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A redefinition of the genus *Diplacina* Brauer, 1868, with the establishment of *Papuathemis* gen. nov. (Odonata: Libellulidae)

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Abstract. The genus *Diplacina* as presently recognised consists of a group of 10 species restricted to the Philippines and Sulawesi and another of 18 species found in the Moluccas and New Guinea. Based on both morphological and molecular data, these geographical assemblages are shown to represent two distinct clades, not even closely related, which should be recognised as separate genera. The holotype of *Diplacina*, *D. nana* Brauer 1868, is a Philippine species hence the 10 species from the Philippines and Sulawesi are retained in *Diplacina*. For the Moluccan and New Guinean species, the new genus *Papuathemis* is erected.

Further key words. Dragonfly, Anisoptera, taxonomy, Philippines, Sulawesi, Moluccas, New Guinea

Introduction

The libellulid genus *Diplacina* Brauer, 1868, contains 28 species occurring in the Philippines (7 species), Sulawesi (3), the Moluccas (1), and New Guinea and adjacent islands (17) (Table 1, Figs 1, 2). None of the species has a wide geographic range and many are restricted to a single island. All species are found at running water and are most commonly encountered at streams in forested areas. No other information on behaviour has been published.

Our knowledge of the larvae is limited. Needham & Gyger (1937) describe and illustrate the larva of the Philippine species, *Diplacina braueri* and *D. bolivari* (by supposition). They state that »The nymph also is easily recognizable by having in *D. braueri* at least, lateral spines on segment 7, 8,

and 9 of the abdomen, and not on 8 and 9 only, as in other genera«. However, the larva they describe as *D. bolivari* does not have a lateral spine on S7, making it unclear if this character can be used to recognise all species of the group. The only other description of a *Diplacina* larva is by Lieftinck (1930), who described and figured a larva tentatively determined as the Moluccan *Diplacina phoebe*, but with strong doubts expressed as to its identity. This specimen was later re-identified as *Agrionoptera similis* Selys, 1879 (van Tol 1992), hence the larva is so far undescribed for any species of *Diplacina* occurring in the Moluccas and New Guinea.

The differences between the two geographic divisions of the genus have long been recognised. In a paper on the *Diplacina smaragdina* group, that is, the species from New Guinea, Lieftinck (1953) suggested that the species of this group were sufficiently distinct from those of the Philippines to warrant their own genus. He also suggested that the same might be true for the species of Sulawesi. However, he concluded that »Until the new

Figure 1. *Diplacina bolivari*, Philippines, Aurora province. Photo: VJK (16.ii.2024).

forms in our collection are carefully analysed and described, and the advisability for a breaking up of the genus has been demonstrated or refuted, *smaragdina* and its near relatives are best left as an eastern group within the genus«. When describing new species from Sulawesi, van Tol (1987) discussed the relations between these groups. Based on characters of venation, he suggested that *D. nana* (the type of the genus from the Philippines) was close to the *D. smaragdina* group with the other species from the Philippines and Sulawesi forming a second group. However, while the integrity of genus has long been suspected, until now it has not been subject to critical study.

The need for this was discovered during a preliminary analysis of COI data of Libellulidae, when it was found that the two geographical groups of *Diplacina* were not retrieved as sister taxa, indicating that they should be regarded as separate genera. In order to test this hypothesis, we analysed the genus in more detail based on both molecular and morphological data.

Figure 2. *Papuathemis phoebe*, Indonesia, Halmahera. Photo: Erland Refling Nielsen (iv.2017).

Table 1. List of species hitherto considered belonging to the genus *Diplacina* with information on their distribution and the proposed new combinations.

