



# The reduced limbed lizards of the genus *Bachia* (Reptilia, Squamata, Gymnophthalmidae); biogeography, cryptic diversity, and morphological convergence in the eastern Caribbean

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## Abstract

The phylogenetic and systematic relationships of the reduced limbed lizards of the genus *Bachia* are poorly understood. Here, we investigate the eastern Caribbean *Bachia* assigned to the *B. heteropa* and *B. flavescens* groups, whose members are characterized by a band of hexagonal or quadrangular scales on the dorsum, respectively. The polytypic *Bachia heteropa* is redefined, and the previous subspecies in the Grenadines (*Bachia heteropa alleni*) and Trinidad (*B. h. trinitatis*) are demonstrated to be species-level lineages. One new species of hex-scaled *Bachia* was formerly assigned intergrade status between *B. heteropa* and *Bachia trinitatis*. Here, it is described as a new species from Caripito, Venezuela. *Bachia h. heteropa*, *B. h. lineata*, and *B. h. marcelae* are elevated to species status. The Tobago species formerly considered a member of the *Bachia flavescens* species group is described as a new species. In this paper, we increase the number of species in the genus *Bachia* from 25 to 31 with the description of two new species and the elevation of four previously described species from the synonymy of *Bachia heteropa*. This work will greatly improve the understanding of the systematics and evolution of *Bachia* in the eastern Caribbean.

**Keywords** Cryptozoic · Dispersal · Fossorial · Grenada · Trinidad · Venezuela

## Introduction

Modern lizards have successfully radiated into many habitats with fossorial and cryptozoic species found throughout numerous clades (Brandley et al. 2008). However, in the Neotropics, one family, the Gymnophthalmidae, has evolved

some exceptional adaptations to a life in the leaf litter and soil. A frequently observed morphological trend in gymnophthalmids is reduced limbs, which may be expressed as simply shortened or lost digits, or with more extreme complete limb loss (Greer 1991). Selection for different body sizes, tail lengths, scale shapes, and altered coloration may

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occur without changes to the animal's body plan. Thus, convergent evolution may drive these small litter-dwelling lizards from different lineages into looking very similar to each other (Lee 1998). This phenomenon has been reported in many fossorial squamates, such as in the South African skink genera *Acontia* (Daniels et al. 2009) and *Scelotes* (Heideman et al. 2011), the Philippine skink genus *Brachymeles* (Siler et al. 2011), the Mediterranean amphisbaenian genera *Blanus* (Albert and Fernandez 2009; Sampaio et al. 2015), *Trogonophis* (Salvi et al. 2018), in the California legless lizard (family Anniellidae) *Anniella pulchra* (Parham and Papenfuss 2009), and in the dipsadid snake genus *Atractus* (Prudente and Passos 2010).

Islands can serve as model systems for biogeographic, evolutionary, and ecological studies and the Lesser Antilles are not an exception, they have geological histories that require complicated biogeographic scenarios to explain their fauna (Tucker et al. 2017). For example, Trinidad is a detached fragment of South America whereas the more northern islands are oceanic in origin. The topographic admixture provides an opportunity for testing hypotheses for contrasting speciation events via vicariance and dispersal (Murphy 1996; Whittaker and Fernández-Palacios 2007).

The gymnophthalmid genus *Bachia* currently contains 25 species (Uetz et al. 2018) of fossorial and cryptozoic lizards, with elongated bodies and tails, significantly reduced or absent limbs, degenerated eyes, no external ear opening, and a lower eyelid with a transparent, unsegmented scale. This combination of traits separates *Bachia* from all other gymnophthalmids. Eleven of these species have been described since Dixon (1973) last revised the genus, an arrangement containing two species groups in the eastern Caribbean. The *Bachia heteropa* group was reported from Grenada and the Grenadines, Trinidad, Tobago, and Little Tobago, as well as western Venezuela, Colombia, and Central America. The *Bachia flavescens* group was considered present in Venezuela, Guyana, Brazil, and Colombia and known from the island of Tobago on the basis of four specimens (Hardy 1982; Murphy 1997; this work). The systematics of both the *B. heteropa* and *B. flavescens* groups are poorly understood and associated with complex nomenclatural issues.

### A short history of the nomenclature surrounding the *Bachia flavescens* group

*Chalcides flavescens* Bonnaterre 1789 is the type species for the genus *Bachia*. Unfortunately, Bonnaterre's original description of *Chalcides flavescens* was based upon Lacépède's (1789) illustration of "Le Chalcide" (Supplemental 1) and a now lost specimen that was presumably in the Museum National d'Historie Naturelle, Paris. The quality of the drawing makes it all but useless for

identification, and no type locality was provided in the original description.

Avila-Pires (1995) defined *Bachia flavescens* as having: 26–34 scales around mid-body; a cloacal plate with 3–5 elongated scales, the middle scale may or may not be horizontally divided; 46–52 transverse rows of scales from nape to the base of the tail; 33–39 transverse rows of ventrals, one or two supraoculars, two or three supraciliaries; three digits on the front limbs and one, two, or three digits on the hind legs; the toes, may or may not have claws. She considered six described species synonyms of *B. flavescens* (Supplemental 2).

### A short history of the nomenclature surrounding the *Bachia heteropa* group

*Chalcides heteropus* Lichtenstein and von Martens (1856) was moved to *Bachia* by Garman (1892), then to *Scolecosaur* by Barbour (1914) and returned to *Bachia* by Ruthven (1925). Members of the *Bachia heteropa* group are distributed from southern Costa Rica to Panama and southward into northern Colombia (*B. pallidiceps*); eastward to Venezuela, and Guyana, and the Lesser Antillean islands of Grenada and the Grenadines, Trinidad and Tobago, and their satellites; as well as the Isla de Margarita (*B. heteropa*). *Bachia guianensis* (Hoogmoed and Dixon 1977) is part of this species group and inhabits the Venezuelan portion of the Guiana Shield. Burt and Burt (1933) and Dixon (1973) placed six names in the synonymy of *Bachia heteropa* (Supplemental 3), and Dixon (1973) recognized five subspecies of *B. heteropa*. No taxonomic changes were made to the *B. heteropa* group until Ribeiro-Júnior et al. (2016) described *Bachia remota* from the Parque Nacional Montanhas do Tumucumaque, Laranjal do Jari municipality, State of Amapá, Brazil. The location is on the Brazilian border with French Guiana and Suriname and about 800 km southeast of the nearest record for *B. heteropa*.

The *Bachia heteropa* group was defined by Hoogmoed and Dixon (1977) as *Bachia* that shared "...four clawed toes on each of limbs, presence of prefrontals, number of supraoculars and supraciliaries, the presence of hexagonal, imbricate dorsals." We should note that this definition is more than a bit confusing because according to Dixon (1973), *B. h. heteropa* has three toes on its rear legs, while *B. h. lineata* and *B. h. marcelae* have two toes on their hind legs. Leaving the only members of the species group with four toes on their rear limbs as *B. h. alleni* and *B. h. trinitatis*, *B. guianensis*, and the recently described *B. remota*. Furthermore, prefrontal scales are absent in *B. h. heteropa*, *B. h. lineata*, and *B. h. marcelae*. Rivas et al. (2012) stated that *Bachia heteropa* is a polytypic species composed of five subspecies, four of which are present in Venezuela (Fig. 1).

Dixon (1973) considered *Bachia* with hexagonal scales in northern Venezuela, Trinidad, Tobago, Grenada and the Grenadines to be *B. heteropa*, despite significant



**Fig. 1** The type localities for the *Bachia* taxa in the eastern Caribbean

morphological variation. Variation included 5–12 longitudinal rows of hexagonal, imbricate, smooth scales on the dorsum; 16–22 longitudinal rows of quadrangular, juxtaposed, lateral, and ventral scales; 24–31 scale rows around mid-body; and 24–36 transverse ventral rows. The number of digits on the hind feet of *B. heteropa* ranges from 2 to 4. Additionally, the number of digits, the presence or absence of prefrontal scales, and the number of supraoculars are all geographically concordant.

Molecular evidence (Kohlsdorf and Wagner 2006; Kohlsdorf et al. 2010) that *Bachia heteropa* (sensu Dixon 1973) is paraphyletic led us to examine the morphology of eastern Caribbean *Bachia*. Here, we compare the morphological and molecular data for eastern Caribbean *Bachia* and adjust the nomenclature following the ICZN rules. We also investigated the identity of *Bachia* in northeastern Venezuela identified by Dixon (1973) to be a *B. h. heteropa* x *B. h. trinitatis* intergrade.

We need to acknowledge the problems associated with the name *Brachypus cuvieri* Fitzinger 1826. Both Barbour (1933) and Brongersma (1946) consider this a valid name. However, it is without a type locality, and the holotype is lost. The original description does not provide the detail needed for diagnosing the taxon, and while Duméril and Bibron (1839) attempted to give a more accurate description, it too proved to be in error. Barbour (1933) demonstrated that the redescription was based on three specimens, each a different species. Both Burt and Burt (1931) and Thomas (1965) suspected that *Bachia alleni* from Grenada should be a junior synonym of

*Bachia cuvieri*. Thomas refrained from this action pending further evidence. *Brachypus cuvieri* Fitzinger is a *nomen dubium* (a name of unknown or doubtful application). The name could be applied to any *Bachia* with four toes on the hind limbs.

### Changing nomenclature with molecular evidence

The morphological similarity of cryptic species from different lineages has frequently resulted in parphyly. The current example is the reduced limbed lizards of the genus *Bachia*. When *Bachia* were tested using molecular data (Kohlsdorf and Wagner 2006; Galis et al. 2010; Kohlsdorf et al. 2010), parphyly was suggested, although no consensus was reached. This has been termed “the burden of heritage in taxonomy” by Pyron and Burbrink (2009).

Recently, Goicoechea et al. (2016) used nucleotide sequences and recognized three tribes within the Cercosaurinae: Bachiini, Cercosaurini, and Ecleopodini. Their molecular evidence rejected Dixon’s (1973) four species groups within the Bachiini because they were non-monophyletic. Thus, their results support the existence of several species of *Bachia* that are currently considered parts of polytypic species. Molecular evidence suggesting that *Bachia heteropa* (sensu Dixon 1973) is paraphyletic comes from multiple sources (Kohlsdorf and Wagner 2006; Kohlsdorf et al. 2010; Goicoechea et al. 2016).

This paper primarily focuses on the polytypic *Bachia heteropa* and *Bachia flavescens* in the eastern Caribbean. As

currently understood, the *B. heteropa* group includes species with a dorsal band of hexagonal scales and an interparietal scale (John et al. 2012); the *B. flavescens* group has a band of quadrangular scales on the dorsum and may or may not have an interparietal scale (Avila-Pires 1995). The *superterranean* leaf-litter and subterranean habitats used by *Bachia* suggested to us that it should have low dispersal abilities and undescribed cryptic diversity.

