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Ctenus igatu sp. nov. (Araneae: Ctenidae): a new subterranean spider from Brazil with an analysis of troglomorphic traits

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Abstract. In this work we describe *Ctenus igatu* sp. nov., the first ctenid spider from South America with conspicuous troglomorphic traits, including elongated appendages, reduction of eyes, and body depigmentation. The new species is only known to occur in a unique sandstone cave from the state of Bahia, north-eastern Brazil. The morphology of the genitalia suggests that *Ctenus igatu* sp. nov. is closely related to *Ctenus fasciatus* Mello-Leitão, 1943, a facultative subterranean species from caves in the state of São Paulo, south-eastern Brazil. In addition, we compared morphological traits possibly related to the isolation in subterranean habitats, such as ratios between carapace length *vs*. leg IV length and eye diameters *vs*. carapace length, of 19 species of *Ctenus* (17 epigean species, *C. fasciatus* and the new troglobitic species described herein). Our analysis showed that both *C. fasciatus* as *C. igatu* sp. nov. have morphological troglomorphisms, with *C. igatu* sp. nov. showing marked specializations to subterranean life.

Keywords: Chapada Diamantina, Cteninae, subterranean biology, troglobitic

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The Ctenidae are a large, mostly tropical spider family, currently with over 500 described species (World Spider Catalog 2020). The family is composed of small to large (4 to 40 mm body length) nocturnal wandering spiders, which do not construct webs to capture prey (Griswold et al. 2005; Polotow & Brescovit 2014). Also known as tropical wolf spiders or tropical wandering spiders (Griswold et al. 2005), they can be found in a variety of environments, ranging from tropical and subtropical forests to subterranean environments, such as caves (Trajano & Bichuette 2010; Polotow & Brescovit 2014).

Worldwide, there are only seven ctenid spiders considered obligatory subterranean (or troglobitic), including *Troglоctenus fagei* (Lessert, 1935) from the Congo, and *T. briali* Ledoux, 2004 from Saint-Paul, Réunion Island. *Amauropelma undara* Raven & Gray, 2001 (described in Raven et al. 2001), *A. matakecil* Miller & Rahmadi, 2012 and *Janusia muiri* Gray, 1973 occur in caves in Southeast Asia and Australia, and *Ciba calzada* (Alayón, 1985) from Cuba (Cueva dos las Anas) and *C. seibo* Alayón & Agnarsson, 2014 from the Dominican Republic (Cueva Seibo) are known from the Neotropical region; the latter *Ciba* sp. was described in Bloom et al. (2014). According to the literature, only three species have been recorded in subterranean environments in Brazil: *Enoploctenus cyclothorax* (Bertkau 1880), *Ctenus fasciatus* Mello-Leitão, 1943 and *Isoctenus corymbus* Polotow, Brescovit & Pellegatti-Franco, 2005 (Trajano & Bichuette 2010; Bichuette et al. 2017, 2019; Gallão & Bichuette 2018). Of these, none has obvious morphological features suggesting specialization to a subterranean environment (i.e., troglomorphisms; Christiansen 2012), such as the reduction or loss of cuticular pigments, reduction or loss of eyes, thinning of the integument, and lengthening of the legs or sensory setae (Fage 1931; Deeleman-Reinhold 1978; Deeleman-Reinhold & Deeleman 1980; Gertsch 1992; Růžička 1999; Cokendolpher 2004; Miller 2005; Arnedo et al. 2007; Růžička et al. 2011, 2013; Marroquín 2014; Pedroso & Baptista 2014; Rodrigues et al. 2018).

Currently, the genus *Ctenus* Walckenaer, 1805, especially diverse in the Neotropical region, is composed of over 210 species, comprising around half of the described diversity within the family Ctenidae (World Spider Catalog 2020). Here we investigate a new *Ctenus* species collected on expeditions to the sandstone caves from Chapada Diamantina, Bahia, Brazil, from 2013 to 2017. Four males, four females, and juveniles of a troglomorphic species were collected in Canal da Fumaça cave, in the village of Igatu, city of Andaraí, state of Bahia, north-eastern Brazil. According to the unique morphology of the specimens, we describe them here as *C. igatu* sp. nov. In addition, we present comparative figures of the male and female of *C. fasciatus* Mello-Leitão, 1943, and analyzed and compared morphological characteristics of 19 Brazilian species of the genus *Ctenus* in order to quantify specializations related to subterranean life.

METHODS

Collection area.—The sandstone cave of Canal da Fumaça is located in the region known as Chapada Diamantina, located in the central portion of the state of Bahia, in the municipality of Andaraí in the district of Igatú (Fig. 1).

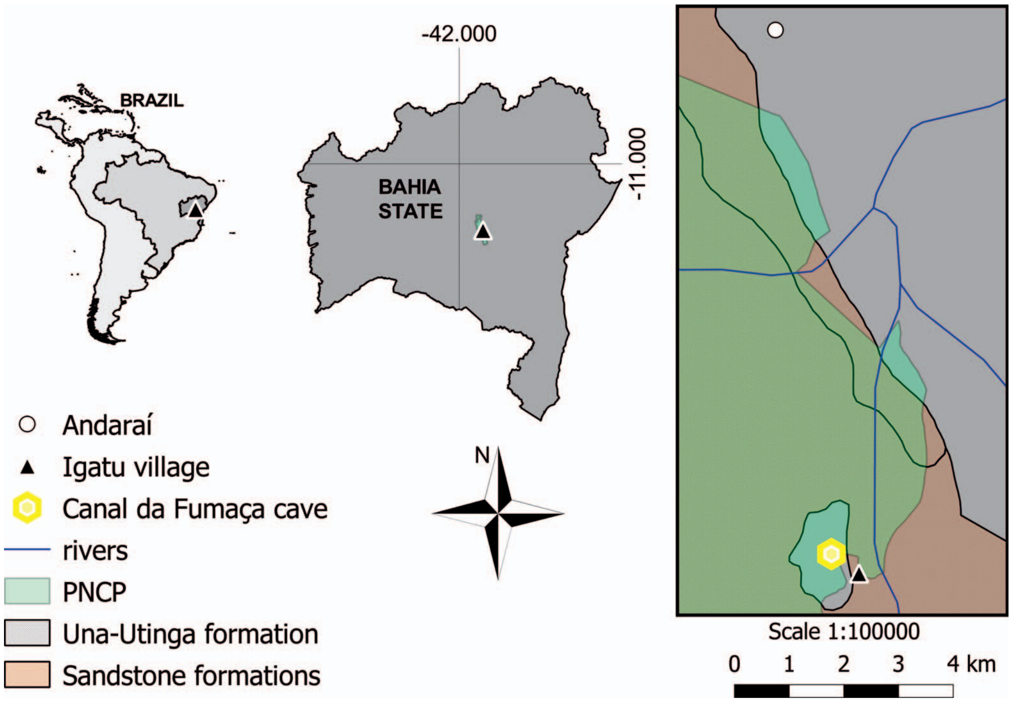

Figure 1.—Distribution of *Ctenus igatu* sp. nov. in Bahia state, Brazil.

