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The *Bugilliesia* Complex of African Baetidae (Ephemeroptera)

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ABSTRACT

The *Bugilliesia* complex is a distinct grouping of Afrotropical Baetidae (Ephemeroptera) genera distinguished by a conspicuous basomedial protuberance on segment 2 of the male genital forceps. It includes *Potamocloeon* Gillies; *Afrobaetodes* Demoulin; *Kivua* McCafferty & Lugo-Ortiz, new genus; *Rhithrocloeon* Gillies; *Bugilliesia* Lugo-Ortiz & McCafferty, new genus; and *Mutelocloeon* Gillies & Elouard. Genera are each highly distinctive as larvae (*Kivua* remains unknown as larvae), but the complex is not definable in the larval stage. Cladistic analysis shows *Potamocloeon* to be the most plesiotypic lineage, with all other genera sharing larval apomorphies. *Kivua, Rhithrocloeon, Bugilliesia,* and *Mutelocloeon* form the next sequential clade, and the latter three form the next. *Bugilliesia* and *Mutelocloeon* are the most apotypic, sister lineages. Relationships are reflected in transitional changes in the unusual male genitalia. The recognition of the six sequenced species groups as genera constitutes a phylogenetic classification. *Kivua* consists of *K. elouardi* (Gillies), new combination, and *K. insueta* (Kopelke), new combination, thereby restricting *Rhithrocloeon* to consist of *R. indicator* Gillies and R. *permirum* (Kopelke). *Bugilliesia* consists of certain species previously considered in *Afroptilum* Gillies: *B. grisea* (Gillies), new combination; *B. guineensis* (Gillies), new combination; *B. nitida* (Ulmer), new combination; *B. notabilis* (Kimmins), new combination; and *B. sudanensis* (Ulmer), new combination. *Potamocloeon macafertiorum* Lugo-Ortiz, new species, is described from northeastern South Africa, and represents a considerable range extension for the genus. *Afrobaetodes intermedius* Lugo-Ortiz & McCafferty, new species, is described from northeastern South Africa. Diagnosis of all genera are given along with species inclusions and distributions.

INTRODUCTION

The faunal composition and phylogenetic relationships of African Baetidae (Ephemeroptera) are poorly known. Attempts to catalogue baetid diversity or devise generic classifications (e.g., Demoulin 1970, Elouard & Vololomboahangy 1990, Gillies 1991b, Wuillot & Gillies 1994, McCafferty & de Moor 1995) have often relied on sparse collections and literature, and thus have been necessarily preliminary. Recent significant revisionary work on African Baetidae (see below) has begun to sort out generic concepts, and will require considerable updating of catalogues and checklists.

Much of the revisionary work on African Baetidae has centered

around species once placed in the genus *Afroptilum* Gillies. Gillies (1990a) erected *Afroptilum* to accommodate all African baetids previously assigned to *Centroptilum* Eaton. In erecting *Afroptilum*, however, Gillies (1990a) did not provide comprehensive nor consistent phylogenetic criteria to characterize it, and it became evident that the genus was polyphyletic because several different evolutionary lineages were represented within it (McCafferty & de Moor 1995).

As Gillies (1990a) originally conceived it, *Afroptilum* was composed of two subgenera: *Afroptilum* s.s. and *Afroptiloides* Gillies. He further subdivided *Afroptilum* s.s. into the so-called *dimorphicum, sudanense, sudafricanum,* and *tarsale* species groups, indicating that the larvae of each group did not differ significantly enough from one another to recognize them as separate genera. Later, however, Wuillot & Gillies (1994) erected the genus *Dicentroptilum* for two distinctive species in the *sudafricanum* group, and Lugo-Ortiz & McCafferty (1996b,c) erected the genera *Crassabwa* and *Dabulamanzia* for various species in the *tarsale* group that were not related to *A. sudafricanum* (Lestage), the type species of *Afroptilum*. McCafferty & de Moor (1995) recombined the type species of the subgenus *Afroptiloides, A. varium* (Crass), with *Acanthiops* Waltz & McCafferty, and Barber-James & McCafferty (1997) provided detailed phylogenetic data showing that most species previously considered in *Afroptilum* (*Afroptiloides*) belonged to *Acanthiops*.

Although the studies mentioned have resolved numerous species that had been placed in *Afroptilum*, other problematic species that are clearly distinct from *A. sudafricanum* and represent other evolutionary lineages have remained in the genus. This paper resolves some of these: we recognize the five species of the *sudanense* group as a new genus separate from *Afroptilum*, as defined by synapomorphies not present in *A. sudafricanum*. The new genus shares highly unusual genitalic traits with certain other genera, including *Potamocloeon* Gillies, *Afrobaetodes* Demoulin, *Rhithrocloeon* Gillies, and *Mutelocloeon* Gillies & Elouard. *Rhithrocloeon*, as previously composed by Gillies (1985, 1989), also has proven to be polyphyletic, containing elements of typical *Rhithrocloeon* and a second new genus described herein. A cladogram depicting the hypothesized relationships of this complex of genera is provided and serves as the phylogenetic basis for our generic revisions and classification. In addition, we review known species of the genera and describe one new species in *Potamocloeon* and one new species in *Afrobaetodes* based on material recently collected from South Africa by one of us (WPM). The generic treatments below are presented in phylogenetic order. The materials examined are housed in the Purdue Entomological Research Collection, West Lafayette, Indiana.

TAXONOMY

Bugilliesia Complex

This grouping is defined by the presence of a large basomedial

protuberance on segment 2 of the adult male genital forceps (Figs. 19-24). In addition, but not exclusive to the complex, adults possess single marginal intercalaries in the forewings and male adults have a distinctive projection between the bases of the genital forceps (Figs. 19-24). Female adults lack reliable morphological features to separate them from other baetids with single marginal intercalaries in the forewings. Larvae of each species group lineage of the complex demonstrate numerous different morphological adaptations, none of which are commonly diagnostic of the entire complex. Diagnosis must be made for individual genera as shown below.

Genus **POTAMOCLOEON** Gillies

Potamocloeon Gillies 1990b:207.

Diagnosis.—LARVA: Antennae nearly 1.5-2.0x length of head capsule. Anterior margin of labrum with ventral edge broadly emarginate and with pairs of dorsal submedian flaps overhanging lateral thirds of emarginations (Fig. 2). Mandibles with incisors deeply cleft; prosthecae slender, apically denticulate; tuft of setae between prosthecae and molae (Figs. 4, 5). Maxillary palps two segmented, extending beyond galealaciniae; segment 2 0.5-0.75x length of segment 1 (Fig. 6; Gillies 1988: Fig. 26). Labium with two-segmented palps; segment 2 broadly wedge-shaped, with long, straight, setose, medially oriented margin; glossae reduced, nearly 0.33x length of paraglossae; paraglossae expanded, robust (Fig. 7; Gillies 1988: Fig. 27). Legs slender, with scattered stout, simple setae; tibiae with small subproximal arc of simple setae; tarsal claws edentate, nearly 0.90x length of tarsi (Fig. 8; Gillies 1988: Fig. 20). Gills on abdominal segments 1-7, asymmetrical, marginally smooth; gills 1-5 with dorsal flap; gills 6-7 simple, platelike (Gillies 1988: Figs. 14-17). Caudal filaments nearly 0.5x length of body; terminal filament subequal to cerci. MALE ADULT: Hindwings present or absent. Genital forceps three segmented; segment 1 with (Fig. 19) acute distomedial projection; segment 2 inwardly bowed, with mediodistally pointed basomedial protuberance; segment 3 appearing partially fused to segment 2 (Fig. 19).

