The African Ephemeridae
(Ephemeroptera)²

by

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ABSTRACT

The known African Ephemeridae presently consist of three genera and seven nominal species. Adults and larvae of *Afroneura* were collected near the Gambia. The genus *Afroneura* is recognized as being distinct from *Ephemera* and is evidently equivalent to the subspecies *Dcypephemerus* (Ephemera) which is the type species. 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, cobble-bottomed rivers in the poorly known savannah. 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 *Afroneura* and *Ephemera* are not consistently 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 silk-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 schoonderli* (Navas) was the first species of African Ephemeridae to be described (Navas, 1911). Today this (perhaps largest of mayflies) species is the best-known African burrower, being widespread throughout much of Africa. The larva of *E. schoonderli* 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 a³

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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 *Eatonogonia* (McCafferty, 1973).

A second species of *Eatonica*, *E. crassus* 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 *Ephemera* 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 aquatorialis* (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 moziana*, 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. moziana* by McCafferty. They were clearly *Ephemera* s.l. larvae.

McCafferty and Edmunds (1973) described three subgenera of *Ephemera* based primarily on larval morphology. The subgenus *DiscrepHEMA* was established for larvae that possessed, among other characteristics, atrophied mandibular teeth (Fig. 8) and an enlarged frontal process. *DiscrepHEMA* was reported from Thailand, India, and South Africa. The latter distributional record was based on young unnamed larvae. Ako, McCafferty and Edmunds (1973) synonymized *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 *DiscrepHEMA*. 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 *DiscrepHEMA*. It appears obvious that the genus *Afromera* of Demoulin (which had been based on adults) is equivalent to the subgenus *DiscrepHEMA* 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 *DiscrepHEMA* as *Afromera siamensis* (Üehara) comb. n. [= *Ephemera* (*DiscrepHEMA*) *siamensis* Üehara], and to recognize the nominal African species as follows:
Ephemera muciana McCafferty
Afromera congolana Demoulin
Afromera aquatorialis (Kimmins)
Afromera evae Gillies sp. n.
Afromera natalensis (Barnard)
Eutonica crassii McCafferty
Eutonica schouledeni (Navas)

It should be kept in mind that Afromera and Ephemerae 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 (1972) to separate adults of Dierepimerae from Ephemerae s.s. can apparently be used to differentiate the African Afromerae from Ephemerae in the same tentative manner. In addition, the fore wings of known Afromerae are generally slightly narrower than those of most Ephemerae. All known species of Afromerae are relatively small for Ephemereae (adult body length ca. 16-14 mm). It is therefore possible that differentiating wing traits of Afromerae will lead to reductionism, and if so, it would not be surprising to discover some of these traits in the smallest species of Ephemerae. Of the characters used by Demoulin (1955) to diagnose Afromerae 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 Ephemerae and Afromerae.

The description and notes on the biology of the new Afromerae species follow. A key to the known African Ephemereae is also included herein along with a discussion of the probable geographical origin and ecological distribution of the African Ephemereae. 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. sequatorialis 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 forelegs subequal to segment 3.
Fig. 5-7. Adult abdominal markings. 5. A. euce abdominal/tergum. 6. A. euce abdominal/sternum. 7. A. aequa abdominal/tergum (after Kinnear, 1958).

Penes broad, narrowly separated; stimulators 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. Maxite 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. Prothorax with pairs of triangular shaped brown patches separated approximately by width of patch.
Branches of rudimentary gills of abdominal segment 1 slimmer and nearly equal in size and shape.

Type material: Adult male holotype: The Gambia, Wali Kunda (12°30′N, 15°57′W), viii, 1973; deposited in the British Museum (Natural History). Paratypes: 1 adult male, 28 subimagoes, and 4 larvae (1 of which is a paratype) kept at Bangong (13°30′N, 15°40′W) collected by P. God."

Remarks. For the adults, the abdominal markings, petals of the mouth, and smaller size serve to distinguish this species from A. aquatorialis. In particular, the pale base and dark apex of each abdominal segment are good diagnostic features.

