

# Definition and Reorganization of the Genus *Pseudocloeon* (Ephemeroptera: Baetidae) With New Species Descriptions and Combinations

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## ABSTRACT

*Labiobaetis* Novikova & Kluge (Ephemeroptera: Baetidae) is synonymized with *Pseudocloeon* Klapálek on the basis of adult morphology now known from throughout its Holarctic, Afrotropical, Oriental, and Australian range and consistent with that of *P. kraepelini* Klapálek, the type of *Pseudocloeon*. Adult and larval stages of *Pseudocloeon* are characterized and compared with those of other genera of the *Baetis* complex. All species previously assigned to *Labiobaetis* and several species previously assigned to *Baetis* are reassigned to *Pseudocloeon*. Tabular summaries of *Pseudocloeon* species show nomenclatural revisions, regional distribution, and diagnostic character variability among larvae. *Pseudocloeon hypodetum*, new species, *P. inconspicuum*, new species, and *P. plicatile*, new species, are described from Australia. *Pseudocloeon involutum*, new species, *P. petersorum*, new species, *P. tuberalpis*, new species, *P. vitile*, new species, *P. vultuosum*, new species, and *P. xeniolium*, new species, are described from Papua-New Guinea. Biogeographic data are shown to be congruent with the revised systematics of *Pseudocloeon*. Occurrences of *Pseudocloeon* in Papua-New Guinea and Australia are probably related to dispersal events as recent as the middle Miocene.

## INTRODUCTION

Klapálek (1905) erected the genus *Pseudocloeon* (Ephemeroptera: Baetidae) for *P. kraepelini* Klapálek, a Javanese species known from three male adults and one male subimago. Klapálek (1905) characterized *Pseudocloeon* by comparing it with *Cloeon* Leach, indicating that, although adults of both genera only possessed one pair of wings, those of *Pseudocloeon* could be distinguished by the presence of double intercalaries along the forewing margin. As a consequence, for the greater part of this century, the absence of hindwings and presence of double marginal intercalaries in the forewings became the primary criteria for assigning baetid adults to *Pseudocloeon*. The larval stage of *P. kraepelini* has never been described. However, beginning with associations of larvae with North American adults known as *Pseudocloeon*, it became generally assumed that baetid larvae that

lacked both hindwings pads and a developed median caudal filament were referable to *Pseudocloeon*. Traver (1932), within the construct of a key to baetid genera based on larvae, was the first to advance such a concept for *Pseudocloeon*. Since then, the combination of these characteristics has been used to assign baetids to *Pseudocloeon* throughout the world. As such, it was a relatively simple matter to assign all baetids either to *Callibaetis* Eaton, *Cloeon* Leach, *Baetis* Leach, or *Pseudocloeon*.

Although the notion that hindwings had been lost numerous times in different evolutionary lineages in Baetidae was being raised (e.g., Spieth 1933; Day 1955; Edmunds *et al.* 1976; Keffermüller 1980; Müller-Liebenau 1981; Waltz & McCafferty 1985ab, 1987c; McCafferty & Waltz 1990), early characterization of *Pseudocloeon* resulted in a virtually uncritical assignment of hindwingless baetids to the genus worldwide. However, studies newly emphasizing larval morphology to delineate baetid taxa (e.g., Müller-Liebenau 1981, 1984ab; Waltz & McCafferty 1985ab, 1987bc) actually revealed that concepts of *Pseudocloeon* were problematic. This was because reductionist characteristics such as lack of hindwings and median caudal filament were being associated with several different morphologically and otherwise distinct lineages.

The taxonomic problems surrounding *Pseudocloeon*, which mainly resulted from the absence of any larval morphology that could be associated with the type species and a poor understanding of reliable adult characterization among most baetid genera, generated considerable opinions and controversy. Keffermüller (1980) proposed the transfer of all species of *Pseudocloeon* to *Baetis* on the basis that several *bona fide* species of *Baetis* lacked hindwings. Müller-Liebenau (1981) attempted to restrict the concept of *Pseudocloeon* to the Oriental region only, speculating that species previously assigned to *Pseudocloeon* in other regions probably were not congeneric. Müller-Liebenau (1981) proposed a list of larval characteristics that might distinguish Oriental *Pseudocloeon*, but that were essentially baseless because the larva of *P. kraepelini* was not known. Waltz & McCafferty (1985a, 1987c) proposed the restriction of the concept of *Pseudocloeon* to *P. kraepelini* as a provisional taxonomic measure, arguing that indiscriminately transferring all species of *Pseudocloeon* to *Baetis* or relying on any presumptive distributional or morphological concepts to assign species to *Pseudocloeon* would hinder phylogenetic and taxonomic studies. Instead, Waltz & McCafferty (1985a, 1987c) indicated that some species of *Pseudocloeon* might be transferred to known genera and that new genera might be erected for other species. McCafferty & Waltz (1990) indeed did demonstrate that North American species of *Pseudocloeon* required reassignment to several genera. Novikova & Kluge (1987) synonymized *Pseudocloeon* with *Baetis* without providing any rationale, and, although that synonymy has not been generally recognized, Gillies (1994) combined all Afrotropical species of *Pseudocloeon* at that time to *Baetis*.

Recipient genera for former species of *Pseudocloeon* have included *Acenitrella* Bengtsson, *Apobaetis* Day, *Baetiella* Uéno, *Baetis*, *Baetodes*

Needham & Murphy, *Barbaetis* Waltz & McCafferty (temporarily), *Cloeodes* Traver, *Labiobaetis* Novikova & Kluge, *Liebiella* Waltz & McCafferty, *Ophelminotostoma* Waltz & McCafferty, *Plauditus* Lugo-Ortiz & McCafferty, and *Pseudopannota* Waltz & McCafferty (Müller-Liebenau 1981; Waltz & McCafferty 1985b, 1986, 1987abc, 1994; Flow-ers 1987; McCafferty & Waltz 1990; Elouard *et al.* 1990; Gillies *et al.* 1990; Waltz 1993; Gillies 1994; McCafferty & Waltz 1995; Lugo-Ortiz & McCafferty 1997, 1998d). Despite revisionary efforts, however, a significant number of species have technically remained in *Pseudocloeon* because of insufficient morphological data associated with them, poor original descriptions and figures, or the loss or inaccessibility of type specimens. In addition, several species initially transferred from *Pseudocloeon* to *Baetis* (e.g., McCafferty & Waltz 1990, Gillies 1994) required further reassignment. Such assignments were begun by Waltz & McCafferty (1987c), McCafferty & Waltz (1990), Waltz *et al.* (1994), and Lugo-Ortiz & McCafferty (1997, 1998d).

We have recently become engaged in the study of baetids from Southeast Asia and Australia in order to assess their faunal composition (Lugo-Ortiz & McCafferty 1998bc, 1999ab). This work and our broad-based studies of species assigned to the genus *Labiobaetis* from throughout the world have revealed sufficient evidence to substantiate the equivalency of *Labiobaetis* and *Pseudocloeon*. We therefore herein synonymize *Labiobaetis* with *Pseudocloeon*, reassign all species of *Labiobaetis* and several species of *Baetis* to *Pseudocloeon*, and for the first time characterize *Pseudocloeon* adequately in both the adult and larval stages. We also describe nine new species of *Pseudocloeon* from Papua-New Guinea and eastern Australia. The material examined is housed in the Purdue Entomological Research Collection, West Lafayette, Indiana, USA.

#### Genus PSEUDOCLOEON Klapálek

*Pseudocloeon* Klapálek 1905: 105.

*Baetis atrebatinus* group Müller-Liebenau 1970: 150.

*Baetis propinquus* group Morihiro & McCafferty 1979a: 130.

*Baetis molawinensis* group Müller-Liebenau 1984b: 260.

*Baetis* (*Labiobaetis*) Novikova & Kluge 1987: 13. New synonym.

*Labiobaetis* Novikova & Kluge: McCafferty & Waltz 1995: 20. New synonym.

*Baetis* (*Mullerbaetis*) Kang & Yang, in Kang *et al.* 1994: 32. New synonym.

*Cymulabaetis* McCafferty & Waltz 1995: 25. New synonym.

**Description.**—LARVA: Antennal scapes usually with distolateral process (Figs. 1, 2; McCafferty & Waltz 1995; Fig. 12), occasionally distolaterally chamfered (Fig. 43; Lugo-Ortiz & McCafferty 1997; Fig. 39), or occasionally unmodified; mandibles with fused incisors and apically denticulate prosthcae (Figs. 11, 12, 21, 22, 33, 34, 46, 47, 58, 59, 70, 71, 82, 83, 94, 95, 106, 107); maxillary palp segment 2 usually distomedially excavated (Fig. 3, 96; McCafferty & Waltz 1995; Fig. 14; Lugo-Ortiz & McCafferty 1997; Figs. 6, 19, 31, 44, 79), sometimes constricted (Figs. 23, 72; Lugo-Ortiz & McCafferty 1997; Fig. 55), or

rarely unmodified (Figs. 13, 35, 48, 60, 84, 108); paraglossae subrectangular (Figs. 14, 24, 36, 49, 61, 73, 85, 97, 109); labial palp segment 2 with distomedial projection usually broad and long (Figs. 24, 73, 97), oftentimes thumblike (Figs. 14, 36, 49, 61, 85, 109), or rarely poorly developed (McCafferty & Waltz 1995; Fig. 8); hindwings pads present, rudimentary, or absent; villopore usually present, sometimes rudimentary, rarely absent, or with any combination of these conditions on different femora; tarsal claws with one row of denticles (Figs. 16, 26, 38, 51, 63, 75, 87, 99, 111); gills on abdominal segment 1 present or absent; abdominal terga with numerous scale bases (Figs. 17, 27, 39, 52, 64, 76, 88, 100, 112); median caudal filament well developed. ADULT: Forewings with double marginal intercalaries (Müller-Liebenau 1981; Figs. 2kn); hindwings present or absent; when present, hindwings somewhat narrow-elongate, with two longitudinal veins, with weakly developed costal process in basal one third (Fig. 4; Gillies 1994; Fig. 2), or entirely lacking costal process (Fig. 5; Barnard 1932; Fig. 12e; Gillies 1949; Figs. 10, 14, 15; Agnew 1961; Figs. 3a, 4b, 5a; Köpcke 1980; Fig. 11b; Müller-Liebenau 1981; Figs. 2hl; Gillies 1993; Fig. 2); males with variously developed sclerotized basomedial process between genital forceps; forceps segment 2 oftentimes medially broadened in basal one third to one half; forceps segment 3 short, oftentimes globular and partially fused to segment 2 (Figs. 6-8; Gillies 1949; Figs. 1, 2; Morihiro & McCafferty 1979a; Figs. 12, 15, 18; Köpcke 1980; Figs. 1a, 10a, 27a, 30, 32a; Müller-Liebenau 1981; Figs. 2gjm; Gillies 1993; Figs. 3, 15; Gillies 1994; Fig. 3; Durfee & Kondratieff 1997; Fig. 2).

*Type species.*—*Pseudocloeon kraepelini* Klapálek 1905: 105.

*Species included and distribution.*— See Table 1.

*Discussion.*—Novikova & Kluge (1987) erected *Labiobaetis* as a subgenus of *Baetis* to incorporate all species in the *B. atrebatinus*, *B. molawinensis*, and *B. propinquus* species groups as defined by Müller-Liebenau (1970, 1984b) and Morihiro & McCafferty (1979a). McCafferty & Waltz (1995) raised *Labiobaetis* to generic rank and showed that it belonged to the *Baetis* complex of genera (see below), defining it by the presence of a distomedial excavation on segment 2 of the maxillary palps and a distolateral process on the antennal scapes in the larval stage. Additionally, McCafferty & Waltz (1995) erected the genus *Cymulabaetis* to include two problematic species whose larvae did not entirely agree with their definition of *Labiobaetis*. Lugo-Ortiz & McCafferty (1997) expanded the concept of *Labiobaetis* somewhat to include species as larvae with or without a distolateral process on the antennal scapes, with a distomedial constriction or excavation on segment 2 of the maxillary palps, with or without hindwings, with a villopore that sometimes is not apparent, and with or without a pair of gills on abdominal segment 1. Gradational characteristics of the antennal scapes, segment 2 of the maxillary palps, and villopore included the concept of *Cymulabaetis*, which was thus synonymized with *Labiobaetis* (Lugo-Ortiz & McCafferty 1997). Kang & Yang (in Kang *et al.* 1994) erected *Müllerbaetis* as a subgenus of *Baetis*. Waltz & McCafferty

(1997) pointed out that the type species of *Müllerbaetis*, *B. molawinensis* Müller-Liebenau, clearly belonged to *Labiobaetis* and thus synonymized *Müllerbaetis* with *Labiobaetis*.

