

# *Oligoneuria* Pictet: phylogenetic analysis and description of three new species from Brazil (Ephemeroptera: Oligoneuriidae)

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**Abstract.** For 150 years *O. anomala* has been the only known species of *Oligoneuria*, the type genus of the Oligoneuriidae (Ephemeroptera). However, two species have been recently described and *Oligoneuria* has been proposed as a senior synonym of the genus *Oligoneurioides*. In the present paper, based on material from the Amazon and Brazilian Atlantic Forest, three new species are described, including information on all life stages. Given these new species, as well as the lack of cladistic support for the proposed synonymy between *Oligoneuria* and *Oligoneurioides*, a phylogenetic analysis was performed in order to address the relationships between all species and to test the status of *Oligoneurioides*. Our results show that the status of the genus is uncertain, mainly due to the lack of knowledge of the type species of *O. anomala*, known exclusively from a female subimago. Taking into account phylogenetic as well as taxonomic arguments, we propose that the genus *Oligoneuria* should be divided into three subgenera: *Oligoneuria* s.s., for *O. anomala*; *Oligoneuria* (*Yawari*) new subgenus, for *Oligoneuria truncata* sp.n.; and *Oligoneuria* (*Oligoneurioides*) for the remaining five species, including *O. amandae* sp.n. and *O. mitra* sp.n.

This published work has been registered in ZooBank, <http://zoobank.org/urn:lsid:zoobank.org:pub:A2AEE4B7-FEA8-4067-8F3B-666095EDB997>.

## Introduction

*Oligoneuria* Pictet, the type genus of the family Oligoneuriidae (Ephemeroptera), was erected to include a mayfly with a unique combination of characteristics: scanty venation, especially regarding cross veins, and atrophied legs (Pictet,

1843). The description of the single species, *O. anomala* Pictet, was based on two female subimagos, one from Rio de Janeiro, Brazil, and another without label. During the following decades, species from all biogeographic realms were attributed to *Oligoneuria* (Imhoff, 1852; Hagen, 1855; McLachlan, 1868; Joly, 1878; Eaton, 1912; Spieth, 1943; Ali, 1971), but subsequently transferred to new and related genera such as *Homoeoneuria* Eaton, *Elassoneuria* Eaton and *Oligoneuriella* Ulmer.

Despite several attributions of other species (e.g. Hagen, 1855; Ulmer, 1921; Puthz, 1973), *O. anomala* remained as the only species in the genus *Oligoneuria*, and no other stage but the female adults could be attributed with confidence to the genus. Two atypical nymphs of Oligoneuriidae, with a 'remarkable frontal shield', were illustrated by Spieth (1943) and Demoulin (1955), from Surinam and the Brazilian Amazon, respectively. Although Spieth tentatively assigned

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the nymph to *Oligoneuria*, Demoulin stated that both nymphs should be attributed to the genus *Spaniophlebia* Eaton. In the same paper, the new genus *Oligoneurioides* was described by Demoulin (1955). The genus was described based on imagos of a single species, *O. amazonicus* Demoulin, 1955, from the same area where the supposed nymphs of *Spaniophlebia* were found.

Salles *et al.* (2007), working on material from the Brazilian Amazon basin, were finally able to associate one of these unusual nymphs to a recognizable taxon with confidence: *Oligoneurioides amazonicus*. Based on this material, the imagos of the species were redescribed, and the nymphs and eggs were described for the first time. In the same year, Kluge (2007) was also able to associate nymphs with a distinctly extended frontal shield to adults of a new species from the Peruvian Amazon.

As indicated by Domínguez *et al.* (2006) in their key to South American mayflies, and pointed out by Kluge (2007) based on the drawing of the type provided by Domínguez *et al.* (2006: fig. 208a), forewing venation is the only reliable difference between *Oligoneuria* and *Oligoneurioides*: in *Oligoneuria* the vein IMP is present and cross veins are found in the costal field and between veins R1 and R4+5/MA1, as well as traces of cross veins in MP field (or spectral cross veins) (examination on the forewing of the type, however, revealed that spectral cross veins are also present between R4+5/MA1 and MP1); in *Oligoneurioides*, IMP is absent and cross veins are present only in costal field and between veins R1 and IRs/R3. In the forewing pads of the mature nymphs studied by Kluge (2007), he was able to observe cross veins in all fields and a well-developed IMP. Adults reared from these nymphs, conversely, had the typical *Oligoneurioides* wing venation (i.e. IMP absent and only few cross veins). According to Kluge (2007), all species of this group probably have complete venation in the nymphal stage, but veins may disappear or be retained in the alate stages. Because of that, Kluge (2007) stated that separation of the two genera could not be justified: *Oligoneurioides*, therefore, was regarded as a junior synonym of *Oligoneuria*, *Oligoneurioides amazonicus* was transferred to *Oligoneuria*, and a new species – *Oligoneuria itayana* Kluge – was described.

After that a new species was also described from Rio de Janeiro, *Oligoneuria macabaiba* Gonçalves *et al.* (2011), based on male and female imagos. Consequently, four nominal species are currently assigned to *Oligoneuria*: *O. anomala* (type species, from Atlantic Forest), *O. amazonica* (Brazilian Amazon), *O. itayana* (Peruvian Amazon) and *O. macabaiba* (Brazilian Atlantic Forest). *Oligoneuria amazonica* and *O. itayana* are known from all stages, whereas the nymph of *O. macabaiba* remains undescribed. Until now *Oligoneuria anomala* has been known exclusively from female adults, the subimago originally described and a single imago from Paraguay, which was compared with the type specimen in Puthz's (1973) redescription of the species.

In the present paper, three new species are described from all life stages. Given this new evidence and taking into account that the synonymy of *Oligoneurioides* and *Oligoneuria* lacks cladistic support, a phylogenetic analysis is performed in order to assess the relationship between the species of *Oligoneuria* and to test the synonymy proposed by Kluge (2007). An identification key for male imago and nymph to all species is also provided.

## Material and methods

### Taxa

Photographs were taken either using a Leica (M165C) stereomicroscope with a DFC420 digital camera. Digital image stacks were produced using the program Leica Application Suite v3.4.1 (2009). Line drawings were prepared with the aid of a camera lucida, photographs, or both. In either case, final illustrations were prepared according to Coleman (2003, 2006). Whole nymphs or dissected parts were dehydrated in a graded ethanol series, dried by critical point-method, before mounting on SEM stubs and sputter-coated with gold, and then observed and imaged with a JSM 6610 LV scanning electron microscope. Terms used in descriptions of the thorax are from Kluge (1994), but for wing venation we follow Pescador & Peters (2007).

As far as possible, all the known life stages of the species were studied directly, under stereomicroscope. In some cases, however, it was only possible to study the species indirectly, based on photographs of the type material (as for *O. anomala*), on the drawings and original description [as for the male imago of *Fittkauneria carina* (Pescador & Peters)] or based on both methods [as was the case for *O. itayana* (Kluge)]. The stages known of the studied species and the way they were studied are presented in Table 1.

Life cycle association, for all the new species, was possible after dissecting the genitalia of the subimago from mature male nymphs and comparing it with those of male imagos collected in the same locality. All the structures of the male genitalia, such as forceps, penis lobes and styliger projections, are already recognizable in this stage.

The holotypes are housed in the Invertebrate Collection of the Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Brazil; paratypes are housed in the following institutions: Coleção Zoológica Norte Capixaba of the Universidade Federal do Espírito Santo (CZNC), São Mateus, Brazil; Instituto de Biodiversidad Neotropical (IBN), Tucuman, Argentina; Musée Cantonal de Zoologie (MZL), Lausanne, Switzerland.

### Cladistics

Characters were scored from the external morphology of the adults (both male and female) and nymphs of the species of *Oligoneuria* and four outgroups (*Homoeoneuria watu* Salles, Francischetti & Soares; *Lachlania* sp.; *Fittkauneria carina*

**Table 1.** Known life stages and form of study of the species of *Oligoneuria* and outgroups utilized in the analyses.

Species	Study of specimens		Known stages		
	Direct	Indirect (literature)	Male imago	Female imago	Nymph
<i>Oligoneuria amandae</i> sp.n.	x	—	x	x	x
<i>Oligoneuria amazonica</i>	x	—	x	x	x
<i>Oligoneuria anomala</i>	—	x	—	x	—
<i>Oligoneuria itayana</i>	—	x	—	x	x
<i>Oligoneuria macabaiba</i>	x	—	x	x	—
<i>Oligoneuria mitra</i> sp.n.	x	—	x	x	x
<i>Oligoneuria truncata</i> sp.n.	x	—	x	x	x
<i>Fittkauneuria carina</i>	x	x	x	x	x
<i>Homoeoneuria watu</i>	x	—	x	x	x
<i>Lachlania</i> sp.	x	—	x	x	x
<i>Spaniophlebia trailiae</i>	x	—	x	x	—

Pescador & Edmunds and *Spaniophlebia trailiae* Eaton), for a total of 57 characters (22 from male imagos, two from female imagos and 33 from nymphs; Table 2). All characters were considered as nonadditive and, in some cases, the contingent coding was preferred instead of multistate. For taxa that lack a particular structure, transformational character states are coded as inapplicable, with a '?' (see Forey & Kitching, 2000). This procedure effectively separates neomorphic and transformational components (Serenó, 2003) and benefits the formation of more inclusive and informative groups, besides respecting the hierarchy of characters and states (see Forey & Kitching, 2000).

For the analysis, we considered three different datasets: (i) the complete dataset, comprising all the eleven species and 57 characters; (ii) a matrix where *O. anomala* was removed (ten species and 57 characters); and (iii) a matrix where only the species with known nymphs were considered, leading to the removal of *Spaniophlebia trailiae*, *O. anomala* and *O. macabaiba* (eight species and 57 characters). Each data matrix was analysed using TNT (Goloboff *et al.*, 2008) under parsimony using equal and implied weights (Goloboff, 1993), the latter with eight different values of  $k$  (3, 5, 7.5, 10, 12.5, 15, 17.5 and 20). This procedure was carried out as a way to evaluate potential topological changes under the different  $k$  values (e.g. Prendini, 2000). Searches were conducted using the implicit enumeration command. Relative Bremer support (RBS, Goloboff & Farris, 2001) was calculated as a measure of group support, using 1000 suboptimal trees up to five steps longer (obtained using traditional search) and frequency differences (GC, Goloboff *et al.*, 2003), using 1000 replications of symmetric jack-knifing.

#### Character list

#### Adults

##### Head

1. Eye size in males: (0) slightly larger than in females (Figs 7, 8); (1) same as in females (Figs 9, 10); (2) eyes contiguous, much larger than in females.

