





Three names, one species: junior synonyms for the Atlantic Forest emerald dragonfly *Navicordulia atlantica* (Odonata: Corduliidae s.s.)

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ABSTRACT

Three Atlantic Forest endemic species of emerald dragonflies of the genus *Navicordulia* Machado & Costa, 1995 are reviewed through a morphological comparative analysis. All name-bearing types and additional specimens of the *Navicordulia atlantica*-complex—*Navicordulia atlantica* Machado & Costa, 1995, *Navicordulia mielkei* Machado & Costa, 1995 and *Navicordulia mielkei* Machado & Costa, 1995 and *Navicordulia mielkei* Machado & Costa, 1995, *Navicordulia mielkei* Machado & Costa, 1995 and *Navicordulia mielkei* Machado & Costa, 1995, *Navicordulia mielkei* Machado & Costa, 1995 and *Navicordulia mielkei* Machado & Costa, 1995, *Navicordulia mielkei* Machado & Costa, 1995 and *Navicordulia* mielkei Machado & Costa, 1995, *Navicordulia* mielkei Machado & Costa, 1995 and *Navicordulia* mielkei Machado & Costa, 1995, *Navicordulia* mielkei Machado & Costa, 1995 and *Navicordulia* atlantica Machado & Costa, 1995 is selected as valid nomen, hence *N. mielkei* **syn. nov.** and *N. miersi* **syn. nov.** are their subjective junior synonyms. Photos, other illustrations, and a new species-level diagnosis are given. Despite of the advances of taxonomic knowledge of *Navicordulia*, the second species-rich corduliid genus in the Neotropical region, the status of some species still necessitates a full revision.

Introduction

The endemic South American emerald dragonflies of *Navicordulia* Machado & Costa, 1995 currently represents the second species-rich corduliid genus in the Neotropical region (Pinto and Lamas, 2010), with 13 species (Fleck and Juillerat, 2019). Among the Corduliidae *s.s.* occurring in the Western Hemisphere, the richness of *Navicordulia* is just behind of the large and diverse Holarctic *Somatochlora* Selys, 1871, with 26 species recorded in North America (cf. Garrison et al., 2006). *Navicordulia* includes corduliids widespread across the three most important biological domains of South America: Amazonia, in Venezuela, French Guiana and Brazil; Cerrado and Atlantic Forest, in Brazil (Machado and Costa, 1995; Pinto and Lamas, 2010; Fleck and Juillerat, 2019). These metallic greenish anisopterans inhabit both forested and open areas, and contrary to many other neotropical corduliid genera, ecological and biological data from adults are generally available in

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the literature (e.g., Machado and Costa, 1995; Pinto, 2019; Fleck and Juillerat, 2019). Despite this, larvae of most species are still unknown; only the ultimate larval stadium of *N. nitens* (De Marmels, 1991) based on the exuvia of the holotype has been described (De Marmels, 1991).

The oldest established species now included in *Navicordulia* was originally described in the Nearctic genus *Dorocordulia* Needham *in* Needham & Betten, 1901, based on a male from Mato Grosso State, Brazil (Calvert, 1909). Baptized as *Dorocordulia errans* Calvert, 1909, it was long considered a biogeographic puzzle. The late odonatologist Newton Dias dos Santos studied the secondary genitalia of the two Nearctic species of *Dorocordulia*, *D. lepida* (Hagen *in* Selys, 1871) and *D. libera* (Selys, 1871), and for the first time, compared it with that of *D. errans*. This led him to cautiously suggest that the Brazilian species of *Dorocordulia* would be distinct from the North American representatives and could be transferred to a proper genus (Santos, 1968). It was finally done many years later by Machado and Costa (1995), when they transferred the three South American *Dorocordulia* N. errans, N. nitens,

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N. vagans (De Marmels, 1989), and additionally described seven new species from Brazil. Since then, three more new species were described, *N. aemulatrix* Pinto & Lamas. 2010 from Atlantic Forest in Brazil (Pinto and Lamas. 2010. 2011) and *N. tumucurakensis* Fleck. 2017 and *N.* pascali Fleck & Juillerat, 2019 from Amazonia in French Guiana (Fleck, 2017; Fleck and Juillerat, 2019). In addition, the distribution data of the Brazilian species was updated (Pinto and Lamas, 2010) and the original taxonomic key has been modified (Pinto and Lamas, 2010, 2011) and later fully updated (Fleck and Juillerat, 2019). However, these keys were offered without a review of the specific status of the species included therein. An unusual tubercle-like tergal process was reported as an exclusive character of some species (Pinto and Lamas, 2010, 2011), though not observed in many other congeners (cf. Pinto and Lamas, 2010; Fleck, 2017; Fleck and Juillerat, 2019). Finally, a putative close phylogenetic relationship between Navicordulia and the Australasian genus Metaphya Laidlaw, 1912 with which females share a similar terminalia was also suggested by Pinto and Lamas (2011) and further evolutionary and biogeographical scenarios were discussed in detail by Fleck (2017). All these can be considered relevant assumptions to be investigated through phylogenetic and biogeographical analyses.

Species delimitation within Navicordulia was originally based on many characters from general external morphology, wing venation, measurements, and coloration, all arranged into five tables (cf. Machado and Costa, 1995). Possibly this style of taxonomic treatment was inspired by the influential paper by May (1992) on Neotropical corduliids of Neocordulia Selys, 1882, published a few years earlier, where similar comparative tables were presented. Despite this, most Navicordulia species were diagnosed based on few characters such as the shape and size of the caudal appendages of males, shape of the supralaminar process of females, and body and pterostigma coloration in both sexes. Two taxonomic groups were proposed based on male cerci: (1) "longistyla-group", now including five species with very long cerci measuring 2.5–3.9 mm; and (2) "errans-group", now including six species with comparatively shorter cerci measuring 1.6-2.0 mm. Two other species of *Navicordulia* are only known from the female holotypes and were not assigned to any group. Adoption of these groups was recognized as for practical purposes only (Pinto and Lamas, 2010; Fleck and Juillerat, 2019), and unlikely to represent phylogenetic relationships between these species. Pinto and Lamas (2010) highlighted the artificiality of these groups and argued that many distinct groups would be assembled following other arbitrary criteria based on a single or combinations of multiple characters. Furthermore, excluding species such as N. errans and N. leptostyla Machado & Costa, 1995, most are known from a few specimens only (Pinto and Lamas, 2011).

