

STUDIES OF THE GENUS *Sialis* (SIALIDAE:
MEGALOPTERA) IN EASTERN NORTH AMERICA

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A Dissertation
Submitted to the Faculty of the
Graduate School of the University of Louisville
in Partial Fulfillment of the Requirements
for the Degree of

Doctor of Philosophy

Biology Department
University of Louisville
Louisville, Kentucky

December 1978

ABSTRACT

Eggs, egg masses, and mature larvae of *Sialis hasta*, *S. iola*, *S. joppa*, *S. infumata*, *S. aequalis*, *S. vagans*, *S. glabella*, *S. mohri*, *S. velata*, and *S. itasca* are described and diagnostic characters are given for their identification. Habitat preferences, adult oviposition site selection, larval behavior, and other life cycle aspects are outlined. Determination keys for the identification of eggs, egg masses, and mature larvae are presented.

Observation of adult behavior and mating confirms previous reports on these aspects of the life cycle of *Sialis*. Adults live for about two weeks, do not feed, are poor flyers, mate in the daylight hours on vegetation over or near the water, and oviposit on vegetation hanging over the water. No preference for a particular species of plant was observed. Some species, however, show a preference for ovipositing on leaves; other species oviposit on twigs or branches. Evidence comparing ovarian egg counts and number of eggs per mass indicate that a single oviposition period usually occurs. Of the species studied, *Sialis joppa* had the smallest number of eggs per mass—170 to 203 eggs—and *S. mohri* had the largest number—500 to 905 eggs per mass.

Position of individual eggs within the egg mass—whether the longitudinal axis of the egg is perpendicular to or parallel to the substrate—divides the egg masses into two groups. Those laid in a vertical arrangement are usually laid on twigs, are darker, and have more prominent surface sculpturing and longer micropylar projections.

Only those eggs of *Sialis glabella* and *S. itasca* were found deposited vertically on leaves. Eggs laid horizontally are usually laid on leaves, are lighter, and have less prominent surface sculpturing and shorter micropylar projections.

Chorion surface and details of the micropylar projections as viewed using the scanning electron microscope (SEM) and photomicrographs provide useful characters for identifying the eggs and egg masses as well as an analysis of the function of these structures.

The distinguishing feature of all Megalopteran eggs is the micropylar projection which varies considerably in size and surface detail in the Sialidae. SEM micrographs show its surface features and aid in diagnosing possible functions of the structure. It provides micropyle orifices and may also function as a respiratory organ or a protective device. The micropylar projection also aids in separating the species. The structure and function of various raised, peltate-like projections on the chorion surface of the egg are also discussed. These projections are larger and more numerous around the micropylar projection. They may function in producing a plastron that protects the eggs when wet. The structure and orientation of the egg burster are revealed clearly in the SEM micrographs, and its function during hatching is discussed.

Larval habitats were found to vary from small streams to large streams and from ponds to large impoundments and lakes. Larvae were always found within areas of quiet water where leaf litter, twigs, and debris had accumulated in the mud and silt. Some species seemed to prefer a particular type of basic habitat.

Detailed descriptions of the mature larvae are presented.

Color patterns on the dorsal surface of the head and thorax are the most reliable characters for species identification. Other features such as the shape and armature of the labrum and mandibles are also used. Based on data obtained from study of eggs and larvae, the origin and relationships of species groups and several sympatric species are discussed.

New distribution records of adults and larvae obtained during this study extend considerably the known ranges of the *Sialis* species.

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INTRODUCTION

The Megaloptera are a small order of aquatic insects. Some authors have treated the group as a suborder of the Neuroptera. Two aquatic groups, the Corydalidae and the Sialidae, are included in the Megaloptera. Some authors also include the Raphidiidae, the snakeflies, in the order as well. The Corydalidae is made up of five genera, all of which have carnivorous larval and large adult stages. The Sialidae is a family of but a single genus—*Sialis*—commonly called alderflies. There are about thirty species in the group worldwide. The adults are small black insects usually found near the water. The larvae are totally aquatic.

The nearctic Sialidae includes twenty-three nominal species (Ross, 1937; Townsend, 1939; Flint, 1964). These records show them to have been found in all the states east of the Mississippi River except Alabama and in all of the Canadian Provinces except Prince Edward Island and Newfoundland. In the western part of the nearctic realm, they are recorded from all the states except Arizona, Colorado, New Mexico, and Nebraska.

The genus was first described by Latreille (1802) from the genotype *Sialis lutaria*. Additional taxonomic work was done by Rambur (1842) who described *S. americana*, by Newman (1838) who described *S. infumata*, and by Banks (1897, 1920) who described four more species. Miall (1895) gave a description of the larvae of *S. lutaria*, a European species. Needham and Betten (1901) and Davis (1903) presented some information about the life cycle of the North American species *S. infumata*. Ross (1937) recognized that *S. infumata* comprised a number of closely related species and using adult genitalic features separated

S. infumata into sixteen species. Lestage (1919) described the life cycle of *Sialis lutaria*, and Dubois and Geigy (1935) gave a detailed account of its life cycle. Townsend (1939) described *Sialis nina* from Lexington, Kentucky, and Flint (1964) described three additional species from eastern North America.

Ross's (1937) work treated adults almost entirely, but he presented a drawing of *Sialis* sp. larva and a sketch of the egg mass of *Sialis mohri*. Azam and Anderson (1969) presented detailed life cycle information on the western North American species *Sialis rotunda* and *S. californica*. Evans (1972) gave descriptions and some details of the life cycle of seven other western North American species. Giani and Laville (1973) added details of the life cycle and production of *Sialis lutaria*. Pritchard and Leischner (1973) gave the life cycle of *Sialis cornuta* and Leischner and Pritchard (1973) gave a detailed description of the immature stages of the same species.

All of the above work treated western North American species or European species. Recent studies of eastern North American species include those of Cuyler (1956) who described the larvae of *Sialis itasca* and *S. americana*; Woodrum and Tarter (1973) who presented ecological data and life cycle information on *Sialis aequalis*, and Lilly (1976) who did a similar study on *S. itasca*. Descriptive details of the immature stages were not given in any of these reports.

The purpose of this study is to present descriptions of the eggs, egg masses, and larvae which will permit recognition and certain determination of species of *Sialis* in eastern North America. Details of the natural history of *Sialis* spp. which would aid in elucidating these species' role in lotic and lentic biocoenoses were also examined.

MATERIALS AND METHODS

Larvae were collected using a hand-held aquatic net with a maximum diameter of 34 centimeters. A simple procedure of collecting was utilized which consisted of dipping up a net full of mud and debris, washing out the excess mud, and handpicking the larvae.

Larvae were reared in the laboratory in plastic boxes 7.5 cm square and 3 cm deep. These were fitted with a friction fit cover of the same size. A plastic tube was fitted into one side for the attachment of an air line and water was added to a depth of 2 cm. A number of these boxes were arranged on a stair-step platform and attached to air lines. Aeration was continuous. Only one larva was placed in each box in order to facilitate separation of species and to collect exuviae after each molt.

Every other day the larvae were fed tubificid worms, and de-chlorinated water was added to maintain the water level at 100 mls. Larvae were transferred to pupation chambers when they showed signs of pupation as observed by Azam and Anderson (1969)—larvae would lie on their sides and curl up into a C-configuration and would not take food. The pupation chamber consisted of about 3 to 4 cm of moist sand in the bottom of a glass vial which was covered with a foam rubber stopper permitting air to enter.

Exuviae found floating in the water of the rearing boxes were removed, preserved in 70% ethyl alcohol, and later mounted on microscope slides in glycerol and ringed with petrolatum for study and measurement. All mature larvae were preserved in Kahle's preservative.

Most adults were taken by hand or with an insect net. Some were taken in a Malaise trap set up in Bernheim Forest, Bullitt County,

Kentucky. Twigs and leaves with egg masses were collected, returned to the laboratory, and suspended over water to await hatching. Newly hatched first instar larvae were also preserved in Kahle's preservative. None of the first instar larvae lived beyond 7 to 10 days in the laboratory.

Details of the egg surfaces were studied using scanning electron micrographs of the hatched eggs. These SEM pictures were made using a Cambridge Stereoscan Microscope at the University of Kentucky Scanning Electron Microscope facility.

GENERAL DESCRIPTIONS AND LIFE CYCLE OF THE SIALIDAE

Alderflies are aquatic or closely linked to the water in all phases of their life cycle. The larvae are totally aquatic, while the adults are found very near water. Pupation is in moist soil not far from the water's edge and the eggs are deposited on vegetation hanging over the water.

ADULT

Adult alderflies are frequently encountered by the collector around lakes and streams in the early spring. The black adults may cover the shoreline vegetation by the hundreds on warm spring days. Adults are distinguished from other Megalopteran members by large black wings which are held tent-like over the body (Pl.I,A). Ocelli are lacking and the fourth tarsal segment is dilated and deeply bilobed. Males can be separated to species by genitalic differences outlined by Ross (1937).

Adults emerge from March to July. A more precise period depends on the particular species and the latitude. Adults live about two weeks, flying short distances during the daylight hours only. They rest on vegetation and retreat under leaves and twigs at night, during cloudy days, or in foul weather. Adults were found hanging motionless during colder, rainy weather or on overcast days. They are poor, awkward fliers, usually traveling only short distances in a flight. They do crawl well on limbs and twigs of trees and shrubs. Their black color makes them conspicuous as they move about on bare twigs before full foliage emerges.

Mating occurs on the leaves and twigs of the shoreline

vegetation. Matings observed in the field during this study closely followed the pattern outlined by Dubois and Geigy (1935) for *Sialis lutaria*, a European species, and that of Azam and Anderson (1969) for species in Oregon. No matings were observed in the laboratory in those specimens returned there for observation.

After mating, the female flies away to select a suitable oviposition site. Oviposition occurs shortly after mating, usually the same day (Azam and Anderson, 1969). The eggs are deposited on vegetation that hangs over the water so that the hatching larvae will fall directly into the water. The eggs are laid singly and stuck to the substrate by a cementing substance secreted by the female's accessory gland. The female swings her abdomen back and forth in an arc as she lays the eggs (Dubois and Geigy, 1935). In the present study oviposition was observed to take over an hour by a female *Sialis vagans* which laid about 500 eggs.

It appears that a female oviposits her mature, ripe eggs during a single period of one or two hours. If she is disturbed during this time, she may begin again at another place. Dubois and Geigy (1935) stated that a second oviposition occurred in *Sialis lutaria*. However, it is likely that such a second oviposition occurred only as a result of disruption of the female and is not a regular occurrence. Counts were made of the eggs in the ovaries of dissected gravid females in this study (Table II). These studies show the ovarian counts to be very similar to the number of eggs per mass, thus indicating that the female deposits all the eggs in a single mass.

Eggs are deposited on the substrate in one of two positions: flat, on their sides, usually on the underside of leaves (Pl.I, B,C) or upright, standing on end, usually on twigs (Pl.I,D). There seems to

be no particular preference for any species of plant on which the *Sialis* female lays her eggs. The female chooses plant material that is usually within one or two meters above the water surface. Several times the eggs of *Sialis hasta* and *S. infumata* were found as high as 5 to 10 meters over the water. Eggs are deposited over still, slow-moving water near the habitat of the larvae. The oviposition sites on twigs are often used repeatedly year after year. The remains of old egg masses were found on overhanging twigs the following winter and spring.

Some species show a preference for the plant part on which the eggs are deposited. *Sialis aequalis*, *S. glabella*, *S. itasca*, *S. iola*, and *S. joppa* eggs were usually laid on the underside of leaves, while *S. hasta*, *S. infumata*, *S. mohri*, and *S. velata* eggs were usually laid on twigs. *S. vagans* eggs were found on both leaves and twigs.

EGG

The average number of eggs per mass ranges from 187 in *Sialis joppa* with the least number of eggs to 718 in *S. mohri* with the largest number per mass. Often several masses may be found side by side. For example, the masses of *S. mohri* and *S. velata* may completely cover a twig.

The eggs range in size from 0.50 mm long and 0.19 mm wide in *S. joppa* (the smallest) to 0.65 mm long and 0.22 mm wide in *S. glabella* (the largest) (Table I). The surface is partially or completely covered by small dot-like structures that under 60x or higher magnification, such as scanning electron micrographs, appear to be raised

peltate projections, resembling a morning glory or *Convolvulus* flower. These projections are especially larger and prominent on the eggs of *Sialis infumata* (Pl.II,B). The projections tend to be larger and more prominent at the micropylar end of those eggs that are laid in the upright position.

