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# A New Species of *Abronia* (Squamata: Anguidae) from the Sierra de Zongolica of Veracruz, Mexico

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**We describe a new arboreal alligator lizard species in the genus *Abronia* from the Sierra de Zongolica in west-central Veracruz, Mexico. The new species is presently known only from the vicinity of the type locality. It is diagnosable from all congeners by the following combination of characters: one occipital scale, two primary temporal scales contacting the postocular series, moderately protuberant posterolateral head scales, lack of protuberant or spine-like supra-auricular scales, 30–34 transverse dorsal scale rows, dorsal scales on the flanks arranged in slightly oblique longitudinal rows relative to the ventrolateral fold, and lateralmost ventral scale row unexpanded relative to the adjacent medial row. The new species occurs sympatrically with *Abronia graminea*, but genomic data assign it to the *oaxacae* group as the sister species of *A. oaxacae*, a finding that is corroborated by morphological evidence. We briefly discuss the regional biogeography of arboreal *Abronia* and comment on the Sierra de Zongolica as a complex transitional area of high species richness and conservation importance.**

**Se describe una nueva especie de lagartija arbórea del género *Abronia* de la Sierra de Zongolica en el centro-oeste de Veracruz, México. Esta nueva especie se conoce actualmente sólo en las cercanías de la localidad tipo. Se puede distinguir de todos sus congéneres por medio de la siguiente combinación de caracteres: una escama occipital, dos escamas temporales primarias en contacto con la serie postocular, escamas posterolaterales de la cabeza moderadamente protuberantes, ausencia de escamas supra-auriculares protuberantes o espinosas, 30–34 hileras transversales de escamas dorsales, escamas dorsales en los flancos dispuestas en hileras longitudinales ligeramente oblicuas con respecto al pliegue ventrolateral, y la hilera de escamas ventral más lateral sin expandir con respecto a la hilera media adyacente. La nueva especie es simpátrica con *Abronia graminea*, sin embargo, los datos genómicos la asignan al grupo *oaxacae* como la especie hermana de *A. oaxacae*, asignación que se corrobora por la evidencia morfológica. Se discute brevemente sobre la biogeografía regional de las especies arbóricolas de *Abronia* y se resalta la Sierra de Zongolica como un área de transición compleja con una alta riqueza de especies e importante para la conservación.**

**V**ERTEBRATES that inhabit tropical forest canopies, and especially arboreal amphibians and reptiles, have long been understudied (Vitt and Zani, 1996; Kays and Allison, 2001). The comparative inaccessibility of arboreal habitats, coupled with the behavioral crypsis of many animals that live there, continues to challenge scientists who investigate organismal diversity within the canopy frontier (Barker and Pinard, 2001; McCracken and Forstner, 2014).

The arboreal herpetofauna of Mexico is a globally important and species-rich assemblage. To name some of the most prominent groups, this assemblage ranges from frogs in the genera *Charadrahyla* and *Ecnomiohyla*, to salamanders in the genera *Bolitoglossa* and *Chiropterotriton*, to lizards in the genera *Abronia* and *Anolis*. Within the past two decades, four new tree-dwelling species of anguimorph lizards have been proposed for recognition in Mexico (Flores-Villela and Sánchez-H., 2003; Werler and Campbell, 2004; Campbell et al., 2016; Clause et al., 2020). These recent finds suggest the

promise of this habitat type for further discoveries. Herein we offer another installment to the growing tally of arboreal species, this one involving the charismatic and imperiled genus *Abronia*.

The alligator lizards of the genus *Abronia* (Anguidae: Gerrhonotinae) occur in mountainous regions throughout much of Middle America. Under the recently expanded concept of this genus (see discussion below regarding work by Gutiérrez-Rodríguez et al., 2021), *Abronia* occur, in Mexico, on both sides of the Isthmus of Tehuantepec, ranging on the Atlantic slope from northeastern Tamaulipas southward to Chiapas, and on the Pacific slope from eastern Michoacán and central Guerrero to Chiapas (Campbell and Frost, 1993; Centenero-Alcalá et al., 2009). Species in *Abronia* also occur to the south and east of Mexico, across Guatemala, northern El Salvador, Honduras, Nicaragua, Costa Rica, and into northwestern Panama (Campbell and Frost, 1993; Gutiérrez-Rodríguez et al., 2021). Over this broad distribution, both arboreal and terrestrial species exist, yet nearly all

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are found exclusively in upper to mid-elevation woodlands, particularly evergreen cloud forests and seasonally dry pine and pine-oak forests (Campbell and Frost, 1993; Gutiérrez-Rodríguez et al., 2021). Due to their often highly restricted geographic distributions and the ongoing deforestation in their native ranges (Campbell and Frost, 1993), many of the arboreal species are considered severely imperiled. This endangerment, coupled with the often-striking appearance of these lizards, has led to substantial recent conservation interest, especially in Mexico (Sánchez-Herrera et al., 2017; Güizado Rodríguez and Porto Ramírez, 2018; SEMARNAT, 2018).

The genus *Abronia* has a lengthy nomenclatural history. Landmark taxonomic revisions by Tihen (1949) and Good (1988) were followed by the classic monograph of Campbell and Frost (1993), which remains the most complete revisionary treatment of *Abronia* to date. Using extensive morphological evidence, Campbell and Frost (1993) diagnosed six species groups (subgeneric clades) and recognized 24 species of *Abronia*, all of them known or presumed to be arboreal. Since this monographic treatment, six new arboreal species of *Abronia* have been described (Campbell, 1994; Campbell et al., 1998, 2016; Campbell and Brodie, 1999; Flores-Villela and Sánchez-H., 2003; Clause et al., 2020). In the first-ever molecular (mitochondrial DNA) phylogenetic analysis of *Abronia*, involving samples from 11 species, Chippindale et al. (1998) subsequently upheld the morphology-based six-clade classification system of Campbell and Frost (1993). Recently, a more well-sampled phylogenetic analysis based on ddRADseq genomic data by Gutiérrez-Rodríguez et al. (2021), which included 17 of 30 recognized species of arboreal *Abronia* and all ten species of the closely related terrestrial genus *Mesaspis*, recovered two main clades distributed in the highlands of Middle America east and west of the Isthmus of Tehuantepec, respectively. Within these two main clades, the authors resolved eight strongly supported species groups, each of which was corroborated by external morphology. Importantly, Gutiérrez-Rodríguez et al. (2021) also resolved multiple independent clades of arboreal and terrestrial species, rendering *Abronia* and *Mesaspis* non-monophyletic relative to one another. Given the nomenclatural priority of *Abronia* over *Mesaspis*, the authors placed *Mesaspis* in the synonymy of *Abronia*. This synonymy increased the content of *Abronia* to 40 species, a tally that includes four species elevated from within the former *Mesaspis moreletii* complex (see Solano-Zavaleta and Nieto-Montes de Oca, 2018).

Among the eight species groups recognized by Gutiérrez-Rodríguez et al. (2021), three constitute the former clade (subgenus) *Abronia* within the genus *Abronia* recognized by Campbell and Frost (1993): Group I (composed of *A. deppii* and *A. martindelcampoi*), Group III (*A. fuscolabialis*, *A. graminea*, and *A. taeniata*), and Group V (*A. cuetzpali*, *A. mixteca*, and *A. oaxacae*). All three groups are arboreal. Gutiérrez-Rodríguez et al. (2021) recovered none of these three groups as sister to one another, but Campbell and Frost (1993) united them based, in part, on two key characters: lack of an enlarged lateral row of ventral scales and lack of strongly protuberant or spine-like supra-auricular scales. Additionally, Campbell et al. (2016) united *A. cuetzpali*, *A. deppii*, *A. martindelcampoi*, *A. mixteca*, and *A. oaxacae* (Groups III and V of Gutiérrez-Rodríguez et al., 2021) in what they called the *deppii* group, based on a synapomorphy of having

dorsal scales on the flanks arranged in oblique longitudinal rows relative to the ventrolateral fold. Hereafter, we have followed Gutiérrez-Rodríguez et al. (2021) by referring to the Group V members of the former *deppii* group (*A. cuetzpali*, *A. mixteca*, and *A. oaxacae*) as the *oaxacae* group, a clade that is especially pertinent to the new lineage which is the subject of this paper.

All members of the *oaxacae* group are endemic or nearly endemic to the Mexican state of Oaxaca. They cumulatively range from 1710–2820 m elevation, largely in seasonally dry pine and pine-oak woodlands (Aldape-López and Santos-Moreno, 2016; Campbell et al., 2016). *Abronia cuetzpali* occurs along a lengthy escarpment of the Sierra Madre del Sur that is commonly called the Sierra de Miahuatlán (Campbell et al., 2016; Schätti, 2019). Farther to the north in the Sierra Madre del Sur, *A. mixteca* occurs on both sides of the continental divide in the Mixteca Alta (=Sierra Mixteca) and also in the Sierra de Cuatro Venados, with localities extending north toward the Puebla border and west into the Malinaltepec region of eastern Guerrero (Campbell and Frost, 1993; Canseco-Márquez and Gutiérrez-Mayén, 2010; Martín-Regalado et al., 2012; Campbell et al., 2016). With a more easterly distribution, *Abronia oaxacae* is found in the Sierra de Juárez, Sierra de Aloapaneca (=Sierra de Monteflor), and Sierra de Cuatro Venados, in addition to seemingly isolated southern populations on Cerro Piedra Larga and near Santo Domingo Chontecomatlán in the western Sierra de Miahuatlán (Aldape-López and Santos-Moreno, 2016; Campbell et al., 2016). Both *A. mixteca* and *A. oaxacae* occur in syntopy in the Sierra de Cuatro Venados (Aldape-López and Santos-Moreno, 2016), and sympatry between *A. cuetzpali* and *A. oaxacae* is suspected but unconfirmed (Campbell et al., 2016).

