

The Biology of *Cloeon cognatum* (Ephemeroptera Baetidae)¹

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ABSTRACT

Ann. Entomol. Soc. Am. 74: 204-208 (1981)

The life history of *Cloeon cognatum* Stephens is described. Details are given on gill regeneration and light-intensity induced metamorphosis. The role of ocelli as possible mediators of metamorphosis is discussed. The function of the subimago is examined.

During the spring and summer of 1977, mayflies appeared—as they had for several years—on the east and west porches of my house in Ashland, Ohio. The mayflies were two-tailed and two-winged and were of three sizes, none of which exceeded 9 mm in body length. The largest were uniformly dingy gray; the medium-sized, light-colored with brown spots; the smallest, similarly marked, but of a darker hue. They were respectively subimagos, female imagoes, and male imagoes.

Some of the imagoes were placed in glass jars without food and water. The females lived at the most 15 days, e.g., 23 May–7 June. The males lived at the most 8 days, e.g., 23–31 May.

Other imagoes were caged during the population peak, 8–24 August, in a pasteboard box turned upside down on a glass dish containing tap water. The mayflies drowned soon after being caged; but not without issue, for an examination of the cage in September revealed that the water contained several mayfly nymphs which had survived on mayfly remains and atmospheric oxygen.

Late in September the few remaining mayflies on the porches were each isolated in glass cages with bottoms of sand or sand and water.

On 27 September, one of the mayflies discharged some matter on the sand and died. The discharge was examined under a compound microscope and identified as transparent ellipsoid eggs and dead nymphs.

Another mayfly was found dead on the water of a cage 28 September. The water contained 467 living nymphs. The female had been placed in the cage 26 September.

On 5 October, some of the 467 nymphs showed gills for the first time—7 pairs per specimen. And as the gills grew larger, the venation became unmistakably palmate.

Now, a two-tailed adult mayfly—to start with Linnaeus' (1758) original dichotomy between *Cauda trifeta* and *Cauda bifeta*—of medium size, which had two wings, that gave birth to living nymphs, which had palmately-veined gills, would normally suggest the name *Cloeon dipterum* (Linnaeus) née *Ephemera dipterum* Linnaeus. But a doubt nagged me. *Cloeon dipterum* was a European mayfly. Burks' (1953) *Mayflies of Illinois*, however, dispelled any doubt I had. Not only did the book contain descriptions that fitted my specimens, it also mentioned that a female *C. dipterum* had been taken in a light trap, 26 August 1939, at Champaign, Illinois, about 300 miles from—and almost due west of—Ashland, Ohio.

To reassure myself of *Cloeon dipterum*'s identity, I sent some specimens to Dr. G. Edmunds for identification. Edmunds (pers. comm.) pointed out that the "species" *C. dipterum* had been split by Sowa (1975) into three species and that Flowers (1978) had placed Pennsylvania specimens in *C. cognatum*. I sent specimens to Flowers who replied that they appeared to be *C. cognatum*. From Sowa's (1975) paper, which Flowers sent me, and which deals chiefly with Polish mayflies, it seems that the differences between the *C. "dipterum"* divisions are very striking, especially in the male eyes:

1. Medial compound eyes cylindrical . . . *C. inscriptum*
- 1'. Medial compound eyes top-shaped 2
2. Eyes yellow *C. dipterum*
- 2'. Eyes liver-red *C. cognatum*.

Materials and Methods

Adult mayflies were caged in lantern globes fitted into fingerbowls; the top of each globe was covered with cheesecloth; the fingerbowl contained a 34 ml stender dish, partly filled with water for oviposition, in its center and the space between the dish and bowl was filled with sand. Nymphs were raised in various dishes, the smallest measuring 15 ml, and fed fish food, dog food, dried hornwort (*Ceratophyllum demersum*), dried grass, etc., in water, which often contained a heavy growth of infusorians, colonial flagellates, etc. Light intensity was measured with an inverse squares apparatus.

Results

Egg.—Eggs were obtained by puncturing the abdominal wall of a 7-day-old, lab-reared, virgin female, 14 November 1977, and found to be smooth (non-faceted and unornamented), clear, vesiculated ellipsoids 0.120×0.090 mm. Eggs were also obtained by bisecting the abdomen of a mature, moribund, wild female, 31 July 1979; measured just seconds before hatching, they were 0.206×0.170 mm.

