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THE LIFE HISTORY OF *MEGISTOCERA LONGIPENNIS* (MACQUART) (TIPULIDAE, DIPTERA), A MEMBER OF THE NEUSTON FAUNA

BY J. SPEED ROGERS

THE essentially tropical genus *Megistocera* (Dolichopezaria, Tipulinae) is represented in the United States by a single species, *longipennis* (Macquart), which is also known from Cuba and Brazil. Originally credited to continental North America on the basis of two specimens labeled "Lake Okechobee" (Florida Everglades), the species is actually widespread and often locally common throughout Florida, with records from Liberty, Leon, Alachua, Nassau, and Putnam counties in the north, from Dade and Collier counties in the south, and from Marion, Lake, Volusia, Orange, Hillsboro, Polk, and Manatee counties in the central and southern part of the peninsula.

Northern Florida is probably near the actual northern limits of the range. In Alachua County, where continuing field work was carried on from 1923 to 1943, *Megistocera* became very rare for several years following the prolonged or unusually cold spells of 1928–29, 1935–36, and 1939–40. The larvae in my aquaria would refuse to feed and become quiescent when the water temperature fell below 50 degrees and were killed by a six-hour exposure to temperatures of 32 to 34 degrees Fahrenheit. The adults appear to be somewhat more tolerant of low temperatures and are able to survive some hours of freezing or slightly below freezing temperatures.

The apparent rarity of the species in Florida is explained by the habits and habitats in the adult and immature stages. The adults are almost wholly crepuscular and nocturnal and, during the day, rest quietly below the tall-herbage stratum of low wet areas: swamps, seepage areas, and especially the margins of swampy rills and creeks. The larvae and pupae are inconspicuous members of the neuston fauna of ponds and quiet backwaters, particularly of the calcareous waters of limestone sinkhole ponds.

Megistocera may be found on the wing throughout the year as far north as Alachua and Putnam counties. In an intensive study of the crane flies of the Welaka (Putnam County) area carried on for more than a year by R. E. Bellamy, Jr., adults were taken in every month except March, with the largest numbers in October and November. My own Alachua County records include collections for every month except August (this exception is doubtless due to the small amount of field work done in August) with decided peaks in April and October–November. This increase is probably not a coincidence, for these periods are ordinarily rather dry seasons in northern Florida; the pond surfaces are at low-water level, and neuston plants and debris are usually more concentrated than they are during the rainy season.

The adults are distinctly gregarious, often during daylight hours forming resting groups of a dozen to several score individuals. In "Sugarfoot Hammock" near Gainesville, Florida, where *Megistocera* was frequently common, a small sluggish stream meanders through the low swampy ("low hammock") woods. This stream for several hundred yards is a succession of small pools and shallows, which are bordered and invaded by a luxuriant growth of lizard's-tail (*Saururus cernuus*). Here in April and in late October one could often find two or three groups of perhaps a score of individuals. Each of these groups was concentrated on the leaves of a few immediately adjacent plants, and no solitary specimen was to be found for many yards of apparently identical cover. Nearly every leaf on the lower half of a plant had two to four adults resting on the top surface, which was inclined at an angle of about 45 degrees. The flies adopt a "shingled" arrangement on the leaf, with the outspread legs of one having a one-third overlap with those of the adjacent individuals, so that the legs, and occasionally the bodies, are in actual contact. If one fly was disturbed all those on the leaf, and usually those on adjacent leaves, took to the wing, so that the whole group would be almost immediately in motion. If not too greatly disturbed, each individual confined its flight to a swift, shuttlelike movement that described an ellipse, vertical to the ground and perhaps twelve to eighteen inches in its long axis. At one end of the ellipse the fly was within an inch or so of the leaf on which it had been resting, and then gliding or flying backward and slightly downward to the other end of the ellipse, it flew forward toward the leaf along the upper side of the elliptical path. During the whole flight, which is remarkably fast and difficult to follow, the fly always faces the leaf and repeats the same path. With a dozen to a score of flies in motion at once, each holding to its own orbit but all close together and flicking in and out of dappled light beneath the uppermost *Saururus* leaves, one often only sees shuttling specks of light that are difficult to recognize as flying insects. When the flies were more greatly disturbed the whole group scattered among the herbage, flying for several to many yards, to become dispersed throughout a long extent of stream-course herbage. Twice when a group was thus broken up in the early afternoon, it reassembled in the original location or a near-by spot a few hours later.

