



Solving a 50-year Mystery: Rediscovery of *Mesaspis antauges* (Squamata: Anguinae)

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Abstract

Vertebrate rediscoveries occur frequently, but must be properly documented for scientific credibility. Ongoing rediscoveries suggest a need for greater caution in declaring species extinct. Here, we report a rediscovery of the mysterious Mexican anguid lizard *Mesaspis antauges* (Cope 1866), a species last recorded by scientists in 1964. Our comparison of newly-collected material against previous specimens, all of which apparently originate from a single isolated volcanic peak, confirms the taxonomic validity of this species and the relegation of the binomen *M. modestus* (Cope 1878) to the status of a junior synonym. We include a brief discussion of the natural history of *M. antauges*, and explore the conservation implications of our rediscovery.

Resumen

Los redescubrimientos de vertebrados ocurren frecuentemente, pero deben ser debidamente documentados para la credibilidad científica. La serie de recientes redescubrimientos sugiere la necesidad de tener mayor precaución al declarar que las especies se han extinguido. Aquí reportamos el redescubrimiento del misterioso ánguido mexicano *Mesaspis antauges* (Cope 1866), una especie que los científicos registraron por última vez en 1964. Nuestra comparación de material recién recolectado y especímenes previos, todos los cuales aparentemente proceden de un solo pico volcánico aislado, confirma la validez taxonómica de esta especie y la relegación del binomio *M. modestus* (Cope 1878) al estatus de sinónimo más moderno. Incluimos una breve discusión de la historia natural de *M. antauges*, y exploramos las implicaciones de nuestro redescubrimiento en conservación.

Key words: Color pattern, *Mesaspis modestus*, Mexico, Morphology, Natural history, Pico de Orizaba, Taxonomy

Palabras clave: Patrón de coloración, *Mesaspis modestus*, México, Morfología, Historia natural, Pico de Orizaba, Taxonomía

Introduction

Species rediscoveries are of great interest to taxonomists, morphologists, and conservationists, and can help to address the Wallacean shortfall (Ladle *et al.* 2011). Vertebrate rediscoveries have substantiated the contemporary existence of living fossils (Holder *et al.* 1999; Biton *et al.* 2013), validated taxonomically controversial species (Robertson *et al.* 2011), provided fresh insights on diagnostic morphological traits (Bille 2001; Yáñez-Muñoz *et al.* 2010; Dever *et al.* 2015), and galvanized preservation efforts (Eames *et al.* 2005; Priddel *et al.* 2008; Ariano-Sánchez *et al.* 2011). However, one high-profile proposed rediscovery (Fitzpatrick *et al.* 2005) is now widely considered to have been inaccurate, emphasizing the necessity of ironclad documentation before a finding is announced (Sibley *et al.* 2006; Ladle *et al.* 2009; Roberts *et al.* 2010). Lack of physical material continues to cloud the credibility of claimed species rediscoveries in some cases (e.g., Grünwald *et al.* 2016).

Method of documentation aside, vertebrate rediscoveries worldwide occur at an average rate of approximately three species per year, and are accelerating in frequency (Scheffers *et al.* 2011). In Mexico alone, over a dozen species of anurans and squamates have been rediscovered in the past 15 years after being “lost” to science for several decades (Flores-Villela *et al.* 2005; Reyes-Velasco *et al.* 2010; Delia *et al.* 2013; Ramírez-Bautista *et al.* 2013; Luría-Manzano *et al.* 2014; Caviedes-Solis *et al.* 2015; Barrio-Amorós *et al.* 2016; Furbush *et al.* 2017). These finds demonstrate that suspicions of extinction are often premature, and suggest that greater restraint against declaring species extinct is warranted for poorly-studied, secretive taxa that occupy remote habitats (Ladle *et al.* 2011; Scheffers *et al.* 2011; Delia *et al.* 2013; Caviedes-Solis *et al.* 2015). Ultimately, many additional little-known, long-lost Neotropical herpetofauna are likely to prove extant, although probably in urgent need of protection (Scheffers *et al.* 2011).

In 2013, we obtained a small series of specimens suspected to represent the mysterious Mexican anguid lizard *Mesaspis antauges* (Cope 1866). This species has a murky systematic history, and was last collected in 1964. We take this opportunity to taxonomically validate the species, clarify its biology, and discuss conservation implications.

Members of *Mesaspis* range from central Veracruz, Mexico, to northern Panama. They are generally moderate-sized, terrestrial, mostly allopatrically-distributed lizards that occupy mesic microhabitats in montane forests. With four endemic species, Mexico stands as a center of diversification in this group. All Mexican *Mesaspis* are classified under Mexican federal law as Special Protection (Sujetas a Protección Especial) on the Norma Oficial Mexicana (NOM-059-SEMARNAT-2010) list. Globally, the IUCN Red List categorizes most species as Least Concern: *M. gadovii* (Boulenger 1913), *M. monticola* (Cope 1878), *M. moreletii* (Bocourt 1872), and *M. viridiflava* (Bocourt 1873). Under the same list, *M. juarezi* (Karges & Wright 1987) is considered Endangered, *M. cuchumatanus* (Solano-Zavaleta, Nieto-Montes de Oca & Campbell 2016) is Not Evaluated, and *M. antauges* is Data Deficient.

