Systematics, distribution patterns and historical biogeography of the Central America wandering spider genus *Kiekie* Polotow & Brescovit, 2018 (Araneae: Ctenidae)

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Abstract

Kiekie Polotow & Brescovit, 2018 is a Neotropical genus of Ctenidae, with most of its species occuring in Central America. In this study, we review the systematics of *Kiekie* and describe five new species and the unknown females of *K. barrocolorado* Polotow & Brescovit, 2018 and *K. garifuna* Polotow & Brescovit, 2018, and the unknown male of *K. verbena* Polotow & Brescovit, 2018. In addition, we describe~~d~~ the female of *K. montanensis* which was wrongly assigned as *K. griswoldi* Polotow & Brescovit, 2018 (both species are sympatric) and extend the southern distribution of *K. panamensis* Polotow & Brescovit, 2018 to Colombia and Ecuador. We inferred a molecular phylogeny using four nuclear (histone H3, 28S rRNA, 18S rRNA and ITS-2) and three mitochondrial genes (cytochrome c oxidase subunit I or COI, 12S rRNA and 16S rRNA) to test the monophyly of the genus and the evolutionary relationships of its species. Lastly, we reconstruct~~ed~~ the historical biogeography and map~~ped~~ diversity and endemism distributional patterns of the different species. This study increased the number of known species of *Kiekie* from 11 to 16, and we describe a new genus, *Eldivo* which is sister lineage of *Kiekie*. Most of the diversity and endemism of the genus *Kiekie* is located in the montane ecosystems of Costa Rica followed by the lowland rainforest of the Pacific side (Limon Basin). *Kiekie* originated in the North America Tropical region, this genus ~~and~~ started diversifying in the Late Miocene ~~dispersed~~ and spread to ~~Lower~~ Central and South America ~~and started diversifying in the Late Miocene~~. In ~~that region~~the lower Central America, *Kiekie* colonized independently several times ~~the~~ montane ecosystems corresponding to periods of uplifting of Talamanca and Central Cordilleras.

Comentado [aa1]: Is it correct? So far, the species is only known from Panama (WSC 2023)

Comentado [aa2]:

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Introduction

The family Ctenidae includes medium to large (5–50 mm) wandering spiders that typically inhabit the forest floor and low vegetation, although a few species are arboreal (Gasnier *et al.*, 2009). To date, more than ~~500~~ 600 species in ~~49~~ 48 genera have been recorded in this family, most of them distributed in the tropics (World Spider Catalog ~~2022~~2023). Their large size and predominant abundance in most Neotropical rainforests suggest that ctenids play an important role in tropical ecosystems as top generalist predators of invertebrates and small vertebrates (Folt & Lapinski, 2017). Recently, Polotow & Brescovit (2018) described the genus *Kiekie* to accommodate two species of the polyphyletic *Ctenus* and other nine new species. As most species of *Ctenus* and *Spinoctenus* (Polotow & Brescovit, 2014; Hazzi *et al.*, 2018), males of *Kiekie* present a slightly to strongly curved metatarsus IV with various small macrosetae (Fig. 5B). In *Kiekie*, this modified male metatarsus is used during courtship (Eberhard, Barrantes & Conejo personal communication). Moreover, in several species of *Kiekie* (e.g., *K. panamensis* Polotow & Brescovit, 2018, *K. laselva* sp.nov, *K.* ~~*sinautipes*~~ *sinuatipes* (F.O. Pickard-Cambridge, 1897), and *K. valeroi* sp. nov.), males and females have strikingly different coloration patterns. While females are mostly black with few gold or orange lines on the abdomen, males are pale brown with dark brown alternating reticular bands (Fig. 5A, C, E and F). *Kiekie* reaches its higher species diversity in Central America with 15 species distributed in Central America (mainly in Costa Rica), ~~and~~ one species in South America, and one species distributed in both regions (Polotow & Brescovit, 2018). Some species of *Kiekie* are restricted to primary forests and their abundances decrease in less ~~preserved~~ pristine habitats (Hazzi *et al.*, 2020). In addition, *Kiekie* species are restricted to different biomes, encompassing high montane to lowland areas, and dry to rain forests biomes.

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Lower Central America is a highly diverse region that provides a geologically complex and dynamic model for studying the assembly and spatial evolution of a Neotropical biota (Bagley & Johnson, 2017; Mendoza *et al.*, 2019). Three important tectonic events have been suggested to summarize the main changes in the structural styles along the forearc of this region: (1) subduction of an ancient ridge during the Neogene (Brandes & Winsemann, 2018); (2) reorganization of tectonic plates during the middle to late Miocene (Mescua *et al.*, 2017; Porras *et al.*, 2021); and arrival of the Cocos Ridge at the Middle America trench in the Pliocene (Abratis & Wo, 2001; Morell, 2016). The high diversity of *Kiekie* in this region, and the restricted distribution of most of its species to specific ecosystems and elevation gradients, makes this genus a good model to study how geological events have contributed to the diversification of the Lower Central American fauna.

While carrying extensive fieldwork in Central America and having examined collections in several natural history museums from Central America, we have discovered several new species of *Kiekie* and new geographic range extensions for the majority of previously described species. In addition, we were able to get fresh samples of most of the *Kiekie* species suitable for genetic sequencing and phylogenetic analysis. Therefore, in this study we review the systematics of *Kiekie* and described six new species and the unknown females of *K. barrocolorado* Polotow & Brescovit, 2018 and *K. garifuna* Polotow & Brescovit, 2018, and the unknown male of *K. verbena*. In addition, we described the female of *K. montanensis* Polotow & Brescovit, 2018 (Polotow & Brescovit (2018) incorrectly assigned a female of *K. griswoldi* Polotow & Brescovit, 2018 as the female of *K. montanensis*- these two species are sympatric). We inferred a molecular phylogeny using four nuclear (histone H3, 28S, 18S and ITS-2) and three mitochondrial genes (12S, 16S and COI) to test the monophyly of *Kieke* and the evolutionary relationships of its

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87 species. With this framework in place, we address the following questions relating to the
88 historical biogeography of the genus: 1) Does the higher diversity of *Kiekie* in Central America
89 correspond with the ancestral area of the genus? or did *Kieke* originate in South America and
90 dispersed to Central America? and 2) Did *Kiekie* originate in lowland or in montane ecosystems?
91 What is the evolutionary history of transitions between lowland and montane habitats? Shortly
92 after the completion of our study two new species of *Kiekie* from Panama were described by
93 Omelko (2023) and these are now included in the taxonomic section with a revised generic
94 diagnosis. Although we have not examined the holotypes of these two latter species, the
95 descriptions and diagnoses are sufficient for accurate identifications. In the present work we
96 have increased the number of described species of *Kiekie* from 11 to 18 and discovered a new
97 genus, *Eldivo* gen. n., which is sister lineage of *Kiekie*.
98
99 ## Materials & Methods
100
101 ## Museum abbreviations
102 The material examined and/or collected belongs to the following museums: MUSENUV, Museo
103 Entomológico de la Universidad del Valle, Cali, Colombia (J. Cabra); MZUCR, Museo de
104 Zoología, Escuela de Biología, Universidad de Costa Rica (G. Barrantes); MNCR Museo
105 Nacional de Costa Rica (M. Sánchez-Ocampo, includes former Instituto Nacional de
106 Biodiversidad de Costa Rica (INBio) collection); MCZ, Museum of Comparative Zoology,
107 Harvard University, Cambridge, USA (G. Giribet); CNAN-AR, National Arachnid Collection at
108 Universidad Nacional Autónoma de México, Mexico (O. Francke and E. González).
109 ## Morphological examination and description of species

Specimens were preserved in 95% ethanol. Descriptions and terminology follow Höfer *et al.* (1994) and Simó & Brescovit (2001). All measurements were given in millimeters and were taken using Leica Application Software (3.4.2) in a Leica M205A ~~stereomircroscope~~stereomicroscope and a Leica DFC425 camera. Epigyna were digested with pancreatin solution (Álvarez-Padilla & Hormiga, 2007) to enable the study of internal structures. Digital images were made with a Leica M205A stereomicroscope adapted to a Leica DFC425 camera digital camera. Extended focal range images were composed using the software package Helicon Focus (version 6.7.1; www.heliconsoft.com) from Helicon Soft Ltd. Digital SEM photographs were taken using a LEO 1430VP scanning electron microscope from the scanning laboratory, Department of Biology of The George Washington University. For SEM preparation, structures were cleaned ultrasonically, transferred to 95% (if they were in 75-80% ethanol originally) and then to 100% ethanol for 10 min in each immersion before being air-dried. The specimens were then coated with Au-Pd. The following abbreviations are used: C, conductor; CD, copulatory ducts; CO, copulatory opening; E, embolus; FD, fertilization ducts; LP, lateral projection; MA, median apophysis; MF, median field of epigynum; RTA, retrolateral tibial apophysis; S, spermathecae. The distribution maps were elaborated with ArcGIS (ESRI) v 10, with the spatial analyst extension.

DNA Sequencing Methods

Sampling design. We sequenced a total of 30 *Kiekie* specimens representing 14 of the 16 known species. When possible, each species was represented by a male and a female, in order to ensure the correct sex was matched for each species. Based on the phylogenetic relationships among genera within Cteninae (Hazzi & Hormiga 2022), we included taxa representing the "American clade" as an outgroup, and rooted the tree with *Anahita* sp. The final matrix includes 57

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terminals, of which 30 belong to *Kiekie* (Table S1). Tissue from the coxae and femora was used for DNA extraction using the Qiagen DNEasy kit and the rest of the specimen was preserved as a voucher. Seven markers were amplified for analyses: mitochondrial ribosomal markers 12S rRNA (~400 bp) and 16S rRNA (~550 bp), cytoplasmic ribosomal markers 18S rRNA (~800 bp), 28S rRNA (~2200 bp) and ITS-2 (~350 bp), nuclear protein-coding gene histone H3 (~320 bp) and mitochondrial protein-coding gene cytochrome c oxidase subunit I or COI (~800 bp). PCR was achieved with the Promega GoTaq kit, using the same primers listed in Hazzi & and Hormiga (2022). Sequence contigs were formed using GENEIOUS 6.0.6 (http://www.geneious.com; Kearse et al., 2012) and protein coding gene sequences were checked for stop codons, then queried against the NCBI BLAST nucleotide database to check for contamination.

Phylogenetic analysis

Phylogenetic analyses were performed using equal weight parsimony (MP) and maximum likelihood (ML). For the model-based analysis, the best partitioning scheme and substitution models were explored using ModelFinder implemented in IQTREE (Nguyen *et al.*, 2015; Kalyaanamoorthy *et al.*, 2017), selecting partition merging and the corrected Akaike information criterion (AICc). We partitioned protein coding genes (H3 and COI) into codon position, and each ribosomal gene was treated as a whole (ITS-2, 28S, 12S, 16S and 18S), for a total of eleven partitions. The maximum likelihood analyses were performed with the package IQ-TREE 1.4.2 (Nguyen *et al.*, 2015) and ultrafast bootstrap (Minh, Nguyen, & Von Haeseler, 2013) were used as a support measure. The parsimony analyses were carried out in TNT v. 1.5 (Goloboff & Catalano, 2016) using 500 random addition sequences followed by TBR branch swapping

algorithm and retaining 10 trees per replicate until the length was hit five times. Branch support was assessed using 1000 replicates of jackknife resampling (Farris *et al.*, 1996).

A Bayesian inference analysis was carried out to estimate a dated phylogeny using BEAST version 2.5.2. (Bouckaert *et al.*, 2014). The analysis was run with linked trees, an uncorrelated lognormal clock, and a birth–death model for the tree prior. All markers were unlinked for site and clock models apart from the mitochondrial rRNA genes 16S and 12S because ModelFinder indicated that these two markers can be treated as a single partition. All the remaining markers were unlinked for site and clock models. Due to reduced computation time and problems of chains convergence in the dating analysis, the likelihood tree topology was constrained by converting it into an ultrametric tree using a penalized likelihood method with the chronos function in R (ape v5.3; Paradis et al., 2019). Three independent runs of 200 million generations each from four Markov Chain Monte Carlo chains were performed and post-burn-in results were combined using Logcombiner 2.5.1. Trees and parameters were sampled every 10,000 generations, 25% of the generations were discarded as burn-in and the remainder were used to calculate posterior parameters. We used Tracer v. 1.7 (Rambaut *et al.*, 2018) to examine chains to convergence (ESS > 200). Trees were summarized with TreeAnnotator, which is distributed as part of the BEAST package.

