

Phylogeny and biogeography of the ephemeral *Campsurus* Eaton (Ephemeroptera, Polymitarcyidae)

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Abstract. To analyse speciation within the large Neotropical genus *Campsurus* Eaton, we examined apparent subgroupings by morphological methods using discrete and continuous character states. In this report, the *albifilum* group is redefined based on redescription of male imagos of *Campsurus albifilum* from the holotype and fresh material and from four closely related new species: *Campsurus yavari* n.sp. and *C. fuliginatus* n.sp. described from male imagos; and *C. homaulos* n.sp. and *C. gracilipenis* n.sp. described from imagos of both sexes. An illustrated key to distinguish the male adults of all species in the *albifilum* group is included. A phylogeny of the group is proposed based on a matrix of seven continuous and 12 discrete characters analysed under implied weights, and includes additional species representing all known or previously proposed groups. This demonstrates the practical application of methods using continuous characters to give additional resolution and support to the phylogeny. The monophyly of the *major* and the *albifilum* groups is confirmed. Based on these results, a biogeographical analysis is conducted (spatial analysis of vicariance) based on distributional records for each species. Two main vicariant events are found: (i) a west–east separation in tropical-subtropical South American lowlands, followed by (ii) a north–south separation of the Amazonas and Paraná regions. Sympatric speciation seems common: most sister species pairs are co-distributed, and show nonoverlapping ranges in body size.

Introduction

Polymitarcyidae part of a larger group known as the burrowing mayflies (the Ephemeroidea or Fossoriae; Ogden *et al.*, 2009), is a cosmopolitan family with its main diversity in the Neotropics (~70% of genera; Kluge, 2003; McCafferty, 2004). Nymphs burrow tunnels in different substrates (Sattler, 1967), including live and dead plant tissues (rotten wood, aerenchyma), clay banks in rivers and soft mud in lake bottoms, acting as very important bioturbators (Leal *et al.*, 2003). Some species have been reported to coat their tunnels with silk (Sattler, 1967) and even to build silk cases (Molineri & Emmerich, 2010). Adults have extremely short lives,

and in the case of Campsurinae they do not even have legs except for the forelegs in males (used to grasp the female) and reduced forelegs in females of some species; they only live some minutes during huge swarms at dusk. Exceptionally the subimaginal moult occurs entirely in flight and dispersal is limited to female adults that at most were caught some kilometres apart from the nearest water body (*C. Molineri*, personal observation). These intrinsic limitations to long-distance dispersal make polymitarcyids an excellent group for studying biogeography.

Campsurus Eaton is the most species-rich genus of Polymitarcyidae, with 41 described species (38 in South America and three in North/Central America; Domínguez *et al.*, 2006; Molineri & Emmerich, 2010; Emmerich & Molineri, 2011). There have been several attempts to recognize groups of species in the genus (Needham & Murphy, 1924; Traver, 1947; Domínguez *et al.*, 2006). *Campsurus* spp. have not been studied in a formal phylogenetic context, but Domínguez *et al.*

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(2006) divided the genus into three groups, *notatus*, *albifilum* and *segnis*, and Molineri & Emmerich (2010) added the *major* group.

Traditionally, taxonomists working with Polymitarciidae used much quantitative variation to distinguish genera and species, mainly in the relative lengths of different veins in the wings, male forelegs and prothorax development, and genital structures (Needham & Murphy, 1924; Hubbard, 1984; Domínguez, 1988). These data never have been analysed in a phylogenetic context.

Our goals are: (i) to explore the phylogenetic and biogeographical relationships of some related *Campsurus* spp. in the *major* and the *albifilum* groups; (ii) to include and test the value of continuous characters treated as such (i.e. not arbitrarily partitioned in discrete states) in the phylogeny of the group; and (iii) to redescribe the male adult of *C. albifilum* Walker and describe four nearly related new species, all from the Amazon basin.

Material and methods

Material treatment and deposition

As in other species of Campsurinae, the penial arm is sclerotized and forms a double articulation: a ventral articulation with pedestal, and a dorsal articulation with posterolateral corners of sternum IX (Figs 8, 9, 11). To study these internal structures, male genitalia were treated with KOH (10%) for 10–15 min (boiling solution), washed in water and mounted in glycerin-jelly (on a slide without cover slip), where they were studied, figured and photographed under magnification. The KOH treatment only was used to study the internal structures. Descriptions and measures were taken from uncleared genitalia. To prevent distortion of genitalia we generally measured critically fine ratios without cover slips, using glycerin-jelly; noticeably distorted or twisted structures in permanent slides were not used.

Material is deposited in the following institutions: Cornell University Insect Collection, Ithaca, NY, U.S.A. (CUIC), Florida A&M University, Tallahassee, FL, U.S.A. (FAMU), Instituto-Fundación Miguel Lillo, Tucumán, Argentina (IFML), Instituto de Biodiversidad Neotropical, Tucumán, Argentina (IBN), Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina (MACN), Museo Ecuatoriano de Ciencias Naturales, Quito, Ecuador (MECN), Museo de la Universidad del Valle, Cali, Colombia (MUSENUV), Royal Belgian Institute of Natural Sciences, Brussels, Belgium (RBINS), Coleção Zoológica Norte Capixaba, São Mateus, Espírito Santo, Brazil (CZNC), Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil (INPA) and Zoologisches Museum Hamburg, Germany (ZMH).

Taxa

The *albifilum* group originally included the following species (Domínguez *et al.*, 2006: 563): *C. albifilum*

(Walker), *C. argentinus* Esben-Petersen, *C. brasiliensis* Traver, *C. burmeisteri* Ulmer, *C. evanidus* Needham & Murphy, *C. major* Needham & Murphy, *C. juradinus* Navás and *C. pallidus* Needham & Murphy. However, Molineri & Emmerich (2010) synonymized *C. major* with *C. brasiliensis*, *C. argentinus* with *C. pallidus*, and described a new species, *C. amapaensis*. They separated these three species (*C. major*, *C. argentinus* and *C. amapaensis*) in the *major* group. Emmerich & Molineri (2011) synonymized *C. evanidus* with *C. juradinus* (from the *albifilum* group of Domínguez *et al.*, 2006), and also described *C. vulturorum*.

Thus the only valid species currently in the *albifilum* group (as delimited by Domínguez *et al.*, 2006) are *C. albifilum*, *C. evanidus* and *C. burmeisteri*. *Campsurus burmeisteri* is a very anomalous species and is not treated here. Traver (1947) suggested that it could pertain to *Tortopus* Needham & Murphy, but this cannot be confirmed since the type material was not studied.

A matrix of 13 taxa (including all the valid species mentioned earlier) and 20 characters was constructed (see File S3). *Campsurus violaceus* Needham & Murphy and *C. truncatus* Ulmer were indistinctly used to root the trees. The material studied from both species includes type material (*C. violaceus* from CUIC, *C. truncatus* from ZMH) and fresh material. To better represent the morphological heterogeneity of the genus and to test the relationship between the *major* and *albifilum* groups, an additional outgroup was included: *C. segnis* Needham & Murphy, scored from type material (at CUIC) and fresh material collected in Venezuela. The three known species of the *major* group (*C. amapaensis* Molineri & Emmerich, *C. argentinus* and *C. major*) were included as they were proposed as sister to the *albifilum* group (Domínguez *et al.*, 2006; Molineri & Emmerich, 2010); a detailed list of material from these species can be found in Molineri & Emmerich (2010). Other species included are: *C. evanidus*, originally in the *albifilum* group (Domínguez *et al.*, 2006) and scored from type material (CUIC) and fresh material from different countries; the morphologically similar *C. vulturorum* Emmerich & Molineri (2011); *C. albifilum* and four related new species (list of material follows).

