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Discovery of two new species of eyeless spiders within a single Hispaniola cave

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Abstract. Vision is a remarkable sensory adaptation; however, natural selection may not favor maintenance of eye function in habitats where eyesight does not contribute to fitness. Vision loss is relatively common in cave-dwelling spiders in the temperate zone, but appears rarer in tropical caves. To date, blind spiders in the (sub)tropical Caribbean have only been described from Cuba and Jamaica, including four pholcids, a barychelid, a ctenid, and a prodidomid with reduced eyes. In our survey of over 40 caves in the Greater Antilles, mainly Puerto Rico, Isla Mona, Cuba, and Dominican Republic, we have not previously found any eyeless spiders. Here we summarize information on blind Caribbean spiders, and describe two newly discovered species representing two families, from a single cave, Cueva Seibo, in the Dominican Republic. These are the eyeless *Ciba seibo* n. gen., n. sp. (Ctenidae) and the vestigial-eyed *Trichopelma maddeni* n. sp. (Barychelidae). Cueva Seibo appears to be an energy-poor system with a relatively small bat population and is physiologically unique amongst caves we surveyed. We postulate that troglobiomorphism in the Caribbean may result from individual cave environments and hypothesize convergent eye loss within this cave, as most members of both families, including epigean species from the Dominican Republic, have normal eyes. However, another blind species, *Ciba calzada* (Alayón 1985) n. comb., occurs in a cave in Cuba and it remains to be tested if eye loss occurred in these two convergently, or if their shared lack of eyes is homologous.

Keywords: Blind spiders, Barychelidae, Caribbean, Ctenidae, troglomorphic, tropical caves

Caves are distinct terrestrial ecosystems in receiving little or no light from the sun. As primary production through photosynthesis is limited, cave systems are supported by energy that enters from outside, such as plant and animal debris, rendering many cave ecosystems energy poor and supported by decomposers (Culver 2000; Cardoso 2012). Caves are thus useful model systems to study adaptation in response to low energy input (Klaus et al. 2013; Niemiller & Zigler 2013). 'Cave adaptations', or troglobiomorphisms, include regressive and constructive traits, as a response to permanent darkness, low food and local conditions (Cardoso 2012; Trontelj et al. 2012). In some cases, direct selection can drive energy-saving strategies such as non-expression of eyes and pigments (Klaus et al. 2013; Niemiller & Zigler 2013). Natural selection can also result in other cave adaptations such as increased life spans and development times, elongation of appendages, and increased non-optic sensory perception (Arnedo 2007; Porter 2007; Klaus et al. 2013; Niemiller & Zigler 2013).

Historically, the study of cave-adapted organisms was focused on temperate ecosystems, where it was hypothesized that the evolution of obligate cave dwellers was related to glaciation periods in the Pleistocene, a time during which tropical regions may have been less affected (Barr 1967; Sbordoni 1982, 2000; Barr & Holsinger 1985; Holsinger 1988). Countless examples of temperate, troglobiomorphic animal lineages exist (Culver 2000; Porter 2007). Although the impact of glaciation periods on cave fauna in the tropics is difficult to evaluate, many tropical caves differ starkly from temperate caves in being energy-rich ecosystems (Mitchell 1969; Ferreira et al. 1998; Bishop et al. 2012). They may contain huge populations of bats, often numbering in thousands or hundreds of thousands, and these systems are driven by the massive influx of energy through bat guano (Ferreira et al. 1998; Pellegrini et al. 2013). Thus animal densities, including decomposers and their predators, can be very high. In such systems, selection for energy-saving traits may be less intense. This seems an intuitively satisfying explanation of why cave adaptations are less frequent in the tropics, but to properly address that question comparative analyses of a range of tropical and temperate cave systems are necessary.