In their comprehensive study Machado and Costa (1995) erected three new species based on material collected from Joinville municipality in the Atlantic Forest of Southern Brazil, i.e., N. mielkei Machado & Costa, 1995 from males and females, N. atlantica Machado & Costa, 1995 from a single male, and N. miersi Machado & Costa, 1995 from a single female. Together these nomina integrate within the Navicordulia atlantica-complex, are morphologically remarkably similar species with weak diagnostic characters and are all from the same type locality. Since the original descriptions in 1995, no additional data were published about these species until adults identified as N. mielkei at Ilha do Cardoso State Park in 2011, extreme south border of São Paulo State, were captured and habitat preference and swarm foraging aggregation behavior, exhibiting a flier type, were also observed (Pinto, 2019). The specific status of these species has been strongly questioned (see discussion in Pinto and Lamas, 2011), partially due to the small number of specimens resulting in a meager knowledge of intraspecific variation, and the poor preservation or young condition (some subteneral) of the specimens studied. Some of these specimens lack structures used for diagnostic purposes or have no definite coloration. Machado and Costa

(1995) based the distinctiveness of these three species on the relative length of male cercus (*N. atlantica* and *N. mielkei*) and existence of a single additional crossvein in hind wing (*N. miersi*).

Our goal is to determine whether minor differences in the size of the caudal appendages of males and number of crossveins in a specific area of the wing in both sexes are reliable for diagnosing among these species. We assess the specific limits using a traditional morphological taxonomic approach for South American emerald dragonflies of the *Navicordulia*, providing a critical review of these three endemic species from Atlantic Forest. For this, all name-bearing types and additional species were examined, photographed, illustrated and a new species level diagnosis are given.

Material and methods

Collections

The examined specimens are deposited in the institutions with the respective acronyms listed below. The material deposited in DZUP was collected under permissions of ICMBIO/SISBIO #25034–1 and COTEC/SMA (IEF/SP) #260108–001.736/2011.

ABMM – Angelo B. M. Machado collection, Centro de Coleções Taxonômicas, Departamento de Zoologia, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais (UFMG), Belo Horizonte, MG, Brazil;

DZUP – Entomological Collection Padre Jesus Santiago Moure, Departamento de Zoologia, Universidade Federal do Paraná (UFPR), Curitiba, PR, Brazil (http://grbio.org/cool/5xp9-edpx);

MNRJ – Entomological Collection, Departamento de Entomologia, Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, RJ, Brazil (https://doi.org/10.15468/7lklen).

General procedures and terminology

The available diagnostic characters enlisted by Machado and Costa (1995), as well as those mentioned by Pinto and Lamas (2010, 2011), Fleck (2017) and Fleck and Juillerat (2019) were critically analyzed and compared with the specimens examined (Table 1; Supplementary data s1–s2). All the name-bearing type specimens from *N. atlantica, N. mielkei* and *N. miersi* were examined and scanned. We also investigated all available data on these three species. Nomina and nomenclatural acts were taken following the recommendations of, and in accordance with, the International Code of Zoological Nomenclature (ICZN, 1999, 2012). Terminology of general morphology is based on Pinto and Lamas (2010, 2011) and references cited therein. The taxonomic status of the specific names, when not explicitly specified here, follows Pinto *in* Taxonomic Catalog of Brazilian Fauna (Pinto, 2022).

Illustrations were made with the aid of a stereomicroscope equipped with a camera lucida. Original drawings from Myrian Morato Duarte published in Machado and Costa (1995) were adapted and herein presented with permission for use granted by Naturalis, Natuurtijdschriften project, S.I.O./Odonatologica (CC BY-SA 4.0). Measurements (in mm) from the type series were obtained from Machado and Costa (1995) and those of the additional material were carried out using a stereomicroscope with an eyepiece with micrometer scale for small dimensions and a caliper for large dimensions. Specimens were photographed or scanned with varied techniques. Stacking focus images were generated using Helicon Focus (https://www.heliconsoft.com) and scans executed using a flatbed scanner. All images were further edited using distinct image editor software.

Table 1

Main diagnostic characters used for *Navicordulia* and *Navicordulia atlantica*-complex species based on literature adapted from Machado and Costa (1995), Pinto and Lamas (2010, 2011), and Fleck and Juillerat (2019). Data from the type series were compiled from Machado and Costa (1995), the additional specimens are from this study. Not applicable = "-".

