Miniaturization in Direct-Developing Frogs from Mexico with the Description of

Six New Species

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ABSTRACT: The *Craugastor mexicanus* Series (Anura: Craugastoridae) includes six species of direct-developing frogs that occur in Mexico and Guatemala. Notably, two of these species have small adult body sizes (< 18 mm SVL) and several have intraspecific polymorphism in color pattern. Using a geographic sampling focused on eastern Mexico (the location of most type localities), we conducted a molecular phylogenetic analysis of two mitochondrial (12S, 16S) and two nuclear (RAG1, TYR) gene fragments. This analysis revealed two widespread species, *C. mexicanus* and *C. pygmaeus*, along with evidence of multiple undescribed taxa from the states of Oaxaca, Mexico, Guerrero, and Jalisco. Interestingly, the widespread species have stratified geographic distributions with the larger-bodied clade restricted to high elevations and the smaller-bodied clade to low elevations. We also identify regions of Guerrero and Oaxaca where multiple species co-occur. To reevaluate the quality of characters that have been previously used to diagnose species, we tested for heterochrony and sexual dimorphism using micro-computed tomography and linear measurements. We found evidence for paedomorphosis as the mechanism of miniaturization in small-bodied taxa. Linear measurements confirmed that tympanum and body size are sexually dimorphic traits in both small and large-bodied species. We used this enhanced understanding of morphological variation in the group to describe six new species. Despite this progress, we suspect that additional species await discovery, particularly in western Mexico and east of the Isthmus of Tehuantepec where our sampling efforts were limited.

Key words: Brachycephaloidea; *Craugastor bitonium* sp. nov.; *Craugastor cueyatl* sp. nov.; *Craugastor candelariensis* sp. nov.; *Craugastor polaclavus* sp. nov.; *Craugastor portilloensis* sp. nov.; *Craugastor rubinus* sp. nov.; Terraranea
The extensive flora and fauna of Mesoamerica make it one of the world’s most ecologically diverse regions. Among amphibians, direct-developing frogs of the genus *Craugastor* Cope 1862, are particularly abundant but have also experienced putative declines in recent times (Crawford 2003; Scheele et al. 2019). Despite the potential threat to these frogs, several groups of *Craugastor* remain poorly studied and are in need of systematic revision. One such group of amphibians is a predominately Mexican radiation, the *C. mexicanus* Series (*sensu* Hedges et al. 2008; Streicher et al. 2014). The Series contains six described species: *C. hobartsmithi* (Taylor 1937), *C. mexicanus* (Brocchi 1877), *C. montanus* (Taylor 1942), *C. omiltemanus* ( Günther 1900a), *C. pygmaeus* (Taylor 1937), and *C. saltator* (Taylor 1941). These direct-developing frogs are denizens of the leaf litter and are distributed throughout subtropical and tropical Mexico, barely extending into western Guatemala. They occur in diverse habitats including highland pine-oak forest and tropical lowland deciduous forest.

Notably, two species have small adult body sizes (*C. hobartsmithi*, males ~14 mm, Taylor 1940; *C. pygmaeus*, males 16 mm, females 19 mm, Taylor 1937). These small species often occur syntopically with larger-bodied species of *Craugastor* creating a situation where they may be confused for juveniles of larger species. Thus, given (1) the expanse and ecological diversity of Mexico and (2) that miniaturized anurans are ‘exceptionally prone to taxonomic underestimation’ (Scherz et al. 2019), it is quite likely that many small-bodied species of the *C. mexicanus* Series are yet to be discovered.

In this study we revised the taxonomy of the *C. mexicanus* Series aided by molecular phylogenetic analyses, morphometrics, micro-computed tomography, analysis of ossification patterns, and qualitative assessments of morphology.
Collectively, our findings allowed us to describe six new species and report that heterochrony has likely contributed to miniaturization in *C. hobartsmithi*, *C. pygmaeus*, and several of the new species. We set the stage for our revision with a summary of the taxonomic history underlying the *C. mexicanus* Series.

**Material and Methods**

**Taxonomic History**

Brocchi (1887) described *Leiuperus mexicanus* from “Mexique.” This locality was later restricted to Cerro San Felipe in Oaxaca by Smith and Taylor (1950).

Günther (1900a,b) described *Syrrhaphus omiltemanus* and *Hyloides calcitrans* both from the locality of Omilteme [Omiltemi] in Guerrero. A small burst of species descriptions occurred during the 1930s and 1940s based solely on the works of E. H. Taylor. Taylor (1936) described both *Eleutherodactylus hobartsmithi* and *E. pygmaeus* with holotypes from Uruapan, Michoacán and Rodríguez Clara, Veracruz, respectively. He also described paratypes of *E. pygmaeus* from Chilpancingo, Guerrero. Taylor (1939) described three species that would later be referred to the *C. mexicanus* Series. The first was *Microbatrachylus albolabris* based on a holotype specimen from Córdoba, Veracruz and paratypes from Portrero Viejo, Veracruz and San Juan Gracia, Veracruz. The second species described was *M. oaxacae* from a holotype and paratypes collected near Cerro San Felipe, Oaxaca. Third, *M. minimus* was described based on a holotype and paratypes from Agua del Obispo, Guerrero and a paratype from Mazatlán, Guerrero. In Taylor (1939), *E. pygmaeus* was also transferred to the genus *Microbatrachylus*. Taylor (1941) described two species; *M. lineatissimus* from a holotype and paratypes originating from Cerro San Felipe, Oaxaca; and *E. saltator* from a holotype and paratypes originating from Omiltemi,
Guerrero. Taylor (1942) described his final two species referable to the *C. mexicanus* Series; *M. montanus* designating a holotype from Mount Ovando, Chiapas and paratypes from La Esperanza, Chiapas, Las Nubes, Chiapas and Salto de Agua, Chiapas; *M. imitator* designating a holotype and from La Esperanza, Chiapas and paratypes from Colonia Hidalgo (8 km north of La Esperanza), Chiapas. The most recent species description was that of Davis and Dixon (1957) who described *M. fuscatus* based on a holotype and paratype from Tulancingo, Hidalgo.

By the early 1960s there was a growing consensus that the genera *Microbatrachylus* (typically species with small adult body sizes) and *Eleutherodactylus* (species with larger adult body sizes) were congeneric. This understanding set the stage for revisionary work that was conducted by W. E. Duellman and J. D. Lynch. Duellman (1961) synonymized *M. albolabris, M. minimus* and *M. imitator* with ‘*M. pygmaeus*’. The rationale for these synonymies was based on overlapping variation that he observed across multiple characteristics (including color pattern, relative length of the hind limb, presence and position of dorsal dermal folds or pustules, relative size of inner and outer metatarsal tubercles, and number of palmar tubercles) rendering the diagnostic features of Taylor (1939; 1942) unreliable. Lynch (1965) synonymized *E. fuscatus* with *E. mexicanus* based on an evaluation of Davis and Dixon’s (1957) diagnostic characters of *E. fuscatus* in some individuals of *E. mexicanus*. Lynch (1965) also moved all species of *Microbatrachylus* to the genus *Eleutherodactylus*. He also introduced a *nomen novum, Eleutherodactylus sartori*, for *E. montanus* because moving it from *Microbatrachylus* to *Eleutherodactylus* created a junior homonym (*Eleutherodactylus montanus* had already been described by Schmidt [1919]). Lynch (1970) placed *E. lineatissimus* and *E. oaxacae* in the synonymy of *E. mexicanus* citing that the type specimens of the latter two taxa were
identical to *E. mexicanus*. Lynch (2000) placed *E. saltator* in the synonymy of *E. mexicanus*.

At the beginning of the 21st century, relationships and species boundaries among members of the *C. mexicanus* Series were still largely uncertain. Lynch (2000) provided a helpful review of the complexities and confusion associated with two groups he described: the *Eleutherodactylus rhodopis* and *E. omiltemanus* groups. The first comprehensive molecular assessment of phylogenetic relationships in these groups was that of Crawford and Smith (2005). Their sampling of the genus *Eleutherodactylus* included six of our focal species (*E. mexicanus*, *E. omiltemanus*, *E. pygmaeus*, *µE. saltator¶*, *E. sartori [= C. montanus]*, and an undescribed species). The results from Crawford and Smith’s (2005) analysis supported (1) moving all of these species to the genus *Craugastor* and (2) creating a new grouping (that they called the ‘*C. mexicanus* group’) to recognize the monophyly of our focal taxa. Moving *E. sartori* to the genus *Craugastor* allowed for the combination *C. montanus* to be used once more. Soon after, Hedges et al. (2008) included two species in their phylogenetic analysis, but redefined the *C. mexicanus* group of Crawford and Smith (2005) as the *C. mexicanus* Series to include seven species. One of these species was *C. saltator*, which they noted should be removed from the synonymy of *C. mexicanus* based on the earlier findings of Crawford and Smith (2005). Streicher et al. (2014) determined that one of the species included by Hedges et al. (2008) in the *C. mexicanus* Series, *C. occidentalis* (Taylor 1941), belonged instead to the *C. rhodopis* Series of Hedges et al. (2008). Collectively, this taxonomic history has resulted in six species assigned to the *C. mexicanus* Series: *C. hobartsmithi*, *C. mexicanus*, *C. montanus*, *C. omiltemanus*, *C. pygmaeus*, and *C. saltator* (Fig. 1).
Geographical and Taxonomic Sampling

We examined 461 specimens from Mexico and Guatemala including the Mexican states of Oaxaca, Guerrero, Nayarit, Sinaloa, Hidalgo, Jalisco, Veracruz, Morelos, Michoacán, Mexico, Colima, and Puebla (Appendix 1). We examined specimens referable to all focal species: *C. hobartsmithi* + *C. cf. hobartsmithi* (*n* = 21), *C. mexicanus* (*n* = 225), *C. montanus* (*n* = 8), *C. omiltemanus* (*n* = 36), *C. pygmaeus* (*n* = 118), and *C. saltator* (*n* = 22). This included type material corresponding to all available names except *Microbatrachylus fuscatus*, however we did examine a near-topotypic specimen from Hidalgo (UTA A-66138) for both morphology and DNA. We also examined 31 specimens with uncertain taxonomic affinities. To examine the geographic distribution of our focal taxa we augmented our sampling localities using VertNet distributional data from several museums in North America. We made maps using QGIS and data layers available from DIVA-GIS.

Throughout the text, GPS coordinates follow WGS84 in all cases.

We extracted DNA from tissues of 59 individuals of the *C. mexicanus* Series (Appendix 2). This sampling included representatives of *C. cf. hobartsmithi*, *C. mexicanus*, *C. omiltemanus*, *C. pygmaeus*, and *C. saltator*. Most samples were collected on field expeditions by the University of Texas at Arlington (UTA) and the National Autonomous University of Mexico (UNAM) over the past two decades (Streicher 2012) and one by Jacobo Reyes-Velasco from Colima (JRV field catalogue). We used representatives of the subgenus *Craugastor* (*C. longirostris* [KU 177803] from the *Craugastor fitzingeri* Series and *C. podiciferus* [mtDNA—UCR 16361, nDNA—MVZFC 13463] from the *Craugastor rhodopis* Series) and the subgenus *Hylactophryne* (*C. uno* [AMCC118080], Hedges et al. 2008; Streicher et al. 2011) as outgroup taxa, sequences downloaded from NCBI GenBank (Benson et al. ...
We included several samples from Hedges et al. (2008) and re-sampled several individuals used in Crawford and Smith (2005). All novel DNA sequences were submitted to NCBI GenBank (Appendix 2).

Molecular Phylogenetic Analysis

We sequenced fragments of the mitochondrial (mtDNA) ribosomal RNA 12S and 16S genes, and nuclear (nDNA) RAG1 and Tyrosinase (Tyr) genes. Sequences were obtained for 58 samples for 12S from Streicher (2012) and for 35 samples from 16S and Tyr from Manuelli (2017). We amplified and sequenced a further three samples for 12S, 26 samples for 16S and TYR, and 47 samples for RAG1 specifically for this study. We amplified DNA fragments using published primers sets (Table 1) and performed Polymerase Chain Reaction (PCR; Saiki et al. 1988) amplification using GoTaq® (Promega). We carried out amplifications in 14.25 µl volumes containing 2 µl of template DNA and 12.25 µl of MasterMix (5.8 µl DEPC treated H2O, 0.1 µl forward primer, 0.1 µl reverse primer, and 6.5 µl GoTaq®). These amplifications were carried out by thermal cycling performed on a Techne® Prime Elite (Techne). We amplified the 12S and 16S gene fragments using the following thermal cycling parameters: An initial cycle of 94°C (4 min) followed by 35 cycles of 94°C (30 s) denaturing, 50°C (30 s) annealing, and a 72°C (2 min) extension. A final phase of 72°C (7 min) followed. We amplified the RAG1 and TYR genes using touchdown PCR (Don et al. 1991) with the following parameters: An initial cycle of 95°C (5 min) followed by 40 cycles of 95°C (30 s) denaturing, 58°C (30 s) annealing, and 72°C (1 min) extension, followed by three touchdown cycles of 95°C (30 s) denaturing, 58°C (-1°C per cycle) (30 s) annealing, and 72°C (1 min) extension. The touchdown cycles were followed by a final set of 40 cycles of 95°C (30 s) denaturing,
55°C (30 s) annealing, and 72°C (1 min) extension, finishing with a final phase of 72°C (10 min). All PCR experiments contained a negative control. All PCR products were quantified on 1% TAE agarose gel and successfully reactions were submitted to the Natural History Museum (London) DNA Sequencing Facility for cleaning and sequencing on an Applied Biosystems 3730 DNA Analyzer (ThermoFisher Scientific).

We assembled forward and reverse chromatographs in Geneious 8.0.4 and constructed multiple sequence alignments on each data set (12S, 446 base pairs; 16S, 601 base pairs; RAG1, 662 base pairs; TYR, 521 base pairs) using the Geneious alignment algorithms (Kearse et al. 2012). We produced a concatenated data set (12S + 16S + RAG1 + TYR, 2230 base pairs) from the aligned sequences using the Geneious concatenation tool. In the protein coding gene alignments (RAG1 and Tyr), we confirmed reading frames were open by visual inspection of alignments. In the ribosomal subunit gene alignments (12S and 16S) we identified hypervariable loop regions as regions of ambiguity in alignment with high densities of indels and removed them to avoid ambiguous alignment. Following alignment, we generated a matrix of genetic distances between and within species using MEGA X (Kumar et al. 2018).

We used Bayesian Markov chain Monte Carlo (MCMC; Yang and Rannala 1997) and Maximum Likelihood (ML) analysis on the concatenated, 12S, 16S, RAG1, and TYR data sets for phylogenetic reconstructions. We partitioned the data set by gene (12S and 16S) and codon position in protein-coding genes (RAG1 and Tyr). We used PartitionFinder 2.1.1 (Lanfear et al. 2016) to select best-fit models of molecular evolution for each partition employing a Bayesian Information Criterion (Table 2). We conducted Bayesian MCMC analysis in MrBayes 3.2.6 (Huelsenbeck
and Ronquist 2001; Ronquist and Huelsenbeck 2003) with sampling occurring every 1000 generations for 10 million generations, and the first 25% of generated trees discarded as burn-in. We used standard deviation split frequencies to assess the convergence (< 0.01). We also carried out ML analyses in MEGA 7.0.26 (Kumar et al. 2016) for each dataset. Nodal support was assessed via 100 bootstrap pseudoreplicates. Gaps and missing data were treated as a partial deletion with a site coverage cut-off of 80%. We visualized phylogenetic trees in FigTree 1.4.3 (Rambaut 2006).

Linear Morphometrics

We collected linear measurements of major body axes from all specimens using digital calipers (accurate to the nearest 0.1 mm). We took all measurements from full-body alcohol preserved specimens. All measurements were taken by the same person (TJ). We used the terminology for the external anatomy of amphibians from Walker (1980). We took 15 measurements from each specimen: (1) snout to vent length (SVL); (2) head width at commissure of the jaw; (3) head length, measured on right side from snout tip to commissure of jaw; (4) maximum tympanum width; (5) maximum eye width; (6) interorbital distance; (7) naris to snout distance, measured on right side from anterior corner of naris to anterior corner of snout; (8) eye to naris distance, measured on right side from anterior corner of eye to posterior corner of naris; (9) brachial length, measured on right side from ventral attachment to body to centre of elbow; (10) antebrachial length, measured on right side from centre of elbow to proximal surface thenar tubercle; (11) manus length, measured on right side from proximal surface of thenar tubercle to tip of finger III; (12) femur length, measured on right side from ventral attachment to body to center of knee; (13) crus
length, measured on right side from center of knee to center of ankle; (14) pes length, measured on right side from center of ankle to proximal surface of inner metatarsal tubercle; (15) toe length, measured on right side from proximal surface of inner metatarsal tubercle to tip of toe IV. All measurements were log-transformed to linearize allometries and equalize variances (Hammer and Harper 2006; Sidlauskas et al. 2011) before input into PAST 3 (Hammer et al. 2001) for morphometric analysis via principal component analysis (PCA) to identify axes of maximal variance (Hammer and Harper 2006).

In PCA of morphology at least one principle component (PC) typically is explained by allometric scaling, as identified by a significant correlation with log centroid size (geometric mean of logs of all measures per specimen; Sidlauskas et al. 2011). We tested for this by correlating scores of each PC with log centroid size. For PCs where a significant correlation with log centroid size was found we performed allometric correction, calculating the residuals of the PC regression with log centroid size to produce a size standardized morphospace (Sidlauskas et al. 2011).

The *Craugastor mexicanus* samples encompassed a size range of 10.9–37.3 mm SVL, including juvenile individuals. To control for the effect of putative juveniles we repeated the PCA excluding all juvenile specimens. The gonads of a subset of the sample were examined to see if mature gonads could be used to separate adult and juvenile specimens, however, size of ova/testes varied dramatically between individuals of the same size (suggesting seasonal variation). No reliable method of separating adult and juvenile specimens was found, in place of this the lower size limit of specimens in this dataset identified as adults by past workers was used to define minimum adult size and all specimens below this size were excluded (Brocchi 1877; Boulenger 1882; Günther 1900; Hedges 1989; Hedges et al. 2008; Lynch 1965,
1970; Parker 1927; Stejneger 1904; Taylor 1936; 1940; 1941; 1942). For example, we excluded specimens < 20.2 mm SVL in *C. mexicanus*; < 10.8 mm SVL in *C. pygmaeus*; < 25.9 mm SVL *C. saltator*.

For *a priori* groups where multiple specimens were available of multiple different sizes we tested for differences in ontogenetic trajectory on size-correlated shape axes by comparing slopes and elevation of reduced-major axis regression lines of size correlated PCs (PCAs carried out on each group individually) with log centroid size (Sidlauskas et al. 2011) using ANCOVA tests in PAST 3 (Hammer et al. 2001). In all statistical reporting we provide degrees of freedom as subscripts of statistics.

**Testing for Heterochrony**

Heterochrony is a change in the timing and/or rates of processes underlying the ontogenetic formation of morphological traits (Alberch et al. 1979; Keller and Lloyd 1992; Gould 2002). The most prevalent form of heterochrony in anurans is paedomorphic miniaturization, driven by deceleration, hypomorphosis, and/or post-displacement (Reilly et al. 1997; Yeh 2002). Because *C. hobartsmithi* and *C. pygmaeus*, have small adult body sizes (< 18 mm), we tested for the signature of miniaturization in their development. Miniaturization is defined as size reduction beyond a threshold at which dramatic changes in morphology, physiology, and ecology occur (Hanken and Wake 1993; Yeh 2002). These reductions relative to ancestral body size are often accompanied by the loss of skeletal elements (de Sá et al. 2019; Scherz et al. 2019).

We scanned 63 alcohol preserved specimens of *Craugastor* at the University of Cambridge Biotomographic Centre using a Nikon Metrology XT ST High
Resolution CT Scanner at 133 kV, 214 µA, with a scan resolution of 0.01–0.07 mm. These specimens were selected to maximize size and phylogenetic variation represented. Reconstructions of skeletal anatomy in 3D were rendered using AMIRA-AVIZO v9.4 (ThermoFisher Scientific). Importantly, these scans included type material for all available names except *Eleutherodactylus fuscatus* (a junior synonym of *C. mexicanus*). We uploaded 3D renders of skeletal anatomy of all specimens investigated in this study to MorphoSource (MorphoSource.org 2020) (Appendix 3)

We investigated osteology of CT scanned specimens by visual inspection of 3D skeletal reconstructions in AVIZO. We identified 19 osteological features that varied among scanned specimen using the osteological terminology of Duellman and Treub (1986): (1) ossification of calcaneum/astragalus epiphyses; (2) ossification of epicorocoid; (3) ossification of the exocipitalprootic; (4) fusion of exocipitalprootic; (5) ossification of femur epiphyses; (6) fusion of frontopareitals; (7) presence of posterolateral projection of the frontopareital; (8) posterior offset of frontopareital-prootic suture; (9) ossification of humeral exterior epiphyses; (10) ossification of humeral interior epiphyses; (11) ossification of hyoid; (12) ossification of prehallux; (13) ossification of prepollex; (14) ossification of palentines; (15) ossification of radioulnar exterior epiphyses; (16), ossification of radioulnar interior epiphyses; (17) ossification of sphenethmoid; (18) ossification of tibiofibular epiphyses; and (19) ossification of vomers. We scored these skeletal characters in terms of presence/absence. Most of these characters appear in a consistent order throughout ontogeny (based on log centroid size), suggesting that there is a distinct ontogenetic sequence for the ossification of skeletal elements in the *C. mexicanus* Series. We used this data to generate a six-stage ossification sequence (Table 3) from which a total ossification score was generated for each individual. Presence of posterolateral
projections of the frontopareitals were not included in the ossification series because they did not have a clear association with ontogeny in all species.