As top invertebrate predators, arachnids are one of the most important and common groups in cave environments. In temperate zones about 20–25% of spiders found in caves are troglobitic (Gertsch 1973a, 1973b; Peck 1990, 1999; Garcia 2000; Culver & Pipan 2009; Trajano & Bichuette 2009; Griswold et al. 2012; Jäger 2012; Miller & Rahmadi 2012), expressing the traditional troglobiomorphic adaptations such as loss of eyes, reduction of pigmentation and elongation of appendages (Culver & Pipan 2009; Niemiller & Zigler 2013). The reduction and absence of eyes is a more frequent condition than other external sensory reductions in spiders (Jimenez & Llinas 2009). In many spider families visual sensory perception is not critical for prey capture, courtship, or mating, with obvious exceptions including families such as Salticidae and Lycosidae. To date there are approximately 1000 described species of eyeless spiders, representing close to 60 families. Not all of these are cave dwellers, but among blind cave species, well over 90% are described from the temperate zone (Gertsch 1973a, 1973b; Peck 1990, 1999; Garcia 2000; Culver & Pipan 2009; Trajano & Bichuette 2009; Griswold et al. 2012; Jäger 2012; Miller & Rahmadi 2012). A small number, as far as we can tell less than 30 species, of eyeless troglobiotic spiders are known from the tropics (Culver &

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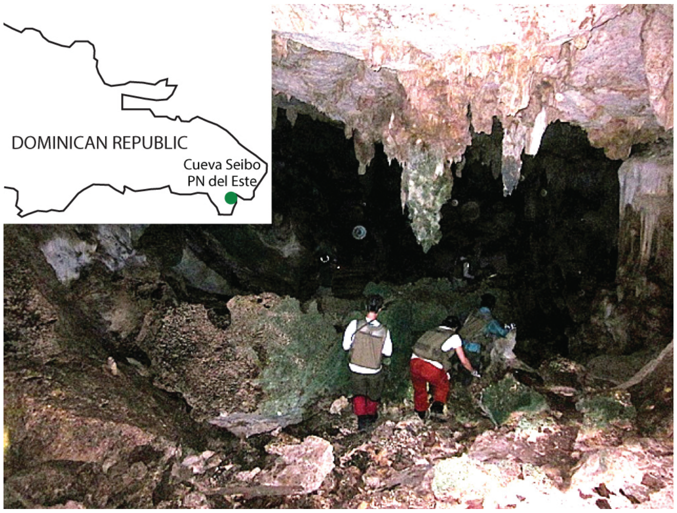

Figure 1.—CarBio team inside the second chamber of Cueva Seibo, Parque Nacional del Este, Provincia de Altagracia, República Dominicana (18.35536°N, 68.61825°W), July 10, 2012. This is the type locality for eyeless *Ciba seibo* sp. nov. and the vestigial-eyed *Trichopelma maddeni* sp. nov., which were found under large limestone slabs shown here. Inset maps show the location of Cueva Seibo.

Pipan 2009). These include species from Hawaiian lava tubes, which are extremely long, shallow, dark and isolated environments (Gertsch 1973b; Howarth 1993), Asian and Australasian caves (Jäger 2012; Miller & Rahmadi 2012), and Neotropical caves including Cuba, Jamaica, the Galapagos, and Mexico (Gertsch 1973a; Peck 1990, 1999; Garcia 2000; Trajano & Bichuette 2009). Although the caverniculous fauna of the Caribbean islands is certainly understudied, current evidence suggests that only a small percentage of Caribbean caves contain blind organisms (Peck 1999).

Here we describe two new species of troglobitic spiders, in two different families, found in Cueva Seibo within Parque Nacional Del Este in the southeast corner of the Dominican Republic. The former, a completely eyeless ctenid, we place in a new genus, *Ciba seibo* n. gen., n. sp., which also contains a blind species from a cave in Cuba. The latter, a Barychelidae species retaining vestigial eyes, belongs to the new species *Trichopelma maddeni* n. sp. These are the first eyeless spiders to be described from Hispaniola, adding to a very short list of seven additional blind spiders from the Caribbean. Given that most lineages found in explored caves do not have reduced eye function, we speculate on what unique aspects of this cave system may explain the occurrence of two lineages independently converging on the reduction of eyes.

METHODS

Specimens were collected in Cueva Seibo (Fig. 1) in Parque Nacional Del Este, Dominican Republic. Approximately ten researchers of our team first descended into the multi-room cave in July 2012. After discovering the first eyeless spiders among the specimens collected, a smaller team returned to target these animals specifically. All *Ciba* and *Trichopelma* specimens, including one adult of each and several juveniles, were found under flat limestone slabs lying on top of other larger stones in the second and completely dark chamber of the cave (Fig. 1). During collection, *Ciba* specimens remained motionless with legs bent in a way similar to *Loxosceles*, which were common throughout the cave but retained their common morphology of six eyes.