Each species is provided with a diagnosis giving key characters for use within the *albifilum* group. To distinguish the species in the *albifilum* group from all other species of *Campsurus*, the group diagnostic characters listed in the diagnosis of the '*albifilum* group' should be used.

New taxa are registered with ZooBank (zoobank.org).

Morphometric data and characters

Measurements were taken following standard descriptions in mayflies (Hubbard, 1995). The length of male foreleg does not include the coxa, this measure was arbitrarily taken from the base of the trochanter to the apex of the claws. Only complete cerci were measured (i.e. with a thinner and setose short portion in the apex). Fore and hind wings have been abbreviated FW and HW, respectively, throughout the text.

Morphometric data were analysed with a multivariate discriminant analysis to test differences among the new species described herein and *C. albifilum*. Due to the large intraspecific variability in size, ratios were used instead of actual measures. The ratios used are those listed as characters 1–6 below (ratios are not always apparent in the two-dimensional figures). Each individual was included separately and was assigned a code classifying it in the corresponding species. The matrix with the morphometric data (File S1) was analysed with the free version of the program INFOSTAT v. 2010 (Di Rienzo *et al.*, 2010). Morphometric characters are defined and explained in File S2.

Characters are scored from external morphological features of male adults, except for character 15, which is scored from internal features of the penial arms (File S2). Except for continuous characters (0–6) and discrete characters 12, 18, 19, all characters were treated as nonadditive. Searches were conducted in TNT (Goloboff *et al.*, 2008) under implied weights (with different values of k : 3, 5, 7), and using the ‘implicit enumeration’ command (under ‘Analyse’). Implied weighting was used because it is a way to decrease the problems of scaling in continuous characters (Goloboff *et al.*, 2006). In some searches, character 0 (FW length, in mm) was deactivated, because its magnitude is much higher than the other continuous characters (which are ratios), and its cost on the tree distorted the support for groups. Relative Bremer support was calculated with 314 suboptimal trees (up to 80% longer than the shortest tree), with the commands ‘suboptimal’ (under ‘Analyse’) and ‘Bremer supports’ (under ‘Trees’). Frequency difference (GC, Goloboff *et al.*, 2003), using 300 replications of symmetric jackknifing, was also calculated as a measure of group support. This value indicates the difference between the frequency of the group (in the shortest tree) and the frequency of the most common contradictory group obtained through the resampling of the matrix. Partial analyses were performed activating only continuous or discrete characters alone, to test their relative importance in the final tree topology, length and group support.

Biogeographical methods

All available geographical records of the species in the *major* and the *albifilum* groups were mapped with DIVA-GIS (version 7.17.2, <http://www.diva-gis.org/>) using delimitation of the freshwater ecoregions of the world by Abell *et al.* (2008), and water lines and bodies provided at the cited website.

Records of *C. albifilum* from Argentina (Santa Fe Province), based on two female adults (Navás, 1926), and from Nova Friburgo (Brazil), based on a damaged female specimen (Navás, 1915: 12, 1916: 19), are not considered valid because these females cannot be attributed to any species with certainty. By contrast, the record of *C. albifilum* based on a male from Maroni (French Guiana) given by Navás (1916: 19) is included in the analysis, as fresh material of this species is present at FAMU (J. Peters, personal communication). An additional record from the literature (Banks, 1913) from

Brazil (Camp 41 and 39, Madeira River) is included. These camps were located at 284 and 306 km from Porto Velho on the road bordering the river (Wolcott, 1912), most probably upstream, near the confluence of the Beni and Mamore rivers. Banks (1913, his fig. 7) illustrated the male genitalia of one of these specimens (coinciding perfectly with *C. albifilum*) but erroneously identifying the species as *C. dorsalis* (Burmeister, 1839).

Spatial analysis of vicariance (Arias *et al.*, 2011), a method that implements the ideas of Hovenkamp (1997, 2001), was used for biogeographical analysis. This method attempts to reconstruct taxon biogeographical history by examining disjunct sister pairs (i.e., barriers), with inputs being a cladogram and distributions of the terminals. The analysis was implemented using the software VIP (Vicariance Inference Program), available at <http://www.zmuc.dk/public/phylogeny/vip> (Arias, 2010). Only data of the ingroup and the root species were analysed in VIP (nine species and 64 distributional records). Other outgroups included in the phylogeny (*C. truncatus*, *C. evanidus*, *C. vulturorum* and *C. segnis*) were omitted as they represent very limited geographic sampling for these species groups. A grid of $2^\circ \times 2^\circ$ was used (maximum fill = 0) in a NASA World Vegetation map (obtained from <http://neo.sci.gsfc.nasa.gov/RenderData?si=1534245&cs=rgb&format=JPEG>) to represent distributions as absence/presence data in each cell. A heuristic search (1000 iterations) was conducted under the default settings, except that overlap was set to 10%, the cost of distribution removal 1.5, and cost of partial removal (activated) 0.75. The heuristic search is used to obtain the better reconstructions of disjunct pairs. Searches using different grid size ($1^\circ \times 1^\circ$) and costs were also conducted for comparative purposes, but the results were similar.

Results

Morphometric analysis

The first principal component (PC1) accounted for 83.3% of total (standardized) variation, chiefly separated all the species. Variables 2 (pedestal length/penes width ratio) and 5 (penes length of inner membrane/length of main lobe ratio) correlated negatively with the first component, and variables 1 (pedestal length/width ratio), 3 (main lobe of penes, length/width ratio), 4 (penes length of secondary/length of main lobe ratio) and 6 (angle of pedestal curvature) correlated positively.

Phylogenetic analyses

The analysis of the whole dataset, including continuous and discrete characters (File S3), yielded the same single tree for each value of k (3, 5, 7) (Fig. 1). The list of synapomorphies and group supports are presented for just one of these values ($k = 3$). The shortest tree presents a length of 46.81 steps (total fit 22.07, total adjusted homoplasy 1.93), and group

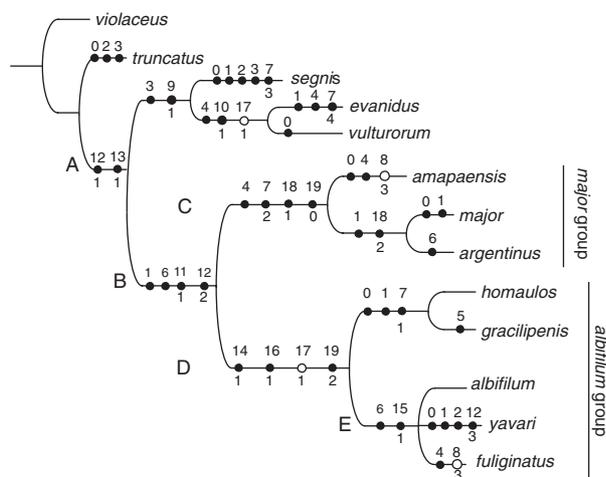


Fig. 1. Phylogenetic hypothesis. Single shortest tree ($k = 3$) with supporting synapomorphies (circles).

supports are high, with frequency difference and/or relative Bremer values > 70 in most of the nodes (Fig. 2). When continuous characters are deactivated, the same single tree is obtained. When discrete characters are deactivated, five equally parsimonious trees are found with continuous characters, with a consensus completely different from the single tree obtained with the entire data set (or discrete characters alone). Group support was calculated also for the 'discrete' dataset and for the complete dataset (i.e. adding the continuous characters, except character 0 to avoid scaling problems as explained earlier): from a total of nine nodes in the shortest tree (Figs 1, 2), the addition of continuous characters increased the group support for four nodes (decreasing it only in one node).

