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150th anniversary of Alberto Santos-Dumont's birth, the father of aviation: the damselfly *Cyanallagma demoiselle* sp. nov. from the Brazilian Atlantic Forest (Odonata: Coenagrionidae)

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Abstract. *Cyanallagma demoiselle* sp. nov. (holotype male deposited in DZUP: Brazil, São Paulo State, Cananéia, Ilha do Cardoso State Park), a new small greenish blue and black damselfly, is described, illustrated, and diagnosed based on males and females from the southeastern Atlantic Forest. This new coenagrionid is named after one of the most celebrated projects, the Demoiselle 20 or *libellule* aircraft, designed by the Brazilian inventor and aviation pioneer Alberto Santos-Dumont (1873–1932). This is the third new odonate species discovered in the same restinga-like formation at São Paulo, and like many other odonates from this assemblage, *C. demoiselle* sp. nov., appears to be a typical inhabitant of this type of environment. Due to its sharing many characteristics with other *Cyanallagma*, the new species can be considered a chimera. Its body coloration and genital ligula are similar to those of *C. trimaculatum*, whereas its caudal appendages closely resemble those of *C. nigrinuchale*. Despite of recent advances in taxonomic knowledge about *Cyanallagma*, this study highlights the need for better understanding the morphological correspondences or homologies among the structures of caudal appendages.

Key words. Dragonfly, Zygoptera, eponym, morphology, neotropical, systematics, taxonomy

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Data Availability Statement:
All relevant data are within the paper.

Introduction

> *"Inventing is imagining something that no one else has; It is believing what no one has sworn; risking what no one has risked; and achieving what no one has attempted. To invent is to transcend."*
> Alberto Santos-Dumont [free translation from a quotation accredited to him]

Cyanallagma Kennedy, 1920 is represented by small blue and black damselflies that are endemic to southern South America, ranging from central Brazil to southern Chile (von Ellenrieder & Garrison, 2008). The genus has one of the most complex taxonomic histories for odonates, with several of the originally included species having since been transferred to other genera throughout the years (see De Marmels 1989, 1997 and von Ellenrieder & Garrison, 2008 for a full background). Its history can be traced back to the groundbreaking studies by Selys (1876) when he included four coenagrionid species in his *Acanthagrion interruptum*-complex: *A. interruptum* Selys, 1876; *A. laterale* Selys, 1876; *A. acutum* Selys, 1876; and

A. cheliferum Selys, 1876. Decades later, Kennedy (1920) proposed the genus *Cyanallagma* based on a laconic diagnosis that distinguished it from the sibling genus *Acanthagrion* Selys, 1876, to accommodate the species of Selys' *Acanthagrion interruptum*-complex, with *A. interruptum* being designated as its type species. Many modifications to the original concept have subsequently been proposed, resulting in the current scenario where only *A. interruptum,* the type species, remains associated with this genus.

The intricate taxonomic inconsistencies were only resolved in the last revision provided for this group, when von Ellenrieder & Garrison (2008) placed the 15 species once associated to *Cyanallagma* s.l. into three distinct genera: *Mesamphiagrion* Kennedy, 1920, *Oreiallagma* von Ellenrieder & Garrison, 2008, and, finally, *Cyanallagma* s.s. that included six species: *C. angelae* Lencioni, 2001; *C. bonariense* (Ris, 1913); *C. ferenigrum* De Marmels, 2003; *C. interruptum* (Selys,1876); *C. nigrinuchale* (Selys, 1876), and *C. trimaculatum* (Selys, 1876). The single new species included in it after von Ellenrieder & Garrison's (2008) review was *C. corbeti* Costa et al., 2009 from the state of Rio Grande do Sul in the southern Atlantic Forest of Brazil. Costa et al. (2009) also provided a new key based on characters that were distinct from those employed by von Ellenrieder & Garrison (2008). Additionally, the ultimate larval stadium of *C. bonariense* and *C. interruptum* were described (see Bulla, 1973).

Analyzing specimens collected in 2011 in the Ilha do Cardoso State Park and an old series of specimens collected in 1968 in the Bertioga municipality, both located on the coast of the Brazilian state of São Paulo, we discovered many phenotypic differences between them and all other currently known *Cyanallagma* species. In this study, we describe them as a new species in the genus *Cyanallagma* (Coenagrionidae: Ischnurinae), already mentioned as new, but left unnamed, by Pinto (2019), paying tribute to the Demoiselle, one of the most famous aircrafts, designed by the outstanding pioneer of aviation, Alberto Santos-Dumont.

Material and methods

The material studied herein is deposited in following collections:

DZUP – Entomological Collection "Pe. Jesus Santiago Moure", Departamento de Zoologia, Setor de Ciências Biológicas, Universidade Federal do Paraná, Curitiba, PR, Brazil;

MZSP – Serviço de Entomologia, Museu de Zoologia, Universidade de São Paulo, São Paulo, SP, Brazil.

Terminology of external morphology and dissection procedures follows standard studies on Zygoptera (e.g., Garrison et al., 2010; Pinto & Araujo, 2020; Pinto & Kompier, 2018). All specific names currently associated with *Cyanallagma* were investigated, and the new name was registered in Zoobank. Specimens were analyzed with the aid of stereomicroscopes, and measurements were taken using a micrometer eyepiece.

Photos were taken using either a DSLR camera with a 100-mm macro lens with the help of Helicon Remote (4.4.3 W), and images were stacked and merged with the software Helicon Focus (v. 8.8.2, https://www.heliconsoft.com/); or with a Leica stereomicroscope equipped with a camera, and source images were combined using the LAS Montage software (version 4.7, https://www.leica-microsystems.com/). Scanning electron microscope (SEM) images were taken with a TESCAN VEGA3 LMU microscope at the Centro de Microscopia Eletrônica (CME) of the Universidade Federal do Paraná (UFPR). The anatomical parts were not metalized and submitted to a low vacuum.

Abbreviations used: Ax = antenodal crossveins; Fw = forewing; GL = genital ligula; Hw = hindwing; L1–2 = segments of genital ligula; S1–10 = abdominal segments 1 to 10. Pt = pterostigma; Px = postnodal crossveins, VS = vesica spermalis.

Cyanallagma demoiselle sp. nov.

Zoobank: https://zoobank.org/NomenclaturalActs/urn:lsid:zoobank.org:act:E875FF5B-B319-4C7C-9A8E-A3A-7EC06DFE4
(Figs 1–6)

Cyanallagma sp. nov.: Pinto (2019: 52, 53, 55, biological data).

Material studied

Holotype

Male; BRAZIL. São Paulo State: Cananéia [municipality], Ilha do Cardoso State Park, [collecting point] PEIC 04–06, along 'Transcardoso', dirt road through the tree-like restinga vegetation, any sort of flooded areas parallel to the road and at some points even on the road (-25.0824, -47.9272; 13 m a.s.l.), 20.X.2011, A.P. Pinto leg. (DZUP 501302).

