UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO

POSGRADO EN CIENCIAS BIOLÓGICAS

FACULTAD DE CIENCIAS

SISTEMÁTICA

LÍMITES DE ESPECIE EN EL COMPLEJO *Holcosus undulatus* (SQUAMATA: TEIIDAE)

TESIS

QUE PARA OPTAR POR EL GRADO DE:

DOCTORA EN CIENCIAS

PRESENTA:

RUBI NELSI MEZA LÁZARO

TUTOR(A) PRINCIPAL DE TESIS: **DR. ADRIÁN NIETO MONTES DE OCA**
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MÉXICO, D.F. **NOVIEMBRE, 2015.**

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ASUNTO: Oficio de Jurado

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

Me permito informar a usted que en la reunión ordinaria del Comité Académico del Posgrado en Ciencias Biológicas, celebrada el día **24 de agosto de 2015**, se aprobó el siguiente jurado para el examen de grado de **DOCTOR EN CIENCIAS** del (la) alumno (a) **MEZA LÁZARO RUBI NELSI** con número de cuenta **98549667** con la tesis titulada: **"Limites de especie en el complejo *Holcosus undulatus* (Squamata: Teiidae)"**, realizada bajo la dirección del (la) **DR. ADRIÁN NIETO MONTES DE OCA:**

Presidente:	DR. JUAN JOSÉ MORRONE LUPI
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Suplente	DRA. ELLA GLORIA VÁZQUEZ DOMÍNGUEZ

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 ESPÍRITU"
Cd. Universitaria, D.F. a 10 de noviembre de 2015

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Coordinadora del Programa

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RESUMEN

Holcosus undulatus (Squamata: Teiidae) era considerada una especie de lagartija, con marcada variabilidad morfológica, ampliamente distribuida en México y Centroamérica. Dicha variabilidad fue reconocida desde su descripción en 1834, en la que se hace referencia a dos variedades. Posteriormente, durante el siglo XX fueron descritas 12 subespecies, que cayeron en desuso. No obstante, la amplia distribución de *H. undulatus* y la marcada variación morfológica en sus poblaciones sugerían que no formaban parte de una sola especie sino de un complejo de especies. El objetivo de este trabajo es reevaluar los límites de especies dentro del complejo *H. undulatus* con base en información morfológica y molecular.

El trabajo se divide en tres partes. La primera y más amplia está constituida por la delimitación de especies basada en información molecular (nuclear y mitocondrial), morfológica y de distribución geográfica. La delimitación de especies fue realizada partiendo del concepto de cohesión de especie. La genealogía mitocondrial mostró una marcada estructuración geográfica dentro de *H. undulatus*, congruente con las subespecies descritas previamente. Así, *H. u. amphigrammus*, *H. u. gaigeae*, *H. u. hartwegi*, *H. u. parvus*, *H. u. pulcher*, *H. u. sinister, H. u. stuarti*, *H. u. thomasi* y *H. u. undulatus* son linajes independientes, basados en la evidencia molecular y morfológica. Por lo tanto, todas estas subespecies fueron elevadas al nivel de especie. La diferenciación morfológica y distribución alopátrida de *H. u. miadis* y *H. u. pulcher*, como así como la divergencia genética alta de esta última especie, sugieren que también representan especies distintas. Los resultados basados en información morfológica y molecular también sugieren diversidad adicional dentro de *H. u. amphigrammus*, *H. u. parvus*, *H. u. sinister* y *H. u. undulatus*. El reconocimiento de la diversidad de especies dentro del género *Holcosus* tiene implicaciones importantes para su conservación, ya que las

especies que conforman el complejo tienen áreas de distribución más reducidas, y pueden ser más vulnerables, por ejemplo, a cambios en el uso de suelo.

La segunda parte consiste de una recopilación de evidencias para restringir correctamente la localidad tipo de *Holcosus undulatus*. Esta parte es relevante debido a que tiene varias consecuencias sobre los nombres usados en las diferentes especies de *Holcosus* en México. La especie *Cnemidophorus undulatus* Wiegmann 1834 fue descrita sobre la base de tres o cuatro ejemplares recolectados por Ferdinand Deppe en "México". Después, *C. undulatus* fue transferido al género *Ameiva* y últimamente al género *Holcosus*. *Holcosus undulatus* fue considerada una especie politípica de 1915 a 1971. El uso del nombre *undulatus* se volvió problemático desde la primera vez que *H. undulatus* fue tratada como especie politípica, ya que la localidad tipo es muy ambigua. La información sobre los viajes de Deppe en México, resguardada por el Museo de Historia Natural de Berlín, permitió restringir la localidad tipo a Alvarado, Veracruz. Las poblaciones del Golfo de México que solían conocerse como a *H. amphigrammus* se asemejan en todos los aspectos a los syntipos, por lo tanto el nombre *H. undulatus* debe aplicarse a estas poblaciones. Las poblaciones de la vertiente Pacífica desde el Istmo hasta el centro de Guerrero, pertenecen a una especie distinta y les corresponde el nombre de *H. dexter*.

La tercera parte de la tesis discute la sinonimia de *H. thomasi* con *H. chaitzami*, considerando caracteres de escamación, patrón de coloración, distribución y modelos geográficos de condiciones climáticas. Considerando que *H. thomasi* y *H. chaitzami* se diferencian en el patrón de coloración y la división de la escama interparietal y que las condiciones ambientales en las que ocurre *H. thomasi* difieren de las condiciones que requiere *H. chitzami,* concluimos que *H. thomasi* es una especie diferente de *H. chaitzami*. Por lo tanto, *H. thomasi* debe ser rescatada de la sinonima de *H. chaitzami.* Por último, para resumir las conclusiones del presente trabajo, se incluyó una lista de especies que históricamente o nominalmente fueron parte de *H. undulatus*, con una breve diagnosis y su distribución.

ABSTRACT

Holcosus undulatus (Squamata: Teiidae) was previously considered a widely distributed species of lizard with marked morphological variability. This variability was recognized since the species original description in 1834, in which two varieties are referred. Along the twentieth century, 12 subspecies were described, to fall, later, into disuse. However, the wide distribution of *H. undulatus* and marked morphological variation in their populations suggested that they were not part of a single species, but a species complex. The aim of this study is to reassess the species boundaries within the complex *H. undulatus*, using morphological and molecular information.

This work is divided into three parts. The first and most comprehensive consists of the delineation of species based on molecular (nuclear and mitochondrial), morphological information, and geographical distribution. The species delimitation was made based on the concept of cohesion of species. Mitochondrial genealogy showed marked geographic structure within *H. undulata*, consistent with the previously described subspecies. Thus, *H. u. amphigrammus*, *H. u. gaigeae*, *H. u. hartwegi*, *H. u. Parvus*, *H. u. pulcher*, *H. u. sinister*, *H. u. stuarti*, *H. u. thomasi* and *H. u. undulatus* are independent lineages, based on molecular and morphological evidence. Therefore, we suggest all these subspecies must be elevated to the species level. Morphological differentiation and allopatric distribution of *H. u. miadis* and *H. u. pulcher*, as well as the high genetic divergence of the latter species, suggest they also represent different species. The results based on morphological and molecular data also suggest additional diversity within *H. u. amphigrammus*, H. u. Parvus, *H. u. sinister* and *H. u. undulatus*. The recognition of the diversity of species within the genus *Holcosus* has important implications for conservation, because those species have smaller distribution areas than the original, and may be more vulnerable, for example, to land conversion.

The second part consists of a collection of evidence to properly restrict the type locality of *Holcosus undulatus*. This is important because it has several consequences on the names used in the different species of *Holcosus* in Mexico. The species *Cnemidophorus*

undulatus Wiegmann 1834 was described on the basis of three or four specimens collected by Ferdinand Deppe in "Mexico". Then, *C. undulatus* was transferred to the genus Ameiva and lately to the genus Holcosus. *Holcosus undulatus* was considered a polytypic species from 1915 to 1971. The use of the name *undulatus* became problematic from the first time that *H. undulatus* was treated as a polytypic species, as the type locality is very ambiguous. Information about the journey of Deppe in Mexico, guarded by the Museum of Natural History in Berlin, allowed us to restrict the type locality to Alvarado, Veracruz. The populations of the versant of the Gulf of Mexico that used to be known as *H. amphigrammus* are similar in all respects to the syntypes; hence the name *H. undulatus* should be applied to these populations. The Pacific slopes populations, from the Isthmus to the center of Guerrero, belong to a different species and their rightful name is *H. dexter*.

The third part of the thesis discusses the synonym of *H. chaitzami* t and *H. thomasi* considering characters of squamation and color pattern, geographical distribution and ecological niche models. Considering that *H. chaitzami* and *H. thomasi* can be distinguished by the adult male color pattern and interparietal scale division, and that the environmental conditions in which *H. thomasi* occurs differs from the conditions required by *H. chitzami*., we concluded that *H. thomasi* is a different species from *H. chaitzami*. Therefore, *H. thomasi* should be rescued from *H. chaitzami* synonymy.

In summary, we suggest that in Mexico at least 12 species are found: *H. undulatus*, *H. podargus*, *H. gaigeae*, *H. hartwegi*, *H. stuarti*, *H. thomasi*, *H. parvus*, *H. sinister*, *H. dexter*, two new species and *H. festivus*. Meanwhile, *H. chatzami* is endemic to Guatemala. To conclude, a list of species that were historically or nominally part of *H. undulatus*, with a brief diagnosis and their distribution, is included.

CAPÍTULO I

INTRODUCCIÓN

La especie es considerada un nivel de organización biológica y una entidad en el proceso evolutivo (Simpson, 1951; de Queiroz & Donoghue, 1988), pero también constituye una categoría taxonómica (Lee, 2003). Las especies son unidades fundamentales de análisis en todos los campos de la biología, incluyendo la anatomía, conducta, ecología, evolución, genética, biología molecular, paleontología, fisiología, sistemática, biogeografía, ecología, macroevolución y biología de la conservación (Hull, 1977; Sites & Crandall, 1997; Sites & Marshall, 2004; de Queiroz, 2005). Además, la especie es la unidad biológica más usada en cuestiones de legislación, agricultura y salud (Hausedorf, 2011).

El término especie ha sido una de las fuentes más prolíficas de discusión y desacuerdos en biología. Debido a la importancia del término "especie", una plétora de conceptos de especie ha sido propuesta (revisiones: Mayden, 1997; de Queiroz, 1998; Harrison 1998; Coyne & Orr, 2004). La discusión sobre los distintos conceptos de especie no es sólo un debate filosófico, ya que diferentes conceptos de especie pueden resultar en distintas conclusiones con respecto a los límites y el número de especies que se reconocen (Isaac et al., 2004; Agapow et al., 2004; Mayden, 1997; de Queiroz, 1998; Harrison, 1998).

El presente trabajo es un estudio de caso, cuyo objetivo es evaluar los límites de especies en el complejo *Holcosus undulatus*. Para llevar a cabo este trabajo fue necesario partir de un concepto de especie y plantear los métodos, criterios y datos que nos permitieran determinar los límites específicos en nuestro grupo de interés. Por ello, en los capítulos siguientes se describen y discuten los conceptos de especie que se consideran de mayor relevancia para el desarrollo de este trabajo y se detallan algunos métodos propuestos para la delimitación de especies. Más adelante, se presenta el estudio de caso que ocupa a este trabajo: los límites de especie en el complejo *Holcosus undulatus* (Squamata: Teiidae).

ANTECEDENTES

1. *CONCEPTO DE ESPECIE*

1.1 Concepto biológico de especie

Lo que hoy se conoce como concepto biológico de especie empezó a utilizarse desde el siglo XIX. Algunas aproximaciones a este concepto aparecen entre las ideas de Buffon (Sloan, 1987), Darwin y otros autores del siglo XIX (Kottler, 1978; Mayr, 1992). No obstante, el desarrollo formal del concepto biológico de especie ocurrió hasta el siglo XX. Ernst Mayr definió a la especie biológica como "un grupo de poblaciones naturales que entrecruzan entre sí y que están reproductivamente aisladas de otros grupos" (Mayr, 1942; Mayr, 2000).

Dicho de otro modo, la especie es un "ensamblaje de poblaciones con cohesión reproductiva" (Mayr, 1942, 2000). Esta definición no hace énfasis en el grado de diferenciación morfológica, sino en las relaciones genéticas. La especiación, de acuerdo con el concepto biológico de especie, es la acumulación de cambios genéticos en dos linajes (Bateson, 1909), que produce aislamiento genético y protección de la integridad de los dos acervos génicos respectivos, que tienen destinos evolutivos independientes (Baker & Bradly, 2006).

Los mecanismos a través de los cuales las especies (acervos génicos adaptados) mantienen su integridad fueron denominados mecanismos de aislamiento (Dobzhansky, 1935, 1937). Los mecanismos de aislamiento son mecanismos fisiológicos que dificultan la entrecruza; estos pueden ser precopulatorios, como el aislamiento ecológico, geográfico, temporal o etológico; postcopulatorios precigóticos, como el aislamiento mecánico, la mortalidad gamética o la incompatibilidad; o postcopulatorios postcigóticos como la inviabilidad de los cigotos, o la esterilidad de la F1 (Templeton 1989; Plate, 1914). Algunos conceptos biológicos de especie hacen referencia a la entrecruza potencial (Mayr, 1942, 1963, 2000). La inclusión de la palabra *potencial* en el concepto biológico de especie tiene como consecuencia que la separación geográfica (aislamiento extrínseco) se vuelve tan importante como el aislamiento reproductor intrínseco en el establecimiento de límites de especies (Brundin, 1966; Hennig, 1966; Wheeler & Nixon, 1990; Meier & Willman, 2000).

Algunos autores consideran que la pérdida del *potencial* reproductor es lo único que garantiza que las entidades funcionen como unidades evolutivas separadas, definida como "punto de no retorno" (de Queiroz & Donoghue, 1988).

Paterson (1985) señala que la especiación ocurre cuando las poblaciones se encuentran separadas por barreras geográficas y que los mecanismos de aislamiento intrínsecos son irrelevantes como barreras de aislamiento durante la especiación, debido a que en alopatría no pueden funcionar como mecanismos de aislamiento. Por tanto, las fuerzas evolutivas responsables del proceso de especiación alopátrida no tienen nada que ver con los mecanismos de aislamiento. El aislamiento es producto del proceso de especiación en algunos casos, pero no debe ser confundido con este proceso (Paterson, 1985).

Algunas críticas al uso del aislamiento reproductor como criterio para delimitar especies son: discernir el potencial reproductor es difícil, consume mucho tiempo, tiene un alto costo y es susceptible de muchos errores (Agapow, 2004). En particular, cuando las poblaciones en cuestión son alopátridas, los organismos podrían ser difíciles de observar en la naturaleza o de criar en el laboratorio (Taylor *et al.*, 1999; Agapow, 2004). Además, no puede ser aplicado cuando se trata de organismos extintos o solo caracterizados por material preservado (Kullander, 1999; Claridge et al.1997) y es inoperante en organismos asexuales (1987) y en casos en los que existe hibridación extensa (Donoghue, 1985). Por lo tanto, el concepto biológico de especie explica solo una pequeña parte del árbol de la vida (Agapow, 2004). Aunque el uso del aislamiento reproductor como propiedad necesaria para reconocer especies distintas ha decaído, la evidencia de interrupción del flujo génico sigue siendo un criterio decisivo en la delimitación de especies, al menos en organismos que se reproducen sexualmente y principalmente en animales.

1.2 Subespecies

El estudio de la variación morfológica entre las poblaciones cobró relevancia bajo el concepto biológico de especie y sobre todo la variación correlacionada con la distribución

geográfica. Las subespecies fueron concebidas como poblaciones genéticamente distintas, geográficamente separadas pero que pertenecen a una misma especie y que, por lo tanto, entrecruzan libremente en las zonas de contacto (Wilson & Brown, 1953). Más tarde el concepto fue extendido para incluir poblaciones genéticamente relacionadas pero aisladas geográficamente, particularmente aquellas que habitan en islas diferentes de los archipiélagos tropicales. Aunque la distintividad de las razas insulares parece ser completamente clara, en realidad en esos casos es incierto si se trata de especies o subspecies (Wilson & Brown, 1953).

El concepto de subespecie es uno de los más ambiguos y problemáticos de la sistemática moderna. Wilson & Brown (1953) catalogaron los problemas que provocan que el concepto de subespecie no pueda reflejar la naturaleza de la variación geográfica y que por lo tanto que carezca de relevancia biológica:

- La tendencia de los caracteres genéticamente independientes de mostrar variación geográfica independiente.
- La aparición de los caracteres en más de un área geográfica, dando lugar a razas politópicas.
- La ocurrencia común de razas microgeográficas.
- La arbitrariedad inevitable en el grado de divergencia poblacional mínima elegida para reconocer formalmente una subespecie.

1.3 Concepto evolutivo de especie

El problema del concepto de especie ("species problem") fue durante mucho tiempo la búsqueda de una sola propiedad o una combinación de propiedades que definieran a la especie (Baum & Shaw, 1995). Sin embargo, las especies son individuos y no clases, y por lo tanto, la especie no tienen propiedades definitorias (Ghiselin, 1974).

Las especies nacen a través de la especiación y mueren a través de la extinción, sus partes pueden cambiar sin cambiar sus nombres, tal como un organismo individual puede reemplazar sus células (Wiley & Lieberman, 2011). También se pueden nombrar y diagnosticar, pero nunca definir. Si las especies son individuos, entonces, las hipótesis de

especie son enunciados históricos singulares, únicos. Estas hipótesis sobre los límites de especie y las relaciones entre ellas se pueden poner a prueba evaluando el peso de la evidencia (Wiley & Lieberman, 2011). Por lo tanto, el concepto de especie debe considerar a las especies como individuos y las consecuencias del concepto de especie deben poder ponerse a prueba (Wiley & Lieberman, 2011).

El concepto evolutivo de especie (Simpson, 1961; Simpson, 1951; Wiley, 1978, 1981) reúne definiciones que enfatizan la extensión temporal de las especies e intentan acomodar tanto las observaciones de que algunas poblaciones parecen mantenerse distintas a pesar de entrecruzarse con otras poblaciones y la idea de que los organismos unisexuales forman especies (de Queiroz, 1998). El concepto evolutivo de especie tiene varias definiciones. Fue originalmente propuesto por Simpson (1961), quien definió a las especies como entidades históricas, temporales y espaciales: “Una especie evolutiva es un linaje (una secuencia de poblaciones con relaciones de ancestría-descendencia), evolucionando separadamente de otros y con su propio rol evolutivo unitario y sus propias tendencias (Simpson, 1961)”. Esta definición fue modificada por Wiley (1978): “Una especie es un solo linaje de poblaciones de individuos que mantienen su identidad de otros linajes, su propia tendencia evolutiva y destino histórico” (Wiley, 1978; Wiley, 1981).

El concepto evolutivo de especie tiene la ventaja de ser aplicable tanto a grupos vivientes como a grupos extintos y a organismos sexuales, unisexuales y asexuales. Ambas definiciones implican unidad y ambas sugieren que la especie es la unidad más inclusiva de evolución. La segunda no implica que las especies deban evolucionar. El concepto evolutivo de especie no exige que haya diferencias morfológicas entre las especies ni se opone a que existan. De acuerdo con Wiley (1978) los linajes evolutivos separados que están reproductivamente aislados de otros mantienen separadas sus identidades, tendencias y destino evolutivos. De este modo, el concepto de especie biológica queda incluido en el concepto de especie evolutiva. No obstante, las especies pueden conservar su identidad a pesar de que no estén aisladas reproductivamente (Wiley, 1978).

El concepto evolutivo ha sido criticado por no poseer criterios empíricos de delimitación precisos (Sokal & Crovello, 1970; Sneath & Sokal, 1973, Templeton, 1989; Mayr, 2000, 2001). Sin embargo, es posible derivar, a partir del concepto evolutivo, hipótesis de límites de especie que se pueden poner a prueba. Es decir, es posible poner a prueba si dos poblaciones o grupos de poblaciones son linajes evolutivos separados (Wiley, 1978; 2011). La evidencia para poner a prueba tal hipótesis proviene de diversas fuentes, dependiendo de la naturaleza del organismo, por ejemplo: evidencia genética, morfológica, espacial, temporal, ecológica, bioquímica o conductual.

De acuerdo con Wiley & Lieberman (2011), el concepto evolutivo de especie es parcial o totalmente sinónimo de varios conceptos de especie: el concepto de linaje de Hennig (1966), el concepto de cohesión de Templeton (1989), el concepto cladista de Ridley (1986), el concepto de linajes de poblaciones (O' Hara, 1993; de Queiroz & Gauthier, 1994) y el concepto Hennigiano de Meier & Willmann (2000).

Como Templeton (1989) admite, el concepto de cohesión de especie está muy relacionado con el concepto evolutivo de especies, y se diferencia de él principalmente en la perspectiva. El concepto de cohesión enfatiza los mecanismos que promueven la cohesión, mientras que el concepto evolutivo enfatiza la manifestación de la cohesión a través del tiempo.

1.4 Concepto de cohesión de especie

El concepto de cohesión de especies la define como un linaje evolutivo o un grupo de linajes con capacidad de intercambio genético o ecológico (Templeton, 2000, 2001). El concepto de cohesión de especie hace énfasis en los mecanismos evolutivos genéticos que operan dentro de las poblaciones de individuos. Los mecanismos de cohesión son de dos tipos, y se enfocan, respectivamente, en los atributos genéticos y geográficos de reproducción de un linaje.

El primer tipo de mecanismos determina los límites de la intercambiabilidad genética y agrupa a los mecanismos de aislamiento reproductor o mecanismos de fertilización. La intercambiabilidad genética determina directamente los límites para el flujo génico y

pueden tener un impacto poderoso, con frecuencia dominante sobre los límites de acción de la deriva génica y la selección (Templeton, 2000). El segundo tipo de mecanismos se ocupa de la demografía básica o la ecología de la reproducción. Si los organismos son en algún sentido equivalentes o intercambiables en su atributos reproductores demográficos o ecológicos, sus descendientes o genes pueden reemplazar (a través de deriva) o desplazar (a través de selección) a los descendientes o genes de otros individuos en el linaje, aun si el linaje no se reproduce sexualmente (Templeton, 2000).

1.5 Concepto general de linaje de especie

Este concepto se refiere a la especies como linajes metapoblacionales (o segmentos de estos linajes) evolucionando separadamente (De Queiroz, 1998; 2007). El término linaje se refiere a series ancestro-descendientes (Simpson, 1961; Hull, 1980) y el término metapoblación a una población formada por conjunto de subpoblaciones conectadas (Levins, 1970; Hanski & Gaggiotti, 2004).

Este concepto, sinónimo del concepto evolutivo, es relevante debido a que ha promovido cambios importantes en la forma en que vemos y estudiamos a las especies. De Queiroz (1998) señaló que todos los conceptos de especie modernos consideran a las especies como linajes evolucionando separadamente. Dicha existencia como un linaje evolucionando separadamente es la única propiedad necesaria de las especies, mientras que otras propiedades tales como la diagnosticabilidad, la exclusividad, o el aslamiento reproductor intrínseco constituyen propiedades secundarias (De Queiroz, 1998; 2007). Éstas últimas no son propiedades necesarias de las especies, pero constituyen líneas de evidencia relevantes para determinar la delimitación de los linajes (De Queiroz, 1998; 2007). El reconocimiento de las especies como linajes evolucionando separadamente como única propiedad necesaria, y el uso de las otras propiedades sólo como criterios operacionales han renovado la discusión sobre la práctica de la delimitación de especies y la integración del conocimiento y los métodos de genética de poblaciones, filogenética, anatomía, fisiología, etología, y ecología.

2. *CRITERIOS DE DELIMITACIÓN DE ESPECIES*

La literatura que se ocupa de los métodos de delimitación de especies ha incrementado considerablemente en los últimos años. Este aumento ha conducido a la práctica de la delimitación de especies a consolidarse como una sólida subdisciplina científica de la sistemática moderna (Wiens, 2007; Padial et al., 2010). En la tarea de la delimitación de especies actualmente se observan tres tendencias generales. La primera es que existe un consenso emergente en la aceptación de que las especies son linajes de poblaciones evolucionando separadamente (Padial et al., 2010, Wiens & Penkrot, 2002; de Queiroz, 2007; Knowles & Carstens, 2007; Shaffer & Thomson, 2007; Raxworthy et al., 2007; Rissler & Apodaca, 2007; Wiens, 2007). Este consenso emergente ha catalizado la integración del conocimiento y los métodos de la biología poblacional, la filogenética y otras disciplinas dentro de la taxonomía (e.g. Leaché et al., 2009; Glow et al., 2010). Esta integración metodológica es la segunda tendencia. La taxonomía integradora se define como la ciencia que se ocupa de delimitar unidades de la diversidad de la vida desde múltiples perspectivas complementarias, como filogeografía, morfología comparada, genética de poblaciones, ecología, desarrollo, conducta, etc. (Dayrat, 2005). La congruencia entre diferentes aproximaciones y fuentes de evidencia es altamente deseable. La congruencia en la identificación de un linaje evolutivo a nivel poblacional entre muchas fuentes de evidencia independientes (por ejemplo, loci diferentes) indicaría que está genéticamente aislado de otros linajes y que califica como especie, ya que es muy improbable que un patrón coherente de concordancia entre caracteres surja por azar (Avise & Ball, 1990; Padial et al., 2010). La concordancia entre fuentes de evidencia para la delimitación de especies incrementa la estabilidad taxonómica. Por ello, algunos investigadores proponen la necesidad de presentar combinaciones, algunas veces muy restrictivas, de múltiples evidencias para delimitar especies (i.e. Dayrat, 2005; Meiri & Mace, 2007; Alström et al., 2007; Carstens et al., 2013). El enfoque de integración por congruencia, sin embargo, podría subestimar el número de especies, ignorando especialmente aquellas especies de origen reciente, ya que el proceso de especiación no siempre es acompañado por cambios

a todos los niveles y las tasas de cambio de los caracteres durante el proceso de divergencia es heterogéneo (Padial et al., 2010).

La congruencia es sin duda deseable, pero una aproximación más flexible que use la información de diferentes disciplinas de manera separada (Schlick-Steiner et al., 2010), podría ser más útil. Esta aproximación, llamada integración por acumulación (Padial et al., 2010) asume que cualquiera de los atributos de los organismos que constituyen caracteres taxonómicos pueden proveer de evidencia para la delimitación de especies. Las concordancias y discordancias entre las fuentes de evidencia acumuladas deben ser explicadas desde una perspectiva evolutiva. La decisión sobre los límites de especie es hecha con base en la información disponible, la cual puede llevar al reconocimiento de una especie con base en un solo grupo de caracteres, si estos se consideran buenos indicadores de la divergencia de linajes y son interpretados apropiadamente.

La tercera tendencia ocurre en el enfoque de los métodos, que ha cambiado hacia los mecanismos genéticos evolutivos que operan dentro de las poblaciones de individuos y las causas del origen de las especies (Templeton, 1989; Padial, 2010). Estos métodos se enfocan en procesos como divergencia, coalescencia, retención del polimorfismo ancestral, hibridación e introgresión, que producen los patrones filogenéticos observados (estructura filogeográfica, polifilia, etc.). Un ejemplo de ellos es el protocolo de delimitación de especies basado en árboles de genes (Baum & Donoghe, 1995). Este método plantea que si una población se divide en dos, al principio los organismos de ambas poblaciones constituirán un solo grupo exclusivo, pero si estas dos poblaciones continúan genéticamente aisladas, muchos de los linajes de genes presentes cuando ocurrió la separación se extinguirán y eventualmente todas las copias de un gen presentes en cada una de las poblaciones coalescerán entre ellas, antes de hacerlo con las copias de dicho gen presentes en la otra población (Baum & Donoghue, 1995; Avise & Ball, 1990). En este punto, ambas poblaciones constituyen grupos exclusivos de organismos (especies genealógicas; Baum & Shaw, 1995). Si la población original se divide asimétricamente, la teoría de coalescencia predice que la población más pequeña alcanzaría antes la exclusividad que la población grande (Avise, 2000). Por lo tanto, habrá un período de

tiempo en el cual la población más pequeña será ya una especie genealógica mientras que la población más grande, de acuerdo con Baum & Donoghue (1995), no pueda ser reconocida como tal. Para decidir si un grupo es exclusivo o no, es necesario evaluar el grado de relación entre los organismos que lo constituyen y el grado de relación con organismos fuera del grupo (Baum & Donoghue, 1995).

Wiens y Penkrot (2002) construyeron una clave dicotómica para tomar decisiones a nivel de especies a partir del planteamiento de Baum & Donoghue (1995). Este método parte de una filogenia de haplotipos de DNA mitocondrial de individuos designados previamente a una especie (especie focal) y de localidad conocida. Esta filogenia deberá incluir haplotipos de tantas especies cercanamente relacionadas a la especie focal como sea posible (para probar la exclusividad de la especie focal) y de dos o más individuos por población para evaluar el flujo génico entre las poblaciones (Slatkin & Maddison, 1989). Si los haplotipos de una población no se reúnen en un clado, esto se toma como evidencia de flujo génico con otras poblaciones (Slatkin & Maddison, 1989), pues el DNA mitocondrial tiene tamaños efectivos poblacionales (N_e) relativamente pequeños, lo cual reduce la posibilidad de que la incongruencia entre el árbol mitocondrial y la distribución geográfica sea causada por la retención del polimorfismo ancestral (Wiens & Penkrot, 2002).

El método de Wiens & Penkrot (2002) evalúa la exclusividad de la especie focal y las especies relacionadas, la distribución geográfica y la evidencia morfológica al asignar a priori cada haplotipo a una especie con base en la taxonomía previa, usualmente basada en morfología. Si los haplotipos de la especie focal son exclusivos y en el interior del clado existen dos o más clados bien apoyados que divergen basalmente y son congruentes con la geografía, esto sugiere la existencia de múltiples especies al interior de la especie focal. En cambio, si hay evidencia de flujo génico entre los linajes basales de la especie focal, entonces se trata de una sola especie. Por otra parte, si la especie focal es polifilética o parafilética con respecto a una o más especies exclusivas, y sus linajes basales son exclusivos, entonces la especie focal representa múltiples especies. En contraste, si hay flujo génico, ésta podría representar una sola especie no exclusiva. Si los haplotipos de la

especie focal interdigitan con los haplotipos de otras especies (volviéndolas polifiléticas o parafiléticas) y no hay evidencia de flujo génico entre los linajes basales de cada especie, entonces cada linaje podría representar una especie que la taxonomía tradicional no había detectado. Si hay flujo génico extensivo entre los linajes basales formados por haplotipos de múltiples especies, entonces todos podrían ser conespecíficos.

El protocolo basado en árboles de DNA mitocondrial tiene una ventaja sobre el análisis de los marcadores con bases nucleares. El tamaño efectivo poblacional del genoma mitocondrial (N_e) causa que los haplotipos de una especie dada coalescan (alcancen la monofilia) cuatro veces más rápido que los de un marcador nuclear. Esta propiedad es importante para delimitar especies porque las especies de formación reciente llegan a ser distintas en sus filogenias de haplotipos mitocondriales antes que en las filogenias de marcadores nucleares. De este modo, el análisis de DNA mitocondrial permite la resolución de los límites de especie en muchos grupos difíciles de resolver. Sin embargo, el uso aislado de datos de secuencias de DNA mitocondrial para la delimitación de las especies ha sido polémica (Moritz et al., 1992; Moritz, 1994; Crandall & Sites, 1997; Puorto et al., 2001; Petit & Excoffier; 2009) debido a que los datos de DNA mitocondrial pueden ser problemáticos porque todos los genes mitocondriales se heredan como un grupo ligado, y como resultado, cualquier incongruencia entre el gen y la historia de las poblaciones, causados por la retención del polimorfismo ancestral o el flujo génico entre las especies afectan al mismo tiempo a todos los genes mitocondriales (Moore, 1995). Además, dado que el mtDNA es heredado por vía materna, las filogenias de haplotipos mitocondriales reflejan los patrones de dispersión y flujo génico de las hembras, que pueden ser muy distintos de los de los machos (Avise, 1994).

Cuando se dispone de filogenias de múltiples genes las historias de los genes deberían ser concordantes entre especies (recuperando su exclusividad en cada caso) y discordante dentro de las especies. Este patrón podría ser otra línea de evidencia para la delimitación de especies (Avise & Ball, 1990; Baum & Donoghue, 1995; Baum & Shaw, 1995; Wiens & Penkrot, 2002). Sin embargo, las expectativas analíticas derivadas de la teoría de genética de poblaciones (Hudson, 1992; Rosenberg, 2002; Wakeley, 2006)

indican que se requiere un tiempo considerable después de la divergencia inicial de las especies antes de que haya una alta probabilidad de observar monofilia recíproca en una muestra de loci múltiples (Hudson & Coyne, 2002; Hudson & Turelli, 2003). Por ejemplo, para que sea posible detectar exclusividad recíproca en 15 loci tendría que transcurrir más de 1 millón de años después de la especiación, si el tamaño efectivo de la población (N_e) es de 100 y suponiendo una generación por año (Knowles & Carstens, 2007). En poblaciones más grandes, el número de años que deben transcurrir aumenta proporcionalmente (Hudson & Coyne, 2002).

