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Nesobasis rito sp. nov. (Zygoptera: Coenagrionidae), a new species of forest damselfly from Vanua Levu, Fiji

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Abstract

Nesobasis rito **sp. nov.** (Holotype ♂, Fiji, Vanua Levu, Drawa, 31 v 2018, A. Rivas-Torres leg.) from the *comosa* group is here described, illustrated, diagnosed, and compared with morphologically close species of the genus. *Nesobasis rito* can be distinguished from its related congeners by the shape of the caudal appendages and the ligula. The most similar species are *N. comosa* and *N. heteroneura*, which, like *N. rito*, have the caudal appendages covered by dense setae (especially the first species), but the shape differs clearly in lateral view, with *N. rito* having longer and more slender appendages, and a basal tooth clearly seen in dorsal view, absent in other members of the *comosa* group. The specific status of the collected specimens is also supported by the results of genetic analyses, where *N. rito* appears as a well-supported monophyletic clade. *Nesobasis rito* also has a distinct distribution from its most similar congeners: it is found on Vanua Levu, while *N. comosa* is found on Viti Levu and the closely related *N. heteroneura* is found on Viti Levu and Ovalau. All species of this group are found in streams with native forest riparian vegetation on their respective islands.

Key words: Odonata, Zygoptera, *Nesobasis*, taxonomy, Vanua Levu, Fiji

Introduction

The genus *Nesobasis* was erected by Selys (1891) to include specimens collected at the islands "Viti", with a general appearance similar to the genus *Pseudagrion* Selys, 1876, but lacking postocular spots, having longer setae in the legs, the lower tooth of the claws almost as long as the upper, the upper anal appendages of males not forked or notched at the end, and a simple prothorax. Later, Tillyard (1924) compiled the knowledge of the odonates of Fiji, describing 13 species, ten in the genus *Nesobasis*, one of which was placed in *Melanesobasis* by Donnelly (1984). Kimmins (1943) described *N. leveri* from a single male collected on Viti Levu. Marinov (2021) introduced *N. martina* and *N. monika* found on Viti Levu and Taveuni, respectively.

Donnelly (1990) reviewed in detail the fauna of Viti Levu, Ovalau and Kadavu, which he divided into three groups, while also describing ten additional species, and indicating that, taking into account the undescribed species from other Fijian islands, this genus is the most speciose example of an odonate island radiation. The results of an extensive study corroborated this fact, with the finding of at least 24 species, including two additional undescribed

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species (Beatty *et al.* 2007). Currently 23 species are described, but 13 more are being prepared for description (Beatty *et al.* 2017; T. Donnelly and M. Marinov, pers. comm.).

Several biological attributes make *Nesobasis* a very unusual genus compared to other coenagrionids. Donnelly (1990) was the first to highlight that some species of *Nesobasis* have a female-biased sex-ratio and he attributed this fact to a sex-role reversal, with territorial females on the streams and males, which are rarely encountered, remaining away from the water. However, sex-role reversal was not found when the behaviour of these species was studied in detail, although for three species male rarity is extreme, and in at least two species males are still unknown (Van Gossum *et al.* 2007). Parthenogenesis has been suggested as the reproductive mode for these female-biased species of *Nesobasis*, but until now the only confirmed case of parthenogenesis in the Odonata remains the Azorean populations of another coenagrionid, *Ischnura hastata* (Say, 1840) (Lorenzo-Carballa & Cordero-Rivera 2009).

Nesobasis is also remarkable because the two main islands, Viti Levu and Vanua Levu, have similarly rich fauna, but do not share any species, whereas smaller islands around them have a subset of the species from the largest islands, making the biogeography of *Nesobasis* a fascinating example of island radiation (Beatty *et al.* 2017; Van Gossum *et al.* 2008). Only one island has species from both assemblages: the island of Koro, located between Viti Levu and Vanua Levu, has a single species from the former island (*N. rufostigma* Donnelly, 1990) along with 3 species from the latter (*N. brachycerca* Tillyard, 1924 and two undescribed species, Van Gossum *et al.* 2008).

Nesobasis is the dominant genus of damselflies found in Fiji, showing wide variation in size, coloration, and morphology (Donnelly 1990), but several species are commonly found in the same stream (as many as 8–12), with apparently little ecological divergence (Beatty *et al.* 2017; Van Gossum *et al.* 2007). Many species of *Nesobasis* have been found to be infected with a variety of strains of *Wolbachia* (Lorenzo-Carballa *et al.* 2019), a bacterium known to influence sex ratios and mate compatibility in several arthropod hosts (Bruzzese *et al.* 2021; Werren *et al.* 2008). While evidence for parthenogenesis in *Nesobasis* is lacking, there is a possible influence of *Wolbachia* infection on the speciation rate of these damselflies (Lorenzo-Carballa *et al.* 2019). Comparative phylogenetic studies and further analyses of the *Wolbachia* infections are needed to understand whether and how these endosymbionts, paired with geographical isolation, have contributed to the high diversity in this genus (Beatty *et al.* 2017; Lorenzo-Carballa *et al.* 2019). However, such a task cannot be completed until all the species within the genus are described. To contribute to this goal, we here describe a new species of *Nesobasis* from Vanua Levu.

Material and methods

Specimen collection and morphological analyses. Specimens were collected during surveys of odonates in different localities of the island of Vanua Levu, in September 2005, August 2009, September 2011 and May-June 2018.

Given the large number of *Nesobasis* species currently awaiting description, we consulted an unpublished key from M. Marinov and notes from T.R. Donnelly, to determine whether the collected specimens were already included in their on-going studies. These specimens were found to be novel. To document the new species, field photographs were taken with a Canon EOS 5D Mark II and 7D Mark II with a Canon 100 mm macro lens. Laboratory photographs were taken with a Leica Flexacam C1 camera attached to an Olympus SZ60 stereomicroscope, and stacked with Adobe Photoshop CS6 to increase depth of field. Specimens were immersed in ethylene glycol to diminish bright areas in the pictures, allowing a sharper view of structures and increasing the contrast between pale and dark areas.

We follow Garrison *et al.* (2010) for body morphology nomenclature. Total body length includes cerci; all measurements are given in mm. Abbreviations for structures used throughout the text are as follows: S1–10: abdominal segments 1 to 10, Fw: forewing, Hw: hindwing.

Specimens are preserved at:

- ECOEVO Laboratory of Evolutionary and Conservation Ecology, Escola de Enxeñaría Forestal, University of Vigo, Pontevedra, Spain.
- NZAC New Zealand Arthropod Collections, Auckland, New Zealand
- USP The University of the South Pacific, Suva, Fiji.

TABLE 1. List of *Nesobasis* and *Melanesobasis* specimens included in the present study. For each specimen, we list voucher ID, sex, collection site information and GenBank accession numbers; n.a. indicates that no sequences were available for a particular marker and/or individual. For biosecurity reasons no coordinates are provided for the new species locations.

Species	Voucher ID	Sex	Collection details	GenBank Accession Nos		Reference
				COI	PRMT	
N. rito	ACR4868	male	Vanua Levu, Drawa,	MZ826789	MZ826788	This study
N. rito	ACR4869	male	Vanua Levu, Drawa,	MZ826791	MZ826790	This study
N. rito	2009-138	female	Fiji, Vanua Levu, Raviravi Creek	MZ826781	n.a.	This study
N. rito	2011-205	female	Fiji, Vanua Levu, Navuturerega creek	MZ826785	MZ826784	This study
N. rito	2011-208	male	Fiji, Vanua Levu, Navuturerega creek	MZ826787	MZ826786	This study
N. rito	2011-184	male	Fiji, Vanua Levu, Navuturerega creek	MZ826783	MZ826782	This study
N. rufostigma	NE015	female	Viti Levu, Vaqo Creek. 18° 04.89’ S; 178° 26.57’ E.	MH348735	MH328150	Lorenzo-Carballa *et al.* 2019
N. rufostigma	NE088	female	Viti Levu, Nukunuku. 17° 37.11’ S, 177° 56.71’ E.	MH348737	MH328151	Lorenzo-Carballa *et al.* 2019
N. rufostigma	NE111	male	Viti Levu, Waikubukubu. 17°32.84’S 177°56.62’ E.	MH348738	MH328152	Lorenzo-Carballa *et al.* 2019
N. rufostigma	NE122	female	Viti Levu, Waikubukubu. 17°32.84’S 177°56.62’ E.	MH348739	MH328153	Lorenzo-Carballa *et al.* 2019
N. monticola	NE1624	female	Viti Levu, Vereni Falls. 17° 40.27’ S; 177° 33.06’ E.	MH348732	MH328145	Lorenzo-Carballa *et al.* 2019
Nesobasis sp. 4	NE452	female	Vanua Levu, Lomaloma Falls. 16°37.38’S, 179°10.00’ E.	MH348764	MH328181	Lorenzo-Carballa *et al.* 2019
Nesobasis sp. 4	NE458	male	Vanua Levu, Lomaloma Falls. 16°37.38’S, 179°10.00’ E.	MH348766	MH328178	Lorenzo-Carballa *et al.* 2019
Nesobasis sp. 4	NE468	female	Vanua Levu, Lomaloma Falls. 16°37.38’S, 179°10.00’ E.	MH348769	MH328179	Lorenzo-Carballa *et al.* 2019
Nesobasis sp. 4	NE1673	male	Vanua Levu, Sauvuqoro Creek. 16° 36.44’ S; 179° 08.87’ E.	MH348774	MH328180	Lorenzo-Carballa *et al.* 2019
Nesobasis sp. 13	NE498	male	Vanua Levu, Lomaloma Falls. 16°37.38’S, 179°10.00’ E.	MH348775	MH328196	Lorenzo-Carballa *et al.* 2019

