

A DIPHYLETIC ORIGIN FOR THE TWO-TAILED BAETID NYMPHS
OCCURRING IN EAST AFRICAN STONY STREAMS WITH A
DESCRIPTION OF THE NEW GENUS AND SPECIES
TANZANIELLA SPINOSA GEN. NOV. SP. NOV.

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ABSTRACT

Several African genera of baetid mayflies are known to have sprawling 2-tailed nymphs. A new genus with these characteristics, *Tanzaniella*, is described from East Africa which, in contrast to the others, is closely related to the Oriental genus *Baetiella*. The higher classification of the Baetidae is discussed, and the three subfamilies, Baetinae, Callibaetinae and Cloeoninae are recognised here. Reasons are given for believing that the Cloeoninae originated in Africa.

INTRODUCTION

Sprawling, 2-tailed baetid nymphs are known in many parts of the world. In Africa, this group is represented by *Afrobaetodes* Demoulin, *Acanthiops* Waltz & McCafferty and *Afroptilum* (*Afroptiloides*) Gillies. The nymph of the latter was defined as being of the sprawling type, the mandibles on one or both sides bearing a tuft of hairs between the prostheca and the molar region, the anterior surface of the tibiae with a line of fine setae, the tarsal claws with a single or double row of denticles and the terminal filament aborted. Both *Afrobaetodes* and *A. (Afroptiloides)* occur in stony streams in the Usambara Mountains of northern Tanzania, the former on the upper surface of rocks, the latter underneath.

On a recent visit to this locality a third type of nymph was found, superficially resembling *Afroptiloides* (Plate I). However, a closer look at the mouthparts and tarsal claws did not confirm this diagnosis. Moreover, it has been possible to associate these nymphs with adults that were previously classified as *Pseudocloeon*. Thus it appears that the resemblance between these two nymphs is the result of convergence and a common life-style and is not an indication of common origin.

This material is described here as the new baetine genus *Tanzaniella*.

***Tanzaniella* gen. nov.**

Adult. Marginal intercalaries of fore wing in pairs; hind wing absent; wing

membrane not pigmented.

Nymph. Antennae about twice length of head. Maxillary palpus short, stout, 2-segmented; canines of mandibles partly fused; 2nd segment of labial palpus greatly reduced, fused with 3rd segment. Femora with ventral setal patch, posterior margin with a fringe of long fine bristles, tibiae with a row of long dorsal bristles; tarsal claws with single row of denticles. Abdomen not dorsoventrally flattened; posterior margins of terga edged with scanty blunt spines. Gills 7, obovate, asymmetrical, margin not serrate. Cerci devoid of hairs; terminal filament reduced to a single segment.

Type species. *T. spinosa* sp. nov.

The adult of *Tanzaniella* resembles other mayflies formerly placed in *Pseudocloeon* Klapálek. The nymph differs from all other Baetidae by the following combination of characters: absence of mandibular hair fringe, reduction of labial palpus, single row of tarsal denticles and suppression of the terminal filament. On the other hand, it resembles the Oriental genus *Baetiella* Uéno, as redefined by Waltz & McCafferty (1987a), notably in the abdominal terga not being dorsoventrally flattened, in the short, stout maxillary palpus, the presence of a ventral setal patch on the femora, single row of long dorsal hairs on the tibiae and unserrated gill margins. It differs from that genus by the canines of the right mandible being divided, and in the greatly reduced second segment of the labial palpus and its fusion with the third segment.

Tanzaniella spinosa sp. n.

Female imago (in life): Eyes coffee-coloured, body pitch-brown. Femora pitch-brown, mid and hind femora pale at knee, tibiae and tarsi colourless, cerci white.