Recientemente se han desarrollado métodos estadísticos para calcular las probabilidades asociadas con diferentes hipótesis de delimitación de especies basados en coalescencia. Estos métodos usan aproximaciones probabilísticas que no requieren monofilia de los alelos o diferencias fijas (Yang & Rannala, 2010). Esta es una característica importante porque no se espera que haya monofilia recíproca entre linajes en la mayoría de los alelos a través del genoma, particularmente en escalas de tiempo de especiación reciente (Hudson & Coin, 2002; Hudson, 1990). Los nuevos métodos de delimitación incrementan el rigor estadístico y la objetividad como resultado de adoptar un modelo multiespecie coalescente (Fujita et al. 2012; Leaché et al., 2014). Los métodos de delimitación de especies que utilizan datos multilocus basados en modelos coalescentes (Yang & Rannala, 2010) son ventajosos porque pueden modelar las probabilidades asociadas con la formación de linajes, lo cual está directamente asociado con los principios de los conceptos de especie basados en linajes (Wiley & Lieberman, 2011). Los datos multilocus capturan la estocasticidad inherente a la coalescencia, incluyendo la incongruencia entre los árboles de genes que surge de la separación incompleta de linajes, la variación en las secuencias moleculares y la variación en los parámetros demográficos que deben ser modelados para delimitar especies de manera precisa (Fujita & Leaché, 2012). Sin embargo, la fortaleza de estos métodos descansa en el número de loci utilizados y no siempre es posible secuenciar un gran número de ellos.

3. *COMPLEJO DE ESPECIES* HOLCOSUS UNDULATUS

Los teiidos suelen ser elementos muy conspicuos de la herpetofauna del Nuevo Mundo y han sido objeto de numerosos estudios. Sin embargo, la taxonomía de la famila Teiidae ha sido por mucho tiempo insatisfactoria, debido a la presencia de grandes géneros polifiléticos que no fueron dignosticados adecuadamente (Harvey et al., 2012). Este problema ha sido particularmente agudo en radiaciones especiosas de cnemidoforinos en las cuales la mayoría de las especies tropicales fueron asignadas a los grandes géneros polifiléticos *Ameiva* y *Cnemidophorus*. Una revisión reciente propone un nuevo arreglo taxonómico para la familia, que resuelve la polifilia de algunos géneros (Harvey et al., 2012). Actualmente la familia Teiidae está formada por tres subfamilias: Callopistinae Harvey, Ugueto & Gutberlet 2012, Teiinae Estes, de Queiroz & Gauthier 1988 y Tupinambinae Presch, 1974. La subfamilia Teiinae está formada por 11 géneros: *Ameiva* Meyer 1795, *Ameivula* Harvey, Hugueto & Gutberlet Jr. 2012, *Aspidoscelis* Fitzinger 1843, Aurivela Harvey, Hugueto & Gutberlet Jr. 2012, *Cnemidophorus* Wagler 1830, *Contomastix* Harvey, Hugueto & Gutberlet Jr. 2012, *Dicrodon* Duméril & Bibron 1839, *Holcosus* Cope 1862, *Kentropyx* Spix 1825, *Medopheos* Harvey, Hugueto & Gutberlet Jr. 2012, y *Teius* Merrem 1820. El género *Holcosus* a su vez, está formado por tres grupos: los grupos *Holcosus orcesi*, *Holcosus septemlineatus* y *Holcosus undulatus* (Harvey et al. 2012).

Las especies del grupo *Holcosus undulatus* se caracterizan por poseer ocho hileras longitudinales de escamas ventrales al nivel de la mitad del cuerpo (Harvey et al. 2012; Fig. 1). La cuarta supraocular está generalmente ausente y la primera es entera. Las placas dorsales de la cabeza no están muy fragmentadas, aunque en *H. leptophrys* puede haber pequeñas escamas separando las parietales (Harvey et al. 2012). La depresión en forma de ojo de cerradura en la región parietal está ausente (Harvey et al. 2012). Las escamas dorsales son suaves y cubren la superficie de forma que asemeja un panal de abejas (Harvey et al. 2012).

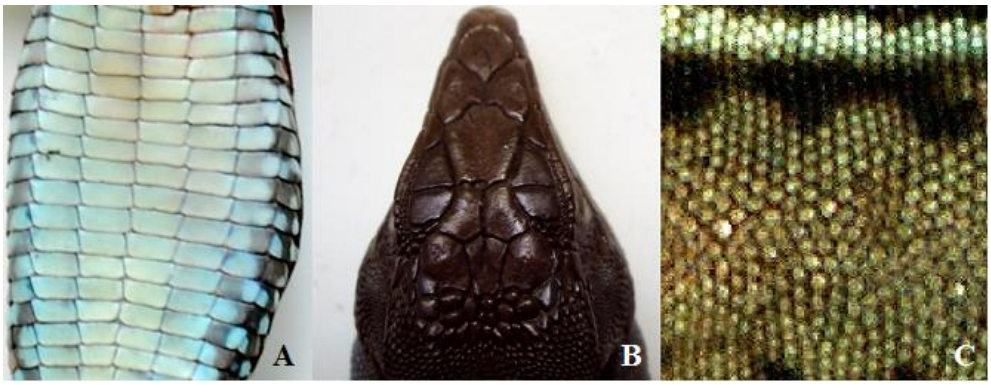

Figura 1. Condición de las escamas ventrales *H. dexter* (A, ANMO 2011), escamación de la cabeza de *H. hartwegi* (B, ANMO 1911) y gránulos dorsales de *H. parvus* (UTA R46792).

El grupo *Holcosus undulatus* está formado por *H. chaitzami*, *H. festivus*, *H. leptophrys*, *H. niceforoi*, *H. quadrilineatus* y *H. undulatus*. Este grupo se distribuye en la mayor parte de México, Centroamérica, noroeste de Colombia, así como en algunas islas del Caribe (Echternacht, 1971).

Las lagartijas del grupo *H. undulatus* habitan diversos tipos de bosques tropicales, pastizales y playas (Hower & Hedges, 2003), son forrajeras activas y se alimentan de insectos y ocasionalmente de lagartijas pequeñas y huevos (Schwartz & Henderson, 1991). En México existen sólo tres especies de *Holcosus*: *H. undulatus*, *H. festivus* y *H. chaitzami* (Echternacht, 1971).

Holcosus undulatus Wiegmann, 1834 es la especie más ampliamente distribuida de estas tres y se encuentra desde Sinaloa hasta Costa Rica por la vertiente del Pacífico y desde Tamaulipas, hasta Honduras por la vertiente del Atlántico (Echternacht, 1971; Global Biodiversity Information Facility, GBIF). También se encuentra en Isla Mujeres, Quintana Roo, México y en Isla del Maíz, Nicaragua (Echternacht, 1971). De esta forma, este taxón ocupa un número considerable de regiones fisiográficas y biogeográficas distintas en México y Centroamérica. Estas lagartijas habitan desde ambientes siempre húmedos (que incluyen bosques lluviosos tropicales y bosques de neblina) hasta ambientes semiáridos y marcadamente estacionales como selvas tropicales semideciduas, deciduas y pastizales.

La extensa variación ontogenética, sexual y geográfica en la morfología de *H. undulatus* se ve reflejada en el número de subespecies que fueron descritas durante el siglo XX (cuadro 1). Las especies que se consideran filogenéticamente más relacionadas a *H. undulatus* son *H. chaitzmani*, que se distribuye en Chiapas y Guatemala y *H. quadrilineata*, de Costa Rica (Echternacht, 1971).

Cuadro 1. Subspecies de *H. undulatus*, localidad tipo y descipción original.

Subspecie	Localidad tipo	Descripción original
H. u. undulatus	"México" (localidad tipo restringida a Tehuantepec por Smith, 1940)	Wiegmann, 1834
H. u. pulcher	de Nicaragua	Hallowell, 1860
H. u. parvus	"Guatemala" (Restringida a Mazatenango por Smith & Laufe (1946)	Barbour & Noble, 1915
H. u. miadis	Isla del Maíz, Nicaragua	Barbour & Loveridge, 1929
H. u. hartwegi,	Chiapas, cruzando el Río Usumacinta a la altura de Piedras Negras, Guatemala	Smith, 1940
H. u. stuarti,	Palenque, Chiapas	Smith, 1940
H. u. amphigrammus	San Andrés Tuxtla, Veracruz	Smith & Laufe, 1945
H. u. gaigeae,	Progreso, Yucatán	Smith & Laufe, 1946
H. u. dexter	Rincón, Guerrero	Smith & Laufe, 1946
H. u. podargus	Victoria, Tamaulipas	Smith & Laufe, 1946
H. u. sinister	Manzanillo, Colima	Smith & Laufe, 1946
H. u. thomasi	La Libertad, Chiapas, cerca de Río Cuilco donde cruza la frontera de Guatemala	Smith & Laufe, 1946

Echternacht (1971) documentó una gran variación morfológica en *Holcosus undulata* a lo largo de su extensa distribución geográfica y también una amplia variación ontogenética. La variación geográfica en algunos caracteres merísticos forma patrones clinales. Las clinas más amplias son las que se forman desde el noreste y noroeste de México hasta el Istmo de Tehuantepec y del Istmo hacia Nicaragua y Costa Rica. Otros caracteres forman clinas más cortas al interior de las anteriores. Echternacht (1971) no reconoció a las subespecies previamente descritas ya que las consideró como divisiones nomentclaturales arbitrarias.

Holcosus undulatus es entonces una especie con una distribución geográfica amplia que abarca diversas regiones fisiográficas y biogeográficas y que presenta una extensa variación geográfica y ontogenética. Estas características sugieren que más que una sola especie, constituye un complejo de especies cuya taxonomía ha sido estudiada

sólo desde la perspectiva morfológica tradicional. Por ello, en este estudio se utilizarán varias fuentes de evidencia (morfología externa y DNA mitocondrial y nuclear) y métodos más rigurosos para la delimitación de especies para reevaluar los límites de especie en el complejo *Holcosus undulatus.*

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Long forsaken species diversity in the Middle American lizard *Holcosus undulatus* (Teiidae)

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Numerous reptile species have been divided into subspecies. Although this classification may capture the morphological variation within species, it often conceals significant species diversity because many subspecies actually represent species under lineage-based species concepts. The lizard *Holcosus undulatus* is a common, widely distributed, monotypic species in Middle America. However, 12 subspecies of this taxon were recognized until the early 1970s. We used two lineage-based methods for species delimitation to re-evaluate species limits within *H. undulatus* with DNA sequence and morphological data. We included all the previously recognized subspecies of *H. undulatus* except *H. u. miadis*. *Holcosus undulatus* was exclusive. In addition, *H. u. amphigrammus*, *H. u. gaigeae*, *H. u. hartwegi*, *H. u. parvus*, *H. u. pulcher*, *H. u. sinister*, *H. u. stuarti*, *H. u. thomasi* and *H. u. undulatus* were supported as distinct evolutionary lineages based on the molecular and morphological evidence. We therefore elevate all of these subspecies to species rank. In addition, two separate mitochondrial lineages may represent cryptic, undescribed species within *H. undulatus*. The morphological distinctness and allopatry of *H. u. miadis* and *H. u. pulcher*, as well as the high genetic divergence of the latter species, suggest that they also represent distinct evolutionary species. Our results also suggest that additional species diversity may still be hidden within the *H. u. amphigrammus*, *H. u. parvus*, *H. u. sinister* and *H. u. undulatus* lineages. This work supports resurrection of overlooked diversity within *Holcosus*, which has important implications for the conservation of this genus in Middle America.

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ADDITIONAL KEYWORDS: *Ameiva* – cryptic species – lineage-based species concept – mtDNA tree – parapatry – phylogeny – species boundaries – species delimitation criteria – species tree – subspecies.

INTRODUCTION

A subspecies is an aggregate of populations, belonging to the same species, inhabiting a geographical subdivision of its range, and differing taxonomically from other populations of that species (Mayr, 1942, 1982). The subspecies were conceived as separate populations inbreeding freely at the zones of contact, but the category was later extended to include geographically isolated populations (Wilson & Brown, 1953). Subspecies has also been conceived as evidence of the adaptive response of species to local climatic conditions (Mayr, 1982), as incipient species (Mayr, 1982) and even as practical devices without biological meaning (Mayr, 1982; Cracraft, 1983). During the mid-20th century, the rank of subspecies became widespread with the expansion of the biological species concept and many populations previously considered as species were combined as subspecies in a single polytypic species (Mayr, 1982; Zink, 2004). In reptiles, many species were divided into subspecies on the basis of geographical variation in scalation and coloration (Wiens, 2008).

Recent studies using lineage-based species concepts (*sensu* Wiley & Lieberman, 2011) and other lines of evidence (e.g. DNA sequences) have revealed that many subspecies actually represent distinct species (e.g. Mulcahy *et al*., 2006; Schulte, Macey & Papenfuss, 2006; Pyron & Burbrink, 2009; Feria-Ortiz, Manríquez-Morán & Nieto-Montes de Oca, 2011; Glor & Laport, 2012).

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Thus, although the diversity was recognized morphologically, embracing the biological polytypic species concept resulted in its inappropriate classification, with the consequent concealment of substantial species diversity (Wiens, 2008). Because this concealment has significant negative consequences for the knowledge and conservation of biodiversity, it is important to investigate whether particular subspecies actually represent distinct, independent lineages and therefore should be recognized as full species (Frost & Hillis, 1990; Wiens, 2008).

The genus *Holcosus* Cope comprises a group of terrestrial, widely foraging teiid lizards that occurs from Mexico to trans-Andean Colombia and Ecuador and includes three species groups: the *H. orcesi*, *H. septemlineatus* and *H. undulatus* groups. The *H. undulatus* group ranges from Central Mexico to Colombia, and contains six species (Harvey, Ugueto & Gutberlet, 2012): *H. chaitzami* Stuart, 1942, *H. festivus* (Lichtenstein & Von Martens, 1856), *H. leptophrys* (Cope, 1893), *H. niceforoi* (Dunn, 1943), *H. quadrilineatus* (Hallowell, 1860) and *H. undulatus* (Wiegmann, 1834). *Holcosus undulatus* is the most extensively distributed of the six species, occurring on the Atlantic slopes from southern Tamaulipas, Mexico, to the Departamentos of Nuevo Segovia and Río San Juan, Nicaragua, and on the Pacific slopes from Nayarit, Mexico, to Puntarenas Province, Costa Rica; it is also found on Isla Mujeres, east of Quintana Roo, Mexico, and the Corn Islands, east of Nicaragua (Echternacht, 1971). The species occurs mainly in shaded habitats in forest or forest-edge areas usually below 1500 m, but it may utilize open areas in the absence of competition from other teiids such as *Aspidoscelis* (Echternacht, 1971).

Holcosus undulatus is currently recognized as a monotypic species (Harvey *et al*., 2012). However, until the publication of Echternacht's (1970, 1971) taxonomic works on Middle and South American *Ameiva* it was divided on the basis of geographical variation in scalation and colour pattern into 12 subspecies (see below). This suggests that adoption of a lineage-based species concept and the analysis of different lines of evidence relevant to species delimitation (e.g. external morphology and DNA sequences) may provide evidence supporting the resurrection of some or all of these subspecies and their elevation to species rank, and thus reveal the existence of more species than currently recognized in the *H. undulatus* group.

Brief taxonomic history of *H. undulatus*

Wiegmann (1834) described *Cnemidophorus undulatus* from 'Mexico' with two varieties: alpha and beta, referred to as varieties A and B by subsequent authors. This author, however, did not provide additional information about the geographical distribution of *C. undulatus* or its varieties. Subsequently, Gray (1845) transferred *C. undulatus* to the genus *Ameiva* Cuvier.

Hallowell (1860) described *Ameiva pulchra* and *Cnemidophorus quadrilineatus* from 'Nicaragua'. However, shortly after this Cope (1862) transferred *C. quadrilineatus* to *Ameiva* (= *A. quadrilineata*). Bocourt (1874), on the basis of Wiegmann's (1834) syntypes and material collected during the labours of the 'Mission scientifique au Mexique et dans l'Amerique Centrale,' provided detailed re-descriptions of *Ameiva undulata* and both of its varieties A and B. Bocourt (1874) also stated that the National Museum of Natural History in Paris had several specimens 'identical' to the type specimens of *C. undulatus* described by Wiegmann (1834), and that all of them had been collected in diverse localities on the Pacific versant of Mexico ('Oaxaca and Tehuantepec') and Central America (scattered localities on the Pacific versant of Guatemala and El Salvador). Furthermore, Bocourt (1874) stated that Wiegmann's (1834) variety A of *A. undulata* inhabited the Atlantic versant of Mexico and Central America [the Petén, the hot lands of Vera Paz, the course of the Rio Polochic, Santa María de Pansos (=Panzós), and Isabal (=Izabal)], whereas variety B had been collected by the Mission Scientifique in the forests of Belize (British Honduras).

Barbour & Noble (1915) treated *Ameiva undulata* as a polytypic species for the first time in the early 20th century. They assigned the Mexican populations to *A. undulata undulata* (suggesting that this taxon was confined to southern Mexico), described *A. undulata parva* from 'Guatemala' and included *A. quadrilineata* in *A. undulata* (*A. u. quadrilineata*). However, Schmidt & Stuart (1941) noted that the specimens of *A. u. quadrilineata* of Barbour & Noble (1915) actually represented *A. pulchra*.

Barbour & Loveridge (1929) described *Ameiva festiva miadis* from Great Corn Island, Nicaragua. Later, Hartweg & Oliver (1937) examined a series of 30 males and 17 females from 32 km south-west of Tehuantepec in Oaxaca, Mexico, and Ranchería Lamanga, 20 km south of Tehuantepec, and concluded that *Ameiva undulata* 'as described by Wiegmann (1834: 27–28) and redescribed and figured by Bocourt (1874: 254–258)' was composed of two forms: *A. u. undulata*, from the region of Tehuantepec, and *A. u. parva*, from the Pacific slopes of Guatemala.

Dunn (1940) suggested that both *Ameiva pulchra* and *A. festiva miadis* were 'a form of *A. undulata* Wiegmann'. In the same year, Smith (1940) described variety A of Wiegmann (1834) and Bocourt (1874) as *A. u. hartwegi* from 'Chiapas, Mexico, across the Usumacinta River from Piedras Negras, Guatemala', and also *A. u. stuarti* from Palenque, Chiapas.

Schmidt & Stuart (1941) recognized four subspecies of *Ameiva undulata*: *A. u. undulata*, ranging along the Pacific coast of Mexico north-westward from Tehuantepec; *A. u. parva*, ranging along the Pacific coast of Mexico and well into that of Guatemala south-eastward from Tehuantepec; *A. u. hartwegi*, from Yucatán, Mexico, and El Petén, Guatemala; and *A. u. stuarti*, from Veracruz, Tabasco and Chiapas in the Atlantic versant of Mexico. Schmidt & Stuart (1941) suggested that both *A. leptophrys* and *A. pulchra* also were forms or races 'of the *undulata* group'. Shortly thereafter, Stuart (1942) described *A. chaitzami* from Alta Verapaz, Guatemala, and Smith & Laufe (1945) described *A. u. amphigramma* from San Andrés Tuxtla, Veracruz.

Smith & Laufe (1946), in their taxonomic review of Mexican *Ameiva*, continued to recognize the previously described subspecies of *A. undulata* and described five more: *A. u. dextra*, *A. u. gaigeae*, *A. u. podarga*, *A. u. sinistra* and *A. u. thomasi*. Also, following Bocourt's (1874) assignment of populations of *Ameiva* to Wiegmann's (1834) varieties A and B of *A. undulata*, Smith & Laufe (1946) concluded that both of these varieties corresponded to *A. u. hartwegi*. Because *A. u. pulchra* and *A. u. miadis* do not occur in Mexico, Smith & Laufe (1946) did not include them in their study. The ten subspecies of *A. undulata* from Mexico recognized by Smith & Laufe (1946), along with the references of their original descriptions, type localities and distributions, are listed in Table 1. Smith & Laufe (1946) also indicated the existence of several putative areas of intergradation among the subspecies (Fig. 1). Smith & Laufe's (1946) taxonomic arrangement of Mexican *Ameiva* was maintained by Smith & Taylor (1950) and Stuart (1963).

Echternacht (1970) discussed the taxonomy of two Middle American *Ameiva*. *Ameiva festiva miadis* was formally designated a subspecies of *A. undulata*, and *A. undulata thomasi* was placed in the synonymy of *A. chaitzami*. Subsequently, Echternacht (1971) performed a detailed analysis of the geographical variation in Middle American *Ameiva* and placed all the other subspecies of *A. undulata* into the synonymy of *A. undulata*. Also, he recognized five other species of *Ameiva* in Middle America: *A. ameiva*, *A. chaitzami*, *A. festiva*, *A. leptophrys* and *A. quadrilineata*. Finally, in a recent, detailed morphological study of the Teiidae, all Mexican and Central American species of *Ameiva* were transferred to the genus *Holcosus* (Harvey *et al.*, 2012).

Herein, we use molecular and morphological data to investigate the potential existence of multiple species within *H. undulatus* and whether their limits correspond to those of the formerly recognized subspecies.

METHODS

Taxon sampling

We sampled broadly from the geographical distribution of *H. undulatus* in Mexico and Central America (Fig. 1, Table S1), including multiple samples from the geographical distribution of each subspecies of *H. undulatus* except for *H. u. pulcher* and *H. u. miadis*, of which only one and no samples were available, respectively. Acronyms for museums and collections follow Sabaj-Pérez (2014). We followed Hallowell (1860), Cope (1862) and Smith & Laufe (1946) to evaluate the subspecific identity of the sampled individuals of *H. undulatus*. 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. Although we tried to include samples from the type locality of each subspecies (e.g. *H. u. amphigrammus* and *H. u. sinister*), this was sometimes not possible, either because the type locality was imprecise (e.g. *H. u. parvus* and *H. pulcher*, from 'Guatemala' and 'Nicaragua', respectively), or because no specimens were found at the type-locality. In such cases we included all available samples from the subspecies reported distribution.

The locality of Finca El Carmen on the Pluma Hidalgo-Huatulco road lies in the putative area of intergradation between *H. u. dexter* and *H. u. undulatus* (Smith & Laufe, 1946). We tentatively assigned our sample of *H. undulatus* from this locality to *H. u. undulatus* because the only male available from this population exhibited the dorsolateral colour pattern described by Smith & Laufe (1946) for this subspecies. Similarly, although our specimens of *H. undulatus* from Honduras fell within the variation range described for *H. u. parvus* by Smith & Laufe (1946), they are from the interior highlands of Honduras, outside of the known distribution of this subspecies (Table 1). Thus, assignment of those samples to *H. u. parvus* was only provisional. Finally, although Echternacht (1971) synonymized *H. u. thomasi* with *H. chaitzami*, examination of most of the types of *H. chaitzami* (the holotype and three paratypes), as well as the holotype, four topotypes and nine additional specimens from the general region of the type locality of *H. u. thomasi*, suggests that these two taxa actually represent distinct species (our pers. observ.). In addition, *H. u. thomasi* and *H. chaitzami* appear to be allopatric and separated by the intervening highlands of the Sierra de los Cuchumatanes. Thus, we consider as an incontrovertible population of *H. chaitzami* only that from its type locality, and tentatively assigned the specimens from Comitán, Chiapas and Huehuetenango, Guatemala, to *H. u. thomasi* following Smith & Laufe (1946). A summary of the

Table 1. Original descriptions, type-localities, and geographic distributions of *H. chaitzami* and the formerly recognized subspecies of *H. undulatus*. Except as otherwise noted, the geographic distributions are taken from Smith & Laufe (1946)

Taxon	Original description	Type locality	Geographical distribution
H. chaitzami	Stuart (1942)	Along Cahabón–Lanquín Trail about 2 km north of Finca Canihor (about 38km ENE [straight line] of Cobán, Alta Verapaz, Guatemala).	Probably distributed thoughout the savanna area of the semi-arid lower Cahabón Valley bellow about 1000 m from Lanquín (30 km [straight line] ENE from Cobán) to Taquincó (56 km [straight line] E from Cobán) (Stuart, 1942) and Poptún (Echternacht, 1971)
H. u. amphigrammus	Smith & Laufe (1945)	San Andrés Tuxtla, Veracruz	Northern Veracruz (exact area uncertain, perhaps in the vicinity of Laguna Tamiahua), southward through most of Veracruz to the Isthmus of Tehuantepec; westward into valleys extending into extreme eastern Oaxaca and probably north-eastern Puebla
H. u. dexter	Smith & Laufe (1946)	Near Rincón, Guerrero	Southern slopes of the Sierra Madre del Sur of Guerrero and perhaps extreme western Oaxaca
H. u. gaigeae	Smith & Laufe (1946)	Progreso, Yucatán	Northern half of the Yucatán Peninsula, and southward to the Island of Carmen along the extreme eastern coast
H. u. hartwegi	Smith (1940)	Chiapas, Mexico, across the Rio Usumacinta from Piedras Negras, Petén, Guatemala	Atlantic slopes of Mexico and Guatemala from the vicinity of the south-eastern end of Laguna de Términos south and eastward across the base of the Yucatán Peninsula to north-western Honduras
H. u. miadis	Barbour & Loveridge (1929)	Great Corn Island, 40 miles off Nicaraguan coast	Known only from Islas del Maíz (Corn Islands), Depto. Zelaya, Nicaragua
H. u. parvus	Barbour & Noble (1915)	Guatemala; restricted to Mazatenango by Smith & Laufe (1946)	Pacific slopes from the Isthmus of Tehuantepec in Oaxaca, near Niltepec, south-eastward to Costa Rica
H. u. podargus	Smith & Laufe (1946)	7 miles west of Victoria, Tamaulipas	Atlantic coast from the latitude of Victoria, Tamaulipas, southward into northern Veracruz
H. u. pulcher	Hallowell (1860)	Nicaragua	Pacific coast of Nicaragua (Echternacht, 1971)
H. u. sinister	Smith & Laufe (1946)	Manzanillo, Colima	Pacific coastal drainage from the arid Balsas Basin at the border of Guerrero and Michoacán north-westward at least to Jalisco, and perhaps farther; the northern drainage of the Río Balsas, at lower elevations and in humid localities, from Michoacán to Puebla
H. u. stuarti	Smith (1940)	Palenque, Chiapas	Atlantic slopes of Mexico from the middle of the Isthmus of Tehuantepec eastward in the lowlands to the southern borders of Laguna de Términos and to Tenosique, Tabasco; southward up the valley of the Río Grijalva at least as far as Tuxtla Gutiérrez, Chiapas
H. u. thomasi	Smith & Laufe (1946)	La Libertad, Chiapas, near Río Cuilco where it crosses the Guatemalan border	Probably in all the dry, hot valleys of the upper tributaries of the Río Grijalva in the interior of Chiapas and of western central Guatemala
H. u. undulatus	Wiegmann (1834)	Mexico (by inference); restricted to Tehuantepec by Smith (1940)	The Pacific slopes of the Isthmus of Tehuantepec in Oaxaca, as far west as Puerto Angel and eastward about to Niltepec

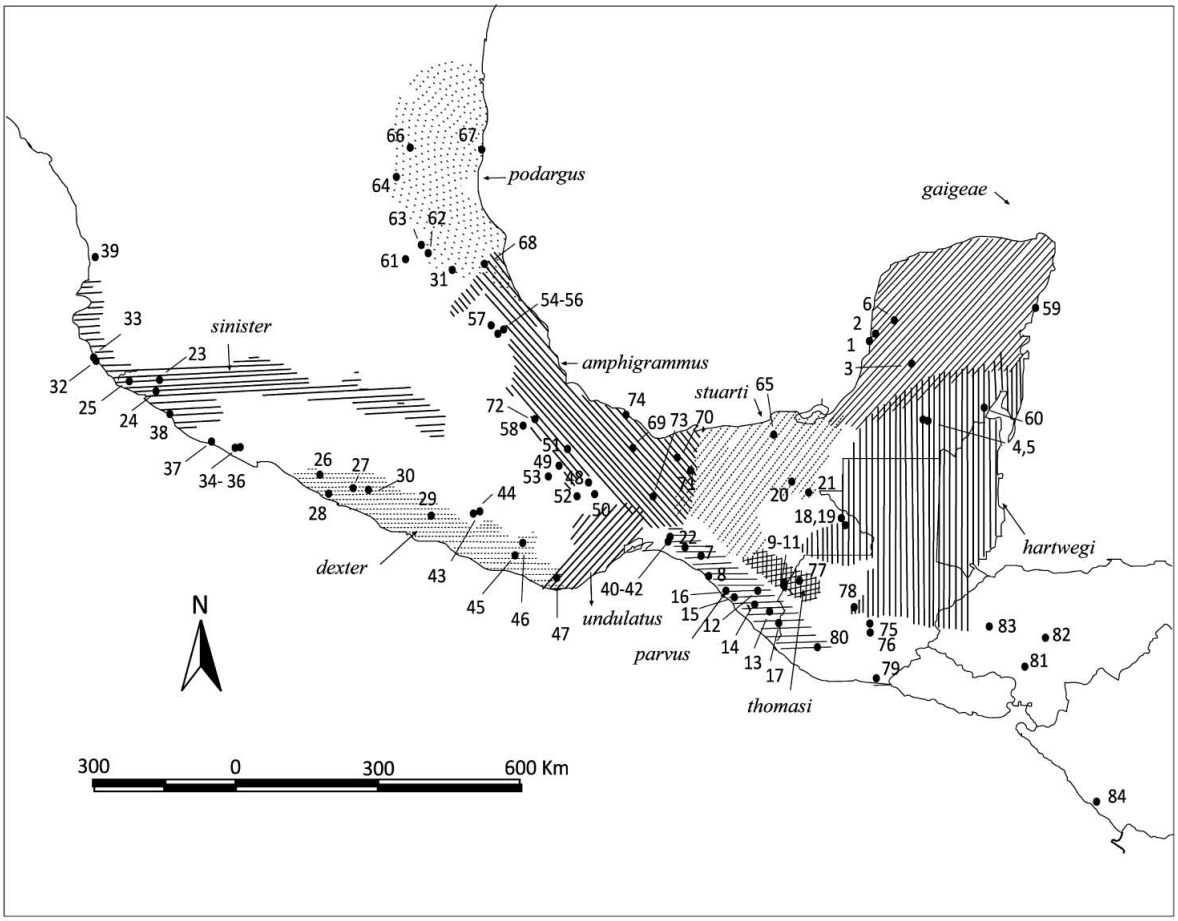

Figure 1. Geographical distribution of the formerly recognized subspecies of *H. undulatus* in Mexico (reproduced from Smith & Laufe, 1946); and sampling localities for *H. undulatus*. Numbers at dots refer to specific sample numbers of *H. undulatus* specimens used in this study. Locality data for these specimens are given in Table S1.

diagnostic characters of the subspecies of *H. undulatus* is given in Table 2.

To evaluate the exclusivity of *H. undulatus*, we included as outgroups representatives of other species of *Holcosus* in Mexico and Central America (*H. festivus* and *H. quadrilineatus*). Unfortunately, no samples of either true *H. chaitzami* (i.e. from its type locality) or of *A. leptophrys* were available. Finally, we included *Aspidoscelis deppii*, *Ameiva ameiva*, *A. auberi* and *A. chrysolaema* (Teiidae) and *Leposoma parietale* (Gymnophtalmidae) in the analysis as more distant outgroups to root the tree.

DATA

Mitochondrial DNA (mtDNA) has well-known advantages and limitations for species delimitation. Because of its low effective population size (one-quarter the size of a given nuclear gene) newly formed species become exclusive in their mtDNA haplotype phylogenies in a quarter of the time they become distinct in nuclear-based markers (Moore, 1995). Therefore, incomplete lineage sorting is less of a concern for mitochondrial than for nuclear loci. Nonetheless, mitochondrial gene trees can be particularly susceptible to the effects of introgressive hybridization, male-biased dispersal (female philopatry) and the development of strong geographical patterns produced by temporary isolation (Palumbi & Baker, 1994; Thorpe, Black & Malhotra, 1996; Wiens & Penkrot, 2002; Funk & Omland, 2003).