##### Wings

2. R3/IRS in relation to R1: (0) divergent (Figs 13–15); (1) parallel.
3. Divergence of R3 in relation to R1 (applicable only to species with divergent R3/ IRS; character 2, state 0): (0) from the base of R1 (around basal 1/10); (1) from the basal 1/5 to 1/2 of R1 (Figs 13–15); (2) from the apical 1/3 of R1.
4. IMP: (0) present (Figs 13–15); (1) absent.
5. IMP (applicable only to species with IMP present; character 4, state 0): (0) complete; (1) spectral (Figs 13–15).
6. IMP origin in relation to MP1 (applicable only to species with IMP present; character 4, state 0): (0) 1/2 of MP1; (1) basal 1/5 of MP1 (Figs 13–15); (2) basal 1/3 of MP1.
7. Cross veins between IRS and R4 + 5: (0) present (Figs 13–15); (1) absent.
8. Cross veins between medial and anal sectors: (0) present; (1) absent (Figs 13–15).
9. Cross veins in the hindwing: (0) present; (1) absent.

##### Male genitalia

10. Forceps: (0) present; (1) absent (Figs 16, 20–25).
11. Number of segments in the forceps (applicable only to species with forceps; character 10, state 0): (0) two segments (Figs 16, 20–23); (1) three segments (Figs 24, 25)
12. Shape of forceps (applicable only to species with forceps; character 10, state 0): (0) slightly curved internally (Figs 16, 20–21, 23–25); (1) strongly curved internally (Fig. 22).
13. Posterior margin of the styliger plate: (0) expanded (Figs 16, 20, 22–25); (1) not expanded (Fig. 21).
14. Expansion of the styliger plate (applicable only to species with styliger plate expanded; character 13, state 0): (0) simple (Figs 24, 25); (1) with paired projections (Figs 16, 20, 22, 23).
15. Paired projections of the expansion of the styliger plate (applicable only to species with styliger plate expanded

**Table 2.** Data matrix of 57 characters and state assignment for the species included in the cladistic analysis. Characters 1–24: imagos; 25–57: nymphs.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
<i>Oligoneuria amandae</i> sp.n.	1	0	1	0	1	1	0	1	0	0	0	1	0	1	1	1	1	0	1	1	0	0	0	0	1	1	0	0	1	0
<i>Oligoneuria amazonica</i>	1	0	1	1	?	1	1	1	1	0	0	0	0	1	0	1	1	0	1	1	0	0	0	0	1	1	0	1	?	0
<i>Oligoneuria anomala</i>	–	0	1	0	1	1	0	0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Oligoneuria itayana</i>	0	0	1	1	?	?	1	1	1	0	0	0	0	1	0	–	1	0	0	1	0	0	0	0	0	–	0	–	–	0
<i>Oligoneuria macabaiba</i>	1	0	1	1	?	?	1	1	1	0	0	0	1	?	?	?	1	1	0	0	0	0	0	0	–	0	–	–	–	–
<i>Oligoneuria mitra</i> sp.n.	0	0	1	0	1	1	0	1	1	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	1	1	0	0	0	0
<i>Oligoneuria truncata</i> sp.n.	1	0	1	0	1	1	0	1	0	0	1	0	0	?	?	0	0	1	1	0	0	0	0	0	1	1	0	0	1	0
<i>Homoconeuria watu</i>	2	1	?	1	?	?	1	1	1	1	?	?	0	0	?	?	0	2	?	1	1	?	1	1	0	0	1	?	?	1
<i>Lachlania</i> sp.	2	0	2	0	0	0	0	1	0	0	0	0	1	?	?	?	0	2	1	1	0	0	1	1	1	1	0	1	?	1
<i>Fitikauneuria carina</i>	1	0	1	0	0	2	0	0	0	1	?	?	0	0	?	?	0	2	?	1	0	1	–	–	1	0	0	1	?	1
<i>Spaniophlebia trailiae</i>	1	0	0	0	0	2	0	1	1	0	0	0	0	?	?	1	0	1	1	0	1	–	–	–	–	–	0	–	–	–
	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57			
<i>Oligoneuria amandae</i> sp.n.	0	0	0	0	1	1	1	0	0	1	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Oligoneuria amazonica</i>	0	0	0	0	0	1	1	0	0	1	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0
<i>Oligoneuria anomala</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Oligoneuria itayana</i>	0	0	0	–	–	–	1	1	–	–	–	–	–	–	0	0	1	0	0	1	0	0	–	0	0	–	0	0	1	–
<i>Oligoneuria macabaiba</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Oligoneuria mitra</i> sp.n.	2	0	0	0	0	1	1	0	0	0	0	0	1	0	1	0	0	1	0	0	1	0	0	1	0	2	0	0	0	0
<i>Oligoneuria truncata</i> sp.n.	1	0	0	0	1	0	1	0	1	1	0	1	1	0	1	0	1	0	0	1	0	0	1	0	0	0	1	0	0	1
<i>Homoconeuria watu</i>	?	0	1	1	?	?	1	0	1	?	1	1	?	0	0	2	1	0	0	1	?	?	2	0	0	1	1	1	?	?
<i>Lachlania</i> sp.	0	0	0	1	?	?	1	1	0	0	1	1	?	1	0	0	0	1	1	0	1	0	1	1	1	1	?	0	0	0
<i>Fitikauneuria carina</i>	3	1	1	1	?	?	1	1	1	?	1	1	?	0	1	?	1	0	1	1	?	?	2	0	0	0	0	0	0	0
<i>Spaniophlebia trailiae</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	–	–	–	–	–	–	–	–	–	–	–	–	–	–

and with paired projections (character 13, state 0; character 14, state 1): (0) tapering gradually from the base (Figs 16, 20, 23); (1) tapering on apical 1/3 (Fig. 22).

16. Paired projections of the expansion of the styliger plate (applicable only to species with styliger plate expanded and with paired projections (character 13, state 0; character 14, state 1): (0) convergent (Figs 16, 23); (1) divergent (Figs 20, 22).
17. Form of apex of penis lobe: (0) rhomb (Figs 24, 25); (1) acute (Figs 16, 20–23).
18. Direction of apices of penis lobes: (0) convergent (Figs 16, 20, 22–25); (1) divergent (Fig. 21); (2) parallel.
19. Penis length in relation to the segment I of forceps: (0) more than 1/2 of the length of segment I (Figs 16, 21, 23); (1) less than 1/2 of the length of segment I (Figs 20, 22, 24, 25).
20. Membranous expansion between the styliger plate and the penis: (0) present (Figs 16, 20, 22–25); (1) absent (Fig. 21).

#### *Thorax*

21. Plumidia: (0) present (Fig. 12); (1) absent.
22. Length of plumidia (applicable only to species with plumidia; character 21, state 0): (0) short (not reaching median length of metanotum) (Fig. 12); (1) long (reaching median length of metanotum).

#### *Female abdomen*

23. Posterolateral projections in the sternum IX of females: (0) present (Fig. 17); (1) absent.
24. Medial projection in the sternum IX of females: (0) strongly excavated (Fig. 17); (1) barely excavated.

### **Nymphs**

#### *Head*

25. Tubercles in the vertex of the head: (0) present; (1) absent (Figs 27, 32, 37, 42, 43, 54).
26. Processes in the apical antennomeres: (0) absent; (1) present (Fig. 55).
27. Anterior projection of the head: (0) present (Figs 27, 32, 37, 42, 43, 54); (1) absent.
28. Carina in the anterior projection of the head (applicable only to species with an anterior projection in the head; character 27, state 0): (0) present (Figs 32, 37, 42, 43, 54); (1) absent (Fig. 27).
29. Length of the carina in the anterior projection of the head (applicable only to species with an anterior projection in the head and with a carina in this projection; character 27, state 0; character 28, state 0): (0) carina extending along the entire projection (Figs 37, 54); (1) carina restricted to the apical third of the projection (Fig 32, 42, 43).
30. Pair of lateral incisions by the side of the eyes: (0) present (Figs 27, 32, 37, 42, 43, 54); (1) absent.

31. Shape of the anterior margin of the anterior projection of the head (applicable only to species with an anterior projection in the head; character 27, state 0): (0) rounded (Figs 27, 32); (1) truncated (Fig 42, 43); (2) tapered just at the apex (Figs 37, 54); (3) tapered from the base to the apex.
32. Length of the antenna in relation to the fore femur: (0) smaller or almost equal to the fore femur (Figs 27, 32, 37, 42, 43, 54); (1) larger than the length of the fore femur.

#### *Thorax/Legs*

33. Epimera and episterna: (0) projected laterally (Figs 37, 43); (1) not projected laterally.
34. Long setae in the outer margin of the fore femur: (0) present (Figs 28, 33, 38, 44); (1) absent.
35. Position of long setae in the outer margin of the fore femur (applicable only to species with long setae in the outer margin of the fore femur; character 34, state 0): (0) restricted to the base of the femur (Figs 28, 38); (1) along the entire outer margin of the femur (Figs 33, 44).
36. Apical projection in the posterior surface of the fore femur: (0) present (Figs 44, 57); (1) absent (Figs 28, 33, 38).
37. Fore tibia and tarsus: (0) fused; (1) not fused (Figs 28, 33, 38, 44).
38. Subapical setae in the inner margin of the mid and hind tarsi: (0) present (Figs 40, 46, 58, 59); (1) absent.
39. Amount of subapical setae in the inner margin of the mid and hind tarsi (applicable only to species with these kind of setae; character 38, state 0): (0) only two distinct medial setae (Figs 40, 59); (1) a tuft of setae (Figs 46, 58).
40. Basal dark band in mid and hind tarsi: (0) present (Figs 39, 40); (1) absent (Figs 29, 34, 45).
41. Protuberances at the base of setae in the inner margin of mid and hind femora: (0) present (Figs 35, 47–49); (1) absent.
42. Development of protuberances at the base of setae in the inner margin of mid and hind femora (applicable only to species with these protuberances present; character 41, state 0): (0) barely developed (Fig. 49); (1) strongly developed (Figs 47, 48).
43. Mid and hind coxae: (0) with a plate barely projected dorsally; (1) with a plate strongly projected dorsally.

#### *Abdomen*

44. Sternal tuft of setae: (0) present (Fig. 56); (1) absent.
45. Form of sternal setae (applicable only to species with a tuft of setae in the sterna; character 44, state 0): (0) short and spiniform; (1) short and thin; (2) long and thin.
46. Posterolateral projections: (0) in the segments II to IX (Figs 26, 31, 36, 41); (1) only in the segments VIII and IX.
47. Lateral margin of the projections of the segments VIII and IX, in relation to the medial line: (0) parallel (Figs 26, 31, 36); (1) oblique (Fig. 41).

48. Posterolateral projection of the segment IX: (0) as long as wide (Fig. 41); (1) longer than wide (Figs 26, 31, 36).

#### Gills

49. External lamella of the gill I: (0) present (Figs 60, 61); (1) absent.
50. Development of external lamella of the gill I (applicable only to species with external lamella in the gill I; character 49, state 0): (0) vestigial (Fig. 60); (1) well-developed (Fig. 61).
51. Length of the dorsal lamella of gill IV in relation to the lateral margin of segment V (including the posterolateral projection): (0) about 1/3 of the lateral margin (Figs 26, 31, 41); (1) about 1/4 of the lateral margin (Fig. 36); (2) greater than 1/2 the length of the lateral margin.

