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Notes on the biology of the mayfly *Povilla adusta* in West Africa

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(With 9 figures in the text)

A study of the mayfly *Povilla adusta* Navas in five West African lakes showed at least one population (in Barombi Mbo) with a clear lunar periodicity of emergence, and at least one without, at Kainji Lake. The seasonal distribution of *Povilla* eggs in fish stomachs at Kainji implies a delayed effect of lake level on adult numbers. The relatively small size and short generation time (probably three months) of *Povilla* in Barombi Mbo, by comparison with the same species in Lake Victoria, may be related to the higher temperature of Barombi Mbo. The eggs of bdelloid rotifers were found attached to *Povilla* larvae from some of the lakes.

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Introduction

Larvae of the mayfly *Povilla adusta* Navás (Fig. 1) are abundant in many African lakes, and Petr (1970) showed that as algal filter-feeders, themselves eaten by fishes, they played an important part in the conversion of algae into fish protein in Volta Lake in Ghana. The species shows a striking lunar periodicity of adult emergence in Lake Victoria (Hartland-Rowe, 1955), but analysis of scattered records from other East African lakes (Hartland-Rowe, 1958) and from Volta Lake (Petr, 1970) did not indicate such periodicity elsewhere. The close synchronisation of emergence in Lake Victoria enabled Corbet (1957) to infer, from length-frequency analysis of larval mandibles, a probable generation time of four or five months. In this paper we report observations made in 1970 to 1972 in West Africa, in crater lakes in Cameroon and at Kainji Lake in Nigeria. The degree of synchronisation of emergence of *Povilla* there varied with season and locality, and at least

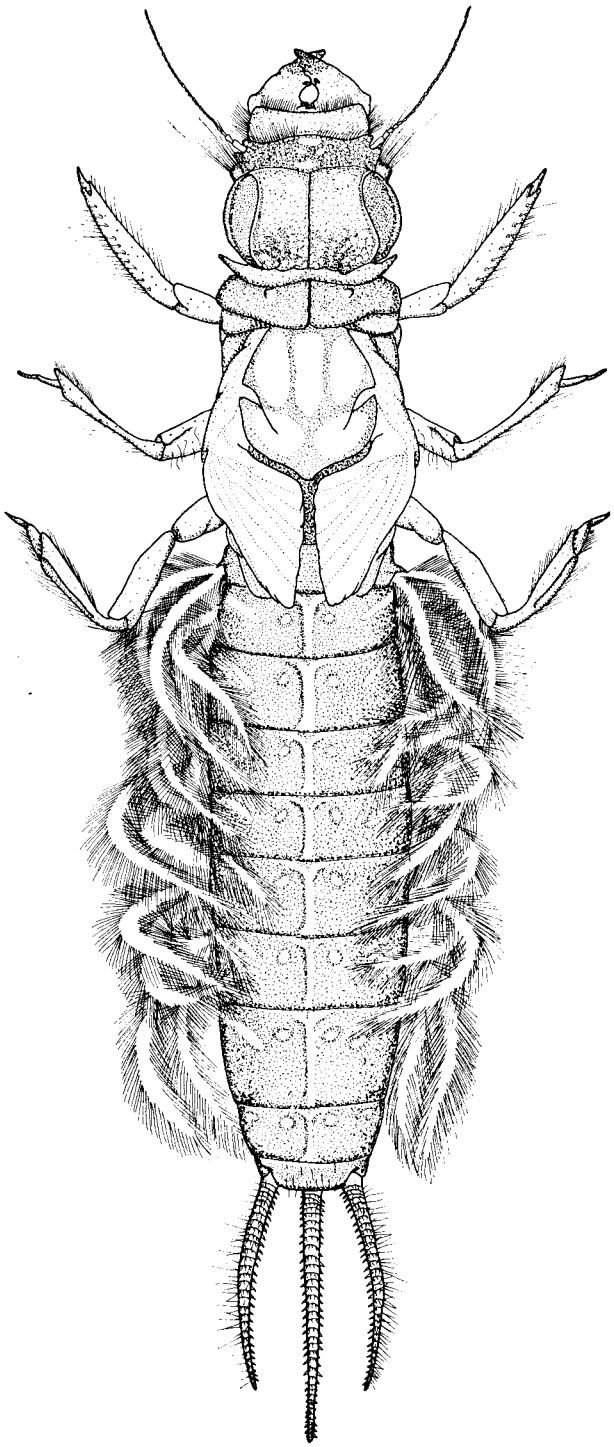

FIG. 1. A final-instar female larva of *Povilla adusta* from Barombi Mbo, 15 mm long, drawn by Diana Harding.

one population, in Barombi Mbo, showed synchronised emergence with a lunar periodicity like that in Lake Victoria. Length-frequency analysis of larvae from Barombi Mbo indicated that the generation time there was commonly shorter than it was in the cooler Lake Victoria. Bdelloid rotifers were found living on the larvae of *Povilla*, and the relationship between the larvae and the rotifers is also discussed.