Nymph.—A male subimago emerged first from the batch of 467 nymphs. His nymphal stage took 35 days and 13 instars at an average temperature of 21°C. The record for the shortest nymphal stage, however, was set by a female from another batch. Her nymphal stage took 21 days and 12 instars at an average 28°C. Currently, the fastest-growing nymph from a third batch of mayflies has reached about two-thirds growth in 52 days and 20 instars at an average 23°C; and an abbreviated composite record of that nymph is given in Table 1.

¹ Received for publication April 8, 1980.

Table 1.—*Cloeon cognatum* nymphal stage.

Instar	Date '80	Body	Length mm Compound eye	Midtail	Other
1	16 Aug	0.525			5-eyed, hind 2 eyes darker; 2-tailed
2	17 Aug	0.600			
3	19 Aug	0.700	0.018		1-7 gill-pads recumbent
4	21 Aug	0.805	0.035		1-6 gills extended & moved
5	22 Aug	0.997	0.044	0.052	Body pigmented to include 6th abdominal segment
6	23 Aug	1.610	0.070	0.280	
7	25 Aug	1.750	0.105	0.700	2-6 gills doubled; outer tails banded
8	26 Aug	2.100	0.140	1.220	Pseudopupils visible
9	28 Aug	2.450	0.175	1.440	Mesothoracic wing-pads; tails with mature hair
10	29 Aug	2.800	0.210	1.750	Midtail banded
11	31 Aug	3.150	0.245	1.925	1st gill with anterior pad
<i>Chiefly enlargement and slower growth in the following omitted instars</i>					
20	6 Oct	4.550	0.385	2.800	Medial (male) compound eyes visible, 0.245 mm long

The end of the nymphal stage was signalled by the blackening of the wing-pads. And the last nymph of the 467 took 153 days to reach that point. Altogether, 65 of the 467 nymphs developed black wing-pads; of the 65, 36 emerged as subimagos. *Cloeon cognatum* adjusted well to the laboratory; and it proved to be very useful in my embryology course.

Subimago.—The first subimago from the 467 batch emerged 2 November 1977, between 7 and 9 p.m.

Imago.—I saw the adult from the above subimago emerge at 10:45 a.m., 3 November 1977. The subimago fluttered his wings for several seconds and then out popped an adult mayfly. The subimago stage thus lasted at the most just under 16 hours at 21°C.

Eaton (1888) says, "Tradition states that Curtis kept a female *Cloeon* alive three weeks"; our laboratory maintained that tradition. One virgin female kept at 21°C lived 22 days (6-28 November 1977) and escaped by flying away on the 22nd day; another lived 29 days at 17°C. A virgin male lived 9 days (3-12 November 1977) at 21°C. On the other hand, wild fertile females lived perhaps no more than 14 days when water was available for them to lay eggs in (see Table 2).

Oviposition.—Needham *et al.* (1935) cite three different authorities to prove that *Cloeon dipterum* is viviparous. Ross (1967) says that *Cloeon* is oviparous with the eggs hatching "almost immediately on touching water." On 31 July 1979, I cut in two the abdomen of

a moribund *C. cognatum*, which was lying on water; eggs sank from the cuts to the bottom of a stender dish and hatched within 2 or 3 seconds—like "popping corn," i.e., the discharge of the nymphs was not only explosive, it left no integumentary remains. That observation, which was repeated, convinced me that *C. cognatum*'s egg was a "pseudovum" like that of the aphid (Comstock 1936); the pseudovum was a thinly-covered nymph or partly-hatched egg; hence Needham *et al.*'s and Ross' views are both acceptable.

In the laboratory, mayflies practiced a method of oviposition like my bisection. On 29 September 1980, I placed a live *Cloeon cognatum* female on water. A hole instantly formed in her belly between the 7th and 8th abdominal segments. Pseudova immediately passed through the hole into the water. The pseudova hatched and the nymphs started to swim within 30 sec; the oviposition took about 1½ min, and its end was marked by the appearance of a bubble of air at the abdominal rupture. The last three—and perhaps one or two other—ovipositions listed in Table 2 were of that type.