Species assigned to *Labiobaetis* have been reported from the Afrotropical, Holarctic, and Oriental regions (see, e.g., Müller-Liebenau 1970, 1981, 1982, 1984ab; Morihiro & McCafferty 1979ab; Müller-Liebenau & Hubbard 1985; Novikova & Kluge 1987; McCafferty & Waltz 1995; Lugo-Ortiz & McCafferty 1997). Specifically in the Oriental region, larvae of *Labiobaetis* usually have reduced hindwings pads or lack hindwings pads, and gills on segment 1 are usually absent; also known adults usually lack hindwings. Reductive trends have been particularly evident in species described from Malaysia, Indonesia, and the Philippines (Müller-Liebenau 1981, 1982, 1984ab). The genitalia of known male adults from these areas, however, remain characteristic, and realization of range of larval characteristics within this group has allowed diagnosis of atypical larvae.

The assignment of certain species to *Labiobaetis* (especially in the Afrotropical and Oriental regions) has relied on a combination of larval characteristics, particularly if the conditions of the antennal scapes, maxillary palps, or villopore are atypical (see relative frequency of characteristics in Description and specifically in Table 2). We have found, however, that male adults are characteristically uniform. The subgenital base of the male genitalia possesses a sclerotized median platelike process, although this process does vary in degree of development (see Description; Figs. 6-8). With respect to the forceps, segment 2 tends to be conspicuously broadened medially, and segment 3 tends to be more or less short, rounded, and partially fused to segment 2. In those species with two pairs of wings, the hindwings are narrow-elongate with two longitudinal veins and with a weakly developed costal process at most (Figs. 4, 5).

Waltz & McCafferty (1985a, 1987c) indicated that the male genitalia of *P. kraepelini* (Fig. 6) were of the same type as those of the *B. atrebatinus* group. Moreover, Waltz & McCafferty (1985a, 1987c) suggested that *P. kraepelini* was probably congeneric with the species in that group. As previously indicated, the larval stage of *P. kraepelini* remains unknown. Nonetheless, because the male genitalia of *P. kraepelini* are equivalent to those of *Labiobaetis*, and in particular with reference to the type of *Labiobaetis*, *L. atrebatinus* (Eaton), as indicated by Waltz & McCafferty (1985a, 1987c), we must conclude that *Pseudocloeon* encompasses the present concept of *Labiobaetis*. We consequently have placed *Labiobaetis* as a junior synonym of *Pseudocloeon*.

Because larvae of *Pseudocloeon* are somewhat morphologically heterogeneous (Table 2) (most apparent when comparing larvae of relatively plesiotypic species of *Pseudocloeon* from the Holarctic with highly apotypic species of *Pseudocloeon* from the Orient and Australia), it might be argued that there are two distinct, but closely related, genera involved. However, close scrutiny of all species reveals numerous species whose larvae are variously the morphological extremes (Table 2). Essentially, there is no consistent morphological gap present

when all species are considered. Any recognition of groups that might be homogeneous on a regional basis becomes untenable on a global scale. Preliminary phylogenetic analysis also reveals that any attempt to maintain *Labiohaetis* for certain plesiotypic species would also create a paraphyletic taxon and leave the placement of several species questionable. Other taxa of Ephemeroptera are also known to express the kinds of phenotypic gradation or global heterogeneity observed in *Pseudocloeon*. For example, in the genus *Acanthiops* Waltz & McCafferty there are species that express extremes of plesiotypic and apotypic characterization, but when all species are considered, the extremes are at the ends of a gradual continuum of character development (Barber-James & McCafferty 1997, Lugo-Ortiz & McCafferty 1998a). The Holarctic and Oriental heptageniid genus *Epeorus* Eaton is a prime example of a globally heterogeneous group in which all attempts to divide it up into different genera that may be consistently characterized in certain regions have failed because intermediate species are always found outside the regions (Jensen 1972).

As a result of the present synonymy, all species of *Labiohaetis* are formally transferred to *Pseudocloeon* (Table 1). It should be noted that Lugo-Ortiz & McCafferty (1997) assigned the Afrotropical species *B. gambiae* Gillies to *Labiohaetis*. Upon further evaluation, however, we have found that that species belongs to the *vernus* group of *Baetis* (Müller-Liebenau 1970), and it is therefore reassigned to *Baetis* (see Table 1).

*Pseudocloeon* is a member of the *Baetis* complex, which has been described and defined by McCafferty & Waltz (1990), Waltz & McCafferty (1997), and Lugo-Ortiz & McCafferty (1998d). The complex is thus currently known to be comprised of the following genera: *Acetrella*, *Baetiella*, *Baetis*, *Barbaetis*, *Demoreptus* Lugo-Ortiz & McCafferty, *Glossidion* Lugo-Ortiz & McCafferty, *Gratia* Thomas, *Heterocloeon* McDunnough, *Liebbiella*, *Platybaetis* Müller-Liebenau, *Plautitus*, *Pseudocloeon*, and *Tanzaniella* Gillies. The presence of a villopore and the lack of a tuft of setae between the incisors and prosthecae together have defined the complex. These characteristics are constant throughout the complex except in certain species of *Pseudocloeon* that do not express the villopore. Because the presence of a villopore is clearly apomorphic among Baetidae, we must conclude that its absence within any lineage of the *Baetis* complex represents a secondary loss, and as a reductive tendency may or may not express species relationships (or common loss). Also because the function of the villopore is unknown, we cannot give any adaptive rationale for its evolution or subsequent loss. Fortunately, one other apparently unique characteristic has been recently associated with the *Baetis* complex by Gaino & Rebra (1999). It involves the presence of flat-tipped sensilla on the larval antennae and elsewhere. Although this finding is preliminary, it is possible that all *Pseudocloeon* larvae will prove to possess this characteristic along with the absence of mandibular tufts of setae, despite the fact that the villopore is not expressed or is inconsistently expressed in some *Pseudocloeon*. For example, we have found that the

highly apotypic Australasian species described herein lack the villopore but possess the flat-tipped sensilla based on our observations made under high magnification with a light microscope.

Larvae of apotypic Australasian species of *Pseudocloeon* demonstrate a remarkable degree of evolutionary parallelism with larvae of the Neotropical baetid genus *Americabaetis* Kluge (see Lugo-Ortiz & McCafferty 1996). Much of this parallelism is due to reductive loss of the hindwings and gills on abdominal segment 1, but also to the development of labial palps. There is also the fact that *Americabaetis* is not a member of the *Baetis* complex because it lacks the villopore, and, as discussed above, the villopore has been secondarily lost in those particular species of *Pseudocloeon*. The adults of the two genera are clearly different, however, and larvae of *Americabaetis* have the mandibular tuft of setae, while larvae of *Pseudocloeon*, characteristic of the *Baetis* complex, do not.

The distribution of *Pseudocloeon* is essentially Arctogean (Table 1). Although the genus is clearly absent from Central and South America, its distribution differs from the traditional Arctogean pattern in that new species we describe here confirm that it also ranges southeast of Wallace's Line. We can only assume that the presence of the genus in Papua-New Guinea and eastern Australia [and possibly New Caledonia (see Peters *et al.* 1978)] represents relatively recent dispersal events, probably beginning in the middle Miocene (approximately 15 million years ago), when Papua-New Guinea and Australia reached their present geographic position (e.g., Stanley 1989). The relative apomorphic characterization of Australasian species supports our conclusion.

*Regional diagnosis of Pseudocloeon larvae.*—In the Nearctic, larvae of *Pseudocloeon* are easily distinguished from all other baetid larvae by the distolateral process of the antennal scapes (Fig. 1; McCafferty & Waltz 1995: Fig. 12) and the distomedially concave maxillary palp segment 2 (Fig. 3; McCafferty & Waltz 1995: Fig. 14). The presence of a broad and long distomedial projection on labial palp segment 2 (McCafferty & Waltz 1995: Fig. 4) usually can also be helpful in this region, with only the relatively uncommon Nearctic species *P. longipalpus* (Moriyama & McCafferty) having a poorly developed palp in this respect (McCafferty & Waltz 1995: Fig. 8).

In the Palearctic, most species are as the majority of Nearctic species (Table 2). Although two species, *P. balcanicum* (Müller-Liebenau) and *P. cleopatrae* (Thomas and Soldán) have atypical antennae and maxillae and the latter lacks hindwing pads and gills 1, all species in the region can easily be diagnosed by the large distomedial projection of labial palp segment 2 (e.g., Müller-Liebenau 1970: Figs. 114c, d, 116, 117; Thomas and Soldán 1989: Fig. 7).

In the Afrotropics, larvae of *Pseudocloeon* are distinguished by having at least a distomedially concave (Fig. 3; Lugo-Ortiz & McCafferty 1997: Figs. 6, 19, 31, 44, 79) or constricted (Lugo-Ortiz & McCafferty 1997: Fig. 55) maxillary palp segment 2. Other typical characteristics often associated with *Pseudocloeon* vary in their frequency in

Afrotropical species (see Table 2).

In the Orient and Australia, larvae of *Pseudocloeon* are distinguished by having at least a broad and long (Figs. 24, 73, 97) or thumblike (Figs. 14, 36, 49, 61, 85, 109) distomedial projection of labial palp segment 2. In addition, it is helpful to remember that along with developed labial palps, lack of the mandibular tuft of setae, and presence of a developed median caudal filament, most presently known Southeast Asian and Australian larvae of *Pseudocloeon* lack gills on abdominal segment 1 and either have no hindwingpads or have only reduced hindwingpads.

*Pseudocloeon hypodelum* Lugo-Ortiz & McCafferty, new species  
Figs. 9-18

*Larva*.—Body length: 5.8 mm; caudal filaments length: unknown. Head: Coloration medium yellow-brown, with faint vermiform markings in vertex. Antennal length unknown; scapes not modified. Labrum (Fig. 9) dorsally with submedial pair of long, fine, simple setae and distal submarginal row of three to four long, fine, simple setae; short, fine, simple setae over surface absent. Hypopharynx as in Figure 10. Left mandible (Fig. 11) with 3 + 3 small denticles. Right mandible (Fig. 12) with 3 + 3 small denticles. Maxillae (Fig. 13) with four denticles on crown of galealaciniae; row of four to five short, fine, simple setae at base of outer denticle absent; one short, fine, simple seta and row of four to five short, fine, simple setae near medial hump; palp segment 1 approximately 0.8x length of segment 2; segment 2 extending beyond galealaciniae, without distomedial concavity. Labium (Fig. 14) with glossae shorter than paraglossae, medially and apically with many long, robust, simple setae; paraglossae apically with three rows of long, distally pectinate setae; palp segment 1 subequal in length to segments 2 and 3; segment 2 approximately 1.3x length segment 3, with moderate thumblike distomedial projection; segment 3 partially fused to segment 2, narrowly rounded, with numerous short, robust, simple setae scattered over surface. Thorax: Coloration medium yellow-brown, with complex faint markings. Hindwingpads absent. Legs (Fig. 15) light to medium yellow-brown; femora without apparent villosity, with faint medium brown broad band submedially, and with row of 20-22 medium sized, somewhat robust, simple setae dorsally and scattered minute, robust, simple setae ventrally; tibiae with row of 16-18 short, somewhat robust, simple setae dorsally and with row of 15-17 short, somewhat robust simple setae ventrally; tarsi basally medium brown, with row of 8-10 short, fine, simple setae dorsally and row of 18-20 simple setae ventrally, increasing in length and girth distally; tarsal claws (Fig. 16) with single row of 10-11 denticles. Abdomen: Coloration light to medium yellow-brown; terga 9 and 10 lighter than rest; tergal posterior margins dark brown; sterna uniformly medium yellow-brown. Terga (Fig. 17) with abundant small scale bases; posterior margin with somewhat irregular spination, spines approximately 1.2x longer than wide. Gills

unknown. Paraprocts (Fig. 18) with 38-40 marginal spines, increasing in length distally.