Periodicity of emergence

In Lake Victoria emergence is confined to a brief period in the evening (about 7.30 p.m. to 8.30 p.m. East African Standard Time, Hartland-Rowe, 1958) and the adults live only about an hour. In Barombi Mbo dead adults floating on the water are quickly removed,

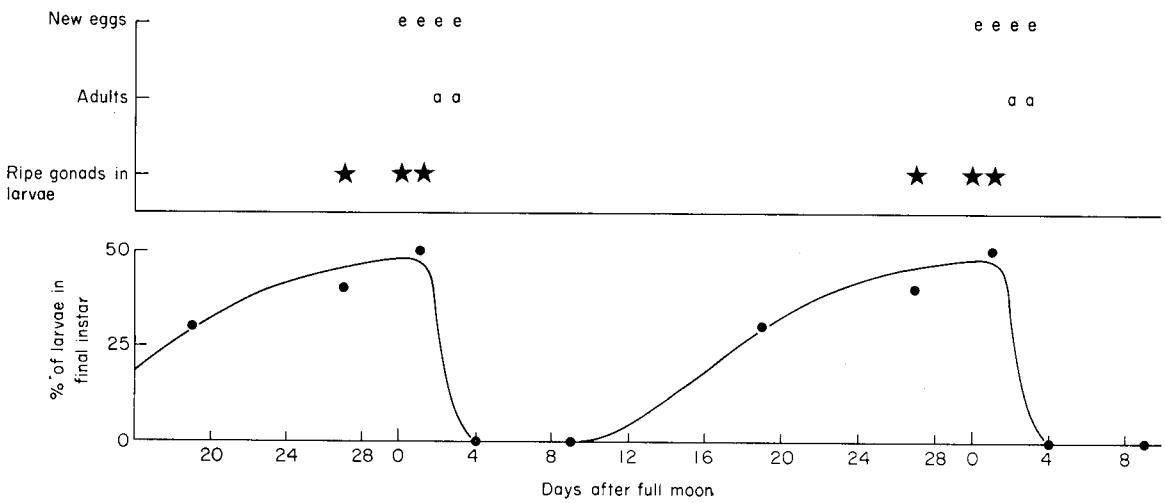

FIG. 2. The periodicity of development of *Povilla* in Barombi Mbo in relation to the phases of the moon. Because the sampling method favoured larger larvae, final-instar larvae probably form a greater percentage of the sample (lower graph) than of the whole population. Sample sizes are given in the legend for Fig. 6.

probably by feeding fishes. In the absence of continuous observation for any lake except Kainji, our evidence about the dates of emergence depends on observations of mass emergences, on the finding of dead adults or of newly-laid eggs, in the lake or in the stomachs of fishes, and on the analysis of stages of development of larvae.

Barombi Mbo (9°22′E, 4°38′N)

Barombi Mbo is a clear crater lake about 2·5 km across and up to 110 m deep, with steep banks clothed in forest (Trewavas, Green & Corbet, 1972). The tunnels of *Povilla* larvae are abundant in the numerous fallen trunks and branches in the shallow water around the edge of the lake. During March and April in 1970 and 1972 we spent a total of 52 days at Barombi Mbo, spanning all days of the lunar month. Although the study of *Povilla* was not our main concern, almost daily visits to the lake made it possible to date emergences fairly accurately from the appearance of newly-laid eggs and of dead adults found floating on the lake the morning after a mass emergence. Figure 2 shows the observations recorded for Mbo in 1970. In 1972 we saw no evidence for adults or new eggs

during a 19-day period from five to 24 days after full moon. It is clear from Fig. 2 that most adults emerged during the four days after full moon. This conclusion receives support from analysis of samples of larvae taken from wood. No final-instar larvae were found in samples taken four or nine days after full moon, but the proportion of final-instar larvae was high just before and at full moon.

Lake Soden (9°17′E, 4°45′N), *Lake Kotto and Mboandong* (9°16′E, 4°27′N)

The three other crater lakes in Cameroon were visited less often than Barombi Mbo; Table I shows the timing of the visits in relation to the lunar month, and the records of eggs and adults of *Povilla*.

TABLE I

The timing in relation to full moon of: v, our visits; a, visits on which we found adults of ***Povilla;*** *e, newly-laid egg masses; and (e), egg-masses of unknown age, at Lakes Kotto and Soden and Mboandong*

	Days after full moon																
Lake	0	2	4	6	8	10	12	14	16	18	20	22	24	26	28	30	
Mboandong						v (e)			v	v							
Kotto	v	v v a	v v		v	v	v (e)	v	v (e)	v	v	v	v	v	v a	v	v				v	v
Soden	v	v e	v e	v	v	v										v	v

Lake Soden is a clear, steep-sided crater lake about 1·25 km across and 80 m deep; Dr John Griffith set gill nets each night, and he found numerous egg masses of *Povilla* on them on the second and third nights after full moon. The periodicity of emergence of *Povilla* there may be similar to that at Barombi Mbo.

