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The African Ephemeridae (Ephemeroptera)[1]

by

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ABSTRACT

The known African Ephemeridae presently consists of three genera and seven nominal species. Adults and larvae of *Afromera evae* sp. n. are described from The Gambia. The genus *Afromera* is recognized as being distinct from *Ephemera* and is evidently equivalent to the subgenus *Dicrephemera* (of *Ephemera*) which is thus synonymized. Larvae of African Ephemeridae are keyed to genus, and adults are keyed to species. The study of African burrowing mayflies may be advanced by sampling the insect drift of large silt-bottomed rivers for the poorly known larvae. The biogeographical affinities of the Ephemeridae of Africa (south of the Sahara) lie with tropical Asia and not with other southern continents. Evolution and dispersal probably were not affected by continental drift. Ecological differences between *Afromera* and *Ephemera* are predicted to be relatively consistent throughout the Afro-Asian area.

The development of our understanding of the burrowing mayfly fauna of the African continent has been gradual and piecemeal. Several factors have contributed to this slow development. First, systematists studying these mayflies have had limited or no field experience in Africa and have had to rely on small series of specimens scattered in museums throughout the world. Second, there have been very little data available from the important larval stage, since the silt-burrowing forms are rarely sampled. And finally, it has not been until very recently that our knowledge of world diversity and generic affinities was such that the African Ephemeridae could be studied in a broader evolutionary and biogeographical framework.

Eatonica schoutedeni (Navas) was the first species of African Ephemeridae to be described (Navas, 1911). Today this (perhaps largest of mayflies) species is the best known of African burrowers, being widespread throughout much of Africa. The larva of *E. schoutedeni* was supposedly described by Crass (1947); however, this description was in fact that of an *Ephemera* (McCafferty, 1971a), and the true *Eatonica* larva was not described until Demoulin (1968) tentatively assigned a

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larva to *E. schoutedeni*. Subsequent study of this larva by the first author further substantiates it as *Eatonica*, particularly in light of its affinities with the closely related Oriental genus *Eatonigenia* (McCafferty, 1973).

A second species of *Eatonica*, *E. crassi* Mc Cafferty, was recently described from adults from Sudan (McCafferty, 1971a). This species has evidently been confused with *E. schoutedeni* for some time and may be relatively widespread in Africa.

Barnard (1932) described *Ephemera natalensis* from adults from South Africa. This species and *E. schoutedeni* remained the only recognized species of African Ephemeridae until Demoulin (1955) described *Afromera congolana* from Elisabethville as the type species of his new "African" genus, *Afromera* (based on rather weak adult characters only). Demoulin also transferred *natalensis* to *Afromera* at that time.

