II 2014 (1, JYC); same data but buffer zone, 10 III 2013 (2, JYC).

O. tzutuhili **Schuster and Reyes-Castillo** (42). GUATEMALA: Alta Verapaz, Salamilá, 7 IV 1982, G. Ibarra (holotype, INECOL); Alta Verapaz, Tucurú, Chelemhá, 2200-2300m, Mt. Yalijux, B. nebular, G. Ibarra, 4 V 1989 (7, UVGC), Alta Verapaz, Chelemhá, marzo 1989, José Monzón (1, UVGC); idem but 22 VI 1989 (1, UVGC); idem but 22 III 1991 (1, UVGC); idem but 22 III 1989 (1, UVGC); Alta Verapaz, Secampana, Finca Esperanza, Q´anixul, 27 VI 1999, b. nuboso, S. Pérez (1, UVGC); Alta Verapaz, San Juan Chamelco, Campamento

Ecoquetzal, aprox. 1 hora en carro y 3 horas a pie de S.J. Chamelco, VI 1998, J.C. Schuster (3, UVGC); Zacapa, San Lorenzo, 1-15 IV 1993, #EER-B, Enio Cano, col. (6, INECOL; 17 UVGC; 1 MNHN); Quiché, Uspantán, aldea Laj Chimel, 2000m, junio 1998, ex bosque nuboso, E.B. Cano (2, UVGC).

***Ogyges* n. sp. 1** (296). MEXICO: Lagunas de Montebello, Mpio. La Trinitaria, Edo. de Chiapas, 1-IX-81, 1556m, P.R.-Castillo et al. cols. bosque mesófilo (1 male, INECOL); idem but 1470m, C. Castillo, col. (1, INECOL); Chiapas, Lagunas de Montebello, 5 VIII 1991, C. Mayorga (1, IBUNAM); Chiapas, Santa Rosa, VIII-62, G. Halffter leg (115, INECOL); Edo. de Chiapas, Santa Rosa, 20 V 1967, G. y V. Halffter y P. Reyes Cols. (18, INECOL); idem but 14-22 IV 62, G. Halffter (1, INECOL); idem but VI.68, P. Reyes leg (1, INECOL); Chiapas, San Antonio Independencia 24-11-87, F. Arias (1); Chiapas, 35 mi N of Las Margaritas, 8 mi N of Leiva Velásquez, 28 VI 1986, J.C. Schuster, 1620m (2, UVGC); Chiapas, Rancho Santa Rosa, 11-17 1975, P. Hubbell (1, UVGC). GUATEMALA: Huehuetenango, Mnt. S of Yalambojoch, rd. to Bulej, 1800m, 5 IV 1996, E. Cano, cloud forest (11, UVGC); Huehuetenango, Nentón, montaña al sur de Yalambojoch, 22 VI 1996, bosque nuboso, P. Lucas, leg (51, UVGC); Huehuetenango, Nentón, Yalambojoch, 1800-1900m, 24 VII 1998, bosque nuboso, col. E.B. Cano (3, UVGC); Huehuetenango, Nentón, San Francisco, Fca. San Francisco, 21 sept 1998, C. Bailey, José Monzón (1, UVGC); Huehuetenango, Barillas, Laguna Maxbal, 27 VII 2000, B. nuboso, 1300m, E. Cano, tronco podrido (47, UVGC); Huehuetenango, Barillas, camino entre Nuevo San Mateo y San Juan las Milpas, cerca de Laguna Maxbal, 28-30 V 1998, E. Cano, bosque nuboso (11, UVGC); Huehuetenango, Barillas, Buena Vista Chiblac, 27 V 1998, E. Cano, b. nuboso (9, UVGC); Huehuetenango, Barillas, Nuevo San Mateo, 1200m, 15685062E, 1761883N, 27 mayo 1998, E.B. Cano, C. Bailey & J. Monzón (1, UVGC); Huehuetenango, Barillas, Malpais, 1200m, 15687633E, 1757386N, junio 1998, E.B. Cano, C. Bailey & J. Monzón (4, UVGC); Huehuetenango, Nentón, Bulej 2 km norte, bosque nuboso, 22-23 sept. 1998, C. Bailey, J. Monzón (2, UVGC); Huehuetenango, Barillas, aldea Malpais, 1100m, oct. 1998, S. Pérez, bosque nuboso (1, UVGC); Huehuetenango, 4 mi NW Barillas, Fca. Chiblac Buena Vista, 19-23 VII 1990, Brody + Campbell, 1300m, female (1, UVGC); Huehuetenango, Barillas, camino entre Ojo de Agua y la Laguna Maxbal, 27 VII 2000, b. nuboso, 1300m, E. Cano, en el suelo (4, UVGC); Huehuetenango Dept., ca 3km NW of Yalhuitz Grande, 1422m, 18-19

July 2012, N15°55.863′, W91°17.960′, R.S. Zack, coll. (1, UVGC); Huehuetenango, Barillas, Unión Las Palmas, 1444m, 15.9311000, -91.2993100, 28 mayo 2011, Camposeco & Monzón (5, UVGC); idem but 15 V 2012, b. nuboso, F. Camposeco, troncos (1, UVGC); idem but 29 VII 2011 (1, UVGC).