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TABLE 1. (Continued)

Species	Voucher ID	Sex	Collection details	GenBank Accession Nos		Reference
				COI	PRMT	
N. longistyla	NE912	male	Viti Levu, Abaca Road 3. 17° 40.11' S; 177° 32.52' E.	MH348721	MH328132	Lorenzo-Carballa *et al.* 2019
N. longistyla	NE918	male	Viti Levu, Abaca Road 3. 17° 40.11' S; 177° 32.52' E.	MH348722	MH328133	Lorenzo-Carballa *et al.* 2019
N. longistyla	NE1644	male	Viti Levu, Vereni Falls. 17° 40.27' S; 177° 33.06' E.	MH348724	MH328137	Lorenzo-Carballa *et al.* 2019
N. campioni	NE1674	female	Viti Levu, Namosi Road 6. 18° 06.74' S; 178° 11.21' E.	MH348646	MH328068	Lorenzo-Carballa *et al.* 2019
Nesobasis sp. 11	NE613	male	Vanua Levu, Raviravi Creek. 16° 36.44' S; 179° 08.87' E.	MH348622	MH328046	Lorenzo-Carballa *et al.* 2019
Nesobasis sp. 11	NE616	male	Vanua Levu, Raviravi Creek. 16° 36.44' S; 179° 08.87' E.	MH348623	MH328049	Lorenzo-Carballa *et al.* 2019
Nesobasis sp. 11	NE638	male	Vanua Levu, Raviravi Creek. 16° 36.44' S; 179° 08.87' E.	MH348624	MH328051	Lorenzo-Carballa *et al.* 2019
N. anguillicolis	NE915	male	Viti Levu island, Abaca Road 3. 17° 40.11' S; 177° 32.52' E.	MH348628	MH328052	Lorenzo-Carballa *et al.* 2019
N. anguillicolis	NE921	male	Viti Levu island, Abaca Road 3. 17° 40.11' S; 177° 32.52' E.	MH348629	MH328053	Lorenzo-Carballa *et al.* 2019
Nesobasis sp. 3	NE1670	female	Vanua Levu, Lomaloma Falls. 16°37.38'S, 179°10.00' E.	MH348639	MH328061	Lorenzo-Carballa *et al.* 2019
N. monticola	NE1657	female	Viti Levu Korowaiwai. 17° 36.18' S; 177° 56.83' E.	MH348733	MH328146	Lorenzo-Carballa *et al.* 2019
N. selysi	NER29	male	Viti Levu, Vaturu Dam Road 2. 17° 46.23' S; 177° 36.58' E.	MH348758	MH328171	Lorenzo-Carballa *et al.* 2019
N. selysi	NER30	male	Viti Levu, Vaturu Dam Road 2. 17° 46.23' S; 177° 36.58' E.	MH348759	MH328172	Lorenzo-Carballa *et al.* 2019
N. flavifrons	NE1662	male	Viti Levu, Vaturu Dam Road 2 17° 46.23' S; 177° 36.58' E.	MH348671	MH328091	Lorenzo-Carballa *et al.* 2019

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TABLE 1. (Continued)

Species	Voucher ID	Sex	Collection details	GenBank Accession Nos		Reference
				COI	PRMT	
N. telegastrum	NE1663	male	Viti Levu, Abaca Road 2: 17° 39.99' S; 177° 31.65' E.	MH348763	MH328177	Lorenzo-Carballa *et al.* 2019
N. erythrops	NE043	female	Viti Levu, Wainikovu 18° 06.39' S; 178° 10.82' E.	MH348658	MH328080	Lorenzo-Carballa *et al.* 2019
N. erythrops	NE124	female	Viti Levu, Waikubukubu 17°32.84'S 177°56.62' E.	MH348661	MH328082	Lorenzo-Carballa *et al.* 2019
N. erythrops	NE065	female	Viti Levu, Korowaiwai. 17° 36.18' S; 177° 56.83' E.	MH348659	MH328081	Lorenzo-Carballa *et al.* 2019
N. erythrops	NE966	female	Viti Levu, Abaca Road 3. 17° 40.11' S; 177° 32.52' E.	MH348665	MH328086	Lorenzo-Carballa *et al.* 2019
N. brachycerca	NE619	male	Vanua Levu, Raviravi Creek. 16° 36.44' S; 179° 08.87' E.	MH348640	MH328062	Lorenzo-Carballa *et al.* 2019
N. brachycerca	NE677	male	Vanua Levu, Raviravi Creek: 16° 36.44' S; 179° 08.87' E.	MH348644	MH328066	Lorenzo-Carballa *et al.* 2019
Nesobasis sp. 17	NE614	male	Vanua Levu, Raviravi Creek. 16° 36.44' S; 179° 08.87' E.	MH348710	MH328123	Lorenzo-Carballa *et al.* 2019
Nesobasis sp. 17	NE621	female	Vanua Levu, Raviravi Creek. 16° 36.44' S; 179° 08.87' E.	MH348713	MH328124	Lorenzo-Carballa *et al.* 2019
Nesobasis sp. 17	NE627	female	Vanua Levu, Raviravi Creek. 16° 36.44' S; 179° 08.87' E.	MH348714	MH328125	Lorenzo-Carballa *et al.* 2019
Nesobasis sp. 17	NE628	female	Vanua Levu, Raviravi Creek. 16° 36.44' S; 179° 08.87' E.	MH348715	MH328126	Lorenzo-Carballa *et al.* 2019
Nesobasis sp. 17	NE1665	male	Vanua Levu, Bagasau Creek. 16° 42.90' S; 179° 43.67' E.	MH348719	MH328130	Lorenzo-Carballa *et al.* 2019
Nesobasis sp. 6	NE1668	male	Vanua Levu, Lomaloma Falls. 16°37.38'S, 179°10.00' E.	MH348734	MH328147	Lorenzo-Carballa *et al.* 2019
Nesobasis sp. 10	NE1672	male	Vanua Levu, Sauvuqoro Creek. 16° 38.50' S; 179° 13.50' E.	MH348672	MH328092	Lorenzo-Carballa *et al.* 2019

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TABLE 1. (Continued)

