UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO

POSGRADO EN CIENCIAS BIOLÓGICAS

FACULTAD DE CIENCIAS

SISTEMÁTICA MOLECULAR Y DESCRIPCIÓN DE ESPECIES NUEVAS DE LOS GÉNEROS *ABRONIA* Y *MESASPIS* (SQUAMATA: ANGUIDAE: GERRHONOTINAE)

TESIS

QUE PARA OPTAR POR EL GRADO DE:

DOCTOR EN CIENCIAS

PRESENTA:

ISRAEL SOLANO ZAVALETA

TUTOR PRINCIPAL DE TESIS: DR. ADRIÁN NIETO MONTES DE OCA
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MÉXICO, CD. MX. **FEBRERO, 2019.**

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POSGRADO
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ASUNTO: Oficio de Jurado

M. en C. Ivonne Ramírez Wence
Directora General de Administración Escolar, UNAM
P r e s e n t e

Me permito informar a usted que en la reunión ordinaria del Subcomité de Ecología y Manejo Integral de Ecosistemas y Biología Evolutiva y Sistemática del Posgrado en Ciencias Biológicas, celebrada el día **04 de noviembre de 2019** se aprobó el siguiente jurado para el examen de grado de **DOCTOR EN CIENCIAS** del estudiante **SOLANO ZAVALETA ISRAEL** con número de cuenta **98174151** con la tesis titulada: **"Sistemática molecular y descripción de especies nuevas de los géneros *Abronia y Mesaspis* (Squamata: Anguidae: Gerrhonotinae"**, realizada bajo la dirección del **DR. ADRIAN NIETO MONTES DE OCA:**

Presidente:	**DR. OSCAR ALBERTO FLORES VILLELA**
Vocal:	**DR. RODRIGO MACIP RÍOS**
Secretario:	**DR. JOSÉ MARTÍN GARCÍA VARELA**
Suplente:	**DR. ALEJANDRO ZALDÍVAR RIVERÓN**
Suplente:	**DR. HIBRAIM ADÁN PÉREZ MENDOZA**

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

A T E N T A M E N T E
"POR MI RAZA HABLARA EL ESPIRITU"
Ciudad Universitaria, Cd. Mx., a 17 de enero de 2020

COORDINADOR DEL PROGRAMA

DR. ADOLFO GERARDO NAVARRO SIGÜENZA

POSGRADO EN CIENCIAS BIOLÓGICAS
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Índice

RESUMEN

Abronia Gray, 1838 y *Mesaspis* Cope, 1877 son dos géneros de lagartijas que se distribuyen en México y Centroamérica, principalmente en bosques templados. *Abronia* se distribuye desde Tamaulipas y Michoacán en la vertiente del Atlántico y del Pacífico, respectivamente, y hacia el sur hasta Honduras y El Salvador; mientras que *Mesaspis* se distribuye desde el norte de Puebla y centro de Veracruz, en la vertiente del Atlántico, y Guerrero en la vertiente del Pacífico, hacia el sur hasta el oeste de Panamá. Debido a la pérdida del hábitat y a que son erróneamente consideradas peligrosas para el ser humano muchas de las especies se encuentran en riesgo, de las 19 especies de *Abronia* que se distribuyen en México 14 están en la Norma Oficial Mexicana (NOM), mientras que de las seis especies de *Mesaspis* cinco están en la NOM. Sin embargo, el comercio ilegal internacional de diversas especies del género *Abronia* ocasionó que recientemente todas las especies se incluyeran en CITES. En la última década dos filogenias con datos moleculares encontraron evidencia que sugiere que *Abronia* y *Mesaspis* no son mutuamente monofiléticos; sin embargo, la diferencia en el número de especies representadas y los marcadores empleados no permite hacer un consenso confiable y, por lo tanto, la monofilia de *Abronia* y *Mesaspis* no ha sido puesta a prueba. En este trabajo se utilizaron marcadores moleculares puntuales para investigar las relaciones filogenéticas y hacer inferencias de delimitación de especies en los géneros *Abronia* y *Mesaspis*. En el capítulo 1 se analizaron los límites de especies dentro de la especie nominal *M. moreletii*, así como sus relaciones filogenéticas, utilizando un fragmento de mtDNA (ND4 y los genes adyacentes $tRNA^{His}$, $tRNA^{Ser}$ y parte de $tRNA^{Leu}$) y tres marcadores nucleares (BMP2, KIAA-1217, PRLR). La especie *M. moreletii* se encuentra distribuida desde Chiapas, México, hacia el sur y hasta el noreste de Nicaragua. A lo largo de su distribución se le reconocen cinco subespecies de las cuales *M. m. rafaeli* y *M. m. salvadorensis*, y tres poblaciones de estatus subespecífico incierto, parecen estar aisladas geográficamente. El análisis de datos moleculares mediante tres metodologías diferentes permitió sugerir que *M. m. moreletii* (incluyendo a *M. m. fulvus*) y las otras subespecies deben elevarse a nivel de especie; sin embargo, el estatus taxonómico de tres poblaciones (*M. moreletii* del este Honduras y de Nicaragua, *M. salvadorensis* del norte de Honduras) se considera incierto hasta no contar con un mayor número de ejemplares, secuencias y/o genes, para analizar estos casos de manera específica. En el capítulo 2 fueron descritas dos especies nuevas, *A. cuetzpali* de la Sierra Madre del Sur, al sur del estado de Oaxaca, México, y *M. cuchumatanus* de la Sierra de Los Cuchumatanes, Departamento de Huehuetenango, Guatemala.

Cabe mencionar que el estatus específico de *M. cuchumatanus* se corroboró en el trabajo de límite de especies de *M. moreletii* (en el capítulo I), ya que era una de las poblaciones asignadas dentro de este taxón. En el capítulo 3 se investigaron las relaciones filogenéticas entre *Abronia* y *Mesaspis* utilizando un fragmento de mtDNA (ND4 y los genes adyacentes $tRNA^{His}$, $tRNA^{Ser}$ y parte de $tRNA^{Leu}$) y tres marcadores nucleares (BMP2, KIAA-1217, PRLR). Se encontró que las especies de *Abronia* y *Mesaspis* se agruparon entre sí en clados fuertemente apoyados y concordantes con la distribución geográfica, y no de acuerdo con la taxonomía actual, lo cual corrobora que ambos géneros no son mutuamente monofiléticos. Adicionalmente, el análisis de límites de especies permitió sugerir que *M. gadovii* no es una especie politípica y que la población de *Abronia* de Laguna Bélgica, Chiapas, corresponde a *A. bogerti*. Se encontró que existe flujo génico en una zona de simpatría entre *A. graminea* y *A. taeniata*, mientras que no se encontró apoyo de la monofilia de *A. vasconcelosii* ni la distintividad de *A. meledona* y *A. campbelli* con respecto a *A. vasconcelosii*. Finalmente, se identificaron cuatro poblaciones (dos *Abronia* de Guerrero, una *Abronia* de Huehuetenango y una *Mesaspis* de Oaxaca) que podrían representar especies no descritas.

ABSTRACT

Abronia Gray, 1838 and *Mesaspis* Cope, 1877 are two lizard genera distributed mainly on temperate forest of México and Central America. *Abronia* distribution ranges from Tamaulipas and Michoacán in the Atlantic and Pacific versant, respectively, southward to Honduras and El Salvador; *Mesaspis* distribution ranges from north of Puebla and central Veracruz, in the Atlantic versant, and Guerrero in the Pacific versant, southward to west Panamá. *Abronia* and *Mesaspis* are endangered because people erroneously think they are dangerous and kill them, and also by loss of habitat; 14 of 19 *Abronia* species distributed in Mexico are protected by Mexican law with the Norma Oficial Mexicana (NOM), and five of six *Mesaspis* distributed in Mexico are protected by NOM. All *Abronia* species were recently added to CITES in scope to fight against illegal international trade. Two independent molecular phylogenies found that *Abronia* and *Mesaspis* are not mutually monophyletic; nevertheless, the difference on the numbers of represented species, and the molecular markers used, does not allow to make a confident consensus, that is why the monophyly of *Abronia* and *Mesaspis* has not been tested. In this work, punctual molecular markers were used to investigate the phylogenetic relationships and species limits of *Abronia* and *Mesaspis* genera. In the first chapter, species limits in the nominal species *Mesaspis moreletii*, as well as their phylogenetic relationships, were evaluated using one mtDNA fragment (ND4 and the adjacent genes $tRNA^{His}$, $tRNA^{Ser}$ and part of $tRNA^{Leu}$) and three molecular markers (BMP2, KIAA-1217, PRLR). *M moreletii* is distributed from Chiapas, México, southward to west Nicaragua. Five subspecies are recognized along its distribution, of which *M. m. rafaeli* and *M. m. salvadorensis*, as well as three populations of uncertain subspecific status, are isolated geographically. The results of three different methodologies recognized that *M. m. moreletii* (including *M. m. fulvus* as synonym) and the other subspecies represent distinct evolutionary independent lineages, and that the populations of uncertain status from Honduras and Nicaragua may represent additional undescribed species but additional information is desired to corroborate it. In the second chapter, two new species were described: *A. cuetzpali* from Sierra Madre del Sur, south of Oaxaca, México, and *M. cuchumatanus* from Sierra de Los Cuchumatanes, Huehuetenango Department, Guatemala. The taxonomic status of *M. cuchumatanus* was corroborated in the previous chapter (Chapter 1) since it was a population assigned to *M. moreletii*. In the third chapter, the phylogenetic relationships of *Abronia* and *Mesaspis* were investigated using one mtDNA fragment (ND4 and the adjacent genes $tRNA^{His}$, $tRNA^{Ser}$ and part of $tRNA^{Leu}$) and three molecular markers (BMP2,

KIAA-1217, PRLR). Species of *Abronia* and *Mesaspis* grouped with each other in strongly supported clades concordant with geography, rather than taxonomy, supporting previous suggestions that *Abronia* and *Mesaspis* are not reciprocally monophyletic. Additionally, our results shed some light on species delimitation problems: *M. gadovii* should not be recognized as a polytypic species, *Abronia* from Laguna Bélgica represents another population of *Abronia bogerti*, *A. vasconcelosii* is not monophyletic and there is no distinctness of *A. meledona* and *A. campbelli* from *A. vasconcelosii*, genetic flow exists between *A. graminea* and *A. taeniata* in a sympatry zone, there are four populations (two *Abronia* from Guerrero, México; *Abronia* from Huehuetenango, Guatemala; *Mesaspis* from Oaxaca, México) that could represent undescribed species.

INTRODUCCIÓN GENERAL

La historia evolutiva de los organismos es uno de los principales objetos de estudio de la biología comparada (p.ej., Good, 1988; Chippindale et al., 1998; Bryson et al., 2007; Esteva et al., 2010). Por lo general esta historia se representa mediante un diagrama conocido comúnmente como árbol filogenético, porque su estructura y sus partes (p.ej., raíz, rama, nodo) denotan y/o se asemejan a la estructura de un árbol (Vandamme, 2009). Se han usado diferentes tipos de datos para investigar las relaciones evolutivas o filogenias de los organismos. La forma tradicional de estimar las relaciones entre las especies estaba basada en el análisis de caracteres morfológicos (Linnaeus, 1758), posteriormente se emplearían diferentes tipos de datos moleculares como las aloenzimas (p.ej., Good, 1987b), secuencias de nucleótidos de genes puntuales (p.ej., Conroy et al., 2005; Pyron et al., 2013) y las obtenidas mediante secuenciación masiva de datos (p.ej., Leaché *et al.*, 2016; Nieto-Montes de Oca *et al.*, 2017; Streicher y Wiens, 2017; Grummer et al., 2018; Natusch et al., 2020) o NGS (Next Generation Sequencing), la cual engloba diferentes metodologías y procedimientos (Harrison y Kidner, 2011). Es importante destacar que los datos moleculares han ayudado a esclarecer las relaciones filogenéticas en muchos grupos de reptiles (Wiens y Slingluff, 2001; Conroy et al., 2005; Lawson et al., 2005; Bryson et al., 2007, 2008; Adalsteinsson et al., 2009). Esto ha permitido poner a prueba la taxonomía tradicional y aclarar el status taxonómico de diversos linajes y/o poblaciones (p.ej., Wiens y Penkrot, 2002; Conroy et al., 2005; Pons et al., 2006; Bryson et al., 2007; Meza-Lázaro y Nieto-Montes de Oca, 2015).

Conceptos y delimitación de especies

Las especies constituyen las unidades fundamentales de la biología, como lo son también, por ejemplo, las células y los organismos en niveles de organización más bajos (Sites y Marshall, 2003; de Queiroz, 2007). Es decir, en trabajos de biogeografía, ecología, evolución, paleontología, sistemática, etc., la unidad básica usualmente es la especie. La definición de "especie" ha sido fuente de controversia durante muchos años pues se han propuesto poco más de 20 conceptos de especie (de Queiroz, 2007) entre los que destacan el concepto biológico (Mayr, 1942, 2000), el evolutivo (Simpson, 1961; Wiley, 1978) y el filogenético (Cracraft, 1992). Todos los conceptos de especie surgieron asociados a la problemática de la

delimitación de las especies en la práctica y se basan en el uso de distintos tipos de datos y criterios operacionales y, por lo tanto, en ocasiones pueden ser parcialmente incompatibles entre ellos (de Queiroz, 1998, 2007; Barberousse y Samadi, 2010; Hausdorf, 2011; Frankham et al., 2012). Sin embargo, la mayoría de los conceptos de especies convergen en que las especies son linajes de meta-poblaciones que evolucionan por separado o independientemente (de Queiroz, 1998, 2007). De manera que las características empleadas por los diferentes criterios para delimitar a las especies aparecen de manera gradual en el proceso de especiación, aunque pueden diferir en el orden de aparición e incluso algunas pueden no presentarse. Como ejemplos de estos criterios operacionales podemos mencionar a la diagnosticabilidad y la incompatibilidad reproductiva (de Queiroz, 2007).

Un objetivo principal de la Sistemática es el de conocer la biodiversidad. Para ello es necesario describir y clasificar a las especies, lo cual tradicionalmente se ha hecho mediante el uso de caracteres morfológicos desde el trabajo de Linnaeus (1758). Podemos diferenciar, diagnosticar e identificar a las especies debido a la variación morfológica presente entre ellas, pero también existe variación entre poblaciones de la misma especie, lo cual está relacionado con el surgimiento del concepto de subespecie. La subespecie puede definirse como "un agregado de poblaciones locales que habitan en una subdivisión geográfica del margen de la especie, y que difieren taxonómicamente de otras poblaciones de la especie" (Mayr y Ashlock, 1991). Esto quiere decir que el término subespecie se ha usado constantemente para reconocer la variación correlacionada con la distribución geográfica (es decir, con el objetivo de nombrar taxonómicamente variaciones geográficas). Sin embargo, la existencia de aislamiento geográfico entre poblaciones puede ocasionar, con el paso del tiempo, un aislamiento reproductivo y provocar su independencia evolutiva. Existen muchos ejemplos de especies de vertebrados que han sido descritas como subespecies basados en diferencias morfológicas mínimas y que ahora se reconocen como especies (p.ej., Feria-Ortiz, Manríquez-Morán y Nieto-Montes de Oca, 2011; Bryson et al., 2014; Meza-Lázaro y Nieto-Montes de Oca, 2015; Nieto-Montes de Oca et al., 2016).

La investigación de los límites entre las especies ha cobrado tal importancia que ahora es uno de los campos principales en la sistemática moderna (Sites y Marshall, 2003; Wiens, 2007). La aceptación generalizada de que las características empleadas por los diferentes criterios para delimitar a las especies aparecen de manera gradual e independiente en la

diversificación de los linajes (de Queiroz, 2007; Knowles y Carstens, 2007; Raxworthy et al., 2007; Rissler y Apodaca, 2007; Wiens, 2007; Wiens y Penkrot, 2002) ha permitido que se propongan diferentes metodologías para delimitar especies usando datos ecológicos (Raxworthy et al., 2007; Rissler y Apodaca, 2007), morfológicos (Zapata y Jiménez, 2012) o moleculares (Wiens y Penkrot, 2002; Pons et al., 2006; Fujita et al., 2012; Grummer et al., 2014; Yang y Rannala, 2014), entre otros. Debido a que las propiedades de las especies, o criterios secundarios, surgen en diferentes momentos durante el proceso de especiación (de Queiroz, 2007; Padial et al., 2010) puede esperarse que los análisis independientes de cada tipo de datos arrojen resultados que no concuerden entre sí y, por lo tanto, el combinar todas las fuentes de información en un solo análisis sea poco conveniente. La "taxonomía integradora" propone dos grandes enfoques para lidiar con la problemática anterior: el de congruencia y el de acumulación. (Padial et al., 2010). Mientras que el enfoque de congruencia apuesta por afirmar que una especie es válida solo cuando diferentes líneas de evidencia seleccionadas a priori lo sugieren; el enfoque de acumulación propone evaluar las concordancias y discordancias desde una perspectiva evolutiva, de manera que la decisión se toma con base en toda la información disponible y el reconocimiento de una especie podría hacerse incluso con solo un tipo de caracteres, siempre y cuando se considere que es un buen indicativo de la divergencia (Padial et al., 2010).

Como se mencionó al final del primer párrafo de esta introducción, los datos moleculares han ayudado a esclarecer relaciones filogenéticas que los datos morfológicos recuperan como ambiguas. Las secuencias de DNA mitocondrial (mtDNA) han sido probablemente los datos moleculares más empleados para inferir relaciones filogenéticas o delimitar especies. Sus características (ausencia de recombinación, modo de herencia materna, tasa de mutación alta y un tamaño de población efectivo pequeño) lo hacen más útil para el estudio de taxones estrechamente emparentados (Funk y Omland, 2003). En el presente trabajo se utilizó un fragmento de mtDNA (parte del gen ND4 y los genes adyacentes $tRNA^{His}$, $tRNA^{Ser}$ y parte de $tRNA^{Leu}$) para investigar las relaciones filogenéticas entre y dentro de los géneros *Abronia* y *Mesaspis* e inferir límites de especies implementando el método de Wiens y Penkrot (2002) de delimitación de especies mediante filogenias de mtDNA. Este método consiste en obtener una filogenia de haplotipos de mtDNA de individuos con localidad conocida y asignados a la especie de estudio o especie focal. Para

evaluar si existe evidencia de flujo genético entre las poblaciones, es necesario incluir haplotipos de dos o más individuos por localidad, mientras que para evaluar la exclusividad de la especie focal se debe incluir haplotipos de tantas especies cercanamente relacionadas con ella como sea posible. En el caso de que los haplotipos de una localidad o de una población no aparezcan todos en el mismo clado, se infiere que existe flujo genético con otra(s) población(es), y en el caso de existir flujo entre linajes basales (es decir, las ramificaciones más antiguas dentro de la especie), se asume que se trata de una sola especie; pero si los haplotipos de la especie focal son exclusivos, con linajes basales fuertemente apoyados y congruentes con la geografía, se toma como evidencia potencial de la existencia de varias especies no reconocidas por la taxonomía previa. También se puede dar el caso de que los haplotipos de la especie focal aparezcan agrupados con haplotipos de las especies cercanamente relacionadas, lo cual puede indicar el reconocimiento de varias especies cuyos límites no habían sido detectados por la taxonomía previa o bien, la presencia de una sola especie con distribución geográfica amplia.

Sin embargo, hacer inferencias únicamente con datos de mtDNA es poco conveniente. Su modo de herencia es materno y por lo tanto sólo refleja los patrones de dispersión y flujo genético de las hembras, de tal manera que las inferencias que pudiéramos hacer carecerían de información relacionada con los patrones de dispersión de los machos (Moore, 1995), y los patrones de dispersión pueden ser muy diferentes entre ambos sexos (Li y Kokko, 2019). Además, la molécula del mtDNA se hereda completa y carece de recombinación, es decir que todos los genes se hereden como un grupo ligado, lo cual hace que eventos como la retención de polimorfismos ancestrales o el flujo génico entre especies afecten a todos los genes del mtDNA y, por lo tanto, el árbol mitocondrial demuestre un patrón diferente al árbol de las especies. Como ya se mencionó anteriormente, la tasa de sustitución del mtDNA es muy diferente con respecto a la que tienen los genes nucleares y, por lo tanto, los patrones de ramificación de los genes nucleares también serán diferentes (Maddison, 1997). Sin embargo, el análisis de varios genes puede lograr que la topología resultante sea un reflejo más fidedigno de la historia evolutiva (Maddison y Knowles, 2006). Con esto en mente, y con el objetivo de obtener una filogenia más robusta, se incluyeron tres genes nucleares (BMP2, KIAA-1212, PRLR).

ANTECEDENTES

Los géneros *Abronia* Gray, 1838 y *Mesaspis* Cope, 1878

Entre todas las especies de lagartijas que habitan en México, sólo algunas de ellas son consideradas venenosas. El nombre escorpión usualmente se emplea para las lagartijas del género *Heloderma*, pero también se utiliza para las especies del género *Lepidophyma* y algunas especies de gerrhonotinos (Anguidae) entre los cuales se encuentran las de los géneros *Abronia* y *Mesaspis* (Campbell y Lamar, 2004).

Las lagartijas del género *Abronia* tienen hábitos arborícolas, aunque ocasionalmente pueden encontrarse en el suelo o sobre arbustos pequeños. Algunas de ellas poseen coloraciones muy llamativas, aunque la mayoría tienen coloraciones crípticas (Campbell y Frost, 1993; Clause et al., 2016a). Pueden distinguirse de los demás gerrhonotinos por la siguiente combinación de características: (1) ausencia de la quinta hilera de escamas temporales; (2) extremidades largas y con garras bien definidas; y (3) pliegue lateral reducido, particularmente entre la extremidad anterior y el tímpano (Campbell y Frost, 1993). El género se distribuye desde el sur de Tamaulipas y Michoacán en México, hacia el sur y el este hasta Honduras y El Salvador (Campbell y Frost, 1993; Centenero-Alcalá et al., 2009). Habitan principalmente en bosques de pino-encino y bosque mesófilo de montaña, entre los 1,500 y los 2,800 metros sobre el nivel del mar, aunque especies como *A. bogerti*, *A. chiszari* y *A. ramirezi* se encuentran en elevaciones entre los 660 y los 1,540 metros (Campbell y Frost, 1993; Clause et al., 2016b).

Las lagartijas del género *Mesaspis* tienen hábitos terrestres. Pueden distinguirse de los demás gerrhonotinos por la siguiente combinación de características: (1) reducción del pliegue lateral; (2) presencia de ocho hileras longitudinales de escamas ventrales a la altura de las extremidades anteriores; (3) escamas subgranulares en los extremos de los costados (Good, 1988; Solano-Zavaleta, 2011). El género se distribuye desde Veracruz (a la altura del Pico de Orizaba) y Guerrero, México, hasta el norte de Panamá (Good, 1988; Solano-Zavaleta, 2011). Habitan principalmente en bosques templados, entre los que destacan el bosque de pino-encino y bosque mesófilo de montaña, usualmente entre los 1,500 y los 3,000 metros sobre el nivel del mar.

Breve historia taxonómica de los géneros *Abronia* y *Mesaspis*

El primer género propuesto para las lagartijas de la subfamilia Gerrhonotinae fue *Gerrhonotus.* En este género se incluía, entre otras especies, a *G. deppii y G. taeniata* (Wiegmann, 1828). Una década después, Gray (1838) dividió a *Gerrhonotus* (sensu Wiegmann) en cuatro géneros: *Abronia*, *Barisia*, *Elgaria* y *Gerrhonotus*, donde *Abronia* incluiría a las especies *A. deppii* y *A. taeniata.* Posteriormente, Fitzinger (1843) reasignó a las especies *A. deppii* y *A. taeniata* a los géneros *Leiogerrhonotus* y *Aspidosoma*, respectivamente. Esta propuesta fue ignorada por los demás especialistas con la excepción de Agassiz (1848), quien los incluyó en su trabajo y utilizó los nombres abreviados y los degeneró en *Liogerrhon* y *Tropidogerrhum* (Tihen, 1949a).

Los géneros propuestos por Gray (1838), incluyendo *Abronia*, fueron reconocidos por algunos autores e ignorados por otros. Sin embargo, no hubo modificaciones en los géneros de gerrhonotinos hasta que Cope (1877) propuso cuatro géneros para clasificar a los gerrhonotinos: *Pterogasterus*, *Gerrhonotus*, *Barissia* y *Mesaspis.* El género *Mesaspis* incluía a las especies *M. moreletii* y *M. fulvus* que habían sido descritas por Bocourt (1872) como *G. moreletii* y *G. fulvus*. La clasificación de Cope (1878) demostró ser poco consistente, por lo que pocos hicieron caso de ella y agruparon a las especies de gerrhonotinos tanto en *Gerrhonotus* como en *Barisia* (p.ej., Cope, 1900; Smith, 1942; Tihen, 1949a, 1949b; Stebbins, 1958; Waddick y Smith, 1974; Rieppel, 1980).

En el trabajo de Tihen (1949a), el autor retomó el género *Abronia* e incluyó diez "formas" en el mismo: *A. aurita*, *A. deppii*, *A. fimbriata*, *A. fuscolabialis*, *A. matudai*, *A. oaxacae*, *A. ochoterenai*, *A. taeniata taeniata*, *A. taeniata graminea*, y *A. vasconcelosii*. Por otra parte, dentro del género *Barisia* incluyó, entre otras "formas", a *B. antauges*, *B. gadovii*, *B. modesta*, *B. monticola*, *B. moreletii moreletii*, *B. m. fulva*, *B. m. rafaeli*, *B. m. salvadorensis*, *B. m. temporalis* y *B. viridiflava* (Tihen, 1949a, 1949b).

Pocos años después Tihen (1954) describió la especie *A. bogerti* y propondría dividir al género en dos grupos: el grupo *deppii*, que incluía a las especies *A. bogerti*, *A. deppii*, *A. fuscolabialis*, *A. graminea*, *A. oaxacae* y *A. taeniata*, y el grupo *aurita*, con las especies *A. aurita*, *A. fimbriata*, *A. matudai*, *A. ochoterenai* y *A. vasconcelosii.* Los autores siguientes adoptarían la propuesta taxonómica de Tihen (1949a, 1954), describiendo dentro del género

Abronia a las especies *A. chiszari*, *A. lythrochila*, *A. mitchelli*, *A. mixteca*, *A. montecristoi*, *A. reidi* y *A. salvadorensis* (Werler y Shannon, 1961; Smith y Álvarez del Toro, 1963; Bogert y Porter, 1967; Smith y Smith, 1981; Campbell, 1982, 1984; Hidalgo, 1983; Good y Schwenk, 1985).

Actualmente, la clasificación de la subfamilia Gerrhonotinae se basa en el trabajo de Good (1988), quien realizó una revisión taxonómica para las especies de este grupo e infirió las relaciones filogenéticas entre sus géneros mediante un análisis de caracteres morfológicos externos, y concluyó que los géneros *Abronia* y *Mesaspis* (reconocido por primera vez desde su erección) son grupos hermanos (Fig. 1).

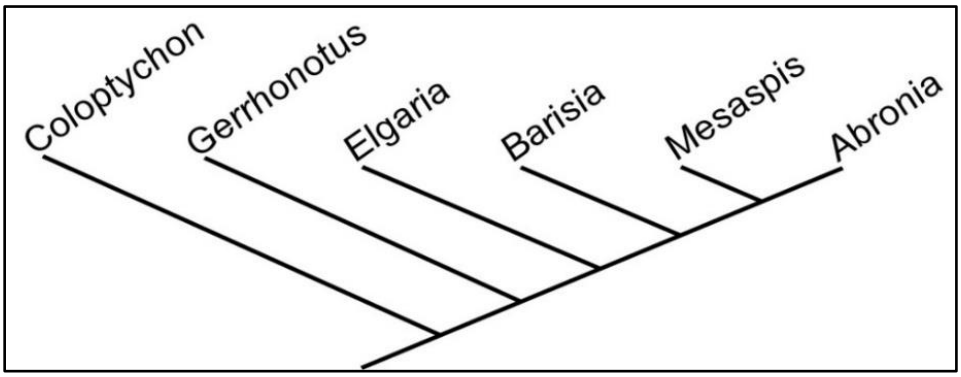

Figura 1. Relaciones filogenéticas entre los géneros de la subfamilia Gerrhonotinae con base en su morfología externa. Tomado de Good (1988).

En el mismo trabajo, Good (1988) propuso dividir al género *Abronia* en cuatro grupos (Fig. 2, Tabla 1): el grupo *mitchelli*, con *A. mitchelli*; el grupo *reidi*, que incluía *A. ornelasi* y *A. reidi*; el grupo *aurita*, con *A. aurita*, *A. lythrochila*, *A. matudai*, *A. montecristoi*, *A. ochoterenai*, *A. salvadorensis* y *A. vasconcelosii*; y finalmente al grupo *deppii*, que incluía a las especies *A. bogerti*, *A. chiszari*, *A. deppii*, *A. fuscolabialis*, *A. graminea*, *A. kalaina*, *A. mixteca*, *A. oaxacae* y *A. taeniata*.

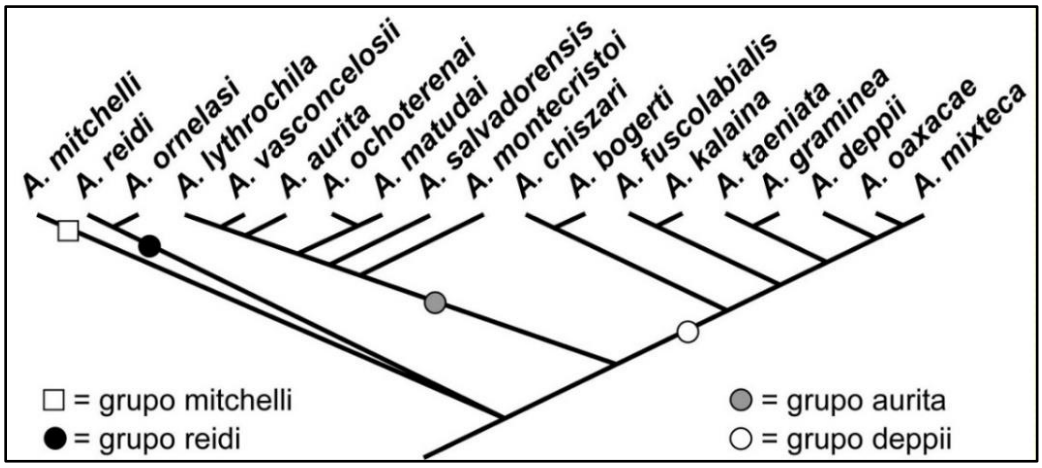

Figura 2. Relaciones filogenéticas entre las especies del género *Abronia* con base en su morfología externa. Modificado de Good (1988).

En el estudio de Good (1988), *Mesaspis* fue dividido en tres grupos (Fig. 3): el grupo *gadovii*, compuesto por *M. gadovii*; el grupo *antauges*, el cual incluye a *M. antauges* y *M. juarezi*; y el grupo *moreletii*, compuesto por *M. monticola, M. moreletii*, y *M. viridiflava*.

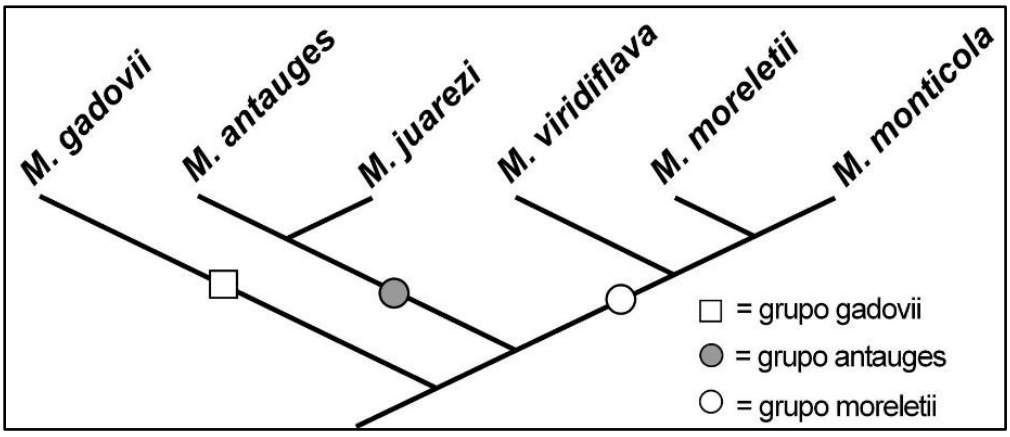

Figura 3. Relaciones filogenéticas entre las especies del género *Mesaspis* con base en su morfología externa. Modificado de Good (1988).

Posteriormente, Campbell y Frost (1993) realizaron un extenso trabajo con el género *Abronia*, en el cual se incluyó la descripción de cuatro especies nuevas, un análisis filogenético empleando datos morfológicos y una clave taxonómica, además de abordar temas de historia natural y conservación. Es importante mencionar que Campbell y Frost (1993) propusieron seis subgéneros para agrupar taxonómicamente a las especies:

Abaculabronia, *Abronia*, *Aenigmabronia*, *Auriculabronia*, *Lissabronia* y *Scopaeabronia* (Cuadro 1).

A pesar de las diferencias entre los datos y los métodos empleados por los distintos autores, la disponibilidad de ejemplares y/o especies, así como las diferencias entre las hipótesis filogenéticas, existen ciertas semejanzas entre los grupos propuestos por Good (1988) y Campbell y Frost (1993). Ambas hipótesis asignan a la especie *A. mitchelli* a un grupo exclusivo (grupo *mitchelli* de Good [1988] y subgénero *Aenigmabronia* de Campbell y Frost [1993]). El grupo *reidi* de Good (1988) agrupa a las especies *A. ornelasi* y *A. reidi*, que junto con *A. montecristoi* forman el subgénero *Abaculabronia* de Campbell y Frost (1993). El grupo *aurita* de Good (1988) podría ser un grupo equivalente al subgénero *Auriculabronia* de Campbell y Frost (1993); sin embargo, Good (1988) incluyó en este grupo a los taxones *A. montecristoi* y *A. salvadorensis*, mientras que Campbell y Frost (1993) ubicaron a estas especies en otros subgéneros. Por otra parte, *A. chiszari* y *A. bogerti* formaban un subgrupo dentro del grupo *deppii* de Good (1988), mientras que están en el subgénero *Scopaeabronia* de Campbell y Frost (1993); las demás especies que formaban el grupo *deppii* de Good (1988) aparecen dentro del subgénero *Abronia* de Campbell y Frost (1993).

Cuadro 1. Taxones reconocidos dentro de los géneros *Abronia* y *Mesaspis*. Se incluye su distribución altitudinal y geográfica, así como su pertenencia a los grupos propuestos por Good (1988) y Campbell y Frost (1993).

Taxón	Distribución	Elevación (msnm)	Grupo (Good, 1988)	Subgénero (Campbell y Frost, 1993)	Referencias
A. ornelasi Campbell, 1984	Cerro Baúl, en Chiapas y Oaxaca, México	1,500 – 1,600	*reidi*	*Abaculabronia*	(Campbell, 1984; Thesing et al., 2017)
A. reidi Werler & Shannon, 1961	Los Tuxtlas, Veracruz, México	1,000 – 1,635	*reidi*	*Abaculabronia*	(Thesing et al., 2017)
A. cuetzpali Campbell, Solano-Zavaleta, Flores-Villela, Caviedes-Solis & Frost, 2016	SMS, Oaxaca, México	1,711 – 2,150	*deppii*[#]	*Abronia*[#]	(Campbell et al., 2016)
A. deppii (Wiegmann, 1828)	FVT, en Guerrero, Michoacán, Morelos y Estado de México	1,850 – 2,600	*deppii** *(A. martindelcampoi*[+]*)*[#]	*Abronia*	(Centenero-Alcalá et al., 2009; Flores-Villela y Sánchez-H, 2003)
A. fuscolabialis (Tihen, 1944)	Sierra Mixe y Sierra de Juárez, Oaxaca, México	1,992 – 2,438	*deppii*	*Abronia*	(Campbell y Frost, 1993; Good y Schwenk, 1985)
A. graminea (Cope, 1864)	Porción Este de la SMO y la FVT, en Puebla, Veracruz y Oaxaca, México	1,170 – 2,740	*deppii*	*Abronia*	(Campbell y Frost, 1993; Clause et al., 2018; Schmidt-Ballardo, 1991)
A. martindelcampoi Flores-Villela & Sánchez-H., 2003	SMS, Guerrero, México	2,100 – 2,600	*deppii*[#] (*A. deppii**)	*Abronia*	(Flores-Villela y Sánchez-H, 2003)
A. mixteca Bogert & Porter, 1967	SMS, región de la Mixteca Alta, Oaxaca, México	2,134 – 2,780	*deppii*	*Abronia*	(Canseco-Márquez et al., 2007; Martín-Regalado et al., 2012)
A. oaxacae (Günther, 1885)	SMS, zona central de Oaxaca, México.	2,100 – 2,743	*deppii*	*Abronia*	(Campbell, 2007a)

A. taeniata (Wiegmann, 1828)	Porción este de la SMO y la FVT, en Tamaulipas, Querétaro, Hidalgo, Veracruz y Puebla	1,000 – 3,000	*deppii*	*Abronia*	(Hudson et al., 2001; Martin, 1958; Stephenson et al., 2008)
A. mitchelli Campbell, 1982	Cara norte de la Sierra de Juárez, Oaxaca, México	Cerca de los 2,750	*mitchelli*	*Aenigmabronia*	(Campbell, 1982)
A. anzuetoi Campbell & Frost, 1993	Volcán de Agua, Departamento de Escuintla, Guatemala	1,219 – 2,286	*aurita*[#] (*A. vasconcelosii**)	*Auriculabronia*	(Campbell y Frost, 1993)
A. aurita (Cope, 1869)	"vast forest of Vera Paz, in the neighborhood of the ancient cities of Peten and Coban", Guatemala	Desconocida	*aurita** (*A. gaiophantasma*[+])[#]	*Auriculabronia*	(Campbell y Brodie, 1999)
A. campbelli Brodie & Savage, 1993	Cerro Tablón de las Minas, Departamento de Jalapa, Eastern Guatemala	1,800 – 1,900	*aurita* [#]	*Auriculabronia*[#]	(Brodie y Savage, 1993)
A. fimbriata (Cope, 1884)	Sierra de Xucaneb y Sierra de las Minas, Departamento de Alta Verapaz, y en la Sierra de Chuacús, Departamento de Baja Verapaz, centro-este de Guatemala	1,400 – 2,100	*aurita* [#]	*Auriculabronia*	(Acevedo et al., 2014; Campbell y Frost, 1993)
A. gaiophantasma Campbell & Frost, 1993	Montañas de los Departamentos de Alta Verapaz y Baja Verapaz, centro de Guatemala	1,600 – 2,400	*aurita*[#] (*A. aurita**)	*Auriculabronia*	(Campbell y Frost, 1993; Eisermann y Acevedo, 2016; Franzen y Haft, 1999)
A. leurolepis Campbell & Frost, 1993	Localidad tipo "Santa Rosa, cerca de Comitán, Chiapas, México"	Probablemente entre 1,800 – 2,300	*aurita*[#]	*Auriculabronia*	(Campbell y Frost, 1993; Townsend Peterson y Nieto-Montes de Oca, 1996)
A. lythrochila Smith & Álvarez del Toro, 1963	MCC, México	1,500 – 3,000	*aurita*	*Auriculabronia*	(Campbell y Muñoz-Alonso, 2007a)

A. matudai (Hartweg & Tihen, 1946)	Volcán Tacaná, Chiapas, México, y los Departamentos de San Marcos y Quetzaltenango, Guatemala	1,950 – 2,630	*aurita*	*Auriculabronia*	(Campbell y Muñoz-Alonso, 2013)
A. meledona Campbell & Brodie, 1999	Entre Mataquescuintla y Jalapa, Departamento de Jalapa, Guatemala	2,200 – 2,660	*aurita*[#]	*Auriculabronia*[#]	(Campbell y Brodie, 1999)
A. ochoterenai (Martin del Campo, 1939)	Localidad tipo "Santa Rosa, cerca de Comitán, Chiapas, México"	Probablemente entre 1,800 – 2,300	*aurita** (*A. smithi*[+])[#]	*Auriculabronia*	(Campbell y Frost, 1993; Townsend Peterson y Nieto-Montes de Oca, 1996)
A. smithi Campbell & Frost, 1993	SMC, Chiapas, México	1,800 – 2,800	*aurita*[#] (*A. ochoterenai**)	*Auriculabronia*	(Campbell y Muñoz-Alonso, 2007b)
A. vasconcelosii (Bocourt, 1871)	Departamentos de Quiché y Suchitepéquez, Guatemala	2,000 – 2,200	*aurita*	*Auriculabronia*	(Campbell y Brodie, 1999; Köhler, 2003)
A. frosti Campbell, Sasa, Acevedo & Mendelson, 1998	Sierra de Los Cuchumatanes, Departamento de Huehuetenango, Guatemala	2,800 – 3,013	*aurita*[#]	*Lissabronia*[#]	(Ariano-Sánchez, 2010; Ariano-Sánchez et al., 2011; Campbell et al., 1998)
A. salvadorensis Hidalgo, 1983	Sierra de Montecillos y Sierra de Opalaca, Honduras	1,900 – 2,250	*aurita*	*Lissabronia*	(Köhler, 2003)
A. montecristoi Hidalgo, 1983	Quebrada Grande, Honduras, y Parque Nacional Montecristo en la frontera entre Guatemala, Honduras y El Salvador	1,370 – 2,250	*aurita*	*Lissabronia*	(Köhler, 2003)
A. bogerti Tihen, 1954	Tierras altas de los Chimalapas (norte de Niltepec, entre Cerro Atravesado y Sierra Madre), Oaxaca, and Cerro Baúl, Chiapas, México	760 – 1,540	*deppii*	*Scopaeabronia*	(Bille, 2001; Clause et al., 2016b)

A. chiszari Smith & Smith, 1981	Los Tuxtlas, Veracruz, México	660 – 800	*deppii*	*Scopaeabronia*	(Flores-Villela y Vogt, 1992; Pérez-Higareda et al., 2002)
A. ramirezi Campbell, 1994	SMC, Chiapas, México	Probablemente entre los 800 – 1,350	*deppii*[#]	*Scopaeabronia*	(Campbell, 1994; Campbell y Muñoz-Alonso, 2007c)
M. antauges (Cope, 1866)	Pico de Orizaba, Veracruz, México	2,200 – 2,700	*antauges*	NI	(Solano-Zavaleta et al., 2017)
M. cuchumatanus Solano-Zavaleta, Nieto-Montes de Oca & Campbell, 2016	Sierra de Los Cuchumatanes y una población aislada en Cumbre del Papal, oeste de Guatemala	2,475 – 3,260	*moreletii*[#]	NI	(Solano-Zavaleta et al., 2016)
M. gadovii (Boulenger, 1913)	SMS, entre Nueva Delhi, Guerrero, and San Pablo Cuatro Venados, Oaxaca, México	2,030 – 3,191	*gadovii*	NI	(Karges y Wright, 1987)
M. juarezi (Karges & Wright, 1987)	Sierra de Juárez y Cuicatlán, Oaxaca, México	2,000 – 2,805	*antauges*	NI	(Canseco-Márquez y Gutiérrez-Mayén, 2010; Karges y Wright, 1987)
M. monticola (Cope, 1878)	Montañas de Costa Rica y oeste de Panamá	1,800 – 3,800	*moreletii*	NI	(Acosta Chaves et al., 2013)
M. m. fulvus (Bocourt, 1871)	Oeste de Guatemala	1,305 – 3,060	*moreletii*	NI	(Ariano-Sánchez et al., 2013; Tihen, 1949a)
M. m. moreletii (Bocourt, 1871)	Alta Verapaz, Guatemala, hacia el oeste, posiblemente hasta Los Cuchumatanes, y al sur hasta Honduras	1,305 – 3,060	*moreletii*	NI	(Ariano-Sánchez et al., 2013; Tihen, 1949a)
M. m. rafaeli (Hartweg & Tihen, 1946)	SMC, Chiapas, México, hasta el Volcán Tajumulco, Guatemala	1,305 – 3,060	*moreletii*	NI	(Ariano-Sánchez et al., 2013; Tihen, 1949a)
M. salvadorensis (Hartweg & Tihen, 1946)	Honduras y El Salvador, hasta Matagalpa, Nicaragua	1,305 – 3,060	*moreletii*	NI	(Ariano-Sánchez et al., 2013; Tihen, 1949a)

M. temporalis (Hartweg & Tihen, 1946)	MCC, Chiapas, México	1,305 – 3,060	*moreletii*	NI	(Ariano-Sánchez et al., 2013; Tihen, 1949a)
M. viridiflava (Bocourt, 1873)	Sierra Mixe and Sierra de Juárez, Oaxaca, México	2,268 – 3,160	*moreletii*	NI	(Campbell, 2007b)

Donde: FVT = Faja Volcánica Transmexicana, MCC = Meseta Central de Chiapas, SMC = Sierra Madre de Chiapas, SMO = Sierra Madre Oriental, SMS =Sierra Madre del Sur, NI = No incluido, * = asignado erróneamente por Good (1988), + = taxón al cual los ejemplares revisados por Good (1988) están asignados actualmente, # = asignado posteriormente y con base en las sinapomorfías propuestas.

Los géneros *Abronia* y *Mesaspis* en filogenias moleculares

La primera filogenia molecular del género *Abronia* fue obtenida por Chippindale et al. (1998), aunque estuvo enfocada en el subgénero *Auriculabronia*. En dicho trabajo se hicieron análisis con diferentes combinaciones de datos, obteniendo un árbol por cada gen y un árbol del análisis combinado de datos morfológicos y moleculares. Además, se empleó una secuencia de *Mesaspis gadovii*, cuya posición resultó incierta y que en la mayoría de sus árboles aparecía como especie hermana de *Barisia imbricata*.

