

THE MATING FLIGHT AND THE VESTIGIAL STRUCTURES OF THE STUMP-LEGGED MAYFLY, *CAMPSURUS SEGNIS* NEEDHAM

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MATING SWARM.

At Kartabo the waters of the Cayuni meet those of the Mazaruni and soon join the great lake-like Essequibo flowing north through the low lying country of British Guiana until it runs into the sea at Georgetown. These rivers are hedged in by the jungle whose undergrowth has invaded the border waters in a persistent attempt to gain more territory. Mangrove roots swing so far out from the banks that fish swim in and out among them. Moccamoccas, the giant arums, have grown out still further. Their clublike stems standing in close rank provide on gigantic scale the kind of animal shelter furnished in more modest form by our own arrow head and pickerel weeds. Many slow flowing creeks feed into these larger streams but their mouths are hidden by creepers, tangles of mangrove, and prickly shrubs, and if the currents are gentle enough they are choked by lush growths of Cabomba.

The mouths of these creeks are flooded every day and the floor of the jungle bordering the shore is covered with water for several feet back from the river by the rise of the fresh water tides. Even at Kartabo Point the daily tides are insistent reminders of the ocean forty miles away. The low tides lay bare stretches of muck and ooze, silt and silty sand, the constant siftings from the side currents of the stream. This silt is soft and loose, rich in organic material. Wherever it occurs in all our more familiar lakes and streams it is the likely dwelling place of nymphs of the burrowing and crawling Mayflies which belong to the subfamily Ephemerinæ including the largest and most familiar Mayflies such as *Ephemera* and *Hexagenia* and the white winged *Polymitarcys*. Among its members is the little known tropical genus, *Campsurus*. Though not absent from smaller streams the burrowers frequent

lakes and rivers where they live in just such silty bottom as that of the Mazaruni and Essequibo. On the Mazaruni side of Kartabo Point there is a short stretch of beach and along it the low tide leaves a band of silt which indicates the nature of the bottom over which the side waters of the Mazaruni flow. Even a glance at this shore would suggest the prediction that burrowing Mayflies might live nearby.

In the late evening of July 8, 1926, Mayflies of the species *Campsurus segnis* were flying in large numbers, above this beach. Burrowing crickets were running, or digging into the moist sand, left where the tide had gone out. They were bewildered by the spotlight and lost their direction if not their speed. Suddenly a shower of Mayflies began falling across the beams of light. In the first glare they looked like the white winged *Polymitarcys alba* of a genus already mentioned. Most of them protested against their fall and their wings fluttered, snowy and opaque. On the sand they toppled helpless. Many fell with outspread wings which at once clung closely to the wet sand; others were tipped over like capsized sail boats. All of them were prone. None had been able to negotiate the ground surface. As they came into the light most of them fluttered straight down from the height of twelve to fifteen feet at which they must have been flying. A few came into view at a low level, evidently borne along near the surface of the water by the breeze coming in from the river. For half an hour they kept falling upon the sand. Then the Mayfly shower ended with the same suddenness with which it began.

Was this a mating flight of fully matured imagos or a company of subimagos which had but just shed their nymphal skins and flown toward the light? Their differing maturity seemed to indicate a mixture of both mating and emerging flights. The cause of the ground flop was seen as soon as one of the Mayflies was picked from the sand. The females did not at first appear to have any legs at all. Only two males were found and these were lying with their front legs extended before them but they were as devoid of other legs as the females and nearly as helpless. This dearth of males argued against there having been any mating flight in progress, since with Mayflies that is characteristically a male performance. In the lake species, *Ephemera simulans*, the flight is predominantly male while in the small species, *Choroterpes basalis* and *Baetis posticus*, males make up at least half of the swarms. The

