Taxonomic assessment of *Craugastor podiciferus* (Anura: Craugastoridae) in lower Central America with the description of two new species

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Abstract.—The systematics and taxonomy of polytypic species *Craugastor podiciferus* are poorly understood due to the high level of phenotypic polymorphism between and within species and the lack of molecular data from topotypic specimens. Herein are reported results of a well-sampled study including all known species of the *C. podiciferus* species group, several localities from highlands in Costa Rica and western Panama, and for the first time, samples from the type locality of *C. podiciferus*. A phylogenetic analysis based on the DNA sequences of the mitochondrial 16S rRNA (16S) and cytochrome oxidase 1 (COI) genes and a morphometric analysis are also included. Based on the results, we restrict *C. podiciferus* to the populations from the Cordillera Volcánica Central and Cordillera de Talamanca in Costa Rica and western Panama. *Craugastor podiciferus sensu stricto* and six additional clades from the highlands of Costa Rica constitute the well-supported *C. podiciferus sensu lato* clade. These analyses support the existence of three additional species from the Pacific slope of southwestern Costa Rica and western Panama. Herein, two lineages are described as new species and revised descriptions for *C. podiciferus* and *C. blairi* are provided. The name *C. blairi* is resurrected and used for populations from the Cordillera de Talamanca and Cordillera Central in western Panama. Two additional species are named. One is easily differentiated by the presence of nuptial pads in adult males, a smooth venter, and flat subarticular tubercles. The other, named for populations from southwestern Costa Rica, is recognized by its coarsely areolate venter, projecting subarticular tubercles, and heel without a projecting tubercle. The recognition of these three species from the lower montane rainforest highlights the role of the highlands on the Pacific slope of Costa Rica and Panama in the diversification of the *C. podiciferus* species group.

Keywords. Brachycephaloidea, cryptic species, DNA barcoding, Talamanca, Terrarana, Costa Rica, Panama

Introduction

The direct-developing frogs of the *Craugastor podiciferus* species group (Hedges et al. 2008) are found from eastern Honduras to Central Panama (AmphibiaWeb 2019; Savage 2002) with most of the species (nine out of ten) restricted to Isthmian Central America. The distribution of this group ranges from sea level to 2,700 m a.s.l. in a wide variety of habitats, from tropical rain forest and cloud forest, to montane forest (Savage 2002). The morphological delimitation between members of the *C.*

podiciferus species group is difficult due to the extremely conserved morphological characters and the high level of phenotypic polymorphism within species and populations. The systematics and taxonomy of the *C. podiciferus* species group has been poorly studied; however, previous molecular studies have suggested the existence of several unnamed species that are masked under the current names (Savage 2002; Crawford 2003; Crawford and Smith 2005; Streicher et al. 2009). For example, Crawford and Smith (2005) examined 10 samples (seven species) of the *C. podiciferus* species group and found

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the presence of two unnamed species (*Craugastor* sp. B and *Craugastor* sp. C); they also found *C. stejnegerianus* (Cope, 1893) to be paraphyletic. Recently, Arias et al. (2016) showed that populations formerly considered to be part of the *C. stejnegerianus* from southwestern Costa Rica and western Panama belonged to a different species and described them as *C. gabbi* Arias, Chaves, Crawford, and Parra-Olea, 2016.

Craugastor podiciferus (Cope, 1875) is the most complicated taxon within the *C. podiciferus* species group. Its morphological polymorphism has been recognized since its description by Cope (1875), who described it based on four varieties plus two additional species (*C. muricinus* and *C. habenatus*) in the same paper, with specimens from the same locality. In addition, Cope (1875) stated that "the colors of this species vary remarkably, more than I have observed to be the case in any other frog." Subsequently, Barbour (1928) described *C. blairi* using specimens from western Panama, which Taylor (1952) later synonymized together with *C. muricinus* and *C. habenatus* under *C. podiciferus*. An additional species, *C. jota* (Lynch 1980), was named using specimens from western Panama, and was suggested to be related to *C. podiciferus*. More recently, the name *C. podiciferus* has been used for specimens from several highland populations (1,089–2,650 m a.s.l.) on both slopes of the mountain ranges in Costa Rica and western Panama (Savage 2002). Streicher et al. (2009) used specimens from several populations referred to as *C. podiciferus* to perform a well-sampled phylogenetic study of this complex. They found *C. podiciferus* is represented by six clades, each likely representing distinct species. In addition, the populations from western Panama were not grouped with the main *C. podiciferus* clade, but were called *Craugastor* sp. B.

Although the molecular and geographical evidence shown by Streicher et al. (2009) supported the presence of several species under the name *C. podiciferus*, taxonomic changes have not yet been implemented, mainly due to the lack of topotypic specimens of *C. podiciferus*. The correct type locality has been discussed by Savage (1970), and Arias and Chaves (2014) concluded it is on the Caribbean slopes of Cerro Kamuk.

Here, specimens of *Craugastor podiciferus* from the type locality are included for the first time together with those from several additional localities from Costa Rica and western Panama. Mitochondrial DNA sequences were used to address three goals: 1) to identify *C. podiciferus sensu stricto* in a phylogenetic context, 2) to evaluate the phylogenetic relationships of the *C. podiciferus* species complex, and 3) to evaluate the taxonomic status of populations from the Pacific slopes of southwestern Costa Rica and western Panama. The result is a comprehensive revision of the *C. podiciferus* species complex, in which two new species are described from southwestern Costa Rica and western Panama. Additionally, an old name is resurrected for a third species in mountainous western Panama.

Materials and Methods

Species criterion: The general metapopulation lineage species concept is followed here (Simpson 1951; Wiley 1978; de Queiroz 2007). Consistent with this concept, a species is recognized when there is evidence of metapopulation lineage separation, preferably based on multiple lines of evidence following a consensus protocol for integrative taxonomy (Dayrat 2005; Padial et al. 2010).

Taxon sampling: The frogs were collected in the field, euthanized, fixed in 10% formalin, and processed in 70% ethanol for long-term storage. A tissue sample was preserved in 96% ethanol or RNAlater and used for genetic analysis. Museum collection acronyms follow Frost (2019) with the addition of AH for Andreas Hertz field numbers, EAP for Erick Arias field numbers, and CRARC for the Costa Rica Amphibian Research Center private collection.

Amplification and sequencing: Partial sequences of the large subunit ribosomal RNA (16S) mitochondrial gene were determined for six specimens of *Craugastor* sp. 1 (Arias et al. 2018), *Craugastor* sp. 2 (Arias et al. 2018), and *Craugastor* sp. B (Crawford and Smith 2005) from the Pacific slopes of southwestern Costa Rica and western Panama (Fig. 1). The sequences obtained herein were compared with those available in GenBank for the *C. podiciferus* species group. The protocols for DNA extraction, amplification, sequencing, and editing follow those of Arias et al. (2018). The list of vouchers and GenBank accession numbers used in this study are provided in Appendix I.

Phylogenetic analyses: Sequence alignments used the MAFFT software (Katoh et al. 2017) under the "auto" strategy and default parameters, and were trimmed to the point where a majority of the taxa had sequence data. The sequence data were partitioned by gene, and the COI data were further partitioned by codon position. PartitionFinder v1.1.1 (Lanfear et al. 2012) and the Bayesian information criterion (BIC) were used to select both the best partition scheme and the best model of sequence evolution for each partition. A single set of branch-lengths were used across all partitions (branchlengths=linked), and the search for the best partition scheme was implemented using a heuristic search (scheme=greedy). Four partitions were defined, *a priori*, one for 16S and three for COI (one for each codon).

Phylogenetic analyses were performed using both the maximum likelihood (ML) and Bayesian inference (BI) methods. The maximum likelihood analysis was performed using Garli 2.01 (Zwickl 2006), with 10 search replicates with the following default setting values: streefname=random, attachmentspertaxon=24, genthreshfortopoterm=100000, significanttopochange=0.00001. For bootstrapping, 1000 replicates were run with the previous settings with the following changes: genthresh-
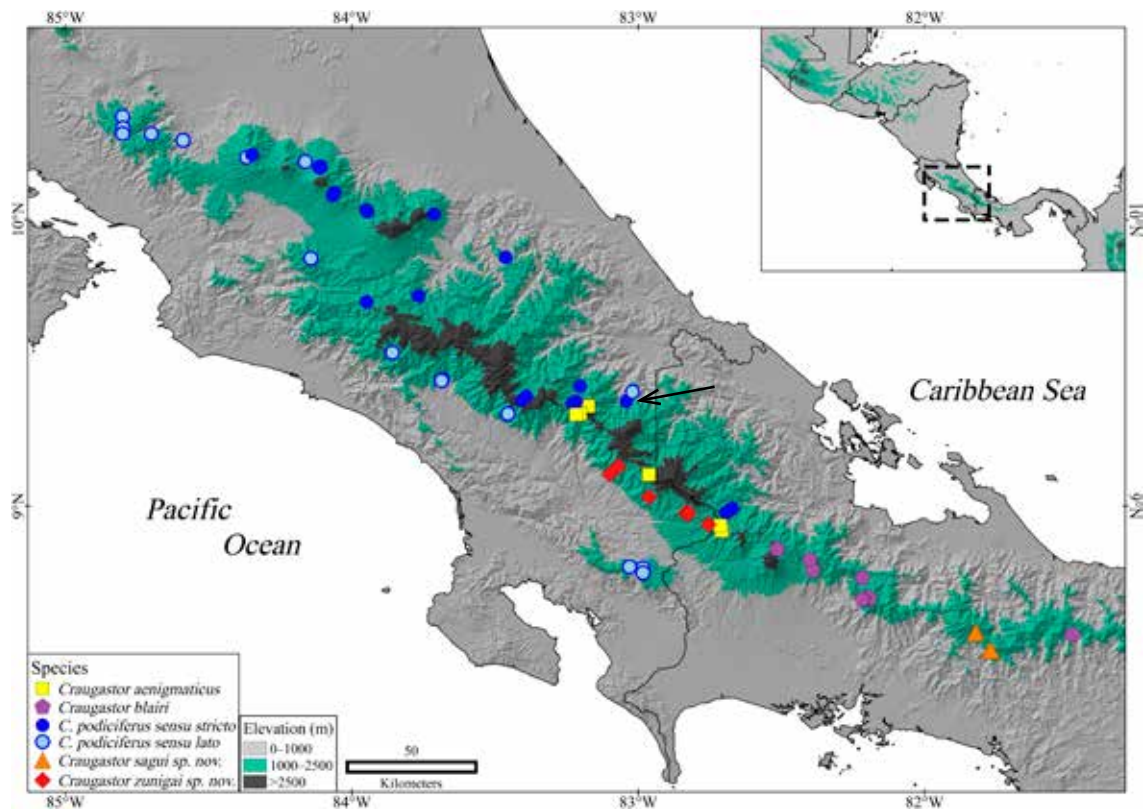
Fig. 1. Map showing the known populations of *Craugastor blairi*, *C. sagui* sp. nov., and *C. zunigai* sp. nov. from the lower montane rainforest in southwestern Costa Rica and western Panama, and populations of other species of the *C. podiciferus* species group inhabiting the highlands of Costa Rica and western Panama. The arrow indicates the type locality of *C. podiciferus*.

fortopoterm=10000, significanttopochange=0.01, treerejectionthreshold=20, as suggested in the Garli manual, to accelerate the bootstrapping. The bootstrap consensus tree was performed using Sumtrees (Sukumaran and Holder 2010b) from the DendroPy package version 4.4.0 (Sukumaran and Holder 2010a). Bayesian phylogenetic analysis was performed using MrBayes 3.2.6 (Ronquist et al. 2012) with the partition scheme and model of sequence evolution for each partition as selected previously. Two separate analyses were run, each consisting of 20 million generations, sampled every 1,000 generations, and four chains with default heating parameters. A time-series plot of the likelihood scores of the cold chain was examined to check the stationarity using Tracer 1.6 software (Rambaut et al. 2014). The first 25% of trees were discarded as burn-in and the remaining trees were used to estimate the consensus tree along with the posterior probabilities for each node and each parameter. Maximum likelihood and Bayesian analyses were run on the CIPRES portal (Miller et al. 2010). Genetic distances (uncorrected *p*-distances) were computed using MEGA6 (Tamura et al. 2013).

Morphometric analyses: A morphometric analysis was performed to compare the three populations from the highlands of southwestern Costa Rica and western Panama. Specimens examined included 19 specimens of *Craugastor* sp. 1, seven specimens of *Craugastor* sp. 2, and 25 specimens of *Craugastor* sp. B (Appendix II). The speci-

mens were deposited in Museo de Zoología (UCR), San José, Costa Rica, and the Senckenberg Research Institute and Nature Museum, Frankfurt, Germany (SMF). The following morphological measurements were recorded as described by Savage (2002), Duellman and Lehr (2009), and Arias et al. (2016): snout-vent length (SVL), head length (HL), head width (HW), inter orbital distance (IOD), width of the upper eyelid (EW), eye-nostril distance (EN), eye diameter (ED), and tympanum diameter (TY). Measurements were performed using dial calipers and rounded to the nearest 0.1 mm. To avoid allometric effects relative to differences in size and shape between species and between individuals, data were transformed using the method of Lleonart et al. (2000). Additional proportions reported herein include: EW/IOD, IOD/HW, TY/ED, EN/ED, ED/HL, HL/HW, and EN/HL. The sex of individuals was determined by gonadal morphology; specimens with opaque seminal vesicles were assumed to be adult males, and those with developed oviducts were assumed to be adult females. The general terminology for morphological characteristics follows Duellman and Lehr (2009). Savage (2002) was followed for the term "supernumerary tubercles," to refer to tubercles on the phalanges (between subarticular tubercles), which is different from the tubercles referred to herein as accessory palmar or plantar tubercles.