The genus *Mesaspis* was coined by Cope (1877), but was subsumed by most later workers into one of several other genera. The name was resurrected from the synonymy of *Barisia* by Good (1988). Today the genus is widely accepted (Savage 2002; Greene *et al.* 2006; Liner & Casas-Andreu 2008; Solano-Zavaleta *et al.* 2016), and seven described species of *Mesaspis* are recognized (Uetz & Hošek 2016). However, recent molecular evidence suggests that *Mesaspis* is paraphyletic with respect to the gerrhonotine genus *Abronia* (Solano-Zavaleta 2011; Pyron *et al.* 2013). Furthermore, mitochondrial DNA sequence data indicates the existence of several undescribed species of *Mesaspis* (Solano-Zavaleta 2011), and *M. moreletii* is suspected to be polytypic (Solano-Zavaleta *et al.* 2016). Pending formal taxonomic revision, we use the genus *Mesaspis* here and recognize seven species-level lineages within the taxon, plus an eighth putative species for the purpose of discussion: *M. modestus* (Cope 1878).

Tihen (1949) was the first to identify subclades within the genus *Mesaspis*, although referring to them as *Barisia*. He denoted the *gadovii* clade (content: *M. antauges*, *M. gadovii*, and *M. modestus*) on the basis of several lepidosis synapomorphies. Good (1988), after an expanded morphological analysis, later erected *M. gadovii* as a stand-alone lineage. He also re-branded the remaining taxa as the *antauges* group, and added the recently-described *M. juarezi* to that group. An unpublished phylogeny based on mitochondrial DNA (Solano-Zavaleta 2011) affirmed the monophyly of the *gadovii* group, but did not resolve *M. gadovii* as sister to all other group members. Hence, for the remainder of this contribution, we take the conservative approach of referring to the *gadovii* group, *sensu* Tihen (1949), as the named clade that encompasses our taxa of interest: *M. antauges*, *M. gadovii*, *M. juarezi*, and *M. modestus*.

The species *Mesaspis antauges* has suffered a torturous nomenclatural history. It has been ascribed over a dozen synonyms in the literature, due to various genus/subgenus combinations, misspellings, and conflation with the problematic species *M. modestus*. Scientific study of both *M. antauges* and *M. modestus* is further plagued by limited physical material. This material is mostly of vague provenance, but appears to have originated entirely from a single volcano far removed from any known congeners. We summarize this history below, to contextualize our find. Institutional collection abbreviations follow Sabaj (2016).

Cope (1866) described *Mesaspis antauges* (as *Barissia antauges*) on the basis of a single specimen (USNM 30221) collected by François Sumichrast. By implication, Cope gave the type locality as “Orizaba, Vera Cruz.” Sumichrast (1882), referring to the species as *Gerrhonotus antauges*, later indicated that the holotype originated from the “Region alpina de Orizaba” (=Región alpina de Orizaba). The city of Orizaba lies in the state of Veracruz, Mexico at an elevation of ca. 1,300 m, well below the alpine zone. Sumichrast’s locality, therefore, probably refers

to the nearby volcano of Pico de Orizaba, whose summit is 5,675 m elevation (Rossotti *et al.* 2006). Gadow (1905) subsequently supported this conclusion, reporting *Gerrhonotus antauges* on “Citlaltépetl” at elevations he variously reported as 8,500 ft, 12,000 ft, and “more than 12,000” ft (2,590 to over 3,650 m). Citlaltépetl is the name for Pico de Orizaba in the local Nahuatl language. A few years later, Gadow (1908) elaborated on his encounters with *Gerrhonotus antauges*, placing them at La Barbara “presumably at 12,500 feet of elevation” on Pico de Orizaba, Veracruz, Mexico. One specimen (BMNH 1903.9.30.122) was collected by Gadow and bears the locality “Xometla,” in reference to a town of that name situated at ca. 2,600 m on the southeast slope of Pico de Orizaba. A third specimen (NMB 3685, formerly MBS 3685), listed as *Gerrhonotus (Barisia) antauges*, possesses the datum “Piz de Orizaba, W.S.M.” and was “obtained from Geneva in 1881” by a man named Lamme or Lamne (H. M. Smith, unpubl. data). On 9 July 1964, a fourth specimen (CAS 98681), listed as *Barisia antauges*, was collected by C. Wemmer from “Mexico: Veracruz: SE slope Mt. Orizaba: along trail (road) between La Perla and Xometla. Alt: 7500 ft.”

