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CONTRIBUTIONS TOWARD A KNOWLEDGE OF THE NATURAL HISTORY AND IMMATURE STAGES OF THE CRANE-FLIES

I. THE GENUS *POLYMERA* WEIDEMANN

BY J. SPEED ROGERS[1]

THE genus *Polymera,* including more than a score of living and one fossil (Baltic Amber, Oligocene) species, is represented in the continental United States by *Polymera georgiae* and *P. rogersiana,* both confined to the southeastern Coastal Plain. The other species of the genus occur in the Antilles and in tropical and subtropical America. It is the purpose of the present paper to describe the habits and immature stages of the two Coastal Plain species and to point out the evidences of the systematic position of the genus provided by the larval and pupal stages.

POLYMERA GEORGIAE ALEXANDER

Polymera georgiae Alexander, C. P., Psyche, 18, 1911: 199, pl. 16, fig. 5.
Alexander, C. P., Proc. Acad. Nat. Sci. Phila., 68, 1916: 535.

GEOGRAPHIC AND SEASONAL DISTRIBUTION

Florida.—Throughout the state with the following records for adults: Alachua County, January to December, inclusive;

[1] Contribution from the Department of Biology of the University of Florida.

Broward, Collier, Glades, Highlands, Levy, Liberty, Manatee, Orange, Palm Beach, Sarasota, and Suwanee counties, January, March, June, July, August, November, and December.

Georgia.—Charlton County, June (Alexander, 1916); Decatur County, July (Alexander, 1916); Dooley County, March; Glynn County, May (Alexander, 1911—type locality). All of these records, except that for Dooley County, are for the extreme southern or southeastern Coastal Plain. Dooley County is near the northern limit of the Coastal Plain, but the three specimens taken there were from a typical Coastal Plain habitat, a pinewoods and cypress swamp margin.

South Carolina.—South Island, Georgetown County, August (Alexander, 1916).

Habits and Habitats

The adults are frequently common, occasionally abundant, about the margins of ponds, lakes, and marshes that have a considerable development of silty or swampy shore line; they are occasionally taken in the cypress and hardwood swamps of creek and river flood plains. They spend the daylight hours within the herb and shrub strata, resting on or beneath the shaded lower stems and leaves. Toward twilight, the flies gradually become more active, and from late twilight until morning range far from their daytime haunts. Numerous "At Light" records are obtained for distances of from several hundred yards to more than half a mile, from any known or probable daytime habitat, and the females are frequently found ovipositing at night along the bare shore lines of ponds that are surrounded by complete and extensive clearings in which no adults can be discovered during the day.

Copulation and oviposition appear to be confined to the early part of the night. A considerable proportion of the flies that come to light between dusk and 9 or 10 o'clock are in copulation; after midnight, most of the records are for single flies. In breeding cages, copulation and oviposition begin shortly after dusk unless inhibited by artificial light. Once either process is begun, however, it is not immediately interrupted by the turning on of lights. I have never observed the beginning of copulation in the field, but from the behavior of the males, both in the field and in large breeding cages, it seems probable that some sort of swarming flight takes place soon after nightfall. Oviposition has been observed in the field at night with the aid of a diffused light. It is of a common crane-fly type, the female walking over saturated silt, probing at irregular intervals with her ovipositor, laying from 3–8 eggs in close proximity when a suitable spot is found, and then walking or flying to another spot a few feet away to repeat the process. The eggs are placed 2–4 mm. below the surface, and the consistency of the silt is such that the tiny puncture made by the ovipositor soon oozes shut.

On one occasion, adults were taken in the field at late dusk from the flowers of *Heliopsis* sp. Actual feeding was not observed but 2 or 3 flies were taken from, or while hovering about, each of 5 or 6 separate flowers. Adults in the breeding cages fed on dilute sugar solution and showed a marked preference to the sugar solution even though unsweetened water was available.