The mean, standard deviation, and range for each morphometric variable were calculated without correction. All variables were used to perform a linear discriminant analy-
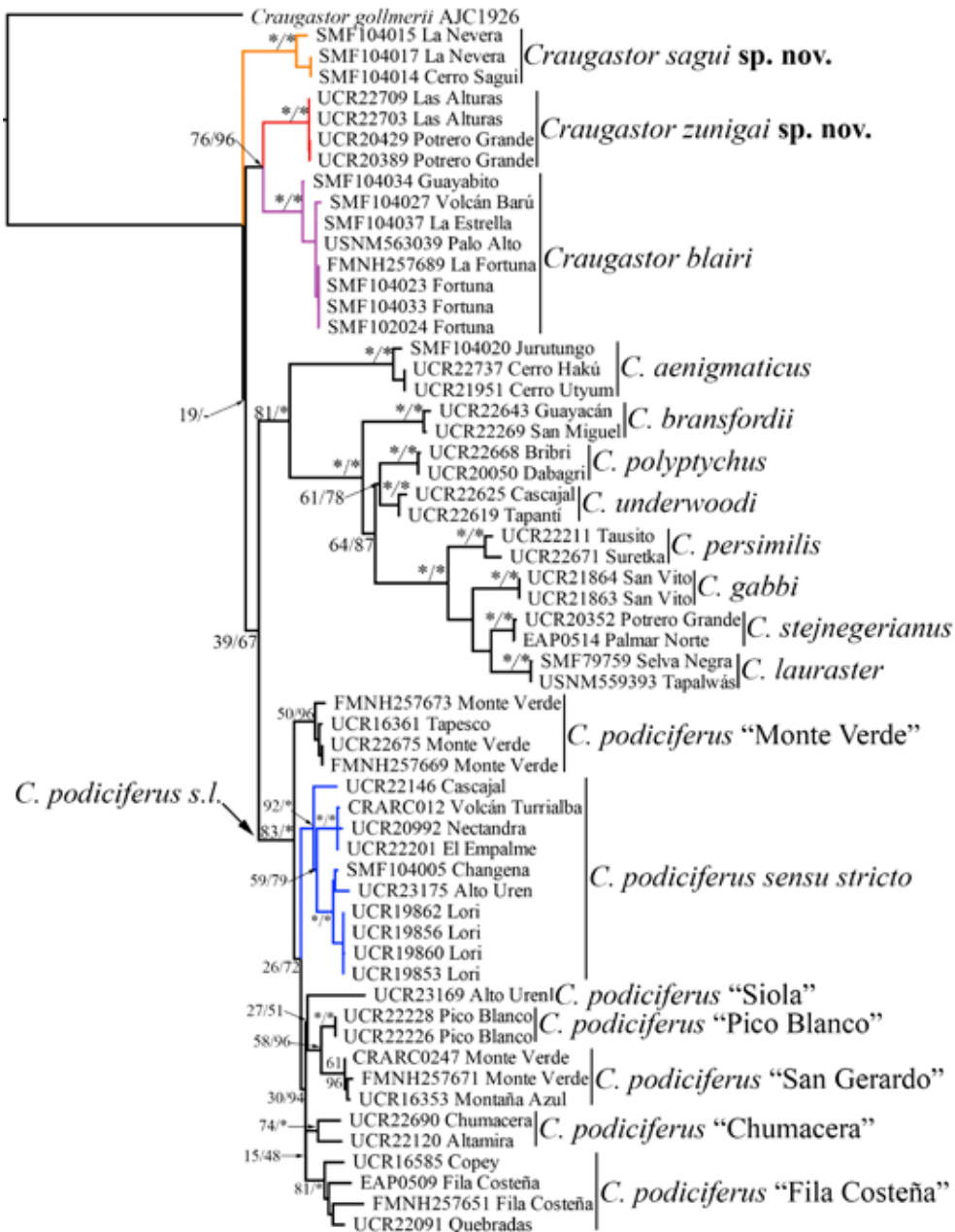
Fig. 2. Maximum likelihood phylogram of the *Craugastor podiciferus* species group based on the 16S and COI mitochondrial DNA gene markers. Bootstrap proportions and posterior probability (multiplied by 100) values obtained with MrBayes before and after the slash, respectively. The scale bar refers to the estimated substitutions per site. Asterisks represent support > 95. The blue clade corresponds to *C. podiciferus sensu stricto*.

sis to determine whether the morphometric variables were effective in predicting the species. The proportion of correctly classified individuals was validated using jackknife accuracy (Manly 1994). All analyses were performed using R v3.3.3 (R Core Team 2017).

Results

Molecular: The resulting mitochondrial data matrix included 59 sequences with a total sequence length of 1,222 bp including gaps; 565 bp for 16S and 657 bp for COI. The best strategy partition contains four partitions, one for 16S and one for each codon in COI. The following substitution models were selected: GTR+G for 16S, K80+I+G for COI

codon position 1, HKY+I+G for COI codon position 2, and GTR+I+G for COI codon position 3. Mitochondrial genetic distances are shown in Table 1. Genetic distances between *Craugastor* sp. 1 and all other members of the *Craugastor podiciferus* species group are 4.9–15.2% for 16S and 13.5–21.6% for COI. *Craugastor* sp. 2 is separated by an uncorrected genetic distance to other members of the *Craugastor podiciferus* species group of 2.9–15.7% for 16S and 14.3–21.3% for COI. Genetic distances between *Craugastor* sp. B and other members of the *Craugastor podiciferus* species group are 2.9–16.2% for 16S and 14.3–19.6% for COI.

The ML and Bayesian trees were similar in topology and show six well-supported clades (Fig. 2). The first is
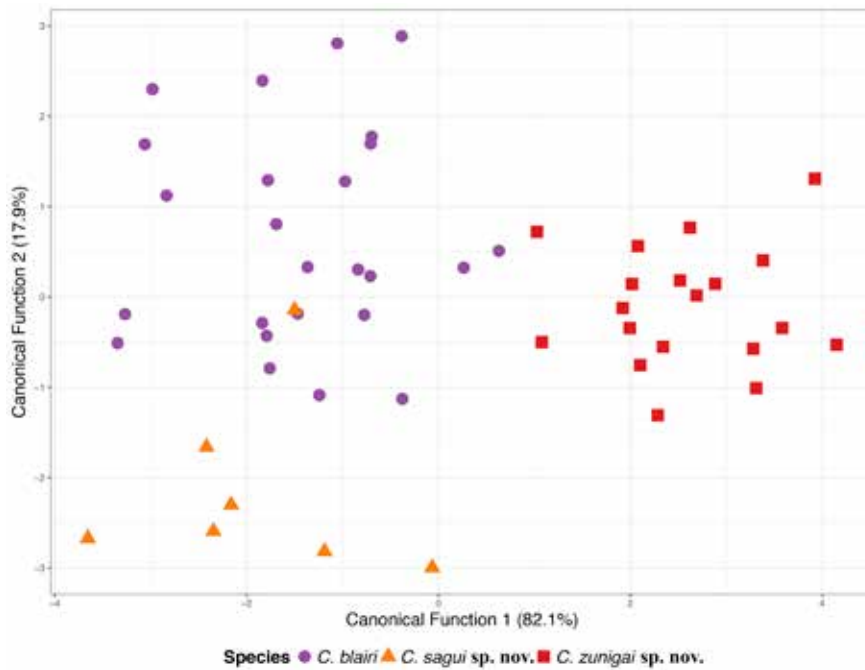
Fig. 3. Linear discriminant analysis showing the morphological separation among the three species from the lower montane rainforest in southwestern Costa Rica and western Panama.

formed by specimens from La Nevera and Cerro Saguí from western Panama. The second and third clades are formed by specimens from southwestern Costa Rica and western Panama, respectively. The fourth clade comprises *C. aenigmaticus* from the montane rainforest of the Cordillera de Talamanca. A fifth major clade includes seven species of the *C. podiciferus* species group that mainly occur from the lowlands to mid-elevations from eastern Honduras to central Panama. Finally, a sixth major clade contains specimens from the type locality of *C. podiciferus* and several other localities from the highlands of Costa Rica and western Panama that are tentatively referred to this species. The main difference between the ML and the Bayesian topology is the position of the clade containing the samples from La Nevera and Cerro Saguí. In the ML tree, this group was the sister to all other members of the *C. podiciferus* species group (although with very low support), while in the Bayesian tree (not shown), it was the sister to a clade containing the samples from Las Alturas and Potrero Grande and *C. blairi*.

Morphometry: Morphometric variation and comparisons among the species are shown in Table 2. The proportion of specimens correctly assigned to the species was 82%, showing a clear morphological separation between the specimens of the three populations of southwestern Costa Rica and western Panama (Fig. 3).

Systematics

Redefinition of *Craugastor podiciferus* (Cope, 1875) and *C. blairi* (Barbour, 1928)

Craugastor podiciferus: The precise type locality of *Craugastor podiciferus* has been a matter of some uncertainty. The taxon was described by Cope (1875) based on material collected by W.M. Gabb from "slope of Cerro Pico Blanco" in 1874. Savage (1974) corrected it to Cerro Utyum, Cantón de Talamanca, Provincia de Limón, 1,524–2,134 m a.s.l. but collected no additional specimens because he did not reach that site. Recently, Arias and Chaves (2014) corrected the type locality to a place between Cerro Pat and the headwaters of the Lari River, elev. 1,520–2,135, Provincia de Limón, Caribbean slope of Cerro Kamuk. The type locality is a remote site within the Parque Internacional La Amistad, in the Cordillera de Talamanca. It is only accessible on foot and requires three days of hiking from the last village (Amubri, Talamanca). For the present study, specimens were collected in the surroundings of the type locality according to Arias and Chaves (2014) [Figs. 1 and 4A]. Based on phylogenetic relationships, we restrict the taxon *Craugastor podiciferus* to the populations from Cordillera Volcánica Central from Costa Rica and Cordillera de Talamanca (Caribbean slopes) in Costa Rica and western Panama (Fig. 1).

Craugastor jota: This species was described by Lynch (1980) based on specimens from the Changena River in western Panama, at 760 m a.s.l., collected by Linda Trueb in 1966. It was placed in the *C. podiciferus* species group based on morphology (Hedges et al. 2008). In this study, specimens from Changena River, western Panama, very near the type locality of *C. jota* (Linda Trueb, pers. comm.) are included. In the phylogenetic analyses these specimens fall within the *C. podiciferus sensu stricto* clade. As a result, we suggest that *C. jota* should be referred to as a junior synonym of *C. podiciferus*.

Table 1. Mean uncorrected genetic distances among lineages of the *Craugastor podiciferus* species group using the COI (above) and 16S (below) mitochondrial genes.

16S/COI	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
1 *C. sagui* sp. nov.	—	14.25	16.51	18.02	16.28	17.60	17.13	18.85	21.34	21.50	19.63	14.43	15.09	16.67	15.58	15.50	15.89	15.19
2 *C. zunigai* sp. nov.	6.05	—	14.62	19.37	18.30	18.54	18.22	20.79	21.34	19.94	19.24	15.71	15.44	18.61	16.59	17.45	17.21	18.61
3 *C. blairi*	6.54	3.19	—	16.34	18.41	18.69	16.85	19.29	19.42	18.35	19.11	16.10	16.04	16.51	14.49	16.85	15.21	16.74
4 *C. aenigmaticus*	13.73	10.95	12.13	—	19.47	18.38	19.21	19.21	20.25	18.30	18.64	16.41	18.31	19.42	17.34	18.30	16.51	17.58
5 *C. bransfordii*	12.50	12.01	11.27	13.97	—	13.08	11.21	17.25	17.83	18.30	18.46	17.50	17.75	19.78	17.13	18.22	17.68	18.11
6 *C. polyptychus*	8.91	10.05	9.80	13.73	8.33	—	8.72	16.43	15.89	16.67	15.89	18.51	19.50	20.02	19.39	20.95	19.00	18.93
7 *C. underwoodi*	8.99	9.31	9.07	13.56	7.11	3.19	—	15.50	16.59	16.90	17.60	16.33	16.88	18.30	16.43	18.38	17.52	17.60
8 *C. persimilis*	11.52	11.52	11.34	15.69	11.27	7.84	8.09	—	14.02	13.71	14.88	18.93	19.28	19.47	19.94	21.03	20.72	21.18
9 *C. gabbi*	13.73	13.73	14.09	17.32	12.99	11.03	10.29	7.11	—	12.93	13.24	19.06	18.82	20.72	19.47	20.48	20.87	21.18
10 *C. stejnegerianus*	14.54	14.22	14.09	16.34	12.99	11.52	10.78	6.62	4.41	—	10.20	19.65	19.95	21.88	19.78	20.95	21.34	21.34
11 *C. lauraster*	14.87	15.69	15.81	17.16	12.01	11.03	10.78	7.60	7.84	5.39	—	18.48	20.75	21.50	20.33	21.34	20.87	20.72
12 *C. podiciferus* "Monte Verde"	6.59	6.21	7.07	12.25	11.03	9.23	8.01	10.54	12.75	13.40	13.73	—	10.20	10.80	9.76	10.93	10.23	10.51
13 *C. podiciferus* sensu stricto	5.69	5.29	5.54	10.62	10.20	8.92	7.75	9.34	12.01	11.91	12.99	3.09	—	11.40	9.11	11.06	10.22	10.88
14 *C. podiciferus* "Siola"	7.84	7.35	6.99	12.91	12.01	9.31	8.33	11.03	12.25	11.76	14.71	6.37	5.20	—	10.44	11.92	10.28	11.84
15 *C. podiciferus* "Pico Blanco"	6.37	5.88	6.13	11.11	10.05	9.56	8.33	10.05	13.24	13.24	12.25	2.45	1.96	5.88	—	6.93	8.88	10.75
16 *C. podiciferus* "San Gerardo"	8.50	8.66	8.78	12.75	11.19	10.38	9.15	11.36	13.56	13.56	12.58	3.65	4.85	7.84	2.94	—	10.98	12.46
17 *C. podiciferus* "Chumacera"	7.35	7.84	7.78	12.34	12.01	10.05	9.31	11.52	13.73	13.24	15.20	4.58	4.00	7.35	4.17	5.07	—	8.72
18 *C. podiciferus* "Fila Costeña"	7.52	7.03	7.11	12.91	11.36	10.05	8.82	10.54	12.42	13.40	13.07	4.25	3.63	7.19	2.45	4.96	5.64	—

Craugastor blairi: The precise type locality of *Craugastor blairi* is unknown. Barbour (1928) indicated the type locality as "from Gutierrez, Bocas del Toro Province, Panama (near Costa Rican frontier)." The type series was collected by Emmett R. Dunn and Chester Duryea in the summer of 1923. Their expedition followed a trail from Chiriquicito at the Laguna de Chiriquí (today in the Corregimiento of Miramar, Bocas del Toro) to Boquete, Province of Chiriquí. Most of their trail climbs up the Atlantic slopes of the Cordillera Central (Savage 1970) before descending into the high valley of Boquete. On the same route, Dunn and Duryea collected several other new species and identified the type localities as either "Gutierrez" or "La Loma." Species with type locality "La Loma" are *Bolitoglossa colonnea* (Dunn, 1924), *Dermophis parviceps* (Dunn, 1924), *Hyloscirtus colymba* (Dunn, 1931), *Pristimantis pardalis* (Barbour, 1928), and *Pristimantis caryophyllaceus* (Barbour, 1928). Each of these species has a vertical distribution range that enters the lowlands to almost sea level (Köhler 2011). Dunn gives the elevation of La Loma as 2,000 feet (610 m) in the description of *D. parviceps* and as 1,500 feet (460 m) in the description of *H. colymba*. In comparison to "La Loma," a species with the type locality "Gutierrez" is *Craugastor obesus* (Barbour 1928). Dunn (1940) also mentioned collecting *C. monnichorum* at "Gutierrez," and both species had a more premontane to montane distribution. Therefore, we believe that "Gutierrez" is further uphill than "La Loma" and thus closer to the continental divide and much closer to Boquete than to the Caribbean lowlands. Several specimens collected at different sites in the vicinity of Boquete on the foothills of Barú Volcano form a separate clade with specimens collected at Cerro La Estrella, Cerro Guayaba, Guayabito, and La Fortuna (Fig. 1 and 4B). For the above reasons, we resurrect the name *C. blairi* for this clade.