Paratypes

(10 ♂♂, 6 ♀). 2 ♂♂, 2 ♀♀, same data as holotype but (DZUP 501303–501304, 501306–501307); 1 ♂, same data but (MZSP); 1 ♂, same data but on 19.x.2011 (DZUP 501305); 1 ♂, 1 ♀, same data but on 21.x.2011 (MZSP); 2 ♂♂, 1 ♀, Bertioga [municipality], Praia do Guaratuba [-23.7658, -45.9122, 7 m a.s.l., 0]1.iii.1968, F[rancisca] C[arolina do] Val leg. (DZUP 501308–501310); 3 ♂♂, 2 ♀♀, same data (MZSP).

Additional material examined

BRAZIL. Minas Gerais State: 1 ♂, Ouro Preto [municipality], 12–13.iv.1968, F[rancisca] C[arolina do] Val leg. (DZUP 501311).

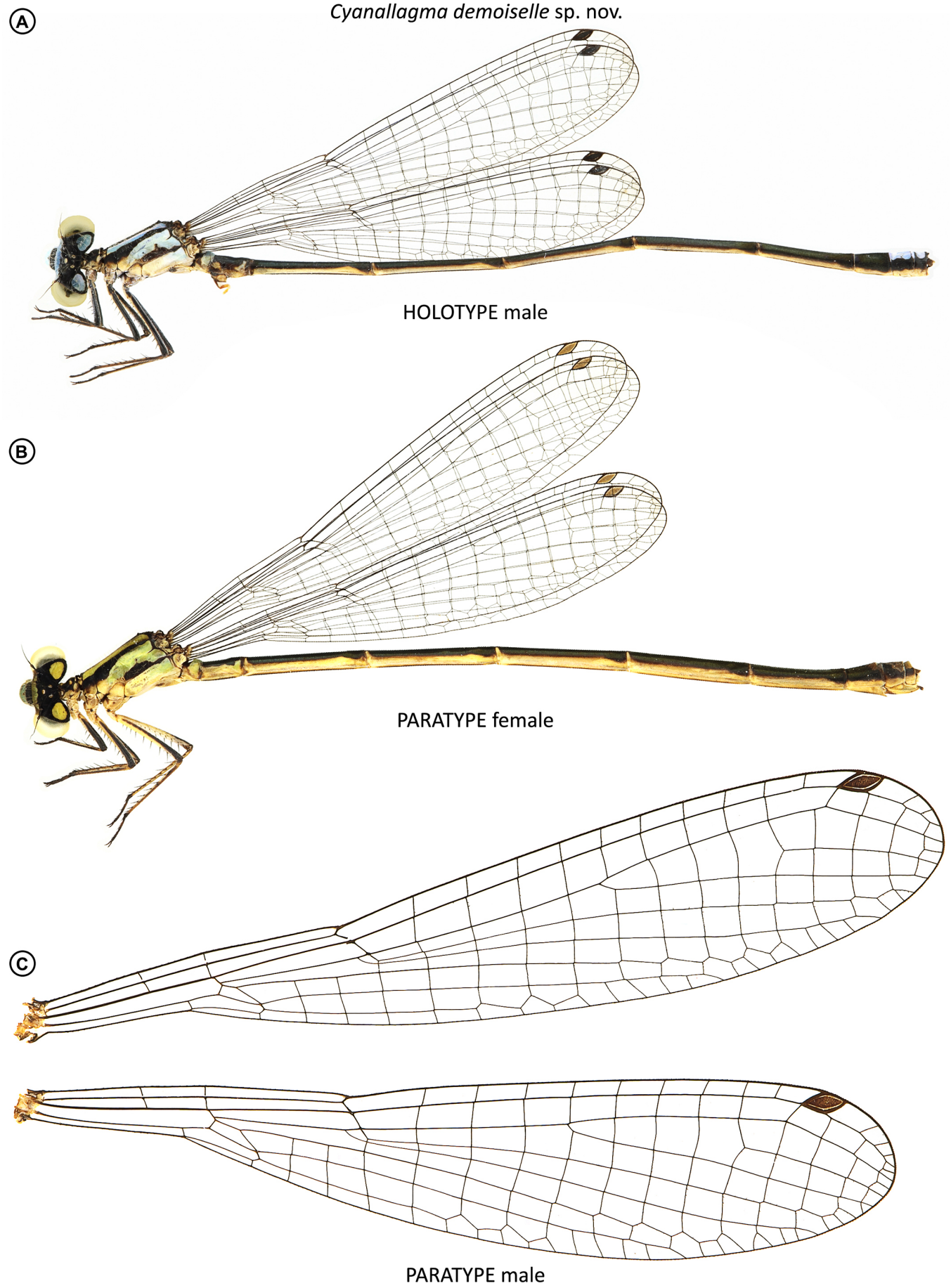

Figure 1. Habitus (A–B) and wings (C) of the type series of *Cyanallagma demoiselle* sp. nov. from Cananéia Municipality, Brazil: (A) Holotype male (DZUP 501302); (B) paratype female (DZUP 501307); (C) paratype male (DZUP 501303).

Diagnosis

A small greenish blue and black coenagrionid damselfly with a rounded frons (Figs 2a–b, 5a), typical of South American Ischnurinae. Both sexes of *Cyanallagma demoiselle* sp. nov. can be distinguished from all other species in this genus by the combination of a large rounded postocular spot (Figs 2a, c), posterior lobe of prothorax trilobate with a large mesially projected plate (Figs 2b, d), truncated posteriorly, occupying 0.5 (female, Fig. 5e) to 0.7 (male, Fig. 5b) of the total width of the posterior lobe, and an uninterrupted, complete mesepisternal stripe (Figs 1a, b).

Males can be distinguished from all other *Cyanallagma* spp. by the second segment of the GL having a single mesial projection on the ental transverse fold (inner process not bifid), lateral lobes strongly rounded laterally, and apical margin concave in ectal view (Figs 4a, b); S10 with a pair of posteriorly projected tubercle-like processes (posterodorsal tubercles; Figs 3a–b, 4e); paraproct short (2.6 times as high as long), quadrate and with a dorsal thorn-like process (Figs 3a, 4e); cercus quadrate in lateral view; a dorsoapical patch of scalariform-like cuticle, inner surface uncarinated and with a large ventro-apical process in laterodorsal view (Figs 3a–b, 4c–f). Females differ from all other *Cyanallagma* spp. by a combination of large yellowish green postocular spots, strongly trilobate posterior lobe of the prothorax with the posterior margin truncated, and a complete mesepisternal pale stripe (Figs 1b; 2c, d).

Based on body coloration, GL shape, and caudal appendages with apical ventral margin of cerci projected into a strong ventro-apical process (Figs 3b, 4d, 5c; this process is considered ventrobasal for *C. nigrinuchale* by von Ellenrieder & Garrison, 2008), males of *C. demoiselle* sp. nov., are similar to *C. nigrinuchale* and *C. trimaculatum*, species which it may be misidentified.