The individuals which comprised these aggregations appeared to be largely males, but since it is necessary either to net a fly or get within a few inches of a resting *Megistocera* to be certain of the sex, the apparently great preponderance of males may be due to insufficient sampling. In the only other crane flies in which marked gregariousness is commonly noted (several species of the related genus *Dolichopeza*) males and females are usually represented in nearly equal numbers. In *Megistocera longipennis* the shuttling flight of a number of adjacent individuals suggests the mating swarms characteristic of many crane fly or other insect species, but I have never seen mating result or found a pair in copula during daylight hours. It is not unlikely, however, that at late dusk, when the flight becomes much more spontaneous, or at night, it may serve a nuptial function.

I have never observed more than an occasional and solitary adult in the immediate vicinity of the larval habitat, and then only at late dusk or at night, probably a female returned to the pond to oviposit. All of the aggregations and most of the individual adults I have seen or have netted were four to twelve hundred yards from the nearest larval habitat. A sinkhole pond in which abundant larvae and pupae were present in five different years, lies in an open dry cultivated field, almost a quarter of a mile from the nearest habitat where an adult was found—or seemed at all likely to occur. There is ample evidence that the adults range widely on humid nights. At such times they come rather freely to light, at distances not infrequently half a mile or more from any known or probable daytime habitat. Nothing is known of the feeding habits of the adult. A single female was once netted at night from a flowering mango tree where other crane flies were feeding in large numbers, but it was not seen feeding. In my rearing cages one would occasionally drink briefly from the sugar solution supplied.

The eggs are deposited in the surface film of the ponds, in the few instances seen, well out from the shore and from the zone of emergent vegetation. The female alights upon the surface, remains for a few seconds, and then flies a few feet to repeat the process. The instances observed were always at late dusk when detailed observation is not possible, but the fly does alight upon the surface and cease to move its wings. I succeeded twice in netting flies after watching them perform, and in both instances they were females which had a partial complement of eggs remaining. I have been able to find only a few eggs in the ponds. These occurred singly and were floating at the surface in contact with an algal strand or bit of debris. In my aquaria the eggs were always placed in or about a stranded bit of algae in the very shallow film of water that was provided. Counts of the egg complement made by dissecting two fully matured, two-day-old females that had not yet oviposited gave 178 and 186 eggs, respectively.

The length of the egg stage in out-of-door aquaria in October was five to ten days. A minimum of five days and a maximum of eight was shown by one clutch of eggs in the same aquarium. No water temperatures were taken, but the air temperature during the period averaged 60 to 70 degrees.

The most striking feature of the pre-adult adaptation to life in the neuston region is the caddis-like, case-dwelling habit of both larva and pupa. The larva does not construct its own case but selects it ready made from floating pieces of hollow stem. The most dependable supply of cases appears to be the abundant fragments of stems and branches of last year's growth of *Nama* (=*Hydrolea*) *quadrivalve*. This is a coarse, bushy, aquatic herb nearly always present in the shallow margins of the waters in which specimens of *Megistocera* occur and is probably an important element of a suitable *Megistocera* habitat. Requirements for the case are that it float barely awash at the surface and be in the form of a tube open at both ends, one to two or three times the length of the larva, with a bore about twice the diameter of the extended larva. Occasionally, a floating segment of a hickory-nut hull that has been tunneled by a husk-boring larva provides a usable case, and I found that bits of "pipe-stem" cane or even short lengths of glass tubing when buoyed up with cork, if left afloat in the pond, were frequently utilized and made fairly efficient traps for securing larvae. The tube-dwelling habit begins some time before the ecdysis of the first instar. For a day or so after hatching the nearly transparent young larvae are free-living members of the infraneuston and may be found among the filaments of surface algae, but by the time they have reached a length of 3 mm., they are almost invariably in cases.

At rest the larva lies wholly in the tube except that the caudal disk is in contact with the water film. If disturbed or moving forward to feed, the caudal disk is drawn wholly within the tube, the long finger-like lobes of the disk closing toward one another to form an elongated air column to the surface, or to hold a large bubble of air that is drawn into the case. When feeding or moving about in the film the head and as much as the anterior third of the body may be protruded from the mouth of the case, the caudal end and attached air bubble or air column drawn far inside the other end. Movement within the case is doubtless aided by the larva's dorsal and ventral creeping welts, but major movement is effected by elongations and contractions of the body with the strongly expansible sixth abdominal segment acting as a hind, and the expansible anterior thoracic segment as a front, anchor. The sixth abdominal segment is *Megistocera*'s most conspicuous and special adaptation for its case-dwelling habit. It is capable of a dorsoventral enlargement to at least three times the normal diameter, and when expanded against the bore of the tube provides so tight a hold that the larva will be torn in two if one attempts to pull it forcibly from the case.