It has been suggested that the above potential problems of mtDNA gene trees may be common, and thus the species limits inferred must be corroborated by other evidence (i.e. Funk & Omland, 2003; Bond & Stockman, 2008; Zink & Barrowclough, 2008). Nuclear DNA gene trees can be used to corroborate mtDNA gene trees

Table 2. Summary of the diagnostic characters of *H. chaitzami* and the subspecies of *H. undulatus*. Data for *H. chaitzami*, the Mexican subspecies and *H. u. pulcher* taken from Stuart (1942), Smith & Laufe (1946), and Hallowell (1860) and Cope (1862), respectively

Taxon/ character	SVL (mm)	Median gular scales			Scale rows between 3rd supraocular and superciliaries	Preanals arrangement	Femoral pores‡	Lamellae under 4th toe	Colour pattern				Male lateral pattern
		Size	Enlargement	Arrangement					Dorsolateral dark line	Dorsolateral light line	Upper lateral light stripe	Upper lateral dark stripe	Lateral vertical bands**	
chaitzami	♂ 70 ♀ 66	Enlarged	Abrupt	One median row	One	Paired	16 (15–17), $N = 4$ (this study)	24.6 (22–26), $N = 4$ (this study)	Continuous	Distinct	Absent	Split into transverse spots, separated by light spots	Few, irregular	
amphigrammus	♂ 105 ♀ 101	Enlarged	Abrupt	Usually one median row (87%); ≤ two of the largest scales divided	One	Paired	17.0 (14–23), $N = 180$; usually ≥ 16 in ♀ (75%)	27.7 (24–33), $N = 187$	Broken into speckles	Absent	Broad, continuous, or broken into blotches§	Split into dorsal and ventral narrow lines by the upper lateral light line	Poorly developed (this study)	
dexter	♂ 113 ♀ 80	Enlarged	Abrupt	One median row	One	One row†, posterior-most usually paired (85%)	18.2 (15–21), $N = 24$	28.9 (27–31), $N = 20$	Broken into speckles in ♂, continuous in ♀	Dim in ♂, distinct in ♀	Broad, continuous, or broken into blotches in ♂	Split into dorsal and ventral narrow lines by the upper lateral light line	Poorly developed, particularly in ♀	
gaigeae	♂ 125 ♀ 107	Small	Usually not abrupt	Irregular	One	Paired	18.5 (15–22), $N = 138$	30.4 (26–36), $N = 132$	Broken into speckles	Absent in ♂, distinct in ♀	Absent	Split into transverse spots, separated by vertical light lines	Well developed; 13.1 (9–18), $N = 57$; usually ≥ 12 (89.5%)	
hartwegi	♂ 138 ♀ 115	Small	Not abrupt	Irregular	Two*	Paired	20.5 (16–23), $N = 100$; usually ≥ 18 (98%)	31.8 (29–36), $N = 97$; ≥ 29 (100%)	Broken into speckles (100%; this study)	Absent or dim (this study)	Absent (this study)	Split into transverse spots, separated by vertical light lines	Well developed; (8–12), $N = 55$; usually ≤ 11 (98.2%)	
parvus	♂ 109 ♀ 95	Enlarged	Abrupt	One median row	Usually two	Paired	16.4 (13–21), $N = 98$	29.1 (26–33), $N = 97$	Broken into speckles	Distinct	Absent	Split into transverse spots, separated by vertical light lines	Well developed	

podargus	♂ 116 ♀ 96	Enlarged	Abrupt	Completely irregular or ≤ two scales forming a row (84.6%)	One	Paired	15.8 (13–18), *N* = 31; usually ≤ 15 in ♀ (64.7%)	29.4 (28–31), *N* = 30; ≥ 28 (100%)	Broken into speckles	Dim	Broad, broken into large blotches¶	Split into dorsal and ventral narrow lines by the upper lateral light line	Present, usually dim
pulcher	No data	Enlarged	Abrupt	Irregular	No data	Paired	20 (holotype)	No data	Continuous (Hallowell, 1860)	No data	Absent	Split into transverse spots, separated by vertical light lines	Numerous, black (Hallowell, 1860)
sinister	♂ 109 ♀ 95	Enlarged	Abrupt	One median row	One	One row†, posterior-most rarely paired (37.7%)	18.1 (15–22), *N* = 121	29.6 (26–32), *N* = 111	Broken into speckles	Absent or dim	Absent	Split into transverse spots, separated by light spots	Well developed in adult ♂
stuarti	♂ 90* ♀ 81*	Enlarged	Abrupt	One median row	No data	Paired	15.5 (13–18), *N* = 73; usually ≤ 17 (97.3%)	25.5 (22–30), *N* = 72; usually ≤ 27 (87.5%)	Usually continuous	No data	Absent	Split into transverse spots, separated by vertical light lines	Narrow in ♂*
thomasi	♂ 92 ♀ 78	Enlarged	Abrupt	One median row	One	Paired	17.2 (14–20), *N* = 18	28.4 (25–30), *N* = 17; usually ≥ 28 (75.5%)	Absent or broken into speckles	Distinct, fused with upper lateral light blotches	Absent	Split into transverse spots, separated by vertical light lines	Present
undulatus	♂ 116 ♀ 95	Enlarged	Abrupt	One median row	One	One row†, posterior-most paired in one-half (52%) of specimens	16.8 (13–20), *N* = 162	27.7 (25–30), *N* = 94	Broken into speckles	Absent except in young	Absent	Split into transverse spots, separated by vertical light lines	Present

*This study (not recorded in the cited references).
†Single median row and on each side a smaller row' (Smith & Laufe, 1946).
‡On one side (both sexes).
§Dark lines between blotches considerably less than half as wide as blotches.
¶Dark bars between light blotches at least half as wide as blotches, usually wider.
**Averages and ranges are for numbers of lateral vertical light lines between the levels of the axilla and groin.

in the search of organismal, as opposed to gene, phylogenies (Moore, 1995, 1997). Because of the intrinsically stochastic nature of the coalescent process and the longer coalescence times of nuclear compared with mitochondrial genes (Moore, 1995; Wiens & Penkrot, 2002; Zink & Barrowclough, 2008), general corroboration between nuclear and mtDNA gene trees is not expected (especially for mtDNA trees with a shallow geographical structure), but when such corroboration is present (at least for some lineages in the phylogeny), it is evidence of probably long lineage isolation. We obtained sequences of an mtDNA fragment encompassing the genes encoding tRNAMet (in part), the second unit of the NADH dehydrogenase (ND2), tRNATrp and tRNAAla (in part), for approximately 1200 bp. In addition, we obtained sequence data from two nuclear markers: the nuclear intron RPS8 (427 bp) (Tod W. Reeder, pers. comm.), and the coding region amplified with the primers for the α-cardiac-actin gene (561 bp) of Waltari & Edwards (2002). The mitochondrial fragment was sequenced for all of the included samples. For the nuclear genes, an effort was made to sequence representative samples of each clade concordant with geography in the mitochondrial tree.

Laboratory protocol

We extracted DNA from liver or tail clips using the standard phenol-chloroform-isoamyl alcohol protocol (Hillis *et al*., 1996), or the extraction protocol for reptile shed skins of Fetzner (1999). All of the sequenced genes were amplified via PCR. The primers used to amplify and sequence these genes are detailed in Table S2. The PCR cycle parameters for the mitochondrial fragment were: an initial denaturation cycle at 94 °C for 5 min, followed by 35 cycles at 94 °C for 1 min, 45–53 °C for 1 min and 72 °C for 2 min, and a final extension at 72 °C for 4 min. The PCR cycle parameters for the nuclear fragments were: an initial denaturation cycle at 94 °C for 5 min, followed by 35 cycles at 94 °C for 1 min, 45–48 °C for 1 min and 72 °C for 2 min, and a final extension at 72 °C for 4 min. PCR products were cleaned with polyethylene glycol precipitation (Lis & Schleif, 1975). DNA templates were sequenced using the Big Dye Terminator v3.1 cycle sequencing kit (Applied Biosystems). The reaction products were cleaned using Sephadex columns and sequenced with an ABI 3100 automated Genetic Analyzer Sequencer.

Phylogenetic analyses

We assembled, edited and aligned sequences using CLC Main Workbench 6.9.1 (CLC Bio). The alignment was adjusted visually with Mesquite v2.75 (Maddison & Maddison, 2011). Regions in the alignment that could not be unambiguously aligned were removed. All of the sequences were deposited in GenBank (Table S1).

We analysed the aligned DNA sequences using Bayesian and maximum-likelihood (ML) methods of phylogenetic inference. We performed partitioned analyses of the mitochondrial fragment and single model analyses of the individual nuclear markers. For the mitochondrial dataset, we assayed different combinations of partitions (partition strategies). To determine the best partition strategy, we used the Bayes factor as described by Brandley, Schmitz & Reeder (2005). To select the best substitution model for each partition, we used the nst = mixed option implemented in MrBayes v3.2 (Ronquist *et al*., 2012). This option uses rjMCMC to sample among all possible reversible substitution models (Ronquist *et al*., 2012). We estimated the marginal likelihood by calculating the harmonic mean of the likelihood values of the Markov Chain Monte Carlo (MCMC) samples. The harmonic mean was calculated by using the sump command in MrBayes (Newton & Raftery, 1994). The partition strategies compared and the selected models of evolution for each strategy are given in Table S3.

Bayesian settings included random starting trees and default priors except for the rate prior, which was set to variable. Analyses consisted of two runs (nruns = 2), each conducted with three heated and one cold Markov chains, sampling every 10000 generations for 10×10^7 generations. The parameters and tree output files from the two individual replicates were combined in LogCombiner 1.8.0 (Drummond, Rambaut & Suchard, 2013). We evaluated stationarity and convergence of likelihood scores between runs visualizing the output parameters with TRACER 1.5.0 (Rambaut & Drummond, 2009). We then discarded burn-in trees and estimated the maximum clade credibility (MCC) tree with nodal posterior probability (PP) support from the postburn-in trees using TreeAnnotator 1.8.0 (Rambaut & Drummond, 2013). We considered nodes with posterior probability values ≥ 95% as significantly supported (Felsenstein, 2004).

We performed ML analyses with RAxML 7.0.4 (Stamatakis, 2006a). We used the same model (GTRGAMMA) for each of four partitions for the mitochondrial fragment (one for the non-coding region and one for each codon position) and each nuclear gene. We used GTRCAT for the bootstrapping face with 1000 fast bootstrap replicates for the final tree inference (Stamatakis, 2006a, b). We considered nodes with a bootstrap value ≥ 70% as significantly supported (Hillis & Bull, 1993). All the phylogenetic analyses were performed in the Cyberinfrastructure for Phylogenetic Research (CIPRES; Miller, Pfeiffer & Schwartz, 2010).

In addition, we estimated a coalescent-based species tree using the program BEAST 1.8.0 (Drummond *et al*., 2012). We assigned the individuals to those sets

of populations supported by the molecular and/or morphological data as distinct, independent evolutionary lineages (see below). We unlinked the three genes (ND2, RPS8 and α-cardiac-actin) and selected the best substitution model for each gene with the use of the Bayesian information criterion implemented with jModelTest 2.1.4 (Darriba *et al*., 2012). We performed the BEAST analyses under a correlated lognormal relaxed molecular clock (mean clock rate fixed to the gene ND2) and the Yule process. We performed two replicates with 100 million generations each, and sampled every 10000 steps. We combined the Log and tree files from the two individual replicates in LogCombiner 1.8.0 (Rambaut & Drummond, 2013), and used the program Tracer 1.5 (Rambaut & Drummond, 2009) to evaluate the convergence of the trees and estimate the burn-in value. Finally, we estimated the MCC tree using TreeAnnotator 1.8.0 (Rambaut & Drummond, 2013).

Testing alternative phylogenetic hypotheses

To test whether alternative phylogenetic hypotheses not present in the preferred tree (i.e. the mitochondrial tree, see below) could be statistically rejected by the data (e.g. an alternative hypothesis holding as monophyletic a paraphyletic taxon in the Bayesian tree), we used a Bayesian approach for hypothesis testing (Huelsenbeck & Rannala, 2004; Brandley *et al*., 2005). If a phylogenetic hypothesis of interest was not included in the 95% set of credible trees for the mtDNA dataset, it was rejected. The hypotheses tested were the monophyly of *H. u. parvus* and *H. u. dexter*.

Species concept

To re-evaluate the species limits in *H. undulatus*, we used the tree-based methods for delimiting species proposed by Wiens & Penkrot (2002) and Bond & Stockman (2008). These methods (hereafter WP and BS, respectively) use a lineage-based species concepts (*sensu* Wiley & Lieberman, 2011) but differ in the species properties or lines of evidence that they use for species delimitation. De Queiroz (2007) proposed that the primary and only necessary defining property of species is their existence as separately evolving lineages. Other properties acquired by lineages during the course of divergence (intrinsic reproductive isolation, genetic exchangeability, diagnosability, same niche or ecological interchangeability, monophyly, etc.) are secondary defining properties of species, many of which are more appropriately interpreted as different lines of evidence relevant to species delimitation only to the extent that they provide evidence of lineage separation.

Thus, a lineage might lack one or more of the secondary defining properties even if it is evolving separately from all other lineages, and does not have to have any of them to be considered a species. However, the presence of any one of those properties (if appropriately interpreted) is evidence for the existence of a species, although more properties and thus more lines of evidence are associated with a higher degree of corroboration (de Queiroz, 2007). This is consistent with the emerging general view that taxonomy needs to be pluralistic and integrate new approaches for species delimitation (e.g. Dayrat, 2005; Bond & Stockman, 2008; Padial *et al*., 2010; Schlick-Steiner *et al*., 2010).

Species delimitation

The WP method is based on a haplotype phylogeny for a set of populations currently classified as a species (the focal species of the study) and as many species as possible that are closely related to this species. The method assumes a phylogeny of non-recombining mtDNA haplotypes of known locality and taxonomic designation. In addition, it assumes that 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 geographical areas from which the haplotypes are found. Species delimitation will depend on the relationship of the focal species to the other species [i.e. whether the focal species is exclusive *sensu* de Queiroz & Donoghue (1990) and subsequent authors] and on the general concordance between phylogeny and geography within the focal species. If the focal species is exclusive, the presence of significantly supported basal lineages (i.e. the oldest split or splits within a focal species) concordant with geography within the species is potential evidence of the absence of gene flow between these lineages (candidate species), and therefore suggests that the focal species may represent multiple species disguised by traditional taxonomy.

The WP method emphasizes the basal lineages that are concordant with geography as potentially distinct species because retained ancestral polymorphisms are most likely in populations that have split very recently (Neigel & Avise, 1986) and the problems of male-biased dispersal, female philopatry and coalescence of temporarily isolated populations are most likely to affect the more recent branches of the haplotype tree. Initially, the focal species of this study was *H. undulatus*. However, because the haplotypes of *H. undulatus* formed an exclusive group and were mainly distributed into lineages of identical subspecies designation, we subsequently added the subspecies of *H. undulatus* as focal species of the study.

The BS method is based on the cohesion species concept of Templeton (1989, 2001). In this concept, the boundaries of an evolutionary lineage are defined by the mechanisms that limit the action of gene flow, genetic drift and natural selection. These mechanisms fall into two major categories: genetic exchangeability and

ecological interchangeability. The first refers to the boundaries for gene flow (Templeton, Maskas & Cruzan, 2000). Individuals from different populations are genetically exchangeable if there is ample gene flow between populations (Crandall, 2000). The second refers to the ability of the descendants or genes of organisms to replace (through drift) or displace (through selection) the descendants or genes of other organisms in the lineage even if the lineage is not reproducing sexually (Templeton *et al*., 2000). Ecological interchangeability can be assessed by 'standard approaches' such as morphological differentiation or less conventional means such as niche-based distribution models. For a set of populations to qualify as a cohesion species they must be derived from a single evolutionary lineage and must be genetically exchangeable (GE) and/or ecologically interchangeable (EI) (Templeton, 2001).

Because several subspecies were previously recognized within *Holcosus undulatus* on the basis of their morphological differentiation, we evaluated the lineages within *H. undulatus* not only for the possibility of gene flow but also adaptive divergence potential (morphological differentiation) between them. For this, we relied on the traditional taxonomy of Hallowell (1860), Cope (1862) and Smith & Laufe (1946), and considered sister lineages to be morphologically differentiated if their populations belonged to different subspecies of *H. undulatus*. Evaluation of morphological differentiation between lineages also is important because recognizing mitochondrial introgression requires evaluating a mitochondrial gene tree against a nuclear background that identifies the participating taxa (nuclear loci or phenotypic differences that presumably have a nuclear basis; Smith, 1992).

Finally, we estimated genetic distances within and among lineages. Genetic distances among lineages have been used frequently to investigate species boundaries (e.g. Hebert *et al*., 2003, 2004; Lefébure *et al*., 2006; Zemlak *et al*., 2009). Although there is not a threshold to separate ranges of intra- and interspecific divergence, comparing genetic distances within and among clades may provide a clue on the divergence level of two clades and support species hypotheses.

RESULTS

Mitochondrial data

The mitochondrial dataset included 137 sequences of *H. undulatus* and 27 of the other taxa included in the analysis: *Ameiva ameiva* (4), *H. festivus* (3), *H. quadrilineatus* (1), West Indian *Ameiva* (13), *Aspidoscelis* (3) and *Leposoma parietale* (1). The dataset consisted of 1044 unambiguously aligned nucleotide positions corresponding to the ND2 gene and 137 corresponding to the adjacent tRNATrp and tRNAAla genes. There were only two indels in the tRNA regions, and no indels or stop codons in the ND2 region. Sequence nucleotide composition showed the typical negatively skewed proportion of guanine of mitochondrial genes (T = 24.0, C = 27.1, A = 39.2, G = 9.7).

Partitioning the dataset into four partitions (one for each ND2 codon position and one for the combined tRNAs) yielded the greatest improvement of mean $-\ln L$ (Table S3). All Bayesian analyses reached stationarity and convergence before 1×10^7 generations.

The MCC tree for the Middle American species of *Holcosus* and representatives of other teiid genera is shown in Figure S1. The haplotypes of *H. undulatus*, *H. festivus*, *A. ameiva*, West Indian *Ameiva* and *Aspidoscelis* all formed significantly supported clades, and *H. quadrilineatus* was significantly supported as sister taxon to the *H. undulatus* clade. Our results suggest that *Ameiva* is paraphyletic with respect to *Aspidoscelis* and do not support the monophyly of *Holcosus*. However, the relationships among the *H. festivus*, (*H. quadrilineatus* + *H. undulatus*) and (*Ameiva* + *Aspidoscelis*) clades were not significantly supported. The above main clades and the significantly supported relationships among them also were significantly supported in the ML tree (data not shown).

The MCC tree for the *Holcosus undulatus* clade showed a pronounced population structure that was strongly concordant with geography at both deep and shallow levels. The clade was composed of six significantly supported clades in both the Bayesian and the ML analyses (Fig. 2). These clades were concordant with geography, allopatric or parapatric, and intermediately to moderately highly divergent from each other (p = 7.4–11.4). Their geographical distributions are shown in Figure 3. Of the six clades, two were geographically distributed on the Pacific versant of Mexico west of the Isthmus of Tehuantepec. One clade was composed of two significantly supported subclades: one with all of the haplotypes of *H. u. dexter* from the Pacific versant of north-western Guerrero (hereafter the north-western *H. u. dexter* lineage), and the other one with all of the haplotypes of *H. u. sinister*. The latter haplotypes were grouped into three significantly supported subclades concordant with geography; however, the relationships among these subclades were not significantly supported. The other clade was composed of all of the haplotypes of *H. u. dexter* from the Pacific versant of south-eastern Guerrero and south-western Oaxaca (hereafter the south-eastern *H. u. dexter* lineage) and a nested, significantly supported clade with all of the haplotypes of *H. u. undulatus*.

Two clades were geographically distributed on the Atlantic versant of Mexico. One was composed of two large, but not significantly supported subclades: one with all of the haplotypes of *H. u. amphigrammus* and the other one with all of the haplotypes of *H. u.*

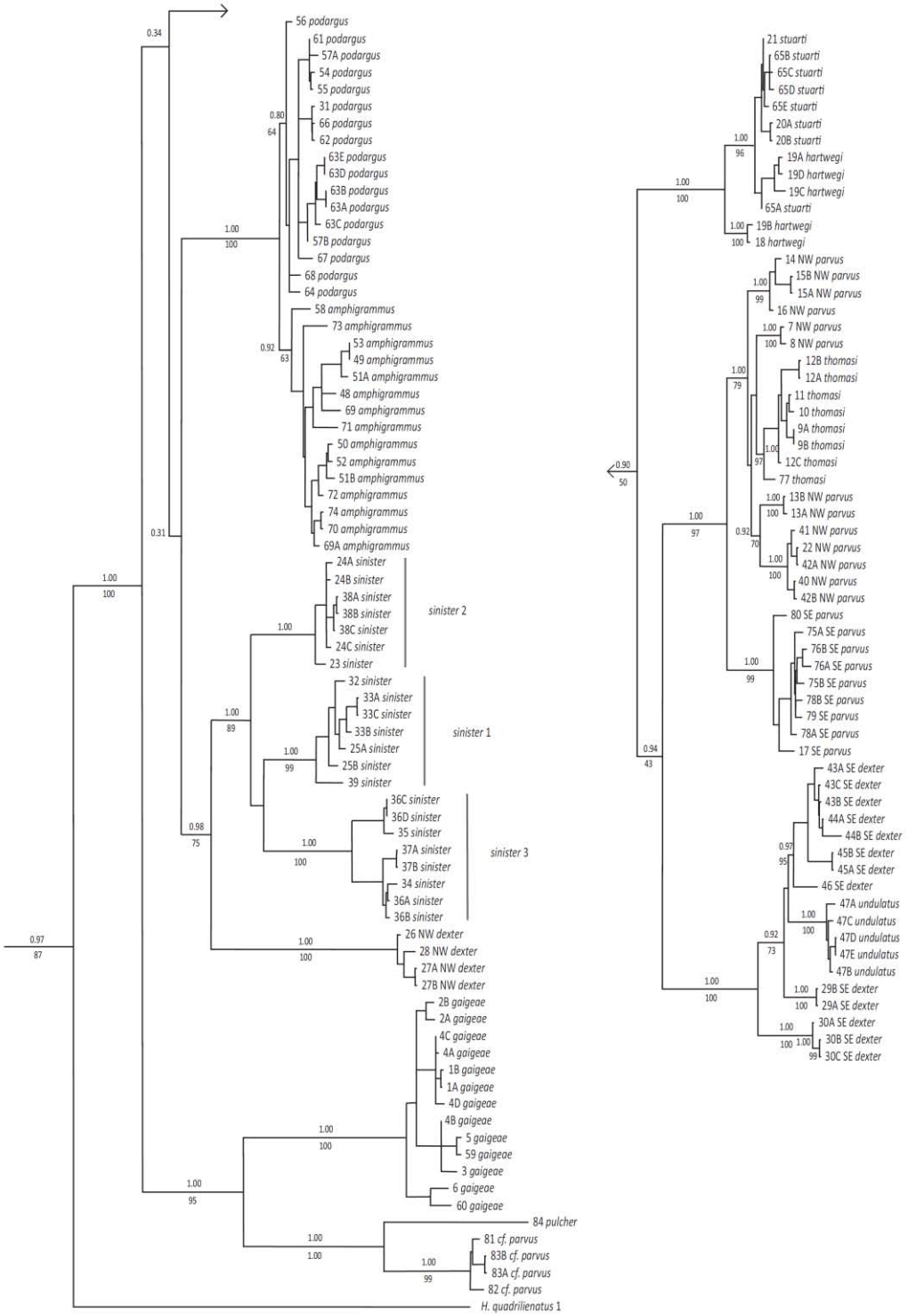

Figure 2. Bayesian MCC tree of *H. undulatus* based on a partitioned analysis of the mitochondrial dataset. Outgroups are not shown. Numbers next to branches indicate posterior probability/bootstrap support values.

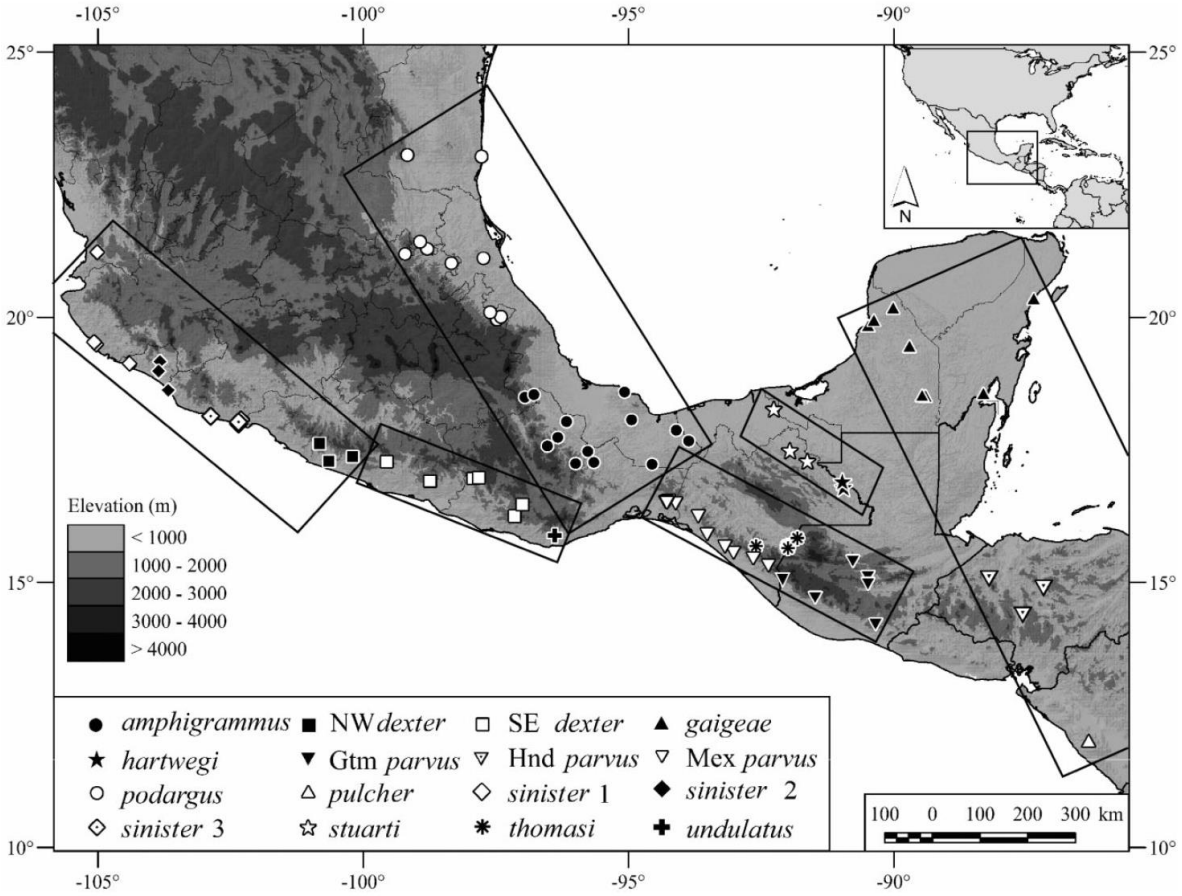

Figure 3. Geographical distribution of the six major, significantly supported haplotype clades identified in the Bayesian and ML phylogenetic analyses of the mitochondrial genes.

podargus. The other clade was composed of all of the haplotypes of *H. u. hartwegi* and *H. u. stuarti*. However, these subspecies were not exclusive with respect to each other.

One clade was geographically distributed mostly on the Pacific versant of Mexico east of the Isthmus of Tehuantepec and Guatemala, but it also included some haplotypes from central Guatemala. This clade was composed of all the haplotypes of *H. u. parvus* from Mexico and Guatemala and a nested, significantly supported clade with all the haplotypes of *H. u. thomasi*.

The last clade was geographically distributed on the Atlantic versant of Mexico (the Peninsula of Yucatán) and Honduras, and the Pacific versant of Nicaragua. This clade was composed of two significantly supported subclades: one with all the haplotypes of *H. u. gaigeae*, and another one with the only haplotype of *H. u. pulcher* as sister to a significantly supported clade with all the haplotypes of *H. u. parvus* from Honduras (hereafter the Honduran *H. u. parvus* lineage).

The relationships among the above six major clades were not significantly supported, although the (Mexican *H. u. parvus* + *H. u. thomasi*) clade was only marginally not significantly supported as sister to the (southeastern *H. u. dexter* + *H. u. undulatus*) clade in the Bayesian analysis (PP = 0.94).

Thus, *H. u. gaigeae*, *H. u. sinister*, *H. u. thomasi* and *H. u. undulatus* were all significantly supported as exclusive lineages concordant with geography, whereas *H. u. amphigrammus* and *H. u. podargus* also were exclusive and concordant with geography, but were not significantly supported. In contrast, the haplotypes of *H. u. dexter* were not exclusive but formed two separate, significantly supported lineages concordant with geography, and one of them was non-exclusive with respect to *H. u. undulatus*. Similarly, the haplotypes of *H. u. parvus* were not exclusive but formed two separate, significantly supported lineages concordant with geography, and one of them was non-exclusive with respect to *H. u. thomasi*. Finally, the combined

Table 3. Genetic divergences (A) among the six significantly supported, major mitochondrial clades of *Holcosus undulatus*, and (B) between lineages within the clades

Clade		1	2	3	4	5	6
A							
1	Gtm *H. u. parvus* + (Mex *H. u. parvus* + *H. u. thomasi*)						
2	SE *H. u. dexter* + *H. u. undulatus*	8.2					
3	*H. u. stuarti* + *H. u. hartwegi*	7.4	8.1				
4	*H. u. amphigrammus* + *H. u. podargus*	7.9	8.8	7.8			
5	NW *H. u. dexter* + *H. u. sinister*	9.1	9.8	8.9	8.2		
6	*H. u. gaigeae* + (Hnd *H. u. parvus* + *H. u. pulcher*)	10.7	11.1	11.2	10.2	11.4	
7	*H. quadrilineatus*	16.1	17.0	16.2	15.6	15.9	16.8
B							
	Gtm *H. u. parvus* – (Mex *H. u. parvus* + *H. u. thomasi*)	4					
	• Mex *H. u. parvus* – *H. u. thomasi*	2.2					
	SE *H. u. dexter* – *H. u. undulatus*	3.2					
	H. u. amphigrammus – *H. u. podargus*	1.7					
	NW *H. u. dexter* – *H. u. sinister*	9					
	• *H. u. sinister* 1 – *H. u. sinister* 2 – *H. u. sinister* 3 (average)	5.9					
	H. u. gaigeae – (Hnd *H. u. parvus* + *H. u. pulcher*)	12					
	• Hnd *H. u. parvus* – *H. u. pulcher*	8.4					

haplotypes of *H. u. hartwegi* and *H. u. stuarti* comprised a significantly supported clade concordant with geography, but were not mutually exclusive. Because only one sample of *H. u. pulcher* was available, the exclusivity of this subspecies could not be evaluated.

The ML tree (not shown) was similar to the Bayesian tree, except that the *H. u. podargus* clade and all of the relationships among the six significantly supported major clades were not significantly supported.

Genetic divergences (uncorrected p-distances, expressed as percentages; Table 3) within the significantly supported, major clades were moderately high between north-western *H. u. dexter* and *H. u. sinister* (9.0), *H. u. pulcher* and Honduran *H. u. parvus* (8.4), and (*H. u. pulcher* + Honduran *H. u. parvus*) and *H. u. gaigeae* (12.0); intermediate among the *H. u. sinister* subclades (5.9); moderate between south-eastern *H. u. dexter* and *H. u. undulatus* (3.0) and Mexican and Guatemalan *H. u. parvus* (4.0); and low between *H. u. amphigrammus* and *H. u. podargus* (1.7).

Nuclear data

The RPS8 and α-cardiac actin datasets consisted of approximately 511 and 561 unambiguously aligned nucleotide positions, respectively. Individual nuclear gene trees showed less resolution and much weaker support than the trees from the mitochondrial dataset (Figs S2, S3). Of the significantly supported mitochondrial lineages included and represented by more than one sample, only the *H. u. gaigeae* and *H. u. podargus* lineages were recovered in both the Bayesian and the ML analyses of RPS8; and of these, only the *H. u. gaigeae* lineage was significantly supported in both analyses. Similarly, only the Honduran *H. u. parvus* and *H. u. sinister* lineages were recovered in the Bayesian and ML analyses of α-cardiac actin; and of these, only the Honduran *H. u. parvus* lineage was significantly supported in the ML (but not the Bayesian) analysis. In addition, the *H. u. stuarti* samples were significantly supported as exclusive and a clade composed of one of the Guatemalan *H. u. parvus*, the two Honduran *H. u. parvus*, and the *H. u. hartwegi* samples was significantly supported in both the Bayesian and the ML analyses of RPS8. None of the six major clades in the mitochondrial tree was recovered. Most importantly, however, the nuclear markers did not contradict the relationships recovered by the mitochondrial marker.