Type Species.—*Cloeon dentatum* Kimmins.

Species Included.—

Potamocloeon dentatum (Kimmins)
Cloeon dentatum Kimmins 1956:77 (male subimago; male adult); Gillies 1988:52 (larva).
Potamocloeon dentatum (Kimmins): Gillies 1990b:207.
Potamocloeon macafertiorum Lugo-Ortiz, NEW SPECIES (larva).

Distribution.— (Fig. 25): Gambia (*P. dentatum*); Guinea (*P. dentatum*); Ivory Coast (*P. dentatum*); South Africa: Mpumalanga (*P. macafertiorum*); Uganda (*P. dentatum*).

Discussion.—Within the *Bugilliesia* complex, *Potamocloeon* possesses the following distinguishing features in the larval stage: a pair of

dorsal submedian flaps overhanging the anterior emarginations of the labrum (Fig. 2), reduced glossae, expanded paraglossae, and labial palps segment 2 that are uniquely wedge-shaped (Fig. 7). Based on the adult of *P. dentatum*, the partial fusion of segments 2 and 3 of the male genital forceps could be diagnostic (Fig. 19); however, the adult of *P. macafertiorum* remains unknown. The labrum and labial palps (Figs. 2, 7) are unique autapomorphies within Baetidae.

Gillies (1990b) believed that *Potamocloeon* shared a conspicuous basomedial projection on segment 1 of the male genital forceps with the Holarctic and Oriental genus *Pseudocentroptiloides* Jacob, thus suggesting a relationship between these genera. Close examination of the genitalia of *Pseudocentroptiloides* (Jacob & Glazaczow 1984: Fig. 1d; Waltz & McCafferty 1989: Fig. 12), however, shows that they do not have a basomedial projection on segment 1 and that actually the basal third of segment 2 is slightly broader than the apical two-thirds of the segment. Moreover, *Pseudocentroptiloides* lacks a basal projection between the male genital forceps. This projection is a common feature of many other baetids with single marginal intercalaries in the forewings, including the *Bugilliesia* complex, but not *Pseudocentroptiloides*.

Potamocloeon macafertiorum Lugo-Ortiz, new species
Figs. 2-9

Larva.—Body length: 5.5 mm; caudal filaments length: 1.8 mm. Head: Coloration pale yellow-brown, with no distinct pattern. Antennae 1.5x length of head capsule. Labrum (Fig. 2) with branched setae anteriorly. Hypopharynx as in Figure 3. Left mandible as in Figure 4. Right mandible as in Figure 5. Maxillae (Fig. 6) with four to five elongate sharp denticles on galealaciniae; palp segment 2 nearly 0.75x length of segment 1; medial margin with three to four short, fine, simple setae. Labium (Fig. 7) with broadly apically round paraglossae. Thorax: Coloration yellow-brown, with variable medium brown markings. Hindwingpads present. Legs (Fig. 8) pale yellow to cream; femora with short, stout, simple setae ventrally; tibiae bare except for medium-sized subapical simple seta ventrally; tarsi with medium-sized simple setae ventrally. Abdomen: General coloration pale yellow-brown. Tergum 1 pale yellow-brown, with median brown transverse dash anteriorly; terga 2, 3, and 6 medium brown, pale yellow-brown anteriorly; tergum 2 with median brown speck anteriorly; tergum 3 with three submedian brown specks anteriorly; terga 4, 5, and 7-9 pale yellow-brown, with median brown speck anteriorly; segment 10 pale yellow-brown, posterior margin brown. Sterna cream to pale yellow-brown. Sterna 2-9 with sublateral longitudinal brown dashes. Gills well tracheated. Paraprocts (Fig. 9) with six to seven sharp marginal spines. Caudal filaments cream to pale yellow, brown every three to five segments; median caudal filament subequal in length to cerci.

Adult.—Unknown.

Type Material Examined.—HOLOTYPE: Larva, South Africa,

Mpumalanga Province, Kruger Natl. Park, Sabie R, NE corner of Old Rhino Camp, X-24-1990, W. P. and N. McCafferty [mouthparts, right foreleg, and paraproct mounted on slide (medium: Euparal)].

Etymology.—This species was collected by Pat and Nadine McCafferty. CRLO is honored to name it after both of them.

Discussion.—*Potamocloeon macafertiorum* is the first species of the genus described from southern Africa. The presence of the genus in South Africa represents a considerable range disjunction for *Potamocloeon, P. dentatum* having been known only from Africa north of the Equator.

Potamocloeon macafertiorum larvae are generally similar to those of *P. dentatum*. However, in *P. macafertiorum*, segment 2 of the maxillary palps (Fig. 6) is considerably longer and more robust than that of *P. dentatum* (Gillies 1988: Fig. 26). The presence of variable small median and submedian speckling on the terga and lateral longitudinal dashes on the sterna also distinguish *P. macafertiorum* from *P. dentatum*. Additionally, *P. macafertiorum* has conspicuous hindwingpads, whereas *P. dentatum* lacks them.

Gillies (1988) collected *P. dentatum* on silt-clay substrate in relatively slow current. *Potamocloeon macafertiorum* was similarly collected in slow current at a water depth of 0.70 m, but in muddy and highly viscous silt-sand substrate.

Genus **AFROBAETODES** Demoulin

Afrobaetodes Demoulin 1970:52.

Diagnosis.—LARVA: Antennae nearly 1.5x length of head capsule. Mandibles with fused left incisors and cleft right incisors; left prostheca (Fig. 12) apically denticulate, right prostheca (Fig. 13) reduced to robust filament. Maxillary palps two segmented; palp segment 1 with filamentous distolateral gill; palp segment 2 subequal to segment 1 (Fig. 14; Kimmins 1955: Fig. 7d; Gillies 1991a: Fig. 14). Labium with three-segmented palps; palp segment 1 subequal in length to segments 2 and 3 combined; segments 2 and 3 subequal in length; segment 3 apically round; glossae and paraglossae subequal in length, relatively narrow and elongate (Fig. 15; Kimmins 1955: Fig. 7e; Gillies 1991a: Fig. 15). Thoracic foresternum with one sublateral filamentous gill on either side. Legs somewhat robust; femora with dorsal row of long, simple setae (Fig. 16; Kimmins 1955: Fig. 6a; Gillies 1991a: Fig. 19, 20); tarsal claws with pair of subapical setae and four to five denticles (Fig. 17; Gillies 1991a: Fig. 18). Gills on abdominal segments 1-6, ventrally oriented (Kimmins 1955: Fig. 6a), marginally smooth (Gillies 1991a: Figs. 9-10), without dorsal flap. Caudal filaments nearly 0.80x length of body; median caudal filament reduced to one segment. MALE ADULT: Hindwings, when present, with hooked costal process (Gillies 1991a: Fig. 2). Genital forceps three segmented; segment 2 inwardly bowed, with blunt (Gillies 1991a: Fig. 5) or acute (Fig. 20) basomedial protuberance; segment 3 nearly 0.33x length of segment 2,

ellipsoidal.

