



The genus *Cloeodes* (Ephemeroptera: Baetidae) in Argentina with new generic synonymy and new species

CAROLINA NIETO1 & BARTON RICHARD2

¹CONICET-INSUE-Facultad de Ciencias Naturales e IML, Miguel Lillo 205, S. M. Tucumán (4000), Tucumán, Argentina. E-mail: macarolina_nieto@yahoo.com.ar

²Entomology, 409 Perry-Paige Building, Florida A&M University, Tallahassee, Florida, USA 32307.

E-mail: barton.richard@famu.edu

Abstract

Three new species of *Cloeodes* are described from Argentina (*C. barituensis*, *C. espinillo* and *C. opacus*), based on nymphs and from adults for the first two species. Two species, *C. stelzneri* and *C. nocturnus*, are proposed as *nomen dubia*. The only other species from Argentina, *C. penai*, is revised. The validity of the monotypic genus *Bernerius* is analyzed. A cladistic analysis including five species of the genus *Cloeodes* and *Bernerius* is presented and the synonymy of the latter is confirmed. A key for South American species of *Cloeodes* is presented.

Key words: Ephemeroptera, Baetidae, Cloeodes, Bernerius, South America

Introduction

The genus *Cloeodes* was originally established by Traver in 1938. In this paper three species were described from Puerto Rico, although only one, *Cloeodes maculipes*, remains in the genus. The genus has been revised and updated in several papers in recent years. Waltz & McCafferty (1987a,b), redefined the genus, described several new species and transferred species placed in other genera. They also synonymized *Centroptella* (Braasch & Soldan, 1980) and established two subgenera, placing *Notobaetis* (Morihara & Edmunds, 1980) as one of them. In 1995, the subgenera were removed by McCafferty & Lugo-Ortiz when they described a new species. Finally, two genera: *Maliqua* Lugo-Ortiz & McCafferty (1997) and *Potamocloeon* Gillies (1990) were synonymized with *Cloeodes* (Jacobus *et al.*, 2006).

Cloeodes has a widespread pantropical distribution in South America, North and Central America, Africa, Madagascar, Southeast Asia and Australia. In South America 13 species are known for this genus, 7 of them described from adults, 4 from nymphs and 2 from both adults and nymphs. These species are distributed in Argentina, Bolivia, Brazil, Guyana, Paraguay, Peru, Uruguay and Venezuela. Three species are previously known from Argentina, two of them described from adults and only Cloeodes penai from both nymphs and adults.

Bernerius is a monotypic South American genus, established by Waltz & McCafferty (1987a). This genus was described based on nymphs from Peru, previously placed in *Baetis* (?) sp. B by Berner (1980). This genus was considered to be the sister group of *Cloeodes* based on, among other characters, the presence of a subproximal arc of long fine setae on each tibia. In this paper, after examination of type material of *Bernerius* and based on a cladistic analysis, this genus is proposed as a synonym of *Cloeodes*.

Finally, three new species of *Cloeodes* are described from Argentina. One is described from nymphs and the other two from both nymphs and adults. Cloeodes stelzneri and Cloeodes nocturnus are proposed as nomen dubia. Keys to the male imagos and nymphs of the South American species of Cloeodes are presented.

Material and methods

The material examined is housed in the following institutions: Fundación-Instituto Miguel Lillo, Tucumán, Argentina (IFML) and Florida A&M University (FAMU).

Cladistic analysis

A matrix of 11 taxa and 54 morphological characters was constructed. The ingroup was composed of 6 species: Cloeodes maculipes (the type species of the genus), Cloeodes penai, the three new species described here, and Bernerius incus. Three taxa, determined in a previous cladistic analysis to be closely related to Cloeodes, were selected as outgroups: Dabulamanzia improvida from Madagascar and both Camelobaetidius phaedrus and Guajirolus queremba from Argentina. The trees were rooted indistinctly in the genera Metamonius (Siphlonuridae) and Siphlaenigma (Siphlaenigmatidae) that are considered to be the closest relatives of the Baetidae (e.g., Kluge et al., 1995).

The characters are from the external morphology of nymphs (44) and adults (10). Thirty nine are binary and the rest (15) are multistate and they are treated as nonadditive (unordered). The list of all characters and their states is presented in Appendix 1. The matrix with the assignment of character states to each taxon is shown in Table 1. Siphlaenigma janae and Cloeodes maculipes were coded from the literature, the other species by examination of the material.

The matrix was analyzed using TNT (Goloboff et al., 2003a), under implied weights (Goloboff, 1993). Shortest trees were obtained with the implicit enumeration command. Group support was calculated as both absolute and relative Bremer supports (Bremer, 1988, 1994) and as Frequency differences (Goloboff et al., 2003b). Bremer supports were calculated for the most parsimonius trees and 10000 suboptimal trees up to 5 steps longer. Suboptimal trees were gathered in ten stages: 0.1, 0.2, 0.3, 0.4, 0.5, 1, 2, 3, 4, 5, each stage saving 1000 trees. Frequency differences were calculated with 500 replicates of jackknifing (Farris et al., 1996) by symmetrical resampling of the original matrix (each character presents the same probability to be positively or negatively reweighed, Goloboff et al., 2003b). Each replicate of jackknifing was calculated by 10 random addition sequences plus TBR (tree bisection and reconnection), saving ten trees per replicate.

TABLE 1. Matrix of 11 taxa and 54 characters. Character state codes as in Appendix 1.

	0	10	20	30	40	50
		1				
Metamonius anceps	000000	0111100000	010110?011	?101120021	0000200010	01000111
Siphlaenigma janae	030033	2111101231	??01010???	???????021	20??????10	01000111
Dabulamanzia improvida	121111	1000011121	112020?020	11010101110	000020?101	21111010
Cloeodes penai	121011	1200011120	101010?110	1001001101	1011010001	11111000
Cloeodes barituensis	111011	1200011120	111010?120	0011001100	1011021101	A0?11000
Bernerius incus	111011	1200001120	111010?110	10010011313	11111100??	,3,3,3,3,3,3
Cloeodes espinillo	121011	1200011120	111010?120	1011001101	1111021101	11111000
Cloeodes opacus	111011	1200011120	101010?120	0011001101	00100211??	, ; ; ; ; ; ; ; ;
Camelobaetidius phaedrus	111121	0000010111	0120210002	?100100011	1000200001	11111001
Guajirolus queremba	112100	2000011111	0120111000	11000000100	00012000?1	10?11???
Cloeodes maculipes	111011	1200011120	??1010??20	00010?0100;	????0???01	.10?11101
A=1.2						

A=1,2

Results

Phylogenetic analysis

By the implicit enumeration of all possible trees, under implied weight, 5 shortest trees (length=98, fit=43.80) were obtained. The strict consensus tree is shown in Fig. A. The synapomorphies of the nodes common to the three shortest trees are listed in Appendix 2.

Rooting the tree in *Metamonius anceps* or *Siphlaenigma janae* did not change the results. Seven synapomorphies sustained the monophyly of the genus *Cloeodes* (Node 15): 1) prostheca of right mandible slender and bifid; 2) setae between prostheca and mola absent; 3) maxillary palpi two-segmented with segment II with an apical constriction; 4) trochanter with spines ventrally; 5) femora with dorsal margin parallel to ventral margin; 6) tarsi with pectinate spines; 7) length of gill/length of tergum 2.0–2.9 times the length of tergum.

The genus from Madagascar, *Dabulamanzia* is the sister group of *Cloeodes* (Node 13) by the synapomorphies of superlinguae with lateral and small spines and tibiae with proximal arc of setae present.

Group support values can be seen in Fig. A. The support obtained under the three estimators obtained good values for *Cloeodes*. The genus *Bernerius* is included within *Cloeodes*. *Cloeodes penai* and *Bernerius incus* are located in the base of the genus. Node 18 separates *C. espinillo* from the other species by apical margin of the femora with a subquadrangulate projection, terminal filament with long spines toward midline dorsally and ventrally every 2 segments. Node 17 separates *C. opacus* from *C. maculipes* + *C. barituensis* by femora with dorsal margin with blunt spines. Finally, Node 16 joins *C. maculipes* and *C. barituensis* which share the character of the hind wing pads absent.

The cladistic analysis is preliminary with regard to *Cloeodes* as it only includes species known from South America. The main purpose of this analysis is not to distinguish different groups within *Cloeodes* but to determine the validity of the genus *Bernerius*.