Current name	New name	Distribution
Diplacina anthaxia Lieftinck, 1933	*Papuathemis anthaxia* (Lieftinck, 1933)	New Guinea
Diplacina antigone Lieftinck, 1933	*Papuathemis antigone* (Lieftinck, 1933)	New Guinea
Diplacina arsinoe Lieftinck, 1953	*Papuathemis arsinoe* (Lieftinck, 1953)	New Guinea
Diplacina bolivari Selys, 1882	*Diplacina bolivari* Selys, 1882	Philippines
Diplacina braueri Selys, 1882	*Diplacina braueri* Selys, 1882	Philippines
Diplacina callirrhoe Lieftinck, 1953	*Papuathemis callirrhoe* (Lieftinck, 1953)	New Guinea
Diplacina clymene Lieftinck, 1963	*Papuathemis clymene* (Lieftinck, 1963)	New Guinea
Diplacina cyrene Lieftinck, 1953	*Papuathemis cyrene* (Lieftinck, 1953)	New Guinea
Diplacina dioxippe Lieftinck, 1963	*Papuathemis dioxippe* (Lieftinck, 1963)	New Guinea
Diplacina erigone Lieftinck, 1953	*Papuathemis erigone* (Lieftinck, 1953)	New Guinea
Diplacina fulgens Ris, 1898	*Papuathemis fulgens* (Ris, 1898)	New Guinea
Diplacina guentherpetersi Villanueva, 2012	*Diplacina guentherpetersi* Villanueva, 2012	Philippines
Diplacina hippolyte Lieftinck, 1933	*Papuathemis hippolyte* (Lieftinck, 1933)	New Guinea
Diplacina holgerhungeri Villanueva, 2012	*Diplacina holgerhungeri* Villanueva, 2012	Philippines
Diplacina ismene Lieftinck, 1933	*Papuathemis ismene* (Lieftinck, 1933)	New Guinea
Diplacina lisa Needham & Gyger, 1941	*Diplacina lisa* Needham & Gyger, 1941	Philippines
Diplacina merope Lieftinck, 1963	*Papuathemis merope* (Lieftinck, 1963)	New Guinea
Diplacina micans Lieftinck, 1953	*Papuathemis micans* (Lieftinck, 1953)	New Guinea
Diplacina militaris Ris, 1909	*Diplacina militaris* Ris, 1909	Sulawesi
Diplacina militaris Ris, 1909	*Diplacina paragua* Villanueva, 2012	Philippines

Current name	New name	Distribution
Diplacina nana Brauer, 1868	*Diplacina nana* Brauer, 1868	Philippines
Diplacina olahi Theischinger & Kovács, 2015	*Papuathemis olahi* (Theischinger & Kovács, 2015)	New Guinea
Diplacina paula Ris, 1919	*Papuathemis paula* (Ris, 1919)	New Guinea
Diplacina persephone Lieftinck, 1933	*Papuathemis persephone* (Lieftinck, 1933)	New Guinea
Diplacina phoebe Ris, 1919	*Papuathemis phoebe* (Ris, 1919)	Moluccas
Diplacina sanguinolenta van Tol, 1987	*Diplacina sanguinolenta* van Tol, 1987	Sulawesi
Diplacina smaragdina Selys, 1878	*Papuathemis smaragdina* (Selys, 1878)	New Guinea
Diplacina torrenticola van Tol, 1987	*Diplacina torrenticola* van Tol, 1987	Sulawesi

Methods

Molecular analyses

For the molecular phylogenetic analysis, the animal barcode fragment of the mitochondrial cytochrome c oxidase subunit I (COI) gene was used.

A total of 41 sequences was obtained from the Barcode of Life Data System (BOLD) and the COI-library of Naturalis Biodiversity Center (see Table 2 for BOLD ID numbers). In addition to *Diplacina*, these include samples of the genera *Nesciothemis*, *Rhyothemis*, *Nannophya*, and *Phyllomacromia*. Our dataset includes eight species of *Diplacina*; three from New Guinea, three from the Philippines, and two from Sulawesi.

Wherever possible, complete sequences of 658 base pairs long without ambiguity were used. However, this was not possible for *Diplacina braueri* as only one complete sequence was available, which contained one nucleotide of ambiguity. This sequence is included in the analysis as well. For the sister taxa, three sequences per species stored by Naturalis Biodiversity Center were used; these include *Rhyothemis phyllis* (Sulzer, 1776), *Nesciothemis farinosa* (Förster, 1898), and *Nannophya dalei* (Tillyard, 1908). For the outgroup, *Phyllomacromia overlaeti* (Schouteden, 1934), only one sequence was available.

All sequences were aligned using MAFFT (Katoh *et al.* 2019). Mesquite was used to determine the codon position of the base pairs. For the phylogeny, both a Bayesian analysis and a Maximum Likelihood estimation were used.