Over a decade after describing *Mesaspis antauges*, Cope (1878) described the remarkably similar *Pterogasterus modestus* on the basis of three specimens (USNM 7084) also collected by Sumichrast. Therein, Cope states that “The precise locality from which the specimens of this lizard were sent to the Smithsonian Institution is uncertain, but is probably Guatemala.” Smith (1942) later emended the type locality for what he called *Gerrhonotus modestus*, describing it variously as “apparently Orizaba, not Guatemala as guessed by Cope,” and “Mount Orizaba, Veracruz.” Smith’s decision appears to have been based on tags labeled “Veracruz” borne by the type specimens (Tihen 1949). In fact, the original USNM catalog ledger for these specimens gives the locality (dittoed from that of USNM 7076) as “Orizaba Mex. Alpine region,” which is replicated in all jar tags for this lot (K. Tighe, pers. comm.). Subsequently, Smith (1984) relegated *Barisia modestus* to the status of a junior synonym of *Barisia antauges*, but without any justification. Karges & Wright (1987) followed the same taxonomic arrangement, citing correspondence with Smith but again providing no further details to support the decision. This synonymy was upheld by Good (1988), who justified his position by claiming a lack of differentiating lepidosis traits, contra Smith (1942) and Smith & Taylor (1950). Good also considered all *M. antauges* specimens to be male, and all *M. modestus* to be female, thus attributing their divergent body proportions to sexual dimorphism, which is known in congeners (Karges & Wright 1987; Solano-Zavaleta *et al.* 2016).

It is evident from this review that at least one species of *Mesaspis* occurs on Pico de Orizaba, Veracruz, Mexico, at a likely elevation range of ca. 2,200–3,800 m. Numerous targeted expeditions to Pico de Orizaba by ourselves, and others, over the last several decades have failed to secure new material (Flores-Villela & Santos-Barrera 2007). However, in 2013 we collected three new specimens of *Mesaspis* from the northeastern slopes of Pico de Orizaba, including adults of both sexes. This material was mentioned by Solano-Zavaleta *et al.* (2016), but we describe it in detail here for the first time. Our morphological analysis of this and all pre-existing material, supplemented with biogeographic evidence, both validates *M. antauges* as a taxon and affirms the synonymy of *M. antauges* and *M. modestus*. We also describe the color pattern of *M. antauges* in life and in preservative, briefly discuss its natural history, and comment on its habitat use and conservation status.

Materials and methods

From February 2013 to August 2013, we made six trips to the northeastern slopes of Pico de Orizaba, Veracruz to conduct general herpetofaunal surveys. We examined high-quality digital photographs or physical specimens of the seven existing individuals of *M. antauges* and *M. modestus*, with the exception of Gadow’s specimen from Xometla (BMNH 1903.9.30.122). This specimen was apparently mis-shelved sometime in the late 1980s and is now lost (Patrick Campbell, pers. comm.). However, we did obtain a set of morphological data for this specimen, recorded prior to its loss.

We maintained wild-collected specimens in captivity for behavioral observation post-capture. All specimens died of natural causes within 10 months of entering captivity, whereupon we fixed them in 10% buffered formalin, followed by preservation in 70% ethanol and deposition in the Museo de Zoología “Alfonso L. Herrera,” Facultad de Ciencias, Universidad Nacional Autónoma de México (MZFC-HE; formerly MZFC). We confirmed sex by post-euthanasia eversion of hemipenes, except in the case of one specimen (subadult MZFC-HE 29312) due to poor preservation after death.

We recorded measurements using dial calipers (to the nearest mm). Scale terminology follows Bogert & Porter (1967), but we adhere to Tihen (1949), Smith & Taylor (1950), and Good (1988) in recognizing the postrostral scale, given this scale's historical diagnostic significance in *Mesaspis*. For bilateral head scales, we recorded counts on both sides, expressed herein as "right/left." Karges & Wright (1987: 6–7) discussed the terminology applied to the lateral head scales situated between the nasal and the orbit. We diverge from these authors' definitions in labeling the single large scale present between the small postnasals and large preocular as the cantholoreal. In some specimens, a small scale is present between the lower postnasal and the cantholoreal, which we interpret as a reduced loreal.

Although we obtained tissue from all three *Mesaspis* captured from Pico de Orizaba in 2013, in this contribution we refrain from inferring their position in a phylogenetic tree. DNA sequencing would be largely uninformative for identification, due to the lack of any historical genetic material for *M. antauges* or *M. modestus*. Multi-locus genetic studies of evolutionary relationships within *Mesaspis* and *Abronia* are ongoing, into which our new samples will eventually be included.

Results

We captured lone *Mesaspis* on each of three separate trips to the Municipio de Alpatláhuac on Pico de Orizaba, Veracruz, in 2013. On 7 May, we collected a subadult of unconfirmed sex (MZFC-HE 29312) at 2,320 m elevation in the vicinity of Ayahualulco (19.10258°N, 97.13828°W). On 7 June, we collected an adult female (MZFC-HE 29311) at 2,620 m elevation from Mesa de Buena Vista (19.12089°N, 97.14344°W). Finally, on 28 June 2013, we collected an adult male (MZFC-HE 29310) at 2,340 m elevation in the vicinity of La Manzanita, a barrio within Ayahualulco (19.09786°N, 97.13817°W). Datum WGS 84 for all coordinates (Fig. 1A).