Chapada Diamantina is partially inserted into the Serra do Espinhaço plateau, formed by siliclastic rocks. The vegetation around the sandstone caves of Chapada Diamantina is formed by 'Campos de Altitude' and remnants of Atlantic Rainforest; the climate is tropical semi-arid (Aw: tropical wet and dry), according to Köppen (1948). The sandstone caves of Chapada Diamantina are located at high altitude (above 500 m a.s.l.) and, inside the caves, the annual mean temperature is ca. 20°C and the relative humidity ca. 95%. The caves have a history of intensive hand mining due to diamond exploration, but nowadays these caves (including Canal da Fumaça cave) are protected within Chapada Diamantina National Park. Canal da Fumaça cave presents many labyrinthine passageways (conduits, tunnels, galleries) handmade by humans due to mining activities. The sandstone caves of the Igatu region already have many studies of the subterranean fauna and are considered a region of high diversity for troglobites, including many obligatory subterranean species of Opiliones, scorpions,

Table 1.—Measurements of the total length of the carapace, leg IV and the ratio of these values for 19 species of *Ctenus*. Also displayed is habitat and habit information for each species. Abbreviations: Amz, Amazonian Forest; Atl, Atlantic Forest; Cam, "Campo de Altitude"; Cav-L, species collected in Limestone cave; Cav-S, species collected in Sandstone cave; Ep, species collected in the Epigean environment; Syn, Synanthropic.

SPECIES	Carapace (mm)	Leg IV (mm)	Leg IV / Carapace	Habitat information	Habit
Ctenus amphora Mello-Leitão, 1930	8.4	36.9	4.39	Atl	Ep
C. crulsi Mello-Leitão, 1930	8.2	35.8	4.37	Amz	Ep
C. fernandae Brescovit & Simó, 2007	8.5	34.9	4.11	Atl	Ep
C. inaja Höfer, Brescovit & Gasnier, 1994	9	34.6	3.84	Amz	Ep
C. maculisternis Strand, 1909	7.4	26.6	3.59	Amz	Ep
C. manauara Höfer, Brescovit & Gasnier, 1994	5.5	26.8	4.87	Amz	Ep
C. medius Keyserling, 1891	12.8	52.2	4.08	Amz, Atl, Syn	Ep
C. minor F. O. Pickard-Cambridge, 1897	5.4	24.4	4.52	Amz	Ep
C. nigritus F. O. Pickard-Cambridge, 1897	8	35.9	4.49	Amz	Ep
C. ornatus (Keyserling, 1877)	9	37.5	4.17	Atl, Syn	Ep
C. paubrasil Brescovit & Simó, 2007	8	34.2	4.28	Atl	Ep
C. pauloterrai Brescovit & Simó, 2007	6.7	28.3	4.22	Atl	Ep
C. rectipes F. O. Pickard-Cambridge, 1897	8.8	32.7	3.72	Atl	Ep
C. serratipes F. O. Pickard-Cambridge, 1897	7.8	33.8	4.33	Amz	Ep
C. similis F. O. Pickard-Cambridge, 1897	4.6	17.6	3.83	Amz	Ep
C. vehemens Keyserling, 1891	7.1	31.1	4.38	Amz	Ep
C. villasboasi Mello-Leitão, 1949	10.6	40	3.77	Amz	Ep
C. fasciatus Mello-Leitão, 1943	8.3	60.5	7.29	Atl	Ep, Cav-L
Ctenus igatu **sp. nov.**	4.13	30.84	7.47	Cam	Cav-S

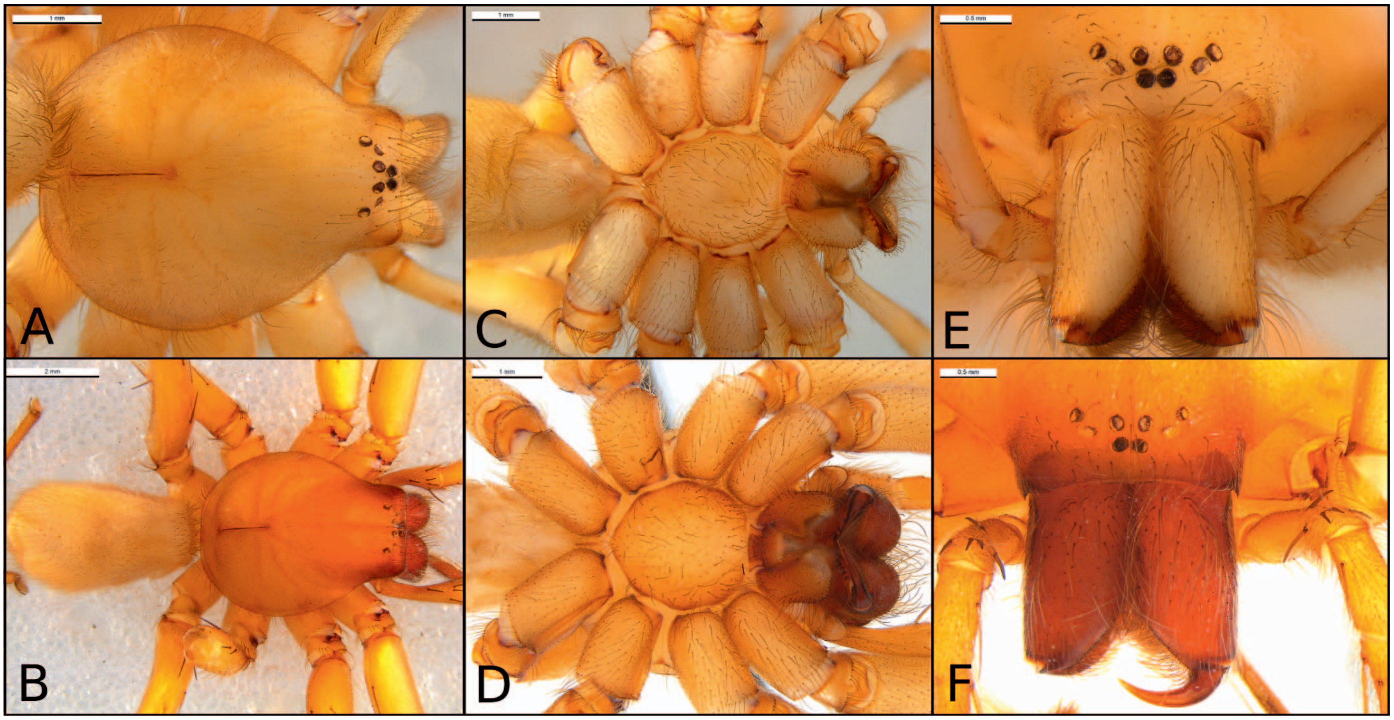

Figure 2.—*Ctenus igatu* sp. nov. (LES 15586, male; LES 15587, female): (A) male prosoma, dorsal view; (B) female habitus, dorsal view; (C) male prosoma, ventral view; (D) female prosoma, ventral view; (E) male ocular area, frontal view; (F) female ocular area, frontal view.

