

Phylogeny of *Callibaetis* (Ephemeroptera: Baetidae) based on morphology of nymphs and adults

PAULO VILELA CRUZ, FREDERICO FALCÃO SALLES & NEUSA HAMADA

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Callibaetis is considered to be one of the most problematic genera among mayflies by a series of taxonomic inaccuracies that have accumulated over the last two centuries. Despite these taxonomic problems, two independent hypotheses of species groups have been proposed. In the first hypothesis, three species groups for North America were proposed, and in the second, three species groups were proposed for South American. In these hypotheses, the generic delimitation and monophyly of *Callibaetis* have not been evaluated under a cladistic framework. Taking this into account, the objectives of this study were to verify the monophyly of *Callibaetis* and whether the groups of species proposed for the genus are corroborated as natural. The matrix included 128 morphological characters and one habitat character, 119 discrete characters were compiled (101 of nymphs and 18 of adults), and six imaginal characters are related to pigmentation pattern. Continuous characters were ratios and were represented by 10 characters (nine for nymphs and one for adults). The data set was analysed under implied weights. Group support was estimated with relative Bremer support and frequency differences. The results corroborated the monophyletic nature of *Callibaetis* and the generic status of *Callibaetoides*; however, the groups proposed for North and South American *Callibaetis* species were not corroborated. Our study indicated four groups of species for the genus, which we proposed as subgenera: *Callibaetis*, *Abaetetuba* **subgen. n.** *Aiso* **subgen. n.** and *Cunbaporanga* **subgen. n.**

Corresponding author: Paulo Vilela Cruz, Universidade Federal de Rondônia – UNIR, CEP: 76940-000, Rolim de Moura, Rondônia, Brazil. E-mail: pvilelacruz@gmail.com

Paulo Vilela Cruz, Universidade Federal de Rondônia – UNIR, CEP: 76940-000 Rolim de Moura, Rondônia, Brazil

Frederico Falcão Salles, Centro Universitário Norte do Espírito Santo, Universidade Federal do Espírito Santo, CEP 29933-415 São Mateus, Espírito Santo, Brazil. E-mail: ffsalles@gmail.com

Neusa Hamada, Coordenação de Biodiversidade, Instituto Nacional de Pesquisas da Amazônia (INPA), CEP 69067-375 Manaus, Amazonas, Brazil. E-mail: nbamada@inpa.gov.br

Introduction

Callibaetis Eaton, 1881 is a Pan-American genus of mayflies with 34 valid species, 13 recorded from North America, five from Central America and 21 from South America. It is considered taxonomically problematic because most of its species were described at the end of 19th century and in the early decades of 20th century, a period when studies of Baetidae were still focused on adult males, which does not provide enough data to allow delimitation of species and genera. At the early time, colour pattern was one of the most important characteristics used in the taxonomy of Baetidae, especially in the case of *Callibaetis*, because usually its species have conspicuous pattern. As many species

descriptions were made based on a single or a few specimens from one locality, intra- and interpopulation variability of characteristics was not known, making specific determination difficult (e.g. Pictet 1843-1845; Eaton 1871, 1881, 1883-1888; Banks 1900, 1918; Needham & Murphy 1924).

In the beginning of the second half of 20th century, descriptions of nymphs began to be used, improving the taxonomy of the family (Edmunds & Allen 1966). At the end of 20th century, use of nymph's morphology to distinguish genera and species in Baetidae was already consolidated (e.g. Lugo-Ortiz & McCafferty 1999). But, only in the last decades, studies were made to associate several of

the previously described adults with their respective nymphal stages in *Callibaetis* (e.g. Check 1982; Kluge 1991; Lugo-Ortiz & McCafferty 1996a; Salles *et al.* 2003; Nieto 2008; Nieto & Cruz 2013; Cruz *et al.* 2014), thus allowing progress in establishing genera concept and in species identification.

Despite the above taxonomic problems, two independent hypotheses for species groups were proposed for the genus, neither of which used a cladistic framework. The first hypothesis (Check 1982) proposed three species groups for North America based on the external morphology of nymphs and colour patterns of adults. The second hypothesis (Gillies 1990) proposed three species groups for South America based only on colour patterns of adults. In addition, the generic delimitation and monophyly of *Callibaetis* were not based on extensive studies (Nieto 2010 and Kluge 2015), and further work is needed, especially considering the recent description of *Callibaetoides* Cruz, Salles & Hamada, 2013, a genus very similar to *Callibaetis*.

As the genus and its internal groups had not been tested under a cladistic framework, the objectives of this study were to verify the monophyly of *Callibaetis* and whether the groups of species proposed by Gillies and Check are corroborated as natural.

Materials and Methods

Taxa

To evaluate the relationships among *Callibaetis* species, we included 28 species from South, Central and North America: *Callibaetis californicus* Banks, 1900; *Callibaetis calloventer* Cruz, Salles & Hamada, 2014; *Callibaetis capixaba* Cruz, Salles & Hamada, 2009; *Callibaetis cruentus* Cruz, Salles & Hamada, 2014; *Callibaetis dominguezi* Gillies, 1990; *Callibaetis fasciatus* (Pictet, 1843); *Callibaetis ferrugineus* (Walsh, 1863); *Callibaetis floridanus* Banks, 1900; *Callibaetis fluctuans* (Walsh, 1863); *Callibaetis gelidus* Cruz, Salles & Hamada, 2014; *Callibaetis gonzalezi* (Navás, 1934); *Callibaetis guttatus* Navás, 1915b; *Callibaetis itannae* Cruz, Salles & Hamada, 2014; *Callibaetis jocosus* Navás, 1912; *Callibaetis montanus* Eaton, 1885; *Callibaetis nigracyclus* Cruz, Salles & Hamada, 2014; *Callibaetis pallidus* Banks, 1900; *Callibaetis pictus* (Eaton, 1871); *Callibaetis pollens* Needham & Murphy, 1924; *Callibaetis pretiosus* Banks, 1914; *Callibaetis radiatus* Navás, 1920; *Callibaetis sellacki* (Weyenbergh, 1883); *Callibaetis willneri* Navás, 1932; *Callibaetis zonalis* Navás, 1915a; *Callibaetis* sp. A, *Callibaetis* sp. B, *Callibaetis* sp. C and *Callibaetis* sp. D. The morphotypes *Callibaetis* A–D represent new species that will be formally described in the future; nymphs of *C. zonalis* and *C. fasciatus* were reared and will be formally described in the future (Table 1).