Character congruence, measured as the adjusted homoplasy of each character (Goloboff *et al.*, 2003), is low for continuous characters 0 and 1 (0.68 and 0.51, respectively; 1 in totally homoplastic characters), which show numerous changes in the

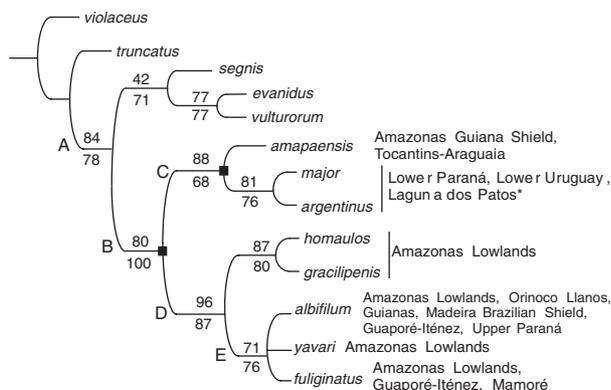


Fig. 2. Group support and vicariant events. Numbers above and below the nodes indicate GC values and relative Bremer support, respectively. Black squares indicate disjunct sister pairs. **Campsurus major* is also recorded from Upper Paraná, Iguassu, Tramandai-Mampituba.

tree. Other characters, both continuous and discrete, are much less homoplastic (< 0.25).

The analysis of the complete data set recovers both groups of species (*major* and *albifilum*) as sister groups, sharing the following synapomorphies: (i) a decrease in pedestal's length/width ratio (character 1, from 1.462–2.057 to 1.120–1.400); (ii) an increase in pedestal curvature (character 6, from 0.155–0.163 to 0.150–0.154); (iii) pedestals flat (character 11, state 1); and (iv) inner apical margin of pedestals broadly convex and slightly projected (character 12, state 2) (later change to strongly projected in *C. yavari*, state 3).

In the *major* group, *C. amapaensis* is sister to *C. argentinus* + *C. major*. Four character state changes define the *major* group: (i) an increase in the ratio length of secondary/main lobes of penes (character 4, from 0.746–0.760 to 0.840–0.853); (ii) abdominal terga widely pigmented (albeit perhaps not strongly pigmented) except on pale transverse dashes at each side (character 7 state 2); (iii) main lobe of penes moderately twisted (character 18 state 1) changing to state 2 (strongly twisted) in *C. argentinus* + *C. major*; and (iv) main lobe of penes hammer-shaped (character 19 state 0).

In the *albifilum* group, *C. gracilipenis* + *C. homaulos* are sister to the other three species that form a tricotomy: *C. albifilum* + *C. yavari* + *C. fuliginatus*. The *albifilum* group is supported by four synapomorphies: (i) penes not curved ventrally, located in the same plane as forceps (character 14 state 1); (ii) pyramidal base of penes with outer margin smoothly continuing through penial lobes (character 16 state 1); (iii) gonopore indistinct (character 17 state 1, non-unique apomorphy, also in other *Campsurus* spp. groups); and (iv) main lobe of penes subtriangular, with straight inner margin and thinner apically (character 19 state 2).

The node uniting *C. homaulos* and *C. gracilipenis* is supported by three synapomorphies: (i) a reduction in size (character 0, FW length in mm, change from 10.1–10.2 to 8.9–9.0); (ii) a change in the length/width ratio of pedestals (character 1, decrease from 1.120–1.400 to 0.750–0.830); and (iii) grey shading on abdominal terga formed by paired rectangles with pale circle inside (character 7 state 1). The second main group, formed by the tricotomy *C. albifilum* + *C. yavari* + *C. fuliginatus*, is defined by two synapomorphies: (i) an increase in pedestal curvature (character 6 change from 0.150–0.154 to 0.142–0.143); and (ii) penial arm with a strong ventral projection on the articulation with pedestal (character 15 state 1).

Biogeography and evolution of the group

Most records from the *major* group are in the Atlantic forests from the Lower Paraná and Lower Uruguay, also from the Uruguayan savannah and Laguna dos Patos (divisions from Abell *et al.*, 2008). The records of *C. amapaensis* are in the Amapá River (near the Amazonas estuary), Tocantins-Araguaia, and the Amazonas Guiana Shield. Records of the five species in the *albifilum* group are mainly from the Amazonas Lowlands and some large tributaries (Mamoré, Guaporé, Madeira), with one species (*C. albifilum*) extending

northward to the Orinoco Llanos, and southward to the Atlantic forests (Upper Paraná). *Campsurus albifilum* is recorded from distant localities in the following basins: Orinoco, Amazonas, Madeira, Guaporé and Paraná. This taxon probably represents a species complex, since some differences exist between their distant populations. It is closely related to a pair of species probably originating from parapatric speciation: *C. yavari* (Colombian Amazonas) and *C. fuliginatus* (Mamoré, Guaporé, Amazonas).

VIP recovered only one reconstruction without removing nodes, with a cost of 5.1, with two disjunct sister pairs: (i) *albifilum* versus *major* groups (barrier 1 in Fig. 3), but with considerable overlap caused by the widely distributed species *C. albifilum*; and (ii) *C. amapaensis* versus (*C. major* + *C. argentinus*) (barrier 2 in Fig. 3). The reconstruction found sympatry between the following species pairs: (i) *C. gracilipennis* + *C. homaulos*; and (ii) *C. major* + *C. argentinus*. Although numerous equally optimal reconstructions were found under other cell sizes and costs, the disjunctions coincide largely with those presented here.

Discussion

Discriminant analysis on morphometric data showed that all species in the *albifilum* group are well distinguished and separated in multivariate space, based on important characters from male genitalia. Together with the autapomorphies listed in the diagnoses, strong support is provided for erection of the new taxa proposed here.

Based on the shortest tree found under parsimony, the sister relationship between the *major* and *albifilum* groups is well supported. *Campsurus evanidus* shares no synapomorphies with either group and is separated here from the *albifilum*

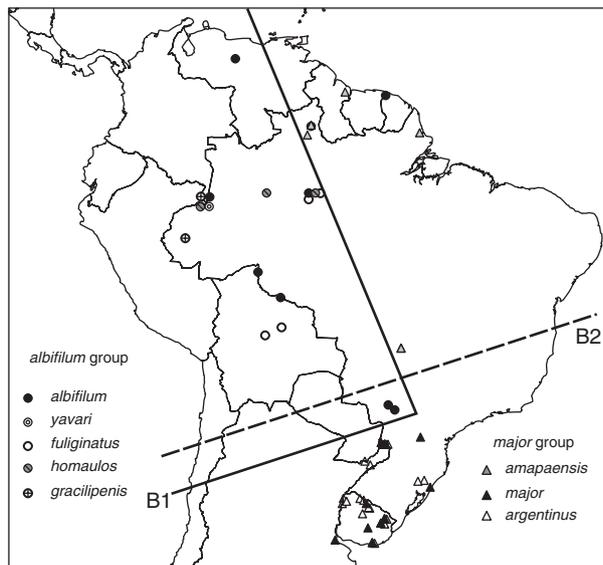


Fig. 3. Distribution map with species records and the two main barriers (or vicariant events) found: B1 and B2.

group, contrary to its previous delimitation (Molineri in Domínguez *et al.*, 2006). This analysis suggests that *C. evanidus* could pertain to the *segnis* group or to a different group of species; this should be tested with the inclusion of more taxa and characters. Synapomorphies that define the *major* group agree with those listed in Molineri & Emmerich (2010), except for a continuous character (character 4) and the character concerning abdominal coloration (character 7), both newly incorporated here. Another exception is that a large male gonopore (character 17) was found to be plesiomorphic in *Campsurus* in this analysis, instead of being a characteristic of the *major* group.

