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Notes on *Amazoneura*, with description of *A. submontana*, a new species of damselfly from Peru (Odonata: Protoneuridae)

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Abstract. *Amazoneura submontana* sp. n. (holotype ♂: Peru, San Martín Región) is described and illustrated. Males of *A. submontana* can be distinguished from the other three known members of the genus by the shape of the cerci and absence of a dark ventral cross band behind the metacoxa in mature specimens. With the description of this fourth species of *Amazoneura* it became clear that some characters attributed to the genus previously are species-specific, so the generic characterization is updated. Furthermore, the species status of *A. westfalli* is confirmed based on genetic information and a key to males of all species is provided.

Keywords: Zygoptera, Andes, San Martín, South America, Yungas

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Data Availability Statement:
All relevant data are within the paper.

Introduction

Amazoneura is a small genus with records known from the Amazon region of northern Peru and the bordering regions of Colombia, Ecuador and Brazil (Bota-Sierra et al., 2024; Koroiva et al., 2020; Mauffray & Tennessen, 2019: Miranda Filho et al., 2022). It was erected by Machado in 2004 to receive the species *A. ephippigera* (Selys, 1886), *A. westfalli* (Machado, 2001) and a new species *A. juruaensis* Machado, 2004. Until then the first two species were placed in the genus *Forcepsioneura,* a genus with similarly built species confined to the Atlantic Forest and Cerrado of eastern Brazil (Machado, 2004, 2008; Pimenta et al., 2019; Pinto & de Araujo, 2021; Pinto & Kompier, 2018).

In 2015 eight males of a hitherto undescribed fourth species were collected in San Martín, Peru. This species closely resembles the other species within *Amazoneura*, but also has some characteristics in common with *Forcepsioneura*. The generic characterization is updated to incorporate the observed intrageneric variation.

Genetic data that was used to show that *A. submontana* represents a separate taxon also shows that *A. westfalli* and *A. ephippigera* are distinct taxa. Due to their very similar morphology this has been questioned in the past (Mauffray & Tennessen, 2019).

Materials and methods

Specimens were collected during a collecting trip in the San Martín Región in northern Peru in 2015. The holotype and five paratypes were deposited in the Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima; three paratypes are housed in the National Museum of Natural History Naturalis, Leiden, the Netherlands.

Photographs of preserved specimens were taken using focus stacking technology (Canon EOS 90D digital camera mounted on a Tamron 90/2.8 macro for overviews and Canon MPE 65/2.8 macro and Nikon CFN 10× microscope objective for smaller details).

To help clarify the position of the new species 2 COI-sequences were compared reciprocally and with that of 23 species from ten neotropical genera within the family Protoneuridae: *Amazoneura, Drepanoneura*, *Epipleoneura*, *Forcepsioneura*, *Idioneura*, *Neoneura*, *Peristicta*, *Protoneura*, *Psaironeura* and *Roppaneura*. Sequences available at RMNH and boldsystems.org were used for the analysis. A phylogenetic tree was constructed using phyML 3.0 (Guindon et al., 2010) and SMS (Smart Model Selection) (Lefort et al., 2017), resulting in best model: GTR +R. Sequences were aligned manually. Branch support values were calculated using the SH-like approximate likelihood ratio test.

Body morphology nomenclature follows Garrison et al. (2010). Measurements are in millimetres, abdominal length excludes appendages. Abbreviations used are as follows: FW – fore wing; HW – hind wing; CuP – Cubitus posterior; CuA – Cubitus anterior; RP2 – Radius posterior, second branch; S1–10 – abdominal segments 1 to 10; MUSM – Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru; RMNH – National Museum of Natural History Naturalis, Leiden, the Netherlands.

Results

Amazoneura submontana sp. nov.

(Figures 1–4)

Etymology

The species is named *submontana*, an allusion to the habitat in which it was found: rather low on the flanks of the Cordillera Oriental (eastern Andes). In Spanish this habitat is referred to as “Bosque Basimontano de Yunga”, a specific type of mountain rainforest within the bioregion of the Yungas.