Species tree

The coalescent-based species tree is shown in Figure 4. The tree was fully resolved but differed from the mitochondrial tree mainly in that: (1) the (*H. u. podargus* + *H. u. amphigrammus*) and (*H. u. stuarti* + *H. u. hartwegi*) clades were significantly supported and marginally not significantly supported (PP = 0.91), respectively; and (2) it recovered all of the major, significantly supported mitochondrial clades except for the (*H. u. gaigeae* + Honduran *H. u. parvus*) clade. In the species tree, the Honduran *H. u. parvus* and *H. u. gaigeae* were the most and second-most closely related species, respectively, to the (Mexican–Guatemalan *H. u. parvus* + *H. u. thomasi*) clade, although these relationships were not significantly

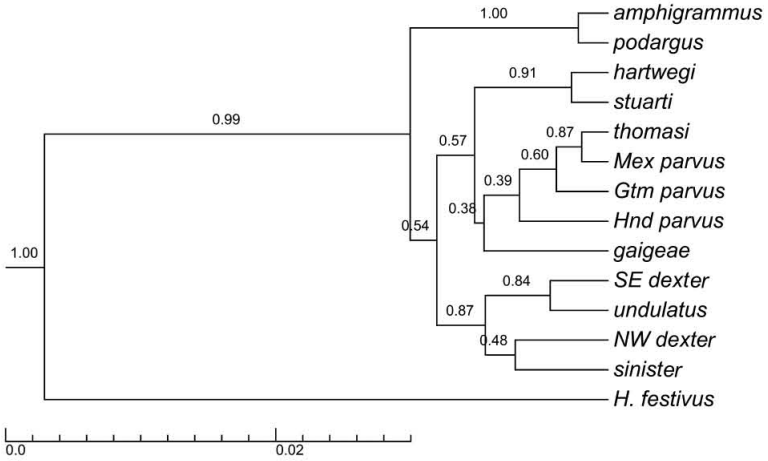

Figure 4. Bayesian MCC species tree of *H. undulatus* inferred by simultaneous gene tree and species tree analysis of the mitochondrial and nuclear genes with *BEAST. Numbers above the branches are posterior probabilities.

supported, and these five species were intermediately supported as the sister group to the (*H. u. hartwegi* + *H. u. stuarti*) clade. All of these species comprise a Central American group that is distributed from the Isthmus of Tehuantepec, Mexico, south and east (including the Yucatán Peninsula) to Nicaragua. This group was intermediately supported as sister to a relatively well-supported group composed of the (south-eastern *H. u. dexter* + *H. u. undulatus*) and (north-western *H. u. dexter* + *H. u. sinister*) clades, which is distributed on the Pacific versant of Mexico from Nayarit to the Isthmus of Tehuantepec in Oaxaca. Finally, the (*H. u. amphigrammus* + *H. u. podargus*) clade, from the Atlantic versant of Mexico west of the Isthmus of Tehuantepec, was significantly supported as sister to all of the other species.

Testing alternative phylogenetic hypotheses

The Bayesian approach to hypothesis testing showed that the alternative hypotheses of the exclusivity of *H. u. dexter* and *H. u. parvus* could be statistically rejected because the alternative sets of relationships were not present in the 95% set of credible trees. In contrast, the south-eastern *H. u. dexter* lineage was recovered as exclusive in 1317 out of 7121 trees in the 95% set of credible trees. Thus, the alternative hypothesis of the exclusivity of this group could not be statistically rejected.

DISCUSSION

Holcosus undulatus was significantly supported as an exclusive lineage distinct and highly divergent from all the other Middle American *Holcosus* in all the mtDNA analyses (see above). However, note that these analyses did not include *H. leptophrys* or *H. chaitzami*. Also, the haplotypes of *H. undulatus* were distributed into six significantly supported, major lineages (see above). All these lineages were concordant with geography, allopatric or parapatric, and highly divergent genetically from each other. The deep genetic structure of the *H. undulatus* populations in the mitochondrial tree and the distribution of the haplotypes predominantly into lineages of identical subspecific designation and concordant with geography suggest strongly that *H. undulatus* is a species complex diversified in Mexico and Central America, and that significant species diversity has been concealed in the genus. Below, we apply the WP and BS methods to the focal species of this study (*H. undulatus* and its subspecies), discuss phylogenetic relationships among the *H. undulatus* lineages and propose pertinent taxonomic changes.

In the WP method, the basal lineages of an exclusive focal species are considered as potentially distinct species if there is no gene flow between them, regardless of their geographical distribution. In the BS method, the daughter lineages of an exclusive focal species also are considered as potentially distinct species if they are allopatric and therefore no gene flow between them is possible (i.e. they are non-GE), whether they are EI or not. However, if there is no evidence of gene flow between the daughter lineages but they are parapatric (i.e. genealogical exchangeability cannot be ruled out), whether they are considered as potentially distinct species depends on the nature of the parapatry and the evidence of adaptive divergence: when the sister lineages are separated by a historical barrier to gene flow (i.e. 'significant' geographical or habitat breaks), they may be interpreted as distinct species

with niche conservation if they are EI, and as potentially distinct species if they are not. When the sister lineages are not separated by a historical barrier to gene flow, they are considered as a single cohesion species if they are EI, and as potentially distinct species if they are not.

Species limits within basal clades

(North-western H. u. dexter + H. u. sinister*) and (*H. u. gaigeae + *(Honduran* H. u. parvus + H. u. pulcher*)) clades*

In each of these clades, the daughter lineages corresponded to distinct subspecies and were significantly supported and concordant with geography. In the WP method, this suggests that the daughter lineages of each clade may represent distinct species. In addition, these lineages were allopatric (Figs 2, 3) and highly divergent genetically (p = 10.0–11.1 and 12.0%, respectively), which supports that suggestion. Furthermore, the subspecies *H. u. sinister* and *H. u. gaigeae* were exclusive. Similarly, in the BS method, the above evidence suggests that the daughter lineages of each basal clade are non-GE. Also, because of their adaptive divergence, they are non-EI (Table 2). Thus, the daughter lineages of each basal clade must be reset as emergent focal taxa.

In the (Honduran *H. u. parvus* + *H. u. pulcher*) emergent focal taxon, the daughter lineages also corresponded to distinct subspecies (if one of them was represented by a single haplotype), and the Honduran *H. u. parvus* lineage was significantly supported and concordant with geography. In addition, the Honduran *H. u. parvus* and *H. u. pulcher* haplotypes originated from distant areas on the Atlantic and Pacific versants of Honduras and Nicaragua, respectively, and were highly divergent from each other (p = 8.4). Thus, gene flow between these subspecies seems unlikely. In the WP method, this suggests that the Honduran *H. u. parvus* lineage and *H. u. pulcher* may represent distinct species; in the BS method, it suggests that they are non-GE and non-EI, and therefore the hypothesis of a single cohesion species for this clade must be rejected.

(South-eastern H. u. dexter + H. u. undulatus*) clade*

In this clade, the basal lineages were significantly supported, concordant with geography, and geographically disjunct. In the WP method, this suggests that the lineages may represent distinct species. However, there were large unsampled areas between their geographical distributions, and the basal-most clades were composed of few individuals from single localities. This suggests instead that the apparent absence of gene flow between the basal lineages is probably an artefact of insufficient sampling, and the basal lineages actually represent a single species.

By contrast, the haplotypes of *H. u. dexter* were not exclusive with respect to those of *H. u. undulatus*, which comprised a significantly supported, exclusive lineage concordant with geography. In the WP method, if there is gene flow between the basal lineages of a focal species, and if the haplotypes of the focal species are not exclusive with respect to the haplotypes of a second species that is distinct and exclusive, then the focal species may represent a single non-exclusive species. Therefore, the south-eastern *H. u. dexter* and *H. u. undulatus* lineages may represent distinct species, even though they were only slightly divergent from each other (p = 3.2). However, our sampling of both *H. u. undulatus* and the area of intergradation between *H. u. dexter* and *H. u. undulatus* in south-central Oaxaca (Smith & Laufe, 1946; Fig. 1) was considerably limited; in fact, our sample of *H. u. undulatus* came from a single locality in the latter area. Thus, additional sampling is needed to conclusively corroborate the existence of two distinct species in this basal clade. For the time being, we conservatively treat this basal clade as a single species (*H. undulatus*, because of the law of priority).

In the BS method, the daughter lineages of this basal clade were concordant with geography and appeared to be geographically disjunct, which suggests they are non-GE. However, one of the lineages was not significantly supported in the Bayesian analysis, and the other was composed of samples from a single locality. Also, the area between their geographical distributions was not sampled. Thus, we consider the daughter lineages to be actually GE. In addition, the populations of *H. u. dexter* in both daughter lineages lacked adaptive divergence. Thus, these populations are EI, and should be treated as a single cohesion species. The low genetic divergence between the daughter lineages supports this suggestion. In addition, the above evidence suggests that the *H. u. undulatus* lineage is both non-GE and non-EI with the *H. u. dexter* lineage, and it may represent a separate cohesion species even though is only slightly divergent genetically from it (but see our reservations above).

(Mexican–Guatemalan H. u. parvus + H. u. thomasi*) clade*

In this clade, the basal lineages were significantly supported and concordant with geography, even though they were parapatric in extreme south-eastern Chiapas and represented by relatively numerous samples (Figs 2, 3). In the WP method, this suggests the absence of gene flow between the daughter lineages and therefore that they may represent two distinct, independent evolutionary lineages, although they were only slightly divergent from each other (p = 4.0): one composed of the populations of *H. u. parvus* from Guatemala and the Tacaná volcano in extreme south-eastern Chiapas

(hereafter the Guatemalan *H. u. parvus* lineage), and the other one composed of the remaining populations of *H. u. parvus* from Mexico (hereafter the Mexican *H. u. parvus* lineage) and the populations of *H. u. thomasi*.

In the (Mexican *H. u. parvus* + *H. u. thomasi*) subclade, the basal lineages were neither consistently significantly supported nor concordant with geography, which suggests they represent the same evolutionary species. However, the haplotypes of *H. u. parvus* were not exclusive with respect to those of *H. u. thomasi*, which comprised a significantly supported, exclusive lineage concordant with geography. In the WP method, this suggests that the Mexican *H. u. parvus* and *H. u. thomasi* lineages may represent distinct species (see above), even though they were only slightly divergent genetically from each other (p = 2.1–2.2). This suggestion is supported by the relatively extensive sampling of both lineages and their geographical isolation by the highlands of the Sierra Madre de Chiapas and western portion of the Central Depression of Chiapas (Figs 1, 3).

In the BS method, the above evidence suggests the absence of gene flow between the daughter lineages of this basal clade. However, because the daughter lineages are parapatric in the absence of major geographical or habitat breaks, they are potentially GE, and considerable weight is placed on evidence of adaptive divergence. Because the populations of *H. u. parvus* in both daughter lineages lacked adaptive divergence, they are EI, and should be treated as a single cohesion species. Genetic divergence between the daughter lineages was low (≤ 4.0). In addition, the above evidence suggests that the *H. u. thomasi* lineage is both non-GE and non-EI with the *H. u. parvus* lineage, and it may represent a separate cohesion species even though it is only slightly divergent genetically from it (see above).

*(*Holcosus u. amphigrammus + H. u. podargus*) clade*

In this clade, the daughter lineages corresponded to distinct subspecies, both of which were concordant with geography and were exclusive. In the WP method, this suggests the absence of gene flow between the *H. u. amphigrammus* and *H. u. podargus* lineages, and therefore that they may represent distinct species. However, these lineages were not significantly supported, and were only slightly divergent genetically from each other (p = 1.7).

Although Smith & Laufe (1946) stated that *H. u. amphigrammus* and *H. u. podargus* intergrade in northern Veracruz, our field work showed that their geographical distributions actually meet at the eastern end of the Mexican Transvolcanic Belt in central Veracruz. A division of the Gulf Coastal Plain into northern and southern portions at central Veracruz has been documented in other groups such as toads (Mulcahy & Mendelson, 2000), frogs (Zaldívar-Riverón, León-Regagnon & Nieto-Montes de Oca, 2004), and reptiles and mammals (Pérez-Higareda & Navarro, 1980). This phylogeographical break has been explained by the repeated inundation of the coastal floodplain resulting from rising and lowering sea levels throughout much of the Pleistocene (Beard, Sangree & Smith, 1982). In the BS method, because there was no evidence of gene flow between the daughter lineages of the basal clade and because the lineages appeared to be parapatric but separated by a phylogeographical break, they are considered to be non-GE. Also, because of their adaptive divergence, the daughter lineages are non-EI, and thus the hypothesis of a single species should be rejected, and these subspecies reset as emergent focal taxa.

It has been argued that poorly supported clades are unreliable because they may have been recovered by chance if their sample size is small (Erixon *et al.*, 2003). However, sample size for both *H. u. amphigrammus* and *H. u. podargus* was rather large (15 and 17 haplotypes, respectively). This suggests that the concordance with geography of the *H. u. amphigrammus* and *H. u. podargus* lineages actually reflects reduced or absent gene flow between them, and that their weak support and low divergence might be explained by causes such as a recent origin or introgressive hybridization from *H. u. amphigrammus* into *H. u. podargus* followed by a complete replacement sweep across its entire distribution (Funk & Omland, 2003; Rheindt & Edwards, 2011). However, until further data corroborate that *H. u. amphigrammus* and *H. u. podargus* are distinct species, we prefer to treat this basal clade as a single species.

*(*Holcosus u. hartwegi + H. u. stuarti*) clade*

In this clade, although both daughter lineages were significantly supported, they were not concordant with geography (i.e. both the haplotypes of *H. u. hartwegi* and *H. u. stuarti* from a given locality failed to cluster together; Figs 2, 3), which is potential evidence for gene flow with other populations. Thus, although the clade was composed of haplotypes of two distinct subspecies, they were not exclusive with respect to each other. In the WP method, this suggests that these taxa represent a single species. Similarly, in the BS method, because the daughter lineages of this basal clade were not concordant with geography or taxonomic designation, they may be considered to be both GE and EI. This suggests that the hypothesis of a single cohesion species cannot be rejected.

However, *H. u. hartwegi* and *H. u. stuarti* differ in body length, size and arrangement of gular scales, numbers of femoral pores and lamellae under the fourth toe, and dorsolateral colour pattern (Smith & Laufe, 1946; Table 2). In fact, Smith & Laufe (1946: 22)

regarded *H. u. stuarti* to be so widely different from *H. u. hartwegi* (and *H. u. gaigeae*) that 'it might well be considered a member of a different species'. Smith & Laufe (1946) also stated that *H. u. hartwegi* and *H. u. stuarti* occur in close geographical proximity, but that no incontrovertible intergrades between the two were known. Furthermore, there appears to be a sharp difference in ecological preference: *H. u. hartwegi* occurs in dense, high inland forest, whereas *H. u. stuarti* inhabits mixed scrub-savanna coastal areas (Smith & Laufe, 1946). Thus, the morphological and ecological evidence suggests strongly that *H. u. hartwegi* and *H. u. stuarti* are distinct species.

However, *H. u. hartwegi* and *H. u. stuarti* were not mutually exclusive in their haplotype phylogeny. This pattern might be explained by incomplete lineage sorting if *H. u. hartwegi* and *H. u. stuarti* actually were sister species that have diverged recently. However, this seems unlikely given the morphological divergence between them. Current gene flow also seems unlikely, as there is no evidence of morphological intermediates (Smith & Laufe, 1946). Another possible explanation for the non-exclusivity of *H. u. stuarti* and *H. u. hartwegi* is introgressive hybridization, as they share similar mtDNA haplotypes but are otherwise divergent species (Funk & Omland, 2003).

An alternative scenario for Holcosus undulatus dexter

The above discussion assumed that the non-monophyly of *H. u. dexter* is explained by imperfect taxonomy (Funk & Omland, 2003), i.e. that the north-western *H. u. dexter* lineage actually represents a cryptic species morphologically similar to, yet distinct from, true *H. u. dexter*. However, we did not find evident morphological differences between the two *H. u. dexter* lineages despite the high genetic divergence between them. Also, it seems odd that such apparently distantly related lineages should be morphologically identical and parapatric.

An alternative explanation is that one of the lineages of *H. u. dexter* does not actually correspond to the native mitochondrial genome of *H. u. dexter* but represents the captured mitochondrial genome of some other lineage. The haplotypes of the south-eastern *H. u. dexter* and *H. u. undulatus* lineages are only slightly divergent from each other, and these two subspecies were reported to intergrade in south-central Oaxaca (Smith & Laufe, 1946). This suggests that the south-eastern *H. u. dexter* lineage might actually represent the captured mitochondrial genome of *H. u. undulatus* (if the latter subspecies actually is distinct from *H. u. dexter*, see above). The north-western *H. u. dexter* lineage is highly divergent from *H. u. sinister* and geographically isolated from it by the Balsas River Basin (Smith & Laufe, 1946); thus, introgressive hybridization from *H. u. sinister* into the north-western *H. u. dexter* lineage seems less likely. Under this scenario, the two mitochondrial lineages of *H. u. dexter* would represent one and the same geographically continuous, morphologically homogeneous lineage that has been introgressed by *H. u. undulatus* over most of its geographical distribution.

A similar scenario could be conceived as an alternative explanation for the non-monophyly of *H. u. parvus*. However, the high genetic distances between the Honduran *H. u. parvus* lineage and its most closely related subspecies in the mitochondrial tree, *H. u. gaigeae* and *H. u. pulcher* (p = 10.7–13.3), do not support this hypothesis.

Species limits at lower levels

The WP method emphasizes the basal lineages of a focal species as potentially distinct species. However, because it is possible that each of these lineages might contain multiple species, it uses the same reasoning to detect such cases. Similarly, in the BS method, the emergent focal taxa are evaluated in the same manner as the basal taxa, and evaluation progresses through the tree towards the tips, until the daughters are determined to be a single cohesion species. This is important because emphasizing only the basal lineages within the focal species might overlook those taxa that represent the most recent adaptations to a changing environment and may be important sources of future evolutionary potential (Wang *et al*., 2008). However, at these progressively lower levels, small sample sizes may limit our ability to confidently rule out gene flow with other lineages.

In this study, sampling of most of the lineages identified as potentially distinct species within the basal clades, as well as the potential areas of contact between the geographical distributions of these lineages, was generally not extensive. Thus, within most of those lineages, the haplotypes generally did not form significantly supported subclades concordant with geography, or, if they did, there were relatively large unsampled areas among their distributions. Also, the populations of each of the potential species were morphologically homogeneous, and their haplotypes only slightly divergent from each other. Thus, the available evidence suggests that all of these lineages each represent a single species. The only clear exception is the *H. u. sinister* lineage.

The three *Holcosus undulatus sinister* lineages were significantly supported, concordant with geography, allopatric or parapatric, and intermediately divergent from each other (p = 4.8–6.4%). Furthermore, in males and females of the *H. u. sinister* 1 and *H. u. sinister* 3 lineages the throat was consistently orange, whereas in males and females of the geographically

intermediate *H. u. sinister* 2 lineage the throat was consistently yellow. This suggests that each lineage may represent a separate species. This is supported by the moderately high genetic divergences and apparently fixed throat colour differences among them. However, throat colour polymorphism is well known to occur in several populations of *H. undulatus* (Echternacht, 1971).

Comparison of used methods

The WP and BS methods differ in the species properties that they use for species delimitation. In the WP method, the basal lineages of a focal species are considered as potentially distinct species if there is no evidence of gene flow between them, regardless of their geographical distribution. In contrast, in the BS method non-GE sister lineages that are parapatric but not separated by a 'significant' geographical or habitat break are not considered as potentially distinct species unless they show evidence of adaptive divergence potential (i.e. they are non-EI). This is because genealogies are influenced by chance in the form of genetic drift. Therefore, phylogeographical breaks in a continuously distributed species might develop in the absence of geographical barriers as a result of stochastic causes, if the average individual dispersal distances and/or population size of the species are low (Irwin, 2002).

Bond & Stockman (2008) used the spiders of the *Aptostichus atomarius* complex as their model system. These spiders are fossorial, sedentary, sit-and-wait predators prone to extreme population structuring (see Bond *et al.*, 2001, 2006; Arnedo & Ferrández, 2007; Starrett & Hedin, 2007). Unlike Bond & Stockman's (2008) model system, most teiids (including *Holcosus*) are good runners and active wide-ranging foragers. These characteristics may hinder the formation of deep phylogeographical breaks as a result of stochastic causes. Additionally, genetic structure in *H. undulatus* did not extend to the tips of the mtDNA tree. Except for the *H. u. sinister* lineage, the basal lineages were moderately to intermediately genetically structured. If small female dispersal distances were the general cause for genetic structure in *H. undulatus*, we would expect that those lineages were structured too, especially if they have wide geographical distributions.

We argue that, rather than being the result of stochastic causes, deep genetic structure in the absence of extrinsic barriers to gene flow in *H. undulatus* probably indicates that some intrinsic reproductive isolation is operating. Therefore, as long as they are well sampled, significantly supported sister lineages concordant with geography and highly divergent in the mtDNA tree probably represent reproductively isolated, evolutionary independent lineages, even in the absence of geographical barriers and adaptive divergence.

Phylogeny

The six major mitochondrial clades were significantly supported in both the Bayesian and the ML analyses, and were also recovered (although most not significantly supported) in the species tree, except for the (*H. u. gaigeae* + Honduran *H. u. parvus*) clade. However, the phylogenetic relationships among the major clades within *H. undulatus* remain poorly resolved.

By contrast, the sister taxa relationship between the daughter lineages of each of the major clades seems highly probable on the basis of their morphology and geographical distribution, except for *H. u. stuarti* and *H. u. hartwegi*, whose actual position in the tree is uncertain, as their relationships are probably obscured by ancestral gene flow. In the species tree, the ((south-eastern *H. u. dexter* + *H. u. undulatus*) + (north-western *H. u. dexter* + *H. u. sinister*)) clade, which is distributed on the Pacific versant of Mexico west of the Isthmus of Tehuantepec, is not only geographically congruent but also contains only those species having one row of preanals (Smith & Laufe, 1946). Similarly, the (((Honduran *H. u. parvus* + (Guatemalan *H. u. parvus* + (Mexican *H. u. parvus* + *H. u. thomasi*))) clade is distributed east of the Isthmus of Tehuantepec, and contains those taxa sharing two rows of preanals and abruptly enlarged median gulars arranged in a single longitudinal row (Smith & Laufe, 1946). Therefore, it can be expected that further data will support these relationships.

Taxonomic conclusions

Our results suggest that, at least, the following lineages should be recognized as distinct evolutionary species:

(*H. u. amphigrammus* + *H. u. podargus*) = *H. amphigrammus*
H. u. gaigeae = *H. gaigeae*
H. u. hartwegi = *H. hartwegi*
(Guatemalan–Mexican *H. u. parvus*) = *H. parvus*
H. u. sinister = *H. sinister*
H. u. stuarti = *H. stuarti*
H. u. thomasi = *H. thomasi*
(South-eastern *H. u. dexter* + *H. u. undulatus*) = *H. undulatus*

However, note that (1) the (*H. u. amphigrammus* + *H. u. podargus*), Guatemalan–Mexican *H. parvus*, and (south-eastern *H. u. dexter* + *H. u. undulatus*) lineages could each be composed of two distinct species; and (2) *Holcosus hartwegi* and *H. stuarti* are recognized on morphological and ecological grounds, and the apparent gene flow between them is attributed to introgressive hybridization.

In addition, the north-western *H. u. dexter* and Honduran *H. u. parvus* lineages may represent cryptic, yet distinct, independent species, provided that the non-monophly of *H. u. dexter* and *H. u. parvus* in the mitochondrial tree is explained by imperfect taxonomy. Further research on the systematics of these two taxa is needed to identify the cause of their non-monophyly and, if appropriate, formally describe the potentially undescribed species. Further research may also uncover additional species within the *H. u. sinister* lineage. Several approaches are available for delimiting species using coalescent techniques (Fujita *et al*., 2012), but the most robust methods rely on the availability of data for several independent loci. Future research with multilocus data, analysed under a coalescent approach, will be decisive for elucidating the species boundaries within *H. dexter*, *H. sinister* and *H. parvus*.

The above conclusions have implications for the status of *H. u. miadis* and *H. u. pulcher*. Evidently, it is realistically not possible that these two subspecies are conspecific with *H. undulatus*. Thus, their status should depend on whether they are distinct from the species identified herein and from each other. We could not include *H. u. miadis* in our analysis. However, this subspecies, known only from Corn Islands, Nicaragua, is allopatric with respect to the other subspecies of *H. undulatus*, and can be distinguished from these subspecies on the basis of its unique colour pattern and several other morphological characters (Echternacht, 1970, 1971). Thus, we also consider *H. u. miadis* to represent a distinct species endemic to Corn Islands. Similarly, both the WP and the BS methods suggest that *H. u. pulcher* may represent a distinct species, although this needs corroboration through additional sampling.

This work has significant implications for the conservation of Mexican and Central American *Holcosus*. Currently, *H. undulatus* is perceived as a common, widely distributed, single species with no conservation problems. Nonetheless, our study indicates that several of its once recognized subspecies actually represent distinct, independent evolutionary species, and therefore the number of species of Mexican and Central American *Holcosus* has been severely underestimated. Evidently, these species have more restricted geographical distributions and their own biological and ecological properties, and their conservation status and extinction risk should be assessed separately. Thus, the basic knowledge of their existence is essential for their conservation.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Figure S1. The inter-relationships of selected lineages of Teiidae, including the phylogenetic placement of *H. undulatus*, inferred by a partitioned Bayesian analysis of the mitochondrial genes. The tree is an MCC tree. Numbers next to branches indicate posterior probability/bootstrap support values.

Figure S2. Bayesian MCC tree of *H. undulatus* based on an analysis of the nuclear marker RPS8. Numbers next to branches indicate posterior probability/bootstrap support values.

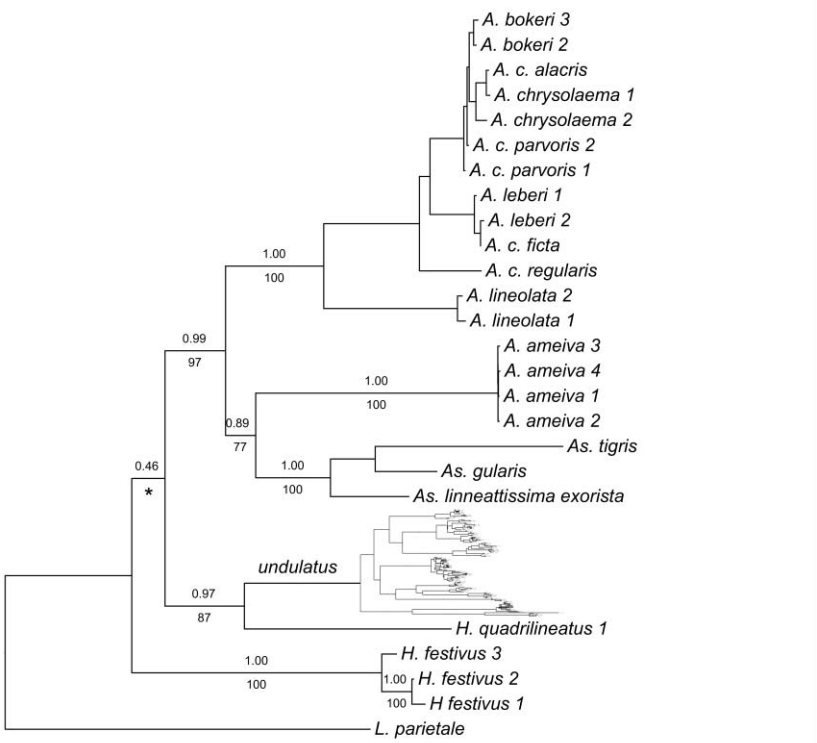
Figure S3. Bayesian MCC tree of *H. undulatus* based on an analysis of the nuclear marker α-cardiac-actin. Outgroups are not shown. Numbers next to branches indicate posterior probability/bootstrap support values.

Table S1. Taxonomic designation, ID, voucher number, locality and GenBank accession numbers for the DNA sequences used in this study. Acronyms for specimen numbers are either scientific collection acronyms (CAS, MVZ, MZFC, UTA) listed in Sabaj-Pérez (2014), field numbers for specimens to be catalogued in the MZFC (AMH, ANMO, ART, DHL, IDF, ISZ, JAC, JCBH, JLAL, JRM, LCM, LNG, LMOO, NLMM, UOGV) or the UTA (MSM) collections, or field numbers assigned to sequences downloaded from Genbank (ALS, BWMC). CR, Costa Rica; Dom Rep, Dominican Republic; Gtm, Guatemala; Hnd, Honduras; Mex, Mexico; Nic, Nicaragua; Sur, Surinam; USA, United States of America.

Table S2. Primers used in study.

Table S3. Partition strategies, harmonic mean of the likelihood values of the MCMC samples, and GTR submodels with the highest posterior probability (the submodels represented by six numbers specify different substitution rates in the order r_{AC}; r_{AG}; r_{AT}; r_{CG}; r_{CT}; r_{GT}).