Nine species were used as outgroups, most in accordance with cladistic analysis of Nieto (2010): *Adebroetus amazonicus* Lugo-Ortiz & McCafferty, 1995; *Apobaetis hamadae* Cruz, Boldrini & Salles, 2011; *Callibaetoides caaigua* Cruz, Salles & Hamada, 2014; *Cryptonympha copiosa* Lugo-Ortiz & McCafferty, 1998; *Paracloeodes atroari* Nieto & Salles 2006; *Paracloeodes bimodulus* Lugo-Ortiz & McCafferty, 1996b; *Rivudiva trichobasis* Lugo-Ortiz & McCafferty, 1998; *Varipes singuil* (Nieto, 2004); and *Waltzoyphius fasciatus* Lugo-Ortiz & McCafferty, 1995. The trees were rooted in *C. copiosa*.

Species without known nymph, species poorly described, species with very damaged types and species in process of taxonomic definition (Authors, review in preparation) were not included in the analysis. These are as follows: *Callibaetis camposi* Navás, 1930b; *Callibaetis distinctus* Lugo-Ortiz & McCafferty, 1996a; *Callibaetis fluminensis* Cruz, Salles & Hamada, 2009; *Callibaetis gregarius* Navás, 1930a; *Callibaetis nigrivenosus* Banks, 1918; *Callibaetis paulinus* (Navás, 1924); *Callibaetis punctilusus* McCafferty & Provonsha, 1993; *Callibaetis skokianus* Needham, 1903; and *Callibaetis viviparus* Needham & Murphy, 1924.

Characters

A matrix of 37 taxa with 128 morphological characters and one habitat character was constructed (Table 2). Characters were scored from the external morphology of the nymphs and adults. A total of 119 discrete characters were compiled, 101 of nymphs and 18 of adults; six characters of imago are related to pigmentation pattern. The continuous characters were ratios (e.g. Molineri & Salles 2013) and were represented by 10 characters, nine for nymphs and one for adults; all characters were treated as non-additive (unordered).

List of continuous and discrete characters

Continuous

0. Length of labrum/width of labrum
1. Maximal length of labrum/minimal length of labrum
2. Length of maxillary palp/length of galea-lacinia
3. Width of distomedial projection/width of base of labial palp segment III
4. Length of labial palp segment III/width of labial palp segment III
5. Length of glossa/length of paraglossa
6. Length of tibia and tarsus/length of femur
7. Length of claw/length of tarsi
8. Length of gill IV/length of segment IV
9. Length of free marginal intercalaries between IMA and MA2 in forewing/distance between IMA and MA2

Discrete

10. Elevation on frons: (0) absent; (1) present.

Table 1 List of material examined (Stage acronyms: N, nymph; ♂I, male imago; ♀I, female imago.)

Species	Examined	Literature
<i>Adebrotus amazonicus</i>	N; UFES	Salles 2010
<i>Apobaetis hamadae</i>	N, ♂I; Holotype, Paratype; INPA	Cruz et al. 2011b
<i>Cryptonympha copiosa</i>	N, ♂I; ♂I reared, not described; INPA	Lugo-Ortiz & McCafferty 1998
<i>Paracloeodes atroari</i>	N, ♂I; Paratype, ♂I reared, not described; INPA	Nieto & Salles 2006
<i>Paracloeodes binodulus</i>	N, ♂I; Holotype. ♂I reared, not described; PURDUE	Lugo-Ortiz & McCafferty 1996b
<i>Rivudiva trichobasis</i>	N, ♂I; Paratype; Lillo	Cruz et al. 2011a
<i>Varipes singuil</i>	N; Paratype; Lillo	Nieto 2004
<i>Waltzoyphius fasciatus</i>	N, ♂I; Literature; ♂I in Preparation by others authors	Lugo-Ortiz & McCafferty 1995
<i>Callibaetis radiatus</i>	N, ♂I, ♀I; Holotype photograph, N and ♂I direct; INPA, UFV, MZB, MNH	Navás 1920
<i>Callibaetis californicus</i>	N, ♂I, ♀ I	Check 1982
<i>Callibaetis cruentus</i>	N, ♂I, ♀I; Holotype and Paratypes; INPA	Cruz et al. 2014
<i>Callibaetis ferrugineus</i>	N, ♂I, ♀I; Type material of <i>C. americanus</i> , <i>C. coloradensis</i> and <i>C. ferrugineus</i> in MHN	Check 1982
<i>Callibaetis floridanus</i>	N, ♀I, ♂I; ♀I in MHN	Check 1982
<i>Callibaetis fluctuans</i>	N, ♀I, ♂I	Check 1982
<i>Callibaetis gonzalezi</i>	N, ♂I, ♀I; Material collected and determined by Cruz P.V.; INPA	Cruz et al. 2014
<i>Callibaetis guttatus</i>	N, ♂I, ♀I; Type material of <i>C. apicatus</i> , <i>C. zonatus</i> , <i>C. guttatus</i> in MZB and new collected and reared in Brazil; INPA	Cruz et al. 2014
<i>Callibaetis jocosus</i>	N, ♂I, ♀I; Type material in MZB and new reared material from Brazil; INPA	Cruz et al. 2014
<i>Callibaetis montanus</i>	N, ♂I, ♀I; Type material in MNH, Purdue	Check 1982
<i>Callibaetis pictus</i>	N, ♂I, ♀I; Type Material and material reared in MNH, Purdue	Check 1982
<i>Callibaetis pallidus</i>	N, ♂I, ♀I; ♂I and ♀I in MHN	Check 1982
<i>Callibaetis pretiosus</i>	N, ♂I, ♀I	Check 1982
<i>Callibaetis willineri</i>	N, ♂I, ♀I; Types and new material collected; Purdue, INPA	Cruz et al. 2014
<i>Callibaetis zonalis</i>	N, ♂I, ♀I; Types MZLP, INPA, Authors, paper in preparation	Cruz et al. 2014
<i>Callibaetis</i> sp. D	N, ♂I, ♀I; INPA	Authors, Paper in preparation
<i>Callibaetis capixaba</i>	N, ♂I, ♀I; Type material; INPA	Cruz et al. 2009
<i>Callibaetis dominguezii</i>	N, ♂I, ♀I; Type material from IFML and material from Nieto & Cruz 2013;	Nieto & Cruz 2013
<i>Callibaetis fasciatus</i>	N, ♂I, ♀I; Type material from MZB; N reared, Authors, paper in preparation; INPA, UFRJ	Cruz et al. 2014
<i>Callibaetis pollens</i>	N, ♂I, ♀I; Type material from Cornell and new material collected and reared; INPA	Cruz et al. 2014