Type specimens

Holotype ♂

Peru, San Martín Región, northwest of Tarapoto, on a south facing mountain slope just south of the Área de conservación regional Cordillera Escalera, elevation 1300 m a.s.l., -6.32551° S, -76.46285° W (27.i.2015), leg. T. Faasen [MUSM].

Paratypes

5♂, same data as holotype, 3♂, same data as holotype except [RMNH].
Females of this species are still unknown.

Description of male holotype

Head. Labium beige. Labrum dark metallic blue with pale anterior border. Mandibles, anteclypeus and genae brown. Postclypeus dark metallic blue. Frons rounded and shiny metallic. Vertex matte black, lacking postocular spots. Eyes, antennae and rear of head dark brown to black (Figures 1A, B).

Thorax. Prothorax pruinose; black, except for greyish anterolateral edge of anterior lobe and entirely greyish propleuron. Middle lobe lacking markings or distinct protuberances, widening posteriorly, with narrowly rounded posterolateral angle. Posterior lobe angled posterolaterally; with continuous, rounded hind edge; medially twice as wide as in lateral corners (Figures 1A, C).

Pterothorax: mesepisternum black with metallic yellow-green reflection, anterior 45% partly covered by greyish pruinosity, narrowing posteriorly, reaching furthest near humeral suture. Mesepimeron with a longitudinal black band, bordered dorsally by an indistinctly delimited grey stripe. Mesinfraepisternum black on dorsal half, grey on ventral half. Metepisternum grey, except for ventral black band from metathoracic spiracle to caudal edge. Metepimeron, venter of pterothorax and coxa whitish. Legs largely whitish, with robust dark dorsal longitudinal stripe on femur, irregular, narrow dark line dorsally and ventrally on tibia, dark spines and small dark areas near joints. Hindtibia with a dark longitudinal line ventrally. Claws dark orange-brown; tip slightly darkened with distinct supplementary tooth. Mesostigmal plates with simple, rounded anterolateral margin (Figures 1C, E).

Wings. Hyaline. Pterostigma covering one cell, brown with thickened marginal veins. CuP slightly closer to antenodal 2 than 1 in both FW and HW. Postnodals: 15 in left FW, 17 in right FW, 13 in left HW and 14 in right HW. RP2 branching at postnodal 7 in FW, at postnodal 5 in HW. CuA extending 0,5 cell length distal to vein descending from subnodus (Figure 1D).

Abdomen. S1–10 black dorsally with faint metallic reflection, except for narrow whitish basal ring on S3–7; ventrally whitish except for entirely dark S10 (Figure 1E). Cerci black, longer than S10, slender, with long dorsal branch and shorter sub-basal ventral branch and ventromedial process. Dorsal branch forcipate, strongly directed dorsoposteriorly. Ventral branch slightly longer than wide and separated from S10 by a distance slightly larger than its width. Ventromedial process brown, tubercle-like, triangular with rounded apex, visible in dorsal, ventral and caudal view, not in lateral view. Rim between ventromedial process and tip of ventral branch of cercus shallowly concave. Paraprocts vestigial (Figures 1F–H, 3C). Genital ligula with terminal fold and large inner fold; terminal segment with two lateral flattened flaps bearing a long curved flagellum (Figures 2A, 2B).

Measurements [mm]. Total length 49.5, abdomen length 43, FW length 29, HW length 28.

Variation in male paratypes

Head. As in holotype, but frons variably rounded to almost angled; dorsum slightly metallic in four paratypes.

Thorax. As in holotype except for: CuP halfway between antenodal 1 and 2 in five paratypes, 14 postnodals in left FW in three paratypes, 16 postnodals in left FW in four paratypes, 15 postnodals in right FW in four paratypes, 16 postnodals in right FW in two paratypes, 14 postnodals in left HW in three paratypes, 13 postnodals in right HW in five paratypes, RP2 branching at postnodal 6 in FW in one paratype, distal to postnodal 7 in left FW in one paratype and distal to postnodal 7 in right FW in three paratypes, RP2 branching proximal to postnodal 5 in right HW in one paratype, at postnodal 6 in right HW in two paratypes. Variation in extent of pruinosity very limited.

Abdomen. As in holotype.

