Revision of South American species of Baetidae (Ephemeroptera) previously placed in *Baetis* Leach and *Pseudocloeon* Klapálek

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Keywords: Ephemeroptera, Baetidae, South America, new combinations.

South American species of small minnow mayflies (Insecta: Ephemeroptera: Baetidae) that have been previously placed in Baetis Leach or Pseudocloeon Klapálek are revised. Species that resided in Baetis are shown to include Camelobaetidius alcyoneus, n. comb., C. coveloae, n. comb., C. dryops, n. comb., C. tantillus, n. comb., Cloeodes nocturnus, n. comb., C. stelzneri, n. comb., Fallceon inops, n. comb., F. murphyae, n. comb., F. yaro, n. comb., Moribaetis aneto, n. comb., M. comes, n. comb., and M. socius, n. comb. Species that resided in Pseudocloeon are shown to include Americabaetis albinervis, n. comb., A. bridarolli, n. comb., A. bruchi, n. comb., A. jorgenseni, n. comb., A. oldendorffi, n. comb., A. peterseni, n. comb., A. weiseri, n. comb., Cloeodes turbinops, n. comb., and C. venezuelensis, n. comb. The bases of the revisions are discussed under each species. The presence of Fallceon and Moribaetis in South America is confirmed for the first time.

Révision des espèces Sud-Américaines de Baetidae (Ephemeroptera) classées auparavant dans les genres *Baetis* Leach et *Pseudocloeon* Klapálek

Mots-clés: Ephemeroptera, Baetidae, Amérique du Sud, combinaisons nouvelles.

Les espèces Sud-Américaines d'Ephémères Pisciforma (Ephemeroptera : Baetidae) qui ont été auparavant classées dans les genres Baetis Leach ou Pseudocloeon Klapálek sont révisées. Il est montré que les espèces regroupées sous Baetis incluent Camelobaetidius alcyoneus, n. comb., C. coveloae, n. comb., C. dryops, n. comb., C. tantillus, n. comb., Cloeodes nocturnus, n. comb., C. stelzneri, n. comb., Fallceon inops, n. comb., F. murphyae, n. comb., F. yaro, n. comb., Moribaetis aneto, n. comb., M. comes, n. comb., and M. socius, n. comb. Il est aussi montré que les espèces regroupées sous Pseudocloeon incluent Americabaetis albinervis, n. comb., A. bridarolli, n. comb., A. bruchi, n. comb., A. jorgenseni, n. comb., A. oldendorffi, n. comb., A. peterseni, n. comb., A. weiseri, n. comb., Cloeodes turbinops, n. comb., and C. venezuelensis, n. comb. Les bases des révisions sont argumentées pour chaque espèce. La présence de Fallceon et de Moribaetis en Amérique du Sud est confirmée pour la première fois.

1. Introduction

Knowledge of the biodiversity of South American small minnow mayflies (Ephemeroptera: Baetidae) has considerably increased recently (e.g., McCafferty & Lugo-Ortiz 1995, Lugo-Ortiz & McCafferty 1995, 1996a-d, 1997, 1998, 1999). The following genera

have come to be known from South America: Adebrotus Lugo-Ortiz & McCafferty, Americabaetis Kluge, Apobaetis Day, Aturbina Lugo-Ortiz & McCafferty, Baetodes Needham & Murphy, Bernerius Waltz & McCafferty, Callibaetis Eaton, Camelobaetidius Demoulin, Cloeodes Traver, Cryptonympha Lugo-Ortiz & McCafferty, Guajirolus Flowers, Harpagobaetis Mol, Mayobaetis Waltz & McCafferty, Moribaetis Waltz & McCafferty, Paracloeodes Day, Prebaetodes Lugo-Ortiz & McCafferty, Rivudiva Lugo-Ortiz & McCafferty, Tomedontus Lugo-Ortiz & McCafferty, Tome

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Varipes Lugo-Ortiz & McCafferty, Waltzoyphius McCafferty & Lugo-Ortiz, and Zelusia Lugo-Ortiz & McCafferty. Three additional genera from the Andes and Patagonia are being described elsewhere by Lugo-Ortiz & McCafferty (1999).