The larvae live in saturated silt, particularly in the fine, black largely organic mud at the margins of small pools and herbage-grown shore lines, and in the thin stratum of saturated, or barely submerged, silt that accumulates in small depressions (cattle tracks, ripple marks, etc.) on the dirty sand shores of swamp-bordered lakes. In any case, the larvae occur within the top 10–15 mm. and usually maintain a respiratory connection with the surface by means of capillary air tubes that lead to the spiracles. The porelike openings of these tubes are very difficult to discern unless one places a larva upon the surface of the silt and observes the formation of the tube as the larva promptly burrows out of sight. When the long brushes of hairs, borne on the ventral lobes of the spiracular disk (Plate II, fig. 8) are drawn beneath the surface, they form a tiny cylinder of evenly spaced and nearly contiguous vertical stays and so provide an unwettable lining for the capillary air passage. The pore that forms the mouth of the air passage is towed slowly about the surface of the silt by the movements of the submerged larva but is seldom closed by a deeper submergence. If the surface of the silt is inundated, or the larva forced deeper into the mud by being probed from above, the air within the tube is entrapped and remains in contact with the spiracles. In the breeding cages, when the surface of the silt had been inundated for several hours, the larvae appeared at the surface of the water, where they hung from the surface film, suspended by the now outspread hairs of the spiracular disk.

The larvae are wholly carnivorous. Small lumbriculid worms, young chironomiid larvae, and the small larvae of other nematocerous Diptera, are fed upon in the breeding cages, and the setae of lumbriculids are often to be found in the guts of larvae taken in the field. Small *Chironomus* and *Erioptera caloptera* larvae are ingested whole and head first. In one instance, a fully grown *Polymera georgiae* larva seized the first abdominal segment of an *Erioptera* and hung on in spite of violent struggles on the part of the victim. A little later, the *P. georgiae* larva began a series of swallowing movements that consisted, in part, of a retraction of its own head capsule back into the thorax and then a strong extrusion of the head capsule with a movement of the mandibles. The body of the *Erioptera* larva was pulled, doubled, into the mouth cavity and then pushed partially out again and at the same time the grip was shifted toward the anterior end. When the hold of the mandibles had reached about the juncture of the first and second thoracic segments of the victim, the latter's head was drawn completely into the mouth cavity of its captor on one of the in-pulling movements. After this, the body of the *Erioptera* larva was progressively swallowed, a millimeter or so at a time, in a series of active swallowing movements, interspaced by longer periods of rest. In a little more than 10 minutes, the *Erioptera* larva was wholly ingested. Other crane-fly larvae that often occur in the same areas of silt with *Polymera georgiae* and may, in their earlier instars, form a part of their food, are: *Pseudolimnophila luteipennis, Pilaria arguta, Erioptera* (*E.*) *vespertina,* and *E.* (*M.*) *caloptera.* Of these, however, *Pilaria arguta* is also predacious and probably feeds on *Polymera* to as great an extent as it is fed upon.

The larvae of *Polymera* are, in turn, preyed upon by the large larvae of *Tabanus* and *Crysops* that commonly occur in the same habitats. At least, the tabanid larvae destroy and feed upon *Polymera* larvae when both are placed in the same jars of wet silt. The chief predators upon the *Polymera* larvae are probably the smaller shore birds, plovers and sandpipers, that frequent the silty lake shores in great numbers.

Pupation takes place just beneath the surface of the silt, the tips of the pupal pronotal breathing-horns in contact with, or protruding slightly above the surface. In the breeding cages, pupae that were submerged for some hours wriggled free of the silt and appeared floating at the surface. In at least one instance, a normal adult emerged from a floating pupa.

The duration of the pupal stage has varied from 6.5 to 9 days in breeding cages exposed to out-of-door fluctuations of northern Florida weather. The duration of the egg and larval stages are unknown, but the time from oviposition to emergence of the adults has ranged from 4.5 to 7 months in out-of-door breeding cages. The 4.5 months' duration was from March 12 to July 20–30; the 7 months' duration was from early November to early June, but in this cage the food was probably far from optimum.