Type Species.—*Afrobaetodes berneri* Demoulin.

Species Included.—

Afrobaetodes berneri Demoulin
Afrobaetodes berneri Demoulin 1970:52 (larva); Gillies 1991a:106 (larva; female adult).
Baetidae nymph A, ? near *Centroptilum* Kimmins 1955:871 (larva).
Afrobaetodes delicatissimus (Barnard)
Cloeon delicatissimum Barnard 1932:216 (female adult).
Afrobaetodes delicatissimus (Barnard): Gillies 1979:153.
Afrobaetodes intermedius Lugo-Ortiz & McCafferty, NEW SPECIES (larva)
Afrobaetodes pugio Gillies
Afrobaetodes pugio Gillies 1991a:106 (larva; male, female adults).
Afrobaetodes pusillus (Navás)
Cloeon pusillum Navás 1930:321 (female adult); Demoulin 1957: 271 (female adult).
Afrobaetodes pusillus (Navás): Gillies 1979:153 (male adult).

Distribution.— (Fig. 26): Malawi (*A. berneri*); South Africa: Mpumalanga (*A. berneri, A. intermedius*), Western Cape (*A. delicatissimus*); Tanzania (*A. berneri, A. pugio*); Zaire (*A. pusillus*).

Discussion.—Within the *Bugilliesia* complex, *Afrobaetodes* possesses the following distinguishing characteristics in the larval stage: ventrally oriented gills on abdominal segments 1-6 (Kimmins 1955: Fig. 6a), cleft right mandibular incisors (Fig. 13; Kimmins 1955: Fig. 7b; Gillies 1991a: Fig. 17), a filamentous distolateral gill on maxillary palp segment 1 (Fig. 14; Kimmins 1955: Fig. 7d; Gillies 1991a: Fig. 14), relatively narrow and elongate glossae and paraglossae (Fig. 15; Kimmins 1955: Fig. 7e; Gillies 1991a: Fig. 15), labial palps with an apically round segment 3 (Fig. 15; Kimmins 1955: Fig. 7e; Gillies 1991a: Fig. 15), prothoracic gills, and reduction of the median caudal filament. Based on our cladistic analysis, these characteristics may be interpreted as autapomorphies within the complex, but are certainly subject to homoplasy in other lineages of Baetidae, other than the *Bugilliesia* complex.

Larvae of *Afrobaetodes* have some phenetic similarity with those of the Panamerican genus *Baetodes* Needham & Murphy and the Afrotropical genus *Thraulobaetodes* Elouard & Hideux. All three genera possess ventrally oriented abdominal gills. As Lugo-Ortiz & McCafferty (1996a) recently showed, *Baetodes* belongs to a distinct monophyletic grouping distinguished by the presence of subapical setae on only one lateral margin of the tarsal claws of the larvae (Lugo-Ortiz & McCafferty 1996a: Figs. 9, 15, 32, 39) and a distinct distomedial projection on segment 1 of the male genital forceps (Lugo-Ortiz & McCafferty 1996a: Figs. 11, 17, 42). Because larvae of *Afrobaetodes* and *Thraulobaetodes* do not possess the lateral setae on the tarsal claws, and

male adults of *Afrobaetodes* (*Thraulobaetodes* adults remain unknown) lack the distomedial projection on segment 1 of the genital forceps, neither of the latter genera is apparently closely related to *Baetodes*. Additionally, adults of *Afrobaetodes* have single marginal intercalaries in the forewings, whereas those of *Baetodes* and its related taxa possess double marginal intercalaries. This suggests that the presence of ventrally oriented gills in *Baetodes* and *Afrobaetodes* and *Thraulobaetodes* is convergent. Lugo-Ortiz & McCafferty (1996a) indicated that the presence of ventrally oriented gills probably represents an adaptation to clinging to the substrate in relatively fast currents [see also Hynes (1970) and Ward (1992)].

The possibility remains that *Afrobaetodes* and *Thraulobaetodes* are related. Both genera have species whose larvae possess dorsal abdominal tubercles (Gillies 1991a: Fig. 7; Elouard & Hideux 1991: Fig. 1a, b) and right mandibles with cleft incisors (Fig. 13; Kimmins 1955: Fig. 7b; Gillies 1991a: Fig. 17; Elouard & Hideux 1991: Fig. 2a, b). We are reluctant to assign *Thraulobaetodes* to the *Bugilliesia* complex at this time, however, because its male adults remain unknown.

Afrobaetodes intermedius Lugo-Ortiz & McCafferty, new species
Figs. 10-18

Larva.—Body length: 3.3 mm. Caudal filaments length: 2.5 mm. Head: Coloration medium brown to yellow-brown, with no distinct pattern. Antennae 1.5x length of head capsule. Labrum (Fig. 10) with long submedian seta and four to five long lateral submarginal setae on either side of midline; anterior margin with branched setae. Hypopharynx as in Figure 11. Left mandible (Fig. 12) with 5 + 3 denticles; tuft of simple setae between prostheca and mola present. Right mandible (Fig. 13) with three denticles on outer set of incisors and four denticles on medial set; tuft of simple setae present between prostheca and mola. Maxillae (Fig. 14) with four denticles on galealaciniae; three to four setae present on medial hump; palps segment 1 nearly 0.45x length of segment 2; distomedial filamentous gill nearly 0.90x length of segment 2. Labium (Fig. 15) with many long, simple setae marginally on glossae and paraglossae; palp segment 3 somewhat broadly rounded. Thorax: Coloration medium brown to yellow-brown, with no distinct pattern. Pronotum with small tuft of short, stout, simple setae in midregion; mesonotum with three tufts of short, stout, simple setae, two submedially in anterior half and one on posterior margin; metanotum with small tuft of short, stout, simple setae on posterior margin. Legs as in Figure 16; tarsal claws (Fig. 17) with five to six sharp denticles increasing in length distally. Abdomen medium brown to yellow-brown, with no distinct pattern. Terga 1-6 each with minute median tuft of short, stout, simple setae posteriorly. Sterna yellow-brown. Gills as long as one and one-half length of corresponding abdominal segments. Paraprocts (Fig. 18) marginally smooth. Caudal filaments pale yellow-brown; clusters of long, fine, simple setae present medially in midregion; medial setae as long as four to six segments

combined.