(In spirit): Eyes fawn, slightly ovoid, narrowly separated. Notum mahogany-brown with darker median suture, metanotum similar with darker median spur. Legs: all femora mahogany-brown, tibiae and tarsi cream. Wings (fig. 1) hyaline, extreme base of Sc and R₁ proximal to costal brace dark brown, the pigment spreading to adjacent wing membrane; marginal intercalaries present from 2nd radial interspace, 2-5 stigmatic crossveins. Abdominal terga I-VI with blunt median spurs, that on I about twice the size of others (fig. 4); terga pale brown with mahogany-brown markings (fig. 2); sterna cream, basal forceps segment brown, remainder cream (fig. 3); cerci white.

Female imago (in life): Head, thorax and abdomen dark brown, metanotum almost black. Abdominal terga IV and V yellow in median area. All femora pitch-brown, mid and hind femora yellow at apex; fore tibiae and tarsi dusky, mid and hind tibiae pale grey, tarsi dusky, cerci dusky.

(In spirit): Body generally mahogany-brown; femora dark brown, tibiae and tarsi pale; wings as in male. Abdominal terga pale brown, posterior margins broadly dark brown; on III-VII or VIII with paired submedian dark spots behind anterior margin; I-VI with small median spur on posterior

margin; cerci white.

Nymph (fig. 5): Generally dark brown, median occipital suture pale. Mouthparts (figs. 9-14). Upper surface of femora yellowish-brown, enclosed on basal and posterior aspect by a broad cream band; a line of fine setae present on dorsal aspect of all tarsi (fig. 6). Metanotum with a blunt median spur; abdominal terga I-VII or VIII each with a small, blunt, median spur on posterior margin. Terga III, VI and VII mainly dark brown, other terga extensively pale; on all terga a pair of oblique, submedian, dark brown dashes present behind anterior margin; posterior margins of all segments dark brown; posterior marginal spines blunt (fig. 8). Gills (fig. 7). Cerci fawn.

Body: Male 4.5-5mm, female 5-6mm. Wing: male 4.5-5mm, female 6mm.

Material: TANZANIA: light-trap by R. Sigi, Chemka, Amani, male holotype [in British Museum (Natural History)], 20.x.61; same locality, 1 male 13.i.53, 3 males 23.iv.61, 1 male 8.x.61, 4 males 11.xii.61, 2 males 28.i.62, 1 male 1.iv.62, 2 males 9.xii.62, 1 male 6.1.63; Amani district, 2 females 31.viii.52, 4 females 27.vi.53 and 7.vii.55, 2 females 27.i.62, 1 female subimago 11.xii.61; Ukungwi stream, Amani, 2 nymphs, 7.iii.85.

Under the name *Baetis (Acentrella)* sp. no. 4, Demoulin (1965) figured an immature 2-tailed nymph from Marangu, Kilimanjaro. It differs from *T. spinosa* in minor details of the mandibles, in the apparent absence of a fringe of hairs along the tarsi and especially in the absence of median spurs on the metanotum and abdominal terga. In other respects it resembles *T. spinosa* closely, and evidently represents a second species of *Tanzaniella*.

Males of *T. spinosa* were not uncommonly caught in light-traps set up beside the River Sigi. Females have been caught on the wing in the afternoon and early evening while egg-laying. The egg masses in life are emerald green. Nymphs were only collected once, in a small stony stream draining into the River Sigi. However, I have several nymphs collected many years earlier on Kilimanjaro, which conform to the description given by Demoulin above. A note made at the time records that they live on the undersides of stones and, if dislodged, make only the feeblest attempts to swim, arching their bodies upwards in an ineffective manner.

ORIGINS OF THE AFRICAN BAETIDAE

The coexistence of these similar but phylogenetically distinct baetid nymphs sheds light on the history of the African Baetidae. In the course of their review of the phylogeny of the Ephemeroptera, Landa and Soldán (1975) recognised the two baetid subfamilies of Kazlauskas (1972), the Baetinae and the Cloeoninae. They drew attention to the taxonomic importance of the tarsal claws. Kazlauskas had used the presence of single or paired marginal intercalaries in the adult wing to separate the two groups. In recent years, the value of marginal intercalaries in the taxonomy of the Baetidae has been seriously doubted (Riek 1973). Mori-hara and Edmunds (1980) even remarked that 'paired marginal intercalaries may have to be regarded as an intragenerically variable character'.

