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"Nada tiene sentido en Biología
si no es a la luz de la evolución"
Theodosius Dobzhansky

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I. RESUMEN

Los roedores constituyen uno de los grupos con mayor riqueza de especies dentro de los mamíferos. No obstante, se considera que esta riqueza esta subestimada debido, entre otras razones, a la existencia de especiación críptica. El género *Reithrodontomys* (Familia Cricetidae, Subfamilia Neotominae) comprende 24 especies, pero diferentes estudios han reportado una alta diversidad genética intraespecífica. Varias de las especies que se han sugerido como complejos crípticos conforman al subgénero *Aporodon*, el cual comprende a los grupos de especies *R. mexicanus* y *R. tenuirostris*. Aunque varios cambios taxonómicos han sido propuestos en este subgénero, estos se han basado principalmente en la información molecular, y no se ha tenido en cuenta otros aspectos importantes para la delimitación de especies, como son la morfología y el nicho ambiental. En esta tesis, se analizaron las relaciones evolutivas entre las especies de *Aporodon*, con énfasis en *R. mexicanus* y *R. microdon*, dos de las especies más cuestionadas taxonómicamente. Para ello, se utilizó un enfoque de taxonomía integradora, donde a partir de métodos moleculares de delimitación se generaron hipótesis de especies que fueron puestas a prueba con datos morfométricos y/o ecológicos. Dentro del grupo *R. mexicanus*, *R. mexicanus* (*sensu stricto*) no pudo recuperarse como monofilética, y el consenso de los métodos de delimitación sugirió cuatro linajes divergentes al nivel de especie, los cuales fueron generalmente soportados por los análisis de morfometría geométrica del cráneo y las comparaciones del espacio ambiental que ocuparon. Para el grupo de especies *R. tenuirostris*, se recuperaron cuatro haplogrupos dentro de *R. microdon*, los cuales se caracterizaron por su distribución alopátrica sin posibles rutas de conectividad espacial, que favoreció la alta diferenciación genética encontrada entre ellos. Además, los análisis morfométricos y ecológicos corroboraron a *R. cherrii* como una especie distinta de *R. mexicanus*. La alta diversidad críptica reportada sugiere incrementar el número total de especies conocidas para *Reithrodontomys*, incluyendo dos especies nuevas para la ciencia. Sin embargo, los rearreglos taxonómicos propuestos también incluyeron reconocer a *R. bakeri* al nivel subespecífico, así como evaluar el posible estatus conespecífico de las poblaciones de *R. spectabilis* con relación a las de *R. gracilis* de México. Estos resultados resaltan la importancia en estudios de sistemática del uso de múltiples fuentes de datos para establecer delimitaciones robustas entre especies consideradas complejas taxonómicamente, sobre todo cuando existen evidencias de procesos de especiación críptica.

II. ABSTRACT

Rodents are one of the groups with the greatest species richness among mammals. However, it is considered that this richness is underestimated because of the existence of cryptic speciation. The genus *Reithrodontomys* (Family Cricetidae, Subfamily Neotominae), comprises 24 species, but different research has reported a high intraspecific genetic diversity. Several species that have been suggested as cryptic complexes belong to the subgenus *Aporodon*, which includes the species groups *R. mexicanus* and *R. tenuirostris*. Although taxonomic changes have been proposed in this subgenus, these have been based mainly on molecular data, and other important aspects for species delimitation, such as morphology and environmental niche, have not been considered so far. In this dissertation, the evolutionary relationships between *Aporodon* species were analyzed, with emphasis on *R. mexicanus* and *R. microdon*, two of the most taxonomically questioned species. For this purpose, an integrative taxonomy approach was implemented using molecular delimitation methods to generate species hypotheses and then test them with morphometric and/or ecological data. Within the *R. mexicanus* group, *R. mexicanus* (sensu stricto) could not be recovered as monophyletic, and consensus delimitation methods suggested four divergent lineages at the species-level, which were generally supported by differences in skull shape and the ecological niche they occupy. For the *R. tenuirostris* group, four haplogroups were recovered within *R. microdon*, which were characterized by their allopatric distribution without possible spatial connectivity routes, which favored the high genetic differentiation between them. Furthermore, morphometric and ecological analyzes confirmed *R. cherrii* as a distinct species from *R. mexicanus*. The high cryptic diversity reported in this dissertation suggests increasing the total number of known species in *Reithrodontomys*, including two new undescribed species. However, the proposed taxonomic rearrangements also included recognizing *R. bakeri* at the subspecific-level, as well as evaluating the possible conspecific status of *R. spectabilis* populations relative to those of *R. gracilis* from Mexico. These results highlight the importance in systematic studies of the use of multiple data sources to establish robust delimitations between species considered taxonomically complex, especially when there is evidence of cryptic speciation processes.

III. INTRODUCCIÓN GENERAL

La categoría de especie es considerada como la unidad básica de la clasificación biológica linneana (Ghiselin, 2001). Las características morfológicas de los organismos fueron de los primeros elementos empleados para identificar estas unidades y realizar agrupaciones. En consecuencia, muchas especies han sido descritas a partir de su morfología, basándose, de manera implícita, en el concepto morfológico o tipológico de especie. Este concepto ha sido ampliamente utilizado en la taxonomía (Mayden, 1997), probablemente por la fácil utilización de cualquier tipo de carácter morfológico para descartar o asignar individuos a una entidad en particular (Cerritos, 2007). No obstante, esta estrategia presenta ciertas limitaciones ya que tiende a subestimar la variación morfológica intraespecífica o incluso puede generar confusión en especies con un marcado dimorfismo sexual (Mori *et al*., 2017). Otra limitación importante de este concepto es en la identificación de especies crípticas, las cuales se refieren a dos o más especies sin características morfológicas distintivas, al menos a simple vista, pero que son genéticamente diferentes (Bickford *et al*., 2007).

La incorporación de los datos moleculares en los estudios de sistemática ha permitido delimitar especies crípticas que anteriormente se consideraban una sola entidad, por lo que, el uso de este tipo de datos se ha convertido en una herramienta útil para esclarecer problemas taxonómicos (Granjon y Montgelard, 2012). Cada vez son más los trabajos que reportan la descripción de nuevas especies con base en diferencias genéticas, empleando generalmente el concepto filogenético de especie (Cracraft, 1989; de Queiroz y Donoghue, 1990). Bajo este concepto, una especie es aquella que pertenece a un grupo monofilético irreducible de organismos que es diagnósticamente distinto de otros grupos similares, y dentro de los cuales existe un patrón parental de ancestría y descendencia (Cracraft, 1989). Por lo tanto, se asume que entre los grupos monofiléticos que representan especies distintas, existe un flujo de genes nulo o casi nulo debido a procesos de especiación (Cerritos, 2007). No obstante, continúa siendo un reto determinar qué concepto de especies resulta más acorde para proponer y delimitar nuevas entidades, ya que no existe una definición única en la que se incluyan todos los conceptos elaborados (Padial *et al*., 2010).

Esta incompatibilidad entre los distintos conceptos de especies se debe en gran medida a la naturaleza de la información que se empleó para conceptualizarlos (de Queiroz, 2007). Por ejemplo, investigadores enfocados en el estudio de aislamiento reproductivo

entre poblaciones, tenderán a usar el concepto biológico de especie (Mayr, 1942), mientras que aquellos que estudien las diferencias entre nichos, usarán de preferencia el concepto ecológico de especie (Van Valen, 1976). Para intentar conciliar el aspecto teórico y el práctico, de Queiroz (1998, 2005, 2007) propuso un concepto unificado de especie (Concepto del Linaje General de especie; de Queiroz, 1998), que emplea distintas "propiedades de las especies", teniendo en cuenta elementos de los conceptos más aceptados. Esta propuesta pone en práctica el uso de múltiples líneas de evidencias para establecer límites entre especies. De manera que, cualquier criterio o propiedad que refleje poblaciones que se están comportando como linajes independientes, va a ser relevante para establecer límites al nivel específico (de Queiroz, 2007). Esta tendencia a emplear diferentes fuentes de información para delimitar entidades taxonómicas se conoce como taxonomía integradora (Dayrat, 2005), y ha sido ampliamente recomendada en estudios de sistemática (Padial *et al*., 2010; Sangster, 2018).

Desde hace algunos años, en mamíferos se han reportado un gran número de linajes crípticos, por lo que se cree que el número total de especies está subestimado (Burgin *et al*., 2018). Para establecer los límites entre especies de este grupo, se ha seguido el concepto genético de especie redefinido por Bradley y Baker (2001) y Baker y Bradley (2006). Estos autores, utilizando la información del gen mitocondrial Citocromo b (Cytb), asociaron valores de divergencia genética superiores al 5% con taxones reconocidos al nivel de especies (Bradley y Baker, 2001). Este gen presenta una tasa de evolución alta en mamíferos, en comparación con otros genes (nucleares o ribosomales), con un ritmo de sustitución que oscila de 3 a 5 % por millón de años (Saccone, 1999). Si se asume que la tasa de evolución del Cytb es similar entre taxones de mamíferos con tiempos de divergencia parecidos, entonces este marcador molecular muestra una adecuada variación que permite estimar las relaciones filogenéticas entre las especies o subespecies (Van Den Bussche y Baker, 1993).

A pesar del uso extendido del Cytb en estudios en mamíferos, utilizar información de un solo gen mitocondrial para establecer límites entre taxones ha sido motivo de crítica (Rubinoff y Holland, 2005; Will *et al*., 2005). Por lo tanto, se recomienda el empleo de genes nucleares, así como de otras fuentes de evidencia para lograr este fin (Will *et al*., 2005; Alström *et al*., 2021). En particular, la incorporación de datos morfológicos y ecológicos a los estudios moleculares ha sido de gran importancia para delimitar especies correctamente, mostrando un enfoque de taxonomía integradora. En ese sentido, la morfometría geométrica (MG) ha demostrado ser una herramienta robusta para discriminar

entre especies muy parecidas morfológicamente (Cordeiro-Estrela *et al*., 2008; Wallace, 2019). Al eliminarse toda variación no asociada a la forma (métodos de superposición), este tipo de análisis favorece una mejor interpretación biológica de los resultados estadísticos, en comparación con las medidas lineales que se emplean en la morfometría tradicional (Zelditch *et al*., 2004). Por su parte, los modelos del nicho ecológico (MNE) también resultan una herramienta eficiente para sugerir límites entre especies, en combinación con las evidencias genéticas (Wiens y Graham, 2005; Rissler y Apodaca, 2007). La información que aportan sobre el rango geográfico de las especies y sus características ambientales permite hacer inferencias sobre cuestiones evolutivas tanto de distribuciones históricas como de procesos de especiación (Hugall *et al*., 2002; Graham *et al*., 2004).

Dentro de los mamíferos, en particular en roedores, numerosos grupos se han considerado complejos taxonómicamente, ya sea porque no han sido lo suficientemente estudiados o porque morfológicamente son muy parecidos (ver D'Elía *et al*., 2019). Muchos de los problemas taxonómicos son el reflejo de una rápida evolución (radiación adaptativa), asociada a procesos de convergencia evolutiva (Triant y DeWoody, 2006). Diversos estudios se han enfocado en esclarecer cuestionamientos taxonómicos asociados a procesos de especiación críptica en este grupo (p. ej.: Engelbrecht *et al*., 2011; Almendra *et al*., 2014; Rivera *et al*., 2018; entre otros). Varios de ellos han empleado los datos morfológicos y ecológicos (en particular la MG y los MNE) para complementar y poner a prueba las hipótesis filogenéticas propuestas acerca de la diversidad encontrada (p. ej.: Martínez-Gordillo *et al*., 2010; Pavan y Marroig, 2016; Almendra *et al*., 2018). No obstante, en muchas especies de roedores con alta diferenciación genética, este tipo de datos no han sido usados para buscar posibles diferencias a partir de una estrategia de múltiples líneas de evidencia, es decir, desde un enfoque de taxonomía integradora, tal como es el caso del género *Reithrodontomys* (Sullivan *et al*., 2000; Arellano *et al*., 2003; 2005; Miller y Engstrom, 2008; Hardy *et al*., 2013; Statham *et al*., 2016).

Reithrodontomys (Familia Cricetidae, Subfamilia Neotominae) presenta una distribución geográfica que abarca desde Canadá en Norteamérica hasta Colombia y Ecuador en Suramérica (Hall, 1981; Arellano, 2015). Este género se compone de 24 especies (Bradley, 2017), agrupadas en los subgéneros *Reithrodontomys* y *Aporodon* (Howell, 1914). Se distinguen de otros cricétidos, por la presencia de un surco longitudinal en el centro de los dientes incisivos superiores (Le Conte, 1853), un tamaño corporal relativamente pequeño y una cola que, en muchas de sus especies, es más larga que el cuerpo. Hooper (1952), considerando atributos morfológicos y de distribución geográfica,

propuso cuatro grupos de especies dentro del género: *R. fulvescens*, *R. megalotis*, *R. mexicanus* y *R. tenuirostris* (Tabla I). Los dos primeros correspondientes al subgénero *Reithrodontomys* y los últimos al subgénero *Aporodon*. En el caso de *Aporodon*, se ha sugerido la existencia de cuatro linajes (Arellano *et al*., 2005), de los cuales dos se corresponden con los grupos propuestos por Hooper (1952) y los otros dos con la propuesta de una especie nueva y la especie *R. creper*, respectivamente (Arellano *et al*., 2005).

Tabla I. Subgéneros y grupos de especies del género *Reithrodontomys* (Cricetidae). Asterisco (*) denota las especies descritas posterior a Hooper (1952); la pertenencia a un grupo de especies fue determinada con base en su parentesco.

Subgénero	Grupos de especies	Especies	
Reithrodontomys	*R. fulvescens*	*R. fulvescens*	*R. hirsutus*
	R. megalotis	*R. humulis*	*R. raviventris*
		R. burti	*R. sumichrasti*
		R. montanus	*R. chrysopsis*
		R. megalotis	*R. zacatecae***
Aporodon	*R. tenuirostris*	*R. microdon*	*R. cherrii***
		R. tenuirostris	*R. bakeri***
		R. rodriguezi	*R. musseri**
		R. creper	
	R. mexicanus	*R. brevirostris*	*R. spectabilis***
		R. darienensis	*R. garichensis***
		R. gracilis	*R. mexicanus*
		R. paradoxus	

En *Reithrodontomys*, seis de sus especies se han considerado complejos de especies crípticas (Sullivan *et al*., 2000; Arellano *et al*., 2005; Miller y Engstrom, 2008; Hardy *et al*., 2013). En este contexto, diferentes autores (p. ej.: Miller y Engstrom, 2008; Gardner y Carleton, 2009) han sugerido la necesidad de estudios adicionales enfocados en esclarecer las relaciones evolutivas intra e interespecíficas en *Reithrodontomys*. Particularmente, en el subgénero *Aporodon* resalta la diversidad críptica de dos de sus especies: *R. mexicanus* (Saussure, 1860) y *R. microdon* Merriam, 1901. La primera, constituye una de las especies con mayor distribución geográfica, desde México hasta el noroeste de Suramérica. En esta amplia distribución, sus poblaciones ocupan diferentes tipos de hábitat como bosques húmedos de pino-encino, bosques mesófilos de montaña y selva baja caducifolia (Hooper, 1952; Hall, 1981). Recientes cambios en su taxonomía (resumidos en Bradley, 2017) han reconocido a varias de sus subespecies al nivel específico, al reportarse linajes divergentes a partir del estudio de genes de diferentes loci

(Arellano *et al*., 2005; Miller y Engstrom, 2008). Por su parte, *R. microdon* se distribuye desde la región central y sur de México hasta el norte de Guatemala, principalmente en bosques mesófilos de montaña y bosques de pino-encino (Hooper, 1952; Hall, 1981). Sus tres subespecies presentan una marcada distribución alopátrica y se ha sugerido, al menos para *R. m. albilabris*, que debe ser reconocida al nivel de especie (Arellano *et al*., 2005).

El uso de diferentes líneas de evidencia podría ser muy útil para el esclarecimiento de las relaciones evolutivas entre y dentro de las especies que conforman el subgénero *Aporodon*. En este sentido, en la presente tesis se utiliza un enfoque de taxonomía integradora para establecer los límites entre estas especies, priorizando aquellas que han sido cuestionadas taxonómicamente, como son *R. mexicanus* y *R. microdon*. Considerando los aspectos mencionados, se plantea la hipótesis de que el subgénero *Aporodon* está compuesto por al menos dos complejos de especies crípticas, en correspondencia con la presencia de linajes divergentes a nivel intraespecífico. Para poner a prueba esta hipótesis, el objetivo principal de este trabajo es evaluar la diversidad críptica contenida en este subgénero a partir de análisis filogenéticos que serán complementados con análisis morfométricos y ecológicos. Esto nos permitirá reevaluar la taxonomía vigente en el subgénero *Aporodon*, al detectar posibles procesos de especiación que deriven en el reconocimiento de nuevas entidades taxonómicas.

La presente tesis se compone de una Introducción General, cuatro capítulos y una Discusión General con sus conclusiones. En los cuatro capítulos, mediante el uso de datos de diferente naturaleza, se analiza la alta diversidad críptica existente en el subgénero *Aporodon* y en particular en los complejos de especies *R. mexicanus* y *R. microdon*. El primer capítulo se corresponde con una publicación en la revista *Mammalian Species* donde se realiza una exhausta revisión de la especie *R*. *mexicanus*, incluyendo aspectos de su taxonomía, distribución geográfica, ecología, genética, entre otros. El segundo capítulo constituye un artículo publicado en la revista *Therya*, en el cual, partiendo de la propuesta de que *R. cherrii* es una especie diferente de *R. mexicanus* (Arellano *et al*., 2005), se comparan ambos taxones utilizando datos morfológicos y ecológicos. El tercer capítulo es un manuscrito en preparación enfocado en delimitar las posibles entidades que componen al complejo de especies crípticas *R. mexicanus*, bajo un enfoque de taxonomía integradora. Los resultados de los análisis moleculares de este manuscrito también permiten comentar sobre aspectos de la taxonomía del grupo de especies *R. mexicanus*. Finalmente, el cuarto capítulo es un artículo publicado en la revista *Journal of Mammalogy*, en el cual se analizan

las relaciones evolutivas entre los representantes del grupo de especies *R. tenuirostris*, con especial énfasis en el complejo de especies *R. microdon*.

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CAPÍTULO I

Reithrodontomys mexicanus (Rodentia: Cricetidae)

MAMMALIAN SPECIES 52(996):114–124

Reithrodontomys mexicanus (Rodentia: Cricetidae)

DAILY MARTÍNEZ-BORREGO, ELIZABETH ARELLANO, FRANCISCO X. GONZÁLEZ-CÓZATL, AND DUKE S. ROGERS

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Abstract: *Reithrodontomys mexicanus* (Saussure, 1860) is a cricetid rodent commonly called the Mexican harvest mouse and is one of 24 recognized species in the genus. It has grooved upper incisors distinctive of *Reithrodontomys*, and a medium to relatively large size, with tail longer than head and body; dorsal pelage varies from brown to cinnamon orange. It is distributed from Mexico to Nicaragua and in the northwestern region of South America. It occupies different habitats including humid pine-oak forests, cloud forests, and deciduous forests at elevations from about 1,000 to 3,800 m. *R. mexicanus* is listed as "Least Concern" by the International Union for Conservation of Nature and Natural Resources, although information about population size throughout its distribution range is unknown.

Key words: cricetid rodent, Mexican harvest mouse, Neotominae, species complex

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Reithrodontomys mexicanus (Saussure, 1860)

Mexican Harvest Mouse

Mus tazamaca Gray, 1843:79. Type locality "Coban, Guatemala." Nomen nudum (see Alston 1876:756).

R [*eithrodon*]. *mexicanus* de Saussure, 1860:109. Type locality "Habite les montagnes de la province de Véra-Cruz [Mexico]," restricted to "Mirador, Veracruz", Mexico by Hooper (1952:140).

Reithrodon mexicana: Tomes, 1861:284. Incorrect subsequent spelling of *Reithrodon mexicanus* de Saussure, 1860.

Ochetodon mexicanus: Coues, 1874:186. Name combination (see "Nomenclatural Notes").

Hesperomys (*Vesperimus*) *cherrii* Allen, 1891:211. Type locality "San José," Costa Rica.

Sitomys cherriei Allen, 1893:238. Name combination. Unjustified emendation of the specific name *cherrii* Allen, 1891.

Fig. 1.—An adult of *Reithrodontomys mexicanus* from Palenque, Chiapas, Mexico. Used with permission of the photographer Oscar Miguel Pérez Macías (CONABIO).

Reithrodontomys mexicanus: Allen, 1895:135. First use of current name combination. Not *Reithrodontomys mexicanus fulvescens* Allen 1894:319.

Reithrodontomys costaricensis Allen, 1895:139. Type locality "La Carpintera (alt. 6000 ft.), Costa Rica."

Reithrodontomys Söderströmi Thomas, 1898:451. Type locality "Quito," Province Pichincha, Ecuador.

Reithrodontomys costaricensis jalapae Merriam, 1901:552. Type locality "[J]alapa, Vera Cruz, Mexico (altitude 4,000 ft.)."

Reithrodontomys goldmani Merriam, 1901:552. Type locality "Metlaltoyuca, Puebla [Mexico] (altitude 800 ft.)."

Reithrodontomys cherriei Osgood, 1907:50. Type locality "San José," Costa Rica. Incorrect subsequent spelling of the specific name *cherrii* Allen, 1891.

Reithrodontomys soderstromi Trouessart, 1910:22. Incorrect subsequent spelling of *R. söderströmi* Thomas, 1898.

Reithrodontomys milleri Allen, 1912:77. Type locality "Munchique (alt. 8325 ft.), Cauca, Colombia."

Reithrodontomys cherriei cherriei: Miller, 1912:129. Incorrect subsequent spelling of the specific name *cherrii* Allen, 1891.

Reithrodontomys cherriei jalapae Miller, 1912:130. Type locality "Jalapa, State of Vera Cruz, Mexico. Altitude, 4,000 feet." Incorrect subsequent spelling of the specific name *cherrii* Allen, 1891.

Reithrodontomys mexicanus goldmani: Howell, 1914:72. Name combination.

Reithrodontomys mexicanus minusculus Howell, 1932:125. Type locality "Comayabuela (just south of Tegucigalpa), Honduras;" corrected to Honduras, Dept. Francisco Morazán, Comayaguela by Hooper (1952:150).

Reithrodontomys mexicanus soederstroemi Arellano, 2015: 63. Justified emendation of spelling of the specific name *Söderströmi* Thomas, 1898 [article 33.2.2 and 32.5.2.1 of the International Code of Zoological Nomenclature (ICZN 1999)].

Context and Content. Order Rodentia, suborder Myomorpha, family Cricetidae, subfamily Neotominae, tribe Reithrodontomyini, genus *Reithrodontomys*, subgenus *Aporodon* (Musser and Carleton 2005). There are 24 species of *Reithrodontomys* (Bradley 2017), grouped into two subgenera (Howell 1914; Hooper 1952). Hooper (1952) also proposed four species groups, two for the subgenus *Reithrodontomys* (*fulvescens* and *megalotis*), and two for the subgenus *Aporodon* (*mexicanus* and *tenuirostris*). *R. mexicanus* was formerly considered a polytypic species with 13 subspecies by Hooper (1952, 1955), but in recent years its taxonomic status has been reviewed and changes have been proposed. *R. cherrii* was proposed as a distinct species by Arellano et al. (2005), and later recognized as such by Gardner and Carleton (2009). Gardner and Carleton (2009) also regarded *R. m. garichensis* as a species, based mainly on craniodental characteristics. In addition, they considered populations of *R. m. potrerograndei* as a synonym of *R. brevirostris*. Here we follow Bradley (2017), who recognizes 10 subspecies:

R. m. eremicus Hershkovitz, 1941:4. Type locality "Near Pimanpiro, Imbabura Province [Valle de la Chota], Ecuador."

R. m. howelli Goodwin, 1932:560. Type locality "Chichicastenango (Santo Tomas) District of El Quiché, Guatemala."

R. m. lucifrons Howell, 1932:125. Type locality "Cerro Cantoral, Honduras." See above; *minusculus* Howell is a synonym.

R. m. mexicanus (de Saussure, 1860:109). See above; *jalapae* (Merriam), *goldmani* (Merriam) are synonyms.

R. m. milleri Allen, 1912:77. See above.

R. m. ocotepequensis Goodwin, 1937:1. Type locality "Monte Verde, Department of Ocotepeque, Honduras, 30 miles northeast of the city Ocotepeque."

R. m. orinus Hooper, 1949:169. Type locality "El Salvador, Dept. Sonsonate, about 12 miles southeast of Sonsonate, near summit of Balsam Range, Hacienda Chilata."

R. m. riparius Hooper, 1955:12. Type locality "México, Michoacán, 2 ½ mi. SW Coalcomán."

R. m. scansor Hooper, 1950:418. Type locality "México, Chiapas, Villa Flores."

R. m. soederstroemi Thomas, 1898:451. See above.

Nomenclatural Notes. *Reithrodontomys mexicanus* was originally classified in the genus *Reithrodon*, which grouped rodents from South America and North America. Coues (1874) recognized the North American species as a different group and included them in the genus *Ochetodon*. However, this name was abandoned because Giglioli (1873, not seen, cited in Merriam 1892) proposed the genus *Reithrodontomys*, including all species of *Ochetodon*. The type specimen of *R. mexicanus* is deposited in the Natural History Museum of Geneva, number 510/100.

The generic name *Reithrodontomys* derives from the Greek *rheithron* (stream or channel), *odous* (tooth), and *mys* (mouse). The specific epithet *mexicanus* comes from Latin, meaning "from or belonging to Mexico," referring to the country where the type specimen was collected. One of the Spanish common names is ratón cosechador mexicano (Tirira 2004).

DIAGNOSIS

Reithrodontomys mexicanus and all other species in the subgenus *Aporodon* (for list of species, see Wilson and Reeder 2005) typically are distinguished from members of the subgenus *Reithrodontomys* by their relatively brighter dorsal fur coloration that can vary in reddish tones. The ventral coloration is generally white, gray, or cinnamon; the dark tail is longer than the head–body length, monochromatic, and with short hairs (members of the subgenus *Reithrodontomys* usually have a bicolored tail with long hairs—Hooper 1952). Molars have a more complex pattern (well-developed enamel loops) than species in the subgenus

Reithrodontomys (Howell 1914). M3 and m3 represent three-quarters of the size of M2 and m2, respectively, constituting compact replicas of these molars versus M3 and m3 equal one-half or less the size of M2 and m2 in members of the subgenus *Reithrodontomys* (Hooper 1952).

Reithrodontomys gracilis (slender harvest mouse) is most closely related to *R. mexicanus* (both are arranged in the *mexicanus* species group—Hooper 1952). The two species differ in overall size (measurements in mm and *R. mexicanus* presented first in each pair): body length (171 versus 181), length of hind foot (19–20 versus 17–20), and skull length (21–24 versus 20–23). The tail of *R. mexicanus* represents 130–160% of the head and body together, whereas in *R. gracilis* it constitutes 97–155%. Although both species are distributed from the southeast portion of Mexico to Nicaragua (Hall 1981), *R. mexicanus* mostly inhabits highlands, mainly pine-oak and subtropical forests, whereas *R. gracilis* is found in tropical arid lowlands (Hooper 1952). *R. mexicanus* is sympatric with other species in the subgenus *Aporodon* such as *R. brevirostris* (short-nosed harvest mouse—Jones and Genoways 1970), *R. tenuirostris* (narrow-nosed harvest mouse), and *R. microdon* (small-tooth harvest mouse—Hall 1981). *R. brevirostris* from Nicaragua resembles *R. mexicanus* but the former is cranially smaller (mean skull length 22.0 mm in *R. b. nicaraguae* versus 23.4 mm in *R. m. lucifrons*) with a much narrower rostrum (Jones and Genoways 1970). *R. tenuirostris* is larger in size of body and skull (mean total length 211 mm versus 181 mm in *R. m. howelli*; mean skull length 24.9 mm versus 22.4 mm in *R. m. howelli*—Hooper 1952). *R. microdon* is slightly smaller than *R. mexicanus* (mean total length 180 mm versus 181 mm), but *R. microdon* has greater depth of the skull (8.9 mm versus 8.4 mm) and longer rostrum (8.3 mm versus 7.7 mm) than does *R. mexicanus* (Hooper 1952).

GENERAL CHARACTERS

Reithrodontomys mexicanus (Fig. 1) is a moderate- to large-sized harvest mouse. Dorsal pelage is brown to cinnamon orange, although it varies geographically and there are more intensely pigmented subspecies such as *R. m. mexicanus* and *R. m. soederstroemi* (Hooper 1952). The underparts can vary from whitish to pale cinnamon. The tail is noticeably longer than head–body length and maintains a uniform color, usually dark brown or blackish, rarely paler below or with a white tip (Hopper 1952; Hall 1981). The ears are fuscous in color and sparsely covered by black hairs. The upper surface of both the forefeet and hindfeet are covered with dark brown hairs and the toes are whitish (Howell 1914). The pelage changes as juveniles transition to adults, and the molting process is very similar throughout the genus (description follows Hooper 1952). Juveniles have a dense coat with long guard hairs and shorter cover hairs, always with a dark and dull coloration. Subadults have thicker and brighter hairs, very similar to adult pelage, which is the most intense and bright with the distinctive marks expressed in their entirety. Hypopigmentation in the fur coat (leucism) has been reported in an individual of the subspecies *R. m. soederstroemi* (Ramírez-Jaramillo et al. 2019).

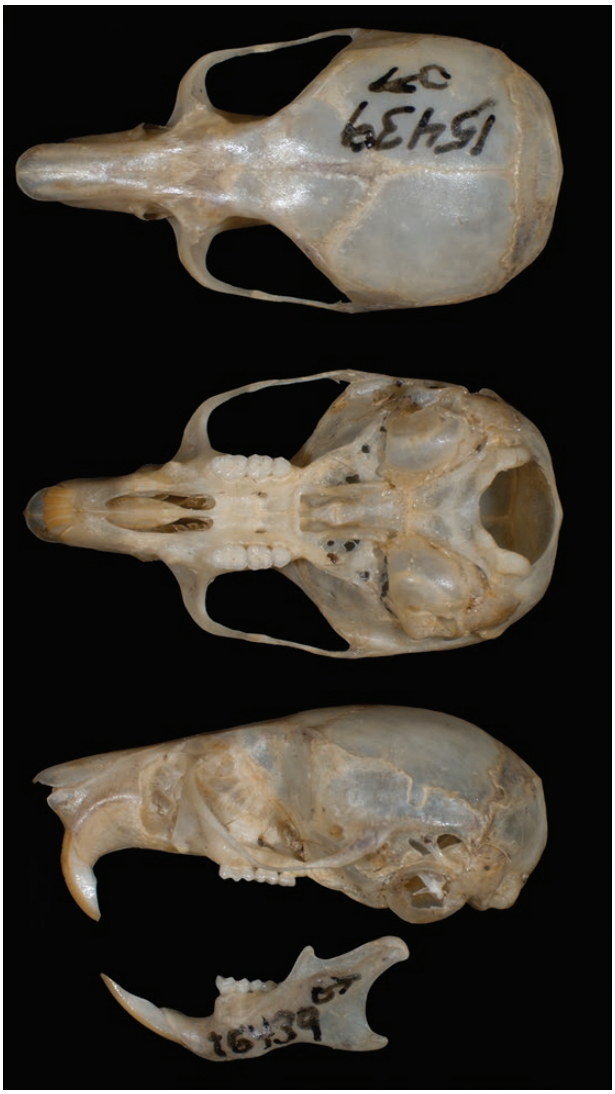

Fig. 2.—Dorsal, ventral, and lateral views of skull, and lateral view of mandible of an adult male *Reithrodontomys mexicanus* (BYU [Monte L. Bean Life Science Museum, Brigham Young University] 15439) from 18 km NW Teocelo, Municipio Ixhuacán, Veracruz, México. Greatest length of skull is 22.4 mm.

The skull of *R. mexicanus* (Fig. 2) shares the general characteristics found in members of the subgenus *Aporodon*. The braincase is wide and shallow, the anterior part of the zygomatic arch is weak (Hooper 1952). The rostrum is wide, and the palate is usually as long as the molar toothrow, but shorter than the incisive foramina (Hall 1981). In comparison to members of the subgenus *Reithrodontomys*, the dentition of *R. mexicanus* has a relatively complex pattern on the occlusal surface of the molars. This pattern is characterized by the presence of mesolophs (ids) and mesostyles (ids) on all

teeth, and a third molar that is essentially a smaller replica of the second (Hooper 1952). The incisors are moderately recurved and, as in all species of *Reithrodontomys*, they have a longitudinal groove located medially on the upper incisors (Le Conte 1853).

An assessment of nongeographic variation in body mass and four external, 13 cranial, and three postcranial measurements showed no sexual dimorphism in a population of *R. mexicanus* from La Esperanza, Oaxaca, Mexico (Arellano et al. 2012). There were significant differences due to age in all but the postcranial measurements, comparing five age classes (I–V) assigned according to the molar wear (I and V being the youngest and oldest age classes, respectively). The most distinct classes were II and III, whereas IV and V were similar in size (Arellano et al. 2012).

Mean external measurements (mm; range in parentheses) for 51 individuals of age class IV (M3 with more than 50% worn occlusal surface) from La Esperanza, Oaxaca were: total length, 198.0 (173–229); tail length, 117.4 (90–144); length of right hind foot, 20.9 (18–24); and length of right ear, 16.1 (13–19—Arellano et al. 2012). Mean body mass (g; range in parentheses) for age class IV was 14.0 (8–18), and mean cranial measurements (mm; range and *n* in parentheses) were: greatest length of skull, 23.8 (22.5–24.9, 51); skull width, 11.5 (10.7–12.1, 54); skull depth, 8.7 (7.9–9.4, 54); zygomatic breadth, 12.4 (11.6–12.7, 10); nasal length, 8.5 (6.4–9.1, 54); length of molars, 3.5 (3.2–4.4, 54), length of incisive foramen, 4.6 (3.8–5.1, 54); rostral length, 8.6 (7.9–9.4, 54); rostral width, 4.3 (3.9–4.6, 54); least interorbital constriction, 3.8 (3.6–4.3, 54); and width of zygomatic plate, 1.8 (1.5–2.1, 54—Arellano et al. 2012).

DISTRIBUTION

Reithrodontomys mexicanus has the largest geographical and elevational range among members of the subgenus *Aporodon* (Arellano 2015). It is distributed from the mountainous systems of northern Mexico south to Nicaragua, and in western Colombia and northwest Ecuador in South America (Fig. 3). *R. mexicanus* can generally be found in an elevational range from near 1,000 to 3,800 m, but this varies depending on the geographic region. In North and Central America, the lowest reported record of occurrence is 91 m, near Gómez Farías in Tamaulipas, Mexico (Jones and Anderson 1958), and the highest is 2,438 m in Los Esesmiles, El Salvador (Hooper 1952). In Colombia, its elevational range varies from 500 to 3,000 m (Marín-C. 2014), and in Ecuador, it occurs from 1,800 to 3,800 m (Tirira 2007).

The distribution of Mexican subspecies includes the Sierra Madre Oriental for *R. m. mexicanus* and the Sierra Madre Occidental for *R. m. riparius* (Hooper 1952, 1955; Hall 1981). *R. m. scansor* is found in Oaxaca and Chiapas and *R. m. howelli* inhabits areas from the center and east of Chiapas to the west and center of Guatemala. Central American subspecies are distributed almost continuously in the highland areas of this region, excluding Costa Rica and Panama (Bradley 2017). In South America, *R. m. milleri* is found in northern Colombia and both

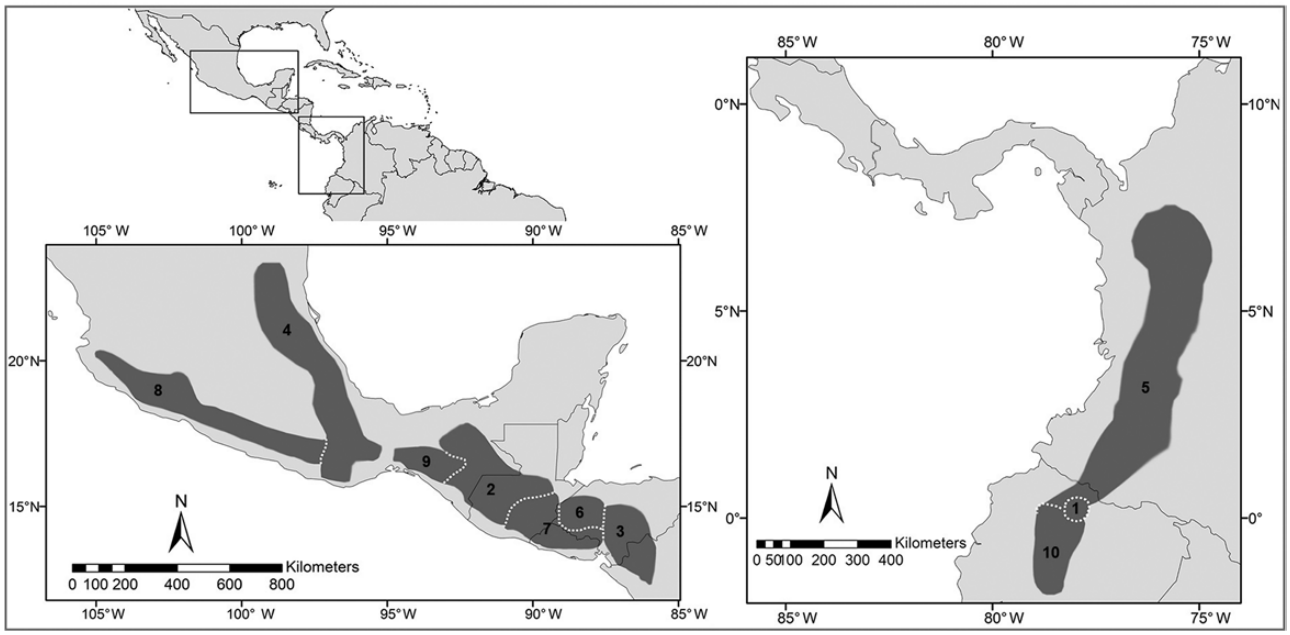

Fig. 3.—Geographic distribution of *Reithrodontomys mexicanus*. Subspecies are: 1, *R. m. eremicus*; 2, *R. m. howelli*; 3, *R. m. lucifrons*; 4, *R. m. mexicanus*; 5, *R. m. milleri*; 6, *R. m. ocotepequensis*; 7, *R. m. orinus*; 8, *R. m. riparius*; 9, *R. m. scansor*; 10, *R. m. soederstroemi*. Map redrawn from Hooper (1952) and Hall (1981) with modifications.

R. m. eremicus and *R. m. soederstroemi* occur in northwestern Ecuador.

FOSSIL RECORD

Information related to fossil remains of *Reithrodontomys* is generally scarce (Ruez 2000). Reports of the subgenus *Aporodon* in northern Ecuador are dated from the late Pleistocene and Holocene (Moreno et al. 2018). A revaluation of the fossil species *Copemyodon ecuadorensis* by Fejfar et al. (1996) resulted in synonymizing this taxon with *Reithrodontomys*. Despite the great similarity of the molars between *R. ecuadorensis* and *R. mexicanus soederstroemi*, it was considered a species-level taxon by Moreno et al. (2018). The remains of two upper molars in a Pleistocene deposit from La Palmera, Costa Rica, were identified by Laurito (2003) as belonging to *R. mexicanus*.

FORM AND FUNCTION

Like other species in the genus, female *Reithrodontomys mexicanus* have six mammae: one pectoral pair and two inguinal pairs (Hooper 1952). The dental formula is i 1/1, c 0/0, p 0/0, m 3/3, total 16 (Emmons and Feer 1999). *R. mexicanus* has a moderately complex molar pattern (Carleton 1980). The groove of the upper incisors is deep, and the molars are bunodont. The lingual root of M1 and M2 is single and large, and M3 has three roots. Also, the labial root of M1 is absent (Carleton 1980). Four main cusps are present in M3, the protoconus is the largest followed by the paraconus, hypoconus, and metaconus. The major fold in M3 is short and deep while the minor fold is usually indistinct. First and second primary and secondary folds are well-developed (Hooper 1952). Both lingual and labial roots are absent in m1, whereas m2 and m3 have two roots each. In m3, the entoconid and hypoconid cusps are greatly reduced and wear to a "C-shape" (Carleton 1980). The major and minor folds in m3 are relatively long and deep, and the second primary fold is well-developed. Mesolophs (ids) and mesostyles (ids) present in all molar teeth, except possibly in m3. The molar toothrow varies in length from about 3.2 mm, in smaller subspecies, to 3.7 mm in larger subspecies (Hooper 1952).

The anterior edge of the zygomatic arch is parallel to the anterior edge of the zygomatic plate in *R. mexicanus*, allowing the former to curve evenly and away from the rostrum (Rinker and Hooper 1950). Stapedial and sphenofrontal foramina are present with a groove existing on squamosal. The foramen ovale is present as is the postglenoid foramen and subsquamosal foramina, which are large. The sphenopalatine vacuities are elongate and extending over one-half the length of the presphenoid bone. When present, the posterolateral palatal pits have one or two small foramina. A pair of palatine foramina are found at the junction of the maxillary and palatine bones. Sometimes, paired foramina are large and have one or two small openings (Carleton 1980). In *R. mexicanus*, there is little difference in size between pterygoid and mesopterygoid fossa (Rinker and Hooper 1950), and the lateral pterygoid fossa is flat. The supraorbital shape is smooth on the sides and the temporal ridges are absent. The zygomatic notch is absent, and the postorbital process and the angular processes of the dentary are not deflected. In the hyoid apparatus, the entoglossal process forms a small knob, the shape of the basihyal bone is arched, and the thyrohyal bone is long, greater than or equal to the length of the basihyal. The malleus is parallel with the manubrium forming a right angle with the frontal plane of the skull. Additionally, an orbicular apophysis is present. The accessory tympanum is large, the small mastoid bullae are unmodified, and the tympanic bullae are also small. The tentorium cerebellum is present as a low relief crest (Carleton 1980).

Reithrodontomys mexicanus possesses 13 thoracic, six lumbar, and more than 36 caudal vertebrae. Additional features of the postcranial skeleton include the presence of an entepicondylar foramen and the second thoracic vertebra with a pronounced neural spine. The first rib articulates with the transverse processes of both the first thoracic and seventh cervical vertebrae. The trochlear process of the calcaneum is broad and it is found at the level with posterior articular facet. The tibia and fibula are extensively fused (Carleton 1980).

Differences in cranial musculature associated with the zygomatic plate and the mesopterygoid fossa were examined between *R. mexicanus* and *R. megalotis* (western harvest mouse) by Rinker and Hooper (1950). *R. mexicanus* has small pterygoideus internus muscles with a minor area for their origin and insertion. The temporalis muscles are large, and their ventral boundaries extend below the dorsal lip of the auditory meatus. The anterior fibers of the masseter lateralis muscle originate slightly medial to the keel of the zygomatic plate, wrapping its anterior margin; and its insertion is posterior to the mental foramen. These myological characteristics have been associated with the movements of the jaw, probably the chewing process. Thereby, muscles responsible for moving the jaw are well-developed while those related to occlusion are relatively weak (Rinker and Hooper 1950).

The anterior ridge of the soft palate is complete with low relief and has two complete and five incomplete palatal ridges (Carleton 1980) in *R. mexicanus*. It has a discoglandular stomach, with a small area of glands located in the ascending part of the greater curvature of the stomach (Carleton 1973). Like all species of *Reithrodontomys*, the incisura angularis is intermediate in development compared to most cricetids (Carleton 1973, 1980); the sulcus on the greater curvature of the stomach is not present and the saclike gallbladder is generally located between the cystic lobes of the liver. The first segment of the large intestine consists of either zero, one, or two coils and the cecum is simple internally, with a moderate length (Carleton 1980).

The glans penis of *R. mexicanus* is similar in shape and structure to other species of *Reithrodontomys* such as *R. fulvescens* (fulvous harvest mouse), *R. megalotis*, and *R. sumichrasti sumichrasti* (Sumichrast's harvest mouse) although larger (mean length = 7 mm, mean diameter = 1.7 mm, n = 2 versus mean

length = 5.9 mm, mean diameter = 1.4 mm, *n* = 5—Hooper 1959). The glans is elongated, and rod-shaped, and consists of two divisions. One is the conical tip, somewhat protractile with soft, flexible, and nonspiny outer tissues, and the other has a main body composed of dense tissue (Hooper 1959). The spines on the glans cover one-half to three-quarters of the spiny body and there are no spines on the inner wall of the crater (Carleton 1980). Compared to *R. megalotis*, the spines are longer and thicker in *R. mexicanus* (Hooper 1959). The urinary meatus is located at the base of the protractile tip (Hooper 1959), in a subterminal position (Carleton 1980). Both ventral and dorsal lappet projections, and the urethral process, dorsal papilla, the lateral bacular mounds, and the crater hood, are absent in *R. mexicanus* (Carleton 1980). The baculum is simple, enlarged toward the base, and blunt distally. It does not consist of a terminal capsule or a cartilage spine, and the bone is much longer than the glans. The mean length of the baculum, based on two specimens, was 8.4 mm (Hooper 1959). Male accessory reproductive glands lack preputials in *R. mexicanus*. The medial and lateral ventral prostates are present as are the dorsal and anterior prostates. In addition, the bulbourethral glands, ampullaries, and vesiculars (J-shaped inverted) are all present, except for the ampullae of ductus deferens (Carleton 1980).

The hind foot of *R. mexicanus* has a bare or slightly furred plantar surface on the heel. The first interdigital plantar pad is positioned back toward the heel, not opposite the fourth, while from the second to the fourth, they are closer to each other. The thenar and hypothenar pads are subsequently displaced and strongly alternated (Carleton 1980).

ONTOGENY AND REPRODUCTION

In Veracruz, Mexico, a female *Reithrodontomys mexicanus* with four embryos was reported in February (Hall and Dalquest 1963), and in Nicaragua a female with the same number of embryos was trapped in July (Jones and Genoways 1970). Females typically have three to four offspring per litter (Reid 1997). Nestling juveniles have been reported in December from El Salvador, and juveniles or subadults were trapped in March and April in Mexico (Hooper 1952). *R. mexicanus* taken in Nicaragua in April had juvenile pelage, and the upper third molar had not fully erupted (Jones and Genoways 1970).