Adult.— Unknown.

Type Material Examined.—HOLOTYPE: Larva, South Africa, Mpumalanga Province, Sabie R at Lisbon Estates, X-27-1990, W. P. and N. McCafferty [mouthparts, foreleg, and paraproct mounted on slide (medium: Euparal)].

Other Material Examined.—Larva, same data as holotype.

Etymology.—The specific epithet is a Latinized form for intermediate. It is in reference to the apparently intermediate position of the species with respect to *A. berneri* and *A. pugio*.

Discussion.—Larvae of *A. intermedius* are more similar to those of *A. berneri* than they are to those of *A. pugio*. As in *A. berneri*, *A. intermedius* lacks the thoracic and tergal tubercles and coxal spurs found in *A. pugio*. But, as in *A. pugio*, *A. intermedius* has small tufts of short, stout, simple setae on the thorax. In contrast to both *A. berneri* and *A. pugio*, *A. intermedius* has more denticles on the mandibular incisors (Figs. 12, 13); minute median tufts of short, stout, simple setae on terga 1-6; and conspicuous medial clusters of long, fine, simple setae on the cerci.

Afrobaetodes intermedius was collected from a small side rivulet of the Sabie River having bedrock substrate with pockets of mixed gravel and sand. Water current was slight to moderate.

Genus **KIVUA** McCafferty & Lugo-Ortiz, new genus

Diagnosis.—LARVA: Unknown. MALE ADULT: Marginal intercalaries nearly 0.5x length of marginal interspace space between main veins (Kopelke 1980: Fig. 39; Gillies 1989: Fig. 1). Hindwings absent. Genital forceps two-segmented; segment 2 inwardly bowed, apically rounded, with blunt basomedial protuberance (Fig. 22).

Etymology.—The generic name is feminine and refers to the Kivu Province in Zaire, from where the type species is known.

Type Species.—*Cloeon insuetum* Kopelke.

Included Species.—

Kivua elouardi (Gillies), NEW COMB.
Rhithrocloeon elouardi Gillies 1989:287 (male adult).
Kivua insueta (Kopelke), NEW COMB.
Cloeon insuetum Kopelke 1980:125 (male adult).
Rhithrocloeon insuetum (Kopelke): Gillies 1985:16.

Distribution.— (Fig. 27): Ivory Coast (*K. elouardi*), Zaire (*K. insueta*).

Discussion.—Gillies (1985) transferred *C. insuetum* to *Rhithrocloeon*, but did not provide a rationale for that transfer. Later, Gillies (1989) described *R. elouardi* from a small series of male adults, and indicated that it was most similar to *C. insuetum*. Our analysis of the morphology of the male genitalia of those species shows that they differ significantly from those of *Rhithrocloeon* as defined herein (see *Rhithrocloeon*, below). The relative cladistic positions of the two lineages amongst others of the *Bugilliesia* complex require that they be classified as different genera (see Phylogeny section, below).

Adults of *Kivua* lack hindwings and possess distinctly short single marginal intercalaries in the forewings. Based on our cladistic analysis, these characteristics may be interpreted as autapomorphies within the complex. Hindwings have been lost independently in one of the species of *Potamocloeon*. This is a common occurrence in many lineages of baetids (see, e.g., McCafferty & Waltz 1990).

Genus **RHITHROCLOEON** Gillies

Rhithrocloeon Gillies 1985:13

Diagnosis.—LARVA: Antennae nearly 2.5x length of head capsule. Mandibles with fused incisors and tuft of setae between prosthecae and molae (Gillies 1988: Figs. 35, 36); right mandibular prostheca reduced to robust filament (Gillies 1988: Fig. 36). Maxillary palps two-segmented, extending beyond galealaciniae; palp segment 2 abruptly narrow in apical fourth, nearly 1.2x length of palp segment 1 (Gillies 1988: Fig. 38); labium with three-segmented palps; palp segment 2 distinctly expanded with convex medial margin in distal half; palp segment 3 poorly demarcated, appearing fused to segment 2, short, somewhat constricted, and caplike (Gillies 1988: Fig. 39). Hindwingpads absent. Legs slender, with scattered stout, simple setae; tarsal claws with one row of minute denticles (Gillies 1988: Figs. 43-45). Gills on abdominal segments 2-7, plate-like, anterodistally serrate, without dorsal flap. Caudal filaments >0.50x length of body; median caudal filament subequal in length to cerci. MALE ADULT: Hindwings absent. Genital forceps two-segmented; segment 2 inwardly bowed, more or less apically pointed, with distomedial straight margin and acute basomedial protuberance (Fig. 21; Gillies 1988: Fig. 26).

Type Species.—*Cloeon permirum* Kopelke.

Included Species.—

Rhithrocloeon indicator Gillies
Rhithrocloeon indicator Gillies 1985:14 (male adult); Gillies 1988:56 (larva).
Rhithrocloeon permirum (Kopelke)
Cloeon permirum Kopelke 1980:123 (male, female adults).
Rhithrocloeon permirum (Kopelke): Gillies 1985:13; Gillies 1988:56 (larva).

Distribution.— (Fig. 28): Tanzania (*R. indicator, R. permirum*), Zaire (*R. permirum*).

Discussion.—Within the *Bugilliesia* complex, *Rhithrocloeon* possesses the following distinguishing characteristics in the larval stage: segment 2 of maxillary palps abruptly narrowed in apical fourth (Gillies 1988: Fig. 38); three-segmented labial palps with segment 2 medially convex in the distal half, and a small segment 3 appearing fused to segment 2 (Gillies 1988: Fig. 39); and the absence of gills on abdominal segment 1. In the adult stage, the distomedially straight edge of segment 2 of the male genital forceps is distinctive (Fig. 21; Gillies

1988: Fig. 26). Based on our cladistic analysis, these characteristics may be interpreted as autapomorphies. The male forceps are unique in Baetidae, but the larval apomorphies are more or less subject to homoplasy in other lineages of Baetidae outside of the *Bugilliesia* complex.