Varios estudios posteriores (Macey et al., 1999; Wiens y Slingluff, 2001; Conroy et al., 2005; Zaldivar-Riverón et al., 2005) apoyan las relaciones propuestas por Good (1988), empezando por la monofilia de Gerrhonotinae. En dichos trabajos, los géneros *Barisia*, *Gerrhonotus* y *Elgaria* se recuperaron como monofiléticos (Macey et al., 1999; Wiens y Slingluff, 2001; Conroy et al., 2005; Zaldivar-Riverón et al., 2005), pero en ninguno de ellos se incluyó más de una especie de *Mesaspis* ni más de dos especies de *Abronia*. Por lo tanto, la monofilia de los géneros *Abronia* y *Mesaspis* aún no se había puesto a prueba de manera rigurosa.

Un trabajo cuyo objetivo fue proponer una hipótesis filogenética robusta del género *Mesaspis* e incluía todas las especies de *Mesaspis*, excepto *M. antauges*, y 12 especies de *Abronia*, encontró que *Abronia* y *Mesaspis* no son mutuamente monofiléticos (Solano-Zavaleta, 2011). Sin embargo, dicho trabajo se basó sólo en un gen mitocondrial, por lo que las relaciones propuestas podían ser consecuencia de la introgresión, duplicación de genes, y/o el sorteo incompleto de linajes; fenómenos que pueden causar una incorrecta estimación de la filogenia (Edwards, 2009; Fujita et al., 2012; Rosenberg, 2013).

Recientemente, Pyron et al. (2013) propusieron una hipótesis filogenética mediante el uso de siete genes nucleares y cinco mitocondriales, y en la cual incluyeron 12 especies de *Abronia* y dos de *Mesaspis*. En este trabajo también se puede apreciar que *Abronia* y *Mesaspis* podrían no ser mutuamente monofiléticos, pero algunas de las relaciones no están fuertemente apoyadas y algunos terminales no tienen datos de todos los genes.

JUSTIFICACIÓN

Las filogenias moleculares previas (Solano-Zavaleta, 2011; Pyron et al., 2013) sugieren que los géneros *Abronia* y *Mesaspis* no son monofiléticos. Este trabajo busca obtener una hipótesis filogenética robusta empleando datos multilocus consistentes en un fragmento de mtDNA (parte del gen ND4 y los genes adyacentes $tRNA^{His}$, $tRNA^{Ser}$ y parte de $tRNA^{Leu}$) y tres marcadores nucleares (BMP2, KIAA-1217, PRLR), e incluyendo el mayor número de especies posibles, para investigar las relaciones filogenéticas de los géneros *Abronia* y *Mesaspis* y poner a prueba su monofilia. Además, se empleará el mismo set de datos para investigar los límites de especies en taxones selectos de ambos géneros.

OBJETIVO GENERAL

Investigar las relaciones filogenéticas y límites de especies dentro del clado formado por los géneros *Abronia* y *Mesaspis*.

OBJETIVOS ESPECÍFICOS

1. Reconstruir las relaciones filogenéticas del clado *Abronia* + *Mesaspis* a partir de secuencias nucleotídicas de los genes mitocondriales ND4 y tRNAs asociados ($tRNA^{His}$, $tRNA^{Ser}$ y parte de $tRNA^{Leu}$) y los genes nucleares BMP2, KIAA-1217 y PRLR.
2. Reevaluar los límites de especies dentro de taxones selectos de *Mesaspis* (*M. gadovii*, *M. moreletii*, *M. viridiflava*) y *Abronia* (*A. graminea* y *A. taeniata*).
3. Describir las especies nuevas descubiertas en este estudio.

El capítulo I aborda la delimitación de especies dentro del complejo *M. moreletii* usando datos moleculares. Primero se identificaron los linajes evolutivos potencialmente independientes utilizando el método de Wiens y Penkrot (2002), y después se evaluaron los límites de especies hipotetizados utilizando datos multilocus (ver arriba) y distintas metodologías propuestas por Grummer et al. (2014) y Yang (2015).

En el capítulo II se describen dos especies nuevas: *A. cuetzpali*, de la Sierra Madre del Sur, al sur del estado de Oaxaca, México, y *M. cuchumatanus*, de la Sierra de Los Cuchumatanes, Departamento de Huehuetenango, Guatemala.

Finalmente, en el capítulo III se propone una hipótesis filogenética del clado (*Abronia* + *Mesaspis*) lo más completa posible y utilizando datos multilocus de los genes mitocondriales ND4 y tRNAs adyacentes ($tRNA^{His}$, $tRNA^{Ser}$ y parte de $tRNA^{Leu}$) y los marcadores nucleares BMP2, KIAA-1217 y PRLR. Además, se evalúan los límites de especies en *M. gadovii*, *M. viridiflava*, *A. graminea* y *A. taeniata*.

CAPÍTULO I

Species limits in the Morelet's Alligator lizard (Anguidae: Gerrhonotinae)

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Species limits in the Morelet's Alligator lizard (Anguidae: Gerrhonotinae)

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ABSTRACT

The widely distributed, Central American anguid lizard *Mesaspis moreletii* is currently recognized as a polytypic species with five subspecies (*M. m. fulvus*, *M. m. moreletii*, *M. m. rafaeli*, *M. m. salvadorensis*, *and M. m. temporalis*). We reevaluated the species limits within *Mesaspis moreletii* using DNA sequences of one mitochondrial and three nuclear genes. The multi-locus data set included samples of all of the subspecies of *M. moreletii*, the other species of *Mesaspis* in Central America (*M. cuchumatanus* and *M. monticola*), and some populations assignable to *M. moreletii* but of uncertain subspecific identity from Honduras and Nicaragua. We first used a tree-based method for delimiting species based on mtDNA data to identify potential evolutionary independent lineages, and then analized the multilocus dataset with two species delimitation methods that use the multispecies coalescent model to evaluate different competing species delimitation models: the Bayes factors species delimitation method (BFD) implemented in *BEAST, and the Bayesian Phylogenetics and Phylogeography (BP&P) method. Our results suggest that *M. m. moreletii*, *M. m. rafaeli*, *M. m. salvadorensis*, and *M. m. temporalis* represent distinct evolutionary independent lineages, and that the populations of uncertain status from Honduras and Nicaragua may represent additional undescribed species. Our results also suggest that *M. m. fulvus* is a synonym of *M. m. moreletii*. The biogeography of the Central American lineages of *Mesaspis* is discussed.

1. Introduction

There are two major goals in systematics: one is to discover and describe species, and the other one to determine the phylogenetic relationships between the species (Wiens, 2007; Wiens and Penkrot, 2002). Traditionally, species have been delimited on the basis of one or more morphological characters whose variation shows no overlap between species or, if there is some overlap, by a unique combination of characters (Wiens, 2007). In addition, subspecies have been similarly delimited in many species exhibiting geographic variation (e.g., in many species of reptiles exhibiting geographic variation in scalation and color pattern; Wiens, 2008). Nevertheless, molecular studies have revealed that many subspecies actually represent distinct species under lineage-based species concepts (Ashton and de Queiroz, 2001; Burbrink and Guiher, 2015; Feria-Ortiz et al., 2011; Glor and Laport, 2012; Kubatko et al., 2011; Meza-Lázaro and Nieto-Montes de Oca, 2015; Mulcahy et al., 2006a,b). Thus, these studies have shown that traditional, morphology-based taxonomy has been underestimating species diversity partly by hiding it in the subspecies category; that is, that considerable diversity has been classified inappropriately (Wiens, 2008).

1.1. The systematics of Mesaspis moreletii

The genus *Mesaspis* Cope, 1878 contains seven recognized species, most of which have small geographic distributions (Good, 1988; Solano-Zavaleta et al., 2016). Of these, *M. antauges*, *M. gadovii*, *M. juarezi*, and *M. viridiflava* occur in the highlands of Guerrero, Oaxaca, and Veracruz, Mexico, west of the Isthmus of Tehuantepec (Good, 1988); *M. cuchumatanus* occurs in the Sierra de los Cuchumatanes in west-central Guatemala (Solano-Zavaleta et al., 2016), and *M. monticola* is distributed on the highlands of Costa Rica and extreme western Panamá (Savage, 2002). *Mesaspis moreletii*, the most widely distributed of the species of *Mesaspis*, occurs in disjunct populations at moderately high elevations in the temperate highlands of Nuclear Central America from both the Meseta Central and the Sierra Madre of Chiapas to northern Nicaragua (Campbell and Vannini, 1989; Good, 1988; Sunyer and Köhler, 2007; Wilson and Johnson, 2010).

Geographic variation in the external morphology of *M. moreletii* has resulted in the recognition of five subspecies (Good, 1988). Tihen

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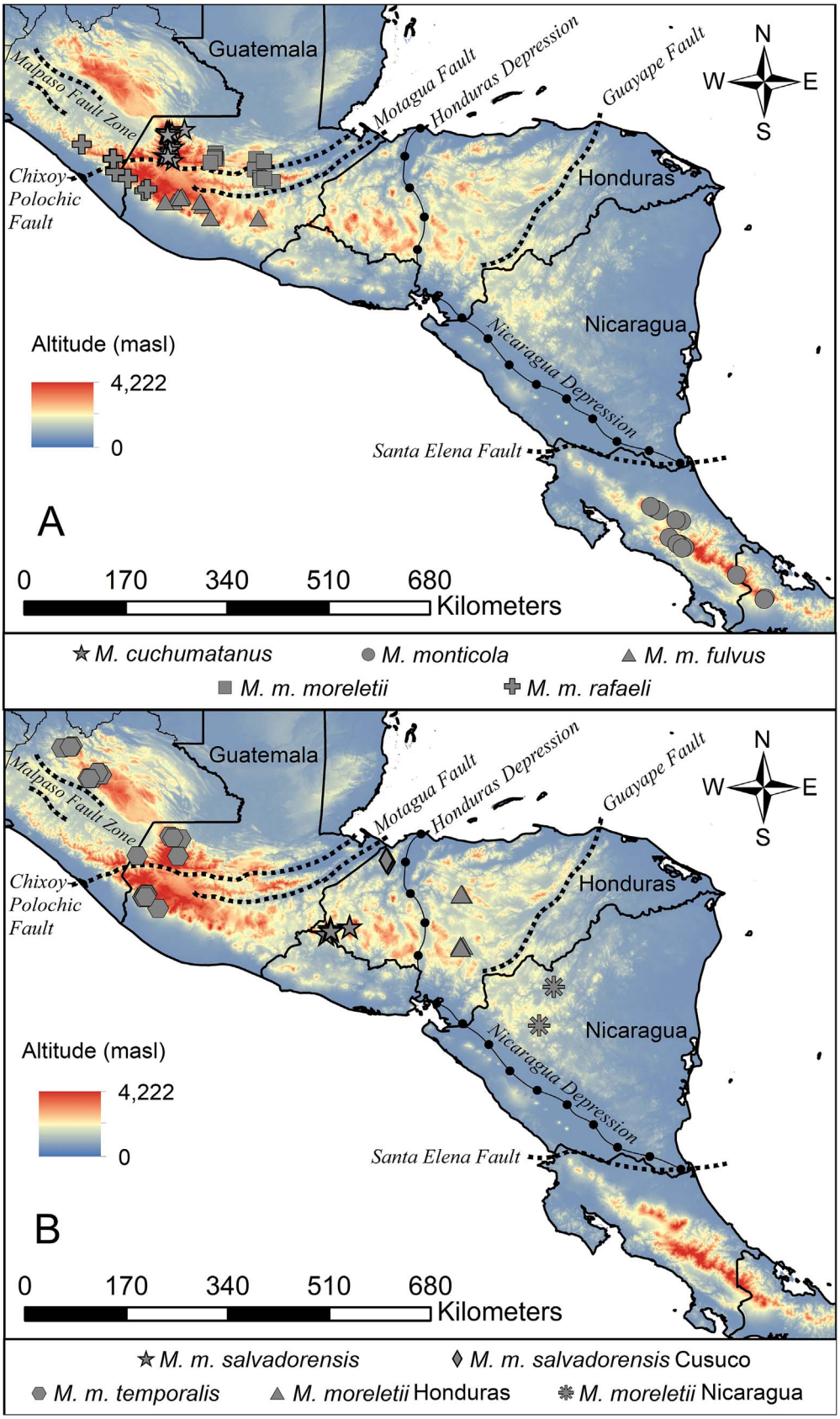

Fig. 1. Distribution records for the Central American clade of *Mesaspis*. A: *Mesaspis cuchumatanus* (stars), *M. monticola* (circles), *M. m. fulvus* (triangles), *M. m. moreletii* (squares), and *M. m. rafaeli* (crosses). B: *M. moreletii* Honduras (triangles), *M. moreletii* Nicaragua (asterisks), *M. m. salvadorensis* (stars), *M. m. salvadorensis* Cusuco (diamond), and *M. m. temporalis* (hexagons).

(1949) stated that *M. m. fulvus* occurs in "northwestern Guatemala, the limits of the range not established," and *M. m. moreletii* is distributed in "Alta Verapaz, Guatemala, westward possibly to, but not beyond, the Cuchumatanes, and southward into Honduras, where presumed intergrades with *M. m. salvadorensis* are found." *Mesaspis m. rafaeli* occurs from the Sierra Madre de Chiapas in southeastern Chiapas to Volcán Tajumulco in northwestern Guatemala (Tihen, 1949); *M. m. salvadorensis* is distributed in Honduras and El Salvador southward to

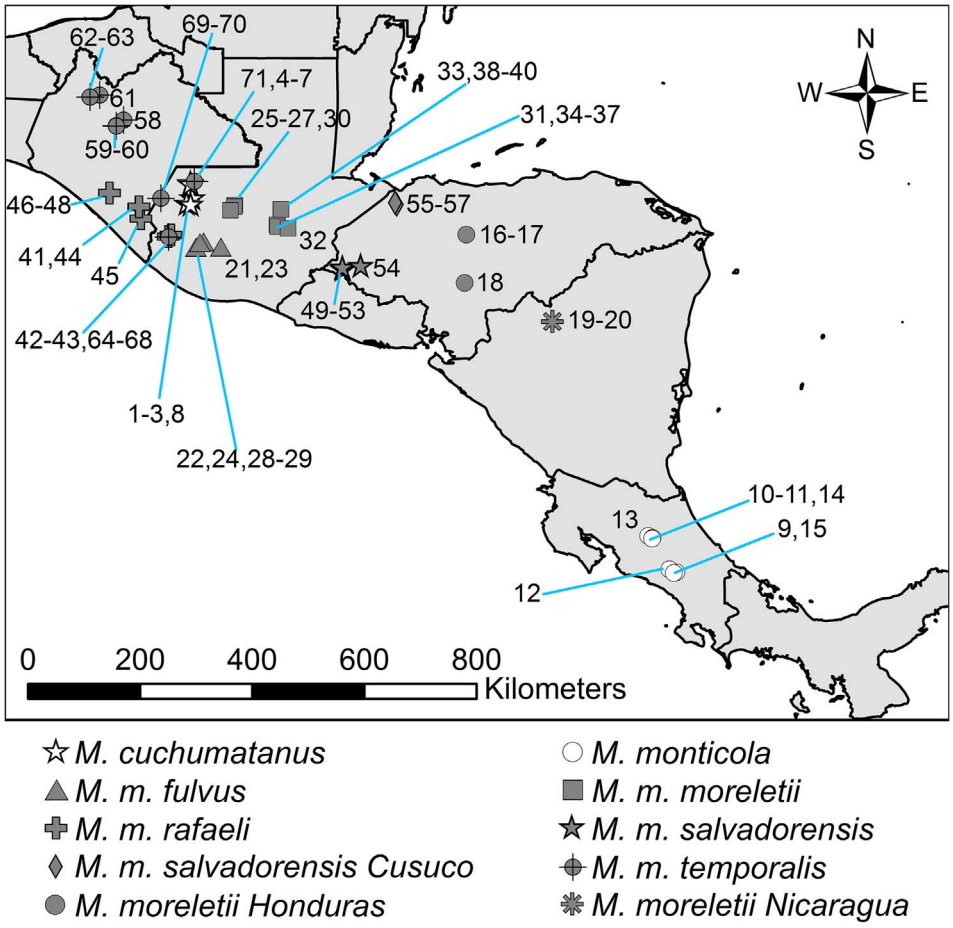

Fig. 2. Collecting localities for the Central American species of *Mesaspis*. Localities for the individual samples are given in Table S1.

Matagalpa, Nicaragua (Tihen, 1949); and *M. m. temporalis* is known only from the vicinity of San Cristóbal de las Casas in the highlands of central Chiapas (Tihen, 1949). The distributions of these subspecies, updated with locality records obtained in this study, are shown in Fig. 1.

However, because of their considerable morphological variation, the limits between these subspecies remain poorly understood (Solano-Zavaleta et al., 2016). For example, Tihen (1949:222) stated that "There is so much individual variation in this form (*M. moreletii*), and the localities from which collections of series of individuals have been made are so scattered that areas of intergradation cannot yet be definitely established. The taxonomic arrangement is therefore far from settled…," and Good (1988) stated that "all of the diagnostic characters vary widely within these subspecies; their validity is therefore questionable." Also, whether these subspecies may represent distinct evolutionary lineages has not been investigated.

Species delimitation, the process by which species boundaries are determined, has recently been a major topic (Carstens et al., 2013; Caviedes-Solis et al., 2015; Fujita et al., 2012; Wiens, 2008, 2007). One of the first methods that used molecular data to delimit species was based on the use of mtDNA phylogenies (Wiens and Penkrot, 2002). Nevertheless, gene trees are expected to deviate from the species tree under a wide variety of realistic evolutionary scenarios; for example, gene duplication, horizontal gene transfer, and incomplete lineage sorting (Edwards, 2009; Fujita et al., 2012; Rosenberg, 2013). Because incomplete lineage sorting can occur in any taxonomic group and in any gene (Edwards, 2009), it has been considered as likely the main source of inconsistency between gene trees and the species tree (Heled and Drummond, 2010). Thus, species delimitation using multi-locus DNA data has been recently based on species trees, which are estimated on the basis of the multispecies coalescent model (e.g. Burbrink et al., 2011; Burbrink and Guiher, 2015; Fujita et al., 2012; Leaché and Fujita, 2010; Pons et al., 2006; Rannala and Yang, 2003; Yang and Rannala, 2010), and it has been suggested that these species delimitation methods outperform analyses of concatenated data (Degnan and Rosenberg, 2009; but see Lambert et al., 2015; Tonini et al., 2015; Xi et al., 2015).

1.2. Biogeography of Mesaspis moreletii

Inferring the evolutionary and biogeographical history of the groups in a region is the first step to elucidate the processes by which the biota of that region originated (Colston et al., 2013). However, relatively few phylogeographical studies of lizard species with broad distributions in Central America have been published (e.g., Hasbún et al., 2005; Phillips et al., 2015). The uplift of Nuclear Central America took place approximately 10–3.8 million of years ago in the late Miocene (Rogers et al., 2002). The processes that caused this uplift acted from Chiapas and Guatemala in Nuclear Central America to Costa Rica and Panamá in the Isthmian Link (Hradecký, 2011; James, 2007; Rogers et al., 2002), causing the highlands in these areas to appear at approximately the same time. Subsequently, a chain of volcanoes (the Pacific volcanic chain) was formed along the western portion of Nuclear Central America during the late Pliocene (Williams, 1960). Thus, the Chiapas and Guatemala highlands were formed during two distinct time intervals (Campbell, 1999). Finally, the repeated expansion and contraction cycles of the coniferous forests during Pleistocene climatic fluctuations isolated many populations of forest-adapted taxa in refugia, leading to speciation (Vanzolini, 1970; Savage, 2002).

Herein, we generate a mitochondrial phylogeny for the Central American species of *Mesaspis* (*M. cuchumatanus*, *M. monticola*, and *M. moreletii*), apply the tree-based species delimitation method of Wiens

and Penkrot (2002) to this phylogeny to investigate the possible existence of multiple evolutionary independent lineages in *M. moreletii*, and apply two coalescent-based species delimitation methods to a multi-locus data set composed of one mitochondrial and three nuclear markers to evaluate the potential evolutionary independent lineages suggested by the former method. We also estimate a time-calibrated tree from the multilocus dataset to evaluate the role of the major orogenic events on lineage diversification in Central America.

2. Material and methods

2.1. Taxon sampling

We sampled broadly from the geographic distribution of *M. moreletii* in Central America, including multiple samples (8–14) from the geographical distribution of each subspecies (Fig. 2; Table S1). We were able to examine most of the vouchers of each taxon. For the subspecific designation of the sampled individuals, we followed Tihen (1949). Also, as an aid in this designation, we examined more than 300 specimens assigned to *M. moreletii* in herpetological collections for comparative purposes (Appendix). However, no genetic data were obtained from these specimens. When single individuals from particular localities could not be easily identified (e.g., female or juvenile specimens), we relied on the examination of other specimens from the same or nearby localities. It was not possible to include samples from the type-locality of each subspecies, either because the type-locality was vague (e.g., the type-locality of *M. m. moreletii*: "le Peten, ainsi que les forêsts de pins de la Haute Vera-Paz [Guatémala]"), or because no specimens were found at the type-locality (e.g., at the type-localities of *M. m. rafaeli* and *M. m. salvadorensis*). In such cases, we included all available samples from the subspecies reported distribution. We also included samples of five individuals that possess the diagnostic characters of *M. moreletii* but could not be assigned to any of its subspecies: three from central Honduras and two from northern Nicaragua (Fig. 2). We regard the taxonomic status of these populations as uncertain, and refer to them as *M. moreletii* Honduras and *M. moreletii* Nicaragua hereafter.

Because a previous phylogenetic analysis of *Mesaspis* in an unpublished M. Sc. thesis (Solano-Zavaleta, 2011) revealed that *M. moreletii* was paraphyletic with respect to *M. monticola* and an undescribed species from Guatemala (recently described as *M. cuchumatanus*; Solano-Zavaleta et al., 2016), and both of these species also are distributed in Central America, we included them in the analysis (eight individuals of *M. cuchumatanus* and seven of *M. monticola*). Finally, we included four Gerrhonotinae genera (*Gerrhonotus liocephalus*, *Barisia imbricata*, *Elgaria multicarinata*, and *Abronia lythrochila*) in the analysis as outgroups and *Celestus enneagrammus* (Diploglossinae) as a more distant outgroup to root the tree (Pyron et al., 2013).

2.1.1. Data

Because mitochondrial DNA (mtDNA) has several important properties for delimitation of newly formed species, including a low effective population size, a maternal mode of inheritance, and a high rate of mutation, among others (Funk and Omland, 2003; Moore, 1995; Wiens and Penkrot, 2002), we sequenced a mtDNA fragment including the gene encoding ND4 (part) and the adjacent genes encoding $tRNA^{His}$, $tRNA^{Ser}$, and $tRNA^{Leu}$ (part, see Arévalo et al., 1994) for all of the sampled specimens of *M. moreletii* (Table S1). This mtDNA fragment has been used previously to investigate evolutionary relationships among anguid lizards (Conroy et al., 2005; Macey et al., 1999; Wiens and Slingluff, 2001; Zaldivar-Riverón et al., 2005). Nonetheless, mtDNA gene trees may be susceptible to the effects of introgressive hybridization, female philopatry, and the development of strong geographical patterns produced by temporary isolation (Funk and Omland, 2003; Wiens and Penkrot, 2002). Thus, we also sequenced three protein-coding nuclear gene regions: BMP2 (Bone morphogenetic protein 2), KIAA1217 (Sickle tail protein), and PRLR (Prolactin receptor). In addition to the stochastic nature of the coalescent process, nuclear genes have longer coalescence times compared with mtDNA genes, thus making congruence between nuclear DNA (nDNA) and mtDNA gene trees unexpected (Moore, 1995; Wiens and Penkrot, 2002; Zink and Barrowclough, 2008). However, when such corroboration is present at least in some lineages in the phylogeny, it is evidence of probably long-term lineage isolation (Meza-Lázaro and Nieto-Montes de Oca, 2015). Because nuclear genes usually are highly conserved (Zink and Barrowclough, 2008), only representative samples of each clade of *M. moreletii* composed of all of the haplotypes from a given area in the mtDNA tree (i.e., concordant with geography) were sequenced for these markers. The localities for the individual samples sequenced are given in Table S1.

2.1.2. Laboratory protocol

Genomic DNA was extracted from tissue previously stored at −60 °C using the standard phenol-chloroform-isoamyl protocol (Hillis et al., 1996), or the extraction protocol for reptile shed skins of Fetzner (1999). All the sequenced genes were amplified via the polymerase chain reaction (PCR). The primers used to amplify and sequence these genes are given in Table S2 (see also Arévalo et al., 1994; Portik et al., 2012). Standard PCR protocols were used to amplify the mtDNA fragment and the nuclear gene KIAA1217, whereas the protocols of Townsend et al. (2008) were used to amplify the nuclear genes BMP2 and PRLR. PCR products were purified with PEG precipitation (Lis, 1980). DNA templates were sequenced with the Big Dye Terminator v.3.1 cycle sequencing kit (Applied Biosystems, Inc.). The reaction products were cleaned using Sephadex columns and sequenced with an ABI 3100 automated Genetic Analyzer Sequencer (Applied Biosystems, Inc.).

2.2. Phylogenetic analyses

Sequences were assembled and edited using Sequencher v4.1.4 (Gene Codes Corporation, Ann Arbor, MI). Sequence alignment was performed using the algorithm Muscle (Edgar, 2004) in Mega v. 6.0 (Tamura et al., 2013), and adjusted visually with Mesquite v3.31 (Maddison and Maddison, 2017). All of the sequences were deposited in GenBank (Table S3).

2.2.1. Mitochondrial data analysis

We estimated the mitochondrial phylogeny using Bayesian inference. We used PartitionFinder v2 (Guindon et al., 2010; Lanfear et al., 2016, 2012) to determine the best partition scheme and the Akaike Information Criterion (AIC) to select the best-fitting model for each partition. Models selected were GTR + I + G for a partition including codon positions 1 and 2 and the tRNAs, and TRN + G for codon position 3. We analyzed the data in MrBayes v3.2 (Ronquist et al., 2012) with two independent runs for a run length of 1×10^8 generations with four chains and the first 25 million generations (25%) discarded as burn-in, saving every 1000th tree. We determined convergence of the two runs onto the stationary distribution by verifying that the average standard deviation of split frequencies approached zero (Ronquist and Huelsenbeck, 2003). The post burn-in trees were used to build a majority consensus tree. Phylogenetic relationships were considered significantly supported if their posterior probabilities (PP) were ≥ 0.95. In addition, we estimated genetic distances within and among lineages. Comparing genetic distances within and among clades may provide a clue on the divergence level of two clades and support species hypotheses, and such comparisons have been used frequently to investigate species boundaries (e.g., Hebert et al., 2004, 2003; Lefébure et al., 2006; Zemlak et al., 2009).

2.2.2. Nuclear data analyses

To evaluate congruence between phylogenies based on mitochondrial and nuclear genes, we estimated the phylogenies for both the

independent and concatenated nuclear genes using Bayesian inference. The best-fitting nucleotide substitution model for each gene was determined with the AIC in jModelTest v2.1.4 (Darriba et al., 2012). Selected models were K80 + I, HKY + G, and HKY for BMP2, KIAA1217, and PRLR, respectively. Ambiguities were treated as missing data and two independent runs were conducted in MrBayes v3.2 (Ronquist et al., 2012) for a length of 1×10^8 generations with four chains and the first 25 million generations (25%) discarded as burn-in, saving every 1000th tree. The same procedure and nucleotide substitution models were employed for both the independent and concatenated gene analyses.

2.2.3. Coalescent-based species tree inference analyses

We estimated species trees using the coalescent-based species tree inference program *BEAST v.1.8.1 (Heled and Drummond, 2010). All nuclear sequences were examined by eye and heterozygous individuals were identified as having two alleles of the same length containing nucleotide substitutions. Gene sequences for heterozygous individuals were phased using PHASE v2.1.1 (Stephens et al., 2001; Stephens and Donnelly, 2003). Input files were prepared using the online tool seqPHASE (Flot, 2010). PHASE outputs were converted back to sequence alignments using SeqPHASE. We used TOPALI v2.5 (Milne et al., 2009, 2004) to test for recombination in the nuclear sequences using the Difference in Sums Square test (McGuire and Wright, 2000). No evidence of recombination was found. Data were partitioned using the same partition scheme for the mtDNA as above and nucleotide substitution models for the nuclear genes (GTR for BMP2, HKY + G for both KIAA1217 and PRLR) were determined as described above for the nuclear genes. All analyses in *BEAST were performed under an uncorrelated lognormal relaxed molecular clock for each locus where the mean clock rate of 1.0 was fixed for the gene ND4 and rates for the other loci were estimated relative to this gene. The tree prior was set to the Yule process while the population size model was set to Piecewise Linear and Constant Root; all other parameters not mentioned were given the same (default) priors across all analyses. For each competing species delimitation model, we ran three replicates using different random starting trees. Analyses were run for 2×10^8 generations with the first 40 million generations (20%) discarded as burn-in, saving every 20,000th tree, and the post-burn-in portion of the posterior distribution from each replicate run was combined using LogCombiner v1.8.1 (Drummond and Rambaut, 2007). We used Tracer v1.6.0 to determine whether the analyses had converged onto similar posterior distributions. Species trees were produced from the combined files of the three replicate runs using TreeAnnotator (Drummond and Rambaut, 2007), where we used the median node heights to construct the maximum clade credibility tree with a minimum clade credibility value of 0.5.

2.3. Species delimitation

There is general agreement that species are independent evolutionary lineages (e.g., de Queiroz, 2007; Raxworthy et al., 2007; Wiens, 2007; Wiley and Lieberman, 2011). Herein, we follow this generalized lineage species concept.

To reevaluate the species limits in *M. moreletii*, we first used the tree-based method for delimiting species based on mtDNA data proposed by Wiens and Penkrot (2002) to identify potential evolutionary independent lineages (e.g., distinct species). In this method, species delimitation is based on a mtDNA phylogeny for a set of populations currently classified as a species (the focal species of the study) and those species that are closely related to this species. In this phylogeny of haplotypes of known locality and taxonomic designation, the failure of haplotypes from a given locality to cluster together is potential evidence of gene flow with other populations, as is the general discordance between haplotype clades and the geographic areas from which the haplotypes are found. Species limits are inferred based on the relationship of the focal species to the other species and on the general concordance between phylogeny and geography within the focal species. If the focal species is exclusive sensu Wiens and Penkrot (2002), the presence of strongly supported basal lineages (i.e., the oldest split or splits) concordant with geography within the species is potential evidence of the absence of gene flow between these lineages (i.e., potential evolutionary independent lineages), and therefore suggests that the focal species may represent multiple species disguised by traditional taxonomy. The method emphasizes basal lineages concordant with geography as potentially distinct species because retained ancestral polymorphisms are most likely in populations that have split very recently, and the problems of male-biased dispersal, female philopatry, and coalescence of temporarily isolated populations are also most likely to affect the more recent branches of the haplotype tree. The focal species of this study was *Mesaspis moreletii*.

We then used the potential evolutionary independent lineages identified using Wiens and Penkrot (2002)'s method to guide species delimitation inference, and generated competing species delimitation models to test alternative species delimitation hypotheses (i.e., the assignment of individuals to alternative lineages or species). To generate the competing species delimitation models, we considered (a) the seven potential evolutionary independent lineages within *M. moreletii* suggested by Wiens and Penkrot (2002)'s method (see below); and (b) the *M. cuchumatanus* lineage. We included the latter lineage in the analysis because its genetic distinctness has not been investigated and because its geographic distribution overlaps those of the *M. moreletii* lineages. In total, we tested 11 species delimitation models (A–K). The first model (A) treats as a single, widely distributed species the above eight potential evolutionary independent lineages, whereas the last model (K) assumes as actually distinct each of these lineages. The remaining models (B–J) lumped one or more pairs of sister lineages and/or one or more pairs of sister clades of lineages in the mitochondrial tree into smaller numbers of lineages (2–7, Fig. 3).

Two methods that simultaneously estimate the species tree and evaluate species-delimitation models are the most recent version of

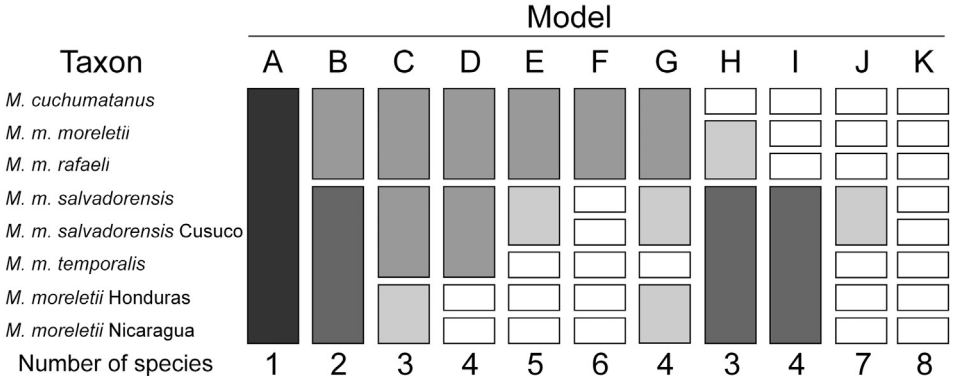

Fig. 3. Species delimitation models (A–K) based on the mtDNA tree. Each species delimitation model comprises a unique combination of lineages (rows). See Section 3.3 for details.

Fig. 4. Bayesian phylogenetic tree for the Central American species of *Mesaspis* inferred from the mtDNA data. Nodal support values are posterior probabilities. Individual samples in boldface are the samples sequenced for nuclear genes. Localities for the individual samples are given in Table S1.

BP&P (BP&P v. 3.1, Yang, 2015) and the implementation of Bayes factors in *BEAST (Grummer et al., 2014; Heled and Drummond, 2010). These two methods use the multispecies coalescent model to compare different hypotheses of species delimitation and species phylogeny in a Bayesian framework, accounting for incomplete lineage sorting due to ancestral polymorphism and gene tree-species tree conflicts (Rannala and Yang, 2013; Yang and Rannala, 2014, 2010). First, we used the method based on Bayes factors (BFD) proposed by Grummer et al. (2014). We used two methods to estimate the marginal likelihood on each of the three replicate runs for each species delimitation model in *BEAST (Drummond and Rambaut, 2007): path-sampling (PS; Lartillot and Philippe, 2006) and stepping-stone (SS; Xie et al., 2011). PS and SS analyses were each run for a chain length of 10^6 generations for 100 path steps (totaling 10^8 generations). The marginal likelihood results of the three replicate *BEAST analyses ran for each species delimitation model were combined in *BEAST and used to calculate the Bayes factor (2lnBf; Grummer et al., 2014). We used the marginal likelihoods values to rank models, and Bayes factors to estimate the support for each model relative to the model with the highest ranking. The Bayes factors (2lnBfs) were evaluated following the recommendations of Kass and Raftery (1995): A 2lnBf = 0–2 means "not worth more than a bare mention", 2lnBf = 2–6 means "positive" support, 2lnBf = 6–10 provides "strong" support, and 2lnBf > 10 means "decisive" support in distinguishing between competing species delimitation hypotheses. We used the same outgroups as in the Bayesian analyses of the independent genes.

We also used the species delimitation method BP&P v. 3.1 (Yang, 2015; Yang and Rannala, 2014) implementing the NNI search algorithm. This method accommodates the species phylogeny as well as incomplete lineage sorting due to ancestral polymorphism. BP&P employs a reverse-jump Markov chain Monte Carlo (rjMCMC) sampling to explore the likelihood of data under models with different numbers of lineages defined a priori. We assigned the *Mesaspis moreletii* samples to the lineages in the species delimitation model with the largest number of potentially distinct species, and included *M. cuchumatanus* and *M. monticola* in the analyses. We used several combinations of priors for ancestral population size (θ) and root age (τ_0) (Table S4), including three combinations used by Leaché and Fujita (2010). The first of the latter combinations assumed relatively large ancestral population sizes and deep divergences: $\theta \sim G(1, 10)$ and $\tau_0 \sim G(1, 10)$. The second combination assumed relatively small ancestral population sizes and shallow divergences among species: $\theta \sim G(2, 2000)$ and $\tau_0 \sim G(2, 2000)$. The third, and more conservative, combination assumes large ancestral population sizes $\theta \sim G(1, 10)$ and relatively shallow divergences among species $\tau_0 \sim G(2, 2000)$, which is a conservative combination that should favor models containing fewer species, and may be the most biologically realistic scenario (Myers et al., 2013). The other divergence time parameters are assigned the Dirichlet prior (Yang and Rannala, 2010: Eq. (2)). Each analysis was run at least twice to confirm consistency between runs.

2.4. Divergence times estimation

We estimated divergence times using *BEAST v1.8.1 (Heled and Drummond, 2010) with the partition scheme selected by PartitionFinder for the mtDNA (see above) and a partition for each nuclear gene. We followed Bryson and Riddle (2012) in using previous rate calibrations for mtDNA employed to estimate divergence times in anguid lizards (0.65–0.69% change/lineage/million years; Macey et al., 1999) and within *Barisia* (0.85% change/lineage/million years; Zaldivar-Riverón et al., 2005). We unlinked the best-fitting models of sequence evolution across partitions and implemented an uncorrelated lognormal clock with a Yule tree prior, and assigned to the ulcd.mean parameter a uniform distribution set to 6.5×10^{-3} and 8.5×10^{-3} substitutions/site/million years as the lower and the upper bound, respectively. The analysis was run for 1×10^{7} generations, with samples retained every 5000 generations. We discarded the first 25 million generations (25%) as burn-in, and the parameter values of the samples from the posterior distribution were summarized on the maximum clade credibility tree using TreeAnnotator (Drummond and Rambaut, 2007), with the posterior probability limit set to zero and mean node heights summarized.

3. Results

3.1. Mitochondrial data

The mtDNA dataset included a total of 76 individuals (Table S1) and consisted of 672 unambiguously aligned nucleotide positions corresponding to the ND4 gene and 171 corresponding to the adjacent $tRNA^{His}$, $tRNA^{Ser}$, and $tRNA^{Leu}$. Of the 76 individuals, 51 represented the five subspecies of *M. moreletii*: *M. m. fulvus* (9), *M. m. moreletii* (11), *M. m. rafaeli* (8), *M. m. salvadorensis* (9), and *M. m. temporalis* (14).

In the inferred Bayesian consensus tree (Fig. 4), the ingroup was monophyletic and composed of two large basal clades. In one basal clade, the haplotypes of *M. m. fulvus* and *M. m. moreletii* were intermingled in a single clade (i.e., were non-exclusive with respect to each other), whereas the haplotypes of *M. m. rafaeli* and *M. cuchumatanus* were exclusive with respect to each other and the haplotypes of *M. m. fulvus* and *M. m. moreletii*. The *M. m. fulvus* + *M. m. moreletii* clade was the sister taxon to *M. m. rafaeli*, and these three taxa comprised the sister group to *M. cuchumatanus*. The uncorrected genetic distances (p) among these three lineages were from 4.17% to 4.73% (Table S5). In the other basal clade, the haplotypes of *M. m. salvadorensis*, *M. m. temporalis*, *M. moreletii* Honduras, *M. moreletii* Nicaragua, and *M. monticola* were exclusive with respect to each other. The genetic distances among these lineages were from 3.08% to 8.15% (Table S5). *Mesaspis m. salvadorensis* was the sister taxon to *M. m. temporalis* and *M. moreletii* Honduras the sister taxon to *M. moreletii* Nicaragua, and these four taxa comprised the sister group to *M. monticola*. All of these relationships were strongly supported, except for the (*M. m. fulvus* + *M. m. moreletii*) – *M. m. rafaeli* sister taxon relationship, which was marginally not strongly supported (PP = 0.94). Furthermore, the samples of *M. m. salvadorensis* from the geographically isolated population at Parque Nacional El Cusuco (*M. m. salvadorensis* Cusuco hereafter) and the samples of *M. m. salvadorensis* from other localities in Honduras formed mutually exclusive clades, although these clades were only slightly divergent from each other (p = 0.44%, Table S5) and not strongly supported. On the basis of their interdigitation in the tree with the clades of other species (*M. cuchumatanus* and *M. monticola*), strong support, concordance with geography, and allopatry (or morphological distinctness), the method of Wiens and Penkrot (2002) suggested the (*M. m. fulvus* + *M. m. moreletii*), *M. m. rafaeli*, *M. m. salvadorensis*, *M. m. salvadorensis* Cusuco, *M. m. temporalis*, *M. moreletii* Honduras, and *M. moreletii* Nicaragua clades of *M. moreletii* as potential evolutionary independent lineages. Except for the (*M. m. fulvus* + *M. m. moreletii*) and *M. m. rafaeli* sister lineages, all sister taxa between these seven lineages are allopatric and, except for the two lineages of *M. m. salvadorensis*, moderately divergent genetically from each other (uncorrected genetic distances ≥ 3.0%). Although the (*M. m. fulvus* + *M. m. moreletii*) and *M. m. rafaeli* sister lineages are possibly parapatric, they are morphologically distinct.

3.2. Nuclear data

The BMP2, KIAA1217, and PRLR datasets consisted of 563, 524 and 557 unambiguously aligned nucleotide positions, respectively. No evidence of intraspecific recombination was detected for any locus. Individual trees showed less resolution and much weaker support than the mitochondrial tree. In all nuclear gene trees (Figs. S1–S3), the samples of *M. moreletii* formed a polytomy that also involved the sample of *Abronia lythrochila*. However, this polytomy was strongly supported only in the BMP2 and PRLR trees. Several of the seven mitochondrial lineages of *M. moreletii* were recovered as monophyletic in one or more of the trees (trees in parentheses): *M. m. moreletii* (BMP2), *M. moreletii* Honduras (KIAA1217 and PRLR), *M. moreletii* Nicaragua (KIAA1217), *M. m. rafaeli* (KIAA1217 and PRLR), and *M. m. salvadorensis* Cusuco (KIAA1217). Similarly, the *M. cuchumatanus* and *M. monticola* lineages were recovered in the BMP2 and KIAA1217 and the BMP2, KIAA1217, and PRLR trees, respectively. All of these lineages were strongly supported except for the *M. cuchumatanus* lineage in the KIAA1217 tree. The *M. m. salvadorensis* and *M. m. temporalis* lineages were not recovered in any tree. In addition, the *M. moreletii* Honduras and *M. moreletii* Nicaragua lineages were strongly recovered as sister taxa in the KIAA1217 tree and formed a strongly supported clade in the PLRL tree, although *M. moreletii* Nicaragua was paraphyletic with respect to *M. moreletii* Honduras in the latter tree. Finally, in the PRLR tree the samples of *M. m. moreletii* and *M. cuchumatanus* formed a strongly supported polytomy, and the clade *M. moreletii* Honduras + *M. moreletii* Nicaragua was strongly supported as sister to a clade with the samples of *M. m. temporalis* and a nested, strongly supported clade with the samples of *M. m. salvadorensis* and *M. m. salvadorensis* Cusuco. There were no strongly supported conflicts between the mitochondrial and individual nuclear trees, except that a strongly supported clade with the samples of *M. m. rafaeli* formed a polytomy with *Abronia lythrochila* and another strongly supported clade with the samples of *M. cuchumatanus*, *M. monticola*, and the remaining samples of *M. moreletii* in the PRLR tree.

The Bayesian concatenated nuclear tree (Fig. S4) recovered most of the relationships in the mitochondrial tree and was mostly congruent with it except for a strongly supported clade with the samples of *M. m. rafaeli*, which formed a polytomy with *Abronia lythrochila* and a strongly supported clade with the samples of *M. cuchumatanus*, *M. monticola*, and the remaining samples of *M. moreletii* as in the PRLR tree. Also, the nuclear tree had fewer strongly supported relationships than the mitochondrial tree.

3.3. Coalescent-based species tree inference analyses

We tested 11 species delimitation models with the BFD method (see above and Fig. 3). The rankings of the 11 models produced by the PS and SS analyses were almost in exact agreement with one another (Table S6). Model K, which recognizes all of the subspecies of *Mesaspis moreletii* but *M. m. fulvus*, three other lineages of *M. moreletii* (*M. moreletii* Honduras, *M. moreletii* Nicaragua, and *M. m. salvadorensis* Cusuco), and *M. cuchumatanus* as distinct species, received "decisive" support over all other models (2lnBF = 200.876–552.612 and 199.346–522.368 in the PS and SS analyses, respectively) with the exception of model J (2lnBF = 4.891 and 3.580 in the PS and SS analyses, respectively). Among the remaining models, excluding model J, model F was the closest in rank to model K (2lnBF = 143.293 and 141.206 in the PS and SS analyses, respectively), and the least favored species delimitation model was the one assuming that all potentially

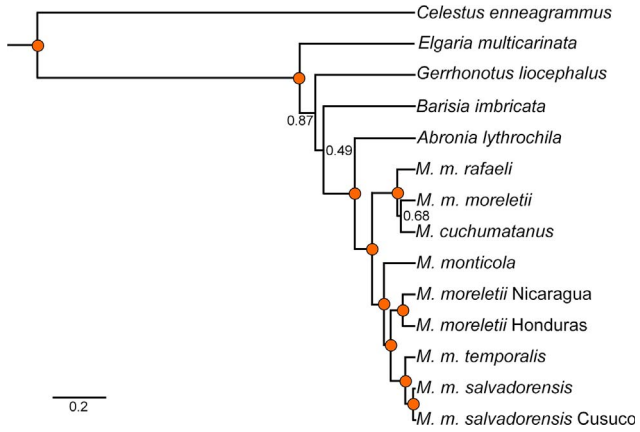

Fig. 5. Species tree for the Central American species of *Mesaspis* inferred from the multilocus data set in *BEAST. Numbers on nodes are posterior probability values. Orange dots represent posterior probability values ≥ 0.95. Localities for individual samples are given in Table S1. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

distinct lineages represent only one species (Model A; Table S6). The species tree for model K (Fig. 5) was generally well supported and similar to the mtDNA tree, except that *M. m. moreletii* was the sister taxon to *M. cuchumatanus*, instead of *M. m. rafaeli*. However, this relationship was not strongly supported.