females of *Campsurus* were borne down to the ground by their heavier bodies and the weight of their eggs, while it may have been that the lighter bodied males had flown on into the trees. This seemed the more probable because many of the females had yellow packets of eggs projecting from the openings of the oviducts. Such egg packets are carried by many kinds of Mayflies and their appearance always indicates that the short span of adult life is about over, that mating has occurred, or if not, at least that full maturity has been reached and the eggs can no longer be retained. One of the Mayflies which is most commonly seen carrying egg packets is the tiny *Caenis* which is often caught and hung, eggs and all, in the meshes of spider webs upon bridges and street lamps. The egg masses of *Campsurus* were carried not only by imagos which had shed their subimago skin entirely but by those over which the subimago skin still fitted completely or partially. When the egg packets were removed from these females, the walls of the oviducts were found far everted with the Malpighian tubules pushed through the membranes and hanging into the air as if the eggs had been forced out so convulsively that the ducts had been torn and the tubules projected through their walls. The females collected had probably swarmed and had been flying over the water to deposit their eggs when they were carried in toward the light.

The subimago stage of *Campsurus segnis* is probably of brief duration, far different from that which is characteristic of its related *Hexagenia bilineata* and *Ephemera simulans* in which this stage lasts twenty-four hours or more. In these and in many other species this subimago period is the one in which there is a rapid elongation of the legs and caudal setæ. These changes are most obvious in the males, the lengthening slenderness of whose front legs is zigzagged across the encasing subimago skin as if in a stocking much too short. No such growth of the legs seemed to have occurred in these *Campsurus* subimagos.

In the extreme specialization which *Campsurus segnis* has attained the brevity of its aerial life has been a necessary parallel to the abbreviation of its legs. The adults are entirely dependent upon their wings for existence. Since they have no legs to rest upon neither males nor females can alight upon anything and if they are forced down there is little chance that they can ever fly again.

VESTIGIAL LEGS AND MODIFICATIONS FOR REPRODUCTION.

In 1876 Eaton published his "Notes on the legless condition of *Campsurus*" and very briefly commented upon specimens of "Campsurus and some of its allies" in which all of the legs had been cast off by some of the females, while in others the front pair of legs had been retained "as it had seemingly in all the males." (Eaton 1876, p. 7). In his "Revisional Monograph of Recent Ephemeridæ" he characterized the genus and described eight species but neither in genus nor species descriptions did he mention the extreme atrophy of the legs which he had previously noted (Eaton 1868, 1876). Although he carefully defined the color of the legs of species of *Campsurus* and referred to the "fore legs yellowish like the hinder legs" in the females of *Campsurus decoloratus* Hagen (Eaton 1883, p. 41) he made no comment as to any vestigial condition. He figured the head, wing, genitalia and front leg of the imago male *Campsurus albifilum* Walker (Eaton 1883 Pl. V., Fig. 8a) but did not there mention any peculiar condition of the middle and hind legs. In 1913 a figure of an unnamed species of *Campsurus* was published by the author (Morgan 1913 p. 394). This was drawn from a specimen kindly loaned by Dr. J. G. Needham. This male imago showed the vestigial middle and hind legs very clearly but some of its structures were broken and so far as the author is aware no description of it has been published. Under the caption, "An Adult 'Peg-leg' *Campsurus* sp?", Dr. Needham included this figure in his interesting paper (Needham 1920, Pl. LXXXI, Fig. 57) on the burrowing Mayflies of the subfamily Ephemerinæ. In connection with his key to this subfamily he pointed out that "*Campsurus* alone has the middle and hind legs aborted," (Needham 1920, p. 277). In his key to the adults, (Needham 1920, p. 277), *Campsurus* was set off by the venational characters, "posterior fork of the median vein in the forewing very deep, almost reaching the base of the wing; two long simple intercalary veins between the first and second anal veins," (Pl. I, Fig. 7).

Campsurus segnīs was first described in the paper. "Neotropical Mayflies" by J. G. Needham and H. E. Murphy 1924. At Dr. Needham's suggestion a further description of it has been included here, together with figures of the male and female imago. The extremes of specialization which are its significant aspects will first be discussed.