Genus **BUGILLIESIA** Lugo-Ortiz & McCafferty, new genus

Diagnosis.—LARVA: Antennae nearly 2.5x length of head capsule. Mandibles with fused incisors; prosthecae apically denticulate, right prostheca more slender and with sharper denticles than left prostheca; tuft of setae present between prosthecae and molae (Gillies 1990a: Figs. 69-73). Maxillary palps two segmented, extending beyond galealaciniae; segment 2 nearly 1.2x length of segment 1 and with (Gillies 1990a: Fig. 76) abrupt distal constriction. Labium with three-segmented palps; palp segment 1 as long as segments 2 and 3 combined; segment 2 with highly pronounced (Gillies 1990a: Fig. 67) or poorly developed (Gillies 1990a: Fig. 74) distomedial projection (labial palp thumb); palp segment 3 rounded. Hindwingpads present. Legs with scattered stout, simple setae (Gillies 1990a: Figs. 79-81); tarsal claws poorly denticulate (Gillies 1990a: Figs. 79-81). Gills on abdominal segments 1-7, plate-like, marginally smooth, without dorsal flaps (Gillies 1990a: Fig. 82). Caudal filaments >0.5x length of body; medial caudal filament subequal in length to cerci. MALE ADULT: Marginal intercalaries as long as marginal interspace between main veins (Kimmins 1956: Fig. 3). Hindwings small, with hooked costal process. Genital forceps (Fig. 23) two segmented; segment 1 with oblique distal margin; segment 2 slightly bowed outwardly, blade-shaped, more or less apically pointed, with rounded basomedial protuberance.

Etymology.—This genus is named in honor of Mick Gillies, for his outstanding contribution to the description of African mayfly fauna, in particular Baetidae. The name consists of an arbitrary combination of letters, with a feminine Latin ending, and incorporates our colleague's last name. Thus, it loosely transliterates as "Gillies' bug."

Type Species.—*Afroptilum guineense* Gillies.

Included Species.—

Bugilliesia grisea (Gillies), NEW COMB.
Afroptilum griseum Gillies 1990a:117 (larva; male, female adults).

Bugilliesia guineensis (Gillies), NEW COMB.
Afroptilum guineense Gillies 1990a:116 (larva; male adult).

Bugilliesia nitida (Ulmer), NEW COMB.
Centroptilum nitidum Ulmer 1916: 17 (male adult).
Cloeon nigroalbum Navás 1932:287 (female adult; male subimago): Demoulin 1957:260.
Cloeon bredoanum Navás 1933:317 (male, female adults): Demoulin 1957:260.
Afroptilum nitidum (Ulmer): Gillies 1990a:99.

Bugilliesia notabilis (Kimmins), NEW COMB.
Centroptilum notabile Kimmins 1956:73 (male adult).
Afroptilum notabile (Kimmins): Gillies 1990a:99.
Bugilliesia sudanensis (Ulmer), NEW COMB.
Centroptilum sudanense Ulmer 1916:18 (male adult); Kimmins 1956:73 (male adult).
Afroptilum sudanense (Ulmer): Gillies 1990a:114 (larva).

Distribution.— (Fig. 29): Gambia (*B. sudanensis*), Guinea (*B. guineensis*), Ivory Coast (*B. guineensis*), Sudan (*B. sudanensis*), Tanzania (*B. grisea, B. notabilis*), Uganda (*B. notabilis, B. sudanensis*), Zaire (*B. nitida*).

Discussion.—Gillies (1990a) considered *B. grisea, B. guineense, B. nitida, B. notabilis,* and *B. sudanensis* to belong to his *sudanense* group of *Afroptilum.* His rationale for including those species in *Afroptilum* was that their larvae did not differ substantially from those of other groups in the genus. Our examination of the mouthparts and male genitalia of those species, however, revealed that they share apomorphies clearly separating them from the type species of *Afroptilum.* Our cladistic analysis also shows this species group to represent a separate lineage classifiable as a genus within the *Bugilliesia* complex. We therefore erect the new genus *Bugilliesia* to accommodate these species.

Within the *Bugilliesia* complex, *Bugilliesia* possesses the following distinguishing characteristics in the larval stage: three-segmented labial palps with a segment 2 that has a distomedial projection (Gillies 1990a: Fig. 67, 74), and poorly defined denticles on the tarsal claws (Gillies 1990a: Figs. 79-81). In the adult stage, the oblique distal margin of forceps segment 1 and the distally divergent orientation of the male genital forceps are distinctive (Fig. 23). The unique blade shape of the genital forceps (Fig. 23) represents an autapomorphy.

Genus **MUTELOCLOEON** Gillies & Elouard

Mutelocloeon Gillies & Elouard 1990:289

Diagnosis.—LARVA: Antennae nearly 0.75x length of head capsule (Gillies & Elouard 1990: Fig. 4). Mandibles with fused incisors; prosthecae apically denticulate; tuft of setae between prosthecae and molae (Gillies & Elouard 1990: Figs. 6, 8). Maxillary palps two segmented, reduced, not reaching galealaciniae (Gillies & Elouard 1990: Fig. 9); segment 2 nearly 0.75x length of segment 1. Labium with two-segmented palps; segment 2 bulbous (Gillies & Elouard 1990: Fig. 10). Hindwingpads rudimentary. Legs bare except for few scattered stout, simple setae on the posterior margin of hindtibiae; tarsal claws edentate (Gillies & Elouard 1990: Figs. 12-14). Gills on abdominal segments 1-7, marginally smooth (Gillies & Elouard 1990: Fig. 15). Caudal filaments 0.17-0.33x length of body; terminal filament subequal to cerci (Gillies & Elouard 1990: Fig. 4). MALE ADULT: Hindwings minute, nearly 0.25 mm (Kimmins 1956: Fig. 6). Genital forceps (Fig. 24) two segmented; segment 2 reduced, slightly bowed outwardly, more or less apically pointed, with rounded to globular basomedial

protuberance.

Type Species.—*Mutelocloeon bihoumi* Gillies & Elouard.

Included Species.—

Mutelocloeon bihoumi Gillies & Elouard

Mutelocloeon bihoumi Gillies & Elouard 1990:290 (larva; female subimago; male adult).

Mutelocloeon corbeti (Kimmins)

Centroptilum corbeti Kimmins 1956:75 (male, female adults).

Mutelocloeon corbeti (Kimmins): Gillies & Elouard 1990:293.

Distribution.— (Fig. 30): Guinea (*M. bihoumi*), Mali (*M. bihoumi*), Uganda (*M. corbeti*).

Discussion.—Within the *Bugilliesia* complex, *Mutelocloeon* possesses the following distinguishing characteristics in the larval stage: shortened antennae (Gillies & Elouard 1990: Fig. 4), reduced maxillary palps (Gillies & Elouard 1990: Fig. 9), two-segmented labial palps with a bulbous segment 2 (Gillies & Elouard 1990: Fig. 10), and three subequal shortened caudal filaments (Gillies & Elouard 1990: Fig. 4). In the adult stage, the aberrant and reduced segment 2 of the male genital forceps is distinctive (Fig. 24). Based on our cladistic analysis, these characteristics may be interpreted as autapomorphies; however, only the aberrant forceps is unique among the Baetidae.