In the BP&P method, all of the combinations of priors yielded posterior probabilities > 0.97 for the species delimitation model K. All the analyses delimited 9 species: the seven potentially distinct lineages of *M. moreletii*, *M. cuchumatanus*, and *M. monticola*, all with posterior probabilities > 0.97, and a species composed of all the populations of *M. m. salvadorensis* with posterior probability < 0.027 (Table S7).

3.4. Divergence times

Our time-calibrated tree (Fig. S5) suggest that the ancestor of the Central American clade of *Mesaspis* was widely distributed in Central America and split into the ancestors of the *M. cuchumatanus* + *M. m. moreletii* (including *M. m. fulvus*) + *M. m. rafaeli* clade (= the *M. cuchumatanus* clade hereafter) and its sister clade (composed of *M. monticola*, *M. moreletii* Honduras, *M. moreletii* Nicaragua, *M. m. salvadorensis*, *M. m. salvadorensis* Cusuco, and *M. m. temporalis*, or the *M. monticola* clade hereafter) probably during the late Oligocene-early Miocene. Within the *M. cuchumanatus* and *M. monticola* clades, all of the following splits took place between the mid Miocene and the early Pliocene (14.52–4.52 Mya), except for the split between *M. m. salvadorensis* and *M. m. salvadorensis* Cusuco, which appears to have occurred as recently as in the Pleistocene.

4. Discussion

4.1. Species delimitation

The application of the species delimitation method based on mtDNA phylogenies of Wiens and Penkrot (2002) to our mtDNA tree suggests that *M. moreletii* is composed of multiple species. First, *Mesaspis moreletii* was not exclusive. Instead, the haplotypes of *M. moreletii* were divided into two strongly supported, geographically overlapping clades, with the haplotypes of *M. m. fulvus*, *M. m. moreletii*, and *M. m. rafaeli* comprising the sister taxon to *M. cuchumatanus* in one clade and the haplotypes of *M. m. salvadorensis*, *M. m. salvadorensis* Cusuco, *M. m. temporalis*, *M. moreletii* Honduras and *M. moreletii* Nicaragua comprising the sister group to *M. monticola* in the other clade (Fig. 4).

Second, the tree showed a deep structure and the *M. moreletii* haplotypes were segregated into five strongly supported, moderately divergent clades of identical subspecific designation (or no subspecific designation but morphologically distinct and concordant with geography) with no evidence of maternal-based gene flow between them, and another clade composed of the haplotypes of *M. m. fulvus* and *M. m. moreletii*, which were nearly identical and intermingled with each other in the clade (Fig. 4). This, and the geographic distribution of these taxa, suggests the existence of gene flow between them, and thus that they represent a single evolutionary lineage (Wiens and Penkrot, 2002). Bocourt (1872) distinguished between these subspecies only based on their apparent geographic isolation and that *M. m. fulvus* is smaller and darker than *M. m. moreletii*. However, we were not able to find any consistent morphological differences between these two forms. Although most of the specimens of *M. m. fulvus* from a given locality were dark brown, there were also some lighter specimens, and any variation found is presumably due to intraspecific variation. This also suggests that *M. m. fulvus* is a junior synonym of *M. m. moreletii*. Regardless, the *M. m. moreletii* (including *M. m. fulvus*) and *M. m. rafaeli* lineages were strongly supported, mutually exclusive, moderately divergent genetically (p = 4.7%), and morphologically distinct (Hartweg and Tihen, 1946; Tihen, 1949) from each other.

In the second *M. moreletii* clade, the haplotypes of *M. m. salvadorensis*, *M. m. temporalis*, *M. moreletii* Honduras, and *M. moreletii* Nicaragua formed strongly supported clades exclusive with respect to each other. In addition, the sister taxa *M. m. temporalis* and *M. m. salvadorensis* are allopatric, moderately divergent genetically (p = 3.1%), and morphologically distinct (Tihen, 1949) from each other. Similarly, the *M. moreletii* Honduras and *M. moreletii* Nicaragua sister lineages seem to be allopatric and are moderately divergent genetically (p = 3.7%) from each other. However, there were large unsampled areas between their known populations, and the apparent absence of gene flow between them might be an artifact of insufficient sampling. Also, morphological differences between these lineages are less evident, and only a few specimens from single localities of each lineage were examined. Similarly, the *M. m. salvadorensis* and *M. m. salvadorensis* Cusuco lineages were allopatric and concordant with geography (Fig. 2) but the former was not strongly supported. This suggests the absence of gene flow between them. However, they were only slightly divergent (p = 0.44%, Table S6), and there were no evident morphological differences between them, which is probably related to their recent split (Figs. 4 and S5).

The BFD method gave model K, which recognizes all of the subspecies of *Mesaspis moreletii* except for *M. m. fulvus*, three other lineages of *M. moreletii* (*M. moreletii* Honduras, *M. moreletii* Nicaragua, and *M. m. salvadorensis* Cusuco), and *M. cuchumatanus* as distinct species, "decisive" support over all the other models except for model J, which does not recognize *M. m. salvadorensis* Cusuco as distinct from *M. m. salvadorensis*. This suggests that the population of *Mesaspis* at Cerro El Cusuco represents an apparently isolated population of *M. m. salvadorensis*. Clearly, because no species should be recognized that are not supported by conclusive evidence, we believe that the more conservative model J should be preferred over model K. On the other hand, all of the analyses performed with the BP&P method delimited 9 species: the seven potentially distinct lineages of *M. moreletii*, *M. cuchumatanus*, and *M. monticola*; all with posterior probabilities > 0.97.

In summary, all of our species delimitation analyses suggest that the (*M. m. fulvus* + *M. m. moreletii*), *M. m. rafaeli*, *M. m. salvadorensis*, *M. m. temporalis*, *M. moreletii* Honduras, and *M. moreletii* Nicaragua lineages, in addition to *M. cuchumatanus* and *M. monticola*, represent distinct evolutionary lineages. Thus, available evidence indicates that *M. moreletii* represents a species complex diversified from Chiapas, Mexico southward to Nicaragua, and that significant species diversity has been concealed in this polytypic species.

4.2. Phylogeny and biogeography

The phylogenetic relationships among the several lineages of

Mesaspis moreletii, *M. cuchumatanus*, and *M. monticola* were strongly supported and identical in the mtDNA and species trees, except that *M. m. moreletii* (including *M. m. fulvus*) was the sister taxon to *M. m. rafaeli* in the mitochondrial tree, and the sister taxon to *M. cuchumatanus* in the species tree. However, none of these relationships were strongly supported. The geographic distribution of the lineages in the *M. cuchumatanus* + *M. monticola* + *M. moreletii* clade is discussed below.

The *Mesaspis* clade composed of *M. cuchumatanus*, *M. monticola*, and *M. moreletii* is distributed throughout the highlands of most of Central America. This clade is isolated from the remaining species of the genus (*M. antauges*, *M. gadovii*, *M. juarezi*, and *M. viridiflava*) by the Isthmus of Tehuantepec, a well-known geographical break and biological barrier for many taxa (e.g., Arellano et al., 2005; Barber and Klicka, 2010; Chippindale et al., 1998; Daza et al., 2010; Esteva et al., 2010; García-Moreno et al., 2006; León-Paniagua et al., 2007; Mulcahy et al., 2006a; Ornelas et al., 2013; Sullivan et al., 2000; Vázquez-Miranda et al., 2009). Central America is divided into the northwestern "Nuclear Central America" and the southeastern "Isthmian Link" by the Santa Elena Fault (James, 2007); in turn, Nuclear Central America is divided into the Maya and Chortis geological blocks by the Motagua Fault zone (James, 2007; Marshall, 2007). The *M. cuchumatanus* clade is distributed exclusively on the highlands of Guatemala and adjacent southeastern Chiapas in Nuclear Central America (Fig. 1), whereas the *M. monticola* clade is distributed from the highlands of the Meseta Central de Chiapas in Nuclear Central America south and east to the highlands of Costa Rica and Panamá in the Isthmian Link (Fig. 1). In addition, the geographic distributions of the *M. cuchumatanus* and *M. monticola* clades overlap in central-west Guatemala and possibly adjacent Mexico (Fig. 1). Although estimates of divergence dates are older and the 95% highest posterior density intervals wider in rate-calibrated trees than in fossil-calibrated trees (Edwards & Beerli, 2000), the geographic distribution of the *M. cuchumatanus* and *M. monticola* clades and our time-calibrated tree (Fig. S5) suggest that the ancestor of these clades was widely distributed in Central America and split long before the elevation of the highlands in the region, approximately 10–3.8 million of years ago in the late Miocene (Rogers et al., 2002). However, the causes that led to the divergence of the *M. cuchumatanus* and *M. monticola* clades are presently unclear.

Our time-calibrated tree (Fig. S5) suggests that the ancestor of the *M. cuchumatanus* clade was already distributed in southern Guatemala and adjacent southeastern Chiapas by the mid Miocene, and diversified posteriorly *in situ* during the late Miocene before the Pacific volcanic chain was formed (Williams, 1960); that is, that the formation of the Pacific volcanic chain was not a key event in the diversification of the *M. cuchumatanus* clade. The known distribution of *M. cuchumatanus* is restricted to the Sierra de los Cuchumatanes (Solano-Zavaleta et al., 2016), where it is isolated from *M. m. moreletii* and *M. m. rafaeli*. The distribution of *M. m. moreletii* is divided into two populations: one on the Pacific volcanic chain and the other one on the inner portion of Guatemala, and these populations are apparently isolated from each other by the basin present along the Motagua-Polochic Fault zone. Lastly, given the small gap between the western-most populations of *M. m. moreletii* and the closest populations of *M. m. rafaeli*, it is possible that these taxa are parapatric or even sympatric in southwestern Guatemala (Fig. 1). The present distribution of these three taxa might be related to the glacial climatic cycles in the late Pliocene-Pleistocene (Castoe et al., 2003; Savage, 2002, 1982).

Similarly, our time-calibrated tree (Fig. S5) and the geographic distribution of the *M. monticola* clade suggest that the ancestor of the clade was already widespread in Central America by the early Miocene, and that the first divergence in the clade, separating *M. monticola* from its sister taxon, took place by the mid Miocene (ca. 14.5 Mya); that is, before the uplift of the highlands of Nuclear Central America and the Isthmian Link (see above). Thus, the causes that led to this divergence are presently unknown. Currently, *M. monticola* and its sister taxon are isolated from each other by the Nicaraguan Depression, which separates the highlands of Honduras and Nicaragua in Nuclear Central America from the highlands of Costa Rica and Panamá in the Isthmian Link (Rogers et al., 2002) and is a major phylogeographical break for many taxa (e.g., Daza et al., 2010; Duellman, 1999; Halas et al., 2005; Parra-Olea et al., 2004). However, it has been suggested that highland lineages across the Nicaraguan Depression diverged as recently as in the late Miocene-Pliocene (Castoe et al., 2009).

The mountainous interior of Honduras is divided into western and eastern portions by a north-south complex of plains and valleys known as the Honduras Depression (McCranie and Wilson, 2002; James, 2007). The interior of Honduras also is traditionally divided into the Northern Cordillera and the Southern Cordillera, distinguished from one another by the presence of Pliocene volcanic ejecta in the latter region (McCranie and Wilson, 2002). These physiographic divisions allow the recognition of four upland areas in Honduras (and adjacent Nicaragua): Northwestern, Southwestern, Northeastern, and Southeastern (Wilson and Townsend, 2007). The (*M. m. salvadorensis* + *M. m. salvadorensis* Cusuco) + *M. m. temporalis* clade is isolated from the *M. moreletii* Honduras + *M. moreletii* Nicaragua clade by the Honduras Depression. *Mesaspis m. salvadorensis* Cusuco is distributed in the Northwestern Highlands and *M. m. salvadorensis* in the Southwestern Highlands, and both of them are isolated from *M. m. temporalis* by the Motagua-Polochic Fault, which has been found to be a physiographical barrier that has caused phylogeographical breaks in different taxa (e.g. Castoe et al., 2009; Devitt, 2006; Halas et al., 2005). *Mesaspis moreletii* Honduras and *M. moreletii* Nicaragua are distributed in the Southeastern Highlands, and the only discernable barrier between their populations is the extensive lowlands between their highlands. Our time-calibrated tree (Fig. S5) suggests that the divergence of the (*M. m. salvadorensis* + *M. m. salvadorensis* Cusuco) + *M. m. temporalis* clade from the *M. moreletii* Honduras + *M. moreletii* Nicaragua clade took place by the mid Miocene (ca. 11 Mya), whereas the following events within each clade took place in the late Miocene-early Pliocene (ca 6.8–4.5 Mya); that is, before and during the uplift of the highlands in Central America approximately 10–3.8 million of years ago in the late Miocene (Rogers et al., 2002), respectively. However, given that rate-calibrated phylogenies may overestimate divergence times (Edwards and Beerli, 2000), it seems possible that the first divergence event took place at the beginning of this uplift. Finally, the split between *M. m. salvadorensis* and *M. m. salvadorensis* Cusuco appears to have taken place in the early Pleistocene, and thus it might be related to the glacial climatic cycles in the late Pliocene-Pleistocene (Castoe et al., 2003; Savage, 2002).

The present distribution of *M. m. temporalis* on the highlands of the Meseta Central of Chiapas, the Sierra de los Cuchumatanes, and the Pacific volcanic chain in Guatemala may be explained by the existence of two highland corridors: a corridor connecting the Guatemalan Plateau with the Cuchumatanes which lacks continuity, and a narrow corridor by which limited exchange of mid-elevation faunas has occurred between the Meseta Central of Chiapas and the northwestern Sierra de los Cuchumatanes (Solano-Zavaleta et al., 2016). These corridors could have allowed the dispersion of *M. m. temporalis* during the glacial climatic cycles in the late Pliocene-Pleistocene (Castoe et al., 2003; Savage, 2002).

5. Taxonomic conclusions

The species delimitation analyses of our molecular data suggest the evolutionary independence of *M. m. moreletii* (including *M. m. fulvus*), *M. m. rafaeli*. *M. m. salvadorensis*, and *M. m. temporalis*. The morphological distinctness of these subspecies supports this suggestion. Those analyses also suggest that *M. moreletii* Honduras and *M. moreletii* Nicaragua may each represent an evolutionary independent lineage. Nonetheless, our samples of these lineages were small, and their distinctness was not supported by conclusive morphological evidence. Also, there were large gaps in our geographic sampling of Honduras and

Nicaragua, and the genetic divergence between *M. m. salvadorensis* and *M. m. salvadorensis* Cusuco was definitely low. At any rate, our results suggest that more species exist within *Mesaspis* than have been recognized by traditional taxonomy.

It has been suggested that species numbers are rapidly increasing (especially in vertebrates) due mostly to "taxonomic inflation," where known subspecies are elevated to species rank because of a change in species concept, rather than new discoveries (Isaac et al., 2004). Evidently, to follow the unified species concept of de Queiroz (2007) to raise the aforementioned subspecies to species status would result in taxonomic inflation. However, we believe that de Queiroz (2007)'s arguments for adopting the unified species concept are compelling, and therefore that elevating subspecies to species rank should be done as long as it is supported by evidence. Also, some of the potential evolutionary independent lineages identified in this study were not known subspecies (the *M. moreletii* Honduras or *M. moreletii* Nicaragua lineages).

Nonetheless, we acknowledge that the suggested evolutionary independence of the several lineages of *M. moreletii* identified in this study is mostly based on data from a few genes, which are not necessarily representative of the genome. Because of this limited sampling of nuclear genes, we suggest that additional genetic evidence, as well as other sources of evidence, are needed to corroborate the status of these lineages as distinct evolutionary species.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ympev.2017.11.011.

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CAPÍTULO II

Descripción de especies nuevas de *Abronia* y *Mesaspis*

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A New Species of *Abronia* (Squamata: Anguidae) from the Sierra Madre del Sur of Oaxaca, Mexico

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Abstract.—A newly discovered species of arboreal alligator lizard of the genus *Abronia* is described from the Sierra Madre del Sur of Oaxaca, Mexico. It appears to be most closely related to *A. mixteca* and *A. oaxacae*, but differs from these species (and others in the subgenus *Abronia*) in a number of features, including the combination of having two primary temporals contacting the postocular series, the anterior superciliary contacting the cantholoreal, six to eight nuchals in a transverse row across the nape, minimally seven to eight scales between large nuchals and ventral scales on neck, and 32–35 transverse rows of dorsal scales. This new species is the only species of *Abronia* known from the central and western portions of the Sierra de Miahuatlán in the southern part of the Sierra Madre del Sur, although *A. oaxacae* occurs to the east in this range. Many of the arboreal and secretive species of *Abronia* have avoided discovery until relatively recently, with about a third of known species described in the last 3 decades.

Resumen.—Se describe una nueva especie de lagartija lagarto arbórea del género *Abronia* de la Sierra Madre del Sur de Oaxaca, México. Parece estar más relacionada a *A. mixteca* y *A. oaxacae*, pero difiere de estas especies y de otras del subgénero *Abronia* en varios caracteres, incluyendo la combinación de tener dos temporales primarias contactando la serie postocular, la superciliar anterior en contacto con la cantoloreal, 6–8 nucales en hilera transversal sobre la nuca, un mínimo de 7–8 escamas entre las nucales grandes y las escamas ventrales del cuello, y 32–35 hileras transversales de escamas dorsales. Esta nueva especie es la única del género *Abronia* conocida de las porciones central y occidental de la Sierra de Miahuatlán en la región sur de la Sierra Madre del Sur, aunque *A. oaxacae* ocurre al oriente de esta serranía. Muchas de las especies de *Abronia* con hábitos secretos y arbóreos han evadido ser descubiertas hasta hace poco, aproximadamente una tercera parte de las especies han sido descritas en las últimas tres décadas.

Many species of the genus *Abronia* are infrequently encountered members of the Middle American highland forest herpetofauna. Their arboreal habits and cryptic coloration often allow them to escape detection. They occur on the Atlantic versant from northeastern Mexico (Tamaulipas) southward across the Isthmus of Tehuantepec through northern Chiapas to the departments of Alta and Baja Verapaz (and almost certainly into Izabal and Zacapa), Guatemala (Campbell and Frost, 1993). The genus occurs in central Mexico along the southern edge of the Transverse Volcanic Cordillera in the states of Morelos, México, and Michoacán (Campbell and Frost, 1993; Flores-Villela and Sánchez-Herrera, 2003; Centeno-Alcalá et al., 2009). On mountains bordering the Pacific coastal plain, one species is known from the highlands of Guerrero, several species in Oaxaca, and several species to the east of the Isthmus of Tehuantepec in Chiapas, Guatemala, El Salvador, and Honduras (Campbell and Frost, 1993).

An interesting aspect of distribution is the almost invariable allopatry of species throughout the extensive range of the genus. Campbell and Frost (1993) discussed the possible instances of sympatry, but were able to document with certainty only one instance of overlap between *A. gaiophantasma* and *A. fimbriata* in Baja Verapaz, Guatemala. The locality data borne by several museum specimens representing three species all collected by a single collector reputedly in 1937 near "Santa Rosa," Chiapas was questioned by Campbell and Frost (1993), and information relating to these specimens and their collector was further elucidated by Peterson and Nieto-Montes de Oca (1996). Another feature of the distribution of *Abronia* is the relatively small ranges of most species. Most occur in single montane forests and often only on a single exposure in those mountains; therefore, for one species to inhabit cloud forest on the windward side and another to occur in pine–oak forest on the drier leeward side is not unusual.

With its diverse topography and climate, along with the diverse historical influxes of fauna (Savage, 1982), Oaxaca harbors more herpetofaunal species than any other state in Mexico (Casas-Andreu et al., 1996, 2004; Campbell, 1999; Ochoa-Ochoa et al., 2013). The extensive highland forests of this state have a temperate climate but the biota is a complex admixture of species of temperate and tropical origin. Hot, humid lowlands bound the state on three sides: the Atlantic Coastal Plain to the north, the Pacific Coastal Plain to the south, and the Isthmus of Tehuantepec to the east. In the west, the highlands of the Sierra Madre del Sur extend into Guerrero, but in western Guerrero this highland corridor is broken by ridgeline elevations that dip to 1,500 m or less. The highlands of Oaxaca often are simplistically regarded as all pertaining to the Sierra Madre del Sur–Mesa del Sur complex (West, 1964). This obscures a complex physiographic picture of many isolated mountain ranges trending in diverse directions and many isolated uplifts. The physiography includes several impressive highlands in the north such as the Sierra de Juárez, Sierra Aloapaneca, the Sierra Mazateca, and the Sierra de Monteflor. Across the extensive central Oaxacan central plateau region, which tends to be xerophytic at lower elevations, there are several isolated ranges including the Sierra de Cuatro Venados, and also many isolated peaks such as the Cerro de Tres Cruces, the Cerro Piedra de Lumbre, and the Cerro Piedra del Sol, all of which have pine–oak forests. Finally, the southern portion of the

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Sierra Madre del Sur in Oaxaca, often referred to as the Sierra de Miahuatlán, runs parallel to the Pacific coast, with considerable areas ranging over 1,500 m that extend unbroken for about 180 km across the south-central portion of the state. Many of the Oaxacan highlands have been poorly explored, but practically all are known to harbor endemic species of amphibians and reptiles. Much of the Pacific versant of the Sierra de Miahuatlán is covered by a magnificent hardwood forest and has been particularly neglected by biologists; this region will undoubtedly provide rewarding results for subsequent field studies.

Materials and Methods

Terminology for defining scales and protocols for making scale counts and measurements have been outlined in Bogert and Porter (1967), Campbell (1982, 1984, 1994), and Campbell and Frost (1993). Specimens examined were fixed in buffered formalin diluted to 10% of stock solution and subsequently transferred into 70% ethanol for permanent storage. Notes of color in life were taken from field notes and photographs of live individuals. Format for the diagnosis and description follow Campbell and Frost (1993) for ease of comparison. Museum abbreviations follow Sabaj Pérez (2014).

Systematic Account

During 2012, a field party from The University of Texas at Arlington teamed with individuals from several institutions including the Universidad Nacional Autónoma de México and the American Museum of Natural History to conduct herpetofaunal inventories of the Oaxacan highlands west of the Isthmus of Tehuantepec. During the course of fieldwork we encountered a specimen of *Abronia* that we were unable to readily identify. Further, this specimen was found in an area where members of the genus were unknown previously. This prompted careful examination and comparison of this specimen with available museum material, which in turn revealed two additional conspecifics. These lizards are distinctly different from all other known species and we propose that this new anguid lizard be known as

Abronia ***cuetzpali*** sp. nov.
(Figs. 1–3, Table 1)

Sierra de Miahuatlán Abronia—Dragoncito de Sierra de Miahuatlán

Holotype.—MZFC 28761, an adult male from near San Miguel Suchixtepec, Sierra de Miahuatlán, approximately 2 km west of the Río Molino, Sierra Madre del Sur, Oaxaca, Mexico, 2,150 m (16.08439°N 96.49042°W), found by I. Caviedes-Solis on 4 November 2011 (Figs. 1–2). The individual was found at 1020 h as it crawled across a trail. The headwaters of the Río Molino occur just to the east of San Miguel Suchixtepec. Suitable habitat occurs throughout the region between 1,500 and 2,500 m.

Paratypes (2).—UTA R-61670, an adult female from 5.4 km eastof Juquila, Sierra de Miahuatlán, Sierra Madre del Sur, Oaxaca, Mexico, 1,711 m (16.23204°N 97.25535°W), found by Oscar Olivares on 8 July 2012 (Fig. 3). The individual was found during the late morning as it crawled on the forest floor. The northward-facing slope on which the holotype was collected drains into the Río Grande, an upper tributary of the Río Verde. UCM 41057, an adult male from near San Miguel Suchixtepec, Oaxaca, Sierra Madre del Sur, Mexico, collected by Thomas MacDougal in May 1967. The specimen was reported by the collector to be from the Río Molino drainage.

Fig. 1. Body (A) and head (B) of *Abronia cuetzpali*, holotype (MZFC 28761), adult male, 108 mm SVL, head length 27.1 mm.

Diagnosis.—A species of *Abronia* in the subgenus *Abronia* defined by Campbell and Frost (1993). Within this subgenus *A. cuetzpali* clearly falls within the *A. deppii* group, containing *A. deppii*, *A. martindelcampoi*, *A. mixteca*, and *A. oaxacae*, all of which have the unique condition in the genus *Abronia* of having scales oriented in oblique rows relative to the ventrolateral fold. *Abronia cuetzpali* differs from *A. deppii* (which occurs along the southern edge of the Mexican Plateau) and *A. martindelcampoi* (which occurs in the western highlands of Guerrero) in having two primary temporals contacting the postocular series (vs. one), an anterior superciliary contacting the cantholoreal (vs. usually no contact), the first postorbital supralabial not enlarged (vs. enlarged), two to three occipitals (vs. one), and 32–35 transverse rows of dorsal scales (vs. 27–29 in *A. deppii* and 24–28 in *A. martindelcampoi*). *Abronia oaxacae* (Fig. 4) and *A. mixteca* (Fig. 5) both occur in Oaxaca, but *A. cuetzpali* may be distinguished from these species by having six to eight nuchals in a transverse row across the nape (vs. four in *A. oaxacae*);

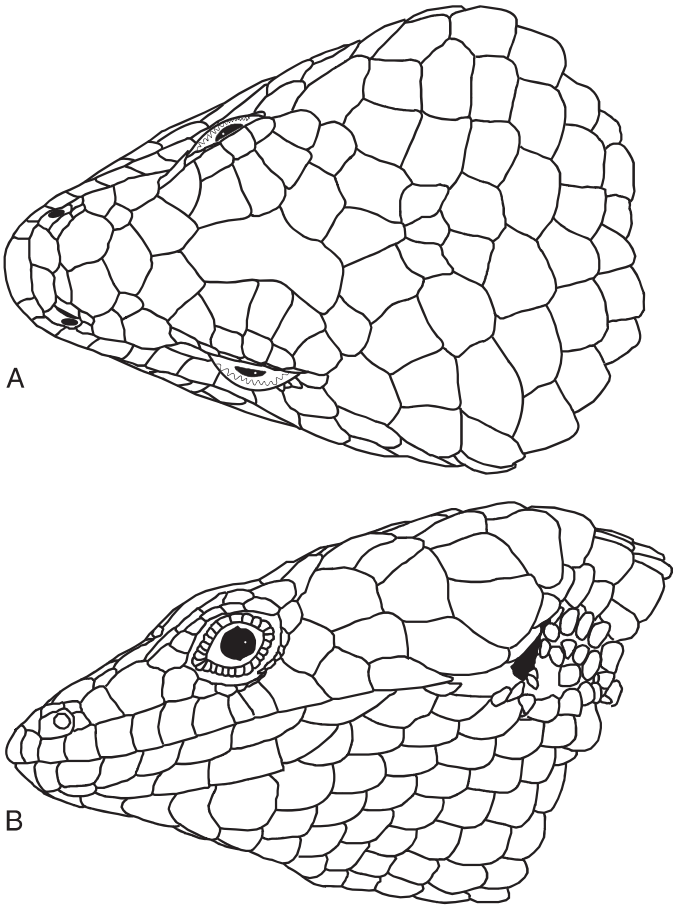

FIG. 2. *Abronia cuetzpali*, dorsal (A) and lateral (B) aspects of head of holotype (MZFC 28761); head length = 27.1 mm.

FIG. 3. Body (A) and head (B) of *Abronia cuetzpali*, paratype (UTA R-61670), adult female, 114 mm SVL, head length 23.7 mm.

relatively small lateral neck scales—minimally seven to eight scales between ventral scales and nuchals (vs. five to six in *A. mixteca*, three to four in *A. oaxacae*; see Fig. 6); the anterior superciliary contacting the cantholoreal (usually no contact in *A. oaxacae*); 32–35 dorsal transverse scale rows (vs. 28–31 in *A. mixteca*, 27–29 in *A. oaxacae*); 39–40 ventral transverse scale rows (vs. 34–37 in *A. oaxacae*); and a more strongly developed ventrolateral fold, containing more granular scales than in *A. mixteca* or *A. oaxacae*.

Description of Holotype.—Adult male, snout–vent length (SVL) 108 mm, head length from rostral to upper anterior edge of auricular opening 27.1 mm, head width at broadest point 21.8 mm (width/length = 80.4%), tail unbroken and unregenerated, tail length 158 mm (1.46 times SVL), and 85 caudal whorls.

One supranasal and two postnasals on each side; upper postnasal slightly larger than lower postnasal; pair of anterior and posterior internasals situated between rostral and frontonasal, with additional scale intervening between anterior and posterior internasals on left side; prefrontals slightly larger than posterior internasals and contact each other medially, precluding frontonasal–frontal contact; single canthal scale on each side, precluding contact between posterior internasal and prefrontal; large cantholoreal extending onto dorsum of canthus rostralis, contacting canthal, prefrontal, and anterior median supraocular; five/five median supraoculars; three/three lateral supraoculars; five/five superciliaries, the anteriormost reaching cantholoreal; frontal large and azygous, fused with left frontoparietal and broadly contacting interparietal; three scales in the occipital region—the interoccipital and slightly larger occipital on either side; two transverse rows of scales separate occipital from first transverse row of nuchals; three primary temporals on each side, lower contacting postoculars, middle contacting postoculars and posterior median supraocular, upper juxtaposed between parietal and median supraoculars, and contacting the frontoparietal; four/four secondary temporals; five/five tertiary temporals; 11/11 supralabials, antepenultimate posteriormost to reach orbit; nine/eight infralabials; postmental divided, followed by four pairs of enlarged chin shields; posteriormost chin shield about half size of preceding scale; five/six sublabials, with anteriormost reaching second (right) or first (left) infralabial, and contacting postmental.

Minimum number of nuchals in transverse series eight with lateralmost scales reduced to about half size of more medial adjacent nuchals; 35 transverse and 14 longitudinal rows of dorsal scales arranged in oblique rows on sides of body; dorsal scales mostly flat but few middorsal scales with feeble, low, rounded ridges; 39 transverse and 14 longitudinal rows of ventral scales; lateral rows of ventral scales not enlarged from more medial ventral scales; head and several anterior rows of nuchals with well-developed osteoderms; more posteriorly on

TABLE 1. Selected transformational series of Oaxacan highland *Abronia* in the subgenus *Abronia* (character numbers pertains to those in Campbell and Frost, 1993).

	A. cuetzpali	*A. mixteca*	*A. oaxacae*	*A. fuscolabialis*
2. Frontonasal scale	Present	Present	Sometimes absent	Present
3. Frontonasal–frontal scale contact	No contact	Variable, usually no contact	Sometimes lacking frontonasal; when present, no contact	No contact
4. Canthal scales (absent when fused with posterior internasal)	Variable	Usually absent	Absent	Present, discrete from posterior internasals
6. Superciliary–cantholoreal scale contact	Present	Present	Usually absent	Present
14. Number of occipitals	2–3	3	3	1
20. Number of transverse rows of dorsal scales	32–35	28–31	27–32	28–32
21. Dorsal scale row orientation	Oblique	Oblique	Oblique	Parallel
22. Osteoderms under first two rows of nuchal scale rows	Moderately developed	Moderately developed	Well developed	Well developed
23. Longitudinal nuchal scale row	6–8; if 8 lateral rows reduced in size	5–6	4	4–6
24. Lateral neck scales	Moderately sized	Enlarged	Enlarged	Granular
25. Ventrolateral fold	Well developed	Reduced	Reduced	Well developed

FIG. 4. *Abronia oaxacae*, adult female from San Juan Tepeuxila, Oaxaca, Mexico. Image courtesy of Luis Canseco-Márquez.

dorsum and flanks of body osteoderms appear very weakly developed or absent; supra-auricular scales granular and nonprotruding; about seven moderately sized scales between lateral nuchals and first large scales on ventrolateral surface of neck; 13 antebranchials from insertion of the forelimb to wrist; ventrolateral fold moderately well developed with small scales and granules interspersed in interstitial skin throughout ventrolateral fold; 19/18 subdigital lamellae on fourth toes.

In preservative (ethanol after formalin), the overall ground color of the dorsum is pale brown, the venter of the head is white, and the body is cream. A slight greenish sheen is present on the anterior flanks and venter. The snout is pale gray, grading to pale brown on dorsum of the head. The ground color of the neck and body is pale brown dorsally, grading to pale gray on the flanks. Darker crossbands are marked with black dots on the flanks and on the tail. The dorsal surfaces of the limbs are grayish; the ventral surfaces of the limbs are cream and the palmar–plantar surfaces and subdigital lamellae are yellowish. The venter of the head and neck are immaculate white and the venter of the body is cream with seven faint crossbands. The dorsum of the tail has 15 brown crossbands. The venter of the tail is pale gray with inconspicuous darker crossbands.

Color in Life.—The holotype has a grayish body ground color; there are seven pale-brown dorsal crossbands on the body, including the nape, extending ventrally to the ventrolateral fold. These crossbands are heavily flecked with black, more so laterally, and are separated from each other by about a single scale middorsally and usually about two scales laterally. The side of the neck and dorsal surfaces of the forelimbs are colored similarly to the body and marked with some black flecking. Several individual scales including the anterior internasals, the

FIG. 5. *Abronia mixteca*, adult female from near Tejocotes, Oaxaca, Mexico, 2,377 m (UTA R-12138).

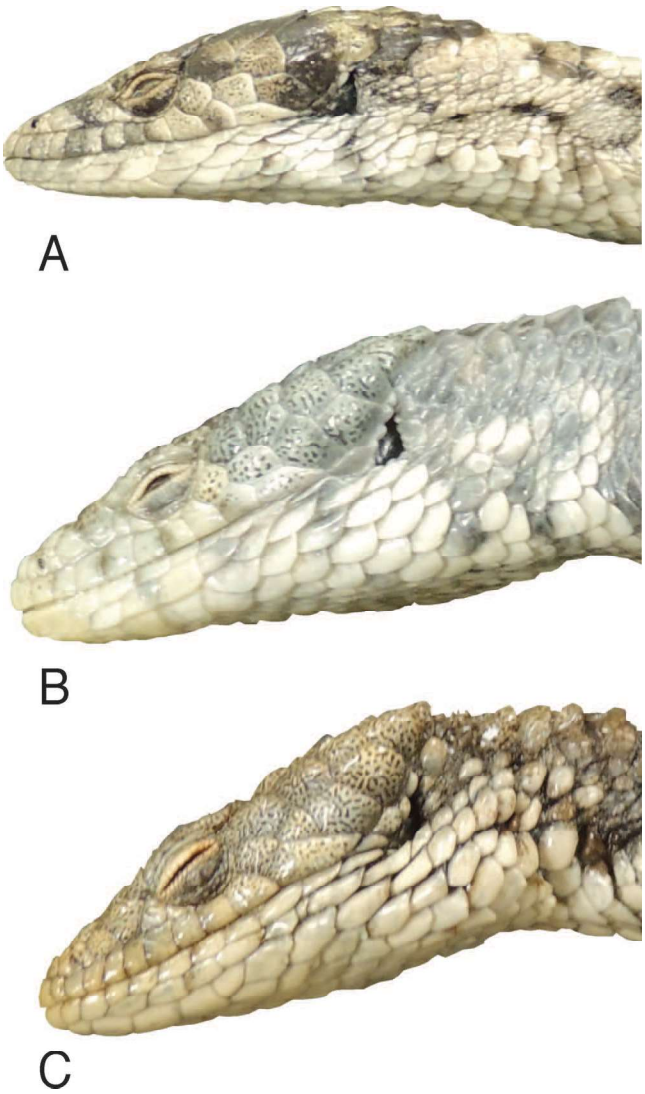

FIG. 6. Variation of lateral neck scales of several species of *Abronia* in the *deppii* group. (A) *A. cuetzpali*, UTA R-61670. (B) *A. mixteca*, UTA R-19650. (C) *A. oaxacae*, UTA R-31197, exposed dark interstitial skin with tiny granules below the nuchals is typical of this species.

left prefrontal, and several scales on the back of the head have a greenish yellow overcast. The top and sides of the head are rugose and accentuated with heavy black vermiculations. The tail is gray with 15 slightly irregular crossbands containing black flecking within their fields. The lower jaw and venter of the head and neck are immaculate white; the venter of the body is very slightly darker than the neck. The iris is whitish with a slight yellowish green sheen.

Variation.—In most respects the two paratypes agree with the holotype. The adult female paratype (UTA R-61670) has a SVL of 114 mm. The length of the head from the rostral to the upper anterior edge of the auricular opening is 23.7 mm, and the head width at the broadest point is 17.8 mm (width/length = 75.1%). The tail is unbroken and unregenerated, having a length of 163 mm and 94 caudal whorls. The upper postnasal is about one-half (left) to two-thirds (right) the size of the lower postnasal. The prefrontals are about 1.5 times the size of the posterior internasals. A large cantholoreal extends onto the dorsum of the canthus rostralis, contacting the internasal, prefrontal, and anterior median supraocular; no canthal scale is present. There are five/six superciliaries. The frontal narrowly contacts the interparietal; there are two scales in the occipital region—the interoccipital and a somewhat smaller occipital on the right side; the posterior portion of the left parietal is highly asymmetrical and extends posteriorly, probably owing to a fusion with the left occipital scale; the usual condition in this species is almost certainly three occipital scales including the interoccipital. There are four/four secondary temporals and five/five tertiary temporals. There are 12/11 supralabials and 8/10 infralabials. There are four/five sublabials, with the anteriormost reaching only the third infralabial. Similar to the holotype the minimum number of nuchals in a transverse series is eight, with the lateralmost scales reduced to about half the size of more medial adjacent nuchals. There are 35 transverse and 14 longitudinal rows of dorsal scales and 40 transverse and 14 longitudinal rows of ventral scales. About eight moderately sized scales occur between the lateral nuchals and the first large scales on the ventrolateral surface of the neck (Fig. 6); there are 12 antebranchials from the insertion of the forelimb to the wrist. There are 19/18 subdigital lamellae on the fourth toes. In preservative (ethanol after formalin) the overall ground color of the dorsum is pale brown and that of the venter of the head and body is cream. A slight greenish sheen is present on the anterior flanks and venter. The dorsum of the head is heavily blotched and mostly dark brown with two irregular crossbands across the snout at the levels of the anterior portion of the internasals and frontonasal. The neck and body are marked with six wide crossbands that extend to the ventrolateral fold. These crossbands have edges of highly irregular dark brown spots. Within the field of the dorsal blotches, a few scattered dark spots are present. The dorsal surfaces of the limbs are mostly pale brown with a few dark brown markings; the ventral surfaces of the limbs are cream and the palmar–plantar surfaces and subdigital lamellae are brown. The venter of the head and neck are immaculate cream and the venter of the body is cream heavily suffused with tan or brown, becoming darker on the lateral portion of the venter. The dorsum of the tail has 15 brown crossbands that are edged with irregular dark brown to black spots. The venter of the tail is mostly gray-brown, marked with only moderately conspicuous, irregular, narrow dark brown and white crossbands, which often do not extend across the venter. In life, UTA R-61670 had a body ground color of tan to pale brown; there were six medium brown dorsal crossbands that extend ventrally to the ventrolateral fold; these crossbands have irregular edges of dark brown to black and are separated from each other by no more than a single scale width middorsally and usually about two scales laterally. The dorsal crossbands also are marked with a few dark spots. The side of the neck and dorsal surfaces of the forelimbs are whitish tan marked with a few small dark spots; the hind limbs are a slightly darker pale brown. The top and sides of the head are medium brown and heavily blotched with dark brown. The tail is medium brown with 15 irregularly blackish edged crossbands; irregular dark spots are scattered within and between the crossbands. The lower jaw and venter of the head and neck are immaculate white; the venter of the body is suffused with brown pigment and darker than the neck but without markings. The iris was whitish silver.

The adult male paratype (UCM 41057) is 115 mm in SVL and has an incomplete tail 114 mm in length; head length 24.6 mm; head width 19.5 mm; head width/length ratio 79.3%; tibia length 12.8 mm; and fourth toe length 11.2 mm. Overall, the specimen agrees in most aspects of scalation, except for the

FIG. 7. Habitat of *A. cuetzpali*, trail through forest 5.4 km east of Juquila, Sierra Madre del Sur, Oaxaca, Mexico, ca. 1,700 m. Photo by Carl Franklin.

following: three scales in occipital region (one interoccipital and two occipitals with the interparietal slightly larger than the flanking occipitals); fewest number of nuchals in transverse row six (all scales in series subequal in size); three/three suboculars and four/four postoculars; nine/nine supralabials and 10/9 infralabials; four/four anterior temporals; about seven lateral neck scales from nuchal row to ventrolateral scales on the neck; 32 dorsal transverse rows and 39 ventral transverse scale rows; 16 ventral longitudinal scale rows; and 19/20 subdigital lamellae on fourth toes. The preserved specimen is uniformly brown dorsally; under magnification each scale on dorsum is finely mottled. The venter of the head and throat are yellow and the venter of the body is yellowish tan. Most of the scales on the chest and belly are black flecked on their anterior portion.

Etymology.—The specific name is a noun in apposition taken from the Nahuatl word for lizard, "cuetzpali," although there are various alternative spellings.

Habitat and Distribution.—On the basis of the three known specimens of *A. cuetzpali*, its distribution extends in the Sierra Madre del Sur of Oaxaca from near Santa Catarina Juquila to San Miguel Suchixtepec, a distance of about 70 km. The known elevational distribution is from 1,711 to 2,150 m. Suitable elevations above 1,500 m and temperate forest are continuous between these localities. There is no reason to believe that *A. cuetzpali* does not range farther to the west and east, where suitable habitat also exists. The area inhabited by *A. cuetzpali* is covered by pine–oak forest (sensu Leopold, 1959) that may have

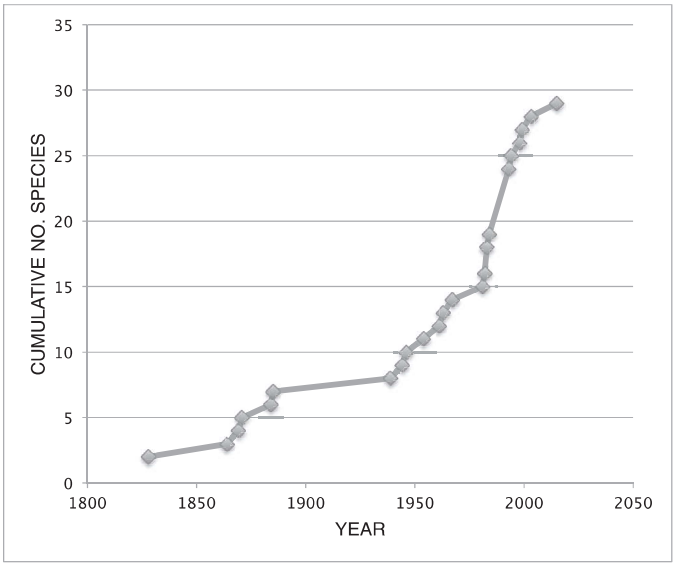

FIG. 8. Accumulation curve for descriptions of new *Abronia* species.

a prominent hardwood component including oaks and a heavy broadleaf understory in some places (Fig. 7).

DISCUSSION

Since the description of the first two species of *Abronia* by Wiegmann (1828), the history of discovery of species in this genus has followed a sigmoid path, increasing exponentially over about the last half century (Fig. 8). As recently as 1938, only 7 species were known; by 1984, some 19 species were recognized; and now, with the addition of *A. cuetzpali*, 29 species are known. Over one-third of *Abronia* species were discovered within the past 30 yr. A cursory examination of the species accumulation curve (Fig. 8) suggests that it is beginning to reach an asymptote, but we are aware of at least two, and possibly up to four, species that await description. One of these is a member of the *A. bogerti* group (subgenus *Scopaeabronia*, sensu Campbell and Frost, 1993) that was mentioned in Campbell and Frost (1993) and Campbell (1994), and another is a member of the subgenus *Auriculabronia* (sensu Campbell and Frost, 1993). Recent collections suggest that additional undescribed species possibly occur in Guerrero and Oaxaca, but we have not examined this material. No other Mexican or Central American lizard genus has experienced a comparable recent surge in known species.