***Ogyges* n. sp. 2** (7). HONDURAS: Yoro, 10 km NO Morazán, 24 III 1991, J.Schuster, #WJe (2, UVGC); Parque Nac. Pico Pijol, Linda Vista, 1450m, N15o09, W87o37′, 8-9 June 2007, RD Cave (1, RC); Pico Pijol, 3 June 2003, R. Turnbow (2, UVGC); Pico Pijol, 2 June 2003, R. Turnbow (2, UVGC).

Capítulo 4

A PRELIMINARY MITOCHONDRIAL PHYLOGENY (12S rRNA) OF THE NEW WORLD TRIBE PROCULINI (COLEOPTERA: PASSALIDAE: PASSALINAE)

A PRELIMINARY MITOCHONDRIAL PHYLOGENY (12S rRNA) OF THE NEW WORLD TRIBE PROCULINI (COLEOPTERA: PASSALIDAE: PASSALINAE)

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ABSTRACT

The non-coding mitochondrial 12S rRNA marker was sequenced for 41 species of New World Passalidae (4 of tribe Passalini, 37 of tribe Proculini), of 18 genera (2 Passalini, 16 Proculini), to resolve the phylogenetic relationships of the tribe Proculini through bayesian inference. The estimated gene tree showed moderate support to the tribe Proculini, but strong support for the following genera: *Ogyges* Kaup, *Undulifer* Kaup, *Heliscus* Zang, *Proculus* Kaup, *Veturius* Kaup, *Chondrocephalus* Kuwert (part), and *Verres* Kaup. Also, the tree recovered flightless species within flying genera (i.e. *Xylopassaloides* Reyes-Castillo, Fonseca and Castillo with *Vindex* Kaup; *Petrejoides* Kaup with *Chondrocephalus*), demonstrating that brachyptery (*i.e*. reduced wings, oval and fused elytra and reduced eyes) evolved several times in Passalidae. The tribe Proculini includes at least 225 described species of which we sequenced only 16.4%. Thus, with some inconsistencies, the 12S phylogeny is a first approximation that supports the molecular monophyly of the tribe Proculini. Further studies increasing taxon sampling and using more genetic markers surely will contribute to resolve divergences and to a more stable molecular phylogeny of Passalidae.

Key words: Passalini, *Passalus*, *Ameripassalus*, *Ogyges*, *Proculus*, *Vindex*, *Chondrocephalus*.

INTRODUCTION

Passalidae, or bess beetles, are black scarabaeoid beetles (tenerals are orange to reddish-brown), of medium to large size (13-80 mm), that live in family groups with overlap of generations in tunnel systems constructed under bark or inside rotten logs. A few species are found in detritus chambers of leaf-cutting ants (Schuster 1984), fern rhizomes (Kabakov 1967, Johki and Kon 1986) or log-ground interface (Kon and Johki 1987). Approximately 930 species are known in the world (Boucher 2006), mostly restricted to the tropics, although some species reach north in United States, Canada, Korea and Japan and others south in Uruguay, Argentina and Tasmania (Schuster 1978). Fossils are very rare, with only two known species: *Passalus indormitus* Cockerell, from the Oligocene (23-34 My) of Oregon (Reyes-Castillo 1977) and *Serrulus sinicus* Hong (= *Macrolinus sinicus* [Hong]), from the Miocene (6-23 My) of Shanwang, east China (Zhang 1989).

In the first systematic treatment of Passalidae, Kaup (1868) created the subfamily Proculinae to include the flightless genera of the New World. Later, Gravely (1918) split Proculinae into two subfamilies, Pseudacanthinae and Proculinae, including both flying and brachypterous species. These criteria were widely accepted until Reyes-Castillo (1970) rearranged the family Passalidae to consist of only two subfamilies: Aulacocyclinae (Asia and Pacific islands, including Australia) and Passalinae (Pantropical), the latter subfamily composed of two tribes, Passalini (Pantropical) and Proculini (restricted to the New World). According to Reyes-Castillo (1970: 83), the clypeus is the only structure that separated clearly Proculini from Passalini: Proculini, with exposed clypeus, dorsally visible, and Passalini with hidden clypeus, located under the frons. But exceptions occur; Jiménez-Ferbans and Reyes-Castillo (2014) described the genus *Ameripassalus* to include a group of Passalini with the clypeus "almost" exposed (as also occurs with *Passalus dominicanus* Doesburg). Also, we have collected species of the Proculini *Vindex* Kaup with the clypeus dorsally "almost" hidden. Thus, phylogenetic analyses of the entire family, based on wide taxon sampling, are urgent.

