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Milen Marinov

A taxonomic and biogeographic discussion on *Rhyothemis regia* (Brauer, 1867) from Samoa and neighbouring islands with introduction of *Rhyothemis regia uveae* subsp. nov. (Odonata: Libellulidae)

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Milen Marinov, Régis Krieg-Jacquier, Jean-Marc Duvernay, Günther Fleck, Joëlle Vincent-Gorlier, Nathalie Mary, Crile Doscher, Florian Le Bail, Hervé Jourdan & Jörn Theuerkauf

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A taxonomic and biogeographic discussion on *Rhyothemis regia* (Brauer, 1867) from Samoa and neighbouring islands with introduction of *Rhyothemis regia uveae* subsp. nov. (Odonata: Libellulidae)

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Abstract

Records of *Rhyothemis regia* (Brauer, 1867) from its eastern distribution range (Swains Island excluded) are reviewed and specimens compared morphologically and by wing colouration to congeners of newly obtained material collected in the field or deposited in entomological collections. The origin of the female holotype of *R. r. chalcoptilon* (Brauer, 1867) has been investigated with new hypotheses of the collector, locality and the probable sampling dates proposed. The holotype was probably mislabelled as from Samoa, while the most likely type locality was Niuafo'ou Island, Tonga. New nomenclature changes are suggested which: assigns *R. r. chalcoptilon* to the population from Niuafo'ou Island, reinstates *R. r. armstrongi* Fraser, 1956 for individuals from Samoan archipelago and introduces a new nomen *R. r. uveae* subsp. nov. for Wallis Island. Biogeography of the species within the investigated area is reviewed and the possible origin of current populations hypothesised. Future hypotheses testing is necessary involving a larger sample size from within the entire species range and comparing them morphologically and molecular to other congeneric from the region, such as *R. phyllis* (Sulzer, 1776) and *R. princeps* Kirby, 1894. The latter two species are briefly discussed in relation to the working hypotheses but due to lack of sufficient material final conclusions are not proposed.

Key words: *Rhyothemis*, new subspecies, Samoa, Wallis, Niuafo'ou, biogeography, Vitiaz Trench

Introduction

Brauer (1867a) established two new species named *Celithemis regia* (type locality Ambon Island, Indonesia) and *Celithemis chalcoptilon* (type locality Samoa). He commented that both were very similar (with the latter having wings widened distally), however, he did not consider them conspecific. No further diagnosis of the two were provided other than a note on the darker wings of *C. chalcoptilon*. Brauer (1867c) transferred both species to *Rhyothemis* Hagen, 1867. Kirby (1894) introduced a new species, *R. princeps* for the dark winged populations in Queensland, Australia and commented that they were 'Probably allied to *R. regia* and *chalcoptilon*, Brauer.' However, no diagnosis was included to differentiate among the three.

This obstacle in the species identification was partly solved by Ris (1909-1919) who reviewed all specimens involved in previous studies, provided synonymic lists, identification keys and established a new subspecies *R. r. exul* Ris, 1913 (type locality Kei Islands, Indonesia). The latter is not considered in my discussions below as its distribution is out of the scope of the present study. Ris (1909-1919) considered holotype specimens of *R. regia* and *R. chalcoptilon* conspecific. He selected *R. regia* as the species nomen (introduced one page before *C. chalcoptiolon* in Brauer 1867a) and kept them as separate subspecies. *Rhyothemis princeps* was included in synonymy of *R. r. chalcoptilon* because of the great similarity in wing patterns which Ris (1909-1919) found almost indistinguishable. The slight widening of the distal part of the fore wings was again noted as the only possible difference between the two. The female holotype of *R. r. chalcoptilon* was the only specimen known from Samoa. The synonymy adopted by Ris (1909-1919) made for a very disjunct distribution of the *R. r. chalcoptilon* – Australia and Samoa with more than a 4,000 km gap in between.

This distribution was briefly mentioned in two studies on the Samoan Odonata by Fraser (1925, 1927). The latter commented that *R. r. chalcoptilon* was never recovered (or even seen in flight!) in the collections consequently made on the Samoan islands. Fraser (1927) had received collections (number not specified) since 1922 made by Dr J.S. Armstrong, Dr P.A. Buxton, Mr. G.H.E. Hopkins, Mr. E.H. Bryan and others. Therefore, Fraser (1927) assumed, following a suggestion by Buxton, that the holotype specimen of *R. r. chalcoptilon*, preserved at the Hamburg Museum, may have been mislabelled as to locality and probably collected from another Pacific island. Another specimen deposited in the British Museum and labelled as ‘type’ may refer to Kirby’s holotype of *R. princeps* which nomen at the time was still considered as a synonym of *R. r. chalcoptilon* (Fraser 1927: 40). In the same study Fraser suggested that the Samoan populations were consubspecific to the Indonesian *R. r. exul*. Such a distribution was used as an evidence of the migratory nature of *R. regia* with two subspecies having highly disjunct distributions – Australia and Indonesian islands north of Australia at one end and Samoa at the opposite. No populations were known in between these two extremes, which is a remarkable phenomenon not discussed by Fraser (1927).

The taxonomic debate on Australian, Papuan and Pacific *Rhyothemis* populations was further elaborated in number of studies published in Lieftinck (1926, 1936, 1942, 1948, 1949, 1953a-b, 1959, 1962). These comprehensive studies are not pertinent here as they include discussions on specimens collected outside of the area of the scope of this paper. A short summary of the most important points is only provided as follows.

Lieftinck (1942) removed *R. princeps* from the synonymy with *R. r. chalcoptilon*. Both were compared and diagnostic traits proposed based on morphology and colour (Lieftinck 1942: 513). No specific trait was given as the most significant diagnostic character but most probably the colouration of the face was considered as the most important: predominantly black in *R. regia* and yellow to orange-red in *R. princeps*. Under his account for *R. r. chalcoptilon*, Lieftinck (1942) admitted that he had not seen this subspecies but had asked Mr. O. H. Swezey, of the Experiment Station, Honolulu (entomology collection now transferred to the Hawaii State Department of Agriculture; D. Polhemus, per. comm.) to check the colour of the face of Samoan specimens preserved in their collection.

Swezy noted that "… vertex and frons shining purplish-black, the postclypeus, labrum and labium are shining black, and the other parts dull brownish …" which Lieftinck justified in assigning Samoan populations to *R. r. chalcoptilon* thus reinstating this subspecies as endemic to Samoa as was previously stated. Lieftinck (1942) further pointed out errors made by Ris (1909-1919) in assigning specimens of *R. princeps* to *R. r. chalcoptilon* and by Fraser (1927) naming Samoan populations as *R. r. exul*. Lieftinck (1942) again noted the highly disjunct distribution and accepted probable wind and migratory dispersal to explain it with centre of origin in the Moluccas whence dispersing as far east as Samoa.

Lieftinck (1948: 303; plate 10) illustrated the wings and provided a distribution map of *R. regia* (1948: 300; fig. 8) from the Malay Archipelago. His study noted the distribution of the species extending as far east as Wallis and Samoa. His review dealt only with species, not subspecies. *Rhyothemis regia* was considered almost without exception insular, '… a species with well-isolated insular populations …', with an '… astonishing ecological plasticity …' and able to overcome geographic barriers, therefore producing some hybrids at contact points between populations. Currency was again given to chance dispersal by air currents and colonisation of the new habitats combined with a lack of competitors at new localities.

The same view was again supported by Lieftinck (1953b) where he provided an overview of the known distribution, ecology and behaviour of the congeners *R. regia* and *R. phyllis*. The most important conclusions for the Lieftinck (1953b) study concerns discussions on status of the populations at the easternmost ends of the ranges for both species. Author argued that both of them are polymorphic 'in a phase of vigorous evolution' with *R. phyllis*, being more advanced and stabilized, was able to occupy the majority of suitable habitats, thus forcing the evolutionary younger *R. regia* to inhabit smaller islands where *R. phyllis* could not reach. Therefore, *R. regia*, although having greater abilities to overcome large oceanic barriers, failed in extending its range due to existing habitats already occupied by *R. phyllis*. Lieftinck (1953b) believed the two species were mutually exclusive with no proof that they actually occur in the same locality. *Rhyothemis r. chalcoptilon* was kept as for the inhabitants of Samoa.

The taxonomic discussion was further exacerbated when Fraser (1956) questioned again the authenticity of the type locality of *R. r. chalcoptilon*. He mentioned that Dr Armstrong, his main collector from Samoa, failed to find specimens of wing colouration matching the holotype of *R. r. chalcoptilon* even after his 30-year stay on Samoan islands between 1921 – 1925 and for another three years from 1950 (Corbet 1978). Fraser (1956) decided that the holotype of *R. r. chalcoptilon* was really mislabelled as to locality and that it probably hailed from Australia, making its distribution in Samoa unsubstantiated. He also restored the synonymy of *R. princeps* to *R. r. chalcoptilon*, elevated it to species rank *R. chalcoptilon* (no rationale for this decision proposed), and considered it confined to Australia thus leaving the Samoan populations without a subspecific nomen. Fraser (1956) assigned the nomen *R. r. armstrongi* to Samoan individuals and included a synonymy for other combinations proposed by earlier authors. His study included illustration of the wing colour of both sexes and a diagnosis, but no designation of a holotype. This was rectified by Kimmins (1966) who assigned a lectotype to *R. r. armstrongi* using one of the specimens identified as *R. r. exul* in Fraser (1927).

Lieftinck (1959) disagreed with this view arguing that Fraser (1956) failed to recognise the distinguishing features proposed by Lieftinck (1942) for differentiation between *R. princeps* and *R. regia*. These were again considered separate species with the former being a 'slow wanderer' confined to Australia-Papuan region and less differentiated, whereas the latter had been very successful in colonising a wide range from Sumatra to Samoa, being predominantly an insular species which had diversified into a number of subspecies and forms with 'almost boundless' variations in the wing pattern. He hypothesised that the holotype of *R. r. chalcoptilon* was properly labelled as to locality (Samoa) and the subspecies exists in two colour forms – a dark-winged (coloration of the holotype) and light-winged, which is the commonest one on the island. His conclusion was based on the fact that females of subspecies from other areas are also bichoromatic with andro- and hetero- forms previously described in the literature (e.g. *R. r. exul* in Ris 1909-1919). Lieftinck argued that he had examined other dark-winged specimens he considered as consubspecific of *R. r. chalcoptilon* collected from neighbouring islands, such as Wallis Island (which he erroneously claimed as being only 17 miles [28km] from Samoa, where it is more than 300 miles [480km] away). Differences in wing pattern were observed in specimens with: Wallis having wings even darker than the holotype. Lieftinck (1959) also investigated specimens from Swains Island, American Samoa, and concluded that they were: "... a little smaller than those from Samoa, but do not show an approach towards the dark extremes mentioned above."None of these forms were illustrated and they unavailable to me during the work on the present study (diagnostic images were obtained later on and will be published separately). A figure comparing wing patterns of both sexes from Samoa with the holotype of *R. r. chalcoptilon* was presented. Lieftinck (1959) emphasised on an important point – in their distribution *R. regia* and *R. princeps* come to a very close contact to each other, but never found in the same locality (distribution map on fig. 2) and no evidences of interbreeding.

Further support for this view was proved by Lieftinck (1962) who, reviewing the Odonata of Micronesia, was unable to differentiate specimens from Mariana Islands (Saipan and Pagan) from Samoa and suggested that they belong to the same subspecies *R. r. chalcoptilon*. His logonymic list was updated and included descriptions of the head and measurements supported wing pattern illustrations of both sexes from Saipan. Commenting on the habitat availability in Mariana Islands, Lieftinck noted that Pagan is pretty dry and the habitat is unknown; moreover, Polhemus (2010) did not find *R. regia* on Pagan Island and considered the possibility of misidentification of earlier material. For Saipan Lieftinck (1962) seemed to cite Gressitt (1954: 50) giving Lake Sasupe as the probable breeding place for *R. r. chalcoptilon*. However, Gressitt (1954: 50) discussed the geography of the island and only mentions the existence of the lake. Lieftinck (1962) proposed a distribution of *R. r. chalcoptilon* as encompassing the Mariana islands (Pagan and Saipan) and Samoa plus neighbouring islands Wallis and Swains. No examples of the dark-winged female (considered typical probably because of the holotype specimen) form was found on the Marianas.

This view remained the dominant one concerning the taxonomy of the species and was never challenged by the consequent researchers of the Samoan Odonata fauna (Donnelly 1986, Papazian et al. 2007, Marinov et al. 2013, 2015). None of them found evidences of the so called 'dark-winged' forms of *R. r. chalcoptilon* from Samoa. Marinov et al. (2015)

established only the so called 'light-winged' form on the islands of Savai'i, Upolu, Tutuila and Aunu'u (missing in Ofu and Olosega) and illustrated two variants of the wing colour of the males and one female. As these studies were faunistic, no taxonomic discussions were attempted.

My study addresses the discrepancies in the previous literature and omissions of earlier studies. New interpretation on the taxonomy and biogeography of the *R. regia* populations from the easternmost range of the species are proposed below. Diagnostic images of specimens collected from Swains Island and deposited in Natural History Museum, London were received after the end of this study and will be published separately.

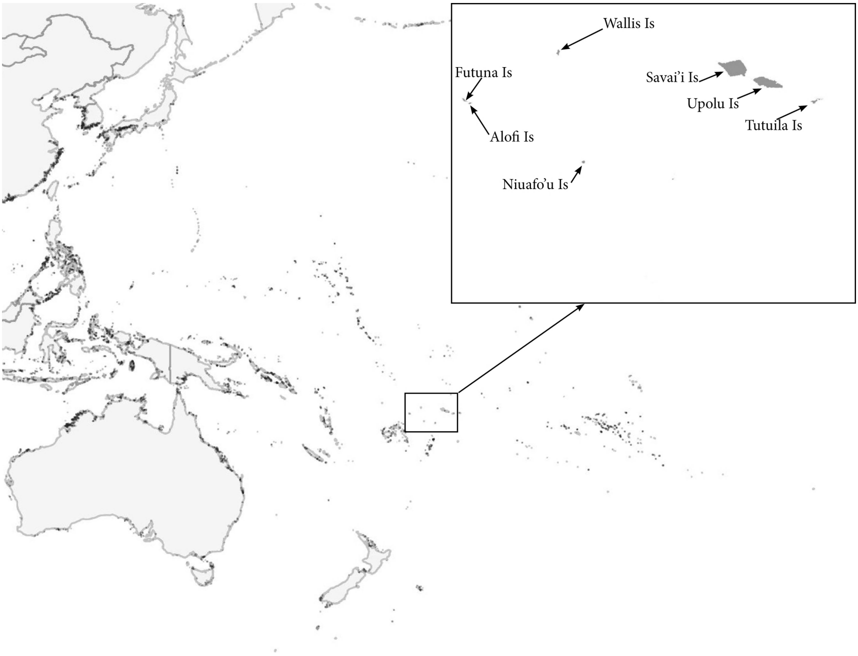


Figure 1. Situation of the study area.

Material and method

The present study focuses on *R. regia* populations from the eastern end of its distribution, mapped in Figure 1, and includes the islands of Wallis (Wallis & Futuna), Samoa (Western Samoa and American Samoa) and Niuafo'ou (Tonga).

Rhyothemis regia specimens deposited in the New Zealand Arthropod Collection were examined and compared to the following conspecifics (collection details recorded with the taxa reviewed in detail below): *R. r. chalcoptilon* type specimen (Zoological Museum Hamburg, Germany), specimens published in Marinov et al. (2015) and new material collected for the period 29 February – 08 March, 2020 from Wallis Island (details of all sampling locations and faunistic results will be published elsewhere). Additionally, all *R. regia* specimens used for the present study was compared to the congeneric *R. princeps* (Australian National Insect Collection) material: AUSTRALIA, 1 ♂ 1 ♀, same ANIC Database No. 014050, N. Queensland, Eubenagee Swamp, N. of Innisfail, 3-4 November 1966, JALW leg. & det.; 1 ♂ 1 ♀, same ANIC Database No. 014051, N. Queensland, Cooktown, 28 January 1951, RD leg., JALW det.; 1 ♂, ANIC Database No. 014055, Mitchell River Settlement Qld, April 1969, AD leg.; 1 ♀, ANIC Database No. 014063, Queensland Mackay, AM leg., JALW det.; NEW GUINEA, 1 ♂ 1 ♀, Western District, Rouku, Morehead River, 19 March – 28 May 1962, WB leg., JALW det.; 1 ♂ 1 ♀, Port Moresby, Mt. Lawes, 1300 ft., 5 March – 12 May 1963, WB leg.

