Universidad Autónoma de Tlaxcala

Posgrado en Ciencias Biológicas

Filogenia de género *Pasimachus* Bonelli (Coleoptera: Carabidae)

TESIS

QUE PARA OBTENER EL GRADO ACADÉMICO DE

MAESTRO (A) EN CIENCIAS BIOLÓGICAS

Presenta

Juan Rafael Cerón Gómez

Director

Dr. Andrés Ramírez Ponce

Tlaxcala, Tlax. Enero, 2019

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PRESENTE

Los abajo firmantes, miembros del jurado evaluador del proyecto de tesis que **Juan Rafael Cerón Gómez** realiza para la obtención del grado de Maestro en Ciencias Biológicas, expresamos que, habiendo revisado la versión final del documento de tesis, damos la aprobación para que ésta sea impresa y defendida en el examen correspondiente. El título que llevará es: **"Filogenia del género Pasimachus Bonelli (Coleóptera: Carabidae)".**

Sin otro particular, le enviamos un cordial saludo.

ATENTAMENTE
TLAXCALA, TLAX., 29 NOVIEMBRE DE 2018

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RESUMEN

El género *Pasimachus* está formado por 34 especies americanas cuyas relaciones con otros géneros ha sido controversial. La propuesta tradicional más aceptada lo considera como el género hermano de *Mouhotia* Castelnau, un género oriental con tres especies y en conjunto ambos géneros conforman la tribu Pasimachini. Otra propuesta coloca a *Mouhotia* en la subtribu Carenina y a *Pasimachus* como único representante de la subtribu Pasimachina, ambas dentro de la tribu Scaritini que es cosmopolita. La única revisión taxonómica data de más de 70 años en la cual se subdivide el género en dos subgéneros, dejando muchas dudas sobre su afinidad y posición dentro de alguna tribu. En el presente trabajo se propone una filogenia para las especies de *Pasimachus*, y se pone a prueba la monofilia de Pasimachini respecto a otras tribus (Scaritini y Carenini), además se analiza la evolución de estructuras taxonómicamente informativas con técnicas filogenéticas y de morfometría geométrica. El análisis filogenético basado en parsimonia, se realizó con seis módulos de caracteres en TNT (uno discreto, uno merístico, y cuatro de morfometría geométrica). El único cladograma obtenido valida la monofilia de Pasimachini, se muestra que *Pasimachus* es monofilético y hermano de *Mouhotia*. Además, dentro de *Pasimachus*, el subgénero *Pasimachus* es un grupo monofilético, no así *Emydopterus* que se muestra como un grupo parafilético, debido a esto se propone una nueva clasificación a nivel de subgéneros en *Pasimachus*. Se discuten dos teorías de la distribución de *Pasimachus* haciendo mención de la relevancia del Cinturón Volcánico Transmexicano como un elemento que ha favorecido la generación de un patrón de vicarianza importante en la evolución del grupo, y aspectos biogeográficos para los patrones filogenéticos a nivel de la tribu Pasimachini. El cladograma indica que la forma del pronoto, de la protibia, y de élitro son considerablemente estable dentro de géneros y tribus a pesar de millones de años que han mantenido separados los linajes, y que tiene además una notable influencia en el patrón de ocupación del morfoespacio a nivel de subtribus, con algunos ejemplos claros de eventos de convergencia.

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I. INTRODUCCIÓN

1.1. Generalidades de la familia Carabidae

A nivel mundial el orden Coleoptera es el más diverso de la clase Insecta, se encuentra dividido en cuatro grandes subórdenes: Adephaga, Myxophaga, Polyphaga y Archostemata, con 211 familias y aproximadamente 360,000 especies descritas (Bouchard y cols. 2011).

Dentro del suborden Adephaga se encuentran familias de coleópteros con gran agilidad para la locomoción terrestre y acuática (Erwin 1991). Una de estas familias es Carabidae, que data del jurásico temprano, hace unos 200 millones de años (Ponomarenko 1992, Bouchard y cols. 2009). Esta familia es muy diversa, y son reconocidos por características morfológicas muy particulares como las patas largas y delgadas, la fórmula tarsal pentámera, la sutura notopleural del pronoto evidente, las antenas filiformes, con muchas de sus especies especializadas en la carnivoría, aunque algunas pueden ser saprófagas u omnívoras necrófagas (Morón y Terrón 1988).

La familia Carabidae ha logrado adaptarse prácticamente a todos los hábitats terrestres del planeta, desde las selvas tropicales hasta los desiertos, exceptuando la Antártida, por lo que se considera una familia cosmopolita (Larochelle y Lariviere 2003).

A diferencia de otros grupos de coleópteros, estos son organismos de hábitos solitarios, y muchas especies en su estado adulto se distinguen por ser braquípteras, es decir, poseen el segundo par de alas reducido, lo que les impide volar, compensando la pérdida del vuelo con el hábito fosorial (Brandmayr 1991, Lövei y Sunderland 1996).

Los adultos se caracterizan por la talla corporal, en un rango entre 1-77 mm, desde la cabeza hasta el ápice de los élitros, la forma del cuerpo plana o muy convexa, y coloración variable, con organismos completamente negro-opacos, o con tonos amarillentos, marrón, manchados, e incluso metálicos (Reichardt 1977). Poseen patas largas y delgadas de tipo corredor, coxas posteriores grandes que interrumpen el primer segmento abdominal, trocánter posterior muy grande, y en la mayoría, la existencia de sutura notopleural muy marcada (Borror y cols. 1989; Fig. 1). Las larvas son campodeiformes con segmentación corporal claramente definida y coloraciones marrón, rojiza o negra. Las larvas que poseen cabeza y antenas prominentes debido a sus hábitos depredadores y desarrollo de órganos sensoriales (Ball y Bousquet 2001).

La estimación de la diversidad de carábidos en el mundo es aproximada, oscila en las 34 mil especies, agrupadas en 23 subfamilias, 100 tribus y 1860 géneros (Lorenz 1998, Bousquet 2012), por lo que es considerada la familia más diversa del suborden Adephaga (Maddison 2006). En México, se han registrado 172 géneros y 1957 especies, de las cuales 1191 (60%) son endémicas (Ball y Shpeley 2000).

La clasificación de la familia Carabidae aún tiene problemas debido a los pocos estudios filogenéticos en la mayoría de los taxones, lo que ha generado un conflicto de clasificación e inestabilidad en las definiciones genéricas (Hogan 2012).

Figura. 1 Ejemplar adulto *de Calosoma aurocinctum* Chaudoir perteneciente a la familia Carabidae.

1.2. El género *Pasimachus* Bonelli

El género *Pasimachus* Bonelli pertenece a la subfamilia Scaritinae compuesta por ocho tribus, 125 géneros y 1850 especies a nivel mundial (Lorenz 2005, Bousquet, 2012). *Pasimachus* está conformado por 34 especies que se distribuyen desde el sur de Canadá hasta Panamá, con la mayor diversidad en México (Bänninger 1950, Erwin 2011, Bousquet, 2012) (Fig. 2).

Este género se distingue por la talla corporal grande, de 17 a 35 mm, la forma del cuerpo deprimida y las patas especializadas para un modo de vida fosorial, es decir, especializado para cavar, además de élitros con reflejos metálicos llamativos generalmente, y por tener hábitos nocturnos como depredadores activos de otros artrópodos (Hogan 2012). Otras características importantes que distinguen a *Pasimachus* son las siguientes: las mandíbulas fuertes y dentadas, que al cerrarse no permiten abertura entre estas y el labro; el cual tiene una forma lobulada con presencia de sedas centrales y laterales; la cabeza con un solo poro supraorbitario; el clípeo carente de sedas; la presencia de un poro sedífero en el antenómero; y la presencia de siete estrías en los élitros (Bänninger 1950).

La taxonomía del género *Pasimachus* ha sido muy poco abordada, hasta ahora sólo existe un trabajo de revisión que incluye una clave y que lo ubica dentro de la subtribu Pasimachina en la tribu Scaritini (Bänninger 1950), sin embargo, otros autores lo clasifican como Pasimachini, la cual es una de las ocho tribus que conforman la subfamilia Scaritinae, y es donde se ubican como taxones hermanos *Pasimachus* Bonelli y *Mouhotia* Castelnau, un género oriental con sólo tres especies (Bousquet 2012).

La propuesta de considerar a Pasimachini con *Pasimachus* y *Mouhotia* como géneros hermanos ha sido rechazada por algunos autores, como Lorenz (2005) y Hogan (2012), quienes han optado por ubicar a *Mouhotia* en Carenina y a *Pasimachus* en Pasimachina, ambos dentro de Scaritini, aunque otros como Bouchard y cols. (2011) y Bosquets (2012) la han validado. Esto ha generado mayor controversia en la clasificación y delimitación de la tribu y de la misma subfamilia, por lo que marcos de referencia filogenéticos, donde se aclaren las relaciones con las otras subtribus, entre los géneros y dentro de éstos, son necesarios para avanzar en el conocimiento del grupo (Bousquet 2012).

La distribución geográfica de los géneros que conforman la tribu Pasimachini es disyunta, además de la talla corporal contrastante, sin embargo, son notables algunas similitudes morfológicas: *Mouhotia* tiene una forma corporal más similar a *Pasimachus* que a cualquier otro género de Carenina, además de otros caracteres como la forma y coloraciones metálicas del pronoto y élitros, la presencia y forma de estrías en los élitros y la forma carinada en el intervalo siete. Sin embargo, *Pasimachus* tiene sedas en diferentes estructuras del cuerpo y *Mouhotia* carece de sedas en casi todo el cuerpo (Bänninger 1950). Además, *Pasimachus* generalmente tiene ocho intervalos elitrales, siendo el 7º el más desarrollado, mientras que *Mouhotia* tiene diez y el 9º es el más desarrollado; en *Pasimachus* las mandíbulas pueden cerrarse por completo y el último segmento de los palpos labiales suele ser delgado o ligeramente dilatado, y las mandíbulas de *Mouhotia* no pueden superponerse de tal manera que no pueden cerrarse completamente y el segmento terminal de los palpos labiales es triangular y en forma de abanico.

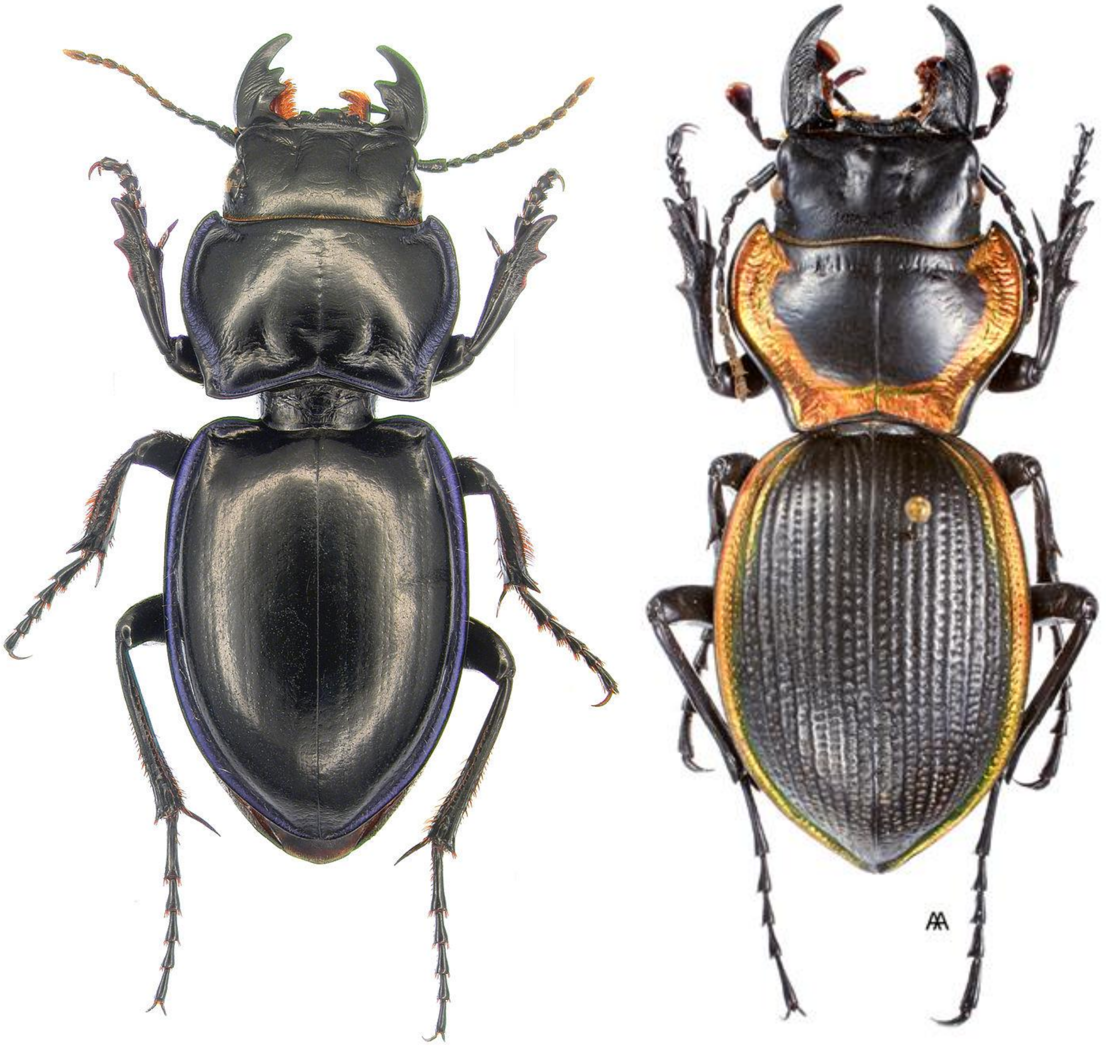


Figura 2. Ejemplar adulto de *Pasimachus elongatus* LeConté y *Mouhotia* sp.

1.3. Morfometría geométrica

El desarrollo de la morfometría a inicios del siglo XX marcó una transición en la morfología y en la biología en general, ya que pasó de abordar las formas de los organismos de manera cualitativa, a una manera cuantitativa, la cual es definida por Bookstein (1996) como el estudio cuantitativo de las formas biológicas (Galán 2015). En las últimas décadas, el desarrollo de distintas técnicas en la morfometría ha permitido incluir la variación de la forma de las estructuras y las trayectorias de cambio bajo un contexto geométrico, que permite eliminar efectos de posición, escala y rotación de las estructuras. De esta manera, la estructura en cuestión no es analizada sólo por sus dimensiones, sino por la relación de sus partes en un espacio (Kendall 1977, Toro y cols. 2010), bajo diferentes contextos como ecológicos, filogenéticos, etológicos, entre otros (Klingenberg 2010, Toro y cols. 2010).

La morfometría geométrica en los últimos años se ha convertido en una herramienta útil en disciplinas como la taxonomía y la sistemática filogenética. Esta contribución no ha sido menor, ya que existen diversos trabajos donde se evidencia la utilidad de estas herramientas en el descubrimiento y descripción de especies crípticas, hipótesis filogenéticas, etc. (Soto-Vivas y cols. 2011).

El propósito de este trabajo es realizar análisis cladísticos con caracteres morfológicos y morfogeométricos para poner a prueba la monofilia de *Pasimachus* y Pasimachini, conocer las relaciones filogenéticas de las especies de *Pasimachus* y además proponer hipótesis sobre la evolución de caracteres con importancia en la taxonomía previa.

II. ANTECEDENTES

2.1. Clasificación de Carabidae, Scaritinae y *Pasimachus*

El origen, evolución y afinidades filogenéticas de los carábidos se ha estudiado durante más de 200 años (Hogan 2012) y diversas clasificaciones han sido propuestas por autores como Dejean (1825), Lacordaire (1854), Chaudoir (1880), Ball (1979), quien hizo una recopilación de las diferentes clasificaciones de Carabidae a lo largo de la historia, dividiéndola en tres periodos: prelinneano (antes de 1758), Linneaeus-Fabricius (1758-1801) y Latreille (1802-presente) (Martínez, 2005). Esto da prueba de la problemática real en la clasificación dentro de la familia, además de que se ha señalado que existen pruebas contradictorias en la convergencia y la reversión de caracteres morfológicos que hace que las relaciones entre los grupos sean difíciles de interpretar (Maddison 2009).

Debido a su aspecto característico, la subfamilia Scaritinae se clasificó originalmente como un grupo separado dentro de los carábidos; Latreille (1802) propone el primer sistema de clasificación global de la familia Carabidae, en donde divide a la familia en “Fossoyers” (Scaritinae) y “Celerigrades” (todos los demás carábidos) (Ball 1979). La clasificación más aceptada los considera como una subfamilia (Bousquet 2012), aunque para algunos autores está inadecuadamente definida, pues se considera en diferentes rangos taxonómicos, por ejemplo, Deuve (2003) los coloca en el rango de familia, Moore y Lawrence (1994) los coloca como una supertribu y Vieira y Bello (2004) los ubican en el rango de tribu.

Una clasificación reciente de Scaritinae divide a esta subfamilia en ocho tribus (Bousquet 2012): Pasimachini, Carenini, Scaritini, Clivinini, Dyschiriini, Salcediini, Promecognathini, Dalyatini, sin embargo, Hogan (2012) considera que Scaritinae sólo contiene cuatro tribus (Fig. 3).

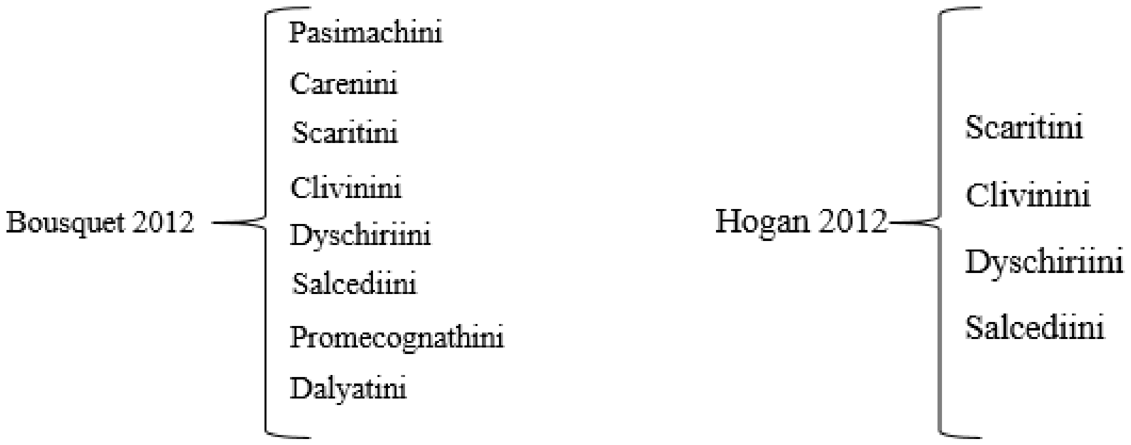


Figura 3. Diferentes clasificaciones a nivel de tribu en la subfamilia Scaritinae.

Algunos autores colocan al género *Pasimachus* en diferentes categorías taxonómicas. Lorenz (2005) lo incluye dentro de Pasimachina, dándole la categoría de subtribu dentro de la tribu Scaritini junto con otros 54 géneros, sin embargo, Bousquet (2012) forma la tribu Pasimachini con *Mouhotia* y *Pasimachus,* aunque en opinión de Bänninger (1950) y Lorenz (2005), Pasimachini no es un grupo monofilético.

Bänninger (1950) revisó las especies y propuso una clave para su determinación sin incluir ninguna ilustración, pero en opinión de autores como Purrington y Drake (2005), el trabajo muestra sesgos importantes por un exceso de detalles no exclusivos del género. *Pasimachus* contiene dos subgéneros: *Pasimachus* (*Emydopterus)* (Laporte) y *Pasimachus* (*Pasimachus*), y dentro de este subgénero se reconocen tres grupos de especies: *Depressus*, *Marginatus* y *Strenuus* (Bousquet 2012). Es por ello que se necesita una revisión taxonómica moderna, así como análisis filogenéticos para resolver problemas pendientes como la delimitación de especies, definiciones subgenéricas claras, así como una filogenia del género y de la tribu.

Hogan (2012) menciona una similitud general entre los géneros *Pasimachus* y *Mouhotia*, sin embargo, este último género lo relaciona con *Oxylobus* Chaudoir, que es un género asiático al igual que *Mouhotia,* y juntos aparecen como hermanos de *Pasimachus*. Hogan (2012) encuentra poco soporte y hace mención a una dificultad para poder hacer afirmaciones sobre estas relaciones, lo que incrementa la incertidumbre acerca de la validez de la tribu Pasimachini.

Tanto para el género *Pasimachus*, como para la tribu Pasimachini y la subfamilia Scaritinae, se carece de antecedentes donde se realicen o combinen análisis de filogenéticos y de morfometría geométrica, sin embargo, se ha explorado para otros grupos de insectos, como el trabajo de Soto-Vivas y cols. (2011) donde analizan filogenéticamente la variación morfométrica de la forma del ala en dos géneros de la tribu Rhodniini (Hemiptera, reduviidae), encontrando evidencia que apoya la taxonomía conocida de esta tribu. De esta manera se puede evidenciar la utilidad y el potencial de los análisis morfométricos en inferencias filogenéticas.

En este trabajo se toma en cuenta la clasificación de Bousquet (2012), ya que es la revisión más extensa y reciente del suborden Adephaga, con lo cual, se pretende poner a prueba la monofilia de la tribu Pasimachini.

III. JUSTIFICACIÓN

Debido a su gran diversidad, abundancia, su distribución, y relativa facilidad de manejo, los carábidos han sido utilizados en numerosas ocasiones como grupos indicadores de perturbación en los ambientes, sin embargo, la clasificación taxonómica dentro de la familia es muy irregular, y poco se podría hacer si no se tiene un conocimiento básico en su identificación y clasificación (Martínez 2005).

La tribu Pasimachini se encuentra inadecuadamente definida, la monofilia de esta tribu es dudosa. Para los géneros que la conforman en la propuesta más aceptada, (*Mouhotia* + *Pasimachus*) no existe un trabajo filogenético previo que ayude a definir las relaciones que existen dentro de la tribu.

La propuesta de una hipótesis filogenética de las especies del género *Pasimachus* es necesaria para esclarecer las relaciones dentro del taxón y establecer una propuesta de clasificación filogenética, en categorías taxonómicas superiores. Esta filogenia aportará evidencia sobre los procesos de especiación, patrones biogeográficos, y un arreglo filogenético para proponer un esquema clasificatorio supraespecífico, el estudio de la evolución de caracteres mediante la optimización de los cambios de estado en el cladograma, y poner a prueba la monofilia de Pasimachini, con alcances en el conocimiento de patrones espaciales a gran escala como temas en biogeografía histórica, evolución morfológica, adaptación, etc., y su potencial aplicación en conservación.

IV. HIPÓTESIS

- El género *Pasimachus* Bonelli es monofilético debido a que muestra constancia morfológica en muchos caracteres y un patrón biogeográfico claro hacia el norte del istmo de Panamá.
- La tribu Pasimachini no es monofilética; los géneros *Pasimachus* y *Mouhotia* no son taxones hermanos por la distancia geográfica tan grande entre en sus distribuciones.

V. OBJETIVOS

5.1. Objetivo general

- Proponer una hipótesis sobre las relaciones filogenéticas del género *Pasimachus B*onelli.

5.2. Objetivos particulares

- Poner a prueba la monofilia de *Pasimachus* y de Pasimachini.
- Definir los grupos naturales del género *Pasimachus* y conocer sus relaciones al interior del taxón.
- Definir marcadores morfológicos que soporten los clados de las topologías resultantes.
- Proponer explicaciones en un contexto evolutivo sobre la presencia de caracteres homólogos y homoplásicos en la interpretación de las hipótesis de homología.
- Establecer una clasificación natural supraespecífica de la tribu Pasimachini

VI. MATRIALES Y MÉTODOS

6.1. Material Biológico

Se obtuvieron en préstamo ejemplares de diversas colecciones científicas nacionales y del extranjero, representantes de todas las especies, subgéneros y grupos de especies del género *Pasimachus,* lo que asegura un muestreo completo de la variación morfológica del taxón y de los criterios taxonómicos y morfológicos de los diversos autores (Tabla 1). De igual forma se incluyeron ejemplares del género *Mouhotia* para conocer el estatus de la tribu Pasimachini, y representantes de Carenini y Scaritini para enraizar el árbol y darle dirección al cambio evolutivo.

Tabla1. Colecciones científicas que han proporcionado material biológico.

Nombre de la colección	**Institución**
Colección Nacional de Insectos (CNIN)	Instituto de Biología, UNAM, CDMX. México
Museo de Zoología Alfonso L. Herrera	Facultad de Ciencias, UNAM, CDMX. México
Colección de coleóptera	Centro de Investigaciones Biológicas, UAEH, Hidalgo. México
Colección de Insectos	Facultad de Ciencias Naturales, UAQ, Querétaro. México.
Colección Entomológica BUAP	Facultad de Biología, BUAP, Puebla. México.
Colección Científica de Insectos	Museo de Historia Natural de Chapultepec, CDMX. México.
Coleoptera Collection NMNH	Smithsonian National Museum of Natural History. EU.
Coleoptera Collection	The Field Museum, Chicago, IL. EU.
Strickland Entomological Museum	University of Alberta, Canada.

El muestro se completó con 270 ejemplares del género *Pasimachus* de las 34 diferentes especies, y cuatro ejemplares representantes de las tres especies del género *Mouhotia*. Como grupo externo se incluyó un género representante de Carenini (*Carenum*) que se ha planteado como la tribu hermana de Pasimachini (Bänninger 1950), así como representantes de cuatro géneros de la tribu Scaritinae (*Scarites, Mamboicus, Haplotrachelus, Dinoscaris*). Como grupo externo funcional se incluyó a *Geoscaptus crassus* también perteneciente a la tribu Scaritini (Tabla 2).

Tabla 2. Ejemplares de estudio.

Tribu	**Distribución**	**Especie**	**No. de ejemplares**
Pasimachini	Costa Rica, Guatemala, El Salvador, México	*P. cordicollis* Chaudoir	7
Pasimachini	México: Oaxaca, Puebla	*P. cuestai* Kohlmann	2
Pasimachini	México: Guerrero, Michoacán, Colima, Estado de México	*P. pacificus* Bänninger	6
Pasimachini	México: Yucatán	*P. purpuratus* Putzeys	10
Pasimachini	México: Oaxaca	*P. quirozi* Flohr	1
Pasimachini	Belice, Nicaragua, México	*P. rotundipennis* Chevrolat	5
Pasimachini	México: Guerrero, Michoacán, Morelos, Veracruz	*P. subangulatus* Chaudoir	6
Pasimachini	México, Estados Unidos	*P. californicus* Chaudoir	17
Pasimachini	México: Durango Guanajuato, Sinaloa	*P. imitator* Bänninger	1
Pasimachini	México: Hidalgo, San Luis Potosí, Estado de México, Ciudad de México	*P. mexicanus* Gray	13
Pasimachini	Estados Unidos: Arizona, Kansas, Nuevo México, Oklahoma, Texas	*P. obsoletus* LeConte	9
Pasimachini	México: San Luis Potosí, Oaxaca, Tamaulipas, Veracruz	*P. sallei* Chaudoir	3
Pasimachini	Estados Unidos: Florida	*P. subsulcatus* Say	20
Pasimachini	México: Ciudad de México, Puebla, Estado de México	*P. tolucanus* Bänninger	5
Pasimachini	México: Jalisco, Michoacán	*P. metallicus* Chaudoir	3
Pasimachini	México: Durango	*P. laevisulcatus* Bates	6
Pasimachini	Belice, El Salvador, Guatemala, México	*P. cardioderus* Chaudoir	1
Pasimachini	Costa Rica, Panamá	*P. intermedius* Chaudoir	11
Pasimachini	Costa Rica, Guatemala, México	*P. sexualis* Bänninger	7
Pasimachini	México, Estados Unidos	*P. atronitens* Casey	5
Pasimachini	Estados Unidos	*P. depressus* Fabricius	24
Pasimachini	México, Estados Unidos	*P. duplicatus* LeConte	6

Pasimachini	Canadá, México, Estados Unidos	*P. elongatus* LeConte	50
Pasimachini	Estados Unidos: Florida, Texas	*P. marginatus* Fabricius	16
Pasimachini	México: Chihuahua, Durango, Sinaloa	*P perpolitus* Casey	5
Pasimachini	Estados Unidos: Florida, Kansas, Ohio, Illinois, Kentucky, Montana, Texas, Wyoming	*P. punctulatus* Haldeman	8
Pasimachini	Estados Unidos: Florida	*P. strennus* LeConte	4
Pasimachini	Estados Unidos: Florida, Illinois, New York, New Jersey, Texas, Indiana	*P. sublaevis* Palisot de Beauvois	9
Pasimachini	México: Chihuahua, Sinaloa, Durango, Sonora. Estados Unidos: Arizona	*P. viridans* LeConte	4
Pasimachini	México: Nayarit, Sinaloa, Jalisco, Michoacán, Colima	*P. ambiguus* Bänninger	3
Pasimachini	México: Oaxaca, Chiapas	*P. aurocinctus* Chaudoir	1
Pasimachini	México: Sinaloa, Sonora	*P. velutinus* Van Dyke	2
Pasimachini	Tailandia	*M. convexa* Lewis	1
Pasimachini	Tailandia, Indonesia, Laos	*M. batesi* Lewis	1
Pasimachini	China	*M. gloriosa* Castelnau	2
Carenini	Australia	*C. interruptum* Macleay	1
Scaritini	Sudáfrica	*H. ignobilis* Chaudoir	1
Scaritini	Madagascar	*D. venator* Chaudoir	1
Scaritini	Italia	*S. buparius* (Foster)	1
Scaritini	Australia	*G. crassus* Sloane	1
Scaritini	Estados Unidos, Canadá	*S. subterraneus* Fabricius	1
Scaritini	Bulgaria	*S. terrícola* Bonelli	1
Scaritini	África	*M. afrellus* Bates	1
Scaritini	Sudamérica	*S. anthracinus*	1

6.2. Revisión de ejemplares

Los ejemplares se trabajaron en el laboratorio de Sistemática de Coleoptera del Laboratorio Regional de Biodiversidad y Cultivo de Tejidos Vegetales del Instituto de Biología-Sede Tlaxcala, UNAM. Estos ejemplares se reblandecieron con agua caliente para disectar la genitalia y se montaron en alfileres entomológicos sobre placas de unicel para su secado. Se observaron los ejemplares para codificar los caracteres de la cabeza, pronoto, patas, élitros, abdomen y genitalia, con ayuda de un microscopio estereoscópico Carl Zeiss Stemi 508. Las medidas se realizaron con un micrómetro asociado a un ocular del microscopio, y las medidas se convirtieron a milímetros con reglas de tres.

6.3. Toma de fotografías

Los ejemplares se fotografiaron con un microscopio multifocal Carl Zeiss Axio Zoom V16 con una cámara Axiocam 506color en el software ZEN para Axio Zoom. Para cada una de las 44 especies (32 *Pasimachus*, 3 *Mouhotia*, 9 grupo externo) se tomaron un par de fotografías por estructura que hicieron un total de 88 fotografías para mandíbula, 88 del pronoto, 88 de élitro y 88 de la protibia.

La primera fotografía se realizó en una sola captura sin profundidad de campo, enfocando en cada estructura a diferentes landmarks previamente seleccionados para tener una fotografía siempre en el mismo plano (figura 4).

Pronoto. Las fotografías se fijaron en los cuatro ángulos externos en el mismo plano focal.

Mandíbula. Las fotografías se tomaron en el mismo plano con referencia del extremo derecho de la base y la punta.

Élitro. Las fotografías se fijaron con referencia en el mismo plano del ápice del escutelo, el húmero y el ápice.

Protibia. Las fotografías se fijaron en el mismo plano con el ángulo basal derecho y el ángulo distal interno.

Figura 4. Pronoto de *Pasimachus quizori* Flohr en una sola captura y sin campo de profundidad.

La segunda fotografía se tomó como una imagen multifocal compuesta con diferentes números de capas que fueron calculadas a partir del grosor de cada estructura y del óptimo de cortes que el programa calculó. Al final se obtuvo una fotografía multifocal de cada una de las estructuras analizadas para cada especie, completamente enfocada en todos sus componentes y profundidad (figura 5).

Figura 5. Fotografía multifocal del pronoto de *Pasimachus quizori* formada por capas superpuestas.

6.4. Codificación de caracteres

6.4.1. Bloque 1. Caracteres continuos

Se registraron ocho medidas en forma de promedios para siete diferentes estructuras morfológicas: 1) largo de la mandíbula izquierda, 2) largo del pronoto, 3) largo élitro, 4) ancho del élitro, 5) largo de protibia, 6) longitud del primer segmento del protarso, 7) largo de metatibia y 8) longitud del primer segmento del metatarso. Estas medidas fueron tomadas para al menos cinco individuos de cada especie con la ayuda de un microscopio estereoscópico graduado Carl Zeiss Discovery V8. En la matriz de caracteres, estos datos continuos formaron parte del primer bloque de datos.

6.4.2. Bloque 2. Caracteres discretos

La codificación de caracteres discretos se realizó con la codificación de caracteres binarios y caracteres multiestado, y para la evaluación de las hipótesis de homología primaria se siguió la prueba de similitud de Remane (1952). La definición semántica de los caracteres sigue la propuesta de Sereno (2007). En total se definieron 90 caracteres morfológicos a partir de la observación de ejemplares, de la revisión de claves taxonómicas (Choate 2001, Purrington y Drake 2005), y de las descripciones originales (Bänninguer 1950, Kohlmann 1993). Se codificaron 82 caracteres binarios y ocho multiestado, que fueron tratados como desordenados (optimización de Fitch), con el mismo peso, y también implementando los pesos implícitos, con valores de concavidad de 3, 7 y 14 (Goloboff 1993). Los caracteres inaplicables se codificaron con un guion medio "-" y los faltantes con un signo de interrogación final "?". La matriz de los caracteres discretos se construyó en el programa Winclada 1.00.08 (Nixon 1999-2002), y después se transformó al formato TNT (Goloboff y cols 2005) con el editor de textos Notepad++.

6.4.2.1. Lista de caracteres

Cabeza

1. Cabeza, color, reflejos metálicos: presentes (0); ausentes (1).
2. Cabeza, región interocular, forma: plana a convexa (0); convexa (1)
3. Antenas, segmentos 2-4, forma: carinado (0); no carinado (1).
4. Antenas, primer segmento, poro setífero: presente (0); ausente (1).
5. Cabeza, canto ocular, forma: sub-angular (0); redondeada (1).
6. Cabeza, canto ocular, forma: laminar, estrecho (0); convexo, amplio (1).
7. Cabeza, un poro setífero supraorbital: presente (0); ausente (1).
8. Cabeza, poro setífero supraorbital posterior: presente (0); ausente (1).
9. Cabeza, poro setífero frontal, al borde del clípeo: presente (0); ausente (1).
10. Labro, superficie: lisa (0); estrigosa (1).
11. Labro, lóbulo medio, longitud en relación a los lóbulos laterales: notablemente mayor (0); similar o menor (1).
12. Labro, lóbulos, forma; marcadamente sinuados (0); ligeramente sinuados (1).
13. Labro, lóbulo medio, forma: redondeado (0); no redondeado (1).
14. Labro, dentículo medio interno: presente (0); ausente (1).
15. Labro, dentículo interno, forma: largo y prominente (0); corto y ancho (1).