Between approximately 1885 and 1971, 22 species of South American Baetidae known only in alate stages were described or placed in either the genus Baetis Leach or Pseudocloeon Klapálek. Since that time, both of these genera have been more thoroughly studied and conceptually restricted, and McCafferty et al. (1992), McCafferty (1998), and Lugo-Ortiz et al. (1999) have recently provided evidence that neither Baetis nor Pseudocloeon is represented in South America. In fact, no Baetis complex genera, of which both Baetis and Pseudocloeon are members, occur in South America. Surveys of extensive collections of larval baetids from throughout South America confirm this, and adult characteristics historically used to place South American species in Baetis or Pseudocloeon no longer apply.

As part of the necessary revision of South American Baetidae, we herein reassign 21 of the 22 species that by default have remained in Baetis or Pseudocloeon, and show them to belong to Americabaetis, Camelobaetidius, Cloeodes, Fallceon Waltz & McCafferty, or Moribaetis. Reassignments have been accomplished with various degrees of certainty, depending on how limited the material or information on the species involved is. Certain of the recombinations could be regarded as provisional and essentially represent our best estimates of where species belong. A few of the species themselves are so obscure with respect to species-level characters that they could be regarded as nomina dubia, and we will doubtfully be able to associate any additional materials with their names in the future. Nonetheless, we maintain that it is important that the generic assignments of all the South American baetids be updated to reflect the considerable recent advances in the systematics of this group. Leaving those species in *Baetis* or *Pseudocloeon* would only confound emerging hypotheses and concepts of world relationships and biogeography.

Fallceon and Moribaetis are documented for the first time from South America in this study, although their occurrences on the continent were predicted by McCafferty (1998). Previously, Fallceon was known from North and Central America and the Antilles (McCafferty et al. 1992, Lugo-Ortiz et al. 1994, McCafferty 1998), and Moribaetis was known from Central America and Mexico (Waltz & McCafferty 1985, Lugo-Ortiz & McCafferty 1994, 1996e,

McCafferty & Lugo-Ortiz 1998). The presence of these two genera also supports their hypothesized Neotropical origin (McCafferty 1998), similar to that of several other Western Hemisphere baetid genera such as Callibaetis and Paracloeodes (McCafferty et al. 1992, Lugo-Ortiz & McCafferty 1996c, McCafferty 1998).

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The 21 revised species are treated below in alphabetical order according to their recombined names under the headings "Species previously in Baetis" and "Species previously in Pseudocloeon." The Argentinian species Baetis weiseri Navás (1922b) is being treated elsewhere because it was found to belong to a new genus described in another study by Lugo-Ortiz & McCafferty (1999).

2. Species previously assigned to *Baetis*

2.1. Camelobaetidius alcyoneus (Traver), new combination

Baetis alcyoneus Traver 1943: 85.

Traver (1943) described this species based on one male adult and one female adult from Venezuela. Traver (1943) indicated that the genital forceps were broken and only illustrated the basal portion thereof (Traver 1943 : Fig. 4a). The hindwings (Traver 1943 : Fig. 4b), however, clearly demonstrate the costal undulation generically diagnostic of Camelobaetidius (e.g., as discussed and illustrated under its junior synonym Dactylobaetis by Edmunds et al. [1976]).

2.2. Camelobaetidius coveloae (Traver), new combination

Baetis coveloae Traver 1971: 61.

Traver (1971) described this species based on a series of 32 male adults from Uruguay. Traver (1971) indicated that she assigned the species to Baetis rather than to Dactylobaetis because of the presence of a spine between the male genital forceps (Traver 1971: Fig. 2). Nonetheless, the morphology of the hindwings (Traver 1971: Fig. 6) is consistent with Camelobaetidius, not Baetis, and immature larvae of Camelobaetidius collected from near the type locality are likely associated with it (Traver 1971). Moreover, the elongate terminal forceps segment of this species is similar to that of many other South American Camelobaetidius. We regard the genital spine as a species variability within Camelobaetidius.

2.3. Camelobaetidius dryops (Needham & Murphy), new combination

Baetis dryops Needham & Murphy 1924: 53.

Needham & Murphy (1924) described this species from one male adult and two female adults from Peru. Our examination of one of the hindwings of the holotype clearly revealed the costal undulation associated with *Camelobaetidius*. The elongate terminal forceps of the holotype, moreover, is characteristic of most *Camelobaetidius* species. The females originally regarded as the same species, however, are neither conspecific nor congeneric with the male holotype.