Species	Voucher ID	Sex	Collection details	GenBank Accession Nos		Reference
				COI	PRMT	
N. heteroneura	NE012	male	Viti Levu, Sauvuqoro Creek. 16° 38.50' S; 179° 13.50' E.	MH348672	MH328092	Lorenzo-Carballa *et al.* 2019
N. heteroneura	NE102	female	Vit Levu, Waikubukubu. 17°32.84'S 177°56.62' E.	MH348677	MH328095	Lorenzo-Carballa *et al.* 2019
N. heteroneura	NE089	female	Viti Levu, Korowaiwai. 17° 36.18' S; 177° 56.83' E.	MH348676	MH328094	Lorenzo-Carballa *et al.* 2019
N. heteroneura	NEX23	female	Viti Levu, Waikubukubu. 17°32.84'S 177°56.62' E.	MH348680	MH328097	Lorenzo-Carballa *et al.* 2019
N. comosa	NE928	male	Viti Levu, Abaca Road 3. 17° 40.11' S; 177° 32.52' E.	MH348647	MH328069	Lorenzo-Carballa *et al.* 2019
N, comosa	NE1001	male	Viti Levu, Abaca Road 3. 17° 40.11' S; 177° 32.52' E.	MH348647	MH328069	Lorenzo-Carballa *et al.* 2019
N. comosa	NE1111	male	Viti Levu, Abaca Road 3. 17° 40.11' S; 177° 32.52' E.	MH348652	MH328075	Lorenzo-Carballa *et al.* 2019
N. comosa	NE1119	female	Viti Levu, Abaca Road 3. 17° 40.11' S; 177° 32.52' E.	MH348653	MH328076	Lorenzo-Carballa *et al.* 2019
Nesobasis sp. 9	NE1667	female	Vanua Levu, Lomaloma Falls 16°37.38'S, 179°10.00' E.	MH348656	MH328079	Lorenzo-Carballa *et al.* 2019
N. malcolmi	NE916	female	Viti Levu, Abaca Road 3. 17° 40.11' S; 177° 32.52' E.	MH348726	MH328139	Lorenzo-Carballa *et al.* 2019
N. malcolmi	NE919	female	Viti Levu, Abaca Road 3. 17° 40.11' S; 177° 32.52' E.	MH348727	MH328140	Lorenzo-Carballa *et al.* 2019
N. malcolmi	NE923	female	Viti Levu, Abaca Road 3. 17° 40.11' S; 177° 32.52' E.	MH348728	MH328141	Lorenzo-Carballa *et al.* 2019
Melanesobasis corniculata	NE1583	male	Viti Levu, Waivudawa Creek. 18° 05.24' S; 178° 21.11' E.	MH348618	MH328042	Lorenzo-Carballa *et al.* 2019

DNA extraction and sequencing. Among the adults captured, six specimens of the putative new *Nesobasis* species (4 ♂♂ and 2 ♀♀), were selected for genetic analyses (see Table 1). Adult individuals were captured using a hand net, and preserved in 80% ethanol prior to DNA extraction. Total genomic DNA was extracted from a single leg of each specimen using the GeneJet DNA extraction kit (ThermoFisher Scientific, Waltham, MA, USA), following the manufacturer's protocol. We amplified a fragment of the mitochondrial Cytochrome Oxidase I (COI) gene, and the nuclear Arginine Methyltransferase (PRMT) gene, using previously published primers (Ferreira *et al.* 2014; Futahashi 2011) (Table 2). PCR reactions were carried out at specific annealing temperatures (Table 2) using the DreamTaq Green PCR Master Mix (ThermoFisher Scientific). Prior to sequencing, unincorporated primers and dNTPs were removed using Shrimp Alkaline Phosphatase and Exonuclease I (New England Biolabs, Ipswich, MA, USA). Cleaned PCR products were sequenced in both directions using BigDye v.3.1 chemistry (Applied Biosystems, Foster City, CA, USA) in an ABI 3730xl DNA Analyzer (Applied Biosystems), at the Macrogen Spain facilities in Madrid.

TABLE 2. Primers used to amplify mitochondrial (COI) and nuclear (PRMT) DNA of the *Nesobasis* species included in this study. Ta indicates the PCR annealing temperature for each primer pair.

Locus	Primer name	Primer sequence (5'-3')	Ta (ºC)	Reference
Cytochrome oxidase I (COI)	COI-S0	TACCAATTATAATTGGAGGATTYGG	48	Futahashi 2011
	COI-AS0	CTTCTGGATGTCCAAARAATCA	48	Futahashi 2011
Arginine methyltransferase (PRMT)	ARG-F2	TGCCGCCAAGGCTGGAGCATC	48	Ferreira *et al* 2014
	ARG-R3	TGCCACCTTCCTAATAGAGCTC	48	Ferreira *et al* 2014

Genetic analyses. After sequencing, chromatograms were visually inspected, trimmed and assembled using Geneious v. 9.1.7 (https://www.geneious.com). BLAST searches were run through Geneious v. 9.1.7 for all DNA sequences, to ensure that they were not derived from contamination. Previously published sequences from several *Nesobasis* species were downloaded from GenBank (https://www.ncbi.nlm.nih.gov/genbank/) and added to our datasets. Sequences of *Melanesobasis corniculata* (Tillyard, 1924) were selected as outgroups for the phylogenetic analyses. Sequences of the species described in the present study have been deposited in GenBank with accession numbers indicated in Table 1.

Sequences were aligned using MAFFT (Katoh *et al.* 2002) as implemented in Geneious v. 9.1.7 (https://www.geneious.com). Alignments were exported into MEGA X (Kumar *et al.* 2018) for estimation of genetic differentiation between the *Nesobasis* species. Genetic p-distances were estimated with the pairwise deletion option, which removes all ambiguous positions for each sequence pair. Phylogenetic relationships among *Nesobasis* were reconstructed using maximum likelihood (ML) and Bayesian inference (BI) approaches. ML analyses were carried out using RAxML 7.2.8. (Stamatakis 2006) as implemented in Geneious v. 9.1.7, using the rapid bootstrapping and search for best scoring ML tree option, under the GTR+G+I model. Support for the nodes in the resulting tree was estimated by running 1,000 bootstrap replicates. BI analyses were conducted using MrBayes 3.2.6 (Huelsenbeck & Ronquist 2001; Ronquist & Huelsenbeck 2003) also implemented in Geneious v. 9.1.7. Searches were run for 1.1 million generations, with default priors and the GTR+G+I substitution model.

Results

Nesobasis rito sp. nov. Rivas-Torres & Cordero-Rivera
(Figs. 1–3)

Holotype. ♂ (currently in ECOEVO, to be deposited at NZAC, accession number NZAC04231068; specimen code ACR-04869), Fiji, Vanua Levu, Drawa, **Drawa River**, altitude 52 m, collected on 31.v.2018, A. Rivas-Torres leg.
Paratypes. ♂ (currently in ECOEVO, to be deposited at USP, specimen code ACR-04868), Fiji, Vanua Levu, Drawa, **Drawa River (**same data as holotype), collected on 31.v.2018. A. Rivas-Torres leg.; ♂ (ECOEVO, specimen code 2011-184, Fiji, Vanua Levu, **Navuturerega creek**, C. Beatty leg.), collected on 16.ix.2011; ♂ (ECOEVO, specimen code 2011-208, Fiji, Vanua Levu, **Navuturerega creek**, C. Beatty leg.), collected on 16.ix.2011.

Paratypes. ♀ (currently in ECOEVO, to be deposited at NZAC, accession number NZAC04231069; specimen code 2009-138), Fiji, Vanua Levu, **RaviRavi**, C. Beatty leg., collected on 7.viii.2009; ♀ (ECOEVO, specimen code 2011-205, Fiji, Vanua Levu, **Navuturerega creek**, C. Beatty leg.), collected on 16.ix.2011.

Etymology. Named ***rito*** (noun in apposition) which in Spanish means ritual, to honour the local community rituals of Drawa village, which we enjoyed before finding the specimens, but also as an acronym of **Ri**vas-**To**rres, as an appreciation of the first author to her family's continuous support.

Description of holotype. Figure 1 shows the habitus of the dried specimen, and the dorsal view of the last abdominal segments. Figure 5 illustrates several live individuals in the field.

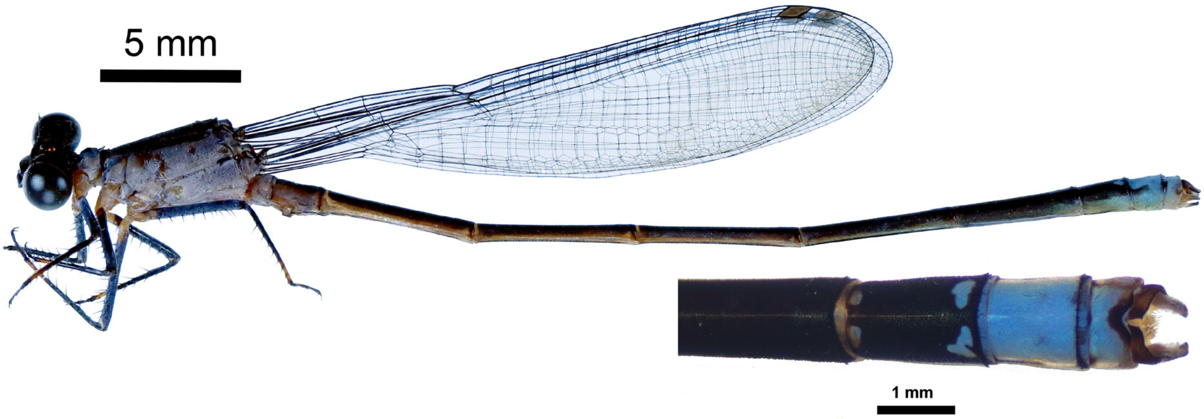

FIGURE 1. *Nesobasis rito* **sp. nov.**, holotype male; habitus and dorsal view of S7–10, showing the blue spots and the caudal appendages.

