

Phylogenetic analyses of *Cloeodes* Traver and related genera (Ephemeroptera: Baetidae)

FREDERICO F. SALLES^{1,2}, JEAN-LUC GATTOLLIAT² and MICHEL SARTORI²

¹Laboratório de Sistemática e Ecologia de Insetos, Depto de Ciências Agrárias e Biológicas, Universidade Federal do Espírito Santo, São Mateus, Brazil and ²Museum of Zoology, Palais de Rumine, Lausanne, Switzerland

Abstract. *Cloeodes* Traver is atypical among Baetidae (Ephemeroptera) because it seems to possess a unique Pan-tropical distribution. Thirty-nine species have been described to date, 26 from the Neotropics, four from the Southern Nearctic, seven from the Afrotropics and two from the Oriental region. Several genera have been considered related to *Cloeodes* during the last decades, of which the following remain valid: *Crassabwa* Lugo-Ortiz & McCafferty, *Dabulamanzia* Lugo-Ortiz & McCafferty (both Afrotropical), *Bungona* Harker (Australasian) and *Chopralla* Waltz & McCafferty (Oriental). Despite their supposed relationship, a phylogenetic analysis between all of these genera has never been performed. In the present paper, based on an extensive analysis of all genera that have been considered related to *Cloeodes*, a phylogenetic analysis using morphological characters (continuous and discrete) was performed in order to address the monophyly of the genus *Cloeodes* within the *Cloeodes* complex of genera. According to our results, *Cloeodes* and the complex are paraphyletic. Based on this, *Cloeodes* is restricted to the New World, *Potamocloeon* is revalidated to include most representatives of Afrotropical *Cloeodes* and is divided into two subgenera: *Potamocloeon* (Africa) and the new *Aquaediva* (Madagascar). In addition, the concept of *Bungona* is expanded to include Australasian and Oriental taxa – namely the subgenera *Chopralla* and the revalidated *Centroptella* – and finally the new genus *Crassolus* is established to include *C. inzingae* **comb.n.** from Africa.

This published work has been registered in ZooBank, <http://zoobank.org/urn:lsid:zoobank.org:pub:C416090E-C43D-481A-9A3D-F3B1EEE41176>.

Introduction

The genus *Cloeodes* Traver (Ephemeroptera: Baetidae) was originally established to encompass three species from Puerto Rico (Traver, 1938). During the following 50 years, no new data were provided, except for the transferral of one of these species to the genus *Paracloeodes* Day (Day, 1955). At the end of the 1980s Waltz & McCafferty (1987a, 1987b) revised the genus and demonstrated that it was much more diverse and widespread than originally conceived. Besides the description of five new species, two from the Neotropics and three

from the Nearctic Region, Waltz & McCafferty (1987a, 1987b) transferred five previously described species to *Cloeodes*, two of them from the Oriental Region (including the type-species of *Centroptella* Braasch & Soldán) and three from the Neotropics (including the type-species of the monotypic genus *Notobaetis* Morihara & Edmunds). Two new genera related to *Cloeodes* were also described by these authors: the monotypic *Bernerius* Waltz & McCafferty from the Neotropics; and *Chopralla* Waltz & McCafferty, a genus erected to include three Oriental species originally described in *Centroptella* which had not been transferred to *Cloeodes*. In the same year, Soldán *et al.* (1987) described two new species of *Centroptella* from Vietnam; these species were not included in Waltz & McCafferty's (1987a) paper and formally remained in *Centroptella*, but clearly fit the concept of *Chopralla*.

Correspondence: Frederico F. Salles, Laboratório de Sistemática e Ecologia de Insetos, Depto de Ciências Agrárias e Biológicas, Centro Universitário Norte do Espírito Santo, Universidade Federal do Espírito Santo (CEUNES/UFES), BR-101 Norte, Km 60, Litorâneo. 29.932-540, São Mateus, Espírito Santo, Brazil. E-mail: ffsalles@gmail.com

During the 1990s and beginning of the 2000s, *Cloeodes* was also reported from continental Africa (Waltz & McCafferty, 1994), Madagascar (Lugo-Ortiz *et al.*, 1999; Gattolliat, 2001) and Australia (Lugo-Ortiz & McCafferty, 1998a). Regarding the presence of *Cloeodes* in Australia, however, Suter & Pearson (2001) considered the two species described by Lugo-Ortiz & McCafferty (1998a) as being conspecific and junior synonyms of *Bungona narilla* Harker. In the meantime, four new genera possibly related to *Cloeodes* were described from the Afrotropical Region: *Crassabwa* Lugo-Ortiz & McCafferty, *Dabulamanzia* Lugo-Ortiz & McCafferty, *Maliqua* Lugo-Ortiz & McCafferty and *Nesydemius* Lugo-Ortiz & McCafferty (Lugo-Ortiz & McCafferty, 1996a, 1996b, 1997, 1998c). In a preliminary outline of the mayfly fauna of Fiji Islands, Flowers (1990) reported and illustrated an undetermined genus of Baetidae apparently related to *Cloeodes* (New genus B). However, except for the presence of setae at the base of tibia, none of the remaining characters presented by Flowers (such as shape of right protheca, shape of labial palp and paraglossa, and tarsal claws) resemble those attributed to *Cloeodes*.

In the last 10 years, the number of papers dealing with *Cloeodes* and related genera increased significantly. Besides descriptions of various life stages of species of *Cloeodes* from the Oriental (Tong *et al.*, 2003), Afrotropical (Jacobus *et al.*, 2006) and Neotropical Regions (Gonçalves *et al.*, 2010), some important new combinations and synonymies have been proposed. For example, *Nesydemius* was considered a junior synonym of *Dabulamanzia* (Gattolliat & Jacobus, 2005), whereas *Maliqua* and *Bernerius* were considered junior synonyms of *Cloeodes* (Jacobus *et al.*, 2006; Nieto & Richard, 2008). One of the species of *Cloeodes* described by Lugo-Ortiz & McCafferty (1998a) from Australia was revalidated and transferred to *Bungona* Harker (Webb & Suter, 2010). Finally, the number of species of *Cloeodes* doubled in the Neotropics during this period, with more than ten species described from Argentina, Brazil and Uruguay (Salles & Lugo-Ortiz, 2003; Salles *et al.*, 2004; Nieto & Richard, 2008; Massariol & Salles, 2011; Nieto & Emmerich, 2011; Massariol *et al.*, 2013).

To date, only four genera historically considered as related to *Cloeodes* remain valid. These include *Crassabwa* and *Dabulamanzia* from the Afrotropical Region (with four and six species, respectively), *Bungona* from the Australian Region (two species), and the Oriental *Chopralla* (four species in *Chopralla* and two species in *Centropella*). *Cloeodes* is the most species-rich genus within the complex, with 39 species described from the Neotropical (26 spp.), Afrotropics (7 spp.), Nearctic (4 spp.) and Oriental (2 spp.) regions.

Despite their supposed relationship, a quantitative phylogenetic analysis among these genera has never been undertaken. A possible relationship between the Oriental genus *Centropella* and the Neotropical genus *Notobaetis* Morihara & Edmunds, now synonyms of *Cloeodes*, has been proposed by Müller-Liebenau (1983) and Waltz & McCafferty (1987b). Lugo-Ortiz & McCafferty (1998c) considered the three Afrotropical genera *Crassabwa*, *Dabulamanzia* and *Nesydemius* as related to *Cloeodes* in a monophyletic clade within the *Cloeodes* complex or Afrotropical *Cloeodes* complex.

This complex has never been formally described and does not encompass the genus *Maliqua*. Moreover, it is not monophyletic based on molecular evidence (Monaghan *et al.*, 2005; Gattolliat *et al.*, 2008). Nieto & Richard (2008) performed a cladistic analysis on South American *Cloeodes*, but it was in order to test the validity of *Bernerius* so ingroup sampling was relatively limited. In a cladistic analysis of primarily South American Baetidae in South America, Nieto (2010) recovered *Cloeodes* as the sister-group of *Dabulamanzia*, both being closely related to a clade comprising the Neotropical genera *Aturbina* Lugo-Ortiz & McCafferty, *Zelus* Lugo-Ortiz & McCafferty and *Tomedontus* Lugo-Ortiz & McCafferty. In all of the cases related above, the most striking character (and potential synapomorphy) associated with the *Cloeodes* complex is the presence of an arc of setae at the base of tibiae and, in the strict case of *Cloeodes*, the presence of a row of setae on some abdominal sterna. The subproximal arc of setae on tibiae, however, may also be present in other members of the family such as *Cloeon* Leach (Gattolliat & Rabeantoandro, 2002) and *Securiops* Jacobus, McCafferty & Gattolliat (Jacobus *et al.*, 2006).

The most recent papers dealing with the classification of Baetidae, with consequent implications in the relationship of *Cloeodes* and other genera, are those recently published by Kluge (2011, 2012) and Kluge & Novikova (2011). According to these authors, *Cloeodes*, *Bungona*, *Centropella* and *Chopralla* form a group within Baetovectata, one of the major groups of Anteropatellata. The position of *Dabulamanzia* and *Crassabwa* is not clear in these papers, but based on the absence of patella-tibial suture and Afrotropical distribution, they should belong to Protopatellata.

Considering the aspects mentioned above, there are some major unresolved questions concerning this group. Is the present concept of *Cloeodes* monophyletic and how are the species of *Cloeodes* related? Do the species from each zoogeographic realm belong to monophyletic lineages? Moreover, do the aforementioned genera (i.e. *Bungona*, *Chopralla*, *Cloeodes*, *Crassabwa* and *Dabulamanzia*) form a monophyletic group, the *Cloeodes* complex *sensu* Waltz & McCafferty (1987a) and Lugo-Ortiz & McCafferty (1998c)? The main purpose of this paper, therefore, is to investigate relationships within *Cloeodes* and among genera in the *Cloeodes* complex based on morphological characters. A phylogeny of the complex is presented, along with a revised classification of the group, including some new taxa.

Material and methods

Taxon sampling and deposition

A matrix of 45 taxa and 132 characters (Tables S1 and S2, Appendix S3) was constructed using the software Mesquite (Maddison & Maddison, 2011). Whenever possible we included the type-species of the studied genera, especially in the case of the ingroups (defined below). Species known at all stages were preferentially included instead of those incompletely described. A detailed list of the material examined, including institutions

where the material is deposited, stages examined, origin and how the material was studied (based on direct examination of the specimens, on photographs or descriptions) is presented in Table S1.

In order to test the monophyly of *Cloeodes* we selected 18 species:

- Neotropical *Cloeodes*: we selected nine out of the 26 species reported from that region. The type-species of *Cloeodes*, *C. maculipes* Traver, the type-species of the genus *Noto-baetis*, *C. penai* Morihara & McCafferty, and seven additional species (two from the Caribbean islands plus five from South America, three of them being undescribed – *Cloeodes* sp. 1, sp. 2 and sp. 3). These species were chosen based on availability of material for direct examination, including nymphs and associated adults, and/or because they represent possible distinct lineages within Neotropical *Cloeodes*. None of the four Nearctic species of *Cloeodes* have been included for the same reasons: they were described based solely on nymphs and seem to be closely related to the three selected Caribbean species. *Cloeodes incus* Waltz & McCafferty, the type species of *Bernerius*, was not included in the analysis because we did not have access to the holotype or any other specimens.
- Afrotropical *Cloeodes*: six of the seven species recognized from this area (two from Africa and four from Madagascar); *C. pusillus* (Navás) was excluded as this species is only known at the imaginal stage;
- Oriental *Cloeodes*: the two species of *Cloeodes* from Asia (which includes the type-species of *Centroptella*), plus an undescribed species from Indonesia (*Cloeodes* sp. 4).

