

The *Centroptiloides* Complex of Afrotropical Small Minnow Mayflies (Ephemeroptera: Baetidae)

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ABSTRACT The *Centroptiloides* complex is a distinctive monophyletic grouping of Afrotropical Baetidae (Ephemeroptera) genera with single marginal intercalary veins in the forewings and 2 subparallel rows of denticles on the larval tarsal claws. The complex includes 30 nominal species in *Acanthiops* Waltz & McCafferty, *Afroptilum* Gillies, *Barnumus* McCafferty & Lugo-Ortiz n. gen., *Centroptiloides* Lestage, *Dicentropitulum* Wuillot & Gillies, *Edmulmeatus* Lugo-Ortiz & McCafferty, *Herbrossus* McCafferty & Lugo-Ortiz n. gen., *Nesoptiloides* Demoulin, *Peuhella* Lugo-Ortiz & McCafferty n. gen., *Susua* Lugo-Ortiz & McCafferty n. gen., and *Thraulobaetodes* Elouard & Hideux. Each genus is detailed and is distinguishable by autapomorphies. The concept of *Afroptilum* is considerably restricted. *Platycloeon* Gillies & Wuillot is a synonym of *Acanthiops* n. syn. Newly described species include *Acanthiops elgonensis* Lugo-Ortiz & McCafferty n. sp. (Kenya), *A. griffithsi* Lugo-Ortiz & McCafferty n. sp. (Kenya), *A. zomba* Lugo-Ortiz & McCafferty n. sp. (Malawi), *Afroptilum confusum* Lugo-Ortiz & McCafferty n. sp. (Madagascar), *A. lepidum* Lugo-Ortiz & McCafferty n. sp. (Madagascar), *Barnumus editus* McCafferty & Lugo-Ortiz n. sp. (South Africa), *Dicentropitulum merina* Lugo-Ortiz & McCafferty n. sp. (Madagascar), and *Herbrossus edmundsorum* McCafferty & Lugo-Ortiz n. sp. (Madagascar). These include the 1st reports of *Afroptilum* and *Dicentropitulum* outside of Africa. New records for previously described species include *Acanthiops tsitsa* Barber-James & McCafferty (Malawi, Mozambique), *Afroptilum sudafricanum* (Lestage) (Lesotho), *Centroptiloides bifasciata* (Esbensen-Petersen) (Kenya, Mozambique), and *Dicentropitulum papillosum* Wuillot (Mozambique, South Africa). New generic assignments include *Acanthiops cooperi* (Gillies & Wuillot) n. comb., *A. erepens* (Gillies) n. comb., *Peuhella christinae* (Wuillot) n. comb., and *Susua niandanensis* (Wuillot) n. comb. *Centroptiloides bifasciata* and *Nesoptiloides intermedia* (Demoulin) are redescribed based on new larval collections.

KEY WORDS *Centroptiloides* complex, new genera, new species, new combinations, Africa, Madagascar

THE FAUNAL COMPOSITION of the mayfly family Baetidae in the Afrotropics has received considerable attention recently (Waltz and McCafferty 1987a, 1994; Gillies 1988, 1990a, b, 1991a-c, 1992, 1993, 1994; Gillies and Elouard 1990; Gillies et al. 1990; Elouard and Hideux 1991; Wuillot and Gillies 1993a, b, 1994; McCafferty and de Moor 1995; Lugo-Ortiz and McCafferty 1996a-c, 1997a-e; Barber-James and McCafferty 1997; Gillies and Wuillot 1997; McCafferty et al. 1997). As a result, the following genera are now known from the region: *Acanthiops* Waltz & McCafferty, *Afrobaetodes* Demoulin, *Afroptilum* Gillies, *Baetis* Leach, *Bugilliesia* Lugo-Ortiz & McCafferty, *Centroptiloides* Lestage, *Cheleocloeon* Wuillot & Gillies, *Cloeodes* Traver, *Cloeon* Leach, *Crassabwa* Lugo-Ortiz & McCafferty, *Dabulamanzia* Lugo-Ortiz & McCafferty, *Demoreptus* Lugo-Ortiz & McCafferty, *Demoulinia* Gillies, *Dicentropitulum* Wuillot & Gillies, *Edmulmeatus* Lugo-Ortiz & McCafferty, *Kivua* McCafferty & Lugo-Ortiz, *Labiobaetis* Novikova & Kluge, *Maliqua* Lugo-Ortiz & McCafferty, *Micksiops* McCafferty,

Lugo-Ortiz, & Barber-James, *Mutelocloeon* Gillies & Elouard, *Nesoptiloides* Demoulin, *Ophelmatostoma* Waltz & McCafferty, *Potamocloeon* Gillies, *Pseudopannota* Waltz & McCafferty, *Rhithrocloeon* Gillies, *Tanzaniella* Gillies, and *Thraulobaetodes* Elouard & Hideux. The several species that have been reported under *Pseudocloeon* Klapálek require study and probably reassignment because the concept of that genus has been severely restricted (Waltz and McCafferty 1985). Species now assigned to *Baetis* also require review to determine more precisely the particular species groups of *Baetis* present in the Afrotropics.

Herein we show the presence of a relatively large and apparently monophyletic Afrotropical complex of baetid genera consisting of *Acanthiops*, *Afroptilum*, *Barnumus* McCafferty & Lugo-Ortiz n. gen., *Centroptiloides*, *Dicentropitulum*, *Edmulmeatus*, *Herbrossus* McCafferty & Lugo-Ortiz n. gen., *Nesoptiloides*, *Peuhella* Lugo-Ortiz & McCafferty n. gen., *Susua* Lugo-Ortiz & McCafferty n. gen., and *Thraulobaetodes*. We refer to this group as the *Centrop-*

tiloides complex. Herein, we diagnose the complex and describe or redescribe each genus. We also describe new species in *Acanthiops*, *Afroptilum*, *Barnumus*, *Dicentropitulum*, and *Herbrossus*, and provide new geographic records for previously known species in *Acanthiops*, *Afroptilum*, *Centroptiloides*, and *Dicentropitulum*. Except where otherwise noted, all materials examined are housed in the Purdue Entomological Research Collection, West Lafayette, IN.

Centroptiloides Complex

The *Centroptiloides* complex consists of baetid mayflies, thus far known only from the Afrotropics, that as larvae possess 2 subparallel rows of denticles on the tarsal claws (Figs. 32, 42, 54, 66) (2nd row reduced in number in some species) and as alate forms possess single marginal intercalaries in the forewings. With regard to diagnoses from other complexes of genera that have been identified in the Afrotropics, larvae of the *Baetis* complex (*Baetis*, *Demoreptus*, *Labiohaetis*, and *Tanzaniella*) are distinguished by a unique femoral villopore (figures 1, 4, 5, and 17 in Waltz and McCafferty [1987b]), and alate forms of the complex have double marginal intercalaries in the forewings. Larvae of the *Bugillesia* complex (*Afrobaetodes*, *Bugillesia*, *Kivua*, *Mutolocloeon*, *Potamocloeon*, and *Rhithrocloeon*) lack the 2 rows of denticles on the tarsal claws, and male adults of the complex have a large basomedial protuberance on segment 2 of the genital forceps (figures 19–24 in Lugo-Ortiz and McCafferty [1996c]).

Acanthiops Waltz & McCafferty

Acanthiops Waltz and McCafferty 1987a: 97.

Afroptiloides Gillies 1990a: 99.

Platycloeon Gillies and Wuillot 1997: 185 n. syn.

Larva. *Head.* Labrum (Figs. 1 and 11) dorsoventrally thin, more or less parallel sided, slightly wider than long, broadly rounded anteriorly, with narrow anteromedial emargination. Hypopharynx (Fig. 2) slightly elongate; lingua with apicomedial marginal convexity and without apical bristle tuft; superlinguae narrow. Left mandible (Fig. 3) with 1 set of incisors; prosthema robust, apically denticulate; tuft of short, fine, simple setae present between prosthema and mola; lateral margin almost straight; basal half bare dorsally. Right mandible (Fig. 4) with 2 sets of incisors; prosthema slender; tuft of short, fine, simple setae present between prosthema and mola; lateral margin almost straight; basal half bare dorsally. Maxillae (Fig. 5) with 4 short, blunt denticles on crown of galealaciniae; palps 2-segmented, reaching or not reaching galealaciniae. Labium (Fig. 6) with glossae subequal to equal in length to paraglossae; glossae basally broad, apically narrow; palps 3-segmented; palp segment 2 with slight distomedial projection; palp segment 3 short, subconical to broadly rounded.

Thorax. Pronotum with slight anteromedial emargination, laterally expanded and flattened (figure 20 in Gillies [1990a]; figure 1 in Barber-James and McCafferty [1997]; figure 6 in Gillies and Wuillot [1997]). Legs held close to body; tibiae and tarsi without dorsal row of long, fine simple setae; forelegs (Fig. 7) with femora without marginal convexity and tibiae without ventrodiscal process. Tarsal claws (figure 15 in Barber-James and McCafferty [1997]) with 2 subparallel rows of denticles.

Abdomen. Segment 1 not enlarged. Terga with poorly developed (figure 30 in Gillies [1990a]; figures 1 and 2 in Barber-James and McCafferty [1997]) to well-developed dorsally oriented medial tubercles (Fig. 8) (figure 3a and b in Demoulin [1967]); posterior marginal spines relatively short and apically blunt. Gills (Fig. 9) on segments 1–7 or 2–7, platelike, relatively broad, marginally smooth, well tracheated, held dorsolaterally. Paraprocts with (Fig. 10) or without (Fig. 12) marginal spines. Medial caudal filament reduced to minute vestige (figure 1 in Barber-James and McCafferty [1997]) or short to ≈ 0.50 times length of cerci (figure 30 in Gillies [1990a]).

Adult. Hindwings somewhat broad; costal process entire, acute, and slightly hooked (figure 25b in Crass [1947]; figure 30 in Gillies [1991a]), or shallowly bifurcated, broadly based, and somewhat hooked (figure 21 in Gillies [1990a]). Male genital forceps (figure 25c in Crass [1947]; figure 12 in Gillies [1991a]) 3-segmented; segment 3 small, tear-drop-shaped.

Type Species. *Centroptilum marlieri* Demoulin (original designation).

Species Included.

Acanthiops cooperi (Gillies & Wuillot) n. comb.

Platycloeon cooperi Gillies and Wuillot 1997: 186 (larva).

Acanthiops elgonensis Lugo-Ortiz & McCafferty n. sp. (larva).

Centroptilum sp. no. 3: Demoulin 1964: 286.

Acanthiops erepens (Gillies) n. comb.

Afroptilum erepens Gillies 1990a: 105 (larva; male, female adults).

Platycloeon erepens (Gillies): Wuillot and Gillies 1997: 186.

Acanthiops griffithsi Lugo-Ortiz & McCafferty n. sp. (larva).

Acanthiops marlieri (Demoulin).

Centroptilum marlieri Demoulin 1967: 230 (larva).

Acanthiops marlieri (Demoulin): Waltz and McCafferty 1987a: 98.

Acanthiops tsitsa Barber-James and McCafferty 1997: 91 (larva).

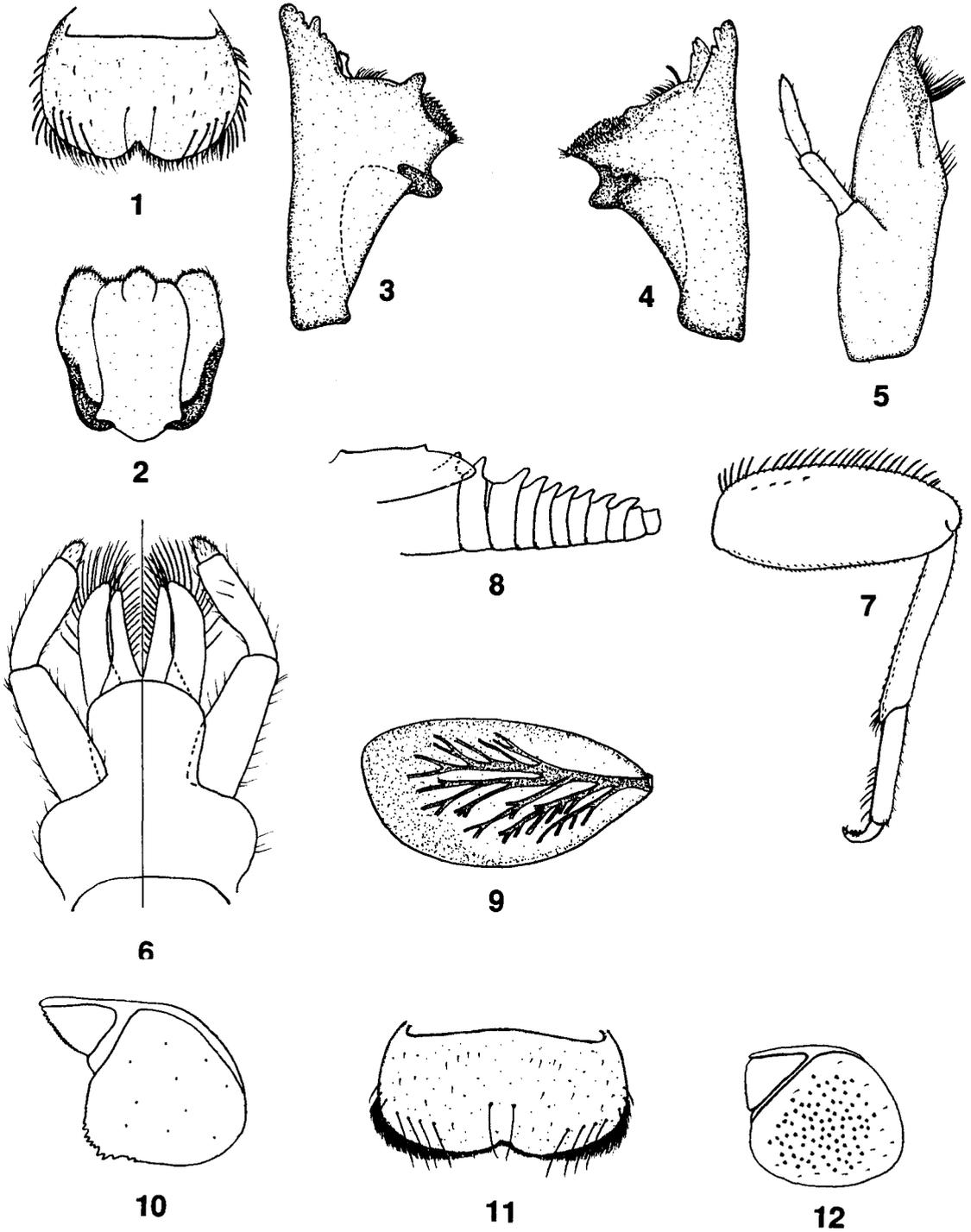
Baetis sp. A: Kimmins 1955: 868.

Acanthiops variegatus (Gillies).

Afroptilum variegatum Gillies 1991a: 111 (larva; male, female adults).

Acanthiops variegatus (Gillies): Barber-James and McCafferty 1997: 88.

Acanthiops varius (Crass).



Figs. 1-12. *Acanthiops* spp., larvae. (1-10) *A. griffithsi* n. sp. (1) Labrum. (2) Hypopharynx. (3) Left mandible. (4) Right mandible. (5) Right maxilla. (6) Labium (left, ventral; right, dorsal). (7) Left foreleg. (8) Abdomen. (9) Gill 4. (10) Paraproct. (11-12) *A. zomba* n. sp. (11) Labrum. (12) Paraproct.

Centroptilum varium Crass 1947: 85 (larva; male, female adults).

Afroptilum varium (Crass): Gillies 1990a: 99.

Acanthiops varius (Crass): McCafferty and de Moor 1995: 468.

Acanthiops zomba Lugo-Ortiz & McCafferty, n. sp. (larva).

Acentrella sp. A: Kimmins 1955: 870.

Centroptilum sp. A: Demoulin 1970: 50.

Afroptilum (*Afroptiloides*) sp. A: Gillies 1990a: 123.