16. Labro, dentículo interno, posición respecto al borde: interna (0); externa (1).
17. Labro, lóbulos laterales, márgenes exteriores, hileras de sedas: presentes (0); ausentes (1).
18. Labro, grupo de sedas mesiales: presente (0); Ausente (1).
19. Labro, seda lateral 2: ausente (0); presente (1).
20. Labio, forma: ancho y amplio (0); angosto, corto (1).
21. Labio, vértices laterales, forma: deprimidos (0); no deprimidos (1).
22. Labio, zona distal, forma: multiseccionada (0); biseccionada (1); no seccionada (2).
23. Labio, artejo distal, forma: delgado (0); ligeramente ancho (1); notablemente ancho (2).
24. Palpo labial, segmento 2, número de sedas: menos de 5 (0); más de 6 (1).
25. Palpo maxilar, longitud del último segmento respecto al penúltimo: más largo (0); similar (1); más corto (2).
26. Mentón, par de poros sedíferos: presentes (0); Ausentes.
27. Submentón, 2 o más poros sedíferos: presentes (0); Ausentes (1).
28. Mandíbula, superficie dorsal: rugosa (0); lisa (1).
29. Mandíbulas, forma: recta con ápices curvos (0); ligera y continuamente curva (1); abruptamente curva en el tercio distal.
30. Mandíbula derecha, forma: Multidentada (0); unidentada (1).
31. Mandíbula derecha, diente basal; subtriangular elevado (0); no subtriangular (1).
32. Mandíbula derecha, diente basal, forma: dentado (0); no dentado (1).
33. Mandíbula derecha, diente 2: Ausente (0); presente (1).
34. Mandíbula derecha, diente 4: Ausente (0); presente (1).
35. Mandíbula izquierda, diente 2: Ausente (0); presente (1).
36. Mandíbula izquierda, diente basal; dentado (0), no dentado (1).
37. Mandíbula izquierda, diente basal, forma: bidentado (0), tridentado (1).

Pronoto

38. Pronoto, borde anterior, área de contacto con abdomen: incrementada (0); marcada (1).
39. Pronoto, borde anterior, ángulos laterales: Ausentes (0), presentes (1).
40. Pronoto, borde anterior, vértices laterales, forma: redondeada (0); constreñida y pronunciada (1); pronunciada hacia el borde humeral (2).
41. Pronoto, vértices posteriores, forma: redondeados (0), ángulo obtuso (1); ángulo recto (2).
42. Pronoto, margen laterobasal: interrumpido, espiniforme (0); uniforme (1).
43. Pronoto, márgenes, color: metálico (0); negro (1).
44. Pronoto, ángulos posteriores, poros sedíferos: presentes (0), ausentes (1).
45. Pronoto, canal lateral, superficie: liso (0); rugoso transversalmente (1).

46. Pronoto, margen anterior; Completo (0), incompleto (1).
47. Pronoto, margen anterior, definido por: Hendidura continua (0), hendidura punteada (1).
48. Pronoto, fosetas laterales superiores; Presentes (0); ausentes (1).
49. Pronoto, fóveas exteriores basales: Ausentes (0); presentes (1).
50. Pronoto, fóveas internas basales: muy marcadas y profundas (0); poco profundas (1).
51. Pronoto, fóveas internas: Conectadas transversalmente (0), no conectadas (1).
52. Prosterno, posición intercoxal: larga (0); corta (1).
53. Prosterno, posición intercoxal, forma: aguda (0), roma (1).

Élitros

54. Húmero, diente humeral: Presente (0); Ausente (1).

55. Húmero, carina humeral: Ausente (0); presente (1).
56. Húmero, carina humeral, forma: Larga (0); corta (1).
57. Élitros, sutura elitral en el tercio distal: Fusionada (0); no fusionada (1).
58. Élitros, estrías: presentes (0); ausentes (1).
59. Élitros, estrías: superficiales (0); Profundas (1).
60. Élitros, estrías: Línea continua (0); definida por puntuación (1).
61. Élitros, costillas elitrales externas: cariadas (0); no carinadas (1).
62. Élitros, costillas elitrales 3-5-7: convergentes hacia el ápice (0); no convergentes (1).
63. Élitros, color: márgenes de color brillante (0); márgenes opacos (1).
64. Élitros, color: metálicos en la parte dorsal (0); colores opacos (1).
65. Élitros, estrías, puntuación: completa (0); porción distal (1).
66. Élitros, superficie apical: poros setífero (0); sin poros setífero (1).
67. Élitros, borde lateral: con poros setífero (0); sin poros setífero (1).

Abdomen

68. Segmentos ventrales 3-5, poros setífero: presentes (0); ausentes (1).
69. Segmento ventral 6, poros setífero: presentes (0); ausentes (1).

Patas

70. Patas, trocánter, poro setífero: ausente (0); presente (1).
71. Patas, metafémur, poros setífero, número: 3-5 (0); 1-2 (1)
72. Patas, protibia, margen externo, dentículos: tridentado (0); multidentado (1).
73. Patas, protibia, margen externo, dentículos basales: deprimidos (0); elevados (1).
74. Patas, espina mesotibial fija, número: 1 (0); más de 1 (1).
75. Patas, espina mesotibial apical fija: larga en forma de punta (0); corta y ancha (0).
76. Patas, segunda espina mesotibial: espiniforme (0); laminar (1).
77. Patas, espina mesotibial, cara interna, parte distal: presente (0); ausente (1).
78. Patas, espina mesotibial, cara interna, seda espiniforme basal: 2 (0); 1 (1).

79. Patas, espina mesotibial, peine en cara interna: ausentes (0); presentes (1).
80. Patas, metatibia, mechón de sedas cara interna: ausente (0); presente (1).
81. Patas, protarsos 2,3,4, parte ventral, carinas: 2 (0); 1 (1).
82. Patas, protarsos 2-4, carina externa: ausente (0); presente (1).
83. Patas, protarso 5, carina mesial: 1 (0); 2 (1).
84. Patas, protarsos, corona de sedas apicales: continua (0); no continua (1).
85. Patas, metatarso 1, seda interna en cara ventral: 0 (0); 1 (1); 2 (2); más de 3 (3).
86. Patas, metatarso 2-4, par de hileras de poros setífero ventrales: ausente (0); presente (1).

Edeago

87. Edeago, parámeros?: corta y chata (0); larga no laminar (1); larga como espátula (2); larga aguda (3)
88. Edeago, placas laterales sedas: cortas (0); largas (1).
89. Edeago, parámeros, mechón de sedas en zona apical: ausente (0), presente (1).

Cuerpo

90. Cuerpo, forma: delgado y alargado (0); robusto y ancho (1).

6.4.3. Bloques 3, 4, 5 y 6. Caracteres morfogeométricos

Para los caracteres de morfometría geométrica se utilizaron configuraciones de dos dimensiones, con landmarks y diseños especiales con plantillas para recuperar la forma de cada estructura morfológica, que fueron elaborados en el programa MakeFan8. En los programas tpsUtil32 ver. 1.70 y tpsDig232 ver. 2.26 se digitalizaron los landmarks sobre las fotografías a partir del diseño de las plantillas y de la forma de cada estructura, y en la intersección de la silueta de cada estructura y los radios de las plantillas se marcaron los puntos. Los diseños de las plantillas para cada estructura fue el siguiente:

1. *Pronoto*. Se digitalizaron cuatro landmarks en los cuatro ángulos externos que conforman al pronoto, partir de los cuales se trazaron un diseño con cuatro peines, que fueron la guía para las 61 marcas de referencia en la digitalización la forma. El peine superior está conformado por 17 puntos, los laterales por 15 puntos, y el inferior por 16 puntos (figura 6).

2. *Mandíbula*. En la mandíbula derecha se realizó desde la base de la mandíbula hasta la punta, un peine digitalizado con 30 landmarks, con lo que se registró sólo la forma del margen externo de la mandíbula (figura 7).
3. *Élitro*. Se realizó un diseño de un abanico de 36 marcas a partir de tres puntos, desde la parte apical del escutelo, hacia el húmero y el ápice para registrar la forma de todo el margen externo (figura 8).
4. *Protibia*. La forma de la protibia derecha se registró con tres peines y un abanico, con un total de 100 landmarks. El primer peine se digitalizo desde el ápice del dentículo distal, hasta el ápice del segundo dentículo. El segundo peine desde el ápice del segundo dentículo, hacia el tercero en su parte apical. El tercer peine desde el ápice del tercer dentículo hacia la base de la protibia. El abanico se diseñó desde la base del margen externo, el ápice del dentículo inferior y hasta el ápice del dentículo superior (figura 9).

Las coordenadas espaciales de cada configuración estructural fueron alineadas en una superposición Procrustes en el programa CoordGen8, que consiste en convertir las configuraciones a una misma escala de tamaño, eliminar el efecto de la posición y rotar los landmarks para minimizar la desviación entre estos (Klingenberg 2010), para posteriormente exportar las coordenadas espaciales en un formato TPS, que son los datos utilizados en los análisis filogenéticos y de morfometría geométrica.

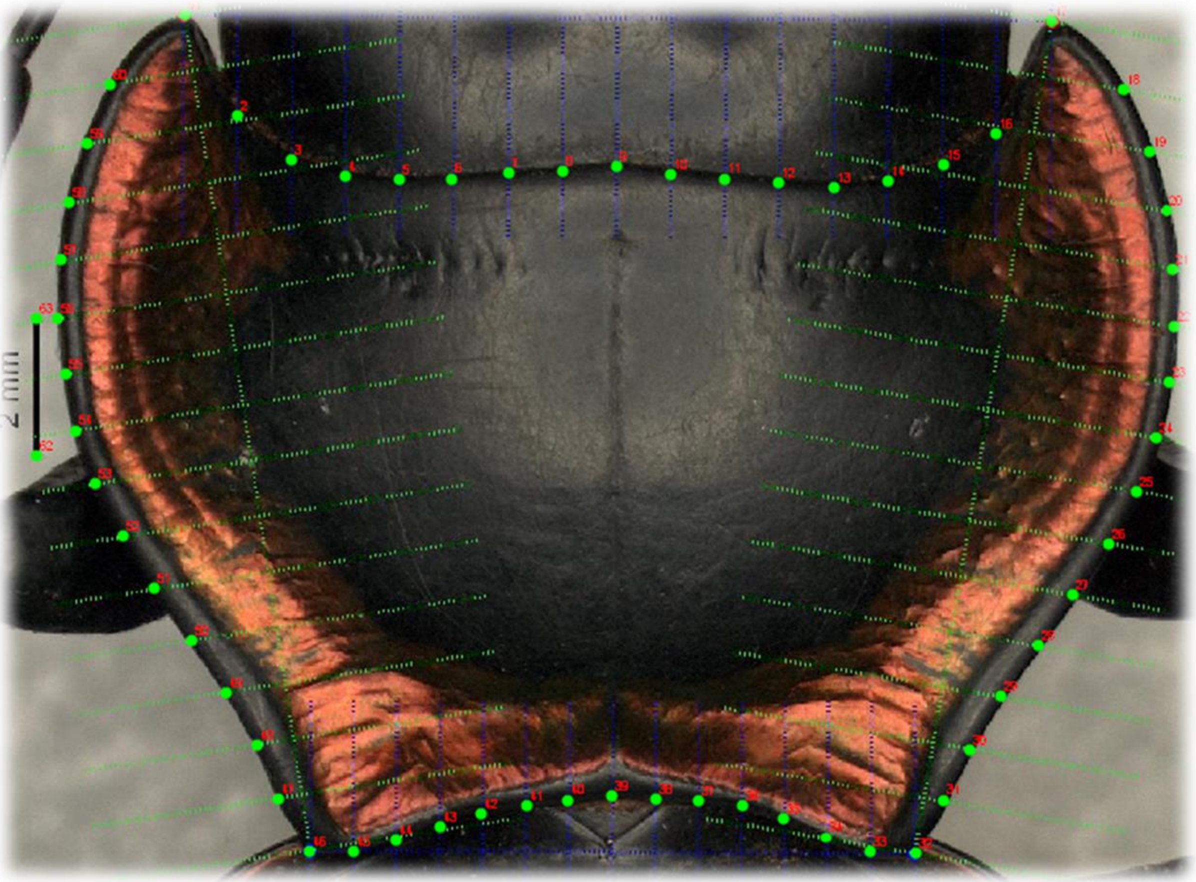


Figura 6. Fotografía del pronoto con cuatro plantillas de peines.

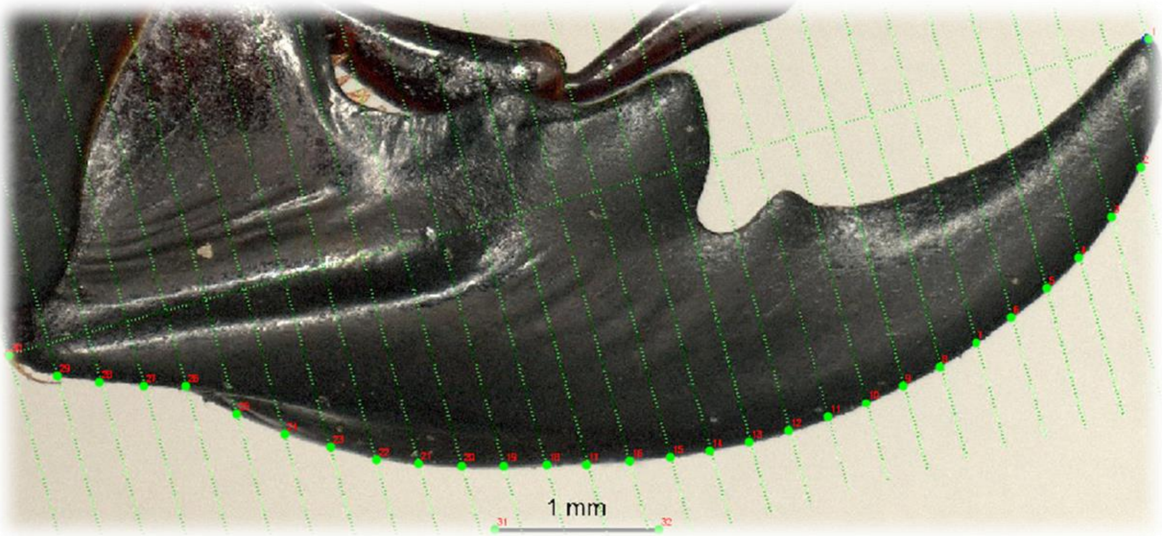


Figura 7. Fotografía de la mandíbula derecha con una plantilla de un peine.

Figura 8. Fotografía del élitro derecho con una plantilla de un abanico.

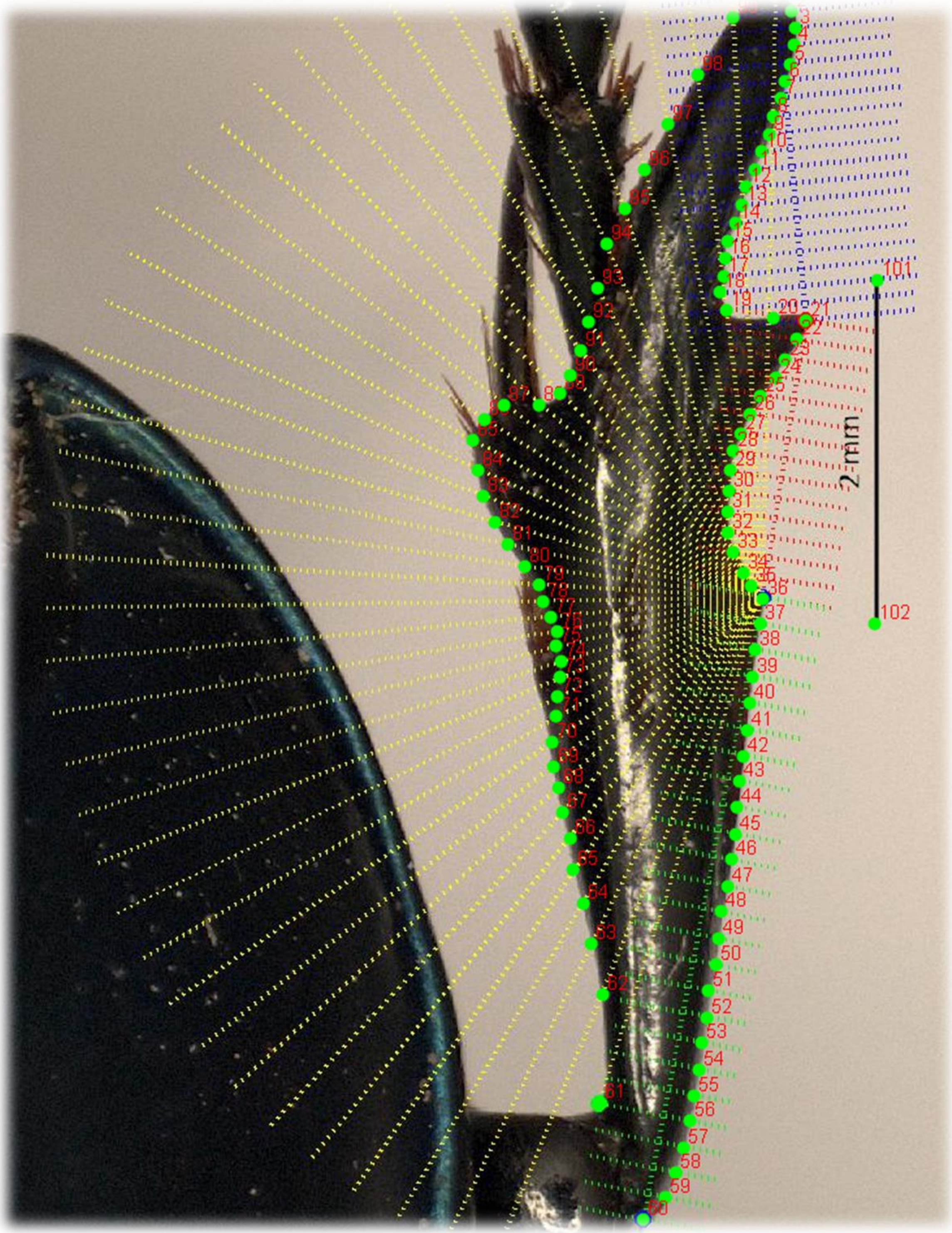


Figura 9. Fotografía de la protibia derecha con una plantilla de un abanico y tres peines.

6.5. Matriz de caracteres

La matriz quedó definida por tres bloques de diferentes tipos de datos morfológicos; caracteres discretos, caracteres continuos y coordenadas morfogeométricas del pronoto, mandíbula, élitro y protibia. La matriz tiene un total de 46 taxones y 102 caracteres a estudiar; 90 caracteres discretos, 8 caracteres continuos y 4 caracteres morfogeométricos con un total de 227 landmarks (Anexo). La matriz fue construida en Winclada 1.00.08 (Nixon 1999- 2002) y editada en Notepad++. Los caracteres morfológicos se trataron como desordenados (optimización de Fitch). Los caracteres inaplicables se codificaron con un guion medio "-" y los faltantes con un signo de interrogación final "?".

6.6. Análisis filogenéticos

El análisis filogenético se realizó implementando el criterio de parsimonia mediante estrategias de búsqueda de nuevas tecnologías en TNT 1.5 (Goloboff y Catalano 2016), utilizando en conjunto los algoritmos Sectorial Searches (Goloboff 1999), Ratchet (Nixon 1999), Tree Drifting (Goloboff 1999) y Tree Fusing (Goloboff 1999), los cuales son utilizados para matrices con un gran número de taxones y caracteres. Posteriormente se realizó una búsqueda de árboles implementando pesos implícitos con valores de concavidad 3, 7 y 14 (Goloboff 1993). La utilidad de hacer búsquedas mediante este criterio permite obtener topologías más optimas, tratando de mejorar la recuperación del mayor número de grupos monofiléticos y con un mejor soporte en las ramas, que es recomendado para matrices grandes en número de taxones y caracteres (Goloboff *et al.* 2008, Ballesteros 2010).

El soporte de ramas se calculó con dos procedimientos en TNT. Bootstrap que elimina algunos de los caracteres al azar y replican los caracteres que quedan, conservando el tamaño original de la matriz, y el análisis de Jackknife quita taxones en el remuestreo mientras produce replicas con una de las pruebas sin taxones (Morrone 2013).

La optimización ambigua en la optimización de las series de transformación de los caracteres se resolvió con la transformación acelerada (ACCTRAN), donde los estados en el paso hacia arriba se colocan más cerca de la raíz, favoreciendo las reversiones hacia el estado plesiomórfico en lugar de los paralelismos y convergencias para la explicación de la homoplasia (Agnarsson & Miller, 2008.).

6.7. Análisis de morfometría geométrica

Se realizaron análisis de la variación de la forma de cada una de las cuatro estructuras codificadas con landmarks, para conocer el cambio evolutivo y los patrones de ocupación de los taxones en el morfoespacio y vincularlas con las filogenias resultantes. La forma de las estructuras morfológicas recuperadas en forma de coordenadas espaciales (en formato tps), y los cladogramas resultantes (en formato nexus) se vincularon en el programa MorphoJ 1.06d (Klingenberg, 2011). El análisis de esta variación morfológica en el espacio asociadas a las filogenias (filomorfoespacio), han tenido aplicaciones en el estudio del orden de las transformaciones morfológicas, diversidad funcional, estudio de patrones de ocupación del morfoespacio, eventos de convergencia, diversificación morfológica de clados, visualizar radiaciones adaptativas, inferir la magnitud y dirección del cambio de la forma a través de clados, etc. (Crusatte y col 2008, Clabaut y col 2007, Rohlf 2002, Sidlauskas 2008 y Ruta 2012).

VII. RESULTADOS

7.1. Filogenia

Con el análisis de caracteres sin pesos se obtuvo un cladograma totalmente resuelto con una longitud de 449 pasos, un índice de consistencia de 0.25 y uno de retención de 0.63 (Figura 10). Los principales resultados son:

Scaritini en el clado más basal, con representantes de cuatro continentes, aparece como un grupo monofilético, y como grupo hermano de Carenini + Pasimachini. Las cuatro especies del género Scarites forman un clado monofilético y hermano de los géneros Haplotrachelus, Mamboicus, Dinoscaris, y Geoscaptus como el más externo.

La posición de *C. interrumptum* (único representante de Carenini), se muestra como el grupo hermano de Pasimachini. Esto está soportado por 13 sinapomorfías entre las que destacan: el canto ocular subangular, la presencia de una segunda seda lateral en el labro, la forma ancha y amplia de labio, la forma ancha del artejo distal del labio y coloraciones en los márgenes laterales del pronoto y de los élitros.

La tribu Pasimachini aparece como monofilética, como los géneros *Pasimachus* y *Mouhotia* monofiléticos y como taxones hermanos, que refiere una congruencia con la clasificación tradicional.

El clado del género *Pasimachus* tiene buen soporte estadístico (Bootstrap 88%, Jacknife 94 %). Los estados de carácter que soportan a este clado son 21, entre los que destacan: la ausencia de un poro setífero supraorbital en la parte posterior, la presencia de estrías elitrales, la fórmula tridentada de las protibias y la elevación de sus dentículos basales del margen externo y la presencia de una carina externa en los protarsos 2, 3 y 4.

El género *Pasimachus* está clasificado tradicionalmente en dos subgéneros, *Pasimachus* y *Emydopterus*. La monofilia de ambos se contrasta, ya que Pasimachus se recupera en un clado y *Emydopterus* aparece como un grupo polifilético.

El clado que conforma *Emydopterus*, por tener a la especie tipo del subgénero, únicamente incluye cuatro especies: *P. metallicus, P. subangulatus, P. pacificus* y *P. rotundipennis* y resultó como el grupo hermano del subgénero *Pasimachus.* El clado de *Emydopterus* presenta un soporte de ramas bajo (Bootstrap 7% y Jacknife 25%), y los estados de caracteres que soportan esta rama son ocho, donde destaca como sinapomorfía importante la forma redonda de los ángulos laterales en el borde posterior del pronoto.

El subgénero *Pasimachus* contiene 19 especies (*P. sallei, P. laevisulcatus, P. velutinus. P. quadricollis, P. imitator, P. punctulatus, P. depressus, P. elongatus, P. marginatus, P. strenuus, P. sublaevis, P. subsulcatus, P. californicus, P. mexicanus, P. viridans, P. duplicatus, P. obsoletus, P. perpolitus* y *P. atronitens*). La posición de este subgénero es estable y concuerda con literatura previa. Este clado presenta un soporte bajo (Bootstrap 6%, Jacknife 15%), y ocho estados de caracteres soportan esta topología: la presencia de un dentículo interno en la zona media del labro, de un poro sedífero en los ángulos posteriores del pronoto y la fusión de los élitros, como los más importantes.

Las otras especies que estaban consideradas como el subgénero *Emydopterus* están en diferentes clados. El primer clado conformado por *P. cordicollis, P. quirozi, P. cuestai, P. tolucanus, P. cardioderus* y *P. purpuratus,* está soportado por ocho estados de carácter, destacando como sinapomorfías la presencia de una carina humeral y un pequeño diente también en la zona del húmero, y la ausencia de una seda en la cara interna del primer metatarso caracteres. Otro clado formado por *P. intermedius, P. sexualis, P. smithi* y *P. aurocinctus,* presenta poca estabilidad en el soporte de Bootstrap y Jacknife, con nueve sinapomorfías, siendo la más destacable, la fuerte marcación de las fóveas internas en la parte basal del pronoto.

Un aspecto notable en los resultados de esta topología es que algunos de los clados formados dentro de *Pasimachus* parecen tener poca congruencia con la clasificación previa, así como pocos caracteres morfológicos que los puedan definir de manera sólida, considerando caracteres neomórficos o transformacionales notablemente conspicuos, y por ello, se decidió a realizar análisis con pesos implícitos para comparar con otras topologías.

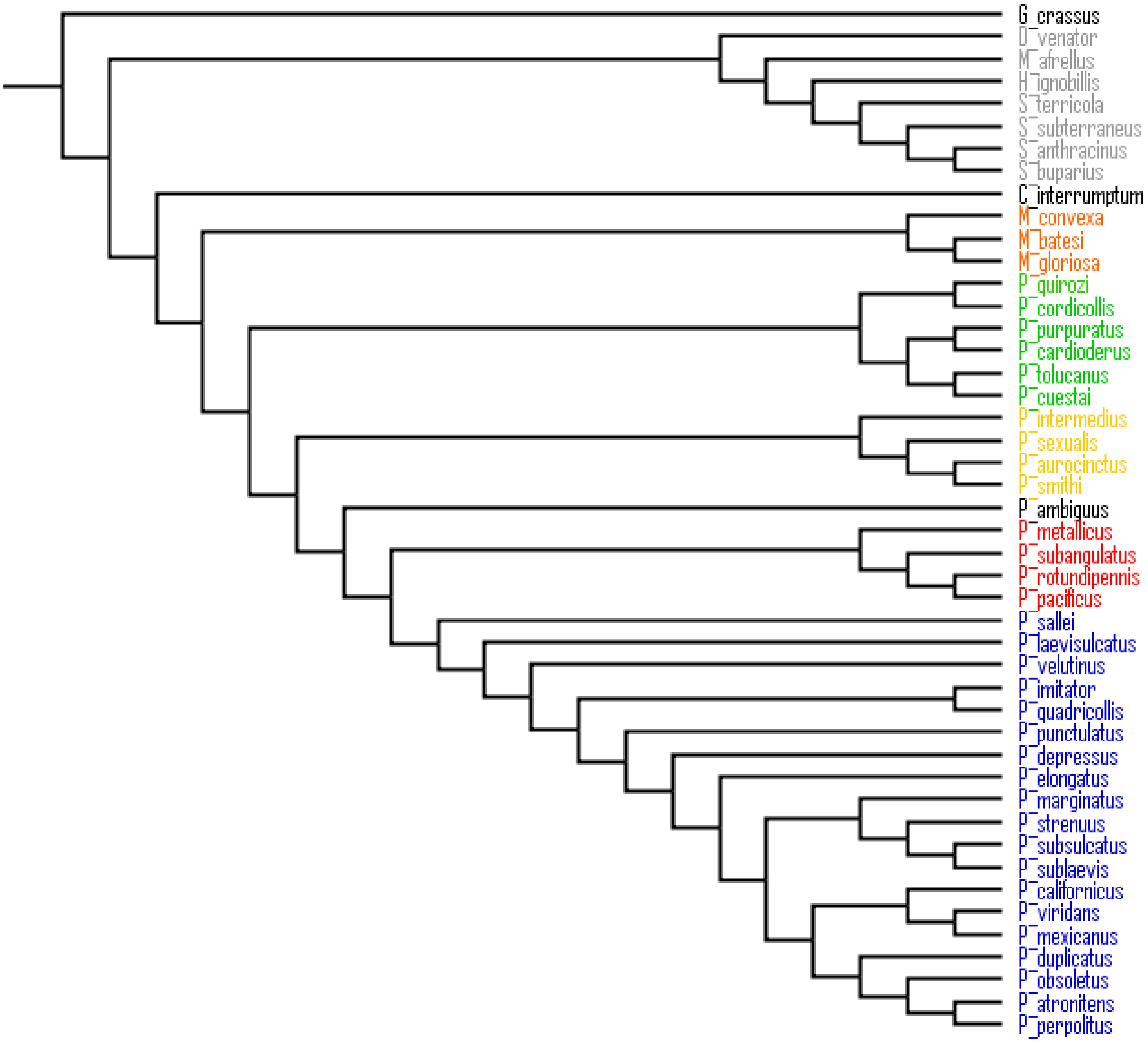


Figura 10. Único cladograma obtenido con cinco módulos usando estrategias de búsqueda con Nuevas Tecnologías. Se muestran como monofiléticos Pasimachini y *Pasimachus* (*Pasimachus*), y como polifilético Pasimachus (*Emydopterus*) en rojo, verde y amarillo.

En los análisis de pesos implícitos con los diferentes valores de concavidad se obtuvo un sólo cladograma en las tres diferentes corridas (Tabla 3). Una tendencia evidente es que a mayor valor de concavidad los valores de ajuste van disminuyendo. Por tanto, el cladograma con el mejor ajuste es el de valor de concavidad 3, que es el que se discute a continuación.

Tabla 3. Resultados de los análisis basados con Nuevas Tecnologías y pesos implícitos.

Análisis	AMP	Longitud	Ajuste	CI	RI	Estatus de Pasimachini
Pesos iguales	1	449	-	0.25	0.63	Monofilético
Pesos implícitos 3	1	457	40.81	0.25	0.62	Monofilético
Pesos implícitos 7	1	453	26.33	0.26	0.65	Monofilético
Pesos implícitos 14	1	452	16.55	0.26	0.65	Monofilético

La topología del cladograma a nivel de tribus igual al análisis anterior (L= 457, Ci= 0.25, Ri= 0.62); Scaritini como grupo hermano de Carenini + Pasimachini (clado 1); Cerenini hermano de Pasimachini (clado 2) y dentro de esta tribu a *Pasimachus* y *Mouhotia* (clado 3) (figura. 11). Las especies de la tribu Scaritini aparecen como un solo grupo y es el más tempranamente divergente. La posición de Carenini (*C. interrumptum*) como tribu hermana de Pasimachini se confirma con un soporte de rama (Boostrap 91% y Jacknife 98%), con las siguientes sinapomorfías: ausencia de un grupo de sedas mesiales en el labro, la forma del labio ancha y amplia, el artejo distal del labio ancho, y la coloración en los márgenes del pronoto y en los élitros.

El género *Mouhotia* está relacionado de la siguiente manera (clado 4); *M. convexa* como el taxón más tempranamente divergente y *M. gloriosa* y *M. batesi* como especies hermanas más derivadas. Esta relación esta soportada principalmente por la forma del pronoto, élitro, mandíbula y protibia, con un soporte de 79% en Bootstrap y un 83% en Jacknife.

La monofilia de Pasimachini (*Pasimachus* + *Mouhotia*, clado 3) se mantiene (Bootstrap 86% y Jacknife 93%), con las siguientes sinapomorfías: ausencia de un poro sedífero supraorbital posterior, la presencia de un número menor a cinco sedas en el segundo segmento del palpo labial, la fórmula tridentada de las protibias, así como elevación de sus dentículos basales del margen externo y la presencia de una carina externa en los protarsos.

En el primer clado de *Pasimachus* diverge el subgénero *Emydopterus* del resto de las especies. Este subgénero (clado 7) con cinco especies (*P. smithi, P. rotundipennis, P. pacificus, P. metallicus* y *P. subangulatus*), presenta un soporte estadístico bajo de 3% de Bootstrap y 4%

en Jacknife, con la forma redondeada de los ángulos posteriores del pronoto como su principal sinapomorfía.

Otros clados se forman a nivel de subgénero (clado 12, 16 y 17), y las especies *P. aurocinctus, P. intermedius* y *P. ambiguus* aparecen como terminales aisladas, que divergen de los clados 5, 13 y 14, que representan nuevos subgéneros monotípicos con autapomorfías.

El clado 12 con *P. sexualis* y *P. quirozi*, se caracterizan por una hendidura punteada en el margen anterior del pronoto y la presencia de una carina humeral.

El clado 16 con *P. cordicollis, P. cuestai, P. tolucanus, P. cardioderus* y *P. purpuratus,* comparten la presencia de una carina humeral. *P. cordicollis* aparece como el taxón más basal de este clado y presenta el canto ocular en forma redondeada y más de seis sedas en el segundo segmento del palpo labial. *P. cuestai* y *P. tolucanus* aparecen como taxones hermanos, presentan los lóbulos del labro ligeramente sinuados, el diente basal de la mandíbula izquierda no dividido y la coloración en todo el cuerpo opaca, este clado tiene un soporte de rama de. Finalmente *P. cardioderus* y *P. purpuratus* presentan un diente basal dentado en la mandíbula derecha, en la mandíbula izquierda un segundo diente, una corona de sedas apicales interrumpida en los protarsos, y la parte apical del edeago larga y ancha.

El clado 17, que corresponde al subgénero *Pasimachus* contiene 19 especies (*P. sallei, P. laevisulcatus, P. velutinus. P. quadricollis, P. imitator, P. punctulatus, P. depressus, P. elongatus, P. marginatus, P. strenuus, P. sublaevis, P. subsulcatus, P. californicus, P. mexicanus, P. viridans, P. duplicatus, P. obsoletus, P. perpolitus* y *P. atronitens*) tienen como sinapomorfías un dentículo interno en la zona media del labro, un poro sedífero en los ángulos posteriores del pronoto y los élitros completamente fusionados.

Respecto a las especies aisladas, *P. aurocinctus* (clado 5) aparece como el más basal y hermana del resto de *Pasimachus*, presenta una carina en la zona del húmero, estrías elitrales superficiales, y coloración metálica en la parte dorsal del élitro; *P. intermedius* (clado 13) presenta el lóbulo medio del labro redondeado, un segundo diente en la mandíbula izquierda y en los machos, un mechón de sedas en el profémur; y *P. ambiguus* (clado 14) posee un par de fosetas laterales en la parte superior del pronoto.