In order to test the monophyly of the *Cloeodes* complex we selected an additional 12 species belonging to genera that have been considered related to *Cloeodes* in previous studies.

- *Chopralla*: three of the four species attributed to this genus [including the type-species *C. ceylonensis* (Müller-Liebenau)], as well as an undescribed species from Indonesia (*Chopralla* sp. 1) and one of the two species described by Soldán *et al.* (1987) in *Centroptella*.
- *Bungona*: one of the two species (*B. narilla* the type species of the genus), plus an undescribed species from Papua New Guinea (deposited at MZL), apparently related to this genus (*aff. Bungona* sp. 1).
- *Crassabwa*: one of the four species [*C. flava* (Crass) is not only the type-species it is also the only species of the genus described for both nymphal and imaginal stages].
- *Dabulamanzia*: four of the six species (two from continental Africa; two from Madagascar).

Given our limited knowledge of higher-level generic relationships of Baetidae, additional taxa belonging to different potentially related lineages were also selected. In this case we chose 15 species of Baetidae matching at least one of the following criteria: (A) the presence of a sub proximal row of setae at the base of tibiae; (B) South American genera that have been considered related to *Cloeodes* previously (i.e.

Nieto, 2010; Kluge & Novikova, 2011); (C) representatives of the distinct lineages recently proposed by Kluge (2011, 2012) and Kluge & Novikova (2011). These included: *Afrop-tilum sudafricanum* (Lestage): criterion C (Protopatellata); *Aturbina georgei* Lugo-Ortiz & McCafferty: criteria B and C [Anteropatellata: Baetovectata: Aturbina/g(1)]; *Baetis monikae* Kopelke: criterion C (Anteropatellata: Baetovectata: Baetungulata); *Bugilliesia margaretae* Gattolliat & Barber-James: criterion C (Protopatellata: Rhithrocloeon/fg1); *Centroptilum luteolum* (Müller): criteria A and C (Anteropatellata: Centroptilum g/1); *Cheleocloeon yolandae* Wuillot & Gillies: criteria A and C [Anteropatellata: Cheleocloeon/g(1)]; *Cloeon dipterum* (Linnaeus): criteria A and C (Anteropatellata: Cloeon/fg1: Cloeon/fg2); *Procloeon pennulatum* (Eaton) and two undescribed species related to *Procloeon* Bengtsson from Indonesia (*Procloeon* sp. 1 and sp. 2): criteria A and C (Anteropatellata: Cloeon/fg1: Procloeon/g1); *Susua niandanensis* (Wuillot) and two undescribed species related to *Susua* Lugo-Ortiz & McCafferty from Africa (*aff. Susua* sp. 1 and sp. 2): criterion A; and *Waltzoyphius fasciatus* McCafferty & Lugo-Ortiz: criteria B and C [Anteropatellata: Baetovectata: Waltzoyphius/g(1)].

Following recent analyses (Nieto & Richard, 2008; Nieto, 2010), we decided to root the tree with *Siphlaenigma janae* Penniket (Siphlaenigmatidae). Despite the results of recent analyses based on molecular and morphological data (Ogden *et al.*, 2009), this family has been historically considered as the sister group of Baetidae (Staniczek, 1997; Kluge, 2004) and the morphological traits found in both families allow a more plausible codification of characters.

The material examined was obtained from the following institutions: Albany Museum, Grahamstown (AMGS), South Africa; Coleção Zoológica Norte Capixaba, Universidade Federal do Espírito Santo (CZNC), São Mateus, Brazil; Musée Cantonal de Zoologie (MZL), Lausanne, Switzerland; Cornell University Insect Collection, Cornell University (CUIC), Ithaca, USA; The Bavarian State Collection of Zoology (ZSM), Munich, Germany; Institute of Entomology, Biology Centre of the Academy of Sciences of the Czech Republic (IECR), České Budějovice, Czech Republic; Collection of Aquatic Insects and Soil Animals, Department of Entomology at South China Agricultural University (SCAU), Guangzhou, China.

Morphological terminology, characters and states

Characters were scored from the external morphology of nymphs and adults, for a total of 132 continuous or discrete characters. For nymphs, 20 continuous and 91 discrete characters; for adults, 11 continuous and 10 discrete characters. A complete list of the characters, their definitions and character states is given in Appendix S1.

The morphological terminology used in this paper follows Hubbard (1995) for calculations of lengths and widths. In the case of the morphological features we follow Hubbard (1995) and Waltz & McCafferty (1987a, 1987b) for terms commonly found in mayfly literature, such as prostheca, gills, caudal filaments or subtending bristle, for example. Some terms recently

proposed (Kluge, 2011, 2012; Kluge & Novikova, 2011) for structures occasionally described by previous workers (e.g. gonovectes) were also adopted. Measurements and ratios used in some characters are illustrated to permit repeatability (Figure S11, Appendix S4). Because TNT does not accept continuous values above 60, angles (characters 2 and 13) and the number of setae on femora (characters 14 and 16) were (respectively) converted into radians and divided by ten in the matrix.

Cladistic analyses

All characters were treated as nonadditive except for continuous characters (chars. 0–30). For discrete characters, in most of the cases, contingent coding was preferred instead of multi-state. For taxa that lack a particular structure, transformational character states are coded as inapplicable, with a ? (see Forey & Kitching, 2000).

The matrix built-in Mesquite software was exported to TNT (Goloboff *et al.*, 2008), where searches were conducted under implied weights ($k=5$), and using the traditional search command (under Analyze). Searches were conducted with 10 000 replications and saving 100 optimal trees per replication. Frequency difference (GC; Goloboff *et al.*, 2003), using 300 replications of symmetric jack-knifing, was also calculated as a measure of group support.

Results

The cladistic analysis resulted in a single tree (Figs 1, 2), with an adjusted homoplasy of 37.40 and a total fit of 84.60. The tree with respective synapomorphies is shown in Figs 1 and 2, group supports are shown in Fig. 2, and apomorphies are depicted in Appendix S2. Of the 132 characters, 10 were uninformative (see Appendix S1) and were excluded from the analysis.

Concerning the *Cloeodes* complex, all genera that have been historically considered as related to *Cloeodes* were recovered in node 59 (Figs 1, 2). This clade has a low GC value, 10, and is characterized by nine synapomorphies (Appendix S2). In addition to being poorly supported, two other genera, supposedly not related to *Cloeodes*, were recovered as belonging to this clade, *Cheleocloeon* Wuillot & Gillies and *Susua*.

In the case of the genus *Cloeodes*, a single clade comprising the species of *Cloeodes* from Africa, Madagascar, Asia and Central and South America, *Chopralla*, *Bungona*, and the undescribed species from Papua New Guinea, was recovered in the analysis (node 67). This clade has a GC value of 43, is characterized by nine synapomorphies (Appendix S2) and is composed in our analysis of four main groups: (i) *Cloeodes dentatus* (Kimmins) plus Malagasy *Cloeodes* (node 66) – a well-supported clade (GC 65, 11 synapomorphies) with the African species *Cloeodes dentatus* sister to the Malagasy species (GC 71, six synapomorphies). (ii) *Cloeodes inzingae* (Crass) – the African species *C. inzingae*, defined by six autapomorphies, is the sister group of the clade comprising the Neotropical *Cloeodes* plus Australasian and Oriental genera. (iii) Neotropical *Cloeodes*

(node 82) – this clade, including the type-species of *Cloeodes* and all other species from the Neotropics, has a GC value of 46 and is characterized by 12 synapomorphies (Appendix S2). (iv) Australasian and Oriental taxa (node 71) – this clade comprises the undescribed species from Papua New Guinea (*aff. Bungona* sp. 1), *Bungona narilla*, Oriental *Cloeodes* and *Chopralla* (GC 80, six synapomorphies). The undescribed species from Papua New Guinea is recovered as the sister group of a clade leading to *Bungona narilla* plus Oriental taxa (GC 78, seven synapomorphies – Appendix S2). The sister relationship between the Oriental taxa, *Chopralla* plus Oriental *Cloeodes* (node 74), is supported by eight synapomorphies, GC 64.

Discussion

The presence of *Cheleocloeon* and *Susua* in node 59 renders the *Cloeodes* complex paraphyletic as conceived by Lugo-Ortiz & McCafferty (1998c). Inclusion of these two genera in the *Cloeodes* complex requires broadening the concept of this complex, which is problematic especially in regard to *Cheleocloeon*. Monaghan *et al.* (2005) and Gattolliat *et al.* (2008) suggested that *Cheleocloeon* was related to *Crassabwa* as well as two other Afrotropical genera that were not included in our analysis, *Rheoptilum* Gattolliat and *Acanthiops* Waltz & McCafferty. The genus *Susua*, in turn, was described by Lugo-Ortiz & McCafferty (1998b) in the *Centroptiloides* complex, a paraphyletic group according to Monaghan *et al.* (2005) and Gattolliat *et al.* (2008). In our analysis *Susua niandanensis* is closely related to *Crassabwa flava* (node 62) as well as two undescribed species from Africa (node 64). Given the low GC value for the clade leading to all genera historically included in the *Cloeodes* complex, we consider that the *Cloeodes* complex (*sensu* Lugo-Ortiz & McCafferty, 1998c) is not valid. Our concept of this complex, excludes the abovementioned genera and thus only contains *Cloeodes*, *Crassolus* **gen.n.**, *Bungona* and *Potamocloeon* Gillies (i.e. node 67), which agrees in part, with *Cloeodes*/g1 of Kluge & Novikova (2011).

The genus *Dabulamanzia* was recovered as paraphyletic according to our analysis (Figs 1–3). Two distinct clades were found, one from continental Africa (node 60) and one from Madagascar (node 61), the latter sister to a clade comprising *Cheleocloeon*, *Susua* and *Crassabwa*. Both clades (60 and 61) are well supported, with GC values above 75, and are characterized by 11 and 8 synapomorphies, respectively (Appendix S2). However, given the low supports found for nodes 59, 58 and 57, we refrain from establishing a new status for the Malagasy species at this moment.