## Materials and methods

### DNA sequencing and analyses

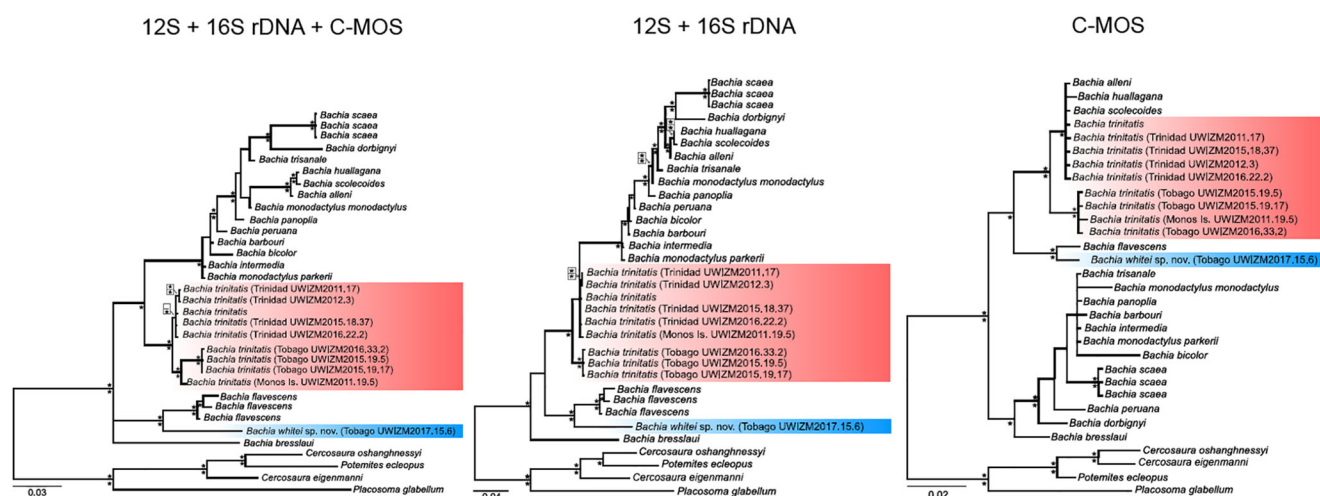
Three mitochondrial gene fragments, 12S rDNA (primers 12Sa and 12Sb; Kocher et al. 1989), 16S rDNA (primers 16SL and 16SH; Palumbi 1996), COI (primers dgLCO1490 and dgLCO2198; Meyer 2003), and a nuclear gene fragment, c-mos (primers G73 and G74; Saint et al. 1998) were amplified. The length of the sequences were 12S rDNA, 323 base pairs (bp); 16S rDNA, 446 bp; COI, 612 bp; and c-mos, 348 bp. We sequenced nine *Bachia* (Genbank accession numbers MG712694-MG712727) from Trinidad ( $n=4$ ), Tobago ( $n=4$ ), and Monos Island ( $n=1$ ). All markers were amplified for these nine individuals, except the COI that was sequenced in seven individuals, because two failed to amplify. Templates were sequenced on both strands, and the complementary reads were used to resolve rare, ambiguous base-calls in Sequencher v.4.9. Sequences were aligned in Seaview v.4.2.11 (Gouy 2010) under ClustalW2 (Larkin et al. 2007) default settings.

We downloaded from GenBank all available *Bachia* for the same molecular markers (see Supplement 4). To assess the phylogenetic relationships between the Lesser Antilles *Bachia*, we included in the analyses *B. heteropa alleni* (from

Grand Etang, Grenada). We used the outgroups from Teixeira et al. (2013) (Fig. 2).

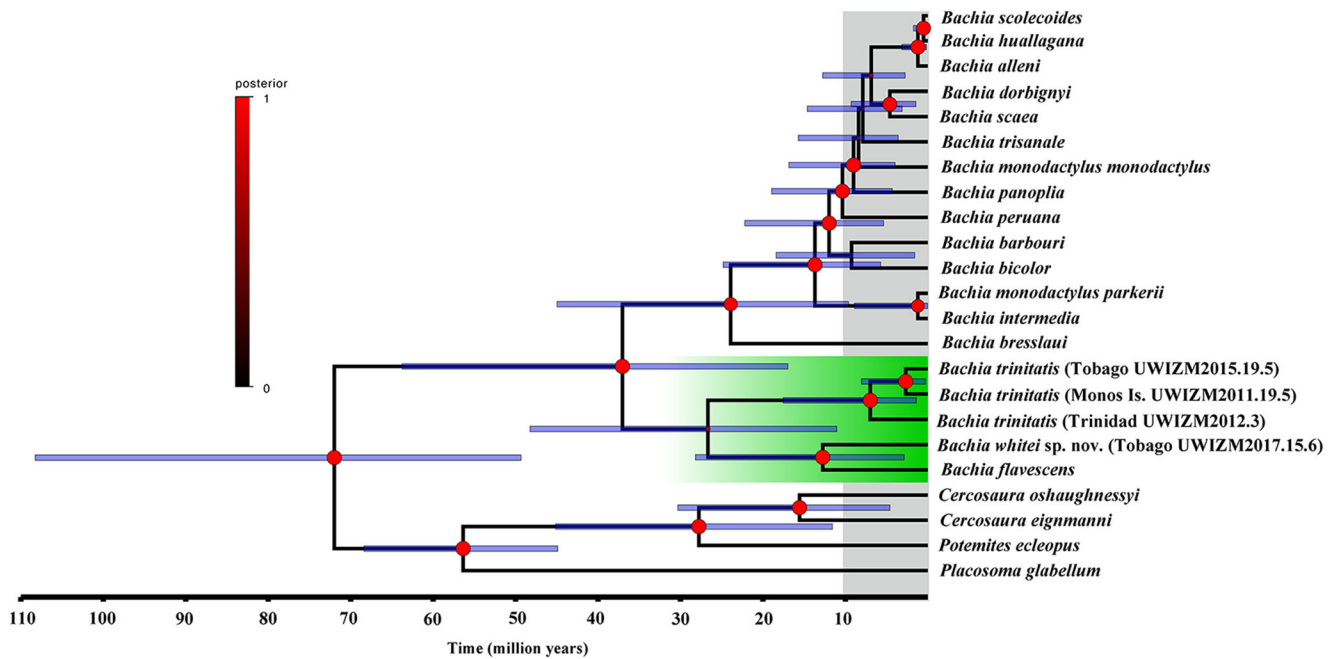
Phylogenetic analyses were conducted using the mitochondrial (12S + 16S rDNA) and nuclear (c-mos) alignments as well as for the concatenated mitochondrial and nuclear (12S + 16S rDNA + c-mos) alignment (with a length of 1733 bp) using a partitioned model of substitution by gene fragment. The most appropriate substitution model for each gene partition was determined by the Bayesian information criterion (BIC) in PartitionFinder v.2 (Lanfear et al. 2012). The best-fitting models for the ribosomal and c-mos fragments were as follows: 12S rDNA + 16S rDNA (GTR + G + I), c-mos (TrNef + G), and COI (by three codon partition scheme in MrBayes v.3.0b4 (Ronquist and Huelsenbeck 2003), 1:HKY, 2:JC, 3:F81, RaxML GTR + G for all partitions). Phylogenetic relationships between taxa were inferred using the Bayesian inference (BI) optimality criterion under the best fitting substitution model for each gene partition. MrBayes was used with default priors and Markov chain settings and with random starting trees. Each run consisted of four chains of 40 million generations, sampled every 1000 generations. Phylogenetic relationships (Fig. 2) were also estimated using a maximum likelihood (ML) approach, as implemented in the software RAXML v7.0.4 (Silvestro and Michalak 2010), using the default settings. All analyses were performed using the CIPRES platform (Miller et al. 2010).

To estimate divergence times between *Bachia* taxa, we used BEAST 1.8.4 (Drummond et al. 2012) (Fig. 3) using a lognormal relaxed clock model. In absence of fossil calibration within *Bachia*, we applied three calibration points resulting from the time-calibrated phylogeny for squamate reptiles by Zheng and Wiens (2016). Accordingly, we set soft bound normal priors with a standard deviation of 10% of the mean on the tree root (mean = 79.37: time root for Gymnophthalmidae in Zheng and Wiens 2016), on the root



**Fig. 2** Best ML trees for the concatenated mitochondrial and nuclear (12S + 16S rDNA + c-mos), mitochondrial (12S + 16S rDNA) and nuclear (c-mos) alignments. Asterisks (\*) by nodes correspond to posterior probabilities (above nodes) recovered from the Bayesian

inference analyses ( $\geq 95\%$ ) and ML bootstrap (below nodes) support ( $\geq 70$ ), respectively. The red clade represents *Bachia trinitatis* and in blue *Bachia whitei* sp. nov.



**Fig. 3** BEAST tree for the concatenated mitochondrial and nuclear (12S + 16S rDNA + c-mos) data set. Red circles and their sizes on nodes correspond to the highest posterior probability and darker to the

lowest. Branch width relates to branch probability. The green clade represents *Bachia trinitatis*, *Bachia whitei* sp. nov., and *Bachia flavescens*

of Cercosaurinae taxa (mean = 59.23), and on the root of Bachinae taxa (mean = 44.45). We applied a Yule speciation tree prior and previously selected substitution model (see “Results” section) for each gene fragment. BEAST was run twice with 50 million generations per run sampling every 5000 steps. Runs convergence was verified in Tracer 1.6 (Rambaut et al. 2013). We used LogCombiner (Rambaut and Drummond 2015a) to combine the runs and TreeAnnotator (Rambaut and Drummond 2015b) to compute the maximum clade credibility tree.

To assess the number of putative species within *Bachia* from Trinidad, Monos Island, and Tobago, we used the Bayesian implementation of the Poisson Tree Processes model (bPTP; Zhang et al. 2013) applied on the ML phylogenetic tree.

### Morphological data collection and analyses

Museum specimens labeled *Bachia heteropa* (including *B. h. alleni*, *B. h. trinitatis*, *B. h. heteropa*) and *B. flavescens* were examined, and a list of materials examined is presented at the end of each species account. The external morphological data collected uses nomenclature following Thomas (1965) and Dixon (1973).

Scales were measured to the nearest 0.1 mm with the aid of a digital caliper and dissection microscope. Total length and tail length measurements were taken to the nearest mm by carefully stretching the specimens along a ruler or placing a measuring tape along the length of the animal. ANOVA

statistical analyses were done with Excel and XLstats (alpha = 0.05). Ventral and subcaudal counts were compared using two sample *t* tests assuming equal variances. Abbreviations are asl—above sea level, *n*—number of specimens,  $\bar{x}$ —mean value, SD—standard deviation, SVL—snout-vent length.

Traits used in the morphological analyses: body length (SVL), head width/SVL, SVL/head length, head width, scales around mid-body, transverse dorsal rows, rows of hexagonal (or hex) scales, number of fingers, number of toes, prefrontal state, gular rows, and the presence or absence of interparietal scale.