Restricting *Craugastor podiciferus* to populations inhabiting the Caribbean slopes of Cordillera de Talamanca of Costa Rica and extreme western Panama and *C. blairi* to populations inhabiting the Cordillera Central from Barú Volcano to the east, results in two allopatric lineages on the Pacific slopes of Cordillera de Talamanca, Costa Rica and those from Cordillera Central, Panama without assignment to an existing taxon. With no available name present in the synonymy of *C. podiciferus* for either of these populations, these two lineages are herein described as new species, and redescriptions are provided for *C. podiciferus* and *C. blairi*.

***Craugastor podiciferus* (Cope, 1875)**
Common name: Polymorphic Dirt Frog
(Figs. 4A and 6)

Syntypes: USNM 30662, USNM 30664–75, and MCZ 11841. All specimens from "5,000 to 7,000 feet (elevation), on the Caribbean slopes of Cerro Pico Blanco," collected by William M. Gabb in 1874.

Table 2. Mean, standard deviation (S.D.), and range for morphometric variables by species.

Variable	*Craugastor podiciferus*		*Craugastor blairi*		*Craugastor sagui* sp. nov.		*Craugastor zunigai* sp. nov.	
	Mean ± S.D.	Range	Mean ± S.D.	Range	Mean ± S.D.	Range	Mean ± S.D.	Range
SVL	25.6±4.3	16.9–33.9	23.2±4.8	13.4–30.6	21.5±6.5	13.0–30.1	20.8±3.9	13.8–26.5
HL	10.4±1.5	7.0–12.9	8.3±1.5	5.6–11.0	8.1±2.5	4.7–10.9	8.4±1.5	5.7–10.3
HW	10.2±1.6	6.5–13.3	8.9±1.8	5.5–12.0	8.0±2.4	4.9–11.5	8.2±1.6	5.6–10.7
ED	3.0±0.5	2.0–3.9	2.9±0.6	1.9–3.8	2.9±0.7	2.0–4.0	2.5±0.3	1.9–2.9
TY	1.8±0.4	1.0–2.7	1.8±0.4	0.8–2.6	1.7±0.6	0.8–2.6	2.0±0.3	1.6–2.9
EW	1.9±0.3	1.2–2.4	1.6±0.3	0.9–2.1	1.5±0.4	0.9–2.0	1.6±0.3	1.2–2.1
IOD	3.3±0.5	2.5–4.2	3.3±0.6	1.8–4.3	2.9±0.8	1.7–3.9	2.7±0.5	1.8–3.7
EN	2.6±0.4	1.9–3.2	2.2±0.4	1.3–3.0	2.1±0.8	1.1–3.2	2.0±0.4	1.3–2.6
EW/IOD	2.8±0.3	2.3–3.6	0.50±0.09	0.34–0.73	0.52±0.06	0.46–0.61	0.59±0.08	0.44–0.76
IOD/HW	0.6±0.1	0.4–0.7	0.37±0.04	0.30–0.45	0.37±0.03	0.34–0.40	0.34±0.02	0.30–0.38
TY/ED	0.6±0.1	0.4–1.0	0.66±0.23	0.40–1.09	0.58±0.18	0.40–0.81	0.81±0.17	0.62–1.34
EN/ED	0.9±0.1	0.7–1.0	0.77±0.08	0.63–0.91	0.71±0.11	0.55–0.88	0.81±0.10	0.63–0.98
ED/HL	0.3±0.1	0.2–0.3	0.35±0.03	0.30–0.43	0.37±0.04	0.31–0.43	0.29±0.02	0.26–0.33
HL/HW	1.0±0.1	0.9–1.1	0.94±0.05	0.84–1.05	1.01±0.06	0.95–1.08	1.03±0.05	0.95–1.14
EN/HL	0.2±0.1	0.2–0.3	0.27±0.02	0.23–0.30	0.26±0.02	0.23–0.29	0.24±0.02	0.20–0.27

Genetic reference specimen: UCR 23175 (EAP 0810), an adult female from Costa Rica: Provincia de Limón: Cantón de Talamanca: Distrito de Telire: Parque Internacional La Amistad, (9.366º, -83.042º; 1,860 m a.s.l.), collected by Erick Arias and Omar Zúñiga on 27 October 2016.

Referred specimens: UCR 23155 (EAP 0803), adult female, same data as the genetic reference specimen. UCR 23145 (EAP 0792), an adult male from Costa Rica: Provincia de Limón: Cantón de Talamanca: Distrito de Telire: Cerro Pat, Parque Internacional La Amistad, (9.393º, -83.025º; 1,450 m a.s.l.), collected by Erick Arias and Omar Zúñiga on 26 October 2016.

Assignment to group: Assigned to *Craugastor* based on molecular analysis and the following characters: cranial crests absent and Toe III larger than Toe V.

Diagnosis: The following combination of characteristics distinguish *Craugastor podiciferus* (Fig. 5A–6) from other described species in the genus: 1) skin on the dorsum is smooth to scattered tubercles; 2) skin on the venter is smooth, at least along the midline; 2) vocal slits in adult males; 3) nuptial pads absent; 4) unwebbed toes; 5) heel with a projecting tubercle; 6) accessory palmar and plantar tubercles absent, usually no supernumerary tubercles under the digits; and 7) subarticular tubercles flat in form. *Craugastor* (*Craugastor*) *podiciferus* is a small species with the following characteristics: (1) skin on the dorsum smooth to scattered tubercles; head smooth; venter smooth; flanks smooth with scattered tubercles to warty; posterior surface of hind limbs surrounding cloaca strongly areolate; some specimens with a pair of scapular, dorsolateral or lateral folds; discoidal fold complete laterally and posteriorly; (2) tympanic membrane round, heavily pigmented; prominent in males, evident in females; annulus evident through the skin; (TY/ED = 44.9–100%); usually with a pair of supratympanic folds; (3) snout subovoid in dorsal view, rounded in profile; loreal region concave; canthus rostralis usually rounded; (4) eyelid granular, with several low tubercles forming a more or less distinct ridge on outer edge of the eyelid continuous with supratympanic fold (EW/IOD = 40.5–71.2%); cranial crests absent; (5) vomerine teeth in two transverse fasciculi, behind choanae; choanae smaller than dentigerous; (6) vocal slits and large single vocal sac in adult males; nuptial pads absent; (7) fingers I and II subequal; discs absent, some specimens with terminal transverse grooves on fingers, especially in males; tips symmetric, usually rounded but pointed in fingers III–IV in some specimens; pads ovoid to triangular; (8) fingers lack lateral fringes; webbing absent; thenar and palmar tubercles low, ovoid, similar in size; supernumerary tubercles absent; accessory palmar tubercles usually absent but 1–2 low barely distinct tubercles visible in some specimens; subarticular tubercles round in basal outline, flat in form and globular in profile; (9) ulnar fold absent but tubercles sometimes visible; (10) heel with a projecting tubercle; inner edge tarsal with an indistinct short ridge, outer smooth or with tubercles; (11) toes lacking lateral fringes; inner metatarsal tubercle elongate, outer rounded, much smaller than inner, inner and outer metatarsal tubercles projecting; supernumerary and plantar tubercles absent; subarticular tubercles rounded to ovoid in basal outline, flat in form and obtuse in profile; (12) Toe III larger than Toe V; discs and terminal transverse grooves present on all fingers; tips symmetrical, disc covers spadate; pads triangular; webbing absent; (13) coloration highly variable; dorsum tan to light or dark brown, nearly uniform or suffused with black or reddish
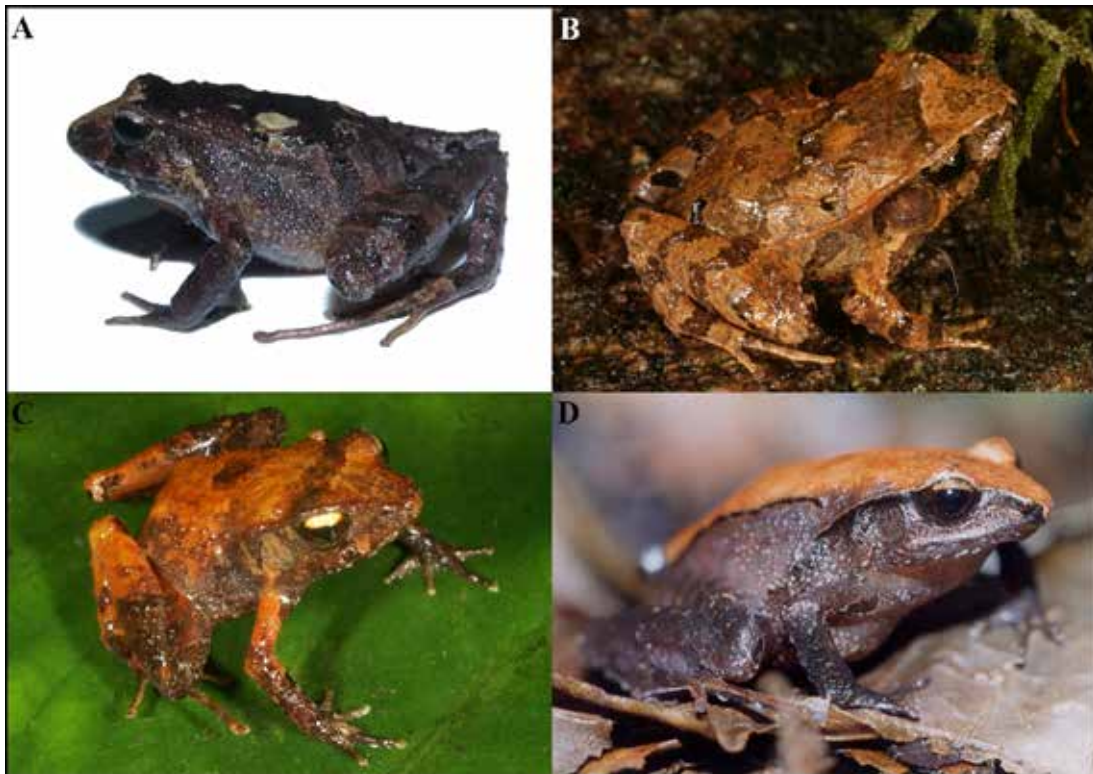
Fig. 4. In life photographs of **(A)** *Craugastor podiciferus* (UCR 23169) from the Caribbean slope of Cerro Kamuk, Costa Rica, **(B)** *C. blairi* (SMF 104032) from Fortuna, Panama, **(C)** *C. sagui* sp. nov. (SMF 104018) from La Nevera, Panama, and **(D)** *C. zunigai* sp. nov. (UCR 20389) from Potrero Grande, Costa Rica. *Photos by E. Arias (A), A. Hertz (B–C), and E. Boza-Oviedo (D).*

pigment; frequently with paired suprascapular dark spots, area between dorsal folds usually contrasting with flank color; several specimens with a dark mask from the snout continuing above the tympanum and often bordered above by a narrow light line; venter yellow, grayish, or reddish, uniform or with light or dark spots; usually forelimbs and hind limbs with dark bars, some specimens with paired dark spots on anterior surface of hind limbs; upper lip has dark bars with white pigment in the form of faded bars; and (14) SVL in males 21–28 mm; SVL in females 23–40 mm.

Comparison: *Craugastor podiciferus* differs from all other craugastorids of Isthmian Central America, excluding those in the *C. podiciferus* species group, by having unwebbed toes and a narrow head (HW 37.0–43.3% of SVL). *Craugastor podiciferus* differs from other members of the *C. podiciferus* species group by having the following characteristics (condition for *C. podiciferus* in parentheses).