The distinguishing feature in all Megalopteran eggs is a prominent micropylar projection (Pls.III & VI). In *Sialis*, the micropylar projection varies in size and surface detail in different species. *Sialis itasca* has the longest micropylar projection (0.21 mm), while *S. joppa* has the shortest (0.06 mm). Ross (1937) described the micropylar projection of *S. mohri* as being a tassel; however, it is more cylindrical with a rugose surface. (Pl.V,B).

Color of the eggs varies with the species also. Colors range from white to dark brown. Those eggs laid in the flat position tend to be lighter in color (white, yellow, or tan) while those laid in the upright position are darker (brown, grey, or reddish-orange).

In each hatched egg shell, the remains of an egg burster can be found. This structure is used to rupture the chorion surface by the hatching larva. The details of the egg burster are best seen with the scanning electron microscope. This structure was described by Azam (1969) and Evans (1972) in western species of *Sialis* and previously by Smith (1920, 1922) for other Megalopteran eggs. The egg burster is a triangular structure with a set of teeth on the inner surface (Pl.III). Evans (1972) showed a photograph of the egg burster of *Sialis hamata* with the egg burster turned so that the teeth were facing the chorion surface. All the scanning electron micrographs from the present study show the teeth projecting inward on the hatched eggs (Pl.III,C-F).

Table I. Sizes of the eggs of Sialidae

Species	Length	Width	Micropyle Length
<i>S. hasta</i>	0.56 mm	0.18 mm	0.09 mm
<i>S. iola</i>	0.58	0.24	0.07
<i>S. joppa</i>	0.50	0.19	0.06
<i>S. infumata</i>	0.58	0.16	0.11
<i>S. aequalis</i>	0.56	0.20	0.09
<i>S. vagans</i>	0.54	0.17	0.08
<i>S. glabella</i>	0.65	0.22	0.09
<i>S. mohri</i>	0.58	0.17	0.20
<i>S. velata</i>	0.58	0.18	0.16
<i>S. itasca</i>	0.57	0.19	0.21

Table II. Number of eggs in ovaries of dissected female Sialidae

Species	Number	Avg. Number Eggs in Ovaries	Range
<i>S. hasta</i>	3	384	305-452
<i>S. iola</i>	2	353	283-423
<i>S. joppa</i>	3	186	158-230
<i>S. infumata</i>	3	480	445-500
<i>S. aequalis</i> ¹	10	657	402-818
<i>S. vagans</i>	3	437	329-498
<i>S. glabella</i>	1	225	—
<i>S. mohri</i>	5	574	463-785
<i>S. velata</i>	4	438	340-533
<i>S. itasca</i> ²	—	539	—

¹ Woodrum and Tarter (1973)² Lilly (1976)

Apparently the side opposite from the teeth is the one that actually ruptures the egg while the teeth may articulate with the head of the embryo or serve some other function. Perhaps the egg burster shown by Evans (1972) was somehow dislodged from the normal position in the process of preparing the slide.

The surface color, chorion structures, micropylar projection morphology, and number of eggs per mass are used to identify the eggs of *Sialis* to species. (See key on page 24.)

Investigators have had little success in obtaining oviposition under laboratory conditions. In this study the eggs were collected in the field, returned to the laboratory, and suspended over water to await hatching. Hatching usually occurs at night. Those in this study hatched at night 6 to 10 days after oviposition.

Occasionally egg masses are attacked by species of Trichogrammatidae, the egg parasitoid wasps. Azam and Anderson (1969), Lestage (1919), and Pritchard and Leischner (1972) all have reported such "parasitism." These wasps were encountered in the eggs of *Sialis velata* at Houghton Lake, Michigan. An example of the destruction of the eggs may be seen in Pl.III,A which shows eggs of *S. velata* with large cavities in the surface where the wasps have hatched.

FIRST INSTAR

The newly hatched first instar larvae fall into the water and begin the aquatic phase of the life cycle of *Sialis*. The distance they fall depends on where the eggs are laid but is usually not more than a few meters. *Sialis hasta* and *S. infumata* eggs were found as high as 8 to 10 meters over the water so their first instars have a long fall.

The rate of cannibalism is high according to Dubois and Geigy (1935).

The first instar larvae resemble the mature larvae except the appendages are not as well developed. All larvae studied conform to the descriptions of Pritchard and Leischner (1972) for *Sialis cornuta* and by Lestage (1919) for *S. lutaria*.

LARVA

Sialis larvae are often found in benthic samples from lakes and streams. They are often the dominant species in collections taken from pockets of accumulated mud and debris. It was found, after collecting in a variety of aquatic habitats, that the larvae are usually confined to the pools and bays of streams. Larvae may be found occasionally in riffles, but they are apparently washed out of their usual habitats by high water. Larvae burrow among the accumulated leaf litter, twigs, and mud that is found in the quiet water areas. Such places are generally rich in their chief source of food—chironomid or midge larvae and tubificid worms. Giani and Laville (1973) found mature *Sialis lutaria* feeding primarily on Chironomidae. In Alberta, Canada, Pritchard and Leischner (1972) found tubificids, chironomids, and ostracods the chief source of food for *S. cornuta*. In West Virginia, Woodrum and Tarter (1973) have reported the same food sources for *S. aequalis*. In this study, nearly all collections had large numbers of chironomid larvae in association with the *Sialis* larvae.

In the fall of the year large numbers of larvae can often be obtained in pools filled with decaying leaves and twigs. Larvae move around in the streams apparently following the shifting pockets of debris as the debris is displaced by increased flow of water. Giani

and Laville (1973) found that *Sialis lutaria* migrated to deeper water in Lake Port-Bielh during the winter months. Larvae were found then out in water from 15 to 20 meters deep.

Some larvae seem to be confined to one type of aquatic habitat. *Sialis joppa* larvae were always found in small clear streams that were 1 to 2 meters wide and one-half meter deep. Such larvae are found in small collections of debris which are less than one meter in diameter that accumulate behind rocks or logs; these accumulations are scattered over the course of a stream. Collecting in each accumulation yields only one or two larvae.

Sialis hasta and *S. infumata*, on the other hand, are found in larger streams that are 10 to 20 meters wide and sometimes have pools 3 to 4 meters deep. As always the larvae are found in the slower moving water with accumulated litter and mud. These two species are frequently found together in the same stream.

Sialis glabella was found in a small woodland pond high on a flat ridge in Nelson County, Kentucky. This isolated pond is only 3 to 4 meters in diameter, but it supports a good population of *S. glabella* which was previously known only from its type locality at Mt. Carmel, Illinois.

Several species are found in the shallow bays and inlets of lakes and impoundments where wave actions emulate the slower moving water of larger streams and rivers. *Sialis mohri*, *S. velata*, and *S. itasca* seem to be confined to these lentic habitats where they burrow in the soft ooze. Such shallow embayments may yield hundreds of larvae.

Sialis vagans seems more diverse in its habitat selection. It was found in streams, sometimes along with *S. hasta* and *S. infumata*,

and also in small lakes. *S. vagans* seems to favor backwater and muddy areas such as pools behind small dams where there is a deep mud layer on the bottom.

Sialis iola was taken from a variety of habitats. It was found in Cedar Bog in Ohio which is a unique area of marl bottom with pH ranges of 7.2 to 7.8 as reported by Hufford and Collins (1976). The species was taken in large numbers in a small pond red with acid-mine water in West Virginia and also in a clear mountain lake in West Virginia. The water quality of the lake is good and it is regularly stocked with trout by the forest service.

Sialis aequalis seems to tolerate extremes of pH conditions. It was reported by Tarter and Woodrum (1972) to survive a pH of 3.0 in a 96 hour TL_m test. The larvae tested were taken from an acid-mine stream which had a pH range of 4.3 to 6.4. The larvae were found to be thriving in this stream. The species is common in the streams in the coal mining areas of eastern Kentucky and West Virginia where pH values are usually low.

Burrowing in the mud, seeking shelter in debris, and choosing locations in small streams, small ponds, and areas of lentic water, all of which offer some degree of protection, seem to characterize the larvae of *Sialis*.

GENERAL DESCRIPTION OF LARVAL ANATOMY

Sialis larvae are of the campodeiform type and may be distinguished from other Megalopteran larvae by lateral filaments projecting from the first seven abdominal segments and a median tapering caudal filament projecting posteriorly from the tenth abdominal

segment (Pl.VII,A & B).

The following general description is based on mature larvae (last three instars of ten eastern North American species) and is a composite of species used in this study.

The head is a flattened subquadrate structure with the lateral margin convex. The lateral edges are generally straight from anterior to posterior curving medially in the rear one fourth. The color of the head varies from pale yellow to a dark reddish brown. The spots and markings are usually light on a dark background color except for *Sialis glabella* which has dark spots on a light background. *Sialis iola* and *S. hasta* have darker reddish-brown heads with distinctive patterns. Other species have heads of a lighter color and usually less distinctive patterns (Pls.X,XI,XII).

The labrum is broadly triangular with the apex blunt to bifid, depending on the species, being about two-thirds wider than long with lateral margins uneven, formed by crenulations in which are set conical marginal setae that number 13 to 17 per side depending on species and instar number (Pl.VI). The anterior-most pair of setae are the longest with the first, shorter setae arising from the ventral side and the second longer setae arising dorsally. Several tiny setae arising from the ventral surface are found between each crenulation and the front teeth. The crenulations may vary per species as to spacing and the type of edge (Pl.VI,D-I). A series of fine hairs are arranged around the dorsal margin of the labrum.

The clypeus is about 9 to 10 times as wide as long and covers the dorsal part of the head capsule. The anterior margins may be elevated and project forward at the midline. Clypeal spots situated

on either side of the median line with long hairs projecting from them may be visible in some species.

The antennae located between the base of the mandibles and the eyes are four-segmented with a broad basal segment or antennal socket. The second segment is about twice as long as the first, while segments III and IV are usually equal in length. In *Sialis aequalis* segments III and IV are more unequal. The fourth segment bears four fine short hairs on its tip. The second has a ring of setae at its distal end with one of these being stouter and projecting laterally.

The mandibles are large and terminate in a long apical hook which curves convexly on the lateral margin (Pl.VI). The terminal hook may be one half of the length of the mandible and in most species is sickle-shaped, but is much straighter in *Sialis infumata* (Pl.VI,B). Two triangular-shaped teeth are borne along the medial margin; the posterior tooth is shortened with its posterior margin tapering obliquely into the mandibular base. A third tooth is present in *Sialis glabella* but is represented by only a slight protuberance in all other species studies (Pl.VI,A). Fine serrations may be present on all hooks and both teeth but are stronger on the first tooth.

The maxillae are strong and well developed. The cardo and stipes are triangular in shape (Pl.VIII,B,B,H). The laciniae are sickle-shaped and bear four large spines on their inner margin (Pl.VIII,B,E). The galeae are cone-shaped and bear very tiny protuberances on the apical tip. The four-segmented palpi are long and project anteriorly; segment II is nearly three times longer than the other segments (Pl.VIII,B,F). Single hairs extend from the tip of the first two segments.

The frons is a semicircular sclerite with a broad point projecting posteriorly at the median ecdysial suture. Two rather large frontal angular markings which open to the lateral margins are usually visible in the center of the frons (Pl.VIII,A,E). A single elongated triangular spot is centered between the frontal angular markings. A few fine hairs may be scattered along the dorsal margin of the frons. The anterior arm of the ecdysial cleavage line is visible in most species (Pl.VIII,A,B).

A pair of long coronal angular markings which are L-shaped are found along the ecdysial cleavage line (epicranial suture)(Pl.VIII, A,G). The occipital suture is incomplete at the midline, curving toward the post-occipital suture but never reaching the ecdysial cleavage line (Pl.VIII,A,H,I). The occipital suture continues ventrally running parallel to the post-occipital suture terminating at the base of the mandible. The post-occipital suture is heavy and dark, terminating at the base of the maxilla. A series of elongated oval marks (genal marks) may be found lateral to the coronal angular markings (Pl.VIII,A,G).

The eyes, positioned just posterior to the antennae bases, are dark black, consisting of six stemmata, each of which is oval in shape. These stemmata are arranged in a circular pattern but blend together under low magnification to appear as a single multifasciated eye.

The labium is elongated and is completely covered by the labrum. The ligulae are pentagon-shaped and small (Pl.VIII,B,G). The palpi are three-segmented, each segment subequal (Pl.VIII,B,A). The mentum and submentum are hexagonal in shape and are wider medially (Pl.VII,B,C & D). A pair of strong spines is found near the posterior

edge of the submentum with a smaller pair anterior to these.