Distribution. Ethiopia (unnamed species), Guinea (unnamed species), Kenya (*A. cooperi*, *A. elgonensis*, *A. griffithsi*), Malawi (*A. tsitsa*, *A. zomba*), Mozambique (*A. tsitsa*), South Africa (*A. tsitsa*, *A. varius*), Tanzania (*A. erepens*, *A. variegatus*), Zaire (*A. marlieri*).

Material Examined. *Acanthiops elgonensis*, *A. griffithsi*, *A. zomba*: see descriptions herein; *A. marlieri*: ZAIRE: Holotype, larva, Bassin de l'Asuwimi-Ituri, riv. Luhule en amont de Vouvoi, 8-II-50, G. Marlier, deposited in the Institute Royal de Sciences Naturelles, Brussels; *A. tsitsa*: SOUTH AFRICA: Mpumalanga Prov.: larva, MacMac R., above MacMac Falls, nr. Graskop, 1,820 m, 18-X-90, W. P. and N. McCafferty; larva, Morite R., nr. Bushbuckridge, 580 m, 19-X-90, W. P. and N. McCafferty; larva, Sabie Sand Game Res., Sabie R., at Londolozi, 20-X-90, W. P. and N. McCafferty; 5 larvae, Kruger Ntl. Pk., Sabie R., at Sabie Gorge, Mozambique-South African border, 22-X-90, W. P. and N. McCafferty; larva, Kruger Ntl. Pk., Sabie R., at Molondozi, 23-X-90, W. P. and N. McCafferty; 30 larvae, Sabie R., at Lisbon Estates, 27-X-90, W. P. and N. McCafferty.

Discussion. Barber-James and McCafferty (1997) indicated that *Acanthiops* could be distinguished from other Afrotropical baetids by the following combination of characters: reduced labial palp segment 3, subequal glossae and paraglossae, 2 rows of denticles on the tarsal claws, presence of tergal tubercles, and 2-tailed condition. Although those characters are useful in most cases, we have found an autapomorphy that clearly defines *Acanthiops* in a cladistic sense, and thus also distinguishes its species from all other genera in the *Centroptiloides* complex. It is the larval pronotum being anteromedially slightly emarginate and laterally expanded and flattened (figure 20 in Gillies [1990a]; figure 1 in Barber-James and McCafferty [1997]; figure 6 in Gillies and Wuillot [1997]). The character can be observed in most larval instars, but it is most evident in mature individuals.

The precise phylogenetic position of *Acanthiops* within the *Centroptiloides* complex cannot be ascertained at this time. *Acanthiops* appears most closely related to *Thraulobaetodes* based on the presence of medial tergal tubercles in the larvae. However, the general morphology of the mouthparts, particularly of the labium, are most reminiscent of *Afroptilum*.

We place *Platycloeon*, which consisted of *A. cooperi* and *A. erepens* (type of *Platycloeon*), as a junior synonym of *Acanthiops* because these species possess the defining pronotal autapomorphy discussed above. Although both species have only a partially reduced medial caudal filament and poorly developed abdominal tubercles (figure 30 in Gillies [1990c]; figure 6 in Gillies and Wuillot [1997]), and *A. erepens* has a slightly bifurcated hindwing costal process (adults of *A. cooperi* are unknown), these species are essentially consistent with our concept of *Acanthiops*. We interpret the longer medial caudal filament, poorly developed abdominal tubercles, and slightly bifurcated costal process as plesiomorphic states within *Acanthiops*. The 2nd row of tarsal claw denticles is absent in *A. cooperi* according to Gillies and Wuillot (1997); however, from their drawing (figure 7 in Gillies and Wuillot [1997]), the claws appear similar to some other species of *Acanthiops* that have a highly reduced 2nd row of denticles (figure 15 in Barber-James and McCafferty [1997]). If the 2nd row proves to be entirely absent, it is an aberrancy within the *Centroptiloides* complex. The simple hooklike hindwing costal process of most species of *Acanthiops* may represent a reversal to the hypothesized plesiomorphic state within the complex (see discussions under *Peuhlella* and *Susua*).

Acanthiops tsitsa was previously known from Mpumalanga and North East Cape in South Africa (Barber-James and McCafferty 1997). Kimmins' (1955) record from Malawi of this species (as *Baetis* sp. A) represents a moderate northeastward extension of its range.

***Acanthiops elgonensis* Lugo-Ortiz & McCafferty
n. sp.**

Larva (figures after Demoulin [1964]). Body length: 6.1 mm; caudal filaments length: 5.0 mm.

Head. Coloration yellow-brown, with faint irregular markings. Labrum (figure 6a) dorsally with submedial pair of long, fine, simple setae and anterior submarginal row of 9–10 long, fine, simple setae. Left mandible (figure 6b) with incisors with 5 denticles. Right mandible (figure 6c) with outer and inner sets of incisors with 3 denticles each. Maxillae (figure 6d) with 4–5 long, fine, simple setae near medial hump; palps slightly extending beyond galealaciniae. Labium (figure 6e) with glossae and paraglossae equal in length; glossae medially and apically with long, robust, simple setae; paraglossae laterally and apically with long, robust, simple setae; palp segment 1 as long as segments 2 and 3 combined; palp segment 3 broadly rounded, with short, fine, simple setae scattered over surface.

Thorax. Coloration yellow-brown, with no distinct pattern. Hindwing pads present. Legs (figure 6 f–h) yellow-brown, medium brown apically; femora with row of long, robust, simple setae dorsally and numerous minute, fine, simple setae ventrally; tibiae with numerous minute, fine, simple setae dor-

sally and short, stout, simple setae ventrally; tarsi with numerous minute, fine, simple setae dorsally and row of robust, simple setae ventrally, increasing in length apically; tarsal claws with 2 rows of 6 denticles each.

Abdomen. Coloration yellow-brown, with no distinct pattern. Tubercles present on segments 1–8. Gills (figure 6 k–m) on abdominal segments 2–7, broad, well tracheated, somewhat translucent marginally, extensively tinged with brown throughout except for border. Medial caudal filament reduced to minute vestige.

Adult. Unknown.

Material Examined. HOLOTYPE: larva, KENYA, Mt. Elgon, obere Waldzone, ≈2,800 m, H. Löffler, no date, deposited in the Collections Nationales Belges d'Insectes et Arachnids, Institute Royal de Sciences Naturelles de Belgique, Brussels. PARATYPE: larva, same data and deposition as holotype.

Etymology. The specific epithet refers to the type locality.

Discussion (figures after Demoulin [1964]). *Acanthiops elgonensis* is distinguished from other species of *Acanthiops* by the absence of gills on abdominal segment 1 and more extensive pigmentation of gills 2–7 (figure 6 k–m).

Acanthiops griffithsi Lugo-Ortiz & McCafferty

n. sp.

(Figs. 1–10)

Larva. Body length: 4.0 mm; caudal filaments length: 3.0 mm.

Head. Coloration yellow-brown, with pale yellow-brown vermiform markings on frons. Antennae ≈1.5 times length of head capsule; scapes and pedicels with short, stout, simple setae scattered over surface. Labrum (Fig. 1) dorsally with submedial pair of long, fine, simple setae and anterior submarginal row 4–5 long, fine, simple setae. Hypopharynx as in Fig. 2. Left mandible (Fig. 3) with incisors with 5 denticles. Right mandible (Fig. 4) with outer and inner sets of incisors with 3 denticles each. Maxillae (Fig. 5) with 4–5 long, fine, simple, setae on medial hump; palps not reaching galealaciniae. Labium (Fig. 6) with glossae and paraglossae equal in length; glossae medially and apically with long, robust, simple setae; paraglossae laterally and apically with long, robust, simple setae; palp segment 1 as long as segments 2 and 3 combined; palp segment 2 dorsally with 2 long, fine, simple setae; palp segment 3 subconical, with short, fine, simple setae scattered over surface.

Thorax. Coloration medium brown; mesonotum with small, blunt tubercles anteriorly and posteriorly; metanotum with large tubercle. Hindwing pads present. Legs (Fig. 7) yellow-brown, medium brown apically; femora with row of long, robust, simple setae dorsally and numerous minute, fine, simple setae ventrally; tibiae with numerous minute, fine, simple setae dorsally and short, stout, simple setae ventrally; tarsi with numerous minute, fine,

simple setae dorsally and row of robust, simple setae ventrally, increasing in length apically; tarsal claws with 2 rows of 4 denticles each.

Abdomen. Coloration medium brown and pale yellow-brown; tergum 1 pale yellow-brown laterally, medium brown anteriorly and posteriorly; terga 2–4, 6, and 7 medium brown, with large sub-lateral oblong pale yellow-brown spots and pale yellow-brown laterally; tergum 5 pale yellow-brown, lightly suffused with brown dots medially; tergum 8 pale yellow-brown, with medium brown circular spot anteromedially, and medium brown posteriorly; tergum 9 pale yellow-brown, medium brown posteriorly; tergum 10 lightly suffused with medium brown spots. Terga 1–8 with robust tubercles (Fig. 8). Sterna cream. Gill 1 narrow, elongate, untracheated, marginally smooth, pale yellow-brown; gills 2–7 (Fig. 9) broad, well tracheated, marginally smooth, pale yellow-brown marginally and in distal third, translucent in midregion. Paraprocts (Fig. 10) with 11–12 irregular marginal spines. Caudal filaments yellow-brown; medial caudal filament reduced to minute vestige.

Adult. Unknown.

Material Examined. HOLOTYPE: larva, KENYA, Turasha R., 2,800 m, 0° 40' S, 36° 40' E, 9-I-91, R. W. Griffiths and S. Cooper (mouthparts, forelegs, gill 4, and paraproct mounted on slide [medium: Euparal]). ADDITIONAL MATERIAL: larva, same data as holotype.

Etymology. We name this species after Ronald W. Griffiths, who collected the specimens and donated them for study.

Discussion. *Acanthiops griffithsi* is distinguished from other species of *Acanthiops* by the number and shape of the abdominal tubercles (Fig. 8), general coloration of the gills (Fig. 9), and number and arrangement of paraproctal spines (Fig. 10).

Acanthiops zomba Lugo-Ortiz & McCafferty

n. sp.

(Figs. 11 and 12)

Larva (figures after Kimmins [1955], except 11 and 12). Body length: 4.2–4.3 mm; caudal filaments length: 4.3–4.4 mm.

Head. Coloration yellow-brown, with pale brown vermiform markings on frons. Scapes and pedicels with minute, fine, simple setae scattered over surface. Labrum (Fig. 11) dorsally with submedial pair of long, fine, simple setae and anterior submarginal row of 4–5 long, fine, simple setae. Hypopharynx slightly elongate (figure 5d). Left mandible (figure 5b) with incisors with 4 denticles. Right mandible (figure 5c) with outer and inner sets of incisors with 3 denticles. Maxillae (figure 5e) with 3 long, fine, simple setae on medial hump; palps not reaching galealaciniae. Labium (figure 5f) with glossae and paraglossae equal in length; glossae medially and apically with long, robust simple setae; paraglossae laterally and apically with long, robust, simple setae; palp segment 1 as long as segments 2 and 3 com-

bined; palp segment 2 dorsally with sublateral row of 5-6 long, fine, simple setae; palp segment 3 apically rounded, with short, fine, simple setae scattered over surface.

Thorax. Coloration pale yellow-brown, with complex markings; metanotum with small tubercle. Hindwing pads present. Legs (figure 5h) yellow-brown, medium brown apically; femora with row of long, somewhat robust, simple setae dorsally and numerous minute, fine, simple setae ventrally; tibiae with numerous minute, fine, simple setae dorsally and short, stout, simple setae ventrally; tarsi with numerous minute, fine, simple setae dorsally and row of somewhat robust, simple setae ventrally, increasing in length apically; tarsal claws with 2 rows of 4 denticles each.

Abdomen. Coloration pale yellow-brown, with no distinct pattern. Terga 1-6 or 1-7 with relatively small, sharp tubercles. Sterna pale yellow-brown. Gill 1 (figure 5j) narrow, elongate, untracheated, marginally smooth, translucent; gills 2-7 (figure 5j) broad, untracheated, marginally smooth, translucent. Paraprocts (Fig. 12) without marginal spines and with abundant scale bases and few minute, fine, simple setae scattered over surface. Caudal filaments yellow-brown; medial caudal filament reduced to minute vestige.

Adult. Unknown.

Material Examined. HOLOTYPE: larva, MALAWI, Mt. Zomba, Mlungusi R., 15-VIII-52, L. Berner, deposited in The Natural History Museum, London (head, thorax, and abdomen mounted on slides [medium: Euparal]). PARATYPE: larva, MALAWI, Mt. Mlanje, Likabula R., 19-VIII-52, L. Berner, same deposition as holotype.

Etymology. The species name is a noun in apposition referring to the type locality.

Discussion. *Acanthiops zomba* is distinguished from other species of *Acanthiops* by the somewhat short and wide labrum with a short row of long, fine, simple submarginal setae (Fig. 11), untracheated gills [figure 5j in Kimmins [1955]], and spineless paraprocts (Fig. 12).

Afroptilum Gillies

Afroptilum Gillies 1990a: 97.

Larva. **Head.** Labrum (Figs. 14 and 25) dorsoventrally thin, more or less parallel sided, slightly wider than long, broadly rounded anteriorly, with narrow anteromedial emargination. Hypopharynx (Figs. 15 and 26) with lingua with tuft of relatively long, robust, stiff, simple setae (bristle tuft) apically on medial marginal convexity; superlinguae apicolaterally rounded. Left mandible (Figs. 16 and 27) with 1 set of incisors; prosthema somewhat robust, apically denticulate; lateral margin almost straight; basal half bare dorsally. Right mandible (Figs. 17 and 28) with 2 sets of incisors; prosthema slender; tuft of short, fine, simple setae between prosthema and mola; lateral margin almost straight; basal half

bare dorsally. Maxillae (Figs. 18 and 29) with 4 short, blunt denticles on crown of galealaciniae; palps 2-segmented, reaching or not reaching galealaciniae. Labium (Figs. 19 and 30) with glossae subequal in length to paraglossae; glossae basally broad, apically narrow; palps 3-segmented; palp segment 2 with slight distomedial projection; palp segment 3 short, subconical.

Thorax. Pronotum medially straight, not expanded or flattened laterally. Legs held close to body; tibiae and tarsi without dorsal row of long, fine simple setae; forelegs (Fig. 31) with femora without marginal convexity and tibiae without ventrodorsal process. Tarsal claws (Fig. 32) with 2 rows of denticles.

Abdomen. Segment 1 not enlarged. Terga without dorsally oriented medial tubercles; posterior marginal spines relatively short and apically blunt. Gills (Figs. 21 and 22) on abdominal segments 1-7 or 2-7, platelike, relatively broad, marginally serrate, well tracheated, held dorsolaterally. Paraprocts (Figs. 23 and 34) with marginal spination. Medial caudal filament 0.50-0.80 times length of cerci.

Adult. Hindwings relatively broad (figure 19 a-d in Crass [1947]; figure 5 in Kimmins [1960]; figures 16 b and c, 19 b-d, and 25 b-d in Kopelke [1980]); costal process narrowly bifurcate, proximal portion narrow and erect, distal portion broadly based and prostrate. Male genital forceps (figure 4a in Kimmins [1960]; figures 15a, 18a, and 24 in Kopelke [1980]) 3-segmented; segment 3 narrow elongate, ≈ 0.20 times length of segment 2.

Type Species. *Centropitilum sudafricanum* Lestage (original designation).

Species Included.

Afroptilum biarcuatum (Kopelke)

Centropitilum biarcuatum Kopelke 1980: 115 (male adult).

Afroptilum biarcuatum (Kopelke): Gillies 1990a: 99.

Afroptilum bicorne (Ulmer)

Centropitilum bicorne Ulmer 1909: 366 (male, female adults).

Afroptilum bicorne (Ulmer): Gillies 1990a: 99.

Afroptilum boettgeri (Kopelke)

Centropitilum boettgeri Kopelke 1980: 111 (male, female adults).

Afroptilum boettgeri (Kopelke): Gillies 1990a: 99.