During recent fieldwork in the forests of the Sierra de Zongolica in west-central Veracruz, Mexico, we collected several unusual individuals of arboreal *Abronia*. Previously, only *A. graminea* was known from this region, and the nearest records of the *oaxacae* group lie dozens of kilometers to the south across inhospitable lowland entrenchments (Canseco-Márquez and Gutiérrez-Mayén, 2010). Based on an integrative analysis of genomic, morphological, and biogeographical evidence, we conclude that these unusual populations in fact belong to the *oaxacae* group and represent a new species which we describe herein.

## MATERIALS AND METHODS

### Molecular procedures

**ddRADseq libraries.**—We extracted genomic DNA from two specimens of the putative new species (MZFC-HE 35663 and 35664) using the EZ-10 Spin Column Genomic DNA Miniprep kit (BIO BASIC; Toronto, Canada). We purified each DNA sample using 1.5x Sera-Mag Magnetic Speed-beads (Thermo Fisher®), and we quantified DNA using a Qubit Fluorometer (Thermo Fisher Scientific®).

We generated ddRADseq libraries following the protocol described by Peterson et al. (2012). The restriction enzymes SbfI (restriction site 5'–CCTGCAGG–3') and MspI (restriction site 5'–CCGG–3') digested the genomic DNA of each sample by incubation at 37°C for two hours in a thermocycler. The digestion reaction contained 21.5 µl of DNA (500 ng), 2.5 µl of 10x Cutsmart® buffer, 0.25 µl MspI at 20 U/µl, and 0.5 µl SbfI at 20 U/µl. We purified the digestion products using 1.5x Sera-Mag Magnetic Speed-beads.

Afterward, we ligated DNA fragments to specific adapters for the enzymes SbfI and MspI. We performed the ligation reaction in a solution of 16.75  $\mu$ l of digested DNA, 1  $\mu$ l of each specific adapter, 2  $\mu$ l of 10x Ligase Buffer (NEB®), and 0.25  $\mu$ l of T4 DNA Ligase at 400 U/ $\mu$ l, and incubated the solution in a thermocycler at 22°C for 40 min, then at 65°C for 10 min. We again purified DNA ligands with 1.5x Sera-Mag Magnetic Speed-beads.

Subsequently, we amplified the restriction-ligation products using polymerase chain reaction (PCR) and specific adapters for the Illumina sequencer. PCR reactions contained 10  $\mu$ l of DNA ligands, 0.5  $\mu$ M of specific adapters, 0.3 mM dNTPs, 1.8 mM MgCl<sub>2</sub>, 5  $\mu$ l of 5x KAPA Long Range Buffer (Kapa Biosystems, Massachusetts), and 1.25 U KAPA Long Range DNA Polymerase. PCR conditions consisted of an initial denaturation step at 94°C for 3 min, followed by 15 cycles of denaturation at 94°C for 25 s, annealing at 57°C for 20 s, and extension at 72°C for 30 s, with a final extension step at 72°C for 10 min.

Finally, we purified the ddRADseq libraries using 1.5x Sera-Mag Magnetic Speed-beads and assessed the success of library construction using a Qubit Fluorometer. We performed the DNA size selection at 500 $\pm$ 50 bp using a Pippin Prep automated size selector (Sage Science®). The ddRADseq libraries were sequenced at the University of Georgia (USA) using an Illumina HiSeq 2500 platform. New sequence data reported in this paper are available in GenBank (SAMN18754171, SAMN18754172).

**Bioinformatic processing.**—We processed the ddRADseq libraries obtained for the putative new species using the pipeline ipyrad ver. 0.7.19 (Eaton and Overcast, 2016), together with libraries previously obtained in Gutiérrez-Rodríguez et al. (2021). We filtered reads using the default offset for quality score of 33, and sequences with more than 10 ambiguous (N) sites were discarded. We used the trimming option for removing all Illumina adapters, selected *de novo* clustering using vSEARCH ver. 1.1.3 (Rognes et al., 2016), and aligned the resulting clusters with Muscle ver. 3.8.31 (Edgar, 2004). We selected a level of sequence similarity of 0.94 based on the results obtained in Gutiérrez-Rodríguez et al. (2021) and following the recommendations of Ilut et al. (2014) to avoid the use of an arbitrary clustering threshold and to minimize false homozygosity and heterozygosity. We generated sequence alignment matrices with increments of one sample in the minimum number of samples with data for a locus to be included in the alignment, to explore the effect on robustness of phylogenetic analyses of (1) different numbers of loci, (2) different corresponding lengths of concatenated sequences, and (3) different percentages of missing data.

### Phylogenetic analyses

We performed phylogenetic analyses using the matrices at different minimum of samples with data for a locus to be included in the alignment. Specifically, we performed maximum likelihood (ML) analyses using the software RAxML ver. 8.0 (Stamatakis, 2014) with the different matrices previously described. The matrices included all concatenated loci with SNPs and invariant sites to improve branch length and topological accuracy in phylogenetic reconstructions (Leaché et al., 2015). We ran all analyses on the CIPRES Science Gateway ver. 3.3 (Miller et al., 2010). We performed a

simultaneous search to obtain the best-scoring ML tree. We also conducted rapid bootstrap analyses with the GTR-GAMMA model, using 1,000 bootstrap replicates starting from random seeds. We used the software FigTree v 1.4.4 (Rambaut, 2018) and Adobe Illustrator CSS to edit the resulting phylogenetic tree.

### Morphological analyses

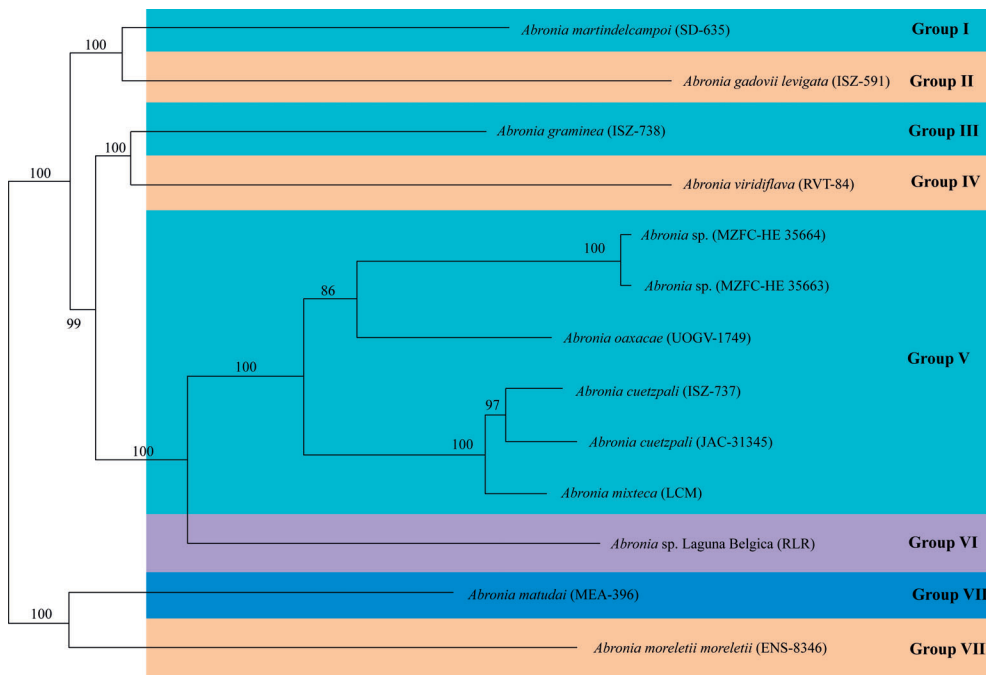
We conducted fieldwork in west-central Veracruz in 2018 and 2019 and collected seven specimens of the putative new species in the Sierra de Zongolica. We euthanized these specimens, fixed them in 10% buffered formalin, and subsequently transferred them to 70% ethanol for permanent storage. We deposited these specimens in the herpetological collection of the Museo de Zoología "Alfonso L. Herrera" of the Facultad de Ciencias, Universidad Nacional Autónoma de México (MZFC-HE) or the Museo de Zoología of the Facultad de Estudios Superiores Zaragoza, Universidad Nacional Autónoma de México (MZFZ). Post-euthanasia and pre-fixation, we gathered liver tissue and preserved it in 95% ethanol for the genomic analyses discussed previously. For other novel field records of both the putative new species and *A. graminea*, we did not euthanize the specimens but instead deposited one or more voucher photographs in the digital collection of the Museo de Zoología of the Facultad de Estudios Superiores Zaragoza, Universidad Nacional Autónoma de México (MZFZ-IMG).

We followed Bogert and Porter (1967) for scale terminology and Campbell (1982) for scale count protocols. We scored bilateral characters on both sides and give the conditions on the left and right sides, in that order, separated by a slash (/). For specimens with divergent transverse dorsal and transverse ventral scale row counts (due to aberrant fission/fusion of scale rows), we express this count as a range. We performed scale counts under a dissecting microscope and took measurements with a ruler (nearest 1 mm), digital calipers (nearest 0.1 mm), or ocular micrometer (nearest 0.1 mm).