*Adult*.—Unknown.

*Type material examined*.—HOLOTYPE: Larva, Australia, Queensland State, Murray Falls, 14-VIII-1983, D. A. Polhemus [mouthparts, forelegs, tergum 4, and paraproct on slide (medium: Euparal)].

*Etymology*.—The specific epithet is a combination of the Greek words *hypo* (less than) and *delos* (clear) that modifies the generic nomen.

*Discussion*.—Larvae of *P. hypodelum* are characterized by the submedial pair of long, fine, simple setae and distal submarginal row of three to four long, fine, simple setae of the labrum (Fig. 9); mandibular denticulation (Figs. 11, 12); moderate thumblike distomedial projection of labial palp segment 2 (Fig. 14); and numerous and relatively acute paraproctal spines (Fig. 18).

We have not been allowed to borrow either recently collected or historically significant specimens of Baetidae housed in Australia, despite our requests, and therefore have not been able to compare our new species with material that has been described previously by Harker (1950) and possibly others. The written descriptions by Harker (1950) are so incomplete that they are essentially of no value for comparative purposes. We are cognizant that new species we describe from Australia will possibly prove to be synonyms of previously published species. Nevertheless, the value of our detailed descriptions and illustrations and the utility of such data for deciphering generic relationships, which we are most concerned with, outweigh any potential inconvenience that an eventual synonymy would cause.

*Pseudocloeon inconspicuum* Lugo-Ortiz & McCafferty, new species  
Figs. 19-30

*Larva*.—Body length: 5.4 mm; caudal filaments length: 4.2 mm. Head: Coloration medium yellow-brown, with no markings. Antennal length unknown; scapes unmodified. Labrum (Fig. 19) dorsally without submedial pair of long, fine, simple setae and with distal submarginal row of four to five long, fine, simple setae; short, fine, simple setae scattered over surface. Hypopharynx as in Figure 20. Left mandible (Fig. 21) with 3 + 3 small denticles. (Prostheca missing in examined specimen.) Right mandible (Fig. 22) 3 + 3 small denticles. Maxillae (Fig. 23) with four denticles on crown of galealaciniae; row of two short, fine, simple setae at base of outer denticles present; short, fine, simple seta on medial hump absent and row of five to six short, fine, simple setae near medial hump present; palp segment 1 approximately 0.7x length of segment 2; segment 2 extending beyond galealaciniae, with distomedial concavity. Labium (Fig. 24) with glossae shorter than paraglossae, medially and apically with many long, somewhat robust, simple setae; paraglossae apically with three rows of long, distally pectinate setae; palp segment 1 approximately 0.7x length of segments 2 and 3 combined; segment 2 approximately 2.3x

length of segment 3, with broad, elongate distomedial projection; segment 3 partially fused to segment 2, subconical. Thorax: Coloration medium yellow-brown, with faint pale markings. Hindwingpads absent. Legs (Fig. 25) light yellow-brown; femora without apparent villopore, with numerous long, somewhat robust, simple setae dorsally and abundant minute, robust, simple setae ventrally; tibiae with numerous short, fine, simple setae dorsally and numerous short, somewhat robust, simple setae ventrally; tarsi with scattered short, fine, simple setae dorsally and row of 14-16 simple setae ventrally, increasing in length and girth distally; tarsal claws (Fig. 26) with single row of 9-10 denticles. Abdomen: Coloration medium yellow-brown, with no distinct markings; sterna uniformly medium yellow-brown. Terga (Fig. 27) with abundant scale bases; posterior margin with somewhat irregular triangular spination, spines approximately 1.3x longer than wide. Gills (Fig. 28) on segments 2-7, untracheated, broadest in midregion; margins (Fig. 29) serrate, with uniform serration and scattered minute, fine, simple, setae. Paraprocts (Fig. 30) with 40-42 marginal spines, increasing in length distally, and with scale bases scattered over surface. Caudal filaments medium yellow-brown; terminal filament approximately 0.5x length of cerci.

*Adult*.—Unknown.

*Type material examined*.—HOLOTYPE: Larva, Australia, New South Wales State, Mt Kosciuszko, 1700 m, creek, 4.5°C, 23-IX-1966, J. Illies [mouthparts, midlegs, tergum 4, gill 4, and paraproct mounted on slide (medium: Euparal)].

*Etymology*.—The specific epithet is Latin for dim.

*Discussion*.—Larvae of *P. inconspicuum* are distinguished by the absence of a submedial row of long, fine, simple setae and the presence of a distal submarginal row of four to five long, fine, simple setae on the labrum (Fig. 19); mandibular denticulation (Figs. 21, 22); small distomedial concavity in maxillary palp segment 2 and two short setae at base of outer denticle of galealaciniae (Fig. 23); broad, elongate medial projection of labial palp segment 2 (Fig. 24); and numerous acute paraproctal spines (Fig. 30).

See the discussion under *P. hypodelum* regarding the integrity of Australian species that of necessity have been described without the advantage of examining comparative baetid material now housed in Australia.

*Pseudocloeon involutum* Lugo-Ortiz & McCafferty, new species  
Figs. 31-42

*Larva*.—Body length: 6.7-8.8 mm; caudal filaments length: 5.5-6.5 mm. Head: Coloration medium yellow-brown, with large, round, light yellow-brown marking in frons and faint vermiform markings in vertex. Antennae approximately 2.0x length of head capsule; scapes slightly chamfered distolaterally (similar to Fig. 43). Labrum (Fig. 31) dorsally with submedial pair of long, fine, simple setae and distal submarginal row of four to five long, fine simple setae; short, fine,

simple setae scattered over surface. Hypopharynx as in Figure 32. Left mandible (Fig. 33) with 3 + 3 small denticles. Right mandible (Fig. 34) with 3 + 5 small denticles. Maxillae (Fig. 35) with four denticles on crown of galealaciniae; row of short, fine, simple setae at base of outer denticle absent; one short, fine, simple setae on medial hump and row of five to six short, fine, simple seta near medial hump; palp segment 1 approximately 0.5x length of segment 2; segment 2 not reaching galealaciniae, without distomedial concavity. Labium (Fig. 36) with glossae shorter than paraglossae, medially and apically with many long, robust, simple setae; paraglossae apically with three rows of long, distally pectinate setae; palp segment 1 subequal in length to segments 2 and 3; segment 2 approximately 1.6x length of segment 3, with small, thumblike distolateral projection; segment 3 broadly rounded, with numerous short, robust, simple setae scattered over surface. Thorax: Coloration light to medium yellow-brown, with complex faint markings. Hindwingpads absent. Legs (Fig. 37) light to medium yellow-brown; femora with villopore present, with broad medium yellow-brown band submedially, and with row of long, somewhat robust simple setae dorsally and scattered minute, robust, simple setae ventrally; tibiae with row of 40-45 short, somewhat robust, simple setae dorsally and numerous short, somewhat robust, simple setae ventrally; tarsi with row of 22-24 short, somewhat robust, simple setae dorsally and row of 12-14 simple setae ventrally, increasing in length and girth distally; tarsal claws (Fig. 38) with single row of 10-12 denticles. Abdomen: Coloration medium yellow-brown to medium brown; terga 1-2 and 7-8 generally medium brown; terga 3-6 and 9-10 generally medium yellow-brown; sterna uniformly medium yellow-brown. Terga (Fig. 39) with abundant small scale bases; posterior margin with somewhat irregular triangular spination, spines approximately as long as wide. Gills (Fig. 40) on segments 2-7, well tracheated, broadest in basal one third; margins (Fig. 41) serrate, with one large serration every two to three small serrations, and with scattered minute, fine, simple setae. Paraprocts (Fig. 42) with 20-22 marginal spines, irregular in length distally, and with scale bases scattered over surface. Caudal filaments light yellow-brown, with broad light brown band in midregion; medial caudal filament approximately 0.7x length of cerci.

*Adult*.—Unknown.

*Type material examined*.—HOLOTYPE: Larva, Papua-New Guinea, Bulolo R, 2950 ft, E of Wau, 15-X-64, W. L. and J. G. Peters. PARATYPES: Eight larvae, same data as holotype [antennae, mouthparts, forelegs, tergum 4, gill 4, and paraproct of two larvae mounted on slide (medium: Euparal)].

*Other material examined*: Sixteen larvae, same data as holotype; larva, Papua-New Guinea, East Sepik Prov, Arin R, W of Wewak, 11-IX-1983, J. T. and D. A. Polhemus.

*Etymology*.—The specific epithet is Latin for complex.

*Discussion*.—Larvae of *P. involutum* are distinguished by the following combination of characteristics: distolaterally chamfered an-

tennal scapes (similar to Fig. 43); labrum with submedial pair of long, fine, simple setae and distal submarginal row of four to five long, fine simple setae (Fig. 31); mandibular denticulation (Figs. 33, 34); absence of distomedial concavity in maxillary palp segment 2 (Fig. 35); small thumblike distomedial projection of labial palp segment 2 and broadly rounded segment 3 (Fig. 36); gill marginal serration (Fig. 41); and somewhat irregular paraproctal spines (Fig. 42). Larvae of *P. involutum* exhibit sexual dimorphism. Females are considerably larger and more robust than males, and their abdominal coloration tends to be uniformly light yellow-brown.

*Pseudocloeon petersorum* Lugo-Ortiz & McCafferty, new species  
Figs. 43-55

*Larva*.—Body length: 6.6-9.0 mm; caudal filaments length: 3.9-4.2 mm. Head: Coloration dark yellow-brown to medium brown, with large, round light yellow-brown marking in frons. Antennae approximately 2.0x length of head capsule; scapes slightly chamfered distolaterally (Fig. 43). Labrum (Fig. 44) dorsally with submedial pair of long, fine, simple setae and distal submarginal row of six to seven long, fine, simple setae; short, fine, simple setae scattered over surface. Hypopharynx as in Figure 45. Left mandible (Fig. 46) with 3 + 4 denticles, outer incisor with large, blade-like denticle and two small denticles, inner incisor with four small denticles. Right mandible (Fig. 47) with 3 + 4 denticles, outer incisor with large, blade-like denticle and two small denticles, inner incisor with four small denticles. Maxillae (Fig. 48) with four denticles on crown of galealaciniae; row of short, fine, simple setae at base of outer denticle absent; one short, fine, simple seta on medial hump and row of four to five short, fine, simple setae near medial hump; palp segment 1 approximately 0.7x length of segment 2; segment 2 not reaching galealaciniae, without distomedial concavity. Labium (Fig. 49) with glossae shorter than paraglossae, medially and apically with many long, robust, simple setae; paraglossae apically with three rows of long, distally pectinate setae; palp segment 1 approximately 0.9x length of segments 2 and 3; segment 2 approximately 1.6x length of segment 3, with small, thumblike distolateral projection; segment 3 distinct from segment 2, narrowly rounded, with numerous short, robust, simple setae scattered over surface. Thorax: Coloration light to medium yellow-brown, with complex markings. Hindwingpads absent. Legs (Fig. 50) light to medium yellow-brown; femora without apparent villopore, with broad medium yellow-brown band submedially, and with row of long, somewhat robust, simple setae dorsally and scattered minute, robust, simple setae ventrally; tibiae with row of 10-13 short, fine, simple setae dorsally and row of 18-20 short, fine, simple setae ventrally; tarsi dark yellow-brown to medium brown distally, with row of 12-14 fine, simple setae dorsally and row of 10-12 simple setae ventrally, increasing in length and girth distally; tarsal claws (Fig. 51) with single row of 11-13 denticles. Abdomen: Coloration light yellow-brown to me-

dium brown; terga 1, 2, and 6-9 generally medium brown; terga 3-5 and 10 generally light yellow-brown; sterna 1-5 light yellow-brown, 6-8 medium yellow-brown, 9 medium brown anteriorly and light yellow-brown posteriorly; sterna 2-5 generally with broad medium brown oblique bands. Terga (Fig. 52) with abundant small scale bases; posterior margin with somewhat irregular triangular spination, spines approximately 2.0x longer than broad. Gills (Fig. 53) on segments 2-7, well tracheated, broadest in basal one third; margins (Fig. 54) serrate, with one large serration between every three to four small serrations, and with scattered minute, fine, simple setae. Paraprocts (Fig. 55) with 20-22 marginal spines, increasing in length distally, and with scale bases scattered over surface. Caudal filaments light yellow-brown; medial caudal filament approximately 0.7x length of cerci.