Adults were collected with an aerial net and either killed in acetone, dried and transferred into paper envelops or preserved in 95% ethanol for molecular analysis.

Microscopic photos for the figures were produced using the Plant Health and Environment Laboratory, Christchurch, Ministry for Primary Industries, equipment in New Zealand. A series of images were taken under high power Nikon AZ100M microscope and stacked with Helicon Focus 6.7.1 software.

Morphological description follows Watson & O'Farrell (1991), wing venation designation follows Riek & Kukalová-Peck (1984).

Abbreviations and CODENS:

Morphology: AL – abdomen length (appendages excluded); HW – hind wing; S1–10 – abdominal segments 1 to 10. Capitalised 'Fig./Figs' refer to figures prepared for this this study, whereas small lettered 'fig./figs' for figures from other studies cited here.

Museum collections: ANIC – Australian National Insect Collection; MLBM – Monty Bean Life Science Museum, Brigham Young University, USA; NZAC – New Zealand Arthropod Collection, Manaaki Whenua Landcare Research, Auckland, New Zealand; ZMH – Zoological Museum Hamburg, Germany (part of the Centrum für Naturkunde).

Collectors: AD – A.L. Dyce, AM – A. Marriage, EG – Eduard Graeffe, JW – John Watt, JALW – J.A.L. Watson, MM – Milen Marinov, RD – R. Dobson, WB – W.W. Brandt.

Results

Morphological comparison of specimens from the area outlined above revealed the existence of three subspecies with one of them new to science. The arrangement below follows the chronology of the subspecies establishment.

Descriptions of the holotype specimens, opposite sexes of known subspecies and illustrations of diagnostic features of all of them are proposed below. Diagnosis is provided with the new subspecies and includes the taxa within the area discussed here only because, based on the biogeography discussed below, I believe that the subspecies are relatively sedentary and do not disperse between islands thus minimising the chances for intrasubspecific mixing.

***Rhyothemis regia chalcoptilon* (Brauer, 1867)** (Figs 2-6)

Holotype female deposited at ZMH, locality label as Samoa, EG leg. (by supposition).

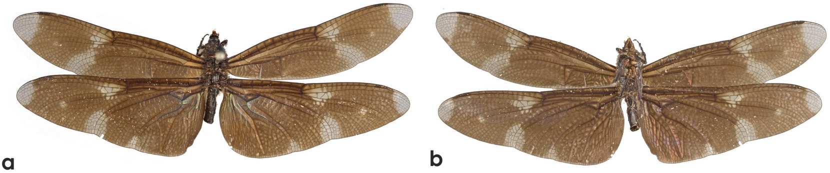


Figure 2. *Rhyothemis regia chalcoptilon*, holotype female: a) dorsal view; b) ventral view.

Figure 3. *Rhyothemis regia chalcoptilon*, female (NZAC04140281): a) head, frontal view; b) vulvar scale.

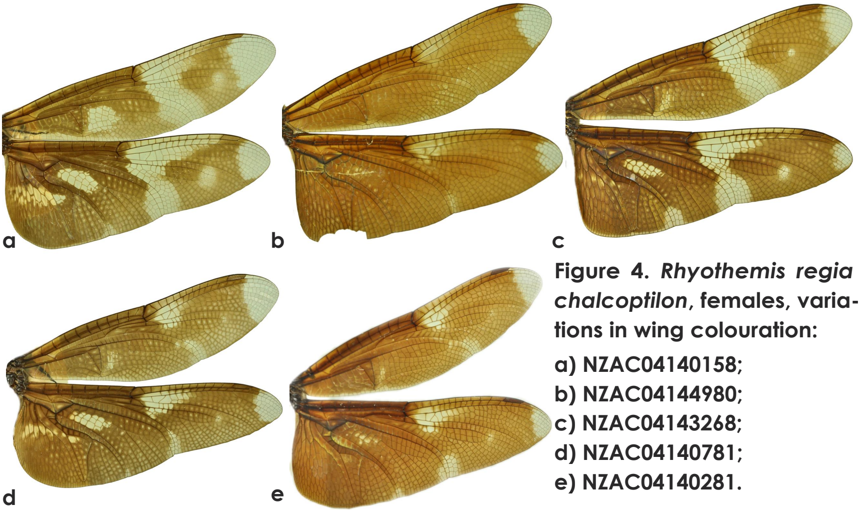


Figure 4. *Rhyothemis regia chalcoptilon*, females, variations in wing colouration:

a) NZAC04140158;
b) NZAC04144980;
c) NZAC04143268;
d) NZAC04140781;
e) NZAC04140281.

Celithemis chalcoptilon m. (Brauer 1867a: 25).

Comparative material: 3 ♂♂ 5 ♀♀, all with the same data: NZAC04143786, NZAC04143154, NZAC04145467; NZAC04140158, NZAC04144980, NZAC04143268, NZAC04140781, NZAC04140281, KINGDOM OF TONGA, Niuafo'ou Island, 15.6035S 175.6252W, 29 January – 01 February 1977, JW leg.

Female NZAC04140281 from the comparative material was found to be the best match to the wing colouration of the female holotype described in Brauer (1867a) (Fig. 2). Their

Figure 5. ***Rhyothemis regia chalcoptilon*, male (NZAC04143786): a) wings; b) anal appendages, lateral view (note, the picture was taken of a pinned specimen, therefore, a view at a clear lateral plane was not possible); c) anal appendages, dorsal view; d) secondary appendages.**

Figure 6. ***Rhyothemis regia chalcoptilon*, males, variations in wing colouration: a) NZAC04143786; b) NZAC04145467; c) NZAC04143154.**

great similarity was my main reason to reopen the debate of the possible mislabelling of the holotype (see Fraser 1927, 1956). Further considerations are provided in under the Discussion.

A redescription of a female specimen was not considered necessary because female was included in Brauer (1867a) and the overall body colouration is almost identical to the male described below. Figure 3 shows the head and vulvar scale, which have not been illustrated so far. Variations in the wing colouration are presented on Figure 4. Measurements (in mm): abdomen (excluding superior appendages) 19.6–20.7; superior appendages 0.6–0.8; HW 29.7–32.0.

Description of male *R. r. chalcoptilon* (NZAC04143786) (Figs 5-6)

Head. Missing.

Thorax. Black throughout with traces of green metallic sheen on metepisternum along metapleural suture close to its dorsal end and a dark yellow edging on ventral side of metepimeron. Legs almost entirely black save for lighter coloration on all trochanters. Wings with dark pattern as on Figure 5a; nodal index 12-10½ / 10½-13 in FW; 11-6 / 6-12 in HW; pt extends over 2.5 cells in FW and 3 cells in HW.

Abdomen. Black throughout including appendages; no paler markings on any segments except for dark red on the intersegmental membranes; S10 with a longitudinally elongate swelling rather than a ridge; superior appendages (Fig. 5b) club shaped with four robust teeth ventrally (Fig. 5b); in dorsal view (Fig. 5c) – curved medially at bases and parallel-sided on apical 2/3.

Measurements (in mm): abdomen (excluding superior appendages) 23.1; superior appendages 1.7; HW 34.2.

Variations in males. One of the other two males is a juvenile (NZAC04145467) which is included in here only with the wing colouration and the number of the teeth on the ventral side of the superior appendages – three on the left and four on the right. Other male (NZAC04143154) has its appendages with broken tips and the number of teeth cannot be determined accurately. There are four teeth on the left appendage and possibly three on the right with a small tubercle on the broken tip which may be another tooth.

Pres. by
Imp.Bur.Ent.
Brit.Mus.
1927—294.

LECTO-
TYPE

Rhyothemis
regia armstrongi
Fraser
LECTOTYPE
D.E.Kimmins det.1964

1684865
BMNH(E)

SAMOAN IS
Tutuila I.
Pagopago
2. xii. 1924.
P.A Buxton
and G H Hopkins.

Rhyothemis
regia
chalcoptilon Br.
det. M. A. Lieftinck 1947

Rhyothemis regia exul
Ris. ♂

Figure 7. ***Rhyothemis regia armstrongi*****, male lectotype (BMNHE_-1684865): a) dorsal view, b) lateral view, c) labels. Courtesy of Ben Price.**

Figure 8. ***Rhyothemis regia armstrongi*****, male (NZAC04146450): a) head frontal view; b) anal appendages, lateral view; c) anal appendages, dorsal view; d) secondary genitalia.**

Figure 9. *Rhyothemis regia armstrongi,* female (NZAC04225-771): vulvar scale.

Wings of two specimens are illustrated on Figure 6. Measurements are given for NZAC04143154 only: abdomen (excluding superior appendages) 21.2; superior appendages 1.5 (tips broken off); HW 30.8.

***Rhyothemis regia armstrongi* Fraser, 1956** (Figs 7–9)

Fraser (1956) did not designate a holotype specimen. Therefore, Kimmins (1966) selected a lectotype (Fig. 7), a male specimen from Tutuila Island, Pago Pago, 2 December 1924, P.A. Buxton & G.H. Hopkins leg.

Rhyothemis regia race *armstrongi* nov. (Fraser 1956: 328); *Rhyothemis regia exul* Ris. (Fraser 1927: 40); *Rhyothemis regia chalcoptilon* Brauer. (Lieftinck 1942: 518); *Rhyothemis regia chalcoptilon* Brauer. (Lieftinck 1959: 46); *Rhyothemis regia chalcoptilon* (Brauer) (Donnelly 1986: 112); *Rhyothemis regia chalcoptilon* (Brauer, 1867) (Marinov et al. 2013: 11); *Rhyothemis regia chalcoptilon* Brauer, 1867 (Marinov et al. 2015: 34); Lieftinck (1948, 1962) mentioned Samoa in the general distribution of *R. regia* and *R. regia chalcoptilon* respectively.

Comparative material (all MM leg.): AMERICAN SAMOA: 3♂♂ 1♀, NZAC04142200, NZAC04144198, NZAC04146450, NZAC04225771, Aunu'u Island, taro field and canals, 14.2848S 170.5573W, 14 m a.s.l., 9 July 2014; 1♂, NZAC04146770, Tutuila Island, wetland at the beginning of the Tuafuna Trail, Vatia Village, 14.2479S 170.6739W, 0 m a.s.l.; WESTERN SAMOA: 1♂, NZAC04144400, Savai'i Island, remnant pools on the bed of a stream above the village of Lalomalava, 13.6934S 172.2308W, 88 m a.s.l., 4 July 2014.

Fraser (1956) illustrated the wings of Samoan populations and provided a diagnosis of his new subspecies *R. r. armstrongi* and is not repeated here. Figures 8-9 include some features of the male anal appendages and secondary genitalia as well as female vulvar scale which are important diagnostic characters of the three subspecies provided below. Measurements (in mm): males - abdomen (excluding superior appendages) 20.0–21.2; superior appendages 1.6–1.8; HW 28.0–29.4; female - abdomen (excluding superior appendages) 17.9; superior appendages 0.6; HW 25.5.

***Rhyothemis regia uveae* subsp. nov.** (Figs 10–13)

Rhyothemis regia chalcoptilon (Brauer, 1867) (Papazian et al. 2007: 56). Lieftinck (1948, 1962) mentioned Wallis in the general distribution of *R. regia* and *R. regia chalcoptilon* respectively.

Holotype. ♂, NZAC04231002; WALIS & FUTUNA, Wallis Island, Lake Kikila, 13.2947S 176.1889W, 14 m a.s.l., 01 March 2020.

Paratypes (all from Wallis Island). 3♂♂, NZAC04231005, MLBM (no accession #), same data as holotype; 2♂♂ 3♀♀, NZAC04231003, MLBM (no accession #), NZAC04230999-1000,

Figure 10. ***Rhyothemis regia uveae*, holotype male: a) head, frontal view; b) wings; c) anal appendages, lateral view; d) anal appendages, dorsal view; e) secondary genitalia.**

Figure 11. ***Rhyothemis regia uveae*, allotype female: a) wings; b) vulvar scale.**

MLBM (no accession #), Lake Alofivai by the College Lano-Alofivai, 13.2573S 176.1718W, 34 m a.s.l., 02 March 2020; 1♂, MLBM (no accession #), Lake Lanumaha, 13.3147S 176.2104W, 40 m a.s.l., 05 March 2020; 1♂, MLBM (no accession #), Lake Lanutuli, 13.3159S 176.2166W, 13 m a.s.l., 04 March 2020; 1♀, MLBM (no accession #), numerous puddles along a section of a secondary road of RT1 north of Lake Lalolalo, 13.2961S 176.2367W to 13.3108S 176.2486W, 41–18 m a.s.l., 05 March 2020.

Allotype. ♀, NZAC04231001, Wallis Island, Lake Alofivai by the College Lano-Alofivai, 13.2573S 176.1718W, 34 m a.s.l., 02 March 2020.

Etymology. The subspecies is named after the island of Wallis using the original name Uvea given by the Polynesian occupants (genitive case *uveae* = Uvea's), emphasising the endemic nature of the taxon to this island.

Description of holotype (Fig. 10)

Head (Fig. 10a). Labium, labrum completely black; anteclypeus edged with dark red laterally fading centrally becoming yellow middorsally; postclypeus almost entirely dark red to black save for yellow border line along frontoclypeal suture; frons with a dark yellow stripe merging dorsally with yellow of postclypeus, remainder of frons dark with violet sheen dorsally, median grove extending to level of median ocellus thus outlining two lobes; vertex dark violet sheen; antennae entirely black; occipital triangle black, bilobed posteriorly.

Thorax. Entirely dark except for dark yellow stripe along ventral margin of metepimeron, entire synthorax with a green-yellow sheen extending to level of metastigma on mesepimeron and metepisternum up to ventral part of metepimeron, but absent on mesinraepisterum. Legs almost entirely black save for lighter trochanters. Wings with dark pattern as on Figure 10b; nodal index 13-10½ / 10½-12 in FW; 12-7 / 7-12 in HW; pt extends over 2.5 cells in FW and 3 cells in HW.

Abdomen. Entirely black throughout including appendages except for dark red intersegmental membranes and yellow areas posteriorly on sternites best expressed on S6 (due to post mortem swelling); S10 with dorsal carina elevated dorsally to about ¼ of its length; superior appendages club shaped with three teeth ventrally (Fig. 10c), in dorsal view (Fig. 10d) – curved basomedially.

Measurements (in mm): abdomen (excluding superior appendages) 22; superior appendages 1.7; HW 33.6.

Description of allotype (Fig. 11)

Head. As in male, but paler on anteclypeus, wider yellow transverse stripe and more extensive green metallic sheen.

Thorax. As in male. Wings with dark pattern as on Figure 11a; nodal index 10-10½ / 10½-10 in FW; 11-6 / 7-11 in HW; pt extends over almost 2 cells in FW and 3 cells in HW.

Abdomen. As in male with slight pruinosity dorsally most conspicuous on S3–5 and ventrally on S3–7; superior appendages weakly divergent in dorsal view slightly longer than S10; vulvar scale as on Figure 11b.

Table 1. *Rhyothemis regia uveae*, variations of the number of the teeth on the ventral side of the superior anal appendages.

Male specimen	Number of teeth on superior appendages	
	left appendage	right appendage
NZAC0431005	4	3
NZAC04231004	4	3
MLBM (no accession #)	3	4
NZAC04231003	3	3
MLBM (no accession #)	3	3
NZAC04231002	3	3
MLBM (no accession #)	4	4

Measurements (in mm): abdomen (excluding superior appendages) 21; superior appendages 0.7; HW 33.0.

Variations within paratype series

Colouration and metallic sheen on head, thorax and abdomen as in holotype and allotype. Wing colour pattern differs slightly in intensity of the occupation of the dark area with some males having almost uniformly dark surface and in females the apical transparent area is reduced to a small spot, but always present on all four wings.

Most notable variation is observed in the number of the ventral teeth on the superior appendages in males which number: three in both appendages in three males, four on both appendages in one specimen and three males having three on one appendage and four on the other (Table 1).