2.4. Camelobaetidius tantillus (Needham & Murphy), new combination

Baetis tantillus³Needham & Murphy 1924: 53.

Needham & Murphy (1924) described this species based on female adults collected from Peru. The holotype we examined has the hindwing costal undulation typical of *Camelobaetidius*. Interestingly, however, the hindwing figure labeled as *B. tantillus* by Needham & Murphy (1924: Fig. 157a) does not agree with the holotype specimen and therefore is either inaccurate or based on another genus and species.

2.5. Cloeodes nocturnus (Navás), new combination

Baetis nocturnus Navás 1922a: 199.

Navás (1922a) described this species from an unspecified number of adults from Córdoba Province, Argentina. According to Alba-Tercedor & Peters (1985), the abdomen of the type is lacking, and evidently because the species is damaged in other respects, they were unable to discern whether it is male or female. Navás (1922a) indicated that the hindwings have a small costal process in the basal one-third of the wing and have two longitudinal veins. This combination is consistent only with species of *Cloeodes* in South America (Waltz & McCafferty 1987).

2.6. Cloeodes stelzneri (Weyenbergh), new combination

Cloe stelzneri Weyenbergh 1883 : 170. Baetis stelzneri (Weyenbergh) : Eaton 1885 : 171.

Weyenbergh (1883) described this species from an unspecified number of male and female adults from Santa Fe Province, Argentina. The type material is apparently lost. Based on body size, geographic distribution, and Weyenbergh's (1883) indication that the hindwings possess a small lancetlike costal process, we assign this species to *Cloeodes*. The similarity with *Cloeodes penai* (Morihara & Edmunds), from Córdoba and Tucumán Provinces, Argentina, is striking (Waltz & McCafferty 1987: Fig. 23), and it is quite possible that *C. penai* will eventually prove to be a synonym of *C. stelzneri*.

2.7. Fallceon inops (Navás), new combination

Baetis inops Navás 1912: 195.

Navás (1912) described this species from an unspecified number of subimagos from Paraguay. There are two specimens labeled "Typus," one of which lacks the abdomen (Alba-Tercedor & Peters 1985), and there is some doubt if they are conspecific. The hooked costal process of the hindwings (Navás 1912: 3a), which in Western Hemisphere baetids with double marginal intercalaries in the forewings is only well developed in Fallceon, allows placement of those subimagos in Fallceon. Because the description was based on subimagos, the species will probably remain dubious.

2.8. Fallceon murphyae (Hubbard), new combination

Baetis melleus Needham & Murphy 1924: 52, nec B. melleus Curtis 1834.

Baetis murphyi Hubbard 1974: 358 (new name). Baetis murphyae Hubbard 1976: 196 (emendation).

Needham & Murphy (1924) described this species based on one male adult from Argentina and two female adults from Peru. The association between the two sexes is probably incorrect, and we base our analysis on the figures of the male provided by Needham & Murphy (1924). It is apparent to us from the hindwings and the morphology of the genital forceps (Needham & Murphy 1924 : Figs. 148a, 158) that this species should be placed in Fallceon. Although the hindwing figure provided by Needham & Murphy (1924: Fig. 148a) shows an erect rather than hooked costal process (both types are found in Fallceon), we believe that the costal process of this species is probably hooked. Traver (1971) indicated that the hindwings of this species and of B. yaro Traver, which has a hooked costal process (Traver 1971: Fig. 7; see below), are similar. Moreover, Traver apparently had access to the type material of this species (although it cannot be found at Cornell) because we have in our possession handwritten notes by her (on her copy of the paper by Needham & Murphy) indicating that the illustration of the hindwings was "fair only." It is likely that, at the time of mounting the hindwing, the costal process folded or was broken, and thus an incorrect rendition was drawn in Needham & Murphy (1924).

2.9. Fallceon yaro (Traver), new combination

Baetis yaro Traver 1971: 62.

Traver (1971) described this species based on one male adult from Uruguay. The hooked costal process of the hindwings (Traver 1971: Fig. 7) and the general morphology of the genital forceps (Traver 1971: Fig. 3) leave no doubt that the species belongs to Fallceon.

260

2.10. Moribaetis aneto (Traver), new combination

Baetis aneto Traver 1971: 58.