#### Filaments

52. Terminal filament: (0) present (Figs 26, 31, 36, 41); (1) absent.
53. Setae in the inner margin of the caudal filaments (Figs 26, 31, 36, 41): (0) abundant (covered with primary swimming setae in most segments); (1) rare (setae absent in most segments, only a few segments with scarce setae).
54. Setation of terminal filament (applicable only to species with terminal filament present; character 52, state 0): (0) almost entirely covered with setae (Fig. 26); (1) covered with setae, except in the basal 1/3 (Fig. 41); (2) covered with setae, except in the basal 1/5 (Figs 31, 36).
55. Shape of the outer lamella of the gills: (0) rounded (Figs 26, 31, 36, 41); (1) spear-shaped.

#### Legs

56. Setae in the inner margin of mid and hind tibiae: (0) present (Figs 50–53); (1) absent.
57. Shape of setae of inner margin of mid and hind tibiae (applicable only to species with the inner margin of middle and hind tibiae covered with setae; character 56, state 0): (0) only with spine-like setae (Figs 50–52); (1) with numerous long and few spine-like setae (Fig. 53).

## Results

#### Phylogenetic analyses

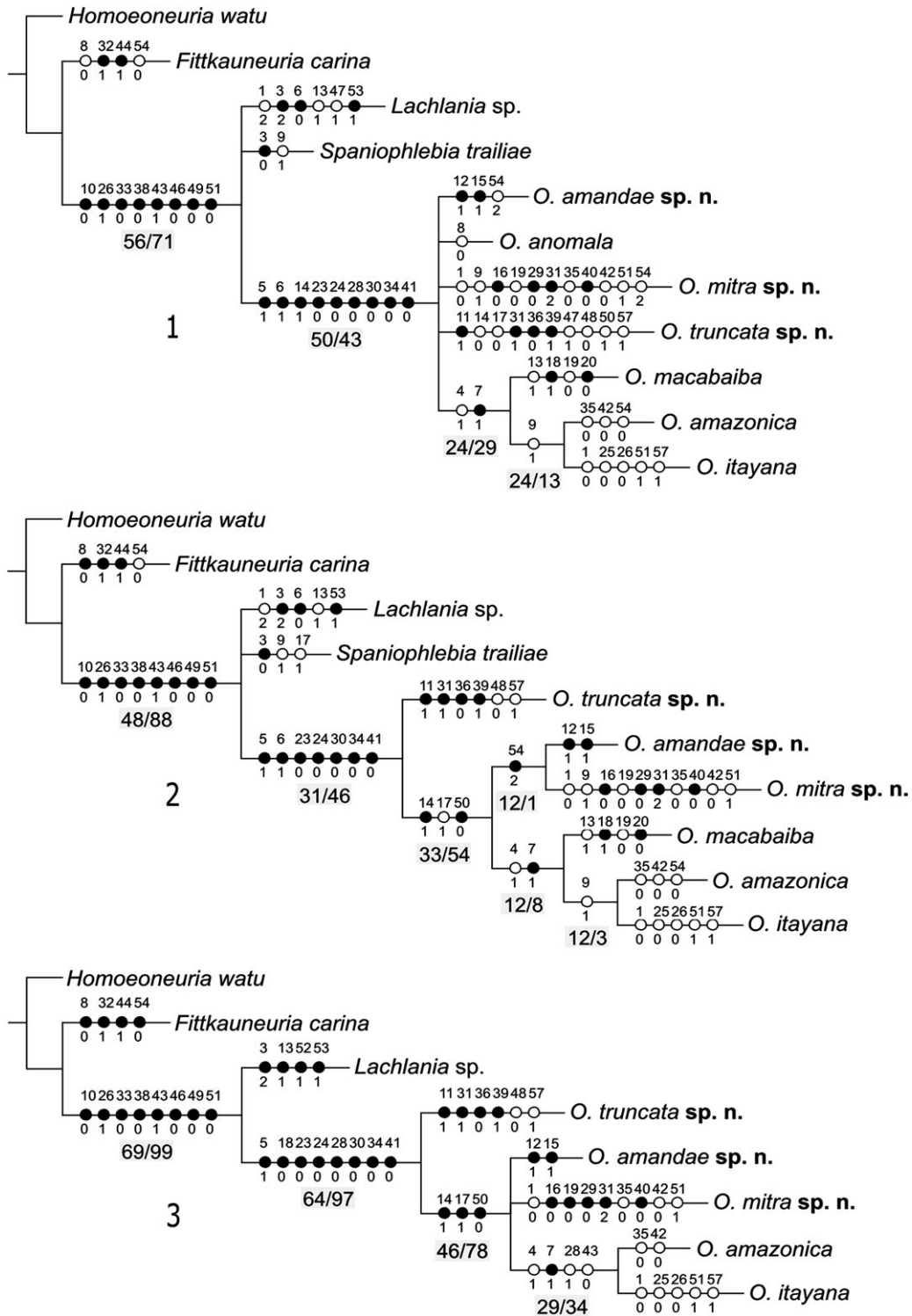
As a whole, we found congruent topologies (Figs 1–3) despite the different weighting schemes utilized, and even the conduct of analyses removing either *O. anomala* or all the species without known nymphs from the dataset. Analysis of the complete dataset yielded the same consensus tree for both equal and implied weights analyses. The same topology was achieved for each value of  $k$  (3, 5, 7.5, 10, 12.5, 15, 17.5, 20) used in the implied weighted analysis (Fig. 1). When *O. anomala* was removed, we also found the same consensus

tree when using equal or implied weights, independent of the value of  $k$  utilized (Fig. 2). When only the species with known nymphs were included (i.e. without *S. trailiae*, *O. macabaiba* and *O. anomala*), we found different topologies under different weighting schemes. A topology that was less resolved but fully congruent with the results from the more complete datasets was retrieved with most weighting schemes (Fig. 3; equal weighting; implied weighting:  $k = 3$ ,  $k = 5$ ,  $k = 15$  and  $k = 17.5$ ). The list of synapomorphies and group supports for each dataset are presented below for the analysis using  $k = 3$  (Figs 1–3).

A clade comprising *Oligoneuria*, *Spaniophlebia* and *Lachlania* (in a tritomy) was recovered in the analysis of total evidence and when *O. anomala* was removed. In the case where just species with known nymphs were analysed, as *Spaniophlebia* was not represented, a sister group relationship between *Oligoneuria* and *Lachlania* was found. Whether *O. anomala* was included or not in the dataset, eight synapomorphies supported the relation among these three genera, and all of these synapomorphies supported *Lachlania* + *Oligoneuria* when just species with known nymphs were considered: (1) forceps present [character 10: state 0]; (2) apical antennomeres with processes [26: 1]; (3) epimere projected [33: 0]; (4) presence of sharpened setae in the inner margin of the apex of the posterior tarsus [38: 0]; (5) mid and posterior coxae with a plate strongly projected dorsally [43: 1]; (6) posterolateral projections in the segments II–IX [46: 0]; (7) outer lamella of gill I present [49: 0]; (8) length of the dorsal lamella of gill IV *c.* 1/3 the length of the lateral margin of fifth abdominal segment (including the posterolateral projection) [51: 0].

*Oligoneuria* was recovered as monophyletic in the analyses of data from the three different matrices. The species of *Oligoneuria* shared nine synapomorphies in the analysis comprising the entire dataset, eight when *O. anomala* was removed and eight in the analysis including only species with known nymphs (see Figs 59–61): (1) spectral IMP [5: 1]; (2) IMP, in relation to MP1, originated in the basal 1/5 [6: 1]; (3) posterior margin of the expansion of the styliger plate with paired projections [14: 1]; (4) presence of a posterolateral projection in the ninth sternite of females [23: 0]; (5) medial projection of the ninth sternite of females heavily excavated [24: 0]; (6) presence of a carina in the anterior projection of the head [28: 0]; (7) pair of lateral incisions by the side of the eyes [30: 0]; (8) presence of long setae in the outer margin of the anterior femur [34: 0]; (9) presence of protuberances in the inner margin of mid and hind femora [41: 0].

Regarding the phylogenetic relationships among the species of *Oligoneuria*, analyses using data from adults and nymphs (both with and without *O. anomala* included) and solely data of species with known nymphs led to a congruent hypothesis. When the complete dataset was analysed, despite the presence of *O. anomala*, a clade comprising *O. amazonica* + *O. itayana* + *O. macabaiba* was recovered supported by two synapomorphies: (i) IMP absent [4: 1] (non-unique apomorphy, also in *H. watu*) and (ii) transverse veins between IRS and R4 + 5 absent [7: 1]. Within this clade,



**Figs. 1-3.** Phylogenetic hypotheses with supporting synapomorphies (circles) and group support (grey rectangles: left Bremer support, right GC values). 1, Complete dataset analysis (11 species and 57 characters), strict consensus of 15 shortest trees; 2, analysis performed after the exclusion of *Oligoneuria anomala* (ten species and 57 characters), strict consensus of three shortest trees; 3, tree obtained with dataset comprising only species with known nymphs (eight species and 57 characters), strict consensus of two shortest trees. In all cases, trees from analysis with  $k = 3$ .

*O. amazonica* and *O. itayana* appeared as sister species, with a single non-unique apomorphy, absence of transversal veins in the hindwing [9: 1] supporting the relationship.

The analysis without *O. anomala* proved to be more resolved than when it was included, and the following relationships were recovered: (a) *Oligoneuria (Yawari) truncata* **sp.n.** as the sister group of the remaining species of the genus; (b) the monophyly of *Oligoneuria (Oligoneurioides)*, including *O. amandae* **sp.n.**, *O. amazonica*, *O. itayana*, *O. macabaiba* and *O. mitra* **sp.n.**, supported by three synapomorphies: (1) posterior margin of the expansion of the styliger plate with paired projections [14: 1]; (2) apex of penis acute [17: 1] (non-unique apomorphy, also in *S. trailiae*); (3) outer lamella of gill I vestigial [50: 0] (within the clade *Oligoneurioides*); (c) a node uniting *O. amandae* **sp.n.** and *O. mitra* **sp.n.**, defined by a single synapomorphy: terminal filament covered with setae, except for the basal 1/5 [54: 2]; (d) the aforementioned clade (*O. macabaiba (O. amazonica + O. itayana)*).