Measurements (in mm): males - abdomen 20.5–22.7; superior appendages 1.7–1.9; HW 31.5–33.7; females - (one not measured because young and body distorted) abdomen 18.5–20.0; superior appendages 0.5–0.6; HW 30.5–32.5.

Figure 12. Comparison between the shape of the male anal appendages in lateral view of: a) *R. r. uveae*; b) *R. r. armstrongi*; c) *R. r. chalcoptilon*.

Differential diagnosis

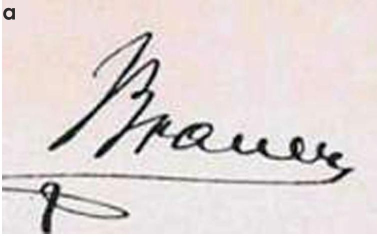
The new subspecies is compared only to the other two known conspecifics from the study area: *R. r. armstrongi* and *R. r. chalcoptilon*. Important consideration must be made in here – the three subspecies considered here lack a clearly defined diagnostic feature that will accord them as separate species. The different morphological characters are not strongly pronounced and the diagnosis noted here work better when comparing a series of specimens of the three subspecies (cf. Fig. 12). The most reliable diagnostic characters were found on the male appendages viewed laterally. *Rhyothemis r. uveae* differs by the following two characters on the superior appendages: more strongly arched than in the other two subspecies; normally with three ventral teeth on each appendage (but check Table 1) vs four in all *R. r. armstrongi* (one specimen with five on

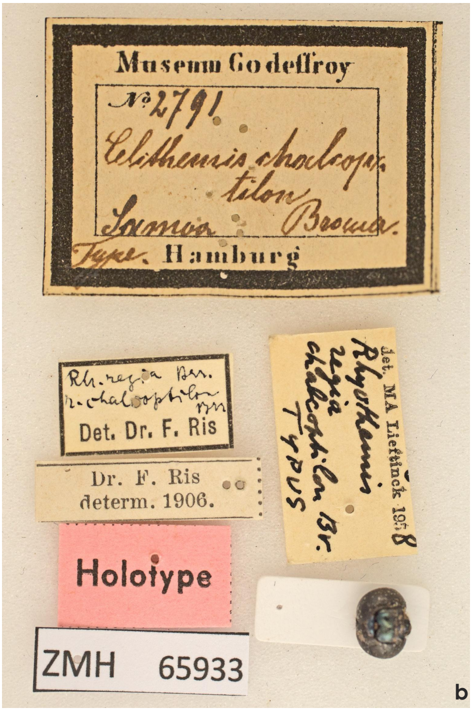
Figure 13. Generalized wing pattern for comparison of males (left column) and females (right column) of: a) *R. r. uveae*; b) *R. r. armstrongi*; c) *R. r. chalcoptilon*.

one appendage) and mostly four in *R. r. chalcoptilon* (two specimens with three on one appendage). Dorsal carina on S10 in all male *R. r. uveae* forming a sharply raised ridge vs less raised (all but one *R. r. armstrongi*) to low and rounded (*R. r. chalcoptilon*). Overall *R. r. uveae* is slightly longer than the other two subspecies, hence the total length of superior appendages is generally slightly longer (1.7-1.9 mm vs 1.6-1.8 mm in *R. r. armstrongi* and 1.7 mm in *R. r. chalcoptilon*). Due to the slightly elongated post-serration section (cf. Fig. 20 for serration ratio), the superior appendages approach the size of that typical of *R. princeps* (see comparison between the two species below). However, these measurements overlap and should be used only in combination with other traits which add to the diagnostic of the three subspecies: geographic situation and wing colouration. The latter is variable, but follows a general pattern shown on Figure 13 separately for the three subspecies.

Discussion

The debate on the origin of *R. r. chalcoptilon* holotype has led to various theories on the taxonomy and biogeography of the species. The distribution has been mapped in Lieftinck (1948, 1959) based on his own data. Marinov (2015) summarised all previous studies, however, was imprecise of the species range presented on figure 27 (showing the distribution of the congeneric *R. phyllis* and *R. regia*). The distributions of *R. regia* was mapped based mainly on the data on the distribution of *R. r. chalcoptilon* available at the time – Mariana Islands to Samoa. Figure 27 shows an extension of the distribution to the Philippines, which is wrong for *R. r. chalcoptilon* because the nominal subspecies occurs there. The map is also incorrect concerning the geographic limits of *R. phyllis* since its border line extends to Futuna only and not to Wallis where both congeneric species coexist in several habitats (M. Marinov, per. obs.). In its northern borders the range includes




Museum Godeffroy
№ 2791
Celithemis chalcoptilon
Samoa Brauer.
Type. Hamburg

Rh. regia Br.
r. chalcoptilon Ris
Det. Dr. F. Ris

Dr. F. Ris
determ. 1906.

Holotype

ZMH 65933

det. MA Lieftinck 1958
Rhyothemis
regia
chalcoptilon Br.
Typus

Figure 14. *Rhyothemis regia chalcoptilon*, investigation of the collector of the holotype female: a) Brauer's own signature; b) label of the holotype.

Pagan, however, the occurrence of *R. regia* on this island needs validation following Polhemus (2010). On the other hand, the map does not include Niuafo'ou, which here is believed to be the actual type locality of the female holotype of *R. r. chalcoptilon*.

Rhyothemis regia has a very wide range where it could be found even on such small islands as Niuafo'ou or Wallis. Therefore, a final taxonomic conclusion should be made when comparing their total known range and an investigation of all potential habitats. My study focuses only on the eastern most range of the species.

Collector of holotype of *Rhyothemis regia chalcoptilon* (Brauer, 1867)

Brauer (1867a) did not provide the name of the collector. Nor do the accompanying label (Fig. 14b). It bears the name of the locality as 'Samoa' at the bottom left corner and a name at the right which is difficult to read. It begins with 'B' and is believed to be the name of the identifier 'Brauer'. It may not be Brauer's own handwriting because his signature is different (Fig. 14a). However, it is very difficult to make 'Brauer' of the handwriting and the following combinations have been investigated as another possibility of locality either in Samoa or within the region: 'Baoma', 'Basma', 'Beoma', 'Broma', 'Baowa' and 'Beowa'. None of them seems to be a likely locality in Samoa because they do not have 'B' in Samoan language (R. Stirnemann, per. comm.). The last two options were ruled out as possible localities in Wallis and Futuna because 'W' does not exit in both Wallisian or Futunian languages (F. Le Bail, per. comm.). The remaining names are certainly not localities in Wallis & Futuna either (J.-M. Duvernay, per. comm.). Therefore, I finally concluded that this should be considered the name of the author of the species.

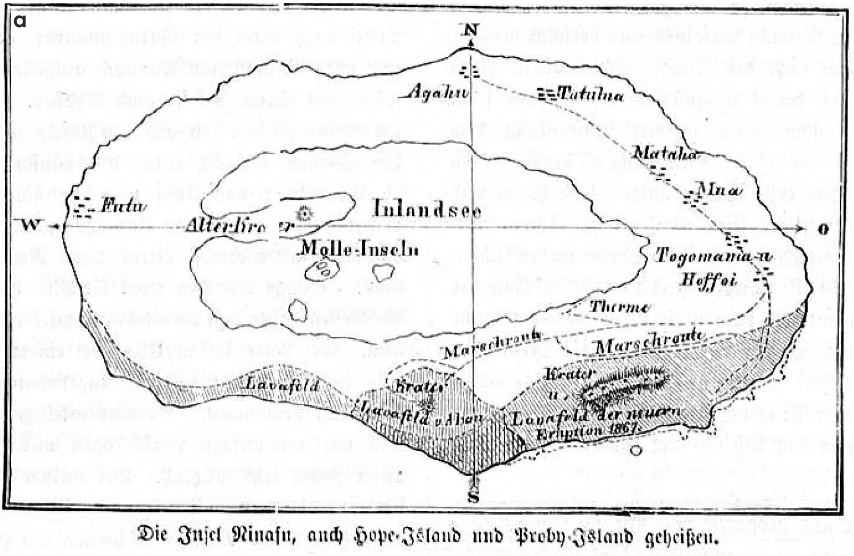
The clue to the collector is provided in Brauer (1867b) who stated that specimens from Viti Levu and Samoa islands were collected by Dr Eduard Graeffe. Kranz (2007) states that Eduard Graeffe (1833-1916), was a Swiss entomologist. At the age of 28 he was employed by Johan Cesar Godeffroy VI (1813-1885), a wealthy Hamburg merchant and ship owner, to build a collection of scientific material from the so called 'Südsee' or 'South seas' for the Godeffroy Museum, Hamburg. Dr Graeffe arrived in Apia, Samoa in 1862, with an initial plan to stay there for three years. However, in May, 1863 his fiancée joined him. They married and their son Edward was born in 1864. They spent ten years with Dr Graeffe surveying the islands of Samoa, Fiji, Tonga, Phoenix (now part of Kiribati) and Gilbert, Ellice (now Tuvalu)), Wallis and Futuna. At the end of 1870 he returned to Hamburg and became the editor of the Journal of the Museum Godeffroy, founded in 1872.

In his autobiography Graeffe (1916) kept a very detailed diary of the journey on board the ship "Sophie" leaving Germany on October 1861 and arriving on Samoa around March 1862. It was not a direct sail from Hamburg to Samoa, but a continuous sampling expedition where Graeffe recorded daily the specimens he had obtained from various sites, including the open ocean, during the voyage. The diary ends in Sydney, Australia and the remaining part of the trip to Samoa are described in less detail by Graeffe.

The first years (1862-1865) of Graeffe's mission in Samoa were spent exploring islands of Fiji (Graeffe 1868b). The next period (1866-1867) of his studies are only briefly recorded (Graeffe 1916) where he referred to a more detailed publication of his work (Graeffe 1868a). This period is pertinent to the present study since provides a probable time table of collection of the holotype specimen of *R. r. chalcoptilon* as discussed below.

Probable collection time

Brauer introduced *R. r. chalcoptilon* in 1867, but his intention to describe several new species was presented on 5th December 1866 during a regular monthly meeting of the Austrian Zoological-Botanical Society (Brauer 1866). A short account on the already described species was presented again on 3rd April 1867 (Brauer 1867b). Therefore, the most likely time when the holotype of *R. r. chalcoptilon* was collected was in 1865-



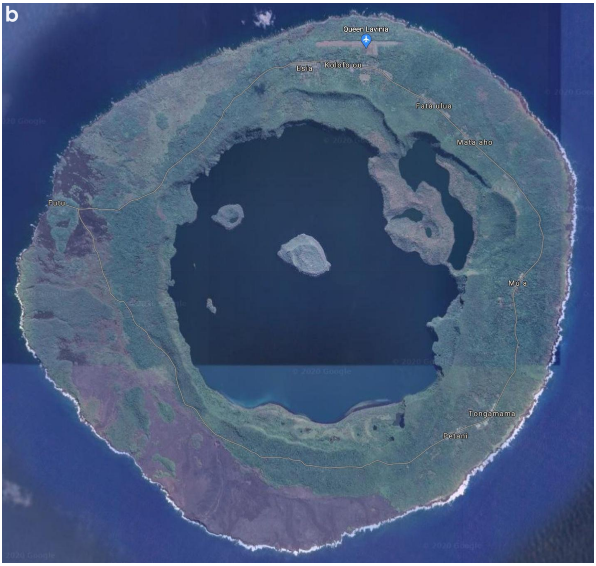


Figure 15. Comparison between the outlines of Niuafo'ou Islands based on: a) maps from Graeffe (1868a); b) present day (Google Maps).

1866 (1863-1865 was mostly dedicated to Fiji). Graeffe (1868a) documented that on 19 October 1866 on board the brig "Susanne" that he sailed towards Niuafo'ou Island, Tonga. The island is spelled Niuafu in the publication and the geographic coordinates (18°38'S 174°55'W) correspond to a location about 90 km west from Vava'u, Tonga. However, there is no doubt that Graeffe visited Niuafo'ou Island, but provided wrong coordinates. Graeffe (1868a) speaks about this island as the northernmost in Tonga group, which is still valid today. He also included maps of the Niuafo'ou Island group which are close to the current outlines (Fig. 15). Another discrepancy on his maps is the position of the peninsula extruding inside the lake; Graeffe (1868a) has it is at the western part of the lake, however a similar structure is now present on the eastern part of the lake. However, the names of the localities are mapped with a high precision and correspond to the present-day settlements on the island. It is not clear if the position of the vegetation is a result of a mistake of the mapping or a consequence of certain geological events. The island has undergone modifications due to earthquakes and volcanic activities. An eruption in April, 1867 was mentioned in Graeffe (1868a) who visited Niuafo'ou again only a few weeks later on May, 1867 in order to study the effect of the volcanic activities.

Graeffe arrived on Niuafo'ou on 21 October, Sunday which is a strict holiday introduced by the Christian missionaries when any work-related activities are forbidden. He began exploring the island on 22 October (Monday) and stayed until 24 October when he left for Futuna. While on the island he visited the interior providing a detailed description of the large lake with a peninsula formed by a volcanic crater, which is said to have erupted about 26 years prior. A trip by canoe inside the largest lake on the island, Vai Lahi (date not specified, but either 22 or 23 October) is thought to be one of the probable times when the holotype of *R. r. chalcoptilon* was collected since he writes about some dragonfly species and snails from genus *Melania* as the only living creatures at the lake. Schmeltz (1869) in the Catalogue of the Godeffroy Museum specimens listed *Melania niuafouana*, which was probably collected during the same trip but Bieler & Petit (2012) consider it as a nomen nudum since no description was ever provided.

However, this trip is about a month and a half before Dr Brauer reported on his intention to establish several new species (5 December 1866), formally published in 1867. This is a very short time for the specimen to arrive by sea from the Pacific to Germany and for Brauer to incorporate this taxon in his report. However, the monthly meetings of the European scientific communities at the time were for members to make short presentations on their scientific results which could be published with a gap with more than a year between (J. Waringer, per. comm.). Therefore, theoretically Brauer may have received the holotype specimen after the presentation on the 5 December 1866 and included it in his publication the following year. It was the last described species in his publication.

This scenario is considered unlikely since in the yearly report of the Austrian Society for 1866 there is a note about the 5th December 1866 meeting and the presenters where the two nomina '*Celithemis regia* und *Malcoptilon*' were included (Brauer 1866: 105). '*Malcoptilon*' was obviously a spelling mistake of '*chalcoptilon*'. This information implies that Brauer had the holotype during his talk in December and even had a nomen which was given for the coppery dark looking wings (Fliedner 2020). Therefore, the actual collection of the holotype must have happened earlier in 1866 (or in 1865) and was therefore collected and given to Graeffe by another collector or sampled during a trip not recorded in the published literature. For example, describing molluscs collected by Graeffe, Mousson (1865) recorded that several species were sampled from Uvea (Wallis Island), which is a trip not recorded in Graeffe's publications of his travels within the region. Trips to Wallis & Futuna were officially recorded as happening in 1866-1867 (Graeffe 1868a), but he may have made short collecting trips within the region earlier or sampling during stopovers on smaller islands. Graeffe (1916) mentions that on his first sail to Fiji in 1862 he had seen the volcanic islands of Tonga on the board of the ship, so probably stopovers may have been contemplated and perhaps realised during some of the trips before Graeffe's official trip to Niuafo'ou in October 1866.

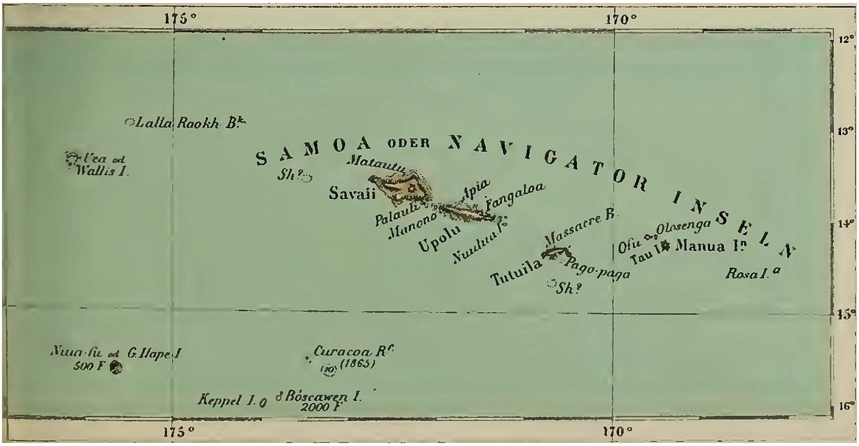


Figure 16. Small scale map of Samoa and neighbouring islands (from Graeffe 1873).