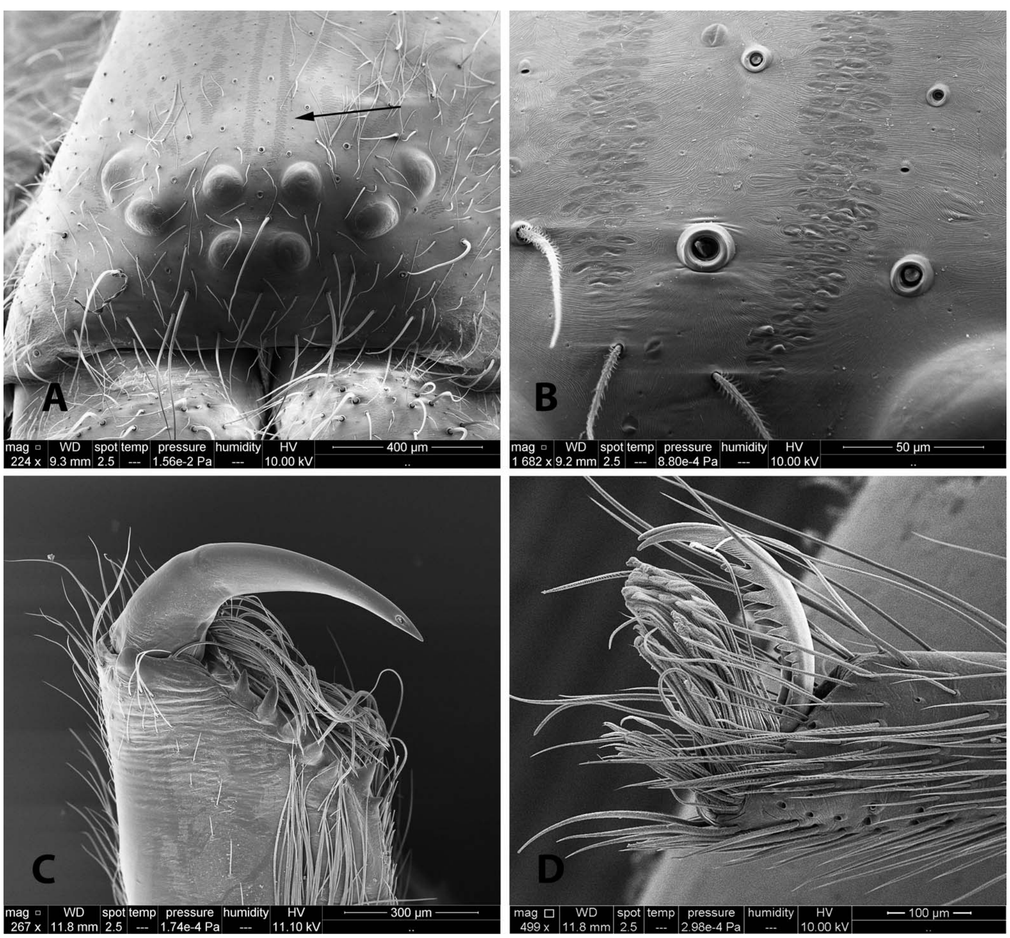

Figure 3.—*Ctenus igatu* sp. nov. (IBSP 189132, male): (A) prosoma, anterior view (arrow to magnified region in B); (B) prosoma, close-up of cuticule posterior to ocular region; (C) chelicerae, retrolateral view; (D) claw and claw tufts of leg I.

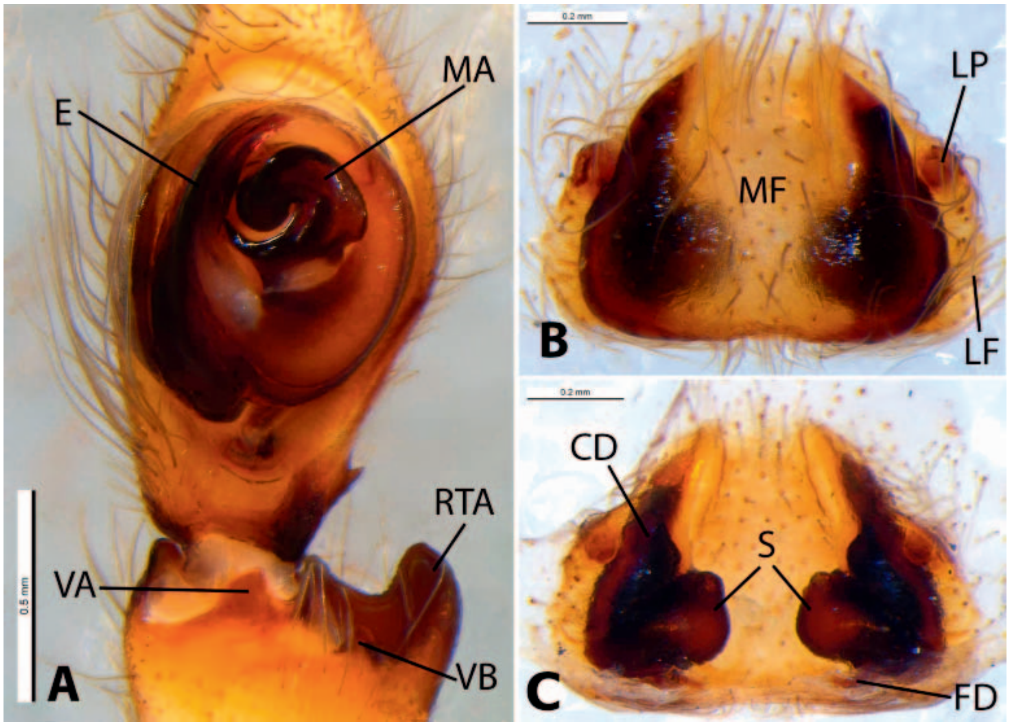

Figure 4.—*Ctenus igatu* sp. nov. (LES15586, male; LES15587, female): (A) male palp, ventral view; (B) male palp, ventral view; (C) epigynum, dorsal view. Abbreviations: CD, copulatory duct; E, embolus; FD, fertilization duct; LF, lateral field; LP, lateral projection; MA, median apophysis; MF, median field; RTA, retrolateral tibial apophysis; S, spermathecae; VA, ventral apophysis; VB, ventral branch of RTA.

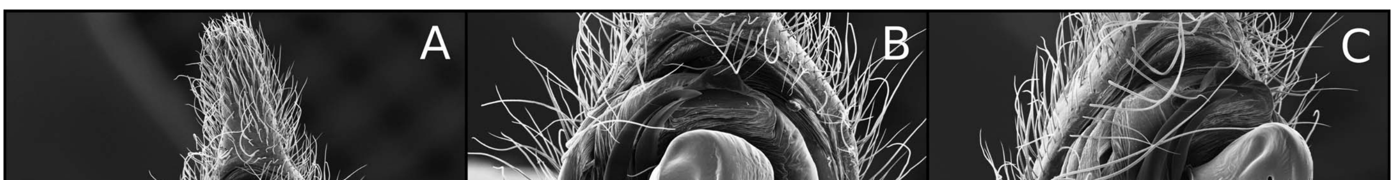

Figure 5.—*Ctenus igatu* sp. nov. (IBSP 189132, male palp): (A, B) ventral view; (C) prolateral view; (D) retrolateral view; (E) retrolateral view of tibia; (F) trichobothrium on tibia. Abbreviations: C, conductor, DT, dorsal tibial projection; E, embolus; Lo, locking lobes; MA, median apophysis; RTA, retrolateral tibial apophysis; Tr, trichobothrium; VA, ventral apophysis; VB, ventral branch of RTA.