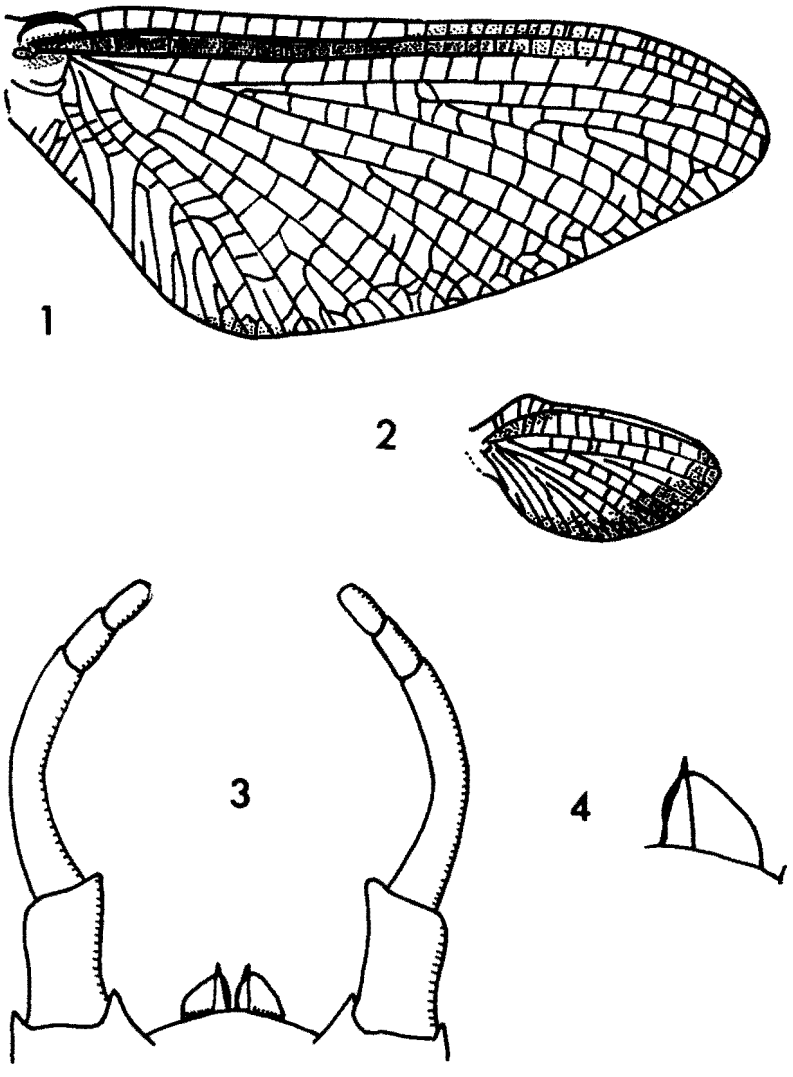
Kimmins (1956) described another species from adults from Uganda: *Afromera aequatorialis* (Kimmins) (originally as *Ephemera*). A key to the adults of the above three species of *Afromera* was given by Demoulin (1970). Larvae of these species, however, remained unknown.

McCafferty (1971a) described a species from South Africa, *Ephemera mooiana*, which was distinct from the three species of *Afromera*. Larvae which had been described by Crass (1947) as *Eatonica* were examined and tentatively assigned to *E. mooiana* by McCafferty. They were clearly *Ephemera* s.s. larvae.

McCafferty and Edmunds (1973) described three subgenera of *Ephemera* based primarily on larval morphology. The subgenus *Dicrephemera* was established for larvae that possessed, among other characteristics, atrophied mandibular tusks (Fig. 8) and an enlarged frontal process. *Dicrephemera* was reported from Thailand, India, and South Africa. The latter distributional record was based on young unnamed larvae. Also, McCafferty and Edmunds (1973) synonymised *Afromera* with *Ephemera* because adult differentiating characters were not believed strong enough to warrant generic status.

McCafferty and Edmunds (1973) indicated that as more larvae from the Ethiopian and Oriental Realms were discovered, they may prove to be *Dicrephemera*. The discovery of a new species (including its associated larvae) from The Gambia is reported herein. Adults of the new species are typical of *Afromera*, and larvae of the new species are typical of *Dicrephemera*. It appears obvious that the genus *Afromera* of Demoulin (which had been based on adults) is equivalent to the subgenus *Dicrephemera* of McCafferty and Edmunds (which had been based on larvae). Although this is a highly probable conclusion, full equivalency of the names cannot be completely confirmed until the larva of the type species of *Afromera*, *A. congolana*, is discovered.

It seems most reasonable at this time to regard *Dicrephemera* as a junior synonym of *Afromera*, and to thus recognize the former type species of *Dicrephemera* as *Afromera siamensis* (Uéno) comb. n. [= *Ephemera (Dicrephemera) siamensis* Uéno], and to recognize the nominal African species as follows:



Figs. 1-4. *Afromera evae* sp. n., adult. 1. Fore wing. 2. Hind wing. 3. Male genitalia. 4. Penis.