Was the holotype mislabelled?

Mislabelling of the holotype of *R. r. chalcoptilon* had been suggested by Prof. Buxton and commented by Fraser (1927, 1956). In raising the question about possible mislabelling, I am not implying a by mistake by Graeffe in the field or Brauer when the latter was working on his manuscript. With the extensive material collected by Graeffe and transport to Germany mistakes with swapping the labels may have happened at many stages of the transportation of the specimens. Whistler (2011) and Whistler & Atherton (2014) reported obvious mistakes with labelling of botanical material collected by Graeffe and labelled as from Tonga, however, those are now known to belong to genera endemic to Fiji.

A possible mistake in labelling may have also resulted from a wrong interpretation of the geography of the region. Mousson (1865) included Wallis Island within Samoa group of islands, which is incorrect. Graeffe (1873) was very precise as to geography of the islands from this part of the Pacific ocean, however, prior to this date the islands of Wallis, Futuna and Niuafo'ou could have been easily mistaken as part of Samoa group because on a small scale map they appear close to Samoa (Fig. 16). Note, that for the type locality ('Patria') of *R. r. chalcoptilon* Brauer (1867a) wrote 'die Samoa oder Schifferinseln' (Samoa or navigator's islands) in plural, whereas when describing other species (e.g. *Hemerobius graeffei* in Brauer 1867b: p. 508) he wrote: 'Vaterland. Upolu Hauptinsel der Samoa- (od. Schiffer-) Gruppe gesammelt von Dr. Gräffe.' (Upolu, main island of the Samoa- (or navigator's) group sampled by Dr Graeffe). Brauer (1867b: p. 505) specified that specimens of the new species have been collected '… auf den Viti- und Samoa-Inseln von Dr. Gräffe …'. Tonga islands were not mentioned which may be a sign that that they were thought to be a part of the Samoa or Navigator's islands; but that also just could mean that there were no specimens from there.

There may even be other scenarios thus far not presented above. We may never find a categorical proof for the view expressed in here but I suggest that the holotype of *R. r. chalcoptilon* was collected on Niuafo'ou Island, Tonga (not Samoa) either by Graeffe, given to him by someone else or that the holotype may have been delivered directly to Godeffroy Museum by one of the many collectors employed by the Museum. Describing his trip to Niuafo'ou in May, 1867, Graeffe (1868a) mentions '… bei meinem früheren Aufenthalte …' (during an earlier stay) instead of '… meinem früheren Aufenthalt …' if he had been there more often (H. Fliedner's translation). Therefore, it is likely that the holotype female was collected by someone else. Moreover, Godeffroy & Son had an agency on Niuafo'ou Island, therefore such a conspicuous insect as *R. r. chalcoptilon*, which Graeffe says was one of the only living creatures on the lake, must have attracted the attention of people inspired by the sampling efforts within the region.

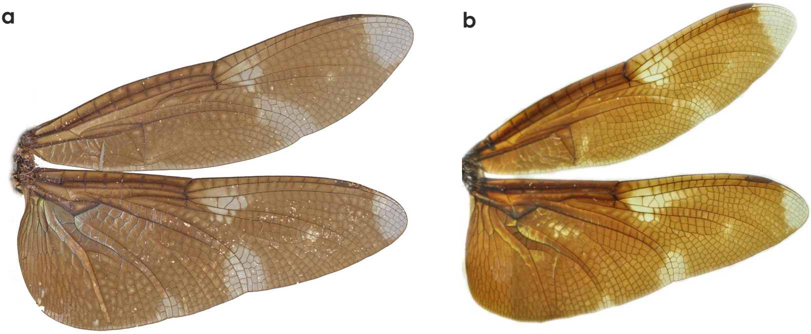


Figure 17. Comparison between the wings of *R. r. chalcoptilon*: a) holotype female; b) NZAC04140281.

The evidence marshalled that the holotype was collected from Niuafo'ou comes from my comparison with the NZAC specimens collected from this island as noted above. Although the colour varies between the female specimens, the wing colour pattern of one female is the best match to the female holotype (Fig. 17) ever reported in the literature so far. The assumption that the type locality is Vai Lahi Lake also makes sense from the taxonomic and biogeographic points of views as expressed below.

Taxonomy of *Rhyothemis regia*

Rhyothemis regia is a polytypic species occupying a wide range (Lieftinck 1948), exhibiting large spectrum of colour variations on the wings with females of certain subspecies proven to be dichromatic (Ris 1909-1919). Therefore, plausible hypothesis concerning species taxonomy can only be suggested when employing specimens from all areas where it is thus far known from. I am suggesting a new approach in studying the taxonomy of the species for this species concerning the small area outlined earlier. Past efforts have been put mainly on the wing pattern. Lieftinck (1942) provided the only information using morphology in comparison with *R. princeps*, but he did not dwell into the diagnostics of the various subspecifies.

Lieftinck (1959) decided that females of *R. r. chalcoptilon* come in two forms: dark-winged (holotype, single female) and light-winged (the common colour pattern illustrated in other sources, e.g. Fraser 1956). I am using the definition of Ford (1955) who defined polymorphism: “as the occurrence together in the same habitat of two or more distinct forms of a species in such proportions that the rarest of them cannot be maintained merely by recurrent mutation.” This definition could be implied in the studies of polychromatism. It excludes the occurrence of continuous variations, but accepts the persistence in sympatry of disjunct colour variants. Female colour polychromatism in *Ischnura elegans* (Vander Linden, 1820) is one of the best studied odonates where the existence of three morphs has been demonstrated to be discrete and heritable (Willink 2018). For Pacific Odonata a similar example (molecular component excluded) would be for *Synthemis miranda* Selys, 1871. Females with differences of dark wing colour have been discovered (Campion 1921; Lieftinck 1971, 1975; Winstanley 1983; Davies 2002), but it was not until Marinov & Richards (2013) proved the sympatry of the two and suggested a possible polychromatism.

Co-existence of *R. r. chalcoptilon* with other forms (as indicated by Lieftinck 1959) has never been proven for Samoa despite the long years of sampling within the area given initially by Fraser (1927, 1956). Other sampling efforts (Donnelly 1986, Marinov et al. 2015) failed to find both colour variants either. Therefore, the hypothesis of existence of two colour forms suggested by Lieftinck (1959) with the dark-winged one to be rediscovered from Samoa could not be proven up to now.

The present study is based on the assumption that the holotype was mislabelled as from Samoa whereas it was more likely collected from Niuafo’ou. Unfortunately, the body of the holotype is broken and the final six abdominal segments lost making it impossible to compare it morphologically to other females within the study area. Morphological comparison of females would have been difficult anyway since no reliable diagnostic features have been discovered in the other female specimens studied here. Wing colour pattern of the holotype is the best match to the female NZAC04140281, which is the main reason to suggest that it was collected from Niuafo’ou. Therefore, my morphological analysis was carried out using males only.

Structure of the male anal appendages and S10 show little variation between populations from the three Pacific islands analysed here. Spatial isolation is obvious with islands apart from each other by at least 264 km (distance between Wallis and Niuafo’ou). Reduced, or no gene flow, and isolation in geological time may help explain the observed

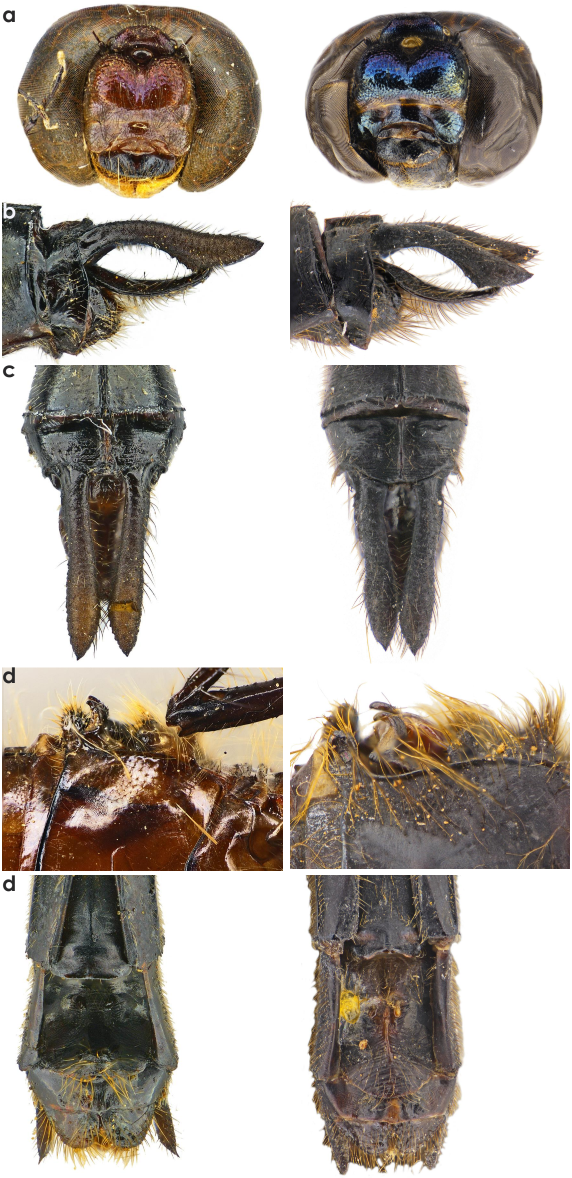


Figure 18. Comparison between *R. princeps* (left column) and *R. regia* (right column): a) head, frontal view; b) male anal appendages, lateral view; c) male anal appendages, dorsal view; d) male secondary genitalia; e) female vulvar scale.

differences that have led to apparent differences in wing pattern but not so morphologically to assure reproductive isolation. I therefore suggest we maintain the subspecific status of *R. regia* populations as described here.

Future studies should focus on morphology of the male anal appendages across the entire range of *R. regia* and comparison with *R. princeps*. The latter is morphologically and by wing pattern very similar to *R. regia*. Lieftinck (1942) claimed that he had found some morphological features to keep them as separate species, used colouration of the face to separate both. Illustrations in Lieftinck (1942: fig. 86-89) of male anal appendages and secondary genitalia are similar for both species. I compared specimens of *R. princeps* housed in the ANIC with the material collected in the present study. Figure 18 compares both sexes of *R. regia* and *R. princeps*. Variations of the wing colour of *R. princeps* are presented in Figure 19.

Both figures indicate that the two species are morphologically close. The following diagnostic features should be used for identification. Males: superior appendages in lateral view club shaped with dorsal edge straight at the level of the ventral serration (*R. regia*) vs dorsal edge concave giving the appendage less club-shaped (*R. princeps*); serration ratio (ventral edge pre-serration / ventral edge post-serration, Fig. 20) 1.7-2.3 (*R. regia*) vs 1.2-1.3 (*R. princeps*); genital hamule arched with tip more or less directed towards genital lobe (*R. regia*) vs arch less pronounced with tip directed externally (*R. princeps*); genital lobe mostly widened along the posterior edge (*R. regia*) vs almost parallel-sided (*R. princeps*). Females: posterior edge of vulvar scale sinious approaching a bilobed appearance (*R. regia*) vs straight (*R. princeps*). In addition to the morphological features the following differences in colouration can be used: face almost completely dark with yellow cross stripe along dorsal edge of postclypeus and ventral edge of frons and lighter areas on anteclypeus (*R. regia*) vs face almost completely bright apart from labrum (*R. princeps*). Wing colouration has not been compared due to the great intra-species/subspecies variations.

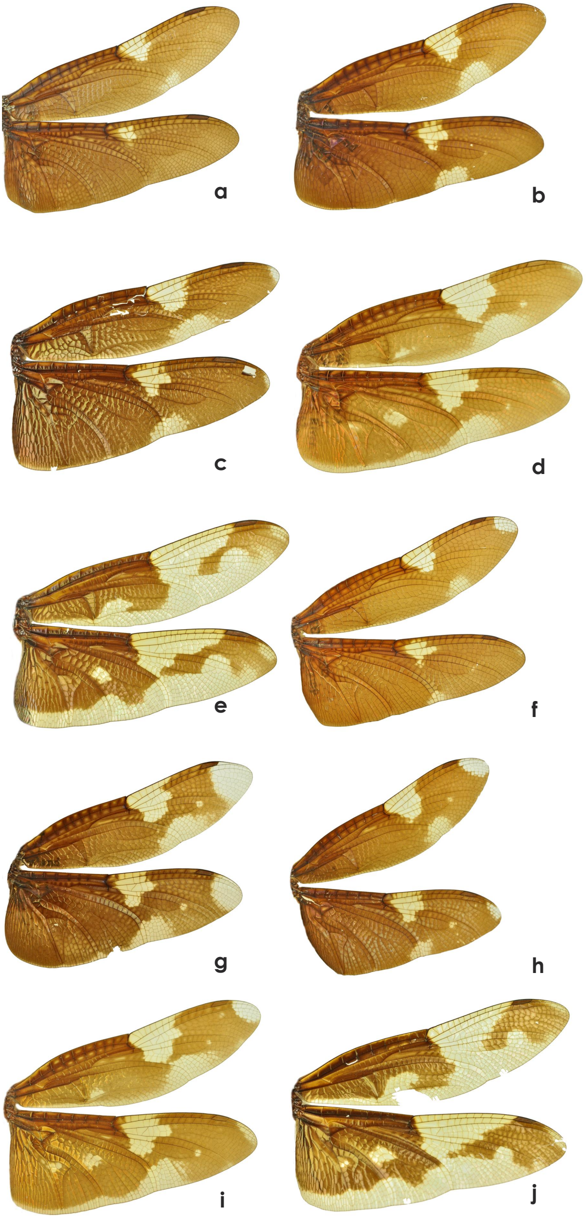


Figure 19. Variations of the wing colour of *R. princeps*, a-e) males; f-j) females: a-c, f-h) Australia; d-e, i-j) New Guinea.

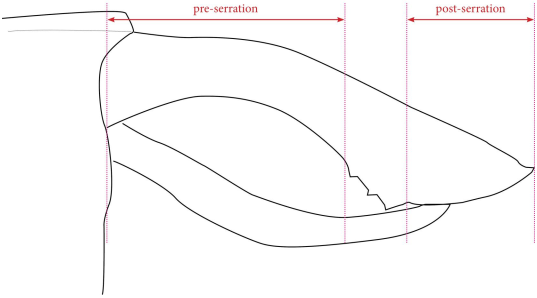


Figure. 20. Measurements of the serration ratio calculated as: ventral edge pre-serration / ventral edge post-serration.

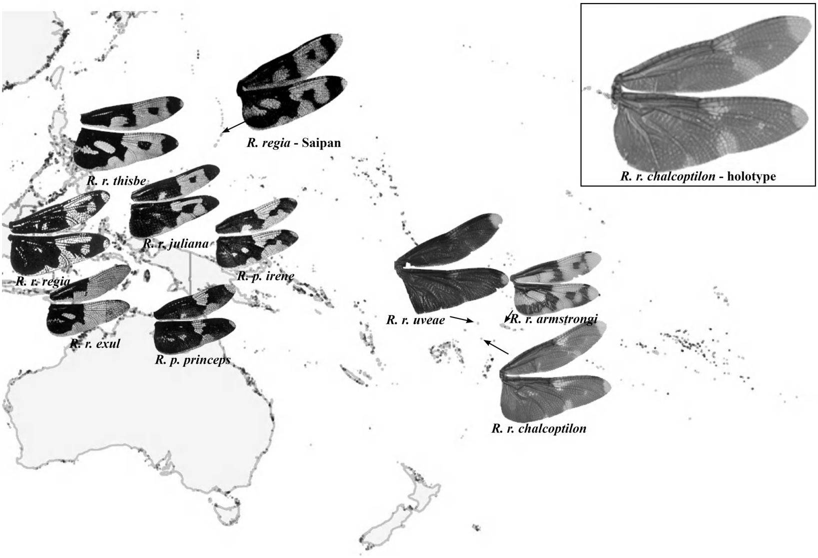


Figure 21. World distribution of *R. regia* and *R. princeps*. Female wings are plotted for comparison with the holotype of R. r. chalcoptilon (top right corner). The map is a reproduction of Lieftinck (1959) and includes summaries from Asahina (1940), Fraser (1925, 1927), Lieftinck (1926, 1936, 1942, 1948, 1949, 1953a-b, 1959, 1962), Michalski (2012), Schmidt (1941) and Ris (1913).