Table 1 Continued

Species	Examined	Literature
<i>Callibaetis sellacki</i>	N, ♂I, ♀I; Types of <i>C. gloriosus</i> , <i>C. lineatus</i> , <i>C. trifasciatus</i> , and new material collected in Argentina; Lillo, NHM, INPA	Cruz et al. 2014
<i>Callibaetis</i> sp. A	N; INPA	Authors, Paper in preparation
<i>Callibaetis itannae</i>	N, ♂I, ♀I; Type material from INPA	Cruz et al. 2014
<i>Callibaetis</i> sp. B	N, ♀I; INPA	Paper in preparation
<i>Callibaetis</i> sp. C	N, ♂I, ♀I; INPA	Authors, Paper in preparation
<i>Callibaetis colloventer</i>	N, ♂I, ♀I; Type material from INPA	Cruz et al. 2014
<i>Callibaetis nigracyclus</i>	N, ♂I, ♀I; Type material from INPA	Cruz et al. 2014
<i>Callibaetis gelidus</i>	N, ♂I, ♀I; Type material from INPA	Cruz et al. 2014
<i>Callibaetoides caaigua</i>	N, ♂I, ♀I; Type material from INPA	Cruz et al. 2013

UFES, Universidade Federal do Espírito Santo; INPA, Instituto Nacional de Pesquisa da Amazonia; MZB, Museu de Zoologia de Barcelona; PURDUE, Purdue University – Entomological Research Collection; Lillo, Museo Miguel Lillo de Ciencias Naturales; Cornell, Cornell University – Insect Collection; UFRJ, Universidade Federal do Rio de Janeiro; MNH, Natural History Museum-London; UFV, Universidade Federal de Viçosa; MLP, Museu de La Plata.

- Type of elevation of frons*: (0) elevated (straight surface); (1) elevated forming a keel (or small tubercle); (2) with two keels; (3) with two keels fused in mid-length.
- Distal margin of labrum forming a lobe* (the distal margin of the labrum, except the midline or area near to medial concavity): (0) no; (1) yes.
- Shape of distal margin of labrum without lobe*: (0) straight; (1) slightly rounded.
- Shape of labrum lobe*: (0) straight; (1) rounded; (2) broadly pointed; (3) broadly rounded.
- Shape of medial concavity*: (0) straight; (1) slightly concave; (2) abruptly concave; (3) deeply concave (V-like).
- Type of anterolateral setae on distal margin of labrum*: (0) simple and pointed; (1) simple and pectinate; (2) bifid; (3) bifid and pectinate; (4) simple and blunt.
- Type of setae near midline of distal margin of labrum*: (0) simple; (1) simple and pectinate; (2) bifid; (3) spatulated; (4) multi-flagellated; (5) serrated.
- Pair of robust denticles on medial emargination of labrum*: (0) absent; (1) present.
- Labrum submedian arc of setae on dorsal surface*: (0) continuous; (1) discontinuous.
- Disposition of dorsal row of setae on labrum*: (0) a row of fine and simple setae; (1) 1 seta centrally and 2–3 setae laterally; (2) flattened and pointed; (3) bifid; (4) spine-like.
- Spine-like setae ventrally on lateral margin of labrum*: (0) absent; (1) present.

22. *Tuft of spine-like setae on ventral surface of anterolateral margin of labrum*: (0) absent; (1) present.
23. *Slender and frayed process at base on right prostbecca*: (0) absent; (1) present.
24. *Prostbecca of right mandible*: (0) stout (with denticles apically); (1) spine-like; (2) thin and bifid.
25. *Prostbecca of left mandible*: (0) stout (with denticles apically); (1) robust and bifid.
26. *Molars of left mandible*: (0) without constrictions; (1) with constrictions.
27. *Fusion of left mandible incisors*: (0) absent; (1) present.
28. *Deepness of fusion of left mandible incisors*: (0) cleft; (1) partially fused; (2) fused but incisors recognizable; (3) completely fused.
29. *Fusion of right mandible incisors*: (0) absent; (1) present.
30. *Deepness of fusion of right mandible incisors*: (0) cleft; (1) completely fused; (2) fused but incisors recognizable; (3) partially fused.
31. *Plane of mandible incisors*: (0) inner and outer incisors in the same plane; (1) inner set of incisors at right angle with outer set.
32. *Setae between prostbecca and mola on right mandible*: (0) absent; (1) present.
33. *Length of setae between prostbecca and mola on right mandible*: (0) shorter than prostbecca; (1) longer than prostbecca; (2) same length of prostbecca.
34. *Lingua projection*: (0) absent; (1) present.
35. *Shape of lingua projection*: (0) lingua with pointed projection; (1) lingua with rounded projection.
36. *Length of lingua*: (0) longer than superlinguae; (1) subequal to superlinguae; (2) shorter than superlinguae.
37. *Distal margin of superlingua*: (0) straight; (1) rounded.
38. *Spines on lateral margin of superlingua*: (0) absent; (1) present.
39. *Ventral setae near maxillary canines*: (0) curved upon denticles; (1) not curved upon denticles.
40. *Number of maxillary palpi segments*: (0) three; (1) two.
41. *Fusion of maxillary palp segments II and III*: (0) complete; (1) incomplete.
42. *Spine-like setae on surface of maxillary palp segment I*: (0) present; (1) absent.
43. *Inner margin of last segment of maxillary palpi on apex*: (0) straight; (1) curved inwardly.
44. *Number of rows of maxillary setae on crown of galea-lacinia*: (0) two; (1) three.
45. *Shape of maxillary canines*: (0) robust and apically blunt; (1) apically pointed (spine-like).
46. *Row of spine-like setae on outer margin of maxilla*: (0) absent; (1) present.
47. *Arrangement of row of spine-like setae on outer margin of maxilla*: (0) complete with many setae; (1) complete with one row; (2) incomplete with tuft at apex; (3) incomplete with two tufts, one apical and other basal.
48. *Arrangement of apical tuft of spine-like on outer margin of maxilla*: (0) restrict on outer margin; (1) basal half of row on dorsal surface.
49. *Shape of glossa*: (0) subtriangular; (1) short oval; (2) roundish-rectangular; (3) subelliptical.
50. *Medial expansion on subelliptical glossa*: (0) absent; (1) present.
51. *Base of glossa*: (0) overlapping base of paraglossa; (1) not overlapping base of paraglossa.
52. *Tuft of long spine-like setae on dorsal surface of glossa*: (0) absent; (1) present.
53. *Shape of paraglossa*: (0) subtriangular; (1) roundish; (2) subrectangular.
54. *Shape of paraglossa apex*: (0) broadly pointed; (1) rounded; (2) truncated.
55. *Number of longitudinal rows of setae on dorsal surface of paraglossa*: (0) one; (1) three; (2) two.
56. *Number of rows of spine-like setae on distal margin of paraglossa*: (0) one; (1) two; (2) three; (3) more than three.
57. *Tuft of fine setae on apex of paraglossa*: (0) absent; (1) present.
58. *Number of tuft of small and simple setae on apex of paraglossa*: (0) one; (1) three.
59. *Spine-like setae on segment I of labial palp*: (0) absent; (1) present.
60. *Distomedial projection on labial palp segment II*: (0) absent; (1) present.
61. *Shape of distomedial projection of labial palpi segment II*: (0) rounded; (1) digitiform; (2) triangular.
62. *Direction of distomedial projection of labial palpi segment II*: (0) lateral (180°); (1) apical (90° to 160°).
63. *Medial concavity on labial palp segment III*: (0) absent; (1) present.
64. *Shape of labial palp segment III without medial concavity*: (0) triangular; (1) globose; (2) quadrangular; (3) rectangular; (4) trapezium; (5) subconical.
65. *Apex of labial palp III without medial concavity*: (0) rounded; (1) truncated; (2) pointed.
66. *Shape of labial palp segment III with medial concavity*: (0) subelliptical; (1) rectangular; (2) subconical.
67. *Apex of labial palp segment III with medial concavity*: (0) rounded; (1) truncated; (2) broadly pointed.
68. *Type of forefemur setae on dorsal margin*: (0) not concave; (1) concave.
69. *Shape of forefemur setae on dorsal margin*: (0) pointed; (1) blunt.
70. *Size and robustness of forefemur setae on dorsal margin*: (0) long and thin; (1) short and thin; (2) short and thick.

