A non-paraphyletic classification of the Afrotropical genus *Acanthiops* Waltz & McCafferty (Ephemeroptera: Baetidae)

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Acanthiops Waltz & McCafferty (Ephemeroptera: Baetidae) is shown to be a monophyletic grouping defined by an anteromedially emarginate and laterally expanded and flattened pronotum in the larva. Attempts to restrict the concept of *Acanthiops* to *Ac. marlieri* (Demoulin) and re-erect *Afroptiloides* Gillies, syn. n., for *Ac. elgonensis* Lugo-Ortiz & McCafferty, *Ac. griffithsi* Lugo-Ortiz & McCafferty, *Ac. tsitsa* Barber-James & McCafferty, *Ac. variegatus* (Gillies), *Ac. varius* (Crass) and *Ac. zomba* Lugo-Ortiz & McCafferty, are shown to be based on inconsistent and inadequate morphological features that result in a paraphyletic taxonomy. The unofficial separate treatment of *Ac. cooperi* (Gillies & Wuillot) and *Ac. erepens* (Gillies) under *Platycloeon* Gillies & Wuillot is also shown to be paraphyletic. *Acanthiops faro* Barber-James & McCafferty, sp. n., is described from larvae from Guinea, and is distinguished by the combination of a papillate projection on labial palp segment 2, small tubercles on terga 1–8 and abdominal colour pattern. *Acanthiops io* Lugo-Ortiz & McCafferty, sp. n., is described from larvae from the Democratic Republic of Congo, and is distinguished by the combination of a papillate projection on palp segment 2, elongate tubercles on terga 1–9 and abdominal colour pattern. The larva of *Ac. erepens* (Gillies) is redescribed to incorporate morphological features and variability previously not accounted for, and larvae originally assigned to *Baetis cataractae* Crass are shown to be equivalent to *Ac. erepens.* New locality data or emendations on locality data are provided for *Ac. griffithsi, Ac. tsitsa* Barber-James & McCafferty and *Ac. varius* (Crass).

Key words: Ephemeroptera, Baetidae, *Acanthiops, Afroptiloides,* new synonym, *Acanthiops faro, Acanthiops io,* new species.

INTRODUCTION

Gillies (1990) erected the subgenus *Afroptiloides* within *Afroptilum* Gillies to accommodate *Afroptilum bicaudatum* Gillies and *Af. varium* (Crass), and selected the latter species as the type of the subgenus. Gillies (1991a) subsequently incorporated *Af. variegatum* Gillies in *Afroptiloides* and redescribed the larva of *Af. varium.* McCafferty & de Moor (1995) transferred *Af. varium* to *Acanthiops* Waltz & McCafferty, a genus originally erected for the distinctive species *Ac. marlieri* (Demoulin) (Demoulin 1967; Waltz & McCafferty 1987a). With that assignment, McCafferty & de Moor (1995) synonymized *Afroptiloides* with *Acanthiops.* Barber-James & McCafferty (1997) reviewed *Acanthiops* and discussed the rationale behind the assignment by McCafferty & de Moor (1995). Barber-James & McCafferty (1997) additionally transferred *Af. variegatum* to *Acanthiops* and described *Ac. tsitsa.* Because *Af. bicaudatum* did not correspond to the concept of *Acanthiops* as defined by Waltz & McCafferty (1987a) and Barber-James & McCafferty (1997), McCafferty *et al.* (1997) erected the genus *Micksiops* for that species.

Lugo-Ortiz & McCafferty (1998) showed that *Acanthiops* belongs in the *Centroptiloides* complex of Afrotropical genera (see also Lugo-Ortiz & McCafferty 1999a), and demonstrated that it was distinguished within that complex by an autapomorphy (see Discussion under *Acanthiops*). Because *Platycloeon* Gillies & Wuillot also possessed that autapomorphy, Lugo-Ortiz & McCafferty (1998) synonymized that genus with *Acanthiops.* The two species originally assigned to *Platycloeon* by Gillies & Wuillot (1997), *P. erepens* (Gillies) and *P. cooperi* Gillies & Wuillot, were consequently transferred to *Acanthiops* (Lugo-Ortiz & McCafferty 1998). Lugo-Ortiz & McCafferty (1998) also described *Ac. elgonensis, Ac. griffithsi* and *Ac. zomba,* thus bringing the number of

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recognized species of *Acanthiops* to nine.

Recently, Gillies (1999) re-erected *Afroptiloides* as a separate genus from *Acanthiops.* Gillies (1999) restricted the concept of *Acanthiops* to *Ac. marlieri,* and transferred *Ac. elgonensis, Ac. griffithsi, Ac. tsitsa, Ac. variegatus, Ac. varius* and *Ac. zomba* to *Afroptiloides.* Without refuting the synonymy of *Platycloeon* with *Acanthiops* by Lugo-Ortiz & McCafferty (1998), or providing any rationale, Gillies (1999) treated it as a valid genus. This explains why he did not transfer *Ac. cooperi* and *Ac. erepens* to *Afroptiloides* or list them under *Acanthiops.* Gillies (1999) identified one autapomorphy to distinguish *Afroptiloides* (see Discussion under *Acanthiops),* but only provided combinations of characters to distinguish *Acanthiops,* and none to distinguish *Platycloeon.*

In this study it is shown that *Acanthiops,* as defined by Lugo-Ortiz & McCafferty (1998), constitutes a distinct monophyletic grouping and that Gillies' (1999) treatment of *Acanthiops, Afroptiloides* and *Platycloeon* as separate genera is paraphyletic. It is demonstrated that the autapomorphy identified by Gillies (1999) to distinguish *Afroptiloides* is invalid because it is inconsistently present in the six species he transferred to that genus, and that it does not delineate any meaningful phylogenetic grouping because it probably is an adaptive character. In addition, the larva of *Ac. erepens* is redescribed to incorporate important features not included in the original description by Gillies (1990), and new locality data from Malawi and South Africa are provided for this species. Emendations to locality data involving *Ac. tsitsa* and *Ac. varius* are additionally provided.

Specimens studied are housed in the following institutions: Albany Museum, Grahamstown, South Africa (AMGS); the British Natural History Museum, London (BMNH); and the Purdue Entomological Research Collection, West Lafayette, Indiana, U.S.A. (PERC). Sexually dimorphic features in baetid larvae, such as the developing turbinate eyes in mature male larvae, are not used for diagnostic purposes. Other features, such as abdominal colouration, claw denticulation and mouthpart morphology, show no sexual dimorphism. It is therefore not necessary to provide information on the sex of the larvae, as male and female larvae of any particular species do not differ from each other any more than individuals of the same sex do.

SYSTEMATICS AND TAXONOMY

Acanthiops Waltz & McCafferty

Acanthiops Waltz & McCafferty, 1987a: 97.
Afroptilum (Afroptiloides) Gillies, 1990: 99.
Platycloeon Gillies & Wuillot, 1997: 185.
Afroptiloides Gillies, 1999: 201. **Syn. n.**

Type species. *Acanthiops marlieri* (Demoulin) (original designation).

Diagnosis. Acanthiops is an endemic African genus. The known distribution of the species are indicated in Fig. 1. Larvae of *Acanthiops* are distinguished by having the pronotum slightly to deeply emarginate anteromedially and expanded and flattened laterally (Figs 2, 3; see also figures in Kimmins 1955: Figs 4g, 5g; Demoulin 1956: Fig. 2a; Demoulin 1967: Fig. 3a; Gillies 1990: Fig. 30; Gillies 1991a: Fig. 23; Barber-James & McCafferty 1997: Fig. 1; Gillies & Wuillot 1997: Fig. 6). Other characteristics that, in combination, aid in distinguishing larvae of *Acanthiops* include the sprawling body shape, reduced labial palp segment 3 (Figs 8, 21), two rows of denticles on the tarsal claws (except in *Ac. cooperi*) (Figs 11, 23) and the presence of variously developed tergal tubercles on at least abdominal segments 1–3. Adults of *Acanthiops* cannot be reliably distinguished from other Afrotropical baetid adults with single marginal intercalaries in the forewings.