Biogeography of *Rhyothemis* in the Pacific

Lieftinck (1942, 1948, 1953b, 1962) commented on the great dispersal abilities of *R. regia*. Lieftinck (1948, 1953b) claimed some evidence of interbreeding between different populations as a result of reintroduction of colonists, either actively by migration, or passively by air currents. However, he offered no supporting evidence. In his hugely important legacy of taxonomic works, Lieftinck generally favoured wind dispersal by a chance and founder effect and often assumed this as the only probable way to explain the contemporary distribution. For example, Lieftinck (1953) opposed to the view in Tillyard (1911) on the non-migratory behaviour of *Hemicordulia australiae* (Rambur, 1842) because he found this species to be very common on the New Zealand North Island when he visited it in January-February, 1949. However, Tillyard (1911) made his suggestion based on the known distribution at the time when the species was only an 'occasional visitor' to the New Zealand islands. Armstrong (1978) documented the invasion history at about the time of the Lieftinck's visit in the 1940's when *H. australiae* was already very common. Had Lieftinck visited New Zealand earlier than 1940's he would have found a completely different scenario.

Lieftinck's view on the great dispersal abilities of odonates, and especially of *R. regia*, is considered below in the light of the known distribution of the *R. regia* subspecies presented on Figure 21.

Dispersalists often assume that a one chance event would be enough for a species to expand its range over a very wide area some thousand kilometres from the supposed centre of origin. Geological history of the earth is given as enough time for this single event to have happened with wind as the dispersal agent. For *R. regia* a chance transport from a probable centre of origin in Australo-Papuan region and dispersal as far as Tutuila Island does not tally with two important points: 1) occurrence of morphological and colour variations which are here considered good enough to establish several subspecific populations on various Pacific islands, and 2) the 'selective distribution' of the populations across the whole *R. regia* range.

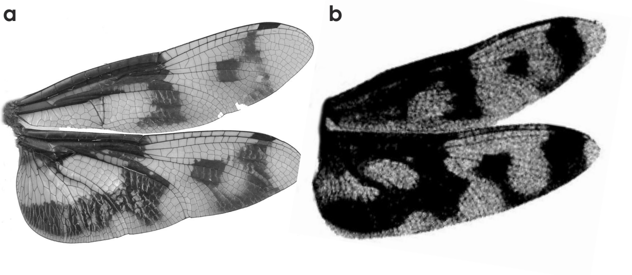


Figure 22. Comparison between the wing pattern of: a) *R. r. armstrongi*; b) *R. regia* from Saipan Island (from Lieftinck 1962).

Insular populations are not just colour variants of the same taxon. Even *R. regia* from Saipan, which Lieftinck (1962) considered as consubspecific to Samoan populations, shows some differences in the wing pattern compared to *R. r. armstrongi* (Fig. 22). I do not consider these differences enough to warrant a separate subspecific status and specimens from Saipan should be compared morphologically to support this assumption. I have removed them from *R. r. chalcoptilon* following the rearrangement of the *R. regia* subspecific taxa in the eastern end of its distribution. Wind dispersal, which is necessary to support the gene flow between Saipan and Samoa, is considered unlikely. *Rhyothemis* r. *armstrongi* in Samoa seems to be isolated morphologically and by wing colour from the closest populations in Wallis and Niuafo'ou islands which are more than 300-400 km apart. Therefore, they are unlikely to have shared the same gene stock with Saipan which is about 5,600 km away.

The term ‘selective distribution’ was introduced by Marinov (2015: figs 23-27) who noticed that the distribution of some Pacific taxa do not occupy all islands as it would have happened if transported by the wind. Some of these maps require updates following new data in order to rectify incorrect distributions. For example, the distribution of *Procordulia* Martin, 1907 (fig. 25) now should encompass Guadalcanal, Solomon Islands after Marinov (2016) and the distribution for *R. phyllis* and *R. regia* (fig. 27) commented above. However, even after those updates, the ‘selective distributions’ are obvious on the maps for certain taxa. An updated distribution for the entire range of *R. regia* is presented here where showing that the species seems to have ‘avoided’ certain islands on its way east; it has never been recorded on New Caledonia, Vanuatu and Fiji. If blown by the wind from Australia or New Guinea, why has it ‘skipped’ these much larger islands and yet become established on smaller islands as Wallis and Swains, for example?

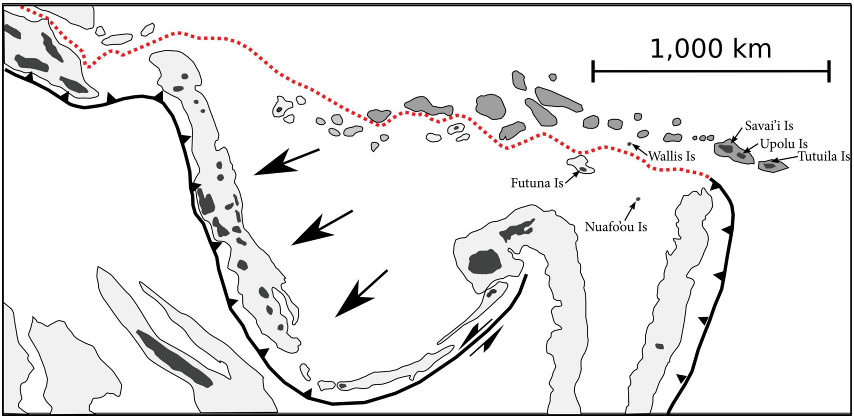


Figure 23. Opening of the North Fiji Basin. The current positions of the investigated islands are shown along the outline of the former Vitiaz Trench (red dotted line).

A vicariance model seems to better explain the distribution of the Pacific representatives of *R. regia* where their distribution follows the western edge of the Pacific plate. Some of the islands from this edge (Bismarck Archipelago, Solomon Islands, Vanuatu, Fiji and Tonga) once formed a continuous island arc, the Vitiaz trench, which was rifted apart into separate arcs by seafloor spreading (Heads 2014: 48). The origin of this trench is thought to have begun 100 Ma and is associated with the so-called rollback of East Gondwana subduction zone (Fig. 23). Expansion of this edge moved towards the Samoan volcanic hot spot. The present islands of this chain are geologically young with Savai’i ~ 5 Ma being the oldest (Koppers et al. 2008), however, there is evidence that presently submerged islands westward were part of the same volcanic chain that was active within the region for at least 40 Ma (cf. Grehan & Mielke 2020). Therefore, the spatial relations between Vitiaz Trench and Samoan volcanic hot spot are tens of millions of years old. Pelletier & Auzende (1995) hypothesised that the current arrangement of the islands in this part of the Pacific is due to the opening of the North Fiji Basin that resulted in pushing the Vanuatu islands southwest and displacing Fijian islands from the alignment of the former Vitiaz Trench creating largely disjunct areas for the ancestral species to occupy the present day islands.

Tectonic spreading events have been correlated by Heads (2014, 2017) for an immense range of animal and plant taxa. Using this model, Grehan & Mielke (2020) commented on the importance of Vitiaz Trench in the distribution of hepialid moths and allopatry of the genera Abantiades Herrich-Schäffer, 1855 (continental Australian) and *Phassodes* Bethune-Baker, 1905 (oceanic islands). This hypothesis has been adopted here for explanation of the distribution of *R. regia*.

The eventual history of the evolution of *R. regia* subspecies within the study area is reviewed in conjunction with the view expressed by Marinov (2015) who commented on the possible relation between the distribution of particular taxa and their geological age plus ecological specialisation. Marinov (2015) hypothesised that the evolution of the taxa may have resulted in a shift from ecological specialisation from eurybionts to stenobionts. Geologically 'older' taxa become more stationary and 'reluctant' to occupy new niches that may not be correspondingly transported with the movement of the islands

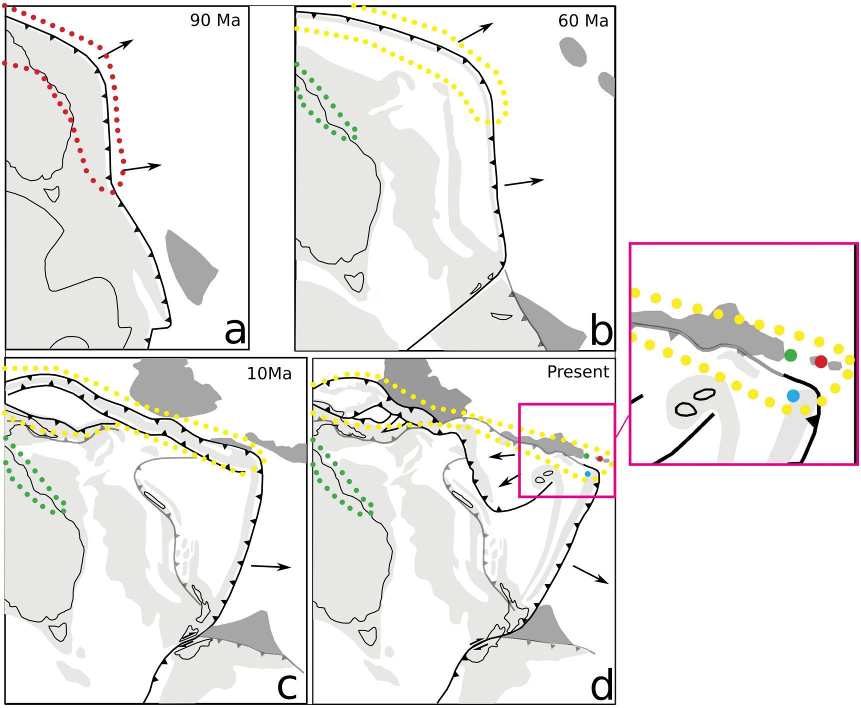


Figure 24. Hypothesised origin of the *R. regia* populations within the study region. Dotted lines are for the possible distribution of: common ancestor (red), green (*R. princeps*), yellow (*R. regia*). Dots represent the current positions of: Samoa (red), Wallis (green) and Niuafo'ou (blue).

or island arcs they live on. However, the age of a taxon may not necessarily result in significant morphological differentiation between spatially isolated populations. Many of the so called 'living fossils' on the planet are evident that the evolution of the organisms is not happening with the same pace constantly over time. Therefore, the model of the evolution of the Pacific *Rhyothemis* assumes that the insular populations, although morphologically insufficient to be considered separate species, may have an age related to geological events tens of millions of years old.

Pacific *Rhyothemis* may have evolved with the so-called rollback of East Gondwana subduction zone. Figure 24 shows a hypothetical predecessor occupying eastern edge of the supercontinent 100 Ma ago. Survival at the edge along the Vitiaz Trench may have been associated with speciation and divergence of the two congeners: *R. regia* and *R. princeps*. Transport of *Rhyothemis* populations eastward probably separated what had become *R. princeps* (remaining around the Australia-New Guinea region) from *R. regia* which was brought closer to the Samoa hot spot allowing it to populate other islands within the area investigated here. The distribution to the neighbouring islands of Niuafo'ou, Wallis, Swains (possibly others with freshwater sources) was not dependant by a long distance dispersal but may have been determined by typical flight dispersal within what was once an archipelago at the junction between Vitiaz and Tonga trenches.

A third member of the genus, *R. phyllis* (Sulzer, 1776), is widely distributed from SE Asia through the Pacific and Australia. This is possible if *R. phyllis* is considered to be with higher ecological plasticity than *R. regia* and *R. princeps*, which may be related to a supposed geologically 'younger' age. Higher mobility of the species and 'readiness' to be transported with the drift of the island arches is different from the long-distance dispersal. The large number of subspecies and wing colour variations of *R. phyllis* is achievable with a spatial isolation which is not possible in a wind assisted dispersal scenario. Both *R. phyllis* and *R. regia* were found to co-exist in multiple habitats over Wallis Island. On the other hand *R. regia* is not established from New Caledonia, Vanuatu and Fiji where only *R. phyllis* has been found so far. It is possible that by the time of the opening of the North Fiji basin (~10 Ma) *R. regia* may have already become well established around the islands marking the outline of the Vitiaz Trench and did not disperse to the islands forming now Vanuatu and Fiji. Assuming *R. regia* 'persisted' along and close to the outlines of the former Vitiaz Trench it could be viewed as another example of the so-called 'subduction zone weed' (Grehan & Mielke 2020) surviving in situ as a metapopulation in a way commented widely for many groups by Heads (2012) for oceanic islands. Molecular analysis is needed to reveal the phylogenetic relationships between the populations but should not be used for predicting the separation times. Calibration of molecular clocks may lead to underestimates of the dating of the actual events (Heads 2014).

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An update of the Odonata fauna of Wallis & Futuna (Insecta: Odonata)

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Abstract

Odonata fauna of the islands of Wallis and Futuna has been investigated during a two week field trip in 2020 and occasional observations in 2007-2012. Updated species checklist and faunistic information following nomenclature changes, new taxonomic information and distribution data are proposed. Presently, 15 species are known from Wallis & Futuna. They are presented with photos of live individuals and exuviae (where available) which is hoped to facilitate easy identification in the field by professionals and general nature lovers.

Abstract in French

Les Odonates des îles de Wallis et Futuna ont été recensés au cours d’une mission de terrain de deux semaines en 2020 et des observations occasionnelles de 2007-2012. Nous proposons dans cette publication, une liste à jour des espèces, des précisions faunistiques et taxonomiques à la suite des changements récents de nomenclature, ainsi que des compléments sur les distributions géographiques. Actuellement, 15 espèces sont connues des îles Wallis & Futuna. Elles sont illustrées par des photos d'individus vivants et d'exuvies (le cas échéant), ce qui devrait faciliter leur identification sur le terrain par les professionnels, et plus généralement, par les amoureux de la nature.

Abstract in Wallisian / Fakamatala fakanounou i te lea faka'uveá

I te ta’u 2020 ne'e tau mai he folau gāue vāha'a lua ki 'Uvea mo Futuna o fakahoko ai 'ia te fakaauau o fa'ahiga pūpū 'e feala ke ma'u i 'otatou motú. Ko gaue aeni ne’e kamata ekenaki i te ta’u 2007 pea mo te ta’u 2012.

Koia, 'e feala anai ke ma’u i te ki’i tohi nei, 'ia higoa o fa'ahiga pūpū kehekehe 'e ma'u nei 'iō tātoú, o fēia ki te 'ū higoa fo'ou mo fakamahino pē logo kehe o 'uhiga mo nātou pea mo kogame'a 'e feala ke natou mā'uli ai.

I te 'aho nei, kua feala ke tou lau ko fa'ahiga pūpū kehekehe e 15 'e ma'u i 'otatou motú.

'E kotou mamata anai ki ai i te 'ū pākí: ko 'ihi ko ni pūpū ma'uli, mo 'ihi leva ko 'onatou ga'asi sinó fakaunú (mokapau ne'e mole feala ni'onatou pāki ma'uli). 'E fīmalie anai kiā nātou 'e gāue ki te 'ū manú kae tāfito age foki lā ia kiā nātou 'e mamana ki te ulufenuá.

Abstract in Futunian

I le fetu’u 2020 na tau mai ai a se folau gā’oi vasa’a lua ki Uvea mo Futuna o fakasoko ai a le fakamaau o fa’asigā mūmū e mafai ke ma’ua i otātou a motu. Ko gā’oi anei na kamata fakatu’utu’u mai mei le fetu’u 2007 ti mo le fetu’u 2012. Koia e mafai ke fakasā i le gā tosi leinei a se lisi mo ‘igoa o fa’asigā mūmū kesekese e ma’ua i otātou la o fela’aki ai ki ‘igoa fo’ou mo fakamatalatala pe logo fo’ou o ‘uiga mo lātou ti mo kogāne’a e mafai ke lotou ma’uli ai. I le ‘aso nei, kua mafai ke tou lau ko fa’asigā mūmū kesekese e 15 e ma’ua i motu e lua la. Ko gā manu anei e fakasā loa i pāki, ko ‘iki e ma’uli ti ko ‘iki loa e fakasā i olātou ga’ati’i tino, koga nei ke fakafaigaofie’i ai kia lātou ko le kau gā’oi a le fakakesekese’i o gā manu, kae tāfito ake loa kia lātou e mamana ki le ulufenua.