Measurements [mm]. Total length 45.7–51.0, abdomen length 38.0–43.5, FW length 26.5–29.5, HW length 25.8–28.7.

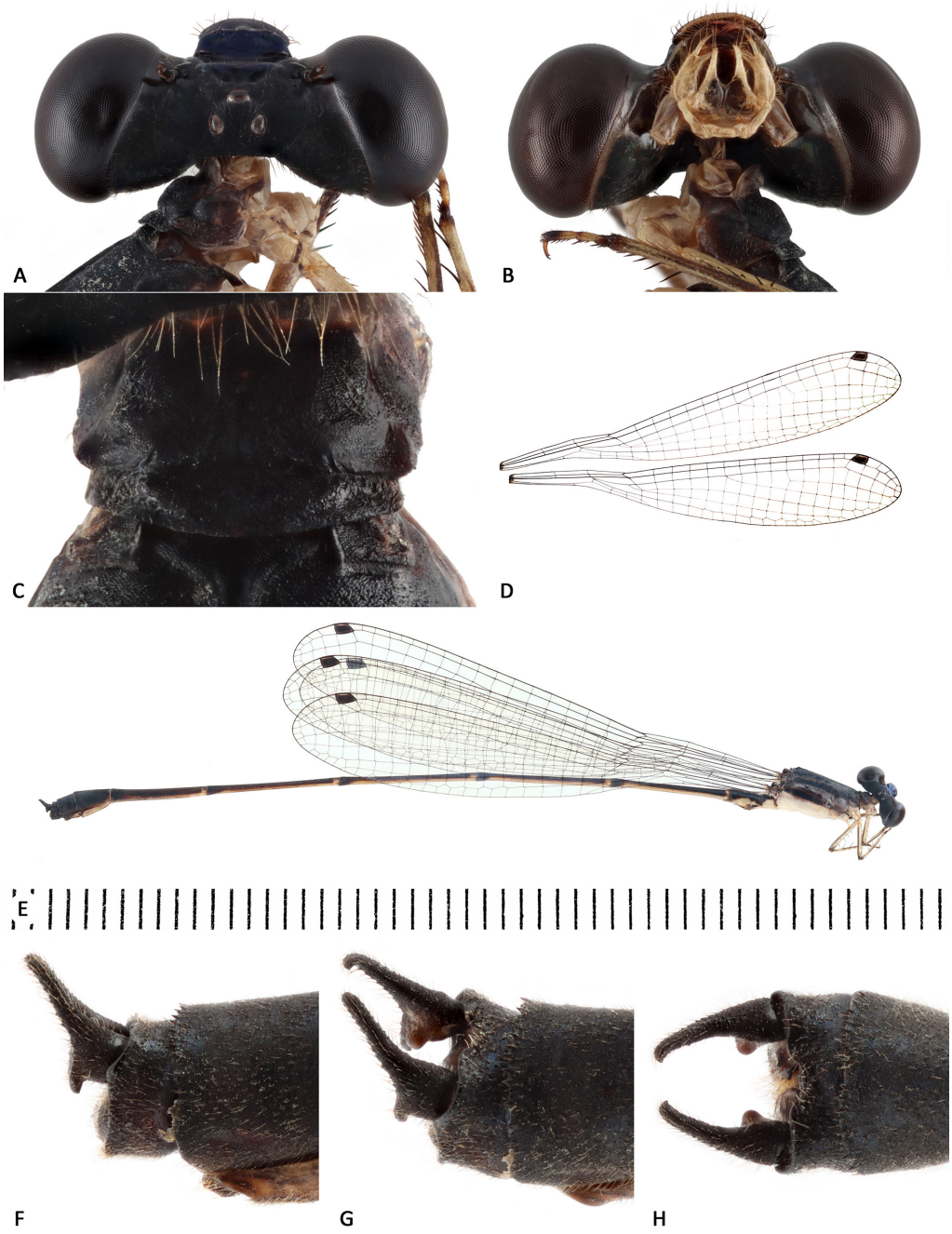


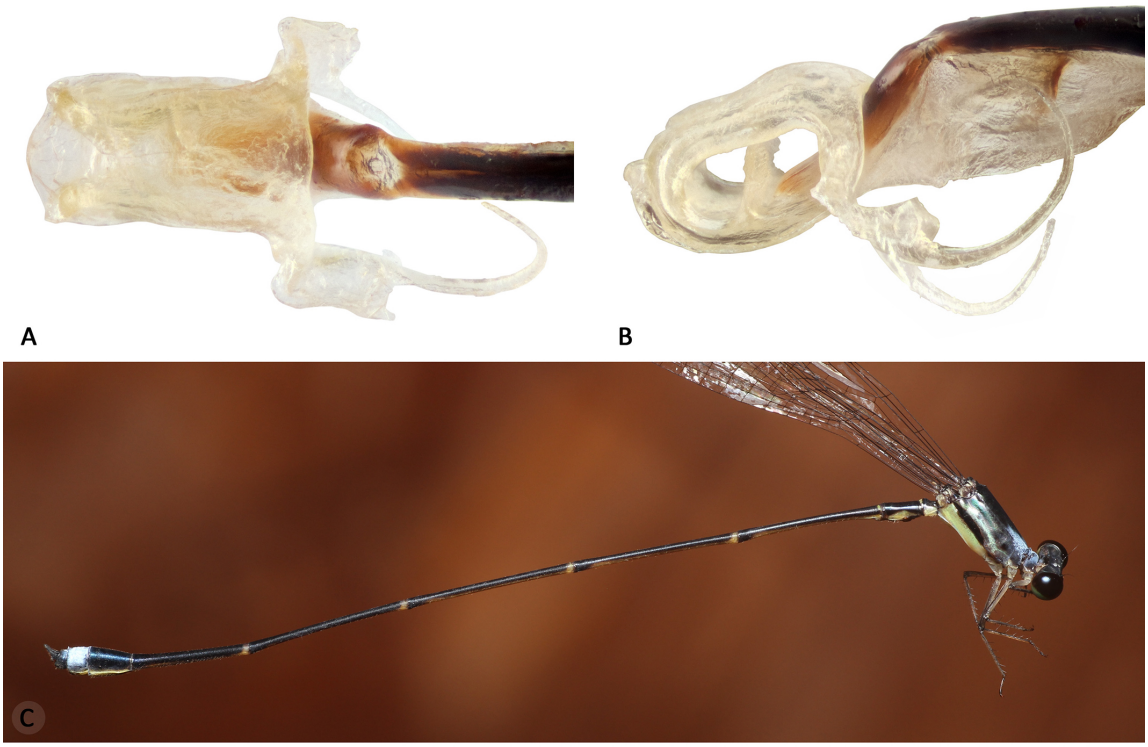
Figure 1. *Amazoneura submontana:* (A) head dorsal view, male paratype; (B) head ventral view, male paratype; (C) prothorax dorsal view, male paratype; (D) wings, male paratype; (E) habitus male paratype; (F) caudal appendages lateral view, male paratype; (G) caudal appendages mediodorsal view, male paratype; (H) caudal appendages dorsal view, male paratype.

Remarks

Two collected specimens were photographed when alive (Figure 2C), providing colour information. Eyes dark brown to black on dorsal ⅔, greenish-yellow on ventral ⅓, sharply demarcated; prothorax and small basal part of pterothorax pruinose; ventral part of thorax and abdomen pale yellow. Tergite of S9 entirely pruinose, base of S10 slightly pruinose dorsally.

Diagnosis

Males of *Amazoneura submontana* can be distinguished from the other members of the genus by the shape of the cerci: ventral branch distinctly separated from the posterior margin of S10 (Figure 1F) [adjacent to S10 in other species]. Additionally mature males can be distinguished by their entirely light ventral side of the thorax (Figure 1F) [with a black cross band in other species].