Our analysis clearly indicates that the current concept of the genus *Cloeodes* is not monophyletic. The Oriental species of *Cloeodes* (node 73) are nested within a clade comprising *Bungona*, *Centroptella* and *Chopralla*, rather than being placed with the Neotropical members of the genus (node 82), which includes the type-species, *Cloeodes maculipes*. Different alternatives can be proposed in order to accommodate the taxonomic implications of our findings. A more conservative approach would lead us to consider all taxa from node 67 as belonging to a single

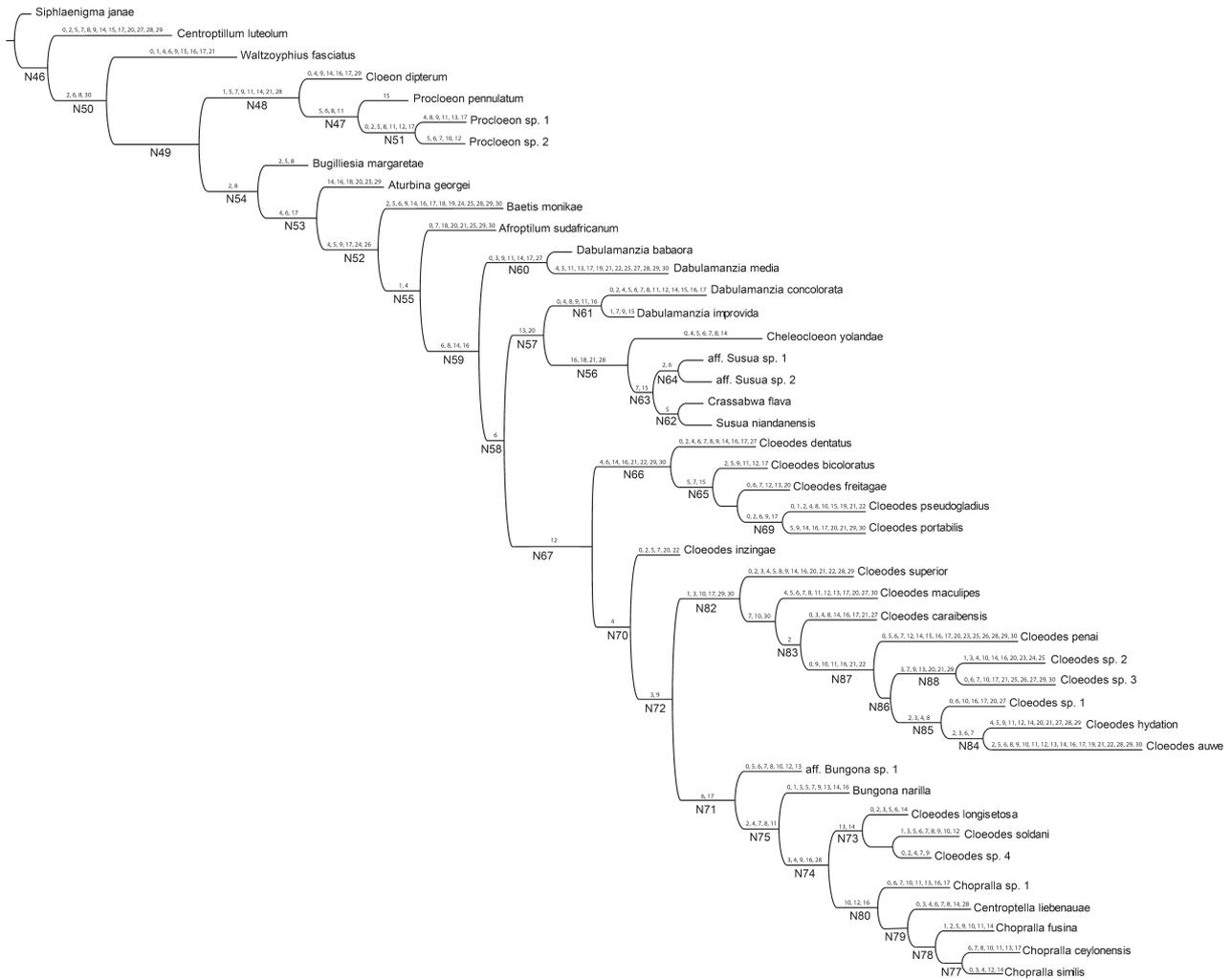


Fig. 1. Tree with changes on continuous characters (numbers above branches are character numbers, see Appendix S1/numbers below branches preceded by N are node numbers, see Appendix S2).

genus, *Cloeodes*, whereas a less conservative approach would lead to the division of this major clade in at least seven genera.

Given the combination of synapomorphies and group support found for each of these clades, along with their distribution in distinct realms, we decided to restrict the concept of the genus *Cloeodes* to the New World species only (node 82, Fig. 3). New generic status, therefore, is assigned below to two clades, one comprising *C. dentatus* and Malagasy *Cloeodes* (node 66) as *Potamocloeon* **stat.n.**, and the singleton *C. inzingae* in *Crasululus* **gen.n.** *Bungona* remains a valid genus but it is more widespread than originally conceived. Based on the morphological similarities found among the representatives sampled here (node 75), the genus is divided into three subgenera, as follows. *Bungona* (*Bungona*) is restricted to the Australasian species *B. narilla* and *B. illiesi*. The status of *Bungona* (*Centropitella*) is revised as a subgenus in order to encompass the Oriental species transferred to *Cloeodes* by Waltz & McCafferty (1987a), the type-species of *Centropitella*, *Cloeodes longisetosus* (Braasch &

Soldán), plus *C. soldani* (Müller-Liebenau) and the undescribed species from Indonesia (node 73). *Bungona* (*Chopralla*), **stat.n.**, is redefined to include all of the species formerly placed in the genus *Chopralla*, the two species described by Soldán *et al.* (1987) not formally transferred to that genus, plus an undescribed species from Indonesia (node 80). ‘Genus No. 2 sp. 1’, described and illustrated by Müller-Liebenau (1984) from West Malaysia, also belongs to *Chopralla*, and based on the shape of the right prostheca, is closely related to *B. (Chopralla) liebenauae* (Soldán, Braasch & Luu). Based on this scenario, a new genus should also be erected in order to include the undescribed species from Papua New Guinea. However, we refrain from doing this presently until we have a more complete knowledge of this taxon, including additional nymphs and ideally the male adult.

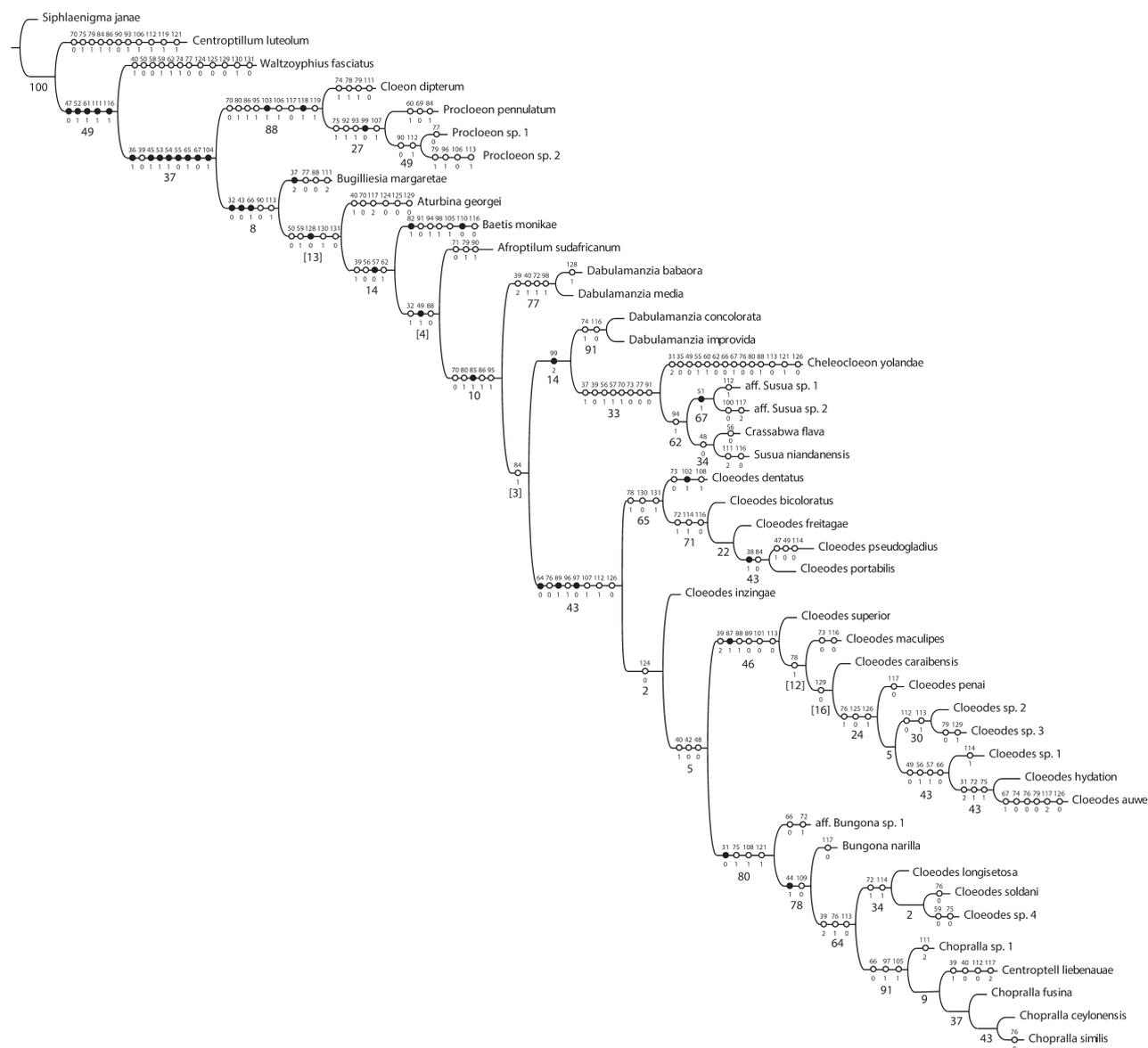


Fig. 2. Tree (same shown in Fig. 1) showing changes on discrete characters. Numbers above and below circles are character and state numbers, respectively, (see Table S1). Numbers below state numbers indicate group support. Black circles indicate unique apomorphies, open circles represent nonunique changes on the tree, either forward or reverse. Brackets indicate negative values.