Although morphological phylogenies of the subfamily Aulacocyclinae (Hosoya *et al*. 2008) and the tribe Passalini (Jiménez-Ferbans and Reyes-Castillo 2014, 2015) have been published, actually only two published phylogenies deal with the entire family Passalidae: Boucher (2006), based on morphological and genital characters, and Fonseca *et al.* (2011),

based on the shape, size and number of diverticula of the hindgut. For 19 genera of the tribe Proculini, Boucher (2006) conserved the tribal level (*sensu* Reyes-Castillo 1970) and, although conserving its integrity, Fonseca *et al.* (2011) elevated the tribe Proculini to subfamily level. Both works, together with the unpublished *Ph.D*. dissertations of Fonseca (1987) and Gillogly (2005), mantained the tribe Proculini as monophyletic, whereas Gillogly (2005) found that the tribe Passalini is paraphyletic with relation to Proculini, as later did Jiménez-Ferbans and Reyes-Castillo (2014: 135, 2015: 8).

The tribe Proculini is poorly represented in North America north of Mexico and south of Panama and is highly diversified, particularly in the mountains, in Mexico and Central America. Many mountainous species of Proculini are brachypterous with the morphological combination of very reduced wings, fused and rounded elytra and reduced eyes. For instance, some genera are characterized by their brachyptery (e.g. *Proculejus* Kaup, *Proculus* Kaup, *Ogyges* Kaup, *Undulifer* Kaup, *Xylopassaloides* Reyes-Castillo, Fonseca and Castillo, and *Pseudacanthus* Kaup), generating doubt that that combination of characters may be homoplasic. As indicated by Marshall (2000: 229, unpublished) related to the phylogeny of *Verres* Kaup: "adding even more distantly related flightless taxa to the analysis (e.g. *Ogyges* Kaup) only continues to group the flightless forms together…". Thus, in order to elucidate the phylogenetic relationships within Proculini, avoiding the use of morphological characters associated with flight, we performed a molecular phylogenetic analysis using the mitochondrial 12s rRNA marker.

Published DNA sequences of Passalidae are scarce. Sequences of six species of Passalidae have been obliquely included in phylogenetic analyses of Scarabaeoidea (Smith *et al*. 2006 [species not indicated], Ahrens *et al.* 2014 [*Aulacocyclus* sp.]), or as outgroups of Lucanidae (Hosoya and Araya 2005 [*Cylindrocaulus patalis* (Lewis)], Kim and Farrel 2015 [*Aceraius* sp., *Ceracupes fronticornis* (Westwood)]) or Staphyliniformia (Caterino *et al*. 2005 [*Aulacocyclus* sp., *Odontotaenius disjunctus* (Illiger)]).

The present work is the first attempt to elucidate the internal relationships of the tribe Proculini, using molecular data. Originally, we focused on the genus *Ogyges* and related genera; nevertheless, because molecular phylogenetic analyses of the family Passalidae are still lacking, we widened the original scope, including more genera of Proculini.

MATERIALS AND METHODS

DNA extraction and sequencing

We used material of Passalidae fixed in 95% ethanol and stored a 4°C at the Arthropod Collection of Universidad del Valle de Guatemala (Table 1). Conceptual taxonomy at generic level was based on Reyes-Castillo (1970) except for the genera *Undulifer* and *Veturius* Kaup, based on Boucher (2006), *Xylopassaloides*, based on Reyes-Castillo *et al*. (1987) and Schuster (1993), *Petrejoides* Kuwert, based on Schuster (1991), and *Ameripassalus* Jiménez-Ferbans and Reyes-Castillo, based on Jiménez-Ferbans and Reyes-Castillo (2014). We selected the non-coding mitochondrial 12S rRNA gene because it is conservative, short (about 450pb), easy to extract and amplify and has been extensively used in molecular taxonomy and phylogeny (Patwardhan *et al*. 2014).