Seven species of *Abronia* are currently recognized from Oaxaca. One species (*A. ramirezi*) is known from an adjacent state and we would not be surprised if it were eventually discovered within the borders of Oaxaca. Two Oaxacan species, *A. bogerti* and *A. ornelasi*, occur east of the Tehuantepec Depression and belong to distinct subgenera (*Scopaeabronia* and *Abaculabronia*, respectively) and are not considered further here. The sole specimen of *A. mitchelli* known from the dense Atlantic versant cloud forest of the Sierra Juárez possesses several unique features and is placed in its own subgenus *Aenigmabronia*. All four remaining Oaxacan species are members of the subgenus *Abronia*; two of these (*A. mixteca*, *A. oaxacae*) are members of the "*deppii*" group characterized by dorsal scales on the flanks that are oriented in oblique rows; these scales are in parallel rows in *A. fuscolabialis* and *A. graminea*. The distributions of species of the subgenus *Abronia* in Oaxaca are as

follows: *A. mixteca* inhabits relatively dry habitat varying from relatively low oak forests with abundant *Tillandsia* and other arboreal bromeliads to pine–oak forests. It occurs from near Tejocotes (Bogert and Porter, 1967), where it occurs on both sides of the Continental Divide northward through the Mixteca Alta region to near the Puebla border and west to the Malinaltepec region of extreme eastern Guerrero (Campbell and Frost, 1993; Canseco-Márquez and Gutiérrez-Mayén, 2010; Martín-Regalado et al., 2012). *Abronia fuscolabialis* is known from several ranges in the northern highlands of Oaxaca, the Sierra Mixe, and the Sierra Juárez (Campbell, 1982; Campbell and Frost, 1993). In the Sierra Mixe it is known from the vicinity of Totontepec and Cerro Zempoaltepec. *Abronia graminea* has been reported from the Sierra Mazateca in extreme northern Oaxaca (Schmidt-Ballardo, 1991).

The distribution of the *A. deppii* group is not without biogeographic peculiarities. All of the species of the group are restricted to the Sierra Madre del Sur and adjacent highlands in Oaxaca and Guerrero, with the exception of *A. deppii*, which occurs along the southern edge of the Mexican Plateau north of the Río Balsas Depression. The closest relative of *A. deppii* appears to be *A. martindelcampoi* in the highlands of Guerrero. The exact nature of how ancestral populations broached the formidable rain-shadow barrier presented by the Balsas Basin remains an open question.

The type locality for *A. oaxacae* is "Oaxaca" and, on the basis of Günther's (1885) description and illustrations of an adult and young (plate 24), there is little doubt that his species pertains to the species that is relatively abundant in the mountains surrounding Oaxaca de Juárez. A*bronia oaxacae* has been reported to range over much of Oaxaca from the mountains north of Oaxaca de Juárez southward into the Sierra de Miahuatlán. Most of the available material of *A. oaxacae* has come from north of the Valley of Oaxaca, particularly in the vicinity of El Punto and Ixtlán de Juárez (Bogert and Porter, 1967; Campbell and Frost, 1993); however, several specimens are known just to the south of Oaxaca de Juárez from near Zaachila and San Vicente Lachixio. Given two obvious aspects of distribution of members of the genus *Abronia* (namely allopatry and confinement to relatively small montane areas), the range of *A. oaxacae*, as previously delimited (Bogert and Porter, 1967; Campbell and Frost, 1993), might have been regarded as suspect. In their analyses, these authors used specimens from several isolated regions in Oaxaca, including the Sierra Aloapaneca, the Sierra de Juárez, and the eastern portion of the Sierra Madre del Sur (Sierra de Miahuatlán). Subsequently, the species was reported from the Sierra de Monteflor (Canseco-Márquez and Gutiérrez-Mayén, 2010). The discovery during the summer of 2012 of *Abronia* in the Sierra de Miahuatlán portion of the Sierra Madre del Sur to the southwest of previous records prompted the re-examination of two specimens available of *A. oaxacae* from this range. This led to the discovery of one of the paratypes of *A. cuetzpali*, which had languished on museum shelves for half a century under the name *A. oaxacae*, and additionally a specimen that had been allocated to *A. mixteca*, here designated as the holotype of *A. cuetzpali*. Another specimen from Santo Domingo Chontecomatlán proves to be *A. oaxacae*, thereby obfuscating what would otherwise be a tidier biogeographic scenario. Perusal of detailed topographic maps show several highland ridges trending from the highlands of central Oaxaca to the east–west-trending Sierra de Miahuatlán, suggesting a possible highland corridor between the two regions.

Campbell and Frost (1993) provided a key for all species of *Abronia* known at the time. Since that publication, several new species in the subgenus *Abronia* have been described. Using the key in Campbell and Frost (1993), *A. martindelcampoi* will key to "*Abronia* species 'Guerrero'" and *A. cuetzpali* will key to *A. mixteca*. Characteristics differentiating the latter two species are provided in the Diagnosis herein.

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A New Species of *Mesaspis* (Squamata: Anguidae) from the High Cuchumatanes of Guatemala

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Abstract.—We describe a new species of anguid lizard of the genus *Mesaspis* from the Sierra de los Cuchumatanes of northwestern Guatemala. This species reaches a maximum snout–vent length of about 72 mm, making it much smaller than *Mesaspis moreletii*. In the Sierra de los Cuchumatanes it occurs sympatrically with *Mesaspis moreletii temporalis*, the only such instance of congeneric sympatry known in Nuclear Central America. The new species appears most similar to the widely distributed species *M. moreletii*, which may be polytypic. *Mesaspis cuchumatanus* may be distinguished from *M. moreletii* by usually having expanded supranasals, 16 longitudinal scale rows, small and granular scales covering the side of the neck from about the level of upper edge of auricular opening to ventrolateral fold, and smaller body size.

Resumen.—Se describe una nueva especie de lagartija del género *Mesaspis* de la Sierra de los Cuchumatanes al noroeste de Guatemala. Esta especie alcanza una longitud hocico-cloaca aproximada de 72 mm, por lo que es significativamente más pequeña que *M. moreletii*. Esta especie se encuentra en simpatria con *M. moreletii temporalis* en la Sierra de los Cuchumatanes, el único caso de simpatría del género en América Central Nuclear. La nueva especie parece ser más similar a *Mesaspis moreletii* que tiene una distribución más extensa y que puede ser politípico. *Mesaspis cuchumatanus* se puede diferenciar de *M. moreletti* por tener las supranasales usualmente expandidas, 16 filas de escamas longitudinales, escamas pequeñas y granulares cubriendo los lados del cuello desde el borde superior de la apertura auricular hasta el pliegue ventrolateral, y un cuerpo más pequeño.

The herpetofauna of the Sierra de los Cuchumatanes of northwestern Guatemala remains poorly known, despite recent discoveries of a multitude of salamanders, anurans, and lizards (e.g., Campbell and Brodie, 1992; Köhler and Smith, 2008; Campbell et al., 2010; Mendelson et al., 2012). Not surprisingly, this range harbors a high number of endemic species, many of which are restricted to relatively modest-sized ranges within the region such as a single mountain slope or peak (e.g., Duellman and Campbell, 1992; Campbell et al., 1998, 2010).

Several genera of anguids are present in the Cuchumatan highlands, but because of their rarity they can hardly be considered to be a conspicuous component of the herpetofauna. The first species of *Abronia* from the region was reported from the southern flanks of the range by Campbell and Frost (1993), who allocated a single individual documented only by photographs to *Abronia aurita*. *Abronia frosti* was described from the northern part of the range by Campbell et al. (1998). Subsequently, several specimens tentatively identified as *Abronia ochoterenai* have been taken at several localities in the northern part of the Cuchumatanes.

Another anguid genus occurring at high elevations in the Cuchumatanes is *Mesaspis*. Among species of the genus *Mesaspis*, *M. moreletii* (Bocourt, 1872) sensu lato has the widest distribution. This species occurs in disjunct populations from the highlands of Chiapas, Mexico, on both the Meseta Central and in the Sierra Madre (Smith and Taylor, 1950), across the Nuclear American highlands (Campbell and Vannini, 1989) to northern Nicaragua (Sunyer and Köhler, 2007). From about central Guatemala through Honduras and El Salvador to northern Nicaragua, *Mesaspis* populations are restricted to several small highland peaks. The range of the species is more extensive in the north where more continuous highlands prevail. Given its wide distribution and many isolated populations, the fact that *M. moreletii* is highly variable in its scale patterns, exhibiting more variability than most other genera in the Gerrhonotinae (Stuart, 1943a; Tihen, 1949), is not surprising. Although characters of lepidosis have been used to differentiate between the five currently recognized subspecies (*Mesaspis moreletii fulvus*, *Mesaspis moreletii moreletii*, *Mesaspis moreletii rafaeli*, *Mesaspis moreletii salvadorensis*, and *Mesaspis moreletii temporalis*), the variability of external morphology and problems of diagnosing these taxa have been noted by practically every author who has considered them. For example, Tihen (1949:222) voiced his frustration stating, "There is so much individual variation in this form, and the localities from which collections of series of individuals have been made are so scattered that areas of intergradation cannot yet be definitely established. The taxonomic arrangement is therefore far from settled . . ." Tihen (1949) further noticed that the population of *M. moreletii* from Sierra de los Cuchumatanes was not typical of *M. m. fulvus*, the geographically most-proximate named taxon. He suggested the Cuchumatan population may possibly represent a three-way intergradation between subspecies (*M. m. moreletii*, *M. m. fulvus*, and *M. m. temporalis*), but because individuals from this population also possessed certain unique characteristics, the situation as he portrayed it may be even more complex. Here we describe a Cuchumatan population of *Mesaspis* that might be easily confused with *M. moreletii*, especially the juveniles and subadults of this species. In doing so, we hope to partially clarify the taxonomic picture of Central American *Mesaspis*. Future studies may reveal the propriety of elevating other isolated *Mesaspis* populations.

Materials and Methods

Scale definitions and protocols for making scale counts follow Bogert and Porter (1967) and Campbell and Frost (1993). The number of longitudinal rows of dorsal scales can be particularly confusing because of the reduced size of one or two rows just

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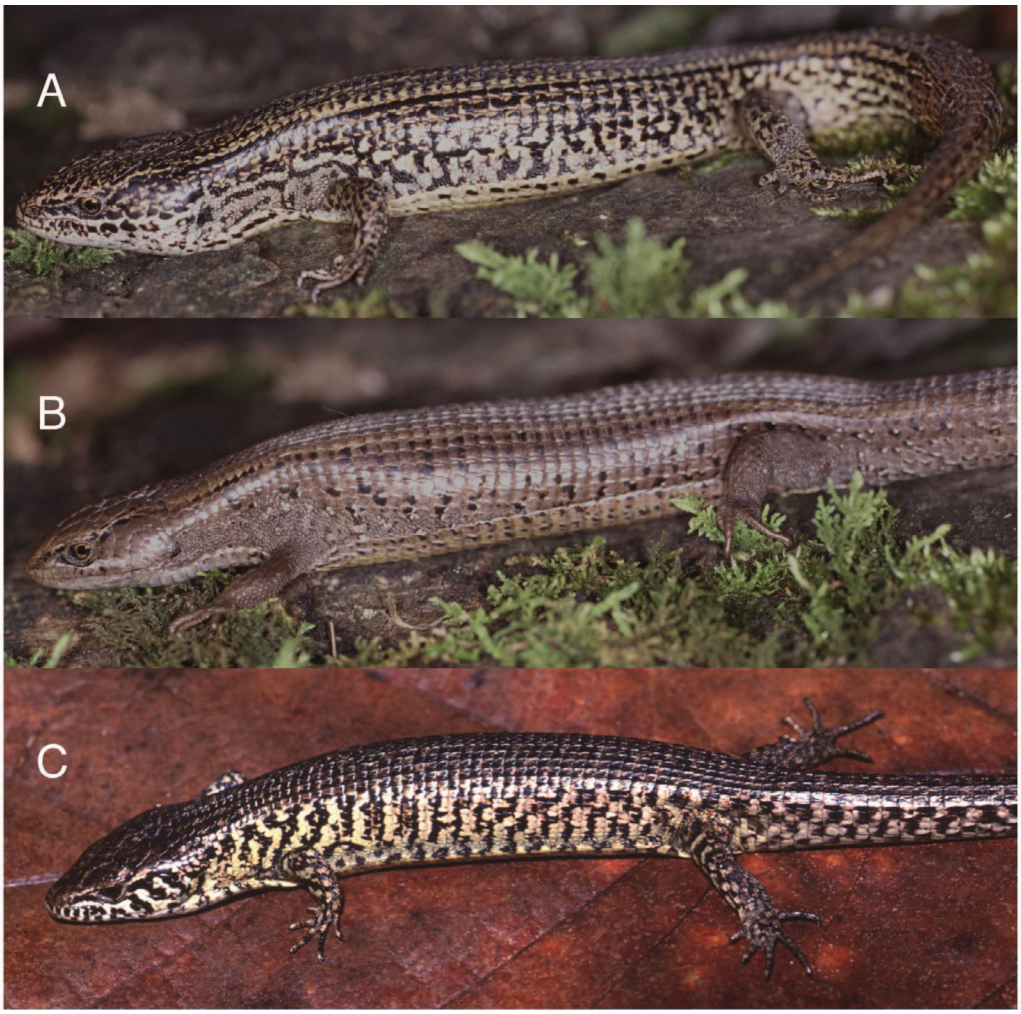

FIG. 1. Species of *Mesaspis* inhabiting the Sierra de los Cuchumatanes, Guatemala. (A) *Mesaspis cuchumatanus*, adult male paratype, UTA R-46014, 12.9 km N Chiantla, ca. 2,900 m. (B) *M. cuchumatanus*, adult female paratypes, UTA R-46015, data same as for UTA R-46014. (C) *M. moreletii*, adult male, UTA R-27398, 2.8 km by road WSW San Mateo Ixtatán.

above the ventrolateral fold; we standardized by counting only rows containing nonreduced scales (Campbell and Frost, 1993:11, footnote 3). Head measurements were made to the nearest 0.1 mm using Vernier calipers held under a dissecting microscope; measurements of the body were made using a metric stick ruler to the nearest 1.0 mm. When the condition of a given character was not identical on the left and right sides, it is indicated as L/R. Data for morphological comparisons were taken from specimens examined and relevant literature (e.g., Tihen, 1949; Karges and Wright, 1987; Good, 1988). Standard abbreviations used are SVL, snout–vent length (front face of rostral to vent); HL, head length (front face of rostral to the upper anterior edge of the auricular opening); and HW, head width (at broadest point). Comparative material was examined from UTA, MVZ, FLMNH, and MZFC (Appendix 1). Museum abbreviations follow Sabaj Pérez (2014). We consulted the published descriptions of morphological features in Campbell and Frost (1993) and Good (1988). Format and terminology in the diagnosis and description follow that of Campbell and Frost (1993).

SYSTEMATIC ACCOUNT

Collections in recent decades have revealed the presence of *Mesaspis* in the Sierra de los Cuchumatanes. Although this is the most-extensive nonvolcanic mountain range in Central America, *Mesaspis* previously was unknown from the region except for one small series reported by Stuart (1943a). This recently secured material has allowed for careful comparisons and analyses of the Cuchumatan sample with those of other highland regions in Central America and Mexico. Somewhat unexpectedly, we have found the Cuchumatan material is representative of two species. We concluded the smaller of the Cuchumatan species has been previously unrecognized and suggest that it be known as:

Mesaspis ***cuchumatanus*** sp. nov.
Figures 1 A–B, 2–4, Table 1

Cuchumatanes Alligator Lizard (English), Escorpioncillo de los Cuchumatanes (Spanish).

Holotype.—UTA R-46096 (original field no. MEA-1645A), an adult male from Cerro Bobic, near San Mateo Ixtatán, Sierra de Los Cuchumatanes, Huehuetenango, Guatemala (15°50′34.57′′N, 91°30′42.33′′W), elevation 2,958 m, collected 20 August 1998 by Manuel Acevedo.

Paratypes.—Thirty-eight specimens from the Sierra de los Cuchumatanes, Huehuetenango, Guatemala. UTA R-27392–27393, 17.1 km (by road) SW San Juan Ixcoy, 3,260 m; UTA R-

TABLE 1. Selected features of *Mesaspis* species. Data are from Tihen (1949), Karges and Wright (1987), Good (1988), and specimens examined.

Character	*M. antauges*	*M. cuchumatanus*	*M. gadovii*	*M. juarezi*	*M. monticola*	*M. moreletii*	*M. viridiflava*
Postmental scale	Divided	Undivided	Divided	Divided	Undivided	Undivided	Undivided
Number of loreals	0	Usually 1, sometimes 2	1	1	1–2	1–3	0
Number of canthals	0–1	Usually 0, rarely 1	1	0	0–2	0–2	0
Number of cantholoreals	1	Often 1	1	1	1–2	0–1	1
Number of suboculars	2	Usually 2, rarely 1 or 3	1	2–3	2–4	1–4	Usually 2, rarely 1
Number of lateral supraoculars	Often 2, sometimes 3	Usually 2, sometimes 3, rarely 4	3	3	2–3	Often 2, sometimes 3, rarely 4	Often 2, sometimes 3
Frontonasal	Absent	Present	Present	Absent	Present	Present	Absent
Prefrontals	Present	Usually fused with frontonasal, sometimes present but reduced	Present	Present	Usually present, often reduced	Present	Present
Dorsal scales	Smooth	Keeled	Keeled	Smooth	Keeled	Keeled	Keeled
Longitudinal dorsal scale rows	16	16, rarely 18	16–18	14, sometimes 16	14–16	18–22	14

27394–27396, 11.1 km (by road) NW Santa Eulalia, 2,760 m; UTA R-36584–36585, 36589, 5.4 km WSW San Mateo Ixtatán, 2,975 m; UTA R-41607, 41610, 3.2 km WSW Patacal, 2,761 m; UTA R-41616, 5.6 km E San Mateo Ixtatán, 2,475 m; UTA R-41617–41619, along road to Patacal, 5.0 km (by road) NW intersection of Guatemala Road 9N (near San Mateo Ixtatán), 2,835 m; UTA R-41621–41622, 5.6 km NW jct of San Mateo Ixtatán to Barillas road and road to Nentón, 2,780–2,800 m; UTA R-46014–46018, 12.9 km N Chiantla, ca. 2,900 m; UTA R-46019–46021, 7.2 km SE Todos Santos, 2,860 m; UTA R-46097–46105, topotypes; MVZ 143480, 143484, 21.8 km N Santa Eulalia, Huehuetenango–Barillas Road; MVZ 143469, 14347, stream below Captzin at km 311 on Huehuetenango-Barillas Road; MVZ 143472, 4.5 km E (by road) Todos Santos on Todos Santos-Paquix Road.

Referred Specimens.—UTA R-39801–39802, Montañas de Cuilco, lado sur de Cumbre del Papal, 2,900–2,970 m.

Diagnosis.—A species of *Mesaspis* characterized by: 1) supranasals usually expanded; 2) frontonasal scale present and usually in broad contact with frontal; prefrontals reduced in size or fused with frontonasal; 3) posterior internasals usually large, sometimes divided; 4) canthals usually absent; 5) parietal not contacting median supraoculars; 6) occipital single; 7) anterior superciliary contacting cantholoreal; 8) postmental single; 9) dorsal scales in 50–58 transverse rows; 10) dorsal scales usually in 16 longitudinal scale rows, scales in lowermost rows half the height of adjacent upper row or triangular shape; 11) ventral scales in 12 longitudinal rows; 12) dorsal scales of neck without keeling; and 13) scales covering lateral side of neck from about level of upper edge of auricular opening to ventrolateral fold small and granular.

Mesaspis cuchumatanus may be distinguished from all species in the *Mesaspis gadovii* and *Mesaspis antauges* groups (sensu Tihen, 1949; Good, 1988) in having one postmental; from all species in the *M. antauges* group in having keeled dorsal scales; from all species in the *M. gadovii* and *M. antauges* groups in usually having two lateral supraoculars; from all species except *M. antauges* in having posterior internasals usually divided; from all congeners in having prefrontals usually fused with frontonasal (Fig. 2), but occasionally prefrontals are present but reduced or lacking on one side. It is most easily distinguished from *M. moreletii*, with which it is sympatric, by its smaller adult body size (<72 mm SVL vs. ≥72 mm SVL); prefrontal scales most-frequently fused with the frontonasal, if prefrontals are present they are much reduced in size; usually having 16 longitudinal dorsal scale rows (vs. 18–22), mostly smooth nuchal scales (vs. keeled), large scales extending down on side of the neck to about the level of the upper edge of the tympanum (vs. level of lower edge of tympanum; see Fig. 3), and a different color pattern. *Mesaspis cuchumatanus* is compared with other species of the genus in Table 1.

Description of Holotype.—Adult male, SVL 56 mm, HL 12.7 mm, HW 9.2 mm (width/length = 0.72); tail complete, 82 mm in length with 68 caudal whorls.

Supranasals elongated and in contact at midline; upper and lower postnasals on each side (the former less than half size of nasal); loreal and nasal scales in contact; two pairs of internasals between rostral and cantholoreals–median supraoculars; posterior internasals about same size as anterior internasals but about twice as wide at widest point; canthals absent such that posterior internasal contacts loreal, cantholoreal, and median supraoculars; single loreal on each side; cantholoreal about as long as high, precluded from contacting supralabial series by contact between loreal and preocular; frontonasal fused with

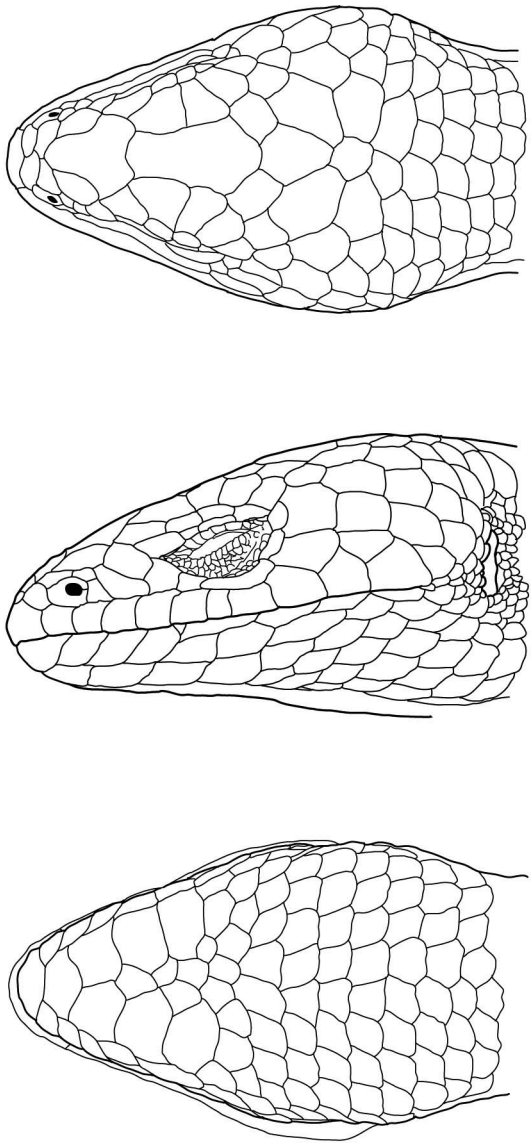

FIG. 2. *Mesaspis cuchumatanus* sp. nov., (upper) dorsal, (middle) lateral, and (lower) ventral aspects of head of holotype (UTA R-46096); head length = 12.7 mm.

FIG. 3. Lateral neck scales of two species of *Mesaspis* inhabiting the Sierra de los Cuchumatanes in the department of Huehuetenango, Guatemala; both adult males. (A) *M. cuchumatanus* sp. nov., UTA R-46101, head length 12.8 mm, Cerro Bobic, near San Mateo Ixtatán, ca. 2,900 m (15.81500°N, 91.47800°W; (B) *M. m. temporalis*, UTA R-59146, head length 18.7 mm, vicinity of Buena Vista Magdalena, 2,429 m (15.55418°N, .91.37424°W). These species vary conspicuously from each other in the size of scales on the side of the neck.

prefrontals, creating broad contact between this azygous scale and frontal; 5/5 median supraoculars, 3/2 lateral supraoculars, and 4/5 superciliaries; first superciliary broadly contacting cantholoreal, narrowly contacting preocular; 1/1 preoculars, 2/2 suboculars, and 3/3 postoculars; frontal broadly contacting interparietal; posterior end of interparietal contacting single occipital; occipital flanked laterally by two parietals and two postparietals; three transverse rows of scales separating occipital from first transverse row of nuchals; 4/4 primary temporals; first primary temporal longitudinally elongated, contacting posterior subocular, lower two postoculars, and two posterior supralabials; second primary temporal as large as first primary temporal, but twice as high, in broad contact with upper postocular, and slightly contacting middle postocular and posteriormost median supraocular; third primary temporal slightly elongated and in narrow contact with posteriormost median supraocular; fourth primary temporal arrowhead in shape and contacting two posterior median supraoculars, frontoparietal, and parietal; 4/4 secondary temporals; 3/3 tertiary temporals; 9/10 supralabials, antepenultimate posteriormost to reach posterior subocular; 8/8 infralabials; postmental not divided, followed by three pairs of enlarged chin shields (scales following posterior pair about half size of chin shields); 4/4 scales in sublabial series, anteriormost reaching only third infralabial and not contacting postmental (Fig. 2).

Minimum number of nuchals in transverse series eight; 52 transverse (from occipital to level of vent); 16 longitudinal rows of dorsal scales, oriented in parallel rows relative to ventrolateral fold; four middorsal longitudinal rows on body keeled with adjacent rows slightly convex, lateral body scales mostly flat; 53 transverse (from posterior chin shield to vent) and 12 longitudinal rows of ventral scales.

Supra-auricular scales granular with about 11 small scales between lateral nuchals and first large scales on ventrolateral surface of neck; 13 antebranchials from insertion of arm to wrist; ventrolateral fold with 2–3 subgranular scales and about 4–5 small granular scales separating adjacent dorsal and ventral longitudinal scale rows; 11/11 subdigital lamellae on fourth toes.

Coloration in Preservative.—(Ethanol after formalin) dorsum of head, body, limbs, and tail predominantly greenish brown with several dark spots or marks; dark irregular marks on head and limbs; dark marks on body tend to group and form three dark lines extending to anterior portion of tail; middorsal line is evident; pale dorsolateral line extending from posterior edge of eye to anterior part of tail, black line bordering below; grayish pale line extending posteriorly from nares and below eyes, around upper portion of auricular opening, and reaching anterior limb insertion; portion of pale grayish line on supralabials surrounded by several dark marks; sides of head, body, and tail predominantly brown with several dark spots or marks; dark marks on side of body tend to be in series forming about 10 dark vertical or V-shaped (or both) bands, usually with small white marks; chin and throat mostly grayish white with dark spots on ventrolateral scales from just below ultimate supra-

labial to anterior limb insertion; venter of body grayish white with several dark spots mostly situated laterally; venter of limbs and tail grayish white with dark spots.

Variation.—Based on 23 of the best-preserved, intact specimens, including holotype, representing different size classes and sexes; seven adult males with SVL of 56–65 mm with cephalic indices (HW/HL) of 0.70–0.76 (mean = 0.73); seven adult females with SVL of 56–72 mm with cephalic indices (HW/HL) of 0.68–0.75 (mean = 0.71); two subadult males with SVL of 54 and 55 mm and cephalic indices of 0.73 and 0.71 (mean = 0.72), respectively; three subadult females with SVL of 48–53 mm and cephalic indices of 0.66–0.74 (mean = 0.71); two juvenile males with SVL of 40 and 45 mm and cephalic indices of 0.65 and 0.70, respectively; two juvenile females with SVL of 42 and 43 mm and cephalic indices of 0.71 and 0.63, respectively; tail complete (unregenerated) in seven specimens, including holotype, 1.19–1.70 (mean = 1.46) times body length with 66–82 (mean = 75.5) caudal whorls.

Single supranasal on each side, unexpanded in 11 individuals, expanded but not reaching midline in 4 individuals, expanded reaching midline in 3 individuals, left scale expanded to midline with right scale expanded but not reaching midline in 3 individuals, right scale expanded at midline and left scale expanded but not reaching midline in 1 individual, right scale expanded but not reaching midline and left unexpanded in 1 individual; postnasals 2/2 in 19 individuals, 2 individuals lacking upper right postnasal, 1 individual lacking both upper postnasals, and 1 individual lacking lower left postnasal; no contact between loreal and nasal scales in 18 individuals, present in 3 individuals, contact on only left side in 2 individuals; 2 pairs of internasals always present; internasals between rostral and cantholoreals–median supraoculars in 9 individuals, between rostral and cantholoreals in 3 individuals, between rostral and cantholoreals–prefrontals in 3 individuals, between rostral and cantholoreal-median supraoculars–prefrontal in 1 individual, with 7 individuals varying on left and right sides; anterior internasals undivided in 20 individuals, 2 individuals with anterior internasals divided, and 1 individual with only left anterior internasal divided; posterior internasals large (about twice size anterior internasals) and undivided in 8 individuals, 11 individuals with divided posterior internasals, 3 individuals with only left posterior internasal divided, and 1 individual with only right posterior internasal divided; no canthals in 19 individuals, 2 individuals with 1/1 small canthal, one individual with small canthal on left side, and one individual with small canthal on right side; 1/1 loreal in 17 individuals, three individuals with 2/2 loreals, two individuals with 1/2 loreals, one individual with 2/1 loreals; cantholoreal about as long as high in 17 specimens, about twice higher than long in 5 specimens, and twice higher than long on left side and as high as long on right side in one specimen; cantholoreal separated from supralabials by contact between loreal and preocular in 12 specimens, separated by small loreal in 2 specimens, and reaching supralabials in 3 specimens; much variation between scalation on sides of head in remaining 6 specimens: cantholoreal on right side reaching supralabials but separated on left side by contact between loreal and preocular in 1 specimen, cantholoreal on left side reaching supralabials, but separated on right side by contact between loreal and preocular in 2 specimens, cantholoreal on left side separated by the contact between loreal and preocular and separated on right side by the presence of small loreal in 2 specimens, and vice versa in 1 specimen; prefrontals lacking in 15 specimens, present in 5 specimens, present on single side in 3 specimens (2 on left, 1 on right); width of contact of frontonasal with frontal is about same width as anterior part of frontal in 15 specimens, about half width of frontal in 3 specimens, extremely reduced and scarcely contacting in 2 specimens, and lacking contact in 3 specimens; 5/5 median supraoculars in 22 specimens, 4/4 in one specimen; 2/2 lateral supraoculars in 11 specimens, 2/3 in four specimens, 3/2 in two specimens, 3/3 in four specimens, 3/4 in two specimens; superciliary series with great amount of variation: one specimen with 2/2 superciliaries, one with 2/4, one with 2/5, two with 3/3, three with 3/4, three with 4/4, four with 4/5, two with 5/4, four have 5/5, and two with 6/6; first superciliary broadly contacting cantholoreal in 22 specimens, in one specimen first superciliary contacting a canthal and a loreal on left side and contacting two loreals on right side; first superciliary narrowly contacting preocular in 20 specimens, no contact in 2 specimens, and 1 specimen with wider contact; 1/1 preoculars in 21 specimens, 2/1 in one specimen, and 2/2 in one specimen; 22 specimens with 2/2 suboculars, one has 1/2, and two have 3/3; 14 specimens with 3/3 postoculars, four with 3/2, two with 2/3, two with 2/2, and one with 4/3; contact between frontal and interparietal about half the width of anterior part of interparietal in 20 specimens, about the same width of anterior part of interparietal in 1 specimen, and about one-third width in 1 specimen; 3 transverse rows of scales separating occipital from first transverse row of nuchals in 13 specimens, separated by 2 rows in 8 specimens, and 1 row in 2 specimens; 4/4 primary temporals in 14 specimens, 3 with 3/4, one with 4/3, three with 5/4, and two with 5/5; lower primary temporal longitudinally elongated in 21 specimens, about as long as high in other 2 specimens; lower primary temporal touching posterior subocular in 19 specimens; lower primary temporal in contact with lower postocular in most specimens (only one specimen with contact absent on right side); lower primary temporal contacting upper and middle postoculars in 16 specimens; second primary temporal as large as the first primary temporal but twice as high in 9 specimens, about same size in 13 specimens, and as large as first primary temporal, but is twice as high on right side but equal in size on left side; second primary temporal in broad contact with upper postocular in 20 specimens (one has slight contact on left side and broad contact on right side, and two specimens lack contact); second primary temporal in narrow contact with middle postocular in 17 specimens, 2 with broad contact, 2 lack contact, 1 with broad contact on left side and narrow contact on right side, and 1 with narrow contact on left side and lacking contact on right side; second primary temporal in narrow contact with median supraocular in 20 specimens, two specimens lack contact and one specimen with contact only on right side; third primary temporal slightly elongated in 17 specimens, three with elongated scale only on right side, one specimen with elongated scale only on left side, and two specimens with no elongated scales; third primary temporal in narrow contact with posterior median supraocular in 16 specimens (in three specimens narrow contact with posterior median supraocular and upper postocular on both sides); one specimen has narrow contact with posterior median supraocular and broad contact with upper postocular on left side, and narrow contact with posterior median supraocular on right side; in two specimens with broad contact with posterior median supraocular and narrow contact with penultimate median supraocular on left side, and narrow contact with posterior median supraocular on right side; one specimen with broad contact with posterior median supraocular

and narrow contact with penultimate median supraocular on right side, and narrow contact with posterior median supraocular on left side; fourth primary temporal arrowhead-shaped in 14 specimens, variously triangular or rhomboidal in shape in other individuals; second primary temporal contacting two posterior median supraoculars in 16 specimens, contacting parietal in 16 specimens (in 3 specimens contact only on right side and in 2 specimens contact only on left, 2 specimens lack contact); 4/4 secondary temporals in 20 specimens (3/4 in two specimens and 3/3 in one specimen); 3/3 tertiary temporals in 14 specimens (2/3 in two specimens, 4/3 in four specimens, and 4/4 in three specimens); 10/10 supralabials in eight specimens (9/9 in four, 9/10 in two, 10/9 in two, 10/11 in two, 11/10 in three, 9/11 in one, and 11/11 in one); antepenultimate supralabial posteriormost to reach posterior subocular in 22 specimens; 7/7 infralabials in 8 specimens (6/6 in one, 6/7 in two, 7/6 in one, 7/8 in three, 8/7 in two, 8/8 in five, and 6/8 in one); postmental not divided in 21 specimens (2 postmentals in one specimen and additional small scale in another); 3/3 enlarged chin shields (3/4 and 4/3 in two specimens, respectively), scales following posterior pair less than half to one-third size of the chin shields; 4/4 scales in sublabial series in 9 specimens (3/3 in two, 3/4 in three, 4/3 in four, 4/5 in two, 5/5 in one, and 5/6 in two); anterior sublabial reaching second infralabial in 13 specimens (reaching 1/2 in one, 2/3 in three, 3/2 in one, 3/3 in four, and 4/4 in one).

Fifty transverse dorsal scale rows (occipital to level of vent) in 6 specimens, 51 in three, 52 in three, 53 in two, 54 in two, 55 in two, 56 in four, 58 in one; 16 longitudinal dorsal scale rows of approximately same size in 9 individuals, 12 individuals with scales in lower lateral rows on one or both sides about half size of other dorsals, only one specimen with 18 dorsal scale rows of about same size and shape; four middorsal longitudinal rows of scales keeled on dorsum (6 in two specimens) and one additional row on each side which is slightly convex in 20 specimens (2 on each side in three specimens); 55 transverse (from posterior chin shield to vent) ventral scale rows in nine specimens (50 in one, 51 in two, 52 in two, 53 in five, 54 in two, 56 in one, and 58 in one); 12 longitudinal rows of ventral scales in all specimens; supra-auricular scales always granular, about 10 small scales between lateral nuchals and first large scale on ventrolateral surface of neck in 6 specimens (8 in five, 9 in six, 11 in four, and 12 in two); 11 antebranchials (counted from the insertion of the arm to wrist) in 12 specimens (10 in six, 12 in four, and 13 in one); ventrolateral fold with 1 subgranular scale separating large dorsal and ventral longitudinal rows of scales in 8 individuals, 1–2 in six, 2 in four, and 2–3 in five; and about 3–4 small granular scales separating these rows of scales in 11 specimens, 2–3 in four, 4 in four, and 4–5 in four; 12/12 subdigital lamellae on the fourth toes in three specimens, 10/10 in one, 10/11 in two, 11/10 in one, 11/11 in one, 11/12 in three, 11/13 in one, 12/11 in two, 12/13 in two, 13/12 in two, 13/13 in one, 13/14 in three, and 14/13 in one.

In preservative (ethanol after formalin), all specimens with dorsum of head, body, limbs, and tail predominantly brown to greenish brown; six males (UTA R-27394, 27396, 39801, 46014, 46096, 46097) with conspicuous irregular dark spots or markings on head and limbs, other specimens with scattered and often smaller spots; three females lacking dorsal black markings or spots on body, no middorsal dark line often present; dark spots or marks along middorsum in seven specimens forming middorsal line, dark spots or markings arranged to form middorsal and dorsolateral lines (dorsolateral lines usually not as evident as vertebral lines) in 13 specimens; conspicuous dorsolateral pale line extending from posterior edge of eye to anterior part of tail in 21 individuals (in two individuals no evident pale line), line inconspicuous posterior to forelimbs in few individuals; dark line (black to dark brown) extending below pale line invariably present; all specimens with grayish pale line extending below eyes (in some specimens extending as far anteriorly as nares), then extending above auricular openings and reaching forelimb insertion; sides of head, body, and tail predominantly brown; dark spots or markings highly variable, especially on head and body; some specimens with few black spots on head and sides of body, others with dark spots and dark vertical or V-shaped (or both) bands covering most of head; in all specimens, some of the dark marks on sides of body have white spots situated at union between two dark scales; ventral surfaces mostly grayish white with small dark spots predominantly arranged laterally, with number and concentration of black spots highly variable among specimens.

Color in Life.—The species is sexually dimorphic; adult males usually have more black spots or markings on their bodies and broader heads. In adult males (Fig. 1A), dorsum and flanks whitish to yellowish tan, heavily marked with black spots on every quadrangular body scale, somewhat irregular on lower flanks but occupying approximately center of each scale on upper flank and dorsum, forming black dorsolateral line extending from behind eye to tail; black markings often forming horizontal black lines on side of neck; supralabials mostly cream with irregular black spots, larger posteriorly. In adult females (Fig. 1B), ground color medium brown with scattered black spots, but not on every scale; a narrow black dorsolateral line from behind eye to base of tail, but not as well defined as in males; supralabials mostly brown, sometimes with small black spots; ground color of flanks may be darker than that of dorsum. In both males and females the black dorsolateral line may be bordered above by a pale line and a middorsal black line may extend from the back of the head to the tail. Juveniles with coppery brown dorsum, dark brown flanks with yellow spots or bars (or both), especially anteriorly; and a few irregular yellow bars on the side of the head.

Etymology.—The species name is taken from the Sierra de los Cuchumatanes, the most extensive mountain range in Central America.

Distribution and Habitat.—*Mesaspis cuchumatanus* is widespread at the higher elevations of the Sierra de los Cuchumatanes, Guatemala, ranging in the south from just north of Chiantla northward to the vicinity of San Mateo Ixtatán (Fig. 4). Several specimens probably attributable to this species have been collected in the isolated highlands of the Montañas del Cuilco, which lie to the southwest of the main portion of the Cuchumatanes. It has not been encountered in the Departamento de Quiché in the eastern portion of the Cuchumatanes, but may occur there. It is sympatric with *M. m. temporalis* in the Sierra de los Cuchumatanes and Montañas del Cuilco.

The main vegetation types reported for the Cuchumatanes are lower montane wet forest, subtropical wet forest, lower montane dry forest, lower montane moist forest, lower montane wet forest, and montane wet forest (Holdridge, 1959). *Mesaspis cuchumatanus* has been taken mostly in the latter three kinds of forest, which occur at high elevations. A predominance of *Abies guatemalensis* forest occurs between 2,900–3,400 m, while at 3,000–3,800 m there prevails a mixed forest of *Juniperus standleyi* and *Pinus hartwegii* (Islebe et al., 1994, 1995; Steinberg and

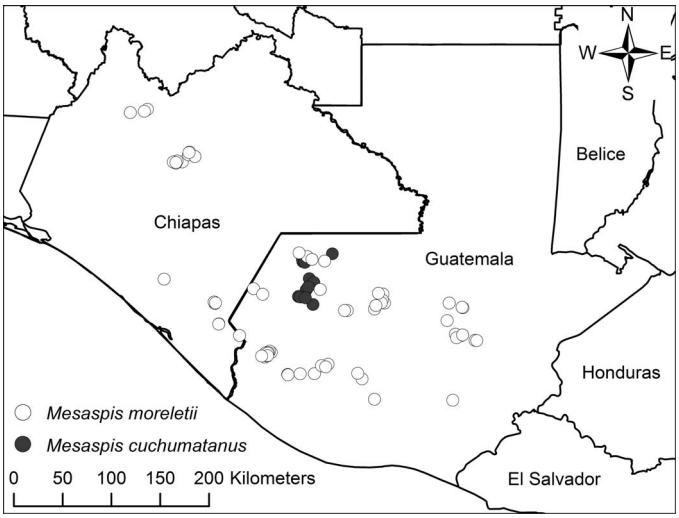

FIG. 4. Distribution of *Mesaspis* in Guatemala and Chiapas, Mexico.

Taylor, 2008). The known elevational distribution for *M. cuchumatanus* is 2,760 m (UTA R-27394–27396) to 3,260 m (UTA R-27392–27393), so it is highly probable that the species is present in a variety of recognized forest types. This species appears to be exclusively terrestrial, as are other members of the genus, and can be found under surface debris or active on the surface. The species has been taken along the edges or forest clearings or in areas that have been recently felled.

One of the collecting sites for *M. cuchumatanus* was close to the type locality of *Abronia frosti*, from where *Bolitoglossa rostrata*, *Pseudoeurycea rex*, *Incilius bocourti*, *Norops crassulus*, *Sceloporus taeniocnemis*, *Thamnophis fulvus*, and *Cerrophidion godmani* have been reported (Campbell et al., 1998).

DISCUSSION

The massive mountain system of the Sierra de los Cuchumatanes extends as a broad arc for some 150 km and reaches elevations of over 3,600 m. In the north the Sierra de los Cuchumatanes trends north–south from near the Mexican border to just north of the city of Huehuetenango, where the highlands curve eastward, extending to a region north of Uspantán in the department of Quiché. The upper reaches of the Cuchumatanes above 2,000 m are isolated from other regions in Guatemala of comparable heights. This range is isolated by lowlands on several sides: to the northwest the basin created by the many tributaries of the Río Grijalva, including the deep entrenchment of the Rio Selegua which separates the Cuchumatanes from the Montañas del Cuilco; to the east and north the low elevations of the Yucatán Platform; and to the southeast by the deep entrenchment of the Río Chixoy and associated tributaries. The Río Chixoy Valley eventually courses northward into the Petén lowlands forming a formidable barrier between highland faunas of the Cuchumatanes and the Verapaces. The single highland corridor into the Cuchumatanes occurs with the Guatemalan Plateau where the highlands separating the Río Grijalva and Río Chixoy drainages reach 1,500–2,000 m. The major tributaries of these two drainages form part of Stuart's (1954a) subhumid corridor. The forest of the highland bridge connecting the Guatemalan Plateau with the Cuchumatanes is covered with sparse pine-oak forest that is very open, lacks continuity, and is devoid of underbrush (Stuart, 1954a; JAC, pers. obs.). This region is relatively xeric and undoubtedly serves as a barrier to mesic-adapted faunas occurring on either side. Based on intensive collecting in this region, *Mesaspis* appears to be absent. Another somewhat tenuous highland connection occurs at the northern periphery of the Cuchumatanes where a narrow ridge scarcely reaching 1,500 m connects the northwestern Cuchumatanes with the Meseta Central of Chiapas. This ridge appears to have provided the corridor by which limited exchange of mid-elevation faunas has occurred.

Although *Mesaspis* has been known from Guatemala since Bocourt (1872), apparently the first report of the genus from the Cuchumatanes was Stuart (1943a), who reported on seven specimens of *M. moreletii* from several localities in the departments of Huehuetenango and Quiché that he assigned to the subspecies *M. m. fulvus*. Stuart (1951) reported two taxa of *Mesaspis* from the Guatemalan Plateau that he considered sufficiently morphologically distinct and geographically isolated to be regarded as separate subspecies. He noted, however, that allocation of individuals to particular taxa often was difficult owing to variation and the frequent presence of atypical individuals within samples. He allocated specimens from the eastern portion of the Guatemalan Plateau to *M. m. fulvus* and those from the western portion of the Plateau and southern range of mountains to *M. m. rafaeli*.

Among the salient characters most frequently separating *M. m. rafaeli* from *M. m. fulvus* are the presence of separated postnasals, presence of posterior prefrontals, and the contact of the posterior loreal with the supralabials; however, *Mesaspis* in general is notorious for the amount of intraspecific variation in head scales within single populations (Tihen, 1949; Karges and Wright, 1987). This is nowhere more evident than in the species described here. Stuart (1963) distinguished *M. m. fulvus* from *M. m. rafaeli* by having an upper postnasal in contact with the lower postnasal and from *M. m. moreletii* by having a belly pattern of scattered, squarish, dark spots and a third infralabial frequently not in contact or just barely in contact with the chin shields. Slevin (1942) reported a large series of *Mesaspis* from "Chichivac" [Chichavac] and Santa Elena in the department of Chimaltenango on the Tecpán Ridge of the Guatemalan Plateau at elevations of 2,640–3,050 m (Slevin, 1939). The frontonasal and frontal were in contact in 84 of these, partially separated in three, and with complete separation in 1 individual; 71 specimens had 18 dorsal longitudinal scale rows and 14 had 20.