Continuous and discrete characters

Several methods have been proposed for dividing a continuous series in an arbitrary set of states (discretization; Mickevich & Johnson, 1976; Archie, 1985; Goldman, 1988; Thiele, 1993). However, an important criticism presented by Farris (1990) concerns their use: taxa with significantly different values may be assigned to the same state, or vice versa. As Goloboff *et al.* (2006) stated, 'when continuous characters are treated as such, rather than distorted through discretization, they seem to carry indeed useful phylogenetic information'. Nevertheless the analysis of continuous characters as such presents the problem of scaling, since the cost of transformation in characters of different magnitude will not be proportional (Goloboff *et al.*, 2006). The use of ratios (six of seven continuous characters used here) greatly reduced these problems.

Another criticism of the use of continuous characters relates to means lacking cladistic content (Cranston & Humphries, 1988). We avoided this by using the complete range of variation for each terminal.

Continuous characters alone were insufficient here to reach a well resolved and supported topology. Of course, only few attributes of each species were coded this way (general size and some ratios in male genitalia, 35% of the data), and thus the weak results using only them are not surprising. Discrete characters alone (65% of the entire dataset) performed much better, and the search using them yields the same shortest tree as the complete data set. Inclusion of continuous characters, however, did result in a general increase of group support values, contributed synapomorphies on almost all the nodes (seven of nine nodes), and added autapomorphies in all but two of the 12 terminals.

Biogeography and evolution of the group

Two main vicariant events seem to have acted on ingroup history. The first represents the split of species groups: the *albifilum* group restricted to the west (in the medium to high Amazonas basin, with *C. albifilum* later expanding its range) from the *major* group restricted to the east (in the lower Amazonas and the Paraná-Uruguay basins). The second vicariant event separated *C. amapaensis* in the north from

C. major + *C. argentinus* in the south. Both events cannot be attributed with certainty to any paleoclimatic or microtectonic event (nodes are not dated) but they coincide largely with results in other groups. With respect to the early east–west vicariance (barrier 1) between the *major* and the *albifilum* groups, it is not possible to recognize a barrier acting today but this pattern is reported also for other taxonomic groups. A possible historic explanation of this pattern (Heads, 2012: 178) concerns Andean uplift that caused the Amazon basin to split in two (before middle Miocene), with westward drainage (west of Purus, 200 km west of Manaus) and eastward drainage (east of Purus). Another, more recent geological explanation of east–west vicariance in tropical South America involves Pleistocene refugia (e.g. Ron, 2000 and references therein). The forest refugia hypothesis (Haffer, 1969) contrasts with a permanent rainforest cover (Colinvaux, 1979, 1987), but Hooghiemstra & van der Hammen (1998) suggested that both scenarios did occur, albeit in different parts of the Amazon basin and at different times. As fossils are almost unknown for Polymitarcyidae, except for an early Cretaceous nymph attributed to Campsurinae (McCafferty, 2004), molecular dating of *Campsurus* clades would be needed to further analyse these hypotheses.

Taking into account the biology of the species in the *major* group, it is not surprising that the dry open forest now separating the low Amazon from the Paraná region has acted as a dispersal barrier (barrier 2). Nymphs of this group live in rivers and streams building soft cases of silk above rocks (Molineri & Emmerich, 2010), and need at least 3 months of permanent water flow before emerging (*C. Molineri*, unpublished data). Once in the alate stage, females show limited dispersal abilities but need riverine habitats to oviposit; the male life span is only a few minutes. The sister relationship between the Paraná and the Amazonas regions has been found also in many other groups (Morrone, 2001).

No reconstruction found allopatry between certain species pairs (*C. homaulos* + *C. gracilipenis*, and *C. major* + *C. argentinus*), suggesting probably that they originated in sympatry. To these pairs could be added the trichotomy *C. albifilum* + *C. yavari* + *C. fuliginatus*, as they are from a rather homogeneous and not fully resolved clade. These three groups present different body sizes where they are found in sympatry. In fact, relatively large gaps in size of each sympatric species pair occur, in spite of a high intraspecific variation (File S3) that suggests a possible mechanism to avoid hybridization. Mate size seems to be one of the main sexual signals for mayflies; males tend to pursue and grab females that fly near or over the swarm, also using other visual signals as coloration and trajectory (Brittain, 1982).

For Berlocher (1998), a testable prediction for the sympatric speciation hypothesis is that early stages of taxa (races, sister species, etc.) would be sympatric. One of the strongest mechanisms of sympatric speciation is sexual selection (Panhuis *et al.*, 2001; Via, 2001). This occurs when a parallel change in mate preference and secondary sexual traits within a population leads to prezygotic isolation between populations, and when this is the primary cause of reproductive isolation. Following

Panhuis *et al.* (2001: 367), ‘two signatures might be recognized for speciation by sexual selection: (1) within species, populations will vary in sexually selected traits and associated preferences and this might generate partial premating isolation between populations; and (2) closely related species will differ markedly in mating signals and preferences; these differences will be the major barrier to gene exchange and the species will differ little in other traits’. Both signatures can be recognized in the populations under study (except in *C. yavari*, known only from two specimens, and thus size range is inadequately known).

Although it is not possible to separate this kind of speciation from others using only these tests (i.e. sympatry of sister species and variations in sexual secondary traits), results indicate a high probability of sympatric speciation. Additional evidence from gene trees, behaviour or microhabitat preferences should be explored.