Species included

Acanthiops cooperi (Gillies & Wuillot)
Platycloeon cooperi Gillies & Wuillot, 1997: 186 (larva).
Acanthiops cooperi (Gillies & Wuillot): Lugo-Ortiz & McCafferty 1998: 2.

Acanthiops elgonensis Lugo-Ortiz & McCafferty
Centroptilum sp. no. 3: Demoulin 1964: 286.
Acanthiops elgonensis Lugo-Ortiz & McCafferty, 1998: 4 (larva).
Afroptiloides elgonensis (Lugo-Ortiz & McCafferty): Gillies 1999: 200.

Acanthiops erepens (Gillies)
Baetis cataractae Crass, 1947: 66. (In part.)
Baetis sp. A Kimmins 1955: 868. (In part.)
Afroptilum erepens Gillies, 1990: 105 (larva; male, female adults).
Platycloeon erepens (Gillies): Gillies & Wuillot 1997: 186.
Acanthiops erepens (Gillies): Lugo-Ortiz & McCafferty 1998: 2.

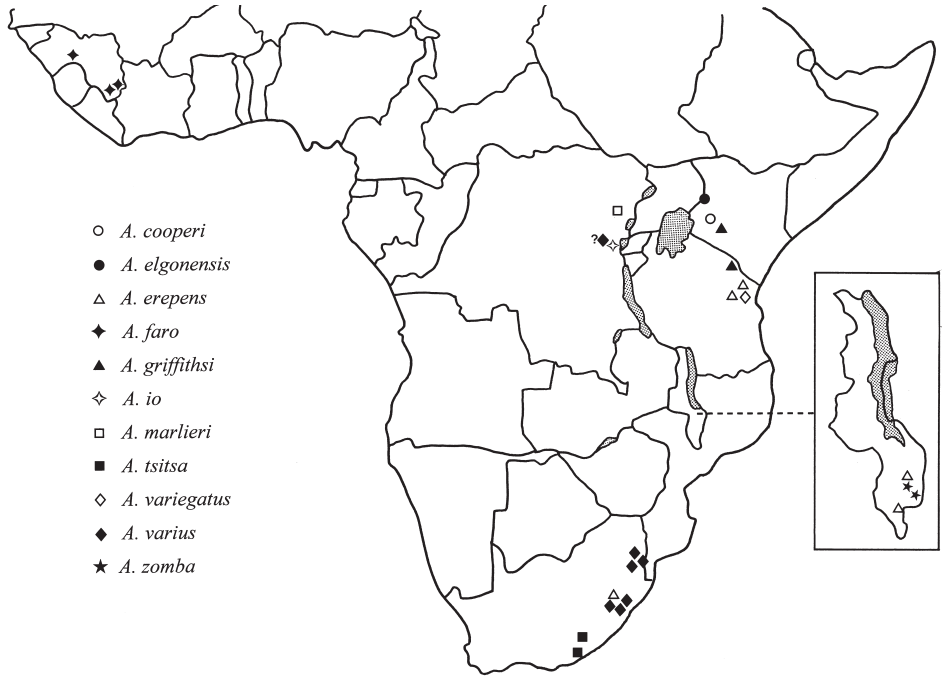


Fig. 1. Distribution of known species of *Acanthiops* in Africa.

Acanthiops tsitsa Barber-James & McCafferty: Lugo-Ortiz & McCafferty 1998: 4. (In part).

Acanthiops faro Barber-James & McCafferty, **sp. n.** (larva).

Acanthiops griffithsi Lugo-Ortiz & McCafferty

Acanthiops griffithsi Lugo-Ortiz & McCafferty, 1998: 5 (larva).

Afroptiloides griffithsi (Lugo-Ortiz & McCafferty): Gillies 1999: 200.

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

Acanthiops marlieri (Demoulin)

Centroptilum marlieri Demoulin, 1967: 230 (larva).

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

Acanthiops tsitsa Barber-James & McCafferty

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

Afroptiloides tsita [sic] Barber-James & McCafferty: Gillies 1999: 200.

Acanthiops variegatus (Gillies)

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

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

Afroptiloides variegatum [sic] Gillies: Gillies 1999: 201.

Acanthiops varius (Crass)

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

Acentrella sp. Demoulin 1956: 7.

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

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

Acanthiops tsitsa Barber-James & McCafferty: Lugo-Ortiz & McCafferty 1998: 4.

Afroptiloides varium [sic] (Crass): Gillies 1999: 201.

Acanthiops zomba Lugo-Ortiz & McCafferty

Acentrella sp. A: Kimmins 1955: 870.

Baetis sp. A: Kimmins 1995: 868. (In part).

Centroptilum sp. A: Demoulin 1970: 50.

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

Acanthiops tsitsa Barber-James & McCafferty: Lugo-Ortiz & McCafferty 1998: 4. (In part).

Acanthiops zomba Lugo-Ortiz & McCafferty, 1998: 5 (larva).

Afroptiloides njombae Gillies, 1999: 200. **Syn. n.**

Distribution of species. Most species of *Acanthiops* seem to be confined to mountainous areas with fast-flowing streams (Fig. 1). From the distribution data available, the mountains along the rift valley appear to be rich in species. The occurrence of

Ac. varius in the Democratic Republic of Congo should be corroborated against the actual specimens examined by Demoulin (1956), as it represents an unexplainable extension of the distribution of that species.

Discussion. Lugo-Ortiz & McCafferty (1998, 1999a) defined the *Centroptiloides* complex as those Afrotropical genera whose larvae possess two subparallel rows of denticles on the tarsal claws (Fig. 11; Gillies 1991a: Fig. 19; Barber-James & McCafferty 1997: Fig. 15; Lugo-Ortiz & McCafferty 1998: Figs 32, 42, 54, 66; Lugo-Ortiz & McCafferty 1999a: Fig. 8). Adults of the *Centroptiloides* complex have single marginal intercalaries in the forewings, but this characteristic is not unique to the complex. Within the *Centroptiloides* complex, Lugo-Ortiz & McCafferty (1998) defined *Acanthiops* by the autapomorphic anteromedially emarginate and laterally expanded and flattened pronotum in the larvae (Figs 2, 3). Lugo-Ortiz & McCafferty (1998) showed that larvae of *Afroptiloides* and *Platycloeon* also possess that autapomorphy (Gillies 1990: Fig. 30; Gillies & Wuillot 1997: Fig. 6), and consequently considered them equivalent to *Acanthiops.*

In re-erecting *Afroptiloides,* Gillies (1999) did not mention or refute the autapomorphy identified by Lugo-Ortiz & McCafferty (1998) for *Acanthiops.* Instead, Gillies (1999) restricted the concept of *Acanthiops* to *Ac. marlieri* by emphasizing the compact body shape and extreme development of the dorsal abdominal tubercles in that species, and considered the presence of a dorsal row of setae on the tibiae of the larvae an autapomorphy of *Afroptiloides.* Gillies (1999) also treated *Platycloeon* separately from *Acanthiops* and *Afroptiloides,* but did not identify any autapomorphies for that genus, nor did he officially re-erect it.

Scrutiny of the tibiae of the larvae of the six species Gillies (1999) assigned to *Afroptiloides* revealed that the dorsal row of setae is absent in *Ac. elgonensis* and *Ac. zomba,* and present in *Ac. griffithsi, Ac. tsitsa, Ac. variegatus* and *Ac. varius.* Such a row of setae is also present in *Ac. erepens* (Fig. 10), but apparently absent in *Ac. cooperi* (Gillies & Wuillot 1997: Figs 6, 7) (although Gillies & Wuillot (1997) indicated that the type material of *Ac. cooperi* was deposited in the BMNH, the institution does not have it (D. Goodger, pers. comm.), and consequently we could not ascertain whether that feature was present or absent in that species. That feature, therefore, cannot be used to separate any species from *Acanthiops,* as Gillies (1999) proposed, and is not a reliable indicator of phylogenetic relationships.