In the analysis comprising only those species where nymphs are known, three slightly different hypotheses were found, depending on the weighting scheme. However, in all cases, regardless of the weighting procedure, the most general relationships, with *O. (Yawari) truncata* **sp.n.** as the sister species of the clade *Oligoneurioides* (besides the monophyly of *Oligoneurioides* itself) were preserved. In all three topologies the monophyly of the species of *O. (Oligoneurioides)* included in the analysis, *O. amandae* **sp.n.**, *O. amazonica*, *O. itayana* and *O. mitra* **sp.n.**, was supported by the same three synapomorphies found in the analysis where only *O. anomala* was excluded. The only difference is that the apex of penis acute [17: 1] appears here as a unique apomorphy, because *S. trailiae* was not considered in this particular data matrix. Finally, a node uniting *O. amazonica* and *O. itayana* also appeared under all the weighting schemes, supported by the following synapomorphies: (1) IMP absent [4: 1] (non-unique apomorphy, also in *H. watu*); (2) transverse veins between IRS and R4+5 absent [7: 1]; (3) carina in the anterior projection of the head absent [28: 1] (non-unique apomorphy, also in *Lachlania* sp. and *F. carina*); and (4) mid and posterior coxae with a plate barely projected dorsally [43: 0] (non-unique apomorphy, also in *H. watu* and *F. carina*).

The differences among the topologies, depending on the weighting scheme, relates to the positions of *O. amandae* **sp.n.** and *O. mitra* **sp.n.** The most common topology (Fig. 3), that was obtained from the analyses under equal and implied weighting with  $k = 3$ ,  $k = 5$ ,  $k = 15$  and  $k = 17.5$ , presented a polytomy among *O. amandae* **sp.n.**, *O. mitra* **sp.n.** and (*O. amazonica + O. itayana*). With implied weighting where  $k = 7.5$  and  $k = 20$ , *O. amandae* **sp.n.** appeared as the sister species of the remaining species, and *O. mitra* **sp.n.** as the sister species of (*O. amazonica + O. itayana*), supported by a single non-unique apomorphy, the absence of transversal veins in the hindwing [9: 1]. Finally, when  $k = 10$  and  $k = 12.5$ , the clade (*O. amandae* **sp.n.** + *O. mitra* **sp.n.**), supported by a single synapomorphy (terminal filament covered with setae, except for the basal 1/5; [54: 2]), appeared as the sister group of the clade (*O. amazonica + O. itayana*).

Despite the significant number of synapomorphies for many clades, group support values varied considerably. The values of RBS and GC for the clades *Oligoneuria* s.l. and *Oligoneurioides* was relatively high in the analysis regarding only the species with known nymphs, but lower values were found for these relationships (when they appeared) in the other analyses. In general, the values were low when considering the internal relationships among *Oligoneuria (Oligoneurioides)* species (Figs 1–3).

## Discussion

Our main objective in this study was to clarify the relationship between *Oligoneuria* and *Oligoneurioides* as well the synonymy proposed by Kluge (2007). Considering the new described species (see below) and the results of the phylogenetic analysis, this clarification is not so simple, especially taking into account the morphological diversity among the species of *Oligoneuria*. If we consider solely the strict consensus tree of the more inclusive analysis (including *O. anomala*; Fig. 1) *Oligoneurioides* is a junior synonym of *Oligoneuria* as we retrieved the type species of *Oligoneuria (O. anomala)* and *Oligoneurioides (O. amazonica)* in a single unresolved clade.

Only the female of *O. anomala* is known, and hence a large number of entries are missing in our data matrix. Empirical and theoretical studies show that including taxa with many missing entries can lead to multiple equally parsimonious trees and poorly resolved consensus trees (Wiens, 2003) failing to reveal relationships that are common to all the most parsimonious trees (Wilkinson, 2003). This is especially problematic when missing data are concentrated in a few taxa (Prevosti & Chemisquy, 2010), as in our case. When we excluded *O. anomala*, and particularly when only the species with known nymphs were considered, we were able to find well-resolved topologies, a much smaller number of most parsimonious trees and clades with higher support values (Figs 2, 3).

In fact, the main problem is that of defining *O. anomala*, especially considering all the implications related to its placement as the type species of the genus. Without a certain determination of *O. anomala*, any attempt to resolve the systematics of the group seems impossible. So far only the females of the type series of this species are known, even after recent comprehensive collecting efforts in different regions of Rio de Janeiro and surrounding states (e.g. Da-Silva *et al.*, 2010; Salles *et al.*, 2010).

In view of the morphological diversity in *Oligoneuria*, and the existence of a well-resolved clade supported by several synapomorphies (*O. amandae* **sp.n.**, *O. amazonica*, *O. itayana*, *O. macabaiba* and *O. mitra* **sp.n.**), and its remarkable difference in relation to *Oligoneuria truncata* **sp.n.**, we propose that the genus be subdivided into three subgenera: (i) *Oligoneuria* s.s. for *O. anomala*, (ii) a new subgenus *Oligoneuria (Yawari)* for *O. truncata* **sp.n.** and (iii) *Oligoneuria (Oligoneurioides)* for the remaining species. By accommodating the variation within *Oligoneuria* in subgenera rather than splitting it into



three genera, we adopt a more conservative and flexible approach. If eventually the hypotheses of relationship proposed here are refuted, in particular with respect to the monophyly of *Oligoneuria* (*Oligoneurioides*) and the exact placement of *O. anomala*, then new combinations will not have to be made.

## Taxonomy

### *Oligoneuria* Pictet, 1843

*Oligoneuria* Pictet, 1843: 291; (Type species *Oligoneuria anomala* Pictet by monotypy)

*Oligoneuria*; Kluge, 2007: 127 (error)

*Oligoneurioides* Demoulin; Kluge, 2007: 127 (proposed synonym)

#### Diagnosis.

*Imago*. R3/IRS divergent in relation to R1 (Figs 13–15); R3/IRS diverging from R1 before or close to middle of wing (Figs 13–15); IMP, when present, diverging from MP1 near its base and spectral (Figs 13–15); plumidia present, short; forceps present, with two or three segments (Figs 16, 20–25); posterior margin of female sternum IX with lateral and medial projections (Fig. 17).

*Nymph*. Antennomeres with inner process (Fig. 55); head with distinct anterior projection (Figs 27, 32, 37, 42, 54); anterior projection of head with a pair of lateral incisions (Fig. 54); epimera and episterna projected (Figs 37, 43); inner margin of mid and hind femora and tibiae with peculiar row of setae (Figs 29, 35, 47–53); inner margin of mid and hind tarsus with subapical setae (Figs 40, 44, 58, 59); sterna with tuft of short, fine setae (Fig. 56); posterolateral projections on segments II–IX (Figs 26, 31, 36, 41); outer lamella of gills rounded (Figs 26, 31, 36, 41); terminal filament present.

### *Oligoneuria* (*Oligoneuria*) Pictet, 1843

#### Diagnosis.

*Male imago and nymph*. Unknown.

*Female imago*. R3/IRS diverging from R1 close to middle of wing (Domínguez *et al.*, 2006, fig. 208A); cross veins (including spectral cross veins) present in all fields of forewing.

*Composition*. *Oligoneuria* (*Oligoneuria*) *anomala* Pictet, 1843

*Distribution*. Atlantic Forest [Rio de Janeiro, Brazil (E. Bauerneind, personal communication) and Ciudad del Este, Paraguay (Puthz, 1973, as Puerto Stroessner)].

### *Oligoneuria anomala* Pictet, 1843

*Oligoneuria anomala* Pictet, 1843: 291 (female subimago); Walker, 1853: 585; Hagen, 1854: 318; Hagen, 1855: 269 (female); Hagen, 1861: 304; Hagen, 1868: 373; Eaton, 1871: 55; Eaton, 1883–1888: 30; Ulmer, 1921:291 (female); Lestage, 1924: 38; Needham & Murphy, 1924: 29 (egg); Lestage, 1931:

60; Spieth, 1943: 12; Ulmer, 1943: 37; Demoulin, 1955: 23; Puthz, 1973: 91 (female, egg); Hubbard, 1982: 269; Mol, 1986: 68; Domínguez *et al.*, 2006: 550; Kluge, 2007:127; Gonçalves *et al.*, 2011:1553.

*Diagnosis and distribution*. See under subgenus section.

### *Oligoneuria* (*Oligoneurioides*) Demoulin, 1955, status rev.

*Oligoneurioides* Demoulin, 1955: 24.

(Type species: *Oligoneurioides amazonicus* Demoulin, original designation).

#### Diagnosis.

*Imago*. R3/IRS diverging from R1 between basal 1/3 and 1/2 of wing (Figs 13, 14); posterior margin of male styliiger plate with paired projections (except in *O. (Od.) macabaiba*) (Figs 20, 22, 23); forceps two-segmented (Figs 20–23); penis simple (i.e. without medial process) (Fig. 16).

*Nymph*. Inner margin of mid and hind tarsi with few setae before apex; outer lamella of gill I vestigial (Fig. 60).

*Composition*. *Oligoneuria* (*Oligoneurioides*) *amazonica* Demoulin, 1955; *Oligoneuria* (*Oligoneurioides*) *itayana* Kluge, 2007; *Oligoneuria* (*Oligoneurioides*) *macabaiba* Gonçalves, Da-Silva & Nessimian, 2011; *Oligoneuria* (*Oligoneurioides*) *amandae* sp.n.; and *Oligoneuria* (*Oligoneurioides*) *mitra* sp.n.

*Distribution*. Amazon (Brazil and Peru) and Atlantic Forest (Brazil) (Figs 4–6).

### *Oligoneuria* (*Oligoneurioides*) *amazonica* Demoulin, 1955

(Figs 4, 5, 20, 26–30)

*Oligoneurioides amazonicus* Demoulin, 1955: 24 (male); Hubbard, 1982: 269; Kluge, 2004: 146; Domínguez *et al.*, 2006:552; Salles *et al.*, 2007: 139 (male, female, nymph, egg); Kluge, 2007:128; Salles *et al.*, 2009: 54.

*Oligoneuria anomala*; Eaton, 1883: 30, plate III (male, female) non Pictet.

*Oligoneuria amazonica*; Kluge, 2007:137; Gonçalves *et al.* 2011:1553.