Afroptilum confusum Lugo-Ortiz & McCafferty n. sp. (larva).

Afroptilum dicentrum (Demoulin)

Centropitilum dicentrum Demoulin 1956: 278 (male, female adults).

Afroptilum dicentrum (Demoulin): Gillies 1990a: 99.

Afroptilum lepidum Lugo-Ortiz & McCafferty n. sp. (larva).

Afroptilum parvum (Crass)

Centropitilum parvum Crass 1947: 84 (larva; male, female adults).

Afroptilum parvum (Crass): Gillies 1990a: 99.

Afroptilum sudafricanum (Lestage)

Centroptilum sudafricanum Lestage 1924: 344 (male adult); Barnard 1932: 224 (larva).

Centroptilum montanum Kimmins 1960: 345.

Centroptilum sp. no. 1: Demoulin 1964: 283.

Afroptilum sudafricanum (Lestage): Gillies 1990a: 98.

Afroptilum montanum (Kimmins): Gillies 1992: 35.

Distribution. Comoros Islands (*A. bicorne*), Ethiopia (*A. sudafricanum*), Kenya (*A. sudafricanum*), Lesotho (*A. sudafricanum*), Madagascar (*A. confusum*, *A. lepidum*), South Africa (*A. parvum*, *A. sudafricanum*), Tanzania (*A. sudafricanum*), Uganda (*A. sudafricanum*), Zaire (*A. biarcuatum*, *A. boettgeri*, *A. dicentrum*, *A. sudafricanum*).

Material Examined. *Afroptilum confusum*, *A. lepidum*: see descriptions herein; *A. sudafricanum*: KENYA: 4 larvae, Malewa R., 2,307.7 m, 0° 20' S, 36° 26' E, 9-I-91, R. W. Griffiths and S. Cooper; LESOTHO: 3 larvae, Mokhotlong-Sengu Basin, below woolshed on Schonhong R., 25-IX-88, P. H. Skelton, deposited in the Albany Museum, Grahamstown, South Africa. SOUTH AFRICA: East Cape Prov.: 10 larvae, Berg R., at Hwy N2, nr. Grahamstown, 13-XI-90, W. P. and N. McCafferty; Kwa-Zulu Natal Prov.: 3 larvae, Impendle area, west fork of Furth R., 1,450 m, 18-IX-90, W. P. and N. McCafferty; 4 larvae, Pietermaritzburg, Natl. Botanical Garden, Dorspruit, 18-IX-90, W. P. and N. McCafferty; 6 larvae, Camberg Nat. Res., Mooi R., 19-IX-90, W. P. and N. McCafferty; Mpumalanga Prov.: 10 larvae, Long Tom State Forest, upper Sabie R., 26-X-90, W. P. and N. McCafferty; Orange Free State: 8 larvae, Little Caledon R., at Golden Gate Camp, 15-X-90; W. P. and N. McCafferty.

Discussion. Gillies (1990a) established the genus *Afroptilum* to include all African species previously assigned to *Centroptilum* Eaton. McCafferty and de Moor (1995) indicated that the genus was polyphyletic, and recent revisionary works by Wuillot and Gillies (1994), Lugo-Ortiz and McCafferty (1996 a-c, 1997a, d), Barber-James and McCafferty (1997), and McCafferty et al. (1997) have sorted out the many lineages involved. Those works, however, had not formally defined *Afroptilum* in its strict sense.

We have found 2 autapomorphies that show *Afroptilum*, as here restricted, to constitute a recognizable monophyletic group within the *Centroptiloides* complex. These are the presence in the hypopharynx of a well-developed bristle tuft at the tip of the lingua (Figs. 15 and 26) and a unique bifurcate costal process of the hindwings consisting of a narrow, erect proximal portion and a prostrate, broadly based distal portion (figure 19 b-d in Crass [1947]; figure 5 in Kimmins [1960]; figures 16c, 19c, and 25c in Kopelke [1980]).

The exact phylogenetic position of *Afroptilum* within the complex is difficult to ascertain at this time. However, we hypothesize that the genus was derived subsequent to *Peuhlella* and *Susua* because

of the presence of the bifurcate costal process of the hindwings. A bifurcate process (different in detail) is also present in *Dicentroptilum*, *Centroptiloides*, and the most plesiotypic species of *Acanthiops*.

Afroptilum confusum Lugo-Ortiz & McCafferty
n. sp.

(Figs. 13-23)

Larva. Body length: 7.7 mm; caudal filaments length: 4.2 mm.

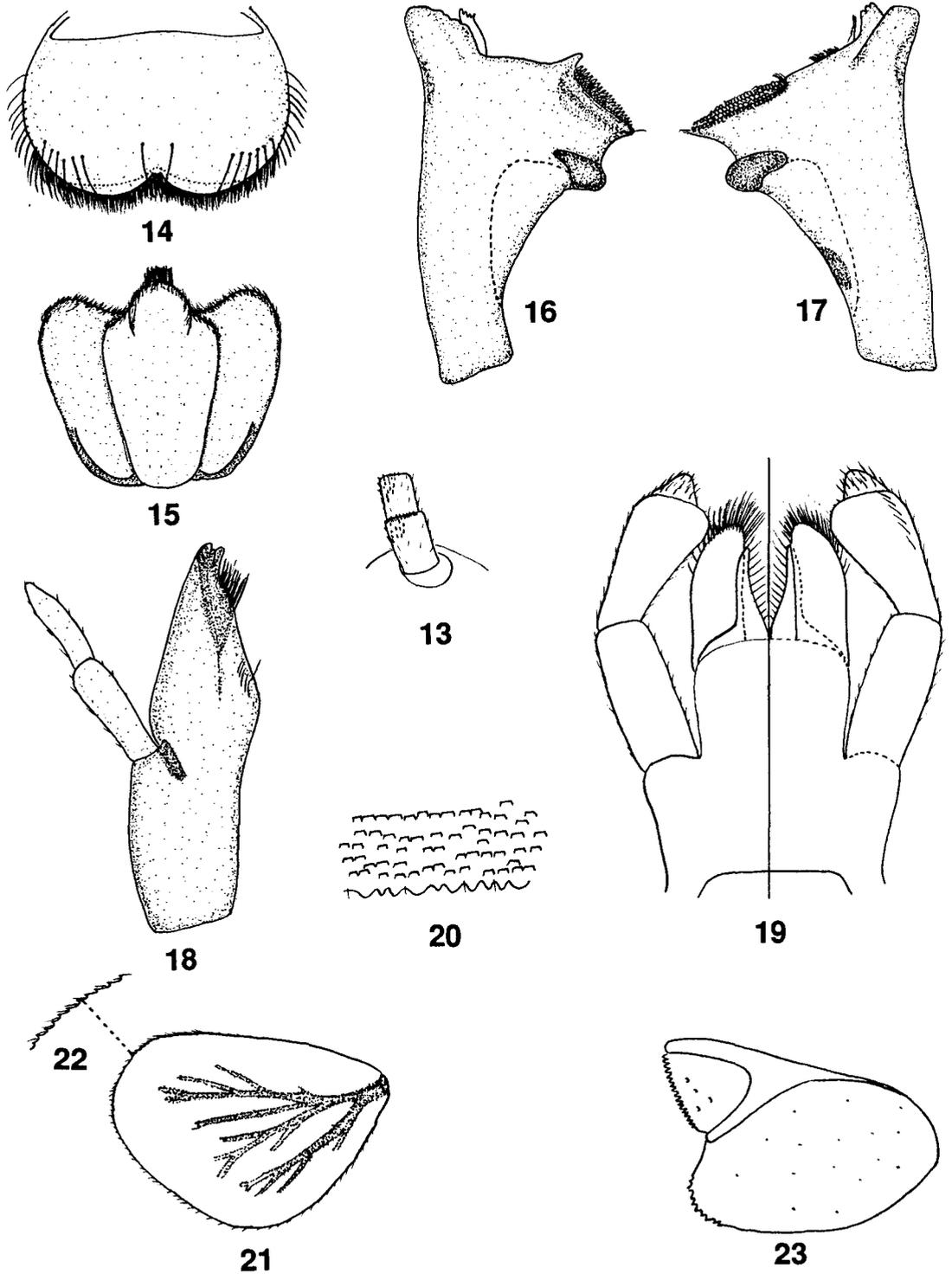
Head. Coloration yellow-brown, with faint pale yellow-brown irregular markings on vertex. Scapes and pedicels (Fig. 13) mediadorsally with numerous short, robust, sharp, simple setae, in addition to minute, fine, simple setae scattered over surface. Labrum (Fig. 14) dorsally with submedial pair of long, fine, simple setae and anterior submarginal row of 5-6 long, fine, simple setae. Hypopharynx as in Fig. 15. Right mandible (Fig. 17) with inner set of incisors with 3 denticles. (Left and right mandibles [Figs. 16 and 17] with incisors worn in material examined.) Maxillae (Fig. 18) with 4-5 long, fine, simple setae on medial hump; palps robust, not reaching galealacinae; palp segment 2 subequal to segment 1. Labium (Fig. 19) with glossae subequal in length to paraglossae; glossae medially and apically with long, fine, simple setae; paraglossae apically broadly rounded, with 3 close rows of long, fine, distally pectinate setae; palp segments somewhat robust; palp segment 1 0.90 times length of segments 2 and 3 combined; palp segment 2 dorsally with lateral submarginal row of 5-6 long, fine, simple setae; palp segment 3 subconical, with long, fine and long, robust simple setae scattered over surface.

Thorax. Coloration yellow-brown, with no distinct pattern. Hindwing pads present. Legs pale yellow-brown; femora with row of long, robust, simple setae dorsally and numerous minute, fine, simple setae ventrally; tibiae with numerous short, stout, simple setae dorsally and short, stout, simple setae ventrally; tarsi with numerous relatively long, fine, simple setae dorsally and row of robust, simple setae ventrally, increasing in length apically; tarsal claws with 2 rows of 4 denticles (similar to Fig. 32).

Abdomen. Coloration pale brown; terga 1-6 and 9-10 pale brown, with faint yellow-brown round markings posterolaterally; tergum 7 pale brown, with large, conspicuous posterolateral pale yellow-brown to cream oblong spot on either side of midline; tergum 8 pale yellow-brown to cream. Terga (Fig. 20) with abundant scale bases; posterior marginal spination irregular. Sterna pale yellow-brown. Gills (Fig. 21) broad, well tracheated, marginally with small serrations and minute, fine, simple setae (Fig. 22). Paraprocts (Fig. 23) apically with 8-10 small spines. Caudal filaments yellow-brown; medial caudal filament \approx 0.75 times length of cerci.

Adult. Unknown.

Material Examined. HOLOTYPE: larva, MADAGASCAR, Antananarivo (=Tanananarive) Prov., stream at Mandraka, 18.6° C, 19-X-71, G. F. and C. H.



Figs. 13–23. *Afroptilum confusum* n. sp., larva. (13) Antennal scape and pedicel. (14) Labrum. (15) Hypopharynx. (16) Left mandible. (17) Right mandible. (18) Right maxilla. (19) Labium (left, ventral; right, dorsal). (20) Detail of tergum 4. (21) Gill 4. (22) Detail of gill margin. (23) Paraproct.

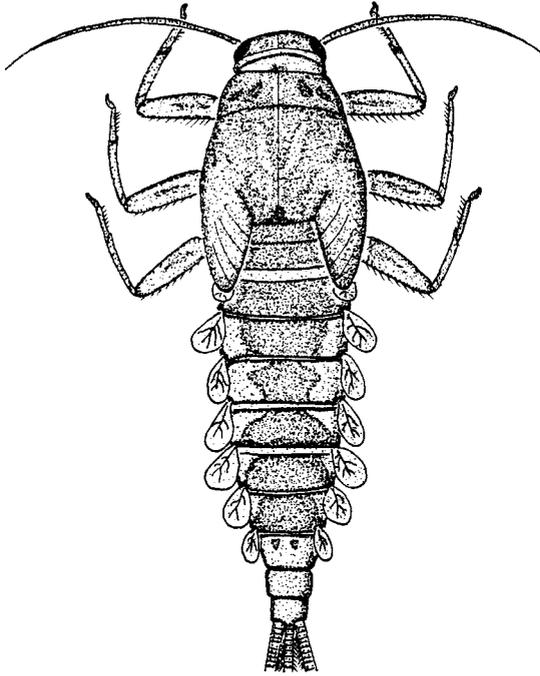


Fig. 24. *Afroptilum lepidum* n. sp., larval habitus.

Edmunds and F. Emmanuel (mouthparts, tergum 4, gill 4, and paraproct mounted on slide [medium: Euparal]).

Etymology. The specific epithet is Latin for confusing.

Discussion. *Afroptilum confusum* differs from the African species *A. parvum* and *A. sudafricanum* and from the Madagascar species *A. lepidum* n. sp. (see below) by having the antennal scapes and pedicels with numerous robust, sharp setae (Fig. 13), more robust maxillary (Fig. 18) and labial palps (Fig. 19), paraglossae with broadly rounded apices (Fig. 19), irregular posterior marginal spination on the abdominal terga (Fig. 20), and few marginal spines on the paraprocts (Fig. 23).

***Afroptilum lepidum* Lugo-Ortiz & McCafferty**

n. sp.

(Figs. 24–34)

Larva (Fig. 24). Body length: 6.5–8.5 mm; caudal filaments length: 5.0–6.0 mm.

Head. Coloration pale brown, with faint pale yellow-brown vermiform markings on vertex. Antennae ≈ 2.5 times length of head capsule; scapes and pedicels with minute, fine, simple setae scattered over surface. Labrum (Fig. 25) dorsally with submedial pair of long, fine, simple setae and anterior submarginal row of 7–8 long, fine, simple setae. Hypopharynx as in Fig. 26. Left mandible (Fig. 27) with incisors with 6 denticles. Right mandible (Fig. 28) with outer set of incisors with 4 denticles, inner set with 3 denticles. Maxillae (Fig. 29) with 4–5

long, fine, simple setae on medial hump; palps slender, reaching apex of galealaciniae; palp segment 1 subequal to segment 2. Labium (Fig. 30) with glossae subequal in length to paraglossae; glossae medially and apically with long, fine, simple setae; paraglossae subrectangular, apically with 3 close rows of long, fine, distally pectinate setae; palp segments slender; palp segment 1 0.90 times length of segments 2 and 3 combined; palp segment 2 dorsally with lateral submarginal row of 7–8 long, fine, simple setae; palp segment 3 subconical, with long, fine and long, moderately robust setae scattered over surface.

Thorax. Coloration yellow-brown to medium brown, with complex pattern. Hindwing pads present. Legs (Fig. 31) yellow-brown; femora with row of long, somewhat robust, simple setae dorsally and numerous short, apically acute, simple setae ventrally; tibiae with numerous minute, apically acute, simple setae dorsally and ventrally; tarsi with numerous minute, apically acute, simple setae dorsally and row of relatively robust, simple setae ventrally, increasing in length apically; tarsal claws (Fig. 32) with 2 rows of 6–7 denticles.