71. *Forefemur longitudinal row of setae near dorsal margin on anterior surface*: (0) absent; (1) present.
72. *Type of setae on forefemur anterior surface near dorsal margin*: (0) spine-like setae; (1) blunt setae; (2) long and thin setae.
73. *Forefemur longitudinal row of setae at middle on anterior surface*: (0) present; (1) absent.
74. *Type of setae on forefemur anterior surface at middle*: (0) pointed; (1) blunt.
75. *Forefemur longitudinal row of setae near ventral margin on anterior surface*: (0) absent; (1) present.
76. *Type of setae in longitudinal row on forefemur anterior surface near ventral margin*: (0) long and pointed; (1) short and blunt; (2) bifid or trifid; (3) short and pointed.
77. *Forefemur transversal row of long setae*: (0) absent; (1) present.
78. *Transverse row of long setae on mid- and hind femora*: (0) absent; (1) present.
79. *Distance of setae sockets of transverse row of long setae on mid- and hind femora*: (0) very near each other, touching each other; (1) not near each other, not touching each other.
80. *Type of setae on ventral margin of foretarsus*: (0) spine-like setae; (1) pectinate spine-like setae; (2) bifid and trifid spine-like setae.
81. *Setae on foretarsus anterior surface*: (0) absent; (1) present.
82. *Type of setae on foretarsus anterior surface*: (0) spine-like setae; (1) pectinate spine-like setae; (2) blunt spine-like setae.
83. *Foreclaw denticles*: (0) absent; (1) present.
84. *Type of foreclaw denticles*: (0) triangular; (1) long and cylindrical; (2) minute; (3) triangular with apical extremely higher than others; (4) conical.
85. *Length of row of foreclaw denticles*: (0) base to apex; (1) less than half; (2) more than half but not all claw; (3) half.
86. *Size of foreclaw denticles*: (0) same size; (1) slightly increasing towards apex.
87. *Type of setae on posterior surface of hind femur*: (0) simple spine-like setae; (1) curved and pectinated spine-like setae; (2) long and pointed.
88. *Mid- and hind claw denticles*: (0) same size of foreclaw; (1) smaller than foreclaw; (2) minute.
89. *Hind wing pads*: (0) present; (1) absent.
90. *Spines on posterior margin of metathorax*: (0) absent; (1) present.
91. *Projection on thoracic mesosternum*: (0) absent; (1) present.
92. *Gills with flap*: (0) no; (1) yes.
93. *Type of gill I without flap*: (0) not racquet-shaped; (1) racquet-shaped.
94. *Number of flaps on gill I*: (0) one; (1) two or more.
95. *Shape of gill I without flaps*: (0) asymmetric; (1) symmetric.
96. *Gills margins*: (0) serrated; (1) smooth.
97. *Shape of gill I with flaps*: (0) rounded; (1) L-like.
98. *Shape of apex of gills*: (0) rounded; (1) apically pointed.
99. *Costal rib moved far from costal margin*: (0) no; (1) yes.
100. *Gills trachea*: (0) pigmented; (1) hyaline.
101. *Posterior margin of abdominal terga*: (0) smooth; (1) with spines.
102. *Type of spines on posterior margin of abdominal terga*: (0) pointed; (1) rounded.
103. *Surface of abdominal terga*: (0) smooth; (1) creased.
104. *Scale-like setae/socket of scale-like setae on abdominal terga*: (0) present; (1) absent.
105. *Type of setae on caudal filaments*: (0) simple setae; (1) flattened setae.
106. *Spines on terminal filament spines*: (0) absent; (1) present.
107. *Arrangement of long spines on terminal filament*: (0) long on each segment; (1) long every second segment; (2) long every four segments.
108. *Spines on cerci*: (0) absent; (1) present.
109. *Arrangement of long spines on cercus*: (0) long on each segment; (1) long every four segments; (2) long every second segment.
110. *Direction of dorsal portion of turbinate eyes*: (0) parallel; (1) anteriorly divergent.
111. *Shape of dorsal portion of turbinate eyes*: (0) oval; (1) circular.
112. *Constriction on turbinate portion of eyes (lateral view)*: (0) absent; (1) present.
113. *Number of free marginal intercalary veins on forewings*: (0) single; (1) double.
114. *Number of longitudinal veins on hind wings*: (0) three; (1) two.
115. *Free marginal intercalary veins on hind wing*: (0) absent; (1) present.
116. *Costal process of hind wing*: (0) absent; (1) present.
117. *Shape of costal process*: (0) pointed; (1) rounded; (2) quadrangular; (3) rectangular.
118. *Spots covering female body*: (0) no; (1) yes.
119. *Unistyliger inner projection*: (0) present; (1) absent.
120. *Unistyliger base*: (0) wider than apex; (1) same width.
121. *Process on subgenital plate*: (0) straight; (1) concave; (2) convex.
122. *Spine on process of subgenital plate*: (0) absent; (1) present.
123. *Habitat*: (0) lentic and/or backwaters of streams; (1) lotic.
124. *Anterior margin of male forewing pigmented*: (0) no; (1) yes.