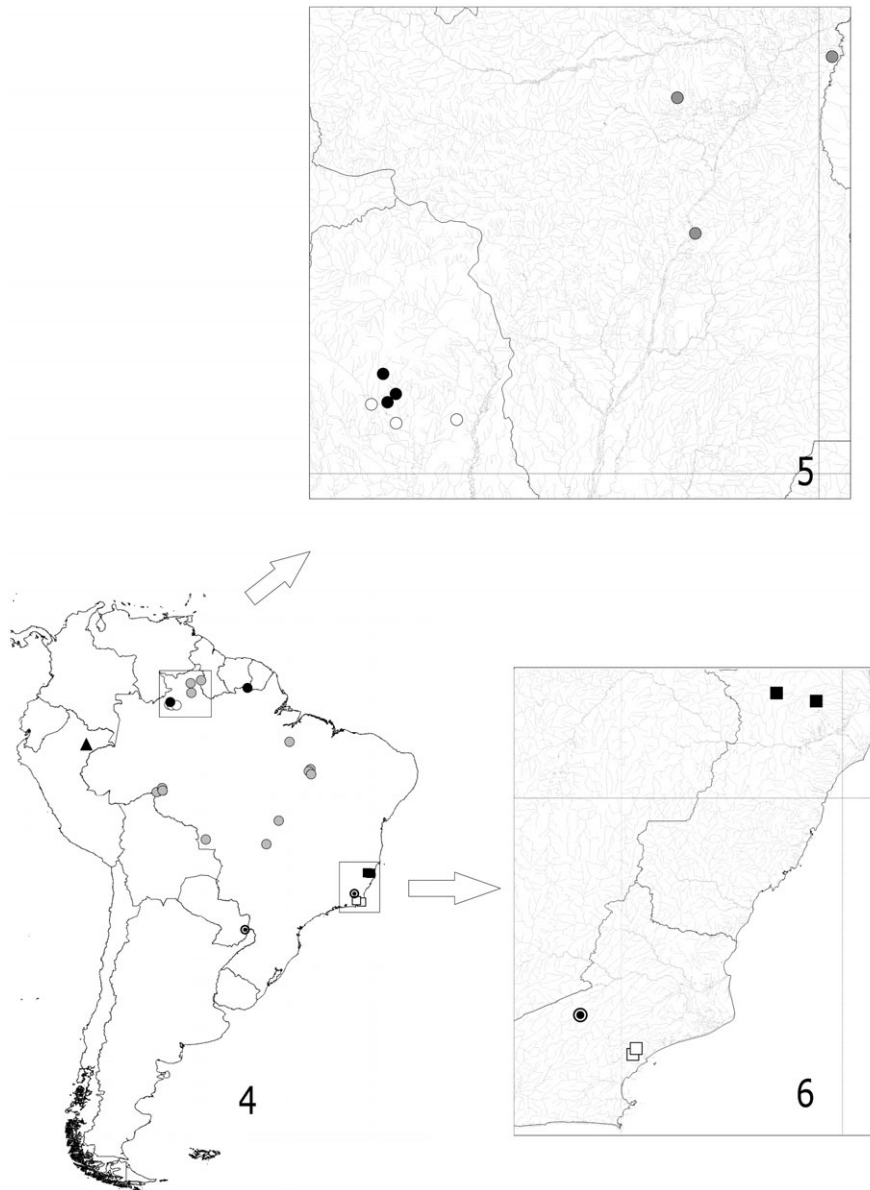
*Spaniophlebia* nymph; Demoulin, 1955:27.

#### Diagnosis.

*Male imago*. IMP absent; styliiger projections divergent, not contiguous at base, apically pointed (Fig. 20); forceps slightly curved inward; penis of medium size (Fig. 20).

*Distribution*. Brazilian Amazon, also in transitional areas between Amazon and Cerrado (Maranhão, Mato Grosso, Pará, Rondônia and Roraima states) (Figs 4, 5).

*Nymph*. Distal margin of anterior projection of head rounded, medial carina absent (Fig. 27); vertex without tubercles; inner margin of mid and hind tibiae with spine-like setae, protuberances at base of setae poorly developed (as Fig. 23).



**Figs. 4-6.** Distribution of *Oligoneuria* species. 4, Distribution of all species in South America; 5, detail of the distribution of *O. (Od.) mitra* sp.n., *O. (Y.) truncata* sp.n. and *O. (Od.) amazonica* in northern Brazil (Amazonas and Roraima states); 6, detail of the distribution of *O. (Og.) anomala*, *O. (Od.) macabaiba* and *O. (Od.) amandae* sp.n. in southeastern Brazil (Rio de Janeiro and Espírito Santo states). Bullseye: *O. (Og.) anomala*; black circles: *O. (Od.) mitra* sp.n.; white circles: *O. (Y.) truncata* sp.n.; grey circles: *O. (Od.) amazonica*; black triangle: *O. (Od.) itayana*; black squares: *O. (Od.) amandae* sp.n.; white squares: *O. (Od.) macabaiba*.

***Oligoneuria (Oligoneurioides) itayana Kluge, 2007***

(Figs 4, 53)

*Oligoneuria itayana* Kluge, 2007: 127 (error)

*Oligoneuria itayana* Kluge, 2007: 130 (original description, male, female, nymph); Gonçalves et al. 2011:1553.

**Diagnosis.**

**Male imago.** IMP absent; styliger projections parallel, not contiguous at base and apically rounded; forceps slightly curved inward; penis of medium size.

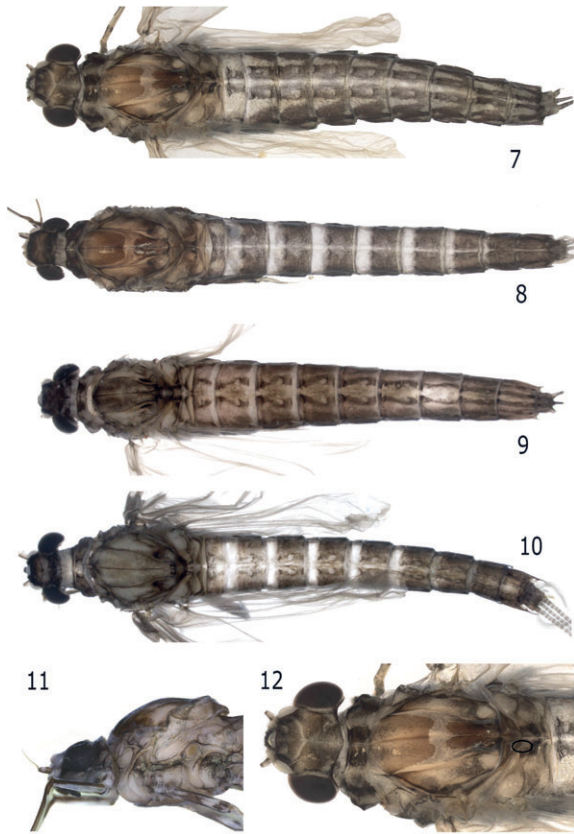
**Distribution.** Peruvian Amazon: Loreto department (Fig. 4).

**Nymph.** Distal margin of anterior projection of head rounded, medial carina absent; vertex with tubercles; inner margin of mid and hind tibiae with spine-like and long setae, protuberances at base of setae strongly developed (Fig. 53).

***Oligoneuria (Oligoneurioides) macabaiba Gonçalves,***

**Da-Silva & Nessimian, 2011**

(Figs 4, 6, 21)



**Figs. 7-12.** *Oligoneuria* spp., adults. 7 and 8, *O. (Od.) mitra* sp.n.; 7, female imago (dorsal view); 8, male imago (dorsal view). 9 and 10, *O. (Od.) amandae* sp.n.; 9, female imago (dorsal view); 10, male imago (dorsal view); 11, *O. (Y.) truncata* sp.n., head and thorax of male imago (lateral view); 12, *O. (Od.) mitra* sp.n., detail of head and thorax of male imago (dorsal view, white ellipse surrounding short plumidia).

*Oligoneuria macabaiba* Gonçalves, Da-Silva & Nessimian, 2011: 1554 (male, female).

*Diagnosis.*

*Male imago.* IMP absent; posterior margin of styliger plate not expanded (Fig. 21); penis long, apically pointed, divergent, and without apical bulb (Fig. 21).

*Nymph.* Unknown.

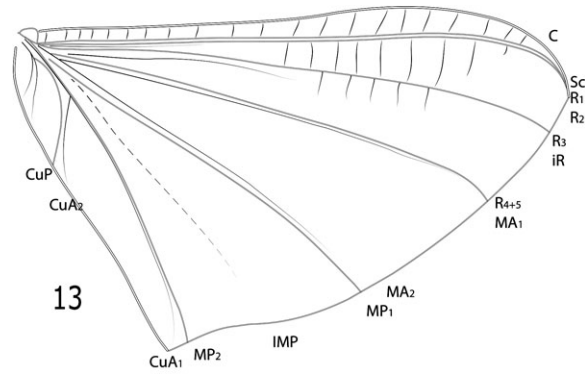
*Distribution.* Brazilian Atlantic Forest (Rio de Janeiro state) (Figs 4, 6).

***Oligoneuria (Oligoneurioides) amandae* sp.n.**

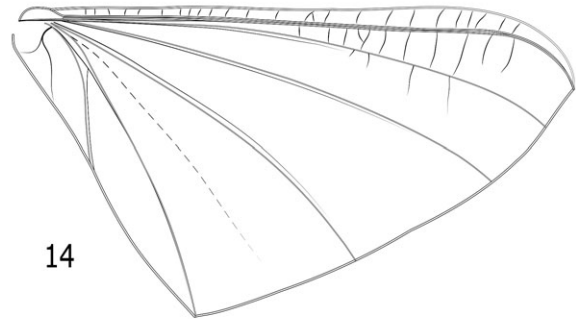
<http://zoobank.org/urn:lsid:zoobank.org:act:78F6196B-2998-4A07-8AE4-FC20E022288A>  
(Figs 4, 6, 9, 10, 13, 17, 22, 31–35, 48, 51)

*Diagnosis.*

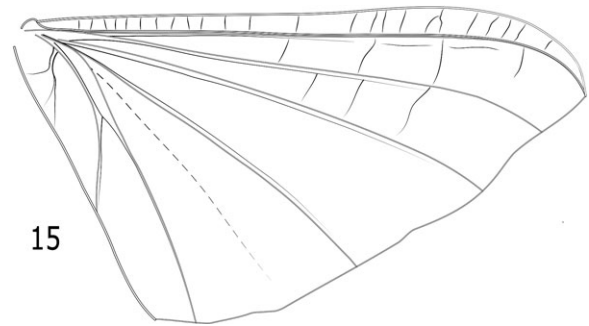
*Male imago.* IMP present, spectral (as in Fig. 13); styliger projections divergent, contiguous at base and broadly pointed



13



14



15

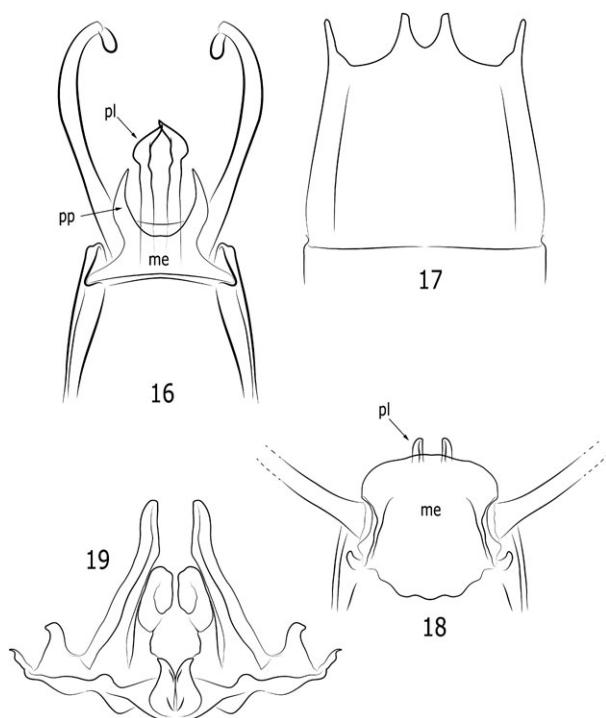
**Figs. 13-15.** *Oligoneuria* spp., forewings. 13, *O. (Od.) amandae* sp.n., female; 14, *O. (Od.) mitra* sp.n., female; 15, *O. (Y.) truncata* sp.n., male.

at apex (or tapering toward apex) (Fig. 22); forceps strongly curved inward; penis of medium size (Fig. 22).