Gillies & Elouard (1990) indicated that *Mutelocloeon* is most closely related to the Southeast Asian genus *Symbiocloeon* Müller-Liebenau because of their symbiotic relationship with bivalves and because they supposedly share a reduction of setation on the legs and gills and both have edentate tarsal claws. Comparison of the figures of the legs of *Symbiocloeon* (Müller-Liebenau & Heard 1979: Fig. 4a) and *Mutelocloeon* (Elouard & Gillies 1990: Figs. 12-14), however, shows that the legs of *Symbiocloeon* are covered with setae, whereas those of *Mutelocloeon* are bare. The absence of denticles on the larval tarsal claws is highly subject to homoplasy within Baetidae. For example, larvae of the distantly related Pantropical genus *Cloeodes* Traver also lack such denticles (Waltz & McCafferty 1987a: Fig. 17; Waltz & McCafferty 1987b: Fig. 8). Also, the cladistic position of *Potamocloeon* (see Phylogeny section, below) indicates another independent loss of claw denticles. We suggest that the absence of denticulate claws in larvae of *Symbiocloeon* and *Mutelocloeon* is possibly independently derived and possibly related to residing on the mantle of bivalves. We remain reluctant to include *Symbiocloeon* in the *Bugilliesia* complex mainly because adults of that genus are unknown, and it is the male genitalia that will or will not place the genus in the complex.

PHYLOGENY

Methods

Cladistic methods employed are after Hennig (1966), Ross (1974), and Wiley (1981). The species group operational taxonomic units, or OTUs, used for cladistic comparative analysis were *Afrobaetodes*, *Mutelocloeon*, *Potamocloeon*, *Rhithrocloeon* (restricted), and the two spe-

Table 1. Structural characters and characters state polarities used to formulate the cladogram of the *Bugilliesia* complex in Figure 1. Numbered characters correspond to the numbered apomorphies distributed on the cladogram.

	Character	Plesiomorphy	Apomorphy
1	Male forceps segment 2	Without basomedial protuberance	With conspicuous basomedial protuberance (Figs. 19-24)
2	Larval tarsal claws	Elongate (Fig. 8)	Reduced (Figs. 16, 17)
3	Gills	With dorsal flaps	Without dorsal flaps
4	Male forceps segment 3	Present	Absent (Figs. 21-24)
5	Male forceps apex	Round or truncate (Figs. 19-21)	More-or-less pointed (Fig. 22-24)
6	Male forceps segment 2 outer margin	Bowed inwardly (rarely appearing straight) (Figs. 19-22)	Slightly bowed outwardly (Figs. 23-24)
7	Male forceps protuberance shape	Pointed (Figs. 19-22)	Globular or round (Figs. 23-24)
8	Labrum shape	Without anterior flaps	With anterior flaps on lateral thirds of emarginations (Fig. 2)
9	Labial palps shape	Not wedge-shaped	Wedge-shaped (Fig. 7)
10	Maxillary gills	Absent	Present (Fig. 14)
11	Forewings marginal intercalaries	>0.5x length of space between veins	<0.5x length of space between veins
12	Male forceps distomedial margin	Without straight edge (Figs. 19-21, 23, 24)	With straight edge (Fig. 22)
13	Male forceps juncture of segments 1 and 2	More or less at right angles to longitudinal plane of body (Figs. 19-22, 24)	Oblique (Fig. 23)
14	Male forceps shape	Not blade-shaped (Figs. 19-22, 24)	Blade-shaped (Fig. 23)
15	Male forceps segment 2	Elongate (Figs. 19-23)	Short (Fig. 24)

cies groups that subsequently were recognized as the new genera *Bugilliesia* and *Kivua*. Cladistic characters and their respective plesiomorphic and apomorphic states are given in Table 1 and are based on considering the outgroup to be all other Baetidae whose adults have single marginal intercalaries. Characters 1-7 demonstrate hypothesized common ancestry, whereas the remaining characters illustrate autapomorphies that define the individual lineages as monophyletic. *Cloeon* Leach best represents a taxon possessing plesiomorphies of the characters used. No analytical programs for handling cladistic data were necessary because of the small number of OTUs and usable comparative characters.

RESULTS

The deduced cladogram depicting the relationships of the OTUs is given in Figure 1. Numbers along the branches of the cladogram (Fig. 1) indicate apomorphies of those numbered characters shared by clades of OTUs or exclusive to individual OTUs.

Except for synapomorphies 2 and 3, which are based on larval characters, all other synapomorphies are based on genitalic characters of male adults. Traditionally in Baetidae, larval characters, particularly those related to mouthparts, have been almost exclusively used to determine species groups or suggest relationships (see, e.g., Müller-Liebenau 1969, Kluge & Novikova 1992, Waltz et al. 1994, Lugo-Ortiz & McCafferty 1996a). This has been the case because of the general lack of differential characters in the adults that are not highly subject to homoplasy, and the absence of male genitalic differences typical of most mayflies. The genitalia of male adults of the *Bugilliesia* complex, however, are atypical of Baetidae in general and have discrete but transitional differences that allow inferences of phylogenetic relationships. Larval characters, on the other hand, provide little evidence for analysis of common ancestry. Each lineage has undergone considerable independent evolution evidently related to diverse niches. We necessarily made assumptions regarding the larval apomorphies 2 and 3 with respect to *Kivua* because it remains unknown in that stage. Its male genitalia are, however, intermediate between those of *Potamocloeon* and *Afrobaetodes* and those of *Rhithrocloeon*, *Bugilliesia*, and *Mutelocloeon*, and therefore predictive of the more apotypic larval claw and gill character within the complex.

CLASSIFICATION

Based on the cladogram (Fig. 1), and allowing for sequencing conventions (Nelson 1973), six phylogenetic classifications are allowable for the species group OTUs in the *Bugilliesia* complex. One alternative would be to consider the entire complex as one genus. A second alternative would be to consider *Potamocloeon* as one genus and *Afrobaetodes*, *Rhithrocloeon*, *Kivua*, *Bugilliesia*, and *Mutelocloeon* as another genus. A third alternative would be to consider *Potamocloeon*,

Afrobaetodes, and *Rhithrocloeon, Kivua, Bugilliesia*, and *Mutelocloeon* as three separate genera. A fourth alternative would be to consider *Potamocloeon, Afrobaetodes, Rhithrocloeon*, and *Kivua, Bugilliesia*, and *Mutelocloeon* as four separate genera. A fifth alternative would be to consider *Potamocloeon, Afrobaetodes, Rhithrocloeon, Kivua*, and *Bugilliesia* and *Mutelocloeon* as five genera. The sixth alternative would recognize the six species group OTUs as six different genera.

Given the distinctiveness of each species group in the complex, especially with respect to the larval stage (see Taxonomy section), we maintain that the only sensible classificatory alternative is to recognize each as a separate genus. Such classification would reflect the diversity and uniqueness of each lineage. Additionally, it would involve the least amount of revision, with the recognition of *Kivua* and *Bugilliesia* as new genera and consequent transfer of species to them (see Taxonomy section) as the most important revisions.

