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Systematics of the *Pseudagrion* red-group from the Bismarck and Solomon archipelagoes (Odonata: Zygoptera: Coenagrionidae)

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Abstract

We examined the structural morphology, colour patterns and genetic relationships of representatives of the *Pseudagrion* red-group occurring on the Bismarck and Solomon archipelagoes. Five species-level taxa are recognised in this group, that we informally call the *P. incisurum* 'complex': *P. bougainville* sp. nov. from Bougainville; *P. brevicornis* sp. nov. from Choiseul; *P. incisurum* Lieftinck from Guadalcanal and Malaita; *P. lorenzi* Gassmann from New Britain and Lihir Island; and *P. simillimum* sp. nov. from the New Georgia group in the Solomons. All of these species are brown-yellow to red damselflies, with a yellow face and with black pattern elements on the head, thorax and abdomen, and differ markedly from all other Papuan *Pseudagrion* by the shape of their male superior anal appendages. When viewed in lateral aspect, the appendages appear more or less parallel sided — at least not subconical — and apically rounded to almost truncate, not subacute or bilobed; and when viewed in a skewed dorsal aspect show a basal excavation anterior to a more or less developed sub-basal to median process and a reflexed apical hook. Similarities in morphology supported by a molecular phylogeny based on mitochondrial and nuclear gene fragments indicate that these five species are closely related, but more extensive sampling of *Pseudagrion* species is required to confirm that they form a monophyletic group.

Key words: *Pseudagrion* red-group, new species, systematics, Papua New Guinea, Solomon Islands, Bougainville, Bismarck archipelago.

Introduction

Pseudagrion is the most speciose genus of damselflies in the family Coenagrionidae, with over 150 species recognized. Its range includes most of Africa, much of Asia, and Australia. The highest diversity is found in Africa, where almost 100 species occur (Schorr & Paul-

son 2025). Nineteen species have been recorded from the New Guinea region, including the Moluccas and the Solomon Islands (Michalski 2012; Kalkman & Orr 2013; Gassmann & Richards 2016; Theischinger et al. 2018), but only two of these, *P. microcephalum* (Rambur, 1842) and *P. incisurum* Lieftinck, 1949, have previously been recorded from the Solomons (Lieftinck 1949). *Pseudagrion microcephalum*, a species with a broad distribution extending from India through southeast Asia to New Guinea, Australia and the South Pacific islands (Michalski 2012), was recorded from Rennell, Russell, Guadalcanal and Malaita islands by Polhemus et al. (2008) and Marinov & Pikacha (2013), and from Bougainville by Richards & Theischinger (2018). *Pseudagrion incisurum* is a reddish species with a black pattern and was placed in the *Pseudagrion* red-group by Seehausen et al. (2025). This group consists of 27 species occurring from mainland southeast Asia to the Solomon archipelago. The species of this group occurring west of Lydekker's line were revised in detail by Seehausen et al. (2025) but the 11 species known from east of Lydekker's line have not been revised. *Pseudagrion incisurum* was described from Guadalcanal Island in 1949 and was reported from there again by Polhemus et al. (2008) who also illustrated a specimen from Malaita. Marinov & Pikacha (2013) claimed that *P. incisurum* is known only from Guadalcanal and Choiseul, presumably unaware of the record from Malaita. Polhemus et al. (2008) also listed and illustrated an undescribed *Pseudagrion* from Vella Lavella, New Georgia, and Kolombangara that is similar to *P. incisurum* but clearly differs from it in the structure of the male anal appendages. These circumstances and the description from New Britain of *Pseudagrion lorenzi* Gassmann 2011, a species apparently closely related to *P. incisurum* (Gassmann 2011) encouraged a closer examination of the *Pseudagrion* red-group species from the Solomon Islands and Bismarck archipelagoes (referred to here as the *P. incisurum* 'complex'). Based on morphology we revise this complex, describing three new species from the Solomon Islands and based on molecular data we test the relationships of all species of the *P. incisurum* 'complex' occurring on the Bismarck and Solomon archipelagoes.

Material and methods

Descriptive terminology largely follows Chao (1953) and Watson & O'Farrell (1991). Coloration is given as assessed from the preserved material in conjunction with photographs taken in life. Measurements are given in millimetres (mm). All line illustrations were done with the aid of a camera lucida and are not to scale. Geospatial coordinates are presented in the WGS 84 datum.

The Solomon Islands archipelago forms a single biogeographic region, but is politically divided between two countries, with Bougainville, Buka and some nearby islands currently part of Papua New Guinea and the remaining islands forming the nation of Solomon Islands. Here we refer to the 'Solomon Islands archipelago', or 'the Solomons' in the biogeographical sense to indicate the entire island chain, and to 'Solomon Islands' to refer to the nation of Solomon Islands, excluding Bougainville and Buka.

Material and relevant information for this study was made available by:

AM — Australian Museum, 1 William St, Darlinghurst NSW 2010, Australia.

BPBM — Bishop Museum, 1525 Bernice Street, Honolulu, Hawaii 96817 USA.

NBCN or **RMNH** — Naturalis Biodiversity Center, Darwinweg 2, 2333 CR Leiden, Netherlands.

NZAC — New Zealand Arthropod Collection Manaaki Whenua – Landcare Research, Private Bag 92170, Auckland 1142, New Zealand.

SAMA — South Australian Museum, North Terrace, Adelaide SA 5000, Australia.

The material is generally less than 20 years old and includes dry papered specimens, some of them treated with acetone, and specimens preserved in ethanol. The diversity in age and preservation of the specimens together with their maturity when collected often made assessing colouration (and its subsequent description) difficult and their use for molecular assessment in many cases impossible using Sanger sequencing technology. However, we sorted all of the material into groups based on structural morphology, determined which were already named, and then named and described the novel forms.

We performed DNA studies to examine species boundaries and interrelationships. Molecular analysis was based on selected samples of most of these groups. Geographical, morphological and molecular information were combined to establish species boundaries and phylogenetic relationships.

In the taxonomic section the species are treated in alphabetical order. Images showing the lateral aspect are presented for both sexes of all recognized species as far as available. Photos of at least dorsal and lateral view of the female pronotum and of the terminal abdominal segments plus anal appendages of the male are shown.

Abbreviations: ca = circa; vs = versus; Pt = pterostigma; S = abdominal segment/s; CL = collection locality numbers used by D. Polhemus to cross-reference localities, photographs, collection notes, and other metadata.

Specimens used for genetic studies, and DNA extraction

We sampled 21 *Pseudagrion* specimens and downloaded sequences from GenBank for a further three specimens to serve as outgroups. Appendix 1 shows the specimens sampled for this study, basic locality data and their museum, BOLD and GenBank accession numbers. We used a mix of dry and ethanol-preserved specimens ranging in age from 7–21 years old.

A single leg was removed from each specimen using sterilized forceps, placed in a sterile 1.5 mL Eppendorf tube, and each leg segment was broken into multiple pieces using the same forceps. Forceps were sterilized between specimens by wiping with a clean tissue, then dipping in 95% ethanol and flaming.

DNA extraction used the Bioline Isolate II kit (Bioline, Everleigh, Australia) with final elution volumes adjusted to 60 μ L.

Amplicon-based generation of DNA sequence data

We targeted the DNA barcode fragment of the COI gene (mitochondrial) and two nuclear genes, Histone 3 (H3) and the second internal transcribed spacer of the rDNA region (ITS2). Polymerase Chain Reaction (PCR) primers are shown in Table 1.

PCR amplification used the primers and followed the method of Mitchell (2015) for COI. In short, a first attempt was made to amplify the full-length DNA barcode fragment, and if that attempt failed, then two smaller overlapping PCR fragments were amplified, and the resulting PCR product reamplified using internal primers.

Table 1. PCR primers, their sequences listed 5'-3' and their source. Note that 5'-M13 tails were added to each primer to facilitate sequencing.

Gene	Forward primer names and sequences (5'-3')	Reverse primer names and sequences (5'-3')	Source
ITS2	ITS2-1Fm (CATGAACATCGACATYTTGAACGC)	28S-25R (TATGCTTAAAYTCAGCGGGT)	Mitchell & Sanways (2005)
Histone H3	HexAF (ATGGCTCGTACCAAGCAGACGGC)	HexAR (ATATCCTTGGGCATGATGGTGAC)	Ogden & Whiting (2003)
COI	AMbc0F1m (TCWACWAAYCAYAARRWTATYGG), AMbc3F1m (GCHCCHGAYATAGCNTTYCCNCG)	AMbc5r1m (GADARWGGNGGRTANACDGTTC), AMbc3r1m (ARYATNGTRATNGCNCNCG) AMbc0r2m (CAAARAAYCARAAYARRTGYTG)	Mitchell (2015)

PCR used the Phire Green Hot Start II PCR Master Mix kit (ThermoFisher Scientific, Scoresby, VIC, Australia) following the manufacturer's recommended conditions. Each 20 μ L reaction contained 2.25 mM MgCl₂, 200 nmol of each primer and 3 μ L of DNA extract (0.3 μ L of PCR product for reamplifications). PCR amplification employed an initial 30s denaturation at 98°C, followed by 38 cycles (32 cycles for reamplifications) of (10s at 98°C, 15s at 51°C, 15s at 72°C), a final extension for 60s at 72°C, then a hold at 10°C.

PCR products were purified using ExoSAP and sequenced in both directions using ABI Big Dye Terminator v.3.1 chemistry by Macrogen Inc. (Seoul, South Korea).

Whole-genome-shotgun-based generation of DNA sequence data

A single leg was removed from each specimen using sterilized forceps and placed into the well of 96-well PCR plate for DNA extraction and subsequent whole genome shotgun sequencing. The laboratory procedures followed Zwick & Zwick (2023). In summary, DNA was extracted using a silica-filter-based approach (DNeasy Blood and Tissue Kit; Qiagen, The Netherlands) and fluorometrically quantified. DNA libraries were built using the fragmentation- and ligation-based QIAseq FX DNA Library Core Kit (Qiagen, Germany; #1120146). Resulting libraries were pooled with other libraries (768 samples total) for sequencing on an Illumina NovaSeq X plus flowcell (10B reads, 150PE).

DNA sequence assembly and phylogenetic analysis

For amplicon sequences, forward and reverse direction sequence trace files were assembled using Geneious v.10.2.6 (Kearse et al. 2012). DNA consensus sequences, sequence trace files, and specimen collection data were uploaded to BOLD (<http://www.boldsystems.org>) where they are accessible as public dataset "DS-SIPSE (dx.doi.org/10.5883/DS-SIPSE)". Sequences were also deposited in GenBank, and two published sequences for outgroups were also downloaded from GenBank (accession numbers, in Appendix 1).

For whole-genome-shotgun sequences, data processing followed Zwick & Zwick (2023). In summary, Illumina reads were demultiplexed, deduplicated, trimmed and de novo assembled into contigs with SPAdes (v3.13.1; Bankevich et al. 2012). Mitochondrial contigs were annotated with MITOS2 (v2.0.8; Donath et al. 2019) to extract the 13 protein-coding mito-

chondrial genes for analyses, while the two nuclear loci H3 and ITS2 were extracted through comparison against the amplicon sequences (BLAST+ suite; v2.10.1; Comacho et al. 2009). We constructed two datasets. The first comprised all data, including up to 11,807 aligned base pairs (bp) from the mitochondrial genomes, 328 bp of the Histone 3 gene and 304 bp from the second internal transcribed spacer (ITS2) from the rDNA repeat, while the second dataset included only 559 bp of the COI gene ('DNA barcodes') plus the ITS2 gene. MEGA X v. 10.0.5 (Kumar et al. 2018) was used to calculate uncorrected distances (p-distances) between sequences.

Phylogenetic analyses were performed on the CIPRES Science Gateway v3.3 (Miller et al. 2010), using IQ-Tree v.2.3.2 (Nguyen et al. 2015) for maximum likelihood and MrBayes v. 3.2.7a (Ronquist et al. 2012) for Bayesian analyses. Initially, the ModelFinder function in IQ-Tree was used to select the best data partitioning scheme and best phylogenetic models to use in MrBayes (i.e., IQ-Tree was run using the options '-mset mrbayes' and 'TESTMERGE-ONLY'), while allowing each branch to have an independent evolutionary rate ('-p'). Initially each of the 13 mitochondrial protein-coding genes was partitioned by codon position, as was Histone 3, while ITS2 had a single partition, for a total of 43 partitions to be tested. IQ-Tree suggested they be combined into 9 data partitions. Five partitions were assigned the HKY + G model, and one each was assigned the HKY + I + G, GTR + I + G, GTR + I, and GTR + G.