Reithrodontomys mexicanus apparently reproduces during several months of the year, although its breeding season is not well-defined (Hooper 1952). Lactating females were noted in February, March, April, and November in El Salvador (Hooper 1952), and in April (Hooper 1952), February, and September (González 2012) in Mexico. Females from Nicaragua collected in July and April did not show evidence of reproductive activity (Jones and Genoways 1970). Scrotal males were collected in Guatemala during January (Matson et al. 2014; Ordóñez-Garza et al. 2014), and in early February both females and males from Cerro Celaque, Honduras were reproductively active (lactating females, females with embryos, and males with testes scrotal or enlarged—Matson et al. 2016). Males with well-developed testes have been captured in Ecuador during November (Vallejo and Boada 2017). Adult males captured in July from Nicaragua had testes with a mean length of 11.3 mm (9–17 mm), and one taken in April had testes measuring 8 mm (Jones and Genoways 1970). Of 11 male *R. mexicanus* trapped in Puebla, Mexico, in May, September, and November, five specimens had testicular measurements, ranging from 5 to 7 mm (González 2012).

ECOLOGY

Population characteristics.—*Reithrodontomys mexicanus* is considered rare to locally common in Central America (Reid 1997), and common in Colombia and Ecuador (Ramírez-Jaramillo et al. 2019). Populations are presumably stable and large (Delgado-V. et al. 2016), although specific data on population sizes or other related characteristics are unknown.

Space use.—*Reithrodontomys mexicanus* is associated with a variety of forests such as humid oak forests, cloud forests, deciduous arid forests, and deciduous lowland forests (Hooper 1952). In Mexico and Central America, *R. mexicanus* is distributed in both mesic and humid forests (Hooper 1952), whereas in southern Colombia it is known from subtropical forests of the western Andes (Hershkovitz 1941). In Ecuador, in addition to subtropical dry forests, it is found in temperate forests and in Andean moors (Tirira 2007). In the Sierra Mixteca, Oaxaca, Mexico, *R. mexicanus* was collected at 2,950 m associated with oak-pine forests (Sánchez-Cordero 2001), whereas, in a temperate forest in Veracruz, Mexico, it was the most commonly trapped mouse in grasses, in both the dry and rainy seasons (Flores-Peredo and Vázquez-Domínguez 2016). In a remnant cloud forest in Cerro Cucurucho, Guatemala, it represented 2.4% of the total of small rodents collected (Ordóñez-Garza et al. 2014), whereas in Chelemhá Cloud Forest Reserve, Guatemala, *R. mexicanus* was one of the most captured species (10% of the total—Matson et al. 2014). Although *R. mexicanus* is mostly associated with primary and secondary forests, it also occurs in disturbed and cultivated areas, near houses (Hooper 1952; Reid 1997); it was reported as inhabiting structures in Colombia (Marín-C. 2014). At Santa María de Ostuma, Nicaragua, five specimens were trapped in a pasture on a farm (Jones and Genoways 1970). *R. m. soederstroemi* was the most abundant captured rodent (317 individuals) in an altered area near Quito Airport, Ecuador, along the Tababela plateau (Ramírez-Jaramillo et al. 2019).

Reithrodontomys mexicanus probably depends on herbs, shrubs, or other plants as food (Hooper 1952). In Mexico and Central America, it has been trapped "in sparse to dense growths of grass, herbs, and shrubs bordering cultivated areas, streams, and marshes; on rocky hillsides; in coffee groves; and in trees" (Hooper 1952:139). In the subtropical arid Valle de la Chota, Ecuador, *R. m. eremicus* occurs "in open situations in light sandy soil" (Hershkovitz 1941:5).

Reithrodontomys mexicanus is a good climber, with semiarboreal habits (Hooper 1952; Delgado-V. et al. 2016). Of the nine specimens of *R. m. scansor* examined by Hooper (1952), seven were trapped in trees, including species in the genus *Erythrina*, between 2 and 2.5 m in height. The subspecies *R. m. howelli* has also been captured in trees at 2.7 m high in Prussia, Chiapas, Mexico (Hooper 1952) and *R. m. mexicanus* at almost 2 m in height in Villa Juárez, Puebla, Mexico (Hooper 1957a).

Reithrodontomys mexicanus may seek shelter under fallen logs, at the base of trees, and under rocks (Marín-C. 2014). Nests are built of vegetable fibers and their size varies between 13 and 20 cm in diameter (Emmons and Feer 1999). In Veracruz, Mexico, a nest was found at the top of a bromeliad, about 2.5 m above the ground. The nest was constructed of grasses and other loose plant fibers and had a diameter of 23 cm (Hall and Dalquest 1963).

Diet.—The diet of *Reithrodontomys mexicanus* includes small seeds, leaves, young shoots, and occasionally insects (Álvarez et al. 1984). In an examination of the gross stomach contents of specimens from Oaxaca, Mexico, Sánchez-Cordero (2001) considered the species as granivorous, with similar proportions of fruit and seed debris. In a temperate forest in central Veracruz, Mexico, it was found that *R. mexicanus* preferred the small seeds of *Pinus patula*, compared to the seeds of four other pine species, and the preferred seeds had high lipid and gallic acid contents (Flores-Peredo and Bolívar Cimé 2016). *R. mexicanus* is sometimes considered a rodent pest in Mexico, where it potentially causes damage to crops (Sánchez-Cordero and Martínez-Meyer 2000; Sánchez-Cordero and García 2003).

Diseases and parasites.—In Mexico, ectoparasites associated with *R. mexicanus* included the following mites: *Dermacarus hypudaei*, *Echinonyssus galindoi*, *Eubrachylaelaps circularis*, *Euschoengastia zapoteca*, *Hoffmannina haramotoi*, *Neotrombicula claudioi*, and *Tyrophagus putrescentiae* (Estébanes-González and Cervantes 2005). The sucking louse *Hoplopleura reithrodontomydis* parasitized specimens from two localities in Oaxaca, Mexico (Sánchez-Montes et al. 2016).

Reithrodontomys mexicanus is not included among the rodents that act as reservoirs of the Sin Nombre virus, which causes Hantavirus Pulmonary Syndrome (Sánchez-Cordero et al. 2005). The species is considered a potential host of the protozoan *Trypanosoma cruzi*, which causes Chagas disease, with *Triatoma dimidiata* as a vector (Rengifo-Corre et al. 2017). Although, in the genus *Reithrodontomys*, the presence of this protozoan has only been confirmed for *R. fulvescens* in Mexico (Mota et al. 2007).

Interspecific interactions.—*Reithrodontomys mexicanus* is broadly distributed in a variety of habitats and thus, it could be sympatric with many species of mammals, depending on their geographic, ecological, or elevational distributions. Some examples of congeneric interactions with *R. mexicanus* include *R. sumichrasti* in southern Mexico and Central America (Hooper 1952). In Santa María de Ostuma, Nicaragua, both species were trapped in the same trapline along with *R. brevirostris* (Jones and Genoways 1970). In some regions in Mexico, *R. mexicanus* occurs with *R. tenuirostris* (Arellano and Rogers 1994) and *R. microdon* (Hooper 1952). In the San Juan del Monte Nature Reserve, Veracruz, Mexico, it was captured with *R. megalotis*, *R. fulvescens*, and *R. sumichrasti* (Flores-Peredo and Vázquez-Domínguez 2016).

Reithrodontomys mexicanus has nocturnal and solitary habits and among its predators are *Tyto alba* (barn owl—Moreno and Román 2013) and *Cerdocyon thous* (crab-eating fox—Delgado-V. 2002). The subspecies *R. m. riparius* was described from a specimen obtained from the stomach of *Masticophis flagellum* (coachwhip snake), which could be recovered due to the slow digestive process (Hooper 1957b). Remnants of *R. mexicanus* were identified in a tree roost belonging to *Chrotopterus auritus* (woolly false vampire bat) in Chiapas, Mexico (Medellín 1988).

Miscellaneous.—Many species of *Reithrodontomys*, including *R. mexicanus*, exhibit audible vocal behavior (Miller and Engstrom 2010). The vocalizations of *R. mexicanus* are intense and have relatively constant frequencies with stereotypic one-, two-, or three-note calls. A slight sexual dimorphism has been reported in the frequencies of the audible element (first carrier), with females using frequencies lower than males (Miller and Engstrom 2010). The content of the information in the first carrier may reflect sexual identity. The calls have both audible and ultrasonic elements and individuals "typically call when they are above the ground; in trees, vine growth, and from rafters in buildings" (Miller and Engstrom 2010:1507). In El Angel Ecological Reserve, Ecuador, vocalizations from an adult male *R. m. soederstroemi* were recorded as a whistle with a dominant frequency of 9.77–10.46 kHz and a duration of 541–1,290 ms (Brito and Battles 2014). *R. mexicanus* emits alarm calls at lower frequencies than expected based on its body size (9–12 kHz versus 15.7 g—García-Navas and Blumstein 2016).

GENETICS

Cytogenetics.—Karyotypes of *Reithrodontomys mexicanus* have mostly acrocentric chromosomes and high diploid numbers (Carleton and Myers 1979; Rogers et al. 1983). The diploid number of chromosomes (2n) and fundamental number of arms (FN) vary among populations. Urbina et al. (2006) reported a karyotype of 2n = 50 and FN = 48 for specimens from Puerto de la Soledad, Oaxaca and El Durazno, Puebla in Mexico. This karyotype differs from those previously described for the subspecies *R. m. howelli* and *R. m. soederstroemi*, from Guatemala and Ecuador, respectively (2n = 52; FN = 52—Carleton and Myers 1979), and for individuals of *R. m. howelli* from Chiapas (2n = 52; FN = 50—Rogers et al. 1983). The karyotype described by Carleton and Myers (1979) also differs by the presence of a pair of biarmed autosomes although the other authors describe all acrocentric chromosomes.

The C-banded karyotypes of *R. mexicanus* showed that constitutive heterochromatin was restricted to centromeric regions. A comparison of the C- and G-banded karyotypes between *R. mexicanus* and *R. fulvescens* showed almost identical karyotypes; the only difference was the addition of a small pair of chromosomes in the former species (Hood et al. 1984). C- and G-banded chromosomes of these two species were compared by Urbina (2011), who concluded that *R. fulvescens* had a more derived karyotype than *R. mexicanus*. In individuals from populations in Oaxaca, Puebla, Veracruz, and Hidalgo, Mexico, heterochromatin was restricted to the centromeric region in all chromosomes, except for the X chromosome that also had heterochromatin as an intercalary band. In addition, the Y chromosome was entirety heterochromatic (Urbina 2011).

Molecular genetics.—The analysis of 31 genetic loci by protein electrophoresis showed relatively high genetic variation among five populations of *Reithrodontomys mexicanus* (one from Mexico, one from Costa Rica, one from El Salvador, and two from Guatemala—Arellano et al. 2003). The samples from Oaxaca, Mexico, differed by alternative fixed alleles in six loci compared to the rest of samples of *R. mexicanus* analyzed. In addition, the population from Costa Rica (assigned at that time to *R. m. cherrii*) differed by alternative fixed alleles at three loci with respect to the samples from Guatemala and El Salvador. Rogers' (1972) distance value between localities from Costa Rica, Guatemala, and El Salvador ranged from 0.07 to 0.22 (Arellano et al. 2003). These authors suggested that populations from Oaxaca, Mexico, and Costa Rica represented undescribed species of harvest mice.

Phylogenetic assessments of sequence data of mitochondrial and nuclear genes demonstrated that *R. mexicanus* does not represent a monophyletic group (Arellano et al. 2005; Miller and Engstrom 2008). Samples of *R. mexicanus* split into three clades based on the mitochondrial cytochrome-*b* gene (Arellano et al. 2005). The first clade included harvest mice from Mexico, Central America, and Colombia, referred to as the "classic" *R. mexicanus*. Specimens from the Sierra Madre Oriental and northern Oaxaca in Mexico formed the second clade. Individuals of the second clade and members of the "classic" *R. mexicanus* lineage were syntopic in northern Oaxaca (Arellano et al. 2005). The third clade was composed of samples still considered as *R. m. cherrii*. These authors proposed this clade represented a distinct species, now recognized as *R. cherrii*, which is most closely allied to representatives of the *R. tenuirostris* species group. The uncorrected *p* distances among these three highly differentiated clades ranged from 12.12% to 12.51% (Arellano et al. 2006). In addition, the uncorrected *p* distances between *R. mexicanus* and its sister species *R. gracilis* varied from 11.45% to 12.68% (Arellano et al. 2006), whereas the genetic distance value with Kimura two-parameter model was 13.51% (Bradley et al. 2004).

In Ecuador, 11 specimens of *R. mexicanus* collected near Río Pastaza (Eastern Andean Corridor) possessed cytochrome-*b* haplotypes not shared between the north and south sides of the river. The north side possessed four haplotypes, with a genetic diversity of 0.694, whereas the south side only had one (Haynie et al. 2006). Additionally, levels of divergence based on the cytochrome-*b* gene and the nuclear interphotoreceptor retinoid-binding protein gene suggested that the Ecuadorian subspecies *R. m. soederstroemi* likely represents a separate species that is related to *R. darienensis* (Darien harvest mouse) from Panama (Chávez 2012).

CONSERVATION

Reithrodontomys mexicanus is categorized as "Least Concern" by the International Union for the Conservation of Nature and Natural Resources, due to its presumed large population size, wide geographic distribution, lack of identified threats, and its ability to tolerate a broad array of habitats. It also occurs in several protected areas and its current population is considered stable and unlikely to decline at a rate that would warrant listing in a threatened category (Delgado-V. et al. 2016). In Mexico, even though its populations are distributed in threatened ecosystems such as cloud forests, *R. mexicanus* is not listed under any risk category in the NOM-059-SERMANAT-2010 (SERMANAT 2019). In Colombia, *R. mexicanus* is not included in any conservation program, yet it is facing threats such as loss of habitat in the Andean mountains, particularly on the slopes of the Valle de Aburra (Marín-C. 2014).

REMARKS

The South American subspecies *Reithrodontomys mexicanus soederstroemi* was suggested as a different species based on morphological, genetic, and ecological data, and *R. m. eremicus* was regarded as a subspecies of *R. m. soederstroemi*. However, a formal description has not been made for *R. m. soederstroemi*, such as that made by Arellano et al. (2005) for *R. cherrii*. Furthermore, *R. m. eremicus* continues to be recognized as a subspecies (Arellano 2015; Bradley 2017). Considering the recent taxonomic changes that have occurred in *R. mexicanus* which include a huge break in its geographical distribution (Mexico to Nicaragua and Colombia–Ecuador), additional studies are necessary for clarifying the taxonomic status of *R. mexicanus* based on the suggestions that it constitutes a species complex (Arellano et al. 2005; Miller and Engstrom 2008; Gardner and Carleton 2009).

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CAPÍTULO II

Morphological and ecological data confirm *Reithrodontomys cherrii* as a distinct species from *Reithrodontomys mexicanus*

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Morphological and ecological data confirm *Reithrodontomys cherrii* as a distinct species from *Reithrodontomys mexicanus*

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The integrative taxonomy approach has recently been widely suggested in systematic studies. Lines of evidence such as the geometric morphometrics and ecological analyses have been useful for discriminating between genetically well-differentiated species. Within the genus *Reithrodontomys*, *R. mexicanus* is one of the more taxonomically complex species, being considered a cryptic species complex. *R. cherrii* was considered a subspecies of *R. mexicanus*, until molecular evidence raised it to the species-level. Herein, we evaluate these two forms using morphological and ecological data based on the premise that they constitute genetically differentiated species. We carried out geometric morphometric analyses on dorsal and ventral views of the skull. Landmark and semi-landmark configurations for both views of the skull were selected based on previous studies of cricetid rodents. We tested the presence of sexual dimorphism, and the skull shape and size differences between species on both cranial views. Additionally, we characterized the environmental space of each species habitat using bioclimatic variables, elevation, and the Normalized Difference Vegetation Index (NDVI). Females and males of *R. mexicanus* and *R. cherrii* did not show sexual dimorphism in shape or size of both skull views. We found significant differences between the two species in both shape and size of the skull. Cranial structures of the ventral view were more useful to differentiate both species. *R. mexicanus* exhibited a broader environmental space than *R. cherrii*, with relatively similar values of temperature and elevation, but not of precipitation. The pairwise comparison showed significant differences in the majority of the environmental variables analyzed. Although for each view, we found statistical differences in the skull shape of *R. cherrii* and *R. mexicanus*, the ventral side showed major resolutive power differentiating both species. Our findings suggest that *R. cherrii* tends to have a larger skull than *R. mexicanus*. However, the morphological and pelage coloration similarity between these species reported in the past, could explain the previous inclusion of *R. cherrii* as a subspecies of *R. mexicanus*. *R. mexicanus* occurs in a variety of vegetation-types coinciding with the broader environmental space that it occupies compared to that of *R. cherrii*. The natural areas where both species are distributed were associated with high NDVI values. Our results complement the molecular evidence and, under an integrative taxonomy approach, support *R. cherrii* as a different species from *R. mexicanus*.

Recientemente, el enfoque de taxonomía integrativa ha sido ampliamente sugerido en estudios sistemáticos. Líneas de evidencia como la morfometría geométrica y los análisis ecológicos han sido útiles para discriminar entre especies genéticamente bien diferenciadas. Dentro del género *Reithrodontomys*, *R. mexicanus* es una de las especies más complejas taxonómicamente, siendo considerada un complejo de especies crípticas. *R. cherrii* se consideró una subespecie de *R. mexicanus*, hasta que la evidencia molecular la elevó al nivel de especie. En este estudio, evaluamos las diferencias entre estas dos formas utilizando datos morfológicos y ecológicos, basados en la premisa de que constituyen especies genéticamente diferenciadas. Se realizaron análisis de morfometría geométrica para las vistas dorsal y ventral del cráneo. Las configuraciones de marcas y semimarcas para ambas vistas fueron seleccionadas utilizando estudios previos en roedores cricétidos. La presencia de dimorfismo sexual y las diferencias en la forma y tamaño del cráneo entre las especies se evaluaron en ambas vistas del cráneo. Asimismo, se caracterizó y comparó el espacio ambiental que cada especie ocupa utilizando variables bioclimáticas, la elevación y el Índice de Vegetación de Diferencia Normalizada (NDVI). Hembras y machos de *R. mexicanus* y *R. cherrii* no mostraron dimorfismo sexual para la forma y el tamaño en ambas vistas del cráneo. Se encontraron diferencias significativas entre las especies para la forma y tamaño del cráneo. Las estructuras craneales de la vista ventral resultaron más útiles para diferenciar ambas especies. *R. mexicanus* exhibió un espacio ambiental más amplio que *R. cherrii*, con valores relativamente similares de temperatura y elevación, pero no de precipitación. La comparación por pares mostró diferencias significativas en la mayoría de las variables ambientales. Aunque para cada vista, encontramos diferencias estadísticas en la forma del cráneo de *R. cherrii* y *R. mexicanus*, el lado ventral mostró mayor poder resolutivo diferenciando ambas especies. Nuestros resultados sugieren que *R. cherrii* tiende a tener el cráneo de mayor tamaño que *R. mexicanus*. No obstante, la gran similitud morfológica y de coloración del pelaje reportada entre estas especies en el pasado, pudiera explicar la previa inclusión de *R. cherrii* como una subespecie de *R. mexicanus*. *R. mexicanus* ocurre en distintos tipos de vegetación, coincidiendo con el espacio ambiental más amplio que ocupa en comparación con el de *R. cherrii*. Las áreas naturales donde se distribuyen ambas especies mostraron asociación con altos valores de NDVI. Nuestros resultados complementan la evidencia molecular y, con un enfoque de taxonomía integrativa, confirman a *R. cherrii* como una especie diferente de *R. mexicanus*.

Keywords: Cricetidae; cryptic species; environmental space; harvest mice; integrative taxonomy; skull morphometry.

Introduction

The morphological species concept has been used historically to describe new taxa (Mayden 1997; Mayr 2000). In fact, the majority of species that we know today were delimited and/or assigned to different taxonomic categories based on their morphological characteristics (Seifert 2014). However, establishing species boundaries in some instances is problematic (Mayr 2000). For example, for cryptic species, which are genetically different entities that do not show distinctive morphological characteristics (Struck *et al.* 2018). In these cases, species concepts with different criteria have been proposed, most of them based on the use of a single operational criterion to describe new species (Sites and Marshall 2003, 2004). In contrast, the General Lineage concept (de Queiroz 1998, 2007) employs multiple lines of evidence (genetic, morphological, ecological, ethological, etc.) to propose species as a separately evolving metapopulation lineage. This approach implements the use of an integrative taxonomy, which has been widely suggested in systematic studies (Dayrat 2005; Alström *et al.* 2008; Sangster 2018).

Recently, Leaché *et al.* (2009) argued that the use of morphological and ecological data, in addition to molecular data, allows better discrimination among species. Geometric morphometric analysis is a robust tool to highlight interspecific variation in zoological groups, such as mammals, corroborating the phylogenetic relationships within them (*e. g.,* Bogdanowicz *et al.* 2005; Camul and Polly 2005; Pavan and Marroig 2016). In addition, ecological niche studies are being increasingly used for these same purposes (*e. g.,* Rissler and Apodaca 2007; Rivera *et al.* 2018; Zhao *et al.* 2019), and for making inferences related to evolutionary questions of both historical distributions and speciation processes (Graham *et al.* 2004).

The genus *Reithrodontomys* (Cricetidae, Rodentia) constitutes a taxon in which species were originally described based on pelage coloration (Allen 1895), and morphological characteristics of the skull and dentition (Merriam 1901; Hooper 1952). However, variation in these characters overlap among populations of different species (Hooper 1952), making taxonomic recognition difficult and leading to misidentifications in many cases.

Reithrodontomys mexicanus (Saussure, 1860) is one of the most taxonomically complex species within the genus, nowadays considered as a complex of cryptic species (Arellano *et al.* 2003, 2005; Miller and Engstrom 2008). Hooper (1952, 1959) recognized 13 subspecies, but currently only 10 are remain valid (Bradley 2017). One of the species that has been subject to taxonomic changes is *R. cherrii* (Allen, 1891), restricted to some highland localities in central Costa Rica (Hooper 1952; Hall 1981). Howell (1914) relegated *R. cherrii* as a subspecies of *R. mexicanus*, without a clear justification for this nomenclatural change. Almost a century later, Arellano *et al.* (2005) raised *R. cherrii* back to the species level based on a molecular phylogenetic analysis of the mitochondrial cytochrome b gene. Specimens of *R. cherrii* were grouped into a genetically well-differentiated clade from *R. mexicanus* (recognized herein as *R. mexicanus* "classic" clade), with a genetic distance value (using the K2P evolutionary model) greater than 12 % (Arellano *et al.* 2006). Also, the species status of *R. cherrii* was recognized by Gardner and Carleton (2009) using traditional morphometrics and pelage coloration. However, it is desirable to complement the taxonomic distinction between *R. cherrii* and *R. mexicanus* with a larger sampling and under an integrative taxonomy approach employing alternative data sources such as geometric morphometrics and ecological attributes. Therefore, the goal of this study is to compare both species using cranial features and environmental characteristics of their habitats, based on the premise that they constitute genetically well-differentiated species.

Materials and methods

Geometric morphometrics data. We examined 47 skulls of adult individuals (M3 erupted, age classes following Arellano *et al.* 2012) from different museum collections (Appendix 1), and each specimen was photographed in the dorsal and ventral views of the skull. We based the selection of specimens; *R. mexicanus* (n = 28) and *R. cherrii* (n = 19); and their localities (Figure 1; Appendix 1), on the *R. mexicanus* "classic" and *R. cherrii* clades obtained in the phylogeny reported by Arellano *et al.* (2005). The specimens used in Arellano *et al.* (2005), but not available for morphometric analysis, were replaced by individuals from the same localities or within a radius less than 60 km. Digital images of skulls were taken using an Olympus DP73 Digital Camera coupled to an optical microscope, and to the computer through the CellSens program. The skulls were positioned on a black background, always keeping the same distance from the camera lens, and using a millimeter rule as a scale bar.

Landmark and semi-landmark configurations for both views were selected based on previous studies of cricetid rodents (*e. g.,* Martínez and Di Cola 2011). Configurations were digitized assuming positional homology among individuals (Zelditch *et al.* 2004), with the TPSdig 2.31 program (Rohlf 2015). We used 17 landmarks, 13 semi-landmarks for the ventral view and 12 landmarks, 23 semi-landmarks for the dorsal view (Figure 2; Appendix 2). We aligned, rotated, and scaled all landmarks and semi-landmarks configurations using a Generalized Procrustes analysis (GPA; Rohlf and Slice 1990) implemented in the package geomorph 3.3.1 (Adams and Otárola-Castillo 2013) from R library (R Core Team 2018). During this processing, semi-landmarks position on the curved structures were allowed to slide along their tangent vectors until reaching the minimum point of bending energy (Bookstein 1997; Zelditch *et al.* 2004). Shape variables (Procrustes distances and Procrustes coordinates) and centroid size (CZ) were obtained from the GPA. The CZ is related to skull size and computed as the square root of the sum of the squared distances between each landmark and the configuration centroid (Bookstein 1991).

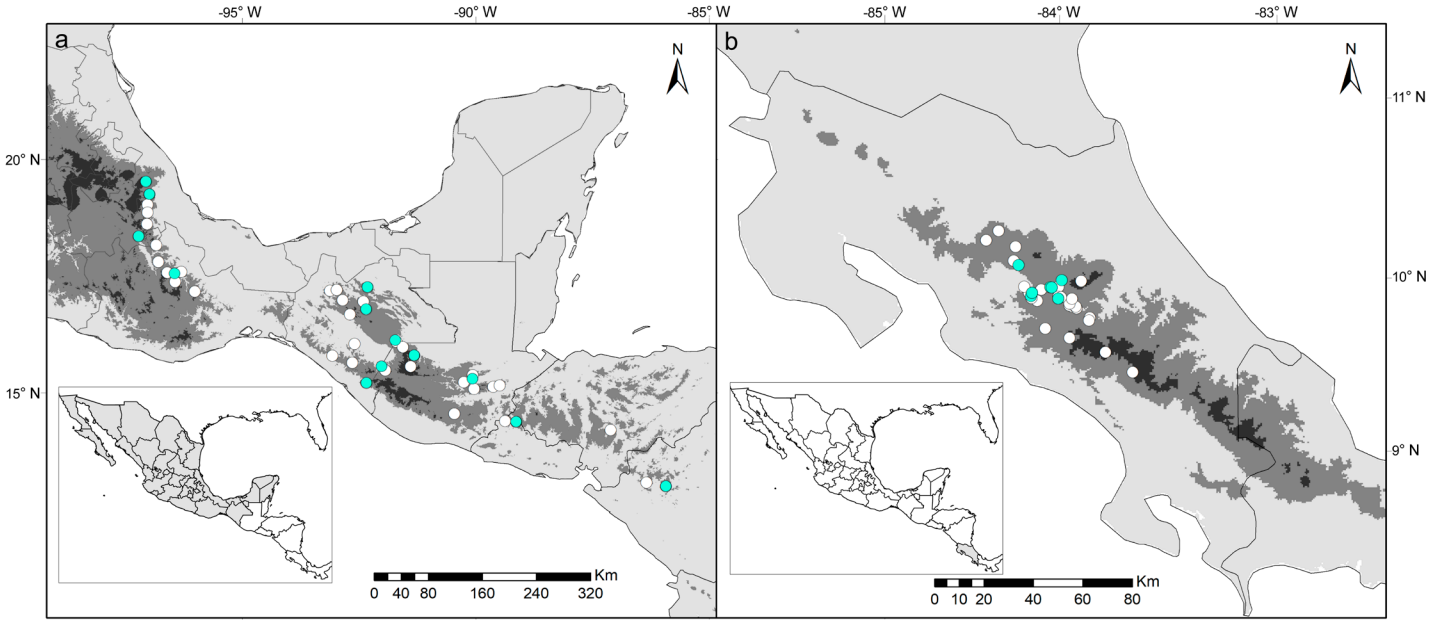

Figure 1. Map showing localities of the specimens used in this study. (a) *Reithrodontomys mexicanus* from Mexico and Central America and (b) *R. cherrii* from Costa Rica. Localities for geometric morphometric analysis are highlight in blue dots. Gray tones depict elevation gradient: light gray < 1,000 m, gray 1,000 to 2,500 m; and dark gray > 2,500 m.

Sexual dimorphism and allometry. We evaluated the sexual dimorphism in shape and size of the skull within species for each view. A Procrustes ANOVA (Goodall 1991; Anderson 2001) was performed for skull shape using the function ProcD.lm, and a factorial design with shape as the dependent variable, sex as the main factor, and CZ as a covariate. Significant differences ($P \leq 0.05$) in skull size between sex were tested using the function lm.rrpp in the R package RRPP (Collyer and Adams 2018). The allometric component (possible effect of the skull size on the shape variation) was analyzed using a Procrustes ANOVA and the same factorial design previously declared. Analyses of sexual dimorphism (shape) and allometry were carried out in geomorph 3.3.1.

Skull shape and size differences. Principal component analysis (PCA) on the Procrustes coordinates were performed for each view of the skull in geomorph 3.3.1. Then, we used the first two components to visualize the ordering of the data according to the skull morphometric variation, and the extreme variation (minimum and maximum) of the shape along component 1 were represented using deformation grids.

We determined shape differences between species for each skull view using a Procrustes ANOVA in geomorph 3.3.1. A factorial design was used with shape as the dependent variable, species as the main factor, and CZ as a covariate. The mean skull shape differences between species were quantified (Procrustes distances) and tested for its statistical significance ($P \leq 0.05$; resampling = 1000), using a pairwise permutation test (function permudist) in the R package Morpho 2.4 (Schlager 2016).

We employed a similar approach to compare skull shape between species for skull size. This analysis was developed for each view with the function lm.rrpp of the RRPP package. The factorial design consisted of CZ as the dependent variable, species as the main factor, and shape as a covariate. We visualized the results of these analyses using the shiny application Extended Boxplot Graphics (Ramirez-Arrieta *et al.* 2020).

Ecological niche data. For the ecological analysis, we included the occurrences localities for the specimens used in the morphometric analysis. Additional localities were incorporated to represent the largest number of sites reported for both species (Figure 1; Appendix 3). Occurrence records were obtained from museums databases or downloaded from the VertNet database (http://portal.vertnet.org). Geographic coordinates were rectified against the known distribution of *R. cherrii* and *R. mexicanus* (Hooper 1952; Hall 1981), to reduce georeferencing errors.

We characterize the species ecological niche using six bioclimatic variables from Wordclim 2.0 (Fick and Hijmans 2017; http://www.worldclim.org): BIO1 = Annual Mean Temperature, BIO5 = Max Temperature of Warmest Month, BIO6 = Min Temperature of Coldest Month, BIO12 = Annual Precipitation, BIO13 = Precipitation of Wettest Month, and BIO14 = Precipitation of Driest Month, with a spatial resolution of ~1 km^2. The selection of variables was based on previous studies that highlight their importance for small mammals ecological analyses (Santos *et al.* 2017; Guevara *et al.* 2018; Stanchak and Santana 2018). Because the distribution of small mammals may also depend on elevation gradient and vegetation quality (Patterson *et al.* 1989; McCain 2005; Umetsu and Pardini 2007), we also used elevation as a topographic variable derived from a digital elevation model (data available at http://www.worldclim.org), and the Normalized Vegetation Difference Index (NDVI; Pettorelli *et al.* 2005). The NDVI layer was obtained from the

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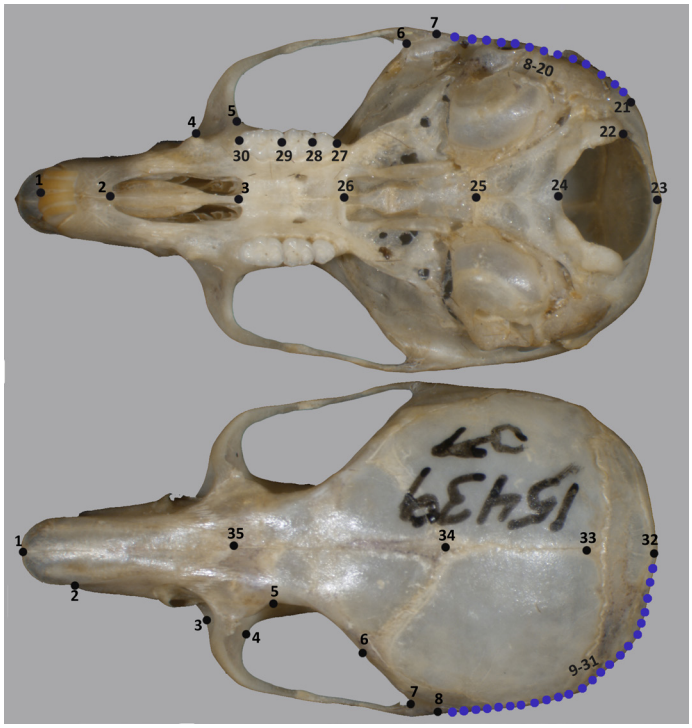

Figure 2. Landmarks (black dots) and semi-landmarks (blue dots) digitized in ventral and dorsal views of the skull. Anatomical positions of landmarks described in Appendix 2. The specimen voucher (BYU 15439) is a male of *Reithrodontomys mexicanus*.

Climate Engine Platform available at http://ClimateEngine.org (Huntington *et al.* 2017), which represents the average conditions of this index in the last five years.

Ecological niche differences. Ecological niche characteristics of *R. cherrii* and *R. mexicanus* were summarized using the predictor variables described above (bioclimatic, elevation, and NDVI). To determinate the environmental ranges of each species, we calculated descriptive statistics (Mean, Standard Error, Maximum and Minimum values, Confidence Intervals constructed from the percentile method, Standard Deviation, and Coefficient of Variation) using information extracted from the occurrence records.

With the predictor variables, we generated an environmental background using ArcGIS 10.8 (ESRI 2020), which included the information extracted from 10,000 random points within a buffer of 100 km^2, around each occurrence record. This buffer selection allows to consider regions with suitable environmental conditions for the species and to minimize the inclusion of areas where they would not be found due to the presence of physical barriers or biotic interactions (Kubiak *et al.* 2017).

The environmental background and the occurrence data were used to visualize the species ecological niche in a three-dimensional space constructed from the first three principal components (which explained over 95 % of the variance in the data). For this, the minimum-volume ellipsoid (Van Aelst and Rousseeuw 2009) and convex polyhedron (Soberón and Nakamura 2009) were displayed as a representation of the fundamental and realized niche (Qiao *et al.* 2016) for each species, respectively. Analyses were performed using NicheA (Qiao *et al.* 2016), a software for exploring and analyzing the environmental and geographic spaces of virtual and real species. Niche similarity between species was quantified in NicheA, based on Jaccard index (Jaccard 1912), and using the minimum-volume ellipsoid calculation method. This index based on the superposition of ellipsoids in the environmental space, captures the fundamental niche rather than the realized.

Additionally, we performed PCA on the environmental data of the occurrence records, to determine whether the ecological niches were significantly different ($P \leq 0.05$) between species, using the first two principal components (which explained 99.7 % of the total variance). Finally, we performed a Mann-Whitney U test for each variable in the program Statistica 8.0 (STATSOFT 2007), to know which of them contributed to the environmental niche differentiation between *R. mexicanus* and *R. cherrii*.

Results

Sexual dimorphism and allometry. Females and males of *R. mexicanus* and *R. cherrii* did not show sexual dimorphism in shape or size of the skull for both ventral and dorsal views (Table 1). Consequently, we did not distinguish between sexes to perform the morphometric analyses. Likewise, none of the species demonstrated significant allometry between shape or size of any skull view, therefore, we used the Procrustes distances matrix in our analyses of interspecific comparison.

Table 1. Results of sexual dimorphism and allometry analyses in *Reithrodontomys mexicanus* and *R. cherrii*, using shape and size (centroid size) of the skull from ventral and dorsal views.

	SS	*MS*	R^2	*F*	*Z*	*P*
A. *Reithrodontomys mexicanus*						
Ventral view						
Shape~Sex	0.002	0.002	0.051	1.416	0.870	0.208
Centroide size~Sex	2.856	2.856	0.028	0.764	0.400	0.404
Shape~Centroide size	0.002	0.002	0.048	1.319	0.809	0.207
Dorsal view						
Shape~Sex	0.002	0.002	0.054	1.554	0.985	0.162
Centroide size~Sex	8.509	8.509	0.064	1.779	0.805	0.207
Shape~Centroide size	0.003	0.003	0.079	2.272	1.556	0.078
B. *Reithrodontomys cherrii*						
Ventral view						
Shape~Sex	0.002	0.002	0.091	2.017	1.569	0.067
Centroide size~Sex	0.165	0.165	0.012	0.210	0.168	0.651
Shape~Centroide size	0.002	0.002	0.092	2.029	1.448	0.084
Dorsal view						
Shape~Sex	0.003	0.003	0.103	1.949	1.288	0.106
Centroide size~Sex	2.310	2.310	0.133	2.612	0.924	0.157
Shape~Centroide size	0.002	0.002	0.063	1.196	0.531	0.283

SS = sum of squares; *MS* = means squares; *Z* and *P* values based on 1000 permutations

Skull shape and size differences. For the ventral view of the skull, the first principal component (PC1) separated *R. cherrii* from *R. mexicanus* almost completely, which together with the second component (PC2) explained 63.12 % of shape variation (Figure 3a). For the dorsal view, the first two principal components overlapped in the skull shape for both species (Figure 3b). The PC1 segregated the two species better than the PC2, explaining 49.67 % and 11.05 % of the skull shape variation, respectively.

Procrustes ANOVA analyses revealed differences between *R. mexicanus* and *R. cherrii* for the ventral ($F_{1.46}$ = 6.42; $P \leq 0.01$) and dorsal ($F_{1.46}$ = 3.19; $P \leq 0.01$) views of the skull shape. Differences between mean shape for the ventral view were found mainly in the posterior region of the cranium (Figure 4). *R. mexicanus* displayed an expansion of the landmarks of the foramen magnum, and a relatively broader braincase than *R. cherrii*. In the dorsal view, the most notable differences were located on the anterior and middle region of the cranium (Figure 4). *R. cherrii* exhibited a relatively longer nasal bones, a broader configuration between the 3-4-5 landmarks that described the zygomatic plate and the interorbital region, and a relatively broader parietal bone. Skull size differences between species (Figure 5) were highly significant for the ventral view ($F_{1.46}$ = 17.01; $P \leq 0.01$), and significant for the dorsal view ($F_{1.46}$ = 4.50; $P \leq 0.05$).

Ecological niche differences. Most variables that characterized the ecological niche of each species were relatively distinct in mean and ranges (Table 2). The environmental space of *R. mexicanus* had ranges with higher values of temperature for the warmest and coldest months, although the mean annual temperature was similar for both species. With respect to precipitation, the environmental space of both species showed similar means for the driest month, but not for the wettest month. Annual precipitation values were notably different, the environmental niche of *R. cherrii* exhibited a higher mean value than that reported for the geographic region where *R. mexicanus* is distributed. The

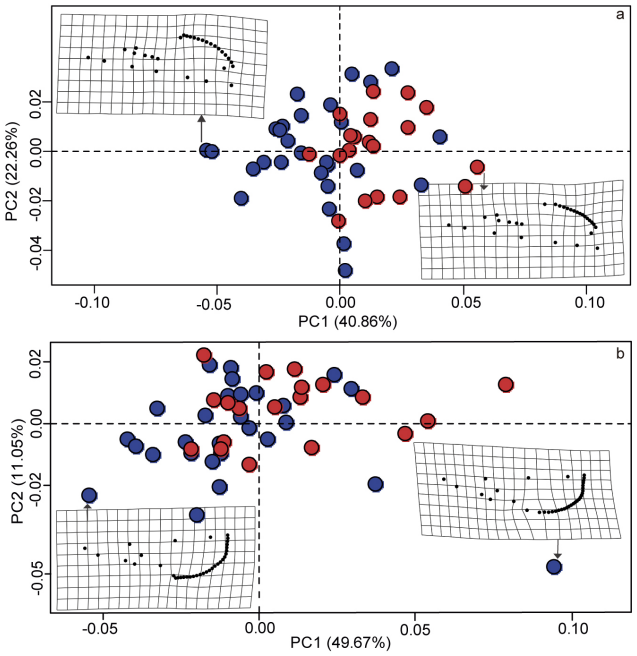

Figure 3. Principal component analysis of ventral (a) and dorsal (b) views of the skull. Red dots = *Reithrodontomys mexicanus* and blue dots = *R. cherrii*. Deformation grids represent the minimum and maximum variation in skull shape along the first component.

Table 2. Descriptive statistics used to summarize the ecological niche characteristics of *Reithrodontomys mexicanus* and *R. cherrii* based on the environmental information from occurrence records.

	Environmental Variables	*Mean ± SE*	*Min - Max*	*CI*	*SD*	*CV*
R. mexicanus	Annual Mean Temperature	17.87 ± 0.53	10.44 - 25.43	12.36 - 21.57	3.61	20.26
	Max Temperature of Warmest Month	25.94 ± 0.62	18.80 - 36.00	19.50 - 31.30	4.21	16.25
	Min Temperature of Coldest Month	9.58 ± 0.50	1 - 18.90	5.50 - 13.20	3.42	35.68
	Annual Precipitation	1906.39 ± 128.08	482 - 4875	1145 - 2943	868.68	45.57
	Precipitation of Wettest Month	346.09 ± 22.38	103 - 886	223 - 546	151.82	43.87
	Precipitation of Driest Month	34.80 ± 4.45	2 - 144	6 - 68	30.16	86.85
	Elevation	1696.91 ± 82.87	438 - 3083	997 - 2434	562.09	33.12
	NDVI	0.77 ± 0.02	0.34 - 0.90	0.58 - 0.87	0.12	15.90
R. cherrii	Annual Mean Temperature	17.88 ± 0.56	8.41 - 22.03	12.51 - 20.42	3.28	18.36
	Max Temperature of Warmest Month	24.35 ± 0.62	14.1 - 29	18.10 - 27.20	3.61	14.85
	Min Temperature of Coldest Month	11.92 ± 0.56	2.3 - 16.3	6.70 - 14.60	3.28	27.55
	Annual Precipitation	2721.65 ± 90.67	1961 - 4052	2197 - 3562	528.75	19.43
	Precipitation of Wettest Month	426.48 ± 11.73	317 - 592	340 - 520	68.42	16.04
	Precipitation of Driest Month	46.29 ± 5.50	10 - 131	10 - 100	32.07	69.29
	Elevation	1629.76 ± 96.25	900 - 3297	1170 - 2573	561.28	34.43
	NDVI	0.67 ± 0.03	0.23 - 0.87	0.38 - 0.83	0.17	25.87

SE = Standard Error, *Min* = Minimum, *Max* = Maximum, *CI* = Confidence Intervals (Percentile method), *SE* = Standard Deviation, *CV* = Coefficient of Variation

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elevation gradient occupied by *R. cherrii* ranged from 900 to almost 3,300 masl, whereas in *R. mexicanus* it ranged from over 400 to around 3,000 masl. Distribution areas of *R. mexicanus* presented NDVI ranges slightly higher than those of *R. cherrii*, although in both species the NDVI means were above 0.6.

The ecological niche visualization using the first three components showed that *R. mexicanus* occurs in a broader environmental space than *R. cherrii* (Figure 6a). The minimum-volume ellipsoids displayed a partial overlap of the environmental conditions of each species, with a low niche similarity of Jaccard index (0.08). The statistical comparison of the principal component scores showed significant differences ($U = 313$; $P = 0.02$) between the environmental niche of each species for the first component, while no differences were found ($U = 458$; $P = 0.25$) for the second component (Figure 6b, 6c). In the pairwise comparisons, all variables were statistically different, except for BIO1, BIO14, and elevation (Figure 7).

Discussion

Geometric morphometrics has shown great applicability in mammal taxonomic studies, mainly for anatomical structures such as the cranium, dentition, or mandibles (*e. g.*, Cordeiro-Estrela *et al.* 2008; Barčiová 2009; Kryštufek *et al.* 2021). As part of an integrative taxonomy, this morphological tool has allowed researchers to corroborate hypotheses derived from phylogenetic studies and to establish species boundaries (Camul and Polly 2005; Pavan and Marroig 2016). This taxonomic approach also includes other lines of evidence, such as ecological data (Dayrat 2005). In particular, the environmental niche characteristics can be useful to delimit cryptic species or phylogenetically related groups, especially when their relationships are known, something that has been confirmed in several rodent species (Martínez-Gordillo *et al.* 2010). This could be the case of the harvest mice *R. mexicanus* and *R. cherrii*, for which genetic differences are well established, but lack modern morphometrics and ecological data. In this study, we tested the premise that differences in the skull and the environmental characteristics would be consistent with the genetic divergence documented between these species (Arellano *et al.* 2003, 2005, 2006).

Our findings of sexual non-dimorphism in both species coincide with that previously described for *Reithrodontomys* (Hooper 1952). In *R. mexicanus*, the absence of sexual dimorphism was reported by Arellano *et al.* (2012) analyzing the morphometric variation in a population from Sierra Juárez, Oaxaca. Whereas for *R. cherrii,* here we report for the first time sexual non-dimorphism for cranial characteristics.

The PCA revealed some overlap in the skull shape for both ventral and dorsal views. However, the cranial structures on the ventral view were more useful to differentiate *R. cherrii* from *R. mexicanus*. The greater discriminative power of the ventral side versus the dorsal of the skull has been noted for other cricetid rodents (Martínez and Di Cola 2011). Particularly for *Reithrodontomys*, Mayares (2012) evaluated the morphometric variation in the skull ventral view among *R. sumichrasti* populations distributed on both sides of the Isthmus of Tehuantepec in Mexico and correctly differentiated populations grouped according to genetic clades suggested as different species by Hardy *et al.* (2013).

Despite the overlap in skull shape, we found statistically significant differences between *R. cherrii* and *R. mexicanus* for ventral and dorsal views. Gardner and Carleton (2009) used craniodental measurements to compare different *Reithrodontomys* taxa distributed in Costa Rica and Panama, including *R. cherrii*, *R. m. garichensis*, and *R. m. potrerograndei*. The skull of *R. cherrii* was differentiated by "its overall robust size and evenly arched dorsal profile, especially over the braincase and occiput; it is notably broad across the braincase and zygomata but has a proportionally shorter rostrum" (Gardner and Carleton 2009:167). These characteristics partially differ from our results, since *R. cherrii* has a narrower foramen magnum region and braincase than *R. mexicanus*, while the nasal bone was relatively longer. Hooper (1952) compared specimens of *R. cherrii* from central Costa Rica to *R. m. lucifrons* central Honduras. Hooper (1952) described *R. m. lucifrons* as possessing a rostrum and incisive foramen that were slightly smaller than that of *R. cherrii*, consistent with the differences we documented for the ventral view of the skull.

The differences in size (CS) for both views of the skull showed that *R. cherrii* tends to have a larger cranium than *R. mexicanus*. These results are consistent with the linear measurements given by Hooper (1952) and traditional morphometric analyses carried out by Gardner and Carleton (2009). Hooper (1952) highlighted *R. cherrii* as one of the largest subspecies within *R. mexicanus*, comparing it in body size and skull length with *Peromyscus maniculatus*.