Cyanallagma demoiselle sp. nov. shares the rounded postocular spot with *C. trimaculatum* (vs. bean-shaped in *C. nigrinuchale*); the well-defined trilobate posterior lobe of the prothorax with mesially projected plate large, > 0.5 of total width of the lobe with *C. nigrinuchale*

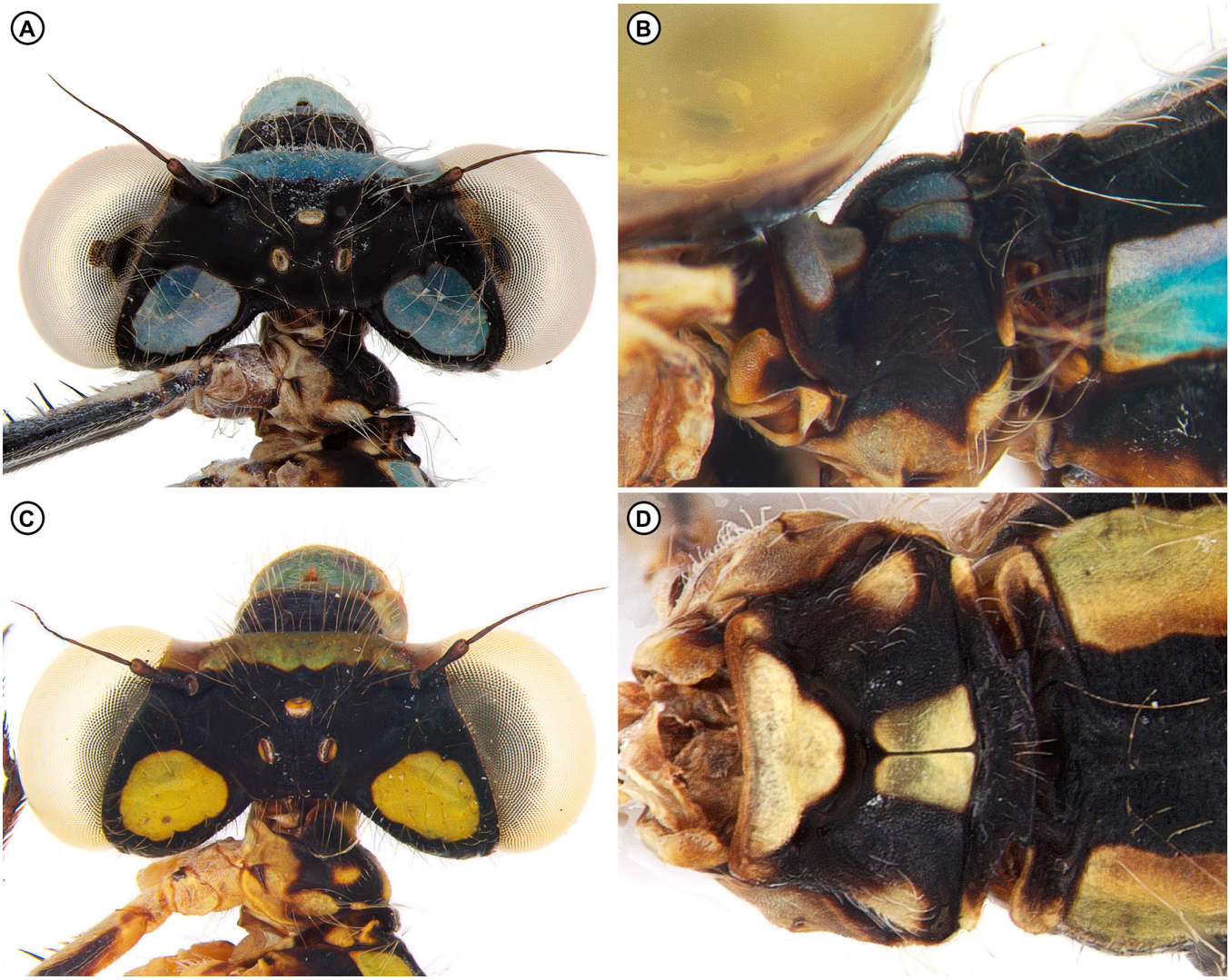

Figure 2. *Cyanallagma demoiselle* sp. nov., Cananéia Municipality, Brazil: (A–B) Holotype male (DZUP 501302): (A) head in dorsal view, (B) prothorax in dorsolateral view; (C–D) Paratypes females: (C) head in dorsal view (DZUP 501307); (D) prothorax in dorsal view (DZUP 501306).

Table 1. Morphological diagnostic characters for males of *Cyanallagma* species. Character states for species not studied in this paper are adopted from von Ellenrieder & Garrison (2008) and Costa et al. (2009). Characters shared with *C. demoiselle* sp. nov. in bold. Abbreviations: GL = genital ligula. 3. Ratio lobe = Ratio between width of mesial lobe / total width of posterior lobe of prothorax; 4. Posterior margin = Posterior margin of mesial lobe of posterior lobe of prothorax; 6. Ental transverse fold = Ental transverse fold projection (inner process) of GL; 8. Paraproct ratio = Ratio between max. height / length of paraproct; 10. Paraproct thorn = Paraproct thorn-like process; 11. Patch of cuticle = Patch of scalariform-like cuticle on cercus; 12. Surface of cercus = Longitudinal-medial surface of cercus; 14. Cercal process = Process on ventral margin of cerci.

Taxon / Character	1. Post-ocular spot shape	2. Posterior lobe of prothorax	3. Ratio lobe	4. Pos-terior margin	5. Mesepi-sternal stripe	6. Ental trans-verse fold	7. Lateral apical lobes of GL	8. Para-proct ratio	9. Para-proct shape	10. Para-proct thorn	11. Patch of cuticle	12. Surface of cer-cus	13. Cercus in lateral view	14. Cercal pro-cess
C. angelae	bean-shaped	**three well-defined lobes**	0.35	convex	interrupted (males) and uninterrupt-ed (females)	**single medial process**	pro-jected	**1.67**	conical	**dorsal**	mesial, subapi-cal	carinated	**quadrate**	basal
C. bonariense	oval-rounded	**three well-defined lobes**	0.45	convex	interrupted	**single medial process**	pro-jected	**2.10**	**quad-rate**	**dorsal**	mesial, subapi-cal	carinated	**quadrate**	basal and apical
C. corbeti	oval-rounded	**three well-defined lobes**	**0.78**	concave	interrupted	**single medial process**	pro-jected	0.95	conical	?	?	**smooth**	**quadrate**	basal
C. ferenigrum	**rounded (small)**	lobes poorly defined	n/a	slightly convex	interrupted	bifid	pro-jected	0.67	conical	medial	lacking	**smooth**	elongated (cylindri-cal)	**apical**
C. interruptum	**rounded**	lobes poorly defined	n/a	convex	interrupted (males) and uninterrupt-ed (some females)	**single medial process**	pro-jected	1.15	conical	**dorsal**	**dorso-apical**	**smooth**	triangular	**apical**
C. nigrinuchale	bean-shaped	**three well-defined lobes**	**0.56**	slightly concave	interrupted	**single medial process**	pro-jected	**1.71**	quad-rate	dorsal	dorso-apical	smooth	quadrate	apical
C. trimacula-tum	**rounded**	lobes poorly defined	**0.78**	concave	**uninter-rupted**	**single medial process**	**not pro-jected**	0.79	**quad-rate**	**dorsal**	ventral, subapi-cal	**smooth**	triangular	basal
C. demoiselle sp. nov.	rounded	three well-defined lobes	0.70	truncate	uninter-rupted	single medial process	not pro-jected	2.64	quad-rate	dorsal	dorso-apical	smooth	quadrate	apical