Key words: Checklist, Central Pacific, melanisation, *Pseudagrion microcephalum*, *Diplacodes trivialis*, *Rhyothemis phyllis*, *Rhyothemis regia uveae*

Introduction

Papazian et al. (2007) is the only published study on the Odonata of the small islands of Wallis (77.9 km^2) and Futuna (46.3 km^2). It was based on a hydrobiological study conducted by one of us (NM) with a summary report produced for the Ministry of Overseas Territories, France (Mary et al. 2006). The study focused on nymphs, but adults of 10 species were also collected and included in Papazian et al. (2007). Grand et al. (2014, 2018) added four species to the Odonata fauna of the two islands by including them in the key to the Odonata of New Caledonia, Wallis & Futuna.

Wallis was mentioned in several previous papers during discussions on the distribution of *Rhyothemis regia chalcoptilon* (Brauer, 1867) (Lieftinck 1948, 1959, 1962). More on these discussions can be found in Marinov (2021), which is another outcome of the present study specifically dealing with the *Rhyothemis regia* (Brauer, 1867) populations from eastern part of the species distribution.

The present study was sparked by members of the public who started discussions on observed dragonflies on Wallis. Coming back from holidays on Wallis Is., Philippe Duvernay posted a picture of a very dark winged *Rhyothemis* Hagen, 1867 and a comment on the Facebook Group "Odonates de France et d'ailleurs" https://www.facebook.com/-groups/336812786402542/permalink/2317433758340425/ "Bonsoir, alors moi, j'y connais rien mais j'ai pris celle ci à Wallis, dans le Pacific sud. Je ne sais pas si elle est endémique, en tous cas, elle est assez fréquente sur l'ile. Merci à ceux qui pourront m'en dire plus." [Good evening, even if I don't know anything about it, but I took this one in Wallis, in the South Pacific. I do not know if it is endemic, in any case, it is quite common on the island. Thanks to those who can tell me more.] The comments followed with the interesting suggestions that it could be *Rhyothemis princeps* Kirby, 1894 which was the logical choice looking the intensively dark wings. However, *R. princeps* is known from Australia and New Guinea (Theischinger et al. 2021) which makes a too disjunct distribution for the species with no reasonable biogeographical explanation.

Further searches on social media platforms revealed another photo of the same species taken at Lalolalo Lake (Wallis Is.) on 10th September 2014 (http://erhanawallis.blogspot.com/2014/). One of us (RKJ) studied the collection of the late Daniel Grand at the Musée des Confluences in Lyon, France and in his bank of pictures. Daniel Grand was known for his passion around the Odonata of French overseas territories resulting in several articles in addition to his well-known book on dragonflies of France, Belgium, and Luxembourg (Grand & Boudot 2006). He studied particularly New Caledonia's Odonatofauna during three trips in 2004, 2010 and 2011 (see Daniel's French overseas territories bibliography), but had investigated some images taken from Wallis & Futuna which resulted in additions to the faunistic list and adding these Pacific islands to the key of the Odonata species from the region (Grand et al. 2014, 2018).

In addition to the *R. regia* records from Wallis Is., photos of what appeared to be *Pseudagrion microcephalum* (Rambur, 1842), another new species for the region, have been communicated to the principal investigator (J. Tennent, R. Garrison, pers. comm.). These all acted as incentive for the present study and contributed to the updated faunistic and taxonomic discussions on the Odonata of Wallis & Futuna presented here.

Unfortunately, these two islands do not have the popularity of their 'neighbours' Fiji (to the southwest) and Samoa (to the east). Therefore, an introduction to the environment, history and people of this interesting part of the Pacific is presented below.

Etymology of the names

Apart from French, the official language, two languages are used on Wallis & Futuna: Wallisian (Faka'uvea) and Futunian (Fakafutuna). Both are Polynesian, a part of the Malayo-Polynesian subgroup of the Austronesian family. The Malayo-Polynesian languages are mainly spoken by the peoples of the island nations of Southeast Asia, the Malay

Peninsula, the Pacific Ocean islands and Madagascar. In French Wallis-et-Futuna is generally written, but it is officially Territoire des îles Wallis et Futuna, and ’Uvea mo Futuna in Wallisian.

In Wallisian (Faka’uvea) ’Uvea is the toponym used to name the main island of Wallis Island (or even only the main island of the cluster occupying the lagoon) but its meaning is not known (C. Moyse-Faurie, in litt.). In French, this toponym is transcribed by Uvea and sometimes Uvéa (or even ‘Uvéa). Ouvéa is a perfect homophone for an island of the Loyalty (New Caledonia). It was named by the Wallisians who populated it during the XVIIIth century. To make the distinction between the two homonymous islands, their descendants use ’Uvea Mama’o (Uvea in the distance) for Wallis, and ’Uvea Lalo (down below ’Uvea or leeward ’Uvea), for Ouvéa in their language, West Uvean (Fagauvea). The first consonant of the toponym ’Uvea is called fakamoga in Wallisian (cough maker) and is a glottal stop, a phonem used all over the Polynesian area. The Academy of Wallisian and Futunian Languages has just validated the writing standards. They use the apostrophe for the glottal stop, even at the initial, while other Polynesian languages use another letter, the ‘okina. Even if the phonem exists in English (used in Cockney or in some vocalic attacks) no letter designates it. When naming *Rhyothemis regia uveae* Marinov, 2021 no apostrophe or ‘okina was used for the subspecific epithet, due to the lack of the phoneme in Latin and the difficulty to transcribe precisely the fakamoga by any other consonant.

Concerning the etymology of Futuna, Smith (1892, p. 33) evokes a possibility, the “place of futu”. Futu is the Futunian name for *Barringtonia asiatica* (L.) Kurz, a tree widespread throughout the Indo-Pacific Region. As Wallisians did for Ouvéa, Futunians reached a remote island in Vanuatu they named Futuna Lalo.

The etymology of the last island, Alofi, seems to be the name of the opposite side of the tau'a place where the kava chiefs sit, opposite the kava dish in the kava ceremony (F. Asi-Talatini, in litt.). It is also the hollow part of the body (e.g. the palm of the hand alofi lima) (https://pollex.shh.mpg.de/).

Geographic and geologic context

The Territory of the Wallis & Futuna Islands is located in the South Pacific Ocean at the western border of the Polynesian Triangle. Its neighbouring archipelagos are Tuvalu to the northwest, Fiji to the southwest, Tonga to the southeast, Samoa to the east and Tokelau to the northeast (Fig. 1). Unlike the latter, Wallis & Futuna is not an archipelago but consists of two groups of islands lying about 230 km away from each other: Wallis has an area of 77.9 km² rising to 151 m at Mt Lulu Fakahega, Futuna with 46.3 km² and a high point of 524 m at Mt Puke, and beyond a 1.8 km strait, Alofi at 17.8 km² (Mt Kolofau, 417 m).

Wallis consists of a low volcanic island, ’Uvea, surrounded by a barrier reef dotted with eight coral islets bordering a 220 km² lagoon from which some eight volcanic islets emerge.

Futuna and Alofi offer a very different aspect from that of 'Uvea. No barrier reef here, but a fringing reef, a hilly inland in Futuna, heavily bevelled by streams and a sloping plateau bordered by sometimes steep slopes for Alofi.

According to Pelletier (2003) the Pacific plate currently carries both groups of Wallis and Futuna Islands, though each of them have a different geological history, being

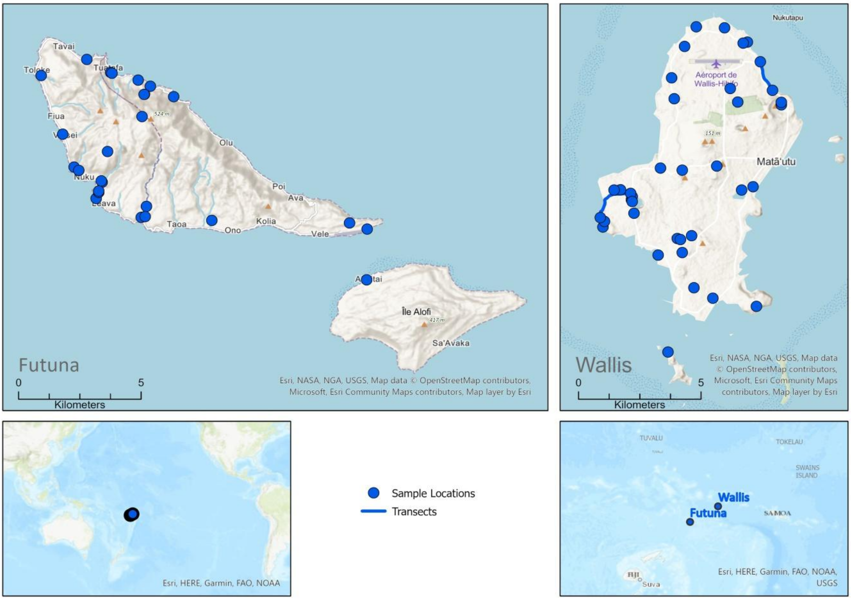

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Figure 1. Geographic situation of the study area.

located on both sides of a fossil subduction zone. The two groups are separated by a succession of deep trenches (over 4,500 m) running from the Tonga trench along the eastern termination of the Vitiaz fossil lineament and through the North Fiji Transform Fault Zone. This lineament separates the Cretaceous Pacific crust (to the north) from the North Fijian and Lau of mio-plio-quaternary age (to the south). Most authors consider this lineament was a converging border zone between the Pacific and Australian plates before the Miocene and the development of the North Fijian basin.

Part of a complex chain of seamounts, banks and islands bordering the Vitiaz lineament to the north, known as the "Northern Melanesian Borderland" (Pelletier 2003), Wallis is located along the middle Miocene to present day Samoan chain or ridge, originating from a hot spot now east of the Samoan Islands. ’Uvea and the volcanic islets are made up of basaltic flows and very recent pyroclastic deposits, of Superior Pleistocene age to sub-actual (less than 0.5 Ma). The nature and age (Late Cretaceous to Miocene?) of the island's bedrock lying on the Cretaceous age Pacific Plate remains unknown.

’Uvea consists of lava flows and associated pyroclastic rocks from 20 closely spaced vents. Some are broad, gently sloping shield volcanoes; others are tuff cinder cones so the island shows a gently undulating plateau, with only slight topographic relief (MacDonald 1945). A conspicuous feature of ’Uvea’s geography is the presence of six or so nearly circular craters with precipitous inner sides containing lakes or swamps resulting from a collapse at the summit of the volcanoes (MacDonald 1945). No perennial streams exist or thalwegs seem to notch the terrane, but the decomposition of rocks is deep.

Stearns (1945) claims that the well-formed barrier reef encircling 'Uvea was able to develop in the rapidly fluctuating seas of the late Pleistocene because of the existence of the gently shelving shore made by the low-dipping Pleistocene (?) lavas and the lack of streams on 'Uvea. He also suggested that the substructure of 'Uvea is a basaltic volcano built from the ocean floor during the Tertiary to about present sea level. During the early ice age, the eustatic low stands of the sea eroded the structure while a fringing reef appeared. Eruptions during the middle Pleistocene built the present 'Uvea. Very recently, 'Uvea entered the fourth phase of volcanism with the eruption of the Lalolalo and Lanutavake volcanoes. The present barrier reef is believed to be the relic of the barrier reef that grew upward from the in the late Pleistocene.

Futuna and Alofi are located south of the fossil Vitiaz lineament, in the junction zone between the Lau and North Fijian basins, near the North Fijian transform fault zone, one of the current segments of the boundary of the Pacific/Australian plates and one of the most active transform faults in the world. This sinistral motion transform zone connects the northern termination of the Tonga Trench to the oceanic accretionary axis of the central North Fijian Basin, through the northern edge of the Fijian plateau.

Grzesczyk et al. (1988) recognized three volcanic units. These indicate: i) the existence of an immature island arc which may correspond to a Pliocene southwards subduction of the Pacific plate along the northern Tonga trench termination, ii) a stage of transitional intraplate volcanism emphasising the end of subduction. After cessation of the volcanism, raised Pleistocene reef limestones evidence the uplift of the islands (more than 500 m). They highlighted the recent age of the volcanic and sedimentary formations (Pliocene to Pleistocene), and the constraints that this imposes on geodynamic reconstructions. They also pointed the rapid evolution of the nature of volcanism that reflects the complex revolution of the North Tonga termination over the last millions of years.

Authors have identified superimposed submarine volcanic formations of Pliocene to Pleistocene age, consisting mainly of pillow lavas, pillow lavas autobreccia, hyaloclastites and rare massive flows. Along the southern coast of Futuna and over almost all of Alofi, stepped reef terraces, rising up to 300 m on Alofi, of presumed Quaternary age covers these volcanic series. Authors interpret the modification of volcanism circa the end of the Pliocene as the marker of the passage from a convergent regime (subduction of Vitiaz-Tonga) to a transforming regime (North-Fijian fracture zone). The presence of pillow-lavas and raised reef limestones suggest that a phase of uplift followed the cessation of volcanism and was succeeded by a phase of over-erection and emersion of volcanic edifices, which is still active (Grzesczyk et al. 1988).

History

According to archaeological research, 'Uvea (presently named Wallis) and Futuna were populated between 900 and 800 B.C. by Austronesians (Sand 2000). Between the 11th and 16th centuries, 'Uvea was dominated by the Tongans, as evidenced by the remains of forts in the south. The first Europeans visited the islands in 1616 (Dutch navigators Lemaire and Schouten to Futuna) and 1767 (British captain Samuel Wallis to 'Uvea).

Many ships then made a stopover in Wallis, especially during the 19th century (Pechberty & Toa 2005) which lead to the introduction of the Catholicism in 1837 to both islands.

The first Western residents to settle permanently in Wallis were missionaries of the Society of Mary, with the aim of evangelising the population (Coffre 2010). The protectorate of Uvea was ratified in 1887. During the referendum of December 27, 1959, 94.4% of the electors voted for the Wallis & Futuna Islands to integrate the French Republic in the form of an Overseas Territory (TOM), a position conferred by the Law of July 29, 1961.

The French government is represented in Wallis & Futuna by a Prefect who ensures the executive of the local authority. There are no municipalities in Wallis & Futuna, but three administrative districts, each with legal entity and a district council chaired by a customary king. The districts correspond to the three kingdoms: 'Uvea in Wallis, and Alo and Sigave in Futuna.

A Territorial Council gets together the three customary kings with three personalities appointed by the prefect after agreement of the Territorial Assembly. The territorial council assists the head of the territory for the administration of the Wallis & Futuna Islands. In particular, it studies all the projects which might be submitted to the territorial assembly (https://www.wallis-et-futuna.gouv.fr/).

In 2003, Wallis and Futuna became a “Collectivité d'Outre-Mer”.

The population of Wallis & Futuna is 11,562 inhabitants (July 2018 census), two thirds of whom live in Wallis and one third in Futuna. In 2014, there were approximately 22,000 inhabitants in New Caledonia who considered themselves as Wallisians and/or Futunians (https://www.wallis-et-futuna.gouv.fr).

Environment

The islands of Wallis and Futuna enjoy a tropical maritime climate characterised by high temperature and high humidity. Precipitation is abundant and the sky is often overcast. Its climate is very regular, with barely marked seasons. The diurnal variations, in particular the thermal amplitude, are also very small (http://www.meteo.nc/19-wf-climat/57-wf-climat).

The average monthly temperatures change little, with an annual amplitude of around 1°C and an average of 27°C. The cooler months are from July to September. Precipitation follows a more marked seasonal rhythm than temperatures. It rains on average half as much in the "winter" months (less than 200 mm) than in January (400 mm). The average annual rainfall is 3,200 mm.

Although devoid of streams, Wallis is punctuated by crater lakes which constitute valuable reserves of fresh water for the island. Significant lakes are Lalolalo, Lanutavake and Lano. Futuna and Alofi islands are crossed by streams (https://fr.wikipedia.org/wiki/-G%C3%A9ographie_de_Wallis-et-Futuna).