Although our morphometric analyses statistically differentiate *R. cherrii* from *R. mexicanus*, both species showed overlap in shape and size of the skull. The degree of morphological overlap among species of *Reithrodontomys* has

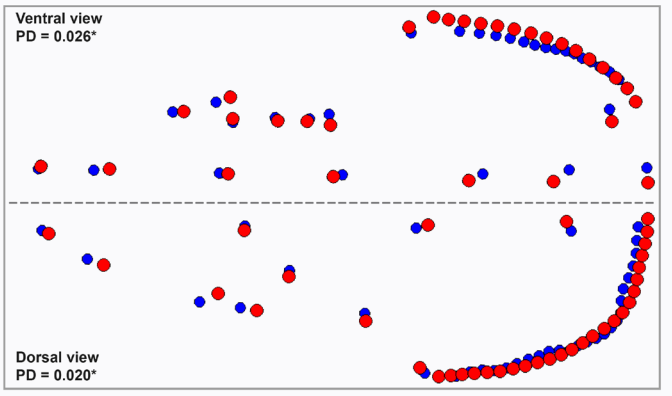

Figure 4. Differences in mean shapes of ventral and dorsal views of the skull, using the Procrustes distances. Red dots = *Reithrodontomys mexicanus* and blue dots = *R. cherrii*, PD = Procrustes distances, asterisks = significant differences based on pairwise permutation test ($P < 0.05$).

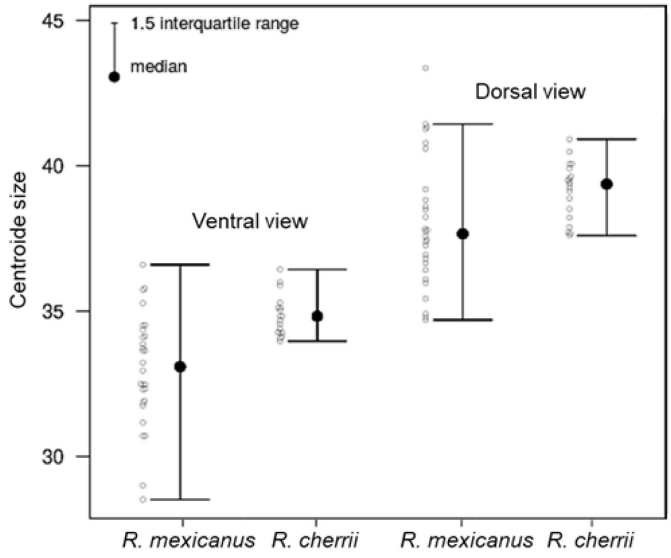

Figure 5. Skull size differences (based on centroid size variable) between *Reithrodontomys mexicanus* and *R. cherrii* for ventral and dorsal views. Statistical significance considered with $P \leq 0.05$.

been evident since the earliest monographs of the genus (Howell 1914; Hooper 1952). This may be why the taxonomic identification of *Reithrodontomys* species is difficult, leading to an underestimation of the actual number of species within this genus. For *R. mexicanus*, Hooper (1952) reported cranial and body measurements very similar or with very wide ranges among all its subspecies, including the former *R. m. cherrii*. The strong similarity of morphological (cranial and body measurements) and pelage coloration among these subspecies explains the inclusion of *R. cherrii* within *R. mexicanus* (Howell 1914), even though it was originally described as a species (Allen 1891).

Reithrodontomys mexicanus has one of the widest distributions within the subgenus *Aporodon* (Arellano 2015), whereas *R. cherrii* is restricted to the highlands of central Costa Rica and the Cordillera de Talamanca (Gardner and Carleton 2009; Villalobos-Chaves *et al.* 2016). Throughout its distribution, *R. mexicanus* is associated with a variety of vegetation-types such as humid oak forests, cloud forests, deciduous arid forests, and deciduous lowland forests (Hooper 1952), which coincides with its broader environmental space here reported compared to that of *R. cherrii*. *R. mexicanus* also occupies areas with high mean values of temperature and low values of precipitation compared to those for the distribution area of *R. cherrii*. The overlap of the minimum-volume ellipsoids in a small region, as well as the low Jaccard similarity index value, may be due to shared environmental characteristics between cloud forests and montane pluvial forests, the main plant formations where *R. mexicanus* and *R. cherrii* occurs, respectively.

The bioclimatic variables used in this study have been previously used in mammal ecological studies (Santos *et al.* 2017; Guevara *et al.* 2018; Stanchak and Santana 2018). BIO5, BIO6, BIO14, and BIO15 are variables that may be limiting the distribution of cloud forest species (Guevara *et al.*

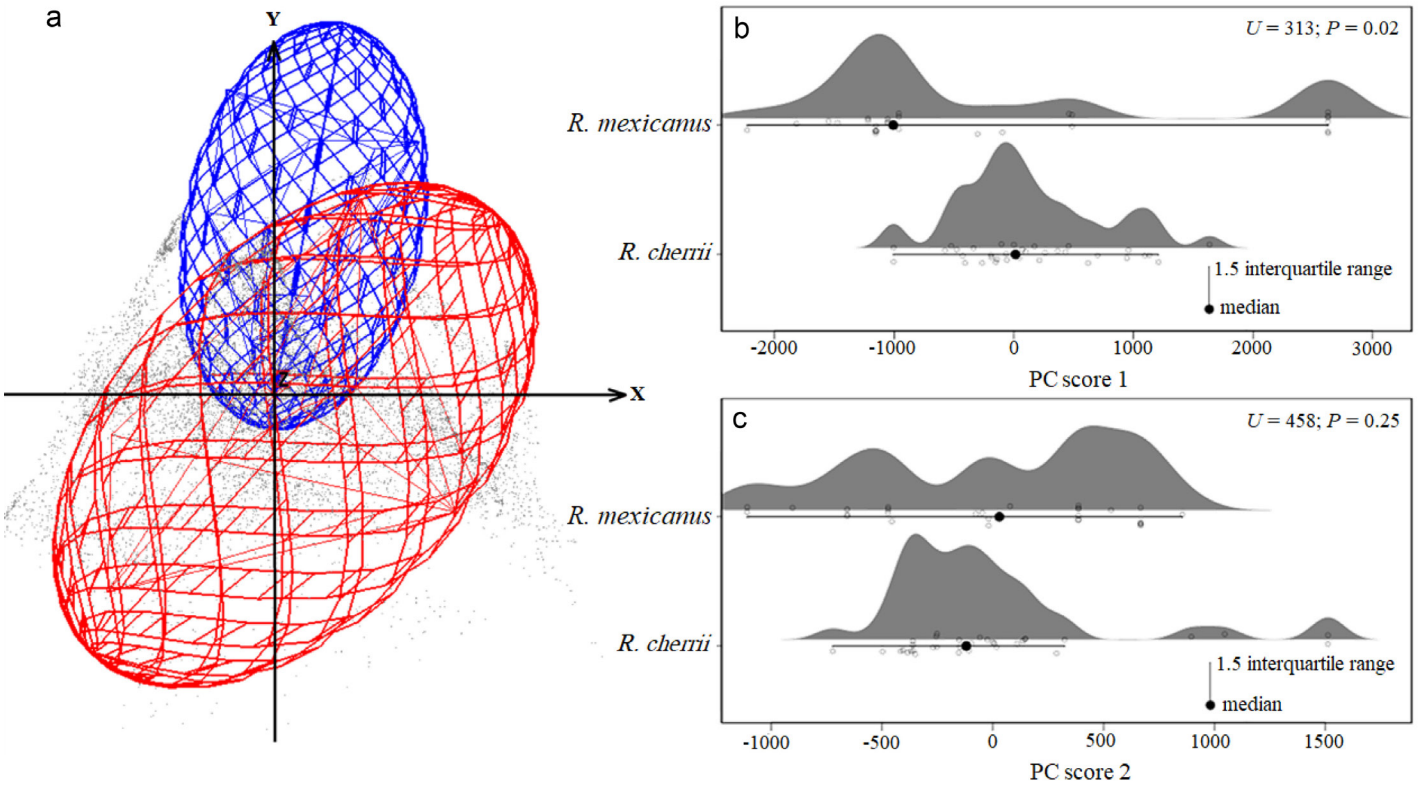

Figure 6. Environmental niche of *Reithrodontomys mexicanus* (red ellipsoid) and *R. cherrii* (blue ellipsoid) displayed in a three-dimensional space and based on the occurrence records and a background data (a). On the right (b and c) show the statistical comparisons using the scores of the first two principal components derived from the environmental variables. Statistical significance considered with $P \leq 0.05$.

2018). Of these four variables, only BIO14 (Precipitation of the driest month) was not significantly different, while the annual precipitation values were the most divergent among regions occupied by these species. These values were higher than 2,000 mm per year for *R. cherrii*, coinciding with the physical-geographical characteristics of the Central Valley (Gómez 1986), which is the climatic region where it is distributed in Costa Rica.

Additionally, we used elevation and NDVI variables to characterize the environmental space of each species. Although the minimum and maximum elevation values were higher for *R. cherrii*, the mean was similar between species. The altitudinal gradient of *Aporodon* species is variable, but most of them inhabit above 1,000 masl (Hooper 1952; Hall 1981). This could explain the lack of statistical differences when comparing this variable between the two species. Elevation has been widely used in studies focused on small rodents (McCain 2005), and it is useful to characterize the habitat in this group. However, this variable should be treated with caution when carrying out ecological analyses, such as niche modeling, due to the high association to temperature and precipitation, especially for small mammals distributed at high elevations (Rubidge *et al.* 2011; Santos *et al.* 2017; Guevara *et al.* 2018).

The NDVI is related to different vegetation parameters (Pettorelli 2013), with values ranging between 0.2 and 0.8, where higher numbers are indicators of photosynthetic activity linked to vegetation types such as temperate forest, rain forest, among others (Meneses-Tovar 2011). Beyond the statistical differences found for this index between *R. mexicanus* and *R. cherrii*, it is important to highlight that the natural areas where these two species are distributed could be considered high quality ecosystems following Pettorelli et al. (2007), considering that the mean values were greater than 0.6. However, quantitative and qualitative indicators are needed to assess integrative ecosystem health (Lu *et al.* 2015). The NDVI application in animal ecology appears to be helpful, especially since it can be linked to animal distribution and abundance (Pettorelli *et al.* 2005). Its use in carnivorous and omnivorous mammal species has been well explored but little is known for small mammals (Pettorelli *et al.* 2011). Our results confirm the utility of this index in habitat characterization and encourages their inclusion in ecological studies for small rodents.

Howell (1914) included *R. cherrii* within *R. mexicanus* as one of its largest and brightest subspecies (Hooper 1952). In mammals, environment can include changes in structures such as skull and jaw, leading to ecophenotypic variations (Camul and Polly 2005). This phenotypic change due to habitat could justify *R. cherrii* misclassification at the subspecific level. However, the high genetic divergence reported between this former subspecies and *R. mexicanus*, translates into different evolutionary histories that vindicates it at the species-level, now as a member of the *R. tenuirostris* species group (Arellano *et al.* 2003, 2005). We found these two species to be different based on the skull morphometry and environmental. Thus, complementing the previous molecular evidence as a whole integrative taxonomy approach that supports *R. cherrii* as a different species from *R. mexicanus*.

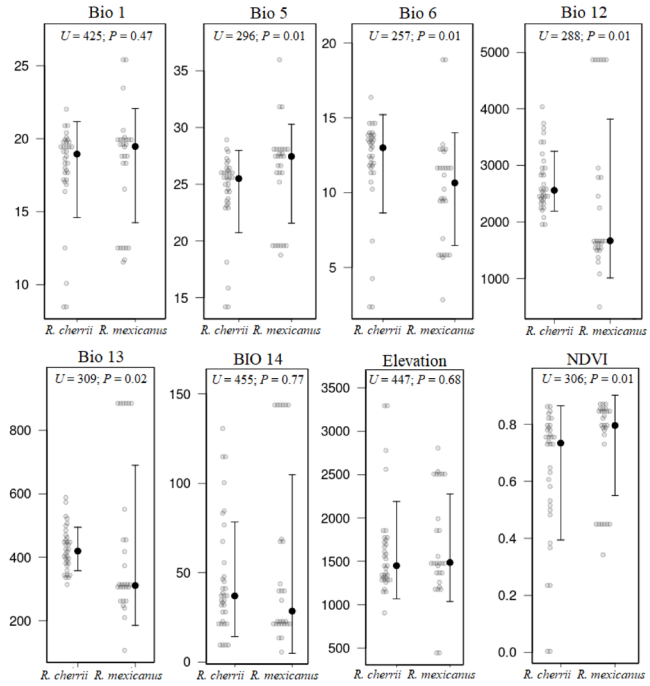

Figure 7. Pairwise comparisons of variables used to characterize the environmental space between *Reithrodontomys mexicanus* and *R. cherrii*. Variable names are in the methods section. Statistical significance considered with $P \leq 0.05$.

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Appendix 1

List of *Reithrodontomys mexicanus* and *R. cherrii* voucher specimens and their associated collecting localities used in the geometric morphometric analyses. Abbreviations before catalogue number represent the mammal collection housing the specimens: AMNH = American Museum of Natural History; BYU = Brigham Young University; CMC = Colección de Mamíferos del Centro de Investigación en Biodiversidad y Conservación; ECOSUR = Colección Mastozoológica de El Colegio de la Frontera Sur, Unidad San Cristóbal; UMMZ = Museum of Zoology, University of Michigan.

Voucher	Species	Locality
UMMZ-109894	*R. mexicanus*	Los Esesmiles, Chalatenango, El Salvador
UMMZ-109897	*R. mexicanus*	Los Esesmiles, Chalatenango, El Salvador
UMMZ-109900	*R. mexicanus*	Los Esesmiles, Chalatenango, El Salvador
UMMZ-109903	*R. mexicanus*	Los Esesmiles, Chalatenango, El Salvador
UMMZ-109905	*R. mexicanus*	Los Esesmiles, Chalatenango, El Salvador
UMMZ-116882-116884	*R. mexicanus*	Santa María de Ostuma, 9 km N of Matagalpa, Nicaragua, 1,400 m
UMMZ-118145-118146	*R. mexicanus*	Municipio La Libertad, Hacienda El Injerto, río Aguacate, Huehuetenango, Guatemala, 1600 m.
UMMZ-118147-118150	*R. mexicanus*	Barillas, Hacienda Santa Gregoria, Huehuetenango, Guatemala
UMMZ-118152-118153	*R. mexicanus*	Barillas, Hacienda Santa Gregoria, Huehuetenango, Guatemala
UMMZ-118154-118155	*R. mexicanus*	Finca Concepción, Tucurú, Alta Verapaz, Guatemala
AMNH-142460	*R. mexicanus*	Coto Brus, Cañas Gordas, Puntarenas, Costa Rica
AMNH-142462-142463	*R. mexicanus*	Coto Brus, Cañas Gordas, Puntarenas, Costa Rica
AMNH-142465	*R. mexicanus*	Coto Brus, Cañas Gordas, Puntarenas, Costa Rica
AMNH-142468-142472	*R. mexicanus*	Coto Brus, Cañas Gordas, Puntarenas, Costa Rica
BYU-15426	*R. mexicanus*	Municipio Santiago Comaltepec, 11 km SW (by road.) La Esperanza, Oaxaca, México
BYU-15436	*R. mexicanus*	Municipio Teotitlán de Flores Magón, 1.5 km S Puerto de la Soledad, Oaxaca, MX
BYU-15439	*R. mexicanus*	Municipio Ixhuacán, 18 km NW Teocelo, Veracruz, México
BYU-20781	*R. mexicanus*	Rancho La Providencia, Chiapas, México, 1775 m
CMC-872	*R. mexicanus*	Municipio Huatusco, 1.9 km N Las Cañadas (Eco reserva), Veracruz, México
CMC-874	*R. mexicanus*	Municipio Huatusco, 1.9 km N Las Cañadas (Eco reserva), Veracruz, México
CMC-877	*R. mexicanus*	Municipio Huatusco, 1.9 km N Las Cañadas (Eco reserva), Veracruz, México
ECOSUR -2842	*R. mexicanus*	Santo Tomás Oxchuc, Mercado Indígena, Chiapas, México
ECOSUR-3000	*R. mexicanus*	Ejido Sombra Chica, 1 km NW Tumbalá, Chiapas, México
ECOSUR-931	*R. mexicanus*	Las Grutas. PN Lagos de Montebello, 3.45 Km N El Vivero, Chiapas, México
AMNH-7905	*R. cherrii*	Cerro La Carpintera, Cartago, Costa Rica
AMNH-123503	*R. cherrii*	Cerro La Carpintera, Cartago, Costa Rica
AMNH-7902-7904	*R. cherrii*	Cerro La Carpintera, Cartago, Costa Rica
AMNH-7908	*R. cherrii*	Cerro La Carpintera, Cartago, Costa Rica
AMNH-131739	*R. cherrii*	Escazú, San José, Costa Rica
AMNH-135258	*R. cherrii*	Vázquez de Coronado, Nubes, San José, Costa Rica
AMNH-135924	*R. cherrii*	Alajuela, Sabanilla, Costa Rica
AMNH-138088	*R. cherrii*	Escazú, Los Higuerones, San José, Costa Rica
AMNH-139284	*R. cherrii*	Montes de Oca, Sabanilla, San José, Costa Rica
AMNH-139289	*R. cherrii*	Montes de Oca, Sabanilla, San José, Costa Rica
AMNH-141878	*R. cherrii*	Alajuelita, Santa Teresa, Peralta, Costa Rica
AMNH-141880-141881	*R. cherrii*	Alajuelita, Santa Teresa, Peralta, Costa Rica
AMNH-141883	*R. cherrii*	Alajuelita, Santa Teresa, Peralta, Costa Rica
AMNH-19187-19188	*R. cherrii*	Montes de Oca, San Pedro, San José, Costa Rica
AMNH-19192	*R. cherrii*	Montes de Oca, San Pedro, San José, Costa Rica

Appendix 2

Anatomical and numerical position (see Figure 2) of landmarks and semi-landmarks used in the geometric morphometric analyses for ventral and dorsal views of the skull.

	Ventral		Dorsal
1	Rostralmost point of the upper incisor tooth next to the midline	1	Rostralmost point of the nasal bone
2	Anteriormost point of the incisive foramen	2	Anteriormost point of suture between nasal bone and nasal process of the incisive
3	Posteriormost point of the incisive foramen	3	Rostral end of zygomatic plate in a dorsal projection
4	Rostral end of zygomatic plate in a ventral projection	4	Anteriormost point of the orbit in a dorsal projection
5	Anteriormost point of the orbit in a ventral projection	5	Narrowest point of the interorbital region
6	Caudalmost point of the orbit in a ventral projection	6	Rostralmost point of the parietal bone
7	Posterior end of zygomatic bar in a ventral projection	7	Caudalmost point of the orbit in a dorsal projection
8-20	Semi-landmarks	8	Posterior end of zygomatic bar in a dorsal projection
21	Lateral margin of the basioccipital	9-31	Semi-landmarks
22	Lateral margin of the foramen magnum	32	Caudal end of the curvature of the occipital bone
23	Posteriormost point of the occipital foramen in the midline	33	Intersection of the sagittal and parietal-interparietal sutures
24	Anteriormost point of the occipital foramen in the midline	34	Intersection of the coronal and sagittal sutures
25	Midpoint of suture between basisphenoid and basioccipital	35	Intersection of the naso-frontal suture in the midline
26	Posteriormost extent of palate at the midline		
27	Posteriormost point of the third molar		
28	Contact point between second and third molars		
29	Contact point between first and second molars		
30	Anteriormost point of the first molar		

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Appendix 3

Geographical coordinates (Datum WGS-84) of localities used in the ecological analysis for *Reithrodontomys mexicanus* and *R. cherrii*.

Species	Longitude	Latitude	Species	Longitude	Latitude
R. mexicanus	-89.133	14.383	*R. mexicanus*	-92.016	15.566
R. mexicanus	-85.925	13.005	*R. mexicanus*	-90.066	15.300
R. mexicanus	-91.315	15.803	*R. mexicanus*	-96.447	17.555
R. mexicanus	-97.220	18.356	*R. mexicanus*	-92.340	15.216
R. mexicanus	-97.064	19.525	*R. mexicanus*	-91.720	16.130
R. mexicanus	-96.984	19.258	*R. cherrii*	-83.984	9.881
R. mexicanus	-92.346	16.794	*R. cherrii*	-84.216	10.076
R. mexicanus	-92.315	17.270	*R. cherrii*	-84.144	9.894
R. mexicanus	-87.106	14.208	*R. cherrii*	-84.136	9.913
R. mexicanus	-96.305	17.599	*R. cherrii*	-84.029	9.947
R. mexicanus	-96.016	17.176	*R. cherrii*	-84.021	9.944
R. mexicanus	-92.340	15.216	*R. cherrii*	-83.962	9.987
R. mexicanus	-93.120	17.190	*R. cherrii*	-84.083	9.933
R. mexicanus	-91.700	16.100	*R. cherrii*	-83.849	9.979
R. mexicanus	-92.640	15.650	*R. cherrii*	-83.798	9.768
R. mexicanus	-93.070	15.800	*R. cherrii*	-83.981	9.896
R. mexicanus	-92.692	16.684	*R. cherrii*	-84.153	9.913
R. mexicanus	-92.400	16.963	*R. cherrii*	-84.406	10.221
R. mexicanus	-90.031	15.089	*R. cherrii*	-84.059	9.705
R. mexicanus	-92.851	16.990	*R. cherrii*	-83.850	9.983
R. mexicanus	-92.975	17.208	*R. cherrii*	-83.902	9.833
R. mexicanus	-91.932	15.485	*R. cherrii*	-83.916	9.839
R. mexicanus	-86.339	13.080	*R. cherrii*	-84.244	10.102
R. mexicanus	-89.366	14.400	*R. cherrii*	-83.982	9.950
R. mexicanus	-90.455	14.558	*R. cherrii*	-84.107	9.868
R. mexicanus	-89.623	15.136	*R. cherrii*	-84.183	9.950
R. mexicanus	-96.605	17.579	*R. cherrii*	-83.548	9.450
R. mexicanus	-96.842	18.168	*R. cherrii*	-83.877	9.823
R. mexicanus	-97.040	18.618	*R. cherrii*	-83.916	9.650
R. mexicanus	-97.028	19.037	*R. cherrii*	-83.881	9.833
R. mexicanus	-96.798	17.811	*R. cherrii*	-83.903	9.879
R. mexicanus	-90.062	15.385	*R. cherrii*	-83.983	9.890
R. mexicanus	-97.024	18.869	*R. cherrii*	-83.803	9.753
R. mexicanus	-91.394	15.571	*R. cherrii*	-84.139	9.883
R. mexicanus	-89.481	15.166	*R. cherrii*	-84.333	10.277
R. mexicanus	-91.560	15.984	*R. cherrii*	-83.707	9.566
R. mexicanus	-90.251	15.236	*R. cherrii*	-83.968	9.888
R. mexicanus	-96.436	17.386	*R. cherrii*	-84.233	10.183
R. mexicanus	-92.591	16.051	*R. cherrii*	-84.465	9.920

CAPÍTULO III

Species delimitation and integrative taxonomy of the *Reithrodontomys mexicanus* (Rodentia: Cricetidae) cryptic complex

Species delimitation and integrative taxonomy of the *Reithrodontomys mexicanus* (Rodentia: Cricetidae) cryptic complex

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Running title: *Integrative taxonomy of the R. mexicanus complex*

ABSTRACT

Species boundaries are difficult to establish in groups with very similar morphology. As an alternative, it has been suggested to integrate multiple sources of data to clarify taxonomic problems in taxa where cryptic speciation processes have been reported. This is the case of the harvest mouse *Reithrodontomys mexicanus*, which has a problematic taxonomy history as it is considered a complex species. Here, we evaluate the cryptic diversity of *R. mexicanus* using an integrative taxonomy approach in order to detect candidate lineages at the species-level. One mitochondrial (cytb) and two nuclear (Fgb-I7 and IRBP) genes were used in the molecular analysis. Species hypotheses were suggested based on three molecular delimitation methods (mPTP, bGMYC, and STACEY), and cytb genetic distances values. Skull and environmental space differences between the delimited species were also tested to complement the discrimination of candidate species. Based on the consensus across the delimitation methods and genetic distance values, four species were proposed, which were mostly supported by morphometric and ecological data: *R. mexicanus* clade I (sensu stricto), *R. mexicanus* clade IIA, *R. mexicanus* clade IIB, and *R. mexicanus* clade III. In addition, the evolutionary relationships between the species that comprise the *R. mexicanus* group were discussed from a phylogenetic approach. Our findings present important taxonomic implications for *Reithrodontomys*, as the number of known species for this genus increases. Furthermore, we highlight the importance of the use of multiple sources of data in systematic studies to establish robust delimitations between species considered taxonomically complex.

Keywords: Cricetidae, rodents, cryptic speciation, molecular delimitation, multiples lines of evidence

INTRODUCTION

A continuing challenge in systematics is the determination of which species concept is most appropriate for proposing and delimiting species. Most species have been described using morphological traits (Mayden 1997), but an increasing number of studies are reporting new species using molecular data (see Jörger and Schrödl 2013). The controversy around species concepts is largely due to the different nature of the information upon which different concepts are based (de Queiroz 2007). For example, the Phylogenetic Species Concept (Cracraft 1989) tends to be used when genetic data are analyzed, while studies focusing on reproductive isolation tend to prefer the Biological Species Concept (Mayr 1942). Bradley and Baker (2001) proposed that mammal species be delimited using the Genetic Species Concept, specifically using genetic distances estimated from the mitochondrial gene Cytochrome b (cytb, Baker and Bradley 2006). In an attempt to eliminate the species problem, de Queiroz (1998, 2005, 2007) proposed the General Lineage Species Concept (GLC). This unified concept uses different species properties, considering elements of the most accepted concepts, and integrates multiple lines of evidence to establish boundaries between species. Therefore, any criterion that evidence a metapopulation lineage evolving separately is considered relevant to identify species (de Queiroz 2005). This multisource approach is known as integrative taxonomy (Dayrat 2005) and has been widely recommended in systematic studies (see Padial et al. 2010; Sangster 2018).

Molecular data have been crucial for studying cryptic species in rodents; they allow both the determination of the number of entities comprising a species complex and the delimitation of those entities (D'Elía et al. 2019, and references therein). Using an integrative taxonomy approach, species phylogenetic hypotheses in rodents have been corroborated by other data sources such as morphology, ethology, biogeography, and ecology (e.g., Almendra et al. 2018, Rivera et al. 2018; Onditi et al. 2021). Thus, the congruence among several lines of evidence indicates robust species hypotheses (Dayrat 2005; Padial et al. 2010).

Reithrodontomys mexicanus (Saussure, 1860) is a cricetid rodent with a discontinuous geographic distribution from Mexico to northwestern South America (Hooper 1952; Hall 1981). Populations occupy a variety of habitats including humid pine-oak forests, cloud forests, and lowland deciduous forests, and they can generally be found in an altitude range from around 1,000 to 3,800 m. Recent changes in its taxonomy (summarized in Martínez-Borrego et al. 2020) have been proposed due to divergent lineages detected using different genetic loci and craniodental characteristics. Arellano et al. (2005), using information from the cytb gene, determined three well-differentiated clades for this species. Based on those findings, they proposed that *R. cherrii* be elevated to the species level and they proposed the existence of an undescribed species distributed in the Sierra Madre Oriental and

northern Oaxaca, Mexico (Arellano et al. 2005). Using mitochondrial and nuclear genes, Miller and Engstrom (2008) also suggested that *R. mexicanus* constitutes a cryptic species complex, while Gardner and Carleton (2009) proposed the former *R. m. garichensis* as a species of the *R. mexicanus* group based on craniodental differences compared to the remaining Central American species of the subgenus *Aporodon*.

As a species complex, *R. mexicanus* sensu lato needs to be reevaluated from a taxonomic point of view. We hypothesize that each of the divergent lineages within *R. mexicanus* constitutes valid species given their significant genetic, morphological, and ecological differences. Here, our goal is to assess the cryptic diversity of this species based on the suggestion by Arellano et al. (2005) that it is composed of at least two species. Putative species will be delimited in accordance with the GLC under an integrative taxonomy approach.

MATERIALS AND METHODS

Molecular analyses of the *R. mexicanus* species complex

Genetic data.

DNA sequences from the mitochondrial gene cytb and the nuclear genes Intron 7 of the beta fibrinogen (Fgb-I7) and Interphotoreceptor retinoid-binding protein (IRBP) were obtained from collected specimens and tissue loans from mammal collections (Fig. 1). The specimens wild-caught followed the Guidelines approved by the American Society of Mammologists (Sikes et al. 2016). Genomic DNA extraction, primers, and PCR procedures for the cytb and Fgb-I7 genes, as well as sequencing protocols for the amplified PCR products of each gene are provided in Martínez-Borrego et al. (2022a). Approximately 1140 pb of cytb was amplified in 47 individuals of *R. mexicanus* while a 608 bp fragment of Fgb-I7 was amplified in 58 individuals. For the IRBP gene, the amplification protocol was only successful in 3 individuals using primers A1 (Stanhope et al. 1992) and B2 (Wickliffe et al. 2003) and the PCR conditions described in Almendra et al. (2018). In individuals for which other tissues were not available, a skin DNA extraction protocol was implemented with modifications from Rogers et al. (2011). The skin DNA amplification was realized using Illustra PuReTaq Ready-To-Go PCR Beads and a series of primer pairs as follows: L14724 (Irwin et al. 1991) and H15149 (Kocher et al. 1989) for cytb, B17 and Bfib (Wickliffe et al. 2003) for Fgb-I7.

Sequences were edited using Codon Code Aligner v.8.0.2 (CodonCode Corporation, Dedham, MA, USA) and aligned against a reference in UGENE v.1.32.0 (Okonechnikov et al. 2012) using the MUSCLE method. Eleven species of the genus *Reithrodontomys* were employed as the outgroup, representing the species groups defined by Hooper (1952): 5 from the *R. mexicanus* group, 3 from the *R. tenuirostris* group, 2 from the *R. megalotis* group, and 1 from the *R. fulvescens* group. The

final dataset comprised 109 sequences for cytb, 68 for Fgb-I7, and 26 for IRBP. The concatenated dataset was only available for cytb + Fgb-I7 (68 sequences, 1750 bp long) and cytb + IRBP (24, 2064 bp long) because very few individuals presented genetic information for all loci. The information of the sequences generated in this study and those downloaded from GenBank is included in Appendix 1.

Phylogenetic analysis and species delimitation.

The evolutionary model and partition scheme (in the case of coding genes) that best fit each dataset was estimated in ModelFinder (Kalyaanamoorthy et al. 2017) according to the Bayesian Informative Criterion (Table 1). Maximum Likelihood (ML) and Bayesian Inference (BI) reconstruction methods were used to estimate phylogenetic relationships for each gene and the concatenated datasets. ML analyses were run in IQ-Tree (Nguyen et al. 2015) using 10000 Ultrafast Bootstrap replicates (UFBoot; Minh et al. 2013) and the GENESITE resampling strategy to estimate branch support. The BI analyses were run in MrBayes v3.2.6 (Ronquist and Huelsenbeck 2003) using eight chains in two independent runs (10 million generations each, sampling once every 1000 generations). We used Tracer v1.7.1 (Rambaut et al. 2018) to verify the convergence and seasonality of each run. The posterior probability (pP) was obtained for individual nodes by constructing a majority-rule consensus after discarding the trees prior to the stationarity phase as burn-in. These analyses were implemented within the CIPRES Science Gateway portal (Miller et al. 2012).

We performed three molecular species delimitation methods: multi-rate Poisson Tree Processes (mPTP; Kapli et al. 2017), Bayesian General Mixed Yule-Coalescent Model (bGMYC; Reid and Carstens 2012), and Species Tree and Classification Estimation, Yarely (STACEY, Jones 2017). These methods were selected because they do not require a priori assignment of individuals to groups. This allowed us to define the cryptic lineages within *R. mexicanus* sensu lato without assumptions regarding the phylogenetic relationships between them.

The cytb gene was used for the two single-locus methods mPTP and bGMYC. The non-coalescent mPTP method was implemented in the Exelisis Lab platform (http://www.exelixis-lab.org) using the BI tree and default parameters. The bGMYC coalescent method was implemented in the bGMYC package (Reid and Carstens 2012) of the R library (R Core Team 2018) using the time-calibrated tree obtained in BEAST2 and the following input parameters: mcmc = 100000, burnin = 90000, thinning = 100, t1 = 11, t2 = 16 (based on the upper range of suggested species with mPTP, considering the outgroup), py1 = 0.5, py2 = 1.5, pc1 = 0.1, pc2 = 0.5, start = c (1.0, 0.1, 11), scale = c(20, 10, 5.00). The multi-locus STACEY method was run using each of the combined datasets (cytb + Fgb-I7 and cytb + IRBP). This coalescent method is implemented as a package within

BEAST2 and uses a modified birth-death-collapsed model for the species tree. The species.tree file generated by STACEY was used as input in the SpeciesDelimitationAnalyzer program (speciesDA.jar, www.indriid.com ; burnin = 1000 collapse height = 0.0001, and similarity cutoff = 1.0) to summarize the posterior tree distribution and calculate the frequency with which each pair of taxa were assigned to the same clade.

The criterion used to define the species limits was congruence among the greatest number of delimitation methods, which supports the correct recognition of the possible species (Carsten et al. 2013). The genetic distances between the lineages proposed as species were estimated using the cytb gene in MEGAX (Kumar et al. 2018) and the Kimura two-parameter evolutionary model (K2P). The 5% cytochrome-b distance value associated with mammalian species recognition (Bradley and Baker 2001) was set as the genetic distance threshold.

Estimation of divergence time for cytb gene.

Divergence times between *Aporodon* clades were inferred in BEAST2 (Bouckaert et al. 2014). We obtained the time-calibrated phylogeny using a Birth-Death model tree prior and an uncorrelated relaxed lognormal clock. Substitution rate and calibration nodes were established in the same way as in Martínez-Borrego et al. (2022a). MCMC analyses were executed with two runs of 10 million generations each, sampling once every 1000 generations. The BEAST log file was examined in Tracer (Rambaut et al. 2018) to assess the convergence of the independent runs, as well as the effective sample size (ESS≥200). A Maxime clade credibility tree was obtained in TreeAnotator after discarding the trees prior to the stationary phase as burn-in.

Geometric morphometric of the *R. mexicanus* species complex

Morphometric data.

We examined 335 adult specimens (fully erupted M^3; following age classes from Arellano et al. 2012) deposited in mammal collections and classified at the time of collection as *R. mexicanus*. However, due to the cryptic diversity reported for this species, only individuals that 1) had a known genetic identity or 2) were collected within less than 60 km of an individual with a known genetic identity were used in the morphometric analyses. In total, 69 specimens (31 males, 38 females) were selected for morphometric analysis (Fig. 1; Appendix 1) and grouped according to the species proposed by the delimitation methods. Individuals from the potential species from El Salvador and Colombia (see Results) were excluded due to a low sample size ($n \leq 5$). Digital images of the dorsal and ventral view of the skull of each specimen were taken using an Olympus DP73 Digital Camera and a millimeter rule as a scale bar

For both views, we digitized landmark and semi-landmark configuration as in Martínez-Borrego et al. (2022b) using TPSdig 2.31 (Rohlf 2015). We also conducted a Generalized Procrustes Analysis

(Rohlf and Slice 1990) that included alignment, rotation, and translation of landmark and semi-landmark configurations. During this processing, semi-landmarks positioned on curved structures were allowed to slide along their tangent vectors until reaching the point of minimum bending energy (Bookstein 1997; Zelditch et al. 2004). This analysis was performed in the R package geomorph 3.3.1 (Adams and Otarola-Castillo 2013). The outputs of this superimposition were the shape variables (Procrustes Distances and Procrustes Coordinates) and the centroid size (CS).

Morphometric comparison between delimited species.

We first explored the shape variation in both views of the skull using a Principal Component Analysis (PCA) of the Procrustes Coordinates to visualize clustering and reduce the dimensionality of the data (see below). We tested shape differences between males and females using a Procrustes ANOVA (Goodall 1991; Anderson 2001) with an OLS estimation method and a resampling procedure based on 1000 iterations. We also assessed size (CS) differences between sexes using the R package stats. Multiple regressions were conducted to evaluate the effect of the skull size on the shape variation (allometry). For this, we used 1000 permutations and a factorial design that included shape as the dependent variable, sex as the main factor, and CZ as a covariate. PCA, shape sexual dimorphism and allometry analyses were performed in geomorph 3.3.1.

For both views of the skull, morphometric differences between delimited species (independent variable) with respect to shape (dependent variable) were determined using a Procrustes ANOVA in geomorph 3.3.1. A similar approach was performed with the function lm.rrpp in the R package RRPP (Collyer and Adams 2018) to test CS differences between the delimited species. The R package MORPHO 2.4 (Schlager 2016) was used to perform pairwise comparison tests to quantify differences in skull shape between delimited species using Procrustes Distances, 1000 permutations, and a significance level of $P \leq 0.05$.

Skull shape differences were visualized with canonical variates analysis (CVA), setting the delimited species a priori. Because CVA cannot be performed when the number of variables is greater than the sample size per group (Kovarovic et al. 2011), we only used the shape information from the first 10 principal components (90% and 92% of the variance explained for dorsal and ventral views, respectively). Finally, we performed Linear discriminant analysis (LDA) to assess the discrimination of individuals against the different delimited species based on skull shape. A cross-validation procedure from the CVA scores was employed to obtain the correct discrimination rate, which allowed us to verify the effectiveness of the LDA to discriminate taxa into their correct groups. For these analyses, we used the R packages geomorph and MASS 7.3-51.4 (Ripley et al. 2020).

Ecological analyses of the *R. mexicanus* species complex

Environmental data.

We used the occurrence data of the individuals grouped in the delimited species to perform an ecological analysis. Localities from museum databases (not included in the phylogeny) collected within less than 60 km of an individual with a known genetic identity were also included in the ecological analyses (Fig. 1; Appendix 1). To reduce georeferencing errors, each geographic coordinate was rectified against the known distribution for *R. mexicanus* sensu lato (Hooper 1952; Hall 1981). We removed duplicate point records and thinned the dataset by setting a distance between localities ≤ 3 km using the R package spThing (Aiello-Lammens et al. 2015). This step was required to reduce spatial autocorrelation and avoid overfitting the model derived from the presence of multiple records in the same 1-km^2 pixel. 56 unique localities were employed in the ecological analysis to test niche differences among delimited species. The individuals from El Salvador (see Results) could not be included because they were collected from a single locality. Six bioclimatic variables at 1-km^2 resolution were downloaded from Wordclim 2.0 (Fick and Hijmans, 2017; http://www.worldclim.org): Bio1 = Annual Mean Temperature, Bio5 = Max Temperature of Warmest Month, Bio6 = Min Temperature of Coldest Month, Bio12 = Annual Precipitation, Bio13 = Precipitation of Wettest Month, and Bio14 = Precipitation of Driest Month. These bioclimatic variables were selected based on previous studies that highlighted their importance in ecological studies of small mammals (e.g.: Santos et al. 2017; Guevara et al. 2018; Stanchak and Santana 2018; Martínez-Borrego et al. 2022b). Due to the arboreal preferences reported for species of subgenus *Aporodon* (Hooper 1952; González-Cozátl and Arellano 2015), we included in our analyses the variable Vegetation Continuous Field (VCF; Hansen et al. 2002; www .landcover.org) as a measure of the percentage of vegetation cover. This product was obtained from the MODIS sensor using 24 scenarios corresponding to the year 2020, with an original resolution of 250 m. We rescaled the VCF product to the same resolution as the bioclimatic variables using ArGis 10.8 (ESRI 2020).

Ecological niche modeling (ENM).

We used MaxEnt (Phillip et al. 2006) to build ENMs for each delimited species using the occurrence points and the environmental variables. To improve the models' fit and predictive ability, different parameter settings were evaluated (Warren and Seifert 2011; Muscarella et al. 2014) using a "checkerboard" method to partition the training and test data. Different values of the regularization multiplier (from 0.5 to 6, in increments of 0.5) and five combinations of feature classes (L = linear, Q = quadratic, H = hinge, P = product, LQHP) were tested. The optimal combination of parameters for each ENM was estimated in the R package ENMeval (Muscarella et al. 2014) and selected according to the lowest delta AICc (Akaike Information Criterion) score

(Supplementary material 1). To obtain the ENMs, calibration areas were defined using the minimum convex polygon. Final models were constructed with 50 replicates, and continuous maps were visualized using the cloglog output. The ENMs were binarized using the 10th-percentile cut-off threshold in ArGis 10.8. Each model's performance was evaluated using the Partial Roc metric implemented in the Niche Toolbox site (http://shiny.conabio.gob.mx:3838/nichetoolb2/), with 1000 Bootstrap iterations and E=0.05.

Ecological niche comparison between delimited species.

We extracted the values of the environmental variables from each occurrence point in order to determine whether the delimited species differed with respect to the ecological space they occupied. In addition, we performed a CVA to evaluate whether the ecological niche of the delimited species allows them to be segregated on the basis of their environmental characteristics. Multivariate statistical analyses and CVA were run in R.

RESULTS

Cytochrome b phylogeny and molecular species delimitation.

The cytb gene trees produced identical topologies using both the BI and ML reconstruction methods (Fig. 2). The *Aporodon* major clade recovered the *R. mexicanus* (*R. brevirostris*, *R. mexicanus*, *R. darienensis*, *R. garichensis*, *R. gracilis*, and *R. spectabilis*) and *R. tenuirostris* (represented here by *R. microdon*, *R. tenuirostris*, and *R. cherrii*) species groups. Specimens from Costa Rica identified as *R. sp.* by Miller and Engstrom (2008) were recovered as closely related to *R. garichensis*. *R. mexicanus* specimens split into three clades that were well-supported in the BI method, but weakly supported by ML. The clade I included individuals from Mexico, Guatemala, and El Salvador, and were recovered as the sister group to *R. brevirostris* from Costa Rica (pP = 1). The clade II corresponded to specimens distributed in Colombia and Ecuador, sister to *R. darienensis* from Panama (pP = 1). The remaining individuals of *R. mexicanus* were grouped into a clade III with geographical distribution in the Sierra Madre Oriental and northern Oaxaca, Mexico. This clade was sister to the *R. mexicanus* and *R. tenuirostris* species groups (pP = 1).

The results of the species delimitation methods were not congruent with each other (Fig. 2). For the *R. mexicanus* group, the mPTP method identified 15 putative species while 11 were delimited by the bGMYC. The multi-locus method STACEY suggested 10 species for both datasets (cytb + Fgb-I7 and cytb + IRBP), excluding species that were not successfully sequenced. The three methods supported the species delimitation of *R. darienensis*, *R. sp.* Volcan Poas, and *R. garichensis*, the latter including the *R. sp*. individual from La Carpentera, Cartago, Costa Rica. In addition, *R. gracilis* and *R. spectabilis* were considered the same species, which was delimited from specimens

of *R. gracilis* distributed in El Salvador. For *R. brevirostris*, each delimitation method proposed different numbers of possible species.

Within the *R. mexicanus* species complex, the *R. mexicanus* clade III was supported at the species level by all three delimitation methods. Within the *R. mexicanus* clade I, STACEY (cytb + Fgb-I7) demarcated 4 possible species, while the other methods delimited two. One of them corresponded to individuals from El Salvador, which were considered a distinct species under all the methods (*R. mexicanus* El Salvador). Within the clade II, the mPTP delimited 5 species, bGMYC 2, and STACEY 3 (cytb + Fgb-I7). In this clade, the consensus between methods demarcated two putative species: *R. mexicanus* clade IIA and *R. mexicanus* clade IIB. The cytb genetic distance values between the delimitation consensus ranged from 4.96 to 18.18, with the highest value generally between *R. mexicanus* clade III and the other delimited species. The cytb genetic distance values between delimited species in the *R. mexicanus* group are shown in Table 2 and Supplementary material 2.

Cytochrome b divergence times.

The time-calibrate cytb tree (Fig. 3) showed that the genus *Reithrodontomys* began to diverge ca. 6.83 mya (95% HPD = 5.46 – 8.36). The most common recent ancestor of the major clade *Aporodon* was at ca. 5.70 mya (95% HPD = 4.53 – 6.84), when the delimited species *R. mexicanus* clade III diverged from the rest of the species of this subgenus. Deep divergences were mostly well supported (pP = 1), except for the split between the *R. mexicanus* and *R. tenuirostris* groups ca. 5.35 mya (95% HPD = 4.31 – 6.48). The earliest divergence in the *R. mexicanus* group occurred ca. 4.45 mya (95% HPD = 3.51 – 5.51) when *R. spectabilis* and *R. gracilis* separated from the rest of the species while the most recent divergences occurred between those species (ca. 0.31 mya, 95% HPD = 0.18 – 0.48), excluding individuals of *R. gracilis* from El Salvador (see Discussion).

Nuclear and concatenated phylogenies.

The topologies resulting from the Fgb-I7 and IRBP nuclear genes were inconsistent with each other and with the cytb tree, showing low support values for the ML and BI reconstruction methods. Neither nuclear trees recovered the *Aporodon* species groups, and most clades were included in polytomies for the ML optimality criteria (Supplementary material 3, 4). In the Fgb-I7 tree, individuals from *R. mexicanus* clade IIB were grouped within the *R. mexicanus* clade III, with generally low support values (pP $\leq$ 0.50, UFB $\leq$ 50). *R. mexicanus* clade I specimens did not form a monophyletic group either, and their relationships with the species with which they were grouped were mostly poorly supported (pP $\leq$ 0.80, UFB $\leq$ 85). The IRBP tree showed minor inconsistencies with the cytb tree, and relationships between *Aporodon* species were mostly better supported compared to the Fgb-I7 tree, at least for the BI analysis (Supplementary material 4b).

Tree topologies obtained with the concatenated dataset cytb + Fgb-I7 were almost identical to the cytb topology (Fig. 4). The only differences were in the ML analysis, where specimens of *R. gracilis* from El Salvador were grouped as the sister clade of *R. mexicanus* clade III, but with low support values (UFB = 43, Supplementary material 5). The phylogenies obtained with the concatenated cytb + IRBP dataset were generally congruent with the cytb tree (Fig. 4). Minor differences were found with respect to the tree resulting from the ML analysis, where *R. garichensis* + *R. sp.* Volcan Poas was recovered as a sister clade to *R. microdon*, although these relationships were not well supported (UFB = 44, Supplementary material 6).

Geometric morphometric of the R. mexicanus species complex.