Ephemera mooiana McCafferty
Afromera congolana Demoulin
Afromera aequatorialis (Kimmins)
Afromera evae Gillies sp. n.
Afromera natalensis (Barnard)
Eatonica crassi McCafferty
Eatonica schoutedeni (Navas)

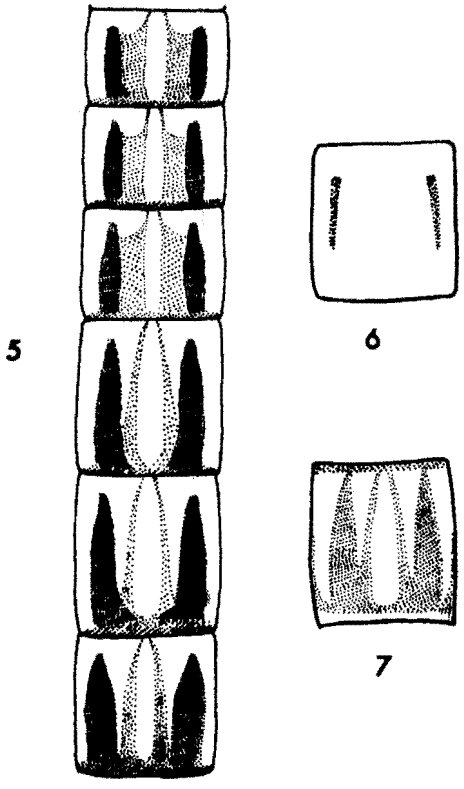
It should be kept in mind that *Afromera* and *Ephemera* are very closely related and that *Afromera* most likely evolved from an *Ephemera* ancestor. Diagnostically the two genera are strongly differentiated as larvae, but may not be as easily differentiated as adults. It remains highly probable that as our knowledge of the burrowing mayfly larvae of tropical Asia increases, the *Afromera* fauna of that area will prove to be much more extensive than is presently recognized. Probable differences in ecological distribution between *Ephemera* and *Afromera* are discussed below under biogeography.

Those characters used by McCafferty and Edmunds (1973) to separate adults of *Dicrephemera* from *Ephemera* s.s. can apparently be used to differentiate the African *Afromera* from *Ephemera* in the same tentative manner. In addition, the fore wings of known *Afromera* are generally slightly narrower than those of most *Ephemera*. All known species of *Afromera* are relatively small for Ephemeridae (adult body length ca. 10-14 mm). It therefore is possible that differentiating wing traits of *Afromera* are related to reductionism, and if so, it would not be surprising to discover some of these traits in the smallest species of *Ephemera*. Of the characters used by Demoulin (1955) to diagnose *Afromera* adults, the only presently reliable one is the shape of the subgenital plate. A complete assessment of adult character differences will require larval-adult associations of many more Afro-Asian *Ephemera* and *Afromera*.

The description and notes on the biology of the new *Afromera* species follow. A key to the known African Ephemeridae is also included herein along with a discussion of the probable geographical origin and ecological distribution of the African Ephemeridae. Authorship of the new species name should be assigned singly to the second author of this paper.

Afromera evae Gillies sp. n. (figs. 1-6,8)

Adult male. Closely resembling *A. aequatoriolis* but differing as follows. Abdominal tergum 1 diffuse purplish brown: terga 2-9 (Fig. 5) cream, each tergum pale anteriorly but with narrow, transverse, dark band at posterior margin, each tergum also with 2 pairs of dark longitudinal markings (narrow submedian pair extending up to anterior margin of segment, and broader, shorter and darker sublateral pair not reaching as far as anterior margin); submedian markings of anterior segments spreading more laterally and blending into darker sublateral markings; tergum 10 brown. Each abdominal sternum with single pair of sublateral dark lines (Fig. 6). Segment 4 of forceps subequal to segment 3.



Figs. 5-7. Adult abdominal markings. 5. *A. evae*, abdominal terga 3-8. 6. *A. evae*, abdominal sternum. 7. *A. aequatorialis*, abdominal tergum 7 (after Kimmins, 1956).

Penes broad, narrowly separated; titillators with more or less straight margins and projecting beyond penes (Fig. 3, 4).

