

OCCASIONAL PAPERS OF THE MUSEUM OF
ZOOLOGY

UNIVERSITY OF MICHIGAN

ANN ARBOR, MICHIGAN

THE ECOLOGICAL DISTRIBUTION, LIFE HISTORY,
AND IMMATURE STAGES OF *LIPSOTHRIX SYLVIA*
(DIPTERA: TIPULIDAE)BY J. SPEED ROGERS¹ AND GEORGE W. BYERS²

THE crane fly *Lipsothrix sylvia* (Alexander) belongs to the small but interesting assemblage of tipulid species that appears to be limited in distribution to the Appalachian Highlands. More widespread than most other species of the group, it is a characteristic spring and early summer member of the streamside fauna of upland rills and brooks throughout the New England, Adirondack, Appalachian Valley, Appalachian Plateau, and Blue Ridge provinces and is present in much of the upland part of the Piedmont region.

Throughout this territory, if one collects along a mountain brook in late May or June, he will usually find a well-marked pattern of ecological distribution of this species from the stream source to the lower valley. As long as the rill or brook is small and has too gentle a gradient to have developed steep banks and a swift, tumbling current, *L. sylvia* is a common and frequent member of the crane-fly fauna. Downstream, as the brook increases in size and in the turbulence of its periodic floods, the occurrence of *L. sylvia* becomes much

¹Dr. Rogers, who was Director of the Museum of Zoology, died May 17, 1955, aged sixty-three years. An obituary and portrait will appear in the Report of the Director for 1954-55. He had completed the parts of this paper on the ecological distribution, life history, and relationships of *Lipsothrix sylvia* and had supervised the drawing of Figures 5-7 by Mr. William L. Brudon. It has seemed best to leave these parts essentially as he prepared them, including his use of the first person singular in some places.

²Lt. G. W. Byers, Department of Entomology, AMSGS, Walter Reed Army Medical Center, Washington 12, D.C., completed this paper by describing the immature stages from material collected by Dr. Rogers and supervised the final drawing by Mr. Brudon of Figures 1-4. After April, 1956, his address will be the Department of Entomology, University of Kansas, Lawrence, Kansas.

more sporadic, restricted to the quieter reaches or to small falls and rapids where logs or tree limbs are strongly lodged in the spray and trickle zones. Still farther downstream, where pools and riffles characterize the stream, *L. sylvia* almost disappears from the streamside fauna except for an occasional restricted population at the juncture of some valley rill with a creek. This pattern of local distribution, which has been quite evident wherever I have been able to follow it in detail—in the Cumberland Plateau in Fentress and Morgan counties, Tennessee, in the Blue Ridge in Macon and Transylvania counties, North Carolina, and in the Ridge and Valley Province at Mountain Lake, Giles County, Virginia—is clearly correlated with the larval habitat and the requirements for oviposition, pupation, and emergence of the adult.

The larval habitat is completely waterlogged wood—sodden logs and limbs that are either largely submerged or lodged beneath permanent trickles or sprays. Oviposition is dependent upon a situation in which some part of this wood is either permanently or frequently emergent, or submerged by no more than a trickle of water; and although the pupae can survive at least forty-eight hours of continued inundation, the emergence of the adult appears to require a surface of wood that extends above the water surface.

Once the larval habitat was discovered, and oviposition and emergence from the pupa had been repeatedly witnessed, some days were spent at Mountain Lake in late May and early June, 1946, in an attempt to ascertain any factors that might limit the availability of the abundant sodden wood for utilization by *L. sylvia*. Some fifty samples of wood (fragments of limbs ten to eighteen inches long and two to six inches in diameter and surface slabs cut from larger limbs and trunks) were collected along the courses of three rills or brooks at Mountain Lake. These pieces were all completely sodden. Some were not submerged, but owed their thoroughly waterlogged condition to the fact that they lay on the mud of permanent boggy springs or in the margin of spring rills; others were totally submerged, lying two or three inches beneath the normal water level of the stream. The rest, showing various degrees of partial submergence, consisted of logs and limbs fallen across the stream course or lodged lengthwise in the streams and with at least one end above the normal water level.