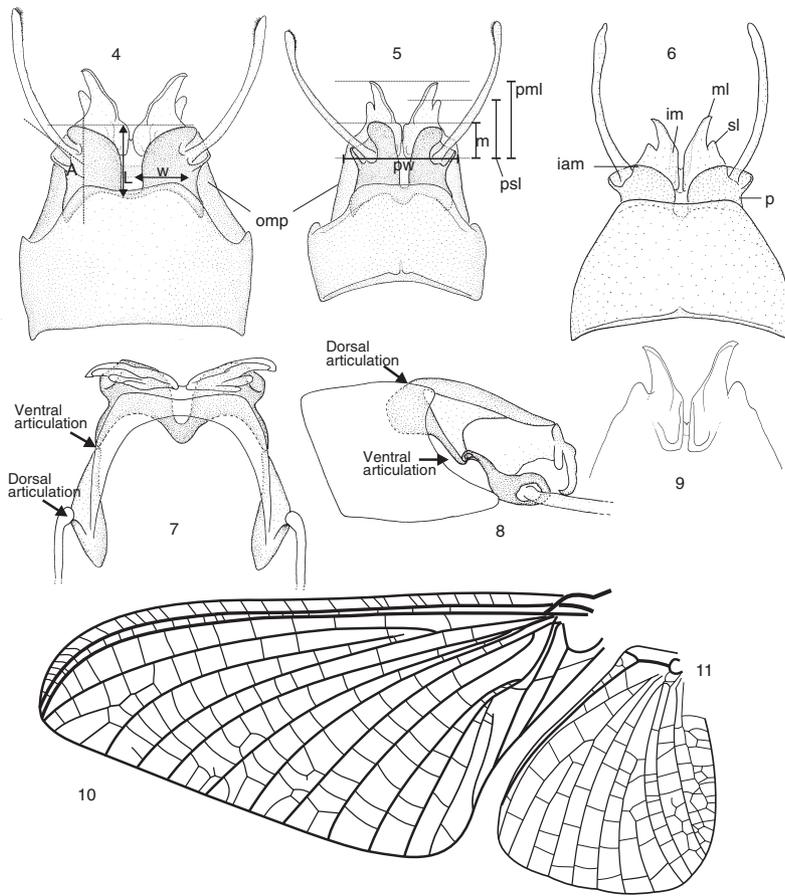
Taxonomy

Albifilum group

The five species comprising the *albifilum* group of *Campsurus* share the following combination of characters that allow their male adults to be distinguished from all other species and species groups in the genus: (i) penes flat, not curved ventrally, and located in the same plane as forceps (character 14 state 1, Figs 4–6, 12–16); (ii) pyramidal base of penes with outer margin smoothly continuing through base of penial lobes (character 16 state 1, omp in Figs 4, 5); (iii) gonopore indistinct (character 17 state 1); (iv) each main lobe of penes subtriangular, with inner margins diverging apically from basal inner membrane (character 19 state 2, Fig. 9), and with a smaller secondary lobe on outer margin (sl in Fig. 6); (v) pedestals broad, flat, medioapically notched (forceps articulation), with inner apical margin broadly convex and outer apical margin less developed (characters 11–12, Figs 4–6, 12, 15); and (vi) apical half of pedestals, or at least the margin, directed laterally (i.e. pedestal curved or at least condyle directed laterally).

Key to the male imagos of the *Campsurus albifilum* species group

1. Abdominal colour pattern pale on terga I–III and very dark on terga IV–IX (Fig. 22); secondary lobe of penes short, knob-like (Fig. 6); FW length about 10.1–13.5 mm; pedestals short (length/width = 1.00–1.40) *C. fuliginatus* – Abdominal color pattern uniform on terga except darker on posterior terga IX or VIII–IX (Figs 21, 22, 24); secondary lobe of penes distinct (Figs 4, 5, 12, 15); FW length variable; pedestals variable 2
2. Body and wings large to medium-sized (FW length > 9.2 mm); pedestals subrectangular, longer than wide (Figs 4, 5) 3



Figs 4–11. Male genitalia: 4, *Campsurus albifilum*, ventral view (vv); 5, *Campsurus yavari*, vv; 6, *Campsurus fuliginatus*, vv; 7, same after treatment with potash; 8, same, lv; 9, detail of penes, vv. Male wings; *Campsurus albifilum*: 10, forewing; 11, hind wing. Abbreviations: A, angle of pedestal curvature; iam, inner apical margin of pedestal; im, inner membrane; L, pedestal length; m, length of inner membrane; ml, main lobe of penes; omp, outer margin of penes; p, pedestal; pml, length of penes main lobe length; psl, length of penes secondary lobe; pw, penes width; sl, secondary lobe of penes; W, pedestal width.

– Body and wings medium to small in size (FW length < 9.0 mm); pedestals small and subquadrate, as wide or wider than long (Figs 12, 15) 4

3. Pedestals very long (length/width ratio > 2.1) and with the apical inner margin strongly projected posteriorly (Fig. 5) *C. yavari*

– Pedestals shorter (length/width ratio > 1.7), inner apical margin broad, not so strongly projected (Fig. 4)..... *C. albifilum*

4. Penes long and slender (length/width = 0.9) (Fig. 15) *C. gracilipenes*

– Penes shorter (length/width = 0.8) (Fig. 12) .. *C. homaulos*

***Campsurus albifilum* (Walker)**

(Figs 4, 10, 11, 20)

Palingenia albifilum Walker 1853: 554

Campsurus albifilum, Eaton 1871: 57; Eaton 1883: 39; Navás 1916: 19; Lestage, 1923: 120; Navás, 1926: 110; Kimmins 1960: 312; Domínguez *et al.* 2006: 566.

Material examined. Holotype, male imago (pinned, NHM) from Para, 45–46 (photographs).

Additional material: six male imagos (a pair of wings on slide 144) and one male subimago (three in MUSENUV, four

in IBN), COLOMBIA, Dpto Amazonas, P.N. Amacayacu, río Amacayacu, S 03°48'28"W 70°15'21", 3.ii.1999, 93 m, light trap 18–20 h, (*Zúñiga, Domínguez & Molineri*); two male imagos (genitalia and forelegs on slide no 522), VENEZUELA, Guarico, 15 km S de Calabozo, N 8°47'W 67°26' (estimated), 1.iii.1986, black light trap (*R. Miller & L. Stange*) (IBN); three male imagos, BOLIVIA, Beni, Versailles, río Iténez, S 12°39'35.9"W 63°22'32.4", 147 m, light trap, 5.v.2006, (*Domínguez & Molineri*) (IBN); one male imago (slide 401), BRAZIL, Mato Grosso do Sul, Ivinheima, S 22°18'38"W 53°49'7.6", 5.v.2005, light trap (*de Melo*) (IBN); two male imagos (slide fcm09, CZNC), AM, Manacapuru, Cristo Ressucitado, Lago Galo (Camoá), 18.ix.2003, N 3°47'58" W 60°49'44.6"; one male imago (CZNC), AM, Arquipelago de Anavilhanas, Manaus, N 2°40'20" W 60°46'40", 31.VII.2000, luz (*Nessimian*); three male imagos, Paraná, Lagoa Patos, S 22°43'12" W 53°17'37", 29.x.1997; 12 male imagos (CZNC), same data except 22.iv.1998.

Diagnosis. (i) FW length 10.2–14.0 mm (male); (ii) dorsum of head generally shaded black except Y-shaped pale median mark (Fig. 20), but vertex shaded completely with black in some males; (iii) abdominal terga shaded with grey as in Fig. 20, slightly darkening posteriorly; (iv) pedestals markedly curved laterally (Fig. 4), relatively long, and with inner apical

margin broadly projected. No autapomorphies were found in the analysis, but ratios listed for continuous characters 1–6 (File S3) can be used as diagnostic.

Male imago. Length (mm): body, 10.3–16.0; FW, 10.2–14.0; HW, 5.1–6.0; foreleg, 5.2–7.0; cerci, 31.0–37.0. General coloration whitish yellow, dorsally shaded grey. Head shaded blackish grey between lateral ocelli except on a median Y-shaped lighter mark (Fig. 20), but variable, some males with vertex completely blackish, others with a pale posteromedian semicircular mark. Antennae yellowish white, shaded slight grey on scape and pedicel. Forelegs shaded grey almost completely, except coxae, trochanter and apex of femora, stronger mark on apex of tibia; vestigial middle and hind legs without grey pigments. Wings (Figs 10, 11). Thorax and abdomen with light grey marks dorsally, except on a mediolongitudinal lighter band on abdomen (Fig. 20). Abdominal terga I–II with a submedian subtriangular mark at each side, terga III–VI with grey[-shaped marks, tergum VII with similar patterns but marks are closed, forming a rectangle on each side, terga VIII–IX widely pigmented except on some small lighter marks (sometimes the pale median line also extends to terga VIII–IX), tergum X whitish. Genitalia (Fig. 4): hind margin of sternum IX with a grey line, pedestals and apical half of penes yellowish, rest whitish. Cerci whitish translucent.

Variations. Some variation is shown in the material from different localities, mainly in details of the genitalia and coloration of the head and abdomen. It is probable that more than one species is represented in the list of material analysed, but the small morphological gaps do not allow the erection of new taxa. Some of this variations include slightly longer penes in the Venezuelan material, shorter pedestals in some males from Mato Grosso do Sul (Brazil), head completely shaded black in these last males and also on the males from Beni (Bolivia), abdomen (including sternum IX and forceps) strongly shaded with black in the males from Beni (but with a similar pattern when compared with the other, much paler males).