*Adult*.—Unknown.

*Type material examined*.—HOLOTYPE: Larva, Papua-New Guinea, Bulolo R, 2950 ft, E of Wau, 15-X-64, W. L. and J. G. Peters. PARATYPES: Nine larvae, same data as holotype [mouthparts, forelegs, tergum 4, gill 4, and paraproct of three larvae mounted on slide (medium: Euparal)].

*Other material examined*: Sixty-eight larvae, same data as holotype; two larvae, Papua-New Guinea, Morobe Prov, Kauli Cr, nr Wau, 17-IX-83, J. T. and D. A. Polhemus; seven larvae, Papua-New Guinea, Morobe Prov, cr on Mt Kaindi Rd, 2000 m, 17-IX-1983, J. T. and D. A. Polhemus; 10 larvae, Western Highlands Prov, 17 km N of Mt Hagen, 6-IX-1983, J. T. and D. A. Polhemus [mouthparts, forelegs, tergum 4, gill 4, and paraproct of one larva mounted on slide (medium: Euparal)].  
*Etymology*.—We are honored in naming this species after W. L. and J. G. Peters, who collected the type material.

*Discussion*.—Larvae of *P. petersorum* are distinguished by the following combination of characteristics: distolaterally chamfered antennal scapes (Fig. 43); labrum with submedial pair of long, fine, simple setae and distal submarginal row of six to seven long, fine, simple setae (Fig. 44); denticulation of the mandibles (Figs. 46, 47); absence of distomedial concavity in maxillary palp segment 2 (Fig. 48); small thumblike distomedial projection of labial palps segment 2 and narrowly rounded segment 3 (Fig. 49); marginal serration of the gills (Fig. 54); and regular paraproctal spines (Fig. 55). As is the case with *P. involutum*, larvae of *P. petersorum* show sexual dimorphism. Females are generally larger and more robust than males, and their abdominal coloration tends to be uniformly light to medium brown.

*Pseudocloeon plectile* Lugo-Ortiz & McCafferty, new species  
Figs. 56-67

*Larva*.—Body length: 6.0 mm; caudal filaments length: unknown. Head: Coloration light to medium yellow-brown, with faint vermiform markings in frons. Antennal length unknown; scapes unmodified. Labrum (Fig. 56) dorsally with submedial pair of long, fine, simple setae and distal marginal row of four to five long, fine, simple

setae; short, fine, simple setae scattered over surface. Hypopharynx as in Figure 57. Left mandible (Fig. 58) with 3 + 3 small denticles. Right mandible (Fig. 59) with 3 + 4 small denticles. Maxillae (Fig. 60) with four denticles on crown of galealaciniae; two long, somewhat robust, simple setae at base of outer denticle present; one short, fine, simple seta on medial hump and row of four to five long, fine, simple setae near medial hump; palp segment 1 subequal in length to segment 2; segment 2 not reaching galealaciniae, without distomedial concavity. Labium (Fig. 61) with glossae shorter than paraglossae, medially and apically with many long, somewhat robust, simple setae; paraglossae apically with three rows of long, distally pectinate setae; palp segment 1 approximately 0.8x length of segments 2 and 3 combined; segment 2 approximately 1.7x length of segment 3, with moderate thumblike distomedial projection; segment 3 narrowly rounded, with numerous short, robust, simple setae scattered over surface. Thorax: Coloration light to medium yellow-brown, with faint complex markings. Hindwings absent. Legs (Fig. 62) light yellow-brown; femora without apparent villopore, with row of 20-22 long, somewhat robust, simple setae dorsally and scattered minute, robust, simple setae ventrally; tibiae with row of 8-10 short, somewhat robust, simple setae dorsally and two poorly defined rows of 16-18 short, somewhat robust, simple setae ventrally; tarsi with row of eight to nine short, fine, simple setae dorsally and row of 16-18 simple setae ventrally, increasing in length and girth distally; tarsal claws (Fig. 63) with single row of 9-11 denticles. Abdomen: Coloration light to medium yellow-brown; terga 1-8 uniformly medium yellow brown; terga 9 and 10 lighter than others; sterna uniformly light yellow-brown. Terga (Fig. 64) with abundant small scale bases; posterior margin with somewhat irregular triangular spination, spines length approximately 0.8x basal width. Gills (Fig. 65) on segments 2-7, well tracheated, broadest in midregion; margins (Fig. 66) serrate, with irregular serration and scattered minute, fine, simple setae. Paraprocts (Fig. 67) with 20-22 marginal spines, increasing in length distally, and with numerous scale bases scattered over surface. Caudal filaments light yellow-brown basally.

*Adult*.—Unknown.

*Type material examined*.—HOLOTYPE: Larva, Australia, New South Wales State, Mt Kosciusko, 1700 m, creek, 4.5°C, 23-IX-1966, J. Illies [mouthparts, forelegs, tergum 4, gill 4, and paraproct on slide (medium: Euparal)].

*Etymology*.—The specific epithet is Greek for complicated.

*Discussion*.—Larvae of *P. plectile* are distinguished by the submedial pair of long, fine, simple setae and distal marginal row of four to five long, fine, simple seta of the labrum (Fig. 56); mandibular denticulation (Figs. 58, 59); absence of distomedial concavity in maxillary palp segment 2 (Fig. 60); moderate thumblike projection of labial palp segment 2 (Fig. 61); marginal serration of the gills (Fig. 66); and somewhat irregular paraproctal spines (Fig. 67).

*Pseudocloeon plectile* co-occurs with *P. inconspicuum*; however, the two species are clearly distinguishable by labral setation, relative size and shape of labial palp segments 2 and 3, shape of tergal spines, and paraproct spination.

*Pseudocloeon tuberpalpus* Lugo-Ortiz & McCafferty, new species  
Figs. 68-79

*Larva*.—Body length: 5.0-6.7 mm; caudal filaments length: unknown. Head: Coloration medium yellow-brown, with large, round light yellow-brown marking in frons. Antennae approximately 2.0x length of head capsule; scapes unmodified. Labrum (Fig. 68) dorsally with submedial pair of long, fine, simple setae and distal submarginal row of four to five long, fine, simple setae; short, fine, simple setae scattered over surface. Hypopharynx as in Figure 69. Left mandible (Fig. 70) with 3 + 3 small denticles. Right mandible (Fig. 71) with 4 + 4 small denticles. Maxillae (Fig. 72) with four denticles on crown of galealaciniae; row of four to five short, fine, simple setae at base of outer denticle present; one short, fine, simple seta on medial hump and row of four to five short, fine, simple setae near medial hump; palp segment 1 approximately 0.8x length of segment 2; segment 2 extending beyond galealaciniae, with distomedial concavity. Labium (Fig. 73) with glossae shorter than paraglossae, medially and apically with many long, robust, simple setae; paraglossae apically with three rows of long, distally pectinate setae; palp segment 1 approximately 0.7x length of segments 2 and 3; segments 2 and 3 fused, with broad, elongate medial projection, and distally subconical. Thorax: Coloration dark yellow-brown to medium brown, without markings. Hindwings absent. Legs (Fig. 74) medium yellow-brown; femora without apparent villopore, with row of long, somewhat robust, simple setae dorsally and scattered minute, robust, simple setae ventrally; tibiae with row of 8-10 short, fine, simple setae dorsally and row of 8-10 short, somewhat robust, simple setae ventrally; tarsi with row of 8-10 short, fine, simple setae dorsally and row of 10-12 simple setae ventrally, increasing in length and girth distally; tarsal claws (Fig. 75) with single row of 9-10 denticles. Abdomen: Coloration dark yellow-brown to medium brown; tergal posterior margins generally dark brown; sterna uniformly dark yellow-brown to medium brown. Terga (Fig. 76) with abundant small scale bases and few scales scattered over surface; posterior margin with somewhat irregular triangular spination, spines approximately as long as wide. Gills (Fig. 77) on segments 2-7, well tracheated, broadest in midregion; margins (Fig. 78) serrate, with uniform serration and scattered minute, fine, simple setae. Paraprocts (Fig. 79) with 30-32 marginal spines, increasing in length distally, and with scale bases scattered over surface. Caudal filaments medium yellow-brown basally.

*Female subimago*.—Body length: 3.8 mm; forewings length: 5.2; caudal filaments length: unknown. Head: Coloration medium to dark brown. Antennae approximately as long as head capsule length;



scapes, pedicels, and flagella light yellow-brown. Thorax: Coloration medium to dark brown. Forewings narrow-elongate, with conspicuous double marginal intercalaries. Legs light to medium yellow-brown. Abdomen: Coloration medium to dark brown, posterior margin of terga dark brown; vestiges of gill insertion apparent on segments 3-7.

*Adult*.—Unknown.

*Type material examined*.—HOLOTYPE: Larva, Papua-New Guinea, Bulolo R. E. of Wau, 2950 ft, 18-X-1964, W. L. and J. G. Peters. PARATYPES: Larva, same data as holotype [antenna, mouthparts, forelegs, tergum 4, gill 4, and paraproct on slide (medium: Euparal)]; larva, Papua-New Guinea, Morobe Prov, Clearwater Cr, nr Luau, 15-IX-1983, J. T. and D. A. Polhemus [mouthparts, forelegs, tergum 4, and paraproct on slide (medium: Euparal)]; larva, Papua-New Guinea, Western Highlands Prov, stream nr Murrmut Pass, 7-IX-1983, J. T. and D. A. Polhemus [mouthparts and forelegs on slide (medium: Euparal)].

*Other material examined*.—Two larvae, same data as holotype; two larvae, same data as holotype, except 27-X-1964; exuviae, female subimago, Papua-New Guinea, Hospital Cr, Wau, 3750 ft, 20-X-1964, W. L. and J. G. Peters; larva, Papua-New Guinea, Western Highlands Prov, stream nr Murrmut Pass, 7-IX-1983, J. T. and D. A. Polhemus.

*Etymology*.—The specific epithet is a combination of the Latin words *tuber* (bulb) and *palpus* (feeler). It refers to the bulbous labial palps and is considered a noun in apposition.

*Discussion*.—Larvae of *P. tuberpalpus* are distinguished by the following combination of characteristics: submedial pair of long, fine, simple setae and distal submarginal row of four to five long, fine, simple setae of the labrum (Fig. 68); mandibular denticulation (Figs. 70, 71); presence of a row of setae at the base of the denticles of the galealacinae and distomedial concavity in palp segment 2 (Fig. 72); broadly elongate segment 2 of the labial palps (Fig. 73); marginal serration of the gills (Fig. 78); and small, sharp, and regularly spaced paraproctal spines (Fig. 79).