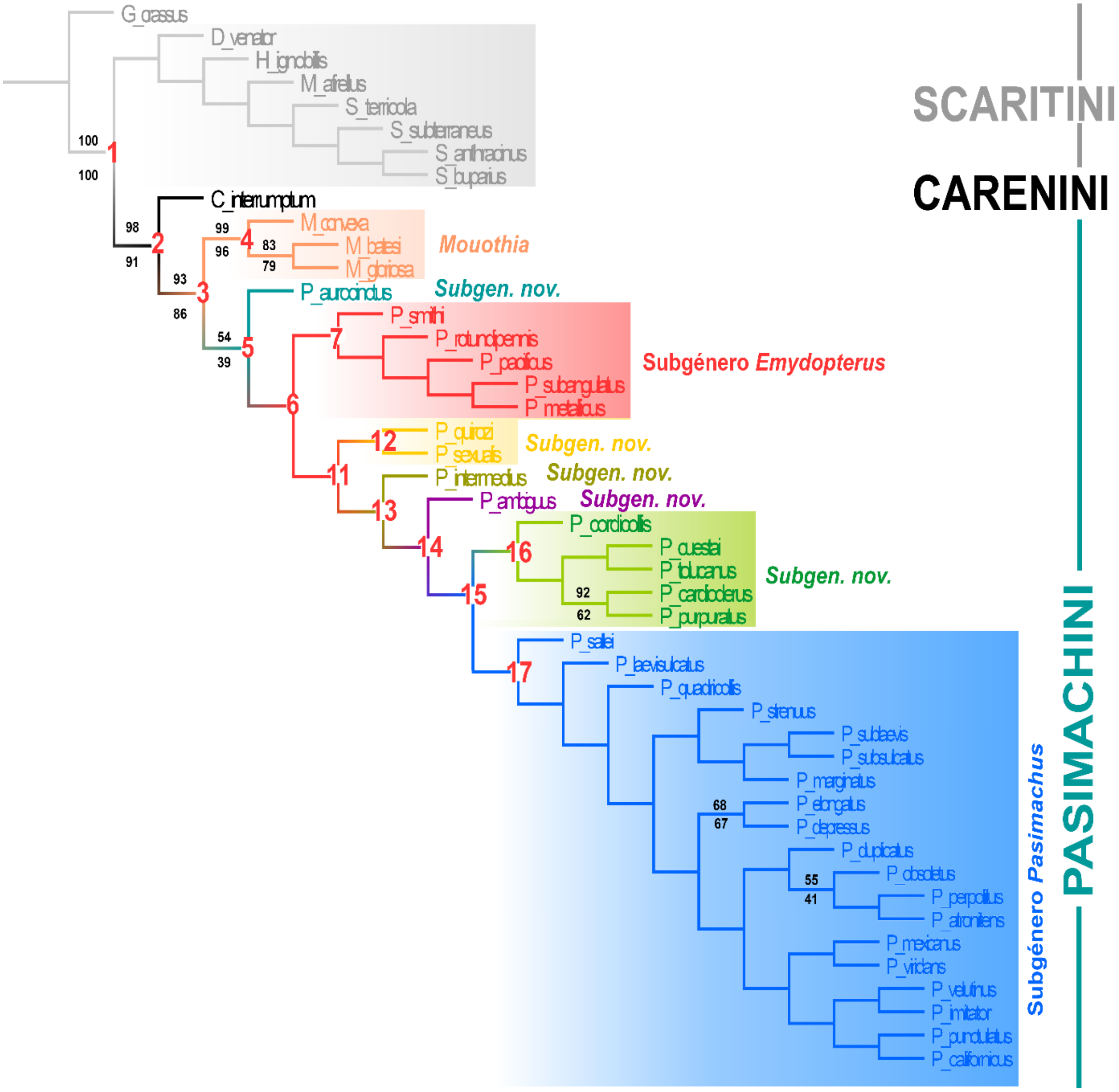


Figura 11. Único cladograma obtenido con pesos implícitos (k=3). Se muestran monofiléticos Pasimachini y *P*. (*Pasimachus*), y como polifilético *P*. (*Emydopterus*) (L= 457, Ci= 0.25, Ri= 0.62).

7.2. Evolución de estructuras morfológicas

7.2.1. Pronoto

El pronoto es una estructura que ha sido considerablemente importante en la taxonomía de los taxones estudiados, al considerarla como taxonómicamente informativa a nivel de tribus, de géneros y subgéneros (Bänninger 1950, Kholman 1993), y los resultados de la filogenia, y del filomorfoespacio evidencian esto.

Para Scaritini la forma del pronoto es muy constante, con los bordes laterales notablemente redondeados y la base considerablemente estrecha, tanto para las especies como para los ancestros reconstruidos (Figura 12). Respecto al único representante de Cerenini (*C. interruptum*), la tribu hermana de Pasimachini, se sigue manteniendo en términos generales la forma de Scaritini. El cambio notable ocurre en Pasimachini, en donde el pronoto se ensancha en la base (se proyectan los ángulos posteriores) y también en la mitad anterior de manera dramática, que es la forma general del género *Mouhotia.*

Respecto al género *Pasimachus*, la forma del pronoto presenta diferentes patrones de cambio. En general es más largo que en *Mouhotia*, aunque en los primeros clados (*P. cordicollis*-*P. purpuratus*), la forma respecto a *Mouhotia* es algo similar, en especial, con *P. quirozi.* En los clados [(*P. intermedius*-*P. aurocinctus*), *P. ambiguus*, (*P. metallicus*-*P. rotundipennis*)], la forma vuele a los bordes laterales redondeados. Finalmente, dentro del clado (*P. sallaei*-*P. atronitens*), ocurre un cambio gradual desde una forma subtrapezoidal, con la base más estrecha que el ápice y los bordes laterales redondeados prominentes en la mitad anterior, hasta un pronoto claramente subrectangular, con la base y el ápice casi de la misma anchura, y los bordes laterales ligeramente curvos, como en el caso del clado (*P. marginatusP.* - *subsulcatus*).

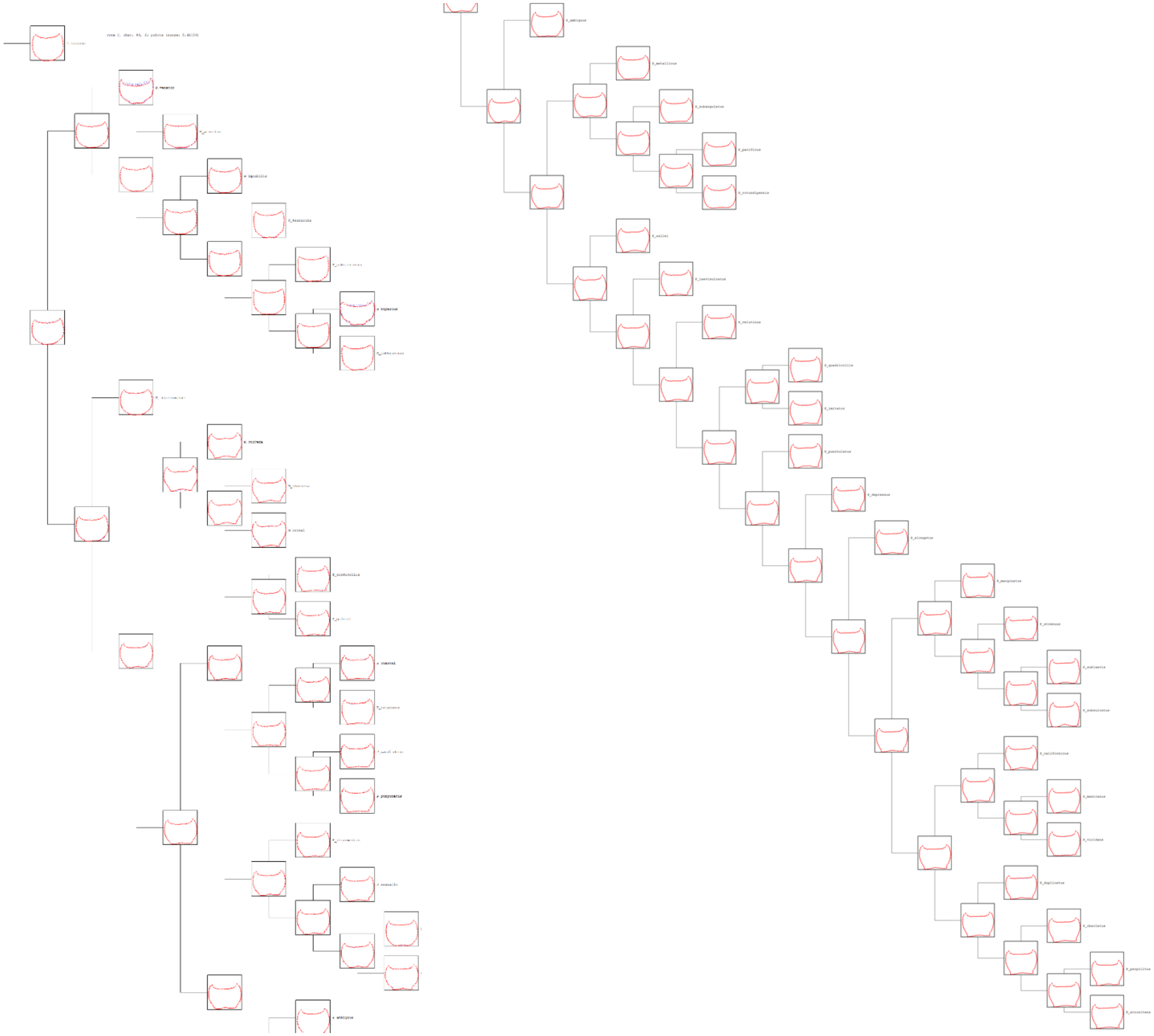


FIGURA 12. CLADOGRAMA RESULTANTE QUE MUESTRA EL CAMBIO EN LA FORMA DEL PRONOTO EN SCARITINI, CARENINI Y PASIMACHINI

7.2.1.1. Análisis de componentes principales y filomorfoespacio

En el análisis de componentes principales los dos primeros componentes explican el 80% de la varianza total, con un patrón de cambio en el CP1 expresado en la reducción de la amplitud de la base, y un ligero ensanchamiento e incremento de la mitad anterior, y en el CP2 por un aumento en la longitud de la estructura, con una pequeña reducción en la anchura, principalmente de la mitad anterior.

La expresión de la variación de la forma del pronoto en el filomorfoespacio (Fig. 13) muestra patrones de ocupación del morfoespacio relativamente estables respecto a la taxonomía a nivel de géneros y tribus, casi sin superponerse entre otros géneros. Por un lado, se encuentran todas las especies del grupo externo que pertenecen a la tribu Scaitini, con una amplia variación morfológica (puntos de color gris), y en otro, Carenini + Pasimachini. Los géneros *Pasimachus* y *Mouhotia* están claramente separados, con excepción de unos pocos casos de convergencia, como *P. aurocinctus* y *P. purpuratus*; la primera es la especie con el pronoto más parecido tanto a *Mouhotia* como a *Carenum*, y la segunda, la más parecida a las dos especies de *Mouhotia*, que además está ubicada en el clado más basal del género.

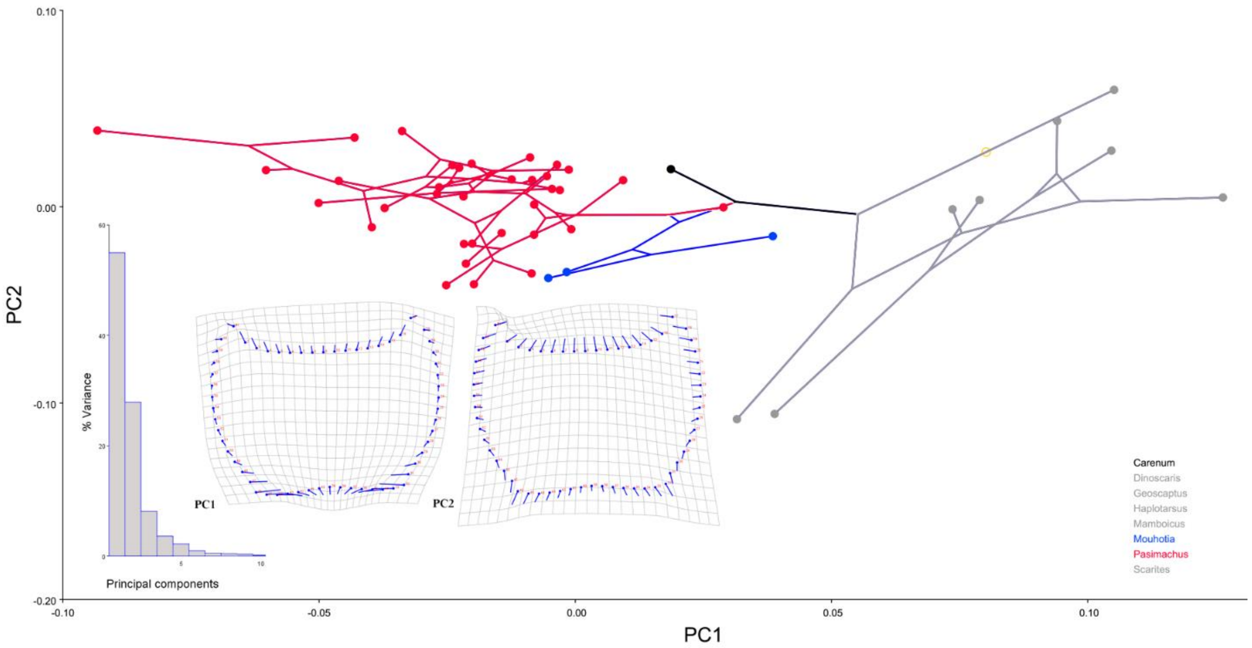


Figura 13. Análisis de componentes principales y filomorfoespacio del pronoto.

7.2.2. Élitro

El élitro se muestra como una estructura estable a lo largo del tiempo a nivel supraespecífico y tribal. La forma del élitro en la tribu Scaritini tiene la misma constancia tanto en el ancestro como en las especies, es un élitro más alargado en forma, la parte del húmero se forma un ángulo de casi 90º y hacia el último tercio apical se comienza a curvear (figura 14). Con *C. interruptum*, único representante de la tribu Carenini, el élitro cambia de forma notable, el ángulo que se forma en la zona del húmero en Scaritini prácticamente desaparece y se observa mucho más redondeado. Este cambio notable se observa también en la tribu Pasimachini, donde se muestra un élitro redondeado en la zona humeral y una curvatura más pronunciada que comienza desde la mitad hacia el ápice del élitro.

FIGURA 14 . CLADOGRAMA RESULTANTE QUE MUESTRA EL CAMBIO EN LA FORMA DEL ÉLITRO EN SCARITINI, CARENINI Y PASIMACHINI

En el género *Pasimachus* se muestran diferencias en la forma. No es tan redondeado como en *Mouhotia* que presenta una curvatura prácticamente desde la zona del escutelo, en *P. aurocinctus* se muestra más esta forma que en cualquier otra especie de *Pasimachus*. En el clado que conforma el subgénero *Emydopterus* la curvatura comienza a notarse desde el primer tercio del élitro, al igual que en el clado (*P. sexualis*-*P. quirozi*), en el clado del subgénero *Cordicollis* se muestra un pequeño cambio en el húmero formando un poco distinguido ángulo. En el subgénero *Pasimachus* se vuelve un poco más alargado en forma, la curvatura vuelve a notarse hacia el tercer tercio hacia el ápice, mostrando una pronunciación elevada en el húmero con respecto al escutelo, lo que asemeja una forma más cuadrada, la cual se nota particularmente en el clado conformado por *P. strenuus, P. marginatus, P. sublaevis* y *P. subsulcatus*.

7.2.2.1. Análisis de componentes principales y filomorfoespacio

En este análisis el primer componente principal explica el 80% de la varianza total de cambio en la forma, que muestra un cambio en la parte del escutelo hacia el humero con una expansión que va hacia el tercer tercio del élitro donde comienza a contraerse hasta el ápice. El CP2 únicamente refleja el 10% de la varianza total de cambio en la forma, mostrando una reducción hacia adentro de la zona del humero y escutelo, se expande desde el primer tercio al tercer tercio donde se vuelve a contraer hasta el ápice.

La variación de la forma del élitro en el filomorfoespacio (figura 15) se muestra congruente en la ocupación de la filogenia en el morfoespacio y se representa claramente la taxonomía a nivel de género (Pasimachini) y a nivel de tribu. La tribu Scaritini presenta una variación morfológica considerable, se muestra a *Scarites buparius* con una forma elitral más parecida a las formas en *Pasimachus.* Carenini-Pasimachini se encuentran bien separadas. Dentro de Pasimachini, *Pasimachus* y *Mouhotia* se muestran claramente diferentes en la forma elitral. *P. viridans* presenta una convergencia con *D. venator* (Scaritini) la cual forma parte del clado del subgénero *Pasimachus*, que es donde la forma alargada y angular del élitro se presenta más similar a la del grupo externo Scaritini.

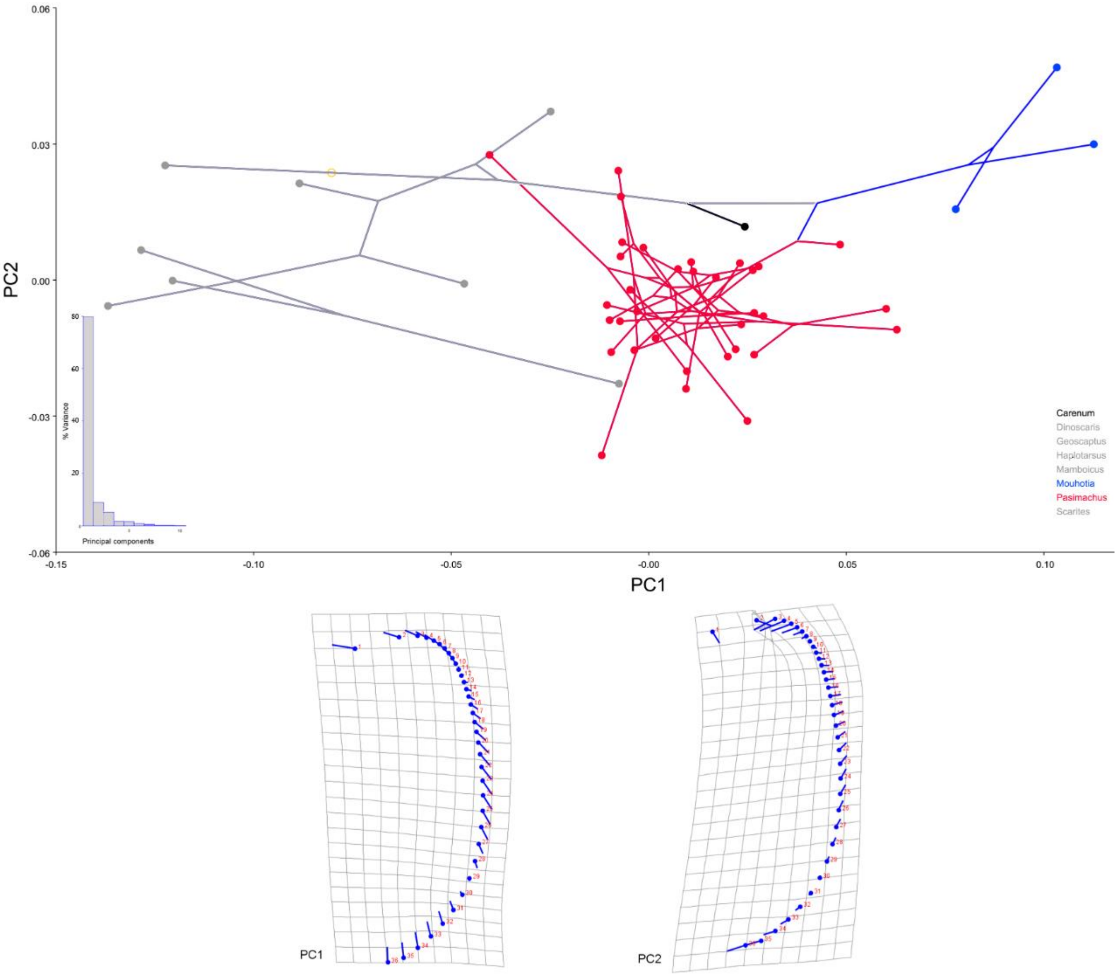


Figura 15. Análisis de componentes principales y filomorfoespacio del élitro derecho.

7.2.3. Mandíbula

Dentro de Scaritini la forma de la mandíbula es muy variable de un género a otro. *G. crassus*, *D. venator*, *M. afrellus* y *H. ignobillis*, comienza expandiéndose la base y contrayéndose el primer tercio para después volver a expandirse, lo que asemejaría un pequeño arco, en el tercer tercio muestran una curvatura notable que culmina justo antes de la punta de la mandíbula, lo cual asemeja una forma recta en el ápice de las mandíbulas. Las especies del género *Scarites* (*S. buparius*, *S. terrícola*, *S. subterraneus* y *S. anthracinus*) presentan una forma casi curva desde la base hasta casi la punta, en su zona apical se muestra la mínima formación de un ángulo recto, que asemeja la terminación de la mandíbula en punta (figura 16). Carenini

+ Pasimachini muestran entre si una estabilidad en la forma desde la base hasta el ápice de la mandíbula, aunque *C. interruptum* es mucho más redonda hacia el ápice.

Dentro de Pasimachini, la forma de *Mouhotia* es mucho más recta, poco curva desde la base y hacia la parte apical forma un pequeño ángulo recto. Para el género *Pasimachus* la forma muestra diferentes patrones de cambio, el clado *P. sexuales* y *P. quirozi* muestra una forma más pequeña y curva que inicia desde la mitad de la mandíbula hacia el ápice al igual que *P. intermedius y P. ambiguus.* El subgénero *Emydopterus* muestra una forma más alargada y poco curva. El subgénero *Pasimachus* muestra la mayor variación de la forma entre las especies. *P. laevisulcatus* presenta una curvatura muy pronunciada desde la mitad de la mandíbula, el clado conformado por *P. strenuus, P.marginatus, P.sublaevis, P.subsulcatus* presenta una cambio más notable que va desde la base en donde se contrae formando un pequeño arco en el primer tercio y poca curvatura hacia la parte apical, dando una forma más alargada a la mandíbula.

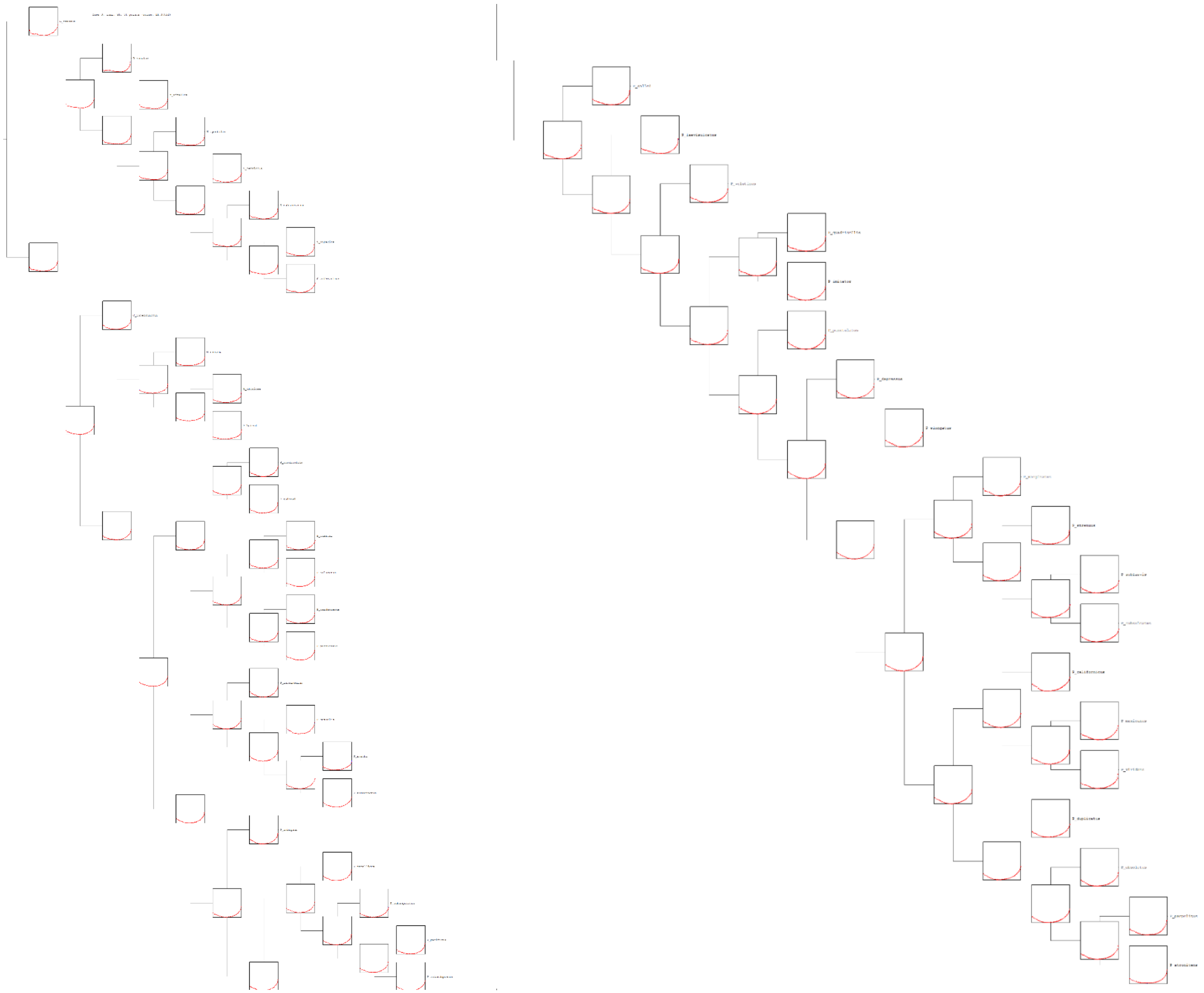


FIGURA 16. CLADOGRAMA RESULTANTE QUE MUESTRA EL CAMBIO EN LA FORMA DE LA MANDÍBULA EN SCARITINI, CARENINI Y PASIMACHINI

7.2.3.1. Análisis de componentes principales y filomorfoespacio

El análisis de componentes principales explica con los dos primeros componentes principales el 83% de la varianza de la forma de la mandíbula. El primer componente principal explica el 55% del 83% muestra una expansión en la base de la mandíbula que termina en el primer tercio, el segundo tercio se contrae hasta el tercer tercio donde vuelve a expandirse casi hasta la parte apical, donde se forma un pequeño ángulo en la punta. El segundo componente principal muestra el 28% de la varianza de la forma, se contrae el primer tercio desde la base se expande y se contrae en el segundo tercio y en el último tercio se expande notablemente para dar una forma en el aumento de la longitud de la estructura.

La expresión de la variación de la forma de la mandíbula en el filomorfoespacio (figura 17) muestra patrones de ocupación no congruentes con la taxonomía a nivel de tribu en el morfoespacio, esto sería una evidencia indirecta de poca información taxonómica y poca señal filogenética . Scaritini, Carenini y Pasimachini se sobreponen en el morfoespacio, a nivel de género se encuentran más estables, ya que dentro de Scaritini, *Scarites* se encuentra conformado, y dentro de Pasimachini *Mouhotia* se encuentra diferenciado de *Pasimachus.*

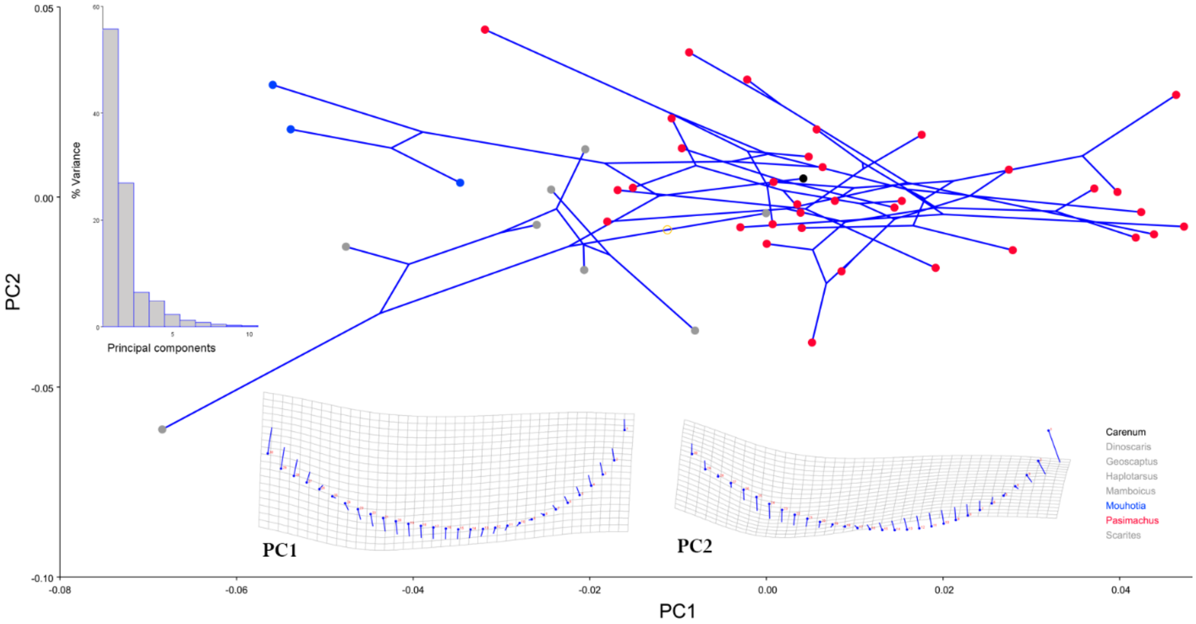


Figura 17. Análisis de componentes principales y filomorfoespacio de la mandíbula derecha.

7.2.4. Protibia

Las patas es una característica constante para la determinación de diferentes grupos en coleópteros. La protibia es una estructura que en este caso se ejemplifica como un carácter importante para la taxonomía a nivel de tribus y géneros, la filogenia y el filomorfoespacio obtenido evidencian de manera clara este aspecto.

En la tribu Scaritini la forma de la protibia es constante, los tres dientes externos muestran muy poca variación en su forma, así como sus dos dientes internos tanto en las especies como para sus ancestros reconstruidos en el cladograma (figura 18). *C. interruptum*, único representante de Carenini, tribu hermana de Pasimachini, presenta cambios muy notables con respecto a Scaritini, únicamente presenta dos dientes externos, y dos internos, aunque el primero notablemente expandido.

Respecto a Pasimachini *Mouhotia* presenta tres dientes en su cara externa, mostrándose notablemente más ancho el primer diente, y un solo diente notable por su cara interna. Para *Pasimachus* este arreglo se mantiene, sin embargo, el tercer diente de la cara externa es mucho más notable.

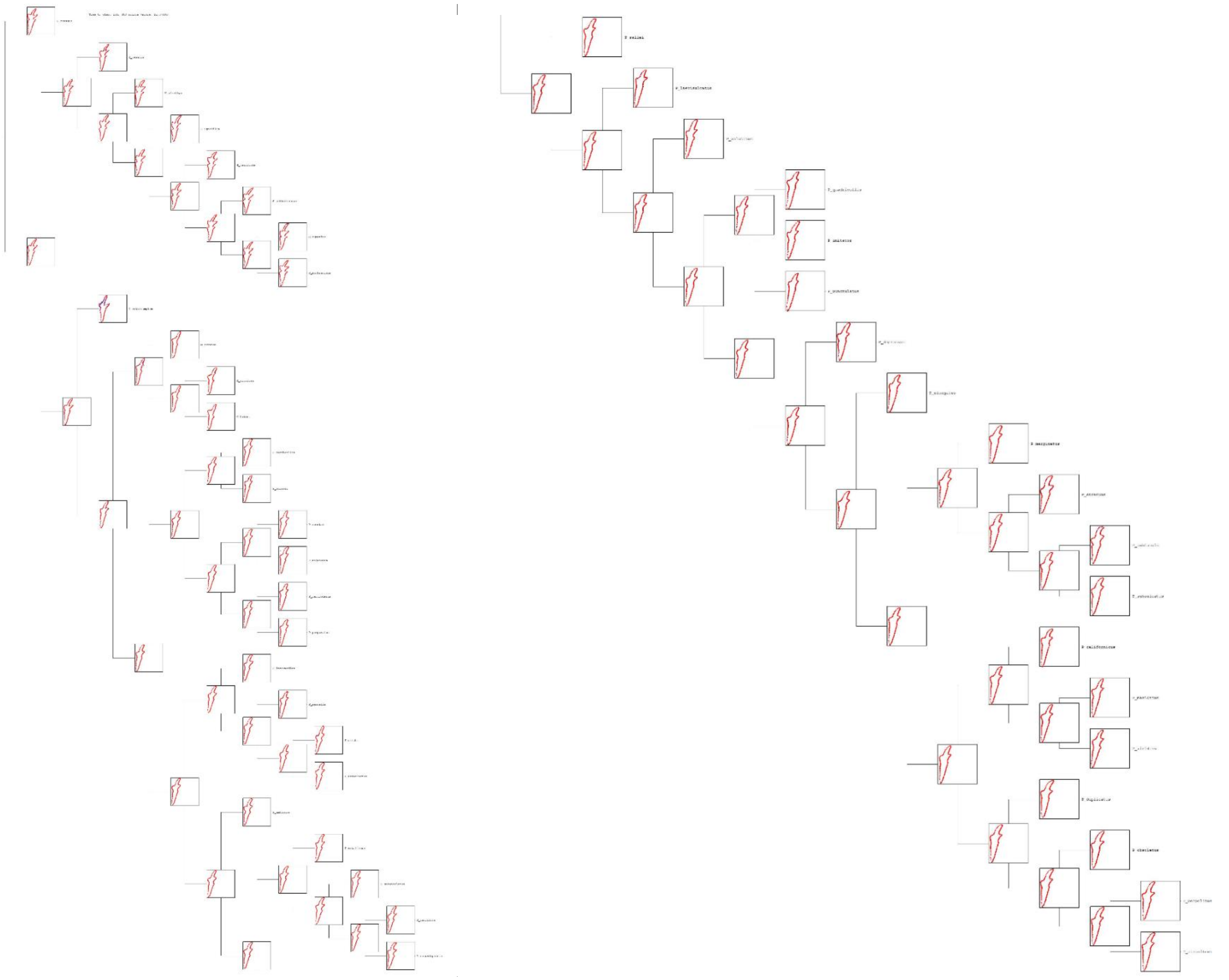


FIGURA 18. CLADOGRAMA RESULTANTE QUE MUESTRA EL CAMBIO EN LA FORMA DE LA PROTIBIA EN SCARITINI, CARENINI Y PASIMACHINI

7.2.4.1. Análisis de componentes principales y filomorfoespacio

El primer componente principal explica el 42% de la varianza total de la forma, muestra la contracción de la parte del primer diente hacia el segundo diente de la cara externa, del segundo al tercer diente se muestra una notable expansión, y del tercer diente a la base, una ligera expansión, desde la base hacia el segundo diente de la cara interna se muestra un ensanchamiento que se reduce desde el segundo hasta el primer diente interno, desde su ápice hacia el ápice del primer diente externo se muestra una ligera reducción. El segundo componente principal explica el 18% de la varianza total, mostrando un cambio en la forma que va desde el primer diente externo y se contrae ligeramente hacia el segundo diente externo, del segundo hacia el tercer diente externo hay una notable reducción en la forma, del tercer diente hacia la base una ligera expansión al igual que de la base hacia el segundo diente de la cara interna, justamente en el segundo diente se refleja una contracción notable para luego expandirse en el primer diente interno, y contraerse hacia el primer diente externo.

La variación de la forma de la protibia en el filomorfoespacio (figura 19) muestra patrones de ocupación del morfoespacio notablemente estables con respecto a la taxonomía a nivel de tribus y géneros. Las especies del grupo externo pertenecientes a Scaritni están bien conformadas con poca variación morfológica. Carenini ocupa un lugar en el morfoespacio muy diferente al de Pasimachini, que es su tribu hermana. *Pasimachus* y *Mouhotia* están claramente separados sin ningún caso de convergencia, lo que refleja una conformación estable en la forma de la protibia en estas tres tribus y dentro de Pasimachini.