Head. (Fig. 2a, c). Epicranium totally black; labrum pale blue, anteclypeus dark brown and postclypeus black; antefrons pale brown, and postfrons black; without postocular spots; antennae, occipital bar and border of postocular lobes black. Eyes pale green in life, dark brown in dried specimens but pale grey when immersed in ethylene glycol (Fig. 2b). Mandibles pale brown (Fig. 2c).

Thorax. (Fig 2b). Prothorax largely black, except anterior and posterior lobes, which have a pale brown bar, the same colour as the propleuron. In dorsal view, the posterior lobe appears slightly bilobed (Fig. 2a). Mesothorax with mesepisternum completely black, mesepimeron pale brown with a black longitudinal stripe occupying about half of its width, metepisternum pale brown with a small dark streak on the posterior end, and a small line at the posterior ventral border; metepimeron pale brown. The pale areas of the thorax are blue in life. In the dried specimen there is a bluish pruinescence covering the sides of the thorax (Fig. 1). Legs mainly pale black, with the coxae and trochanters pale brown, and the last third of tibiae reddish (Fig. 1).

Wings. (Fig. 2f). Hyaline, venation dark, 14 antenodals, pterostigma brown, about 0.8 mm width. A single line of cells distal of pterostigma.

Abdomen. (Fig. 1). Mostly black, S1 and S2 black dorsally, pale laterally (bluish alive, brown post-mortem); S3–6 black dorsally and pale ventrally; S7 black and pale ventrally, but with a blue ventral part, covering the last quarter; S8 black dorsally with two blue irregular spots posteriorly and two blue dots in the anterior part, blue laterally; S9 and S10 almost blue, with a dark area in the distal part of S10 dorsally.

Caudal appendages. (Fig. 2e, g). In dorsal view, only the cerci are clearly visible, convergent, with a terminal tooth and a small basal tooth (arrow in Fig. 2e) and covered with a dense pale pilosity. In lateral view, cerci and paraprocts slightly longer than S10. Cerci dark brown, oriented downwards and with rounded end. Paraprocts light brown basally and dark brown distally, almost horizontal, with rounded tip.

Genital ligula. (Fig. 3). Distal segment simple, similar to a spoon, without flagella, but with an indentation that creates a rounded lateral lobe in each side.

Measurements. Body length: 41.2, Hw: 23.8.

Male paratypes. The paratypes are very similar to the holotype. Specimen ACR-04868 has the general appearance of a younger specimen. The pale areas of thorax are bluish in life (as shown for other specimens in Fig. 5a–c) and the black stripe of mesepimeron broader, fused with the black mesepisternum (Fig. 2d). The distal blue spots in S8 are larger than in the holotype and drop-shaped (Fig. 2i). Caudal appendages very similar to holotype (Fig. 2h). Blue spots on S8 are reduced in specimen 2011-184. Specimen 2011-208 shows some pruinescence on the last abdominal segments, indicating it is an older individual.

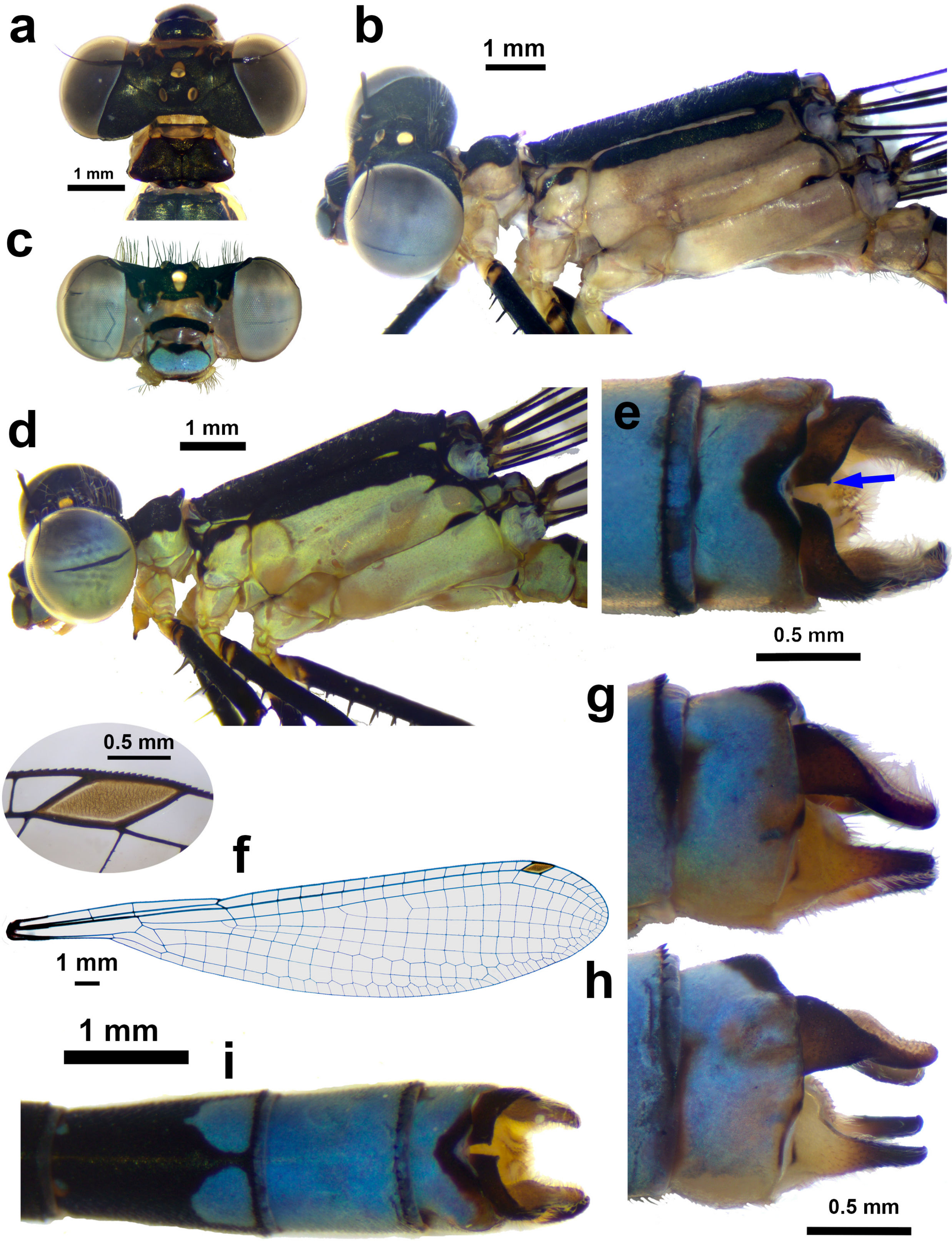

FIGURE 2. *Nesobasis rito* **sp. nov.**, **holotype** male from Vanua Levu, Fiji: (2a) head in dorsal view. Note the notch at posterior lobe of prothorax; (2b) lateral view of the thorax; (2c) head in frontal view; (2e) caudal appendages in dorsal view, with the basal tooth of the cerci indicated by the arrow; (2g) caudal appendages in lateral view; (2f) hw and a detail of the pterostigma; **paratype** male: (2d) lateral view of head and thorax, showing extended black pattern on the mesepimeron compared to the holotype; (2h) lateral view of the caudal appendages; (2i) dorsal view of S8–10, showing large blue spots in S8.