*Nymph.* Distal margin of anterior projection of head rounded, medial carina present (Fig. 32); vertex without tubercles; inner margin of mid and hind tibiae with spine-like setae, protuberances at base of setae strongly developed (Figs 48, 51).

*Description.*

*Male imago.* Body: 11–12 mm; forewing: 8.5–9 mm; hind-wing: 4.5–5 mm; caudal filament (broken at apex): 5–8 mm. Coloration (Fig. 8): Head yellowish with diffuse dark brown pigmented marks. Thorax yellowish. Medioscutum and outer margin of submedioscutum with diffuse brownish pigmented marks; posterior scutal protuberance with diffuse dark brown pigmented marks; scutellum surrounded with dark brown. Fore



**Figs. 16–19.** *Oligoneuria* spp., ventral view of adults segment IX. 16, *O. (Od.) mitra* sp.n., general view of male genitalia; 17, *O. (Od.) amandae* sp.n., female. 18 and 19, *O. (Y.) truncata* sp.n.; 18, general view of male genitalia; 19, detail of penis (me, membrane expansion of styliiger plate; pp, paired process of styliiger plate; pl, penis lobe).

leg yellowish with diffuse brownish pigmented marks. Mid and hind leg with femora yellowish with diffuse brownish pigmented marks; tibiae and tarsi whitish. Abdomen whitish uniformly pigmented with grey, except for submedial longitudinal dark grey stripe. Head: Compound eye not enlarged. Forewing (similar to Fig. 13): IMP present, spectral. Cross veins present between IRS and R4 + 5 and absent between medial and anal sectors. Hindwing: Spectral cross veins present in cubito-anal field. Genitalia (Fig. 22): Forceps strongly curved inwardly. Styliiger projection short, broad, contiguous at base, and apically divergent and broadly pointed. Penis of medium size (*c.* 1/3 length of forceps segment I), apically acute, convergent.

**Female imago.** Body: 14 mm; forewing: 12–12.5 mm; hindwing: 5–5.5 mm; caudal filaments: 4–5 mm. **Coloration** (Fig. 9): Similar to male imago, except abdomen uniformly pigmented with orange brown.

**Nymph.** Male. Body: 10–12 mm; caudal filament: 2–3.5 mm. Female. Body: 15–16 mm; caudal filaments: 4–5 mm. **Coloration** (Fig. 31): Yellowish with diffuse brownish pigmented marks. Tibia without subapical mark. Mid and hind tarsi without basal stain. Abdomen with submedial longitudinal dark brown stripe and posterolateral dark brown mark. Caudal filaments dark brown, apical 1/4 yellowish. Head (Fig. 32): Vertex without tubercles. Anterior projection with medial carina in apical 1/3, distal margin rounded. Thorax: Mid and hind coxae strongly projected dorsally. Fore



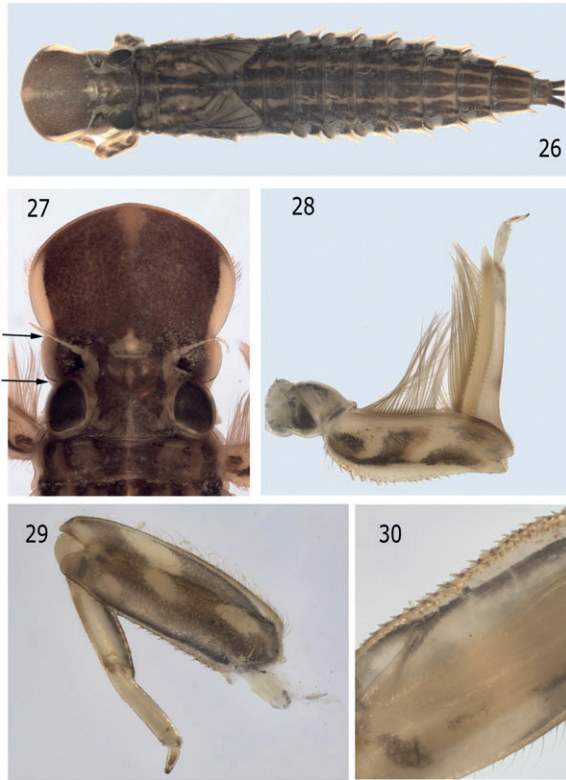
**Figs. 20–25.** *Oligoneuria* spp., male genitalia. 20, *O. (Od.) amazonica*; 21, *O. (Od.) macabaiba*; 22, *O. (Od.) amandae* sp.n. (arrow showing apex of styliiger projection); 23, *O. (Od.) mitra* sp.n.; 24 and 25, *O. (Y.) truncata* sp.n. 24, general view; 25, detail.

femur (Fig. 29) with long setae along entire outer margin; posterior surface without apical projection. Ventral surface of mid and hind femora with long setae near inner margin; inner margin with well-developed protuberances at base of thick setae (Fig. 48). Inner margin of mid and hind tibiae with short, thick setae (Fig. 51). Inner margin of hind tarsus with two setae at apex. Abdomen: Lateral margin of posterolateral projections VIII and IX parallel to midline; posterolateral projection of segment IX longer than wide. Dorsal lamella of gill IV approximately 1/3 length of lateral margin of segment V (including posterolateral projection). Terminal filament covered with setae, except for basal 1/5.

**Etymology.** The specific epithet honors Amanda Oliveira, a brilliant student and close friend who devoted herself to entomology (mainly forensic flies) during her undergraduate studies and departed from life on 20 April 2012.

#### *Material examined.*

**Holotype.** Male imago, Brazil, Espírito Santo, Sooretama, São José River, 23/i/2012, 19°07'33.1''S, 40°14'26.1''W, 24 m, Salles, F.F.; Molineri, C.; Nascimento, J.C. (INPA). **Paratypes.**



**Figs. 26–30.** *Oligoneuria (Od.) amazonica*, nymph. 26, General habitus; 27, head and pronotum (arrows indicating lateral incision); 28, fore leg; 29, hind leg; 30, hind leg, detail of posterior surface of femur.

Four male imagos, two female imagos, six nymphs, sama data as holotype (one male imago, one female imago and three nymphs at IBN, three male imagos, one female imago and three nymphs at CZNC); one male imago, same information as holotype except for 14.ii.2011, Massariol, F.C.; Nascimento, J.M.C.; Silva, P.B., cols. (CZNC); Five nymphs, Brazil, Espírito Santo, São Gabriel da Palha, Parque da Ilha, São José River, 06.ii.2012, 19°02'53.1''S, 40°35'35.7''W, 108 m, Massariol, F.C.; Rozário, E.M., col. (CZNC).

**Distribution.** Brazilian Atlantic Forest (Espírito Santo state) (Figs 4, 6).

***Oligoneuria (Oligoneurioides) mitra* sp.n.**

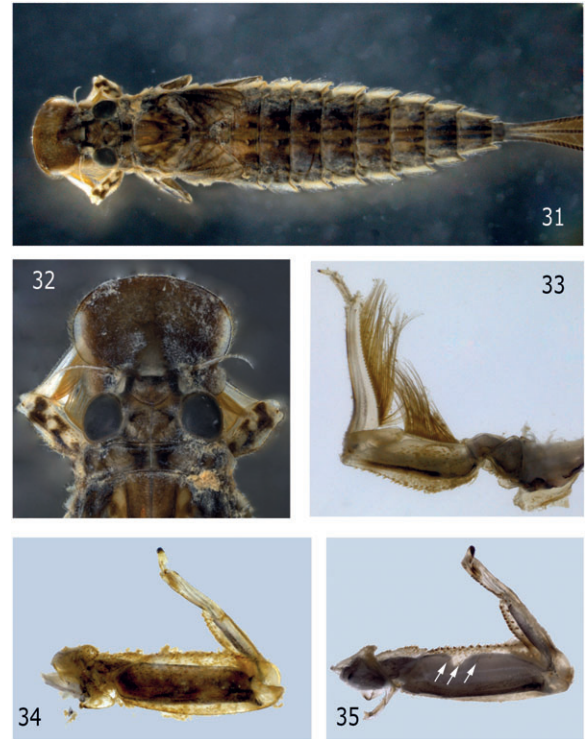
<http://zoobank.org/urn:lsid:zoobank.org:act:3EFE67A4-3FB6-4E2B-83E6-0D797FA29749>

(Figs 4, 5, 7, 8, 12, 14, 16, 23, 36–40, 49, 52, 54, 55, 58)

*Oligoneuria* sp. Spieth, 1943: 12 (nymph); Domínguez et al., 2006: 550; Kluge, 2007: 127.

**Diagnosis.**

**Male imago.** IMP present, spectral (as in Fig. 14); styliger projections curved inward, contiguous at base, apically pointed (Figs 16, 23); penis long, with apical bulb (Figs 16, 23).



**Figs. 31–35.** *O. (Od.) amandae* sp.n., nymph. 31, General habitus; 32, head and pronotum; 33, fore leg; 34, hind leg (anterior view); 35, hind leg (posterior view).

**Nymph.** Distal margin of anterior projection of head pointed, medial carina present (Figs 37, 54); vertex without tubercles; inner margin of mid and hind tibiae with spine-like setae, protuberances at base of setae poorly developed (Figs 49, 52).

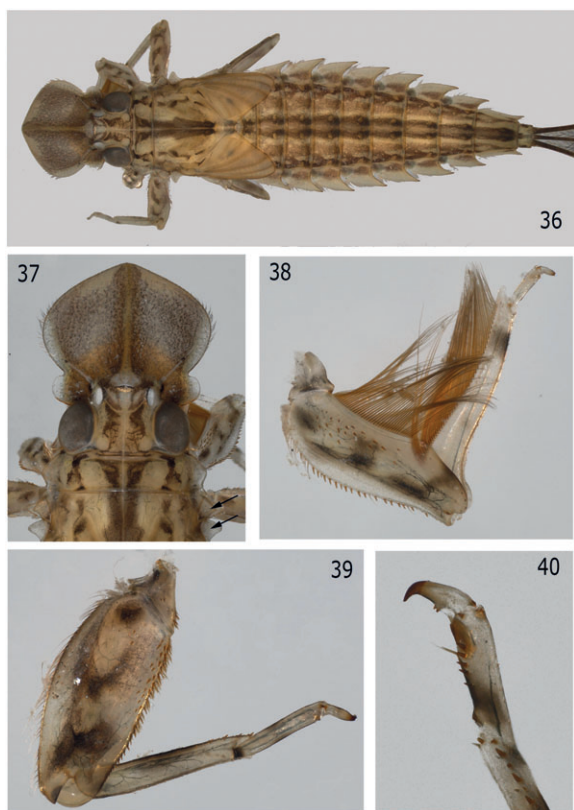
**Description.**

**Male imago.** Body: 10–11 mm; forewing: 9–10 mm; hindwing: 5–5.5 mm; caudal filaments (broken at apex): 4 mm.

**Coloration** (Fig. 8): Head and abdomen yellowish with diffuse brownish pigmented marks, except abdominal segment X. Thorax yellowish; medioscutum with diffuse dark brown pigmented marks; scutellum surrounded with dark brown. Femora yellowish with diffuse dark brown pigmented marks; tibiae and tarsi yellowish. **Head:** Compound eye enlarged. **Forewing** (similar to Fig. 14): IMP present, spectral. Cross veins present between IRS and R4 + 5 and absent between medial and anal sectors. **Hindwing:** Cross veins absent. **Genitalia** (Figs 16, 23). Forceps two-segmented, slightly curved inwardly. Styliger projection long, curved inwardly, contiguous at base, and thinner toward apex. Penis long (longer than 1/2 of forceps segment I), with apical bulb and apically acute, convergent.