This form and the genus to which it belongs present an extreme in the development of those parts directly or indirectly concerned with reproduction and a relative suppression of those not necessary to that end. The whole tribe of Mayflies includes many similar but less striking examples and the wings, front legs, and caudal setæ are always modified for action in the vertical flights undertaken during the Mayfly mating dance. Corresponding parts are less specialized in the more conservative females. Mayflies have developed mechanisms which are extremely efficient in these unique flights during which they mate. They are poor and unwilling walkers and no Mayfly can run. Their legs are always slender and delicate, giving only a weak support to the body which in many species is carried mainly by the middle and hind legs, the front ones, especially in the males, being held forward in an attitude of cordiality with no reference to locomotion or support. Observation of the male individuals of *Siphonurus*, *Heptagenia*, *Ephemerella* or *Chirotenetes* will show the small part which the front legs take in supporting the body and will indicate their tendency to have less and less to do with the work of walking. This general ineffectuality of the legs for their original function and the shift in the use of the front legs of the male into structures accessory to mating is but a hint of the extreme disparagement of pedal locomotion which occurs in *Campsurus*.

In *Campsurus segnis* the middle and hind legs of the male are but stumps made up of three poorly defined segments, the terminal ones being pointed and heavily chitinized at the tips. (Pl. I, Fig. 2). These legs are too short to be of any use. When alive the insects are able to move them only a little and even when the legs have been pushed ventrally by force their tips hardly reach to the underside of the thorax. The front legs of the male are similar and not proportionately longer than those of males of other related forms of the *Ephemerinæ*. As is usual in Mayflies there is a twist in the joint which articulates the first tarsus with the tibia; this allows the supination of the tips of the front legs which are clasped about the female in mating. The male approaches the female from beneath and throws his front legs upward about her thorax, bending the tip of his abdomen upward, so that its ventral side comes so closely in contact with that of the female that the forceps may clasp her abdomen and the hooks of the penis, (Pl. I,

Fig. 5), be extended into the openings of the oviducts between the seventh and eighth segments.

The front, middle and hind legs of the female *Campsurus* are all aborted stumps each consisting of three weakly defined segments, (Pl. I, Fig. 4). The front legs are shortest and consist like the others of what is probably coxa, femur and tibia. What first appear to be the coxæ of the third legs are elevations of the thoracic wall, (Pl. I, Fig. 4). The ventral views of both the male and female thorax make the legs appear further ventral than they really are, (Pl. I, Figs. 2, 4). The side view of the male (Pl. I, Fig. 1) gives a truer picture of their position as it obtains in both sexes. Among the sixty females examined there were five in which one leg was noticeably longer than its mate, (Pl. I, Fig. 4). This plasticity of the leg form was further demonstrated by one female in which the left front leg was long enough to reach the front margin of the head and included a well grown femur, tibia and tarsus with tarsal claw although the corresponding front leg had but three ill defined segments and happened to be even shorter than the average, (Pl. I, Fig. 3). Reversion like this, and such irregularities of size and form are characteristic of vestigial structures and here they are good evidence of the unsteadiness of this extreme specialization which has not yet become firmly implanted in the pattern of the organism. Among Mayflies it represents an extremity of the reduction of the standing and walking function of the legs, and the predominance of degenerate limbs among which more normal ones still make their appearance.

Here pedestrianism has become as much a matter of the past as food getting became long ago among adults of the whole Ephemeropterid society. *Campsurus segnis* is similar to related species, such as *Hexagenia recurvata*, (Murphy 1922, Pl. VI, Figs. 88-98), in the atrophy of its mouth parts. In the female here figured all of the mouth parts are easily seen except the labrum, (Pl. I, Fig. 4). The long soft processes of the mandibles are usually crossed above the mouth cavity in which the papilla like hypopharynx is visible. They are similar to those of species of *Hexagenia* and *Ephemera* and other burrowers, and are the vestiges of the tusk like rami of the mandibles. The unknown nymph of this species must have such mandibular tusks. (Nymph of an unknown species of *Campsurus*. Needham and Murphy, 1924, Plate IV.) These atrophied mandibles

showed clearly in both of the captured males but were more shrunken in them than in the females, a difference which may have been due to greater maturity or to individual variation.

Like other Mayflies this species has long caudal setæ, held stiffly extended behind in flying, outriggers especially long in the males; in *Campsurus segnis* they are three times the length of the body. But the unique specialization of *Campsurus segnis* remains in the abbreviation of legs of which it is a superlative example.