The fourteen samples of wood in which larvae, pupae, or empty pupal skins were found were all from the partly submerged group, and all were from flowing water. In most instances the wood was not identified, but rhododendron, hickory, and ash were represented

among the samples. The inhabited wood had lost all traces of bark, was heavy enough to sink in water, and usually had a moderately hard surface, apparently formed of summer wood, the softer spring wood of the annual ring being quickly eroded when exposed. All of the logs or limbs inhabited by *L. sylvia* were very firmly lodged and had the appearance of having been in place for a considerable time, perhaps a year or longer. Two logs some twelve to sixteen inches in diameter, lying across Hunters' Branch and forming partial dams, had frequently been used for observation of oviposition and emergence in 1946. These were still in position and inhabited by continuing generations of larvae when revisited in September, 1947, and April, 1949.

From these and additional observations and collections in other areas it seems evident that the most critical condition necessary for the maintenance of a population of *L. sylvia* is a stable supply of dead wood, partly submerged in, or continuously wetted by, well-aerated water. Water temperature seems not to be a controlling factor, for spring and summer temperatures in a rill may vary widely, at least from 45° to 65° F. Occasional total submergence for some hours or even days is not detrimental so long as the wood is not dislodged. The necessary conditions are thus most commonly and dependably provided by small, spring-fed streams so near their sources that torrential floods do not occur. Here, sizable trunks or limbs falling into or across the streams will remain in place for the whole period of their gradual decay, and if, as is usual, the area is wooded, there is a constant and ample supply of falling logs and branches. As the stream increases in size and in the violence of its spring and summer-rain floods, the sufficiently stable lodgment of logs in the required in-and-out-of-water position becomes much more dependent upon chance, or upon some special feature of stream topography, such as miniature waterfalls, where logs carried downstream by unusually high floods may lodge and remain in place through the normal floods of succeeding years.

Several of the logs inhabited by the immature stages of *L. sylvia* extended for a considerable distance beyond the stream. In these the nonimmersed part was often in an advanced stage of decay, being most decomposed at the greatest distance from the water. From these unsubmerged but still rather sodden parts the larvae of *Epiphragma fascipennis* and *Elephantomyia westwoodi* were obtained.

The imagines of *L. sylvia* are rarely found more than a few yards from the stream courses. They may often be swept from the vegetation of the banks, or be found hovering over or walking about on the wet

wood that protrudes from the stream. Oviposition and mating may be observed at almost any time of day in shaded situations; on several occasions, in places where large logs or several smaller logs piled in a jam against the face of a waterfall provided extensive areas suitable for larval habitat, several scores of the flies could be seen at one time ovipositing, mating, or walking on or flying near the wet surface of the wood. Mating appeared to be initiated by chance encounters between walking or hovering flies; the frequency with which the mating pair included a rather teneral female suggests that the males may seek recently emerged females as they rest and harden on the damp logs, close to their empty pupal skins.

Although light-trapping was carried on intensively at Mountain Lake, and traps were operated throughout the night within fifty yards of a rill where *L. sylvia* occurred, no light-trap records were obtained.

THE LIFE CYCLE

When laying eggs in the saturated fiber of barely submerged wood, the female fly stands at the edge of the water, or even in shallow margins, where foothold and current permit. Probing the surface with her ovipositor and apparently seeking minute crevices or softer spots in the wood, the female here and there inserts her ovipositor briefly to a depth approximately half to three-quarters of its length, that is, about 0.75 to 1 mm. In only three instances was I able to find the small, delicate egg at the base of the puncture, and I cannot be certain whether more than one egg was laid at a time. The three found were in the soft but firm spring wood just beneath the harder layer of summer wood that formed the thin, outer crust.