Craugastor bransfordii (Cope, 1886), *C. gabbi*, *C. laurasterr* (Savage, McCranie, and Espinal, 1996), *C. persimilis* (Barbour, 1926), *C. polyptychus* (Cope, 1886), *C. stejnegerianus* (Cope, 1893), and *C. underwoodi* (Boulenger, 1896) differ from *C. podiciferus* by the following features: a) dorsum usually granular or warty (dorsum smooth to scattered tubercles); b) subarticular tubercles projecting (subarticular tubercles flat); and c) venter coarsely areolate, including the midline (venter smooth, at least in mid-

line). *Craugastor aenigmaticus* Arias, Chaves, and Parra-Olea, 2018 differs from *C. podiciferus* by the following features: a) absence of prominent calcar tubercle on heel, although some specimens can have one to three small tubercles (prominent calcar tubercle on the heel); b) venter violet-brown with white blotches (venter yellow, orange, grayish or olive in adults); and c) white prominent folds between subarticular tubercles on hands of adults (absence of white folds between subarticular tubercles on hands of adults). *Craugastor blairi* (Barbour, 1928) differs from *C. podiciferus* by the following features: a) skin on venter coarsely areolate (venter smooth, at least in midline); b) absence of prominent calcar tubercle on heel (prominent calcar tubercle on heel); c) having accessory palmar tubercles (accessory palmar tubercles absent); and d) having subarticular tubercles projecting (subarticular tubercles flat). *Craugastor sagui* differs from *C. podiciferus* by the following features: a) nuptial pads in adult males (nuptial pads absent); b) absence of prominent calcar tubercle on heel (prominent calcar tubercle on heel); and c) absence of vocal slits in adult males (vocal slits in adult males). *Craugastor zunigai* differs from *C. podiciferus* by the following features: a) skin on venter coarsely areolate (venter smooth, at least in midline); b) absence of prominent calcar tubercle on heel (prominent calcar tubercle on heel); c) accessory palmar tubercles (accessory palmar tubercles absent), and d) subarticular tubercles projecting (subarticular tubercles flat).

Fig. 5. Variation of the ventral views of the right hands. **(A)** *Craugastor podiciferus* (UCR 23175), **(B)** *C. blairi* (SMF 104032), **(C)** *C. sagui* sp. nov. holotype (SMF 104018), and **(D)** *C. zunigai* sp. nov. holotype (UCR 22703). *Photos by E. Arias (A and D) and G. Köhler (B-C).*

Natural history: *Craugastor podiciferus* inhabits the lower montane rainforest (Holdridge 1967; Bolaños et al. 2005), which is characterized by a very short dry season (one to three months), annual precipitation ranging from 3,600–7,500 mm, and annual temperature from 12–17 ºC. Very little is known about the natural history of *C. podiciferus*; however, it is noteworthy that the species was abundant during the months of fieldwork. Individuals were always found on the forest floor and observed jumping during the active search. Schlaepfer and Figeroa-Sandí (1998) described the call of *C. podiciferus* from Las Cruces, herein referred to as *C. podiciferus* "Fila Costeña." The advertising call of *C. podiciferus sensu stricto* is unknown, although it is known to vocalize.

Distribution: *Craugastor podiciferus sensu stricto* is restricted to the highlands of the Cordillera Volcánica Central in Costa Rica and Caribbean slopes of the Cordillera de Talamanca in Costa Rica and western Panama (Fig. 1). The altitudinal range of *C. podiciferus* is 1,700–2,700 m a.s.l. All known populations of *C. podiciferus* are found in primary forests, and several localities are within protected areas, (i.e., Parque Internacional La Amistad, Parque Nacional Tapantí-Macizo de la Muerte, Parque Nacional Braulio Carrillo, and Parque Nacional Juan Castro Blanco). More fieldwork is necessary to clarify the distribution of *C. podiciferus*, especially on the northern end of the Cordillera de Talamanca and in the adjacent zone between the Cordillera Volcánica Central and the Cordillera de Tilarán.

Remarks: Several populations from the highlands of Costa Rica are tentatively assigned to *Craugastor podiciferus*. However, these populations are phylogenetically structured and show uncorrected *p*-distances in the 16S rRNA gene between 2.45 and 6.37% (Table 1), and some differ morphologically from typical *C. podiciferus* and thus may represent as many as six additional unnamed species. These six populations are as follows: 1) the *C. podiciferus* "Monte Verde" clade, which corresponds to clade A of Streicher et al. (2009), restricted to Cordillera de Tilarán and Volcánica Central, at 1,500–1,931 m a.s.l. The specimens in this clade are morphologically very similar to *C. podiciferus sensu stricto*. 2) The *C. podiciferus* "San Gerardo" clade, which corresponds to clade B of Streicher et al. (2009), restricted to Cordillera de Tilarán and Cordillera Volcánica Central, at 1,470–1,500 m a.s.l. The specimens in this clade differ from *C. podiciferus s.s.* in having projecting subarticular tubercles. 3) The *C. podiciferus* "Pico Blanco" clade, which contains a single population from the northern end of the Cordillera de Talamanca in the Central valley, at 2,242 m a.s.l. The specimens in this clade differ from *C. podiciferus s.s.* by having an areolate venter and projecting subarticular tubercles. 4) The *C. podiciferus* "Fila Costeña" clade, corresponding to clades E and F of Streicher et al. (2009), restricted to South Pacific Costa Rica, at 1,350–1,550 m a.s.l. The specimens in this clade differ from *C. podiciferus s.s.* by having an areolate venter and accessory palmar tubercles. 5) The *C. podiciferus* "Chumacera" clade, which is known for only
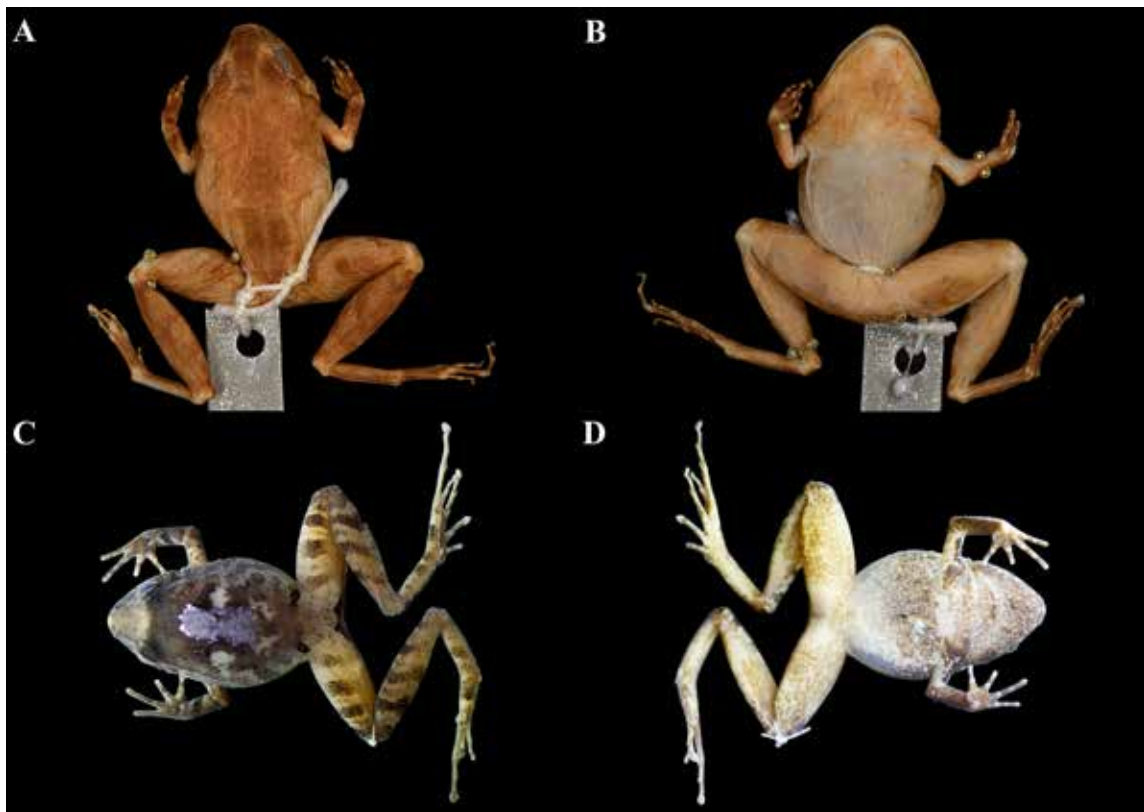
Fig. 6. Dorsal and ventral views in ethanol of *Craugastor podiciferus* **(A, B)** syntype (USNM 30672) and **(C, D)** molecular specimen reference (UCR 23175). *Photos by E.M. Langan (A–B) and E. Arias (C–D).*

one population on the Pacific slopes of Cordillera de Talamanca, at 1,750–1,850 m a.s.l. The specimens in this clade differ from *C. podiciferus s.s.* by having accessory palmar tubercles. 6) The *C. podiciferus* "Siola," which is known for only one population on the Caribbean slope of the Cordillera de Talamanca, at 1,300–1,350 m a.s.l. The specimens in this clade differ from *C. podiciferus s.s.* by having an areolate venter and by the prominent pungent calcar tubercle on the heel.

Despite the molecular results and morphological differences between some of these clades, there is little to distinguish some populations for particular characters, especially *C. podiciferus sensu stricto*, *C. podiciferus* "Monte Verde," and *C. podiciferus* "Chumacera." In addition, this group forms a monophyletic group, thus agreeing with the definition of the taxon by Savage (2002), Leenders (2016), and Cossel and Kubicki (2017). For these reasons and until new morphological evidence support the distinctiveness, we refrain from raising these clades to the species level.

***Craugastor blairi* comb. new. (Barbour, 1928)**
Common name: Blair's Dirt Frog
(Figs. 4B and 7)

Holotype: MCZ 13036 from Gutierrez, Bocas del Toro Province, Panama (near Costa Rican border), collected by E.R. Dunn and Chester Duryea in summer 1925.

Genetic reference specimen: SMF 104032 (AH 379), an adult male from Panama: Provincia de Chiriquí: Distrito

de Gualaca: La Fortuna, western slope of Cerro Pata de Macho (8.679º, -82.193º; 1,793 m a.s.l.), collected by Andreas Hertz and Sebastian Lotzkat on 20 May 2010.

Referred specimens: SMF 104030 (AH 377) and SMF 104031 (AH 378), adult males; same date as genetic reference specimen. SMF 104025 (AH 196), adult female from Panama: Provincia de Chiriquí: Distrito de Gualaca: La Fortuna, (8.672º, -82.200º; 1,400 m a.s.l.), collected by Andreas Hertz and Sebastian Lotzkat on 20 March 2009. SMF 104026 (AH 238) and SMF 104027 (AH 239), adult females from Panama: Provincia de Chiriquí: Distrito de Bugaba: Volcán Barú, Sendero Los Quetzales (8.849º, -82.515º; 2,134 m a.s.l.), collected by Andreas Hertz and Sebastian Lotzkat on 8 April 2009.

Assignment to group: Assigned to the genus *Craugastor* based on molecular data and on the following characters: cranial crest absent and Toe III larger than Toe V. Assigned to the *C. podiciferus* species group based on the following features: narrow head (HW/SVL = 34.6–42.8%), dorsum smooth to scattered tubercles, unwebbed toes, vocal slits in adult males, and nuptial pads absent.

Diagnosis: The combination of the following characteristics can be used to distinguish *Craugastor blairi* (Figs. 5B and 7) from other described species of the genus: 1) skin on dorsum is smooth or has scattered tubercles; 2) skin on venter is coarsely areolate; 3) vocal slits and vocal
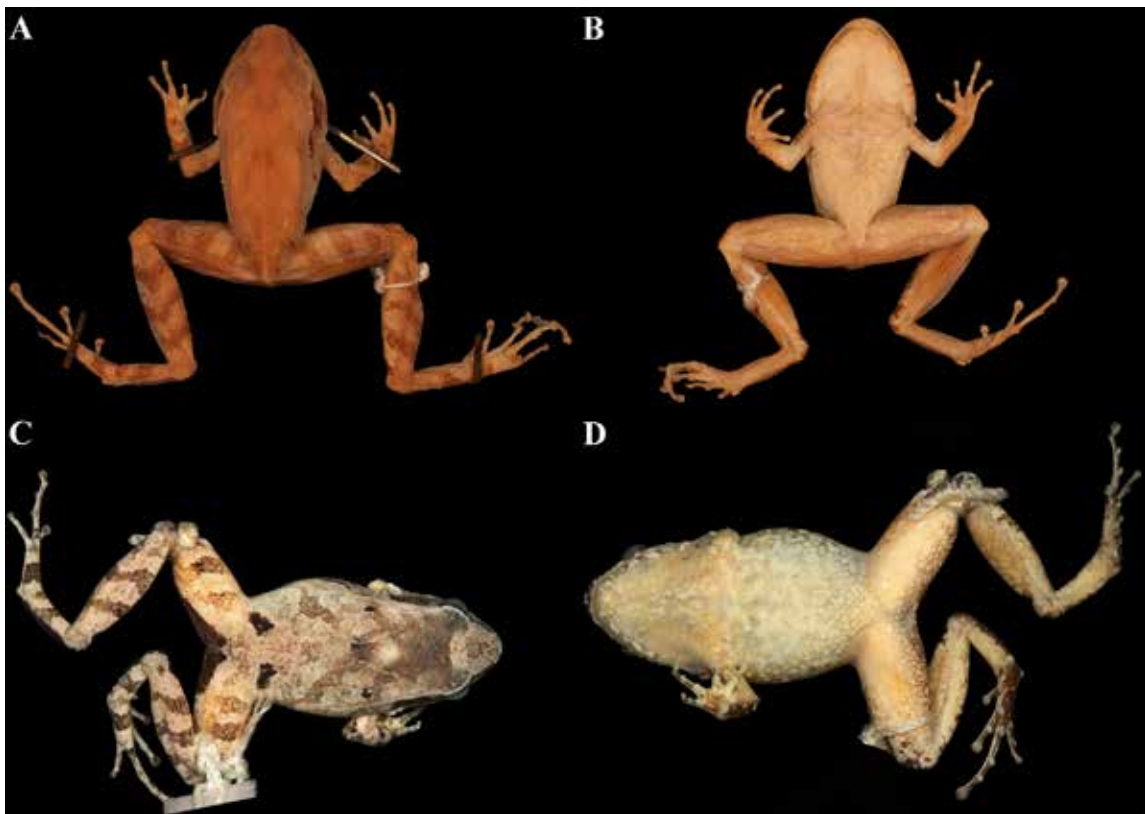
Fig. 7. Dorsal and ventral views in ethanol of *Craugastor blairi* **(A, B)** holotype (MCZ A-13036) and **(C, D)** molecular specimen reference (SMF 104032). *Photos by the Museum of Comparative Zoology, Harvard University (A–B) and G. Köhler (C–D).*

sac present in adult males; 4) nuptial pads absent; 5) unwebbed toes; 6) heel without an enlarged calcar tubercle, although one to three small tubercles or granules can be present on heel; 7) accessory palmar and plantar tubercles present, and absence of supernumerary tubercles; and 8) subarticular tubercles projecting.