The presence of a dorsal row of setae in the larvae of *Ac. erepens, Ac. griffithsi, Ac. tsitsa, Ac. variegatus* and *Ac. varius* is better interpreted as an adaptation to keep purchase in the swift-current biotopes where they are found (Crass 1947; Barber-James & McCafferty 1997). This feature is also present in the larvae of numerous baetid genera that occur in similar biotopes, including *Acentrella* Bengtsson, some *Baetis* Leach, *Baetodes* Needham & Murphy, *Deceptiviosa* Lugo-Ortiz & McCafferty, *Dicentroptilum* Wuillot & Gillies, *Echinobaetis* Mol, *Gratia* Thomas, *Herbrossus* McCafferty & Lugo-Ortiz, *Jubabaetis* Müller-Liebeneau, *Liebebiella* Waltz & McCafferty, *Micksiops* McCafferty, Lugo-Ortiz & Barber-James, *Papuanatula* Lugo-Ortiz & McCafferty, *Platybaetis* Müller-Liebeneau, *Prebaetodes* Lugo-Ortiz & McCafferty and *Tanzaniella* Gillies (Morihara & McCafferty 1979; Müller-Liebeneau 1980, 1982; Waltz & McCafferty 1987b; Mol 1989; Gillies 1991b; Thomas 1992; McCafferty *et al.* 1994, 1997; Wuillot & Gillies 1994; Lugo-Ortiz & McCafferty 1996, 1998, 1999b,c; Gattolliat & Sartori 1998). Significantly, in *Acentrella* (Morihara & McCafferty 1979, McCafferty *et al.* 1994) and *Herbrossus* (Lugo-Ortiz & McCafferty 1998, Gattolliat & Sartori 1998) it has been documented that whereas some species have a well-developed dorsal row of setae on the tibiae, others have a row with short setae or lack one.

Gillies (1999) additionally rejected the concept of a stepwise progression in the development of the tergal tubercles in *Acanthiops,* as discussed by Barber-James & McCafferty (1997), considering it applicable only to those species he transferred to *Afroptiloides.* Gillies (1999) argued that the presence of such tubercles in *Acanthiops* and *Afroptiloides* was a homoplasy, adducing that they also occur in several unrelated genera of Baetidae. Although it is true that several unrelated baetid genera possess such tubercles, it is incorrect to consider the different expressions of this feature an instance of homoplasy between, on the one hand, *Ac. marlieri* and, on the other, *Ac. cooperi, Ac. elgonensis, Ac. erepens, Ac. griffithsi, Ac. tsitsa, Ac. variegatus, Ac. varius* and *Ac. zomba.* This is because all nine species possess the autapomorphic pronotal character discussed above. Significantly, Gillies (1999) obviated the critical species

Ac. griffithsi, which has well-developed tubercles on terga 1–8 (Lugo-Ortiz & McCafferty 1998: Fig. 8) similar to those of *Ac. marlieri* (Demoulin 1967: Fig. 3a, b). Moreover, *Ac. griffithsi* has a compact body shape that is reminiscent of that of *Ac. marlieri,* with abdominal segments 2–3 or 2–4 tightly overlapping (segments 2–6 or 2–7 are tightly overlapping in *Ac. marlieri*). Also, the morphology of its mouthparts, particularly with respect to the labium and mandibles (Lugo-Ortiz & McCafferty 1998: Figs 2, 3, 6), is essentially the same as in *Ac. marlieri* (Demoulin 1967: Fig. 4b, c, f). It is therefore evident that Gillies's (1999) isolation of *Ac. marlieri,* and concomitant separate treatment of the other eight species under either *Afroptiloides* or *Platycloeon,* represent an arbitrary taxonomic decision based primarily on the extreme development of the tergal tubercles of the apparently most apotypic species thus far known in the lineage. Such a classificatory scheme is paraphyletic, and therefore not permissible in a strictly phylogenetic system (Hennig 1966; Ross 1974).

A similar, instructive case of a stepwise progression in the development of tergal tubercles is found in the baetid genus *Papuanatula,* from New Guinea and New Britain (Lugo-Ortiz & McCafferty 1999c). *Papuanatula copis* Lugo-Ortiz & McCafferty has well-developed tubercles on terga 1–8 (Lugo-Ortiz & McCafferty 1999c: Fig.16), whereas *P. lenos* Lugo-Ortiz & McCafferty, *P. plana* Lugo-Ortiz & McCafferty and *P. vaisisi* Lugo-Ortiz & McCafferty lack such tubercles. Between these extremes, *P. bessa* Lugo-Ortiz & McCafferty shows submedial pairs of minute tubercles on terga 1–5 or 1–6 (Lugo-Ortiz & McCafferty 1999c: Fig. 5) and *P. tuber* Lugo-Ortiz & McCafferty shows small medial tubercles on terga 1–8 (Lugo-Ortiz & McCafferty 1999c: Fig. 34). The six species, however, constitute a distinct monophyletic grouping because they possess the autapomorphic character of labial palp segment 3 being more convex laterally than medially (Lugo-Ortiz & McCafferty 1999c: Figs 4, 14, 21, 29, 37). Separating *P. copis* from the other five species of *Papuanatula* based on the extreme development of its tergal tubercles would result in a paraphyletic classification similar to the one proposed by Gillies (1999).

Although *Acanthiops* is a monophyletic grouping, precise phylogenetic relationships among its 11 constituent species cannot be ascertained from the information available at present. This is in part a result of the male adults of only *Ac. variegatus* and *Ac. varius* being known. Preliminary cladistic analysis, however, indicates that *Ac. cooperi* and *Ac. erepens* are the most ancestral species because they retain a well-developed medial caudal filament. *Acanthiops cooperi* is probably the most basal species because it has tergal tubercles on terga 1–3 or 4 only, whereas *Ac. erepens* is more similar to the other nine species in having more extensive tergal tuberculation. The co-occurrence of *Ac. erepens* with *Ac. varius* in South Africa, *Ac. zomba* in Malawi and *Ac. variegatus* in Tanzania (Fig. 1) is of biogeographic and phylogenetic interest because it suggests that *Ac. erepens* is ancestral to at least those three species. *Acanthiops elgonensis, Ac. faro, Ac. griffithsi, Ac. io, Ac. marlieri, Ac. tsitsa, Ac. variegatus, Ac. varius* and *Ac. zomba* have a minute medial caudal filament, indicating that they are more derived species. Among those species, *Ac. griffithsi* and *Ac. marlieri* are clearly the most derived, as demonstrated by their highly developed tergal tuberculation and compressed bodies with at least segments 2–3 or 4 tightly overlapping. Relationships among *Ac. elgonensis, Ac. faro, Ac. io, Ac. tsitsa, Ac. variegatus, Ac. varius* and *Ac. zomba* are unresolved, but it appears that *Ac. elgonensis* and *Ac. zomba* are more closely related to *Ac. griffithsi* and *Ac. marlieri,* because the four species have variously pigmented gill lamellae and segment 2 of the labial palps tends to be narrow-elongate. In contrast, *Ac. faro, Ac. io, Ac. tsitsa, Ac. variegatus* and *Ac. varius* have unpigmented gill lamellae and segment 2 of the labial palps tends to be shorter and more robust. These latter features are similar to those observed in *Ac. cooperi* and *Ac. erepens,* and it is therefore probable that *Ac. faro, Ac. io, Ac. tsitsa, Ac. variegatus* and *Ac. varius* have ancestral positions in relation to *Ac. elgonensis, Ac. griffithsi, Ac. marlieri* and *Ac. zomba.* On the other hand, it is possible that *Ac. io* is more closely related to *Ac. griffithsi* and *Ac. marlieri* because it has relatively large abdominal tubercles on terga 1–9 also. The above preliminary observations are summarized in Table 1 and Fig. 36.