**Female imago.** Body: 13–17 mm; forewing: 11–14 mm; hindwing: 6–8 mm; caudal filaments: broken. **Coloration** (Fig. 7): Similar to female nymph (Fig. 36).

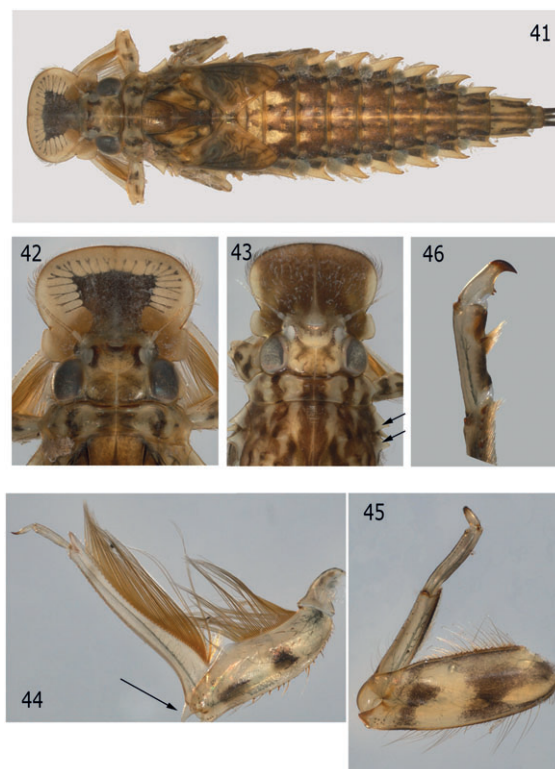
**Nymph.** Male. Body: 12.5–14 mm; caudal filament: 4–5 mm. Female. Body: 17–18 mm; caudal filaments:



**Figs. 36–40.** *O. (Od.) mitra* sp.n., nymph. 36, General habitus; 37, head and pronotum; 38, fore leg; 39, hind leg; 40, detail of hind tarsus and claw.

5–6 mm. *Coloration* (Fig. 36): Yellowish with diffuse brownish pigmented marks. Tibia with subapical mark. Mid and hind tarsi with basal stain. Abdomen with submedial longitudinal dark brown stripe. Caudal filaments dark brown, apical 1/4 light yellow. *Head* (Fig. 37): Vertex without tubercles. Anterior projection with medial carina along entire length, distal margin acute toward apex. *Thorax*: Mid and hind coxae strongly projected dorsally. Fore femur (Fig. 38) with long setae present at base of outer margin; posterior surface without apical projection. Ventral surface of mid and hind femora without long setae; inner margin of mid and hind femora with barely discernible protuberances at base of thick setae (Fig. 49). Inner margin of mid and hind tibiae with short, thick setae (Fig. 52). Inner margin of hind tarsus with two subapical setae (Fig. 40). *Abdomen*: Lateral margin of posterolateral projections VIII and IX parallel to midline; posterolateral projection of segment IX as long as wide. Dorsal lamella of gill IV approximately 1/4 length of lateral margin of segment V (including posterolateral projection). Terminal filament covered with setae, except for basal 1/5.

*Etymology.* After the shape of the frontal shield of the head resembling a mitre, the ceremonial head-dress in some Christian churches.



**Figs. 41–46.** *O. (Y.) truncata* sp.n., nymph. 41, General habitus; 42, head and pronotum of a pharate nymph; 43, head and pronotum of a nearly mature nymph (arrows indicating epimera and episterna); 44, fore leg (arrow indicating projection on apex of femur); 45, hind leg; 46, detail of hind tarsus and claw.

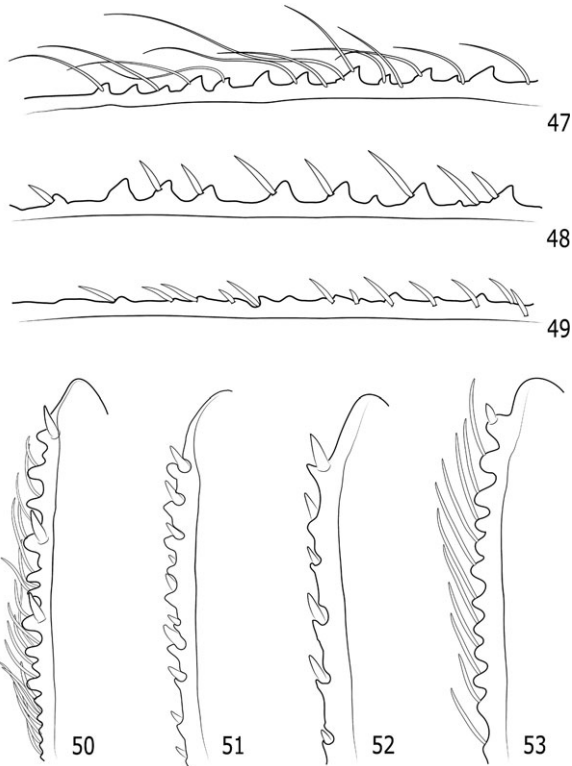
#### *Material examined.*

*Holotype.* Male imago, Brazil, Amazonas, Barcelos, Serra do Aracá, Comunidade Ukukii, 26.vii.2009, 00°48'0.28''N, 63°29'22.92''W, Pensilvânia, Salles, F.F., col. (INPA). *Paratypes.* Three female imagos, same information as holotype (INPA); 62 nymphs, same information as holotype except for 21.vii.2009 (28 at INPA, 28 at CZNC, 4 at IBN, 2 at MZL); three female imagos, same information as holotype (CZNC); two nymphs, Brazil, Amazonas, Barcelos, Serra do Aracá, 23.vii.2009, 00°34'14.84''N, 63°27'32.15''W, Salles, F.F., col. (MZL); one male imago, same information as holotype except for 24–25.vii.2009, lençol (CZNC); 25 nymphs, Brazil, Amazonas, Barcelos, Serra do Aracá, 23.vii.2009, 00°34'14.84''N, 63°27'32.15''W, Salles, F.F., col. (CZNC); 19 nymphs, Brazil, Amazonas, Barcelos, Serra do Aracá, Igarapé Jauari, 23.vii.2009, 00°37'59.16''N, 63°23'26.88''W, Salles, F.F., col. (CZNC).

*Distribution.* Brazilian (Amazonas state) and Surinamese Amazon (Figs 4, 6).

#### *Oligoneuria (Yawari), new subgenus*

<http://zoobank.org/urn:lsid:zoobank.org:act:0FB1CA7D-4FED-45FB-930F-44750E1BBDC9>



**Figs. 47–53.** *Oligoneuria* spp. nymphs, details of legs. 47–49, Inner margin of femur; 47, *O. (Y.) truncata* sp.n.; 48, *O. (Od.) amandae* sp.n.; 49, *O. (Od.) mitra* sp.n.; 50–53, detail of inner margin of hind tibia; 50, *O. (Y.) truncata* sp.n.; 51, *O. (Od.) amandae* sp.n.; 52, *O. (Od.) mitra* sp.n.; 53, *O. (Od.) itayana*.

#### Diagnosis.

*Imago.* R3/IRS diverging from R1 between 1/6 (male) and 1/5 (female) of wing (Fig. 15); IMP present, spectral (Fig. 15); posterior margin of styliger plate of male strongly expanded and without projections (Figs 18, 19, 24, 25); penis lobes with ventrally curved medial process (Figs 18, 19, 24, 25).

*Nymph.* Distal margin of anterior projection of head truncate, medial carina present (Figs 42, 43); inner margin of mid and hind tarsi with tuft of setae before apex (Figs 46, 58); outer lamella of gill I present (Fig. 61); inner margin of mid and hind tibiae with numerous long and few short, thick setae, protuberances at base of setae strongly developed (Figs 47, 50).

*Type species.* *Oligoneuria (Yawari) truncata* sp.n.

*Composition.* *Oligoneuria (Yawari) truncata* sp.n.

*Distribution.* Brazilian Amazon (Serra do Aracá) (Figs 4, 6).

*Etymology.* From yawa'ri the Tupi word for the palm tree jauari (*Astrocaryum jauari*), a species common in the region where the material was collected. Noun in apposition, the gender is feminine.

#### *Oligoneuria (Yawari) truncata* sp.n.

<http://zoobank.org/urn:lsid:zoobank.org:act:572B7AF6-43C9-494E-A4BB-C424FFC9B510>

(Figs 4, 5, 11, 15, 18, 19, 24, 25, 41–47, 50, 56–58, 61)

*Diagnosis.* See under subgenus section.