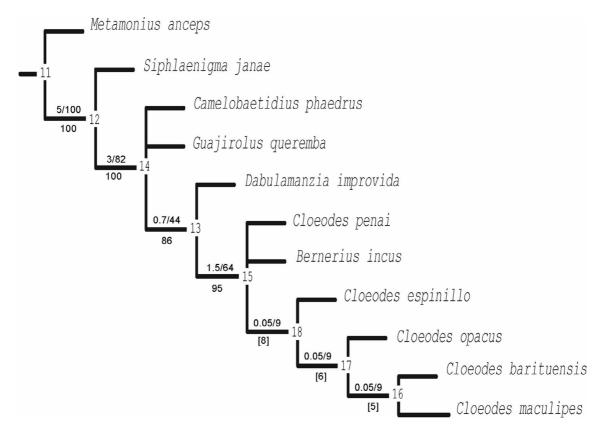


FIGURE A. Strict consensus of the 5 shortest trees obtained. Numbers above nodes represent absolute and relative Bremer supports. Numbers below nodes represent the support as Frequency differences.

Taxonomy

Cloeodes Traver

Cloeodes Traver, 1938: 32; Waltz & McCafferty, 1987a: 177; 1987b: 192; McCafferty & Lugo-Ortiz, 1995: 33 (Type species: Cloeodes maculipes Traver, original designation.

Notobaetis Morihara & Edmunds, 1980: 606; McCafferty & Lugo-Ortiz, 1995: 33 (Type species: *Notobaetis penai* Morihara & Edmunds, original designation).

Centroptella Braasch & Soldán, 1980: 123 (in part).

Maliqua Lugo-Ortiz & McCafferty, 1997: 368.

Potamocloeon Gillies, 1990: 207.

Bernerius Waltz & McCafferty, 1987a: 179. SYN. NOV.

Diagnosis. The genus *Cloeodes* can be distinguished from the other genera of the family by the following combination of characters. In the adults, 1) fore wings with paired or single marginal intercalary veins; 2) hind wings if present with 2 or 3 longitudinal veins, never bifurcate; 3) genitalia with forceps three-segmented, segment III rounded. In the nymphs, 1) antennae 1.5–3 times the head capsule, scape 1–1.5 times the length of pedicel; 2) labrum scarcely wider than long; 3) mandibles with or without setae between prostheca and mola; 4) left mandible with incisors fused apically, prostheca with denticles apically; 5) right mandible with incisors cleft in two sets, prostheca slender and branched; 6) superlinguae with apicolateral margins with short spines; 7) maxillae with palpi 1–1.5 times the length of galea-lacinia, two-segmented, segment II with a constriction; 8) segment II of labial palpi without projection; 9) dorsal margin of femora with spines, tibiae with a subproximal arc of fine setae; 10) tarsal claws 0.3–0.6 times the length of tarsi, if denticles present minute; 11) hind wing pads absent or present; 12) posterior margin of abdominal terga with spines, sterna II–VI each with long fine setae; 13) gills present on abdominal segments I–VII; 14) paraprocts with spines apically; 15) terminal filament subequal to cerci.

The above diagnosis applies to *Cloeodes* of South America and is modified from the diagnoses of Waltz & McCafferty (1987a,b) and Domínguez *et al.* (2006).

Bernerius was established by Waltz & McCafferty (1987a) and was considered to be the sister group of Cloeodes based on the shared synapomorphies of 1) left mandible with incisors fused apically, and a stout prostheca, 2) right mandible with incisors partially fused but separated apically, 3) right prostheca slender and furcate, 4) the presence of an arc of long, fine setae subproximally on the tibia, and 5) simple asymmetrically lamellate and broadly pointed gills. A comparison of the diagnostic characters listed for the two genera yields the following distinct character differences; Bernerius has the thumb of the molar area of the left mandible in the same plane as the anterior margin and abundant long, fine setae ventrally on most abdominal segments, while Cloeodes has the thumb of the molar area transverse to the anterior margin and ventral setae of the abdomen restricted to small tufts of long, fine setae laterally on each side of segments II-VI. Bernerius is said to retain the plesiomorphous condition of abundant long, fine setae on the venter of most abdominal segments, but no examples are given, nor an explanation to explain why this character state would be considered plesiomorphic. None of the outgroup taxa used in this analysis possessed any long, fine setae on the venter of the abdomen. The character of the thumb of the molar area of the left mandible being transverse to the plane of the anterior margin is also ambiguous with regard to ancestral state within the Baetidae. The majority of South American baetid genera have left mandibles with the thumb of the molar area transverse to the plane of the anterior margin. Only a few taxa possess a left mandible with the thumb of the molar area in the same plane as the anterior margin as does Bernerius. This cladistic analysis suggests that these two characters are autapomorphies for Bernerius incus.

The results of the phylogenetic analysis found *Bernerius* to be included within the genus *Cloeodes*. For this reason *Bernerius* is placed as a junior subjective synonym of *Cloeodes* and *B. incus* is transferred to this genus.

Key to South American Cloeodes

Male imagos ¹
1 Hind wings present
- Hind wings absent5
2(1) Hind wings with costal projection in the center of anterior margin (Fig. 53b)
- Hind wings with costal projection in the first third of anterior margin (Fig. 17b)
3(2)Hind wings with 3 longitudinal veins (Fig. 17b)
- Hind wings with 2 longitudinal veins
4(3)Segment II of forceps with a basal constriction (McCafferty & Lugo-Ortiz, 1995: Fig. 12) C. hydation
- Segment II of forceps without constriction
5(1)Apical margin of subgenital plate with a short spine (Traver, 1943: Fig. 7)
- Apical margin of subgenital plate without spines
6(5)Compound eyes erect, almost contiguous apically
- Compound eyes not as above and not contiguous apically
Compound eyes not as above and not configuous apreary
Nymphs
1 Hind wing pads absent
- Hind wing pads present
2(1)Labium with segment III of palpi truncate; maxillae with palpi longer than galea-lacinia
- Labium with segment III of palpi conical (similar to Fig. 61); maxillae with palpi subequal to galea-
lacinia (Fig. 10)
3(2)Abdominal tergum I with posterior margin smooth; abdominal color pattern as in Fig. 5; nymphs bigger
(6 mm)
- Abdominal tergum I with spines on posterior margin; abdominal color pattern not as above; nymphs
smaller (4 mm)
4(1)General color pattern with head, thorax, and segments I–V of abdomen dark
- General color pattern not as above
5(4)Femora with 2–3 spatulate spines apically (Fig. 26)
- Femora with 2–3 pointed spines apically (Fig. 63)
6(5)Dorsal edge of femora with blunt spines (Fig. 48);
- Dorsal edge of femora with pointed spines, except a pair of blunt spines apically (Fig. 26); abdominal
color pattern not as above
7(6)Tarsal claws at least half the length of tarsi
- Tarsal claws less than half the length of tarsi
8(7)Labial palpi with segment III truncate; mesonotum with distinct spots; nymphs smaller (3.5–4.5 mm)
- Labial palpi with segment III rounded (Fig. 24); mesonotum without spots (Fig. 20); nymphs bigger (6–
6.5 mm)
9(5)Maxillary palpi longer than galea-lacinia (Fig. 35); thumb of molar area of the left mandible in the same
plane as anterior margin (Fig. 32); tarsal claws with minute denticles basally (Fig. 38) C. incus n. comb.
- Maxillary palpi subequal to galea-lacinia (Fig. 60); thumb of molar area of the left mandible transverse to
anterior margin (Fig. 57); tarsal claws without denticles (Fig. 64)

^{1.} *C. turbinops* is not included in the key because the original description does not have enough characters to distinguish this species from the others.

^{2.} *C. anduzei* and *C. binocularis* are presently indistinguishable.

Cloeodes barituensis n. sp.

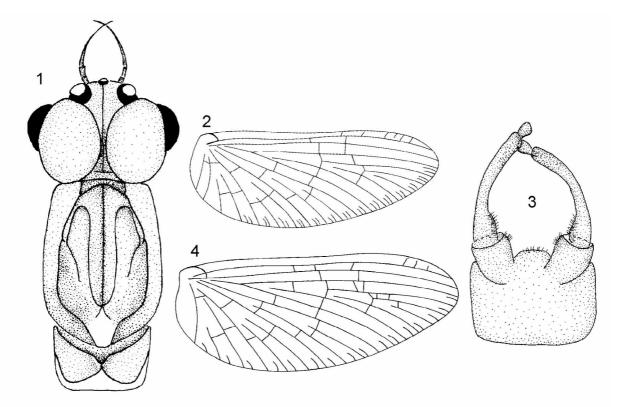
(Figs. 1–14)

Male imago (Fig. 1). Length: body, 5.9–6.1 mm; fore wings, 6.7–6.8 mm. Head yellowish brown. Compound eyes orange brown, height of stalk half length of eye diameter. Antennae yellowish brown. Thorax yellowish brown. Legs pale yellow. Leg I: tibia 1.5 times the length of femur; tarsi as long as tibia with 4 segments decreasing in length apically. Fore wings (Fig. 2) hyaline, except costal and subcostal spaces translucent, hind wings absent. Abdomen: segments I, VII–X yellowish brown; segments II–VI pale yellow, posterior margins of terga with a dark transverse line. Genitalia (Fig. 3) with bases of forceps close together, segment III rounded. Cerci yellow.