I never counted the eggs of *Cloeon cognatum*. But I did count the freshly-hatched nymphs from 13 normal (uncut) female adults (Table 2). The range of freshly-hatched nymphs was 300-1,178. That compares favorably with an estimate of 450-500 eggs for *Callibaetis floridanus* (Berner 1950) but is well below the estimate of 2,200-8,000 eggs for *Hexagenia* (Edmunds *et al.* 1976). In addition to the nymph count given in Table 2, Haj Abed (pers. comm.) reported an estimate of 1,068 nymphs from a female caged 8 days during the summer of 1978.

Breeding sites.—Strand (pers. comm.) reported taking *Cloeon cognatum* from a local creek during the summer of 1979; but when I rechecked the creek with him we found only *Callibaetis*. Strand (pers. comm.) also took *Cloeon cognatum*, another *Cloeon* or *Centropitilum*, and *Callibaetis* from my neighbors' fishpond; I took similar mayflies from the same place. The pond was located 23 m from my east porch and it had an area of approximately 25 m². It was spring-fed and filled with hornwort. It was also very likely the source of my mayflies.

Gill loss and regeneration.—In looking for help to raise mayflies in the fall of 1977, I found this advice in

Table 2.—Freshly-hatched *Cloeon cognatum* nymph count.

Days adults caged prior to discharge	No. nymphs	Time
2	467	Fall, 1977
9	758	Fall, 1977
10	667	Fall, 1977
14	653	Fall, 1977
13	1067	Spring, 1979
11	1178	Spring, 1979
9	997	Summer, 1979
5	685	Summer, 1980
12	559	Summer, 1980
1	567	Summer, 1980
11	300	Summer, 1980
6	419	Fall, 1980
8	329	Fall, 1980

953) Berner (1950): "If more than a day or two elapses between the time the living nymphs are collected and the time subimagoes appear, it is advisable to change the water in the rearing pans." I followed Berner's advice and several of my mayflies developed swollen gills that eventually broke off. That happened when the mayflies were transferred from culture water with much organic matter to fresh tap water. In the spring of 1978, it occurred to me that it would be a good exercise to have my embryology² students try to reconstruct my experience. Half of the class studied gill loss in culture water; half, in tap water, i.e., nymphs were transferred from culture water to tap water. The results surprised me: there was no appreciable difference; 19 nymphs in culture water each lost an average of 2.5 gills; 17 nymphs in tap water lost an average of 2.2 gills; and not a single nymph suffered a massive loss of gills such as marked my original specimens. The gill losses totalled:

Abdominal segment	Gills lost
1	6
2	13
3	16
4	22
5	13
6	11.5
7	2

Since abdominal segment 7 lost the fewest gills, and since those gills were never moved (except rarely in an early instar), gill loss was apparently caused by gill movement. The gills were first regenerated as single gills, then as double gills, nicely illustrating the biogenetic principle, or a regeneration variant of it: ontogeny recapitulates ontogeny.

In 1979, my embryology students were instructed to see if they could eliminate the gills without killing the nymphs. Kessler (pers. comm.) reported that he got rid of 9 gills by placing a nymph in water containing 1 ppm sodium hypochlorite; the nymph survived for 48 hours, but it regenerated no gills. We subsequently learned that the city water—the source of our tap water—sometimes had 1.6–1.7 ppm of chlorine. Thus chlorine may have caused the gill loss in my original mayfly specimens.

Light intensity and metamorphosis.—Since subimagoes and imagoes emerged every month in the laboratory from October until March, it was obvious that *Cloeon cognatum* was not affected by changes in the length of the light period. But the effect of light intensity was another matter. Again I had my embryology students (1978–79) study the emergence of subimagoes from blackwing nymphs kept on the window sill and from blackwing nymphs kept on a table on the opposite side of the room. The light was 13 (7–19) times as great at the window sill as it was at the table; and the temperature was 4 degrees (17–21°C) colder at the window sill than it was at the table. The results (Table 3), which show that twice as many emergences took place at the window sill as at the table, were suggestive rather than

Table 3.—Emergence of *Cloeon cognatum* under variable light intensities.

	Window/Live- Dead	Wall/Live- Dead	Total
Male	6 12	4 17	41
Female	6 8	3 10	27
Total	14 20	7 27	68

statistically significant. And the results suggested that light intensity might have governed the metamorphosis of the blackwing nymphs.

Discussion

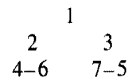
Mediators of metamorphosis.—If light intensity governs the metamorphosis of the mayfly nymphs, as I think it does, then it must register on their eyes. But which one(s)?