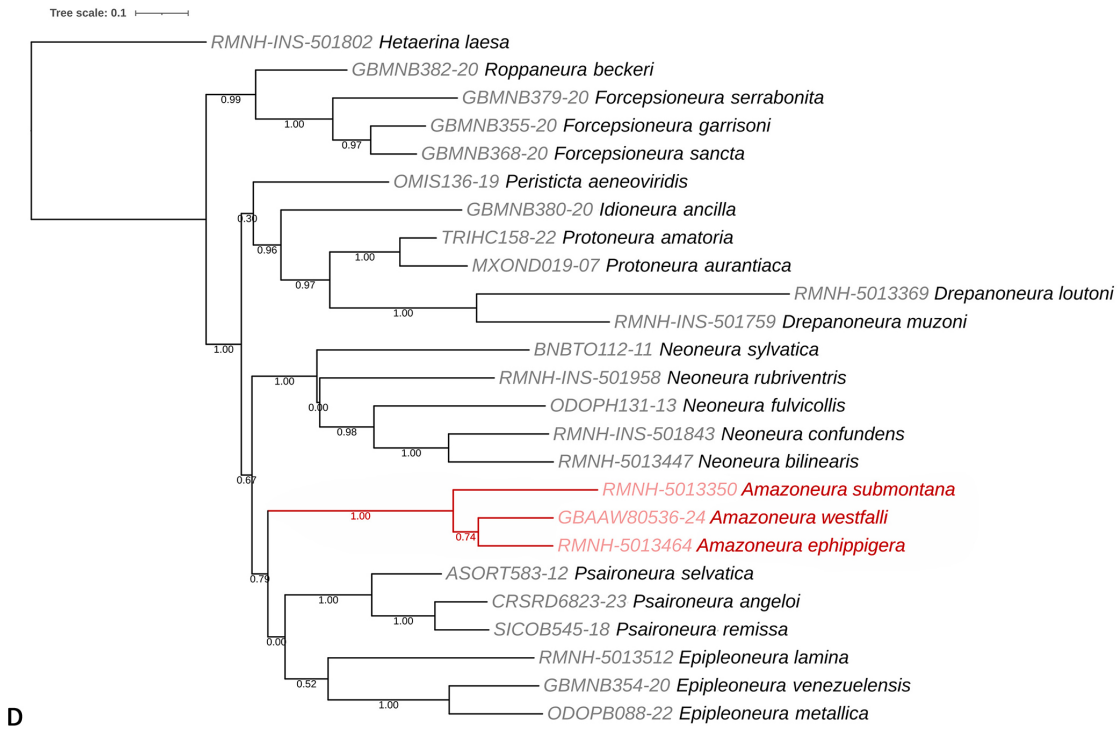


Figure 2. *Amazoneura submontana:* (A) genital ligula ventral view, male paratype; (B) genital ligula lateral view, male paratype; (C) habitus male paratype *in vivo*; (D) Section of rooted maximum likelihood phylogram (based only on COI-5P) with neotropical representatives of Protoneuridae including branch support values.

Table 1. characters separating the males of the four species of *Amazoneura*. * In Machado, 2004 it is stated that *A. ephippigera* has pruinescence on the thorax. In Peruvian specimens it is present on S9, not on the thorax, as in *A. westfalli*.

Character	*A. juruaensis*	*A. ephippigera*	*A. westfalli*	*A. submontana*
Body length	46 mm	37–42 mm	38–41 mm	45.7–51 mm
Cerci in lateral view	not strongly directed upwards	strongly directed upwards	strongly directed upwards	strongly directed upwards
Ventral branch of cercus	poorly-developed, bordering S10	moderately developed, strongly curved anteromedially, bordering S10	well-developed, moderately curved, projecting medioventrally, bordering S10	well-developed, hardly curved, projecting ventrally, separated from S10
Apex of ventromedial process of cercus	without teeth, not visible in lateral view	with two teeth, narrowly visible in lateral view	without teeth, not visible in lateral view	without teeth, not visible in lateral view
Rim between ventromedial process and apex of ventral branch of cercus	details unknown	deeply notched	deeply notched	shallowly concave
Posterolateral corner of median lobe	without tubercle	with poorly-developed tubercle	with poorly-developed tubercle	with poorly-developed tubercle
RP2 origin closest to postnodal	6 in FW and 4 in HW	5-6 in FW and 4-5 in HW	5-6 in FW and 4-5 in HW	6-7 in FW and 5-6 in HW
Genital ligula terminal segment	'with two filaments' details unknown	gradually narrowing into two filaments	gradually narrowing into two filaments	abruptly narrowing into two filaments
Ventral side of thorax in mature males	with black cross band	with black cross band	with black cross band	without black cross band
Pruinescence in mature males	present on S9, not on thorax	variable (present on S9 and/or thorax)*	present on S9, not on thorax	present on S9 and thorax