Character / specimen	<i>N. atlantica</i> Male (n = 1)	<i>N. mielkei</i> Males (n = 3) and Females (n = 4)	<i>N. miersi</i> Female (n = 1)	<i>N. atlantica</i> "morph" Male (n = 1)	<i>N. mielkei</i> "morph" Male (n = 1)	N. mielkei / N. miersi "morph" Female (n = 1)
1. Pt coloration	brownish black	pale yellow to brown	pale yellow	dark brown	dark brown	dark brown
2. Membranule coloration	destroyed in both wings	white to brown	light brown	light brown	light brown	light brown
3. Space between CuP- crossing and base of triangle in Hw (cubito- anal area)	one-celled (lacking supernumerary crossvein)	one-celled (lacking supernumerary crossvein)	two-celled (with one supernumerary crossvein)	one-celled (lacking supernumerary crossvein)	one-celled (lacking supernumerary crossvein)	one-celled (lacking supernumerary crossvein)
4. Anal field of Hw	destroyed in both wings	2–3 cells row (3 rows for 1–4 cells distance)	2–3 cells row (3 rows for 3–4 cells distance)	2 cells row throughout	2 cells row throughout	2 cells row throughout
5. Genital lobe	quadrangular	quadrangular	-	quadrangular	quadrangular	-
6. Supralaminar process	-	cup-shaped lacking setae on posterior margin	dish-shaped with setae on posterior margin	-	-	dish-shaped with setae on posterior margin
7. Length of supralaminar process (ratio between total length of supralaminar process and total length of subgenital plate taken from posterior margin of S8)	_	0.66	0.66	_	_	0.62
8. Pilose complex on the sternite of S7	missing S7–8	1 transversal carina	-	1 transversal carina	1 transversal carina	-
9. Cercus length (ratio of cercus / epiproct)	as long as or slightly longer than epiproct (1.00)	shorter than epiproct (0.85-0.95)	-	as long as or slightly longer than epiproct (1.10)	shorter than epiproct (0.89)	-
10. Cercus in dorsal view	Almost parallel, slightly convergent to the apex, ending in a rounded tip	Almost parallel, slightly convergent to the apex, ending in a rounded tip	-	Almost parallel, slightly convergent to the apex, ending in a rounded tip	Almost parallel, slightly convergent to the apex, ending in a rounded tip	-
11. Length of ventro- lateral carina of cercus (ratio of carinated / uncarinated part)	twice as long as uncarinated part (2.20)	twice as long as uncarinated part (2.00-2.60)	_	twice as long as uncarinated part (2.10)	twice as long as uncarinated part (2.70)	_
12. Ventro-medial carina	developed [?]	developed [?]	_	developed	developed	_
13. Ventro-medial tubercle	-	-	_	weakly developed	weakly developed	_
14. Ventro-lateral carina	developed	developed	_	developed	developed	_
15. Dorso-basal tubercle	weakly developed	weakly developed	-	weakly developed	weakly developed	-
16. Ventro-lateral tubercle	well developed	developed	_	well developed	developed	_
17. Setae distribution (fringe or brush of long hair)	sparse setae (without a brush of long hairs)	sparse setae (without a brush of long hairs)	_	sparse setae (without a brush of long hairs)	sparse setae (without a brush of long hairs)	_

The following abbreviations are used: Ax = antenodal crossveins; CuP = cubitus posterior; Fw = fore wing; Hw = hind wing; Pt = pterostigma; S1-10 = abdominal segments.

Geographic coordinates not provided on the collection labels or original papers were acquired from toponyms list of IBGE (2011). Missing data from the original labels are written in square brackets, hence they correspond to our interpretation.

Results

We analyzed 101 characters / parameters (Supplementary data s1-s2) based on examination of all name-bearing types (Figs. 1a-c; 2i-j; 3a-b, e-f), and additional material held in collections (Figs. 2a-h; 3c-d, g-h; 4a-f; 5a-b), totaling 12 specimens. The compilation of main diagnostic

characters used in the original descriptions and the taxonomy of genus (Table 1) show no character or suits of characters to justify allocation of the three names as valid. The minor differences in shape, width/robustness, and size of caudal appendages (Figs. 2g–j; 3–4), we hypothesized are due to intraspecific variation, condition of preservation, and biased taxonomic interpretation. Comparison of the diagnostic characters among *N. miersi* and all known females of *Navicordulia*, including that recorded from Atlantic Forest, show no consistent differences than one additional crossvein in the cubito-anal area of Hw. We found the female holotype of *N. miersi* (Figs. 1c; 2j) being remarkably similar to other females determined as either *N. mielkei* (Fig. 2i) or *N. aemulatrix.*

Based on our comprehensive study we considered the three available names as a single species, therefore the hypothesis that specimens determined as *N. atlantica*, *N. mielkei* and *N. miersi* represent distinct species is no longer supported. Our results were



Figure 1 Habitus of the holotypes of Navicordulia species and their respective labels: (a) Navicordulia atlantica male; (b) Navicordulia mielkei male; (c) Navicordulia miersi female. All specimens in ABMM. Scale bars = 10 mm.

based on comparisons side by side of all type material with additional specimens from Ilha do Cardoso State Park, that unquestionably proved to belong to the same species and "combine" characters previously selected as diagnostic for these species. Since the three names were published simultaneously, we, as first reviewers (ICZN, 1999, Article 24: 24.2., 24.2.1: https://bit.ly/3NQDjun), select *N. atlantica* as senior synonym, subsequently *N. mielkei* and *N. miersi* are subjective junior synonyms. The full nomenclatural and taxonomic treatments, including status, synonymy, diagnosis, and distribution are presented below.

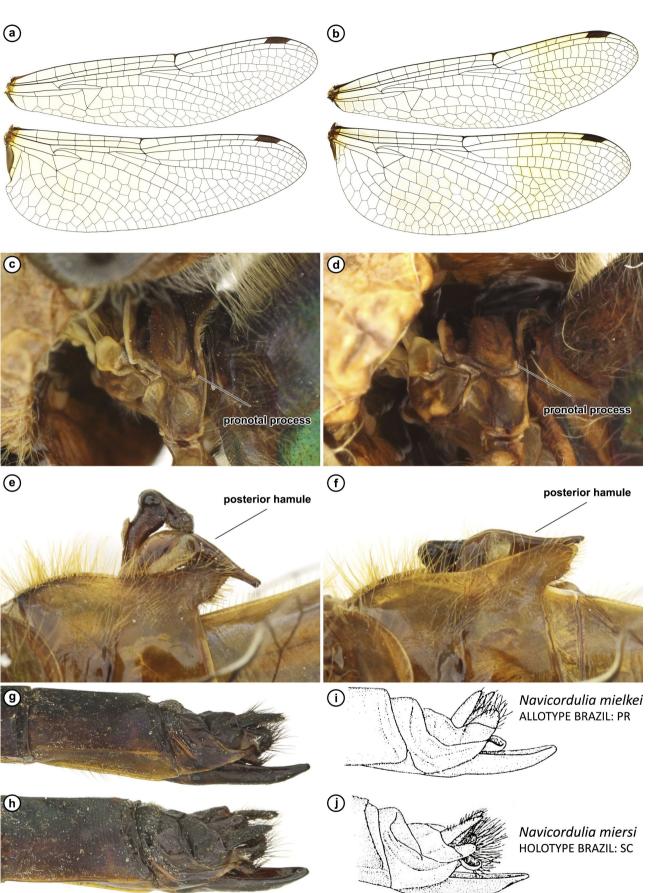


Figure 2 Males (a, c-f) and females (b, g-j) of *Navicordulia atlantica*: (a-b) wings; (c-d) prothorax in dorsolateral view; (e-f) secondary genitalia in lateral view; (g-h) S8-10 in lateral (g), and dorsolateral (h) views; (i) allotype from Paraná State (ABMM); (j) holotype from Santa Catarina State (ABMM). (a-h) specimens from Ilha do Cardoso State Park, São Paulo State (DZUP); (i-j) adapted from Machado and Costa (1995, figs. 29-30).