Evolution of selected characters

A row or arc of conspicuous setae at the base of tibiae, or sub proximal arc of setae, was the main character used by Lugo-Ortiz & McCafferty (1996a, 1996b, 1998c) to hypothesize the relationships between *Cloeodes* and different taxa, such as *Dabulamanzia*, *Nesydemius* (junior synonym of the latter), *Crassabwa* and *Maliqia* (junior synonym of *Cloeodes*). This character, however, is not restricted to these genera and is more complex than the simple attribution of its presence or absence can reveal. It involved several characters in our analysis, such as: presence (char. 86), distance between the insertions of setae

(char. 87), extension of this row on the anterior surface of tibia (char. 10) and the angle formed by this row on posterior surface in relation to the outer margin of tibia (char. 13). Its presence, for example, evolved independently three times throughout the tree, on node 48 (*Cloeon* + *Procloeon*), node 59 and the terminal containing *Centroptillum luteolum*. Therefore, it cannot be used to define the complex *sensu* Lugo-Ortiz & McCafferty (1998c). Although this row of setae is long in *Potamocloeon* (node 66), *Crassolus inzingae* and in *Bungona* (node 71), in *Cloeodes* (node 82) the extension of this row decreases (from 0.32–0.64 to 0.24) and the insertions of the setae are contiguous. Both are synapomorphic character states for the genus and, to some

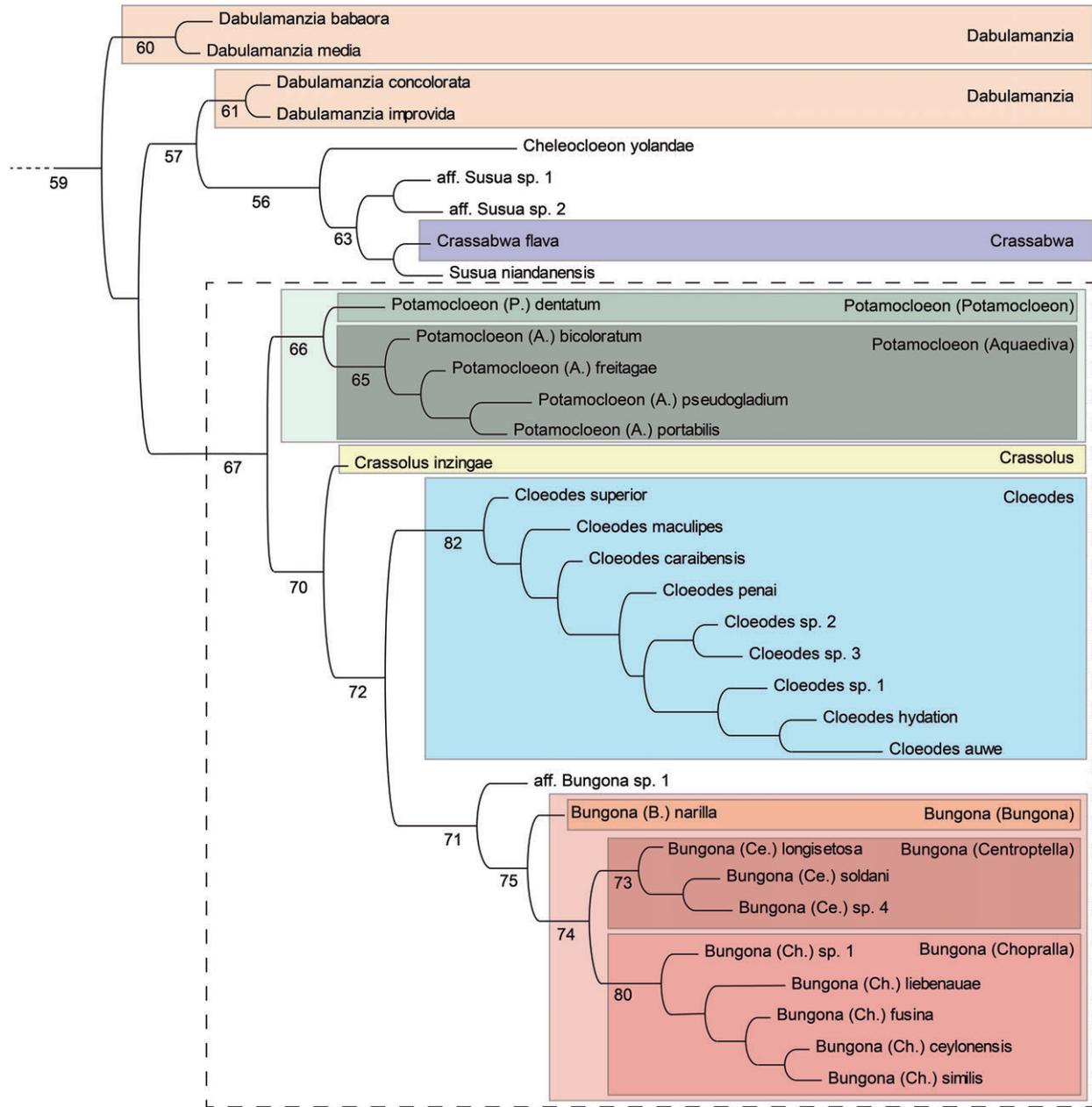


Fig. 3. Partial tree from Figs 1 and 2 showing only node 59 showing classification applied here. Taxa historically attributed to *Cloeodes* complex of genera are highlighted, genera belonging to the current concept of the *Cloeodes* complex are inside the dashed area. Numbers below branches are node numbers.

extent, might be related to the restoration of the patella-tibial suture in this clade (see next paragraph). The relative angle on posterior surface of tibia is also an important feature concerning this row of setae, because a decrease of this angle on node 73 (from 1.03–1.04 to 0.57) is one of the few synapomorphies defining the subgenus *Centroptella*.

The evolution of character 88 is also relevant because it has implications for the systematics of the family. According to Kluge (Kluge, 2011, 2012; Kluge & Novikova, 2011)

the presence (or restoration) of a patella-tibial suture on forelegs of nymphs and female adults is the synapomorphy of Anteropatellata. Based on our analysis, the presence of this suture is ancestral and it has disappeared twice, once in *Bugilliesia margaretae* and once in node 55. Nevertheless, in this node a reversal has occurred twice with the suture present in *Cheleocloeon yolandae* and in *Cloeodes* (node 82). Anteropatellata, therefore, is polyphyletic according to our results. Regarding the location of this suture on the mid and

hind legs (char. 89), the plesiomorphic condition is origin of the suture at the base of tibiae. The position of this suture in the middle of the tibiae found on node 67, the *Cloeodes* complex, is one of the synapomorphies of the clade. A single reversal, however, occurred in *Cloeodes* where the suture is located at the base of tibiae.

Taxonomic account

Cloeodes complex

Diagnosis. Apex of maxillary palp slightly narrowing between 1/2 and apical 1/3 (Fig. 5A–C); row of long conspicuous setae at the base of tibiae present (Figs 6A–E, F, G, I, 10A); conspicuous long setae on tarsi, arranged in row (Fig. 6F, G, I); Denticles on tarsal claws absent (except in *Bungona* (*Chopralla*)] (Figs 6F–I, 10C, D); row of conspicuous long setae on abdominal sterna present (Fig. 10E–G); shape of apex of gill III or IV pointed (except in a few species of *Cloeodes* s.s.) (Fig. 7A, C). There are no adult characters defining the complex.

Genera included. *Cloeodes* Traver, *Bungona* Harker, *Bungona* (*Centroptella*) Braasch & Soldán, *Bungona* (*Chopralla*) Waltz & McCafferty, *Crassolus* **gen.n.**, *Potamocloeon* Gillies, **stat.n.**, and *Potamocloeon* (*Aquaediva*) **subgen.n.**

Distribution. Neotropical, Nearctic, Afrotropical, Oriental and Australasian regions.

Comments. Based on results of analyses by Monaghan *et al.* (2005) and Gattolliat *et al.* (2008), *Dabulamanzia* and *Crassabwa* are more related to other Afrotropical genera than to *Cloeodes* s.l. The row or arc of setae at the base of tibiae is plesiomorphic and can no longer be used to define the members of the *Cloeodes* complex. The presence of a row of conspicuous long setae on abdominal sterna, on the other hand, is one of its main striking synapomorphies (although it has also evolved independently in *Procloeon*). When Waltz & McCafferty (1987a) redefined the genus *Cloeodes*, they overlooked the presence of this row on the species of *Chopralla* (in this group, however, they are present on segments IV or V–VI, instead of on II–VI).

Cloeodes Traver

Diagnosis. *Nymph.* Prosthema of right mandible bifid, i.e. slender and with a thin medial process (Fig. 4B); long or spine-like setae absent between prosthema and mola of both mandibles (Fig. 4B, I, J); distal margin of labial palp rounded (Fig. 5D) to straight (Fig. 5E); hindwing pad absent (Fig. 6K) or present (Fig. 6L); setae on outer margin of femora short (Fig. 6F); row of conspicuous long setae on anterior surface of fore tibia extending for a short distance (Fig. 6A, F); insertions of conspicuous long setae on fore tibia contiguous (Fig. 6A, F); patella-tibial suture present on fore tibia (Fig. 6A,

F); patella-tibial suture located at base of tibiae (Fig. 6A, F); row of conspicuous long setae present on abdominal sterna II–VI (Fig. 10E–G). *Adult.* Free marginal intercalary veins double on male forewing (Fig. 8B), double or single in females (Fig. 8A); hindwing, when present, with costal projection broad at base, hooked and located on basal 1/3 (except in *C. penai*, present in the middle of hindwing) (Fig. 8C); marginal intercalary veins of forewing generally double (Fig. 8B), single in female of some species (Fig. 8A) Gonovectes (Figs. 9A, B): free and deeply situated on sternum IX; forceps segment I with outer and inner margins parallel (Fig. 9A); forceps segment III short and almost as wide as long (Fig. 9A).

Type species. *Cloeodes maculipes* Traver, 1938: 33.

Species included. *C. maculipes* Traver; *C. anduzei* (Traver); *C. auwe* Salles & Batista; *C. ayмара* (Traver.); *C. aymore* Massariol & Salles; *C. barituensis* Nieto & Richard; *C. binocularis* (Needham & Murphy); *C. carabensis* Hofmann & Thomas; *C. consignatus* Traver; *C. dialutoi* Nieto & Emmerich; *C. espinillo* Nieto & Richard; *C. excogitatus* Waltz & McCafferty; *C. guenoa* Nieto & Emmerich; *C. hydration* McCafferty & Lugo-Ortiz; *C. incus* (Waltz & McCafferty); *C. inferior* Kluge; *C. irvingi* Waltz & McCafferty; *C. itajara* Massariol & Salles; *C. jaragua* Salles & Lugo-Ortiz; *C. macrolamellus* Waltz & McCafferty; *C. maracatu* Lima, Pinheiro & Massariol; *C. opacus* Nieto & Richard; *C. penai* (Moriyama & Edmunds); *C. peninsulus* Waltz & McCafferty; *C. redactus* Waltz & McCafferty; *C. spaceki* Queiroz, Oliveira & Salles; *C. superior* Kluge; *C. turbinops* (Needham & Murphy); *C. vaimaca* Nieto & Emmerich; and *C. waltzi* Wiersema & Baumgardner.

Distribution. South America to southern North America.

Comments. This is the most species-rich genus within the complex, with 30 species described so far (four from southwestern North America, 26 from South and Central America), and also one of the most species-rich genera of mayflies in the Neotropics. In fact, at least ten undescribed species of this clade have been recently collected from South America (FFS, unpublished data). Consequently, this is also the clade with most variation in character states among the complex (especially characters such as hindwings present or absent; double or simple marginal intercalary veins, sometimes double in males and simple in females; nymphs with short to long projections of apex of femora; body length ranging from less than 4 mm to more than 12 mm). Critical, at this point, is the monophyletic condition of this group and the fact that *C. incus*, although excluded from our analysis, possesses most of the synapomorphies attributed to the genus *Cloeodes*.