We based our diagnosis and comparisons with other taxa on a review of the descriptive literature, including Campbell and Frost (1993) and all subsequent relevant works (Brodie and Savage, 1993; Campbell, 1994; Campbell et al., 1998, 2016; Campbell and Brodie, 1999; McCranie and Wilson, 1999; Flores-Villela and Sánchez-H., 2003; Solano-Zavaleta et al., 2016, 2017; Clause et al., 2020). For ease of comparison, description format largely follows the revisionary treatment by Campbell and Frost (1993). We here adopt the evolutionary species concept as detailed by Wiley and Mayden (2000a, 2000b, 2000c) and follow an integrative approach that relies on genetic distinctiveness, fixed differences in morphological traits (see Wiens and Servedio, 2000), and geographical isolation to delimit the presence of distinct species-level lineages.

### RESULTS

We obtained a total of 5,519,032 single-end sequence reads from two ddRADseq libraries in an Illumina HiSeq platform. Samples of the putative new species had a mean sequence read of 2,759,526 (min = 2,166,498; max = 3,352,534). The most informative matrix had a minimum taxon coverage of eight samples with a total of 2,994 loci. The number of parsimony-informative characters was 6,913 for the datasets.



**Fig. 1.** Maximum-likelihood consensus tree based on 2,994 loci. Color boxes indicate taxonomic assignments *sensu* Campbell and Frost (1993): subgenus *Abronia* (turquoise), subgenus *Scopaeabronia* (violet), subgenus *Auriculabronia* (bluish gray), or former genus *Mesaspis* (pale orange). Group names (I–VIII) indicate taxonomic assignments *sensu* Gutiérrez-Rodríguez et al. (2021). See Data Accessibility for tree file.

Finally, the ipyrad analyses estimated a mean heterozygosity of 0.011 and mean error rate of 0.0036.

We recovered a robust ML phylogenetic tree with high support (Fig. 1). The dataset resolved 100% of the deeper and recent nodes with bootstrap support >85. We recovered the same topology between the eight groups within the genera *Abronia* and *Mesaspis* that were previously defined by Gutiérrez-Rodríguez et al. (2021). The specimens of the putative new species grouped into Group V (*oaxacae* group). This clade is now composed of *A. cuetzpali*, *A. mixteca*, *A. oaxacae*, and the putative new species, with the latter two being sister to one another (Fig. 1).

Corroborating this phylogenetic hypothesis, our morphological analyses also showed that the putative new species is assignable to the *oaxacae* group, yet it is readily distinguishable morphologically from all other species in this group (see below). Furthermore, all known populations of the putative new species are allopatric with respect to other members of the *oaxacae* group. The nearest recorded population is attributed to *A. oaxacae* itself, from Peña del Águila near Coyula (=San Juan Coyula) in the northern Sierra de Juárez, Oaxaca (Canseco-Márquez and Gutiérrez-Mayén, 2010). This site lies some 75 km south of the nearest confirmed population of the putative new species, on the opposite side of the semi-arid, lowland (<550 m elevation) canyon of the Río Santo Domingo, which almost certainly acts as a regional dispersal barrier to *Abronia*. The nearest known localities for *A. mixteca* and *A. cuetzpali* are even more distant (100 km and 260 km to the southwest, respectively), and are isolated from the putative new species by the arid lowland barrier of the Valle de Tehuacán-Cuicatlán (Canseco-Márquez and Gutiérrez-Mayén, 2010; Campbell et al., 2016). Based on these multiple lines of evidence, we conclude that the samples of *Abronia* from the Sierra de Zongolica do indeed represent a new species, which we name and describe below.

### ***Abronia zongolica*, new species**

urn:lsid:zoobank.org:act:0A5746B6-D2CE-4F46-AD2E-

19C9CD2E6D30

Sierra de Zongolica Arboreal Alligator Lizard

Dragoncito de la Sierra de Zongolica

Figures 2, 3, 4; Tables 1, 2

*Abronia graminea*.—Guzmán Guzmán, 2011: 125 (in part).

**Holotype**.—MZFC-HE 35664 (field number LOR 251), adult male, Ayahuatlulco, Municipality of Mixtla de Altamirano, Sierra de Zongolica, Veracruz, Mexico, 18.60°N, 97.02°W, datum WGS84, 1600 m elevation, J. R. Hernández Ginez, 20 December 2018.

**Paratypes**.—6 specimens, all collected in the Sierra de Zongolica, Veracruz, Mexico. MZFC-HE 35663, 1 subadult female, same collection data as the holotype; MZFC-HE 35665, 1 adult male, MZFC-HE 35662, 1 neonate, Teopantecoalco, Municipality of San Juan Texhuacán, 18.60°N, 97.05°W, datum WGS84, 1785 m elevation, M. Á. de la Torre-Loranca, J. C. Sánchez-García, and U. O. García-Vázquez, 23 November 2018; MZFC 4408, 1 adult male, MZFC 4406, 1 adult female, MZFC 4407, 1 neonate, Atiopa, Municipality of San Juan Texhuacán, 18.61°N, 97.04°W, datum WGS84, 1670–1760 m elevation, M. Á. de la Torre-Loranca and J. R. Hernández Ginez, between October 2018 and February 2019.

**Referred specimens**.—5 vouchers, all from the Sierra de Zongolica, Veracruz, Mexico: MZFC-IMG 309–311, Huapanango, Municipality of Astacinga; MZFC-IMG 312, Atiopa, Municipality of San Juan Texhuacán; MZFC-IMG 313, Ayahuatlulco, Municipality of Mixtla de Altamirano. All locality data in this and the preceding two paragraphs are masked; see the first paragraph of the Conservation subsection for details.

**Diagnosis**.—*Abronia zongolica* can be distinguished from all described congeners (including members of the former genus *Mesaspis*) by the following combination of characters: (1) one occipital scale; (2) two primary temporal scales contacting



**Fig. 2.** *Abronia zongolica*, new species, head of holotype (MZFC-HE 35664, head width 25.2 mm) in dorsal view (top), right lateral view (middle; image intentionally mirrored horizontally) and ventral view (bottom), in preservative. Scale bars represent 10 mm.

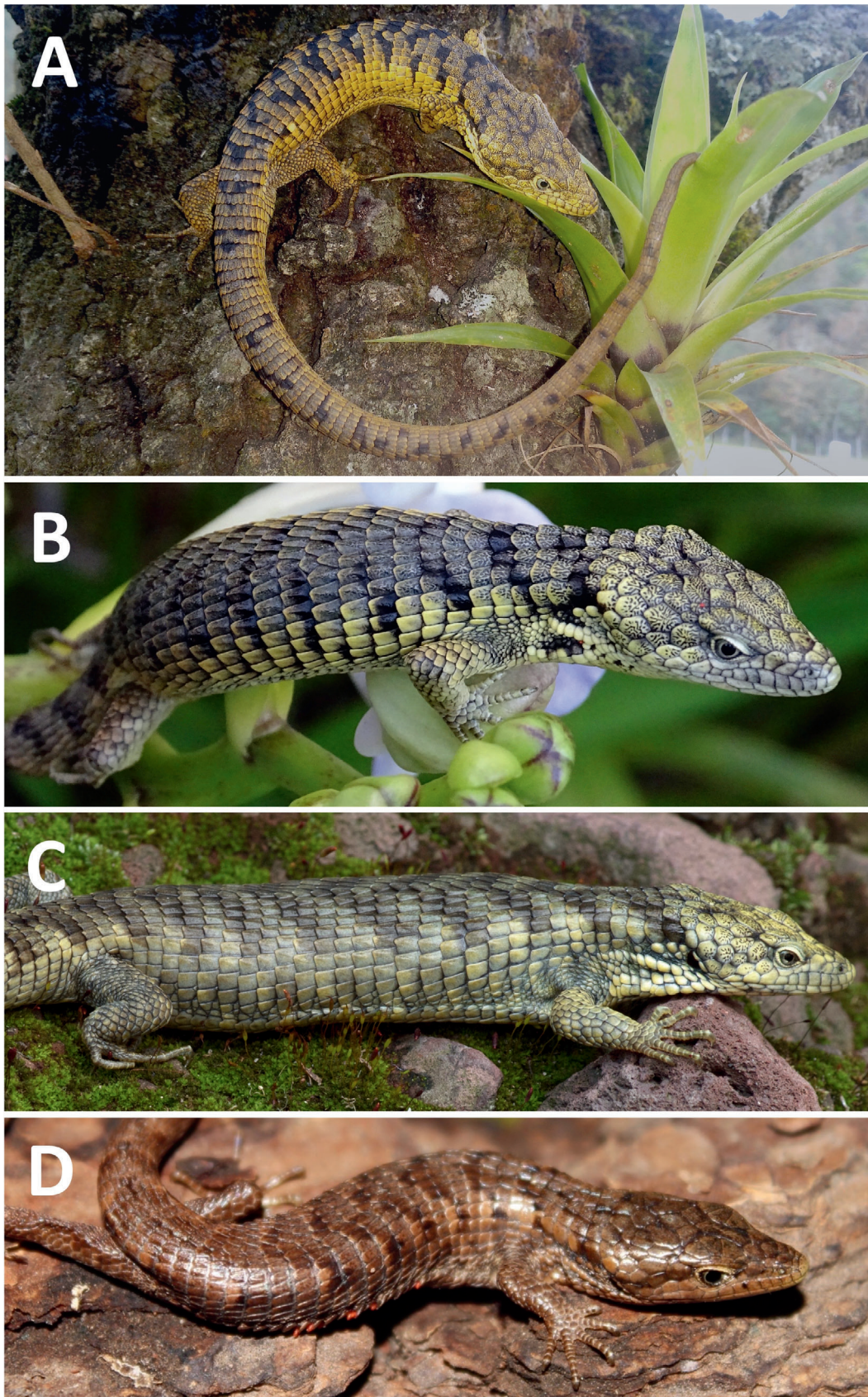
the postocular series; (3) posterolateral head scales moderately protuberant; (4) supra-auricular scales granular, not protuberant or spine-like; (5) 30–34 transverse dorsal scale rows; (6) dorsal scales on the flanks arranged in slightly oblique longitudinal rows relative to the ventrolateral fold; (7) lateralmost row of ventral scales unexpanded relative to the adjacent medial row.