Subsequent to these collections, we became aware of a fourth, uncatalogued adult specimen of *Mesaspis* deposited at the Instituto Tecnológico Superior de Zongolica in Veracruz (ITSZ). This specimen was collected from the southeastern slopes of Pico de Orizaba at "El Pilancón," Municipio de La Perla, at approximately 3,300 m elevation (18.98°N, 97.23°W). We have viewed a photograph of this specimen in life, and tentatively attribute it to *M. antauges* based on gross morphology and biogeography, but do not mention it further due to lack of access for close study.

We personally examined three specimens from the Texas A&M Biodiversity Research and Teaching Collections (TCWC 22098–22100) listed as *Mesaspis antauges* and collected in 1959 from "Los Cambres de Acultzingo" (=Los Cumbres de Acultzingo), Veracruz, Mexico. We determined that they actually represent adult *Barisia imbricata*, on the basis of (1) fusion of supranasal and upper postnasal scales; (2) incomplete superciliary scale series; (3) strongly keeled dorsal scales of head, body, and tail; and (4) robust body with snout-to-vent length >100 mm. We also examined specimen MNHN 000.2920, listed as *Gerrhonotus antauges*, from the collection of the Muséum National d'Histoire Naturelle. Although supposedly collected from "Veracruz" (Bocourt 1878), this may be in error because the collection data on file at the MNHN lists only "Mexique: Sans localité précise." Regardless, upon examination the specimen is clearly attributable to *Mesaspis viridiflava* on the basis of (1) postmental scale undivided, (2) postrostral scale absent, (3) frontonasal scale absent, (4) eight longitudinal nuchal scale rows, (5) 14 longitudinal dorsal scale rows, and (6) moderately keeled dorsal scales. We do not discuss any of these specimens further.

Of the lot of three specimens that apparently constitute the type series for *Mesaspis modestus* (USNM 7084), only one specimen has a snout-to-vent length (72 mm) that corresponds to the measurement given in the original description by Cope (1878). We therefore designate this specimen as the lectotype, and the other two specimens in the lot as paralectotypes. Through courtesies extended to us by USNM staff, the two paralectotypes are now re-catalogued with their own unique numbers: USNM 591589–591590. The lectotype retains the original catalogue number USNM 7084. Hereafter in this contribution, we will refer to the type series using these three unique catalog numbers.

Morphology. We assessed physical features that previous authors (Tihen 1949; Smith & Taylor 1950; Karges & Wright 1987; Good 1988) have considered diagnostic for the *M. gadovii* group or members of its component species. We include data for all previously known *M. antauges* and *M. modestus* exemplars. Selected features are provided in Table 1.

None of the seven specimens attributed to *M. antauges* or *M. modestus* have their hemipenes everted or their tail bases dissected, with the possible exception of Gadow's specimen BMNH 1903.9.30.122, which we could not examine because it is now lost. As such, it is unclear why Good (1988) attributed supposed differences between these species to sexual dimorphism. We were unable to secure permission to dissect these specimens for independent physical confirmation of their sex.

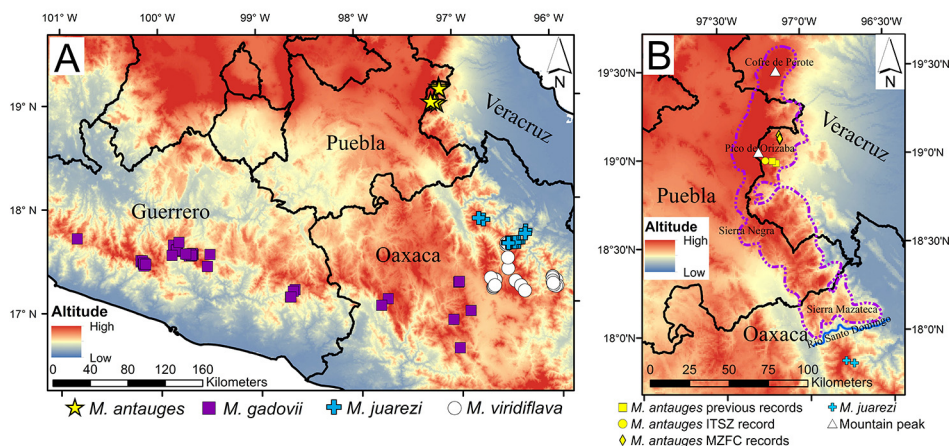


FIGURE 1. Distribution of *Mesaspis* in Guerrero, Oaxaca, and Veracruz, Mexico. The dashed blue line in part B delineates our rough prediction of the possible geographic range of *M. antauges*.