I was unable to obtain any data on the duration of the egg stage and did not find any first instar larvae. Since all third and fourth instar larvae were taken from beneath the surface of the submerged part of the log within 1 to 4 mm. of the surface, I assume that on hatching the first instar larvae begin to feed on and tunnel through the soft spring wood, keeping within or moving toward completely saturated conditions.

Eight of the some hundred larvae taken from two logs on May 26 and 28, 1946, are considered to be in the second instar, about fifty in the third, and forty in the fourth. These must all have overwintered as larvae. Their numbers and stage of development seem to correlate rather well with observations on the time of year that the imagines are on the wing at Mountain Lake. This is from May 23 to July 18,

the population increasing rapidly from late May to a maximum in the second week of June and then declining gradually until only occasional individuals, chiefly females, are to be found in the second week of July.

The larvae, in the soft wood, form persistent tunnels that are only slightly larger in diameter than the animals themselves. The tunnels could frequently be traced for lengths of 10 to 15 cm. and were usually parallel to the axis of the log and within one, two, or three annual rings of the surface. The tunnels are chiefly in the softer spring wood of the annual ring, but occasionally bend abruptly to penetrate the summer wood and enter the spring wood of the next annual ring. Guts dissected from larvae were found to be filled with cylindrical pellets of wood fibers that probably represent successive bites, each pellet being slightly shorter than the mesal length of the mandibles. This wood contained abundant mycelia of fungi and minute, unicellular objects that cannot be identified in the alcohol-preserved gut contents, but which may be intestinal symbionts.

The pupal stage occurs in late May and early June and lasts from five to six days. Fully grown larvae brought into the laboratory on May 26 began pupation within four or five hours; nearly all had pupated by May 28. The first emergence of an adult from these pupae occurred on May 30; others emerged May 31 and June 1 and 2. Removing part of a log from the water and allowing it to dry out slowly resulted in the prompt pupation of all the fully grown and even nearly fully grown larvae it contained. This forced pupation resulted in the production of a considerable proportion of smaller than average adults which barely reached or slightly exceeded the minimum size of adult flies taken in the field. In another experiment pieces of the same log were totally submerged for four days; during this time pupation was apparently inhibited, but was resumed at the end of this period, when the originally exposed surface was brought slightly out of water. The larger part of the log was left undisturbed in its position in the brook, and adults of *Lipsothrix sylvia* continued to emerge from it for several weeks.

Young pupae are found in the larval burrows, occasionally several centimeters from the pre-cut mouth of the burrow. Actual protrusion of the pupa from the burrow takes place not more than an hour before the emergence of the adult. The position of all but the oldest pupae within the larval tunnel and the fact that a definite opening to the surface could often be found at the end of the burrow several centimeters cephalad of the pupa lead to the inference that the larva makes an opening through the comparatively compact, thin outer layer of

summer wood and then retreats for some distance within the burrow before pupation. Only in the instances of a few newly formed pupae was I able to find the last larval skin near the caudal end of the pupa; this is evidence that the pupa travels for some distance within the larval tunnel. Shortly before the emergence of the adult, the pupa pushes its way through the opening of the burrow and projects out into the air as far as the tips of its wing pads. The pupal body is now bent, with the head, thorax, and upper abdomen projecting at nearly a right angle to the surface of the wood and the caudal half of the pupa lying parallel to the surface, within the burrow. Emergence of the adult is rapid, the entire process requiring something less than a minute. The newly emerged adult, after not more than two or three minutes, usually moves a short distance along the wood to rest and harden on some vertical or overhanging surface.

IMMATURE STAGES

A large collection of larvae and pupae of *Lipsothrix sylvia*, taken at Mountain Lake, Giles County, Virginia, on May 26 and 28, 1946, includes representatives of three larval instars and a series of pupae that appear to range from those recently pupated to those ready to emerge.