Each thoracic segment is subquadrate, flattened, and bears a median dorsal ecdysial suture. The pronotum is almost twice as long as the meso- and metanotum. The dorsal sclerotized portion curves downward at the lateral margins, while the side appears straight with the posterolateral corners rounded. Three pairs of elongated light pronotal medial spots usually appear on either side of the median suture (Pl.VIII,A,K). Lateral elliptical marks of varying numbers and shapes appear lateral to the elongated medial spots (Pl.VII,A,J). These usually point toward the medial suture at an angle. The arrangement and distinctness of the pronotal medial spots and the lateral elliptical marks may be used to separate several species.

The mesonotum is more rounded than the pronotum with its sides tapering inward posterolaterally. A figure roughly the shape of the letter M (mesonotal angular markings) appears on the mesonotal disc (Pl.VIII,A,P). The details of this figure vary with each species and these patterns are useful in the determination of species. An irregularly shaped spot is found lateral of the mesonotal angular markings (Pl.VIII,A,O). Elongated spots are situated lateral of the outer arms of the mesonotal angular markings (Pl. VIII,A,W). These spots may coalesce and form distinguished figures in different species. Usually two spots (posterolateral membraneous marks), one round and the other elongated are found in the unsclerotized portion of the mesonotum (Pl.VIII,A,Q). The lateral margin has a light crescent-shaped mark that increases in size with the later instars which are the developing wing pads (Pl.VIII,A,L). Two pairs of small, open posterior circles may be visible at the posterior base of the mesonotal disc (Pl.VIII,

A, N).

The metanotum is similar in shape to the mesonotum but slightly shorter, and the unsclerotized portions have small triangles at the posterolateral margins. The metanotal angular markings are made up of several spots found along the midline that combined roughly form an inverted V (Pl.VIII, A,R). The upper portion of this figure is usually question mark-shaped (Pl. VIII,A,S). This metanotal angular marking varies in each species and like the similar marking of the mesonotum is useful in species identification. A rather large, generally O-shaped spot (posterolateral semicircular spot) is found near the posterior base of the metanotal angular markings (Pl.VIII,A,T). Crescent-shaped spots are found at the lateral margin of the metanotum as in the mesonotum.

The ventral surface of the thorax lacks any patterns of distinct figures. Some setae are present and some species have darkened pigmented areas in the center. Small thoracic spiracles are present between the pro- and mesothorax which are most visible in prepupal larvae.

The legs are long and project laterally from the thorax; each has a long, large coxa, a triangular trochanter, a long femur, a shorter tibia, and a single-segmented tarsus which bears two unequal length claws (Pl.VIII,C). The coxae generally bear only lateral setae (Pl.VIII,C,B). The trochanter has a small series of stout setae at the posterior margin (Pl.VIII,C,A). The femur has a row of numerous short setae in the center, with a group of scale-like structures lateral to it; both edges are fringed with long hairs (Pl.VIII,C,C). The tibia also has a center row of stouter but fewer setae, the number varying per

Table III. Number of central tibial setae on the legs of *Sialis* larvae (N = 5)

Species	Leg I	Leg II	Leg III
<i>S. hasta</i>	11	12-13	12
<i>S. iola</i>	10	15	15
<i>S. joppa</i>	9	12	12
<i>S. infumata</i>	11	12	12
<i>S. aequalis</i>	11	13-14	14-15
<i>S. vagans</i>	8-10	10-12	10-13
<i>S. glabella</i>	5	9	9
<i>S. mohri</i>	9	12	13
<i>S. velata</i>	10-11	13-14	14-15
<i>S. itasea</i>	9	12	13

species and instar (Pl.VIII,C,E). Scale-like structures are present but smaller than those in the femur. A few strong setae may be present at the posterior edge and hairs are present at both edges. These central tibial setae vary in number with different species and, while not providing a reliable character for species identification, may be useful in separating some species (Table III). The proximal end is slightly less wide than the distal part which is more oval in shape. The tarsus is short and round in cross section and lacks a center row of setae (Pl.VIII,C,D). The lateral edges have four to five strong setae on leg I and leg II. The tarsus and often the tibia of leg I is darker than those of legs II and III. The tarsal claws are unequal in length, one about one-third longer than the other.

The abdomen is long and tapering posteriorly (Pl.VII,A,B). Its dorsal surface is always darkened and in some species the ventral surface may also be pigmented. Light-colored filaments extend laterally from the anterolateral membranous parts of the first seven segments. Those on segments I and II have four sections while the others have five sections. The basal section of each filament is broader than the distal portions. Each filament is fringed by numerous tiny hairs. The first abdominal segment is shorter than the others. Segments II to VII become increasingly longer and narrower. Each segment appears to be connected to the next by a pigmented, broadened, triangular area at the anterior margin of each segment. This area may be covered by the next segment if the abdomen is contracted. Segments I to VII have C-shaped or chevron-shaped light markings to either side of the midline; these markings become straight on segments VIII and IX. A row of small dots appear near the posterior margin of each segment. These

become more prominent in the last instar and may blend together. These chevron-like markings are joined in the center in *S. vagans* producing an anchor-like figure in each segment (Pl.VII,B). The lateral edges of each segment have lighter branchlike markings protruding inward from the light colored basal section of the lateral filament. Segment IX is narrow and short, while segment X appears as a small median triangle and a pigmented spot on either lateral margin. A light colored filament which is fringed by long hairs extends posteriorly from segment X.

Small abdominal spiracles are present on the lateral edges of the segments at the basal area of the lateral filaments. These spiracles enlarge and become functional in the prepupal stages. The spiracles apparently function to allow the larvae to migrate out of the water and live in a terrestrial environment until pupation occurs.

The venter of the abdomen may be pigmented darkly or be very light in color depending upon the species (Pl.IX). *Sialis iola* has the entire segment darkened while other species have only bands of pigment across each segment. This character may be used in identification of the species. Those species with a dark venter usually have a series of 2 to 3 round dots across the middle of each segment and the pigmentation is usually incomplete at the center of the last three segments.

PUPA

The mature (perhaps tenth instar) larva leaves the water in the early spring and forms the pupa in a cell made in the soil. This migration occurs at night, according to Azam and Anderson (1969).

Prepupae were found in the present study under leaves and under a thin layer of soil. Pupae of *S. joppa* and *S. hasta* were within a meter of the water's edge. None of the prepupae were found more than two meters from the water. The pupation cell was formed 1 to 2 cm deep in the soil. The pupae are usually found at the point where leaves or grass first occur on the bank of the stream or lake, this area offering more protection and ease of digging in the soft moist soil. The pupal cells are often very close to one another in the soil. Over a half dozen pupae were dug out of an area a few square centimeters in size on Harrod's Creek in Kentucky. Larval exuviae were found with the pupae.

Successful pupation occurred on several occasions in laboratory reared specimens. Many of these specimens died in the pupal stage, and many larvae died during the final molt before pupation. Pupation lasts 10 to 14 days in the lab. Pupae returned to the lab from the field took 7 to 10 days to emerge. The pupae assumed a scarabaeiform shape in the cell and were active during the pupal stage.

Pupae conform closely to the descriptions of pupae presented by Pritchard and Leischner (1972) and Dubois and Geigy (1935). The active pupa has well-developed white wing pads or cases, long filiform antennae, and is dark brown, darkening to black as development proceeds.

Emergence occurred at night in the laboratory and also in the field as reported by Azam and Anderson (1969). By daybreak or mid-morning, the adult wings are dry and the alderfly is ready for flight.

KEYS TO EGGS, EGG MASSES, AND MATURE LARVAE OF *SIALIS*

The following keys are given to the eggs, egg masses and mature larvae of the ten species discussed in this study. Effective use of these keys may be made only if larvae are carefully preserved in Kahle's Preservative, FAA, or KAAD. Ethyl alcohol (70%) is unsatisfactory since it causes fading of the colors and patterns and shrinkage of the specimens. Although scanning electron micrographs presented in Plates I to V of the eggs and egg masses emphasize details, identification may be made by careful observation using a stereomicroscope with 60x or higher magnification.

EGGS AND EGG MASSES

1. Eggs arranged in a flat position, often on the underside of leaves (Pl.I,B,C).....2
 - Eggs placed in an upright position, usually on twigs but sometimes on leaves (Pl.I,D).....5
2. Eggs tan; micropylar projection widened at base as Pl.IV,D *S. iola*
 - Eggs white to cream colored; micropylar projection otherwise....3
3. Egg mass usually with less than 200 eggs; eggs small in size (0.50 mm long, 0.19 mm wide or less); white in color...*S. joppa*
 - Egg mass usually with more than 200 eggs; eggs larger than above; color other than white.....4
4. Micropylar projection with a constriction at base (Pl.IV,E); eggs cream to yellow in color, deposited on leaves or twigs (Pl, II, E).....*S. vagans*
 - Micropylar projection lacking a constricted base (Pl.IV,B); eggs white, usually found on leaves.....*S. aequalis*
5. Eggs found on the under side of leaves.....6
 - Eggs found on twigs or other vertical plant parts.....7

6. Micropylar projection with a long constriction at base (Pl.V, A); eggs reddish-orange in color.....*S. glabella*
 Micropylar projection conical, very rough in appearance, resembling a pine cone (Pl.V,D)..... *S. itasca*
7. Micropylar projection long (over 0.15 mm).....8
 Micropylar projection shorter (less than 0.15 mm).....9
8. Micropylar projection cylindrical, lacking knob at tip; eggs greyish-brown in color (Pl.V,B).....*S. mohri*
 Micropylar projection with a rough knob at tip; eggs dark brown in color.....*S. velata*
9. Micropylar projection cylindrical with a small round, rough knob at tip (Pl.IV,A); eggs brown, laid at a slight slant..*S. hasta*
 Micropylar projection with a swollen base tapering to a tip with projections (Pl.IV,C); eggs dark brown with large peltate structures around the micropylar end (Pl.II,B)... *S. infumata*

MATURE LARVAE

1. Venter of the abdomen with distinct cross bands or solidly dark with pigment (Pl.IX,A,C).....2
 Venter of abdomen light in color lacking distinct cross bands, or with incomplete bands (Pl.IX,B).....5
2. Background color of head and thorax dark with distinct lighter markings on head and pronotum (Pl.X,A,B).....3
 Background color of head and thorax with faint markings on head and pronotum.....4
3. Labrum with a snout-like front (Pl.VI,E); venter of the abdomen with all but last segment darkened completely, a narrow white line along the lateral edges (Pl.IX,A).....*S. iola*
 Labrum lacking a snout as above (Pl.VI,D); venter of abdomen with dark bands incomplete at the edge of each segment (Pl. IX, C).....*S. hasta*
4. Pronotum with only posterior pronotal medial spot visible, lateral elliptical spots large and ovoid on a dark background; labral marginal setae, usually 12 per side; meso- and metanotal patterns as (Pl.XI,C).....*S. joppa*

- Pronotum with pronotal medial spots faint; labral marginal setae usually 15 per side; meso- and metanotal patterns as (Pl.X,C) with parts thickened and joined.....*S. aequalis*
5. Mandible with a third tooth present (Pl.VI,A); markings on head and thorax dark on a light background (Pl.XI,A)....*S. glabella*
- Mandible without a distinct third tooth, represented only by a slight protuberance (Pl.VI,B,C); head and thoracic figures light on a darker background.....6
6. Dorsum of abdomen with markings forming an anchor-like figure on each segment; pronotum with rectangular light area at center (Pl.VII,B).....*S. vagans*
- Dorsum of abdomen with usual chevron markings (Pl.VII,A); pronotum not as above.....7
7. Pronotum with small, dark elliptical pronotal spots, median portion light (Pl.XI,B); venter of the abdomen with cross bands incomplete at midline or absent.....*S. infumata*
- Pronotum without dark elliptical pronotal spots, pattern may be indistinct; venter of the abdomen usually white.....8
8. Head with darkened markings; pronotal medial spots dark; mesonotum and metanotum as (Pl.XII,A).....*S. itasca*
- Head with patterns faint; pronotal medial spots barely visible if at all (Pl.XII,B,C); mesonotum and metanotum not as above....9
9. Mesonotal figures with parts thickened and fused at median suture (Pl.XII,C).....*S. velata*
- Mesonotal figures with parts slim and not fused as above (Pl.XII,B)*S. mohri*

DESCRIPTIONS OF SPECIES

Sialis hasta Ross

Sialis hasta ranges from 80° longitude in the east to 95° longitude in the west. It has not been found south of 35° north latitude. It is rather common in the northern parts of the Ohio River drainage and the streams of northern lower Michigan (Pl.XIV).

This species is often found along with *Sialis infumata* and, to a lesser extent, with *S. vagans*. Adults of *Sialis hasta* and *S. infumata* were taken together on the same day and sometimes on the same vegetation on several occasions at localities on Harrod's, Wilson's, and CornCreeks in Kentucky. *Sialis hasta* was taken along with *S. vagans* on May 29 at Lovells, Michigan, the type locality of *S. hasta*. Adult males of these species are easily recognized by the genitalic features given by Ross (1937).