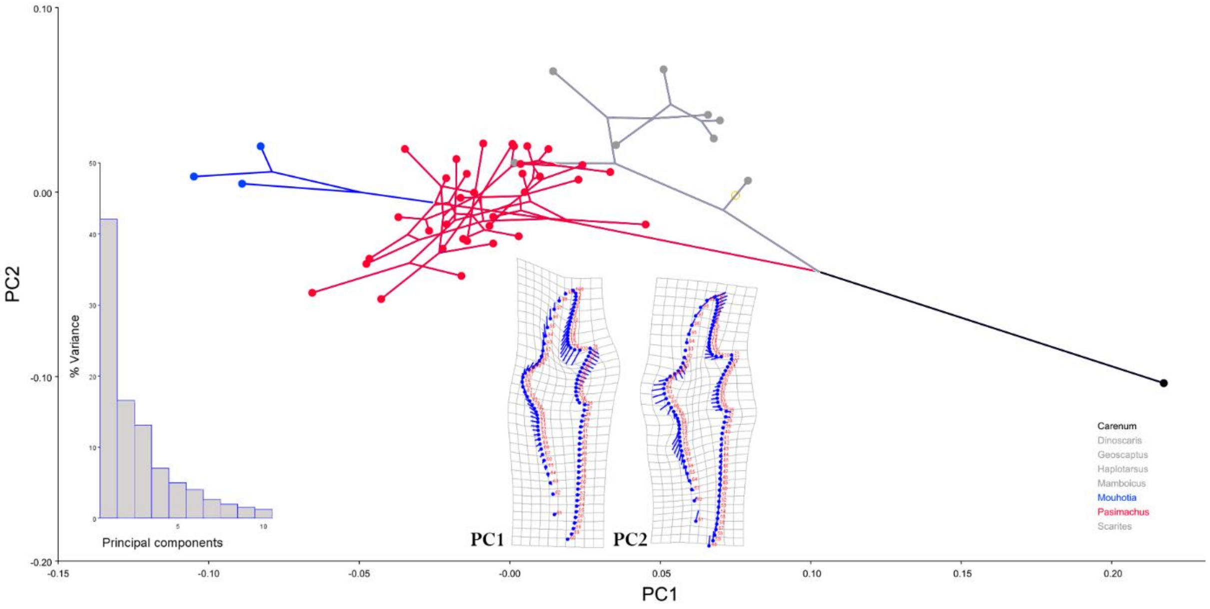


Figura 19. Análisis de componentes principales y filomorfoespacio de la protibia derecha.

VIII. DISCUSIÓN

8.1. Filogenia de Pasimachini

Bänninger (1950) hace mención de la dudosa monofília de esta tribu, la cual se discute a continuación.

Carenini (*C. interrumptum* única especie representante en este trabajo) es una tribu endémica de Australia. Sloane en 1905 postulaba a Carenini y Pasimachini bajo un mismo grupo familiar, lo que sugería una estrecha relación entre ambos grupos debido a las similitudes morfológicas, Bänninger también hace referencia a esta tribu, como la más emparentada con Pasimachini, lo cual ha sido sustentado por otros autores (Nichols 1988). Hogan en 2012 realizó una filogenia molecular de la subfamilia Scaritinae, donde Carenini también aparece como la tribu hermana de Pasimachini, sin embargo, Hogan no toma en cuenta todas las especies que conforman a la tribu Pasimachini.

Tanto en el cladograma obtenido a partir de estrategias de búsqueda con Nuevas Tecnologías con el mismo peso y con pesos implícitos se puede validar la monofilia de Pasimachini, incluyendo como únicos integrantes a *Pasimachus* como a *Mouhotia,* y esta tribu, como el grupo hermano de Carenini, lo cual difiere con la opinión que presentó Bänninger en su revisión, donde no asegura a Pasimachini como un grupo natural, indicando que *Mouhotia* debería ser ubicado fuera de Pasimachini para formar una tribu única sin dar una propuesta formal.

El género *Mouhotia* está conformado por tres especies distribuidas en el sudeste de Asia. Esta distribución ha sido una de las principales razones por las cuales la tribu Pasimachini es cuestionada como un grupo natural. Lorenz (2005) incluso coloca a *Mouhotia* fuera de Pasimachina y lo incluye en Carenini, mientras que Bousquets (2012) evita la propuesta de un nuevo grupo familiar para colocar a *Mouhotia* y lo incluye como miembro de Pasimachini. Sin embargo, las características morfológicas dan muestra clara de la afinidad filogenética entre *Mouhotia* y *Pasimachus*. Los caracteres más notables que validan esto son: la ausencia de un poro sedífero supraorbital en la zona posterior del ojo, la ausencia de un poro sedífero frontal en el borde del clípeo, la ausencia de una hilera de sedas en los márgenes exteriores en los lóbulos laterales del labro, la presencia de más de 6 sedas en el segundo segmento del palpo labial, formación de ángulos en la parte basal en el pronoto, ausencia de poros setíferos en la zona apical de los élitros, la forma tridentada en el margen externo de la protibia, elevada de los dentículos basales de la protibia elevados, la ausencia de una espina en la cara interna en la parte distal de la mesotibia y la presencia de una carina en la parte externa de los protarsos 2, 3 y 4.

8.2. Relaciones filogenéticas dentro de Pasimachini

Partiendo del establecido en que Pasimachini es un grupo monofilético conformado por *Pasimachus* y *Mouhotia*, las relaciones entre las especies de cada género no son sencillas de exponer. *Mouhotia* es un género que está representado únicamente por tres especies (*M. gloriosa*, *M. convexa* y *M. batesi*), las cuales aparecen en nuestro cladograma como las más que se separan primero de y como los parientes inmediatos respecto de la tribu Carenini. Sin embargo, a pesar de que este género esta poco representado en número de especies, sus relaciones no habían sido definidas. Pouillaude (1914) y Csiki (1927) hacen sinopsis breves acerca de este género y definen a las especies por características como el tamaño corporal, el cual es muy variable. Mawdsley en 2011 hace una diagnosis y proporciona una clave mejorada donde incluye características más particulares para el reconocimiento de especies, sin proporcionar afinidades entre las especies. En los cladogramas obtenidos, tanto en el de pesos iguales como el de pesos implícitos, se muestran a las especies de *Mouhotia* en un clado con el mismo arreglo; *M. convexa* como la especie basal y *M. gloriosa* y *M. batesi* como especies hermanas y derivadas, esto se describió anteriormente y los caracteres que soportan esta relación son merísticos y morfogeométricos.

El género *Pasimachus,* de acuerdo con la literatura está compuesto por dos subgéneros; *Pasimachus* Hope 1838 y *Emydopterus* Lacordaire 1854. Esta clasificación se mantuvo vigente por Bänninger al momento de hacer su revisión de la subtribu Pasimachina, la cual proporciona el único trabajo previo acerca de *Pasimachus*. Esta clasificación a nivel de subgéneros está basada en características morfológicas y también coincide con un patrón de distribución biogeográfico, en donde *P. (Pasimachus)* presenta una distribución neártica, que va desde el centro hasta el norte de México, prácticamente en todo Estados Unidos hasta y hasta el sur de Canadá, y mientras que *P. (Emydopterus)* presenta con una distribución neotropical, que va desde el centro y sur de México hasta Panamá, que refleja una separación vicariante entre las especies de ambos subgéneros por la barrera que representa el Eje Volcánico Transversal.

Esto es considerablemente relevante en el contexto del establecimiento del género en México y su posterior distribución y especiación, ya que implicaría que al menos algunas especies o linajes, o bien, son antiguos y tuvieron una amplia distribución antes de la elevación del Eje Volcánico, y después, al elevarse esta cadena montañosa, quedaron aislados en ambos lados. Este escenario se ajusta al Patrón de Distribución Paleoaméricano descrito por Halffter (1964, 1976, 1978), que se caracteriza por taxones con penetración antigua a América por vía septentrional y que han diversificado en la EVT durante el Plioceno, con sus parientes más próximos en el Viejo Mundo.

El subgénero *Pasimachus* en nuestro cladograma aparece como un grupo monofiletico. De acuerdo a la designación de este subgénero existen 21 especies reconocidas (Erwin 2011), aunque, en nuestro cladograma dos de estas especies, *P. tolucanus* y *P. aurocinctus* están ubicadas en otros clados. Hogan (2012) hace mención a 3 grupos de especies dentro de este subgénero; *depressus, marginatus,* y *strenuus,* aunque no indica ningún criterio morfológico para ello. Las especies de cada uno de estos grupos no forman clados en nuestros resultados, por lo que el arreglo y la inclusión de nuevas especies a estos tres grupos, es una posibilidad real con los resultados finales de nuestros análisis filogenéticos.

En el caso del subgénero *Emydopterus*, nuestros resultados no muestran congruencia con lo establecido tradicionalmente. *Emydopterus*, con respecto a *Pasimachus* representa un grupo parafilético, distribuido en tres diferentes clados, y algunas especies se encuentran en ramas terminales aisladas, como en el caso de *P. aurocinctus, P. intermedius* y *P. ambiguus*, cuyos epítetos específicos de al menos las dos últimas, podrían indicar la compilación del autor para reconocer su afinidad con el resto de las especies. *P. rotundipennis*, que es la especie tipo del subgénero *Emydopterus*, aparece en el clado más basal de *Pasimachus* que incluye 4 especies más (*P. smithi, P. pacificus, P. metallicus* y *P. subangulatus*), y por ello, para considerar a *Emydopterus* como un taxón valido, se tendría que ser redefinida su composición de especies.

8.3. Clasificación supraespecífica

La condición de polifilia en el subgénero *Emydopterus*, refleja la necesidad de una nueva clasificación a nivel de subgéneros dentro de *Pasimachus*. En el siguiente apartado se presenta una propuesta basada en los clados obtenidos en nuestra filogenia, para proponer una clasificación filogenética de la tribu Pasimachini, así como una clave dicotómica para las 34 especies del género.

8.3.1. Clasificación filogenética

Con base a la topología resultante del cladograma obtenido, y siguiendo las reglas de nomenclatura, básicamente la subordinación y secuenciación se propone la siguiente clasificación filogenética.

Orden Coleoptera Linnaeus 1758
  Familia Carabidae Latreille 1802
    Subfamilia Scaritinae Bonelli 1810
      Tribu Pasimachini Putzeys 1867
        Género *Mouhotia* Castelnau 1862
            M. convexa Lewis 1883
            M. gloriosa Castelnau 1862
            M. batesi Lewis 1879
        Género *Pasimachus* Bonelli 1813
          Subgénero *Aurocinctus* Cerón-Gómez y Ramírez-Ponce 2018
            P. aurocinctus Chaudoir 1880

Subgénero *Emydopterus* Lacordaire 1854

- *P. rotundipennis* Chevrolat 1834
- *P. smithi* Bates 1891
- *P. pacificus* Bänninger 1950
- *P. metallicus* (Chaudoir, 1880)
- *P. subangulatus* Chaudoir 1862

Subgénero *Sexualis* Cerón-Gómez y Ramírez-Ponce 2018

- *P. sexualis* Flohr 1887
- *P. quirozi* Bänninger 1950

Subgénero *Intermedius* Cerón-Gómez y Ramírez-Ponce 2018

- *P. intermedius* (Chaudoir) 1880

Subgénero *Ambiguus* Cerón-Gómez y Ramírez-Ponce 2018

- *P. ambiguus* Bänninger 1950

Subgénero *Cordicollis* Cerón-Gómez y Ramírez-Ponce 2018

- *P. cardioderus* (Chaudoir 1880)
- *P. cordicollis* Chaudoir 1862
- *P. cuestai* Kohlman 1993
- *P. tolucanus* Chaudoir 1880
- *P. purpuratus* (Putzeys, 1845)

Subgénero *Pasimachus* Bonelli 1813

- *P. sallei* Chaudoir 1862
- *P. laevisulcatus* Bates 1891
- *P. quadricollis* Chaudoir 1880
- *P. strenuus* LeConte 1874
- *P. marginatus* (Fabricius, 1787)
- *P. sublaevis* (Palisot de Beauvois, 1811)
- *P. subsulcatus* Say 1823
- *P. elongatus* LeConte 1846
- *P. depressus* (Fabricius, 1787)
- *P. duplicatus* LeConte 1853

P. obsoletus LeConte 1848

P. perpolitus Casey 1913

P. atronitens Casey 1913

P. mexicanus Gray 1832

P. viridans LeConte 1858

P. velutinus Van Dyke 1943

P. imitator Bänninger 1950

P. punctulatus Haldeman 1843

P. californicus Chaudoir 1850

8.3.2. Clave taxonómica para determinar las especies del género *Pasimachus* Bonelli

1. Formación de carina en la zona humeral (foto 9); Pronoto con ángulos en los bordes laterales posteriores……………………………………..……………………………………...2

1´ Ausencia de carina en la zona humeral; Forma del pronoto sin ángulos en los bordes laterales posteriores…………………… Subgénero *Emydopterus* Putzey….………..……………26

2. Coloración con reflejos metálicos en la cabeza; presencia de un dentículo medio interno en el labro (foto 1); poros sedíferos presentes en los ángulos posteriores del pronoto (foto 12); sutura elitral fusionada…………...Subgénero *Pasimachus* Bonelli…..…....…..…………3

2´ Coloración opaca en la cabeza; ausencia de un dentículo en el labro; sin poros sedíferos en los ángulos del pronoto; élitros no fusionados (foto 13)…………………….............Subgénero *Cordicollis* Cerón……………………...……22

3. Lóbulos del labro notablemente sinuados (foto 2); margen incompleto en la zona anterior del pronoto (foto 14); estrías elitrales sin puntuación………….………………...….………..4

3´ Lóbulos en el labro ligeramente sinuados; margen completo en la zona anterior del pronoto; estrías elitrales definidas por puntuación………………………....…......*P. sallei* Hogan

4. Superficies del labro estrigosa; presencia de fóveas exteriores en el pronoto……….………5

4´ Superficie del labro lisa, ausencia de fóveas exteriores basales del pronoto (foto 15); parte apical del edeago larga no laminar…………………………...………*P. laevisulcatus* Bates

5. Lóbulo medio del labro similar o menor en relación a los lóbulos laterales; diente basal de la mandíbula derecha no dentado (foto 16); ausencia de un segundo diente en la mandíbula izquierda……………………..………………………….……………………………6

5´ Lóbulo medio del labro notablemente mayor en relación a los lóbulos laterales; diente basal de la mandíbula derecha dentado; presencia de un segundo diente en la mandíbula izquierda……………………..…………………..…….….….*P. quadricollis* Chaudoir

6. Costillas elitrales 3-5-7 convergentes hacia el ápice del élitro (foto 17); ausencia de poros sedíferos en los segmentos ventrales 3-5; forma corporal cuadrada amplia en la zona humero que se va angostando hacia el ápice……....…………………………………7

6´ Costillas elitrales 3-5-7 no convergentes hacia el ápice del élitro; presencia de poros sedíferos en los segmentos ventrales 3-5…………………………………………………13

7. Presencia de más de 6 sedas en el segundo segmento del palpo labial; mandíbula derecha multidentada; más de tres sedas internas en la cara ventral del primer metatarso……………………………...……………………………..*P. strenuus* LeConte

7´ Menos de 6 sedas en el segundo segmento del palpo labial; mandíbula derecha con solo un diente; menos de tres sedas internas en la parte ventral del primer metatarso (foto 18)…...8

8. Dentículo interno del labro largo y prominente; corona de sedas apicales continua en los protarsos (foto 19)…..…………………………………………………….…………9

8´ Dentículo interno del labro corto y ancho; corona de sedas apicales interrumpida en protarsos……………..........……..……………………………*P. marginatus* (Fabricius)

9. Espina mesotibial apical fija corta y ancha; placas laterales del edeago con sedas largas..10

9´ Espina mesotibial apical fija larga y en forma de punta (foto 20); placas laterales del edeago con sedas cortas……………………………..…………………………….……………13

10. Región interocular de la cabeza plana (foto 4); ángulos posteriores del pronoto forman un ángulo obtuso; fóveas internas basales en el pronoto poco marcadas y profundas…....……..……………..……………………*P. sublaevis* (Palisot de Beauvois)

10´ Región interocular de la cabeza convexa; ángulos posteriores del pronoto redondeados; Foveas internas basales en el pronoto muy marcadas y profundas ………………………………...…………………………………... *P. subsulcatus* Say

11. Segmentos antenales 2-4 carinados; ausencia de estrías elitrales visibles…….….……….12

11´ Segmentos antenales 2-4 no carinados; presencia de estrías elitrales visibles..…………..24

12. Región interocular plana; superficie lisa del canal lateral del pronoto……………………………………..…………………*P. depressus* (Fabricius)

12´ Región interocular convexa; superficies rugosa del canal lateral del pronoto (foto 9)…………………..………………..……………………………*P elongatus* LeConte

13. Longitud del último segmento del palpo maxilar más corto con respecto al penúltimo segmento; costillas elitrales externas carinadas……………………..…………………14

13´ Longitud del último segmento del palpo maxilar más largo con respecto al penúltimo segmento; costillas elitrales externas no carinadas…………………………...………...15

14. Ausencia de sedas en el metatarso 1 por su cara ventral; placas laterales del edeago largas……………………..……………..……………….…...*P. duplicatus* LeConte

14´ Presencia de dos sedas internas en el metatarso 1 por su cara ventral; placas laterales del edeago cortas……………..……………………………..………*P. obsoletus* LeConte

15. Mandíbulas abruptamente curvas hacia el tercio distal; ausencia de fosetas laterales superiores en el pronoto…….……………………….………………….…………..16

15´ Mandíbulas no curvas en el tercio distal; presencia de fosetas laterales superiores en el pronoto…………………………..……………………………………………......17

16. Dentículo interno del labro corto y ancho; superficie lisa en la parte dorsal de la mandíbula derecha…………...………………...……………..………….....…….*P. atronitens* Casey

16´ Dentículo interno del labro largo y prominente; superficie rugosa en la parte dorsal de la mandíbula derecha……………..………………….……………….………*P. perpolitus* Casey

17. Margen del pronoto definido por una endidura punteada; fóveas internas basales del pronoto muy marcadas; profundas y conectadas transversalmente..………………..……………..18

17´ Margen del pronoto definido por una endidura continua; fóveas internas basales del pronoto poco marcadas………………………………..…..……….…………………………...19

18. Vertices posteriores del pronoto formando un ángulo obtuso; ausencia de poros sedíferos en los ángulos posteriores del pronoto……………......................……….*P. mexicanus* Gray

18´ Vértices posteriores del pronoto formando un ángulo recto; presencia de poros sedíferos en los ángulos posteriores del pronoto……………………………………..*P. viridans* LeConte

19. Presencia de 1 seda interna en la cara ventral del metatarso 1; ausencia de un mechón de sedas en la cara interna de la metatibia ………..……………………….………..……..…20

19´ Presencia de más de una seda interna en la cara ventral del metatarso 1; presencia de un mechón de sedas en la cara interna de la metatibia……………………………………...21

20. Foveas internas basales no conectadas transversalmente; longitud del último segmento del palpo maxilar más largo con respecto al penúltimo……………..…*P. velutinus* Van Dyke

20´ Foveas internas basales conectadas transversalmente; último segmento del palpo maxilar con longitud similar al penúltimo segmento……...………….……..…..*P. imitator* Bänninger

21. Margen anterior del pronoto incompleto; foveas internas basales muy marcadas y profundas y conectadas transversalmente………………………….....………*P. californicus* Chaudoir

21´ Margen anterior del pronoto completo; fóveas internas basales poco marcadas y no conectadas transversalmente……………….……………………*P. punctulatus* Haldeman

22. Canto ocular con forma sub-angular; lóbulo medio del labro de tamaño similar o menor a los lóbulos laterales; segundo segmento del palpo labial con menos de 5 sedas…..……...23

22´ Canto ocular con forma redondeada; lóbulo medio del labro mayor a los lóbulos laterales; segundo segmento del palpo labial con más de 6 sedas......................*P. cordicollis* Chaudoir

23. Lólubos del labro ligeramente sinuados; diente basal de la mandíbula izquierda no dentado……………………………………………..………………………………..24

23´ Lóbulos del labro marcadamente sinuados; diente basal de la mandíbula izquierda dentado…………………………………………………...………………………..25

24. Parte distal del labio no segmentada; forma unidentada de la mandíbula derecha; márgenes del pronoto de coloración metálico……...…………………...……….*P. cuestai* Kohlmann

24´ Parte distal del labio bisegmentada; forma multidentada de la mandíbula derecha; márgenes del pronoto de coloración negro..……..……………………………...*P. tolucanus* Chaudoir

25. Presencia de un segundo diente en la mandíbula derecha; posición intercoxial en el prosterno en forma chata………………………………..……..……………*P. purpuratus* Putzeys

25´ Ausencia de un segundo diente en la mandíbula derecha; posición intercoxal en el prosterno en forma de punta……………………………..…..…..……….*P. cardioderus* (Chaudoir)

26. Coloraciones iridiscentes verde-anaranjado en el borde del pronoto y en los élitros; ausencia de fóveas exteriores en la base del pronoto; diente basal de la mandíbula izquierda bidentado………………………………..…......................................….*P. smithi* Bates

26´ Coloraciones iridiscentes rojas-verdes-azules en el borde del pronoto y élitros; presencia de fóveas exteriores en la base del pronoto; diente basal de la mandíbula izquierda tridentado……………………………......…………………..…..*P. rotundipennis* Chevrolat

27. Parte distal del labio bisegmentada; diente basal de la mandíbula izquierda bidentado; margen anterior del pronoto incompleto; coloraciones metálicas en la parte dorsal de los élitros………………………………………..………..28

27´ Parte distal del labio no segmentada; diente basal de la mandíbula izquierda tridentado; margen anterior del pronoto completo; coloración verde metálico en los surcos elitrales……………………………………...……...………..…*P. pacificus* Bänninger

29. Vértices laterales del labio deprimidos; ausencia de un cuarto diente en la mandíbula derecha; fóveas internas del pronoto conectadas transversalmente……………………………………………..*P. metallicus* (Chaudoir)

29´ Vértices laterales del labio no deprimidos; presencia de un diente 4 en la mandíbula derecha; fóveas internas del pronoto no conectadas transversalmente…………………………….…………………..*P. subangulatus* Chaudoir

30. Diente basal de la mandíbula derecha dentado; parte apical del edeago larga no laminar; posición intercoxial larga en el prosterno………….……………...….*P. sexualis* Bänninger

30´ Diente basal de la mandíbula derecha no dentado; parte apical del edeago corta y chata; posición intercoxial corta en el prosterno……………………………..….*P. quirozi* Flohr

31. Lóbulo medio del labro redondeado; fosetas laterales superiores del pronoto ausentes; mechón de sedas en el profemur…………………………….……*P. intermedius* (Chaudoir)

31´ Lóbulo medio del labro chato; fosetas laterales superiores del pronoto presentes; coloración verde metálica en los élitros……………………………..………*P. ambiguus* Bänninger

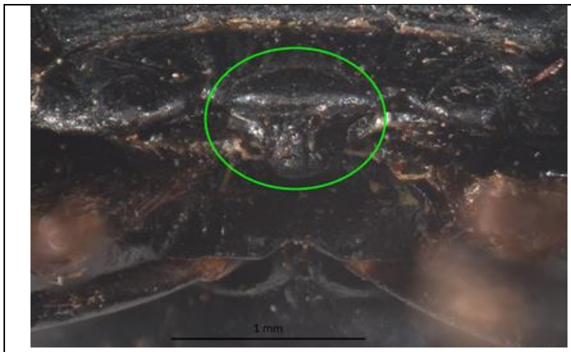


Foto 1. Dentículo medio interno en el labro

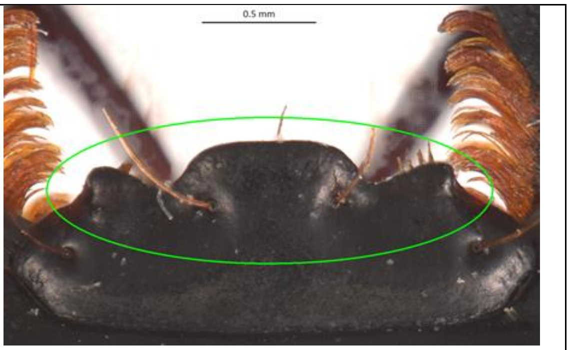


Foto 2. Lóbulos del labro

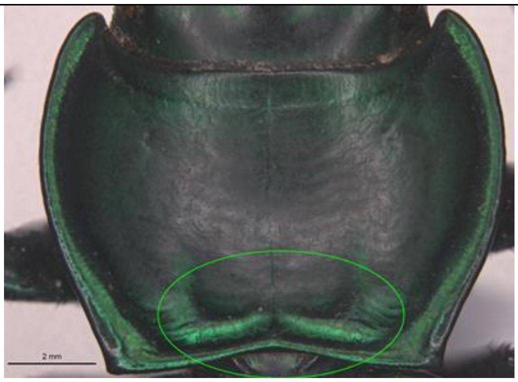


Foto 3. Fóveas internas pronotales conectadas

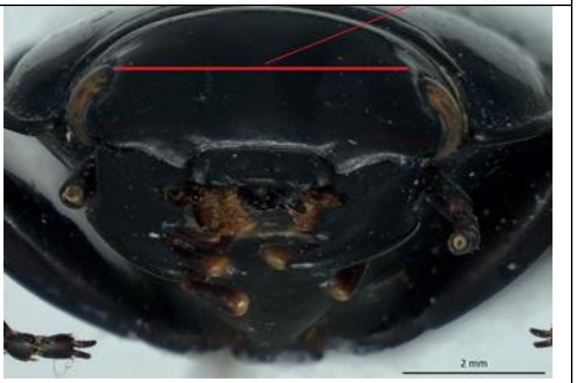


Foto 4. Región interocular

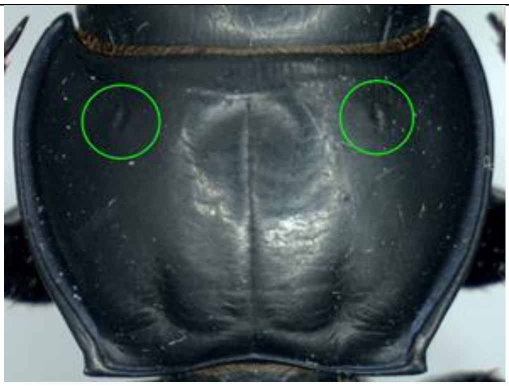


Foto 5. Fosetas superiores pronotales

Foto 6. Espina mesotibial fija

Foto 7. Mechon de sedas en profemur (*P. intermedius*)

Foto 8. Prosterno, posición intercoxial prominente, larga y en punta

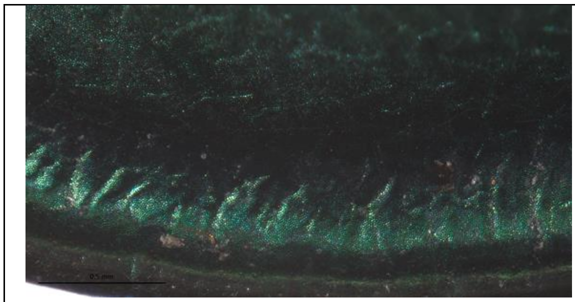


Foto 9. Canal lateral del pronoto con superficie rugosa

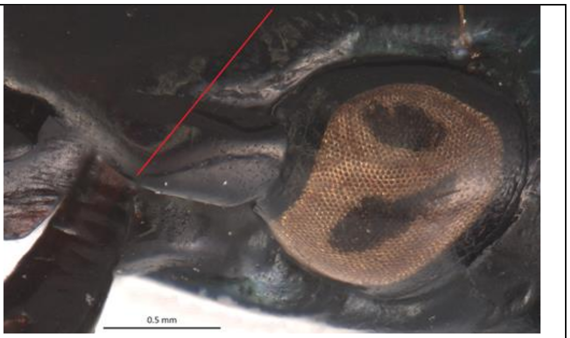


Foto 10. Canto ocular

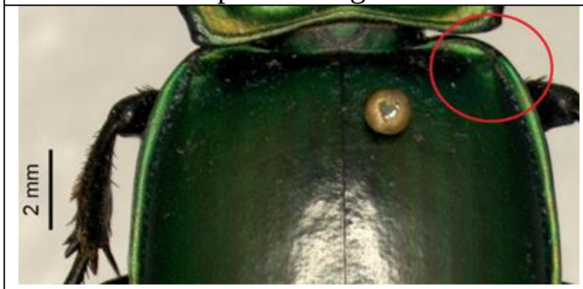


Foto 11. Carina humeral

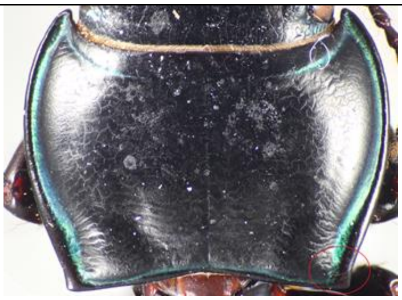


Foto 12. Poros sediferos en los ángulos posteriores del pronoto

Foto 13. Élitros no fusionados

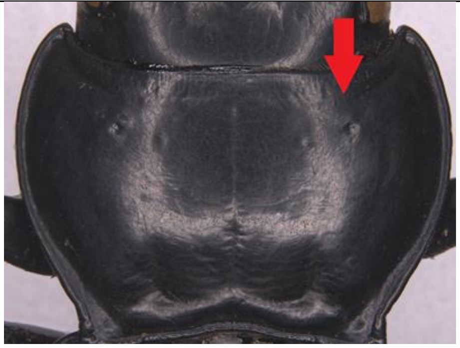


Foto 14. Márgen anterior pronotal incompleto

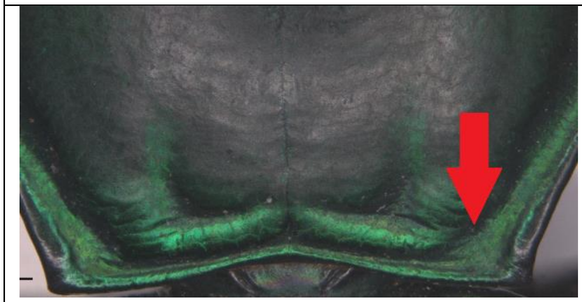
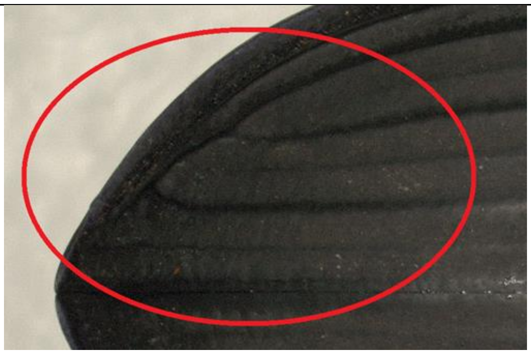
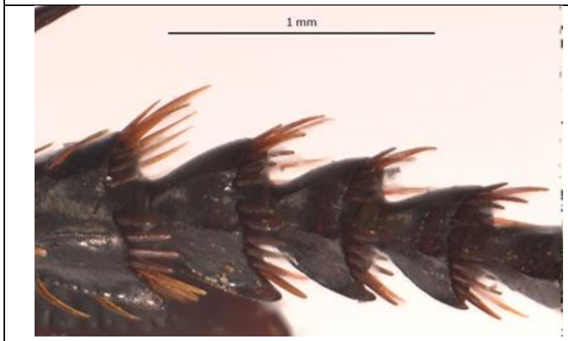


Foto 15. Fóveas exteriores del pronoto

Foto 16. Diente 2 de mandíbula derecha no dentado

 Foto 17. Estrías elitrales 3-5-7 convergentes en el ápice del élitro	 Foto 18. Sedas en la cara interna del metatarso
 Foto 19. Corona de sedas apicales continuas en los protarsos	 Foto 20. Espina mesotibial fija larga

8.4. Afinidades biogeográficas de Pasimachini

La distribución actual de las especies de ambos géneros es disyunta; las tres especies que conforman a *Mouhotia* se distribuyen en el sudeste de Asia (Tailandia, Indonesia, China, Laos), mientras que *Pasimachus* se distribuye exclusivamente en América, desde el sur de Canadá hasta Panamá. Hasta el momento no se ha generado una explicación para este patrón biogeográfico, sin embargo, es necesario considerar la fragmentación de Gondwana. Esta propuesta es mencionada por Hogan (2012) para explicar la distribución actual de Pasimachina y Carenina (que es una tribu exclusivamente australiana), y su parentesco como subtribus hermanas. Sin embargo, *Pasimachus* pudo haber tenido una distribución septentrional y la ausencia actual de *Pasimachus* en Sudamérica se podría explicar por eventos de extinción. Este evento geológico debió haber ocurrido a finales del triásico y principios del jurásico, hace unos

250-200 millones de años. En la era mesozoica, lo cual coincide con los primeros registros fósiles de carábidos, un ejemplo es la tribu Hiletinae, un grupo contemporáneo con Scaritinae.

Otra propuesta que podría ser aceptada para la distribución actual de los miembros de Pasimachini, es la que menciona Erwin (1985), denominada como un patrón de distribución anfiántico. Este patrón que va desde el sur del neotrópico hasta llegar a la parte norte de la región neártica, se explica por una ruta de dispersión que debió pasar desde Australia por la Antártida hasta llegar a Sudamérica. El desplazamiento por la Antártida tiene congruencia, ya que hace 200 millones de años las condiciones eran distintas en esa zona del planeta y no estaba cubierta por una extensa capa de hielo.

Otra posible ruta para explicar el petrón disyunto en Pasimachini y la presencia de *Pasimachus* en América pudo haberse dado por el hemisferio norte del planeta. Halffter (1962-1964) ha estudiado los patrones de distribución de los taxones en la zona de transición mexicana, y propone un patrón de distribución Paleoamericano, en el cual hubo especies que llegaron a América del Norte desde Eurasia y tuvieron una distribución hacia el sur, con distribuciones presentes en las zonas bajas tropicales. Esto podría haber sucedido con *Pasimachus*, ya que Halffter habla de taxones cosmopolitas con este patrón de distribución, una característica de los carábidos. Esta distribución debió haber ocurrido en el cenozoico temprano, antes del desarrollo del Cinturón Volcánico Transmexicano, el cual parece ser fundamental para la evolución de *Pasimachus*. Esto explicaría la ausencia de Pasimachini en África y Sudamérica.

IX. CONCLUSIONES

La hipótesis filogenética resultante en este trabajo nos da un marco de referencia estable de las relaciones entre las especies del género *Pasimachus*, ya que las topologías resultantes en los diferentes análisis, con y sin bloques de morfometría geométrica, son en la mayoría de los casos, congruentes.

La filogenia ha generado información relevante que ha servido para proponer una clasificación natural desde el nivel de tribus, así como al interior de *Pasimachus*, a nivel de subgéneros, la cual no había sido abordada desde el trabajo de Bänninger (1950).

La conformación de la tribu Pasimachini (*Pasimachus* y *Mouhotia)* es validada como un grupo monofilético y soportada por 17 sinapomorfías. Esto descarta la hipótesis inicial de este trabajo sobre la naturaleza de un grupo artificial, como lo mencionaba Bänninger (1950) y Lorenz (2005).

El género *Pasimachus* es un grupo monofilético, con el subgénero *Pasimachus* como monofilético, y el subgénero *Emydopterus* polifilético.

Se proponen una clasificación taxonómica con 4 subgéneros nuevos: *Aurocinctus, Intermedius, Sexuallis y Cordicollis* basados en la filogenia resultante.

Se analiza la forma del cuatro estructuras morfológicas en un contexto evolutivo, y se encuentra evidencia de que el pronoto, el élitro y la protibia son notablemente extables en su forma a nivel de géneros y tribus, por lo que proporcionan información filogenética importante, sin embargo, la mandíbula no muestra patrones de ocupación en el morfoespacio acordes con la taxonomía a nivel de tribus ni de géneros.

Se abordan dos posibles explicaciones acerca de la distribución geográfica actual de los miembros de la tribu Pasimachini. Una distribución con un origen Gondwanico y otra distribución desde Eurasia hacia Norteamérica, interpretando los resultados obtenidos en nuestra hipótesis filogenética con los eventos geológicos sucedidos en la era mesozoica.