Table 2. Sequenced material, obtained from the Barcode of Life Data System (BOLD) and the COI-library of Naturalis Biodiversity Center (RMNH), used for molecular analyses in this study.

Genus	New placement	Species/ ssp.	Origin	Sample ID Bold	Source/ Bold process ID (Sequence page)
Rhyothemis		*phyllis*	Philippines	RMNH.INS.509579	ODOBP7037-16
Rhyothemis		*phyllis*	Myanmar	CCDB-32138-H10	SICOB1424-18
Rhyothemis		*phyllis*	Pakistan	NIBGE ODO-00301	MAODO301-12
Nesciothemis		*farinosa*	Angola	RMNH.INS.508304	ODOBP6091-16
Nesciothemis		*farinosa*	DR of the Congo	RMNH.INS.505419	ODOBP3091-16
Nesciothemis		*farinosa*	South Africa	RMNH.5008145	ODOBP227-16
Nannophya		*dalei*	Australia	RMNH.INS.505228	ODOBP2932-16
Nannophya		*dalei*	Australia	RMNH.INS.505226	ODOBP2930-16
Nannophya		*dalei*	Australia	RMNH.INS.504877	ODOBP2801-16
Phyllomacromia		*overlaeti*	Cameroon	RMNH.INS.500171	ODOBP7807-16
Diplacina		*bolivari*	Philippines	RMNH.INS.506532	ODOBP3941-16
Diplacina		*bolivari*	Philippines	RMNH.INS.509535	ODOBP6994-16
Diplacina		*bolivari*	Philippines	RMNH.INS.509436	ODOBP6896-16
Diplacina		*bolivari*	Philippines	RMNH.INS.509459	ODOBP6918-16
Diplacina		*bolivari*	Philippines	RMNH.INS.506585	ODOBP3988-16
Diplacina		*bolivari*	Philippines	RMNH.INS.506538	ODOBP3947-16
Diplacina		*braueri*	Philippines	RMNH.INS.506639	ODOBP4036-16
Diplacina		*braueri*	Philippines	RMNH.INS.509536	ODOBP6995-16
Diplacina		*braueri*	Philippines	RMNH.INS.506529	ODOBP3938-16
Diplacina		*braueri*	Philippines	RMNH.INS.506544	ODOBP3952-16
Diplacina	*Papuathemis*	*dioxippe*	Indonesia	RMNH.INS.500633	ODOBP8045-16
Diplacina	*Papuathemis*	*dioxippe*	Indonesia	RMNH.INS.500536	ODOBP7966-16
Diplacina	*Papuathemis*	*ismene*	Indonesia	RMNH.INS.500586	ODOBP8007-16
Diplacina	*Papuathemis*	*ismene*	Indonesia	RMNH.INS.500585	ODOBP8006-16
Diplacina	*Papuathemis*	*ismene*	Indonesia	RMNH.INS.500584	ODOBP8005-16
Diplacina	*Papuathemis*	*ismene*	Indonesia	RMNH.INS.500583	ODOBP8004-16
Diplacina		*militaris*	Indonesia	RMNH.INS.557575	ODOBP4607-16
Diplacina		*militaris*	Indonesia	RMNH.INS.557582	ODOBP4614-16
Diplacina		*militaris*	Indonesia	RMNH.INS.557540	ODOBP4572-16
Diplacina		*militaris*	Indonesia	RMNH.INS.557563	ODOBP4595-16
Diplacina		*militaris dumogae*	Indonesia	RMNH.INS.509744	ODOBP4251-16
Diplacina		*militaris dumogae*	Indonesia	RMNH.INS.509718	ODOBP4226-16
Diplacina		*militaris dumogae*	Indonesia	RMNH.INS.509716	ODOBP4224-16
Diplacina		*nana*	Philippines	RMNH.INS.509537	ODOBP6996-16