The highlands in southeastern Guatemala are not as extensive as those to the west and *Mesaspis* is restricted to a few of the higher peaks. Stuart (1954b) reported *M. m. fulvus* from the Soledad Grande highlands, although the presence of this taxon in the region was missed by subsequent authors (e.g., Good, 1988). In his monograph of the Guatemalan herpetofauna, Stuart (1963) delimited the ranges of *Mesaspis* as *M. m. moreletii* in the mountains of the Verapaces, *M. m. rafaeli* in the mountains of the Sierra Madre of Chiapas into extreme southwestern Guatemala, and *M. m. fulvus* in high elevations of the Plateau of Guatemala. Interestingly, Stuart (1963) makes no mention of the highest, most-continuous massif in Guatemala—the Cuchumatanes—as being within the range of *Mesaspis*, a region from which he previously reported the species (Stuart, 1943a). Stuart (1948) considered *M. m. moreletii* to be restricted to the mountains of Alta Verapaz; however, this taxon was subsequently found in the mountains to the south, including the Sierra de las Minas (Campbell, 2000). In general, most populations of *Mesaspis* in Guatemala occur to well over 2,000 m, and several authors have noted that in mesic regions of cloud forest these lizards may descend to about 1,500 m or even a little

lower (Stuart, 1951; Campbell and Vannini, 1989; Sunyer and Köhler, 2007). This is true in the region of Granja Lorena on the Pacific Versant of Guatemala and in the northeastern cloud forests of Baja Verapaz (Campbell, 2000). The southernmost records for *Mesaspis* in Nicaragua are the lowest at just above 1,300 m (Sunyer and Köhler, 2007). It has been our experience in the highlands of Guatemala that populations of *Mesaspis* are restricted to and isolated at rather high elevations and that populations tend to be highly fragmented and noncontinuous.

Stuart (1943a) noted the herpetofaunal assemblage of the Cuchumatanes to be quite different from adjacent regions and suggested that it comprised a unique faunal area worthy of recognition from any of the adjacent regions. Based on salamander distributions, Stuart (1943b, 1950) recognized the Sierra de los Cuchumatanes as one of the nine major "biotic areas" in Guatemala. Campbell and Vannini (1989) reassessed the faunal area of Guatemala based on the entire herpetofauna. They realized the close relationships between three mountainous regions in Guatemala (the Cuchumatanes, the Montañas del Cuilco, and the Guatemalan Plateau) but divided these highland areas into separate regions. With specific reference to the allopatric populations of *Mesaspis* in the Cuchumatanes and Alta Verapaz, Stuart (1950:27) showed considerable insight by observing it is "probable that differentiation from a widespread prototypic stock took place independently in the two areas."

Previously, only a single, widespread species, *M. moreletii*, was recognized across the Nuclear Central American highlands. The type localities of all described taxa of *M. moreletii* have come from regions to the south of the Cuchumatanes: *M. m. moreletii* from the department of Alta Verapaz at 1,440 m, *M. m. fulvus* from the department of Totonicapan on the southern slopes of the Sierra de Chuacús at 2,460 m, and *M. m. rafaeli* at 2,300 m, near Siltepec in Chiapas in the Sierra Madre of Chiapas. The discovery of *M. cuchumatanus* with *M. m. temporalis* in the Sierra de los Cuchumatanes was somewhat unexpected. *Mesaspis cuchumatanus* is broadly sympatric with *M. m. temporalis* at several localities around San Mateo Ixtatán.

Isolation or reproductive barriers between the two species of *Mesaspis* in the area remain to be ascertained. It is probable that a sexual barrier exists in size because *M. cuchumatanus* is substantially smaller and less corpulent than is *M. m. temporalis*. The color pattern of adult male *M. cuchumatanus* and *M. m. temporalis* is considerably different. Adult male *M. cuchumatanus* tend to have a greenish-brown coloration and darker side patterns whereas adult male *M. m. temporalis* tend to have a predominantly pale-brown coloration and are usually marked with black and white bands on their flanks.

We have made no effort to ascertain exactly what material or information previous authors may have had when dealing with *Mesaspis* from the Cuchumatanes. Indeed, this would not be feasible in most instances. The extreme variation noted in Cuchumatan material by these authors may result from the commingling of *M. cuchumatanus* and *M. m. temporalis*. Therefore, certain names by Tihen (1949), Stuart (1943a), and Good (1988) should possibly be considered synonyms, at least in part, with *M. cuchumatanus*.

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Appendix 1
Specimens Examined

Mesaspis antauges: MEXICO: VERACRUZ: Municipio Alpatlahuac (MZFC 29310-29312).

Mesaspis cuchumatanus. See species account.

Mesaspis gadovii: MEXICO: GUERRERO: Municipio General Heliodoro Castillo: Carretera Puerto del Gallo – El Jilguero (MZFC 16451); Municipio Leonardo Bravo: 3.8 km by road E Carrizal (Corral) de Bravo (MZFC 15252, 15254, 15255); Municipio San Miguel Totolapan: Carretera Nueva Dehli – La Guitarra (MZFC 16452, 16453); Municipio Zirándaro: 50 m del Crucero del Carrizal (MZFC 689, 690); El Puerto (MZFC 587–589, 656–658); 1.6 km S Omiltemi, 2,750 m (UTA R-4127–4150); 0.8–1.6 km S Omiltemi, 2,195–2,286 m (UTA R-4410–4414); 1.6 km E Omiltemi, 2,591 m; (UTA R-4865–4671); Omiltemi, 2,134 m (UTA R-4872–4880). OAXACA: El Tejocote, 2,286 m (UTA R-5793–5798); El Tejocote, 2,134 m (UTA R-25773–25779).

Mesaspis juarezi: MÉXICO: OAXACA: Municipio Concepción Pápalo: Peña Verde, NE de Cuicatlán (MZFC 8695–8697); Municipio Santa María Pápalo: Peña Verde, NE de Cuicatlán (MZFC 8693, 8694); Municipio Santiago Comaltepec: Brecha 60 (MZFC 4508, 4509), N Cerro Pelón, 10.6 km N Cerro Machín (turnoff for Comaltepec) on Hwy 175 (MZFC 15903); 8.5–10.8 km N (by road) crest Cerro Pelón, 2,073–2,451 m (UTA R-25780); 9.8 km N crest Cerro Pelón, 2,438 m (UTA R-4863–4864); 10.8–15.6 km N (by road) Cerro Pelón, 2,027–2,057 m (UTA R-25781–25782); 51 km S Valle Nacional Bridge on Mex Hwy 175 (UTA R-58925–58926).

Mesaspis monticola: COSTA RICA: CARTAGO: Cerro de la Muerte, 11.1 km by road NW Villa Mills, near km post 84 on Ruta Nacional 2, 3,250 m (UTA R-27000–27023); Cerro de la Muerte, 20.3 km by road NW Villa Mills, near km post 75 on Ruta Nacional 2, 3,005 m (UTA R-27024–27027); Cerro de la Muerte, 21.0 km by road NW Villa Mills, near km post 74 on Ruta Nacional 2, 3,000 m (UTA R-27028–27034).

Mesaspis moreletii: GUATEMALA: ALTA VERAPAZ: Cáquipec (UTA R-19693, 19696, 19698, 19700); Montaña Yalijux, Chelemhá (UTA R-27453); near Cáquipec Mines, 20 km E and 6 km S Cobán (MVZ 143464–143467); San Pedro Carcha, Aldea Chirrucbiquim (UTA R-33660); Sierra de Xucaneb, Chelemhá (UTA R-40104–40106). BAJA VERAPAZ: 4 km ENE Chilascó (MVZ 144538); Cerro Quisís (UTA R-6564); Cerro Quisís, near La Unión Barrios (UTA R-19732–19734, 19739–19740); Rta. Nacional 5, 2.6–4.8 km S (by road) Purulhá (MVZ 109365); Finca Quisís, Purulhá (MVZ 146503); Finca San Jorge, 5 km ENE Chilascó (MVZ 160610–16014); near La Unión Barrios (UTA R-28920–28922); Niño Perdido (UTA R-28932); Plantación Santa Teresa, 7.7 km SSE Purulhá (UTA R-6272–6273, 6421, 6423, 6425–6426, 6430, 6500); Refugio Universitario para Quetzal Vuelta del Quetzal (UTA R-7811); Sierra de las Minas, vicinity of Chilascó (UTA R-38852–38857); Sierra de las Minas, Chilascó, Finca San Jorge (UTA R-38851, 38861–38862); vicinity of La Unión Barrios (UTA R-7844–7845, 30818, 46756–46758); Vuelta del Quetzal, 3.8 km SE de Purulhá (UTA R-19731, 19735–19738); Vuelta del Quetzal, Biotopo Mario Dary (UTA R-22122). HUEHUETENANGO: Sierra de los Chuchumatanes, 2.8 km by road WSW San Mateo Ixtatán (UTA R-27398–27399); Montañas del Cuilco, La Democracia, Cumbre entre Ojo de Agua y Hoja Blanca, 1,900–2,200 m (UTA R-41592–41605); 3.2 km WSW Patacal, 2,761 m (UTA R-41608–41609, 41611–41612); 5.6 km E San Mateo Ixtatán, 2,475 m (UTA R-41613-41615); Sierra de los Cuchumatanes, 14.0 km NW jct of San Mateo Ixtatán to Barillas road and road to Nentón, 2,780 m (UTA R-41620); vicinity of San Mateo Ixtatán (UTA R-46110); 1.4 km E Yalambojoch at Río Salchilá (UTA R-52244); vicinity of Buena Vista Magdalena, 2,429 m (UTA R-59146–59148); JALAPA: 4.7 km SW Miramundo (UTA R-28918); between Soledad Grande and Miramundo (UTA R-33176–33177, 33179); Cerro Miramundo, ca. 2,600 m (UTA R-46111); La Soledad, on road to Guatel Tower (UTA R-33158, 33160–33170); Miramundo highlands, near Torre de Guatel (UTA R-46880, 52242); Miramundo, Guatel Tower (UTA R-33190, 33193–33195, 33649–33653, 33655–33658); Soledad Grande, along road to Guatel Tower (UTA R-33183). PROGRESO: San Agustín Acasaguastlán, Sierra de las Minas, S of Cerro Pinalón (UTA R-28934). QUETZALTENANGO: 15.1 km NE Colomba (UTA R-40114–40115, 40578); 3.8 km S (by road) Las Nubes, on road from San Martín to Colomba (MVZ-104163); Finca Lorena on road from San Martín to Colomba (MVZ 104164); Meseta Norte, Volcán Santa María (UTA R-52240); N Volcán Zunil (UTA-R 42014–42017). QUICHÉ: 20.5 km N Uspantán y 4.5 km N Aldea Caracol (UTA R-52241); 19.3 km N Uspantán, N of Aldea El Caracol (UTA R-41994); 3.0 km SSE Chichicastenango, valley between Paxot and Camanibal (UTA R-19691–19692, 19741, 27446–27450, 28930, 28930–

28931); 7.8 km NE (by road) from junction of Carretera Nacional #2 and road to Santa Rosa, on road to Santa Rosa, 2,390 m (UTA R-33184–33185); 9.0 km NE (by road) Nebaj, on road to San Juan Cotzal, 2,010 m (UTA R-33186); ca 4.8 km NE (by road) Nebaj, on road to San Juan Cotzal, 1,760 m (UTA R-33187–33188); Chichicastenango (UTA R-33199); Cordillera de Los Cuchumatanes, 3.5 km NW (by air) Uspantán (MVZ-160728–160731); Ruta Depto. 3, 10.7 km S (by road) Nebaj (MVZ 109384); Uspantán, Camino El Chimel, 1,600–2400 m (UTA R-41988–41989, 41991–41993); 19.3 km N Uspantán, N of Aldeas El Caracol, 2,140 m (UTA R-41994); Uspantán, El Chimel, Colonia Patoja (UTA R-41998); Uspantán, Cumbre El Chimel–San Pablo El Baldio (Lado Este), 2,350 m (UTA R-41990); Santa Cruz del Quiché (UTA R-46108); 20.5 km N Uspantán (UTA R-52241). SAN MARCOS: between km 259–261 on road between San Marcos and San Rafael Pie de la Cuesta, ca. 10–12 km SW of San Marcos, 2,200–2,400 m (UTA R-28916); Aldea La Fraternidad, Finca La Esperanza, 1,825–1,860 m (UTA R-3885–3860, 40010–40015); Municipio Esquipulas Palo Gordo, Aldea La Fraternidad, Finca La Esperanza, 1,880 m (UTA R-40016–40017); vicinity of Aldea Feria y La Trinidad a Aldea La Fraternidad, Finca La Esperanza, 1,200–1,900 m (UTA R-40018–40021); Esquipulas Palo Gordo, Aldea La Fraternidad, Finca La Esperanza (UTA R-40403, 40404, 41581–41589, 41591); Fields above Rta. Nacional 1, 14.1 km W (by road) San Marcos (MVZ 109411); Finca Insula, El Rincón Transect 3, W side of slope, ca. 2–2.5 km W by air) El Rincón (MVZ 104169–10470); NE-trending ridge, 1.0–2.0 km W, 0.0–1.0 km N (by air) El Rincón (MVZ 117107, 117097); ridge 2 km W (by air) El Rincón (MVZ-109460); Ridge W of El Rincón (MVZ 140639, 140641); roadside area along Rta. Nacional 1, 9.5 km W San Marcos (MVZ 117098); Rta. Nacional 1, 14 km W (by road) San Marcos (MVZ-113671); W-facing ridge, ca. 1.0–2.0 km S of summit, between Palo Gordo and La Fraternidad, of Rta. Nacional 1 (MVZ 117099–11104). TOTONICAPAN: 9.5 km W Río Nahualá bridge, 26.0 km WSW Los Encuentros–Atitlán turnoff (UTA R-23733–23738); 34.4 km S Río Pucal on Guatemala Hwy CA–1, 2,620 m (UTA R-27445); just W of summit of Zunil Ridge, along Pan American Hwy (MVZ 228782); María Tecúm Block, Rta. Nacional 1.5 km N, 6 km E (by air) Nahualá (MVZ 109454); W summit of Zunil Ridge, along Pan American Hwy (MVZ 150168). HONDURAS: CORTÉS: Parque Nacional El Cusuco (FLMNH 144734, 144735); Parque Nacional El Cusuco, Bosque Enano (FLMNH 144727); Parque Nacional El Cusuco, Cerro Cusuco landslide (FLMNH 147635); Parque Nacional El Cusuco, Cerro Jilinco (FLMNH 147632, 147633); Parque Nacional El Cusuco, Quebrada de Cantiles (FLMNH 147634, 147636). FRANCISCO MORAZÁN: La Tigra (UTA R-53230); Parque Nacional La Tigra (UTA R-53231–53233); San Juancito (FLMNH 124827). OCOTEPEQUE: 20.1 km E de Nueva Ocotepeque (FLMNH 124828–12429); Carretera Nueva Ocotopeque – La Labor (UTA R-46866, 52245); Reserva Biológica Güisayote, 3.5 km S (by air) of CA-4 at El Portillo de Ocotepeque (MVZ-263868). MEXICO: CHIAPAS: Cerro Mozotal, 16.7 mi (via road to Siltepec) from pass on continental divide above Huixtla (MVZ 191590–19193, 193586–19387); Municipio Unión Juárez: foot road above Colonia Talquian, Volcán Tacaná (MVZ 159516–15917); above Colonia Talquian, Volcán Tacaná (MVZ-159495–159505); 10.9 km ESE San Cristóbal on Mex Hwy 190 (UTA R-8881–8883); 10.5 km E Rayón Mezcala (El Mirador), 1,878 m (UTA R-12192–12193); Grutas de San Cristóbal (UTA R-19685–19690). NICARAGUA: JINOTEGA: Santa María de Ostuma (MVZ 203676); Reserva Natural Cerro Kilambé (FLMNH 156197–15699). EL SALVADOR: CHALATENANGO: E slope Los Esesmiles (MVZ 40273–40280, 40288–40289, 40291–40294, 40296–40298); Los Esesmiles (MVZ 40281–40285, 40300–40302).

Mesaspis viridiflava: MEXICO, OAXACA: Municipio Ixtlán de Juárez: Llano de las Flores, 16.5 mi N de Guelatao, Sierra de Juárez (MZFC 7474); Municipio Santiago Comaltepec: Upslope from Comaltepec, Sierra de Juárez (MZFC 11091); 1 km N Cerro Pelón on Hwy 175 (MZFC 15904); Municipio Santa María Tlahuitoltepec: Carretera Coconales – Zacatepec (MZFC 16084); Municipio Teotitlán del Valle: on road from Teotitlán del Valle, just downslope from Benito Juárez (MZFC 11144); Municipio Totontepec Villa de Morelos, along road above Totontepec (MZFC 16081); ca. 11 miles W Totontepec (MZFC 16074–16078); Sierra Mixe, ca. 13 miles W Totontepec (MZFC 16169–16171); Sierra Mixe, 5.6 miles W Totontepec (MZFC 16186–16188); Sierra Mixe, 11.4 km W Totontepec (MZFC 16189, 16190); 5 km S Totontepec (MZFC 11586–11589); 23.7 km NE Díaz Ordaz, 3,000 m (MZFC 16087); ca. 17.7 km W Totontepec, 2,641 m (UTA R-51934–51940); Carretera Coconales to Zanatepec, 2,490 m (UTA R-51941–51942); Sierra Mixe, ca. 21 km W Totontepec, 2,550 m (UTA R-51943–51944); Cerro San Felipe, 2,900 m (UTA R-51945); Sierra Mixe, 9 km W Totontepec, 2,386 m (UTA R-51946); Sierra Mixe, 13.8 km W Totontepec, 2,606 m (UTA R-51947–51949).

CAPÍTULO III

Relaciones filogenéticas del clado (*Abronia* + *Mesaspis*) inferidas a partir de un fragmento de mtDNA (parte del gen ND4 y los genes adyacentes $tRNA^{His}$, $tRNA^{Ser}$ y parte de $tRNA^{Leu}$) y los genes nucleares BMP2, KIAA-1217 y PRLR

Molecular phylogeny of *Abronia* and *Mesaspis* Alligator Lizards (Anguidae: Gerrhonotinae) reveals multiple origins of arboreality

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ABSTRACT

For nearly four decades, the anguid lizard genera *Abronia* and *Mesaspis* have been regarded as putatively distinct, sister taxa. Recently, two molecular phylogenetic studies have suggested that these genera are not mutually monophyletic. However, their monophyly has not been tested and their phylogenetic relationships remain only partially known. We performed a phylogenetic study of the *Abronia-Mesaspis* clade based on DNA sequences of one mitochondrial and three nuclear genes, including all the species of *Abronia* available to us (18) and all of the species of *Mesaspis*, in addition to multiple representatives of their closest relatives (*Barisia*, *Gerrhonotus*, and *Elgaria*) as well as more distant outgroups, in order to test the monophyly of the former genera and investigate their phylogenetic relationships. Also, we preliminarily address several species delimitation problems in the clade, involving both already described taxa and previously unknown populations of uncertain taxonomic status. Our results suggest that *Abronia* and *Mesaspis* are not mutually monophyletic, and that species of *Abronia* and *Mesaspis* west and east of the Isthmus of Tehuantepec form two reciprocally monophyletic groups. Also, some species of *Abronia* and *Mesaspis* on the highlands of eastern Mexico west of the Isthmus form a strongly supported clade nested within the first of those groups. Our results also suggest that the subgenera *Auriculabronia* and *Scopaeabronia* may be monophyletic groups. In contrast, the subgenus *Abronia* is paraphyletic with respect to several lineages of *Mesaspis*. Furthermore, our phylogenetic hypotheses suggest the existence of several undescribed species in the *Abronia-Mesaspis* clade, the non-exclusivity of the subspecies of *M. gadovii*, and potential gene flow between *A. graminea* and *A. taeniata*. However, our results do not support the distinctness of *A. campbelli* nor *A. meledona*.

Key words: *Abronia* – *Mesaspis* – phylogeny – systematics - species tree

1. Introduction

Lizards of the genus *Abronia* are mainly arboreal, although they can be occasionally found on the ground. *Abronia* lizards are generally stout-bodied, with relatively long and well-clawed limbs (the other Gerrhonotinae genera usually have shorter limbs), a widened depressed head, and a prehensile tail. Most species of *Abronia* inhabit *Pinus*, *Pinus-Quercus*, *Quercus*, and cloud forests, mainly between 1,500 and 2,800 meters of elevation, although some species like *A. bogerti*, *A. chiszari*, and *A. ramirezi* can be found at elevations as low as 660 meters (Campbell and Frost, 1993; Clause et al., 2016b). Although some species are brightly colored, most of them have cryptic colorations (Campbell and Frost, 1993; Clause et al., 2016a). Currently, 29 species of *Abronia* are recognized (Campbell et al., 2016), most of which have small geographic distributions. The known distribution of the genus extends from the highlands of Tamaulipas and Michoacán on the Atlantic and Pacific versants of Mexico, respectively, south and east to Honduras and El Salvador (Campbell and Frost, 1993; Centenero-Alcalá et al., 2009; Fig. 1).

In contrast, lizards of the genus *Mesaspis* are terrestrial, tend to have slender bodies, shorter limbs and claws, and a narrower depressed head than lizards of the genus *Abronia*; also, they lack a prehensile tail. Species of *Mesaspis* inhabit mainly *Pinus*, *Quercus*, *Pinus-Quercus* and cloud forests between 1,100 and 3,800 meters of elevation (Good, 1988; Solano-Zavaleta et al., 2016; Solano-Zavaleta and Nieto-Montes de Oca, 2018). These lizards have mostly brown to dark brown colorations that can favor camouflage in terrestrial habitats. The genus contains 10 recognized species, most of which also have small geographic distributions, and occurs from the highlands of Veracruz and Guerrero, on the Atlantic and Pacific versants of Mexico, respectively, south and east through Central

America to extreme western Panamá (Good, 1988; Savage, 2002; Solano-Zavaleta et al., 2016, 2017; Solano-Zavaleta and Nieto-Montes de Oca, 2018; Fig. 2). Based on some differences in their morphology and presumably their habits (e.g., arboreal vs terrestrial), *Abronia* and *Mesaspis* have been unquestioned as distinct genera for nearly the last four decades.

1.1.The systematics of *Abronia* and *Mesaspis*

The anguid lizard subfamily Gerrhonotinae is thought of as composed of five genera: *Abronia*, *Barisia*, *Elgaria*, *Gerrhonotus*, and *Mesaspis* (Uetz et al., 2018). The phylogenetic relationships among and within these genera has been the subject of numerous studies. Good (1988) provided a pioneering phylogenetic hypothesis of the relationships among gerrhonotine genera based on external morphology. In his phylogenetic hypothesis (Fig. 3), *Abronia* and *Mesaspis* were sister taxon to each other, and their closest relatives were *Barisia*, *Elgaria*, *Gerrhonotus*, and *Coloptychon* (now transferred to *Gerrhonotus*, see García-Vázquez et al., 2018), in that order. A few years later, Campbell and Frost (1993) performed a taxonomic revision of *Abronia* that included the description of four new species, a phylogenetic analysis based on external morphology, natural history and conservation notes, and a key. In this work, Campbell and Frost (1993) recognized 23 species, classifying them into six subgenera: *Abaculabronia*, *Abronia*, *Aenigmabronia*, *Auriculabronia*, *Lissabronia* and *Scopaeabronia*. The contents and geographic distribution of these subgenera are given in Table S1 (see also Fig. 1). In their phylogenetic analysis, Campbell and Frost (1993) employed *Mesaspis* and *Barisia* as first and second outgroups,

99 respectively, based on the phylogenetic hypothesis of Good (1988), and assuming the
100 monophyly of *Abronia* with respect to *Mesaspis*.
101 The first phylogenetic analysis of *Abronia* based on DNA sequence data
102 (Chippindale et al., 1998) was focused on the subgenus *Auriculabronia*; it included only 11
103 species of *Abronia* and was based on fragments of the cytochrome b and 12S ribosomal
104 RNA mitochondrial genes. Chippindale et al. (1998) also employed representatives of
105 *Gerrhonotus*, *Barisia*, and *Mesaspis* (*G. liocephalus*, *B. imbricata*, and *M. gadovii*,
106 respectively) as outgroups based on the phylogenetic hypothesis of Good (1988), and also
107 assuming the monophyly of *Abronia* with respect to *Mesaspis*. Subsequent molecular
108 phylogenetic analyses of the relationships among anguid lizards (e.g., Macey et al., 1999;
109 Wiens and Slingluff, 2001) were based on few mitochondrial genes and included a single
110 representative each of *Abronia* and *Mesaspis*. Thus, although these analyses found support
111 for the monophyly of Gerrhonotinae and the *Abronia-Mesaspis* sister taxon relationship,
112 they did not provide clues about the monophyly of these genera. Other works have
113 addressed the relationships within *Barisia* (Bryson and Riddle, 2012; Zaldivar-Riverón et
114 al., 2005) or *Elgaria* (Leavitt et al., 2017); the phylogenetic placement of particular taxa
115 (*Gerrhonotus parvus*; Conroy et al., 2005), the relationships within *Gerrhonotus* and the
116 phylogenetic placement of *Coloptychon* (García-Vázquez et al., 2018), or the species limits
117 within the former *Mesaspis moreletii* (Solano-Zavaleta and Nieto-Montes de Oca, 2018).
118 These studies used a single representative of *Abronia* (Bryson and Riddle, 2012; Conroy et
119 al., 2005; Leavitt et al., 2017; Solano-Zavaleta and Nieto-Montes de Oca, 2018) or two
120 representatives of *Abronia* and one of *Mesaspis* (García-Vázquez et al., 2018; Zaldivar-
121 Riverón et al., 2005) as outgroups, and in none of them the monophyly of *Abronia* and
122 *Mesaspis* was tested. Nonetheless, when two species of *Abronia* and one of *Mesaspis* were

included (García-Vázquez et al., 2018; Zaldivar-Riverón et al., 2005), some analysis suggested that *Abronia* may not be monophyletic with respect to *Mesaspis*.

In an unpublished M. Sc. thesis, Solano-Zavaleta (2011) performed a phylogenetic analysis of gerrhonotine lizards, based on one mitochondrial gene, that included 12 species of *Abronia* and all of the species of *Mesaspis* recognized at the time, except for *M. antauges*. In this analysis, *Abronia* and *Mesaspis* were not reciprocally monophyletic. Also, a supermatrix phylogeny of Squamata based on seven nuclear and five mitochondrial genes (Pyron et al., 2013) suggested that *Abronia* and *Mesaspis* are not reciprocally monophyletic. This work included 12 species of *Abronia*, but only two of *Mesaspis*. Thus, in summary, the systematics of *Abronia* and *Mesaspis* has been relatively neglected and, although there is some evidence that *Abronia* and *Mesaspis* are not reciprocally monophyletic, their monophyly has not been rigorously evaluated.

In this study, we perform a phylogenetic study of the *Abronia-Mesaspis* clade based on DNA sequences of one mitochondrial and three nuclear genes, including all the species of *Abronia* available to us (18) and all of the species of *Mesaspis*, in addition to multiple representatives of their closest relatives (*Barisia*, *Gerrhonotus*, and *Elgaria*) as well as more distant outgroups, in order to test the monophyly of the former genera and investigate their phylogenetic relationships.

2. Materials and methods

2.1. Taxon sampling

Because previous works (Pyron et al., 2013; Solano-Zavaleta, 2011) and preliminary results suggested that *Abronia* and *Mesaspis* are not reciprocally monophyletic, we sampled from the geographic distribution of both genera in Mexico and Central America including representative samples of as many species of each genus as possible (18 and all 10 recognized species of *Abronia* and *Mesaspis*, respectively). Previous works and/or preliminary results also have suggested the need to reevaluate the species limits between *A. graminea* and *A. taeniata* (Clause et al., 2018), between *A. campbelli* and *A. meledona* (Chippindale et al., 1998), and between the subspecies of *M. gadovii* (Solano-Zavaleta, 2011). Thus, an effort was made to include multiple samples of each of these taxa. In addition, we included samples of several populations of uncertain taxonomic status which might represent undescribed taxa (treated here as "*Abronia* sp.": *A.* sp. Guerrero ANMO-3343, *A.* sp. Guerrero MZFC-28966, *A.* sp. Laguna Bélgica, Chiapas, and *A.* sp. Huehuetenango, MVZ-265219. Finally, we included representatives of three Gerrhonotinae genera (*Barisia*, *Elgaria*, and *Gerrhonotus*) and more distantly related taxa (*Shinisaurus*, *Xenosaurus*, *Anniella*, *Celestus*) to root the tree (Pyron et al., 2013). The individual samples sequenced and their localities are given in Table S2 (See also Fig. 4).

2.2.1. Data

We sequenced a mtDNA fragment including the gene encoding ND4 (part) and the adjacent genes encoding $tRNA^{His}$, $tRNA^{Ser}$, and $tRNA^{Leu}$ (part) for all specimens included in this study (Table S2). This mtDNA fragment has been used previously to investigate evolutionary relationships among and within anguid genera (Solano-Zavaleta, 2011; Solano-Zavaleta and Nieto-Montes de Oca, 2018; Zaldivar-Riverón et al., 2005). In

addition, we sequenced three protein-coding nuclear gene (nDNA) regions: BMP2 (Bone morphogenetic protein 2), KIAA1217 (Sickle tail protein), and PRLR (Prolactin receptor). Congruence between mtDNA genes trees and nDNA genes trees is unexpected (Moore, 1995; Wiens and Penkrot, 2002; Zink and Barrowclough, 2008) because nuclear genes have longer coalescence times compared with mtDNA genes, and because the stochastic nature of the coalescent process. However, if congruence is present in at least some lineages in the phylogeny, it may constitute evidence of probably long-term lineage isolation (Zink and Barrowclough, 2008). Because nDNA genes are highly conserved compared to mtDNA genes (Zink and Barrowclough, 2008), only representative samples of each clade concordant with geography in the mtDNA tree were sequenced for nDNA markers (Table S2).

2.2.2. Laboratory protocol

Genomic DNA was extracted from tissue previously stored at -70 °C using the standard phenol-chloroform-isoamyl protocol (Hillis et al., 1996) or the extraction protocol for reptile shed skins of Fetzner (1999). All the sequenced genes were amplified via the polymerase chain reaction (PCR). The primers used to amplify and sequence these genes are given in Table S3. Standard PCR protocols were used to amplify the mtDNA fragment and the nuclear gene KIAA1217, whereas the nuclear genes BMP2 and PRLR were amplified using the protocols of Townsend et al. (2008). PCR products were purified with PEG precipitation (Lis, 1980). DNA templates were sequenced with the Big Dye Terminator v.3.1 cycle sequencing kit (Applied Biosystems, Inc.). The reaction products

were cleaned using Sephadex columns and sequenced with an ABI 3100 automated Genetic Analyzer Sequencer (Applied Biosystems, Inc.).

2.3. Phylogenetic analyses

Sequences were assembled and edited using Sequencher v 4.1.4 (Gene Codes Corporation, Ann Arbor, MI). Sequence alignment for each locus was performed using the Muscle algorithm (Edgar, 2004) in Mega v. 7.0 (Kumar et al., 2016), and adjusted visually in Mesquite v 3.5 (Maddison and Maddison, 2018). Ambiguities were treated as missing data. All the sequences were deposited in GenBank (Table S4).

Phylogenetic analysis of the DNA alignments was performed using Bayesian inference (BI) and maximum likelihood (ML) methods. For the analysis of each alignment, we used PartitionFinder v 2.1.1 (Lanfear et al., 2016) to select the best-fitting partitioning scheme and substitution model for each partition with the corrected Akaike Information Criterion (AICc), the MrBayes models option, and the three codon positions of each protein-coding gen and the combined mitochondrial tRNA sequences as data blocks. For the Bayesian analyses, the partitioning schemes and substitution models (in parentheses) for each alignment were as follows: a single partition for the mtDNA fragment (GTR+I+G), each of the individual nuclear genes (BMP2 [SYM+I], KIAA1217 [GTR+I], and PRLR [HKY+G]), and the concatenated nuclear genes (GTR+G) alignments, and two partitions (one including the ND4 first and third codon positions and the third codon position of all nuclear genes, and the other one including the ND4 second codon position, tRNA fragments, and first and second codon positions of all nuclear genes) for the concatenated mitochondrial and nuclear genes alignment (GTR+I+G for both partitions).

The partitioned Bayesian analysis of each dataset was performed using MrBayes v 3.2.6 (Ronquist et al., 2012) in the CIPRES Science Gateway (Miller et al., 2010) and consisted of two independent runs, each with four chains, which were run for 1×10^8 generations, sampling every 1,000 generations. We evaluated convergence between the two runs onto the stationary distribution using the average standard deviation of split frequencies and potential scale reduction factor diagnostics in MrBayes (Ronquist and Huelsenbeck, 2003), and by ensuring that all parameters had ESS values > 1000 using Tracer v 1.7 (Rambaut et al., 2018). In addition, we assessed topological convergence using the R package RWTY v 1.01.1 (Warren et al., 2017) in R v 3.4.0 (R Core Team, 2017), verifying that each run had mixed well and converged on a stationary distribution, that independent runs were sampling from similar areas of tree space and that the posterior probabilities were correlated (correlation coefficient > 0.95), and that the topological ESS values were > 1000. The first 25 million generations (25%) were discarded as burn-in, and the post burn-in trees were used to build a 50% majority-rule consensus tree. Nodes were considered significantly supported if their posterior probabilities (PP) were ≥ 0.95 (Huelsenbeck and Rannala, 2004).

The ML analysis of each dataset was performed using RAxMLGUI v 1.5b1 (Silvestro and Michalak, 2012). For each dataset, we used the selected partitioning scheme (see above) and the following substitution model: mtDNA fragment, GTRGAMMAI; BMP2 and KIAA1217, GTRI; PRLR, GTRGAMMA; concatenated nuclear genes, GTRGAMMA; and concatenated mitochondrial and nuclear genes, GTRGAMMAI. We performed rapid bootstrap analyses with 1000 replicates (Stamatakis et al., 2008). Nodes were considered as significantly supported if their bootstrap value was ≥ 70% (Hillis and Bull, 1993).

241 In addition, we estimated the species tree using the coalescent-based species tree
242 inference program *BEAST v.1.8.1 (Heled and Drummond, 2010). All nuclear sequences
243 were examined by eye and heterozygous individuals were identified as having two alleles
244 of the same length containing nucleotide substitutions. Gene sequences for heterozygous
245 individuals were phased using PHASE v2.1.1 (Stephens et al., 2001; Stephens and
246 Donnelly, 2003). Input files were prepared using the online tool seqPHASE (Flot, 2010).
247 PHASE outputs were converted back to sequence alignments using SeqPHASE. We used
248 TOPALI v2.5 (Milne et al., 2009, 2004) to test for recombination in the nuclear sequences
249 using the Difference in Sums Square test (McGuire and Wright, 2000). No evidence of
250 recombination was found. The best partitioning scheme and substitution model for each
251 partition were determined as described above and were as follows (models in parentheses):
252 a single partition for the mtDNA fragment (GTR+I+G+X) and each of the individual
253 nuclear genes: BMP2 (GTR+I+X), KIAA1217 (GTR+G+X), and PRLR (HKY+G+X).
254 The all-genes analysis in *BEAST was performed under an uncorrelated, lognormal
255 relaxed molecular clock for each locus where the mean clock rate of 1.0 was fixed for the
256 ND4 gene and rates for the other loci were estimated relative to this gene. The tree prior
257 was set to the Yule process, while the population size model was set to Piecewise Linear
258 and Constant Root; all other parameters not mentioned were given the same (non
259 informative) priors across all analyses. Analyses consisted of two independent runs, which
260 were run for 2×10^8 generations each, with the first 40 million generations (20%) discarded
261 as burn-in, saving every 20,000th tree. Convergence was assessed as above. Species trees
262 for each analysis were produced using TreeAnnotator (Drummond and Rambaut, 2007),
263 where we used the median node heights to construct the maximum clade credibility tree
264 with a minimum clade credibility value of 0.5.

3. Results

The mtDNA dataset included a total of 228 individuals (Table S2) and consisted of 672 unambiguously aligned nucleotide positions corresponding to the ND4 gene and 171 corresponding to the adjacent $tRNA^{His}$, $tRNA^{Ser}$, and $tRNA^{Leu}$ genes. Of the 228 individuals, 115 represented all known (10) species of *Mesaspis* and 75 represented 18 species of *Abronia*. The BMP2, KIAA-1217, and PRLR nuclear marker datasets consisted of 563, 524, and 557 unambiguously aligned nucleotide positions and included 76, 64, and 69 individuals, respectively, where 31, 30 and 30 sequences represented nine species of *Mesaspis* and 36, 28 and 31 represented 16, 14 and 15 species of *Abronia*, respectively.

3.1. Phylogenetic relationships of *Abronia* and *Mesaspis*

3.1.1. Mitochondrial tree

The Bayesian mitochondrial tree was moderately well resolved and supported (Figs. 5, S1). *Abronia* and *Mesaspis* comprised a strongly supported clade whose closest relatives were the genera *Barisia*, *Gerrhonotus*, *Elgaria*, and *Anniella*, in that order. All these relationships were strongly supported, except for the sister taxon relationship between *Barisia* and the (*Abronia* + *Mesaspis*) clade. Nonetheless, *Abronia* and *Mesaspis* were not reciprocally monophyletic. Instead, several clades of haplotypes of *Abronia* or *Mesaspis* were intermingled across the tree and grouped into larger clades concordant with geography, rather than taxonomy.

289 In the following description, all the clades and relationships were strongly
290 supported, unless noted otherwise. The (*Abronia* + *Mesaspis*) clade was approximately
291 symmetrical, and one basal clade was composed of all the haplotypes of *Abronia* and
292 *Mesaspis* from Mexico west of the Isthmus of Tehuantepec (Western *Abronia-Mesaspis*
293 clade hereafter), whereas the other basal clade was composed of all the haplotypes of
294 *Abronia* and *Mesaspis* from Mexico and Central America east of the Isthmus (Eastern
295 *Abronia-Mesaspis* clade hereafter). The only exception were the haplotypes of *A. bogerti*,
296 which came from the Sierra Madre of Oaxaca east from the Isthmus of Tehuantepec but
297 were placed in the Western *Abronia-Mesaspis* clade.
298 In the Western *Abronia-Mesaspis* clade, haplotypes were arranged in six well
299 resolved clades of *Abronia* and/or *Mesaspis*; however, the majority of the relationships
300 among these clades were unresolved or weakly supported: (1) a small clade of *Abronia* with
301 *A. chiszari*, from the Los Tuxtlas range at the northern end of the Isthmus of Tehuantepec,
302 and *A. bogerti* (which included the sample of *A.* sp. Laguna Bélgica, see below), from the
303 Sierra Madre of extreme eastern Oaxaca; (2) and (3) a clade each of *Abronia* (*A. oaxacae* +
304 (*A. cuetzpali* + *A. mixteca*)) and *Mesaspis* (*M. viridiflava*) from the Sierra Madre del Sur of
305 Oaxaca, which were strongly supported as sister taxon to each other; (4) a clade of *Abronia*
306 from the Sierra Madre del Sur of Guerrero (*A.* sp. Guerrero ANMO-3343 + (*A. deppii* + (*A.*
307 sp. Guerrero MZFC-28966 + *A. martindelcampoi*))); (5) a clade of *M. gadovii*, from the
308 Sierra Madre del Sur of Guerrero and Oaxaca, and (6) a clade with a subclade of *Abronia*
309 (*A. fuscolabialis* + (*A. graminea* and *A. taeniata*, which were not reciprocally
310 monophyletic)) and another one of *Mesaspis* (*M. antauges* + *M. juarezi*) from the highlands
311 of the Atlantic versant of Mexico west of the Isthmus of Tehuantepec (Sierra Madre
312 Oriental, eastern extreme of the Trans-Mexican Volcanic Belt, and northern mountain

313 ranges of the Sierra Madre del Sur of Puebla and Oaxaca, or Mexican Eastern Highlands
314 for simplicity hereinafter).

315 The Eastern *Abronia-Mesaspis* clade was composed of a weakly supported subclade
316 with *A. ornelasi*, from the Sierra Madre of extreme southeastern Oaxaca, as sister taxon to a
317 clade with all the haplotypes of *Mesaspis* from Central America, and a subclade with all the
318 haplotypes of *Abronia* also from Central America. The *Mesaspis* clade was composed of
319 two asymmetrical basal clades. In the smaller basal clade, *M. moreletii* was the sister taxon
320 to *M. rafaeli*, and these two taxa comprised the sister group to *M. cuchumatanus*. In the
321 larger basal clade, *M. salvadorensis* was the sister taxon to *M. temporalis* and *M. moreletii*
322 Honduras the sister taxon to *M. moreletii* Nicaragua, and these four taxa comprised the
323 sister group to *M. monticola*. In the *Abronia* clade, *A. smithi*, from the Sierra Madre of
324 Chiapas, was the sister taxon to all the remaining haplotypes in the clade, which were
325 divided into two clades: a small clade with the haplotypes of *A. lythrochila* and *A.*
326 *fimbriata*, from the highlands of central Chiapas and central Guatemala, respectively, and a
327 larger clade from the highlands of the Sierra Madre of southern Chiapas and Guatemala. In
328 the latter clade, the haplotypes of *A. campbelli* and *A. meledona*, from the eastern portion of
329 the Sierra Madre of Guatemala, formed a deeply nested polytomy whose closest relative
330 was one of the two haplotypes of *A. vasconcelosii* (UTA R-22558), followed by the other
331 one, UTA R-35035 (both from the central portion of the Sierra Madre of Guatemala), the
332 haplotype of *A.* sp. Huehuetenango MVZ-265219, and the haplotypes of *A. matudai* from
333 the southwestern extreme of the Sierra Madre of Guatemala, in that order.

334 The ML tree (Fig. S2) was very similar to the BI tree, except that some nodes
335 strongly supported in the latter tree (especially the basal-most nodes) were not strongly
336 supported. Also, in the ML tree *M. rafaeli* was the sister taxon to *M. cuchumatanus*,

337 whereas in the BI tree *M. rafaeli* was the sister taxon to *M. moreletii*. However, neither of
338 these relationships was strongly supported.
339
340 3.1.2 Concatenated nuclear tree
341
342 In the concatenated nuclear tree (Fig. 6), the (*Abronia* + *Mesaspis*), Western *Abronia-*
343 *Mesaspis*, and Central American *Abronia* clades of the mitochondrial tree were similarly
344 recovered and strongly supported; however, the Mexican Eastern Highlands *Abronia-*
345 *Mesaspis* and Central American *Mesaspis* clades were not recovered. Instead, the (*Abronia*
346 + *Mesaspis*) clade was composed of a basal polytomy formed by *M. rafaeli*, a clade with
347 the remaining Central American *Mesaspis*, and a weakly supported clade with the Western
348 *Abronia-Mesaspis* and Central American *Abronia* clades as sister taxon to each other.
349 Within the Western *Abronia-Mesaspis* clade, some of the taxa in the mitochondrial
350 tree could not be included (e.g., *M. antauges*), and only five of the six strongly supported
351 mitochondrial clades were recovered, since the samples of *A. bogerti* and *A. chiszari* did
352 not form a clade, but were placed within a strongly supported polytomy with the samples of
353 *Abronia* from the Sierra Madre del Sur of Oaxaca. The relationships among the five
354 remaining, strongly supported mitochondrial clades were somewhat different from those in
355 the mitochondrial tree. However, there were no strongly supported conflicts between these
356 trees. For instance, whereas in the nuclear tree the *M. gadovii* clade was strongly supported
357 as sister to the clade of *Abronia* from the Sierra Madre del Sur of Guerrero, in the
358 mitochondrial tree the relationships of *M. gadovii* within the Western *Abronia-Mesaspis*
359 clade were unresolved; similarly, whereas in the mitochondrial tree the clade of *Abronia*
360 from the Sierra Madre del Sur of Oaxaca and the *M. viridiflava* clade were strongly

supported as sister taxa, in the nuclear tree the relationships of the latter clade within the Western *Abronia-Mesaspis* clade were uncertain.

Within the Central American *Abronia* clade, some of the taxa in the mitochondrial tree also could not be included (i.e., *A. ornelasi*, *A. vasconcelosii*), and some relationships were in conflict with those in the mitochondrial tree. In the latter tree, *A. matudai* was strongly supported as the sister taxon to the (*A.* sp. Huehuetenango MVZ-265219 + (*A. vasconcelosii* UTA R-35035 + (*A. vasconcelosii* UTA R-22558 + (*A. campbelli* + *A. meledona*)))) clade, whereas in the nuclear tree *A. matudai* was not monophyletic; instead, one sample (UTA-R 40643) was strongly supported as the sister taxon to a clade with all the other Central American *Abronia*, whereas another sample (MVZ 270036) was the sister taxon to the (*A. campbelli*/*A. meledona*) clade, although this relationship was not strongly supported. Also, whereas in the mitochondrial tree *A. smithi* was strongly supported as sister taxon to all the other Central American *Abronia*, in the nuclear tree *A. smithi* was the sister taxon to the (*A. matudai* + (*A. campbelli* + *A. meledona*)) clade, although this relationship was not strongly supported either.

Finally, whereas in the mitochondrial tree the Central American *Mesaspis* clade was strongly supported and its relationships were completely resolved and strongly supported, in the nuclear tree *M. rafaeli* was not included in the clade (see above) and the relationships within the clade were not well resolved nor generally strongly supported. However, except for the position of *M. rafaeli*, these relationships were not in conflict with those in the mitochondrial tree.

The ML tree (Fig. S3) was very similar to the BI tree, except that some nodes strongly supported in the latter tree (especially the basal-most nodes) were not strongly supported. Also, in the ML tree the (*M. temporalis* + *M. salvadorensis*) clade was the sister

taxon to the (*M. cuchumatanus* + *M. moreletii*) clade, whereas in the BI tree the (*M. temporalis* + *M. salvadorensis*) clade was the sister taxon to the (*M. moreletii* Honduras + *M. moreletii* Nicaragua) clade. However, neither of these relationships was strongly supported.