**Comparisons.**—(Tables 1, 2) Among members of the former genus *Mesaspis*, which was recently placed in the synonymy of *Abronia* based on genomic evidence (Gutiérrez-Rodríguez et al., 2021), *Abronia zongolica* differs from all species by

having dorsal scales on the flanks arranged in slightly oblique longitudinal rows relative to the ventrolateral fold (vs. parallel longitudinal rows), and by having 30–34 transverse dorsal scale rows (vs. >40 rows). The new species further differs from *A. cuchumatanus*, *A. gadovii*, and the *A. moreletii* complex by having 14 longitudinal dorsal scale rows (vs. 16 or 18, 16–18, and 18–22, respectively); from *A. antauges* and *A. juarezi* by having vertebral and paravertebral dorsal scales distinctly keeled at midbody in adults (vs. smooth to slightly convex); from *A. viridiflava* by having the frontonasal scale present (vs. absent); and from *A. monticola* by having a divided postmental scale in 6/7 or 86% of specimens (vs. undivided).

Among members of *Abronia* not formerly attributed to the genus *Mesaspis*, *Abronia zongolica* differs from all species except the *deppii* group (*sensu* Campbell et al., 2016; *contra* Campbell and Frost, 1993) by having dorsal scales on the flanks arranged in at least slightly oblique longitudinal rows relative to the ventrolateral fold (vs. parallel longitudinal rows in other species), and differs from all species except the subgenera *Abronia*, *Aenigmabronia*, and *Scopaeabronia* (plus a few individuals of *A. lythrochila*; see Campbell and Frost, 1993) by having the lateralmost row of ventral scales unexpanded relative to the adjacent medial row (vs. expanded in other species). The new species further differs from the subgenera recognized by Campbell and Frost (1993) as follows. Unlike the subgenus *Abaculabronia*, the new species has a dorsum with dark, sometimes interrupted or faint crossbands in living adults (vs. dorsum with no trace of crossbands in living adults), and the supranasal scales not in contact (vs. in contact in 8/9 or 89% of specimens). Unlike the subgenus *Aenigmabronia*, the new species has one occipital scale (vs. two occipitals), and protuberant head shields on the posterolateral “corners” of the head are present (vs. absent). Unlike the subgenus *Auriculabronia*, the new species has protuberant or spine-like supra-auricular scales absent (vs. present). Unlike the subgenus *Lissabronia*, the new species has protuberant head shields on the posterolateral “corners” of the head present (vs. absent). Unlike the subgenus *Scopaeabronia*, the new species has the lower primary temporal unexpanded (vs. expanded), six longitudinal nuchal scale rows (vs. eight rows), and 30–34 transverse dorsal scale rows (vs. 38–47 rows).

Additionally within the subgenus *Abronia*, the new species shares with the *deppii* group the morphological synapomorphy of having dorsal scales on the flanks arranged in at least slightly oblique longitudinal rows relative to the ventrolateral fold. Because both the *deppii* group and the subgenus *Abronia*, unlike all other subgenera mentioned in the previous paragraph, are non-monophyletic based on the genomic analysis of Gutiérrez-Rodríguez et al. (2021), we here compare the new species to each species within the subgenus *Abronia*. Among non-*deppii*-group members of this subgenus (*A. fuscolabialis*, *A. graminea*, and *A. taeniata*; Group III of Gutiérrez-Rodríguez et al., 2021), the new species differs by having an oblique row of enlarged lateral neck scales, each  $\geq 3$  times larger than adjacent scales (vs. row of enlarged scales absent, or poorly developed and not reaching nuchal scales); flanks at least partially yellow and contrasting with darker back in adult males (vs. flanks and back similar in color); and dorsal scales on the flanks arranged in slightly oblique longitudinal rows relative to the ventrolateral fold (vs. parallel longitudinal rows). Within the *deppii* group, the



**Fig. 3.** *Abronia zongolica*, new species, color variation in life (photos not to scale). (A) Adult male holotype (MZFC-HE 35664, snout–vent length [SVL] 112 mm); (B) adult male paratype (MZFC-HE 35665, SVL 95.8 mm); (C) adult female paratype (MZFC 4406, SVL 86.6 mm; image intentionally mirrored horizontally); (D) neonate paratype (MZFC 4407, SVL 45.6 mm). Photos by Miguel Ángel de la Torre-Loranca and Antonio Esaú Valdenegro-Brito.

**Table 1.** Character states for selected features of *Abronia zongolica* and all other species in the *oaxacae* group.

	<i>A. zongolica</i>	<i>A. cuetzpali</i>	<i>A. mixteca</i>	<i>A. oaxacae</i>
Canthal scale separate from posterior internasal scale	yes	yes or no	usually no	no
Anterior superciliary scale contacting the cantholoreal scale	yes	yes	yes	usually no
Temporal scales between posterior supralabial and posterolateral “corner” of head in adult males*	3	2	2–3	1–2
Occipital scale(s)	1	2–3	3	3
Scale rows between the occipital scale(s) and first row of nuchal scales	1–2	2	3	1–2
Longitudinal nuchal scale rows	6	6–8 (if 8, lateral rows reduced in size)	5–6	4
Lateral neck scales between ventral scales and nuchal scales	5–6	7–8	5–6	3–4
Transverse dorsal scale rows	30–34	32–35	28–31	27–29

\* =adult females sometimes also correctly segregate based on the character states presented for each species

new species differs from *A. deppii* and *A. martindelcampoi* (Group I of Gutiérrez-Rodríguez et al., 2021) by having the anterior superciliary scale contacting the cantholoreal scale (vs. usually not in contact), the first postorbital supralabial scale not enlarged (vs. enlarged), two primary temporal scales contacting the postocular series (vs. one), and 30–34 transverse dorsal scale rows (vs. 27–29 in *A. deppii* and 24–28 in *A. martindelcampoi*). Within the *oaxacae* group nested within the *deppii* group (*A. cuetzpali*, *A. mixteca*, and *A. oaxacae*; Group V of Gutiérrez-Rodríguez et al., 2021), the new species differs by having one occipital scale (vs. two or three).

**Description of the holotype.**—(Figs. 2–4) Adult male with both hemipenes partially everted, snout–vent length (SVL) 112 mm, head length from rostral to upper anterior edge of

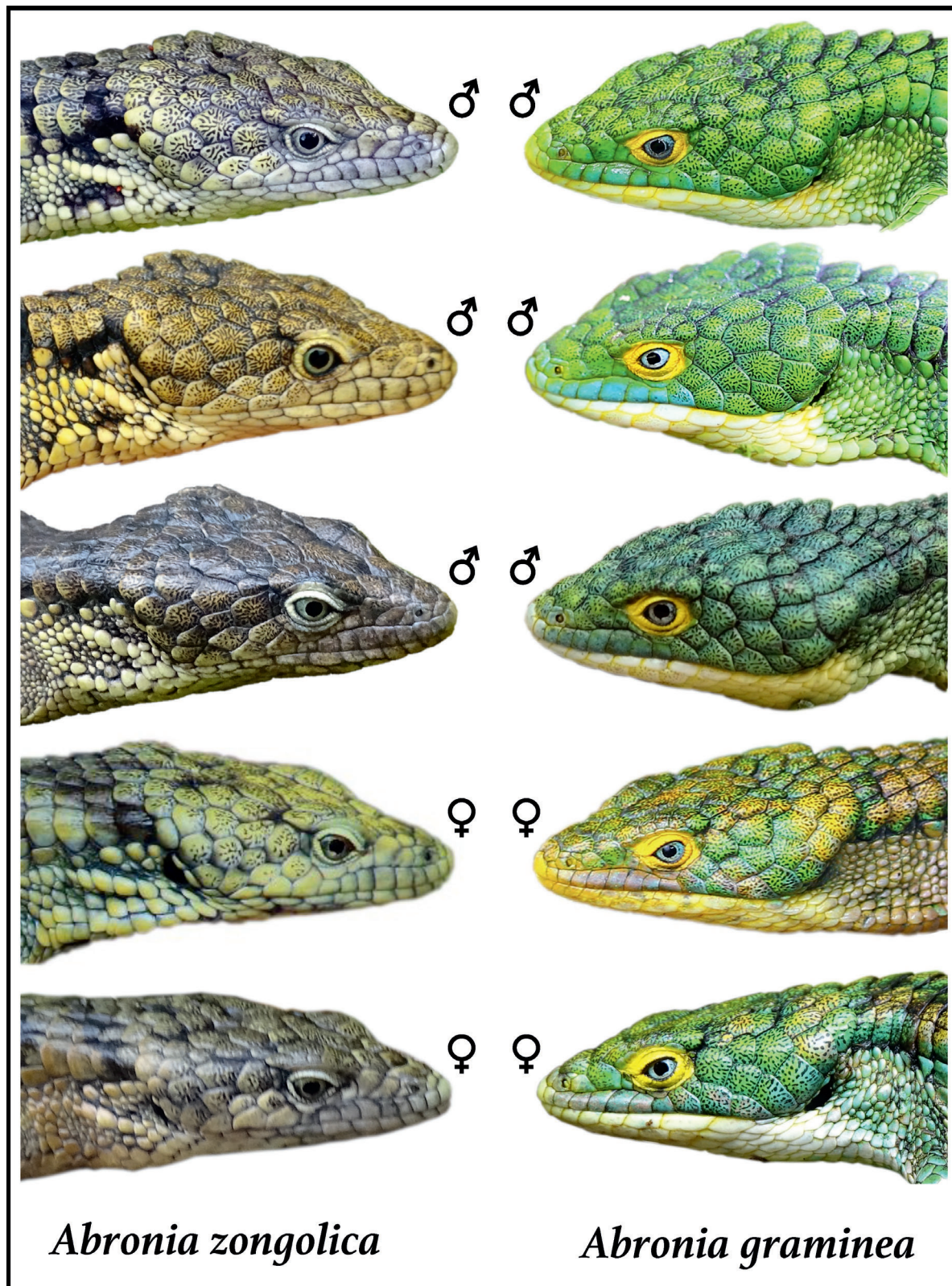
auricular opening 25.2 mm, head width at broadest point 19.6 mm, head width/length ratio = 78.4%, tail unbroken and unregenerated, tail length (TL) 154 mm (1.37 times SVL), and 81 caudal whorls. Supranasals 1/1, somewhat expanded medially; postnasals 2/2, upper slightly smaller than lower; one pair of anterior and posterior internasals situated between rostral and frontonasal; prefrontals over twice as large as posterior internasals, contacting each other medially; canthals 1/1, preventing contact between posterior internasal and prefrontal; loreals 1/1, about one-half size of cantholoreals, and contacting both postnasals; cantholoreals 1/1, extending onto dorsum of canthus rostralis, broadly contacting anterior median supraocular, canthal, prefrontal, and fifth supralabial; median supraoculars 5/5; lateral supraoculars 3/3; superciliaries 6/5, anteriormost on left side contacting cantholoreal and similar in length to adjoining