DNA was extracted using the method of Henry *et al*. (1990), consisting in homogenizing the legs with liquid nitrogen and washing the rest with two buffers, TENT (10mM Tris-HCl, pH 7.4; 24mM EDTA; 10mM NaCl and 0.5% Triton X-100) and TEN (the buffer TENT without Triton X-100). Two extractions with phenol-chloroform were made and DNA was precipitated in 100% isopropanol. The 12s marker (400-450 pb) primers SR-J-14199 (5'-TAC TAT GTT ACG ACT TAT- 3') and SR-N-14594 (5'-AAA CTA GGA TTA GAT ACCC-3') were used. PCR reaction was performed in a final volume of 25µl with the following recipe: 16.80 µl of H_2O, 2.5 µl Buffer 10x, 1.5 µl of MgCl, 0.5 µl of each primer, 1.00 µl of DNTP´s, 0.20 µl of Taq and 200 ng of DNA. The PCR products were visualized on a 1% agarose gel. The amplified segments were purified with the kit Wizard PCR Preps DNA Purification System, Promeg, and sending for sequencing to Macrogen, USA, with a concentration of 30ng/µl, together with the primers of 12s (5pmol/µl). The obtained sequences (forward and reverse) were edited with the programs Seqman Pro and Editseq of Lasergene 8 (DNASTAR, Inc. Privacy Statement - NetNation). The sequences were aligned with Clustal W, with the program Megalign (DNASTAR, Inc. Privacy Statement - NetNation).

Phylogenetic analysis

For 62 sequences of 41 species (4 of Passalini, 37 of Proculini), of 18 genera (2 of Passalini, 16 of Proculini), we performed a phylogenetic analysis using MrBayes 3.1.2 (Huelsenbeck

and Ronquist 2003) for Bayesian Inference. The evolutionary model that best fitted the sequence data was selected using JModelTest 2 and the Akaike information criterium (Darriba *et al*. 2012, Guindon and Gascuel 2003). The Bayesian tree was inferred using the TrN+G model (derived fixed transition frequencies = 1.0000, 5.1209, 1.0000, 1.0000, 2.9636, 1.0000 for rAC, rAG, rAT, rCG, rCT, rGT, respectively; fixed nucleotide frequencies = 0.4020, 0.0624, 0.1453, 0.3903 for A, C, G and T, respectively), under one million generations, sampling each hundredth tree, and discarding 1000 trees as burn-in. Phylogeny was manually re-rooted with the Passalini tribe + *Undulifer* + *Pseudacanthus subopacus* clade using the program Mesquite (Maddison and Maddison 2015). Statistical support for recovered clades was assessed using posterior probabilities (PP).

RESULTS AND DISCUSSION

The estimated mitochondrial gene tree of Bayesian inference (Figure 1) shows a moderate support to the tribe Proculini (PP= 0.65) and strong support for some genera: *Ogyges*, *Undulifer, Heliscus*, *Proculus*, *Veturius*, *Chondrocephalus* (part), and *Verres*. Not surprisingly, the clade *Vindex* + *Proculejus* + *Xylopassaloides* resolves *Vindex* Kaup as paraphyletic. As Schuster (1993: 118) indicated, the only character that separates *Xylopassaloides* from *Vindex* is the form of clypeus, which seems to be a matter of degree. Thus, here, we present some molecular evidence to conclude that *Xylopassaloides* (but, only one species sequenced) is just a brachypterous group of *Vindex*, and suggests that *Xylopassaloides* should be merged with *Vindex*. On the other hand, the genus *Proculejus* is in urgent need of systematic revision and our results are provisional because only one species was considered in the analysis. Nevertheless, Schuster and Reyes-Castillo (1981) also suggested a close relationship of *Vindex* with *Proculejus* based on larval similarities.

The three Mesoamerican species of *Petrejoides* of the clade *Chondrocephalus* (part) + *Petrejoides*, are brachypterous. Previously, Boucher (2006: 347) transferred *P. salvadorae* Schuster to *Chondrocephalus*, based on characters of the frons. Our tree supports the statement of Boucher (2006) adding to the group an undescribed species of *Petrejoides* from El Salvador and the very rare *P. pokomchii* Schuster, from Sierra de las Minas in Guatemala. Strangely, the flying and widely distributed *Ch. granulifrons*, remained outside *Chondrocephalus*.