Specimens were preserved in 95% ethanol and rough sorted to morphospecies in the field. Using a Visionary Digital BK Plus digital imaging system, we took standard taxonomic photographs of adult females (Figs. 2, 3). The limited availability of adult specimens—one female of each species—and the fragility of the genitalia, especially of the barychelid, hampered their detailed dissection and illustration and limited the taxonomic utility of the photographs. Therefore, we also extracted DNA and amplified sequences of Cytochrome Oxidase 1 (CO1) (for extraction methods and primers see Agnarsson & Rayor 2013, Agnarsson et al. 2013b, Kuntner et al. 2013) to provide further diagnostic characters through DNA barcodes. These barcodes could also aid in determining the family placement of these species. We blasted the sequences against sequences in GenBank and BOLD; however, Genbank turned out to have too limited DNA barcode data available to help identification of these species (Garston et al. 2013a). In BOLD the *Ciba* specimen has the highest blast hit with an unidentified Ctenidae (90.1 percent identity), supporting its placement in this family. However, there are no public records of Barychelidae in BOLD, and the closest blast hit was with a Theraphosidae species (85.5% *Poecilotheria miranda*) in this case not allowing precise family placement based on barcodes alone.

TAXONOMY

Family Ctenidae Keyserling 1877
Subfamily Cteninae Keyserling 1877
Ciba n. gen.

Justification.—We describe the new genus *Ciba* based on unique features of the female genitalia, including absence of basal and median epigynal spurs and form of spermathecae and copulatory ducts that differ clearly from other Ctenidae genera. The two included species both occur in caves with no known epigean relatives. Given the poor knowledge of Caribbean spiders we hypothesize that epigean *Ciba* species are yet to be discovered, a taxonomic hypothesis that will require testing through further sampling of specimens and phylogenetic analyses.

Type species.—*Ctenus calzada* Alayón 1985. Designated here.

Etymology.—The specific name is an arahuac word meaning big rock. The gender is feminine.

Diagnosis.—Females resemble those of genera *Ctenus* and *Ohvida* by the general features of the epigyne, but can be distinguished from these two genera by the absence of basal and median epigynal spurs.

Description.—Median size ecribellate spiders (Fig. 2). Total body lengths (females): 7.9–9.0 mm. Carapace prolonged and anterior truncated; thoracic groove longitudinal. Ocular area 1/5 of the cephalic region; eyeless or with six small eyes (in three files of two). Chilum inconspicuous. Clypeus with few bristles or no bristles at all. Chelicerae with scattered white setae in frontal area and margins; promargin with three teeth;