Except for size differences, all three larval instars are very much alike and have a striking appearance. The unusually elongate, dull white body, jet black head capsule, somewhat laterally expanded anterior thorax, tapering caudal end, and the very sluggish movements give the larva superficially an appearance more like certain buprestid beetle larvae than typical crane-fly larvae. Removed from their burrows and placed on a moist, flat surface, larvae of *L. sylvia* appear unable to make the strong body contractions characteristic of most crane-fly larvae; when stimulated, they bend the body into a series of open S-curves, thereby accomplishing a slow locomotion. When the larva is stimulated or in motion, the lobes of the caudal disk are tightly closed, and the caudal end of the body tapers to a conical point with no indication of stigmata, caudal disk, or lobes. Left undisturbed and in a well-moistened condition, the larva opens its caudal disk, revealing that it consists of four long, tapering lobes, which even at maximum spread are still directed strongly caudad, concealing the spiracles on the proximomesal faces of the dorsal lobes. After they were killed in hot water and preserved in 80 per cent alcohol, many of the smaller larvae were observed to become somewhat translucent (apparently

because of the slight development of body musculature and fat bodies), making visible the broad, brownish, wood-filled intestinal tract.

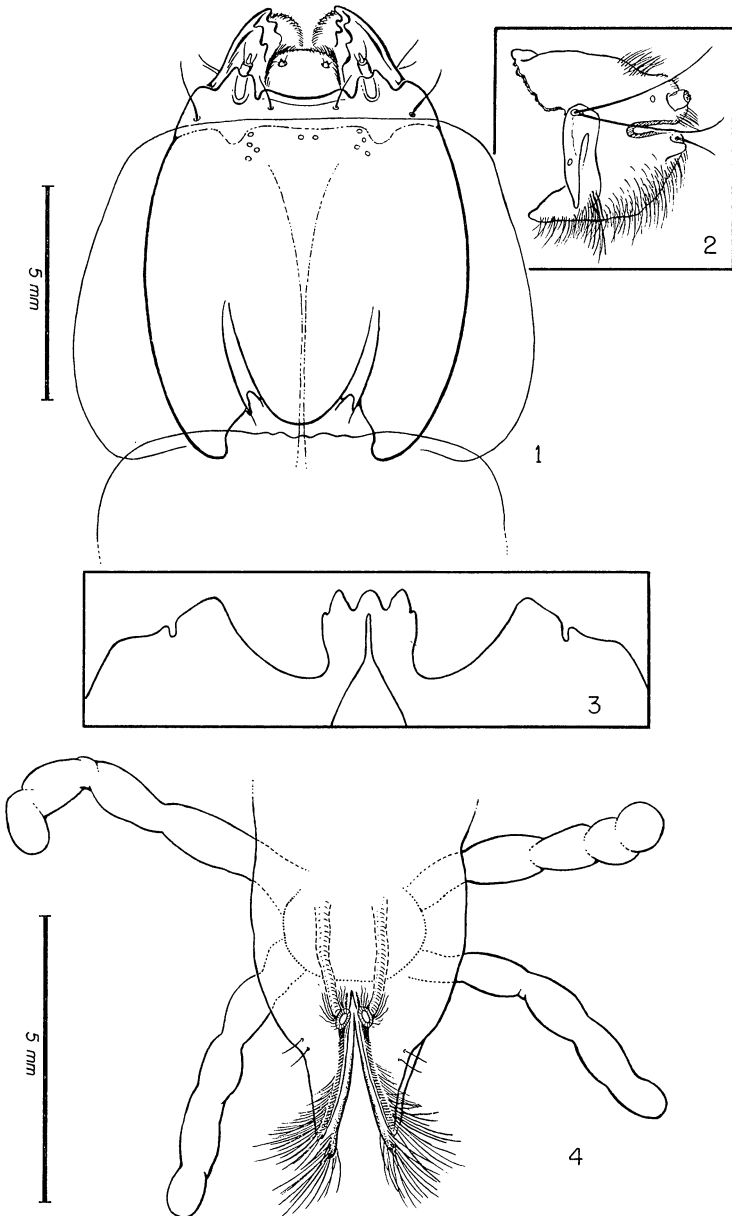
The visible part of the pupa found protruding from a piece of decaying wood is inconspicuous. Although the large, crownlike thoracic respiratory appendages are much lighter than the dark chestnut-brown dorsum of the thorax and leg sheaths and the blackish brown eyes and wing pads, they are so shaded as to blend with the darker browns, thus minimizing the color contrast between the protruding part of the pupa and the wood surface and making a living pupa less readily detected than an empty pupal skin. The part (approximately three-fifths) of the pupa concealed within the burrow is, on the other hand, of the same dull white as the larva. Even the tarsal sheaths are pale, in contrast to the darker color of the more proximal exposed parts of the leg sheaths. Pupae that were found hidden within the larval tunnels ranged, with age, from a nearly uniform white through various degrees of increasing pigmentation to the condition of coloration seen at emergence, with first the eyes, then the dorsomedian margins of the respiratory appendages, and finally the wing pads beginning to show traces of pigmentation.

