

COLONIZATION OF A PARTHENOGENETIC MAYFLY (CAENIDAE: EPHEMEROPTERA) FROM CENTRAL AFRICA

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ABSTRACT

A new parthenogenetic species of *Caenis* s.l. collected from Gabon, and maintained as a laboratory colony for 3 years in London, is formally described and notes are given on its biology in culture.

INTRODUCTION

In February, 1984, in the course of a survey of the molluscan hosts of human schistosomiasis in Gabon, Central Africa, one of us (RJK) brought some material back to London for further study. The collection included the snails (*Bulinus forskalii*) together with tadpoles (*Leptopleis*) and leaf-litter from the bed of a forest stream. The *Bulinus* were set up as a laboratory colony in enamel dishes, while the tadpoles and detritus were put in an aquarium tank.

When the aquarium was set up a few mayfly nymphs were seen amongst the litter, and a few days later the decomposing bodies of adults were floating on the surface. Several weeks later numerous small nymphs were noticed on the bottom and sides of the tank. They were fed on sycamore (*Acer pseudoplatanus*) leaves and lettuce, and in due course another hatch of adults occurred. The adults were almost exclusively females, and since then a self-perpetuating colony has been maintained.

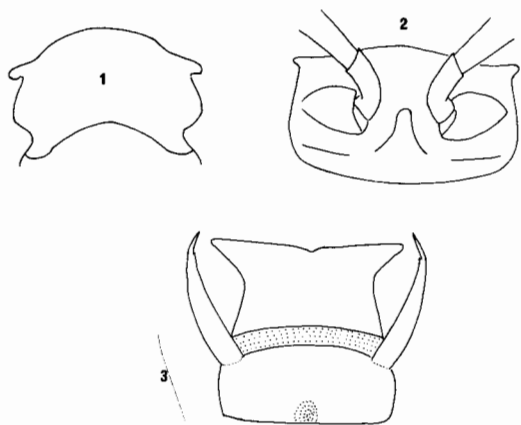
A description of this material follows. Owing to uncertainty as to the validity of some of the genera currently recognised in the Caenidae (Malzacher 1984), this new taxon is placed in the genus *Caenis*. The type, a male subimago mounted on a slide, has been deposited in the British Museum (Natural History).

DESCRIPTION

Caenis knowlesi sp. nov.

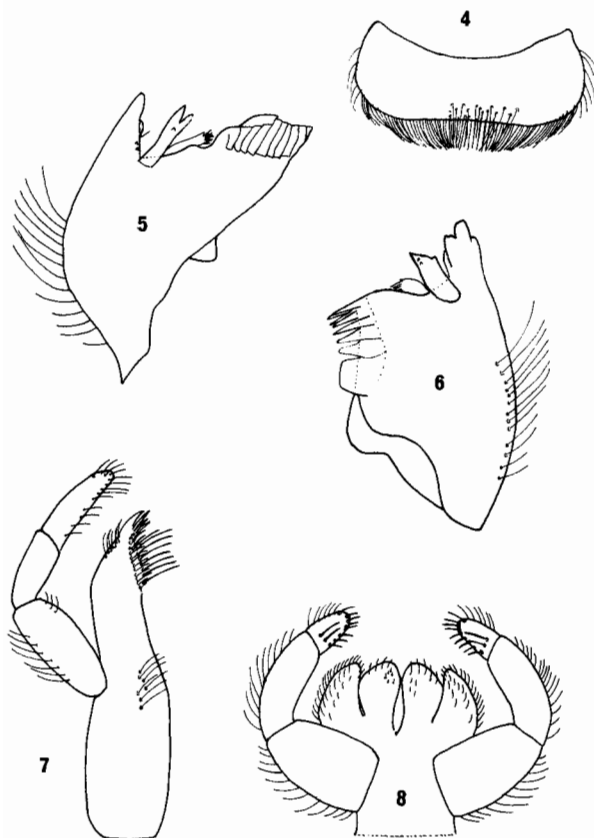
Male subimago. Head and pronotum purplish brown, antennae white, rest of thorax pale brown; antero-lateral margin of pronotum deeply notched before apex to form a blunt process at the corner (Fig. 1); prosternum *ca* 1.6 times as broad as long, coxae separated by a distance about equal to or slightly less than width of coxa (Fig. 2). Fore femur and tibia purplish brown, mid and hind legs cream. Anterior wing veins purple, remainder clear. Abdominal terga I-IX purplish brown, on III-VIII with a median pale interruption, IX with indefinite brown markings, X mostly pale. Tails cream, basal segments tinged with brown. Venter generally pale, antero-median portion of meso- and metasterna purplish brown, lateral margins of abdominal sterna VII-IX purple; posterior angles of V-IX ending as fine points. Terminalia (Fig. 3); forceps purplish brown including terminal process; forceps base narrowly dark posteriorly; penes white.