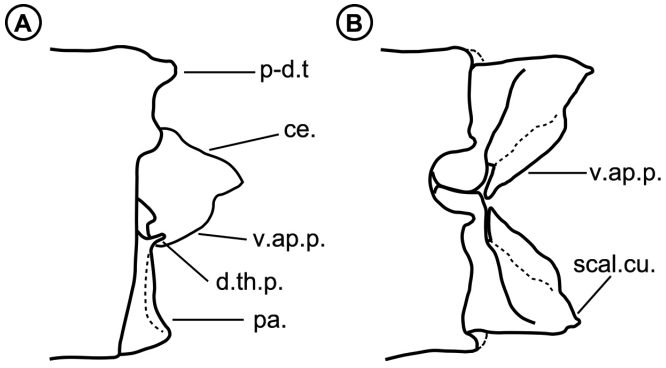

Figure 3. Diagrammatic outline of caudal appendages based on the holotype of *Cyanallagma demoiselle* sp. nov., Cananéia Municipality, Brazil: (A) lateral view, (B) dorsal view. Abbreviations: ce. = cercus, d.th.p = dorsal thorn-like process, pa. = paraproct, p-d.t = posterodorsal tubercle, scal.cu = scalariform-like cuticle, v.ap.p. = ventro-apical process.

(vs. lobes poorly defined and mesially projected plate also large in *C. trimaculatum*); posterior margin of the mesially projected plate truncated (vs. slightly concave in *C. nigrinuchale* to concave in *C. trimaculatum*); the complete, uninterrupted mesepisternal stripe is shared with *C. trimaculatum* (vs. interrupted in *C. nigrinuchale*); GL is very similar to *C. trimaculatum* with a single mesial projection (inner process) on the ental transverse fold, and lateral apical lobes not projected (vs. also with a single inner process on mesial projection, but lateral lobes projected in *C. nigrinuchale*); the appearances of cercus and paraproct quadrate in lateral view are shared with *C. nigrinuchale* (vs. roughly triangular in *C. trimaculatum*); cercus with a dorso-apical white patch with a scalariform-like cuticle, and the paraproct with a dorsal thorn--like process are similar to *C. nigrinuchale* (vs. white patch ventral and subapical, and paraproct longer than cercus and lacking a dorsal

thorn-like process in *C. trimaculatum*; but see the discussion about correspondences between ventrobasal/apical processes of cercus). Caudal appendages are also similar to those of *C. interruptum* from which *C. demoiselle* sp. nov. can be distinguished based on the posterior lobe of prothorax having three well-defined lobes with the posterior margin truncated, and by the complete pale mesepisternal stripe (poorly defined lobes, posterior margin convex and mesepisternal stripe interrupted). Females of *C. demoiselle* sp. nov. can be told

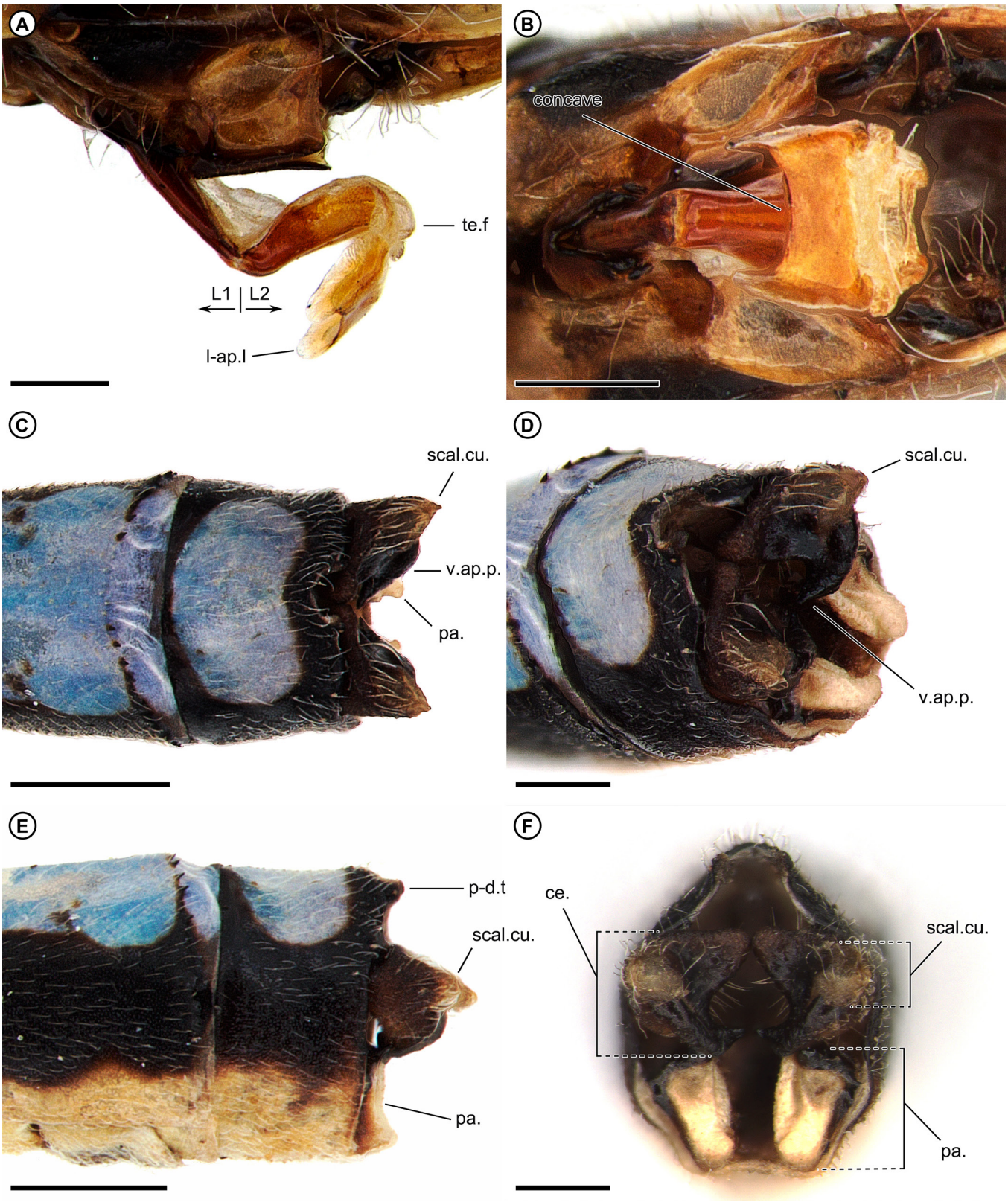

Figure 4. Holotype male (DZUP 501302) of *Cyanallagma demoiselle* sp. nov., Cananéia Municipality, Brazil: (A–B) secondary genitalia in lateral (A) and ventral (B) views; (C–F) caudal appendages in dorsal (C), dorsolateral (D), lateral (E) and caudal (F) views. Abbreviations: ce. = cercus, l-ap-l. = latero-apical lobe, L1–2 = segments of genital ligula, pa. = paraproct, p-d.t = posterodorsal tubercle, scal.cu = scalariform-like cuticle, te.f = terminal fold, v.ap.p. = ventro-apical process.