Acanthiops erepens (Gillies) (Figs 2–16)

Redescription of larva

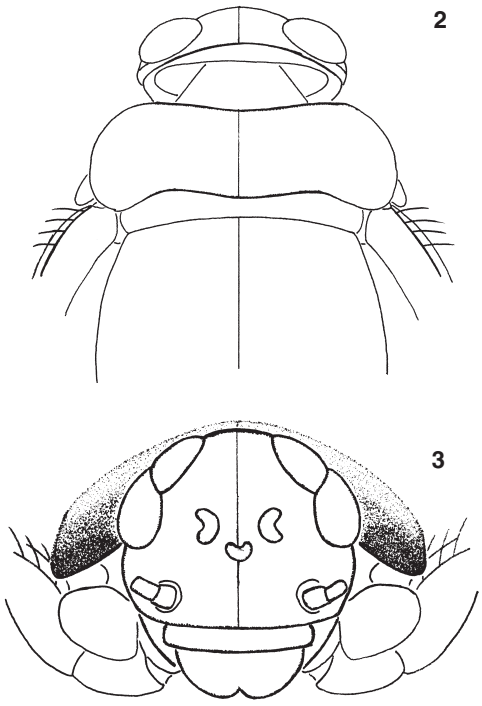
Lengths. Body: 5.5–7.0 mm; medial caudal filament: 2.5–3.0 mm; cerci: 2.5–3.0 mm.

Head. Pale to medium yellow-brown, with faint vermiform markings on frons and vertex.

Table 1. Structural characters and character state polarities used to formulate the cladogram in Fig. 36. Numbered characters correspond to the numbered apomorphies distributed in the cladogram. All characters refer to the larval stage. See text for discussion.

Character	Plesiomorphy	Apomorphy
1. Pronotum	Anteromedially straight and laterally not flattened	Anteromedially emarginate and laterally flattened (Figs 2, 3)
2. Abdominal tuberculation	On terga 1–4 only	On terga 1–6 to 9 (Figs 14–16, 24, 25, 33, 34)
3. Medial caudal filament	Developed	Undeveloped (Fig. 25)
4. Gills	Unpigmented	Pigmented
5. Abdominal terga	Not overlapping	Terga 2–3 or 4 tightly overlapping

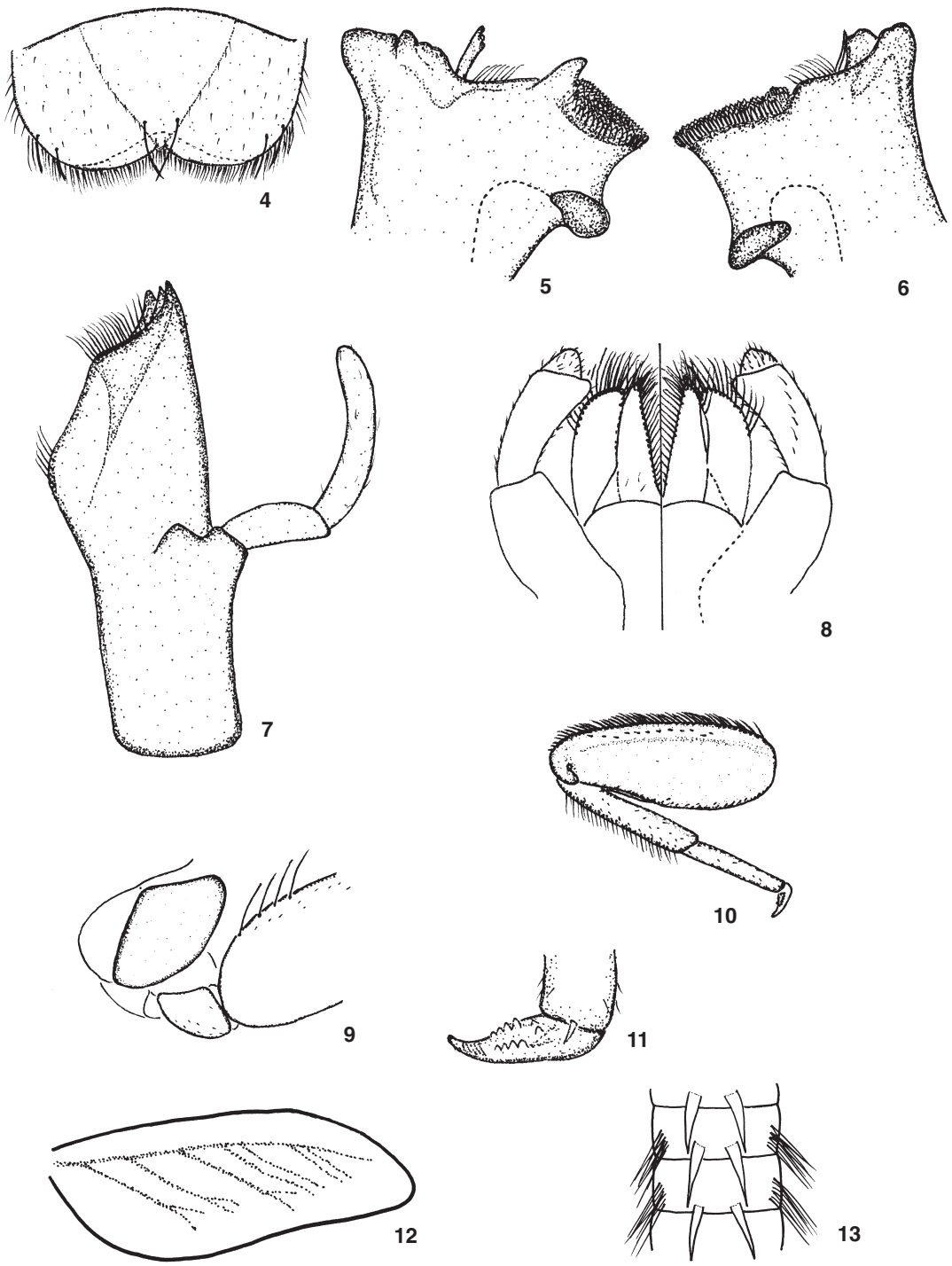
Antennae approximately 1.2 times length of head capsule. Labrum (Fig. 4) broadly rounded anteriorly, medially raised; dorsally with submedial pair of long, fine, simple setae and apicolaterally with 2–3 long, fine, simple setae. Hypopharynx (Kimmins 1955: Fig. 4d) with no distinctive features. Left mandible (Fig. 5) with four denticles; prostheca robust, apically denticulate; tuft of minute, fine, simple setae present between prostheca and mola. Right mandible (Fig. 6) with outer incisor with large denticle, inner incisor with three small apical denticles; prostheca slender, apically pointed; tuft of minute, fine, simple setae present between prostheca and mola. Maxillae (Fig. 7) with 4–5 fine, simple setae near medial hump; palps reaching galealaciniae; palp segment 1 approximately 0.75 times length of segment 2; palp segment 2 apically without fused papillate projection. Labium (Fig. 8) with glossae slightly longer than paraglossae; glossae medially with long, robust, simple setae and apically with long, robust, simple setae and few short, stout, 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 slightly produced distomedially, dorsally with 5–6 minute, fine, simple setae; palp segment 3 subconical, with short, fine, simple setae scattered over surface.