I prefer to look at it another way. There is a small homogeneous group of baetids which is distinguished from all the rest by a striking, derived character state, namely a cuticle ornamented, to a greater or a lesser extent in both adult and nymph, with a conspicuous sprinkling of small pigmented depressions. I refer, of course, to *Callibaetis*. If one accepts that it represents a distinct phylogenetic line, then the rest of the family fall naturally into two groups, those with paired and those with single marginal intercalaries. The former is presumably the ancestral condition.

What are the arguments to support this statement? The most compelling reasons come from a comparison of the fauna of the two southern continents. In South America, with the exception of one species of *Cloeodes*, Waltz and McCafferty (1987), all known recent baetid genera have paired marginal intercalaries. In Africa, on the other hand, there is a rich and varied fauna of baetids with single marginal intercalaries. Something like 2/3 of the 100-odd described species and 8 out of 13 genera belong to this group. In both continents there has been a parallel tendency towards further reduction in marginal venation, in South America in those with paired intercalaries, in Africa in those with single. In the former continent there is the single example of *Cloeodes*. In Africa one can cite the restriction of intercalaries to the middle of the wing margin in *Afrobaetodes* and the elimination of alternate intercalaries in certain species of *Cloeon* (figs. 15, 16). I have even seen a female of an unknown genus from Senegal in which intercalaries are entirely absent (fig. 17). The effects of evolution over a long period of time are surely manifest here.

The nymphs have two character states that correlate to a high degree with the venational differences in the adult, (1) a setal tuft at the base of the prostheca of the mandible, as noted by Demoulin (1965) and (2) the presence of a double row of denticles on the tarsal claws, (Jacob, 1972, Landa and Soldán, 1985).

(1) The setal tuft is present (on the right mandible, if not always on the left) in practically all genera with single marginal intercalaries. The exceptions are the two genera *Centroptiloides* Lestage and *Raptobaetopus* Müller-Liebenau, which are carnivorous and have highly modified mandibles, and *Baetopus* Keffermüller. On the other hand, the mandibular setal tuft is absent from 15 out of 18 known genera with paired intercalaries, the exceptions being *Acerpenna* Waltz and McCafferty, *Fallceon* Waltz and McCafferty and *Guajirolus* Flowers.

(2) The denticles on the tarsal claws correlate less closely with the adult venational state. This is probably because the claws have sometimes been highly modified in response to adaptive pressures. The denticles may even be entirely absent, as for example in *Apobaetis* Day or *Symbiocloeon* Müller-Liebenau. Or, in some genera such as *Afrobaetodes* Demoulin and *Afroptilum* Gillies, the denticles may be biseriata in some species and uniseriate in others; the second 'row' may even be represented by a single tooth. Thus, there are two rows of teeth in 9 out of 16 currently recognised genera with single marginal intercalaries in the adult. On the other hand, in those with

paired marginal intercalaries, the tarsal denticles are in a single row or absent in 16 out of 18 currently recognised genera, the exceptions being the Nearctic *Heterocloeon* McDunnough and the Oriental *Chopralla* Waltz & McCafferty.

All known species of the African fauna, with single marginal intercalaries in the adult have one or both of the above nymphal characters.

The third group of Baetidae, those with a stippled cuticle, i.e. *Callibaetis*, have nymphs of all known species with a well developed mandibular tuft of setae and the tarsal claws have 2 rows of teeth, sometimes very long ones. Morihara and McCafferty (1979) have expressed the opinion that the latter condition is the ancestral state. Since in certain Siphonuridae, for example the New Zealand genus *Nesameletus* Tillyard and the closely related *Siphlaenigma* Penniket, the tarsal teeth are in two rows, this conclusion would seem to be correct. Similarly, in certain other siphonurids, there is a mandibular fringe of setae, (Edmunds 1975), and this character would also seem to be ancestral. The mouthparts of *Callibaetis* show at least one derived character state, not shared by other Baetids. As pointed out to me by Dr R. Wills Flowers, the terminal segment of the labial palps is rotated through 90° and held down over the other mouthparts.