We plotted ossification score against log centroid size for each species to allow the relationships between size/ontogeny and ossification to be compared among species (Alberch et al. 1979; Mitteroecker et al. 2005; Piras et al. 2011; Scanferla 2016; Esquerré et al. 2017; Hipsley and Müller 2017; Da Silva et al. 2018). We compared the relationships between size/ontogeny and ossification in more detail for groups with sufficiently large sample sizes (C. mexicanus, C. pygmaeus, C. saltator, and C. hobarstsmithi) by comparing slopes and elevation of reduced-major axis regression lines of ossification score against log centroid size. We used ANOVA to tests if slopes of ontogeny versus ossification differ significantly from zero and between-species pairwise $\chi^2$ tests of reduced-major axis regression slopes to test if the rates of ossification versus ontogeny different between species. We carried out all statistical analysis in PAST 3 (Hammer et al. 2001). In all statistical reporting we provide degrees of freedom as subscripts of statistics.

Geometric Morphometrics of the Skull

We undertook geometric morphometric analysis on the skulls of 56 of the CT scanned specimens using 14 landmarks that were placed on the 3D reconstructions of skulls using the landmarking function in AVIZO. Our landmarks were based on those used on anuran skulls by Simon et al. (2016): (1) anterior midline tip premaxilla; (2) maxilla premaxillary suture; (3) anterior tip nasal; (4) posterior lateral tip frontopareital; (5) posterior dorsal tip frontopareital; (6) posterior dorsal tip squamosal (7) anterior frontopareital prootic suture; (8) lateral tip nasal; (9) squamosal maxillary suture; (10) posterior tip maxilla; (11) anterior tip parasphenoid;
(12) posterior tip parasphenoid; (13) lateral tip parasphenoid; and (14) pterygoid maxillary suture (Fig. 2).

We aligned landmark configurations by Procrustes superimposition (Hammer and Harper 2006) and performed PCA in the R package Geomorph 3.0.6 (Adams et al. 2018). We visualized shape change across principle components in MorphoJ 1.8 (Klingenberg 2011).

Testing for Sexual Dimorphism

Little is known regarding the reproductive biology of our focal species, but sexual dimorphism in tympanum size and pigmented gonads have been reported in some species (Taylor 1940, 1947). We compared SVL to tympanum width in three species where males have been reported to have larger tympana than females: C. *mexicanus* (*n* = 149), C. *omiltemanus* (*n* = 27) and C. *pygmaeus* (*n* = 86). We compared correlation coefficients (using non-parametric Spearman’s ρ tests) between tympanum width and body size (SVL) to those between putatively non-sexually dimorphic characters and SVL. We expected that if tympana are sexually dimorphic, they would have a lower correlation coefficient with SVL than non-dimorphic characters (which should scale more linearly with body size). For non-dimorphic characters, we used eye width in C. *pygmaeus* and C. *omiltemanus* and crus length in C. *mexicanus*. We were unable to use the same non-dimorphic characters across all species because of logistical issues, however we had all measurements for C. *omiltemanus* and analyzed both eye width and crus length to confirm that these characters have similar scaling relationships with SVL (see results). In C. *mexicanus*, we were able to dissect 27 individuals and confirm sex. We used this analytical framework instead of direct statistical comparisons between males and females.
because we were not able to dissect most specimens to confirm sex. All statistical analyses of sexual dimorphism were performed in R version 3.6.2 (R Core Team 2019) and plots made in SYSTAT 13.2 (Systat Software, San Jose, California). In statistical reporting we provide the correlation coefficient ($r_s$), sum of all squared rank differences ($S$), probability of the null hypothesis that $\rho$ is equal to 0 ($P$) and sample sizes ($n$).

### Criteria for Species Recognition

We used similar philosophical criteria to those described by Meik et al. (2018) to determine species boundaries. First, we considered the evolutionary history of putative lineages using both concatenated and standalone analyses of mitochondrial and nuclear DNA sequences. Specifically, we surveyed for evidence that species were (1) monophyletic (if there was more than one individual sampled) and (2) had proportionally similar branch lengths distinguishing them from other taxa in both mitochondrial and nuclear phylogenetic reconstructions. We viewed similar divergence in both mtDNA and nDNA datasets as strong evidence of organismal divergence, and thus a reasonable proxy for speciation patterns. Second, we made comparisons with two taxa that are closely related but easily differentiated by morphology (C. mexicanus and C. omiltemanus), to calibrate a minimum threshold of genetic divergence (4.9%; Table 4) that we would expect between most species. Third, we compared external morphology and skull osteology among species to identify differences among species. In summary, we recognized a new species if they met two or more of the following criteria; (1) Phylogenetic distinctiveness in both mitochondrial and nuclear DNA, (2) ‘large’ genetic distances from other species, and (3) morphological differentiation from other species.
RESULTS

Phylogenetic Analyses and Genetic Distances

Overall, maximum likelihood analysis recovered lower branch support than Bayesian analysis (Fig. 3). We discuss phylogenetic relationships within species in the taxonomic accounts below. In this analysis, *C. montanus* was found with limited support to be the sister taxon of all other species in the *C. mexicanus* Series (66 ML; 0.99 BAYES). *Craugastor omiltemanus* and *C. saltator* were weakly supported as sister taxa (44 ML; 0.74 BAYES). Together these two species were supported as the sister taxon to *C. mexicanus* in the concatenated and mtDNA-only analyses (Figs. 3 and 4). *Craugastor pygmaeus* and *C. hobartsmithi* were more closely related to one another than any other species, however they belong to a clade that also includes six undescribed species (all of which were found to have levels of mtDNA and nDNA divergence similar to recognized species; Figs. 4 and 5). Thus, our phylogenetic results supported the recognition of six currently recognized species in the *C. mexicanus* Series: *C. hobartsmithi*, *C. mexicanus*, *C. montanus*, *C. omiltemanus*, *C. pygmaeus*, *C. saltator* and six undescribed species. These six new species are described herein as *C. bitonium*, *C. candelariensis*, *C. cueytatl*, *C. polaclavus*, *C. portilloensis*, *C. rubinus*.

The phylogenetic results revealed several interesting geographical patterns. Two species, *C. mexicanus* and *C. pygmaeus*, are widely distributed throughout Mexico and appear to have non-overlapping elevational distributions, with *C. mexicanus* being restricted to the highlands of the Sierra Madre Oriental and Sierra Madre del Sur (Fig. 6). We observed a difference in elevational distribution using locality data from museum specimens and confirmed that *C. mexicanus* and *C.*
pygmaeus have largely non-overlapping elevational distributions (Fig. 7). Another widely distributed species is C. hobartsmithi + C. cf. hobartsmithi, which putatively ranges from the state of Guerrero in the east to the state of Sinaloa in the northwest (Fig. 8). Although we had relatively few individuals represented, our results suggest that C. omiltemanus ranges more widely in the Sierra Madre del Sur than previously thought with a distribution extending into Oaxaca. The remaining species in the C. mexicanus Series (C. bitonium, C. candelariensis, C. cuelatl, C. montanus, C. polaclavus, C. portilloensis, C. rubinus, and C. saltator) appear to have generally restricted geographical distributions (Figs. 6 and 8) and four species (C. candelariensis, C. portilloensis, C. polaclavus, and C. pygmaeus) occur in near sympatry in the region of Candelaria, Loxicha in Oaxaca. Genetic distance analysis of the concatenated alignment (Table 4) revealed that between species divergence ranged from 3.4% (C. hobartsmithi and C. rubinus) to 10% (C. polaclavus to C. saltator). Within species genetic distances ranged from 0.3% (C. candelariensis) to 2.2% (C. mexicanus).

Morphology and Development

Multivariate analyses of linear measurements suggested that there are two main morphological groups in our dataset (Fig. 9). The first group consisted of mostly small-bodied species (C. bitonium, C. candelariensis, C. cuelatl, C. hobartsmithi, C. polaclavus, C. portilloensis, C. pygmaeus, and C. rubinus). The second group consisted of large-bodied species (C. mexicanus, C. montanus, C. omiltemanus, and C. saltator). The small-bodied morphological group corresponds to a clade in our phylogenetic analyses (Figs. 3, 4, and 5). This may suggest that small adult body sizes evolved once within the C. mexicanus Series.
Despite the difference in adult body sizes, the developmental trajectories (log centroid size vs. PC1 scores) among well-sampled species (C. hobartsmithi, C. mexicanus, C. omiltemanus, and C. pygmaeus) had mostly indistinguishable slopes (Fig. 10). While the slope of C. hobartsmithi was distinct from the other taxa (ANCOVA, $F_{4,93} = 11.6, P = 1.268e^{-07}$), this may be related to small sample sizes. In contrast, the slopes of C. mexicanus, C. omiltemanus, C. pygmaeus and C. saltator were not significantly different (ANCOVA, $F_{3,91} = 1.072, P = 0.3652$) suggesting that most taxa, regardless of body size have similar ontogenetic trajectories.

The similarity in ontogenetic trajectory between the large-bodied taxa (C. mexicanus, C. omiltemanus, and C. saltator) and the small-bodied taxon C. pygmaeus suggests that miniaturization of C. pygmaeus (and potentially other members of the small-bodied clade) is due to a halt in body size increase at an earlier stage of development in small-bodied taxa relative to large-bodied taxa. This suggests that the mechanism for miniaturization is hypomorphic paedomorphosis (Reilly et al. 1997).

The results of our ossification staging analysis (Fig. 11) revealed that multiple small-bodied species (C. bitonium, C. candelariensis, C. hobartsmithi and C. pygmaeus) complete the same ossification sequence as their large bodied relatives (C. mexicanus, C. omiltemanus, and C. saltator). We found a correlation between centroid size and ossification score for the whole sample (ANOVA, $F_{1,64} = 4.784, P = 0.03239$) and each species individually ($P < 0.05$) for which enough taxa were available for statistical analysis. C. pygmaeus had a steeper slope of ontogeny versus ossification than C. mexicanus ($\chi^2_{1,32} = 10.069, P = 0.0015078$; Fig. 11). In other words, C. pygmaeus reaches the same level of ossification as C. mexicanus at an earlier stage of ontogeny/smaller size. Two specimens of C. mexicanus had unexpected placements including the examined paratype of ‘M. lineatissimus’ which
had a unique body size for having a relatively well-ossified skeleton (similar to C. *montanus*), and a small heavily ossified individual.

Completing the same ossification sequence as large-bodied species suggests that although *C. pygmaeus* and at least three other small-bodied species (*C. bitonium*, *C. candelariensis*, and *C. hobartsmithi*) may be miniaturized through a process of heterochronic hypomorphosis, heterochronic processes have not affected ossification. Alternatively, other small-bodied species (*C. ceuyatl*, *C. polaclavus*, *C. portilloensis*, and *C. rubinus*) had low levels of ossification but putatively mature gonads. This suggests that these species are paedomorphic both in terms of size and level of ossification (Reilly et al. 1997; also see Discussion).

### Skull Morphometrics and Sexual Dimorphism

Geometric morphometrics of 3D skulls revealed that members of the *Craugastor mexicanus* Series fall into two groups based on skull shape. These two groups are mainly defined by variation in the shape of the frontoparietals and parasphenoid, as described by PC2 (Fig. 12). These skull shape groups largely overlap with the large and small-bodied clusters identified using linear measurements (Fig. 9). The skull shape data suggests clades within the *Craugastor mexicanus* Series can be recognised morphologically by skull shape. The smaller-bodied species (*C. bitonium*, *C. candelariensis*, *C. ceuyatl*, *C. hobartsmithi*, *C. pygmaeus*, and *C. rubinus*) typically have a more recessed anterior frontoparietal-prootic suture and a more anterior tip of the parasphenoid, compared to the larger-bodied species that form a monophyletic clade (*C. mexicanus*, *C. omiltemanus*, *C. saltator*). *Craugastor montanus* has an intermediate skull morphology between these groups. *Craugastor polaclavus* and *C. portilloensis* are distinct within this framework, for possessing small body sizes but
skull morphologies that are similar to larger-bodied species. One specimen of *C. mexicanus* had unexpected placement; the examined paratype of ‘*M. lineatissimus*’ which overlapped more with the small-bodied cluster.

In *C. mexicanus*, tympanum width was less associated with body size ($r_s = 0.604, S = 218318, P = 3.508e^{-16}, n = 149$) than crus length was with body size ($r_s = 0.977, S = 12653, P < 2.200e^{-16}, n = 149$). In *C. pygmaeus*, tympanum width was less associated with body size ($r_s = 0.462, S = 56959, P = 7.306e^{-06}, n = 86$) than eye width was with body size ($r_s = 0.776, S = 23690, P < 2.200e^{-16}, n = 86$). In *C. omiltemanus*, tympanum width was less associated with body size ($r_s = 0.603, S = 1300, P = 0.008644, n = 27$) than eye width ($r_s = 0.933, S = 220, P = 1.403e^{-12}, n = 27$) or crus length ($r_s = 0.862, S = 451, P = 7.417e^{-09}, n = 27$). These results are consistent with sexual dimorphism in tympanum size in *C. mexicanus*, *C. omiltemanus* and *C. pygmaeus*. Using the specimens of *C. mexicanus* with confirmed sexes revealed that males have larger tympanum sizes than females (Fig. 13). A handful of *C. omiltemanus* and *C. pygmaeus* specimens that we were able to dissect also followed this pattern with males having larger tympana. Thus, as in other species of anuran (e.g. Werner et al. 2009) multiple species of the *Craugastor mexicanus* Series have males with larger tympana than females suggesting that bioacoustic communication/signaling is important to these frogs.

Taxonomic Revision

In light of our phylogenetic and morphological analyses, we provide updated taxonomic accounts for the *C. mexicanus* Series. Our taxonomic revision includes re-descriptions of six species and the description of six new species. Each account includes a description, diagnosis, commentary on phylogenetic and osteological
variation, and available natural history information. Diagnoses and comparisons are
summarized in Table 4 (intraspecific and interspecific genetic distances), Table 5
(sex-specific body size and gonad pigmentation), Table 6 (diagnostic character
comparisons), and Figs. 14–21 (body, head, hand, and foot comparisons). We also
provide a dichotomous key for the group. Morphological diagnoses are intended to be
used with adult specimens (unless otherwise noted).

TAXONOMIC ACCOUNTS

_Craugastor bitonium_ sp. nov.

_Holotype._—UTA A-64254 (field ID: JAC 22117; Fig. 22, A), adult female
from road between Yerba Santa and Yextla (HWY 196), Guerrero, Mexico,
17.52666°N, 99.9579°W, 2071 m, collected by J. A. Campbell and colleagues on 10
June 2002.

_Paratypes (5)._—MZFC-HE-35600–01 and UTA A-66117–18 adult females,
and UTA A-66119 adult male (Fig. 22, B–D), all same collection data as holotype.

_Diagnosis._—A species of _Craugastor_ distinguished by the following
combination of characters: (1) small adult size (maximum SVL = 16.7 mm); (2) full
ossification of skeletal elements in adults; (3) absence of posterolateral projection of
frontoparietal; (4) absence of vomerine odontophores; (5) presence of raised tubercles
on eyelids; (6) supratympanic fold absent or poorly developed; (7) face flank barred
or with supralabial pale stripe, and with or without dark canthal stripe; (8) single
postrictal tubercle; (9) gular region peppered with melanocytes; (10) dorsal surface
two-toned, usually with a dark suprascapular “Λ,” or almost unicolored; (11) pale or
ground color middorsal ridge; (12) scattered fine tubercles on dorsum; (13) body
flank barred darker anteriorly, slightly shagreened to smooth; (14) inguinal glands present and axillary glands absent in adults; (15) when leg adpressed to body, heel reaches middle of eye to slightly beyond snout; (16) outer tarsal ridge with 1–6 small mostly round tubercles, no raised fringe; (17) finger and toe tips round, slightly lanceolated, slightly expanded; (18) inner metatarsal tubercle larger than outer metatarsal tubercle.

**Comparisons.**—*Craugastor bitonium* can be differentiated from *C. mexicanus*, *C. montanus*, *C. omiltemanus*, and *C. saltator* due to their large adult body sizes of SVL > 20 mm (< 20 mm in *C. bitonium*), the presence of vomerine teeth (absent in *C. bitonium*), and the presence of three palmar tubercles (one palmar tubercle in *C. bitonium*). *Craugastor bitonium* can be differentiated from *C. candelariensis*, *C. cueyatli*, *C. hobartsmithi*, and *C. portilloensis* by the presence of metatarsal tubercles of similar sizes (different sizes in *C. bitonium*). *Craugastor bitonium* can be differentiated from *C. rubinus* by the presence of posterolateral projections of the frontoparietal (absent in *C. bitonium*). *Craugastor bitonium* can be differentiated from *C. polaclavus* by its shorter eye–nostril distance with an eye–nostril distance 9–10% SVL in *C. bitonium* and 10–13% SVL in *C. polaclavus*. *Craugastor bitonium* is most similar to *C. pygmaeus* (in morphology, osteology, and genetic distance), but may be differentiated from this taxon by the condition of the outer tarsal ridge; 1–6 small tubercles in *C. bitonium* versus no tubercles (= smooth) in *C. pygmaeus*.

**Holotype description.**—Holotype small female with unpigmented developing ova (SVL = 15.8 mm); snout rounded and short (0.9 mm naris–snout; 6% SVL); short eye–nostril distance (1.42 mm; 9% SVL); tympanum 1.4 mm (8.9% SVL); small supratympanic fold terminating in shoulder tubercle; finger length formula III < IV <
II < I; single palmar tubercle; single prepollical tubercle; subarticular tubercles present on all fingers; no supernumerary tubercles present on hands; toe length formula IV < III < V < II < I; inner metatarsal tubercle larger than outer metatarsal tubercle; subarticular tubercles present on all toes; supernumerary tubercles present on plantar surface; small dark supracloacal fold present; white lip bar in life (Fig. 22, A), still evident in preservative (Fig. 19, A); 2–3 incomplete bands on each arm; one leg removed for genetic analysis and 4 bands on thigh of remaining leg; dorsum brown and mottled on head and anterior-most third of body, eclipsed by lighter coloration on posterior two thirds of body; ventral surface lightly colored in preservative; skull of holotype lacks vomerine odontophores (although vomers present).

**Variations in Paratypes.**—Body sizes (SVL) 15.8 mm (MZFC-HE-35600), 15.2 mm (MZFC-HE-35601), 16.9 mm (UTA A-66117), 16.7 mm (UTA A-66118), 12.3 mm (UTA A-66119); eye–nostril distance 9–10% SVL; tympanic ratios 7–9%; dorsal color patterns variable, often with two distinctive patches of differing ground coloration ranging from orange to tan.

**Etymology.**—The specific epithet is a combination of the Latin prefix bi- meaning two and tonium meaning tone. It is a reference to the two distinctive patches of color found on the holotype and several paratypes that create the appearance of a ‘two-tone’ dorsal coloration.

**Distribution.**—This species is known only from the Sierra Madre del Sur of central Guerrero (~2071 m). The closest named places to the type locality are Izotepec to the north and Los Bajos to the southwest. The habitat at the type locality is montane pine-oak forest.
Diet.—CT-scan of the holotype revealed the presence of a small millipede (Diplopoda) in the stomach. We also noted the presence of a small red ant (Formicidae) in the mouth of the holotype.

Phylogenetics.—*Craugastor bitonium* was inferred to be the sister taxon of *C. pygmaeus* with high support in the concatenated analyses (ML = 99; BAYES = 1.0; Fig. 3). This sister relationship was also recovered in both mtDNA and nDNA analyses, although with lower support in the nDNA-only analyses (ML = 54, BAYES = 0.67; Figs. 4 and 5). *Craugastor bitonium* is separated from *C. pygmaeus* by a p-distance of 4.7% (Table 4).

Remarks.—The skull of *C. bitonium* is similar to *C. hobartsmithi*, *C. montanus*, and *C. pygmaeus*. *Craugastor bitonium* displays a developmental pattern similar to *C. pygmaeus* (with high levels of ossification at small sizes) suggesting small adult body sizes (Fig. 11). This species likely co-occurs with *C. pygmaeus*, *C. omlitemanus* and *C. saltator* in central Guerrero (Figs. 6 and 8). The specimen UTA A-66132 is referred with some hesitation as it was collected from a lower elevation than the type locality and has a Finger I length nearing *C. pygmaeus* (which also occurs in Guerrero). Six of the specimens were adult females containing unpigmented ovaries with yolked eggs and thick oviducts, the seventh (UTA A-66119; Fig. 22, C, far left) is an adult male with pigmented testes.

*Craugastor candelariensis* sp. nov.

Holotype.—UTA A-64253 (field ID: JAC 21885), male collected by E. N. Smith and colleagues N of Candelaria on the road to Oaxaca; Sierra Madre del Sur,
Oaxaca, Mexico, 15.94960°N, 96.47110°W, 668 m, on 21 January 2002 between 11:30 and 12:00 hrs, near stream bordering coffee plantation and secondary forest.

**Paratypes (3).**—MZFC-HE-35617 (formerly UTA A-64252; field ID: JAC 21873; Fig. 23), male with heavily pigmented testes, same data as holotype except collected 1.2 mi on rough road towards Pluma Hidalgo on the Candelaria–Portillo road, 15.95610°N, 96.44930°W, 1051 m, on 21 January 2002 at 10:00 hrs in leaf litter of coffee plantation. UTA A-66116 (field ID: JAC 21851), male with pigmented testes collected by E. N. Smith and colleagues from San Gabriel Mixtepec, Puente de Hamaca, Oaxaca, Mexico, 16.10510°N, 97.06310°W, 710 m, on 20 January 2002 at 15:20 hrs on forest floor. UTA A-55247 (field ID: ENS 9698), female with unpigmented gonads and extended oviducts collected by Karin S. Castaneda along the Carretera San Gabriel Mixtepec–Miahuatlán of the Sierra Madre del Sur, Oaxaca, Mexico, 16.160556°N, 97.00111°W, 1270–1350 m, on 15 March 1998 at 16:30 hrs from pine forest habitat.