SUPPORTING INFORMATION



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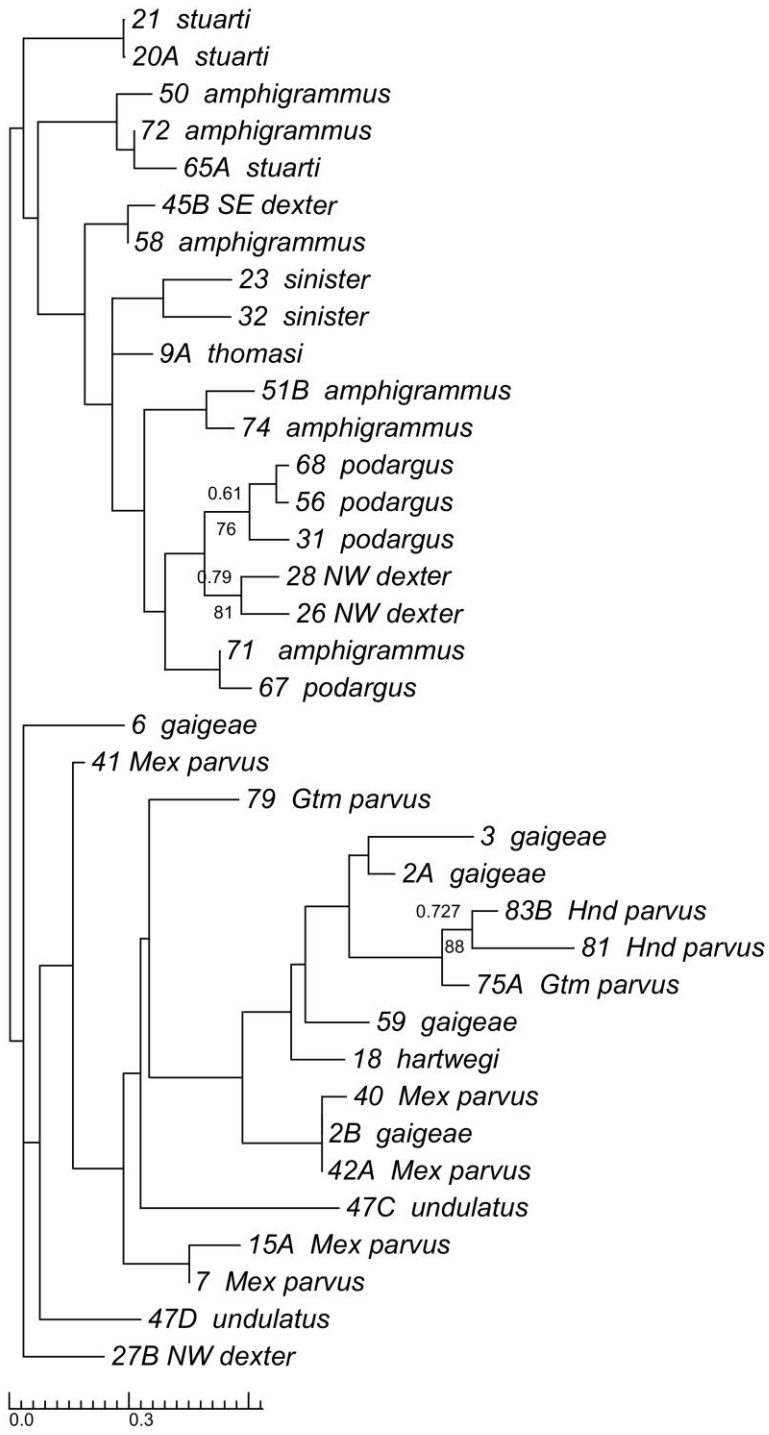

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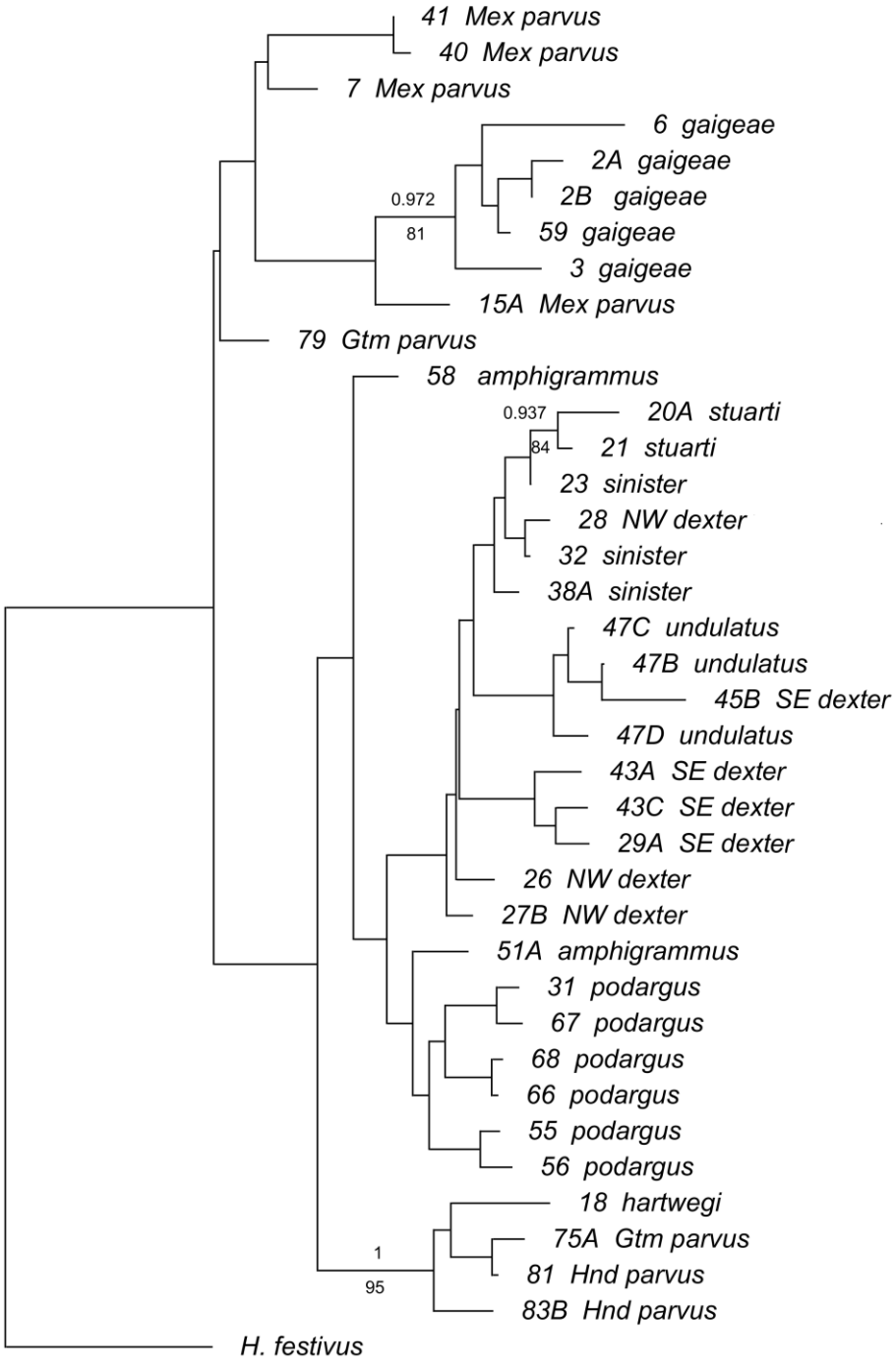

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SUPPORTING INFORMATION

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Taxon	ID	Specimen		Locality	Country	Latitude	Longitude	ND2	RPS8	actine
H. festivus	*H. festivus 1*	MVZ	207357	San José: Moravia	CR			KR058105		
H. festivus	*H. festivus 2*	MVZ	207358	San José: Moravia	CR			KR058106		
H. festivus	*H. festivus 3*	LNG	50	Chiapas: Ocosingo, Tres Lagunas	Mex	16.84277	-91.14552	KR058107	KR058136	
H. quadrilineatus	*H. quadrilineatus*	MVZ	149853	Limón: Tortuguero	CR			KR058019		
H. u. amphigrammus	48	AMH	--	Oaxaca: San Juan Cotzocón, 3 km W of Santa María Asunción Puxmetacán	Mex	17.26193	-95.65324	KR057967		
H. u. amphigrammus	49	ANMO	2268	Oaxaca: Valle Nacional, Los Cantiles, 5 km S of San Mateo Yetla	Mex	17.731861	-96.3313333	KR057968		
H. u. amphigrammus	50	JAC	21592	Oaxaca: Distrito Mixe, Zacatepec - Jesús Carranza road	Mex	17.239969	-95.9972861	KR058043		KR058167
H. u. amphigrammus	52	UOGV	1747	Oaxaca: San Juan Lalana, 10 km N of Santiago Jalahuy	Mex	17.468917	-95.76625	KR058056		
H. u. amphigrammus	53	UOGV	1748	Oaxaca: Santiago Comaltepec, Metates - La Esperanza road	Mex	17.569606	-96.5293722	KR058058		
H. u. amphigrammus	58	JLAL	324	Puebla: Eloxochitlán	Mex	18.486978	-96.9546639	KR058090		KR058170
H. u. amphigrammus	70	ANMO	1820	Veracruz: Las Choapas	Mex	17.86575	-94.0995833	KR057966		
H. u. amphigrammus	71	UOGV	655	Veracruz: Las Choapas: Las Choapas - Tuxtla Gutiérrez road	Mex	17.663639	-93.8630833	KR058044		
H. u. amphigrammus	72	UOGV	903	Veracruz: Tezonapa, Ejido Rancho Nuevo	Mex	18.538139	-96.7830278	KR058047		
H. u. amphigrammus	73	UOGV	1917	Veracruz: Uxpanapa, Ejido Pancho Villa	Mex	17.225167	-94.5543056	KR058045		
H. u. amphigrammus	74	UOGV	1954	Veracruz: San Andrés Tuxtla, Los Tuxtlas Biology Station	Mex	18.586783	-95.0731417	KR057965		KR058178
H. u. amphigrammus	51A	UOGV	1733	Oaxaca: San Juan Bautista Tuxtepec, Tuxtepec	Mex	18.025278	-96.1669167	KR058057		
H. u. amphigrammus	51B	UOGV	1738	Oaxaca: San Juan Bautista Tuxtepec, Tuxtepec	Mex	18.025278	-96.1669167	KR058055		KR058176
H. u. amphigrammus	69A	ANMO	1794	Veracruz: Acayucan, Ixtacapa	Mex	18.058806	-94.9402778	KR058089		
H. u. amphigrammus	69B	ANMO	1795	Veracruz: Acayucan, Ixtacapa	Mex	18.058806	-94.9402778	KR058094		
H. u. dexter	26	JCBH	42	Guerrero: Tecpan de Galeana, Bajos de Balzamar	Mex	17.61375	-100.825611	KR058071	KR058147	KR058169
H. u. dexter	28	UOGV	1517	Guerrero: Tecpan de Galeana, Acapulco - Zihuatanejo MEX 200 Hwy	Mex	17.284167	-100.648056	KR058070	KR058120	KR058148
H. u. dexter	46	JAC	21754	Oaxaca: San Francisco Sola, 11 km SSW of San Fancisco Sola	Mex	16.465	-96.999	KR058091		
H. u. dexter	27A	JAC	29537	Guerrero: Atoyac de Álvarez, Nueva Delhi - Paraiso road	Mex	17.370389	-100.20025	KR058092		
H. u. dexter	27B	UOGV	807	Guerrero: Atoyac de Álvarez, Nueva Delhi - Paraiso road	Mex	17.370389	-100.20025	KR058050	KR058146	KR058179
H. u. dexter	29A	UOGV	1821	Guerrero: Malinaltepec, San Luis Acatlán - Tlapa de Comonfort road	Mex	16.905194	-98.7412222	KR058066		
H. u. dexter	29B	UOGV	1820	Guerrero: Malinaltepec, San Luis Acatlán - Tlapa de Comonfort road	Mex	16.905194	-98.7412222	KR058065		
H. u. dexter	30A	ANMO	2938	Guerrero: About 6 km from El ocotito, road El Ocotito - Zoyatepec, "Poza Azul"	Mex	17.276889	-99.555222	KR057984		
H. u. dexter	30B	ANMO	2939	Guerrero: About 6 km from El ocotito, road El Ocotito - Zoyatepec, "Poza Azul"	Mex	17.27689	-99.555223	KR058002		
H. u. dexter	30C	ANMO	2940	Guerrero: About 6 km from El ocotito, road El Ocotito - Zoyatepec, "Poza Azul"	Mex	17.276891	-99.555224	KR058005		
H. u. dexter	43A	ANMO	2010	Oaxaca: Tlaxiaco, Putla Villa de Guerrero, Putla - Pinotepa road	Mex	16.9565	-97.9263611	KR058003		

H. u. dexter	43B	ANMO	2012	Oaxaca: Tlaxiaco, Putla Villa de Guerrero, Putla - Pinotepa road	Mex	16.9565	-97.9263611	KR058004			
H. u. dexter	43C	ANMO	2011	Oaxaca: Tlaxiaco Putla, Villa de Guerrero, Putla - Pinotepa road	Mex	16.9565	-97.9263611	KR058038			
H. u. dexter	44A	ANMO	1976	Oaxaca: Tlaxiaco, Santiago Nuyoo, Media Cuesta - Yucuhuiti road	Mex	16.96725	-97.8201389	KR058036			
H. u. dexter	44B	ANMO	1977	Oaxaca: Tlaxiaco, Santiago Nuyoo, Media Cuesta - Yucuhuiti road	Mex	16.96725	-97.8201389	KR058037			
H. u. dexter	45A	ANMO	739	Oaxaca: 25 km from San Pedro, Oaxaca - Puerto Escondido MEX Hwy 131	Mex	16.248017	-97.1473833	KR058052			
H. u. dexter	45B	ANMO	740	Oaxaca: 25 km from San Pedro, Oaxaca - Puerto Escondido MEX Hwy 131	Mex	16.248017	-97.1473833	KR058080	KR058132	KR058162	
H. u. gaigeae	3	ANMO	1848	Campeche: Dzibalchen - Xpujil road	Mex	19.449361	-89.7022222	KR057974	KR058111	KR058157	
H. u. gaigeae	5	ANMO	1888	Campeche: Escárcega, Becán archaeological site	Mex	18.517111	-89.4642778	KR057978			
H. u. gaigeae	6	ISZ	216	Campeche: Hecelchakán, Xcalumkin	Mex	20.171722	-90.0104167	KR058041	KR058121	KR058165	
H. u. gaigeae	59	CAS	80RCV	Quintana Roo: Tulum, Akumal, Cenote Xunaan Ha	Mex	20.344	-87.361	KR058083	KR058126	KR058163	
H. u. gaigeae	60	QROO	60	Quintana Roo: Chetumal	Mex	18.558378	-88.309121	KR058017			
H. u. gaigeae	1A	ANMO	1837	Campeche: Campeche, Cuidad Concordia	Mex	19.835	-90.4836389	KR057970			
H. u. gaigeae	1B	ANMO	1838	Campeche: Campeche, Cuidad Concordia	Mex	19.835	-90.4836389	KR057971			
H. u. gaigeae	2A	ANMO	1839	Campeche: Campeche, Hampolol	Mex	19.941944	-90.37525	KR057972	KR058123	KR058155	
H. u. gaigeae	2B	ANMO	1842	Campeche: Campeche, Hampolol	Mex	19.941944	-90.37525	KR057973	KR058110	KR058156	
H. u. gaigeae	4A	ANMO	1874	Campeche: Calakmul, Xpujil archaeological site	Mex	18.508861	-89.4007778	KR057975			
H. u. gaigeae	4B	ANMO	1875	Campeche: Calakmul, Xpujil archaeological site	Mex	18.508861	-89.4007778	KR057976			
H. u. gaigeae	4C	ANMO	1876	Campeche: Calakmul, Xpujil archaeological site	Mex	18.508861	-89.4007778	KR058018			
H. u. gaigeae	4D	ANMO	1877	Campeche: Calakmul, Xpujil archaeological site	Mex	18.508861	-89.4007778	KR057977			
H. u. hartwegi	18	ANMO	1911	Chiapas: Ocosingo, La Trinitaria - Palenque Hwy, road to Frontera Corozal	Mex	16.783333	-90.9459167	KR058022	KR058116	KR058160	
H. u. hartwegi	19A	ART	450	Chiapas: Ocosingo, Yaxchilán archaeological site	Mex	16.896386	-90.9682167	KR058029			
H. u. hartwegi	19B	ART	468	Chiapas: Ocosingo, Yaxchilán archaeological site	Mex	16.896386	-90.9682167	KR058031			
H. u. hartwegi	19C	ART	479	Chiapas: Ocosingo, Yaxchilán archaeological site	Mex	16.896386	-90.9682167	KR058030			
H. u. hartwegi	19D	ART	466	Chiapas: Ocosingo, Yaxchilán archaeological site	Mex	16.896386	-90.9682167	KR058028			
H. u. parvus	7	UOGV	961	Chiapas: Jiquipilas, Las Ventanas, 2.3 km NE of Tierra y Libertad	Mex	16.247556	-93.6842222	KR058051	KR058134	KR058180	
H. u. parvus	8	UOGV	880	Chiapas: Pijijiapan, Tonalá - Pijijiapan MEX Hwy 200	Mex	15.903667	-93.5183889	KR058063			
H. u. parvus	14	AMH	390	Chiapas: Acacoyagua, main road from Golondrinas to Rosario Zacatonal	Mex	15.450778	-92.6458611	KR058082			
H. u. parvus	16	UOGV	877	Chiapas: Pijijiapan - Mapastepec MEX Hwy 200, Rancho Ojo de Agua	Mex	15.673694	-93.1826944	KR058062			
H. u. parvus	17	ANMO	1937	Chiapas: Unión Juárez, Cerro del Carmen, Pico de Loro	Mex	15.053667	-92.0971944	KR058008			
H. u. parvus	22	JAC	23177	Chiapas: Cintalapa, Rizo de Oro, Arroyo El Chorro	Mex	16.489833	-94.110611	KR058076			
H. u. parvus	40	IDF	181	Oaxaca: Santo Domingo Zanatepec, mountains N of Zanatepec	Mex	16.539889	-94.2449444	KR058081	KR058112	KR058164	
H. u. parvus	41	ANMO	1043	Oaxaca: Foothills of the Sierra Madre N of Zanatepec	Mex	16.515611	-94.2984444	KR058068	KR058142	KR058151	
H. u. parvus	79	UTAR	41377	Santa Rosa: Barberena - Taxasco road	Gtm	14.209358	-90.3411	KR058102	KR058141	KR058181	
H. u. parvus	80	UTAR	41376	Quetzaltenango: Volcan Zunil, Finca El Carmen	Gtm	14.711378	-91.4790972	KR058020			
H. u. parvus	81	MSM	435	Comayagua: Aldea Las Mesas	Hnd	14.384756	-87.5694111	KR058098	KR058127	KR058173	
H. u. parvus	82	JHT	2027	Francisco Morazán: Marale, Río Maralito	Hnd	14.890869	-87.1770694	KR058009			
H. u. parvus	13A	ANMO	1927	Chiapas: Motozintla - Frontera Comalapa road, Bridge El Chorro	Mex	15.315472	-92.3620556	KR058039			
H. u. parvus	13B	ANMO	1928	Chiapas: Motozintla - Frontera Comalapa road, Bridge El Chorro	Mex	15.315472	-92.3620556	KR058007			
H. u. parvus	15A	LMOO	129	Chiapas: Pijijiapan - Mapastepec MEX Hwy 200, Jericó	Mex	15.559417	-93.0178611	KR058086	KR058122	KR058171	
H. u. parvus	15B	LMOO	101	Chiapas: Pijijiapan - Mapastepec MEX Hwy 200, Jericó	Mex	15.559417	-93.0178611	KR058077			
H. u. parvus	42A	UOGV	1631	Oaxaca: 8km NE Zanatepec, El Boquete	Mex	16.503333	-94.2745	KR058060		KR058175	
H. u. parvus	42B	UOGV	1632	Oaxaca: 8km NE Zanatepec, El Boquete	Mex	16.503333	-94.2745	KR058061			
H. u. parvus	75A	UTAR	41387	Baja Verapaz: Rabinal, Cerro La Capilla	Gtm	15.101333	-90.487	KR058104	KR058125	KR058182	
H. u. parvus	75B	UTAR	41389	Baja Verapaz: Rabinal, Cerro La Capilla	Gtm	15.101333	-90.487	KR058023			
H. u. parvus	76A	UTAR	41390	Baja Verapaz: Rabinal, near La Quebrada (Chol village)	Gtm	14.968453	-90.4831361	KR058095			
H. u. parvus	76B	UTAR	41391	Baja Verapaz: Rabinal, near La Quebrada (Chol village)	Gtm	14.968453	-90.4831361	KR058024			
H. u. parvus	78A	UTAR	41384	Quiché: Chicamán, Chixoy	Gtm	15.398667	-90.767925	KR058021			
H. u. parvus	78B	UTAR	41385	Quiché: Chicamán, Chixoy	Gtm	15.398667	-90.767925	KR058108			
H. u. parvus	83A	UTAR	41245	Santa Bárbara: Ilama, Aldea La Cañada	Hnd	15.067222	-88.2025	KR058016			
H. u. parvus	83B	MSM	420	Santa Bárbara: Ilama, Aldea La Cañada	Hnd	15.067222	-88.2025	KR058096	KR058140	KR058172	
H. u. podargus	31	JAC	25952	Hidalgo: Altapexco, Río Altapexco	Mex	21.01619	-98.33889	KR058075	KR058117	KR058168	
H. u. podargus	66	NO	645	Tamaulipas: Gómez Farías, 3 km NNW of Gómez Farías	Mex	23.052578	-99.1670639	KR058078	KR058119		
H. u. podargus	67	ANMO	1752	Tamaulipas: Aldama, 1 km W of Barra del Tordo	Mex	23.024861	-97.7718611	KR058053	KR058118	KR058152	

H. u. podargus	68	ANMO	1759	Veracruz: Álamo Temapache, Alazán	Mex	21.112056	-97.7354167	KR058054	KR058131	KR058153
H. u. podargus	54	UOGV	473	Puebla: Tlatlauquitepec, Ejido El Canal, Rio Zontalaco	Mex	19.960306	-97.4871389	KR058084		
H. u. podargus	55	UOGV	644	Puebla: Tlatlauquitepec, Macuicuila	Mex	19.958694	-97.4755556	KR058069		
H. u. podargus	56	AMH	437	Puebla: Tlatlauquitepec, Casa de Máquinas	Mex	20.0105	-97.4028889	KR058079	KR058139	KR058150
H. u. podargus	61	MZFC	9878	Querétaro: Landa de Matamoros, 2 km NE Tangojó	Mex	21.193989	-99.2107611	KR058087		
H. u. podargus	62	ANMO	1678	San Luis Potosí: Tamazunchale , Itztiamen	Mex	21.289056	-98.7928333	KR058059		
H. u. podargus	64	DHL	441	San Luis Potosí: El Naranjo, Salto de Agua	Mex	22.58675	-99. 38156	KR057969		
H. u. podargus	57A	MZFC	22079	Puebla: Huehuetla	Mex	20.09225	-97.6078333	KR058048		
H. u. podargus	57B	IDF	11	Puebla: Huehuetla	Mex	20.09225	-97.6078333	KR058046		
H. u. podargus	63A	ANMO	1688	San Luis Potosí: Axtla de Terrazas, Santa Fe Texacal	Mex	21.425472	-98.9301111	KR058049		
H. u. podargus	63B	ANMO	1690	San Luis Potosí: Axtla de Terrazas, Santa Fe Texacal	Mex	21.425472	-98.9301111	KR058097		
H. u. podargus	63C	ANMO	1691	San Luis Potosí: Axtla de Terrazas, Santa Fe Texacal	Mex	21.425472	-98.9301111	KR058099		
H. u. podargus	63D	ANMO	1692	San Luis Potosí: Axtla de Terrazas, Santa Fe Texacal	Mex	21.425472	-98.9301111	KR058101		
H. u. podargus	63E	ANMO	1689	San Luis Potosí: Axtla de Terrazas, Santa Fe Texacal	Mex	21.425472	-98.9301111	KR058100		
H. u. pulcher	84	UTAR	44846	Managua: Finca El Pescado	Nic	12.0105	-86.3246667	KR058109		
H. u. sinister	23	ANMO	494	Colima: Colima, around Colima city	Mex	19.165694	-103.831869	KR058074	KR058143	KR058161
H. u. sinister	32	NLMM	1	Jalisco: La Huerta, Chamela Biology Station	Mex	19.486272	-105.033842	KR058072	KR058145	KR058174
H. u. sinister	34	ANMO	1099	Michoacán: Lázaro cárdenas, 10 km N of Playa Azul	Mex	18.065389	-102.309222	KR058093		
H. u. sinister	35	ISZ	612	Michoacán: Lázaro cárdenas, 1 km NNW of Playa Azul	Mex	17.98828	-102.35442	KR057985		
H. u. sinister	39	ISZ	663	Nayarit: Compostela, Mesillas, 15 km E of Las Varas	Mex	21.22268	-105.01433	KR058073		
H. u. sinister	24A	ISZ	627	Colima: Tecomán, Puerta de Caleras, 7.9 km NNE of Tecomán	Mex	18.97843	-103.85824	KR057994		
H. u. sinister	24B	ISZ	629	Colima: Tecomán, Puerta de Caleras, 7.9 km NNE of Tecomán	Mex	18.97843	-103.85824	KR057995		
H. u. sinister	24C	ISZ	630	Colima: Tecomán, Puerta de Caleras, 7.9 km NNE of Tecomán	Mex	18.97843	-103.85824	KR057996		
H. u. sinister	25D	ISZ	638	Colima: Manzanillo, near El Naranjo, 15 km NW of Manzanillo	Mex	19.12497	-104.40789	KR057997		
H. u. sinister	25E	ISZ	639	Colima: Manzanillo, near El Naranjo, 15 km NW of Manzanillo	Mex	19.12497	-104.40789	KR057998		
H. u. sinister	33A	LCM	1972	Jalisco: La Huerta, Chamela	Mex	19.528053	-105.075014	KR058000		
H. u. sinister	33B	LCM	1971	Jalisco: La Huerta, Chamela	Mex	19.528053	-105.075014	KR058035		
H. u. sinister	33C	LCM	1963	Jalisco: La Huerta, Chamela	Mex	19.528053	-105.075014	KR057999		
H. u. sinister	36A	ISZ	613	Michoacán: Lázaro cárdenas, 5 km N Playa Azul	Mex	18.02371	-102.35302	KR057987		
H. u. sinister	36B	ISZ	621	Michoacán: Lázaro cárdenas, 5 km N Playa Azul	Mex	18.02371	-102.35302	KR057990		
H. u. sinister	36C	ISZ	614	Michoacán: Lázaro cárdenas, 5 km N Playa Azul	Mex	18.02371	-102.35302	KR058001		
H. u. sinister	36D	ISZ	615	Michoacán: Lázaro cárdenas, 5 km N Playa Azul	Mex	18.02371	-102.35302	KR057986		
H. u. sinister	37A	ISZ	617	Michoacán: Aquila, Las Salinas, 13 km W of Caleta de Campos	Mex	18.13261	-102.87709	KR057988		
H. u. sinister	37B	ISZ	618	Michoacán: Aquila, Las Salinas, 13 km W of Caleta de Campos	Mex	18.13261	-102.87709	KR057989		
H. u. sinister	38A	ISZ	622	Michoacán: Coahuayana, 0.6 km SW of Ojo de Agua de San Telmo	Mex	18.62001	-103.67873	KR057991	KR058124	
H. u. sinister	38B	ISZ	623	Michoacán: Coahuayana, 0.6 km SW of Ojo de Agua de San Telmo	Mex	18.62001	-103.67873	KR057992		
H. u. sinister	38C	ISZ	624	Michoacán: Coahuayana, 0.6 km SW of Ojo de Agua de San Telmo	Mex	18.62001	-103.67873	KR057993		
H. u. stuarti	21	ANMO	1906	Chiapas: La Trinitaria - Palenque MEX Hwy 307, 1 km SE of Angel Albino Corzo	Mex	17.281556	-91.6245	KR058034	KR058115	KR058159
H. u. stuarti	20A	ANMO	1901	Chiapas: Palenque, road to Kan Kan Há	Mex	17.478611	-91.9565	KR058014	KR058114	KR058158
H. u. stuarti	20B	ANMO	1902	Chiapas: Palenque, road to Kan Kan Há	Mex	17.478611	-91.9565	KR058015		
H. u. stuarti	65A	ANMO	1829	Tabasco: Jonuta, Tres Brazos - Jonuta road	Mex	18.259806	-92.2569722	KR058011		KR058154
H. u. stuarti	65B	ANMO	1830	Tabasco: Jonuta, Tres Brazos - Jonuta road	Mex	18.251139	-92.2259444	KR058012		
H. u. stuarti	65C	ANMO	1832	Tabasco: Jonuta, Tres Brazos - Jonuta road	Mex	18.251139	-92.2259444	KR058013		
H. u. stuarti	65D	ANMO	1833	Tabasco: Jonuta, Tres Brazos - Jonuta road	Mex	18.251139	-92.2259444	KR058033		
H. u. stuarti	65F	ANMO	1834	Tabasco: Jonuta, Tres Brazos - Jonuta road	Mex	18.251139	-92.2259444	KR058010		
H. u. thomasi	10	ANMO	1924	Chiapas: Frontera Comalapa, 1 km SE of Ciudad Cuauhtémoc	Mex	15.658944	-92.0018889	KR057981		
H. u. thomasi	11	ANMO	1926	Chiapas: Frontera Comalapa, Las Champas	Mex	15.646167	-91.9907778	KR057983		
H. u. thomasi	77	UTAR	41383	Huehuetenango: Nentón, La Fortuna, Hacienda Miramar	Gtm	15.834667	-91.8163333	KR058103		
H. u. thomasi	12A	ANMO	1942	Chiapas: Monte Cristo de Guerrero, San Nicolas - Nueva Independencia road	Mex	15.683722	-92.5948889	KR057979		
H. u. thomasi	12B	ANMO	1948	Chiapas: Monte Cristo de Guerrero, San Nicolas - Nueva Independencia road	Mex	15.683722	-92.5948889	KR058032		
H. u. thomasi	12C	ANMO	1949	Chiapas: Monte Cristo de Guerrero, San Nicolas - Nueva Independencia road	Mex	15.683722	-92.5948889	KR058040		
H. u. thomasi	9A	ANMO	1922	Chiapas: Frontera Comalapa, Ciudad Cuauhtémoc	Mex	15.685722	-92.0041667	KR057980		
H. u. thomasi	9B	ANMO	1923	Chiapas: Frontera Comalapa, Ciudad Cuauhtémoc	Mex	15.685722	-92.0041667	KR057982		

H. u. undulatus	47A	ISZ	473	Oaxaca: Pluma Hidalgo - Huatulco road, Finca El Carmen	Mex	15.879194	-96.3886389	KR058088			
H. u. undulatus	47B	ISZ	474	Oaxaca: Pluma Hidalgo - Huatulco road, Finca El Carmen	Mex	15.879194	-96.3886389	KR058085			
H. u. undulatus	47C	ISZ	478	Oaxaca: Pluma Hidalgo - Huatulco road, Finca El Carmen	Mex	15.879194	-96.3886389	KR058067	KR058113	KR058166	
H. u. undulatus	47D	UOGV	1765	Oaxaca: Pluma Hidalgo - Huatulco road, Finca El Carmen	Mex	15.879194	-96.3886389	KR058064	KR058135	KR058177	
H. u. undulatus	47E	UOGV	1766	Oaxaca: Pluma Hidalgo - Huatulco road, Finca El Carmen	Mex	15.879194	-96.3886389	KR058006			
A. ameiva	*A. ameiva 1*	MVZ	247600	Brokopondo Reservoir: Brownsberg Nature Park	Sur			KR058025			
A. ameiva	*A. ameiva 2*	MVZ	247601	Brokopondo Reservoir: Brownsberg Nature Park	Sur			KR058026			
A. ameiva	*A. ameiva 3*	MVZ	247602	Brokopondo Reservoir: Brownsberg Nature Park	Sur			KR058042			
A. ameiva	*A. ameiva 4*	MVZ	247603	Brokopondo Reservoir: Brownsberg Nature Park	Sur			KR058027			
A. chrysolaema	*A. chrysolaema 1*	MEG	320	Hispaniola	Dom Rep			EU781090.1			
A. chrysolaema	*A. chrysolaema 2*	MEG	88	Hispaniola	Dom Rep			EU781080.1			
A. chrysolaema boekeri	*A. c. boekeri 2*	ALS	94	Azua: Biyeya	Dom Rep			AY561667.1			
A. chrysolaema boekeri	*A. c. boekeri 3*	ALS	98	Azua: Biyeya	Dom Rep			AY561668.1			
A. chrysolaema ficta	*A. c. ficta*	ALS	29	Pedernales: 4 km SSE of Los Tres Charcos	Dom Rep			AY561660.1			
A. chrysolaema parvoris	*A. c. parvoris 1*	ALS	193	Los Bancos	Dom Rep			AY561677.1			
A. chrysolaema parvoris	*A. c. parvoris 2*	ALS	22	Isla Catalina	Dom Rep			AY561654.1			
A. chrysolaema regularis	*A. c. regularis*	BWMC	6861	Nueva Judea	Dom Rep			AY561648.1			
A. crysolaema alacris	*A. c. alacris*	BWMC	6854	2.1 km NW Rio Yaque	Dom Rep			AY561646.1			
A. leberi	*A. leberi 1*	ALS	41	Pedernales: 6 km SSE Los Tres Charcos	Dom Rep			AY561661.1			
A. leberi	*A. leberi 2*	ALS	83	Pedernales: 5 km SSE Los Tres Charcos	Dom Rep			AY561663.1			
A. lineolata	*A. lineolata 1*	BWMC	6852	2.1 km NW Río Yaque	Dom Rep			AY561636.1			
A. lineolata	*A. lineolata 2*	BWMC	6855	3.5 km S Río Yaque	Dom Rep			AY561639.1			
Aspidoscelis gularis	*As. gularis*	JRM	4650		Mex						
Aspidoscelis lineatissima exorista	*As. lineatissima exorista*	UOGV	1526	Michoacán	Mex						
Aspidoscelis tigris	*As. tigris*	MVZ	179799	California	USA			U71332.1			

Table S2. Primers used in study.

Marker	Name	Primer 3'-5'	
NADH2	tMetR	AAG CTY TYG GGC CCC ATA CCC C G	Amplification and sequencing
	tAla	CTT AAT KAA AGT GTK TGA GTT GCA TTC AG	Amplification and sequencing
	ND2	CAY CTV TGA YTR CCA GAA GTW ATA CAA GG	Sequencing
	L514	CCT ACT CAT CCA TTG CAA ACA TRG GMT GAA	Sequencing
	H514	TTC AKC CYA TGT TTG CAA TGG ATG AGT AGG	Sequencing
	H655	CAT GTT GTG CTA ATR GTT TTR A	Sequencing
RPS8	RPS8f	GCC TTC TGG AGG AGC AGT TCC A	Amplification and sequencing
	RPS8r	TCC TGG TCT GGA GGC AAT GCA G	Amplification and sequencing
α-cardiac actin	a-cardiac f	GAGCGTGGCTAYTCCTTTGT	Amplification and sequencing
	a-cardiac r	GTGGCCATTTCATTCTCAAA	Amplification and sequencing

Table S3. Partition strategies, harmonic mean of the likelihood values of the MCMC samples, and GTR submodels with the highest posterior probability (the submodels represented by six numbers specify different substitution rates in the order r_{AC}; r_{AG}; r_{AT} ; r_{CG}; r_{CT}; $r_{GT)}$.

Mitochondrial DNA	Partition strategy	Harmonic mean	Partitons and models			
	4 Partitions	-13034.51	Non-coding	Codon-pos 1	Codon-pos 2	Codon-pos 3
			121121	123423	123123	121343
	3 Partitions	-13095.06	Non-coding	Codon-pos 1&2	Codon-pos 3	
			121121	121121	121343	
	2 Partitions	-13396.85	Non-coding	ND2		
			121121	121134		
	0 Partitions	-13255.15	Complete matrix			
			123454			
	RPS8	-1356.46				
			1123312			
	α-cardiac actin	-1126.26				
			123113			

CAPITULO III

Resolution of the type locality of *Holcosus undulatus* Wiegmman, 1834 (Squamata, Teiidae)

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Abstract

Cnemidophorus undulatus Wiegmann 1834 was described on the basis of three or four specimens collected by Ferdinand Deppe from "Mexico". Then, *C. undulatus* was transferred to the genus *Ameiva*, and lately to the genus *Holcosus*. *Holcosus undulatus* was, from 1915 to 1971, considered a polytypic species. Recently most of its subspecies were elevated to species level. The use of the name *undulatus* became problematic from the first time *H. undulatus* was treated as polytypic, because the type locality is ambiguous. Records of Deppe travels in Mexico and information from Museum für Naturkunde, Berlin and the morphological revision of the syntypes may help resolve the type locality of *Holcosus undulatus*.