Lake Kotto and the nearby lake called Mboandong are both shallow lakes with turbid water. Lake Kotto is about 2 km across and up to 6 m deep; Mboandong is about 400 m across and up to 5 m deep (Corbet, Green, Griffith & Betney, 1973). The finding at Kotto of a few adults on the 19th day after full moon, and of egg masses in the stomachs of *Tilapia kottae* Trewavas on the 12th and 14th days after full moon, indicate that emergence there is not confined to the four days after full moon, although it may show a peak at that time. At Mboandong, too, the finding of large numbers of egg masses on the tenth day after full moon may indicate emergence later than four days after full moon; egg masses in Barombi Mbo did not remain intact and conspicuous for so long after full moon.

Kainji Lake (10°20′N, 4°25′E)

In Kainji Lake in Northern Nigeria, formed by the damming of the River Niger, *Povilla* larvae are common in tunnels in the submerged trunks of the trees that were killed when the land was flooded. The University of Ife's field station at Shagunu, on a peninsula in the lake, is close to the water's edge, and research workers there recorded the presence or absence of *Povilla* adults coming to the laboratory lights at 8 p.m. local

time (=19.00 hrs GMT) each day between March and October 1972 (Fig. 3). Between March and June there is evidence of slight periodicity, with a poorly-marked peak of emergence a few days after full moon and a rather clearer decrease in the few days before full moon. For seven weeks during June and July no adults came to the lights and then (after a period without regular records in the first three weeks of August) adults re-appeared after the August full moon. From that time until records ended in mid-October periodicity of emergence was not apparent.

There are several possible reasons for the absence of records of *Povilla* adults at the Shagunu lights in late June and July: windy, rainy weather is normally experienced there between late May and September; the shore-line was further from the lights during the

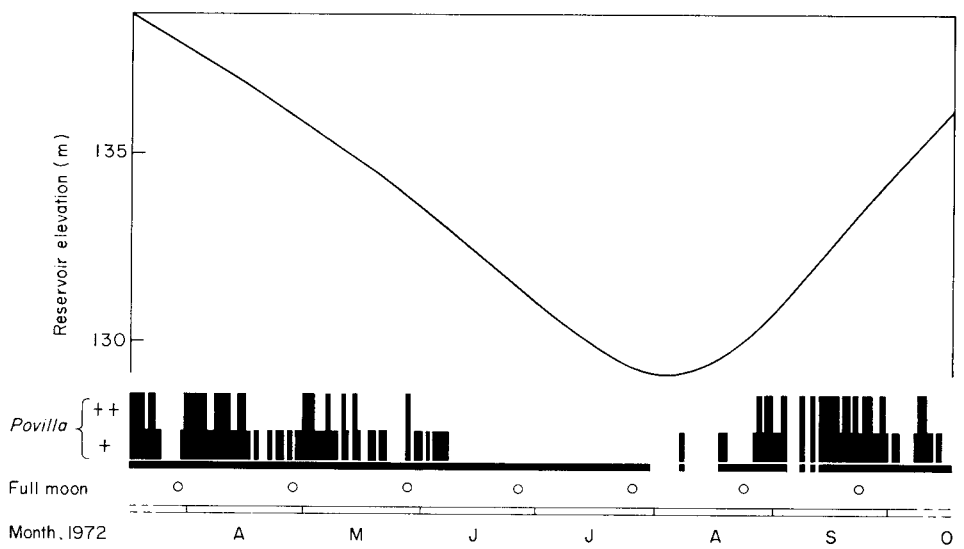

FIG. 3. The arrival of *Povilla* adults at lights at Shagunu in 1972, in relation to full moon and the water level of Kainji Lake. Breaks in the horizontal black bar represent evenings when no records were made.

annual period of low water level (the drawdown) which is such an important feature of Kainji Lake (Figs 3 and 4); and in late June sunset was about 40 minutes later than it was in late December, so that in late June the recording time (standardised in relation to Standard Time, not sun time) may have preceded the arrival of *Povilla* at the lights. *Povilla* adults were not absent from the lake, because some eggs appeared in the stomachs of fishes at that time.

The eggs and newly-hatched larvae of *Povilla* are found close inshore. When the water level was falling these relatively immobile stages might be stranded, although older larvae might be able to leave their tunnels and move down with the water. We have records of stomach contents for several species of *Synodontis* (N.W.) and *Alestes* (R.S.) caught in Kainji Lake in 1971 and 1972. Members of both these genera of fishes commonly eat larvae and eggs of *Povilla*, and the seasonal variation in the percentage occurrence of *Povilla* eggs in the stomachs of 3202 specimens of *Alestes baremose* (Joannis) is shown in Fig. 4. Fluctuations in the number of eggs in the fishes' diets may be at least partly due to fluctuations in the numbers of egg-laying *Povilla* adults; and these will depend on the

numbers of larvae of that generation that have completed their development. If the drawdown is a major cause of mortality for eggs and small larvae, fluctuations in adult numbers (and therefore in the numbers of eggs) may be expected to be related to the water level one generation (three months) earlier. In Fig. 4 the dashed line shows the graph of fluctuations in lake level displaced three months forwards; it shows fair correlation with the frequency of occurrence of *Povilla* eggs in the stomachs of *A. baremose*.