A. submontana can be distinguished from *A. westfalli* and *A. ephippigera* specifically also by its relatively large overall size: 45.7–51.0 mm [37–42 mm in *A. westfalli* and *A. ephippigera*], by the shallowly concave rim between ventromedial process and ventral branch of the cerci [deeply notched in *A. westfalli* and *A. ephippigera*] (Figure 3A–C) and by the genital ligula which abruptly narrows into two filaments (Figure 2A) [narrowing gradually in *A. westfalli* and *A. ephippigera*].

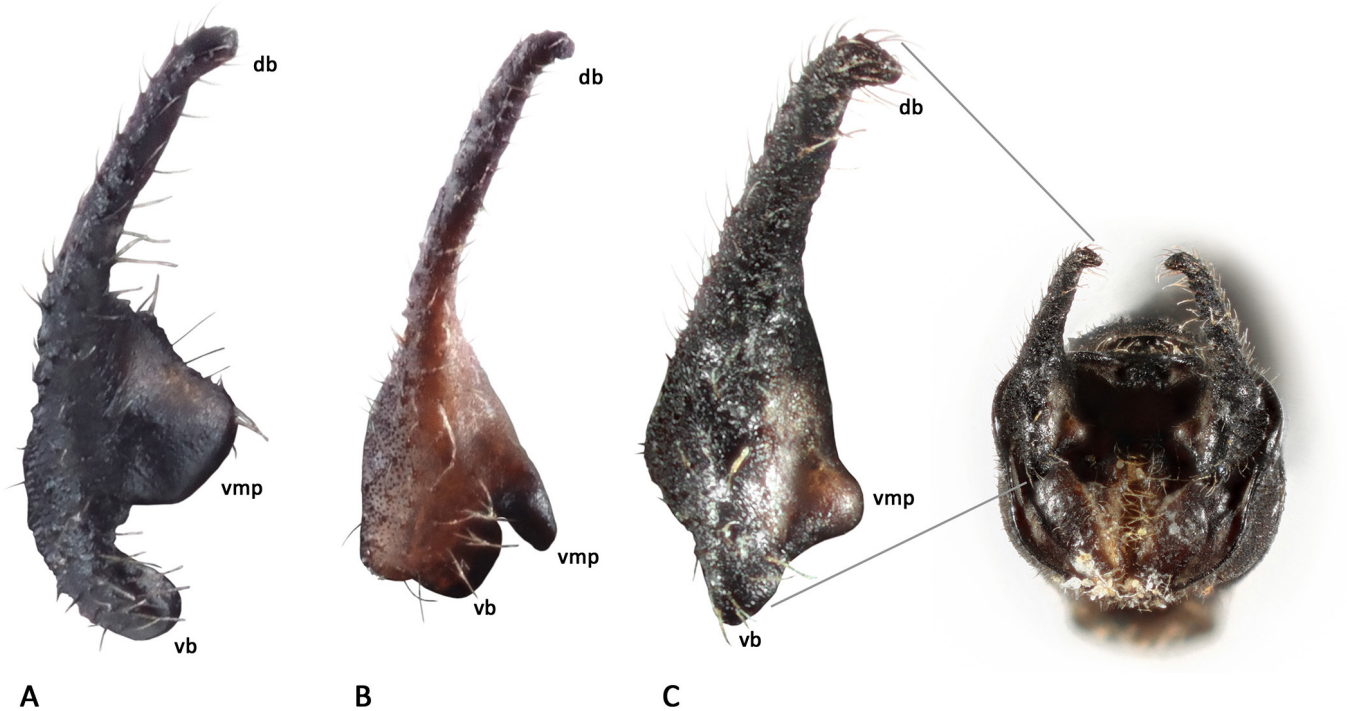


Figure 3. Left cercus caudal view. Abbreviations: db – dorsal branch, vb – ventral branch, vmp – ventromedial process. (A) *Amazoneura westfalli*; (B) *Amazoneura ephippigera*; (C) *Amazoneura submontana* (paratype).