MrBayes analyses was set to run for 30 million generations, with a sample frequency of 1,000, using 2 runs, setting the number of chains to 4. The stopping rule was used to end the analysis when the average standard deviation of split frequencies dropped below 0.01, suggesting probable convergence of the chains. The burnin fraction was set to 0.25.

Maximum Likelihood analyses in IQ-Tree implemented the newer models (option 'TESTNEW-MERGE'), allowed each branch to have an independent evolutionary rate (option '-p'), used the more thorough and slower nearest neighbour interchange option ('-allnni') for tree searching, and implemented 10,000 ultrafast bootstrap replicates.

Results & Discussion

Systematics

Common morphological characters of the species of the *Pseudagrion incisurum* complex

We use the terms "species complex" and "species group" for convenience when discussing certain clades resolved by our phylogenetic analysis. Future analysis of such clades using more refined molecular techniques may reveal additional structure. In this context, the geographically defined *Pseudagrion incisurum* complex (Bismarck and Solomon Islands archipelagos) is also defined based on the following set of characters:

All known species and geographically identifiable forms are rather small coenagrionid damselflies, with males largely yellow to dark red in life (Figs 1, 5, 10a, 16a) and females brown to dark red (Fig. 5), and usually with a yellow face and small black pattern elements on head and thorax and larger elements on much of the abdomen. The body coloration does not vary markedly or consistently between different local populations. The wings have black venation and a dark pterostigma.



Figure 1. *Pseudagrion bougainville* sp. nov., live mature male. Photo by S. Richards.

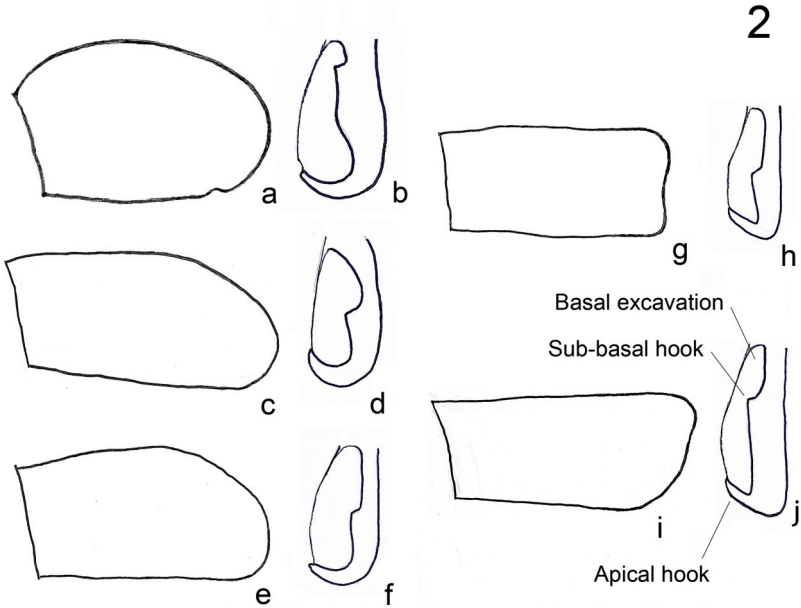


Figure 2. *Pseudagrion* spp., male terminalia. (a, c, e, g, i) left superior anal appendage, lateral; (b, d, f, h, j) right superior anal appendage, skewed dorsal view: (a, b) *P. lorentzi*; (c, d) *P. bougainville* sp. nov.; (e, f) *P. simillimum* sp. nov.; (g, h) *P. brevicornis* sp. nov.; (i, j) *P. incisurum*.

Table 2. Grouping of the *Pseudagrion incisurum* complex based on structure of male superior appendage and distribution (can also be used to identify adult males)

Name population from codes used in trees	Male superior anal appendages	Known Distribution
<p><i>P. lorentzi</i> ODO 1, 2, 3, 4</p>	<p>In lateral view not more than 50% longer than wide, medially swollen with dorsal margin strongly curved (Fig. 2a); in an inwardly skewed dorsal view basal excavation less than 1/4 the length of appendage, inner margin beyond sub-basal process long and sinuous, apical hook uniformly curved and somewhat wrapped around membranous apical portion (Fig. 2b).</p>	<p>PNG: Bismarck Archipelago, New Britain</p>
<p><i>P. incisurum</i> 421, 422</p>	<p>In lateral view more than 50% longer than wide, almost parallel sided (Fig. 2i); in an inwardly skewed dorsal view basal excavation ca 1/3 length of appendage, beyond sub-basal process inner margin straight and parallel to outer margin, apical hook basally angulate, otherwise straight, thin and recurved (Fig. 2j).</p>	<p>Solomon Is: Guadalcanal</p>
<p><i>P. brevicornis</i> Choiseul ODO 7, 8, 9, 11, 12, 13, 14</p>	<p>In lateral view more than 50% longer than wide, almost parallel sided (Fig. 2g); in an inwardly skewed dorsal view basal excavation ca 1/2 the length of appendage, inner edge beyond median process tapering gently as far as angle of apical hook, apical hook basally angulate, otherwise straight, thin and recurved (Fig. 2h).</p>	<p>Solomon Is: Choiseul</p>
<p><i>P. bougainville</i> Bougainville 201, 202, 203, ODO 15, 16</p>	<p>In lateral view more than 50% longer than wide, dorsal margin slightly curved beyond midpoint creating a slight swelling followed by a narrowed rounded apex (Fig. 2c); in an inwardly skewed dorsal view basal excavation ca 1/2 the length of appendage, inner margin with large sub-basal process with inner margin beyond tapering towards apex; apical hook uniformly curved and thick, somewhat wrapped around membranous apical portion (Fig. 2d).</p>	<p>PNG: Bougainville</p>
<p><i>P. simillimum</i> New Georgia group ph3D1, ph3E2, ph3E1 (ODO6</p>	<p>In lateral view than more than 50% longer than wide, dorsal margin curved beyond midpoint creating a slight swelling followed by a narrowed subtruncate apex (Fig. 2e); in an inwardly skewed dorsal view basal excavation ca 1/2 the length of appendage, median process rather small and inner margin not tapered towards apex, apical hook uniformly curved basally, distally rather straight and weakly recurved (Fig. 2f).</p>	<p>Solomon Is: Kolombangara Rendova Vella Lavella</p>

1) *Structural Morphology*: In lateral aspect the short superior anal appendages (cerci) of the male appear more or less parallel sided with the apex simply rounded to sub-truncate (Figs 3c, d; 8d–f; 10c–f; 14b, c; 16c–e), rather than conical with apex pointed or bifid as in all other Papuan *Pseudagrion* species. In a skewed dorsal aspect they have a well-defined basal excavation followed by a sub-basal to median angle, sometimes produced and referred to here as a 'process', and an apical hook (Fig. 2). The posterior lobe of the female pronotum bears a forward-pointing thorn-like to finger-shaped lobe on each side

(Figs 4c, d; 11c, d; 14e, f). While the shape of the male superior anal appendages distinguishes members of this complex from all New Guinean mainland species, the detailed form of these elements may be useful for distinguishing taxa within the complex. The size and shape of the female pronotal lobes distinguishes members of the complex from some other Papuan *Pseudagrion* and may prove useful for distinguishing taxa within the complex when more material is available.

- 2) *Colour* (Figs 3, 4): Small black pattern elements are generally present on the head, thorax, and abdomen. They include on the head a patch along the inner side of the lateral ocelli, sometimes a patch along the posterior margin of the median ocellus, and patches bordering much of the postocular lobes, including the temples; on the pronotum part of the furrow between the anterior and median lobes, almost all of the furrow between the median and posterior lobes, and the midline and two longitudinal stripes on each side of the median lobe; on the synthorax black pattern elements form lines and patches of variable length and width along the middorsal carina, along the antealar and subalar ridges extending posteriorly as far as the metapleural suture, along parts or all of the sutures delimiting the mesokatepisternum and across it, a patch in the dorsal 1/5–1/3 of the humeral suture potentially continued by a line/strip along its whole length, a potential thin line and patch along the dorsal 1/3 of the intersegmental suture, a patch on the dorsal 1/6–1/3 of the metapleural suture potentially continued by a line along its whole length, and a thin dorsal delimitation of part of the metapostepimeron; and on the abdomen tergites 1–8, apical rim of tergite 9 and dorsal apical rim of S10 and the superior anal appendages.

The above characters readily distinguish members of the *Pseudagrion incisurum* complex from all other described New Guinea mainland *Pseudagrion* species but vary only slightly among members of the complex. We therefore rely on consistent differences in the shape and proportion of the male anal appendages (as given in Table 2) to create a robust classification of species within the complex.

Taxonomy

Pseudagrion bougainville Theischinger, Richards & Polhemus sp. nov.

(Figs 1, 2c–d, 3a–f, 4a–d, 5, 6, 7, 21, 22a)

Polhemus et al. (2008) listed and illustrated an undescribed *Pseudagrion* species from Rendova, Vella Lavella, New Georgia, and Kolombangara that is similar to *P. incisurum* but differs in some aspects of coloration and structure of the male appendages. Specimens closely resembling this new species were subsequently encountered at Mapisi and Pipikei during an Odonata survey on Bougainville (Richards & Theischinger 2020). Although we initially grouped all these populations as a single taxon, we now consider the Bougainville specimens to belong to a separate and new species, described here as *Pseudagrion bougainville* sp. nov. The other similar populations from the New Georgia group we treat as *Pseudagrion simillimum* sp. nov., described later in this paper.

Holotype ♂. (Fig. 22a), SAMA 07-001679, Papua New Guinea, The Autonomous Region of Bougainville, Bougainville Island, Pipikei (5.8077° S, 154.8067° E; 240 m a.s.l.), 20-x-2019, S. Richards; deposited in the South Australian Museum, Adelaide, Australia.

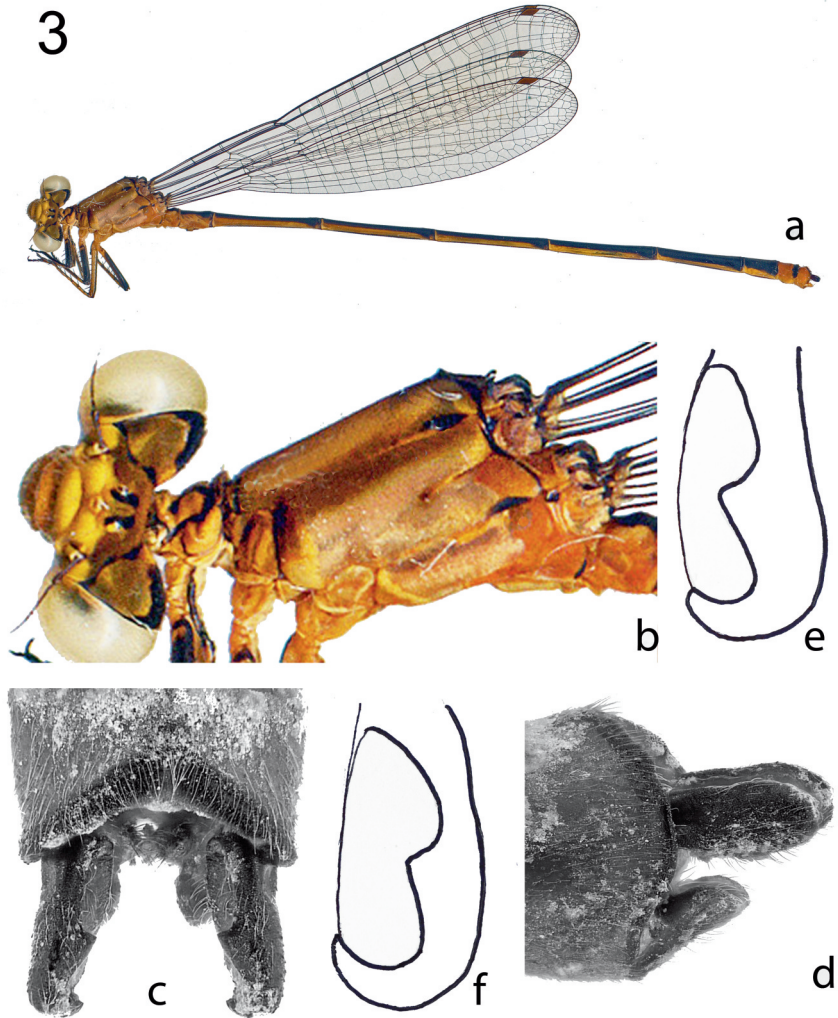


Figure 3. *Pseudagrion bougainville* sp. nov., male. (a) habitus, lateral; (b) head and thorax, dorsal/lateral; (c, d) terminalia: (c) dorsal; (d) lateral; (e, f) right superior appendage, skewed dorsal view.