Adults were collected in large numbers at sites in Kentucky and Indiana. Emergence is in the early spring—late March to early April in Kentucky and mid-May in Michigan. Adults are easily seen on the bare twigs at this time of year and seem to prefer the limbs of the larger trees as they crawl about.

Egg masses are found on the bare twigs of overhanging trees. The masses were often found high over the water. Those found at the Covered Bridge Boy Scout Reservation on Harrod's Creek in Kentucky were as high as ten meters over the water. The mass of this species is brownish and is usually laid along the long axis of the twig. The eggs are deposited in the upright position on the twigs at a slight slant (Pl.I,D). Eggs for this study were collected from the above site and

and also from Corn Creek in Kentucky. Those eggs hatched in the laboratory in six days.

The larval habitat is that of larger streams and rivers that are 10 to 20 meters or more wide. *Sialia hasta* seems to favor areas where large numbers of twigs and plant debris accumulate in the soft muddy sediments of the slower moving water. Large larval populations were found in the black organic ooze under alder thickets at Lovells, Michigan. At this site two distinct larval sizes were taken in April and May indicating that the life cycle is probably two years in duration in the northern parts of its range. No distinct differences were seen in material collected from the streams of Kentucky. This observation suggests a one-year life cycle in the southern parts of its range.

Larvae for this study were taken from the following sites:

Indiana: Silver Creek, 1 mile east of Henryville, Clark County.

Kentucky: Harrod's Creek at Covered Bridge Boy Scout Reservation, Oldham County; Wilson Creek, Bernheim Forest, Bullitt County; Corn Creek, Trimble County. Michigan: East Branch of Au Sauble River, Lovells, Crawford County; Middle Branch of Au Sauble River, Rt. F-97, near Hardwick Pines, Crawford County; Maple River, near Brutus, Emmet County. Ohio: Mad River, Urbana, Champaign County.

Egg: Color medium brown, darker at the micropylar end, micropylar projection light tan (Pl.II,A). Length 0.50 mm, width 0.18 mm, micropylar projection 0.09 mm long. Micropylar projection cylindrical, tapering slightly to a round knob at the apex, knob with projections (Pl.IV,A). Surface covered with peltate projections which are larger at the micropylar end. Number of eggs per mass 227 to 477, \bar{x} 334. (Based on 6 masses)

Larva: Dark reddish-brown ground color, dorsal markings very distinct (Pl.X,A), venter with dark brown bands on segments I to XII. Length 11.11 mm to 15.18 mm \bar{x} 12.73 mm. Head width 1.58 mm to 2.57 mm \bar{x} 2.20 mm. Labrum 1.04 mm to 1.24 mm wide \bar{x} 1.14 mm, length 0.65 mm to 0.82 mm \bar{x} 0.76 mm. Labrum with crenulations projected at anterior edges (Pl.VI,D). Labral marginal setae 14 per side. Clypeus with distinct medial spots elongated laterally. Frontal angular markings and center triangle stout and prominent, hat-shaped in appearance. Coronal angular markings very distinct; genal spots elongated and prominent. Pronotal patterns always with three distinct medial pairs of spots, the posterior pair with their bases broader. Lateral elliptical spots numerous and distinct, arranged to form a crescent that opens toward the lateral margin. Mesonotal angular markings distinct on a background of dark reddish-brown; lateral arms often disjoined, slender with upper portions separated at the top of the median suture, medial segment broader posteriorly, base of lateral arms ovoid and pointing inward. Lateral spots forming triangles, the outer two often fused to form an inverted V. Metanotal angular markings with medial arms narrow. Posterolateral semicircular marks open. Ventral thoracic surface without figures. Abdomen robust, very dark almost black with pigmentation on dorsal surface. Lateral edges of each segment unpigmented (Pl.IX,C). (Based on 19 specimens)

Sialis iola Ross

This species is in Ross' Californica group due to genitalic features of the male, but it is definitely an eastern species. *Sialis iola* ranges from 85° longitude in the west to the east coast. It is

found in most of the eastern coastal states (Pl.XIII). Adult genitalia of the male is similar to *Sialis joppa* but the larvae of these two species are distinct. *Sialis iola* was not found in association with any other species.

Emergence is usually later than in most other species, ranging from mid-May through early June. Most adults in this study were taken at Summit Lake in West Virginia in mid-June.

Numerous egg masses were found laid flat on the underside of leaves at Summit Lake. These were not far over the water and were found mostly on leaves of red maple (*Acer rubrum*). The mass is light tan and is spread out in a circular pattern. One mass of *Sialis iola* was found on a board of a small bridge in Cedar Bog at Urbana, Ohio. Eggs were taken in the greatest number at Summit Lake. These hatched in the laboratory in ten days.

The larval habitat is varied for this species. A rather large population was found at Cedar Bog in Ohio which is a unique area with pH ranges of 7.2 to 7.8 and considerable marl formations according to Hufford and Collins (1976). On the other hand, large numbers of larvae were taken from an acid-mine pond in West Virginia. This pond was by the side of a road constructed of coal and slate and was red with the accumulation of iron and acid-mine water. Also a large population was found in a cold mountain lake, Summit Lake, in West Virginia, that was regularly stocked with trout. The larvae seem to be quite tolerant of a variety of conditions. Most larvae were taken in the mud at the base of clumps of grass and sedge. Indications are that a two-year life cycle may occur since two distinct sizes of larvae were taken at the collection sites.

Larvae for this study were taken from the following sites:

Ohio: Cedar Bog, Urbana, Champaign County. West Virginia: A roadside pond near Babcock State Park, Fayette County; Summit Lake, Monongahela National Forest, Greenbrier County.

Egg: Evenly colored light tan, micropylar projection white (Pl.II,F). Length 0.58 mm, width 0.24 mm, micropylar projection 0.07 mm long. Micropylar projection short, broad at base tapering at the tip and lacking a well defined knob at the tip, sides spongy, micropyles forming a ring near apex (Pl.IV,D). Chorion surface evenly covered with small dot-like projections evenly scattered over the surface (Pl.II,F). Number of eggs per mass 289 to 655 \bar{x} 479. (Based on 10 masses)

Larva: Very dark reddish-brown ground color, abdomen dark brown, venter dark brown all the way to the lateral edges (Pl.X,B). Length 19.42 mm to 23.15 mm \bar{x} 20.91 mm. Head width 2.41 mm to 2.90 mm \bar{x} 2.68 mm. Labrum 0.97 mm to 1.3 mm wide \bar{x} 1.11 mm, 0.60 mm to 0.78 mm long \bar{x} 0.66 mm. Labral marginal setae numbering 14 per side. Labrum with a snout-like tip (Pl.VI,E). Head with a dark-reddish background, patterns very distinct on this background. Head and thoracic markings similar to *S. hasta* but more robust. Frontal angular markings lacking medial inward projection of *S. hasta*. Submentum darkened at lateral and posterior edges, cardo similarly darkened. Pronotum with distinct medial spots as in *S. hasta*. Sternum with a triangular spot on each thoracic segment. Mesonotal angular markings very distinct, parts slim and not fused at medial suture. Metanotal angular markings with figures widely separated at median suture, upper portion of metanotal angular markings shaped

like a question mark with an elongated tail, posterolateral semi-circular marks closed or nearly so. Abdomen robust, very dark brown in color, venter with all but last segment completely dark; a thin white branched line runs near the lateral edge of each segment, appearing continuous from one segment to another (Pl.IX,A). (Based on 16 specimens)

Sialis joppa Ross

Sialis joppa ranges east of 90° longitude to the east coast. Except for one record (Tarter, 1978) in Louisiana, it is not found south of 35° latitude. It seems to be mostly concentrated in the Ohio River drainage and in the mountains of New England (Pl.XIV).

Sialis joppa is a member of the Californica group of Ross (1937). In this group the male genitalia are all similar.

Emergence is from mid-April to mid-June, being taken in Kentucky in April and May and later in June in the northern parts of its range. Adults are rather solitary and were never found in large numbers. They seem to be scattered out over the small streams in which they are found. Sometimes 2 to 3 hours of collecting would yield only one or two specimens.

Eggs were found deposited in the flat position on the under side of leaves. The mass is the smallest of any of those studied (\bar{x} 187). The mass appears white in color, is circular in shape, and similar in appearance to that of *Sialis vagans* but has fewer eggs. Egg masses for this study were taken from Morgan's Creek and Overall's Creek in Kentucky. These hatched in the laboratory in 9 to 10 days.

Larvae seem to be confined to small, shallow woodland streams

often no more than 1 to 3 meters wide and less than one-half meter deep. Larvae are found in small pockets of accumulated debris and mud on the edges of the stream bed. As with the adults, the larvae are scattered out along the stream and are few in number. Indications are that a two-year life cycle occurs. Larvae from Morgan's Creek in Kentucky were maintained in the laboratory from September to August of the following year before they died in pupation attempts.

Larvae for this study were taken from the following sites: Kentucky: Morgan's Creek, Otter Creek Park, Meade County; Overall's Creek, Bernheim Forest, Bullitt County; South Fork of Harrod's Creek, Sleepy Hollow, Oldham County; Branch of Harrod's Creek on Rt. 329, Jefferson County.

Egg: Color white, micropylar projection white (Pl.I,E). Length 0.58 mm, width 0.19 mm, micropylar projection 0.06 mm long. Micropylar projection short with a slightly swollen base and a very slight rounded knob at tip, sides spongy in appearance (Pl.IV,F). Chorion surface covered with very small, evenly scattered peltate projections with smaller dot-like structures between them. Number of eggs per mass 170 to 203 \bar{x} 187. (Based on 4 masses)

Larva: Reddish-tan ground color, head and pronotum lighter in color, abdomen dark reddish-brown, venter with dark bands on each segment (Pl.XI,C). Length 8.50 mm to 14.75 mm \bar{x} 10.62 mm. Head width 1.60 mm to 2.31 mm \bar{x} 1.87. Labrum 0.68 mm to 1.04 mm wide \bar{x} 0.85 mm, 0.39 mm to 0.75 mm long \bar{x} 0.56 mm. Labral marginal setae numbering 12 per side. Labral crenulations forming a smooth edge (Pl.VI,H). Head pattern faint, coronal angular markings usually visible, genal spots faint. Post-occipital suture very dark and strong. Medial pronotal spots thickened and ovoid, only posterior

one of group visible; lateral spots large and irregular in shape in mature larvae, posterior margin darker in color. Mesonotal patterns distinct, mesonotal angular markings rather slim in appearance, medial arms broadened at base and somewhat triangular in shape, touching at medial suture, lateral arms with parts fused, bases pointing inward, lateral spots elongated, posterolateral membraneous marks distinct. A heart-shaped spot at the center of the sternum. Metanotal pattern with slim figures, question mark in appearance not touching at median suture, parts usually joined, posterolateral semicircular marks somewhat reniform. (Based on 11 specimens)

Sialis infumata Newman

This species ranges from 95° longitude in the west to the east coast, with none found south of 32° latitude. It is widely distributed north of the Ohio River (Pl.XIV).

Sialis infumata was one of the three nearctic species of *Sialis* prior to Ross' (1937) treatment of the genus. Davis' (1903) work on the life cycle of *S. infumata* in New York may have been based upon several eastern species of *Sialis*.

This species is often collected along with *Sialis hasta* and sometimes with *S. vagans*. Ross (1937) cites *S. infumata* and *S. vagans* as both being taken on May 20, 1936 on a branch of the Cass River at Vassar, Michigan. *S. infumata*, *S. hasta*, and *S. vagans* can be taken with regularity from the streams of Kentucky and Indiana. These species are not similar in the male genitalia or in larval characteristics.

Adults emerge in the early spring at the same times as *S. hasta*,

i.e. in the early part of April in the southern range and in May in the northern part of the range.

Egg masses were found deposited upright on bare twigs, sometimes along with those of *Sialis hasta* on Harrod's Creek in Kentucky. The mass is darker brown than that of *S. hasta* and is larger in size. Both are found high over the water, as high as ten meters. Eggs were taken from Harrod's Creek at Covered Bridge Boy Scout Reservation and Corn Creek in Kentucky. These eggs hatched in six to seven days in the laboratory.

The larval habitat is similar to that of *Sialis hasta* being found in larger sized streams and rivers. Indications are that the life cycle is not more than one year in duration since only one size class of larvae were taken in this study.