Univariate analyses of morphological data, ANOVA, principal component analysis (PCA), cluster analysis, and discriminant analysis (DA) were applied when necessary. Statistical analyses were done with Excel using XLstat. Additionally, morphological data were analyzed in a cladistic framework using the maximum parsimony method as implemented in TNT v1.5 (Goloboff et al. 2008) in order to compare the estimated relationships between species with those recovered based on molecular data. For this purpose, we scored 23 external characters based upon the data we collected and from the literature. Given the limited number of morphological characters available, we limited our analysis to the *Bachia heteropa* group, using *B. pyburni* as the outgroup. Twenty-one characters were binary and the remaining two were multistate. Characters used were as follows: 1: frontonasal scale (0 = present, 1 = absent); 2: shape of frontonasal (0 = heptagonal, 1 = not heptagonal); 3: prefrontal scales (0 = present, 1 = absent); 4: interparietal scale (0 =

present, 1 = absent); 5: number of supraocular scales (0 = two, 1 = four); 6: number of upper labial scales (0 = five or six, 1 = less than four); 7: number of dorsal rows (0 = 42 or less, 1 = more than 42); 8: number of lower labials (0 = five, 1 = four or less); 9: dorsal scales' surface (0 = smooth, 1 = keeled); 10: dorsal scales' shape (0 = hexagonal, 1 = quad); 11: ventral scales' shape (0 = hexagonal, 1 = squared); 12: second pair of chin shields in contact (0 = yes, 1 = no); 13: ventral scales' surface (0 = smooth, 1 = other); 14: femoral pores presence (0 = yes, 1 = no); 15: digits (0 = free 1 = fused); 16: number of toes on hind limbs (0 = four, 1 = three or less); 17: prefrontals medial contact (0 = yes, 1 = no); 18: DSR (0 = 45 or less, 1 = more than 45); 19: gular scale rows (0 = seven or eight, 1 = five); 20: scales on mid-dorsal line (0 = more than 50, 1 = less than 50); 21: tail scales similar to body scales (0 = yes, 1 = no); 22: number of rear toes (0 = four, 1 = three, 2 = two); 23: number of digits on hand (0 = five, 1 = four, 2 = three). Maximum-parsimony tree searches were carried out using equal weights for all characters and treating characters as non-additive. Traditional search parameters were specified as follows: initial addseqs = 1000, tree saved per replication = 1000, swapping algorithm = TBR. Nodal support was assessed by standard bootstrap analysis with 1000 replicates.

Specimens examined are listed at the end of each species account. Acronyms for museums are listed in the Acknowledgements.

## Results

### Molecular analyses

The complete data set (1733 bp) of the sequenced *Bachia heteropa trinitatis* (*B. trinitatis* hereafter) from Trinidad, Tobago, and Monos Island resulted in six haplotypes. The three gene alignments recovered the following haplotypes for the nine *Bachia* individuals from Trinidad, Tobago, and Monos Island: 12S rDNA + 16S rDNA (six haplotypes; two from Tobago, three from Trinidad, one from Monos Island), c-mos (three haplotypes; one from Tobago, one from Trinidad, one from Monos Island), 12S + 16S rDNA + c-mos (six haplotypes; two from Tobago, three from Trinidad, one from Monos Island), COI (six haplotypes: two from Tobago, three from Trinidad, one from Monos Island, Supplemental 5).

The effective sample size (ESS) values for all Bayesian phylogenetic analyses were over 300, thus confirming good convergence mixing of all Markov chain Monte Carlo (MCMC) runs. The analysis based on the concatenated mitochondrial and nuclear dataset recovered a well-supported monophyletic clade (Bayesian Posterior Probability, BPP: 1.00: ML: 100%) of all *Bachia trinitatis* from Trinidad, Tobago, and Monos Island, with the latter forming a subclade (Figs. 2 and 3). Unlike the mitochondrial tree, which

shows a close relationship between specimens from Trinidad and Monos Islands, the c-mos tree recovered the Monos Island specimen sister to the Tobago specimens. *Bachia alleni* is grouped with the South American *B. huallagama* and *B. scolecooides*. This clade is monophyletic with Trinidad's *B. trinitatis* in the c-mos tree, but this relationship was not recovered from the mitochondrial trees. *B. flavescens* and *B. whitei* sp. nov. are monophyletic (BPP: 1.00: ML: 100%) in all trees and analyses (Figs. 2 and 3). The c-mos and BEAST tree recover a sister clade relationship between this clade and the *B. trinitatis* + *B. alleni* + *B. huallagama* + *B. scolecooides* clade.

Divergence time estimates between *Bachia trinitatis* and the clade formed by *Bachia whitei* sp. nov. + *B. flavescens* are dated circa 26 million years ago (MYA), whereas the split between *Bachia trinitatis* from Trinidad and Monos Island + Tobago dates to about 7 MYA (Table 1).

The bPTP identifies two putative species within *Bachia* from Trinidad, Monos Island, and Tobago corresponding to *Bachia trinitatis* specimens (support = 0.71) and the *B. whitei* sp. nov. from Tobago (support = 1.00). *Bachia* cf. *flavescens* (*Bachia whitei* sp. nov. hereafter see next section) is monophyletic with *B. flavescens* in all analyses (BPP: 1.00: ML: 100) (Figs. 2 and 3).

### Morphological analyses

A discriminate functional analysis (DA) (Fig. 4) using 12 morphological traits and 62 specimens of *Bachia* from the eastern Caribbean separated the taxa. The DA illustrates their morphological similarities, which are not necessarily concordant with the molecular results. The DA recovered three clusters of *Bachia trinitatis* (Trinidad, Tobago, and Little Tobago Island) and the remarkable similarity of *B. alleni* to *B. trinitatis*. The eastern Caribbean taxa previously assigned to *B. heteropa* represent at least three different species. Details of the DA are in Supplemental 6.

The cladistic analyses of morphological characters recovered 20 most parsimonious trees, and their 50%-majority-rule consensus tree shows a complete lack of phylogenetic resolution (result not shown). The sister relationships between *B. alleni* and *B. trinitatis* and between *B. whitei* sp. nov. and *B. flavescens* were the only ones recovered in more than 50% of the most parsimonious trees (85 and 100%, respectively) and with a bootstrap support (BS) close to 50 (45 and 54, respectively; BS of all other relationships < 23).

Morphologically, the mainland and eastern Caribbean island groups are readily distinguished. Mainland taxa have no prefrontals; they have two or three supraocular scales (as opposed to four in island species), two or three toes on the feet (as opposed to four in island species), and quadrangular scales on the tail (as opposed to hexagonal tail scales in the island

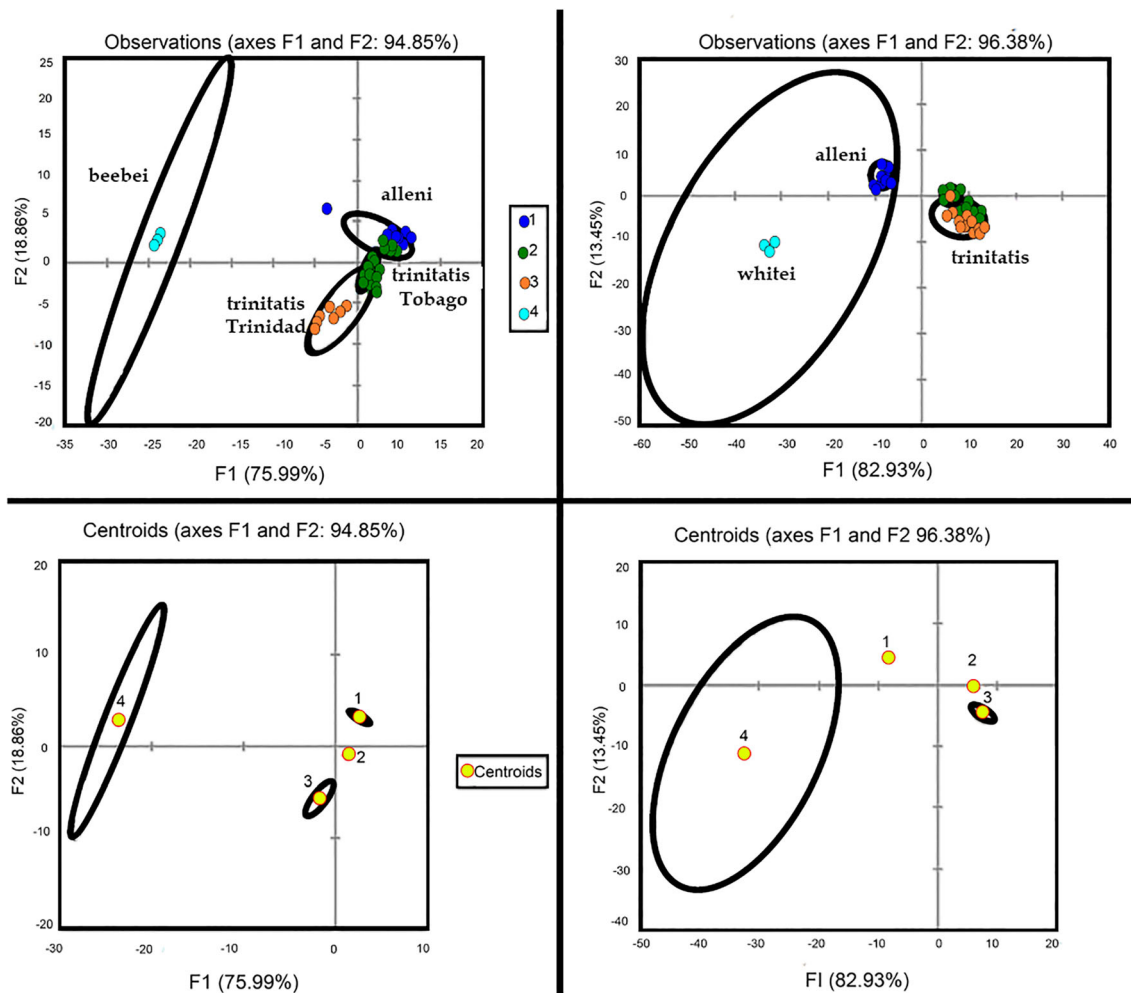
**Table 1** Time divergence estimates in millions of years (MYA) and 95% height (height 95% HPD) for lineages and groups of taxa discussed

Species clade comparison	Median range MYA (height 95% HPD)
<i>B. alleni</i> (Grenada)- <i>B. huallagama</i> + <i>B. scoleicoides</i>	1.2 (0.16–3.13)
<i>B. trinitatis</i> Tobago-Monos Island	2.68 (0.27–8.06)
<i>B. trinitatis</i> Trinidad-Monos Island + Tobago	6.98 (1.37–17.54)
<i>B. flavescens</i> - <i>B. whitei</i> sp. nov	12.7 (2.88–28.18)
<i>B. flavescens</i> + <i>B. whitei</i> sp. nov.- <i>B. trinitatis</i>	26.67 (11.0–48.2)

species). Table 2 compares the morphological traits found in taxa associated with Dixon’s (1973) *B. heteropa* group. A taxonomic key and a taxonomic revision of the *Bachia* of the eastern Caribbean with the description of new species follow.

**A key to the *Bachia* in the eastern Caribbean**

- 1a. Band of quadrangular dorsal scales ... *Bachia whitei* sp. nov. (Tobago).
- 1b. Band of hexagonal dorsal scales ... 2.