**Diagnosis.**—A species of *Craugastor* distinguished by the following combination of characters: (1) small adult size (maximum SVL = 18.6 mm); (2) full ossification of most skeletal elements in adults, lacking ossification only of stage 6 (Table 3); (3) absence of posterolateral projection of frontoparietal; (4) presence of vomerine odontophores; (5) absence of raised tubercles on eyelids; (6) supratympanic fold absent or poorly developed; (7) face flank with nostril-canthal-supratympanic stripe, lips colored as dorsum; (8) two postrictal tubercles; (9) gular region uniformly pale to slightly evenly peppered with melanocytes; (10) dorsal surface unicolored pale; (11) pale middorsal ridge, sometimes with few tiny spots; (12) evenly fine tubercles on dorsum; (13) body flank unicolored pale, shagreened with fine tuberculation; (14) inguinal glands present and axillary glands absent in adults; (15)
when leg adpressed to body, heel reaches between eye and tip of snout; (16) outer tarsal ridge with 3–8 tiny and pointed tubercles on slightly raised fringe; (17) finger and toe tips lanceolate to mucronate (toes and outer two fingers); (18) similar sizes of inner and outer metatarsal tubercles.

**Comparisons.**—*Craugastor candelariensis* can be differentiated from *C. bitonium, C. mexicanus, C. montanus, C. omiltemanus, C. polaclavus, C. pygmaeus, C. rubinus,* and *C. saltator,* by a larger inner metatarsal tubercle (inner and outer metatarsal tubercles are similar sizes in *C. candelariensis*). *Craugastor candelariensis* can be differentiated from *C. cueytal* and *C. hobartsmithi* by the absence of vomerine odontophores (present in *C. candelariensis*). It can be differentiated from *C. portilloensis* by the presence of posterolateral projections of the frontoparietal (absent in *C. candelariensis*).

**Description of holotype.**—Holotype small male (SVL = 13.3 mm); snout rounded and short (0.5 mm naris–snout; 4% SVL); long eye–nostril distance (1.7 mm; 13% SVL); tympanum 1.2 mm (7.6% SVL); no supratympanic fold and no shoulder tubercle; finger length formula III < IV < II = I; single palmar tubercle; single prepollical tubercle; subarticular tubercles present on all fingers; supernumerary tubercles present on Finger III; toe length formula IV < III < V < II < I; inner metatarsal tubercle and outer metatarsal tubercle equal size; subarticular tubercles present on all toes; supernumerary tubercles present on plantar surface; unable to verify supracloacal fold state as posterior end damaged when removing leg for genetic analysis; entire body lightly colored in preservative (appears some saponification may have occurred).
Variations in Paratypes.—Body sizes (SVL) 12.4 mm (MZFC-HE-35617), 14.3 mm (UTA A-66116), 18.6 mm (UTA A-55247); eye–nostril distance 10–13% SVL (males), 9% SVL (female); tympanic ratios 7–10%.

Etymology.—The name is an abbreviated allusion to the municipality of Candelaria Loxicha (near the type locality) and the Latin suffix -ensis meaning place. It is simultaneously a reference to the Latin noun candēla meaning a fire or light made of wax given the translucent yellow appearance of several type specimens in preservative, as if someone were shining a candle through them.

Distribution.—This species is known from intermediate elevations of southern Oaxaca (668–1350 m), an area that mostly consists of Sierra Madre del Sur pine-oak forest habitat.

Phylogenetics.—Craugastor candelariensis was strongly supported as monophyletic in the concatenated analysis (ML = 100; BAYES = 1.0; Fig. 3). In this analysis, the sister taxon of C. candelariensis was inferred to be C. polaclavus (ML = 80; BAYES = 0.99). We also observed this sister relationship in the nDNA-only analysis (Fig. 5), however, in the mtDNA-only analysis C. candelariensis was inferred to be the sister taxon of a clade containing C. bitonium + C. pygmaeus (Fig. 4). In terms of genetic distances, Craugastor candelariensis is most similar to C. polaclavus and C. pygmaeus (both 6.4%; Table 4).

Remarks.—The skull of C. candelariensis is similar to C. bitonium, C. hobartsmithi, C. montanus, and C. pygmaeus with more posteriorly placed anterior suture of the frontopareital and prootic than other species. Two type specimens appear white-yellowish in preservative (possibly having been saponified). This species likely co-occurs with C. pygmaeus, C. polaclavus, and C. portilloensis in southcentral
Oaxaca (Figs. 6 and 8). In terms of body size and ossification level it is the smallest member of the *C. mexicanus* Series to complete stage 5 of our ossification series.

*Craugastor cueyatli* sp. nov.


**Holotype.**—UTA A-62348 (field ID: JAC 27244; Fig. 24, B), male collected by J. W. Streicher, C. L. Cox, J. Reyes-Velasco, G. Weatherman, and C. M. Sheehy III on the road from Avandaro to El Manzano, East of Cerro Gordo, Estado de México, Mexico, 19.12209°N, 100.13969°W, 2311 m on 18 June 2008.

**Paratypes (2).**—MZFC-HE-35614 (Fig 24, A), female with developed ova covered in mildly pigmented connective tissue, same data as holotype, except 19.11735°N, 100.13940°W, 2282 m. AMNH A-57809 (Fig. 24, C), male from Tepozteco, Morelos, Mexico (Aztec archaeological site, 19.00079°N, 99.10156°W, 2000 m).

**Referred Specimens (4).**—USNM 122054–55, and USNM 139380 from Estado de México and Morelos, respectively. MZFC 1089, from Tepoztlán, Barrio de Ixaltepec, central Morelos.

**Diagnosis.**—A species of *Craugastor* distinguished by the following combination of characters: (1) small adult size (maximum SVL = 15.7 mm); (2) reduced ossification of the skeleton relative to other members of the Series, lacking ossification of any skeletal elements beyond stage 2 (Table 4); (3) presence of posterolateral projection of frontoparietal; (4) absence of vomerine odontophores; (5)
presence of raised tubercles on eyelids; (6) supratympanic fold absent or poorly
developed; (7) face flank barred, with snout-nostril-canthal-supratympanic stripe; (8)
on postictal tubercle; (9) gular region lightly pigmented; (10) dorsal surface
unicolored dark; (11) dark middorsal ridge; (12) evenly tubercular dorsum; (13) body
flank unicolored pale with or without a dark supra-/post-axillary band, shagreened;
(14) inguinal glands present and axillary glands absent in adults; (15) when leg
adpressed to body, heel reaches anterior corner of eye; (16) outer tarsal ridge with 3–7
rounded tubercles, no raised fringe; (17) finger tips round and not expanded, toe tips
slightly lanceolate and barely expanded; (18) similar sizes of inner and outer
metatarsal tubercles.

**Comparisons.**—*Craugastor cueyatl* can be differentiated from *C.
candelariensis*, *C. mexicanus*, *C. montanus*, *C. omiltemanus*, *C. portilloensis*, and *C.
saltator* by the presence of vomerine odontophores (absent in *C. cueyatl*). It can be
differentiated from *C. bitonium*, *C. hobartsmithi*, *C. polaclavus* and *C. pygmaeus* by
the absence of posterolateral projections of the frontoparietal (present in *C. cueyatl*). It can be differentiated from *C. rubinus* by a larger inner metatarsal tubercle (inner
and outer metatarsal tubercles are similar sizes in *C. cueyatl*).

**Description of the holotype.**—Holotype small male (SVL = 12.3 mm);
highly pigmented testes; snout rounded and short (0.6 mm naris–snout; 4% SVL);
medium eye–nostril distance (1.4 mm; 11% SVL); tympanum 1.2 mm (10% SVL);
supratympanic fold terminating in small shoulder tubercle; finger length formula III <
IV < II < I; single palmar tubercle; single prepollical tubercle; subarticular tubercles
present on all fingers; supernumerary tubercles not present on hand; left arm removed
for genetic analysis; toe length formula IV < III < V < II < I; inner metatarsal tubercle
and outer metatarsal tubercle equal in size; subarticular tubercles present on all toes;
supernumerary tubercles present on plantar surface; small supracloacal fold; 1–2 bands of melanocytes on remaining arm; bands on legs evident in life barely visible in preserved specimen.

**Variations in Paratypes.**—Body sizes (SVL) 15.7 mm (MZFC-HE-35614), 11.7 mm (AMNH A-57809); eye–nostril distance 7% SVL (female), unavailable (male); tympanic ratios 8% (female), 11% (male); crus ratio 51% (female), 54% (male).

**Etymology.**—The specific epithet is taken from the word for frog in Nahuatl, an Aztec language that has been spoken in the Valley of Mexico since the 7th Century, a region that includes the type locality of *C. cueyatl*.

**Distribution.**—The new species occurs throughout the central region of the Trans Volcanic Mexican Cordilleras slopes, those facing the Río Balsas, in the states of Mexico and Morelos (1670–2264 m), an area of mesic pine-oak forest habitat. Castro-Franco et al. (2006) associated *C. cueyatl* (as *E. hobartsmithi*) with dry tropical forests and cultivated areas.

**Diet.**—The holotype’s stomach was found to contain a small spider of unknown taxonomy.

**Phylogenetics.**—Craugastor *cueyatl* was inferred to be the sister taxon of *C. bitonium* + *C. pygmaeus* with strong support in the concatenated analysis (87 ML; 0.99 BAYES; Fig. 3). The placement of *C. cueyatl* was less certain in the mtDNA and nDNA-only analyses (Figs. 4 and 5). In terms of genetic distances, Craugastor *cueyatl* is most similar to *C. pygmaeus* (5.9%; Table 4).

**Remarks.**—The skull of *C. cueyatl* is similar to that of *C. hobartsmithi*, *C. montanus*, and *C. pygmaeus* with a more posteriorly placed anterior suture of frontoparietal and prootic than other species. Several of the referred specimens are
based on geographic occurrence and general gestalt and should be further examined.

One referred specimen of *C. cueyatl* (USNM 139380) is reported to be collected from Distrito Federal (= Mexico City). We georeferenced this locality as being in the city (Fig. 8), but it is most likely the specimen was collected from outside the metropolis.

Very rarely do species of vertebrate occurring near/in major metropolitan areas remain hidden from science, the late discovery of this new species is likely explained by the diminutive size of *C. cueyatl* and previous confusion with *C. hobartsmithi* and *C. pygmaeus*.

**Craugastor hobartsmithi** (Taylor 1937)

*Eleutherodactylus hobartsmithi* Taylor 1937:355. Holotype male (FMNH 100114) from “Uruapan, Michoacán, Mexico.” [examined].


*Microbatrachylus pygmaeus* Duellman 1961:34. [misidentification].

*Craugastor pygmaeus* Ahumada-Carrillo et al. 2013:1338. [misidentification].

**Diagnosis.**—Based on six specimens. A species of *Craugastor* distinguished by the following combination of characters: (1) small adult sizes (males 11.3–15.2 mm, females ~16.7 mm; Table 5); (2) full ossification of most skeletal elements in adults, lacking ossification beyond stage 4 (Table 3); (3) absence of vomerine odontophores; (4) absence of posterolateral projection of frontoparietal; (5) presence of a row of 4–6 rounded tubercles along outer edge, and 1–3 in mid upper eyelid; (6) supratympanic fold poorly developed; (7) face flank barred with or without distinctive canthal stripe; (8) one or two postrictal tubercles; (9) gular region peppered with
melanocytes; (10) dorsal surfaces finely blotched, usually with dark interorbital bar and suprascapular “Λ,” some individuals with pale dorsal color and 4 stripes, paravertebral and lateral, originating at corners of eyes and ending above groin (lateral more prominent); (11) middorsal ridge (dark or background color); (12) mostly smooth dorsum or with just fine tubercles or folds towards back; (11) body flank darker anteriorly, around axilla, slightly tubercular; (14) inguinal glands present and axillary glands absent in adults; (15) when leg adpressed to body, heel reaches between anterior corner of eye and snout; (16) outer tarsal ridge with 4–6 rounded to slightly pointed tubercles, no raised fringe; (17) finger and toe tips round, finger tips slightly expanded, toe tips expanded; (18) similar sizes of inner and outer metatarsal tubercles.

**Comparisons.**—*Craugastor hobartsmithi* can be differentiated from *C. bitonium, C. mexicanus, C. montanus, C. omiltemanus, C. polaclavus, C. pygmaeus,* and *C. rubinus* by an inner metatarsal tubercle that is twice the size of the outer (these are similar sizes in *C. hobartsmithi*). It can be differentiated from *C. candelariensis* and *C. saltator* by the presence of vomerine odontophores (absent in *C. hobartsmithi*). It can be differentiated from *C. cueyatl* and *C. portilloensis* by the presence of posterolateral projections of the frontoparietal (absent in *C. hobartsmithi*).

**Description.**—In previous literature, *C. hobartsmithi* has been described as small-bodied with pigmented gonads (Taylor 1937; 1940); presence of tubercles on the tarsus (Duellman 1961); two palmar tubercles (Lynch 1965); tarsus bearing a row of tubercles along its outer edge (Lynch 1970).

Holotype (FMNH 100114) small male (13.5 mm); snout rounded and short (0.9 mm naris–snout; 6% SVL); short eye–nostril distance (1.18 mm; 8.7% SVL); tympanum 1.9 mm (14% SVL). We further examined two specimens of *C. cf.*
hobartsmithi from coastal Michoacán (UTA A-66133–34; Fig. 25, B and C) and noted the following characteristics: supratympanic fold terminating in two posttricial tubercles; finger length formula III < IV = II < I; toe length formula IV < III < V < II < I; inner metatarsal tubercle and outer metatarsal tubercle equal size.

**Distribution.**—Craugastor hobartsmithi occurs in the pine oak forest of Michoacán. Craugastor cf. hobartsmithi occurs throughout western Mexico in low to intermediate habitats of Jalisco, Nayarit, Michoacán, Guerrero, and Sinaloa (Fig. 8; Hardy and McDiarmid 1969). Flores-Cobarrubias et al. (2012) reported C. hobartsmithi from Hostotipaquillo, Jalisco. García and Ceballos (1994) reported C. hobartsmithi from coastal Jalisco. The records of C. pygmaeus reported in Duellman (1961) and Ahumada-Carrillo et al. (2013) are all likely C. hobartsmithi or C. cf. hobartsmithi, as our molecular results indicate that C. pygmaeus does not occur west of Guerrero. Similarly, many iNaturalist (https://www.inaturalist.org, accessed June 2019) accounts of C. cf. hobartsmithi are listed under C. pygmaeus—these accounts also suggest that C. cf. hobartsmithi is much more widely distributed in western Mexico than museum collections indicate.

**Phylogenetics.**—Craugastor cf. hobartsmithi was found to be the sister taxon of C. rubinus with strong support (ML = 100; BAYES = 1.0) in both the concatenated and separate mtDNA and nDNA analyses (Figs. 3, 4 and 5). The pairwise p-distances between C. cf. hobartsmithi and C. rubinus is 3.4% (Table 4); the smallest genetic distance between any species of the C. mexicanus Series, suggesting recent divergence.

**Remarks.**—The skull of C. hobartsmithi is similar to C. montanus and C. pygmaeus, with more posteriorly placed anterior suture of frontoparietal and prootic than other species. We tentatively referred several museum collections to C.
hobartsmithi (Fig. 8) as C. cf. hobartsmithi, but these should be further examined. The specimens of C. pygmaeus reported by Duellman (1961) from Arteaga, Michoacán are referred to C. cf. hobartsmithi because we examined several C. pygmaeus from Oaxaca with tubercles on the outer edge of the tarsus rendering Duellman’s (1961) apomorphic character for C. hobartsmithi unreliable. Craugastor hobartsmithi may co-occur with C. pygmaeus in southcentral Guerrero (Figs. 6 and 8). The tissues of C. cf. hobartsmithi used in our phylogenetic analysis originated from Colima. While we lack a voucher specimen for the tissue, the collector of the tissue (J. Reyes-Velasco) provided us with photographs of C. cf. hobartsmithi from Montitlan; near where the tissue was collected (Fig. 25, E and F). One female specimen of C. hobartsmithi from near Uruapan (UMMZ 94230) had several intradermal trombiculid mites on its venter (Fig. 15, D).

Craugastor mexicanus (Brocchi 1877)

Leiuperus mexicanus Brocchi 1877:184. Holotype unsexed (MNHNP 6218) from "Mexico" (= Cerro San Felipe, Oaxaca, Mexico [Smith & Taylor 1950]). [examined].


Pleurodema mexicana (Brocchi): Parker 1927:475.

Microbatrachylus oaxaceae Taylor 1940:505. Holotype male (FMNH 100001) from "Cerro San Flipe, near Oaxaca, Oaxaca, Mexico.” [examined].

Microbatrachylus lineatissimus Taylor 1941:87. Holotype male (FMNH 1000036) from “Cerro San Flipe, near Oaxaca, Oaxaca, Mexico.” [examined].
*Microbatrachylus fuscatus* Davis and Dixon 1957:146. Holotype female (TCWC 12171) from “20 miles east of Tulancingo, Hidalgo, Mexico.” [not examined; near-topotypic specimen from Hidalgo examined (UTA A-66138)].


*Eleutherodactylus mexicanus* (Brocchi): Gorham 1966:86.

*Craugastor mexicanus* (Brocchi): Crawford and Smith 2005:351.

**Diagnosis.**—Based on 26 specimens. A species of *Craugastor* distinguished by the following combination of characters: (1) large adult size (maximum SVL = 40.5 mm); (2) full ossification of the skeleton in adults; (3) presence of posterolateral projection of frontoparietal (Fig. 26, B); (4) presence of vomerine odontophores (in larger individuals); (5) presence or absence of raised tubercles on eyelids, < 4 smooth to round and only slightly protruding tubercles; (6) supratympanic fold developed; (7) face flank, labium barred with or without distinctive canthal stripe; (8) one (or two fused) posttrital tubercles; (9) gular region peppered with melanocytes; (10) dorsal surface extremely variable, ranging from dark or light stripes, dark hour glass, dark or pale dorsal stripe of different widths, being unicolored dark or pale brown, to bird dropping coloration (black peppered grayish dorsum with a dirty white medial streak and bright-white heels), all color morphologies have variable presence of interocular band and suprascapular or rump blotching or stripping; in most snout colored as rest of body but sometimes pale; (11) variable middorsal ridge; (12) dorsal skin smooth or tubercular and may have hourglass and/or vertebral and/or paravertebral ridges; (13) body flank unicolored pale, slightly darker anteriorly, or spotted posteriorly and or anteriorly, supratympanic dark coloration sometimes reaching posterior axillary area;
smooth to shagreened; (14) inguinal gland present and axillary gland sometimes present in adults; (15) when leg adpressed to body, heel reaches snout tip or beyond; (16) outer tarsal ridge with 0–5 rounded tubercles; smooth or with thick but only slightly raised fringe; (17) finger and toe tips round and expanded (rarely slightly spatulate or barely expanded and somewhat pointed); (18) inner metatarsal tubercle larger than outer metatarsal tubercle.

**Comparisons.**—*Craugastor mexicanus* can be differentiated from *C. candelariensis*, *C. cueyat*, *C. hobartsmithi*, and *C. portilloensis* by the equal sizes of the inner and outer metatarsal tubercles (unequal sizes in *C. mexicanus*). It can be differentiated from *C. bitonium* and *C. pygmaeus* by the absence of a posterolateral projection of the frontoparietal (present in *C. mexicanus*). It can be differentiated from *C. polaclavus* and *C. rubinus* by the absence of vomerine odonotophores (present in *C. mexicanus*). It can be differentiated from *C. montanus* by the condition of supratympanic folds in adults; developed in *C. mexicanus* versus moderate to poorly developed in *C. montanus*. It can be differentiated from *C. omiltelmannus* by ventral skin texture in life; smooth to granular in *C. mexicanus* versus areolate in *C. omiltelmannus*. *Craugastor mexicanus* is most similar to *C. saltator*. We were unable to identify any reliable morphological characters to differentiate *C. mexicanus* and *C. saltator*, however, they have non-overlapping geographic distributions with *C. saltator* only occurring in western Guerrero (Fig. 6).

**Description.**—In previous literature, described as large-bodied, long-legged with row of small tubercles on outer edge of the tarsus (Taylor 1941); variable palmar tubercle arrangements (palmar tubercle divided, single, or evaginated; Lynch 1965); inner metatarsal tubercle larger than outer metatarsal tubercle; lack of tarsal tubercles (Lynch 2000).
Holotype (MNHN 6318) is large (~40 mm SVL); owing to poor preservation, columella of holotype partially ruptured the tympana on both sides (Fig. 1, B); finger lengths III > IV > II > I; toe length IV > V = III > II > I.

**Distribution.**—This species is widespread throughout eastern Mexico in high elevation habitats (1554–2700 m) of Oaxaca, Puebla, Hidalgo and Veracruz (Fig. 6). These habitats span the Sierra Madre Oriental and Sierra Madre del Sur. Canseco-Márquez and Gutiérrez Mayén (2010) report *C. mexicanus* occurs in the forests adjacent to the Tehuacán-Cuicatlán valley in Puebla and Oaxaca. It is likely this species occurs in Guerrero, however most specimens resembling *C. mexicanus* we examined from Guerrero are referable to *C. saltator*.

**Phylogenetics.**—The concatenated dataset placed *C. mexicanus* as the sister taxon to a clade of *C. omiltemanus* + *C. saltator* with high support in the BAYES analysis (0.98) but moderate support in the ML analysis (75; Fig. 3). This appears to be a relationship supported exclusively by the mtDNA dataset, as separate analysis of the nDNA markers did not confidently infer a sister taxon of *C. mexicanus* (Figs. 4 and 5). While BAYES analyses strongly supported the monophyly of *C. mexicanus* (> 0.90), the ML analyses recovered variable support ranging from 79 (concatenated analysis) to 54 (nDNA-only analysis). In terms of genetic distances (Table 4), *C. mexicanus* was most similar to *C. omiltemanus* (4.9%), followed by similarity to *C. saltator* (5.1%).