Larvae for this study were taken from the following: Illinois: Salt Fork of Vermillion River, near Oakwood. Indiana: Silver Creek, 1 mile east of Henryville, Clark County. Kentucky: Harrod's Creek, Covered Bridge Boy Scout Reservation, Oldham County; South Fork of Harrod's Creek, Sleepy Hollow, Oldham County; Wilson Creek, Bernheim Forest, Bullitt County; Corn Creek, Trimble County.

Egg: Color dark brown, appearing darker at the micropylar end, micropylar projection light brown (Pl.II,B). Length 0.58 mm, width 0.15 mm, micropylar projection 0.11 mm long. Micropylar projection swollen at base, surface smooth, tip with several sharp projections giving a burr-like appearance (Pl.IV,C). Chorion surface covered with large peltate structures, these larger at the micropylar end, appearing as white scale-like coverings from a top view. Number of eggs per mass 440-451 \bar{x} 444. (Based on 7 masses)

Larva: Dark brown ground color, abdomen dark brown on dorsal surface (Pl.XI,B), venter with dark brown bands usually incomplete at center or worn off giving a white venter. Length 8.7 mm to 17.2 mm \bar{x} 14.82 mm. Head width 1.65 mm to 2.44 mm \bar{x} 1.91 mm. Labrum 0.85 mm to 1.52 mm wide \bar{x} 1.12 mm, 0.54 mm to 1.04 mm long \bar{x} 0.77 mm. Labral marginal setae 14 per side. Crenulations form a rolling edge. Mandible with outer edge straighter than most (Pl.VI,B). Head yellow in color, patterns not distinct, usually not visible at all. Medial pronotal spots not usually visible, posterior one may be visible and triangular in shape, lateral spots form a double row of small dark spots. Mesonotal angular markings with lateral arms closely applied to medial arm, touching at medial suture; posterior lateral spots usually two, sometimes three, often appearing as two triangles with apices pointing in opposite directions. Posterolateral membranous spots fuse to form a large comma-shaped figure. Metanotum with parts of metanotal angular markings joined, halves not fused at median suture, upper portion more ovoid than most species. Posterolateral semicircular marks thickened and roughly L-shaped. Abdomen with dorsal surface dark brown, venter varying, dark bands incomplete at edge usually incomplete at center or narrowing at center giving the appearance of a row of two spots on each segment. In some individuals the bands appear worn off and barely visible. (Based on 11 specimens)

Sialis aequalis Banks

This species occurs in the eastern half of the continent, ranging from 95° longitude to the east coast. No material has been seen from south of the 32nd parallel. This species is primarily

found in the eastern coastal states (Pl.XIII).

The adults of this species appear to be related to *Sialis vagans* since in the male the 9th abdominal sternal plate is produced as a flap which covers the genitalia of these species. Larvae are similar in that the head and thoracic patterns are broadly merged (Pl.VII, B & C). The abdomen of *Sialis aequalis* is dark brown and has the chevron markings typical of most species (Pl.X,C) and the venter has dark bands of pigment (Pl.IX,C). However, in *S. vagans* the abdomen is quite different. In this species the chevron markings are connected in the center by a mark that extends forward forming an anchor-like figure on each segment (Pl.VII,B). The venter of *S. vagans* lacks the dark bands also (Pl.IX,B). The eggs are also similar in these two species but differ in micropylar details (Pl. IV, B & E).

Emergence is from mid-April to early May. Adults were not taken of this species in the present study. Their habits were reported by Woodrum and Tarter (1973) in a life cycle study on the species in West Virginia.

Larvae are found in small to medium streams with sandy, rocky bottoms. As with other species of the genus, larvae are found in pockets of accumulated litter and debris along the margins of streams where decreased flow is seen. Larvae of this species are apparently quite tolerant of low hydrogen ion concentration (pH). Woodrum and Tarter (1972) reported that *Sialis aequalis* larvae were able to withstand a pH of 3.0. The species seemed to be thriving in Camp Creek, an acid-mine stream, in Wayne County, West Virginia where Woodrum and Tarter (1972) had taken their specimens and was still

abundant in the fall of 1977.

Egg masses for this species were found deposited in the flat position on the underside of leaves along Flatfoot Creek in Cabell County, West Virginia. The mass is small, white, and round to oval in shape. It is very much like that of *Sialis vagans*, which is sometimes found on leaves. The eggs of these two species are separated by details of the micropylar projection (Pl.IV,B & E). The eggs hatched in the laboratory in eight to ten days.

Larvae for this study were taken from Camp Creek, Wayne County, West Virginia and Flatfoot Creek, Cabell County, West Virginia.

Egg: Color white, darkening with age, micropylar projection white also (Pl.II,D). Length 0.56 mm, width 0.20 mm, micropylar projection 0.09 mm long. Micropylar projection cylindrical without a pronounced knob at apex, slightly constricted at the base, surface spongy in appearance (Pl.IV,B). Chorion surface covered with small, evenly scattered granular structures. Number of eggs per mass 262 to 335 \bar{x} 298. (Based on 2 masses)

Larva: Head and pronotum light yellowish-brown color, ground color otherwise medium brown, abdomen with dorsal surface dark brown, venter with dark brown bands on each of segments I to VII, each band incomplete laterally (Pl.X,C). Length 12.5 mm to 17.9 mm \bar{x} 13.5 mm. Head with 1.90 mm to 2.24 mm \bar{x} 2.09 mm. Labrum 1.04 mm to 1.30 mm wide \bar{x} 1.16 mm, width 1.90 mm to 2.24 mm \bar{x} 2.09 mm. Labral marginal setae 15 per side. Crenulations forming a squarish edge (Pl.VI,F). Coronal angular markings usually distinct as are the frontal angular markings. Genal spots usually faint. Antennae with segment III one fourth as long as segment IV. Pronotal pattern faint, medial spots

barely visible if at all, darkened areas between lateral spots forming a crescent opening to the lateral edges; prosternum with two dark crescent-shaped spots near the anterior margin. Mesonotal pattern distinct, mesonotal angular markings may be fused at median suture, lateral arms of figure closely applied to median arm, posterior bases ovoid, pointing inward; posterior lateral spots thick and oval in shape. Metanotum with rather thick parts, usually joined, markings not touching at median suture. Posterolateral semicircular marks closed with dark spots in the center. (Based on 16 specimens)

Sialis vagans Ross

This species ranges from 95° longitude in the west to the east coast; none have been reported south of the 30th parallel (Pl. XIII). It is found in most of the eastern region exclusive of the Appalachian Mountains.

Sialis vagans is quite similar to *S. aequalis* in that the male of both has the 9th abdominal segment projected as a flap that covers the genitalia (see *S. aequalis*). These two are also alike in the larval stage to some degree. Despite these similarities, Ross' (1937) records and collections from the present study do not show these two species being collected together at the same locality. However, *S. vagans* is frequently taken with *S. hasta* or *S. infumata*.

Emergence of *S. vagans* is in the early spring, occurring in early April in northern Kentucky and southern Indiana and later in mid-May to mid-June further north. Adults were taken in mid-May in Michigan, and Tennessen (1968) reports the species taken through June 20 in northern Wisconsin.

Egg masses were taken on twigs and on the underside of leaves at Tom Wallace Lake and Harrod's Creek in Kentucky. The mass is white and laid in a fan shape on the leaves or spread out along the twigs. On the leaves eggs are not deposited on the veins by the female. One female *Sialis vagans* was observed to take over an hour to lay her eggs on the underside of a leaf. The mass is somewhat similar to that of *Sialis joppa* or *S. aequalis* but may be distinguished from the former by the number of eggs and by the micropylar projection details. The eggs hatched in the laboratory in seven days.

Larvae have been collected in both streams and lakes. A sizeable population was found in a small lake, Tom Wallace Lake, in Kentucky. Other populations were found in streams. The habitat appears to be muddy, slow-moving water, such as areas behind dams or in stream backwater. Larvae were most often found in these areas where a deep mud layer covered the bottom. All indications point to a one-year life cycle in this species since only one size class of larvae were taken at the collecting sites.

Larvae were taken for this study from the following sites:
Kentucky: Tom Wallace Lake, Jefferson County; Branch of Harrod's Creek on Rt. 329, Jefferson County; Harrod's Creek, Bridge on Rt. 393, Oldham County; South Fork of Harrod's Creek, Sleepy Hollow, Oldham County.
Michigan: East Branch Au Sauble River, Lovells, Crawford County;
Middle Branch of Au Sauble River, Rt. F-97 near Hardwick Pines, Crawford County.

Egg: Color light cream to yellow, darkening with development, micropylar projection white (Pl.II,E). Length 0.54 mm, width 0.17 mm, micropylar projection 0.08 mm long. Micropylar projection short, base

constricted, tip with a rounded knob formed by a ring of micropylar openings (Pl.IV,E). Chorion surface covered with small peltate projections, with white dot-like projections evenly scattered between them. Number of eggs per mass 437 to 573 \bar{x} 479.
(Based on 12 masses)

Larva: Light brown ground color, abdomen dark brown, venter white, lacking pigmented bands (Pl.I,B). Length 11.94 mm to 15.25 mm \bar{x} 13.22 mm. Head width 1.66 mm to 2.07 mm \bar{x} 1.87 mm. Labrum 0.65 mm to 0.91 mm wide \bar{x} 0.81 mm, length 0.45 mm to 0.56 mm \bar{x} 0.51 mm. Labral marginal setae numbering 14 to 15 per side. Crenulations form a rolling edge. Head light yellow in color, patterns faint, usually coronal and frontal angular markings visible; genal spots rounded and faint. Pro-notum light yellow in color, medial spots not visible, medial area very light, bounded by a series of lateral spots in two rows. Mesonotal angular markings have parts joined; lateral arms fused to medial arm, forming a rectangular figure; lateral spots usually fused forming another lighter area. Metanotal angular markings fused anteriorly, posterior bases broadly rounded. Posterolateral semicircular marks absent or nearly so. Dorsal surface of the abdomen with anchor-like figure on each segment, these from a center spot joining the lateral chevron marks (Pl.VII,B). Pigmented areas usually not reaching the lateral edge. (Based on 12 specimens)

Sialis glabella Ross

This apparently rare species was reported by Ross (1937) from only two localities: Mt. Carmel, Illinois, the type locality, and Muncie, Illinois. Both sites are on the Wabash River. During the

present study a population of *Sialis glabella* was found in Nelson County, Kentucky. This site is a very small woodland pond on a high, isolated ridge in Knobs State Forest. The pond is only about ten meters in diameter but contains a sizeable population of this species.

Adults of *Sialis glabella* are much like those of *S. americana* in the male genitalia according to Ross (1937) but the two species differ in the coloration of the head. During this study, a trip was made to Mt. Carmel but neither adults nor larvae were found.

Cuyler (1956) described the larvae of *Sialis americana* from Wake County, North Carolina. His specimens had a third tooth on the mandible as do those taken from the site in Kentucky. However, the color patterns of the head and thorax of the Kentucky specimens are different from those described by Cuyler. No *Sialis americana* were taken in the present study but based on the adults and larvae I believe that the material from Nelson County represents *S. glabella*.

Emergence is in late May to June. Material from the Kentucky site was taken in early June, while Ross' (1937) records show *S. glabella* flying in late May on the Wabash River.

Several egg masses were taken at the pond in Knobs State Forest. These masses are unusual in that they show a red-orange color and eggs are laid upright on the underside of leaves. The eggs are deposited in a tight circular mass and are the largest eggs of any of those studied (Table I). Eggs returned to the laboratory hatched in eight days.

Larvae were taken from the pond in Kentucky at Knobs State Forest which had a deep layer of fine sediment and leaf litter on the bottom. The small tributaries at Mt. Carmel flowing into the Wabash River also

have deep mud bottoms. These observations seem to indicate that *S. glabella* prefers to burrow deep in the sediment and mud.

Egg: Color reddish-orange, micropylar projection a paler reddish-orange. Length 0.65 mm, width 0.22 mm, micropylar projection 0.09 mm long. Micropylar projection is a large club-like structure borne on a thick base, with the micropylar openings forming a slightly constricted ring at the apex (Pl. V,A). The chorion surface is covered with very tiny dot-like structures that are evenly distributed. Number of eggs per mass 192 to 312 \bar{x} 242. (Based on 7 masses)

Larva: Dark yellow ground color, abdomen a dark reddish-brown, venter usually white (Pl.XI,A). Length 14.51 mm to 16.51 mm. Head width 2.07 mm. Labrum 0.60 mm wide, 0.38 mm long. Labral marginal setae numbering 13 per side, crenulations deep (Pl.VI,I). Mandibles long with three narrow sharp teeth (Pl.VI,A). Head pattern with all markings dark-reddish brown on a yellow background. Pronotal pattern also dark on a lighter background with spots encircled with a light halo. Mesonotal figures light on a darker background as with other species. Mesonotal angular markings with parts disjoined, medial arm formed by two triangles fused at the base along median suture. Metanotal angular markings disjoined, widely separated medially, upper portion like a question mark. Dorsal surface of the abdomen with a center spot in each segment in addition to the usual lateral chevron marks. These central spots form a cross-like figure on each segment. (Based on 4 specimens)

Sialis mohri Ross

This species ranges from 95° longitude to the east coast. It

is not found south of 36⁰ latitude. It is widely distributed in the lakes north of the Ohio River (Pl.XIII).