Due to the lack of fossils in Ctenidae, we used gene substitution rates reported for lycosoid spiders (Piacentini & Ramírez, 2019). We prefer to use these rates rather than the rates reported in Hazzi & Hormiga (2022) because of the lower rates reported in mitochondrial genes due to genome saturation. In addition, we incorporated one calibration point within Ctenidae based on a biogeographic event related to biome formation in the Tropical Andes (Jaramillo, 2019). We set

a maximum crown age of 10 Ma with a uniform distribution for *Spinoctenus* Hazzi *et al*., 2018. The genus *Spinoctenus* is composed of 12 species distributed in the tropical Andes and Chocó biogeographical regions (Hazzi *et al*., 2018). Most *Spinoctenus* diversity is found in the Andes (eight species) and using event-based biogeographic analyses on a morphological phylogeny, Hazzi *et al*. (2018) inferred an Andean origin for this genus. Both the most recent molecular phylogeny of Ctenidae (Hazzi & Hormiga 2022) and the morphological phylogeny of Hazzi et al. (2018) indicate that the Andean species *Spinoctenus eberhardi* Hazzi et al., 2018 and *S. stephaniae* Hazzi et al., 2018 diverged early within the genus. These two species are endemic to cloud forest ecosystems above 2000 m, a biome that was completely absent from the north of South America before 10 Ma (Jaramillo, 2019).

Species model distributions and Distribution patterns of diversity and endemism.

We estimated the distribution of *Kiekie* species using the Maxent algorithm (Phillips, Anderson, & Schapire, 2006; Elith *et al.*, 2011). We used occurrence records from the literature, fieldwork and museum specimens. To mitigate the impact of uneven sampling in our occurrence data, we applied a distance correction by taking only one point within a radius of 10 km. We obtained 19 bioclimatic predictor layers summarizing annual trends, seasonality and extremes in precipitation and temperature at a spatial resolution of 30 arc-seconds (i.e. 1 km2) from the WorldClim database (Fick & Hijmans, 2017). To reduce collinearity of the predictor variables, we selected the following variables (Pearson <0.7): annual mean temperature (Bio1), mean diurnal range (Bio2), temperature seasonality (Bio4), annual precipitation (Bio12), precipitation seasonality (Bio15) and precipitation of warmest quarter (Bio18). The area selected for modelling was the trans-Andean region ~~until~~ through the Neotropical Caribbean area of Mexico.

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We ran the models selecting a logistic output and random seed, and the maximum number of background points maintained at 10,000. To assess model performance, we applied k-fold cross validation procedure splitting the occurrences into training and testing records (70% and 30%, respectively), and replicating this process 15 times. Models were evaluated using the Area Under the Curve Metric (AUC) that compares model results with null expectations using a threshold-independent measure. We averaged the AUC values obtained in the replicates and created confidence intervals values to assess model significance from random model expectations (AUC> 0.5). To make the binary distribution maps, habitat suitability values were converted in presence and absence using the 5^{th} percentile as the threshold value (Liu *et al.*, 2005; Liu, White, & Newell, 2013). In addition, areas with high probability of presence, but disjunct from areas where specimens have been recorded, were excluded from the prediction (Helgen *et al.*, 2013). For species of *Kiekie* ~~species~~ with less than five records, we generated minimum convex polygon corrected by elevation range. For species with less than three records, we generated buffers of 10km^2 for each record.

Species richness and endemism maps were generated in Biodiverse package (Laffan, Lubarsky, & Rosauer, 2010) based on the distribution ranges estimated for each *Kiekie* species described above and using 0.05° of spatial resolution. Endemism maps were computed using weighted endemism. In this metric, species richness is weighted by the inverse of the distribution range size of each species, so that pools of species that occur over smaller ranges are given higher scores. In addition, weighted endemism corrects for unweighted species richness, to distinguish per-species endemism from richness-based endemism (Crisp *et al.*, 2001).

Historical Biogeography Analysis

Based on the geographical distribution patterns of the species of *Kiekie*, we conducted the analysis using the following biogeographical units: Trans-Andean, Lower Central America, Talamanca Cordillera and Tropical North America. These regions are divided by well-known topographical and climatic barriers ~~that divided~~for other taxa in Central America (Bagley & Johnson, 2017; Mendoza *et al.*, 2019), and additionally supported by the distribution patterns of *Kiekie* species. We carried out biogeographic analyses using the RASP package (Yu *et al.*, 2015) which compares models of range evolution in a phylogenetic framework. We tested six biogeographic models using the Akaike information criterion (AICc): DIVA (Ronquist, 1997), DEC (Ree & Smith, 2008) and BayAREA (Landis *et al.*, 2013). Each model was run with and without the founder-speciation event (j) (Matzke, 2014). The statistical comparisons of biogeographic models with and without the inclusion of the J parameter has been previously criticized upon the argument that the J parameter artificially inflates the contribution of cladogenetic events to the likelihood, and leads to underestimates of anagenetic, time-dependent ranges evolution (Ree & Sanmartín, 2018). However, models without the J parameters are usually inadequate in the common situations when most species have narrowed geographical ranges (single areas) (Matzke, 2022) . Additionally, statistical comparison between models with and without the J parameter are identical to comparison of two ClaSSE submodels (Matzke, 2022). Therefore, we considered valid the used and statistical comparison between biogeographic models with and without the inclusion of the J parameter.

Nomenclatural acts

According to the International Commission on Zoological Nomenclature (ICZN), the electronic version of this article in portable document format (PDF) will represent a published work. The new species names contained in the electronic version are effectively published under that Code

from the electronic edition alone. This article and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix http://zoobank.org/. The LSID for this publication is: urn:lsid:zoobank.org:pub:A693D4C7-C4DD-4F69-9D2A-DDD62527B4CF.

Results

Phylogenetics

The likelihood analysis indicated that *Kiekie* is monophyletic with high support (Fig. 1) and placed within a clade of North and Central American ctenids of the genera *Leptoctenus* and *Ctenus*. The parsimony analysis also showed *Kiekie* as monophyletic but with low support (Fig. S1). The sister group of *Kiekie* is an undescribed species from Mexico which lacks *Kiekie*'s morphological synapomorphies and diagnostic characters, and therefore is proposed here as a new genus (*Eldivo* n. gen.). This sister group relationship is highly supported in both the likelihood and parsimony analyses. Both analyses also show several well-supported intrageneric groups in *Kiekie*. *Kiekie garifuna* is placed sister to the remaining species in the genus and two well-supported clades are identified. The first clade includes the species *Kiekie barrocolorado*, *K. verbena*, *K. montanensis* and *K. curvipes* (Keyserling, 1881). Within this clade the sister relationship between *K. curvipes* and *K. montanensis* is highly supported. The second clade includes the species *K. sarapiqui* Polotow & Brescovit, 2018, *K. valeroi*, *K. laselva* sp.nov, *K. panamensis*, and *K.griswoldi* .

Biogeography

The species richness map indicated that *Kiekie* reaches its highest diversity in montane ecosystems of Costa Rica, followed by the lowlands of the Pacific area of Costa Rica (Fig. 2A). In addition, most of the endemism of this genus is concentrated in the montane ecosystems of Costa Rica (Fig. 2B). Model testing provided stronger support for models with the jump dispersal parameter over models without it. Models with the j parameter gave similar results in the ancestral area reconstruction for *Kiekie*, and they could not be statistically distinguished from each other (AIC weights: DEC+J= 0.38, DIVA+J=0.35, BAYESAREA+j=0.28). These analyses support an origin of *Kiekie* during the Late Miocene in the Tropical North America region and subsequently dispersed to Central America, where its highest diversity arises (Fig. 3A and B, event 1). The following description of the historical biogeography of *Kiekie* is based on the results of DEC+J model. One event of dispersal (event 2) from Talamanca Cordillera to Lower Central America originated two species: *Kiekie tirimbina* and *K. barrocolorado*. Then, there was an event of dispersal (event 3) from Lower Central America back to the cordillera Talamanca originating the species *K. verbena* and *K. montanensis*. The widespread species *K. curvipes* originated from the latter lineage of montane species, dispersing into the lowlands of Central and Tropical North America (event 4). The clade comprising the montane species *K. ~~sinautipes~~ sinuatipes* and *K. barrentesi* likely originated ~~in~~ from the lowlands of Central America (event 5) but there is a high uncertainty in the area reconstruction of the node preceding this lineage. Finally, there were two dispersal events (event 6 and 7) from the lowlands of Central America to Talamanca Cordillera and the Trans-Andean region, originating the montane clade *K. lascruces* and *K. griswoldi*, and the ~~South~~ Central America species *K. panamensis*, respectively.

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Taxonomy

Family Ctenidae Keyserling, 1877

Subfamily Cteninae Keyserling, 1877

Genus *Kiekie* Polotow & Brescovit, 2018

Type **species**: *Kiekie* ~~*sinautipes*~~ *sinuatipes* F.O. Pickard-Cambridge, 1897.

Composition: 16 species: *Kiekie sinuatipes* (F.O. Pickard-Cambridge, 1897), *K. curvipes* (Keyserling, 1881), *K. garifuna* Polotow & Brescovit, 2018, *K. verbena* Polotow & Brescovit, 2018, *K. sarapiqui* Polotow & Brescovit, 2018, *K. griswoldi* Polotow & Brescovit, 2018, *K. barrocolorado* Polotow & Brescovit, 2018, *K. panamensis* Polotow & Brescovit, 2018, *K. montanensis* Polotow & Brescovit, 2018, and *K. antioquia* Polotow & Brescovit, 2018, *K. laselva* sp. nov., *K. valeroi* sp. nov., *K. barrentesi* sp. nov., *K. lamuerte* sp. nov., *K. bernali* sp. nov., *K. tirimbina* sp. nov.

Diagnosis. Males of *Kiekie* can be distinguished from the remaining Ctenidae by three synapomorphies: an elongated embolus with a laminar process (Figs. 23A–F, 24A–F), conductor resembling an open fan (Figs. 23A–F, 25A–F), and locking lobes located at posterior and sometimes in retro-posterior side (Figs. 25B, 26C), instead of posterior prolateral as most ctenines. Some females of *Kiekie* (*K.* ~~*sinautipes*~~*sinuatipes*, *K. barrentesi*, *K. sarapiqui*, *K. laselva*, *K. valeroi*, *K. panamensis*, *K. griswoldi* and *K. lascruces*) differ from the remaining Ctenidae by elongate curved copulatory ducts that projects in the anterior area of the epigynum (Figs. 6B, 16B and 20B) as opposed to short and straight, and large copulatory openings instead of small. However, females of the remaining species cannot be accurately distinguished from *Eldivo* or other Mesoamerican ctenids.

Natural History. *Kiekie* species live in a variety of ecosystems and across a wide elevational range, from sea level to 2500m. As other ctenines, *Kiekie* species are nocturnal forest dwellers,

living on ground covered with leaf litter and on some ~~occasions~~ cases on vegetation in the understory. During the day, these spiders can be found hiding under leaf litter or decaying fallen logs. *Kiekie sarapiqui*, *K. valeroi*, *K. curvipes*, *K. garifuna*, *K. tirimbina*, *K. laselva* and *K. panamensis* are found in lowland tropical rain forests ~~ecosystems with low elevation~~ (>700m). However, *K. curvipes* and *K. panamensis* are widespread species that can be found in less humid ecosystems and higher elevations (~1500m). In Costa Rica, there are high levels of species sympatry in *Kiekie*. The most striking case occurs in the Tirimbina Biological ~~Ttation~~Station, where five species can be found in sympatry: *K. vale~~o~~roi*, *K. curvipes*, *K. sarapiqui*, *K. laselva* and *K. tirimbina*, the latter being rarely observed. *Kiekie valeroi* and *K. sarapiqui* are more abundant in the preserved forest and *K. curvipes* is abundant in both preserved and disturbed environments. These species live also in sympatry with other ctenids, such as *Phoneutria depilata* (Strand, 1909) and the arboreal species *Phymatoctenus cf. sassii* Reimoser, 1939. In ~~montane ecosystems of~~the Talamanca cordillera, there are four species restricted to montane ecosystems: *K. bernali*, *K. griswoldi*, *K. las cruces*, *K. lamuerte*, *K. ~~sinautipes~~sinuatipes*, *K. barrentesi*, *K. verbena*, and *K. montanensis*. In the north of Costa Rica, it is possible to find in some localities *K. griswoldi*, *K. sinautipes*, *K. verbena* and *K. barrentesi* in sympatry. In the campus of Universidad of Costa Rica, *K. barrentesi* and *K. verbena* are easily found in very disturbed environments. In the southern part of the cordillera, *K. lascruces* inhabits in sympatry with *K. montanensis*. Hazzi et al. (2020) studied the effects of forest succession and microenvironmental variables on the abundance of ctenid spiders in Las Cruces Biological Station, a tropical montane rainforest. This study found four ctenids living in sympatry: *Spinoctenus escalerete* Hazzi et al., 2018, *K. griswoldi*, and three species with much lower abundances. The larger species, *K. griswoldi* was significantly more abundant in primary than in

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342 secondary forest. Conversely, *S. escalerete* was more abundant in the secondary forest. In
343 addition, this study found that while abundance of *K. lascruces* was positively related with leaf
344 litter depth, the abundance of *S. escalerete* was negatively related to litter depth. This study also
345 reported an event of intraguild predation where an adult female of *K. griswoldi* was eating an
346 adult male of *S. escalerete* in the primary forest. In Cali, Colombia, females of *K. panamensis*
347 were observed with egg sacs in both captivity and in the field. The egg sacs were white with a
348 flat face attached to the substrate (i.e. litter leaf or the wall of the terrarium) and a convex face. In
349 captivity, we observed that females protected the egg sacs by standing over them. Spiderlings
350 emerged between 29–31 days (n=2). After hatching, spiderlings emerged and built an irregular
351 web where they remained until their second molt. These small observations about the
352 reproductive behavior of *K. panamensis* are consistent with those reported in *Phoneutria*
353 *depilata* (Hazzi 2014).
354 ***Kiekie antioquia* Polotow and Brescovit, 2018**
355 *Holotype: Female holotype deposited in* MCZ30617, not examined.
356 Diagnosis. Females of *Kiekie antioquia* (fig. 14A–B, Polotow & Brescovit 2018) resemble those
357 of *K. sinuatipes* (fig. 5A–B, Polotow & Brescovit 2018) by the large median field of the
358 epigynum, but it can be distinguished by the narrow median field and elongated and narrow
359 lateral projections. Internally, it can be distinguished by smaller spermathecae and sinuous
360 copulatory ducts (Polotow & Brescovit 2018).
361
362 ***Kiekie almae* Omelko, 2023**
363 *Kiekie almae* Omelko, 2023: 276, f. 1–5, 11–14, 19–22, 27–30, 36–37 (male holotype and three
364 female paratypes from Panama, deposited in ZMMU, Moscow, not examined).