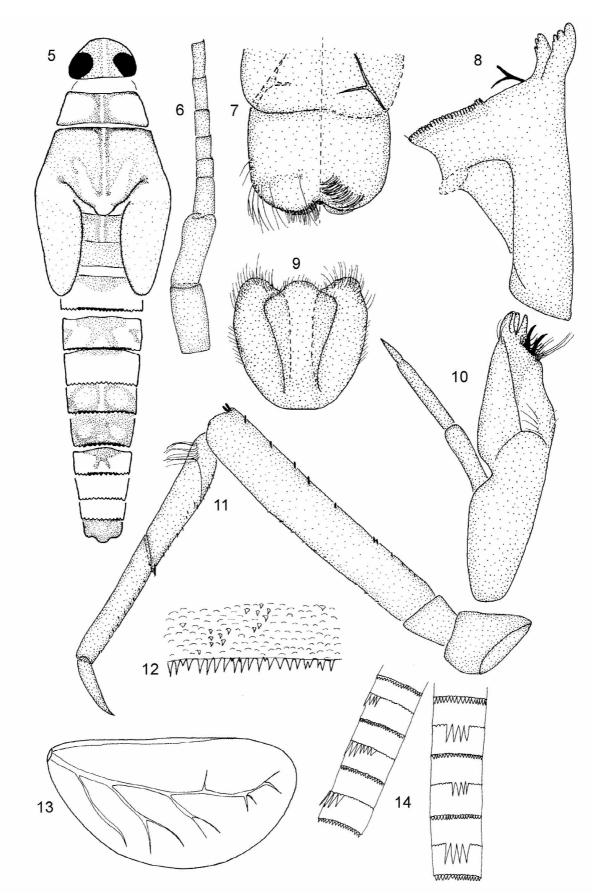
Female imago. Length: body, 7.2–7.3 mm; fore wings, 8 mm. Similar to male imago except head yellow. Fore wings (Fig. 4) with marginal intercalary veins single. Cerci yellowish brown.

Nymph (Fig. 5). Length: body, 5.0–6.5 mm; cerci, 1.6–1.8 mm; terminal filament, 1.5–1.6 mm. Antennae, 1.4–1.7 mm. Head yellow, longer than wide; compound eyes of the male grey brown. Antennae (Fig. 6) pale yellow, 1.5 times the head capsule, pedicel 1.5 times the length of scape. Mouthparts: labrum (Fig. 7) with one subapical seta centrally and two setae near lateral margin, anterior margin with basally bifid setae near midline and apically bifid setae near lateral margin. Left mandible (similar to Fig. 57), without setae between prostheca and mola, thumb of molar area transverse to anterior margin. Right mandible (Fig. 8) without setae between prostheca and mola. Hypopharynx (Fig. 9): lingua with a rounded projection. Maxillae (Fig. 10), palpi as long as galea-lacinia, two segmented, segment II with a constriction. Labium (similar to Fig. 61), with segment III of palpi rounded.

Thorax yellowish brown, median line yellow. Fore wing pads yellow. Sterna pale yellow. Legs yellow, tarsi and tarsal claws yellowish brown. Femora (Fig. 11) dorsally with a row of short blunt spines, ventrally with spines, apically with a subquadrangular projection (similar to Fig. 48). Tibia with bipectinate spines. Tarsi with short spines. Tarsal claws 0.4 times the length of tarsi. Hind wing pads absent.



FIGURES 1–4. *Cloeodes barituensis* **n. sp.** Male imago. 1, head and thorax, d.v.; 2, fore wing; 3, genitalia v.v. Female imago. 4, fore wing.



FIGURES 5–14. *Cloeodes barituensis* **n. sp.** Nymph. 5, general view, dorsal. 6, antennae. Mouthparts (Figs. 7–10): 7, labrum, left d.v., right v.v.; 8, right mandible v.v.; 9, hypopharynx v.v.; 10, maxilla v.v. 11, leg I. 12, posterior margin of tergum IV. 13, gill IV. 14, terminal filament, left cercus, right caudal filament.

Abdominal color pattern with segments I, X and anterior margin of segment II yellowish brown, segments IV, VIII and IX yellow, other segments yellowish brown with yellow spots as in Fig. 5. Posterior margin of terga with spines as in Fig. 12, except tergum I smooth. Sterna pale yellow, sterna II–VI with a small tuft of long fine setae laterally on each side. Paraprocts with spines apically, similar to Fig. 67. Gills (Fig. 13) translucent white, 2 times the length of each tergum, trachea pigmented. Caudal filaments yellow, 1/3 apically yellowish brown, with flattened setae basally sclerotized (similar to Fig. 30). Cerci with long spines toward external margin every two segments, terminal filament with long spines toward midline dorsally and ventrally every two segments (Fig. 14).

Etymology. Baritú is the name of one of the rivers where this species was collected.

Diagnosis. Cloeodes barituensis **n. sp.** can be distinguished from the other species of the genus by the following combination of characters. In the imago, 1) female with fore wings with single marginal intercalary veins, male with fore wings with paired marginal intercalary veins; 2) hind wings absent; 3) male with genitalia (Fig. 3) with bases of forceps close together, segment III rounded. In the nymph, 1) hind wing pads absent; 2) posterior margin of abdominal tergum I smooth (Fig. 5); 3) abdominal color pattern with segments I, X and anterior margin of segment II yellowish brown, segments IV, VIII and IX yellowish, other segments yellowish brown with yellow spots as in Fig. 5; 4) femora apically with a subquadrangular projection (similar to Fig. 48); 5) dorsal edge of femora with a row of blunt spines (similar to Fig. 48); 6) caudal filaments with flattened setae basally sclerotized (similar to Fig. 30), cerci with long spines toward to external margin every two segments and terminal filament with long spines toward midline dorsally and ventrally every two segments (Fig. 14).

Material. Holotype: male nymph: ARGENTINA, Salta, Río Colorado, S 23°22'09", W 64°28'11", 406 m, 1/ VI/ 2000, Romero, Molineri, Manzo & Nieto colls. Paratypes: 30 nymphs same data as holotype; 1 male imago (reared), 3 male and 2 female imagos, 20 male and 4 female subimagos: Depto. Santa Victoria, Baritú, Río Baritú, 1500 m, 10–17/ IX/ 1981, Domínguez col.; 5 nymphs: Aguas Blancas, Estación Jakulica, Río Pescado, Arroyo Arrazayal, 7–11/ XII/ 1984, Domínguez col. Material housed in IFML.

Cloeodes espinillo n. sp. (Figs. 15–30)

Male imago (Fig. 15). Length: body, 6.4–6.5 mm. Fore wings, 5.9–6.0; hind wings 1.1–1.2 mm. Head yellowish brown, compound eyes pale yellow, height of stalk half length of eye diameter. Antennae pale yellow. Thorax yellowish brown, sterna yellowish brown. Legs pale yellow. Leg I: tibia 1.5 times the length of femur, tarsi as long as tibia with 4 segments decreasing in length apically. Fore wings (Fig. 16) hyaline, except costal and subcostal spaces translucent. Hind wings (Figs. 17 a and b) present, 0.2 times the length of fore wing; costal projection pointed and located in the basal third of anterior margin. Posterior margin of the metanotum strongly projected dorsoventrally (Fig. 18). Abdomen pale yellow. Genitalia (Fig. 19) with bases of forceps close together, segment III rounded. Cerci pale yellow.

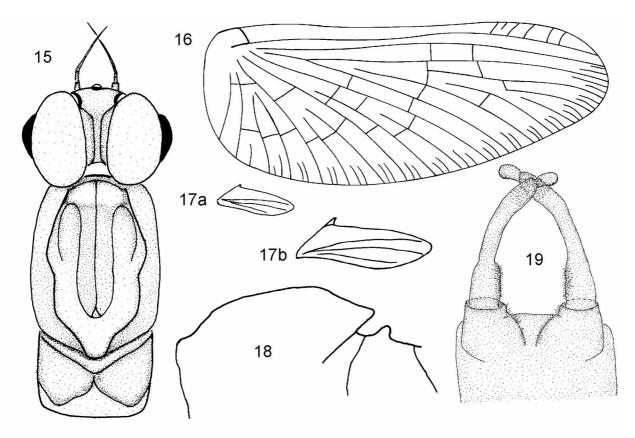
Female imago. Length: body, 6.6–6.7 mm. Fore wings, 7.2 mm; hind wings, 1.2 mm. Similar to male imago except thorax yellow. Abdomen yellow with tracheae pigmented.