We found no evident relationship between the phase of the moon and the frequency of occurrence of *Povilla* eggs in the fish stomachs; this confirms the absence of any clear

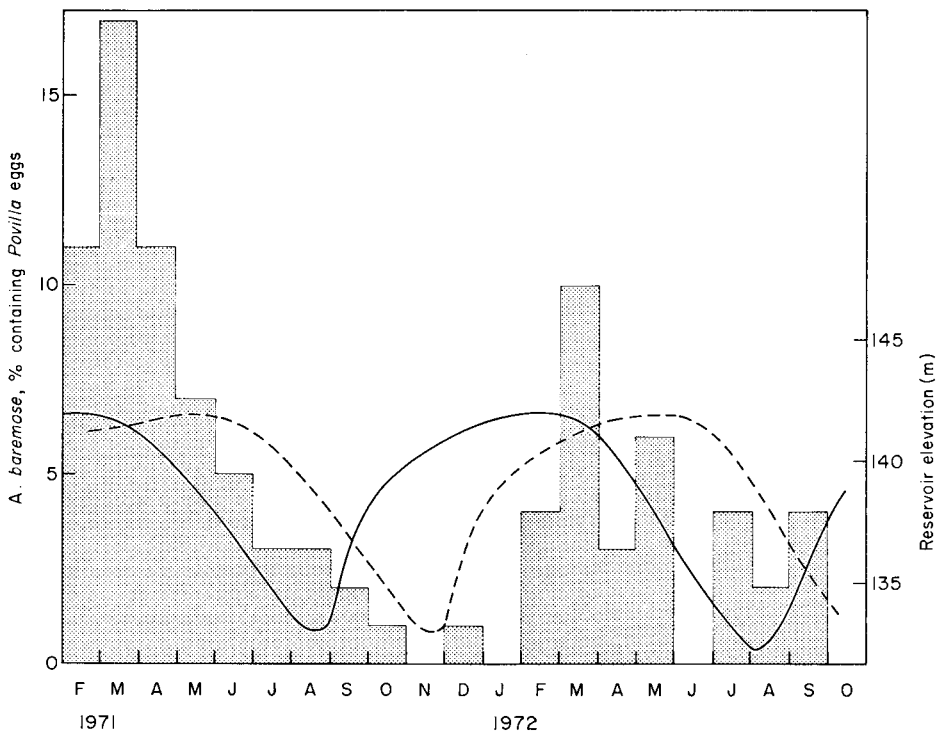

FIG. 4. Seasonal variation in the percentage occurrence of *Povilla* eggs in the stomachs of the fish *Alestes baremose* (Joannis) in Kainji Lake (stippled histogram) and the lake level (continuous line). The dashed line shows the lake level line moved three months forwards (see text).

lunar periodicity, deduced from the records of adults at light (Fig. 3). Even before the drawdown, the emergence of *Povilla* was less closely synchronised than it was at Barombi Mbo, and after the drawdown periodicity was not apparent (Fig. 3). If the drawdown is a cause of loss of synchronisation, this effect may be understood in relation to Hartland-Rowe's (1955) observation that larvae from Lake Victoria, kept in the laboratory, emerged within three days of full moon unless they had been subjected to a disturbance (breakdown of their aeration supply; being collected in the field eleven days before full moon when ready to emerge). If pharate adults time their emergence in relation to the intensity of light that they perceive when they leave their tunnels at night, any disturbance (such as shortage of oxygen, or field collection) that forced them to leave the darkness of

their tunnels during daylight might result in precocious emergence. The changing water level associated with the drawdown at Kainji might produce a similar effect.

Discussion

Emergence of *Povilla* in Barombi Mbo (and perhaps in Lake Soden) shows a distinct periodicity with the same relation to the lunar month as Hartland-Rowe (1955) found in Lake Victoria. In Lake Kotto, Mboandong and Kainji Lake emergence seems less closely synchronised. These three lakes are much more turbid than the very clear Barombi Mbo