Diagnosis. Males of *K. almae* resemble those of *K. lamuerte* sp. nov, in the general conformation of the palp (Fig. 22; Omelko 2023: fig. 12) but differ by the medial position of the RTA (Omelko 2023, fig: 12), in contrast with the more apical RTA in *K. lamuerte* (Fig. 13). Females of *K. almae* resemble those of *K. garifuna* in the wide anterior area of the epigynal median sector (Fig. 13D; Omelko: figs. 27 and 28), but differ by being ~~more square and flat~~squarer and flatter, in contrast with the ovoid and elevated anterior area in *K. garifuna*.

Distribution. Known only from the type locality in the Chiriquí Province of Panama.

***Kiekie barrantesi* sp. nov.**

Figs. 6, 24B, 26B.

Type Material.

Holotype. COSTA RICA: Male from San Jose province, San Pedro, campus of Universidad of Costa Rica (9.9376N, -84.0507, 1200m), 10.VI-2018, N. Hazzi (MCZ IZ 167568). *Paratypes*. ~~3~~ Three males and ~~3~~ three females, same data as holotype; ~~2~~ two females from William ~~Eberhard~~ and Mary Jane Eberhard~~s~~ house, San Antonio de Escazu, San Jose province (9.8975N, 84.1377, 1330m), 20.VII.2018, N. Hazzi (MCZ IZ 167569).

Other material examined. COSTA RICA: San Jose province: One male and one female, San Jose, Sabanas Sur (9.9308N, -84.0933W), 12.V.1981, G. Biamonte (UCR); one female and one male, San Rafel de Moravia (9.9688N, -84.0489W), 00.V.1963, C. Valerio (UCR); Tibas, Parques del Norte (9.9666N, -84.0736W), C. Herrera (MNCR); Alajuela province: One Male, Palmares (10.0607N, -84.4377), 20.IV.2013, S. Zamora; Cartago province: One female, Jimenez, Pejibaye, Copal Biological Station (9.7834N, -83.7519W), 00.IV.2005 (MNCR); Heredia province: One female, Calle los Gemelos (9.9834N, -84.1136W), 27.IV.1990, J. Carvajal

(MNCR); San Joaquin, Flores (10.0062N, -84.1537W), 14.IV.1997 (MNCR); two males, Santo Domingo, Santa Rosa (9.9736N, -84.0944), 15.II.1995, C. Viquez (MNCR). PANAMA: Chiriquí province: One male and one female, Fortuna Reserve (8.711N, -82.171, 1800m), 4.XII.2018, N. Hazzi (MCZ IZ 167570).

Etymology. This species is dedicated to Gilbert Barrantes, professor from Universidad of Costa Rica, who has made important contributions to the study of spider behavior and natural history.

Diagnosis. Males resemble ~~to~~ those of *K. panamensis* and *K. valeroi*, but can be distinguished from them by the orientation of the sclerotized process at the base of the embolus (Fig. 6B and 24B), circular shaped-bulb (Fig. 6B and 26B) (the other two species have oval bulbs being longer than wide) and a small RTA (Fig. 6B–C and 24B). Females resemble those of *K. sinautipes* by the conformation of the copulatory ducts (Figs. 6E and 18E) but can be distinguished from them by an internal projection of the spermatheca (Fig. 6E), and anterior area of the median sector narrow (Fig. 6D) instead of wide.

Male (MCZ IZ 167568 from Campus of Universidad of Costa Rica, San Pedro, San José province, Costa Rica). Total length 27.00. Carapace 16.62 long and 12.08 wide. AME 0.60 ALE 0.52, PME 0.71, PLE 0.76. Sternum 6.73 long and 5.88 wide, labium 1.92 long and 1.70 wide, endites 2.93 long and 1.88 wide. Leg measurements: I: femur 18.81, patella 6.85, tibia 22.4, metatarsus 17.40, tarsus 6.12, total; II: 19.44, 6.27, 20.21, 16.55, 6.50, total; III: 15.83, 6.03, 15.95, 16.17, 5.50, total; IV: 20.40, 6.10, 20.50, 22.90, tarsus (missing), total. Leg spination: leg I-II tibia v2-2-2-2-2, d0-0-1-0, p1-1-0, r1-1-0, metatarsus v2-2-2; leg III-tibia v2-2-2, d1-1-1, p1-0-1, r1-0-1, metatarsus v2-2-2, d0-1-0, p1-1-2, r1-1-2; leg IV-tibia v-2-2-2, d1-1-1, p1-01, r1-0-1, metatarsus modified. Palp: RTA spiniform in ventral view and with wide apex (Fig. 6C), embolus elongated and flagelliform, presence of sclerotized process at the base of the embolus

(Figs. 6B and 24B), median apophysis with cup-shaped aperture visible ventrally (Fig. 24B and 26B); conductor with a narrow base and large apex, covering the tip of the embolus (Fig. 6B, 24B and 26B).

Female (MCZ IZ 167569-1, from Campus of Universidad of Costa Rica, San Pedro, San José province, Costa Rica). Total length 35.18. Carapace 16.22 long and 12.64 wide. AME 0.70, ALE 0.50, PME 0.80, PLE 0.80. Sternum 6.73 long and 6.06, labium 2.27 long and 2.13 wide, endites 4.61 long and 2.50 wide. Leg measurements: I: femur 15.16, patella 7.10. tibia 16.71, metatarsus 12.83, tarsus 5.40, total 57.20; II: 15.13, 6.63, 15.39, 12.33, 5.02, total 54.50; III: 13.56, 5.50, 12.60, 12.44, 4.50, total 48.60; IV: 17.08, 6.35, 16.68, 19.14, 5.50, total 64.75. Leg spination: tibia I-II v2-2-2-2-2, metatarsus I-II v2-2-2-2-2, tibia III v-2-2-2, d1-1-1, p1-0-1, r1-0-1, metatarsus v-2-2-2, p1-1-2, r1-1-1; tibia IV v2-2-2 d1-1-1, r1-0-1, p1-0-1, metatarsus v-2-2-2, d0-1-0, p1-1-2, r1-1-2. Epigynum (Fig. 6AD: median sector with anterior area narrow and posterior area wide, with margins sclerotized; lateral fields with a large hyaline projection, lateral projections elongated, originated medially. Vulva (Fig. 6E). Copulatory ducts elongated, curved, with a 360° turn (as in *K. sinautipes*); spermathecae elongated with an internal projection; fertilization ducts small and located posteriorly.

Variation. Males (n=4): Total length 27.00–34.09, carapace 14.98–19.11, femur I 18.81–20.30. Females (n=6): Total length 26.89–36.50, carapace 13.76–16.22, femur I 13.90–15.16.

Distribution. Montane ecosystems of Costa Rica (Fig. 27).

***Kiekie barrocolorado* Polotow & Brescovit, 2018**

Fig. 7.

Holotype: Male holotype from Panama, Canal Zone, Barro Colorado Island (9.15, -79.85), VI–VII.1936,
A.M. Chickering coll., (deposited in MCZ 79093, not examined).

Material examined. PANAMA: ~~2~~ Two males and ~~1~~ one female from Chiriquí province, Puerto Amuelles, banana plantations (8.3408N, 82.8069W, 10m), 29.VII.2019, N. Hazzi, T. Rios and J. Bernal (MCZ IZ 167571). COSTA RICA: Puntarenas province, Tres Colinas Station (9.3374N, 83.9108W), 17.IX. 2002, R. Gonzalez (MNCR).

Diagnosis. Males of *Kiekie barrocolorado* resemble those of *K. garifuna* by the embolus shape and conductor, but differ by the RTA position, which is distant from the apical border of the tibia (Figs. 7C) as opposed to be positioned at the apex, and by the median apophysis shape, with a narrow and longer base (Figs. 7B) instead of wide and long as most species (Polotow & Brescovit 2018). Females differ from all other species in the genus by the uniquely shaped pigynal median sector (Figs. 17D), with a pointed projection in the posterior area and anterior area broad, with two lobes, and by having small and inconspicuous copulatory openings (Figs. 7E).

Female (MCZ IZ 167571 , Puerto Amuelles, Chiriquí province, Panama). Total length 20.30. Carapace 10.77 long and 8.72 wide. AME 0.50, ALE 0.38, PME 0.63, PLE 0.60. Sternum 4.60 long and 4.40 wide, labium 1.56 long and 1.38 wide, endites 2.89 long and 1.89 wide. Leg measurements: I: femur 8.73, 4.32, 8.06, 6.87, 2.60, total 30.58; II: 8.02, 3.72, 7.52, 6.70, 2.54, total 28.50; III: 6.57, 3.12, 6.08, 6.49, 2.30, total 24.56; IV: 8.96, 3.71, 8.72, 10.07, 3.07, total 34.53. Leg spination: tibia I-II v2-2-2-2-2, metatarsus I-II v2-2-2-2-2, tibia III v-2-2-2, d1-1-1, p1-0-1, r1-0-1, metatarsus v2-2-2, d0-1-0, p1-1-2, r1-1-2; IV-tibia v2-2-2, d1-1-1, 1-0-1, p1-0-1, metatarsus v-2-2-2, d0-1-0, p1-1-2, r1-1-2. Epigynum (Fig. 7D): median sector with a pointed or

oval projection in the posterior area, anterior area broad with two lobes, lateral fields without large hyaline projection and copulatory openings small and inconspicuous, lateral process elongated and originated medially. Vulva (Fig. 7E). Copulatory ducts curved, with a broad less sclerotized area at the beginning of the copulatory openings; spermathecae bean-shaped; fertilization ducts small and located posteriorly.

Male. Described by Polotow & Brescovit (2018).

Distribution. Lowland ecosystems of Costa Rica and Panama (Fig. 27).

***Kiekie bernali* sp. nov.**

Figs. 4D, 8, 23B and 25B.

Type material.

Holotype. PANAMA: Male from Chiriquí province, Fortuna Reserve (8.711N, -82.171, 1800m), 4.XII.2018, N. Hazzi (MCZ IZ 167572). *Paratype*s: ~~6~~ Six males and ~~5~~five females, same data as holotype (MCZ IZ 167573).

Diagnosis. This is the smallest species of *Kieke* and it differs from the other congeneric species by the following unique combination of characters: males with prominent subtegulum in the exterior face of the embolus (Figs. 8B, 23B and 25B, in the remaining species the subtegulum is visible in the exterior face), retrolateral tibial apophysis apically truncated (Fig. 8C), leaf-shaped median apophysis (Figs. 8B, 23B and 25B) and metatarsus IV unmodified. The epigynum resembles that of *K. lamuerte* by the short copulatory ducts and small copulatory openings (Figs. 8D–E and 13D–E)), but it differs by the less sclerotized margins of the median sector and the bean-shaped spermathecae instead of kidney-shaped (Fig. 8D).

Etymology: This species is dedicated to the memory of the late Juan Bernal, entomologist from Universidad of Chiriquí who contributed with numerous studies to the diversity and distribution of aquatic insects in Panama.