Nymph (Fig. 20). Length: body, 5.5–6.0 mm; cerci, 2.8–3.0 mm; terminal filament, 2.5 mm. Head yellowish brown, longer than wide; compound eyes of the male yellowish brown. Antennae pale yellow, 3 times the head capsule; pedicel 1.5 times the length of scape. Mouthpart: labrum (Fig. 21) with one subapical seta centrally and two setae near lateral margin, anterior margin with basally bifid setae near midline and apically bifid setae near lateral margin. Left mandible (Fig. 22) without setae between prostheca and mola, thumb of molar area transverse to anterior margin. Right mandible without setae between prostheca and mola (similar to Fig. 58). Hypopharynx (Fig. 23): lingua with a rounded projection. Maxillae (similar to Fig. 60), palpi as

long as galea-lacinia, two segmented, segment II with a constriction. Labium (Fig. 24) with segment III of palpi rounded.

Thorax yellowish brown (Fig. 20). Fore wing pads pale yellow. Sterna pale yellow. Legs (Fig. 25) yellow. Dorsal edge of femora with a row of pointed spines, apically with a subquadrangular projection with a pair of blunt spines (Fig. 26). Tarsi with a row of short spines. Tarsal claws 0.4 times the length of tarsi. Hind wing pads present.

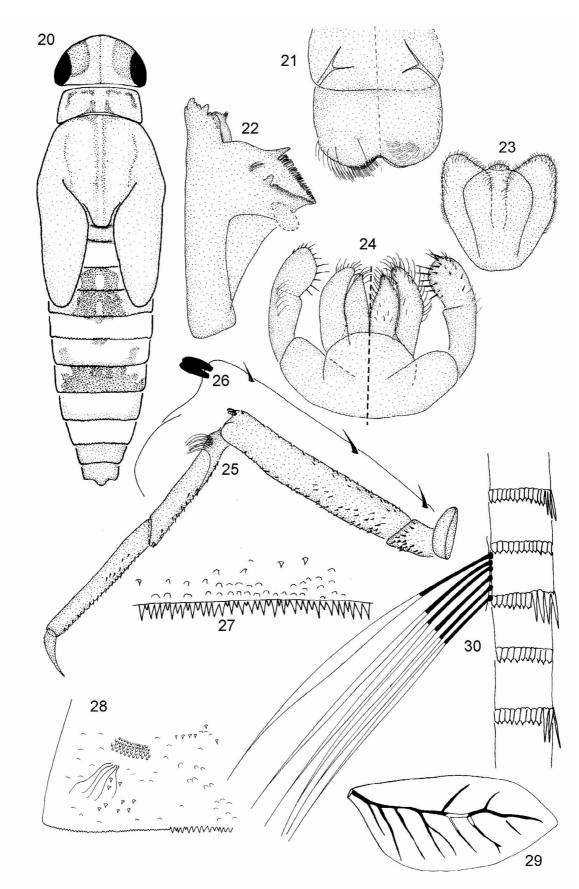
Abdomen yellowish brown, segments II–III and VI with brown spots as in Fig. 20, segment IX–X brown, posterior margin of terga with spines (Fig. 27). Sterna pale yellow, segments II–VI with a small tuft of long fine setae laterally on each side (Fig. 28). Paraprocts with spines apically (similar to Fig. 51). Gills translucent white, 2 times the length of each tergum, main trachea pigmented (Fig. 29). Caudal filaments yellow, apical third yellowish brown, with flattened setae basally sclerotized (Fig. 30). Cerci (Fig. 30) with long spines toward external margin every two segments, terminal filament with long spines toward midline dorsally and ventrally every two segments (similar to Fig. 14).



FIGURES 15–19. Cloeodes espinillo **n. sp.** Male imago: 15, head and thorax, dorsal; 16, fore wing; 17a, hind wing; 17b, hind wing detail; 18, thorax lateral view; 19, genitalia v.v.

Etymology. Espinillo is the name of one of the rivers where this species was collected.

Diagnosis. Cloeodes espinillo **n. sp.** can be distinguished from the other species of the genus by the following combination of characters. In the male imago, 1) hind wings 0.2 times the length of the fore wings (Figs. 16, 17a); 2) hind wings (Fig. 17b) with costal projection located in the first third of the anterior margin; 3) genitalia (Fig. 19) with bases of forceps close together, segment III rounded. In the nymph, 1) hind wing pads present; 2) lingua with a rounded projection (Fig. 23); 3) dorsal edge of femora with a row of pointed spines, apically with a subquadrangular projection with a pair of blunt spines (Fig. 26); 4) abdominal color pattern yellowish brown with segments II–III and VI with brown spots as in Fig. 20, segments IX–X brown; 5) caudal filaments with flattened setae basally sclerotized (Fig. 30), cerci with long spines toward external



FIGURES 20–30. *Cloeodes espinillo* **n. sp.** Nymph. 20, general view. Mouthparts (Figs. 21–24): 21, labrum, left d.v., right v.v.; 22, left mandible v.v.; 23, hypopharynx v.v.; 24, labium, left d.v., right v.v. 25, leg I; 26, dorsal margin of femur I. 27, posterior margin of tergum IV; 28, sternum IV. 29, gill IV. 30, cercus.

margin every two segments and terminal filament with long spines toward midline dorsally and ventrally every two segments (similar to Fig. 14).

Material. Holotype: male nymph: ARGENTINA, Córdoba, Río Los Espinillos, 13–16/ IX/ 1997, Nieto & Molineri colls. Paratypes: 4 nymphs, 5 male imagos (reared) and 16 male imagos, same data as holotype. 18 nymphs: Depto. Pocho, arroyito afluente Río Pocho, S 31°13'17", W 65°08'26", 1030 m, 14/ XI/ 2001, Orce & Nieto colls. Material housed in IFML.

Cloeodes incus (Waltz & McCafferty) n. comb. (Figs. 31–42)

Bernerius incus Waltz & McCafferty, 1987a: 181. Baetis (?) sp. B. Berner, 1980: 190.

Diagnosis. Cloeodes incus n. comb., known from nymphs, can be distinguished from the other species of the genus by the following combination of characters: 1) labrum (Fig. 31) with one subapical seta centrally and two setae near lateral margin, anterior margin with basally bifid setae near midline and apically bifid setae near lateral margin; 2) mandibles without setae between prostheca and mola; 3) left mandible with thumb of molar area in the same plane as anterior margin (Fig. 32); 4) right mandible with incisors cleft in two sets (Fig. 33); 5) lingua with a rounded projection (Fig. 34); 6) maxillary palpi long, 1.5 times the length of galealacinia, two segmented, segment II with a constriction (Fig. 35); 7) labium with segment III of palpi rounded (Fig. 36); 8) hind wing pads present; 9) dorsal edge of femora (Fig. 37) with a row of pointed spines and apically rounded (as in Fig. 63), femora, tibiae and tarsi with bipectinate spines; 10) tarsal claws with minute denticles basally (Fig. 38); 11) posterior margins of abdominal terga with spines (Fig. 39), sterna with long fine setae randomly distributed throughout; 12) gills pointed apically (Fig. 40); 13) posterior margin of paraprocts with spines apically (Fig. 41); 14) caudal filaments with simple setae, and with whorl of spines on each segment (Fig. 42).