POLYMERA ROGERSIANA Alexander

Polymera rogersiana Alexander, C. P., Can. Ent., 61, 1929: 18.

Geographical and Seasonal Distribution

Florida.—Alachua County, April, May, June, July, September, and November.

According to Alexander, the nearest known relative of *P. rogersiana* is *P. obscura* Macquart, a northern South and Central American species that ranges into western Cuba.

Habits and Habitats

All of the specimens of *P. rogersiana* that have been taken thus far, some 20–30 adults and about the same number of larvae and pupae, were from the south slopes of the Devil's Mill Hopper, a deep, lime-sink with mesophytic vegetation and numerous springs and small rills. Here the adults, which appear to be strongly crepuscular or nocturnal, occur within dense shaded growths of ferns along small rill courses, or on the damp mosses and liverworts that line the miniature, intrenched rill courses. On the few occasions when lighting has been employed at the Devil's Mill Hopper, this species was not taken and few observations have been made on adult habits. The flies are hard to flush during the day and when disturbed, usually keep within the fern stratum, flying deeper among the dense growth of stems and fronds. Twice, in late afternoon, females have been flushed from the margin of a comparatively open rill course or seepage area, and were presumably engaged in ovipositing when disturbed.

The larvae and pupae occur in boggy seepage areas or the margins of spring rills where the disintegration of the soft limestone has left a residue of sticky, strongly basic clay. The surface of this clay deposit is more or less mixed with coarse sand and a scanty plant débris and varies from slightly to distinctly plastic. The immature stages have all been taken from this sandy clay, usually from small local patches where a slight accumulation of organic débris makes the saturated earth least plastic. Even these surface patches have a pH of 8.3 to 8.7. This larval habitat differs markedly from the usually slightly acid, largely organic silt occupied by the larvae of *P. georgiae* and has an entirely different association of crane-fly larvae. Occurring in the same or in overlapping habitats with *P. rogersiana* are: *Pseudolimnophila contempta, Limnophila* (*P.*) *epimicta, Gonomyia slossonae,* and *Erioptera* (*M.*) *needhami*. The last, together with several non-tipulid nematocerous Diptera and some very small lumbriculid worms, appears to form the chief food for *P. rogersiana*. Annelid setae have been found in the digestive tracts of larvae taken in the field, but in the breeding cages the larvae of *E.* (*M.*) *needhami* and of two other small nematocerous Diptera (Psychodidae ? and Dixidae ?) formed the chief food.

In the breeding cage, eggs were oviposited in October and adults appeared in early April, a generation with 5–6 months at out-of-door temperatures.

Descriptions of the Immature Stages

By Alexander's keys to the immature stages of the crane-flies,[2] the larvae of *Polymera* would key to the tribe Hexatomini, subtribe Limnophilaria, group Limnophilae. The pupae would key to the tribe Hexatomini, where they would end in couplet 5, neither fitting the subtribe Pseudolimnophilaria nor the group Ulomorphae of the subtribe Limnophilaria, although rather closer to the latter.

The corresponding immature stages of *P. georgiae* and *P. rogersiana* are so similar in all respects that dissection and detailed measurements are required to separate them. Even then, I believe, the two species can be more surely distinguished by accurate habitat data than on morphological grounds. The following descriptions of larva and pupa, drawn from an examination of 21 larvae and 9 pupae of *P. georgiae* and 15 larvae, 5 pupae, and 6 pupae skins of *P. rogersiana,* apply to both species. Such apparently constant specific characters as I can discern are given in keys to the larvae and pupae that follow the descriptions.

THE EGG

(based on *P. georgiae,* only)

Slender, slightly curved spindle-shaped; terete; markedly elongate. Dimensions: length, 0.53–0.54 mm.; greatest diameter (at midlength), 0.125–0.13 mm.; diameter at ends, about 0.03–0.04 mm. Chorion thin, delicate, transparent; contents an opaque, yellowish white. General appearance with reflected light, smooth, moderately shining.