Introduction

The understanding of Earth's biodiversity depends critically on the accurate identification and nomenclature of species (Cappellini, 2014). However, many species were described centuries ago, and in a surprising number of cases the nomenclature or type material remain unclear or inconsistent (Cappellini, 2014). For instance, *Holcosus undulatus* was described by Wiegmann in 1834, as *Cnemidophorus undulatus,* with a variety α, from "Mexico", without additional information about the type locality. During the first half of the XX century twelve subspecies were described for *H. undulatus* and the use of the name *undulatus* became problematic, because the type locality of the species was ambiguous and the original description brief and uninformative.

After its description, *C. undulatus* was transferred to the genus *Ameiva* Cuvier (Gray, 1845). Later, Bocourt (1874) on the basis of Wiegmann (1834)'s syntypes and material collected during the labors of the "Mission scientifique au Mexique et dans

l'Amerique Centrale," provided detailed redescriptions of *Ameiva undulata* and two varieties, A and B. Bocourt (1874) stated that the National Museum of Natural History in Paris had several specimens "identical" to the type specimens of *C. undulatus* described by Wiegmann (1834), and that they had been collected in diverse localities on the Pacific versant of Mexico ("Oaxaca and Tehuantepec") and Central America (scattered localities on the Pacific versant of Guatemala and El Salvador).

Therefore, Bocourt (1874) established for the first time the scope of the geographic distribution of *A. undulata,* which encompassed the Pacific versant of Mexico and Central America. Additionally, Bocourt (1874) stated that the variety A (Wiegmann, var. A) of *A. undulata* inhabited the Atlantic versant of Mexico and Central America (the Petén, the hot lands of Vera Paz, the course of the Rio Polochic, Santa María de Pansos [= Panzós], and Isabal [= Izabal]), and the variety B the forests of Belize (British Honduras).

Later, Barbour & Noble (1915), in their revision of the lizards of the genus *Ameiva*, treated *A. undulata* as a polytypic species for the first time, describing *A. u. parva* and treating *A. quadrilineata* (Hallowell, 1860) as a subspecies of *A. undulata*. They considered *A. u. parva* "a race apparently confined to Guatemala", related to *A. u. undulata* and *A. u. quadrilineata*, "from which could be distinguished in having a short stocky head and in having the gular scales, except for the median group, very small". Additionally, they assigned the Mexican populations to *A. u. undulata*, and described an adult male from Colima as representative of this subspecies, which considered "apparently confined to southern Mexico." This revision was based almost wholly on the collection in the Museum of Comparative Zoology, but also on loans from other institutions (Barbour & Noble, 1915). However, Barbour and Noble apparently made their decision on the basis of only three specimens (the type M. C. Z. 5831, an adult male, a female, and a young specimen, collected by Van Patten [Smith & Taylor, 1950], from Guatemala and a single adult male from Colima).

Later, Hartweg & Oliver (1937) recorded the following data from a series of 30 males and 17 females (UMMZ 81895-904) collected in the Isthmus of Tehuantepec during

the summer of 1936: “Femoral pores, ♂ 15 to 20 (17.7), ♀ 14 to 18 (16.1); ventrals to anus, 7 to 10 (7.7); lamellae on inner ventral surface of fourth toe, 25 to 30 (27.7). There is a single row of median enlarged preanals (3 to 4 in number) in 43 (91.5 percent) specimens; the remaining 4 specimens each have anteriorly 2 median enlarged scales and the third (posterior) paired...” Hartweg & Oliver (1937) assigned their specimens to *A. undulata*, and suggested that “Bocourt had both *undulata undulata* (from Tehuantepec) and *undulata parva* (from the Pacific slope of Guatemala) but did not recognize the differences... *Ameiva undulata* as described by Wiegmann (1834:27-28) and re-described and figured by Bocourt (1874: 254-258) “is composed, we feel, of two forms, *undulata undulata* and *undulata parva.”*

Thus, Hartweg & Oliver (1937) settled that true *A. u. undulata* occurred at Tehuantepec and had a single row of median enlarged preanals. Hartweg and Oliver (1937) knew the works by Wiegmann (1834) and Bocourt (1874), but apparently they did not examine the syntypes of *A. u. undulata*, as they did not make any reference to them or their characters.

Later, Smith (1940) stated that *Ameiva undulata undulata* “was restricted by Hartweg and Oliver (1937) to Tehuantepec”. However, Stuart (1942) clarified that the type locality of *A. u. undulata* was “Mexico by inference; restricted to the Tehuantepec, Mexico, race by Smith (1940) and not by Hartweg & Oliver as stated by Smith.”

During the first half of the XX century twelve subspecies were described for *A. undulata,* and the need for a revision became evident. Echternacht (1970, 1971) formally designated *A. festiva miadis* as a subspecies of *A. undulata*, and placed *A. undulata thomasi* in the synonymy of *A. chaitzami*, and all of the other subspecies of *A. undulata* in the synonymy of *A. undulata*. Recently, all Mexican and Central American species of *Ameiva* were transferred to the genus *Holcosus* (Harvey et al., 2012). Finally, *H. undulatus undulatus*, *H. u. parvus*, *H. u. thomasi*, *H. u. hartwegi*, *H. u. gaigeae*, *H. u. amphigrammus* and *H. u. miadis* were resurrected from the synonymy of *H. undulatus* and elevated to species level (Meza-Lázaro & Nieto-Montes de Oca, 2015). *Holcosus undulatus dexter* from

southwestern Oaxaca and southeastern Guerrero was regarded as a junior synonym of *H. undulatus.* Thus, *H. undulatus* occurs on the Pacific versant of Mexico from the Isthmus of Tehuantepec to west-central Guerrero.

Nevertheless, examination of the type series of *H. undulatus* suggests that this taxon, as described by Wiegmann (1834:27-28), may not be composed of the species *H. undulatus* and *H. parvus* as understood today, and furthermore that the application of the name to populations in the Pacific versant of Mexico may not be justified.

The type series was composed of three syntypes: ZMB 867–869 (according to a handwritten comment added by the first curator of the Museum für Naturkunde, Berlín Wilhelm Peters around 1958). Of these, ZMB 867 represented a variety with a "scuta (illegible word) divido" and ZMB 869 represented variety alpha (hand-written catalogue; pers. comm.) What variety ZMB 868 represented apparently was not recorded. We examined (directly or through photographs) the three specimens. The specimens ZMB 867 and 868 are similar each other in most respects, including the presence of paired enlarged preanals. The arrangement of the enlarged preanals is one of the few characters which almost all students who have dealt critically with this group (undulata) have realized are of primary significance (Smith and Laufe, 1946). The syntype ZMB 869 had been reported (Echternacht, 1971). However, ZMB 869 is kept at the Museum für Naturkunde, Berlín (fig. 2), and has paired preanals (fig. 3), and abruptly enlarged gulars irregular in arrangement.

The arrangement of the preanals allows differentiating thespecies occupying the Pacific versant of Mexico at the west of the Isthmus of Tehuantepec (single row of median enlarged preanals; posterior most might be paired) from all other species (paired preanals). From our knowledge of the morphological variation among species in the *H. undulatus* complex (Bocourt, 1874; Smith, 1940; Hartweg & Oliver, 1942; Echternatch, 1971; Meza-Lázaro & Nieto-Montes de Oca, 2015), it is evident that the morphological characters of the syntypes do not correspond to the characters in the populations along the Pacific coast of Mexico from the Isthmus of Tehuantepec to Sinaloa

Hartweg and Oliver (1942) probably suggested that *Holcosus undulatus* as composite because in Bocourt (1874) plate XX A (*planche XX A*) figures 7a- 7d are labeled as "*Ameiva undulata*, type (Wiegmann)... *Mexique et Guatemala occidental*" (fig. 1). All the illustrations correspond to ZMB 868, except Figure 7d. Figure 7d (Bocourt, 1874) shows the preanals arranged in a single row. Figure 7d does not correspond to any of the syntypes. Additionally, in Bocourt (1874), the illustration labeled as "Figure 8. *Ameiva undulata* var. A type (Wiegmann)... Du Mexique et du Guatemala oriental" is not based on ZMB 869. Figures 7d an 8 must be based on other specimens different from Wiegmann's type series, probably from the *Mission scientifique au Mexique*.

According to the inventory catalogue of the Museum für Naturkund, ZMB 867-769 were collected in the 1820's by Ferdinand Deppe in "Mexico". Ferdinand Deppe visited Mexico from December 1824 to January 1827 and from 1828 to 1838 (Stresemann, 1954). Deppe collected mainly birds, but also mammals, a quantity of reptiles, amphibians, fishes, snails, and thousands of insects for scientific purposes (Stresemann, 1954). Deppe collected at several localities in Mexico, such as Alvarado, the swamps and lagunas near Tlacotalpan, Misantla, and Papantla in Veracruz, Temascaltepec, Las Cruces, Tenancingo and Sacualpán (Zacualpan), Real (de) Arriba and Volcan Toluca (Nevado de Toluca) in Mexico State, Jantepeque and Cuernavaca in Morelos, Tlalpaxahua (Tlalpajahua) in Michoacán, Cimapan (Zimapán) in Hidalgo, Tehuacán, Puebla, and Tehuantepec, and Oaxaca, Oaxaca (Stresemann, 1954). Deppe also visited a place called Valle Real, Veracruz (Valle Nacional, Oaxaca; Binford, 1989).

There are hundreds of pages of handwritten correspondence between Deppe and the Zoological Museum Berlin. Although the lists are somewhat detailed and collecting time and locality are given, the naming of the specimens is not detailed enough to figure out which one becomes later a type specimen. However, the contents of the shipments were checked after their arrival by Lichtenstein. He wrote a table of contents for every single box. In addition, on June 21, 1826, Lichtenstein (the director of ZMB at the time) acknowledged having received a box from Deppe containing "4 *Agama undulata* n. [=nobis]," a preliminary new (working) name used by Lichtenstein. This material was

collected between December 1824 and January 1825 in “Alvarado in Mexico.” Deppe send also in 1826, 1828 and 1829 lizards from different localities to Berlin that Lichtenstein named in his different lists as *Ameiva* n.sp. or simply new genus of lizard.

Discussion

The use of a taxonomic name is not always straightforward. Ambiguous descriptions and imprecise type localities might obscure the name application. The name *undulatus* has a long history and it is not always clear. However, we can infer the origin of type specimens and clarify the use of the name. From morphology data, the itinerary of Deppe's journey and the Lichtenstein's list of acquisitions, we can obtain the following information:

1) The syntypes (ZMB 867 and 868) of the Museum für Naturkund could be from Tehuantepec, since Deppe visited this locality, but they do not correspond morphologically with the specimens reported in Hartweg & Oliver (1937). Ferdinand Deppe visited the populations of the versant of the Mexican Gulf, and in the Pacific versant the surroundings of Tehuantepec. However, he did not visit Chiapas, Tabasco or Yucatan Peninsula. This information restricts the places where syntypes could be collected to populations in the Pacific versant, that have paired preanals and central gular scales abruptly enlarged regularly or irregularly arranged.

2) There are no evidences suggesting that the syntypes came from different localities. Wiegmann (1834) described variety α after a specimen that has abruptly enlarged central gular scales arranged irregularly. Scales arrangement would be the only evidence suggesting that the syntypes could be from different localities. However both conditions, central gular scales regularly or irregularly arranged, are present in the populations from the versant of the Gulf of Mexico, from Tamaulipas to south of Veracruz (Smith & Laufe, 1945; 1946).

3) The syntypes ZMB 867, 768 and 769 are most probably from Alvarado, Veracruz. The following evidences support this conclusion: a) the syntypes have abruptly enlarged gular scales and paired preanals that characterize to *Holcosus* from the versant of the

Mexican Gulf and Pacific versant of Chiapas; b) the itinerary of the travel of Ferdinand Deppe allows us to restrict the probable origin localities for the syntypes to the versant of Gulf of Mexico; c) four specimens were labeled by Lichtenstein as "Agama undulata", collected between December 1824 and January 1825 at “Alvarado in Mexico. Other specimens were labeled as *Ameiva*, but not as *undulata*.

Therefore it seems justified to restrict the type locality of *H. undulatus* to Alvarado, Veracruz, Mexico. This modification would have implications on the circumscription of *H. undulatus*. Populations from Gulf of Mexico versant would be known as *H. undulatus*. *Holcosus amphigrammus* would be synonymous of *H. undulatus*.

Meanwhile, populations occupying the Pacific versant from Tehuantepec Isthmus to southeastern Guerrero cannot be known as *H. undulatus* since they belong to a different lineage, they should be known as *Holcosus dexter,* Smith and Laufe, 1946, with its type locality at near Rincon, Guerrero (Holotype: adult male, EHT-HMS No. 11966, collected by Edward H. Taylor and Hobart M. Smith).

The syntypes of *H. undulatus* remain in good condition, allowing the evaluation of all scalation characters. The color pattern is still visible in ZMB 867 and 869. Designation of a lectotype as the single name-bearing specimen is necessary to fix the identity of the species for all future work on its biology, phylogeny, and conservation. Based on this evidence, and in conformity with Article 74.7 of the ICZN, we hereby designate ZMB-868, as the lectotype of *H. undulatus* Wiegmann, 1834.

Figure 1. A) *Cnemidophorus undulatus* (*Holcosus undulatus*) taken from plate XX (planche XX; Bocourt, 1874); B) Reproduced from plate XXA (planche XX A; Bocourt, 1874), labeled in the original as 7, 7a, 7b, 7d and 7e (see text).

Figure 2. Syntype of *Holcosus undulatus* ZMB 869.

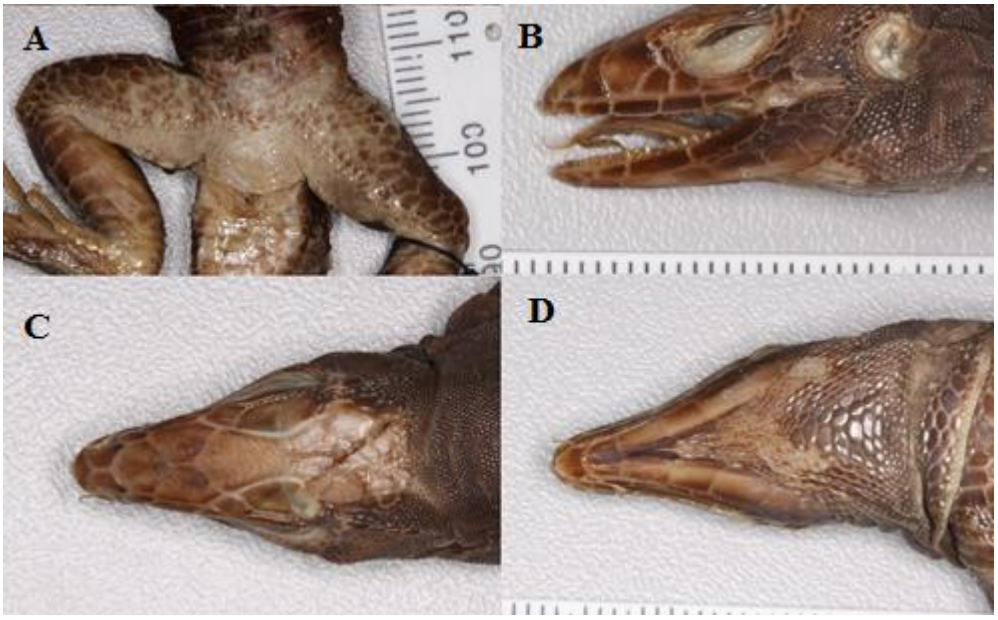

Figure 3. Syntype of *H. undulatus* ZMB 869, A) arrangement of preanal scales, B) lateral, C) dorsal, D) ventral view of the head.

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CAPÍTULO IV

Morphological and ecological perspective of *Holcosus chaitzami* and *H. thomasi (Squamata: Teiidae)*

Meza-Lázaro, R. N.; López-Alcaide, S.; Nieto Montes de Oca, A.

Introduction

Holcosus chaitzami Stuart 1942 is an uncommon and poorly known species of teiid lizard (Campbell & Muñoz-Alonso, 2013), which was originally described from the semi-arid Cahabón Valley along Cahabón-Lanquin trail about 2Km north of finca Canihor (about 38Km ENE [straight line] of Cobán) in Alta Verapaz, Guatemala. This species was considered endemic to the Cahabón Valley (Stuart, 1950; 1963), though Echternacht (1970) synonymized *H. undulatus thomasi* from the upper tributaries of the Río Grijalva in Chiapas, Mexico, and west-central Guatemala with *H. chaitzami.* Therefore, the current distribution of *H. chaitzami* ranges from the valleys of the upper tributaries of the Río Grijalva in Chiapas, Mexico, and west-central Guatemala, to the vicinity of Finca Canihor, Alta Verapaz and nearby areas of Poptún, El Petén, Guatemala (Echternacht, 1970; 1971; Campbell & Muñoz-Alonso, 2013). This distribution leaves *H. chaitzami* restricted to three widely separated areas (Campbell, 1999). The allopatric distribution and the presence of morphological differences among the populations of *H. chaitzami* thus suggest that they could belong to separate species.

Holcosus chaitzami was mentioned to be almost identical with *H. u. stuarti*, from which could "readily be distinguished, by the fact that the median parietal is divided longitudinally to produce four instead three parietals and by its smaller size" (Stuart, 1942) (Fig.1). *Holcosus u. stuarti* was described two years before from Palenque, Chiapas, as a small lizard having two rows of preanals and a median row of enlarged gulars (Smith, 1940). *Holcosus u. thomasi* Smith & Laufe 1946 was on the other hand described from La Libertad, near Río Cuilco in Chiapas, where it crosses the Guatemalan border (Holotype:

Adult male, EHT-HMS No. 15327). According to Smith & Laufe (1946), *H. u. thomasi* is probably restricted to the dry, hot valleys of the upper tributaries of the Rio Grijalva in the interior of Chiapas, Mexico, and western central Guatemala (Smith & Laufe, 1946). These authors considered *H. u. thomas*i a member of the *undulata* group, due to it possess paired preanals, abruptly enlarged gulars, lacks a secondary row of superciliary granules, and with supraoculars broadly contacting the frontoparietals. The adult male color pattern of *H. thomasi* differs from that of all other forms of *Holcosus* in having the upper lateral light spots merged with the dorsolateral light line to form a continuous light band, the dorsal border of which is regular, the ventral irregular and giving rise to the vertical light bars. However, no information about the interparietal condition was given for *H. u. thomasi* nor *H. u. stuarti* by Smith (1940) or Smith & Laufe (1946).

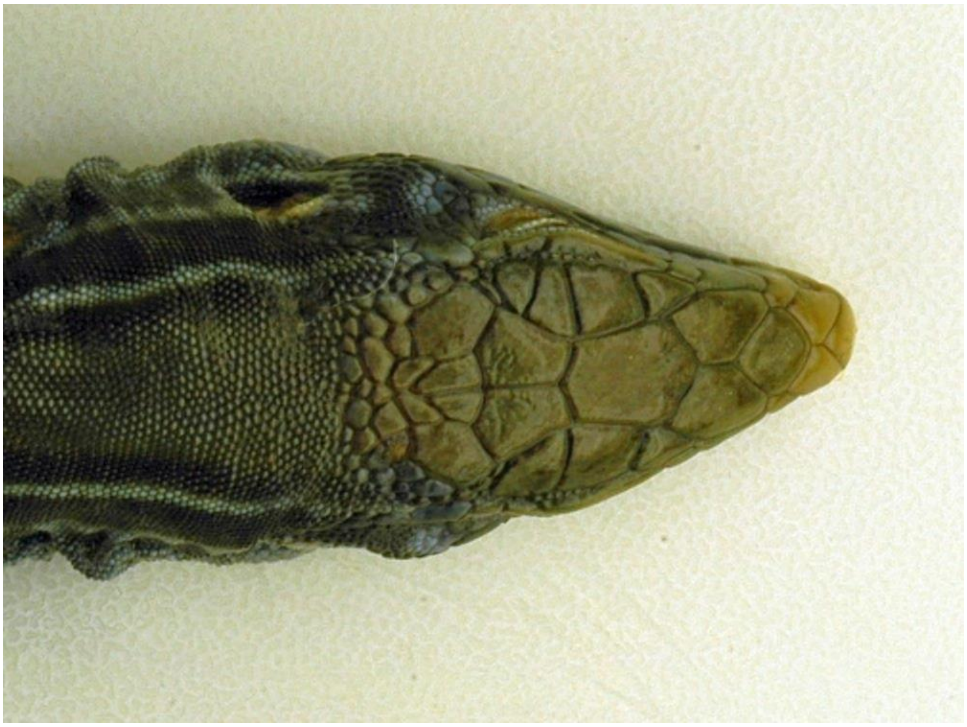

Figure 1. Head scutelation of the holotype of *H. chaitzami*.

Years later, Echternacht (1970) argued that “the posterior scales on the dorsal surface of the head is an unstable character among Middle American species of *Ameiva*, and diagnoses based on scales in the area are unreliable”, and that “the description of *H. u.*

thomasi (Smith & Laufe, 1946) agrees with that of Stuart (1942) for *H. chaitzami* in most respects". Then, this author synonymized *H. u. thomasi* (Smith & Laufe, 1946) with *H. chaitzami*, whereas *H. u. stuarti* was synonymized with *H. undulatus* (Echternacht, 1970, 1971). He also reported that "*Ameiva undulata*" from Middle America has the median parietal divided or semidivided in 22% out of 1043 specimens obtained throughout the range of the species, and that this was probably a conservative estimate of the frequency of occurrence of this condition.

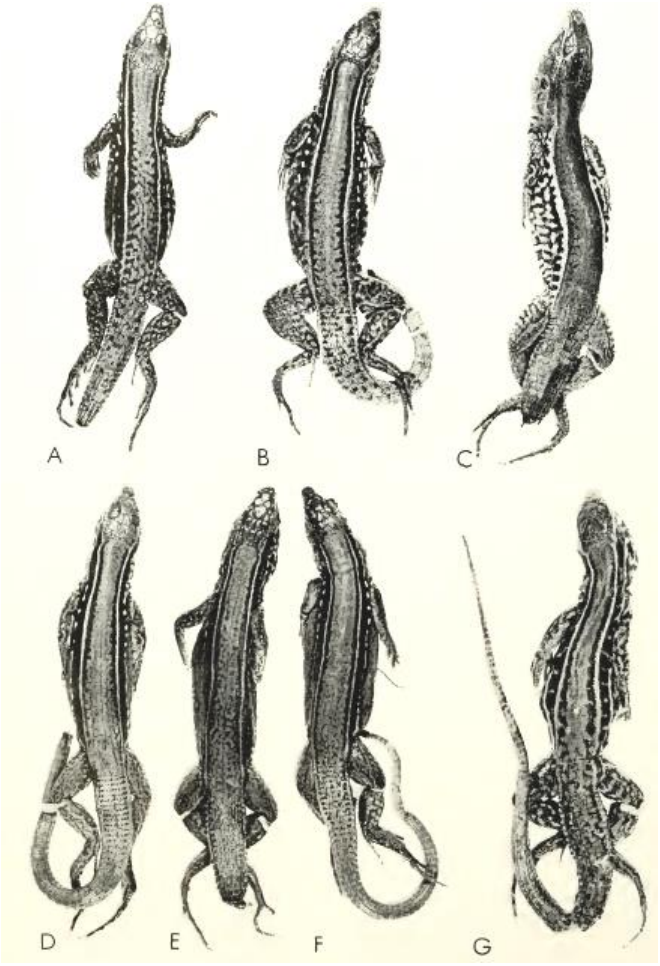

Figure . Originally from Echternacht (1971). Ontogenetic change in pattern of *Holcosus chaitzami*. A-D and F, UMMZ 94905, E, UMMZ 94901, all from the vicinity of Comitan, Chiapas, Mexico. Field Tag Numbers and SVL are: Males, (A) 473, 45 mm, (B) 482,68 mm,

(C) 461, 73 mm. Females, (D) 483, 55 mm, (E) 365, 68 mm, (F) 501, 75 mm. (G) For comparison, UMMZ 90640, a male paratype 68 mm SVL from along the Cahabon-Languin trail about 2 km N Finca Canihor, Alta Verapaz, Guatemala.

Table 1 summarizes the information recorded by Echternacht (1970) for samples of *H. hartwegi*, *H. chaitzami,* a population from Nicaragua and a population from Eastern Mountains of Chiapas having the high frequency of occurrence of division of the median parietal. According to the author, divided interparietal frequency ranges from 48 to 90% and there seem to be no geographic trends associated with the condition of the median parietal. Echternacht (1971) subsequently recorded as a single character state the divided or semi-divided interparietal, inflating the frequency of the presence of divided interparietal in populations with high semi-divided interparietal frequency.

Table 1. Frequency of the longitudinally divided or semi-divided interparietal (Echternacht, 1970). * From the range of *H. thomasi* as described by Smith & Laufe (1946)

Taxon	**Samples having a high frequency of occurrence of division were as follow:**	**Individuals with divided or subdivided interparietal**
-	Near Chinandega, Depto. Chinandega, Nicaragua	55 % (N=31)
H. hartwegi	Piedras Negras, Depto. El Petén	72 % (N= 32)
H. hartwegi	Canihor, Depto. Alta Verapaz, Guatemala	50% (N=30);
H. hartwegi	Sabana de San Quintín, Chiapas, México	100% (N=10)
-	Near Las Tazas and Florida, Chiapas, México	90% (N=30)
H. chaitzami*	Comitán, Chiapas, México,	3 % (N=30)
H. chaitzami*	Near San Antonio, Huista, Depto. Huehuetenango, Guatemala	10% (N=31)
H. chaitzami	Near Finca Canihor, Depto. Alta Verapaz, Guatemala and near Poptún, Depto. El Petén, Guatemala. Six of the nine in the sample constitute the type series.	89% (N= 9)

For assessing whether populations of *H. thomasi* and *H. chaitzami* belong or not to the same species, we recorded the diagnostic morphological features of both taxa, as well as of *H. stuarti, H. parvus* and *H. hartwegi*. We also built niche-based distribution models for

each taxon to evaluate adaptive divergence or allopatry between their known populations. Gene flow among *H. thomasi*, *H. stuarti* and *H. chaitzami* could be disrupted if they have dissimilar climatic niche envelopes, or the geographic area between them has no acceptable environmental conditions for them (Wiens & Graham, 2005).

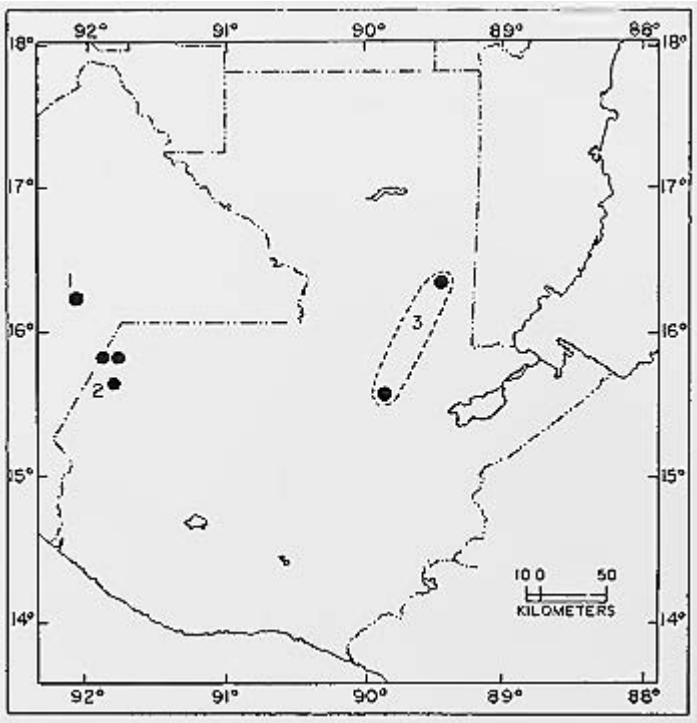

Figure 1. Originally from Echternacht (1971). Map showing locality records of "*Ameiva" chaitzami* (*Holcousus chaitzami*): (1) Comitan, Chiapas, Mexico, (2) Vicinity of San Antonio Huista, Depto. Huehuetenango, Guatemala, (3) combined sample of those specimens originally designated by Stuart (1942) as holotype and paratypes from the Languin-Cahabón road near Finca Canihor, Depto. Alta Verapaz, Guatemala, and specimens from the vicinity of Poptún, Depto. El Peten, Guatemala, later collected by Stuart and identified as *A. chaitzami*.

Methods

Taxa

We examined specimens (Table 1) of *Holcosus chaitzami*, *H. thomasi*, *H. stuarti*, *H. hartwegi*, and *H. parvus* to assess the stability of the interparietal condition and the

dorsolateral color pattern on each taxon. We additionally examined part of the type series of *H. chaitzami*, and the holotype of *H. thomasi*.

Niche-based distribution models were built based on reliable locality records. Most of the localities for *H. thomasi* and *H. stuarti* have coordinates collected from a GPS, and the identity of the collected specimens confirmed by morphological and molecular data (Table 2). The localities of *H. chaitzami* were georeferenced following the locality description of Stuart (1942) and a map shown in Stuart (1948).

Morphological data

We examined scutelation, color and pattern features for assessing morphological differentiation among *H. chaitzami*, *H. stuarti* and *H. thomasi.* We also gathered available information in literature about specimens and localities of the *Holcosus undulatus* complex from Chiapas and Guatemala (Stuart, 1942; Smith and Laufe, 1946; Stuart, 1948; Echternacht 1970; Echternacht 1971).

We recorded snout-vent length (SVL), gular scales, dorsolateral light stripe, and ventrolateral light stripe following Echternacht's (1971) nomenclature. The interparietal condition was recorded as longitudinally divided interparietal, longitudinally semi-divided or complete interparietal.

Distribution Modeling

We created niche-based distribution models for *H. thomasi* and *H. stuarti* with the program Maxent version 3.3.3k (Phillips et al., 2006; for free download see: http://www.cs.princeton.edu/~schapire/maxent/) using default values: convergence threshold = 10-5, maximum iterations = 500, regularization multiplier = 1, and auto features selected. We used 19 bioclimatic, recently updated variables derived from the monthly precipitation and temperature values (Cuervo-Robayo et al., 2013).

Jackknife model testing

To test predictive performance, we implemented a jackknife test (Pearson et al., 2006). This is an appropriate approach when few observed locality points are available. Multiple predictions were made per species, with one of the observed localities excluded in each case. We conservatively removed from the training data set all localities situated within 10 km of the test locality for each jackknife model run to lessen the effect of locality clustering and non-spatial independence (Pearson et al. 2006). For each prediction, a decision threshold was applied (based on the training localities), and the ability to predict the excluded locality was tested. A P value was then calculated for each species across the set of jackknife predictions using the program P-Value Compute (Pearson et al., 2006). The jackknife validation approach requires the application of a threshold to distinguish 'suitable' from 'unsuitable' areas (Pearson et al., 2004). We considered a conservative approach and identified the minimum predicted area possible whilst maintaining zero omission error in the training data set (Pearson et al., 2006).

Table 2. Localities used in this study. Gtm = Guatemala; Mex = Mexico.

Taxon	Latitud	Longitud	Locality	Contry	Source
H.chaitami	16.308009	-89.416705	Petén; 2 km SW Poptún	Gtm	Echternacht, 1971
H.chaitami	15.610091	-89.86348	Alta Verapaz; Cahabon-Lanquintrail about 2Km north of finca Canihor	Gtm	Stuart, 1942
H.chaitami	16.349483	-89.416518	Petén; 1Km N Poptún	Gtm	Echternacht, 1971
H. thomasi	15.659108	-91.777418	Huehuetnango; 1Km N San Antonio Huista	Gtm	Echternacht, 1971
H. thomasi	15.65624	-91.76041	Huehuetenango; 1Km E San AntonioHuista	Gtm	Echternacht, 1971
H. thomasi	15.8346667	-91.8163333	Huehuetenango; Hacienda Miramar, La Fortuna, Nentón	Gym	This study
H. thomasi	15.6857222	-92.0041667	Chiapas; Crossroads of Paso Hondo and Ciudad Cuahutemoc,Comitán	Mex	This study
H. thomasi	15.6461667	-91.9907778	Chiapas; Las Champas, Cuahutemoc City, on the Guatemalan border	Mex	This study
H. thomasi	15.6837222	-92.5948889	Chiapas; Between Montecristo and San Nicolas Plan de Aquila	Mex	This study
H. thomasi	15.828671	-92.279102	Chiapas; Pablo L. Sidar	Mex	This study

H. thomasi	15.435219	-92.10784	Chiapas; La Libertad, near Río Cuilcowhere it crosses the Guatemalan border	Mex	Smith and Laufe, 1946
H. stuarti	17.4786111	-91.9565	Chiapas; Road to KanKanHá, Palenque	Mex	This study
H. stuarti	17.2815556	-91.6245	Chiapas; Highway Angel Albino Corzo-Yaxchilán	Mex	This study
H. stuarti	17.482588	-91.424237	Tabasco; Tenosique	Mex	This study
H. stuarti	18.2598056	-92.2569722	Tabasco; Road Tres Brazos-Jonutla	Mex	This study
H. stuarti	18.2511389	-92.2259444	Tabasco; Road Tres Brazos-Jonutla	Mex	This study
H. stuarti	18.547798	-92.647386	Tabasco; Frontera	Mex	Smith and Laufe, 1946
H. stuarti	17.574323	-92.941486	Tabasco; Teapa	Mex	Smith and Laufe, 1946
H. stuarti	18.413074	-91.499748	Tabasco; Balchacaj	Mex	Smith and Laufe, 1946

Results

Morphology

Holcosus chaitzami, *H. thomasi* and *H. stuarti* are small lizards, around 90mm of SVL. *Holcosus chaitzami* is particularly small, the largest specimen recorded reaches only 70mm. Echternacht (1971) suggested that specimens in the type series of *H. chaitzami* were juveniles and compared them with those of *H. thomasi* (fig. 2).