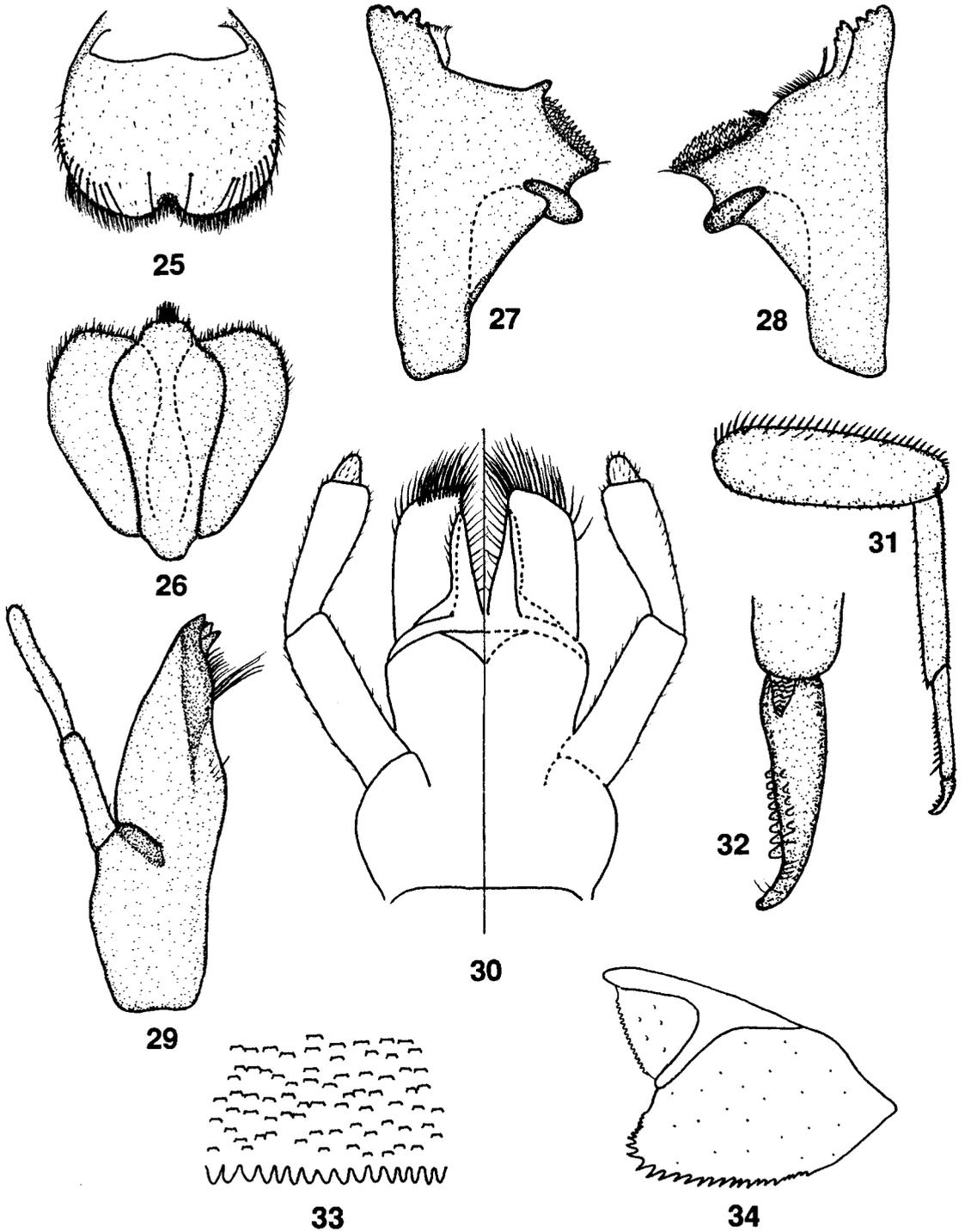
Abdomen. Coloration medium brown, with cream to pale yellow-brown markings; tergum 1 medium brown; terga 2 and 5–7 medium brown, with lateral subtriangular cream to pale yellow-brown subtriangular markings; terga 3 and 4 medium brown, with large lateral cream to pale yellow-brown markings; tergum 7 in some specimens with small posterior sublateral cream to pale yellow-brown round markings; tergum 8 yellow-brown, with anterior submedial pair of small subtriangular pale yellow-brown markings; terga 9 and 10 uniformly yellow-brown. Terga (Fig. 33) with abundant scale bases; posterior marginal spination somewhat irregular. Sterna cream to pale yellow-brown. Gills (similar to Fig. 21) broad, well tracheated, marginally with small serrations and minute, fine, simple setae (similar to Fig. 22). Paraprocts (Fig. 34) with 16–17 marginal spines, distal and proximal spines smaller than others. Caudal filaments yellow-brown; medial caudal filament ≈ 0.50 times length of cerci.

Adult. Unknown.

Material Examined. HOLOTYPE: larva, MADAGASCAR, Fianarantsoa Prov., small creek, at Ranomafana, 21° C, 6-XI-71, G. F. and C. H. Edmunds and F. Emmanuel. PARATYPES: 13 larvae, same data as holotype (mouthparts, forelegs, gill 4, and paraproct of 1 larva mounted on slide [medium: Euparal]). ADDITIONAL MATERIAL: 23 larvae, same data as holotype.

Etymology. The specific epithet is Latin for elegant and is a reference to the color pattern.

Discussion. *Afroptilum lepidum* is distinguished from the African species *A. parvum* and *A. sudafricanum* and the Madagascar species *A. confusum* by its distinct abdominal coloration (Fig. 24). It is further distinguished from *A. confusum* by having more slender maxillary (Fig. 29) and labial (Fig. 30) palps, subrectangular paraglossae (Fig. 30), more regular



Figs. 25-34. *Afroptilum lepidum* n. sp., larva. (25) Labrum. (26) Hypopharynx. (27) Left mandible. (28) Right mandible. (29) Right maxilla. (30) Labium (left, ventral; right, dorsal). (31) Left foreleg. (32) Tarsal claw. (33) Detail of tergum 4. (34) Paraproct.

posterior marginal spination on the abdominal terga (Fig. 33), and more marginal spines on the paraprocts (Fig. 34).

***Barnumus* McCafferty & Lugo-Ortiz n. gen.**

Larva. Head. Labrum (Fig. 35) dorsoventrally thick, conspicuously wider than long, with broad, deep, V-shaped anteromedial emargination. Hypopharynx (Fig. 36) with lingua with small apicomedial marginal convexity and superlinguae somewhat acute apicolaterally. Left mandible (Fig. 37) with 1 set of incisors; incisors base broad and extended; prosthema robust, apically denticulate; tuft of setae between prosthema and mola absent; lateral margin with conspicuous convex angulation; basal half with abundant short, fine, simple setae dorsally. Right mandible (Fig. 38) with 1 set of incisors; denticles united for ≈ 0.75 times their length; incisors base broad and extended; prosthema robust, apically denticulate; tuft of setae between prosthema and mola absent; lateral margin with conspicuous convex angulation; basal half with abundant short, fine, simple setae dorsally. Maxillae (Fig. 39) with galealacinae with 4 long, acute denticles; palps 2-segmented, not reaching galealacinae. Labium (Fig. 40) with glossae shorter than paraglossae; glossae basally broad, apically narrow; palps 3-segmented; palp segment 3 short, subconical.

Thorax. Pronotum anteromedially straight, not expanded or flattened laterally. Legs outstretched; tibiae and tarsi without dorsal row of long, fine simple setae; forelegs (Fig. 41) with femora without ventral marginal convexity and tibiae without ventrodorsal process. Tarsal claws (Fig. 42) with 2 rows of denticles.

Abdomen. Segment 1 not enlarged. Terga (Fig. 43) creased, without scale bases; posterior marginal spines short and apically blunt; dorsally oriented medial tubercles absent. Gills (Figs. 44 and 45) on abdominal segments 1–7, platelike, broad, untracheated, marginally smooth, held dorsolaterally. Paraprocts (Fig. 46) without marginal spines. Medial caudal filament reduced to minute vestige.

Adult. Unknown.

Type Species. *Barnumus editus* McCafferty & Lugo-Ortiz n. sp.

Species Included. *Barnumus editus* McCafferty & Lugo-Ortiz n. sp. (larva).

Material Examined. *Barnumus editus*: see description herein.

Etymology. This genus is named in honor of Andrew H. Barnum, an early and influential mentor in the career of W.P.M.

Discussion. *Barnumus* is distinguished from other genera in the *Centroptiloides* complex by the following autapomorphies: the broad, deep, V-shaped anteromedial emargination of the labrum (Fig. 35); the distinct cleft of the incisors of the right mandible (Fig. 38); and the somewhat robust and apically

denticulate prosthema of the right mandible (Fig. 38).

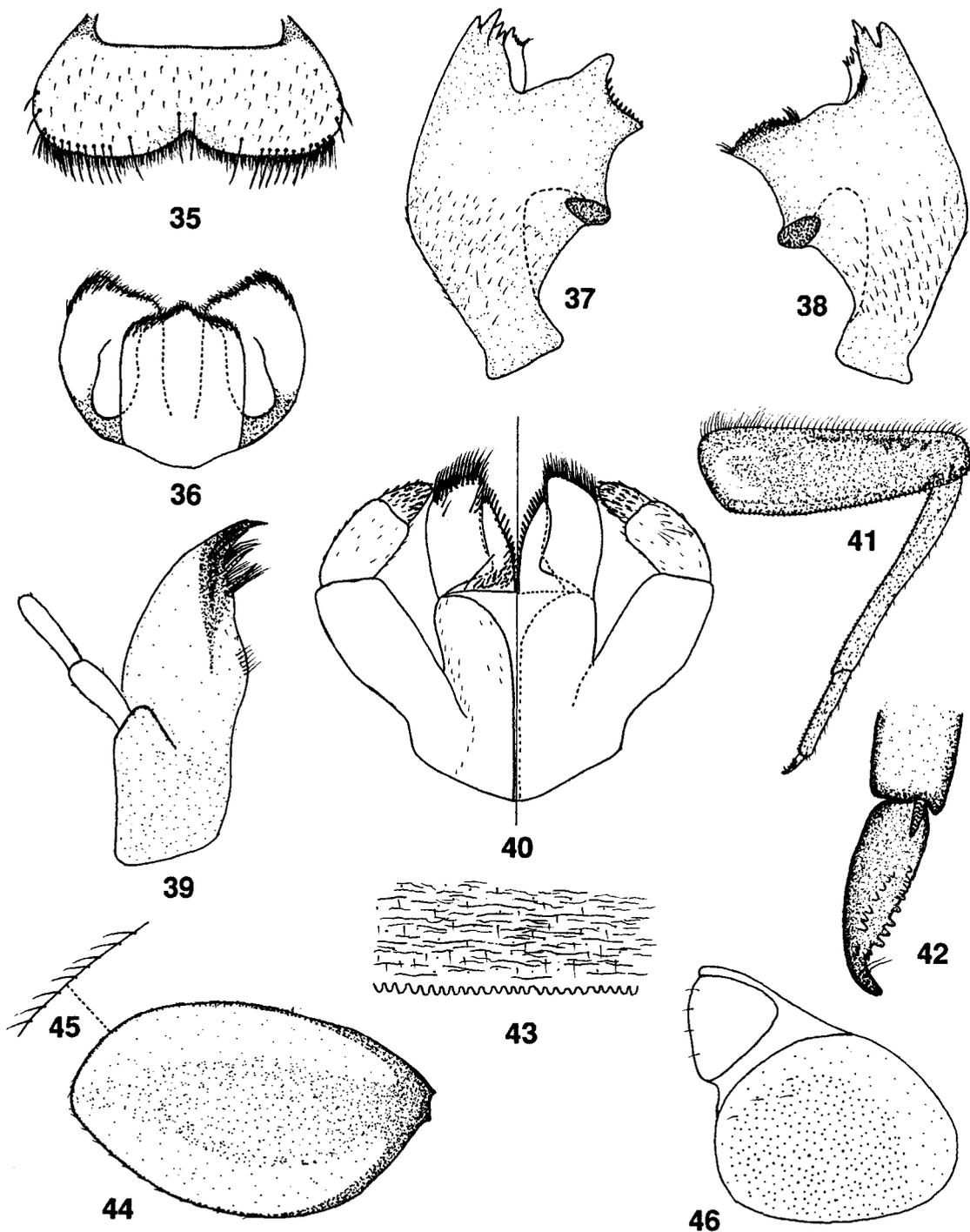
Preliminary cladistic analysis indicates that *Barnumus* is part of a complex also containing *Centroptiloides*, *Herbrossus* n. gen., and *Nesoptiloides*. *Barnumus* shares with those genera a labrum that is dorsoventrally thick and conspicuously wider than long (Figs. 35, 47, 71, 81); mandibles with a conspicuous lateral convex angulation and abundant setae in the basal half (Figs. 37, 38, 49, 50, 73, 74, 83, 84); and long, acute maxillary denticles on the apex of the galealacinae (Figs. 39, 51, 75, 85). Within this clade, *Barnumus* and *Centroptiloides* appear to be sister lineages because they share numerous apomorphies, including mandibles with a conspicuous convex angulation on the lateral margin and somewhat elongate and slender incisors (Figs. 37, 38, 49, 50), the absence of a tuft of setae between the prosthema and molar region of the right mandible (Figs. 38 and 50), and creased terga (Figs. 43 and 55). *Herbrossus* appears to be a sister lineage of *Barnumus* + *Centroptiloides* because their labra have a relatively wide anteromedial emargination (Figs. 35, 47, 71), and *Nesoptiloides* appears to be ancestral to the other genera in the clade, demonstrating the most plesiomorphic character states.

The lateral angulation of the mandibles and morphology of the mandibular incisors are important in hypothesizing behavioral evolution in this clade. *Herbrossus* and *Nesoptiloides* have mandibles that are moderately convex laterally (Figs. 73, 74, 83, 84). This condition is similar to that of most other baetids, and it is therefore likely that those 2 genera are collector-gatherers. In contrast, in *Barnumus* and *Centroptiloides* the lateral margin of the mandibles has become conspicuously convex (Figs. 37, 38, 49, 50). Additionally, the mandibular incisors have become somewhat narrow elongate (Figs. 37, 38, 49, 50). We associate those conditions with predatory behavior. *Barnumus*, however, is probably omnivorous because its mouthparts are intermediate compared with *Centroptiloides*. The molars and incisors of *Centroptiloides* are clearly modified for impaling (Figs. 49 and 50), a condition observed in other mayflies mainly or exclusively predatory (e.g., *Anepeorus* McDunnough, *Echinobaetis* Mol, *Harpagobaetis* Mol, *Pseudiron* McDunnough, *Raptoabaetopus* Müller-Liebenau, and *Raptoheptagenia* Whiting & Lehmkuhl).

***Barnumus editus* McCafferty & Lugo-Ortiz n. sp.**
(Figs. 35–46)

Larva. Body length: 9.5–13.0 mm; caudal filaments length: 10.0–13.0 mm.

Head. Coloration medium brown, with pale yellow-brown to cream vermiform markings on vertex and frons, and clypeus and labrum pale yellow-brown to cream with medium brown margins. Antennae as long as head capsule. Labrum (Fig. 35) with abundant short, fine, simple setae and 8–10 long, fine, simple setae on either side of midline



Figs. 35-46. *Barnumus editus* n. sp., larva. (35) Labrum. (36) Hypopharynx. (37) Left mandible. (38) Right mandible. (39) Right maxilla. (40) Labium (left, ventral; right, dorsal). (41) Left foreleg. (42) Tarsal claw. (43) Detail of tergum 4. (44) Gill 4. (45) Detail of gill margin. (46) Paraproct.

dorsally. Hypopharynx as in Fig. 36. Left mandible (Fig. 37) with incisors with 5 denticles. Right mandible (Fig. 38) with outer set of incisors with 2 denticles, inner set with 4 denticles. Maxillae (Fig. 39) with 6–7 long, fine, simple setae on medial hump. Labium (Fig. 40) with glossae with abundant short, stout, simple setae ventrally near base; paraglossae apically with 3 rows of long, distally pectinate setae; mentum with scattered short, fine, simple setae; palp segment 1 \approx 1.20 times length of segments 2 and 3 combined; palp segment 2 with sublateral row of 3–4 long, fine, simple setae dorsally and scattered short, fine, simple setae over surface; palp segment 3 with abundant short, fine and short, robust, simple setae over surface.

Thorax. Coloration yellow-brown to medium brown, with complex pale yellow-brown to cream markings. Hindwing pads present. Legs (Fig. 41) dark yellow-brown to medium brown; femora anteriorly medium brown with U-shaped yellow-brown marking proximally, posteriorly uniformly yellow-brown, with row of long, fine, simple setae and numerous short, stout, simple setae dorsally and numerous short, stout, simple setae ventrally; tibiae with short, fine, simple setae randomly distributed dorsally and numerous short, stout, simple setae ventrally; tarsi with short, fine, simple setae dorsally and numerous short, stout, simple setae ventrally; tarsal claws (Fig. 42) with 2 rows of 6–7 denticles each and subapical pair of long, fine, simple setae.