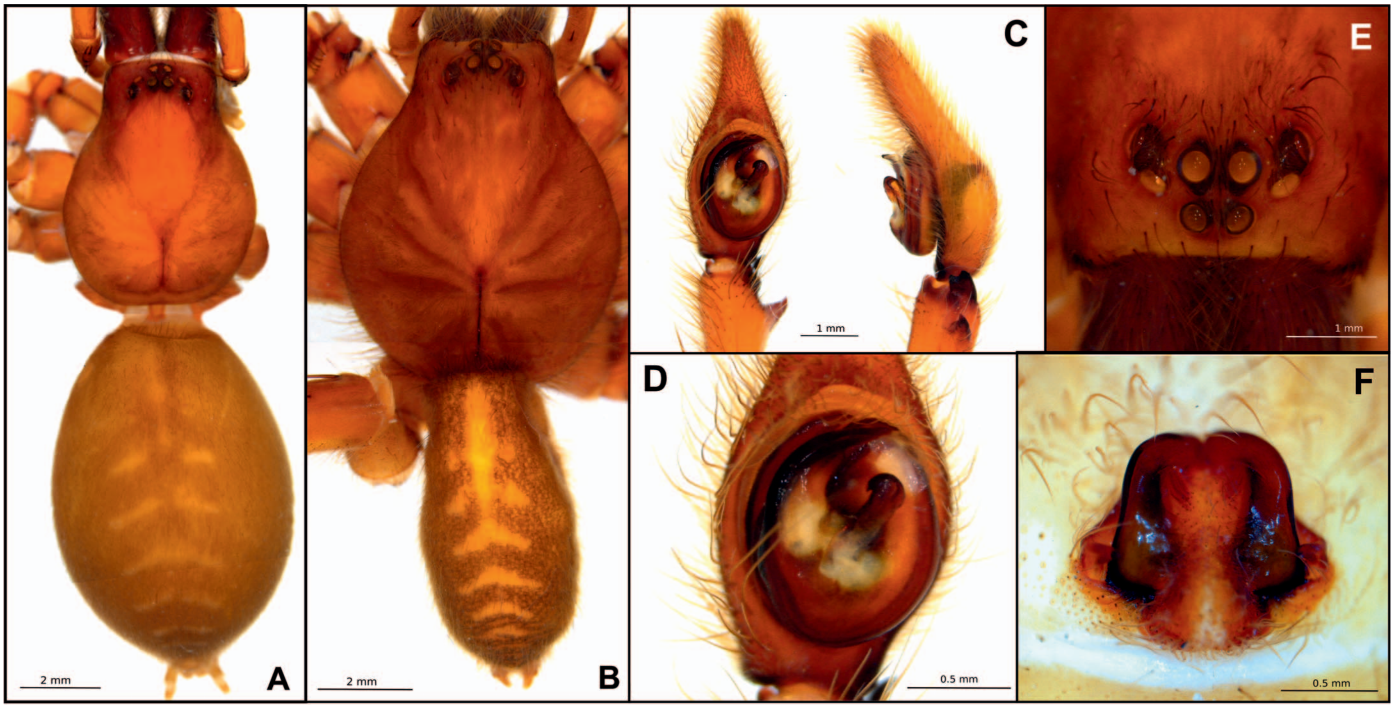

Figure 6.—*Ctenus fasciatus* Mello-Leitão, 1943: (A) female; (B) male; (C) male palp, ventral and retrolateral views; (D) male palp, ventral view; (E) female ocular area, frontal view; (F) epigynum, ventral view.

mygalomorph spiders, isopods, chilopods and fish (Trajano et al. 2016).

Analysis and preparation.—The material examined is deposited in the arachnological collection of Instituto Butantan, São Paulo (IBSP; curator A. D. Brescovit) and Laboratório de Estudos Subterrâneos, Universidade Federal de São Carlos, São Carlos (LES; curator: M. E. Bichuette). Morphological observations, measurements, and photographs were made using a Leica M165C stereomicroscope. For scanning electron microscopy (SEM) images, body parts were dehydrated in a series of graded ethanol washes (80% to 100%), dried by critical point, mounted on metal stubs using adhesive copper tape and nail polish for fixation and covered with gold. SEM photographs were taken with a FEI Quanta 250 scanning electron microscope at the Laboratório de Biologia Celular of Instituto Butantan, São Paulo, Brazil. Epigynes were carefully excised and placed in a pancreatin solution for 24–48 hours to digest extraneous tissue (Álvarez-Padilla & Hormiga 2008) then placed in water and manually cleaned. All measurements are in millimeters, and the mapping of coordinates and the map were made using QGIS 3.14.1 development Team (2020).

Abbreviations: ALE, anterior lateral eyes; AME, anterior median eyes; C, conductor; CD, copulatory duct; CRP, cymbial retrobasal projection; d, dorsal; DT, dorsal tibial projection; E, embolus; FD, fertilization duct; Lo, locking lobes; LP, lateral projection of epigynum; MA, median apophysis; MF, median field of epigynum; PLE, posterior lateral eyes; PME, posterior median eyes; r, retrolateral; RPE, retrolateral projection of embolus; RTA, retrolateral tibial apophysis; S, spermathecae; Ti, tibia; Tr, trichobothria; v, ventral; VA, ventral apophysis of tibia; VB, ventral branch of RTA.

To quantify and compare morphological troglomorphisms, we compiled information for 17 epigean species of *Ctenus* (see Table 1), all formally described (Höfer et al. 1994; Höfer & Brescovit 1997; Brescovit & Simó 2007; Polotow & Brescovit 2007, 2012). Information relating to *C. fasciatus* was obtained from three specimens deposited at the Instituto Butantan, as follows: 1 ♂, IBSP 2740 from Caverna de Santana, Parque Estadual Turístico do Alto Ribeira [PETAR], Iporanga, São Paulo, Brazil, F. Pellegatti-Franco ; 1 ♂, IBSP 232627 from Parque Estadual do Alto da Ribeira, Bulhas D'água cave, Iporanga, São Paulo, Brazil, F. Pellegatti-Franco (Figs. 6A, C, D); and 1 ♀, IBSP 232633 (Figs. 6B, E, F).

A morphometric database was developed to analyze the following morphological characteristics: length of the appendices by comparing the ratio of leg IV length / carapace length (Table 1); and eye reduction by comparing the proportion of eye diameter / carapace length ratio (Table 2). Interspecific comparisons were made between individual eyes (i.e., ALE, AME, PLE and PME) and between the mean ocular size (Table 2). For morphological analyses, we used only males since not all females are known (e.g., *C. maculisternis* Strand, 1909). The reduction or loss of cutaneous pigmentation was evaluated by visual comparison. Besides morphological information, environmental data for each of the species were considered: species collected only inside cave habitats (restricted to subterranean environments); only in the epigean (=surface) environment; or in both environments (Table 1).

TAXONOMY

Family Ctenidae Keyserling, 1877
Subfamily Cteninae Keyserling, 1877
Genus *Ctenus* Walckenaer, 1805

Table 2.—Eye diameter measurements (ALE, AME, PLE and PME) for 19 species of *Ctenus*, and the ratios of eye diameters to carapace length for each species.