The Interparietal conditon varies within populations, but a complete interparietal is by far the most frequent state (Table 3). Partial division of the interparietal can also be considerably frequent (*H. parvus* 32%, *H. hartwegi* 23%). In contrast, a divided interparietal is unfrequent. The only population where we observed a relatively high frequency of this condition was in *H. hartwegi* from Yaxchilán, Chiapas (19.23%), though it was not as high as the frequency reported by Echternacht (1970).

Comparison of color pattern among *Holcosus* species is hampered by ontogenic change in pattern and sexual dimorphism. Comparisons are usually based on adult males. Two remarkable characters present in the type series of *H. chaitzami* are the continuous, well-defined dorsolateral and ventrolateral light lines. A continuous dorsolateral light line is

uncommon in adult males of most species, except *H. stuarti* and *H. thomasi.* The latter color pattern feature can be present in some juveniles or females of *H. parvus*, but is virtually absent in males. Juvenile specimens of *H. thomasi* on the other hand have broken or discontinuous ventrolateral light line (fig. 2). All the specimens of the type series of *H. chaitzami* have continuous and well-defined dorsolateral light lines (fig. 3)

Table 3. Interparietal condition, ventrolateral light line and dorsolateral light line in *H. chaitzami*, *H. thomasi* and *H. stuarti*.

	n	**SVL (mm)**	**Interparietal**			**Lateral light line**			**Dorsolateral light line**		
			Complete	semidivided	divided	absent	broken	continuous	absent	broken	continuous
***chaitzami* (S)**	6	70f, 66f	0	0	**100%**	0	0	**100%**	0	0	100%
hartwegi	26	130.8m, 115.3f	61.53%	23%	19.23%	19.23%	80.77%	0	11.53%	88.46%	0
parvus	67	101.4m, 91.8f	65.7%	32.8%	1.5%	27.9% (n=43)	69.76% (n=43)	2.32% (n=43)	30.95% (n=42)	52.38%(n=42)	16.66% (n=42)
stuarti	11	89.54m, 80.82f	90.9%	9.09%	**0**	30% (n=10)	70% (n=10)	**0**	0	40% (n=10)	60% (n=10%)
thomasi	14	89.56m, 81.81f	92.8%	0	7.1%	57.14	42.85%	**0**	0	7.14%	92.85%
***thomasi* (SL)**	9	92m, 78f	No data	No data	No data	?	occasionally	0	0	22.22%	77.77%

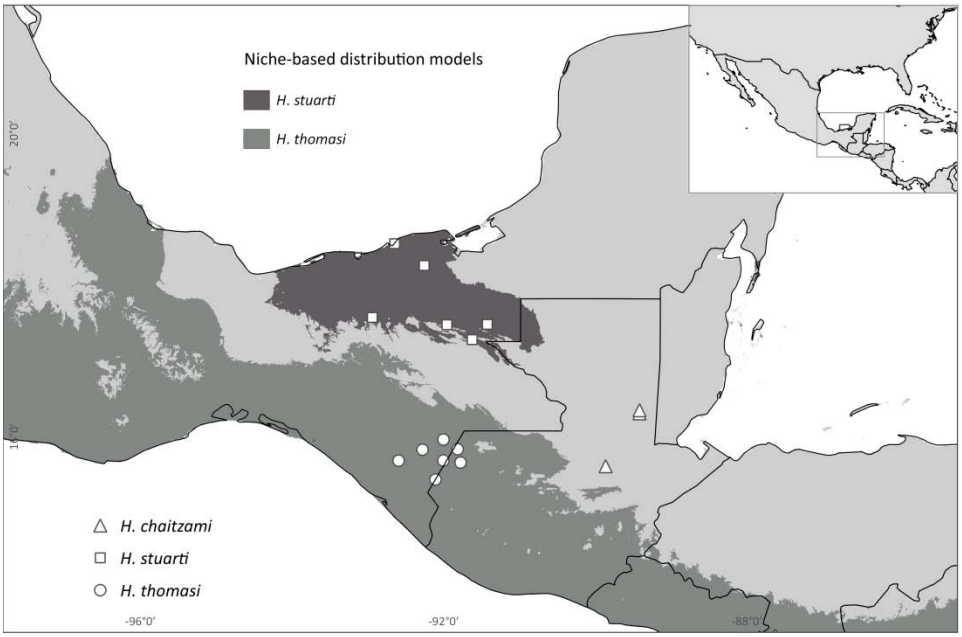

Figure 4. Maxent Niche-based distribution models created for *H. stuarti* and *H. thomasi*. Gray shading depicts areas predicted as suitable habitat using a T16 and T27 fixed umbral respectively (predicted 100% of the data with p<0.05 [0.00-and 0.00-]).

Niche Distribution Models

Figure 4 summarizes the niche distribution models reconstructed for *H. u. thomasi* and *H. chaitzami.* Niche-based distribution models of *H. thomasi* and *H. stuarti* were developed maximizing the area predicted, excluding only areas with probabilities below the probability of the threshold that predicts all the localities. Even under this approach, the models the niche-based distribution models of *H. thomasi* and *H. stuarti* do not predict the area where *H. chaitzami* has been recorded. Niche distribution models for *H. chaitzami* were not developed because only one reliable locality is known, and Poptún populations were not examined and could actually belong to a different species.

Discussion

Our following morphological and niche modeling results indicate that *H. thomasi* is different from *H. chaitzami*: 1) differences in the frequency of divided interparietal, 2) the

presence of continuous ventrolateral light line, 3) their allopatric distribution, and 4) the differences in the climatic niche envelope.

The divided interparietal is not an exclusive character of *H. chaitzami*, since it can be present in other species such as *H. hartwegi*. However, the proportion of individuals with this condition in the type series of *H. chaitzami* (table 3) is unusually high (100%). The populations of *Holcosus*, different from the type series of *H. chaitzami*, that have a high proportion of individuals with divided or semi-divided interparietal are populations of *H. hartwegi* (72-100%), and populations from near Chinandega, Depto. Chinandega, Nicaragua (likely *H. pulcher*; 55%). Those populations can be distinguished on the bases of other characters from *H. chaitzami* and *H. thomasi*. Therefore, even if the frequency of the interparietal condition are not useful to differentiate *H. chaitzami* from *H. hartwegi*, it could be useful to differentiate it from *H. thomasi* (divided interparietal = 3-10%; Table 1, 3).

Holcosus thomasi has marked ontogenetic change and sexual dimorphism in color pattern. Echternacht (1971) mentioned that a series of specimens from the vicinity of Comitán, Chiapas, México have the ontogenetic change, and compared a young specimen (SVL= 68mm) with the holotype of *Holcosus chaitzami*. Based on our observations, we suggest that there is not notable geographic variation in color between these two taxa, and presume that the type series of *H. chaitzami* only consists of juvenile specimens.

We also suggest that the type series *H. chaitzami* consists of adults and that this species is especially small. First, the original description of *H. chaitzami* details the color in alcohol of the holotype (SVL=70mm). The holotype had the legs and arms olive brown above, mottled with black and bluish white, the anterior surfaces of the thighs black with blue spots, the ventral surfaces are bluish, darkest on abdomen, and the sides of the head are blue mottled with black. Juvenile specimens of *Holcosus* lack of blue coloration. Additionally, one of the specimens of the type series, a female with a head-body length of 66mm, had well-formed eggs (Stuart, 1942), showing *H. chaitzami* is actually a small size species with a lateral color pattern that allows to distinguish it from *H. thomasi*.

The holotype and paratypes of *H. chaitzami* have continuous dorsolateral and ventrolateral light lines. The dorsolateral light line is also continuous in *H. thomasi* and *H. stuarti*. However, continuous ventrolateral light line in adults is only characteristic of *H. chaitzami.*

Holcosus chaitzami can be distinguished from *H. thomasi* and *H. stuarti* by the presence of the divided interparietal and continuous and well-defined lateral light line commencing at the eye and extending posteriorly onto the tail. *Holcosus chaitzami* also has dorsolateral light line extending from the posterior corner of the eye to about one third the way back on the tail. Well-defined continuous dorsolateral and ventrolateral lines are also present in *H. quadrilineatus.* However, *H. quadrilinatus* is different, having central gular scales moderately enlarged, irregular in arrangement, scales of posterior one-half of gular region abruptly smaller than scales of anterior one-half, and larger preanals irregularly arranged.

The geographic distribution and niche-based distribution models also support the three lineages (*H. thomasi, H. stuarti* and *H. chaitzami)* hypothesis. We used a liberal threshold to distinguish suitable areas from unsuitable areas for *H. thomasi* and *H. stuarti*, but maintaining zero omission error in the prediction of the excluded locality. Niche-based distribution models *H. thomasi* and *H. chaitzami* do not predict the localities of *H. chaitzami*, neither the type locality, or the localities near Poptún, Guatemala. The model for *H. thomasi* predicted extremely wide area where obviously does not occurs, including the areas of distribution of *H. parvus* (its closest relative). In contrast, the model for *H. stuarti* predicts an area restricted to the probable area of distribution of the species. Models developed using the jackknife approach with small sample sizes identify regions that have similar environmental conditions where the species is known to occur (Pearson et al., 2007). If a set of populations occur under climatic conditions that do not overlap those of closely related species (e.g., Graham et al., 2004), then gene flow between these population and other species may be unlikely, and these populations may represent a distinct species. Therefore, we propose that *H. thomasi* must be resurrected from its synonymy with *H. chaitzami*. *Holcosus thomasi* thus is restricted to the valleys of the upper tributaries of the Río Grijalva in the interior of Chiapas, Mexico, and western central

Guatemala. *Holcosus stuarti* is on the other hand restricted to northern Chiapas and Tabasco, and *H. chaitzami* to the Cahabón Valley, Petén, Guatemala.

Neither *H. thomasi* nor *H. chaitzami* seem to occur at the southern portion of Guatemala, since the southern portion of Guatemala is occupied by *H. parvus* (Meza-Lázaro & Nieto-Montes de Oca, 2015). *Holcosus chaitzami* was recorded near Poptún, Petén, but those specimens morphologically differ from the ones from Cahabón. Thus, we suggest that the actual distribution of *H. chaitzami* is in fact extremely reduced, restricted to the Cahabón Valley. Laurence Cooper Stuart contributed largely to the knowledge of the herpetofauna of Guatemala. In April 1940 this author collected six small lizards in Finca Canihor at the Cahabón Valley in Alta Verapaz, Guatemala and described them as *Ameiva chaitzami*. Finca Canihor is a small cacao plantation on the banks of the Rio Cahabón, 41 kilometers east-northeast of Cobán, at an altitude, probably, about 270 meters (Stuart, 1948). In 1940, little of the region remained virgin, and the heavily cultivated area was burned over every few years (Stuart, 1942) with dominant vegetation formed by savanna grasses with some pine and a *little nance* (Byrsonima) and sahá (Curatella). The Cahabón savannas are restricted to the lower Cahabón Valley (Stuart, 1948). If the geographic distribution of *H. chaitzami* is restricted to Cahabón Valleys, this species could be severely endangered, especially if the burn agricultural practice continues to date.

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CAPÍTULO V

DISCUSIÓN

Holcosus undulatus fue objeto de múltiples estudios durante el siglo XX. Fueron descritas 12 subespecies y fueron propuestas algunas hipótesis sobre el origen y la diversificación de la especie y sobre la evolución de sus caracteres (Stuart, 1940; Smith & Laufe, 1946; Echternacht, 1971). Sin embargo, después de la sinonimización de las subespecies de *H. undulatus,* siguió un largo periodo sin estudios amplios, con sólo algunos ejemplos de estudios aislados sobre aspectos ecológicos (e.g. Pérez Higareda, 1991; Macip-Ríos et al., 2013). La reevaluación de los límites de especies dentro de *H. undulatus* puede atraer renovado interés en el conocimiento de este grupo de escamados.

Holcosus undulatus no es una especie ampliamente distribuida en México y Centroamérica, sino un grupo de especies, cuyo número aún no es definitivo. Este trabajo propone que en México existen, al menos, 12 especies. De acuerdo con los registros del Museo de Historia Natural de Berlín (Museum für Naturkund) y la revisión morfológica de los ejemplares tipo, la localidad tipo de *H. undulatus* es Alvarado Veracruz. Esta especie tan solo ocupa los estados de Veracruz, sur de Puebla y noreste de Oaxaca. Las otras especies mexicanas del género son: *H. podargus*, *H. gaigeae*, *H. hartwegi*, *H. stuarti*, *H. thomasi*, *H. parvus* (en las faldas del volcán Tacaná), *H. sinister* y *H. dexter*, además, de *H. sp*. del noroeste de Guerrero (Fig.) y *H. sp*. de Chiapas y este de Oaxaca que aún requieren una descripción formal. Al sureste de México también se encuentra *H. festivus*.

La información sobre la morfología externa y la distribución de *H. chaitzami* sugiere que ésta no se encuentra en México. Las poblaciones mexicanas pertenecen a *Holcosus thomasi*. Ambas especies se distribuyen en áreas reducidas. *Holcosus chaitzami* está probablemente restringida a los valles del Río Cahabón, Guatemala y *H. thomasi* a los valles de los ríos tributarios del río Grijalva en la Depresión Central de Chiapas. En Honduras se encuentra una especies cercanamente relacionada con *H. gaigeae,* que requiere de una descripción formal y una caracterización morfológica adecuada y en Nicaragua se encuentran *H. pulcher* y *H. miadis*.

Además de éstas especies*, H. sinister*, *H. dexter* y *H. sp* de Chiapas y Oaxaca presentan marcada estructuración geográfica y variación en el patrón de coloración y podrían representar pequeños grupos de especies. Por lo tanto, aún es necesario continuar obtener más evidencias que nos permitan evaluar la diversidad del género en México y Centroamérica. Gracias a las tecnologías de secuenciación masiva, la obtención de miles de loci es cada vez más accesible para organismos no modelo como las especies del grupo *H. undulatus*. Este tipo de datos, combinados con información morfológica y ecológica, serán de gran utilidad en un futuro para resolver las relaciones entre las especies, descubrir nuevas especies, poner a prueba las hipótesis de especies generadas a partir de los datos mitocondriales y morfológicos y reconstruir los mecanismos que promovieron la diversificación en el grupo.

A partir de este estudio, también trabajo surge la necesidad de evaluar el estado de conservación de estas especies, cuyos intervalos de distribución son mucho más reducidos que el de "*H. undulatus*." La distribución de las especies de *Holcosus* aparentemente continua, está en realidad limitada a áreas sombreadas con hojarasca (Macip-Ríos et al., 2013; observación personal). Por esta razón, la mayoría de ellas (excepto *H. stuarti,* que fue colectada en áreas más abiertas) pueden ser incluso más abundantes en bosques perturbados, pero no pueden ocupar áreas convertidas es pastizales. El cambio de uso de suelo en México durante los últimos años ha sido extensivo y es representativo de los otros países en desarrollo (Fuller et al. 2007) y cada especie del género puede tener mayor o menor sensibilidad al cambio de uso de suelo. Por ello, no es posible asumir de antemano que no se encuentran en ninguna categoría de riesgo.

CONCLUSIÓN

Como conclusión presento una lista de especies del género *Holcosus* de México, Guatemala, Honduras, y Nicaragua que solían ser parte de *Holcosus undulatus*. En total son 14 especies. Incluyo en la lista tres especies nuevas que requieren de una descripción formal: *Holcosus sp* de Honduras, *Holcosus sp* del Noroeste de Guerrero, y *Holcosus sp* de Chiapas y este del Istmo de Tehuantepec, Oaxaca. Aparecen también las modificaciones en los nombres sugeridas en los capítulos tres y cuatro de esta tesis: *Holcosus undulatus* ocupando el Golfo de México, *Holcosus dexter* en el pacífico y *Holcosus thomasi* de la Depresión Central de Chiapas (diferente de *Holcosus chaitzami* de Cahabón-Lanquín, Guatemala). En eta lista también está incluida *Holcosus podargus,* aunque no fue elevada al nivel de especie en el artículo (capítulo 2). Sin embargo, existen evidencias que señalan que se trata de una especie diferente. *Holcosus u. podargus* es monofilética, morfológicamente diagnosticable y separada de *H. undulatus* por un punto de ruptura filogeográfica que afecta también a otros grupos (Pérez-Higareda & Navarro, 1980).
Por último aparece *Holcosus miadis*, que aunque no fue incluida en el análisis mitocondrial, considerando que es alopátrida y morfológicamente diagnosticable, indudablemente se trata de un linaje independiente. No se cuenta con muestras de tejido o especímenes de El Salvador, Costa Rica y Belice, por lo que es de esperarse que haya aún más especies dentro del género *Holcosus*. Otra fuente de diversidad críptica es la que podríamos hallar en las especies con pronunciada estructura genética como *Holcosus undulatus*, *H. parvus*, *H. dexter* y *H. sinister*. Además, *Holcosus dexter* presenta variación geográfica muy pronunciada en el patrón de coloración dorsolateral de los machos como puede apreciarse en las figuras 21, 22 y 23.

***Holcosus gaigeae* (Smith & Laufe)**

Sinónimos: *Ameiva undulata gaigeae* — SMITH & LAUFE 1946
Ameiva undulata — ECHTERNACHT 1971
Holcosus undulatus — HARVEY, UGUETO & GUTBERLET 2012
Holcosus gaigeae — MEZA-LÁZARO & NIETO-MONTES DE OCA 2015

Holotipo. Macho adulto (EHT-HMS No. 11927) de Progreso, Yucatán. Recolectado por Hobart M. Smith, 1935.

Paratipos. Sesenta y tres, incluyendo seis topotipos (EHT-HMS Nos. 11925-6, 11928-31), 59 (EHT-HMS No. 11985, UMMZ Nos. 68215, 72934-72957, 80847-80860, 80861 (3), 80862 (5), 83289 (3), 80890 (5) de Chichen Itza, Yucatán; tres (UMMZ No. 78586) de 8 Km tierra adentro de Vigía, Quintana Roo; y dos (UMMZ No. 78587) de Bahía de la Ascensión, Yucatán.

Diagnosis. *Holcosus gaigeae* puede distinguirse de todas las otras especies de *Holcosus,* excepto de *H. hartwegi*, porque presenta escamas gulares centrales pequeñas (más pequeñas que las escamas preanales y mesoptiquiales) arregladas irregularmente (escamas gulares centrales abruptamente agrandadas, iguales o mayores que las escamas preanales y mesoptiquiales en las otras especies de *Holcosus*). Puede distinguirse de *H. hartwegi* por la presencia de coloración (amarilla o naranja y también azul) en las superficies ventral y lateral de la cabeza en machos (ausente en *H. hartwegi*), 12 o más franjas verticales claras en el costado entre los niveles del axila y la ingle (11 o menos en *H. hartwegi*) y una sola hilera de gránulos entre las escamas supraoculares y superciliares (dos hileras de gránulos en *H. hartwegi*).

Figura 2. *Holcosus gaigeae*, Cobá, Quintana Roo. Foto de Tom Riggle.

Figura 3. *Holcosus gaigeae* de Muyil, Yucatán, México. Foto por Tore Grebberg.

Distribución. Península de Yucatán, México. Probablemente también se encuentre en el norte de Guatemala (Fig. 3).

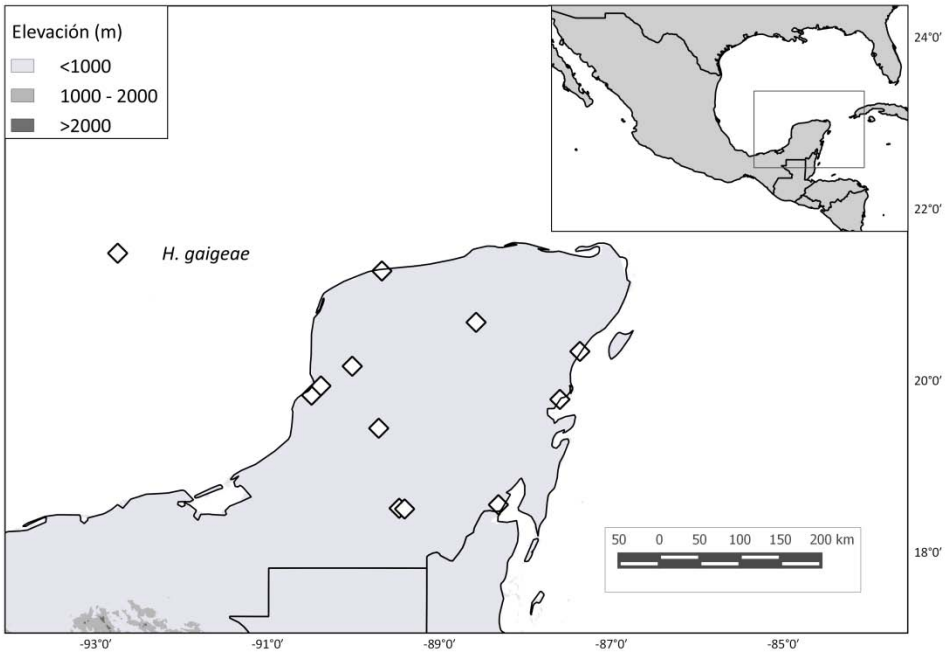

Figura 4. Registros de *Holcosus gaigeae*.

***Holcosus hartwegi* (Smith)**

Sinónimos: *Ameiva undulata hartwegi* — SMITH 1940

Ameiva undulata — ECHTERNACHT 1971

Holcosus undulatus — HARVEY, UGUETO & GUTBERLET 2012

Holcosus hartwegi — MEZA-LÁZARO & NIETO-MONTES DE OCA 2015

Holotipo. U. S. Nat. Mus. No. 108600 de Chiapas, México, atravesando el Río Usumacinta desde Piedras Negras, Petén, Guatemala. Colectado por Hobart M. Smith, 1939.

Diagnosis. *Holcosus hartwegi* se caracteriza por presentar escamas gulares centrales pequeñas (más pequeñas que las escamas preanales y mesoptiquiales) arregladas irregularmente (escamas gulares centrales abruptamente agrandadas, iguales o mayores que las escamas preanales y mesoptiquiales en las otras especies de *Holcosus, excepto en H. gaigeae*) y preanales pareadas (preanales centrales arregladas en una hilera central en *H. dexter* y *H. sinister*). Puede distinguirse de *H. gaigeae* por la presencia de una hilera secundaria de gránulos entre la tercera escama supraocular y las superciliares, y por la presencia de 11 o menos franjas verticales dorsolaterales entre los niveles de la axila y la ingle.

Figura 5. *Holcosus hartwegi* de Yaxchilán, Chiapas. Foto por Luis Canseco Márquez.

Distribución. Este de Chiapas, Petén y Alta Verapaz, Guatemala, y Belice (Fig. 5).

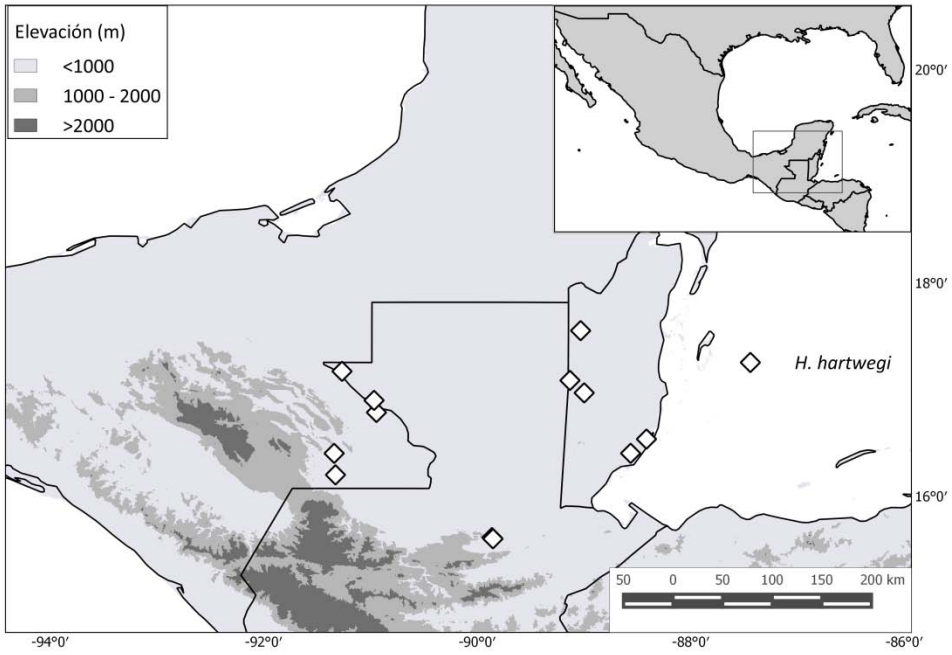

Figura 6. Registros de *Holcosus hartwegi*.

***Holcosus thomasi* (Smith & Laufe)**

Sinónimos: *Ameiva undulata thomasi* — SMITH & LAUFE 1946

Ameiva chaitzami — ECHTERNACHT 1970

Holcosus chaitzami — HARVEY, UGUETO & GUTBERLET 2012

Holcosus thomasi — MEZA-LÁZARO & NIETO-MONTES DE OCA 2015

Holotipo. Macho adulto (EHT-HMS No. 15327) de La Libertad, Chiapas, cerca de Río Cuilco donde cruza la frontera de Guatemala. Colectado por Henry D. Thomas.

Paratipos. Ocho, incluyendo siete topotipos (EHT-HMS Nos. 15323-15326, 15328-15330) y uno de "Chiapas" probablemente de la misma localidad (EHT-HMS 15374).

Diagnosis. Posee preanales pareadas, escamas gulares centrales abruptamente agrandadas arregladas en una hilera longitudinal, carece de una hilera secundaria de gránulos entre la supraocular y las escamas superciliares. Los machos adultos difieren de todas las otras especies de *Holcosus* en el patrón de coloración lateral. En los machos de esta especie las franjas verticales claras en el área lateral superior se fusionan con la línea dorsolateral clara, que forma una banda continua con el borde dorsal regular y el ventral

irregular; el borde ventral de esta banda da origen a las líneas verticales claras en el área lateral (la línea clara dorsolateral, si está presente, no se fusiona con las franjas o manchas claras en el área lateral superior en las otras especies).

Figura 7. Macho de *H. thomasi* de Ciudad Cuauhtémoc, Frontera Comalapa, Chiapas, México. Foto por Luis Canseco.

Distribución. Los valles de los ríos tributarios del Río Grijalva en Chiapas, México y en el oeste de Guatemala.

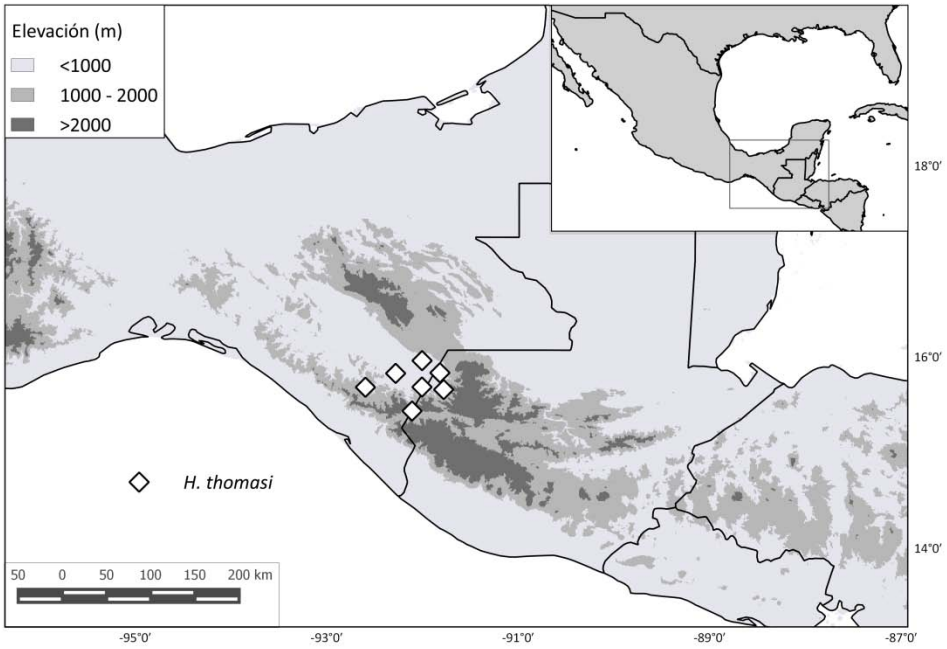

Figura 8. Registros de *Holcosus thomasi*.

***Holcosus stuarti* (Smith)**

Sinónimos: *Ameiva undulata stuarti* — SMITH 1940

Ameiva undulata stuarti — SMITH & LAUFE 1946

Ameiva undulata — ECHTERNACHT 1971

Holcosus undulatus — HARVEY, UGUETO & GUTBERLET 2012

Holcosus stuarti — MEZA-LÁZARO & NIETO-MONTES DE OCA 2015

Holotype. U. S. Nat. Mus. No. 108601 de Palenque, Chiapas

Paratipos. Treinta y nueve especímenes de Palenque, Chiapas (H.M.S. field Nos. 8471-4, 8483-5, 8502-4, 8506-11, 8550-2, 8673, 8684-6, 8750, 8754, 8762-3, 8790-1, 8798-9, 8814-8, 8880,8899, 8927).

Diagnosis. Esta especie se caracteriza por su tamaño reducido, la presencia de escamas gulares abruptamente agrandadas arregladas en una hilera y dos hileras de escamas preanales. El patrón de coloración lateral de los machos permite diferenciar a esta especie de todas las otras. La línea clara dorsolateral es continua y bien definida. El área dorsolateral presenta líneas verticales delgadas, claras amarillas o cafés en un fondo negro (el área lateral presenta coloración azul o verde en los machos de otras especie). La Línea ventrolateral es discontinua (regularmente ausente o tenue en los machos de otras

especies, y continua en *H. chaitzami*). La región gular, mesoptiquial y los lados de la cabeza son de color rojo ladrillo.

Distribución. Tabasco y norte de Chiapas.

Figure 9. Macho de *H. stuarti* de Palenque, Chiapas.

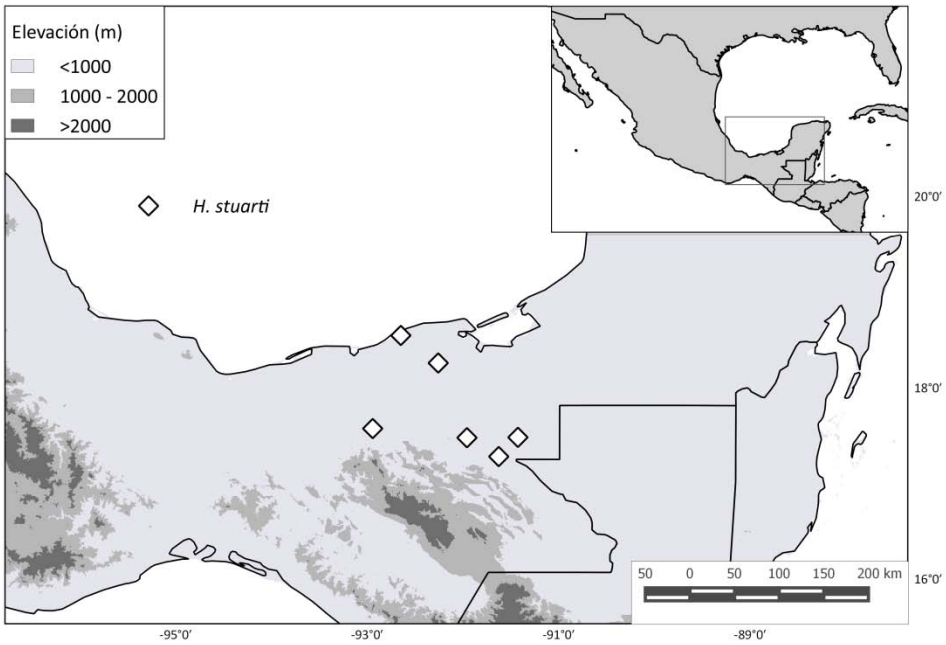

Figura 10. Registros de *Holcosus stuarti.*

***Holcosus sinister* (Smith & Laufe)**

Sinónimos: *Ameiva undulata sinistra* — SMITH & LAUFE 1946

Ameiva undulata — ECHTERNACHT 1971

Holcosus undulatus — HARVEY, UGUETO & GUTBERLET 2012

Holcosus sinister — MEZA-LÁZARO & NIETO-MONTES DE OCA 2015

Holotipo. Macho adulto (EHT-HMS No. 11908) de Manzanillo, Colima, colectado por Hobart M. Smith en 1935.