Locomotion of larva and case is effected either by the larva grasping some external object in the mandibles and hauling the case forward by a body contraction, or by protruding the anterior third of the body from the tube and, lashing alternately to right and left, towing the case slowly through the water film.

Since the larva grows and the bore and length of the case are fixed, a succession of progressively larger hollow stems must be utilized. As the old case becomes tight, new ones are explored, without the larva completely leaving the old one, until a suitable new case is found. Not infrequently a new case investigated proves to be already occupied and, if so, is stoutly defended by the occupant. Defense is by vigorous pushing and biting, the invaded larva, if taken in the rear, turning quickly within the tube to face the trespasser, which soon retreats to explore another hollow stem.

In daylight feeding the larva extends as much as the anterior third of its body from the tube to find algal strands and other floating vegetation. Feeding is rapid and vigorous, and entire algal filaments are ingested lengthwise by a series of hauling movements with mandibles and head capsule. Succulent floating leaves are taken piecemeal by biting out pieces from the margin. Intestinal pellets, dissected out or voided by wild larvae, were preponderantly composed of the empty but often still connected cell walls of filamentous algae, with lesser quantities of leaf epidermis and, in April, of pine pollen.

The shortest timed larval period in my aquaria, from hatching to pupation, was eight weeks, within one or two days; the longest was slightly more than twelve weeks. The individual lengths of the apparently four instars were not obtained, but the first is relatively short, usually not more than a week.

Pupation takes place in one end of the last larval case, with the pupa completely enclosed save for the long pronotal breathing horns, the tips of which reach the surface film. The pupa is capable of some movement within the case and, if submerged, moves to regain contact with the surface film. Just before emergence it protrudes its anterior third beyond the mouth of the case, dorsal surface uppermost and in or above the surface film.

Pupae that were removed from their cases and returned to the water behaved as normal infraneuston forms, floating just beneath the surface with the pronotal horns in contact with the surface film. Just before emergence these pupae came to float dorsal surface uppermost in the surface film, and the adults emerged successfully and rested unwetted on the surface film until sufficiently hardened to fly. The hardening period is short, perhaps three to five minutes or less, and the "take-off" in flight from the water surface is without struggle or undue effort. In fact the newly emerged adult seems unwettable and able to utilize the water film like a leaf surface for a resting place. Possibly there is some relation between this ability to lie unwetted upon the water surface and the characteristic sprawl of the adult upon a leaf, the legs in contact with the surface and the tips of the feet extending beyond its periphery.

The length of the pupal stage in the rearing jars has been as short as six days, but in cool weather it may be considerably longer. The minimum life cycle, from oviposition to adult, may thus be as short as ten or eleven weeks. This would permit four generations each year, and the very definite April and October–November peaks in the adult population may be interpreted as indicating either that the completion of the life cycle in nature averages nearly six months, or that the dry seasons are more favorable for emergence and survival of the adult.

DESCRIPTION OF IMMATURE STAGES

EGG.—The egg is slender, cylindrical, with a hardly perceptible curve at mid-length and bluntly rounded ends; length, 0.65 mm.; diameter, 0.12 mm. Chorion opaque brown, thin, and smooth.

LARVA.—There appear to be four instars that may be distinguished by their head-capsule lengths of approximately 0.3, 0.6, 1.0, and 1.5 mm., respectively. The last three are very similar in all respects except size; the first differs in several details, especially in the form and appearance of the spiracular disk. All measurements were made from specimens that had been killed in hot water and preserved in alcohol, and they show an intermediate state between maximum contraction and maximum extension, although somewhat nearer the latter.