Material and method

Most specimens come from the field studies of the first author from 29 February to 14 March 2020. Mainly adult odonates were collected with an aerial net and either killed in acetone, dried and transferred into paper envelopes or preserved in 95% ethanol for molecular analysis. Field notes on the biology and ecology of the species were also recorded, however, no specific investigations on these two topics have been carried out. Therefore, the results from the field visit should be considered preliminary. For some species, data on morphology and body colour are included as well as these were found important for taxonomic discussions. Microscopic pictures of diagnostic characters were produced using the equipment of the Plant Health and Environment Laboratory, Christchurch, Ministry for Primary Industries, in New Zealand. A series of images were taken under high power Nikon AZ100M microscope and stacked with Helicon Focus 6.7.1 software.

Additional observations and samples were taken by some of us: JT (2007-2009, 2011-2012) and HJ (2007-2008). Figure 1 shows the geographic situation of the islands and sampling localities for each of them. Some *R. regia* specimens collected from islands within the investigated area (Wallis and Swains) and deposited in Natural History Museum, London (NHMUK) were examined by photos only (courtesy of Ben Price) and shortly discussed in the section for this species.

Morphological description follows Watson & O'Farrell (1991) and wing venation designation is after Riek & Kukalová-Peck (1984).

Species checklists include photographs of all species recorded during the present study. Almost all of them were taken by the principal investigator from one of the studied islands. Additional photographs were selected from the archive of the late D. Grand (DG) taken during his studies on the Odonata of New Caledonia (Grand et al. 2019) and Haomiao Zhang (HZ) from China.

Two identifiers of the investigated islands were used: 'Wallis & Futuna' when referring to them as an administrative unit and 'Wallis and Futuna' for the geographic units.

Distribution records follow Papazian et al. (2007) and Grand et al. (2014).

The list of localities is mainly based on the data from the 2020 study (dates where no year included). Records from all other sampling dates and localities have been used by Grand et al. (2014) where the general species distribution was presented only. Here they are presented in detail for the first time. The following localities were investigated (districts/kingdoms in bold):

Wallis Island

1. Lake Kikila, **Hahake** (13.2947S, 176.1889W; 14 m a.s.l.): 29 February, 01, 06 March; 13 November 2007 (HJ).
2. Floods at Talietumu, Fort Tongien, **Mu'a** (13.3375S, 176.2094W; 24 m a.s.l.): 29 February.
3. Bushes at Pointe Matala'a, **Mu'a** (13.3456S, 176.1825W; 69 m a.s.l.): 29 February.
4. Lake Lanutavake, **Mu'a** (13.3220S, 176.2145W; 24 m a.s.l.): 29 February, 04 March; 14 November 2007 (JT, HJ).
5. Accommodation place, Mala'e, **Hihifo** (13.2502S, 176.1938W; 48 m a.s.l.): 29 February.
6. Canals in Nefunefu at Vaitupu, **Hihifo** (13.2298S, 176.1864W; 7 m a.s.l.): 29 February.
7. Lake Alofivai by the College Lano-Alofivai, **Hihifo** (13.2573S, 176.1718W; 34 m a.s.l.): 02 March.
8. Stream by the College Lano-Alofivai, **Hihifo** (13.2562S, 176.1718W; 37 m a.s.l.): 02 March.
9. RT1 S of Lake Lalolalo, **Mu'a** (13.3048S, 176.2352W; 53 m a.s.l.): 03 March.

10. RT1 by the Lake Lalolalo, **Hahake** (13.2989S, 176.2364W; 46 m a.s.l.): 03 March.
11. RT1 N of Lake Lalolalo, **Hahake** (13.2976S, 176.2360W; 47 m a.s.l.): 03 March.
12. Numerous puddles along a section of a secondary road of RT1 north of Lake Lalolalo, **Hahake** (13.2961S, 176.2367W to 13.3108S, 176.2486W; 41 – 18 m a.s.l.): 03, 05 March.
13. Marais sanglants, 'Bloody swamps', **Mu'a** (13.3084S, 176.2480W; 8 m a.s.l.): 03 March.
14. Ocean beach Tetoki, **Mu'a** (13.3067S, 176.2498W; 0 m a.s.l.): 03 March.
15. Lake Lano, **Hahake** (13.2945S, 176.2410W; 14 m a.s.l.): 03 March.
16. Lake Lanutuli, **Mu'a** (13.3159S, 176.2166W; 13 m a.s.l.): 04 March.
17. Open grass vegetation near the Chapelle Saint Pierre Chanel, **Mu'a** (13.3163S, 176.2152W; 65 m a.s.l.): 04 March.
18. Lake Lanumaha, **Mu'a** (13.3147S, 176.2104W; 40 m a.s.l.): 05 March.
19. Transect with canals in east part of the island close to chapelle du Sacré Cœur, Mafu Tapu Alele, **Hihifo** (13.2384S, 176.1808W to 13.2510S, 176.17554W; 5 – 6 m a.s.l.): 07 March.
20. Nefunefu Taro fields, NE part of the island Vaitupu, **Hihifo** (13.2303S, 176.1882W; 5 m a.s.l.): 08 March.
21. Vaimea Taro fields, NE part of the island Vailala, **Hihifo** (13.2236S, 176.1962W; 7 m a.s.l.): 08 March.
22. Gravel pit in the NW part of the island Tufuone, **Hihifo** (13.2231S, 176.2084W; 11 m a.s.l.): 08 March.
23. Secondary road, W part of the island Lalokea Tufuone, **Hihifo** (13.2317S, 176.2135W; 19 m a.s.l.): 08 March.
24. RT1, W part of the island Ulugivai Tufuone, **Hihifo** (13.2455S, 176.2190W; 18 m a.s.l.): 08 March.
25. RT1, W part of the island, **Hihifo** (13.2546S, 176.2179W; 50 m a.s.l.): 08 March.
26. RT1, W part of the island close to the junction with RT3, **Hahake** (13.2850S, 176.2238W; 26 m a.s.l.): 08 March.
27. RT3 N of Mount Hologa, **Hahake** (13.2859S, 176.2145W; 56 m a.s.l.): 08 March.
28. Small pond (ca 5 m²) in a pine plantation W of Mt Loka, N of RT11, **Hihifo** (13.2561S, 176.1905W; 60 m a.s.l.): 02 November 2007 (JT)
29. Taro field by Mala'efo'ou, Mu'a (13.3420S, 176.2013W; 6 m a.s.l.): 10 November 2007 (HJ)
30. Mangrove by Mala'etoli, Mu'a (13.3231S, 176.2249W; 5 m a.s.l.): 12 November 2007 (HJ)
31. Secondary forest by Lake Lano, **Hahake** (13.2947S, 176.2439W; 27 m a.s.l.): 12 November 2007 (JT)
32. Taro field by Taumata, **Hahake** (13.2932S, 176.1839W; 12 m a.s.l.): 13 November 2007 (HJ)
33. Lalolalo Lake, **Hahake** (13.2997S, 176.2360W; 46 m a.s.l.): 14 November 2007 (HJ)
34. Mt Holo, garden, **Hahake** (13.2842S, 176.1996W; 125 m a.s.l.): 26 November 2008 (JT)

Nukuatea Island

35. Pointe Mata'aho, **Mu'a** (13.3656S, 176.2206W; 7 m a.s.l.): 12 November 2007 (HJ)

Futuna Island

36. Accommodation place Ono, **Sigave** (14.3068S, 178.1166W; 30 m a.s.l.): 09 March.
37. Vaifau pond, **Sigave** (14.2820S, 178.1548W; 252 m a.s.l.): 10 March.
38. Leava River and taro fields, **Sigave** (14.2930S, 178.1568W; 7 m a.s.l.): 10 March.
39. Floods in Nuku village, **Sigave** (14.2876S, 178.1670W; 15 m a.s.l.): 10 March.
40. Stretch of Vainifao River, **Sigave** (14.3057S, 178.1424W to 14.3018S, 178.1405W; 11-101 m a.s.l.): 11 March.
41. Stream in Vaisei, **Sigave** (14.2757S, 178.1712W; 8 m a.s.l.): 11 March.
42. Roadside N part of the island Tavai, **Sigave** (14.2487S, 178.1624W; 0 m a.s.l.): 11 March.
43. Taro field Tuatafa near Vai stream, **Alo** (14.2534S, 178.1536W; 9 m a.s.l.): 11 March.
44. Trickle crossing the RT1 Tuatafa near Vai stream, **Alo** (14.2537S, 178.1532W; 9 m a.s.l.): 11 March.
45. Taro field by Ogea, **Alo** (14.2584S, 178.1391W; 12 m a.s.l.): 11 March.
46. Roadside puddle by Pouma, **Alo** (14.2622S, 178.1305W; 32 m a.s.l.): 11 March.
47. Streams crossing the road about 3-4 km NW from Poi, **Alo** (14.2751S, 178.1161W; 2 m a.s.l.): 11 March.
48. Open grass area by the chapelle de la Sainte Famille Toatafa, Kapau, **Alo** (14.2562S, 178.1436W; 10 m a.s.l.): 12 March.
49. Touristic track to Mt Puke, Tuatafa, **Alo** (14.2613S, 178.1413W; 236 m a.s.l.): 12 March.
50. Stream crossing the touristic track to Mt Puke Tuatafa, **Alo** (14.2613S, 178.1414W; 236 m a.s.l.): 12 March.
51. Pond under Mt Puke, **Alo** (14.2693S, 178.1421W; 457 m a.s.l.): 12 March; 18 November 2008 (JT); 18 May 2011 (JT)
52. Mangrove by Leava, **Sigave** (14.2989S, 178.1590W; 6 m a.s.l.): 07 November 2007 (JT)
53. Leava, garden, **Sigave** (14.2967S, 178.1580W; 14 m a.s.l.): 09 November 2007 (JT); 19 November 2008 (JT)
54. Taro field by Nuku, **Sigave** (14.2888S, 178.1653W; 5 m a.s.l.): 16 November 2008 (JT); 17-18 November 2008 (JT); 12 May 2009 (JT)
55. Vainifao river, pool, **Alo** (14.3055S, 178.1410W; 96 m a.s.l.): 16 November 2008 (JT)
56. Taro field by Toloke, **Sigave** (14.2545S, 178.1791W; 13 m a.s.l.): 16 November 2008 (JT)
57. Leava, taro field, **Sigave** (14.2926S, 178.1571W; 9 m a.s.l.): 12 May 2009 (JT)
58. Ditch, service de l'environnement (Department of the Environment), **Sigave** (14.2967S, 178.1580W; 14 m a.s.l.): 17 May 2009 (JT)
59. Coco plantation, Vele, **Alo** (14.3078S, 178.0661W; 72 m a.s.l.): 13 May 2011 (JT)
60. Mangrove, Vele, **Alo** (14.3100S, 178.0596W; 17 m a.s.l.): 14 May 2011 (JT)
61. Leava, supermarket, **Sigave** (14.2962S, 178.1580W; 18 m a.s.l.): 05 June 2012 (JT)

Alofi Is.

62. Coast and fields, Alofitai, **Alo** (14.3283S, 178.0598W; 13 m a.s.l.): 21 November 2008 (JT)

Results

Species checklist

Family Coenagrionidae Kirby, 1890

Agriocnemis exsudans Selys, 1877 (Fig. 2)

Localities: 1; 8; 12-13; 15-16; 18-19; 21-22; 29; 38-40; 44; 50-51 (12 March 2020, 18 November 2008); 54 (17-18 November 2008); 56

Adults did not seem to have any special habitat preference and were observed at most localities.

Previously reported for Wallis (Papazian et al. 2007; Grand et al. 2014) and Futuna (Grand et al. 2014).

Figure 2. *Agriocnemis exsudans*: a) mature male; b) immature male; c) mature female; d) immature female (DG).

Figure 3. *Ischnura aurora*: a) tandem with an immature female; b) adult female.

Ischnura aurora (Brauer, 1865) (Fig. 3)

Localities: 1; 7; 16; 18; 32; 38-39; 46; 54 (16 November 2008, 12 May 2009); 56

Very common species, which is easily overlooked due to its small size. Typical occupant of marginal emergent vegetation where mating pairs were observed even during rain. Previously reported for Wallis and Futuna (Papazian et al. 2007; Grand et al. 2014).

Pseudagrion microcephalum (Rambur, 1842) (Fig. 4)

Localities: 1; 4; 10; 12; 15; 17; 33

Figure 4. *Pseudagrion microcephalum*: a) male perched on a dead twig; b-c) males perched on leaves of *Hibiscus tiliaceus*.

Figure 5. *Hibiscus tiliaceus* growing along the water edge. Leaves and dead twigs are the most likely places to observe *P. microcephalum*.

Imagines keep very close to the riparian bush vegetation represented mainly by *Hibiscus tiliaceus* L. (Fig. 5). The tips of dead branches sticking out of the water were the most common perching sites (Fig. 4a). Adults perched on leaf surfaces as well (Fig. 4b-c).

Selected sites were always at least in half shadow. One teneral female was found in bushes high on the hilltop about 500 m from the closest possible place suitable for the development of the nymphs of the species.

Pseudagrion microcephalum individuals looked darker compared to populations from other islands, however, no illustrations of the diagnostic traits are provided in here for comparison (but see the Discussion).

First record for Wallis. Not known from Futuna.

Family Aeshnidae Rambur, 1842

Anaciaeschna jaspidea (Burmeister, 1839) (Fig. 6)

Locality: 61

A single dead specimen found in the supermarket of Leava.

Previously reported for Futuna (Grand et al. 2014). Not known from Wallis.

Figure 6. *Anaciaeschna jaspidea*, male (HZ).

Anax guttatus (Burmeister, 1839) (Fig. 7)

Localities: 1; 4; 7; 15-16; 18; 37; 51 (12 March, 18 May 2011); 57

In addition to the localities given above only one individual was observed crossing the over-vegetated bottom of the lake at Locality 16 (Fig. 8) without any evidences for breeding. *Anax guttatus* was established as a common breeder in other lakes on both islands. Exuviae were found from low in the grass vegetation (Fig. 9a) to about 2.75 m above the water (Fig. 9b). Females were observed to oviposit alone.

Previously reported for Wallis (Papazian et al. 2007; Grand et al. 2014) and Futuna (Grand et al. 2014).

Figure 7. ***Anax guttatus*****: a) male (DG); b) male, close view; c) female, close view; d) exuvia.**

Figure 8. Overgrown water bodies on the bottom of Lake Lanutuli, Locality 16.

Figure 9. ***Anax guttatus*****, exuviae (arrow): on tree branch at about 2.75 m above the water.**

Family Libellulidae Rambur, 1842

Diplacodes bipunctata (Brauer, 1865) (Fig. 10)

Localities: 1-2; 4 (14 November 2007); 7; 12-13; 16-18; 37-40; 42-43; 45; 48; 51-52; 54 (12 May 2009); 55

Adults have been observed in the grass vegetation close to the water edge or perching directly on the ground of secondary roads away from the wetlands.

Previously reported for Wallis (Grand et al. 2014) and Futuna (Papazian et al. 2007; Grand et al. 2014).

Figure 10. *Diplacodes bipunctata*, male.

Figure 11. *Diplacodes trivialis:* a) mature male.

Diplacodes trivialis (Rambur, 1842) (Fig. 11)

Localities: 1-2; 7; 18; 21

This species is probably more widespread than the localities presented in here. It may have been overlooked due to its size and colouration especially of tenerals (Fig. 11b). In Locality 1 the adults were more abundant in the grasses where they were active even during rain.

First record for Wallis. Not known for Futuna.

Figure 11. *Diplacodes trivialis:* b) immature male; c) immature female. Note the infestation of mites on the body.

Figure 12. *Lathrecista asiatica*, male.

Lathrecista asiatica (Fabricius, 1798) (Fig. 12)

Localities: 12-13; 19; 28; 35; 46; 49; 53 (19 November 2008)

Observed predominantly in shaded places with almost complete vegetation cover from the trees along the secondary roads (Fig. 13), deep inside forests, or roadsides puddles overshadowed by the trees.

Previously reported for Wallis and Futuna (Grand et al. 2014).