A number of authors have discussed the higher classification of the Baetidae. As long ago as 1933 Spieth distinguished "three distinct lines of evolution", *Callibaetis*, *Baetis* with *Pseudocloeon*, and *Centroptilum* together with *Cloeon*. Kazlauskas (1972) proposed the recognition of two subfamilies, Baetinae and Cloeoninae. Riek (1975) listed the two subfamilies, Baetinae and Callibaetinae, and included the Siphlaenigmatinae in the Baetidae. More recently, Landa and Soldán (1985) also recognised three subfamilies, Baetinae, Cloeoninae (including *Callibaetis*) and Siphlaenigmatinae.

In the light of the arguments given above, I am recognising the three subfamilies, Baetinae Leach, Cloeoninae Kazlauskas and Callibaetinae Riek, this last containing *Callibaetis* only. I follow Edmunds *et al.* (1976) in treating *Siphlaenigma* Penniket as a distinct family.

Table I summarises the characters used in defining the subfamilies, the derived character state being indicated by the + sign. In fig. 18 their relationships are presented as a simple cladogram.

Edmunds (1972) argued that the Baetidae arose in South America and spread to Africa, and that a secondary radiation occurred there. I would take his argument further and identify this radiation with the emergence of the Cloeoninae. It would follow from this that the origins of the Cloeonine fauna of other zoogeographical Regions should be sought in Africa.

In proposing these names, I am doing no more than formalising the ideas of Spieth. It must be admitted that this system leaves a number of problems. It also leaves the Baetinae as a large and unwieldy group, the complexity of which has been emphasised by the recent studies of Waltz & McCafferty. As regards the two 2-tailed baetids from East Africa, one clearly belongs to the Cloeonine genus *Afroptilum* (*Afroptiloides*), while the other is the new baetine genus, *Tanzaniella*. The similarity of this taxon to *Baetiella* Uéno suggests

that it may represent a relatively recent invasion of Africa from the Palaearctic or Oriental Regions.

ACKNOWLEDGEMENTS

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Table I. Derived character states (+) used in the definition of subfamilies of the Baetidae.

Character state	Callibaetinae	Cloeoninae	Baetinae
1. Stippled cuticle in adult	+	-	-
2. Reduced hind wing, few cross-veins	-	+	+
3. Single marginal intercalaries	+, -	+	-
4. Loss of setal tuft at base of prosthema of mandible of nymph	-	-	+