Comments. Photographs of the type specimen of *C. albifilum* from Pará (Brazil) were studied. In the figure of Kimmins (1960) both lobes of the penes (main and secondary) appear as of the same length, but in the photographs of the types it is clear that the secondary lobe is shorter. The measures and general aspect of the genitalia of the type coincide very well with new material collected in different localities of Brazil, Bolivia, Colombia and Venezuela, from which new drawings and redescriptions have been presented here. Figures 4, 10, 11 and 20 are from a male from Colombia (Leticia). Given the large geographic range of this species, together with small differences in morphometric characters and color pattern, it may be possible that the different populations are experiencing speciation or divergence events. To separate these possibly cryptic species, it would be necessary to conduct some molecular work, but more material is needed.

Navás (1926) cited *C. albifilum* from Argentina (Santa Fe) based on two female adults, but this is taken here as a spurious record since these females could not be attributed to any species with certainty at that time. Banks (1913) illustrated the male genitalia of *C. albifilum* but he erroneously identified the species as *C. dorsalis*; his fig. 7 is useful to recognize the species, and thus the record from Brazil (Camp 41 and 39, Madeira River) is taken here as valid. Navás (1915, 1916) recorded *C. albifilum* from Nova Friburgo (Brazil) and Maroni (French Guiana); he based these records on a damaged female adult from Nova Friburgo and a male adult from Maroni, he identified the female by direct comparison with the male, but he did not provide any comments or figures on the male justifying his identification. Here the record from Nova Friburgo is taken as invalid and that from Maroni as possible.

Campsurus albifilum is quite similar to *C. yavari* **sp.nov.**, but the strong development and length of pedestals in the last species are clear characters distinguishing both. A short redescription of the male imago is presented here to amend the original descriptions.

***Campsurus yavari* sp.nov.**

(Figs 5, 21)

<http://zoobank.org/urn:lsid:zoobank.org:act:>

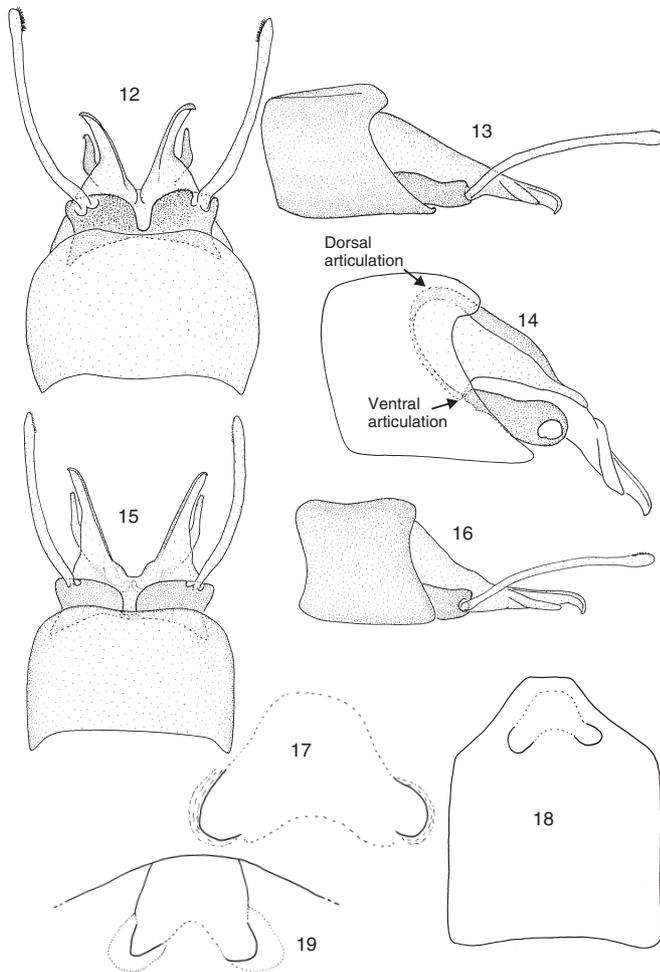
B0B593B7-5E16-4BCD-A8B7-0040DCDEE3B9

Material examined. *Holotype*, (MUSENUV) and one *Paratype* (IFML), male imagos, COLOMBIA-BRAZIL, R. N. Palmari, río Yavari, Muelle Centro Administrativo, 120 m, 29.v.2002, light trap, S 04° 17' 10" W 70° 17' 49" (Zúñiga *et al.*).

Etymology. The name 'yavari' ('javari' in Portuguese) refers to the name of the river where the specimens were collected; noun in apposition.

Diagnosis. (i) FW 9.2–9.5 mm (male); (ii) dorsum of head shaded black except Y-shaped pale median mark (Fig. 21); (iii) abdominal terga VIII–IX marked blackish grey much stronger than the rest (Fig. 21); (iv) pedestals markedly curved laterally, inner posterior margin strongly developed (Fig. 5). Four autapomorphies were found in the analysis: a FW size decrease (character 0 from 10.2–10.3 to 9.2–9.5 mm), a great increase in pedestal length/width ratio (character 1, from 1.200–1.400 to 2.102–2.115), increase in pedestal length/penes width ratio (character 2, from 0.453–0.625 to 0.715–0.764), and inner apical margin of pedestals broadly convex and strongly projected (character 12, state 3).

Male imago. Length (mm): body, 10.5–11.0; FW, 9.2–9.5; HW, 4.0–4.1; forelegs, 4.5–4.6; cerci (broken), 23.0. General coloration yellowish white with blackish grey marks on dorsum, abdominal terga VIII–IX darker. Head completely shaded blackish grey on dorsum, lighter on vertex and median Y mark. Antennae yellowish white slightly shaded grey. Forelegs completely shaded blackish grey from trochanter to



Figs 12–19. Male genitalia: 12, *Campsurus homaulos*, genitalia vv; 13, same lv; 14, same after treatment with potash; 15, *Campsurus gracilipenis*, genitalia vv; 16, same lv. Female genitalia, vv: 17, *Campsurus gracilipenis*, detail of sockets; 18, same, abdominal sternum VIII; 19, *Campsurus homaulos*, detail of sockets.

claws, tarsi and claws lighter. Thorax pattern as in Fig. 21. Abdomen (Fig. 21) with blackish grey marks on dorsum except on a mediolongitudinal lighter band (band thinner on terga VIII–IX); tergum I with small submedian marks, terga II–VII with] marks (outer margins of marks nearly closed in II and VII); terga VIII–IX almost black with some small lighter marks; tergum X lighter, yellowish-white shaded grey on lateral one-third. Sterna without grey mark except on VII–IX diffusely shaded grey (stronger on VIII). Genitalia (Fig. 5): sternum IX with a blackish line on hind margin, pedestals yellowish, penes whitish yellow, forceps translucent white shaded grey. Cerci whitish translucent.

Comments. *Campsurus yavari* is similar to *C. albifilum* and *C. fuliginatus*, but can be separated mainly because of its smaller size and the strong medial projection of pedestals.

***Campsurus fuliginatus* sp.nov.**

(Figs 6–9, 22)

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41F3FE3E-C66A-42F4-AD82-2E15CF1B7805

Material examined. *Holotype*, male imago (UMSA, slides no 402a, b), BOLIVIA, na. Once Por Ciento, río Blanco, S 15°21'39.7" W 63°17'28.8", 250 m, 14.vi.2000 (*Domínguez*); one *Paratype*, male imago and two male genitalia (slides fcm 07 and 08, CZNC), BRAZIL, AM, Ilha da Paciência, Nossa Senhora da Conceição, Lago Jacitara, S 3°16'40.7" W 60°16'34.5", 19.ix.2003, light trap; and one male genitalia (slide fcm 010 CZNC), BRAZIL, AM, Manacapuru, Cristo Ressucitado, Lago Galo (Camoá), S 3°34'47.8" W 60°49'44.6", 18.ix.03.