Genus	New placement	Species/ ssp.	Origin	Sample ID Bold	Source/ Bold process ID (Sequence page)
Diplacina		*nana*	Philippines	RMNH.INS.509487	ODOBP6946-16
Diplacina		*nana*	Philippines	RMNH.INS.506667	ODOBP4064-16
Diplacina	*Papuathemis*	*smaragdina*	Indonesia	RMNH.INS.500617	ODOBP8032-16
Diplacina	*Papuathemis*	*smaragdina*	Indonesia	RMNH.INS.500535	ODOBP7965-16
Diplacina		*torrenticola*	Indonesia	RMNH.INS.509760	ODOBP4267-16
Diplacina		*torrenticola*	Indonesia	RMNH.INS.509759	ODOBP4266-16
Diplacina		*torrenticola*	Indonesia	RMNH.INS.509727	ODOBP4235-16

For the inference of a Maximum Likelihood phylogeny, the IQ-tree web server (Nguyen *et al.* 2015), which applied thousand generations of Ultrafast Bootstrap (Hoang *et al.* 2018), was used. Besides this, IQ-tree was used to find the best fitting evolutionary models (Kalyaanamoorthy *et al.* 2017) for the partitions (Chernomor *et al.* 2016) – in this case the three different codon positions. The evolutionary models used were HKY for codon position 1, TIM3 for codon position 2, and F81 for codon position 3.

MrBayes 3.2.7a (Ronquist *et al.* 2012) was used for the inference of a Bayesian phylogeny. Since the evolutionary models provided by IQ-Tree are not implemented in MrBayes 3.2.7a (Ronquist *et al.* 2012), they were translated: nst=2 rates=gamma for codon position 1, nst=6 rates=gamma for codon position 2, and nst=1 rates=equal for codon position 3. The analysis consisted of two runs of four independent chains for 10 million generations with a sample frequency of 1 000. The Bayesian analysis creates a posterior probability which is interpreted as a probability that the topology is accurate when comparing it to the existing data (Huelsenbeck *et al.* 2001). The analysis was carried out through the CIPRES gateway to quicken the process (Miller *et al.* 2010).

The convergence was examined in Tracer v1.2.7 (Rambaut *et al.* 2018), by checking if the effective sample size (ESS) was above 200 for all parameters after a burn-in of 10 %. Additionally, the standard deviation of split frequencies was checked to be lower than 0.01. FigTree 1.4.4 was used to visualise both the Bayesian and Maximum Likelihood phylogenies. Since IQ-Tree gives unrooted phylogenies, the Maximum Likelihood phylogeny was manually rooted in *Phyllomacromia overlaeti*.

Morphological analyses

We first made a preliminary study of the specimens of *Diplacina* available at Naturalis Biodiversity Center, Leiden, The Netherlands. Based on this, we constructed a list of characters that seemed to differ between the Philippine-Sulawesi group and the Molucca-Papuan group. With this list we scored the character states of the species, using collection material or based on the description in literature (Lieftinck 1933, 1953, 1963; Villanueva 2012; Theischinger & Kovács 2015). When possible, each character was scored on five specimens of each sex. The following characters were scored (*cf*. Table 3):

C1 – Frons with green metallic sheen
C2 – Synthorax with green metallic sheen
C3 – Front of synthorax with yellow humeral stripes
C4 – Male: hind wing base with dark spot
C5 – Male: abdominal segments 3–4 with a thin mid-dorsal yellow line
C6 – Male: abdominal segments 4–8 with extensive lateral yellow to yellow-red marks
C7 – Male: base of abdomen in with red pattern
C8 – Triangle in fore wing with cross-vein
C9 – Triangle in hind wing with cross-vein
C10 – Supratriangle in fore wing with cross-vein

Results

Neither the Bayesian nor the Maximum Likelihood phylogenies retrieved *Diplacina* as a monophyletic group (Figs 3, 4). Rather, *Diplacina* sequences split into two groups with representatives of other distant genera in between. The five species from the Philippines and Sulawesi form one cluster (Posterior Probability (PP) = 99 and Ultrafast Bootstrap (UFB) = 83) and the three species from New Guinea the other cluster (PP = 100 and UFB = 98).