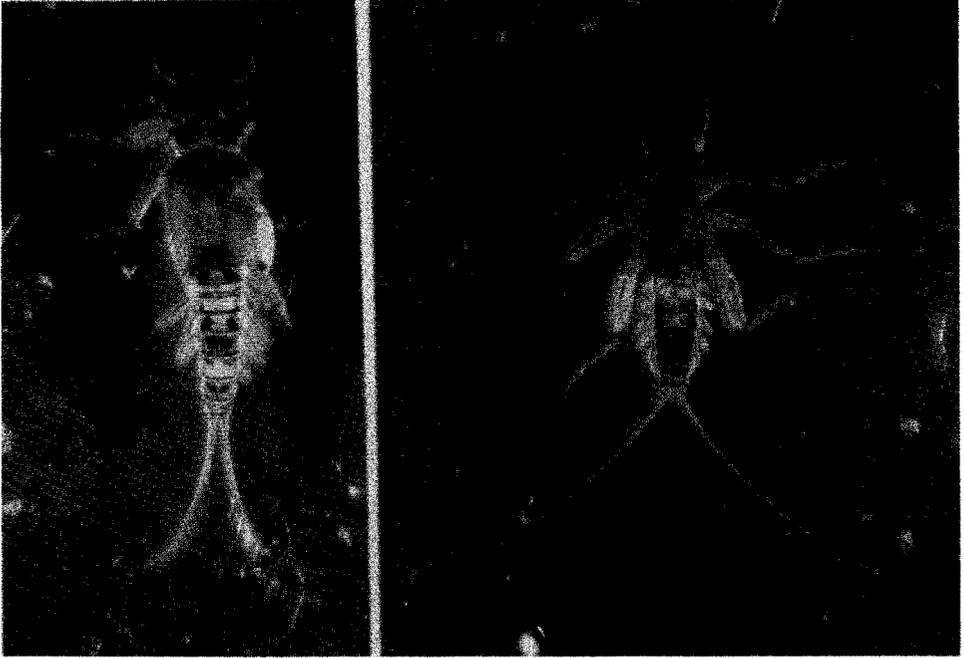


Plate I. Two nymphs from the Usambara Mountains, Tanzania. A. *Afroptilum* (*Afroptiloides*) sp. B. *Tanzaniella spinosa* sp. nov.