No skull views showed sexual dimorphism in shape (dorsal: $F = 1.18$, $p = 0.28$; ventral: $F = 1.09$, $p = 0.36$) or CS (dorsal: $t = 0.25$, $p = 0.80$; ventral: $t = 0.93$, $p = 0.35$). For the dorsal view of the skull, there was no significant correlation between CS and shape ($F = 0.70$; $p = 0.55$). For the ventral view, the CS-shape correlation was significant ($F = 8.39$; $p = 0.001$), with CS explaining 9.10 % of the shape variation. Despite being statistically significant, this allometric effect was considered relatively weak and the original Procrustes Distance values were used for the remaining analyses.

Procrustes ANOVA revealed significant differences in skull shape (dorsal: $F = 3.41$, $p = 0.004$; ventral: $F = 8.92$, $p = 0.001$) among the delimited species. For the dorsal view, pairwise comparisons showed significant differences among all putative species (Fig. 5). The mean shape of *R. mexicanus* clade IIB differed from *R. mexicanus* clade I in having a relatively longer nasal bone (landmarks 1 and 2), a slightly narrower interorbital region (landmark 5), and the braincase with a tendency to narrow towards the caudal region of the occipital bone. When compared to *R. mexicanus* clade III, it showed a narrowing of the anterior-medial region of the skull (landmarks 1-8; 35) although the braincase is slightly wider towards the ends of the parietal-interparietal bones. *R. mexicanus* clade I and *R. mexicanus* clade III differed in most of the landmarks that characterized the skull shape, the latter having a longer rostrum and a braincase that was wider towards the parietal-interparietal region but narrower towards the curvature of the occipital bone.

In the ventral shape, only *R. mexicanus* clade I - *R. mexicanus* clade IIB did not differ significantly in skull shape. Differences in the mean shape between *R. mexicanus* clade IIB and *R. mexicanus* clade III occurred in the anterior region of the skull; *R. mexicanus* clade III had a longer incisive foramen, but a shorter palate. The *R. mexicanus* clade III skull shape showed a notable contraction of the landmarks (22-24) describing the foramen magnum with respect to the other delimited species analyzed. This putative species also differed from *R. mexicanus* clade I in that it had a shorter line of molars and slightly wider basicranium towards the posterior region of the zygomatic

bar, but with a tendency to narrow towards the tympanic bullae. No view showed significant skull size differences (CS) between delimited species (dorsal: F = 2.19; p = 0.12; ventral: F = 1.72; p = 0.18).

The CVA performed on the two views showed a partial overlap in the morphospace of the delimited species for the dorsal side and considerable discrimination of *R. mexicanus* clade III for the ventral side along the positive CV1 axis (Fig. 5). The LDA based on skull shape did not assign 100% of the individuals to the corresponding delimited species (Table 3). The dorsal side had a lower correct discrimination rate (0.65%) than the ventral side (0.77%). In both views, most of the misclassed individuals belonged to *R. mexicanus* clade IIB, while the best classification accuracy was in *R. mexicanus* clade III, with a majority of individuals correctly assigned.

Ecological analyses of the R. mexicanus species complex.

The partial ROC tests showed a significant predictive ability of the models for all delimited species ($p < 0.05$; Supplementary material 7). ENMs predicted high-suitability areas for each of the delimited species (Fig. 6). *R. mexicanus* clade I had the largest suitability areas, mainly distributed in the Sierra Madre Oriental, northern Oaxaca, and the Central Highlands of Chiapas and Guatemala. For *R. mexicanus* clade III, suitability areas were found mostly in the Sierra Madre Oriental and northern Oaxaca. The suitability areas of *R. mexicanus* clade IIA were restricted to the northern region of the western and central Cordillera of the Colombian Andes, while for *R. mexicanus* clade IIB they were distributed from the southwestern region of the Colombian Andes to the northern Ecuadorian Andes.

There were significant pairwise differences between the delimited species for all environmental variables except for Bio1 and Bio5 (Fig. 7a-g). The environmental niche of *R. mexicanus* clade III presented the lowest temperature values for the coldest month (Bio6, mean of 6.5 °C). *R. mexicanus* clade IIA presented on average the highest values of annual precipitation (Bio12, mean of 2483 mm) and precipitation of the driest month (Bio14, mean of 95.2 mm) but showed similar average values of precipitation of the wettest month, together with *R. mexicanus* clade I (Bio13, mean of 340.3 y 345.9 mm, respectively). The CVA completely segregated the *R. mexicanus* clade IIA – *R. mexicanus* clade IIB environmental niches from those of *R. mexicanus* clade I – *R. mexicanus* clade III, but there was still a small region of overlap in their environmental space (Fig 7h).

DISCUSSION

Taxonomy of the R. mexicanus species group.

Within the subgenus *Aporodon*, the *R. mexicanus* group currently comprises the species *R. mexicanus*, *R. brevirostris*, *R. paradoxus*, *R. gracilis*, *R. spectabilis*, *R. darienensis*, and *R. garichensis*. The overall distribution of this group ranges from Mexico to South America, although

most species are concentrated in Central American (Hall 1981). Here, all the members of this group could be analyzed using molecular data, which allowed us to clarify the evolutionary relationships between them, with the exception of *R. paradoxus*.

Reithrodontomys brevirostris was recovered as the sister group to the clade *R. mexicanus* clade I and confirmed as a valid species by all molecular delimitation methods. However, populations of this species have tended to be confused with those of *R. mexicanus* from Central America. Indeed, most of the individuals that exemplified the *R. brevirostris* clade in this study had originally been identified by their collectors as *R. mexicanus* (another two as *R. gracilis* by Miller and Engstrom 2008). Similarly, in the phylogeny of Arellano et al. (2005) one individual from Costa Rica, grouped in their Clade I, was later reclassified as *R. brevirostris* by Gardner and Carleton (2009). Furthermore, these authors assign *R. m. potrerograndei*, a former *R. mexicanus* subspecies, as part of *R. brevirostris* "because of their comparably small size and other morphological resemblances" (Gardner and Carleton 2009: 172). Hooper (1952) noted that many of the morphological and cranial features of *R. brevirostris* were reminiscent of *R. mexicanus*, but the absence of evidence of interbreeding allowed them to be maintained as species. The separation between *R. brevirostris* and *R. mexicanus* clade I occurred approximately 1.49 mya, and its genetic divergence for cytb was 5.68%, slightly higher than the 5% used to separate species in mammals (Baker and Bradley 2006). The relatively low genetic differentiation could account for the strong morphological similarity historically reported between these clades. They also share similar habitat characteristics, being distributed mainly in the cloud forest (Hooper 1952, Gual-Díaz and Rendón-Correa 2014). Both clades would fall within the gray zone described by de Queiroz (2007), in which the decision as to whether they constitute one or two taxonomic entities depends on the species criteria used. Based on our results, we propose that they remain distinct entities, under the assumption that they have been evolving as divergent lineages for sufficient time to separate but continue to maintain many of the common ancestral characteristics they share (de Queiroz 1998).

Hooper (1952) considered *R. darienensis* and *R. gracilis* to be superspecies because they did not show major differences in morphological traits, pelage coloration, or cranial or body size. The term superspecies was proposed by B. Rensch and later by E. Mayr to refer to monophyletic and allopatric taxa that formed a single entity and later evolved to the species level (Amadon 1966). However, our phylogenetic results did not recover *R. darienensis* and *R. gracilis* as a monophyletic group, and the genetic distances between them reached values of almost 14%. Furthermore, *R. darienensis* was more closely related to the clade containing *R. mexicanus* specimens from South America (although they were genetically well-differentiated) than to *R. gracilis*. This is consistent with its restricted distribution in eastern Panama (Bradley 2017). The *R. gracilis* specimens from

Yucatan and Campeche, Mexico were unequivocally delimited as the same entity as *R. spectabilis*, while those from El Salvador were recognized at the species level. According to their geographical distribution, these two specimens correspond to the subspecies *R. g. anthonyi* (Hall, 1981), but the genetic distances of almost 8% between these and *R. gracilis* + *R. spectabilis* clade suggest the need to reevaluate the Central American populations of *R. gracilis*, in search of completed speciation processes (Futuyma 2013).

Reithrodontomys spectabilis, whose distribution is restricted to Cozumel Island, Mexico, was described as one of the largest species of the genus (Jones and Lawor 1965). Although many aspects of its morphology were reminiscent of *R. gracilis* from Yucatan, marked differences in body size, darker coloration, and broader and heavier zygomatic arches prompted its recognition at the species level. Jones and Lawlor (1965) suggested that the precursor of *R. spectabilis* arrived from the Yucatan Peninsula during the Late Pleistocene, which assumes a relatively long period of isolation between these two species. Our results suggest that the divergence between these species (95% HPD = 0.19-0.47) occurred at some point in the Middle Pleistocene (from 0.781 to 0.126 Mya, Walker et al. 2018), indicating a very recent separation between their populations compared to those reported for other species of the subgenus *Aporodon* (Martínez et al. 2022a; this study). This recent separation is also consistent with the low cytb genetic differentiation between these species (0.7 %), which fall within the intraspecific range values proposed for *Reithrodontomys* (Baker and Bradley 2006). The phylogenetic relationships between *R. spectabilis* and *R. gracilis* have been analyzed in the past with allozymes and the cytb gene, arriving at results similar to ours and suggesting the island effect as a possible cause of their morphological differences (Arellano et al. 2003; 2005). Rodents frequently exhibit island gigantism with respect to conspecific populations on the mainland (Lomolino 1985). This phenomenon is known as the Island rule (Foster 1964) and is affected by different factors including the resource availability and the absence of natural predators (Lomolino 2005). We agree with Arellano et al. (2005) that this could be the explanation for why the harvest mice populations of Isla Cozumel differ, mainly in body size, from the *R. gracilis* populations of Yucatan. Recognizing *R. spectabilis* as a conspecific of *R. gracilis* entails reevaluating its populations in many ways, considering that it is an endemic species classified as Critically Endangered by the IUCN Red List of Threatened Species (Vázquez et al. 2018). Additional studies that compare populations of both species with different sources of evidence such as geometric morphometric, ecological niche, population genetics, among others, facilitate reaching a conclusion about their taxonomic status.

Reithrodontomys mexicanus cryptic species complex.

Reithrodontomys mexicanus originally comprised 13 subspecies (Hooper 1952; Hooper 1955), though 10 are currently recognized (Bradley 2017). Our phylogenies included samples of the formerly subspecies *R. garichensis* for the first time. We confirmed that it is distinct from *R. mexicanus* but belongs to the *R. mexicanus* group (Gardner and Carleton 2009). Surprisingly, the Costa Rican specimens considered to be *Reithrodontomys sp.* by Miller and Engstrom (2008) showed a close relationship with this species. These authors suggested the two specimens from Volcan Poas as a new species based on their morphological and genetic differences with respect to *R. mexicanus*. The three species delimitation methods supported this proposal. On the other hand, these methods failed to differentiate the specimen from La Carpentera from *R. garichensis*, identifying it as the same taxonomic unit; we therefore propose that it be reclassified as *R. garichensis*.

In this study, *R. mexicanus* was recovered as a non-monophyletic taxon formed by non-sister clades that are highly divergent from each other, in agreement with what was reported by Arellano et al. (2003; 2005). All delimitation methods demarcated individuals from Parque Nacional Montecristo, El Salvador to the species level, although the cytb genetic distance between this grouping and the remaining individuals of the clade was at the 5 % lower limit estimated by Baker and Bradley (2006) for separating mammal species. Specimens from El Salvador could not be examined morphologically, except for 5 individuals from Los Esesmiles (Cerro El Pital), which were not included in the molecular or morphometric analyses. Compared to individuals of *R. mexicanus* clade I distributed in Mexico and Guatemala, these specimens from Los Esesmiles differ morphologically by their relatively shorter nasal bones, broader palatal, and rounded braincase. The pelage exhibits a cinnamon coloration, and the tail tends to be not much longer than the head and body together. The two localities in El Salvador are separated by ca. 30 km, so they could be assumed to have the same genetic identity. Thus, populations from El Salvador could be assumed to be a diverging lineage, but more evidence is needed to reach a conclusion regarding their taxonomic status, such as molecular analyses that include a representative sampling of individuals from this country.

The strongest morphometric similarities were found between the putative species *R. mexicanus* clade I and *R. mexicanus* clade IIB, which showed no significant differences in the ventral skull shape. It has been reported that the ventral view tends to be the best view to recover phylogenetic relationships (Camul and Polly 2005). Consequently, our morphometric results are consistent with the molecular data, which showed that these clades are more closely related to each other than to *R. mexicanus* clade III. In mammals, it has been reported that the environment can influence the development of bone structures such as the skull and jaw (Camul and Polly 2005). The few

morphometric differences found between these delimited species could be due to the fact that they share similar habitat characteristics in general (Hooper 1952). However, the ecological analyses allowed to correctly segregate their environmental space, based mainly on precipitation and VCF variables. Although their separation was weakly supported by geometric morphometrics, the genetic and environmental differentiation of these clades strongly support their demarcation as distinct species.

The bGMYC delimitation method proved to be the most conservative for proposing possible species within the clade that grouped the *R. mexicanus* specimens from South America. Despite the number of species proposed by the different methods, most pairwise comparisons did not exceed cytb genetic distance values of 5% (K2P distances range from 1.50 to 4.20%, Supplementary material 2). The low levels of genetic differentiation reported for South American rodents have been explained as a consequence of recent speciation processes (Patton and Smith 1992). Such would be the case in the genus *Reithrodontomys*, whose diversification processes began ca. 6.83 mya according to our results, expanding from North America to South America, of which only subspecies of *R. mexicanus* are known (Hooper 1952).

Arellano et al. (2005) analyzed a specimen from Colombia but retained it as part of *R. mexicanus* sensu stricto. In their analyses, *R. darienensis* from Panama was not included. Our phylogenetic analyses included *R. darienensis* and a good representation of specimens from Colombia and Ecuador that had been classified a priori as *R. mexicanus*. Our evidence supported the conclusion that South American specimens form a distinct clade from *R. mexicanus* which is sister to *R. darienensis*. Within this clade, delimitation methods and cytb genetic distances agreed that the Colombian specimens (*R. mexicanus* clade IIA) from Risaralda (ICN16579) and Antioquia (FMNH78179) constitute an entity apart from the other South American individuals. Although it was not possible to corroborate the species-level with morphological evidence, the ENM delimited its distribution to the northwestern region of the western and central Cordillera, with a habitat characterized mainly by high precipitation values. These individuals could be considered a divergent lineage that is already distinct from the rest of the South American populations in at least two species properties (genetic and ecological niche; de Queiroz 2007).

The remaining individuals from Colombia and Ecuador (*R. mexicanus* clade IIB) were validated at the species level by genetic and ecological data, and to a lesser extent with morphometric evidence. Hooper (1952) reported three subspecies of *R. mexicanus* in South America: *R. m. milleri*, *R. m. soederstroemi*, and *R. m. eremiscus*. The known distribution of *R. m. milleri* ranges from Colombia to northern Ecuador, including the suitability areas found for the two delimited species. However, the distribution of *R. mexicanus* clade IIA was restricted to a small region of the western and central

Cordillera, while *R. mexicanus* clade IIB was distributed mainly in the Cordillera Oriental, a region not reported for *R. m. milleri* (Hooper 1952). In addition, the suitability areas of *R. mexicanus* clade IIB included localities recognized for the other two subspecies, distributed only in Ecuador (Hooper 1952; Arellano et al. 2015). In the future, an analysis focused on the harvest mice populations of South America is essential to correctly establish the taxonomic designation of the *Reithrodontomys* species that inhabit this region, since they undoubtedly do not belong to *R. mexicanus*.

Reithrodontomys mexicanus clade III was considered a candidate species using allozymes (Arellano et al. 2003), cytb sequences (Arellano et al. 2005), and chromosomal data (Urbina et al. 2006). In our analyses, we were able to include a wide sampling that allowed us to support this new species not only with molecular data but also with morphological and ecological data. The phylogenetic position of this delimited species in the trees confirms that it is a much older lineage (divergence time estimates ranging from 4.53 to 6.84 mya) and has a different evolutionary history from the rest of the subgenus *Aporodon* clades. Although its representatives have historically been classified as *R. mexicanus*, they are genetically very distant from this species, even those that coexist in sympatry in the localities of La Esperanza and Puerto de la Soledad in Oaxaca, Mexico. Specimens of this clade could be discriminated correctly by morphology, especially by ventral skull shape. The phylogenetic signal that exhibits structures located on the ventral side of the skull (Lockwood et al. 2004; Macholán 2008) could explain the more marked morphometric differentiation that this clade presented in accordance with its position in the phylogenetic trees. The environmental characteristics of this putative species partially overlap with those of *R. mexicanus* clade I. This is expected, given that they share part of their distribution in the Mexican cloud forests (Gual-Díaz and Rendón-Correa 2014). However, comparisons of the environmental variables were mostly statistically significant, with *R. mexicanus* clade III occupying a geographic area characterized by low values of temperatures and annual precipitation, and high forest cover (VCF). The congruence between the independent datasets is essential for the delimitation of this clade as a new species since only molecular data had been used to differentiate it until now.

Species delimitation and its taxonomic implications.

Establishing species boundaries is difficult when dealing with taxonomically complex groups whose descriptions have been based primarily on their morphology (Dayrat 2005). Many of these species exhibit such strong morphological resemblance to each other that they are recognized as cryptic species (Bickford et al. 2007). This is the case of *R. mexicanus*, where molecular (Arellano et al. 2003, 2005; Miller Engstrom 2008) and craniodental (Gardner and Carleton 2009) data have revealed broad cryptic variation leading to its recognition as a species complex. Integrating multiple approaches to delimit species has been strongly recommended to better confirm the species taxa

hypothesis (Dayrat 2005; Will et al. 2005). In this study, we implemented an integrative taxonomy approach to test whether there are cryptic lineages within *R. mexicanus* that are evolving separately. We employed different criteria in accordance with the GLC (de Queiroz 1998; 2007), seeking as much evidence as possible to support the delimited species (Sangster 2018).

Species proposals were not always congruent among the delimitation methods. The limitations of these methods based on DNA data have been discussed previously (see Luo et al. 2018), mainly those related to non-compliance with the assumptions of the method (Carsten et al. 2013). However, in *Reithrodontomys*, the efficacy of the delimitation methods used here (mPTP, bGMYC, and STACEY) to demarcate cryptic lineages has been demonstrated (Martínez-Borrego et al. 2022a). On the other hand, the use of different molecular markers showed conflicting results among the phylogenies, with a high discordance between the topology with cytb and those with Fgb-I7 and IRBP, respectively. This mito-nuclear discordance has been suggested to be a consequence of introgression or incomplete lineage sorting (Toews and Brelsford 2012; Firneno et al. 2020). Although including more genetic markers can help to elucidate species limits, sometimes the use of multiple loci has complicated this purpose for taxonomists (Firneno et al. 2021). Therefore, in our study, the recognition of taxonomic entities was based primarily on molecular species delimitation methods, including the cytb genetic distances traditionally used in mammal genetic studies (Bradley and Baker 2001; Baker and Bradley 2006), but other evidence such as skull morphometry and ecological niche were also used.

Geometric morphometrics and niche modeling have shown great applicability in taxonomic studies in mammals (Barčiová 2009; Martínez Gordillo et al. 2010) and allowed the corroboration of species limits hypotheses derived from phylogenetic studies (e.g., Camul and Polly 2005; Rivera et al. 2018). However, the species-level clades proposed here by the three delimitation methods and genetic distances were not always strongly supported by ecological and/or morphological data. Under the GLC, failure to meet any of the species criteria does not mean that it does not correspond to a divergent lineage (de Queiroz 2007). Rather, GLC recognizes that species properties may evolve at different times during divergence (Sangster 2018), hence the importance of integrating multiple data sources to support or reject the species hypothesis (Padial et al. 2010).

In summary, we confirm that *R. mexicanus* sensu lato is a cryptic species complex composed of at least four putative species: *R. mexicanus* clade I (*R. mexicanus* sensu stricto), *R. mexicanus* clade IIA, *R. mexicanus* clade IIB, and *R. mexicanus* clade III. In addition, specimens from El Salvador should be reevaluated taxonomically including a better sampling of multiple lines of evidence. For *R. mexicanus* sensu stricto, additional analyses are necessary to estimate its phylogenetic relationship with respect to the subspecies *R. mexicanus riparius*, which was not included in our

611 analyses but has evident geographic isolation from the other Mexican populations (Hooper 1955;
612 Hall 1981). Finally, *R. mexicanus* clade III constitutes a new species, pending formal description
613 and assignment of a scientific name according to the International Code of Zoological
614 Nomenclature rules.

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878 Table 1. Evolutionary models and partition schemes used in the phylogenetic analyses of the
879 *Reithrodontomys mexicanus* species complex.

Gene	Scheme partition	Codon Position 1	Codon Position 2	Codon Position 3
cytb	partitioned (1 + 2 + 3)	TN+I+G4	HKY+F+I+G4	TN+F+G4
Fgb-I7	noncoding	HKY+F+I		
IRBP	partitioned (1-3 + 2)	TN+F+G4	K2P	

880 Table 2. Matrix of Kimura 2-parameter genetic distances (%) for Cytochrome b gene sequence data
881 between delimited species of the *R. mexicanus* group (genus *Reithrodontomys*). Taxon labels
882 correspond to the delimited species under the consensus of the mPTP, bGMYC, and STACEY
883 methods, shown in Figure 2.

Species delimitation	1	2	3	4	5	6	7	8	9	10
R. mexicanus clade III										
R. mexicanus clade I	15.92									
R. mexicanus ES	15.92	4.96								
R. mexicanus clade IIA	16.86	8.26	8.72							
R. mexicanus clade IIB	15.88	8.32	8.96	6.06						
R. brevirostris	16.15	5.68	5.23	8.31	8.34					
R. darienensis	16.68	8.48	7.69	8.30	7.54	9.22				
R. garichensis	18.18	14.59	12.92	16.09	14.24	14.0	15.62			
R. sp. Volcan Poas	17.12	13.83	13.98	14.86	13.93	13.37	13.95	11.31		
R. grac- spect	14.70	13.43	13.26	15.53	14.56	12.91	13.86	16.60	15.23	
R. gracilis ES	15.16	13.43	14.50	16.72	16.22	14.29	15.55	17.38	16.38	7.91

884 Table 3. Discrimination of individuals to the delimited species within the *Reithrodontomys*
885 *mexicanus* complex base on the skull shape. CDR = Correct discrimination rate in percentage; N =
886 sample size per delimited species.

	1	2	3	% / N
A. Dorsal view				
1. *R. mexicanus* clade I	11	5	4	55 / 20
2. *R. mexicanus* clade IIB	4	5	4	30.77 / 13
3. *R. mexicanus* clade III	5	30	1	83.33 / 36
CDR	0.65%			
B. Ventral view				
1. *R. mexicanus* clade I	12	5	3	60 / 20
2. *R. mexicanus* clade IIB	4	2	7	53.84 / 13
3. *R. mexicanus* clade III	2	34	0	94.44 / 36
CDR	0.77%			

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Figure 1

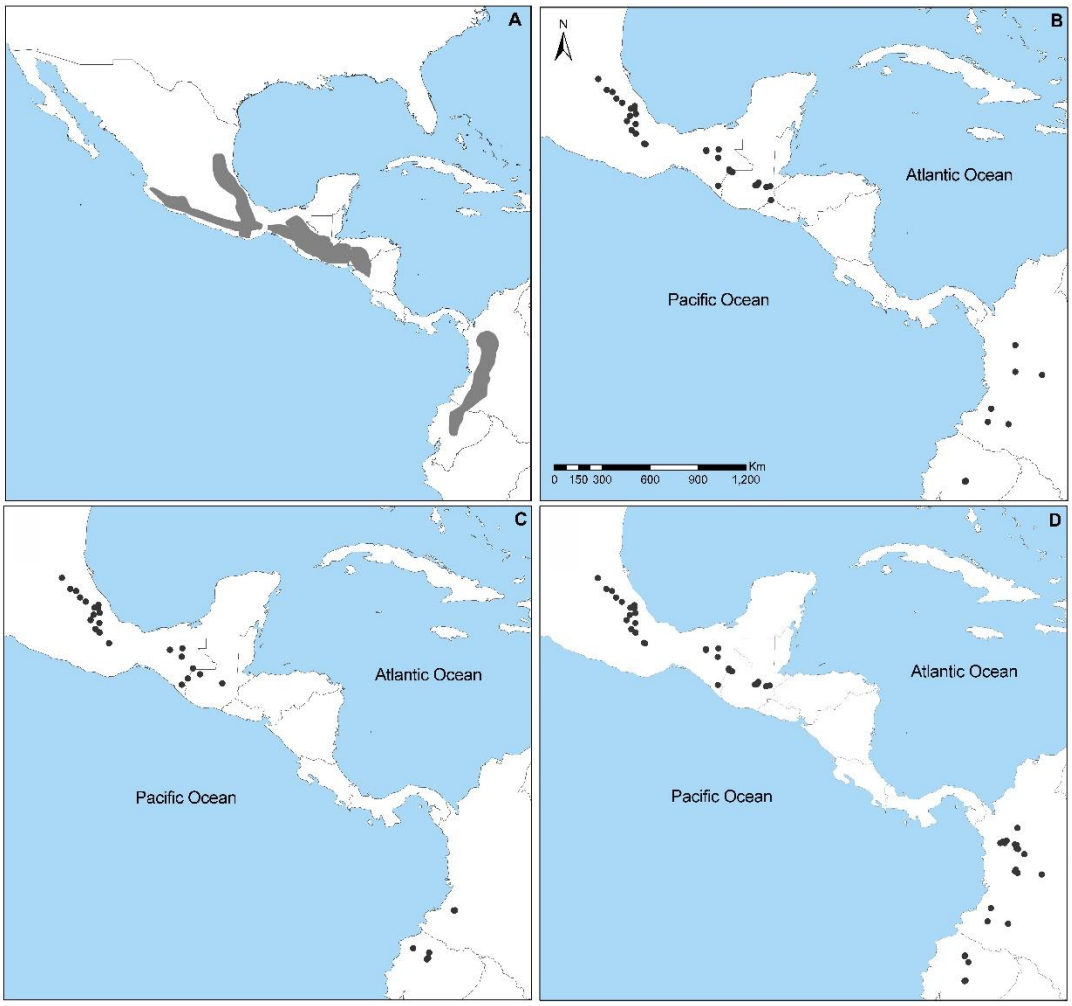


Figure 1. Localities of the *Reithrodontomys mexicanus* specimens used in this study. A = Current distribution (gray shading) of *R. mexicanus* sensu lato modified from Hooper (1952) and Hall (1981); B-D = localities utilized in the molecular, geometric morphometric, and ecological analyses, respectively.

Figure 2

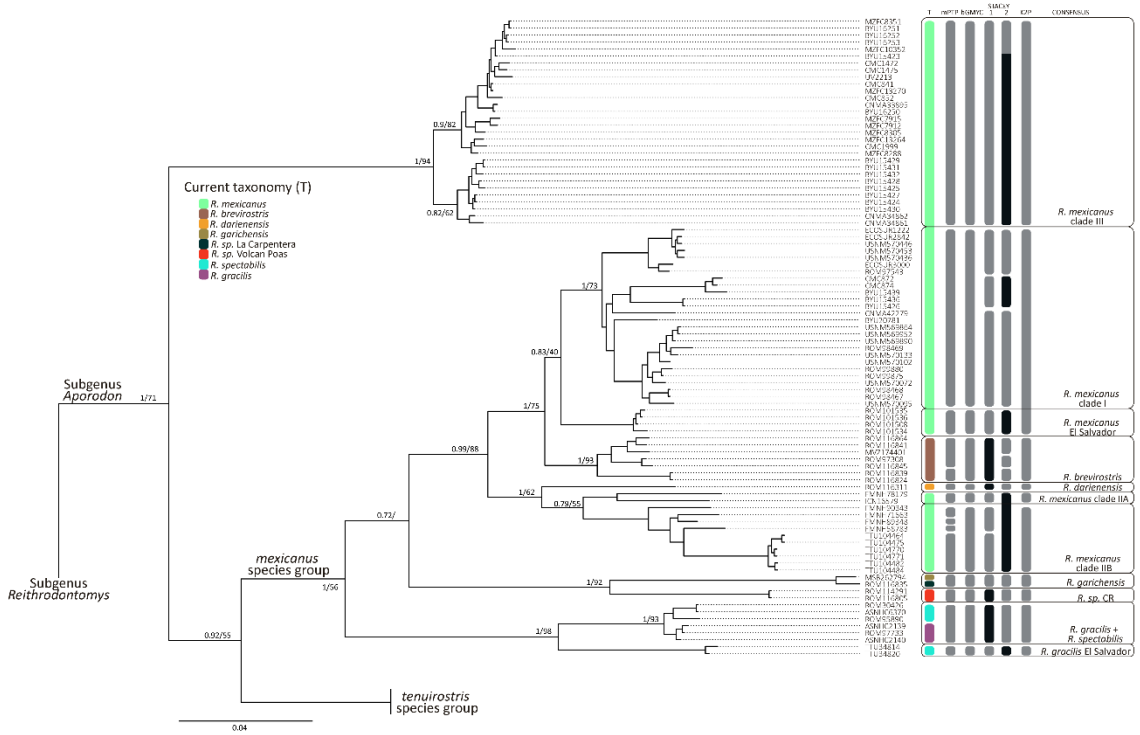


Figure 2. Phylogenetic relationships among species of the *R. mexicanus* group using sequences data of the mitochondrial gene Cytochrome b. Branches values represent nodal support for BI/ML analysis. Right bars represent taxa delimited as species-level by the single-locus methods mPTP and bGMYC, and the multiple-loci method STACEY with probability values above 0.95. T = Current taxonomy; STACEY 1 = Cytochrome b + Intron 7 of the beta fibrinogen; STACEY 2 = Cytochrome b + Interphotoreceptor retinoid-binding protein. When DNA information was not available, a black bar was used. Terminal labels are named according to mammal collection voucher numbers (see Appendix 1).

Figure 3.

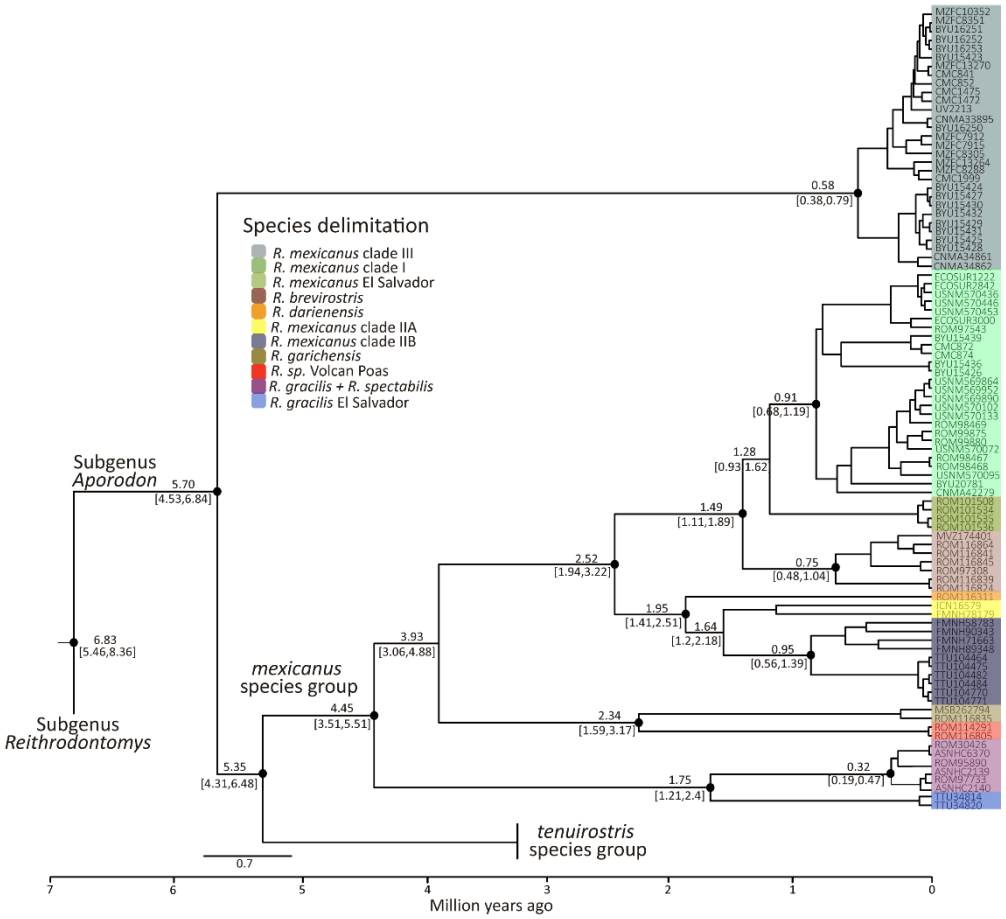


Figure 3. Maximum clade credibility tree obtained with BEAST2 for species of the *R. mexicanus* group using Cytochrome b sequence data. Values above branches represent mean divergence times and below the branches are the 95% highest posterior density (HPD) intervals. Black points represent posterior probability = 1. Terminal labels are named according to mammal collection voucher numbers (see Appendix 1).

Figure 4.

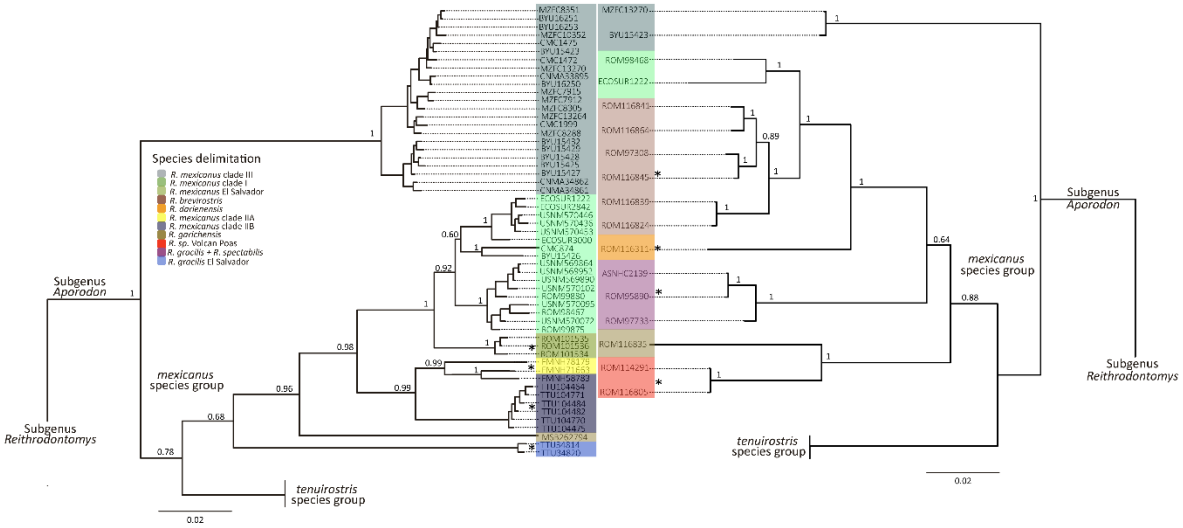
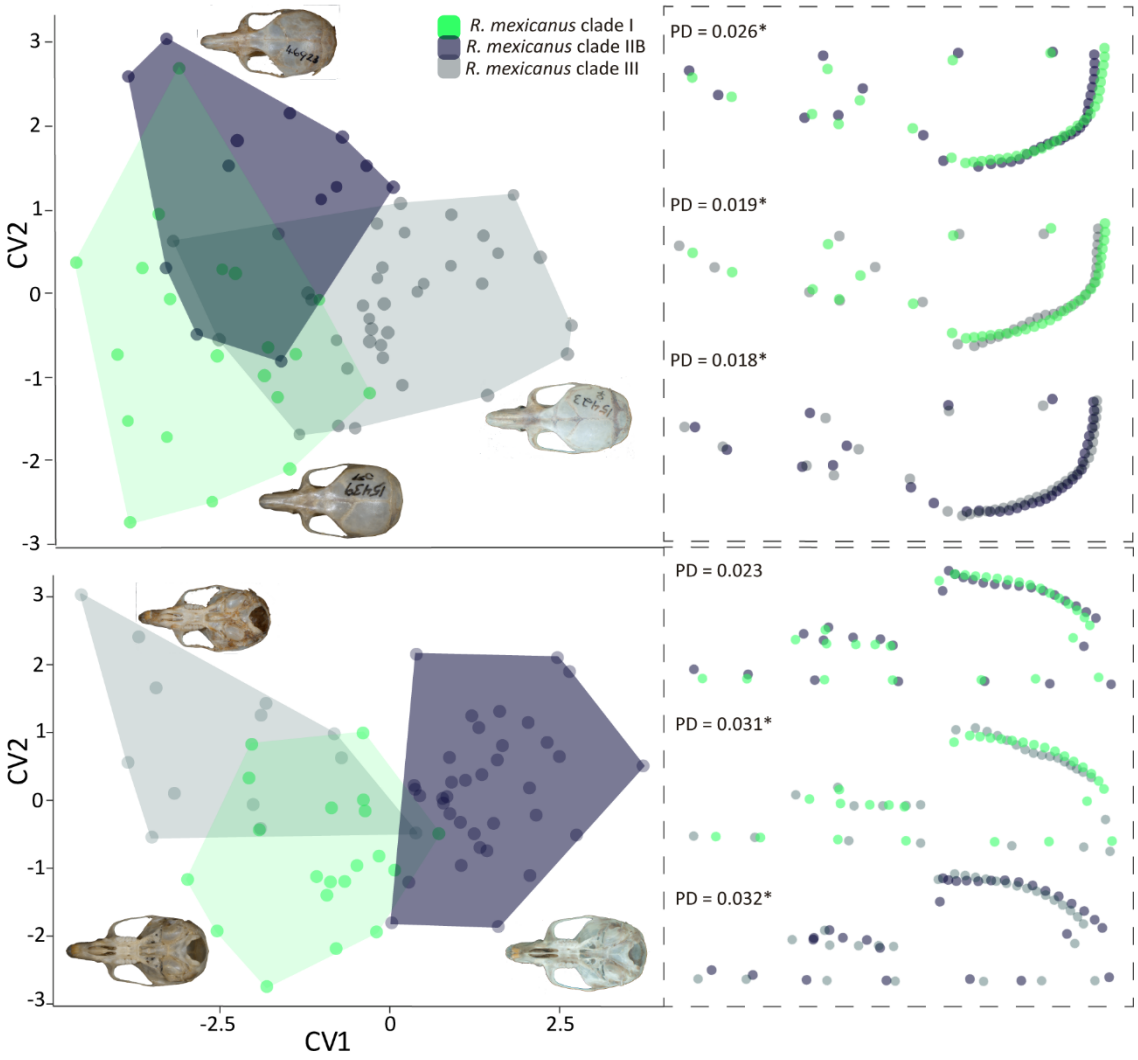


Figure 4. Phylogenetic relationships among species of the *R. mexicanus* group using sequence data of the concatenated dataset Cytochrome b + Intron 7 of the beta fibrinogen (left) and Cytochrome b + Interphotoreceptor retinoid-binding protein (right). Values above branches represent nodal support for BI analysis. Asterisks = delimitated species not represented in both phylogenies. Terminal labels are named according to mammal collection voucher numbers (see Appendix 1).

948 Figure 5.



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950 Figure 5. Canonical variable analysis of dorsal (top) and ventral (bottom) views of the skull for
951 delimited species within the *Reithrodontomys mexicanus* complex. The right panel represents the
952 differences in mean shapes of each skull view, using the Procrustes distances (PD). Asterisks =
953 significant differences based on pairwise permutation test ($p < 0.05$).

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Figure 6.

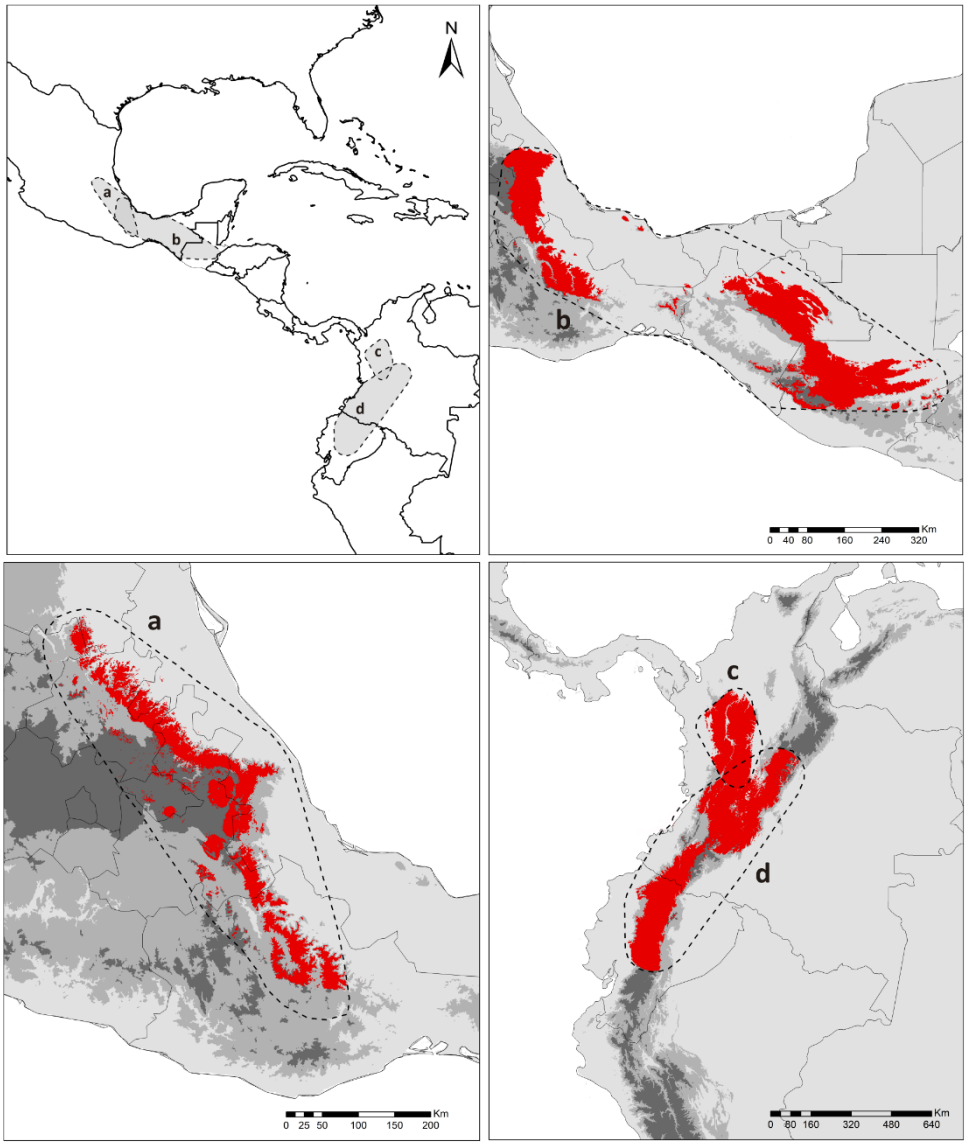


Figure 6. Ecological niche modeling of the delimited species within the *Reithrodontomys mexicanus* complex using six bioclimatic variables and the vegetation continuous field product. Red color represents the high suitability areas for each species using the 10th-percentile cut-off threshold: a = *R. mexicanus* clade III, b = *R. mexicanus* clade I, c = *R. mexicanus* clade IIA, d = *R. mexicanus* clade IIB. The calibration areas used in the construction of each final model are represented with dashed lines. Gray hues depict an elevation gradient: light gray < 1000 m; gray 1000-2500 m; and dark gray > 2500 m.

Figure 7.

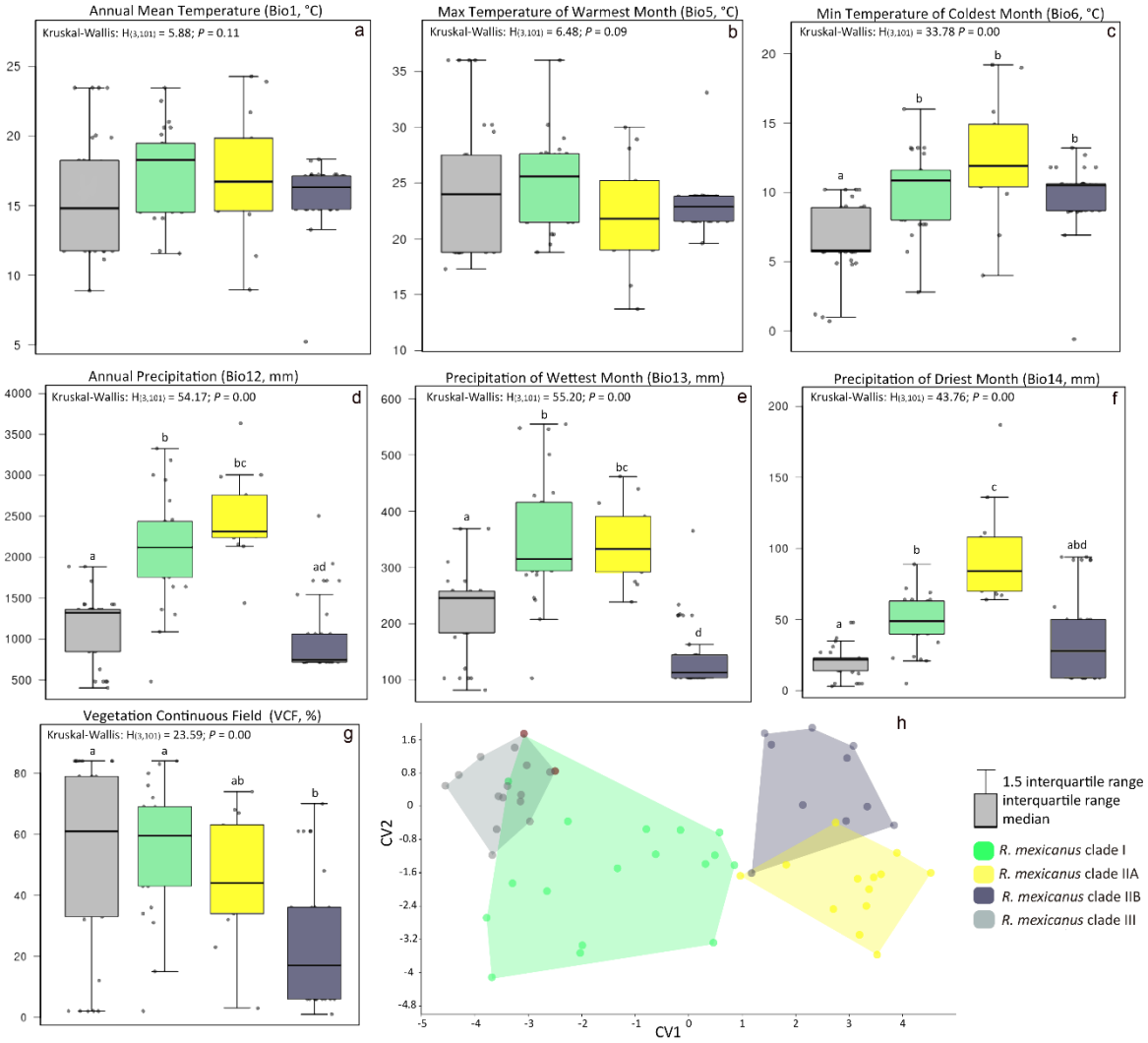


Figure 7. Statistical comparisons (a-g) and canonical variable analysis (h) between delimited species of the *Reithrodontomys mexicanus* complex using six bioclimatic variables and the vegetation continuous field product. Statistical significance was considered with $p \leq 0.05$.