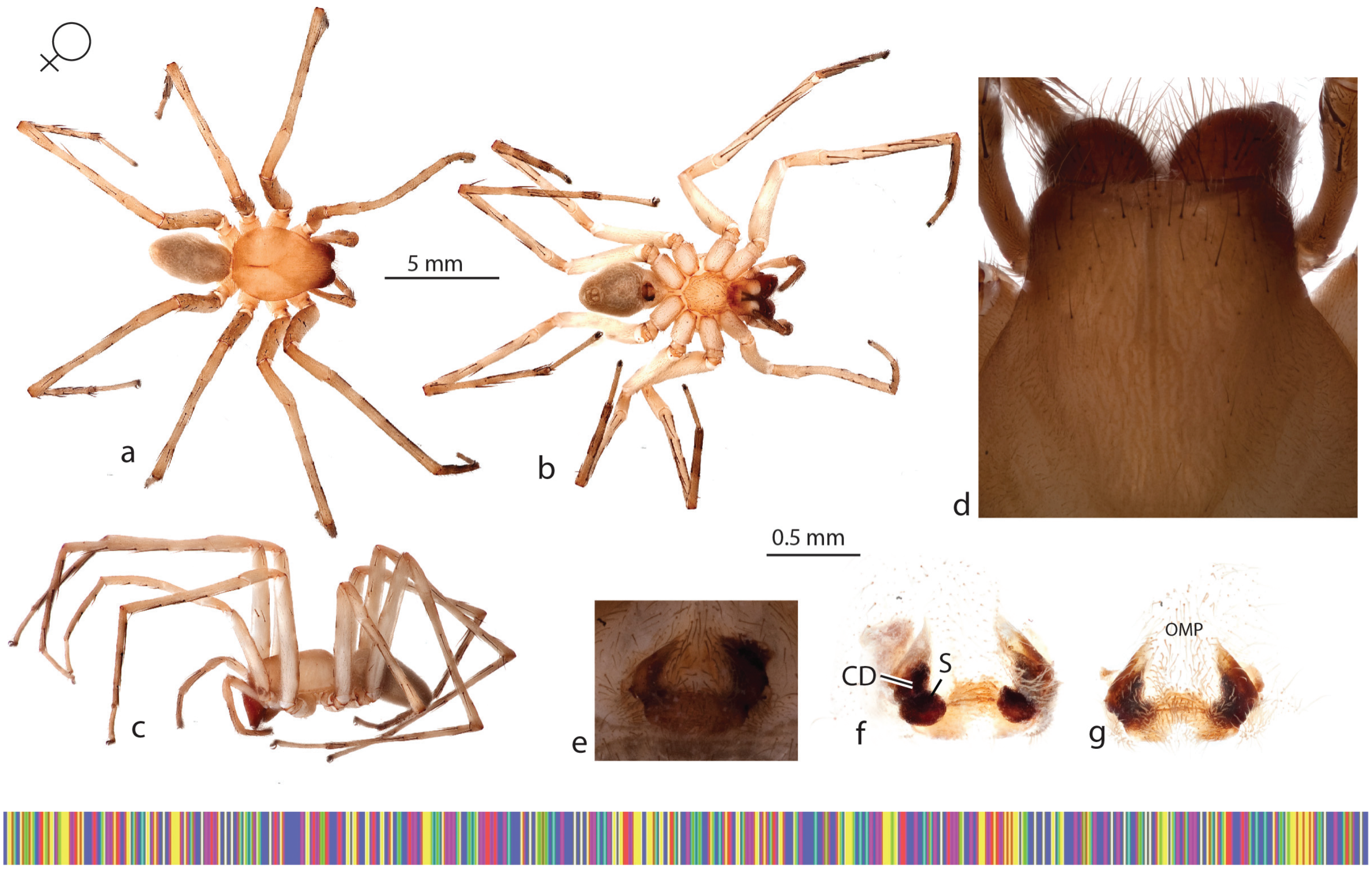

Figure 2.—Female holotype *Ciba seibo* sp. nov. a) dorsal habitus; b) ventral habitus; c) lateral habitus; d) dorsal carapace, note absence of eyes; e) external epigynum; f) internal epigynum dorsal, CD=copulatory duct, S=spermathecae; g) internal epigynum ventral, OMP=oval median plate. DNA barcode is displayed below illustrations.

retromargin with four-five large and regularly spaced teeth and a small denticle. Endites convergent and with internal lateral margins excavated, distally semi-rounded bearing dense apical scapulae and setae. Sternum oval, not extending between coxae IV. Leg formulae 4312 or 4231. Trochanters notched. Abdomen oval with filiform setae in the anterior dorsal area. Epigyne (Figs 2e–g): subtriangular with projected and sclerotized lateral margins; lateral spurs absent. Internal genitalia: with very short and curved copulatory ducts emerging from basal area of spermathecae.

Composition.—Two species: *Ciba calzada* and *C. seibo* n. sp

Distribution.—Cuba and Hispaniola.

Ciba calzada (Alayón 1985) n. comb.

Ctenus calzada Alayón, 1985:3–4, Fig. 1 (female holotype from Sistema Cavernario Majagua Cantera, Cueva de las Dos Anas, Sierra de San Carlos, Luís Lazo, Municipio Matahambre, Provincia de Pinar del Río, Cuba, deposited in the MNHNCu, examined).

Diagnosis.—Females can be distinguished from *Ciba seibo* sp. nov. by the weakly sclerotized marginal area of the epigynum and the presence of six reduced eyes.

Description.—*Male*. Unknown.