Paratypes. Papua New Guinea, The Autonomous Region of Bougainville, Bougainville Island: 6 ♂♂, 2 ♀♀, SAMA 07-001680–07-001687, type locality, 17-20-x-2019, S. Richards (SAMA); 1 ♂, SAMA 07-001688, Kaitare-ei, (5.7915° S, 154.8393° E; 730 m a.s.l.), 24-x-2019, S. Richards and local assistants (SAMA); 1 ♂, BPBMENT1000005427, Buin, 0–100 m, October 1971, N. L. H. Krauss (BPBM); 1 ♂, BPBMENT1000005428, Baretemba, 100–200 m,

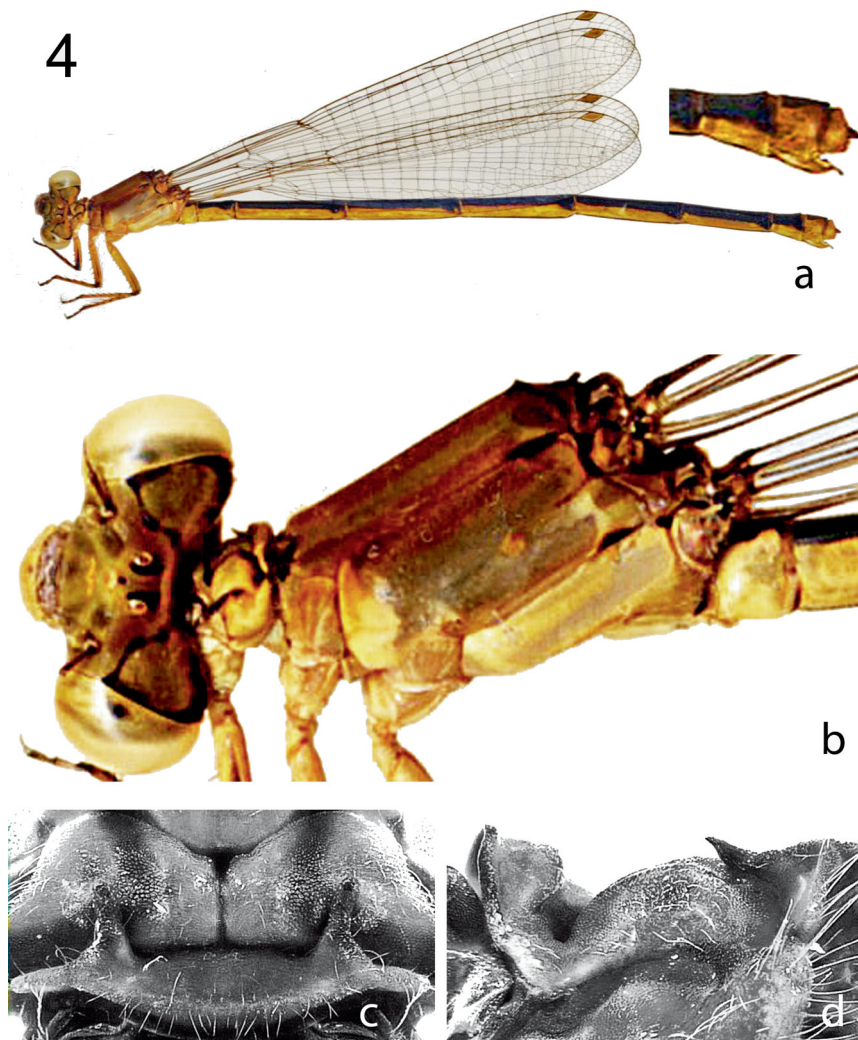


Figure 4. *Pseudagrion bougainville* sp. nov., female. (a) habitus, lateral; (b) head and thorax, dorsal/lateral; (c, d) part of pronotum: (c) dorsal; (d) lateral.

26 October 1971, N. L. H. Krauss (BPBM); 2 ♂♂, 1 ♀, BPBM100005429–100005431, Mutahi, near hot water spring, 650 m, 13 March 1968, R. Straatman (BPBM); 1 ♂, BPBM100005429, same data as preceding but 650 m, 13 March 1968, R. Straatman (BPBM).

Etymology. Named after Bougainville Island, the type locality for the new species.

Description of the holotype

Head. Labium, face including labrum, clypeus, genae, base of mandibles and antennae, scape and frons up to just beyond median ocellus yellow to pale brownish yellow, only a tiny spot posterior to median ocellus black; pedicel, top of frons from level of lateral ocelli, post-ocular lobes, vertex and dorsal portion of occiput largely yellowish grey with black patches and variably narrow to wider lines along inner margin of lateral ocelli, suture between frons and postocular lobe, along top eye margin and broadly along most of postgenae black; apex of mandibles and antennal flagellum black; postgenae black with yellow band along lateral eye margin.

Thorax. Largely pale brownish yellow. Pronotum largely yellow to pale brownish yellow, posterior lobe greyish yellow to yellowish grey, part of furrow between anterior and median, and almost all of furrow between median and posterior lobe, and midline and two longitudinal stripes each side of median lobe black. Synthorax largely pale to darker greyish yellow and brownish yellow; middorsal carina, antealear ridge and most of subalar ridge black, as are a narrow patch covering dorsal 1/5 along and of the humeral suture, a patch covering more than 1/5 along and of the metapleural suture and a smaller patch at posterodorsal end of metapostepimeron; very fine lines along most of suture separating mesanepisternum from mesokatepisternum and metepimeron from metapostepimeron also black. Humeral plates and terga largely pale to darker greyish yellow and brownish yellow. Legs with coxae and trochanters very pale greyish yellow to very pale brownish yellow, femora pale greyish yellow to pale brownish yellow with lateral and posterior face almost completely black, tibiae largely pale greyish yellow to brownish yellow with most of inner/anterior face black, protibia also with lateral face partly darkened, tarsi and spines black, claws pale to dark greyish and brownish yellow. Post-coxae and poststernum pale greyish yellow. Wings with venation black and membrane hyaline. Postnodals 15/13–14. Pt distinctly sloping, overlying slightly less than 1 cell, yellowish grey to blackish grey.

Abdomen. Tergites 1–8 dorsally black, laterally very pale greyish yellow to brownish yellow with thin extension reaching close to midline at base of S3–7, tergite 9 yellow, with broad black apical rim dorsally; S10 yellow with thin dorsal apical rim. Most of sternite 1 yellow with narrow midventral black patch in basal 2/3; secondary genitalia largely yellow with second joint of penis black; sternites 3–7 largely black; sternite 8 yellow with black midline; sternite 9 including pointed valvae yellow. Superior anal appendages black, in lateral view more than 50% longer than wide, dorsal margin slightly curved beyond midpoint creating a slight swelling followed by a narrowed rounded apex; in an oblique dorsal view – inner dorsolateral view basal excavation ca 1/2 the length of appendage, inner margin with large sub-basal process with inner margin beyond tapering towards apex; apical hook uniformly curved and thick, somewhat wrapped around membranous apical portion. Inferior anal appendages medium to dark yellow, in lateral view almost parallel sided with apex rounded, at least half as thick as superiors.

Dimensions. Hind wing 25.5 mm; abdomen (including anal appendages) 39.0 mm.

Female

Head. Much as in male, only genae and band along eye in postgenae yellow, remainder largely variably dark greyish yellow to yellowish grey, postclypeus darkest, black patches less distinct.

Figure 5. *Pseudagrion bougainville* sp. nov., pair in copula, in life. Photo by S. Richards.

Thorax. Much as in male, but with two forwardly-directed, conical lobes on posterior lobe of pronotum, appearing sharply pointed in lateral view (Figs 4c, d). Synthoracic pleura largely somewhat darker than in male except for most of metepimeron, black markings very much as in male with addition of thin black line along dorsal 1/5 of interpleural suture and black spot some distance ventral to it. Legs much as in male but with lateral and posterior darkening of femora, and inner/anterior face of tibiae reduced to black streaks extending only part of their length, tarsi dull yellow and brown. Wings much as in male but Pt pale grey to pale yellowish grey. 15–16/13–14 postnodals. *Abdomen.* S1–2 much as in male except for lack of secondary genitalia; thin extension of lateral



yellow reaches close to midline at base of S3–6; S8 dorsally and laterally black, a dull yellow patch in posterior 1/6; S9 laterally largely dull yellow with cup-shaped black dorsal patch; S10 yellow with similar but smaller black patch or only black along anterior margin; anal appendages black; outer valves dull yellow, finely denticulate ventrally, reaching close to end of S10; ovipositor black, styles brownish yellow.

Dimensions. Hind wing 25.4–25.6 mm; abdomen 35.4–36.6 mm.

Variation in the male paratypes

The five paratypes differ from the holotype in the following characters:

Head. Face slightly brighter to bright yellow; top of head darker yellowish grey, making black elements hard to discern.

Thorax. Slightly to markedly darker greyish yellow, particularly mesokatepisternum which may also have a diagonal black stripe; metepisternum and metepimeron somewhat darker with reddish touch, black elements up to 1/3 the length of humeral and intersegmental suture, the humeral suture just appearing as a thin black line for most to all of its length



Figures 6, 7. Habitat along two streams that supported *Pseudagrion bougainville* sp. nov. populations at the type locality, Pipikei, Kunua District, Bougainville Is. Photos by S. Richards.

and the adjacent $\frac{1}{4}$ of mesanepisternum darkened. Additional thin black line along dorsal $\frac{1}{5}$ of interpleural suture and black spot some distance ventral to it. Legs darker with lateral and posterior face of femora and all of protibia nearly or completely black, also lateral face of meso- and metatibia lined black. Postnodals 15–16/13–15. Pt dark yellowish grey.

Abdomen. With a slight to stronger touch of reddish on yellow sides of S1 and S2, yellow coloration on the side of abdomen extended to close to middorsal at base of S3-6 only.

Dimensions. Hind wing 22.3–25.3 mm; abdomen 35.0–36.5 mm.

Differential diagnosis. The male of *Pseudagrion bougainville* sp. nov. can be distinguished from *P. lorenzi* and *P. incisurum* by the relatively longer basal excavation of its superior anal appendages (ca 1/2 length vs less than 1/4–ca 1/3 length), from *P. breviconis* sp. nov. by the apically more widely rounded vs sub-conical superior anal appendages, and from *P. simillimum* sp. nov. by a larger inner median process and a strongly curved vs straighter apical hook of the superior anal appendages (Figs 3c–f). The male lateral pterothorax is bright red in living specimens (Figs 1, 5), fading to a more brownish yellow in preserved specimens (Figs 3a, b).

Distribution and habitats. Currently known only from Bougainville Island (Fig. 21). Adults were common in sunny patches along slow- and fast-flowing streams where they perched on low, riparian vegetation in both severely disturbed habitats such as plantations, and in patches of good quality remnant forest.

Pseudagrion breviconis Theischinger, Polhemus & Richards sp. nov.

(Figs 2g–h, 8a–f, 9, 21, 22b)

Holotype. ♂, BPBMENT 0000081507 (Fig. 22b), Solomon Islands, Choiseul Province, Choiseul Island: Vangamole River at logging road, 3 km N of Mole (6°48'40"S, 156°32'43"E; 25 m a.s.l.), flying along stream corridor/margin, 17-iii-2005, R. A. Englund (BPBM).