The eyes of *Cloeon cognatum* differentiate as early as the first instar, when the future ocelli appear lighter colored than the future compound eyes. They also differ in position, with the future ocelli numbered 1–3 and the future compound eyes numbered 4–5 in the following diagram:



The mature female nymph retains the above pattern, except for the compound eyes moving sideways.

The mature male nymph has 7 eyes:



I shall use the male to illustrate the differences between the eyes.

The first eye faces forward. It is the smallest eye, having regressed from a size equal to that of the other eyes. Seen only in the full-grown nymph, it appears vestigial, as if it had already performed its function. It shows practically no detail at 30×.

The second and third eyes face sideways. Each eye is several times larger than the first eye, and appears to be lined with a white material, perhaps guanine. Seen from above, the second and third eyes look like saucers; actually they are covered with flat transparent cuticles that have to be felt to be detected.

The fourth and fifth eyes face mostly sideways. They are several times larger than the second and third eyes. Each eye's surface is convex, hexagonally faceted, clear, with a sprinkling of black pigment through which a pseudopupil can be seen from overhead as well as from the side.

The sixth and seventh eyes face upward from a medial position. They are larger than the fourth and fifth eyes, faceted, and have an opaque brown color that never changes. They have no pseudopupils.

The sixth and seventh eyes may be eliminated as mediators of metamorphosis because they are not common to both sexes. The fourth and fifth may be eliminated

² It is perhaps not without interest to note that Darwin (1866) introduced his section on Embryology in the 4th and subsequent editions of the *Origin of Species* with a reference to the metamorphosis of "Chloëon."

because they turn black during the closing hours of the full-grown nymph's life, a condition present also in dead and dying nymphs.

On the other hand, the ocelli, especially the second and third, bear a striking resemblance to the eyes of the crustacean *Gigantocypris*—even to the point of glowing. According to Land (1978), *Gigantocypris* has mirror-equipped eyes with an f-number of 0.3 that produce images 17 times brighter than those made by fish lens eyes (f-number 1.25). The ocelli of *Cloeon cognatum* may have similar biological mirrors composed of guanine that increase the intensity of light and bring about metamorphosis.

After reaching the above conclusion largely by conjecture, I was presented with a nice piece of supporting evidence. On 3 May 1979, Strand gave me some live *Leptophlebia* females that he took in Ashland county. I beheaded one and she discharged 5,220 eggs. The eggs hatched 11 May 1979. The emerging nymphs had three ocelli. Precursors of the compound eyes did not appear until the second instar. That made me think ocelli almost certainly control the hatching of the egg and the molting of the first instar and very likely control the molting of the other instars. From the large size of the first eye in the first instar, a size that is soon lost, I would go a step further and say that the control of hatching of the egg rests solely on the first ocellus. A picture of the first instar nymph is shown in Fig. 1.

Function of the subimago.—In contrast with the *Cloeon* male imago, the male subimago has forelegs whose tibiae and tarsi are one-half shorter; tails, one-fourth shorter; darker wings and abdomen; fainter veins; hairs on the trailing edges of the wings; smaller and more globular medial eyes; shorter and straighter claspers; a larger and (it is to be inferred) heavier body. The differences between the female imago and subimago are less noticeable, and will be ignored.

Needham *et al.* (1935) mention most of the above characters; yet they accord the subimago only a limited status:

"Mayflies are peculiar in having a partial shedding of skin after the adult form has been assumed. This has been the subject of much speculation—and over-emphasis. It has been looked upon as the equivalent of a pupal stage. It is only a casting of the delaminated, hairy outer covering. It does not occur in all mayflies (*Paligenia* is an exception). It is partial in some. It does not represent a growth period, and is therefore not a true instar."

According to Needham *et al.*, the changes that occur in the last molt which forms the imago are directed at improving flight. The chief change has been a loss of weight—over 20%—brought on almost entirely by desiccation following the shedding of the subimago skin. The mayflies are thus better able to swarm. Mayflies that do not swarm do not have subimagos.

Needham *et al.* notwithstanding, there is very little speculation and overemphasis on the subimago—at least in print. The only other view that I have found which offers an explanation is Schaefer's (1975): the subimago is a relict perpetuated by the synchronous emergence of such a crowd of mayflies that predators are swamped and travel to find mates is eliminated. Schaefer accounts

for the subimago's "adaptive basis" by saying that "there may indeed be none."