Traver (1971) described this species from a large series of male and female adults from Uruguay. The illustrations of the hindwing and male genitalia provided by Traver (1971: Figs. 1, 4) are clearly typical of *Moribaetis*. As in *Moribaetis*, the relatively broad hindwings have a small, erect costal process in the basal one-third of the wing and three longitudinal veins. With respect to the genitalia, *M. aneto* shows the apomorphic distomedial process on the first segment characteristic of the *Baetodes* complex and the two small humps between the forceps also found in the type species of *Moribaetis*, *M. maculipennis* (Flowers) (Lugo-Ortiz & McCafferty 1996a: Fig. 11).

2.11. Moribaetis comes (Navás), new combination

Baetis comes Navás 1912: 194.

Navás (1912) described this species from an unspecified number of adults from São Paulo, Brazil. Although the hindwings are broken of the type specimen (Alba-Tercedor & Peters 1985), the illustration of the hindwing provided by Navás (1912: Fig. 1a) clearly indicates that this species belongs to *Moribaetis* (see Lugo-Ortiz & McCafferty 1996a). Moreover, Navás (1912) stated that the species was similar to *Baetis salvini* Eaton, a species that was shown to belong to *Moribaetis* by Waltz & McCafferty (1985).

2.12. Moribaetis socius (Needham & Murphy), new combination

Baetis socius Needham & Murphy 1924: 52.

Needham & Murphy (1924) described this species from one female subimago from Peru. One hindwing of the holotype (see Needham & Murphy 1924: Fig. 153a), which we were able to examine, is entirely characteristic of *Moribaetis* (see Lugo-Ortiz & McCafferty 1996). It will be difficult, however, to know this species precisely because it was based on a female subimago — a sex and stage often devoid of specific diagnostic characters.

3. Species previously in Pseudocloeon

3.1. Americabaetis albinervis (Navás), new combination

Pseudocloeon albinerve Navás 1923: 443.

Navás (1923) described this species from a series of adults from Valparaiso Province, Chile. Certain characteristics associated with this species (i.e., the

absence of hindwings, body size, and collection data) are highly suggestive that it belongs to *Americabaetis* (see Lugo-Ortiz & McCafferty 1996d). Alba-Tercedor & Peters (1985) indicated that the remaining type of this species lacks the head and the apex of the abdomen. We regard the generic recombination provisional, and, given the very brief and inconsequential description of species-level characteristics in Navás (1923), it may be impossible to assign any material to this specific name in the future.

3.2. Americabaetis bridarolli (Navás), new combination

Pseudocloeon bridarolli Navás 1933: 113.

Navás (1933) described this species from an unspecified number of male and female adults from Santa Fe Province, Argentina. We have been unable to locate the type, and assume that it is lost. We provisionally assign this species to *Americabaetis* based on the absence of hindwings, body size, and collection data (Lugo-Ortiz & McCafferty 1996d). Further supporting this assignment are notations by Navás (1933) that the species was similar to *Pseudocloeon bruchi* Navás and *P. jorgenseni* (Esben-Petersen). This is significant because there are sufficient characteristics associated with the latter species for an undoubted placement in *Ameri-cabaetis* (see below).

3.3. Americabaetis bruchi (Navás), new combination

Pseudocloeon bruchi Navás 1926: 34.

Navás (1926) described this species from an unspecified number of male and female adults from Córdoba Province, Argentina. Based on the absence of hindwings, the body size, the collection data, and the statement by Navás (1926) that this species was similar to *P. jorgenseni*, a species clearly assignable to *Americabaetis* (see below), we provisionally are able to place it in *Americabaetis*. According to Alba-Tercedor & Peters (1985), the type lacks the head, right wing, and abdomen. The condition of the type and the incomplete description by Navás (1926) suggest that any species-level concept associated with the name will probably remain dubious.

3.4. Americabaetis jorgenseni (Esben-Petersen), new combination

Cloeon jorgenseni Esben-Petersen 1909: 551.

Pseudocloeon jorgenseni (Esben-Petersen): Ulmer 1920: 125.

Esben-Petersen (1909) described this species from an unspecified number of male and female adults from Mendoza Province, Argentina. The fate of the type material is unknown. The absence of hindwings, the body size range, and most significantly the figure of the male genitalia provided by Esben-Petersen (1909: Fig. 1), which is typical of *Americabaetis* (see Lugo-Ortiz & McCafferty 1996d), clearly indicate that this species belongs to *Americabaetis*.