Color Pattern. In preservative, adult male MZFC-HE 29310 and subadult MZFC-HE 29312 are generally similar in appearance (Fig. 2). The dorsum of the head, body, and tail is medium brown with a few small, irregular dark marks. A dark dorsolateral line, bordered above in places by pale spots that sometimes converge into a line, extends from mid-neck to near the insertion of the forelimbs. The sides of the head, body, and tail are predominantly dark chocolate brown. On the flanks, and sometimes on the neck, several dark marks occur in irregular series. These marks form up to 14 interrupted dark vertical bands, usually with small adjacent white marks posteriorly. A pale line extends posteriorly from the cantholoreal scale to below the eye, and the pale supralabial scales form another line surrounded by dark marks. Two white marks or bars, bordered by dark pigment, extend posteriorly from the upper and lower portion of the eye. The chin and throat are mostly gray-green with heavy dark vermiculations and dark and white spots, which begin ventrolaterally just below the orbits. The limbs have several irregular dark marks and white spots, and the venter of the body, limbs, and tail is gray-green with many dark and white spots. The only noticeable variation on subadult MZFC-HE 29312 with respect to adult MZFC-HE 29310 is the presence of irregular dark marks that form a thin, nearly continuous vertebral stripe, becoming interrupted on the tail; and the presence of two dorsolateral, discontinuous dark lines on the body. The adult female (MZFC-HE 29311) differs from the above description in being generally less dramatically marked, as follows. The dorsum of the body above the lateral fold, including the head, limbs, and tail, is uniform brown save for a few small, irregular dark marks on the anterior part of the head. On the body, small irregular dark brown marks that suggest a thin vertebral line extend from the middle of the neck to the tip of the tail. Additional irregular dark marks, generally forming a discontinuous dorsolateral line on each side of the body, extend from the middle of the neck to almost the tip of the tail. The flanks, neck, and sides of the head and tail are predominantly brown. A pale gray line extends posteriorly from the tip of the snout to the last supralabial scale, delimited above by a dark line in the area below the orbit. The venter of the body, limbs, and tail is generally paler, contrasting noticeably with the dorsum along the lateral line.

In life, color pattern differs only minimally from color in preservative. For the adult male (MZFC-HE 29310) and subadult (MZFC-HE 29312), this pattern is as described herein. The dorsum of the head, body, and tail is dull medium brown (subadult) or bright rufous brown (adult), with a few small, irregular dark marks. A thin, dark, partial vertebral stripe is present (subadult) or absent (adult). The body shows a thin, complete (subadult) or interrupted (adult) dorsolateral dark stripe, demarcated dorsally on the neck, pectoral, and pelvic regions by pale yellow to white spots that occasionally fuse into a stripe. The sides of the head, body, and tail are mostly gray-

brown (subadult) or charcoal gray (adult), and notably darker than the dorsum. The flanks and sometimes the neck are marked with a few (subadult) or many (adult) black spots that tend to occur in series, forming up to 14 thin vertical stripes and usually bordered posteriorly by pale yellow to white spots. The labial scales anterior to the orbit are dirty white, mottled with varying amounts of light or dark gray. The labial scales ventral and posterior to the orbit are marked with distinct or amorphous alternating black and white bars that are slanted posteriorly. The chin and throat are pale gray-green, with dark ventrolateral vermiculations that originate roughly at the level of the orbits. The venter of the body, limbs, and tail is pale gray-green with heavy vermiculations, composed of black spots usually bordered posteriorly and laterally by white spots. The limbs are gray to brown, and irregularly marked with black and white spots. The color pattern of the adult female (MZFC-HE 29311) differs notably from the others, as follows. The dorsum and sides of the body, limbs, and tail are almost uniform medium brown, with limited contrast between the paler dorsum and darker flanks. The body is marked with an indistinct, dark vertebral stripe, and with dorsolateral spots that converge into thin, partial stripes. The tail has a series of dark, posteriorly directed chevrons. Indistinct markings are visible on the face. The labial scales are pale gray with dark spots, and bordered above with a dark line near the orbit; no obvious black or white bars are visible. The venter of the body, limbs, and tail is similar to the males' but generally paler, contrasting more strongly with the dorsum along the lateral fold.

Natural History. Gadow (1905; 1908) provides the only pre-existing field data on the habitat and biology of *M. antauges*. In his 1905 article, he states that the species inhabits “pine-forests,” “the grass near little streams,” and “tussocks of grass,” adding that it is viviparous, and lives on “insects and worms.” In a popular account of his travels, Gadow (1908) also noted that *M. antauges* “shed their skin, fingers, eyelids and all, in one continuous piece.” This observation matches all available ecdysis data for other gerrhonotine anguids (Spengler & Smith 1983; González-Romero & López-González 1990). Rieppel (1978) included specimen NMB 3685 in an analysis of tooth replacement patterns.



FIGURE 2. Habitus of *Mesaspis antauges* in life. Top photo: subadult MZFC-HE 29312. Middle and bottom photos: adult male MZFC-HE 29310. Photos by Nelson Martín Cerón de la Luz.

We captured all of our new material while the lizards were basking in the morning, always in open areas near forest edges and close to microhabitat refuges (tall grass, bare roots, rotting logs, rocks, bushes). The lizards were terrestrial in habit. We encountered the adult male (MZFC-HE 29310) in a church courtyard, the adult female (MZFC-HE 29311) moving over leaf litter in a fragmented patch of *Alnus acuminata* (Fig. 3), and the subadult (MZFC-HE 29312) hiding among the roots of a shrub within an orchard of *Prunus domestica*. Natural vegetation in the surrounding areas is composed mainly of *Alnus acuminata* forest, although tracts dominated by *Quercus* spp. and *Pinus* spp. are also present. Undisturbed forest in the region is now largely restricted to the ridgelines and steep upper slopes of the generally east-west trending valleys. The zones where we encountered the specimens retain only fragments of forest, embedded in a matrix of pastures, cropland, orchards, and rural residences.