Paratipos. Son 60, incluyendo 8 de Quesería, Cuauhtémoc, Colima (EHT-HMS Nos. 11906-7, 11946-8, 14499, 15121; UMMZ No. 80109); 20 de Hacienda Paso del Rio, Colima (EHT-HMS Nos. 11909-16, 11949- 51, 14500, 15122-9; UMMZ Nos. 80110, 80111 [3], 80112 [5], 80115 [3], 80120); Salvador (UMMZ No. 80116); Pascuales (UMMZ Nos. 80113 [3], 80114); y Periquillo (UMMZ Nos. 80117 [11], 80118 [2], 80119).

Diagnosis. Esta especie se caracteriza por presentar una sola hilera de escamas preanales, la escama posterior a veces dividida y una hilera de escamas gulares abruptamente agrandadas. La combinación de estos dos caracteres diferencia a las especies de *Holcosus* que se distribuyen al oeste del Istmo de Tehuantepec de todas las otras especies de Holcosus. *Holcosus sinister* difiere de *H. dexter* en el patrón de coloración de los machos: las barras verticales claras del área dorsolateral se continúan con barras en el área ventrolateral adoptando un patrón atigrado.

Figura 11. Macho de *Holcosus sinister* de Chamela, Jalisco, México. Foto por Luis Canseco Márquez.

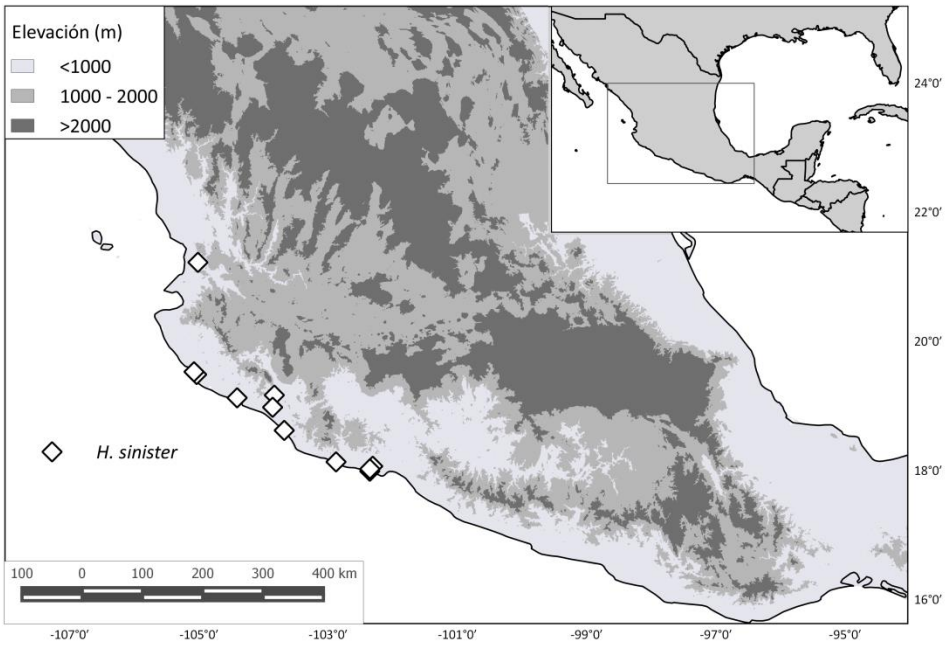

Figura 12. Registros de *Holcosus sinister*.

***Holcosus parvus* (Barbour & Noble)**

Sinónimos: *Ameiva undulata parva* (BARBOUR & NOBLE, 1915)

Ameiva undulata parva — SMITH & LAUFE 1946

Ameiva undulata — ECHTERNACHT 1971

Holcosus undulatus — HARVEY, UGUETO & GUTBERLET 2012

Holcosus parvus — MEZA-LÁZARO & NIETO-MONTES DE OCA 2015

Holotipo. Macho adulto (MCZ No. 5831) de Guatemala. Localidad tipo restringida posteriormente a Mazatenango (Smith & Laufe, 1915).

Descripción. Esta especie se caracteriza por la presencia de escamas preanales pareadas, escamas gulares abruptamente agrandadas arregladas en una hilera central. Puede distinguirse de *Holcosus sp.* de Chiapas y este de Oaxaca, de *H. thomasi*, *H. chaitzami* y *H. stuarti* en el patrón de coloración lateral. El área ventrolateral presenta líneas claras verticales muy definidas y marcadas (líneas fragmentadas o punteadas en *H. sp*. de Chiapas y este de Oaxaca y en *H. thomasi*). El área lateral superior puede presentar una banda clara continua o fragmentada. En el caso de que esté fragmentada, los fragmentos se fusionan con las líneas verticales claras en el área ventrolateral formando líneas que abarcan toda el área lateral.

Figura 13. *Holcosus parvus* joven de Pico de Loro, Unión Juárez, Chiapas. Foto por Luis Canseco Márquez.

Distribución. Sierra Madre, Guatemala y faldas del volcán Tacaná en Chiapas, México, sobre los 1000 msnm.

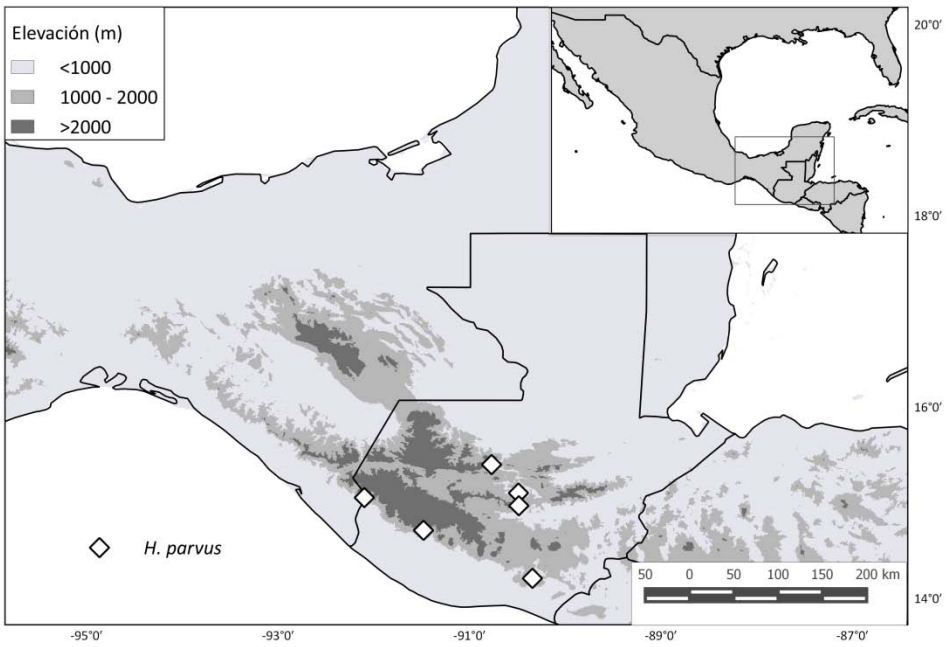

Figura 14. Registros de *Holcosus parvus*.

Holcosus sp.

Holotipo. Macho adulto, Museo de Zoología "Alfonso L. Herrera", No. XXXXX (ANMO 2820). Colectado en abril 15, 2012 por M.E. Ferreira, I. Solano-Zabaleta, R.N. Meza-Lázaro. **Localidad tipo**. Puente Palopique, Carrizal, Cintalapa, Chiapas 16^{o} 31' 15", 93^{o} 51' 5.6".

Diagnosis. Se caracteriza por la presencia de escamas preanales pareadas y escamas gulares centrales abruptamente agrandadas, generalmente arregladas en una hilera (una o dos escamas pueden estar dividida). El área lateral inferior presenta líneas formadas por puntos, separados entre sí o fusionados.

Distribución. Vertiente del Pacífico de Chiapas y este del Istmo de Tehuantepec, Oaxaca.

Figura 15. *Holcosus sp*. de Laguna Bélgica, Ocozocuautla, Chiapas. Foto por Fausto Méndez.

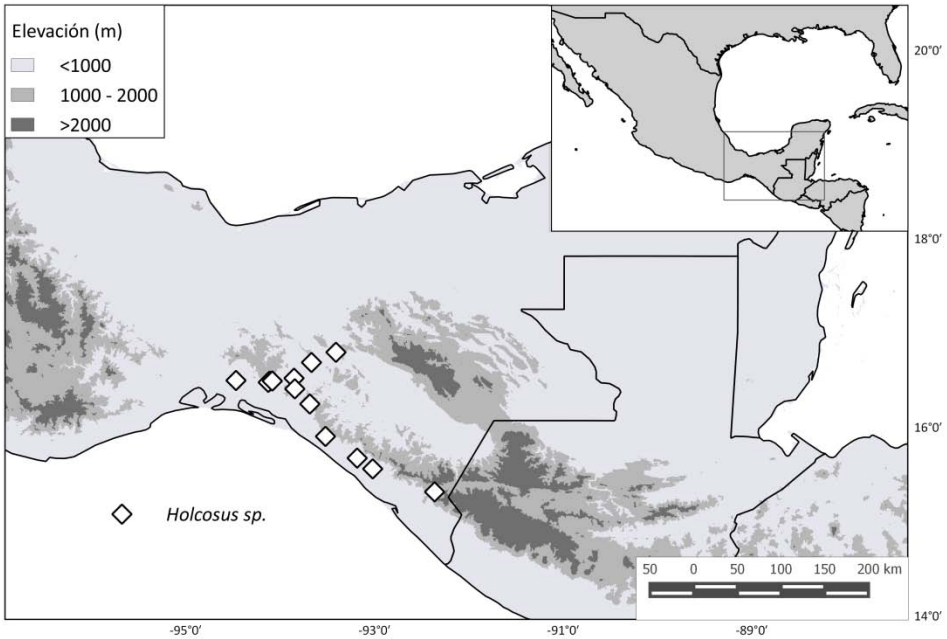

Figura 16. Registros de *Holcosus sp.* de Chiapas y este del Istmo de Tehuantepec, Oaxaca, México.

***Holcosus undulatus* (Wiegmann)**

Sinónimos: *Cnemidophorus undulatus* — WIEGMANN 1834

Ameiva undulata amphigramma — SMITH & LAUFE 1945

Ameiva undulata — ECHTERNACHT 1971

Holcosus undulatus — HARVEY, UGUETO & GUTBERLET 2012

Holcosus amphigrammus — MEZA-LÁZARO & NIETO-MONTES DE OCA 2015

Holcosus undulatus — MEZA-LÁZARO, TILLACK & NIETO-MONTES DE OCA en preparación

Holotipo. ZMB 868, Alvarado, Veracruz.

Paratipos. ZMB 867 y 869, Alvarado Veracruz.

Diagnosis. *Holcosus undulatus* puede distinguirse de otras especies por la siguiente combinación de caracteres: preanales pareadas, gulares centrales abruptamente agrandadas arregladas regularmente. La banda lateral clara continua o interrumpida por espacios oscuros delgados.

Figura 17. *Holcosus undulatus* de San Isidro Lachiguche, Oaxaca N (17° 53.868', O 95° 18.655'). Fotos por Luis Canseco Márquez.

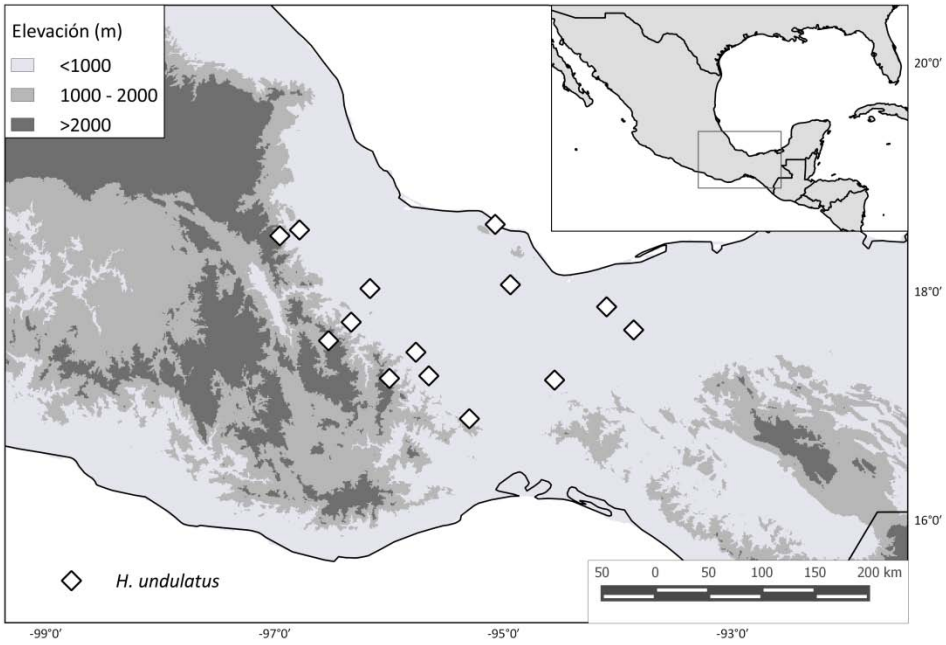

Figura 18. Registros de *Holcosus undulatus.*

***Holcosus podargus* (Smith & Laufe)**

Sinónimos*:* *Ameiva undulata podarga* — SMITH & LAUFE 1946

Ameiva undulata — ECHTERNACHT 1971

Holcosus undulatus — HARVEY, UGUETO & GUTBERLET 2012

Holcosus amphigrammus — MEZA-LÁZARO & NIETO-MONTES DE OCA 2015

Holotipo. Macho adulto (EHT-HMS No. 14471) de 11.3 Km al oeste Ciudad Victoria, Tamaulipas, colectado por Hobart M. Smith y David H. Dunkle en 1934.

Paratipos. Quince, incluyendo 5 (EHT-HMS Nos. 14472-4, USNM Nos. 106141-2) de Hacienda La Clementina, cerca de Forlon, Tamaulipas; tres (EHT-HMS Nos. 11959-61) de Antiguo Morelos, Tamaulipas; dos (UMMZ No. 88232 [2]) de Rio Guayala, near Magiscatzin; tres (EHT-HMS Nos. 11677-9) de Ciudad Maíz, San Luis Potosí; uno (EHT-HMS No. 11962) de Valles, San Luis Potosí; y uno (HMS No. 1597) de Huichihuayan, San Luis Potosí.

Diagnosis. Se caracterizan por tener escamas preanales pareadas y escamas gulares abruptamente agrandadas arregladas de manera irregular. Se distingue de *H. undulatus* por la ausencia de la franja clara en el área lateral superior.

Distribución. Norte de Veracruz, Norte de Puebla, Hidalgo, Querétaro San Luis potosí y Tamaulipas

Figura 19. *Holcosus podargus* de la Sierra Madre Oriental, Tamaulipas, México. Foto por Toby Hibbitts.

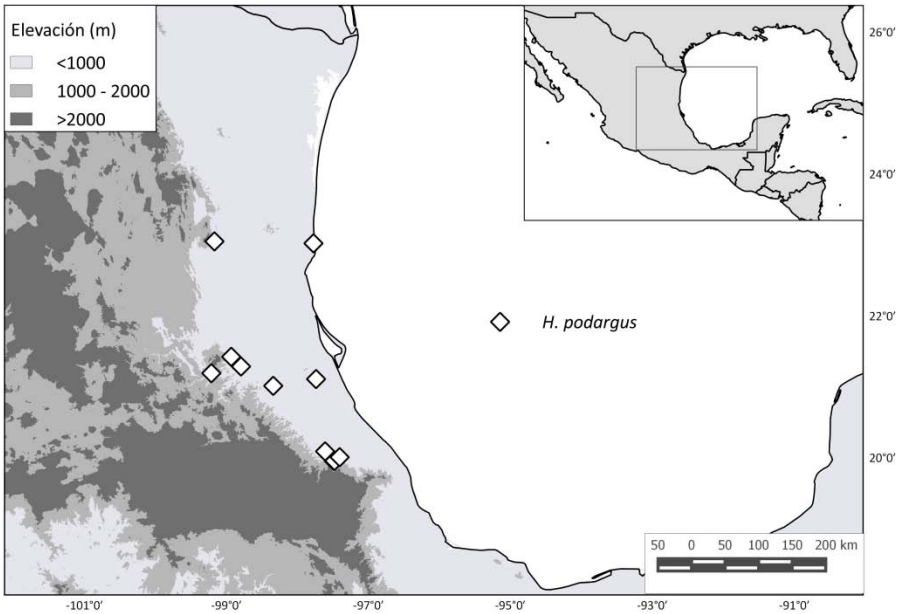

Figura 20. Registros de *Holcosus podargus.*

***Holcosus dexter* (Smith & Laufe)**

Sinónimos: *Ameiva undulata dextra* — SMITH & LAUFE 1946

Ameiva undulata — ECHTERNACHT 1971

Holcosus undulatus — HARVEY, UGUETO & GUTBERLET 2012

Holcosus undulatus — MEZA-LÁZARO & NIETO-MONTES DE OCA 2015

Holotipo. Macho adulto (EHT-HMS No. 11966) de Rincón, Guerrero, colectado por Edward H. Taylor and Hobart M. Smith).

Descripción. Presentan una hilera media de escamas preanals y una hilera media de escamas gulares centrales abruptamente agrandadas. La coloración lateral de los machos está caracterizada por la tendencia a formar una franja clara en el área lateral superior (Figs. 21 y 22). Sin embargo, en las poblaciones que ocupan las áreas cercanas a Huatulco, Oaxaca, los machos presentan franjas verticales claras en un fondo obscuro en el área lateral superior en vez de una franja clara continua (Fig. 23).

Figura 21. Macho de *Holcosus dexter* de El Ocotito, Guerrero. Foto por Peter Heimes

Figura 22. Macho de *Holcosus dexter* de Sierra de Malinaltepec, Guerrero. Foto por Oscar Rivera.

Figura 23. *Holcosus dexter* de Huatulco, Oaxaca. Foto por Fabiola Balcazar.

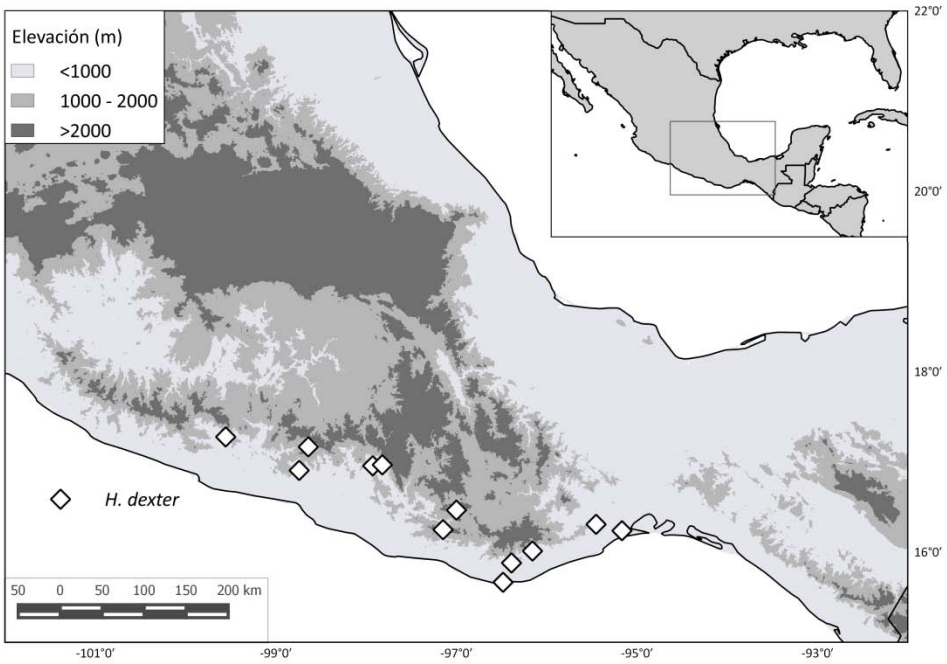

Figura 24. Registros de *Holcosus dexter.*

Holcosus sp.

Holotipo. El Paraíso, Atoyac de Álvarez, Guerrero, México.

Descripción. Se caracteriza como el resto de los *Holcosus* al oeste del Istmo de Tehuantepec por la presencia de escamas preanales arregladas en una sola hilera o en forma de roseta, pero no en hileras pareadas. Presentan escamas gulares centrales abruptamente agrandadas formando una hilera longitudinal. Se distingue de *H. sinister* en la tendencia a formar una banda clara en el área lateral superior en los machos adultos (área lateral superior ocupada por manchas claras separadas por franjas verticales obscuras en *H. sinister*). Puede diferenciarse de *H. dexter* por la coloración amarilla de la gula y los lados de la cabeza de los machos adultos (rojo ladrillo o naranja en *H. dexter*) aunque es necesario establecer la estabilidad de éste carácter).

Distribución. Noroeste de Guerrero.

Figura 25. *Holcosus sp.* El paraíso, Guerrero. Foto por Stephen Davies.

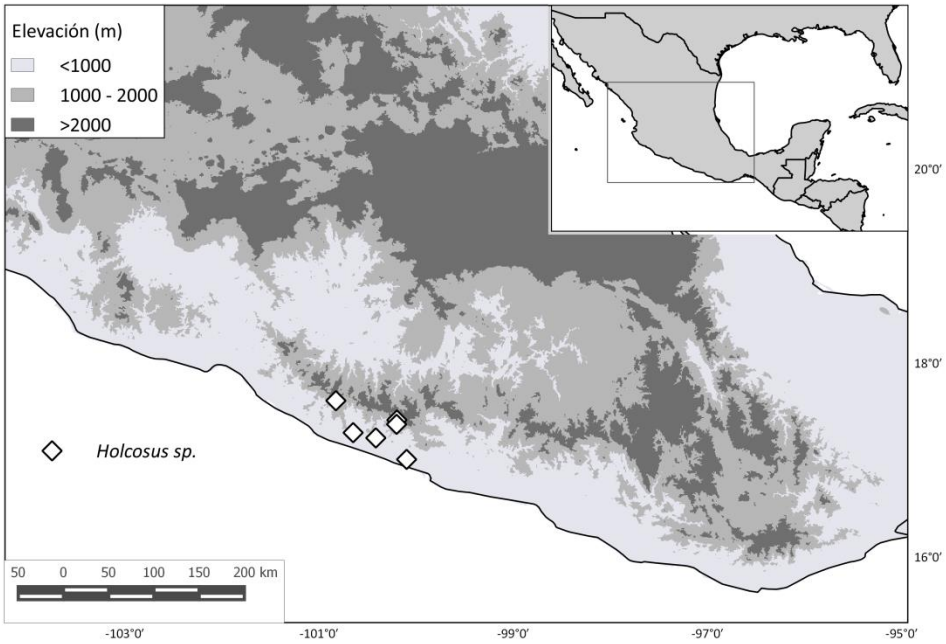

Figura 26. Registros de *Holcosus sp*. de Guerrero, Mexico.

Holcosus sp.

Comentario. Esta especie presenta escamas preanales pareadas y escamas gulares centrales abruptamente agrandas (*H. gaigeae* y *H. hartwegi* presentan escamas gulares

centrales pequeñas). No se conoce caracteres o una combinación de caracteres diagnósticos que permitan diferenciarla *H. parvus*, *Holcosus sp.* de Chiapas y de otras poblaciones en Centroamérica.

Figura 27. *Holcosus sp*. de San Pedro Sula, Honduras

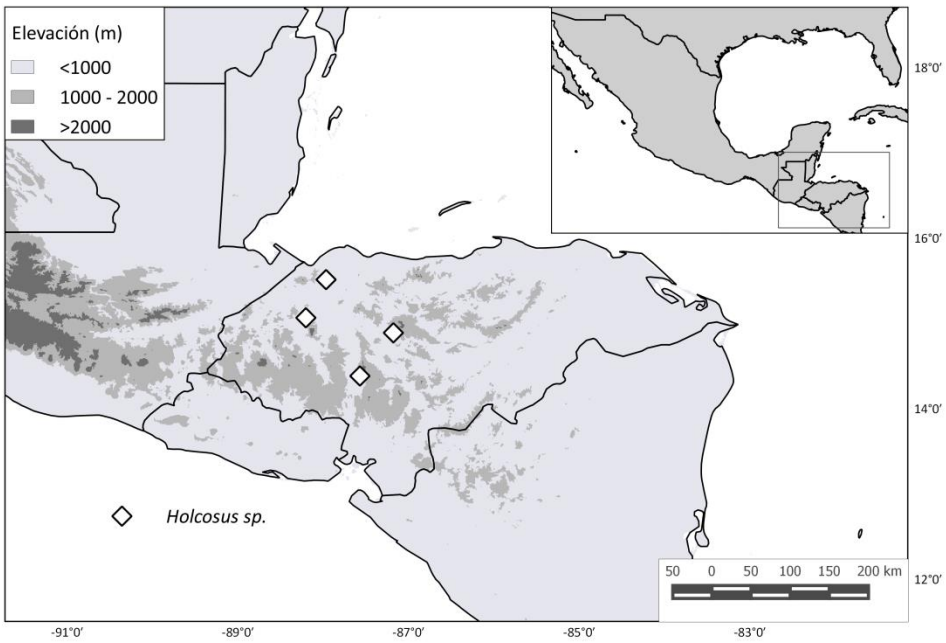

Figura 28. Registros de *Holcosus sp.*

***Holcosus pulcher* (Hallowell)**

Sinónimos: *Ameiva pulchra* — HALLOWELL 1860

Ameiva undulata quadrilineata — BARBOUR & NOBLE 1915

Ameiva undulata — ECHTERNACHT 1971

Holcosus undulatus — HARVEY, UGUETO & GUTBERLET 2012

Holcosus pulcher — MEZA-LÁZARO & NIETO-MONTES DE OCA 2015

Syntypes: ANSP 9133-9134 de Nicaragua.

Diagnosis. *Holcosus pulcher* se caracteriza por presentar escamas preanales pareadas, escamas gulares agrandadas arregladas irregularmente, rodeado por escamas pequeñas, y la última supraocular separada de las occipitales por dos o tres hileras de escamas granulares. El dorso es color olivo, con líneas laterales color marrón. Puede distinguirse de todas las otras especies de *Holcosus,* excepto de *H. podargus* del grupo *undulatus* por la presencia de escamas abruptamente agrandadas en la gula arregladas irregularmente. Sin embargo, *H. podargus* es muy lejana geográficamente y no está estrechamente relacionada con esta especie.

Distribución. Costa Pacífica de Nicaragua (Echternacht, 1971). Existen pocos registros: Chinandega (Barbour y Noble, 1915), Managua y Laguna de Apoyo (Fig. 30).

Figura 29. Hembra de *Holcosus pulcher* de Laguna de Apoyo, Nicaragua. Foto de Kolby Kirk.

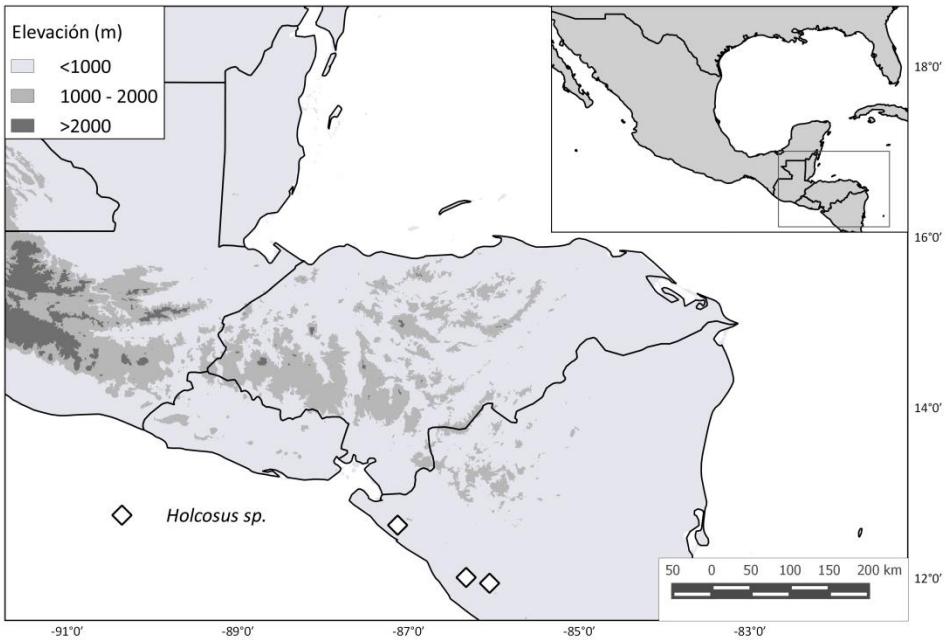

Figura 30. Registros de *Holcosus pulcher*.

***Holcosus miadis* (Barbour & Loveridge)**

Sinónimos: *Ameiva festiva miadis* — BARBOUR & LOVERIDGE 1929

Ameiva undulata miadis — VILLA 1983

Ameiva undulata miadis — ECHTERNACHT 1970

Ameiva undulata — ECHTERNACHT 1971

Holcosus undulatus — HARVEY, UGUETO & GUTBERLET 2012

Holcosus miadis — MEZA-LÁZARO & NIETO-MONTES DE OCA 2015

Holotipo. MCZ-26970, colectado por James L. Peters en Great Corn Island, Departamento de Zelaya, Nicaragua.

Paratipos. Cinco especímenes (MCZ-26971-75) de Great Corn Island Nicaragua.

Dianosis. *Holcosus miadis* se caracteriza por presentar escamas preanales pareadas, escamas gulares centrales abruptamente agrandadas arregladas en una hilera longitudinal. Puede distinguirse de todas las otras especies de *Holcosus* en el patrón de coloración dorsolateral de machos y hembras adultos (Fig. 31). El patrón lateral de barras azules (en machos) o marrones (en hembras) en un fondo negro se extienden desde franja medio-dorsal hasta los escudos ventrales (Echternacht, 1970).

Distribución. Endémica de Islas del Maíz, Departamento de Zelaya, Nicaragua (Fig. 32): Great Corn Island de 10.3 Km^2 y Little Corn Island de 2.9 Km^2 (Sunyer, 2013).

Figura 31. *Holcosus miadis* de Isla del Maíz Grande. Tomado de Sunyer *et al.* (2013)

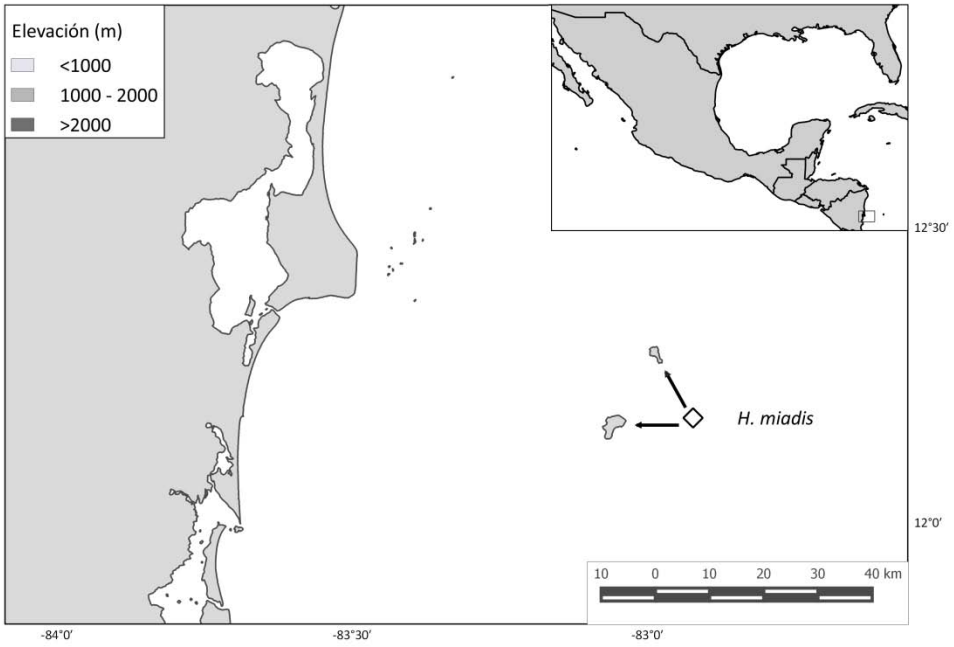

Figura 32. Registros de *Holcosus miadis.*

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