

GILL MOBILITY IN THE BAETIDAE (EPHEMEROPTERA): RESULTS OF A SHORT STUDY IN AFRICA

MICHAEL T. GILLIES

Whitfield, Hamsey, Lewes, Sussex, BN8 5TD, England

Afropitulum was the only genus of Baetidae observed with mobile gills in African streams. Other members of the *Cloeon* group of genera from fast-running water, including *Dicentropitulum*, *Rhithroclaeon*, *Afrobaetodes*, *Centropitiloides* and *Platycloeon* had rigid gills. No gill movements were observed in any species of *Baetis* s.l. No structural features of the gills appear to be correlated with this behaviour. Gill movement is seen as an adaptation by *Afropitulum* to lower current speeds. Mobility of the gills is thought to be the plesiomorphic state.

INTRODUCTION

KLUGE *et al.* (1984) were the first to note that in the family Baetidae gill vibration is confined to the subfamily Cloeninae (referred to here as the *Cloeon*-group of genera). They concluded it had been lost in the subfamily Baetinae (*Baetis*-group of genera). In a later paper, NOVIKOVA & KLUGE (1987) remarked that *Baetis* was sharply differentiated from all members of the *Cloeon*-group genera in which gills are developed as a mean of creating a current of water round the body of the nymph. KLUGE & NOVIKOVA (1992) reaffirmed the taxonomic importance of this character, while noting that in this subfamily *Baetopus* was an exception to the rule.

At first sight this is an exciting and revealing observation. In Europe I have long puzzled over the fact that there was some difference between the general appearance of *Centroptilum luteolum* (MÜLLER) and of species of *Baetis* LEACH that could not be explained in anatomical terms. Now it seems the elusive difference lies in the function of the gills.

A recent visit to East Africa gave me the opportunity to make a short study of this facet of behaviour in certain African genera of Baetidae. Kluge and his co-workers expressed the opinion that it was a taxonomic character at the subfamily level, this being based on their studies of the Palearctic fauna. The object of the present investigation was to test out their thesis in the Afrotropical Region.

METHODS

The site chosen for this study was the River Sigi basin in the Eastern Usambara Mountains of north-east Tanzania in

the vicinity of the research station of Amani. It lies at an altitude of 600-900 m and is fed by a number of streams draining the forested slopes of the surrounding hills. It had the advantage that intermittent studies of the mayfly fauna have been made in the past so that the identity of most taxa could be firmly established. The availability of laboratory facilities was also a great help. The study was limited to a tree-week period during the months of November and December, 1993.

The essential observations were made at the riverside. I collected nymphs with a sweep net and transferred them directly from the holding pan into individual dishes for study under a portable stereomicroscope at a magnification of 20 diameters. The instrument was made up from a pair of Zeiss 8x20 binoculars together with a pair of low-power objectives, the two parts being fitted together when required on a lightweight stand. All the bits can be carried in a camera case and in one's pocket.

Each nymph was watched for three 1-minute periods, separated by 1-minute pauses. When present, gill movement normally consists of alternating periods of vibration and resting. I scored the number of such «episodes» by counting the number of times a new bout of gill movement began during each test period. The results for each specimen were taken as the mean of three counts. They were then transferred into individual tubes for preservation in spirit and later identification. It would obviously have been easier to do the counting in comfort in the laboratory. But no motor transport was available, and the terrain being steep and sometimes precipitous it was seldom possible to get the nymphs back to the Amani labs in a viable condition.

Identification was based on examination on mouthparts and noting the presence or absence of a 1st gill and of hind wing buds. In Africa, the presence of a tuft of setae at the base of prosteca of the right mandible is a reliable key character of the *Cloeon* group of genera (GILLIES, 1991). Gill structure was studied in temporary mounts in glycerine.

RESULTS

The behaviour of 93 live nymphs is shown in Table 1, together with notes on their normal habitat. Fig. 1 depicts the same results graphically. Of the 10 taxa observed, it will be seen

that vibration of the gills was restricted to species of the genus *Afroptilum*. The commonest species was *A. tarsale*, and it will be noted that in 2 out of 34 specimens examined no gill movements were observed during the test period. On the other hand, none of the other 5 genera of the *Cloeon* group showed any similar movements. As would be expected, the same was true of all the *Baetis* s.l. studied.