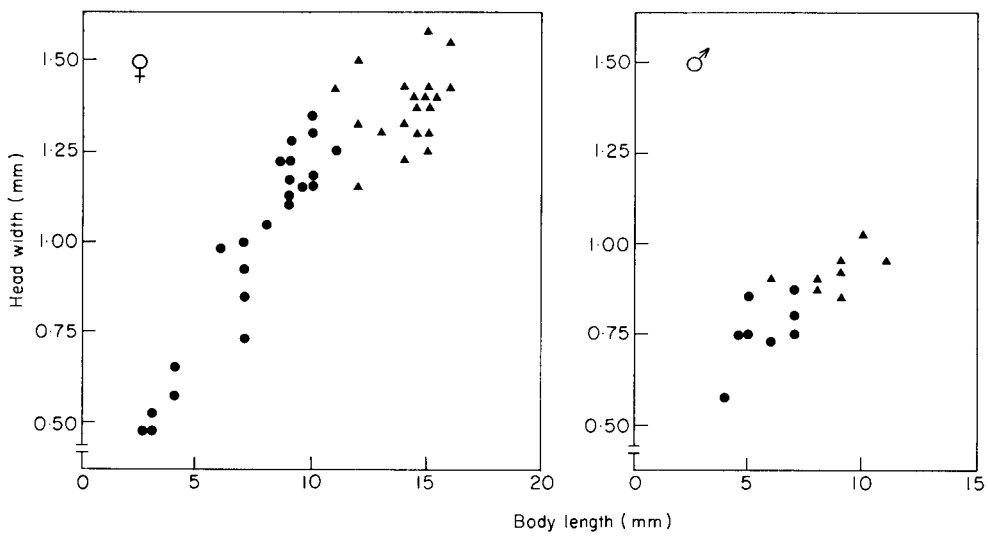

FIG. 5. The relationship between "head width" and body length in a sample of *Povilla* larvae taken from Barombi Mbo one day after full moon. Triangles: final instar larvae; dots: younger larvae.

and Lake Soden; a secchi disc was visible down to 595 cm in Barombi Mbo but only to 80 cm in Lake Kotto in April 1972. If synchronisation of emergence depends on a response to nocturnal light intensity the closer synchronisation in Barombi Mbo may be related to the clarity of its water.

Duration of immature stages

From measurements of larval mandibles from the stomachs of the fish *Mormyrus kannume* Forsk. in Lake Victoria, Corbet (1957) deduced a usual generation time of four or five months for *Povilla adusta* there. The distinct periodicity of emergence of *Povilla* in Barombi Mbo has made it possible to study the duration of larval life there in a similar way. Samples of larvae, collected from submerged wood in Barombi Mbo during March and April in 1970 and 1972, were sexed by examination of the external genitalia, and the length of the anterior margin of the frontoclypeus ("head width") (Fig. 8) was measured for each larva. In Fig. 6(a) and (b) these values are plotted for females and males in relation to the phase of the moon. The stippled lines show the pattern of growth that seems most likely for most larvae.

Figure 5 shows the relationship between head width and body length measured from the

anterior margin of the head to the base of the cerci. These larvae appear to be only about half the length of larvae at corresponding stages of development from Lake Victoria (shown in Fig. 4 in Corbet, 1957); 20 female final-instar larvae from Mbo ranged from 11 to 16 mm, whereas nine female final-instar larvae from Lake Victoria ranged from 22 to 30 mm. Dwarfing in Barombi Mbo is a feature of several species of zooplankters, too (Green, 1972).