The Fully Grown Larva

Length 20 to 24 mm.; dextrosinistral and dorsoventral diameters both 0.8–0.9 mm., except first two thoracic segments and the creeping welts; dextrosinistral diameter of prothorax 1.15–1.20 mm.; dorsoventral diameter through creeping welts 1.0–1.1 mm.

Form (Fig. 7) strikingly elongate and vermiform, terete except for prothorax, mesothorax, and region of creeping welts, and nearly uniform in diameter from thoracic segment 3 to abdominal segment 7; thoracic segments 1 and 2 somewhat expanded and depressed; abdominal segments 8 and 9 tapering to caudal end. Integument white, opaque in life, almost bare; pile soft, scanty, and microscopic; body setae long, pale, very slender, and pliable, hardly noticeable except with lens and contrasting background. Creeping welts on dorsal and ventral surfaces of abdominal segments 2 through 7 each with some 20 to 30 transverse rows of microscopic hooks that are erected when welt is expanded. Magnified only ten times, these hooks appear as rows of minute points. Abdominal segments 2–6 elongate, each longer than total length of thorax or combined length of abdominal segments 7+8+9; first abdominal segment intermediate in length.

Head capsule (Fig. 1) compact and massive. Length 0.65 mm. (from posterior apices of lateral plates to anterior curvature of closed man-



Details of larva of *Lipsothrix sylvia* (Alexander)

FIG. 1. Head capsule and prothoracic segment of fourth instar larva, dorsal aspect. FIG. 2. Right maxilla, ventrolateral aspect. FIG. 3. Mentum and anteroventral margin of head capsule, ventral aspect. FIG. 4. Terminal abdominal structures, showing spiracles, anal gills, and caudal lobes.

dibles); dorsal plate length 0.56 mm.; width at mid-length 0.63 mm.; depth 0.50 mm. Dorsal and lateral plates broad and strongly sclerotized, glossy black in life, dark brownish black after preservation in alcohol, so strongly fused in anterior half that sutures between adjoining plates are obliterated; lateral plates strongly fused to bars of mentum. The anterior cranial margin appears crenulate in dorsal aspect, with a broad, shallow emargination at labral suture and small, flat projecting plates above and below points of mandibular articulation. Labrum a gently convex, nearly quadrate plate, its anterolateral angles obtusely rounded, with a small, oval sensory papilla situated mesally from and behind each anterolateral angle. Antennae inserted beneath the small plates or crenulations above bases of mandibles and concealed beneath (but not attached to) these plates to about mid-length; basal joint elongate (about three times as long as wide) and cylindrical; apical joint small and ovoid, subtended on either side by a much longer, slightly curved bristle. Mandibles of cutting type, strong, heavy, and rather elongate, overlapping by nearly one-third of their length when closed; the apical halves of their mesal faces concave, the heavy margins bearing two dorsal, one apical, and three ventral teeth; the basal parts heavy and subcylindrical with a strong, low, rounded mesal tooth. Mentum (Fig. 3) heavily sclerotized, with three subequal teeth; the central tooth deeply cut behind by a median cleft, each lateral tooth with a basolateral notch that may represent a vestige of an additional lateral tooth; bars of mentum firmly fused with head capsule; a subtriangular, bladelike extension of anteroventral margin of lateral plate situated on either side of mentum. Hypopharynx a narrow, sclerotized collar, the ventral plate with four small teeth. Maxillae (Fig. 2) deeply cleft; the palp concealed by the mandible in dorsal view, but the lacinia conspicuous and brushy.