Bungona Harker

Diagnosis. Selected autapomorphies: *Nymph.* Antenna short (little longer than head capsule); right prosthema with thin medial process (Fig. 4C–E); spine-like setae between prosthema and

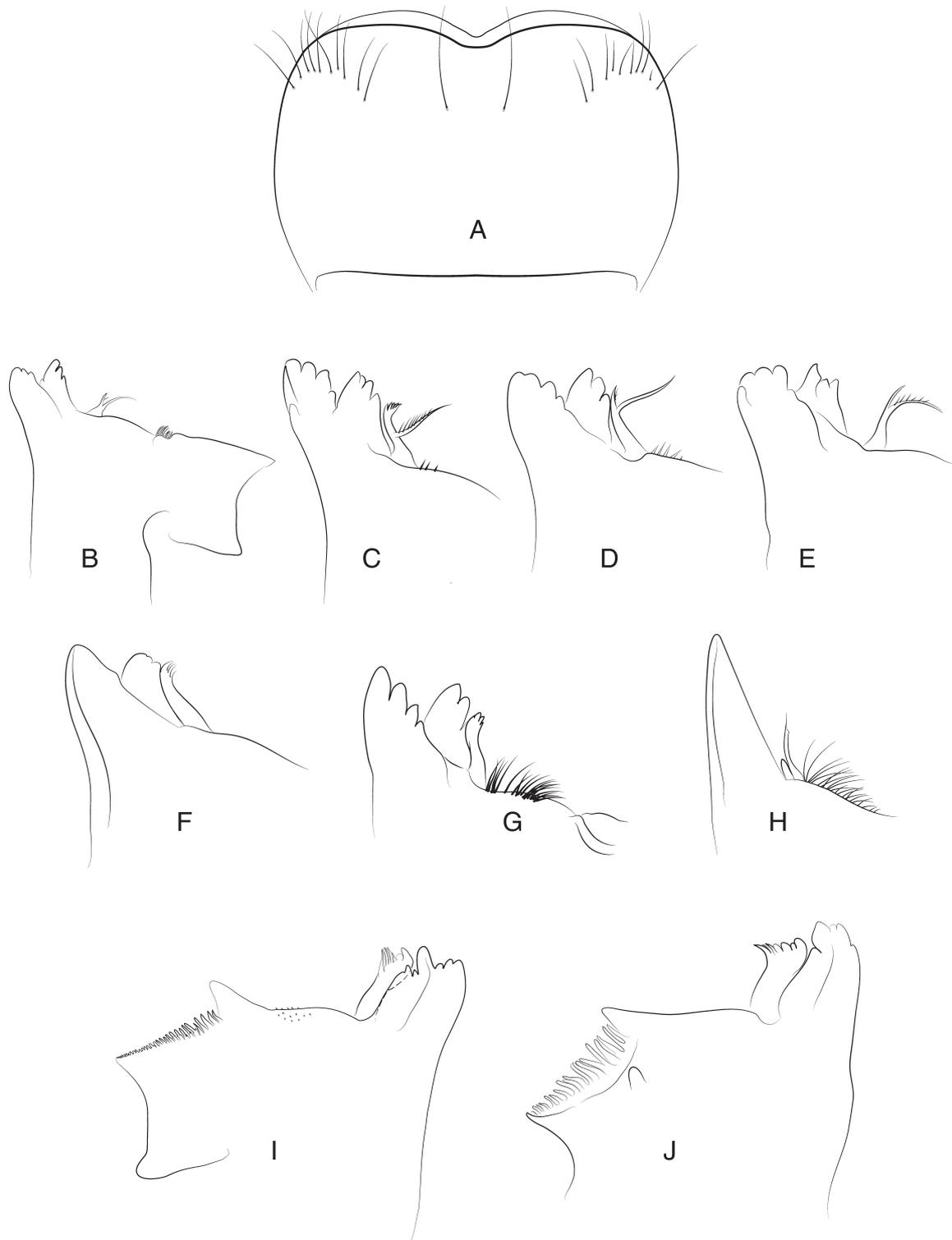


Fig. 4. Mouthparts of selected species of Baetidae studied in the current analysis (A, labrum; B–H, right mandible; I, J, left mandible): (A) *Potamocloeon (Aquaediva) freitagae*; (B) *Cloeodes maculipes*; (C) *Bungona (Bungona) narilla*; (D) *Bungona (Centroptella) soldani*; (E) *Bungona (Chopralla) ceylonensis*; (F) *Crassolus inzingae*; (G) *Potamocloeon (Potamocloeon) dentatum*; (H) *Potamocloeon (Aquaediva) pseudogladium*; (I) *Cloeodes maculipes*; (J) *Cloeodes auwe*.

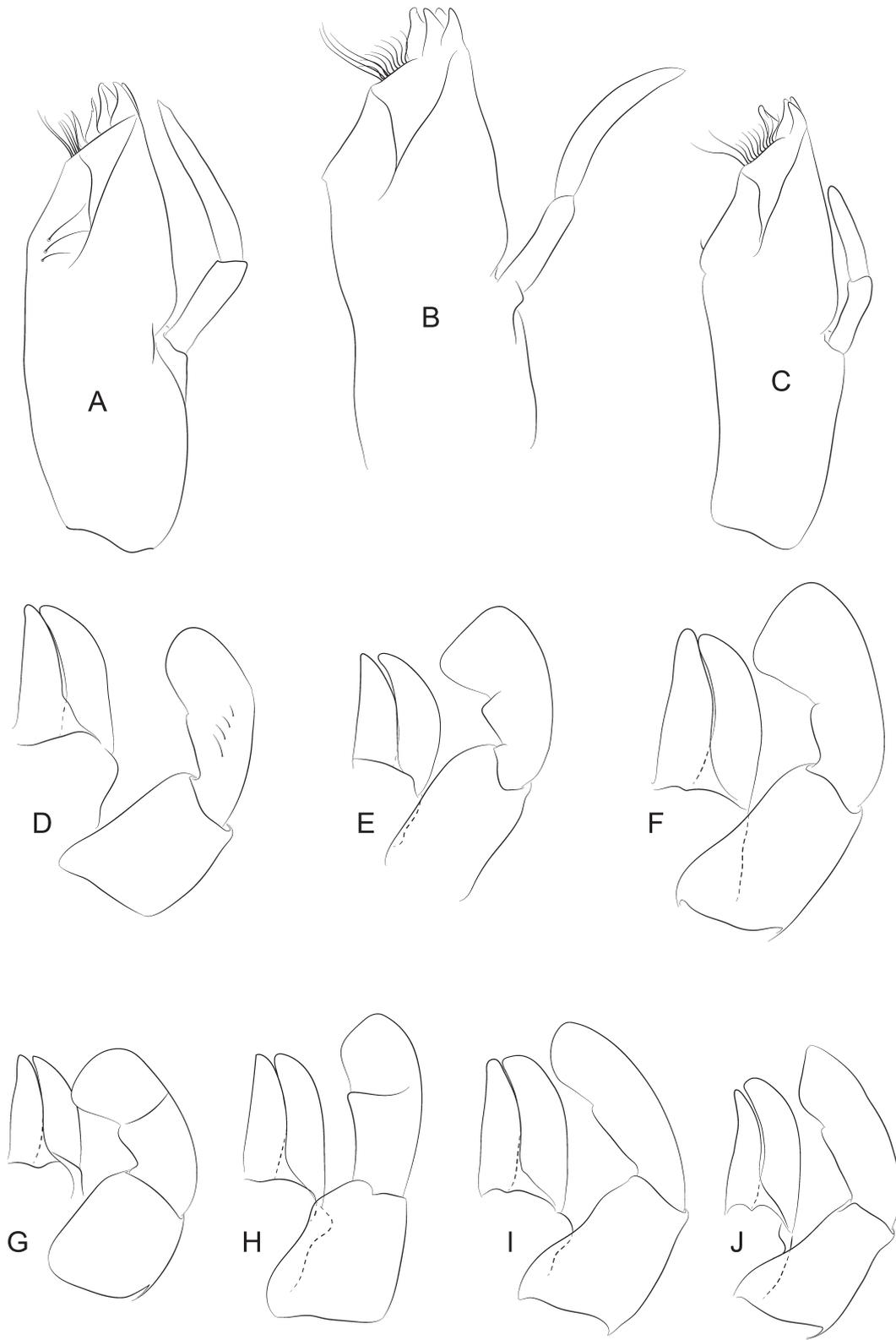


Fig. 5. Mouthparts of selected species of Baetidae studied in the current analysis (A–C, maxillae; B–J, labia): (A) *Cloeodes superior*; (B) *Bungona (Centroptella) soldani*; (C) *Potamocloeon (Potamocloeon) dentatum*; (D) *Cloeodes maculipes*; (E) *Cloeodes auwe*; (F) *Bungona (Centroptella) soldani*; (G) *Bungona (Chopralla) ceylonensis*; (H) *Crassolus inzingae*; (I) *Potamocloeon (Potamocloeon) dentatum*; (J) *Potamocloeon (Aquaediva) freitagae*.