3.1.3 Concatenated mitochondrial and nuclear tree

The concatenated mitochondrial and nuclear genes tree (Fig. 7) was highly similar to the mitochondrial tree, except for some minor details: within the Western *Abronia-Mesaspis* clade, the *Abronia* clade from the Sierra Madre del Sur of Oaxaca (*A. oaxacae* + (*A. cuetzpali* + *A. mixteca*)) was strongly supported as sister taxon to the (*A. bogerti* + *A. chiszari*) clade, whereas in the mitochondrial tree it was strongly supported as sister taxon to the *M. viridiflava* clade. Also, in the *Abronia* clade from the Mexican Eastern Highlands, *A. graminea* and *A. taeniata* were reciprocally monophyletic, whereas in the mitochondrial tree they were not (however, it should be noted that not all the samples in the mitochondrial tree could be included in the multi-locus tree). In addition, in the Eastern *Abronia-Mesaspis* clade, *A. ornelasi* was the sister taxon to the Central American clade of *Abronia*, whereas in the mitochondrial tree it was the sister taxon to the Central American clade of *Mesaspis*; however, neither relationship was strongly supported. Also, *M. moreletii* was the sister taxon to *M. cuchumatanus*, and these two taxa comprised the sister group to *M. rafaeli*, whereas in the mitochondrial tree *M. moreletii* was the sister taxon to *M. rafaeli*, and these two taxa comprised the sister group to *M. cuchumatanus*.

The ML tree (Fig. S4) was very similar to the BI tree, except that some basal nodes within the *Abronia-Mesaspis* clade strongly supported in the latter tree were not strongly

409 supported, and vice versa. Also, in the ML tree the *Abronia-Mesaspis* clade from the
410 Mexican Eastern Highlands was the sister taxon to the (*M. gadovii* + (*A.* sp. Guerrero
411 ANMO-3343 + (*A. deppii* + (*A.* sp. Guerrero MZFC-28966 + *A. martindelcampoi*)))) clade,
412 whereas in the BI tree the former clade was the sister taxon to the ((*A. chiszari* + *A. bogerti*)
413 + (*A. oaxacae* + (*A. mixteca* + *A. cuetzpali*))) clade. Also, in the ML tree *A. ornelasi* was
414 the sister taxon to the Central American clade of *Mesaspis* as in the mtDNA tree, while in
415 the BI tree *A. ornelasi* was the sister taxon to the Central American clade of *Abronia*.
416 However, neither of these relationships was strongly supported.
417
418 3.1.4 Species tree
419
420 The species tree (Fig. 8) was, in general, similar to the mitochondrial tree. However,
421 several nodes within the *Abronia-Mesaspis* clade that were strongly supported in the
422 mitochondrial tree were weakly supported in the former tree, including the basal-most
423 nodes (e.g., those of the Western and Eastern *Abronia-Mesaspis* clades) as well as some
424 more recent nodes. The species tree recovered the same six strongly supported clades
425 recovered within the mitochondrial Western *Abronia-Mesaspis* clade (see above);
426 furthermore, whereas in the mitochondrial tree the relationships among these clades were
427 predominantly unresolved, in the species tree they were completely resolved. Nonetheless,
428 whereas in the mitochondrial tree the (*A. oaxacae* + (*A. mixteca* + *A. cuetzpali*)) clade was
429 strongly supported as sister taxon to the *M. viridiflava* clade, in the species tree it was the
430 sister taxon to the (*A. bogerti* + *A. chiszari*) clade. All other relationships among the six
431 clades were weakly supported. Also, whereas in the mitochondrial tree *M. moreletii* was
432 sister to *M. rafaeli* and *M. cuchumatanus* was sister to these two taxa, in the species tree *M.*

moreletii was sister to *M. cuchumatanus* and *M. rafaeli*. However, the sister taxon relationship of *M. moreletii* was weakly supported in both trees.

The species tree was even more similar to the concatenated all-genes tree, as it recovered the same six strongly supported clades within the Western *Abronia-Mesaspis* clade and the only strongly supported sister-taxon relationship among these clades, with the (*A. oaxacae* + (*A. mixteca* + *A. cuetzpali*)) clade as sister to the (*A. bogerti* + *A. chiszari*) clade; all other relationships among those clades that differed between the trees were weakly supported. Additionally, within the Eastern *Abronia-Mesaspis* clade the species tree recovered *A. ornelasi* as sister taxon to the Central American clade of *Mesaspis*, whereas in the all-genes concatenated tree *A. ornelasi* was the sister taxon to the Central American clade of *Abronia*. However, neither relationship was strongly supported.

4. Discussion

4.1 Phylogenetic relationships of *Abronia* and *Mesaspis*

Overall, despite the differences in taxon sampling, missing data, and coalescence times across datasets, there were few strongly supported conflicts between the mitochondrial and concatenated nuclear trees (namely, in the relationships of *A. matudai* and –-to a lesser extent–- *A. smithi*; see above). With that caveat in mind, the inference of a phylogenetic hypothesis from the concatenated mitochondrial and nuclear sequence data seems justified. In addition, the concatenated all-genes tree and the species tree were nearly identical, except for the position of *A. ornelasi*, weakly supported in both trees, and the relationships within the clade composed of *M. cuchumatanus*, *M. moreletii*, and *M. rafaeli*, which were

457 weakly supported in the species tree. In both trees, the phylogenetic positions of *A. matudai*
458 and *A. smithi* were the same as in the mitochondrial tree. On the other hand, the
459 mitochondrial tree included many more samples than the concatenated all-genes tree and
460 showed good resolution and support at the more recent nodes, thus being often more
461 informative for species limits estimation than the latter tree. In all the trees, the deeper the
462 nodes the lower it was the resolution and support. Also, relationships among the *Abronia-*
463 *Mesaspis* clade and the other Gerrhonotinae genera (*Elgaria*, *Gerrhonotus*, and *Barisia*)
464 differed across the trees. This suggests that inclusion of more slow-evolving markers is
465 needed to obtain a robust phylogenetic hypothesis across the phylogeny.
466 Although the monophyly of *Abronia* and *Mesaspis* was often assumed (e.g.,
467 Campbell and Frost, 1993; Chippindale et al., 1998), some previous unpublished (Solano-
468 Zavaleta, 2011) and published (Pyron et al., 2013) studies suggested the non-monophyly of
469 these genera. By performing a phylogenetic analysis of a multi-locus dataset with the
470 largest number of species of *Abronia* included so far in a molecular phylogenetic analysis
471 (18) and all the species currently recognized of *Mesaspis*, we were able to test the
472 monophyly of these genera and generate the most comprehensive hypothesis of
473 relationships within the *Abronia-Mesaspis* clade to date.
474 Our phylogenetic hypothesis supports previous suggestions that *Abronia* and
475 *Mesaspis* are not reciprocally monophyletic. In this hypothesis, species of *Abronia* and
476 *Mesaspis* grouped with each other in strongly supported clades concordant with geography,
477 rather than taxonomy: most noticeably, the Western and Eastern *Abronia-Mesaspis* clades
478 and, nested within the Western *Abronia-Mesaspis* clade, an *Abronia–Mesaspis* clade ([*A.*
479 *fuscolabialis* + [*A. graminea* + *A. taeniata*]] + [*M. antauges* + *M. juarezi*]) on the Mexican
480 Eastern Highlands. The relationships of *M. gadovii* and *M. viridiflava* were uncertain; still,

481 they were more closely related to species of *Abronia* west of the Isthmus of Tehuantepec
482 than to other *Mesaspis* east of the Isthmus. Also, within the Eastern *Abronia-Mesaspis*
483 clade, *A. ornelasi* was sister to the Central American clade of *Mesaspis* in the species tree;
484 however, this relationship was weakly supported.

485 Given these results, it may seem surprising that the monophyly of *Abronia* and
486 *Mesaspis* has been usually assumed. Clearly, of the putative synapomorphies at least the
487 presence and absence of relatively long, well-clawed limbs in species of *Abronia* and
488 *Mesaspis*, respectively, appears to be related to their arboreal vs. terrestrial habits.
489 However, according to our results arboreality appears to have evolved not once, but several
490 times within the *Abronia-Mesaspis* clade, rendering *Abronia* a non-monophyletic group.
491 Evidently, other putative synapomorphies of *Abronia* or *Mesaspis* must be homoplastic
492 similarities.

493 Of the six subgenera of *Abronia* recognized by Campbell and Frost (1993), we
494 could include representatives of only four, since we could not include the only member of
495 *Aenigmabronia* nor any member of *Lissabronia*. Also, regarding the subgenus
496 *Abaculabronia*, we could not include but one of its two members (*A. ornelasi*); thus, the
497 monophyly of this subgenus could not be evaluated. Nonetheless, *A. ornelasi* was placed
498 within the Eastern *Abronia-Mesaspis* clade as sister taxon to the subgenus *Auriculabronia*
499 in the concatenated all-genes tree (in Campbell and Frost [1993]'s preferred tree, it was the
500 sister taxon to the [*Auriculabronia* + *Lissabronia*] clade) and as sister taxon to the Central
501 American clade of *Mesaspis* in the species tree; however, none of these relationships was
502 strongly supported. Biogeographically, the placement of *A. ornelasi* as sister taxon to either
503 the Central American clade of *Abronia* or *Mesaspis* seems plausible since it represents the
504 western-most distributed taxon within the Eastern *Abronia-Mesaspis* clade.

505 The subgenus *Scopaeabronia* was strongly supported as monophyletic, which
506 supports its morphological distinctness (Campbell and Frost, 1993), although it was
507 represented by only two of its three members, since we could not include *A. ramirezi*.
508 Nonetheless, the included members nearly encompass the geographic distribution of the
509 subgenus on moderate elevations west and east of the Isthmus of Tehuantepec, evidently a
510 geographic barrier for the genus: *A. bogerti*, from the Sierra Madre of extreme eastern
511 Oaxaca, and *A. chiszari*, from the Sierra de Los Tuxtlas in extreme southern Veracruz.
512 *Abronia ramirezi* is known only from the type-locality in the Sierra Madre de Chiapas of
513 western Chiapas.
514 In contrast, we included all the members of the subgenus *Abronia*. However, they
515 did not form a single clade, but three strongly supported clades that were not each other's
516 sister taxon: one on the Trans-Mexican Volcanic Belt and the Sierra Madre del Sur of
517 Guerrero (*A.* sp. Guerrero ANMO-3343 + (*A. deppii* + (*A.* sp. Guerrero MZFC-28966 + *A.*
518 *martindelcampoi*))), whose relationships to other clades in the concatenated all-genes and
519 species trees were weakly supported, another one on the Mexican Eastern Highlands (*A.*
520 *fuscolabialis* + (*A. graminea* + *A. taeniata*)), sister taxon to the (*M. antauges* + *M. juarezi*)
521 clade, also from the same highlands; and the other one on the Sierra Madre del Sur of
522 Oaxaca (*A. oaxacae* + (*A. mixteca* + *A. cuetzpali*)), which was sister taxon to the subgenus
523 *Scopaeabronia*, although this relationship was not strongly supported in the species tree. In
524 addition, relationships among the members of the subgenus were more concordant with
525 geography than they were in Campbell and Frost (1993)'s preferred hypothesis. In the latter
526 hypothesis, *A. fuscolabialis* and *A. graminea* were sister taxa; however, *A. taeniata*, sister
527 taxon to the geographically closest *A. graminea* in our hypothesis, was more closely related
528 to the species of the subgenus in Guerrero and Oaxaca than to *A. graminea*, which seems

529 less plausible. Also, although Campbell and Frost (1993)'s preferred hypothesis recovered
530 a clade with two species from the Trans-Mexican Volcanic Belt and the Sierra Madre del
531 Sur of Guerrero (*A. deppii* and *A.* "Guerrero" [=*A. martindelcampoi*], respectively) and two
532 from the Sierra Madre del Sur of Oaxaca (*A. mixteca* and *A. oaxacae*), in this clade *A.*
533 *oaxacae* was more closely related to the former species than to the geographically closer *A.*
534 *mixteca* as it was in our hypothesis, which also seems less plausible.
535 The subgenus *Auriculabronia* was strongly supported as monophyletic, although it
536 was represented by most, but not all, of its members (7 out of 12). This suggests the early
537 split of an ancestor on the highlands of Nuclear Central America and the subsequent and
538 parallel diversification of the *Abronia* (*Auriculabronia*) and *Mesaspis* clades in these
539 highlands. Whether the subgenera *Auriculabronia* and *Lissabronia*, whose geographic
540 distributions overlap in Nuclear Central America, are strongly supported as reciprocally
541 monophyletic remains to be investigated.
542 When the taxonomy of Chippindale et al. (1998)'s mitochondrial phylogeny for the
543 subgenus *Auriculabronia* (their molecular-only tree without step-matrices, Fig. 4E) is
544 updated following Campbell and Brodie (1999), this phylogeny and our multi-locus
545 phylogeny for *Auriculabronia* are similar. In both hypotheses, the representatives of the
546 *aurita* subgroup of Campbell and Brodie (1999), composed of *A. anzuetoi*, *A. aurita*, *A.*
547 *campbelli*, *A. meledona*, and *A. vasconcelosii*, formed a strongly supported clade, although
548 both hypotheses failed to include *A. aurita* and our hypothesis also failed to include *A.*
549 *anzuetoi*. In both hypotheses, *A. matudai* was sister to the *aurita* subgroup, and the (*A.*
550 *fimbriata* + *A. lythrochila*) clade was sister to the (*aurita* subgroup + *A. matudai*) clade.
551 Furthermore, in our hypothesis *A. smithi*, which was not included in Chippindale et al.
552 (1998)'s phylogeny, was sister to all of these taxa.

553

554 4.2 *Abronia* classification

555 Clearly, the subgenus *Abronia* is paraphyletic with respect to several lineages of
556 *Mesaspis*. In addition, the monophyly of most of the other *Abronia* subgenera (since none
557 [*Lissabronia*] or only some of their members [*Abaculabronia*, *Auriculabronia*,
558 *Scopaeabronia*] were included in the analysis) remains uncertain. Thus, the current
559 subgeneric classification of *Abronia* is logically inconsistent with our molecular
560 phylogenetic hypothesis. Evidently, this classification must be modified if its future use is
561 considered useful. However, ideally this modification should not be performed until a more
562 comprehensive and robust phylogeny for the *Abronia-Mesaspis* clade is available.

563

564 4.3 Species delimitation problems

565

566 Although performing specific analyses to investigate species delimitation problems in the
567 *Abronia-Mesaspis* clade is beyond the goals of this work, our results shed some light
568 towards their resolution. We comment about these problems below.

569 Populations of *Abronia* of uncertain taxonomic status from Guerrero. The sample of
570 *Abronia* sp. Guerrero MZFC-28966 was morphologically most similar to *A.*
571 *martindelcampoi* and was strongly supported as sister taxon to all the other samples of this
572 taxon in both the mitochondrial and concatenated all-genes trees (Figs. 5, 7, S1, S2, S4).
573 However, it was moderately divergent genetically from those samples, which suggests that
574 it may represent either a relatively divergent population of *A. martindelcampoi* or an
575 undescribed species. Similarly, the sample of *Abronia* sp. Guerrero ANMO-3343 was
576 significantly supported as sister taxon to the (*A. deppii* + (*A.* sp. Guerrero MZFC-28966 +

A. martindelcampoi)) clade in the above trees, and moderately more divergent genetically from the taxa in this clade than they are from each other. This suggests that this population likely represents an undescribed species. Additional material and data (morphological and molecular) are needed from both problematic populations to confidently determine their taxonomic status.

Population of *Abronia* of uncertain taxonomic status from the Huehuetenango region. In the mitochondrial and concatenated all-genes trees (Figs. 5, 7, S1, S2, S4), the sample of *Abronia* sp. Huehuetenango MVZ-265219 was strongly supported as sister taxon to the *aurita* subgroup clade. However, it was more divergent from all the samples of this subgroup (i.e., the samples of *A. vasconcelosii*, *A. campbelli*, and *A. meledona*) than they were from each other; also, it was taken in a region where none of the latter taxa is known from. Thus, it is possible that it represents an undescribed species. Additional material and data (morphological and molecular) are needed to corroborate this hypothesis.

Population of *Abronia* of uncertain taxonomic status from Laguna Bélgica, Chiapas. Campbell and Frost (1993) reported a specimen of *Abronia* from Laguna Bélgica, Chiapas, suggesting that it represented an undescribed species. However, the sample from a road-killed specimen from the same area was nested within the strongly supported clade with the samples of *A. bogerti* and very similar to them. This indicates that the Laguna Bélgica population represents another population of *Abronia bogerti*. Morphological examination of the specimen reported by Campbell and Frost (1993) and recently collected specimens of *A. bogerti* (unpublished data) supports this notion.

The *aurita* subgroup. In Chippindale et al. (1998)'s hypothesis, *A. campbelli* and *A. meledona* were sister taxon to each other, and these two taxa formed a polytomy with *A. anzuetoi* and their two samples of *A. vasconcelosii*, which did not form a clade. In our

mitochondrial and concatenated all-genes trees (Figs. 5, 7, S1, S2, S4), the sample of *A. meledona* formed a polytomy with all the samples of *A. campbelli* and was essentially identical to them. The closest relatives to this polytomy were the two samples of *A. vasconcelosii*; however, these samples did not form a clade. Thus, *A. vasconcelosii* was paraphyletic with respect to *A. campbelli* and *A. meledona*. These results do not support the distinctness of *A. meledona* claimed by Chippindale et al. (1998) and Campbell and Brodie (1999). It is worth noting that the single sample of *A. meledona* in both Chippindale et al. (1998)' and our study was the same and was taken from the holotype of the name. Our results also do not support the monophyly of *A. vasconcelosii* nor the distinctness of *A. meledona* and *A. campbelli* from *A. vasconcelosii*, and suggest that further study on this subgroup is needed to reevaluate its species limits.

Abronia graminea and *A. taeniata*. These nominal species have been considered closely related and broadly allopatric for many years (Campbell and Frost, 1993; Canseco-Márquez and Mendoza-Quijano, 2007; Flores-Villela and Santos-Barrera, 2007). In fact, *A. graminea* was considered once a subspecies of *A. taeniata* by Tihen (1949) and subsequent authors (Smith and Taylor, 1950; Smith et al., 1952; Tihen, 1954; Werler, 1951; Werler and Smith, 1952). Recently, Clause et al. (2018) reported the existence of a broad zone of sympatry (of about 100 km) between these two taxa in the southern Sierra Madre Oriental. These workers examined three morphological traits that were regarded useful to discriminate between *A. graminea* and *A. taeniata* in 21 specimens of the first taxon and 14 of the second from the zone of sympatry: (1) number of transverse dorsal scale rows (25–29 in *A. graminea* and 30–36 in *A. taeniata*); (2) longitudinal nuchal scale rows (4–6 in *A. graminea* and 6 in *A. taeniata*); and (3) adult dorsal body coloration (uniform or occasionally with faint transverse dark bands, particularly in females, in *A. graminea*;

625 always with dramatic transverse dark bands, occasionally fused along the dorsal midline, in
626 both sexes in *A. taeniata*). However, they found no evidence of character displacement in
627 the zone. Instead, morphological differentiation was reduced, intergrades were widespread
628 across the zone, and of the three characters examined only the dorsal body coloration was
629 reliable for identifying *Abronia*, and that only in adult male individuals. Although this
630 suggested gene flow between *A. graminea* and *A. taeniata* in the zone of sympatry, Clause
631 et al. (2018) preferred to retain these taxa as species-level entities until genetic data from
632 them were available.

633 In the mitochondrial trees (Figs. 5, S1, S2), the haplotypes of *A. graminea* and *A.*
634 *taeniata* formed a large clade with a moderately deep structure and a clear pattern of
635 geographic distribution of the genetic variation. Whereas one basal clade included all the
636 haplotypes of *A. graminea* from south of the Trans-Mexican Volcanic Belt, in the other
637 basal clade the first and second subclades to branch off were composed of intermingled
638 haplotypes of both *A. graminea* and *A. taeniata* from the eastern end of the Trans-Mexican
639 Volcanic Belt and the southern end of the Sierra Madre Oriental, and the last subclade to
640 branch off was composed of the haplotypes of *A. taeniata* from the central and northern
641 portions of the Sierra Madre Oriental. Thus, *A. graminea* was paraphyletic with respect to
642 *A. taeniata*, and the tree suggests a south-north dispersal of *Abronia* along the Mexican
643 Eastern Highlands. Also, this genetic structure seems congruent with the reduced
644 morphological differentiation in specimens of *A. graminea* and *A. taeniata* from the
645 sympatry zone reported by Clause et al. (2018), and suggests the existence of gene flow
646 between these taxa in the area. However, if this were the case, then *A. graminea* and *A.*
647 *taeniata* might represent a single species with clinal variation in some morphological
648 characters or, alternatively, two distinct lineages with a sympatry zone where introgressive

649 hybridization between them has occurred. Like Clause et al. (2018), we prefer to retain, for
650 the time being, recognition of these two taxa as distinct species until further research solves
651 this matter. It should be noted that, although in the concatenated all-genes tree (Figs. 7, S4)
652 *A. graminea* and *A. taeniata* were reciprocally monophyletic, the samples of *A. graminea*
653 from the sympatry zone of Clause et al. (2018) included in the mitochondrial tree (MVZ-
654 191068, ISZ-971, RPS-31, RPS-41) were not included, since they lacked data for the
655 nuclear genes.

656 *Mesaspis gadovii*. Although in the mitochondrial trees (Figs. S1, S2) the haplotypes
657 of *M. g. gadovii* and *M. g. levigata* were only slightly divergent from each other, they
658 showed some tendency to form mutually exclusive clades from Guerrero and Oaxaca,
659 respectively. However, the clade of *M. g. gadovii* was weakly supported, and several
660 samples of *M. g. levigata* did not group either with the other samples of *M. g. levigata* or
661 the samples of *M. g. gadovii*. Additionally, Solano-Zavaleta (2011) found that the
662 morphological characters proposed to distinguish between the two subspecies (Spengler et
663 al., 1982; Tihen, 1949b) actually do not allow to do so. At any rate, the subspecies were not
664 mutually exclusive, which suggests that they are not natural groups, and therefore *M.*
665 *gadovii levigata* should not be recognized.

666 *Mesaspis viridiflava.* In the mitochondrial, concatenated nuclear, and concatenated
667 all-genes trees, the samples of *M. viridiflava* from Cerro San Felipe y la Sierra Alopaneca,
668 Oaxaca (n = 6), formed a strongly supported clade sister to, and fairly divergent from, a
669 clade with the remaining samples of *M. viridiflava*. This arrangement of the samples of *M.*
670 *viridiflava* into strongly supported, mutually exclusive, genetically divergent basal clades
671 concordant with geography suggests the absence of gene flow between their respective
672 populations, even though they are not geographically far from each other (approximately ≥

673 28.5 km), and thus that *M. viridiflava* is composed of two cryptic, evolutionary independent
674 lineages. Additional material and data (morphological and molecular) are needed to
675 corroborate this hypothesis.
676
677 **5. Taxonomic conclusions**
678
679 1. *Abronia* and *Mesaspis* are not mutually monophyletic. Because the name *Abronia* Gray,
680 1838 has priority over the name *Mesaspis* Cope, 1877, *Mesaspis* should be placed in
681 synonymy under the senior name *Abronia*.
682 2. *Mesaspis gadovii* should not be recognized as a polytypic species.
683 3. *Mesaspis viridiflava* appears to be composed of two cryptic, evolutionary independent
684 lineages; however, additional material and data (morphological and molecular) are
685 needed to corroborate this hypothesis.
686 4. The potential evidence of gene flow between *Abronia graminea* and *A. taeniata* in the
687 zone of sympatry documented by Clause et al. (2018) suggest that these nominal
688 species might represent the same lineage or, alternatively, the existence of a broad zone
689 where introgressive hybridization between them has occurred.
690 5. The specimens of *Abronia* sp. from Guerrero, México (*A.* sp. Guerrero MZFC-28966
691 and *A.* sp. Guerrero ANMO-3343) and Huehuetenango, Guatemala (*A.* sp.
692 Huehuetenango MVZ-265219) might represent three undescribed species. Additional
693 material and data (morphological and molecular) are needed from these problematic
694 populations to confidently determine their taxonomic status.

6. Neither the monophyly of *A. vasconcelosii* nor the distinctness of *A. meledona* and *A. campbelli* from *A. vasconcelosii* or from each other are supported by our molecular data. Further study on this subgroup is needed to reevaluate its species limits.

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889

890 FIGURE LEGENDS

891

892 Figure 1. Geographic distribution of *Abronia* species. In the cases of *A. aurita* (cross inside
893 a circle), *A. leurolepis* (diamond), *A. mitchelli* (star), and *A. ochoterenai* (triangle) no exact
894 locality is known.

895

896 Figure 2. Geographic distribution of *Mesaspis* species.

897

898 Figure 3. Good (1988)'s hypothesis of phylogenetic relationships among gerrhonotine
899 lizards based on external morphology.

900

901 Figure 4. Sampling localities for *Abronia* and *Mesaspis* species.

902

903 Figure 5. Bayesian phylogenetic tree for the species of *Abronia* and *Mesaspis* inferred from
904 the mtDNA data. Orange dots on nodes represent posterior probability values ≥ 0.95.
905 Localities for the individual samples are given in Table S2.

906

907 Figure 6. Bayesian phylogenetic tree for the species of *Abronia* and *Mesaspis* inferred from
908 the concatenated nuclear genes. Orange dots on nodes represent posterior probability values
909 ≥ 0.95. Localities for individual samples are given in Table S2.

910

911 Figure 7. Bayesian phylogenetic tree for the species of *Abronia* and *Mesaspis* inferred from
912 concatenation of all genes. Orange dots on nodes represent posterior probability values ≥
913 0.95. Localities for individual samples are given in Table S2.

914

915 Figure 8. Species tree for the species of *Abronia* and *Mesaspis* inferred from the multi-
916 locus data set in *BEAST. Orange dots represent posterior probability values ≥ 0.95.
917 Localities for individual samples are given in Table S2.

918

919 Figure S1. Bayesian phylogenetic tree for the species of *Abronia* and *Mesaspis* with all
920 sequenced samples shown inferred from the mtDNA data. Orange dots on nodes represent
921 posterior probability values ≥ 0.95. Individual samples in boldface are samples sequenced
922 for the nuclear genes. Localities for the individual samples are given in Table S2.

923

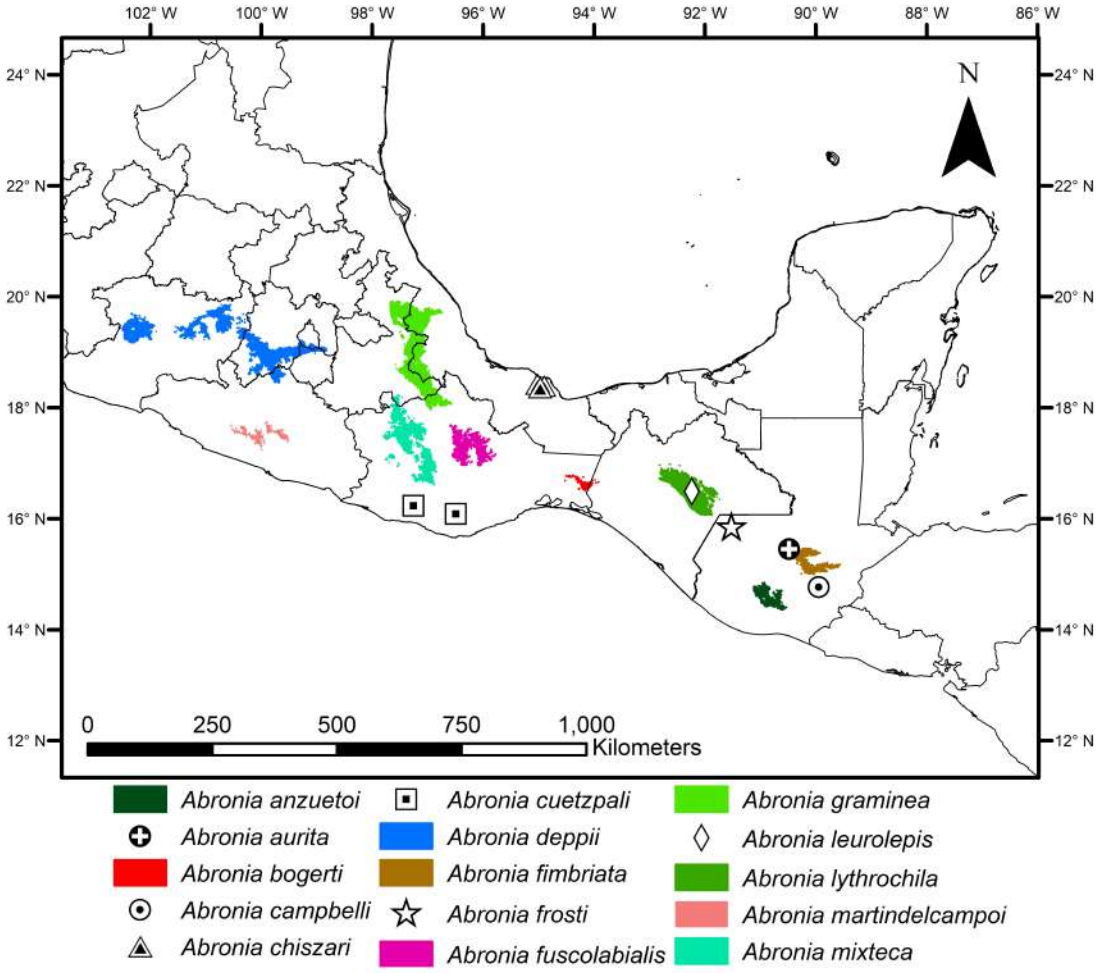
924 Figure S2. Maximum Likelihood phylogenetic tree for the species of *Abronia* and *Mesaspis*
925 with all sequenced samples shown inferred from the mtDNA data. Orange dots on nodes
926 represent bootstrap values ≥ 0.70. Individual samples in boldface are samples sequenced for
927 the nuclear genes. Localities for the individual samples are given in Table S2.

928

929 Figure S3. Maximum Likelihood tree for the species of *Abronia* and *Mesaspis* inferred
930 from the concatenated nuclear genes. Orange dots on nodes represent bootstrap values ≥
931 0.70. Localities for individual samples are given in Table S2.

932

933 Figure S4. Maximum Likelihood tree for the species of *Abronia* and *Mesaspis* inferred
934 from concatenation of all genes. Orange dots on nodes represent bootstrap values ≥ 0.70.
935 Localities for individual samples are given in Table S2.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16° N
14° N
12° N
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750
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Kilometers
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Abronia aurita
Abronia bogerti
Abronia campbelli
Abronia chiszari
Abronia cuetzpali
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Abronia fimbriata
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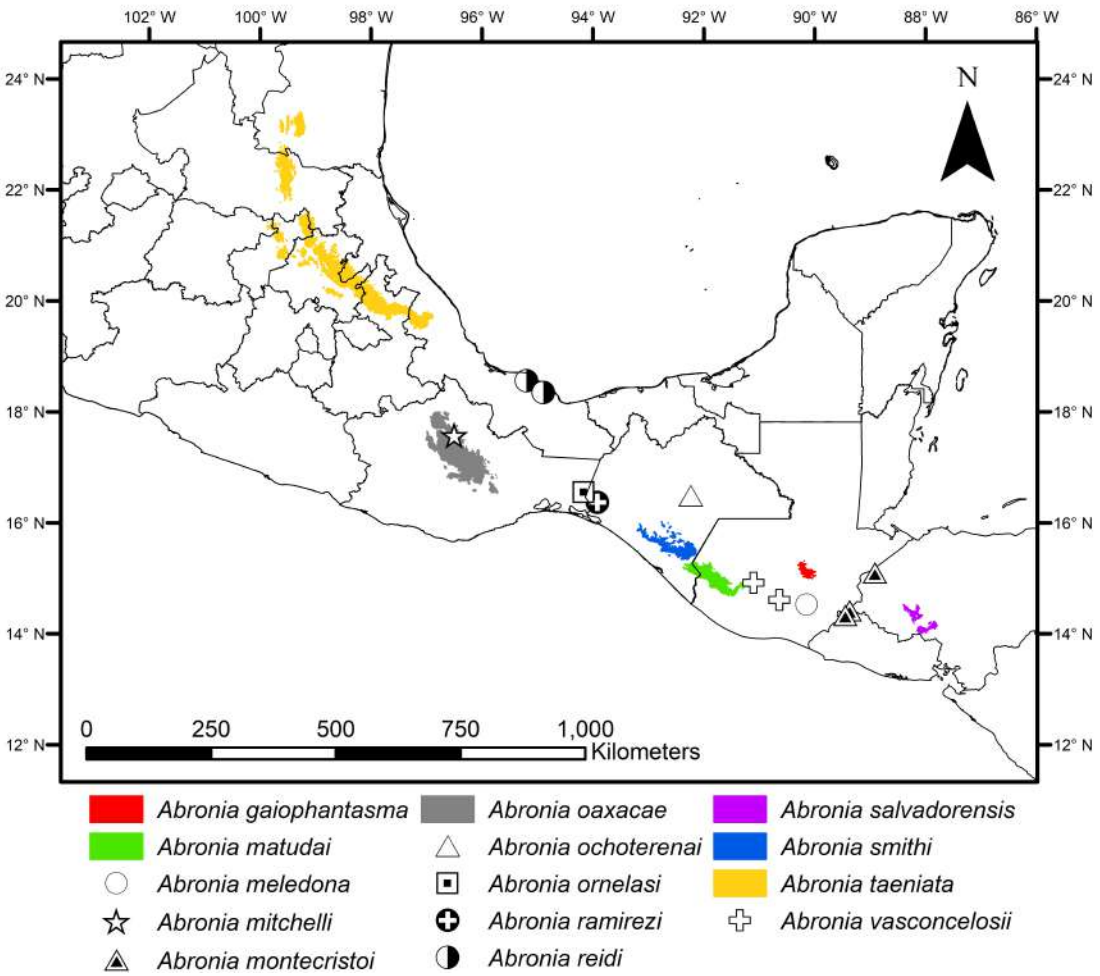
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Kilometers
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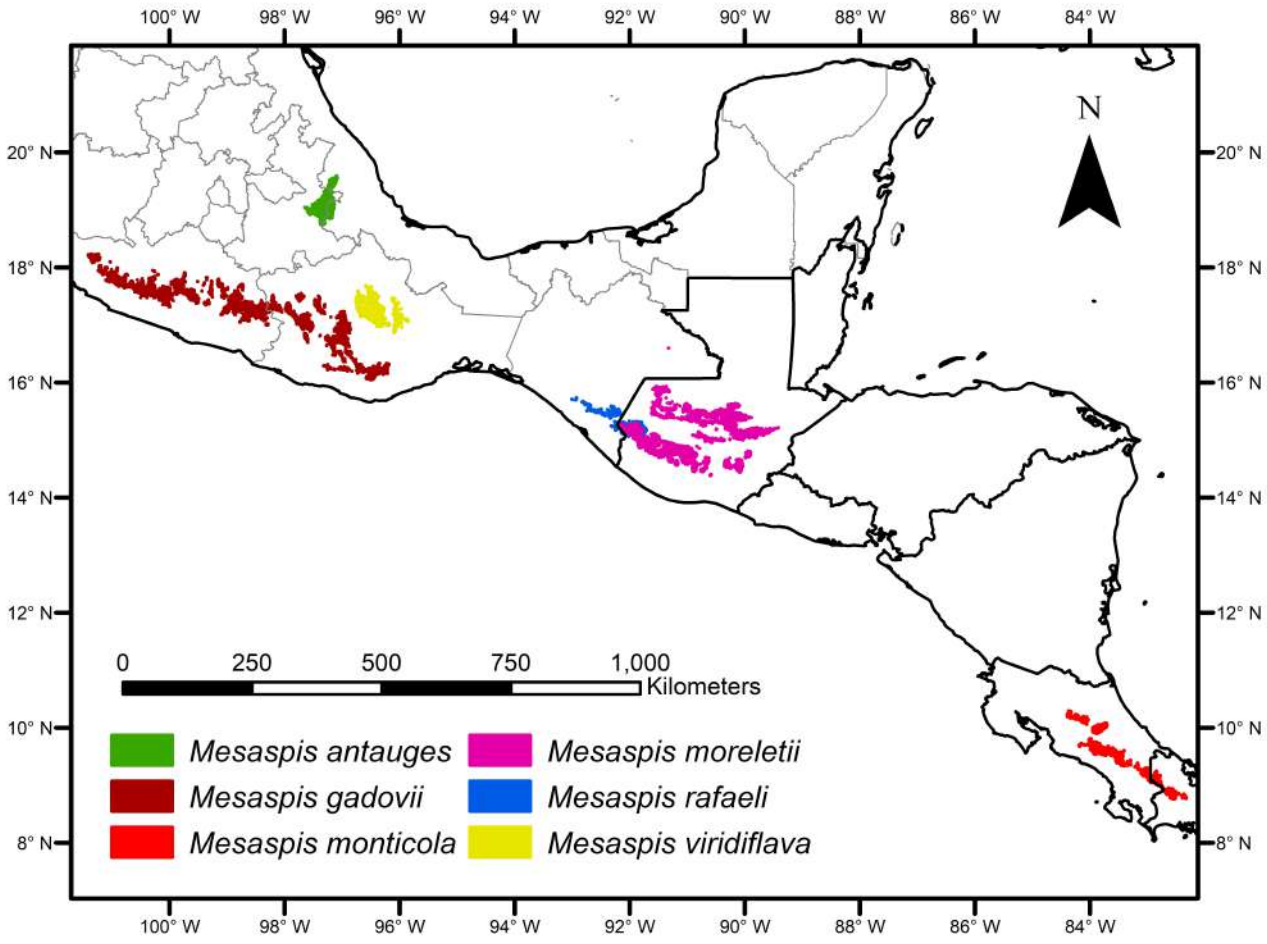
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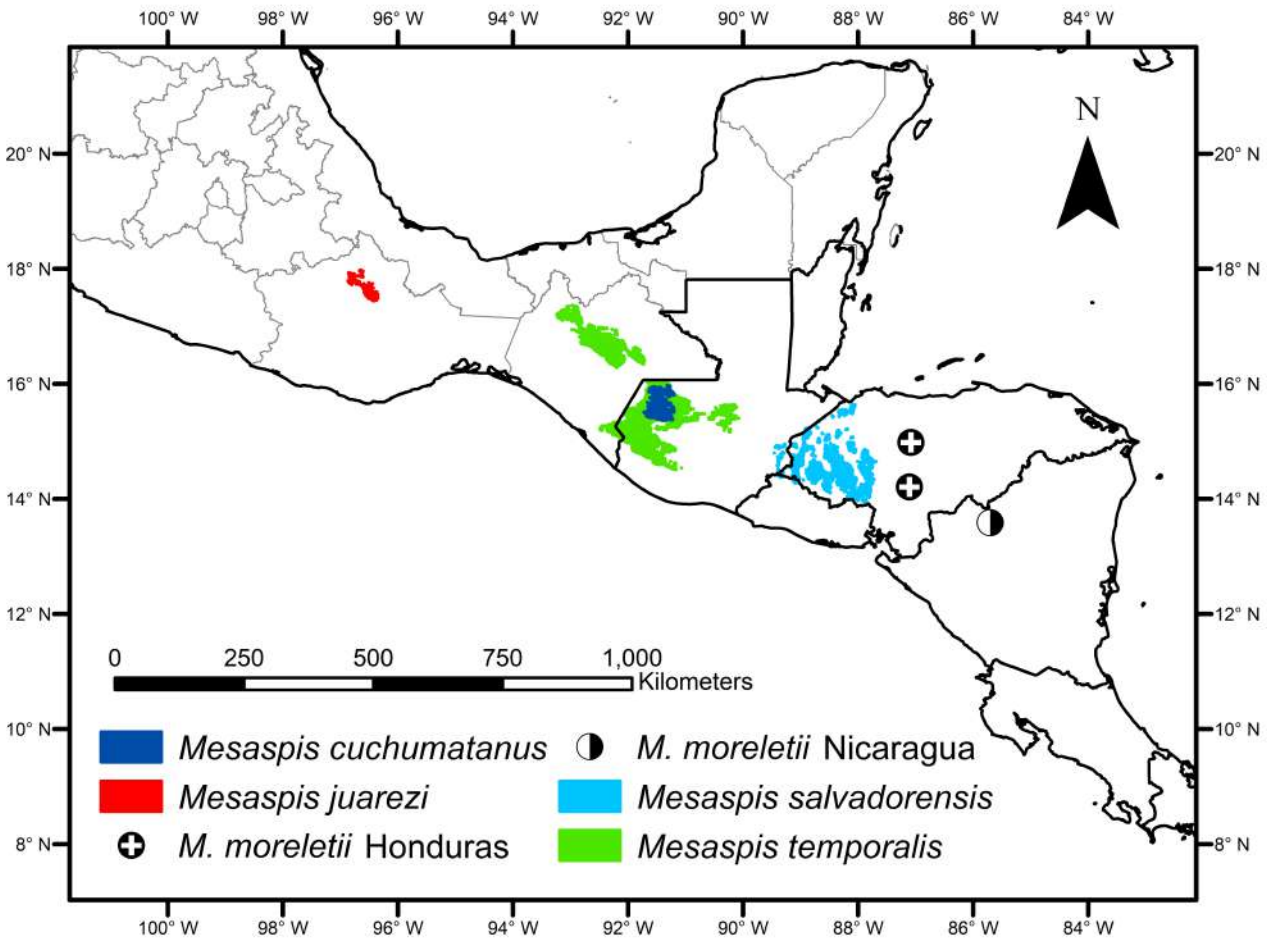
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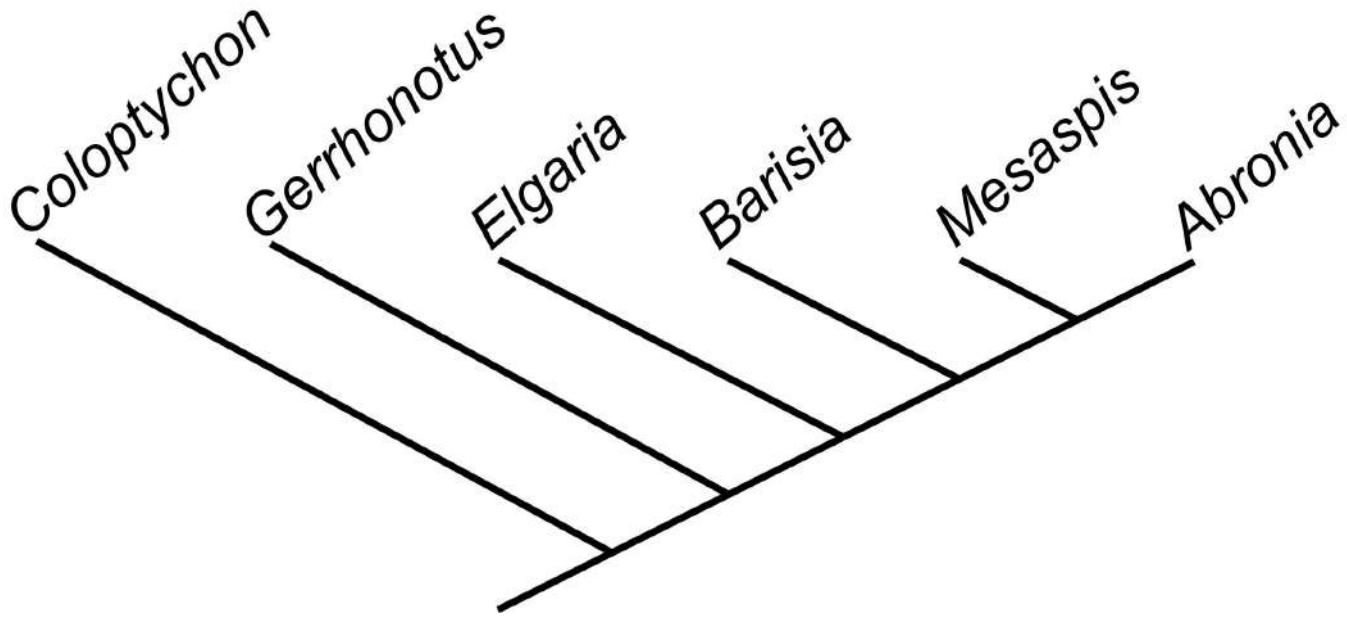
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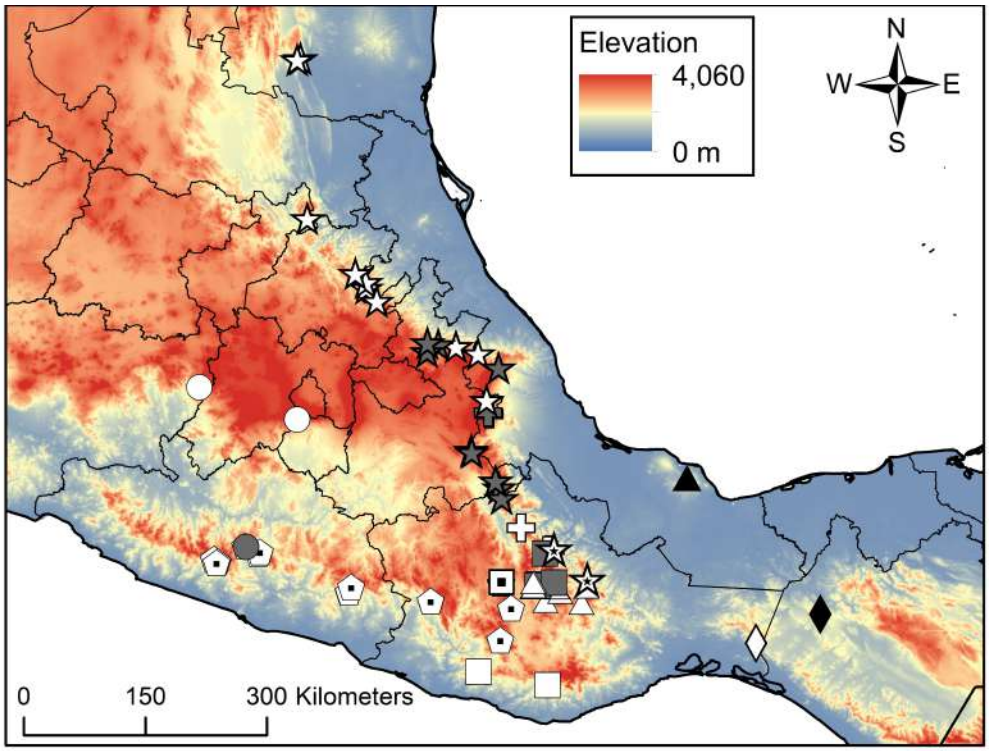