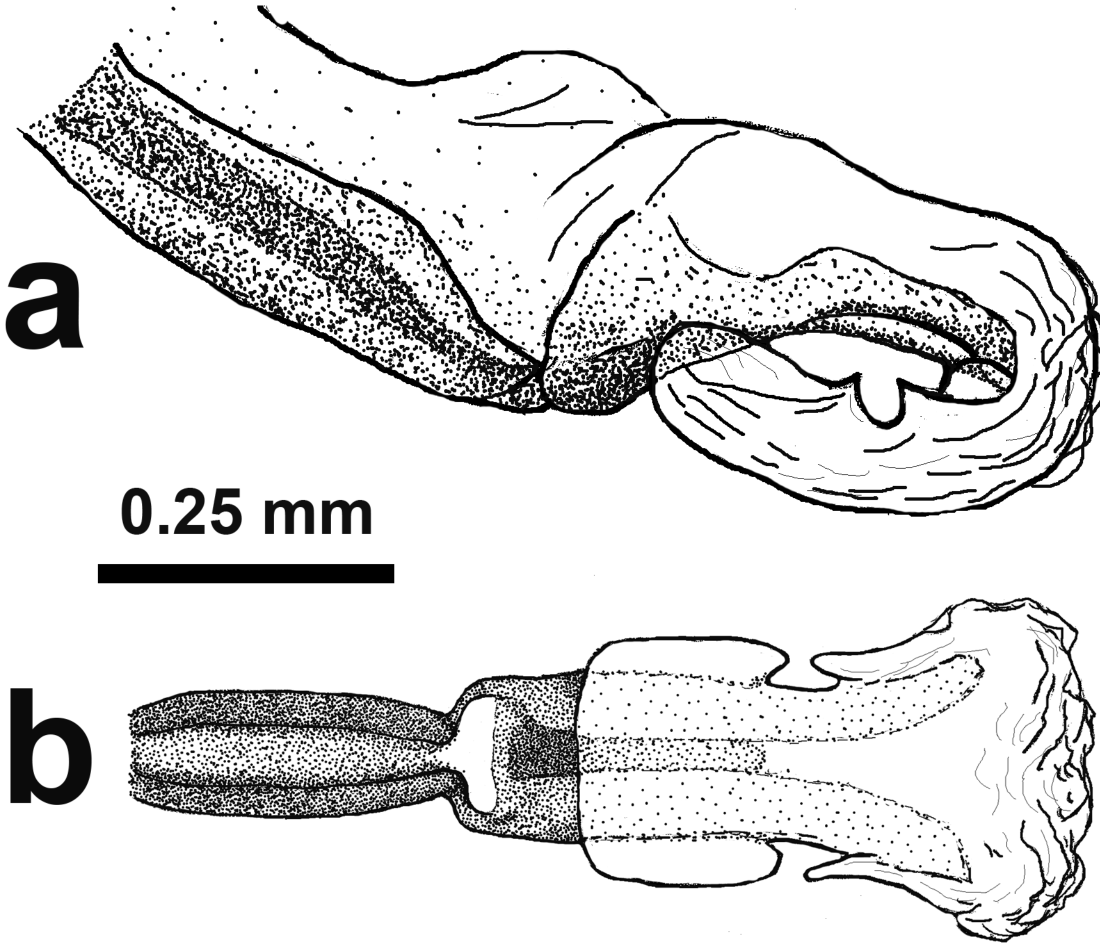

FIGURE 3. *Nesobasis rito* **sp. nov.**, **holotype** male from Vanua Levu, Fiji; (3a) lateral view of the genital ligula; (3b) ectal view.

Measurements. Specimen ACR-04868: Body length: 40.8, Hw: 23.8; specimen 2011-184: Body length: 40.2, Hw: 21.4; specimen 2011-208: Body length: 40.8, Hw: 22.0.

Female paratypes: Very similar to the male in general appearance (Fig. 4). The pale areas of the body were reddish in life (Fig. 5d–e) but pinkish in the preserved specimens (Fig. 4a, f). The pronotum is trapezoidal in dorsal view, with two small triangular expansions on the frontal border. The posterior lobe with a narrow elevated tubercle in lateral view (Fig. 4f). The valves of the ovipositor reach almost to the tip of the cerci (Fig. 4c, d). The pterostigma is uniformly light brown (Fig. 4e).

Measurements. Specimen 2009-138: Body length: 36.2; specimen 2011-205: Hw: 22.6; body length: 37.5, Hw: 22.8.

Discussion

Differential diagnosis. According to its morphology, *N. rito* belongs to the *comosa* group as defined by Donnelly (1990), which includes *N. comosa*, *N. heteroneura*, *N. aurantiaca*, *N. malcolmi* and *N. martina*. Based on the phylogeny of Beatty *et al.* (2017) this is a highly supported clade. One unique feature of *N. rito* is a notch at around the middle from the posterior lobe of the prothorax that makes it somewhat bilobed (Fig. 2a). *Nesobasis rito* differs markedly in its appendages from *N. malcolmi* and *N. aurantiaca,* two species that have very short caudal appendages. *Nesobasis rito* resembles *N. comosa* because the caudal appendages are covered by dense setae, although their shape differs clearly in lateral view: *N. rito* has longer and more slender appendages, and a basal tooth that can be seen in dorsal view (Fig. 2e) which is absent in *N. comosa*. The general body colouration and the cerci resemble also those of *N. heteroneura*, although, in *N. rito*, the cerci are longer, with more pilosity and differ also by the presence of the basal teeth. Furthermore, the blue spots of S8 are not mentioned in the description of *N. heteroneura* or *N. comosa*. The genital ligula in lateral view (Fig. 3a) is similar to that of *N. comosa,* but with the distal segment broader and the lateral lobes more pronounced (compared to Fig. 103, Donnelly, 1990). In ectal view (Fig. 3b) more elongated than the ligula of *N. comosa* and the lateral lobes clearly visible (compared to Fig. 104, Donnelly, 1990). Like *N. heteroneura*, the wings of *N. rito* have a single row of cells distal from the pterostigma but in *N. comosa* wings have mostly double rows of cells (M. Marinov, personal communication).