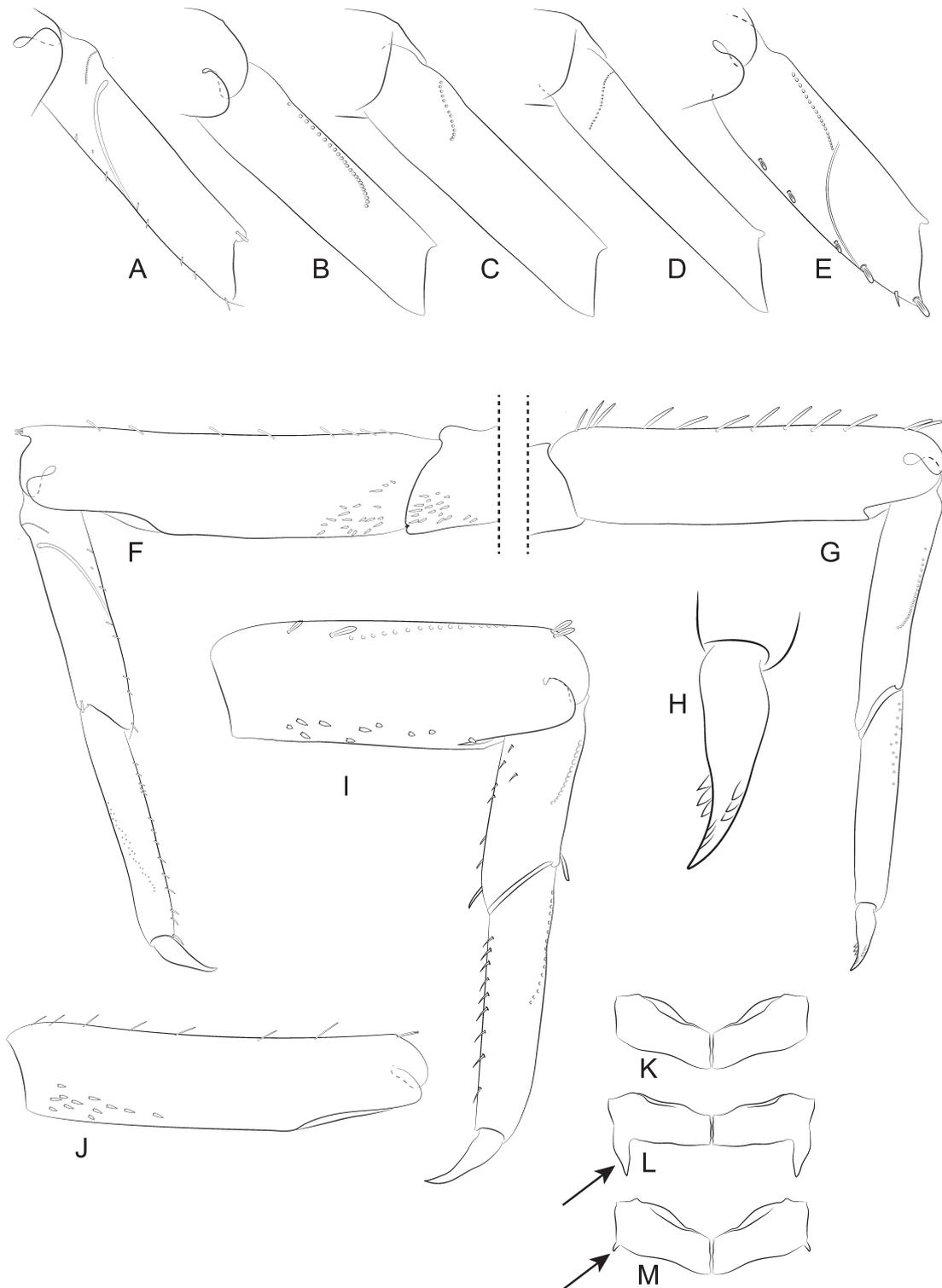


Fig. 6. Thoracic structures of selected species of Baetidae studied in the current analysis (A–D, fore tibiae; E, hind tibia; F, G and I, legs; H, tarsal claw; J, femur; K–M, hind thorax, arrow showing hindwing pad): (A) *Cloeodes* sp. 1 (anterior surface); (B) *Bungona* (*Centroptella*) *longisetosa* (anterior surface); (C) *Bungona* (*Centroptella*) *longisetosa* (posterior surface); (D) *Bungona* (*Chopralla*) *liebenauae* (posterior surface); (E) *Potamocloeon* (*Potamocloeon*) *dentatum* (anterior surface); (F) *Cloeodes* sp. 1; (G, H) *Bungona* (*Chopralla*) *ceylonensis*; (I) *Potamocloeon* (*Potamocloeon*) *dentatum*; (J) *Crassolus* *inzingae*; (K) *Bungona* (*Centroptella*) *longisetosa*; (L) *Cloeodes* sp. 1; (M) *Bungona* (*Chopralla*) *ceylonensis*.

mola of right mandible present (Fig. 4C–E); labial palp segment III distally expanded (Fig. 5F, G); setae on outer margin of fore femur long, $\frac{1}{3}$ width of femur (Fig. 6G); patella-tibial suture absent on fore tibia and located at middle length of mid and hind tibiae (Fig. 6B–E, G); row of conspicuous setae on anterior surface of fore tibia long distance (exceeding half of length of tibia, Fig. 6B, E, G, as in Fig. 10B); row of conspicuous long setae present on abdominal sterna IV or V–VI (Fig. 10G); distance between insertions of conspicuous long setae on abdominal sterna greater than diameter of insertions (Fig. 10G); secondary swimming setae present (Fig. 7F). *Adults*. Forewing with double marginal intercalary veins (as in Fig. 8C); hindwing absent (although vestiges of hindwing pads are present in some species, Fig. 6M); forceps segment I narrowing toward apex (Fig. 9C); forceps segment III elongate (Fig. 9C).

Type species. *Bungona narilla* Harker, 1957: 73.

Species included. *Bungona (Bungona) narilla* Harker; *Bungona (Bungona) illiesi* (Lugo-Ortiz & McCafferty); *Bungona (Centroptella) longisetosa* (Braasch & Soldán), **comb.n.**; *Bungona (Centroptella) soldani* (Müller-Liebenau), **comb.n.**; *Bungona (Centroptella) sp4*. (present paper); *Bungona (Chopralla) ceylonensis* (Müller-Liebenau), **comb.n.**; *Bungona (Chopralla) colorata* (Soldán, Braasch & Luu), **comb.n.**; *Bungona (Chopralla) fusina* (Tong & Dudgeon), **comb.n.**; *Bungona (Chopralla) liebenauae* (Soldán, Braasch & Luu), **comb.n.**; *Bungona (Chopralla) pusilla* (Müller-Liebenau), **comb.n.**; *Bungona (Chopralla) similis* (Müller-Liebenau), **comb.n.**; *Bungona (Chopralla) sp1*. (present paper); Genus No. 2 sp. 1 (Müller-Liebenau, 1984).

Distribution. Australia, New Guinea, and southern, eastern and southeastern Asia.

Comments. The genus *Bungona* was erected by Harker, (1957) to include a single species from Australia, *B. narilla*. The original description is succinct and the relationship of *Bungona* to other genera such as *Centroptella* and *Chopralla*, was overlooked by Waltz & McCafferty (1987a) while reviewing the genus *Cloeodes*. In fact, the distinction among *Bungona*, *Chopralla* and *Centroptella*, and especially between *Bungona* and *Centroptella* is very subtle, relying on a few unusual characters.

Bungona (Bungona) Harker, 1957

Diagnosis. *Nymph*. Dorsal surface of labrum with two setae on anterolateral corner; prostheca of right mandible very close to incisors (Fig. 4C); right prostheca narrow (not slender as in other subgenera of *Bungona*) and with thin medial process (Fig. 4C); angle of row of long setae on posterior surface of fore tibia around 60° (as in Fig. 6D); large spines present on every segment of cercus (large spine as in Fig. 10I).

Type species. *Bungona narilla* Harker, 1957: 73.

Species included. *Bungona (Bungona) narilla* Harker; *Bungona (Bungona) illiesi* (Lugo-Ortiz & McCafferty).

Distribution. Australia.

Bungona (Centroptella) Braasch & Soldán, 1980, stat.n.

Diagnosis. *Nymph*. Prostheca of right mandible relatively far from incisors [in comparison with *Bungona (Bungona)*], slender and with thin medial process (Fig. 4D); distal margin of labial palp segment III straight (Fig. 5F); few setae on outer margin of fore femur (around six); angle of row of long setae on posterior surface of fore tibia around 30° (Fig. 6C); gills weakly serrate; gill VII long, reaching caudal filaments.

Type species. *Centroptella longisetosa* Braasch & Soldán, 1980: 123.

Species included. *Bungona (Centroptella) longisetosa* (Braasch & Soldán), **stat.n.**; *Bungona (Centroptella) soldani* (Müller-Liebenau), **stat.n.**; *Bungona (Centroptella) sp. 4* (present paper).

Distribution. Southern and southeastern Asia.

Bungona (Chopralla) Waltz & McCafferty, 1987, stat.n.

Diagnosis. *Nymph*. Prostheca of right mandible relatively far from incisors [in comparison to *Bungona (Bungona)*], slender and with thin medial process (Fig. 4E – except in *B. (Ch.) liebenauae* and Genus No. 2 sp 1, *sensu* Müller-Liebenau, 1984); base of glossa not reaching inner $\frac{1}{3}$ of paraglossa (Fig. 5G); length of row of long setae on anterior surface of fore tibia extending for about 0.8× length of tibia (Fig. 6G); width of row of long setae on posterior surface of fore tibia around 0.7× width of tibia (Fig. 6D); peculiar denticles on tarsal claws present (Figs 6H, 10D); scales on tergal surface lanceolate (Fig. 10H); characteristic contrasting body colour pattern (Fig. 7E); gills weakly serrate.

Type species. *Centroptella ceylonensis* Müller-Liebenau, 1983: 486.

Species included. *Bungona (Chopralla) ceylonensis* (Müller-Liebenau), **comb.n.**; *Bungona (Chopralla) colorata* (Soldán, Braasch & Luu), **comb.n.**; *Bungona (Chopralla) fusina* (Tong & Dudgeon), **comb.n.**; *Bungona (Chopralla) liebenauae* (Soldán, Braasch & Luu), **comb.n.**; *Bungona (Chopralla) pusilla* (Müller-Liebenau), **comb.n.**; *Bungona (Chopralla) similis* (Müller-Liebenau), **comb.n.**; *Bungona (Chopralla) sp. 1* (present paper); Genus No. 2 sp 1 (Müller-Liebenau, 1984).

Distribution. Southern and southeastern Asia.

Crassolus, gen.n.

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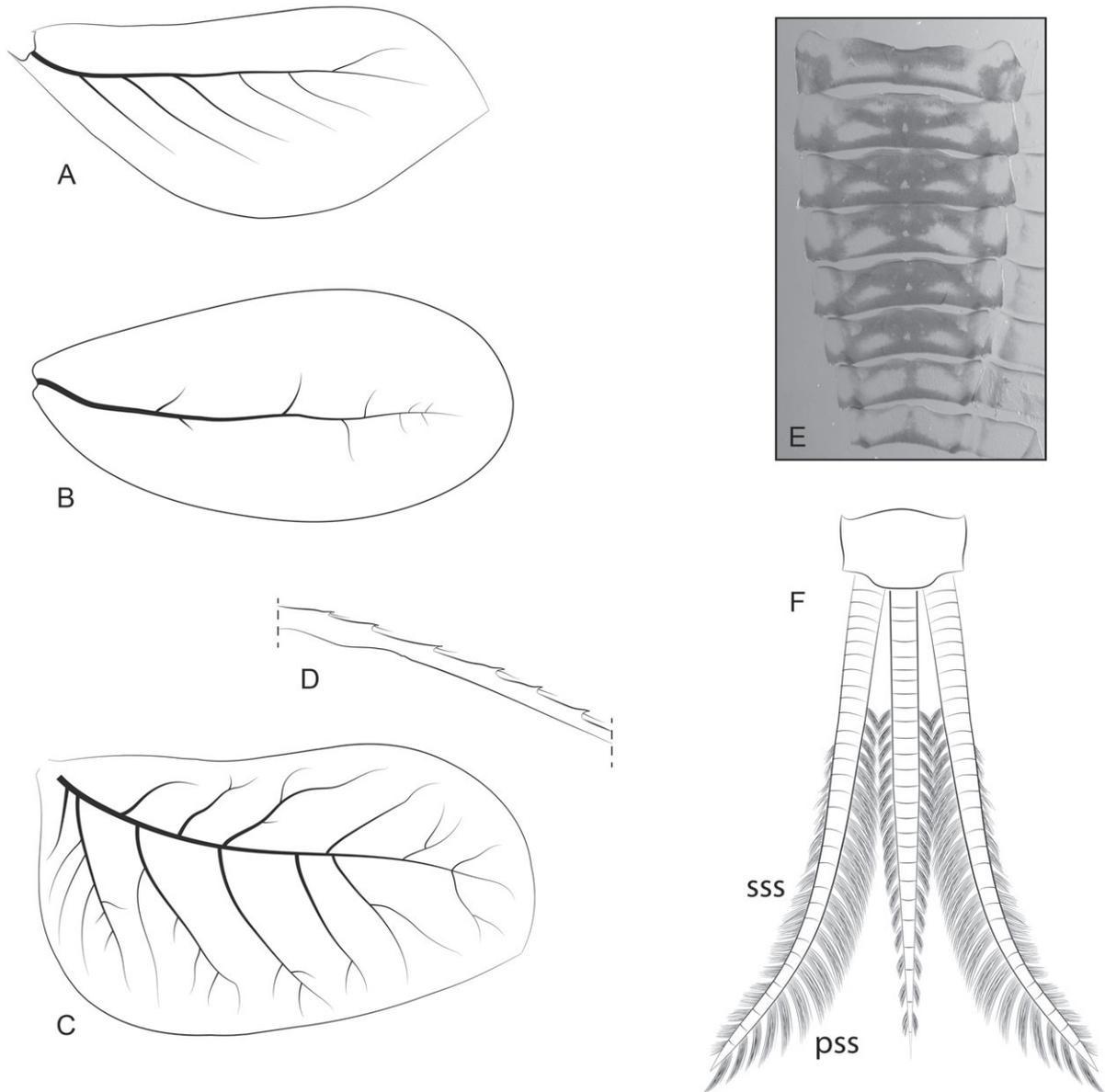


Fig. 7. Abdominal structures of selected species of Baetidae studied in the current analysis (A–E, gills; F, terga I–VIII; F, caudal filaments): (A) *Bungona (Chopralla) ceylonensis*; (B) *Cloeodes* sp.; (C, D) *Potamocloeon (Aquaediva) freitagae*; (E) *Bungona (Chopralla)* sp.; (F) *Bungona (Centroptella) longisetosa*. pss, primary swimming setae; sss, secondary swimming setae.