3.5. Americabaetis oldendorffi (Weyenbergh), new combination

Oxycypha oldendorffii Weyenbergh 1883: 173. Cloeon oldendorffii (Weyenbergh): Eaton 1885: 191. Baetis oldendorffi (Weyenbergh): Banks 1913: 85. Pseudocloeon oldendorffii (Weyenbergh): Ulmer 1920: 125.

We can only provisionally assign this species to Americabaetis based on the absence of hindwings, its body size, and its known geographic distribution in northern Argentina and southern Brazil. The specific epithet has been spelled in various ways (see synonymy above); however, the spelling "oldendorffi" is correct because the species was named after C. Oldendorff. The type material of this species is apparently lost and Weyenbergh's (1883) description and figure of the forewing (Weyenbergh 1883: Pl. 10, Fig. 6) provide no clues. The incomplete figure of the male genital forceps provided by Needham & Murphy (1924: Fig. 161) is inconsequential, and in any case could not be relied on because there is no assurance that the specimens studied by Needham & Murphy were actually Weyenbergh's species.

3.6. Americabaetis peterseni (Hubbard), new combination

Cloeon brunneum Esben-Petersen 1909: 552, nec C. brunneum Rambur 1842.

Pseudocloeon brunneum (Esben-Petersen): Ulmer 1920: 125.

Cloeon peterseni Hubbard 1974 : 357 (new name). Pseudocloeon peterseni (Hubbard) : Hubbard et al. 1992 : 204.

Esben-Petersen (1909) described this species from an unspecified number of male and female adults and subimagos from Mendoza Province, Argentina. Based on the absence of hindwings, the body size, the collection data, and the generically diagnostic figure of the male genitalia provided by Esben-Petersen (1909: Fig. 3), it is clear that this species belongs to *Americabaetis*.

3.7. Americabaetis weiseri (Navás), new combination

Pseudocloeon weiseri Navás 1926: 34.

Navás (1926) described this species from an unspecified number of female adults from Catamarca and Córdoba Provinces, Argentina. Absence of hindwings, the body size, the collection data, and its evidently close similarity to females of other species of Americabaetis allow a provisional placement in Americabaetis. One specimen labeled "Typus" and deposited in the Museo de Zoología del Ayuntamiento in Barcelona, Spain, lacks the head, legs, and caudal filaments (Alba-Tercedor & Peters 1985). Another female specimen, also labeled "Typus," is deposited in the Museo Argentino de Ciencias Naturales Bernardino Rivadavia in Argentina (Domínguez 1989). Although the species is most appropriately placed in Americabaetis, the fact that the species was based on females will make any future identification of the species difficult.

3.8. Cloeodes turbinops (Needham & Murphy), new combination

Pseudocloeon turbinops Needham & Murphy 1924: 57.

Needham & Murphy (1924) described this species from two male adults and one female adult from British Guiana. Our examination of the holotype of this species provided little data for placing it generically because of its extremely poor condition. However, based on the figures of the forewings and the genital forceps of the holotype provided by Needham & Murphy (1924 : Figs. 150, 160), we provisionally assign this species to Cloeodes. The forewing is relatively narrow-elongate and is somewhat pointed apically, and the forceps are relatively erect with a broad segment 2 and a relatively elongate and ovoid segment 3. These characteristics are commonly found in male adults of Cloeodes (Waltz & McCafferty 1987). The female adult that Needham & Murphy (1924) associated with the holotype is neither conspecific nor congeneric. This was also the opinion of R. D. Waltz when he formerly examined the material (personal communication). It will be difficult to associate future specimens with this species because of uncertainties regarding its specific characteristics.

3.9. Cloeodes venezuelensis (Traver), new combination

Pseudocloeon venezuelensis Traver 1943: 92.

Traver (1943) described this species from two male adults and three female adults from Venezuela. Traver (1943) indicated that the male turbinate eyes were erect, cylindrical, and with a slightly larger diameter apically than basally. As far as we know, only male adults of *Cloeodes* show a similar eye morphology in

South America, and on that basis we provisionally assign the species to *Cloeodes*. The male genitalia of *C. venezuelensis* are somewhat similar to those of other species of *Cloeodes*; however, *C. venezuelensis* has a distinctive spine between the forceps (Traver 1943: Fig. 7).

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