125. Pigment on male forewing forming transversal bands: (0) no; (1) yes.
 126. Anterior margin of female forewing pigmented: (0) no; (1) yes.
 127. Pigment on female forewing forming transversal bands: (0) no; (1) yes.
 128. Female forewing completely pigmented: (0) no; (1) yes.

Analysis

The matrix was analysed with TNT (Goloboff *et al.* 2008) under implied weights ($k = 4$); implied weighting was used because it is a means of decreasing problems of scaling in continuous characters (Goloboff *et al.* 2006). Searches were conducted by traditional search, with 500 replicates of random addition sequences followed by tree bisection–reconnection, saving 10 trees per replication. Group support was calculated with relative Bremer support (Goloboff & Farris 2001) and frequency differences (GC, Goloboff *et al.* 2003). Bremer supports were calculated for the most parsimonious trees and 1000 suboptimal trees up to 10 steps longer than the shortest tree. Frequency differences were calculated with 300 replicates by symmetrical resampling of the original matrix (GC, Goloboff *et al.* 2003). Each replicate was calculated by 10 random addition sequences plus TBR (tree bisection and reconnection), saving 10 trees per replicate.

The matrix ready to run in TNT is in the supplementary file.

Results and discussion

Cladistic analysis

Analysis of the data set (continuous and discrete characters) yielded one tree (Fig. 1) with a length of 275.990 steps (total fit 80.41, adjusted homoplasy 18.59, consistency index 57.9 and retention index 78.5).

The clade *Callibaetoides* + *Callibaetis* (GC = 100 and Relative Bremer = 85) was recovered based on 14 synapomorphies (seven unique) (Fig. 1). This relationship was already hypothesized by Kluge (2015) as taxon *Callibaetis*/fg2 which is divided into a monospecific genus *Callibaetoides* and a holophyletic taxon *Callibaetis*/fg3 (genus *Callibaetis*), based on two morphological synapomorphies also recovered in this study: (i) costal rib moved far from costal margin (Char. 99 – unique) and (ii) reduced size of mid- and hind claw denticles (Char. 88 – non-unique). Kluge (2015) included the viviparous behaviour as a third synapomorphy of *Callibaetis*/fg2, such behaviour needs to be confirmed in most of the species and was not included in the matrix.

Callibaetoides was corroborated as a distinct taxa characterized by the following: (i) increase of ratio length of labrum/width of labrum (0.720–0.760 → 1.180) (Char. 0); (ii) increase of ratio maximum length of labrum/minimum

length of labrum (1.320–1.430 → 4.000) (Char. 1); (iii) increase of ratio length of maxillary palp/length of galea-lacinia (1.480–1.760 → 1.810) (Char. 2); (iv) decrease of ratio length of labial palp segment III/width of labial palp segment III (1.080–1.250 → 0.400) (Char. 4); (v) decrease of ratio length of glossa/length of paraglossa (0.810–0.870 → 0.770) (Char. 5); (vi) decrease of ratio length of gill IV/length of segment IV (2.000 → 1.500) (Char. 8); (vii) labrum lobe broadly pointed (fig. 3B in Cruz *et al.* 2013) (Char. 14); (viii) midline of distal margin of labrum with multiflagellated setae (fig. 3C in Cruz *et al.* 2013) (Char. 17); (ix) maxillary palp with three segments (fig. 3G in Cruz *et al.* 2013) (Char. 40); (x) three rows of maxillary setae on crown of galea-lacinia (fig. 6D–G in Cruz *et al.* 2013) (Char. 44); (xi) tuft of long spine-like setae on glossa dorsal surface present (fig. 3I in Cruz *et al.* 2013) (Char. 52); (xii) apex of paraglossa truncate (fig. 3J in Cruz *et al.* 2013) (Char. 54); (xiii) dorsal margin of femora with rounded setae (fig. 7D in Cruz *et al.* 2013) (Char. 69); (xiv) presence of longitudinal row of rounded setae near dorsal margin on femora (fig. 7D in Cruz *et al.* 2013) (Char. 72); (xv) surface of abdominal terga smooth (fig. 7A in Cruz *et al.* 2013) (Char. 103); (xvi) abdominal terga with scale-like setae or their socket (fig. 7A in Cruz *et al.* 2013) (Char. 104). Additionally, the genus possesses the third segment of labial palp quadrangular (fig. 3I in Cruz *et al.* 2013); third segment of labial palp without concavity; absence of trifold setae on legs (fig. 4A in Cruz *et al.* 2013); gill I oval and with one flap (fig. 5A in Cruz *et al.* 2013); costal process of hind wing on medial third (fig. 2A in Cruz *et al.* 2013) and two longitudinal veins (fig. 2A in Cruz *et al.* 2013).