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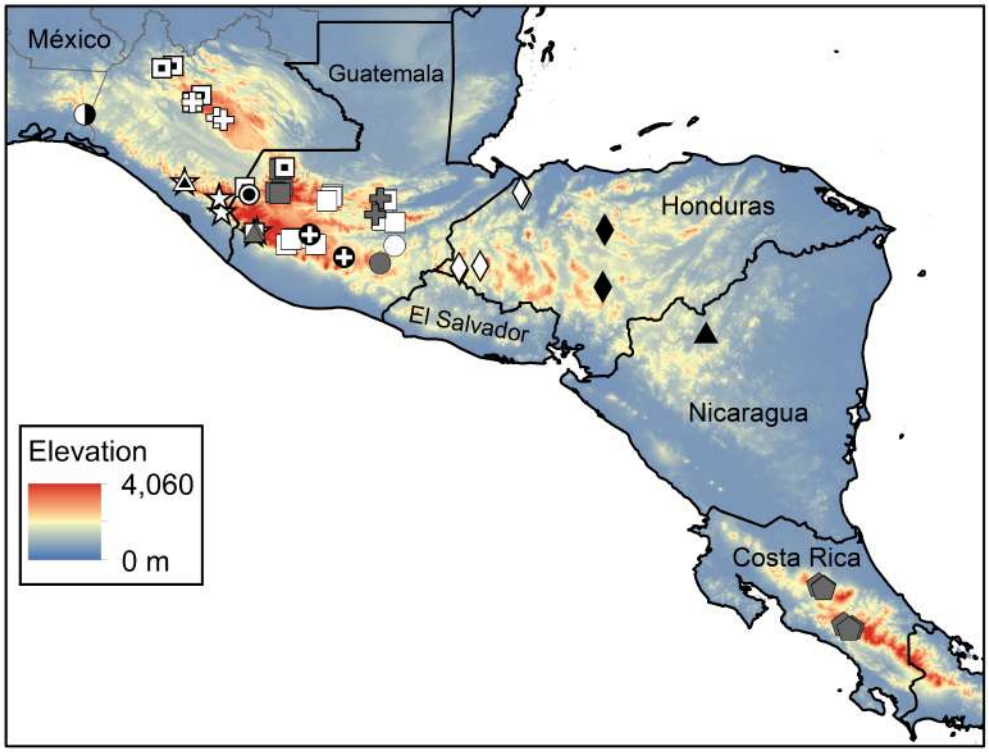

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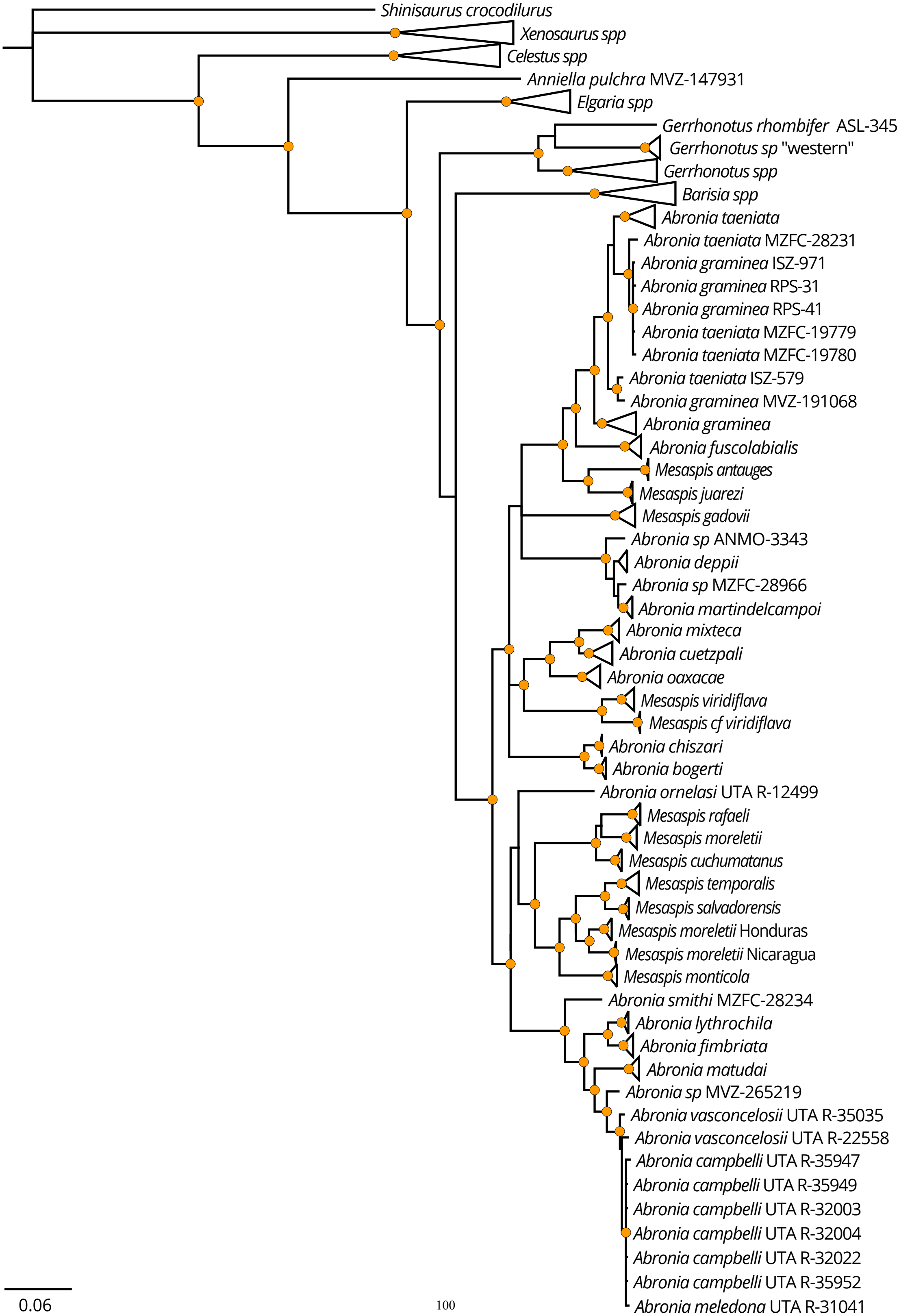
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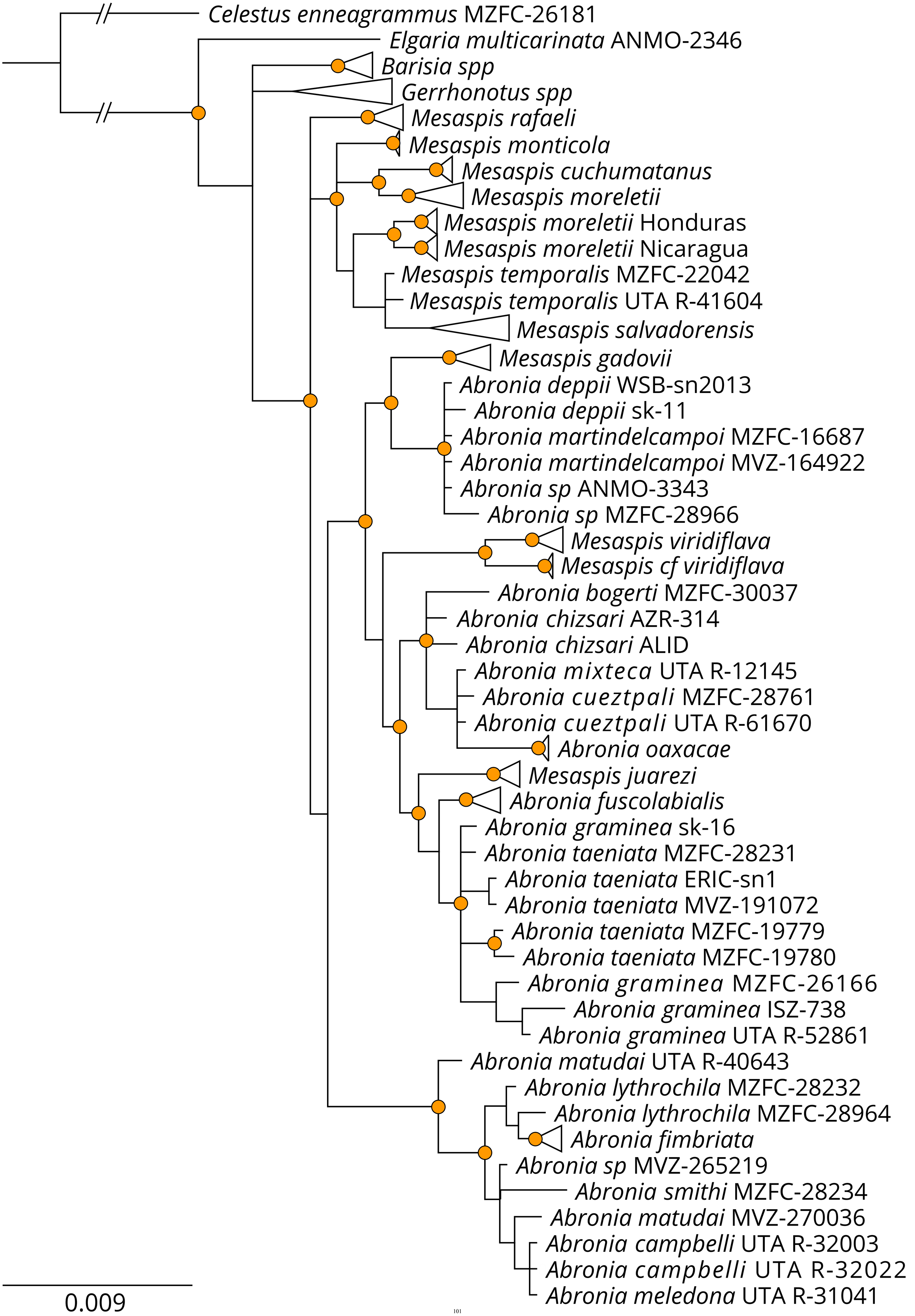
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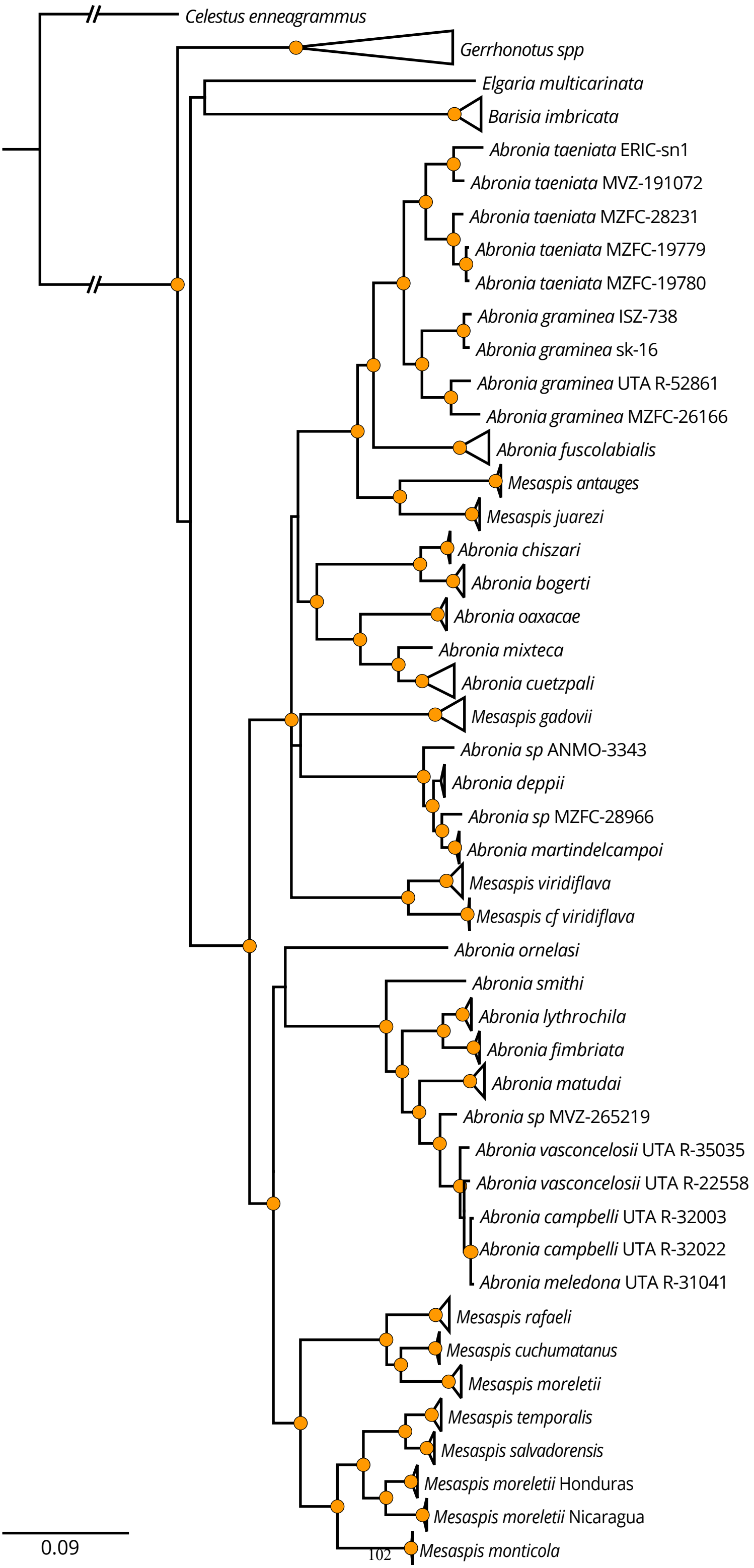
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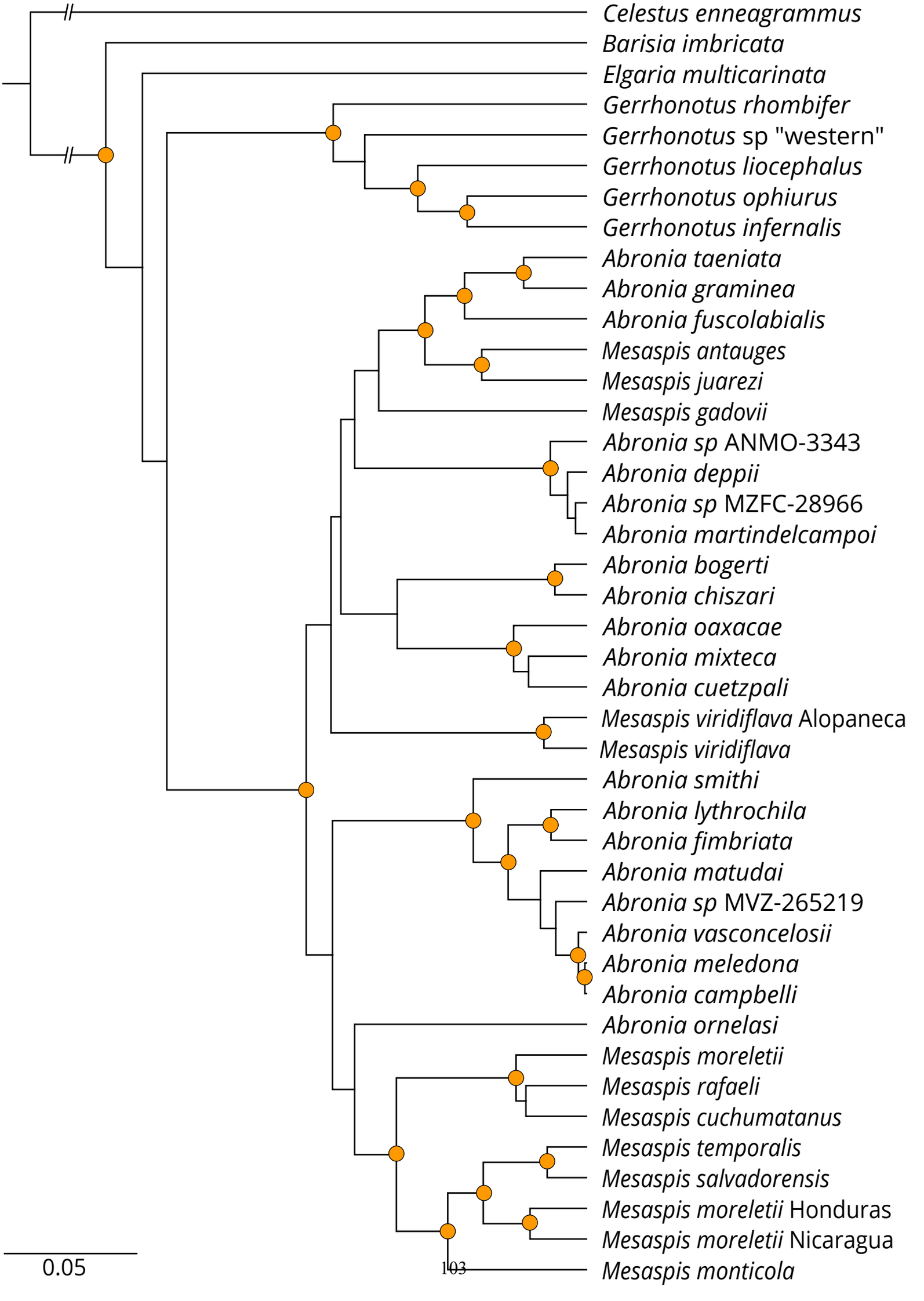
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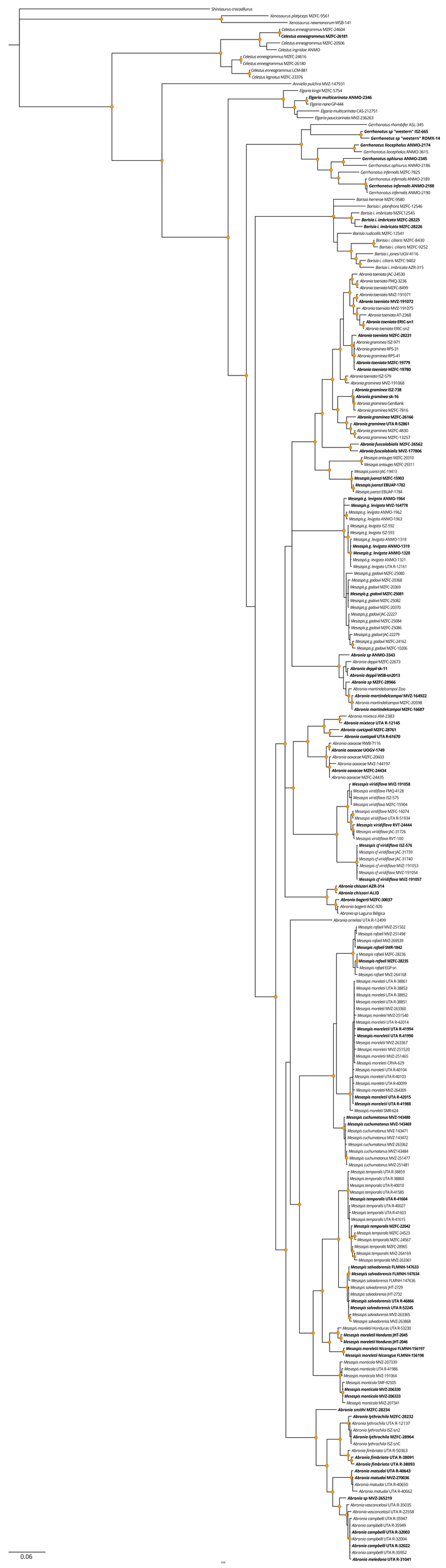
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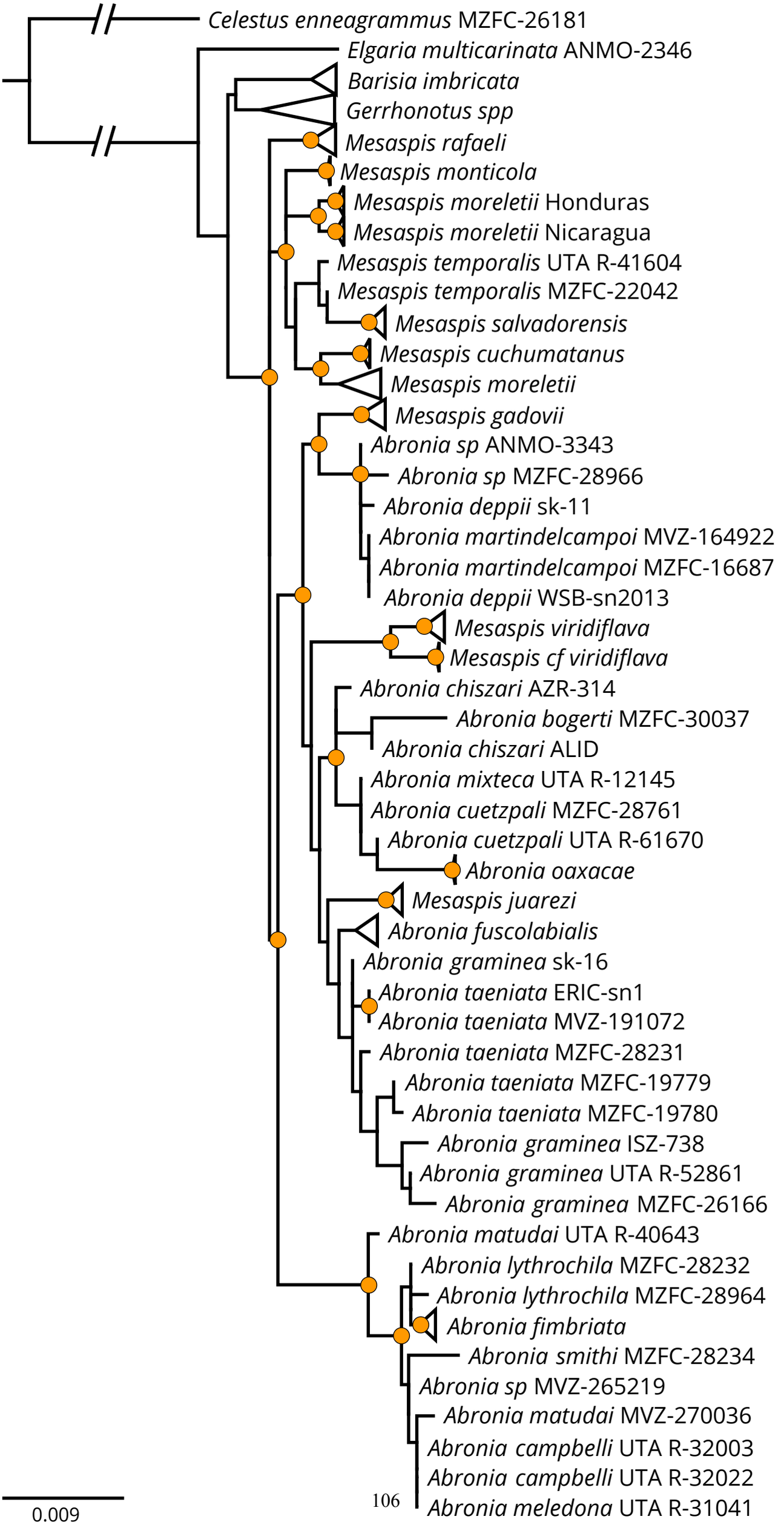
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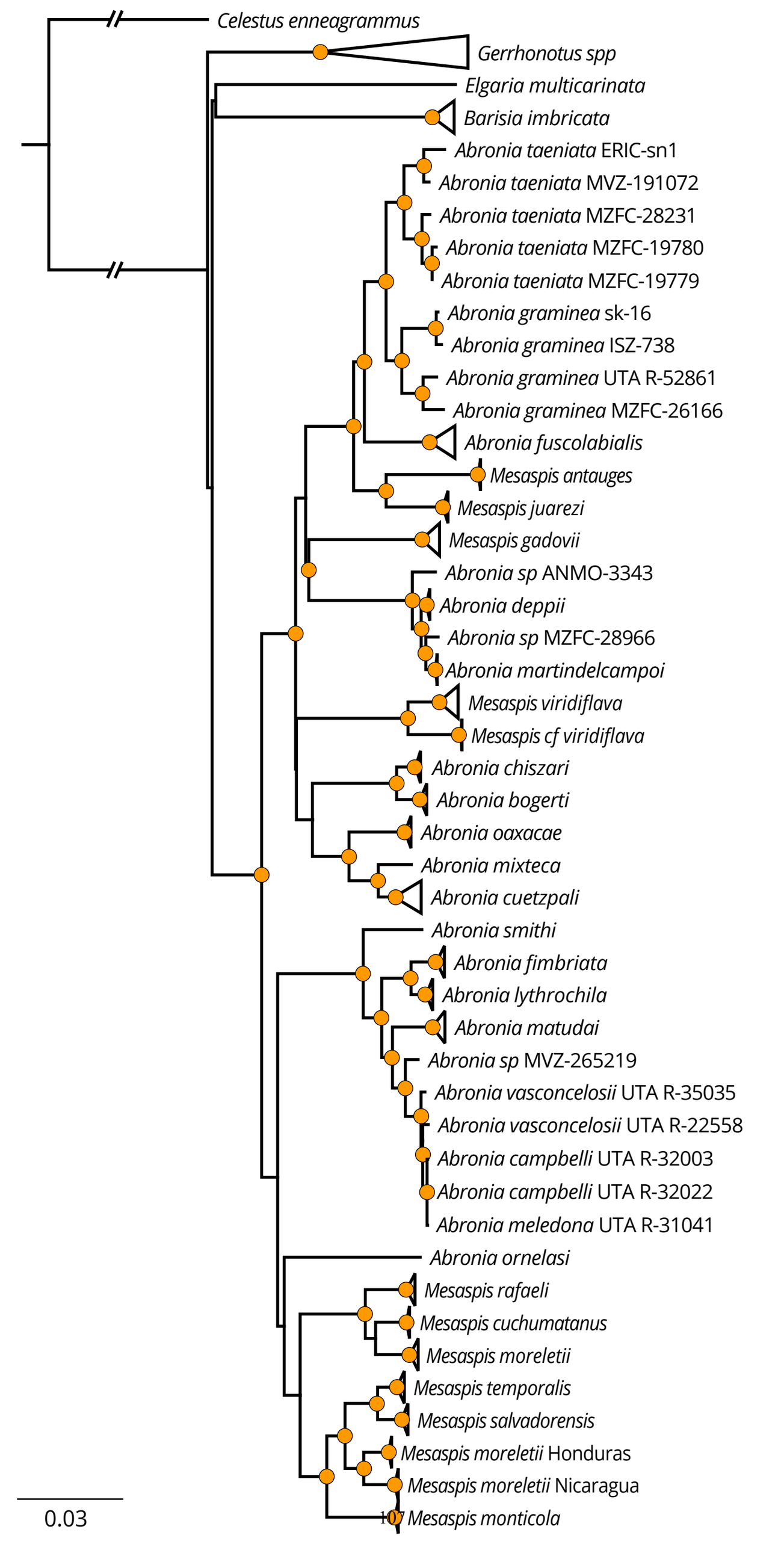
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Mesaspis monticola
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Table S1. Recognized species of *Abronia* and *Mesaspis* and their known geographic distribution. Subgenus membership for *Abronia* species is also shown.

Species	Subgenus	Distribution	Elevation (m)	References
Abronia ornelasi Campbell, 1984	*Abaculabronia*	Cerro Baúl, in the border between Chiapas and Oaxaca, México	1,500-1,600	(Campbell, 1984; Thesing et al., 2017)
A. reidi Werler & Shannon, 1961	*Abaculabronia*	Los Tuxtlas, Veracruz, México	1,000-1,635	(Thesing et al., 2017)
A. cuetzpali Campbell, Solano-Zavaleta, Flores-Villela, Caviedes-Solis & Frost, 2016	*Abronia*	Sierra Madre del Sur, in the Mexican state of Oaxaca	1,711-2,150	(Campbell et al., 2016)
A. deppii (Wiegmann, 1828)	*Abronia*	Trans-Mexican Volcanic Belt in the Mexican states of Guerrero, Michoacán, Morelos and Estado de México	1,850-2,600	(Centenero-Alcalá et al., 2009; Flores-Villela y Sánchez-H, 2003)
A. fuscolabialis (Tihen, 1944)	*Abronia*	Sierra Mixe and Sierra de Juárez, Oaxaca, México	1,992-2,438	(Campbell y Frost, 1993; Good y Schwenk, 1985)
A. graminea (Cope, 1864)	*Abronia*	Eastern Sierra Madre Oriental and Trans-Mexican Volcanic Belt, in the Mexican states of Puebla, Veracruz and Oaxaca	1,170-2,740	(Campbell y Frost, 1993; Clause et al., 2018; Schmidt-Ballardo, 1991)
A. martindelcampoi Flores-Villela & Sánchez-H., 2003	*Abronia*	Sierra Madre del Sur, in the Mexican state of Guerrero	2,100-2,600	(Flores-Villela y Sánchez-H, 2003)

A. mixteca Bogert & Porter, 1967	*Abronia*	Sierra Madre del Sur, Mixteca Alta region, in the Mexican state of Oaxaca	2,134-2,780	(Canseco-Márquez et al., 2007; Martín-Regalado et al., 2012)
A. oaxacae (Günther, 1885)	*Abronia*	Sierra Madre del Sur, highlands in central Oaxaca, México.	2,100-2,743	(Campbell, 2007a)
A. taeniata (Wiegmann, 1828)	*Abronia*	Eastern Sierra Madre Oriental and Trans-Mexican Volcanic Belt, in the Mexican states of Tamaulipas, Querétaro, Hidalgo, Veracruz and Puebla	1,000-3,000	(Hudson et al., 2001; Martin, 1958; Stephenson et al., 2008)
A. mitchelli Campbell, 1982	*Aenigmabronia*	North slope of Sierra de Juárez, Oaxaca, México	Around 2,750	(Campbell, 1982)
A. anzuetoi Campbell & Frost, 1993	*Auriculabronia*	Volcán de Agua, Department of Escuintla, Guatemala	1,219-2,286	(Campbell y Frost, 1993)
A. aurita (Cope, 1869)	*Auriculabronia*	"vast forest of Vera Paz, in the neighborhood of the ancient cities of Peten and Coban", Guatemala	Unknown	(Campbell y Brodie, 1999)
A. campbelli Brodie & Savage, 1993	*Auriculabronia*	Cerro Tablón de las Minas, Department of Jalapa, Eastern Guatemala	1,800-1,900	(Brodie y Savage, 1993)
A. fimbriata (Cope, 1884)	*Auriculabronia*	Sierra de Xucaneb and	1,400-2,100	(Acevedo et al., 2014; Campbell y

		Sierra de las Minas, Department of Alta Verapaz, and Sierra de Chuacús, Department of Baja Verapaz, in central-eastern Guatemala		Frost, 1993)
A. gaiophantasma Campbell & Frost, 1993	*Auriculabronia*	Mountains of the Departments of Alta Verapaz and Baja Verapaz, central Guatemala	1,600-2,400	(Campbell y Frost, 1993; Eisermann y Acevedo, 2016; Franzen y Haft, 1999)
A. leurolepis Campbell & Frost, 1993	*Auriculabronia*	Type locality "Santa Rosa, near Comitán, Chiapas, México"	Probably between 1,800-2,300	(Campbell y Frost, 1993; Townsend Peterson y Nieto-Montes de Oca, 1996)
A. lythrochila Smith & Álvarez del Toro, 1963	*Auriculabronia*	Meseta Central of Chiapas, México	1,500-3,000	(Campbell y Muñoz-Alonso, 2007a)
A. matudai (Hartweg & Tihen, 1946)	*Auriculabronia*	Volcán Tacaná, southeastern México, and Departments of San Marcos and Quetzaltenango, southwestern Guatemala	1,950-2,630	(Campbell y Muñoz-Alonso, 2013)
A. meledona Campbell & Brodie, 1999	*Auriculabronia*	Between Mataquescuintla and Jalapa, Department of Jalapa, southeastern Guatemala	2,200-2,660	(Campbell y Brodie, 1999)
A. ochoterenai (Martin del Campo, 1939)	*Auriculabronia*	Type locality "Santa Rosa, Comitán,	Probably between	(Campbell y Frost, 1993; Townsend Peterson y Nieto-Montes de Oca,

		Chiapas", México"	1,800-2,300	1996)
A. smithi Campbell & Frost, 1993	*Auriculabronia*	Sierra Madre de Chiapas, southeastern Chiapas, México	1,800-2,800	(Campbell y Muñoz-Alonso, 2007b)
A. vasconcelosii (Bocourt, 1871)	*Auriculabronia*	Guatemala Plateau, in the Departments of Quiché and Suchitepéquez, southern Guatemala	2,000-2,200	(Campbell y Brodie, 1999; Köhler, 2003)
A. frosti Campbell, Sasa, Acevedo & Mendelson, 1998	*Lissabronia*	Sierra de Los Cuchumatanes, Department of Huehuetenango, western Guatemala	2,800-3,013	(Ariano-Sánchez, 2010; Ariano-Sánchez et al., 2011; Campbell et al., 1998)
A. salvadorensis Hidalgo, 1983	*Lissabronia*	Sierra de Montecillos and Sierra de Opalaca, Honduras	1,900-2,250	(Köhler, 2003)
A. montecristoi Hidalgo, 1983	*Lissabronia*	Quebrada Grande, western Guatemala, and Montecristo National Park at the border between Guatemala, Honduras and El Salvador	1,370-2,250	(Köhler, 2003)
A. bogerti Tihen, 1954	*Scopaeabronia*	Chimalapas highlands (north of Niltepec, between Cerro Atravesado and Sierra Madre), Oaxaca, and Cerro Baúl, Chiapas, México	760-1,540	(Bille, 2001; Clause et al., 2016)

A. chiszari Smith & Smith, 1981	*Scopaeabronia*	Los Tuxtlas, Veracruz, México	660-800	(Flores-Villela y Vogt, 1992; Pérez-Higareda et al., 2002)
A. ramirezi Campbell, 1994	*Scopaeabronia*	Sierra Madre de Chiapas, western Chiapas, México	Probably between 800-1,350	(Campbell, 1994; Campbell y Muñoz-Alonso, 2007c)
M. antauges (Cope, 1866)		Pico de Orizaba, Veracruz, México	2,200-2,700	(Solano-Zavaleta et al., 2017)
M. cuchumatanus Solano-Zavaleta, Nieto-Montes de Oca & Campbell, 2016		Sierra de Los Cuchumatanes, and an apparent isolated population in Cumbre del Papal, in western Guatemala	2,475-3,260	(Solano-Zavaleta et al., 2016)
M. gadovii (Boulenger, 1913)		Sierra Madre del Sur, between Nueva Dehli, Guerrero, and San Pablo Cuatro Venados, Oaxaca	2,030-3,191	(Karges y Wright, 1987)
M. juarezi (Karges & Wright, 1987)		Sierra de Juárez, and an apparent isolated population northeast Cuicatlán, in Oaxaca, México	2,000-2,805	(Canseco-Márquez y Gutiérrez-Mayén, 2010; Karges y Wright, 1987)
M. monticola (Cope, 1878)		Central Volcanic range and Talamancan range in Costa Rica and western Panamá	1,800-3,800	(Acosta Chaves et al., 2013)
M. moreletii (Bocourt, 1871)		Central and southern Guatemala, and isolated populations in eastern Honduras and	1,230-3,244	(Solano-Zavaleta y Nieto-Montes de Oca, 2018)

		north Nicaragua		
M. rafaeli (Hartweg & Tihen, 1946)		Sierra Madre de Chiapas, southeastern Chiapas, México, and apparently to southwestern Guatemala	2057-3760	(Solano-Zavaleta y Nieto-Montes de Oca, 2018)
M. salvadorensis (Hartweg & Tihen, 1946)		Western Honduras	1,770-2411	(Solano-Zavaleta y Nieto-Montes de Oca, 2018)
M. temporalis (Hartweg & Tihen, 1946)		Meseta Central of Chiapas, México, and western-central Guatemala	1,123-3,053	(Solano-Zavaleta y Nieto-Montes de Oca, 2018)
M. viridiflava (Bocourt, 1873)		Sierra Mixe and Sierra de Juárez, Oaxaca, México	2,268-3,160	(Campbell, 2007b)

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Table S2. Localities (in alphabetical order) for samples utilized in this study. All samples were sequenced for the mitochondrial fragment. Samples in boldface are samples sequenced for nuclear genes. Acronyms for museums and collections follow Sabaj Pérez (2010). In the case of vouchers yet to be catalogued in the MZFC we provide their field numbers

Sample number	Taxon	Voucher	Locality
	Anniella pulchra	MVZ-147931	United States: California: Hwy. 58 at crest of Temblor Range
	Celestus enneagrammus	MZFC-24604	México: Oaxaca: Totontepec Villa de Morelos: Campamento de la SCT, saliendo de Totontepec
	C. enneagrammus	MZFC-24616	México: Puebla: Chilchotla: Aprox. 0.9 km al E de Ahuatla
	C. enneagrammus	LCM-881	México: Oaxaca
	C. enneagrammus	MZFC-20506	México: Puebla: Eloxochitlán: Paraje El Mirador, carretera Zoquitlán-Eloxochitlán
	C. enneagrammus	MZFC-26180	México: Veracruz: Aprox. 0.8 km al W de Tecoac
	C. enneagrammus	**MZFC-26181**	México: Oaxaca: Totontepec Villa de Morelos: Campamento de la SCT, saliendo de Totontepec
	C. ingridae	ANMO-	México
	C. legnotus	MZFC-23376	México: Puebla: Tlatlauquitepec: Xocayucan
	Shinisaurus crocodilurus		
	Xenosaurus newmanorum	WSB-141	México: San Luis Potosí: aproximadamente 7.2 km NE de Xilitla

	X. platyceps	MZFC-9561	México: Tamaulipas: Jaumave, Ciudad Victoria
1	***Abronia sp***	**ANMO-3343**	México: Guerrero
2	***Abronia sp***	**MZFC-28966**	México: Guerrero
3	*Abronia sp*	Laguna Bélgica	México: Chiapas: Ocozocoautla de Espinosa: Parque Laguna Bélgica
4	***Abronia sp***	**MVZ-265219**	Guatemala: Huehuetenango: 11.6 km (by road) from Colotenango-Cuilco road, past San Francisco El Retiro, Montañas de Peña Blanca,
5	***A. bogerti***	**MZFC-30037**	México: Chiapas: Cerro Baúl
6	*A. bogerti*	AGC-926	México: Chiapas: Cerro Baúl
7	***A. campbelli***	**UTA R-32003**	Guatemala: Jalapa: Cerro Tablón de Las Minas, near La Pastoría
8	*A. campbelli*	UTA R-32004	Guatemala: Jalapa: Cerro Tablón de Las Minas, near La Pastoría
9	***A. campbelli***	**UTA R-32022**	Guatemala: Jalapa: Cerro Tablón de Las Minas, near La Pastoría
10	*A. campbelli*	UTA R-35947	Guatemala: Jalapa: Cerro Tablón de Las Minas, near Potrero Carrillo
11	*A. campbelli*	UTA R-35949	Guatemala: Jalapa: Cerro Tablón de Las Minas, near Potrero Carrillo
12	*A. campbelli*	UTA R-35952	Guatemala: Jalapa: Cerro Tablón de Las Minas, near Potrero Carrillo
13	***A. chiszari***	**AZR-314**	México: Veracruz: Los Tuxtlas
14	***A. chiszari***	**ALID**	México: Veracruz: Los Tuxtlas
15	***A. cuetzpali***	**MZFC-28761**	México: Oaxaca: San Miguel Suchixtepec: near San Miguel Suchixtepec, Sierra de

			Miahuatlán, approximately 2 km west of the Río Molino
16	***A. cuetzpali***	**UTA R-61670**	México: Oaxaca: Juquila: 5.4 km east of Juquila, Sierra de Miahuatlán, Sierra Madre del Sur
17	*A. deppii*	MZFC-22673	México: Michoacán: Zitácuaro: 3.5 km SE Lázaro Cárdenas, Cerro El Molcajete
18	***A. deppii***	**sk-11**	México: Morelos: Huitzilac
19	***A. deppii***	**WSB-sn2013**	México: Morelos: Huitzilac: vicinity of Huitzilac
20	***A. fimbriata***	**UTA R-38091**	Guatemala: Alta Verapaz: near Chirrucbiquim, 2.0 km NNE Minas Cáquipec
21	***A. fimbriata***	**UTA R-38093**	Guatemala: Alta Verapaz: near Chirrucbiquim, 2.0 km NNE Minas Cáquipec
22	*A. fimbriata*	UTA R-50363	Guatemala: Baja Verapaz: vicinity La Unión Barrios
23	***A. fuscolabialis***	**MVZ-177806**	México: Oaxaca: bus stop shed, 16.6 km N (by road) summit Hwy. 175, Cerro Pelón, Sierra Juárez
24	***A. fuscolabialis***	**MZFC-26562**	México: Oaxaca: Totontepec Villa de Morelos: 2.5 km by road to the west of Totontepec
25	*A. graminea*	Genbank	NC_005958.1
26	*A. graminea*	MVZ-191068	Mexico: Veracruz: Acajete: forest W of La Joya
27	*A. graminea*	MZFC-4830	México: Oaxaca: Teotitlán de Flores

			Magón: Puerto de La Soledad
28	*A. graminea*	MZFC-13257	México: Oaxaca: Teotitlán de Flores Magón: Puerto de La Soledad
29	*A. graminea*	MZFC-7816	México: Puebla: Tepeyahualco: Tepeyolulco
30	***A. graminea***	**sk-16**	México: Veracruz: Acultzingo: Puerto del Aire
31	***A. graminea***	**ISZ-738**	México: Veracruz: Acultzingo: Puerto del Aire
32	***A. graminea***	**MZFC-26166**	México: Puebla: Ajalpan: Cinco Señores
33	*A. graminea*	ISZ-971	México: Puebla: Tetela de Ocampo: Tepexácatl
34	*A. graminea*	RPS-31	México: Puebla: Tetela de Ocampo: La Cañada, SW of Tetela de Ocampo
35	*A. graminea*	RPS-41	México: Puebla: Cuautempan: SW of San Esteban Cuautempan
36	*A. graminea*	UTA R-52861	México: Puebla: Sierra Negra
37	***A. lythrochila***	**MZFC-28232**	México: Chiapas: Teopisca
38	***A. lythrochila***	**MZFC-28964**	México: Chiapas: Zinacantán: Parque San José Bocomtenelté
39	*A. lythrochila*	ISZ-snC	México: Chiapas: Zinacantán: Parque San José Bocomtenelté
40	*A. lythrochila*	ISZ-sn2	México: Chiapas: Zinacantán: Parque San José Bocomtenelté
41	*A. lythrochila*	UTA R-12137	México: Chiapas: 12.1 km ESE Teopisca, Tulanc
42	***A. martindelcampoi***	**MVZ-164922**	México: Guerrero: Carrizal de Bravo, Sierra Madre del Sur

43	***A. martindelcampoi***	**MZFC-16687**	México: Guerrero: Leonardo Bravo: 3.4 km S Carrizal de Bravo
44	*A. martindelcampoi*	MZFC-20598	México: Guerrero: Carrizal de Bravo, Sierra Madre del Sur
45	***A. martindelcampoi***	**Zoo**	**México:**
46	***A. matudai***	**MVZ-270036**	Guatemala: San Marcos: San Marcos municipal forest, ca. 200 m S of high point on road from El Rincón to Barranca de Galvez
47	***A. matudai***	**UTA R-40643**	Guatemala: San Marcos: Esquipulas Palo Gordo: Aldea La Fraternidad, Finca La Esperanza
48	*A. matudai*	UTA R-40650	Guatemala: San Marcos: Esquipulas Palo Gordo: Aldea La Fraternidad, Finca La Esperanza
49	*A. matudai*	UTA R-40662	Guatemala: San Marcos: Esquipulas Palo Gordo: Aldea La Fraternidad, Finca La Esperanza
50	***A. meledona***	**UTA R-31041**	Guatemala: Jalapa: Miramundo, Guatel Tower
51	*A. mixteca*	AM-2383	México: Oaxaca: El Tecojote
52	***A. mixteca***	**UTA R-12145**	México: Oaxaca: El Tecojote
53	*A. oaxacae*	MVZ-144197	México: Oaxaca: Cerro San Felipe, 20 km NNE (by Mexican Hwy. 175) Oaxaca to La Cumbre, 4 km NW (by dirty road), 9500 ft
54	*A. oaxacae*	MZFC-20603	México: Oaxaca: El Punto, Sierra de Juárez
55	***A. oaxacae***	**MZFC-24434**	México: Oaxaca: Santa María Yavesía: Santa María Yavesía