**Table 2.** Character states for selected features of *Abronia zongolica* and all species in Group III of Gutiérrez-Rodríguez et al. (2021).

	<i>A. zongolica</i>	<i>A. fuscolabialis</i>	<i>A. graminea</i>	<i>A. taeniata</i>
Circumorbital area color different from surrounding scales in adults	usually no (if yes, then white or pale cream)	no	usually yes (bright to pale yellow)	no
Canthal scale separate from posterior internasal scale	yes	yes	no	no
Postnasal supralabial scales and lower temporal scales similar in color to lower jaw and throat	yes	yes	no, lower jaw and throat much paler	yes
Lateral neck scales	oblique row of enlarged scales each $\geq 3$ times larger than adjacent scales	row of distinctly enlarged scales absent	row of distinctly enlarged scales absent or poorly developed	row of distinctly enlarged scales absent
Longitudinal nuchal scale rows	6	6 (rarely 4)	4–6	6 (very rarely 4)
Trunk coloration in adult males*	flanks at least partially yellow, back brown or gray, often with broken black transverse bands	flanks and back green or turquoise, with entire or broken dark or yellow transverse bands	flanks and back bright green, scales often with black bases and/or yellow tips	flanks and back yellow or cream with wide dark transverse bands
Arrangement of dorsal scales on flanks relative to the ventrolateral fold	slightly oblique longitudinal rows	parallel longitudinal rows	parallel longitudinal rows	parallel longitudinal rows

\* =adult females sometimes also correctly segregate based on the character states presented for each species





**Fig. 4.** Head comparison of adult *Abronia zongolica* and *Abronia graminea*, illustrating differences in (1) circumorbitral area color, (2) upper and lower jaw color pattern, and (3) presence/absence of well-developed oblique row of enlarged lateral neck scales. Locality and voucher information for each image is as follows, listed from top-to-bottom. *Abronia zongolica*: Teopantzacalco (paratype, MZFC-HE 35665), Ayahualulco (holotype, MZFC-HE 35664), Huapango (referred specimen, MZFC-IMG 310), Atiopa (paratype, MZFC 4406), Huapango (referred specimen, MZFC-IMG 311). *Abronia graminea*: El Sumidero (MZFC-HE 32991), Puerto del Aire (MZFC-IMG 322), Acultzinapa (MZFC-IMG 336), Puerto del Aire (Clause et al., 2016: fig. 2), Puerto del Aire (MZFC-IMG 338). All photos taken within 1 month of capture. From top, first and third images of *A. zongolica* and fifth image of *A. graminea* intentionally mirrored horizontally. Photos by Miguel Ángel de la Torre-Loranca, Adam G. Clause, and Antonio Esaú Valdenegro-Brito.

superciliary, on right side fused with adjoining superciliary; preoculars 1/1; suboculars 2/2, posteriormost barely separated from lowermost primary temporal by ninth (left side) or eighth (right side) supralabial; postoculars 3/3; frontal large, separated from frontonasal and interparietal; parietal separated from median supraoculars; one large occipital, slightly larger than interparietal, abnormally divided into a small triangular anterior scale and a much larger posterior scale; one transverse row of scales separating occipital from first transverse row of nuchals; primary temporals 4/4, only lowermost two contacting postoculars on each side; secondary temporals 4/4; tertiary temporals 4/4; supralabials 10/11, antepenultimate the posteriormost to reach orbit; infralabials 9/9; postmental divided; four pairs of enlarged chinshields posterior to postmental, posteriormost ones subequal in size to adjacent ones, separated by two scales; sublabials 4/4, anteriormost contacting third infralabial but not postmental.

Minimum longitudinal nuchal scale rows 6; transverse dorsal scale rows 32–33; longitudinal dorsal scale rows 16, arranged in slightly oblique longitudinal rows on sides of body; eight dorsal-most longitudinal scale rows strongly keeled, others entirely smooth or with faint partial keels; transverse ventral scale rows 33; longitudinal ventral scale rows 12; lateralmost row of ventral scales unexpanded relative to the adjacent medial row of ventral scales; head and several anterior rows of nuchals with well-developed osteoderms; more posteriorly on dorsum and flanks of body, osteoderms appear very weakly developed or absent; supra-auricular scales granular and non-protruding; about seven moderately sized scales (lateral neck scales) between lateral nuchals and first large scales on ventrolateral surface of neck; lateral neck scales with enlarged oblique row reaching the lateral nuchals, each scale in row  $\geq 3$  times larger than adjacent lateral neck scales; antibrachial from insertion of the forelimb to wrist 12–13; ventrolateral fold moderately well developed with small scales and granules interspersed in interstitial skin throughout ventrolateral fold; subdigital lamellae on fourth toes 21/21.

**Coloration of the holotype.**—(Figs. 2–4) In life, body gray-brown, becoming bright yellow with scattered dark speckles on paravertebral scale rows and flanks. Body with distinct but narrow and uneven black chevron-shaped crossbands, often interrupted on flanks. Many vertebral and paravertebral dorsal scales with bright yellow posterior blotch, especially at midbody. Scales in and along ventrolateral fold bright to pale yellow with scattered dark speckles, some scales with black wedge-shaped markings at anterior margin. Lateral neck scales predominantly bright to pale yellow, but some entirely black scales consolidate into one or two oblique, oblong markings. Interstitial skin between lateral neck scales often dark gray and prominent. Partial black bar borders the dorsal-most lateral neck scales. Dorsal surface of forelimbs and hindlimbs mostly yellow, but many scales flecked with medium gray-brown, sometimes heavily, especially on the hindlimbs. Digits predominantly gray-brown with yellow flecks. Head predominantly cream-colored with yellow highlights and some gray-tinged scale margins, nearly all scales moderately to faintly rugose; rugosity accentuated by heavy black vermiculations, which extend onto all nuchal scales and across 2–3 transverse dorsal scale rows posterior to the forelimb insertion. Scales between orbit and rostral on sides of head cream to pale yellow with some darker

marbling; rugosity and vermiculations absent. Tail medium gray-brown with yellow anterior margins or blotches on some lateral scales, particularly anterior third of tail. Tail with roughly 22 indistinct dark brown to black crossbands that do not or only faintly extend to venter, many reduced to a single dorsal blotch. Lower jaw, chin, and throat pale yellow, many scales flecked or blotched with dark gray, sometimes heavily. Venter of body and limbs bright yellow, some scales with dark gray flecks. Iris pale gray-green.

In preservative (ethanol after formalin), overall color pattern unchanged except all yellow dramatically faded to various shades of cream, and dorsum of back and tail with slight green tinge. Manus and pes cream-colored with faint rusty tinge. Subdigital lamellae medium gray-brown.

**Morphological variation.**—(Figs. 3–4) All six paratypes similar to the holotype in most respects. Two adult males (MZFC-HE 35665, MZFZ 4408) with SVL 95.8 and 97.7 mm, head length from rostral to upper anterior edge of auricular opening 20.5 and 22.4 mm, head width at broadest point 16.3 and 16.6 mm, respectively, tail broken in MZFC-HE 35665 and broken and regenerated in MZFZ 4408. One adult female (MZFZ 4406) with SVL 86.6 mm, head length 19.1 mm, head width 14.4 mm, tail unbroken and unregenerated, TL 127.4 mm (1.47 times SVL). One subadult female (MZFC-HE 35663) with SVL 81.1 mm, head length 17.6 mm, head width 13.1 mm, tail broken and regenerated, TL 104.2 mm (including 26.7 mm regenerated tissue). Two neonates (MZFC-HE 35662, MZFZ 4407) with SVL 44.2 and 45.6 mm, head length 10.5 and 10.8 mm, head width 7.1 and 7.5 mm, respectively, tail broken in MZFZ 4407, and broken and regenerated in MZFC-HE 35662.