Female (holotype). Total length (mm) 9.00. Carapace 4.20 long. 3.40 wide. Abdomen 4.80 long, 2.80 wide. Labium 0.70 long. Sternum 1.95 long, 1.80 wide. Leg measurements: I, femur 6.30, tibia 6.90; II, femur 6.60, tibia, 6.30; III, femur 6.80, tibia 6.90; IV, femur 7.30, tibia 7.20. Leg formulae 4312. Leg spination: tibia I and II ventral 2-2-2-2-2 (shorts), dorsal 1-1, prolateral 1-1; metatarsus I and II ventral 2-2-2; tibia III and IV ventral 2-2, dorsal 1-1, prolateral 1-1; metatarsus III and IV ventral 1-1-1, dorsal 1-1, prolateral 1-1. Epigyne: sub-triangular, lateral margins weakly sclerotized, head of spermathecae rounded.

Additional material examined.—Two females (paratypes) from the type locality.

Distribution.—Only known from the type locality.

Natural history.—Found in crevices on the floor, under rocks, and low parts of the walls of the cave.

Ciba seibo Alayon and Agnarsson n. sp.
(Figs. 2a–g)

Type material.—Female holotype from Cueva Seibo, Parque Nacional del Este, Altagracia province, Dominican Republic (18.35536°N, 68.61825°W), July 10, 2012, Col. Team CarBio, deposited in the NMNH Smithsonian.

Etymology.—The species name is a toponym in apposition referring to the type locality.

Diagnosis.—The females of *Ciba seibo* sp. nov. resemble those of *C. calzada* by the morphology of the epigynum, but can be distinguished by the most heavily sclerotized margins of