Description of *Campsurus segnis* Needham

Male imago (Pl. I, Fig. 1). (Alcoholic specimen). Length of body, 10 mm.; length of setæ, 32 mm.; front legs, 4.5 mm.; middle legs, 1 to 2 mm.; hind legs, 1 to 2 mm.

General color pinkish buff, becoming subhyaline on the abdomen with brownish shadings, ridges brownish. Head, unevenly brown; eyes uniformly dark brown, small, oval and widely separated; lateral ocelli distant from each other, larger than the median ocellus; antennæ with the terminal segment hair-like and longer than the other two together. Thorax, pinkish buff, translucent; mesonotum with a broadly triangular spot of brown; metanotum tipped with brown. Wings hyaline (Pl. I, Fig. 7), costal border brownish; costa, subcosta, and radius of the front wing and costa and subcosta of the hind wing brown. Front legs with femur and tibia brown, equal or subequal in length; fore tarsi whitish, the joint between the tibia and tarsus appearing like a short segment; middle legs vestigial with three poorly defined segments, the terminal one pointed; hind legs similar to the middle pair, but slightly longer, (Pl. I, Fig. 2), legs sometimes variable in length and asymmetrical. Abdomen brownish with pale sutures, flecks and dashes; a pale mid-dorsal line extending through segments 3-10; a corresponding but more distinct line on the ventral side; conspicuous elevations on segments 2-8, each terminating at the hind angle of the sternite, showing the former position of six of the nymphal gills, (Pl. I, Fig. 1). Setæ two, hyaline, sparsely plumose at the tips. Forceps inserted each upon a separate base distinct from the posterior margin of the ninth sternite, and with a short process extending lateral to each forceps limb, (Pl. I, Figs. 5, 6). Penis strongly chitinized, curved ventrally above a pair of shorter, club-shaped processes which broaden into the spoon-shaped subgenital plates, (Pl. I, Fig. 6).

Female Imago.—Encased in subimago skin but sexually mature with the oviducts everted and abdomen cleared of eggs. (Alcoholic specimen). Length of body, 9 mm.; length of setæ, 18 mm.; length of front, middle and hind legs, each less than 3 mm.

General color buff, brownish shadings on abdomen, ridges brown. Head unevenly brown; eyes oval, same size as in the male; ocelli obscurely banded with brown, the lateral ocelli distant from each other and larger than the median one. Pronotum pale; mesonotum with

brown markings confluent in a triangular spot; front legs aborted into short stumps with three poorly defined segments, (Pl. I, Fig. 4); middle and hind legs likewise aborted and segmented but slightly longer than the first pair; legs sometimes asymmetrical, (Pl. I, Figs. 3, 4). Abdomen with lateral elevations in segments 2-7 marking the positions of nymphal gills. Setæ two, hyaline to whitish, not plumose at the tip as in the male.

Described from two males and ten females taken at Kartabo, British Guiana, July 8, 1926. The nymph is not known and no specimens nor molted skins of it were discovered.

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EXPLANATION OF PLATE.

- Fig. 1. *Campsurus segnis* Needham. Adult male, showing vestigial middle and hind legs. Note the lateral elevations on the abdomen.
- Fig. 2. Ventral view of adult male, showing the three segments of the vestigial legs. Front legs with four tarsi, and a twisted joint between the tibia and tarsus which allows the supination of the tarsi.
- Fig. 3. Ventral view of adult female, showing asymmetry of the front legs. The vestigial mandibles have their rami extended forward.
- Fig. 4. Ventral view of adult female, showing the vestigial condition of the legs and a common asymmetry. Note the vestigial mouth parts; clypeus, (labrum not visible), mandibles, maxillæ, labium, and the papilla-like hypopharynx showing within the mouth cavity.
- Fig. 5. Side view of male genitalia, showing each forceps limb flanked by a short process and the double penis curving ventrally over the extensions of the subgenital plates.
- Fig. 6. Ventral view of the same. Note the incurving hooks upon the median edges of the subgenital plates. The plates on either side of the anus shown in outline appear disproportionately large when the body is in this position.
- Fig. 7. Front and hind wing of *Campsurus segnis*. Veins named by homology with those of *Hexagenia*, (Morgan 1912). Note the depth of the posterior fork of the median vein.