The six paratypes closely resemble the holotype in scalation, with exceptions as follows. Supranasal markedly expanded medially on left side and contacting right posterior internasal in MZFC-HE 35662 and MZFZ 4407; postnasals subequal in size in MZFC-HE 35665; postnasal on right side absent in MZFC-HE 4406; prefrontals in narrow contact with each other in MZFC-HE 35662; cantholoreal in narrow contact with supralabials on right side and separated from supralabials on left side by expanded preocular in MZFZ 4408; superciliaries 6/4 in MZFC-HE 35662, 5/5 in MZFZ 4408, 6/5 in MZFZ 4407, and 6/6 on all other paratypes; anteriormost superciliary markedly elongate on right side on MZFZ 4408, due to aberrant fusion with adjacent superciliary; postoculars 2–4 on left side and 3–4 on right side across all paratypes (mean = 3.1); frontal–interparietal contact absent in MZFZ 4407, narrow contact in all other paratypes; parietal–median supraocular contact broad in MZFZ 4406, narrow in MZFC-HE 35663, absent in all other paratypes; one large occipital entire and not aberrantly divided in all paratypes except MZFC-HE 35663, in which a small triangular scale separates the occipital from the interparietal (same as holotype); two transverse rows of scales separating occipital from first transverse row of nuchals in MZFC-HE 35665, MZFZ 4406, and MZFC-HE 35662; primary temporals 4/2 with uppermost on left side very small in MZFC-HE 35663, 4/3 with medial temporals presumably fused on right side in MZFZ 4407, 3/2 in MZFZ 4406; tertiary temporals 4/5 in MZFZ 4406 and MZFZ 4407, 5/5 in MZFC-HE 35665; supralabials 10–12 (mean = 10.8); infralabials 9–11 (mean = 9.1); postmental single in MZFZ 4407; sublabials 4–5 (mean = 4.5).

Transverse dorsal scale rows 30–34 (mean = 32.3); transverse ventral scale rows 32 in MZFC-HE 35663 and MZFC 4406; lateralmost row of ventral scales weakly enlarged overall in MZFC-HE 35662; osteoderms appear weakly developed in MZFC-HE 35662 and MZFC 4407; lateral neck scales as few as 5 in MZFC-HE 35663; subdigital lamellae on fourth toes 17–22 (mean = 19.8), excluding the counts from MZFC 4408 which is missing both toe tips.

**Color pattern variation.**—In life, the two adult male paratypes (MZFC 4408 and MZFC-HE 35665) differ from the holotype as follows: dorsum medium gray; black chevron-shaped crossbands 0.5–2 scales wide, often extend to ventrolateral fold in MZFC 4408, reduced to narrow interrupted paravertebral dashes in MZFC-HE 35665; many scales in and along ventrolateral fold with black wedge-shaped anterior marking in MZFC 4408; lateral neck scales mostly pale cream to whitish; partial black bar bordering dorsal-most lateral neck scales broken and indistinct in MZFC-HE 35665; dorsum of head with indistinct, arrowhead-shaped dark marking centered at occipital scale in MZFC 4408; dorsum of head medium gray with cream highlights in MZFC 4408, cream with light gray margins on some scales in MZFC-HE 35665; black vermiculations extend across all nuchal scales and onto 3–4 transverse dorsal scale rows posterior to forelimb insertion in MZFC 4408; sides of head from rostral to orbit medium gray with pale cream marbling in MZFC 4408, uniform pale gray in MZFC-HE 35665; supralabial scales posterior to orbit, and lowermost temporal scales, medium-gray with cream marbling and light to moderate black vermiculations in MZFC 4408, these scales cream to pale gray with vermiculations only on temporals in MZFC-HE 35665; anterior to autotomy point, tail with roughly 13 indistinct dark gray-brown crossbands in MZFC 4408, 3 heavily obscured dark gray crossbands in MZFC-HE 35665; ventral scales on head and body with hairline dark margins in MZFC 4408, only some scales with dark margins in MZFC-HE 35665; venter of head, body, and tail, and limbs mostly pale cream to whitish.

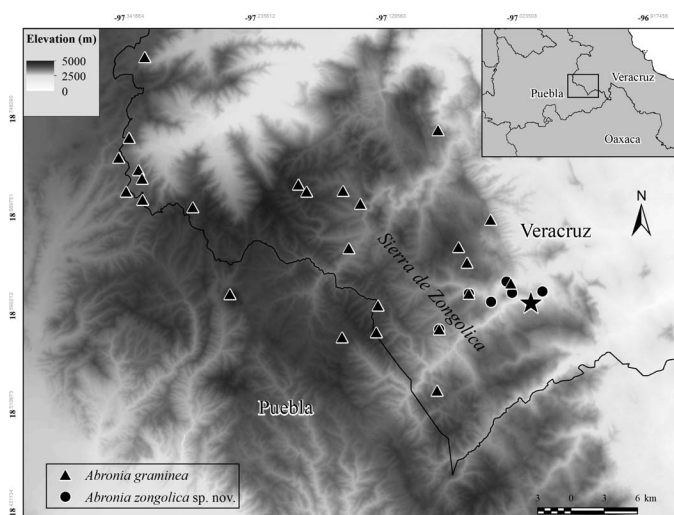
In life, the adult female paratype (MZFC 4406) differs from the holotype as follows: body medium brown-gray with strong green tinge, becoming pale gray on paravertebral scale rows and flanks; chevron-shaped crossbands dark gray, 1–2 scales wide, often offset and partially fused along dorsal midline, terminate on flanks; posterolateral margins of some dark crossbands cream or pale yellow; scales in and along ventrolateral fold pale gray or cream, some with dark speckling; lateral neck scales mostly pale cream, lack adjacent dark dorsal bar; dorsum of all limbs pale gray with green tinge, hindlimbs blotched with medium gray-brown; digits tan to brown with green tinge; dorsum of head pale yellow with green tinge, most scales faintly rugose; rugosity accentuated by faint to moderate dark gray vermiculations, which extend onto most vertebral and paravertebral nuchal scales; sides of head from rostral to orbit to lowermost secondary temporal scale pale yellow with green tinge, with hairline black margins on many scales and some dark marks; temporal scales with moderate to weak black vermiculations, absent on supralabial scales; tail medium gray-brown becoming pale gray on sides with green tinge throughout; tail with roughly 24 broken, often offset crossbands, none reduced to a single dorsal blotch; lower jaw, chin, and throat cream to pale yellow, lack green tinge, lateralmost scales

often with black to dark gray margins; venter of body, limbs, and tail pale yellow to cream, becoming pale gray laterally; dark crossbands on tail weakly visible on venter, most prominent on posterior half of tail.

In preservative, the subadult female paratype (MZFC-HE 35663) differs from the holotype as follows: body medium-brown, becoming slightly rusty brown on flanks; black chevron-shaped crossbands 0.5–1 scales wide, some broken at dorsal midline, usually with pale yellow or cream blotch or dash at posterolateral margin; scales in and along ventrolateral fold rusty brown with pale yellow to cream highlights; lateral neck scales mostly pale brown or cream, lack adjacent dark dorsal bar; interstitial skin on lateral neck inconspicuous, medium-gray, not forming oblique dark markings; limbs rusty brown, becoming dark gray posterolaterally; dorsum of head medium-brown with some gray highlights; black vermiculations weak on lateralmost nuchal scales, terminate at forelimb insertion; sides of head from rostral to orbit to lowermost secondary temporal scale cream with brown tinge, many scales with hairline dark gray margins; temporal scales with weak black vermiculations, absent on supralabial scales; tail medium-brown with rusty and gray highlights; anterior to autotomy point, tail with roughly 13 broken, often offset dark gray to black crossbands, none reduced to a single dorsal blotch, some with pale yellow to cream spot at posterior or posterolateral margin; regenerated portion of tail uniform medium-brown; lower jaw, chin, and throat pale cream to very pale brown with dark flecking; venter cream to pale gray or pale brown, often with moderate to heavy dark flecking.

In preservative, the two neonate paratypes (MZFC 4407 and MZFC-HE 35662) differ from the holotype as follows: body pale gray to medium brown-gray lacking green tinge; dorsal crossbands black to dark gray, partly bordered posteriorly by pale gray to white; vertebral and paravertebral dorsal scales lack pale posterior blotches; lateral neck scales mostly pale gray; dorsum of all limbs pale gray to medium brown-gray, moderately to heavily flecked or blotched with black or dark gray; fingers and toes dark gray to medium brown-gray; dorsum of head same color as body, scales flat, most scales with hairline black margins, few scales rugose and only faintly so; rugosity accentuated with limited black vermiculations, not extending onto nuchal scales or transverse dorsal scales; sides of head from rostral to orbit to lowermost secondary temporal scale pale gray to pale brown-gray with hairline black margins on most scales, otherwise unmarked; tail same color as body with black to dark gray crossbands; regenerated portion of tail in MZFC-HE 35662 uniform dark gray; lower jaw, chin, and throat pale gray lacking green tinge; cream tinge on anterior half of jaw in MZFC-HE 35662; venter of body and limbs pale gray, nearly all scales moderately to heavily flecked with dark gray; venter of tail same as body except for uniform dark gray regenerated portion in MZFC-HE 35662; venter of tail mostly brown-gray with heavy dark gray flecking in MZFC 4407.