Description. *Male* (MCZ IZ 167572, from Fortuna Reserve, Chiriquí province, Panama). Total length 10.60. Carapace 5.90 long and 4.99 wide, eye diameters: AME 0.34, ALE 0.21, PME 0.40, PLE 0.38. Clypeal height 0.17, sternum long, wide; labium 1.65 long, 1.30 wide. Sternum 2.58 long and 2.50 wide, labium 0.54 long and 0.86 wide, endites 1.40 long and 0.88 wide. Leg measurements: I: femur 6.52, patella 1.9, tibia 7.42, metatarsus 5.49, tarsus 2.72, total 24.05; II: 6.69, 2.22, 6.49, 5.64, 2.21, total 23.25; III, 5.98, 2.00, 5.01, 5.38, 2.01, total 20.38; IV 7.58, 2.03, 7.10, 8.80, 3.18, total 28.69. Leg spination: leg I tibia v2-2-2-2-2, p0-1-0, r1-0-0, metatarsus v2-2-2, p1-1-0 r0-1-0 leg II tibia v-2-2-2-2-2, d0-0-1-0, p0-1-0, r1-1-0, metatarsus v2-2-2, p1-1-0, r1-1-0, leg III v2-1-2-2, p1-0-1-0, r1-1-1, metatarsus v2-2-2-2, d0-1-0, r1-1-1, leg IV tibia v2-2-2, d1-1-1, p-0-1-1-0, r0-1-1-0, metatarsus v2-2-2, d0-1-1, p0-1-2, r0-1-2. Palp: RTA small and truncated at the apex (Fig. 8C); embolus flagelliform and laminar with a sclerotized dark area at the base (Fig. 8B, 23B and 25B); median apophysis with a long base and horizontally oriented (Fig. 8B, 23B and 25B); conductor with a narrow base and large apex, covering the tip of the embolus (Fig. 8B, 23B and 25B).

Female (MCZ IZ 167573-1, from Fortuna Reserve, Chiriquí province, Panama). Total length 12.22. Carapace 6.34 long and 4.94 wide, eye diameter: AME 0.34, ALE 0.25, PME 0.37, PLE 0.38. Clypeal height 0.15, sternum long 2.59 and 2.54 wide, endites 1.79 long and 1.04 wide, labium 0.72 long and 0.91 wide. Leg measurements: I: femur 4.87, patella 1.95, tibia 4.91, metatarsus 3.65, tarsus 1.65, total 17.03; II, 4.66, 2.14, 4.33, 3.55, 1.60, total 16.28; III 4.17, 2.03, 3.55, 3.67, 1.71, total 15.13; IV 5.52, 1.80, 4.74, 6.15, 2.46, total 20.67. Leg spination: tibia

I-II v2-2-2-2-2, metatarsus I-II v2-2-2-2-2; III tibia v2-2-2, d0-1-1-0, r1-0-1, p1-0-1; metatarsus v2-2-2, p1-1-1, r1-1-1; IV tibia v2-2-2, d0-1-0-0, p0-1-1-0, r0-1-1-0; metatarsus v2-2-2-2, p1-1-1 r1-1-1. Epigynum (Fig. 8A): median sector sub quadrangular with margins sclerotized, posterior area wide and anterior area narrow, lateral process small, originated medially. Vulva (Fig. 18B). Copulatory ducts short and curved, spermathecae small and bean-shaped, fertilization ducts small and posteriorly located.

Variation. Males (n=6): Total length 9.70–10.60, carapace 4.86–5.90, femur I 5.90–6.72. Females (n=5): Total length 12.22–15.22, carapace 6.33–6.97, femur I 5.20–5.86.

Distribution. Montane ecosystems of Chiriquí Province, Panama (Fig. 27).

***Kiekie curvipes* Polotow & Brescovit, 2018**

Figs. 5E–F, 10, 11, 26E**.**

Microctenus curvipes Keyserling, 1881: 579, pl. 16, fig. 24 (male holotype from Panama, deposited in C.L. Koch personal collection, not examined, probably lost).

Ctenus curvipes: Simon 1897:107, fig. 100; F.O. Pickard-Cambridge 1897: 86, pl. 3, figs 6a, 7e; Polotow & Brescovit 2014: 355, fig. 12C.

Ctenus incolans F.O. Pickard-Cambridge, 1900: 111, pl. 7, figs 35–36 (female holotype from Guatemala, deposited in BMNH 1901.3.3.142–143).

Material examined. COSTA RICA. Alajuela province: one female from Upala, Finca la ''Selva'' (10.8977N, 85.0166W, 50m) (UCR); one male from San Ramón, Concepción (10.1213N, 84.4402W, 1100m), 00.V.2015, N. Conejo (UCR); San Pedro de Poas (10.0722N, 84.2461W, 1100m), 15.VIII.2017, T. Roman (UCR); one female from Los Chiles, Finca de la Compañía Comercial San Luis (10.9616N. 84.6517W), 08.II. 2009 (MNCR); Guanacaste

province: one female from Pitilla Biological Station (10.9926N, 85.4295W, 700m), J. Huff (MNCR); one female from Monte Alto de Pilangosta, Hojancha Fila Maravilla (10.0085N, 85.4124W, 800m), W. Porras (MNCR); Heredia province: one female from Sarapiquí, La Selva Biological Station (10.4306N, 84.0069W), C. Valerio (UCR); five females and five males from Sarapiquí, Tirimbina Rainforest Center (10.4150N, 84.1210W, 160m), 15.VI.2019, N. Hazzi (MCZ IZ 167574); Limon Province: one female from Liverpool, Veragua (9.9248N, 83.1912W, 400m), L.S egura (UCR); one female from Santa Rosa (10.3525N, 83.8044W, 100m), 00.04.2009, R. Madrigal (UCR); one female from Reserva Hitoy Cerere (9.6717N, 83.0277W), 28.III.2003 (MNCR); one male from Guacimo, Pocora (10.2458N, 83.5766W) 00.V.2000, C. Víquez (MNCR); four females and four males PNN Tortugueros (10.4498N, -83.4730W, 10m), 10.VI.2019, N. Hazzi. Puntarenas province: one female from Playa Nicoya-Curu, Bosques Marianas (9.791N, 84.9281W), 3.XII.1988 (UCR); one female, San Vito, Coto Brus (8.9541N, 83.0704), C. Valerio (UCR); one female from PNN Corcovado, San Pedrillo (8.6230N, 83.7366W), 27.IX.1998, M. Lobo (MNCR); one female from Peninsula la Osa, Puerto Jiménez (8.5387N, 83.3061W), 10.I.1998, M. Lobo (MNCR); one female, Rincon Station (8.6049N, 83.5295W), 9.IX.1996; S. Avila (MNCR); Puesto en la Isla del Cano y Sendero sitio arqueológico (8.7097N, 83.8736W), 23.II.1998, A. Azofeifa; two males and two females from Cirenas (9.720N, 85.211W), 08.VI.2018, N. Hazzi (MCZ IZ 167575). San Jose province: one female from Puriscal, Maztatal (9.6737N, 84.3691W, 400m), 27.III.2009, M. Ramírez (UCR); one female from Pérez de Zeledon, Escuela Naranjo (9.2035N, 83.6366W, 800m); one female from Puriscal, PN La Cangrejera (9.7003N, 84.3978W), B. Gamboa (MNCR). PANAMA. Chiriquí province: two females and two males from Chiriqui University (8.4318N, 82.4515W, 30m), 28.VII.2018, N. Hazzi (MCZ IZ 167576). MEXICO: Chiapas province: one female and

one male from Marqués de Comillas, Playón de la Gloria (16.1513N, 90.8966W), 05.VII.2013 (CAN-AR 3462); one female and one male from Ocosingo, El Taller, Sierra de la Cojolita (16.804N, 90.901W), 09.VIII.2005, R. Paredes (CNAN-AR 6695), one female from Ocosing, Arroyo Nayte, Sierra de la Cojolita (16.792N, 91.042W), R. Paredes (CNAN-AR: 6692); Marquez de Comillas, Playon de la Gloria (16.1504N, 90.8965W), 7.VIII.2013 (CNAN-AR 4979); Veracruz Province: four females and four males, Los Tuxlas Biological Station (18.5822N, 9.0755W), F. Alvarez Padilla (2016-2017) (CNAN-AR-Ar011669).

Diagnosis. Males of *Kiekie curvipes* differ from all congeneric species by the S-shaped and cylindrical RTA, medially located at the palpal tibia (Figs. 9B–C and 10B–C). Females resemble those of *K. montanensis* by the absence of a hyaline area in the lateral field, close to the copulatory opening (Figs 9D, 10D and 15D); but can be distinguished by the shorter copulatory ducts (Fig. 9E and 10E).

Taxonomic remarks: Polotow & Brescovit (2018) mentioned the round projection at the embolus base and the bimarginated median apophysis (Fig. 46C) as diagnostic characters of *K. curvipes*. However, during examination of specimens from Mexico, we found specimens with neither the round projection at the embolus base nor the bimarginated median apophysis (Fig. 15B). In addition, we found specimens from Mexico with the round projection at the embolus base, but without the bimarginated median apophysis. Therefore, males of *Kiekie curvipes* should be diagnosed based on the S-shaped and cylindrical RTA. ~~The f~~Females from these localities have larger spermathecae with conspicuous posterior granules (Fig. 16B) than those of the southern populations of Costa Rica and Panama. Future studies should examine in more detail whether this variation could indicate the existence of more than one species.

Distribution. Lowland ecosystems of Costa Rica, Panama, Mexico, Honduras and Nicaragua (Fig. 27).

***Kiekie dietrichi* Omelko, 2023**

Kiekie dietrichi Omelko, 2023: 280, f. 6-10, 15-18, 23-26, 31-35, 38-39 (male holotype and four female paratypes from Panama (deposited in ZMMU(Moscow)), not examined)**.**

Diagnosis. Males of *K. ~~dietriche~~ dietrichi* resemble those of *K. montanensis* in the shape of the median apohysis (Fig 15; Omelko, 2023: figs 15–17), but can be distinguished by the larger and curved RTA with a sharp tip (vs. a tiny, straight, bifurcated tip as in *K. montanensis*, Fig15C; Omelko, 2023: fig. 17). Females of *K. dietrichi* resemble those of *K. curvipes* in the shape of the median sector of the epigynum (Figs. 9D and 10D; Omelko, 2023: figs. 31 an 32) and the orientation of the copulatory ducts (Figs 9E and 10E; Omelko 2023, fig. 34), but differ by the small lateral processes of the epigynum pointing towards each other and by the reniform spermathecae (Omelko, 2023: figs. 31 and 32), in contrast with the large downward-pointing lateral projections and the piriform spermathecae of *K. curvipes* (Figs. 9D and 10D).

Distribution. Known only from the type locality in the Chiriquí Province of Panama.

***Kiekie garifuna* Polotow & Brescovit, 2018**

Figs. 11, 24C and 26E.

Holotype: Male holotype from Guatemala, ~~deposited~~ (deposited in BMNH 1901.3.3.142–143, not examined)**.**

Material examined. MEXICO**:** Veracruz province: two females and two males, Los Tuxlas Biological Station (18.5822N, 9.0755W), F. Alvarez-Padilla (2016-2017) (CNAN-AR-

Ar011670). Chiapas province: four females from Ocosingo, Arroyo Nayte, Sierra de la Cojolita (16.792N, 91.042W), A. Valdez, O. Francke, C. Santibáñez y J. Cruz (CNAN-AR:9528, 6668, 6695, 6696).

Diagnosis. Males of *Kiekie garifuna* can be distinguished from congeneric species by the shape of the RTA, with a wide and flat tip, and a large base (Fig. 11B and 24C). Females of *Kiekie garifuna* differ from all other ~~the~~ species in the genus by an ovoid projection in the anterior area of the median sector of the epigynum (Fig. 11D) and by their large and thick curved copulatory ducts (Fig. 11E).

Female (CNAN-AR-Ar011670, from Los Tuxlas Biological Station, Veracruz province, Mexico). Total length 18.40. Carapace 9.00 long and 7.00 wide. AME 0.38, ALE 0.30, PME 0.45, PLE 0.48. Sternum 3.78 long and 3.38 wide, labium 1.18 long and 1.30 wide, endites 2.24 long and 1.32 wide. Leg measurements: I: femur 8.47, patella 3.66, tibia 7.85, metatarsus 6.53, tarsus 2.70, total 29.21; II: 7.81, 3.40, 7.81, 6.38, 2.45, total 27.84; III: 7.0, 2.85, 6.31, 6.15, 2.41, total 24.71; IV: 8.96, 3.71, 8.72, 10.07, 3.07, total 34.53. Leg spination: tibia I-II v2-2-2-2-2, metatarsus I-II v2-2-2-2-2, tibia III v-2-2-2, d1-1-1, p1-0-1, r1-0-1, metatarsus v2-2-2, d0-1-0, p1-1-2, r1-1-2; IV-tibia v2-2-2, d1-1-1, 1-0-1, p1-0-1, metatarsus v-2-2-2, d0-1-0, p1-1-2, r1-1-2. Epigynum (Fig. 11D): median sector with an oval projection in the anterior area, lateral fields without large hyaline projection and copulatory openings small and inconspicuous, lateral process elongated and originated medially. Vulva (Fig. 11E). Copulatory ducts curved, with a broad less sclerotized area at the beginning of the copulatory openings; spermathecae nearly rounded; fertilization ducts small and located posteriorly.

Male. Described by Polotow & Brescovit (2018).

Variation. Males (n=3): Total length 14.20–15.10, carapace 8.40–10.10, femur I 9.25–10.10. Females (n=3): Total length 18.22–19.00, carapace 9.10–9.55, femur I 8.34–8.90.

Distribution. Lowland ecosystems from Mexico to Nicaragua.

***Kiekie griswoldi* Polotow & Brescovit, 2018**

Figs. 5C–D, 12, and S2.