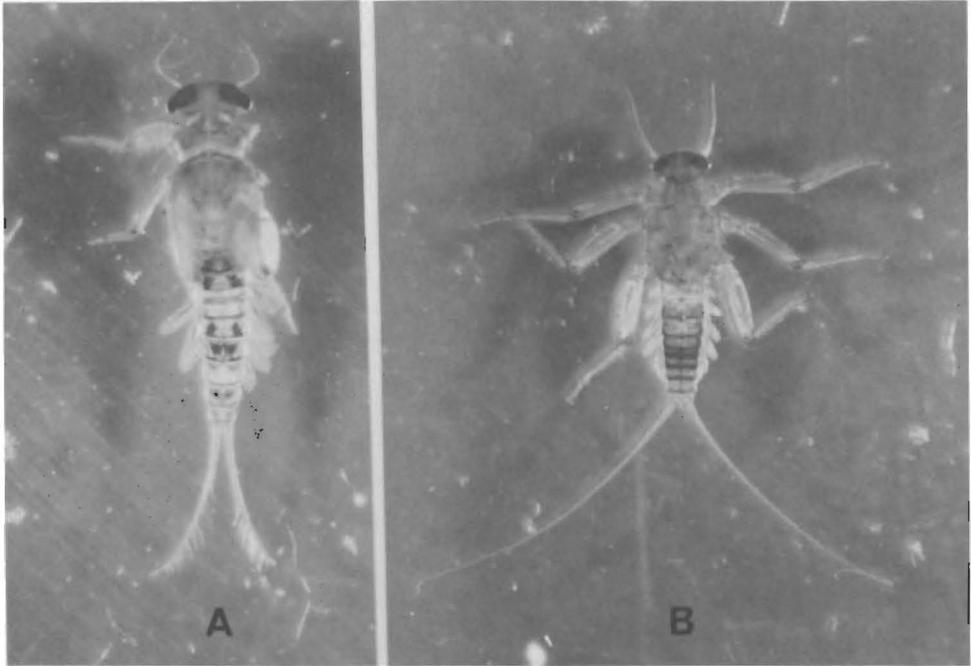


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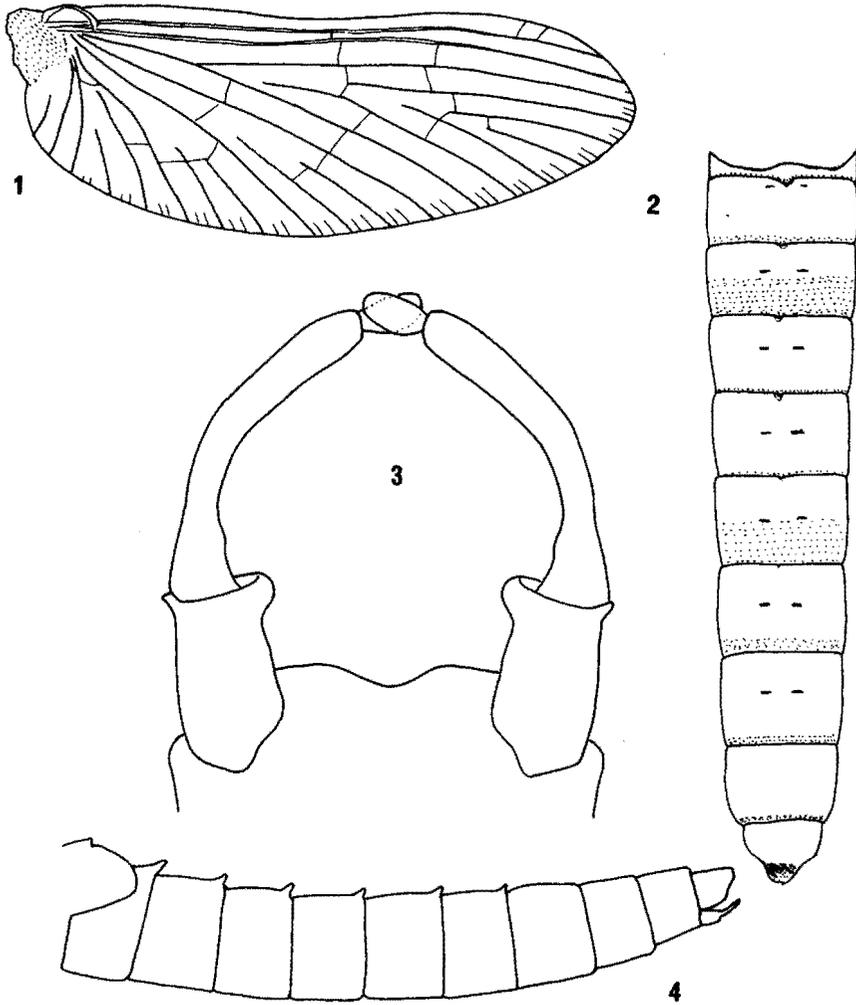


Plate 2, Figs. 1-4. *Tanzaniella spinosa*, male imago. 1. Forewing. 2. Abdominal terga, dorsal view. 3. Genital forceps. 4. Abdomen, lateral view.