[2] Alexander, C. P., "The Crane-Flies of New York," Part II, "Biology and Phylogeny," *Cornell Univ. Agr. Exp. Sta., Memoir,* 38 (1920): 690–1133.

The egg complement, as counted for two females, was 180–200.

THE FULLY GROWN LARVA

Length: 9–12 mm. Form: slender, cylindrical; dorso-ventral and dextro-sinistral diameters equal and approximately uniform from second thoracic to sixth abdominal somites, inclusive, 0.9–1.1 mm., varying with state of contraction and sex; first thoracic and eighth–ninth abdominal somites slender, conical, tapering to apices of body; seventh abdominal somite capable of moderate dilation. Color: in life, yellowish white, dark brown sclerotized portions of head capsule and minute markings of spiracular disk in marked contrast; in preserved specimens more opaque white, contrast with head capsule less marked. Integument: thin, nearly transparent, faint to marked amber tinge; with dense, long, appressed, microscopic pilosity; no evidence of creeping welts, inter-somitic incisures hardly evident with low magnification; setae few and nearly vestigial except on ninth abdominal somite.

Spiracular disk (Pl. II, fig. 8) reduced, markedly concave caudally and capable of closing so that caudal face is concealed and the spiracles apposed. Dorso-median lobe vestigial, barely indicated when expanded disk is viewed with magnification; paired dorso-lateral and ventral lobes distinct, cylindro-conical, their margins fringed with long hairs; dorso-lateral lobes shorter, blunt, their apical hairs 3–5 times as long as lobes; ventral lobes much longer, fingerlike, their apical hairs 8–10 times as long as lobes, caudal face of each with elongate brown stripe; spiracles oblique, oval, blackish brown. Anal gills 4, small, egg-shaped; their closely contiguous bases borne from common circum-anal ring.

Head capsule (Pl. II, figs. 1, 2) of limnophiline type, moderately reduced; heavily sclerotized portions include the elongate, paired, dorso-lateral and ventral rods (anterior end of each rod with distinct, and apparently freely movable, articulation with anterior portion of capsule); a dorsal, anterio-lateral framework of short rods; a massive, U-shaped, internal structure, that apparently represents the hypopharynx; and the conspicuous mandibles. The prefrons, labrum, and lateral plates are represented by thin, non-sclerotized, connected membranes, supported by and enclosing the anterior sclerotized framework. Dimensions: caudal margin to cephalic edge of labrum, 0.75–0.8 mm.; caudal margin to apices of maxillae, 0.95–1.1 mm.; width at base of mandibles, 0.22–0.24 mm.; depth at base of mandibles, 0.1–0.15 mm.; length of maxillae, 0.27–0.3 mm.; of antennae, 0.09–0.12 mm.

Antenna (Pl. II, figs. 4, 6): elongate cylindrical; basal joint cylindrical, second joint elongate cylindrical, bearing apically an elongate, segmentlike papilla, 1 elongate curved seta and several, indistinct, rodlike pegs; apical papilla 0.5–0.7 as long as second joint, slender cylindrical with rounded apex and faintly sculptured surface. Mandible (Pl. II, figs. 3, 5) of carnivorous type; base massive; 1 strong, conical, curved, long apical tooth; 2 small, flattened teeth on mesal surface at base of apical tooth. Maxilla principally or entirely developed as an elongate, slender, conical lobe, extending far cephalad of head; moderately sclerotized on basal half and along mesal margin of apical half, otherwise membraneous and delicate but turgid; with 2–3 minute, peg-bearing papillae near base of membraneous portion. Labrum thin, transparent; cephalic margin with minute sensory papillae on either side of median line; cephalo-lateral margins with elongate brushes of hairs (possibly pilose, projecting plates); epipharyngeal region not conspicuously developed. Mentum reduced, scarcely discernible, wholly membraneous and, apparently, completely cleft.[3] Hypopharynx massive, heavily sclerotized; caudal margin of cephalo-median portion with numerous, small, slender, caudally projecting teeth; lateral arms articulating with cephalic ends of ventral bars. Cephalic end of oesophagus with 20–30 parallel rows of close-set, minute points, making the oesophageal lining a conspicuous part of the