Female imago. Head and pronotum purplish brown, meso- and metanota pale brown; fore coxae separated by a space equal to three-quarters of width of coxal base. Abdominal terga purplish



Figs 1-3. Adult of *C. knowlesi*. 1. Pronotum of male. 2. Prosternum. 3. Terminalia of male subimago.

brown; sterna cream medially, lateral third purplish brown; basal portion of tails (for a distance about equal to length of IXth and Xth terga combined) deep purplish brown, remainder cream.



Figs 4-8. Mouthparts of *C. knowlesi*. 4. Labrum. 5-6. Right and left mandibles. 7. Maxilla. 8. Labium.

Legs purplish brown, mid and hind legs paler. Costal and subcostal areas of wing semi-opaque, purple; remaining veins purple.

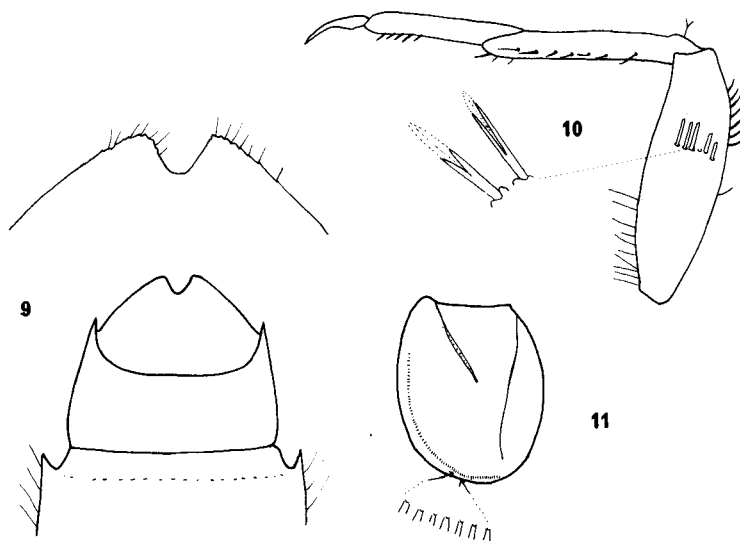
Body. Male 3.5 mm, female 3.0-3.5 mm. Wing: male 2.5 mm, female 2.8 mm. Tails: male (subimago) 2 mm, female 2 mm.

Nymph. General colour dark brown, legs with broad pale bands at apices of all femora, tibiae and tarsi. Mouthparts Figs 4-8. Fore femur (Fig. 10), upper surface with a transverse line of 5-6 broad, blunt, spine-like setae. Underside of gill operculum with a line of single, hair-fine scales (Fig. 11). Subanal plate of abdomen deeply cleft (Fig. 9).

Holotype male subimago, reared in laboratory from material collected in Gabon, Kéri, 12 km east of Lambaréné, ii.84. Numerous female imagines, subimagines and nymphs, same provenance.

The site from which the material was originally collected was an open stretch of an otherwise forested stream, some 90 cm across and 16 cm deep. At the time of the visit the water was very clear and slow-flowing over a substratum of bedrock and gravel. The stream bed was covered with a layer of detritus, composed of twigs and decaying leaves, but there was an absence of macrophytes. The *Caenis* nymphs were presumably concealed in this litter, some of which was brought back to the laboratory along with the snails.

The female of *C. knowlesi* differs from all other described species in the deep brown colour of the base of the tails. On the basis of the terminal process of the male forceps the species falls into the group of *Caenis* s.l. that Thew (1960) treated as *Caenodes* Ulmer. Compared with other Afrotropical members of this group, *knowlesi* differs from *jinjana* Kimmins, *kungu* Eaton and *ulmeri* Kimmins by the form of the penes, and from *hoggarimensis* Grandi by the smooth edge of the forceps base and the abdominal markings. The excision in the antero-lateral margin of the pronotum in *knowlesi* would also seem to be diagnostic.



Figs 9–11. Nymph of *C. knowlesi*. 9. IXth sternum, apical notch at higher magnification shown above. 10. Fore leg. 11. Underside of gill lamella, showing microtricheal band at higher magnification.

BIOLOGY

Parthenogenesis

Only a single male has been identified from several hundred adults reared in the laboratory colony and all the mature nymphs examined. Hatching of eggs and the emergence of nymphs has been observed from egg-batches laid by female imagines, as well as from the bodies of female subimagines trapped by the water surface. Even when dead females are in an advanced stage of decomposition and invasion by saprophytes, the ovaries remain intact and the eggs hatch normally. The ovaries are also ignored by turbellarians, ostracods and browsing snails. Successful hatching can also take place from eggs contained in mature nymphs. When a mature nymph was killed by decapitation, the eggs hatched some 10 days later and viable nymphs emerged. A similar result has been seen when dead or dying last instar nymphs have been isolated.