Paratypes: Solomon Islands, Choiseul Island: 4♂♂, BPBMENT 0000081508–0000081514, (ODO9, 10, 13, 14), same data as holotype; 3♂♂ (ODO7, 8, 12), Choiseul Prov., Vangamole River at logging road, 3 km N of Mole, 25 m a.s.l., 6°48'40"S, 156°32'43"E, flying along stream corridor/margin, 17-iii-2005, CL 7389, D.A. Polhemus (BPBM).

Etymology. The name *breviconis* = Latin for “with short cones” referring to the short superior anal appendages (cerci).

Description of holotype (ODO11)

Head. Labium and face including labrum, clypeus, genae, base of mandibles and antennae, scape and frons, dark yellow; top of head, including vertex, postocular lobes and occiput largely pale brownish yellow; pedicel dark brown; a small spot posterior to median ocellus, patches and variably narrow to wider lines along inner margin and posterior margin of lateral ocelli, suture between frons and postocular lobe, along top eye margin and broadly on postocular lobe and along most of postgenae black; apex of mandibles and antennal flagellum dark brown to black; postgenae black with thin pale brownish yellow band along part of eye margin.

Thorax. Pronotum largely pale brownish yellow, posterior lobe with top rim, part of furrow between anterior and median lobe, and almost all of furrow between median and posterior lobe, and midline and two wide curved longitudinal stripes each side of median lobe, black. Synthorax largely pale brownish yellow; antealar ridge, most of subalar ridge, anteroven-

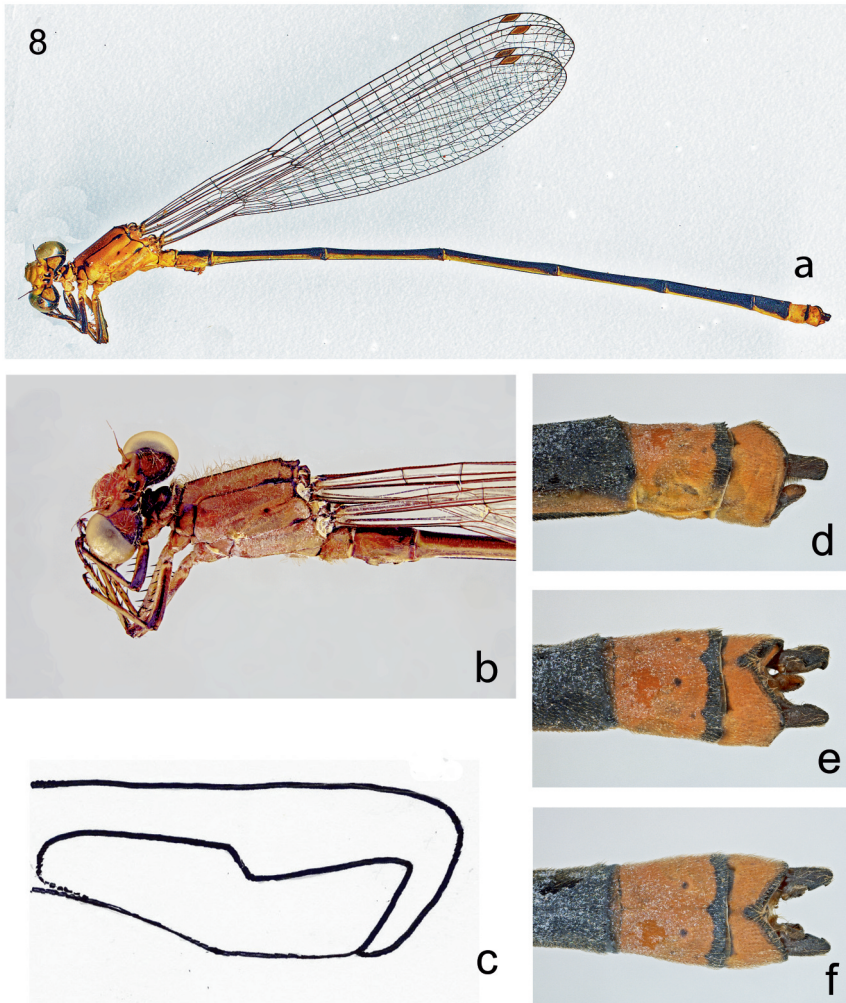


Figure 8. *Pseudagrion breviconis* sp. nov., male. (a) habitus, lateral; (b) head and thorax, dorsal/lateral; (c) right superior appendage, skewed dorsal view, showing configuration of apical hook, median process and basal excavation; (d–f) male abdominal terminalia in multiple views: (d) lateral; (e) dorsal oblique; (f) dorsal (specimen from lower Vangamole River, Choiseul Is., CL 7389).

tral and dorsal edge of mesokatepisternum and connecting diagonal stripe, line on and along mid-dorsal carina, humeral patch about 1/3 length of suture merging into thick humeral line, line along almost dorsal 1/3 of interpleural suture and slightly thicker patch somewhat ventral to it, patch covering about dorsal 1/3 along metapleural suture and on and along remaining 2/3 of it, black; small patch at posterodorsal end of metapostepimeron and very fine



Figure 9. Type-locality habitat for *Pseudagrion brevicornis* sp. nov., at lower Vangamole River, 0–15 m a.s.l., Choiseul Is., CL 7389 (D. A. Polhemus photo).

line along most of the suture separating metepimeron from metapostepimeron, black. Humeral plates and terga largely pale to darker greyish yellow and brownish yellow. Legs with coxae and trochanters very pale greyish yellow to very pale brownish yellow, lateral and posterior face of pro- and meso-femur almost completely black, pro- and meso-tibia pale greyish yellow to brownish yellow with most of inner/anterior and part of lateral face black, tarsi and spines black, claws pale to dark greyish and brownish yellow, hind-leg missing. Post-coxae and poststernum dull to pale greyish yellow. Wings with venation black and membrane hyaline. Postnodals 15/13. Pt distinctly sloping, overlying slightly less than 1 cell, yellowish grey.

Abdomen. Tergites 1–8 dorsally black, laterally pale to dull yellow to brownish yellow with thin extension reaching close to midline at base of S3–6, tergite 9 yellow, with broad black apical rim dorsally; S10 yellow with thin black dorsal apical rim. Sternite 1 yellow with narrow midventral black patch in basal 2/3; secondary genitalia largely yellow with second joint of penis black; sternites 3–8 largely black; sternite 9 including pointed valvae yellow. Superior anal appendages black, in lateral view more than 50% longer than wide, almost parallel sided; in an oblique dorsal view – inner dorsolateral view basal excavation ca 1/2 the length of appendage, inner edge beyond median process tapering gently as far as angle of apical hook, apical hook basally angulate, otherwise straight, thin and recurved. Inferior anal appendages medium to dark brown, in lateral view more than half as thick as superiors, subconical.

Dimensions. Hind wing 21.8 mm; abdomen 34.0 mm.

Variation in male paratypes (ODO7-10, 12-14)

One of the seven paratypes is very dark all over (discoloured) with darker pattern elements that are conspicuous on the other paratypes barely discernible.

Six other paratypes:

Head. Face paler and base of top of head and dark pattern elements slightly paler or slightly darker than in holotype.

Thorax. With dark pattern elements including lines and patches very slightly more or less extensive than in holotype. Legs with metafemur paler yellow with black posterolateral line, metatibia largely paler yellow with much of inner face blackish. Postnodals 15/13–17/15; Pt longer, overlying up to an entire cell.

Abdomen. Much as in holotype to slightly darker.

Dimensions. Hind wing 22.3–24.0 mm; abdomen (including anal appendages) 34.3–37.9 mm.

Female

Unknown

Differential diagnosis. The male of *Pseudagrion breviconis* sp. nov. can be distinguished from *P. lorenzi* and *P. incisurum* by the relatively longer basal excavation of its superior anal appendages (ca 1/2 length vs less than less than 1/4–ca 1/3 the length), and from *P. bougainville* sp. nov. and *P. simillimum* sp. nov. by the apically sub-conical vs more widely rounded to truncate superior anal appendages (Figs 8c–f).

Distribution and habitats. Known only from, and possibly endemic to, Choiseul Island in the Solomon Islands (Fig. 21) where it is known only from the coastal lowlands at 25 m a.s.l. (Fig. 9)

Pseudagrion incisurum Lieftinck, 1949

(Figs 2i–j, 10a–g, 11a–d, 12, 13, 17a–b, 21)

Pseudagrion incisurum Lieftinck, 1949, p. 336.

Material examined.

Solomon Islands, Guadalcanal Province, Guadalcanal Island: 2 ♂♂ (dry), 5 ♂♂ (EtOH), Tenaru River at Tenaru Falls, 12 km SE of Honiara, 40 m., water temp. 25° C., 21 November 2004 9°31'01"S, 160°00'59"E CL 7337, D. A. Polhemus (BPBM); 20 ♂♂ (EtOH), Charebuma River, above Gold Ridge mine, 390–460 m., water temp. 23.5° C., 3 August 2005, 11:00–15:00 hrs. 9°35'39"S, 160°07'28"E, CL 7421, D. A. Polhemus and R. A. Englund (BPBM); 2 ♂♂ (421, 422), Charebuma River, above Gold Ridge mine, 390 m, 9°35'40"S, 160°07'28"E, 3 August 2005, D.A. Polhemus (BPBM); 1 ♂, Tenaru River at Tenaru Falls, SE of Honiara, 40 m, 9°31'01"S, 160°00'59"E, flying along stream margins, 21 November 2004, D.A. Polhemus (all preceding in BPBM). 1 paratype ♂, RMNH.INS.975686, C.H.Foggitt coll., E,C.Van Dyke don., coll. Calif. Acad.; 1 ♂, RMNH.INS.975683, Lavono, 18-ii-1934, No. 752, R.A. Lever; 1 ♂, 1 ♀, RMNH.INS.975684, Ilu farm, sloot, 30-x-1964, G.S. Slooff; 1 ♂, 1 ♀, RMNH.INS.-

975685, Betikama, ix-1960; all in RMNH. 1 ♂, NZAC04134249, Sulapuka River in the Honiara Botanical Garden, 21 m a.s.l., 9.4363°S/159.9417°E, 28-iv-2012, M. Marinov; 1 ♀, NZAC04137347, same data; 1 ♀, NZAC04141745, same data; 1 ♂, NZAC04144126, same data; 1 ♂, NZAC04140297, RAP-, light trap at Haviha Campsite, 1221 m a.s.l., 9.6688°S/160.0570°E, 16-ix-2015, T. Cakacaka; 1 ♂, NZAC04144413, RAP-, stream and tributaries below Valevahalo camp, 760 m a.s.l., 9.6664°S/160.0443°E, 9-ix-2015, M. Marinov; 1 ♂, NZAC041447175, same data; 1 ♂, NZAC04135708, RAP-, Mbeambea River, 672 m a.s.l., 9.6670°S/160.0501°E, 10-ix-2015, M. Marinov; 1 ♂, NZAC04139951, Kovi River above Kongulae Village, 251 m a.s.l., 9.4610°S/159.8936°E, 1-v-2012, M. Marinov; all in NZAC. Malaita Prov., Malaita: 3 ♂♂, Kwaisale River at Kwaisale Falls, nr. Anomasu village on road from Auki to Atori, 48 road km. NE of Auki, 120–200 m., 8°41'53"S, 160°49'40"E, water temp. 25.5° C., 30 July 2005, 11:30–14:00 hrs., CL 7410, D. A. Polhemus & R. Englund (BPBM); 1 ♂, Kapolo Creek (trib. to Koa River), 7.5 km. N. of Auki on road to Dala, 5 m., 8°42'09"S, 160°41'59"E, water temp. 25.5° C., 31 July 2005, 09:00–10:30 hrs, CL 7412, D. A. Polhemus & R. Englund (all in BPBM).

A yellow-faced *Pseudagrion*, with the male having the top of the head pale to bright brownish yellow, distinctively framed and marked black; the thorax bright red in life (Fig. 10a) fading to largely pale to bright brownish yellow in preserved specimens (Fig. 10b), rather thinly lined with black along some sutures; and the abdomen brownish yellow with S1–8 dorsally black, S9 and S10 almost all yellow and dark anal appendages. The female coloration is somewhat darker. Details of the colour pattern were provided by Liefinck (1949) and Gassmann (2011).