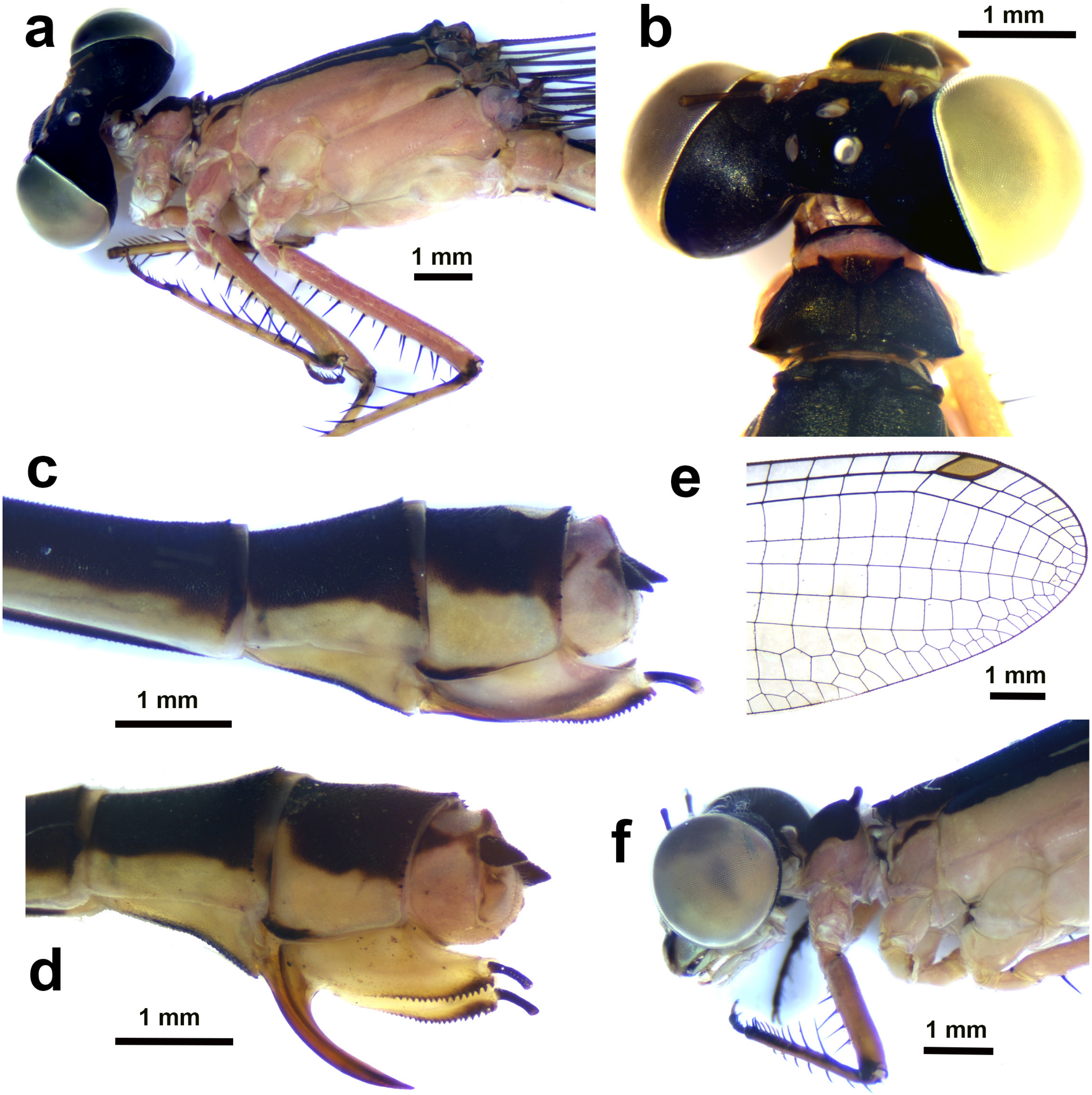

FIGURE 4. *Nesobasis rito* **sp. nov.**, paratype females from Vanua Levu, Fiji; (4a) female 2009-138, lateral view of the head and thorax; (4b) dorsal view of the head and the pronotum; (4c) S7–10 in lateral view; (4e) detail of the left hindwing; (4d) S8–10 of female 2011-205, showing the stylus; (4f), lateral view of the head and prothorax of female 2011-205.

It is of note that specimens of *N. comosa* and *N. heteroneura* resemble one another; while generally *N. comosa* males have more dense setae on their caudal appendages (similar to *N. rito*) and are somewhat more robust, these traits can be variable, making it difficult to resolve *N. comosa* and *N. heteroneura* in some locations. In the phylogenies of Beatty *et al.* (2017), Lorenzo-Carballa *et al.* (2019) and in our genetic results here (Figs. 6 and 7, Table 3), a close relationship between these species is suggested. It is possible that *N. comosa* and *N. heteroneura* represent a species complex; it has been noted that specimens more closely resembling *N. comosa* are found at higher elevation localities, with more characteristic *N. heteroneura* individuals appearing in lower-elevation streams (CDB pers. obs.). Thus, these two species may represent two morphotype extremes along a habitat gradient, a hypothesis that needs further research.

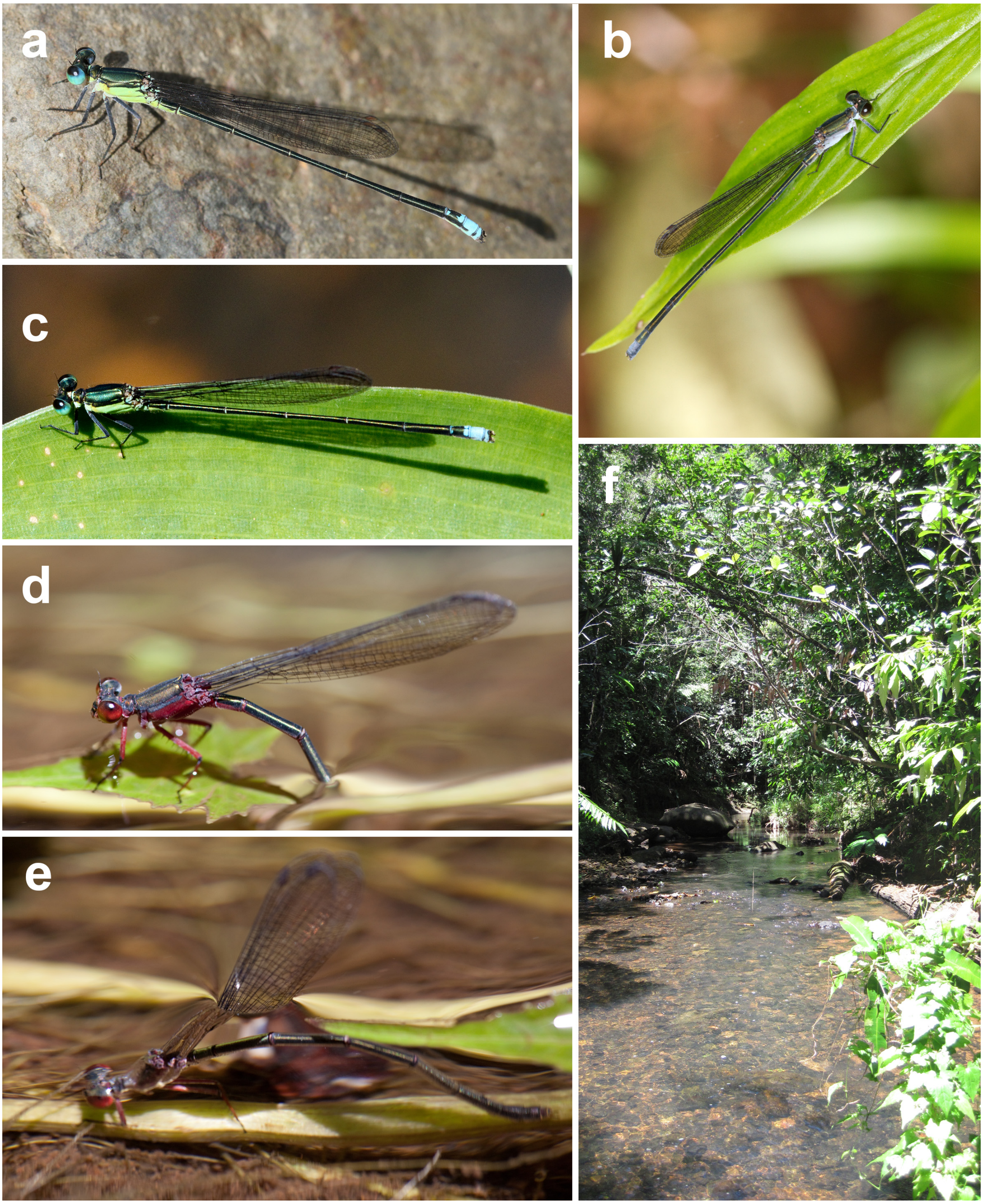

FIGURE 5. Live specimens of *Nesobasis rito* **sp. nov.** and habitat. (5a) A young male from the type locality, Drawa River; (5b) a pruinescent male and a mature male (5c) from Navuturerega creek; (5d–e) a female laying eggs in the Navuturerega creek, a section of which is shown in (5f). Pictures by AC-R.

Habitat and ecology. The species was found in shallow but wide streams (about 4–5 m wetted channel width, Fig. 5f), commonly in shaded areas, with native riparian vegetation, but in the open as well. Males perched both in the vegetation (Fig. 5b, c) and on stones in the middle of the stream (Fig. 5a). Females lay eggs alone and may go underwater to oviposit (Fig. 5d, e).