Development

Fecundity was measured by egg counts in the ovaries of 10 females. Mean clutch size 526, s.d. 151, range 271–755. The time interval between the

death of spent females and the appearance of newly hatched nymphs ranged from 7–10 days in a short series recorded. The hatching rate was high, with the percentage hatched or embryonated between 88.2–99.4%, (mean 93.0%) from the ovaries of 5 females dissected after hatching of the eggs had started. The developmental period was highly variable. For example, eggs which had been dissected out of a spent female hatched a week later. The first adult emerged after 35 days, but emergence continued sporadically over the next two months up to a maximum of 97 days (Fig. 12).

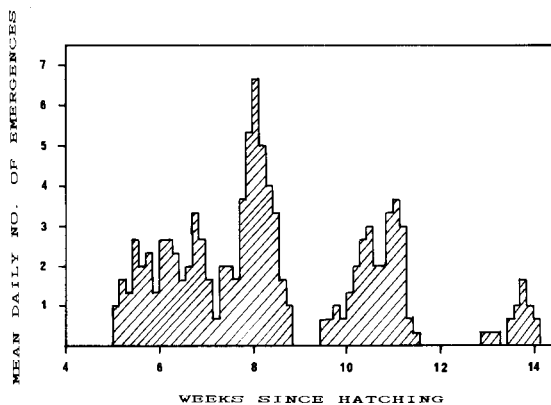


Fig. 12. Diagram to show duration of nymphal life, from hatching of eggs to emergence of adults, in the progeny of a single egg batch.

Culture conditions

Nymphs are reared in shallow dishes in 2–3 cms of water at a constant temperature of 25–26°C and a light regime of 12 h on, 12 h off. The dishes are covered with glass lids to prevent the escape of emerging adults. The arrangement often prevents subimagines escaping from the surface film and may interfere with normal oviposition. However, since full hatching of eggs appears to take place as readily in the decomposing bodies of females as in isolated egg-masses, this is not a problem.

The bodies of emerged female mayflies are placed in water containing the faeces of the snail, *Bulinus*, which have been fed on a diet of sycamore leaves and a blue green alga, *Oscillatoria*. Without this, there is a high mortality of the early instar nymphs although it may lead to contamination of the culture with other organisms, and problems have been encountered with ostracod infestations. Once the nymphs are big enough to be easily seen they are given a diet of air-dried sycamore leaves that have been soaked for a few days in water.

DISCUSSION

Parthenogenesis occurs widely in the Ephemeroptera (Degrange 1960, Mingo 1978, Bergman and Hilsenhoff 1978, Humpesch 1980), with most examples being occasional or accidental parthenogenesis (*sensu* Humpesch 1980). They exhibit a very low hatch rate of unfertilised eggs, and adult populations do not show marked distortions of sex-ratios. Their ecological importance is not clear. In a small minority of cases parthenogenesis is "normal" and obligatory. Males are rare or absent and the hatching rate of eggs is more than 80 percent. An example of the latter type is provided by *Caenis cuniana* from Brazil, in which males were not observed but several consecutive generations were reared in the laboratory (Froelich 1969). *C. knowlesi* is very similar but at least one male has been produced in the culture.

No other examples of obligatory parthenogenesis have yet been reported from the Caenidae.

The adaptive value of parthenogenesis for *C. knowlesi* is not immediately obvious. It inhabits permanent streams in the stable climate of equatorial rain forest so perhaps the answer lies in the stability of the environment. In this situation one would expect genetic variation to be reduced to a minimum, and the evolutionary dead-end of parthenogenesis might well prove to be the most appropriate strategy.

A possible consequence of parthenogenesis is the lesser importance of synchrony in the emergence of adults. Unlike bisexual species, they have no need to aggregate for reproduction, and a steady dribble of emergence should suffice to ensure the survival of the species. This lack of synchrony has been noted for the parthenogenetic species *Cloeon triangulifer* in North America by Gibbs (1977), and our data on *Caenis knowlesi* suggests that the same may apply. However, in at least one non-parthenogenetic tropical caenid, *Tasmanocoenis* in northern Australia, lack of synchrony is well marked (Marchant 1982).

Zimmerman (1957) reported *Caenis nigropunctata* Klapalek, a widely distributed Oriental species, on the oceanic island of Hawaii where its presence was first noticed in 1944, and by 1948 it was said to be abundant. Zimmerman assumed that the insect was introduced by plane from the Western Pacific as an adult, however in view of the extremely short life of adult Caenids, the introduction of an egg-mass or of nymphs with a parthenogenetic strain seems much more likely.

ACKNOWLEDGEMENTS

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