	Eyes diameter (mm)				Eyes / Carapace*				
SPECIES	AME	ALE	PME	PLE	AME	ALE	PME	PLE	(x)
Ctenus amphora Mello-Leitão, 1930	0.38	0.26	0.52	0.52	0.09	0.06	0.12	0.12	0.10
C. crulsi Mello-Leitão, 1930	0.45	0.23	0.5	0.47	0.11	0.06	0.12	0.11	0.10
C. fernandae Brescovit & Simó, 2007	0.35	0.25	0.35	0.4	0.08	0.06	0.08	0.09	0.08
C. inaja Höfer, Brescovit & Gasnier, 1994	0.57	0.37	0.57	0.52	0.13	0.08	0.13	0.12	0.11
C. maculisternis Strand, 1909	0.4	0.26	0.4	0.43	0.11	0.07	0.11	0.12	0.10
C. manauara Höfer, Brescovit & Gasnier, 1994	0.32	0.17	0.4	0.41	0.12	0.06	0.15	0.15	0.12
C. medius Keyserling, 1891	0.5	0.4	0.6	0.5	0.08	0.06	0.09	0.08	0.08
C. minor F. O. Pickard-Cambridge, 1897	0.34	0.23	0.37	0.37	0.13	0.09	0.14	0.14	0.12
C. nigritus F. O. Pickard-Cambridge, 1897	0.4	0.25	0.42	0.5	0.10	0.06	0.11	0.13	0.10
C. ornatus (Keyserling, 1877)	0.45	0.37	0.57	0.6	0.10	0.08	0.13	0.13	0.11
C. paubrasil Brescovit & Simó, 2007	0.36	0.24	0.52	0.52	0.09	0.06	0.13	0.13	0.10
C. pauloterrai Brescovit & Simó, 2007	0.3	0.26	0.4	0.4	0.09	0.08	0.12	0.12	0.10
C. rectipes F. O. Pickard-Cambridge, 1897	0.42	0.3	0.5	0.45	0.10	0.07	0.11	0.10	0.09
C. serratipes F. O. Pickard-Cambridge, 1897	0.47	0.26	0.51	0.51	0.12	0.07	0.13	0.13	0.11
C. similis F. O. Pickard-Cambridge, 1897	0.21	0.16	0.22	0.2	0.09	0.07	0.10	0.09	0.09
C. vehemens Keyserling, 1891	0.36	0.22	0.44	0.44	0.10	0.06	0.12	0.12	0.10
C. villasboasi Mello-Leitão, 1949	0.53	0.27	0.6	0.58	0.10	0.05	0.11	0.11	0.09
C. fasciatus Mello-Leitão, 1943	0.3	0.26	0.33	0.3	0.07	0.06	0.08	0.07	0.07
Ctenus igatu **sp. nov.**	0.12	0.13	0.13	0.14	0.06	0.06	0.06	0.07	0.06

* See Table 1 for information on total length of the species carapace.

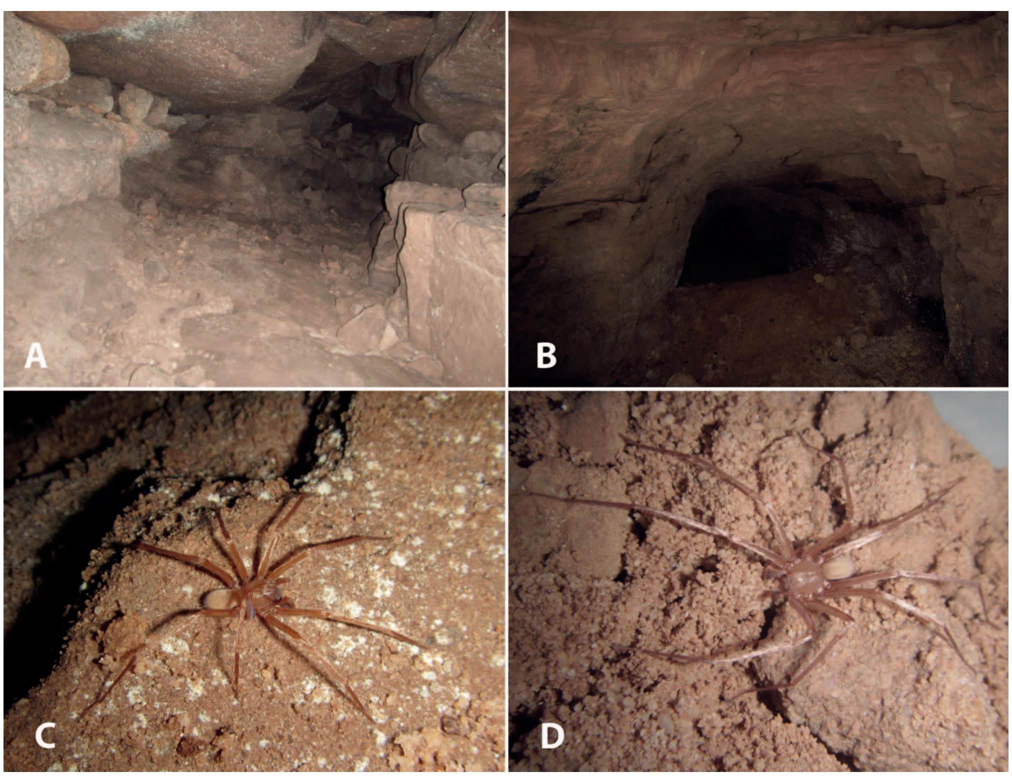

Figure 7.—*Ctenus igatu* sp. nov.: (A, B) Type-locality, galleries of Canal da Fumaça cave; (C) male *C. igatu* sp. nov. in natural environment; (D) male of *C. igatu* sp. nov. in laboratory conditions three months following capture.