Table 3 summarises the morphological character states. Where appropriate, we merged the character states for males and females as these were largely identical in the two sexes. Most characters were found to be clearly different between the Philippine-Sulawesi group (Fig. 1) and the Molucca-Papuan group (Fig. 2). Males of most species of the Philippine-Sulawesi group have yellow lateral marks on S4–S8 but these were absent in some

species. However, it could be that the yellow marks are present in these species earlier in their adult lives with the yellow becoming obscured as they age. All species of the Philippine-Sulawesi group have a reddish base of the abdomen except for *D. torrenticola*. Characters 8–10 (triangle in hind and fore wing and supratriangle in fore wing with cross-vein) also clearly differ between the two groups. However, in two species of the Philippine-Sulawesi group (*D. lisa* and *D. nana*) the cross-vein in the triangle and supratriangle can be either absent or present.

The shape of the secondary genitalia was not scored as character states are often difficult to define. The shape of the hamule has the same general form in all species considered. However, it was noted that in all Philippine and Sulawesi species the anterior lamina is small and lower than the hamule, while the genital lobe is well-developed (Fig. 5). In New Guinean and Moluccan species, the situation is exactly opposite, with a small and barely developed genital lobe and a large anterior lamina (Fig. 6). The females of

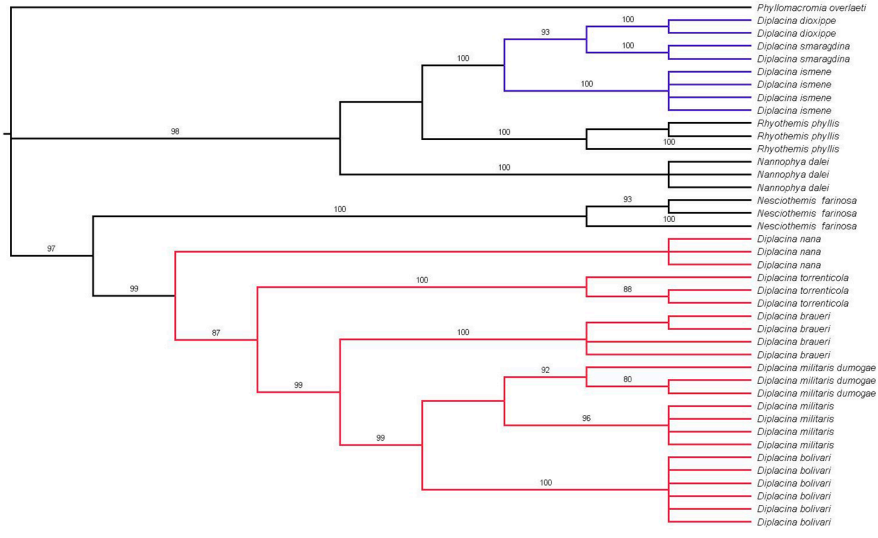

Figure 3. Phylogenetic reconstruction of the Bayesian Analysis of the COI gene. The Posterior Probabilities are shown when above 70. The Papuan *Diplacina* species (here reassigned to *Papuathemis*) are shown in blue; the Philippine-Sulawesi *Diplacina* species are shown in red.

two species, *D. sanguinolenta* and *D. torrenticola*, were found to have large and well-developed flaps at the side of S8 whereas in all other species these were small to absent.

Conclusion

The molecular data demonstrates that the species of *Diplacina* from the Moluccas and New Guinea included in our analyses are not closely related to those of Sulawesi and the Philippines. This is supported by morphological data allowing us to show that the division applies also to the species not included in our molecular analyses. Based on these results, we propose to