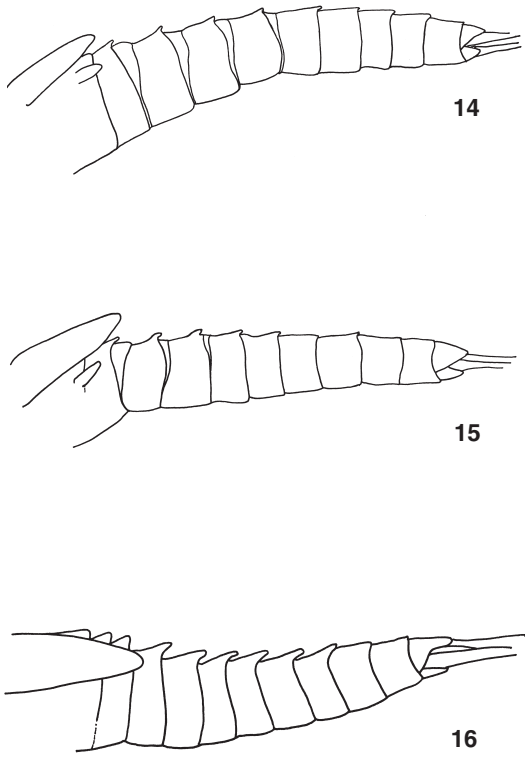
Figs 2, 3. *Acanthiops erepens*, larva, showing anteromedian emarginate and flattened pronotum. **2**, pronotum (dorsal view); **3**, pronotum (frontal view).

Thorax. Pale to medium yellow-brown, with various markings. Hind wing pads present. Pronotum (Figs 2, 3) with shallow anteromedial emargination; meso- and metanotum each with small, blunt, medial tubercle posteriorly. Forecoxal plate (Figs 3, 9) broadly rounded. Legs (Fig. 10) medium yellow-brown; femora with row of long, robust, simple setae dorsally and numerous minute fine and robust simple setae ventrally; tibiae with dorsal row of long, fine, simple setae dorsally and minute, robust, simple setae ventrally; tarsi with numerous minute, fine, simple setae dorsally and ventrally; tarsal claws (Fig. 11) with two rows of 4–5 denticles each.

Abdomen (Figs 14–16). Pale to medium yellow-brown, with no distinct markings, or with faint markings only. Terga 1–7 medially with small, posteriorly oriented, single tubercles; tergum 8 with minute medial crest; terga 9–10 without tubercles



Figs 4–13. *Acanthiops erepens,* larva. **4**, labrum; **5**, left mandible; **6**, right mandible; **7**, left maxilla; **8**, labium (left, ventral view; right, dorsal view); **9**, procoxal plate (angular view); **10**, right foreleg; **11**, tarsal claw; **12**, gill 3; **13**,detail of ventral surface of medial caudal filament [modified from Gilles (1990)].



Figs 14–16. *Acanthiops erepens*, larva, tergal tuberculation. **14**, Loteni River (KwaZulu-Natal Province, South Africa); **15–16**, Mlungusi Stream (Malawi).

or crests. Gill 1 narrow-elongate; gills 2–7 (Fig. 12) subtriangular, well tracheated, marginally smooth. Paraprocts with 4–5 small, irregular spines. Cerci and medial caudal filament pale yellow-brown. Medial caudal filament ventrally with medial pairs of spines (Fig. 13).

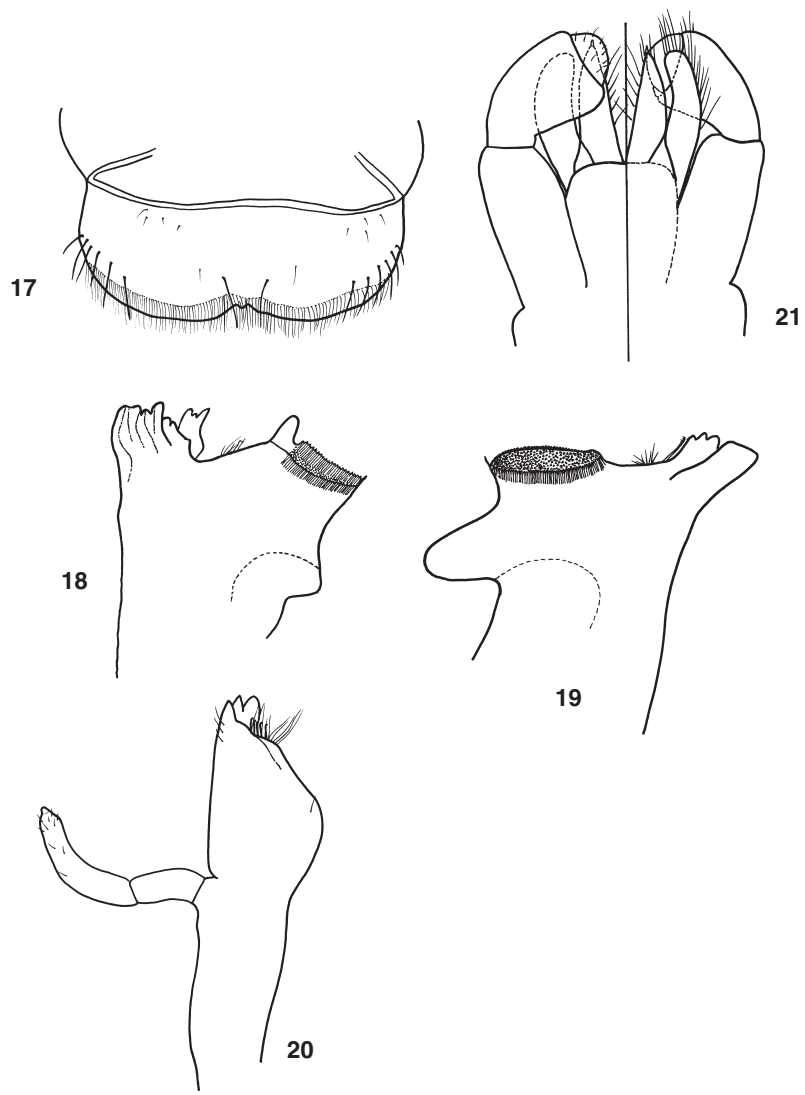
Material examined. SOUTH AFRICA: *KwaZulu-Natal Province,* two larvae, Loteni (Lotheni) R., nr Nkangala, nr 29°35′S 29°40′E, iii.1946, R.S. Crass (AMGS Nos. RSC2A, RSC2B) [mouthparts and left foreleg of one larva on slide (medium: Euparal)]. MALAWI: two larvae, Mt Zomba, Mlungusi Stream, 15.viii.1952, L. Berner (BMNH); two larvae, 22 mi N of Chiromo, 24.vii.1952, L. Berner (BMNH) [mouthparts and left foreleg of one larva mounted on slide (medium: Euparal)].

Discussion. Gillies (1990) described *Ac. erepens* from larvae and female adults from several locations in Tanzania. Gillies' (1990) description of the larva is, however, brief and the figures he provided are schematic. Importantly, Gillies (1990) did not document the considerable variation in the development of the dorsal tubercles on the terga. Early-instar larvae tend to have relatively small tubercles (Figs 14, 15), whereas middle-instar and mature larvae tend to have more developed tubercles (Fig. 16). In some larvae, the tuberculation on terga 1–2 or 1–3 appears to be hooked (Fig. 15), whereas in others it is straighter (Figs 14, 16). More significantly, Gillies (1990) overlooked the dorsal row of long, fine, simple setae on the tibiae (Fig. 10), which he considered a unique feature of those species he assigned to *Afroptiloides* (Gillies 1999).

Body length is also highly variable in *Ac. erepens.* However, it should be noted that, prior to moulting, individuals conspicuously expand the arthrodial membrane between the abdominal segments, thus causing them to appear elongate (Figs 14, 15). This condition, in combination with the variation of the tergal tubercles, may misleadingly give the impression that multiple species are involved.

The shallow anteromedial emargination of the pronotum (Fig. 2) and the presence of pairs of spines on the ventral side of the medial caudal filament (Fig. 13) should be sufficient to identify *Ac. erepens* correctly. *Acanthiops cooperi,* the other known species of the genus with a well-developed medial caudal filament, has a deep anteromedial emargination (Gillies & Wuillot 1997: Fig. 6) and lacks the ventral spines on the caudal filament.