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ANEXO 1. Matriz de caracteres morfológicos y morfogeométricos

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Matrix Pasimachus
'
102 46

&[continuous]
G_crassus 0.36 0.53 1.32 0.61 0.52 0.11 0.46 0.13
M_afrellus0.26 0.35 0.82 0.38 0.34 0.05 0.31 0.05
H_ignobilis           0.44 0.42 1.03 0.53 0.47 0.09 0.37 0.06
D_venator 0.81 0.64 1.72 0.96 0.83 0.18 0.72 0.16
S_anthracinus         0.36 0.38 0.08 0.46 0.54 1.11 0.38 0.36
S_buparius            0.59 0.51 1.42 0.75 0.68 0.11 0.58 0.11
S_terricola0.27 0.38 0.99 0.45 0.38 0.07 0.33 0.06
S_subterraneus        0.31 0.35 0.89 0.43 0.38 0.05 0.28 0.05
C_interrumptum        0.33 0.52 1.05 0.45 0.47 0.11 0.45 0.15
M_batesi  0.71 0.86 2.29 1.24 0.98 0.23 1.15 0.51
M_convexa             0.68 0.87 2.21 1.25 0.85 0.22 1.03 0.42
M_gloriosa            0.78 0.90 2.35 1.40 1.05 0.21 1.08 0.40
P_quirozi 0.40 0.40 1.00 0.50 0.71 0.10 0.53 0.17
P_purpuratus          0.56 0.60 1.46 0.81 0.64 0.16 0.66 0.23
P_rotundipennis       0.48 0.58 1.33 0.62 0.62 0.15 0.60 0.18
P_sallei  0.41 0.48 1.17 0.63 0.51 0.11 0.57 0.24
P_sexualis0.43 0.45 1.15 0.55 0.51 0.11 0.60 0.18
P_subsulcatus         0.33 0.46 1.10 0.73 0.44 0.11 0.53 0.18
P_tolucanus           0.38 0.48 1.13 0.62 0.50 0.12 0.56 0.19
P_viridans0.44 0.56 1.32 0.66 0.56 0.12 0.62 0.22
P_californicus        0.58 0.70 1.60 0.89 0.71 0.18 0.76 0.26
P_cardioderus         0.62 0.64 1.43 0.89 0.70 0.16 0.74 0.24
P_cuestai 0.39 0.43 1.11 0.59 0.46 0.10 0.50 0.18
P_imitator0.58 0.64 1.71 0.90 0.70 0.16 0.76 0.23
P_intermedius         0.42 0.48 1.23 0.60 0.56 0.13 0.55 0.18
P_mexicanus           0.46 0.59 1.39 0.75 0.60 0.14 0.69 0.26
P_obsoletus           0.43 0.54 1.24 0.72 0.56 0.14 0.61 0.21
P_pacificus           0.39 0.45 1.09 0.56 0.46 0.10 0.49 0.15
P_atronitens          0.42 0.53 1.22 0.67 0.55 0.15 0.58 0.21
P_duplicatus          0.42 0.59 1.30 0.74 0.57 0.16 0.61 0.22
P_perpolitus          0.49 0.55 1.23 0.67 0.57 0.15 0.62 0.22
P_punctulatus         0.57 0.65 1.42 0.84 0.63 0.18 0.76 0.29
P_strenuus0.62 0.73 1.65 1.05 0.73 0.23 0.78 0.32
P_sublaevis           0.46 0.64 1.27 0.86 0.59 0.16 0.58 0.21
P_cordicollis         0.34 0.41 1.04 0.53 0.45 0.10 0.48 0.14
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P_subangulatus          0.45 0.50 1.19 0.59 0.55 0.12 0.56 0.23
P_depressus             0.57 0.62 1.41 0.79 0.60 0.14 0.74 0.30
P_marginatus            0.47 0.61 1.56 0.91 0.56 0.16 0.75 0.32
P_elongatus             0.52 0.61 1.40 0.74 0.59 0.15 0.71 0.29
P_metallicus            0.37 0.44 1.06 0.56 0.45 0.11 0.44 0.15
P_aurocinctus           0.37 0.43 1.02 0.48 0.44 0.11 0.45 0.18
P_ambiguus              0.43 0.55 1.26 0.61 0.58 0.13 0.59 0.21
P_velutinus             0.52 0.64 1.55 0.79 0.64 0.15 0.73 0.27
P_laevisulcatus         0.40 0.44 1.08 0.55 0.44 0.12 0.54 0.21
P_quadricollis          0.38 0.38 0.92 0.50 0.36 0.10 0.4 0.17
P_smithi    0.25 0.32 0.75 0.32 0.33 0.09 0.28 0.11

&[numeric]

G_crassus 1 0 1 1 1 1 1 0 ? 0 0 0 0 1 - - 0 0 0 1 - - 0 1 0 1 0 0 1 0 1 1 0 1 0 0 0 1 0 0 0 1 1 1 0 0 0 1 0 - - 1 0 1 0 - 1 0 0 0 1 - 1 1 - 0 0 0 0 0 1 1
0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 1 - - 0
M_afrellus1 0 1 1 1 0 1 0 0 0 1 0 0 1 - - 0 0 0 1 - - 0 1 0 0 0 0 0 0 0 1 0 1 0 0 0 1 0 0 0 0 1 1 0 0 0 1 0 - - 1 0 0 0 - 0 0 1 0 0 1 1 1 - 0 0 0 0 1 1 1
1 0 0 0 0 0 0 0 0 0 0 0 1 0 0 ? ? ? 0
H_ignobilis             1 0 1 1 1 0 1 0 0 0 1 1 1 1 - - 1 0 0 1 - - 0 1 0 0 0 0 0 0 0 1 0 0 0 0 0 1 0 0 0 1 1 1 0 0 0 1 0 - - 1 0 0 0 - 0 0 1 0 0 1 1 1 0 0
0 0 0 1 1 1 1 0 0 0 0 0 0 0 0 0 0 2 0 0 0 - - 0
D_venator 1 0 1 1 1 0 1 0 ? 0 1 0 0 1 - - 0 0 0 1 - - 0 1 0 0 0 0 0 0 0 1 ? ? ? 0 1 0 0 0 0 1 1 1 0 0 0 0 0 - - 1 0 1 0 - 0 1 - - 0 - 1 1 - 0 0 0 0 1 1 1 0
1 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0
S_anthracinus           1 1 1 1 1 0 1 0 0 0 1 1 0 1 - - 0 0 0 1 - - 0 1 0 0 0 0 0 0 0 1 1 0 0 0 0 1 0 0 0 0 1 1 0 0 0 1 0 - - 1 0 0 0 - 1 0 0 0 1 1 1 1 0 0
0 0 0 0 1 1 1 1 - 0 0 0 0 0 0 0 0 2 0 0 0 0 0 0
S_buparius              1 2 1 1 0 0 1 0 0 1 1 0 0 1 - - 0 0 0 1 - - 0 1 0 0 0 0 0 0 0 1 0 0 1 0 0 0 0 0 0 0 1 1 0 0 0 1 0 - - 1 0 0 0 - 1 0 0 0 1 1 1 1 0 0
0 0 0 0 1 1 0 1 1 0 0 0 0 0 0 0 0 2 0 0 - - - 0
S_terricola1 2 1 1 1 0 1 0 0 0 1 0 0 1 - - 0 0 0 1 - - 0 1 0 0 0 0 1 0 0 1 0 0 0 0 1 1 0 0 0 0 1 1 0 0 0 1 0 - - 1 0 0 0 - 1 0 1 0 1 1 1 1 0 0 1 0 0 0 1 1
1 0 1 0 0 1 0 0 ? 0 0 2 0 0 0 0 - 0
S_subterraneus          1 2 1 1 1 0 1 0 0 0 1 0 0 1 - - 0 0 0 1 - - 0 1 0 0 0 0 0 0 0 1 1 0 0 0 0 1 0 0 0 0 1 1 0 0 0 1 0 - - 1 0 0 0 - 1 0 1 0 1 1 1 1 0 0
0 0 0 0 1 1 1 1 1 0 0 0 0 0 0 0 0 0 2 0 0 1 0 0 0
C_interrumptum          1 2 1 1 0 1 0 0 0 0 0 0 0 1 - - 0 1 1 0 1 0 2 1 0 1 1 0 1 0 0 1 0 1 0 0 0 1 0 0 0 1 0 1 0 1 0 1 0 1 1 0 0 0 1 1 0 1 - - 1 - 0 1 - 0
0 0 0 1 1 1 0 0 1 0 0 0 0 0 0 0 0 1 0 0 1 ? ? ? 0
M_batesi  1 2 1 1 0 1 1 1 1 1 - - - 1 - - 1 1 0 0 1 0 2 0 0 1 1 0 1 1 1 0 0 0 0 0 - - 1 1 1 1 0 1 1 1 1 0 0 - - 0 0 1 0 - 0 0 1 1 1 1 0 1 0 1 1 1 1 0 - 0 1
1 0 1 1 0 0 0 0 1 1 [12] 0 1 ? ? ? 1
M_convexa               1 2 1 1 0 1 1 1 1 1 - - - 1 - - 1 1 0 0 1 0 2 0 0 1 1 0 1 1 1 1 0 0 0 0 - - 1 1 1 1 0 1 1 1 1 1 0 - - 0 0 1 0 - 0 0 1 1 1 1 0 1 0 1 1
1 1 0 - 0 1 1 0 1 1 0 0 0 0 1 ? ? ? 1 0 0 0 1
M_gloriosa              1 2 1 1 0 1 1 1 0 1 - - - 1 - - 1 1 0 0 1 0 2 0 0 1 1 0 1 1 1 1 0 0 0 0 - - 1 1 1 1 0 1 1 1 1 1 0 - - 0 0 1 0 - 0 0 1 1 1 1 0 1 0 1 1
1 1 0 - 0 1 1 0 1 1 1 1 0 0 1 1 [12] 1 1 ? ? - 1
P_quirozi  0 0 ? 0 0 1 0 1 1 1 0 1 1 1 - - 1 1 1 0 1 2 1 0 0 1 0 0 0 0 1 1 0 0 0 0 0 - 1 1 2 1 0 1 0 0 1 1 0 0 0 1 1 0 1 1 1 0 1 1 1 0 0 1 1 1 0 0 0 1 1
0 1 0 1 - 1 1 - 0 0 1 1 0 0 1 0 0 0 0
P_purpuratus            1 1 1 0 0 1 0 1 1 1 1 0 1 1 - - 1 1 1 0 1 1 1 0 0 1 0 0 1 0 1 0 1 0 1 0 1 - 1 1 2 1 0 1 0 1 0 1 0 1 0 1 1 0 1 1 1 0 1 0 1 0 0 1 1
1 0 0 0 1 1 0 1 0 1 - 1 0 - 0 0 1 1 0 0 1 1 0 1 1
P_rotundipennis         0 1 1 0 0 1 0 1 1 1 1 1 1 1 - - 1 1 1 0 1 2 1 0 0 1 0 0 1 0 1 1 1 0 1 0 0 - 0 0 0 1 0 1 0 1 0 1 1 0 0 1 1 1 0 - 1 0 1 1 1 0 0 1 0
1 0 0 0 1 0 0 1 0 1 - 1 1 - 0 0 1 1 0 0 1 ? ? ? 1
P_sallei    0 0 1 0 0 1 0 1 1 1 1 1 1 0 1 1 1 1 1 0 0 1 1 0 0 1 0 0 1 0 1 1 0 0 0 0 0 - 1 1 2 1 0 0 1 0 0 1 1 0 0 0 0 1 1 1 0 0 1 1 1 0 0 1 0 1 0 0 0 1 1
0 1 0 1 - 1 0 - 0 1 1 1 [12] 0 1 0 1 0 0
P_sexualis1 0 1 0 0 1 0 1 1 1 0 0 1 1 - - 1 1 1 0 1 2 1 0 0 1 0 0 1 0 1 0 1 0 1 0 1 - 1 1 2 1 0 1 1 1 1 1 0 0 0 0 0 1 1 1 1 0 1 1 1 0 0 1 1 1 0 0 0 1 1
0 1 0 0 - 1 0 - 0 1 1 1 0 0 1 1 1 0 0
P_subsulcatus           1 0 1 0 1 1 0 1 1 1 1 0 1 0 0 0 1 1 1 0 0 1 1 0 1 1 0 1 1 1 1 1 0 0 0 0 0 - 1 2 2 1 0 0 0 1 0 1 1 0 1 1 1 0 1 0 0 0 0 0 1 0 0 1 -
1 0 1 0 1 1 0 1 0 1 - 1 0 - 0 0 1 1 0 0 1 1 1 0 1
P_tolucanus             1 1 1 0 0 1 0 1 1 0 1 1 1 0 1 1 1 1 1 0 0 1 1 0 1 1 0 0 1 0 1 1 0 0 0 1 - - 1 1 1 1 1 1 0 1 0 1 0 1 0 0 0 0 1 1 0 1 - - 1 - 1 1 - 1
0 0 0 1 1 0 1 0 1 - 1 0 - 0 1 1 1 0 0 1 0 0 0 0
P_viridans0 1 1 0 0 1 0 1 1 1 1 0 1 1 - - 1 1 1 0 0 1 1 0 1 1 0 0 1 0 1 1 0 1 0 0 0 - 1 1 2 1 0 0 1 0 1 1 1 0 0 1 1 0 1 1 0 1 - - 1 - 0 1 - 1 0 0 0 1 0 0
1 0 1 - 1 0 - 0 1 1 1 [12] 1 1 2 0 1 0
P_californicus          1 0 0 0 0 1 0 1 1 1 1 0 1 0 0 0 1 1 1 0 0 1 1 1 1 1 0 0 1 0 1 1 0 1 0 0 0 - 1 1 2 1 0 0 0 1 0 0 1 0 0 1 0 0 1 1 0 1 - - 1 - 0 1 - 1
0 0 0 1 1 0 1 0 1 - 1 0 - 1 0 1 1 [12] 0 1 2 0 1 1
P_cardioderus           1 1 1 0 0 1 0 1 1 1 1 0 1 1 - - 1 1 1 0 0 1 1 0 0 1 0 0 1 0 1 0 0 0 1 0 1 - 1 1 1 1 0 1 1 1 0 1 1 1 0 0 0 0 1 1 1 0 1 0 1 0 0 1 1
1 0 0 0 1 1 0 1 0 1 - 1 - - 0 0 1 1 0 0 1 1 0 1 1
P_cuestai  1 1 1 0 0 1 0 1 1 1 1 1 1 1 - - 1 1 1 0 1 2 1 0 0 1 0 0 1 1 1 1 0 0 0 1 - - 1 1 2 1 0 1 0 1 0 1 0 1 1 0 0 0 1 1 1 1 - - 1 - 1 1 - 1 0 0 0 1 1 0
1 0 1 - 1 0 - 0 0 1 1 0 0 1 ? ? ? 0
P_imitator 0 0 0 0 0 1 0 1 1 1 0 0 1 0 1 0 1 1 1 0 0 1 1 0 1 1 0 0 1 1 1 1 0 0 0 0 0 - 1 1 2 1 0 0 0 0 0 0 0 0 1 1 0 0 0 0 - 0 0 0 0 1 1 0 0 - 1 0 0 0 1 1
0 1 0 1 - 1 0 - 0 0 1 1 1 0 1 ? ? ? 0
P_intermedius           1 0 1 0 0 1 0 1 1 1 0 0 0 1 - - 1 1 1 0 1 2 1 0 0 1 0 0 1 0 1 1 0 0 1 0 0 - 1 1 2 1 0 1 1 1 0 1 1 0 0 1 0 1 0 - 1 0 1 0 1 0 0 1 1
1 0 0 0 1 1 0 1 0 0 - 1 0 - 0 0 1 1 1 0 1 0 1 0 0
P_mexicanus             0 0 0 0 0 1 0 1 1 1 1 0 1 0 0 0 1 1 1 0 0  1 1 0 1 1 0 0 1 0 1 1  0 1 0 0 0 - 1 1 1 1 0 1 1 0 1 0 1 0 0 0 0 0 1 1 0 1 - - 1 - 0 0 -
1 0 0 0 1 0 0 1 0 0 - 1 0 - 0 1 1 1 [12] 1 1 2 1 1 0
```

```
P_obsoletus     1 0 0 0 1 1 0 1 1 1 0 0 0 0 0 0 1 1 1 0 0 1 1 ? 2 1 0 0 1 0 1 1 0 1 0 0 0 - 1 1 2 1 1 0 1 1 1 0 1 0 0 0 0 0 1 0 0 0 0 1 0 1 1 1 -
1 0 0 0 1 0 0 1 0 1 - 1 0 - 0 0 1 1 2 1 1 2 0 1 0
P_pacificus     0 1 1 0 0 1 0 1 1 1 0 0 1 1 - - 1 1 1 0 1 2 1 0 0 1 0 0 1 0 1 0 1 0 0 0 1 - 0 0 0 1 0 1 0 0 0 1 1 1 0 1 0 1 0 - 1 0 1 0 1 0 0 1 1
1 0 0 0 1 1 0 1 0 1 - 1 1 - 0 1 1 1 0 0 1 0 1 0 0
P_atronitens     1 0 0 0 1 1 0 1 1 0 0 0 0 0 1 0 1 1 1 0 0 1 1 0 2 1 0 1 2 0 1 1 0 1 0 0 0 - 1 1 2 1 1 0 1 0 0 1 1 0 1 1 1 0 1 0 0 1 0 1 0 - 1 1 -
1 0 0 0 1 0 0 1 0 0 - 1 0 - 0 1 1 1 2 1 1 2 0 1 0
P_duplicatus     1 0 0 0 1 1 0 1 1 0 1 0 1 0 0 0 1 1 1 0 0 1 1 0 2 1 0 0 1 0 1 1 0 1 0 0 0 - 1 1 2 1 0 0 1 1 0 0 1 1 1 0 0 0 1 0 0 1 - - 0 - 0 1 - 1
0 0 0 1 0 0 1 0 1 - 1 0 - 0 1 1 1 0 0 1 2 1 1 0
P_perpolitus     1 1 0 0 0 1 0 1 1 0 0 0 0 0 0 0 0 1 1 1 0 0 1 1 0 2 1 0 0 2 0 1 1 0 1 0 0 0 - 1 1 2 1 1 0 1 0 0 1 1 0 1 1 1 0 1 1 0 1 - - 1 - 1 1 - 1
0 0 0 1 0 0 1 0 0 - 1 0 - 0 0 1 1 [01] 0 1 2 0 1 0
P_punctulatus     1 0 0 0 0 1 0 1 1 1 1 1 1 0 1 1 1 1 1 0 0 1 1 0 1 1 0 0 2 0 1 1 0 0 0 0 0 - 1 1 2 1 0 0 0 0 0 1 1 1 1 0 0 0 1 0 0 1 - - 1 - 0 1 - 1
0 0 0 1 1 0 1 0 0 - 1 0 - 1 1 1 1 2 1 1 3 0 ? 1
P_strenuus1 0 1 0 1 1 0 1 1 1 1 0 1 0 0 0 1 1 1 0 0 1 1 1 2 1 0 0 1 0 1 1 0 1 0 0 0 - 1 1 2 1 0 0 1 1 0 1 1 1 1 0 0 0 1 0 0 0 0 0 1 0 0 1 - 1 0 1 0 1 0
0 1 0 0 - 1 0 - 0 0 1 1 3 0 1 2 0 0 1
P_sublaevis     1 1 1 0 1 1 0 1 1 1 1 0 1 0 0 0 1 1 1 0 0 1 1 0 1 1 0 0 1 1 1 1 0 0 0 0 0 - 1 2 1 1 0 0 1 1 0 1 1 1 1 1 1 1 0 1 0 0 0 0 1 1 0 0 1 0
1 0 1 0 1 0 0 1 0 1 - 1 0 - 0 1 1 1 1 0 1 2 1 0 1
P_cordicollis     1 0 1 0 1 1 0 1 1 1 0 0 0 1 - - 1 1 1 0 0 1 1 1 0 1 0 0 1 0 1 1 0 0 0 0 0 - 1 1 2 1 0 1 1 1 0 1 1 0 0 1 1 0 1 1 1 0 1 0 1 0 0 1 1
1 0 0 0 1 1 0 1 0 1 -  1 0 - 0 1 1 1 0 0 1 0 0 0 0
P_subangulatus     0 0 1 0 0 1 0 1 1 1 1 0 1 1 - - 1 1 1 0 1 1 1 0 0 1 0 0 1 0 1 1 0 1 0 0 0 - 0 0 0 1 0 1 1 1 0 1 1 1 1 0 0 1 0 - 1 0 1 0 1 0 0 0 - 1
0 0 0 1 1 0 1 0 1 - 1 1 - 0 1 1 1 0 0 1 0 1 0 0
P_depressus     1 1 0 0 0 1 0 1 1 1 1 0 1 0 0 0 1 1 1 0 0 1 1 0 2 1 0 1 1 1 1 1 0 0 0 0 0 - 1 1 2 1 0 0 0 0 0 1 1 1 1 0 0 0 1 0 0 1 - 0 1 - 0 1 -
1 0 0 0 1 0 0 1 0 0 - 1 0 - 0 1 1 1 2 1 1 3 0 0 0
P_marginatus     1 0 0 0 1 1 0 1 1 1 1 0 1 0 1 0 1 1 1 0 0 1 1 0 1 1 0 0 1 1 1 1 0 0 0 0 0 - 1 2 2 1 0 0 1 1 0 0 1 1 1 0 0 0 1 0 0 0 0 1 1 0 0 1
01 0 1 0 1 1 0 1 0 0 - 1 0 - 0 1 1 1 2 1 1 2 0 0 1
P_elongatus     1 0 0 0 0 1 0 1 1 1 1 0 1 0 0 0 1 1 1 0 0 1 1 0 1 1 0 1 1 1 1 1 0 0 0 0 0 - 1 1 2 1 0 0 1 1 0 1 1 1 1 0 0 0 1 0 0 1 - - 1 - 0 1 - 1
0 0 0 1 [01] 0 1 0 0 - 1 0 - 0 1 1 1 2 1 1 3 0 0 0
P_metallicus     0 1 1 0 0 1 0 1 1 1 1 0 1 1 - - 1 1 1 0 0 1 1 0 0 1 0 0 1 0 1 0 0 0 0 0 0 - 0 0 0 1 0 1 0 1 0 1 1 1 0 1 1 1 0 - 1 0 1 0 1 0 0 0 - 1
0 0 0 1 1 0 1 0 0 - 1 0 - 0 0 1 1 [01] 0 1 0 1 0 0
P_aurocinctus     0 1 1 0 0 1 0 1 1 1 0 0 1 1 - - 1 1 1 0 1 2 1 0 0 1 0 0 1 0 1 1 0 1 0 0 0 - 1 1 2 1 0 1 0 1 0 1 0 0 1 1 0 0 0 - 1 1 0 1 1 - 0 0 0 1
0 0 0 1 1 0 1 0 0 - 1 0 - 0 1 1 1 0 0 1 0 1 0 0
P_ambiguus     1 0 1 0 0 1 0 1 1 1 1 0 1 1 - - 1 1 1 0 0 1 1 0 0 1 0 0 1 0 1 1 0 0 0 0 0 - 1 1 2 1 0 1 0 1 0 0 1 1 0 1 0 1 0 - 1 0 1 0 1 0 0 1 - 1
0 0 0 1 1 0 1 0 0 - 1 0 - 0 0 1 1 1 0 1 0 1 0 0
P_velutinus     1 1 0 0 0 1 0 1 1 1 1 0 1 0 1 0 1 1 1 0 0 1 1 0 0 1 0 0 1 0 1 1 0 0 0 0 0 - 1 1 2 1 0 0 0 0 0 0 1 1 1 1 0 0 1 1 0 1 - - 1 - 0 1 - 1
0 0 0 1 1 0 1 0 0 - 1 0 - 0 1 1 1 1 0 1 ? ? ? 0
P_laevisulcatus     0 0 1 0 0 1 0 1 1 0 1 0 1 0 1 0 1 1 1 0 0 1 1 0 0 1 0 0 1 1 1 1 0 0 0 0 0 - 1 1 2 1 0 0 0 1 0 1 0 1 0 1 1 1 1 1 0 0 0 0 1 1 0 1 -
1 0 0 0 1 1 0 1 0 0 - 1 0 - 0 1 1 1 2 0 1 1 0 0 0
P_quadricollis     0 ? ? 0 0 ? 0 1 1 1 0 0 1 ? ? ? 1 1 1 ? ? ? 1 0 1 1 0 0 1 1 1 0 1 1 1 0 0 - 1 1 2 1 0 0 1 0 0 1 1 0 1  0 0 0 1 0 0 0 1 0 0 1 0 1 0
1 0 0 0 1 1 0 1 0 0 - 1 ? - 0 1 - 1 ? 0 1 0 0 0 0
P_smithi   1 ? ? 0 0 ? 0 1 1 1 1 0 1 ? ? ? 1 1 1 ? ? ? 1 0 0 1 0 0 1 0 1 1 1 0 0 0 0 - 1 0 0 1 0 1 1 1 0 ? 0 0 1 ? 0 1 0 - 1 0 1 1 1 0 0 1 1 1 0 0 0 1 1 0
1 0 0 - 1 ? - 0 1 - 1 ? 0 1 ? ? ? 0