**Intraspecific variation.**—We examined over 220 specimens of *C. mexicanus* for this revision (Appendix 1), and briefly provide some patterns of intraspecific variation that we observed. Many populations have substantial color pattern polymorphism (Fig. 27), similar to what is observed in the *C. rhodopis* Series (Lynch 1966; Streicher et al. 2014). In some northern populations (Hidalgo and Puebla), the
canthal mask is broken into a black spot posterior to the tympanum (often with a thin yet distinctive white margin). Specimens throughout Oaxaca varied in whether they had a single or divided palmar tubercle (as reported by Lynch 1965, see his Fig. 2); in six specimens we examined there was asymmetry with a single palmar tubercle on one hand and divided on the other.

Patterns of dorsal ridging and coloration often coincide, with observations of the following morphs: (1) straight raised ridges that are tubercular and darker in coloration than the rest of the dorsum, (2) straight raised dorsal ridges that are tubercular but of the same color as the rest of the dorsum, (3) straight lines of color that are dark but with no tubercular raised ridges, (4) ridges that are not straight but form an hourglass shape and are tubercular, (5) ridges that are not straight but form an hourglass shape and are not tubercular, (6) scattered tubercles on the dorsum which are sometimes dark and sometimes same color as the background, (7) pale or dark unicolored dorsum, (8) a unicolored dorsum with a pale median stripe that can be ridged or smooth, (9) a wide dark band on the dorsum which usually co-occurs with a pale upper labium, and (10) ‘white hills’ of coloration and a peppered grayish dorsum sometimes with a diffused lighter cream color a pattern which may mimic bird droppings (appearing superficially as a smear of uric acid and digestive waste).

Remarks.—The skull of *C. mexicanus* is similar to that of *C. omiltemanus* and *C. saltator* with more anteriorly placed anterior suture of the frontoparietal and prootic than in other species. We noticed that the ‘*M. lineatissimus*’ morphotype (raised and parallel ridges on the dorsum) occurs widely throughout the range of *C. mexicanus*. Interestingly, the examined paratype of ‘*M. lineatissimus*’ has a unique skull shape for *C. mexicanus*. The shape is similar to that of *C. hobartsmithi*, *C. montanus*, and *C. pygmaeus*, with a more posteriorly placed anterior suture of the
frontoparietal and prootic than in other species, coupled with a narrower back of the
skull than in any other species (Fig. 27, A). This unique condition likely explains the
specimen as an outlier in several of our statistical analyses (Figs. 9, 11, and 12).
However, we were unable to CT-scan other individuals with the ‘M. lineatissimus’
morphotype (or the holotype of M. lineatissmus), so future investigation is necessary
to determine if the examined paratype (FMNH 104548) is an aberrant individual of
C. mexicanus or represents a valid taxon.

Lynch (1965) reports that ‘E. oaxaca’ has parotoid glands. However, we saw
no evidence of these glands in the two type specimens that we examined (FMNH
100001 and FMNH 126638), nor are we aware of any species of Craugastor that
possess parotoid glands (= large poison glands on the nuchal region). Craugastor
mexicanus likely co-occurs with C. o miltemanus at high elevation localities of central
Oaxaca (Figs. 6 and 8). At intermediate elevation localities in Veracruz and Oaxaca, it
may overlap with C. pygmaeus (Fig. 7). Male C. mexicanus have significantly larger
tympana than female C. mexicanus (Fig. 13).

Craugastor montanus (Taylor 1942)
Microbatrachylus montanus Taylor 1942:67. Holotype female (USNM 115507) from
“Mount Ovando, Chiapas, Mexico.” [examined].
Eleutherodactylus sartori Lynch 1965:10. [replacement name].
Craugastor montanus (Taylor): Crawford and Smith 2005:351.

Diagnosis.—Based on holotype (Fig. 1, E). A species of Craugastor
distinguished by the following combination of characters: (1) moderate adult size
(holotype, SVL = 24.5 mm); (2) ossification of most of skeleton in adults; (3)
presence of posterolateral projection of frontoparietal; (4) presence of vomerine
odontophores; (5) presence or absence of raised tubercles on eyelids; (6)
supratympanic fold moderate to poorly developed; (7) face flank barred with or
without canthal stripe, 1–2 particularly dark bars below eye; (8) one (or two fused)
postriectal tubercles; (9) gular region with pale spotting; (10) dorsal surface blotched
or unicolored pale; diffuse interorbital bar, small suprascapular spots; sometimes with
2 dark rump spots (11) middorsal ridge present; (12) dorsum smooth with only few
fine tubercles; (13) body flank darker anteriorly (post axillary), slightly shagreened to
smooth; (14) inguinal gland present and axillary gland present in adults; (15) when
leg adpressed to body, heel reaches snout tip or beyond; (16) outer tarsal ridge with
0–2 small and round tubercles close to heel, no raised fringe; (17) finger and toe tips
round, finger tips slightly or not expanded, toe tips expanded; (18) inner metatarsal
tubercle larger than outer metatarsal tubercle.

Comparisons.—Craugastor montanus can be differentiated from C.
candelariensis, C. cueyat, C. hobartsmithi, and C. portilloensis by equal sizes of the
inner and outer metatarsal tubercles (unequal sizes in C. montanus). It can be
differentiated from C. bitonium and C. pygmaeus by the absence of a posterolateral
projection of the frontoparietal (present in C. montanus). It can be differentiated from
C. polaclavus and C. rubinus by the absence of vomerine odontophores (present in C.
montanus). It can be differentiated from C. mexicanus, C. omiltemanus, and C.
saltator by the general shape of its skull (Fig. 12). It can be differentiated from C.
mexicanus by the condition of supratympanic folds in adults; moderate to poorly
developed in C. montanus versus developed in C. mexicanus. It can be differentiated
from C. omiltemanus by ventral skin texture in life; smooth to granular in C.
montanus versus areolate in C. omiltemanus. It can be differentiated from C. saltator
by relative leg length; crus 53–59% SVL in *C. montanus* versus 62–73% SVL in *C. saltator*.

**Description.**—In previous literature, described as moderately-sized (males average 16.2 mm SVL, females average 24.0 mm SVL); finger I shorter than finger II; 3 palmar tubercles; testes black; inner metatarsal tubercle larger than outer metatarsal tubercle (Lynch 2000). Lynch (2000) redescribed *C. montanus* (as *E. sartori*) owing to ‘errors in Taylor’s (1942) original description that were repeated by Lynch (1965, 1970).’

**Distribution.**—This species is known from intermediate to high elevations (~2000 m) of the Sierra Madre de Chiapas in the state of Chiapas, Mexico (Lynch 2000) and adjacent regions of the Department of San Marcos, Guatemala (Crawford and Smith 2005). This region contains a complex mixture of dry forests, mixed forests, cloud forests, and pine-oak forests.

**Phylogenetics.**—In the concatenated analysis, *C. montanus* was recovered as the sister taxon of all other members of the *C. mexicanus* Series (ML = 66, BAYES = 0.99; Fig. 3). It also had this placement in the mtDNA-only analysis (Fig. 4), but not in the nDNA analysis where it was found with weak support to be the sister taxon of a clade containing all taxa except *C. mexicanus* and *C. omiltemanus* (ML = 33, BAYES = 0.73; Fig. 5). This differs from the phylogenetic placement of *C. montanus* (as *E. sartori*) in the nDNA-only analysis of Crawford and Smith (2005). In terms of genetic distances (Table 4), *C. montanus* was most similar to *C. polaclavus* (5.7%) followed by similarity with *C. mexicanus* (6.1%).

**Remarks.**—The skull of *C. montanus* is similar to *C. hobartsmithi* and *C. pygmaeus*, with more posteriorly placed anterior suture of the frontoparietal and prootic than other species. The skull of *C. montanus* was also described by Lynch
(2000) as *E. sartori*. Lynch (1965) created the neonym, *Eleutherodactylus sartori*, because *Eleutherodactylus montanus* was preoccupied by a West Indian species. This is the most southerly distributed species in the *C. mexicanus* Series. *Craugastor montanus* likely co-occurs with *C. pygmaeus*.

The type locality of *C. greggi* (Bumzaheim 1955) is Volcan Tajumulco in San Marcos, Guatemala near where we sampled *C. montanus* for our molecular analysis (Fig. 6). Although *C. greggi* was placed in the *C. laticeps* Series of Hedges et al. (2008), it is allied to the *C. mexicanus* Series by having Finger I shorter than Finger II. This affinity was noted in the original description: “*Eleutherodactylus greggi* seems to agree most closely with the member of the *Eleutherodactylus mexicanus* group…” (Bumzaheim 1955). However, *C. greggi* was differentiated from *C. montanus* (= *E. sartori*) by Lynch (2000) on the basis of fusion between the last presacral vertebrae and sacrum (not fused in *C. montanus*). Nonetheless, our preliminary examinations of the holotype of *C. greggi* (Fig. 28) and collections from the Sierra de Chiapas suggest that future research is needed to confirm *C. greggi* can be differentiated from *C. montanus* as the taxa are united by multiple characters including (but not limited to) adult body size, presence of vomerine odonotophores, presence of posterolateral projection of frontoparietal, gular region with pale spotting, finger lengths, toe lengths, unequal sizes of the inner and outer metatarsal tubercles, and geographic distribution.

*Craugastor omiltemanus* (Günther 1900)

*Syr rhaphus omiltemanus* Günther 1900:213. Holotype unsexed (BMNH 1901.12.19.7) from “Omilteme, Guerrero, Mexico.” [examined].

**Eleutherodactylus omiltemanus** (Günther): Lynch 1970:175.

**Craugastor omiltemanus** (Günther): Crawford and Smith 2005:351.

**Diagnosis.**—Based on *Hylodes calcitrans* type series of 25 individuals and 1 additional specimen. A species of *Craugastor* distinguished by the following combination of characters: (1) large adult size (maximum SVL = 38.8 mm); (2) reduced ossification of skeleton in adults relative to other members of Series, lacking ossification of any elements beyond stage 2 (Table 3) except for the sphenethmoid; (3) presence of posterolateral projection of frontoparietal; (4) presence of vomerine odontophore; (5) presence or absence of raised tubercles on eyelids, smooth, 6 round and only slightly protruding tubercles, sometimes a few aligned at the outer edge; (6) supratympanic fold developed; (7) face flank barred or dark; canthus dark, pale, or spotted; canthus with or without a stripe (complete or broken); (8) one or two postrictal tubercles; (9) gular region from evenly scattered fine pigmentation, to densely pigmented with a mid-pale stripe; (10) dorsal surface unicolored pale brown or grey; unicolored to lightly spotted above the scapular and/or rump areas, or tubercles and ridges (if present), interorbital bar; (11) with or without a middorsal ridge; (12) dorsum smooth with only few fine tubercles towards flanks and urostyle or with ridges forming hourglass patterns and medium tuberculation; (13) body flank darker anteriorly (post axillary) due to posterolateral expansion of supratympanic stripe; sometimes with contrasting white/dark blotching inguinal area, otherwise pale colored; shagreened; (14) inguinal gland present and axillary gland present in adults; (15) when leg adpressed to body, heel reaches middle of eye to mid-canthal area; (16)
outer tarsal ridge 0–5 rounded and only slightly raised tubercles, no raised fringe; (17) finger and toe pads round, fingertips slightly or not expanded, toe tips expanded; (18) inner metatarsal tubercle larger than outer metatarsal tubercle.

**Comparisons.**—*Craugastor omiltemanus* can be differentiated from all other members of the *C. mexicanus* Series by the combination of rough (and often raised) areolate skin on its venter and a massive inner metatarsal tubercle (Figs. 21, G and 29; Lynch 1970, 2000).

**Description.**—In previous literature described as large-bodied, short-legged, with toe III < toe V; inner metatarsal tubercle up to five times larger than outer metatarsal tubercle (Fig. 29, A); subarticular tubercles conical; vomerine odontophores; few supernumerary plantar tubercles (Taylor 1941; Lynch 2000).

There are two syntypes of *C. omiltemanus*, BMNH 1901.12.19.7 (re-registered as BMNH 1947.2.16.62; Fig. 1, J) and BMNH 1901.12.19.8 (re-registered as BMNH 1947.2.16.63). We designate the former as the lectotype and the latter as the paralectotype of this species. Both specimens appear to have partially desiccated at some point in their history, whereas the type series of *Hylodes calcitrans* is in much better condition (Fig. 1, K; Fig. 23, A and B). We designate BMNH 1901.12.19.29 (re-registered as BMNH 1947.2.16.47) as the lectotype of *H. calcitrans*. Relative finger lengths of the types are III > IV > II > I and relative toe lengths are IV < III < V < II < I. Dorsal skin texture raised often with an ‘X’ pattern of sebaceous glands in life (Fig. 30, A–D).

**Distribution.**—Prior to our study, *C. omiltemanus* was known only from Guerrero (Günther 1900; Crawford and Smith 2005). Our discovery of a specimen from Oaxaca (UTA A-64264) that is both phylogenetically and morphologically assignable with *C. omiltemanus* extends the distribution of this species eastward. This
species occurs in high elevation pine-oak forest habitats of the Sierra Madre del Sur in the states of Guerrero and Oaxaca (Fig. 8; Fig. 30, E and F).

**Phylogenetics**.—In all analyses, *C. omiltemanus* was found to be monophyletic with strong support (ML > 90; BAYES > 0.90; Figs. 3 and 4). In the concatenated analysis *C. omiltemanus* was found to be the sister taxon of *C. saltator*, although with limited support (ML = 44; BAYES = 0.74; Fig. 3). There was less support for the sister relationship with *C. saltator* in the mtDNA-only analysis (ML = 33; BAYES = 0.82; Fig. 4). In the nDNA-only analysis (which did not include *C. saltator*), *C. omiltemanus* was placed in basal polytomy with two other clades: (1) *C. mexicanus* and (2) all other species of the *C. mexicanus* Series (Fig. 5). In terms of genetic distances (Table 4), *C. omiltemanus* was most similar to *C. mexicanus* (4.9%), followed by similarity to *C. saltator* (5.6%).

**Remarks**.—The skull of *C. omiltemanus* is similar to *C. mexicanus* and *C. saltator* with a more anteriorly placed anterior suture of frontoparietal and prootic than in other species. Skull examination was also conducted on a smaller subadult individual (UTA A-55240, SVL = 16.5 mm), that had only stage 1 of the ossification sequence complete and only two features of stage 2 present. Unlike the adult specimen, the nasals are completely unossified and the frontoparietal greatly reduced and while vomerine odontophores are present the posterolateral projection of the frontoparietal is absent. *Craugastor omiltemanus* likely shares a similar distribution with other *Craugastor* species endemic to the Sierra Madre del Sur (e.g. *C. uno*; Streicher et al. 2011). Lynch (2000) reports that *C. omiltemanus* has white testes, but we observed pigmented testes in this species (Table 6). Throughout its range, *C. omiltemanus* likely co-occurs with *C. bitonium*, *C. mexicanus*, *C. pygmaeus*, and *C.
Male *C. omiltemanus* have significantly larger tympana than female *C. omiltemanus* (Lynch 2000; this study).

*Craugastor polaclavus* sp. nov.

**Holotype.**—UTA A-62392 (field ID: JAC 21230; Fig. 31), female collected by E. N. Smith and colleagues in Portillo del Rayo, Distrito San Pedro Pochutla, Sierra Madre del Sur, Oaxaca, Mexico, 15.97303°N, 96.99711°W, 1550–1585 m, 24 September 2001.

**Paratypes (4).**—UTA A-55246, a recent hatchling collected by E. N. Smith and José Luis Camarillo Rangel from Río Salado, Sierra Madre del Sur, Oaxaca, Mexico, 16.194167°N, 97.0975°W, 1245 m, 26 September 1997. UTA A-66098 and MZFC-HE-35582–83, adult or subadult specimens all collected with the holotype.

**Referred Specimen (1).**—UTA A-66097, female, same data as holotype.

**Diagnosis.**—A species of *Craugastor* distinguished by the following combination of characters: (1) small adult size (maximum SVL = 14.7 mm); (2) highly reduced ossification of skeleton in adults relative to other members of Series; (3) presence of posterolateral projection of the frontoparietal; (4) absence of vomerine odontophores (5) presence of raised tubercles on eyelids; (6) supratympanic fold absent or poorly developed; (7) face flank barred with no distinctive canthal stripe, 1–2 particularly dark bars below eye; (8) one or two postrictal tubercles; (9) gular region with pale spotting; (10) dorsal surface blotched; suprascapular chevron, interorbital bar; (11) pale or as background middorsal ridge; (12) dorsum smooth with only large scattered tubercles; (13) body flank darker anteriorly, no sharp delineation of color change, smooth to shagreened; (14) inguinal glands present and axillary glands absent
in adults; (15) when leg adpressed to body, heel reaches nostril; (16) outer tarsal ridge
with 0–4 extremely small, flat, and round tubercles, no raised fringe; (17) finger and
toe pads round, finger tips not expanded, toe tips slightly expanded; (18) inner
metatarsal tubercle larger than outer metatarsal tubercle.

**Comparisons.**—*Craugastor polaclavus* can be differentiated from *C. candelariensis*, *C. mexicanus*, *C. montanus*, *C. omiltemanus*, and *C. saltator* by the
presence of vomerine odontophores (absent in *C. polaclavus*). It can be differentiated
from *C. bitonium*, and *C. cueytatl* by the condition of adpressed leg where the heel
does not reach the nostril (reaches nostril in *C. polaclavus*). It can be differentiated
from *C. hobartsmithi* and *C. pygmaeus* by the absence of a posterolateral projection of
the frontoparietal (present in *C. polaclavus*). It can be differentiated from *C.
portilloensis* by metatarsal tubercles of equal size (unequal in *C. polaclavus*). It can be
differentiated from *C. rubinus* by relative finger lengths of IV = II (IV > II in *C.
polaclavus*).

**Description of holotype.**—Holotype small female (SVL = 14.7 mm); snout
rounded and short (0.8 mm naris–snout; 5% SVL); short eye–nostril distance (1.4
mm; 7% SVL); tympanum 1.4 mm (10% SVL); mild supratympanic fold terminating
in small shoulder tubercle; finger length formula III < IV = II < I; single palmar
tubercle; single prepollical tubercle; subarticular tubercles present on all fingers;
supernumerary tubercles not present on hand; toe length formula IV < III < V < II < I;
inner metatarsal tubercle larger than outer metatarsal tubercle; subarticular tubercles
present on all toes; supernumerary tubercles present on plantar surface; small
supracloacal fold; dark supratympanic fold in life with orange shoulder tubercle (Fig.
25), shoulder tubercle color not visible in preservative; many bands present on arms
and legs; left leg removed for genetic analysis.
Variations in Paratypes.—Body sizes in SVL 8.2 mm (UTA A-55246), 12.3 mm (UTA A-66098), 11.6 mm (MZFC-HE-35582), 13.5 mm (MZFC-HE-35583); eye–nostril distance 11–13% SVL; tympanic ratios 7–8%.

Distribution.—Intermediate elevations in the foothills of the Sierra Madre del Sur in Oaxaca 1245 ± 15 m (Fig. 7). These habitats are comprised of mixed tropical dry and temperate sierra forests.

Etymology.—The specific epithet is a combination of the Latin pola meaning small and clavus meaning wart. The name is an allusion to the small size and rugose appearance of several individuals in the type series.

Phylogenetics.—Craugastor polaclavus was inferred to be the sister taxon of *C. candelariensis* with strong support in the concatenated analysis (90 ML; 0.99 BAYES; Fig. 3) and nDNA-only analysis (ML > 90, BAYES > 0.90; Fig. 5). The placement of *C. polaclavus* was less certain in the mtDNA where it was found to be the sister taxon of a clade containing *C. cf. hobartsmithi* + *C. rubinus* (ML = 51, BAYES = 0.74; Fig. 4). In terms of genetic distances (Table 4), *C. polaclavus* was most similar to *C. portilloensis* (5.8%), followed by similarity to *C. bitonium* (5.9%).

Remarks.—The skull of *C. polaclavus* is similar to *C. mexicanus*, *C. omiltemanus*, and *C. saltator* with more anteriorly placed anterior suture of the frontoparietal and prootic than in other species. Specimens were dissected, three seem to be subadult females, UTA A-62392, 66098 and MZFC-HE-35582 with unpigmented ovaries and thin undeveloped oviducts, UTA A-66097 is an adult female, with a thickened oviduct and also unpigmented ovaries, containing yolked eggs, UTA A-66098 adult and MZFC-HE-35582 subadult are males with pigmented testes (smaller on second specimen), the hatchling (8.2 mm SVL) was not dissected. This species likely co-occurs with *C. candelariensis*, *C. portilloensis*, and *C.
*pygmaeus* in southcentral Oaxaca (Figs. 6 and 8). It was collected in sympatry with *C. portilloensis* at Portillo del Rayo, Oaxaca, Mexico (Fig. 8). The hatchling paratype specimen (UTA A-55246) had no evidence of skeletal ossification (Fig. 11).

*Craugastor portilloensis* sp. nov.

**Holotype.**—UTA A-62393 (field ID: JAC 21431; Fig. 32), subadult female collected by E. N. Smith and colleagues in Portillo del Rayo, Distrito San Pedro Pochutla, Sierra Madre del Sur, Oaxaca, Mexico, 15.979444°N, 96.516667°W, 1550 m, 1 October 2001.

**Paratypes (4).**—MZFC-HE-35580 and UTA A-66095, juvenile males. MZFC-HE-35581 subadult female, and UTA A-66096 subadult male. All collected at the type locality between 1550 and 1585 m on 24 September 2001 by E. N. Smith and colleagues.