The taxonomy of *Ac. erepens* requires explanation. Crass (1947) described *B. cataractae* from KwaZulu-Natal, South Africa, and associated larvae and adults based only on geographical proximity. Although Crass (1947) did not designate any types from the series of specimens he studied, it is evident from his discussion that his species concept of *B. cataractae* was based on the male adult. The male adults in that series do not agree with the concept of *Acanthiops* (Lugo-Ortiz & McCafferty 1998), because they have double marginal intercalaries in the forewings and the hind wings are slender and lack a costal process (Crass 1947: Fig. 12a, b). We consequently do not transfer *B. cataractae* to *Acanthiops.* Our examination of the four larvae assigned by Crass (1947) to *B. cataractae* revealed, however, that two of them are clearly *Ac. erepens* (see Material examined). The other two specimens are actually pharate subimagos that were unable to emerge and are in extremely poor condition. Significantly, those two



Figs 17–21. *Acanthiops faro*, larva. **17**, labrum; **18**, left mandible; **19**, right mandible; **20**, right maxilla; **21**, labium (left-ventral view; right-dorsal view).

specimens do not show any dorsal tuberculation on the terga, and it is therefore possible that they do belong to *B. cataractae.*

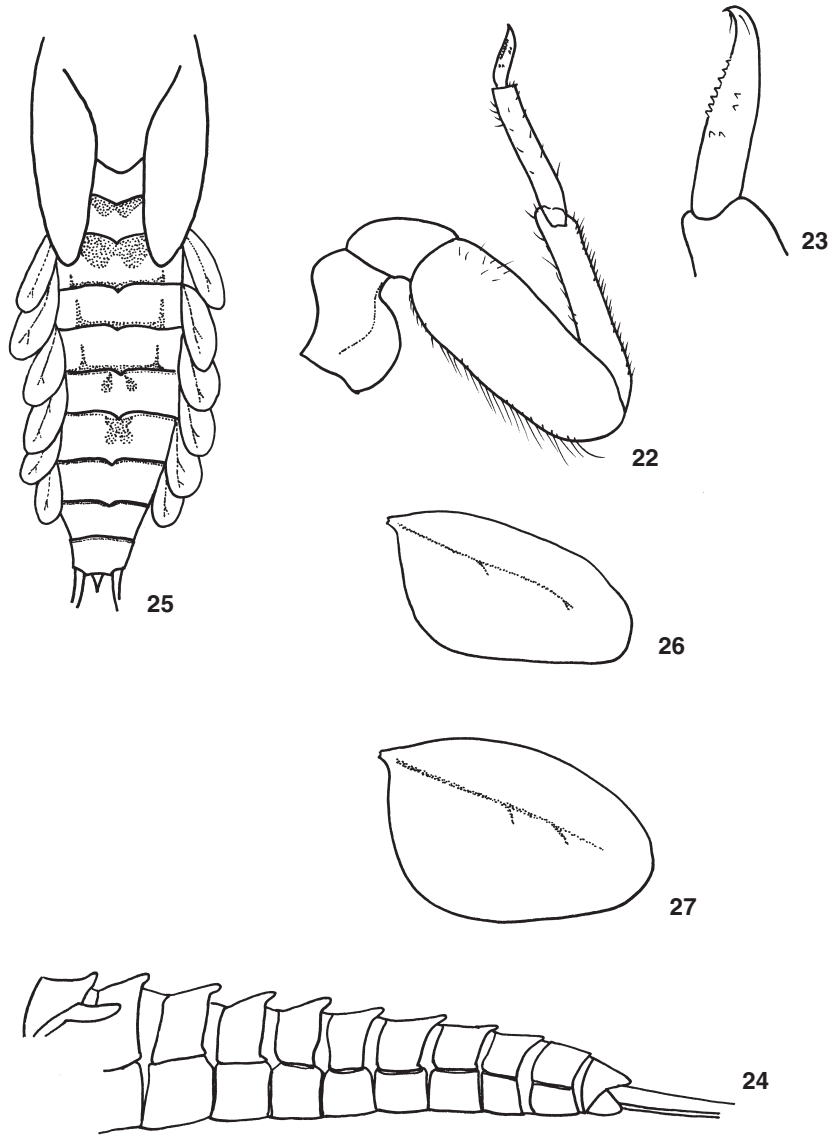
Kimmins (1955) described several larvae from different localities in Malawi as *'Baetis* sp. A.' Eventually, Lugo-Ortiz & McCafferty (1998) assigned those larvae to *Ac. tsitsa.* Our more recent study of Kimmins' (1955) larvae, however, shows that they actually constitute three species; none of them is assignable to *Ac. tsitsa.* One larva (unidentified stream 13.5 mi E of Fort Johnson, 7.vii.1953, L. Berner) belongs to *Baetis harrisoni* Barnard; another larva (Likabula stream, Mt Mlanje, 19.viii.1953, L. Berner) belongs to *Ac. zomba*; all other specimens belong to *Ac. erepens* (see Material examined), but they show considerable variation, as documented above.

Acanthiops faro Barber-James & McCafferty, **sp. n.** (Figs 17–27)

Description of larva

Lengths. Body: 4.0–4.8 mm; medial caudal filament: reduced to pointed stub; cerci: 2.6–2.9 mm.

Head. Medium yellow-brown, with no distinctive markings. Antennae approximately 2.5 times



Figs 22–27. *Acanthiops faro*, larva. **22**, foreleg; **23**, tarsal claw; **24**, abdomen (lateral view); **25**, abdomen (dorsal view); **26**, gill 1; **27**, gill 4.

length of head capsule. Labrum (Fig. 17) broadly rounded anteriorly; dorsally with submedial pair of long, fine, simple setae and row of six long, fine, simple setae. Hypopharynx with no distinctive features. Left mandible (Fig. 18) with six denticles; prostheca robust, apically denticulate; tuft of minute, fine, simple setae present between prostheca and mola. Right mandible (Fig. 19) with outer incisor with large denticle, inner incisor with three small denticles; prostheca slender, apically pointed; tuft of minute, fine, simple setae present between prostheca and mola. Maxillae (Fig. 20) with single fine, simple seta near medial hump; palps reaching galealaciniae; palp segment 1 approximately 0.50 times length of segment 2; palp segment 2 apically with fused papillate projection. Labium (Fig. 21) with glossae and paraglossae equal in length; glossae medially with long, robust, simple setae and apically with short, robust, simple setae; paraglossae laterally and

apically with long, robust, simple setae; palp segment 1 subequal in length to segments 2 and 3 combined; palp segment 2 slightly produced distomedially, dorsally with sparsely scattered minute, fine, simple setae; palp segment 3 round, cap-like, with short, fine, simple setae scattered over surface.

Thorax. Pale to medium yellow-brown, without distinct markings. Hind wing pads present. Pronotum (similar to Figs 2, 3) with shallow anteromedial emargination; meso- and metanotum each with small, blunt, posteromedial tubercle. Procoxal plate (similar to Figs 3, 9) broadly rounded. Legs (Fig. 22) yellow-brown; femora with row of long, robust, simple setae dorsally and minute, fine, simple setae ventrally, more numerous proximally; tibiae with dorsal row of short, fine, simple setae dorsally and minute, robust, simple setae ventrally; tarsi with numerous minute, fine, simple setae scattered over surface; tarsal claws (Fig. 23) with two rows of 2–7 denticles each, and with paired setae at apex of each claw.

Abdomen (Figs 24, 25). Pale to medium yellow-brown. Terga 1–10 uniformly pale yellow-brown; terga 2 and 3 with pale yellow-brown background, and dark brown W-shape marking extending from anterior margin; terga 3–5 with dark brown stripe along posterior margin, ending in single vertical bars parallel to lateral margin on either side; tergum 6 with medial pair of large oblong to round spots; tergum 7 with anteromedial pair of large oblong markings joining along anterior margin. Terga 1–8 medially with elongate, posteriorly oriented, single tubercles; terga 9 and 10 without tubercles or crests. Gill 1 reduced, oblong, untracheated (Fig. 26); gills 2–7 oblong to subtriangular, poorly tracheated, opaque, marginally smooth (Fig. 27). Paraprocts with 6–8 irregular spines. Cerci pale yellow-brown.