apart from all congeneric species except *C. trimaculatum* and some female individuals of *C. angelae* and *C. interruptum*, by the complete mesepisternal (antehumeral) stripe (antehumeral stripe interrupted in the remaining species). *Cyanallagma demoiselle* sp. nov. has the lateral margins of the mesostigmal plates convex as opposed to the linear margins of *C. angelae*. The posterior margin of the mesially projected plate of the prothorax is truncated, with conical posterolateral edges slightly protruding posteriorly in *C. demoiselle* sp. nov., while in *C. trimaculatum*, the posterior margin of the medial lobe is rounded and separated from lateral ones by a marked concavity on each side. Also, in *C. demoiselle* sp. nov. females, the posterior margin of the medial lobe of the posterior lobe of the pronotum is developed into a plate that caudally projects beyond the lateral lobes and in this manner differs from the posterior margin of *C. trimaculatum* and *C. interruptum* in which it is indented mesially and not projected.

Etymology

From French, a noun in apposition, not declinable, in allusion to the aircraft Demoiselle 20 or libellule (dragonfly or damselfly in English) designed by one of the pioneers of aviation, the Brazilian Alberto Santos-Dumont (1873–1932) who created many aircrafts, was one of the greatest individuals at the beginning of aviation, an admirable person, and also considered a pacifist (see Ramalho, 2013; Wier, 2019). His model 14-bis was the very first powered heavier-than-air aircraft to fly in Europe, and he was celebrated for it in Paris, France, as the first man to fly (Wier, 2019). We dedicate this specific name to one of his most famous and celebrated projects the Demoiselle ("young women"), also a popular name for zygopteran odonates in France, country where he created and made public most of his inventions.

Description of the male (holotype)

Head (Figs 1a, 2a). Labium ivory-yellow. Mandibles, light blue dorsally, darkening to dark brown ventrally. Labrum light blue, dorsally with a thin black line from clypeolabral suture, extended mesially into a minute spot. Anteclypeus grayish blue, postclypeus black. Frons rounded, antefrons light blue, anterior half of postfrons dark blue and black posteriorly, anterior limit of the black mark crenulated. Remaining parts of epicranium and rear of head black, with a pair of large pale yellow spots laterally on the postocciput. A large light blue postocular spot, covering 0.6 of the ocular lobe. Antennifer light blue, scape black with tip brown, pedicel and flagellum brown.

Thorax (Figs 1a, 2b). Prothorax black with pale blue spots dorsally, ventrally yellowish brown; a large triangular blue spot on the anterior lobe; median lobe with a pair of blue parallel-sided stripes mesially, covering the posterior 0.8 of the lobe; posterior lobe black, with small yellowish brown spots on the lateral edges (Fig. 2b), posterior margin of pronotum trilobate; mesial projected plate rectangular, as wide as about 0.7 of the lobe's total width, posterior margin truncated, conical lateral edges protruded (as in Fig. 5b for a paratype). Synthorax (Fig. 1a) black dorsally, lightening to yellowish brown ventrally, with three pale blue stripes, one each on mesepisternum, mesepimeron-metepisternum, and on metepimeron; mesepisternal stripe continuous over the full length, parallel to the humeral suture, as wide as half the sclerite width, slightly narrowed posteriorly by a concave black marking; meso-metathoracic pale stripe covering 0.5 ventrally, widening dorsally to roughly the entire sclerite width; metepimeron pale throughout, light blue dorsally to yellowish brown ventrally, with small dark dorsal spot on metapleural suture; metapostepimeron ivory-yellow, ventrolateral angle with a black spot. Legs dark, coxa pale, femur and articulations black, tibia and tarsus dark brown, ventral surface of coxa, trochanter and femur ivory-yellow, pretarsal claws with distinct acute supplementary inferior tooth in distal 0.8; anteroventral surface of femora with long thin spurs, 4 (plus 3 spatulate ones) in pro-, 6–7 in meso-, and 9 on the metathoracic femora, all more or less the same size, anteroventral surface of tibia 10–11 (6–7 of tibial comb) in pro-, 6 in meso-, and 7–8 on the metathoracic tibia.

Wings (Figs 1a, c). Membrane hyaline, venation dark brown to black, Pt rhomboidal, black, enclosed by a very thin pale line, adjacent veins dark brown; MP reaching anal margin distally at level of Px 7 in Fw, Px 6 in Hw; CuA reaching anal margin distally at Px 7 in Fw Px 7 in Hw; Px in Fw 12; Hw 9; RP2 originating at proximal Px 5 in Fw, at proximal Px 4 in Hw.

Abdomen (Figs 1a, 3a–b, 4c–f): Tergites black dorsally, light brown to ivory yellow lateroventrally, pale blue spots on S1–2 and S8–10. S1 pale spot light to dark blue, large covering up to posterior 0.7; S2 with a single lateral pale spot, formed by connection of a small anterolateral yellow spot and a large triangular posterolateral light blue spot; S8 posterior field dorsally blue; S9–10 with large rounded dorsal blue spots, covering S9 length, including posterior field; S10 with an oval spot (Fig. 4c); S10 posterodorsal margin with a u-shaped cleft margined by a pair of tubercle-like processes (Figs 3b, 4d). Secondary genitalia (Figs 4a–b) typical of Coenagrionoidea with anterior hamule quadrangular; posterior hamule small, black, almost entirely internalized; VS longer than wide; genital ligula with L1 smooth; a sclerotized latero-apical fold on flexure; L2 proximal portion more sclerotized, distal portion rectangular with lateral margin arched inwards, its distal margin concave with rounded latero-apical lobes, broader section three times the width of proximal portion of L2, lacking inner fold. With a transverse fold between latero-medial lobes and inner process on the second

transverse fold. Cercus (Figs 3a–b, 4c–f) dark brown to black, tip yellowish-brown; shorter than S10; in dorsal view outer margin straight, inner margin touching anteriorly, diverging posteriorly and ending in an acute tip (Figs 3b, 4c); ventral margin projected anteroventrally in a curved spur-shaped process directed anteriorly (Figs 3b, 4c, the ventral-apical process); in dorsolateral view the dorsal margin arcuate with a broad rounded well defined carina at base of the appendage (Fig. 4d), ventral margin slightly concave, strongly curved into a