**Diagnosis.**—A species of *Craugastor* distinguished by the following combination of characters: (1) small adult size (maximum SVL = 11.4 mm); (2) reduced ossification of skeleton in adults relative to other members of the Series, lacking ossification of any skeletal elements beyond stage 2 (Table 3); (3) presence of posterolateral projection of frontoparietal; (4) absence of vomerine odontophores (5) presence or absence of raised tubercles on eyelids; (6) supratympanic fold absent or poorly developed; (7) face flank darker than dorsum, faintly barred lips, snout-nostril-canthal-supratympanic stripe; (8) one or two postrictal tubercles; (9) gular region with pale spotting; (10) dorsal surface unicolored pale, diffuse interorbital bar, sometimes with two dark rump spots; (11) with or without a middorsal ridge; (12) dorsum smooth or with scattered fine tubercles; (13) body flank has dark supratympanic stripe
extending towards lower mid-flank, smooth, very few small tubercles; (14) inguinal

(15) when leg adpressed to body, heel reaches between eye and slightly past snout; (16) outer tarsal ridge smooth or with 1–3 extremely small, flat, and round tubercles, no raised fringe; (17) finger and toe pads round, finger tips not expanded, toe tips slightly expanded; (18) similar sizes

of inner and outer metatarsal tubercles.

Comparisons.—Craugastor portilloensis can be differentiated from C. candelariensis, C. mexicanus, C. montanus, C. omiltemanus, and C. saltator by the presence of vomerine odontophores (absent in C. portilloensis). It can be differentiated from C. bitonium, C. hobartsmithi, and C. pygmaeus by the absence of a posterolateral projection of the frontoparietal (present in C. portilloensis). It can be further differentiated from C. pygmaeus by the absence of a canthal mask (present in C. portilloensis). It can be differentiated from C. pygmaeus by the absence of a canthal mask (present in C. portilloensis). It can be differentiated from C. pygmaeus by the absence of a canthal mask (present in C. portilloensis). It can be differentiated from C. pygmaeus by the absence of a canthal mask (present in C. portilloensis). It can be differentiated from C. pygmaeus by the absence of a canthal mask (present in C. portilloensis). It can be differentiated from C. pygmaeus by the absence of a canthal mask (present in C. portilloensis). It can be differentiated from C. pygmaeus by the absence of a canthal mask (present in C. portilloensis). It can be differentiated from C. pygmaeus by the absence of a canthal mask (present in C. portilloensis). It can be differentiated from C. pygmaeus by the absence of a canthal mask (present in C. portilloensis). It can be differentiated from C. pygmaeus by the absence of a canthal mask (present in C. portilloensis). It can be differentiated from C. pygmaeus by the absence of a canthal mask (present in C. portilloensis). It can be differentiated from C. pygmaeus by the absence of a canthal mask (present in C. portilloensis). It can be differentiated from C. pygmaeus by the absence of a canthal mask (present in C. portilloensis). It can be differentiated from C. pygmaeus by the absence of a canthal mask (present in C. portilloensis). It can be differentiated from C. pygmaeus by the absence of a canthal mask (present in C. portilloensis). It can be differentiated from C. pygmaeus by the absence of a canthal mask (present in C. portilloensis). It can be differentiated from C. pygmaeus by the absence of a canthal mask (present in C. portilloensis).

Description of holotype.—Holotype small female (SVL = 11.4 mm); snout rounded and short (0.8 mm naris–snout; 6% SVL); short eye–nostril distance (1.1 mm; 9.8% SVL); tympanum 0.8 mm (6.8% SVL); no supratympanic fold; small shoulder tubercle; finger length formula III < IV < II < I; single flat palmar tubercle; single flat prepollical tubercle; subarticular tubercles present on all fingers; supernumerary tubercles not present on hand; toe length formula IV < III < V < II < I; inner metatarsal tubercle and outer metatarsal tubercle equal size; subarticular tubercles present on all toes; supernumerary tubercles present on plantar surface; right leg removed for genetic analysis; small supracloacal fold; dark mask extending from
snout through eye and past tympanum onto flanks (Fig. 32; coloration also in
paratypes). Some bands present on arms and legs.

**Variations in Paratypes.**—Body sizes in SVL 8.7 mm (MZFC-HE-35580),
8.4 mm (UTA A-66095), 12.1 mm (MZFC-HE-35581), 12.6 mm (UTA A-66096);
eye–nostril distance 10–11% SVL; tympanic ratios 7%.

**Etymology.**—The name is an abbreviated allusion to the type locality near the
town of Portillo del Rayo and the Latin suffix -ensis meaning place.

**Distribution.**—Intermediate elevations in the foothills of the Sierra Madre del
Sur in Oaxaca 1550–1585 m (Fig. 8). These habitats are comprised of mixed tropical
dry and temperate sierra forests.

**Phylogenetics.**—In the concatenated analysis, *Craugastor portilloensis* is the
sister taxon to a clade of small-bodied species (*C. bitonium, C. candelariensis, C.
cueyatl, C. hobartsmithi, C. polaclavus, C. pygmaeus, and C. rubinus*), but with low
branch support (ML = 53, BAYES = 66; Fig. 3). It occupies the same phylogenetic
placement in the mtDNA-only dataset (Fig. 4), but in the nDNA-only dataset is the
sister taxon of a clade including (*C. bitonium, C. cueyatl, C. hobartsmithi, C.
ygmaeus, and C. rubinus*) with moderate support in the Bayesian analysis (ML = 43,
BAYES = 0.78; Fig. 5). In terms of genetic distances (Table 4), *C. portilloensis* was
most similar to *C. montanus* (5.7%), followed by similarity to *C. polaclavus* (5.8%).

**Remarks.**—The skull of *C. portilloensis* is similar to *C. mexicanus, C.
omiltemanus, and C. saltator* with a more anteriorly placed anterior suture of
frontoparietal and prootic than other species. We dissected all specimens of *C.
portilloensis*, males possess pigmented testes and females unpigmented ovaries. This
species likely co-occurs with *C. candelariensis, C. polaclavus, and C. pygmaeus in
southcentral Oaxaca (Figs. 6 and 8). It was collected in sympatry with *C. polaclavus*

at the type locality of Portillo del Rayo, Oaxaca, Mexico (Fig. 8).

*Eleutherodactylus pygmaeus* (Taylor 1937)


*(Microbatrachylus albolabris* Taylor 1940:502. Holotype female (FMNH 100071) from “two miles west of Córdoba, Veracruz, Mexico.” [examined].


*(Microbatrachylus minimus* Taylor 1940:507. Holotype male (FMNH 100323) from “Agua del Obispo, Guerrero, Mexico.” [examined].

*(Microbatrachylus imitator* Taylor 1942:70. Holotype female (USNM 115508) from “La Esperanza, Chiapas, Mexico.” [examined].

*Diagnosis.*—Based on 37 specimens. A species of *Craugastor* distinguished by the following combination of characters: (1) small adult size (mean SVL = 13.5 mm [SD = 1.77], n = 29); (2) full ossification of skeletal elements in adults; (3) lack of posterolateral projection of frontoparietal; (4) lack of vomerine odontophores; (5) presence or absence of raised tubercles on eyelids; (6) supratympanic fold absent or poorly developed; (7) face flank barred canthus and jaws (rarely dark and blotched), no canthal stripe; (8) one (or two fused) postrictal tubercles; (9) gular region pigmentation present or absent; (10) dorsal surface two-toned usually with dark suprascapular “∧,” or striped and with pale middorsal stripe, (11) variable middorsal ridge; (12) dorsum smooth or with only some large scattered tubercles; (13) body
flank barred darker anteriorly, slightly shagreened to smooth; (14) inguinal glands present and axillary glands absent in adults; (15) when leg adpressed to body, heel reaches between eye and slightly beyond tip of snout; (16) outer tarsal ridge smooth, no raised fringe; (17) finger and toe pads round, expanded; (18) inner metatarsal tubercle larger than outer metatarsal tubercle.

**Comparisons.**—*Craugastor pygmaeus* can be differentiated from *C. candelariensis*, *C. cueyat*, *C. hobartsmithi*, and *C. portilloensis* by equal sizes of the inner and outer metatarsal tubercles (unequal sizes in *C. pygmaeus*). It can be differentiated from *C. mexicanus*, *C. montanus*, *C. omiltemanus*, *C. polaclavus*, *C. rubinus*, and *C. saltator* by the presence of a posterolateral projection of the frontoparietal (absent in *C. pygmaeus*; Fig. 26, C). *Craugastor pygmaeus* is most similar to *C. bitonium* (in morphology, osteology and genetic distance), but may be differentiated from this taxon by the condition of the outer tarsal ridge which is smooth in *C. pygmaeus* versus 1–6 small tubercles in *C. bitonium*.

**Description.**—In previous literature, described as small-bodied (“diminutive”) and short-limbed, with unequal inner and outer metatarsal tubercle sizes; distinct subarticular tubercles; barely visible supernumerary tubercles; no vomerine teeth (Taylor 1937); rounded canthus; two palmar tubercles (Taylor 1942).

Holotype (UIMNH 16125) ~18 mm SVL. Among select specimens we examined we observed short, rounded snout (naris–snout = 0.78 mm [SD = 0.14], \(n = 29\); 5.8% SVL); long eye–nostril distance (1.19 mm [SD = 0.24], \(n = 29\); 8.9% SVL); some specimens with single palmar tubercle; relative finger lengths III > IV > II = I; relative toe lengths IV < III < V < II < I; color pattern in life variable (Fig. 33).

**Distribution.**—Widely distributed throughout lowland to intermediate localities in the states of Chiapas, Puebla, Oaxaca, and Veracruz (also possibly
Tabasco, Mexico, and western Guatemala) from near sea level to 2000 m (Fig. 6).

Canseco-Márquez and Gutiérrez-Mayén (2010) report *C. pygmaeus* occurs in the forests adjacent to the Tehuacán-Cuicatlán valley in Puebla and Oaxaca. The western range edge of *C. pygmaeus* is uncertain; we examined one specimen (UTA A-66131) a male with pigmented testes, from San Vicente de Benítez (17.29061°N, 100.27955°W, 951 m), Guerrero, collected 17 June 2004, that appears referable to *C. pygmaeus*.

**Diet.**—One male specimen (UTA A-64263, determined by the presence of pigmented testes), was found to contain ants (Formicidae) in its stomach.

**Phylogenetics.**—*Craugastor pygmaeus* was inferred to be the sister taxon of *C. bitonium* with high support in the concatenated analyses (ML = 99; BAYES = 1.0; Fig. 3). This sister relationship was also recovered in both mtDNA and nDNA analyses, although with lower support in the nDNA-only analyses (ML = 54, BAYES = 0.67; Figs. 4 and 5). *Craugastor pygmaeus* is separated from *C. bitonium* by a p-distance of 4.7% (Table 4).

**Remarks.**—The skull of *C. pygmaeus* is similar to *C. hobartsmithi* and *C. montanus*, with more posteriorly placed anterior suture of the frontoparietal and prootic than other species. Despite how common this species is in most museum collections, we know very little about its natural history, including reproductive behavior, call, and diet. This species likely co-occurs with *C. candelariensis*, *C. polacalvus* and *C. portilloensis* in southcentral Oaxaca and (possibly) *C. bitonium* in central Guerrero. It may overlap with (1) *C. montanus* in Chiapas, (2) *C. mexicanus* at intermediate elevations of the Sierra Madre del Sur and Sierra Madre Oriental (Fig. 7), and (3) *C. hobartsmithi* in central/western Guerrero. Males likely have larger tympana than females (Figs. 13 and 33).
Craugastor rubinus sp. nov.

**Holotype.**—UTA A-62345 (field ID: JAC 30720; Fig. 34, A), male collected by J. W. Streicher, C. L. Cox, C. M. Sheehy III, R. U. Tovar, and M. J. Ingrasci on the road between Talpa de Allende and El Cuale, Jalisco, Mexico, 20.37707°N, 105.04793°W, 1771 m, 8 July 2009.

**Paratypes (2).**—UTA A-62347 (Fig. 34, C) and MZFC-HE-35616 (formerly UTA A-62346; Fig. 34, B), same collection data as holotype.

**Diagnosis.**—A species of Craugastor distinguished by the following combination of characters: (1) small adult size; (2) reduced ossification of the skeleton in adults relative to other members of Series, lacking ossification of any skeletal elements beyond stage 2 (Table 3); (3) presence of posterolateral projection of frontoparietal; (4) absence of vomerine odontophores; (5) presence of raised tubercles on eyelids; (6) supratympanic fold absent or poorly developed; (7) face flank barred, with snout-nostril-canthal-supratympanic stripe, sometimes broken canthaly and postocularly; (8) one postrictal tubercle; (9) gular region with pale spotting; (10) dorsal surface blotched or unicolored pale; diffuse interorbital bar, small suprascapular spots, sometimes 2 dark rump spots; (11) middorsal ridge present; (12) dorsum smooth with no tubercles; (13) body flank dark supratympanic stripe extending towards lower mid-flank, broken, paler towards groin, smooth to finely shagreened; (14) inguinal glands present and axillary glands absent in adults; (15) when leg adpressed to body, heel reaches nostril; (16) outer tarsal ridge with 0–4 extremely small, flat, and round tubercles, no raised fringe; (17) finger and toe pads
round, finger tips not or just barely expanded, toe tips slightly lanceolate and barely expanded; (18) inner metatarsal tubercle larger than outer metatarsal tubercle.

**Comparisons.**—*Craugastor rubinus* can be differentiated from *C. candelariensis, C. cueyatl, C. hobartsmithi,* and *C. portilloensis* by equal sizes of the inner and outer metatarsal tubercles (unequal sizes in *C. rubinus*). It can be differentiated from *C. mexicanus, C. montanus, C. omiltemanus, C. polaclavus,* and *C. saltator* by the presence of vomerine odontophores (absent in *C. rubinus*). It can be differentiated from *C. bitonium* and *C. pygmaeus* by the absence of a posterolateral projection of the frontoparietal (present in *C. rubinus*).

**Description of holotype.**—Holotype small male (SVL = 12.6 mm); snout rounded and short (0.8 mm naris–snout; 7% SVL); short eye–nostril distance (1.3 mm; 10% SVL); tympanum 1.2 mm (9.1% SVL); no supratympanic fold or shoulder tubercle; finger length formula III < IV < II < I; single flat palmar tubercle; single flat prepollical tubercle; subarticular tubercles present on all fingers; supernumerary tubercles not present on hand; right arm removed for genetic analysis; toe length formula IV < III < V < II < I; inner metatarsal tubercle larger than outer metatarsal tubercle; subarticular tubercles present on all toes; supernumerary tubercles present on plantar surface; right leg removed for genetic analysis; small dark supracloacal fold; dorsal color in life included brown and grey mottling, orange coloration on arms extending to posterior edge of tympanum (Fig. 34, A); venter coloration in life included pale, almost blue speckling similar to other species of *C. mexicanus* Series (Fig. 35); grey in preservative; many bands present on arms and legs.

**Variations in Paratypes.**—Body sizes (SVL) 10.8 mm (MZFC-HE-35616), 11.5 mm (UTA A-62347); eye–nostril distance both 10% SVL; tympanic ratios both
9%; dorsal color pattern mottled (MZFC-HE-35616; Fig. 34, B) or with dark stripe extending from snout to flank (UTA A-62347, Fig. 34, C).

**Distribution.**—Known only from the type locality in Jalisco (Talpa de Allende), habitat of pine-oak forest at the southern extent of the Sierra Madre Occidental.

**Etymology.**—The specific epithet is derived from the Latin *rubinus*, which means ruby. This name is inspired by the garnet mines found near the type locality of Talpa de Allende in the Sierra Madre Occidental of Jalisco.

**Phylogenetics.**—*Craugastor rubinus* was strongly supported as monophyletic in the concatenated analysis (ML = 99; BAYES = 1.0; Fig. 3). The new species is also strongly supported as the sister taxon of *C. cf. hobartsmithi* (ML = 100; BAYES = 1.0). *Craugastor rubinus* is separated from *C. cf. hobartsmithi* by a p-distance of 3.4% (Table 4).

**Remarks.**—The skull of *C. rubinus* is similar to that of *C. hobartsmithi*, *C. montanus*, and *C. pygmaeus* with more posteriorly placed anterior suture of the frontoparietal and prootic than other species. The type series was collected from the leaf litter surrounding a mountain stream. The male holotype has slightly pigmented testes. A female paratype, UTA A-62345, has large pigmented ovaries. This species may co-occur with *C. hobartsmithi* in Jalisco. Despite the small genetic distances separating *C. rubinus* and *C. cf. hobartsmithi*, there are many skeletal and morphological differences between these two species including relative metatarsal tubercle sizes, condition of the posterolateral projection of frontoparietal, and relative snout length (Table 6).
Eleutherodactylus saltator Taylor 1941:89. Holotype female (FMNH 100116) from "Omitleme, Guerrero, Mexico." [examined].

Eleutherodactylus mexicanus: Lynch 2000:134. [misidentification].


Diagnosis.---Based on holotype and three additional specimens. A species of Craugastor distinguished by the following combination of characters: (1) large adult size (maximum SVL = 44 mm); (2) full ossification of skeleton in adults but under a different ossification sequence to other members of the Series (Table 3); (3) presence of posterolateral projection of the frontoparietal; (4) presence of vomerine odontophores; (5) presence or absence of raised tubercles on eyelids; (6) supratympanic fold developed; (7) face flank, labium barred or dark with a cream stripe above; canthal stripe complete or broken; (8) one or two postrictal tubercles; (9) gular region with trace of mid-pale stripe; (10) dorsal surface unicolored, blotched, or with wide middorsal stripe bordered by cream colored stripes, dark interorbital bar, sometimes with small suprascapular and/or rump spots; (11) middorsal ridge present; (12) dorsum smooth or slightly tuberculate; (13) body flank unicolored, rarely supratympanic stripe extending to area behind insertion of arm, making anterior area darker; finely shagreened; (14) inguinal gland present and axillary gland present in adults; (15) when leg adpressed to body, heel reaches beyond snout; (16) outer tarsal ridge with 0–5 extremely small, flat, and round tubercles, no raised fringe or ridge; (17) finger and toe pads round and expanded; (18) inner metatarsal tubercle larger than outer metatarsal tubercle.

Comparisons.---Craugastor saltator can be differentiated from C. bitonium, C. cueyatl, C. hobartsmithi, C. pygmaeus and C. rubinus by the absence of vomerine
odontophores (present in *C. saltator*). It can be differentiated from *C. candelariensis* and *C. portilloensis* by equal sizes of the inner and outer metatarsal tubercles (unequal sizes in *C. saltator*). It can be differentiated from *C. omiltemanus* by ventral skin texture in life; smooth to granular in *C. saltator* versus areolate in *C. omiltemanus*. It can be differentiated from *C. montanus*, and *C. polaclavus* by shorter relative leg sizes with a crus ratio of 50–58% SVL (long relative leg sizes of 62–73% SVL in *C. saltator*). *Craugastor saltator* is most similar to *C. mexicanus*, however they do not overlap in geographic range (see *C. mexicanus* account for additional information).

**Description.**—Detailed description in Taylor (1942). Described as large-bodied, long-legged, with pigmented testes, unequal inner and outer metatarsal tubercle sizes, large vomerine teeth, and generally smooth dorsal skin (Taylor 1941); with less population-level chromatic variation than its relative *C. mexicanus* (Lynch 2000).

Holotype (FMNH 100166) large female (SVL = 44 mm; Fig. 36) with relative finger lengths III > IV > II > I and relative toe lengths IV > III > V > II > I. A subadult individual used in the molecular analysis, UTA A-66120 (Fig. 36) had the following characteristics: SVL = 14.5 mm; tympanum width = 1.2 mm; naris–snout length = 0.7 mm (4.7% SVL); eye–nostril distance = 1.5 mm (10.3% SVL); relative finger lengths III > IV > II > I; relative toe lengths IV > III > V > II > I; unlike adult specimens, inner metatarsal tubercle and outer metatarsal tubercle near equal in length.

**Distribution.**—Known only from the high elevation pine-oak forests of Guerrero in the Sierra Madre del Sur (Fig. 6).

**Phylogenetics.**—As we were only able to sequence mtDNA data for *C. saltator*, it was only included in the concatenated and mtDNA analyses. In the
concatenated analysis it was recovered as the sister taxon of *C. omiltemanus* with limited support (ML = 44; BAYES = 0.74; Fig. 3). In the mtDNA-only analysis support for this relationship was lower in the ML analysis, but higher in the BAYES analysis (ML = 33, BAYES = 0.82; Fig. 4). In terms of genetic distances (Table 4), *C. saltator* was most similar to *C. mexicanus* (5.2%), followed by similarity to *C. omiltemanus* (5.6%).

**Remarks.**—The skull of *C. saltator* is similar to that of *C. mexicanus* and *C. omiltemanus* with more anteriorly placed anterior suture of the frontoparietal and prootic than in other species. Taylor (1941) makes multiple references to *C. saltator* and *C. omiltemanus* (as *Eleutherodactylus calcitrans*) being similar and states that these two species can be differentiated by the “very long limb, and the reduced inner metatarsal tubercle [of *C. saltator*].” Lynch (2000) noted that *C. saltator* is actually far more similar to *C. mexicanus* from adjacent Oaxaca and subsequently synonymized *C. saltator* with *C. mexicanus* (see Methods, Taxonomic History). Despite the finding of Crawford and Smith (2005) which were used to revalidate *C. saltator*, at one point in our study one of us (JWS) was convinced by Lynch’s (2000) argument that *C. saltator* should be a junior synonym of *C. mexicanus*. The basis for this suspicion was (1) a specimen collected by J. D. Godman from Omilteme, Guerrero (the type locality) identified by J. D. Lynch as *C. saltator* on 13 January 1972 (BMNH 1901.12.19.24) is similar in morphology to *C. mexicanus*, (2) the nDNA analysis of Crawford and Smith (2005) found *C. mexicanus + C. saltator* to be monophyletic, and (3) we did not observe range overlap between *C. mexicanus* and *C. saltator* (Fig. 6), which may be consistent with a single large-bodied, long-legged species inhabiting the Sierra Madre del Sur. However, as in Crawford and Smith (2005) our mtDNA phylogenetic results did not recover *C. mexicanus + C. saltator* as
monophyletic (Fig. 3) and the specimens of *C. saltator* we examined had on average larger body sizes and differing toe length formulae than *C. mexicanus* (Figs. 10 and 11; Table 6). As such, we continue to recognize *C. saltator* as a distinct species pending further taxonomic investigation. *Craugastor saltator* likely co-occurs with *C. bitonium*, *C. pygmaeus*, and *C. omiltemanus* in the Sierra Madre del Sur of Guerrero. It may overlap with *C. mexicanus* in eastern Guerrero/western Oaxaca (Fig. 6).