*Pseudocloeon vitile* Lugo-Ortiz & McCafferty, new species  
Figs. 80-91

*Larva*.—Body length: 6.6-6.9 mm; caudal filaments length: unknown. Head: Coloration medium yellow-brown, with no markings. Antennal length unknown; scapes unmodified. Labrum (Fig. 80) dorsally with submedial pair of long, fine, simple setae and distal marginal row of four to five long, fine, simple setae; short, fine, simple setae scattered over surface. Hypopharynx as in Figure 81. Left mandible (Fig. 82) with 3 + 4 small denticles. Right mandible (Fig. 83) with 3 + 4 small denticles. Maxillae (Fig. 84) with four denticles on crown of galealacinae; row of short, fine, simple setae at base of outer denticle absent; short, fine, simple seta on medial hump absent and row of four to five short, fine, simple setae near medial hump present; palp segment 1 approximately 0.8x length of segment 2; segment 2

extending beyond galealacinae, without distomedial concavity. Labium (Fig. 85) with glossae shorter than paraglossae, medially and apically with many short, robust, simple setae; paraglossae apically with three rows of long, distally pectinate setae; palp segment 1 approximately 0.9x length of segment 2 and 3; segments 2 and 3 fused, with small, thumblike distomedial projection, and distally rounded. Thorax: Coloration light to medium yellow-brown, with faint markings. Hindwingpads absent. Legs (Fig. 86) medium yellow-brown; femora without apparent villopore, with row of long, somewhat robust, simple setae dorsally and scattered minute, robust, simple setae ventrally; tibiae with row of 20-25 short, fine, simple setae dorsally and row of 15-20 short, somewhat robust simple setae ventrally; tarsi with row of 10-12 short, fine, simple setae dorsally and row of 10-12 simple setae ventrally, increasing in length and girth distally; tarsal claws (Fig. 87) with single row of 10-11 denticles. Abdomen: Coloration pale brown to medium yellow-brown; terga 5, 9, and 10 light yellow-brown; sterna light to medium yellow brown; sterna 7 and 8 pale brown. Terga (Fig. 88) with abundant small scale bases; posterior margin with somewhat irregular triangular spination, spines approximately as long as wide. Gills (Fig. 89) on segments 2-7, untracheated or poorly tracheated, broadest in midregion; margins (Fig. 90) serrate, with uniform serration and scattered minute, fine, simple setae. Paraprocts (Fig. 91) with 22-24 marginal spines, increasing in length distally, and with abundant small scale bases over surface.

*Adult*.—Unknown.

*Type material examined*.—HOLOTYPE: Larva, Papua New Guinea, Western Highlands Prov, Kaugel R, nr Alkena, IX-7-1983, J. T. and D. A. Polhemus. PARATYPE: Two larvae, same data as holotype [mouthparts, forelegs, tergum 5, gill 5, and paraproct of one larva mounted on slide (medium: Euparal)].

*Other material examined*.—Three larvae, same data as holotype.

*Etymology*.—The specific epithet is Latin for interwoven.

*Discussion*.—Larvae of *P. vitile* are distinguished by the following combination of characteristics: labrum with submedial pair of long, fine, simple setae and distal submarginal row of four to five long, fine, simple setae (Fig. 80); mandibular denticulation (Figs. 82, 83); absence of distomedial concavity in maxillary palp segment 2 (Fig. 84); small thumblike distomedial projection of labial palp segment 2 and fused, somewhat elongate segment 3 (Fig. 85); gill marginal serration (Fig. 90); and paraproctal spination (Fig. 91).

*Pseudocloeon vultuosum* Lugo-Ortiz & McCafferty, new species  
Figs. 92-103

*Larva*.—Body length: 8.5-9.0 mm; caudal filaments length: unknown. Head: Coloration medium brown, without markings. Antennae approximately 3.0x length of head capsule; scapes unmodified. Labrum (Fig. 92) dorsally with submedial pair of long, fine, simple

setae and distal submarginal row of eight to nine long, fine, simple setae; short, fine, simple setae scattered over surface. Hypopharynx as in Figure 93. Left mandible (Fig. 94) with 3 + 3 small denticles. Right mandible (Fig. 95) with 3 + 4 small denticles. Maxillae (Fig. 96) with four denticles on crown of galealaciniae; row of short, fine, simple setae at base of outer denticle absent; one short, fine, simple seta on medial hump and row of five to six short, fine, simple setae near medial hump; palp segment 1 subequal in length to segment 2; segment 2 extending beyond galealaciniae, with distomedial concavity. Labium (Fig. 97) with glossae shorter than paraglossae, medially and apically with robust, simple setae; paraglossae apically with three rows of long, distally pectinate setae; palp segment 1 approximately 0.9x length of segments 2 and 3 combined; segment 2 approximately 1.5x length of segment 3, with broad, elongate distomedial projection; segment 3 narrowly rounded apically. Thorax: Coloration medium brown, with complex faint markings. Hindwingspads absent. Legs (Fig. 98) light to medium yellow-brown; femora without villopore, with broad medium brown band submedially, and with row of relatively short, somewhat robust, simple setae dorsally and scattered minute, robust, simple setae ventrally; tibiae with row of 15-20 short, somewhat robust, simple setae dorsally and numerous short, somewhat robust, simple setae ventrally; tarsi with scattered short, somewhat robust, simple setae dorsally and row of 15-18 simple setae ventrally, increasing in length and girth distally; tarsal claws (Fig. 99) with single row of 8-10 denticles. Abdomen: Coloration uniformly medium brown; sterna uniformly light to medium brown. Terga (Fig. 100) with abundant small scales bases; posterior margin with somewhat irregular triangular spination, spines approximately as long as wide. Gills (Fig. 101) on segments 2-7, well tracheated, broadest in midregion; margins (Fig. 102) serrate, with one large serration every two to three small serrations, and with scattered minute, fine, simple setae. Paraprocts (Fig. 103) with 30-35 marginal spines, increasing in length distally, and with abundant scale bases scattered over surface. Caudal filaments basally dark yellow-brown to medium brown.

*Adult*.—Unknown.

*Type material examined*.—HOLOTYPE: Larva, Papua-New Guinea, Western Highlands Prov, 17 km N of Mt Hagen, 6-IX-1983, J. T. and D. A. Polhemus. PARATYPE: Larva, same data as holotype [mouthparts, foreleg, tergum 4, gill 4, and paraproct mounted on slide (medium: Euparal)].

*Other material examined*.—Four larvae, Papua-New Guinea, Morobe Prov, Poverty Cr, Mt Missim, 1600 m, 18-IX-1983, J. T. and D. A. Polhemus; larva, Papua-New Guinea, Morobe Prov, Clearwater Cr, 3 km S of Mummeng, 19-IX-1983, J. T. and D. A. Polhemus.

*Etymology*.—The specific epithet is Latin for "full of expression." *Discussion*.—Larvae of *P. vultuosum* are distinguished by the following combination of characteristics: labrum with submedial pair of long, fine, simple setae and distal submarginal row of eight to nine long, fine, simple setae (Fig. 92); mandibular denticulation (Figs. 94,

95); distomedial concavity in maxillary palp segment 2 (Fig. 96); medial projection of labial palp segment 2 (Fig. 97); long, slender legs (Fig. 98); gill tracheation and marginal serration (Figs. 101, 102); and sharp paraproctal spination (Fig. 103).

*Pseudocloeon xeniolium* Lugo-Ortiz & McCafferty, new species  
Figs. 104-115

*Larva*.—Body length: 10.0-10.5 mm; caudal filaments length: 6.5-7.0 mm. Head: Coloration dark yellow-brown; frons with large pale yellow-brown circular spot. Antennae approximately 1.5x length of head capsule; scapes unmodified. Labrum (Fig. 104) with submedial pair of long, fine, simple setae and distal submarginal row of seven to nine long, fine, simple setae; short, fine, simple setae scattered over surface. Hypopharynx as in Figure 105. Left mandible (Fig. 106) with 3 + 3 denticles. Right mandible (Fig. 107) with 2 + 4 denticles. Maxillae (Fig. 108) with four denticles on crown of galealaciniae; row of short, fine, simple setae at base of outer denticle absent; one short, fine, simple seta on medial hump and row of four to five simple setae near medial hump; palp segment 1 approximately 1.1x length of segment 2; segment 2 not reaching galealaciniae, without distomedial concavity. Labium (Fig. 109) with glossae shorter than paraglossae, medially and apically with robust, simple setae; paraglossae apically with three rows of long, distally pectinate setae; palp segment 1 approximately 1.1x length of segments 2 and 3 combined; segment 2 approximately 4.8x length of segment 3, apically broader than basally, with almost straight distomedial projection; segment 3 broadly rounded apically. Thorax: Coloration pale to dark yellow-brown, with complex faint markings. Hindwingspads absent. Legs (Fig. 110) light to medium yellow-brown; femora with rudimentary villopore, with large oblong to subrectangular subproximal and subdistal cream markings, and with row of relatively short, somewhat robust, simple setae dorsally and scattered minute, robust, simple seta ventrally; tibiae with abundant short-fine and short-robust, simple setae dorsally and ventrally; tarsi with abundant short-fine and short-robust, simple setae dorsally and ventrally; tarsal claws (Fig. 111) with single row of 8-10 denticles; forelegs relatively shorter and more robust than mid- and hindlegs. Abdomen: Coloration cream to medium brown; segments 1, 9, and 10 uniformly medium brown; segments 2-5 medium brown, with medial pair of cream longitudinal dashes; segment 6 cream; segment 7 medium brown, with large cream subtriangular marking medially; segment 8 medium brown, with narrow cream longitudinal marking medially; arthrodistal membrane between segments 1-9 dark purple brown; sterna pale to medium brown. Terga (Fig. 112) with abundant scale bases; posterior margin with irregular triangular spination. Gills (Fig. 113) on segments 2-7, well tracheated, broadest in midregion; margins (Fig. 114) serrate, with scattered minute, fine, simple setae. Paraprocts (Fig. 115) with poorly defined marginal spines, and with scale bases and minute fine, simple setae scattered over surface.

Caudal filaments dark yellow-brown to medium brown; median caudal filament approximately 0.7x length of cerci.

*Adult*.—Unknown.

*Type material examined*.—HOLOTYPE: Larva, Papua-New Guinea, Morobe Prov., Poverty Cr., Mt Missim, 1600 m, 18-IX-1983, J. T. and D. A. Polhemus. PARATYPES: Two larvae, same data as holotype [mouthparts, forelegs, tergum 4, gill 4, and paraproct of one larva and mouthparts, forelegs, and paraproct of the other larva mounted on slides (medium: Euparal)].

*Etymology*.—The specific epithet is a Latin noun in apposition meaning "small gift to a guest."

*Discussion*.—Larvae of *P. xeniothum* are distinguished by the following combination of characteristics: presence of a submedial pair of long, fine, simple setae and distal submarginal row of seven to nine long, fine, simple setae on the labrum (Fig. 104); mandibular denticulation (Figs. 106, 107); labial palps with segment 2 apically broad and basally narrow and segment 3 short and broadly rounded (Fig. 109); presence of a rudimentary villopore; relatively short and robust forelegs (Fig. 110); irregular posterior marginal spination of the terga (Fig. 112); well-tracheated gills (Fig. 113); and paraprocts with poorly defined marginal spination (Fig. 115).

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Table 1. Species of *Pseudocloeon*, species possibly assignable to *Pseudocloeon*, and species assigned to *Pseudocloeon* that require reassignment. (Note: When authors of newly combined species are not parenthetical it indicates a reversion to the original combination.)

#### Pseudocloeon

#### AFROTROPICS

- P. aquacidum* (Lugo-Ortiz & McCafferty), n. comb.  
*P. bellum* (Barnard), n. comb.  
*P. boussoultium* (Gillies), n. comb.  
*P. elouardi* (Gillies), n. comb.  
*P. fabulosum* (Lugo-Ortiz & McCafferty), n. comb.  
*P. fastigiatum* Kopelke, n. comb.  
*P. glaucum* (Agnew), n. comb.  
*P. grandiculum* Kopelke, n. comb.  
*P. insolitum* (Kopelke), n. comb.  
*P. kalengoense* (Kopelke), n. comb.  
*P. latum* (Agnew), n. comb.  
*P. masai* (Lugo-Ortiz & McCafferty), n. comb.  
*P. mtone* (Gillies), n. comb.  
*P. nadineae* (Lugo-Ortiz & McCafferty), n. comb.  
*P. piscis* (Lugo-Ortiz & McCafferty), n. comb.  
*P. plumbago* (Lugo-Ortiz & McCafferty), n. comb.  
*P. quintum* (Agnew), n. comb.  
*P. tenuicrinium* Kopelke, n. comb.  
*P. vinosum* Barnard, n. comb.