Adult. Unknown.

Etymology. The specific epithet is a noun in apposition after the sky and water god of the Bambara people of West Africa.

Type material. Holotype: larva, GUINEA, M'Boo River near Moyendougou, ii.1989 (PERC). Paratypes: two larvae, GUINEA, tributary of the Milo River near Konsankoro, iii.1977 (one mature larva in PERC; one smaller larva in AMGS, No. CAW 292A) [mouthparts, antenna, gills 1 and 5, and right foreleg of mature larva mounted on slide (medium: Euparal)].

Additional material examined. GUINEA: larva, Leleko River near Konsankoro, vii-1988 (PERC); three larvae, Kaba River, no date (PERC).

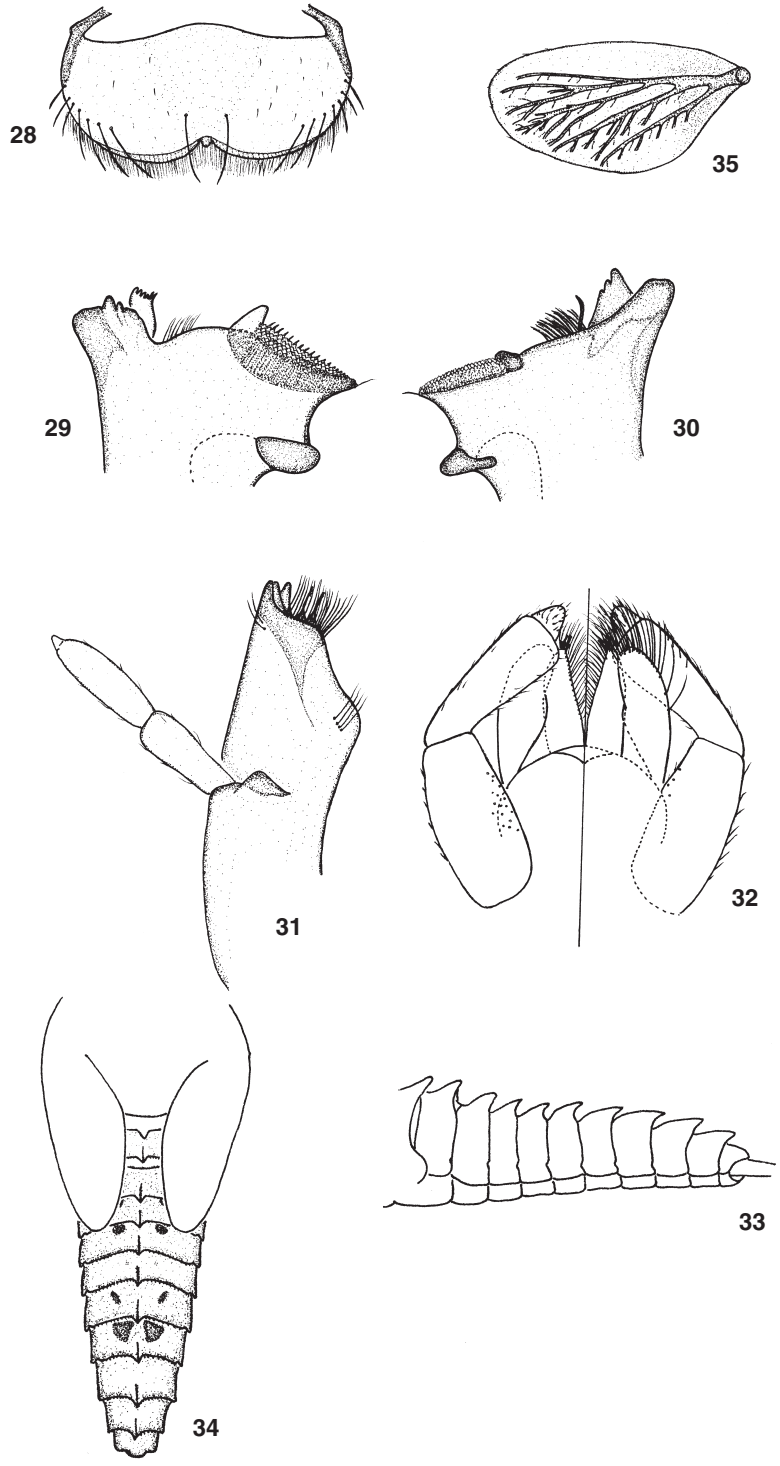
Discussion. Larvae of *Ac. faro* are similar to those of *Ac. tsitsa* and *Ac. varius,* particularly with respect to the morphology of the labial palps (Fig. 21) and abdominal tuberculation (Figs 24, 25), but they differ from them in having a papillate apical projection on segment 2 of the maxillary palps (Fig. 20) and a different abdominal colour pattern (Fig. 25). Larvae of *Ac. faro* are further distinguished from those of *Ac. tsitsa* by having a narrower labrum with an anteromedial denticle (Fig. 17), and from those of *Ac. varius* by being less robust. Although *Ac. io* sp. n.(described below) has a papillate projection on maxillary palp segment 2, *Ac. faro* is readily distinguished from it because the latter lacks a medial tubercle on tergum 9 and has less elongate tubercles on terga 1–8 (Figs 24, 25), and gills have less pronounced tracheation (Figs 27, 35).

Acanthiops io Lugo-Ortiz & McCafferty, **sp. n.** (Figs 28–35)

Description of larva

Lengths. Body: 5.0–5.5 mm; medial caudal filament: reduced to pointed stub; cerci: 4.5–6.0 mm.

Head. Pale to medium yellow-brown, with faint vermiform markings on frons and vertex. Antennae approximately 1.2 times length of head capsule. Labrum broadly rounded anteriorly, medially slightly raised (Fig. 28); dorsally with submedial pair of long, fine, simple setae and row of 4–6 long, fine, simple setae. Hypopharynx with no distinctive features. Left mandible with four denticles (Fig. 29); prostheca robust, apically denticulate; tuft of minute, fine, simple setae present between prostheca and mola. Right mandible with outer incisor with large denticle, inner incisor with three small denticles (Fig. 30); prostheca slender, apically pointed; tuft of minute, fine, simple setae present between prostheca and mola. Maxillae with 4–5 fine, simple setae near medial hump (Fig. 31); palps reaching galealaciniae; palp segment 1 approximately 0.75 times length of segment 2; palp segment 2 apically with fused papillate projection. Labium with glossae and paraglossae equal in length (Fig. 32); glossae medially with long, robust, simple setae and apically with long, robust, simple setae and few short, stout, simple setae; paraglossae laterally



Figs 28–35. *Acanthiops io,* larva. **28**, labrum; **29**, left mandible; **30**, right mandible; **31**, right maxilla; **32**, labium (left, ventral view; right, dorsal view); **33**, abdomen (lateral view); **34**, abdomen (dorsal view); **35**, gill 4.

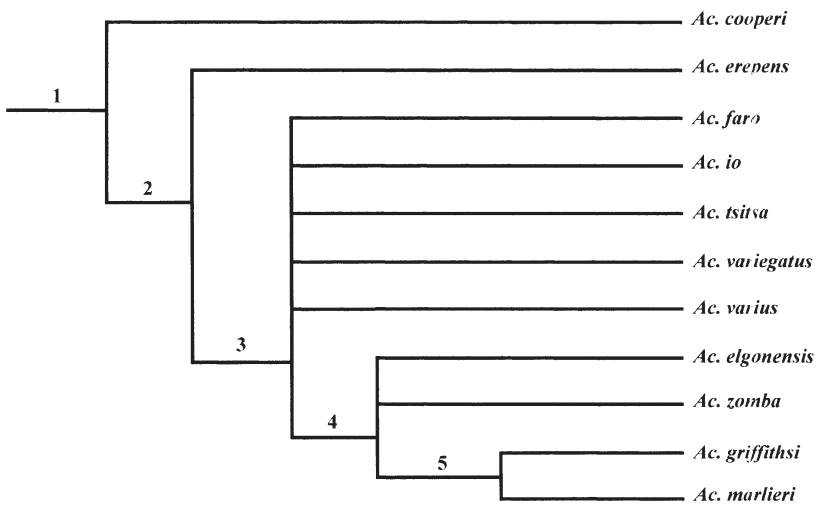


Fig. 36. Cladogram expressing relationships among known species of *Acanthiops*. Numbered apomorphies correspond to numbered apomorphies in Table 1. See text for discussion.

and apically with long, robust, simple setae; palp segment 1 approximately 0.95 times length of segments 2 and 3 combined; palp segment 2 slightly produced distomedially, dorsally with 4–5 minute, fine, simple setae; palp segment 3 subconical, with short, fine, simple setae scattered over surface.