**DICHOTOMOUS KEY TO THE CRAUGASTOR MEXICANUS SERIES**

1a. Large or medium sized adults (females > 20 mm SVL, males > 16 mm SVL); axillary gland present or absent; supratympanic fold usually developed (except for moderately to poorly developed in *C. montanus*); both vomerine odontophores and posterolateral projection of frontoparietal present (except for some *C. montanus* with no odontophores [but with frontoparietal projection], and some *C. mexicanus* with no frontoparietal projection [but with vomerine odontophores]) ................................................................. 2

1b. Small sized adults (females < 20 mm SVL, males < 16 mm SVL); axillary gland always absent; supratympanic fold absent or poorly developed; with no vomerine odontophores (except in *C. candelariensis*) ........................................... 5

2a. Heel not reaching nostril when leg adpressed to body; 2 or 3 metacarpal tubercles (including thenar; outer smallest, middle largest); outer/inner metatarsal tubercle ratio 0.40–0.55; testis usually unpigmented (sometimes lightly pigmented); ovaries unpigmented; from the highlands of Guerrero and Central Oaxaca (1900–2600 m elevation) . *Craugastor omiltemanus* (Günther)
2b. Heel reaching tip of snout or beyond when leg adpressed to body; always 3 metacarpal tubercles (including thenar); outer/inner metatarsal tubercle ratio variable (0.36–0.75); testis strongly pigmented; ovaries always pigmented (strongly or lightly) .................................................................3

3a. Medium sized adult females (< 16 mm SVL); crus 53–59% SVL; with or without vomerine odontophores; supratympanic fold moderately to poorly developed; labium always barred; middle metacarpal tubercle largest and outer very small; outer tarsal heel tubercles ≤ 2 (close to heel); ovaries pigmented; highlands east of the Isthmus of Tehuantepec (from the Sierra Madre del Sur of eastern Chiapas and western Guatemala)......Craugastor montanus (Taylor)

3b. Large sized adult females (> 16 mm SVL); crus 53–73% SVL; always with vomerine odontophores; supratympanic fold well-developed; labium variable in pattern; middle metacarpal tubercle about same size as thenar, outer smaller; outer tarsal heel tubercles 0–5; ovaries pigmented or not; highlands west of the Isthmus of Tehuantepec (from Oaxaca and Guerrero to Puebla and Hidalgo, including the central highlands of Veracruz).................................4

4a. Crus > 62% SVL (62–73%); heel always beyond tip of snout when leg adpressed to body; outer/inner metatarsal tubercle ratio (0.36[0]–0.58); ovaries unpigmented or only slightly pigmented; from the Sierra Madre del Sur of Guerrero west of Chilpancingo (1900–2850 m elevation) Craugastor saltator (Taylor)

4b. Crus < 69% SVL (53–69%); heel at snout tip or sometimes beyond when leg adpressed to body; outer/inner metatarsal tubercle ratio (0.50–0.75); ovaries pigmented or not; from Guerrero east of Chilpancingo to Oaxaca and to the
north in Puebla, Hidalgo and the adjacent Veracruz highlands (1500–3015 m elevation). Craugastor mexicanus (Brocchi)

Small species

5a. Vomerine odontophores present; outer two fingers and toes lanceolate to mucronate; body flank unicolor pale; no raised eyelid tubercles; gular region not pigmented or only lightly and uniformly peppered; face never barred; postrictal tubercles 2; metacarpal tubercles about equal in size; outer tarsal ridge with 3–8 tiny and pointed tubercles on slightly raised fringe; posterolateral projection of frontoparietal absent; from the Sierra Madre del Sur of Oaxaca, mountains above Puerto Escondido and Puerto Angel (668–1350 m elevation) Craugastor candelariensis Jameson et al.

5b. Vomerine odontophores absent; fingers and toes usually round or at most, slightly lanceolate; body flank darker anteriorly (towards axilla, except uniformly pale in some C. cueyatl); usually with raised eyelid tubercles; gular region blotched or heavily peppered (rarely lightly peppered in C. pygmaeus); face barred or not; postrictal tubercles 1 or 2; outer metacarpal tubercle usually longer and/or wider than inner (except about equal in size in C. cueyatl and C. pygmaeus); outer tarsal ridge with no raised fringe and variable number of tubercles (0–7), flat and round (sometimes slightly pointed); posterolateral projection of frontoparietal present or absent

6a. Face barred, one or two prominent bars below eye; no distinctive canthal stripe; one distinctive dark and rectangular blotch under lower jaw and at level of canthus (prominent in ventral view); gular region with pale spotting; finger tips not expanded; outer tarsal ridge with 0–4 extremely small, flat and round tubercles; posterolateral projection of frontoparietal present; from the Sierra
Madre del Sur of Oaxaca in the mountains above Puerto Escondido (1245–1585 m elevation) ........................................... *Craugastor polaclavus* Jameson et al.

6b. Face barred or not, bars below eye variable; canthal stripe present or absent; no distinctive rectangular blotches under lower jaw and at level of canthus (not prominent in ventral view); gular region variable but, usually spotted or peppered; finger tips expanded or not; outer tarsal ridge with 0–7 extremely small, flat and round to slightly pointed tubercles; posterolateral projection of frontoparietal present or absent; .................................................................

7a. Finger and toe tips round and conspicuously expanded; face barred, never with a canthal stripe; postrictal tubercles 1 (sometimes look like 2 fused); dorsal pattern two-toned or striped, and with a pale middorsal stripe; metacarpal tubercles about equal in size; outer tarsal ridge smooth and lacking tubercles; posterolateral projection of frontoparietal absent; from the lowlands of southern Mexico, from Puebla and Veracruz on the Gulf versant and southern Guerrero on the Pacific versant to Escuintla, Chiapas and possibly adjacent Guatemala (0–1580 m elevation) ...................... *Craugastor pygmaeus* (Taylor)

7b. Finger tips round or lanceolate, not expanded or only slightly; toe tips slightly expanded to expanded, sometimes slightly lanceolated; face barred or with a pale supralabial stripe, canthal stripe present or absent (some *C. bitonium* and *C. hobartsmithi*); postrictal tubercles 1 or 2; dorsal pattern variable; outer tarsal ridge smooth or tuberculated (*C. portillensis* and *C. rubinus*) or always tuberculated; posterolateral projection of frontoparietal present or absent ......

8a. Always with a canthal stripe and softly barred lips; dorsum uniformly dark; postrictal tubercles always 1, on each side; body flank uniformly pale or slightly darker anteriorly; gular region with evenly distributed fine
melanocytes (evenly peppered); metacarpal tubercles about equal in size;
finger tips not expanded round and not expanded; outer tarsal ridge with 3–7
rounded tubercles; posterolateral projection of frontoparietal present; from the
slopes facing the Balsas River depression in the states of Mexico and Morelos
(1670–2311 m elevation)......................... *Craugastor cuyatl* Jameson et al.

8b. Canthal stripe present or absent, and with soft or prominent bars on lips or
with a supralabial pale stripe; dorsum uniformly pale, two-toned, or striped,
ever uniformly colored and darker than flanks; postrictal tubercles 1 or 2;
body flank always darker anteriorly; gular region variable but usually
melanocyte distribution forming light spotting (particularly under lower jaws
and mid-gular area); outer metacarpal tubercle slightly larger than inner;
finger tips not or just barely expanded, round or slightly lanceolated; outer
tarsal ridge with 0–7 tubercles; posterolateral projection of frontoparietal
present or absent ................................................................. 9

9a. Canthal stripe present or absent, and with bars on lips or a supralabial pale
stripe; dorsum usually two-toned or striped; gular region with small
melanocyte distribution forming a few small light spots under lower jaws and
mid-gular area; finger tips slightly expanded, round or slightly lanceolated (*C.
bitonium*); outer tarsal ridge with 1–6 tubercles, round to slightly pointed;
posterolateral projection of frontoparietal absent ........................................ 10

9b. Canthal stripe always present, and with bar(s) on lips; dorsum uniformly pale
(as compared to flanks, one specimen of *C. rubinus* with traces of ill-defined
and light blotching); gular region with melanocyte distribution forming
prominent light spots under lower jaws and mid-gular area; finger tips usually
not expanded (somewhat expanded in one specimen of *C. rubinus*), round,
never lanceolated; outer tarsal ridge with 0–4 tubercles, extremely small, flat, and round; posterolateral projection of frontoparietal present................. 11

10a. Postrictal tubercles 1, on each side; finger and toe tips slightly lanceolated;

finger lengths III > IV ≥ II > I; toe lengths always IV > III > V > II > I;

outer/inner metatarsal tubercle 0.40–0.75; not less than four outer tarsal tubercles, 4–6; from the Sierra Madre del Sur de Guerrero, south of Yextla (2071 m elevation).................................Craugastor bitonium Jameson et al.

10b. Postrictal tubercles 1–2, on each side; finger and toe tips rounded, not lanceolated; finger lengths always III > IV > II > I; toe lengths IV > III ≥ V > II > I; outer/inner metatarsal tubercle 0.62–0.67; outer tarsal tubercles 1–6;

from near Uruapan, Michoacán (1450–1700 m elevation)................................................Craugastor hobartsmithi (Taylor)

11a. Eyelid raised tubercles present or absent; postrictal tubercles 1–2, on each side; toe tips round and slightly expanded; finger lengths III > IV > II > I; toe lengths IV > III ≥ V > II > I; outer/inner metatarsal tubercle 0.67–1.25; from the Sierra Madre del Sur of Oaxaca at Portillo del Rayo (1550–1585 m elevation)............................................. Craugastor portilloensis Jameson et al.

11b. Eyelid raised tubercles present; postrictal tubercles 1, on each side; toe tips slightly lanceolated and barely expanded; finger lengths III > IV = II > I; toe lengths always IV > III > V > II > I; outer/inner metatarsal tubercle 0.50–0.55;

from the Pacific slopes of Jalisco west of Talpa de Allende (1771 m elevation)..............................................Craugastor rubinus Jameson et al.

DISCUSSION

Overview
The description of six new species brings the total number of species in the *C. mexicanus* Series to 12. With the exception of *C. montanus*, all species are endemic to Mexico (though some populations of *C. pygmaeus* may range into Guatemala; Fig. 6). As in other miniaturized anurans, we suspect micro-endemism is common and there are still many undescribed species, particularly among the populations of *C. hobartsmithi* that occur in western Mexico and populations of *C. pygmeus* that occur east of the Isthmus of Tehuantepec.

While our examinations of tympanum size and gonad coloration/morphology have revealed new insights, we still know little regarding the reproductive biology of members of the *C. mexicanus* Series. Bioacoustic communication is clearly important to some species (Fig. 13) and may provide a mechanism for assortative mating in communities with multiple sympatric species living in the leaf litter. Although most species we examined had pigmented gonads, notably in testes (Table 5, Fig. 37, A, C), not all ovaries were pigmented. It is unclear if testis pigmentation is present in the gonadal tissue, the mesorchia, or both. Recent research has demonstrated that the degree of pigmentation on gonads of anurans is regulated by testosterone (Zieri et al. 2015). This may explain why some females of *C. mexicanus* and *C. pygmaeus* (and several of the new species) did not have melanocytes in the visceral peritoneum of their developing ova. However, we note that many other species of *Craugastor* do not have pigmented testes (Fig. 37). Thus, exploring both bioacoustics and gonadal morphology are exciting future directions of reconnaissance.

We conclude this monograph by briefly revisiting (1) the putative causes of body miniaturization, (2) morphology of the *C. mexicanus* Series relative to other *Craugastor* from Mexico, and (3) the conservation status of our focal species through the clarified lens of our taxonomic revision.
Small Bodies and Miniaturization

The occurrence of heterochronic miniaturization in the *C. mexicanus* Series is consistent with the existing literature on miniaturization in anurans. Rittmeyer et al. (2012) described several expectations for miniaturization in anurans: (1) Direct-development; (2) belonging to a clade that includes larger direct developing species; (3) reduced and simplified morphology; (4) inhabiting a wet-forest leaf litter niche.

Four of the miniaturized focal species fulfill expectations 1, 2, and 4 (*C. bitonium*, *C. candelariensis*, *C. hobartsmithi*, and *C. pygmaeus*); whilst the other four small-bodied species may fulfill all expectations (*C. cueyatl*, *C. polaclavus*, *C. portilloensis*, and *C. rubinus*), with reduced ossification of the skeleton. Our data support heterochrony as explaining miniaturization in the four species that complete the ossification sequence at small adult body sizes (Table 3; Fig. 1). However, we are less confident about what explains the species with less-ossification. We hesitate to implicate hypomorphic paedomorphism as a mechanism of miniaturization and reduced ossification in *C. cueyatl*, *C. polaclavus*, *C. portilloensis* and *C. rubinus* for two reasons: (1) possible artificial decalcification and (2) a lack of evidence that specimens we examined are adult frogs.

Preservation of museum specimens in alcohol can cause decalcification of skeletal elements owing to the acidity of some solutions (Dingerkus 1982). Given that we were unable to control for differences in how specimens have been stored at different institutions and over time, we are unable to rule out preservation-related effects as explaining the reduced ossification and/or loss of skeletal elements we observed in some species. While two of the less-ossified small species had putatively mature gonads (*C. cueyatl* and *C. rubinus*), skull characteristics of *C. polaclavus* and
C. portilloensis are more similar to large bodied species, indicating the specimens we examined may be subadults (Fig. 12). We did, however, note that subadults of large-bodied species sometimes lacked adult skull characteristics such as the posterolateral process of the frontoparietal (see C. omiltemanus species account), which is consistent with paedomorphism explaining some skull morphology in small-bodied species. Despite some limitations we assign two developmental modes to species of the C. mexicanus Series; ancestral and heterochronic miniaturization (Table 7). Parsimony suggest that heterochronic miniaturization evolved once in the group (in the ancestor of the monophyletic clade containing C. bitonium, C. candelariensis, C. cueyatl, C. hobartsmithi, C. polaclavus, C. portilloensis, C. pygmaeus, and C. rubinus; Fig. 3) and has been maintained within all species. Even accounting for the possibility that some species may only be known from subadult individuals the small-bodied clade of the C. mexicanus Series are still among the world’s smallest frogs and indeed tetrapods. As with other miniature frogs, members of the small-bodied clade of the C. mexicanus Series occupy a wet forest leaf litter niche (Lehr and Coloma 2008; Kraus 2011; Rittmeyer 2010; Oliver et al. 2017; Scherz et al. 2019). Wet forest leaf litter represents an adaptive zone for miniature anurans, facilitating access to prey not available to larger species and shelter from predators, whilst providing a high humidity microclimate limiting desiccation associated with the high surface-area-volume ratios that occur at small sizes (Kraus 2011; Rittmeyer 2010; Scherz et al. 2019). Our study adds to a growing body of literature illustrating that miniature leaf litter frogs have evolved convergently multiple times around the world, constituting a distinct ecological guild ubiquitous throughout tropical regions (Lehr and Coloma 2008; Kraus 2011; Rittmeyer 2010; Oliver et al. 2017; Scherz et al. 2019).
Comparisons to Other Mexican *Craugastor*

Given that the *C. mexicanus* Series is mostly endemic to Mexico, we provide some guidelines for differentiating them from other Mexican congeners of *Craugastor*. There are 31 other species of *Craugastor* that occur in Mexico (sensu Hedges et al. 2008); subgenus *Campbellius* (*C. matudai*); subgenus *Hylactophryne* consisting of the *C. augusti* Series (*C. augusti* and *C. tarahumaraensis*) and *C. bocourtii* Series (*C. alfredi*, *C. batrachylus*, *C. decoratus*, *C. galacticorhinus*, *C. glaucus*, *C. guerreroensis*, *C. megalotympanum*, *C. polymniae*, *C. silvicola*, *C. spatulatus*, *C. stuarti*, *C. taylori*, *C. uno*, and *C. yucatanensis*); subgenus *Craugastor* consisting of the *C. laticeps* Series (*C. greggi*, *C. laticeps*, and *C. lineatus*), *C. punctariolus* Series (*C. berkenbuschii*, *C. brocchi*, *C. palenque*, *C. pozo*, *C. psephosypharus*, *C. rugulosus*, *C. vocalis*, and *C. vulcani*), and *C. rhodopis* Series (*C. loki*, *C. occidentalis*, and *C. rhodopis*).

The *C. mexicanus* Series is most similar in morphology to species of the *C. rhodopis* Series and the *C. laticeps* Series. In *C. loki*, *C. occidentalis*, and *C. rhodopis* the relative length of Finger I > II, whereas Finger I ≤ II in the *C. mexicanus* Series (Table 6; however, we note that we encountered some rare specimens of *C. mexicanus* and *C. omiltemanus* that had Finger I > II). Adult body size differentiates *C. laticeps* from all species of the *C. mexicanus* Series; the smallest adult males of *C. laticeps* are ~31 mm SVL and females of *C. laticeps* are typically ~60 mm SVL (Savage 1987) whereas the largest adult female of any species of the *C. mexicanus* Series is ~40 mm SVL (Table 5). *Craugastor lineatus* can be differentiated from species of the *C. mexicanus* Series by a strongly developed series of outer tarsal tubercles (Savage 1987), whereas *C. mexicanus* Series taxa have small to no tubercles on their outer
tarsal ridge. As mentioned in the *C. montanus* species account above, we were unable to identify any external characters that can reliably differentiate *C. greggi* from *C. montanus* (but see Lynch 2000 for osteological comparison).

Relative finger lengths can also be used to differentiate the *C. mexicanus* Series from *C. matudai, C. augusti, C. tarahumaraensis, C. alfredi, C. batrachylus, C. decoratus, C. galacticorhinus, C. glaucus, C. guerreroensis, C. megalotympanum, C. polymniae, C. silvicola, C. spatulatus, C. stuarti, C. taylori, C.uno, C. yucatanensis, C. berkenbuschii, C. brocchi, C. palenque, C. pozo, C. psephosypharus, C. rugulosus, C. vocalis, and C. vulcani;* these species all have Finger I > II (Finger I ≤ II in the *C. mexicanus* Series; Table 6 [however, see note above about some rare specimens of *C. mexicanus* and *C. omiltemanus*]). Furthermore, finger disks can be used to differentiate the *C. mexicanus* Series from *C. alfredi, C. batrachylus, C. decoratus, C. galacticorhinus, C. glaucus, C. guerreroensis, C. megalotympanum, C. polymniae, C. silvicola, C. spatulatus, C. stuarti, C. taylori, C.uno, and C. yucatanensis;* these species all have expanded disks on Fingers III and IV (absent in the *C. mexicanus* Series).

Conservation Status

Conservation assessments for all previously recognized species in the *C. mexicanus* Series were most recently made by the IUCN Species Survival Commission (SSC) Amphibian Specialist Group in 2020. Most species are classified as Least Concern (*C. hobartsmithi, C. mexicanus, C. omiltemanus, C. pygmaeus*) (IUCN SSC Amphibian Specialist Group 2020a, b, c, d), whilst *C. montanus* and *C. saltator* have been placed in the Endangered category (IUCN SSC Amphibian Specialist Group 2020e, f). Three species (*C. montanus, C. omiltemanus, and C.
saltator) are included on the Mexican Federal List of Endangered Species (NOM-059-SEMARNAT-2010) under the Special Protection (Pr) risk category (Semarnat 2020). We recommend that *C. bitonium*, *C. candelariensis*, *C. cueyatl*, *C. polaclavus*, *C. portilloensis*, and *C. rubinus*, be considered either Data Deficient or Endangered given their limited geographic distribution.

A classification of Endangered for the above species would be consistent with the classifications of *C. montanus* and *C. saltator* (IUCN SSC Amphibian Specialist Group 2020e, f) based on criteria B1ab(iii) of the IUCN Red List Categories and Criteria, version 3.1 (IUCN 2012): Extent of occurrence estimated to be less than 5,000 km²; severely fragmented or known to exist at no more than five locations, with continued decline in area, extant, and quality of habitat inferred. Furthermore, given that populations of *C. ceuyatl* have previously been misidentified as *C. hobartsmithi* (see *C. ceuyatl* species account above), the conservation status of *C. hobartsmithi* requires reassessment. We suspect that misidentification of populations has led to an overestimate of the range size of *C. hobartsmithi*, and hence an underestimate of the species threatened status.

Inspection of the known localities of the *C. mexicanus* Series (Figs. 6 and 8) suggests the presence of at least two diversity hotspots for the group where multiple species co-occur: (1) Central Guerrero where *C. bitonium*, *C. omiltemanus*, *C. pygmaeus*, and *C. saltator* co-occur, and (2) southcentral Oaxaca where *C. candelariensis*, *C. polaclavus*, *C. portilloensis*, and *C. pygmaeus* co-occur. Comparison of species occurrence maps to maps of registered protected areas (UNEP-WCMC and IUCN 2018) indicate that both *C. mexicanus* Series diversity hotspots receive minimal protection. Within the central Guerrero hotspot the only protected areas are two small voluntary conservation areas, the 20 km² Área de Conservación y...
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Desarrollo Silvopastoril Acahuizotla and the 8 km² El Borbollón, La Pandura y La Yerbabuena. Within the southcentral Oaxaca hotspot the only protected areas are one small voluntary conservation areas (11 km² El Gavilán) and an additional 21 tiny (< 1 km²) voluntary conservation areas around the town of Pluma Hidalgo. We recommend that future conservation action should be taken in these regions to expand and link the existing small protected areas to safeguard these diversity hotspots.

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**Published on** ## Month 202##
APPENDIX I

Specimens Examined

An asterisk indicates inclusion in both molecular and morphological analyses.