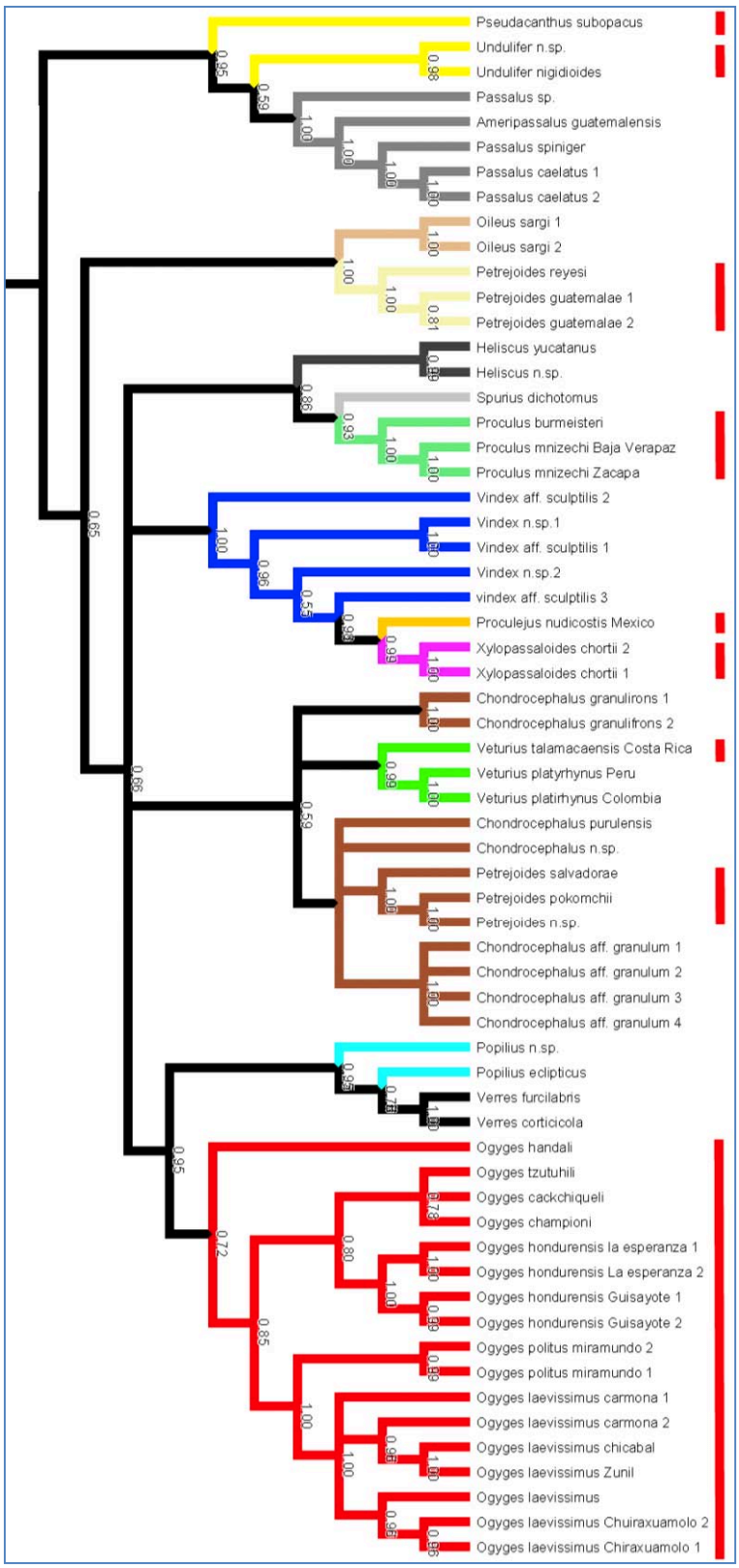

Figure 1. Mitochondrial 12S rRNA phylogeny of the tribe Proculini. The tribe Passalini in light gray and *Ogyges* in red. Numbers at nodes represent the bayesian posterior probabilities.

The red vertical bars indicate the brachypterous taxa. Provenance of specimens and species as indicated in Table 1.

The genus *Veturius* includes flightless and flying species (Boucher 2006); *V. standfussi* Boucher and *Veturius* sp., has normal wings while *V. talamacaensis* Boucher is brachypterous. The species *Petrejoides reyesi* Schuster and *P. guatemalae* Schuster and Reyes-Castillo are also flightless. Then, as seen on Figure 1 (red vertical bar), molecular data demonstrate that brachyptery has evolved several times in Passalidae.

The analysis recovered *Ogyges* as monophyletic (six species of 25 described) and related to *Verres* + *Popilius*. Neither Marshall (2000, unpublished), who estudied *Verres*, nor Gillogly (2005, unpublished), who estudied *Popilius* Kaup, or Cano *et al*. (in prep.) who studied *Ogyges*, have considered this relationship. Boucher (2006) related *Ogyges* to the flightless genera *Proculus* and *Proculejus*. The internal clades of *Ogyges*, similarly, were resolved in a manner that is not congruent with the morphological phylogeny (Cano *et al*. in prep.). These inconsistencies may be resolved using more species of *Ogyges* in the molecular analysis and using more genes. Nevertheless, the 12S phylogeny is an interesting first approximation confirming monophyly in some genera and suggesting paraphyly in others. Also, its results relating the tribe Passalini with *Pseudacanthus subopacus* + *Undulifer* is similar to relationships of some Passalini with some Proculini, as indicated by Jiménez-Ferbans and Reyes-Castillo (2014, 2015) and Gillogly (2005). In fact, *Undulifer nigidioides* (Hincks) was described originally as a *Passalus* (*Phoroneus*) section "Petrejus".