**Fig. 4** The discriminate function analysis (DA) on the left was done using 58 specimens of eastern Caribbean *Bachia* and 12 traits. *Bachia alleni* (1 dark blue). The blue outlier labeled *alleni* is the type specimen of *B. a. parviceps*. (3, 4) *Bachia trinitatis* is shown as two populations: Trinidad (orange), Tobago, and Little Tobago (green). (4) *Bachia beebei* sp. nov. (light blue). The DA on the right was done with 61 specimens of eastern Caribbean *Bachia*. *Bachia alleni* (dark blue). *Bachia trinitatis* is shown as two populations: Trinidad (orange), Tobago and Little

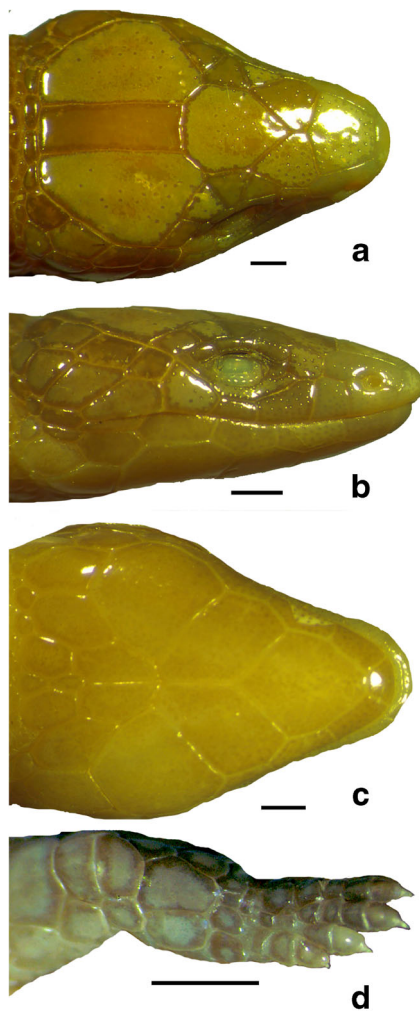
Tobago (green). (4) *Bachia whitei* sp. nov. (light blue). *Bachia alleni* (1 dark blue). (3, 4) *Bachia trinitatis* is shown as three populations: Trinidad (orange), Tobago (green), and Little Tobago (green). Traits used in the morphological analyses: head width/SVL, head width/head length, SVL/head length, scales around mid-body, transverse dorsal rows, longitudinal dorsal scale rows, rows of hex scales, number of fingers, number of toes, prefrontal condition, gular rows, presence or absence of interparietal scale

**Table 2** A comparison of the morphology of the *Bachia heteropa* group (JR) Data from Ribeiro et al. (2016), (D) Data from Dixon (1973), (HD) Hoogmoed and Dixon (1977) and numbers refer to the number of specimens seen and data we collected

	<i>Alleni</i>	<i>Trinitatis</i>	<i>Beebei</i>	<i>Heteropa</i>	<i>Lineata</i>	<i>Marcelae</i>	<i>Pallidiceps</i>	<i>Remota</i>	<i>Guianensis</i>
Type localities	St. George, Grenada	Caparo, Trinidad	Caripito Venezuela	La Guaira, District Federal Venezuela	Duaca, Falcon, Venezuela	Bosque La Luz, Estado Barinas, Venezuela	Rio Truando Region, Colombia	Parque Nacional Montanhas do TumucumaqueBrazil (JR)	Bolivar, Venezuela
Source	this study	this study	this study	(D)	(D)	(D)	(D)	(JR)	(HD)
Supraoculars	4	4	4	2	2	2	2	2	2
Frontonasal	pent	Pent	oct	hept	hept	hept	hept	oct	pent
Prefrontals	yes	Yes	no	no	no	no	no	no	yes
PFMC	yes	Variable	no	no	no	no	no	no	yes
Digits on hand	4	5	4	4	4	4	4	4	4
Digits on feet	4	4	3	3	2	2	3	2	4
SAB range	27–31	26–29	26–28	28–30	24–26	25	21–25	28	26
Mean SAB	29.23	26.67	28.8	29.3	nd	nd	nd	nd	nd
SD =	1.15	0.99	0.4	nd	nd	nd	nd	nd	nd
N =	30	13	5	nd	nd	nd	nd	nd	nd
TDSR	38–41	36–40	39–40	45–47	45–49	39–42	43–48	54	50
Mean TDSR	40.16	38.17	39.4	45.3	47.2	40.7	nd	nd	nd
SD =	1.08	1.53	0.49	nd	nd	nd	nd	nd	nd
Rows of gulars	8	7 or 8	6 or 7	7	7	5	7	8	9
Range of ventrals	25–27	26–29	27–28	27–30	24–26	nd	30–34	40	40
Interparietal	yes	Yes	yes	yes	yes	Yes	yes	no	yes

$\bar{X}$  mean, *SD* standard deviation, *n* number, *nd* no data, *pent* pentagonal, *Oct* octagonal, *Hept* heptagonal, *hex* hexagonal, *PFMC* prefrontals in medial contact, *SAB* scales around body, *TDSR* transverse dorsal scale rows





**Fig. 5** *Bachia alleni*. KU315771 from Grenada. **a** Crown. **b** Profile. **c** Gular view. **d** Rear leg with four digits. Each bar is about 1 mm

- 2a. No prefrontals ... go to 3.
- 2b. Prefrontals present ... go to 6.
- 3a. Hindlimbs with two toes ... go to 4.
- 3b. Hindlimbs with three toes ... go to 5.
- 4a. Seven rows of gular scales ... *Bachia lineata*.
- 4b. Five rows of gular scales ... *Bachia marcelae*.
- 5a. Two supraoculars ... *Bachia heteropa*.
- 5b. Four supraoculars ... *Bachia beebei* sp. nov.
- 6a. Hexagonal scales usually in 8 rows, four digits on *manus* ... *Bachia alleni*.
- 6b. Hexagonal scales in 9 or 10 rows, five digits on *manus* ... *Bachia trinitatis*.

### The hex-scaled *Bachia* from Grenada and the Grenada Bank

The morphological and molecular results suggest that *Bachia alleni* is restricted to Grenada and the Grenadines and is not conspecific with the hex-scaled *Bachia* present on Trinidad, Tobago, or Little Tobago.

*Bachia alleni* (Barbour, 1914).

Fig. 5

*Scolecocaurus alleni* Barbour 1914:316. Type locality St. George, Grenada (12°3'N 61°45'W). Holotype: MCZ 7793.

*Scolecocaurus alleni alleni*—Barbour 1933:76.

*Scolecocaurus alleni parviceps* Barbour 1933:77. Type locality Canouan, Grenadine Islands (12° 43'N, 61° 19' W). Holotype: MCZ 32345. The specimen was collected by David Fairchild and H. F. Loomis, on February 6, 1932. Barbour (1933) wrote, “Similar to *S. a. alleni* of Grenada but with smaller head and body shorter in proportion to the total length.” Thomas (1965) reported that *B. a. parviceps* has a prefrontal/frontal suture length of 0.14, and he considered it within the range of Grenada specimens. Dixon (1973) entirely overlooked this name but listed Barbour’s 1933 paper in his literature cited. One of us (ALB) examined the type specimen of *B. a. parviceps*, and all of the morphometric and meristic traits fall within the ranges for *Bachia alleni* from Grenada. This specimen has seven rows of hexagonal scales on the dorsum, while most *Bachia alleni* have eight rows, but six of the 34 specimens of *B. alleni* we examined had seven rows. Pending future study, this name is best regarded as conspecific with *B. alleni*.

[*Bachia*] *alleni*—Vanzolini 1961:204.

*Scolecocaurus trinitatis*—Underwood 1962:94 (in part).

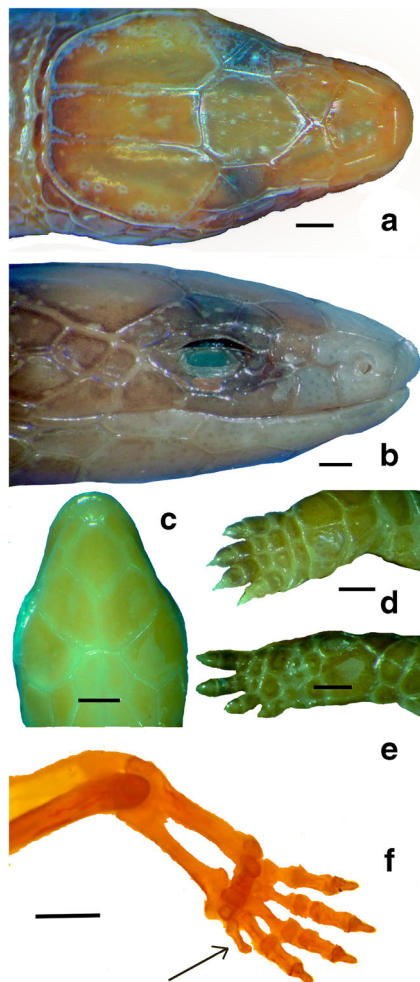
*Bachia alleni alleni*—Thomas 1965:145.

*Scolecocaurus* sp. Groome 1970:36.

*Bachia heteropa alleni*—Dixon, 1973:32.

**Diagnosis** A *Bachia* with (1) prefrontal scales in medial contact; (2) the second supraocular the longest; (3) the frontonasal is pentagonal; (4) four digits on the *manus* and *pes* (phalange formulas: *manus* 2–3–3–2–0, *pes* 4–4–2–2–0); (5) a band of eight (7–11) hexagonal scales on the dorsum; (6) scales around mid-body 27–31; (7) transverse dorsal rows 38–41; (8) the fifth upper labial may or may not contact the last supraocular; (9) eight rows of gulars; (10) the second pair of chin shields is not in contact; (11) an interparietal scale is present.