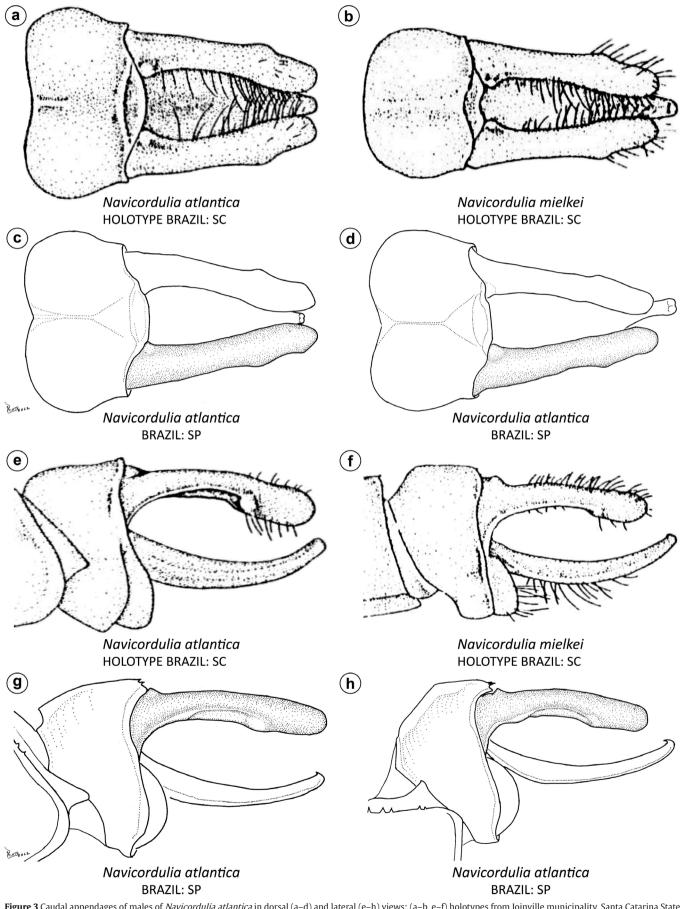


Figure 3 Caudal appendages of males of *Navicordulia atlantica* in dorsal (a–d) and lateral (e–h) views: (a–b, e–f) holotypes from Joinville municipality, Santa Catarina State (ABMM), adapted from Machado and Costa (1995, figs. 11, 13, 17–18); (c–d, g–h) original illustrations of specimens from Ilha do Cardoso State Park, São Paulo State (DZUP).





e



C

b



Figure 4 Caudal appendages of males of Navicordulia atlantica in dorsal (a, d), lateral (b, e), and ventral view (c, f). All from Ilha do Cardoso State Park, São Paulo State (DZUP).

Based on the revised status, *N. atlantica* does not properly key out using the keys by Machado and Costa (1995) and Fleck and Juillerat (2019) for males, and Pinto and Lamas (2011) for females. Males may key out either as *N. atlantica* or *N. mielkei* based on ratio of caudal

appendages, and the females may erroneously key to either as *N. mielkei* or *N. miersi*. The keys referred to above can be modified allowing for the correct determination of *N. atlantica*. We refrain from providing another new key until a full revision of the genus has been carried out.

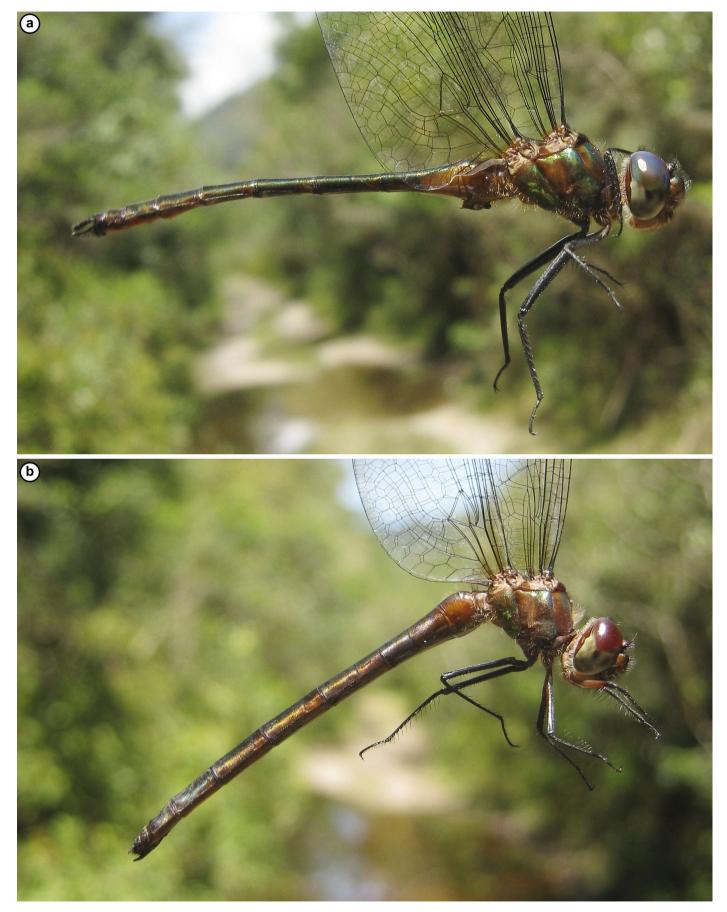


Figure 5 Habitus of male (a) and female (b) of Navicordulia atlantica at Ilha do Cardoso State Park, Cananéia municipality, São Paulo State (DZUP). Photos by APP in 2011.