Craugastor (*Craugastor*) *blairi* is a small species with the following characteristics: (1) skin on dorsum smooth or has scattered tubercles; head smooth; venter coarsely areolate: flanks smooth with scattered tubercles to warty; posterior surface of hind limbs surrounding cloaca strongly areolate; some specimens with a pair of scapular, dorsolateral or lateral folds; discoidal fold complete laterally and posteriorly; (2) tympanic membrane round, heavily pigmented in females, translucent in adult males; prominent in males, evident in females; annulus evident through the skin; (TY/ED = 40–109%); usually with a pair of supratympanic folds; (3) snout subovoid in dorsal view, rounded in profile; loreal region concave; canthus rostralis usually rounded; (4) eyelid granular, with an evident supraocular tubercle and a more or less distinct ridge on outer edge of eyelid continuous with supratympanic fold (EW/IOD = 37.2–72.7%); cranial crests absent; (5) vomerine teeth in two transverse fasciculi, behind choanae; choanae smaller than dentigerous; (6) vocal slits and a single vocal sac that is large in adult males; nuptial pads absent; (7) Finger I and II subequal; discs absent, some specimens with terminal transverse grooves on fingers, especially in males;

tips symmetric, usually rounded; pads ovoid to triangular; (8) fingers lacking lateral fringes; webbing absent; thenar and palmar tubercles low, ovoid, similar in size; supernumerary tubercles absent; 1–2 accessory palmar tubercles; subarticular tubercles round in basal outline, projecting in form and globular in profile; (9) ulnar fold absent but tubercles visible; (10) heel without an enlarged calcar tubercle, although one to three small tubercles or granules can be present on heel; inner edge tarsal smooth, outer with an incomplete fold and/or tubercles; (11) toes lacking lateral fringes; inner metatarsal tubercle elongate, outer rounded, much smaller than inner, inner and outer metatarsal tubercles projecting; supernumerary tubercles absent; several low plantar tubercles; subarticular tubercles rounded to ovoid in basal outline, projecting in form and obtuse in profile; (12) Toe III larger than Toe V; discs and terminal transverse grooves present on all fingers; tips symmetrical, disc covers palmate to spadate; pads triangular; webbing absent; (13) coloration very variable; dorsum tan to light or dark brown, nearly uniform or suffused with black or reddish pigment; frequently paired suprascapular dark spots; some specimens with dark mask from snout continuing above tympanum and downward behind axilla, often bordered above by a narrow light line; venter yellow, grayish, or reddish, uniform or with light or dark spots; usually forelimbs and hind limbs with dark bars, some specimens with paired dark spots on anterior surface of hind limbs; upper lip with dark bars with white pigment

Table 3. Main diagnostic characteristics and character states for secondary sexual characteristics of the species forming the *Craugastor podiciferus* species group.

| Species	Dorsal skin texture	Ventral skin texture	Thenar and palmar tubercles in size relation	Subarticular in profile	Super-numerary tubercles	Accessory palmar tubercles	Heel skin texture	Nuptial pads	Vocal slits	Vocal sac
C. aenigmaticus	Smooth to weakly granular	Smooth with granules laterally	Thenar tubercle much smaller than palmar tubercle	Flat	Absent	Absent	Smooth to three low granules not projecting	Absent	Absent	Absent
C. bransfordii	Granular to warty	Coarsely areolate	Thenar tubercle equal or slightly smaller than palmar tubercle	Projecting	Present	Present	Granular	Present	Absent	Absent
C. blairi	Smooth to shagreen with scattered tubercles	Coarsely areolate	Thenar tubercle equal or slightly smaller than palmar tubercle	Projecting	Absent	Present	Smooth to several low granules not projecting	Absent	Present	Present
C. gabbi	Shagreen with scattered granules to granular	Coarsely areolate	Thenar tubercle much smaller than palmar tubercle	Projecting	Present	Present	Granular	Absent	Absent	Absent
C. lauraster	Granular to warty	Coarsely areolate	Thenar tubercle much smaller than palmar tubercle	Projecting	Present	Present	Granular	Absent	Absent	Absent
C. persimilis	Granular	Coarsely areolate	Thenar tubercle much smaller than palmar tubercle	Projecting	Present	Present	Granular	Absent	Absent	Absent
C. podiciferus	Smooth to scattered tubercles	Smooth	Thenar tubercle equal or slightly smaller than palmar tubercle	Flat	Absent	Absent	A projecting tubercle	Absent	Present	Present
C. polyptychus	Granular to warty	Coarsely areolate	Thenar tubercle equal or slightly smaller than palmar tubercle	Projecting	Present	Present	Granular	Absent	Absent	Absent
C. sagui sp. nov.	Smooth to shagreen with scattered tubercles	Smooth	Thenar tubercle equal or slightly smaller than palmar tubercle	Usually flatted, but projecting in some specimens	Absent	Absent	Smooth to several low granules not projecting	Present	Absent	Absent
C. stejnegerianus	Granular to warty	Coarsely areolate	Thenar tubercle much smaller than palmar tubercle	Projecting	Present	Present	Granular	Absent	Absent	Absent
C. underwoodi	Granular to warty	Coarsely areolate	Thenar tubercle equal or slightly smaller than palmar tubercle	Slightly projecting	Usually absent	Present	Granular	Present	Absent	Absent
C. zunigai sp. nov.	Smooth to shagreen with scattered tubercles	Coarsely granular	Thenar tubercle equal or slightly smaller than palmar tubercle	Slightly projecting	Absent	Present	Granular to two low granules not projecting	Absent	Present	Present
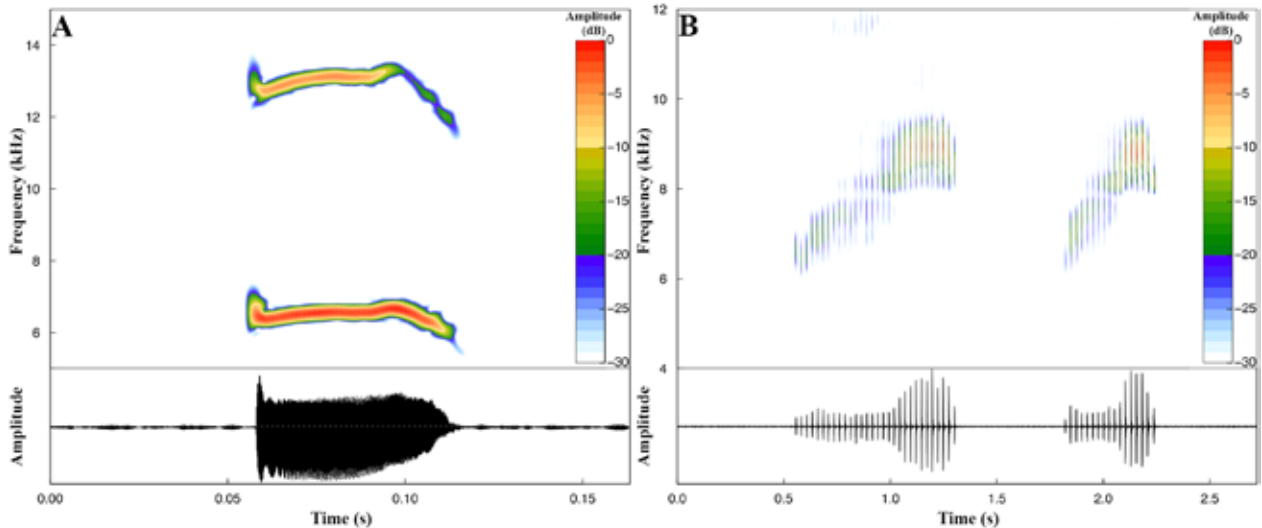
Fig. 8. Spectrograms and oscillogram of **(A)** the advertisement call (squeak) and **(B)** pulsed call (chirp) of *Craugastor blairi.*

in the form of faded bars; and (14) SVL in males 15.9–21 mm; SVL in females 13.4–30.6 mm.

Comparisons: *Craugastor blairi* differs from all the other Isthmian Central America craugastorids (except for those in the *C. podiciferus* species group) by having unwebbed toes and a narrow head (HW 34.6–42.8% of SVL). *Craugastor blairi* differs from other members of the *C. podiciferus* species group by having the following characteristics (condition for *C. blairi* in parentheses). *Craugastor bransfordii*, *C. gabbi*, *C. lauraster*, *C. persimilis*, *C. polyptychus*, *C. stejnegerianus*, and *C. underwoodi* differ from *C. blairi* by the following features: a) dorsum usually granular or warty (dorsum smooth to having scattered tubercles); b) subarticular tubercles obtuse to pointed, at least the distal subarticular tubercles under Toe III and IV (subarticular tubercles projecting, globular); and c) altitudinal range, 0–1,600 m a.s.l. (altitudinal range is 1,280–2,134 m a.s.l. for *C. blairi*). *Craugastor podiciferus* differs from *C. blairi* by the following features: a) prominent calcar tubercle on heel (absence of prominent calcar tubercle on heel); b) subarticular tubercles flat (subarticular tubercles projecting); and c) venter smooth, at least in midline (venter coarsely areolate, including midline). *Craugastor aenigmaticus* differs from *C. blairi* by the following features: a) venter smooth (venter coarsely areolate); b) subarticular tubercles flat (subarticular tubercles projecting, globular); and c) prominent white folds between subarticular tubercles (absence of white folds between subarticular tubercles). *Craugastor sagui* differs from *C. blairi* by the following features: a) venter smooth (venter coarsely areolate); b) nuptial pads in adult males (nuptial pads absent); c) absence of vocal slits (vocal slits in adult males); and d) subarticular tubercles flat (subarticular tubercles projecting). *Craugastor zunigai* differs from *C. blairi* by the absence of an evident supraocular tubercle (eyelid with an evident supraocular tubercle).

Natural history: *Craugastor blairi* inhabits the lower montane rainforest (Holdridge 1967; Bolaños et al. 2005), which is characterized by a very short dry season (one to three months). Annual precipitation ranges from 3,600–7,500 mm and annual temperature from 12–17 ºC. Very little is known about the natural history of *C. blairi*; however, it is noteworthy that the species was abundant during the months of fieldwork. The specimens were always found on the floor in leaf litter, possibly active during the day. Males call during periods of lower light due to dark clouds or in evening hours. Calling activity is greater during rain.

Vocalization: Vocalizations of four male specimens (AH 375, 1,430 m, dusk, 19.5 °C, 100% RH, AH 377–379, 1,793 m, 18.5 °C, 100% RH) have been recorded on the slopes of Cerro Pata de Macho. All specimens were calling at dusk, between 18:00 h and 19:00 h after a moderate rain. Calling sites were elevated positions only a few centimeters above the ground such as low vegetation, twigs, or roots. Calling stopped completely after dark. One male (AH375) was recorded at 19.5 °C and 100% relative humidity. The other three males were recorded at 18.5 °C and 100% relative humidity. Two very different call types could be distinguished (Fig. 8). The first that was emitted by all four males was a "squeak" of 0.035–0.065 (0.050 ± 0.007) seconds in length, given in frequent intervals after 7.938–29.124 (11.974 ± 4.825) seconds, resulting in a call rate of 4.66–9.63 (6.67 ± 2.41) calls per minute. The call has two harmonics, the fundamentals of which also contain the dominant frequency at 6,844–8,063 (7,306 ± 313) Hz. The dominant frequency is reached in the middle or towards the end of the call, 0.009–0.053 (0.030 ± 0.012) seconds after ignition of the call. The frequency range of the fundamental harmonic is between 4,705–6,674 (5,680 ± 634) Hz low frequencies and 7,181–9,343 (7,965 ± 467) Hz high frequencies. The higher harmonic has a frequency range of 9,566–14,057 (12,057 ± 1,159) Hz low frequen-
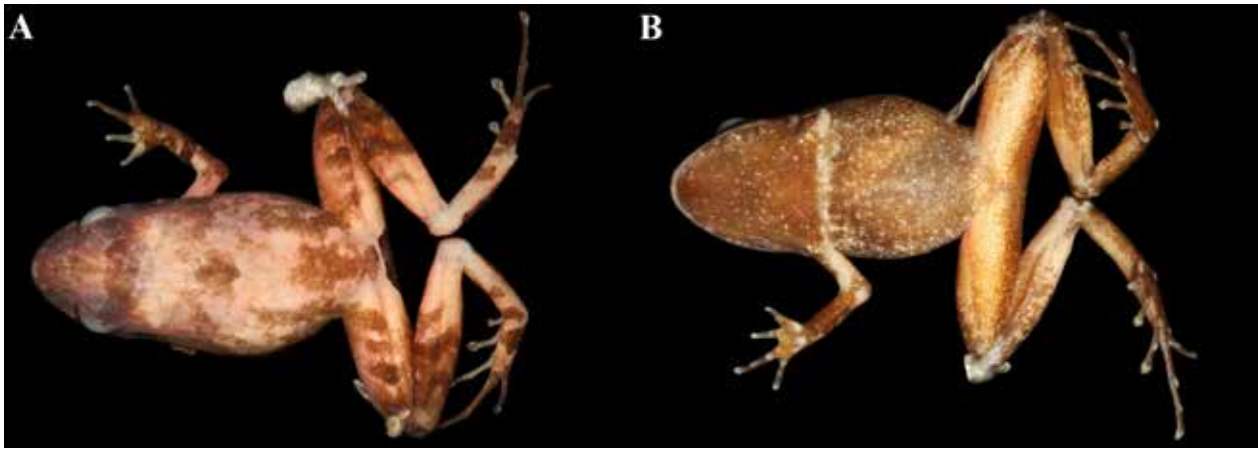
Fig. 9. Dorsal and ventral views in ethanol of the holotype (SMF 104018) of *Craugastor sagui* sp. nov. *Photos by G. Köhler.*

cies and 14,182–16,617 (15,175 ± 650) Hz high frequencies, with the highest acoustic intensity at 13,313–15,656 (14,147 ± 626) Hz.