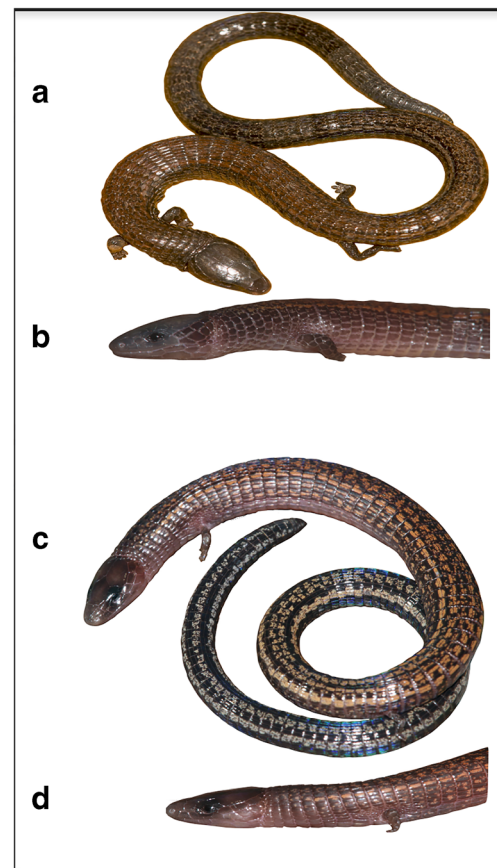
**The status of the Bequia Island *Bachia*** Thomas (1965) noted that two specimens of *Bachia* from Bequia Island (12° 58' N, 61° 14'W) have prefrontals in apical contact and suggests that they may represent a distinct species. We have examined one of them (AMNH 90516). The scale counts fall within the ranges of Grenada *B. alleni* (Table 2). However, the prefrontals are triangular (pentagonal in Grenada *B. alleni*), the fourth supraocular is the smallest (first and fourth about the same size in Grenada *B. alleni*), and the posterior edge of the interparietal is rounded (squared off in Grenada *B. alleni*). Most remarkably, the limbs are long, the forelimbs are 0.166 of the SVL, and



**Fig. 6** *Bachia trinitatis*. **a** Crown view UWIMZ2010.12.44c. **b** Profile FMNH 49881. **c** Gular view. **d** *Manus*. **e** *Pes*. **f** FMNH 49880d cleared and stained *manus*; arrow points to the reduced first digit, not readily visible in complete specimens. Each bar is about 1 mm

the hind limbs are 0.195 of the SVL. The Grenada *B. alleni* has forelimbs that are 0.09–0.118 ( $x = 0.099$ ,  $n = 4$ ) and legs that are 0.100–0.133 ( $x = 0.120$ ,  $n = 4$ ) of the SVL. The Bequia specimen also has an elongated head, 0.242 of the SVL. In Grenada, *B. alleni* has a head that is 0.149–0.159 of the SVL. Given the small size of this specimen (21 mm SVL), we suspect that it is a hatchling, although no umbilical scar was noted. We cannot rule out the possibility that the long head and limbs are a product of allometry. Thus, the status of Bequia Island *Bachia* remains uncertain but worthy of future investigation; it is the most northern population of *B. alleni*.

**Similar species** *Bachia alleni* has four digits on each limb and usually eight rows of hexagonal scales on the dorsum, two traits that will separate it from *Bachia trinitatis* (five digits on the *manus* and usually 10 rows of hexagonal scales). It has prefrontal scales that make medial contact a trait that will separate it from *B. heteropa* and *B. beebei* sp. nov. (both lack



**Fig. 7** **a, b** *Bachia trinitatis* from Flagstaff Hill, Tobago (JCM). **c, d** *Bachia whitei* sp. nov. UWIZM.2017.15.6. A female from Main Ridge Reserve, Tobago (JCM)

prefrontal scales). It can be distinguished from *B. whitei* sp. nov. by the band of hexagonal scales. To separate *B. alleni* from other former members of the *B. heteropa* group, see Table 2.

**Material examined** *Bachia alleni* ( $n = 34$ ) GRENADA—Albert A. Schwartz collection AAS6847–48, 6998, 7144–7155, 7158, 7175, 7197–99, 7368; AMNH 38968; KU 315771–76; USNM 43219, 67219–20, 79190, 286940. GRENADINES—Bequia Island AMNH 90516; Canouan Island MCZ 32345.

### The Trinidad and Tobago hex-scaled *Bachia*

*Bachia trinitatis* is present on Trinidad as well as the Bocas Islands (Chacachacare, Monos, and Gasparee), Tobago, and Little Tobago Island. Additionally, we suspect its presence on the Isla de Margarita and in the Peninsula de Paria in northern Venezuela. We have seen few specimens from Margarita and Paria and tentatively assign them to *Bachia trinitatis* pending further investigation.

*Bachia trinitatis* (Barbour 1914).

Figs. 6 and 7a, b

*Scolecosaurus trinitatis* Barbour 1914:316. Type locality “Capara,” Trinidad. Holotype: MCZ 8947. We suspect the type locality is Capara, Trinidad (10°27' N, 61°20' W).

[*Bachia*] *trinitatis*—Vanzolini 1961:204.

*Bachia alleni trinitatis*—Thomas 1965:152.

*Scolecosaurus* sp.—Groome 1970:36.

*Bachia heteropa trinitatis*—Dixon 1973:32.

*Bachia heteropus*—Schwartz and Thomas 1975:109.

**Diagnosis** A *Bachia* with (1) the prefrontal scales in narrow contact, or not in contact (2) the second supraocular the longest; (3) the frontonasal is pentagonal; (4) there are five digits on the *manus* and four digits on the *pes* (phalange formulas: *manus* 1–2–3–3–1, *pes* 2–3–3–2); (5) there is a band of ten (8–11) hexagonal scales on the dorsum; (6) scales around mid-body 26–29; (7) transverse dorsal scales in 36–42 rows; (8) the fifth upper labial does not usually make contact with the last supraocular; (9) seven or eight rows of gulars; (10) the second pair of chin shields are completely separated; (11) an interparietal scale is present.

**Variation** The prefrontals of most Tobago specimens make full medial contact, while on Trinidad, they may make apical

contact or no contact. Supraoculars four; supraculars three; upper labials six, rarely five, or seven; lower labials are five, rarely six. Gular scale rows number eight on Tobago, and usually seven on Trinidad. Five specimens have fused rows such that the number falls between seven and eight.

Configuration of the pectoral shields on 77 specimens is as follows: 2 + 1 + 1 + 2 (51%), 1 + 1 + 1 + 1 (25%), 2 + 1 + 1 + 1 (6%), 1 + 1 + 1 + 2 (3%), 2 + 1 + 2 + 2 or 2 + 2 + 1 + 2 (9%), and other odd combinations (6%). The lateral pectoral shields are about one half the width of the medial shields in most instances.

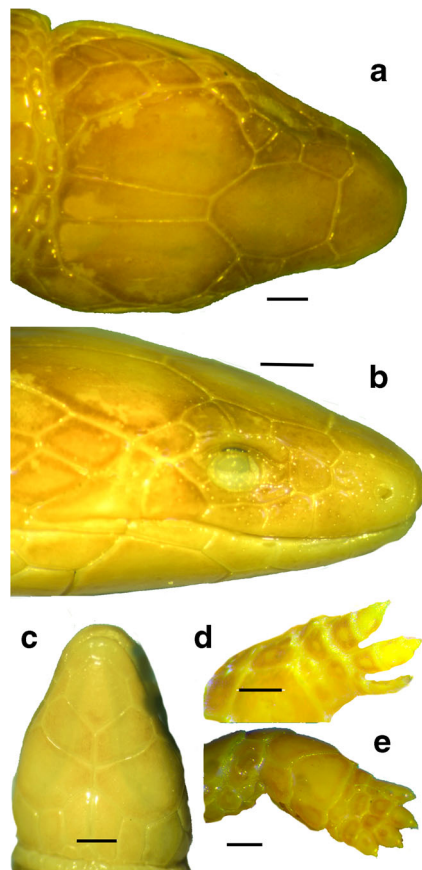
Scale rows around the middle of the body (SAB) range from 26 to 30. The band of hexagonal scales on the dorsum ranges from 8 to 11 (usually nine on Tobago and 10 on Trinidad). DSRs ranged from 36 to 41. Transverse ventral rows range from 22 to 29.

Only 21% of the adult and juvenile Tobago samples appeared to have original tails. Four mature females average 95.8 (95–97) caudal scale rows, five mature males average 99.2 (98–101), eight hatchlings average 96.4 (90–100), and six juveniles average 98.3 (95–101). Caudal scales, like the dorsal body scales, are hexagonal and imbricate. However, unlike the dorsal body scales, the dorsal, caudal scales appear slightly keeled.

The average tail length/total length ratio for six freshly measured hatchlings is 0.567 (0.560–0.573). All males greater than 40 mm SVL have four well-developed preanal pores, two at the base of each rear leg. Males between 36 and 40 mm SVL show varying degrees of preanal pore development, with some appearing to have two, one at the base of each rear leg. Two specimens deviate from the standard configuration of preanal shields. One adult female has a triangular middle posterior shield. A small juvenile has the three posterior shields fused into one. Females lack preanal pores and most have a single large scale where males have two or three smaller scales in the preanal pore area.

All specimens have four clawed digits on all uninjured hind feet. The anterior limbs have a remnant fifth digit readily visible in cleared and stained specimens (Fig. 8) and somewhat visible when the hand is viewed from below.

All specimens appear to be dark brown in coloration; however, close examination reveals a pattern of light and dark stripes and lines, obscured by flecking and mottling. The pattern is more distinct on hatchlings and juveniles and is progressively obscured with age. The head of hatchlings is darker than the body. The dorsal pattern consists of a dark vertebral line extending posteriorly from the occiput, faint paravertebral light stripes mottled with brown, dorsolateral pale stripes bordered by dark brown stripes, lateral surfaces darker than the dorsum, and a uniform gray/tan venter. The longitudinal stripes present on the trunk are more distinct on the tail, and there is a trace of lateral and ventrolateral indistinct pale stripes. The head of adults is not noticeably darker than the



**Fig. 8** *Bachia beebei* sp. nov. AMNH 137630. **a** Crown view note absence of prefrontals. **b** Profile. **c** Gular view. **d** *Manus*, with three digits. **e** *Pes* with four digits. Each bar is about 1 mm

body. The pattern on a few adults is nearly as distinct as on hatchlings. The dorsum is tan with dark brown mottling and flecking. The dark vertebral stripe is usually faint or entirely obscured on the body, but visible on the tail. The dorsolateral light stripes usually are indistinct on the body, become bolder on the tail, and are bordered above and below by a dark brown line that also is more evident on the tail. Laterally, the dark brown grades into a gray/tan venter that becomes mottled and flecked with dark brown pigment on some larger specimens. Encroachment of ventral pigmentation is most apparent in the gular, pectoral, and pelvic regions. The ventral surface of the tail is darker and more heavily mottled than the belly. The lines and stripes are absent or disrupted on regenerated portions of tails.

Sexual dimorphism is apparent in dorsal and ventral scale row counts, head length/snout-vent length ratios, and presence or absence of preanal pores (ANOVA). Also, sexual dimorphism appears to exist in the mean number of caudal scale rows and in scale morphology of the preanal pore area. Adult body lengths (> 40 mm SVL) are sexually dimorphic ( $p = 0.006$ ) with females ( $X = 47.31$ ,  $n = 26$ ) slightly larger than males ( $X = 44.59$ ,  $n = 25$ ).

Regression of head length on snout-vent length reveals that adult females have a relatively longer body than adult males of similar head size. Sub-adult samples are small, but the separation between males and females appears to coincide with the onset of sexual maturity.

Eight hatchlings have an average SVL/HL ratio of 4.89 (4.52–5.35), 19 juveniles have a ratio of 5.85 (5.0–6.4), 24 adult males have a ratio of 6.65 (6.14–7.06), and 29 adult females have a ratio of 7.19 (6.52–7.70).

The relatively longer body of females is likely an adaptive feature that allows housing mature eggs end to end, thus maintaining a smaller body diameter when gravid. A slim build would appear to be advantageous in the forest floor habitat.