&[landmark 2d]
G_crassus -0.107216,0.115172     -0.0933052,0.106219     -0.0803721,0.0969213     -0.0671695,0.0912338     -0.0540037,0.0878402     -
0.0408749,0.0867405  -0.0274131,0.0853183  -0.014612,0.0842133  -0.00185303,0.0857298  0.0115771,0.0862738  0.0246585,0.0881233
0.0370844,0.0899622 0.0504776,0.0928 0.0631943,0.0969381 0.0765454,0.102397 0.0891988,0.110468 0.10181,0.12116 0.122766,0.102158
0.12794,0.0861804  0.131792,0.0708369  0.134017,0.0548116  0.135248,0.0394258  0.136484,0.0237124  0.137382,0.00864907  0.137636,-
0.0070802 0.134263,-0.0215567 0.129913,-0.0363768 0.123263,-0.050906 0.113644,-0.064172 0.100425,-0.0778237 0.0839074,-0.0902174
0.0670678,-0.102944   0.0582834,-0.107019   0.0501333,-0.109772   0.0416291,-0.110893   0.0328025,-0.112346   0.0236376,-0.113149
0.0147899,-0.113291  0.00661869,-0.114734  -0.00256199,-0.114554  -0.0110715,-0.115347  -0.0195862,-0.115811  -0.0284339,-0.115954  -
0.0373027,-0.114785  -0.0458438,-0.113612  -0.0550773,-0.110155  -0.0729679,-0.0983152  -0.0902084,-0.0861372  -0.104172,-0.0739064  -
0.114214,-0.060957   -0.121983,-0.0466598   -0.127791,-0.0320033   -0.132616,-0.017331   -0.135486,-0.00197162   -0.136394,0.0137471   -
0.136642,0.0291487 -0.136568,0.0448832 -0.135515,0.0609613 -0.132185,0.0780593 -0.127206,0.0945284 -0.107544,0.115167
M_afrellus-0.120844,0.105309     -0.106046,0.100974     -0.0908981,0.0954315     -0.075829,0.0920213     -0.0614251,0.0901114     -
0.0464568,0.0894423   -0.0314886,0.0887731   -0.0168585,0.0890064   -0.00159696,0.088653   0.0124352,0.0885594   0.0276632,0.0891197
0.0425754,0.0899733     0.057183,0.0908157     0.0723326,0.0935079     0.0871327,0.0974071     0.101471,0.105559     0.1159,0.111274
0.132443,0.0926698     0.137616,0.0763917     0.140929,0.06096     0.143023,0.0454835     0.143572,0.0305601     0.14411,0.0159412
0.144343,0.00131118    0.142445,-0.0133973    0.139915,-0.0275191    0.136775,-0.0416633    0.126835,-0.053313    0.115688,-0.0653121
0.0980659,-0.0754146   0.0780078,-0.0856067   0.0612886,-0.095371   0.0537531,-0.097783   0.0458906,-0.0995972   0.0380056,-0.100802
0.0297825,-0.101105  0.0224731,-0.101374  0.0142052,-0.100458  0.00657998,-0.100434  -0.00132736,-0.101029  -0.00894135,-0.10131  -
0.0165441,-0.101894 -0.0244627,-0.102186 -0.0323812,-0.102477 -0.0403222,-0.102159 -0.0480482,-0.0993938 -0.0684741,-0.0913011 -
0.0852789,-0.0821603  -0.104814,-0.073425  -0.117715,-0.0626157  -0.129116,-0.0511413  -0.134505,-0.0373108  -0.138664,-0.0237401  -
0.141029,-0.00918849   -0.142187,0.00571251   -0.143356,0.0209181   -0.143894,0.0355369   -0.14265,0.0514413   -0.140503,0.0676838   -
0.135941,0.084625 -0.120844,0.105309
H_ignobilis     -0.118859,0.108073   -0.103979,0.0961029   -0.0892325,0.0886684   -0.0748685,0.0839466   -0.0596507,0.0810658   -
0.0453402,0.0781583   -0.0304605,0.0764782   -0.0158921,0.0750916   -0.00104805,0.0746211   0.0131556,0.0753424   0.027617,0.0775845
0.0423719,0.0801379     0.0568156,0.0829849     0.0715081,0.0876551     0.0858715,0.0932235     0.0998613,0.101202     0.114278,0.115247
0.128705,0.0981177     0.135216,0.0825715     0.139299,0.0672563     0.142146,0.0528127     0.143187,0.0380132     0.143615,0.0234983
```

0.142522,0.00924119 0.140504,-0.00443784 0.139108,-0.0187038 0.135881,-0.0324185 0.128998,-0.0453329 0.118761,-0.0574382 0.105519,-0.0702374 0.0907201,-0.0815692 0.0752986,-0.092314 0.0651331,-0.0965481 0.0555812,-0.101067 0.0462961,-0.104367 0.036086,-0.107089 0.0267564,-0.108877 0.0167595,-0.108567 0.00676272,-0.108256 -0.00350977,-0.108861 -0.0131953,-0.108844 -0.0228808,-0.108827 -0.0328776,-0.108516 -0.0429279,-0.106391 -0.0530228,-0.102754 -0.0628064,-0.0994106 -0.0815554,-0.0896728 -0.0982233,-0.0786631 -0.110062,-0.0672084 -0.121607,-0.0554423 -0.129239,-0.0429557 -0.13478,-0.0294994 -0.137618,-0.0153582 -0.139558,-0.000887839 -0.141178,0.0129866 -0.141614,0.027804 -0.141455,0.0429415 -0.139473,0.0578301 -0.13661,0.0736526 -0.131648,0.0901423 -0.119162,0.108064

D_venator -0.13353,0.107209 -0.115774,0.0731006 -0.0985076,0.0648157 -0.0820301,0.0599054 -0.0656181,0.057033 -0.0492279,0.0548399 -0.0318188,0.0526795 -0.0157792,0.0508151 0.000567261,0.0499805 0.0168264,0.0518631 0.0333707,0.0554548 0.049893,0.0597258 0.065758,0.0632956 0.0825982,0.0682568 0.0987482,0.0735358 0.114855,0.0801734 0.129562,0.119745 0.144428,0.101524 0.149356,0.0857022 0.151151,0.0721602 0.1523,0.0575774 0.152419,0.0433015 0.151497,0.0296722 0.149556,0.0160101 0.147615,0.00234796 0.143944,-0.0103498 0.140283,-0.0233872 0.133182,-0.0351752 0.122334,-0.0467437 0.108046,-0.0570627 0.0920486,-0.0670967 0.0773882,-0.0764077 0.0666494,-0.0913726 0.0566457,-0.097474 0.0461495,-0.0988314 0.0363108,-0.0994876 0.0257382,-0.0984675 0.0152093,-0.0988059 0.00502006,-0.0991334 -0.00548702,-0.100151 -0.0156654,-0.100818 -0.0258328,-0.101825 -0.0363617,-0.102163 -0.0465947,-0.101132 -0.0577143,-0.0936699 -0.0672886,-0.0813979 -0.0842258,-0.0727625 -0.100823,-0.0641162 -0.114375,-0.0550319 -0.125593,-0.0445127 -0.132417,-0.0331723 -0.137237,-0.0207474 -0.141716,-0.00831167 -0.14453,0.00519761 -0.147684,0.018696 -0.149797,0.0315478 -0.150913,0.0451117 -0.150692,0.0593985 -0.150461,0.0733456 -0.148213,0.0880376 -0.13354,0.107549

S_anthracinus -0.122723,0.103409 -0.107973,0.100712 -0.0924321,0.0905866 -0.0768269,0.0854479 -0.0616802,0.0820621 -0.0466371,0.0804499 -0.03126,0.0792131 -0.0163206,0.0793744 -0.000984949,0.078847 0.0138923,0.0800725 0.0287281,0.0820073 0.0439186,0.083963 0.0590054,0.0876921 0.0744055,0.0921515 0.0893472,0.0983637 0.103455,0.106663 0.119627,0.110099 0.135227,0.092859 0.138936,0.0781268 0.14012,0.063959 0.139906,0.0493536 0.140005,0.0354783 0.139749,0.0215822 0.139139,0.00766549 0.137423,-0.00560404 0.134705,-0.0199999 0.131174,-0.0326637 0.125181,-0.0458273 0.118458,-0.0586776 0.10631,-0.0700654 0.0916792,-0.0815983 0.0777164,-0.0923802 0.0677407,-0.0983022 0.0572859,-0.102117 0.0474575,-0.104471 0.0372123,-0.105781 0.0265502,-0.106049 0.0162635,-0.10665 0.0062693,-0.106166 -0.00399667,-0.107122 -0.0146795,-0.107035 -0.024904,-0.1087 -0.0349397,-0.107507 -0.0456018,-0.107774 -0.0561166,-0.104474 -0.0663181,-0.100443 -0.0804606,-0.0898797 -0.0963974,-0.0790656 -0.109517,-0.067731 -0.118381,-0.0561476 -0.125219,-0.0426662 -0.129888,-0.0297698 -0.133159,-0.0164358 -0.135762,-0.00235096 -0.137321,0.0121508 -0.138505,0.0263186 -0.140065,0.0408204 -0.140226,0.0557599 -0.139282,0.0700521 -0.136585,0.0848027 -0.122723,0.103409

S_buparius -0.13165,0.0981539 -0.114729,0.0828905 -0.098087,0.074247 -0.0818474,0.067998 -0.06512,0.0644826 -0.0487442,0.0621582 -0.0326694,0.059821 -0.0160181,0.058111 0.000031,0.0563757 0.0162423,0.057963 0.032979,0.0613812 0.0491392,0.0641721 0.0646976,0.0669377 0.0810573,0.0721486 0.0970527,0.0788513 0.112921,0.0885631 0.128723,0.107014 0.14725,0.0894066 0.15024,0.0756663 0.153532,0.0619387 0.154077,0.0489997 0.154635,0.0357598 0.153036,0.0236348 0.151135,0.0114971 0.148633,-0.000665962 0.144012,-0.0126168 0.138451,-0.023703 0.134118,-0.0353403 0.123691,-0.0454258 0.11112,-0.0546972 0.0955013,-0.0631927 0.0795693,-0.0714 0.0694973,-0.0899108 0.0588675,-0.0951817 0.0483484,-0.0959263 0.0378674,-0.0975737 0.027323,-0.0977165 0.0161387,-0.0969819 0.00556898,-0.096523 -0.00464918,-0.0972549 -0.0151048,-0.0995041 -0.0259121,-0.100562 -0.0364819,-0.100103 -0.0467888,-0.0987289 -0.0578116,-0.0946717 -0.0688158,-0.0767474 -0.0854071,-0.0693075 -0.102011,-0.0615668 -0.115004,-0.0536738 -0.128336,-0.0448909 -0.133933,-0.0336719 -0.138339,-0.0221014 -0.14425,-0.0105942 -0.147465,0.00132794 -0.150092,0.0135764 -0.152116,0.0258502 -0.154153,0.0384249 -0.154698,0.0513638 -0.15345,0.0646798 -0.150423,0.0786736 -0.131349,0.0981666

S_terricola-0.116886,0.111216 -0.102035,0.101874 -0.0875979,0.0947648 -0.0732012,0.0886179 -0.0586178,0.0856924 -0.0447161,0.0837025 -0.0302132,0.0827017 -0.0154028,0.0820352 -0.000980232,0.0829593 0.0130947,0.0845115 0.0271831,0.085743 0.0415386,0.0882711 0.0555599,0.0911065 0.0701692,0.095252 0.0843638,0.10163 0.0984914,0.109611 0.112606,0.117914 0.126843,0.100191 0.131671,0.0846464 0.133277,0.0692882 0.134535,0.0545583 0.135165,0.0394807 0.134833,0.024363 0.133845,0.00953918 0.132845,-0.00496381 0.131189,-0.0191728 0.127287,-0.0334757 0.123052,-0.0474711 0.113643,-0.0607186 0.100666,-0.0731513 0.0848011,-0.0857045 0.0734142,-0.0977493 0.0645266,-0.108083 0.0547159,-0.111706 0.0451455,-0.113392 0.0352008,-0.113807 0.02555,-0.113568 0.0158858,-0.113008 0.00590082,-0.112461 -0.00373656,-0.112542 -0.0132935,-0.114549 -0.0232249,-0.115285 -0.0325012,-0.116315 -0.0424996,-0.115448 -0.0525784,-0.112655 -0.0624437,-0.107283 -0.0735797,-0.0945727 -0.0898217,-0.0827184 -0.103805,-0.0710911 -0.117173,-0.0587954 -0.120663,-0.0444801 -0.126079,-0.0302452 -0.129262,-0.0155957 -0.131509,-0.000264377 -0.132767,0.0144656 -0.134373,0.0298237 -0.135017,0.0452221 -0.134698,0.0606606 -0.132788,0.076487 -0.12866,0.0930489 -0.116873,0.110895

S_subterraneus -0.121281,0.108297 -0.106022,0.0996343 -0.0911682,0.0935667 -0.0760381,0.0891375 -0.0606418,0.0866722 -0.0458969,0.0841872 -0.0309056,0.0843175 -0.0159143,0.0844478 -0.00156447,0.0842326 0.013407,0.0850142 0.0286744,0.0867829 0.0432905,0.0885317 0.0578569,0.0919089 0.0727293,0.0959474 0.0878678,0.10195 0.10199,0.109225 0.117069,0.117182 0.130671,0.0986889 0.133762,0.0828098 0.135531,0.0675424 0.136658,0.0519295 0.136788,0.0369382 0.137244,0.0219568 0.137059,0.00662992 0.135886,-0.00840103 0.13273,-0.0225144 0.12763,-0.0370129 0.123832,-0.0514718 0.116402,-0.0644113 0.102755,-0.0765621 0.0838666,-0.0878945 0.0692322,-0.0997494 0.0598766,-0.102968 0.0514981,-0.106157 0.0420731,-0.107096 0.0332896,-0.107689 0.0241705,-0.107967 0.0147059,-0.107603 0.00557692,-0.107555 -0.00320659,-0.108148 -0.012,-0.108416 -0.0214151,-0.10968 -0.0305242,-0.110283 -0.0393573,-0.109248 -0.0488318,-0.108559 -0.0577244,-0.105569 -0.0743554,-0.0946662 -0.0922793,-0.0841283 -0.106631,-0.0731557 -0.115505,-0.0600605 -0.120806,-0.0465305 -0.126453,-0.0323591 -0.131123,-0.018158 -0.133198,-0.00355183 -0.134315,0.0117354 -0.135432,0.0270226 -0.134596,0.0423694 -0.135071,0.0580021 -0.136504,0.0729537 -0.134079,0.0896527 -0.121281,0.108297

C_interrumptum -0.107218,0.104015 -0.0934503,0.0893098 -0.0800173,0.0819361 -0.0667731,0.0787065 -0.0539204,0.0770562 -0.0404447,0.0757538 -0.0273313,0.0753932 -0.0142324,0.0753513 -0.00110449,0.0746719 0.0119072,0.0765427 0.0249479,0.077776 0.038322,0.078705 0.0509858,0.0811988 0.0642436,0.084678 0.0771246,0.0894178 0.0898311,0.0979829 0.102943,0.111677 0.120231,0.0968129 0.128535,0.0828167 0.133623,0.0693128 0.136813,0.0554029 0.139031,0.0417682 0.141902,0.0278438 0.143164,0.0141655 0.142499,0.000718773 0.141849,-0.0130467 0.138924,-0.0259575 0.134419,-0.0392598 0.128306,-0.0523159

0.119628,-0.0651695 0.107125,-0.0781975 0.0894776,-0.0905016 0.0780026,-0.0980522 0.0658609,-0.104994 0.054197,-0.108401 0.0422142,-0.111822 0.0301589,-0.113649 0.0180309,-0.113883 0.00556959,-0.113812 -0.00619605,-0.114987 -0.0179762,-0.115843 -0.0298436,-0.114787 -0.0424211,-0.112166 -0.0543611,-0.109516 -0.0667651,-0.103692 -0.0785462,-0.0975209 -0.097254,-0.0865543 -0.110905,-0.074399 -0.120397,-0.0623736 -0.127702,-0.0492901 -0.133065,-0.036757 -0.135921,-0.0231514 -0.138444,-0.00984999 -0.139373,0.00352406 -0.13936,0.0172605 -0.139666,0.0309823 -0.138392,0.0450956 -0.135829,0.0589483 -0.131368,0.0732069 -0.124372,0.0879005 -0.107218,0.104015

M_batesi -0.119001,0.112673 -0.103567,0.0860319 -0.0885701,0.0749573 -0.0738961,0.0709776 -0.0593962,0.0708181 -0.045219,0.0717378 -0.0302729,0.0737862 -0.0155748,0.0752765 -0.00116196,0.0770272 0.0134001,0.0755034 0.0281853,0.0750835 0.0424247,0.0746388 0.0574952,0.0739585 0.072156,0.0762674 0.08668,0.081578 0.100497,0.0904111 0.114124,0.121385 0.134059,0.103972 0.141925,0.0873774 0.147273,0.0720347 0.149632,0.0562824 0.150613,0.0407408 0.149933,0.0256703 0.147057,0.0107732 0.142544,-0.00419858 0.135811,-0.0184512 0.126882,-0.0325304 0.118226,-0.0465972 0.108466,-0.0604409 0.100951,-0.0755495 0.0944661,-0.0892439 0.0874722,-0.103782 0.0754407,-0.103783 0.0632724,-0.100783 0.051848,-0.0961085 0.0404983,-0.093071 0.0287148,-0.0925143 0.0169562,-0.0925034 0.00545796,-0.0922071 -0.00649894,-0.0938459 -0.0176123,-0.0959931 -0.0295319,-0.0984505 -0.0405458,-0.102781 -0.0521303,-0.10659 -0.0637273,-0.110127 -0.0751757,-0.110922 -0.0842817,-0.0971178 -0.0909442,-0.0829289 -0.0997774,-0.0691123 -0.10969,-0.0556184 -0.120433,-0.0418889 -0.129526,-0.0283577 -0.137541,-0.0145038 -0.143372,-0.000550487 -0.146512,0.0143459 -0.149665,0.0295151 -0.149555,0.0451065 -0.148069,0.0604872 -0.143878,0.076538 -0.138336,0.0929239 -0.119001,0.112673

M_convexa -0.118281,0.10633 -0.103463,0.0874626 -0.0882918,0.0743353 -0.0733134,0.0669295 -0.058491,0.0641553 -0.0440511,0.0646413 -0.029902,0.0656631 -0.0154988,0.067239 -0.00108644,0.0685424 0.0133718,0.0684835 0.0284025,0.0676256 0.0426066,0.0670127 0.0570281,0.0680437 0.0713397,0.072344 0.0855595,0.0793689 0.0999233,0.0902173 0.112956,0.116295 0.132296,0.100854 0.139894,0.0858347 0.145302,0.071015 0.148259,0.0561127 0.150379,0.0417279 0.150866,0.027288 0.149989,0.0128022 0.148277,-0.00116617 0.14494,-0.015462 0.13559,-0.0294147 0.126222,-0.0428225 0.117681,-0.0564752 0.109158,-0.0706729 0.103613,-0.0842247 0.0967429,-0.0989122 0.0839285,-0.0990708 0.0708142,-0.0984212 0.0576173,-0.0953195 0.0444296,-0.0924903 0.030942,-0.0888529 0.0181093,-0.0884666 0.00474082,-0.088371 -0.00802769,-0.0898919 -0.0210411,-0.0922392 -0.0339629,-0.0973111 -0.0469397,-0.100748 -0.0599439,-0.103368 -0.0729849,-0.104898 -0.0857901,-0.105329 -0.093614,-0.0916817 -0.101429,-0.0783067 -0.108962,-0.0651951 -0.118402,-0.0521476 -0.129195,-0.0394185 -0.138082,-0.0266251 -0.142908,-0.0128769 -0.145837,0.00120805 -0.147404,0.0153388 -0.14789,0.0297787 -0.147023,0.0445369 -0.144794,0.059341 -0.140657,0.0742092 -0.135431,0.0891142 -0.118281,0.10633

M_gloriosa -0.117845,0.106149 -0.102701,0.0816859 -0.087671,0.0723814 -0.0728265,0.0675135 -0.0580805,0.0649944 -0.043922,0.0640193 -0.0290682,0.0651649 -0.0144753,0.0662995 -0.000415332,0.0676732 0.0147542,0.0675248 0.0288908,0.0670716 0.0432227,0.0681953 0.0578046,0.0695909 0.072549,0.0733462 0.0864121,0.0794175 0.100567,0.0909912 0.114448,0.115364 0.134482,0.0989488 0.140836,0.0845747 0.145635,0.069874 0.149369,0.0556515 0.150514,0.0407977 0.150561,0.0272049 0.149064,0.0130246 0.147295,-0.000905655 0.142395,-0.0149672 0.13459,-0.0283662 0.126536,-0.0420371 0.118482,-0.055708 0.11121,-0.069346 0.10445,-0.0827012 0.0979723,-0.0965675 0.0843796,-0.0966144 0.0712869,-0.0961175 0.0576504,-0.0951205 0.0442093,-0.0925467 0.0310072,-0.08944 0.017849,-0.0873773 0.00450627,-0.0871523 -0.00874889,-0.0890151 -0.0219165,-0.0929658 -0.0350514,-0.0976993 -0.0479909,-0.100856 -0.0614961,-0.102991 -0.0742511,-0.10431 -0.0877892,-0.105662 -0.0949044,-0.0918424 -0.102509,-0.0788279 -0.110102,-0.0660744 -0.118783,-0.0523208 -0.128736,-0.0394047 -0.136352,-0.0261293 -0.142662,-0.0127991 -0.146385,0.00116241 -0.148019,0.0152114 -0.148882,0.0295543 -0.148201,0.0444847 -0.145932,0.0589588 -0.142901,0.0739877 -0.136468,0.0888979 -0.117845,0.106149

P_quirozi -0.116009,0.110799 -0.101684,0.085365 -0.086774,0.0771793 -0.0724491,0.0713324 -0.0578318,0.0684089 -0.0432145,0.0660702 -0.0291819,0.0666549 -0.0151493,0.0672396 -0.00082432,0.0678242 0.0135006,0.069286 0.0281179,0.070163 0.0424429,0.0707477 0.0564755,0.0727941 0.0705081,0.077764 0.084833,0.0839033 0.0988656,0.0950124 0.112314,0.117815 0.125469,0.102906 0.131024,0.0882885 0.135994,0.0733788 0.140379,0.0587615 0.143887,0.0438519 0.144764,0.0295269 0.144472,0.0146173 0.141256,0.000292346 0.137455,-0.0137403 0.131608,-0.0280652 0.122838,-0.0426825 0.113775,-0.0567151 0.106174,-0.0710401 0.102374,-0.085365 0.105005,-0.100275 0.0909723,-0.102906 0.0766473,-0.103198 0.0626147,-0.102029 0.0485821,-0.100275 0.0342572,-0.0999823 0.0202246,-0.0973512 0.00560729,-0.0958895 -0.00813297,-0.0982282 -0.0221656,-0.101444 -0.0361982,-0.104367 -0.0502308,-0.107583 -0.0645557,-0.109922 -0.0785883,-0.110507 -0.0926209,-0.109045 -0.0923286,-0.093843 -0.0972985,-0.0795181 -0.106069,-0.0660702 -0.116009,-0.0520376 -0.125364,-0.0385897 -0.132672,-0.0242647 -0.137935,-0.00993976 -0.141443,0.00467753 -0.143197,0.0190025 -0.142904,0.0339121 -0.141443,0.0488218 -0.138519,0.0640237 -0.135303,0.0789334 -0.130041,0.0947201 -0.116301,0.110799

P_purpuratus -0.121136,0.103569 -0.105707,0.0829169 -0.0906338,0.074516 -0.075384,0.0698273 -0.0604772,0.0671248 -0.0453187,0.0655702 -0.0301768,0.0645854 -0.0150598,0.0644553 -0.000521063,0.0645936 0.0148477,0.0656115 0.0296468,0.0666128 0.0447058,0.0684771 0.0597398,0.0711962 0.0741708,0.0750384 0.0887872,0.0823088 0.103362,0.0910028 0.117848,0.112525 0.131403,0.0975215 0.137231,0.0834335 0.14135,0.0692957 0.144605,0.0554179 0.146738,0.040937 0.146851,0.0272529 0.146395,0.0135521 0.144221,0.000087 0.141208,-0.0139734 0.136177,-0.0272371 0.128866,-0.0405672 0.121555,-0.0538973 0.112811,-0.066984 0.103506,-0.0803722 0.102195,-0.0940978 0.0882919,-0.0964989 0.0746492,-0.0980368 0.0609236,-0.0967257 0.0472228,-0.0962693 0.0332288,-0.0955363 0.0195115,-0.09451 0.00581903,-0.0943385 -0.00781533,-0.0961614 -0.0214746,-0.0971296 -0.0354105,-0.098391 -0.0487516,-0.10049 -0.0626543,-0.102892 -0.0763385,-0.103005 -0.0900973,-0.100554 -0.0927667,-0.0872296 -0.103665,-0.0752853 -0.114874,-0.0624946 -0.125219,-0.049964 -0.131576,-0.0373171 -0.136524,-0.0240589 -0.139487,-0.0104578 -0.143581,0.00282531 -0.145404,0.0164597 -0.146095,0.0304122 -0.145362,0.0444061 -0.14235,0.0584665 -0.138215,0.0731299 -0.134649,0.0877766 -0.121136,0.103569

P_rotundipennis -0.114206,0.103787 -0.0992377,0.0809437 -0.0846786,0.0725944 -0.0707369,0.0660527 -0.05652,0.0631374 -0.042312,0.0614302 -0.0287125,0.0603225 -0.0145135,0.0598233 -0.000010,0.0590244 0.013567,0.0609368 0.027444,0.0631536 0.0416275,0.0647685 0.0555,0.0675892 0.0690526,0.0728238 0.0825986,0.0789644 0.0964109,0.0899395 0.109834,0.112691 0.128366,0.0980283 0.13542,0.083583 0.140352,0.0700281 0.143171,0.0564576 0.146293,0.0425873 0.147904,0.0290079 0.148608,0.0154218 0.148407,0.00182897 0.146693,-0.011473 0.143773,-0.0250859 0.139641,-0.0381037 0.132793,-0.0514435 0.125038,-0.0647901 0.114866,-0.0778525 0.0974384,-0.0900624 0.0844831,-0.0943865 0.0712057,-0.0959947 0.0582236,-0.0966947 0.0452326,-

0.0961866 0.0316375,-0.0956829 0.0186487,-0.0954768 0.00566218,-0.0955728 -0.00761969,-0.0965769 -0.0208971,-0.0981852 -0.034179,-0.0991894 -0.0468591,-0.0998871 -0.0601454,-0.100287 -0.0731342,-0.100081 -0.0861408,-0.097459 -0.10676,-0.0864362 -0.117424,-0.0738297 -0.126274,-0.0615119 -0.13271,-0.0488742 -0.13794,-0.0359255 -0.141361,-0.0226615 -0.143273,-0.00908432 -0.145485,0.00418864 -0.14619,0.0177748 -0.145084,0.0316763 -0.143675,0.045278 -0.141363,0.0594905 -0.137238,0.0734143 -0.131005,0.0882598 -0.114206,0.103787

P_sallei -0.11119,0.103356 -0.096664,0.0825721 -0.0828092,0.0763325 -0.0691043,0.0723715 -0.0555681,0.0709739 -0.0415372,0.070753 -0.0278661,0.0716526 -0.0142512,0.0734066 -0.000808655,0.073433 0.0122928,0.0742951 0.026305,0.074359 0.0400136,0.074689 0.0533811,0.0758546 0.0665987,0.0792988 0.0806333,0.0833689 0.0935886,0.0908005 0.106746,0.112548 0.122246,0.0986932 0.130607,0.0846549 0.13669,0.0704667 0.140778,0.0561473 0.14369,0.0423226 0.145767,0.0281568 0.145565,0.0138411 0.14392,-0.000283482 0.141135,-0.014483 0.135522,-0.0291548 0.130155,-0.0432383 0.123365,-0.0574154 0.116878,-0.0718586 0.110372,-0.086017 0.108746,-0.100426 0.093726,-0.102559 0.0785184,-0.101843 0.0637679,-0.0993814 0.0489987,-0.0966347 0.0341921,-0.0933183 0.0192505,-0.0922991 0.0047062,-0.0929701 -0.0100292,-0.0950839 -0.0245173,-0.0966094 -0.0393501,-0.10159 -0.0542391,-0.105716 -0.0689745,-0.10783 -0.0834626,-0.109356 -0.0981568,-0.107748 -0.100196,-0.094152 -0.107417,-0.0800387 -0.114905,-0.0662291 -0.122659,-0.0527229 -0.127014,-0.0387071 -0.133059,-0.0250885 -0.13825,-0.0114137 -0.14175,0.00265836 -0.142668,0.0166143 -0.142181,0.0309487 -0.141106,0.0450359 -0.138037,0.0592542 -0.133259,0.0735849 -0.125936,0.0883692 -0.11119,0.103356

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P_tolucanus -0.112466,0.104323 -0.0978854,0.0864256 -0.084151,0.0803712 -0.0704951,0.0777867 -0.0565761,0.0763654 -0.0426767,0.0758116 -0.0287774,0.0752578 -0.0151737,0.0749866 -0.00130698,0.0758786 0.0125728,0.0761923 0.0261438,0.077367 0.0397148,0.0785416 0.0532858,0.0797162 0.0671133,0.0823432 0.0805797,0.0881444 0.0937112,0.0959633 0.107205,0.113337 0.122582,0.0986409 0.130427,0.0843527 0.135965,0.0697231 0.139755,0.0556326 0.14066,0.0411876 0.141848,0.0270382 0.141879,0.0128628 0.140477,-0.00192369 0.138195,-0.0161514 0.134743,-0.029827 0.128708,-0.0444289 0.12266,-0.0584524 0.115173,-0.0727978 0.107969,-0.0868475 0.103077,-0.100845 0.0892238,-0.102315 0.0750418,-0.102057 0.0611489,-0.101792 0.047243,-0.100949 0.0336328,-0.100389 0.0194508,-0.100131 0.0055645,-0.100156 -0.0083022,-0.101048 -0.0224385,-0.102814 -0.0362855,-0.104573 -0.0501588,-0.105176 -0.0637167,-0.106929 -0.077866,-0.108117 -0.0917523,-0.108141 -0.0975666,-0.0940964 -0.104525,-0.0806561 -0.113513,-0.0669723 -0.121338,-0.0535517 -0.12802,-0.0395265 -0.132665,-0.0260339 -0.135877,-0.0119303 -0.137925,0.00191022 -0.139409,0.0163422 -0.13944,0.0305176 -0.138899,0.0449953 -0.136617,0.0592231 -0.132034,0.0740814 -0.125428,0.0889855 -0.112466,0.104323

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P_cardioderus -0.117376,0.0998751 -0.102174,0.0825649 -0.0877762,0.0728978 -0.0733628,0.0680405 -0.0581734,0.0661176 -0.0440432,0.0657306 -0.0292743,0.0653839 -0.0148248,0.0650171 -0.000734985,0.0652686 0.013953,0.0661992 0.0283216,0.0671096 0.0430095,0.0680402 0.0573175,0.0699085 0.0714838,0.0740119 0.0858278,0.0803706 0.0999493,0.0902417 0.113884,0.108116 0.131758,0.0941805 0.138735,0.0801963 0.143756,0.0667293 0.146202,0.0534197 0.148349,0.0397706 0.14888,0.0263396 0.148432,0.0131673 0.147964,0.00031424 0.144643,-0.0130402 0.140303,-0.0254974 0.134726,-0.0386741 0.126554,-0.0513741 0.117784,-0.0647531 0.109612,-0.0774531 0.102738,-0.0903914 0.0882322,-0.0941957 0.0745022,-0.0950656 0.060671,-0.094339 0.046561,-0.0942713 0.0330693,-0.0938437 0.0185793,-0.0928383 0.00482904,-0.0933889 -0.00852099,-0.0951965 -0.0222308,-0.0963857 -0.036559,-0.0979346 -0.0499697,-0.0987843 -0.0642776,-0.100653 -0.0780279,-0.101203 -0.0919805,-0.0985608 -0.0988564,-0.086173 -0.110522,-0.0740887 -0.119633,-0.0618426 -0.128126,-0.0492367 -0.134064,-0.036469 -0.138725,-0.0236203 -0.14179,-0.0106705 -0.144236,0.00263906 -0.145724,0.0160093 -0.146255,0.0294403 -0.146106,0.0422731 -0.144741,0.0561447 -0.140182,0.0702187 -0.134986,0.0843331 -0.117376,0.0998751

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P_imitator -0.113523,0.105404 -0.0985612,0.0836276 -0.0842236,0.0759964 -0.0699478,0.0710187 -0.0560218,0.0683929 -0.04213,0.0672413 -0.0282451,0.0663845 -0.0143671,0.0658226 -0.000201135,0.0655624 0.0136288,0.0670643 0.0274657,0.0682714 0.0412819,0.070363 0.0550981,0.0724546 0.0691749,0.0760273 0.0826208,0.0813553 0.0962929,0.0896385 0.109279,0.114721 0.123466,0.100891 0.131166,0.0869104 0.136522,0.0722851 0.140684,0.0582221 0.142488,0.0441041 0.144003,0.0296845 0.143736,0.0158133 0.142598,0.0013319 0.139383,-0.0126079 0.135585,-0.0268562 0.130312,-0.0411389 0.12445,-0.0554353 0.119472,-0.0697111 0.113898,-0.0837058 0.110402,-0.0982421 0.0956596,-0.0985853 0.0800331,-0.0989491 0.0649895,-0.0990043 0.0499252,-0.0981749 0.0345387,-0.0961731 0.0194608,-0.0947541 0.00409482,-0.0936368 -0.0106128,-0.0954542 -0.0255741,-0.0990475 -0.0405559,-0.101756 -0.0558464,-0.103882 -0.0705883,-0.104225 -0.0855839,-0.106344 -0.100881,-0.108175 -0.103871,-0.0937902 -0.109501,-0.0800563 -0.115727,-0.0660413 -0.122241,-0.052328 -0.129057,-0.0383267 -0.134104,-0.0242843 -0.138259,-0.0105161 -0.140358,0.00359498 -0.141284,0.0180284 -0.141024,0.0321943 -0.139886,0.0466758 -0.137274,0.0611915 -0.132886,0.0754536 -0.125858,0.0903671 -0.113516,0.105109

P_intermedius -0.114183,0.108548 -0.0992453,0.082145 -0.0846735,0.0744519 -0.0707871,0.0704274 -0.0569427,0.0685501 -0.0427975,0.0669854 -0.028989,0.0669483 -0.0148618,0.0663038 -0.000752551,0.0665795 0.0127312,0.0674566 0.0271172,0.0692719 0.0411965,0.0710812 0.054957,0.0734979 0.0686876,0.0774483 0.0830017,0.0829442 0.0963177,0.0924096 0.109653,0.116604 0.126209,0.101585 0.132938,0.0869882 0.138746,0.0723734 0.142709,0.0580294 0.144518,0.0439501 0.14602,0.0298649 0.146001,0.0151362 0.145663,0.00101501 0.143173,-0.0128414 0.138228,-0.0267458 0.13175,-0.0406802 0.122198,-0.0543677 0.111107,-0.0677785 0.0987895,-0.0812133 0.0975315,-0.0953524 0.0841256,-0.100217 0.0712852,-0.102616 0.0581022,-0.10318 0.0449131,-0.103438 0.0319828,-0.101236 0.0181444,-0.0996651 0.00555077,-0.0989906 -0.00760233,-0.101089 -0.0204307,-0.104101 -0.0339025,-0.105591 -0.0464542,-0.107064 -0.059938,-0.107941 -0.073151,-0.106972 -0.086424,-0.102936 -0.0903743,-0.0892049 -0.102293,-0.0759369 -0.113888,-0.063583 -0.124574,-0.0505977 -0.131898,-0.036933 -0.136763,-0.0235271 -0.139799,-0.00947182 -0.142222,0.00459546 -0.143105,0.018386 -0.143387,0.0328019 -0.143061,0.0475366 -0.140582,0.0620065 -0.136269,0.076819 -0.130121,0.0919743 -0.113876,0.108554

P_mexicanus -0.109245,0.107417 -0.094972,0.0844933 -0.0813475,0.0749146 -0.0676174,0.071878 -0.0542569,0.0719588 -0.0409041,0.0723237 -0.0278277,0.0723968 -0.0141908,0.0727694 -0.000830243,0.0728502 0.0127911,0.0737911 0.0261284,0.0747242 0.0394656,0.0756573 0.0528417,0.0751699 0.0661401,0.0775235 0.0795829,0.0849987 0.0923798,0.0952994 0.105197,0.115267 0.122647,0.10096 0.129577,0.0866492 0.134519,0.0722842 0.138339,0.05732 0.141284,0.0431848 0.142533,0.0287189 0.142929,0.0142297 0.141052,-0.00032158 0.138891,-0.0148806 0.135025,-0.0294863 0.129163,-0.0438622 0.122457,-0.0585454 0.115742,-0.0729446 0.10932,-0.0876201 0.107443,-0.102171 0.0926696,-0.102575 0.0781649,-0.102403 0.0636369,-0.101378 0.0490933,-0.0997856 0.034511,-0.0967723 0.0196523,-0.0940509 0.00483243,-0.09275 -0.00960241,-0.0951347 -0.0236988,-0.0995003 -0.0383789,-0.103313 -0.0527827,-0.106834 -0.0669334,-0.109211 -0.0816757,-0.110751 -0.0961649,-0.111147 -0.100822,-0.0967745 -0.107461,-0.0827402 -0.114107,-0.0684219 -0.12189,-0.0541345 -0.127107,-0.0400614 -0.132617,-0.025712 -0.137559,-0.011347 -0.139943,0.0030878 -0.141192,0.0175537 -0.141035,0.0326266 -0.13915,0.0468938 -0.136437,0.0620366 -0.132571,0.0766422 -0.126441,0.0915941 -0.109245,0.107417

P_obsoletus -0.112229,0.103036 -0.0978489,0.0832241 -0.0836368,0.0755474 -0.069807,0.0718021 -0.0556947,0.0713411 -0.0419148,0.0712035 -0.0281441,0.0717219 -0.0150383,0.0728873 -0.000944102,0.0737382 0.0128312,0.0739286 0.0262876,0.0734586 0.0403818,0.0743095 0.054139,0.0758119 0.0672266,0.0782891 0.0812755,0.0824199 0.0949465,0.090154 0.107106,0.112301 0.128287,0.098816 0.135375,0.08448 0.139505,0.0704311 0.142652,0.0563686 0.144159,0.0422835 0.144682,0.0281847 0.143889,0.0143958 0.141788,0.000260752 0.136407,-0.0139196 0.133322,-0.0280683 0.127613,-0.0422532 0.119932,-0.0561373 0.1116,-0.0703585 0.109827,-0.084489 0.109038,-0.0986059 0.094301,-0.10045 0.0795509,-0.10131 0.06445,-0.100534 0.0496771,-0.0997545 0.0348725,-0.0966788 0.0197853,-0.0968873 0.00467085,-0.095128 -0.00973323,-0.0972954 -0.0247933,-0.0994719 -0.0391792,-0.102951 -0.0539022,-0.105779 -0.0689532,-0.108612 -0.0833799,-0.109139 -0.0981845,-0.106063 -0.0990354,-0.091969 -0.10349,-0.0782527 -0.110235,-0.064896 -0.118297,-0.0512295 -0.125699,-0.037882 -0.131793,-0.0241883 -0.137231,-0.0104855 -0.140045,0.00325353 -0.142208,0.0173296 -0.143059,0.0314238 -0.142926,0.0455317 -0.140825,0.0596667 -0.137412,0.0738199 -0.131708,0.0883328 -0.112229,0.103036