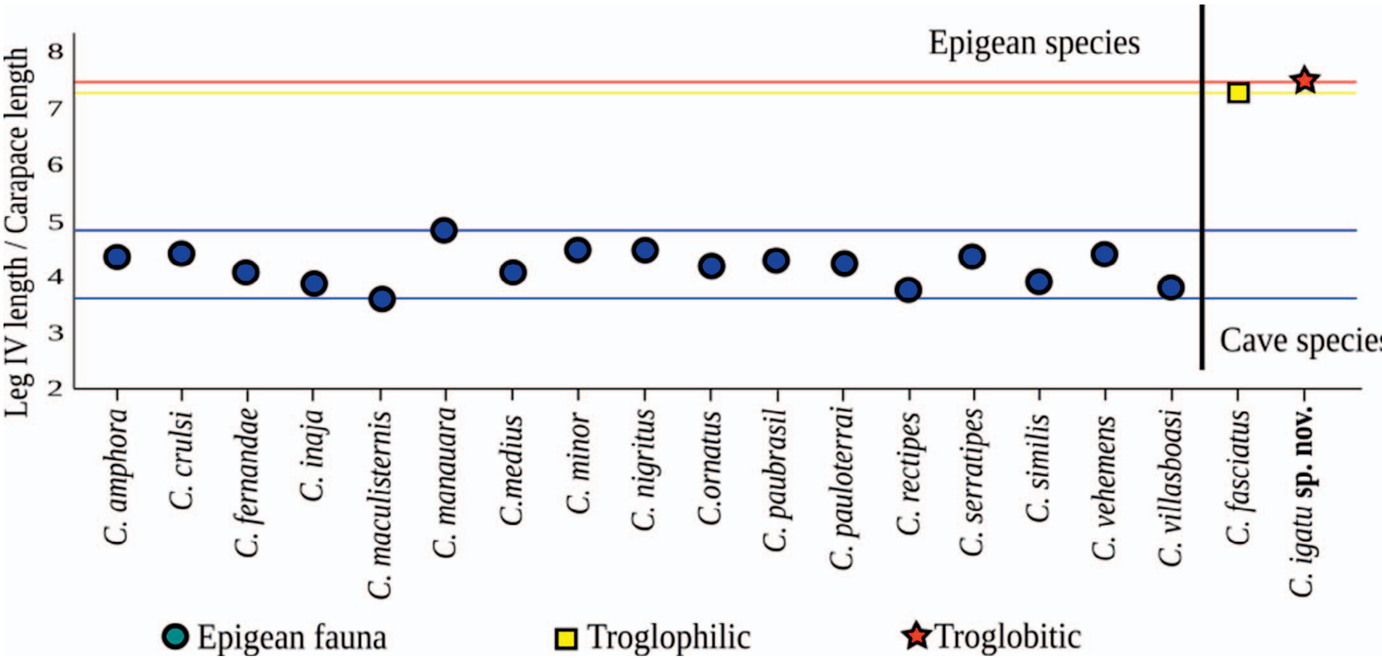

Figure 8.—Graph plotting the ratio of the length of leg IV versus the length of the carapace, for 19 epigean and cave species of *Ctenus* (see Table 1).

Ctenus igatu Polotow, Cizauskas & Brescovit, sp. nov.
http://zoobank.org/?lsid=urn:lsid:zoobank.org:act:4D1BCFDA-B6A1-4783-96DE-40AD3BA40FB2
(Figs. 2–5)

Isoctenus 'sp.n.1': Gallão & Bichuette, 2015: appendix S1.
Enoploctenus 'sp.': Gallão & Bichuette, 2018: 13.

Type material.—*Holotype male*. BRAZIL: *Bahia*: Andaraí, Igatu, Canal da Fumaça cave, 12°53′35″S, 41°19′19″W, 23 March 2013, J. E. Gallão, M. E. Bichuette and D. M. von Schimonsky (IBSP 189131).

Paratypes: 1 ♀, same data as holotype (IBSP 189131); 1 ♂, same data (LES 15586); 1 ♂ same data as holotype (LES 14013); 1 ♀, same locality data, 19 May 2016, J. E. Gallão. (LES 11425); 1 ♀, same locality data, 22 October 2014 (LES 15587; drawings and measurements); 1 ♀, same locality data, 21 May 2017 (LES 14006).

Other material examined.—BRAZIL. *Bahia*: 1 ♂, same data as holotype (IBSP 189132, MEV); 3 juveniles, same data (IBSP 189133, 189134, 196189).

Etymology.—The specific epithet is a noun in apposition taken from the region of the type locality, 'Igatu', which harbors many caves and numerous troglobitic arthropods.

Diagnosis.— Males and females resemble *Ctenus fasciatus* by the elongated legs, but *C. igatu* can be distinguished by the presence of reduced eyes (Figs. 2A, B, E, F, 3A) and by the homogeneous coloration of the dorsal abdomen (Fig. 2B; in contrast to the foliate pattern described by Eickstedt 1975: fig. 7). Males of *C. igatu* sp. nov. further resemble those of *C. fasciatus* (Eickstedt 1975: figs. 3–4) by the presence of a dorsal tibial projection on the male palp (Fig. 5E), an embolus continuous with the tegulum (i.e., without a hyaline division), tapering to the tip (Figs. 4A, 5A–C), and a wider than longer hyaline conductor (Fig. 5D). Males of *C. igatu* sp. nov. can be distinguished from *C. fasciatus* (Eickstedt 1975: fig. 4) by the presence of curved median apophysis in ventral view, with an elongated prolateral basal projection (Figs. 4A, 5A–D), and by the presence of an additional projection ventral to the RTA (ventral branch of RTA; Figs. 4A, 5D). Females of *C. igatu* sp. nov. can be distinguished from *C. fasciatus* (Eickstedt 1975: figs. 5, 6) by the sub-trapezoidal and smooth median field of the epigynum, lacking a posterior round projection and anterior folds (Fig. 4B).

Description.—*Male* (LES 15586). Prosoma uniformly light brown, darker around the ocular region and borders of the carapace (Figs. 2A, C, E); fovea brown (Fig. 2A); eyes with black rings (Fig. 2E); legs light brown; opisthosoma uniformly beige. Total length 7.60. Carapace 4.13 long, 3.55 wide, with rows of cuticular plates (Figs. 3, 4). Eye diameters: AME 0.12, ALE 0.13, PME 0.13, PLE 0.14. Chelicerae (Fig. 3C): promargin with three teeth, the median almost twice as high as the laterals; retromargin with five similar-sized teeth. Leg measurements: I: femur 7.22, patella 2.32, tibia 8.20, metatarsus 7.55, tarsus 3.00; total 28.29; II: 6.63, 2.45, 7.33, 6.80, 2.93, 26.14; III: 6.37, 2.12, 6.34, 6.63, 2.70, 24.16; IV: 7.43, 2.17, 8.13, 9.80, 3.31, 30.84. Leg formula: 4123. Leg spination: tibia I–II v2-2-2-2-2, r0-1-0, p1-1-0; tibia III–IV v2-2-2, r0-1-1, p1-0-1; metatarsus I–II–III v2-2-2, r1-1-1, p1-1-1, IV v2-1-1-1-1, r1-1-1, p1-1-1. Palp (Figs. 4A, 5A–F): tibia and cymbium elongated; tibia approximately three quarters length of cymbium; RTA with ventral branch subtriangular and dorsal branch short and truncated, scoop-shaped; tibia with short and subtriangular ventral apophysis; tibia with several trichobothria on base of RTA; cymbium elongated at the tip and with retrobasal spiniform projection; tegulum oval and subtegulum prolateral; embolus continuous from tegulum, tapering to tip; median apophysis positioned in the center of tegulum; conductor hyaline and short.