The monophyly of *Callibaetis* (node A) was corroborated (GC = 61 and Relative Bremer = 85) and the species of this genus share: (i) decrease of ratio length of maxillary palp/length of galea-lacinia (1.480–1.760 → 1.360–1.370) (Char. 2); (ii) decrease of ratio length of tibia and tarsus/length of femur (1.130–1.140 → 1.120) (Char. 6); (iii) increase of ratio length of claw/length of tarsus (0.380–0.430 → 0.620–0.630) (Char. 7); (iv) prosthema of left mandible robust and bifid (fig. 2D in Cruz *et al.* 2014) (Char. 25); (v) presence of medial concavity on labial palp segment III (fig. 2H and 6H in Cruz *et al.* 2014) (Char. 63); (vi) bifid and trifold setae on foretarsus ventral margin (reverted to simple in node F) (fig. 7B in Cruz *et al.* 2014) (Char. 80); (vii) dorsal portion of turbinate eyes parallel (fig. 1A in Cruz *et al.* 2014) (Char. 110); and (viii) spots covering female body (Char. 118). Additionally, all species in the genus share a row of simple and thin spine-like setae near distal margin on ventral surface of labrum; bifid and trifold setae near ventral margin of forefemur on anterior surface (reverted to simple in node F); abdominal terga without

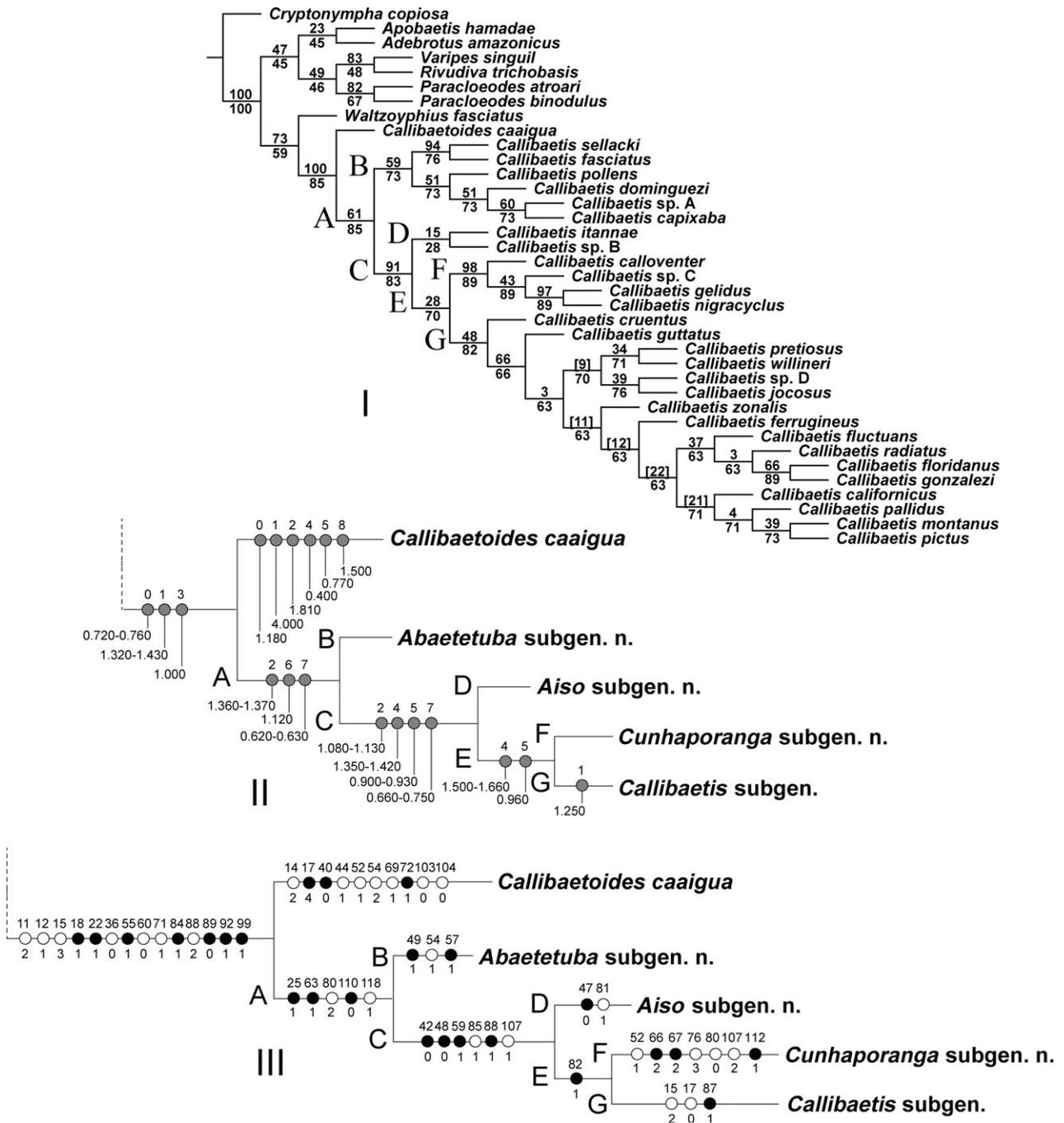


Fig. 1 I. Phylogenetic hypotheses with $k = 4$. Values above branches correspond to GC, and values below branches correspond to Relative Bremer. II. Detail of subgenera with continuous synapomorphies. III. Detail of subgenera with discrete synapomorphies. Black circles indicate synapomorphies; white circles represent nonunique changes on the tree, either forward or reverse; above are the character numbers and below are the character states.

scale-like setae or their sockets; gill I L-shaped with three lamella (figs. 4C–D in Cruz *et al.* 2014); costal process of hind wing on basal third (fig. 1K in Cruz *et al.* 2014); and hind wing with three longitudinal veins.

One of four synapomorphies, which sustains *Callibaetis*, is in accordance with Kluge (2015) hypothesis (*Callibaetis*/fg3): (i) spots covering imago body (Char. 118), and two of 12 synapomorphies are in accordance with Nieto (2010): (i)

presence of medial concavity on labial palp segment III (Char. 63) and (ii) bifid and trifid setae on foreleg (Char. 80). These three synapomorphies independently recovered (Nieto 2010; Kluge 2015 and here) are common features attributed to *Callibaetis* and notably allow the differentiation from others genera.