#### AUSTRALIAN

- P. hypodelum* Lugo-Ortiz & McCafferty, n. sp.  
*P. inconspicuum* Lugo-Ortiz & McCafferty, n. sp.  
*P. involutum* Lugo-Ortiz & McCafferty, n. sp.  
*P. kraepelini* Klapálek  
*P. petersorum* Lugo-Ortiz & McCafferty, n. sp.  
*P. plectile* Lugo-Ortiz & McCafferty, n. sp.  
*P. tuberpalpus* Lugo-Ortiz & McCafferty, n. sp.  
*P. vitile* Lugo-Ortiz & McCafferty, n. sp.  
*P. vultuosum* Lugo-Ortiz & McCafferty, n. sp.  
*P. xeniolum* Lugo-Ortiz & McCafferty, n. sp.

#### NEARCTIC

- P. apache* (McCafferty & Waltz), n. comb.  
*P. dardanum* (McDunnough), n. comb.  
*P. ephippiatum* (Traver), n. comb.  
*P. frondale* (McDunnough), n. comb.  
*P. longipalpus* (Moriwara & McCafferty), n. comb.  
*P. propinquum* (Walsh), n. comb.

#### ORIENTAL

- P. boetigeri* Ulmer  
*P. borneoense* (Müller-Liebenau), n. comb.  
*P. difficile* (Müller-Liebenau), n. comb.  
*P. diffundum* (Müller-Liebenau), n. comb.  
*P. dipsicum* (Gillies), n. comb.

- P. fulmeki* (Ulmer), n. comb.  
*P. germinatum* (Müller-Liebenau & Hubbard), n. comb.  
*P. inopinum* (Gillies), n. comb.  
*P. kraepelini* Klapálek  
*P. molainense* (Müller-Liebenau), n. comb.  
*P. moriharai* (Müller-Liebenau), n. comb.  
*P. morum* (Chang & Yang), n. comb.  
*P. multum* (Müller-Liebenau), n. comb.  
*P. necopinatum* (Müller-Liebenau), n. comb.  
*P. numeratum* (Müller-Liebenau), n. comb.  
*P. operosum* (Müller-Liebenau), n. comb.  
*P. ordinatum* (Müller-Liebenau & Hubbard), n. comb.  
*P. palmyrae* (Gillies), n. comb.  
*P. pulchellum* (Müller-Liebenau & Hubbard), n. comb.  
*P. sumigarensis* (Müller-Liebenau), n. comb.  
*P. ulmeri* (Müller-Liebenau), n. comb.

#### PALEARCTIC

- P. atrebatinum* (Eaton), n. comb.  
*P. bulcanicum* (Müller-Liebenau & Soldán), n. comb.  
*P. calcarratum* (Keffermüller), n. comb.  
*P. cleopatrae* (Thomas & Soldán), n. comb.  
*P. desertum* (Novikova & Kluge), n. comb.  
*P. tricolor* (Tshernova), n. comb.

#### Possibly Pseudocloeon

#### AFROTROPICS

- Baetis lawrenci* Crass  
*B. magae* (Barnard)  
*B. monikae* Kopelke  
*B. spatulatus* Gillies  
*B. tripunctatus* Gillies

#### ORIENTAL

- B. tigroides* Gillies  
*Cloeon papuanum* van Bruggen  
*P. rubellum* Navás

#### Not Pseudocloeon

- Baetis gambiae* Gillies, n. comb.

#### NEOTROPICS

- P. albinerve* Navás  
*P. bridarolii* Navás  
*P. bruchi* Navás  
*P. jorgenseni* (Esben-Petersen)  
*P. oldendorffi* (Weyenbergh)  
*P. peterseni* (Hubbard)  
*P. tarbinops* Needham & Murphy  
*P. venezuelensis* Traver  
*P. weiseri* Navás

#### ORIENTAL

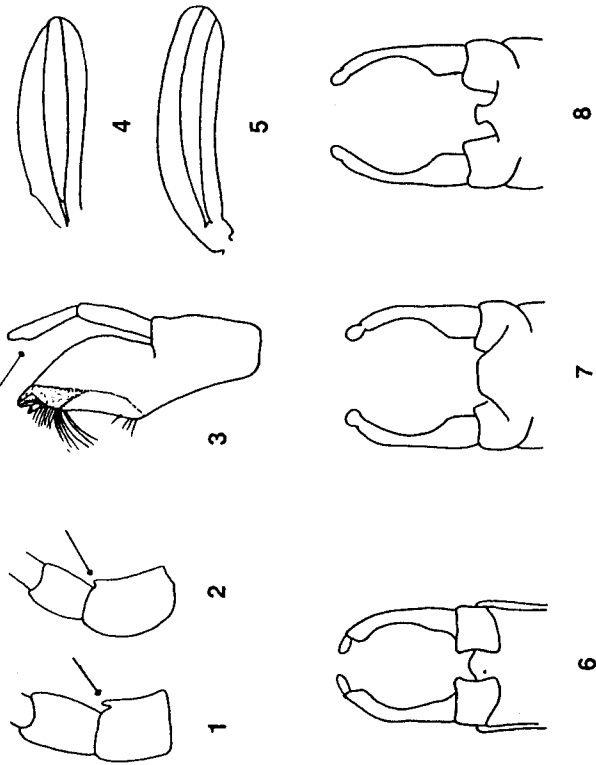
- P. obscurum* Ulmer

Table 2. Character distribution among known *Pseudocloeon* larvae (\* = poorly developed).

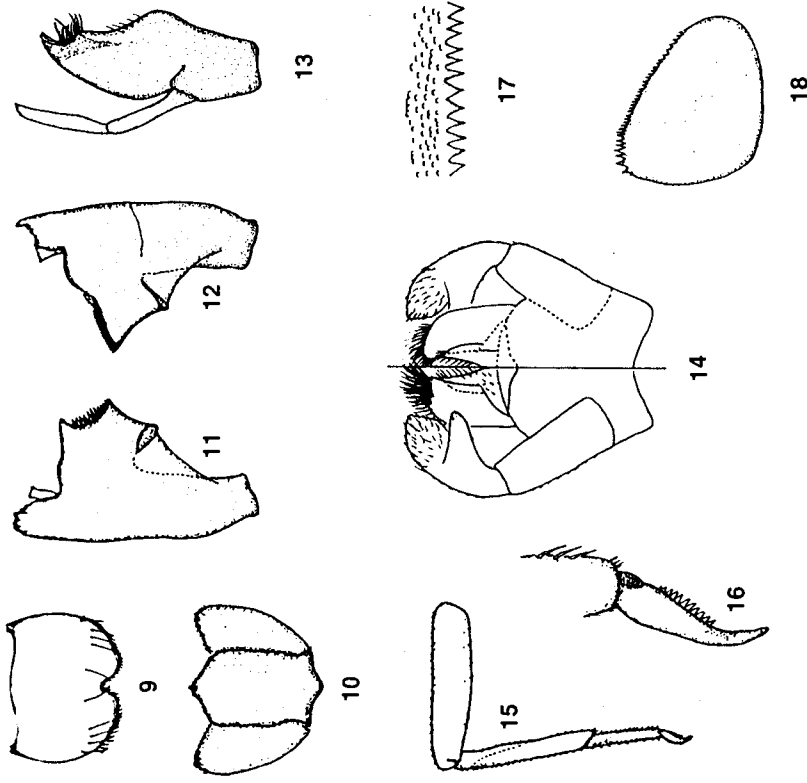
Species	Antennal process (Figs. 1, 2)	Maxillary palp segment 2 excavation (Figs. 3, 96)	Labial palp segment 2 enlargement pads (Figs. 24, 73, 97)	Developed hindwing-pair pads	1" gill pair
<b>NEARCTIC</b>					
<i>P. apache</i>	X	X	X	X	X
<i>P. ephippiatum</i>	X	X	X	X	X
<i>P. frondale</i>	X	X	X	X	X
<i>P. longipalpus</i>	X	X	X	X	X
<i>P. propinquum</i>	X	X	X	X	X
<b>PALEARCTIC</b>					
<i>P. atrebatinum</i>	X	X	X	X	X
<i>P. balcanicum</i>	X	X	X	X	X
<i>P. calcaratum</i>	X	X	X	X	X
<i>P. cleopatrae</i>	X*	X	X	X	X
<i>P. desertum</i>	X	X	X	X	X
<i>P. tricolor</i>	X	X	X	X	X
<b>AFROTROPICS</b>					
<i>P. aquacidum</i>	X	X	X	X	X
<i>P. bellum</i>	?	X*	X	X	X
<i>P. boussoulium</i>	X*	X	X	X	X
<i>P. elouardi</i>	X	X	X	X	X
<i>P. fabulosum</i>	X	X	X	X	X
<i>P. glaucum</i>	?	X*	X	X	X
<i>P. latum</i>	?	X	X	X	X
<i>P. masai</i>	X*	X*	X	X	X
<i>P. mtone</i>	X	X	X	X	X
<i>P. nadineae</i>	X*	X*	X	X	X
<i>P. piscis</i>	X*	X*	X	X	X
<i>P. plumbago</i>	X	X	X	X	X
<i>P. quintum</i>	?	X	X	X	X
<i>P. vinosum</i>	X*	X*	X	X	X
<b>ORIENTAL</b>					
<i>P. borneense</i>	X	X*	X	X	X
<i>P. difficile</i>	X	X*	X	X	X
<i>P. diffundum</i>	X*	X*	X	X	X

CONTINUES

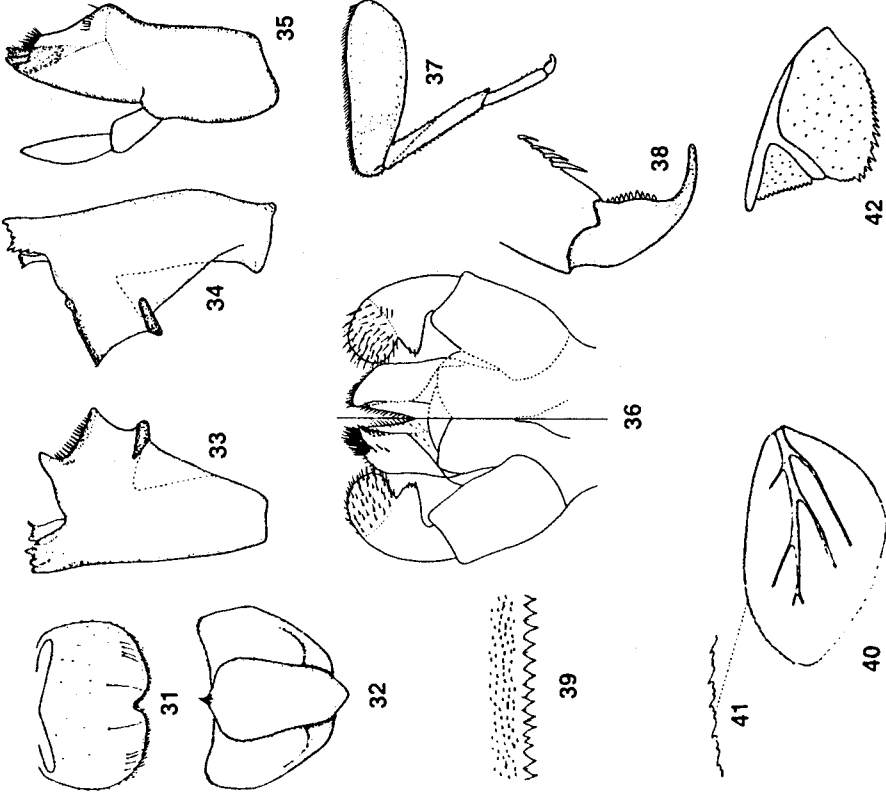
Species	Antennal process (Figs. 1, 2)	Maxillary palp segment 2 excavation (Figs. 3, 96)	Labial palp segment 2 enlargement pads (Figs. 24, 73, 97)	Developed hindwing-pair pads	1" gill pair
<i>P. serminatum</i>	X*	X*	X	X	X
<i>P. molavoivense</i>	X*	X*	X	X	X
<i>P. moriharai</i>	X	X	X	X	X
<i>P. morum</i>	X	X	X	X	X
<i>P. multum</i>	X	X	X	X	X
<i>P. numeratum</i>	X*	X*	X	X	X
<i>P. operosum</i>	X*	X*	X	X	X
<i>P. ordinatum</i>	X	X	X	X	X
<i>P. pulchellum</i>	X*	X*	X	X	X
<i>P. sumigarensense</i>	X*	X*	X	X	?
<b>AUSTRALIAN</b>					
<i>P. hypodelum</i>		X*	X*	X*	X*
<i>P. inconspicuum</i>		X*	X*	X*	X*
<i>P. involutum</i>		X*	X*	X*	X*
<i>P. petersorum</i>		X*	X*	X*	X*
<i>P. plectile</i>		X*	X*	X*	X*
<i>P. tuberpalpus</i>		X*	X*	X*	X*
<i>P. vitile</i>		X*	X*	X*	X*
<i>P. vultuosum</i>		X	X	X	X
<i>P. xeniolum</i>		X	X	X	X