Filiation

A basic phylogenetic analysis of the COI-5P barcode of *Amazoneura submontana* indicates a relationship with *A. ephippigera* and *A. westfalli* (Figure 2D), thus supporting its placement within the same genus, despite the lack of a black ventral thoracic cross band previously thought characteristic for all species within the genus.

As a byproduct the constructed phylogenetic tree also supports the split between *Amazoneura* and *Forcepsioneura*, as proposed by Machado (Machado, 2004, 2008) and recently confirmed by Pessacq (Pessacq et al., 2025). As this tree is based on a limited amount of information from only one gene, no firm conclusions should be drawn from it regarding clades within Protoneuridae. It does however support the species status of *A. westfalli*. In the past it has been suggested that *A. westfalli* might by a synonym of *A. ephippigera* (Mauffray & Tennessen, 2019). Despite it being morphologically quite similar to *A. ephippigera*, it differs from the latter genetically by almost 11% (50 basepairs within 463 basepairs).

Update generic characterisation

In his paper revalidating the genus *Amazoneura* (Machado, 2008) Machado mentions eight characteristics for males of the genus. Two of these are not present as such in *A. submontana* sp. n.: it has the ventral branch of the cercus pointed instead of mammillary or truncate. Furthermore the species lacks a dark metepimeral stripe extending ventrally behind the metacoxae when mature, which is present in all other species in the genus. Also the frons is not always as clearly rounded as in the other species of *Amazoneura*.

With the description of *Forcepsioneura regua* Pinto & Kompier, 2018 also it became clear that weakly developed tubercles on the posterolateral margin of the prothorax was not confined to *Amazoneura*.

Nonetheless *Amazoneura* can still be separated from *Forcepsioneura* based on morphology and habitus based on the following characteristics sensu Machado (2008): rear of head black [pale in *Forcepsioneura*], ventral branch of cercus short, not overpassing ½ the distance to ventral border of S10 [overpassing ½ this distance in *Forcepsioneura*], first antenodal costal spaces longer than third [equal or shorter in *Forcepsioneura*].

Additionally the genera can be separated based on the shape of the ventromedial process on the cerci, which is short and tubercle-like in *Amazoneura* [well-developed and plate-like in *Forcepsioneura*].

In their book on Damselfly-genera of the New World (Garrison et al., 2010) Garrison et al. give a range in length for *Amazoneura* of 40–46 mm. This should be stretched to 37–51 mm. The upper end of this range is covered by *A. submontana*; the low end by *A. ephippigera* specimens collected at Tamshiyacu-Tahuayo Reserve in northern Peru.

Key to species of the genus Amazoneura

The main text of the key presents structural characteristics. Smaller indented texts provide additional information, including known distribution and size and colour characteristics. Although the latter are considered less stable than structural characteristics they can be useful as a control option or as a workaround when studying specimens in the field or specimens that are damaged.

Key to males

1. Ventral branch of cercus moderately to well developed (though sometimes bent anteromedially and then poorly visible in lateral view); basal height of cercus in lateral view, including ventral branch, 2.5× the height of cercus at mid length or more 2

   Cerci strongly directed upwards. Mature males with or without ventral black thoracic cross band behind metacoxa.

1'. Ventral branch of cercus poorly developed: basal height of cercus in lateral view, including ventral branch, 2× the height of cercus at mid length or less ..... *A. juruaensis*

   Cerci only slightly directed upwards. Mature males with ventral black thoracic cross band behind metacoxa. Total body length ± 46 mm. Known from lowland Amazonian forests in state of Acre, Brazil (Figure 4B).