[3] I believe that the structure that I am interpreting as the hypopharynx in *Polymera* is homologus with the "transverse chitinized crossbar which is finely grooved," which Alexander (*tom. cit.*, 858) has interpreted as the mentum. If my interpretation is correct the mentum in the Limnophilae is likewise membraneous and largely vestigial.

cleared head capsule. Caudo-dorsal margin of the head capsule with paired, small, triangular, sclerotized plates; their caudal angles more or less prolonged into truncate flaps.

THE PUPA

Length, inclusive of pronotal breathing horns, 9.0–10.5 mm.; length pronotal breathing horns, 1.3–1.4 mm. (*P. rogersiana*) to 1.8–1.9 mm. (*P. georgiae*); dorso-ventral diameter at base of wing pads, 0.85–1.0 mm.; dextro-sinistral diameter, 0.8–0.9 mm.

Form slender, almost terete; elongate conical abdomen tapering to slender cauda. Head small, short; minute, simple, thornlike tubercles of cephalic crest nearly concealed in ventral view by bases of antennae. Antennal sheaths, arising at about midlength of mesal margins of eyes, rounded, prominent; straight lateral portion of each sheath with 7–10 distinct, short-cylindrical annuli of more heavily sclerotized bands; apices uniformly sclerotized, almost acicular; apices in male ending opposite caudal fifth of wing; in female, ending slightly beyond base of wing. Labrum small, narrow, caudal margin rounded; labial lobes fused, their common, caudo-median margin emarginate. Maxillary lobes straight, conical, their apices almost acicular. Caudo-lateral angles of genae flattened, slightly projecting.

Pronotal breathing horns (Pl. II, fig. 7) elongate, erect; except for apices, with fine but distinct, spirally wound corrugations; apical portion of each, 2 thin, lanceolate flaps. Pronotum with latero-cephalic angles slightly inflated, each projecting as small, subconical wart, armed with single minute seta on slender papilla; median line slightly keeled. Dorsum of mesonotum with cephalic angle abruptly convex, slightly crenulate; without spines or setae but simulating a crest by its elevation above caudal margin of pronotum. Wing sheaths ending at caudal margin of abdominal somite 2; sheaths of halteres, just beyond base of 1; sheaths of tarsi on basal annuli of 4; apices of tarsi varying from nearly coterminal to conspicuously uneven.

Abdomen with somites 2–7 divided into basal and distal annuli; basal annuli of terga and sterna 3–7 subdivided into 2 narrow, sclerotized, transverse plates. Caudal margins of distal annuli of terga and sterna with terminal rows of minute, setiferous tubercles. Basal annuli of pleura with 1 setiferous tubercle on each side; distal annuli with 2–4, very minute, setiferous tubercles on each side. Eighth somite with 1 large, conical tubercle on each caudo-lateral angle; region of caudal lobes with a low, conical elevation, spiracles not evident. Cauda of male elongate; ventral lobe short, truncate; lateral lobes elongate, oval, their mesal margins contiguous, flattened; dorsal plate with apex furcate and ending in divergent, pointed lobes, directed mesad. Cauda of female with lobes elongate; tergal lobes slightly longer than sternal.