Male terminalia. Superior anal appendages brown to black, in lateral view more than 50% longer than wide, almost parallel sided; in an oblique dorsal view – inner dorsolateral view basal excavation ca 1/3 length of appendage, beyond sub-basal process inner margin straight and parallel to outer margin, apical hook basally angulate, otherwise straight, thin and recurved. Inferior anal appendages orange to medium and dark brown, in lateral view slightly conical, more than half as thick as superiors (Figs 10c–f).

Secondary genitalia. Largely yellow with second joint of penis black (Figs 17a, b)

Differential diagnosis. *Pseudagrion incisurum* can be distinguished from *P. lorentzi* by the straight vs sinuous inner margin beyond the sub-basal process and the relatively longer basal excavation of its superior anal appendages (ca 1/3 length vs less than 1/4 the length), from *P. bougainville* sp. nov., *P. simillimum* sp. nov. and *P. breviconis* sp. nov. by the relatively shorter basal excavation of its superior anal appendages (ca 1/3 length vs ca 1/2 length), and from *P. lorentzi*, *P. bougainville* sp. nov. and *P. simillimum* sp. nov. by its almost parallel sided vs at least distally narrowed superior anal appendages (Figs 10c–f).

Female

As illustrated in Figs 11a–d.

Distribution and habitats. Solomon Islands, Guadalcanal and Malaita islands (Fig. 21). Flying along the margins of rocky upland streams (Figs 12, 13), recorded from 40–1221 m a.s.l.

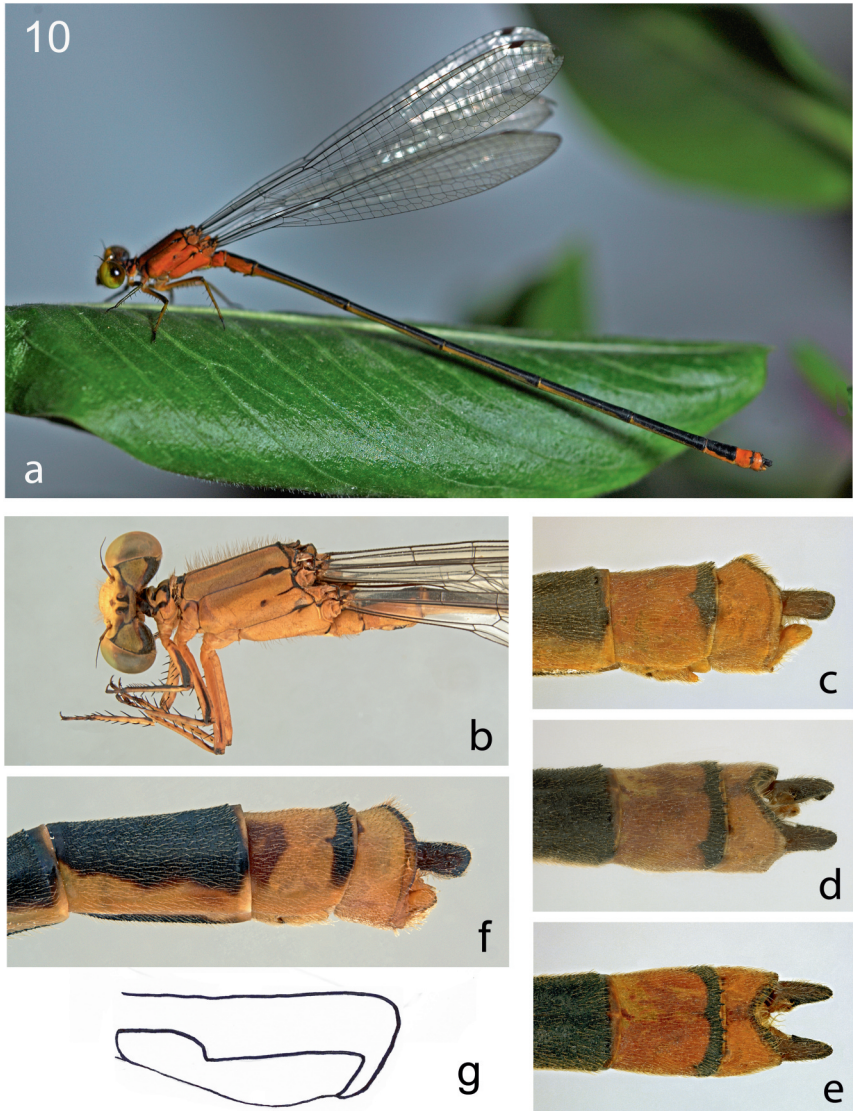


Figure 10. *Pseudagrion incisurum* Lieftinck, male. (a) habitus, left lateral, photograph of living specimen; (b) head and thorax, dorsolateral; (c-f) male abdominal terminalia in multiple views: (c) lateral; (d) dorsal oblique; (e) dorsal; Figs 10 a-e based on specimens from Tenaru Falls, Guadalcanal Is., CL 7337 (D. A. Polhemus photos); (f) male abdominal terminalia in lateral view, specimen from Kwarea River, Malaita Is., CL 7410; (g) right superior appendage, skewed dorsal view, showing configuration of apical hook, sub-basal hook and basal excavation.

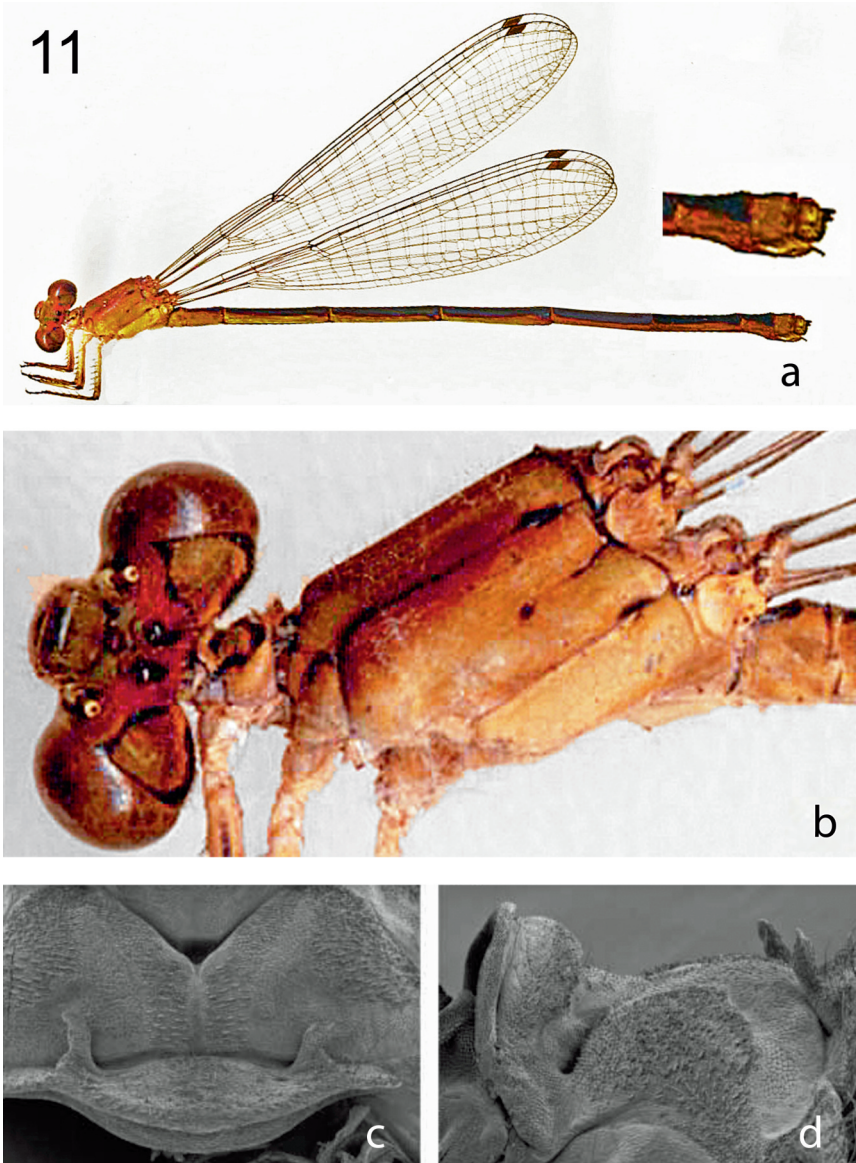


Figure 11. *Pseudagrion incisurum* Lieftinck, female. (a) habitus, left lateral, with detail of ovipositor; (b) head and thorax, dorsal/lateral; (c, d) pronotum: (c) dorsal; (d) left lateral.



Figures 12, 13. Habitats for *Pseudagrion incisurum* Lieftinck, on Guadalcanal Is.: (12) Tenaru River at Tenaru Falls, CL 7337; (13) upper Charebuma River near Gold Ridge mine, 440 m a.s.l., CL 7421, with discoloration in the water at right center from local gold prospecting, (D. A. Polhemus photos).

***Pseudagrion lorenzi* Gassmann, 2011**

(Figs 2a–b, 14a–f, 15, 21)

Pseudagrion lorenzi Gassmann, 2011, p. 152.

Material examined. Papua New Guinea, West New Britain Province, New Britain Island: 1 ♂, Wilaumez Peninsula, springs and clear outflow creeks above Walindi Plantation, N. of Kimbe, 50 m., 5°25'47"S, 150°04'43"E, water temp. 26° C., 13 January 2005, 09:30–15:30 hrs., CL 7345, D. A. Polhemus (BPBM); 1 ♂, Wilaumez Peninsula, trib. to Vulevulu River, W. slope of Mt. Welcker, 15 m., 5°26'15"S, 149°58'14"E, water temp. 27° C., 15 January 2005, 11:30–12:30 hrs., CL 7349, D. A. Polhemus (BPBM). New Ireland Province, Lihir Is.: 4 ♂ ♂, 1 ♀, town area, (3° 03'S, 152 36'E), 20–26 Oct. 2001, M. Humphrey & M. Moulds (AM); 1 ♂, Dolan village (3°13'S, 151°53'E), 14 Nov. 2001, M.S. Moulds & M.A. Humphrey (AM).

A yellow-faced *Pseudagrion*, male with top of head dull brownish yellow framed and marked black; thorax largely dull brownish yellow, rather indistinctly striped with brown to black along some sutures; abdomen dull brownish yellow with S1–8 dorsally black, S9 and S10 almost all yellow and dark anal appendages (Figs 14a, d). The female is somewhat darker with colour pattern that is less clearly defined, see Gassmann (2011) for further details.

Male terminalia. Superior anal appendages black, In lateral view not more than 50% longer than wide, medially swollen with dorsal margin strongly curved; in an inwardly skewed dorsal view basal excavation less than 1/4 the length of appendage, inner margin beyond sub-basal process long and sinuous, apical hook uniformly curved and somewhat wrapped around membranous apical portion. Inferior appendages yellow, in lateral view appearing approximately half as thick as superiors (Figs 14b, c).

Differential diagnosis. The male of *Pseudagrion lorenzi* can be distinguished from all other species of the *P. incisurum* complex by the relatively shorter basal excavation of its basally and distally narrowed superior anal appendages (less than 1/4 the length vs ca 1/3 – ca 1/2 the length) and by the sinuous vs straight inner edge beyond the sub-basal process (Fig. 14b, c).

Female

As illustrated in Figs 14e, f.

Distribution and habitats. Papua New Guinea, New Britain and Lihir Island only; given this distribution, the species is likely more widespread in the Bismarck archipelago, and almost certainly occurs on intervening New Ireland. *Pseudagrion lorenzi* is mainly found along medium-sized, sun-exposed and fast flowing stony streams (Gassmann 2011, and see our Fig. 15), across an altitudinal range from 0–860 m. However, it was also sighted at larger and more shady creeks (Malalimi), and even at large ponds near Tompoi Camp in the Nakanai Mountains at about 850 m a.s.l. where individuals were found flying in sunny areas (Gassmann & Richards 2011). This species also occurred along a creek at Numundo Plantation that was situated in a partially logged area.