Appendix 1

List of *Reithrodontomys* specimens used in the molecular analysis and geometric morphometric and ecological analyses in the case of *R. mexicanus*. Collecting localities and GenBank accessions numbers for Cytochrome *b*, Intron 7 of the beta fibrinogen, and Interphotoreceptor retinoid-binding protein genes are given (GenBank accessions highlighted in bold represent DNA sequences generated in this study). Abbreviations for analysis, countries, and mammal collections housing the specimens we included are as follows: E = ecology; GM = geometric morphometric; M = molecular; COL = Colombia; CR = Costa Rica; ECU = Ecuador; ES = El Salvador; GU = Guatemala; MX = Mexico; NIC = Nicaragua; PAN = Panama; AMNH = American Museum of Natural History; ASNHC = Angelo State Natural History Collections; BYU = Brigham Young University; CMC = Colección de Mamíferos del CIByC; CNMA = Colección Nacional de Mamíferos, Universidad Nacional Autónoma de México; ECOSUR = Colección de Mamíferos de El Colegio de la Frontera Sur, San Cristóbal; FMNH = Field Museum of Natural History; ICN = Colección de Mamíferos, Instituto de Ciencias Naturales; LSUMNS = Louisiana State University Museum of Zoology; MVZ = Museum of Vertebrate Zoology; MZFC = Colección de Mamíferos, Museo de Zoología "Alfonso L. Herrera", Universidad Nacional Autónoma de México; ROM = Royal Ontario Museum; TTU = Mammal Collection, Texas Tech University; UMMZ = Museum of Zoology, University of Michigan; USNM = Division of Mammals, National Museum of Natural History; UV = Colección de Mamíferos, Universidad Veracruzana.

Current species name / Voucher	Locality	Analysis	GenBank Accession		
			cytb	Fgb-I7	IRBP
R. mexicanus AMNH 32582	COL: Popayán, Cerro Munchique, Cauca.	GM			
R. mexicanus AMNH 32584	COL: Popayán, Cerro Munchique, Cauca.	GM			
R. mexicanus AMNH 32590	COL: Popayán, Cerro Munchique, Cauca.	GM			
R. mexicanus AMNH 32599	COL: El Tambo, Cocal, Cauca.	GM			
R. mexicanus AMNH 46908	ECU: Quito, Pichincha.	GM			
R. mexicanus AMNH 46920	ECU: Quito, Pichincha.	GM			
R. mexicanus AMNH 46923	ECU: Quito, Pichincha.	GM			
R. mexicanus AMNH 46977	ECU: Santo Domingo, Alobuela, Pichincha.	GM			
R. mexicanus AMNH 46978	ECU: Santo Domingo, Alobuela, Pichincha.	GM			
R. mexicanus AMNH 46980	ECU: Santo Domingo, Alobuela, Pichincha.	GM			

R. mexicanus AMNH 46982	ECU: Santo Domingo, Alobuela, Pichincha.	GM			
R. mexicanus AMNH 46997	ECU: Quito, Perucho, Pichincha.	GM			
R. mexicanus AMNH 47003	ECU: Guayllabamba River, Pichincha.	GM			
R. mexicanus BYU15432	MX: 28 km SW (by road.) La Esperanza, Municipio Santiago Comaltepec, Oaxaca.	M, E	AY859435	**ON156946**	
R. mexicanus BYU15429	MX: 11 km SW (by road.) La Esperanza, Municipio Santiago Comaltepec, Oaxaca.	M, GM, E	AY859444	**ON156933**	
R. mexicanus BYU15431	MX: 11 km SW (by road.) La Esperanza, Municipio Santiago Comaltepec, Oaxaca.	M, GM, E	AY859446		
R. mexicanus BYU15427	MX: 11 km SW (by road.) La Esperanza, Municipio Santiago Comaltepec, Oaxaca.	M, GM, E	AY859442	**ON156936**	
R. mexicanus BYU15430	MX: 11 km SW (by road.) La Esperanza, Municipio Santiago Comaltepec, Oaxaca.	M, GM, E	AY859445		
R. mexicanus BYU15424	MX: 11 km SW (by road.) La Esperanza, Municipio Santiago Comaltepec, Oaxaca.	M, GM, E	AY859434		
R. mexicanus BYU15428	MX: 11 km SW (by road.) La Esperanza, Municipio Santiago Comaltepec, Oaxaca.	M, GM, E	AY859443	**ON156927**	
R. mexicanus BYU15425	MX: 11 km SW (by road.) La Esperanza, Municipio Santiago Comaltepec, Oaxaca.	M, GM, E	AY859441	**ON156947**	
R. mexicanus BYU16250	MX: 1.5 km S Puerto de la Soledad, Municipio Teotitlán de Flores Magón, Oaxaca.	M, GM, E	AY859437	**ON156945**	
R. mexicanus BYU16251	MX: 1.5 km S Puerto de la Soledad, Municipio Teotitlán de Flores Magón, Oaxaca.	M, GM, E	AY859438	**ON156941**	
R. mexicanus BYU16252	MX: 1.5 km S Puerto de la Soledad, Municipio Teotitlán de Flores Magón, Oaxaca.	M, GM, E	AY859439		
R. mexicanus BYU16253	MX: 1.5 km S Puerto de la Soledad, Municipio Teotitlán de Flores Magón, Oaxaca.	M, GM, E	AY859440	**ON156942**	
R. mexicanus BYU15423	MX: 6 km S Zacualtipán, Rancho la Mojonera, Municipio Zacualtipán, Hidalgo.	M, GM, E	AY859433	**ON156948**	**ON156971**
R. mexicanus BYU15439	MX: 18 km NW Teocelo, Municipio Ixhuatlán, Veracruz.	M, GM, E	AY293822		
R. mexicanus BYU15436	MX: 1.5 km S Puerto de la Soledad, Municipio Teotitlán de Flores Magón, Oaxaca.	M, GM, E	AY859448		

R. mexicanus BYU15426	MX: 11 km SW (by road.) La Esperanza, Municipio Santiago Comaltepec, Oaxaca.	M, GM, E	AY859449	MW117093	
R. mexicanus BYU20781	MX: Rancho La Providencia, Chiapas.	M, GM, E	HQ269733		
R. mexicanus CMC852	MX: Xometla (ravine over the bridge), Municipio La Perla, Veracruz.	M, GM, E	**ON156862**		
R. mexicanus CMC1472	MX: 3.4 km SW from desviation to Mazatepec, Mesa de la Yerba, Veracruz.	M, GM, E	**ON156863**	**ON156937**	
R. mexicanus CMC1475	MX: Matlalapa, Municipio Xico, Veracruz.	M, GM, E	**ON156865**	**ON156939**	
R. mexicanus CMC841	MX: 2.9 km E Puerto del Aire, Municipio Acultzingo, Veracruz.	M, GM, E	**ON156868**		
R. mexicanus CMC1999	MX: Rancho 22 de marzo, km 75.8 Ahuazotepec-Zacatlán road, Puebla.	M, GM, E	**ON156872**	**ON156934**	
R. mexicanus CMC872	MX: 1.9 km N Las Cañadas (Eco reserve), Municipio Huatusco, Veracruz.	M, GM, E	**ON156879**		
R. mexicanus CMC874	MX: 1.9 km N Las Cañadas (Eco reserve), Municipio Huatusco, Veracruz.	M, GM, E	HQ269734	HQ269796	
R. mexicanus CMC877	MX: 1.9 km N Las Cañadas (Eco reserve), Municipio Huatusco, Veracruz.	GM, E			
R. mexicanus CMC842	MX: 2.9 km E Puerto del Aire, Municipio Acultzingo, Veracruz.	GM, E			
R. mexicanus CMC844	MX: 2.9 km E Puerto del Aire, Municipio Acultzingo, Veracruz.	GM, E			
R. mexicanus CMC845	MX: 2.9 km E Puerto del Aire, Municipio Acultzingo, Veracruz.	GM, E			
R. mexicanus CMC846	MX: 2.9 km E Puerto del Aire, Municipio Acultzingo, Veracruz.	GM, E			
R. mexicanus CMC865	MX: Xometla (ravine over the bridge), Municipio La Perla, Veracruz.	GM, E			
R. mexicanus CMC868	MX: Xometla (ravine over the bridge), Municipio La Perla, Veracruz.	GM, E			
R. mexicanus CMC1377	MX: 3.4 km SW from desviation to Mazatepec, Mesa de la Yerba, Veracruz.	GM, E			
R. mexicanus CNMA34862	MX: 5 km N Cerro Zempoaltepelt, Santa María Yacochi, Oaxaca.	M, GM, E	**ON156860**	**ON156929**	
R. mexicanus CNMA33895	MX: Puerto de la Soledad, Municipio Teotitlán de Flores Magón, Oaxaca.	M, GM, E	AY859436	**ON156932**	

R. mexicanus CNMA42279	MX: Rancho La Providencia, Unión Juárez, Chiapas.	M, E	AY859450		
R. mexicanus CNMA34861	MX: 5 km N Cerro Zempoaltepelt, Santa María Yacochi, Oaxaca.	M, GM, E	**ON156874**	**ON156928**	
R. mexicanus ECOSUR1222	MX: 3.45 km N El Vivero, Las Grutas, Lagos de Montebello National Park, Chiapas.	M, E	**ON156880**	**ON156964**	**ON156968**
R. mexicanus ECOSUR2842	MX: Mercado Indígena, Santo Tomás Oxchuc, Chiapas.	M, GM. E	**ON156881**	**ON156952**	
R. mexicanus ECOSUR3000	MX: Ejido Sombra Chica, 1 km NW Tumbalá, Chiapas.	M, GM, E	**ON156883**	**ON156962**	
R. mexicanus ECOSUR931	MX: 3.45 km N El Vivero, Las Grutas, Lagos de Montebello National Park, Chiapas.	GM			
R. mexicanus FMNH78179	COL: Las Palmas, Medellín, Antioquia.	M, E	**ON156896**	**ON156925**	
R. mexicanus FMNH90343	COL: 650m Guachicono River, Cauca.	M, E	**ON156897**		
R. mexicanus FMNH71663	COL: San Cristóbal, Cundinamarca, Bogotá.	M, E	**ON156901**	**ON156935**	
R. mexicanus FMNH58783	COL: Las Cuevas Parque, Upper Cabana, cocina, Huila.	M, E	**ON156902**	**ON156931**	
R. mexicanus FMNH89348	COL: Charguayaco, Cauca.	M, E	**ON156903**		
R. mexicanus FMNH71680	COL: Guapantal, Urrao, Antioquia.	E			
R. mexicanus FMNH71666	COL: Paramo Frontino, Urrao, Antioquia.	E			
R. mexicanus FMNH71666	COL: 15 km E Negrito River, Sonson, Antioquia.	E			
R. mexicanus FMNH71658	COL: Termales River, Manizales, Caldas.	E			
R. mexicanus FMNH71685	COL: Santa Barbara, Urrao, Antioquia.	E			
R. mexicanus FMNH71686	COL: Urrao River, Urrao, Antioquia.	E			
R. mexicanus FMNH70166	COL: Valdivia, Quebrada Valdivia, Antioquia.	E			
R. mexicanus FMNH69653	COL: Santa Elena, Medellín, Antioquia.	E			
R. mexicanus ICN16579	COL: Vereda La Pastora, road to Las Cascadas, PRN Ucumar, Corregimiento La Florida, Municipio Pereira, Risaralda.	M, E	AF108708		
R. mexicanus ICN16097	COL: 4 km S, Vereda Puente Peláez, farm Cañaveral, Retiro, Antioquia.	E			
R. mexicanus ICN16760	COL: Vereda El Tambo, farm Cde. Margarita Molina., La Unión, Antioquia.	E			

R. mexicanus ICN11684	COL: Vereda Cocora, Estación Forestal, farm La Montaña, Salento, Quindío.	E			
R. mexicanus MVZ139529	ECU: 22 km NNE Quito, Pichincha.	E			
R. mexicanus MVZ 139530	ECU: 26 km NNE Quito, Pichincha.	E			
R. mexicanus MZFC7915	MX: El Pemoche, Landa de Matamoros, Querétaro.	M, GM, E	**ON156861**	**ON156940**	
R. mexicanus MZFC10352	MX: Puerto de la Soledad, Municipio Teotitlán de Flores Magón, Oaxaca.	M, GM, E	**ON156864**	**ON156938**	
R. mexicanus MZFC8351	MX: Puerto de la Soledad, Municipio Teotitlán de Flores Magón, Oaxaca.	M, GM, E	**ON156867**	**ON156926**	
R. mexicanus MZFC13270	MX: Xochititan, Puebla.	M, GM, E	**ON156869**	**ON156949**	**ON156970**
R. mexicanus MZFC8305	MX: 6 km NE Zacualpan, Municipio Zacualpan, Estado de México.	M, GM, E	**ON156870**	**ON156944**	
R. mexicanus MZFC13264	MX: Xochititan, Puebla.	M, GM, E	**ON156871**	**ON156930**	
R. mexicanus MZFC8288	MX: 6 km NE Zacualpan, Municipio Zacualpan, Estado de México.	M, GM, E	**ON156873**	**ON156950**	
R. mexicanus MZFC7912	MX: El Pemoche, Landa de Matamoros, Querétaro.	M, GM, E	**ON156875**	**ON156943**	
R. mexicanus ROM101534	ES: Montecristo National Park, Los Planes, Santa Ana.	M	**ON156876**	**ON156961**	
R. mexicanus ROM101535	ES: Montecristo National Park, Los Planes, Santa Ana.	M	**ON156877**	**ON156963**	
R. mexicanus ROM101536	ES: Montecristo National Park, Los Planes, Santa Ana.	M, E	**ON156878**	**ON156960**	
R. mexicanus ROM101508	ES: Montecristo National Park, Los Planes, Santa Ana.	M, E	AY859453		
R. mexicanus ROM97543	MX: 6 km E of Rayon, Chiapas.	M, E	AY859447		
R. mexicanus ROM98468	GU: 5 km E of Purulhá, Baja Verapaz.	M, E	**ON156885**		EF989911
R. mexicanus ROM98467	GU: 5 km E of Purulhá, Baja Verapaz.	M, E	AY859451	MW117094	
R. mexicanus ROM98469	GU: 5 km E of Purulhá, Baja Verapaz.	M, E	**ON156886**		
R. mexicanus ROM99880	GU: 2 km N of San Lorenzo, Sierra De Las Minas, Zacapa.	M, E	**ON156891**	**ON156957**	
R. mexicanus ROM99875	GU: 2 km N of San Lorenzo, Sierra De Las Minas, Zacapa.	M, E	**AY859452**	**ON156951**	
R. mexicanus TTU104464	ECU: 1.5 km S, 3 km W Baños, Tungurahua Lahar zone.	M, E	**ON156898**	**ON156922**	
R. mexicanus TTU104482	ECU: 1.5 km S, 1 km E Baños, Runtún.	M, E	**ON156899**	**ON156919**	

R. mexicanus TTU104770	ECU: 5 km E Baños, Represa Agoyán.	M, E	**ON156900**	**ON156920**	
R. mexicanus TTU104771	ECU: 5 km E Baños, Represa Agoyán.	M, E	**ON156904**	**ON156923**	
R. mexicanus TTU104475	ECU: 1.5 km S, 3 km W Baños, Tungurahua Lahar zone.	M, E	**ON156905**	**ON156921**	
R. mexicanus TTU104484	ECU: 1.5 km S, 1 km E Baños, Runtún.	M, E	**ON156906**	**ON156924**	
R. mexicanus UMMZ118145	GU: Aguacate river, Hacienda El Injerto, Municipio La Libertad, Huehuetenango.	GM, E			
R. mexicanus UMMZ118146	GU: Aguacate river, Hacienda El Injerto, Municipio La Libertad, Huehuetenango. .	GM, E			
R. mexicanus UMMZ118147	GU: Barillas, Hacienda Santa Gregoria, Huehuetenango.	GM, E			
R. mexicanus UMMZ118148	GU: Barillas, Hacienda Santa Gregoria, Huehuetenango.	GM, E			
R. mexicanus UMMZ118149	GU: Barillas, Hacienda Santa Gregoria, Huehuetenango.	GM, E			
R. mexicanus UMMZ118150	GU: Barillas, Hacienda Santa Gregoria, Huehuetenango.	GM, E			
R. mexicanus UMMZ118152	GU: Barillas, Hacienda Santa Gregoria, Huehuetenango.	GM, E			
R. mexicanus UMMZ118153	GU: Barillas, Hacienda Santa Gregoria, Huehuetenango.	GM, E			
R. mexicanus UMMZ118154	GU: Finca Concepción, Tucurú, Alta Verapaz.	GM, E			
R. mexicanus UMMZ118155	GU: Finca Concepción, Tucurú, Alta Verapaz.	GM, E			
R. mexicanus UMMZ127159	ECU: 8.9 km by road W Papallacta, Napo.	E			
R. mexicanus USNM570453	GU: 1.1 km NE (by road) Yalambojoch, Huehuetenango.	M, E	**ON156882**	**ON156965**	
R. mexicanus USNM570095	GU: 9.5 km NW Gualan, El Limo, Sierra de las Minas, Zacapa.	M, E	**ON156884**	**ON156954**	
R. mexicanus USNM570102	GU: 3 km S Tucuru, Finca Concepción, Tucurú, Alta Verapaz.	M, E	**ON156887**	**ON156956**	
R. mexicanus USNM569890	GU: Chelemhá Cloud Forest Reserve, Yalijux Mountain, Alta Verapaz.	M, E	**ON156888**	**ON156955**	
R. mexicanus USNM570133	GU: 9 km S of Pasmola, between km 166 and 167 on CA-14, Hotel Country Delights, Baja Verapaz.	M, E	**ON156889**		
R. mexicanus USNM570072	GU: 9.5 km NW Gualan, El Limo, Sierra de las Minas, Zacapa.	M, E	**ON156890**	**ON156953**	

R. mexicanus USNM569864	GU: Chelemhá Cloud Forest Reserve, Yalijux Mountain, Alta Verapaz.	M, E	**ON156892**	**ON156958**	
R. mexicanus USNM569952	GU: Chelemhá Cloud Forest Reserve, Yalijux Mountain, Alta Verapaz.	M, E	**ON156893**	**ON156959**	
R. mexicanus USNM570436	GU: 3.5 km N (by air) Aldea la Trinidad, Huehuetenango.	M, E	**ON156894**	**ON156966**	
R. mexicanus USNM570446	GU: 1.7 km NE (by road) Yalambojoch, Huehuetenango.	M, E	**ON156895**	**ON156967**	
R. mexicanus UV2213	MX: 3 km N Zongolica, Municipio Zongolica, Veracruz.	M, GM, E	**ON156866**		
R. brevirostris ROM97308	CR: Monte Verde, Puntarenas.	M	EF990005		EF989906
R. brevirostris ROM116845	CR: Monte Verde, Puntarenas.	M	EF990007		EF989908
R. brevirostris ROM116841	CR: foothills near Pico Blanco, San José, San Antonio de Escazú.	M	EF990011		EF989912
R. brevirostris ROM116839	NIC: Cerro Madera, Ometepe Island.	M	EF990016		EF989917
R. brevirostris ROM116804	CR: 10 km E of Sucre, Juan Castro Blanco National Park, Alajuela.	M	EF990017		EF989918
R. brevirostris ROM116824	NIC: Cerro Madera, Ometepe Island.	M	EF990020		EF989921
R. brevirostris MVZ174401	CR: Colima Tapanti, 1.6 km S Tapanti Bridge over Rio Grande de Orosi, Cartago.	M	AF108709		
R. darienenis ROM116311	PAN: Mount Pirri, Darien Province.	M	EF990015		EF989916
R. garichensis MSB262794	PAN: Jurufungo, Chiriqui, Renacimiento, La Amistad International Park.	M	**ON156907**	**ON156918**	
R. sp. Cartago ROM116835	CR: Cerro de la Carpentera, Iztaru Scout Camp, Cartago.	M	EF990012		EF989913
R. sp. Poas ROM114291	CR: Volcan Poas National Park, Alajuela.	M	EF990018		EF989919
R. sp. Poas ROM116805	CR: Volcan Poas National Park, Alajuela.	M	EF990019		EF989920
R. gracilis TTU34814	ES: about 3 miles NW San Luis Talpa, La Paz.	M	**ON156908**	**ON156916**	
R. gracilis TTU34820	ES: about 3 miles NW San Luis Talpa, La Paz.	M	**ON156909**	**ON156917**	
R. gracilis ROM95890	MX: 52 km SW of Champoton, Municipio Champoton, Campeche.	M	AY859432		EF989905
R. gracilis FN30426	MX: Laguna Becanchen, Yucatán.	M	AY293817		
R. gracilis ASNHC6370	MX: Laguna Becanchen, Yucatán.	M	AY859431		

R. spectabilis ASNHC2140	MX: 30 km SE San Miguel, Isla Cozumel, Quintana Roo.	M	AY859462		
R. spectabilis ROM97733	MX: 1.5 km N of El Cedral, Isla Cozumel, Quintana Roo.	M	EF990022		EF989923
R. spectabilis ASNHC2139	MX: 30 km SE San Miguel, Isla Cozumel, Quintana Roo.	M	EF990021		EF989922
R. microdon Ecosur1930	MX: Cerro Mozotal 30 km N Motozintla by road Buenos Aires-El Porvenir, Municipio El Porvenir, Chiapas.	M	MW117046	MW117100	**ON156969**
R. microdon Ecosur2671	MX: 2 km NE San Cristóbal de las Casas, Reserva Ecológica Huitepec Hillside, Chiapas.	M	MW117051	MW117101	
R. microdon ROM98300	GU: 12 km NW of Santa Eulalia (by road), Huehuetenango.	M	EF990014		EF989914
R. microdon ROM98382	GU: 16 km NW of Santa Eulalia (by road), Huehuetenango.	M	AY859458		EF989915
R. tenuirostris BYU 14479	MX: Cerro Tzontehuitz, 13 km NE San Cristóbal de las Casas, Municipio Chamula, Chiapas.	M	AY859463	MW117095	
R. tenuirostris ECOSUR1817	MX: Cerro Tzontehuitz, 11 km NE San Cristóbal de las Casas, Municipio Chamula, Chiapas.	M	MW117045	MW117096	
R. cherrii LSUMNS25169	CR: 1 km (by road) SW Poas, San José.	M	MW117038	MW117074	
R. cherrii LSUMNS381	CR: Cartago.	M	**ON156912**	**ON156913**	
R. cherrii LSUMNS466	CR: San José.	M	**ON156911**	**ON156914**	
R. cherrii LSUMNS380	CR: Cartago.	M	MW117037	MW117077	
R. cherrii MSB61867	CR: 2 km NE Getzemani, Heredia.	M	**ON156910**	**ON156915**	
R. megalotis ASNHC2133	MX: 3 km S of Parres, Ciudad de México.	M	EF990008		EF989909
R. megalotis ASNHC2136	MX: 3 km S of Parres, Ciudad de México.	M	EF990009		EF989910
R. megalotis CMC1072	MX: 4.7 km NE Teziutlán (by road), Municipio Teziutlán, Puebla.	M	HQ269732	HQ269795	
R. sumichrasti ROM98383	GU: 10 km SW of Santa Eulalia, Santa Eulalia, Huehuetenango.	M	HQ269715	HQ269787	EF989924
R. sumichrasti ROM98384	GU: 15 km SW of Santa Apolonia, Santa Apolonia, Chimaltenango.	M	HQ269716	HQ269788	EF989925
R. fulvescens BYU20914	MX: Río de la Arena 6 km E (by road) Pinotepa Nacional, Municipio Pinotepa Nacional.	M	HQ269730	HQ269794	
R. fulvescens ASNHC3465	MX: 4.8 km N of Santiago, Santiago, Nayarit.	M	EF990000		EF989901

Supplementary material 1

Parameters of 50 ecological niche models, obtained in Wallace (Kass et al. 2018) for *Reithrodontomys mexicanus* species complex (Rodentia: Cricetidae). The best fit model parameters used to obtain the final ecological niche model are highlighted in bold. Features classes: L=Linear; Q=Quadratic; H=Hinge; P=Product. AUC=Area Under Curve. 10p=10th-percentile; mtp=Minimum training presence. AIC=Akaike Informative Criterion. rm=Regularization multiplier.

Reithrodontomys mexicanus clade III									
rm	Features	AUC train	AUC val avg	AUC diff avg	or 10p avg	or mtp avg	AICc	delta AICc	w AIC
1.5	**LQH**	**0.92**	**0.83**	**0.10**	**0.62**	**0.22**	**360.06**	**0.00**	**0.46**
2.5	H	0.88	0.83	0.07	0.37	0.11	363.47	3.41	0.08
3	LQH	0.89	0.84	0.08	0.42	0.22	363.48	3.42	0.08
1	LQ	0.87	0.85	0.04	0.29	0.17	363.77	3.70	0.07
1.5	LQ	0.87	0.84	0.04	0.37	0.17	364.98	4.92	0.04
2.5	LQH	0.89	0.84	0.08	0.48	0.22	365.67	5.61	0.03
3.5	LQH	0.88	0.84	0.07	0.37	0.22	366.01	5.95	0.02
3	H	0.88	0.84	0.06	0.37	0.06	366.02	5.96	0.02
3	LQHP	0.88	0.83	0.08	0.42	0.22	366.02	5.96	0.02
2	LQ	0.87	0.84	0.03	0.35	0.17	366.55	6.48	0.02
1	L	0.86	0.84	0.02	0.24	0.17	366.75	6.69	0.02
3	LQ	0.87	0.81	0.01	0.17	0.17	366.93	6.86	0.01
2	LQH	0.90	0.84	0.08	0.48	0.22	367.42	7.36	0.01
2.5	LQHP	0.88	0.83	0.08	0.48	0.22	367.77	7.71	0.01
2.5	LQ	0.87	0.82	0.00	0.17	0.17	368.46	8.40	0.01
5	LQH	0.86	0.80	0.01	0.17	0.17	368.49	8.43	0.01
4.5	LQH	0.87	0.83	0.03	0.17	0.17	368.53	8.47	0.01
4	LQH	0.88	0.84	0.06	0.29	0.22	368.93	8.87	0.01
2	LQHP	0.90	0.83	0.08	0.48	0.17	369.00	8.94	0.01
3.5	LQ	0.86	0.80	0.01	0.17	0.17	369.16	9.10	0.00
3.5	H	0.88	0.85	0.03	0.31	0.06	369.16	9.10	0.00
3.5	LQHP	0.88	0.84	0.06	0.37	0.22	369.16	9.10	0.00
0.5	L	0.85	0.84	0.03	0.29	0.11	369.37	9.31	0.00
3.5	L	0.84	0.82	0.01	0.24	0.17	369.44	9.38	0.00
5.5	LQ	0.81	0.80	0.01	0.17	0.17	369.52	9.45	0.00
6	LQ	0.81	0.80	0.01	0.17	0.17	369.87	9.81	0.00
6	LQH	0.81	0.80	0.01	0.17	0.17	369.87	9.81	0.00
2.5	L	0.84	0.83	0.00	0.24	0.17	370.01	9.95	0.00
4	L	0.84	0.82	0.01	0.17	0.17	370.44	10.37	0.00
4.5	LQ	0.82	0.80	0.01	0.17	0.17	370.70	10.64	0.00
3	L	0.84	0.82	0.01	0.24	0.17	371.10	11.03	0.00

2	L	0.85	0.83	0.01	0.24	0.17	371.15	11.09	0.00
4.5	L	0.84	0.81	0.01	0.17	0.17	371.55	11.49	0.00
5	H	0.84	0.83	0.01	0.24	0.06	371.63	11.57	0.00
5	LQHP	0.84	0.82	0.01	0.24	0.17	371.63	11.57	0.00
4	LQ	0.84	0.80	0.01	0.17	0.17	371.77	11.71	0.00
5	LQ	0.81	0.80	0.01	0.17	0.17	371.79	11.73	0.00
5.5	LQH	0.81	0.80	0.01	0.17	0.17	371.84	11.77	0.00
0.5	LQ	0.88	0.84	0.07	0.29	0.22	371.87	11.81	0.00
1.5	L	0.86	0.84	0.01	0.24	0.17	372.15	12.09	0.00
5.5	H	0.84	0.83	0.01	0.24	0.06	372.54	12.48	0.00
5.5	LQHP	0.84	0.82	0.01	0.24	0.17	372.54	12.48	0.00
4	LQHP	0.87	0.85	0.01	0.24	0.17	372.84	12.78	0.00
4	H	0.87	0.85	0.01	0.24	0.06	372.84	12.78	0.00
4.5	H	0.86	0.85	0.01	0.24	0.06	373.22	13.15	0.00
4.5	LQHP	0.86	0.84	0.01	0.24	0.17	373.22	13.15	0.00
6	H	0.84	0.83	0.01	0.24	0.06	373.51	13.45	0.00
6	LQHP	0.84	0.82	0.01	0.24	0.17	373.51	13.45	0.00
5	L	0.84	0.65	0.00	0.17	0.17	375.69	15.63	0.00
2	H	0.90	0.83	0.08	0.31	0.11	375.99	15.93	0.00
Reithrodontomys mexicanus clade I									
0.5	**LQ**	**0.91**	**0.82**	**0.08**	**0.42**	**0.16**	**425.32**	**0.00**	**0.31**
4	H	0.89	0.82	0.07	0.25	0.12	426.71	1.39	0.15
4	LQHP	0.89	0.82	0.07	0.25	0.12	426.71	1.39	0.15
3.5	LQHP	0.89	0.82	0.07	0.25	0.12	428.84	3.52	0.05
3.5	H	0.89	0.82	0.07	0.25	0.12	428.84	3.52	0.05
4.5	H	0.89	0.82	0.06	0.25	0.12	428.85	3.52	0.05
4.5	LQHP	0.89	0.82	0.06	0.25	0.12	428.85	3.52	0.05
5	LQHP	0.89	0.82	0.06	0.25	0.12	430.82	5.50	0.02
5	H	0.89	0.82	0.06	0.25	0.12	430.82	5.50	0.02
5	LQH	0.89	0.80	0.07	0.25	0.12	430.98	5.66	0.02
4	LQH	0.89	0.80	0.07	0.25	0.12	431.09	5.77	0.02
6	LQH	0.89	0.67	0.04	0.07	0.07	431.37	6.05	0.01
3	H	0.89	0.82	0.07	0.25	0.12	431.81	6.49	0.01
3	LQHP	0.89	0.82	0.07	0.25	0.12	431.81	6.49	0.01
5.5	LQH	0.89	0.80	0.07	0.25	0.12	432.81	7.49	0.01
1	L	0.84	0.79	0.07	0.40	0.26	432.85	7.53	0.01
5.5	LQHP	0.89	0.83	0.06	0.25	0.12	432.91	7.59	0.01
5.5	H	0.89	0.83	0.06	0.25	0.12	432.91	7.59	0.01
4.5	LQH	0.89	0.80	0.08	0.25	0.21	433.12	7.80	0.01
1.5	L	0.84	0.79	0.07	0.40	0.26	433.80	8.47	0.00
1	LQ	0.89	0.80	0.08	0.28	0.21	433.86	8.54	0.00

2.5	LQ	0.85	0.78	0.07	0.25	0.12	434.47	9.15	0.00
4	LQ	0.85	0.79	0.06	0.25	0.12	434.52	9.20	0.00
2	L	0.84	0.79	0.07	0.32	0.12	435.05	9.73	0.00
3	LQ	0.85	0.78	0.07	0.25	0.12	435.52	10.20	0.00
3	L	0.83	0.80	0.06	0.32	0.12	435.53	10.21	0.00
4.5	LQ	0.84	0.79	0.05	0.25	0.12	435.76	10.44	0.00
1.5	H	0.90	0.82	0.11	0.47	0.26	436.57	11.25	0.00
1.5	LQHP	0.90	0.82	0.11	0.47	0.26	436.57	11.25	0.00
2.5	L	0.84	0.79	0.06	0.32	0.12	436.60	11.28	0.00
3.5	LQ	0.85	0.78	0.07	0.25	0.12	436.71	11.39	0.00
5	LQ	0.84	0.80	0.03	0.25	0.12	437.13	11.81	0.00
2	LQ	0.85	0.78	0.07	0.32	0.12	437.29	11.97	0.00
3.5	L	0.83	0.80	0.04	0.25	0.12	437.32	12.00	0.00
5.5	LQ	0.84	0.80	0.02	0.25	0.12	438.65	13.33	0.00
6	H	0.89	0.67	0.04	0.07	0.07	439.03	13.70	0.00
6	LQHP	0.89	0.67	0.04	0.07	0.07	439.03	13.70	0.00
4.5	L	0.83	0.66	0.01	0.07	0.07	439.06	13.74	0.00
2	H	0.90	0.83	0.11	0.40	0.26	439.36	14.04	0.00
2	LQHP	0.90	0.83	0.11	0.40	0.26	439.36	14.04	0.00
4	L	0.83	0.66	0.01	0.07	0.07	439.44	14.12	0.00
0.5	L	0.84	0.79	0.06	0.32	0.14	439.49	14.17	0.00
3.5	LQH	0.89	0.82	0.07	0.25	0.12	439.59	14.27	0.00
5	L	0.83	0.50	0.00	0.00	0.00	440.13	14.81	0.00
6	LQ	0.83	0.67	0.01	0.00	0.00	440.32	15.00	0.00
5.5	L	0.83	0.50	0.00	0.00	0.00	441.36	16.04	0.00
2.5	LQHP	0.89	0.83	0.09	0.47	0.19	442.12	16.80	0.00
2.5	H	0.89	0.83	0.09	0.47	0.19	442.12	16.80	0.00
1.5	LQ	0.87	0.78	0.07	0.32	0.12	442.32	17.00	0.00
6	L	0.83	0.50	0.00	0.00	0.00	442.77	17.45	0.00
Reithrodontomys mexicanus clade IIA									
1.5	**H**	**0.70**	**0.62**	**0.15**	**0.61**	**0.10**	**289.96**	**0.00**	**0.06**
1.5	LQH	0.70	0.58	0.21	0.61	0.23	289.96	0.00	0.06
1.5	LQHP	0.70	0.59	0.19	0.61	0.23	289.96	0.00	0.06
2	H	0.70	0.67	0.05	0.41	0.10	290.33	0.37	0.05
2	LQH	0.70	0.61	0.13	0.41	0.23	290.33	0.37	0.05
2	LQHP	0.70	0.63	0.11	0.41	0.23	290.33	0.37	0.05
1	LQ	0.69	0.63	0.13	0.35	0.35	290.73	0.77	0.04
2.5	H	0.70	0.67	0.05	0.41	0.10	290.79	0.84	0.04
2.5	LQHP	0.70	0.58	0.13	0.41	0.41	290.79	0.84	0.04
2.5	LQH	0.70	0.55	0.12	0.41	0.35	290.79	0.84	0.04
1.5	LQ	0.69	0.56	0.13	0.41	0.35	291.08	1.12	0.04

3	LQH	0.70	0.55	0.12	0.41	0.35	291.34	1.38	0.03
3	H	0.70	0.59	0.01	0.10	0.10	291.34	1.38	0.03
3	LQHP	0.70	0.55	0.12	0.41	0.35	291.34	1.38	0.03
2	LQ	0.69	0.56	0.13	0.41	0.35	291.57	1.61	0.03
0.5	L	0.69	0.62	0.09	0.35	0.35	291.91	1.95	0.02
3.5	LQH	0.70	0.46	0.11	0.31	0.25	291.97	2.01	0.02
3.5	H	0.70	0.50	0.00	0.00	0.00	291.97	2.01	0.02
3.5	LQHP	0.70	0.46	0.11	0.31	0.25	291.97	2.01	0.02
2.5	LQ	0.69	0.46	0.11	0.31	0.25	292.18	2.23	0.02
1	L	0.69	0.63	0.12	0.35	0.35	292.22	2.27	0.02
4	H	0.70	0.50	0.00	0.00	0.00	292.67	2.71	0.02
4	LQH	0.70	0.46	0.11	0.31	0.25	292.67	2.71	0.02
4	LQHP	0.70	0.46	0.11	0.31	0.25	292.67	2.71	0.02
1.5	L	0.69	0.58	0.12	0.41	0.35	292.82	2.87	0.02
3	LQ	0.69	0.46	0.11	0.31	0.25	292.92	2.96	0.01
0.5	LQ	0.69	0.62	0.11	0.35	0.29	293.34	3.38	0.01
4.5	LQHP	0.70	0.46	0.11	0.31	0.25	293.45	3.49	0.01
4.5	LQH	0.70	0.46	0.11	0.31	0.25	293.45	3.49	0.01
4.5	H	0.70	0.50	0.00	0.00	0.00	293.45	3.49	0.01
3.5	LQ	0.69	0.46	0.11	0.31	0.25	293.77	3.81	0.01
5	H	0.70	0.50	0.00	0.00	0.00	294.31	4.35	0.01
5	LQHP	0.70	0.46	0.11	0.31	0.25	294.31	4.35	0.01
5	LQH	0.70	0.46	0.11	0.31	0.25	294.31	4.35	0.01
4	LQ	0.69	0.46	0.11	0.31	0.25	294.74	4.78	0.01
2.5	L	0.69	0.46	0.11	0.31	0.25	294.99	5.04	0.01
5.5	LQH	0.70	0.46	0.11	0.31	0.25	295.24	5.29	0.00
5.5	LQHP	0.70	0.46	0.11	0.31	0.25	295.24	5.29	0.00
5.5	H	0.70	0.50	0.00	0.00	0.00	295.24	5.29	0.00
2	L	0.69	0.46	0.11	0.31	0.25	296.63	6.67	0.00
3	L	0.50	0.46	0.11	0.31	0.25	303.98	14.03	0.00
3.5	L	0.50	0.46	0.11	0.31	0.25	303.98	14.03	0.00
4	L	0.50	0.46	0.11	0.31	0.25	303.98	14.03	0.00
4.5	L	0.50	0.46	0.11	0.31	0.25	303.98	14.03	0.00
5	L	0.50	0.46	0.11	0.31	0.25	303.98	14.03	0.00
5.5	L	0.50	0.50	0.00	0.00	0.00	303.98	14.03	0.00
6	L	0.50	0.50	0.00	0.00	0.00	303.98	14.03	0.00
4.5	LQ	0.50	0.46	0.11	0.31	0.25	303.98	14.03	0.00
5	LQ	0.50	0.46	0.11	0.31	0.25	303.98	14.03	0.00
5.5	LQ	0.50	0.46	0.11	0.31	0.25	303.98	14.03	0.00
Reithrodontomys mexicanus clade IIB									
2	**LQ**	**0.79**	**0.68**	**0.13**	**0.60**	**0.20**	**247.87**	**0.00**	**0.23**

1.5	L	0.79	0.68	0.13	0.60	0.20	248.27	0.39	0.19
2.5	LQ	0.79	0.68	0.13	0.60	0.20	248.54	0.66	0.16
2	L	0.79	0.68	0.13	0.60	0.20	249.09	1.22	0.12
2.5	L	0.79	0.68	0.13	0.60	0.20	250.07	2.20	0.08
3	L	0.79	0.68	0.13	0.60	0.20	251.17	3.30	0.04
3.5	L	0.79	0.68	0.13	0.60	0.20	252.37	4.50	0.02
3	LQ	0.79	0.68	0.13	0.60	0.20	252.47	4.59	0.02
3.5	LQ	0.79	0.68	0.13	0.60	0.20	253.25	5.37	0.02
4	L	0.79	0.68	0.13	0.60	0.20	253.66	5.79	0.01
6	LQ	0.70	0.68	0.13	0.60	0.20	253.92	6.04	0.01
6	LQH	0.70	0.68	0.13	0.60	0.20	253.92	6.04	0.01
4	LQ	0.79	0.68	0.13	0.60	0.20	254.04	6.17	0.01
4	LQH	0.79	0.68	0.13	0.60	0.20	254.04	6.17	0.01
1.5	LQ	0.80	0.68	0.13	0.60	0.20	254.44	6.57	0.01
4.5	LQH	0.78	0.68	0.13	0.60	0.20	254.83	6.96	0.01
4.5	LQ	0.78	0.68	0.13	0.60	0.20	254.83	6.96	0.01
4.5	L	0.79	0.62	0.05	0.20	0.20	255.02	7.14	0.01
5	LQ	0.77	0.68	0.13	0.60	0.20	255.62	7.75	0.00
5	LQH	0.77	0.68	0.13	0.60	0.20	255.62	7.75	0.00
5	H	0.72	0.50	0.00	0.00	0.00	255.88	8.01	0.00
0.5	L	0.83	0.75	0.09	0.40	0.10	256.00	8.13	0.00
5.5	LQHP	0.70	0.50	0.00	0.00	0.00	256.23	8.36	0.00
5.5	LQ	0.75	0.68	0.13	0.60	0.20	256.41	8.54	0.00
5.5	LQH	0.75	0.68	0.13	0.60	0.20	256.41	8.54	0.00
5	L	0.79	0.62	0.05	0.20	0.20	256.44	8.57	0.00
6	LQHP	0.70	0.50	0.00	0.00	0.00	256.68	8.80	0.00
5.5	H	0.72	0.50	0.00	0.00	0.00	257.00	9.13	0.00
5	LQHP	0.77	0.50	0.00	0.00	0.00	258.58	10.71	0.00
1	L	0.82	0.71	0.12	0.60	0.20	259.14	11.27	0.00
3.5	LQH	0.80	0.68	0.13	0.60	0.20	263.15	15.28	0.00
4	H	0.81	0.60	0.04	0.20	0.10	265.76	17.88	0.00
1	LQ	0.83	0.71	0.12	0.50	0.20	266.88	19.00	0.00
4.5	H	0.79	0.50	0.00	0.00	0.00	267.60	19.73	0.00
4.5	LQHP	0.78	0.62	0.05	0.20	0.20	267.73	19.86	0.00
2.5	LQH	0.83	0.68	0.16	0.60	0.20	269.62	21.74	0.00
5.5	L	0.50	0.62	0.05	0.20	0.20	269.96	22.09	0.00
6	L	0.50	0.50	0.00	0.00	0.00	269.96	22.09	0.00
6	H	0.50	0.50	0.00	0.00	0.00	269.96	22.09	0.00
3	LQH	0.82	0.68	0.13	0.60	0.20	270.89	23.01	0.00
3	H	0.82	0.61	0.16	0.30	0.10	271.52	23.65	0.00
3.5	H	0.81	0.60	0.04	0.20	0.10	272.99	25.12	0.00

3.5	LQHP	0.83	0.68	0.14	0.70	0.10	273.01	25.14	0.00
0.5	LQ	0.87	0.75	0.11	0.50	0.20	273.96	26.08	0.00
4	LQHP	0.83	0.69	0.14	0.60	0.20	274.80	26.93	0.00
2	H	0.86	0.63	0.17	0.70	0.10	310.11	62.23	0.00
2	LQHP	0.86	0.66	0.17	0.70	0.10	310.21	62.34	0.00
2	LQH	0.86	0.67	0.16	0.60	0.20	310.68	62.81	0.00
2.5	LQHP	0.83	0.66	0.17	0.70	0.10	315.20	67.33	0.00
3	LQHP	0.83	0.67	0.16	0.70	0.10	316.48	68.61	0.00

Supplementary material 2

Tables 1-4. Matrixes of Kimura 2-parameter genetic distances (%) for cytochrome-b gene sequence data between species of the *mexicanus* group. Taxon labels correspond to species delimited by mPTP, bGMYC, and STACEY methods.