P_pacificus -0.114269,0.104566 -0.0998755,0.0823317 -0.085445,0.0751499 -0.0710616,0.0699474 -0.0574982,0.0659136 -0.0435956,0.0642645 -0.029316,0.0634166 -0.0150553,0.0633604 -0.00119987,0.0636906 0.013042,0.0644262 0.0272744,0.0655576 0.0414785,0.0678766 0.0552962,0.0697903 0.0686331,0.0752574 0.0823565,0.0811298 0.0963153,0.0937415 0.109303,0.113856 0.124309,0.0991618 0.131765,0.0854762 0.137656,0.0709611 0.142331,0.0576054 0.145046,0.0434107 0.146168,0.0295741 0.146489,0.0161146 0.145226,0.00261728 0.142785,-0.0113042 0.139543,-0.0248487 0.134718,-0.0384309 0.129101,-0.052032 0.121504,-0.0656802 0.111919,-0.0789798 0.101146,-0.0923077 0.0873941,-0.0969925 0.0735859,-0.0993021 0.0601263,-0.0996229 0.0466856,-0.100735 0.0332261,-0.101056 0.0193801,-0.101782 0.00552465,-0.102113 -0.00871721,-0.102848 -0.0217809,-0.103159 -0.0356363,-0.10349 -0.0490865,-0.104206 -0.0629324,-0.104933 -0.0768351,-0.103283 -0.0903984,-0.0992497 -0.101398,-0.0864407 -0.112785,-0.0740371 -0.121409,-0.0611715 -0.128837,-0.0486736 -0.133512,-0.0353178 -0.137801,-0.0215567 -0.1393,-0.00852134 -0.142797,0.00525861 -0.143127,0.019114 -0.142656,0.0325925 -0.141007,0.0464951 -0.137775,0.0604354 -0.133364,0.0747999 -0.126588,0.0896169 -0.114269,0.104566

P_atronitens -0.113126,0.105358 -0.0989728,0.0820621 -0.0850102,0.0760585 -0.0709964,0.0730334 -0.0572595,0.0737737 -0.0432735,0.0748027 -0.0292282,0.0750249 -0.0148545,0.0744599 -0.00136683,0.0749115 0.0123106,0.0764587 0.0265854,0.0772385 0.0403618,0.0774409 0.0541184,0.0779122 0.0678157,0.0791905 0.0818727,0.0829289 0.095364,0.090682 0.108574,0.113287 0.126089,0.0994326 0.133403,0.084557 0.138197,0.070848 0.141437,0.0562135 0.142735,0.0422473 0.143535,0.0277036 0.141855,0.0137886 0.140752,-0.000624653 0.137458,-0.0146583 0.132051,-0.0293882 0.124703,-0.0434498 0.117355,-0.0575113 0.110046,-0.0721108 0.105636,-0.0856857 0.10807,-0.10038 0.0933955,-0.103082 0.0788122,-0.103344 0.0643,-0.100896 0.0495979,-0.0995439 0.0349157,-0.0984608 0.0203324,-0.0987225 0.0059587,-0.0981576 -0.00854543,-0.0994952 -0.0233185,-0.100853 -0.0377435,-0.103266 -0.0519193,-0.105391 -0.0663443,-0.107804 -0.0811174,-0.109161 -0.0955504,-0.10779 -0.0968287,-0.0940924 -0.102739,-0.0799247 -0.109974,-0.0661249 -0.118284,-0.0524042 -0.125788,-0.0386242 -0.131409,-0.0247057 -0.135935,-0.0109769 -0.138578,0.00289032 -0.140742,0.017604 -0.141482,0.0313409 -0.140648,0.0457344 -0.138739,0.060207 -0.135195,0.0745294 -0.12954,0.0895481 -0.113126,0.105358

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P_perpolitus -0.109165,0.108605 -0.0950464,0.0832047 -0.0816687,0.07765 -0.0685844,0.0732272 -0.0552539,0.0730604 -0.0419308,0.0737444 -0.0283191,0.0738637 -0.0147025,0.0734159 -0.00137198,0.0732491 0.0119486,0.0742167 0.0249931,0.074331 0.0386047,0.0744503 0.0519254,0.0754179 0.0649574,0.0769501 0.0785367,0.0807559 0.0915116,0.0888104 0.104322,0.115581 0.122317,0.100991 0.130098,0.0868798 0.135894,0.0727507 0.13914,0.0583157 0.141533,0.0441568 0.142513,0.0294183 0.14207,0.0152346 0.140211,0.00075481 0.137789,-0.0140135 0.132525,-0.0282395 0.124714,-0.0430551 0.118602,-0.0575721 0.111356,-0.0720991 0.107513,-0.0865963 0.109341,-0.101044 0.0946024,-0.102024 0.0801524,-0.103568 0.0654065,-0.103698 0.0506605,-0.103827 0.0358848,-0.100553 0.0208379,-0.0986999 0.00636555,-0.0976924 -0.00864905,-0.0995256 -0.0230915,-0.101921 -0.0377977,-0.106587 -0.0522427,-0.108699 -0.0666727,-0.112512 -0.0814037,-0.114343 -0.0961969,-0.109084 -0.0966097,-0.094341 -0.101838,-0.080207 -0.108771,-0.0658043 -0.118534,-0.0519936 -0.125748,-0.0378769 -0.132397,-0.0234717 -0.136772,-0.00961382 -0.139735,0.00482369 -0.140999,0.0195597 -0.141692,0.0340171 -0.140969,0.0484869 -0.138832,0.0635363 -0.134421,0.0780384 -0.127742,0.0925605 -0.109165,0.108605

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P_strenuus-0.11209,0.100569 -0.097003,0.072805 -0.0834852,0.0690682 -0.0697993,0.0681951 -0.055929,0.0698694 -0.0420092,0.0705946 -0.0280894,0.0713198 -0.014486,0.0720285 -0.000566185,0.0727537 0.0130537,0.0731461 0.0266901,0.0732221 0.0406264,0.0736309 0.0545791,0.0737234 0.0682155,0.0737994 0.0820364,0.0764228 0.0953926,0.0818769 0.10861,0.10826 0.128333,0.0950129 0.135669,0.0820719 0.140191,0.0683499 0.143114,0.0548618 0.144439,0.0416077 0.144498,0.0282877 0.143942,0.0146183 0.143368,0.00126534 0.14123,-0.0124864 0.138109,-0.0256549 0.133107,-0.0392387 0.126839,-0.0528883 0.119623,-0.0665875 0.109859,-0.0801021 0.112166,-0.0939395 0.0970299,-0.0956797 0.0818941,-0.0974199 0.0670911,-0.0994599 0.0511413,-0.0977532 0.0358078,-0.0956971 0.0208565,-0.0948899 0.00558887,-0.0940992 -0.00956339,-0.0955231 -0.0246497,-0.0982124 -0.0394527,-0.100252 -0.0551882,-0.102658 -0.0703734,-0.103449 -0.0849754,-0.103259 -0.101192,-0.102517 -0.10285,-0.0889634 -0.111435,-0.0764047 -0.120069,-0.0628969 -0.126788,-0.0496067 -0.132542,-0.0365833 -0.137047,-0.0231777 -0.140603,-0.00972256 -0.142577,0.00381495 -0.14327,0.017102 -0.143978,0.0307054 -0.143089,0.0440749 -0.14095,0.0578267 -0.136597,0.0716938 -0.130346,0.0856599 -0.112106,0.100885

P_sublaevis -0.106941,0.106166 -0.092969,0.0799139 -0.0794206,0.0737816 -0.0665598,0.072594 -0.0534197,0.0719958 -0.0403104,0.0728555 -0.0274988,0.0740006 -0.0143772,0.0742772 -0.00155331,0.0748392 0.0115683,0.0751157 0.0246961,0.0751006 0.0378238,0.0750856 0.0506354,0.0762308 0.0637325,0.0776737 0.0765072,0.0805684 0.089202,0.0872538 0.100865,0.115213 0.117495,0.101269 0.124789,0.0874203 0.128589,0.0732061 0.1318,0.0592711 0.135017,0.0450446 0.137644,0.0310974 0.139403,0.0168401 0.139698,0.00284369 0.137971,-0.0120705 0.137391,-0.0260853 0.134199,-0.0407387 0.129543,-0.0551311 0.123144,-0.069852 0.116453,-0.0845791 0.112969,-0.0992386 0.0976564,-0.106271 0.0822327,-0.108055 0.0670638,-0.108082 0.0515542,-0.105784 0.0362869,-0.101146 0.0208018,-0.100014 0.00562679,-0.0997505 -0.00951754,-0.100945 -0.025202,-0.104193 -0.0400056,-0.107713 -0.0550946,-0.111532 -0.0705183,-0.113316 -0.0856872,-0.113344 -0.101587,-0.106386 -0.106839,-0.0924939 -0.11384,-0.0786388 -0.12114,-0.0644983 -0.126975,-0.0506187 -0.131364,-0.0361251 -0.132528,-0.0224388 -0.133996,-0.00817534 -0.135165,0.00580262 -0.134883,0.0201029 -0.134316,0.0347009 -0.133153,0.048728 -0.131407,0.0627675 -0.127923,0.0774269 -0.121226,0.0918624 -0.106941,0.106166

P_cordicollis -0.107658,0.1039 -0.0932405,0.0799796 -0.0799349,0.0740524 -0.06671,0.0715884 -0.0538637,0.0705016 -0.0403087,0.0687384 -0.0271241,0.068006 -0.0136013,0.067628 -0.000432897,0.0675883 0.0127194,0.0682413 0.0258474,0.0699332 0.0389674,0.0719714 0.0520794,0.074356 0.0651913,0.0767405 0.0782629,0.0808567 0.0912135,0.0901678 0.103165,0.112623 0.117679,0.0994472 0.125967,0.0857798 0.132515,0.0724183 0.136994,0.0586622 0.14078,0.0448899 0.142488,0.0310691 0.14385,0.0172404 0.143488,0.0030249 0.142426,-0.0108604 0.139639,-0.0251323 0.134429,-0.0394607 0.127133,-0.0534912 0.118121,-0.0682547 0.112564,-0.0825912 0.113918,-0.0960737 0.0984461,-0.101285 0.0825232,-0.102003 0.0672768,-0.102012 0.0516599,-0.100989 0.0364055,-0.100652 0.0211269,-0.0992751 0.00519593,-0.0996462 -0.0103887,-0.100009 -0.0252242,-0.102781 -0.0407846,-0.104183 -0.0559503,-0.107655 -0.0714945,-0.109749 -0.0870872,-0.109766 -0.102438,-0.105273 -0.102777,-0.0907269 -0.110373,-0.0770433 -0.120385,-0.0637626 -0.128681,-0.0497489 -0.134553,-0.0356786 -0.137985,-0.0222446 -0.140393,-0.00809369 -0.140716,0.00575931 -0.141385,0.0196042 -0.139984,0.0338439 -0.136852,0.0481239 -0.134058,0.0620495 -0.128485,0.0756933 -0.121543,0.0900621 -0.107658,0.1039

P_subangulatus -0.115019,0.103022 -0.100116,0.0818942 -0.0856582,0.0729986 -0.0713492,0.0681807 -0.0571317,0.065872 -0.0429713,0.0651317 -0.0288109,0.0643913 -0.0149984,0.0645805 -0.000895196,0.0654084 0.0132309,0.0656091 0.0273342,0.066437 0.0420419,0.0679151 0.0554949,0.0693475 0.0701341,0.0727076 0.0834272,0.0785312 0.0973984,0.0916033 0.110177,0.111542 0.128291,0.0971259 0.134753,0.0835421 0.139984,0.0692851 0.142671,0.0558778 0.145055,0.0421453 0.146499,0.0283786 0.147316,0.014589 0.146878,0.000753709 0.144523,-0.0122092 0.140926,-0.0255315 0.137026,-0.0391788 0.130919,-0.0525925 0.122605,-0.0657725 0.111457,-0.0787418 0.100018,-0.0923498 0.0866562,-0.0962914 0.0731917,-0.0974102 0.0596472,-0.0963333 0.0464506,-0.096186 0.0326725,-0.0973161 0.01886,-0.0975053 0.00533836,-0.0970558 -0.00781248,-0.0981631 -0.0212998,-0.0986545 -0.0347758,-0.0994596 -0.0485539,-0.10059 -0.0622864,-0.102975 -0.0755287,-0.101573 -0.0891303,-0.0989274 -0.103691,-0.087209 -0.113871,-0.0750169 -0.121891,-0.0618038 -0.128632,-0.0491723 -0.134433,-0.0365065 -0.139013,-0.0228541 -0.142316,-0.00978325 -0.14376,0.00398349 -0.144565,0.0174594 -0.144127,0.0312947 -0.14305,0.0448392 -0.141369,0.0590339 -0.137481,0.0729949 -0.131419,0.0876633 -0.115019,0.103022

P_depressus -0.113673,0.105935 -0.0987796,0.0822016 -0.0846878,0.075953 -0.0709137,0.0729298 -0.0566459,0.0728752 -0.0423861,0.0733588 -0.0289499,0.0749068 -0.0149634,0.0756555 -0.000972732,0.076135 0.0127528,0.0763414 0.0267394,0.0770901 0.0407341,0.0773005 0.0544515,0.0780452 0.068426,0.0796013 0.0823721,0.0830412 0.0962413,0.0915947 0.109089,0.1144 0.125455,0.10011 0.132406,0.0854087 0.136934,0.0706714 0.140113,0.056183 0.142208,0.0422167 0.144037,0.0279771 0.143721,0.013167 0.142317,-0.000851965 0.138494,-0.0151765 0.132246,-0.0292683 0.124651,-0.0433803 0.117595,-0.0574842 0.110005,-0.0718654 0.106448,-0.0859167 0.105321,-0.10047 0.0910933,-0.103107 0.0765644,-0.103594 0.0625617,-0.103266 0.0479923,-0.101063 0.033688,-0.098586 0.0193838,-0.0961092 0.00482252,-0.0944438 -0.00886256,-0.0973415 -0.023355,-0.100251 -0.037289,-0.104499 -0.0512351,-0.107939 -0.0654706,-0.110037 -0.0800156,-0.109448 -0.0934883,-0.108574 -0.0953216,-0.0940653 -0.100911,-0.0804207 -0.109195,-0.0665474 -0.117206,-0.0529393 -0.125759,-0.03907 -0.132429,-0.0251725 -0.137214,-0.0112466 -0.139851,0.00298077 -0.141138,0.0169593 -0.141083,0.0312271 -0.13996,0.0460494 -0.138833,0.0606026 -0.135284,0.0751922 -0.129586,0.0900832 -0.113404,0.10594

P_marginatus -0.107098,0.103451 -0.0930816,0.0786732 -0.0794225,0.072155 -0.0666975,0.0693667 -0.0535368,0.0695493 -0.0406538,0.069991 -0.0277892,0.0709695 -0.0146378,0.0714204 -0.00175472,0.0718621 0.0111467,0.0717671 0.0242705,0.0730232 0.0374312,0.0732057 0.050351,0.0725738 0.0629564,0.0732748 0.0762474,0.0774924 0.0889464,0.0833021 0.100872,0.111657 0.117982,0.0985394 0.126235,0.085118 0.132341,0.0716231 0.135772,0.0577677 0.138925,0.0441715 0.141551,0.0302885 0.143103,0.0163687 0.143045,0.00239367 0.141117,-0.0119142 0.138652,-0.0262404 0.134559,-0.0400851 0.13103,-0.0547165 0.126955,-0.069098 0.121528,-0.083257 0.117463,-0.0979069 0.101488,-0.102217 0.0856523,-0.10276 0.0694657,-0.100896 0.0533067,-0.0998379 0.0376753,-0.0984929 0.021461,-0.0958243 0.00523762,-0.0928873 -0.0104597,-0.0974562 -0.0258795,-0.102284 -0.0419833,-0.102836 -0.0574859,-0.105249 -0.073516,-0.107948 -0.0893606,-0.108223 -0.105566,-0.105823 -0.111144,-0.0920408 -0.117268,-0.0780091 -0.122587,-0.0639497 -0.126832,-0.0498535 -0.131336,-0.036035 -0.135832,-0.0224848 -0.138744,-0.00807419 -0.139214,0.00561403 -0.139433,0.0198482 -0.138292,0.0335917 -0.136336,0.0470943 -0.133335,0.061439 -0.128714,0.0755704 -0.121668,0.0895163 -0.107107,0.10372

P_elongatus -0.115576,0.106958 -0.100275,0.0825975 -0.086184,0.0754513 -0.0714958,0.0733745 -0.0576659,0.0728573 -0.0433264,0.0728913 -0.0295382,0.0734348 -0.0152406,0.0745294 -0.000625604,0.0743087 0.0133859,0.0759232 0.027195,0.0759363 0.0409937,0.0762146 0.0550366,0.0770336 0.0690377,0.0789132 0.0831995,0.0834549 0.0969602,0.0914332 0.11037,0.115066 0.1261,0.100018 0.133579,0.0854405 0.137591,0.0712579 0.141347,0.0567996 0.142718,0.0422473 0.143558,0.027674 0.143581,0.0135998 0.141494,-0.000823224 0.136999,-0.01481 0.131741,-0.0296236 0.124319,-0.0434601 0.116377,-0.0575827 0.109507,-0.0719287 0.104757,-0.0861911 0.103996,-0.100562 0.0899949,-0.102441 0.0757077,-0.103801 0.0618777,-0.103284 0.0480164,-0.101971 0.0338585,-0.0998737 0.0196902,-0.0975108 0.00558459,-0.0967389 -0.00817225,-0.0980778 -0.0218664,-0.101008 -0.0355605,-0.103937 -0.0500188,-0.107694 -0.0640617,-0.108513 -0.0776161,-0.108251 -0.0912018,-0.107193 -0.0928372,-0.0926508 -0.10054,-0.0791448 -0.107977,-0.0656283 -0.117006,-0.0521745 -0.125504,-0.0386998 -0.131881,-0.0251415 -0.136943,-0.0112658 -0.139893,0.00295862 -0.141518,0.0172353 -0.143143,0.031512 -0.141862,0.0461689 -0.139795,0.0611222 -0.135852,0.0756184 -0.129808,0.0907285 -0.115587,0.107223

P_metallicus -0.112203,0.100104 -0.0978395,0.0816976 -0.0839029,0.0749096 -0.069864,0.0715472 -0.0559171,0.0706907 -0.042198,0.0698259 -0.0283014,0.0703363 -0.0146158,0.0703828 -0.00091348,0.0699736 0.0134388,0.0705007 0.0266269,0.0716695

0.0411819,0.0728885 0.0547922,0.0749852 0.068369,0.0779933 0.0821402,0.0819209 0.0957272,0.0908605 0.108718,0.109815 0.125665,0.09561 0.132782,0.081956 0.137629,0.0679905 0.141768,0.0546834 0.144084,0.0413093 0.145953,0.0276907 0.146911,0.0140385 0.145565,0.000986196 0.14492,-0.0124967 0.141304,-0.0258605 0.136753,-0.0385744 0.129948,-0.0520554 0.121076,-0.065156 0.110829,-0.0780791 0.0996709,-0.0910356 0.086228,-0.0976887 0.0728288,-0.0993214 0.0591599,-0.0998235 0.0457273,-0.100545 0.0318139,-0.1006 0.0185588,-0.0999461 0.00511777,-0.10044 -0.00832326,-0.100933 -0.0219419,-0.102802 -0.0353662,-0.103752 -0.0490099,-0.104937 -0.062451,-0.105431 -0.0757897,-0.102499 -0.089187,-0.0979725 -0.101494,-0.0858778 -0.112653,-0.0739691 -0.121778,-0.0615295 -0.128853,-0.0490146 -0.135017,-0.0364662 -0.139148,-0.0233869 -0.141911,-0.0102573 -0.14308,0.00293079 -0.144257,0.0163467 -0.143376,0.0296102 -0.141836,0.0435821 -0.138904,0.0569209 -0.134638,0.0712211 -0.128306,0.0851409 -0.112211,0.100332

P_aurocinctus -0.113068,0.10589 -0.0986561,0.0870883 -0.0844427,0.0796085 -0.070673,0.0775406 -0.0569034,0.0754727 -0.0429795,0.0755351 -0.0292822,0.0753527 -0.0153764,0.0758864 -0.00143441,0.0754774 0.0119819,0.0764645 0.0261144,0.077243 0.0397755,0.0780034 0.0534184,0.0792351 0.0672609,0.0814187 0.0807954,0.0854788 0.0946112,0.0945065 0.107775,0.114367 0.127499,0.0986013 0.135158,0.0835528 0.139735,0.068858 0.143596,0.0543718 0.146287,0.0396046 0.147546,0.0252545 0.147137,0.0113125 0.146039,-0.003128 0.142557,-0.0169519 0.137896,-0.0308211 0.130851,-0.0440736 0.121939,-0.0578699 0.108994,-0.0711129 0.0927208,-0.0837755 0.0897192,-0.097817 0.0776713,-0.103708 0.0663309,-0.103436 0.0540388,-0.102963 0.0419733,-0.102246 0.0300801,-0.0998701 0.0176703,-0.0963338 0.00561388,-0.0958524 -0.00631593,-0.0986707 -0.0182367,-0.101725 -0.0304113,-0.104316 -0.0423682,-0.106428 -0.0541347,-0.107351 -0.0663816,-0.108057 -0.0783381,-0.104032 -0.0812469,-0.0897448 -0.09798,-0.0781131 -0.111658,-0.066128 -0.123233,-0.0535902 -0.130584,-0.0404181 -0.136992,-0.0272098 -0.141523,-0.0136935 -0.144187,0.00036658 -0.145428,0.0142453 -0.145282,0.0288853 -0.143722,0.0435796 -0.140276,0.0583463 -0.13731,0.0733306 -0.131299,0.0889038 -0.113059,0.105655

P_ambiguus -0.107654,0.109443 -0.0937672,0.0858051 -0.0805206,0.0778853 -0.0666943,0.0730439 -0.053969,0.0721524 -0.0409899,0.0708013 -0.0273452,0.0704171 -0.0146676,0.0706986 -0.00152082,0.0709992 0.0116164,0.0715343 0.0249978,0.0718444 0.0373835,0.0735239 0.050698,0.0754761 0.0634859,0.0788169 0.0766475,0.0845226 0.0892635,0.092086 0.101632,0.117263 0.120082,0.102741 0.127741,0.0877789 0.133973,0.0732288 0.138544,0.0590811 0.141952,0.044651 0.144187,0.0301731 0.14477,0.0158629 0.14418,0.00150488 0.142163,-0.0124413 0.138767,-0.0271485 0.13417,-0.0411998 0.126054,-0.0553944 0.116755,-0.0694022 0.105336,-0.0832614 0.097952,-0.0981311 0.0845176,-0.102908 0.0714473,-0.105085 0.0580372,-0.104692 0.0451346,-0.105217 0.0322128,-0.105274 0.0190278,-0.104636 0.00535449,-0.103548 -0.00771585,-0.105725 -0.0205898,-0.106955 -0.0337175,-0.107724 -0.0468452,-0.108494 -0.0597478,-0.10902 -0.0731674,-0.108391 -0.0861943,-0.105867 -0.0944997,-0.0923417 -0.107047,-0.0785189 -0.117689,-0.0653234 -0.126482,-0.0513476 -0.133136,-0.0379897 -0.136769,-0.0238037 -0.140392,-0.00985234 -0.141679,0.00442919 -0.141802,0.0189931 -0.140499,0.0331452 -0.138051,0.0480488 -0.134674,0.0632252 -0.129646,0.078234 -0.123201,0.0930655 -0.10741,0.109218

P_velutinus -0.111027,0.104988 -0.096814,0.0834567 -0.0826957,0.076491 -0.0690224,0.0746069 -0.0553877,0.0736927 -0.0415299,0.073273 -0.0281955,0.0738037 -0.0146188,0.0743441 -0.000760931,0.0739244 0.0130486,0.0747168 0.0265965,0.0759846 0.0399019,0.0772426 0.0537211,0.0777927 0.067211,0.0805151 0.0811666,0.0837416 0.0944538,0.0915553 0.106939,0.113421 0.121832,0.0992013 0.127735,0.0851095 0.133163,0.070756 0.137369,0.0565966 0.14012,0.0423793 0.141417,0.0281042 0.141986,0.0138001 0.140858,-0.000571607 0.138257,-0.0145163 0.135189,-0.0289651 0.129921,-0.043016 0.123459,-0.0575999 0.116978,-0.071699 0.110488,-0.0855556 0.109127,-0.100179 0.0942214,-0.103929 0.0794131,-0.104033 0.0647893,-0.102673 0.0498459,-0.0993822 0.0349025,-0.0960918 0.0198229,-0.0954778 0.00524735,-0.0953295 -0.00927025,-0.0966358 -0.0240013,-0.0986791 -0.0384128,-0.102652 -0.0530571,-0.106878 -0.0673129,-0.108659 -0.0827713,-0.110731 -0.0971527,-0.109361 -0.101359,-0.0952018 -0.109182,-0.0816721 -0.116064,-0.0673764 -0.123413,-0.053585 -0.129083,-0.0392411 -0.134462,-0.0260997 -0.137466,-0.0116497 -0.139257,0.00284864 -0.140311,0.0171335 -0.139426,0.0314955 -0.137813,0.0458864 -0.134019,0.0603642 -0.129506,0.0751134 -0.124761,0.0901147 -0.111027,0.104988

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0.122346,0.100249 0.128269,0.0852393 0.13291,0.0711102 0.136916,0.0572658 0.140339,0.0424628 0.141237,0.028488 0.14185,0.0138784 0.142424,0.000201422 0.140834,-0.0138777 0.137989,-0.0276982 0.1339,-0.0415708 0.126677,-0.0549521 0.11698,-0.0687486 0.105081,-0.0820147 0.0950468,-0.0952025 0.0819154,-0.101358 0.069936,-0.105286 0.056972,-0.10801 0.0445514,-0.108842 0.03112,-0.107849 0.018919,-0.106492 0.00613536,-0.106094 -0.00684172,-0.108507 -0.0192232,-0.110272 -0.0316308,-0.111415 -0.0444144,-0.111018 -0.0569262,-0.109674 -0.0698272,-0.106479 -0.0831694,-0.100188 -0.0948943,-0.0879128 -0.10693,-0.0756508 -0.11679,-0.0632975 -0.124824,-0.0499335 -0.130967,-0.0371129 -0.134636,-0.0238771 -0.136479,-0.0096306 -0.137688,0.00433116 -0.138896,0.0182929 -0.138253,0.0326438 -0.137298,0.0470077 -0.134181,0.0617737 -0.13074,0.0762419 -0.126055,0.0907623 -0.113354,0.107176

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S_buparius 0.252158,0.18763 0.251856,0.11387 0.23896,0.0841415 0.22546,0.0583029 0.21088,0.037897 0.193783,0.0204923 0.177298,0.00625886 0.159079,-0.0049309 0.140774,-0.0145563 0.121951,-0.0218563 0.10226,-0.0276346 0.0829182,-0.0326094 0.0626876,-0.0356712 0.0424357,-0.038342 0.0217076,-0.0394696 0.000567126,-0.0402274 -0.0194426,-0.0401392 -0.0418202,-0.0397876 -0.0626334,-0.0393508 -0.0842926,-0.0377834 -0.105603,-0.0354124 -0.126544,-0.0326291 -0.150329,-0.0280393 -0.172613,-0.022191 -0.195722,-0.0156031 -0.219265,-0.00825429 -0.24209,0.00031036 -0.264331,0.00537642 -0.286985,0.0108123 -0.313101,0.0293965
S_terricola0.27432,0.148047 0.261175,0.106809 0.245984,0.0821092 0.22892,0.0619432 0.211217,0.0460932 0.193064,0.0305775 0.175405,0.0171397 0.155887,0.00543158 0.137706,-0.00447495 0.118566,-0.0133205 0.0988018,-0.0206546 0.0791395,-0.0259689 0.0588528,-0.0297717 0.0380576,-0.0328479 0.0184395,-0.0357499 -0.00280611,-0.0384918 -0.0224823,-0.0410015 -0.0430012,-0.0432349 -0.0647111,-0.0428379 -0.0851859,-0.042659 -0.108261,-0.0384545 -0.130391,-0.0325063 -0.152463,-0.0269505 -0.173737,-0.0240832 -0.196593,-0.0186435 -0.217533,-0.0153258 -0.239663,-0.00937766 -0.262141,-0.00107533 -0.285694,0.00907273 -0.310873,0.0302069
S_subterraneus 0.26342,0.168697 0.256988,0.109462 0.242436,0.0829205 0.227192,0.0615028 0.21098,0.0421855 0.193372,0.0249467 0.175996,0.0115894 0.158082,0.000354539 0.139222,-0.0092088 0.120747,-0.0178925 0.100898,-0.0249266 0.0805544,-0.0306961 0.0618384,-0.0346624 0.0412975,-0.0365722 0.0208004,-0.0393397 -0.00100521,-0.0417441 -0.0207761,-0.0418947 -0.0427132,-0.041726 -0.0647161,-0.0402708 -0.0855201,-0.0370344 -0.107094,-0.0355572 -0.128843,-0.0306493 -0.151967,-0.0240917 -0.174684,-0.0170833 -0.197785,-0.0109545 -0.21848,-0.0098624 -0.240207,-0.00538329 -0.262276,-0.0026415 -0.285872,0.00475188 -0.311885,0.0257808
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M_batesi 0.271956,0.150832 0.264023,0.0937281 0.248716,0.0699162 0.232034,0.0507062 0.214221,0.0373225 0.19626,0.0251139 0.176779,0.0154994 0.157492,0.00750104 0.138205,-0.000497339 0.118672,-0.00653718 0.0986972,-0.0122346 0.0786735,-0.0175403 0.0585512,-0.0220627 0.0384289,-0.026585 0.0178163,-0.0303732 -0.00294423,-0.0329862 -0.0233624,-0.0351583 -0.0450542,-0.0366949 -0.0656695,-0.0373001 -0.0865314,-0.0359468 -0.108618,-0.0343497 -0.13095,-0.030794 -0.153283,-0.0272384 -0.174783,-0.0239758 -0.196774,-0.0199792 -0.219745,-0.0145143 -0.241245,-0.0112518 -0.263235,-0.0072551 -0.286943,0.000902435 -0.311388,0.0117526
M_convexa 0.27779,0.140222 0.265178,0.0986117 0.25005,0.0716781 0.232724,0.05334 0.214324,0.0388652 0.195855,0.0256935 0.176813,0.015105 0.157246,0.006231 0.138044,-0.00131699 0.118362,-0.00801922 0.0985878,-0.012984 0.0775107,-0.0180176 0.0576909,-0.0221137 0.0374366,-0.0262327 0.0161301,-0.0269228 -0.00554195,-0.0289388 -0.0254995,-0.0304288 -0.0463717,-0.0310958 -0.0667636,-0.0326087 -0.0880701,-0.0332988 -0.110337,-0.0322973 -0.131621,-0.0334217 -0.152585,-0.0323513 -0.17364,-0.0295435 -0.196091,-0.0250672 -0.21813,-0.0201335 -0.240192,-0.0147655 -0.262277,-0.00896307 -0.285369,-0.000600421 -0.311252,0.0193752

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P_quirozi 0.262531,0.174096 0.257089,0.10974 0.242475,0.0827912 0.227127,0.0597997 0.210578,0.0415299 0.193428,0.0256208 0.175246,0.0124381 0.156896,0.00125076 0.138878,-0.00910496 0.119462,-0.0171669 0.0999781,-0.0244308 0.0806589,-0.0288677 0.0605751,-0.0337707 0.0394584,-0.0359473 0.0191398,-0.0380569 -0.00131294,-0.0385703 -0.0208669,-0.0402137 -0.0428153,-0.0420584 -0.0637007,-0.0422062 -0.0850186,-0.0419885 -0.106005,-0.0409392 -0.127158,-0.0378945 -0.149211,-0.0337198 -0.171032,-0.0275161 -0.194684,-0.0186532 -0.218802,-0.00902578 -0.240224,-0.00278862 -0.263376,0.00491062 -0.286395,0.0110136 -0.312921,0.0397289

P_purpuratus 0.2691,0.160449 0.256758,0.116192 0.242208,0.0884677 0.226657,0.0656373 0.209683,0.0458386 0.192064,0.0301755 0.174492,0.0163837 0.155788,0.00224582 0.138309,-0.0078032 0.11822,-0.0174124 0.099282,-0.0259269 0.0800444,-0.0314379 0.0597121,-0.035798 0.0393985,-0.0394095 0.0194686,-0.0426561 -0.000040,-0.0440408 -0.0214018,-0.0446301 -0.042754,-0.0448451 -0.0640687,-0.043563 -0.0850372,-0.0434131 -0.106689,-0.0406246 -0.12834,-0.0378361 -0.149561,-0.0328113 -0.172242,-0.026252 -0.195213,-0.0163149 -0.217426,-0.0060223 -0.239751,-0.000220908 -0.262834,0.00522494 -0.284383,0.0121304 -0.311442,0.0382735

P_rotundipennis 0.270446,0.157466 0.259212,0.108132 0.243413,0.0847076 0.227155,0.0639503 0.210034,0.0466148 0.192475,0.0311815 0.174097,0.0176394 0.156048,0.00602132 0.136785,-0.00333377 0.117511,-0.0123062 0.0981938,-0.0197483 0.0784939,-0.0272012 0.0595157,-0.0331019 0.0389526,-0.0371331 0.0191439,-0.0407599 -0.00184533,-0.0432715 -0.0217085,-0.0449853 -0.0419651,-0.0463273 -0.0630196,-0.0465432 -0.0840741,-0.0467592 -0.105577,-0.0446903 -0.127494,-0.0414845 -0.149073,-0.0367374 -0.171897,-0.0285794 -0.194372,-0.0192628 -0.218474,-0.0065461 -0.240927,0.00200537 -0.263686,0.00786767 -0.286565,0.0179387 -0.310798,0.0352467

P_sallei 0.262956,0.168602 0.254287,0.117837 0.240333,0.0896849 0.225087,0.0663459 0.208615,0.0459537 0.191638,0.0292812 0.174569,0.0152218 0.155993,0.00148288 0.138445,-0.00960337 0.119364,-0.0196226 0.100603,-0.0281354 0.0814032,-0.0347949 0.0617506,-0.0392279 0.0413515,-0.0436873 0.0216725,-0.0473737 0.00110166,-0.0469803 -0.0198425,-0.0466001 -0.0419065,-0.0462595 -0.0624906,-0.0454928 -0.084647,-0.0425391 -0.105657,-0.0402924 -0.127906,-0.0347257 -0.149821,-0.0280259 -0.173309,-0.0191391 -0.196331,-0.0128522 -0.21782,-0.00763239 -0.239389,-0.000172774 -0.262837,0.00759409 -0.285565,0.016134 -0.311649,0.0350204

P_sexualis 0.263122,0.176021 0.253355,0.1217 0.238108,0.0945729 0.223172,0.0710867 0.206729,0.0512151 0.188801,0.0335041 0.172328,0.0158139 0.155096,0.000294551 0.135994,-0.0116152 0.117599,-0.0220604 0.099546,-0.0310461 0.0799973,-0.0371442 0.0604383,-0.0425152 0.0404844,-0.0457101 0.0204993,-0.0467237 -0.000571304,-0.0481164 -0.0209304,-0.048408 -0.0420166,-0.0487101 -0.0620069,-0.0493601 -0.082366,-0.0496518 -0.103483,-0.0477725 -0.124253,-0.0447974 -0.146487,-0.0411159 -0.168399,-0.0345209 -0.190738,-0.0235683 -0.214956,-0.00827921 -0.23917,0.00664638 -0.26263,0.0197646 -0.285742,0.0339787 -0.311519,0.0565181

P_subsulcatus 0.275488,0.147645 0.261817,0.10636 0.246623,0.0791565 0.229325,0.0604408 0.210782,0.0461496 0.192579,0.0329833 0.17359,0.021281 0.154972,0.00958948 0.135929,-0.000255828 0.116482,-0.00899773 0.0981168,-0.0165931 0.0778625,-0.0231282 0.0575867,-0.0289205 0.0380213,-0.033577 0.0176807,-0.0371409 -0.00305273,-0.0399729 -0.0226936,-0.0420296 -0.0441914,-0.0441403 -0.064575,-0.0462186 -0.0850556,-0.0449544 -0.105875,-0.0448152 -0.128245,-0.0424907 -0.149937,-0.0379162 -0.171279,-0.0325882 -0.19416,-0.0254463 -0.217107,-0.0160761 -0.238928,-0.00704488 -0.263564,0.00933877 -0.286989,0.0224122 -0.311201,0.0369496

P_tolucanus 0.269971,0.156945 0.260006,0.105134 0.24452,0.0810119 0.227998,0.0617967 0.210783,0.0446853 0.193225,0.0303772 0.17497,0.0171221 0.156371,0.0059697 0.137074,-0.00448003 0.119186,-0.0124821 0.0995457,-0.0204788 0.0795597,-0.0270734 0.0599271,-0.0326181 0.0392491,-0.0364083 0.0189235,-0.0394991 -0.00104871,-0.04154 -0.0213701,-0.0432296 -0.0430883,-0.0435139 -0.0637514,-0.0424002 -0.0847659,-0.0416358 -0.106828,-0.0398173 -0.128185,-0.0365998 -0.150587,-0.0312775 -0.173682,-0.0235011 -0.196772,-0.0143236 -0.219863,-0.00514615 -0.24192,-0.00157629 -0.263976,0.00234385 -0.284983,0.00556025 -0.310489,0.0266546

P_viridans 0.263357,0.171191 0.257171,0.109683 0.241716,0.082863 0.225675,0.062224 0.209568,0.0434067 0.192251,0.0278292 0.174478,0.014789 0.156653,0.00320612 0.138034,-0.00658118 0.119011,-0.0152885 0.0995593,-0.0221873 0.0801072,-0.029086 0.0609542,-0.03415 0.040682,-0.0385245 0.0203706,-0.041806 -0.000370352,-0.0432789 -0.0203696,-0.04509 -0.041488,-0.0462116 -0.0622681,-0.0465914 -0.0834779,-0.0451627 -0.10431,-0.0440852 -0.126717,-0.039781 -0.149177,-0.0340194 -0.171754,-0.0249788 -0.195489,-0.0141557 -0.219654,-0.00152395 -0.242425,0.00276725 -0.263727,0.00674633 -0.286225,0.0136009 -0.312135,0.0341958

P_californicus 0.271142,0.159323 0.258464,0.112596 0.242387,0.089044 0.224907,0.0699193 0.207081,0.0520004 0.189717,0.0356507 0.171644,0.0213164 0.153603,0.00777487 0.135316,-0.00218214 0.115426,-0.0124692 0.0968416,-0.020031 0.077481,-0.0271632 0.0569477,-0.0338492 0.0384629,-0.0390325 0.0187888,-0.0441659 -0.00242123,-0.0480437 -0.0215827,-0.0504187 -0.0415537,-0.053157 -0.0622843,-0.0550692 -0.0833284,-0.0549826 -0.104406,-0.055689 -0.124144,-0.0528772 -0.146559,-0.0475706 -0.16841,-0.0383164 -0.191368,-0.0270301 -0.21454,-0.0113666 -0.239809,0.0111359 -0.262371,0.0224055 -0.285626,0.0360869 -0.309804,0.056161