Emendations to the available keys

Key to males modified from Fleck and Juillerat (2019, couplet 7 deleted).

6. Cerci in lateral view with a large ventrobasal tooth
Fleck & Juillerat, 2019
- Cerci in lateral view without ventrobasal tooth7
[go directly to couplet 8]
8. Cerci with ventrolateral tubercle. Genital lobe triangular or
quadrangular9
- Cerci without ventrolateral tubercle. Genital lobe triangular10
9. Proximal carinated part of cerci four times as long as the distal non-
carinated one. Genital lobe triangular
(De Marmels, 1989)
- Proximal carinated part of cerci twice as long as the distal non-
carinated one. Genital lobe quadrangular <i>N. atlantica</i>

Machado & Costa, 1995 (= *N. mielkei*, = *N. miersi*)

Key to females modified from Machado and Costa (1995, couplet 3 deleted), including the emendations from Pinto and Lamas (2011).

7'. Ratio between total length (from S8 posterior margin) of supralaminar process and total length of subgenital plate 0.80*N. aemulatrix* Pinto & Lamas, 2010

Navicordulia atlantica Machado & Costa, 1995 stat. rev.

ZooBank: http://zoobank.org/NomenclaturalActs/69ba84cc-caa4-49ad-b9ba-5b49c57ba7c7

(Figs. 1–5; Table 1; Supplementary data s1–s2)

- Navicordulia atlantica Machado & Costa, 1995: 188–189, 192, 194, 197, 199, 201, 204–207, 209, 216–217, figs. 11, 17, 23 (description of Holotype male, BRAZIL. Santa Catarina State: Joinville municipality, XII.1957, J. Lane leg. in ABMM, key, biological notes, illustrations of secondary genitalia in lateral view, caudal appendages in dorsal and lateral views); —Garrison et al. (2006: 161–162, mention); —Heckman (2006: 87–89, key, reproduction of illustrations from Machado and Costa, 1995); —von Ellenrieder (2009, assessed as Data Deficient in IUCN Red List); —Pinto and Lamas (2010: 608, 612–614, map, records from Brazil); —Pinto (2016: 22, catalog); —Fleck (2017: 257, mention); —Fleck and Juillerat (2019: 560–561, key, map); Garrison and von Ellenrieder (2019: 52, synonymic list [printed version from Garrison and von Ellenrieder, 1991]).
- Navicordulia mielkei Machado & Costa, 1995 syn. nov. ZooBank http://www.zoobank. org/NomenclaturalActs/4dfe3e98-e19c-42f2-aa02-55fbf3d525cc: 190, 192, 194-199, 201, 204, 210-213, 215-217, figs. 13, 18, 25, 30 (description of Holotype male, BRAZIL. Santa Catarina State: Joinville municipality, Serrinha, 31.X.[19]87, O. Mielke leg. in ABMM, key, biological notes, illustrations of female caudal appendages in lanterodorsal view, secondary genitalia in lateral view, caudal appendages in dorsal and lateral views of holotype); -Garrison et al. (2006: 161, mention); -Heckman (2006: 85, 87, 90, key, reproduction of illustrations from Machado and Costa, 1995); -Pinto and Lamas (2010: 608-609, 612-614, map, records from Brazil); -Pinto and Lamas (2011: 701-702, key, discussion on the taxonomic status and comparison with N. aemulatrix and N. miersi, biological notes); -Hämäläinen (2015: 107, eponymic species list); -Pinto (2016: 22, catalog); -Fleck (2017: 257, mention); -Fleck and Juillerat (2019: 559-561, key, map); - Garrison and von Ellenrieder (2019: 52, synonymic list [printed version from Garrison, 1991); -Pinto (2019: 52-53, 55-56, record to São Paulo State, behavioral and biological notes); -Pinto et al. (2020: 11, fig.

8 of male habitus, mention); — Vilela & Guillermo-Ferreira (2021a, assessed as Vulnerable in IUCN Red List).

Navicordulia miersi Machado & Costa, 1995 syn. nov. ZooBank http://www. zoobank.org/NomenclaturalActs/e31c8be8-18ea-4af4-ba49-202632bb3a89: 188, 194–197, 206, 211, 214–217, fig. 29 (description of Holotype female, BRAZIL. Santa Catarina State: Joinville municipality, 3–250 m, 26.XI.[19]79, H. Miers leg. in ABMM, key, biological notes, illustrations of caudal appendages in laterodorsal view of holotype); –Garrison et al. (2006: 161–162, mention); –Heckman (2006: 85, 89, key, reproduction of illustrations from Machado and Costa, 1995); –Pinto and Lamas (2010: 608, 612–614, map, records from Brazil); –Pinto and Lamas (2011: 702, discussion on the taxonomic status and comparison with *N. aemulatrix* and *N. mielkei*, biological notes); –Hämäläinen (2015: 107, eponymic species list); –Pinto (2016: 22, catalog); –Fleck (2017: 257, mention); –Fleck and Juillerat (2019: 560–561, map, comparison with *N. pascali*); –Garrison and von Ellenrieder (2019: 52, synonymic list [printed version from Garrison, 1991]); –Vilela & Guillermo-Ferreira (2021b, assessed as Data Deficient in IUCN Red List).

Type material examined

Navicordulia atlantica (1 male). BRAZIL. Santa Catarina State: male Holotype, Joinville municipality, XII.1957, J. Lane leg. (ABMM).

Navicordulia mielkei (3 males and 4 females). BRAZIL. Santa Catarina State: male Holotype, Joinville municipality, Serrinha [road], 31.X.[19]87, O. Mielke leg. (ABMM); 1 female paratype, Joinville municipality, 24.X.[19]82, [without collector] (ABMM); 1 male paratype, same data but 16.XII.[19]83, H. Miers leg. (ABMM); 1 female paratype, same data but 02.II.1985 (MNRJ 441); 1 female paratype, same data but collected into the forest, [0]8.XII.1985, [without collector] (ABMM); 1 male paratype, same data but 23.XII.1985, H. Miers leg. (MNRJ 440); Paraná State: female allotype, Estação Ecológica de Guaraqueçaba, collected in a forested trail at 5:00 pm, 13.II.[19]88, P.A. Machado leg. (ABMM).