Newly hatched larva: Length, 1.8 mm.; diameter, 0.18 mm.; length of head capsule, 0.29–0.31 mm. Integument semitransparent, light brownish gray; dorsal, pleural, and ventral surfaces alike in pattern and color. Anal gills not discernible; caudal disk with four evident, subequal lobes, the laterals and ventrals; these triangular in caudal view and only slightly longer than basal width. The apical third of the lateral lobes with about six and the apical two-fifths of the ventrals with about twelve strong, flexible setae that are about twice as long as the lobes that bear them. These setae lack the enlarged bases of the caudal-lobe setae of the later instars. The larvae appear to attain a length of about 3.5 to 4.0 mm. and a diameter of 0.35 mm. before the first ecdysis.

Fully grown larva, at end of last instar (Pl. I, Fig. 3): Length, 21–23 mm.; diameter at second thoracic segment, 1.8–2.0 mm; dorsoventral diameter of sixth abdominal, 2.8–3.0 mm.; dextrosinistral diameter, 2.2–2.4 mm.; dorsoventral diameter of caudal disk, 0.5 mm.; dextrosinistral diameter, 0.8 mm.; length of dorsal, lateral, and ventral lobes of disk, 0.5, 0.8, and 1.4 mm., respectively.

Form nearly terete, slightly greater in dorsoventral than dextrosinistral diameter; diameter increasing very gradually from thorax to sixth abdominal segment, thence decreasing somewhat more rapidly to caudal disk.

Color reddish brown in specimens preserved in alcohol; a more grayish and translucent brown in life, with the thoracic and seventh and eighth abdominal segments perceptibly darker. Color largely caused by dense microscopic hairs; those of dorsal and ventral surfaces in form of close (100 per mm.) parallel transverse rows of thickly set, uniform, rather stiff hairs, some 0.02 mm. long. The pilosity of the pleural surfaces nearly equally dense, but longer, softer, and set in irregular whorls that produce a somewhat mottled appearance. The different hair patterns of the pleural, dorsal, and ventral surfaces producing a distinct striped apppearance, especially in the living larva. The usual setae present; elongate and erect, but very slender, soft, and pale.

Caudal disk conspicuous, both in size and markings, with conspicuous stigmata and lobes. Lobes somewhat flattened in the plane of the disk when extended, their margins fringed with an even single row of long specialized setae or sensory hairs, which arise from slightly enlarged, papilla-like bases. These hairs range from 0.15 to 0.6 mm. in length and are longest on the apical two-thirds of each lobe. The four conspicuous anal gills are slender and cylindrical and markedly contractile; those of the most extended set in the preserved material before me are 1.6 mm. long and 0.3 mm. in diameter. The two gills on each side have a common base; the bases of the right and left sets widely separated ventrally.

Head capsule (Pl. II, Fig. 3) of typical tipuline form. Length, 1.4–1.6 mm.; greatest breadth, 0.85–1.0 mm.; dorsomedian suture of lateral plates arched strongly dorsad in its caudal third so that caudally the head capsule is as deep as it is wide. Labrum broad, with a broadly rounded anterior lobe that bears a dense brush of stiff hairs on its ventral surface and anterolateral margin; proximad of this brush each laterodorsal area with about five pairs of small, setae-bearing papillae. Antennae comparatively elongate; first segment nearly globular, uncolored and little chitinized; second segment cylindrical, three to four times as long as diameter, well chitinized, brown; apex with a small papilla and a conspicuous slender, conical spine two-fifths as long as second segment. Maxillae flattened and subrectangular in ventral view; their median and cephalic margins with dense brushes of short stiff hairs, their palpi short cylindrical, a small cushion of strong setae on membranes between palpi and apical brushes of setae. Mentum (Pl. II, Fig. 2) with anterior plate extensive and well chitinized, subrectangular; cleft extending to base of central tooth; anterior margin rounded, with nine teeth; central tooth largest but projecting less than half its length beyond apices of adjacent laterals; laterals progressively smaller laterad, the outer tooth on either side subvestigial. Hypopharynx narrow; upper plate heavily membranous with dense short hairs, lower plate with five teeth, the central slightly larger and more projecting than the laterals. Mandibles typically tipuline, in lateral view about three times as long as wide; mesially with a strong ridge at about mid-length, its crest projecting disto-mesad; the dorsal angle of this ridge prolonged into a strong, subconical tooth, the ventral angle produced into a flattened cutting edge, the margin between slightly serrate. Distad of the ridge the margin of the mandible bears six teeth, a large apical, a smaller and more dorsal but still conspicuous subapical tooth, and two smaller teeth on both dorsal and ventral margins, basad of the apical teeth.