14

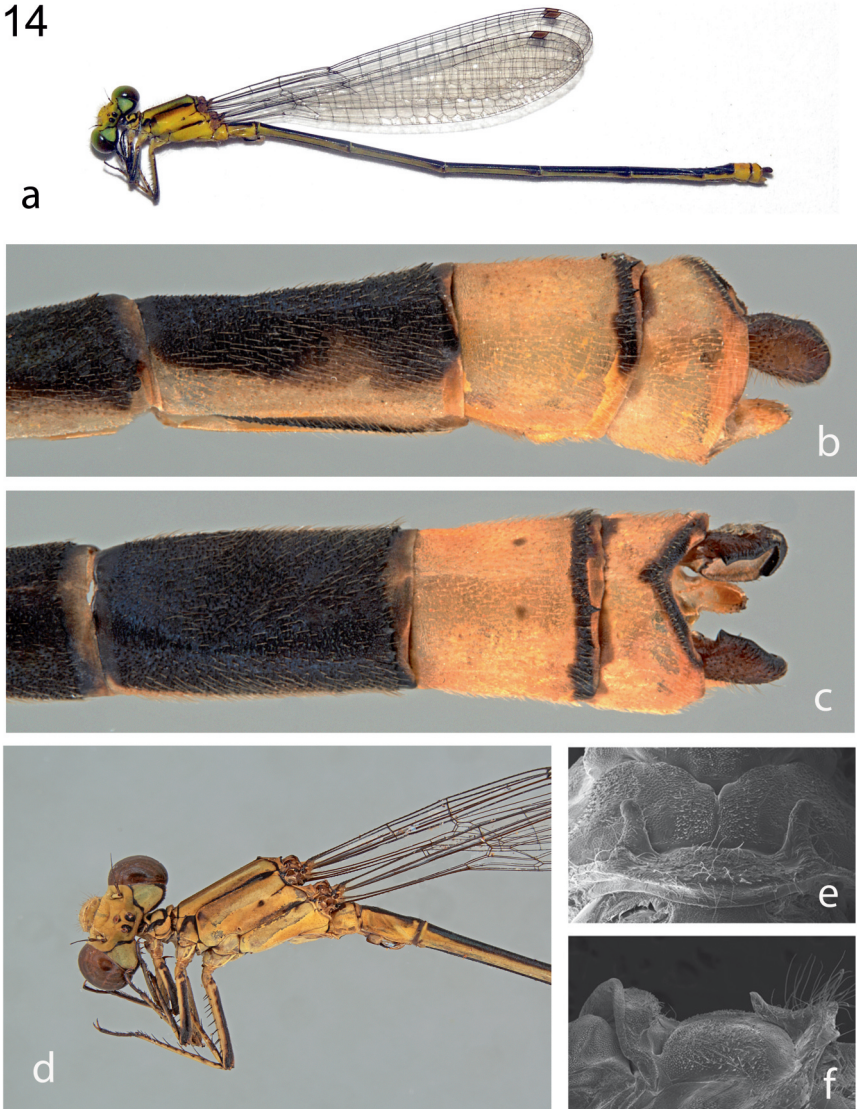


Figure 14. *Pseudagrion lorenzi* Gassmann (a) male habitus, left lateral; (b, c) male abdominal terminalia in multiple views; specimen from Vulevulu River trib., New Britain Is., CL 7349: (b) lateral; (c) dorsal; (d) male head and thorax, dorsal/lateral; (e, f) female pronotum: (e) dorsal; (f) lateral.



Figure 15. Habitat for *Pseudagrion lorenzi* Gassman, at springs above Walindi Plantation, 50 m a.s.l., New Britain Is., CL 7345 (D. A. Polhemus photo).

***Pseudagrion simillimum* Theischinger, Polhemus & Richards sp. nov.**

(Figs 2e–f, 16a–h, 17c–d, 18–21, 22d)

Polhemus et al. (2008) listed and illustrated an undescribed *Pseudagrion* from Vella Lavella, New Georgia, and Kolombangara in the Solomon Islands that was similar to *P. incisurum* but differed in some aspects of coloration and structure of the appendages. Based on morphology and geography this is described below as *Pseudagrion simillimum* sp. nov.

Holotype. ♂, BPBMNT 0000081516 (Fig. 22c), Solomon Islands: Western Province, Rendova Island, trib. to Toropi River at road, 5.5 km SE of Kenole (8°30'30"S, 157°18'45"E; 230–250 m a.s.l.), flying along stream corridor, 21-iii-2005, CL 7399, D. A. Polhemus & R.A. Englund (BPBM).

Paratypes: Solomon Islands: Rendova Island: 1 ♂, BPBMNT 0000081516, same data as holotype (BPBM); Kolombangara Is.: 1 ♂, BPBMNT 0000081517, Western Prov., rocky forest stream 5.5 km N of Ringgi harbour, 120 m. a.s.l., 7°12'03"S, 156°54'40"E, hovering along stream margins, 19-iii-2005, CL 7394, D. A. Polhemus & R.A. Englund (BPBM); 2 ♂♂, BPBMNT 0000081518, 0000081519, Vila River, 8.5 km. N of Ringgi harbor, 140–150 m. a.s.l., 8°02'39"S, 157°07'16"E, water temp. 24° C., 20 March 2005, 10:00–13:00 hrs., CL 7397, D. A. Polhemus & R. A. Englund (BPBM). Vella Lavella Is.: 1 ♂, BPBMNT 0000081520, Western Prov., Bainapo Kasi Creek, trib. to Sileri River 5–15 m a.s.l., 7°45'54"S, 156°36'17"E, hovering along stream margins, 15-iii-2005, CL 7385, D. A. Polhemus & R.A. Englund (BPBM). New Georgia Is.: 5 ♂♂, BPBMNT 0000081521–0000081525, Western

Prov., upper Sakumbare River near former Sakumbare logging camp, 15.5 km. E. of Putagita harbor, 190 m a.s.l., water temp. 26° C., 8°24'28"S, 157°41'34"E, 22 March 2005, 11:00–15:00 hrs., CL 7401, D. A. Polhemus & R. A. Englund (BPBM). Mono Is.: 2 ♂♂, 1 ♀, BPBM ENT 0000081526–0000081529, Mono Is., 10 m., 7 November 1980, J. L. Gressitt (BPBM).

Etymology. Superlative of Latin adjective *similis*, -e because of strong similarity to *Pseudagrion bougainville* sp. nov.

Description of holotype (D1)

Head. Labium pale brownish yellow; face including labrum, clypeus, genae, base of mandibles and antennae, scape and frons, red in life (Fig. 16a), fading to pale yellowish brown in preserved specimens; top of head, including vertex, postocular lobes and occiput also largely yellowish brown; pedicel dark brown; median ocellus laterally and posteriorly surrounded by black; patches and variably narrow to wider lines along inner margin and posterior margin of lateral ocelli, suture between frons and postocular lobe, along top eye margin and broadly along most of postgenae, black; apex of mandibles and antennal flagellum dark brown to black; postgenae black with pale brownish yellow band along lateral eye margin.

Thorax. Thorax predominantly bright red in living individuals (Figs 16a, b), fading to yellowish-brown in preserved specimens; pronotum largely yellow to pale yellowish brown, posterior lobe with top rim, part of furrow between anterior and median lobe, and almost all of furrow between median and posterior lobe, and midline and two longitudinal stripes each side of median lobe, black. Synthorax largely pale to darker brownish yellow with slight reddish touch. Antealar ridge, most of subalar ridge, anteroventral and posterodorsal edge of mesokatepisternum and connecting diagonal stripe, thick line on and along middorsal carina black; humeral patch 1/4–1/3 length of suture merging into thick humeral line, line along almost dorsal 1/2 of interpleural suture ending in slightly thicker patch, a patch covering about dorsal 1/4–1/3 along metapleural suture and a smaller patch at posterodorsal end of metapostepimeron, black; very fine line along more than 2/3 of metapleural suture and along most of the suture separating metepimeron from metapostepimeron, black. Humeral plates and terga largely pale to darker greyish yellow and brownish yellow. Legs with coxa and trochanter very pale greyish yellow to very pale brownish yellow, profemur almost completely black, protibia pale greyish yellow to brownish yellow with most of inner-/anterior and part of lateral face black, tarsi and spines black, claws pale to dark greyish and brownish yellow, mid- and hind-leg missing. Postcoxae and poststernum pale yellow. Wings with venation black and membrane hyaline. Postnodals 14/13. Pt distinctly sloping, overlying slightly less than 1 cell, yellowish grey to blackish grey.

Abdomen. Tergites 1–8 black dorsally, pale to dull yellow to brownish yellow laterally with thin extension reaching close to midline at base of S3–6; tergite 9 yellow, with broad black apical rim dorsally; S10 yellow with irregular brownish lateral patch and thin black dorsal apical rim. Most of sternite 1 yellow with midventral black patch in basal 1/2; secondary genitalia largely yellow with second joint of penis black (Figs 17c, d); sternites 3–7 largely black; sternite 8 yellow with black midline; sternite 9 including valvae yellow. Superior anal appendages largely brown to black, in lateral view more than 50% longer than wide, dorsal margin curved beyond midpoint creating a slight swelling followed by a narrowed subtruncate apex; in an oblique dorsal view – inner dorsolateral view basal excavation ca

1/2 the length of appendage, median process rather small and inner margin not tapered towards apex, apical hook uniformly curved basally, distally rather straight and weakly recurved. Inferior anal appendages yellow to medium and dark brown, slightly conical in lateral view.

Dimensions. Hind wing 23.7 mm; abdomen 36.2 mm.

Variation in the male paratypes

The paratype from Vella Lavella (E1) has labium, face including labrum, clypeus, genae, base of mandibles and antennae, scape and frons up to just beyond median ocellus yellow, with only a tiny spot posterior to median ocellus black; pedicel, top of frons from level lateral ocelli, postocular lobes, vertex and dorsal portion of occiput are largely pale yellowish grey with black patches and variably narrow to wider lines along inner margin of lateral ocelli; apex of mandibles and antennal flagellum are black.

Pronotum largely yellow to pale brownish yellow, posterior lobe greyish yellow to yellowish grey. Synthorax with most of dorsum pale to darker greyish yellow and yellowish brown, darkest but not well-defined for about 1/3 of mesanepisternum along middorsal carina, sides pale brownish yellow to very pale greyish yellow from humeral suture to posterior margin of metepimeron; middorsal carina, antealar ridge, most of subalar ridge, a wider patch covering dorsal 1/5–1/4 along and of the humeral suture, a thinner patch covering more than 1/5 of and along interpleural suture with ill-defined dark patch not far ventral to it, and a slightly wider patch again along and of the dorsal 1/5 of metapleural suture, black; small patch at posterodorsal end of metapostepimeron, very fine lines along remainder of humeral, interpleural and metapleural sutures black. Legs with pro- and mesofemur pale greyish yellow to pale brownish yellow with lateral and posterior face almost completely black, pro- and mesotibia largely pale greyish yellow to brownish yellow with most of inner/anterior face black, protibia also with lateral face partly darkened, tarsi and spines black; hindleg missing. Postcoxae and poststernum yellow to pale greyish yellow. Postnodals 14–15/13–14. Pt overlying up to all of 1 cell, yellowish grey.

Abdominal tergites 1–8 dorsally black, laterally very pale greyish yellow to brownish yellow with thin extension to close to midline at base of S3–7, S10 yellow with thin dorsal apical rim. Most of sternite 1 yellow with substantial midventral black patch in basal 2/3; sternite 8 largely dark grey to black; sternite 9 including valvae yellow. Superior anal appendages largely black, inferiors yellow to brown, in lateral view about half as thick as superiors.

Dimensions. Hind wing 20.9 mm; abdomen 30.8 mm.

The paratype from Kolombangara (E2) has face and top of head yellowish brown to brownish yellow with the usual black elements, but the occiput and midline between lateral ocelli dark brownish yellow; and the pale margin of postgenae thin and fragmentary; top of head largely dark yellowish grey making black elements hard to detect/distinguish.