Abdomen. Coloration yellow-brown to medium brown, with no distinct color pattern. Terga 2–9 generally with 2 conspicuous pairs of medium brown to dark brown dots in anterior half. Terga (Fig. 43) with minute, fine, simple setae scattered over surface; posterior marginal spination uniform, spines as long as basally wide. Sterna cream to pale yellow-brown; sternum 1 generally uniformly cream to pale yellow-brown; sterna 2–8 with anterior submedial pair of medium brown dots and oblique dashes and sublateral longitudinal medium brown dashes; sternum 9 medium brown. Gills as in Figs. 44 and 45. Paraprocts (Fig. 46) with short, fine, simple setae scattered over surface. Caudal filaments yellow-brown to dark brown, becoming paler distally; medial caudal filament reduced to vestige.

Adult. Unknown.

Material Examined. HOLOTYPE: larva, SOUTH AFRICA, KwaZulu-Natal Prov., Highmoor For., trib. Little Mooi R., 1,800 m, 19-IX-90, W. P. and N. McCafferty. PARATYPES: larva, same data as holotype; 2 larvae, SOUTH AFRICA, KwaZulu-Natal Prov., Sani Pass Rd., at police post, 1,950 m, 16.4° C, 1-X-71, G. F. and C. H. Edmunds (mouthparts and forelegs of 1 larva on slide [medium: Euparal]), 1 larva deposited in the Albany Museum, Grahamstown, South Africa; larva, SOUTH AFRICA, Mpumalanga Prov., Long Tom Sta. For., upper Sabie R., 26-X-90, W. P. and N. McCafferty (mouthparts, forelegs, tergum 3, and paraproct on slide [medium: Euparal]). ADDITIONAL MATERIAL: SOUTH AFRICA: 5 larvae, same data as holotype; 18 larvae,

KwaZulu-Natal Prov., Sani Pass Rd., at police post, 1,950 m, 16.4° C, 1-X-71, G. F. and C. H. Edmunds.

Etymology. The specific epithet is Latin for high, in reference to the high altitudes from where the species was collected.

Discussion. The dorsal setation of the labrum (Fig. 35), mandibular denticulation (Figs. 37 and 38), relative lengths of the segments of the maxillary palps (Fig. 39), labial setation and development of the labial palps (Fig. 40), and uniform posterior marginal spination of the terga (Fig. 43) are distinguishing characteristics of *B. editus*. The species was collected at relatively high elevations, in narrow, swift streams with rocky bottom.

Centroptiloides Lestage

Centroptiloides Lestage 1918: 108.

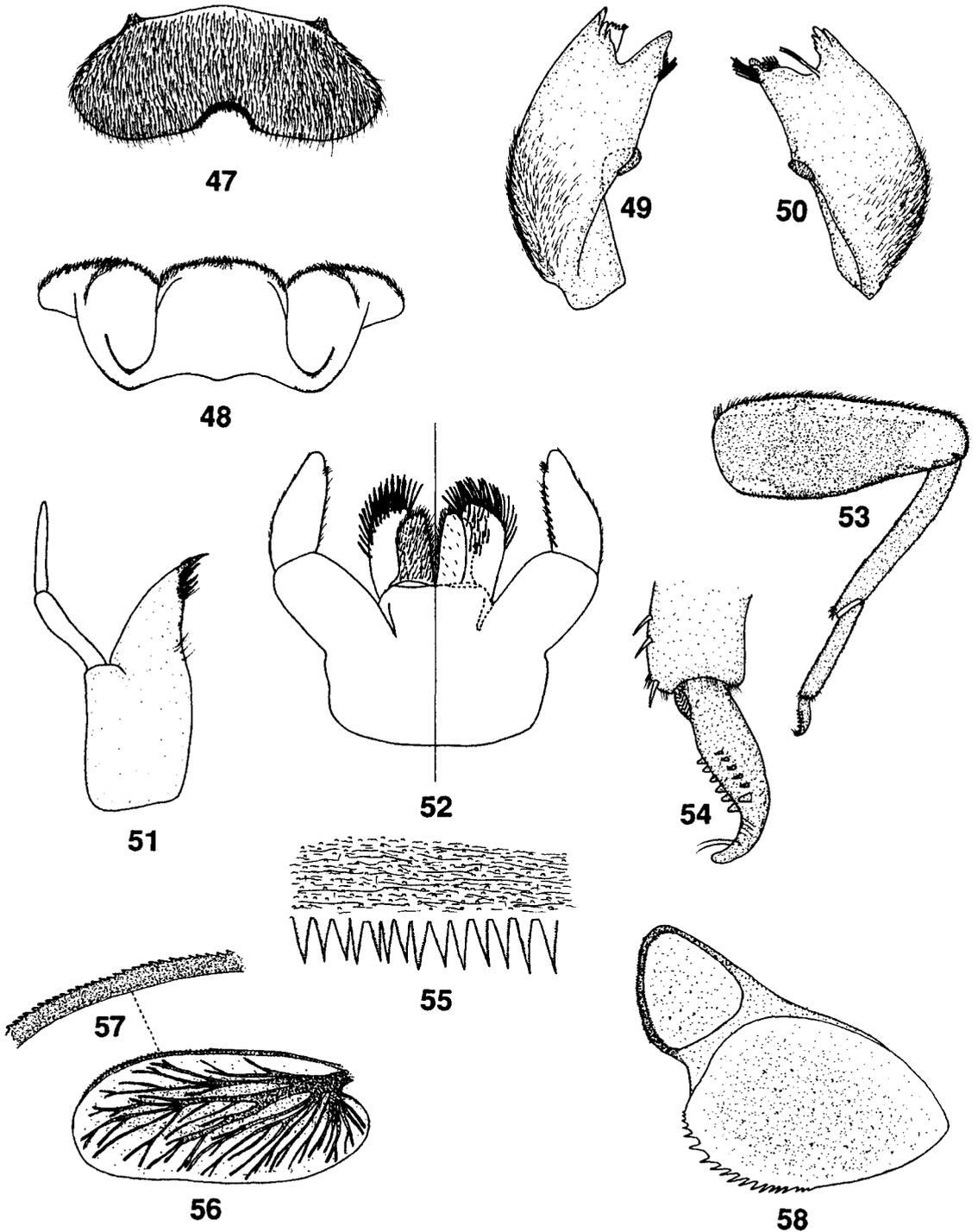
Haplobaetis Navás 1922: 115.

Larva. Head. Labrum (Fig. 47) dorsoventrally thick, conspicuously wider than long, with broad, deep, U-shaped anteromedial emargination. Hypopharynx (Fig. 48) with lingua apically truncate and without apicomedial bristle tuft; superlinguae apicolaterally produced. Left mandible (Fig. 49) with 1 set of incisors; incisors base broad and extended; prostheca robust, apically denticulate; tuft of setae between prostheca and mola absent; lateral margin with conspicuous angulation; basal half with abundant short, fine, simple setae dorsally. Right mandible (Fig. 50) with 1 set of incisors; incisors base broad and extended; prostheca slender, apically bifid; tuft of setae between prostheca and mola absent; lateral margin with conspicuous angulation; basal half with abundant short, fine, simple setae dorsally. Maxillae (Fig. 51) with galealaciniae with 4 long, acute denticles; palps 2-segmented, reaching galealaciniae. Labium (Fig. 52) with glossae subequal in length to paraglossae; glossae and paraglossae uniformly broad; palps 2-segmented; palp segment 2 subconical.

Thorax. Pronotum anteromedially straight, not expanded or flattened laterally. Legs outstretched; tibiae and tarsi without dorsal row of long, fine simple setae; forelegs (Fig. 53) with femora without ventral marginal convexity and tibiae without ventrodistal process. Tarsal claws (Fig. 54) with 2 rows of denticles.

Abdomen. Segment 1 not enlarged. Terga (Fig. 55) creased and with scale bases; posterior marginal spines long and acute; dorsally oriented medial tubercles absent. Gills (Figs. 56 and 57) on abdominal segments 1–7, platelike, somewhat narrow-elongate, well tracheated, marginally serrate and sclerotized, held dorsolaterally. Paraprocts (Fig. 58) with marginal spines. Medial caudal filament \approx 0.50 times length of cerci.

Adult (figures after Crass [1947]). Hindwings (figure 29b) broad, with 3 longitudinal veins; middle vein bifurcate in midregion; several crossveins present; 2 almost contiguous costal processes in basal 0.33. Male genital forceps (figure 29c) 3-seg-



Figs. 47-58. *Centroptiloides bifasciata* (Esben-Petersen), larva. (47) Labrum. (48) Hypopharynx. (49) Left mandible. (50) Right mandible. (51) Right maxilla. (52) Labium (left, ventral; right, dorsal). (53) Left foreleg. (54) Tarsal claw. (55) Detail of tergum 4. (56) Cill 4. (57) Detail of gill margin. (58) Paraproct.

mented; segment 3 \approx 0.20 times length of segment 2, somewhat teardrop-shaped.

Type Species. *Centroptilum bifasciatum* Esben-Petersen (original designation).

Species Included.

Centroptiloides bifasciata (Esben-Petersen)

Centroptilum bifasciatum Esben-Petersen 1913: 182 (male, female adults); Crass 1947: 90 (larva).

Centroptiloides bifasciatus (Esben-Petersen): Lestage 1918: 108.

Centroptiloides bifasciatum (Esben-Petersen): Ulmer 1920: 53.

Haplobaetis umbratus Navás 1922: 115.

Centroptiloides bifasciata (Esben-Petersen): Navás 1922: 115.

Centroptiloides marginata Lestage 1924: 341.

Centroptiloides collarti Navás 1930: 319.

Centroptiloides umbratus Lestage 1945: 89.

Distribution. Kenya, Mozambique, South Africa.

Material Examined. *Centroptiloides bifasciata*: see description herein.

Discussion. *Centroptiloides* is distinguished from all other genera in the complex by the following autapomorphies: broad, deep, U-shaped anteromedial emargination of the labrum (Fig. 47); laterally produced superlinguae (Fig. 48); reduced and medially produced molae (Figs. 49 and 50); uniformly broad glossae (Fig. 52); 2-segmented labial palps (Fig. 52); and long and acute, posterior marginal spines of the terga (Fig. 57). Details of the possible phylogenetic relationships of *Centroptiloides* are discussed under *Barnumus*.

***Centroptiloides bifasciata* (Esben-Petersen)**
(Figs. 47–58)

Larva. Body length: 12.5–14.5 mm; caudal filaments length: 9.5–10.5 mm.

Head. Coloration medium brown, with large yellow-brown to cream round marking on clypeus. Antennae \approx 2.5 times length of head capsule. Labrum (Fig. 47) with abundant long, fine, simple setae dorsally. Hypopharynx as in Fig. 48. Left mandible (Fig. 49) with incisors with 5 denticles. Right mandible (Fig. 50) with incisors with 5 denticles. Maxillae (Fig. 51) with 4–5 long, fine, simple setae near medial hump; palp segment 1 slightly longer than segment 2. Labium (Fig. 52) with glossae with abundant short, fine, simple setae ventrally; paraglossae with abundant long, relatively robust, simple setae laterally and apically; palp segment 1 as long as segment 2; palp segment 2 with submedial row of relatively short, robust, simple setae dorsally.

Thorax. Coloration medium brown, with complex pale yellow-brown to cream markings; pronotum usually with submedial pair of large, round, pale yellow-brown to cream markings and sublateral pair of anteriorly narrow and posteriorly broad oblique pale yellow-brown to cream markings. Hindwing pads present. Legs (Fig. 53) medium brown and pale yellow-brown or cream; femora medium brown, with pale yellow-brown to cream submarginal areas

dorsally, ventrally, and apically, and with row of long, fine, simple setae dorsally and numerous short, fine and short, stout simple setae dorsally and ventrally; tibiae with numerous short, fine, simple setae dorsally and ventrally; tarsi with numerous short, fine, simple setae dorsally and ventrally; tarsal claws (Fig. 54) with 2 rows of 5–6 denticles each and subapical pair of long, fine, simple setae.

Abdomen. Coloration generally medium brown; terga with dark brown posterior margins; mature males with medial and lateral dark brown markings on terga 2–8. Terga (Fig. 55) with minute, fine, simple setae scattered over surface; posterior marginal spines \approx 2.5 times as long as basally wide. Sterna generally pale yellow-brown; mature males with sternum 1 anteriorly and laterally purplish, sterna 2–8 with medial and sublateral purplish markings, and sterna 9 and 10 pale brown. Gills as in Figs. 56 and 57; immature larval gills sometimes with basal folds. Paraprocts (Fig. 58) with 16–18 marginal spines and few scale bases scattered over surface. Caudal filaments medium brown, turning pale-yellow brown to cream distally.

Adult. Adequately described by Barnard (1932) and Crass (1947).

Material Examined. KENYA: larva, Ewaso Ng'iro R., at Samburu Lodge, Samburu Isiolo Res., 20-XI-71, G. F. and C. H. Edmunds. SOUTH AFRICA: Eastern Cape Prov.: larva, Tsitsa R., at Tsitsa Falls, 31° 00' 55" S, 28° 29' 20" E, 26-III-91, H. M. Barber-James and F. de Moor, deposited in Albany Museum, Grahamstown, South Africa; KwaZulu-Natal Prov.: larva, Umlaas R., at Durban waterworks, filtration plant nr. Pinetown, 22.3° C, 4-X-71, G. F. and C. H. Edmunds; 18 larvae, Mooi R., at Niekerks Fontein, below weir, 20-IX-90, W. P. and N. McCafferty and B. Fowles; 10 larvae, Umgeni R., below Nagel Dam, 1,100 m, 21-IX-90, W. P. and N. McCafferty and B. Fowles; larva, Umgeni R., just above Nagel Dam impoundment, 21-IX-90, W. P. and N. McCafferty and B. Fowles; Mpumalanga Prov.: larva, Kruger Natl. Pk., Sabie R., at Sabie Gorge, Mozambique-South Africa border, 22-X-90, W. P. and N. McCafferty; 6 larvae, Kruger Natl. Pk., Sabie R., at Molondozi, 23-X-90, W. P. and N. McCafferty.

Discussion. Esben-Petersen (1913) described *C. bifasciata* based on male and female adults. Crass (1947) associated the larval and adult stages through rearing, and Demoulin (1970) redescribed the larva. Crass's (1947) and Demoulin's (1970) descriptions of the larva are brief, and their figures are somewhat schematic and, in some cases, inaccurate. We have therefore redescribed the larval stage and provided new figures showing characters not formerly given.

The dorsal setation of the labrum (Fig. 47), mandibular denticulation (Figs. 49 and 50), relative length of the maxillary palps (Fig. 51), setation of the labium (Fig. 52), long posterior marginal spines of the terga (Fig. 55), gill tracheation (Fig. 56), abdominal coloration, and paraproctal spination (Fig. 58) are distinguishing characteristics of *C. bifasciata*.

One of us (W.P.M.) has closely observed the behavior of *C. bifasciata* larvae in the field. In the Sabie River, South Africa, larvae crawled on the tops of algae-covered bedrocks in ≈ 20 –50 cm depth, facing the extremely fast current and rather remarkably were able to maintain purchase. This crawling in such rapids was apparently part of their midge hunting behavior.

Centroptiloides bifasciata was previously known from eastern South Africa. The new record from Kenya considerably extends its range, and indicates that the species is probably widely distributed in eastern Africa.

Dicentropitulum Wuillot & Gillies

Dicentropitulum Wuillot and Gillies 1994: 133.