FIGURE 3. Disturbed *Alnus acuminata* forest habitat for *Mesaspis antauges* in the Municipio de Alpatláhuac, Pico de Orizaba, Veracruz. Photos by Nelson Martín Cerón de la Luz.



FIGURE 4. Copulating *Mesaspis antauges* in captivity. Male MZFC-HE 29310 (top), and female MZFC-HE 29311 (bottom). Photo by Carlos Javier Pérez Alvarado.

We fed captive lizards with house crickets, *Acheta domestica*, and American cockroaches, *Periplaneta americana*. The lizards became active at about 9 am most mornings, and activity ceased by 5 pm when they sought shelter. Of particular interest was a captive mating event between MZFC-HE 29310 and 29311, observed on 6 July 2013. Almost immediately upon the adult male and subadult being introduced to the female's enclosure, they began to display their gular areas to her with brief, subtle movements while she remained passive. The subadult soon disengaged, and moved to the opposite end of the terrarium from the female. The adult male continued to display, and subsequently approached and bit the neck of the female, while holding and lifting the base of her tail for hemipenial insertion (Fig. 4). The pair remained copulating in this position for just over four hours, from 1037 to 1420 h. This is the first copulation event reported for the genus, but is generally consistent with copulatory behavior documented in the gerrhonotine genera *Abronia* (Campbell & Frost 1993; Schmidt Ballardo & Mendoza-Quijano 1999), *Elgaria* (Banta & Leviton 1961; Beaman & Reining 2003), and *Gerrhonotus* (Lazcano Jr. *et al.* 1993).

Discussion

Our re-analysis of all historical material attributed variously to *M. antauges* or *M. modestus*, and analysis of our new series of specimens, confirms our rediscovery of one of the most enigmatic Mesoamerican squamates.

All *Mesaspis* specimens we examined from Pico de Orizaba possess a divided postmental scale and complete superciliary scale series, except possibly in MZFC-HE 29312 for which poor preservation precluded an evaluation. Presence of these features confirms these specimens' placement in the *gadovii* group (*M. antauges*, *M. gadovii*, *M. juarezi*, and *M. modestus*). Some past authors (e.g., Tihen 1949) have considered additional features to be diagnostically relevant for the *gadovii* group. However, recent work has revealed dramatic intra- and inter-species variation in *Mesaspis*, showing those features to be uninformative for diagnosis of *gadovii* group members (Karges & Wright 1987; Solano-Zavaleta *et al.* 2016).

Our analysis of the type material for both *M. antauges* and *M. modestus* shows that only the frontonasal scale (present in the former, absent in the latter) can potentially be used to separate them (Table 1). However, the existence of the frontonasal scale is variable in the closely related and geographically proximate *M. juarezi* (Karges & Wright 1987). The additional *Mesaspis* material from Pico de Orizaba bears out this variability in the presence/absence of the frontonasal, with no correlated variation in other traits. We conclude that no feature of lepidosis can diagnose *M. modestus* from *M. antauges*.

Substantiating the identity of our new material on the basis of color pattern in life is impossible. The sole written description of living *M. antauges* simply refers to them as "brown" (Gadow 1908), and no description of color in life exists for *M. modestus*. Descriptions of color pattern in the preserved type specimens by Cope (1866; 1878) are more detailed, but are still too superficial to separate *M. antauges* or *M. modestus* from congeneric species recognized today. A later color description by Cope (1900) for *M. antauges* is unreliable, because it draws upon material now attributed to *M. viridiflava*. The re-description by Lynch & Smith (1965) of the color pattern of the *M. antauges* holotype, although concise, is in general agreement with ours.

Karges & Wright (1987) identified two diagnostic color-pattern traits for *M. antauges* (including *M. modestus* in their concept of that species): supralabial scales mottled with dark and light pigment but lacking stripes or bars; and dorsum lacking even traces of dark, posteriorly directed chevron markings. Recent digital imagery of the type specimens of both *M. antauges* and *M. modestus* reveals that they have become severely faded, even bleached. Their vestiges of remaining pattern, however, correspond well to our new material, as does the pattern of more well-preserved specimens of Pico de Orizaba *Mesaspis* (CAS 98681 and NMB 3685) that we have personally examined, both of which appear to be males. On the basis of this analysis, we concur with Karges & Wright (1987) that a dorsum lacking any traces of dark chevron markings is a consistent trait of *Mesaspis* from Pico de Orizaba, and unique among members of the *gadovii* group. However, in life, and to a somewhat lesser extent in preservative, our new adult male and subadult specimens in fact clearly show distinct, uninterrupted light and/or dark bars on the supralabial scales ventral and posterior to the orbit (Fig. 2). Similarly distinct marks, in the same position on the face, are also visible on specimens CAS 98681 and NMB 3685, contra Karges & Wright (1987). As such, facial pattern is now best regarded as uninformative for diagnosing *Mesaspis* from Pico de Orizaba.