The female body proportions probably account for much of the larger size of females. The snout-vent length of the five largest males examined (49, 48.5, 48, 48, and 47 mm) is lower and does not overlap with the five largest females (56, 52.5, 52, 51.5, and 51.3 mm).

Ontogenetic variation is evident in the head length/snout-vent length ratios and the preanal pore development of males. Also, the color-pattern of adults is less distinct than the juvenile's color pattern.

**Similar species** *Bachia trinitatis* has five digits on each *manus* and four on each *pes* (*Bachia alleni* has four digits on each limb). The prefrontals may make narrow medial contact or make no contact (*B. alleni* prefrontals make medial contact). *Bachia heteropa* has no prefrontals; three digits on the *pes*; and the second pair of chin shields are in contact (not so in *B. trinitatis*). It can be distinguished from *B. whitei* sp. nov. by the band of hexagonal scales (*B. whitei* sp. nov. has

quadrangular scales) and *B. whitei* sp. nov. lacks an interparietal scale (*B. trinitatis* has an interparietal scale). To distinguish *B. trinitatis* from other former members of the *B. heteropa* group, see Table 2.

**Ecology** Dixon (1973) concluded they are supraterranean leaf litter inhabitants. *Bachia trinitatis* collections generally support this idea. A few specimens were beneath rocks, but most were collected in leaf litter, rotten logs, piles of cacao pods and coconut hulls, and other piles of downed vegetation. However, underlying soil strata were not sampled, and to what extent *B. trinitatis* might use that habitat remains unknown. However, they do not hesitate to enter burrows in the soil. *Bachia trinitatis* appears to be the most abundant reptilian forest litter inhabitant on Tobago. It seems less abundant on Trinidad.

No literature references to any aspects of reproduction could be found for eastern Caribbean *Bachia*. Dixon (1973) gives the clutch size for *B. intermedia* and *B. barbouri* as two. Beebe (1945) reported on one egg laid by a *B. cophias* (= *monodactylus*).

Eggs were found in August and December (Table 3). The two eggs in each of the four clutches were located within 10 cm of each other. The exact placement of the eggs could not be determined due to substrate disturbance by collecting activities. Nests were found in leaf litter under cacao trees, and one nest was in a mound of humus laden soil where a tree had been uprooted. Adults were typically in the vicinity of the nests, and all nests were on moderate slopes in or at the edge of forests.

Eleven *B. trinitatis* females were examined that had mature or developing eggs. Based on information from these females and the egg clutches found in the wild, the standard clutch size appears to be two. Mature oviductal eggs are arranged end to end, rather than side by side. A protracted and probably continuous breeding season is apparent with eggs and gravid females occurring in April, August, and December.

Testes enlargement and overt preanal pore development suggests that males become sexually mature at about 40 mm SVL. Preanal pores are fully apparent only in males over 40 mm SVL. The smallest female with enlarging yokes was 45.0 mm SVL, suggesting a larger size at the onset of sexual maturity for females.

**Distribution** *Bachia trinitatis* occurs on Trinidad, the Bocas Islands (Chacachacare, Gaspar Grande, and Monos), Tobago, and Little Tobago; and on Margarita Island and the Paria Peninsula of Venezuela.

**Material examined** *Bachia trinitatis* ( $n = 107$ ) TRINIDAD—FMNH 10900, 25013, 40000, 40447, 40447, 49873–91, 55390–91, 215813. LITTLE TOBAGO ISLAND—USNM 227715–24. TOBAGO—ALB collection 3600.1–2, 3615.1–

**Table 3** Data on eggs and hatchlings of *Bachia trinitatis* from Tobago. SVL = snout-vent length. SVL and total mm fresh measurements. Hatchling's SVL mm taken after preservation, nd = no data

No. eggs	Date collected	Date hatched	SVL mm	Total mm	Hatchlings SVL mm
2	18-Dec-78	24-Dec-78	nd	nd	22.4
			nd	nd	22.6
2	23-Dec-78	12-Jan-79	24.0	55.6	23.5
			23.3	54.6	23.5
2	23-Aug-80	4-Sep-80	24.4	55.8	23.0
			24.4	57.2	23.5
2	28-Aug-80	5-Sep-80	24.8	56.7	24.0
			24.0	54.6	23.5

2; FMNH 55932; USNM 90240, 90283–84, 902300, 22791, 227945–60, 27962–66, 227968–84, 227985–94, 227997–99, 228000–01, 228003–11. VENEZUELA—Yacua, Paria, Sucre MCZ 43880.

### Hex-scaled *Bachia* from the Caribbean coastal range of Venezuela

Five specimens collected at Caripito, Venezuela, were examined by Dixon (1973) and identified as *Bachia heteropa heteropa* × *Bachia h. trinitatis*. The presence of three toes on the feet, the lack of prefrontals, and the second pair of chin shields in medial contact suggest to us that these represent an undescribed species, and we describe it below.

*Bachia beebei* sp. nov.

Fig. 8

*Bachia heteropa heteropa* × *Bachia heteropa trinitatis*—Dixon 1973:33.

**Holotype** An adult male, AMNH 137630 from Caripito Venezuela (10°7'N, 63°6'W).

**Diagnosis** A *Bachia* with (1) no prefrontal scales; (2) the first supraocular is the longest, and extends over the loreal; (3) the frontonasal is hexagonal; (4) four digits are present on the *manus* and three on the *pes* (phalange formulas: *manus* 1–2–2–1–0, *pes* 1–2–2–0–0); (5) a band of 12 rows of imbricate hexagonal scales on the dorsum; (6) scales around mid-body 26–28; (7) 39–40 transverse rows of dorsals; (8) the fifth upper labial contacts last supraocular; (9) the gulars are in six or seven; (10) the second pair of chin shield are in medial contact; (11) an interparietal present.

**Variation** Two males were 40 and 55 mm in SVL; one female was 40 mm SVL. The tails were all damaged. Beebe (1945) describes one individual that had a total length of 165 mm before breaking its tail. Forelegs were 0.08–0.99 of the SVL and legs were 0.08–0.10 of the SVL. Head widths were 0.09–0.11 of the SVL, head lengths were 0.14–0.15 of the SVL of

the SVL. Supraciliaries range from 2 to 4 (usually three), one specimen has two on both sides, another has three on one side and four on the other; two other specimens have three on both sides. The number of lower labials can be five or six; gular rows are seven, one specimen has six. Scale rows around mid-body are 29, one specimen has 28 ( $X = 28.80$ ,  $SD = 0.40$ ); dorsal scale rows are 39–40 ( $X = 39.4$ ,  $SD = 0.49$ ). Transverse ventral scale rows are 27 or 28 ( $X = 27.20$ ,  $SD = 0.40$ ).

**Description of the holotype** A male, SVL 55 mm, front leg 4.6 mm, rear leg 4.6 mm, head length 8.2 mm, head width 5.5 mm, head depth 4.5 mm. Body elongate, a sulcus between the head and nuchal region, snout rounded, tail broken. Rostral small, barely visible from above, contacting first supralabial (same as the lower lobe of the nasal scale), nasal, and frontonasal. Viewed from above, the rostral is about twice as wide as high; in lateral view, it projects slightly over the anterior margin of the jaw. Prefrontals are absent. Frontonasal hexagonal, broader than long, with anterior margin flat, lateral margins straight and expand laterally, in contact with loreal and first supraocular, and the first two upper labials. Frontal is octagonal, longer than wide, and in contact with the frontonasal, the first two supraoculars, the parietals, and interparietal. Parietals large, longer than wide, slightly longer and slightly wider than frontal, roughly pentagonal. Interparietal narrow anteriorly widens posteriorly. Posterior borders of parietals and interparietal coincide with the cervical sulcus in the occipital region. Four supraoculars, the first is the longest, the third the smallest. Two superciliaries are present. Nasal large, longer than tall and complete; nare in the anterior middle of the nasal, fused to first upper labial. Loreal pentagonal, undivided and in contact with upper labials 2–3, preocular, frontal, internasal, and supranasal. Six upper labials (counting the lower portion of the nasal as the first upper labial); the first is below the nare and forms the bottom half of the nasal; 3–5 contacting suboculars, the fifth is the tallest, the fourth is the shortest, the sixth longest. Scales around the orbit are one subocular; one preocular, one postocular. Eyelid

present with an undivided semitransparent scale. Ear-opening is absent. All head scales smooth and juxtaposed. Mental broader than long, slightly broader than the ventral surface of rostral. Postmental roughly hexagonal; longer than wide. Two pairs of chin shields, both pairs are in medial contact; the anterior pair is smaller; followed by a row of five pre-gulars, the medial pre-gulars are divided into smaller scales at the sulcus. Six lower labials, first two pairs contact the post mental. Gulars smooth, imbricate, rounded posteriorly, in seven transversal rows; gular scales gradually increase in size toward the pectoral region. The pectoral region has two central plates, each longer than wide, and a pair of two smaller scales laterally (scale on left divided), pectoral formula 2112. Lateral scales of neck rectangular, smooth, imbricate, and slightly rounded posteriorly, wider than long. Gular fold present. Dorsal scales are imbricate and in 39 transverse rows between interparietal sulcus and the level of hind limbs. Lateral scales about the same size as the dorsals; those closer to ventrals slightly wider. Granular scales at the insertion point of limbs. Scales around mid-body 28, 12 rows of these on the dorsum are hexagonal. Ventral scales smooth, longitudinally imbricate, laterally juxtaposed, almost square, those after mid-body narrower; 27 transverse rows between interbranchials and preanals. Four preanal pores present. Cloacal shield composed of four scales, lateral scales small. The front limbs have four clawed digits on each hand the rear legs have three digits on each foot. The front limbs are equal to five rows of transverse lateral scales, and the hind limbs are equal to about seven rows of transverse lateral scales.

We have not observed this lizard alive. However, Beebe (1945) described the coloration in life as “Chestnut brown above with a wide band down the back of dull cinnamon gray stippled with chestnut, fading into solid chestnut toward the tail. A tan row stripe of chestnut down the center of the dorsal band. The band is edged on each side with a linear series of arrowheads of pale olive buff. Inner border of these marks edged with chestnut. The arrowheads get smaller and fade out entirely toward the tail. Iris straw yellow.”

**Similar species** *Bachia alleni* and *B. trinitatis* have four digits on each *pes* and prefrontal scales (*B. beebei* sp. nov. has three digits on each *pes* and no prefrontal scales). *Bachia heteropa* has 45–47 transverse scale rows (39–40 in *B. beebei* sp. nov.). *Bachia whitei* sp. nov. has quadrangular scales on the dorsum and no interparietal scale (*B. beebei* sp. nov. has hexagonal scales on the dorsum and an interparietal scale is present). To distinguish *B. beebei* sp. nov. from other former members of the *B. heteropa* group, see Table 2.

**Etymology** *Bachia beebei* sp. nov. is named in honor of William Beebe, the premier American naturalist of the early twentieth century. Beebe made many contributions to the ecology of tropical forests as well as early deep ocean exploration.

His contributions to the herpetology of the Caribbean Coastal Ranges as well as Trinidad and Tobago are often overlooked because of his more publicized contributions to natural history.