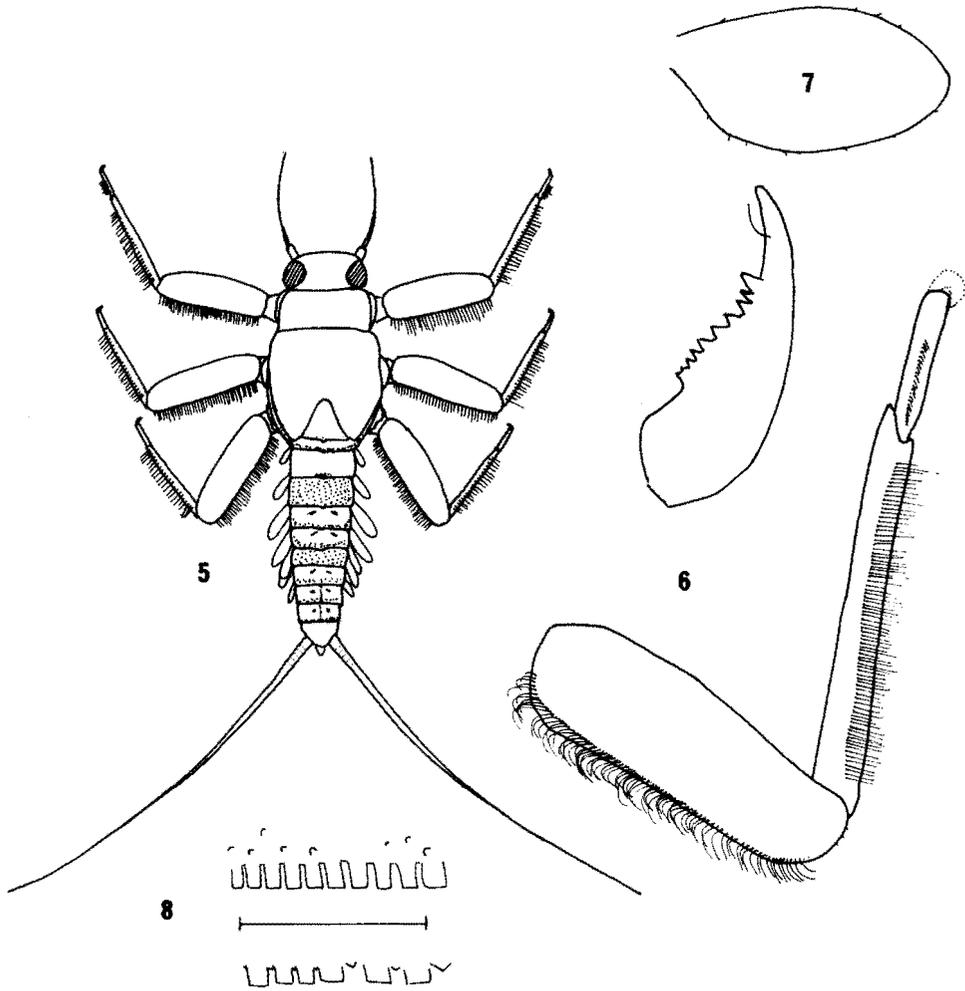


Plate 3, Figs. 5-8. *Tazantella spinosa*, nymph. 5. Mature nymph. 6. Foreleg, inset tarsal claw at higher magnification. 7. Gill lamella. 8. Posterior margins of two abdominal terga. (Scale = 0.1 mm.)