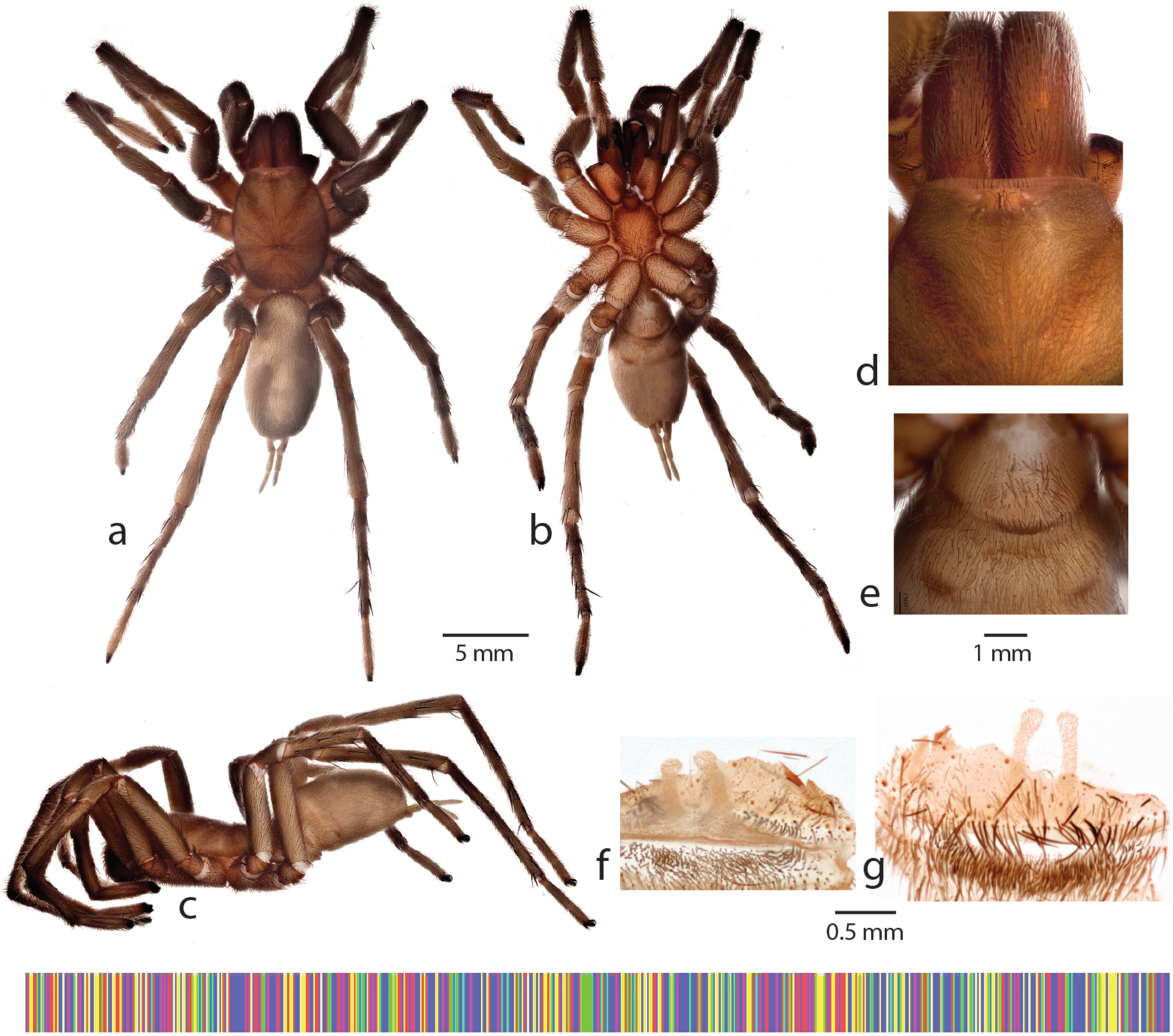

Figure 3.—Female holotype *Trichopelma maddeni* sp. nov. a) dorsal habitus; b) ventral habitus; c) lateral habitus; d) dorsal carapace, note small white vestigial eyes; e) external epigynum; f) internal epigynum dorsal; g) internal epigynum ventral. DNA barcode is displayed below illustrations.

the epigynum, the low position of the spermathecae, and the presence of two small 'eye spots', or vestigial eyes.

Description.—Male unknown.

Female (holotype).—Total length (mm) 7.97. Carapace 4.33 length and 3.28 wide. Sternum 1.88 long and 1.88 wide. Labium 0.91 long and 0.79 wide. Leg measurements: I femur, 4.09; tibia 5.37; II femur 5.48; tibia 5.57; III femur 4.77; tibia 4.76; IV femur 5.91; tibia 6.27. Leg formulae 4231. Leg spination: tibia I and II ventral 2-2-2-2-2 (shorts), no dorsal or prolateral spines; metatarsus I and II ventral 2-2-2; tibia III and IV with an irregular pattern of 6–7 spines both ventrally and dorsally; metatarsus III and IV with an irregular pattern of 5–7 spines both ventrally and dorsally. Epigyne: median plate sub-cuadrate, margins curved and sclerotized.

Additional material examined.—Only known from holotype female and several juveniles from the type locality.

Distribution.—Only known from the type locality.

Natural history.—Found on cave floor under stones in the dark area of the cave.

Barcode.—partial barcode, positions 18–658 of the standard barcode: TTGGACTTGACCAGCTTAASCAGGTACGGGGATAAGAGTTTTAATTCGTATAGAATTAGGTCATTCTGGTAGATTGTTAGGGGATGATCATTTGTATAATAGTTGTTGTTACTGCTCATGCTTTTGTAATGATTTTTTTTATGGTAATACCAATTTTAATTGGTGGATTTGGTAATTGGTTAGTTCCTTTAATATTAGGGGCTCCTGATATATCGTTTCCTCGTATAAATAATTTATCTTTTTGATTGTTGCCACCTTCTTTATTTTTGTTGTTGATATCTTCTAT

GGTGGAAATAGGGGTTGGGACTGGTTGAACTGTTTATCCTCCTTTAGCTTCTAGAATTGGTCATATAGGTAGATCAATGGATTTTGCTATTTTTTCTTTACATTTAGCTGGGGCTTCTTCTATTATAGGGGCGGTAAATTTTATTTCTACTATTGTTAATATACGTTTATTAGGGATAAGAATAGAGAGGGTGCCTTTGTTTGTTTGGTCGGTTTTTATTACAGCTATTTTATTGTTATTGTCTTTACCTGTGTTAGCGGGTGCTATTACTATATTGTTGACTGATCGAAATTTTAATACTTCTTTCTTTGATCCTGCGGGAGGAGGAGATCCTGTTTTATTTCAACATTTGTTT.

Family Barychelidae Simon 1889

Trichopelma maddeni Esposito and Agnarsson n. sp.

(Figs. 3a–g)

Type material.—Female holotype from Cueva Seibo, Parque Nacional del Este, Altagracia province, Dominican Republic (18.35536°N, 68.61825°W), July 10, 2012, Col. Team CarBio, deposited in the NMNH Smithsonian.

Etymology.—A noun in apposition, named in honor of the Caribbean naturalist Hannah Madden.