Holotype: Male from Costa Rica, Puntarenas Province, Santa Elena, near Monteverde (deposited in MCZ 30607, not examined).

Kiekie sanjose Polotow & Brescovit, 2018: 10, Fig. (Female holotype from Costa Rica, deposited in MCZ 79098, and female paratype deposited in AMNH, not examined). **New synonymy.**

Material examined. COSTA RICA: Alajuela Province: One female, Arenal, San Ramón Reserve (10.2276N, 84.6008W), C. Víquez (MNCR); one female, Upala, around San Ramón de dos Rios (10.8832N, 85.4135W), 22.VI.1994 (MNCR), one male, San Ramón, Villa Blanca Cloud Forest Hotel (10.2025N, 84.4844W), 21.VII.2018, N. Hazzi and N. Conejo (MCZ IZ 167577); Cartago Province: One male, National Park Tapantí, Quebrada Segundo area (9.7625N, 83.7883W), R. Delgado (MNCR); Guanacaste province: One female, Faldas Volcán Tenorio (10.658N, 84.9961W), 08.II.1986, C. Bernal (UCR); One female, Biological Station Pitilla, 9km from Santa Cecilia (10.9926N, 85.4295W), 01.V.1989, P. Rios (MNCR); Puntarenas Province: One female, Arenal, Monteverde, La Casona Station (10.2984N, 84.7925W), 23.V.1995, K. Martínez (MNCR); One female, Arenal, Monteverde, Tropical Scientific Center (10.3014N, 84.7954W), 17.VIII.2009, D. Gutierrez (MNCR); three males and three females, Coto Brus, Las Cruces Biological Station (8.7840N, 82.9590W), 25.VI.20018, N. Hazzi and N. Conejo (MCZ IZ

167578). PANAMA: Chiriquí province: One male, Lagunas de Volcan (8.7638N, -82.6772W, 1368m), 31.VII.2018, N. Hazzi (MCZ IZ 167579).

Diagnosis. Males of *Kiekie griswoldi* are easily distinguished from all other species of the genus by the large and curved RTA, emerging from the retrodorsal area of the tibia to ventral direction (Fig. 12B-C and S2B-C), and by a large median apophysis at the apex with C-shaped in ventral view (Fig. 12B and S2B). Females of *Kiekie griswoldi* differ from all species by the lateral and straight elongation of the spermathecae (fig. 12E).

Taxonomic Remarks: Polotow & Brescovit (2018: fig. 10C) diagnosed females of *Kiekie griswoldi* by the short and anterior position of the lateral process of the epigynum. However, during examination of museum specimens, we discovered that females instead have lateral processes positioned medially, as usual in most species, but some specimens lack them, probably because they lost them during mating. Therefore, the lateral process that Polotow & Brescovit pointed in their fig. 10C, is not the lateral process, but ~~just~~ is just part of the conformation of the lateral field of the epigynum. Polotow & Brescovit (2018) differentiate *Kiekie sanjose* from *K. griswoldi* by the longer median field of the epigynum. However, examination of specimens from areas close to the type localities and other regions in Costa Rica, indicate ~~that~~ there is a continuum of variation between shapes in the middle field with high overlap. In addition, the males associated with females with longer median epigynal field have the diagnostic characters of *K. griswoldi*. Therefore, we synonymize *K. sanjose* with *K. griswoldi.* This species presents a large morphological variation across its geographic distribution range. Populations from the southern area of Cordillera Talamanca are considerably larger in size than the populations from the mountain ranges of Central Cordillera, Guanacaste and Tilaran. In addition, populations of the southern part of Talamanca have larger and robust median tegular projection compared to the

660 populations of the northern area (Fig. 12 and S2). Due to the limited sampling and continuous
661 morphological variation, we prefer to consider this variability as intraspecific. However, we
662 acknowledge that more studies are needed to determine if *K. griswoldi* could be more than one
663 species.
664 **Distribution.** Montane ecosystems of Costa Rica and Panama (Fig. 38A).
665
666 ***Kiekie lamuerte* sp. nov.**
667 Figs. 13, 23A and 25A.
668 **Type material**
669 *Holotype.* COSTA RICA: Male from San Jose Province, Cerro de la Muerte (9.55N, -83.72W),
670 21.III. 1993, G. Hormiga (MCZ IZ 167580). *Paratypes.* ~~1~~ One male and one~~1~~ female, same data
671 as holotype (MCZ IZ 167581).
672 **Etymology.** The species name is a toponym in apposition in reference to the type locality.
673 **Diagnsosis.** Males of *K. lamuerte* resemble those of *K. bernali* in the general palp conformation,
674 but differ by the hook-shaped median apophysis (Figs. 13B, 23A and 25A), presence of a
675 sclerotized process (Fig 13B, 23A), apically bifid RTA (Fig. 13C) and the presence of modified
676 metatarsus IV. The epigyna resemble those of *K. bernali* by the short copulatory ducts and small
677 copulatory openings, but differ by the stronger sclerotized margins of the median sector (Fig.
678 13D) and the spermathecal shape, with a well-defined base (Fig. 13E).
679 **Male** (MCZ IZ 167580, from Cerro de la Muerte, San Jose Province, Costa Rica). Total length
680 18.57. Carapace 10.18 long and 8.27 wide. Eye diameters: AME 0.43, ALE 0.33, PME 0.35,
681 PLE 0.52. Clypeal height 0.24, sternum 4.55 long and 4.31 wide, endites 2.82 long and 1.50
682 wide, labium 1.26 long and 1.47. Leg measurements: I: femur 10.27, patella 3.87, tibia 10.15,

metatarsus 9.17, tarsus 3.78, total 37.24; II: 9.31, 3.43, 10.19, 8.24, 3.78, total 34.95; III: 8.85, 2.99, 8.37, 8.29, 3.30, total 31.80; IV: 3.22, 10.68, 11.24, 11.59, 3.67, total 40.40. Leg spination: tibia v2-2-2-2-2, p0-1-0, 0-1-0 metatarsus v2-2-2, II tibia v2-2-2-2-2, r2-2-0, p2-2-0, metatarsus v2-2-2, III v-2-2-2, d1-1-1, p 1-0-1, r1-0-1, metatarsus v2-2-2, 0-1-0, p1-1-2, r1-1-2; IV tibia v-2-2-2, d1-1-1, p1-0-1 r1-0-1, metatarsus modified. Palp: RTA small and apically bifid (Fig. 13C), embolus flagelliform and laminar, with a sclerotized process at the base of the embolus (Fig 13B and 23A), median apophysis vertically oriented (Figs. 13B and 23A, 25A); conductor with a narrow base and large apex, covering the tip of the embolus (Figs. 13B and 23A, 25A).

Female (MCZ IZ 167580-1, from Cerro de la Muerte, San Jose Province, Costa Rica). Total length 27.76. Carapace 12.35 long and 9.35 wide. AME 0.47, ALE 0.35, PME 0.55, PLE 0.50. Clypeal height 0.26, sternum 5.14 long and 4.62 wide, endites 2.45 long and 2.36 wide, labium 1.15 long and 1.55 wide. Leg measurements: I, femur 9.31, patella 4.60, tibia 9.12, metatarsus 7.01, tarsus 2.90, total; II: 8.04, 3.47, 6.75, 6.308, 3.00, total; III: 7.51, 3.50, 6.16, 6.10, 2.30, total; IV: 9.55, 3.84, 9.10, 9.54, 3.50, total. Leg spination tibia I-II v2-2-2-2-2, metatarsus I-II v2-2-2-2-2; III tibia v2-2-2, p1-1-0, r1-1-0, metatarsus v2-2-2, d0-1-0, p1-1-1 r1-1-1; IV tibia v2-2-2, d0-1-1-0, r0-1-1-0, p0-1-1-0, metatarsus v2-2-2, p1-1-1, r1-1-1, r1-1-1-2. Epigynum (Fig. 13D): median sector sub quadrangular with margins sclerotized, posterior area wide and anterior area narrow, lateral process small, originated medially. Vulva (Fig. 13E). Copulatory ducts short and curves, spermathecae bean-shaped, with a well-defined base; fertilization ducts small, posteriorly located.

Variation. Males (n=2): Total length 18.57–19.32, carapace 10.75–10.90, femur I 10.27–10.75.

Distribution. Montane ecosystems of San Jose Province, Costa Rica (Fig. 27).

***Kiekie laselva* sp. nov.**

Figs. 4E–F, 24A and 26A.

Type material.

Holotype. COSTA RICA: Female from Heredia Province, Sarapiquí, La Selva Biological Station (10.4305N, 84.0073W), 18.VI.2018, N. Hazzi (MCZ IZ 167582). *Paratypes*: ~~3~~ Three males and ~~5~~ five females, Limón Province, PNN Tortugueros (10.4498N, -83.4730W, 10m), 10,VI.2019, N. Hazzi (MCZ IZ 167583); ~~1~~ one female, Heredia Province, Sarapiquí, Tirimbina Rainforest Center (10.4150N, -84.1210, 160m), 25.VI.2018, N. Hazzi (MCZ IZ 167584).

Other material examined. **Costa Rica:** One female, Limón Province, River fri (10.4014N, -83.6000W), 04.X.1997, C. Víquez (MNCR).

Etymology. The species name is a noun in apposition to ‘’La Selva’’ Biological station, which was established as a research station in 1968 by the organization of tropical studies (OTS).

Diagnosis. Males of *K. laselva* resemble those of *K. valeroi* and *K. panamensis* but can be distinguished from them by a white conspicuous laminar process of the embolus (Fig. 14A and 24A) and by a longer whip-shaped embolus (Figs. 14A, 24A, 26A). Females of *K. laselva* also resemble those of *K. panamensis* and *K. valeroi* in the general epigynal configuration but differ by the more complex ~~rolled~~ coiled conformation of the copulatory ducts (Fig. 14E).

Female (MCZ IZ 167582, from La Selva Biological Station, Sarapiquí, Heredia Province, Costa Rica). Total length 37.12. Carapace 16.57 long and 13.22 wide. AME 0.62, ALE 0.56, PME 0.69, PLE 0.82. Clypeal height 0.26, sternum 6.70 long and 6.03 wide, endites 4.00 long and 2.66 wide. Leg measurements: I: femur 14.19, patella 6.00, tibia 13.88, metatarsus 9.80, tarsus 4.06, total; II: 13.10, 5.55, 11.82, 9.86, 3.60, total III: 11.49, 4.71, 9.98, 9.05, 2.90, total; IV: 14.05, 5.83, 12.78, 14.82, 4.00, total. Leg spination: tibia I-II v2-2-2-2-2, metatarsus I-II v2-2-2-

Comentado [aa8]: Numbers lower than ten are written in letters, change throughout text accordingly

Comentado [aa9]: ??

2-2, tibia III v-2-2-2, d1-1-1, r1-0-1, p1-0-1, metatarsus v-2-2-2, d0-1-0, p1-1-2, r1-1-2; IV tibia v2-2-2 d1-1-1, r1-0-1, p1-0-1, metatarsus v-2-2-2, d0-1-0, p1-1-2, r1-1-2. Epigynum (Fig. 14D): median sector sub pentagonal and vertically elongated, lateral fields with a large hyaline projection, posterior area wide and anterior area narrow, lateral process sharp, originated medially. Vulva (Fig. 14E). Copulatory ducts elongated forming complex loops, spermathecae small and bean-shaped; fertilization ducts small and located posteriorly.

Male (MCZ IZ 167583-1, La Selva Biological Station, Sarapiquí, Heredia Province, Costa Rica). Total length 36.84. Carapace 20.02 long and 15.80 wide. AME 0.65, ALE 0.50, PME 0.74, PLE 0.86. Clypeal height 0.20, sternum 8.81 long and 7.36 wide, labium 2.44 long and 2.24, endites 4.48 long and 2.60 wide. Leg measurements: I: femur 19.84, patella 7.18, tibia 19.55, metatarsus 17.74, tarsus 6.69, total; II: 18.40, 7.38, 17.52, 15.29, 5.30, total; III: 16.64, 6.3, 14.64, 13.45, 4.60; IV: 20.80, 8.05, 20.10, 20.33, 6.38, total. Leg spination: leg I tibia v2-2-2-2-2, p1-1-1-0, r1-0-0, metatarsus v-2-2-2, Leg II, tibia v2-2-2-2, p-1-1, r1-1, metatarsus v-2-2-2; III: v2-2-2, d1-1-1, , p 1-0-1, r1-0-1, metatarsus v2-2-2, d0-1-0, p1-1-2, r1-1-2, IV tibia v2-2-2, d1-1-1, p1-01, r1-0-1, metatarsus modified. Palp: RTA spiniform in ventral view, with wide apex (Figs. 14B, C), embolus elongated, flagelliform with a large white laminar process, presence of sclerotized process at the base of the embolus (Figs. 14B, 24A), median apophysis with cup-shaped aperture visible ventrally (Figs. 24A, 26A); conductor with a narrow base and large apex, covering the tip of the embolus (Figs. 24A, 26A).