With the exception of one specimen, Kimmins' (1956) material of A. aquatorialis 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 Nyala, 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 A. aquatorialis in West Africa. Specimens in the British Museum of A. marinae from Lake Nyanza and of probably 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 were 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 Mc-Cafferty and Emmans, 1973) in a number of respects. First, the mature larvae of A. evae are somewhat smaller in size. Second, the fronsal 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 at mud dredged from the bottom of the river were unsuccessful. However, it was later found that this flyfly was much more abundant at Bamang, 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 A. evae in the River Gambia. The proved unpractical because of the periodic reversal of the flow direction with the change of 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
below the surface of the water. In the course of two evenings’ trawling at dusk, in
this somewhat precarious manner, a small number of Aprosore larval skins
together with 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 stinging nettle walls of a
prefabricated nest. They rest with their tails held close together and firmly
pressed 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. Frntal process of head oblate, never bifurcate
   ............ Etonica ............ 2
   Frntal process large and bifurcate (Figs. 8, 9) ............ 2

2. Mandibular tusks well developed and projecting anteriorly
   beyond frontal process (Fig. 9) ............ Ephemerina
   Tusks greatly reduced and not discernible from above (Fig. 8) ............ Afromera

Adults

1. Males with ra incompetnt median caudal filament and 3-segmented genital forcip; females and males with one MP of hind wings attached to vein MP, basally and free from vein CuA ......... Etonica, 2

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

2. Males with rounded pens lacking acute lateral projections; dorsal strips of abdomen not right to somewhat concave medially at each tergum ......... Etonica creta
   Males with rounded pens possessing small sharp lateral projections near the apex; dorsal strips of abdomen somewhat convex medially at each abdominal tergum ......... Etonica scarabaeina

3. Fore wing longer than 18 mm and with MP, originating basally from CuA; males with forcip bases only slightly projected beyond posterior margin of subgenital plate; males with pair of continuous dorsal longitudinal (sometimes faint) stripes along abdomen ......... Afromera manolai
   Fore wing less than 15 mm long and with MP, usually attached at its base to MP (Fig. 1); males with forcip bases protruding somewhat beyond median posterior margin of subgenital plate, often giving appearance of exargnate subgenital plate; abdominal color pattern variable ......... Afromera scarabaeina

4. Abdominal sternum 1-8 unmarked ......... Afromera manolai
   Abdominal sternum 1-8 with some dark markings ............ 5

5. Abdominal terga 2-9 each with single pair of submedian dark lines ......... Afromera confusa
   Abdominal terga 2-9 each with both submedian and sublateral markings (Fig. 5) ............ 6

6. Abdominal terga each with anteriorly but with narrow dark band at posterior margin (Fig. 5) ......... Afromera scarabaeina
   Abdominal terga each with narrow dark bands anterior margin and pair at posterior margin (Fig. 7) ............ Afromera anapustulata

* According to Derooifin (1970).
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B. GEOGRAPHY

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

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

The African species of Ephemeridae all appear to be relatively highly derived, including Ephemeromorpha, Afromera, Eatoecia, Eatoecia, and Ephemeromorpha 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 ephemeditid 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 Ephemeridae having been distributed in the Southern Hemisphere via continental drift.

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

Afromera appears to be specially adapted to permanently warm waters and substrates. Afromera habitats (including warm lentic environments as well as typical eutrophic environments) clearly support this conclusion. Known larval habitats of the relatively more ancestral and diverse genus Ephemerida include waters which are somewhat warmer and characterized by a substrate of sand, sand-gravel, and sand-silt (McCafferty, 1975). Ephemerida, therefore, is more typical of middle and lower alitron (and perhaps some upper peramol) environments as well as cold lakes with sufficient wave action.

Our discussion of Africa is applicable to the Ethiopian or Afrotropical Region only. Thus (area north of the Sahara is assumed to be Palaearctic in affinity if indeed Ephemeridae occur, for example, in the large river of Montecito.

Lotication terminology is used in a general sense and after Ilaea and Bontanerean (1963).
On the bases of habitat data from North America and Europe and preliminary data from the Afro-Asian area and from biogeographic patterns, it can be hypothesized that habitat preferenda of Ephemer a and A f romera remain relatively distinct and for the most part are genetically valid. It appears possible that much of what has been called Ephemer a (based on adults only) in southern and lowland Asia will prove to be A f romera, while actual Ephemer a may be found in temperate Asia and highlands of tropica-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 Ephemer a's restriction in the Ethiopian Realm to South Africa and its absence from the Neotropics.

LITERATURE


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