Diagnosis.—The female of *Trichopelma maddeni* n. sp. is the first blind species in this genus and is therefore readily diagnosed from other congeners. The transverse pallid weakness (suture) of tarsus IV, characteristic of the genus, is present. The only other species recorded from Hispaniola is known from a single, fully eyed, male specimen (*Trichopelma nitida* Simon 1888), so a meaningful comparison cannot be made.

Description.—*Female* (holotype). Light brown coloration of carapace and chelicerae, abdomen greyish-tan, legs light brown with the exception of the conspicuously greyish-tan femur. Covered entirely in fine, acuminate setae, ventral surfaces of the cephalothorax are covered in additional coarse macrosetae. A cluster of macrosetae present at the center of the ocular area, as is a line of 12 macrosetae, slightly anterior to the ocular cluster, on the anteromedian margin of the carapace (Fig. 3d). The tibia and metatarsus of legs I and II each with six spines; femur through metatarsus of legs III and IV covered with numerous elongate spines. Paired tarsal claws with single denticular row. Chelicerae without conspicuous rastellum, and single row of teeth on the cheliceral promargin. Ocular area nearly flat, eyes absent with slightly lighter pigmentation at the sites of absent eyes (Fig. 3d). Thoracic furrow transverse and straight. Labium subquadrate with ~100 cuspules on the anterior third. Total length (mm) 159. Carapace length 66.8, width 53.8. Sternum length 30.4, width 26.8. Labium length 10.0, width 10.2. Leg measurements: I femur 64.4, tibia 60.6; II femur 53.1, tibia 53.8; III femur 55.0, tibia 48.8; IV femur 74.4, tibia 69.4. Leg formulae 4123. Spermathecae width 12.5, divided into two capitated regions (Fig. 3f, g).

Male. Unknown.

Additional material examined.—Only known from holotype female and several juveniles from the type locality.

Distribution.—Only known from the type locality.

Natural history.—Collected from the dark zone of a limestone cave under stones on the cave floor.

Barcode.—partial barcode, positions 38–658 of the standard barcode:

GTAGGAACTGCTATAAGAGTTGTTATTCGTATTGAGTTGGGACAAGTTGGAAGATTATTAGGTGATGATCATTTATATAATGTGGTGGTAACGGCTCATGCTCTTGTGATGATTTTTTTTATAGTAATACCTATTTTAATTGGAGGATTTGGGAATTGAATGTTACCTTTAATATTAGGAGCTCCTGATATAGCTTTTCCGCGAATGAATAATTTGAGATTTTGGTTATTACCTCCTTCTTTATTTTTGTTGATTTTATCTTCTTTGACTGATGTTGGTGTAGGAGCTGGATGGACAATTTACCCCCCCTTATCATCTTTTATTGGACACTCAGGTGGTGGAATGGATTTCGCTATTTTTTCTTTACATTTGGCTGGTGCTTCGTCTATTATGGGATCTATTAATTTTATTACTACAGTAATAAATATACGGGGCATAGGAATAAAGTTGGAGCGAGTTCCTTTGTTTGTCTGGTCGGTTGTTATTACAACTGTTTTGCTTTTACTTTCCTTGCCTGTGTTGGCTGGTGCAATTACTATATTGTTGTTTGATCGTAATTTTAATACCTCTTTTTTTGATCCTGCGGGTGGGGGTGATCCTATTTTGTTTCAACATTTATTT.

PREVIOUSLY DESCRIBED TROGLOMORPHIC CARIBBEAN SPIDERS

Barychelidae.—*Troglothele coeca* (Fage 1929) – Cuba. This was the first troglomorphic mygalomorph found in Cuba, and the Caribbean. Only two juvenile females have been collected in the type locality, Cuevas de Bellamar, Matanzas, in northwest Cuba near Havana. Lack of genitalic and genetic material hinders comparison and speculation on possible relationship with *T. maddeni*.

Pholcidae.—*Anopsicus cubanus* (Gertsch 1981) – Cuba. This species, only known from a male, is the only blind pholcid in Cuba, type locality Cueva Grande, Punta Caguanes, Yaguajay, de Sancti Spiritus Province.

Anopsicus clarus Gertsch 1982 – Jamaica. Known only from a female, type locality Caves of Clarendon Parish.