Variation. Males (n=3): Total length 36.50–37.68, carapace 19.00–20.68, femur I 19.00–20.51. Females (n=7): Total length 34.53–40.32, carapace 17.63–20.01, femur I 14.19–17.6.

Distribution. Lowland ecosystems of Costa Rica (Fig. 27).

***Kiekie montanensis* Polotow & Brescovit, 2018.**

Fig. 5–B, 15.

Holotype: Male holotype from Costa Rica, Puntarenas Province, San Vito (deposited in CAS, not examined).

Material examined. PANAMA: 10 females and 10 males from Panama, Chiriquí province, Lagunas de Volcán (8.7638N, -82.6772W, 1368m), 31.VII.2018, N. Hazzi (MCZ IZ 167585); COSTA RICA: 3 males and 3 females from Puntarenas province, Las Cruces Biological Station (8.7840N, 82.9590W, 1200m), 25.VI.2018, N. Hazzi (MCZ IZ 167586); 3 males and 1 female, Puntarenas Province, Las Alturas Biological Station (8.9450, -82.8330, 1300m), 29.VI.2018, N. Hazzi (MCZ IZ 167587). COSTA RICA: Puntarenas Province: One female, Buenos Aires. Durika Reserve (9.2617N, 83.2469W), 00.II.1990, one male, Coto Brus, Sabalito, Finca Marco Morales (8.9064N, 82.8047W), 08.V.1995 (MNCR); one male, Coto Brus, 500m from Cerro Pelon (8.9136N, 82.7965W) (MNCR).

Diagnosis. Males of *K. montanensis* resemble those *of K. curvipes and K. verbena* by having a prominent tegular process (Figs. 9B, 15B and 21B), but can be distinguished from them by a median apophysis with a long and straight stem and a small RTA (Fig. 15B–C), not visible in ventral view. Females differ from all other congeneric species by the unique configuration of the copulatory ducts (Figs. 15E), which are ~~rolled~~ coiled and connecting posteriorly (below) with the spermathecae, and by the presence of numerous granules ~~below~~ under ~~of~~ the copulatory ducts.

Female (MCZ IZ 167585-1, Lagunas de Volcán, Chiriquí province, Panama). Total length 24.00. Carapace 11.19 long and 9.18 wide. AME 0.52, ALE 0.38, PME 0.59, PLE 0.60. Sternum 4.73 long and 4.31 wide, labium 1.51 long and 1.48 wide, endites 3.07 long and 1.73 wide. Leg measurements: I: femur 8.96, patella 4.20, tibia 8.74, metatarsus 6.52, tarsus 2.80, total 31.22; II:

8.82, 3.99, 7.70, 6.52, 2.70, total 29.73; III: 7.80, 3.23, 6.54, 6.26, 2.87, total 26.70; IV: 9.58, 4.02, 9.28, 9.63, 3.00, total 35.51. Leg spination: tibia I-II v2-2-2-2-2, metatarsus I-II v2-2-2-2-2, tibia III v-2-2-2, d1-1-1, p1-0-1, r1-0-1, metatarsus v2-2-2, d0-1-0, p1-1-2, r1-1-2; IV-tibia v2-2-2, d1-1-1, 1-0-1, p1-0-1, metatarsus v-2-2-2, d0-1-0, p1-1-2, r1-1-2. Epigynum (Fig. 15D): median sector sub pentagonal, anterior area narrow, lateral fields without large hyaline projection, lateral process robust and originated medially. Vulva (Fig. 15E). Copulatory ducts elongated, ~~rolled~~ coiled and connecting posteriorly (below) of the spermathecae; rounded spermathecae; fertilization ducts small, posteriorly located, with multiple granules between the copulatory and fertilization ducts.

Male. Described by Polotow & Brescovit (2018).

Variation. Males (n=10): Total length 20.08–21.53, carapace 10.87–11.85, femur I 10.67–11.03. Females (n=10): Total length 19.39–25.57, carapace 10.42–11.88, femur I 8.04–9.54.

Distribution. Montane ecosystems of Costa Rica and Panama (Fig. 46).

***Kiekie panamensis* Polotow & Brescovit, 2018**

Figs. 4A–C, 16, 23E 25E.

Holotype: Male holotype from Panama, Canal Zone, Barro Colorado Island (deposited in MCZ 79100, not examined).

Material examined. PANAMA: Coclé Province: One female, 50km west of Penonome Via el Cope (8.6680N, 80.5925W), 08.VI.2008, G. Hormiga (MCZ IZ 167588); three females and three males, Colón Province, Gamboa (9.0980N, 79.0738W), 05.VIII.2018, N. Hazzi and S. Meneses (MCZ IZ 167589). COLOMBIA: Antioquia Department: one female and one male, Valle del Aburra (6.2375N, 75. 5804W), N. Hazzi and A. Arroyave (MUSENUV); Valle del Cauca

Department: One female, Tulua, Botanical Garden INCIVA (4.0396N, 76.1683W), 00.X.2013, N. Hazzi (MUSENUV); one female and one male; Buga, Parque Natural Regional ''El Vínculo'' (3.8373N, 76.3002W), 00.X.2013, N. Hazzi (MUSENUV); ~~One~~ one male, Cali, Universidad del Valle Melendez, Biological Station (3.3712N, 76.5331), 00.X.2010, N. Hazzi (MUSENUV); one female and one male, Buenaventura, Pericos River Forest Reserve (3.8443N, 76.7901W), 04.I.2014, N. Hazzi (MUSENUV); one female, Buenaventura, Bahía Chucheros (3.9369N, 77.2967W), 00.XI.2011, N. Hazzi (MUSENUV). ECUADOR: Esmeraldas, Caimito (3.9369N, 77.2967W), 05.X.2019, N. Hazzi (MCZ IZ 167589).

Diagnosis. Males of *K. panamensis* resemble those of *K. valeroi* but can be distinguished from them by a shorter, sclerotized tegular process at the base of the median apophysis (Fig. 16B, 23E, 25E), and by median apophysis without a small peak (Fig. 25E). Females of *K. panamensis* can be distinguished from *K. valeroi* by sharper lateral process of the epigynum (Fig. 16D), anterior area of the median sector of the epigynum wide (Fig. 16D); and small ~~spermathecas~~ spermathecae (16E).

Distribution. Lowland and premontane ecosystems of Panama, Colombia and Ecuador (Fig. 27).

***Kiekie sarapiqui* Polotow & Brescovit, 2018**

Figs. 17, 24D, 26D.

Holotype: Male from Sarapiquí Heredia province, Costa Rica (deposited in MCZ 79099, not examined)

Material examined. COSTA RICA. Heredia province: two males and two females from Sarapiquí, Tirimbina Rainforest Center (10.4150N, 84.1210W, 160m), 15.VI.2019, N. Hazzi (UCR). Alajuela province: one male and one female from Reserva Alberto Manuel Brenes

(10.2301N, -84.6271W, 700m), 00.IV.2009, A. Rojas (UCR); Limon province: one female from Tortugueros, Campus Escuela Agricola Regional del Trópico Húmedo (10.20N, 83.6167W, 50m), 18.IX.2000, C. Víquez (MNCR); one female from Pococi, Finca del INBIO (10.1867N, -83.8569W, 300m) (MNRC); Puntarenas province: one female from R.B. Hitoy Cerere (9.6650N, 83.0271W, 250m) (MNCR).

Diagnosis. Males of *Kiekie sarapiqui* resemble those of *K. sinuatipes* by the conformation of the RTA and embolus but differ by the wider and shorter median apophysis with the aperture not visible in ventral view (Figs. 17B, 24D, 26D). Females of *Kiekie sarapiqui* resemble those of *K. sinautipes* but differ by a longer median epigynal field and shorter lateral process (Fig. 17D); and by copulatory ducts folded over themselves before connecting to the spermathecae (Fig. 17E).

Kiekie ~~***sinautipes***~~ ***sinuatipes*** **(F.O. Pickard-Cambridge, 1897)**

Figs. 18, 24F, 26F**.**

Holotype: Male from San José Province, Costa Rica (deposited in BMNH 1896.3.20.26–29, not examined)

Material examined. COSTA RICA: Alajuela province: one male from Zarcero (10.1834N, 84.3927W, 1700m), 18.IV.2013, A. del Valle (UCR), one male from the same locality, 27.10.1997 (MNCR). Cartago Province: One male from Dulce Nombre (9.8456N, 83.9095W), 02.IV.1978 (UCR); one female from San Rafael, Sierras de la Unión (9.9084N, 83.9719W, 1400m), 06.09.2017, M. Springer (UCR); one female from Alto de Ochomogo (9.8878N, 83.9413W, 1500m) (UCR). Heredia Province: one male from San Rafael (10.0116N, 84.1035W), 6.19.2019 (MNCR); one female from San Joaquín de Florez (10.0062N, 84.1537W), 01.05.1997, C. Víquez (1997). Puntareas province: one female fron Monteverde (10.2749N,

Comentado [aa10]: Change misspellings throughout text

844 84.8255W), C. Valerio (UCR); one female from Coto Brus, Estación Pitter, ‘’Cerro Pitter’’ trail
845 (9.0256N, 82.9627W, 1670m), E. Núñez (MNCR), two females from the same locality,
846 16.I.2000 (MNCR); one female from Buenos Aires, Pila Sector Altamira (9.0329N, 83.0109W,
847 1400m), 25.VIII.2005 (MNCR). San José province: one male from Curridabat, Granadilla
848 (9.9221, 84.0177W), C. Valerio (UCR); one male from Alajuelita, San Juan de Dios de
849 Desamparados (9.9013N, 84.0995W), 08.IV.1981 (UCR); one male and one female from Montes
850 de Oca (9.9407N, 84.0250W), 08.V.1981, A. del Valle (UCR), One female from San Antonio de
851 Alajuelita (9.8858N, 84.1144W), 10.VII.1986, M. Garcia (UCR); one female from San Rafael de
852 Moravia (9.9688N, 84.0489W), 00.V.1963, C. Valerio (UCR); one male from Guadalupe
853 (9.9471N, 84.0535W), 06.II.1972 (S. Salas); one male from San Jose, Barrio Cuba (9.9245N,
854 84.0901W), (UCR); one female from Tibas (9.9576N, 84.0816W, 1200m), 00.III.1998, L.
855 Bonatti (UCR); Estación Cuericí, 4.6km E de Villa Mills (9.5552N, 83.6703W), A. Mora
856 (MNCR); two males from Curridabat, Los Prados (9.9339N, 84.0284W), 10.II.1995 (MNCR);
857 San Antonio de Escazu, William Eberhard and Mary Jane Eberhard house (9.8975N, 84.1377W),
858 20.VII.2018, N. Hazzi (MCZ IZ 167590).
859 **Diagnosis.** Males of *Kiekie sinuatipes* resemble those of *K. sarapiqui* (Fig. 18A–B) by the shape
860 of the embolus and RTA but can be distinguished by the elongated hook-shaped median
861 apophysis (Figs. 18B, 24F, and 26F). Females resemble those of *K. barrentesi* by the
862 conformation of the copulatory ducts (Fig. 18E) but can be distinguished from them by the
863 narrower anterior area of the median sector narrow (Fig. 18D) and rounded spermathecae
864 without an internal projection (Fig. 18E).
865 **Distribution.** Montane ecosystems of Costa Rica (Fig. 27).
866

***Kiekie tirimbina* sp. nov.**

Figs. 19, 23C, 25C

Type Material.

Holotype. COSTA RICA: Male from Heredia Province, Sarapiquí, Tirimbina Rainforest Center (10.4150N, 84.1210, 160m), 15.VI.2019, N. Hazzi (MCZ IZ 167591).

Diagnosis. Males of *K. tirimbina* differ from the remaining species of the genus by the combination of the following unique characters: thin and straight median apophysis, rounded at the apex (Figs. 19B, 23C and 25C); conductor large and deeply folded (Figs. 19B, 23C and 25C), tegulum with numerous and small grooves (Fig. 25C).

Etymology. The species epithet is a noun in apposition taken from the Tirimbina Biological Reserve, a protected tropical rainforest in Sarapiquí.

Male (MCZ IZ 167591, from Tirimbina Rainforest Center, Sarapiquí, Heredia province). Total length 19.12. Carapace 9.88 long and 7.91. AME 0.57, ALE 0.31, PME 0.59, PLE 0.62, sternum 4.12 long and 3.75, labium 1.40 long and 1.25 wide, endites 2.82 long and 1.41. Leg measurements: I: femur 9.91, patella 4.45, tibia 12.05, metatarsus 9.72, tarsus 3.80, total 37.93; II: 9.84, 4.24, 10.81, 9.77, 3.30, total 37.96; III: 9.54, 3.48, 8.39, 8.74, 2.81, total 32.96; IV: 11.51, 3.91, 11.13, 13.99, 4.18, total 44.72. leg I tibia v2-2-2-2-2, p1-1-0, r1-1-0, metatarsus v2-2-2; p1-1-0, r1-1-0; II-tibia v2-2-2-2-2, d1-1-1, p1-1-0, r1-1-0, metatarsus v2-2-2, p1-1-0, r1-1-0; III-tibia v2-2-2, d1-1-1, p1-0-1, r1-0-1, metatarsus v2-2-2, d0-1-0, p1-1-1, r1-1-1; IV-tibia v2-2-2, d1-1-1, p1-01, r1-0-1, metatarsus modified. Palp: RTA short and robust (Fig. 19C), embolus elongated and flagelliform, with laminar process (Figs. 23C and 25C); presence of sclerotized process at the base of the embolus (Figs. 23C and 25C); median apophysis thin and straight, apically rounded, cup-shaped with aperture not visible ventrally (Figs. 19B, 23C and 25C);

conductor with a narrow base and large apex, covering the tip of the embolus (Figs. 23C and 25C).