Adult female. Abdominal markings as in male. Contained eggs orange.

Fore wing length. 9 mm.

Larva. Mature length 11-13 mm, caudal filaments 4-4.5 mm. Color pattern of abdomen as in adult although dorsal markings appearing more diffuse. Frontal process deeply bifurcate, not quite twice as long as wide, with slightly rounded lateral margins, and with apices of forks slightly upturned. Labrum slightly emarginate medially. Head with distinct dark brown bar extending between lateral ocelli and pair of lighter brown patches between eyes. Pronotum with pairs of triangular shaped brown patches separated approximately by width of patch.

Branches of rudimentary gills of abdominal segment 1 slender and nearly equal in size and shape.

Type material. Adult male holotype: The Gambia, Wali Kunda (13°34'N, 14°57'W), viii-1973; deposited in the British Museum (Natural History). Paratypes: 19 adult males, 3 adult females, 29 subimagines, and 4 larvae (3 exuviae), same locality and Bansang (13°26'N, 14°40'W) (collected by P. Goll).

Remarks. For the adults, the abdominal markings, penes of the male, and smaller size serve to distinguish this species from *A. aequatorialis.* In particular, the pale base and dark apex of each abdominal tergum are good diagnostic features.

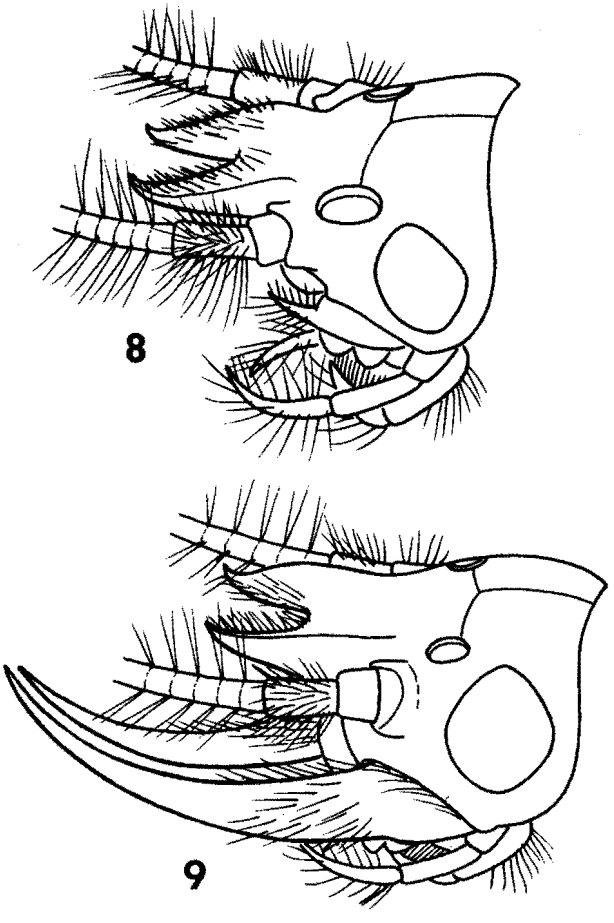
With the exception of one specimen, Kimmins' (1956) material of *A. aequatorialis* came from Lake Victoria. Examination of this material has indicated that they correspond closely with the published description. However, there is a single specimen from Njala, Sierra Leone, which, although pinned and dried, is clearly the same as the Gambian material described herein. This specimen is accordingly referred to *A. evae,* which thus appears to replace *aequatorialis* in West Africa. Specimens in the British Museum of *A. natalensis* from Lake Nyasa and of problably the same species from Ukara Island in Lake Victoria, collected by Dr. A. Smith, were also examined.

Although adults of *A. evae* were not reared from larvae, the larval abdominal markings are well developed and allowed adults to be confidently associated with larvae. A number of adults were collected at a light-trap at the same locality and time that the larval stage was taken.