Additional material: nine male imagos (IBN), BOLIVIA, Cochabamba, Laguna de inundación II, río Ichilo, S 16°04'45" – W 64°44'20" (*Goitía*).

Etymology. From Latin *fuliginatus*, meaning black, because of the dark general coloration of the abdomen.

Diagnosis. (i) FW 10.1–13.5 mm (male); (ii) dorsum of head shaded black widely except on two submedian triangular marks after median ocellus (Fig. 22); (iii) abdominal segments VII–IX much darker than rest of body, abdominal terga IV–IX

shaded with black on a medial band (Fig. 22); (iv) pedestals curved laterally (Fig. 6), secondary lobe of penes reduced in length (Figs 6, 9). Two autapomorphies define this species: (i) a decrease in length of secondary lobe of penes (character 4 from 0.736–0.753 to 0.543–0.702), and unique abdominal coloration (character 8, state 3).

Male imago. Length (mm): body, 11.6–14.0; FW, 10.1–13.5; HW, 5.5–6.0; forelegs 4.5–6.0; cerci, 27.0–39.0. General coloration whitish yellow strongly shaded with black, darker on distal half of abdomen. Head (Fig. 22) shaded black among ocelli, vertex not shaded, occiput greyish. Antennae whitish shaded on apical margin of scape and pedicel. Grey markings on remnants of mouthparts. Thorax (Fig. 2): Grey shading present on coxae I–II, femur II, entire leg I, and median mesosternal membrane. Wings: FW shaded blackish grey in the area delimited by costal brace; veins C, Sc and R₁ brownish grey, rest hyaline; HW veins hyaline except vein Sc and thick costal crossvein, greyish. Abdomen (Fig. 22) with very thin medial line without black pigments. Terga I–II with greyish submedian marks; terga IV–IX strongly shaded with black on a medial band (more extensively shaded in VIII–IX); also shaded on a transverse band towards hind margin of terga III–VII; tergum X shaded grey except medially. Abdominal sterna shaded with grey, getting darker posteriorly, as follows: sternum III slightly marked laterally, sterna IV–VII with stronger lateral marks and with median zone widely pigmented; sterna VII–IX very strongly pigmented; sternum X whitish. Genitalia (Figs 6–9): sternum IX with yellowish margins, shaded completely with black except on median line; some small subcircular marks without pigments are interspersed in the pigmented area. Pedestals and penes yellowish white, forceps whitish, with diffuse grey shadings; penes with secondary lobe very short and wide (Fig. 9). Cerci whitish translucent.

Comments. As stated in the discussion of the previous species, *C. fuliginatus*, *C. albifilum* and *C. yavari* are similar but can be separated by the characters listed in the specific diagnosis, mainly by the form of pedestals and penes.

Campsurus homaulos sp.nov.

(Figs 12–14, 19, 23)

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EA0AD5D1-DCCA-493B-A49D-9052DDAE528E

Material examined. Holotype, male imago (MUSENUV), *Paratypes* 19 male (five in MUSENUV, 14 in IFML) and 16 female (five in MUSENUV, 11 in IFML) imagos, COLOMBIA, Dpto Amazonas, P.N. Amacayacu, río Amacayacu, S 03°48'28" W 70°15'21", 3.ii.1999, 93 m, light trap, 18–20 h, (Zúñiga, Domínguez & Molineri).

Additional material: five male imagos (IBN), COLOMBIA-BRAZIL, R. N. Palmari, río Yavarí, Muelle Centro Administrativo, 120 m, 29.v.2002, light trap, S 04°17'10" W

70°17'49" (Zúñiga *et al.*); two male imagos (CZNC), BRAZIL, Manaus, Ilha da Paciência, Nossa Senhora da Conceição, Lago Jacitara, S 3°16'40.7" W 60°16'34.5", 19.ix.2003, lighthouse, and one male and one female imagos (CZNC), BRAZIL, Manaus, Tefé, São Francisco da Boca da Capivara, Barra do Solimões, S 3°16'56, W 64°37'18, 10.9.03, light trap.

Etymology. From Greek *homaulos*, meaning 'living together', in reference to the sympatric distribution with its sister species *C. gracilipenis*.

Diagnosis. (i) FW 6.2–9.0 mm (male), 8.9–10.5 (female); (ii) dorsum of head shaded black widely between ocelli (Fig. 23); (iii) abdominal terga shaded slightly darker posteriorly, pattern as in Fig. 23; (iv) pedestals rounded and short (Fig. 12).

Male imago. Length (mm): body, 7.0–9.6; FW, 6.2–9.0; HW, 3.0–4.3; forelegs, 3.0–3.7; cerci, 17.5–23.5. General coloration yellowish white, shaded with grey dorsally. Head (Fig. 23) shaded dorsally with grey, some males with lighter coloration on medial line and around median ocellus; vertex without marks, some males with a grey postero-marginal shading. Antennae whitish shaded with grey, stronger at margins of scape and pedicel. Thorax (Fig. 23): pronotum whitish translucent shaded slightly with grey on median zone, on a pair of small elongated sublateral marks and along hind margin; mesonotum shaded grey on carinae and on posterior one-fourth [between Posterior Scutal Protuberances (PSP)]; metanotum yellowish, shaded slightly with grey. Forelegs whitish shaded completely grey, lighter on tarsi; legs II–III yellowish translucent. Wings: veins whitish translucent, shaded with purplish grey at the base of longitudinal veins, shading more extensive on veins Sc and R₁ (on basal half). Abdomen (Fig. 23): terga shaded widely with grey; tergum I lightest, IX darkest; terga II–VII with a lighter subcircular mark at each side of median line; thin medial line without grey pigments. Ventrally without grey shadings, except laterally on sternum IX. Genitalia (Figs 12–14): yellowish except median zone of sternum IX and base of penes whitish; pedestals, forceps and secondary lobes of penes in some males with a light grey shading. Cerci whitish translucent.

Female imago. Length (mm): body, 7.0–10.0; FW, 8.9–10.5; HW, 3.0–4.3; forelegs, 1.3–1.4; cerci, 2.7–3.5. General coloration as in male. Head as in male except grey shading more strongly marked, vertex without markings. Thorax: pronotum shaded grey on a pair of small elongated marks (as in male) and also on a pair of anterior oblique lines (posteriorly convergent). Mesonotum as male, some females with median zone between PSP strongly shaded grey forming a transverse band. Foreleg shaded grey except tibia. Abdomen: terga shaded grey except on a mediolongitudinal whitish band, color pattern similar to male but more widely shaded, sternum X whitish; sternum VIII with a pair of small anteromedian

sockets (Fig. 19). Terminal filament light grey basally, cerci whitish translucent.

Eggs. Length, 250 µm; width, 200 µm. Hemispheric, yellowish, with one whitish polar cap formed by a compound thread (ca. 5.0 mm long) formed by numerous thin filaments tightly braided.

Comments. *Campsurus homaulos* is very similar to *C. gracilipenis*, but in the former, the penes are shorter, the female has deeper sockets, and the eggs have thinner polar caps.