The mitochondrial marker 12S rDNA is highly conserved and has been used to detect genetic diversity of higher taxa levels such as phyla (Arif *et al*. 2009). Also, has been used to resolve phylogenetic relationships of several taxonomic groups, such as sharks (Masstor *et al*. 2014), gobioid fishes (Wang *et al*. 2001), wolf spiders (Park *et al*. 2007), crustaceans (Tomikawa *et al.* 2007), hyloid frogs (Darst and Cannatella 2004), fruit flies (Han and Ro 2005), and beetles (Magro *et al*. 2010). In our laboratories it has not been useful to detect intraspecific differences in *Anopheles albimanus* (Mérida *et al*. 1999), nor has been successful for *Bemisia tabaci* biotypes (Palmieri *et al*. 2002). Norris *et al*. (1999) reported that 12S rDNA with ticks is not as good as 18S rDNA, not even combined with 16S. Though, the combination of CO1 and 12S is appropriate to distinguish at different taxonomic levels (Patwardhan *et al*. 2014).

Although considered as fast evolving (Brown *et al*. 1979), the patterns of evolutionary change of 12S apparently are not equivalent in widely separated taxa. Our results with the populations of *Ogyges laevissimus* (Kaup) and *O. hondurensis* Schuster and Reyes-Castillo (Figure 1) indicate that the 12S rRNA works well for distinguishing species and populations of Passalidae. As species are well characterized, the marker is useful for taxonomic studies at the generic level, and in combination with other markers, is promising at higher phylogenetic levels. Actually, the tribe Proculini includes at least 225 described species; for this reason, conclusions of the study are limited: we sequenced only 37 species that represent only the 16.4% of the known species. Further studies increasing taxon sampling and using more genetic markers surely will contribute to resolve divergences and to a more stable molecular phylogeny of Passalidae.

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ACKNOWLEDGEMENTS

Collecting permits in Guatemala were provide by Consejo Nacional de Areas Protegidas (CONAP). Financial support was provided by Consejo Nacional de Ciencia y Tecnología de Guatemala (CONCYT). For academic support we thank Universidad del Valle de Guatemala (UVG). Enio B. Cano thanks the Programa de Doctorado en Ciencias Biológicas of the Universidad Nacional Autónoma de México (UNAM) for support. This work forms part of the doctoral thesis of Enio B. Cano.

Table 1. Checklist of sequenced material and geographical distribution.

Oileus sargi	Guatemala: Chiquimula, Plan de la Arada.	1968m
Oileus sargi	Guatemala: no data.	no data.
Xylopassaloides chortii	Guatemala: Zacapa, La Unión.	1500m
Xylopassaloides chortii	Guatemala: Chiquimula, aldea Cafetales, Chanmagua.	1484m
Chondrocephalus granulum 1	Guatemala: Huehuetenango, Soloma, Cerro Cruz Maltín.	1900m
Chondrocephalus granulum 2	Guatemala: Huehuetenango, Soloma, Cerro Cruz Maltín.	1900m
Chondrocephalus granulum 3	Guatemala: Huehuetenango, Soloma, Cerro Cruz Maltín.	1900m
Chondrocephalus granulum 4	Guatemala: Huehuetenango, Soloma, Cerro Cruz Maltín.	1900m
Chondrocephalus purulensis	Guatemala: Chiquimula, Plan de la Arada.	1968m
Chondrocephalus n.sp.	Guatemala: Santa Rosa, Cerro Miramundo.	1810m
Chondrocephalus granulifrons 1	Guatemala: El Progreso, Sierra de las Minas.	2500m
Chondrocephalus granulifrons 2	Guatemala: Sacatepequez, Volcán Acatenango.	2700m
Spurius dichotomus	Guatemala: Baja Verapaz, Purulhá.	1600m
Passalus spiniger	Guatemala: no data.	no data.
Passalus caelatus	Guatemala: Huehuetenango, Soloma, Cerro Cruz Maltín.	1900m
Passalus sp.	Guatemala: no data.	no data.
Ameripassalus guatemalensis	Guatemala: no data.	no data.
Petrejoides guatemalae	Guatemala: Huehuetenango, Chiantla, Laguna Magdalena.	3200m
Oileus sargi	Guatemala: Chiquimula, Plan de la Arada.	1968m
Petrejoides guatemalae	Guatemala: Huehuetenango, San Mateo Ixtatán, Cerro Bobi.	3015m
Petrejoides salvadorae	Guatemala: Chiquimula, Plan de la Arada.	1900m
Petrejoides reyesi	Honduras: Tegucigalpa, P.N. La Tigra.	1700m
Petrejoides n.sp.	El Salvador: Chalatenango, Cerro El Pital.	2700m
Petrejoides pokomchii	Guatemala: El Progreso, Cerro Pinalón, Sierra de las Minas.	2500m
Proculejus nudicostis	Mexico: Guerrero, Omiltemi.	2450m
Proculus mnizechi	Guatemala: Baja Verapaz, Purulhá.	1600m
Proculus miniszechi	Guatemala: Zacapa, La Unión.	1500m
Proculus burmeisteri	Honduras: Ocotepeque, El Portillo (Güisayote)	1900m
Pseudacanthus subopacus	Guatemala: Quetzaltenango, Fuentes Georginas.	2400m
Pseudacanthus n.sp.	Guatemala: Huehuetenango, Nentón, Yalambojoch.	1800m
Pseudacanthus nigidioides	Guatemala: Quetzaltenango, Volcán Lacandón.	2200m
Vindex aff. *sculptilis*	Guatemala: Huehuetenango, Barillas, La Joya.	2159m
Vindex aff. *sculptilis*	Guatemala: no data.	no data.
Vindex aff. *sculptilis*	Guatemala: Huehuetenango, Barillas, aldea La Joya.	2159m