**Distribution** *Bachia beebei* sp. nov. is known only from the type locality, Caripito, Venezuela.

**Ecology** The environment at the type locality was described by Beebe (1943). He found the area to be highly seasonal with an extended dry period. Two species of *Bachia* were present at Caripito, *B. cophais* and *B.* [formerly *heteropa*] *beebei* sp. nov. The lizards were found while digging pits, or after they had fallen into the pits; but he also extracted them from decomposing logs. He commented on their readiness to autotomize their tail and their similarity in their appearance (coloration and fine longitudinal stripes) to the snake *Atractus trilineatus*. This snake is also sympatric with *Bachia trinitatis* on Trinidad and Tobago.

**Material examined** AMNH137630–34. Venezuela, Caripito.

*Bachia heteropa* (Lichtenstein and von Martens).

*Chalcides heteropus* Lichtenstein and von Martens 1856:17. Holotype is in the Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt-am-Main (SMF 39900) from La Guaira, Venezuela (10° 35'N, 66° 55'W).

*Bachia heteropus*–Garman, 1892:97.

*Bachia heteropa heteropa*–Peters and Donoso Barros 1970:80.

**Diagnosis** A *Bachia* with (1) no prefrontal scales; (2) the third supraocular is the longest; (3) the frontonasal is hexagonal; (4) four digits are present on the *manus* and three on the *pes* (5) a band of imbricate hexagonal scales on the dorsum; (6) scales around mid-body 28–30; (7) 4–47 transverse rows of dorsals; (8) the fifth upper labial contacts primary temporal; (9) the gulars are in six or seven; (10) the second pair of chin shield are in medial contact; (11) a sub-triangular interparietal present.

**Material examined** Venezuela (1) UMMZ 55880.

*Bachia lineata* (Boulenger).

*Bachia lineata* Boulenger 1903:432. Type-locality, Duaca, Venezuela. (10° 16'N, 69° 08'W) (Holotype, British Museum Holotype, British Museum of Natural History (NHM) 1946.8.2.41 (formerly 1902.7.29.90), an adult, collected by Mr. Wayman (purchased from Mr. Rosenberg), date of collection unknown, but registered into the collection on 29 July 1902.

*Bachia anomala* Roux 1929:31. Type-locality, El Mene, District Acosta, Falcon Province, Venezuela (11° 02'N, 68° 29'W). Holotype, Naturhistorisches Museum, Basel (NMBA) 9912, an adult male (SVL 52 mm), collected by H.G. Kugler

and presented to the museum in 1929. Shreve (1947) suggested that *B. lineata* and *B. anomala* might not be conspecific. He noted that Boulenger's description stated the dorsal scales were quadrangular and suggests this led Roux into thinking his specimen was new. Burt and Burt (1931) placed *B. lineata* in the *B. cophias* group. Boulenger's description also reports five longitudinal dorsal stripes, with Shreve noting that none of the specimens he examined had more than three.

*Bachia heteropa lineata*: Mijares-Urrutia and Arends 1999:115.

**Diagnosis** A *Bachia* with (1) no prefrontal scales; (2) the third supraocular is the longest; (3) the frontonasal is hexagonal; (4) four digits are present on the *manus* and three on the *pes* (5) a band of imbricate hexagonal scales on the dorsum; (6) scales around mid-body 24–26; (7) 42–45 transverse rows of dorsals; (8) the fifth upper labial contacts primary temporal; (9) the gulars are in six or seven; (10) the second pair of chin shield are in medial contact; (11) a sub-triangular interparietal present.

**Material examined** Data from the literature.

*Bachia marcelae* Donoso-Barros and Garrido.

*Bachia marcelae* Donoso-Barros and Garrido 1964:1. Type-locality, La Luz, Edo. Barinas, Venezuela (8° 23' N, 69° 49' W). Holotype, Museo de Zoología de la Universidad de Concepción, Chile (MZUC) 8578, male holotype (D-B 6312061 in the original publication). Collected on 12 December 1963 by R. Donoso-Barros and A. Garrido.

*Bachia lineata marcelae*–Donoso-Barros 1968:117.

*Bachia heteropa marcelae*–Dixon 1973:33.

**Diagnosis** A *Bachia* with (1) no prefrontal scales; (2) two supraoculars; (3) the frontonasal is hexagonal; (4) four digits are present on the *manus* and two on the *pes* (5) a band of imbricate hexagonal scales on the dorsum; (6) scales around mid-body 25; (7) 39–42 transverse rows of dorsals; (8) the fifth upper labial contacts primary temporal; (9) the gulars are in five rows; (10) the second pair of chin shield are in medial contact; (11) a sub-rectangular interparietal present.

**Material examined** Data from the literature.

The Quad-scaled *Bachia* from Tobago.

Three specimens collected in the late 1970s have been previously considered to be related to *Bachia flavescens*. This taxon is a previously undescribed species, distinct from the Guyana specimens of *flavescens*-like *Bachia* that we examined. A fourth specimen was collected on Tobago in 2017. We believe this species is a Tobago endemic.

*Bachia whitei* sp. nov.

Fig. 7c, d.

*Bachia* cf. *flavescens*–Hardy 1982:78.

*Bachia flavescens*–Murphy 1997:133.

**Holotype** USNM 227942, a male from Hillsborough Dam, Tobago (11°13' 32"N, 60°40' 10"W). Collected 21 December 1978 by Alvin L. Braswell.

**Referred material** USNM 227944, 227943, UWIZM 2017.15.6.

**Diagnosis** A *Bachia* with (1) no prefrontal scales; (2) the second supraocular is slightly longer than the first; (3) the frontonasal is hexagonal; (4) three clawed digits on each *manus* and two digits on each *pes*; (5) there are quadrangular scales on the dorsum; (6) scales around mid-body 31–32; (7) transverse dorsals in 47–49 rows; (8) the fifth upper labial does not contact the last supraocular; (9) there are eight rows of gulars; (10) the second pair of chinshields are widely separated; (11) an interparietal scale is absent.

**Measurements** SVL–58.5 mm, head width 3.98 mm, head length 6.75 mm, head depth 3.02 mm.

**Description of the holotype** Body elongate, with a sulcus between the head and nuchal region, snout rounded, tail broken. Rostral small, barely visible from above, contacting the first supralabial, nasal and frontonasal scales; viewed from above the rostral is about twice as wide as high; in lateral view, it projects slightly over the anterior margin of the jaw. Prefrontals are absent; frontonasal heptagonal, longer than wide, with anterior margin pointed, lateral margins straight to slightly concave, in contact with loreal and three superciliaries. Parietals large, longer than wide, slightly longer and slightly narrower than frontal, roughly pentagonal; posterior borders of parietals and dorsals coincide with the cervical sulcus in the occipital region. Three supraoculars, the second is the largest three superciliaries. Nasal large, longer than high and completely divided; nostril in the anterior lower margin of the nasal, invading the upper border of the first supralabial. Loreal square, undivided and in contact with upper labials 2–3, the preocular, the frontal, the internasal and the supranasal. Six upper labials; first is below the nare and forms the bottom half of the nasal; 3–5 contact the oculars, the second is the tallest, fourth is smallest, sixth is longest. Scales around the orbit are: one subocular; one preocular, a postocular absent. Eyelid present with an undivided semitransparent scale. Ear-opening is absent. All head scales smooth and juxtaposed. Mental wider than long, slightly broader than the ventral surface of rostral. Postmental roughly heptagonal; longer than wide. Two pairs of chin shields, contacting lower labials 2–3; the anterior pair smaller, in broad contact at the midline; second pair separated by a pair of smaller scales, followed by a row of pre-gulars, inner scales are the largest. Five lower labials, first pair contact first and second lower labials. Gulars are smooth, imbricate, rounded posteriorly, in eight transversal rows; gular scale rows are increasing gradually in size toward

the pectoral region. The pectoral region with two central scales, longer than wide, a pair of two smaller scales laterally (scale on left divided). Lateral scales of neck rectangular, smooth, imbricate, and slightly rounded posteriorly, longer than wide, in regular transverse rows and becoming gradually similar to adjacent dorsal and ventral scales. Gular fold present. Dorsal scales are imbricate and in 47 transverse rows between interparietal sulcus and the level of hind limbs. Lateral scales are about the same size as the dorsals but smooth; those closer to the ventrals slightly wider. A distinctive area with granular scales present around insertion of limbs. Scales around mid-body are 32. Ventral scales smooth, longitudinally imbricate, laterally juxtaposed, almost square just after the interbrachial row, becoming gradually longer than wide, rounded posteriorly, those after mid-body narrower; 38 transverse rows between interbrachials and preanals. Four preanal pores are present. Cloacal shield composed of five scales, with small lateral scales. The front limbs have three clawed digits on each hand the rear legs have two digits on each foot.

Color in alcohol based on a fresh specimen. Head is a uniform brown; the lower surface is cream to tan. The dorsum is brown; ventral surface is cream to beige. Some dark flecking on the anterior gulars. Two dorsolateral stipes edge the sides of the hexagonal band. There is a dark gray-brown indistinct mid-dorsal stripe. Lateral body and limbs are slightly darker than the dorsum. The tail's dorsum has three dark stripes on the base of the tail, and they fade posteriorly, the ventral surface of the tail becomes darker distally.

**Similar species** This species can be readily distinguished from all other *Bachia* in the eastern Caribbean by the absence of hexagonal scales (it has only quadrangular shaped scales on the dorsum), three digits on the hands, two digits on the feet, it has 31–32 scale rows around the body and 47–49 transverse rows of dorsals from the occiput to just behind the back legs. *Bachia alleni* and *B. trinitatis* all have a band of hexagonal scales on the dorsum that is usually seven to 12 scales wide, they have four or five digits on the *manus*, and four digits on the *pes*. All of the specimens of the *B. flavescens* group we examined lacked the band of hexagonal scales, some have three fingers and one toe, others have three fingers and two toes, but all have seven rows of gular scales (instead of eight), two supraoculars (instead of three), and four or five upper labials instead of six. This species also has a uniquely shaped cloacal plate composed of three plate-like scales. All other species examined have a cloacal plate consisting of four plate-like scales. Parietal scales are not separated by an interparietal as they are with *B. trinitatis*.

Because *B. flavescens* is a composite species, it is impossible to provide a comparison of *B. whitei* sp. nov. to *B. flavescens*. We did compare *B. whitei* sp. nov. to two candidate species (species A and B) of the *B. cf. flavescens* group

from Guyana. *Bachia whitei* sp. nov. has a more slender-body, a lighter base color in the preserved state, and their heads tend to be narrower (HW/HL  $x = 0.5986$ ,  $n = 2$ ). Guyana *B. cf. flavescens* sp. A have a more robust body, they are darker in color in the preserved state, and their heads tend to be slightly wider (HW/HL  $x = 0.6182$ ,  $n = 2$ ). They have 26 scales rows at mid-body, 35–37 scale rows between the pectoral and anal plates, seven gular scale rows, a pentagonal lower posterior temporal, two supraoculars, four upper labials, and distinctive chin scale morphology. Guyana *B. cf. flavescens* sp. B has a robust body, darker base color with characteristic longitudinal striping pattern in the preserved state, and the head is quite broad (HW/HL = 0.6849,  $n = 1$ ). The specimen has 32 scale rows at mid-body, 38 scale rows between the pectoral and cloacal plates, seven gular scale rows, a quadrangular lower posterior temporal, two supraoculars, five upper labials, and chin scale morphology that closely resembles that of Guyana *Bachia* sp. A.