PUPA (Pl. I, Figs. 1–2).—Length (cephalic crest to tip of caudal), 15.5–18.0 mm.; cephalic crest to apex of wing pad, 7.5–8.0 mm.; length of wing pad, 5.6–6.0 mm.; of longer pronotal breathing horn, 6.7–7.3 mm.; of shorter, 4.2–4.8 mm. Diameters at base of wing pads; dorsoventral, 2.5–2.7 mm.; dextrosinistral, 2.3–2.5 mm.

Form nearly cylindrical, with cephalic end truncate, and last three abdominal segments tapering to bases of caudal sheaths. Color varying from pale yellowish brown to dark reddish brown with age; the pleural region of abdomen, and large mottlings on head and dorsum of thorax distinctly paler; bases of prothoracic respiratory tubes blackish. Wing sheaths extending to caudal margin of second abdominal segment; mesothoracic and metathoracic tarsal sheaths, to nearly midlength of fifth abdominal segment; prothoracic tarsal sheaths, to about caudal margin of third. Antennal and palpal sheaths distinct, the basal part of antennal sheath forming ventral part of cephalic crest, and bearing small outward projecting "thorns." Cauda conspicuous, comprising thorny sheaths of the six caudal lobes of larvae and, ventrad of these, sheaths of the adult genital terminalia; the terminalia in female pupa extending caudad of apices of middle (lateral) caudal lobes; in male, not beyond mid-length of these lobes. Pronotal breathing horns directed more or less cephalad, elongate but conspicuously unequal, the longer subequal to slightly longer than wing pad, the shorter two-thirds or less as long; each a spirally sculptured slender tube; the apex smooth, abruptly widened, somewhat flattened, and showing an open suture along one margin. The inequality in the length of the breathing horns appears to be invariable and usually to approximate the proportion of two to three, but the longer horn was dextral in ten and sinistral in six of sixteen pupae, with no apparent correlation with sex.

A COMPARISON OF THE KNOWN LARVAL FORMS AND HABITATS OF THE DOLICHOPEZARIA

The immature stages and habitats of representatives of three genera of the Dolichopezaria, *Dolichopezia* (*Oropeza*) *obscura, D.*(*O.*) *sayi, D.*(*O.*) *subalbipes,* and *D.*(*O.*) *walleyi; Brachypremna dispellans;*[1] and *Megistocera longipennis,* may now be compared.

The most striking impression obtained by such a comparison is that tremendous dissimilarity exists between the larvae and, to a lesser extent, the pupae of the three genera. I can find no character common to the three genera that would separate their larvae as a group from the larvae of *Tipula* or *Nephrotoma.* Indeed the only feature common to the three, or to any two of the three, is the similarity of head capsules, but these are of so typical a tipuline form as to be equally difficult to distinguish from those of *Tipula* or *Nephrotoma.* In all other respects the larvae appear to differ far more

[1] I am indebted to Dr. R. E. Bellamy, Jr., for the loan of larvae and a pupa of *Brachypremna dispellans,* reared by him from the eggs at Welaka, Florida. By comparing his specimens with a large number of unknown Florida larvae and pupae that had been taken in the field and had detailed habitat data, it was possible to identify unmistakably nearly a score of larvae and several pupae as *Brachypremna dispellans.*

from each other than they do from the *Tipula* larvae that share the same or similar habitats, so that, in view of the evident relationships in the adult structure and even in the adult behavior patterns of members of the three genera, one is forced to conclude that the evident differences in larval characters are adaptive rather than phylogenetic. The possession of a common type of head capsule is not an exception to this conclusion for, in common with the great majority of *Tipula* larvae, all these larvae are herbivorous, feeding on algae, mosses, liverworts, and the very tender parts of herbaceous plants.

All of the known larvae of *Oropeza* live in or adjacent to mosses or liverworts, tunneling down to or shallowly into the substratum of rock, wood, or wet earth, and feeding on the more succulent parts of mosses or liverworts. All are strikingly alike, with a mottled gray-green integument, a large, rather truncate caudal disk, development of the anal gills into a quadrate-lobed, rather bulbous pushing organ, and with one apparently unique feature, a prominent conical lobe on each caudal dorsolateral point of the eighth abdominal segment, just cephalad of the somewhat similar dorsolateral lobes of the caudal disk. Aside from these eighth abdominal lobes the known larvae of *Oropeza* are like the moss-inhabiting larvae of *Tipula* (*S.*) *hermannia* or (barring the form of the gills), of *T.* (*Y.*) *iroquois* or *T.*(*N.*) *nobilis*.