The adults are often found in large numbers around lakes and impoundments. *Sialis mohri* occurs occasionally with *S. velata* and to a lesser extent with *S. itasca*. Adults males are easily distinguished by their distinctive genitalia. Mature larvae of these three species are all similar in appearance.

Emergence of *Sialis mohri* occurs in May to late June or early July in some parts of the range. Large numbers of adults were taken in Kentucky and Indiana lakes and impoundments in mid-May. Emergence times extend from mid-June to early July in Michigan and through mid July in some parts of the Upper Peninsula of Michigan.

Numerous egg masses of this species were found on the shoreline vegetation of several lakes. The mass is usually laid on twigs although some were found on the leaves of cattail (*Typha* sp.) The eggs are deposited in an upright position and often placed so the mass completely encircles the twig (Pl.I,A). The long, white micropylar projections are prominent above the masses. Ross (1937) described the micropylar projection as a "tassel" but the projection is cylindrical and straight-sided (Pl.V,B). Often several egg masses are laid side by side, literally covering the twig with eggs. Eggs used in this study were taken from Deam Lake, Monroe Reservoir, in Indiana; Houghton Lake, Mio Pond, Burt Lake, Douglass Lake, in Michigan; and Sympson Reservoir in Kentucky. Egg masses returned to the laboratory hatched in ten to eleven days.

The larvae were all taken from larger lakes and impoundments. They were found in the bottom mud and litter in the bays and inlets of

these lakes. They probably migrate to the deeper water in winter months. Giani and Laville (1973) reported a migration for *Sialis lutaria* in Lake Port-Bielh in the Pyrennes Mountains. In the present study no larvae could be found in water less than a meter deep during the winter months at Deam Lake, Indiana.

Larvae for this study were taken from the following sites:
Indiana: Deam Lake, Clark County. Michigan: Houghton Lake, Roscommon County; Power Dam at Mio, Oscoda County.

Egg: Color grayish-brown, slightly darker at the micropylar end, micropylar projection white (Pl.II,C). Length 0.58 mm, 0.17 mm wide, micropylar projection 0.20 mm long. Micropylar projection columnar, longer than most, lacking a knob or projections at apex, surface spongy in appearance (Pl.V,B). Chorion surface with raised peltate structures that diminish in size toward the egg base. Number of eggs per mass 500 to 905 \bar{x} 718. (Based on 17 masses)

Larva: Medium brown ground color, abdomen dark brown, venter light, some with faint cross bands (Pl.XII,B). Length 11.52 mm to 14.43 mm \bar{x} 13.02mm. Head width 1.41 mm to 1.91 mm \bar{x} 1.67 mm. Labrum 0.65 mm to 0.91 mm \bar{x} 0.59 mm, 0.45 mm to 0.52 mm long \bar{x} 0.38 mm. Labral marginal setae numbering 14 to 15 per side. Head yellow with faint patterns, frontal angular markings visible, coronal angular markings faint and elongated, occipital suture curving gradually. Pronotal patterns not usually visible, a lighter rectangular area in the center instead of the usual medial spots, faint darkened lines at the median suture, posterior margin with dark wavy lines. Mesonotal angular markings with parts thickened and joined, the halves touching at the median suture, the anterolateral irregular spots may join the

figure near the anterior end. Metanotal angular markings with parts thickened also and disjoined, lateral arm with anterior part shaped like an exclamation mark. Posterolateral semicircular marks partially closed. (Based on 9 specimens)

Sialis velata Ross

This species ranges from 100° longitude to the east coast and, except for one record in Texas (Ross, 1937), is not found south of 35° latitude. This is the most widely distributed species of the genus (Pl.XIII).

The species is occasionally encountered with *Sialis mohri*. Adults males of these two species possess distinctive genitalia, but the larvae of these two are somewhat similar.

Emergence of the adults is similar to that of *S. mohri* running from mid-May through late June. *Sialis velata* adults were taken in large numbers in late May and early June in Michigan.

Egg masses are large and similar to those of *S. mohri* in arrangement and basic features. Those of *Sialis velata* are darker brown and lack the grayish tint of *S. mohri* eggs. The micropylar projection is not as white as in *S. mohri* and differs in surface structure. The egg masses often completely cover the twigs or grass blades on which they are laid. Eggs for this study were taken from Lake Margarethe in Michigan. These hatched in the laboratory in eight to nine days.

Larvae in this study were taken only from lakes; however, Ross (1937) found this species on streams as well. Larvae were found burrowed in the sandy bottoms of the lakes in Michigan.

Larvae for this study were taken from Lake Margarethe, near Grayling, Michigan and Houghton Lake, Roscommon County, Michigan.

Egg: Color grayish brown, micropylar projection white (Pl.III, A). Length 0.58 mm, width 0.18 mm, micropylar projection 0.16 mm long. Micropylar projection long with a burr-like knob at the apex, sides smooth (Pl.V,C). Chorion surface with small peltate structures diminishing in size and number toward the egg base. Number of eggs per mass 577 to 780 \bar{x} 679. (Based on 18 masses)

Larva: Dark brown ground color, abdomen medium brown, venter light with some light brown spots on later segments (Pl.XII,C). Length 12.20 mm to 15.93 mm \bar{x} 13.82 mm. Head width 1.83 mm to 2.07 mm \bar{x} 1.93 mm. Labrum 0.84 mm to 0.91 mm wide \bar{x} 0.88 mm, length 0.58 mm to 0.60 mm \bar{x} 0.59 mm. Labral marginal setae numbering 15 per side. Head yellow, patterns barely visible, postoccipital suture heavy and dark, with streaks of pigment projecting from it. Pronotum yellow, usual pattern of spots not visible, some darker areas present on lateral and posterior edges. Mesonotal angular markings with parts joined, very thick, lateral arms fusing with median arm, halves of figure touching at the median suture. Metanotal angular markings with parts joined, upper portion of lateral arms appearing as exclamation marks which touch at the anterior part along the median suture. Posterolateral semicircular marks closed and irregular in shape. (Based on 7 specimens)

Sialis itasca Ross

This species ranges from 90° longitude to 75° longitude and is not found south of 30° latitude (Pl.XIII).

The adult males resemble closely those of *S. velata*, but they may be separated by minute details of the genitalia (Ross, 1937). The larvae are also somewhat similar in these two species.

Emergence is later than most species, occurring in late May through early July. No adults were taken in this study but several were studied by Lilly (1976) at a small pond in West Virginia.

Egg masses were found at the above pond in Wayne County, West Virginia. These were deposited on the underside of leaves with the eggs placed upright. These eggs along with those of *Sialis glabella* were the only ones found to be laid upright on leaves. The mass is light brown, circular in shape and with long, whiteish micropylar projections. The eggs taken from this site on June 15, 1978 had already hatched so no hatching time is given for this species.

Larval habitat seems to be similar to that of *Sialis mohri* and *S. velata* in that all tend to favor lakes. Larvae for this study were taken from a small pond—Wayne County Coon Hunter's Pond, Lavalete, West Virginia where Lilly (1976) had studied the life cycle of this species. The larvae were found at the inlet of the pond in a deep layer of mud and leaf litter.

Egg: Color light brown, micropylar projection white (Pl.III,B). Length 0.57 mm, width 0.19 mm, micropylar projection 0.21 mm long. Micropylar projection tapering, covered with short, numerous projections, base somewhat constricted (Pl.V,D). Chorion surface with large peltate structures that diminish in size and number toward the egg base. Number of eggs per mass 330 to 583 \bar{x} 560. (Based on 3 masses)

Larva: Dark brown ground color, abdomen dark brown, venter lacking pigmented bands (Pl.XII,A). Length 13.61 mm to 15.68 mm \bar{x} 14.57 mm,

Head width 1.83 mm to 2.16 mm \bar{x} 2.01 mm. Labrum 0.78mm to 1.05 mm wide \bar{x} 0.95 mm, 0.49 mm to 0.71 mm long \bar{x} 0.58 mm. Labral marginal setae numbering 16 per side, lateral crenulations rolling with a slightly projected anterior edge (Pl.VI,G). Head yellow, patterns faint, coronal angular markings darker than background, genal spots also darkened. Pronotum light brown, pronotal medial spots usually visible, lateral spots dark with a lighter halo surrounding each, posterior margin very dark. Mesonotal patterns distinct, similar to *Sialis mohri*, mesonotal angular markings with parts joined, slim in appearance, medial arms rounded at posterior base, halves of figure touching at median suture, posterior lateral spots long and thin. Metanotal angular markings slim, disjoined, and distinct. Posterolateral semicircular marks irregularly shaped with a dark spot in the center. (Based on 15 specimens)

DISCUSSION

Ross (1937) in his study of nearctic alderflies arranged the species of *Sialis* into phylogenetic units based primarily on male genitalic features. He divided the genus into four units. In one group male genitalia are relatively simple and none of the anatomical parts are greatly enlarged. In this category two units were recognized—the Californica group, with short, hooked genital arms included five western species, *Sialis arvalis*, *S. californica*, *S. cornuta*, *S. hamata*, and *S. occidentis* and two eastern species, *Sialis iola* and *S. joppa*. The other group—the Americana Group possessed long, straight genital arms and included *Sialis americana* and *S. glabella*.

The other two groups—the Infumata group with the genital plate (modified 10th sternite) anteriorly directed with long hooks—consisted of *Sialis velata*, *S. itasca*, *S. concava*, *S. infumata*, *S. hasta*, and *S. mohri*; and the Aequalis group in which the ninth sternite is enlarged and produced as a ventral flap which covers the genitalia. This group includes *Sialis aequalis* and *S. vagans*. In the present study of *Sialis* eggs and larvae as well as the behavior of adults, additional evidence has been obtained that substantiates the relationship that Ross (1937) outlined in his divisions of the family.

The Americana group is distinct, for the eggs and larvae are different from those of any other species. The eggs of *Sialis glabella* have a reddish-orange color, are laid upright on leaves, and are the largest of any of those studied. Eggs of *Sialis americana* have not been described, but probably are very similar to those of *S. glabella*. The larva of *S. glabella* has the color patterns of the head and thorax reversed (dark on a light background while all other species have lighter

patterns on a dark background). An extra tooth on the mandible is found on *Sialis glabella*. Cuyler (1956) described *S. americana* larvae as having the extra mandibular tooth also. Indications are that both species are found in the small pond type of habitat. Perhaps *S. glabella* and *S. americana* are the remnant of some prototype from which the other species have developed.

The Aequalis group forms a natural unit since the eggs and larvae of the two species are similar. The eggs differ slightly in the details of the micropylar projection. The larvae share some features, such as the coalescing parts of the mesonotal pattern, but differ in the anchor-like figures found on the dorsum of the abdomen of *S. vagans* that are lacking in *S. aequalis*. The larva of *S. vagans* seems to be more adapted to lakes, although it was found in slower moving water of streams. *Sialis aequalis* has been taken only in streams.

The Californica group that included *Sialis joppa* and *S. iola* makes up a more heterogenous unit and presents more of a problem. Eggs of these two species are alike. In both species the eggs are laid flat and are small in size with short micropylar projections. However, the larvae of *S. iola* are much more like that of *S. hasta* than any other of those studied. The habitat of *Sialis joppa* seems rather restricted, i.e. small streams, while *S. iola* was found in a variety of habitats.

The members of the Infumata group, with the exception of *S. hasta* are all rather similar. The eggs are laid upright, their micropylar projections are long and the chorion colors are darker in this group. The larvae have a light ground color and rather faint head and thoracic patterns, except for *S. hasta* which has a darker ground color and distinct patterns more like those of *S. iola*.

Most of the group was found to inhabit lakes, except for *Sialis infumata* and *S. hasta*.

Several species of *Sialis* are sympatric. In most of the species, there seems to be a preference for different habitats which separates them. For example, *Sialis joppa* inhabits small streams, while *S. mohri* and *S. velata* are usually found in lakes. Some species, *Sialis hasta*, *S. infumata* and *S. vagans*, are encountered together literally on the same tree or other vegetation. This sympatry appears to violate the principle of competitive exclusion as proposed by some ecologists. However, the food resources do not seem to be limiting in the larval habitats, even though the larvae may be found in close proximity to one another. There is usually an abundance of food in the mud and debris. Also the larvae are not dependent upon an exact source of food since they are carnivorous or to an extent omnivorous.