2. Ventral branch of cercus in lateral view bordering S10. Area between ventromedial process and ventral branch of cercus deeply notched in caudal view (Figure 3A, B). Ventromedial process on cercus in dorsal view semicircular or triangular, but then with two minute teeth. Genital ligula gradually narrowing into two long filaments 3

   Mature males with ventral black thoracic cross band behind metacoxa, pruinescence present or absent. Total body length 37–42 mm. Known from lowland Amazonian terra firme forests in northern Peru and bordering areas of Brazil, Colombia and Ecuador (< 500 m a.s.l.).

2'. Ventral branch of cercus in lateral view separated from S10 by at least its own width (Figure 1F). Area between ventromedial process and tip of ventral branch of cercus only slightly concave in caudal view (Figure 3C). Ventromedial process on cercus in dorsal view triangular with broadly rounded tip, without teeth (Figure 1H). Genital ligula abruptly narrowing into two long filaments (Figure 2A) ..... *A. submontana*

   Mature males without ventral black thoracic cross band behind metacoxa, but with pruinescence on both thorax and S9 (Figures 1E, 2C). Total body length 45.7–51.0 mm. Known from forests on East Andean mountains of Peru (> 800 m a.s.l.) (Figure 4B).

Figure 4. (A) Habitat *Amazoneura submontana* (type-locality); (B) known distribution *Amazoneura*-species.

3. Ventral branch of cercus not strongly curved anteromedially, projecting ventromedially. Ventromedial process on cercus semicircular in dorsal and caudal view (Figure 3A), not visible in lateral view ..... *A. westfalli*

   Known from Peru, Ecuador and Colombia (Figure 4B).

3'. Ventral branch of cercus strongly curved anteromedially and not very pronounced in lateral or caudal view (Figure 3B). Ventromedial process on cercus in dorsal view triangular with two minute teeth ..... *A. ephippigera*

   Known from Peru, Ecuador and Amazonas state Brazil (Figure 4B).

Notes on females

The females of *A. juruaensis* and *A. submontana* are not known, so a reliable key based on morphology cannot be constructed yet. However, based on differences in body size and distributional ranges females of these two species might be tentatively identified. Regarding the sympatric species *A. westfalli* and *A. ephippigera*: these are very similar in appearance, but in female specimens of A. *ephippigera* collected in northern Peru the black band on the ventral side of the metepisternum at its widest point is as wide as or slightly wider than the pale band dorsally bordering it. In female specimens of *A. westfalli* collected in northern Peru this metepisternal black band is narrower at its widest point than the pale band dorsally bordering it. Additionally in *A. westfalli* the anterior margin of the antefrons is yellow for a slightly larger part (⅔ or more) than in *A. ephippigera* (⅓ or less). More specimens should be studied though to check how stable these characteristics are.

Habitat and ecology

All eight type specimens of *Amazoneura submontana* were collected on the same day within the wet season (end of January) at the same locality northwest of Tarapoto. The place was located at 1300 m a.s.l. in primary forest of the type "Bosque Basimontano de Yunga". This forest type can be found on the eastern slopes and valleys of the Peruvian Andes. It is a non-cloudy montane ecosystem located between 600 and 1800 m above sea level. It forms a closed canopy forest with canopy trees of at least 25 meters tall and with a high floristic richness (Tovar Narváez, 2018).

The specimens were perching solitary, low on branches in the undergrowth of a small, very shallow, natural, subcanopy swamp with standing water only a few centimetres deep. The swampy area was at most 15–20 m long and had an organic bottom layer of decaying leaves. It was the only stagnant swampy place encountered in this area in which in general non sloping areas were scarce. Most likely scenario is these males were all mature and waiting for a female. The swamp probably being a reproductive site (Figure 4A).

Distribution and threats

Amazoneura submontana is so far known only from the type locality northwest of Tarapoto (San Martín Región) (Figure 4B). This region is densely populated and suffers from habitat degradation and ongoing deforestation. The type locality is situated near but outside of the boundaries of the Área de conservación regional Cordillera Escalera.

Further north, in the Valle del Alto Mayo, the species was not found, though this area was studied in the first half of February 2024.

As *A. submontana* seems to live in shallow stagnant swamps, it is likely to some extent vulnerable to extreme droughts, which are becoming more frequent due to climate change (Clarke et al., 2024).

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