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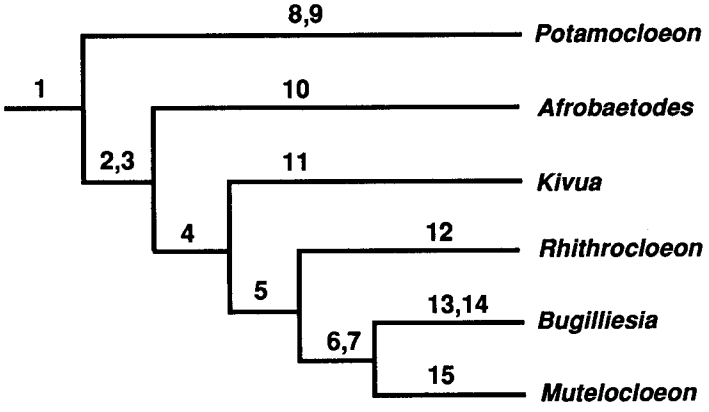
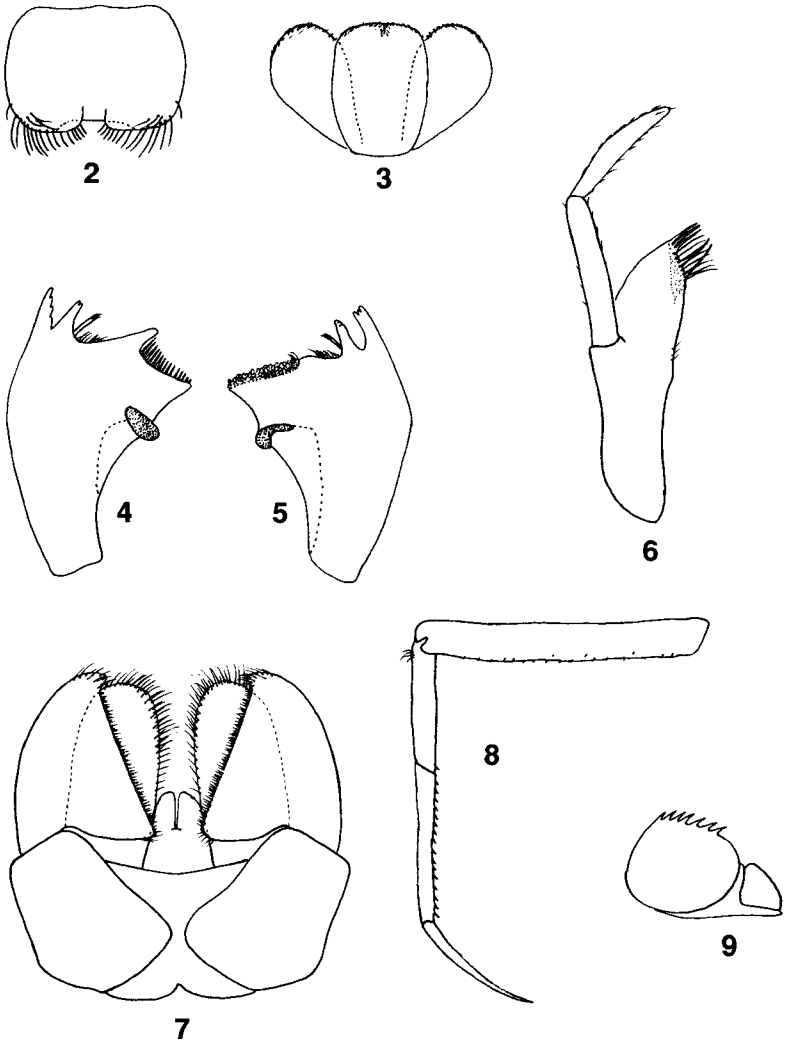
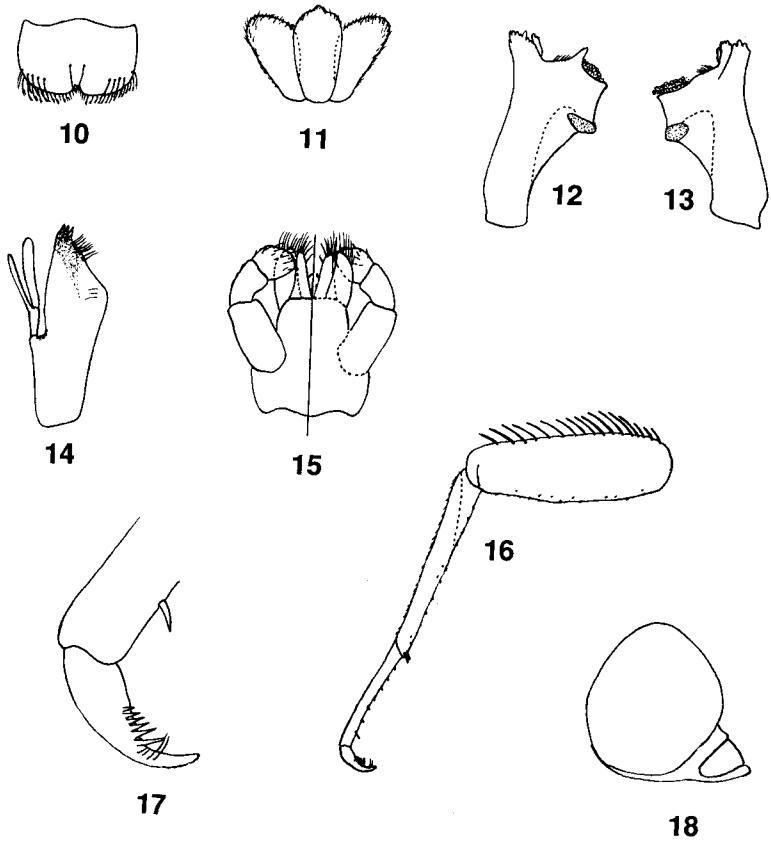


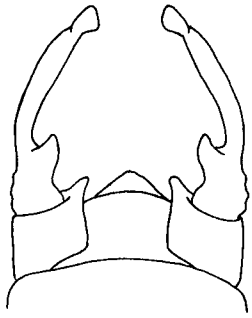
FIGURE 1. Cladogram of the species group OTUs of the *Bugilliesia* complex. Numbered apomorphies correspond to the numbered apomorphies in Table 1.



FIGURES 2-9. *Potamocloeon macafertiorum* Lugo-Ortiz, new species, larva. 2. Labrum (dorsal). 3. Hypopharynx. 4. Left mandible. 5. Right mandible. 6. Right maxilla. 7. Labium (ventral). 8. Right foreleg. 9. Paraproct.



FIGURES 10-18. *Afrobaetodes intermedius* Lugo-Ortiz & McCafferty, new species, larva. 10. Labrum (dorsal). 11. Hypopharynx. 12. Left mandible. 13. Right mandible. 14. Right maxilla. 15. Labium (left-ventral; right-dorsal). 16. Right foreleg. 17. Tarsal claw. 18. Paraproct.