The larvae of *A. evae* differ from those of *A. siamensis* (described from Thailand by McCafferty and Edmunds, 1973) in a number of respects. First, the mature larvae of *A. evae* are somewhat smaller in size. Second, the frontal process of the African species is not as narrow-elongate as it is in *siamensis.* Third, the transverse band of the head of *evae* is more striking; and fourth, the rudimentary gills of abdominal segment 1 of *evae* have both branches quite similar, while the branches of the gill 1 of *siamensis* are very dissimilar in size and shape.

Biology of A. evae. Adults have been caught occasionally at lights at the type locality, Wali Kunda, some 260 km up the River Gambia from the ocean. The river at this point is close to a kilometer wide, and it is perhaps not surprising that attempts to collect larvae in small samples of mud dredged from the bottom of the river were unsuccessful. However, it was later found that this mayfly was much more abundant at Bansang, some 40 km above Wali Kunda, where the river is only 160-250 m wide. At both localities the river is tidal with a twice daily rise and fall of about one meter, and its substrate is composed of a deep layer of fine silt.

Since sampling the drift of large rivers in North America had been productive for capturing burrowing mayflies, it seemed that the use of drift nets could be an effective method for collecting in the River Gambia. This proved impractical because of the periodic reversal of the flow direction with the change in tides. The problem was solved by fixing a series of nets to a boom balanced across the bows of a fisherman's dugout canoe, with the nets arranged so that they just dipped



Figs. 8-9. Larval heads. 8. *Afromera evae*. 9. *Ephemera mooiana* (?).

below the surface of the water. In the course of two evenings' trolling at dusk in this somewhat precarious manner, a small number of *Afromera* larval skins together with a live immature larva were collected.

The subimagines hatch from the water at dusk and adults emerge during the course of the night. Male adults can sometimes be found in the daytime resting in relatively exposed situations, for example, on the shining metal walls of a prefabricated hut. They rest with their tails held close together and firmly appressed against the surface of their perch, while the whole body is tilted over to one side. This habitus would appear to provide support against dislodgement by the wind.

Key to the African Ephemeridae

Larvae

1. Frontal process of head obtuse, never bifurcate ..... *Eatonica*

   Frontal process large and bifurcate (Figs. 8, 9) 2

2. Mandibular tusks well developed and projecting anteriorly beyond frontal process (Fig. 9) ..... *Ephemera*

   Tusks greatly reduced and not discernible from above (Fig. 8) ..... *Afromera*

Adults

1. Males with rudimentary median caudal filament and 3-segmented genital forceps; females and males with vein MP_2 of hind wings attached to vein MP_1 basally and free from vein CuA ..... *Eatonica*, 2

   Males with well developed median caudal filament and 4-segmented genital forceps (Fig. 3); females and males with vein MP_2 of hind wings not attached to MP_1 basally and either free basally (Fig. 2) or often attached basally to vein CuA 3

2. Males with rounded penes lacking acute lateral projections; dorsal stripes of abdomen straight to somewhat concave medially at each tergum ..... *Eatonica crassi*

   Males with rounded penes possessing small sharp lateral projections near the apices; dorsal stripes of abdomen somewhat convex medially at each abdominal tergum..... *Eatonica schoutedeni*

3. Fore wing longer than 16 mm and with MP_2 originating basally from CuA; males with forceps bases only slightly projected beyond posterior margin of subgenital plate; males with pair of continuous dorsal longitudinal (sometimes faint) stripes along abdomen . . *Ephemera mooiana*

   Fore wing less than 15 mm long and with MP_2 usuallly attached at its base to MP_1 (Fig. 1); males with forceps bases protruding somewhat beyond median posterior margin of subgenital plate, often giving appearance of emarginate subgenital plate; abdominal color pattern variable ..... *Afromera*, 4

4. Abdominal sterna 1-8 unmarked[2] ..... *Afromera natalensis*

   Abdominal sterna 1-8 with some dark markings 5

5. Abdominal terga 2-9 each with single pair of sublateral dark lines ..... *Afromera congolana*

   Abdominal terga 2-9 with both submedian and sublateral markings (Fig. 5) 6

6. Abdominal terga each pale anteriorly but with narrow dark band at posterior margin (Fig. 5) ..... *Afromera evae*

   Abdominal terga each with narrow dark band at anterior margin and pale at posterior margin (Fig. 7) ..... *Afromera aequatorialis*

[2] According to Demoulin (1970).