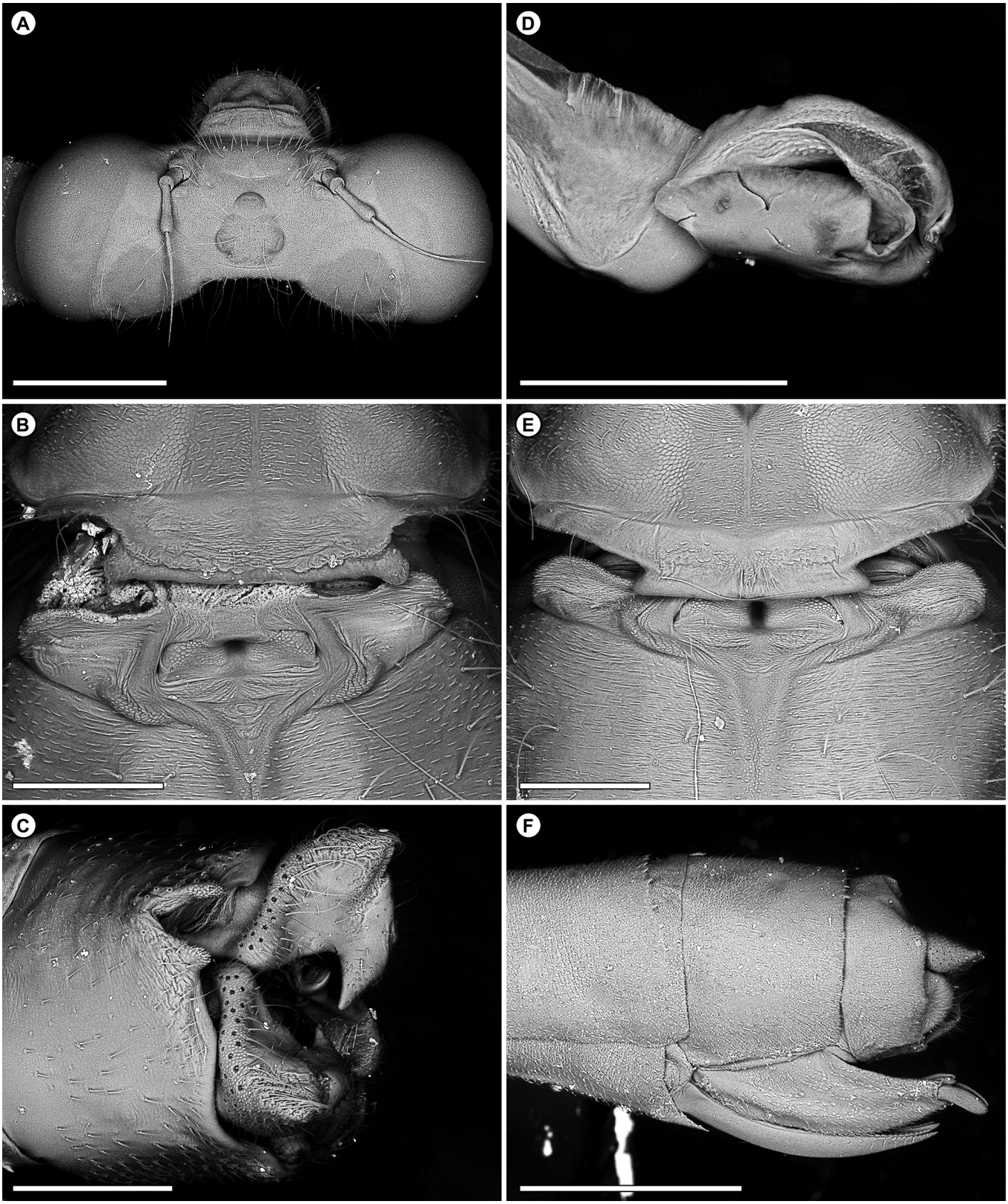

Figure 5. SEM of *Cyanallagma demoiselle* sp. nov., Cananéia Municipality, Brazil: (A–D) Paratype male (DZUP 501303): (A) head in dorsal view, (B) prothorax in dorsal view, (C) caudal appendages in dorsolateral view, (D) genital ligula in lateral view; (E–F) paratype female (DZUP 501306): (E) prothorax in dorsal view, (F) terminalia in lateral view.

tapering ventral-apical process; in lateral view (Fig. 4e) rectangular, tip rounded, projected into a membranous rounded area (patch of scalariform-like cuticle sensu von Ellenrieder & Garrison, 2008), ventral-apical process partially visible, curved anteriorly; cercus in posterior view touching basally (Fig. 4f), tip widely separated and ventral-apical process curved inwards, close to each other, dorsal margin straight, outer margin convex, inner margin concave (Fig. 4f). Paraproct ivory-yellow, black dorsally (Fig. 4c), small, quadrate, projected dorsally into a sclerotized thorn-like tip (dorsal thorn-like process) visible in lateral view (Figs 3a, 4e).

Measurements (mm). Total length (incl. caudal appendages) 33; abdomen length (excluding caudal appendages) 27.5; head maximum width 3.63; Fw length 18.5; Hw length 17; Fw maximum width 4.2; Hw maximum width 3.76; Pt length 0.5 in Fw; 0.52 in Hw; length of metathoracic femur 2.88; metathoracic tibia 2.82; length of S9+10 in lateral view 1.85; total length of cercus in lateral view 0.27.

Female paratype

Very similar to holotype, except for the sex-linked characters. All parts, dots and stripes that are blue in the male are yellowish green (most likely green in life). The pale spots in the lateroventral parts of the abdominal tergites also have a green hue.

Head. Labrum dark blue, all other pale spots with a yellow-green tone (Fig. 2c).

Thorax. Median lobe of prothorax with an additional, rounded, pale ivory-yellow spot, covering 10% of the prothorax (Fig. 2d). In dorsal view, anterior margin of pronotum slightly concave, posterior margin of pronotum with mesial projected plate as wide as about 0.5 of the lobe's total width, margin truncated, conical lateral edges less protruded posteriorly, mesostigmal lobe straight (Figs 2d, 5e). Legs with dorsal stripes on femur lighter brown. Tibia paler ventrally than in the holotype.

Wings. Pterostigma light brown (Fig. 1b).

Abdomen. Green spots on S1–2; greenish brown dorsal spots in S8 covering 0.3, S9 covering 0.6, and S10 covering 0.5 dorsally (Fig. 1b). Ovipositor extending distally beyond the level of the cercus in lateral view (Fig. 5f).

Variation in male paratypes

Numbers of Px in Fw 9–11 and 8–9 in Hw. The specimens from Bertioga lack the minute spot on the labrum and the Pt is noticeably darker in color. Most specimens from Bertioga lack the pale spots on the median lobe of the prothorax, whereas it is present in all specimens from Ilha do Cardoso State Park (PEIC), even if not as visible as in the females.

Measurements (mm, n = 10). Total length (incl. caudal appendages) 24–33; abdomen length (excluding caudal appendages) 18.27–27.5; head maximum width 3.33–3.63; Fw length 15.5–18.5; Hw length 13.8–17; Fw maximum width 3.40–4.2; Hw maximum width 3.2–3.76; Pt length 0.43–0.5 in Fw; 0.41–0.52 in Hw; length of metathoracic femur 2.47–2.88; metathoracic tibia 2.59–3.0; length of S9+10 in lateral view 1.35–1.85; total length of cercus in lateral view 0.23–0.27.