Female. Unknown.

Distribution. Lowland ecosystems of Costa Rica (Fig. 27).

***Kiekie valeroi* sp. nov.**

Figs. 20, 23F and 25F.

Type Material

Holotype. COSTA RICA: Male from Heredia Province, Sarapiquí, Tirimbina Rainforest Center (10.4150N, -84.1210, 160m), N. Hazzi (MCZ IZ 167592). *Paratypes.* ~~5~~Five males and ~~5~~ five females same data as holotype (MCZ IZ 167593).

Additional material examined. Costa Rica: San José Province: One male, Perez Zeledón, San Isidro del General (9.3547N, -83.6348), 3.VI.1972, J. Bolenige (UCR); One female, Puriscal, PN la Cangreja (9.7003N, -84.3978W), B. Gamboa (MNCR); Two females, Alajueja Province, San Ramón, Reserva Alberto Manuel Brenes (10.2301, -84.6271), 15.V.2013, M. Salazar; Upala. Finca ‘’La Selva’’ (10.8977N, -85.0166) (UCR); One female, Upala, El Pilón (10.8166N, -84.9500W), 16.X.2003 (MNCR), One female (10.7046, -84.9923), 23.VIII.2009, A. Azofeida (MNCR); Cartago Province, Turrialba (9.9067N, -83.6801), 03.VII.1986, C. Valerio (UCR); Jimènez, Pejibaye, Copal Biological Station (9.1963N, -83.5975W), R. González (MNCR); Guanacaste Province: One male Arenal, Tilaran (10.4563N, -84.9713), C. Valerio; Liberia, Colorado river (10.6842N, -85.4430) (UCR); one female and one male, La ~~cruz~~Cruz, Pitilla Biological Estation (10.9926N, -85.4295W), 31.VII. 1991, C. Moraga (MNCR); Heredia Province, Sarapiquí, Tirimbina Biological Station (10.4190N,-84.1210W), (MNCR); 2 females,

Con formato: Fuente: Sin Cursiva

Limon Province, Hitoy Cerere Biological Reserve (9.6717N, -83.0277W), 14.V.1998 (MNCR); Cocori (10.5942N, -83.7165W), 00.XI.1997, E. Rojas (MNCR); Limón, Espavel trail (9.6680N, -83.0236W), 25.IX.2003 (MNCR); Pococi, Finca INBIO (10.1867N, -83.8569) (MNCR); Puntarenas Province: San Pedrillo Station, Osa Peninsula (8.6230N, -83.7366W) (MNCR); Parrita (9.5230N, -84.5387W) (MNCR).

Diagnosis. Males of *K. valeroi* resemble those of *K. panamensis* in the general palp conformation, but can be distinguished from them by a wider tegular process at the base of the median apophysis (Fig. 20B), which is not sclerotized (Fig. 23F); and a robust base of the median apophysis with a small peak (Fig. 25F). Females of *K. valeroi* can be distinguished from *K. panamensis* by less sharp lateral process of the epigynum (Fig. 20D), more narrow anterior area of the median sector of the epigynum (Fig. 20D); and larger ~~spermathecas~~ spermathecae projecting internally and contacting with the copulatory ducts (Fig. 20E), while in *K. panamensis* the ~~spermathecas~~ spermathecae do not contact the copulatory ducts.

Etymology. This species is dedicated to Carlos E. Valerio, who made important contributions to the knowledge of spider diversity in Costa Rica.

Male (MCZ IZ 167592, from Tirimbina Rainforest Center, Sarapiquí, Heredia province). Total length 31.55. Carapace 17.50 long and 14.95 wide. AME 0.77, ALE 0.51, PME 0.81, PLE 0.87. Sternum 7.87 long and 7.01 wide, labium 2.40 long and 2.23 wide, endites 4.99 long and 2.41 wide. Leg measurements: I: femur 19.10, patella 6.86, tibia 17.99, metatarsus 15.03, tarsus 5.92, total 64.90; II: 17.37, 6.43, 18.10, 15.16, 5.06, total 62.12; III: 16.32, 6.82, 14.63, 14.44, 4.62, total 56.83; IV: 19.86, 7.63, 19.33, 20.61, 6.62, total 74.05. Leg spination: leg I tibia v2-2-2-2-2, d1-0-1, p1-1-0, r1-1-0, metatarsus v2-2-2; p1-1-0, r1-1-0; II-tibia v2-2-2-2-2, d1-1-1, p1-1-0, r1-1-0, metatarsus v2-2-2, p1-1-0, r1-1-0; III-tibia v2-2-2, d1-1-1, p1-0-1, r1-0-1, metatarsus v2-2-

2, d0-1-0, p1-1-1, r1-1-1; IV-tibia v2-2-2, d1-1-1, p1-01, r1-0-1, metatarsus modified. Palp: RTA spiniform (ventral view) and with wide apex (Fig. 20C), embolus elongated and flagelliform with laminar process (Figs. 23F, 25F), with a sclerotized process at the base of the embolus (Figs. 23F, 25F); median apophysis with cup-shaped aperture visible ventrally (Figs. 20B, 23F, 25F); conductor with a narrow base and large apex, covering the tip of the embolus (Figs. 20B, 23F, 25F).

Figs. 20, 23F and 25F

Female (MCZ IZ 167593-1, from Tirimbina Rainforest Center, Sarapiquí, Heredia province). Total length 34.76, Carapace 17.30 long and 15.23 wide. AME 0.74, ALE 0.56, PME 0.87, PLE 0.90. Sternum 7.50 long and 6.76 wide; labium 2.36 long and 2.26 wide, endites 4.30 long and 2.91 wide. Leg measurements: I: femur 16.45, patella 7.63, tibia 16.90, metatarsus 13.58, tarsus 4.57, total 59.13; II: 15.94, 7.60, 15.35, 12.36, 4.57, total 55.82; III: 12.79, 6.35, 11.29, 11.37, 4.27, total 46.07; IV: 17.29, 6.77, 15.85, 18.73, 5.38, total 64.02. Leg spination: tibia I-II v2-2-2-2-2, metatarsus I-II v2-2-2-2-2, tibia III v-2-2-2, d1-1-1, p1-0-1, r1-0-1, metatarsus v2-2-2, d0-1-0, p1-1-2, r1-1-2; IV-tibia v2-2-2, d1-1-1, 1-0-1, p1-0-1, metatarsus v-2-2-2, d0-1-0, p1-1-2, r1-1-2. Epigynum (Fig. 20D): median sector sub pentagonal, vertically elongated and with anterior area narrowed, lateral fields with a large hyaline projection, lateral process originated medially. Copulatory ducts elongated, with one loop and folded; large spermathecae projecting internally and contacting copulatory ducts; fertilization ducts small and posteriorly located (Fig. 20E).

Variation. Males (n=6): Total length 25.00–36.74, carapace 14.50–21.00, femur I 18.81–20.30. Females (n=6): Total length 26.44–37.03, carapace 12.56–18.14, femur I 10.78–16.45.

Distribution. Lowland ecosystems of Costa Rica (Fig. 27).

***Kiekie verbena* Polotow & Brescovit, 2018**

Figs. 21, 23D and 25D.

Holotype: Female from Costa Rica, San José Province, San José, La Verbena (deposited in MCZ 79102, not examined)

Material examined. COSTA RICA: Two females and five males from San José province, San Pedro, campus of Universidad of Costa Rica (9.9376N, -84.0507W, 1200m), 10.VI-2018, N.Hazzi (MCZ IZ 167594); 3 males and 3 females, San Antonio de Escazu, San Jose province (9.8975N, 84.1377W, 1330m), N. Hazzi, (MCZ IZ 167595); three females from Punta Arenas, Monteverde, UGA, (10.2829, 84.799W, 1100m), 12.06.2018, N. Hazzi (MCZ IZ 167596). Alajuela Province, San Ramón, Alberto Manuel Brenes Reserve (10.2283N, 84.6396W) (UCR); Cartago Province: Tres Rios, Concepcion (9.8638N, 83.9161W) 1981, C. Valerio (UCR); one female, La Union, San Rafael, Sierras la Unión (9.9083N, 83.9764W), 16.VIII.2015, M. Springer (UCR); Guanacaste Province: Tilaran (10.4563N, 84.9713W), 15.VII. 1967, C. Valerio (UCR); Volcán Miravalles (10.7471N, 85.1512W), 19.III.1967 (UCR); Puntarenas Province: Monteverde, San Luis (10.2852N, -84.8199W) 00.XI.1993 (MNCR). San José Province: One female, San Pedro, Universidad of Costa Rica (9.9369N, -84.0510W), 20.V.2009, R. Quesada (UCR); one female, Escazú, Agres River (9.9369N, 84.0510W), 14.III.2009, R. Arias (UCR); one female, Curridabat, Granadilla (9.9221N, 84.0177W), C. Valeroi (UCR); one female, Montes de Oca (9.9407N, 84.0250W), 21.IV.1967, C. Valerio (UCR); two males, Curridabat, Los Prados (9.9339N, 84.0284W), 10.II.1995 (MNCR).

Diagnosis. Males of *K. verbena* resemble those *of K. curvipes and K. montanensis* in having a prominent tegular process (Figs. 21B), but can be distinguished from them by a not strongly

sclerotized tegular process, whitish in coloration. In addition, males have a bifid RTA at the base, forming two divergent apophyses (Figs. 21B-C), a short embolus and a small conductor (Figs. 21B, 23D and 25D) in contrast with all other congeneric species. Females are distinguished from all other ~~congeners~~ species by the configuration of the epigynum with a short and wide median sector, long lateral projection of the lateral field and short copulatory openings (Fig. 21D) and short copulatory ducts (Fig. 21E).

Male (MCZ IZ 167594-1, from Campus of Universidad of Costa Rica, San Pedro, San José province, Costa Rica). Total length 15.09. Carapace 8.48 long and 7.00 wide. AME 0.40, ALE 0.25, PME 0.40, PLE 0.41. Sternum 3.70 long and 3.38 wide, labium 0.95 long and 1.08, endites 1.92 long and 1.03 wide. Leg measurements: I: femur 8.05, patella 2.77, tibia 7.43, metatarsus 6.66, tarsus 2.88, total 27.78; II: 7.62, 2.90, 7.10, 6.26, 2.43, total 26.31; III: 6.93, 2.92, 5.65, 6.15, 2.59, total 24.24; IV: 8.36, 2.91, 8.28, 8.75, 3.28, total 31.58. Leg spination: leg I tibia v2-2-2-2-2, p1-1-0, r1-1-0, metatarsus v2-2-2; d1-0-1, p1-1-0, r1-1-0; II-tibia v2-2-2-2-2, d0-1-0, p1-1-0, r1-1-0, metatarsus v2-2-2, p1-1-0, r1-1-0; III-tibia v2-2-2, d1-1-1, p1-0-1, r1-0-1, metatarsus v2-2-2, d0-1-0, p1-1-1, r1-1-1; IV-tibia v2-2-2, d1-1-1, p1-01, r1-0-1, metatarsus modified. Palp: RTA at the base forming two divergent apophyses (Fig. 21B), embolus short without laminar process (Fig. 23D); embolus base without a sclerotized process (Fig. 23D); median apophysis large with cup-shaped aperture visible ventrally (Fig. 23D, 25D); conductor reduced, covering the tip of the embolus (Fig. 23D, 25D).

Variation. Males (n=9): Total length 11.83–16.03, carapace 6.47–9.78, femur I 6.65–9.22. Females (n=6): Total length 15.10–21.08, carapace 7.44–10.26, femur I 5.51–8.05.

Distribution. Montane ecosystems of Costa Rica (Fig. 27).

Female. Described by Polotow & Brescovit (2018).

***Eldivo* gen. nov.**

Figs. 22 and 26G–H.

Type Material

Holotype. MEXICO: Male from Veracruz Province, Los Tuxlas Biological Station (18.5822N, 9.0755W), F. Álvarez Padilla (2016-2017) (CNAN-AR-T01865). *Paratypes.* ~~3~~Three females, same data as holotype (CNAN-AR-T01866).

Other Material Examined. Mexico: Oaxaca province: One female, Huautla de Jiménez, San Agustín, Zaragosa (18.11N, 96.80W), 13.X.2014, O. Francke and J. Cruz (CNAN-AR). One male, San José, Nuevo Rio Manzo, cerro Chango (17.706N, 96.899W), 05.IX.2018 (CNAN-AR).