Four groups of species were recovered in *Callibaetis*; given the high values of support and synapomorphies, these four groups are proposed as subgenera: *Callibaetis*, *Abaetetuba* **subgen. n.**, *Aiso* **subgen. n.** and *Cunbaporanga* **subgen. n.**

The first group is the node B or *Abaetetuba* **subgen. n.** (GC = 59 and Relative Bremer = 73). Species in this subgenus share the following: (i) short oval glossa (fig. 42A in Cruz et al. 2009) (Char. 49); (ii) apex of paraglossa rounded (fig. 8a in Nieto 2008) (truncated in clade that *C. (Ab.) dominguezii*, *C. (Ab.)* sp. A and *C. (Ab.) capixaba* belong) (fig. 42A in Cruz et al. 2009) (Char. 54); (iii) tuft of fine setae on apex of paraglossa present (fig. 42A in Cruz et al. 2009) (Char. 57). Additionally, all species in this subgenus share subrectangular paraglossa; segment I of labial and maxillary palp without spine-like setae; labrum with deep V medial emargination; apex of segment III of labial palp truncated; cerci and terminal filament with long spines on all segments; four species have three rows of setae on crown of galea-lacinia (*C. (Ab.) dominguezii*, *C. (Ab.)* sp. A, *C. (Ab.) fuscatus* and *C. (Ab.) capixaba*).

Abaetetuba **subgen. n.**, at first examination, can be mistakenly considered to be *Callibaetoides* due to the presence of deep V-like medial emargination on labrum and third segment of labial palp subquadrangular. However, all species in *Abaetetuba* **subgen. n.** share characters and states that define the genus, especially the presence of medial concavity on labial palp segment III and bifid and trifid setae on foretarsus ventral margin. Adults of *Abaetetuba* **subgen. n.** are easily distinguished from that of *Callibaetoides* by its small costal process and three veins on hind wing, while *Callibaetoides* possess vestigial hind wing with L-shaped costal process and two veins. This subgenus is morphologically distinct from the other subgenera by, notably, the unique synapomorphy presence of short oval paraglossa (Char. 49), which is changed to subelliptical in all others subgenera of *Callibaetis*.

The three remaining groups (node C) are closely related, (GC = 91 and Relative Bremer = 83), the species belonging to these groups share: (i) decrease of ratio length of maxillary palp/length of galea-lacinia (1.360–1.370 → 1.080–1.130) (Char. 2); (ii) increase of ratio length of labial palp segment III/width of labial palp segment III (1.250 → 1.350–1.420) (Char. 4); (iii) increase of ratio length of glossa/length of paraglossa (0.810–0.870 → 0.900–0.930) (Char. 5); (iv) increase of ratio length of claw/length of

tarsi (0.620–0.630 → 0.660–0.750) (Char. 7); (v) segment I of maxillary palp with spine-like setae (fig. 2F in Cruz et al. 2014) (Char. 42); (vi) apical tuft of spine-like on outer margin of maxilla restrict on outer margin (fig. 2F in Cruz et al. 2014) (Char. 48); (vii) segment I of labial palp with spine-like setae (fig. 2H in Cruz et al. 2014) (Char. 59); (viii) row of foreclaw denticles less than the length of claw (fig. 3A in Cruz et al. 2014) (Char. 85); (ix) mid- and hind claw denticles smaller than foreclaw (Char. 88); and (x) long spines on cercus every second segment (change to every four segments in node F) (Char. 107). Additionally, all species share subelliptical labial palp segment III (changed to subconical in node F); subelliptical glossa; subtriangular paraglossa; and two rows of setae on crown of galea-lacinia.

The second group is represented by node D or *Aiso* **subgen. n.** (GC = 15 and Relative Bremer = 28). Species in this subgenus share the following: (i) row of spine-like setae on outer margin of maxilla complete and with many setae (fig. 14G in Cruz et al. 2014) (Char. 47) and (ii) anterior surface of foretarsus with spine-like setae (fig. 15A in Cruz et al. 2014) (Char. 81). Additionally, all species share labrum with large V-like medial emargination (fig. 14B in Cruz et al. 2014); dorsal surface near apex of glossa and paraglossa with small tuft of fine simple setae; and anterior surface of tibiae with spine-like setae (fig. 15A in Cruz et al. 2014). The distance between setae sockets (Char. 47) on outer margin of maxilla probably is variable (instars), but always with a complete row (without interruptions) in last instar.

The third group is represented by node F or *Cunbaporanga* **subgen. n.** (GC = 98 and Relative Bremer = 89). Species in this subgenus share the following: (i) presence of tuft of long spine-like setae on glossa dorsal surface (fig. 2G in Cruz et al. 2014) (Char. 52); (ii) subconical labial palpi segment III (fig. 2G in Cruz et al. 2014) (Char. 66); (iii) apex of segment III of labial broadly pointed (fig. 2G in Cruz et al. 2014) (Char. 67); (iv) anterior surface of forefemur with one row of simple spine-like near ventral margin (reversion) (fig. 3B in Cruz et al. 2014) (Char. 76); (v) spine-like setae ventrally on foretarsus (fig. 3A in Cruz et al. 2014) (Char. 80); (vi) long spines on every four segments on terminal filament and cerci (independent acquisition) (fig. 16H in Cruz et al. 2014) (Char. 107); and (vii) presence of constriction on stalk of turbinate portion of eyes (fig. 10B in Cruz et al. 2014) (Char. 112). This subgenus possesses three of seven synapomorphies against the common features attributed to *Callibaetis* at the beginning of this study (absence of trifid setae on forefemur and foretarsus, and terminal filament with long spines on every four segments). We formerly considered that this group could be closely related to the outgroup because of

the absence of common features, but, after analysis, absence of trifold setae was considered to be reversion and long spines on every four segments were recovered as independent acquisition (also present in *Paracloedes*). Therefore, *Cunbaporanga* **subgen. n.** can be differentiated from others subgenera notably by those tree nonunique synapomorphies.

Only in *Cunbaporanga* **subgen. n.** one subgeneric unique synapomorphy based on adult characters was recovered (Char. 112). As *Callibaetis* species cannot be placed in a subgenus without knowledge on the nymphs, due the lack of synapomorphies, the following species receive the temporary subgeneric status of *incertae sedis*: *Callibaetis camposi*, *Callibaetis distinctus*, *Callibaetis gregarius*, *Callibaetis nigrivenosus*, *Callibaetis paulinus* and *Callibaetis viviparus*. *Callibaetis skokianus* did not receive a subgeneric allocation because its nymphs were not studied.