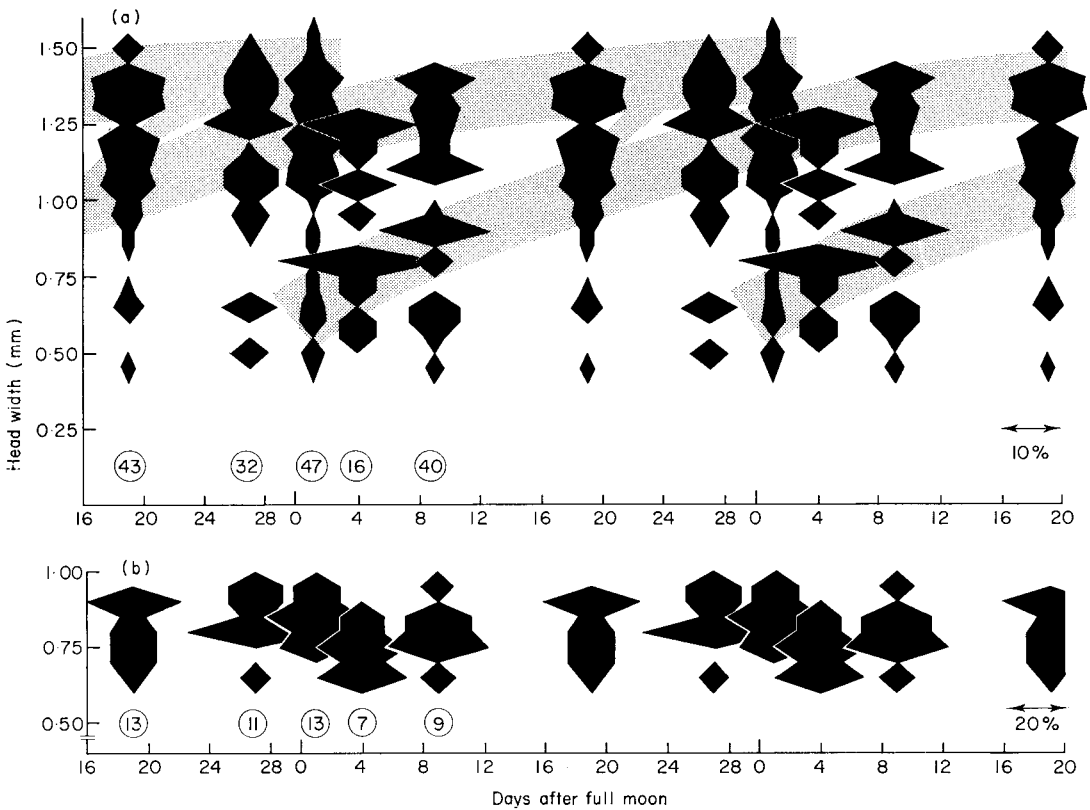

FIG. 6. Growth of *Povilla* larvae in Barombi Mbo in relation to the phases of the moon: (a) for female larvae; (b) for males. The stippled band indicates the pattern of development that is probably followed by the majority of females. The numbers in circles are the numbers of larvae of each sex in each of the five samples. The data from the same five samples are plotted two or three times to make the pattern clearer.

In the female larvae (Fig. 6(a)) with head widths of more than 0·95 mm on the first and 27th days after full moon, two groups can be distinguished by inspection; some larvae had the large wing buds of the final instar of the dark colour that indicates readiness to emerge; and the others had the smaller wing buds of earlier instars. By day four from full moon the final-instar larvae had emerged, leaving only earlier instars in the group of larvae with head widths greater than 0·95 mm. The proportion of final-instar larvae increased towards the next full moon, as shown for the same samples in Fig. 2. Although our sampling probably favoured larger larvae, and certainly ignored the early stages not found in wood, it is possible to trace a third size group with a head width of 0·50 to

0·65 mm on the first and 27th days after full moon. Larvae that first appear in these samples at a head width of about 0·50 mm (corresponding to a length of about four mm, Fig. 5) at about full moon must originate from eggs laid one or two months earlier. In Lake Victoria the eggs usually hatch after 11 or 12 days (Corbet, 1957; Hartland-Rowe, 1958); they may hatch a day or two sooner in the warmer water of Barombi Mbo. Corbet (1957) inferred that larvae in Lake Victoria reached a mandible length of six of his eye-piece units (equivalent to a body length in Lake Victoria of ten mm) in about four weeks from hatching. If a similar stage is reached at about half the length in Barombi Mbo, larvae there may reach a length of about five mm (or a head width of 0·75 mm, Fig. 5) about five and a half weeks after oviposition; and the generation time for females, corresponding to the growth pattern shown in Fig. 6(a), will be three lunar months. Similarly,

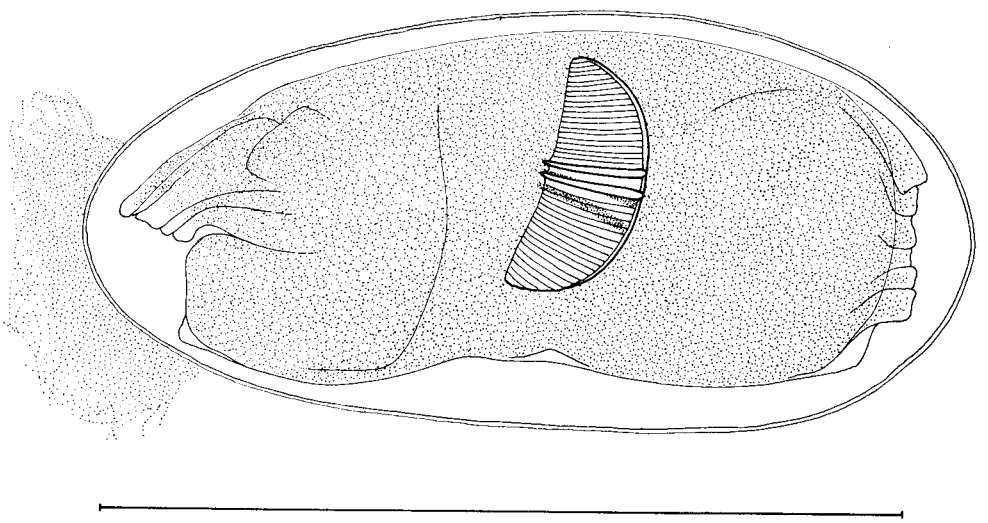

FIG. 7. The egg of a bdelloid rotifer found on a *Povilla* larva from Barombi Mbo, showing the ramate trophi, and the glue at one end of the egg.

the more limited data for male larvae shown in Fig. 6(b) are compatible with a generation time of three months for male *Povilla*.