The second call type could only be recorded in two of the four males. It was identified as a trilling, i.e., strongly pulsed "chirp" composed of mostly two, or less often one or three, notes. The notes are 0.266–0.692 (0.450 ± 0.116) seconds in length, and the total call duration is 0.745–1.551 (0.914 ± 0.206), depending on how many notes are contained in the call. Calls are repeated after 5.911–18.265 (10.196 ± 3.522) seconds. A single note contains 12–25 (19 ± 4) pulses that are emitted at a pulse rate of 36–46 (43 ± 2) pulses per second. The dominant frequency of 8,813–10,313 (9,654 ± 236) Hz is reached in the middle or towards the end of the note at pulse 6–21 (13 ± 5). Calls are frequency modulated with the lowest frequencies of 6,044–7,640 (6,617 ± 508) Hz in the first pulses gradually rising towards 10,298–12,002 (10,848 ± 466) Hz high frequencies in the last pulses of each note.

Distribution: *Craugastor blairi* is restricted to western Panama, on the Cordillera Central from Barú Volcano to the east over the La Fortuna depression into the Serranía de Tabasará. The specimens were collected around Barú Volcano, Cerro La Estrella, Cerro Guayaba, Guayabito, and La Fortuna (Fig. 1). The altitudinal range of the species is 1,280–2,134 m a.s.l. To our current knowledge, the continuous distribution of *C. blairi* is interrupted between La Fortuna and Guayabito. Both sites are separated by ~80 airline kilometers. Within this gap, another distinct clade was found that seems restricted to the surroundings of Cerro Saguí and Cerro Santiago, and is described below as *C. sagui*. More fieldwork will be necessary to clarify the distribution of *C. blairi* with respect to *C. sagui*, especially in the area between La Fortuna and Guayabito. It would also be interesting to explore the eastern distribution limits of *C. blairi*, as far east as Santa Fé, Veraguas.

Craugastor sagui sp. nov.

urn:lsid:zoobank.org:act:27F02325-D86E-4A4E-9311-B6FDD977C1E0

Common name: Sagui Dirt Frog
(Figs. 4C and 9)

Holotype: SMF 104018 (AH481), an adult male from Panama: Comarca Ngöbe-Buglé: Distrito de Nole Duima: southeastern slope of Cerro Saguí (8.563º, -81.821º; 1,991 m a.s.l.), collected by Andreas Hertz and Sebastian Lotzkat on 9 September 2010.

Paratypes: SMF 104014 (AH483), adult female; same date as the holotype. SMF 104017 (AH342), adult male and SMF 104015 (AH045), adult female from Panama: Comarca Ngöbe-Buglé: Distrito de Nole Duima: La Nevera, southern slopes of Cerro Santiago (8.500º, -81.772º; 1,700 m a.s.l.), collected by Andreas Hertz and Sebastian Lotzkat on 13 November 2009.

Assignment to group: Assigned to genus *Craugastor* based on our molecular data and on the following morphological characters: cranial crests absent, and Toe III longer than Toe V. Assigned to *C. podiciferus* species group based on the following features: narrow head (HW/SVL = 35.8–40.9%), length of Finger I equal to Finger II, dorsum smooth, toes unwebbed, and nuptial pads in adult males.

Diagnosis: The combination of the following characteristics can distinguish *Craugastor* (*Craugastor*) *sagui* (Figs. 4C, 5C, and 9) from the other described species in the genus: 1) skin on dorsum smooth; 2) skin on venter smooth; 3) vocal slits absent; 4) nuptial pads in adult males; 5) unwebbed toes; 6) heel without an enlarged calcar tubercle, although one to three small tubercles or granules may be present on heel; 7) accessory palmar, plantar, and supernumerary tubercles absent; and 8) subarticular tubercles flat.

Comparison: *Craugastor sagui* differs from all other Isthmian Central America craugastorids (except for those in *C. podiciferus* species group) by having unwebbed toes and a narrow head (HW 35.8–40.9% of SVL). *Craugastor sagui* differs from other members of the *C. podiciferus* species

group by having the following characteristics (condition for *C. sagui* in parentheses). *Craugastor bransfordii, C. gabbi, C. lauraster, C. persimilis, C. polyptychus, C. stejnegerianus,* and *C. underwoodi* differ from *C. sagui* by the following features: a) dorsum usually granular or warty (dorsum smooth to shagreen with scattered tubercles); b) subarticular tubercles projecting (subarticular tubercles flat); and c) venter coarsely areolate, including the midline (venter smooth, at least in midline). *Craugastor podiciferus* differs from *C. sagui* by the following features: a) prominent calcar tubercle on heel (Fig. 6) (calcar tubercle absent, although some specimens can have one to three small tubercles); b) vocal slits present in adult males (vocal slits absent); and c) absence of nuptial pads (nuptial pads present in adult males). *Craugastor aenigmaticus* differs from *C. sagui* by the following features: a) venter coloration of violet-brown with white blotches (venter yellow, orange, grayish, or olive in adults); b) white prominent folds between subarticular tubercles on hands of adults (absence of white folds between subarticular tubercles on hands of adults); and c) absence of nuptial pads (nuptial pads present in adult males). *Craugastor blairi* differs from *C. sagui* by the following features: a) venter coarsely areolate (venter smooth); b) absence of nuptial pads (nuptial pads present in adult males); c) vocal slits present in adult males (vocal slits absent in adult males); and d) projecting subarticular tubercles (flat subarticular tubercles). *Craugastor zunigai* differs from *C. sagui* by the following features: a) venter coarsely areolate (venter smooth); b) subarticular tubercles projecting (subarticular tubercles flat); c) absence of nuptial pads (nuptial pads present in adult males); and d) vocal slits in adult males (vocal slits absent).

Description of the holotype: Adult males have an SVL of 18.7 mm (Figs. 4–5). Head relatively narrow, HW = 35.8% of SVL; snout subovoid in the dorsal view, rounded in profile; snout relatively long (HL = 7.0 mm, 37.4% of SL), with nostrils directed laterally; in the ventral view, tip of the snout protruding slightly beyond the edge of lower lip. Internarial area convex; canthus rostralis rounded; intercanthal area flat; loreal region slightly concave; vocal slits absent. Eye moderate (EN/ED = 74.07%), not protruding beyond dorsal and ventral outline of head, directed laterally. Tympanic membrane distinct, covered in skin; tympanic annulus prominent, round, relatively large (77.77% of ED). Skin on all dorsal and lateral surfaces of head smooth to shagreen. Upper eyelid granular, without superciliar or supraocular tubercles but with a more or less discernible ridge on outer edge of eyelid continuous with supratympanic fold and downward behind the axilla. Postrictal tubercles fused to form a short ridge posteroventral to tympanum. Skin on dorsum and limbs smooth to shagreen. Skin of chest and throat smooth, venter smooth; ventral surfaces of thighs smooth; skin of groin nearly smooth. Flanks shagreen, especially along antero-ventral flank region. Discoidal fold complete.

Forelimb relatively short and slim; fingers moderately long and slim without lateral fringes. Discs absent; fingers with grooves; tips of fingers unexpanded, rounded in dorsal view; pads ovoid. Supernumerary tubercles absent; accessory palmar tubercles absent; subarticular tubercles rounded in basal outline, flat in form and globular in profile; thenar and palmar tubercles elongate and flat; thenar and palmar tubercles similar in size. Ulnar fold absent but several tubercles visible. Fingers not webbed.

Legs relatively long and slim; heel granular, lacking enlarged tubercles. Discs and grooves on all toes, palmate on Toe IV, spadate on others; pads triangular on Toe IV, ovoid in others. Supernumerary and plantar tubercles absent; subarticular tubercles rounded in basal outline, flat in form and obtuse in profile; inner metatarsal tubercle elongate, globular; outer metatarsal tubercle rounded, globular; outer much smaller than inner; outer edge tarsal with several tubercles, inner smooth. Cloacal opening directed posteriorly at mid-level of thighs.

Coloration of the holotype in life: Dorsal background color dark orangeish-brown with dark blotches, and a dark interorbital bar. Dorsal surfaces of legs and arms with dark bars, anterior surface of legs with white spots. Upper lip brown-orange with dark bars and scattered white spots. Flanks with a similar dorsal coloration but paler orange, with fine white-bluish mottling. Ventral surface of body and legs dark reddish-brown with bluish-white pigment forming blotches; ventral surface of throat similar to venter but with fewer pale spots. Soles of feet and hands dark brown with cream-colored tubercles.

Coloration of the holotype in ethanol: After eight years in ethanol (70%), the overall dark orangeish-brown on dorsum faded to pale cream-pinkish with dark brown blotches. The dark orangeish-brown on ventral surface of the body and legs faded to dark brown.

Measurements of the holotype (mm): SL 18.7; HL 7.0; HW 6.7; IOD 2.7; EW 1.4; EN 2.0; ED 2.7; TY 2.1. Measurements in related percentages: EW/IOD 51.85%; IOD/HW 40.3%; TY/ED 77.78%; EN/ED 74.07%; ED/HL 38.57%; HL/HW 104.48%; EN/HL 28.57%.

Etymology: The species was discovered on Cerro Saguí, in western Panama. The specific name is a noun in the apposition.

Natural history: *Craugastor sagui* inhabits the lower montane rainforest (Holdridge 1967; Bolaños et al. 2005), characterized by a very short dry season (one to three months), annual precipitation ranging from 3,600–7,500 mm and annual temperature from 12–17 ºC. Very little is known about the natural history of *C. sagui*; however, it is noteworthy that it was relatively abundant during the months of fieldwork. The specimens were exclusively
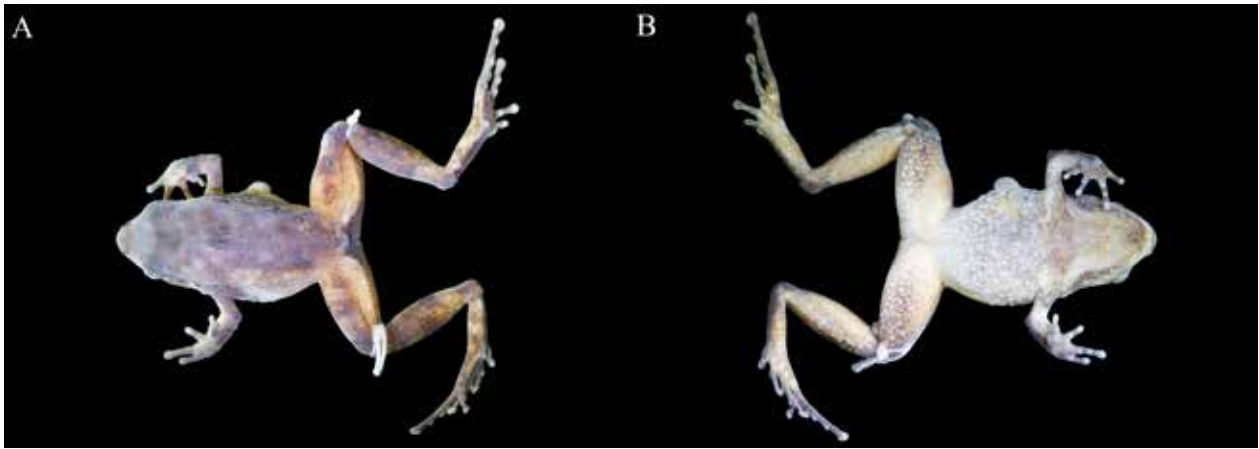
Fig. 10. Dorsal and ventral views in ethanol of the holotype (UCR 22703) of *Craugastor zunigai* sp. nov. *Photos by E. Arias.*

found in the leaf litter on the forest floor, and also typically observed jumping during the active search. We never recorded a vocalization that could be attributed to *C. sagui*; however, it is possible that it does vocalize.

Distribution: *Craugastor sagui* is restricted to western Panama, on the pacific slopes of Cordillera Central. The specimens were collected on the slopes of Cerro Saguí and Cerro Santiago (Fig. 1). The known altitudinal range is 1,700–1,991 m a.s.l.

Craugastor zunigai sp. nov.

urn:lsid:zoobank.org:act:70A61278-3E9F-454D-8F08-436F453F7116

Common name: Zúñiga's Dirt Frog
(Figs. 4D and 10)

Holotype: UCR 22703 (EAP 0618), adult male from Costa Rica: Provincia de Puntarenas: Cantón de Coto Brus: Distrito de Sabalito: Finca Las Alturas, Zona Protectora Las Tablas, (8.976º, -82.834; 1,732 m a.s.l.), collected by Erick Arias, Gerardo Chaves, and Omar Zúñiga on 15 September 2015.

Paratypes: UCR 23014 (EAP 0725), UCR 23016 (EAP 0727), UCR 23017 (EAP 0728), and UCR 23018 (EAP 0729), adult females from Costa Rica: Provincia de Puntarenas: Cantón de Buenos Aires: Distrito de Potrero Grande: Tres Colinas, Parque Internacional La Amistad, (9.123º, -83.066º; 1,846 m a.s.l.), collected by Erick Arias, Fanny Hernández, and Omar Zúñiga on 10 September 2016. UCR 23176 (EAP 0831), adult male and UCR 23177 (EAP 0832), adult female from Costa Rica: Provincia de Puntarenas: Cantón de Coto Brus: Distrito de Pittier: Santa María de Pittier, Parque Internacional La Amistad, (9.031º, -82.962; 1,920 m a.s.l.), collected by Erick Arias and Omar Zúñiga on 27 March 2018.

Assignment to group: Assigned to the genus *Craugastor* based on molecular data and on the following char-

acters: cranial crests absent and Toe III larger than Toe V. Assigned to the *C. podiciferus* species group based on our phylogeny and on the following characters: narrow head (HW/SVL = 35.8–41.9%), dorsum smooth to shagreen with scattered tubercles, unwebbed toes, vocal slits in adult males, and absence of nuptial pads.