Vindex n.sp.2	Guatemala: Huehuetenango, San Mateo Ixtatán, Chibalasum.	2823m
Vindex n.sp.1	Guatemala: Quetzaltenango, Volcán Lacandón.	2200m
Heliscus yucatanus	Guatemala: Petén, Biotopo Dos Lagunas.	280m
Heliscus n.sp.	Guatemala: Izabal, Sierra Caral.	1150m
Popilius n.sp.	Guatemala: no data.	no data.
Popilius eclipticus	Guatemala: Baja Verapaz, Purulhá.	1600m
Verres furcilabris	South America: no data.	no data.
Verres corticicola	Guatemala: Izabal, Sierra de Caral.	1150m
Veturius standfussi	Colombia: Huila, Gigante.	2250m
Veturius sp.	Perú: Huánuco, Tingo María.	670m
Veturius talamacaensis	Costa Rica: Alajuela, Volcán Poás.	2500m
Ogyges laevissimus	Guatemala: Sacatepéquez, Volcán de Agua.	2700m
Ogyges laevissimus	Guatemala: Quetzaltenango, Volcán Chicabal.	2500m
Ogyges laevissimus	Guatemala: Sololá, Chuiraxamoló.	3000m
Ogyges laevissimus	Guatemala: Sacatepéquez, Cerro Carmona.	2100m
Ogyges laevissimus	Guatemala: Quetzaltenango, Fuentes Georginas.	2400m
Ogyges hondurensis	Honduras: Intibuca, La Esperanza.	1800m
Ogyges hondurensis	Honduras: Ocotepeque, El Portillo (Güisayote).	1900m
Ogyges politus	Guatemala: Santa Rosa, Cerro Miramundo.	1800m
Ogyges cackchiqueli	Guatemala: Huehuetenango, Cuilco mountain.	2100m
Ogyges tzutuhili	Guatemala: Zacapa, San Lorenzo, Sierra de las Minas.	2400m
Ogyges championi	Guatemala: Baja Verapaz, Purulhá.	1600m
Ogyges handali	Guatemala: Chiquimula, Plan de la Arada.	1600m

DISCUSIÓN GENERAL Y CONCLUSIONES

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DISCUSIÓN

Ogyges es un género braquíptero y, en consecuencia, comparte con otros géneros y especies de Passalidae al menos cuatro caracteres: ojos reducidos, alas reducidas y élitros redondeados y fusionados. Esa asociación de caracteres que no parecen relacionadas (particularmente los ojos reducidos), así como la forma convexa del cuerpo, sugieren que a nivel genético podría estar ocurriendo pleiotropía (el efecto de un gen sobre dos o más caracteres) o desequilibrio de ligamiento (la asociación no aleatoria de alelos en loci distintos), dos explicaciones alternativas que, para otros taxa, se han sugerido cuando existe correlación entre conjuntos de rasgos adaptativos (e.g Baer y Lynch 2003). En todo caso, tradicionalmente los grupos braquípteros se han considerado filogenéticamente cercanos, aunque molecularmente parecen alejados o viceversa (e.g. *Vindex* y *Xylopassaloides*). A *Ogyges* se le ha relacionado con *Proculus* y *Proculejus*; sin embargo, el análisis molecular (Capítulo 4) coloca a *Proculus* y a *Proculejus nudicostis* alejados de *Ogyges*. *Proculus* ya ha sido revisado (Schuster *et al*. 2003), pero el clado que incluye *Vindex* + *Xylopassaloides* + *Proculejus nudicostis*, necesita urgentemente de ser estudiado. *Ogyges* fue separado del género hermano *Proculejus* por Kaup (1871) por las estrías elitrales superficiales y la ausencia de setas a los lados de los élitros. Pero fue Kuwert (1896) quien separó a *Ogyges* de *Proculejus* por las diferencias en el clípeo, con una clara sutura en *Proculejus* y un clípeo convexo (y aparentemente sin sutura) en *Ogyges* [*laevissimus*]. Este último criterio ha permanecido desde que Reyes-Castillo (1970) revivió el género y fue seguido por Schuster y Reyes-Castillo (1990) y por Schuster *et al*. (2005). Boucher (2006) fue el primero que consideró poco convincente la separación de ambos géneros basado únicamente en la ausencia de sutura frontoclipeal; sin embargo, en su análisis filogenético, aunque sostiene a *Ogyges* como monofilético, no encontró alguna autapomorfía. Los resultados del presente trabajo demuestran (Capítulo 3) que la sutura frontoclipeal es un carácter variable y homoplásico, particularmente porque una nueva especie de Honduras presenta una sutura frontoclipeal claramente visible. Sin embargo, también se demostró (Capítulos 1 y 3), que la forma de los dientes internos de la mandíbula constituyen una autapomorfía de *Ogyges*, presente incluso en la especie con la sutura frontoclipeal bien delimitada.