Navicordulia miersi (1 female). BRAZIL. Santa Catarina State: female Holotype, Joinville municipality, 3–250 m, 26.XI.[19]79, H. Miers leg. (ABMM).

Additional material examined

(2 males and 1 female). BRAZIL. São Paulo State: 1 male and 1 female, Cananéia municipality, Parque Estadual da Ilha do Cardoso (PEIC_04, 06) coordinates between points 04 and 06, 25°04'56.54"S, 47°55'38.02"W, 13 m a.s.l., along to 'Trans Cardoso', a dirt road through the tree-like restinga vegetation, flooded areas parallel to road and at some points even on the road, 21.X.2011, A.P. Pinto leg. (DZUP 501065–501066); 1 male, same data but 22.X.2011 (DZUP 501067).

Diagnosis

Medium-sized (37–47 mm), brown corduliid with dark metallic green reflections (Figs. 1; 5). The anal margin of Hw with an accentuated excavation posterior to anal triangle (Fig. 2a), posterior hamule unbranched with a recurved apex (Figs. 2e–f) and a pilose complex on sternite of S7 in males; a large boat shaped subgenital plate and supralaminar process (sternite S9), both strongly projected posteriorly in females (Figs. 2g–j), both sexes with pronotal tergal process (Figs. 2c–d), typical of *Navicordulia* (cf. Pinto and Lamas, 2010).

Males of *N. atlantica* can be distinguished from the congeners within the "*longistyla*-group" (i.e., *N. aemulatrix, N. kiautai* Machado and Costa, 1995, *N. longistyla*, *N. nitens* and *N. tumucurakensis*) by the short cerci (1.70–1.92 mm) with scattered setae on their distal half and epiproct as long as or longer than cerci (ratio epiproct / cercus = 0.95–1.30) (Figs. 3–4), while in "*longistyla*-group" the cerci are longer (2.5–3.9 mm), with a brush of long hair-like setae in their distal half, epiproct shorter than cerci (ratio epiproct / cercus = 0.52–0.82). The quadrangular genital lobe (Figs. 2e–f; triangular in *N. errans, N. leptostyla, N. pascali*, and *N.* *vagans*), the pilose complex of S7 with a single transversal process (two in *N. errans, N. leptostyla*, and *N. pascali*), proximal 0.2 of cerci ventrally smooth, lacking a projected tubercle-like process (with a basal ventral tooth in *N. pascali*) distinguishes *N. atlantica* from the other four species of the "*errans*-group". Except by their strongly disjunct distribution, i.e., Atlantic Forest and Amazonia, distinction of males of *N. atlantica* from *N. amazonica* Machado & Costa, 1995—only known from its female holotype—can be difficult when not in association with females.

Females of *N. atlantica* can be distinguished from almost all other known females by the wider than long supralaminar process, "dish-shaped" (Figs. 2g–j; longer than wide in *N. amazonica, N. errans, N. leptostyla*, and *N. longistyla*, and rather "tongue-shaped" or "spoon-shaped"). The short and wide supralaminar process is similar to that of *N. aemulatrix*, possibly of *N. nitens* too, and most likely it is also true for the unknown female of *N. kiautai*. The longer subgenital plate of *N. atlantica* (Figs. 2g–j; supralaminar process / subgenital plate = 0.62–0.67) separates it from the sympatric *N. aemulatrix* (supralaminar process / subgenital plate = 0.80). Except by the disjunct distribution, females of *N. atlantica* cannot be distinguished from the montane Amazonian supposed *N. nitens*. Females of *Navicordulia* are still poorly known, thus, it may be risky to determine isolated females without accompanying males and caution is required when determining females.

Measurements

Males. Total length (incl. caudal appendages) 41.0–44.3; abdomen length (excluding caudal appendages) 29.6–32.3; maximum width of head 6.3–6.5; eyes seam length 0.94–1.0; length of Fw 30.0–31.9, Hw 29.0–31.0; width of wing (proximal to costal nodus) 7.0–7.2 in Fw, 9.8–10.0 in Hw; length of distance of base-nodus 16.0–17.2 in Fw, 13.0–14.0 in Hw; ratio between base-nodus distance / total length of wing 0.53–0.55 in Fw, 0.44–0.45 in Hw; Pt length 2.0–2.4 in Fw, 2.1–2.5 in Hw; length of postnodal space (*sensu* May, 1991) 0.47–0.49 in Fw, 0.44–0.53 in Hw; length of metathoracic femur 6.3–6.8; length of metathoracic tibia 6.2–6.8; length of genital lobe 1.1–1.4; width of base of genital lobe 0.6–0.7; length of hamule in lateral view (anterior to posterior margins) 1.8–2.0; length of S9+10 in lateral view 2.5–2.6; total length of cercus in lateral view 1.70–1.92; length of carinated part of cercus in lateral view 1.20–1.38; length of uncarinated part of cercus in lateral view 0.50–0.62; length of epiproct in lateral view 1.82–2.14.

Females. Total length (incl. subgenital plate) 37.0–47.0; abdomen length (excluding subgenital plate) 33.5–36.0; maximum width of head 6.4; eyes seam length 0.70–0.96; length of Fw 32.0–34.8, Hw 31.0–33.0; width of wing (proximal to costal nodus) 8.0 in Fw, 10.5 in Hw [DZUP only]; length of distance of base-nodus 16.7–18.5 in Fw, 13.2–14.5 in Hw; ratio between base-nodus distance / total length of wing 0.52–0.53 in Fw, 0.43–0.44 in Hw; Pt length 2.2–2.5 in Fw, 2.3–2.4 in Hw; length of postnodal space (*sensu* May, 1991) 0.40–0.48 in Fw, 0.45–0.46 in Hw; length of metathoracic femur 6.5; length of metathoracic tibia 6.6; length of cercus in lateral view 0.8–0.9; length of epiproct in lateral view 0.59; length of subgenital plate (from S8 posterior margin) 1.7; length of subgenital plate (from S8 posterior margin) in lateral view 2.4–2.7; ratio between total length of supralaminar process and subgenital plate 0.62–0.67.