Anopsicus jarmila Gertsch 1982 – Jamaica. Known only from a female, type locality Worthy Park, Cave No. 2, St. Catherine Parish.

Anopsicus nebulosus Gertsch 1982 – Jamaica. Known only from a female, type locality Duanwary, Cave No. 1, St. Elizabeth Parish.

Ctenidae.—*Ciba calzada* (Alayon 1985) new combination – Cuba. *Ciba calzada* is described from the Majagua-Cantera cave system as well as Cueva de Las Dos Anas and Sierra de San Carlos, all in the province of de Pinar del Río in western Cuba. The species is only known from females, which have six highly reduced eyes. At least an additional two eyeless ctenids have been described from Australia: *Janusia muiri* (Gray 1973) and *Amauropelma undarra* (Raven et al. 2001).

Prodidomidae.—*Lygromma gertschi* (Platnick & Shadab 1976) – Jamaica. *Lygromma gertschi* is the only known troglobitic gnaphosid. Its troglomorphisms include the loss of functional eyes, elongation of the legs, tarsal trichobothria, and spinnerets, and the loss of teeth on the tarsal claw. Male and female holotypes were described from Falling Cave, Douglas Castle, St. Ann Parish, northern Jamaica.

RESULTS AND DISCUSSION

We describe two new blind spider species, from two spider families, discovered in a single karst cave in southeast Dominican Republic. *Ciba seibo* lacks eyes altogether, while *T. maddeni* retains vestigial eyes. This discovery is significant for several reasons. First, there are few troglobitic spiders in the region, with only seven previously described blind cave species, four from Jamaica and three from Cuba (Platnick 1976; Gertsch 1982; Peck 1999; Alayon 2000). Second, no cave explored to date has contained more than a single blind species. Third, of all the caves explored in the karst regions of the Greater Antilles islands to date, only a small fraction contain any troglobiomorphic animals (Peck 1999; Alayon 2000; Garcia 2000), certainly much less than 20–25%. Therefore, in the tropics, the occurrence of troglobiomorphism appears to be caused by a set of conditions unique to a single cave rather than a regional pattern.

That Cueva Seibo contains two blind spider species while most hitherto explored Caribbean caves harbor no blind spiders is likely the result of a combination of factors including cave age, energy input into the cave, and historical characteristics of the cave, such as openings to the surface. It is unlikely that cave age alone explains the evolution of troglobiomorphic traits, as karst caves typically are of similar age across a karst region, and the morphology of a cave, such as the depth, darkness, and connectivity to the outside environment is not directly related to the age of the karst development (Jones & Smith 1988). Strikingly, molecular genetic estimates of divergence indicate that significant eye reduction can occur in as little as one hundred years in cave-dwelling invertebrates (Caccone & Sbordoni 2001; Arnedo et al. 2007). Hawaiian lava tubes, for example, much younger than Caribbean karst formations, contain blind spiders (Gertsch 1973; Gray 1973; Clarke 2010). Troglobitic spiders have been hypothesized to adapt to particular ecological niches within a cave, determined by a number of physical factors such as light availability, stability, humidity, percentage of CO_2 and the amount of available nutrients (Arnedo et al. 2007). The relatively small and localized population of bats, and relatively low abundance of decomposing animals (pers. obs.) suggests that Cueva Seibo may be a low energy system due to the low import of external nutrients via guano. The large limestone slabs on the cave floor indicate a recent collapse of the cave roof at the only known entrance to the cave. We hypothesize that historically this was a largely closed cave with insufficient surface connections to allow significant use by bats, and that troglobiomorphism evolved during this period of extremely low energy input.

CONCLUSIONS

The finding of two eyeless spider species *T. maddeni* and *C. seibo* in a single cave is unique in light of the paucity of troglobiomorphic spiders in the Caribbean. Although troglobiomorphisms occur ubiquitously in temperate region caves, the evolution of troglobites in the tropics may be influenced by characteristics of individual caves such as morphology and energy input. Troglobitic species express a high degree of endemism; often species are restricted to individual caves (Cardoso 2012; Niemiller & Zigler 2013). Further morphological and phylogenetic comparison of subterranean and surface populations of related spider species will advance our understanding of factors such as speciation, ecological adaptation and morphological change that generate subterranean biodiversity.

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