P_cardioderus 0.267119,0.167718 0.257987,0.112806 0.242497,0.0858399 0.226178,0.0636177 0.210173,0.0443559 0.192506,0.028263 0.174754,0.0145074 0.15612,0.00184293 0.138023,-0.00888276 0.118784,-0.0178247 0.0987676,-0.0246888 0.0795131,-0.0306356 0.0601034,-0.034903 0.0397766,-0.0384082 0.0192947,-0.040234 -0.00104814,-0.0407441 -0.0223777,-0.0411499 -0.0433784,-0.0415904 -0.0644138,-0.0423599 -0.0850508,-0.0425063 -0.106864,-0.0411979 -0.127517,-0.0383491 -0.149416,-0.0347034 -0.17192,-0.0273352 -0.194284,-0.0186513 -0.216373,-0.0136551 -0.239135,-0.00559422 -0.261569,0.00243187 -0.28523,0.014579 -0.31302,0.0474514

P_cuestai 0.27537,0.149231 0.262542,0.105391 0.24614,0.0806237 0.228976,0.0626989 0.211406,0.0457827 0.192681,0.0308629 0.174798,0.0190945 0.155458,0.00861513 0.136846,-0.00250873 0.11736,-0.0105858 0.0978526,-0.0183196 0.0778976,-0.0243585 0.0575784,-0.0300751 0.0378411,-0.0340339 0.0173336,-0.0366618 -0.00315286,-0.0396329 -0.0230367,-0.0411894 -0.043971,-0.0424655 -0.0642189,-0.0436998 -0.0862246,-0.0443522 -0.106983,-0.0428619 -0.128147,-0.040363 -0.150103,-0.03619 -0.172569,-0.0292924 -0.195265,-0.0186198 -0.217877,-0.00931989 -0.240238,-0.00413823 -0.262579,0.000700243 -0.284421,0.00866922 -0.311294,0.0369992

P_imitator 0.268962,0.159216 0.257945,0.114442 0.24269,0.0882686 0.226026,0.0665974 0.208839,0.0473356 0.191738,0.0294258 0.173927,0.0163133 0.155189,0.00461788 0.137551,-0.00579054 0.119259,-0.0158176 0.0984142,-0.0233051 0.0799792,-0.0302684 0.0596679,-0.0347355 0.0396729,-0.0395622 0.0194267,-0.0430153 -0.00109259,-0.0454326 -0.0208274,-0.0462032 -0.0416847,-0.0485989 -0.0633392,-0.0475494 -0.0845906,-0.0455075 -0.106202,-0.0437819 -0.126963,-0.0393956 -0.149328,-0.0335489 -0.171815,-0.0243003 -0.195948,-0.0142674 -0.219067,-0.00429943 -0.241137,0.00084961 -0.26215,0.00660963 -0.284471,0.0131324 -0.310671,0.0385711

P_intermedius 0.267197,0.170858 0.255935,0.121055 0.240077,0.0924921 0.223671,0.070742 0.206589,0.0509236 0.189967,0.0336013 0.171987,0.0173044 0.154356,0.00429855 0.134856,-0.00694264 0.117003,-0.0183586 0.0983619,-0.0270481 0.0783061,-0.0343146 0.0591086,-0.0390294 0.0387745,-0.0443086 0.0190126,-0.0478867 -0.000296111,-0.0518066 -0.0202806,-0.0537948 -0.0408853,-0.0542488 -0.0616012,-0.0539078 -0.0828816,-0.0524302 -0.10297,-0.0507856 -0.126222,-0.0439104 -0.148337,-0.0364708 -0.171009,-0.0250566 -0.192377,-0.0142703 -0.215685,-0.00699763 -0.238023,0.00203183 -0.260298,0.0135017 -0.28382,0.0252021 -0.310515,0.0595579

P_mexicanus 0.265222,0.166406 0.253686,0.120826 0.238932,0.0925753 0.223498,0.069309 0.207552,0.0497808 0.190378,0.0330463 0.172674,0.0170857 0.154989,0.00408932 0.136359,-0.00819002 0.118446,-0.0195251 0.0997776,-0.0284249 0.0804662,-0.0357202 0.0614566,-0.042128 0.0412186,-0.045742 0.021396,-0.0492993 0.000817196,-0.0504213 -0.0194031,-0.0510712 -0.0405676,-0.051004 -0.061544,-0.0492186 -0.0828789,-0.0479054 -0.104026,-0.044874 -0.125815,-0.0402381 -0.148361,-0.033167 -0.17102,-0.0252652 -0.194247,-0.01321 -0.218532,0.000392979 -0.241436,0.00699198 -0.263094,0.0137614 -0.285753,0.0216632 -0.310191,0.0394763

P_obsoletus 0.270525,0.158884 0.259271,0.110687 0.243115,0.0864391 0.226597,0.0665231 0.208906,0.0475999 0.191276,0.032317 0.173585,0.0177562 0.155293,0.00605355 0.136549,-0.00459612 0.117325,-0.0138318 0.0980095,-0.0219843 0.0785742,-0.0286928 0.0590185,-0.0339571 0.0385904,-0.0374765 0.0185234,-0.0409658 -0.00169408,-0.04265 -0.0222425,-0.0447253 -0.0429112,-0.0453565 -0.0635197,-0.0467097 -0.0841884,-0.0473409 -0.105007,-0.0461669 -0.126579,-0.0446921 -0.148029,-0.040299 -0.170353,-0.0341609 -0.192946,-0.0247736 -0.216383,-0.0140023 -0.239337,-0.000282655 -0.264398,0.0168969 -0.287052,0.0270062 -0.310518,0.0425009

P_pacificus 0.26607,0.167937 0.256406,0.111674 0.242197,0.0851532 0.226153,0.0630999 0.210059,0.0448821 0.192444,0.0286097 0.175461,0.0141231 0.156799,0.002843 0.137612,-0.00764856 0.118637,-0.0164064 0.0999785,-0.0242714 0.0802702,-0.0305592 0.0601415,-0.0368992 0.0400679,-0.0402444 0.020206,-0.0418559 -0.000024,-0.04394 -0.0209355,-0.0439744 -0.0423716,-0.0432202 -0.0638598,-0.0420457 -0.0845595,-0.0403464 -0.106468,-0.039224 -0.128113,-0.0367884 -0.149914,-0.0330916 -0.172133,-0.0260318 -0.194981,-0.0173427 -0.218145,-0.00954653 -0.240311,-0.00290712 -0.262895,0.00709527 -0.286163,0.0157322 -0.311629,0.0351945

P_atronitens 0.266766,0.16396 0.259944,0.107761 0.244401,0.0812077 0.227534,0.0598672 0.211814,0.0413747 0.193613,0.0256499 0.17535,0.0127462 0.157848,0.00187559 0.13912,-0.00821573 0.119523,-0.0155037 0.0995137,-0.0223975 0.0798722,-0.0276703 0.0601951,-0.0313309 0.0400971,-0.0341945 0.0183513,-0.0354815 -0.00216749,-0.0375479 -0.0227487,-0.0367931 -0.0441181,-0.0368621 -0.0654964,-0.0365281 -0.086445,-0.0373943 -0.107411,-0.0374544 -0.128405,-0.0363055 -0.15023,-0.0339653 -0.172504,-0.0296188 -0.194016,-0.0232394 -0.217184,-0.0148805 -0.24038,-0.00531246 -0.264363,0.00343169 -0.286287,0.0102052 -0.312186,0.0326167

P_duplicatus 0.271506,0.154819 0.25971,0.110352 0.24432,0.085472 0.22767,0.0626527 0.210186,0.0442248 0.192215,0.0305098 0.174271,0.0174644 0.1554,0.00646683 0.13693,-0.00286992 0.117468,-0.0118326 0.0980985,-0.018452 0.0783808,-0.025393 0.0587153,-0.0309949 0.0387151,-0.0365837 0.0184848,-0.0394813 -0.00107597,-0.042405 -0.0226061,-0.0442459 -0.0434406,-0.0454434 -0.0648923,-0.0452757 -0.0843353,-0.0451865 -0.105774,-0.044684 -0.127482,-0.0424945 -0.148429,-0.0379878 -0.17101,-0.0324114 -0.193178,-0.0248394 -0.217881,-0.0134802 -0.240739,0.0021656 -0.264129,0.0128029 -0.286658,0.0197184 -0.310442,0.0374121

P_perpolitus 0.261276,0.172664 0.252545,0.118903 0.238887,0.0911908 0.223785,0.067579 0.207601,0.0469495 0.19144,0.0285482 0.174191,0.0127579 0.156591,-0.00117176 0.139014,-0.0128733 0.120353,-0.0215925 0.100598,-0.0284433 0.0812225,-0.0345553 0.0618659,-0.0388105 0.0414146,-0.0411974 0.0209632,-0.0435843 0.000156014,-0.0444819 -0.0202915,-0.0464974 -0.0414662,-0.0470198 -0.060788,-0.0479329 -0.0823302,-0.04808 -0.104186,-0.0426531 -0.12642,-0.037965 -0.148644,-0.0321628 -0.17123,-0.0256141 -0.194165,-0.0168334 -0.217452,-0.00619208 -0.241822,0.00743164 -0.264772,0.0147269 -0.287359,0.0212757 -0.310978,0.0356343

P_punctulatus 0.267103,0.169206 0.255896,0.115925 0.240741,0.0908394 0.224097,0.0694733 0.207132,0.0508998 0.189806,0.0354681 0.171782,0.0199562 0.153907,0.00622977 0.135133,-0.00583148 0.116587,-0.0168054 0.0981499,-0.0256446 0.0792834,-0.0338259 0.0599074,-0.0406509 0.0402905,-0.0453814 0.0198151,-0.0487959 -0.000083,-0.0510828 -0.0204096,-0.0527117 -0.0413264,-0.0522863 -0.0618941,-0.0518207 -0.0826223,-0.0499588 -0.104907,-0.046861 -0.126225,-0.0429448 -0.147704,-0.0376322 -0.169343,-0.0309232 -0.192631,-0.0190985 -0.215678,-0.00936816 -0.238657,0.00284584 -0.261757,0.0161071 -0.285205,0.0293282 -0.311186,0.055345

P_strenuus0.264308,0.166814 0.259225,0.102232 0.244125,0.0778952 0.227514,0.0579483 0.210979,0.0423643 0.193281,0.0283873 0.175206,0.015607 0.156756,0.00402348 0.138347,-0.00518032 0.119555,-0.013584 0.100401,-0.0199978 0.0800495,-0.0267876 0.060519,-0.0320046 0.0406124,-0.0360248 0.0203298,-0.0388484 0.000068,-0.0404821 -0.0217809,-0.0420884 -0.041612,-0.0417458 -0.0630366,-0.0417724 -0.0840576,-0.0414093 -0.105858,-0.0402392 -0.127242,-0.0378861 -0.150129,-0.0307461 -0.173024,-0.0240028 -0.19665,-0.0136761 -0.222191,0.000651113 -0.243205,0.00141087 -0.265382,0.00377768 -0.286348,0.0073138 -0.310761,0.0180508

P_sublaevis 0.278087,0.143127 0.26483,0.099977 0.248002,0.0774577 0.229713,0.0598535 0.211528,0.0460908 0.193096,0.0336474 0.173216,0.0231183 0.154293,0.0133136 0.135428,0.00392926 0.116201,-0.00497653 0.0971487,-0.0126212 0.0772555,-0.0201495 0.0573623,-0.0276777 0.037702,-0.0335245 0.0168387,-0.0387763 -0.00355903,-0.0406651 -0.0240731,-0.0433947 -0.0439341,-0.044501 -0.0650562,-0.0454327 -0.0860618,-0.0455236 -0.107313,-0.0442952 -0.128086,-0.0427047 -0.149292,-0.0380551 -0.172484,-0.0322738 -0.194848,-0.0236081 -0.217936,-0.0139853 -0.240242,-0.00489917 -0.261824,0.00322978 -0.285345,0.0159116 -0.310646,0.0374083

P_cordicollis 0.269157,0.158314 0.256971,0.116183 0.242124,0.0893367 0.225122,0.0685849 0.208101,0.0488551 0.191359,0.0325377 0.173237,0.0172174 0.155059,0.00496285 0.136515,-0.0059354 0.117947,-0.0154711 0.0993609,-0.023985 0.0793996,-0.0318423 0.0604171,-0.0372967 0.0400535,-0.0417539 0.0200306,-0.0462049 -0.000054,-0.0472497 -0.0204668,-0.0489819 -0.0419261,-0.0493701 -0.0627165,-0.0490647 -0.0835439,-0.0467156 -0.105412,-0.043363 -0.126598,-0.0399982 -0.149562,-0.0325766 -0.171838,-

0.0254834 -0.195204,-0.0146618 -0.217851,-0.00587155 -0.240827,0.00223124 -0.2628,0.0113744 -0.285416,0.0184615 -0.310639,0.0377679

P_subangulatus 0.272539,0.152616 0.261162,0.106968 0.244915,0.0829957 0.227434,0.0626602 0.21134,0.0449893 0.193274,0.0300368 0.174614,0.0166956 0.156098,0.00588393 0.137033,-0.00373057 0.117742,-0.0112747 0.0980377,-0.0188638 0.0794854,-0.0254897 0.0582686,-0.0307295 0.038663,-0.0353751 0.0189224,-0.0387784 -0.00173647,-0.0414436 -0.0229895,-0.0424976 -0.0433693,-0.0438756 -0.0640193,-0.0427691 -0.0858664,-0.0422118 -0.106606,-0.0402771 -0.127301,-0.0387566 -0.149878,-0.0353457 -0.171941,-0.0289463 -0.194824,-0.0188652 -0.219039,-0.00809097 -0.240922,-0.00334784 -0.264129,0.0058601 -0.286102,0.0114314 -0.310804,0.0305321

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P_ambiguus 0.266376,0.167221 0.256771,0.117483 0.240992,0.0883269 0.225557,0.0646587 0.208749,0.0444207 0.190912,0.0289849 0.173761,0.0159503 0.155238,0.00463073 0.136372,-0.0060028 0.117849,-0.0149212 0.0979542,-0.0224676 0.0790883,-0.0286419 0.0585073,-0.0344732 0.0396413,-0.0389324 0.0190603,-0.0430486 -0.000148641,-0.0447637 -0.0214157,-0.0471648 -0.0413107,-0.0485369 -0.0622347,-0.049566 -0.0831587,-0.0492229 -0.104083,-0.0471648 -0.126036,-0.0447637 -0.147989,-0.0406475 -0.169599,-0.0337872 -0.193267,-0.0234967 -0.215563,-0.010805 -0.240261,0.00325866 -0.263586,0.0162933 -0.286568,0.0289849 -0.311608,0.0481939

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P_viridans -0.114454,0.163463 -0.054565,0.179955 -0.0400121,0.179902 -0.0308629,0.176096 -0.0200967,0.172284 -0.0104085,0.168476 0.000349905,0.162508 0.00679438,0.156016 0.012157,0.148451 0.0180546,0.139805 0.0217943,0.130629 0.02446,0.122534 0.0271217,0.113362 0.0292445,0.104191 0.0313613,0.0934031 0.0334743,0.0815374 0.0355853,0.0691327 0.0366203,0.0572709 0.0376475,0.0432531 0.0386746,0.0292353 0.039155,0.0130635 0.0396314,-0.00418627 0.039563,-0.0230511 0.0389477,-0.0440699 0.0377837,-0.0677818 0.0333896,-0.0904039 0.0300579,-0.117342 0.0234844,-0.146424 0.0136808,-0.174417 0.00280123,-0.201866 -0.0118435,-0.227146 -0.0307846,-0.248099 -0.0502529,-0.265815 -0.0718831,-0.285141 -0.0956575,-0.301225 -0.121014,-0.307601

P_californicus -0.142413,0.169508 -0.0771964,0.186142 -0.0513405,0.187497 -0.0319425,0.185972 -0.0159605,0.181725 -0.00547565,0.175666 -0.000034,0.168834 0.00596777,0.161014 0.0114891,0.152661 0.0160762,0.142734 0.0211702,0.132834 0.0247168,0.12336 0.0287969,0.113407 0.0309288,0.101826 0.0335676,0.0902717 0.0362862,0.0771965 0.0374837,0.0640416 0.0397219,0.0504328 0.0415327,0.0352766 0.0434763,0.0175855 0.0443794,0.000348187 0.0458958,-0.0188904 0.0454639,-0.0397563 0.0451117,-0.062143 0.0422246,-0.0846626 0.0372831,-0.106781 0.0303401,-0.129513 0.0228902,-0.152272 0.0123188,-0.173669 -0.000814145,-0.194692 -0.0149876,-0.215261 -0.0318553,-0.232921 -0.0502439,-0.250661 -0.0695403,-0.270481 -0.0903841,-0.289875 -0.114934,-0.296753

P_cardioderus -0.158729,0.17073 -0.082193,0.190796 -0.0485843,0.194281 -0.0288318,0.19099 -0.0204529,0.185065 -0.0125044,0.17861 -0.00498629,0.171624 0.00172093,0.163099 0.0100179,0.153283 0.0152847,0.144609 0.0202207,0.134444 0.0242463,0.1237 0.0283217,0.112476 0.0320164,0.100241 0.0351813,0.0884373 0.0386448,0.0737526 0.0409988,0.0604086 0.0425418,0.0455248 0.0446645,0.0297304 0.0469863,0.0120156 0.0489275,-0.0067093 0.0485179,-0.0261632 0.0486879,-0.0465275 0.0469375,-0.0670909 0.043896,-0.0892441 0.0389837,-0.112076 0.0325813,-0.134578 0.0231489,-0.155938 0.0122263,-0.176967 -0.000286011,-0.196705 -0.0153483,-0.215251 -0.0315201,-0.232457 -0.0493314,-0.247892 -0.0692623,-0.261605 -0.0902032,-0.274937 -0.11252,-0.279677

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P_mexicanus -0.142482,0.177567 -0.0763451,0.189379 -0.0289185,0.192124 -0.0193681,0.186554 -0.0114288,0.180363 -0.00567109,0.174071 0.000111871,0.167233 0.00542526,0.158734 0.0101932,0.15021 0.0138451,0.14218 0.0175475,0.133059 0.0213005,0.122848 0.0250534,0.112637 0.0271954,0.101804 0.0305041,0.0893858 0.0321007,0.0785279 0.0343691,0.0649682 0.0366881,0.0503176 0.038487,0.0350963 0.0403617,0.0182387 0.0411709,0.000785149 0.0414852,-0.0177845 0.0418501,-0.0374451 0.0406798,-0.0593632 0.037848,-0.0808117 0.0345972,-0.105013 0.0291141,-0.128224 0.0214747,-0.152082 0.0127191,-0.175445 0.000716195,-0.199505 -0.0126051,-0.218707 -0.0286282,-0.23858 -0.0468836,-0.257464 -0.065735,-0.275283 -0.0869956,-0.288294 -0.109777,-0.292083

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P_pacificus -0.128942,0.16594 -0.0626974,0.18497 -0.0382394,0.18528 -0.0262843,0.182295 -0.0168138,0.177397 -0.00921673,0.171848 -0.00161172,0.165672 0.00411985,0.158846 0.00987526,0.150137 0.0143685,0.14204 0.0188776,0.132689 0.0221245,0.123949 0.0253873,0.113955 0.028023,0.103952 0.0306745,0.0926958 0.0327069,0.0808043 0.0360174,0.0670472 0.0386928,0.0539093 0.0395107,0.0388662 0.0422258,0.0225927 0.0430675,0.00566816 0.0433139,-0.0137728 0.0435682,-0.0338409 0.0419412,-0.0539328 0.0397188,-0.0765412 0.0356229,-0.0998005 0.0302888,-0.12433 0.0230891,-0.150138 0.0133809,-0.175977 0.00112445,-0.198713 -0.0136564,-0.220226 -0.0309537,-0.241143 -0.0488781,-0.262069 -0.0699938,-0.278645 -0.0930148,-0.293363 -0.117417,-0.298062

P_atronitens -0.13436,0.174096 -0.0671896,0.18752 -0.0295769,0.188528 -0.0189341,0.183832 -0.00993577,0.178538 -0.00424143,0.172601 0.000944259,0.164991 0.00500887,0.157904 0.00910312,0.149711 0.0126294,0.142056 0.016215,0.132189 0.019203,0.123966 0.0222207,0.114637 0.0252828,0.103649 0.0283449,0.0926602 0.0303304,0.0805358 0.0328839,0.0678732 0.0349435,0.0529832 0.0364204,0.0391847 0.0379714,0.0226205 0.039552,0.00495007 0.0400264,-0.01275 0.0417108,-0.0342923 0.0412123,-0.0570002 0.0396224,-0.0802909 0.0358348,-0.104194 0.0309855,-0.129786 0.0244767,-0.155423 0.0146344,-0.180595 0.00249057,-0.202508 -0.0118806,-0.223927 -0.0296594,-0.242116 -0.0474827,-0.258646 -0.0669506,-0.275774 -0.0893175,-0.287997 -0.112519,-0.289726

P_duplicatus -0.133662,0.171988 -0.0663988,0.186655 -0.0422254,0.18748 -0.0297234,0.183604 -0.0177402,0.179173 -0.0094623,0.173002 -0.00172159,0.166813 0.00444423,0.159494 0.00903518,0.151045 0.0141633,0.142616 0.0176982,0.133593 0.0223259,0.124071 0.0258975,0.113974 0.028413,0.103304 0.0320397,0.0915959 0.0351474,0.0793323 0.0372175,0.0659576 0.0393243,0.0515086 0.0403567,0.0370229 0.0419996,0.0204068 0.0436792,0.00271635 0.04484,-0.0155297 0.0450365,-0.0370355 0.0436214,-0.0585963 0.0417424,-0.0823242 0.0366037,-0.105088 0.0309278,-0.12787 0.0231582,-0.152337 0.0126842,-0.176358 0.000543742,-0.198823 -0.0138189,-0.219212 -0.0308857,-0.239156 -0.049082,-0.257525 -0.0694454,-0.275431 -0.0916587,-0.286407 -0.115075,-0.293661

P_perpolitus -0.142552,0.17726 -0.0757912,0.189451 -0.0455096,0.190202 -0.025274,0.186891 -0.0129114,0.18137 -0.00678318,0.174887 0.000520733,0.167905 0.00561599,0.15964 0.0101056,0.15191 0.0140965,0.143004 0.0187288,0.132994 0.0221854,0.123482 0.0257134,0.11283 0.0287071,0.101573 0.0317364,0.0897457 0.0348371,0.0767783 0.0367978,0.0637396 0.0382241,0.0500952 0.0403276,0.0347764 0.0419323,0.018282 0.0442499,-0.000456773 0.044323,-0.0199083 0.0444319,-0.0399298 0.0430091,-0.0629084 0.0403037,-0.0836783 0.0360309,-0.106835 0.0300124,-0.129529 0.0223197,-0.1529 0.0128812,-0.175808 0.00119835,-0.199429 -0.0135843,-0.219239 -0.0296496,-0.236839 -0.047995,-0.254582 -0.0675517,-0.271257 -0.0890326,-0.284619 -0.111654,-0.288896

P_punctulatus -0.140612,0.183967 -0.0752204,0.191472 -0.0305869,0.191644 -0.0177304,0.186488 -0.0108378,0.180946 -0.00492404,0.173707 0.00153187,0.166503 0.00476991,0.158547 0.0096696,0.150153 0.013485,0.141689 0.0162511,0.132613 0.0201719,0.122523 0.0240927,0.112432 0.0269292,0.102272 0.0299765,0.0888581 0.0329536,0.0765288 0.0348814,0.0635871 0.0364077,0.0484415 0.0377934,0.0354646 0.0382705,0.0197066 0.0399725,0.00185022 0.0412026,-0.0171257 0.0409117,-0.0378335 0.0401489,-0.0596608 0.0377947,-0.0821357 0.0344617,-0.106307 0.0289248,-0.130078 0.0221982,-0.152292 0.0118169,-0.17692 0.000647485,-0.197789 -0.0132679,-0.218291 -0.0289153,-0.237272 -0.045647,-0.256323 -0.0646528,-0.273889 -0.0849539,-0.288272 -0.107916,-0.295205

P_strenuus-0.162066,0.169379 -0.0876348,0.189756 -0.0500062,0.194251 -0.0299906,0.191095 -0.0159193,0.186065 -0.0090075,0.179028 -0.000792513,0.171313 0.00463088,0.162885 0.0100543,0.154457 0.0156976,0.144004 0.0191835,0.134546 0.0240606,0.123599 0.0277225,0.112521 0.0306181,0.100949 0.0336457,0.0881627 0.0371224,0.0750149 0.0403699,0.0602028 0.0432123,0.0453467 0.0454204,0.0287824 0.0472235,0.012174 0.0488414,-0.00650371 0.0485658,-0.0266166 0.0487392,-0.0470905 0.0469752,-0.0685945 0.0440399,-0.0906355 0.0394844,-0.112852 0.0319173,-0.133757 0.0237599,-0.156775 0.0129082,-0.177626 -0.000232718,-0.196266 -0.0151259,-0.213868 -0.0325816,-0.230518 -0.0496761,-0.246718 -0.0687961,-0.263139 -0.0901081,-0.27447 -0.112256,-0.278104

P_sublaevis -0.1342,0.155836 -0.0626384,0.183088 -0.0409194,0.185341 -0.0261346,0.182799 -0.0123453,0.179717 0.00051692,0.174068 0.00531272,0.167134 0.00965351,0.158664 0.0134538,0.151189 0.0157695,0.142651 0.0191148,0.13364 0.020452,0.124055 0.0228018,0.114504 0.0241562,0.104412 0.026051,0.0933253 0.0284691,0.0817491 0.030381,0.0701558 0.0323613,0.0565374 0.0333289,0.0428847 0.035918,0.0262457 0.0390475,0.00861112 0.0407265,-0.0110998 0.0424568,-0.0323297 0.0432428,-0.0556188 0.0425613,-0.080478 0.0408843,-0.105878 0.0357145,-0.132916 0.0284684,-0.158504 0.0181503,-0.183181 0.0052496,-0.206426 -0.0113148,-0.226245 -0.0294492,-0.244598 -0.0497285,-0.259474 -0.0726588,-0.270892 -0.0956061,-0.281804 -0.119248,-0.287164

P_cordicollis -0.136661,0.176566 -0.073866,0.187986 -0.0530857,0.188053 -0.0374449,0.184643 -0.0164617,0.180992 -0.00808569,0.173988 -0.000270053,0.167486 0.00600953,0.159835 0.0123181,0.151652 0.017622,0.142349 0.0218921,0.132456 0.0256309,0.122535 0.0282491,0.113618 0.0310412,0.101513 0.0327126,0.0904128 0.0355337,0.0777766 0.0367607,0.0650534 0.0386061,0.0507651 0.0405094,0.0354141 0.0424417,0.0195318 0.0439297,0.00202652 0.0444709,-0.0176621 0.0445097,-0.0379111 0.0430415,-0.0598411 0.0411289,-0.0833941 0.037062,-0.106532 0.0314879,-0.13135 0.0231413,-0.154188 0.0132875,-0.178708 0.00116347,-0.200686 -0.0137622,-0.220153 -0.0309003,-0.238141 -0.0492459,-0.253531 -0.0690986,-0.270602 -0.090188,-0.284542 -0.11348,-0.287412

P_subangulatus -0.134322,0.176413 -0.0699068,0.188135 -0.0428352,0.188098 -0.0295072,0.184484 -0.0183568,0.179172 -0.00996765,0.173807 -0.00265156,0.166764 0.00467504,0.159169 0.0103554,0.15099 0.0165984,0.142269 0.0200907,0.132944 0.0235935,0.123066 0.0271067,0.112636 0.0295155,0.102185 0.0319452,0.0906294 0.0343855,0.0785215 0.0368468,0.0653091 0.0387663,0.051534 0.0407384,0.0349975 0.0426895,0.0195655 0.0441513,0.000809457 0.0445086,-0.0179676 0.0443136,-0.0367552 0.0419516,-0.0577939 0.0390374,-0.0788432 0.0350816,-0.103227 0.0294481,-0.126538 0.022752,-0.152079 0.0121481,-0.175484 0.000439551,-0.198911 -0.0140513,-0.221285 -0.0297203,-0.239815 -0.0481506,-0.258397 -0.0683007,-0.273697 -0.0901392,-0.287372 -0.113229,-0.293336

P_depressus -0.134322,0.176413 -0.0699068,0.188135 -0.0428352,0.188098 -0.0295072,0.184484 -0.0183568,0.179172 -0.00996765,0.173807 -0.00265156,0.166764 0.00467504,0.159169 0.0103554,0.15099 0.0165984,0.142269 0.0200907,0.132944 0.0235935,0.123066 0.0271067,0.112636 0.0295155,0.102185 0.0319452,0.0906294 0.0343855,0.0785215 0.0368468,0.0653091 0.0387663,0.051534 0.0407384,0.0349975 0.0426895,0.0195655 0.0441513,0.000809457 0.0445086,-0.0179676 0.0443136,-0.0367552 0.0419516,-0.0577939 0.0390374,-0.0788432 0.0350816,-0.103227 0.0294481,-0.126538 0.022752,-0.152079 0.0121481,-0.175484 0.000439551,-0.198911 -0.0140513,-0.221285 -0.0297203,-0.239815 -0.0481506,-0.258397 -0.0683007,-0.273697 -0.0901392,-0.287372 -0.113229,-0.293336

P_marginatus -0.140614,0.163575 -0.0706537,0.183689 -0.0373992,0.187004 -0.0231987,0.184352 -0.0111689,0.179682 -0.000951348,0.173395 0.00551889,0.166146 0.0104943,0.158437 0.0151318,0.149949 0.0190321,0.141041 0.0218164,0.131693 0.0234642,0.122284 0.0258697,0.112916 0.0279781,0.102012 0.0300866,0.0911077 0.0310791,0.0797635 0.0325322,0.0669245 0.0340057,0.0537066 0.0355406,0.0393523 0.0371778,0.0231039 0.0388355,0.00647663 0.0394589,-0.0121061 0.0393861,-0.0318662 0.0393746,-0.0527627 0.0375713,-0.0756557 0.0347133,-0.100125 0.0299613,-0.124697 0.0225779,-0.149791 0.0136384,-0.174209 0.00208798,-0.199528 -0.0122778,-0.221959 -0.029459,-0.241503 -0.0477766,-0.261109 -0.0685922,-0.27667 -0.0905442,-0.292293 -0.114697,-0.302335

P_elongatus -0.132233,0.171616 -0.0737916,0.184288 -0.032532,0.187986 -0.0184722,0.18441 -0.00981738,0.178183 -0.0046484,0.171855 0.0010331,0.165044 0.00571865,0.158203 0.0109458,0.149883 0.0146936,0.141021 0.0184269,0.132657 0.0211933,0.123268 0.0244722,0.113396 0.0272823,0.102513 0.0296089,0.091118 0.0324481,0.0792393 0.0338078,0.0668189 0.0362072,0.0529337 0.0381523,0.03754 0.0390723,0.0231132 0.0405922,0.00521501 0.0406181,-0.0127268 0.0407168,-0.0331585 0.0408591,-0.0550841 0.0385115,-0.0770825 0.0336886,-0.0996517 0.028924,-0.124213 0.0216694,-0.148847 0.01295,-0.17452 0.0011699,-0.197791 -0.0131437,-0.219641 -0.0294347,-0.242046 -0.0473069,-0.261508 -0.0682543,-0.278069 -0.0896997,-0.294645 -0.113428,-0.301319

P_metallicus -0.142403,0.174175 -0.0775246,0.187986 -0.0318438,0.191129 -0.0222188,0.186972 -0.0164262,0.180459 -0.00786287,0.174593 -0.000936868,0.167557 0.00489159,0.159928 0.00964045,0.151148 0.0138136,0.142908 0.0174649,0.133534 0.0211342,0.123602 0.0248214,0.113112 0.0279508,0.102605 0.0300007,0.0909464 0.0320684,0.07873 0.0341362,0.0665136 0.0368514,0.0515264 0.0384331,0.037061 0.0418316,0.0181876 0.0429274,0.0014734 0.0435551,-0.0180474 0.0448122,-0.0397813 0.0438385,-0.0615869 0.0412273,-0.0845618 0.0381123,-0.109228 0.0327304,-0.13285 0.0251355,-0.157102 0.014716,-0.180328

0.0025875,-0.202492 -0.0129951,-0.221418 -0.0303047,-0.238724 -0.0487835,-0.254392 -0.0690432,-0.266768 -0.089771,-0.281951 -0.112567,-0.284917

P_aurocinctus -0.132002,0.182309 -0.07532,0.188895 -0.053713,0.18927 -0.0393006,0.185125 -0.0248882,0.180981 -0.0162009,0.175015 -0.00643876,0.168567 0.000735051,0.160956 0.00740439,0.152796 0.0135692,0.144088 0.0187032,0.134809 0.0228061,0.124961 0.0264266,0.114037 0.0305955,0.102608 0.0337335,0.0906096 0.036345,0.0785889 0.0406239,0.0645282 0.0428628,0.0488002 0.0456283,0.0330943 0.0474067,0.0157649 0.0492731,-0.0036703 0.050635,-0.023654 0.0504615,-0.0447565 0.0487525,-0.0669779 0.0454862,-0.0897918 0.0411669,-0.11265 0.0331624,-0.135661 0.0245874,-0.157642 0.0133582,-0.179206 -0.000021,-0.199806 -0.0150674,-0.218365 -0.032856,-0.234402 -0.0517856,-0.248377 -0.0701227,-0.263909 -0.0917286,-0.276941 -0.114279,-0.279993

P_ambiguus -0.128884,0.168436 -0.0635189,0.184232 -0.0395518,0.185321 -0.0270235,0.181508 -0.0188529,0.177696 -0.0101376,0.172248 -0.0025117,0.165712 0.00348007,0.158086 0.00947185,0.15046 0.0154636,0.142834 0.0187319,0.133574 0.0236342,0.12377 0.0263578,0.113965 0.029626,0.103615 0.0312601,0.0927212 0.033439,0.080193 0.0356178,0.0676647 0.0367072,0.0551365 0.0394307,0.0404294 0.0399754,0.0235434 0.0410649,0.00774694 0.0432437,-0.0124072 0.042699,-0.0331061 0.042699,-0.0543497 0.0405201,-0.0788615 0.0372519,-0.104463 0.0323495,-0.128975 0.0247236,-0.15512 0.0143742,-0.179632 0.00239066,-0.20251 -0.0134058,-0.222664 -0.0302918,-0.242274 -0.0499012,-0.259159 -0.0706001,-0.274956 -0.0929331,-0.28694 -0.1169,-0.293476

P_velutinus -0.130175,0.171611 -0.0614535,0.186139 -0.0380954,0.185715 -0.0267452,0.182108 -0.0168853,0.177351 -0.0088924,0.171437 -0.00127605,0.165518 0.0056137,0.157706 0.0106259,0.14949 0.0156381,0.141275 0.0195312,0.13229 0.0222892,0.123666 0.0254451,0.113541 0.0289935,0.102292 0.0310249,0.091774 0.0327011,0.079745 0.0351356,0.0673499 0.0364511,0.0541859 0.0389175,0.0395314 0.0398989,0.0233494 0.041644,0.00642494 0.0426731,-0.0131462 0.042965,-0.0338576 0.0413793,-0.0549722 0.0394383,-0.0775983 0.0352379,-0.100256 0.0303268,-0.125937 0.023135,-0.150144 0.012936,-0.17477 0.000466927,-0.198674 -0.0135403,-0.220341 -0.0305972,-0.239413 -0.0491711,-0.257754 -0.0696331,-0.275745 -0.0912035,-0.295258 -0.1148,-0.30463

P_laevisulcatus -0.122416,0.164068 -0.0537383,0.183621 -0.0406975,0.182426 -0.0325639,0.17964 -0.0238954,0.175762 -0.0136092,0.170239 -0.00494975,0.165274 0.00369177,0.158133 0.00961009,0.150472 0.0138927,0.14228 0.0170878,0.134097 0.0208222,0.125365 0.0250869,0.114998 0.0288033,0.104092 0.0314322,0.0931949 0.0351397,0.0812011 0.0377552,0.0686727 0.0387305,0.0550702 0.042411,0.039814 0.0444513,0.0234838 0.0448559,0.00662336 0.0452426,-0.0124121 0.0456203,-0.032535 0.0443533,-0.0542756 0.0419988,-0.0760073 0.0374514,-0.099896 0.0312728,-0.123771 0.0239843,-0.150356 0.013995,-0.174744 0.00128698,-0.199109 -0.0141173,-0.220733 -0.0322358,-0.241791 -0.0514283,-0.261208 -0.0727643,-0.276802 -0.095745,-0.294013 -0.120815,-0.300875

P_quadricollis -0.125633,0.174126 -0.0628909,0.18897 -0.0389259,0.189706 -0.0240649,0.186472 -0.0114375,0.180863 -0.00202199,0.174694 0.00327405,0.167476 0.00810923,0.160244 0.012526,0.151615 0.0155602,0.142943 0.0190836,0.133364 0.0221602,0.12331 0.0243151,0.113227 0.0269451,0.102698 0.0291566,0.0907724 0.0318432,0.0783998 0.0326863,0.0659706 0.0340469,0.0517121 0.0354359,0.0365318 0.0364064,0.0199548 0.0378378,0.00339196 0.0374824,-0.015071 0.0376586,-0.0358241 0.0364522,-0.0566197 0.0343807,-0.0792871 0.0304799,-0.102472 0.0256857,-0.126607 0.0190763,-0.15172 0.0110844,-0.176876 -0.000190269,-0.200287 -0.0128617,-0.22328 -0.0279507,-0.242657 -0.0449681,-0.259325 -0.0628789,-0.276944 -0.083179,-0.291868 -0.104684,-0.297603

P_smithi -0.126657,0.177806 -0.0696864,0.187201 -0.0327756,0.187435 -0.0231981,0.183955 -0.0149786,0.178538 -0.00814729,0.17213 -0.00178884,0.165707 0.0036542,0.158308 0.0081667,0.150406 0.013152,0.142519 0.0167642,0.133168 0.0218252,0.122917 0.0259404,0.112636 0.0300708,0.101882 0.0318522,0.0905796 0.0331457,0.0797348 0.0344996,0.0669987 0.0358686,0.0537898 0.0377861,0.0382318 0.038773,0.0221708 0.0412238,0.00473668 0.0418589,-0.0151221 0.0420514,-0.0359416 0.0412982,-0.0567914 0.039187,-0.0795778 0.0342389,-0.102455 0.0293815,-0.128169 0.0215813,-0.150664 0.0119805,-0.176057 0.000427871,-0.199618 -0.0135645,-0.220892 -0.0294935,-0.240807 -0.0483502,-0.257976 -0.0667038,-0.276075 -0.0879095,-0.293792 -0.111475,-0.296913

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