The larvae of *Brachypremna dispellans* are nonaquatic dwellers in the wet to saturated black organic soil of seepage areas, damp shaded stream banks, or low, wet grasslands. They occur beneath the liverworts or damp moss mats of swamp hummocks and beneath and among the matted stolons and roots of the luxuriant carpet grass sods of low, wet, meadow-like situations. Most of the larvae I collected were with the larvae of *Tipula* (*S.*) *synchroa* and show a remarkable resemblance to them in the form of caudal disk, the lack of evident anal gills, and especially in the conspicuous hairy outgrowths dorsad and cephalad of the caudal disk. The larvae of *B. dispellans,* however, differ markedly from those of *T. synchroa* in the strikingly hairy integument of the entire body surface, caudad of the relatively bare first two thoracic segments. These dense body hairs retain a coat of the mud in which the larva lives, so that most specimens require a rather careful brushing and washing to disclose the integument and the close set pattern of stiff, moderately elongate hairs.

The larvae of both *Oropeza* and *Brachypremna* are noticeably sluggish in contrast to the quick movements and generally alert behavior of the larva of *Megistocera longipennis,* which in general appearance is much more like that of various amphibious members of the *Tipula* (*Y.*) *tricolor* group. The only other neuston-inhabiting cranefly larva that I know, *Limonia* (*D.*) *distans,* belongs to the subfamily *Limoninae* and is hardly comparable in appearance or type of adaptations.

PLATE I

Larva and pupa.

FIG. 1. Female pupa (× 7), side view.
FIG. 2. The same specimen, ventral view.
FIG. 3. A partly extended fully grown larva (× 6), side view.

Drawn by Mr. Jon Herring, Department of Biology, University of Florida, from specimens preserved in alcohol.