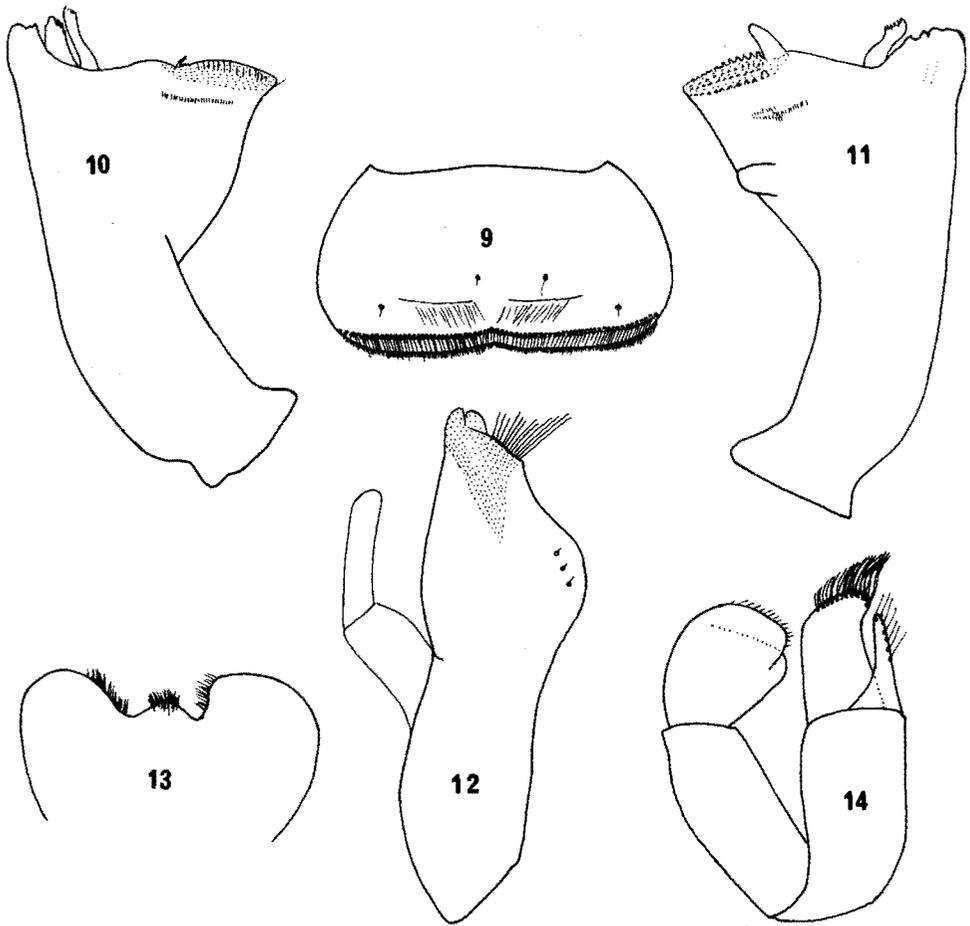


Plate 4, Figs. 9-14. *Tanzaniella spinosa*, mouthparts of nymph. 9. Labrum. 10. Right mandible. 11. Left mandible. 12. Maxilla. 13. Hypopharynx. 14. Labium.

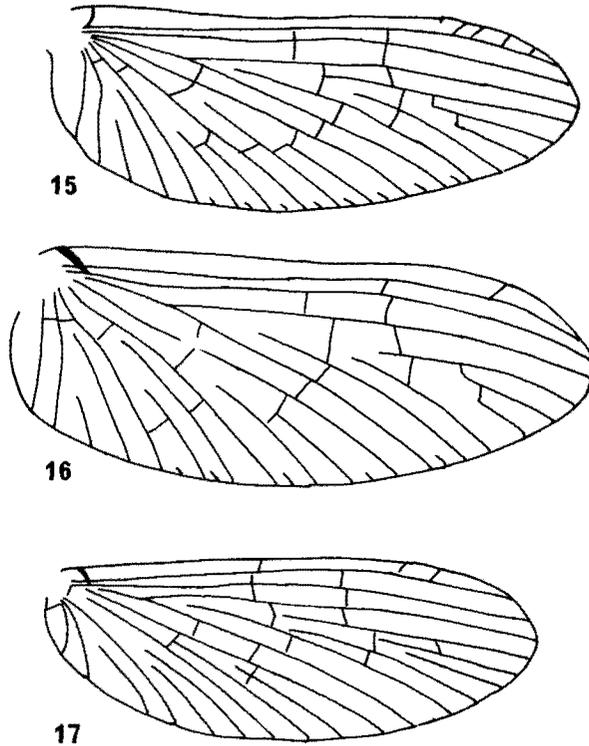


Plate 5, Figs. 15-17. Forewings in African Cloeoninae. 15. *Afrobaetodes pusillus* (Nav.). 16. *Cloeon cylindroculum* Kim. 17. Unknown female from Senegal.

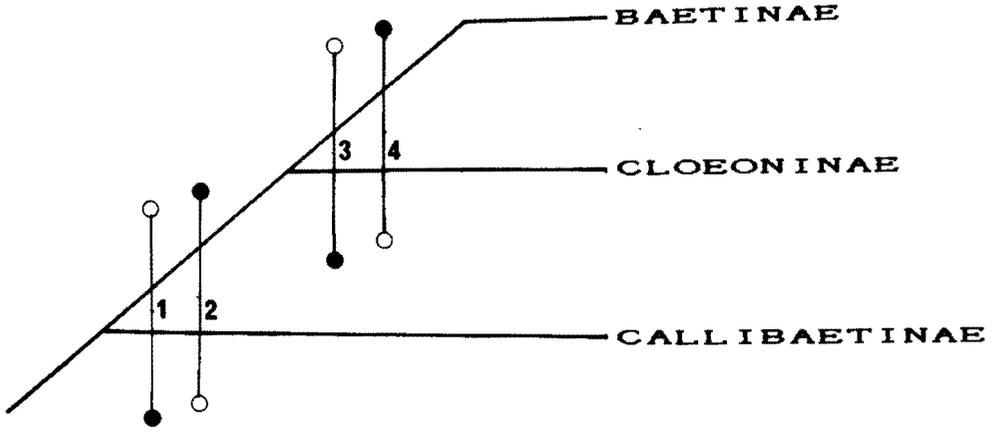


Plate 6, Fig. 18. Phylogenetic relationships of the subfamilies of the Baetidae. The derived character state is indicated by solid circles. Numbers refer to characters listed in Table I.