**Etymology** Named in honor of Graham White, for his contributions to the natural history and conservation of the Trinidad and Tobago fauna. He has extensive knowledge of the biodiversity of Trinidad and Tobago, is an avid birder and a member of the Trinidad and Tobago Rarities Committee since its inception in 1996. He is a long-standing member of the Trinidad and Tobago Field Naturalists' Club (TTFNC) and has served on the Editorial Committee of the Living World Journal published by the TTFNC from 1999 to 2014 and as the Editor 2015-present. Mr. White is also the Chairman of the Asa Wright Nature Centre.

**Distribution** Of the four known specimens, reliable locality data is available only for the type specimen (Hillsborough Dam) and UWIZM.2017.15.6 which was found on Spring Trail, in the Main Ridge Forest Reserve of Tobago (11°16' N 60°35'W). Both locations are on the Tobago's Main Ridge and are about 10.5 km apart.

**Natural history** The first specimen of *B. whitei* sp. nov. collected came from a pile of cut grass/lawn debris that it shared with *Bachia trinitatis*. The debris pile was about 50 m from the forest edge. The other two specimens collected in the late 1970s came from unknown localities. The most recent specimen collected was along a Main Ridge Trail and was under a piece of palm that was laying on wet, bare soil in the closed canopy forest. The female specimen behaved much differently than *B. trinitatis* when we photographed it. *Bachia trinitatis* tried to hide under leaves and debris, while *B. whitei* sp. nov. used its tail to propel its body into the air in attempts to escape.

**Material examined** *Bachia whitei* sp. nov. ( $n = 4$ ) TOBAGO USNM 227942–44, UWIMZ 2017.15.6. *Bachia cf. flavescens* ( $n = 18$ ): BRAZIL–AMNH 64869–71;



COLOMBIA–USNM 65437; GUIANA–AMNH 25086, 29084, 140924, 151917, 151922, 151924, 151931–32; FMNH 23801, MCZ 1688, UMMZ 65170, USNM 566424, 566426. No data: AMNH 3580.

## Discussion

### Systematics and biogeography of the eastern Caribbean *Bachia*

*Bachia trinitatis* from Trinidad, Tobago, and Monos Island form a clade and represent a distinct species as suggested by species delimitation analyses. However, the position of the Monos Island lizard differed between the mitochondrial and nuclear gene trees and suggests further investigation to assess its phylogenetic status in respect to the other two islands. In addition, we cannot exclude the possibility of introgression in the Monos Island population from either Trinidad or Tobago. The calibration ranges remain too broad to point out a particular precise period or mode of colonization. However, dispersal limitations of this leaf litter dweller could suggest vicariance between South America and Trinidad and Tobago as the time estimates predate considerably the late Miocene (circa 5 MYA) when Trinidad detached from Paria Peninsula in northern Venezuela.

The close systematic relationship of *B. alleni* (Grenada), to *B. scolecooides* (southern Amazonia of Brazil) and *B. huallagana* (eastern versant of the Peruvian Andes) and a Pleistocene divergence as shown in our analyses, cannot be explained by a parsimonious biogeographic interpretation. *Bachia huallagana* and *Bachia scolecooides* lack prefrontals, two of them have keeled lanceolate scales covering the body, and only *B. huallagana* has hexagonal scales on the dorsum. The question of *Bachia alleni*'s phylogenetic relationships remains unresolved. In view of the unexpected systematic positioning of *B. alleni* (a formalin preserved specimen, voucher 11769), Galis et al. (2010) addressed the need for further sequencing of fresh individuals from this subspecies. Similarly, *B. alleni*'s sister taxa, *B. scolecooides* (voucher MCZ R-154229) and *B. huallagana* (voucher NHM 193004) were formalin preserved specimens too, and fresh samples may help further clarify the systematics of the genus.

To answer the major biogeographical question on how *Bachia* colonized the non-continental islands of Tobago, Grenada, and the Grenadines, some insight comes from the geology of the islands. Despite geographical proximity, Trinidad and Tobago sit on different tectonic plates and therefore were never part of the same geological structure, ruling out vicariance as a means of speciation between islands. Marine depths separating both islands imply that sea level drops up to circa 100 m are necessary for the formation of dry land bridges and possible crossing over of species

(Murphy 1997). Shallow marine waters (less than 100 m) in the area (and repeated sea level falls throughout the Pliocene–Pleistocene) would have formed multiple dry land connections. Further evidence comes from Jowers et al. (2015) on the centrolenid frog *Hylinobatrachium orientale*, present in Tobago and northern Venezuela but not in Trinidad. Molecular calibrations estimated a Pliocene connection when Tobago was proximal to the Paria Peninsula, and thus accounting for their presence in Tobago and Paria Peninsula but not in Trinidad.

Grenada has a considerable number of faunal links to South America. Germano et al. (2003) list one frog *Leptodactylus validus*; one tortoise *Geochelone carbonaria*; two lizards, *Thecadactylus rapicauda*, *Iguana iguana*; and three snakes *Corallus grenadensis*, *Clelia clelia*, and *Mastigodryas bruesi* that tie the islands to the continent at least at the generic level. Additionally, two snakes collected in the late 1870s, *Liophis melanotus* and *Pseudoboa newwiedii*, have not been seen since and may represent colonization followed by extirpation. Three specimens of *Plica plica* were collected in the nineteenth century on Grenada. These may represent an extirpated population or merely a failed attempt at colonization (Henderson and Murphy 2012; Murphy and Jowers 2013). All of the mainland squamates reported from Grenada and nearby islands are arboreal or terrestrial species with the exception of *Bachia*, a pattern that agrees with the expectation for dispersal suggested by Inger and Voris (2001), for the southeastern Asian herpetofauna.

Few Grenada taxa have been genetically compared to their mainland counterparts for times of divergence. However, Henderson and Hedges (1995) found that the Grenada treeboa *Corallus* was most closely related to Guyana *Corallus*. Colston et al. (2013) suggested over-water dispersal of the boid snake ancestor of *Corallus grenadensis* and *C. cookii* from a northern, Guyanan Shield ancestor. However, their divergence estimates place the age of the time since the most recent common ancestor (TMRCA) of these two species and *C. hortulanus* from Guyana at approximately 2 MYA in the early Pleistocene. Since no evidence exists for a land connection between the Guyana Shield and the Lesser Antilles and the distribution of the common ancestor of *C. grenadensis* and *C. cookii* was in the Lesser Antilles during the Pleistocene, over-water dispersal from South America is suggested. Dispersal of vertebrates from mainland South America to the Lesser Antilles may be the result of the North Brazil–Guyana littoral current combined with the outflow of the Orinoco River (Warne et al. 2002). Furthermore, Camargo et al. (2009) examined *Leptodactylus validus* from the mainland, Trinidad, Tobago, Grenada, and St. Vincent and found the Grenada population was derived from Trinidad animals about 1.25 MYA.

Recent biogeographic work on the fossorial snake *Atractus trilineatus* from Trinidad, Tobago, and Guyana has revealed a close genetic affinity between these locations, suggesting

dispersal through Pleistocene land bridge formations or rafting (Murphy et al. in review). Such findings are surprising given the physical constraints of fossorial species. These studies add to the understanding of the complexity of biogeographic events in the Lesser Antilles and the contrasting modes of speciation (e.g., vicariance, land bridge formations, and rafting) in the area by some taxa.

## Taxonomic implications

Reduced and lost digits and limbs can be found in almost every major clade of squamate reptiles, iguanian, and xantusiid lizards being the exceptions (Wiens et al. 2006). Reduced limbs result in a simplified body plan that constrains morphology and reduces the options of evolution resulting in a convergence of morphology so similar that it has confounded and confused systematic researchers for the last two centuries. The degree of confusion was significant enough that it allowed researchers to place *Bachia* with different numbers of toes into a single species. Such is the case with *Bachia heteropa* and the species confused with it.

*Bachia heteropa* remains a valid taxon. It has three toes, 28–30 scales around mid-body and seven rows of gulars. We have removed the two subspecies: *B. h. lineata* has two toes, 45–49 transverse dorsal scale rows, and seven rows of gulars; and *B. h. marcelae* which has two toes, 39–42 transverse rows of dorsal scales, and five rows of gulars. Both these subspecies are reassigned species status based upon the morphology. Furthermore, we suspect that *B. anomala* Roux is a valid species that was placed in the synonymy of *B. lineata* by Burt and Burt (1933), but there is not enough information available on its morphology to distinguish it from that species.

The identity of *Brachypus cuvieri* Fitzinger remains an enigma. It may be one of the four-toed species discussed here (*Bachia alleni*, *B. trinitatis*, or mainland species awaiting re-discovery). The clue to the identification of this species lies in the four digits on each hind limb with the fourth toe reduced to a single, rounded phalange as suggested by Barbour (1933). *Bachia alleni* has the fourth toe with two phalanges. This suggests that *B. alleni* or *B. trinitatis* could be *Brachypus cuvieri*. However, neither Barbour (1933) nor Thomas (1965) could decide on this and Thomas suggested that the head scalation of *cuvieri* may be distinct from both of these species. We consider *Brachypus cuvieri* Fitzinger *nomen nudum*.

## Conclusions

The morphological diagnosis for *Bachia heteropa* now distinguishes it from other eastern Caribbean *Bachia* and the species is no longer polytypic. The Grenada and Grenadine *B. alleni* is morphologically and genetically distinct from the continental

*B. trinitatis* and *B. heteropa*. With the elevation of most of the former subspecies of *B. heteropa* to species level, the description of a new member of the hex scaled *Bachia* from Caripito, Venezuela, and the description of a new member of the quad scaled *B. flavescens* group from the island of Tobago there are now 31 species in the genus *Bachia*.

Given the holotype and type locality are unknown for *Bachia flavescens*, we suggest the name be considered *nomen nudum* pending further findings. A substantial number of taxa are currently obscured by this name and a complete understanding of the evolution of *Bachia* will require the identification of the various lineages presently concealed by the name *B. flavescens*.

*Bachia whitei* sp. nov. becomes the tenth endemic taxon in the Tobago herpetofauna; joining: the lizard *Gonatodes ocellatus*, the snakes *Erythrolamprus ocellatus*, *Leptophis haileyi*, *Mastigodryas dunni*, *Pristimantis charlottevillensis*, *P. turpinorum*, and the frogs *Mannophryne olmonae*, and *Hyalinobatrachium orientale tobagense*. Tobago's Main Ridge appears to be a micro-biodiversity hot-spot that has been overlooked and under-appreciated. The presence of these species on Tobago and their apparent absence on Trinidad suggests a land connection between Tobago and central Venezuela in the past. Alternatively, the connection may have been Tobago's accretion to Venezuela before it moved to its present position.

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