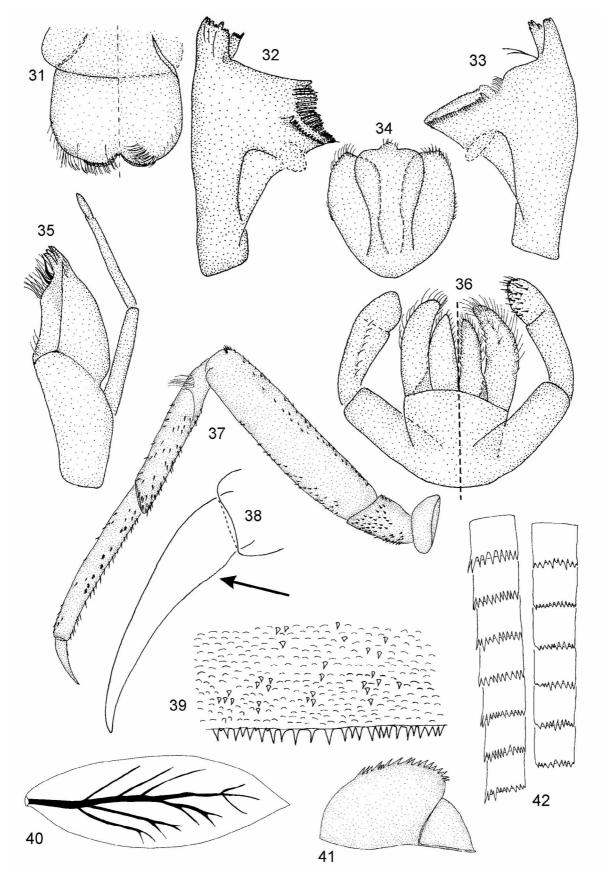
Material examined. Paratypes: 2 nymphs: BOLIVIA, trib. Río Umalo o Grande, below Calamarca on La Paz, Oruro Rd, 18/VII/ 1977, S. S. Roback & L. Berner colls. Material housed in FAMU.

Cloeodes nocturnus (Navás) Nomen dubium

Baetis nocturnus Navás, 1922: 199. Cloeodes nocturnus; Lugo-Ortiz & McCafferty, 1999: 259.

Discussion. This species was originally described by Navás (1922) from adults and was placed in the genus *Baetis*. Alba-Tercedor and Peters (1985) noted that the type was very damaged with only head and thorax remaining and thus did not indicate the sex of the specimen. Lugo-Ortiz & McCafferty (1999) examined the description and based on the location of the costal process and venation of the hind wings they transferred this species to *Cloeodes*. However, the original description is incomplete. A hind wing with 2 longitudinal veins and a costal process located in the basal third of the anterior margin are characters that are not restricted to *Cloeodes*. Finally, the holotype is in bad condition, thus making it impossible to assign fresh material to this species. For these reasons, *Cloeodes nocturnus* is proposed here as a *nomen dubium*.

Distribution. Argentina: Córdoba.



FIGURES 31–42. *Cloeodes incus* n. comb. Nymph. Mouthparts (Figs. 31–36): 31, labrum d.v., left d.v., right v.v.; 32, left mandible v.v.; 33, right mandible v.v.; 34, hypopharynx v.v.; 35, maxilla v.v.; 36, labium, left d.v., right v.v. 37, leg I; 38, tarsal claw I. 39, posterior margin of tergum IV. 40, gill IV. 41, paraproct. 42, terminal filament, left cercus, right caudal filament.

Cloeodes opacus n. sp.

(Figs. 43–51)

Nymph (Fig. 43). Length: body, 5.3–5.5 mm; cerci, 2.2–2.3; terminal filament, 1.9–2.0 mm. Antennae, 1.8–1.9 mm. Head dark brown, longer than wide; compound eyes in the male brown. Antennae: scape and pedicel dark brown, flagellum pale yellow, 2 times the head capsule; pedicel 1.5 times the length of the scape. Mouthparts: labrum (Fig. 44) with one subapical seta centrally and two setae near lateral margin, anterior margin with basally bifid setae near midline and apically bifid setae near lateral margin (Fig. 45). Left mandible (similar to Fig. 57), without setae between prostheca and mola, thumb of molar area transverse to anterior margin. Right mandible (similar to Fig. 58) without setae between prostheca and mola, prostheca bifid. Hypopharynx (similar to Fig. 9): lingua blunt apically. Maxillae (similar to Fig. 60), palpi as long as galea-lacinia, two segmented, segment II with a constriction. Labium (Fig. 46), segment III of palpi subquadrangular.

Thorax dark brown, with spots as in Fig. 43. Fore wings yellowish brown, sterna pale yellow. Legs (Fig. 47) dark brown. Femora dorsally with a row of blunt spines, apically with a quadrangular projection with two blunt spines (Fig. 48). Tarsi with a row of spines. Tarsal claws 0.3 times the length of tarsi. Hind wing pads absent.

Abdomen dark brown, color pattern with segments I–IX with medial yellow markings as in Fig. 43, segment X brown. Posterior margin of terga with spines as in Fig. 49. Sterna pale yellow, segments II–VI with a small tuft of long fine setae laterally on each side. Gills (Fig. 50) translucent white and rounded, 2 times the length of each tergum, main branch of trachea and a few secondary branches pigmented. Paraprocts, with spines apically as in Fig. 51. Cerci pale yellow, apical third yellowish brown with flattened setae basally sclerotized (similar to Fig. 30). Cerci with long spines toward external margin every two segments, terminal filament with long spines toward midline ventrally and dorsally every two segments (similar to Fig. 14).

Etymology. Opacus: from Latin, dark. For the general coloration of this species.

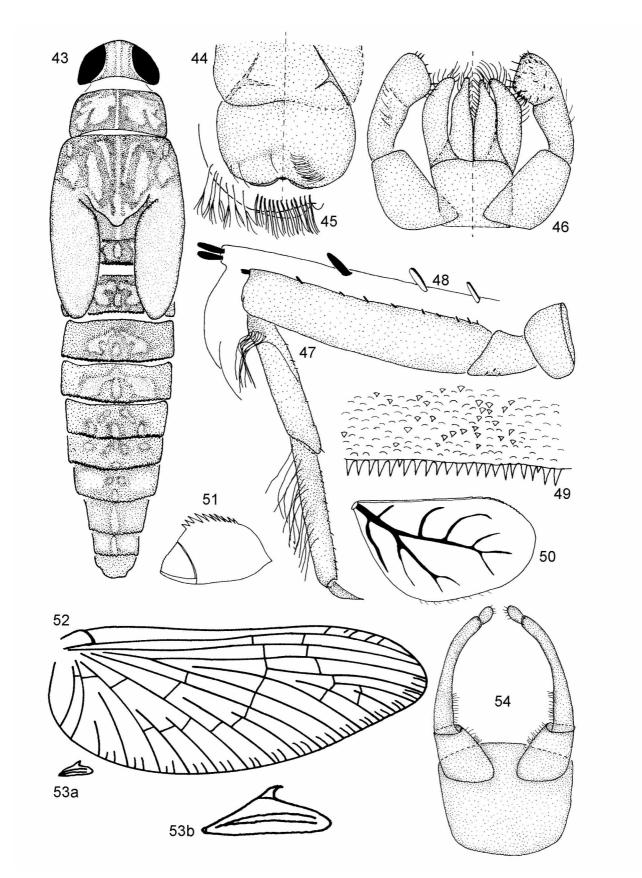
Diagnosis. Cloeodes opacus **n. sp.** can be distinguished from the other species of the genus by the following combination of characters: 1) dorsal edge of femora with a row of blunt spines, apically with a subquadrangular projection (Fig. 48); 2) abdominal color pattern dark brown with segments I–IX with medial yellow markings as in Fig. 43, segment X brown; 3) hind wing pads absent; 4) segment III of labial palpi subquadrangular (Fig. 46); 5) caudal filaments with flattened setae basally sclerotized (similar to Fig. 30), cerci with long spines toward external margin every two segments, terminal filament with long spines toward midline dorsally and ventrally every two segments (similar to Fig. 14).

Material. Holotype: female nymph: ARGENTINA, Misiones, Pque. Prov. Urugua-i, Paraje Ma. Soledad, arroyo afluente Río Tateto, S 25°51'39", W 53°58'55", 410 m, 30/ XI/ 2001, Domínguez, Orce & Nieto colls. Paratypes: 7 nymphs, same data as holotype. Material housed in IFML.