Diagnosis: The combination of the following characteristics can be used to distinguish *Craugastor* (*Craugastor*) *zunigai* (Figs. 4D, 5D, and 10) from other described species in the genus: 1) skin on dorsum smooth to shagreen with scattered tubercles; 2) skin on venter coarsely areolate; 3) vocal slits present in adult males; 4) nuptial pads absent; 5) unwebbed toes; 6) heel without a projecting tubercle, although one to three low tubercles or granules can be present; 7) accessory palmar and plantar tubercles present, usually with no supernumerary tubercles under the digits; and 8) subarticular tubercles projecting.

Comparison: *Craugastor zunigai* differs from all other Isthmian Central America craugastorids (except for those in the *C. podiciferus* species group) by having unwebbed toes and a narrow head (HW 35.8–41.9% of SVL). *Craugastor zunigai* differs from other members of the *C. podiciferus* species group by having the following characteristics (condition for *C. zunigai* in parentheses). *Craugastor bransfordii*, *C. gabbi*, *C. lauraster*, *C. persimilis*, *C. polyptychus*, *C. stejnegerianus*, and *C. underwoodi* differ from *C. zunigai* by the following features: a) dorsum usually granular or warty (dorsum smooth to shagreen with scattered tubercles); b) subarticular tubercles obtuse to pointed, at least distal subarticular tubercles under Toe III and IV (subarticular tubercles projecting, globular); and c) altitudinal range, 0–1,600 m a.s.l. (altitudinal range is 1,500–2,100 m a.s.l. for *C. zunigai*). *Craugastor podiciferus* differs from *C. zunigai* by the following features: a) prominent calcar tubercle on heel (Fig. 6) (calcar tubercle absent, although some specimens can have one to three small tubercles in *C. zunigai*); b) venter smooth (venter coarsely areolate); c) subarticular tubercles flat (subarticular tubercles projecting); and d) absence of accessory

palmar tubercles (accessory palmar tubercles present). *Craugastor aenigmaticus* differs from *C. zunigai* by the following features: a) venter smooth (venter coarsely areolate); b) subarticular tubercles flat (projecting subarticular tubercles, globular); and c) prominent white folds between subarticular tubercles (absence of white folds between subarticular tubercles). *Craugastor blairi* differs from *C. zunigai* by the presence of an evident supraocular tubercle (eyelid smooth to granular but without an evident supraocular tubercle). *Craugastor sagui* differs from *C. zunigai* by the following features: a) nuptial pads in adult males (nuptial pads absent); b) absence of vocal slits (vocal slits in adult males); c) venter smooth (venter coarsely areolate); and d) flat subarticular tubercles (projecting subarticular tubercles, globular).

Description of the holotype: Adult male having an SVL of 19.8 mm (Fig. 10). Head relatively narrow, HW = 35.86% of SVL; snout subovoid in the dorsal view, rounded in profile; snout relatively long (HL = 7.6 mm, 38.38% of SL), with nostrils directed laterally; in ventral view, tip of snout protruding markedly beyond edge of lower lip. Internarial area convex (IN 2.2 mm); canthus rostralis rounded; intercanthal area flat (IC = 3.6 mm); loreal region slightly concave; vomerine teeth transverse, in two fascicles behind choanae. Tongue round in shape, lacking a distinct posterior notch; teeth absent; choanae moderately large, rounded on the posterior half but flat on anterior half, hemispherical; paired elongate vocal slits under posterolateral margins of tongue and a single internal subgular vocal sac. Eye moderate (EN/ED = 84.1%), protruding beyond dorsal outline of head in ventral view, directed laterally. Tympanic membrane prominent, translucent, and slightly pigmented; tympanic annulus prominent, round, large (134% of ED). Skin on dorsal and lateral surfaces of head smooth. Upper eyelid smooth, without superciliar or supraocular tubercles but with a more or less discernible ridge on outer edge of eyelid continuous with supratympanic fold and downward behind axilla. Elongate and projecting postrictal tubercle, postero-ventral to tympanum. Skin on dorsum and limbs smooth to shagreen with a pair of incomplete dorso-lateral folds, extending from axillary to inguinal level. Skin of chest and throat smooth, venter coarsely areolate with low granules; ventral surfaces of thighs areolate; skin of groin smooth. Flanks shagreen with scattered tubercles to areolate, especially along antero-ventral flank region. Discoidal fold complete.

Forelimb relatively short and robust; fingers moderately long and slim without lateral fringes. Discs absent; fingers III–IV with grooves; tips of fingers unexpanded, rounded in dorsal view; pads ovoid. Supernumerary tubercles absent; four small and rounded accessory palmar tubercles; subarticular tubercles rounded in basal outline, slightly projecting in form, and globular in profile; thenar tubercle elongate and palmar tubercle rounded, flat, similar in size. Ulnar fold absent but some tubercles visible. Fingers not webbed.

Legs relatively long and slim (TL = 55.3% SVL); heel smooth with two barely visible low granules, lacking a projecting tubercle. Discs and grooves on all toes, palmate on Toe IV, spadate in others; pads triangular on Toe IV, ovoid in others. Supernumerary tubercles absent; plantar tubercles small and rounded; subarticular tubercles ovoid in basal outline, projecting in form, and obtuse in profile; inner metatarsal tubercle elongate, projecting; outer metatarsal tubercle rounded, globular; outer metatarsal tubercle much smaller than inner; outer edge tarsal with an indistinct short ridge and low granules, inner smooth. Cloacal opening directed posteriorly at mid-level of thighs.

Coloration of the holotype in life: Dorsal background color dark brown suffused laterally with pale brown, head uniform dark brown. Dorsal surfaces of legs and arms with dark bars, posterior surface of legs cream suffused with red. Cloacal opening darker than posterior surface of legs. Flanks pale brown, groin suffused with red. Ventral surface of body and legs yellowish-cream with dark pigment; throat cream with dark pigment. Absence of bars on lips, mask, and blotches on dorsal surface.

Coloration of the holotype in ethanol: After three years in ethanol (70%), the overall dark brown on dorsum remained very similar to that in life. The yellowish-cream color on ventral surface of body and legs faded to pale brown.

Measurements of the holotype (mm): SL 25.9; HL 10.3; HW 10.3; IOD 3.7; EW 1.7; EN 2.5; ED 2.9; TY 1.9. Measurements in related percentages: EW/IOD 68.82%; IOD/HW 28.18%; TY/ED 54.12%; EN/ED 81.12%; ED/HL 27.24%; HL/HW 107%; EN/HL 24.34%.

Variation: The morphometric variation is summarized in Table 2. *Craugastor zunigai* shows a relatively high level of intraspecific polymorphism. In some specimens, a pair of lateral folds is present, and some specimens show a supraocular tubercle. In some specimens, two unfused postrictal tubercles are visible. Palmar and thenar tubercles are equal in size in some specimens, thenar slightly smaller than palmar in others. The palmar tubercle is heart-shaped in some specimens and ovoid in others. UCR 20389 with a pair of lateral folds from the axillar level to cloaca bordered by black pigment, the area between folds and from snout to cloaca a lighter, cream-yellowish color in ethanol. UCR 20428 with a pattern of dark brown on the dorsum with a lighter interorbital mark and area anterior to it more pale than dorsum. Mask absent in some specimens. Throat has a nearly uniform cream color in UCR 20401, heavily mottled in UCR 20421, and nearly uniform dark brown in UCR 20389. Venter ranges from nearly uniform cream color without dark pigment in UCR 20401 to heavily mottled in UCR 20389.

Etymology: The name *zunigai* is a patronym, honoring the field-guide Omar Zuñiga in recognition of his im-

portant aid during the fieldwork within the Cordillera de Talamanca. Omar Zuñiga took part in the fieldwork that yielded the specimens from Tres Colinas, Las Alturas, Las Tablas, and Santa María de Pittier.

Natural history: *Craugastor zunigai* inhabits the lower montane rainforest (Holdridge 1967; Bolaños et al. 2005), which is characterized by a very short dry season (one to three months), annual precipitation ranging from 3,600–7,500 mm and annual temperature from 12–17 ºC. Very little is known about the natural history of *C. zunigai*; however, is noteworthy that the species was relatively abundant during the months of fieldwork. The specimens were always found on the forest floor jumping among the leaf litter during the active search. We never recorded a vocalization that could be attributed to *C. zunigai*; however, it is possible that it vocalizes. At Las Alturas, *C. zunigai* occurs very near the known *C. gabbi* localities; however, we did not find them in sympatry since they are not known to overlap altitudinally. In Tres Colinas, the above-mentioned pattern is similar to *C. stejnegerianus*.

Distribution: *Craugastor zunigai* is restricted to southwestern Costa Rica, on the Pacific slopes of Cordillera de Talamanca. The specimens were collected from Santa María de Pittier, Tres Colinas, Las Alturas de Cotón, and road to Las Tablas (Fig. 1). The altitudinal range of the new species is 1,500–2,100 m a.s.l. All populations were found in primary forests, the populations from Santa María de Pittier and Tres Colinas are in La Amistad International Park and the population from Las Alturas de Cotón and road to Las Tablas is in Zona Protectora Las Tablas. The known populations of *C. zunigai* are fragmented over ~43 km. This species was not found on the Pacific slope of Cerro Utyum and Cerro Dúrika (to the west). Additional fieldwork is necessary to clarify the distribution of *C. zunigai*. The locality "road to Las Tablas" is very close to the Costa Rica-Panama border, so *C. zunigai* is likely also present in Panama.

Discussion

With the recognition of *Craugastor blairi*, *C. zunigai*, and *C. sagui*, the *C. podiciferus* species group is now formed by 12 species, all of which are collectively distributed in Costa Rica and western Panama (Savage 2002; AmphibiaWeb 2019). The species in this group have been difficult to delineate historically because of morphological variability between and within populations. However, using molecular sequence data, we found well-supported clades and large genetic distances between several of these populations (Table 1). Although the sole use of genetic distances for species delimitation is not recommended, we believe that the combination of large genetic distances and close geographic proximity between phylogenetically related species provide an important measure to identify cryptic species with a conservative morphology. The

genetic distances presented herein between members of the *C. podiciferus* species group are above the thresholds of 3% in the 16S rRNA and 10% in the COI mitochondrial genes suggested by Fouquet et al. (2007) and Vences et al. (2005). For amphibians, the 16S rRNA gene fragment has been suggested as a DNA barcode marker for amphibian diversity inventories (Vences et al. 2005) to complement the standard COI-5' marker used for animals in general (Smith et al. 2008). Although the species recognized herein are not cryptic *sensu stricto* (Pérez-Ponce de León and Nadler 2010), they are in taxonomic practice. As suggested by Pérez-Ponce de León and Nadler (2010), the use of molecular data within morphologically conserved groups allow delineation of taxa that otherwise would be considered a single taxon. The use of phylogenies based on molecular data has been essential to solve taxonomic problems in this group.

Taylor (1952) synonymized *C. blairi* under *C. podiciferus* without further discussion, nor was it discussed in the comprehensive seminal work of Savage (2002). The results presented here support the validity of *Craugastor blairi* (previously shown as *Craugastor* sp. B), and it is not a sister to *C. podiciferus* (Crawford and Smith 2005; Streicher et al. 2009). However, *C. blairi* and *C. podiciferus* are morphologically similar and show a high level of polymorphism, and thus the taxonomic decision of Taylor (1952) is not surprising given the technical limitations at the time of that publication. The distinctiveness of *C. blairi* is provided by its phylogenetic position. The same rules apply to *C. sagui*, the phylogenetic position of which provides significant evidence for its distinct evolutionary trajectory as a species beyond the observation that it resembles *C. podiciferus* and *C. blairi* morphologically. The morphological similarity among nonsister species can be explained either as plesiomorphy or convergence (Castroviejo-Fisher et al. 2017). All species analyzed herein have inhabiting the ground leaf litter in highland forest habitats (lower montane zonation) in common, which has likely played a role in the maintenance of this morphology.

A more complicated situation lies in the recognition of *Craugastor zunigai*, given its morphological resemblance to its sister species *C. blairi*. Although the morphological divergence between *C. blairi* and *C. zunigai* is weak, we believe that both are valid species supported by phylogenetic distinctiveness based on mitochondrial analysis. These species are geographically very close (~10 airline km); thus, it seems unlikely that the large genetic distances (2.9% in 16S and 14.3% in COI) are explained by isolation due to distance. Our taxonomic decision to recognize these two as separate species will be strengthened with additional evidence, especially the comparison of mating calls of *C. zunigai* with the call of *C. blairi*. Future sampling efforts must also be conducted on the highlands of extreme western Panama and adjacent Costa Rica between Barú Volcano and Cerro Pando to explore the species distribution limits and possible contact zones of *C. aenigmaticus*, *C. blairi*, *C. zunigai*, and *C. podiciferus*.

The presence of several additional species within *Craugastor podiciferus* is uncertain. Streicher et al. (2009) suggested that the current concept of *C. podiciferus* could be masking six distinct species that are geographically structured, but with two instances of sympatry. However, the findings of Streicher et al. (2009) and our own results agree with *C. podiciferus* being a monophyletic entity; thus, there is currently no need to split *C. podiciferus* into several species until such division is supported by detailed morphological or other evidence. The performance of an extensive, integrative analysis of the *C. podiciferus* species complex is strongly suggested to reevaluate the taxonomic status of its different genetic clades. For now, the recognition of *C. podiciferus sensu lato* as a single species results in a highly variable morphological group, given that even those few useful characters (i.e., skin on venter, subarticular tubercles, vocal slits, and nuptial pads) are highly variable between populations. The clades shown herein should be reevaluated using other types of data that can provide evidence of lineage divergence, such as geographical distribution, ecological niche, mating calls, or detailed morphometric data.