Species delimitation (mPTP)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
R. mexicanus clade III														
R. mexicanus clade I	15.92													
R. mexicanus ES	15.92	4.96												
R. mexicanus clade IIA	16.86	8.26	8.72											
R. mexicanus clade IIB	13.20	5.20	7.20	1.60										
R. mexicanus clade IIC	14.30	6.50	8.60	3.60	2.20									
R. mexicanus clade IID	13.50	4.30	6.10	3.10	1.50	3.20								
R. mexicanus clade IIE	15.70	7.10	9.0	3.40	2.20	4.20	3.90							
R. brevirostris clade IA	14.40	3.20	4.10	5.70	5.20	6.50	4.80	8.10						
R. brevirostris clade IB	15.60	4.80	5.10	6.70	6.90	8.70	6.50	9.50	2.80					
R. darienensis	16.68	8.48	7.69	5.60	5.0	7.60	5.80	8.30	8.30	9.70				
R. garichensis	18.18	14.59	12.92	13.60	12.80	14.70	12.90	13.30	12.60	13.20	15.62			
R. sp. Volcan Poas	17.12	13.83	13.98	14.0	12.30	12.90	12.40	14.20	12.50	13.60	13.95	11.31		
R. grac- spect	14.70	13.43	13.26	12.0	14.10	15.30	12.50	14.0	11.60	12.90	13.86	16.60	15.23	
R. gracilis ES	15.16	13.43	14.50	15.30	15.70	16.30	14.0	15.80	13.30	14.20	15.55	17.38	16.38	7.91

Species delimitation (bGMYC)

	1	2	3	4	5	6	7	8	9	10
R. mexicanus clade III										
R. mexicanus clade I	15.92									
R. mexicanus ES	15.92	4.96								
R. mexicanus clade IIA	16.86	8.26	8.72							
R. mexicanus clade IIB	15.88	8.32	8.96	6.06						
R. brevirostris	16.15	5.68	5.23	8.31	8.34					
R. darienensis	16.68	8.48	7.69	8.30	7.54	9.22				
R. garichensis	18.18	14.59	12.92	16.09	14.24	14.0	15.62			
R. sp. Volcan Poas	17.12	13.83	13.98	14.86	13.93	13.37	13.95	11.31		
R. grac- spect	14.70	13.43	13.26	15.53	14.56	12.91	13.86	16.60	15.23	
R. gracilis ES	15.16	13.43	14.50	16.72	16.22	14.29	15.55	17.38	16.38	7.91

Species delimitation (STACEY: cytb + Fgb- I7)*

	1	2	3	4	5	6	7	8	9
R. mexicanus clade III									
R. mexicanus clade IA	14.60								
R. mexicanus clade IB	13.30	2.0							
R. mexicanus clade IC	14.80	2.40	2.70						
R. mexicanus ES	15.92	3.90	4.0	4.40					
R. mexicanus clade IIA	16.86	4.90	5.0	5.20	8.72				
R. mexicanus clade IIB	12.60	5.80	5.30	5.70	7.10	1.50			
R. mexicanus clade IIC	15.70	7.60	8.50	8.10	9.0	3.90	2.10		
R. garichensis	18.18	13.40	12.70	13.20	12.92	16.09	12.50	13.30	
R. gracilis ES	15.16	12.60	12.60	12.30	14.50	16.72	15.0	15.80	17.38

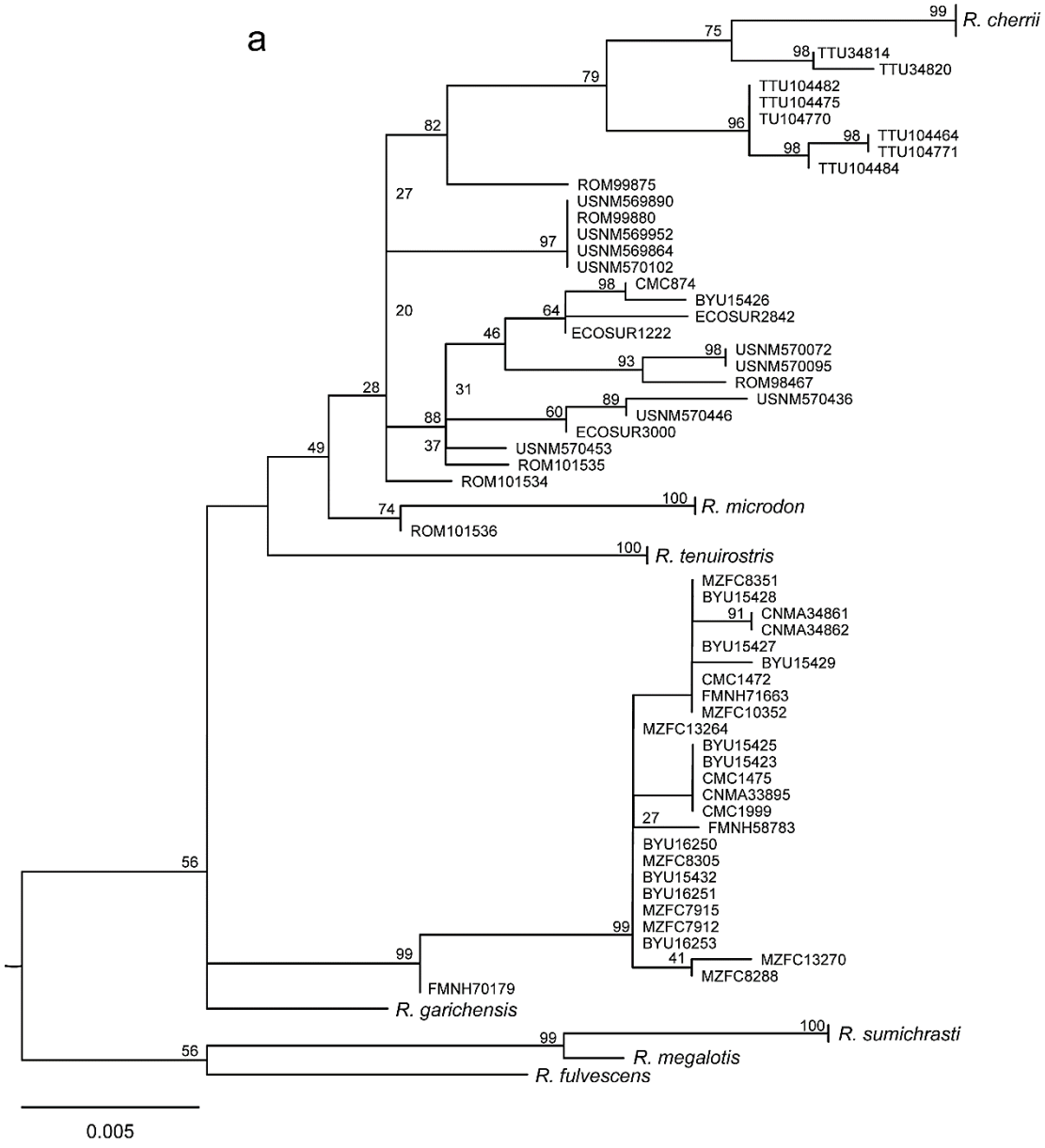
* Concatenated data set not available for *R. brevirostris*, *R. darienensis*, *R. sp*. Volcan Poas, and *R. gracilis* + *R. spectabilis*.

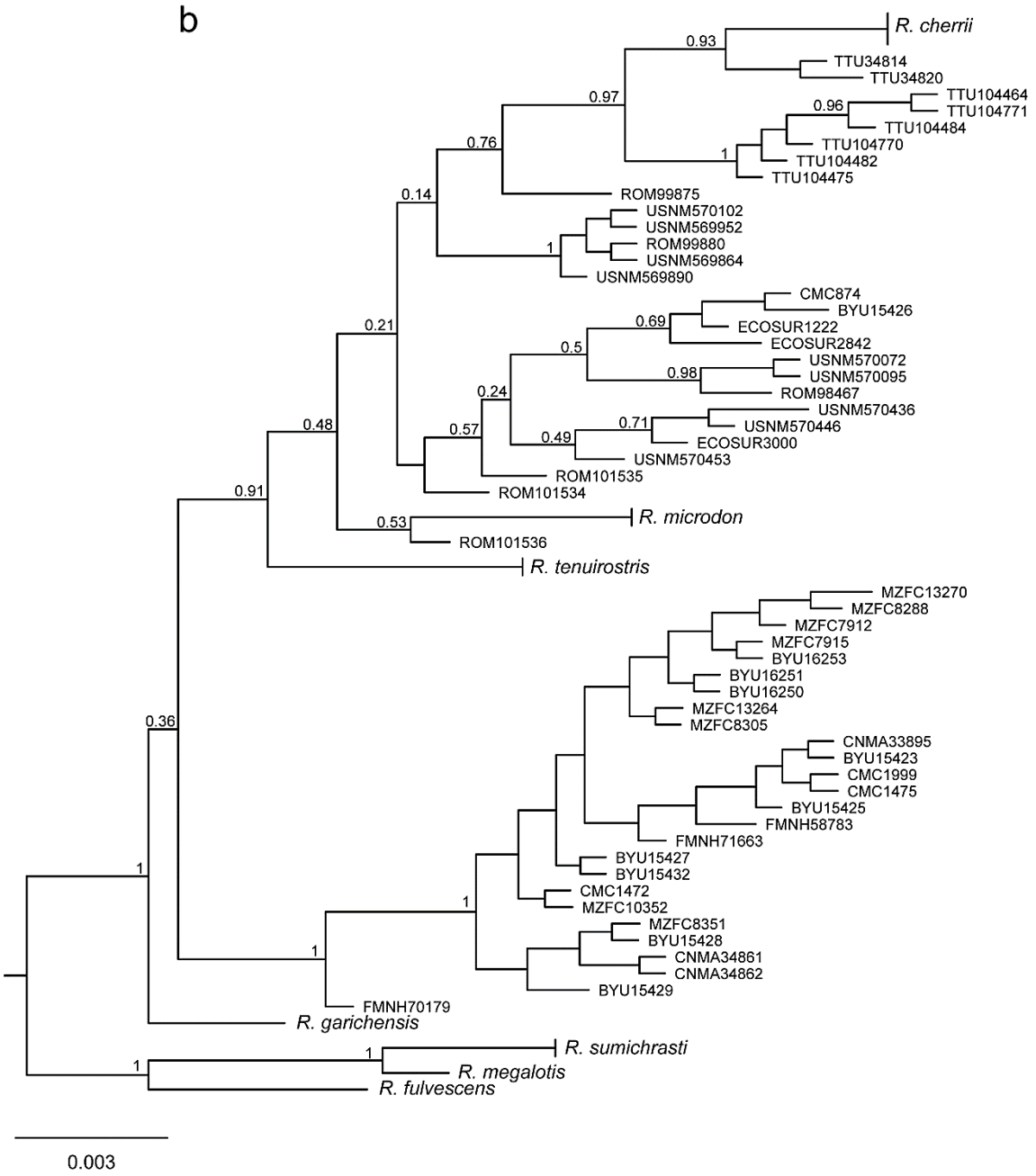
Species delimitation (STACEY: cytb + IRBP)*

	1	2	3	4	5	6	7	8	9
R. mexicanus clade III									
R. mexicanus clade IA	15.92								
R. mexicanus clade IB	14.80	2.0							
R. brevirostris clade IA	14.70	3.50	4.80						
R. brevirostris clade IB	15.10	4.0	4.90	1.30					
R. brevirostris clade IC	15.60	4.70	6.30	2.80	3.60				
R. darienensis	16.68	7.30	7.80	8.60	8.80	9.70			
R. garichensis	18.18	12.70	13.20	12.80	13.40	13.20	15.62		
R. sp. Volcan Poas	17.12	12.60	13.20	12.80	13.10	13.60	13.95	11.31	
R. grac- spect	14.70	11.50	12.70	11.70	12.0	12.80	13.86	16.60	15.23

* Concatenated data set not available for *R. mexicanus* ES, *R. mexicanus* (Colombia and Ecuador), and *R. gracilis* ES.

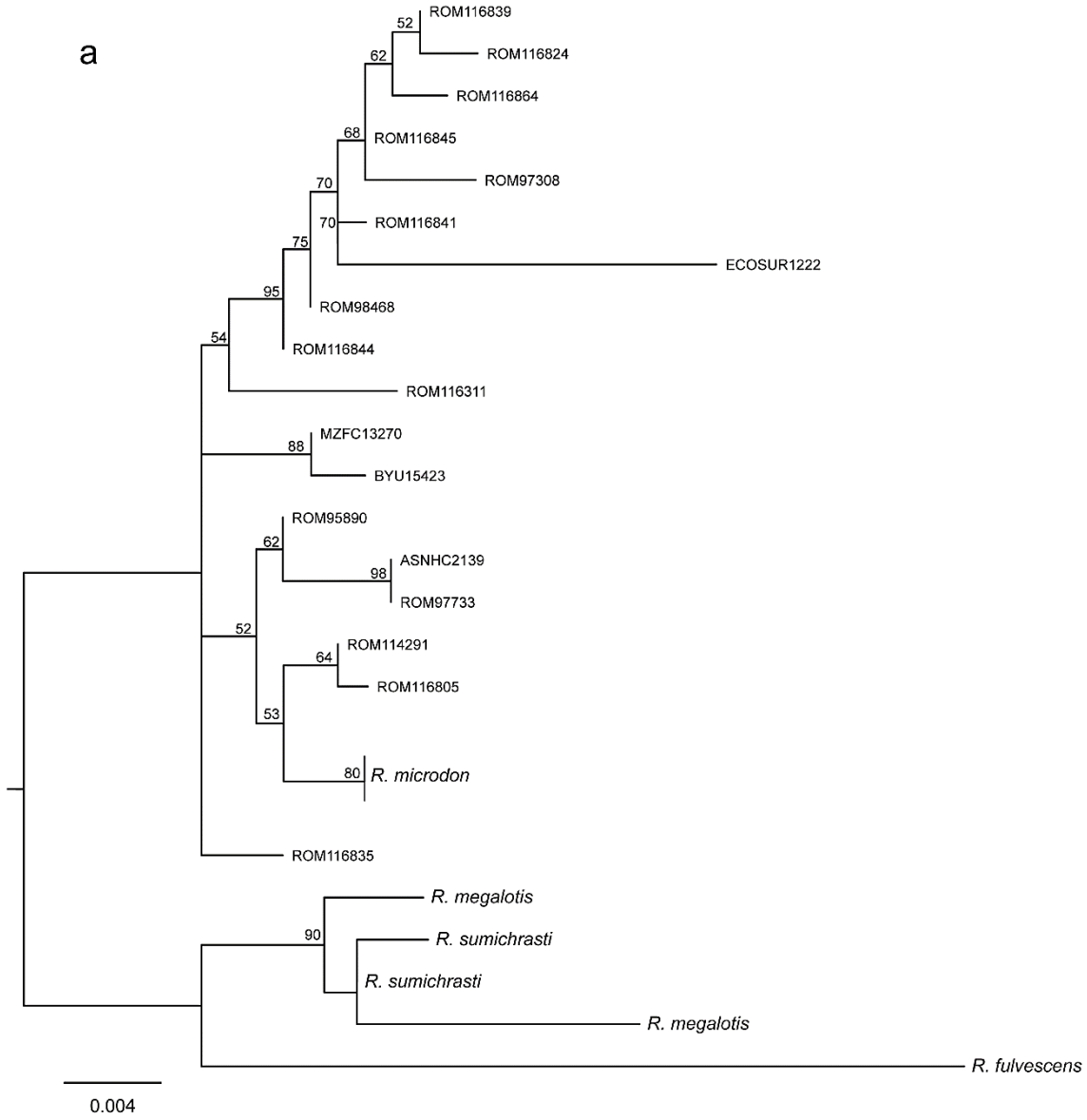
Supplementary material 3





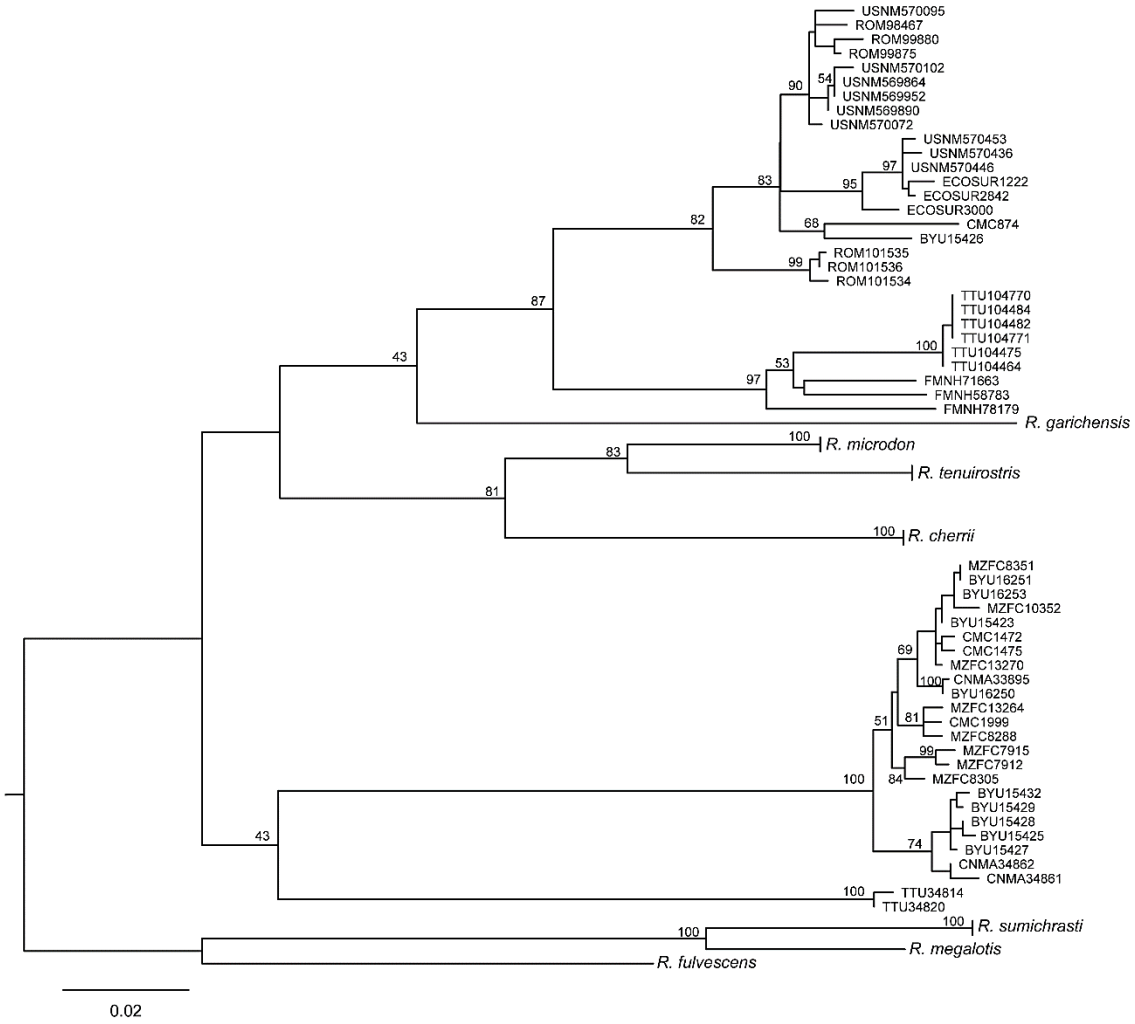
Phylogenetic relationships among species of the *Reithrodontomys mexicanus* group (Rodentia: Cricetidae) using the intron 7 of the beta fibrinogen sequences data set and the reconstructive methods of Maximum Likelihood (a) and Bayesian Inference (b). Values above branches represent nodal support. Terminal labels are named according to mammal collection voucher numbers (see Appendix 1).

Supplementary material 4



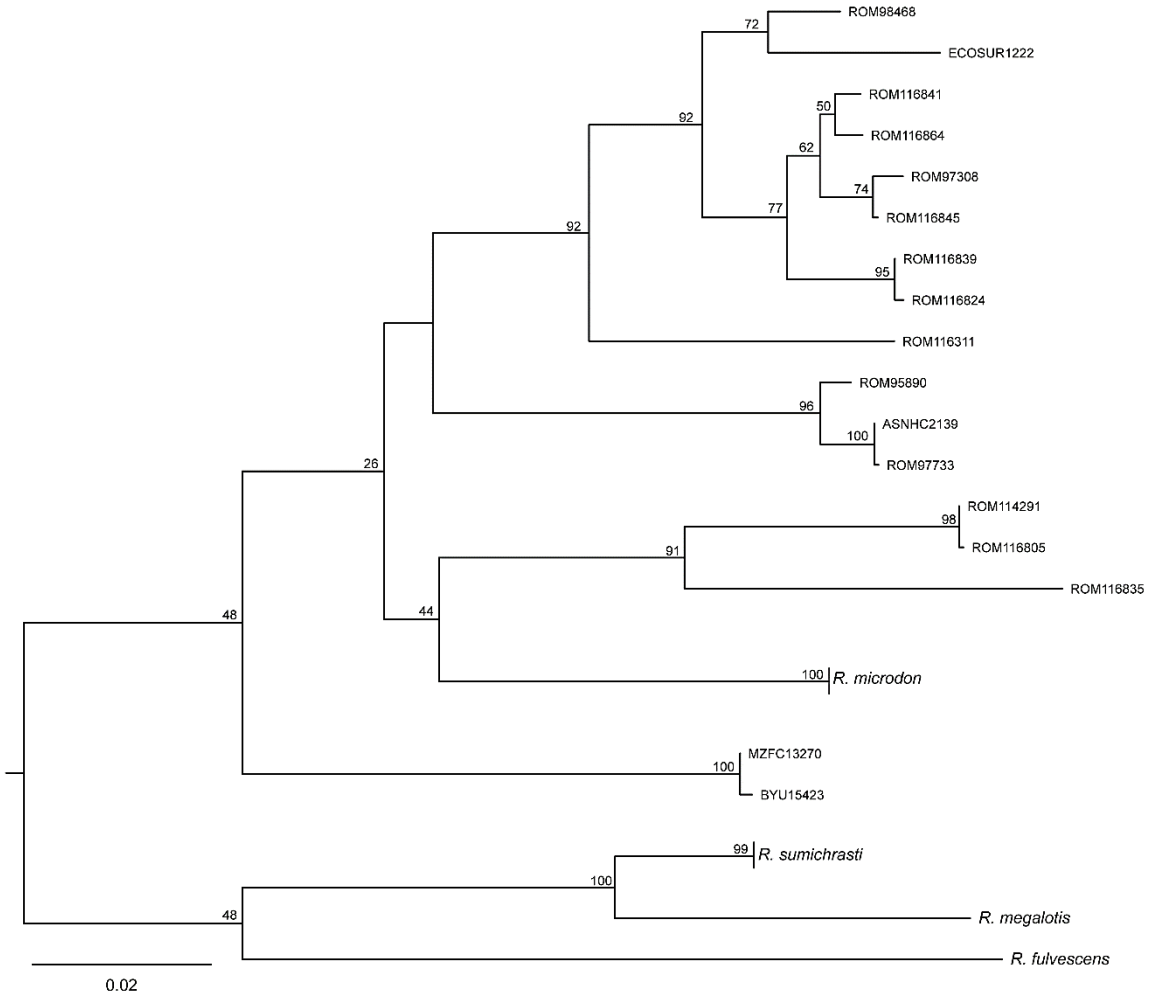
Phylogenetic relationships among species of the *Reithrodontomys mexicanus* group (Rodentia: Cricetidae) using the Interphotoreceptor retinoid-binding protein sequences data set and the reconstructive methods of Maximum Likelihood (a) and Bayesian Inference (b). Values above branches represent nodal support. Terminal labels are named according to mammal collection voucher numbers (see Appendix 1).

Supplementary material 5



Phylogenetic relationships among species of the *Reithrodontomys mexicanus* group (Rodentia: Cricetidae) using sequence data of the concatenated dataset Cytochrome b + Intron 7 of the beta fibrinogen and the reconstructive method of Maximum Likelihood. Values above branches represent nodal support. Terminal labels are named according to mammal collection voucher numbers (see Appendix 1).

Supplementary material 6



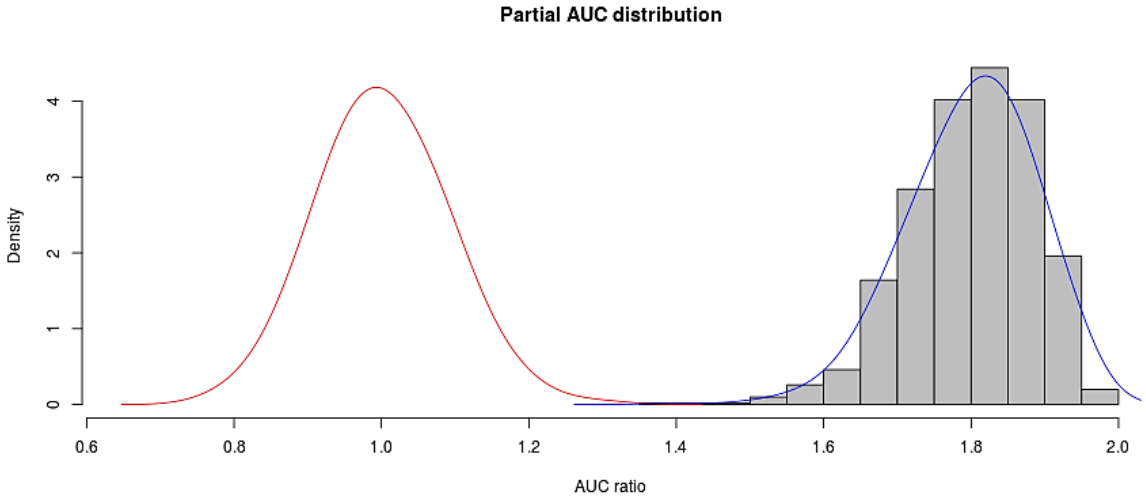
Phylogenetic relationships among species of the *Reithrodontomys mexicanus* group (Rodentia: Cricetidae) using sequence data of the concatenated dataset Cytochrome b + Interphotoreceptor retinoid-binding protein and the reconstructive method of Maximum Likelihood. Values above branches represent nodal support. Terminal labels are named according to mammal collection voucher numbers (see Appendix 1).

Supplementary material 7.

Partial-ROC values and distribution of AUC ratios; red distribution represents the null model; blue distribution represents the distribution of expectations using a random points percentage of 50% of the total available points and 1000 resampling replicates.

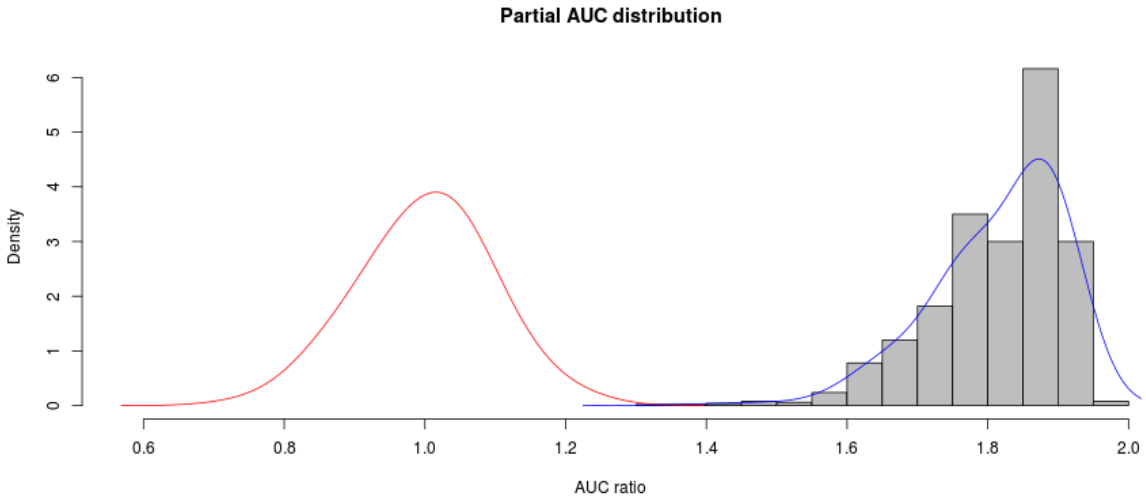
Reithrodontomys mexicanus clade III

Mean AUC ratio after 1000 simulations: 1.799753 (p = 0)



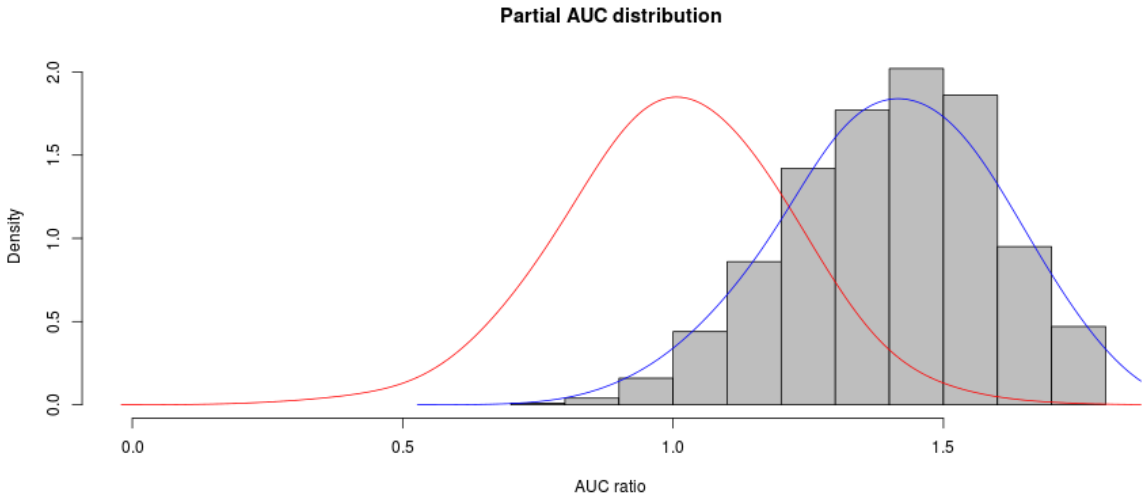
Reithrodontomys mexicanus clade I

Mean AUC ratio after 1000 simulations: 1.814829 (p = 0)



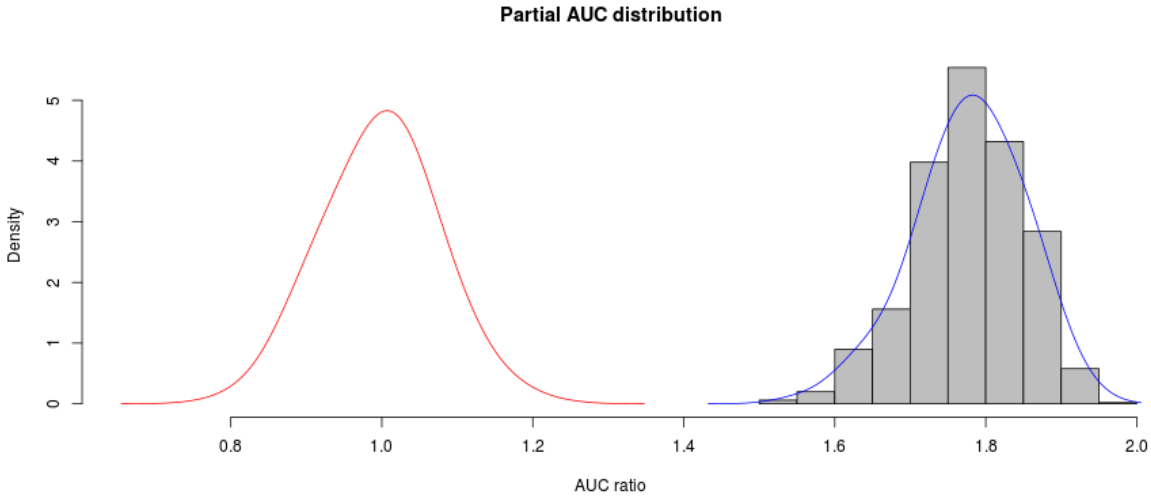
Reithrodontomys mexicanus clade IIA

Mean AUC ratio after 1000 simulations: 1.403082 (p = 0.021)



Reithrodontomys mexicanus clade IIB

Mean AUC ratio after 1000 simulations: 1.777717 (p = 0)



CAPÍTULO IV

Molecular systematics of the *Reithrodontomys tenuirostris* group (Rodentia: Cricetidae) highlighting the *Reithrodontomys microdon* species complex

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Molecular systematics of the *Reithrodontomys tenuirostris* group (Rodentia: Cricetidae) highlighting the *Reithrodontomys microdon* species complex

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The *Reithrodontomys tenuirostris* species group is considered "the most specialized" within the genus *Reithrodontomys* from morphological and ecological perspectives. Previous studies based on molecular data recommended changes in the taxonomy of the group. In particular, *R. microdon* has been the most taxonomically questioned, with the suggestion that it constitutes a complex of cryptic species. We analyzed the phylogenetic relationships of the *R. tenuirostris* species group using DNA sequences from the mitochondrial Cytochrome *b* gene and Intron 7 of the nuclear beta fibrinogen gene. In addition, divergence times were estimated, and possible new taxa delimited with three widely used species delimitation methods. Finally, possible connectivity routes based on shared haplotypes were tested among the *R. microdon* populations. All species were recovered as monophyletic with the exception of *R. microdon*, whose individuals were grouped into four different haplogroups, one of which included specimens of *R. bakeri*. Diversification within the *R. tenuirostris* species group began about 3 Ma, in the Pleistocene. The bGMYC and STACEY delimitation methods were congruent with each other, delimiting at the species-level each haplogroup within *R. microdon*, while the mPTP suggested a greater number of species. Moreover, none of the haplogroups showed potential connectivity routes between them, evidencing lack of gene flow. Our results suggest the existence of a higher number of species in the *R. tenuirostris* group, because we show that there are four species within what is currently recognized as *R. microdon*.

Key words: Cricetid rodent, Cytochrome *b*, *Fgb*, harvest mice, species delimitation

Dentro del género *Reithrodontomys*, el grupo de especies *R. tenuirostris* es considerado "el más especializado" morfológica y ecológicamente. Estudios moleculares previos recomendaron cambios en su taxonomía, proponiendo a *R. microdon* como un complejo de especies crípticas. Se analizaron las relaciones filogenéticas del grupo de especies *R. tenuirostris* con base en información de un gen mitocondrial, Citocromo b, y uno nuclear, el intrón 7 del beta fibrinógeno. Se estimaron los tiempos de divergencia, y se delimitó a posibles nuevos taxa aplicando tres métodos comúnmente utilizados, y se evaluaron posibles rutas de conectividad con base en los diferentes haplotipos identificados en las poblaciones de *R. microdon*. Todas las especies del grupo se recuperaron como monofiléticas excepto *R. microdon*, cuyos individuos formaron cuatro haplogrupos diferentes, uno de los cuales incluyó a especímenes de *R. bakeri*. Según la datación obtenida, la diversificación del grupo *R. tenuirostris* comenzó en el Pleistoceno, hace aproximadamente 3 Ma. Los métodos de análisis de delimitación de especies bGMYC y STACEY resultaron congruentes entre sí, logrando delimitar cada haplogrupo dentro de *R. microdon* a nivel de especie, mientras que con el método de mPTP se delimitó un número mayor de especies.

No se identificaron rutas de conectividad entre haplogrupos, lo que resultaría en una ausencia de flujo génico. Se sugiere la existencia de un mayor número de especies en el grupo *R. tenuirostris*, ya que hay cuatro especies incluidas en lo que actualmente se reconoce como *R. microdon*.

Palabras clave: Citocromo b, delimitación de especies, *Fgb*, ratón cosechero, roedor cricétido

Establishing boundaries among species constitutes one of the main challenges for systematics, especially in taxa for which speciation processes have not resulted in obvious morphological differentiation (Goldstein and de Salle 2011). Faced with this problem, one approach has been to use multiple lines of evidence (e.g., ecology, behavior, biogeography, and genetics) to infer species boundaries (Dayrat 2005; Padial *et al.* 2010). The incorporation of molecular data in systematics studies has been particularly useful in resolving taxonomic problems in different zoological groups, especially those where multiple cryptic species have been identified (Bickford 2007; Jörger and Schrödl 2013; Struck *et al.* 2018). Within mammals, Rodentia is a clear example of a group that comprises a relatively large number of taxonomically complex and/or insufficiently studied lineages that contain cryptic species (Fabre *et al.* 2012; Burgin *et al.* 2018). One explanation is that by exhibiting relatively high evolutionary rates, rodents reflect rapid evolution (adaptive radiation), which often is associated with convergence during evolution (Hartenberger 1985; Pagel *et al.* 1991; Triant and DeWoody 2006).

Harvest mice of the genus *Reithrodontomys* Giglioli, 1874 constitute an example of cryptic species complexes. Of the 24 species in the genus, at least six have been found to be composite based on molecular data (Sullivan *et al.* 2000; Arellano *et al.* 2003, 2005; Miller and Engstrom 2008; Hardy *et al.* 2013; Statham *et al.* 2016). These studies have revealed values of intraspecific genetic divergence above 5%, which are in the same order of magnitude of those reported for distinct rodent species (Bradley and Baker 2001). Additional studies focused on clarifying both intraspecific and interspecific evolutionary relationships therefore remain necessary (Arellano *et al.* 2005; Miller and Engstrom 2008; Gardner and Carleton 2009).

The genus *Reithrodontomys* is comprised of two subgenera: *Reithrodontomys* Giglioli, 1874 and *Aporodon* Howell, 1914. Within *Aporodon*, Hooper (1952) defined the *R. mexicanus* and *R. tenuirostris* species groups, but the existence of at least two additional species groups has been suggested (Arellano *et al.* 2005). The *R. tenuirotris* species group originally included *R. tenuirostris* Merriam, 1901 (narrow-nosed harvest mouse), *R. microdon* Merriam, 1901 (small-toothed harvest mouse), *R. creper* Bangs, 1902 (Talamancan harvest mouse), and *R. rodriguezi* Goodwin, 1943 (Rodriguez's harvest mouse), which were considered by Hooper (1952) the most specialized in the genus, both morphologically and ecologically. Later, the species *R. bakeri* Bradley, Mendez-Harclerode, Hamilton and Ceballos, 2004 (Baker's small-toothed harvest mouse) and *R. musseri* Gardner and Carleton, 2009 (Musser's harvest mouse) were added to the *R. tenuirostris* group, and *R. cherrii* (Allen, 1891—Costa Rican harvest mouse) was shown to be more related to the *R. tenuirostris* group than to *R. mexicanus* species group (Arellano *et al.* 2003, 2005), to which it originally belonged.

Within the *R. tenuirostris* group, the most taxonomically complex species has been *R. microdon*. It currently is recognized as polytypic, with three subspecies: *R. m. microdon* Merriam, 1901; *R. m. albilabris* Merriam, 1901; and *R. m. wagneri* Hooper, 1950; each allopatrically distributed in pine-oak and cloud forests of central and southern Mexico and northern Guatemala (Hooper 1952; Hall 1981). The species is considered rare and museum records are from above 2300 m; semi-arboreal habits are considered the norm (Hooper 1952; Musser and Carleton 2005; González-Ruíz *et al.* 2007). However, a mainly arboreal preference was reported recently (González-Cózatl and Arellano 2015). Hooper (1952) indicated that *R. m. microdon*, *R. m. albilabris*, and *R. m. wagneri* were reproductively isolated from each other, but with so few morphological differences that he declined to recognize them as separate species. In their analyses based on Cytochrome *b* (*Cytb*) gene sequences, Arellano *et al.* (2005) included samples of *R. m. microdon* from east of the Isthmus of Tehuantepec and *R. m. albilabris* from western Oaxaca in Mexico. They failed to recover *R. microdon* as monophyletic. Instead, mice from east of the Isthmus of Tehuantepec were found to be more closely related to *R. tenuirostris*, and those from western Oaxaca were sister to *R. bakeri*, from Central Mexico. As a result, Arellano *et al.* (2005) suggested that *R. m. albilabris* should be considered a species-level taxon.

Given the complex taxonomic history of the genus *Reithrodontomys*, particularly so within the *R. tenuirostris* species group, our goals here are to assess the evolutionary relationships among its members and, based on the resulting phylogenetic patterns, to identify and delimit putative cryptic species within this group, emphasizing populations of *R. microdon*. To accomplish these objectives, we developed additional taxon and geographic sampling for both the mitochondrial *Cytb* gene and the nuclear Intron 7 of the beta fibrinogen (*Fgb*) gene.

Materials and Methods

Sampling

Specimens used in this study were obtained from field work using methods approved in the ASM Guidelines (Sikes *et al.* 2016), by means of tissue loans from mammal collections, or from GenBank (Fig. 1; Supplementary Appendix I). For initial identifications of the wild-caught animals, we followed the morphological key developed by Hooper (1952). For the *R. tenuirostris* species group, 59 *Cytb* and 43 *Fgb* sequences were included in the molecular analyses. For both genes, the largest number of samples (40 and 32, respectively) corresponded

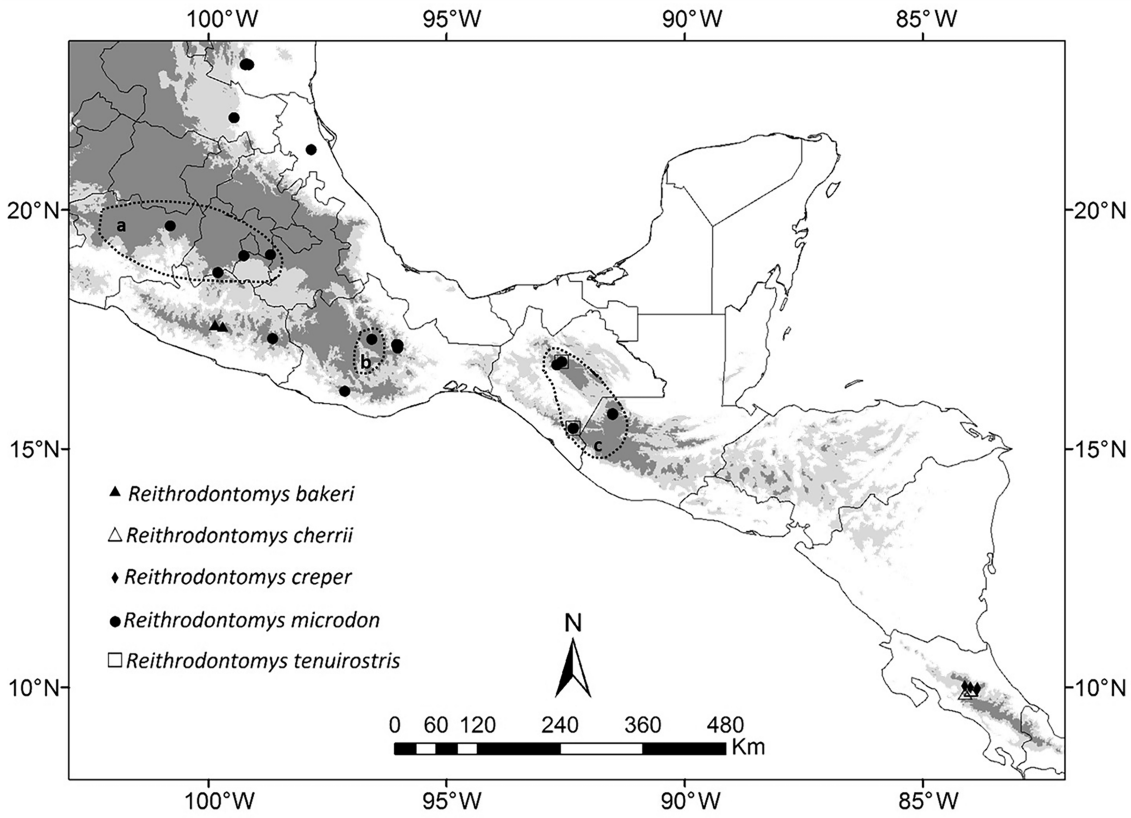

Fig. 1.—Map of Mexico and Central America showing localities for specimens of the *Reithrodontomys tenuirostris* species group analyzed in this study. Dotted dots represent the geographical distribution (proposed by Hall 1981) of the *R. microdon* subspecies [a) *R. m. wagneri*; b) *R. m. albilabris*; c) *R. m. microdon*]. Gray hues depict an elevation gradient: white <800 m; light gray 800–1700 m; and dark gray >1700 m.

to specimens identified a priori as *R. microdon*. The other representatives of the *R. tenuirostris* group we included were *R. bakeri*, *R. creper*, *R. cherrii*, and *R. tenuirostris*. Three species of the *R. mexicanus* group (*R. mexicanus*, *R. brevirostris*, and *R. gracilis*) and three of the subgenus *Reithrodontomys* (*R. megalotis*, *R. sumichrasti*, and *R. fulvescens*) were used as outgroups in the phylogenetic analyses. An additional 36 *Cytb* and 5 *Fgb* sequences were downloaded from GenBank (see Supplementary Appendix I).

DNA extraction, amplification, and sequencing

Total genomic DNA was extracted from liver tissue frozen or preserved in 95% ethanol following the protocol of Fetzner (1999) or using the Qiagen DNeasy Blood & Tissue Kit extraction kit (QIAGEN Inc., Valencia, California). Polymerase chain reactions (PCRs) were undertaken to amplify the *Cytb* and *Fgb* genes. The complete *Cytb* gene (1143 bp) was amplified using the MVZ05 and MVZ14-M primers following the conditions of Smith and Patton (1993), as modified by Arellano *et al.* (2005). The combination of primers MVZ-16 (Smith and Patton 1993)–L14724 (Irwin *et al.* 1991) was used for samples with fragmented DNA. For the *Fgb* gene, 608 bp were amplified with primers B17 and Bfib (Wickliffe *et al.* 2003).

The thermal profile for the *Cytb* gene consisted of an initial denaturing of 4–5 min at 94°C, followed by 37–40 cycles of 1 min at 94°C, 1 min for the annealing at 43–45°C, and 1 min for the final extension at 72°C. For the *Fgb* gene, a 2-step touchdown was necessary. The PCR thermal profile included an initial 2 min 20 s denaturation at 94°C, followed by 45 s at 94°C, 35 s at 63°C, 1 min 30 s at 72°C (9 cycles); and 45 s at 94°C, 35 s at 53°C, 1 min 30 s at 72°C (24 cycles); and 7 min for the final extension at 72°C. Negative controls were used to ensure that there was no contamination in the products of all PCR amplifications.

The amplified PCR products of each gene were sequenced at Macrogen Inc., Seoul, Korea or at the DNA Sequencing Center at Brigham Young University. The resulting sequences were assembled and corrected by eye using the Codon Code Aligner v.8.0.2 program (CodonCode Corporation, Dedham, MA), and aligned against a reference sequence with the MUSCLE method in the UGENE v.1.32.0 program (Okonechnikov *et al.* 2012). The GenBank accession numbers for the DNA sequences generated in this study are listed in Supplementary Appendix I.

Phylogenetic analysis

Cytb and Fgb data set.—The model of nucleotide substitution that best fit each data set was selected with the Bayesian informative criterion (BIC), using ModelFinder (Kalyaanamoorthy *et al.* 2017). This program provides guidance about data partitioning. The models of evolution selected for the *Cytb* sequences were TIM2e + I + G, HKY + I, and TN + G for the first, second, and third codon positions, respectively. In addition, saturation of the codon positions was tested in DAMBE7

(Xia 2018). The model of evolution that best fit the *Fgb* sequences was HKY + I. These models of evolution and the DNA partition scheme (for *Cytb*) were used to estimate phylogenetic relationships in the *R. tenuirostris* species group based on the reconstructive methods of Maximum Likelihood (ML) and Bayesian Inference (BI).

Phylogenetic relationships with ML and BI were estimated in IQ-Tree (Nguyen *et al.* 2015) and MrBayes v3.2.6 (Ronquist and Huelsenbeck 2003), respectively. Both software programs were implemented within the CIPRES Science Gateway portal (Miller *et al.* 2012). In the ML analysis, branch support was calculated using 10000 Ultrafast Bootstrap replicates (UFBoot; Minh *et al.* 2013) and the GENESITE resampling strategy, which allows resample of partitions and sites within partitions (Gadagkar *et al.* 2005). Branches with UFBoot support values > 95% were considered reliable (Minh *et al* 2013). For the BI analyses, eight chains in two independent runs with 10 million Metropolis Coupled Markov Chain Monte Carlo (MCMC) generations were used. The default parameters of the model were not modified, and the trees were sampled every 1000 generations, starting the analysis with a random tree. The convergence and seasonality of each run was verified using the probability parameters in the Tracer v1.7.1 program (Rambaut *et al.* 2018), and then all trees prior the stationarity phase were discarded as burn-in. The posterior probability (pP) was obtained for individual nodes by constructing a majority-rule consensus with the trees not discarded as burn-in. Values of pP > 0.95 were considered strongly supported (Huelsenbeck and Ronquist 2001).