Caudal disk (Fig. 4) with four subequal, elongate, tapering lobes extending almost directly backward. Each lobe, in cross section, approximates a "quarter-round," the outer surfaces forming the anatomically cephalic parts of the lobes, and the concealed inner surfaces forming the posterior "face" of the spiracular disk. When closed, the lobes are brought into complete, opposed contact, fitting tightly together to form an unbroken terminal cone that resembles the slender caudal end of an earthworm. When opened, the caudal lobes resemble a cone that has been divided at right angles by two axial incisions, with the quadrants somewhat separated apically to a distance somewhat greater than their own width. The margins of each lobe bear a row of slender, pale setae that increase in length toward the apex of the

lobe and extend backward in inconspicuous tufts or brushes, about half as long as the lobes themselves. When the lobes are closed, the four tufts combine to form a short, slender caudal filament. The rather small, somewhat elliptical stigmata lie at the bases of the dorsal lobes in the narrow, sclerotized and pigmented bands that separate the ventral and mesal surfaces of those lobes.

Four anal gills (Fig. 4) are borne from a common, transverse, oval, protruding base on the ventral surface of the abdominal segment 8. Each gill is a slender, delicate, elongate tube, divided by slight but evident and apparently persistent constrictions into a slightly conical base and four subequal, subelliptical segments. Each gill appears to be formed of a single layer of columnar epithelial cells beneath a thin cuticle. The gills seem not to be retractile, and it is unlikely that either they or their common base can have a propulsive function such as is shown by the anal gills of other wood-burrowing crane-fly larvae.