Larva. *Head.* Labrum (Fig. 59) dorsoventrally thin, wider than long, medially raised near base. Hypopharynx (Fig. 60) with lingua with large apicomedial marginal convexity and apically broad superlinguae, without lingual bristle tuft. Left mandible (Fig. 61) with 1 set of incisors; denticles medially oriented; prosthema somewhat robust, apically denticulate; tuft of short, fine, simple setae present between prosthema and mola; lateral margin with basal angulation; basal half bare dorsally. Right mandible (Fig. 62) with 2 sets of incisors; prosthema slender; tuft of short, fine, simple setae present between prosthema and mola; lateral margin with basal angulation; basal half bare dorsally. Maxillae (Fig. 63) with 4 short, blunt denticles on crown of galealaciniae; palps 2-segmented, reaching galealaciniae. Labium (Fig. 64) with glossae subequal in length to paraglossae; glossae basally broad, apically narrow; palp segment 2 slightly (Fig. 64) or moderately (figure 8 in Wuillot and Gillies [1994]) produced apicomedia; palp segment 3 short, broadly rounded, partly fused to segment 2.

Thorax. Pronotum anteromedially straight, not expanded or flattened laterally. Legs (Fig. 65) outstretched; tibiae and tarsi with dorsal row of long, fine, simple setae; forelegs with femora without ventral marginal convexity and tibiae without ventrodorsal process. Tarsal claws (Fig. 66) with 2 rows of denticles.

Abdomen. Segment 1 not enlarged. Terga without dorsally oriented medial tubercles; posterior marginal (Fig. 67) spines short and blunt. Gills (Figs. 68 and 69) on abdominal segments 1–7, platelike, relatively broad, marginally serrate, well tracheated, held dorsolaterally. Paraprocts (Fig. 70) with marginal spines. Medial caudal filament 0.33–0.50 times length of cerci.

Adult. Hindwings (figure 5 in Gillies [1990a]; figure 2 in Wuillot and Gillies [1994]) broad, with broadly bifurcate costal process, proximal portion narrow and erect or broadly based and prostrate, distal portion broadly based and prostrate. Male genital forceps (figure 4 in Wuillot and Gillies [1994]) 3-segmented; segment 3 narrow elongate, ≈ 0.20 times length of segment 2.

Type Species. *Afroptilum decipiens* Gillies (original designation).

Species Included.

Dicentropitulum decipiens (Gillies).

Afroptilum decipiens Gillies 1990a: 100 (larva; male, female adults).

Dicentropitulum decipiens (Gillies): Wuillot and Gillies 1994: 134.

Dicentropitulum merina Lugo-Ortiz & McCafferty n. sp. (larva).

Dicentropitulum papillosum Wuillot, in Wuillot and Gillies 1994: 134 (larva; male adult).

Dicentropitulum spinulosum (Demoulin).

Centroptiloides spinulosa Demoulin 1970: 37 (male adult).

Afroptilum spinulosum (Demoulin): Gillies 1990a: 99.

Dicentropitulum spinulosum (Demoulin): Wuillot and Gillies 1994: 137.

Distribution. Guinea (*D. papillosum*), Liberia (*D. papillosum*), Madagascar (*D. merina*), Mozambique (*D. papillosum*), South Africa (*D. papillosum*, *D. spinulosum*), Tanzania (*D. decipiens*), Zaire (*D. papillosum*).

Material Examined. *D. merina*: see description herein; *D. papillosum*: SOUTH AFRICA: Mpumalanga Prov.: 6 larvae, Kruger Natl. Pk., at Sabie Gorge, Mozambique–South Africa border, 22-X-90, W. P. and N. McCafferty; 25 larvae, Kruger Natl. Pk., Sabie R., at Molondozi, 23-X-90, W. P. and N. McCafferty; 7 larvae, Sabie R., at Lisbon Estates, 27-X-90, W. P. and N. McCafferty.

Discussion. The following autapomorphies distinguish *Dicentropitulum* from other genera in the *Centroptiloides* complex: the medially raised, short, and broad labrum (Fig. 59) and the dorsal row of long, fine, simple setae on the tibiae and tarsi (Fig. 65). Wuillot and Gillies (1994) considered the presence of sinuosities on the cerci a distinguishing characteristic of the genus; however, that characteristic applies only to known African larvae of the genus.

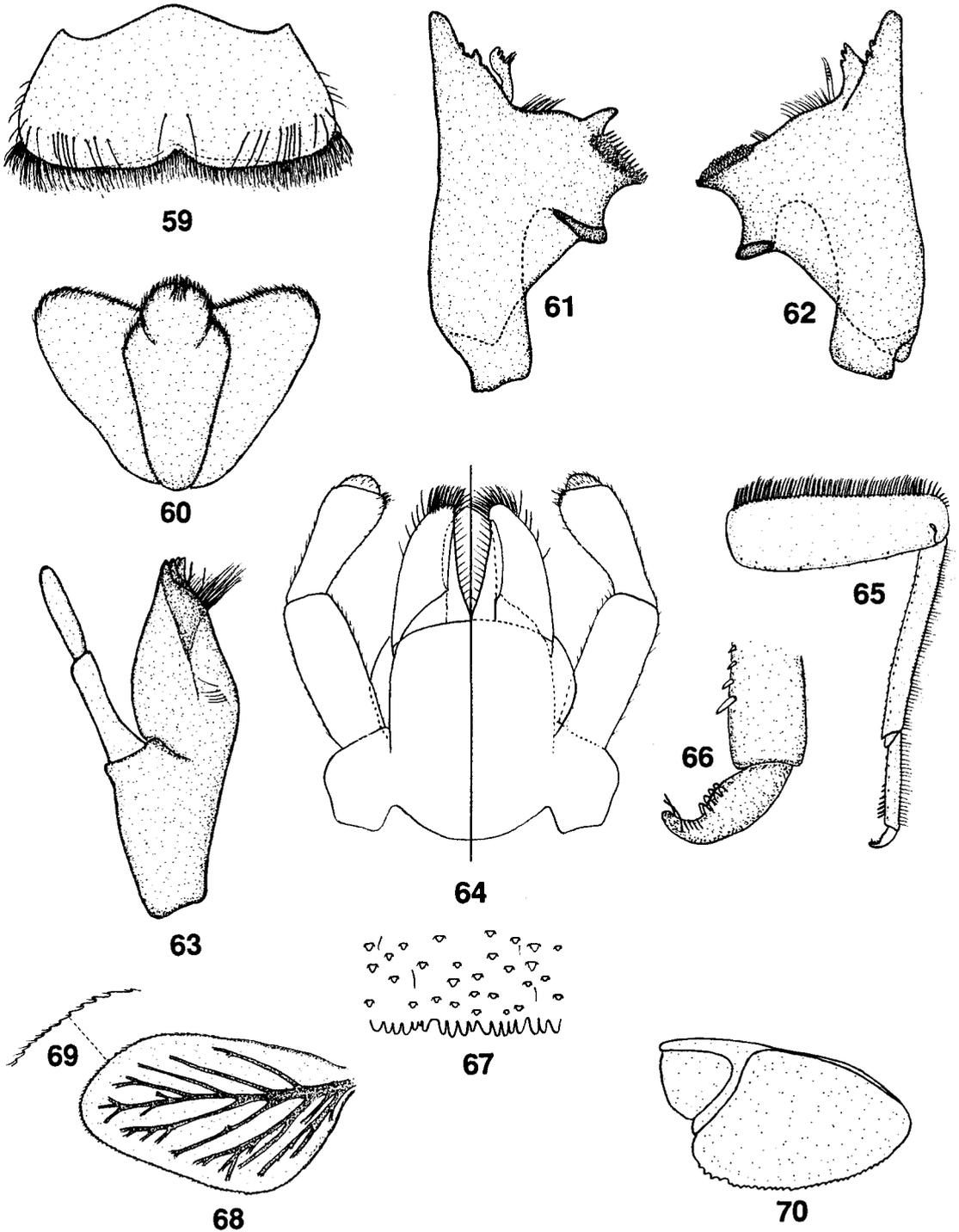
The costal process of the hindwings of *D. decipiens* (figure 5 in Gillies [1990a]) is similar to that of known adults of *Afroptilum*. However, in *D. decipiens* the process is broadly bifurcate, whereas in *Afroptilum* it is narrowly bifurcate. The broadly bifurcate hindwing costal process of *D. decipiens* and *D. papillosum* is very similar to that of *C. bifasciata*, possibly suggesting that *Dicentropitulum* is a sister lineage to the clade comprising *Barnumus*, *Centroptiloides*, *Herbrossus* and *Nesoptiloides*.

Dicentropitulum merina Lugo-Ortiz & McCafferty n. sp.

(Figs. 59–70)

Larva. Body length: 7.3–7.5 mm; caudal filaments length: 9.6–9.8 mm.

Head. Coloration medium brown, females with pale yellow-brown to cream vermiform markings on frons and vertex. Antennae ≈ 2.5 times length of head capsule. Labrum (Fig. 59) dorsally with sub-



Figs. 59-70. *Dicentropilum merina* n. sp., larva. (59) Labrum. (60) Hypopharynx. (61) Left mandible. (62) Right mandible. (63) Right maxilla. (64) Labium (left, ventral; right, dorsal). (65) Left foreleg. (66) Tarsal claw. (67) Detail of tergum 4. (68) Gill 4. (69) Detail of gill margin. (70) Paraproct.

medial pair of long, fine, simple setae and anterior submarginal row of 10–12 long, fine, simple setae. Hypopharynx (Fig. 60) with lingua with apicomедial tuft of long, fine, simple setae. Left mandible (Fig. 61) with incisors with 4 denticles. Right mandible (Fig. 62) with outer set of incisors with 4 denticles, inner set with 3 denticles. Maxillae (Fig. 63) with 4–5 long, fine, simple setae on medial hump; palp segment 1 \approx 1.2 times length of segment 2. Labium (Fig. 64) with glossae medially and apically with long, fine, simple setae; paraglossae apically with 3 close rows of long, fine, distally pectinate setae; palp segment 1 1.13 times length of segments 2 and 3 combined; palp segment 2 slightly distomedially produced, dorsally without lateral submarginal row of setae; palp segment 3 with long, fine and long, relatively robust, simple setae scattered over surface.

Thorax. Coloration yellow-brown, with complex medium brown markings. Hindwing pads present. Legs (Fig. 65) yellow-brown, with no distinct color pattern; femora with row of long, relatively robust, simple setae dorsally and short, sharp, simple setae ventrally; tibiae with row of long, fine simple setae dorsally and short, sharp, simple setae ventrally; tarsi with row of long, fine, simple setae dorsally and short, sharp, simple setae and row of relatively robust, simple setae ventrally, increasing in length apically; tarsal claws (Fig. 66) with 2 rows of 4 denticles each.

Abdomen. Coloration pale brown to cream; tergum 1 cream, posterior margin medium brown; terga 2–6 pale brown, with anterior submedial pair of medium brown oblique dashes (terga 4–5 somewhat paler than others); tergum 7 pale brown, with anterior submedial pair of medium brown dots; tergum 8 medium brown anteriorly, cream posteriorly, with pair of medium brown submedial dots in midregion; terga 9–10 cream, with no markings. Terga (Fig. 67) with scales and minute, fine, simple setae scattered over surface; posterior marginal spination irregular. Sterna cream to pale yellow brown; sterna 2–8 with small subanterolateral medium brown dots. Gills (Figs. 68 and 69) well tracheated, marginally serrate and with minute, fine, simple setae. Paraprocts (Fig. 70) with numerous small marginal spines. Caudal filaments pale yellow-brown; cerci without medial sinuosities; medial caudal filament 0.33–0.44 times length of cerci.

Adult. Unknown.

Material Examined. HOLOTYPE: larva, MADAGASCAR, Antananarivo (=Tanarive) Prov., stream at Mandraka, 18.6° C, 19-X-71, G. F. and C. H. Edmunds and F. Emmanuel. PARATYPES: 4 larvae, same data as holotype (mouthparts, tergum 4, gill 4, and paraproct of 1 larva mounted on slide [medium: Euparal]); 6 larvae, MADAGASCAR, Antananarivo (=Tanarive) Prov., Amboromptsy R., nr. Sambaina, 3-XI-71, G. F. and C. H. Edmunds and F. Emmanuel. ADDITIONAL MATERIAL: 24 larvae, same data as holotype; 44 larvae, MADAGASCAR, Antananarivo (=Tanarive) Prov., Antanifotsy R.,

at forest station, 20° C, 31-X-71, G. F. and C. H. Edmunds and F. Emmanuel; 197 larvae, MADAGASCAR, Antananarivo (=Tanarive) Prov., Amboromptsy R., nr. Sambaina, 3-XI-71, G. F. and C. H. Edmunds and F. Emmanuel; 3 larvae, MADAGASCAR, Antananarivo (=Tanarive) Prov., Ankeniheny R., 28° C, 4 km S of Manjakatempo Forest Station, 1-XI-71, G. F. and C. H. Edmunds and F. Emmanuel; 16 larvae, MADAGASCAR, Antananarivo (=Tanarive) Prov., Ankeniheny R., 15.5° C, Manjakatempo For. Stat., 2-XI-71, G. F. and C. H. Edmunds and F. Emmanuel; 75 larvae, MADAGASCAR, Fianarantsoa Prov., Namarona R., at Ranomafana, 22° C, 5-XI-71, G. F. and C. H. Edmunds and F. Emmanuel; 100 larvae, MADAGASCAR, Fianarantsoa Prov., Tsaratango R., 9 km E of Ranomafana, 23° C, 6-XI-71, G. F. and C. H. Edmunds and F. Emmanuel.

Etymology. The specific epithet is a noun in apposition and refers to the indigenous ethnic group of the region where most of the specimens were collected.

Discussion. *Dicentropitulum merina* is distinguished from *D. decipiens* and *D. papillosum* by the lack of medial sinuosities on the cerci, the relatively long submarginal row of long, fine, simple setae on the labrum (Fig. 59), the slight distomedial projection of labial palp segment 2 (Fig. 64), and the numerous small marginal spines on the paraprocts (Fig. 70).

Edmulmeatus Lugo-Ortiz & McCafferty

Edmulmeatus Lugo-Ortiz and McCafferty 1997c: 191.

Larva (figures after Lugo-Ortiz and McCafferty [1997c]). **Head.** Capsule (figures 1 and 2) enlarged relative to body, hemispherical. Labrum (figure 3) dorsoventrally thin, more or less parallel sided, slightly broader than long, with somewhat deep and narrow anteromedial emargination. Left mandible (figure 5) massive and robust, with 1 set of incisors; incisors base broad and short; prosthema robust, apically adenticulate; tuft of setae between prosthema and molar region absent; molar region with well-developed, broadly based denticles; lateral margin almost straight; basal half bare dorsally. Right mandible (figure 6) massive and robust, with 1 set of incisors; incisors base broad and short; prosthema robust, apically adenticulate; tuft of setae between prosthema and molar region absent; molar region with well-developed, broadly based denticles; lateral margin almost straight; basal half bare dorsally. Maxillae (figure 7) short and broad; palps 2-segmented. Labium (figures 9 and 10) reduced relative to other mouthparts; glossae basally broad, apically narrow, with slight apicomедial emargination; paraglossae somewhat narrow elongate; palps relatively long, extending beyond apices of glossae and paraglossae; palp segment 2 with well-developed distomedial projection; segment 3 somewhat elongate, subconical.

Thorax. Pronotum anteromedially straight, not expanded laterally. Legs held close to body; tibiae and tarsi without dorsal row of long, fine simple setae; forelegs (figure 11) with femora without ventral marginal convexity and tibiae without ventrodistal process. Tarsal claws (figure 12) with 2 rows of denticles.

Abdomen. Segment 1 not enlarged. Terga without dorsally oriented medial tubercles; posterior marginal spines short and blunt. Gills (figures 14 and 15) on abdominal segments 2–7, platelike, marginally serrate, well tracheated, held dorsolaterally. Medial caudal filament subequal to cerci.

Adult. Unknown.

Type Species. *Edmulmeatus grandis* Lugo-Ortiz & McCafferty (original designation).

Species Included. *Edmulmeatus grandis* Lugo-Ortiz & McCafferty 1997c: 193 (larva).

Distribution. Madagascar.

Discussion (figures after Lugo-Ortiz and McCafferty (1997c)]. *Edmulmeatus* is distinguished from other genera in the *Centroptiloides* complex by the following autapomorphies: enlarged, hemispherical head capsule (figures 1 and 2); massive mandibles with strongly denticulate incisors and molae (figures 5 and 6); highly reduced maxillae and labium (figures 7 and 9); and apicomedial emargination of the glossae (figure 10). This highly unusual genus remains enigmatic in that its phylogenetic affinities within the complex cannot be ascertained at this time because the larvae are so specialized and the male adult is unknown.