56	*A. oaxacae*	MZFC-24435	México: Oaxaca: Santa María Yavesía: Santa María Yavesía
57	*A. oaxacae*	RWB-7116	México: Oaxaca: Puerto del Sol, km 117 Hwy 175
58	***A. oaxacae***	**UOGV-1749**	México: Oaxaca: Santiago Comaltepec: Sierra de Juárez, desviación a Santiago Comaltepec
59	*A. ornelasi*	UTA R-12499	México: Oaxaca: Colonia Rodulfo Figueroa, 19 km NW Rizo de Oro (Chiapas)
60	***A. smithi***	**MZFC-28234**	México: Chiapas: Mapastepec: Reserva de El Triunfo, campamento de la CONANP en la zona núcleo 1
61	*A. taeniata*	MVZ-191071	México: Hidalgo: 4.3 km E junction of Mexico Hwy. 105 and old Hwy. to Tianguistengo
62	***A. taeniata***	**MVZ-191072**	México: Hidalgo: 4.3 km E junction of Mexico Hwy. 105 and old Hwy. to Tianguistengo
63	*A. taeniata*	MVZ-191075	México: Hidalgo: 3.2 km NW (by road) Agua Blanca Iturbide
64	***A. taeniata***	**MZFC-19779**	México: Puebla: Tlatlauquitepec: Atalpa
65	***A. taeniata***	**MZFC-19780**	México: Puebla: Tlatlauquitepec: Atalpa
66	***A. taeniata***	**MZFC-28231**	México: Veracruz: Altotonga: Aprox. 2.78 km W de Altotonga
67	*A. taeniata*	AT-2368	México: Veracruz: Huayacocotla: Viborillas
68	***A. taeniata***	**ERIC-sn1**	México: Veracruz: Huayacocotla: La Selva
69	*A. taeniata*	ERIC-sn2	México: Veracruz: Huayacocotla: La Selva
70	*A. taeniata*	ISZ-579	México: Puebla: Quimixtlán: aprox. 1 km al

			E de Ahuatla
71	*A. taeniata*	JAC-24530	México: Querétaro: roadside park alongside Mexican Hwy 120º
72	*A. taeniata*	FMQ-3236	México: Tamaulipas: Rancho El Cielo
73	*A. taeniata*	MZFC-8499	México: Tamaulipas: Gómez Farías: aprox. 5 km al SE de la Estación Canindo, Reserva de la Biósfera Rancho El Cielo
74	*A. vasconcelosii*	UTA R-22558	Guatemala: Quiché: 3 km SSE Chichicastenago, in valley between Paxot and Camnibal
75	*A. vasconcelosii*	UTA R-35035	Guatemala: Sacatepéquez: San Lucas Sacatepéquez: Cerro Alux (W of Guatemala City)
	Barisia herrerae	MZFC-9580 AY605120	México: Estado de México: approximately 4 km E Ocuilan
	B. i. ciliaris	MZFC-8430 AY605107	México: Querétaro: Cadereyta: 1 km NE El Doctor
	B. i. ciliaris	MZFC-9252 AY660759	México: Querétaro: Pinal de Amoles: 6 km NW Rancho Los Velázquez.
	B. i. ciliaris	MZFC-9402 AY660760	México: Querétaro: Colón: Pinal de Zamorano
	B. i. imbricata	MZFC-12545 AY605114	México: Oaxaca: Peña Verde, Cañada de Cuicatlán
	B. i. imbricata	**MZFC-28225**	México: Veracruz: La Perla: About 2 km W San Miguel Pilancón y San Miguel Chinela
	B. i. imbricata	**MZFC-28226**	México: Veracruz: La Perla: About 2 km W San Miguel Pilancón y San Miguel Chinela
	B. i. imbricata	AZR-315	México: Veracruz: Pico de Orizaba

	AY605109	
B. i. jonesi	UGV-4116	México: Michoacán: Coalcomán
	AY605118	
B. i. planifrons	MZFC-12546	México: Oaxaca: Sierra de Juárez, Yuvila
	AY605119	
B. rudicollis	MZFC-12541	México: Estado de México: Avándaro, Valle
	AY660761	de Bravo
Elgaria kingii	MZFC-5754	México: Chihuahua: Cascada de
	AY605103	Basaseachic
E. multicarinata	CAS-212751	United States: California: Little Sullivan
	DQ364660	Creek, Colusa Co.
E. multicarinata	**ANMO-2346**	México: Baja California: La Oliva, Puerto
		Trampa
E. nana	GP-444	México: Baja California Norte: Coronados
	DQ364661	Island
E. paucicarinata	MVZ-236263	México: Baja California Sur: San Antonia
	DQ364662	de la Sierra
Gerrhonotus sp "western"	**ISZ-665**	México: Nayarit: Compostela: Mesillas,
		aprox. 15 km al E de Las Varas
G. sp "western"	**ROMX-14**	México: Jalisco: Chamela
G. infernalis	**MZFC-7825**	México: Querétaro: Cadereyta de Montes:
		Aproximadamente 4 Km NE por terracería
		al Rancho El Arbolito, Mesa de León,
		carretera Termoeléctrica Zimapán
G. infernalis	**ANMO-2188**	México: Coahuila: Sierra de Jimulco
G. infernalis	ANMO-2189	México: Coahuila: Sierra de Jimulco
G. infernalis	ANMO-2190	México: Coahuila: Sierra de Jimulco
G. liocephalus	**ANMO-2174**	México: Oaxaca: Guelatao de Juárez

	G. liocephalus	ANMO-3615	México: Guerrero: Tlapa de Comonfort: Camino a Olinalá, en la desviación a Coachimaico
	G. ophiurus	**ANMO-2345**	México: Veracruz: Cuautlapan
	G. ophiurus	ANMO-2186	México: Veracruz: Misantla: Manuel Gutiérrez Nájera
76	*Mesaspis antauges*	MZFC-29310	México: Veracruz: Alpatlahuac: La Manzanita
77	*M. antauges*	MZFC-29311	México: Veracruz: Alpatlahuac: Mesa de Buena Vista
78	***M. cuchumatanus***	**MVZ-143469**	Guatemala: Huehuetenango: km 311, at stream below Captzin, on Huehuetenango-Barillas Rd.
79	*M. cuchumatanus*	MVZ-143471	Guatemala: Huehuetenango: km 311, at stream below Captzin, on Huehuetenango-Barillas Rd.
80	*M. cuchumatanus*	MVZ-143472	Guatemala: Huehuetenango: Cuchumatanes Mts., 4.5 km E (by road) Todos Santos on Todos Santos-Paquix Rd.
81	*M. cuchumatanus*	MVZ-263362	Guatemala: Huehuetenango: 3 km (by road) N of junction with road to Todos Santos Cuchumatán, on road from San Juan Ixcoy to Huehuetenango
82	***M. cuchumatanus***	**MVZ-143480**	Guatemala: Huehuetenango: 13.6 mi N Santa Eulalia, Huehuetenango-Barillas Rd.
83	*M. cuchumatanus*	MVZ-143484	Guatemala: Huehuetenango: 13.6 mi N Santa Eulalia, Huehuetenango-Barillas Rd.
84	*M. cuchumatanus*	MVZ-251477	Guatemala: Huehuetenango: 11.4 km north

			of Santa Eulalia by road
85	*M. cuchumatanus*	MVZ-251481	Guatemala: Huehuetenango: 11.4 km north of Santa Eulalia by road
86	*M. gadovii gadovii*	MZFC-24162	México: Guerrero: Chilpancingo: aprox., 2 km E Omiltemi (por camino)
87	*M. g. gadovii*	MZFC-10206	México: Guerrero: Chilpancingo: aprox. 2 Km N Omiltemi, Barranca Agua Fría
88	*M. g. gadovii*	MZFC-20368	México: Guerrero: Sierra de Malinaltepec, carretera San Luis Acatlán-Tlapa de Comonfort, km 73.
89	*M. g. gadovii*	MZFC-20369	México: Guerrero: Sierra de Malinaltepec, carretera San Luis Acatlán-Tlapa de Comonfort, km 73.
90	*M. g. gadovii*	MZFC-25080	México: Guerrero: Malinaltepec: Ejido Tres Marías
91	***M. g. gadovii***	**MZFC-25081**	México: Guerrero: Malinaltepec: Ejido Tres Marías
92	*M. g. gadovii*	MZFC-25082	México: Guerrero: Malinaltepec: Ejido Tres Marías
93	*M. g. gadovii*	MZFC-20370	México: Guerrero: Sierra de Malinaltepec: carretera San Luis Acatlán-Tlapa de Comonfort
94	*M. g. gadovii*	MZFC-25084	México: Guerrero: Atoyac de Álvarez: (Cerro Teotepec) Carretera Filo de Caballos-Puerto del Gallo
95	*M. g. gadovii*	JAC-22227	México: Guerrero: Carretera Nueva Delhi-La Guitarra
96	*M. g. gadovii*	MZFC-25086	México: Guerrero: Cerro Teotepec

97	*M. g. gadovii*	JAC-22279	México: Guerrero: between Filo de Caballo and Carrizal de Bravo
98	***M. g. levigata***	**MVZ-164778**	México: Oaxaca: Santa María Sola: 10.4 mi WSW (by road) San Vicente Lauhixio
99	*M. g. levigata*	ANMO-1318	México: Oaxaca: El Tejocote, Camino al Cerro Metate
100	***M. g. levigata***	**ANMO-1319**	México: Oaxaca: El Tejocote, Camino al Cerro Metate
101	***M. g. levigata***	**ANMO-1320**	México: Oaxaca: El Tejocote, Camino al Cerro Metate
102	*M. g. levigata*	ANMO-1321	México: Oaxaca: El Tejocote, Camino al Cerro Metate
103	*M. g. levigata*	UTA R-12161	México: Oaxaca: El Tejocote
104	*M. g. levigata*	ANMO-1962	México: Oaxaca: Santa Maria Yucuhuiti: Llano Grande
105	*M. g. levigata*	ANMO-1963	México: Oaxaca: Santa Maria Yucuhuiti: Llano Grande
106	***M. g. levigata***	**ANMO-1964**	México: Oaxaca: Santa Maria Yucuhuiti: Llano Grande
107	*M. g. levigata*	ISZ-592	México: Oaxaca: La Nevería, 4 km S, San Pablo Cuatro Venados
108	*M. g. levigata*	ISZ-593	México: Oaxaca: La Nevería, 4 km S, San Pablo Cuatro Venados
109	***M. juarezi***	**EBUAP-1782**	México: Oaxaca: Peña Verde (NE de Cuicatlán)
110	*M. juarezi*	EBUAP-1784	México: Oaxaca: Peña Verde (NE de Cuicatlán)
111	***M. juarezi***	**MZFC-15903**	México: Oaxaca: N. Cerro pelon, 10.6 km N

			cerro machin (turnoff for comaltepec) on Hwy 175 turnoff for
112	*M. juarezi*	JAC-19413	México: Oaxaca: 31.9 mi S Valle Nacional bridge on Hwy # 175
113	*M. monticola*	MVZ-191064	Costa Rica: San José: Villa Mills, Cerro de La Muerte
114	*M. monticola*	MVZ-207339	Costa Rica: Cartago: 20.7 km SE El Empalme junction on Hwy 2
115	*M. monticola*	UTA R-41986	Costa Rica: San José: Cerro de La Muerte, Las Torres
116	***M. monticola***	**MVZ-206330**	Costa Rica: Heredia: Braulio Carrillo National Park
117	***M. monticola***	**MVZ-206333**	Costa Rica: Heredia: Braulio Carrillo National Park
118	*M. monticola*	MVZ-207341	Costa Rica: Heredia: 0.6 km W Vara Blanca junction on Hwy 120
119	*M. monticola*	SMF-92505	Costa Rica: Heredia: Volcán Barva, Los Ángeles de Paso Llano
120	*M. moreletii*	MVZ-251465	Guatemala: Chimaltenango: Top pf Cerro Tecpan
121	*M. moreletii*	CRVA-629	Guatemala: Chimaltenango: Top pf Cerro Tecpan
122	*M. moreletii*	SMR-624	Guatemala: El Progreso: Albores cabins, Sierra de las Minas Biosphere Reserve
123	*M. moreletii*	MVZ-251520	Guatemala: Totonicapan: Paquix
124	*M. moreletii*	MVZ-263367	Guatemala: Totonicapan: Nuevo Santa Caterina Ixtahuacán
125	*M. moreletii*	UTA R-42014	Guatemala: Quezaltenango: N del Volcán

			Zunil
126	***M. moreletii***	**UTA R-42015**	Guatemala: Quezaltenango: N del Volcán Zunil
127	*M. moreletii*	MVZ-263360	Guatemala: Baja Verapaz: Finca Foresta, 1.5 km (by road) from Chilasco
128	*M. moreletii*	UTA R-38851	Guatemala: Baja Verapaz: Finca San Jorge, Chilasco, Sierra de las Minas
129	*M. moreletii*	UTA R-38852	Guatemala: Baja Verapaz: Chilasco (town) and surroundings, Sierra de las Minas
130	*M. moreletii*	UTA R-38853	Guatemala: Baja Verapaz: Chilasco (town) and surroundings, Sierra de las Minas
131	*M. moreletii*	UTA R-38861	Guatemala: Baja Verapaz: Finca San Jorge, Chilasco, Sierra de las Minas
132	*M. moreletii*	UTA R-40099	Guatemala: Alta Verapaz: Chelemhá, Sierra de Xucaneb
133	*M. moreletii*	UTA R-40103	Guatemala: Alta Verapaz: Chelemhá, Sierra de Xucaneb
134	*M. moreletii*	UTA R-40104	Guatemala: Alta Verapaz: Chelemhá, Sierra de Xucaneb
135	*M. moreletii*	MVZ-264309	Guatemala: Alta Verapaz: Chelemhá, 12.1 km NNE (by air) of Tucuru, Montañas de Yalijux
136	*M. moreletii*	MVZ-251540	Guatemala: Quiché: 3.4 km N Uspantán, on road to Caracol
137	***M. moreletii***	**UTA R-41988**	Guatemala: Quiché: Uspantán: El Chimel, Colonia Patoja
138	***M. moreletii***	**UTA R-41990**	Guatemala: Quiché: Uspantán: Cumbre El Chimel-San Pablo El Baldío (East side)

139	***M. moreletii***	**UTA R-41994**	Guatemala: Quiché: 19.3 km N Uspantán, N of Aldea El Caracol
140	***M. moreletii* Honduras**	**JHT-2045**	Honduras: Francisco Morazán: Parque Nacional Montaña de Yoro
141	***M. moreletii* Honduras**	**JHT-2046**	Honduras: Francisco Morazán: Parque Nacional Montaña de Yoro
142	*M. moreletii* Honduras	UTA R-53230	Honduras: Francisco Morazán: Parque Nacional La Tigra
143	***M. moreletii* Nicaragua**	**FLMNH-156197**	Nicaragua: Jinotega: Reserva Natural Cerro Kilambé
144	***M. moreletii* Nicaragua**	**FLMNH-156198**	Nicaragua: Jinotega: Reserva Natural Cerro Kilambé
145	***M. rafaeli***	**SMR-1842**	Mexico: Chiapas: Motozintla: 200 m (by road) S of summit of Cerro Mozotal
146	*M. rafaeli*	MVZ-264168	Mexico: Chiapas: east side of Cerro Mozotal
147	*M. rafaeli*	MVZ-251498	Guatemala: San Marcos: Finca La Ínsula, km 263 of RN1
148	*M. rafaeli*	MVZ-251502	Guatemala: San Marcos: Caxaque
149	*M. rafaeli*	MVZ-269539	Mexico: Chiapas: Motozintla: Cerro Boquerón, 1.1 km WSW (by air) of Ejido Boquerón
150	*M. rafaeli*	EGP-sn	México: Chiapas: El Triunfo Biosphere Reserve
151	***M. rafaeli***	**MZFC-28235**	México: Chiapas: El Triunfo Biosphere Reserve
152	*M. rafaeli*	MZFC-28236	México: Chiapas: El Triunfo Biosphere Reserve
153	*M. salvadorensis*	JHT-2729	Honduras: Ocotepeque: along road below

			towers, El Güisayote Biological Reserve
154	*M. salvadorensis*	JHT-2732	Honduras: Ocotepeque: along road below towers, El Güisayote Biological Reserve
155	*M. salvadorensis*	MVZ-263365	Honduras: Ocotepeque: comunication tower, 5.3 km (by road) S CA-4, El Güisayote Biological Reserve
156	*M. salvadorensis*	MVZ-263868	Honduras: Ocotepeque: 3.5 km S (by air) of CA-4 at El Portillo de Ocotepeque, El Güisayote Biological Reserve
157	***M. salvadorensis***	**UTA R-46866**	Honduras: Ocotepeque: Carretera Nueva Ocotopeque - La Labor
158	***M. salvadorensis***	**UTA R-52245**	Honduras: Ocotepeque: Carretera Nueva Ocotopeque - La Labor
159	***M. salvadorensis***	**FLMNH-147633**	Honduras: Cortés: Cerro Jilinco, El Cusuco National Park
160	***M. salvadorensis***	**FLMNH-147634**	Honduras: Cortés: Quebrada de Cantiles, El Cusuco National Park
161	*M. salvadorensis*	FLMNH-147636	Honduras: Cortés: Quebrada de Cantiles, El Cusuco National Park
162	*M. temporalis*	MVZ-263361	Mexico: Chiapas: 6.5 km (by road) W of San Cristóbal de las Casas on old road to Tuxtla Gutiérrez
163	*M. temporalis*	MZFC-28965	Mexico: Chiapas: Zinacantán
164	*M. temporalis*	MVZ-264169	Mexico: Chiapas: top of Cerro Tzontehuitz
165	***M. temporalis***	**MZFC-22042**	México: Chiapas: Pueblo Nuevo Solistahuacán: Paradero Selva Negra
166	*M. temporalis*	MZFC-24523	Mexico: Chiapas: Tapalapa: between km 5 and 6 on Coapilla-Tapalapa road

167	*M. temporalis*	MZFC-24567	Mexico: Chiapas: Tapalapa: between km 5 and 6 on Coapilla-Tapalapa road
168	*M. temporalis*	UTA R-38859	Guatemala: San Marcos: Esquipulas Palo Gordo: Finca La Esperanza, Aldea La Fraterrnidad
169	*M. temporalis*	UTA R-38860	Guatemala: San Marcos: Esquipulas Palo Gordo: Finca La Esperanza, Aldea La Fraterrnidad
170	*M. temporalis*	UTA R-40010	Guatemala: San Marcos: Esquipulas Palo Gordo: Finca La Esperanza, Aldea La Fraterrnidad
171	*M. temporalis*	UTA R-40027	Guatemala: San Marcos: Esquipulas Palo Gordo: Finca La Esperanza, Aldea La Fraterrnidad
172	*M. temporalis*	UTA R-41585	Guatemala: San Marcos: Esquipulas Palo Gordo: Finca La Esperanza, Aldea La Fraternidad
173	*M. temporalis*	UTA R-41603	Guatemala: Huehuetenango: La Democracia, between Ojo de Agua and Hoja Blanca
174	***M. temporalis***	**UTA R-41604**	Guatemala: Huehuetenango: La Democracia, between Ojo de Agua and Hoja Blanca
175	*M. temporalis*	UTA R-41615	Guatemala: Huehuetenango: 5.6 km E San Mateo Ixtatán
176	***M. viridiflava***	**MVZ-191058**	México: Oaxaca: Santiago Comaltepec: Cerro Pelon [Humo], 49 km N Guelatao on Mexico Hwy. 175

177	*M. viridiflava*	ISZ-575	México: Oaxaca: Santiago Comaltepec: 1 km N (por camino) del mirador de Cerro Pelón, Ixtlán
178	*M. viridiflava*	FMQ-4128	México: Oaxaca: Llano de las Flores, carretera Oax-Tuxtepec Km 118.3
179	***M. viridiflava***	**MZFC-24444**	México: Oaxaca: Santa María Yavesía
180	*M. viridiflava*	RVT-100	México: Oaxaca: Santa María Yavesía
181	*M. viridiflava*	JAC-31726	México: Oaxaca: 15 kms WSW Santo Domingo Xagacia
182	*M. viridiflava*	MZFC-15904	México: Oaxaca: 1 km N Cerro Pelon on Hwy 175
183	*M. viridiflava*	UTA R-51934	México: Oaxaca: ca. 11 mi (17.7 km) W Totontepec
184	*M. viridiflava*	MZFC-16074	México: Oaxaca: ca. 11 miles W Totontepec
185	*M. cf viridiflava*	MVZ-191053	México: Oaxaca: Nuevo Zoquiapam: Cerro San Felipe, 15.4 km NW (by road) La Cumbre
186	*M. cf viridiflava*	MVZ-191054	México: Oaxaca: Nuevo Zoquiapam: Cerro San Felipe, Micro-Ondas, 12.9 km NW (by road) La Cumbre
187	***M. cf viridiflava***	**MVZ-191057**	México: Oaxaca: Nuevo Zoquiapam: Cerro San Felipe, Micro-Ondas, 12.9 km NW (by road) La Cumbre
188	***M. cf viridiflava***	**ISZ-576**	México: Oaxaca: Estación de microondas Corral de Piedra, Cerro San Felipe
189	*M. cf viridiflava*	JAC-31739	México: Oaxaca: 10 kms W Santa Catarina Ixtepeji, Sierra de Aloapaneca
190	*M. cf viridiflava*	JAC-31740	México: Oaxaca: 10 kms W Santa Catarina

Table S3. Primers used in this study.

Primer Name	Primer Sequence	Source
BMP2_f6	5' CAKCACCGWATTAATATTTATGAAA 3'	(Townsend et al.,
BMP2_r2	5' CGRCACCCRCARCCCTCCACAACCA 3'	2008)
KIAA1217_f1	5' WYGGAGGAYATTGCTTTCATG 3'	(Portik et al., 2012)
KIAA1217_r2	5' RATTTCAAAYCTTTTWGCCTCYTTATGT 3'	
PRLR_f1	5' GACARYGARGACCAGCAACTRATGCC 3'	(Townsend et al.,
PRLR_f3	5' GACYTTGTGRACTTCYACRTAATCCAT 3'	2008)
ND4	5' CACCTATGACTACCAAAAGCTCATGTAGAAGC 3'	(Arévalo et al.,
Leu	5' CATTACTTTTACTTGGATTTGCACCA 3'	1994)

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DISCUSIÓN GENERAL

Esta tesis se dividió en tres capítulos y cada uno de ellos se enfocó en una problemática diferente. Cada capítulo busca cumplir con uno o más objetivos, y debido a ello esta discusión seguirá el orden de dichos capítulos.

Límites de especies

En el **Capítulo 1** se investigaron los **límites de especies en *Mesaspis moreletii*** (parte del objetivo 2, ya que los problemas de límites de especies en *M. gadovii*, *M. viridiflava*, *A. graminea* y *A. taeniata* se abordan de manera breve en el Capítulo 3). De todos los límites de especies que se deseaba trabajar, era este el que resultaba más interesante. En primer lugar, este taxón presentaba una distribución geográfica amplia con respecto a los demás gerrhonotinos y, en segundo lugar, se le reconocían cinco subespecies. En esta sección de la tesis se identificó a las subespecies *M. m. moreletii* (incluyendo a *M. m. fulvus*), *M. m. rafaeli*, *M. m. salvadorensis* y *M. m. temporalis* como linajes evolutivamente independientes y, dado que existen diferencias morfológicas entre cada uno de estos linajes (Hartweg y Tihen, 1946; Solano-Zavaleta, 2011), se sugirió elevar estas subespecies a nivel de especie. Adicionalmente se corroboró la validez taxonómica de *M. cuchumatanus* (Solano-Zavaleta et al., 2016), una especie descrita como parte de este trabajo de tesis.

Además, se detectaron algunas poblaciones que podrían representar especies no descritas: poblaciones asignadas a *M. moreletii* del este Honduras, *M. moreletii* de Nicaragua y *M. salvadorensis* del norte de Honduras. Aunque los métodos empleados con caracteres moleculares (Grummer et al., 2014; Wiens y Penkrot, 2002; Yang, 2015) sugieren el reconocimiento de estas poblaciones como especies distintas, es posible que estos resultados se deban al pequeño número de ejemplares revisados, así como a la falta de ejemplares de localidades intermedias (problemas de muestreo) entre estas poblaciones y con respecto a las otras especies reconocidas. Adicionalmente, el reducido número de secuencias representativas de estas poblaciones podría estar causando una sobreestimación de los valores para inferir los límites de especies. Por otra parte, los caracteres morfológicos no permiten distinguir de manera clara entre las poblaciones asignadas a *M. moreletii* del este Honduras y *M. moreletii* de Nicaragua; lo mismo sucede entre las poblaciones de *M. salvadorensis* y *M. salvadorensis* del norte de Honduras (Solano-Zavaleta, 2011), las cuales presentan además distancias genéticas muy pequeñas (p = 0.44%) entre ellas. Con base en los argumentos anteriores, se prefirió seguir

un enfoque conservador y concluir que el estatus taxonómico de estas tres poblaciones sigue incierto hasta no contar con un mayor número de ejemplares, secuencias y/o genes, para analizar estos casos de manera específica.

El caso de ***A. graminea*** y ***A. taeniata***. Análisis preliminares de este trabajo de tesis revelaron que los haplotipos de los ejemplares de *Abronia graminea* en el árbol de mtDNA se agruparon en dos clados, uno con los ejemplares del extremo norte de la distribución (Pico de Orizaba-Cumbres de Acultzingo) y el otro conformado por los ejemplares del extremo sur de la distribución (Sierra Negra de Puebla-Puerto Soledad, Oaxaca). Es decir, clados representativos de las poblaciones del norte y sur, respectivamente, de la distribución de *A. graminea*. La coloración dorsal de ambas poblaciones es diferente. La mayoría de los individuos del norte presentan una coloración dorsal verde uniforme aunque algunas hembras pueden tener bandas transversales visibles e incluso una coloración dorsal con tonos anaranjados brillantes u opacos (Clause et al., 2016a). En las poblaciones del sur, los machos tienen una coloración dorsal verde menos brillante que los ejemplares del norte, mientras que las hembras presentan una coloración dorsal más opaca, predominando los tonos grises claros y oscuros, con bandas transversales evidentes de color marrón oscuro o negro.

La diferencia en los patrones de coloración entre estas dos poblaciones, así como el arreglo de los haplotipos en el árbol de mtDNA y el aparente aislamiento geográfico, parecía sugerir que existía un problema de límite de especies al interior de *A. graminea*. Sin embargo, no se encontraron diferencias morfológicas que permitieran diferenciar entre ambas poblaciones y el análisis exploratorio con verosimilitudes marginales, mediante Path-sampling (Lartillot y Philippe, 2006) y Stepping-stone (Xie et al., 2011), arrojó cifras del factor Bayes por debajo del valor que Grummer et al. (2014) recomiendan para reconocer a dos linajes como distintos (estos deben ser >10). Todo lo anterior sugería que el arreglo de los haplotipos en dos clados sólo reflejaba el aislamiento geográfico entre las poblaciones o aislamiento por distancia; en otras palabras, que las poblaciones representadas en este estudio (Pico de Orizaba-Cumbres de Acultzingo y Sierra Negra de Puebla-Puerto Soledad) son los extremos opuestos dentro de la distribución de *A. graminea*.

Sin embargo, el presente trabajo encontró problemas relacionados con los límites de especies entre *Abronia graminea* y *A. taeniata* al incluir ejemplares de la Sierra Norte de Puebla, una zona de simpatría entre estos dos taxones recientemente descubierta entre estos dos taxones. Hasta hace algunos años se creía que ambos taxones tenían distribución alopátrica, es decir estaban aisladas geográficamente entre sí (Campbell y Frost, 1993; Canseco-Márquez y

Mendoza-Quijano, 2007; Flores-Villela y Santos-Barrera, 2007). De acuerdo con Martin (1955), los caracteres diagnósticos más importantes para distinguir entre las especies *A. graminea* y *A. taeniata* son: número de hileras transversales de escamas dorsales (25-29 en *A. graminea* vs. 30-36 en *A. taeniata*), número de hileras longitudinales de escamas nucales (4-6 en *A. graminea* vs. 6 en *A. taeniata*) y la coloración de los ejemplares adultos (*A. graminea* usualmente con coloración dorsal verde uniforme o en ocasiones con algunas bandas apenas visibles principalmente en hembras, mientras que ambos sexos de *A. taeniata* poseen bandas transversales muy evidentes que se fusionan en ocasiones en la parte media del dorso). Sin embargo, en la revisión de ejemplares de la Sierra Norte de Puebla (Clause et al., 2018) se encontró que los caracteres morfológicos propuestos por Martin (1955) presentan sobrelapamiento en ejemplares de la zona de simpatría (Sierra Norte de Puebla) y que, en el mejor de los casos, la coloración dorsal de los adultos es la única manera de poder diferenciar entre *A. graminea* y *A. taeniata*.

Los haplotipos de la zona de simpatría asignados tanto a *A. graminea* como a *A. taeniata* formaron dos clados, uno pequeño con sólo dos haplotipos (ISZ-579 y MVZ-191068) y uno grande con seis haplotipos (ISZ-971, RPS-31 y 41, MZFC-19779, 19780 y 28231), y ambos compuestos por los haplotipos de los dos taxones, lo cual sugiere la existencia de flujo génico entre estas especies en la zona de simpatría. Sin embargo, no fue posible obtener secuencias de genes nucleares de los ejemplares provenientes de esta zona. Con la evidencia disponible, existen dos posibles explicaciones: que *A. graminea* y *A. taeniata* formen parte de una sola especie con variación clinal en algunos caracteres morfológicos, o la hipótesis preferida de que en la zona de simpatría existe un fenómeno de introgresión y por lo tanto se debe seguir reconociendo a *A. graminea* y *A. taeniata* como especies válidas. Sin embargo, es necesario aumentar el muestreo en esta zona y hacer una evaluación más a fondo. Por lo tanto, este trabajo queda abierto a futuras investigaciones.

En el caso de ***M. gadovii***, los haplotipos de *M. g. gadovii* y *M. g. levigata* fueron ligeramente divergentes y mostraron una tendencia a formar clados exclusivos de Guerrero y Oaxaca, respectivamente. Sin embargo, el clado de *M. g. gadovii* mostró un valor de soporte bajo, mientras que algunas de las muestras de *M. g. levigata* no se agruparon con otras muestras de *M. g. levigata* o muestras de *M. g. gadovii*. Aunado a lo anterior, los caracteres morfológicos propuestos para distinguir entre ambas subespecies (Spengler et al., 1982; Tihen, 1949a) no permiten diferenciarlas (Solano-Zavaleta, 2011). Las subespecies no son mutuamente

excluyentes y, por lo tanto, *M. g. levigata* no debería ser reconocida pues no existe evidencia de que represente un grupo natural.

Con respecto a ***M. viridiflava***, en el árbol de mtDNA se observó que los haplotipos de la Sierra Mixe-Sierra de Juárez se agruparon en un clado, mientras que los haplotipos de Cerro San Felipe se congregaron en otro; es decir, que el arreglo de las secuencias dentro del árbol de mtDNA parece sugerir que se trata de dos linajes independientes (*M. viridiflava* y *M. cf. viridiflava*). Este arreglo resultó desconcertante al tener en cuenta que los ejemplares de *M. cf. viridiflava* se encontraron aproximadamente a 27 km en línea recta de los ejemplares de *M. viridiflava*. La búsqueda de caracteres morfológicos que permitieran distinguir entre ambas poblaciones no arrojó resultados contundentes, mientras que el análisis preliminar de delimitación de especies utilizando varios genes arrojó resultados no concluyentes. Si bien cabe la posibilidad que estos dos linajes representen dos especies diferentes, las muestras secuenciadas para los árboles de los genes nucleares BMP2 y PRLR forman un clado pero no presentan el mismo arreglo mostrado en el árbol de mtDNA. Sin embargo, dicha topología sí se presenta en el árbol del gen nuclear KIAA-1217 y además con valores de soporte altos, lo cual resulta llamativo si consideramos que este gen fue el que menos resolución presentó. Cabe la posibilidad que las diferencias moleculares detectadas entre ambas poblaciones se deban a un evento de especiación peripátrica (aislados periféricos o "budding speciation", véase Funk y Omland, 2003) ya que la población de *M. cf. viridiflava* pudo haber sufrido un evento de deriva génica y posterior cuello de botella, lo cual habría causado que se fijaran solo unos alelos en esta población. Esto último podría explicar los patrones similares entre el árbol de mtDNA y el árbol de KIAA-1217 a pesar de que los genes nucleares generalmente tienen tasas de mutación mucho más bajas (Zink y Barrowclough, 2008). Este fenómeno ya se ha detectado en otros organismos (Hedin, 1997; Marko, 1998).

Descripción de especies nuevas de *Abronia* y *Mesaspis*

El objetivo principal del **Capítulo 2** era la descripción de especies nuevas de *Abronia y Mesaspis*. En esta sección de la tesis se describieron dos especies nuevas: *Abronia cuetzpali* (Campbell et al., 2016) de la Sierra Madre del Sur de Oaxaca, y *Mesaspis cuchumatanus* (Solano-Zavaleta et al., 2016) de los Cuchumatanes, Guatemala. Para la descripción de *A. cuetzpali* se contó únicamente con tres ejemplares, por lo que la variación morfológica dentro de la especie podría no estar del todo representada. La posición de los haplotipos dentro del

árbol de mtDNA sugiere que se trata de un linaje evolutivamente independiente que tiene como especie hermana a *A. mixteca*. Con base en los tres ejemplares conocidos, la distribución de *A. cuetzpali* se restringe a la Sierra Madre del Sur de Oaxaca. Resulta deseable ampliar el muestreo en la Sierra Madre del Sur con el propósito de tener una idea más clara acerca de la distribución de esta especie, así como corroborar que *A. mixteca* y *A. oaxacae* se encuentran ausentes de la zona (Campbell, 2007a; Canseco-Márquez et al., 2007) y validar el aislamiento geográfico de *A. cuetzpali*.

En el caso de la descripción de *M. cuchumatanus,* existen varias fuentes de información que corroboran su validez taxonómica. Anteriormente Tihen (1949) reconoció que los ejemplares de *Mesaspis* de Los Cuchumatanes presentaban características morfológicas atípicas de *M. m. fulvus* (el taxón descrito más cercano geográficamente) y sugirió que podría ser una zona de hibridación entre las subespecies *M. m. moreletii*, *M. m. fulvus* y *M. m. temporalis,* o bien que la situación podría ser incluso más compleja. La revisión morfológica de ejemplares de esta zona no solo permitió describir a la especie *M. cuchumatanus*; también demostró que la especie *M. m. temporalis* (que se sugiere elevar a nivel de especie como parte de los resultados de esta tesis) se encuentra presente en el área. Aunque las diferencias morfológicas entre *M. cuchumatanus* y *M. temporalis* sean evidentes, es muy probable que los ejemplares jóvenes de *M. temporalis* pudieran haber causado los problemas en las interpretaciones de Tihen (1949). Los datos moleculares (ver Capítulo 1) confirman la validez de *M. cuchumatanus*, pero también sugieren que el flujo génico entre *M. cuchumatanus* y *M. temporalis* parece poco probable.

Relaciones filogenéticas dentro del clado *Abronia* + *Mesaspis*

El objetivo general de esta tesis fue investigar las relaciones filogenéticas y problemas de delimitación de especies dentro del clado formado por los géneros *Abronia* y *Mesaspis*, lo cual se aborda ampliamente en el **Capítulo 3**. Sin embargo, los casos de evaluación de límites de especies se trataron en párrafos anteriores y en esta sección nos enfocaremos en la discusión de la hipótesis filogenética obtenida del clado (*Abronia* + *Mesaspis*) a partir de un fragmento del mtDNA (parte del gen ND4 y los genes adyacentes $tRNA^{His}$, $tRNA^{Ser}$ y parte de $tRNA^{Leu}$) y los genes nucleares BMP2, KIAA-1217 y PRLR.

El árbol de mtDNA obtenido muestra que los géneros *Abronia* y *Mesaspis* no son mutuamente monofiléticos, resultado que era de esperarse de acuerdo con filogenias previas (Solano-Zavaleta, 2011; Pyron et al., 2013;). Los valores de soporte en los nodos del árbol del

mtDNA son altos (>0.95), lo cual sugiere que el árbol obtenido es confiable, a menos que existan problemas de hibridación, separación incompleta de linajes, etc. El árbol de mtDNA se divide en dos grandes clados, uno con ejemplares al este y otro con los ejemplares al oeste del Istmo de Tehuantepec. Este patrón, que sugiere el Istmo de Tehuantepec como barrera geográfica, es recurrente en diversos grupos de organismos (Arellano et al., 2005; Castoe et al., 2009; Devitt, 2006; Esteva et al., 2010; García-Moreno et al., 2006; León-Paniagua et al., 2007; Mulcahy et al., 2006; Sullivan et al., 2000; Vázquez-Miranda et al., 2009).

Debido a que los tiempos de coalescencia dependen directamente del tamaño poblacional efectivo, y que el tamaño poblacional de los genes nucleares es aproximadamente cuatro veces más grande que el de los genes mitocondriales, las topologías de los genes nucleares (BMP2, KIAA-1217 y PRLR) presentan menor resolución en comparación con el árbol de mtDNA, aunque en general los valores de soporte de los nodos fueron más bajos. El análisis de los tres genes nucleares en conjunto arrojó una topología más resuelta donde el clado mitocondrial del oeste del Istmo de Tehuantepec se recupera con un valor de soporte alto, mientras que el clado mitocondrial del este del Istmo de Tehuantepec no se recupera: el subclado del árbol mitocondrial con muestras de *Abronia* del este del Istmo de Tehuantepec se recupera con un valor de soporte alto; mientras que el subclado del árbol mitocondrial con muestras de *Mesaspis* del este del Istmo de Tehuantepec se recupera excepto por *M. rafaeli*, el cual no aparece relacionado con los otros *Mesaspis* del este del Istmo de Tehuantepec. Sin embargo, a pesar de las diferencias de muestreo de los taxones representados, los datos faltantes, y los diferentes tiempos de coalescencia entre los diferentes conjuntos de datos, no hay casi ningún conflicto fuertemente apoyado entre el árbol mitocondrial y el árbol de los genes nucleares; esto quiere decir que es válido concatenar los datos de los diferentes genes esperando que su información sea complementaria. El árbol obtenido del análisis de todos los genes concatenados arroja una topología que en su mayoría presenta nodos con valores de soporte alto y muy similar al árbol de especies, excepto por la posición de *A. ornelasi*, con valores de soporte bajo en ambos árboles, y las relaciones dentro del clado compuesto por *M. cuchumatanus*, *M. moreletii* y *M. rafaeli*.

Debido a que se esperaba que los genes nucleares presentaran menor resolución o información que los genes mitocondriales, se secuenciaron sólo muestras representativas de cada especie; en otras palabras, en los análisis con nDNA hay un menor número de muestras que en el árbol de mtDNA. Además, hubo muestras de las cuales no fue posible secuenciar genes nucleares debido a diferentes razones (por ejemplo *A. ornelasi*). Estas secuencias

hubieran permitido proponer un arreglo taxonómico con mayor apoyo. También hubo varios taxones de los cuales no se pudieron conseguir muestras de tejido (*A. anzuetoi*, *A. frosti*, *A. gaiophantasma*, *A. leurolepis*, *A. ochoterenai*, *A. mitchelli*, *A. montecristoi*, *A. reidi*, *A. salvadorensis*).

Para poder sugerir un arreglo taxonómico que refleje las relaciones obtenidas en los árboles es necesario mencionar que Campbell y Frost (1993) resaltaron que la evidencia de la monofilia del género *Abronia* no era contundente, y que incluso las características osteológicas propuestas como sinapomorfías (Gauthier, 1982; Good, 1987b) fueron sugeridas mediante el análisis de pocos taxones disponibles. Campbell y Frost (1993) concluyeron que de las sinapomorfías sugeridas por Good (1988) sólo tres parecen ser válidas (pérdida de una quinta hilera de escamas temporales, reducción de la altura del pliegue lateral entre el oído y la extremidad, presencia de extremidades largas y con garras bien desarrolladas). El caso de las sinapomorfías propuestas por Good (1988) para *Mesaspis* no parece muy diferente; de las cinco sinapomorfías propuestas, al menos dos no están presentes en todas las especies (rayas labiales características y vientre moteado) y comparten la reducción del pliegue lateral con el género *Abronia*, mientras que las otras dos (ocho hileras de escamas ventrales (vs 10) a la altura de las extremidades, escamas subgranulares en la superficie delantera de las pantorrillas) no han sido evaluadas. Ahora bien, con base en los árboles moleculares obtenidos podemos inferir que las sinapomorfías propuestas para ambos géneros no son válidas y, por lo tanto, parece que es necesario sugerir cambios taxonómicos.

Arreglo taxonómico

Hay dos posibles opciones y comenzaré discutiendo la primera de ellas. La primera propuesta se basa en la divergencia que concuerda con la barrera geográfica del Istmo de Tehuantepec. En este caso, el clado del oeste del Istmo debería conservar el nombre *Abronia* ya que la especie tipo se encuentra en este clado (Gray, 1838). Por lo tanto, este género incluiría a 16 especies descritas: *A. bogerti*, *A. chiszari*. *A. cuetzpali*, *A. deppii*, *A. fuscolabialis*, *A. graminea*, *A. martindelcampoi*, *A. mitchelli*, *A. mixteca*, *A. oaxacae, A. ramirezi*, *A taeniata*, así como a las especies actualmente reconocidas como *Mesaspis antauges*, *M. gadovii*, *M. juarezi* y *M. viridiflava*. Por otra parte, el clado al este del Istmo de Tehuantepec podría dividirse en dos géneros, uno correspondiente a *Mesaspis* debido a la ubicación de la especie tipo (Cope, 1878) y compuesto por seis especies descritas (*M. cuchumatanus*, *M. monticola*, *M. moreletii*, *M.*

rafaeli, *M. salvadorensis*, *M. temporalis*), y el género *Auriculabronia*, compuesto por 18 especies descritas (*A. anzuetoi*, *A. aurit*a, *A. campbelli*, *A. fimbriata*, *A. frosti*, A. *gaiophantasma*, *A. leurolepis*, *A. lythrochila*, *A. matudai*, *A. meledona*, *A. montecristoi*, *A. ochoterenai*, *A. ornelasi*, *A. reidi*, *A. salvadorensis*, *A. smithi* y *A. vasconcelosii*). El problema en seguir esta propuesta radica en que no se tienen representados los subgéneros *Aenigmabronia* (*A. mitchelli*) y *Lissabronia* (*A. frosti*, *A. montecristoi*, *A. salvadorensis*) y tampoco se tienen representados todas las especies de los subgéneros *Abaculabronia* (sólo se tiene secuencia de mtDNA de *A. ornelasi* y no existe muestra de *A. reidi*) y *Scopaeabronia* (se tienen representadas *A. bogerti* y *A. chiszari*, pero no existe muestra de *A. ramirezi*). Entonces, dado que los subgéneros no se tienen bien representados y que es probable que la inclusión de las secuencias de las especies faltantes modifique la hipótesis filogenética obtenida, la idea de la clasificación mencionada en este párrafo se descarta por el momento.

La segunda propuesta tiene un enfoque más conservador, implica un menor número de cambios taxonómicos, y probablemente no se vea afectada al incluir, posteriormente, a representantes de los subgéneros *Aenigmabronia* (*A. mitchelli*) y *Lissabronia* (*A. frosti*, *A. montecristoi*, *A. salvadorensis*), así como a las secuencias de las especies *A. reidi* (subgénero *Abaculabronia*) y *A. ramirezi* (subgénero *Scopaeabronia*). Esta propuesta sugiere simplemente que *Mesaspis* sea sinonimizado con *Abronia* (la sinapomorfía morfológica más evidente es la reducción del pliegue lateral).

CONCLUSIONES GENERALES

1. *Abronia* y *Mesaspis* no son mutuamente monofiléticos. Debido a que el nombre *Abronia* Gray, 1838 tiene prioridad sobre el nombre *Mesaspis* Cope, 1878, *Mesaspis* debe ser sinonimizado con *Abronia*.
2. De las cinco subespecies reconocidas dentro de *M. moreletii,* cuatro (*M. m. moreletii, M. m. rafaeli, M. m. salvadorensis* y *M. m. temporalis*) deben ser elevadas a nivel específico, mientras que *M. m. fulvus* debe sinonimizarse con *M. m. moreletii.*
3. La potencial evidencia de flujo génico entre *Abronia graminea* y *A. taeniata* en la zona de simpatría documentada en Clause *et al.* (2018) sugiere que estas especies nominales podrían representar el mismo linaje o, de manera alternativa, la existencia de una zona extensa donde eventos de hibridación han ocurrido entre ambas especies.
4. La especie *M. gadovii* no debe reconocerse como especie politípica.

5. La especie *M. viridiflava* parece estar compuesta por dos linajes crípticos, pero evolutivamente independientes; sin embargo, se requiere de material y datos (morfológicos y moleculares) adicionales para corroborar esta hipótesis.
6. Existen ejemplares de Guerrero, México (*Abronia* sp. MZFC-28966, *Abronia* sp. ANMO-3343) y de Huehuetenango, Guatemala (*Abronia* sp. MVZ-265219) así como tres poblaciones (*M. moreletii* del este de Honduras, *M. moreletii* de Nicaragua y *M. salvadorensis* del noreste de Honduras) que podrían representar especies no descritas. Se requiere de material y datos (morfológicos y moleculares) adicionales para determinar de manera confiable su estatus taxonómico.
7. Los datos moleculares obtenidos no apoyan la monofilia de *Abronia vasconcelosii* ni la distintividad de *A. meledona* y *A. campbelli* con respecto a *A. vasconcelosii* o entre ellas. Se requiere de realizar más investigación dentro de este grupo con el objetivo de reevaluar sus límites de especies.

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