In preservative (ethanol after formalin), all other paratypes maintain their general color pattern as described above, but like the holotype all yellow or cream is faded to pale cream or whitish, and brown areas are more gray and occasionally have a green tinge. Also, as in the holotype, manus and pes cream or whitish with faint rusty tinge, and subdigital lamellae medium gray-brown.



**Fig. 5.** Geographic distribution of *Abronia zongolica* and proximate populations of the only known sympatric congener, *A. graminea* in Mexico. The star represents the type locality of *A. zongolica*. See Appendix 1 for locality information of mapped records of *A. graminea*.

**Etymology.**—The specific epithet *zongolica* is a feminine singular adjective in the nominative case and refers to the Sierra de Zongolica of Veracruz, Mexico. This mountain range supports the only confirmed populations of the new species. The name “zongolica” appears to be derived from the words “tzoncolican” or “tzoncolihucan” in the Nahuatl language, which roughly translate as “where hair is braided” (Melgarejo Vivanco, 1950).

**Distribution and ecology.**—Based on vouchered material, the distribution of *A. zongolica* extends across less than 10 km in the Sierra de Zongolica from near Ayahuatulco to Huapango (Fig. 5). All confirmed localities lie within the Río Alpatlahuaya drainage, and span an elevational range of 1,500–2,200 m. Suitable elevations above 1,500 m and mesic tropical forests are continuous between the known localities, and thus *A. zongolica* likely occurs in other regions of the Sierra de Zongolica. We are aware of records of *Abronia* from nearby forested areas of west-central Veracruz that also might represent *A. zongolica*. Pending detailed analysis of these populations and deposition of museum vouchers, we have

considered their taxonomic allocation uncertain at this time. Additionally, Guzmán Guzmán (2011) published a photograph from an unspecified locality of what is identified as a female *A. graminea*, but which is actually an adult *A. zongolica* (likely a male) based on multiple diagnostic features as given in Table 2.

*Abronia zongolica* is found in mature pine-oak forest (*sensu* Rzedowski, 2006), with dominant tree species including *Quercus conspersa*, *Q. crassifolia*, *Q. laurina*, and *Q. rugosa*; the arboreal stratum also regularly contains *Alnus acuminata*, *Cupressus benthamii*, *C. lindleyi*, and *Pinus patula* (Fig. 6). Epiphytes are typically abundant and primarily consist of bryophytes, but also include the bromeliad *Tillandsia imperialis* and fern *Elaphoglossum paleaceum*. *Abronia zongolica* seems to be both arboreal and diurnal. Most individuals were found hidden behind or within bromeliads on tree trunks or branches, ranging from the root or buttress level up to 4 m in height. Individuals were also directly observed while active by day amongst the branches of trees and shrubs. An analysis of fecal material from two individuals of *A. zongolica* (MZFZ-IMG 312 and 313) indicates that the species feeds on insects (Orthoptera, Coleoptera, Lepidoptera, and Hemiptera) along with other unidentified small invertebrates. To our knowledge, this is the first published wild dietary data for any arboreal species of *Abronia*. Like all arboreal congeners for which data exist (Schmidt-Ballardo et al., 2015), *A. zongolica* is a viviparous species that gives birth in the spring: a captive female (MZFZ-IMG 309) birthed four neonates in early May that measured 30–33 mm SVL.

*Abronia zongolica* is sympatric with *A. graminea* in the municipalities of Astacinga and San Juan Texhuacán (Fig. 5). Both species occupy similar forest microenvironments, but *A. graminea* is usually more abundant and is also distributed at higher elevations in coniferous forests, where *A. zongolica* appears to be absent. The only other gerrhonotine anguid lizard species that shares habitat with *A. zongolica* in the Sierra de Zongolica is the terrestrial *Barisia imbricata*.

**Conservation.**—None of the vouchered populations of *A. zongolica* occur in designated protected areas. However, the species might eventually be documented in the Parque Nacional Cañón del Río Blanco, the Reserva Ecológica Natural en la Cuenca Alta del Río Atoyac, or even the Reserva del Bicentenario (Castillo-Hernández and Flores-Olvera, 2017; Pérez-Sato et al., 2018). Regionally, deforesta-



**Fig. 6.** Habitat of *Abronia zongolica* at the type locality in Veracruz, Mexico.

tion has caused extensive habitat loss and fragmentation (Gómez-Díaz et al., 2018), including to the surroundings of all vouchered localities for *A. zongolica*. Due to agricultural demands and other livelihood requirements for the growing human population in the Sierra de Zongolica, we expect that this deforestation will continue. Climate change is also forecasted to dramatically reduce the area of cloud forests in this region (Ponce-Reyes et al., 2012; Rojas-Soto et al., 2012). Because *A. zongolica* also occurs in more widespread mid-elevation forests, the threat posed by climate change remains difficult to quantify (but see Elsen et al., 2020). Additionally, the species could be threatened by direct killing due to mistaken beliefs that it is dangerously venomous (Penguilly Macías et al., 2010) and by harvest for the pet trade (Altherr, 2014; Auliya et al., 2016; Hernández Mares, 2018), although we consider these factors less important compared to deforestation and climate change. Nonetheless, based on the risk of hobbyist commercialization, we have preemptively masked the locality data reported herein by (1) rounding all GPS coordinates to the nearest hundredth of a decimal degree, and (2) not giving distances or cardinal directions from the nearest settlement or landmark.

Given this available threat data, together with the aforementioned distribution and ecology of *A. zongolica*, we propose its categorization under three relevant species-imperilment frameworks. First, we suggest that *A. zongolica* be provisionally assessed as Endangered (B1ab[iii]+2ab[iii]) on the International Union for Conservation of Nature's (IUCN) Red List of Threatened Species. Second, we evaluate *A. zongolica* as having an Environmental Vulnerability Score (EVS; Wilson et al., 2013) of 18 out of 20, placing it in the High Vulnerability category. Contributory geographic distribution, ecological distribution, and human persecution scores of 6, 8, and 4, respectively, substantiate this EVS, but if the species is shown to have a broader distribution and/or becomes commercially exploited for the pet trade, the latter two scores would warrant being updated to 7 and 6, respectively. Lastly, we recommend a categorization of Amenazada (Threatened) for *A. zongolica* on the Norma Oficial Mexicana list (SEMARNAT, 2010), which is the only legally binding imperiled-species list in Mexico. We base this recommendation on the species meeting Criteria A.(I)+B.(II)+C.(II)+D.(II) as defined by the Anexo Normativo I. All three proposed categorizations are consistent with those of many other arboreal species of *Abronia* (SEMARNAT, 2010; Wilson et al., 2013; Clause et al., 2020).

## DISCUSSION

Genomic and morphological evidence are concordant in supporting the recognition of *A. zongolica* and its assignment as the newest member of the *oaxacae* group (Gutiérrez-Rodríguez et al., 2021), which is composed of *A. cuetzpali*, *A. mixteca*, and *A. oaxacae*. *Abronia zongolica* is morphologically assignable to the *oaxacae* group, which is nested within the *deppii* group, which is itself nested within the subgenus *Abronia* (*sensu* Campbell et al., 2016), because: (1) the new species does not differ from the subgenus *Abronia* by any single character, in contrast to every other recognized subgenus; (2) the new species is united with the *deppii* group by the unique shared character of having dorsal scales on the flanks arranged in at least slightly oblique longitudinal rows relative to the ventrolateral fold; and (3) the new species

differs from all members of the *oaxacae* group by only a single shared character (one occipital scale vs. two or three), which is fewer characters than for any other cluster of species within the subgenus *Abronia*. For additional diagnostic clarity, we offer an expanded list of characters that separate the new species from the *oaxacae* group (Table 1) and from the non-*deppii*-group members of the subgenus *Abronia* (Table 2), which together comprise the most morphologically similar and geographically proximate congeners. Based on our genomic data (Fig. 1), *A. oaxacae* is sister to the new species, yet they are well differentiated morphologically (Table 1), consistent with obvious biogeographic barriers to dispersal. The new species is now the northernmost representative of the *oaxacae* group, and the only one to occur in the state of Veracruz.

With the addition of *Abronia zongolica*, the content of the genus *Abronia* is increased to 41 species, of which 31 are known or suspected to be highly arboreal. Our discovery of this new species highlights Mexico as a globally important area of diversification for the genus, with 19 arboreal and four terrestrial species of *Abronia* now considered endemic to the country (Gutiérrez-Rodríguez et al., 2021). The state of Veracruz itself presently contains 232 recognized species of native non-avian reptiles including *A. zongolica* (Torres-Hernández et al., 2021). This tally ranks the state second behind the state of Oaxaca, with 319 species (Mata-Silva et al., 2021).