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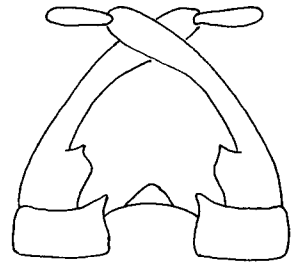

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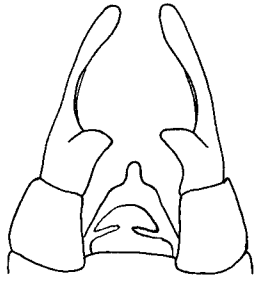

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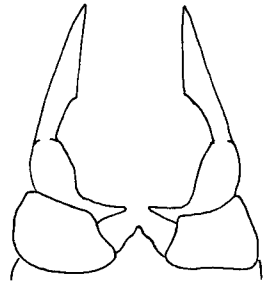

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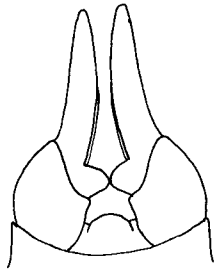

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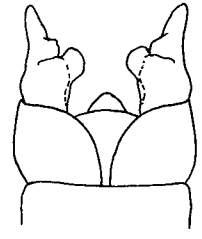

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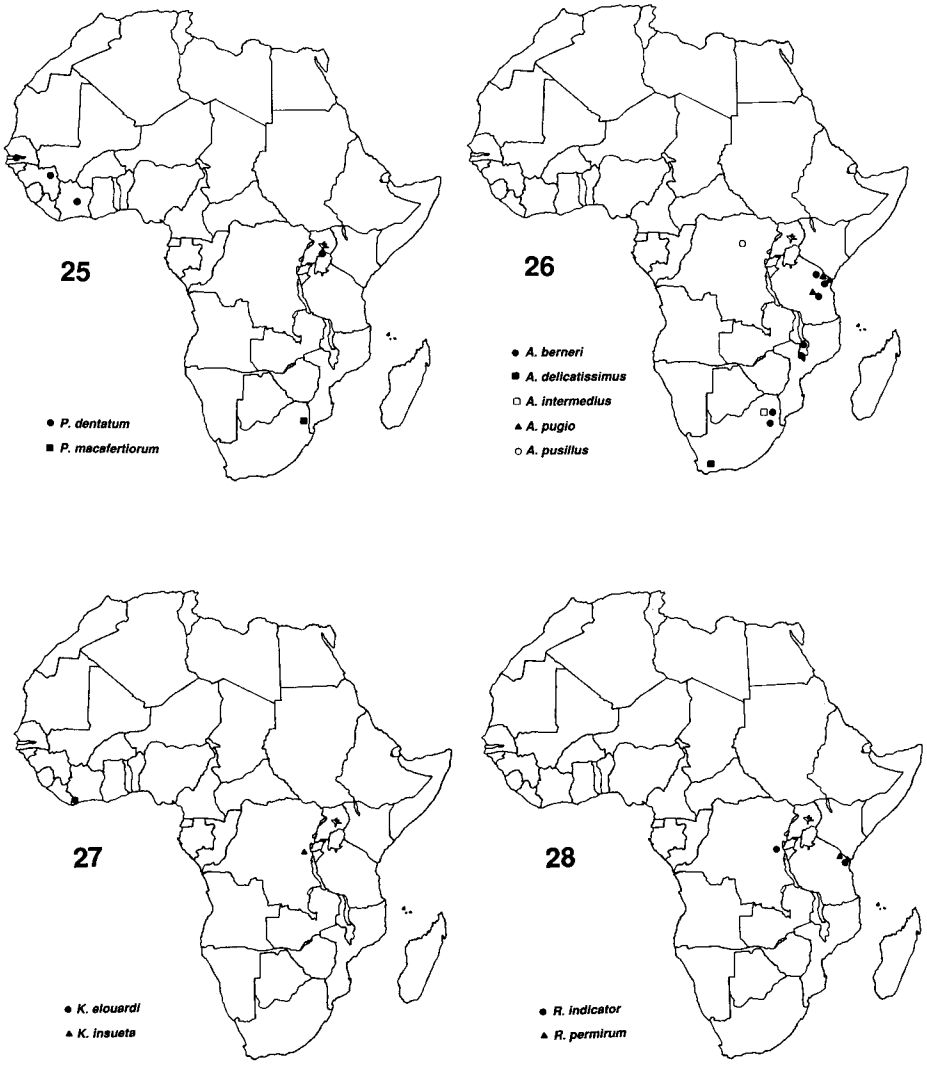
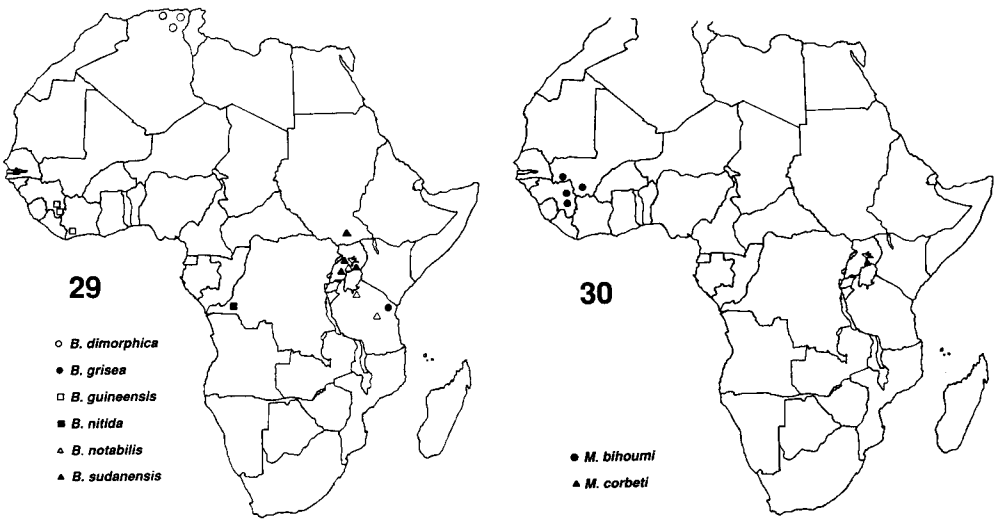
FIGURES 19-24. Male adult genitalia (ventral). 19. *Potamocloeon dentatum*. 20. *Afrobaetodes pusillus*. 21. *Rhithrocloeon permirum*. 22. *Kivua insueta*. 23. *Bugilliesia sudanensis*. 24. *Mutelocloeon corbeti*. [Redrawn from Kimmins (1956), Gillies (1979), and Kopelke (1980)].



FIGURES 25-28. Distributions of genera. 25. *Potamocloeon* spp. 26. *Afrobaetodes* spp. 27. *Kivua* spp. 28. *Rhithrocloeon* spp.



FIGURES 29-30. Distributions of genera. 29. *Bugilliesia* spp. 30. *Mutelocloeon* spp.