Diagnosis. *Nymph.* Length of setae on outer margin of fore femur relatively long (around $\frac{1}{5}$ of width of femur, Fig. 6J); absence of long setae between prostheca and mola of both mandibles (Fig. 4F); labial palp segment III quadrangular, not expanded (Fig. 5H); absence of spines on posterior margin of metanotum. *Adult.* Forewing relatively narrow (ratio length/width of forewings around 2.8, Fig. 8D); double marginal intercalary veins on forewing (Fig. 8D); forceps segment I narrowing toward apex (Fig. 9D); forceps segment III elongate (Fig. 9D); and gonovectes free, not fused to penial bridge, and located at base of forceps (not deeply invaginated in sternum IX) (Fig. 9D).

Type species. *Pseudocloeon inzingae* Crass, 1947: 60.

Species included. *Crassolus inzingae* (Crass), **comb.n.**

Distribution. South Africa.

Etymology. Named after the describer of the type-species, R.S. Crass, and with the Latin adjective *solus*, meaning unique, alone, to refer to the monotypy of the genus. The gender is masculine.

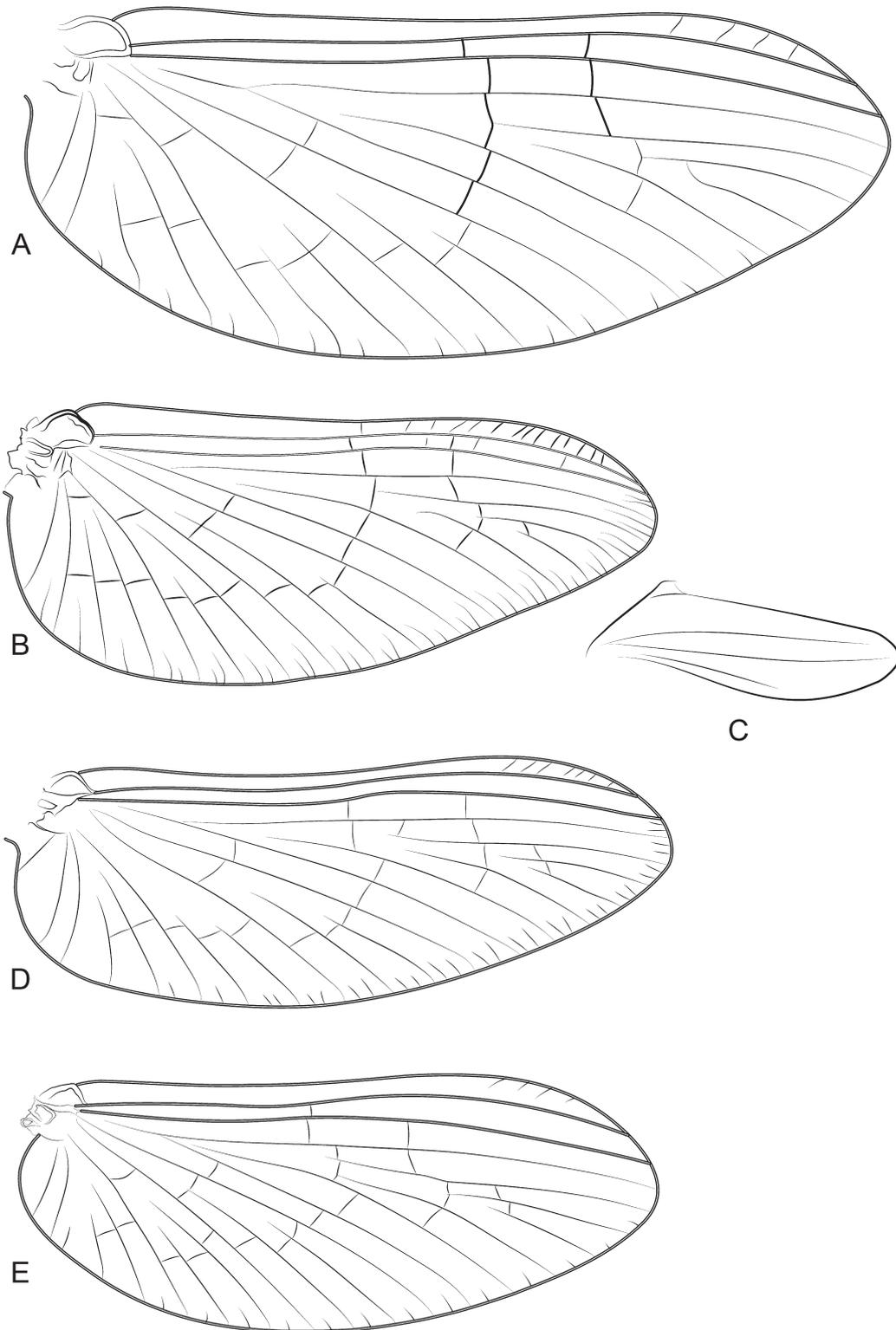


Fig. 8. Wings of selected species of Baetidae studied in the current analysis (A, B, D, E, forewings; C, hindwing): (A) *Cloeodes maculipes* (female); (B) *Cloeodes* sp. 1 (male); (C) *Cloeodes* sp. 1 (male); (D) *Crassolus inzingae* (male); (E) *Potamocloeon* (*Potamocloeon*) *dentatum* (male).

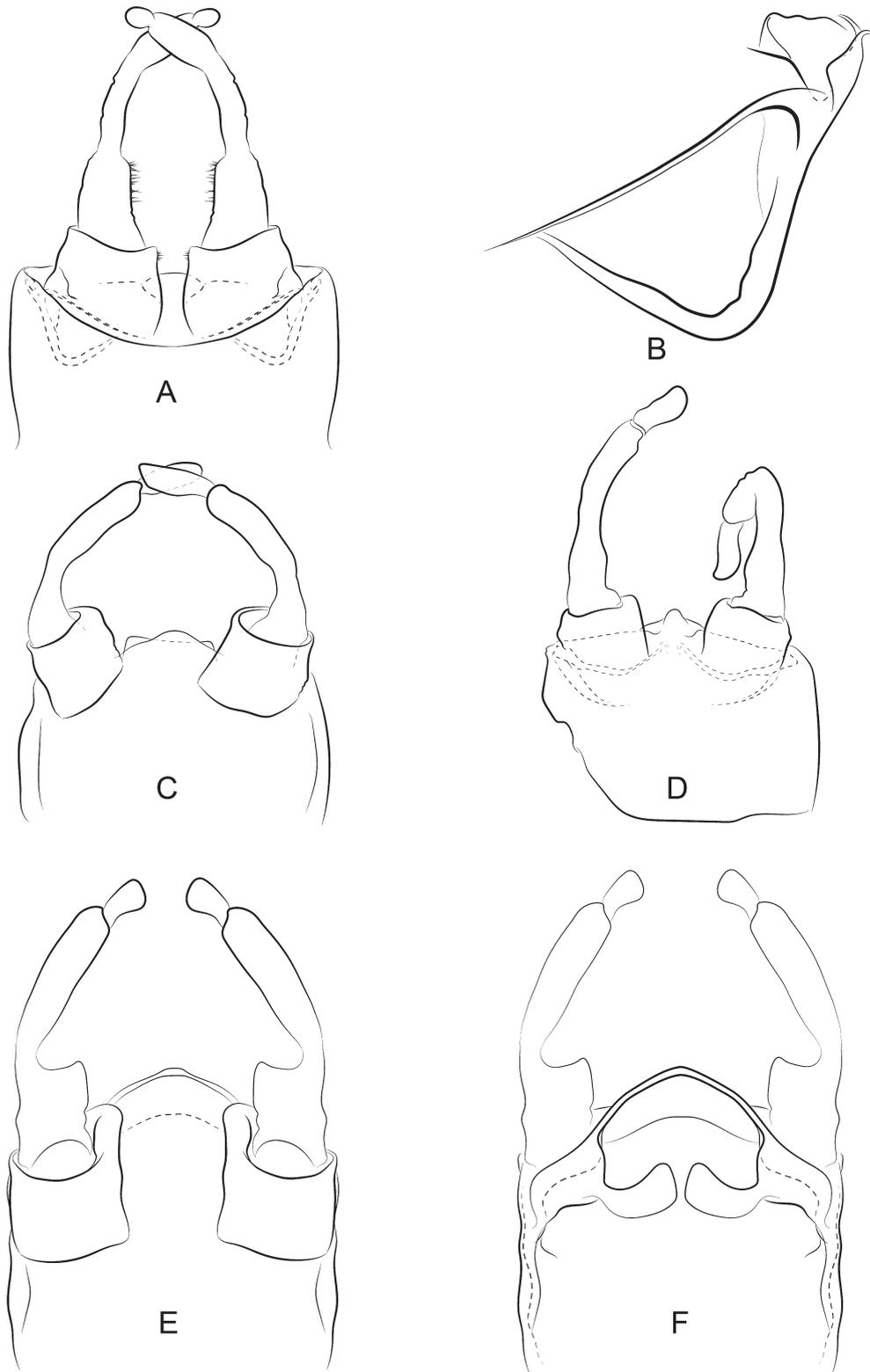


Fig. 9. Male genitalia of selected species of Baetidae studied in the current analysis (A, C–E, ventral view; B, detail of gonovectes; F, dorsal view, tergum IX detached): (A, B) *Cloeodes* sp. 1; (C) *Bungona* (*Centroptella*) *longisetosa*; (D) *Crassolus inzingae*; (E, F) *Potamocloeon* (*Potamocloeon*) *dentatum*.