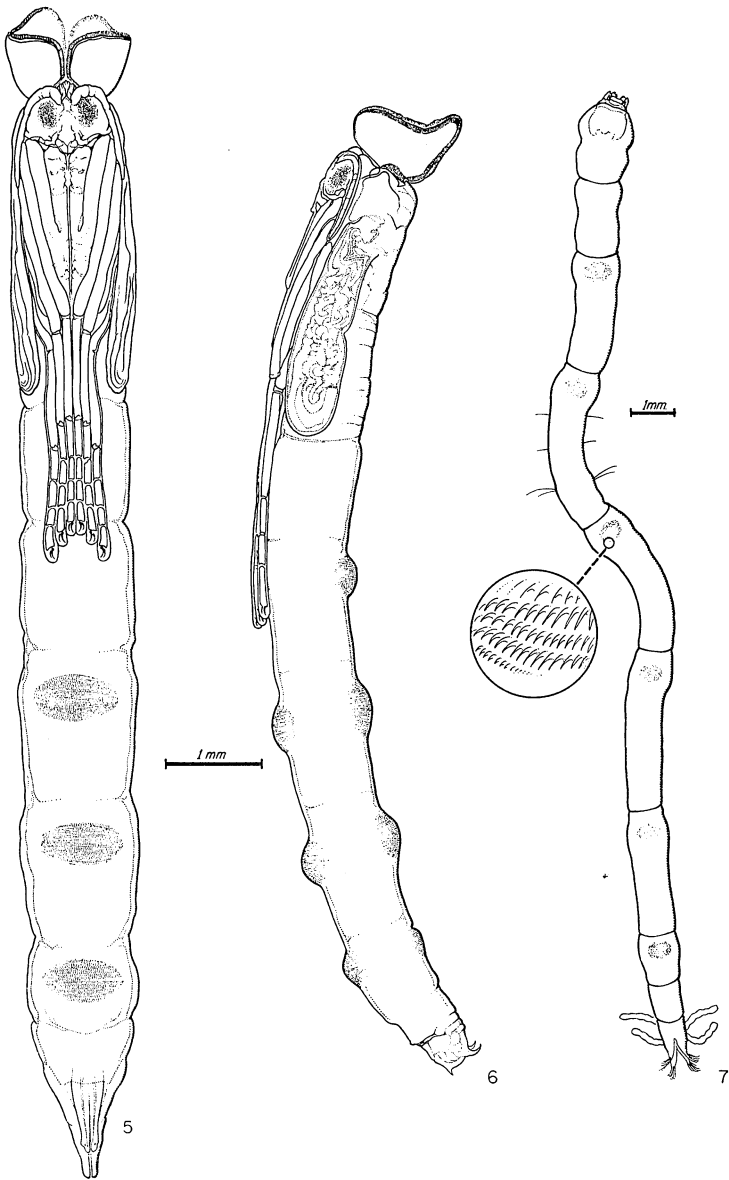
Third Instar Larva

More than half the larvae collected in late May are classed as third instar because they form a distinct and fairly compact size group. They resemble the fourth instar closely in all details except size: head capsule length 0.42–0.48 mm.; width 0.40–0.44 mm.; body size ranging from 11 mm. long and 0.42 mm. in diameter to 14 mm. long and 0.53 mm. in diameter, with an average of about 13 mm. in length and 0.51 mm. in diameter. All measurements are of larvae killed in hot water and preserved in 80 per cent alcohol.

Second Instar Larva

Eight out of nearly one hundred larvae from the late May collections are classed as second instar on the basis of the following measurements: head capsule 0.31 mm. long, 0.30 mm. wide, and about 0.17 mm. in maximum dorsoventral depth; body size from 7.0 to 7.5 mm. long and from 0.30 to 0.34 mm. in diameter (on the basis of specimens killed in hot water and preserved in alcohol). Very like larvae of instars III and IV except in size and in increased transparency resulting from thinner cuticle and lesser development of fat bodies.

Two larvae are intermediate in size between those classed as second and third instar and probably represent freshly mounted third instar larvae killed before hardening. No first instar larvae were obtained.



Immature stages of *Lipsothrix sylvia* (Alexander)

FIG. 5. Pupa, female, ventral aspect. FIG. 6. Pupa, male, left lateral aspect. FIG. 7. Larva, fourth instar, dorsal aspect. Inset: Microscopic hooks of creeping welt.

Pupa

Length 10.5–13.3 mm., females average 1.5 to 2.0 mm. longer than males; diameter at base of wing 1.0–1.1 mm. Form (Figs. 5, 6) terete, slender, gradually tapering from base of wing pads to the slender cauda. Color: abdomen dull white; dorsum of thorax pale brownish tan, becoming darker with age; wing pads and proximal parts of leg sheaths dark brown; breathing horns with apical margins yellowish, mesal margins brown; eyes changing from reddish to dark blackish brown with age. Integument thin, without abdominal "thorns" or ornaments; details of wings, legs, antennae, and genitalia of developing imago visible within sheaths in older pupae; small, roughened median crests on dorsocephalic and ventrocephalic angles of head, the latter crests, situated between antennal bases, twice minutely furcate cephalad; small, curved dorsal hooks on cauda of both sexes, in male conspicuous and curved dorsocephalad, in female smaller and projecting dorsad from near apices of sheaths of tergal valves; male with additional pair of short, sharp projections near ventrolateral margin of cauda. Ventral creeping welts on abdominal segments 5 through 7 and dorsal welts on segments 4 through 7; these raised to make dorsoventral body diameter through opposite welts as great as that at base of wing pads. Structure of pupal welts like that of larval counterpart, with 20 to 30 parallel rows of minute, hook-shaped points.