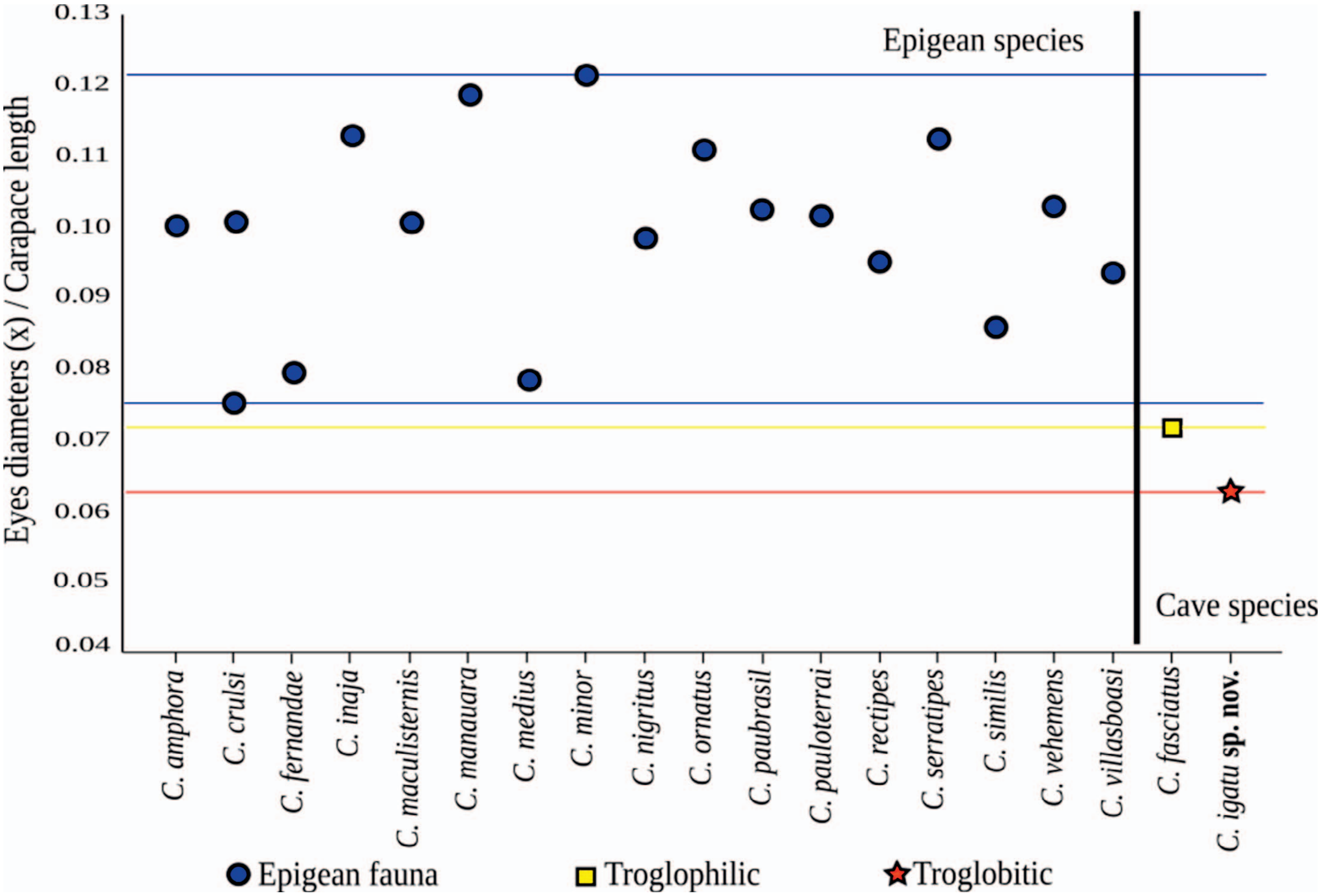

Figure 9.—Graph plotting the ratio of the mean eye diameter versus the length of the carapace, for 19 epigean and cave species of *Ctenus* (see Table 2).

Female (LES 15587). Coloration and cuticular markings as in male (Figs. 2B, D, F). Total length 8.76. Carapace 4.50 long and 3.60 wide. Eye diameters: AME 0.12, ALE 0.14, PME 0.13, PLE 0.13. Chelicerae as in male. Leg measurements: I: femur 6.00, patella 2.37, tibia 6.50, metatarsus 4.99, tarsus 2.36, total 22.22; II: 5.83, 2.14, 6.00, 4.99, 2.30, 21.26; III: 5.00, 2.00, 5.65, 4.62, 2.10, 19.37; IV: 6.27, 2.12, 7.00, 7.40, 2.96, 25.75. Leg formula: 4123. Leg spination: tibia I–II v2–2-2-2-2, r0, p0; tibia III–IV v2-2-2, r1-1, p1-1; metatarsus I–II v2-2-2, r0, p0; metatarsus III v2-2-2, r1-1-1, p-1-1-1; metatarsus IV v2-1-1-1-1, r1-1-1, p1-1-1. Epigynum (Figs. 4B, C): divided in median and lateral fields; median field, without folds or wrinkles; lateral spurs short with a pointed tip; copulatory ducts short; spermathecae each with a small and rounded head and large base; fertilization ducts short.

Distribution.—Known only from the type locality, in the state of Bahia, north-eastern Brazil (Fig. 1).

Natural history.—Fauna species from the sandstone caves of Chapada Diamantina (Figs. 7A, B) are heavily influenced by the rainy season (Gallão & Bichuette 2015), when drastic floods impact the caves. Due to this factor, specimens of Amblypygi, Opiliones, scorpions and adult specimens of *C. igatu* sp. nov. (Figs. 7C, D) were more easily found at the end of the rainy season (Gallão 2017). Even with high sampling effort during field trips to subterranean and epigean habitats in surrounding areas, no additional specimens of *C. igatu* sp. nov. were found. The absence of this species in surface habitats, along with the presence of morphological troglomorphisms such as depigmentation, reduced eyes and elongated appendages (Table 1, 2), corroborate the hypothesis of isolation of this species in subterranean habitats. Thus, we propose a troglobitic status for *C. igatu* sp. nov. (i.e., the source population is only in subterranean environments, *sensu* Trajano 2012). It is important to highlight that while troglomorphisms do not define troglobitic species, they are frequently the cause of an incompatibility to epigean life (Trajano & Carvalho 2017). According to Trajano & Carvalho (2017), the primary criterion for defining a troglobite is geographic isolation, or more precisely habitat restriction. *Ctenus igatu* sp. nov. is the fourth troglobitic arachnid described for the Igatu region and the first one in the genus *Ctenus* from the South America.

Ctenus fasciatus Mello-Leitão, 1943
(Fig. 6)

Distribution.—Known only from Iporanga, in the state of São Paulo, south-eastern Brazil.