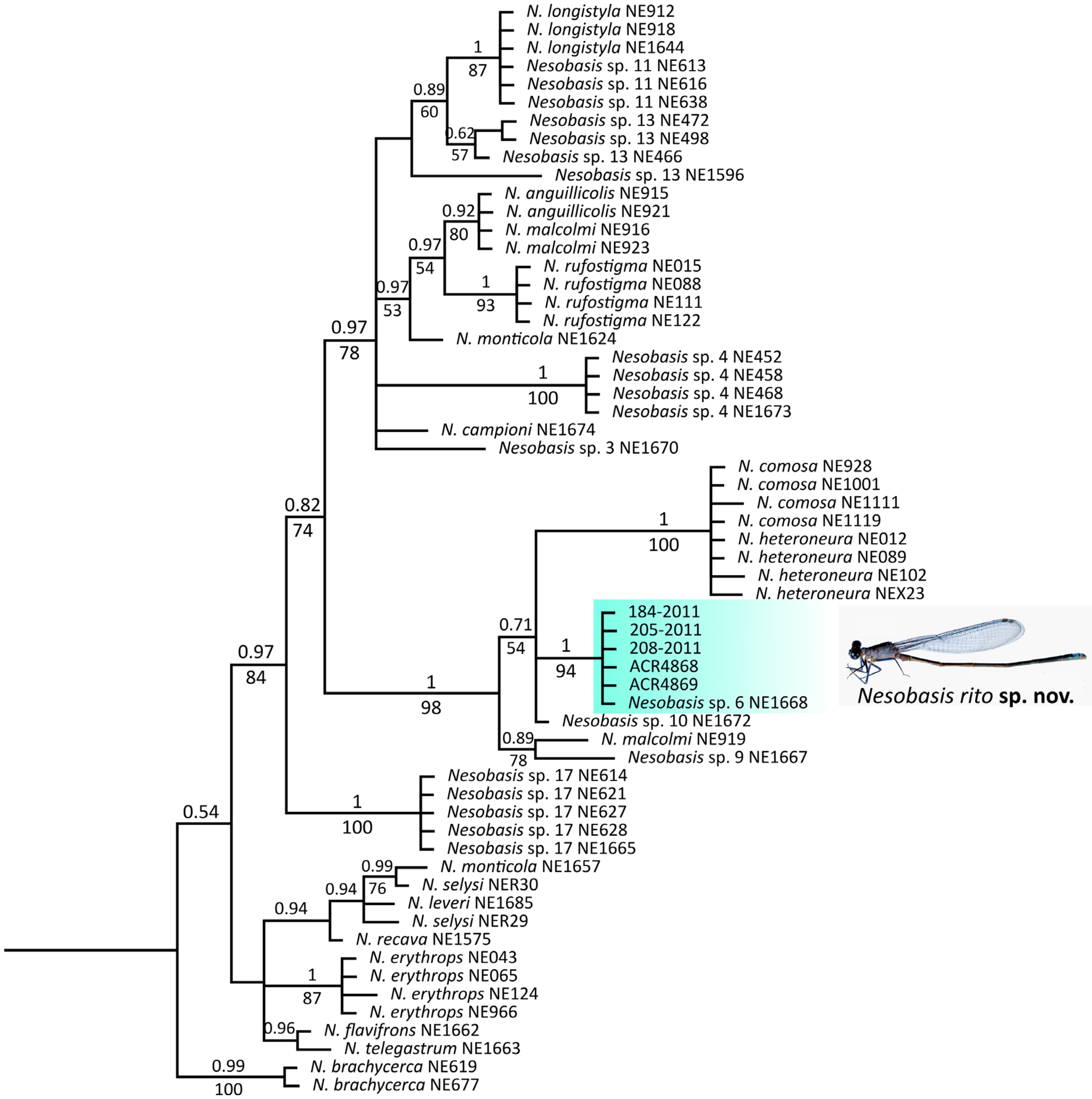

FIGURE 6. Phylogenetic tree representing the relationships among the *Nesobasis* species included in the present study for the PRMT nuclear marker. The tree illustrates the position of *Nesobasis rito* **sp. nov.** within the *comosa* group. Values above/below branches represent BI posterior probability and ML bootstrap support values, respectively. Only bootstrap support values ≥ 50% are shown. *Melanesobasis corniculata* was used as the outgroup in these analyses (see main text and Table 1 for details) but for the purposes of illustration, only the ingroup (i.e. *Nesobasis*) is shown here.

Genetic relationships with other *Nesobasis* species. The genetic analyses showed that, for the nuclear DNA marker, *N. rito* **sp. nov.** appears as a well-supported, monophyletic clade, within the *comosa* group (Figs. 6–7). For the mitochondrial DNA, some discordance with the nuclear DNA phylogeny is observed, regarding the placement of *N. rito* in relation to the clade that includes *N. heteroneura* and *N. comosa* (Fig. 7). These results are likely due to the widespread *Wolbachia* infections that are found within the species of *Nesobasis* (Lorenzo-Carballa *et al.* 2019). Yet, the fact that the specimens of *N. rito* appear in both cases as a well-supported, monophyletic clade, provides strong support for the distinctiveness of these specimens and corroborates the results of the morphological analyses. In agreement with the phylogenetic analyses, the genetic distances between *N. rito* and *N. heteroneura* and *N. comosa* are the lowest for both sequenced markers (Table 3).

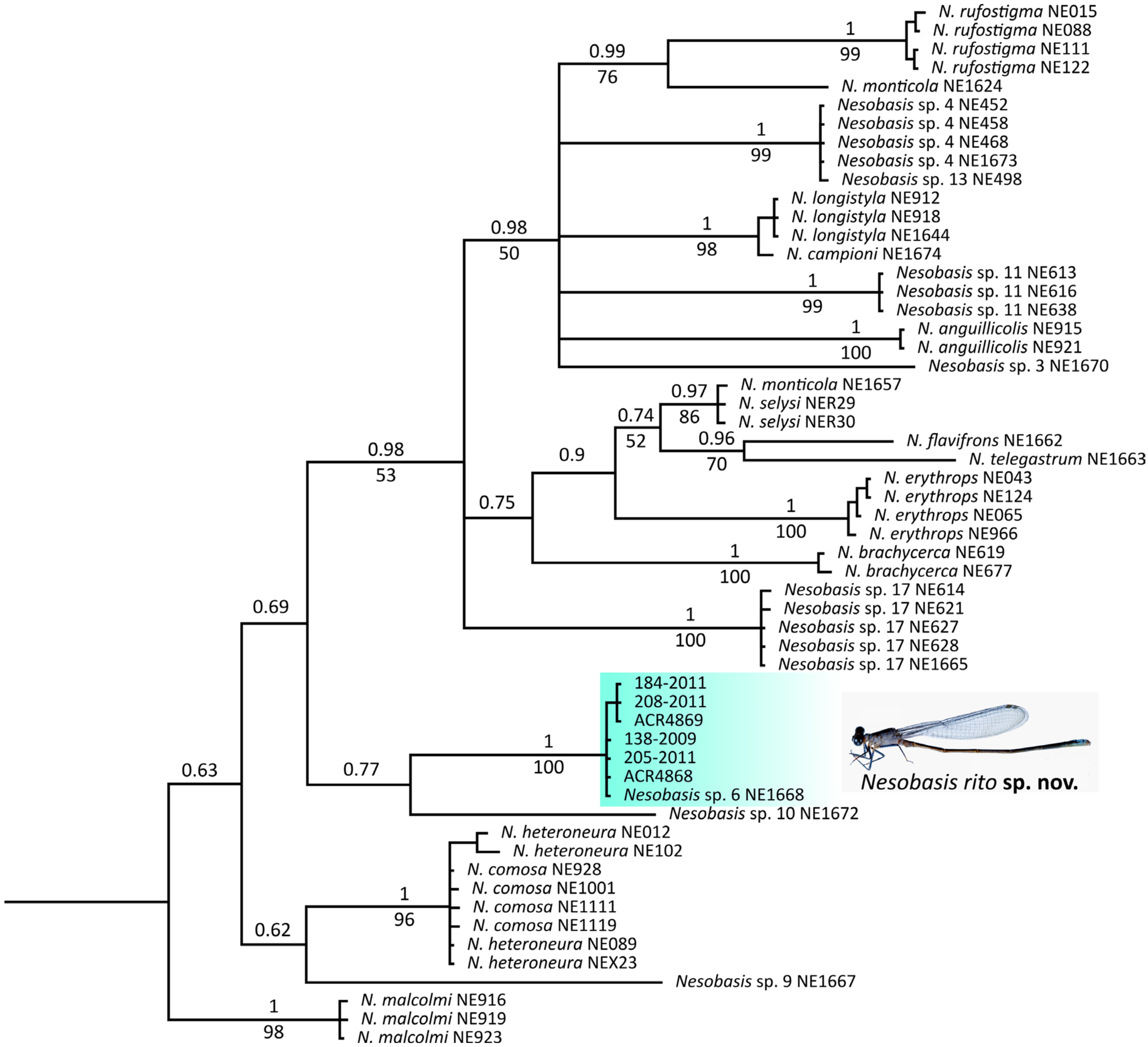

FIGURE 7. Phylogenetic tree representing the relationships among the *Nesobasis* species included in the present study for the COI mitochondrial marker. Values above/below branches represent BI posterior probability and ML bootstrap support values, respectively. Only bootstrap support values ≥ 50% are shown. *Melanesobasis corniculata* was used as the outgroup in these analyses (see main text and Table 1 for details) but, for the purposes of illustration, only the ingroup (i.e. *Nesobasis*) is shown here.