Dorsum and sides of synthorax greyish yellow, metepisternum and metepimeron somewhat darker with slight reddish touch, mesokatepisternum somewhat darker, also black anterodorsally and posteroventrally with thick diagonal black stripe. Black line on and along middorsal carina thick; humeral patch, 1/3 the length of suture merging into thick line for the remainder of the suture, line along dorsal 1/5 of interpleural suture and spot some distance ventral to it, connected to make one quite distinct black element. Legs missing. Postcoxae

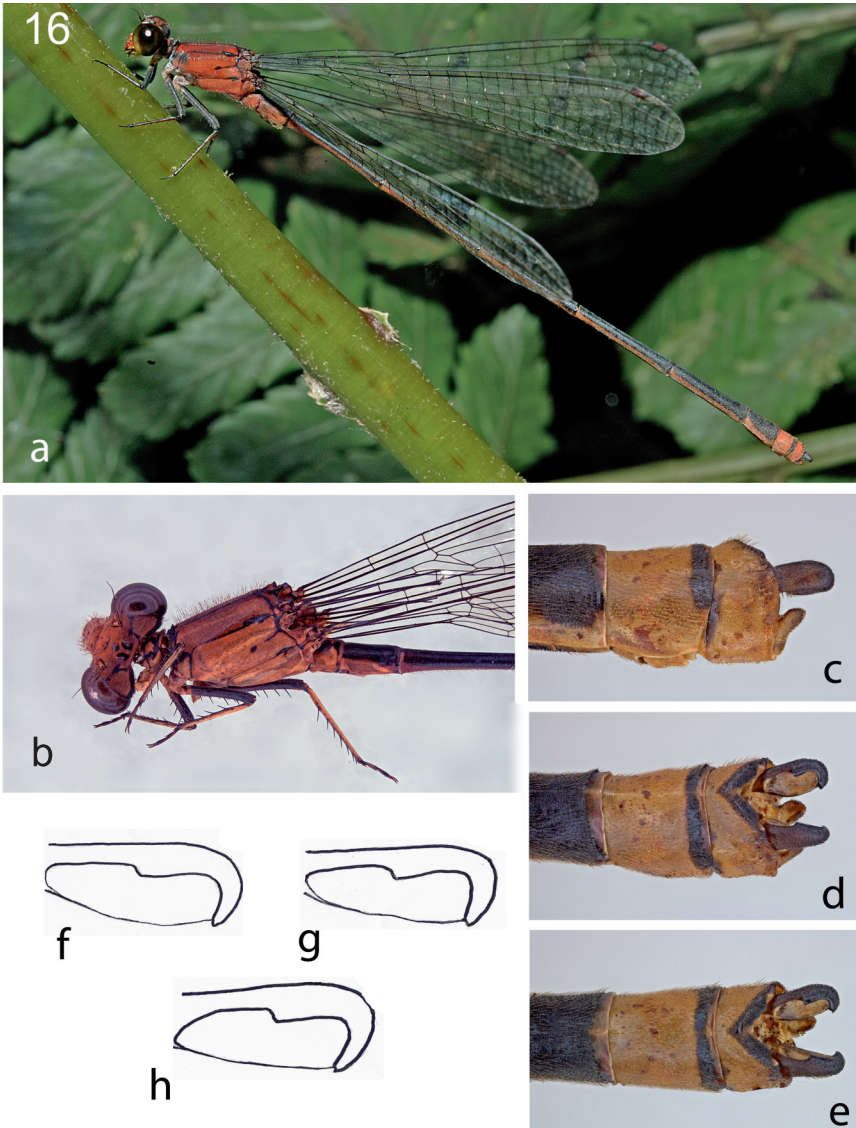


Figure 16. *Pseudagrion simillimum* sp. nov., male. (a) habitus, left lateral, photograph of living specimen from Toropi River trib., Rendova Is., CL 7399 (D. A. Polhemus photo); (b) head and thorax, dorsal/lateral; (c–e) male abdominal terminalia in multiple views; Figs 16a–e based on specimen from upper Toropi River trib., Rendova Is., CL 7399: (c) lateral, (d) dorsal oblique, (e) dorsal; (f–h) right superior appendage, skewed dorsal view, showing configuration of apical hook, sub-basal process and basal excavation: (f) from Kolombangara; (g) from Rendova; (h) from Vella Lavella.



Pseudagrion incisurum – Guadalcanal

Pseudagrion simillimum – Kolombangara

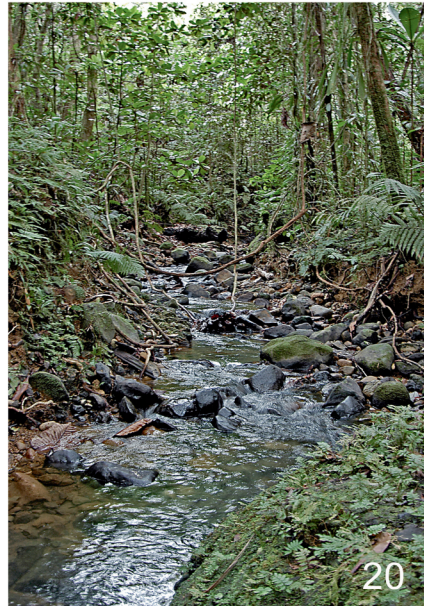
Figure 17. Male secondary genitalia of *Pseudagrion* species. (a, b) *Pseudagrion incisurum* Lieftinck: (a) dorsal, (b) lateral; specimen from Tenaru Falls, Guadalcanal, CL 7337; (c, d) *Pseudagrion simillimum* sp. nov.: (c) dorsal, (d) lateral; specimen from Toropi River trib., Rendova Is., CL 7399.

variably broadly black along midline. Postnodals 14/12–13. Pt dark yellowish grey.

Yellow sides of S1 and S2 with slight touch of reddish, pale coloration on side of S3–7 somewhat reduced, rather yellowish brown, reaching close to mid-dorsum at base of S3–6 only. Sternites greyish brown to black. Inferior anal appendages pale brownish yellow, rather thin. Valvae pointed.

Hind wing 21.7 mm; abdomen 33.4 mm.

Differential diagnosis. The male of *Pseudagrion simillimum* sp. nov. can be distinguished from *P. lorenzi* and *P. incisurum* by the relatively longer basal excavation of its superior anal appendages (ca 1/2 the length vs less than 1/4–ca 1/3 the length), from *P. brevicornis* sp. nov. by the apically more widely rounded to truncate vs sub-conical superior anal appendages, and from *P. bougainville* sp. nov. by the less prominent median process and the abruptly reflexed vs uniformly curved apical hook (Figs 16c–h).



Figures 18–20. Habitats for *Pseudagrion simillimum* sp. nov.: (18) upper Toropi River trib., 250 m a.s.l., Rendova Is., CL 7399; (19) Bainapo Kasi Creek, 15 m a.s.l., Vella Lavella Is., CL 7385; (20) stream 5.5 km. N. of Ringgi Harbor, 120 m a.s.l., Kolombangara Is., CL 7394 (D. A. Polhemus photos).

Distribution and habitats. Restricted to the Solomon Islands where it occurs in the New Georgia group of islands: Kolombangara, New Georgia, Rendova, Vella Lavella, and somewhat more distant Mono (Fig. 21). Adults were taken flying along the margins of rocky upland streams (Figs 18–20), across an elevation range of 5–250 m a.s.l.

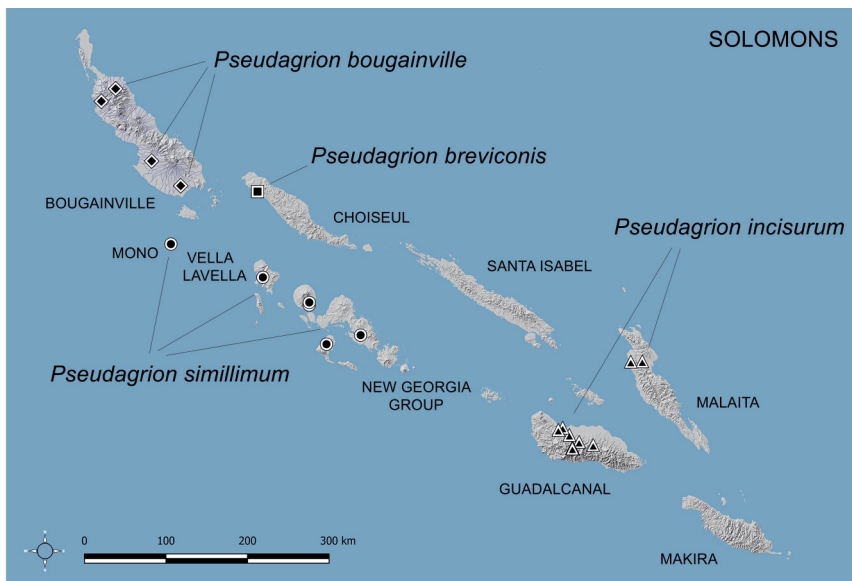


Figure 21. Distribution of yellow-faced *Pseudagrion* species in the Solomons.

Molecular Results & Discussion

Relationships

The histone gene is highly conserved within the ingroup, with only a single variable site in an alignment of 328 bp (0.3%) with sequences from only *P. bougainville* sp. nov. and *P. incisurum*. ITS2 has 17 sites that vary within the ingroup in an alignment of 302 bp (5.6%), including two indels, while COI has 7 sites which vary within the ingroup out of 559 bp (1.3%), however there are 38 variable sites between ingroup and outgroup (6.8%). Only half-length COI sequences (304 bp) were obtained for the two *P. simillimum* sp. nov. specimens.

The BI tree from the “all data” dataset is shown as Appendix 2. This tree has a polytomy at the base, and fails to demonstrate that the ingroup is monophyletic, with *P. ignifer* possibly being placed within the ingroup.

P. lorentzi is clearly separated from the other ingroup species with strong support, posterior probability (PP) equal to 1. However, there is very little DNA variation among the remaining species.

There is no support for any of the remaining species being monophyletic in our trees, in part due to the lack of DNA variation. For *P. simillimum* sp. nov., the two Sanger sequences

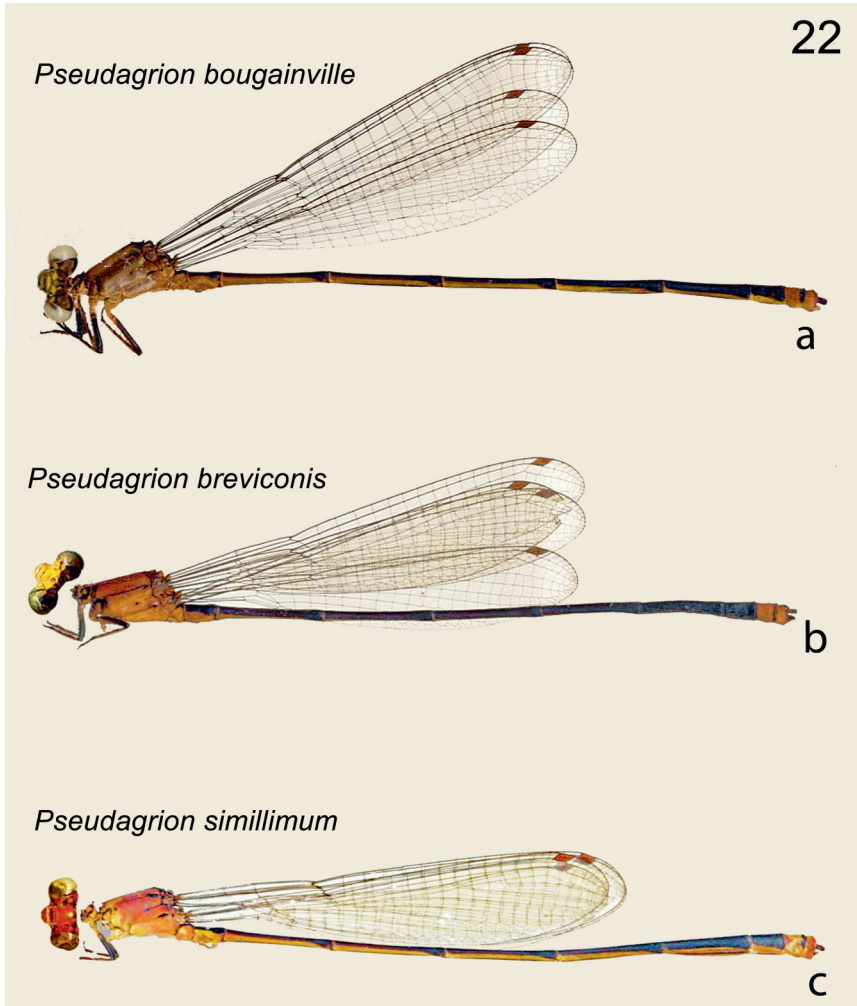


Figure 22. Holotypes of the *Pseudagrion* species described as new in this paper, male, habitus, left lateral view. (a) *P. bougainville* sp. nov.; (b) *P. breviconis* sp. nov.; (c) *P. simillimum* sp. nov.

derived for COI (specimens D1 and E2) are short (304 bp) and most similar to *P. incisurum*, while the Illumina sequence for a third specimen (ODO8) is identical to the *P. bougainville* sp. nov. sequences. For ITS2 the ODO6 sequence again is identical to the *P. bougainville* sp. nov. sequences, while the single Sanger sequence (from specimen D1) is unique and quite distinct from the remaining ITS2 sequences (3.0% p-distance). There are too few samples of this species to determine whether there is indeed substantial variation within

this species or if cross-contamination among samples is the reason for sample ODO6 being placed within *P. bougainville* sp. nov.