Six of the 31 female final-instar larvae in the samples collected one day and 27 days after full moon were noticeably smaller than the rest, with head widths of 1·15 and 1·30 mm (and body lengths of 12 to 15 mm). In the other samples shown in Fig. 6(a) ten of the 11 female final-instar larvae had head widths of 1·35 to 1·50 mm; and 24 of the 25 female larvae with head widths of 1·15 to 1·30 mm were not yet in their final instar. The exception was a final-instar larva with a head width of 1·30 mm 19 days after full moon. The presence of these larvae with the wing pads of final instars and the small size of penultimate instars may indicate that a few precocious individuals can emerge a month earlier than their batch-mates, perhaps with a generation time of two instead of three months.

Discussion

The difference in rate of development between the population of *Povilla* in Lake Victoria and that in Barombi Mbo may be related to the higher temperature of Barombi Mbo. In

Lake Victoria the temperature ranged in a year from 23·8° to 25·8°C at the surface and from 23·4° to 25·6°C at 10 m (Talling, 1965). In Barombi Mbo in March 1972 the temperature was 30·1°C at the surface and 29·4°C at 10 m. It is known for several arthropods that individuals reared at higher temperatures mature earlier and at a smaller size (for example *Aëdes aegypti* (L.) (Christophers, 1960, van den Heuval, 1963), *Bruchus obtectus* Say

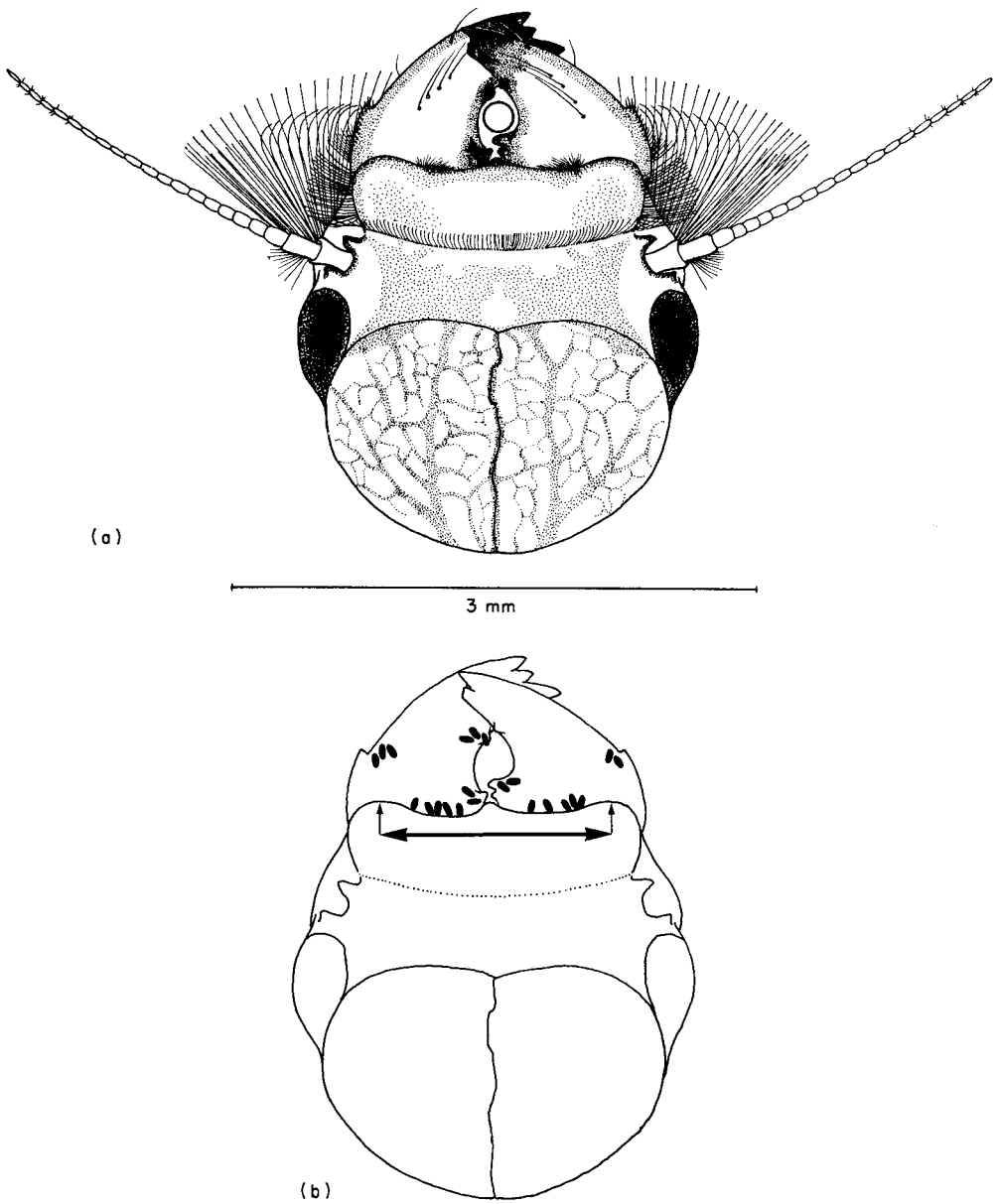

FIG. 8. (a) Dorsal view of the head of a ten-mm-long *Povilla* larva from Barombi Mbo, with a broken cercus between its mandibles. (b) Outline of the head showing how the length of the anterior margin of the frontoclypeus ("head width") was measured, and showing the positions where rotifer eggs commonly occur.