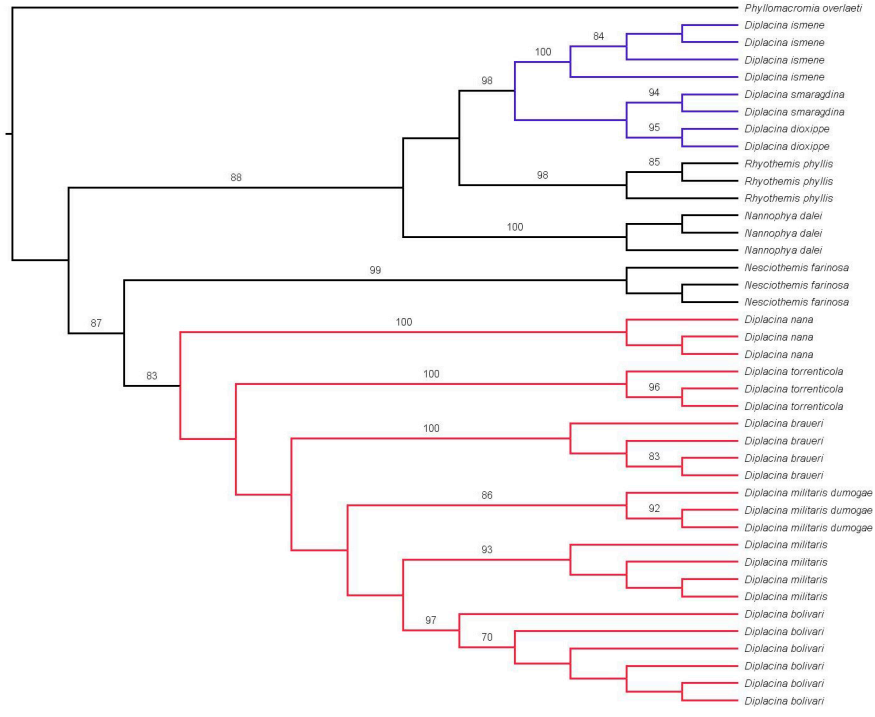

Figure 4. Phylogenetic reconstruction of the Maximum Likelihood analysis of the COI gene. The Ultrafast Bootstrap values are shown when above 70. The Papuan *Diplacina* species (here reassigned to *Papuathemis*) are shown in blue; the Philippine-Sulawesi *Diplacina* species are shown in red.

Table 3. List of *Diplacina* and *Papuathemis* species and their origin, showing the scored character states for morphological analysis (C1–C10; for definition, see text). + – character present, +/- – character partly present.

	C1	C2	C3	C4	C5	C6	C7	C8	C9	C10
Moluccas										
Papuathemis phoebe (Ris, 1919)	+	+			+					
New Guinea										
Papuathemis anthaxia (Lieftinck, 1933)	+	+			+					
Papuathemis antigone (Lieftinck, 1933)	+	+			+					
Papuathemis arsinoe (Lieftinck, 1953)	+	+			+					
Papuathemis callirrhoe (Lieftinck, 1953)	+	+			+					
Papuathemis clymene (Lieftinck, 1963)	+	+			+					
Papuathemis cyrene (Lieftinck, 1953)	+	+			+					
Papuathemis dioxippe (Lieftinck, 1963)	+	+			+					
Papuathemis erigone (Lieftinck, 1953)	+	+			+					
Papuathemis fulgens (Ris, 1898)	+	+			+					
Papuathemis hippolyte (Lieftinck, 1933)	+	+			+					
Papuathemis ismene (Lieftinck, 1933)	+	+			+					
Papuathemis merope (Lieftinck, 1963)	+	+			+					
Papuathemis micans (Lieftinck, 1953)	+	+			+					
Papuathemis olahi (Theischinger & Kovács, 2015)	+	+			+					
Papuathemis paula (Ris, 1919)	+	+			+					
Papuathemis persephone (Lieftinck, 1933)	+	+			+					
Papuathemis smaragdina (Selys, 1878)	+	+			+					
Philippines										
Diplacina bolivari Selys, 1882			+	+		+	+	+	+	+
Diplacina braueri Selys, 1882			+			+	+	+	+	+
Diplacina guentherpetersi Villanueva, 2012			+	+			+	+	+	+
Diplacina holgerhungeri Villanueva, 2012			+	+			+	+	+	+
Diplacina lisa Needham & Gyger, 1941			+				+		+	+/-
Diplacina nana Brauer, 1868			+			+	+			+/-
Diplacina paragua Villanueva, 2012			+	+			+	+	+	+
Sulawesi										
Diplacina militaris Ris, 1909			+	+		+/-	+	+	+	+
Diplacina sanguinolenta van Tol, 1987			+	+			+	+	+	+
Diplacina torrenticola van Tol, 1987			+	+		+		+	+	+

split the genus. *Diplacina nana*, the type species of the genus, is from the Philippines so that the genus *Diplacina* is restricted to the ten species occurring in Sulawesi and the Philippines. For the 18 species from the Moluccas and New Guinea we erect the new genus *Papuathemis*.