Even if the identity of the *P. ignifer* specimen is correct, our main point still stands, and that is that the large amount of missing data in the “all data” dataset casts doubt on the trees derived from it. We therefore analysed a smaller dataset from the same specimens but including only COI and ITS2 data. The latter dataset gives much more robust results. In that tree (Appendix 3) *P. lorentzi* is sister group to all other in *Pseudagrion* species sampled here, while *P. ignifer* branches off next, as sister-group to the remaining *Pseudagrion*.

Given that the “all data” dataset has very large gaps in the data matrix with >50% missing data, we thought it prudent to also analyse a subset of the data with a low proportion of missing data, hence our second dataset comprising just COI and ITS2 data. The Bayesian tree derived from this dataset is shown as Appendix 3, with PP and ML ultrafast bootstrap values shown above branches, when >0.9 and 90% respectively. Appendix 3 indicates that the ingroup is not monophyletic with respect to the “*P. ignifer*” sequence, with *P. lorentzi* placed as sister-group to a clade comprising *P. ignifer* and the rest of the ingroup. There is strong support (PP = 1) in this tree for the monophyly of *P. bougainville* sp. nov. plus the single sample *P. simillimum*. In this tree *P. brevicornis* sp. nov. and *P. incisurum* are recovered as monophyletic, although they are each subtended by very short branches with no statistical support. It appears that these species have radiated very recently.

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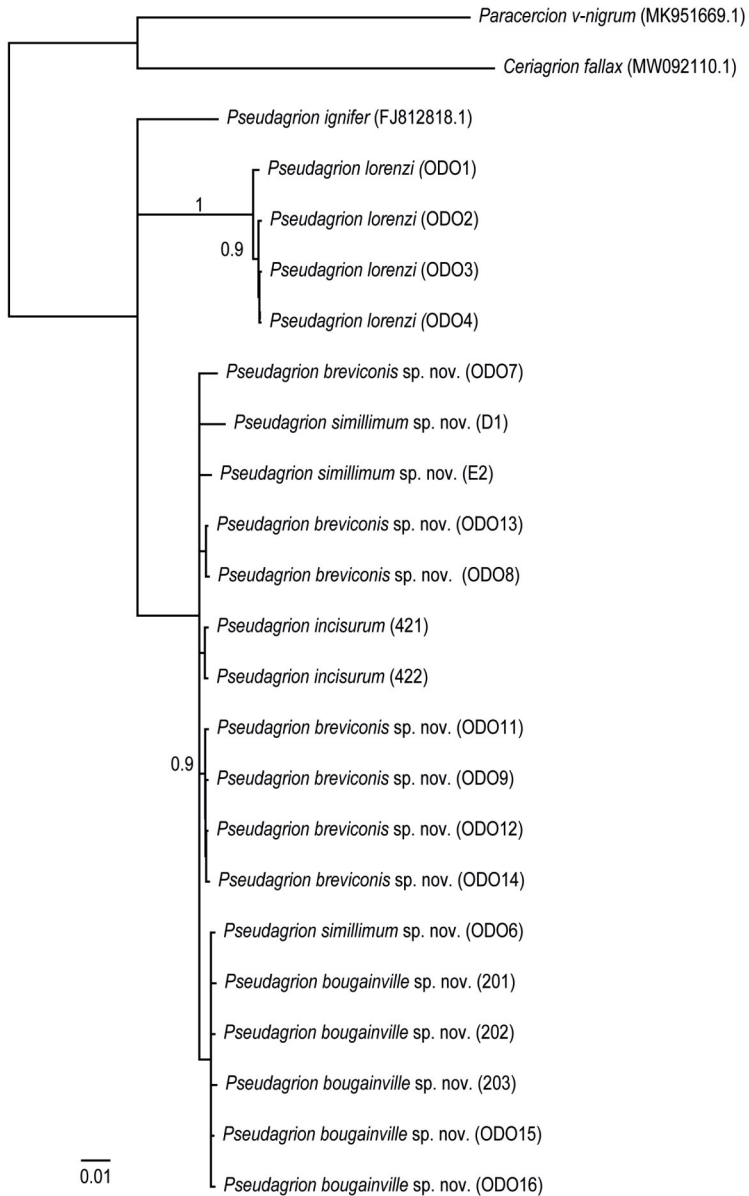
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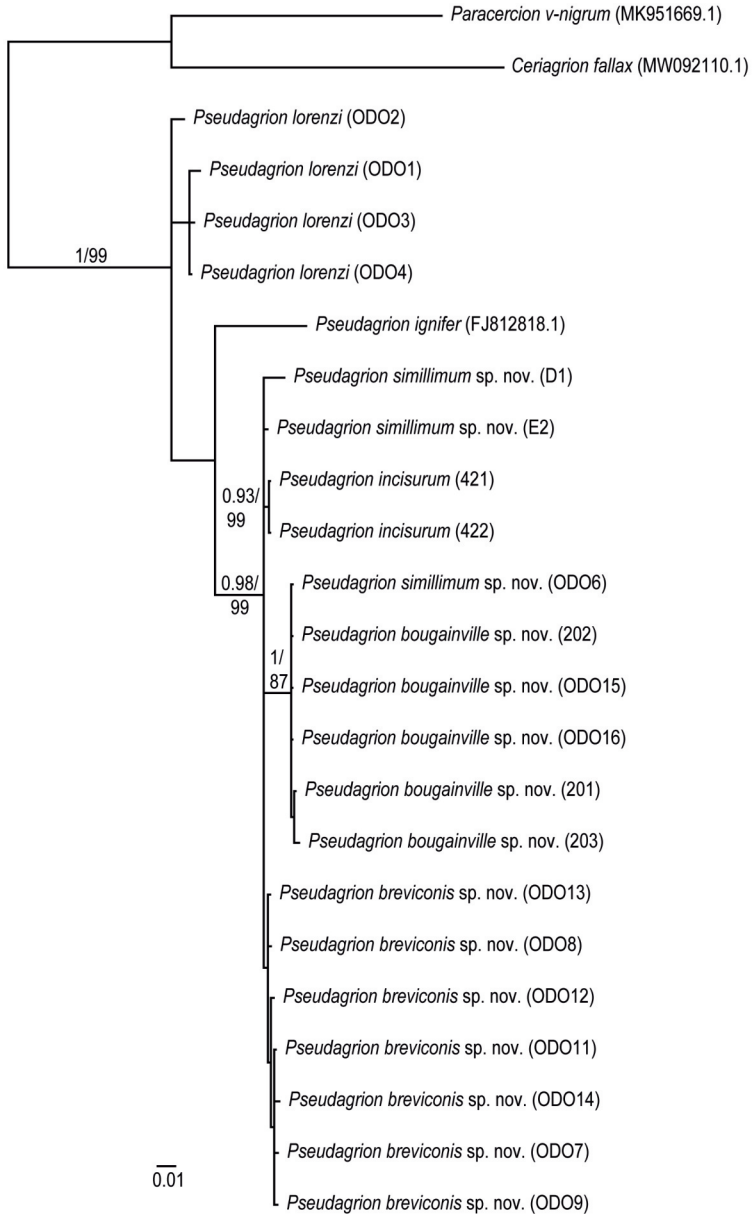
Appendix 1. Samples used for DNA analysis, specimen collection locality and sequence database accession numbers.

Species	Locality	Sample ID	Museum Accession	GenBank Accession COI (For mt genome)	GenBank Accession Histone 3	GenBank Accession ITS2
<i>Paracercion v-nigrum</i>	Unknown			MK951669.1		
<i>Ceriagrion fallax</i>	Unknown			MW092110.1		
<i>Pseudagrion ignifer</i>	Unknown			FJ812818.1		
<i>Pseudagrion lorentzi</i>	Papua New Guinea, New Ireland	ODO1	K.668522	PX222956		
<i>Pseudagrion lorentzi</i>	Papua New Guinea, New Ireland	ODO2	K.668523			
<i>Pseudagrion lorentzi</i>	Papua New Guinea, New Ireland	ODO3	K.668524	PX222955		
<i>Pseudagrion lorentzi</i>	Papua New Guinea, New Ireland	ODO4	K.668525	PX222954		
<i>Pseudagrion breviconis</i> sp. nov.	Solomon Islands, Choiseul Is	ODO7	BPBMENT 0000081508			PX222970
<i>Pseudagrion breviconis</i> sp. nov.	Solomon Islands, Choiseul Is	ODO8	BPBMENT 0000081509			PX222971
<i>Pseudagrion breviconis</i> sp. nov.	Solomon Islands, Choiseul Is	ODO9	BPBMENT 0000081510	PX222950		PX222972
<i>Pseudagrion breviconis</i> sp. nov.	Solomon Islands, Choiseul Is	ODO11	BPBMENT 0000081511	PX222951		PX222973
<i>Pseudagrion breviconis</i> sp. nov.	Solomon Islands, Choiseul Is	ODO12	BPBMENT 0000081512	PX222939	PX222978	PX222960
<i>Pseudagrion breviconis</i> sp. nov.	Solomon Islands, Choiseul Is	ODO13	BPBMENT 0000081513	PX222940		PX222961
<i>Pseudagrion breviconis</i> sp. nov.	Solomon Islands, Choiseul Is	ODO14	BPBMENT 0000081514	PX222949		PX222969
<i>Pseudagrion incisurum</i>	Solomon Islands, Guadalcanal	421		PX222952	PX222984	PX222974
<i>Pseudagrion incisurum</i>	Solomon Islands, Guadalcanal	422		PX222953	PX222985	PX222975
<i>Pseudagrion simillimum</i> sp. nov.	Solomon Islands, Vella Lavella Is	ODO6E1	BPBMENT 0000081520	PX222948		PX222968
<i>Pseudagrion simillimum</i> sp. nov.	Solomon Islands, Rendova Is	D1	BPBMENT 0000081517	PX222941		PX222962
<i>Pseudagrion simillimum</i> sp. nov.	Solomon Islands, Kolombangara Is	E2	BPBMENT 0000081516	PX222942		
<i>Pseudagrion bougainville</i> sp. nov.	Papua New Guinea, Bougainville	ODO15	SAMA 07-001684	PX222947	PX222983	PX222967
<i>Pseudagrion bougainville</i> sp. nov.	Papua New Guinea, Bougainville	ODO16	SAMA 07-001686	PX222946	PX222982	PX222966
<i>Pseudagrion bougainville</i> sp. nov.	Papua New Guinea, Bougainville	201	SAMA 07-001685	PX222943	PX222979	PX222963
<i>Pseudagrion bougainville</i> sp. nov.	Papua New Guinea, Bougainville	202	SAMA 07-001687	PX222944	PX222980	PX222964
<i>Pseudagrion bougainville</i> sp. nov.	Papua New Guinea, Bougainville	203	SAMA 07-001688	PX222945	PX222981	PX222965

Appendix 2. All data Bayesian Tree (Specimen collection localities provided in Appendix 1)



Appendix 3. COI, ITS2 Bayesian Tree.



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