Figure 13. Typical perching sites of *L. asiatica*, puddles along a secondary road at Locality 12. Note the tree canopy provides almost a 100% cover on the site.

Macrodiplax cora (Kaup in Brauer, 1867) (Fig. 14)

Localities: 1; 3; 4; 7; 15; 18; 30-31; 34

In wetlands individuals most often perch on dead branches just above the water surface or as high as 3 m. Oviposition was observed in tandem.

Previously reported for Wallis (Grand et al. 2014). Not known from Futuna.

Figure 14. *Macrodiplax cora*, male.

Orthetrum serapia Watson, 1984 (Fig. 15)

Localities: 1-2; 4 (14 November 2007); 7-8; 11-13; 15-19; 22; 37-38; 40-43; 45-46; 51 (18 May 2011); 53 (09 November 2007); 54 (12 May 2009); 55

One of the most abundant species on both islands. Observed in a wide range of habitats; one of the compulsory faunistic elements in taro fields (Fig. 16).

Figure 15. *Orthetrum serapia*, male.

Figure 16. Taro field plantations, typical habitat of *O. serapia*, *D. bipunctata*, *P. flavescens*: a) Locality 20; b) Locality 45.

Figure 17. Comparison between *O. serapia* with increased melanisation (a) and the most common type of colouration (b).

Individuals with increased melanisation (Fig. 17a) were often observed during the study. The differences were impossible to be related to age.

Previously reported as *O. sabina* (Drury, 1798) for Wallis (Papazian et al. 2007; Grand et al. 2014) and Futuna (Grand et al. 2014).

Pantala flavescens (Fabricius, 1798) (Fig. 18)

Localities: 1; 3; 7; 10-12; 15; 18; 22; 26; 36; 38-40; 42-43; 45-46; 48; 51 (12 March 2020, 18 November 2008); 55; 62

Very common on both islands often found away from the wetlands along the roadside vegetation.

Previously reported for Wallis and Futuna (Papazian et al. 2007; Grand et al. 2014).

Figure 18. ***Pantala flavescens*****: a) immature male (DG); b) mature male in flight (DG); c) exuvia.**

Rhyothemis phyllis (Sulzer, 1776) (Fig. 19)

Localities: 1-2; 7; 12; 16; 18-21; 23-24

Prefers open waters with areas of emergent vegetation (Fig. 20a). Individuals were observed also in Locality 16 which is overgrown almost completely leaving for a few small ponds (Fig. 20b). They were perching on dense vegetation or single emergent plants close to the water edge (Fig. 20c). Often found away from the wetlands along the roadside vegetation.

The wing colourations of a total of 20 (seven specimens checked in the lab and 13 live individuals) have been compared using images taken under a microscope or caught and released in the field. With only one exception they were all found to be almost identical (Fig. 21a). The only deviation from this pattern was observed in one specimen with increased melanisation (Fig. 21b). The dominant wing colour pattern was found to be closer to specimens collected from Vanuatu (Fig. 21c) than to *R. p. dispar* Brauer, 1867, Fiji (Fig. 21d). A comparison (*R. phyllis* from Wallis in brackets) between the wings shows that *R. p. dispar* has darker wings especially on the leading edges of both wings with a characteristic dark band between C and RA proximal to nodus which expands to RP1 distally; the band is almost complete with a lighting for a few postnodal cells in FW (reduced to a dark spot around the nodus, base of the wings clear or restricted to a few patches on crossveins close to the base); in HW the band occupies similar area with an additional lightening close to the pt where the dark reaches RA and is obscure to RP1 (completely transparent); FW triangle area covered with amber colour (clear) and HW dark spots: anterior covers the triangle reaching to MP (may pass through the posterior end of the triangle) and posterior crosses anal loop reaching MA (going half way through the anal loop or to AA1; if reaching MA it is a short elongation of the spot along a single vein). Therefore, no subspecific name is proposed here for the populations from Wallis.

Previously reported for Wallis (Papazian et al. 2007; Grand et al. 2014). Not known for Futuna.

Figure 19. *Rhyothemis phyllis*, male.

Figure 20. Habitats for *R. phyllis*: a) Locality 18, wide areas with emergent aquatic vegetation were found to be a favourite site; b) Locality 16, one of the few pools found at the bottom of Lake Lanutuli; c) two species at Locality 16: *R. phyllis* (right) and *M. cora* (left).

Figure 21. Comparison between the wing pattern of males of: a) *R. phyllis*, Wallis Island – most common colour pattern; b) *R. phyllis*, Wallis Island – increased melanisation; c) *R. phyllis*, Aneityum Island, Vanuatu; d) *R. p. dispar*, Fiji.

Rhyothemis regia uveae Marinov, 2021 (Fig. 22)

Localities: 1-2; 4; 7; 10; 12; 15-18; 22-23

Dark *Rhyothemis*-like individuals observed at three localities in Futuna (29-30, 42), however, no specimens collected. Therefore, the species is not included for Futuna.

Figure 22. *Rhyothemis regia uveae*, male.

Figure 23. Perching positions for *R. r. uveae*, males usually select dead branches and face to the wetland.

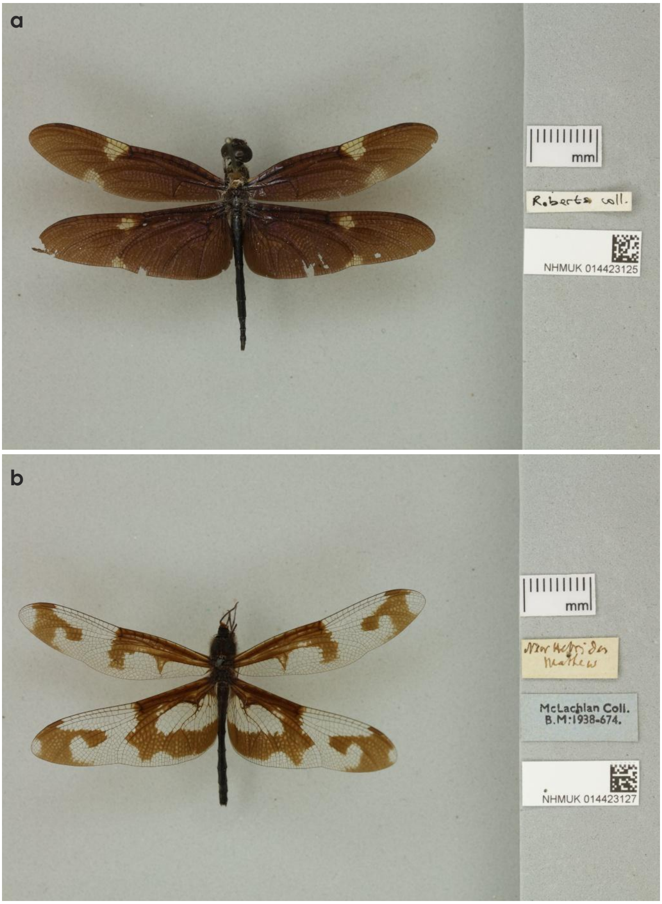

Figure 24. Wing colouration of *Rhyothemis regia* specimens deposited in NMHUK: a) male, NHMUK014423125, locality label not available; b) female, NHMUK014423127, locality label difficult to read, but probably 'New Hebrides', now Vanuatu; c) female, NHMUK014423128, Wallis Island; d) male, NHMUK014423129, Swains Island.

No evidence for reproduction in Locality 16 (overgrown lake) – only passing individuals and a few perched on the emergent vegetation. Adults were active for most of the day. Males fight for perching sites with conspecifics. No aggressive interactions observed with *R. phyllis*. Adults predominantly select branches of bushes where they usually perch facing the wetland (Fig. 23). Mating was observed early in the morning. Female oviposited guarded by the male from the air. Often found away from the wetlands along the roadside vegetation.

Previously reported for Wallis as *R. r. chalcoptilon* (Lieftinck 1948, 1959, 1962; Papazian et al. 2007; Grand et al. 2014). Grand et al. (2014) reported it for Futuna, however, this record needs validation because the species was not established as surely breeding for the island during the most recent field study (Marinov 2021).

Lieftinck (1959) commented on the distribution and polychromatism of *R. regia* specimens from Wallis, Swains and Samoa deposited in NHMUK. These records have been discussed in Marinov (2021), however, photos of the museum specimens were unavailable and not included in the study. Images of 19 specimens (NHMUK014423118 – 36) collected from the three island groups were inspected for the present study. Not all hand written labels were easy to read, therefore most of the specimens were not considered further in the analysis. Figure 24 shows the wing patterns of four selected specimens. Discussion is provided below.

Figure 25. *Tholymis tillarga*: a) adult male (DG); b) immature male (DG); c-e) exuviae.

Tholymis tillarga (Fabricius, 1798) (Fig. 25)

Localities: 1; 4; 6-8; 11-12; 15; 19-21; 46; 51 (18 May 2011)

Active mainly early in the morning or late afternoon. One of the few species which remained on wing during light rain. Mating occurs in flight for about 25 s and oviposition commences immediately. Female oviposits were rarely guarded alone.

Previously reported for Wallis (Papazian et al. 2007; Grand et al. 2014) and Futuna (Grand et al. 2014).

Tramea transmarina Brauer, 1867 (Fig. 26)

Localities: 1; 3-5; 7; 9; 13; 15-19; 25-27; 37; 39; 51 (12 March, 18 May 2011); 58-60

One of the most common species on both islands found in various habitats (Fig. 27). Imagines were often observed away from the wetlands along the roadside vegetation. Oviposition was performed in tandem or alone.

Previously reported for Wallis and Futuna (Papazian et al. 2007; Grand et al. 2014).

Figure 26. *Tramea transmarina*: a) male; note the photo was taken of an individual which was caught and released on the twig; b) exuvia.

Discussion

This study adds two new species to the Odonata fauna of Wallis & Futuna: *P. microcephalum* and *D. trivialis*, both found on Wallis only. These faunistic results are in accordance with what we would expect considering the wide global distribution of the species found on the two islands with endemism confined only to the subspecies level (see Marinov 2021 for discussion on *R. r. uveae*).

We could not validate the presence of *Agriocnemis argentea* Tillyard, 1906, which was included in the key of Grand et al. (2014) based on archived photos. The species turned out to be *P. microcephalum*. *Agriocnemis argentea* is known only from Australia thus far (Theischinger et al. 2021) and is unlikely to be found in Wallis & Futuna.

Anaciaeschna jaspidea is known from one dead specimen found in a shop in Leava. It is unclear if the single specimen was an accidental visitor to the island or a member of an established population. Therefore, the autochthony of the species needs validation from further studies. This is a predominantly crepuscular species, which occasionally may be seen during daylight (Marinov et al. 2015) and may have been overlooked so far for Futuna. *A. jaspidea* may also be only an accidental vagrant to this region.

The lack of observations of Corduliidae is surprising. *Hemicordulia* Selys, 1870 is a genus with a wide distribution across the Pacific and has been discussed by several studies but still needs a thorough revision (Marinov et al. 2019b). It is represented with at least three species in Samoa (Marinov et al. 2013) and at least two species in Fiji (Marinov 2019). On several occasions, we saw dark green *Hemicordulia*-like individuals in flight. However, those may have been mistaken with the melanistic variant of *O. serapia*.

Figure 27. Habitats for *T. transmarina*: a) Locality 4; b) Locality 29; c) Locality 51.

Increased melanisation has been observed on some individuals of the following species: *O. serapia, P. microcephalum* and *T. transmarina* (a female with very dark at the base of the wings). It was most obvious on *O. serapia* with some individuals having almost completely black abdomen on the dorsum of S3-10 spared for a yellow area on the middle of S6 (Fig. 16a). No specimens were collected to check their affinity under a microscope. All have been identified in the field as darker variants of *O. serapia* because this species is not known to produce any subspecies and to express a significant age-related colour morphism within its range. This is an interesting topic for future studies. It is unclear if the increased melanisation could be attributed to environmental factors such as temperature. The water temperatures were measured to as high as 35.2°C (under the *H. tiliaceus* bushes, which were typical perching sites of *P. microcephalum*) and 37.6°C (open areas where exuviae of *T. transmarina* and *A. gutattus* have been found) with one extreme of 41.4°C at Locality 1 (Fig. 27).

Melanisation on the bodies of *P. microcephalum* has to be proven by further lab work on comparison between specimens from the entire species range as done on the morphology of the male appendages in Vanuatu (Marinov et al. 2019a). No updates are provided in this study because Pacific representatives of genus *Pseudagrion* Selys, 1876 have been passed on to students from Brigham Young University, USA. The results of this study will be published elsewhere.

Increased melanisation was contemplated by previous authors as a possible explanation of the observed differences between the wing patterns of populations of *R. regia* inhabiting Wallis and the neighbouring islands of Samoa and Tonga. Those have been considered as variants/forms or subspecies (for a review on this topic see Marinov 2021) until the taxonomic revision where Marinov (2021) proposed the following endemic taxa for the region: *R. r. armstrongi* Fraser, 1956 (Samoa), *R. r. chalcoptilon* (Brauer, 1867) (Niuafo'ou Is, Tonga) and *R. r. uveae* (Wallis). Wing colour pattern was demonstrated to be of a diagnostic importance because it was found to be in congruence with certain morphological features on the male superior appendages (Marinov 2021).

Important updates to the discussion in Marinov (2021) have been derived after completion of the study. Images of specimens collected from Wallis, Swains and Samoa and deposited at the NHMUK collection have been inspected and some of them presented here on Figure 24 with the following discussion points:

1) NHMUK014423125 has no locality label, but the wing colouration is closest to the pattern presented in Marinov (2021: fig. 19b) for *R. princeps* from Australia. However, precise identification is not possible unless morphology is studied from the actual specimen.

2) According to the locality label specimen, NHMUK014423127 may have been collected from 'New Hebrides' which is a former name of Vanuatu. However, *R. regia* has never been reported from Vanuatu (Marinov et al. 2019). Therefore, the presence of this species in Vanuatu needs validation.

3) NHMUK014423128 is a female specimen which bears identification label '*Rhyothemis regia* subspec.' by Lieftinck dated 1947. It is unclear why Lieftinck did not provide a subspecific name for what he categorically defended in Lieftinck (1959) to be the dark-wing form of *R. r. chalcoptilon*. The way the label is written implies more that the specimen might be an unknown subspecies.

4) NHMUK014423129 is a male specimen from Swains Island which is very similar in wing colouration to Samoan populations (compare Marinov 2021: fig. 7a, male lectotype of *R. r. armstrongi*). However, its subspecific affiliation has to be established by investigating the morphology. The specimen was not available for such examination during the present study.

Subspecific status of *R. phyllis* has not been assessed. So far, the wing colouration is the only proposed diagnostic trait to differentiate between the subspecies of *R. phyllis* within its range. However, Marinov et al. (2019a) did not propose subspecific status of Vanuatu populations because of the observed differences in wing colourations within the individuals of the same locality and between the islands. Individuals/specimens studied in here from Wallis were different in the wing pattern from *R. p. dispar* from Fiji and were closer to Vanuatu populations (cf. Fig. 21). Therefore, we propose to remove *R. p. dispar* from the faunistic lists of Wallis published so far (Papazian et al. 2007, Grand et al. 2014) until more detailed studies employing morphological features from the male abdominal appendages. They are needed in order to propose a more plausible hypothesis of the subspecific arrangements within the Pacific. Wing colouration only is insufficient to explain the great diversity of variations among the archipelagos.

One last comment which may help in future studies on the Pacific representatives of the genus *Rhyothemis* is on some observed behaviour differences in the field from Locality 1, lake Kikila, Wallis Island. *Rhyothemis phyllis* seemed to prefer emergent vegetation inside the lake as perching substrates. Those were usually sites which were accessible only by wading in grassy vegetation in the shallow areas. *Rhyothemis r. uveae* individuals were found more commonly close to the lake margin where they selected dead branches of bushes as perching sites often facing towards the wetland. No aggressive interactions have been observed between individuals of the two species. *Rhyothemis phyllis* disappeared from the lake earlier than *R. r. uveae*. The activity of both decreased sharply with the rain with single *R. r. uveae* males seen seeking shelters in the bushes. Both species have been observed away from the lakes in what have been considered as feeding flights. One must consider that the behaviour observations were not the main focus on the present study. These notes are given to facilitate future studies in this interesting topic.

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