Combined data set (Cytb + Fgb).—A concatenated data set was generated (1751 bp) for the individuals in which DNA sequences for both genes could be evaluated. For these analyses, the models of evolution previously established for the *Cytb* and *Fgb* genes were used, as well as the same parameters for the phylogenetic reconstructions with ML and BI. The Wiens (1998) methodology was followed to detect inconsistencies between the resulting topologies of the phylogenetic trees with a single gene (*Cytb* or *Fgb*) and the combined data set. In this way, the branches detected with incongruities between the topologies were treated with caution (Almendra *et al.* 2014).

Estimation of divergence times.—Divergence times between clades recovered in the *Cytb* phylogeny were estimated using BEAST2 v2.6.3 (Bouckaert *et al.* 2014). For each partition (unlinked substitution model), the same parameters and models of nucleotide substitution were established as those used in the phylogenetic analyses. The analyses were carried out using a Calibrated Yule Model prior under the assumption of an uncorrelated lognormal relaxed-clock model (Drummond *et al.* 2006), which allows variation in substitution rates between branches (Arbogast *et al.* 2002), and using the average established for mammals of 0.086 substitutions per site per million years (Steppan and Schenk 2017). In addition, for the calibration of the subgenus *Reithrodontomys* node, fossil records of the extinct species *R. moorei*, *R. wetmorei*, *R. galushai*, *R. pratincola*, and *R. rexroadensis* were integrated to construct a log-normal distribution of priors, with an offset of 1.8 Ma (M = 1.13; S = 0.3) and a probability of densities for the age of the node (HD = 95%) between 3.69 and 6.87 Ma (Dalquest 1978; Czaplewski 1987; Martin *et al.* 2002; Martin and Peláez-Campomanes 2014). The posterior distribution of the parameters, tree topology, and divergence times was determined with MCMC analysis using two runs of 10 million generations each, and trees sampled every 1000 generations. Convergence of the independent runs and the effective sample size (appropriate ESS > 200) were assessed using Tracer v1.7.1 (Rambaut *et al.* 2018). All trees prior stationary phase were discarded as burn-in, and the maximum credibility tree then was selected using TreeAnotator v2.6.2, included in BEAST2.

Species delimitation.—We used three different methods to delimit putative new species, which allows a better interpretation of the results because congruence among the methods supports the recognition of the new taxonomic entities (Carstens *et al.* 2013). Two single-locus and one multiple-loci species delimitation methods therefore were used in this study.

Species-level lineages for the *R. tenuirostris* group were identified from the *Cytb* tree using the single-locus species delimitation methods: multi-rate Poisson Tree Processes (mPTP; Kapli *et al.* 2017) and Bayesian General Mixed Yule-Coalescent Model (bGMYC; Reid and Carstens 2012). The mPTP non-coalescent method models the branching processes, under the assumption that within species branching events will be more common, whereas among species they will be rare. This method considers the potential divergence in intraspecific diversity (Kapli *et al.* 2017) and uses the Akaike informative criterion to decide the number of resulting species according to the phylogenetic tree (Zhang *et al.* 2013). This analysis used the BI tree and the Model specifications and MCMC settings established by default in the Exelisis Lab platform (http://www.exelixis-lab.org) as input. The bGMYC coalescent method assumes that one of two events occurs at the branch points of a tree: divergence events between two species (speciation) or coalescence events between lineages within a species (Zhang *et al.* 2013). The last 100 ultrametric trees derived from the divergence time analysis were selected using LogCombiner v2.6.3 from the BEAST2 package and used as input data. The delimitation analysis was implemented in the bGMYC package (Reid and Carstens 2012) of the R library (R Core Team 2018), with the input parameters as follows: mcmc = 100000, burnin = 90000, thinning = 100, t1 = 11, t2 = 16 (based on the upper range of suggested species with mPTP, considering the outgroup), py1 = 0.5, py2 = 1.5, pc1 = 0.1, pc2 = 0.5, start = c (1.0, 0.1, 11), scale = c (20, 10, 5.00).

The Kimura 2-parameter (K2P; Kimura 1980) genetic distances for *Cytb* were estimated between the lineages suggested as new species using MEGA X (Kumar *et al.* 2018). This model of evolution allowed us to make intra- and inter-specific comparisons with genetic distance values reported in rodents (Bradley and Baker 2001; Baker and Bradley 2006).

The Species Tree and Classification Estimation, Yarely (STACEY, Jones 2017) coalescent method was used to delimit possible new species from the combined DNA sequence data (*Cytb* + *Fgb*). This multiple-loci method does not require a

priori assignations of individuals to species and does not require a guide tree. Also, the number of delimited species (minimal cluster tree) can vary from one to the total number of terminals (Jones 2017). The STACEY analysis uses the birth-death-collapsed tree model as a prior and is implemented as a package within BEAST2. The SpeciesDelimitationAnalyzer program (speciesDA.jar, www.indriid.com) was used to summarize the tree posterior distribution and calculate the frequency with which each pair of taxa were assigned to the same clade. The species.tree file generated by STACEY (burnin = 1000 collapse height = 0.0001, and similarity cutoff = 1.0) was used as input data.

Population connectivity based on shared haplotypes

Genetic connectivity patterns were explored between the demarcated species within *R. microdon* by the bGMYC and STACEY delimitation methods (see Results section). We used the method implemented by Chan *et al.* (2011), which integrates ecological niche models (ENM) and haplotype networks to estimate putative dispersal corridors based on habitat suitability and shared haplotypes. This analysis allows making inferences about the existence of gene flow (population connectivity) or, on the other hand, the identification of possible barriers to dispersal (Chan *et al.* 2011). In addition, hypotheses about speciation processes among populations that display high genetic divergence can be corroborated.

TCS haplotype networks for *Cytb* and *Fgb* genes were constructed using PopARTv1.7 (Leigh and Bryant 2015) with 1000 permutations. This program allowed us to obtain the frequency of each haplotype, as well as the genealogical relationships among them. For the ENM, 8 Worldclim bioclimatic layers (Hijmans *et al.* 2005; Supplementary Data SD1) with a spatial resolution of ~ 1 km^2 were used as environmental predictors. Points of occurrence for *R. microdon* were taken from SNIB-CONABIO project No. JM043 (González-Cózatl 2014), and each geographic coordinate was rectified against the known distribution (Hooper 1952; Hall 1981; González-Cózatl and Arellano 2015) to reduce georeferencing errors. A spatial thinning of occurrences was undertaken to avoid autocorrelation, establishing a minimum distance of 5 km between the localities. The model calibration areas were determined with a 70 km^2 buffer around each occurrence record. The data processing and selection of the best fit parameters for the construction of the final model was carried out in Wallace (Kass *et al.* 2018; Supplementary Data SD1) of the R library. The final model was obtained in Maxent v3.4.0 (Phillips *et al.* 2006) with 50 bootstrap replicas and keeping the maxent logistic output (range from 0 to 1).

A data set comprised of *Fgb* haplotypes and the geographical coordinates of the site(s) where they were distributed was used as input data in the landscape connectivity analysis. This data set included the haplotypes present in *R. bakeri,* given their phylogenetic position relative to *R. m. wagneri* (see below). A friction layer was generated from the ENM obtained for *R. microdon*, where the areas of little or no probability of presence of the species depicted areas of high cost for dispersal (Chan *et al.* 2011). Least cost corridors and least cost paths then were calculated among the populations analyzed. For each comparison, the lower cost paths were classified into three categories as suggested by Chan *et al.* (2011), and the least cost corridors with higher connectivity values were interpreted as probable migration routes. This analysis was carried out with the SDMtoolbox extension (Brown *et al.* 2017) in ArcGIS v10.1 (ESRI 2011). Based on the low presence of shared *Cytb* haplotypes among the populations of the *R. microdon* species complex, we did not to use this marker in the population connectivity analysis.

Results

Phylogenetic analysis with Cytb

Of the 1143 nucleotides comprising the *Cytb* gene, 430 were variable; of those, 366 were parsimony-informative sites. The phylogenetic analyses with ML and BI resulted in the same tree topologies, although in general the analysis with BI showed greater nodal support (Fig. 2). In both analyses, the *R. tenuirostris* species group was recovered as a clade, with the exception of *R. creper*, which was more closely related to the *R. mexicanus* species group. Species comprising the *R. tenuirostris* group were recovered as monophyletic clades with high nodes support, with the exception of *R. microdon*.

The 40 individuals identified a priori as *R. microdon* were recovered as four haplogroups (Fig. 2; see Fig. 6 for geographic distribution of haplogroups), each strongly supported by high pP values in the BI analysis. Haplogroup I comprised samples from Tamaulipas, San Luis Potosí, and a specimen from Veracruz, Mexico. Haplogroup II was made up of individuals distributed in Michoacán, Morelos, and Estado de México, Mexico, all currently recognized as members of the subspecies *R. m. wagneri* together with *R. bakeri*. Haplogroup III included individuals representing the subspecies *R. m. microdon* distributed in Chiapas, Mexico and northern Guatemala. *R. tenuirostris* was recovered as the sister taxon of haplogroup III; this relationship was well supported by BI analysis (pP = 0.9), but not in the ML analysis (UFBoot = 56). Haplogroup IV included specimens classified as *R. m. albilabris* from the Oaxacan Highlands and an individual from southern Guerrero (CMC1627).

Phylogenetic analysis with Fgb

Of the 608 nucleotides comprising the *Fgb* gene, 89 were variable, with 58 parsimony-informative sites. In addition, five regions with indels were identified: (i) at position 74, a bp deletion was inferred for haplogroup I; (ii) at position 281, a bp insertion occurred in outgroup *R. fulvescens*; (iii) at position 366, *R. creper* had a bp insertion; (iv) at position 451, there was a bp insertion for outgroups *R. megalotis* and *R. sumichrasti*; (v) at positions 563–573, a 10 bp insertion was inferred for outgroups *R. megalotis* and *R. sumichrasti*. Phylogenetic analyses with the *Fgb* nuclear intron based on ML and BI optimality criteria revealed similar tree topologies, but the BI tree was more fully resolved than

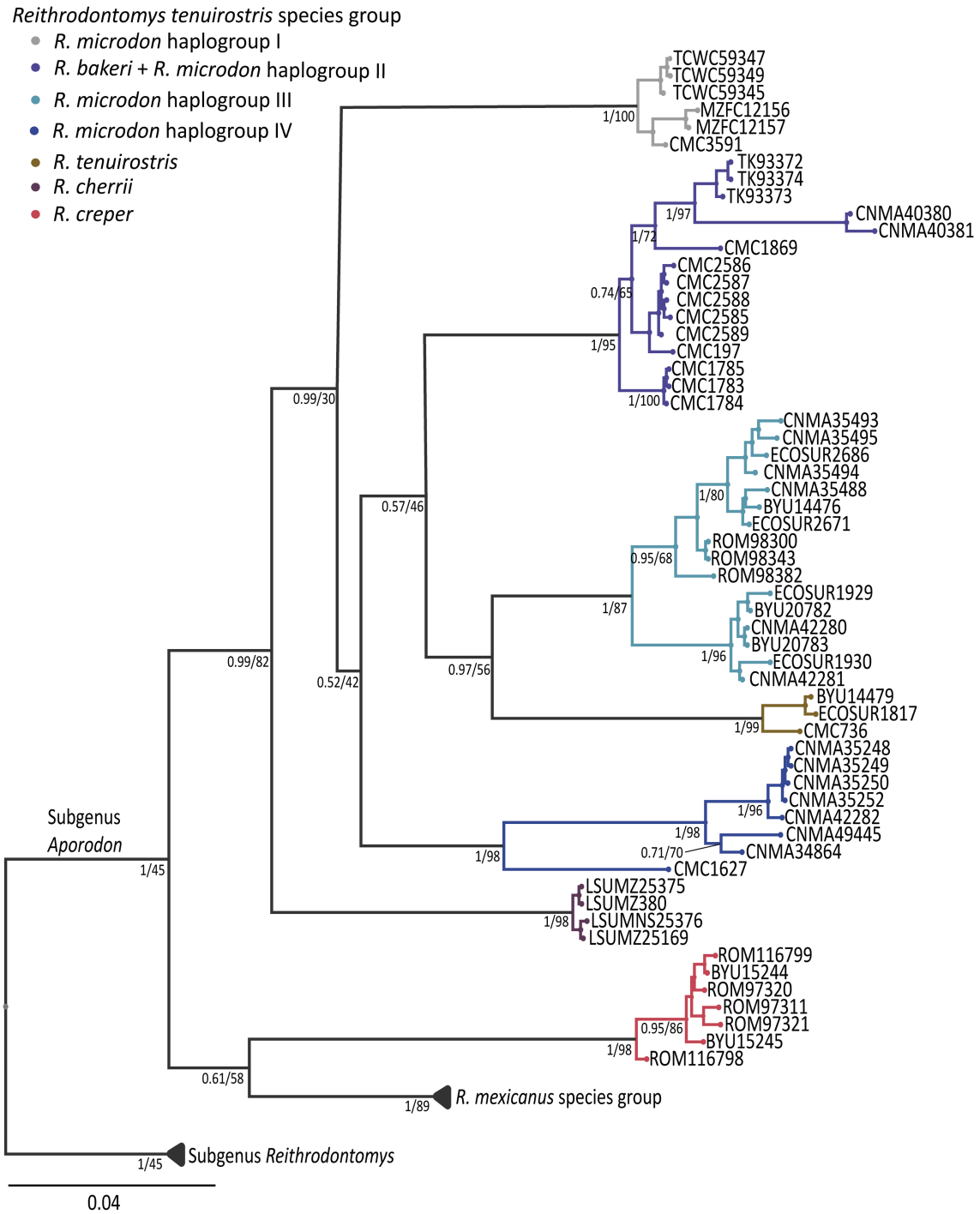

Fig. 2.—Phylogenetic relationships among species of the *Reithrodontomys tenuirostris* group using sequences data of the mitochondrial gene Cytochrome *b*. Values below branches represent nodal support for BI/ML analysis. Terminal labels are named according to mammal collection voucher numbers (see Supplementary Appendix I).

the ML tree (Fig. 3). In general, both analyses showed weak nodal support, and the trees were not concordant with the phylogenetic relationships found between and within clades and haplogroups recovered in the *Cytb* tree. However, the species of the *R. tenuirostris* group were recovered in well-supported clades as well as the four haplogroups found in *R. microdon*, with the exception of haplogroup II. In addition, individuals CMC1627 and CNMA49445 did not group into haplogroup IV.

Phylogenetic analysis of the combined data

Tree topologies obtained with the combined data set (1751 bp) using the BI and ML optimality criteria displayed inconsistencies between each other. The ML analysis represented essentially the same topology as the *Cytb* tree but with low UFBoot values (Supplementary Data SD2), whereas the BI tree recovered the majority of the major clades with a high nodal support (pP> = 0.95; Fig. 4). The incongruities between the BI

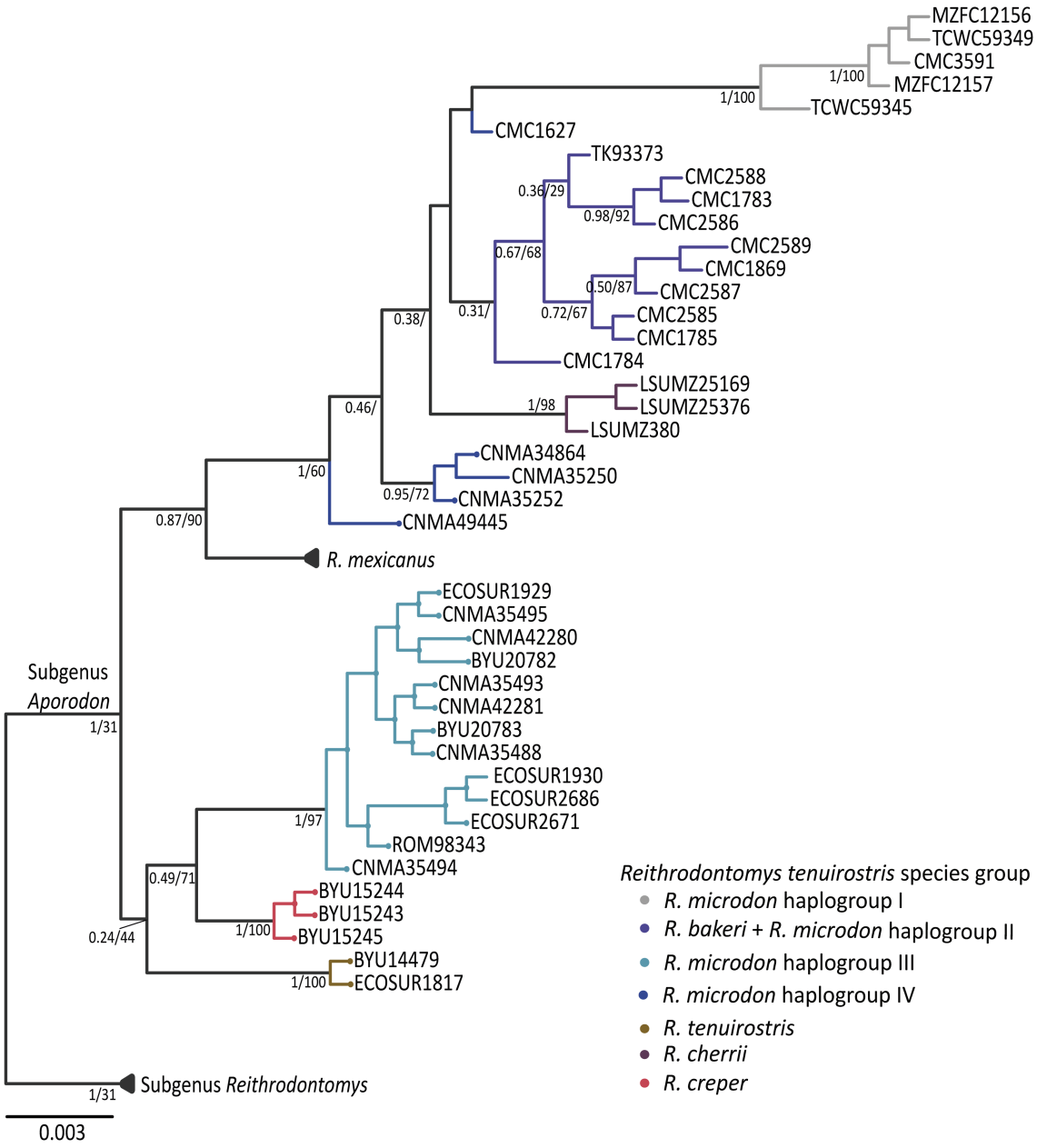

Fig. 3.—Phylogenetic relationships among species of the *Reithrodontomys tenuirostris* group using sequences data of the Intron 7 of the nuclear gene beta fibrinogen. Values below branches represent nodal support for BI/ML analysis. Terminal labels are named according to mammal collection voucher numbers (see Supplementary Appendix I).

combined and the *Cytb* tree topologies were in the positions of the haplogroup IV (*R. m. albilabris*) and *R. creper*. In the former, the samples of *R. m. albilabris* were recovered as the sister group of haplogroup II (*R. m. wagneri* + *R. bakeri*), a relationship that was well-supported (pP = 0.95). In addition, *R. creper* was recovered as the sister group of the *R. tenuirostris* species group, albeit with low nodal support (pP = 0.44).

Estimation of divergence times

The BEAST MCMC analysis converged on a tree topology almost identical to that obtained with the ML and BI criteria for *Cytb* (Fig. 5). The root of the most recent common ancestor (MRCA) for the genus *Reithrodontomys* had a mean age of 5.4 Ma. Within the subgenus *Aporodon* the split between the *R. tenuirostris* species group (except *R. creper*) and *R. mexicanus* was at ~ 4.5 Ma (95% HPD = 3.1–6.1). The MRCA mean age for the *R. tenuirostris* species group was estimated at 3.0 Ma (95% HPD = 1.9–4.2), when *R. cherrii* split as a different lineage. Within the four haplogroups identified for *R. microdon*, haplogroup IV diverged ~2.7 Ma (95% HPD = 1.7–3.7), whereas haplogroup I did ~2.6 Ma (95% HPD = 1.7–3.6). Haplogroup II split from haplogroup III and *R. tenuirostris* at a mean age of 2.2 Ma (95% HPD = 1.4–3.1), whereas the mean time of divergence for the latter two was estimated at 1.9 Ma (95% HPD = 1.2–2.8).

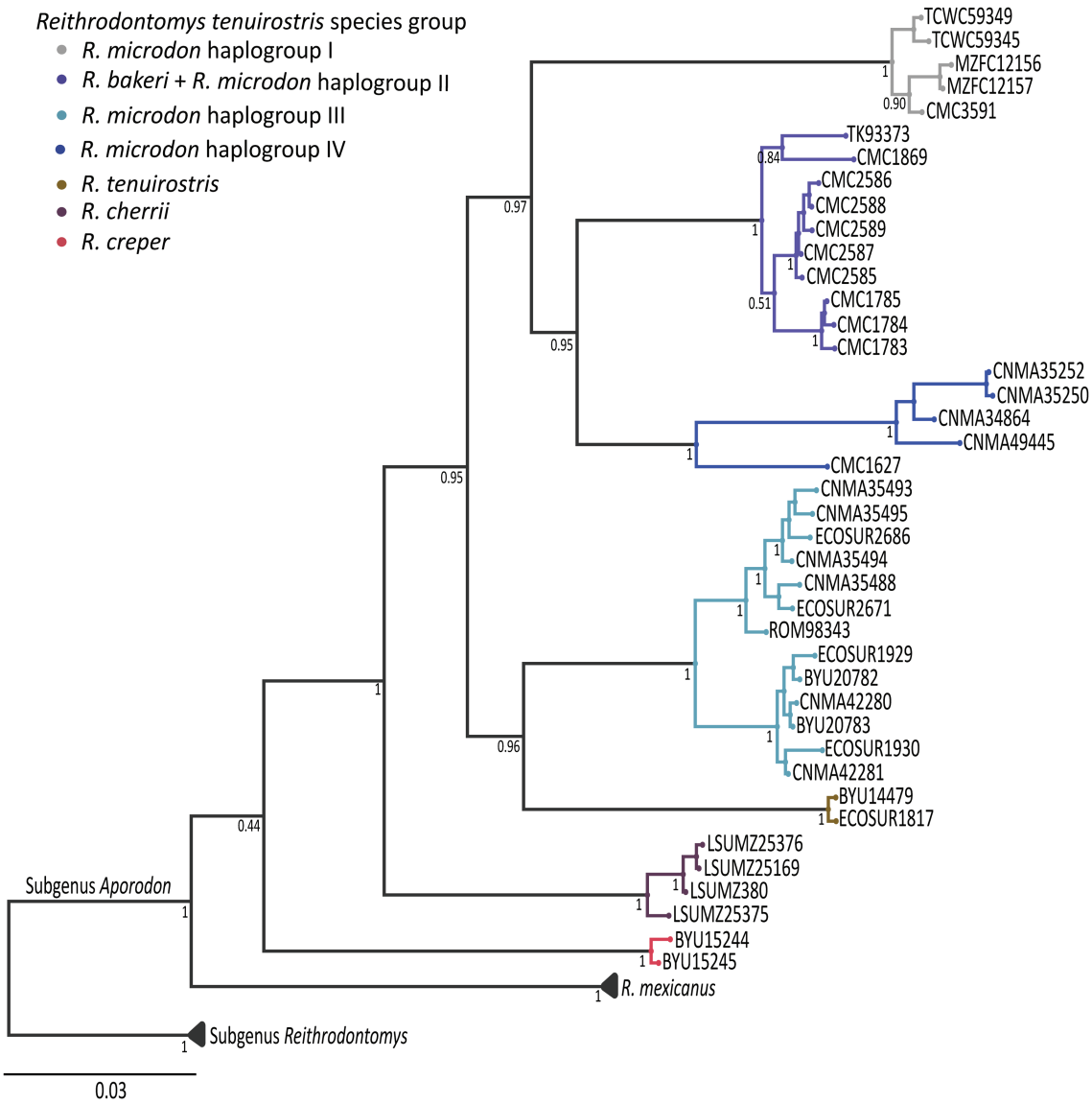

Fig. 4.—Phylogenetic relationships among species of the *Reithrodontomys tenuirostris* group using a concatenated sequences data set (Cytochrome *b* + Intron 7 of the beta fibrinogen). Values below branches represent nodal support for BI analysis. Terminal labels are named according to mammal collection voucher numbers (see Supplementary Appendix I).

Species delimitation

The single-locus mPTP and bGMYC delimitation methods recovered *R. creper*, *R. cherrii*, and *R. tenuirostris*, as species-level clades. Likewise, both methods inferred the presence of a species complex within *R. microdon*, although the number of delimited species (including *R. bakeri*) was not congruent across methods (Fig. 5). Specimens from Cerro Mozotal, Chiapas, Mexico were demarcated by the mPTP as a second species within haplogroup III (*R. m. microdon*), whereas the bGMYC delimited this haplogroup as a single species. The K2P genetic distance (GD-K2P; Table 1) between these putative species suggested by mPTP was 2.8%. Similarly, for haplogroup II (*R. m. wagneri* + *R. bakeri*), mPTP suggested three species-level clades, but bGMYC delimited it as a single taxon. The GD-K2P among these three lineages ranged from 1.6% to 2.4%. For haplogroup IV (*R. m. albilabris*), the mPTP and bGMYC methods delimited three (GD-K2P ranged from 1.7% to 9.2%) and two (GD-K2P 8.3%) putative species, respectively. Both methods agreed that CMC1627 represented a different species within this haplogroup. Furthermore, both delimitation methods supported haplogroup I as a species-level clade. The lineages recovered at the species-level with the multiple-loci STACEY were consistent with those delimited by the bGMYC method (Fig. 5).

Population connectivity in Reithrodontomys microdon

The *Cytb* haplotype network consisted of 25 haplotypes, 16 of which were exclusive to single individuals, and none shared among populations (Supplementary Data SD3). Only haplogroup III contained a haplotype shared between two localities, from northwest of San Cristóbal de las Casas, Chiapas, Mexico. The *Fgb* haplotype network consisted of nine

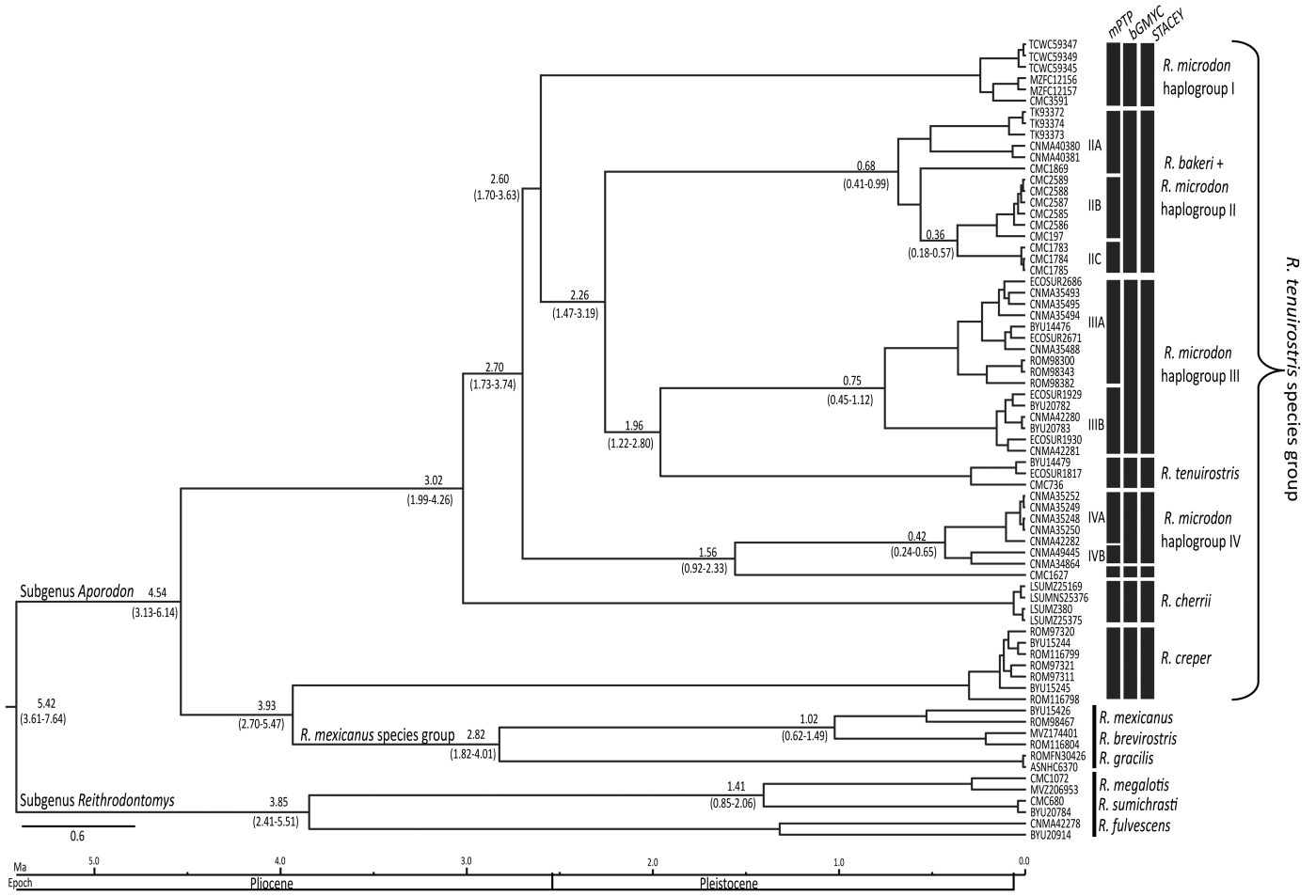

Fig. 5.—Maximum clade credibility tree obtained with BEAST2 for species of the *Reithrodontomys tenuirostris* group using Cytochrome *b* sequences data. Values above branches represent mean divergence times and below the 95% highest posterior density (HPD) intervals. Dark gray bars represent taxa delimited as species-level by the single-locus methods mPTP and bGMYC with probability values above 0.95, and the multiple-loci method STACEY.

haplotypes, five of which were exclusive to a locality, and none of which was shared among the four haplogroups (Fig. 6C).

The dispersal network among sites based on shared *Fgb* haplotypes did not show potential migration routes among the four haplogroups delimited as species-level clades by STACEY (Fig. 6C). Within haplogroup IV (*R. m. albilabris*), a possible migration route existed between populations of the Oaxacan Highlands and individual CMC1627 from Sierra Madre del Sur, but it was supported by relatively low connectivity values. Samples within each haplogroup showed cost paths crossed with a medium to low frequency, except for a low-cost path that connected the two northwestern populations of San Cristóbal de las Casas, Chiapas, Mexico. Within haplogroup II, *R. bakeri* showed a dense potential migration route with the remaining individuals of this group, in particular with those from Zacualpan, Estado de México, the geographically most proximal locality.

Discussion

Molecular data confirm the existence of two monophyletic subgenera (*Aporodon* and *Reithrodontomys*) within *Reithrodontomys* (Howell 1914; Hooper 1952). This finding is consistent with previous molecular studies based on mitochondrial and nuclear genes (Arellano *et al.* 2003, 2005; Miller and Engstrom 2008). The mean divergence time between subgenera was the late Pliocene (5.42 Ma), followed by a relatively rapid colonization and diversification processes that favored the establishment of cryptic lineages characterized by high genetic divergence (Sullivan *et al.* 2000; Arellano *et al.* 2005; Miller and Engstrom 2008; Hardy *et al.* 2013). Within *Aporodon*, most diversification of the *R. tenuirostris* species group occurred during the Pleistocene; this finding is supported by information on environmental fluctuations and the existence of biogeographic corridors at the time (Ceballos *et al.* 2010) that favored continued expansion followed by a post-glacial isolation (Martin 1961).

The *R. tenuirostris* group currently comprises the species *R. tenuirostris*, *R. microdon*, *R. creper*, *R. bakeri*, *R. cherrii*, *R. musseri*, and *R. rodriguezi*, but the last two species were not included in this study. Our results corroborate the membership of *R. cherrii* in this species group (Arellano *et al.* 2003, 2005) but fail to support inclusion of *R. creper* because its phylogenetic relationships in the *Cytb*, *Fgb*, and combined data set trees were ambiguous. Hooper (1952) proposed that this

Table 1.—Matrix of Kimura 2-parameter genetic distances (%) for Cytochrome *b* gene sequence data between species of the *Reithrodontomys tenuirostris* group. Taxon labels correspond to species delimited by mPTP (A) and bGMYC (B) methods in Fig. 5.

	Species delimitation										
(A) mPTP	1	2	3	4	5	6	7	8	9	10	11
1. Haplogroup I											
2. Haplogroup IIA	10.7										
3. Haplogroup IIB	10.6	1.9									
4. Haplogroup IIC	10.7	2.4	1.6								
5. Haplogroup IIIA	9.9	8.2	8.1	8.1							
6. Haplogroup IIIB	10.9	8.3	8.6	8.5	2.8						
7. Haplogroup IVA	11.8	10.2	10.5	10.9	10.6	10.0					
8. Haplogroup IVB	10.2	9.3	9.4	9.8	9.3	8.9	1.7				
9. CMC1627	11.6	7.7	9.3	8.5	8.7	8.9	9.2	7.3			
10. *R. tenuirostris*	10.5	9.1	9.6	9.7	7.7	8.5	10.3	9.5	9.4		
11. *R. cherrii*	11.6	10.6	11.5	11.4	11.2	10.5	11.5	10.7	11.0	11.1	
12. *R. creper*	12.8	13.7	13.9	14.0	12.6	13.3	13.9	13.1	13.5	13.3	12.6
(B) bGMYC	1	2	3	4	5	6	7				
1. Haplogroup I											
2. Haplogroup II	10.0										
3. Haplogroup III	9.6	6.9									
4. Haplogroup IV	10.9	9.1	8.9								
5. CMC1627	11.6	7.9	8.1	8.3							
6. *R. tenuirostris*	10.5	8.8	7.3	9.7	9.4						
7. *R. cherrii*	11.6	10.5	10.2	10.9	11.0	11.1					
8. *R. creper*	12.8	13.2	12.2	13.3	13.5	13.3	12.6				

species should be treated as part of the *R. tenuirostris* group based on morphological and ecological characteristics that make this species group the most specialized within the genus. However, he also indicated that *R. creper* was the least related to the rest of the species in this group and only shared cranial and body size measurements and coloration patterns with *R. tenuirostris* and *R. rodriguezi*, and none with *R. microdon*. Moreover, *R. creper* is morphologically distinct from species in the *R. mexicanus* group with which it overlaps in some regions, because the latter species are "much smaller; in them [N. B.: referring to *R. mexicanus* (Saussure, 1860); *R. gracilis* Allen and Chapman, 1897; *R. brevirostris* Goodwin, 1943; and *R. darienensis* Pearson, 1939] the rostrum is short and broad and the brain case is small" (Hooper 1952:176). Our results based on *Cytb* and the combined data set are partially consistent with those of Arellano *et al.* (2005), who recommended considering *R. creper* as an independent lineage within *Aporodon*. However, due to the uncertain position of this species (low values of UFBoot and Pp) among the distinct phylogenetic trees generated by the different algorithms, we were not able to support their recommendation. Phylogenetic analysis of all representatives of this species group, including other sources of evidence (morphological data), is needed to clarify the phylogenetic position of *R. creper* within the subgenus *Aporodon*.

The phylogenetic analysis with *Fgb* did not recover the same relationships among clades and haplogroups as the *Cytb* and the combined data set. Although the *R. tenuirostris* species group clade was recovered with a high nodal support, *R. mexicanus* was placed within this group, which clearly differs from the topologies generated with *Cytb* and the combined data set. Also, in the *Fgb* gene phylogeny, *R. creper* was grouped as part of the *R. tenuirostris* species group, but this was supported by low values of pP and UFBoot. These conflicting results may be due to the relatively low substitution rate that this nuclear gene presents in comparison to the mitochondrial *Cytb* gene (Wickliffe *et al.* 2003). Similar results have been reported in other rodent genera such as *Handleyomys* Voss, Gómez-Laverde and Pacheco, 2002 and *Oligoryzomys* Bangs, 1900, suggesting incomplete lineage sorting and retention of ancestral polymorphisms (Almendra *et al.* 2014; Rivera *et al.* 2018). In addition, the incongruence in topology between *Cytb* and *Fgb* trees could be explained by differences in the number of individuals and species that were used in the construction of each tree. Although at least two individuals for each clade/haplogroup obtained with *Cytb* data were represented in the *Fgb* tree, some members of the *R. mexicanus* group were missing. The absence of these species and individuals could have affected the resulting topology.

Among the four haplogroups recovered within *R. microdon*, the bGMYC and STACEY delimitated haplogroup III (*R. m. microdon*) as a species-level clade. The *Cytb* genetic distances between this haplogroup and other haplogroups or previously recognized species range from 6.9% to 9.6%. These values all were larger than the range of intraspecific divergence values reported by Bradley and Baker (2001). Although the mPTP method delimited two possible species within haplogroup III, the mean *Cytb* genetic distance (2.8%) was at the upper limit of that reported in *Reithrodontomys* for the intraspecific level (Baker and Bradley 2006). Given this relatively low genetic distance value, which coincides with a relatively short divergence time (~ 0.75 Ma), we recognize haplogroup III as a single taxon (see below). However, non-culminating speciation events (Futuyma 2013) could be occurring between the population from Cerro Mozotal, Chiapas, and the remaining populations of this haplogroup in Central Chiapas and Guatemala.

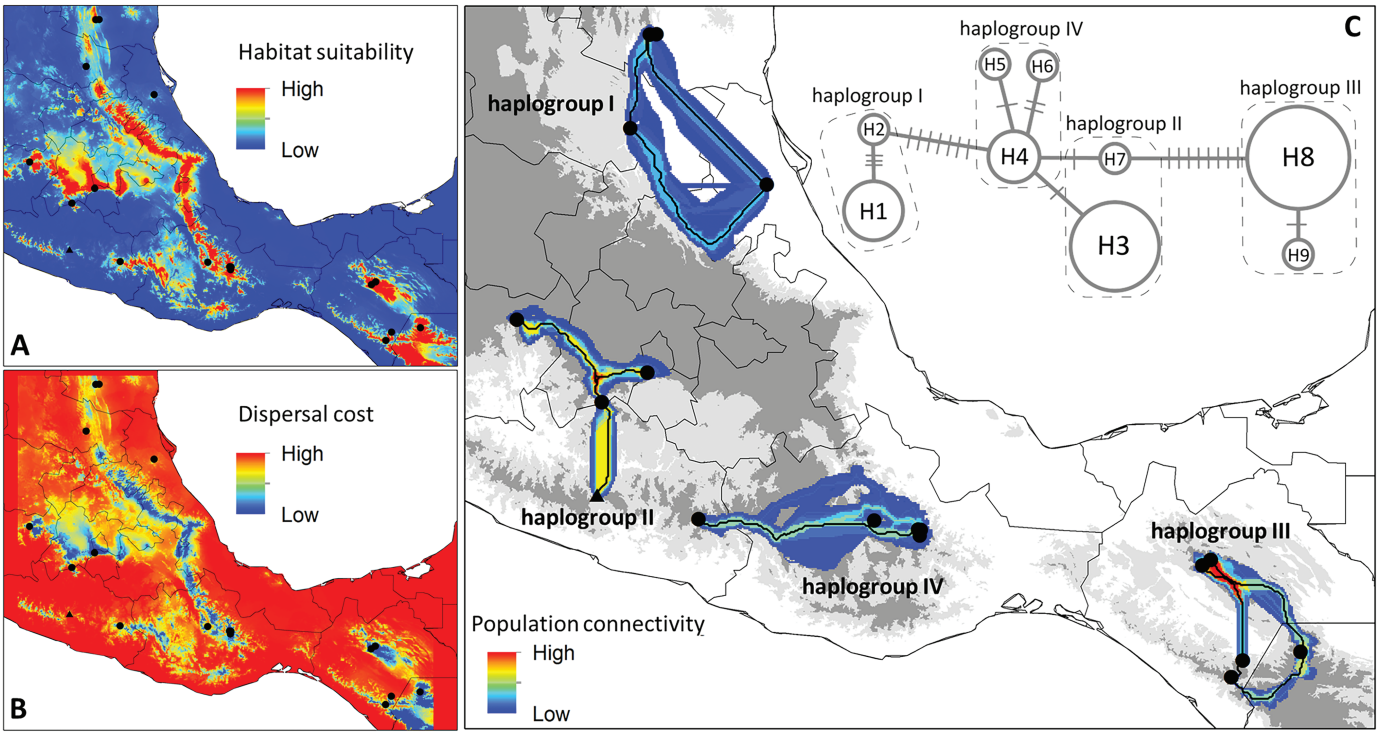

Fig. 6.—Landscape connectivity analysis based on the Intron 7 of the beta fibrinogen shared haplotypes in *Reithrodontomys microdon*. A) Ecological niche modelling of *R. microdon*; warmer colors depict high suitability areas. B) Friction layer obtained from the Ecological niche modelling; warmer colors depict areas with a high cost to dispersal. C) *Fgb* haplotype network and dispersal network with the least-cost paths; warmer colors depict paths traversed more frequently and higher population connectivity. The black circles and triangle represent the occurrence points of *R. microdon* and *R. bakeri*, respectively.

Phylogenetic relationships as ascertained with *Cytb* data recovered haplogroup IV (*R. m. albilabris*) as the sister taxon of a clade that was comprised haplogroups II, III, and *R. tenuirostris*, but this relationship was weakly supported. However, with the combined data set, haplogroup IV was closely related to haplogroup II, agreeing with Arellano *et al.* (2005), who found that *R. m. albilabris* was related to individuals of *R. bakeri* (here included in haplogroup II). The known distribution for this subspecies is restricted to the northern Oaxacan Highlands, Mexico (Hooper 1952; Hall 1981). An individual from Tejocote, Guerrero, Mexico (CMC1627) was included with this haplogroup based on its close phylogenetic relationship to specimens of *R. m. albilabris*. However, the three species delimitation methods were consistent in defining this individual as representing a distinct species-level clade, with high values of *Cytb* genetic differentiation (7.3%–11.6%) with respect to other haplogroups or species in the *R. tenuirostris* group. The divergence time between CMC1627 and the populations of *R. m. albilabris* occurred approximately 1.56 Ma (95% HPD = 0.9–2.3), which is comparable with the diversification time reported between species of various rodent genera, including *Reithrodontomys* (Schenk *et al.* 2013; Almendra *et al.* 2014; Platt *et al.* 2015).

The Oaxacan Highlands do not constitute a natural biotic unit and the affinity of the southern part of this region with the eastern part of the Sierra Madre del Sur has been previously reported (León-Paniagua and Morrone 2009). In this study, the *Fgb* dispersal network revealed a potential migration route between CMC1627 (Sierra Madre del Sur) and individuals from Cerro Zempoaltepetl (Oaxacan Highlands) by sharing the H4 haplotype, although this path showed relatively low connectivity values. The accumulated mutations in mitochondrial DNA (over 25 mutational steps with *Cytb*; Supplementary Data SD3) during the time that these populations have been geographically isolated, along with the results of species delimitation methods and the *Cytb* genetic distances, all constitute sufficient DNA evidence to suggest that CMC1627 represents an undescribed species within the *R. tenuirostris* group. However, studies including more individuals would be necessary to confirm this conclusion.

Within haplogroup IV, the mPTP method delimited the specimens CNMA49445 and CNMA34864 as a distinct species distributed in Ixtepeji and Cerro Zempoaltepec, Oaxaca, Mexico, respectively. The *Cytb* genetic distances between these two individuals (haplogroup IVB) and haplogroup IVA was 1.7%, a value lower than the range reported for rodents recognized sister species (Bradley and Baker 2001; Baker and Bradley 2006). In accordance with the results of the bGMYC and STACEY species delimitation methods and the relatively recent splits between these two groups (~0.42 Ma), we consider them as a single taxonomic group at the species level, which differs genetically from the individual CMC1627 and from the two subspecies currently recognized for *R. microdon*.

Reithrodontomys bakeri was described based on genetic distances of the *Cytb* gene and morphological measurements, which differentiated it from *R. microdon*. However, Bradley *et al.* (2004) compared their new species to *R. m. albilabris*

and were not able to compare to the geographically most proximal subspecies of *R. microdon*: *R. m. wagneri*. In our study, we included 10 specimens of *R. m. wagneri*, distributed in the Mexican states of Michoacán, Estado de México, and Morelos. The results with *Cytb*, *Fgb*, and the combined data set showed a close relationship between these populations and *R. bakeri*, with generally high nodal support. In addition, the connectivity values of the *Fgb* dispersal network were relatively high, evidencing a potential migration route between the *R. bakeri* population from Filo de Caballo, Guerrero, and that of Zacualpan, Estado de México (*R. m. wagneri*), separated by approximately 120 km. This analysis suggests, at least for the nuclear data, the probable existence of gene flow between these populations. It could be possible that certain geographical and demographic characteristics may have favored this gene flow in the past. Although populations of *R. m. wagneri* and *R. bakeri* did not share any *Cytb* haplotypes, we assume that the relatively high rate of nucleotide substitution exhibited by mitochondrial genes compared to nuclear genes accounts for this observation (Saccone *et al.* 1999; Palumbi *et al.* 2001). Finally, *R. bakeri* and individuals representing *R. m. wagneri* were considered the same species both by the single-locus bGMYC and by the multiple-loci STACEY, with $P > 0.95$. The assumption that these populations were connected in the past also can be corroborated with *Cytb* data. The divergence mean time estimation between these populations was 0.68 Ma, which is consistent with the low degree of *Cytb* genetic differentiation found between *R. bakeri* (haplogroup IIA) and the other two groupings proposed as candidate species by the mPTP (haplogroup IIB-1.9% and haplogroup IIC-2.4%).

Haplogroup I was represented by individuals identified a priori as *R. mexicanus* given their geographic distribution north of Sierra Madre Oriental and Sierra de Otontepec in Mexico (Hooper 1952). After an exploratory analysis with the *Cytb* gene, these individuals were assigned to a part of the *R. tenuirostris* species group, and due to their morphological similarity as "*R. microdon* like." This haplogroup was not genetically similar to any of the other haplogroups, and all the species delimitation methods recovered it as a distinct putative species. *R. mexicanus* and *R. microdon* share great similarities in cranial characteristics and pelage coloration (Hooper 1952), and they occur in sympatry in some regions in southern Mexico (Hall 1981). However, the geographical distribution of haplogroup I individuals is close to that known for *R. mexicanus* in that region, and this could explain their previous identifications as *R. mexicanus*. Otherwise, only three specimens of *R. mexicanus* have been reported from Tamaulipas, Mexico (Hooper 1952; Jones and Anderson 1958), and those records constituted the northernmost distribution for *Aporodon* at that time. The altitudinal records of those specimens are near or well below the known elevational range of *R. mexicanus* (~1,000 to 3,800 m; Martínez-Borrego *et al.* 2020) but are similar to those registered for haplogroup I specimens analyzed in this study (see Supplementary Appendix I). Given the geographical distribution and morphological similarity between the haplogroup I specimens and *R. mexicanus*, we suggest that individuals from Tamaulipas reported by Hooper (1952) and Jones and Anderson (1958) should be reclassified as part of this new candidate species.