Table 1. Selected traits for *Mesaspis antauges* and “*M. modestus*.”

Specimen	postmental	supranasals	postnasals	loreal	cantholoreal	superciliary series complete	suboculars	postrostral	frontonasal	posterior internasal	dorsal scales	sex/age/SVL
“ <i>M. modestus</i> ” USNM 7084 Lectotype	divided	expanded	2/2	0/1	1/1	yes/yes	3/3	present	present	divided	smooth	female (?) adult 72 mm†
“ <i>M. modestus</i> ” USNM 591589 Paralectotype	divided	expanded	2/2	0/1	1/1	yes/yes	3/3	present	present	divided	smooth	female (?) adult 80 mm†
“ <i>M. modestus</i> ” USNM 591590 Paralectotype	divided	expanded	3/3°	0/0	1/1	yes/yes	3/3	present	present	divided	smooth	female (?) subadult 54 mm†
<i>M. antauges</i> USNM 30221 Holotype	divided	expanded	2/2	1/1	1/1	yes/yes	3/3	present	absent	divided	smooth	male (?) adult 85 mm*
<i>M. antauges</i> † BMNH 1903.9.30.122	divided	expanded	2/2	1/1	1/1	yes/yes	3/3	present	absent	divided	smooth	male (?) adult 72 mm
<i>M. antauges</i> NMB 3685 (MBS 3685)	divided	expanded‡	2/3	0/0	1/1	yes/yes	2/3	present	absent	divided	smooth	male (?) adult 82 mm
<i>M. antauges</i> CAS 98681	divided	expanded	2/3	0/0	1/1	yes/yes	3/3	present	present	divided	smooth	male (?) adult 79 mm
<i>M. antauges</i> MZFC-HE 29310	divided	expanded	2/2	0/0	1/1	yes/yes	2/2	absent	absent	divided on left side	smooth	male adult 75 mm
<i>M. antauges</i> MZFC-HE 29311	divided	expanded	2/2	0/0	1/1	yes/yes	2/2	absent	absent	entire	smooth	female adult 82 mm
<i>M. antauges</i> MZFC-HE 29312	–	expanded	2/2	0/0	1/1	–	2/3	present	present	divided	slightly convex	male (?) subadult 64 mm

* = measured by Lynch & Smith 1965, and Karges & Wright 1987

° = lowermost scale on right side partly fused with cantholoreal

† = data courtesy of J. P. Karges

‡ = left supranasal only slightly expanded

Sexual dimorphism and sexual dichromatism are both suggested in our small series of newly-collected material, consistent with similar sexual differences documented in congeners (Karges & Wright 1987; Solano-Zavaleta *et al.* 2016). Conspecificity of these new specimens is strongly indicated by our observation of a captive copulation event. Sexual differences have been cited as a reason to taxonomically sink *M. modestus* into *M. antauges* (Good 1988), a claim of uncertain validity because the sex of the type material could not be confirmed through analysis of sex organs. Ultimately, because *Mesaspis* are notorious for dramatic within-population variation in morphology and color pattern, any emergent pattern of divergence between the sexes may disappear once additional material comes to light. Furthermore, every specimen attributable to these two supposed taxa are known or suspected to have originated from the slopes of a single volcano well isolated from congeneric populations, providing biogeographic evidence that a single species is likely involved (Fig. 1).

On the basis of this combined evidence, we affirm the validity of *M. antauges* (Cope 1866) as a diagnosable taxon, and corroborate the taxonomic decision by Good (1988) to relegate *M. modestus* (Cope 1878) to the status of a junior synonym. Nearly 50 years after it was last collected, we hereby announce the persistence of wild populations of *Mesaspis antauges* on Pico de Orizaba, Veracruz, Mexico. This species can be distinguished from all described congeners using the following combination of identifiers: (1) postmental scale divided; (2) smooth or slightly convex dorsal scales; (3) dorsum lacking even traces of posteriorly directed dark chevron-shaped markings (although dark spots may be present); (4) moderate size, with adult snout-to-vent length up to 85 mm; (5) known geographic range restricted to Pico de Orizaba, Veracruz, Mexico.

Mesaspis antauges is the northernmost representative of the genus. All existing and historical localities for the species on Pico de Orizaba lie over 130 km NNW of the nearest congeneric populations of *M. juarezi* in the extreme northern Sierra de Juárez, Oaxaca (Canseco-Márquez & Gutiérrez-Mayén 2010) (Fig. 1A). *Mesaspis viridiflava* is also known from the Sierra de Juárez, sympatric in places with *M. juarezi* (Karges & Wright 1987). North of the Sierra de Juárez lies an uninterrupted north-south trending montane corridor that has variously been considered as part of the Trans-Mexican Volcanic Belt or Faja Volcánica Transmexicana (Rovito & Parra-Olea 2016), the southern reaches of the Sierra Madre Oriental (Campbell & Duellman 2000), or a unique range called the Sierra Negra or Sierra Negra de Puebla (Canseco-Márquez & Gutiérrez-Mayén 2010). The southernmost expansion of this corridor is known as the Sierra Mazateca. These highland peaks and ridgelines extend continuously from the foothills of Pico de Orizaba to the Sierra Mazateca, in excess of 2,300 m elevation throughout. However, the Sierra Mazateca is sharply separated from the Sierra de Juárez by the low-elevation valley of the Río Santo Domingo, biogeographically isolating *M. antauges* from possible congeneric contact (Fig. 1B). Although reports of congeneric sympatry exist both within *Mesaspis* (Karges & Wright 1987; Solano-Zavaleta *et al.* 2016) and *Abronia* (Campbell & Frost 1993; Peterson & Nieto-Montes de Oca 1996; Torres *et al.* 2013), allopatry is nevertheless a dominant pattern of evolutionary diversification in these genera. For these reasons, we predict that *Mesaspis antauges* will remain allopatric to all congeners even after additional sampling, further emphasizing its validity as a species.