Both views—Needham *et al.*'s swarming and Schaefer's swamping—link subimago flight with reproduction. The views are very plausible. They are also simplistic. And they force us to return to our basics. The classical and still viable view of locomotion is that it was developed for two functions; thus Lamarck (1809) says this about animals: "il étoit nécessaire qu'ils aient la faculté de mouvoir, et même de déplacer, afin de pouvoir se procurer les alimens (sic) dont ils ont besoin." And "il étoit encore nécessaire qu'ils pussent se déplacer pour se mettre à portée d'effectuer des actes de fécondation."

The gist of Lamarck's remarks is that locomotion is used for both feeding and reproduction. And the two can—perhaps often do—compete so that one has to be subordinated to the other. Thus in a study of *Bittacus apicalis* (hangingfly), I (1957) discovered that the male feeds the female at the time of copulation. In another study of *Leptogaster annulatus* (robberfly), I (1963) discovered that the males and females feed during the day, court at dusk, and mate in the dark just before dawn, and are more common than seven other species of *Leptogaster* (combined) whose males try to mate while the females try to feed in the daytime. In another study, I

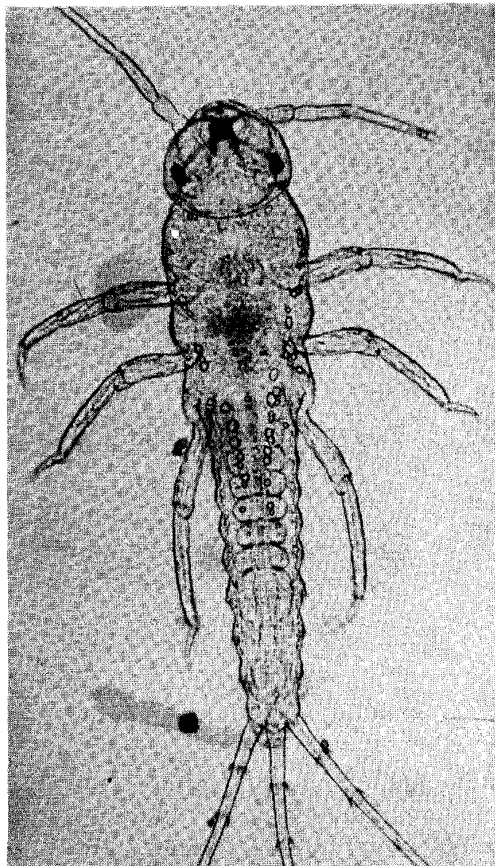


FIG. 1.—First instar *Leptophlebia* nymph.

partly supervised Brownson's (1964) discovery that *Bittacus strigosus* (hangingfly) males copulate at dusk, freeing females to feed in trees; both then mate heterosexually on low-growing plants at dawn without exchanging food. And in still another study, I (1970) confirmed Steyskal's discovery that *Rhamphomyia longicauda* (dancefly) males feed swarming females at the time of mating. Now, those four species were among the dominant insects of Ashland county woods. And I think their dominance was attained by the way they removed the conflict between feeding and mating.

The subimago is extremely common in the order Ephemeroptera. And its commonness assures it a survival value. And because Darwin (1869) made natural selection synonymous with survival of the fit, its survival value is to be equated with its selective value. But the value we are interested in here is what Darwin (1859) called the "adaptive or analogous" character. Though unique in itself, the subimago is part of a life history that is analogous to that of *Leptogaster annulatus* or *Bittacus strigosus*, a life history that exhibits a conflict between feeding and reproduction which is resolved by scheduling the events at different times. The young nymphs feed only; the old mayflies (imagoes) reproduce only. The subimagoes do neither. But they contribute to both. By flying they disperse the population and eliminate the competition for food. And then by molting they lighten the imagoes' weight and make reproductive swarming more efficient. And in both cases they contribute to the unity and integrity of the species.

Acknowledgment

I thank Drs. G. F. Edmunds, Jr. and R. W. Flowers for presenting me with valuable papers and for identifying specimens of *Cloeon cognatum*, Dr. Warren Segelkin for use of the inverse squares apparatus, Dr. and Mrs. Thomas Vanosdall for use of their fishpond, Dr. John Hadder and Mr. Gerald Strand for the *Leptophlebia* photograph, and my students, particularly Mrs. Andrée Haj Abed and Mr. Dave Kessler. I especially thank my reviewer for his constructive criticism.

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