***Campsurus gracilipenis* sp.nov.**

(Figs 15–18, 24)

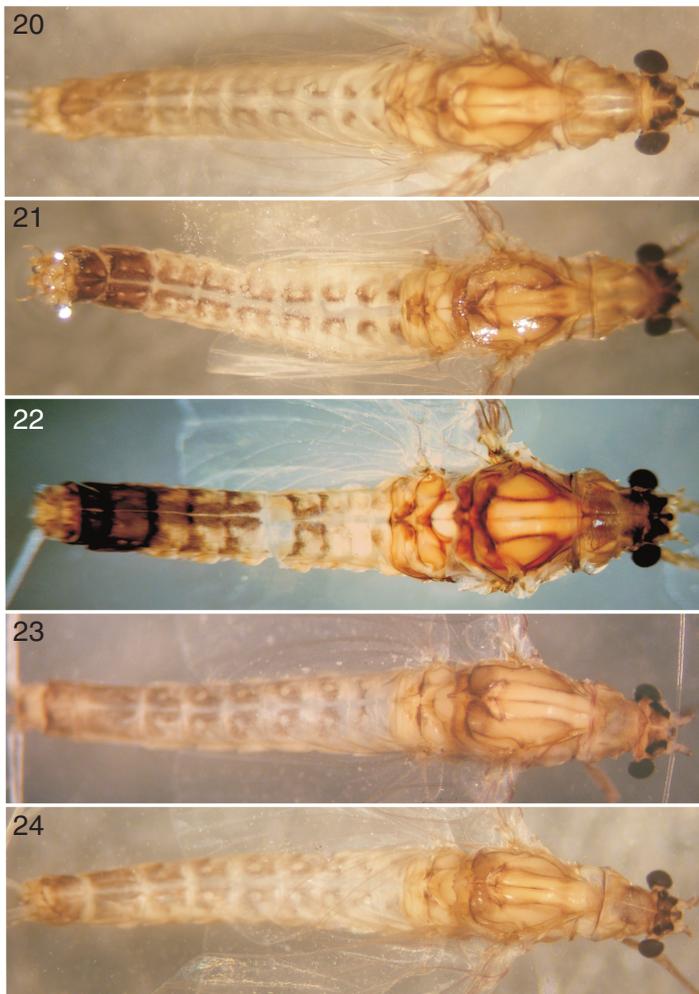
[http://zoobank.org/urn:lsid:zoobank.org:pub:](http://zoobank.org/urn:lsid:zoobank.org:pub:3AC19827-54E0-428C-8812-AAE38E608EE6)

3AC19827-54E0-428C-8812-AAE38E608EE6

Material examined. *Holotype*, male imago (MUSENUV) and *Paratypes* 11 (three in MUSENUV, eight in IFML) male imagos (in four vials), COLOMBIA, Amazonas, Puerto

Nariño, Loreto Yacu, 5.ii.1999, light trap 18–20 h (*Domínguez et al.*); three male, two female imagos, one male subimago from COLOMBIA, Dpto Amazonas, P.N. Amacayacu, río Amacayacu, S 03°48'28" W 70°15'21", 3.ii.1999, 93 m, light trap 18–20 h, (*Domínguez et al.*) (IFML); one male imago, COLOMBIA, Dpto Amazonas, P.N. Amacayacu, Quebrada Mata-Mata, S 03°48'28" W 70°15'21", 4.ii.1999, 93 m, light trap 4–6 h, (*Domínguez et al.*) (MUSENUV); two male imagos, COLOMBIA, Dpto Amazonas, Monillamena, confluencia quebradas Orejón y Yavarí, S 04°7'12" W 69°55'43.3", 25.vi.2009, 109 m, (*Domínguez & Torres*) (IFML).

Additional material: four male and ten female imagos, Brazil, Amazonas St, Ipixuna, comunidade Santa Catarina, light trap, 10.v.2011 (*Somavilla*); nine male and four female imagos, BRAZIL, Amazonas St, comunidade Estirão da Preta, Rio Liberdade, light trap, 07°21'46"S W 71°52'07", 13.v.2011, A. (*Somavilla*) col.; one male, BRAZIL, Amazonas St, Ipixuna, comunidade Lago Grande, Rio Gregório, light trap, 07°10'11"S 70°49'10"W, 18–23.v.2011 (*Somavilla*). Two males and two females housed in IBN, two males and two females at CZNC, remaining material at INPA.



Figs 20–24. Male adults, dorsal view: 20, *Campsurus albifilum*; 21, *Campsurus yavari*; 22, *Campsurus fuliginatus*; 23, *Campsurus homaulos*; 24, *Campsurus gracilipenis*.

Etymology. From Latin *gracilis* (thin) and *penis*, due to the slender aspect of the penes.

Diagnosis. (i) FW 7.2–8.9 mm (male), 10.0–11.0 (female); (ii) dorsum of head shaded black widely, mainly between lateral ocelli (Fig. 24); (iii) abdominal terga shaded slightly darker posteriorly, pattern as in Fig. 24; (iv) pedestals rounded and short (Fig. 15). One autapomorphy resulted from the analysis: a decrease in inner membrane/penes length ratio (character 5, from 0.320–0.360 to 0.250–0.282).

Male imago. Length (mm): body, 7.5–9.7; FW, 7.2–8.9; HW, 3.0–4.2; forelegs, 2.9–4.0; cerci, 17.0–25.0. General coloration yellowish white, shaded with grey dorsally, darker on head. Head shaded black among ocelli, darker medially forming a black triangle between lateral ocelli (Fig. 24); vertex shaded slightly grey. Antennae whitish shaded grey. Thorax (Fig. 24): pronotum shaded diffusely with grey; mesonotum shaded grey on carinae and apices of PSP; metanotum with light grey marks. Forelegs shaded completely with grey. Wings: veins whitish translucent, shaded with purplish grey on the basal portion of longitudinal veins. Abdomen (Fig. 24): terga shaded extensively with grey; tergum I lightest, IX darkest; terga II–VII with a lighter subcircular mark at each side of median line; thin medial line without grey pigments. Ventrally without grey shadings, except laterally on sterna IX–X. Genitalia (Figs 15, 16): yellowish except median zone of sternum IX and base of penes whitish; pedestals, forceps and penes with light grey shading. Terminal filament shaded with grey. Cerci whitish translucent.

Female imago. Length (mm): body, 9.5–10.7; FW, 10.0–11.0; HW, 3.7–4.8; forelegs, 1.7–2.0; cerci, 3.2–3.7. General coloration whitish yellow, eggs filling the abdomen yellowish to orange-yellow. Head: as in male, the darkest portion of the body. Thorax: as in male, except mesonotum shaded more strongly on three longitudinal bands (one medial, two laterals), the median band is interrupted anteriorly by a whitish oval mark with a dark spot inside. Forelegs shaded grey except on tibia. Abdomen as in male but grey shading more widely distributed, except on a medial whitish band; abdominal sterna without grey marks. Sternum VIII with a pair of small anteromedian sockets (Figs 17, 18). Caudal filament whitish, median filament shaded grey on a basal ring.

Eggs. Length 290–310 µm; width 245–260 µm. Hemispheric, yellowish, with one whitish polar cap formed by a single very long compound thread spirally arranged; this thread is composed of many (> 30) very thin filaments, tightly braided.

Comments. *Campsurus gracilipenis* is very closely related to *C. homaulos*, but they can be separated because the first species does not present small elongated grey marks on the pronotum, and the penes are long and slender. Furthermore, the

females of *C. gracilipenis* show shallower sockets and wider polar caps in the eggs.

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference:

10.1111/j.1365-3113.2012.00656.x

File S1. Morphometric data of the male imagos of the *albifilum* group used in the multivariate discriminant analyses. Variables 1–6 are defined in File S2 (as characters 1–6).

File S2. Definition of characters and states.

File S3. Data matrix of seven continuous and 13 discrete characters and state assignment for each species used in the cladistic analysis; matrix ready to run in TNT.

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