Details of gill structure are shown in Fig. 2. Two species with mobile gills are illustrated, *A. tarsale* (Fig. 2A) and *A. griseum* (Fig. 2B). It will be seen that there are no obvious structural differences to separate them from most of the other six genera shown (Figs 2D-2I). For instance, the gill lamella of *A. tarsale* (Fig. 2A) is almost identical with that of *Dicentropilum decipiens* (Fig. 2H). Yet, the former has mobile gills and lives in moderate currents, while the latter the gills are rigid and it is found, sometimes abundantly, in the shallow water cascading over the surface of rocks. The nymphs of *Baetis spatulatus* has, like all other known members of the *Baetis* group, rigid gills (Fig. 2D). Their structure, however, is much the

same as in those with mobile gills (Figs 2A, 2B). *Afrobaetodes* (Fig. 2E) has ventrally attached gills and lives in the upper surface of rocks in fast flowing water. Gill surface is much reduced. On the other hand, the opposite development has occurred in *Centroptiloides* (Fig. 2I), which is often found in brushwood caught up in the fastest sections of streams. Both have immobile gills.

In addition to the results detailed here, I must record brief but relevant observations I made on a different fauna in a different part of the world. In the Departamento de Maldonado in Uruguay there is a Baetid nymph that lives in the margins of clear flowing streams. Its habitat is reminiscent of *Centroptilum* in Europe, and, sure enough, from time to time it vibrates its gills. But there the resemblance ends.

Firstly, examination of the mouthparts shows that it belongs to the dominant grouping of Baetidae in South America. Secondly, the vibration of the gills did not take the usual metachronous form (ERIKSEN & MOEUR, 1990), but appeared to be synchronous and highly irregular.

Table 1. Species and numbers of African Baetidae tested for gill mobility.

	Gills mobile		Habitat
	+	-	
<i>Afroptilum tarsale</i> Gil.	32	2	Trailing vegetation, stony or sandy substrate
<i>Afroptilum griseum</i> Gil.	7	0	ditto
<i>Afroptilum</i> sp. (lowland)	1	0	ditto
<i>Afroptilum</i> sp. (highland)	0	2	Stony substrate
<i>Dicentropilum decipiens</i> (Gil.)	0	9	Cascades
<i>Afrobaetodes</i> sp.	0	2	Surface of rocks in torrents
<i>Platycloeon erepens</i> (Gil.)	0	5	Vertical rockface, splash-zone
<i>Rhithrocloeon</i> sp.	0	1	Trailing vegetation, stony substrate
<i>Centroptiloides</i> sp.	0	1	Brushwood in torrents
<i>Baetis</i> s.l. species	0	31	Trailing vegetation, under stones in riffles

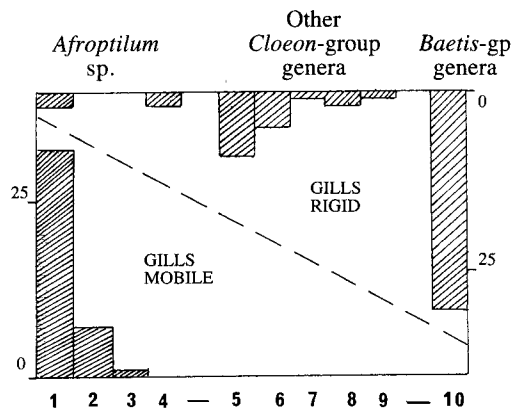


Fig. 1. Numbers of nymphs observed with mobile or rigid gills in 10 taxa of Afrotropical Baetidae. 1: *Afroptilum tarsale*; 2: *A. griseum*; 3: *Afroptilum* sp. lowland; 4: *Afroptilum* sp. highland; 5: *Dicentropilum decipiens*; 6: *Platycloeon erepens*; 7: *Rhithrocloeon* sp.; 8: *Afrobaetodes* sp.; 9: *Centroptiloides* sp.; 10: *Baetis* s.l. sp.

DISCUSSION

In mountain streams in East Africa, *Afroptilum* sp. and *Baetis* s.l. sp. occur together. They are caught in the same sweep of a net, they look much the same, their gills are the same and they can only be reliably distinguished by examining the mouthparts. Yet the one is instantly separable from the other by the rhythmically vibrating gills of *Afroptilum*.