*Craugastor bitonium* (6).—MEXICO: GUERRERO: Road between Yerba Santa and Yextla HWY 196, 2071 m (UTA A-64254*, holotype; UTA A-66117–19, paratypes; MZFC-HE 35600–01, paratypes).

*Craugastor candelariensis* (4).—MEXICO: OAXACA: Sierra Madre del Sur: 1.2 mi from the Candelaria-Portillo road on rough road towards Pluma Hidalgo, 1051 m (MZFC-HE-35617* [formerly UTA A-64252], paratype); Carretera San Gabriel Mixtepec–Miahuatlán, 16.160556°N, 97.00111°W, 1270 [–1350] m (UTA A-55247, paratype); North of Candelaria on the road to Oaxaca, 15.94960°N, 96.47110°W, 668 m (UTA A-64253*, holotype); San Gabriel Mixtepec, Puente de Hamaca, 710 m (UTA A-66116, paratype).


*Craugastor hobartsmithi* (6).—MEXICO: MICHOACÁN: Uruapan (FMNH 100114, holotype; FMNH 100579, paratype; FMNH 100899, paratype); Tzararaca Falls, 5–6 miles south of Uruapan (UMMZ 94230–31; UMMZ 115440).

*Craugastor cf. hobartsmithi* (15).—MEXICO: GUERRERO: 2 km east of Río Santiago and 25 km northeast of Atoyac (MVZ 106335–38). MICHOACÁN: Carretera Playitas–Torre de Microondas, after logging Station, 1656 m (UTA A-66133–34;
NZARIT: 7 miles east of San Blas and 1 mile northwest of HWY 46 (CAS 17448–49); 2.9 miles south of Laguna Santa María and 11.1 miles east of junction between HWY 15 and Santa María del Oro to Laguna Santa María roads (CAS 99052). SINALOA: HWY 40, 4.0 miles west of Santa Lucía (CAS 159232; CAS 159235–36; CAS 159238–40).

*Craugastor mexicanus* (225).—MEXICO: OAXACA: Cerro San Felipe

(MNHNP 6318, holotype; FMNH 100001, holotype of *Microbatrachylus oaxaca*; FMNH 12663, paratype of *Microbatrachylus oaxaca*; FMNH 100036, holotype of *Microbatrachylus lineatissimus*; FMNH 104548, paratype of *Microbatrachylus lineatissimus*; USNM 47905; USNM 47907; AMNH A-74410; AMNH A-81435); La Parada (USNM 47911); Lachiguiri (USNM 116475–80); 4–10 miles south of La Esperanza, along HWY 175 (USNM 224504–09); Power line service road, 3.0 miles north of Cerro Pelón and 0.5 miles east of HWY 175 (USNM 224510–26); San Andrés Chica Huaxtla (UTA A-55232*); Municipio Putla de Guerrero, Carretera Putla–San Andrés Chica Huaxtla (UTA A-56558); Sierra Mazateca, Puerto Soledad (UTA A-56559*); Carretera Coconales–Zacatepec (UTA A-64285–86*); Vicinity of San Felipe Cieneguilla, Rancho Los Encinos (UTA A-64287*); Sierra Mazateca, Puerto Soledad (UTA [Field ID: JAC 22781]*); Sierra Mixe, Carretera Ayutla–Zacatepec, 13.2 miles from the junction of Totontepec toward Zacatepec (UTA A-64255–57*); 8.1 miles south of Sola de Vega (UTA A-64258*; UTA A-66103*; MZFC-HE-35584–86); HWY 175, 6.1 miles south of San Miguel Suchixtepec (UTA A-64259*; MZFC-HE-35587–89); Carretera Sola de Vega–Juquila (UTA A-64260*; UTA A-64271*); Sierra Miahuatlán (UTA A-64413*); Carretera Sola de Vega–Juquila (UTA A-66107*; UTA A-64415*; MZFC-HE-35590–98); Along road above Totontepec (MZFC-HE-35578–79); 2 miles east of Puerto de la Soledad (ANSP
30325; Puerto de la Solidad (ANSP 30289); Villa Alta and Yelagago (AMNH A-71145–56); Northern extension of the Zempoaltepetl ridge (AMNH A-165097); Río Cimatan between Chacalapa and Sadani (AMNH A-13828); Huautla (AMNH A-60414–23); 1 mile north of El Punto on the northwest slope of northeastern Cerro San Felipe (AMNH A-69487); Llano de las Flores, Sierra Juárez (AMNH A-60488–91; AMNH A-76436); 11 miles south by road of Sola de Vega (AMNH A-72645);

Cumbre del Estudiante (AMNH A-76437); 3.6 miles south of El Punto (AMNH A-76438); Sierra Aloapaneca, 14 miles northeast by road from San Juan del Estado (AMNH A-76439); Cofradia, Distrito Sola de Vega (AMNH A-76440–41; AMNH A-80647); 10 mi southeast of Llano de las Flores on eastern side of headwaters of Río Soyalápan, Sierra Juárez (AMNH A-78849); Río Molino, Sierra de Mihuatlan (AMNH A-78850); 3 miles northwest by road of Santa Inez del Monte, Sierra de Cuatro Venados (AMNH A-78851); 12 mi northeast of Cerro Pelón on Tuxtepec road (AMNH A-78855–64); 6 miles northeast of Cerro Pelón (AMNH A-78864); 7 miles east of Cerro Pelón (AMNH A-80608–38); 4.5 miles north of Jaltianguis, Sierra de Juárez (AMNH A-80639); 6.7 miles southwest of Ayutla (AMNH A-80640); 6.2 miles northwest of Asunción Mixtepec, Distrito Zimatlán (AMNH A-80641–45); 5.5 miles northwest of Santa Ines del Monte, Sierra de Cuatro Venados (AMNH A-80646); Slopes to Summit of Cerro San Felipe (AMNH A-164795); 17.5 miles south of Vista Hermosa (AMNH A-164797); 15.5 miles north of Ixtlan de Juarez (AMNH A-164798); Llano de las Flores, 16.4 miles north of Guelatao de Juarez (AMNH A-164799–801; Huautla (AMNH A-179573–615; AMNH A-179616 [A–F]). Hidalgo: 20 miles east of Tulancingo (UTA A-66138*). Puebla: Sierra Negra, 2382 m (UTA A-56579); Tlatlauquitepec (MZFC-HE-23062*).
Craugastor montanus (8).—GUATEMALA: SAN MARCOS: Esquipulas Palo Gordo, Aldea La Fraternidad (UTA A-51105). MEXICO. CHIAPAS: Mount Ovando (USNM 115507, holotype); Mount Ovando 1600 m (UMMZ 87970; UMMZ 87973);

Mount Ovando 1800 m (UMMZ 87999; UMMZ 88002); Montecristo (UMMZ 135479); Soconusco District, vicinity of Escuintla (UMMZ 133272).

Craugastor omiltemanus (36).—MEXICO: GUERRERO: Omiltemi (BMNH 1901.12.19.7 [= BMNH 1947.2.16.62], lectotype; BMNH 1901.12.19.8 [= BMNH 1947.2.16.43–61], type series [part] of Hylodes calcitrans; BMNH 1906.6.6.101–103); "Omiltemi,” trail to la Joya, Omiltemi State Park (USNM 304807);

Between Filo de Caballo and Carrizal de Bravo, 2572 m (UTA A-66122); 0.25 miles east of Omiltemi (UTA A-4102); 6.4 km southwest of Filo de Caballo (UTA A-8007); Northwest of Chilpancingo and 28.6 km by road west of Asoleadero (UTA A-52669–70); Sierra de Malinaltepec, Road between San Luis Acatlán and Tlapa de Comonfort, 2370 m (UTA A-60788), 2169 m (UTA A-60785), 2200 m (UTA A-60786), 2295 m (UTA A-60795); 2298 m (UTA A-60789–90); Road from Chichihualco to HWY 200, west of Chilpancingo, 17.5559°N, 99.87862°W, 2221 m (UTA A-66139–40); Sierra Madre del Sur, Carretera Xochipala–Campo de Aviación (UTA A-55240*); 13.2 km (by road) west of Mazatlán, 17.435770°N, 99.539380°W, 2114 m (MZFC-HE-35699). OAXACA: Near Ayutla, 1900 m (UTA A-64264); 1 mile north of El Punto on northeast slope of Cerro San Felipe (AMNH A-69484–86);

Vivero Rancho Teja, 2 miles east of Ixtlán de Juárez (AMNH A-72644).

paratypes; UTA A-66097); Río Salado, Sierra Madre del Sur, 16.194167°N, 97.0975°W, 1245 m (UTA A-55246*, paratype; UTA [Field ID: JAC 21236]).


*Craugastor pygmaeus* (118).—MEXICO: VERACRUZ: One mile north of Rodríguez Clara (UIMNH 16125, holotype); two miles west of Córdoba (FMNH 100355, holotype of *Microbatrachylus albolabris*; FMNH 100071, paratype of *Microbatrachylus albolabris*); Portrero Viejo (USNM 115447–76, USNM 116840–42, USNM 116864–75); Cuautlapan, on slopes near and above Casa de Senon (USNM 224792–93); Municipio Zongolica, Tepetlampa, Cascada Atlhuitzia (UTA A-60776–77); Cuautlapan (MZFC-HE-22115* [Field ID: UOGV 338]). CHIAPAS: La Esperanza (USNM 115508, holotype of *Microbatrachylus imitator*; USNM 115477–79; USNM 116831–33); La Esperanza, 8 km north of Colonia Hidalgo (USNM 116834–37); La Esperanza, 8 km from Las Nubes on Mt. Obando (= Cerro Ovando; USNM 116849–52; USNM 116854); Acacoyagua (USNM 116827); Escuintla, 28 km northeast of Finca Juarez (USNM 116828–30); Salto de Agua (USNM 116855–63); Escuintla, La Esperanza Rancho (AMNH A-52244). GUERRERO: Agua del Obispo (FMNH 100323, holotype of *Microbatrachylus minimus*; FMNH 100192, paratype of *Microbatrachylus minimus*; USNM 115446; USNM 116817–19; USNM 116821–22; USNM 116824–25); Grutas de Juxtlahuaca, 931 m (UTA A-64263*); Road between Carretera Vallecitos and El Durazno (UTA [Field ID: JAC 25170]); Highway 134 from Ixtapa to Ciudad Altamirano, 17.87525°N, 101.35073°W, 447 m (UTA A 66141); Caserio Nuevo Dehli, Sierra Madre del Sur (UTA A-55241 [Field ID: ENS.
9492); Grutas de Juxtlahuaca (UTA A-64263); Chilpancingo, Acahuizotla (MZFC-HE-35701* [Field ID: IDF 59]); Chilpancingo, Agua de Obispo (MZFC-HE-35698* [Field ID: LCM 1209]). OAXACA: San Gabriel Mixtepec, Puente de Hamaca, 710 m (UTA A-64262*); Municipio Santa María Chimalapa: Carretera Santa María Chimalapa-Lazaro Cardenas, 250 m (UTA A-64270*; UTA A-64261); Road to El Progreso near intersection with highway MEX 185, 62 m (UTA A-64269*; UTA A-64288); Carretera Santa María Guienagati–Lachidola (UTA A-57976; UTA A-64268*); Municipio Santa María Chimalapa, Carretera Santa María Chimalapa–Lazaro Cardenas, 250 m (UTA A-64267*); Sierra Mazateca, Carretera Puente de Fierro–Chilchotla, 1221 m (UTA A-64266*); North of Candelaria on the road to Oaxaca City, 668 m (UTA A-64265*); Carretera Santa María Guienagati–Lachidola (UTA A-64272*); Road from Santo Domingo Petapa to Loma Santa Cruz, 16.91191°N, 95.22102°W, 560 m (UTA A-64283*); Road between San Juán Mazatlán and La Mixtequita, 17.13646°N, 95.41718°W, 633 m (UTA A-64284*); Municipio San Miguel Chimalapa, Cerro Atravezado northeast of El Palmar, 1345 m (UTA A-64289–90*); Road between San José Pacifico and Candelaria Loxicha, 550 m (UTA A-64414*); Matías Romero (USNM 116826); 1.6 miles north of Chacalapa and then east to Cafetal Concordia (AMNH A-164805).


*Craugastor saltator* (22).—MEXICO: GUERRERO: Omiltemi, about 8000 feet (FMNH 100116, holotype; FMNH 100235–36, paratypes); Omiltemi (BMNH 1901.12.19.24); “Omiltemi” (USNM 134261; USNM 148861–62); “Omiltemi,” 3.5 km west of Canada de Agua Fria (USNM 304808); Between Filo de Caballo and
Carrizal de Bravo, 2572 m (MZFC-HE-35602 [Field ID: JAC 22302]); Road from Chichihualco to HWY 200, W of Chilpancingo, 17.5559°N, 99.87862°W, 2221 m (MZFC-HE-35615 [Field ID: JAC 27696]); Area above Corral de Bravo, 2560–2590 m (UTA A-66120*); Puerto del Gallo, 2543 m (UTA A-66121); Between Puerto del Gallo and Vuelta del Sur, 2850 m (UTA A-66123); 1 mile west of Omiltemi (UTA A-4100–01); west-northwest of Chilpancingo, 2 miles east by road of Puerto Gallo on the south slope of Cerro Teotopec (UTA A-52688; UTA A-52689); Carretera Pto. El Gallo-Nueva Dehli (UTA A-55239; UTA A-55238); "Asoleadero" west-northwest of Chilpancingo (UTA A-52673); west-northwest of Chilpancingo, 5 miles south of Puerto Gallo (UTA A-52701); 2.4 miles east of Carrizal (Corral) de Bravo (UTA A-54931–32).
### Molecular Data Examined

Genbank accession numbers for molecular loci used in the study. All localities are states in Mexico unless otherwise noted.

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**Outgroups**

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*Sequence too short to be submitted to GenBank. Contact authors for sequence.*
### APPENDIX 3

#### 3D Scan Data Examined

MorphoSource identifiers for 3D models of specimens from mico-CT scans.

All localities are states in Mexico unless otherwise noted.

<table>
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<th>MorphoSource ID</th>
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UTA A-64286   Oaxaca   uta:uta-a:64286
UTA A-64287   Oaxaca   uta:uta-a:64287

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USNM 115507   Chiapas   usnm:amphibians & reptiles:115507

* Craugastor omiltemanus *
USNM 116481   Guerrero   usnm:amphibians & reptiles:116481
UTA A-55240   Guerrero   uta:uta-a:55240
UTA A-64264   Guerrero   uta:uta-a:64264

* Craugastor polaclavus *
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UTA A-62392   Oaxaca   uta:uta-a:62393

* Craugastor portilloensis *
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* Craugastor pygmaeus *
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USNM 224792   Veracruz   usnm:amphibians & reptiles:224792
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UTA A-60777   Veracruz   uta:uta-a:60777
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*Crugastor rubinus*

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TABLE 1. Primers used to amplify the fragments of the mitochondrial (mtDNA) and nuclear (nDNA) genes examined in this study.

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<td>Bossuyt and Milinkovitch (2000)</td>
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<td>ACACACCCGCCCGTCACCCTC</td>
<td>Liu et al. (2000)</td>
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<td>16S</td>
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<td>CGCCTGTATTAYCAAAAACAT</td>
<td>Kessing et al. (1989)</td>
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<td>16SBR</td>
<td>CCGGTCTGAACCTCAGATCAGT</td>
<td>Kessing et al. (1989)</td>
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<tr>
<td>RAG1</td>
<td>R182</td>
<td>GCCATAACTGCTGGAGCATYAT</td>
<td>Heinicke et al. (2007)</td>
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<td>AGYAGATGTTCCTGGGCTTC</td>
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TABLE 2. Best-fit models selected for Bayesian phylogenetic analysis in Mr. Bayes 3.2.1 by Partition Finder under both Bayesian Information Criteria (BIC) and Akaike Information Criteria (AIC).

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<th>BIC</th>
<th>AICc</th>
<th>ln Likelihood</th>
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<td>GTR+G</td>
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<td>4971.775</td>
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<td>RAG1, 1st position</td>
<td>K2+G</td>
<td>2286.308</td>
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<td>1946.933</td>
<td>1175.064</td>
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Table 3. Six-stage ontogenetic sequence for skeletal development used to diagnose development in the *Craugastor mexicanus* Series.

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<th>Stage 4</th>
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<td>Palatines ossified</td>
<td>Sphenethmoid ossified</td>
<td>Exoccipital-prootic fusion</td>
<td>Prepollex present</td>
<td>Frontopareitals Fused</td>
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<tr>
<td>Vomers ossified</td>
<td>Humeral interior epiphyses ossified</td>
<td>Frontopareital-prootic suture offset posteriorly</td>
<td>Prehallux present</td>
<td>Epicorocoid Ossified</td>
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<tr>
<td>Hyoid ossified</td>
<td>Radioulnar exterior epiphyses ossified</td>
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<td></td>
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<tr>
<td>Humeral exterior epiphyses ossified</td>
<td>Femur epiphyses ossified</td>
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<tr>
<td>Radioulnar interior epiphyses ossified</td>
<td>Tibiofibular epiphyse ossified</td>
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<tr>
<td>Calcaneum/astragalus epiphyses ossified</td>
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<td>cueyatl</td>
<td>hobartsmithi</td>
<td>mexicanus</td>
<td>montanus</td>
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For species contained within the Craugastor mexicanus Series, bolded distances on diagonal are within species, p-distances (if more than a single individual was used to estimate mean genetic distance).

Table 4. Genetic p-distances derived from the concatenated alignment of 2230 base pairs of 12S and 16S (mtDNA) + RAG1 and TYR (nDNA).
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- *polaclavus* 0.059 0.064 0.067 0.068 0.060 0.066 0.067 0.013
- *portilloensis* 0.065 0.070 0.073 0.077 0.056 0.057 0.065 0.058
- *pygmaeus* 0.047 0.064 0.059 0.070 0.056 0.068 0.067 0.061
- *rubinus* 0.072 0.083 0.076 0.034 0.066 0.080 0.079 0.066
- *saltator* 0.097 0.070 0.081 0.089 0.051 0.088 0.056 0.100
- *nirvanus* 0.061 0.061 0.009
- *melanomelas* 0.063 0.073 0.088
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Note: Sometimes very slightly pigmented
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Uncertainty: If greater than one, number of specimens examined is indicated in parentheses.
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<td>10 ± 11% (5)</td>
<td>7 ± 12% (48)</td>
<td>10 ± 11% (3)</td>
</tr>
<tr>
<td>Crus ratio</td>
<td>50 ± 55% (6)</td>
<td>51 ± 58% (4)</td>
<td>51 ± 54% (2)</td>
<td>53 ± 61% (5)</td>
<td>53 ± 69% (191)</td>
<td>51 ± 59% (5)</td>
<td>32 ± 65% (39)</td>
<td>0.50 ± 0.58 (6)</td>
<td>51 ± 61% (5)</td>
<td>50 ± 66% (48)</td>
</tr>
</tbody>
</table>
TABLE 7. Developmental modes in species of the *Craugastor mexicanus* Series.

*Species with putative miniaturization and character reduction given the observation of low levels of skeletal ossification (but also see Discussion).

<table>
<thead>
<tr>
<th>Mode I</th>
<th>Mode II</th>
<th>Uncertain</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Presumed ancestral)</td>
<td>(Miniature species)</td>
<td></td>
</tr>
</tbody>
</table>

- *mexicanus*  
- *montanus*  
- *omiltemanus*  
- *saliator*  

- *bitonium*  
- *candelariensis*  
- *hobartsmithi*  
- *pygmaeus*

- *cueyatl*  
- *polaclavus*  
- *portilloensis*  
- *rubinus*
Fig. 1.—Male holotype of *Eleutherodactylus hobartsmithi* Taylor (A, FMNH 100114, SVL = 14.4 mm); female holotype of *Leiuperus mexicanus* Brocchi (B, MNHNP 6318, SVL = 40 mm); male holotype of *Microbatrachylus oaxacae* Taylor (C, FMNH 100001, SVL = 18.1 mm); male holotype of *Microbatrachylus lineatissimus* Taylor (D, FMNH 100036, SVL = 20.0 mm); female holotype of *Microbatrachylus montanus* Taylor (E, USNM 115507, SVL = 27.0 mm); female holotype of *Eleutherodactylus pygmaeus* Taylor (F, UIMNH 16125, SVL = 17.0 mm); female holotype of *Microbatrachylus albolabris* Taylor (G, FMNH 100071, SVL = 16.5 mm); male holotype of *Microbatrachylus minimus* Taylor (H, FMNH 100323, SVL = 15.0 mm); female holotype of *Microbatrachylus imitator* Taylor (I, USNM 115508, SVL = 14.2 mm); male lectotype of *Syrrhaphus omiltmanus* Günther (J, BMNH 1947.2.16.62, SVL = 19.8 mm); female lectotype of *Hylodes calcitrans* Günther (K, BMNH 1947.2.16.47, SVL = 34.9 mm); female holotype of *Eleutherodactylus saltator* Taylor (L, FMNH 100166, SVL = 44.0 mm). Symbols correspond to current taxonomic assignments (square = *C. hobartsmithi*, triangle = *C. mexicanus*, crossed-square = *C. montanus*, pentagon = *C. omiltmanus*, circle = *C. pygmaeus*, rotated-triangle = *C. saltator*).

Fig. 2.—Skull of *Craugastor mexicanus* (USNM 47905) in anterior, dorsal, lateral, and ventral views showing placements of landmarks. Landmarks are (1) anterior mid-line tip premaxilla, (2) maxilla-premaxilla suture, (3) anterior tip nasal, (4) anterior tip frontoparietal, (5) posterior lateral tip frontoparietal, (6) posterior
dorsal tip squamosal, (7) anterior frontoparietal prootic suture, (8) lateral tip nasal, (9) squamosal maxillary suture, (10) posterior tip maxilla, (11) anterior tip parasphenoid (12) posterior tip parasphenoid, (13) lateral tip parasphenoid, and (14) pterygoid maxillary suture.