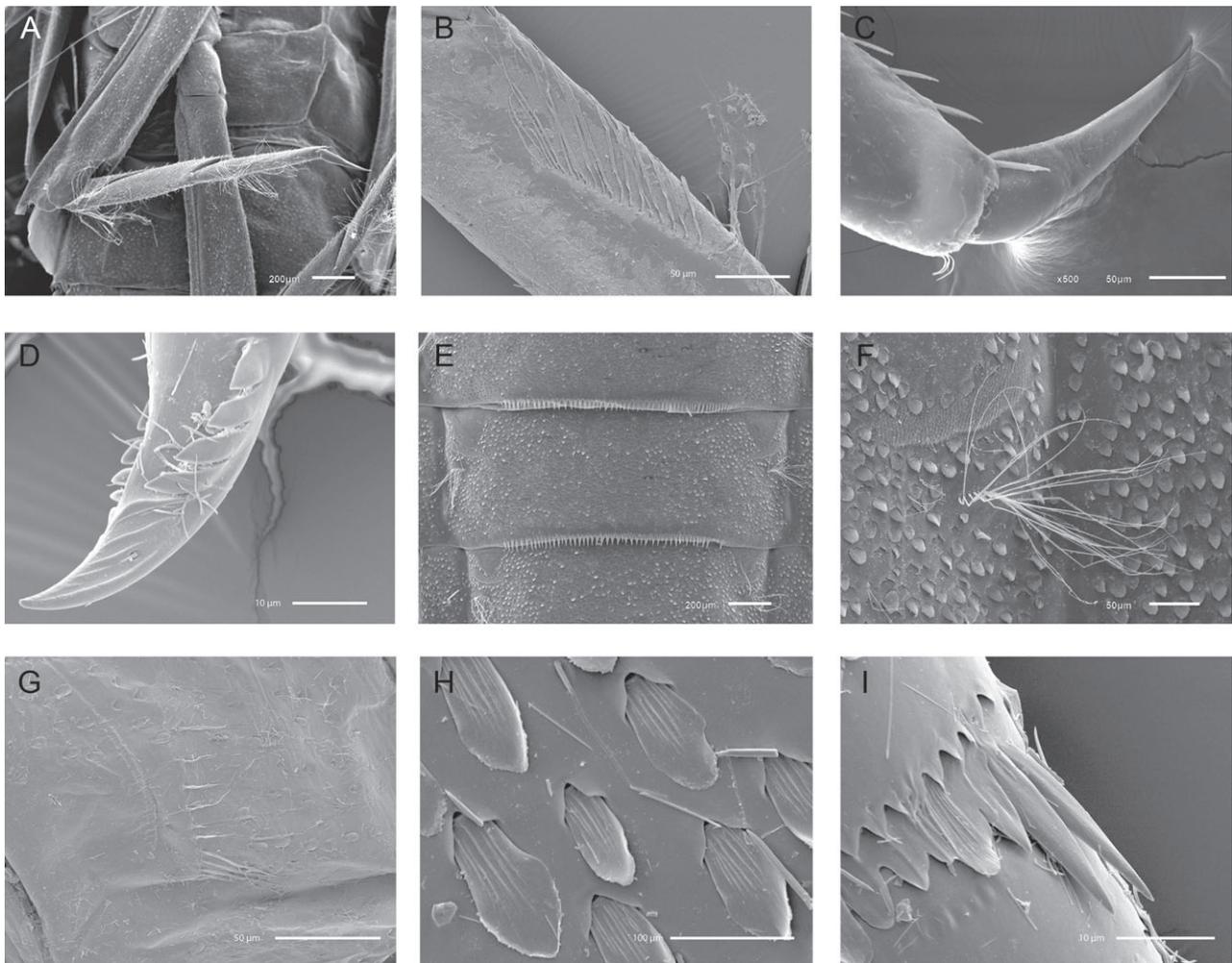


Fig. 10. SEM photographs of selected species of Baetidae studied in the current analysis. (A) *Cloeodes* sp., ventral view of thorax showing mid and hind leg; (B) *Potamocloeon (Aquaediva) portabile*, detail of anterior surface of fore tibia; (C) *Cloeodes penai*, tarsal claw; (D) *Bungona (Chopralla)* sp. 1, tarsal claw; (E) *Cloeodes* sp., abdominal sterna III–V; (F) *Cloeodes* sp., detail of abdominal sternum IV; (G) *Bungona (Chopralla)* sp. 1, detail of abdominal sternum V; (H) *Bungona (Chopralla)* sp. 1, detail of tergal surface; (I) *Bungona (Chopralla)* sp. 1, detail of caudal filaments.

Comments. *Crassolus inzingae* new combination was originally described by Crass (1947) in *Pseudocloeon* and was the first member of the *Cloeodes* complex reported from Africa (Waltz & McCafferty, 1994). Despite its distribution, it has more affinities with Oriental, Australasian and Neotropical species, than to the other Afrotropical species here below assigned to *Potamocloeon*. Based on the available material for study, this species seems to be much less common than *P. dentatum*, the other representative of the complex in continental Africa.

Potamocloeon Gillies stat.n.

Diagnosis. Nymph. Right prostheca stout and in contact with incisors and without thin medial process (Fig. 5F); long setae between prostheca and mola of both mandibles present (Fig. 4G, H); fore femur stocker (Fig. 6H); row of long conspicuous setae on femora present (Fig. 6I); patella-tibial suture absent on fore tibia and located at middle length of mid and hind tibiae (as

in Fig. 6E); spine-like setae on trochanter serrate (char. 78); strong serration on distal $\frac{1}{3}$ of outer margin of gill present (Fig. 7C, D). **Adults.** Broadening of forewing close to middle length (Fig. 8C); marginal intercalary veins of forewing single (Fig. 8C); hindwing absent; forceps segment III short (Fig. 9E, F); apex of forceps segment III straight (Fig. 9E, F); gonovectes fused to sclerotized penial bridge (Fig. 9F).

Type species. *Cloeon dentatum* Kimmins, 1956: 76.

Species included. *Potamocloeon (Potamocloeon) dentatum* (Kimmins), **comb.reinst.**; *P. (Aquaediva) portabile* (Lugo-Ortiz & McCafferty), **comb.n.**; *P. (Aquaediva) bicoloratum* (Gattolliat), **comb.n.**; *P. (Aquaediva) freitagae* (Gattolliat), **comb.n.**; *P. (Aquaediva) pseudogladium* (Gattolliat), **comb.n.**

Distribution. Afrotropics, Africa and Madagascar.

Comments. The taxonomic history of the genus *Potamocloeon*, and its type species *Cloeon dentatum* is rather complex: the species was originally described based on adults in the genus *Cloeon* (Kimmins, 1956). Later, based on the description of the supposed nymph of the species, (Gillies, 1990) established the genus *Potamocloeon*. Jacobus *et al.* (2006), however, found out that the association between nymphs and adults made by Gillies was incorrect; the true nymph of *Potamocloeon dentatum* belonged in fact to *Cloeodes*, whereas the remarkable nymphs, wrongly associated by Gillies, were assigned to a new genus named *Securiops* Jacobus, McCafferty & Gattolliat (see Jacobus *et al.*, 2006 and Table S2). Moreover, Jacobus *et al.* (2006) also synonymized *Maliqia plumosa* (Wuillot) and *Maliqia abdalahi* McCafferty with *C. dentatus*. Consequently, *Potamocloeon* and *Maliqia* were considered as junior synonyms of *Cloeodes*. Based on the paraphyly of *Cloeodes* and the monophyly at node 73, we revalidate *Potamocloeon* **stat.n.** to encompass most of the species previously assigned to *Cloeodes* from Africa. *Maliqia* is a junior synonym of *Potamocloeon*.

Within the *Cloeodes* complex, the sister lineage to the remaining genera is the Afrotropical genus *Potamocloeon*, with (*P.*) *Potamocloeon* in mainland Africa and the subgenus *Aquaediva* endemic to Madagascar. Based on ancestral state likelihood analysis, Monaghan *et al.* (2005) proposed that what they called the *Cloeodes* lineage (i.e. *Potamocloeon*) originated in Madagascar with subsequent dispersal to tropical Africa. This may explain the restricted number of species in Africa (a single species with a wide distribution) compared to Madagascar (four species).

***Potamocloeon* (*Potamocloeon* Gillies, 1990)**

Diagnosis. Nymph. Labial palp segment III oblong to rounded (Fig. 5I); spines on posterior margin of metanotum present; row of conspicuous long setae on abdominal sterna IV–VI. *Adults.* Forceps segment I with distomedial projection (Fig. 9E).

Type species. *Cloeon dentatum* Kimmins, 1956: 76.

Species included. *Potamocloeon* (*P.*) *dentatum* (Kimmins), **comb.reinst.**

Distribution. Sub-Saharan Africa.

Comments. The single species of *Potamocloeon* is widely distributed in sub-Saharan Africa. The diagnostic characters presented above readily distinguish the subgenus from the other Afrotropical members of the *Cloeodes* complex. *Cloeon pusillum* Navás was described based on female adults from Zaire. Later, Demoulin (1957) redescribed additional females and Gillies (1979), based on adults of both sexes from Zaire, described the supposed males and transferred it to the genus *Afrobaetodes* Demoulin. Based on wing venation and general shape of male genitalia illustrated by Gillies (1979); Jacobus *et al.* (2006) transferred this species to *Cloeodes*. *Cloeodes*

pusillum, indeed, may also belong to *Potamocloeon* based on wing venation and shape of forceps segment I. However, the elongate forceps segment III (Gillies, 1979: fig. 1) is not in accordance with our concept of the genus. In order to avoid further nomenclatural changes involving this species, we consider that it should remain as *incertae sedis* until nymphs (and male adults) are associated with female adults.

***Potamocloeon* (*Aquaediva*), subgen.n.**

<http://zoobank.org/urn:lsid:zoobank.org:act:4B05DAEE-8D90-4AD2-A02B-05F6926C1421>

Diagnosis. Nymph. Up to eight setae on distolateral corner of labrum (Fig. 4A); distal margin of labial palp segment III straight (Fig. 5J); gill VII long, reaching caudal filaments; large spines on cercus absent. *Adults.* Forceps segment I narrowing toward apex, as wide as base of segment II (as in Fig. 9C, D).

Type species. *Cloeodes portabilis* Lugo-Ortiz & McCafferty, 1999: 208.

Species included. *P. (A.) portabile* (Lugo-Ortiz & McCafferty), **comb.n.**; *P. (A.) bicoloratum* (Gattolliat), **comb.n.**; *P. (A.) freitagae* (Gattolliat), **comb.n.**; *P. (A.) pseudogladium* (Gattolliat), **comb.n.**

Distribution. Madagascar.

Etymology. Named from the Latin words Aqua (water) and Diva (Fairy), literally the fairy of the water; the gender is feminine.

Comments. Gattolliat (2001) described three new species of *Cloeodes* from Madagascar and pointed out some of the striking features shared exclusively by the four Malagasy species. Most of these characteristics, in fact, are also found in *P. dentatum* and are autapomorphies that define the genus *Potamocloeon*.

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: 10.1111/syen.12144

Table S1. List of material examined (stage acronyms: N, nymph; MI, male imago, FI, female imago. Determiner acronyms: AS, Arnold Staniczek; AW, André Wagner; CN, Carolina Nieto; FFS, Frederico Falcão Salles; JLG, Jean-Luc Gattolliat; JW, Jeff Webb; MS, Michel Sartori).

Table S2. List of the species currently attributed to the *Cloeodes* complex of genera with respective original designation and synonyms.

Appendix S1. List of continuous and discrete characters. For details on measurements, check Figure S11. Consistency index for each character is presented between brackets.

Appendix S2. List of apomorphies from terminals and nodes. Arrows separate plesiomorphic from apomorphic states.

Appendix S3. Matrix of characters and states. Ready to use in TNT (psp1, *Procloeon* sp. 1; psp2, *Procloeon* sp. 2; ssp1, aff. *Susua* sp. 1; ssp2, aff. *Susua* sp. 2; bsp1, aff. *Bungona* sp. 1; clsp1 to 4, *Cloeodes* sp. 1 to sp. 4; chsp1, *Chopralla* sp. 1).

Appendix S4. Descriptions.

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