Larva

Unknown.

Biological and ecological data

Few data on natural history exist for this species, except for short notes on field envelopes and by Pinto (2019, cited as *N. mielkei*). Based on collecting sites, it is a low land Atlantic Forest corduliid (0–140 m of elevation) occurring in the highly diverse coastal formations from tree-like restinga to tropical rainforest vegetation. Adults of *N. atlantica* (Fig. 5) were observed exhibiting typical flier and swarm aggregation behaviors side by side with *Lauromacromia picinguaba* Carvalho et al., 2004, both foraging near to the lower tree canopies in sunny environments. At that site '*Schizocordulia' rustica* (Hagen *in* Selys, 1871) was sympatric, adults of this species showing similar behavior (see Machado, 2005). Larvae were searched for, but results were unsuccessful at the Ilha do Cardoso State Park. The habitat preferences of adults may differ from those of larval sites, the latter can be being associated with more highland areas in rocky streams or streamlets due to its dependency on forested areas.

Distribution coordinates

An endemic species of Brazil with records for São Paulo State: Ilha do Cardoso State Park (25°04'56.54"S, 47°55'38.02"W, 13 m a.s.l.); Paraná State: Estação Ecológica de Guaraqueçaba (25°17'02"S, 48°25'32"W, at sea level); Santa Catarina State: Serrinha (26°19'03.45"S, 48°58'06.76"W, 140 m a.s.l.), Joinville (26°18'14"S, 48°50'45"W, 10 m a.s.l.).

Conservation status

In the first assessment of the conservation status of dragonflies at global level by the International Union for Conservation of Nature in 2009, Navicordulia atlantica (under this name) was the only name of the Navicordulia atlantica-complex to be included in the Red List of Threatened Species (IUCN Red List) as Data Deficient (DD). In the more recent versions of Red List, all three names were assessed with N. mielkei categorized as Vulnerable (VU) based on the criteria B1ab(iii) and *N. atlantica* and *N. miersi* as Data Deficient. However, considering the revised status here with the three names now representing the same species, N. atlantica does not meet the requirements to be considered Vulnerable since it is distributed in an area of about 4.500 km² with the northernmost and southernmost localities separated by 175 km in straight line. This occupancy region includes many protected areas, such as Ilha do Cardoso State Park, Environmental Protection Area of Guaraqueçaba and National Parks of Saint-Hilaire/Lange, Superagui and Guaricana, all located among the best-preserved fragments of the Atlantic Forest (see Ribeiro et al., 2009). Therefore, its revised conservation status in IUCN Red List may be considered as Least Concern (LC) or in a more conservative view, as Near Threatened (NT).

Remarks

All type specimens of *N. mielkei* preserved in MNRJ were lost in the catastrophic fire of 2018. These specimens and their data were digitized and will be freely available elsewhere in a forthcoming study (Pinto et al., in prep.).

Discussion

Doubts of specific status of *Navicordulia* occurring in Brazilian Atlantic Forest were raised by Pinto and Lamas (2011), indeed they put under the spotlight that the knowledge about Atlantic species of *Navicordulia* still meager on many aspects of their biology, behavior, and taxonomy. Pinto and Lamas (2011) questioned whether the differences observed in the three species of the *N. atlantica*-complex could not be due to the few known specimens and conditions of preservation, thus the distinctness would be explained both by intraspecific variation or by young and bad preserved specimens. All known specimens of this complex were collected during spring and summer seasons, between October and February, and except for a female from Guaraqueçaba Ecological Station in Paraná and the three specimens (two males and one female) from Ilha do Cardoso State Park in São Paulo, all others are from the same type locality in the municipality of Joinville in Santa Catarina.

Navicordulia atlantica (one male) was originally distinguished from *N. mielkei* (3 males and 4 females) based on the relative length of male cercus and coloration of pterostigma as follows: cercus longer or about the same length as epiproct (Figs. 3a, e; superior and inferior appendages *sensu* Machado and Costa, 1995) and pterostigma brownish black in *N. atlantica* versus cercus shorter than epiproct (Figs. 3b, f) and pterostigma vellowish brown in *N. mielkei* (Machado and Costa. 1995). Shape and size of caudal appendages are used as source of taxonomic data for specific delimitation in many families of Odonata since the foundations of odonatology (e.g., Selys, 1871), and they were considered by Machado and Costa (1995) the "most important character" to distinguish among species of Navicordulia. However, it can be misleading when not associated to other characters or when not considering intraspecific variation. Drastic variation in size and shape of caudal appendages have been documented in Anatya guttata (Erichson in Schomburgk, 1848) by De Marmels (1992) and Micrathyria mengeri Ris, 1919 by Dunkle (1995). The caudal appendages morphology has been shown to be useless to species recognition for large groups of Neotropical Libelluloidea, in special genera of Libellulidae, such as the dragonlets of the ubiquitous species of Erythrodiplax Brauer, 1868 (Borror, 1942).