Fig. 3.—Concatenated Maximum Likelihood analyses of two mitochondrial (12S and 16S) and two nuclear (RAG1 and TYR) gene fragments sequenced from the *Craugastor mexicanus* Series (total of 2230 base pairs). Node values correspond to bootstrap support from Maximum Likelihood analysis and posterior probabilities from a Bayesian analysis of the same dataset, respectively. Support values are not reported for nodes that had less than 50/0.50. ‘NS’ indicates no support in the Bayesian analysis for a depicted relationship. Locality abbreviations are as follows: COL = Colima, HID = Hidalgo, GRO = Guerrero, JAL = Jalisco, MEX = Estado de México, OAX = Oaxaca, PUE = Puebla, and VER = Veracruz.

Fig. 4.—Maximum Likelihood analyses of mitochondrial DNA (mtDNA) markers sequenced from the *Craugastor mexicanus* Series (total of 1047 base pairs). Black circles indicate nodes receiving bootstrap support values greater than 90 from the Maximum Likelihood analysis and 0.90 posterior probabilities in corresponding Bayesian analyses. Where posterior probabilities were higher than 0.90 but Maximum Likelihood bootstrap support was less than 90, a number indicates the bootstrap support. ‘NS’ indicates no support in the Bayesian analysis for a depicted relationship. Locality abbreviations are as follows: COL = Colima, HID = Hidalgo,
Fig. 5.—Maximum Likelihood analysis of nuclear DNA (nDNA) markers sequenced from the Craugastor mexicanus Series (total of 1183 base pairs). Black circles indicate nodes receiving bootstrap support values greater than 90 from the Maximum Likelihood analysis and 0.90 posterior probabilities in corresponding Bayesian analyses. Where posterior probabilities were higher than 0.90 but Maximum Likelihood bootstrap support was less than 90, a number indicates the bootstrap support. ‘NS’ indicates no support in the Bayesian analysis for a depicted relationship. Locality abbreviations are as follows: COL = Colima, GRO = Guerrero, JAL = Jalisco, MEX = Estado de México, OAX = Oaxaca, PUE = Puebla, and VER = Veracruz.

Fig. 6.—Distribution of Craugastor mexicanus, C. montanus, C. pygmaeus, and C. saltator in Mexico and Guatemala. Dots inside symbols indicate individuals used in the molecular analyses in this study. Relevant type localities are indicated by text and arrows.

Fig. 7.—Box plots depicting elevational distribution of Craugastor mexicanus and C. pygmaeus inferred from locality data associated with museum specimens. Results are shown for both specimens used in the molecular analysis (Molecules +
Morphology) and for specimens assigned to species using only morphology. Asterisks represent potential outliers, which are greater than 1.5 times the inter-quartile range (range inside the box).

Fig. 8.—Distribution of *Craugastor hobartsmithi*, *C. cf. hobartsmithi*, *C. omiltemanus* and six new species from Mexico. Dots inside symbols indicate individuals used in the molecular analyses in this study. Inset depicts region of Oaxaca where three of the new species exist in near sympatry. A question mark indicates uncertain georeferencing. Relevant type localities are indicated by text and arrows.

Fig. 9.—Body size and shape variation within the *Craugastor mexicanus* Series as depicted by principal components analysis of 15 linear measurements. Principal component scores for the first two components (left) are depicted along with their residuals (right). Large bodied species are those with an adult body size > 20 mm Snout-vent length (*C. mexicanus, C. montanus, C. omiltemanus, C. saltator*), and small-bodied species are those with adult body sizes < 20 mm (*C. bitonium, C. candelariensis, C. cueyatl, C. hobartsmithi, C. polacalvus, C. portilloensis, C. pygmaeus*, and *C. rubinus*).

Fig. 10.—Difference in ontogenetic trajectories between select large-bodied (*Craugastor mexicanus, C. omiltemanus, C. saltator*) and small-bodied species (*C.
hobartsmithi, C. pygmaeus) of the C. mexicanus Series as evidenced by reduced-
major axis regression of size-correlated shape axes with log-centroid size following
Sidlauskas et al. (2011).

Fig. 11.—Ossification levels within the Craugastor mexicanus Series compared to body size (estimated as log centroid size). Ossification scores are based on the six-stage ossification sequence described in Table 3.

Fig. 12.—Skull shape variation within the Craugastor mexicanus Series as depicted by principal components analysis of 14 geometric morphometric landmarks (Fig. 10). The first seven principal components explained ~75% of the variance. The second and third principal components are depicted because they maximized differences between large-bodied and small bodied species.

Fig. 13.—Evidence of sexual dimorphism of tympanum width in Craugastor mexicanus (left) and C. pygmaeus (right). Sex was determined by directly examining gonads for select specimens of C. mexicanus and is implied by scaling patterns in those specimens where sex was not directly determined.

Fig. 14.—Dorsal body surface in representative specimens of the Craugastor mexicanus Series. Female holotype of C. bitonium (A, UTA A-64254, SVL = 15.8
mm); male holotype of *C. candelariensis* (B, UTA A-64253, SVL = 13.3 mm); male
holotype of *C. cueyatl* (C, UTA A-62348, SVL = 13.0 mm); male *C. hobartsmithi* (D, UMMZ 94231, SVL ~11 mm, photo by J. David Curlis); male *C. mexicanus* (E, UTA A-6907, SVL = 22.3 mm); male *C. montanus* (F, UMMZ 88002, SVL = 21.8 mm); female *C. omiltemanus* (G, UTA A-66140, SVL = 30.9 mm); female holotype of *C. polaclavus* (H, UTA A-62392, SVL = 14.7 mm); female holotype of *C. portilloensis* (I, UTA A-62393, SVL = 11.4 mm); female *C. pygmaeus* (J, UTA A-54809, SVL = 17.3 mm); male holotype of *C. rubinus* (K, UTA A-62345, SVL = 12.6 mm); female *C. saltator* (L, UTA A-55239, SVL = 38.2 mm).

Fig. 15.—Ventral body surface in representative specimens of the *Craugastor mexicanus* Series. Female holotype of *C. bitonium* (A, UTA A-64254, SVL = 15.8 mm); male holotype of *C. candelariensis* (B, UTA A-64253, SVL = 13.3 mm); male holotype of *C. cueyatl* (C, UTA A-62348, SVL = 13.0 mm); female *C. hobartsmithi* (D, UMMZ 94230, SVL ~12 mm, photo by J. David Curlis); female *C. mexicanus* (E, UTA A-28754, SVL = 35.9 mm); male *C. montanus* (F, UMMZ 88002, SVL = 21.8 mm); female *C. omiltemanus* (G, UTA A-66140, SVL = 30.9 mm); female holotype of *C. polaclavus* (H, UTA A-62392, SVL = 14.7 mm); female holotype of *C. portilloensis* (I, UTA A-62393, SVL = 11.4 mm); female *C. pygmaeus* (J, UTA A-54809, SVL = 17.3 mm); male holotype of *C. rubinus* (K, UTA A-62345, SVL = 12.6 mm); female *C. saltator* (L, UTA A-55239, SVL = 38.2 mm).
Fig. 16.—Lateral body surface in representative specimens of the *Craugastor mexicanus* Series. Female paratype of *C. bitonium* (A, UTA A-66118, SVL = 16.7 mm); female paratype of *C. candelariensis* (B, UTA A-55247, SVL = 18.6 mm); female paratype of *C. cuyatl* (C, MZFC-HE-35614. SVL = 17.2 mm); male *C. hobartsmithi* (D, UMMZ 94231, SVL ~11 mm, photo by J. David Curlis); female *C. mexicanus* (E, UTA A-6907, SVL = 22.3 mm); female *C. montanus* (F, UMMZ 87970, SVL = 25.8 mm); male *C. omiltemanus* (G, UTA A-66139, SVL = 18.1 mm); female holotype of *C. polaclavus* (H, UTA A-62392, SVL = 14.7 mm); female holotype of *C. portilloensis* (I, UTA A-62393, SVL = 11.4 mm); male *C. pygmaeus* (J, UTA A-64414, SVL = 10.3 mm); male holotype of *C. rubinus* (K, UTA A-62345, SVL = 12.6 mm); male *C. saltator* (L, UTA A-54931, SVL = 18.4 mm).

Fig. 17.—Dorsal surface of the head in representative specimens of the *Craugastor mexicanus* Series. Female paratype of *C. bitonium* (A, UTA A-66118, SVL = 16.7 mm); female paratype of *C. candelariensis* (B, UTA A-55247, SVL = 18.6 mm); female paratype of *C. cuyatl* (C, MZFC-HE-35614. SVL = 17.2 mm); female *C. hobartsmithi* (D, UMMZ 94230, SVL ~12 mm, photo by J. David Curlis); female *C. mexicanus* (E, UTA A-28754, SVL = 35.9 mm); female *C. montanus* (F, UMMZ 87970, SVL = 25.8 mm); male *C. omiltemanus* (G, UTA A-66139, SVL = 18.1 mm); female holotype of *C. polaclavus* (H, UTA A-62392, SVL = 14.7 mm); female holotype of *C. portilloensis* (I, UTA A-62393, SVL = 11.4 mm); female *C. pygmaeus* (J, UTA A-54809, SVL = 17.3 mm); male holotype of *C. rubinus* (K, UTA A-62345, SVL = 12.6 mm); male *C. saltator* (L, UTA A-54931, SVL = 18.4 mm).
Fig. 18.—Ventral surface of the head in representative specimens of the *Craugastor mexicanus* Series. Female paratype of *C. bitonium* (A, UTA A-66118, SVL = 16.7 mm); female paratype of *C. candelariensis* (B, UTA A-55247, SVL = 18.6 mm); female paratype of *C. cueyatl* (C, MZFC-HE-35614, SVL = 17.2 mm); male *C. hobartsmithi* (D, UMMZ 94231, SVL ~11 mm, photo by J. David Curlis); male *C. mexicanus* (E, UTA A-6907, SVL = 22.3 mm); female *C. montanus* (F, UMMZ 87970, SVL = 25.8 mm); male *C. omiltemanus* (G, UTA A-66139, SVL = 18.1 mm); female holotype of *C. polaclavus* (H, UTA A-62392, SVL = 14.7 mm); female holotype of *C. portilloensis* (I, UTA A-62393, SVL = 11.4 mm); male *C. pygmaeus* (J, UTA A-64414, SVL = 10.3 mm); male holotype of *C. rubinus* (K, UTA A-62345, SVL = 12.6 mm); male *C. saltator* (L, UTA A-54931, SVL = 18.4 mm).

Fig. 19.—Lateral surface of the head in representative specimens of the *Craugastor mexicanus* Series. Female holotype of *C. bitonium* (A, UTA A-64254, SVL = 15.8 mm); female paratype of *C. candelariensis* (B, UTA A-55247, SVL = 18.6 mm); male holotype of *C. cueyatl* (C, UTA A-62348, SVL = 13.0 mm); female *C. hobartsmithi* (D, UMMZ 94230, SVL ~12 mm, photo by J. David Curlis); female *C. mexicanus* (E, UTA A-28754, SVL = 35.9 mm); male *C. montanus* (F, UMMZ 88002, SVL = 21.8 mm); female *C. omiltemanus* (G, UTA A-66140, SVL = 30.9 mm); female holotype of *C. polaclavus* (H, UTA A-62392, SVL = 14.7 mm); female holotype of *C. portilloensis* (I, UTA A-62393, SVL = 11.4 mm); female *C. pygmaeus* (J, UTA A-54809, SVL = 17.3 mm); male holotype of *C. rubinus* (K, UTA A-62345, SVL = 12.6 mm); male *C. saltator* (L, UTA A-54931, SVL = 18.4 mm).
FIG. 20.—Ventral surface of the hand in representative specimens of the *Craugastor mexicanus* Series. Female paratype of *C. bitonium* (A, UTA A-66118, SVL = 16.7 mm); female paratype of *C. candelariensis* (B, UTA A-55247, SVL = 18.6 mm); male holotype of *C. cueyatl* (C, UTA A-62348, SVL = 13.0 mm); female *C. hobartsmithi* (D, UMMZ 94230, SVL ~12 mm, photo by J. David Curlis); female *C. mexicanus* (E, UTA A-28754, SVL = 35.9 mm); male *Craugastor montanus* (F, UMMZ 88002, SVL = 21.8 mm); female *C. omiltemanus* (G, UTA A-66140, SVL = 30.9 mm); female *C. polaclavus* (H, UTA A-66097, SVL = 16.0 mm); female holotype of *C. portilloensis* (I, UTA A-62393, SVL = 11.4 mm); female *C. pygmaeus* (J, UTA A-54809, SVL = 17.3 mm); male holotype of *C. rubinus* (K, UTA A-62345, SVL = 12.6 mm); male *C. saltator* (L, UTA A-54931, SVL = 18.4 mm).

FIG. 21.—Ventral surface of the foot in representative specimens of the *Craugastor mexicanus* Series. Female paratype of *C. bitonium* (A, UTA A-66118, SVL = 16.7 mm); female paratype of *C. candelariensis* (B, UTA A-55247, SVL = 18.6 mm); female paratype of *C. cueyatl* (C, MZFC-HE-35614. SVL = 17.2 mm); male *C. hobartsmithi* (D, UMMZ 94231, SVL ~11 mm, photo by J. David Curlis); male *C. mexicanus* (E, UTA A-6907, SVL = 22.3 mm); male *Craugastor montanus* (F, UMMZ 88002, SVL = 21.8 mm); male *C. omiltemanus* (G, UTA A-66139, SVL = 18.1 mm); female holotype of *C. polaclavus* (H, UTA A-62392, SVL = 14.7 mm); female paratype of *C. portilloensis* (I, MZFC-HE-35581, SVL = 12.1 mm); female *C. pygmaeus* (J, UTA A-54809, SVL = 17.3 mm); male paratype of *C. rubinus* (K,
MZFC-HE-35616, SVL = 10.8 mm); female *C. saltator* (L, UTA A-55239, SVL = 38.2 mm).

**Fig. 22.**—Female holotype of *Craugastor bitonium* (A, UTA A-64254, SVL = 15.8 mm); female paratype (B, UTA A-66117, SVL = 16.9 mm); (B); one male and two female paratypes (C, left to right, UTA A-66119, SVL = 12.3 mm; MZFC-HE-35600, SVL = 15.8 mm; MZFC-HE-35601, SVL = 15.2 mm); female paratype (D, UTA A-66118, SVL = 16.7 mm). Note ‘two tone’ dorsal color pattern in A, B, and C. All collected from the road between Yextla and Vuelta del Sur, Guerrero, Mexico, 2071 m.

**Fig. 23.**—Male paratype of *Craugastor candelariensis* (MZFC-HE-35617, SVL = 12.4 mm) from Sierra Madre del Sur, 1.2 miles on the road between Candelaria and Portillo del Rayo, Pluma Hidalgo, Oaxaca, Mexico, 1051 m.

**Fig. 24.**—Female paratype (A, MZFC-HE-35614, SVL = 15.8 mm) and male holotype (B, UTA A-62348, SVL = 12.3 mm) of *Craugastor cueyatl* from type locality; male paratype (C, AMNH A-57809, SVL = 11.7 mm) from Tepozteco, Morelos, Mexico, ~2000 m (C). Leaf litter habitat near the type locality east of Cerro Gordo, Estado de México, Mexico, 2282 m (D).
Fig. 25.—View from the type locality of *Craugastor hobartsmithi*, Uruapan, Michoacán looking towards Cerro Tancitaro (A). *Craugastor cf. hobartsmithi*; female (B, UTA A-66134, SVL = 13.2 mm); male (C, MZFC-HE-35613, SVL = 9.6 mm); female (D, UTA A-66133, SVL = 18.3 mm); all from near Las Playitas (Carretera Playitas–Torre de Microndas), Michoacán, Mexico, 1565 m. *Craugastor cf. hobartsmithi* from Montitlan, Colima, Mexico photographed 13 April 2020 (E, F, not collected, photo by Jacobo Reyes-Velasco).

Fig. 26.—Skulls of *Microbatrachylus lineatissimus* (A, paratype, FMNH 104548), *Craugastor mexicanus* (B, UTA A-56558) and *C. pygmaeus* (C, UTA A-64272) in dorsal and lateral views. Posterolateral projection of the frontoparietal on *C. mexicanus* (B) is indicated by an arrow and grey shading.

Fig. 27.—Examples of intraspecific polymorphism in *Craugastor mexicanus* from Mexico; female (A, UTA A-56558, SVL = 37.3 mm) from Putla de Guerrero municipality; Oaxaca, female (B, UTA A-64415, SVL = 28.3 mm) from Carretera Sola de Vega–Juquila, Oaxaca; subadult (C, UTA A-64271, SVL = 11.9 mm) from Carretera Sola de Vega–Juquila, Oaxaca; subadult and adult (D, UTA A-64258, SVL = 13.6 mm and MZFC-HE-35584, SVL = unavailable) both from 8.1 miles south of Sola de Vega, Oaxaca; adult (E, UTA A-66107, SVL = unavailable) from Carretera Sola de Vega–Juquila, Oaxaca; subadult (F, UTA A-64260, SVL = 16.6 mm) from Carretera Sola de Vega–Juquila, Oaxaca; female (G, UTA A-64413, SVL = 23.5) from Sierra Miahuatlán, Oaxaca; female (H, UTA A-56579, SVL = 21.3 mm) from...
Sierra Negra, Puebla; female (I, UTA A-56559, SVL = 35.4 mm) from Sierra  
Mazateca, Puerto Soledad, Oaxaca; subadult (J, UTA A-64257, SVL = 17.6 mm)  
from Sierra Mixe, Carretera Ayutla–Zacatepec, Oaxaca; subadult (K, UTA A-64259,  
SVL = 10.9 mm) from 6.1 miles south of San Miguel Suchixtepec, Oaxaca; subadult  
(L, UTA A-66138, SVL = unavailable) from 20 miles east of Tulancingo, Hidalgo.

Fig. 28.—Female holotype of Craugastor greggi (FMNH 20876, SVL = 36.0  
mm) of the C. laticeps Series from Volcan Tajumulco, near San Marcos, Guatemala  
in dorsal (left) and ventral (right) views. Images courtesy of Alan Resetar and the  
Field Museum of Natural History.

Fig. 29.—Ventral coloration and areolate skin texture of Craugastor  
omiltemanus. Venter in preservative, an arrow indicates the large inner metatarsal  
tubercle that is characteristic of the species (A, BMNH 1947.2.16.44, SVL = 36.5  
mm, photo by Wai-Yee Cooper); venter in preservative (B, BMNH 1947.2.16.47,  
SVL = 39.6 mm, photo by Wai-Yee Cooper); venter in life (C, UTA Field ID: JAC  
27695); venter in life (D, UTA Field ID: JAC 27694).

Fig. 30.—Adult Craugastor omiltemanus (A, MZFC-HE-35699 [field ID:  
TJD 780], SVL = unavailable, photo by Thomas Devitt) from near Mazatlán,  
Guerrero; female (B, UTA A-66140, SVL = 30.5 mm) from habitat along the road  
between Chichihualco and Chilpancingo, Guerrero, 2221 m; male (C, UTA A-64264,
SVL = 12.9 mm) from near Ayutla, Oaxaca, 1900 m; female (D, UTA A-60796, SVL = 27.5 mm) from Sierra de Malinaltepec (Carretera San Luis Acatlán–Tlapa de Comonfort), 2298 m; habitat found 13.2 km west of Mazatlán, Sierra Madre del Sur (E, photo by Thomas Devitt); habitat found in the Sierra Madre del Sur west of Chilpancingo, Guerrero (F).

Fig. 31.—Subadult female holotype of Craugastor polaclavus (UTA A-62392, SVL = 14.7 mm) from San Pedro Pochutla district, Portillo del Rayo, Oaxaca, Mexico, 1550–1585 m.

Fig. 32.—Female holotype of Craugastor portilloensis (UTA A-62393, SVL = 11.4 mm) from Portillo del Rayo, Oaxaca, Mexico, 1550 m. The specimen’s leg was removed for genetic analysis.

Fig. 33.—Male Craugastor pygmaeus (A, UTA A-64283, SVL = 14.6 mm, photo by Matthew Ingrasci) from Oaxaca, Mexico; female (B, UTA A-64262, SVL = 13.7 mm) from Oaxaca, Mexico; female (C, UTA A-64266, SVL = 17.0 mm) from Oaxaca, Mexico; male (D, UTA A- 64263, SVL = 12.4) from Guerrero, Mexico.

Fig. 34.—Male holotype of Craugastor rubinus (A, UTA A-62345, SVL = 12.6 mm), male paratype (B, MZFC-HE-35616, SVL = 10.8 mm) and male paratype
(C, UTA A-62347, SVL = 11.5 mm). All from Talpa de Allende, Jalisco, Mexico, 1771 m. Leaf litter at the type locality where the specimens were collected (D).

**Fig. 35.**—Ventral coloration in life from some member of the *Craugastor mexicanus* Series. *Craugastor rubinus* (A, UTA A-62345); *C. pygmaeus* (B, UTA A-64284), *C. cueyatl* (C, UTA A-62348). Note varying levels of bluish-white speckling.

**Fig. 36.**—Subadult *Craugastor saltator* (left, UTA A-66120, SVL = 14.5 mm) from area above Corral de Bravo, Guerrero, Mexico, 2560–2590 m; female holotype (right, FMNH 100166, SVL = 44.0 mm) from Omiltemi, Guerrero, Mexico.

**Fig. 37.**—Gonad coloration and morphology in the genus *Craugastor*:

- pigmented testes in *C. mexicanus* (A, UTA A-66090); partially pigmented ovaries in
- *C. mexicanus* (B, UTA A-56558); pigmented maturing ova in *C. mexicanus* (C, UTA A-64413); unpigmented testes in *C. fitzingeri* (D, BMNH 1979.344), unpigmented ovaries in *C. fitzingeri*, (E, BMNH 1979.343); unpigmented testes in *C. noblei* (F, BMNH 1987.779); maturing ova and oviducts in *C. loki* (G, BMNH 1973.2439);
Figure 3