KEY TO LARVAE AND PUPAE

Larvae

Pubescence of abdominal somites 7–9 brown; antenna (including apical papilla) 0.7–0.8 times as long as longest chord of mandible; caudal angles of caudo-median triangles of dorsum of head capsule distinctly projecting, flaplike. Average size of larvae and average length of head capsules slightly greater .... *Polymera georgiae*

Pubescence of abdominal somites 7–9 light golden yellow; antenna 1.1–1.3 times as long as longest chord of mandible: caudal angle of caudo-median triangles of dorsum of head capsule weak, acute rather than straplike. Average size and average length of head capsule somewhat less .... *Polymera rogersiana*

Pupae

Lanceolate apical flaps of pronotal breathing horns relatively short, contained 6–7 times in total length of horn; straight, lateral portion of antennal sheath with about 10 distinct sclerotized annuli.
Polymera georgiae

Lanceolate flaps of pronotal breathing horns relatively longer, contained 4–5 times in total length of horn; lateral portion of antennal sheath with about 7 distinct sclerotized annuli ...... *Polymera rogersiana*

Indications of the Systematic Position of *Polymera* Shown by the Immature Stages

In 1920, Alexander[4] proposed a greatly revised and detailed classification of the *Tipulidae,* based, in large part, upon his extensive and fundamental studies of the immature stages. *Polymera,* with its larvae and pupae at that time unknown, was assigned to a provisional subtribe, the Polymeraira and placed in the tribe Hexatomini. Later,[5] and largely on the basis of venational characters, *Polymera* was placed in the subtribe Epiphragmaria of the Hexatomini. More recently still, Alexander[6] has placed the genus in a more isolated position among the limnophiline subtribes of the Hexatomini.

As far as larval and pupal characters are concerned, *Polymera* appears to belong clearly to the subtribe Limnophilaria of the Hexatomini, somewhat closer to the group Limnophilae than to the Ulomorphae. The larvae of *Polymera* show clear affinities with those of the subgenera Dicranophragma, Limnophila, and especially Phylidorea of Limnophila. The chief disparity, the massive structure of the internal, sclerotized element of the head capsule of *Polymera,* that I have identified as the hypopharynx,[7] is suggested on a smaller scale in Phylidorea, particularly in a Florida specimen of this subgenus that is almost certainly *Limnophila (Phylidorea) epimicta.* The other peculiar feature, the relatively caudal position and marked development of the articulations of the ventral and especially the dorso-lateral, sclerotized bars of the head capsule, is also chiefly different in degree and position from the condition shown by Phylidorea, where similar articulations are less marked and much more cephalad in position. In other respects, the structure of mandibles, maxillae, antennae, and labrum, and in the charac-

[4] Alexander, C. P., *tom. cit.*: 690–1133.

[5] Alexander, C. P., ''The Interpretation of the Radial Field of the Wing in the Nematocerous Diptera with Special Reference to the Tipulidae,'' *Proc. Linn. Soc. New South Wales,* 42 (1927): 42–72.

[6] Alexander, C. P., Manuscript keys to genera and subgenera of North American Tipulidae, April 30, 1932.

[7] See footnote 3, page 9.

ters of the integument and body, *Polymera* differs little more from Phylidorea and Dicranophragma than they differ from each other or from Lasiomastix.

The characters of the pupae are in no way inconsistent with placing *Polymera* with or close to the group Limnophilae. The "key-character," the lanceolate flap of the apices of the pronotal breathing horns, can hardly have a phylogenetic significance since very similar structures are shown by such divergent groups as the subtribe Pseudolimnophilaria, and the group Ulomorphae of the subtribe Limnophilaria as well as certain species of the subfamily Tipulinae. In all other respects the pupae of *Polymera* hardly differ more from the pupae of the various groups—subgenera Lasiomastix, Dicranophragma, Limnophila, and Phylidorea—than these do from one another.

PLATE I. Larva, Female Pupa, and Male Adult of *Polymera georgiae* Alexander, drawn from specimens from Alachua County, Florida, by Grace Eager.