Herbrossus McCafferty & Lugo-Ortiz n. gen.

Larva. Head. Labrum (Fig. 71) dorsoventrally thick, conspicuously wider than long, with relatively narrow, deep, U-shaped anteromedial emargination. Hypopharynx (Fig. 72) with lingua with small apicomedial marginal convexity and superlinguae slightly acute apicolaterally. Left mandible (Fig. 73) with 1 set of incisors; incisors base broad and short; prosthema robust, apically denticulate; tuft of setae between prosthema and mola absent; lateral margin with moderate angulation; basal half with abundant short, fine, simple setae dorsally. Right mandible (Fig. 74) with 1 set of incisors; incisors base broad and short; prosthema slender, apically bifid; tuft of setae between prosthema and mola present; lateral margin with moderate angulation; basal half with abundant short, fine, simple setae dorsally. Maxillae (Fig. 75) with galealacinae with 4 long, acute denticles; palps 2-segmented, reaching galealacinae. Labium (Fig. 76) with glossae subequal in length to paraglossae; glossae basally broad, apically narrow; palps 3-segmented; palp segment 3 short, subconical.

Thorax. Pronotum anteromedially straight, not expanded or flattened laterally. Legs outstretched; tibiae and tarsi without dorsal row of long, fine simple setae; forelegs (similar to Fig. 41) with femora without ventral marginal convexity and tibiae

without ventrodistal process. Tarsal claws (similar to Fig. 42) with 2 rows of denticles.

Abdomen. Segment 1 not enlarged. Terga (Fig. 77) not creased, with scale bases; posterior marginal spines short and blunt; dorsally oriented medial dorsal tubercles absent. Gills (Figs. 78 and 79) on abdominal segments 1–7, platelike, broad, well-tracheated, marginally smooth, held dorsolaterally. Paraprocts (Fig. 80) with marginal spines. Medial caudal filament ≈ 0.50 times the length of cerci.

Adult. Unknown.

Type Species. *Herbrossus edmundsorum* McCafferty & Lugo-Ortiz n. sp.

Species Included. *Herbrossus edmundsorum* McCafferty & Lugo-Ortiz n. sp. (larva).

Material Examined. *Herbrossus edmundsorum*: see description herein.

Etymology. This genus is named in honor of Herbert H. Ross, an influential and later mentor in the career of W.P.M.

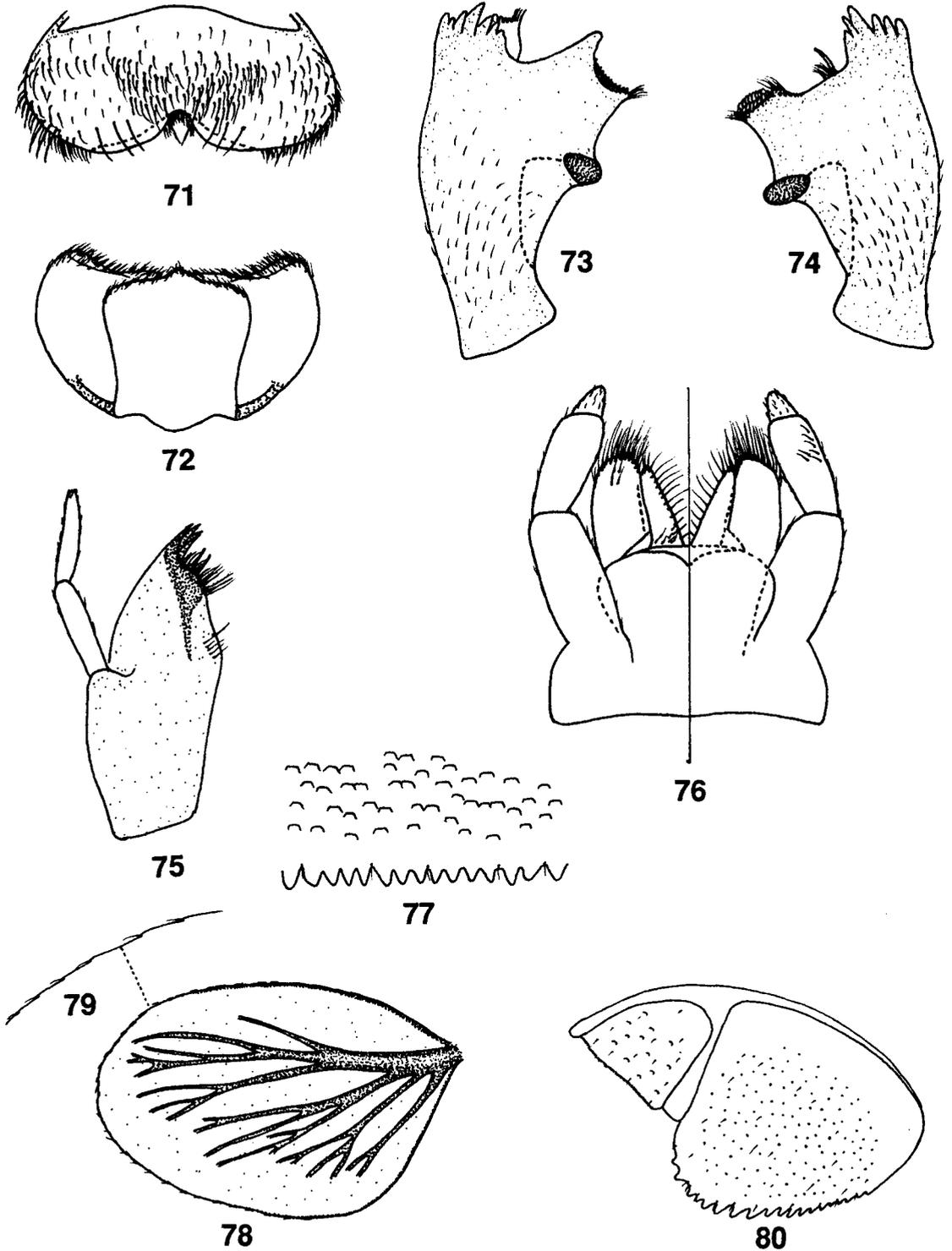
Discussion. *Herbrossus* is distinguished from all other genera in the *Centroptiloides* complex by the narrowly U-shaped labral anteromedial emargination (Fig. 71). The particulars of the possible phylogenetic relationships of *Herbrossus* are discussed under *Barnumus*.

Herbrossus edmundsorum McCafferty & Lugo-Ortiz n. sp. (Figs. 71–80)

Larva. Body length: 8.5–10.0 mm; caudal filaments length: 9.0–10.5 mm.

Head. Coloration medium brown, with yellow-brown to cream vermiform markings on vertex and frons and large yellow-brown to cream round marking on clypeus. Antennae ≈ 2.0 times length of head capsule. Labrum (Fig. 71) with submedial long, fine, simple seta and 3–5 long, fine, simple setae on either side of midline; long, fine, simple setae dorsally, most abundant in midregion. Hypopharynx as in Fig. 72. Left mandible (Fig. 73) with incisors with 7 denticles. Right mandible (Fig. 74) with incisors with 6 denticles. Maxillae (Fig. 75) with 4–5 long, fine, simple setae on medial hump. Labium (Fig. 76) with glossae ventrally with scattered short, stout, simple setae near base; paraglossae apically with abundant long, distally pectinate setae; mentum bare; palp segment 1 as long as segments 2 and 3 combined; palp segment 2 with sublateral row of 7–8 fine, simple setae dorsally; palp segment 3 apically narrow, with short, fine, simple setae over surface.

Thorax. Coloration medium brown, with irregular medium brown markings. Hindwing pads present. Legs (similar to Fig. 41) yellow-brown to medium brown; femora with row of long, fine, simple setae dorsally and numerous short, stout, apically blunt and apically pointed, simple setae ventrally; tibiae with short, fine, simple setae randomly distributed dorsally and numerous short, stout, apically pointed, simple setae ventrally; tarsi with short, fine, simple setae randomly distributed dorsally and numerous



Figs. 71-80. *Herbrossus edmundsorum* n. sp., larva. (71) Labrum. (72) Hypopharynx. (73) Left mandible. (74) Right mandible. (75) Right maxilla. (76) Labium (left, ventral; right, dorsal). (77) Detail of tergum 4. (78) Gill 4. (79) Detail of gill 4. (80) Paraproct.

short, stout, apically pointed, simple setae ventrally; tarsal claws (similar to Fig. 42) with 2 rows of 7–8 denticles and subapical pair of long, fine, simple setae.

Abdomen. Coloration medium brown to yellow-brown, with no distinct color pattern. Terga 1–3 and 6–7 generally medium brown; terga 4–5 and 8–10 generally yellow-brown. Terga (Fig. 77) with abundant scale bases and short, fine, simple setae randomly arranged along posterior margin; posterior marginal spines somewhat irregular, nearly as long as basally wide. Sterna pale yellow-brown to cream. Gills as in Figs. 78 and 79. Paraprocts (Fig. 80) with 16–17 marginal spines and short, fine, simple setae scattered over surface. Caudal filaments yellow-brown to pale brown; medial caudal filament ≈ 0.50 times length of cerci.

Adult. Unknown.

Material Examined. HOLOTYPE: larva, MADAGASCAR, Antananarivo (=Tananarive) Prov., Amborompsy R., nr Sambaina, 3-XI-71, G. F. and C. H. Edmunds and F. Emmanuel. PARATYPES: 3 larvae, same data as holotype; 2 larvae, MADAGASCAR, Antananarivo (=Tananarive) Prov., stream at Mandraka, 18.6° C, 19-X-71, G. F. and C. H. Edmunds and F. Emmanuel (mouthparts, forelegs, tergum 4, and paraproct of 1 larva mounted on slide [medium: Euparal]). ADDITIONAL MATERIAL: MADAGASCAR: 18 larvae, same data as holotype; larva, Antananarivo (=Tananarive) Prov., stream at Mandraka, 18.6° C, X-19-71, G. F. and C. H. Edmunds and F. Emmanuel; 4 larvae, Fianarantsoa Prov., Namaron R., at Ranomafana, 22.0° C, 5-XI-71, G. F. and C. H. Edmunds and F. Emmanuel; 3 larvae, Toamasina (=Tamatave) Prov., Amboasary R., Perinet (=Andasibe), 12-13-X-71, G. F. and C. H. Edmunds and F. Emmanuel.

Etymology. This species is named after George F. and Christine H. Edmunds, who collected it.

Discussion. The relatively large tergal scale bases (Fig. 77), relatively well-tracheated gills (Fig. 78), and the number and arrangement of paraproctal spines (Fig. 80) are diagnostic of *H. edmundsorum*.

Nesoptiloides Demoulin

Nesoptiloides Demoulin 1973: 2.

Larva. Head. Labrum (Fig. 81) dorsoventrally thick, conspicuously wider than long, with shallow anteromedial emargination. Hypopharynx (Fig. 82) with linguae broadly pointed apically and without apicomedial bristle tuft; superlinguae apicolaterally broadly rounded. Left mandible (Fig. 83) with 1 set of incisors; incisors base broad and short; prosthema robust, apically denticulate; tuft of setae between prosthema and mola absent; lateral margin with moderate angulation; basal half with abundant short, fine, simple setae dorsally. Right mandible (Fig. 84) with 1 set of incisors; incisors base broad and short; prosthema slender, apically bifid; tuft of setae between prosthema and mola absent; lateral margin with moderate angulation; basal half with abundant

short, fine, simple setae dorsally. Maxillae (Fig. 85) with galealacinae with 4 long, acute denticles; palps 2-segmented, reaching galealacinae. Labium (Fig. 86) with glossae subequal in length to paraglossae; glossae basally broad, apically narrow; palps 3-segmented; segment 3 subconical.

Thorax. Pronotum anteromedially straight, not expanded or flattened laterally. Legs outstretched; tibiae and tarsi without dorsal row of long, fine simple setae; forelegs (Fig. 87) with femora with pronounced ventral marginal convexity and tibiae with ventrodistal process. Tarsal claws (similar to Fig. 42) with 2 rows of denticles.

Abdomen. Segment 1 not enlarged. Terga (Fig. 88) not creased, with scale bases; posterior marginal spines short and apically blunt; dorsally oriented medial tubercles absent. Gills (Figs. 89 and 90) on abdominal segments 1–7, platelike, broad, well tracheated, marginally smooth, held dorsolaterally. Paraprocts (Fig. 91) with marginal spines. Medial caudal filament ≈ 0.40 times length of cerci.

Adult. Unknown.

Type Species. *Nesoptiloides intermedia* Demoulin (original designation).

Species Included. *Nesoptiloides intermedia* Demoulin 1973:2 (larva).

Distribution. Madagascar.

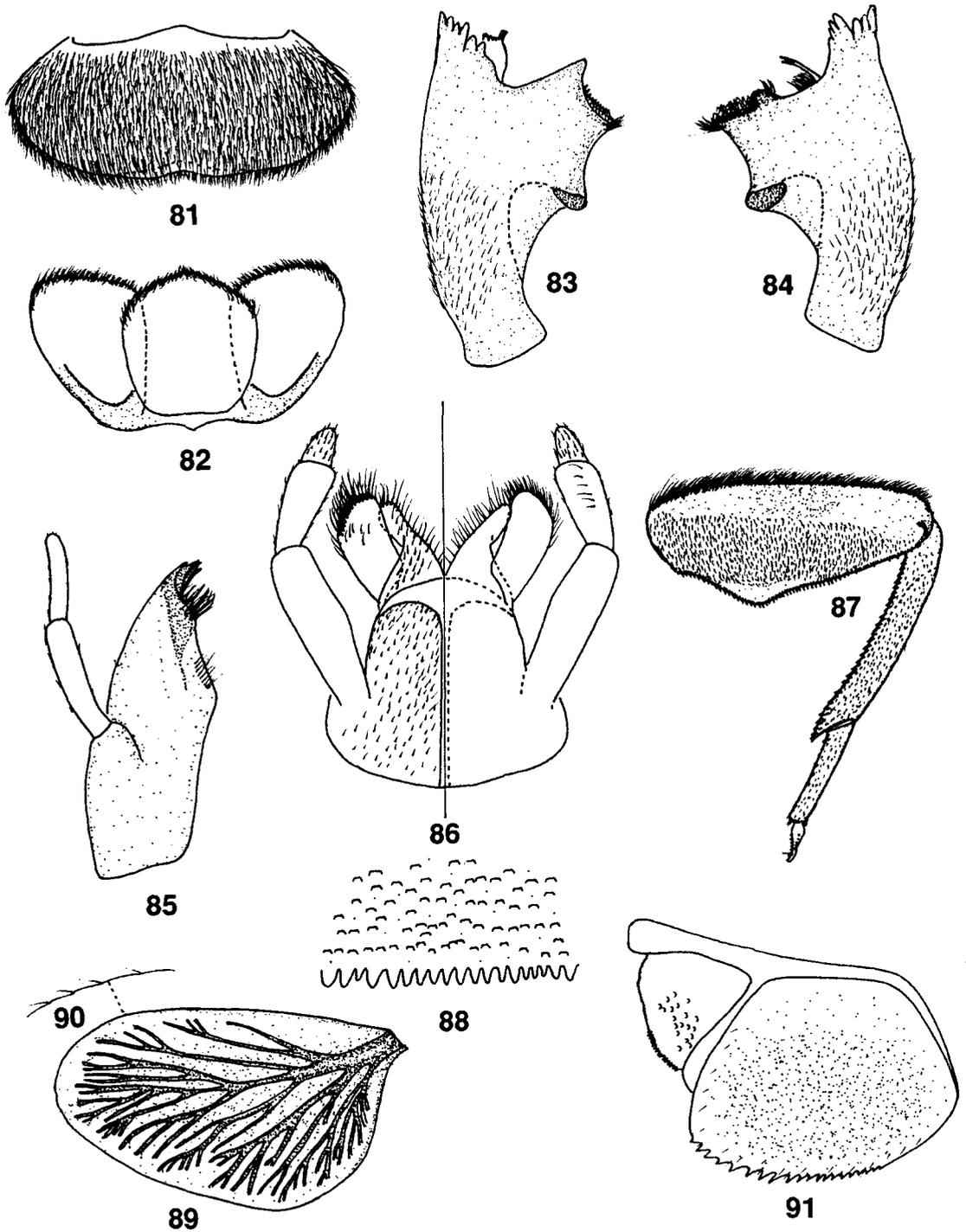
Material Examined. *Nesoptiloides intermedia*: see redescription herein.