Variations in the length ratio between cercus and epiproct have also been recorded in many corduliids s.l. including the Asian Macromiidae Epophthalmia Burmeister, 1839, the incertae sedis Corduliidae s.l. from North-Central and South America Neocordulia batesi (Selys, 1871) and in the Amazonian *Lauromacromia dubitalis* (Fraser, 1939); all these species show considerable variation in the relative size of the caudal appendages. In his revision of Epophthalmia, Lieftinck (1931: 37) keys-out Epophthalmia vittata vittata Burmeister, 1839 with "Inferior appendage [epiproct] as long as or slightly longer than upper pair [cerci] (fig. 7)", further in the same paper (p. 48) on *Epophthalmia elegans* (Brauer, 1865) he stated: "According to Hagen (loc. cit., p. 60) the appendix inferior [epiproct] of the male may be as long as the superiors [cerci] or even slightly shorter. In the specimen from Japan, it overlaps the tips of the superior ones for a trifle, as already observed by De Selys who described this male in the Synopsis". In the same way, May (1991: 37) based on the examined specimens and literature data from Selys-Longchamps (1871) and Martin (1906) reached the same conclusion for *N. batesi*, a species in which the cercus varies from longer to shorter than the epiproct. Specimens of *N. batesi batesi* in MNRJ from the provinces of Manabi, Napo, and Pichincha in Ecuador (all lost in the fire of 2018, Pinto et al., in prep.) have the cercus either longer or shorter than the epiproct. For Lauromacromia Geijskes, 1970, a poorly represented genus in collections, a recently studied male from Brazil has the cercus shorter than the epiproct, in contrast to the holotype in which it is longer than the epiproct (Ehlert and Pinto, 2020: 84).

The darkened coloration of the pterostigma in *N. atlantica* is most likely due to the mature condition of the holotype, while the three males in the type series of *N. mielkei* may be young individuals captured during the prereproductive period or even suffered postmortem effects. Moreover, the female allotype of *N. mielkei* (not from the type locality), a fully mature specimen and different from the holotype, has a dark brown pterostigma.

The two additional males of *N. atlantica* from the Ilha do Cardoso State Park were formerly considered to belong to a single species (Pinto, 2019, cited as *N. mielkei*). Reexamining these specimens, we

also find them individuals belonging to the same species, even though one has the cercus slightly longer than the epiproct and in the another the cercus is shorter than the epiproct (Figs. 3c–d, g–h; 4); both have a dark brown pterostigma. Excluding these minor differences in cercus and epiproct lengths, no other consistent differences were observed between males of *N. atlantica* and *N. mielkei*, hence, given the current evidence, this led us to consider them individuals of the same species.

In their study, Machado and Costa 1995 diagnosed Navicordulia miersi exclusively due to an additional crossvein to the CuP-crossing in Hw, and by a subjective cup-shaped supralaminar process without setae on its posterior margin. In the same paper, females of Navicordulia mielkei were considered to have a dish-shaped supralaminar process with setae on the posterior margin, while the female of *N. atlantica* was unknown. Pinto and Lamas (2011) pointed out the weakness of comparing the single female of *N. miersi* with the single male of *N.* atlantica, the latter lacking the essential anal area in Hw, and the males and females of N. mielkei. They also gave examples in other dragonflies to show how unreliable is this character alone for species delimitation. Rácenis (1970: 37) described a female from the Auyantepui region in the Guyana Shield of Venezuela as belonging to Paracordulia sericea (Selys, 1871) also with an additional crossvein to the CuP-crossing in the cubito-anal area but this specimen is now considered as possible N. nitens (De Marmels, 1991; Pinto and Lamas, 2011). A similar argument was used by Garrison and von Ellenrieder (2005) to justify the synonym in the damselfly genera *Mesagrion* Selys, 1885 and *Heteropodagrion* Selys, 1885 (Heteragrionidae-Mesagrionidae complex) that was supported only by an extra subcostal antenodal crossvein in Hw.

Finally, apart from the controversies on levels of homoplasy in wing venation characters, many variations are well known and easy to see in species description, including in *Navicordulia*. As samples of biological entities, the overall morphology of specimens is the result of many processes at the interface between gene expression and ontogenetic changes, thus no single character should necessarily be adopted as evidence of a species-specific benchmark.

The distinction between females of N. atlantica and N. amazonicaknown only from its female holotype-and supposed N. nitens-female also known from a single specimen-is difficult, except for its greatly disjunct distribution: Atlantic Forest for N. atlantica and Amazonia for *N. amazonica* and *N. nitens*. Females of *N. atlantica* have the supralaminar process wider than long ("dish-shaped"), while in N. amazonica it is longer than wide ("tongue-shaped"). This character cannot be observed in the figure of N. nitens in Rácenis (1970: 37, fig. 7). However, Machado and Costa (1995) used very detailed aspects of the tergal extension of the S9 to distinguish supposed *N. nitens* from *N. atlantica* (cited as N. miersi). These differences seem to us doubtful and until these specimens are reexamined, these details should not be adopted. Pinto and Lamas (2011) argued that the number of cell rows in the anal field of Hw (Figs. 2a-b), already mentioned as diagnostic among these species by Machado and Costa (1995), would represent a more consistent character. However, it, too, shows great variation, indicating no more than a phenetic trend. Our study reveals inconsistencies (see Table 1) and most likely this character is also not a reliable when used alone.

The establishment of these names, assumed as three distinct species in Machado and Costa (1995), was biased in favor of the paucity of specimens and, somehow, by adoption of a typological species concept. After the key study by Machado and Costa (1995) erecting the genus, which represented a doorway to an unknown biodiversity with introduction of most species discovered so far, many advances in taxonomic knowledge about *Navicordulia* have been published although is the second most species-rich of corduliids genus in the Neotropical region, and many investigations are waiting to be conducted.

In addition to the revisions on the taxonomic status of some species, data on natural history, ecology, and habitat preferences, mainly on larvae, should be produced. The assumptions implied in the recently proposed speculative evolutionary and biogeographic scenarios must be thoroughly investigated through phylogenetic and biogeographical analyses upon to a sounder knowledge of these marvelous dragonflies be available.

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Conflicts of interest

The authors declare no conflicts of interest.

Author contribution statement

APP conceived the study, compiled, organized, and analyzed the data, wrote the manuscript, revised, and approved its definitive version; MVOA and JE measured specimens, analyzed the data, wrote the manuscript, revised, and approved its definitive version.

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Supplementary data

The following online material is available for this article:

Table S1 - Comparative characters of male and female used by Machado & Costa (1995, Tables II–III) based on wing venation for *N. atlantica*, *N. mielkei* and *N. miersi*. Not applicable = "—".

Table S2 - Comparative characters of male and female based on measurements used by Machado & Costa (1995, Tables IV–V) for *N. atlantica*, *N. mielkei* and *N. miersi*. Not applicable = "—".