PLATE I

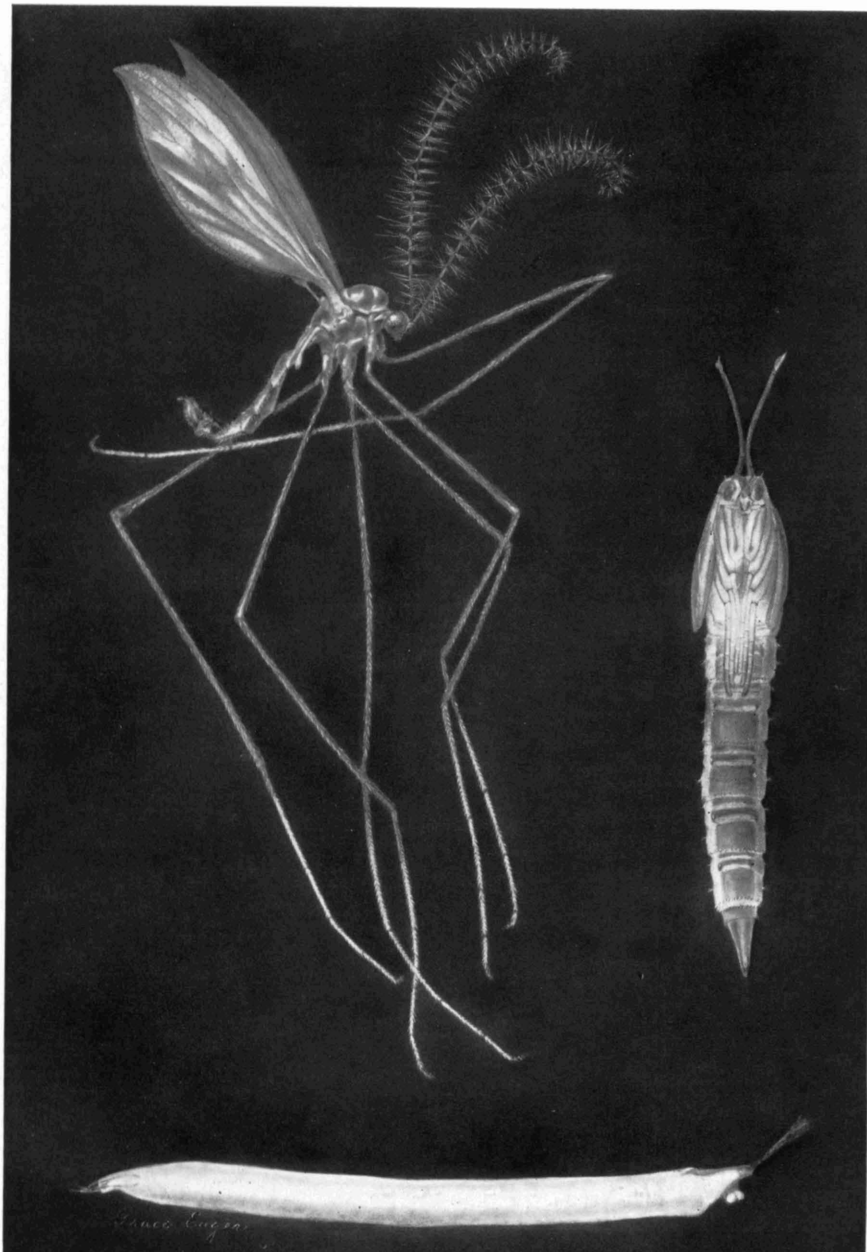

PLATE II. Details of Larval and Pupal Structure in *Polymera*.

FIG. 1. Head capsule of *Polymera georgiae*. Drawn in dorsal view from balsam mount.

FIG. 2. Head capsule of *Polymera georgiae*. Drawn in ventral view from alcoholic and balsam specimens.

FIG. 3. Left mandible of *Polymera georgiae*, dorsal view.

FIG. 4. Antenna of *Polymera georgiae*.

FIG. 5. Left mandible of *Polymera rogersiana*, dorsal view.

FIG. 6. Antenna of *Polymera rogersiana*.

FIG. 7. Pronotal breathing horn of pupa, side view, *Polymera georgiae*.

FIG. 8. Caudal end and spiracular disk of *Polymera georgiae*, dorsal view.

Plate II