Six species of *Abronia* (one terrestrial, five arboreal) are now documented from Veracruz. The terrestrial species is *A. antauges* (formerly *Mesaspis antauges*), which is currently reported only from the eastern flanks of Pico de Orizaba (Solano-Zavaleta et al., 2017), although it could conceivably prove to be sympatric with *A. zongolica*. Two of the arboreal species (*A. reidi* and *A. chizari*) are endemic to the isolated volcanic Tuxtla region of east-central Veracruz. These species are members of the *Abaculabronia* and *Scopaeabronia* clades, respectively, and thus neither appears to be a close relative of *A. zongolica* (Campbell and Frost, 1993; Gutiérrez-Rodríguez et al., 2021). The remaining two species, *A. taeniata* and *A. graminea*, are widely distributed in the northern and central parts of Veracruz (Clause et al., 2018), and *A. graminea* is broadly sympatric with *A. zongolica* (Fig. 5). However, adult male *A. graminea* and *A. taeniata* are strikingly differentiated from *A. zongolica* based on multiple scale characters and aspects of color pattern (Table 1, Fig. 4). Neonates, juveniles, and females of *A. graminea* and *A. zongolica* are more similar, but the presence of a canthal scale and the oblique row of distinctly enlarged lateral neck scales in *A. zongolica* reliably distinguish it from *A. graminea* at any age.

Allopatry among the arboreal species of *Abronia*, driven by adaptation to montane habitat patches isolated by lowland barriers, has until recently been considered almost invariable (Campbell and Frost, 1993; Campbell et al., 2016). The co-occurrence of *A. graminea* and *A. zongolica* is therefore notable. However, several recent studies have revealed exceptions to the allopatry narrative (e.g., Aldape-López and Santos-Moreno, 2016; Thesing et al., 2017; Clause et al., 2018), which cumulatively make this newest example of sympatry less surprising. Importantly, within the *oaxacae* group to which *A. zongolica* belongs, dramatic biogeographic barriers appear to have long isolated this new species from its closest relatives. The semi-arid tropical dry forest of the steep Río Santo Domingo canyon prevents contact with *A. oaxacae*

in the northern Sierra de Juárez, while the arid scrubland of the broad Tehuacán-Cuicatlán Valley similarly segregates *A. mixteca* and the even more distant *A. cuetzpali* from contact with the new species. Somewhat unusually however, *A. oaxacae* and *A. mixteca* are themselves syntopic southwest of the Valle de Oaxaca in the Sierra de Cuatro Venados (Aldape-López and Santos-Moreno, 2016), suggesting a complex historical biogeographic interplay within the heterogeneous highlands of the Sierra Madre del Sur in central Oaxaca.

The biogeographic heterogeneity of the Sierra de Zongolica, which supports the only known populations of *A. zongolica*, is also apparent. This north–south trending karstic massif, with its eastern slopes dissected by multiple river valleys draining onto the broad Gulf coastal plain (Fig. 5), lies at the junction of three major mountain chains: the Sierra Madre Oriental to the north, and Trans-Mexican Volcanic Belt to the northwest, and the Sierra Madre del Sur to the south. The regional boundaries of these three mountain chains are inconsistently circumscribed. Recent authors have variously considered the Sierra de Zongolica to be part of the Sierra Madre Oriental (Ponce-Reyes et al., 2012; Rojas-Soto et al., 2012), the Trans-Mexican Volcanic Belt (Morrone, 2014; Torres-Hernández et al., 2021), the Sierra Madre del Sur (Morrone et al., 2017), or part of what was historically termed the Oaxaca province (Ferrusquía-Villafranca, 1990; Morrone et al., 1999), among other names (see list in Morrone, 2014). The high local/regional richness of birds (Arizmendi and Márquez-Valdemar, 2000), mammals (Escalante et al., 2014; Macario-Cueyactle et al., 2019), and plants (Castillo-Hernandez and Flores-Olvera, 2017) further underscores the status of the Sierra de Zongolica as a zone of interchange between major biotic provinces in Mexico.

The multiple names given to the Sierra de Zongolica itself also highlight its complexity. It has been previously called the Región de las Altas Montañas de Veracruz (Pérez-Sato et al., 2017), while the southern portions of the mountain range in the states of Puebla and Oaxaca are commonly called the Sierra Negra and Sierra Mazateca, respectively (Schmidt-Ballardo, 1991; Canseco-Márquez and Gutiérrez-Mayén, 2010; García-Vázquez et al., 2010; Canseco-Márquez et al., 2018). Biological or geological distinctions between the Sierra de Zongolica and the topographically contiguous Sierra Negra and Sierra Mazateca nevertheless remain unclear.

Regardless of its name and precise geographical boundaries, the Sierra de Zongolica has received scant attention from herpetologists. Most fieldwork has focused on the herpetofauna of the more northerly Orizaba-Cuautlapan-Cordoba corridor (e.g., Ceron de la Luz et al., 2016; Peralta-Hernández et al., 2020; Vázquez-Cruz et al., 2021), or the forested escarpments even farther north between Pico de Orizaba and Cofre de Perote (e.g., Murrieta-Galindo et al., 2013; García-Castillo et al., 2018; Parra Olea et al., 2020). As might be expected, recent visits to underexplored reaches of the Sierra de Zongolica have yielded two newly discovered squamate reptile species in the genera *Lepidophyma* (García-Vázquez et al., 2010) and *Geophis* (Canseco-Márquez et al., 2016). Together with other recent herpetofaunal records (Canseco-Márquez et al., 2018; de la Torre-Loranca et al., 2019, 2020), these results strongly suggest that the diversity of the Sierra de Zongolica is higher than currently known—particularly for secretive species that are difficult to encounter, as exemplified by the present work. Our work also emphasizes that, along with other Mexican highland areas within the

Mesoamerica biodiversity hotspot (Myers et al., 2000), the Sierra de Zongolica lies in a predicted global hotspot of undescribed species, particularly reptiles (Moura and Jetz, 2021).

Given this remarkable species diversity, together with multiple pressing anthropogenic threats, increased conservation attention is urgently needed in the Sierra de Zongolica. Establishing new community-based protected areas in partnership with resident stakeholders is potentially of great value (Ochoa-Ochoa et al., 2009). Ecotourism involving both national and international visitors is another possible form of sustainable development that shows regional promise (Mikery-Gutiérrez et al., 2014). There are currently several ecotourism projects in the Sierra de Zongolica that are promoted by local inhabitants and by the Instituto Nacional de los Pueblos Indígenas of the Mexican Federal Government. These projects have identified part of the type locality of *A. zongolica* for recognition as an Environmental Management Unit (UMA). We hope that the formal announcement of *Abronia zongolica* as a microendemic, high-profile lineage will help to further stimulate these and other conservation actions.

#### DATA ACCESSIBILITY

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#### APPENDIX 1. Other specimens referred.

The following museum specimens, photo vouchers, or literature references substantiate records of *Abronia graminea* in Mexico from the region surrounding the populations of the new species *A. zongolica*. Most of these records of *A. graminea* are novel, being announced and mapped herein for the first time (Fig. 5). To protect these sensitive populations from poaching pressure, we have masked the locality data and do not provide coordinates (see Conservation subsection in the main text for further details). Institutional abbreviations follow Sabaj (2020), except for MZFZ for the Museo de Zoología of the Facultad de Estudios Superiores Zaragoza, Universidad Nacional Autónoma de México.

*Abronia graminea*: Puebla: Ajalpan, Municipality of Cinco Señores (MZFZ-HE 26166–26168); Alhuaca, Municipality of Vicente Guerrero (MZFZ-IMG 329); El Sumidero, 2.72 road km SSE of Mex-150, Municipality of Nicolás Bravo (MZFC-HE 32991); Lagunas de San Bernardino, Municipality of Vicente Guerrero (Canseco-Márquez and Gutiérrez-Mayén, 2010); Parque Ecoturístico Jabes (MZFZ-IMG 330) and Puente Colorado (UMMZ 89328), Municipality of Chapulco. Veracruz: Acultzinapa, Municipality of Soledad Atzompa (MZFZ-

IMG 314, 336); Atiopa (MZFZ-IMG 334), El Mirador (MZFZ-IMG 335) and Las Cruces (MZFZ-IMG 320), Municipality of San Juan Texhuacán; Atotonilco, Municipality of Calchahuaco (MZFZ 4417); Ayahualulco, Municipality of Alpatlahuac (MZFZ-IMG 316); Cascadas el Paraiso (MZFZ-IMG 328) and Villas Pico (MZFZ-IMG 325), Municipality of La Perla; Cubanicuico (MZFZ 4422) and Ejido Zoquiapa (MZFZ-IMG 321), Municipality of Los Reyes; Cumbre de Aquila, Municipality of Aquila (MZFZ-IMG 331); Ejido Santa Cruz Muyuapan, Municipality of Nogales (MZFZ 4419); El Xuchilt, Municipality of Maltrata (MZFZ-IMG 323); Huapango (MZFZ-IMG 332) and Loma Guitarra (MZFZ-IMG 318), Municipality of Astacinga; La Joya, Municipality of Acajete (MZFZ 4413); Llano Grande, Municipality of Tlaquilpa (MZFZ-IMG 317); Loma Grande, Municipality of Mariano Escobedo (MZFZ-IMG 324); Puerto del Aire (MZFZ-IMG 322), 4 mi SE of Puerto del Aire (LACM 67703), Puerto del Aire, ca. 1.0 km (by dirt road) SE of Mex Hwy 150 (MZFZ-IMG 308), and Macualtzingo, 3.42 road km N of Mex-150 (MZFC-HE 32989), Municipality of Acultzingo; San Miguel Acultzinapan (MZFZ-IMG 316) and Terrero (MZFZ-IMG 333), Municipality of Atlahuilco; Tepeica, Municipality of Tehuipango (MZFZ-IMG 319); Tequila, Municipality of Tequila (MZFZ-IMG 337); Tetelzingo, Municipality of Coscomatepec (MZFZ-IMG 327); Xoxocotla, Municipality of Xoxocotla (MZFZ-IMG 315).