The members of the *Craugastor podiciferus* species group have qualities such as high abundance, broad distribution (collectively), and high genetic diversity that makes them suitable for use in various studies in ecology and evolution. However, these species have been poorly studied, likely because of the difficulty in clearly identifying the species. Therefore, it is necessary to clarify the taxonomy of this species group. Upon revisiting study objectives, the following conclusions are offered: 1) *Craugastor podiciferus sensu stricto* is restricted to those populations at Cordillera Volcánica Central, Costa Rica and Cordillera de Talamanca (Caribbean slopes) in Costa Rica and western Panama; 2) seven well-supported clades are found within the current concept of *C. podiciferus*, and these seven clades require extensive taxonomic revision; and 3) the populations from southwestern Costa Rica and western Panama are grouped in three clades, one potentially referring to an existing name, *C. blairi*, which is resurrected herein, and two representing new species that are herein named *C. sagui* from western Panama and *C. zunigai* from southwestern Costa Rica.

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Erick Arias is a Costa Rican herpetologist; who earned a bachelor's degree in biology at Universidad de Costa Rica in 2013. Erick then joined Parra's Lab at Universidad Nacional Autónoma de México (UNAM) where he received a doctorate in systematics in 2019 focusing on molecular systematics, taxonomy, and biogeography of the *Craugastor podiciferus* species group. Erick's current research focuses on the systematics, taxonomy, and biogeography of the amphibians and reptiles of Costa Rica, especially of direct-developing frogs and salamanders.

Andreas Hertz earned a diploma degree in biology at Goethe-University, in cooperation with the Senckenberg Research Institute in Frankfurt am Main, Germany, where he studied reptiles and amphibians from Venezuela. In a subsequent doctorate, Andreas worked on the systematics, taxonomy, and conservation of Panamanian amphibians. Andreas then joined University of Massachusetts Boston (USA) as a DFG postdoctoral fellow to work on amphibian chytridiomycosis. His current research is on recovering amphibian populations in upland areas of Panama that have survived mass extinction through chytridiomycosis. This research focuses on the mechanisms of host adaption in recovering frog populations which allow coexistence with the pathogen.

Gabriela Parra Olea earned a Ph.D. at University of California, Berkeley working on the molecular systematics of neotropical salamanders. In 2001, Gabriela obtained a full-time research position at the Instituto de Biología, UNAM in Mexico City. Her current research focuses on molecular systematics, taxonomy, and conservation of neotropical amphibians, especially salamanders. A second line of Gabriela's research is based on studying the impact of chytridiomycosis on the conservation of Mexican amphibians.

Appendix I. Institutional voucher numbers, locality information, and GenBank accession numbers for the specimens used in the molecular phylogenetic analyses. Museum collection acronyms follow Frost (2019) with the addition of EAP to refer to Erick Arias field numbers and CRARC to refer to the Costa Rica Amphibian Research Center private collection. CR = Costa Rica, HN = Honduras, NI = Nicaragua, PA = Panama.

| Species | Institutional vouchers | Collection locality | Elevation (m) | Geographic coordinates | | GenBank Number | |
				Lat	Lon	16S	COI
C. aenigmaticus	SMF: 104020	Changuinola, Bocas del Toro, PA	2388	8.9139	-82.7088	MK211615	MK211577
C. aenigmaticus	UCR: 21951	Telire, Talamanca, CR	2700	9.3488	-83.1750	MK211616	MK211578
C. aenigmaticus	UCR: 22737	Buenos Aires, Puntarenas, CR	2660	9.3224	-83.2028	MK211617	MK211579
C. blairi	FMNH: 257689	Gualaca, Chiriquí, PA	1000	8.7500	-82.2170	EF562353	——
C. blairi	SMF: 102024	Gualaca, Chiriquí, PA	1730	8.6775	-82.1980	MK211627	MK211583
C. blairi	SMF: 104023	Gualaca, Chiriquí, PA	1280	8.6781	-82.2101	MK211628	MK211584
C. blairi	SMF: 104027	Bugaba, Chiriquí, CR	2134	8.8494	-82.5154	MK211629	MK211585
C. blairi	SMF: 104033	Gualaca, Chiriquí, PA	1456	8.6740	-82.2154	MK279367	——
C. blairi	SMF: 104034	Ñurum, Ngöbe Buglé, PA	1541	8.5512	-81.4833	MK279368	——
C. blairi	SMF: 104037	Boquete, Chiriquí, PA	1952	8.7757	-82.3901	MK279369	——
C. blairi	USNM: 563039	Boquete, Chiriquí, PA	1663	8.3136	-82.4000	EF562356	——
C. bransfordii	UCR: 22269	Alajuela, Alajuela, CR	466	10.3121	-84.1778	KT950295	MK211571
C. bransfordii	UCR: 22643	Siquírres, Limón, CR	537	10.0595	-83.5452	MK211610	MK211572
C. gabbi	UCR: 21863	Coto Brus, Puntarenas, CR	1200	8.7889	-82.9583	KT950271	MK211567
C. gabbi	UCR: 21864	Coto Brus, Puntarenas, CR	1200	8.7889	-82.9583	KT950272	MK211568
C. lauraster	SMF: 79759	Matagalpa, Matagalpa, NI	1300	12.9993	-85.9092	MK211608	MK211565
C. lauraster	USNM: 559393	Puerto Lempira, Gracias a Dios, HN	190	14.9275	-84.5339	KU323364	MK211566
C. persimilis	UCR: 22211	Paraíso, Cartago, CR	1050	9.7841	-83.7517	KT950293	MK211570
C. persimilis	UCR: 22671	Talamanca. Limón, CR	121	9.5773	-82.9343	MK211609	MK211569
C. podiciferus sensu strictii	CRARC: 0012	Turrialba, Cartago, CR	2250	10.0192	-83.7132	MK211633	MK211589

Appendix I (continued). Institutional voucher numbers, locality information, and GenBank accession numbers for the specimens used in the molecular phylogenetic analyses. Museum collection acronyms follow Frost (2019) with the addition of EAP to refer to Erick Arias field numbers and CRARC to refer to the Costa Rica Amphibian Research Center private collection. CR = Costa Rica, HN = Honduras, NI = Nicaragua, PA = Panama.

Species	Institutional vouchers	Collection locality	Elevation (m)	Geographic coordinates		GenBank Number	
				Lat	Lon	16S	COI
C. podiciferus sensu stricto	SMF: 104005	Changuinola, Bocas del Toro, PA	1766	8.9908	-82.6716	MK211641	MK211597
C. podiciferus sensu stricto	UCR: 19853	Telire, Talamanca, CR	1817	9.3580	-83.2294	MK211639	MK211595
C. podiciferus sensu stricto	UCR: 19856	Telire, Talamanca, CR	1817	9.3580	-83.2294	MK211637	MK211593
C. podiciferus sensu stricto	UCR: 19860	Telire, Talamanca, CR	2108	9.3645	-83.2164	MK211636	MK211592
C. podiciferus sensu stricto	UCR: 19862	Telire, Talamanca, CR	2108	9.3645	-83.2164	MK211638	MK211594
C. podiciferus sensu stricto	UCR: 20992	Alfaro Ruiz, Alajuela, CR	2143	10.2272	-84.3482	MK211632	MK211588
C. podiciferus sensu stricto	UCR: 22146	Vázquez de Coronado, San José, CR	1700	10.0263	-83.9448	MK211635	MK211591
C. podiciferus sensu stricto	UCR: 22201	Dota, San José, CR	2395	9.7126	-83.9488	MK211634	MK211590
C. podiciferus sensu stricto	UCR: 23175	Talamanca, Limón, CR	1860	9.3659	-83.0417	MK211640	MK211596
C. podiciferus "Chumacera"	UCR: 22120	Buenos Aires, Puntarenas, CR	1821	9.3218	-83.4546	MK211642	——
C. podiciferus "Chumacera"	UCR: 22690	Pérez Zeledón, San José, CR	1793	9.3267	-83.4706	MK211631	MK211587
C. podiciferus "Fila Costeña"	EAP: 0509	Golfito, Puntarenas, CR	1546	8.7878	-83.0306	——	MK211605
C. podiciferus "Fila Costeña"	FMNH: 257651	Coto Brus, Puntarenas, CR	1350	8.7833	-82.9833	EF562367	——
C. podiciferus "Fila Costeña"	UCR: 16585	Dota, San José, CR	1400	9.5353	-83.8580	MK211647	——
C. podiciferus "Fila Costeña"	UCR: 22091	Pérez Zeledón, San José, CR	1488	9.4410	-83.6830	MK211646	MK211604
C. podiciferus "Monte Verde"	FMNH: 257669	Monte Verde, Puntarenas, CR	1500	10.2773	-84.5891	EF562372	MK211598
C. podiciferus "Monte Verde"	FMNH: 257673	Monte Verde, Puntarenas, CR	1500	10.2773	-84.5891	EF562343	MK211603
C. podiciferus "Monte Verde"	UCR: 16361	Alfaro Ruiz, Alajuela, CR	1930	10.2176	-84.3671	EF562371	——

Appendix I (continued). Institutional voucher numbers, locality information, and GenBank accession numbers for the specimens used in the molecular phylogenetic analyses. Museum collection acronyms follow Frost (2019) with the addition of EAP to refer to Erick Arias field numbers and CRARC to refer to the Costa Rica Amphibian Research Center private collection. CR = Costa Rica, HN = Honduras, NI = Nicaragua, PA = Panama.

Species	Institutional vouchers	Collection locality	Elevation (m)	Lat	Lon	16S	COI
C. podiciferus "Monte Verde"	UCR: 22675	Puntarenas, Puntarenas, CR	1726	10.3202	-84.7987	——	MK211606
C. podiciferus "Pico Blanco"	UCR: 22226	Escazú, San José, CR	2242	9.8646	-84.1429	MK211644	MK211601
C. podiciferus "Pico Blanco"	UCR: 22228	Escazú, San José, CR	2242	9.8646	-84.1429	MK211643	MK211600
C. podiciferus "San Gerardo"	CRARC: 0247	Tilarán, Guanacaste, CR	1470	10.3600	-84.8000	MK211645	——
C. podiciferus "San Gerardo"	FMNH: 257671	Monte Verde, Puntarenas, CR	1500	10.2773	-84.5891	EF562374	MK211599
C. podiciferus "San Gerardo"	UCR: 16353	Sarapiquí, Heredia, CR	1500	10.2022	-84.1625	EF562349	MK211602
C. podiciferus "Siola"	UCR: 23169	Talamanca, Limón, CR	1300	9.3987	-83.0200	MK211630	MK211586
C. polyptychus	UCR: 20050	Talamanca, Limón, CR	900	9.6178	-83.2681	MK211614	MK211576
C. polyptychus	UCR: 22668	Talamanca, Limón, CR	198	9.6064	-82.9115	MK211613	MK211575
C. sagui sp. nov.	SMF: 104014	Nole Duima, Ngöbe Buglé, PA	1762	8.5571	-81.8245	MK211623	——
C. sagui sp. nov.	SMF: 104015	Nole Duima, Ngöbe Buglé, PA	1700	8.4997	-81.7724	MK211624	MK211580
C. sagui sp. nov.	SMF: 104017	Nole Duima, Ngöbe Buglé, PA	1815	8.4955	-81.7672	MK279370	——
C. stejnegerianus	EAP: 0514	Osa, Puntarenas, CR	45	8.9655	-83.4411	MK211607	MK211563
C. stejnegerianus	UCR: 20352	Buenos Aires, Puntarenas, CR	900	9.0863	-83.1105	KT950284	MK211564
C. underwoodi	UCR: 22619	Paraíso, Cartago, CR	1412	9.7518	-83.7792	MK211611	MK211573
C. underwoodi	UCR: 22625	Vázquez de Coronado, San José, CR	1708	10.0254	-83.9456	MK211612	MK211574
C. zunigai sp. nov.	UCR: 20389	Buenos Aires, Puntarenas, CR	1500	9.1112	-83.1006	MK211625	MK211581
C. zunigai sp. nov.	UCR: 20428	Buenos Aires, Puntarenas, CR	1800	9.1381	-83.0700	MK279371	——

Appendix I (continued). Institutional voucher numbers, locality information, and GenBank accession numbers for the specimens used in the molecular phylogenetic analyses. Museum collection acronyms follow Frost (2019) with the addition of EAP to refer to Erick Arias field numbers and CRARC to refer to the Costa Rica Amphibian Research Center private collection. CR = Costa Rica, HN = Honduras, NI = Nicaragua, PA = Panama.

Species	Institutional vouchers	Collection locality	Elevation (m)	Geographic coordinates		GenBank Number	
				Lat	Lon	16S	COI
C. zunigai sp. nov.	UCR: 22703	Coto Brus, Puntarenas, CR	1732	8.9759	-82.8344	MK279372	——
C. zunigai sp. nov.	UCR: 22709	Coto Brus, Puntarenas, CR	1980	8.9751	-82.8243	MK211626	MK211582

Appendix II. Specimens used in the morphometric analysis. Museum collection acronyms follow Frost (2019) with the addition of AH to refer to Andreas Hertz field numbers and HAU to refer to Frank Hauenschild field numbers.

Craugastor blairi: PANAMA: *Chiriquí*: Bajo Mono, Los Naranjos, Boquete (AH: 0289–0290; SMF: 104028); Cerro La Estrella, Jaramillo, Boquete (SMF: 104037); Cerro Guayaba, Caldera, Boquete (HAU: 023; SMF: 104035); Volcán Barú, Los Naranjos, Boquete (AH: 0240–1; SMF: 104026–7); Fortuna, Hornito, Gualaca (AH: 0079–0080, 0372, 00376; HAU: 008, 010; SMF: 102024, 104023, 104025, 104029–33). *Ngöbe Buglé*: Guayabito, Ñurüm (SMF: 104034).

Craugastor sagui sp. nov.: PANAMA: *Ngöbe Buglé*: Cerro Saguí, Jädeberi, Nole Duima (SMF: 104014, 104018–9); La Nevera, Nole Duima (AH: 0168; SMF: 104015–7).

Craugastor zunigai sp. nov.: COSTA RICA: *Puntarenas*: Las Alturas, Pittier, Coto Brus (UCR: 22703–4, 22709–10); Tres Colinas, Potrero Grande, Buenos Aires (UCR: 20257–8, 20389, 20395, 20401, 20411, 20419, 20421, 20423, 20428, 23014, 23016–8); road to Las Tablas, Sabalito, Coto Brus (UCR: 23170).