Thorax. Pale to medium yellow-brown, with various markings. Hind wing pads present. Pronotum (similar to Figs 2, 3) with shallow anteromedial emargination; meso- and metanotum each with small, blunt, posteromedial tubercle. Forecoxal plate (similar to Figs 3, 9) broadly rounded. Legs (similar to Fig. 10) yellow-brown; femora with row of long, robust, simple setae dorsally and numerous minute, fine and robust, simple setae ventrally; tibiae with dorsal row of long, fine, simple setae dorsally and minute, robust, simple setae ventrally; tarsi with numerous minute, fine, simple setae dorsally and ventrally; tarsal claws (similar to Fig. 11) with two rows of 4–5 denticles each.

Abdomen (Figs 33, 34). Pale to medium yellow-brown. Terga 1, 2, 5 and 8–10 uniformly pale yellow-brown; terga 3 and 4 uniformly pale yellow-brown, with anteromedial pair of large round spots; tergum 6 with medial pair of large oblong or round spots; tergum 7 with anteromedial pair of large subtriangular markings. Terga 1–9 medially with elongate, posteriorly orientated, single tubercles; tergum 10 without tubercles or crests. Gill 1 narrow-elongate; gills 2–7 (Fig. 35) subtriangular, well tracheated, marginally smooth. Paraprocts with 4–5 irregular spines. Cerci pale yellow-brown.

Adult. Unknown.

Etymology. The specific epithet is a noun in apposition from Greek mythology, referring to the daughter of the river-god, Inachus.

Type material. Holotype: larva, DEMOCRATIC REPUBLIC OF CONGO, small stream near Lake Kivu, Goma-Bukavu Rd, iii.1981 (PERC). Paratypes: three larvae, same data as holotype (one larva in AMGS, No. CAW 291A; two larvae in PERC) [mouthparts and left foreleg of one larva mounted on slide (medium: Euparal)].

Additional material examined. Larva, same data as holotype (PERC). DEMOCRATIC REPUBLIC OF CONGO: larva, Lake Kivu stream, Bukavu-Nigona Rd, iii.1981 (PERC).

Discussion. Acanthiops io is similar to *Ac. faro* in having an apical papillate projection on segment 2 of the maxillary palps (Fig. 31) and elongate tubercles on terga 1–9 (Figs 33, 34). Other characteristics that may aid in distinguishing *Ac. io* include the morphology and setation of the labrum (Fig. 28), the abdominal colour pattern (Fig. 34) and the much denser gill tracheation (Fig. 35).

Acanthiops griffithsi Lugo-Ortiz & McCafferty

Material examined. KENYA: larva, Malewa R., 9.i.1991, R. Griffiths (AMGS No. CAW 175A); two larvae, Nanyuki R., at Nanyuki, 19.xi.1971, G.F.

Edmunds (PERC); TANZANIA: two larvae, Mt Kilimanjaro, 1700 m, iii.1981 (PERC).

Discussion. Lugo-Ortiz & McCafferty (1998) described *Ac. griffithsi* from the Turasha River in Kenya. The new records above extend the range of the species slightly southward.

Acanthiops tsitsa Barber-James & McCafferty

Material examined (all material housed in AMGS, No. ECR 330A). SOUTH AFRICA: *Eastern Cape Province,* ten larvae, Nahoon River on Fairview Farm, W of East London, 32°51'S 27°44'E, 240 m, 5.v.2000, F.C. de Moor and H.M. Barber-James.

Discussion. The new record above represents a southward extension of the range of *Ac. tsitsa.* The specimens, however, are more darkly pigmented than the original material described (Barber-James & McCafferty 1997), and the dorsal abdominal tubercles may extend to segment 9 and are slightly more pointed.

Acanthiops varius (Crass)

Material examined (all material housed in PERC, except where otherwise indicated). Larva, SOUTH AFRICA: *KwaZulu-Natal Province,* Mkomazi R. at Staebraes, 29°59'10"S 30°09'17", 410 m, 12.x.1996, F.C. de Moor and H.M. Barber-James (AMGS No. UMK 121AH); 13 larvae (3 immature), Mkomazi R. below SAICOR weir, 30°10'11"S 30°41'55"E, 30 m, 12.x.1996, F.C. de Moor, H.M. Barber-James and C. Dickens (AMGS No. UMK 106AV); larva, Mkomazi R. at Gravesend Estate, 30°10'40"S 30°44'12"E, 10 m, 6.v.1996, F.C. de Moor and C. Dickens (AMGS No. UMK 77AL). *Mpumalanga Province,* larva, MacMac R., above MacMac Falls, nr Graskop, 1820 m, 18.ix.1990, W.P. and N. McCafferty; larva, Marite R., nr Bushbuckridge, 580 m, 19.x.1990, W.P. and N. McCafferty; larva, Sabie Sand Game Reserve, Sabie R., at Londolozi, 20.x.1990, W.P. and N. McCafferty; larvae, Kruger National Park, Sabie R., at Sabie Gorge, Mozambique–South Africa border, 22.x.1990, W.P. and N. McCafferty; larva, Kruger National Park, Sabie R., at Molondozi, 23.x.1990, W.P. and N. McCafferty; larvae, Sabie R., at Lisbon Estates, 27.x.1990, W.P. and N. McCafferty. TANZANIA: larva, Korogwe, Pangani R, vi.1981.

Discussion. The South African material examined above corresponds to that examined by Lugo-Ortiz & McCafferty (1998) and assigned to *Ac. tsitsa.* Our re-examination of that material indicated that it is actually assignable to *Ac. varius.* These new assignments, along with those from Malawi based on the Kimmins (1955) material (see Discussion under *Ac. erepens),* indicate that *Ac.tsitsa* is confined to the rivers draining the southern Drakensberg and Amatola mountain ranges, and is currently recorded from the Pot, Tsitsa, Wildebees and Nahoon Rivers in the Eastern Cape Province, South Africa (Barber-James & McCafferty 1997; see above). *Acanthiops tsitsa* has a more narrow-elongate body than *Ac. varius,* and its tergal tubercles are more erect (Barber-James & McCafferty 1997: Figs 1, 4). Both species are found in swift-flowing streams at a wide altitudinal range, but they apparently do not co-occur.

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ADDENDUM

Since this paper was accepted for publication, the authors have received a publication describing three new species of *Afroptiloides* from Madagascar (Gattolliat 2000). This provides significant new distribution records, which could not be included in Fig. 1. Following the discussions presented in our paper, the species described by Gattolliat should be included as members of the genus *Acanthiops* and not as *Afroptiloides.* The following synonymies are therefore proposed:

Acanthiops delphinae (Gattolliat) **Comb. n.**
Afroptiliodes delphinae Gattolliat 2000: 310 (larva).

Acanthiops namorona (Gattolliat) **Comb. n.**
Afroptiloides namorona Gattolliat 2000: 310 (larva).

Acanthiops spinosum (Gattolliat) **Comb. n.**
Afroptiloides spinosum Gattolliat 2000: 307 (larva).

Reference

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