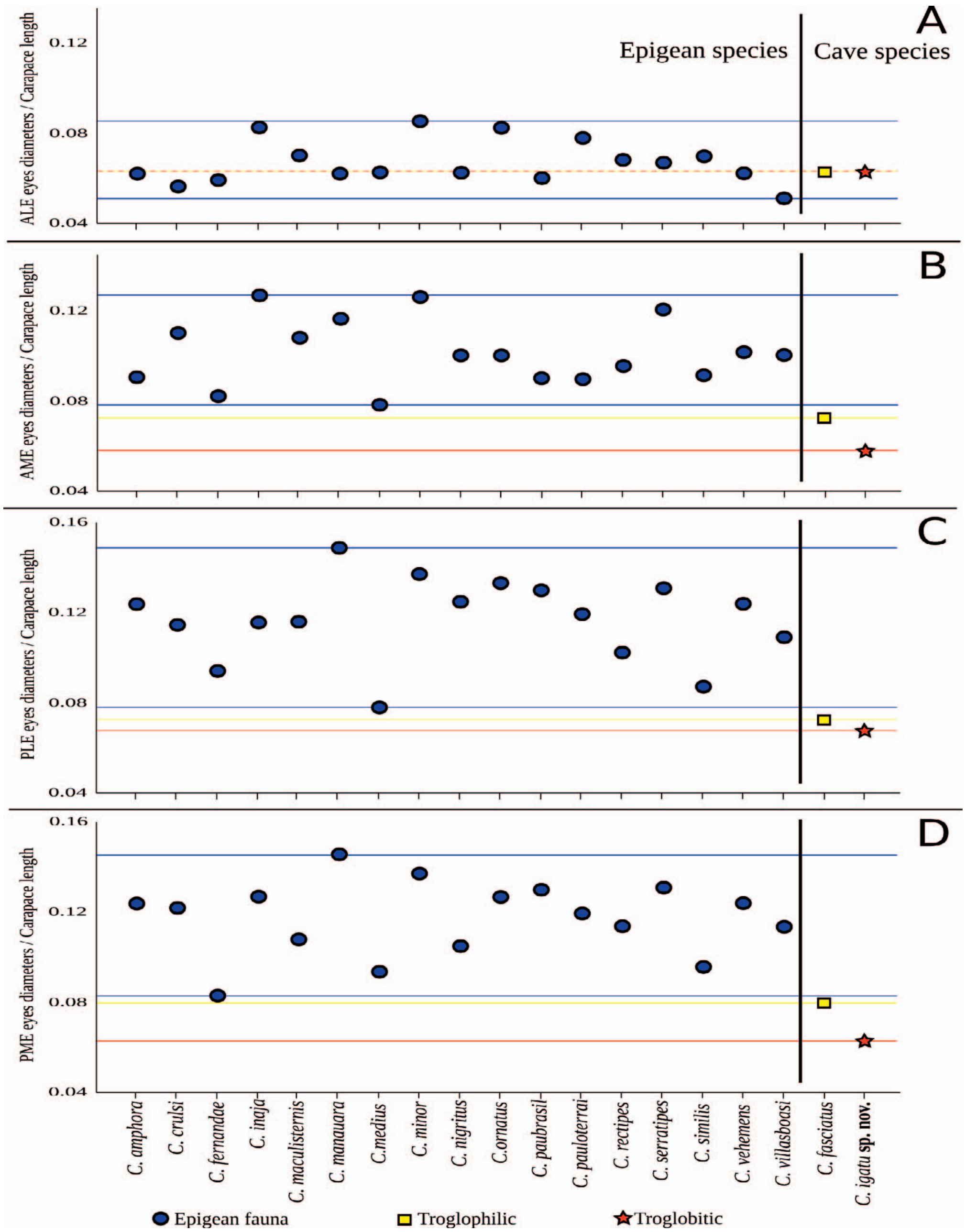

Figure 10.—Graphs plotting the ratios of each eye diamteter versus the length of carapace, for 19 epigean and cave species of *Ctenus* (see Table 2): (A) PLE; (B) ALE; (C) PME; (D) AME.

DISCUSSION

Ctenus igatu sp. nov. features morphological characters such as depigmentation, ocular reduction and lengthening of the appendices suggesting evolution within, and consequently specialization to, the subterranean environment. Compared with their epigean relatives, obligatory subterranean spider species often develop longer legs (Gertsh 1992; Cokendolpher 2004; Miller 2005; Mammola & Isaia 2017; Rodrigues et al. 2018). The ratio of the length of leg IV versus the length of the carapace for epigean versus subterranean species of the genus *Ctenus* was recorded as: leg IV 3.59–4.87 × carapace length for epigean species ($n = 17$); leg IV 7.28 × carapace length for *C. fasciatus* ($n = 1$); and leg IV 7.46 × carapace length for *C. igatu* sp. nov. ($n = 1$). *Ctenus fasciatus* is also a subterranean species with troglophilic status (source populations in both epigean and subterranean environment, *sensu* Trajano 2012) and the ratio of the length of leg IV versus the length of the carapace is similar to that of *C. igatu* sp. nov. (Fig. 8). Christiansen (2012) reported that troglomorphisms may be present in troglophiles and troglobites (e.g., antennae lengths in crickets and coleopterans, barbel lengths in fish).

The lengthening of the legs relative to the carapace observed both in *C. igatu* sp. nov. and *C. fasciatus* implies that this morphological trait may be a specialization to the hypogean environment. An ecological characteristic shared by *C. igatu* sp. nov. and *C. fasciatus* is the preference for the rocky substrate present mostly in caves (e.g., blocks of rock and walls). Epigean species are more likely to be found in the organic substrate of the edaphic surface environment (e.g., leaflet, trunks), usually in forested habitats.

The ratio of the eyes size/s versus the length of the carapace for epigean versus subterranean species of *Ctenus* was recorded as: eyes 0.078-0.121 × smaller than carapace length for epigean species ($n = 17$); eyes 0.072× smaller than carapace length for *C. fasciatus* ($n = 1$); and eyes 0.063 × smaller than carapace length for *C. igatu* sp. nov. ($n = 1$). When comparing the mean of the diameter of all eyes for each species, we observed that both *Ctenus igatu* sp. nov. and *C. fasciatus* have smaller eyes compared with epigean species (Fig. 9).

Opell (1988) observed variation in the size, number, and positioning of eyes in epigean species of Uloboridae, and concluded that ocular loss is accompanied by increased visual angles, optical material investment and potential visual acuity of the retained eyes. In addition, the same author considered that species with fewer eyes had increased retinal cell density, improving potential visual acuity. In the case of *C. igatu* sp. nov., the decrease in eye size likely implies a lower visual capacity. Eye reduction is a typical troglomorphism, and a specialization correlated with isolation in subterranean habitats (Fig. 9). Posterior lateral eyes (PLE), posterior median eyes (PME) and anterior median eyes (AME) are reduced in the subterranean species *C. igatu* sp. nov. and *C. fasciatus*, compared to epigean species (Figs. 10B, C, D). However, the ratio of the size of the anterior lateral eyes (ALE) relative to carapace length is similar for all species (Fig. 10A, see Table 2).

Another trait observed in subterranean ctenid species also reported here is the presence of a dorsoventrally flattened body compared to epigean species. This morphological feature could facilitate the vertical movement of the spiders through the caves, for the purposes of predation, predator avoidance and oviposition. We also observed differences in maternal behavior when comparing subterranean and epigean ctenids. *Ctenus fasciatus* fixes the egg sac on the rocky substrate, as does *Enoploctenus cyclothorax* (see Pellegatti-Franco, 2004), while some epigean *Ctenus* spiders carry the egg sac in the chelicerae (e.g., *C. ornatus* (Keyserling, 1877), *C. medius* Keyserling, 1891). The same morphological and behavioral characteristics described for *C. fasciatus* are also observed in *E. cyclothorax*, another subterranean species (troglophilic or trogloxene) of the family Ctenidae (Pellegatti-Franco 2004). *Ctenus fasciatus* and *E. cyclothorax* are commonly found in Brazilian caves (Pinto-da-Rocha 1995; Bichuette et al. 2017, 2019) and represent a significant component of the invertebrate predators in these habitats (Trajano 2000; Zepon & Bichuette 2017), sometimes in high abundance as seen in caves from Alto Ribeira karst area (Pellegatti-Franco 2004). In contrast, *C. igatu* sp. nov. is present in low abundance and occurs in a unique cave from Chapada Diamantina, which means that this species is probably endemic.

Although knowledge concerning subterranean spiders is increasing, most information is still restricted to the taxonomic description of species. Studies that focus on the natural history of subterranean spiders, and research on population biology and behavior, are still scarce and need more attention. The small number of troglobitic ctenids worldwide reinforces the importance of karst conservation, and the necessity for conservation projects focusing on aspects of their distribution, life history and population ecology.

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