The Sierra Madre Oriental is recognized as one of the oldest and most complex geological regions in Mexico (Ferrusquía-Villafranca 1993; Marshall and Liebherr 2000) and has been associated with cryptic speciation events in rodents (e.g., Sullivan *et al.* 2000; Arellano *et al.* 2005, Ávila-Valle et al. 2012; Almendra *et al.* 2014). The divergence times analysis estimated that the separation of haplogroup I occurred about 2.6 Ma; this group therefore has been genetically isolated from other species in the *R. tenuirostris* group for a long time. Perhaps as a consequence of similar habitats, such as the cloud forests (Gual-Díaz and Rendón-Correa 2014), members of this haplogroup maintained morphological similarities common to almost all species of *Aporodon* (Hooper 1952). Consequently, this has led to underestimating the number of species that exist in this subgenus.

Hooper (1952) noted the reproductive isolation that exists among the three subspecies of *R. microdon*, which has been corroborated in this study with the absence of possible connectivity routes among them. However, assuming little morphological differentiation, Hooper (1952) maintained them in the same species while recognizing three allopatrically distributed subspecies (Fig. 1). The subspecies *R. m. albilabris* and *R. m. microdon* are distributed in the Oaxacan Highlands and the mountains of Chiapas and northern Guatemala, respectively. Between these two regions, the Isthmus of Tehuantepec constitutes an effective geographic barrier which has presumably acted to gene flow, and thus favoring speciation events (Sullivan *et al* 2000; León-Paniagua *et al.* 2007; Esteva *et al.* 2010; Hardy *et al.* 2013), in which the high genetic divergence between populations on either side of the Isthmus has resulted in hypotheses about the occurrence of a vicariance event that affected the small mammal fauna of this Mexican region (e.g., Rogers *et al.* 2007). The distribution of *R. m. wagneri* is restricted to the Neovolcanic Belt. This may be the result of suitable habitat contractions that occurred during the Pleistocene, where these mountainous regions could have served as a refuge (Ceballos and Rodríguez 1993). In this way, they were isolated and differentiated at a specific level, a trend also reported in other genera of rodents such as *Peromyscus* Gloger, 1841 and *Microtus* Schrank, 1798 (Ceballos *et al.* 2010).

The high precision of methods for delimiting species, as well as knowledge of the assumptions made during the process (Rannala 2015), gives them advantages over empirical ways of setting limits such as using a cut-off or arbitrarily determined distance thresholds (Fujisawa and Barraclough 2013; Alström *et al.* 2021). Yet, these methods often are computationally demanding and/or their performance is potentially affected by factors that cause an under- or overestimation of the lineages to be delimited, such as variation in population sizes, number of species, ongoing gene flow, accuracy of input trees, and rate of molecular change, among others (Rannala 2015; Luo *et al.* 2018). Using alternative delimitation methods in search of congruence therefore can lead to more realistic hypotheses on species boundaries (Muñoz-Tobar and Caterino 2020). The taxonomic

proposal of our study is mainly based on the results generated with three widely used delimitation methods (PTP, GMYC, and STACEY—Alström *et al.* 2021), two of which were completely congruent with each other. If we assume that speciation usually is a gradual process, then the incongruence presented by mPTP could be explained by the statistical power of each method to detect independent lineages (Carstens *et al.* 2013). Likewise, one of the main limitations of the three employed methods is the presence of gene flow (Luo *et al.* 2018). However, given that all clades representing putative new species have allopatric distributions, it is unlikely that there is ongoing gene flow between them and, as a result, the performance of these species delimitation methods would not have been affected.

Based on our results and those of Arellano *et al*. (2003, 2005), we propose that there is sufficient evidence to recognize each of the *R. microdon* subspecies as a valid species, as follows:

Reithrodontomys microdon Merriam, 1901
Type locality. "Todos Santos, Guatemala (altitude 10,000 ft.)".

Synonym. Reithrodontomys microdon microdon Merriam, 1901:548. Type locality: see above.

Distribution. Highlands of Guatemala (Howell 1914), and the extreme southern portion of Mexico (Hooper 1952). This species is distributed from the highlands of central and southern Chiapas in Mexico to the southwestern region of Guatemala.

Remarks. For additional information on type material, cranial measurements, morphological characteristics, habitat, and comparisons with other species of the subgenus *Aporodon,* see Hooper (1952:170).

Reithrodontomys albilabris Merriam, 1901
Type locality. "Cerro San Felipe, Oaxaca, Mexico (altitude 10,000 ft.)".

Synonym. Reithrodontomys microdon albilabris Merriam, 1901:549. Type locality: see above.

Distribution. Oaxacan Highlands. Known range (in addition to type locality) included Cerro Zempoaltepec, Vista Hermosa, Llano de las Flores, Cerro Pelón (Hall 1981), and Ixtepeji (this study), Mexico.

Remarks. Reithrodontomys albilabris comprises the specimens representing haplogroup IV, with the exception of the individual CMC1627. Information on type material and morphological characteristics is available in Merriam (1901) and Howell (1914).

Reithrodontomys wagneri Hooper, 1950
Type locality. "México, Michoacán, about 10 miles northwest of Ciudad Hidalgo, western flanks of Cerro San Andrés, 9400 feet elevation".

Synonym. Reithrodontomys microdon wagneri (Hooper 1950:169). Type locality: see above.

Distribution. The Neovolcanic Belt in Mexico, with records in Michoacán, Ciudad de México, Estado de México, Morelos and Guerrero, Mexico (Hooper 1952; Hall 1981; González-Cózatl and Arellano 2015).

Remarks. We recommend inclusion within this species of the two populations from Guerrero, Mexico, recognized as *Reithrodontomys bakeri*, which according to the Principle of Priority (Article 23; ICZN 1999) should be renamed as *R. wagneri*. Also, we suggest the recognition of two subspecies within *R. wagneri*: *R. w. wagneri* and *R. w. bakeri*. For additional information on type material, cranial measurements, morphological and habitat characteristics, see Hooper (1952: 170).

Finally, haplogroup I should be considered as a candidate for a new species, with a known geographic distribution in the north of Sierra Madre Oriental (Tamaulipas and San Luis Potosí, Mexico) and Sierra de Otontepec (Veracruz, Mexico). This new species candidate represents the northernmost distribution known within the *R. tenuirostris* species group, increasing its distribution range to the mountainous regions of northeastern Mexico. Additional information sources (together with the already existing genetic information) such as morphological and ecological, among others, still are necessary to undertake the formal description of this candidate new species.

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Conflict of Interest

The authors have no conflicts of interest to declare.

Supplementary Data

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Worldclim Bioclimatic layer used to obtain the ecological niche model of *Reithrodontomys microdon* (Rodentia: Cricetidae) and the parameters of 50 ecological niche models obtained in Wallace. The best fit model parameters used to obtain the final ecological niche model are highlighted in red.

Supplementary Data SD2.—Phylogenetic relationships among species of the *Reithrodontomys tenuirostris* group (Rodentia: Cricetidae) using a concatenated sequences data set (Cytochrome *b* + Intron 7 of the beta fibrinogen) and the reconstructive method of Maximum Likelihood (ML). Values above branches represent nodal support for ML analysis. Terminal labels are named according to mammal collection voucher numbers (see Supplementary Appendix I).

Supplementary Data SD3.—TCS network for Cytochrome *b* haplotypes of *Reithrodontomys microdon* (Rodentia: Cricetidae). Haplogroup II included *R. bakeri* haplotypes. Numbers in parentheses represent mutational steps between haplotypes, and the filled gray circles are theoretical consensus sequences (unsampled or extinct).

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Appendix I

List of *Reithrodontomys* specimens with collecting localities and GenBank accessions numbers for Cytochrome *b* and Intron 7 of the beta fibrinogen genes (asterisks depict DNA sequences generated in this study). Abbreviations for countries and mammal collections (Dunnam et al. 2018[+]) housing the specimens we included are as follows: CR = Costa Rica; GU = Guatemala; MX = Mexico; USA = United States of America; ASNHC = Angelo State Natural History Collections; BYU = Brigham Young University; CMC = Colección de Mamíferos del CIByC; CNMA = Colección Nacional de Mamíferos, Universidad Nacional Autónoma de México; ECO-SC-M = Colección de Mamíferos de El Colegio de la Frontera Sur, San Cristóbal; LSUMNS = Louisiana State University Museum of Zoology; MVZ = Museum of Vertebrate Zoology; MZFC = Colección de Mamíferos, Museo de Zoología "Alfonso L. Herrera", Universidad Nacional Autónoma de México; ROM = Royal Ontario Museum; TCWC = The Biodiversity Research and Teaching Collections, Texas A&M University; TK = Mammal Collection, Texas Tech University.

Current species name	N	Locality	Museum/Mammal Collection Voucher	GenBank Accession (*Cytb*)	GenBank Accession (*Fgb*)
R. microdon	1	MX-Tamaulipas, Estación Biología Los Cedros Gómez Farias, Reserva de la Biosfera El Cielo, 320 m	TCWC59345	MW117039*	MW117073*
R. microdon	1	MX-Tamaulipas, Hotel El Pino, Alta Cima, Reserva de la Biosfera El Cielo, 910 m	TCWC59347	MW117040*	
R. microdon	1	MX-Tamaulipas, San José, Reserva de la Biosfera El Cielo, 1320 m	TCWC59349	MW117041*	MW117072*
R. microdon	1	MX-Veracruz, Sierra de Otontepec 7.6 km SE Citlaltepec, 1100 m	CMC3591	MW367885*	MW367886*
R. microdon	2	MX-San Luis Potosí, Las Guapas, Rayón, 1062 m	MZFC12156 MZFC12157	MW117042* MW117043*	MW117070* MW117071*
R. microdon	1	MX-Michoacán, Municipio Hidalgo, Mil Cumbres 8.9 km (by road), 2625 m	CMC1869	MW117053*	MW117089*
R. microdon	3	MX-Estado de México, municipio Zacualpan, 8 km SW Zacualpan by road Zacualpan-Mamatla, 2315 m	CMC1783 CMC1784 CMC1785	MW117056* MW117054* MW117055*	MW117086* MW117087* MW117092*

R. microdon	1	MX-Estado de México, 10.5 km SE de Amecameca by road Amecameca-Tlamacas, 2970 m	CMC197	MW117057*	
R. microdon	5	MX-Morelos, Municipio Tepoztlán, 6.5 km E of Coajumulco, old railroad track, 2500 m	CMC2585	MW117062*	MW117091*
			CMC2586	MW117058*	MW117084*
			CMC2587	MW117060*	MW117090*
			CMC2588	MW117061*	MW117085*
			CMC2589	MW117059*	MW117078*
R. microdon	1	MX-Guerrero, Municipio Malinaltepec, 3 km E of El Tejocote, 2620 m	CMC1627	MW117063*	MW117080*
R. microdon	1	MX-Oaxaca, Municipio San Juan Lachao, El Polvorín 5.3 km S (by road) from turn off to Lachao Viejo, 1735 m	CNMA42282	AY859461	
R. microdon	3	MX-Oaxaca, Municipio Santa María Tlahuitoltepec, Santa María Yacochi 4.5 km N Cerro Zempoaltepelt, 2450 m	CNMA35248	MW117064*	
			CNMA35249	MW117065*	
			CNMA35250	MW117066*	MW117082*
R. microdon	1	MX-Oaxaca, Municipio Santa María Tlahuitoltepec, Santa María Yacochi 5 km N Cerro Zempoaltepelt, 2450 m	CNMA34864	MW117068*	MW117081*
R. microdon	1	MX-Oaxaca, Municipio Santa María Tlahuitoltepec, Santa María Yacochi Cerro Zempoaltepec, 2450 m	CNMA35252	AY293819	MW117083*
R. microdon	1	MX-Oaxaca, Ixtepeji, 1892 m	CNMA49445	MW117067*	MW117079*
R. microdon	2	MX-Chiapas, Municipio El Porvenir, Cerro Mozotal 30 km N Motozintla by road Buenos Aires- El Porvenir	ECO-SC-M1929	MW117047*	MW117103*
			ECO-SC-M1930	MW117046*	MW117100*
R. microdon	4	MX-Chiapas, Municipio El Porvenir, Cerro Mozotal, 2930 m	BYU20782	MW117049*	MW117105*
			BYU20783	MW117048*	MW117111*
			CNMA42280	AY859460	MW117104*
			CNMA42281	AY859459	MW117110*
R. microdon	5	MX-Chiapas, Municipio Chamula, Cerro Tzontehuitz 13 km NE San Cristóbal de las Casas, 2880 m	CNMA35488	AY859454	MW117112*
			CNMA35493	AY859455	MW117107*
			CNMA35494	AY859456	MW117108*
			CNMA35495	AY859457	MW117109*
			BYU14476	AY293818	
R. microdon	2	MX-Chiapas, Reserva Ecológica Huitepec Hillside W, 2 km NE San Cristóbal de las Casas	ECO-SC-M2686	MW117052*	MW117102*
			ECO-SC-M2671	MW117051*	MW117101*
R. microdon	2	GU-Huehuetenango, 16 km NW of Santa Eulalia (by road)	ROM98382	EF990014	
			ROM98343	MW117050*	MW117106*
R. microdon	1	GU-Huehuetenango, 12 km NW of Santa Eulalia (by road)	ROM98300	AY859458	
R. bakeri	2	MX-Guerrero, Municipio Chilpancingo, Omiltemi	CNMA40380	AY293815	
			CNMA40381	AY293816	
R. bakeri	3	MX-Guerrero, Municipio Chichihualco, Filo de Caballo	TK93372	AY293812	
			TK93373	AY293813	MW117088*
			TK93374	AY293814	
R. tenuirostris	1	MX-Chiapas, Municipio El Porvenir, Cerro Mozotal, 2930 m	CMC736	MW117044*	
R. tenuirostris	1	MX-Chiapas, Municipio Chamula, Cerro Tzontehuitz 13km NE San Cristóbal de las Casas, 2880 m	BYU14479	AY859463	MW117095*

R. tenuirostris	1	MX-Chiapas, Municipio Chamula, Cerro Tzontehuitz 11 km NE San Cristóbal de Las Casas, 2890 m	ECO-SC-M1817	MW117045*	MW117096*
R. creper	1	CR-Heredia, Municipio Heredia, Los Ángeles de Paso Llano, Barva, San José de la Montaña, 2050 m	BYU15243		MW117099*
R. creper	2	CR-Heredia, Municipio Heredia, San José de la Montaña, 2050 m	BYU15244 BYU15245	AY859429 AY859430	MW117097* MW117098*
R. creper	2	CR-Cartago, 12 km N of Potrero Cerrado (by road), Rio Birrís	ROM97320 ROM97321	AY859428 DQ861372	
R. creper	1	CR-Cartago, 12 km N of Porter, Rio Birrís	ROM97311	EF989996	
R. creper	2	CR-Cartago, Parque Nacional Volcán Irazú	ROM116798 ROM116799	EF989999 EF989998	
R. cherrii	3	CR-San José, 1 km (by road) SW Poás, 1500 m	LSUMNS25169 LSUMNS25375 LSUMNS25376	MW117038* MW117036* AY293821	MW117074* MW117076* MW117075*
R. cherrii	1	CR-Cartago	LSUMNS380	MW117037*	MW117077*
R. mexicanus	1	MX-Oaxaca, Municipio Santiago Comaltepec, 11 km SW (by road) La Esperanza	BYU15426	AY859449	MW117093*
R. mexicanus	1	GU- Baja Verapaz, 5 km E of Puruhla	ROM98467	AY859451	MW117094*
R. brevirostris	1	CR-Cartago, Colima Tapanti 1.6 km S Tapanti Bridge over Rio Grande de Orosi, 1290 m	MVZ174401	AF108709	
R. brevirostris	1	CR-Alajuela, Parque Nacional Juan Castro Blanco, 10 km E of Sucre	ROM116804	EF990017	
R. gracilis	2	MX-Yucatán, Laguna Becanchen	ROMFN30426 ASNHC6370	AY293817 AY859431	
R. megalotis	1	USA-California, Berkeley, Contra Costa Co., 300-400 m Big Springs picnic area on Arroyo trail, Tilden Regional Park, 392 m	MVZ206953	KR611945	
R. megalotis	1	USA-Texas, Lubbock Co., Lubbock Lake Landmark State Historical Park, 975 m	TK22460		KJ697789
R. megalotis	1	MX-Puebla, Municipio Teziutlán, 4.7 km NE Teziutlán (by road), 1750 m	CMC1072	HQ269732	HQ269795
R. sumichrasti	2	MX-Chiapas, Municipio El Porvenir, 2930 m	CMC680 BYU20784	MW117069* HQ269707	MW117113* HQ269781
R. fulvescens	1	MX-Oaxaca, Municipio Pinotepa Nacional, Rio de la Arena, 6 km E (by road) Pinotepa Nacional, 60 m	BYU20914	HQ269730	HQ269794
R. fulvescens	1	MX-Chiapas, Municipio Mazapa de Madero, 5 km NE (by road) Mazapa de Madero, 1100 m	CNMA42278	AY859465	
R. fulvescens	1	USA-Oklahoma, Mcintosh Co., 1.9 km E Dustin	TK23469		AY274211

[+]Dunnum, J. L., B. S. McLean, and R. C. Dowler. 2018. Mammal collections of the Western Hemisphere: a survey and directory of collections. Journal of Mammalogy 99:1307–1322.

Supplementary Data SD1

Worldclim Bioclimatic layer (Hijmans et al. 2005) used to obtain the ecological niche model of *Reithrodontomys microdon* (Rodentia: Cricetidae).

	Bioclimatic layer
Bio2	Mean Diurnal Range (Mean of monthly (max temp - min temp)
Bio6	Min Temperature of Coldest Month
Bio9	Mean Temperature of Driest Quarter
Bio11	Mean Temperature of Coldest Quarter
Bio12	Annual Precipitation
Bio14	Precipitation of Driest Month
Bio16	Precipitation of Wettest Quarter
Bio18	Precipitation of Warmest Quarter

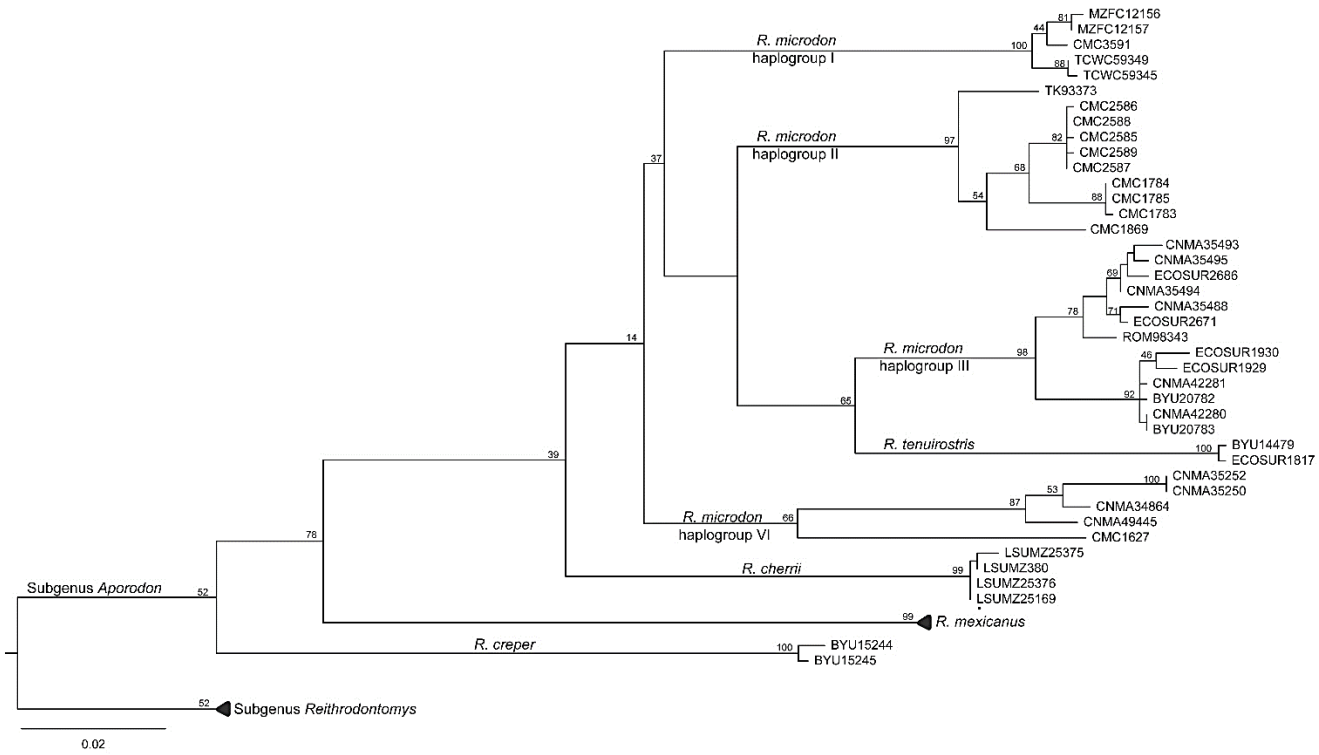
Parameters of 50 ecological niche models, obtained in Wallace (Kass et al. 2018) for *Reithrodontomys microdon* (Rodentia: Cricetidae). The best fit model parameters used to obtain the final ecological niche model are highlighted in red. L=Linear; Q=Quadratic; H=Hinge; P=Product. AUC=Area Under Curve. MTP=Minimum training presence. AIC=Akaike Informative Criterion. RM=Regularization multiplier.

Features	RM	Train AUC	Avg test AUC	Avg diff AUC	Avg test or MTP	Avg test or 10pct	AICc	delta AICc	wAIC
H	2.5	0.91	0.89	0.02	0.01	0.12	1353.08	0.00	0.80
LQHP	3	0.91	0.89	0.02	0.01	0.13	1357.60	4.52	0.08
H	3	0.90	0.89	0.02	0.01	0.12	1359.93	6.85	0.03
LQHP	2.5	0.91	0.90	0.02	0.01	0.15	1360.18	7.10	0.02
H	2	0.91	0.89	0.02	0.01	0.12	1361.44	8.36	0.01
H	4	0.90	0.89	0.02	0.01	0.13	1361.93	8.85	0.01
H	4.5	0.90	0.88	0.02	0.01	0.13	1362.26	9.18	0.01
LQHP	3.5	0.91	0.89	0.02	0.01	0.12	1363.08	10.00	0.01
LQH	3.5	0.90	0.89	0.02	0.01	0.12	1363.91	10.83	0.00
LQHP	4	0.90	0.89	0.02	0.01	0.13	1364.12	11.04	0.00
LQH	3	0.90	0.89	0.02	0.01	0.10	1364.21	11.13	0.00
H	3.5	0.90	0.89	0.02	0.01	0.12	1364.38	11.30	0.00
LQ	0.5	0.91	0.89	0.03	0.04	0.12	1364.44	11.35	0.00
LQHP	2	0.91	0.90	0.02	0.01	0.15	1365.28	12.19	0.00
H	5	0.90	0.88	0.02	0.01	0.15	1365.58	12.50	0.00
LQH	5	0.90	0.89	0.02	0.03	0.12	1365.62	12.54	0.00
LQ	4.5	0.89	0.88	0.02	0.02	0.12	1365.89	12.80	0.00
LQ	1.5	0.90	0.88	0.02	0.00	0.14	1366.20	13.12	0.00
LQ	5	0.89	0.88	0.02	0.02	0.12	1366.55	13.47	0.00
LQH	4	0.90	0.89	0.02	0.01	0.13	1366.75	13.67	0.00

LQ	2.5	0.90	0.88	0.02	0.02	0.12	1366.80	13.72	0.00
LQ	1	0.91	0.89	0.02	0.04	0.12	1367.28	14.19	0.00
LQ	4	0.89	0.88	0.02	0.02	0.12	1367.52	14.44	0.00
LQHP	5	0.90	0.89	0.02	0.01	0.13	1367.78	14.70	0.00
LQ	3.5	0.89	0.88	0.02	0.02	0.12	1368.27	15.19	0.00
LQ	3	0.90	0.88	0.02	0.02	0.12	1368.97	15.89	0.00
LQ	2	0.90	0.88	0.02	0.02	0.14	1369.00	15.92	0.00
LQH	4.5	0.90	0.89	0.02	0.01	0.13	1369.53	16.45	0.00
LQHP	4.5	0.90	0.89	0.02	0.01	0.13	1370.86	17.78	0.00
LQHP	1.5	0.91	0.89	0.02	0.01	0.13	1373.47	20.39	0.00
H	1	0.92	0.90	0.03	0.01	0.12	1376.80	23.72	0.00
LQH	2.5	0.90	0.89	0.02	0.01	0.10	1377.90	24.81	0.00
H	1.5	0.91	0.90	0.02	0.01	0.13	1378.47	25.39	0.00
LQH	1.5	0.91	0.89	0.02	0.01	0.15	1378.73	25.65	0.00
LQHP	1	0.92	0.89	0.03	0.04	0.15	1379.17	26.09	0.00
LQH	2	0.91	0.89	0.02	0.01	0.12	1385.30	32.22	0.00
L	5	0.88	0.87	0.02	0.02	0.13	1385.78	32.70	0.00
L	4	0.88	0.87	0.02	0.02	0.12	1387.71	34.63	0.00
L	2	0.88	0.87	0.03	0.02	0.10	1389.47	36.39	0.00
L	2.5	0.88	0.87	0.02	0.02	0.10	1389.61	36.53	0.00
L	3	0.88	0.87	0.02	0.02	0.10	1389.78	36.70	0.00
L	3.5	0.88	0.87	0.02	0.02	0.10	1390.00	36.92	0.00
L	4.5	0.88	0.87	0.02	0.02	0.12	1390.56	37.48	0.00
L	1.5	0.88	0.87	0.03	0.02	0.10	1391.69	38.61	0.00
LQH	1	0.92	0.89	0.03	0.04	0.15	1395.53	42.45	0.00
L	1	0.88	0.86	0.03	0.02	0.10	1396.77	43.69	0.00
L	0.5	0.88	0.86	0.03	0.02	0.12	1403.60	50.52	0.00
H	0.5	0.93	0.89	0.04	0.05	0.17	1472.59	119.50	0.00
LQH	0.5	0.93	0.88	0.05	0.07	0.19	1538.29	185.21	0.00

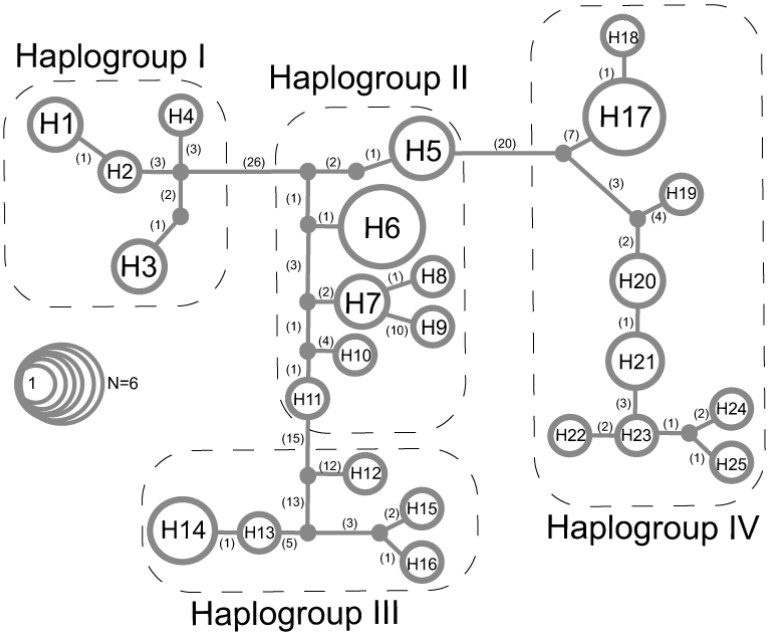
LQHP	0.5	0.93	0.88	0.05	0.07	0.17	1552.60	199.52	0.00

Supplementary Data SD2



Phylogenetic relationships among species of the *Reithrodontomys tenuirostris* group (Rodentia: Cricetidae) using a concatenated sequences data set (Cytochrome *b* + Intron 7 of the beta fibrinogen) and the reconstructive method of Maximum Likelihood (ML). Values above branches represent nodal support for ML analysis. Terminal labels are named according to mammal collection voucher numbers (see Appendix I).

Supplementary Data SD3



TCS network for Cytochrome *b* haplotypes of *Reithrodontomys microdon* (Rodentia: Cricetidae). Haplogroup II included *R. bakeri* haplotypes. Numbers in parentheses represent mutational steps between haplotypes, and the filled gray circles are theoretical consensus sequences (unsampled or extinct).

VIII. DISCUSIÓN GENERAL Y CONCLUSIONES

La premisa que un gran número de especies permanecen desconocidas para la ciencia (Wilson, 2003) ha direccionado muchas ramas de la biología para lograr, en el menor tiempo posible, describir nuevas entidades taxonómicas y comprender los procesos que han dado origen y mantienen a la diversidad biológica actual. En ese sentido, los resultados de este trabajo buscan esclarecer la taxonomía y las relaciones evolutivas entre las especies del subgénero *Aporodon*, donde una alta diversidad críptica intraespecífica ha caracterizado a muchos de sus integrantes. Para ello, se utilizaron diferentes grupos de datos que aportaron información molecular, morfométrica y ecológica de los taxones analizados, un enfoque altamente recomendado en estudios de sistemática y conocido como taxonomía integradora (Dayrat, 2005; Padial *et al*., 2010).

Los primeros estudios del género *Reithrodontomys* se enfocaron principalmente en la descripción de nuevas especies, teniendo en cuenta aspectos de su morfología y distribución geográfica (p. ej.: Allen, 1895; Merriam, 1901). Hooper (1952), con su monografía del género, propuso arreglos taxonómicos al nivel específico e intraespecífico. Además, proporcionó información de características morfológicas y ecológicas de las especies del género, proponiendo cuatro grupos, acorde con las relaciones de parentesco entre ellas. La taxonomía propuesta por Hooper (1952) se mantuvo casi inalterable hasta hace algunos años, cuando estudios empleando técnicas moleculares evidenciaron la ocurrencia de procesos de especiación críptica (Sullivan *et al*., 2000; Arellano *et al*., 2003, 2005; Miller y Engstrom 2008; Hardy *et al*., 2013; Statham *et al*., 2016). Estas evidencias de especiación constituyeron un indicio de que el número real de especies que componen a *Reithrodontomys* está subestimado; no obstante, solo ha sido corroborado con datos moleculares, mientras que otros aspectos importantes de su biología, como son sus características morfológicas y de hábitat, han sido poco abordados.

En la mayoría de los casos, los resultados apoyaron que la diferenciación entre las especies de *Aporodon* analizadas no solo es genética, sino también morfométrica y ecológica. Tal es el caso de *R. cherrii*, anteriormente considerada una subespecie de *R. mexicanus*, hasta que fue elevada al estatus específico utilizando información del gen Cytb (Arellano *et al*., 2005). Se pudo corroborar que *R. cherrii* también se diferencia de *R. mexicanus* por la morfometría de su cráneo, el cual tiende a ser de mayor tamaño y con huesos nasales más largos, pero con una caja craneana más estrecha. Además, *R. cherrii* ocupó un espacio ambiental más reducido que el de *R. mexicanus*, como consecuencia quizás de su distribución restringida a las tierras altas de Costa Rica (Hall, 1981). El nicho

climático de ambas especies compartió valores similares de temperaturas, pero pudo diferenciarse correctamente en cuanto a las precipitaciones. Complementar los resultados genéticos con análisis morfométricos y ecológicos, no solo permitieron concluir que, inequívocamente se trata de dos entidades taxonómicas diferentes, sino también, resaltaron la utilidad de otras líneas de evidencia distintas a la molecular para discriminar entre especies crípticas (Alström *et al*., 2021).

Para establecer límites entre especies de mamíferos se han empleado los valores de distancias genéticas estimados por Bradley y Baker (2001) y Baker y Bradley (2006), a partir del gen Cytb, el cual ha mostrado gran efectividad en estudios de sistemática en este grupo (Irwin *et al*., 1991; Tobe *et al*., 2010). De esta manera, los valores estimados de divergencia genética del grupo en estudio se comparan con los previamente reportados en la literatura, y en conjunto con las relaciones evolutivas obtenidas en las filogenias permite arribar a conclusiones taxonómicas donde se aceptan o rechazan las hipótesis sobre especies. No obstante, establecer un umbral de corte (a partir de las distancias genéticas) para la discriminación interespecífica ha sido criticado, ya que es un valor definido de manera arbitraria (Blair y Bryson, 2017). Además, el uso de un solo gen para la descripción de especies también ha sido cuestionado, al reflejar la historia evolutiva de ese gen en particular, que no necesariamente corresponde con la de otros genes (Rubinoff y Holland, 2005; Will *et al*., 2005). Es por lo que, en los análisis para sugerir los límites entre especies, se implementaron diferentes métodos matemáticos que utilizan la información molecular de uno o varios *loci* para sugerir los linajes que potencialmente constituyen especies distintas, además de los valores de diferenciación genética con Cytb. En particular, fueron empleados tres de los métodos más ampliamente usados para este fin (Alström *et al*., 2021); dos de ellos tuvieron en cuenta la información de Cytb (mPTP y bGMYC), mientras que un tercer método multi-loci (STACEY) empleó la información concatenada de Cytb y los genes nucleares Fgb-I7 e IRBP, según fuera el caso.

La congruencia entre el mayor número de métodos de delimitación permitió dar mayor confianza al reconocimiento de las nuevas entidades taxonómicas (Carstens *et al*., 2013), así como corroborar los límites entre las especies ya reconocidas para el subgénero *Aporodon*. Dentro del grupo *R. mexicanus*, la mayoría de sus especies fueron ratificadas como válidas. No obstante, para *R. gracilis* y *R. spectabilis* se encontraron ciertas incongruencias con la taxonomía actualmente aceptada (ver Bradley, 2017). Todos los métodos de delimitación reconocieron a las poblaciones de ambas especies como conespecíficas, lo cual fue soportado por un valor de distancia genética entre ellas de

apenas 0,7%. La baja divergencia genética entre estas especies ya había sido sugerida por Arellano *et al*. (2005). Aunque existen estudios que resaltan la diferenciación morfológica entre ambas especies, principalmente en cuanto a su tamaño corporal (Hooper, 1952; Jones y Lawlor, 1965), en la presente tesis este tipo de datos no pudo incluirse. No obstante, se sugiere como posible causa de la diferenciación morfológica el efecto de isla (Foster, 1964), debido a la distribución geográfica de *R. spectabilis*, restringida a Isla Cozumel, México (Hall, 1981). Por lo tanto, en el presente trabajo se recomienda que, las poblaciones de *R. gracilis* de México y las de *R. spectabilis* deben ser analizadas con un enfoque integrador incluyendo múltiples fuentes de datos (genética poblacional, morfometría, ecología) que pongan a prueba la premisa de que constituyen la misma especie.

Por otra parte, debe prestarse especial interés a las poblaciones de *R. gracilis* de Centroamérica. Si bien en los análisis realizados solo pudieron incluirse dos individuos de El Salvador, y estos muestran una relación muy estrecha con las muestras de *R. gracilis* y *R. spectabilis* de México, todos los métodos sugirieron que esos dos individuos representan una entidad diferente a nivel de especie. Lo anterior también es soportado por una divergencia genética de 8%, superior a la magnitud de 5% asociada al reconocimiento de especies en mamíferos (Baker y Bradley, 2001). Aunque, un mejor muestreo resulta imprescindible para apoyar que estos individuos pertenecen a una especie aún no descrita, se podría asumir que eventos de especiación alopátrica han estado ocurriendo entre las poblaciones de *R. gracilis* distribuidas en México y Centroamérica. Esto podría explicarse considerando las barreras geográficas evidentes que existen entre estas regiones, tal como el Istmo de Tehuantepec, el cual ha favorecido el aislamiento geográfico y por ende la ausencia de flujo de genes entre poblaciones de diferentes especies de pequeños mamíferos, incluido el género *Reithrodontomys* (Sullivan *et al*., 2000; León-Paniagua *et al*., 2007; Hardy *et al*., 2013).

Dentro del grupo *R. mexicanus*, la mayor variación intraespecífica se reportó para *R. mexicanus*. Estos hallazgos coinciden con otros autores, donde esta especie no pudo ser recuperada como monofilética en ninguno de los casos (Arellano *et al*., 2003, 2005; Miller y Engstrom, 2008). En su lugar, tres clados altamente divergentes se habían reportado en las reconstrucciones filogenéticas, uno de ellos perteneciente a la actual especie *R. cherrii*. En el presente trabajo, los análisis filogenéticos incluyeron un muestreo extensivo de individuos clasificados *a priori* como *R. mexicanus*, con la única excepción de la subespecie *R. m. riparius*, y ratifican a esta especie como un complejo críptico. Los resultados de todos los métodos de delimitación coincidieron en que las poblaciones

distribuidas en la Sierra Madre Oriental y el norte de Oaxaca, México, constituyen una especie diferente que se posicionó como el grupo hermano del subgénero *Aporodon*. Este resultado fue apoyado por altos valores de distancia genética (> 12 %), así como por los análisis morfométricos y ecológicos, validando este clado como una especie no descrita. En al menos dos localidades en Oaxaca, esta nueva especie se distribuye de manera simpátrica con poblaciones agrupadas en otro clado bien diferenciado genéticamente, y que retuvo el nombre de *R. mexicanus*. Este clado incluyó localidades de México, Guatemala y El Salvador, aunque los especímenes de esta última región necesitan ser reevaluados taxonómicamente dada la evidencia molecular de que sus poblaciones se encuentran en un proceso de especiación no concluido (Futuyma, 2013). Al reconocer este clado como *R. mexicanus sensu stricto*, se restringe considerablemente la amplia distribución geográfica, históricamente reconocida para esta especie, algo que sin dudas resulta valioso en términos de conservación de sus poblaciones.

En cuanto a las poblaciones de Suramérica, si bien los resultados hacen evidente que no pertenecen a *R. mexicanus*, la sugerencia de que dichas poblaciones representan distintas especies fue incongruente entre los métodos de delimitación. No obstante, el consenso entre la mayoría de los métodos apoya la existencia de dos especies en esta región; una de ellas confinada geográficamente a las cordilleras occidental y central de Colombia (*R. mexicanus* clado IIA), mientras que la otra abarca desde la cordillera oriental de Colombia hasta la región norte de los andes ecuatorianos (*R. mexicanus* clado IIB). Estas posibles especies pudieron ser comparadas entre sí con la información molecular y ecológica, donde la diferenciación genética fue menos marcada que aquella entre los nichos que ocupan. Los bajos valores de diferenciación genética entre especies de roedores suramericanos han sido previamente reportados y justificados por la relativamente reciente colonización y radiación de este grupo en esa región (Patton y Smith, 1992). No obstante, la asignación taxonómica de las dos posibles especies, delimitadas por los análisis, tiene sus complicaciones. Hooper (1952) reportó tres subespecies de *R. mexicanus* en Suramérica: *R. m. milleri*, *R. m. soederstroemi* y *R. m. eremiscus*. De ellas, *R. m. milleri* tiene registros en localidades de Colombia y Ecuador. En Colombia, las localidades de esta subespecie coinciden con la distribución potencial de *R. mexicanus* clado IIA, pero no con la de *R. mexicanus* clado IIB. Mientras que, en Ecuador, la distribución potencial de *R. mexicanus* clado IIB comparte localidades reportadas para las tres subespecies. En este contexto, es claro que se necesitan estudios adicionales que incluyan individuos de la

mayor cantidad de localidades posibles de esta región, para la correcta asignación taxonómica de los linajes a nivel de especie reconocidos.

Dentro del subgénero *Aporodon*, también pudieron ser analizadas las relaciones evolutivas entre las especies que conforman el grupo *R. tenuirostris*. Dentro de este grupo, la mayoría de las especies estuvieron más emparentadas entre sí, con respecto a las especies del grupo *R. mexicanus*. La única excepción fue *R. creper* cuya posición en los árboles filogenéticos fue variable y generalmente con bajos valores de soporte para los métodos de reconstrucción de máxima verosimilitud y bayesiano. La posición incierta de esta especie en las filogenias del subgénero *Aporodon* ya había sido resaltada por Arellano *et al*. (2005), quienes la propusieron como un linaje diferente de los grupos de especies sugeridos por Hooper (1952). Se requieren evidencias complementarias para generar una conclusión taxonómica más robusta referente a la inclusión de esta especie en el grupo *R. tenuirostris*.

La única especie dentro del grupo *R. tenuirostris* que no se recuperó como una entidad monofilética fue *R. microdon*. Sus individuos se agruparon en cuatro clados bien diferenciados (definidos aquí como haplogrupos) por los métodos de delimitación, las distancias genéticas para Cytb superiores al 5% y los análisis de conectividad del paisaje, que combinaron haplotipos con modelos de nicho climático. De estos cuatro haplogrupos, tres de ellos corresponden a las subespecies descritas para *R. microdon*, mientras que el restante constituye una especie nueva no descrita, con la distribución geográfica más al norte reportada para el grupo *R. tenuirostris*. Las recomendaciones taxonómicas derivadas de estos análisis sugirieron elevar a cada una de estas subespecies al nivel específico, pero también incluir a *R. bakeri* como una subespecie de *R. wagneri* y no como una especie válida (Bradley *et al*., 2004). Esto se debe a que ningún método de delimitación logró separar las poblaciones de *R. bakeri* de las de *R. wagneri*, algo soportado por bajos valores de diferenciación genética con Cytb y por valores relativamente altos de rutas de conectividad entre estas poblaciones en un tiempo evolutivo reciente. La diversidad críptica encontrada en *R. microdon* constituye un claro ejemplo de especiación alopátrica (Futuyma, 2013), pero el ocupar un hábitat con características muy similares, como los bosques mesófilos de montañas (Gual-Díaz y Rendón-Correa, 2014), puede haber favorecido la retención de características morfológicas que impidieron su reconocimiento como especies distintas en anteriores revisiones. Si se pone en práctica el concepto de Linaje General de Especie (de Queiroz 1998, 2005, 2007), estaríamos ante especies que ya han “cumplido” el criterio operacional de diferenciación genética, pero que aún no completan su

diferenciación teniendo en cuenta otras líneas de evidencias como la morfológica. No obstante, para corroborar esta hipótesis es necesario llevar a cabo análisis morfométricos entre las especies ahora reconocidas dentro de *R. microdon*.

Los tiempos de divergencia y las relaciones evolutivas estimados con el gen Cytb entre los representantes del subgénero *Aporodon*, fueron congruentes entre sí, al comparar los árboles obtenidos para los dos grupos de especies. No obstante, en ambos casos, las historias evolutivas obtenidas para los genes nucleares fueron incongruentes con las del gen mitocondrial. La principal justificación propuesta para esta discordancia mitonuclear (Toews y Brelsford, 2012) ha sido la introgresión y la retención de polimorfismos ancestrales o separación incompleta de linajes (*incomplete lineage sorting*; Firneno *et al*., 2021), esta última ampliamente reportadas en distintos grupos zoológicos, incluidos los mamíferos (p. ej.: Almendra *et al*., 2014; Rivera *et al*., 2018). Es por lo que, este estudio se enfoca en análisis integradores, donde, siempre que fuera posible, las hipótesis filogenéticas se pusieron a prueba con datos morfológicos y ecológicos (Sangster, 2018). Estas hipótesis filogenéticas fueron generadas principalmente a partir de las sugerencias de los tres métodos de delimitación de especies. Aunque estos métodos presentan limitaciones asociadas con los supuestos que se deben cumplir para poder implementarlos (Luo *et al*., 2018), resultan muy superiores a otros métodos de delimitación como son el umbral de corte de distancia genética, que puede variar entre casi todos los grupos zoológicos (Alström *et al*., 2021). En el grupo *R. tenuirostris,* solo el método mPTP tendió a sobrestimar el número de especies, los restantes dos métodos sí fueron congruentes. De manera contraria, las incongruencias entre los métodos de delimitación para el grupo *R. mexicanus* fueron más evidentes, quizás porque está conformado por una mayor cantidad de linajes recientes crípticos que todavía están experimentando procesos de divergencia, algo que pudiera resultar desafiante desde el punto de vista metodológico para los métodos de delimitación empleados (Fujita *et al*., 2012; Firneno *et al*., 2021).

En conclusión, los resultados expuestos presentan importantes implicaciones para la sistemática y taxonomía del género *Reithrodontomys*, en particular para el subgénero *Aporodon*. Actualmente, dentro de este género 24 especies son reconocidas, pero la alta diversidad críptica reportada, sugiere al menos 6 especies adicionales. Las sugerencias de arreglos taxonómicos incluyen que cada una de las subespecies de *R. microdon* sean reconocidas como especies válidas: *R. microdon* (*sensu stricto*), *R. albilabris* y *R. wagneri*. En esta última especie quedaría incluida *R. bakeri*, la cual sería reasignada al nivel subespecífico. Además, se propone para el grupo *R. tenuirostris* una nueva especie

pendiente de descripción formal y distribuida hasta el momento en Tamaulipas, San Luis Potosí, y Sierra de Otontepec, en Veracruz, México. Se proponen 4 especies dentro de *R. mexicanus*: *R. mexicanus* (*sensu stricto*), dos especies para Suramérica y una especie nueva pendiente de descripción formal, distribuida hasta el momento en Sierra Madre Oriental y norte de Oaxaca, México. Son necesarios estudios adicionales para esclarecer el estatus taxonómico de *R. spectabilis* con relación a *R. gracilis*, así como la posición taxonómica de *R. creper* dentro del subgénero *Aporodon.* Además, es recomendable la revaluación taxonómica de las poblaciones de El Salvador tanto de *R. gracilis* como de *R. mexicanus* (*sensu stricto*), por las evidencias moleculares de que cada una constituyen linajes que están evolucionando de manera independiente. Finalmente, estos resultados resaltan la importancia del uso de múltiples líneas de evidencias para establecer delimitaciones robustas entre especies consideradas complejas taxonómicamente, sobre todo cuando están implícitos procesos de especiación críptica. Este enfoque de taxonomía integradora favorece la estabilidad taxonómica de estos grupos, lo cual, repercute de manera directa en las acciones de conservación, en caso de requerirse.

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Tesis: Caracterización de la diversidad críptica en ratones del subgénero *Aporodon* (Rodentia: Cricetidae)

Alumno que lo presenta a revisión: DAILY MARTÍNEZ BORREGO

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