The species previously known as *Nesobasis* sp. nov. 6 and represented in our analyses by a single individual from Lorenzo-Carballa et al. (2019) (voucher ID NE1668; see Table 1), falls within the *N. rito* clade for both nuclear and mitochondrial DNA (Figs. 6–7). Also, the genetic distances between this individual and the specimens of *N. rito* sequenced in the present work are 0 and 0.1% for the nuclear and mitochondrial DNA, respectively, thus indicating that this individual is in fact a representative of *N. rito*. This would correlate to species *N.* sp. nov. 6 in Beatty *et al.* (2017), which is referred to as Uds2 in Beatty *et al*. (2007).

This species description is another step toward documenting the diversity of the genus *Nesobasis* in the Fiji Islands. A number of other congeneric species remain to be described, and the diversity of this group and the factors driving it need to be further explored.

TABLE 3. Estimates of divergence over sequence pairs between the *Nesobasis* species included in this study (uncorrected p-distances), as estimated by MEGA X. The percentage of base differences per site from averaging over all sequence pairs between groups are shown. Values above diagonal correspond to genetic distances estimated from the nuclear DNA dataset, whereas values below diagonal correspond to distances estimated using the mitochondrial DNA dataset; n.a. indicates that no data were available for a particular species/marker

	N. rito	*N. angullicolis*	*N. brachycerca*	*N. campioni*	*N. comosa*	*N. erythrops*	*N. flavifrons*	*N. heteroneura*	*N. leveri*	*N. longistyla*	*N. malcolmi*	*N. monticola*
Nesobasis rito		2.9	3.9	2.7	2.3	3.6	3.2	2.4	4,0	3.1	2.4	3.4
N. angullicolis	15.9		2.5	1.0	4.4	2.6	2.1	4.4	2.9	1.4	1,0	1.8
N. brachycerca	13.1	14.0		2.5	5.3	2.2	1.4	5.3	2.4	2.9	2.9	2.4
N. campioni	13.1	12.2	13.4		4.0	2.1	1.7	4.0	2.5	1.2	1.6	1.7
N. comosa	9.8	15.0	11.9	12.3		5.5	4.7	0.1	5.1	4.6	3.8	4.7
N. erythrops	14.9	14.6	12.8	12.7	13.7		1.0	5.5	1.5	2.8	3.0	2.0
N. flavifrons	14.4	14.5	12.2	13.0	13.7	11.2		4.7	1.2	2.3	2.4	1.7
N. heteroneura	9.7	14.8	12.1	12.5	0.8	13.4	13.7		5.2	4.6	3.8	4.7
N. leveri	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.		3.1	3.2	1.7
N. longistyla	12.9	12.0	13.2	0.6	12.1	13.3	12.8	12.3	n.a.		2,0	2,0
N. malcolmi	10.5	15.5	14.3	13.2	9.8	15.2	13.9	10.0	n.a.	13.0		2.4
N. monticola	14.0	13.7	12.3	11.8	13.2	11.3	9.3	13.3	n.a.	12.0	14.6	
N. recava	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
N. rufostigma	12.8	13.8	13.6	11.4	13.8	14.1	12.8	14.1	n.a.	12.1	15.5	12.1
N. selysi	15.0	13.8	11.0	12.4	12.4	8.2	7.8	12.3	n.a.	12.6	13.9	7.0
Nesobasis sp. 3	14.4	14.3	15.2	12.4	15.3	14.2	13.4	15.7	n.a.	12.6	16.2	14.0
N. sp. 4	13.6	13.7	12.4	12.6	13.9	11.2	12.2	13.4	n.a.	12.4	13.4	12.5
N. sp. 9	12.9	17.2	16.4	14.7	11.0	14.2	13.9	11.4	n.a.	14.5	12.8	14.3
N. sp. 10	10.1	15.5	14.3	14.9	11.3	12.9	13.2	11.1	n.a.	14.7	12.5	12.8
N. sp. 11	16.1	15.5	15.5	13.7	16.1	15.7	14.7	15.9	n.a.	13.9	17.8	13.6
N. sp. 13	13.8	13.4	12.2	12.4	14.1	11.0	12.0	13.6	n.a.	12.2	13.6	12.3
N. sp. 17	14.6	15.8	13.2	12.3	12.4	14.4	12.3	12.6	n.a.	11.6	13.6	12.4
N. sp. 6	0.1	15.8	13.0	13.0	9.7	15.0	14.3	9.6	n.a.	12.8	10.6	13.9
N. telegastrum	14.0	14.3	13.0	13.9	13.8	11.6	9.0	13.5	n.a.	14.1	14.6	11.1

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TABLE 3. (Continued)

	N. recava	*N. rufostigma*	*N. selysi*	*Nesobasis* sp. 3	*N.* sp. 4	*N.* sp. 9	*N.* sp. 10	*N.* sp. 11	*N.* sp. 13	*N.* sp. 17	*N.* sp. 6	*N. telegastrum*
Nesobasis rito	3.5	3.1	4.1	3.3	4.2	1.7	0.6	3.1	2.9	3.3	0,0	3.4
N. angullicolis	2.4	0.8	2.9	1.3	2.6	3.3	2.7	1.5	1.5	2.4	2.8	2.3
N. brachycerca	1.9	2.9	2.3	3.3	4.0	4.2	3.7	3.0	3.0	2.5	3.8	1.7
N. campioni	2.0	1.2	2.5	1.5	2.5	3.1	2.5	1.3	1.2	1.8	2.6	1.9
N. comosa	4.5	4.6	5.3	4.9	5.5	3.1	1.7	4.7	4.5	4.6	2.3	4.8
N. erythrops	1,0	2.8	1.3	3.1	4,0	4.1	3.6	2.8	2.6	2.8	3.5	0.9
N. flavifrons	0.8	2.3	1.2	2.6	3.4	3.5	2.9	2.4	2.1	2.1	3.1	0.2
N. heteroneura	4.6	4.6	5.4	5,0	5.5	3.2	1.8	4.7	4.6	4.6	2.3	4.9
N. leveri	0.4	3.1	0.4	3.4	4,0	4.2	3.7	3.2	2.9	2.9	4,0	1.5
N. longistyla	2.6	1.3	2.9	1.9	2.9	3.6	2.9	0.0	0.9	2.4	3,0	2.3
N. malcolmi	2.8	1.6	3.3	2.0	3.1	2.6	2.1	2.1	2.0	2.7	2.4	2.6
N. monticola	1.4	1.9	1.6	2.5	3.3	3.7	3.2	2.1	2.1	2.5	3.3	1.7
N. recava		2.6	0.4	2.9	3.7	3.6	3.3	2.7	2.3	2.4	3.5	1,0
N. rufostigma	n.a.		3.0	1.9	2.9	3.6	2.9	1.3	1.7	2.4	3.1	2.3
N. selysi	n.a.	14.2		3.5	4.0	4.1	3.8	3.0	2.8	2.8	4,0	1.3
Nesobasis sp. 3	n.a.	14.4	14.2		2.7	3.9	3.2	1.9	1.9	3,0	3.2	2.7
N. sp. 4	n.a.	13.0	12.0	14.5		4.8	4.0	2.9	3.0	3.9	4.1	3.5
N. sp. 9	n.a.	16.1	14.3	15.8	15.1		1.2	3.6	3.3	3.8	1.7	3.3
N. sp. 10	n.a.	13.8	13.0	15.5	13.2	12.8		3.0	2.9	3.1	0.6	3.2
N. sp. 11	n.a.	14.7	14.9	15.3	12.8	15.5	16.6		0.9	2.5	3,0	2.3
N. sp. 13	n.a.	12.8	11.8	14.3	0.2	14.9	13.0	13.0		2.6	2.9	2.2
N. sp. 17	n.a.	13.6	10.8	14.6	13.2	13.9	14.2	15.7	13.0		3.3	2.1
N. sp. 6	n.a.	12.7	14.9	14.3	13.7	13.0	10.1	16.0	13.9	14.5		3.3
N. telegastrum	n.a.	15.0	8.8	13.0	12.2	15.8	11.8	14.7	12.0	13.2	13.9	

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