Apices of wing pads situated at juncture of abdominal segments 2 and 3; apices of all tarsal sheaths on cephalic end of abdominal segment 4; antennal sheaths terminating near proximal ends of metathoracic femora. Breathing horns broad and curved, together forming a conspicuous cephalic cup or crown slightly greater in diameter than the thorax. The structure of these respiratory appendages appears to be nearly identical with that found in the European *Lipsothrix remota* Walker by Hinton (1955) and may be seen to include a superficial network of minute air passages on the outer surface of most of the "gill" and a series of short, unconnected air tubes curved over the free edges of the gill.

RELATIONSHIPS

The genus *Lipsothrix* includes about a score of nominal living species and one well-preserved form from the Baltic Amber of the lower Oligocene, the latter originally described (Alexander, 1931) as *Electrolabis extincta* (see Alexander, 1945). The living species (with the exception of a single record from Panama) are holarctic, with a

wide distribution in Europe, Asia, and North America. In addition to the eastern *Lipsothrix sylvia*, three other North American species are known from the Pacific northwest—from California, Oregon, Washington, and British Columbia.

The genus has been arbitrarily placed in the tribe Eriopterini on the basis of the lack of tibial spurs in combination with a three-branched radial sector. In venation and general appearance, however, the adults resemble *Limnophila* of the Hexatomini; both *Lipsothrix sylvia* (Alexander) and *L. nigrolineata* (Doane) were originally described in the genus *Limnophila*. In one other well-marked character, the strongly toothed tarsal claws, *Lipsothrix* differs from nearly all Hexatomini and Eriopterini and resembles the genus *Limonia* of the Limoniini.

Thus, the immature stages of *Lipsothrix sylvia* are of particular interest for the light they may throw on the taxonomic relationships of the genus. Here I am inclined to place the most reliance upon the characteristics of the larval head capsule. This is owing to the fact that in the considerable series of crane-fly larvae that I have been able to study, the characteristics of the head capsules in closely related forms from diverse habitats have been markedly more conservative than body form, integument, chaetotaxy, or any other comparable external structure. Conversely, less closely related species occupying essentially similar habitats and often superficially alike in general appearance can be readily distinguished on the basis of the head capsule and its appendages. Characteristics of the larval head capsule of *L. sylvia* show affinities with the primitive Hexatomini, or with what might perhaps be better designated as a proto-Hexamini stem not markedly differentiated from the more primitive species of the other tribes of the Limoniinae.

Of the North American crane-fly larvae known to me, the most similar to *Lipsothrix* in head structure are those of *Epiphragma*. Even more closely similar, apparently, is the larva of *Limnophilomyia lacteitarisus* (Alexander) of South Africa, described by Wood (1952). This larva, like that of *Lipsothrix sylvia*, is elongate, with expanded thoracic segments and a compact but less heavily sclerotized head capsule; the anal gills are also similar, although the general aspects of the caudal ends of the larvae of the two species are unlike. The larval habitat of *Limnophilomyia* (Wood, 1952: 214) is remarkably like that of *Lipsothrix*. In the pupa of *Limnophilomyia* the respiratory appendages are not gill-like, but are slender.

The larval head capsule of *Lipsothrix sylvia* is probably nearer to

the presumed ancestral eucephalous type than is that of any crane-fly larva heretofore described. Evidence derived from study of the larval structures leads me to consider *Lipsothrix* as occupying an isolated position, but as related to the common ancestral form from which the main tribes of the Limoniinae have been derived.

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Received for publication September 16, 1955