This study has made clear that the behaviour of these Tanzanian species of *Afroptilum* is identical with that of its sister-group, *Centroptilum*, in the Palaearctic. The results confirm the thesis of Kluge and his co-workers that gill mobility is shared by other members of the *Cloeon* group but not by those of the *Baetis* group genera. On the other hand, members of the *Cloeon* group that are adapted to fast-flowing waters have rigid gills as in *Baetis*.

I was unable to establish any correlation between the structure of the gills and their mobility. In contrast to this, NOVIKOVA & KLUGE (1987) described the immobile gills of

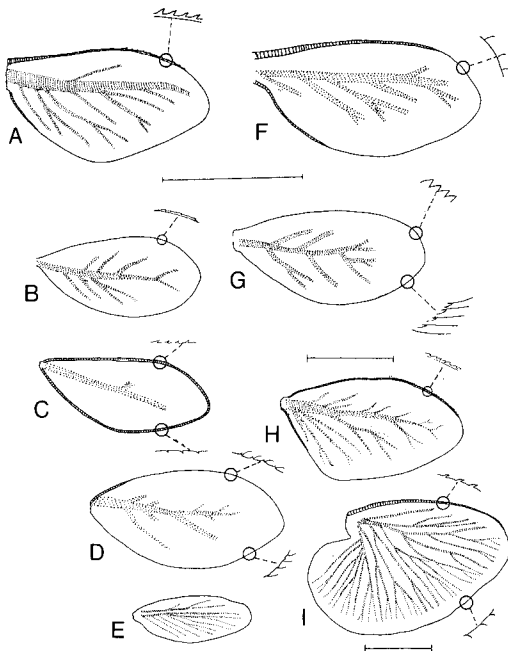


Fig. 2. Gill lamellae of 9 taxa of Afrotropical Baetidae. A: *Afroptilum tarsale*; B: *A. griseum*; C: *A. sudafricanum*; D: *Baetis spatulatus*; E: *Afrobaetodes* sp.; F: *Platycloeon erepens*; G: *Rhithrocloeon* sp.; H: *Dicentroptilum decipiens*; I: *Centroptiloides* sp.

Table 2. Gill mobility in the Baetidae in relation to habitat.

MOBILE GILLS			FIXED GILLS
Ponds	Lakes	Stream margins	Mid stream Torrents
<i>Callibaetis</i> (New World)	-	-	<i>Baetis</i> lineage
<i>Cloeon</i> s.str. (Old World)	<i>Centroptilum</i> lineage	<i>Centroptilum</i> lineage	<i>Centroptiloides</i> + other lotic genera

the *Baetis* group as bordered on all sides with sclerotised ribs. In the African species of *Baetis* s.l. that I studied, the thickening («ribs») was confined to the basal part of the anterior margin only. The same is true of most members of the *Cloeon* group, whether they have rigid or mobile gills.

Fossil evidence suggests that the ancestral forms of the Siphonuroidea were inhabitants of lakes or slow-moving waters (SINITSHENKOVA, 1984). Recent forms of the superfamily have mobile gills, and it seems possible that the same was true of their predecessors from the Mesozoic. With the appearance of the Heptagenioidea and their invasion of flowing-water habitats (McCAFFERTY, 1991), it no longer remained obligatory for nymphs to invest supplementary movements. In the case of the Baetidae, one can postulate that they first moved out of the lakes into the side of streams, a habitat still used by *Centroptilum* and *Procloeon* today. The second step would have been into the main torrents, where it would have been the *Baetis* group that first abandoned the brackwaters and at the same time lost the ability to vibrate their gills (Table 2).

The same sequence of events occurred in those members of the *Cloeon* group lineage that invaded torrents and acquired fixed gills, among them the big, carnivorous nymphs of *Centroptiloides* in Africa. Thus one can regard mobile gills that are capable of metachronous movement, as the plesiomorphic state. On the other hand, it is tempting to suggest that in South America the development of synchronous gill movements in a member of the *Baetis* group lineage may have been a secondary development after it had moved back into the sides of streams.

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