Discussion. *Nesoptiloides* is distinguished from all other genera of the complex by the broadly based hump on the ventral margin of the forefemora and the ventrodistal process of the foretibiae (Fig. 87). Details of the possible phylogenetic relationships of *Nesoptiloides* are discussed under *Barnumus*.

Nesoptiloides intermedia Demoulin (Figs. 81–91)

Larva. Body length: 11.5–14.5 mm; caudal filaments length: 4.3–4.5 mm.

Head. Coloration medium brown, with yellow-brown to cream vermiform markings on frons and large yellow-brown to cream round marking on clypeus. Antennae ≈ 3.0 times length of head capsule. Labrum (Fig. 81) densely covered with long, fine, simple setae dorsally. Hypopharynx as in Fig. 82. Left mandible (Fig. 83) with incisors with 6 denticles. Right mandible (Fig. 84) with incisors with 7 denticles. Maxillae (Fig. 85) with 7–9 long, fine, simple setae on medial hump; palp segment 1 slightly longer than segment 2. Labium (Fig. 86) with glossae subequal in length to paraglossae; glossae ventrally with abundant short, stout, simple setae; paraglossae apically with abundant long, distally pectinate setae and scattered short, fine, simple setae ventrally, particularly in apical half; mentum with abundant short, fine, simple setae; palp segment 1 ≈ 1.33 times length of segments 2 and 3 combined; segment 2 with row of 6–7 long, fine, simple setae dorsally; segment 3 short, subconical, with short, fine, simple setae scattered over surface.



Figs. 81-91. *Nesoptiloides intermedia* Demoulin, larva. (81) Labrum. (82) Hypopharynx. (83) Left mandible. (84) Right mandible. (85) Right maxilla. (86) Labium (left, ventral; right, dorsal). (87) Left foreleg. (88) Tergum 4. (89) Gill 4. (90) Detail of gill margin. (91) Paraproct.

Thorax. Coloration yellow-brown to medium brown, with complex markings. Hindwing pads present. Legs pale yellow brown, anteriorly with light brown markings. Forelegs (Fig. 87) with femora with row of long, fine, simple setae dorsally, numerous short, stout, apically blunt setae ventrally, and abundant short, fine, simple setae anteriorly; tibiae with short, stout, apically pointed setae ventrally and abundant short, fine, simple setae scattered over surface; tarsi with short, fine, simple setae scattered over surface; tarsal claws (similar to Fig. 42) with 2 rows of 6–7 denticles and subapical pair of long, fine, simple setae.

Abdomen. Coloration yellow-brown to medium brown. Terga 1, 4, and 8 generally pale yellow-brown; tergum 4 with medium brown markings forming a large pale yellow-brown solid circle in anterior half; terga 2, 3, and 5–7 medium brown, with 2 pairs of small dots submedially in anterior half; terga 9 and 10 medium brown, with faint yellow-brown markings. Terga (Fig. 88) with abundant scale bases; posterior marginal spines ≈ 1.2 times as long as basally wide. Sterna pale to medium yellow-brown. Gills as in Figs. 89 and 90. Paraprocts (Fig. 91) with 18–20 marginal spines and short, fine, simple setae submarginally. Caudal filaments basally medium brown, gradually becoming cream in midregion and pale yellow-brown in distal third.

Adult. Unknown.

Material Examined. MADAGASCAR: Antananarivo (=Tananarive) Prov.: larva, stream at Mandraka, 18.6° C, 17-X-71, G. F. and C. H. Edmunds and F. Emmanuel; 6 larvae, same data, except 19-X-71; 4 exuviae, 7 larvae, Ankeniheny R., Manjakatompo Forest Station, 15.5° C, 2-XI-71, G. F. and C. H. Edmunds and F. Emmanuel; Toamasina (=Tamatave) Prov.: 3 larvae, Anevoka R., 15 km E of Perinet (=Andasibe), 16° C, 11-X-71, G. F. and C. H. Edmunds and F. Emmanuel; 2 exuviae, 2 larvae, stream at Gri-Gri, RN 2, 23° C, 19-X-71, G. F. and C. H. Edmunds and F. Emmanuel.

Discussion. Demoulin (1973) described *N. intermedia* from a small series of larvae. Demoulin's (1973) description is rather brief and his figures are somewhat schematic. We have therefore redescribed the species and provided new figures showing characters not previously indicated.

The setation of the labrum (Fig. 81), mandibular denticulation (Figs. 83 and 84), relative length of the maxillary and labial palps (Figs. 85 and 86), degree of development of the femoral ventral convexity and ventrodiscal tibial process of the forelegs (Fig. 87), size of tergal scale bases (Fig. 88), and paraproctal spination (Fig. 91) are diagnostic of *N. intermedia*.

Peuhlella Lugo-Ortiz & McCafferty n. gen.

Larva (figures after Wuillot and Gillies [1993a]). **Head.** Labrum (figure 5) dorsoventrally thin, more or less parallel sided, slightly broader than long, with narrow anteromedial emargination. Left mandible

(figure 7) with 1 set of incisors; prostheca robust, apically denticulate; tuft of setae between prostheca and mola present; lateral margin almost straight; basal half bare dorsally. Right mandible (figure 6) with 1 set of incisors; prostheca slender; tuft of setae between prostheca and mola present; lateral margin almost straight; basal half bare dorsally. Maxillae (figure 9) with 4 short, blunt denticles on crown of galealaciniae; palps 2-segmented, not reaching galealaciniae. Labium (figure 8) with glossae subequal in length to paraglossae; glossae basally broad, apically narrow; palps 3-segmented; palp segment 2 with slight anteromedial projection; palp segment 3 subconical, somewhat elongate.

Thorax. Pronotum anteromedially straight, not expanded or flattened laterally. Legs held close to body; tibiae and tarsi without dorsal row of long, fine simple setae; forelegs with femora without marginal convexity and tibiae without ventrodiscal process. Tarsal claws (figure 10) with 2 rows of denticles.

Abdomen. Segment 1 (figure 12) enlarged compared to other segments. Terga without dorsally oriented medial tubercles; posterior marginal spines short and blunt. Gills (figure 11) on abdominal segments 1–7, platelike, relatively broad, marginally serrate, held dorsolaterally; gills 1 and 7 poorly tracheated; gills 2–6 well tracheated. Medial caudal filament ≈ 0.75 times length of cerci.

Adult (figures after Wuillot and Gillies [1993a]). Hindwings (figure 2) narrow-elongate, with single, relatively short, hooked costal process. Male genital forceps (figure 4) with segment 2 basally broad, tapering gradually apically; segment 3 ovoid, somewhat elongate.

Etymology. This genus is named after the Peuhl people of Guinea.

Type Species. *Afroptilum christinae* Wuillot.

Species Included.

Peuhlella christinae (Wuillot) n. comb.

Afroptilum christinae Wuillot in Wuillot and Gillies 1993a: 270 (larva; male adult).

Distribution. Guinea.

Discussion (figures after Wuillot and Gillies [1993a]). The enlarged abdominal segment 1 of the larvae (figure 12) is an autapomorphy that distinguishes *Peuhlella* from all other genera in the *Centroptiloides* complex.

Peuhlella is most similar to *Susua* n. gen. However, larvae of *Peuhlella* lack the enlarged apical denticles on the tarsal claws (figure 10) found in *Susua*, and the prostheca of the right mandible of *Peuhlella* is more slender (figure 6). Male adults of *Peuhlella* differ from those of *Susua* in that they do not have segment 2 of the genital forceps basally swollen (figure 4). Adults of both genera have a single hooked costal process in the hindwings (Fig. 2, 14). We consider the presence of such process to be plesiomorphic, and hypothesize that both genera have a basal position relative to other genera in the *Centroptiloides* complex. The relatively slender prostheca of the right mandible of *Peuhlella* (figure 6), which it shares with all other genera of the

complex except *Susua*, however, suggests that *Peuhlella* is derived with those other genera.

Susua Lugo-Ortiz & McCafferty n. gen.

Larva (figures after Wuillot and Gillies [1993a]). **Head.** Labrum (figure 17) dorsoventrally thin, more or less parallel sided, slightly broader than long, with narrow anteromedial emargination. Left mandible (figure 19) with fused incisors; prostheca robust, apically denticulate; tuft of setae between prostheca and mola absent; lateral margin almost straight; basal half bare dorsally. Right mandible (figure 18) with 1 set of incisors; prostheca robust, apically denticulate; tuft of setae between prostheca and mola present; lateral margin almost straight; basal half bare dorsally. Maxillae (figure 21) with 4 short, blunt denticles on crown of galealaciniae; palps 2-segmented, extending beyond galealaciniae. Labium (figure 20) with glossae subequal in length to paraglossae; glossae basally broad, apically narrow; palps 3-segmented; palp segment 2 with slight anteromedial projection; palp segment 3 subconical, somewhat elongate.

Thorax. Pronotum anteromedially straight, not expanded laterally. Legs held close to body; tibiae and tarsi without dorsal row of long, fine simple setae; forelegs with femora without marginal convexity and tibiae without ventrodiscal process. Tarsal claws (figure 22) with 2 rows of denticles, apical denticles in both rows distinctly larger than the rest.

Abdomen. Segment 1 not enlarged. Terga without dorsally oriented medial tubercles; posterior marginal spines short and blunt. Gills on abdominal segments 1-7; gill 1 (figure 23) narrow-elongate, untracheated, marginally serrate; gills 2-7 (figure 23) platelike, relatively broad, poorly tracheated, marginally serrate, held dorsolaterally. Medial caudal filament ≈ 0.75 times length of cerci.

Adult (figures after Wuillot and Gillies [1993a]). Hindwings (figure 14) narrow-elongate, with 2 longitudinal veins and long, single, hooked costal process. Male genital forceps (figure 4) with segment 2 basally broad, abruptly narrow ≈ 0.40 from base, apically somewhat bulbous; segment 3 small, somewhat teardrop-shaped.

Etymology. This genus is named after the Soussou (also Susu) people of Guinea.

Type Species. *Afroptilum niandanensis* Wuillot.

Species Included.

Susua niandanensis (Wuillot) n. comb.

Afroptilum niandanensis Wuillot in Wuillot and Gillies 1993a: 272 (larva; male adult).

Distribution. Guinea.

Discussion (figures after Wuillot and Gillies [1993a]). The following autapomorphies distinguish *Susua* from all other genera in the *Centrop-tiloides* complex: tarsal claws with apical denticles conspicuously larger than the rest (figure 22), narrow-elongate gill 1 (figure 23), and basally broad

segment 2 of the male genital forceps (figure 16). The prostheca of the right mandible differs from the prosthecae of all other members of the *Centrop-tiloides* complex in that it is robust (figure 18). We consider that characteristic, along with the single hooked costal process of the hindwings, to be pleiomorphic. *Susua* is apparently the most basally derived genus in the complex, with all others sharing an apomorphic prostheca (see discussion under *Peuhlella*).

Thraulobaetodes Elouard & Hideux

Larva (figures after Elouard and Hideux [1991]). **Head.** Left mandible (figure 2 c and d) with 1 set of incisors; prostheca robust, apically denticulate; tuft of setae between prostheca and mola present; lateral margin almost straight; basal half bare dorsally. Right mandible (figure 2 a and b) with 2 sets of incisors; prostheca slender; tuft of setae between prostheca and mola present; lateral margin almost straight; basal half bare dorsally. Maxillae (figure 2e) with 4 short, blunt denticles on crown of galealaciniae; palps 3-segmented, not reaching galealaciniae. Labium (figure 2g) with glossae and paraglossae equal in length; glossae fused in basal half; palp segment 2 with slight distomedial projection; palp segment 3 somewhat short, subconical.

Thorax. Pronotum anteromedially straight, not expanded laterally. Legs outstretched; tibiae and tarsi without dorsal row of long, fine simple setae; forelegs with femora without marginal convexity and tibiae without ventrodiscal process. Tarsal claws (figure 3f) with 2 rows of denticles.

Abdomen. Segment 1 not enlarged. Terga (figure 1 a and b) with well-developed dorsally oriented medial tubercles; posterior marginal spines short and blunt. Gills (figure 3a) on abdominal segments 2-7, elongated basally, fringed with long projections, untracheated, held ventrally. Medial caudal filament reduced to minute vestige.

Adult. Unknown.

Type Species. *Thraulobaetodes cumminsorum* Elouard & Hideux (original designation).

Species Included. *Thraulobaetodes cumminsorum* Elouard and Hideux 1991: 170 (larva).

Distribution. Guinea.

Discussion (figures after Elouard and Hideux [1991]). We consider the basally fused glossae (figure 2g) and ventrally oriented, marginally fringed gills (figure 3a) autapomorphies that distinguish *Thraulobaetodes* from all other genera in the *Centrop-tiloides* complex. *Thraulobaetodes* appears to be closely related to *Acanthiops* (both genera, for example, have medial abdominal tubercles). *Thraulobaetodes* larvae, however, lack the anteromedially emarginate and laterally expanded and flattened pronotum that distinguishes *Acanthiops*.

Key to the Larvae of the *Centroptiloides* Complex of Afrotropical Baetidae

1. Tarsal claws with apical denticles conspicuously larger than basal denticles *Susua*
Tarsal claws as in Figs. 32, 42, 54, 66 2
2. Abdominal segment 1 much larger than other segments *Peuhlella*
Abdominal segment 1 not enlarged 3
3. Dorsal abdominal tubercles present 4
Dorsal abdominal tubercles absent 5
4. Pronotum anteromedially slightly emarginate, laterally expanded and dorsoventrally flattened; gills dorsolaterally oriented, not marginally fringed (Fig. 9); glossae not fused (Fig. 6) *Acanthiops*
Pronotum anteromedially straight, not expanded or flattened; gills ventrally oriented, marginally fringed; glossae basally fused *Thraulobaetodes*
5. Lingua with bristle tuft (Figs. 15 and 26) *Afroptilum*
Lingua without bristle tuft (Figs. 36, 48, 60, 72, 82) 6
6. Head capsule enlarged, hemispherical in lateral view; mandibles massive, with incisors and molae forming series of large denticles; maxillae and labium highly reduced *Edmulmeatus*
Head, mandibles (Figs. 3, 4, 16, 17, 27, 28, 37, 38, 49, 50, 61, 62, 73, 74), maxillae, and labium not as above 7
7. Labrum medially raised (Fig. 59); tibiae and tarsi with dorsal row of long, fine, simple setae (Fig. 65) *Dicentroptilum*
Labrum not medially raised (Figs. 35, 47, 71, 81); tibiae and tarsi without dorsal row of long, fine, simple setae (Figs. 41, 53, 87) 8
8. Forefemora with broadly based ventral hump; foretibiae with ventrodiscal process (Fig. 87) *Nesoptiloides*
Forefemora without broadly based ventral hump; foretibiae without ventrodiscal process (Figs. 41, 53) 9
9. Labrum with narrowly U-shaped anteromedial emargination (Fig. 71) *Herbrossus*
Labrum with broad anteromedial emargination (Figs. 35, 47) 10
10. Labrum with broad, deep, V-shaped anteromedial emargination (Fig. 35); right mandible with incisors distinctly cleft and with robust and apically denticulate prostheca (Fig. 38); labial palps 3-segmented (Fig. 40) *Barnumus*
Labrum with broad, deep, U-shaped anteromedial emargination (Fig. 47); right mandible with incisors not cleft and with slender prostheca (Fig. 50); labial palps 2-segmented (Fig. 52) *Centroptiloides*

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