As Ross (1937) found with *Sialis velata* and *S. mohri* there is a temporal spacing in the emergence of some species. *Sialis velata* invariably emerges first when associated with *S. mohri*. No such temporal spacing has been observed for *S. hasta* and *S. infumata*, although *S. vagans* was found to emerge slightly earlier than *S. hasta* at Lovells, Michigan where the two occur together.

Rupprecht (1975) reported a system of communication between the sexes by *Sialis lutaria* and *S. fuliginosa*, two European species. The communication involved vibrations of the abdomen and the tapping of the abdomen by the wings that was different for each species. Dubois and Geigy (1935) described sensory structures on the labrum of the male and discs on the wings of the female of *S. lutaria* that were used to locate mates. While none of these features have been seen in

any American species, there is probably a premating behavioral pattern that is species specific which separates the sympatric species. These were not observed in this study since no laboratory matings were achieved by any of the species studied.

Alderflies are probably much more abundant than collection records indicate. If one looks at the proper time and place, large numbers of adults may be found. Hundreds of adult *Sialis velata* were seen at a site on the north shore of Houghton Lake in Michigan. Visits to this site for three consecutive years always yielded large numbers of adults. Every suitable oviposition site is usually covered with egg masses and adult alderflies. In the collection of the Illinois Natural History Survey, I found two full half-pint jars of adult *S. velata* labeled paratypes. These were taken from Lake Margarethe in Michigan in 1936. This certainly indicates a very large population at that time. I found a large population still at the same lake during several visits over the course of this study. Similar large hatches were observed in *Sialis mohri* at Deam Lake and Monroe Reservoir in Indiana and at Sympson Lake in Kentucky. Dredging of these lakes would yield large numbers of larvae as well.

Larvae occur in many streams and they can be found if sought in their preferred habitat. Generally, stream samples are taken from riffle areas and these collections fail to yield a large number of sialid larvae. The larvae inhabit pools and the slower moving margins of the streams with muddy, silty bottom deposits and accumulated debris. In such places larger numbers of larvae may be taken.

The sialid larvae along with the odonate larvae found in this

habitat are the secondary carnivores in this system. The larvae also provide food for fish and higher invertebrates. The first instar larvae would be particularly subject to prey of small fish. A fish could pick them off as the helpless larvae drop from the egg mass into the water.

The stream species are usually found in smaller numbers. The larvae play the important role of carnivore in the food chain of the mud-litter habitat. This may account for the fact that few larvae are usually taken close together. As predators the larvae would tend to scatter out since the number of prey in an area could support only a limited number of predators.

The number of eggs laid by those species inhabiting lakes is much larger than those in the stream species. *Sialis mohri* and *S. velata* usually have over 600 to 700 eggs per mass while those stream species such as *Sialis hasta*, *S. infumata*, or *S. joppa* have 300 to 400 eggs per mass. The large number of eggs may compensate for the loss of the first instar larvae to predators or cannibalism. These younger larvae have little protection on the lake bottom, since they usually drop into shallow, clear water where there are few hiding places. The surviving mature larvae migrate into deeper water and burrow into the muddy bottom. Stream species are also subject to some predation as well, but may find better cover on the stream bottom than on the lake bottom. Many larvae would be swept away by the current but eventually find a quiet pool to inhabit.

The burrowing adaptation affords the larvae some protection from predators and puts them close to a source of food in the mud and litter. The nocturnal feeding activity as reported by Azam and Anderson (1969) is also apparently an adaptation which allows some protection from predators.

Probably the greatest competition between species is for suitable oviposition sites. For example, adults of *Sialis velata* and *S. mohri* that fly together might exhibit this competition. *Sialis velata*, by emerging earlier, could gain an advantage in choosing oviposition sites. This is of no great consequence, however, unless there is a shortage of such sites.

With the encroachment of more civilization on lakes and streams, many oviposition sites are being destroyed as the shoreline vegetation is made scarce. The collection site, for example, at Houghton Lake, Michigan is a vacant lot on the north shore of the lake. This lot was cleared in 1978 probably with plans to build a summer cottage. In the process much of the shoreline vegetation was destroyed eliminating some of the choice oviposition sites on the overhanging branches. Similar results might occur from clear cutting of timber along a stream.

The number of larval instars and the length of the life cycle seems to vary among the species of *Sialis*. Pritchard and Leischner (1972) found 8, 9, or 10 instars in the rearing they did of *S. cornuta*. Azam and Anderson (1969) found ten instars in *S. rotunda* and *S. californica*. Woodrum and Tarter (1973) reported ten instars for *S. aequalis* based on head capsule widths.

In the laboratory rearings of specimens for this study produced no more than three molts between August and the time the specimen pupated in the following spring. This would suggest fewer than ten instars for most species. There is, however, strong evidence of a life cycle of more than one year's duration for *Sialis joppa*, *S. iola* and perhaps *S. hasta* which could account for the low number of instars found in

these species. There may be more frequent molting from spring until August by the young larvae. None of the larvae were collected during this time from the field and none were reared from the first instar in the laboratory. Azam and Anderson (1969) felt the length of the life cycle of *S. californica* was determined by the amount of food available. It would seem that temperature is more important as a factor in the life cycle of *S. hasta* since a longer life cycle is apparent in Michigan than in Kentucky. Probably the instar number is due to an interaction of temperature and the amount of food available during the critical winter months.

Emergence of *Sialis* adults may vary considerably annually depending upon the prevailing climatic conditions. Emergence seems to depend upon the time that spring breaks and not how severe the winter itself was.

This is illustrated by the fact that in 1977 the emergence was very early for all species despite the extremely cold temperatures that occurred during that winter. In 1978, however, all emergences were late due to the heavy snow accumulation and the late arrival of spring. Ice remained on the lakes of Michigan until almost May 1st.

Sialis velata was taken in mid-May in 1977 at Houghton Lake while prepupae were taken on May 8, 1978 at Houghton Lake and Lake Margarethe, but no adults were found flying until May 27 that year. In 1977 *Sialis hasta* and *S. infumata* were taken in early April in Kentucky while in 1978 emergence was delayed until the end of April.

This annual variation might account for some of the records of *Sialis* adults being taken in July or August. It is thus difficult to predict an exact order of emergence for *Sialis* adults but it appears

that *Sialis vagans* emerges earliest in the spring in any area within its range. *Sialis hasta* and *S. infumata* would follow closely behind with *S. aequalis* and *S. joppa* emerging next. Where the two occur together *S. velata* emerges before *S. mohri* as suggested by Ross (1937). Only one *S. mohri* adult was taken among hundreds of *S. velata* at Houghton Lake in June of 1978, while about equal numbers of these two were found in May of 1977 and June of 1976. *Sialis itasca* and *S. iola* were the latest to emerge with *S. glabella* slightly before them, although so few records of this species exist that a precise emergence pattern is hard to predict.

The oviposition site the female selects is usually one that will allow the newly hatched larvae to fall directly into the water. There is no particular preference for a species of plant in this selection. The female apparently chooses a site for oviposition by its proximity to the water rather than the site's surface structure, type of plant, or species. *Sialis velata* eggs were found hanging over the water on the rough, scaly bark of pine twigs, and within a few meters other masses were found on the smooth blades of grasses hanging over the water. The eggs of *Sialis vagans* were found on box elder leaves and also on twigs of birch that were hanging over the water at the same locality, Harrod's Creek, Kentucky. Azam and Anderson (1969) found eggs of *Sialis rotunda* and *S. californica* laid on bridges and culverts in Oregon. Pritchard and Leischner (1972) induced *S. cornuta* to oviposit on artificial substrates made of plywood that they placed in their study pond. In the present study all egg masses were found on natural materials, except for one mass of *S. iola* that was found on a bridge board in Cedar Bog, Ohio.

No evidence was found in this study of more than one oviposition by the female as reported by Dubois and Geigy (1935) for *Sialis lutaria*, a European species. The counts of eggs in the ovaries and the number of eggs per mass are close, with the exception of *S. aequalis*.

If a female is disturbed while laying her eggs, she would probably finish laying her eggs at another site. One female *Sialis vagans* was observed to take over an hour to lay her 500 eggs in the field. Considerable energy must be expended in the maturation and oviposition of the eggs, so it is doubtful that a female has additional energy to expend for a second oviposition. Matsuzaki (1977) showed that only 3 to 4 mature eggs are present in the ovariole as did Dubois and Geigy (1935). In the dissected gravid females of the present study only 1 to 2 mature eggs were present in the follicular portion of the ovarioles. It would take some time for subsequent eggs to develop to a mature stage in the ovariole. This would also indicate that a second oviposition is unlikely.

There is no substantial evidence of actual feeding by the adults of *Sialis*. Dubois and Geigy (1935) reported that *S. lutaria* squeezed nectar from *Antriacus silvestris* flowers. Azam and Anderson (1969) also saw adults of *Sialis rotunda* and *S. californica* with their mouth parts appressed to flowers. Their dissections of adults showed that the alimentary canal was not developed, however; so actual feeding could not occur. This lack of food intake would also suggest that a female would not have enough energy reserve to oviposit more than one egg mass.

The chorion surface and micropylar projections of the sialid egg are adorned with raised structures that are only vaguely discern-

ible using light microscopy. The scanning electron microscope permits these surface structures to be perused in greater detail and confirms that the chorion surface adornment varies in size and arrangement in the alderfly species studied here. These chorionic structures are larger in those eggs which are oviposited in an upright position. In these upright eggs, the surface structures also diminish in size and complexity toward the attached base of the egg. Eggs oviposited in a horizontal position in the egg mass tend to have smaller evenly distributed structures over the chorion surface.

The distribution of chorionic structures and the arrangement of the eggs in the mass confirm their usefulness in providing the collective mass with a combined plastron surface that protects the eggs from wetting as found by Hinton (1959, 1960). Eggs arrayed vertically in the mass are usually exposed to wetting, since these masses are usually oviposited on unshielded twigs and leaves. Horizontally arrayed eggs are found in egg masses that are placed in more protected, unexposed areas. These masses are perhaps subjected to heavy dew condensation but not to direct precipitation.

The micropylar projection details are also made quite clear by the scanning electron microscope. Several forms of this structure are revealed which serve as distinguishing characters in separating the eggs. The exact function of such an extended structure needs further study, for its function may be variable.

The micropylar projection surface is porous or spongy in appearance on the sides. This along with its hollow feature might allow for the exchange of gases for the developing egg particularly since no aeropyles are apparent on the chorion surface. The extended

micropylar projection may serve as a snorkel-like apparatus, especially when the eggs are wet. Such a device might function in addition to the above mentioned plastron respiration.

The long micropylar projection might also serve as an aid to the fertilization process. Fertilization occurs as the eggs pass by the bursa copulatrix which stores the sperm from a spermatophore deposited by the male as reported by Dubois and Geigy (1935). As the eggs pass by this bursa the long micropylar projection could help in picking up sperm from this storage sac. The knobbed or spiny apex of the micropylar projection might stimulate the release of sperm from the bursa.

Finally it is possible that the rugose surface with spines and projections that adorns the surface of the micropylar projection may act as some sort of protective device against parasitoid wasps and other such insects. Such a surface might deter an insect from walking over the surface of the egg mass.

Another feature of the egg revealed in detail by the scanning electron microscope is the egg burster. The exact function of the tooth-like structures on the inner surface of the egg burster is unknown. These may articulate with the head of the embryo providing a contact point and leverage as it ruptures the egg in hatching. Another more likely possibility is that they serve to rupture the embryonic envelope as the larva emerges from the egg. Such a sac was reported by Smith (1920,1922) to occur in the eggs of other Megaloptera. Remains of this sac may be seen at the posterior end of dead larvae still attached to the egg mass.

Perhaps the egg burster is oriented within the unhatched egg

near the micropylar end so that the pushing and movement of the hatching larva causes the triangular untoothed surface to rupture the chorion surface. As the action continues, the break enlarges resulting in the openings seen in the micrographs. The egg burster is then left extending out from the surface as seen in the micrographs (Pl.III) with the teeth decurving downward leaving a surface on which the embryonic envelope could catch and tear open.

Evans (1972) presented a photograph of the egg of *Sialis hamata* showing the teeth turned outward toward the chorion surface. This slide was apparently of a cleared, stained egg. In the preparation process the egg burster may have been dislodged and disoriented from its normal, functional position.

Hopefully, this work has added considerably to the knowledge of the immature stages of the eastern North American Sialidae and has also raised some interesting questions that need further study. Precise identification of the larval and egg stages should permit easy collection of detailed ecological data in the future.