Cloeodes penai (Morihara & Edmunds) (Figs. 52–67)

Notobaetis penai Morihara & Edmunds, 1980: 606. Cloeodes penai Waltz & McCafferty, 1987a: 179. Cloeodes (Notobaetis) penai, Waltz & McCafferty, 1987b: 196

Diagnosis. Cloeodes penai can be distinguished from the other species of the genus by the following combination of characters. In the adult, 1) hind wings small, 0.1 times the length of fore wings (Figs. 52, 53a), costal projection located in the center of anterior margin (Fig. 53b); 2) genitalia (Fig. 54) bases of forceps close together, segment III rounded. In the nymphs, 1) antennae with scape subequal in length to pedicel (Fig. 55); 2) labrum (Fig. 56) with one subapical seta centrally and two setae near lateral margin, anterior margin with



FIGURES 43–51. *Cloeodes opacus* **n. sp.** Nymph. 43, general view, dorsal. Mouthparts (Figs. 44–46): 44, labrum, left d.v., right v.v.; 45, labrum: anterior margin; 46, labium, left d.v., right v.v. 47, leg I; 48, dorsal margin of femur I. 49, posterior margin of tergum IV. 50, gill IV. 51, paraproct. Figs. 52–54. *Cloeodes penai*. Male imago: 52, fore wing; 53a, hind wing; 53b, hind wing detail; 54, genitalia v.v.

basally bifid setae near midline and apically bifid setae near lateral margin; 3) left mandible without setae between prostheca and mola, thumb of molar area transverse to anterior margin (Fig. 57); 4) right mandible with prostheca bifid (Fig. 58); 5) lingua with a rounded projection (Fig. 59); 6) maxillary palpi subequal to galea-lacinia (Fig. 60); 7) labial palpi with segment III rounded (Fig. 61); 8) hind wing pads present, though very small; 9) dorsal edge of femora with a row of pointed spines, and apically rounded (Fig. 63), femora, tibiae and tarsi with bipectinate spines (Figs. 62, 64); 10) tarsal claws without denticles (Fig. 64); 11) posterior margin of abdominal terga with spines (Fig. 65); 12) gills elongate, broadly acute posteriorly, sometimes rounded (Fig. 66); 13) posterior margin of paraprocts with spines (Fig. 67); 14) caudal filaments with simple setae, and with whorl of spines on each segment (as in Fig. 42).

Distribution. Argentina: Córdoba and Tucumán.

Material examined. Paratypes: 2 nymphs: ARGENTINA, Córdoba prov, Copina (ca. 25 km WNW Alta Gracia) elev. 1650 m, 11–14/ IV/ 1967, L. Peña. (FSCA E1010T); 1 male imago (reared): Tucumán prov, La Cascada, La Sala, 7/ XI/ 1981, Domínguez col.; 8 nymphs: Tucumán, San Javier, Arroyo Los Noques, 3/ VIII/ 1978, Bertikian col. Paratypes housed in FAMU, other material in IFML.

Cloeodes stelzneri (Weyenbergh) Nomen dubium

Cloë stelzneri Weyenbergh, 1883: 170. Baetis stelzneri; Eaton, 1885: 171.

Cloeodes stelzneri; Lugo-Ortiz & McCafferty, 1999: 259.

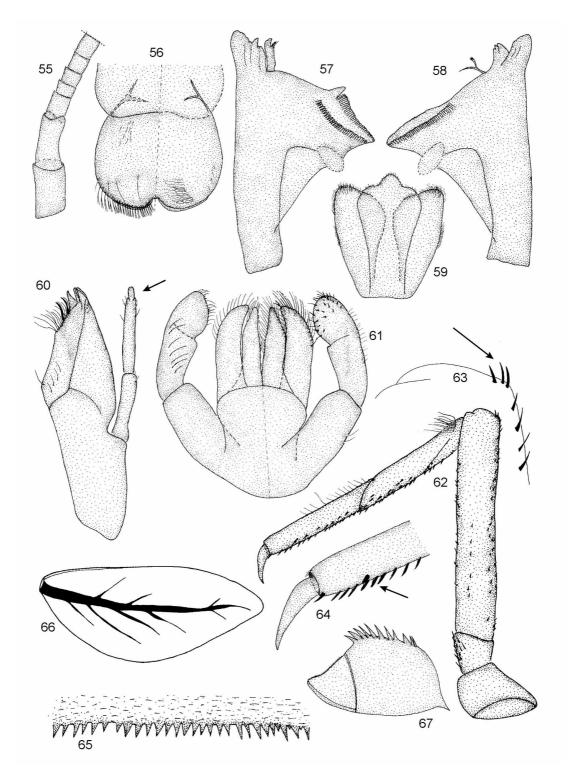
Discussion. This species was originally described by Weyenbergh (1883) from adults from Santa Fe and was placed in *Cloë*. Eaton (1885) transferred this species to the genus *Baetis*, but he worked with material from Córdoba, Argentina (see Eaton, 1885: 171). Later, Lugo-Ortiz & McCafferty (1999) concluded, based on size, distribution, and possession of a small lancetlike costal process on the hind wings, that this species belonged to *Cloeodes*. They also suggested a possible synonymy between this species and *Cloeodes penai* based on similarity of the hind wings. However, this single characteristic is not sufficient for the synonymy of the two species. Moreover, the type material is apparently lost (Lugo-Ortiz & McCafferty, 1999) so it will be impossible to assign fresh material to this species. For these reasons, *Cloeodes stelzneri* is proposed here as a *nomen dubium*.

Distribution. Argentina: Santa Fe and Córdoba.

Discussion

There are presently fifteen species of *Cloeodes* recognized in South America. Four species are known from both nymphs and adults: *C. barituensis, C. espinillo, C. hydation* and *C. penai*. Five species are known only from adults: *C. anduzei, C. aymara, C. binocularis, C. turbinops* and *C. venezuelensis*. The following six species are known only from nymphs: *C. auwe, C. incus, C. irvingi, C. jaragua, C. opacus* and *C. redactus*. Four of the fifteen species of *Cloeodes* listed above are known from Argentina and are discussed here.

The adults of *Cloeodes barituensis*, *C. espinillo*, and *C. penai* are known only from Argentina at this time. *Cloeodes barituensis* is unique among the three species in that it lacks hind wings. It is also notable that in *C. barituensis* the males have paired marginal intercalary veins while the females have single marginal intercalary veins. This has been noted previously in *Cloeodes* (Waltz & McCafferty, 1987a,b), but not recorded in South America. Both *C. espinillo* and *C. penai* possess hind wings but differ in that the costal projection of *C. espinillo* is located in the first third of the anterior margin while that of *C. penai* is located at the center of the anterior margin. The males of all three species have genitalia with forceps bases that are close together.



FIGURES 55–67. *Cloeodes penai.* Nymph. 55, antennae. Mouthparts (Figs. 56–61): 56, labrum, left d.v., right v.v.; 57, left mandible v.v.; 58, right mandible v.v.; 59, hypopharynx v.v.; 60, maxilla v.v.; 61, labium, left d.v., right v.v. 62, leg I; 63, femur I apical margin; 64, tarsal claw I. 65, posterior margin of tergum IV. 66, gill IV. 67, paraproct.

Cloeodes opacus, known only from nymphs, is added to the three species discussed above that are known from both nymphs and adults in Argentina. Cloeodes barituensis is unique among the nymphs in lacking hind wing pads. Cloeodes penai differs from the other three species in having femora that are apically rounded and in having caudal filaments with simple setae and whorls of spines on each segment. Cloeodes barituensis, C. espinillo and C. opacus nymphs share the characters of femora with a subquadrangulate projection apically

and cerci with long spines toward external margin every two segments, and terminal filament with long spines toward midline dorsally and ventrally every two segments. *Cloeodes espinillo* and *C. opacus* can be differentiated from each other by the spines of the dorsal edge of the femora which are blunt in *C. opacus* and pointed in *C. espinillo*. Each of the above species of *Cloeodes* also has a distinctive abdominal color pattern which may be useful in distinguishing the species.

Acknowledgments

We want to thank E. Domínguez and C. Molineri for reading the manuscript. Financial support from the Argentine National Council of Scientific and Technological Research (CONICET) to which one of the authors belongs, is acknowledged.