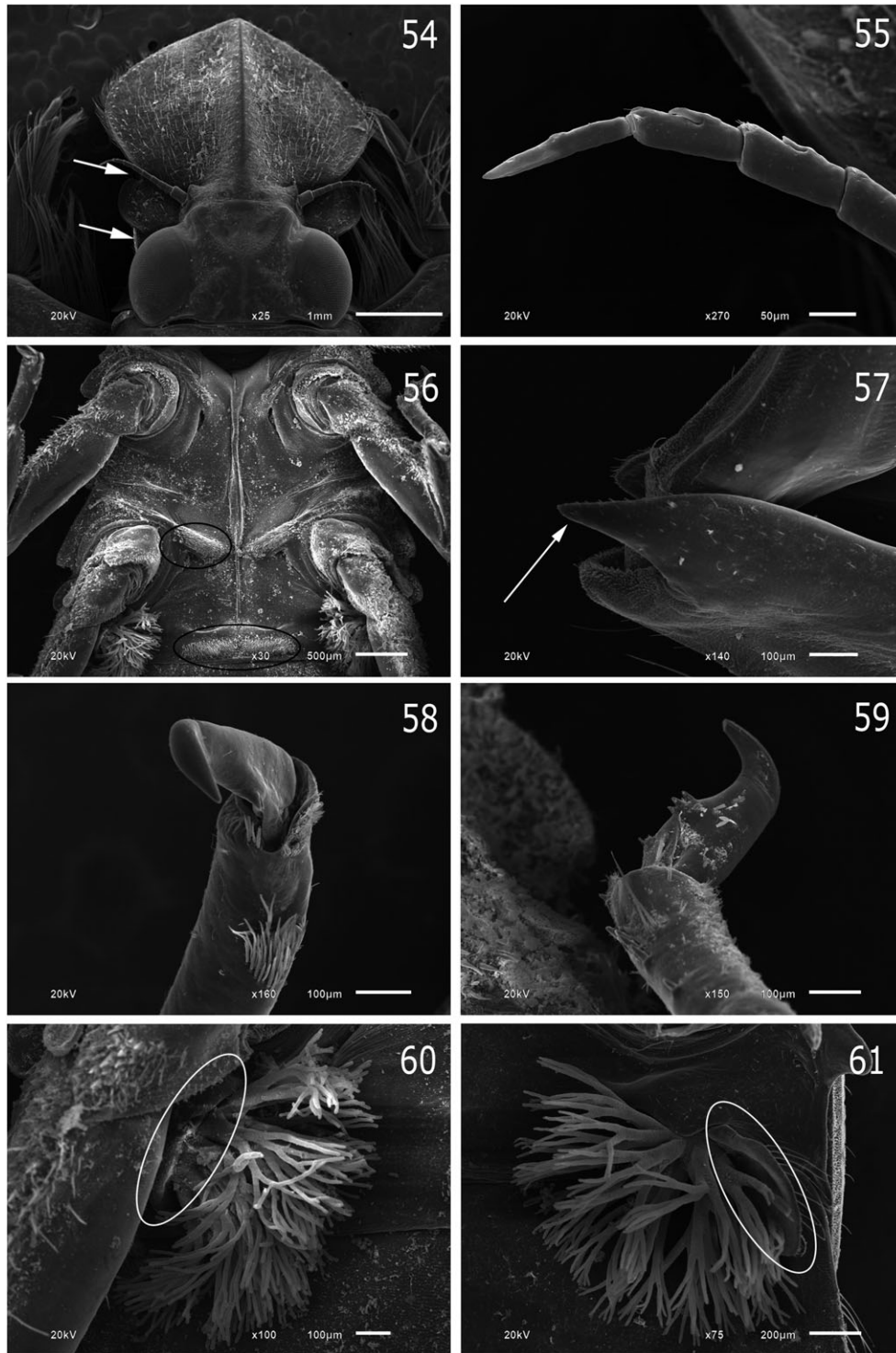
#### Description.

*Male imago.* Body: 9.5–10.5 mm; forewing: 7.5–9 mm; hindwing: 4–5 mm; caudal filaments (broken at apex): 4–7 mm. *Coloration* (Figs 11, 12): Head yellowish with diffuse brownish pigmented marks. Thorax yellowish brown with H-shaped unpigmented mark. Medioscutum anteriorly with diffuse dark grey pigmented marks; submedioscutum with diffuse dark brown pigmented marks; scutellum completely dark grey. Fore leg yellowish with diffuse dark grey pigmented marks. Mid and hind leg with femora with diffuse dark grey pigmented marks; tibiae and tarsi whitish. Abdomen completely dried, coloration not visible. *Head:* Compound eye not enlarged. *Forewing* (Fig. 15): IMP present, spectral. Cross veins present between IRS and R4 + 5 and absent between medial and anal sectors. *Hindwing:* Spectral cross veins present in cubito-anal field. *Genitalia* (Figs 18, 24, 25): Forceps three-segmented, slightly curved inwardly. Posterior margin of styliger plate expanded, distally rounded and without projections. Penis lobes with ventrally curved medial process (Fig. 19).

*Female imago.* Body: 9.5–11 mm; forewing: 8–10 mm; hindwing: 4–5 mm; caudal filaments: broken. *Coloration:* Similar to male imago, abdomen whitish with diffuse dark brown pigmented marks, except for sublateral longitudinal stripe on segments II–IX and segment X.

*Nymph.* Male. Body: 10–11 mm; caudal filament: 3–4 mm. Female. Body: 13–15 mm; caudal filaments: 3.5–4.5 mm. *Coloration* (Fig. 41): Yellowish with diffuse dark brown pigmented marks. Tibia without subapical mark. Mid and hind tarsi without basal stain. Caudal filaments dark brown, lighter toward apex. *Head* (Figs 42, 43): Vertex without tubercles. Anterior projection with medial carina in apical 1/3, distal margin truncate. *Thorax:* Mid and hind coxae strongly projected dorsally. Fore femur (Fig. 44) with long setae along entire outer margin; posterior surface with apical projection. Ventral surface of mid and hind femora without long setae near inner margin; inner margin with well-developed protuberances at base of long, thick setae (Fig. 47). Inner margin of mid and hind tibiae with numerous long and few short, thick setae (Fig. 50). Inner margin of hind tarsus with tuft of setae at before apex (Figs 46, 58). *Abdomen:* Lateral margin of posterolateral projections VIII and IX oblique in relation to midline; posterolateral projection of segment IX as long as wide. Outer lamella of gill I present; dorsal lamella of gill IV approximately 1/3 of length of lateral margin of segment V (including posterolateral projection). Terminal filament covered with setae, except for basal 1/3.

*Etymology.* After the shape of the distal margin of the anterior projection of the nymphal head.



**Figs. 54–61.** *Oligoneuria* spp., nymphs, SEM photographs. 54–56, *O. (Od.) mitra* sp.n.: 54, head (setae showing lateral incisions); 55, apex of antenna; 56, ventral view of meso- and metathorax and abdominal segment I (white ellipses surrounding sternal tuft of setae); 57 and 58, *O. (Y.) truncata* sp.n.: 57, apex of fore femur (posterior view, arrow indicating apical projection); 58, hind tarsus and claw; 59 and 60, *O. (Od.) mitra* sp.n.: 59, hind tarsus and claw; 60, detail of gill I (ellipse surrounding external lamella); 61, *O. (Y.) truncata* sp.n., detail of gill I (ellipse surrounding external lamella).



*Material examined.*

*Holotype.* Male imago, Brazil, Amazonas, Barcelos, Rio Aracá, 06.viii.2009, Pensilvânia 3, 00°24'33.88"N, 63°23'17.16"W, Salles, F.F., col. (INPA). *Paratypes.* Thirty-nine nymphs, Brazil, Amazonas, Barcelos, Serra do Aracá, Tributário do Rio Jauari, 03.viii.2009, 00°33'24.37"N, 63°35'09.67"W, Salles, F.F., col. (15 at INPA, 15 at CZNC, 6 at IBN, 3 at MZL); ten female imagos and one male imago, Brazil, Amazonas, Barcelos, Boca do Rio Demeni, 08–09.viii.2009, 00°25'28.72"N, 62°54'20.02"W, Pensilvânia, Salles, F.F., col. (four female imagos at INPA, four female imagos and one male imago at CZNC, two female imagos at IBN). One male imago, Brazil, Amazonas, Barcelos, Rio Aracá, 03–06.viii.2009, 00°24'33.88"N, 63°23'17.16"W, Salles, F.F., col. (CZNC); one male imago, Brazil, Amazonas, Barcelos, Rio Aracá, 29.vii.2009, 00°24'33.88"N, 63°23'17.16"W, Salles, F.F., col. (CZNC). Two nymphs, Brazil, Amazonas, Barcelos, Rio Aracá, 01.viii.2009, 00°24'33.88"N, 63°23'17.16"W, Salles, F.F., col. (MZL).

*Distribution.* See under new subgenus section.

**Key to male imagos**

1. Forceps three-segmented (Fig. 24); lobes of penis with medial process (Fig. 19); styliger plate strongly expanded (Figs 19, 24, 25) ..... *O. (Y.) truncata* **sp.n.**
  - Forceps two-segmented (Figs 16, 20–23); lobes of penis without medial process; styliger plate usually expanded and with paired projections (Figs 16, 20–23, except in one species) ..... 2
- 2(1). Penis very long, apically pointed and divergent (Fig. 21); styliger plate not expanded and without projections (Fig. 21) ..... *O. (O.) macabaiba*
  - Penis medium sized to long, apically convergent (Figs 20, 22, 23); styliger plate expanded and with paired projections (Figs 16, 20, 22, 23) ..... 3
- 3(2). Penis long, with apical bulb (Figs 16, 23); styliger projections curved inward (Figs 16, 23) ..... *O. (O.) mitra* **sp.n.**
  - Penis of medium size, without apical bulb (Figs 20, 22); styliger projections parallel or divergent (Figs 20, 22) ..... 4
- 4(3). IMP present, spectral (Fig. 13); forceps strongly curved inward (Fig. 22); bases of styliger projections contiguous (Fig. 22) ..... *O. (O.) amandae* **sp.n.**
  - IMP absent; forceps slightly curved inward (Fig. 20); bases of styliger projections not contiguous (Fig. 20) ..... 5
- 5(4). Styliger projections apically rounded (Fig. 23 in Kluge, 2007) ... *O. (O.) itayana*
  - Styliger projections apically pointed (Fig. 20) ..... *O. (O.) amazonica*

**Key to nymphs**

1. Distal margin of anterior projection of head truncate (Figs 42, 43); inner margin of hind tarsus with tuft of setae before apex (Fig. 58); outer lamella of gill I well developed (Fig. 61) ..... *O. (Y.) truncata* **sp.n.**
  - Distal margin of anterior projection of head rounded or broadly pointed (Figs 27, 32, 37); inner margin of hind tarsus without tuft of setae (Figs 40, 59); outer lamella of gill I vestigial (Fig. 60) ..... *O. (Oligoneurioides)* ..... 2
- 2.(1). Anterior projection of head with carina along its entire length, distal margin broadly pointed (Figs 37, 54) ... *O. (O.) mitra* **sp.n.**
  - Anterior projection of head without carina or with carina restricted to apical third, distal margin rounded (Figs 27, 32) ..... 3
- 3(2). Vertex with tubercles (Figs 2, 3 in Kluge, 2007); inner margin of mid and hind tibiae with spine-like and long setae (Fig. 53) ..... *O. (O.) itayana*
  - Vertex without tubercles; inner margin of mid and hind tibiae with spine-like setae (Figs 51, 52) ..... 4
- 4(3). Protuberances at base of setae on inner margin of mid and hind femora well developed (Fig. 26); posterior surface of mid femur with long setae close to inner margin (Fig. 35) ..... *O. (O.) amandae* **sp.n.**
  - Protuberances at base of setae on inner margin of mid and hind femora poorly developed (as in Fig. 49); posterior surface of mid femur without long setae close to inner margin ..... *O. (O.) amazonica*

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Amaral and Rosaflor Oliveira who departed in their prime on 20 April 2012.

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