(Menusan, 1936) and *Daphnia magna* Strauss (MacArthur & Baillie, 1929)). A similar effect may be responsible for the smaller size and faster development of *Povilla* in the warmer lake Barombi Mbo.

Sex ratio

Of the 231 larvae on which Fig. 6 is based, 53, or 23 %, were males. Petr (1970) found a similar proportion of males (25 %) in his samples of *Povilla* larvae from Volta Lake in Ghana, and in a sample of 84 larvae from Lake Victoria Hartland-Rowe (pers. comm.) found that 32, or 38 %, were males.

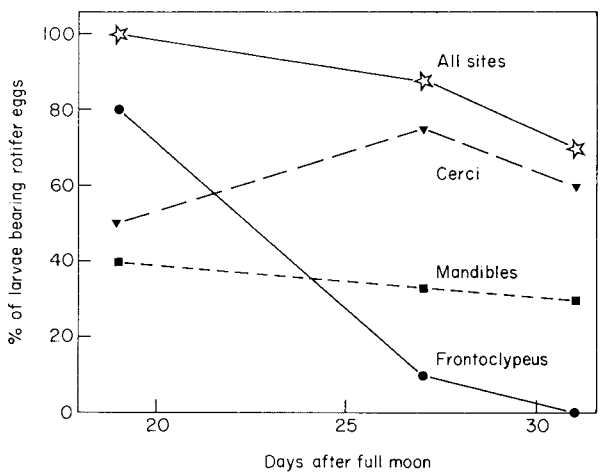

FIG. 9. Graph showing the relationship between the distribution of rotifer eggs on final-instar larvae of *Povilla* and the day of the lunar month.

Epibiotic rotifers

Bdelloid rotifers, similar to, and perhaps identical with, *Embata commensalis* (Western), were common at the bases of the cerci of *Povilla* larvae in Kainji Lake (J. Green, pers. comm.), and there were numerous bdelloid rotifers associated with preserved *Povilla* larvae from Barombi Mbo. Some of the many small eggs attached to larvae from Mbo and Kotto contained recognisable trophi of the ramate form characteristic of bdelloid rotifers (Fig. 7). These rotifers may well prove to be one or more species of the family Philodinidae, but firm identification, as well as elucidation of their relationship with *Povilla*, will require work with living animals. The finding of bdelloid rotifers with *Povilla* larvae in the three lakes (Mbo, Kotto, Kainji) from which collections are available may indicate some kind of regular association. Nearly all the rotifer eggs on the larvae in the samples from Barombi Mbo were attached in one of three sites: at the bases of the cerci; on the anterior margin of the frontoclypeus; or on the mandibles (Fig. 8(b)). Because of the synchronised development of the population in Mbo, and the resulting synchronised moult to the final instar, it was possible to see how the distribution of rotifer eggs changed towards the time of emergence. Figure 9 shows the results of counts of eggs on ten final-instar larvae from each of the three samples in which these were present (see Fig. 2). The percentage of larvae bearing eggs decreased only a little towards metamorphosis, although the number of eggs per ten larvae (72 on day 19 after full moon, 55 on day 27, and 42 on

day 1, just before emergence) decreased more noticeably. Presumably eggs laid just before emergence would stand a lower chance of hatching in a suitable habitat. The percentage of larvae with eggs on the anterior margin of the frontoclypeus decreased markedly from 80% at the beginning of the final instar to none at the end. Possibly pioneer rotifers arriving to colonise a newly-moulted larva are at first excluded from other parts of the larva by the feathered setae on the legs and head (Fig. 8a, and Hartland-Rowe, 1953); later, when more of them have gained access to the region behind the sieve, more of the eggs are laid on the cerci. The numbers of eggs on the mandibles varied less. They may not have been laid there, but may have stuck there as the larva used its mandibles to groom its cerci while the rotifer egg glue was still wet. One preserved specimen had the mandibles clamped around a broken cercus (Fig. 8(a)) and the curious shapes of the mandibles of *P. adusta* may be related to grooming the cerci and other parts as well as to burrowing in wood and smoothing silk. The disposition of rotifer eggs on the mandibles indicates that both the median bays and the lateral notches may be used in grooming. The harvest of rotifer eggs might form a valuable supplement to a diet of phytoplankton; but no rotifer trophi could be found in the gut contents of five final-instar *Povilla* larvae from Barombi Mbo preserved one day after full moon.

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