References

- Alba-Tercedor J. & Peters W.L. (1985) Types and additional specimens of Ephemeroptera studied by Longinos Navás in the Museo de Zoología del Ayuntamiento, Barcelona, Spain. *Aquatic Insects*, 7, 215–227.
- Berner L. (1980) II: Ephemeroptera nymphs. pp. 187–194 *in* Roback *et al.* Results of the Catherwood Bolivian-Peruvian altiplano expedition. Part I. Aquatic insects except Diptera. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 132, 176–217.
- Braasch D. & Soldán T. (1980) *Centroptella* n. gen., eine neue Gattung der Eintagsfliegen aus China (Ephemeroptera: Baetidae). *Reichenbachia*, 18, 123–127.
- Bremer K. (1988) The limits of amino-acid sequence data in angiosperm phylogenetic reconstructions. *Evolution*, 42, 795–803.
- Bremer K. (1994) Branch support and tree stability. Cladistics, 10, 295–304.
- Domínguez, E., Molineri, C., Pescador, M.L., Hubbard, M.D. & Nieto, C. (2006) Ephemeroptera of South America. *In*: Adis, J., Arias, J.R., Rueda-Delgado, G. & K.M. Wantzen (Eds.), *Aquatic Biodiversity in Latin America (ABLA). Vol.* 2. Pensoft, Sofia-Moscow, 646 pp.
- Eaton A.E. (1883–1888) A revisional monograph of recent Ephemeridae or mayflies. *Transaction of the Linnean Society of London*, 2nd Ser Zool, N3, 352 pp.
- Farris J.S., Albert V.A., Källersjö M., Lipscomb D. & Kluge A.G. (1996) Parsimony jackknifing outperforms neighborjoining. *Cladistics*, 12, 99–124.
- Gillies, M.T. (1990) A new genus for the Afrotropical mayfly, *Cloeon dentatum* Kimmins (Ephem., Baetidae). *Entomologist's Monthly Magazine*, 126, 207–208.
- Goloboff P. (1993) Estimating character weights during tree search. Cladistics, 9, 83–91.
- Goloboff P., Farris J.S. & Nixon K. (2003a) TNT: Tree Analysis Using New Technology-version 1.0. Program and documentation available from the authors, and at http://www.zmuc.dk/public/phylogeny (accessed 7 January 2008)
- Goloboff P.A., Farris J.S., Källersjö M., Oxelman B., Ramirez M.J. & Szumick C. (2003b) Improvements to resampling measures of group support. *Cladistics*, 19, 324–332.
- Jacobus L.M., McCafferty W.P. & Gattolliat J-L. (2006) Taxonomy of Afrotropical *Securiops*, a new genus, and *Cloe-odes* Traver (Ephemeroptera: Baetidae). *African Entomology*, 14(1), 129–140.
- Kluge N.J., Studemann D., Landolt P. & Gonser T. (1995) A reclassification of Siphlonuroidea (Ephemeroptera). *Bulle-tin de la Société Entomologique Suisse*, 68, 103–132.
- Lugo-Ortiz C.R. & McCafferty W.P. (1997) *Maliqua*: a new genus of Baetidae (Ephemeroptera) for a species previously assigned to *Afroptilum*. *Entomological News*, 108(5), 367–371.
- Lugo-Ortiz C.R. & McCafferty W.P. (1999) Revision of South American species of Baetidae (Ephemeroptera) previously placed in *Baetis* Leach and *Pseudocloeon* Klapálek. *Annales of Limnologie*, 35(4), 257–262.
- McCafferty W.P. & Lugo-Ortiz C.R. (1995) *Cloeodes hydation*, **n. sp.** (Ephemeroptera: Baetidae): an extraordinary, drought tolerant mayfly from Brazil. *Entomological News*, 106(1), 29–35.
- Morihara D.K. & Edmunds G.F. (1980) *Notobaetis*: a new Genus of Baetidae (Ephemeroptera) from South America. *International Revue gesamten Hydrobiologie*, 65(4), 605–610.
- Navás L. (1922) Estudis sobre Nevropters (Insectes). Arxius de l'Institut de Ciències Barcelona, 7, 179-203.
- Traver J.R. (1938) Mayflies of Puerto Rico. The Journal of Agriculture of the University of Puerto Rico, 22(1), 5–42.
- Traver J.R. (1943) New Venezuelan mayflies. Boletin de Entomologia Venezolana, 2, 79–98.

- Waltz R.D. & McCafferty W.P. (1987a) Generic Revision of *Cloeodes* and description of two new Genera (Ephemeroptera: Baetidae). *Proceedings of the Entomological Society of Washington*, 89(1), 177–184.
- Waltz R.D. & McCafferty W.P. (1987b) Revision of the Genus *Cloeodes* Traver (Ephemeroptera: Baetidae). *Annals of the Entomological Society of America*, 80, 191–207.
- Weyenbergh H. (1883) Bjdrage tot de kennis der Zuid-Amerikaansche Ephemeriden. *Tijdschrift voor Entomologie*, 26, 159–174.

Appendix 1. List of characters and states

- {0 Frontoclypeal suture: 0-at the level of or above the ocelli; 1-below the ocelli.
- {1 Antennae length: 0-short (0.5 times the head capsule); 1-intermediate (1–2.5 times the head capsule); 2-long (3–5.5 times the head capsule).
- {2 Labrum, anterior margin: 0-lightly concave; 1-concave with medial lobe; 2-deeply concave without lobe.
- {3 Labrum, shape: 0-base width=apex width; 1-apex wider than base.
- {4 Labrum, apical lateral setae: 0-simple setae; 1-bifid setae; 2-bifid and bipectinate setae.
- {5 Labrum, apical setae near midline: 0-simple setae; 1-bifid setae; 2-bifid and bipectinate setae.
- {6 Labrum, subapical setae: 0-a row of setae; 1-1 central seta and 2-3 lateral setae; 2-absent.
- {7 Prostheca of right mandible: 0-normal (with denticles apically); 1-seta-like; 2-slender and bifid.
- {8 Prostheca of right mandible: 0-without a transverse seta; 1-with a transverse seta.
- {9 Prostheca of left mandible: 0-normal (with denticles apically); 1-seta-like.
- {10 Prostheca of the left mandible: 0-without a transverse seta; 1-with a transverse seta.
- {11 Thumb of the mola of left mandible: 0-in the same plane as anterior margin; 1-transverse to anterior margin.
- {12 Incisors of mandibles: 0-strongly elongate; 1-normal.
- {13 Incisors of left mandible: 0-fused; 1-fused but denticles visible; 2-deeply cleft in two sets of denticles.
- {14 Incisors of right mandible: 0-fused; 1-fused but denticles visible; 2-incisors cleft in two sets; 3-incisors deeply cleft in two sets.
- {15 Setae between prostheca and mola: 0-absent; 1-present.
- {16 Superlinguae: 0-without spines; 1-with lateral and small spines.
- {17 Lingua: 0-longer than superlinguae; 1-subequal to superlinguae.
- {18 Maxillary palpi: 0-three-segmented; 1-two-segmented, segment II with apical constriction; 2-two-segmented.
- $\{19\ Glossae:\ 0\hbox{--}overlapping\ paraglossae};\ 1\hbox{--}not\ overlapping\ paraglossae}.$
- {20 Glossae: 0-glossae wider than paraglossae; 1-glossae subequal to paraglossae; 2-paraglossae wider than glossae.
- {21 Labial palpi, segment II: 0-without projection; 1-with projection.
- {22 Labial palpi, segment II: 0-medial projection; 1-enlarged anteromedial projection.
- {23 Trochanter: 0-without spines ventrally; 1-with spines ventrally.
- {24 Femora (I,II,III) with spines apically: 0-absent; 1-pointed spines; 2-blunt spines.
- {25 Femora (I,II,III), dorsal margin: 0-with spines; 1-with setae and spines intercalated; 2-with setae.
- {26 Femora (I,II,III), dorsal margin: 0-with blunt spines; 1-with pointed spines.
- {27 Femora (I,II,III): 0-dorsal margin parallel to ventral margin; 1-ventral margin concave.
- {28 Apical margin of the femora: 0-without projection; 1-with a subquadrangulate projection.
- {29 Tibiae and tarsi: 0-tibiae longer than tarsi; 1-tarsi subequal to the tibiae.
- {30 Tibiae (I,II,III): 0-without a row of setae; 1-with a row of long setae dorsally.
- {31 Tibiopatelar suture: 0-shorter than half of length of tibia; 1-longer than half of length of tibia; 2-absent.
- {32 Tarsi (I,II,III): 0-with simple spines; 1-with pectinate spines.
- {33 Tibiae (I,II,III) with a proximal arc of setae: 0-absent; 1-present.
- {34 Claw denticles: 0-absent; 1-with 1 row; 2-with two rows; 3-with minute denticles.
- {35 Hind wing pads: 0-absent; 1-present.
- {36 Gills: 0-serrated margins; 1-smooth margins.
- {37 Gills: 0-rounded; 1-pointed apically.
- {38 Length of gill/length of tergum: 0-1.1-1.9 times the length of tergum; 1-2.0-2.9 times the length of tergum.
- {39 Length/width of gills: 0-1.1-1.9 times the width; 1-2.0-2.9 times the width.
- {40 Abdominal sterna: 0-with a small tuft of long fine setae laterally on each side; 1-with long fine setae distributed throughout; 2-without long fine setae.
- {41 Caudal filaments; 0-simple setae; 1-flattened setae; 2-flattened setae basally sclerotized.
- {42 Terminal filament: 0-with whorl of spines on each segment; 1-with long spines toward midline dorsally and ventrally every 2 segments.
- {43 Cerci, posterior margin: 0-with spines on each segment; 1-with long spines toward external margin every 2 seg-

ments.