PLATE I

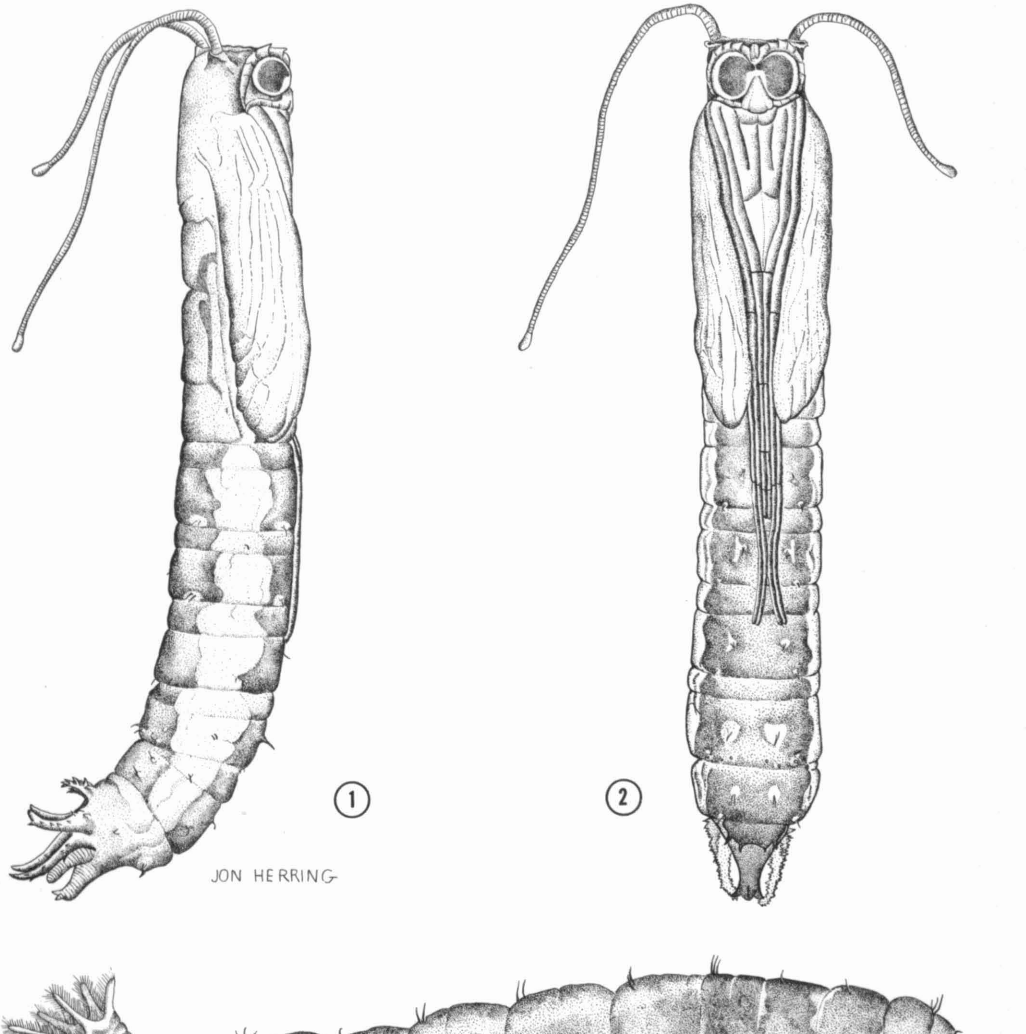


PLATE II

Details of larval structure

FIG. 1. Anal gills (× 12) alcoholic specimens. In life the gills may be extended until they are longer than the lobes of the caudal disk (shown here in silhouette) or contracted into a pair of rounded bulges.

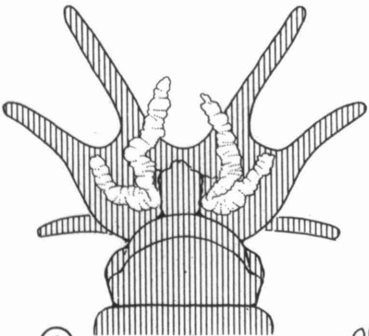
FIG. 2. Mentum of head capsule (× 35); ventral view of cleared specimen.

FIG. 3. Head capsule (× 35) dorsal view. The left mandible has been removed to show mesal aspect of outer half of left maxilla. Drawn from opaque and cleared specimens.

FIG. 4. Caudal disk (× 30). Drawn from flattened and cleared slide mount, color pattern from alcoholic specimen. This is the view seen when the disk is expanded in the surface film. The setae of the lobes are accurate as to number, position, and size, but since they are whitish hyaline in color, they are less conspicuous than indicated.

Drawn by William H. Brudon from specimens preserved in alcohol and from cleared slide mounts.

PLATE II



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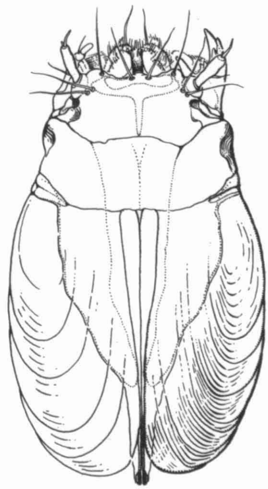

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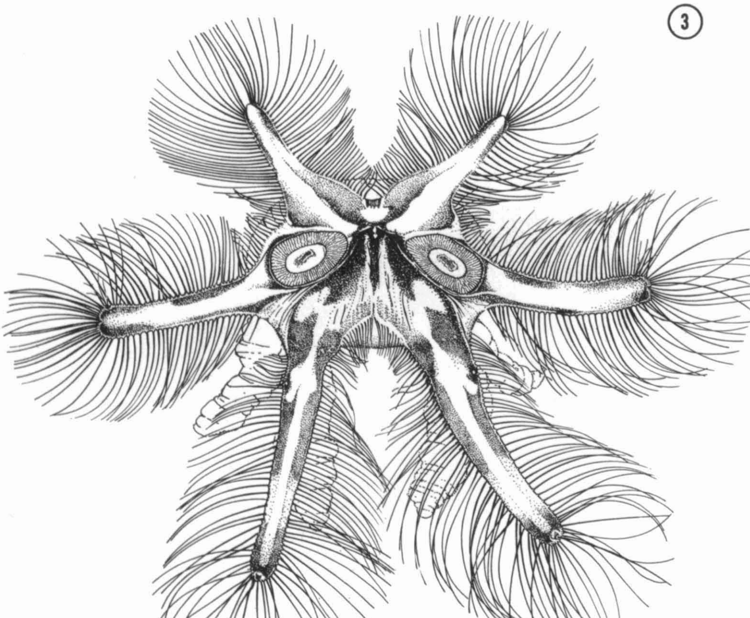

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