Variation in female paratypes

Numbers of Px in Fw 10–12 and 8–10 in Hw; the specimens from Bertioga lack the minute spot on labrum, similar to the male paratypes, and only one has the pale spots on the median lobe of prothorax.

Measurements (mm, n = 6). Total length (incl. caudal appendages) 29.2–34.3; abdomen length (excluding caudal appendages) 22.54–26.60; head maximum width 3.38–3.65; Fw length 16.5–19; Hw length 15.5–17.5; Fw maximum width 3.56–4.16; Hw maximum width 3.24–4.12; Pt length 0.38–0.6 in Fw; 0.4–0.6 in Hw; length of metathoracic femur 2.7–3.03; metathoracic tibia 2.6–3.09; length of S9+10 in lateral view 1.1–1.57; total length of cercus in lateral view 0.13–0.23.

Notes

Specimens from the Bertioga population in the north are clearly smaller than those from Ilha do Cardoso State Park and have also undergone postmortem modifications in that their coloration was dulled and hues are dramatically less clear. This is the third new odonate species discovered in the same restinga-like formation as the protoneurids *Forcepsioneura lopii* Pinto & Araujo, 2020 and *Idioneura furieriae* Lencioni, 2021. *Cyanallagma demoiselle* sp. nov. appears to be a typical inhabitant of restinga-like formations, rendering the provenance data of the single male from Quadrilátero Ferrífero in the state of Minas Gerais highly suspect to the point of being unlikely (Fig. 6), most likely is a labeling mistake.

Biological and ecological data

Both Ilha do Cardoso State Park and the Bertioga municipality (that has more than half of its area protected by the Serra do Mar State Park) exhibit typical formations of the Atlantic Forest of the southeastern coastal region of Brazil, with an estimated distance of 250 kilometers between them. Pinto (2019) and Pinto & Araujo (2020) have described in detail the habitat where our specimens from Ilha do Cardoso were collected. Adults of *C. demoiselle* sp. nov. were seen perched and flying in shaded areas along the drainage channels of the transcardoso dirt road crossing through the tree-like restinga vegetation. This boggy terrain hosts shallow puddles with a very slow flux at which larvae and adults

of other endemic restinga-dwelling odonates, such as the protoneurine *Forcepsioneura lopii* and the corduliids *Schizocordulia rustica* (Hagen in Selys, 1871), and *Lauromacromia picinguaba* Carvalho et al., 2004 were collected (Ehlert & Pinto, 2020; Pinto, 2019; Pinto & Araujo, 2020). Although no additional information on the habitat of the population in Bertioga is known, we are confident that it is strongly similar to that in the Ilha do Cardoso State Park.

Discussion

Since the establishment of the *Acanthagrion interruptum*-complex by Selys (1876), this group of South American damselflies has been both challenging and intriguing for students of odonates for more than a century, with difficult taxonomic placement and unknown phylogenetic relationships (see De Marmels 1989, 1997; von Ellenrieder & Garrison, 2008). Putative specimens of the three genera *Cyanallagma*, *Mesamphiagrion*, and *Oreiallagma* can be virtually unambiguously assigned to them based on the current genus-level concept. However, this classification is not supported by unique characteristics (Garrison et al., 2010; von Ellenrieder & Garrison, 2008). Despite these limitations, *C. demoiselle* sp. nov. is consistent with its genus' diagnostic criteria, even displaying such rare features as a continuous mesepisternal stripe that has so far been found only in *C. trimaculatum* and in some females of *C. angelae* and *C. interruptum* (Bulla, 1973; von Ellenrieder & Garrison, 2008). Recent phylogenomic investigations (Bybee et al., 2021) supported this genus' placement within the Ischnurinae (core Coenagrionidae sensu Dijkstra et al., 2014), but its monophyly and composition is still pending corroboration, requiring more specific studies with larger taxon sampling focused on resolving the "*Cyanallagma* problem".

This taxonomic difficulty and instability are reflected in the morphological correspondence of structures of caudal appendages proposed by von Ellenrieder & Garrison (2008), which may trigger misleading assumptions. Despite the necessity of naming structures for comparative purposes, it is clear to us that the same names do not necessarily correspond to the "same" structures in *Cyanallagma*, violating logical hypothesis of homology (see Fitzhugh, 2006; Sereno, 2007). The correspondence of the caudal appendage processes in one of the most recent keys to males of *Cyanallagma* (von Ellenrieder & Garrison, 2008) can lead to misidentifications due to different interpretations as to which are ventrobasal or ventro-apical processes. We do not believe that the ventrobasal and ventro-apical processes are homologous among *C. interruptum*, *C. nigrinuchale*