- {44 Eyes of male: 0-tuberculate; 1-not tuberculate.
- {45 Vein MA2: 0-joined to MA1; 1-detached basally from MA1.
- {46 Fore wings, crossveins (marginal intercalaries): 0-absent; 1-double; 2-single.
- {47 Hind wings: 0-absent; 1-present.
- {48 Hind wings: 0-with several longitudinal veins; 1-with 2-3 longitudinal veins.
- {49 Tarsal claws I of male: 0-two pointed claws; 1-single blunt pointed claws.
- {50 Number of segments of tarsi I: 0-five; 1-four.
- {51 Forceps: 0-three-segmented; 1-four-segmented.
- {52 Forceps: 0-apical segment rounded; 1-apical segment elongate.
- {53 Forceps: 0-bases expanded medially and close together; 1-bases not expanded medially.

Appendix 2. Synapomorphies common to the 5 shortest trees

Character numbers are in parentheses (See Appendix 1).

Numbered nodes refer to nodes on consensus tree (Fig. A).

Metamonius:

All trees:

-No autapomorphies.

Siphlaenigma janae:

All trees:

-Glossae (20): 1-glossae subequal to paraglossae --> 0-glossae wider than paraglossae

Dabulamanzia improvida:

All trees:

- -Tibiopatelar suture (31): 0-shorter than half of length of tibia --> 1-longer than half of length of tibia
- -Fore wings, cross veins (46): 1-double --> 2-single

Some trees:

- -Glossae (20): 1-glossae subequal to paraglossae --> 2-paraglossae wider than glossae
- -Femora (I,II,III) with spines apically (24): 1-pointed spines --> 2-blunt spines
- -Cerci, posterior margin (43): 0-with spines on each segment --> 1-with long spines toward external margin every 2 segments

Cloeodes penai:

All trees:

-Lingua (17): 1-subequal to superlinguae --> 0-longer than superlinguae

Cloeodes barituensis:

All trees:

-No autapomorphies.

Bernerius incus:

All trees:

- -Thumb of the mola of left mandible (11): 1-transverse to anterior margin --> 0-in the same plane as anterior margin Some trees:
- -Claws denticles (34): 0-absent --> 3-with minute denticles
- -Gills (37): 0-rounded --> 1-pointed apically
- -Abdominal sterna (40): 0-with a small tuft of long fine setae laterally on each side --> 1-with long fine setae distributed throughout

Cloeodes espinillo:

- -Some trees:
- -Gills (37): 0-rounded --> 1-pointed apically

Cloeodes opacus:

All trees:

- -Lingua (17): 1-subequal to superlinguae --> 0-longer than superlinguae
- -Gills (36): 1-smooth margins --> 0-serrated margins
- -Length/width of gills (39): 1-2.0-2.9 times the width --> 0-1.1-1.9 times the width

Camelobaetidius phaedrus:

Some trees:

- -Labrum, apical lateral setae (4): 0-simple setae --> 2-bifid and bipectinate setae
- -Incisors of mandibles (12): 1-normal --> 0-strongly elongate
- -Glossae (20): 1-glossae subequal to paraglossae --> 2-paraglossae wider than glossae
- -Femora(I,II,III),dorsal margin (25): 0-with spines --> 2-with setae
- -Gills (36): 0-serrated margins --> 1-smooth margins

Guajirolus queremba:

- -All trees:
- -Hindwing pads (35): 1-present --> 0-absent
- -Hind wings (47): 1-present --> 0-absent

Some trees:

- -Labrum, anterior margin (2): 1-concave with medial lobe --> 2-deeply concave without lobe
- -Labial palpi, segment II (22): 0-medial projection --> 1-enlarged anteromedial projection
- -Length/width of gills (39): 0-1.1-1.9 times the width --> 1-2.0-2.9 times the width

Cloeodes maculipes:

All trees:

- -Apical margin of the femora (28): 1-with a subquadrangulate projection --> 0-without projection
- -Tarsi (I,II,III) (32): 1-with pectinate spines --> 0-with simple spines
- -Forceps (51): 0-three-segmented --> 1-four-segmented
- -Forceps (53): 0-bases expanded medially and close together --> 1-bases not expanded medially

Node 12:

All trees:

-No synapomorphies

Node 13:

All trees:

- -Superlinguae (16): 0-without spines --> 1-with lateral and small spines
- -Tibiae (I,II,III) with a proximal arc of setae (33): 0-absent --> 1-present

Some trees:

- -Labrum, apical lateral setae (4): 0-simple setae --> 1-bifid setae
- -Labrum, subapical setae (6): 0-a row of setae, or 2-absent --> 1-1 central seta and 2-3 lateral setae
- -Incisors of right mandible (14): 1-fused but denticles visible --> 2-incisors cleft in two sets
- -Labial palpi, segment II (21): 1-with projection --> 0-without projection
- -Femora (I,II,III) with spines apically (24): 0-absent --> 1-pointed spines, or 2-blunt spines
- -Forceps (53): 1-bases not expanded medially --> 0-bases expanded medially and close together

Node 14:

All trees:

- -Frontoclypeal suture (0): 0-at the level of or above the ocelli --> 1-below the ocelli
- -Prostheca of right mandible (7): 1-seta-like --> 0-normal (with denticles apically)
- -Prostheca of right mandible (8): 1-with a transverse seta --> 0-without a transverse seta
- -Prostheca of left mandible (9): 1-seta-like --> 0-normal (with denticles apically)
- -Prostheca of the left mandible (10): 1-with a transverse seta --> 0-without a transverse seta
- -Thumb of the mola of left mandible (11): 0-in the same plane as anterior margin --> 1-transverse to anterior margin
- -Maxillary palpi (18): 0-three-segmented --> 2-two-segmented
- -Glossae (19): 1-not overlapping paraglossae --> 0-overlapping paraglossae
- -Claw denticles (34): 2-with two rows --> 1-with 1 row
- -Vein MA2 (45): 0-joined to MA1 --> 1-detached basally from MA1
- -Fore wings, cross veins (46): 0-absent --> 1-double

- -Tarsal claws I of male (49): 0-two pointed claws --> 1-single blunt pointed claws
- -Number of segments of tarsi I (50): 0-five --> 1-four

Some trees:

- -Labrum, anterior margin (2): 0-lightly concave --> 1-concave with medial lobe
- -Labrum, shape (3): 0-base width=apex width --> 1-apex wider than base
- -Eyes of male (44): 1-not tuberculate --> 0-tuberculate
- -Hind wings (48): 0-with several longitudinal veins --> 1-with 2-3 longitudinal veins
- -Forceps (51): 1-four-segmented --> 0-three-segmented

Node 15:

All trees:

- -Prostheca of right mandible (7): 0-normal (with denticles apically) --> 2-slender and bifid
- -Setae between prostheca and mola (15): 1-present --> 0-absent
- -Maxillary palpi (18): 2-two-segmented --> 1-two-segmented, segment II with apical constriction
- -Trochanter (23): 0-without spines ventrally --> 1-with spines ventrally
- -Femora (I,II,III) (27): 1-ventral margin concave --> 0-dorsal margin parallel to ventral margin
- -Tarsi (I,II,III) (32): 0-with simple spines --> 1-with pectinate spines
- -Length of gill/length of tergum (38): 0-1.1-1.9 times the length of tergum --> 1-2.0-2.9 times the length of tergum Some trees:
- -Labrum, shape (3): 1-apex wider than base --> 0-base width=apex width
- -Claw denticles (34): 1-with 1 row --> 0-absent
- -Gills (36): 0-serrated margins --> 1-smooth margins
- -Length/width of gills (39): 0-1.1-1.9 times the width --> 1-2.0-2.9 times the width
- -Abdominal sterna (40): 2-without long fine setae --> 0-with a small tuft of long fine setae laterally on each side
- -Caudal filaments (41): 0-simple setae --> 1-flattened setae

Node 16:

All trees:

-Hind wing pads (35): 1-present --> 0-absent

Node 17:

All trees:

-Femora (I,II,III), dorsal margin (26): 1-with pointed spines --> 0-with blunt spines

Node 18:

All trees:

- -Apical margin of the femora (28): 0-without projection --> 1-with a subquadrangulate projection
- -Terminal filament (42): 0-with whorl of spines on each segment --> 1-with long spines toward midline dorsally and ventrally every 2 segments

Some trees:

- -Femora (I,II,III) with spines apically (24): 1-pointed spines --> 2-blunt spines
- -Caudal filaments (41): 1-flattened setae --> 2-flattened setae basally sclerotized
- -Cerci, posterior margin (43): 0-with spines on each segment --> 1-with long spines toward external margin every 2 segments