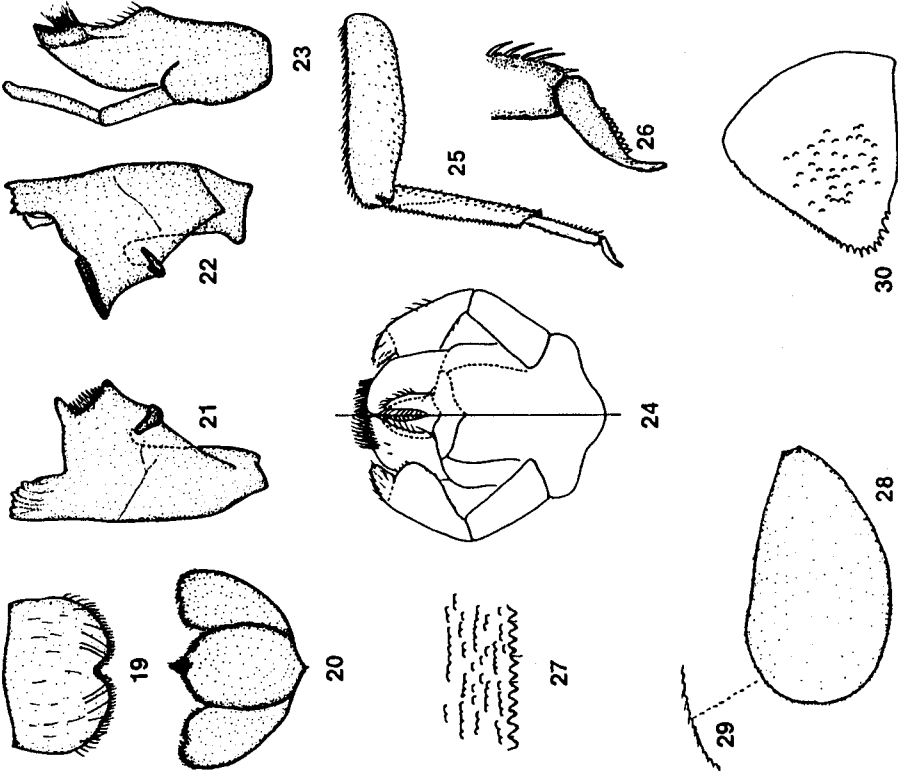
FIGURES 1 - 8. Larval and adult structures of *Pseudocloeon* spp. 1. *P. aquacidum*, antennal scapes (pointer towards distolateral process)(after Lugo-Ortiz & McCafferty 1997: Fig. 1). 2. *P. molawinense*, antennal scapes (pointer towards distolateral process)(after Müller-Liebenau 1982: Fig. 4d). 3. *P. plumbeo*, left maxilla (pointer towards excavation)(after Lugo-Ortiz & McCafferty 1979a: Fig. 19). 4. *P. propinquum*, hindwing (after Morihara & McCafferty 1979a: Fig. 67). 5. *P. kalengoense*, hindwing (after Kopelke 1980: Fig. 2c). 6. *P. kraepelini*, male genitalia (after Waltz & McCafferty 1985a: Fig. 3). 7. *P. ephippiatum*, male genitalia (after Morihara & McCafferty 1979a: Fig. 14). 8. *P. longipalpus*, male genitalia (after Morihara & McCafferty 1979a: Fig. 13).



FIGURES 9 - 18. Larval structures of *Pseudocloeon hypodelium*. 9. Labrum (dorsal). 10. Hypopharynx. 11. Left mandible. 12. Right mandible. 13. Right maxilla. 14. Labium (left: ventral; right: dorsal). 15. Right foreleg. 16. Tarsal claw. 17. Tergum 4 (detail). 18. Paraproct.

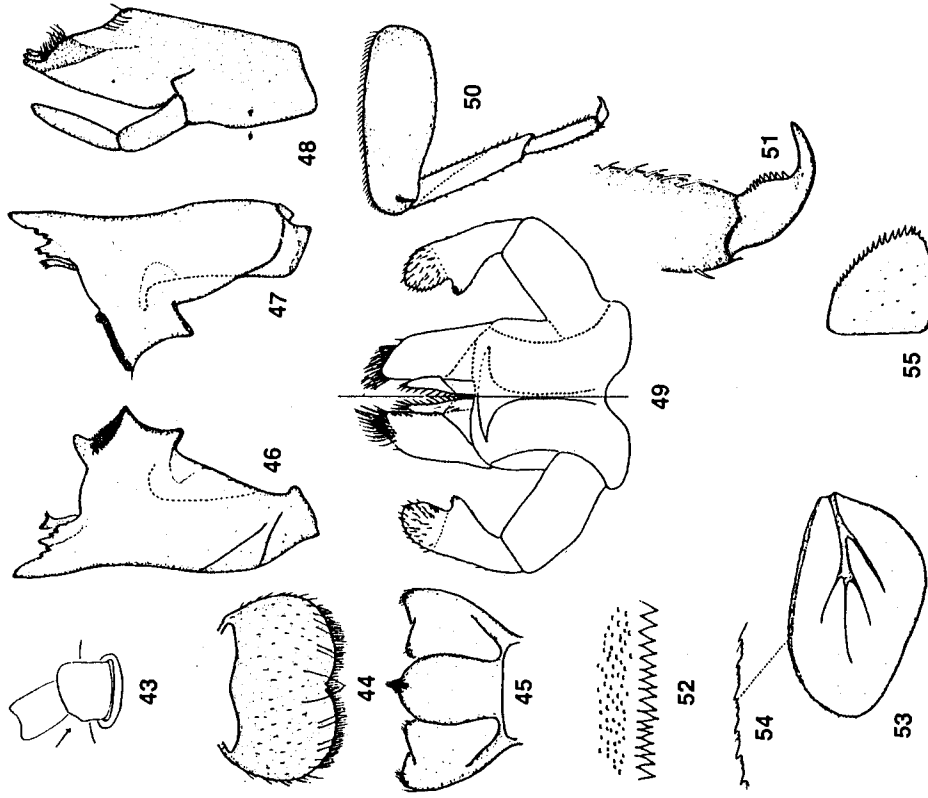


FIGURES 31 - 42. Larval structures of *Pseudocloeon involutum*. 31. Labrum (dorsal). 32. Labium (left: ventral; right: dorsal). 33. Hypopharynx. 34. Right mandible. 35. Right maxilla. 36. Labium (left: ventral; right: dorsal). 37. Right foreleg. 38. Tarsal claw. 39. Tergum 4 (detail). 40. Gill 4. 41. Gill margin (detail). 42. Paraproct.

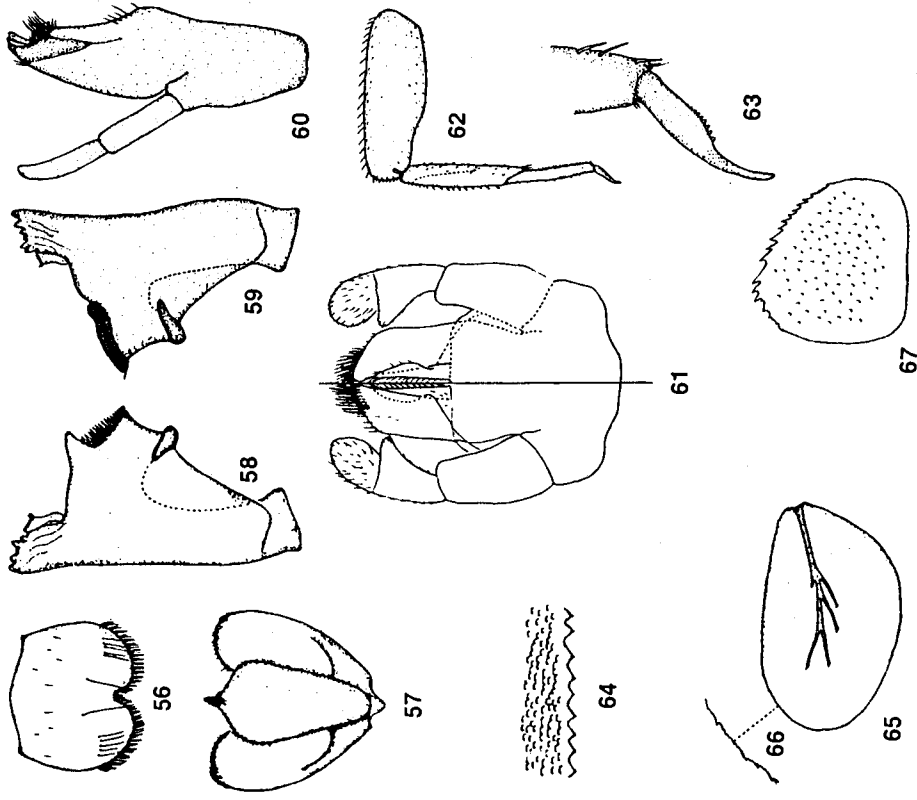


FIGURES 19 - 30. Larval structures of *Pseudocloeon inconspicuum*. 19. Labrum (dorsal). 20. Labium (left: ventral; right: dorsal). 21. Hypopharynx. 22. Right mandible. 23. Right maxilla. 24. Labium (left: ventral; right: dorsal). 25. Right foreleg. 26. Tarsal claw. 27. Tergum 4 (detail). 28. Gill 4. 29. Gill margin (detail). 30. Paraproct.