The fourth group is represented by node G or *Callibaetis* subgenus (GC = 48 and Relative Bremer = 82). Species in this subgenus share the following: (i) decrease ratio maximal length of labrum/minimal length of labrum (1.260–1.280 → 1.250) (Char. 1); (ii) medial concavity of labrum abruptly concave (fig. 18B in Cruz *et al.* 2014) (Char. 15); (iii) simple setae near midline on labrum (fig. 18B in Cruz *et al.* 2014) (Char. 17); and (iv) posterior surface of hind femur with two rows of curved and pectinated spine-like setae (fig. 19F in Cruz *et al.* 2014) (Char. 87). Additionally, all species share a row of spine-like setae on outer margin of maxilla incomplete, with two tufts, one apical and the other basal (fig. 18F in Cruz *et al.* 2014); and long spines on every segment on terminal filament and cerci. This subgenus can be differentiated from the others subgenera by the unique synapomorphy posterior surface of hind femur with two rows of curved and pectinated spine-like setae (Char. 87).

Subgenus *Callibaetis* is the most specious and an unique group with record in all America continent, while all others are restrict to South America. The non-cladistic proposal of groups (Check 1982 and Gillies 1990) was mainly based on species allocated in this subgenus; consequentially, classical proposals were not corroborated in this study.

All species studied by Check (1982) were included in *Callibaetis* subgenus. The species studied by Gillies (1990) were included in *Callibaetis* subgen. and *Abaetetuba* subgen. n. subgenera. Gillies (1990) arranged the species in the groups based on wing pigmentation, but our study showed that the elements composing wing pigmentation (characters 124–128) possess independent acquisition and loss. Females of *C. (Cu.) calloventer* and *C. (Ca.) cruentus*, for example, possess identical forewings (Cruz *et al.* 2014) but belong to different groups. Both species were collected in marginal vegetation of large Amazonian rivers (Cruz *et al.* 2014);

another example of colour homoplasy occurs with *C. (Ab.) pollens* and *C. (Ai.) itamae*, both without pigmentation on forewing and usually collected in small- to medium-sized lakes (Cruz *et al.* 2014), but with morphologically distinct nymphs. The independent acquisition and loss of pigmentation elements may be related to landscape, which could be a stronger influence in *Callibaetis* females than in other Baetidae because of their longevity. Longevity is probably correlated with viviparity, which is a process that requires a longer lifetime to allow egg–nymph development (5–14 days) (Trost & Berner 1963; Brittain 1982). In this scenario, the conspicuous female pigmentation (body and wing) is an excellent camouflage tool (probably disruptive). This hypothesis does not exclude the possibility that pigmentation can improve the effectiveness of distinguishing females in flight, but it is unlikely that males recognize females exclusively or specifically through the colour pattern (e.g. mate size and flight trajectory [when the female moves from one ommatidia to the next] (see Brittain 1982; Brodskiy 1973; Horridge *et al.* 1982).

Taxonomy

Subgenus *Callibaetis* Eaton, 1881

Type species. *Baetis pictus* Eaton, 1871 (original designation).

Composition. *C. (Ca.) californicus*, *C. (Ca.) cruentus*, *C. (Ca.) ferrugineus*, *C. (Ca.) floridanus*, *C. (Ca.) fluctuans*, *C. (Ca.) fluminensis*, *C. (Ca.) gonzalezi*, *C. (Ca.) guttatus*, *C. (Ca.) jocosus*, *C. (Ca.) montanus*, *C. (Ca.) pallidus*, *C. (Ca.) pictus*, *C. (Ca.) punctilusus*, *C. (Ca.) pretiosus*, *C. (Ca.) radiatus*, *C. (Ca.) willineri*, *C. (Ca.) zonalis*, *C. (Ca.)* sp. D.

Diagnosis. (i) Medial concavity of labrum abrupt (fig. 4 in Nieto 2008); (ii) simple setae near midline (distal margin) on labrum (fig. 6B in Cruz *et al.* 2014); (iii) posterior surface of hind femur with two rows of curved and pectinated spine-like setae (fig. 19F in Cruz *et al.* 2014); and (iv) long spines on every segment of terminal filament and cerci (fig. 8J in Cruz *et al.* 2014). (See more in cladistic results).

Subgenus *Abaetetuba* subgen. n

Type species. *Cloe fasciata* Pictet, 1843 (original designation).

Composition. *C. (Ab.) capixaba*, *C. (Ab.) dominguezi*, *C. (Ab.) fasciatus*, *C. (Ab.) pollens*, *C. (Ab.) sellacki*, *Callibaetis (Ab.)* sp. A.

Etymology. The subgeneric epithet means ‘place with special things or people’ in the Tupi-Guarini language, an allusion to detached morphological difference of nymphs.

Diagnosis. (i) Labrum with deep V medial emargination (fig. 37a in Cruz *et al.* 2009); (ii) segment I of labial and maxillary palp without spine-like setae; (iii) subrectangular paraglossa (fig. 42a in Cruz *et al.* 2009); and (iv) apex of segment III of labial palp truncated. (See more in cladistic results).

Subgenus Aiso subgen. n

Type species. *Callibaetis itannae* Cruz, Salles & Hamada, 2014.

Composition. *C. (Ai.) itannae*, *Callibaetis (Ai.)* sp. B.

Etymology. The subgeneric epithet means ‘lovely’ in the Tupi-Guarani language, an allusion to the beauty of the nymphs and females.

Diagnosis. (i) Labrum with V medial emargination; (ii) row of spine-like setae on outer margin of maxilla complete and with many setae (fig. 14G in Cruz *et al.* 2014). (See more in cladistic results).

Subgenus Cunhaporanga subgen. n

Type species. *Callibaetis calloventer* Cruz, Salles & Hamada, 2014.

Composition. *C. (Cu.) calloventer*, *C. (Cu.) gelidus*, *C. (Cu.) nigracyclus*, *Callibaetis (Cu.)* sp. C.

Etymology. The subgeneric epithet means ‘the most beautiful woman’ in the Tupi-Guarani language, an allusion to the beauty of the females.

Diagnosis. (i) Labrum with V medial emargination; (ii) subconical labial palpi segment III (fig. 22G in Cruz *et al.* 2014); (iii) anterior surface of forefemur without bifid and trifid setae (fig. 23B in Cruz *et al.* 2014); and (iv) long spines on every four segments on terminal filament and on cerci (figs 4I and 4J in Cruz *et al.* 2014). (See more in cladistic results).

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Supporting Information

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

Appendix S1. Matrix ready to run in TNT.