***Papuathemis* gen. nov.**

Type species: *Diplacina smaragdina* Selys, 1878, by present designation.

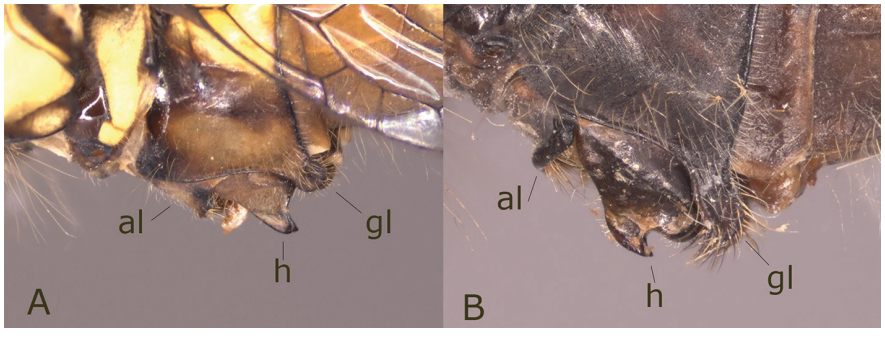

Figure 5. Secondary genitalia of (a) *Diplacina nana* and (b) *D. militaris* showing the relatively small anterior lamina (lower than the hamule) and the well-developed genital lobe. al – anterior lamina; h – hamule; gl – genital lobe.

Figure 6. Secondary genitalia of (a) *Papuathemis smaragdina* and (b) *P. phoebe* showing the small and barely developed genital lobe and a large anterior lamina. al – anterior lamina; h – hamule; gl – genital lobe.

Etymology. A combination of Papua, referring to the main distribution of the genus and -themis, an often used suffix for genera of the family Libellulidae, derived from the name of the Greek goddess of justice, law, custom, order, truth, and wisdom.

Diagnosis. Small and slender libellulids with relatively long legs. Frons with (often bright) green metallic sheen. Thorax dark with a metallic green gloss and a yellow pattern. Front of thorax without ante-humeral stripes but with the mid-dorsal line yellow and in many species a humeral yellow mark. Side of thorax with an extensive yellow pattern in most species, which is often rather irregular (see Michalski 2012; Orr & Kalkman 2015). Abdomen dark with or without a yellow mid-dorsal pattern; in most species the yellow pattern is more prominent on S7 forming a yellow mark. Body never with red or blue markings. Genital lobe small and weakly developed. Anterior lamina large and about as high as the hamule (Fig. 6). Fore wing with 11–12 antenodal cross-veins; triangle and supertriangle in both Fw and Hw without cross-vein; pterostigma uniform dark brown to black. Anal appendages dark, with upper appendages of simple shape; lower appendage in many species widened at tip and bifid. All species of modest size, abdomen with appendages 18–24 mm, hind wing 21–30 mm.

Identification. The species of this genus are all relatively uniform and identification is largely based on pattern on the head and thorax, the shape of the anal appendages, and the secondary genitalia. Most species have been (re)described by Lieftinck (1933, 1953, 1963) who provided good drawings of the key characters but nonetheless identification is not always easy. The key presented by Michalski (2012) contains all species with the exception of *Papuathemis olahi* (Theischinger & Kovács, 2015), while Orr & Kalkman (2015) provide diagnostic drawings of all species occurring on the main island of New Guinea, again excepting the then unknown *P. olahi*.

Distribution, habitat, and behaviour of *Papuathemis*

Table 1 presents the known distribution of *Diplacina* and *Papuathemis*. *Diplacina* is known from seven species in the Philippines and three species on Sulawesi, while *Papuathemis* has 17 species in New Guinea and adjacent

islands and one species occurring in the Moluccas. Species of *Papuathemis* are found at exposed brooks and rivers in forest environments, being absent from largely shaded brooks and seemingly preferring streams with a swift current and a rocky substrate. Individuals, mostly males, sit on stones or vegetation near the water. Detailed information on territoriality, mating behaviour, and oviposition is not available. It is likely that undescribed species remain to be found.

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