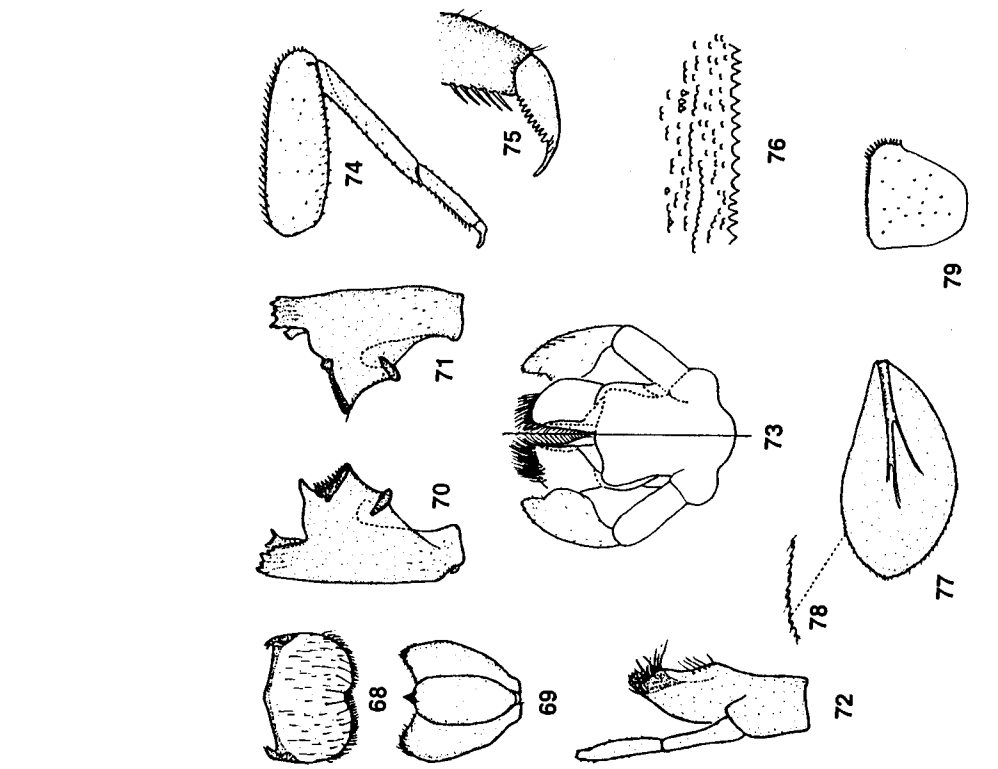




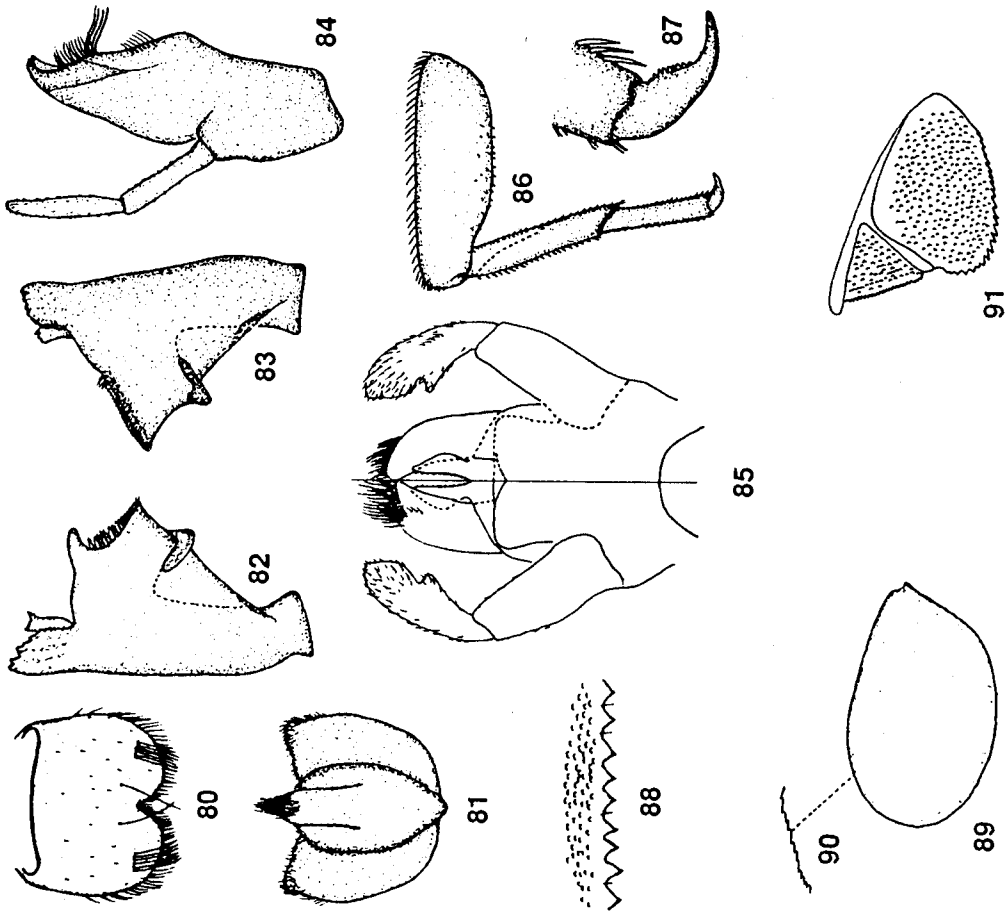
FIGURES 43 - 55. Larval structures of *Pseudocloeon petersorum*. 43. Antennal scape and pedicel. 44. Labrum (dorsal). 45. Hypopharynx. 46. Left mandible. 47. Right mandible. 48. Right maxilla. 49. Labium (left: ventral; right: dorsal). 50. Right foreleg. 51. Tarsal claw. 52. Gill 4. 53. Gill margin (detail). 54. Gill margin (detail). 55. Paraproct.



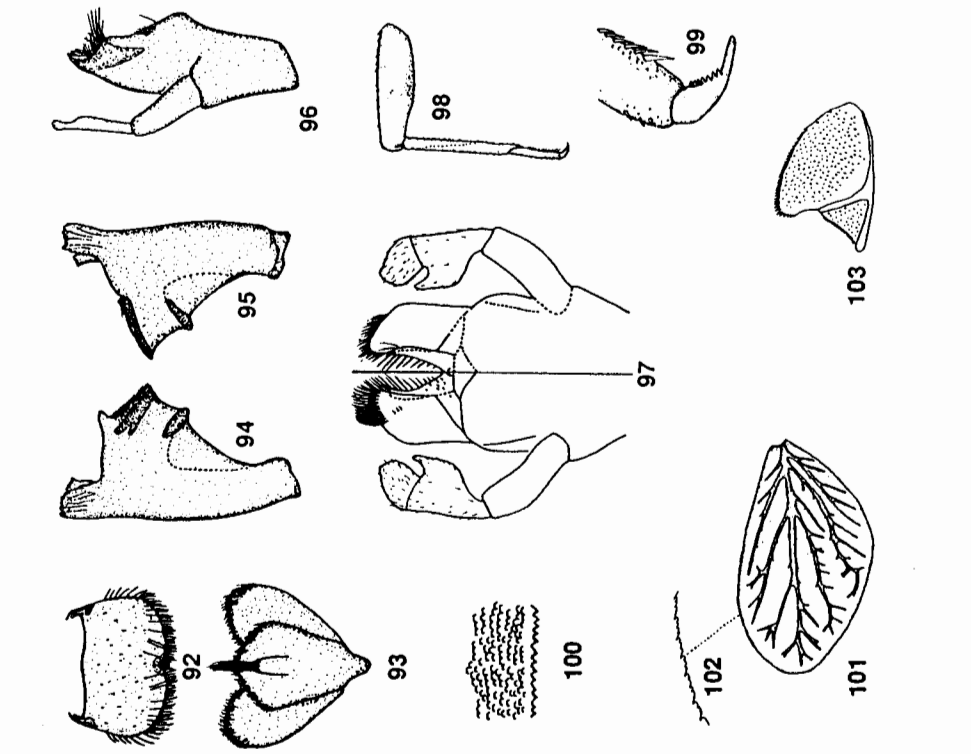
FIGURES 56 - 67. Larval structures of *Pseudocloeon plectile*. 56. Labrum (dorsal). 57. Hypopharynx. 58. Left mandible. 59. Right mandible. 60. Right maxilla. 61. Labium (left: ventral; right: dorsal). 62. Right foreleg. 63. Tarsal claw. 64. Tergum 4 (detail). 65. Gill 4. 66. Gill margin (detail). 67. Paraproct.



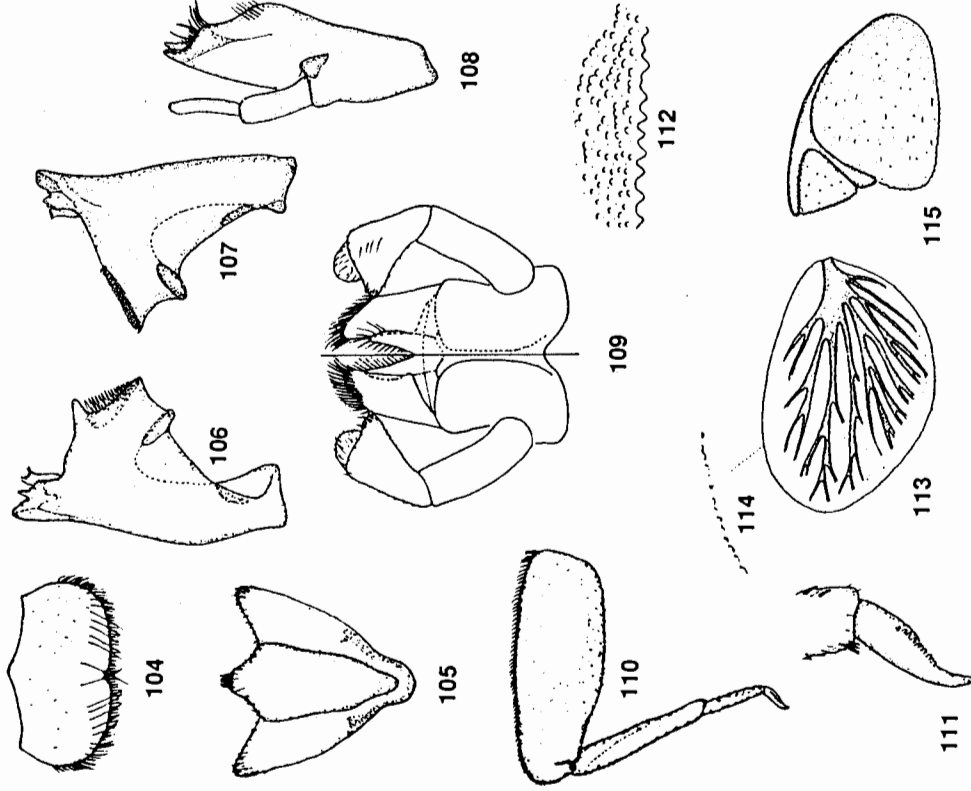
FIGURES 68 - 79. Larval structures of *Pseudocloeon tuberculipes*. 68. Labrum (dorsal). 69. Hypopharynx. 70. Left mandible. 71. Right mandible. 72. Right Maxilla. 73. Labium (left: ventral; right: dorsal). 74. Left foreleg. 75. Tarsal claw. 76. Tergum 4 (detail). 77. Gill margin (detail). 78. Gill 4. 79. Paraproct.



FIGURES 80 - 91. Larval structures of *Pseudocloeon vitile*. 80. Labrum (dorsal). 81. Hypopharynx. 82. Left mandible. 83. Right mandible. 84. Right maxilla. 85. Labium (left: ventral; right: dorsal). 86. Tergum 5 (detail). 87. Gill margin (detail). 88. Tergum 5 (detail). 89. Gill 5. 90. Gill margin (detail). 91. Paraproct.



FIGURES 92 - 103. Larval structures of *Pseudocloeon multuosum*. 92. Labrum (dorsal). 93. Hypopharynx. 94. Left mandible. 95. Right mandible. 96. Right maxilla. 97. Labium (left: ventral; right: dorsal). 98. Left foreleg. 99. Tarsal claw. 100. Tergum 4 (detail). 101. Gill 4. 102. Gill margin (detail). 103. Paraproct.



FIGURES 104 - 115. Larval structures of *Pseudocloeon xeniolum*. 104. Labrum (dorsal). 105. Hypopharynx. 106. Left mandible. 107. Right mandible. 108. Right maxilla. 109. Labium (left: ventral; right: dorsal). 110. Left foreleg. 111. Tarsal claw. 112. Tergum 4 (detail). 113. Gill 4. 114. Gill margin (detail). 115. Paraproct.