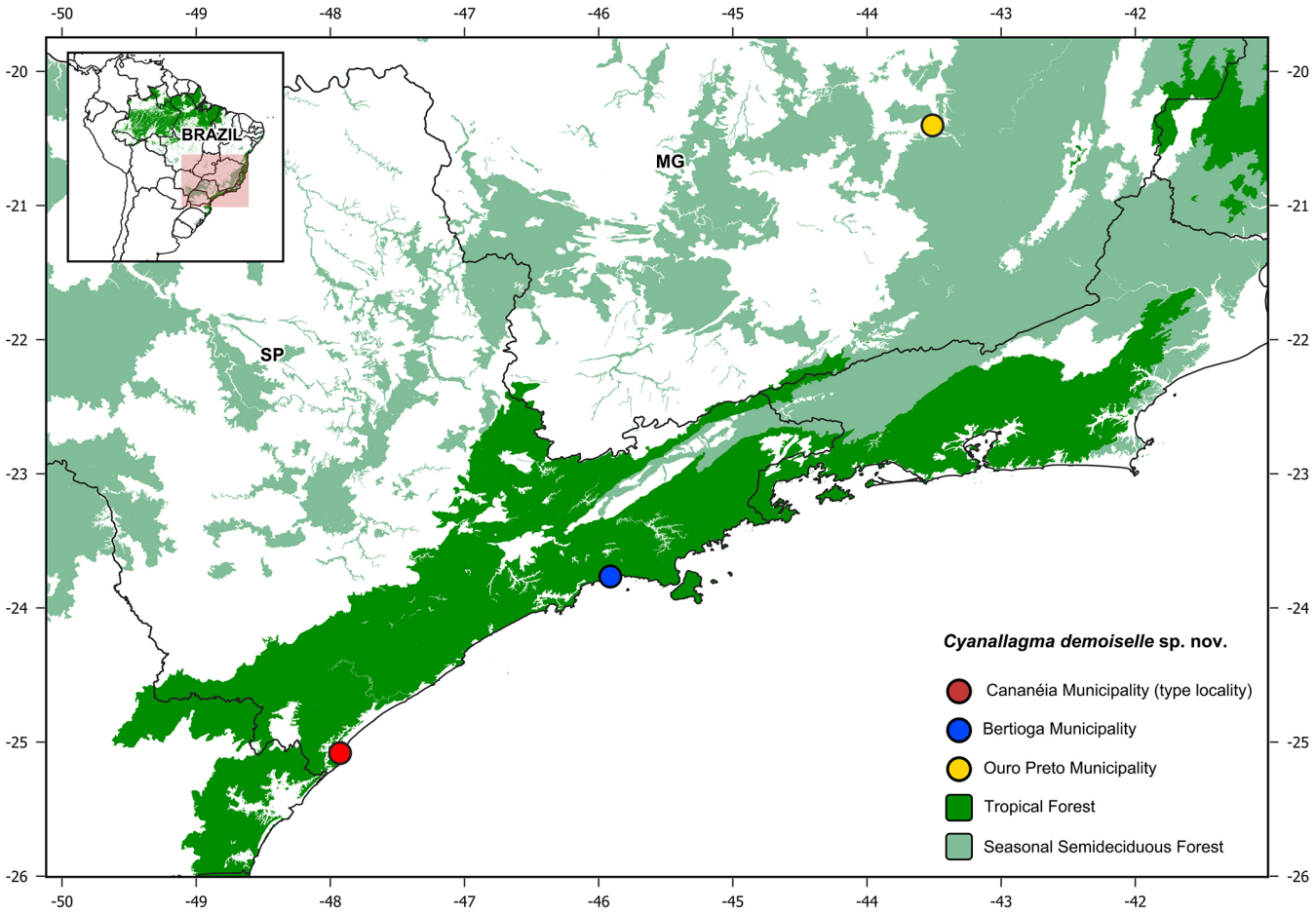

Figure 6. Distributional records of *Cyanallagma demoiselle* sp. nov. and vegetational type within the Atlantic Forest domain, Brazil. MG = Minas Gerais State, SP = São Paulo State. The record for MG is questionable; see Discussion section.

and *C. demoiselle* sp. nov. Using the key from von Ellenrieder & Garrison (2008), males of *C. demoiselle* sp. nov. key out either as *C. interruptum* (couplet 2) if the large process on the cercus is considered ventroapical, or as *C. trimaculatum* (couplet 5') if it is considered a ventrobasal process, while in the key provided by Costa et al. (2009), which uses different characters, *C. demoiselle* sp. nov. would either key out as *C. interruptum* (couplet 2), or as *C. trimaculatum* (couplet 3). Females in von Ellenrieder & Garrison's (2008) key out as *C. bonariense*. Despite of *C. demoiselle* sp. nov. not agreeing adequately with any of these keys, we refrain from providing a new key, since we did not examine specimens from all *Cyanallagma* species. Therefore, to facilitate comparisons between the species included in the genus *Cyanallagma* we here provide instead a comparative table that includes the main diagnostic characters mentioned by von Ellenrieder & Garrison (2008).

This difficulty in taxonomic identification at species-level in *Cyanallagma* is aggravated by the discovery of *C. demoiselle* sp. nov., which has a chimera-like character set in that it shares many characteristics also observed in other species of its genus. Its head coloration is remarkably similar either to *C. interruptum* or *C. trimaculatum*; the large mesial plate quadrate of the posterior lobe of the prothorax resembles that of *C. angelae* and *C. nigrinuchale,* the last species additionally shares the shape of the caudal appendages, while synthorax coloration and GL exhibit a strong resemblance of those found in *C. trimaculatum.*

We believe that *C. demoiselle* sp. nov. is an endemic species of the restinga-like formation in coastal areas of the Brazilian Atlantic Forest and that the single male labeled as originating from the municipality of Ouro Preto in the state of Minas Gerais, an area with a very distinct phytophysiographical and biogeographical evolutionary histories, is likely to be a mislabeled specimen. The series from Bertioga and the specimen from Ouro Preto were both collected by the dipterist Francisca Carolina do Val in 1968, in March and April, respectively. We suspect the Ouro Preto specimen was then mislabeled, since this site is located at more than 1200 meters of elevation and hosts a quite different vegetation type within the Atlantic Forest domain, the Seasonal Semideciduous Forest (Fig. 6). In contrast, all other specimens, including those observed alive and collected by one of us (APP), come from sea level and a highly specific vegetation type within the coastal Tropical Forest of the Atlantic Forest, composed of herbaceous shrub and woody plant species growing on sandy soils, known as Restinga (Fig. 6). However, only additional data may show up the true occurrence of this species in such biotype in Minas Gerais.

Restinga forests are considered one the most threatened ecosystems in the highly fragmented and threatened Brazilian Atlantic Forest (Agapito et al., 2023), a domain considered the hottest of the biodiversity hotspots in the world (Laurance, 2009). The state of conservation of *C. demoiselle* sp. nov. is unknown, but its areas of occurrence are conserved by lying in well-established protected areas (i.e., Ilha do Cardoso and Serra do Mar State Parks). However, monitoring these and nearby sites is important to future investigations of these populations and so is the identification of threats.

Our selected specific name *demoiselle* honors the famous aircraft created by Santos-Dumont, a Brazilian historical figure of global fame; thus, it can be considered an eponym. Since the introduction of the first available names for odonates by Linnaeus in 1758, about 23% of dragonfly and damselfly species have been baptized honoring individuals (Hämäläinen, 2016). This practice has increased dramatically over the last 30 years, accounting for 40 to 45% of all names for odonates introduced within this period (Hämäläinen, 2016, 2021), which appears to be significantly higher than the average for other metazoans (compare with data in Ceríaco et al., 2023). Such a phenomenon can be explained by a variety of reasons, including egocentrism, but sometimes it appears to be related to efforts to draw more attention to the biodiversity agenda from the public. The establishment of eponyms (scientific names after people) is currently a heated debate about who, if, and when individuals should be honored by a specific name, with a major focus on moral concerns (e.g., Raposo et al., 2023). These concerns are legitimate to avoid offensive names and to minimize a culture that may reinforce the legacy of colonialism, racism, and slavery (e.g., Harris & Xavier, 2023), and Guedes et al. (2023) have suggested a radical solution by eradicating all eponyms from taxonomy practices, but such policies are also harmful. Clearly, this crusade would have a strong impact on how taxonomic practices are carried out and on nomenclatural stability (e.g., Ceríaco et al., 2023).

When we chose to name this new damselfly after one of the Santos-Dumont's inventions, we wanted to celebrate a fascinating personality who played a crucial role in the early days of aviation, thus, being worthy of honoring. Consequently, whether Santos-Dumont's actions and beliefs are deemed inadequate or incompatible with future or even contemporary culture makes no difference. Finally, Alberto Santos-Dumont received many homages over the years, and his 150th birthday has been widely celebrated in Brazil.

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Conflict of interest

The authors declare no conflict of interest, and their organizations had no role in any steps of the development of this study, from its design to submission for publication.

Authors contributions

All authors contributed equally to this study, designed, compiled, organized, and wrote the manuscript, revised, and approved its final version.

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