BIOGEOGRAPHY

The faunal affinities of African[3] Ephemeridae undoubtedly are with tropical Asia including the Indian subcontinent. Whether this affinity was a result of post-Gondwana dispersal or was mediated by continental drift can only be suggested from phyletic relationships and known distributions of extant Ephemeridae. On these bases, the former theory is much more tenable at this time.

Ephemera is a large and diverse genus, and is known from southern Africa, tropical Asia, and throughout the Holarctic. *Afromera* was most likely derived from an *Ephemera* or at least an *Ephemera*-like ancestor, and *Afromera* occurs exclusively in Africa and tropical Asia. *Eatonica* is a highly derived genus which is indigenous to Africa but very closely related to the genus *Eatonigenia* which is found in tropical Asia. The common ancestor of these latter sister genera was probably *Eatonigenia*-like or *Litobrancha*-like. *Litobrancha* is presently Nearctic and possibly eastern Palearctic (McCafferty, 1973).

The African species of Ephemeridae all appear to be relatively highly derived, including *Ephemera mooiana. Afromera, Eatonica, Eatonigenia,* and *Ephemera mooiana* are restricted to the Ethiopian and/or Oriental Realms. On the other hand, ancestral genera or congeners which were likely to have produced the immediate forebears of this fauna are distributed in the northern continents and conspicuously absent from Neotropical and Australian Realms.

All of the above leads to the conclusion that the present African Ephemeridae or their recent ancestors were derived from Asian or Afro-Asian Ephemeridae. Furthermore, recent ephemerid stocks appear to have reached Africa via the Oriental Realm, most likely after the Indian subcontinent had become connected with the Asian mainland.

There is no phyletic or distributional evidence of the family Ephemeridae having been affected by continental drift. This does not, however, rule out the possibility of other families of Ephemeroidea having been distributed in the Southern Hemisphere via continental drift.

Observations on the ecological distribution of *Afromera* and *Ephemera* are interesting and may tend to support the present generic classification as well as have important biogeographic implications as follows:

The derived genus *Afromera* appears to be specially adapted to perennially warm waters and silt substrates. *Afromera* habitats (including warm lentic environments as well as typical potamon[4] lotic environments) clearly support this conclusion. Known larval habitats of the relatively more ancestral and diverse genus *Ephemera* include waters which are not perennially warm and substrates of sand, sand-gravel, and sand-silt (Mc Cafferty, 1975). *Ephemera,* therefore, is more typical of middle and lower rhithron (and perhaps some upper potamon) environments as well as cold lakes with sufficient wave action.

[3] Our discussion of Africa is applicable to the Ethiopian or Afrotropical Region only. That fauna north of the Sahara is expected to be Palearctic in affinity (if indeed Ephemeridae occur, for example, in the large rivers of Morocco).

[4] Lotic zonation terminology is used in a general sense and after Illies and Botosaneanu (1963).

On the bases of habitat data from North America and Europe and preliminary data from the Afro-Asia area and from biogeographic patterns, it can be hypothesized that habitat preferenda of *Ephemera* and *Afromera* remain relatively distinct and for the most part are generically valid. It appears possible that much of what has been called *Ephemera* (based on adults only) in southern and lowland Asia will prove to be *Afromera,* while actual *Ephemera* may be found in temperate Asia and highlands of tropical Asia. The study of larvae from the Afro-Asian area will be the real test of this hypothesis. Furthermore, if the hypothesis is correct, it may help explain *Ephemera*'s restriction in the Ethiopian Realm to South Africa and its absence from the Neotropics.

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