Ogyges fue revisado por Schuster y Reyes-Castillo (1990), quienes basaron su definición del género en el trabajo clásico de 1970, por lo cual no lo redescribieron. Con ese trabajo el número de especies aumentó a 12, con distribución en Chiapas, Guatemala, El Salvador y Honduras. En el presente trabajo, se aumentó el número de especies a 27 (de las cuales, 25 ya estaban descritas), por lo cual, se hizo necesario realizar una nueva descripción del género (Capítulo introductorio). Así, con una mayor amplitud filogenética, el análisis biogeográfico basado en el análisis filogenético (Capítulo 3), contrasta con las hipótesis biogeográficas de Schuster y Reyes-Castillo (1990), quienes relacionan especies del grupo de *O. crassulus* de Honduras con especies del grupo de *O. championi* del norte de Guatemala.

Por otro lado, este trabajo presenta un análisis detallado de las barreras biogeográficas de América Central Nuclear, para pasálidos de montaña que no pueden volar, evidenciando vicarianza para los tres grupos de especies. Es posible que estudios posteriores puedan confirmar esta hipótesis de vicarianza y que igualmente pueda aplicar a otros grupos de organismos.

CONCLUSIONES GENERALES

1. *Ogyges* Kaup es un género monofilético, demostrado por el análisis molecular (12S rRNA) y el morfológico (53 caracteres). El análisis filogenético morfológico demostró la existencia de al menos 5 sinapomorfías, una de ellas, la forma del diente interno de la mandíbula, es exclusiva del género y es una clara autapomorfía.

2. La braquiptería, con el conjunto de caracteres asociados (ojos reducidos, alas reducidas y élitros redondeados y fusionados), ha evolucionado múltiples veces en Passalidae, demostrado por el árbol del gen 12S rRNA.

3. El análisis biogeográfico basado en la filogenia morfológica mostró que los tres clados (grupos de especies) presentan una distribución mayormente alopátrica, con el grupo de *O. championi* distibuido en el bloque Maya y los grupos de *O. laevissimus* y *O. crassulus* distribuidos en el bloque Chortís.

4. Con base en el análisis filogenético morfológico se demostró que las principales barreras

que han afectado la distribución de *Ogyges* son: el Istmo de Tehuantepec en México, que separa a *Ogyges* del grupo hermano *Proculejus*; las zonas de sutura de Motozintla-Comaltitlán en Chiapas y del Motagua-Cuilco en Guatemala, que separan el grupo de especies de *O. championi* de los otros grupos de especies; el sistema de fallas del río Guayape en Honduras, que representa el límite oriental del grupo de especies de *O. crassulus*; el intrincado sistema de valles secos del sistema Ulúa-Chamelecón-Olancho, en el centro de Honduras que separa parcialmente a los grupos de especies de *O. crassulus* y *O. laevissimus*; y los valles de tierras bajas de los ríos Colón y Comalí entre las fronteras de Honduras y Nicaragua (o quizás, la sutura norte del Terreno Siuna en Nicaragua), que representan el límite de distribución sur para el género *Ogyges*.

5. La complicada historia taxonómica de *Ogyges* proviene de tres motivos: 1) el método de clasificación quinario (taxones con únicamente cinco miembros) adoptado por Kaup en 1871; 2) la confusión introducida por Kuwert (1896) al confundir el *Proculejus championi* de Bates con el *Proculejus laevior* (=*Veturius laevior*] de Kaup; y 3) el único especímen tipo de *P. laevior* (= *V. laevior*) permaneció inaccesible para la mayoría de los autores relevantes en el estudio de *Ogyges*.

6. La ausencia de sutura frontoclipeal como un caracter diagnóstico de *Ogyges* se rechaza. Al menos una especie de *Ogyges* presenta una sutura frontoclipeal completa, y el clípeo se presenta con diferentes grados de separación de la frente en varias especies del género.

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