Con formato: Inglés (Estados Unidos)

Etymology. This species is dedicated to the memory of Alberto Aguilera Valadez, known professionally as Juan Gabriel and colloquially as "El Divo". Juan Gabriel was a Mexican singer and songwriter that was known for his histrionic style, which overcame barriers within the Latin music.

Diagnosis. Males of *Eldivo* resemble those of *Kiekie* by the presence of a modified metatarsus IV, but can be distinguished from them by the shorter embolus with a laminar fold in the internal side (Figs. 22B, 26H), locking lobes located at posterior prolateral side (Fig. 26G); in contrast with the elongated embolus and locking lobes in the posterior retrolateral side in *Kiekie*. Females cannot be accurately distinguished morphologically from *Kiekie* or other Mesoamerican ctenids.

Description. Large-sized ecribellate spiders, total length 24.00–27.00. Carapace piriform, dark brown, black pigment around eyes; thoracic groove longitudinal, in the posterior third. Ctenid eye pattern 2–4-2, with anterior and posterior rows recurved in dorsal view. Eyes round, except

oval anterior lateral eyes, with white setae around PLE and PME and lateral of AME. Chilum divided. Clypeus with long erect black bristles. Chelicerae brown, retromargin with four similar-sized teeth and two small proximal teeth; with intermarginal denticles between the promargin and the retromargin; prominent basal condyle. Endites brown with anterolateral serrula and anteromedian scopulae. Labium dark brown, slightly longer than wide. Sternum truncated anteriorly and posteriorly pointing, not extending between coxae IV. Ventral faces of coxae light brown with dark brown spots. Male legs longer and slender than female legs. Trochanter notched. Tarsus with claw tufts composed of tenent setae. Abdomen oval, brown, dorsum with a black anterior border, lighter centrally and with a folium-like pale brown longitudinal band, venter brown with four divergent series of white dots. Spinnerets: anterior laterals (ALS) long and wide in the apex; posterior medians (PMS) roughly conical, short and narrow in the apex; posterior laterals (PLS) long and conical. Palp: RTA short and truncated in the apex (Fig. 22C), embolus short without laminar process (Fig. 22B and 26I); lacking a sclerotized process at the base (Fig. 22B and 26I); median apophysis large with cup-shaped aperture ventrally visible (Fig. 22B, 26G-I); conductor reduced, covering the embolus tip (Figs. 39B, 47B). Epigynum (Fig. 22D): median sector with a pointed or oval projection in the posterior area, anterior area broad with two lobes, lateral fields without large hyaline projection and copulatory openings small and inconspicuous, lateral process elongated and originated medially. Copulatory ducts curved, with a broad, less sclerotized area at the beginning of the copulatory openings; spermathecae reniform-shaped; fertilization ducts small and posteriorly located (Fig. 22E).

Composition: Only the type species, *Eldivo tuxlas*.

***Eldivo tuxlas* sp. nov.**

Etymology. The species epithet is a noun in apposition after the type locality, Reserva de la Biosfera Los Tuxtlas, a protected tropical rainforest in Veracruz.

Diagnosis. As in genus description.

Male (CNAN-AR-T01865, from Los Tuxlas Biological Station, Veracruz province, Mexico). Total length 26.87. Carapace 14.11 long and 11.04 wide. AME 0.54, ALE 0.42, PME 0.53, PLE 0.54. Sternum 6.16 long and 5.42 wide, labium 1.90 long and 1.70, endites 3.23 long and 1.89 wide. Leg measurements: I: femur 16.87, patella 5.67, tibia 18.67, metatarsus 16.84, tarsus 6.84, total 64.89; II: 16.61, 6.45, 16.88, 15.85, 6.47, total 62.26; III: 14.68, 5.34, 13.85, 13.83, 5.20, total 52.90; IV: 17.82, 5.86, 18.30, 11.81, 6.2, total 31.58. Leg spination: leg I tibia v2-2-2-2-2, p1-1-0, r1-1-0, metatarsus v2-2-2; d1-0-1, p1-1-0, r1-1-0; II-tibia v2-2-2-2-2, d0-1-0, p1-1-0, r1-1-0, metatarsus v2-2-2, p1-1-0, r1-1-0; III-tibia v2-2-2, d1-1-1, p1-0-1, r1-0-1, metatarsus v2-2-2, d0-1-0, p1-1-1, r1-1-1; IV-tibia v2-2-2, d1-1-1, p1-01, r1-0-1, metatarsus modified. Palp: as in genus description.

Female (CNAN-AR-T01866, from Los Tuxlas Biological Station, Veracruz province, Mexico)**.**Total length 24.78. Carapace 11.28 long and 8.89 wide. AME 0.50, ALE 0.35, PME 0.50, PLE 0.50. Sternum 4.52 long and 4.32 wide, labium 1.23 long and 2.54 wide, endites 2.24 long and 1.70 wide. Leg measurements: I: femur 11.61, patella 4.85, tibia 12.32, metatarsus 9.89, tarsus 4.06, total 42.73; II: 11.09, 4.76, 11.13, 9.02, 3.71, total 39.71; III: 12.40, 4.08, 8.70, 8.35, 3.04, total 36.57; IV: 12.23, 4.32, 11.28, 12.28, 4.10, total 44.21. Leg spination: tibia I-II v2-2-2-2-2, metatarsus I-II v2-2-2-2-2, tibia III v-2-2-2, d1-1-1, p1-0-1, r1-0-1, metatarsus v2-2-2, d0-1-0, p1-1-2, r1-1-2; IV-tibia v2-2-2, d1-1-1, 1-0-1, p1-0-1, metatarsus v-2-2-2, d0-1-0, p1-1-2, r1-1-2. Epigynum: as in generic description. Epigynum: as in genus description.

Distribution. Lowland and premontane ecosystem of Mexico (Fig. 27).

Discussion

This study presents a molecular phylogeny of *Kiekie* including 15 of the 16 currently described species. Our phylogenetic analyses support the monophyly of *Kiekie* and reveal a new genus from Mexico as its sister lineage. The monophyly of *Kiekie* is supported by three morphological synapomorphies: an elongated embolus with a laminar process (Figs. 42A–E, 43A–E), conductor resembling an open fan (Figs. 25A–F, 26A–F), and locking lobes located at posterior and sometimes in retro-posterior side (Figs. 25B, 26C), instead of posterior prolateral as most ctenines. The sister relationship of *Eldivo* and *Kiekie* is supported by the presence of a modified IV metatarsus in males (Fig.4C), although this character has evolved convergently several times in South American ctenines. The *Eldivo* monophyly ~~*Eldivo*~~ is supported by one male morphological synapomorphy: a laminar fold in the internal side of the embolus.

Most of the intrageneric relationships of *Kieke* are well supported by molecular data, and some of them also by morphological characters. The first clade comprises the species *K. curvipes*, *K. verbena* and *K. montanensis* shared a prominent tegular process. The second clade contains the larger species of the genus: *K.* ~~*sinautipes*~~*sinuatipes*, *K. barrentesi*, *K. sarapiqui*, *K. laselva*, *K. valeroi*, *K. panamensis*, *K. griswoldi* and *K. lascruces*. Although the second clade is recovered with low support, it also presents several synapomorphies, providing more support to its monophyly: elongate and curved copulatory ducts that project in the anterior area of the epigynum, and large copulatory openings. In addition, males of the second lineage have longer flagelliform embolus compared to the remaining species. Within this clade, the sister relationship between *K. sinautipes* and *K. barrentesi* is supported by the copulatory ducts having a 360° turn that completely covers the anterior side of the spermatheca~~l~~, while in the remaining species of this clade the copulatory ducts fold over itself before it enters the spermathecae.

Con formato: Español (Perú)

The highest species diversity in *Kiekie* occurs in the montane ecosystems of Costa Rica, followed by the lowland rainforest of the Pacific side (Limón Basin). This diversity arose after a dispersal event from the tropical region of North America to Lower Central America (Costa Rica) during the Late Miocene (10-7ma). The northern origin of *Kiekie* and subsequently colonization of Lower Central and South America is supported not only by the early divergent North American species *K. garifuna* and the sister genus *Eldivo*, but also by a more basal lineage of North American species of the genera *Ctenus* and *Leptoctenus* (Peck, 1981). Therefore, the northern origin of *Kiekie* and subsequent dispersal and diversification in Lower Central America is well supported. Interestingly, the species diversity of *Kiekie* starts to decrease toward the south and in the Trans-Andean region of South America is only represented by two species, being *K. panamensis* the most common species found in Colombia and Ecuador. The high diversity of *Kiekie* in Lower Central America which can reach up to five species in one locality of tropical rainforest is replaced in South America by another ecological equivalent ctenid, *Spinoctenus* (Hazzi *et al*., 2018).

The geological evolution of the Costa Rica forearc has a complex history related to subduction along the Middle America Trench (Porras *et al*., 2021). Geochronological, geochemical, and petrological data from the Talamanca Cordillera tracks the key turning point (12–8 Ma) from the evolution of an oceanic arc depleted in incompatible elements to a juvenile continent (Gazel *et al*., 2019). The first event of dispersal from Tropical North America during the late Miocene temporally corresponds with these dates in which Costa Rica started becoming a young continental land.

Although there is no information about the different elevation stages of the mountain ranges in Costa Rica at different time periods, there are contractional deformation periods in Cordillera

Central and Talamanca from 11 to 5mya (Mescua et al., 2017; Porras et al., 2021). In the case of Cordillera Central the period of deformation is from 10 to 5mya, which it could be enough time to allow the formation of mild elevation mountains (Porras et al., 2021). In Talamanca Cordillera, the deformation in the Fila Costeña was probably linked to deformation and uplift of this Cordillera in the middle to late Miocene (Mescua *et al.*, 2017). These deformations are also related with a change of the chemistry of the volcanic rocks which could indicate mountain uplift (Porras et al., 2021). The four independently events of Colonization from lowland ecosystems to the montane ecosystems of Cordillera Central and Talamanca during the Late Miocene (9-4ma) temporally match the geological time assumed in which Central and Talamanca Cordilleras started uplifting. The divergence times of montane species of *Kiekie* also correspond with the time of diversification of montane palm-pitviper snakes (*Bothriechis*) in Costa Rica which occurred during the Late Miocene (Mason *et al.*, 2019). These events of deformation and uplift also coincided with the deposition of the Limón basin (Pacific side of Costa Rica) which contributed to the final closure of the Isthmus, and possibly causing the speciation of the three lowland endemic species of this region: *K. laselva*, *K. tirimbina* and *K. sarapiqui*, around 7-4mya. The diversification of these lowland species also coincides to some extent with the origin times of *Brachyrhaphis* fishes (Poecilidae) in the Pacific Region of Central America (Ingley *et al.*, 2015).

Con formato: Fuente: Cursiva

Conclusions

In conclusion, this study increased the number of known species of *Kiekie* from 11 to 16 and documented a new genus, *Eldivo* which is the sister lineage of *Kiekie*. Most of the diversity and endemism of *Kiekie* is located in the montane ecosystems of Costa Rica followed by the lowland rainforest of the Pacific side (Limon Basin). *Kiekie* originated in the North America Tropical region and dispersed to Lower Central America where it started diversifying during the Late

Miocene. In Lower Central America, *Kiekie* colonized independently several times the montane ecosystems corresponding to periods of uplifting of Talamanca and Central Cordilleras. Then, during the Pliocene *Kiekie* dispersed to South America as attested by ~~originating~~ the species *Kiekie panamensis*.

Comentado [aa11]: The species apparently originated in Panama, Central America, and then dispersed to South America

Acknowledgements

We are grateful to Gilbert Barrentes (MZUCR), Marcela Sanchez Ocampo (MNCR), Oscar Francke and Edmundo Gonzalez (CNAN) and Jimmy Cabra (MUSENUV) for making available some of the specimens for this study. We also want to thank to La Tirimbina Rainforest Center for their great hospitality and help during fieldwork. N. Hazzi is ~~in~~ deeply in debt with Gilbert Barrantes, Natalia Conejo, Bernal Rodríguez Herrera, Ronald Cordero, Juan Bernal and Tomas A. Rios for fieldwork logistics and travel. N. Hazzi also want to thanks to William Eberhard and Mary West-Eberhard for their hospitality. Collecting in Costa Rica and exporting the specimens out the country was permitted by Sistema Nacional de Areas de Conservacion (SINAC) and Ministerio de Ambiente de Energia (SINAC-ACC-PI-R-045-2019 and PE-DCUSBSE-SE325-2019). Collecting in Panama and exporting the specimens out the country was permitted by Ministerio de Ambiente (SEX/A-79-18). We want to thank to the Department of Biological Sciences of The George Washington University, the Harlan Fellowship and the Explorers Club Washington DC group for fieldwork financial support. We also want to thank to the Ernst Mayr Travel Grants (MCZ) to support the examination of the ctenid specimens of the Museums in Costa Rica (MZUCR and MNCR). Additional support was provided by ~~a~~ US National Science Foundation grants (DEB 1754289, DEB 1754289) to GH.

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Comentado [aa12]: Some grammar typos, and at least one wrong, check again all references

Comentado [aa13]:

Comentado [aa14R13]: Check reference

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