We hypothesize that the restriction of *M. antauges* to Pico de Orizaba is a sampling artifact. Pico de Orizaba is geologically young, with an estimated age of just 650,000 yr (Rossotti *et al.* 2006). It supports no additional species of microendemic vertebrate save for the salamanders *Thorius lunaris* and *T. spilogaster*, which are known only from the volcano's lower flanks (Hanken & Wake 1998; Wake & Vredenburg 2008). This speciose genus of dwarfed salamanders is evolutionarily and ecologically very different from *Mesaspis*, however, being characterized as an "adaptive radiation in miniature" with high rates of localized speciation driven by extremely low vagility (Rovito *et al.* 2013). Geographically proximate, unbroken highland corridors suggest that the range of *M. antauges* could extend south as far as the Sierra Mazateca, or north along the edge of the Trans-Mexican Volcanic Belt to the base of Cofre de Perote (Fig. 1B). We encourage biologists to be attentive to the possibility of *Mesaspis* in the subalpine forests of these montane regions. However, identifications must be made with care because the anguids *Abronia graminea*, *Barisia imbricata*, *Celestus enneagrammus*, and *Gerrhonotus ophiurus* also occur throughout this mountainous region (e.g., Canseco-Márquez & Gutiérrez-Mayén 2010). Indeed, we ourselves encountered *B. imbricata* in syntopy with our new *M. antauges* material.

Historic records for *M. antauges* by Gadow (1905; 1908) indicate that the species potentially ranges up to the edge of the pine belt at ca. 3,800 m elevation on Pico de Orizaba. However, the only specimen actually collected by Gadow (BMNH 1903.9.30.122) bears locality data indicating that it was taken much lower, at ca. 2,600 m elevation. Gadow's material, plus specimen CAS 986681 and our own recent specimens, cumulatively represent

the only verifiable, specific known sites for *M. antauges*. Based on this material, we here confirm that the species inhabits the lower eastern slopes of Pico de Orizaba, in forested landscapes variously dominated by *Alnus acuminata*, *Quercus* spp. and *Pinus* spp. at elevations from ca. 2,200–2,700 m. Additional field surveys are needed to clarify the true elevation and habitat range of *M. antauges*.

The habitat data for our recent specimens shows that *M. antauges* can persist in highly human-modified habitats, with minimal adjacent natural forest cover. Further study is required to evaluate whether such degraded, fragmented habitats support densities of *M. antauges* comparable to those in more intact habitats. The apparent adaptability by *M. antauges* to anthropogenic disturbance is nonetheless encouraging for its conservation status.

Neither existing nor historical localities for *M. antauges* lie within any protected areas. However, we consider it plausible that the species' range extends into nearby Parque Nacional Pico de Orizaba, a 19,750-ha federal preserve centered roughly on the volcano's summit. On the northeastern slopes of the volcano, the park boundary descends to ca. 3,000 m elevation, where it encloses large swaths of generally intact forest that might currently support *M. antauges*. Assuming sufficient connectivity of habitat fragments at lower elevations, the park also has potential as a future refuge for *M. antauges* under climate change-driven altitudinal migration scenarios.

Using the published IUCN Red List criteria, we conservatively re-evaluate *M. antauges* as Endangered, based on an extent of occurrence estimated at < 3,000 km² and an area of occupancy estimated at < 50 km², fulfilling criteria B1ab(iii) and B2ab(iii). An alternative system for assessing threat level in herpetofauna is the Environmental Vulnerability Score (EVS), which has been applied widely across Mesoamerica (Wilson *et al.* 2013a; Wilson *et al.* 2013b; Johnson *et al.* 2015). An advantage of this metric compared to the current IUCN system is that it does not “penalize” little-known species, as the Data Deficient category sometimes does (Johnson *et al.* 2015; Bland & Böhm 2016). Under this system, *M. antauges* was previously assessed as having an EVS of 16, placing it in the high vulnerability category (H) (Wilson *et al.* 2013b). We suggest that this EVS remain unchanged.

Despite limited data, two independent threat assessment systems thus indicate that *M. antauges* is imperiled. We make the case that *M. antauges* is a taxonomically valid, diagnosable lineage that warrants immediate conservation attention. We hope that this contribution will stimulate such action.

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