PLATE I. Eggs and Oviposition Types in Sialidae

- A. Female *Sialis mohri* ovipositing on a twig
- B. Egg masses of *Sialis vagans* laid flat on twigs and leaves
- C. Eggs laid in flat position, *Sialis joppa*
- D. Eggs laid in upright position, *Sialis hasta*
- E. SEM of the eggs of *Sialis joppa* (a) micropylar projection
- F. Micropylar projection and egg bursters of *Sialis itasca*
(a) micropylar projection (b) egg bursters

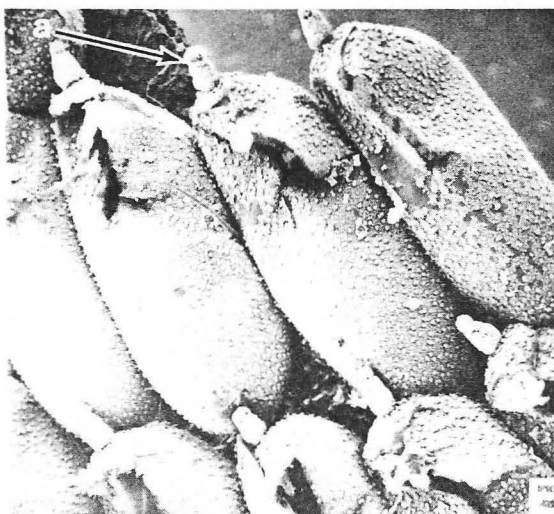
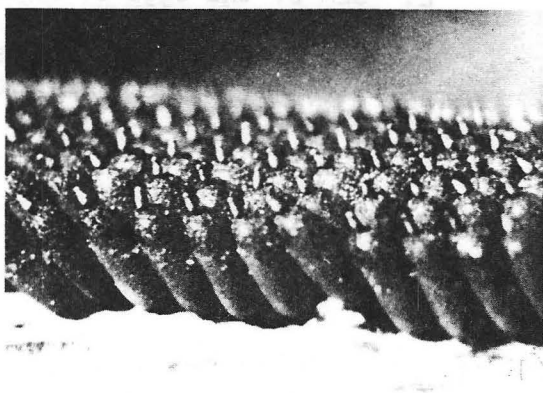
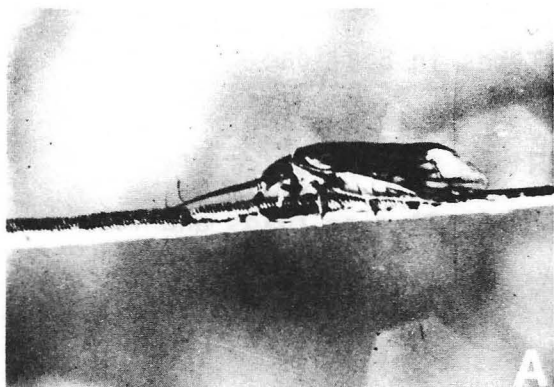
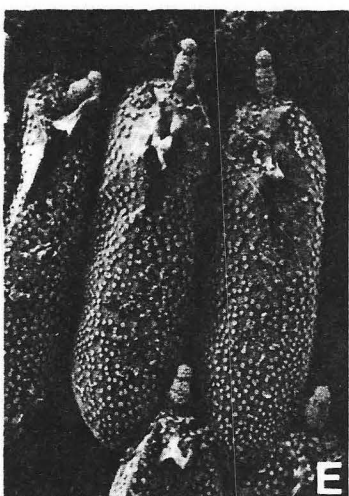
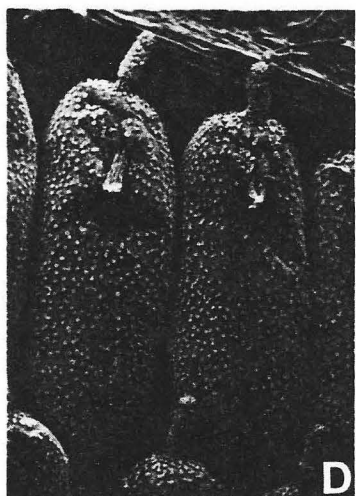
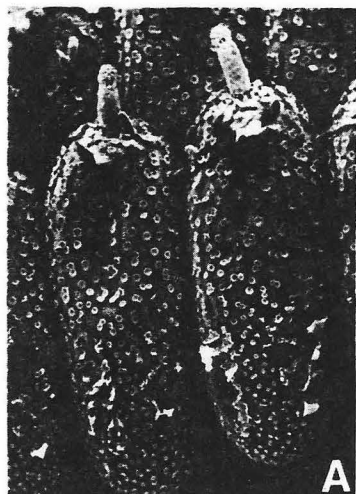


PLATE II. Eggs of *Sialis*

- A. Eggs of *Sialis hasta*.
- B. Eggs of *Sialis infumata*
- C. Eggs of *Sialis mohri*
- D. Eggs of *Sialis aequalis*
- E. Eggs of *Sialis vagans*
- F. Eggs of *Sialis iola*



←→
.25 mm

PLATE III. Eggs and Egg Bursters

- A. Eggs of *Sialis velata* (arrow represents 0.50 mm)
- B. Eggs of *Sialis itasca* (arrow represents 0.50 mm)
- C. Egg burster of *Sialis hasta* (arrow represents 0.05 mm)
- D. Egg burster of *Sialis iola* (arrow represents 0.05 mm)
- E. Egg burster of *Sialis vagans* (arrow represents 0.05 mm)
- F. Egg burster of *Sialis infumata* (arrow represents 0.05 mm)

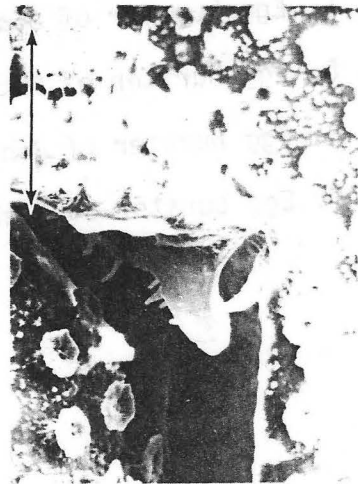
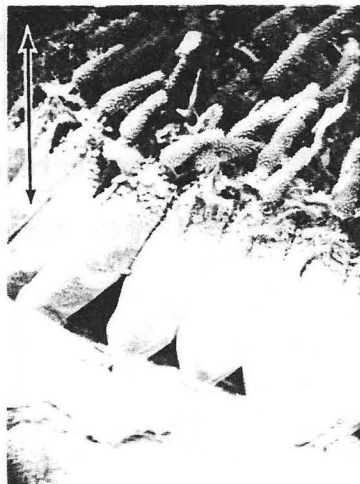
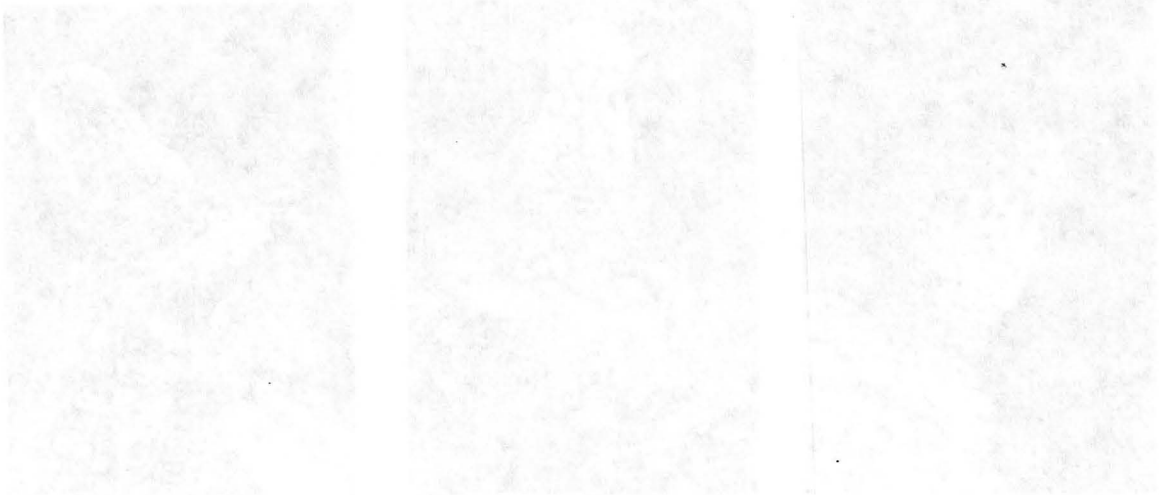
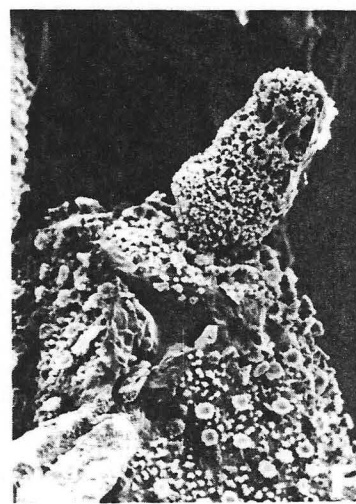
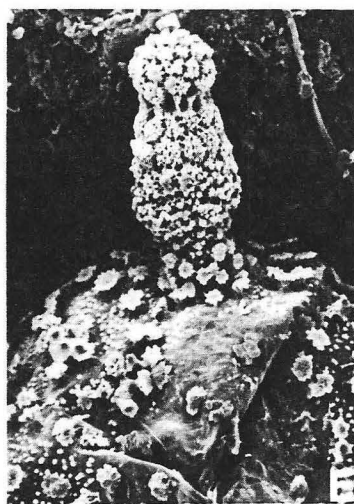
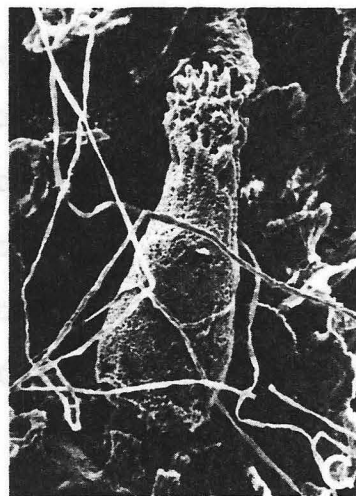
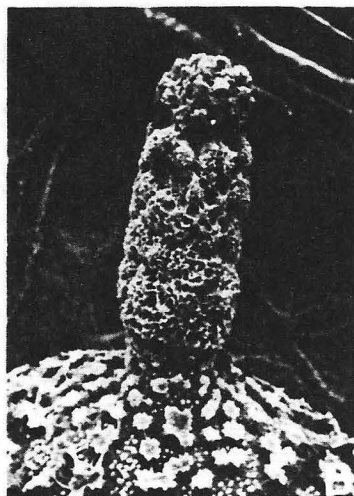
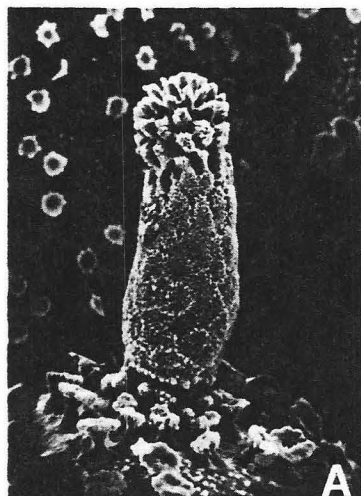


PLATE IV. Micropylar Projections

- A. Micropylar projection of *Sialis hasta*.
- B. Micropylar projection of *Sialis aequalis*.
- C. Micropylar projection of *Sialis infumata*.
- D. Micropylar projection of *Sialis iola*.
- E. Micropylar projection of *Sialis vagans*.
- F. Micropylar projection of *Sialis joppa*.

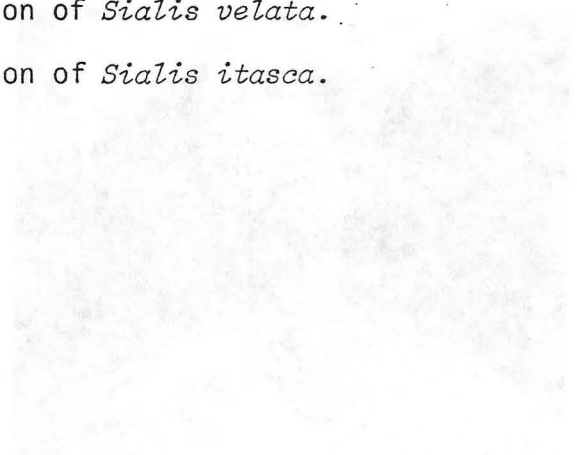
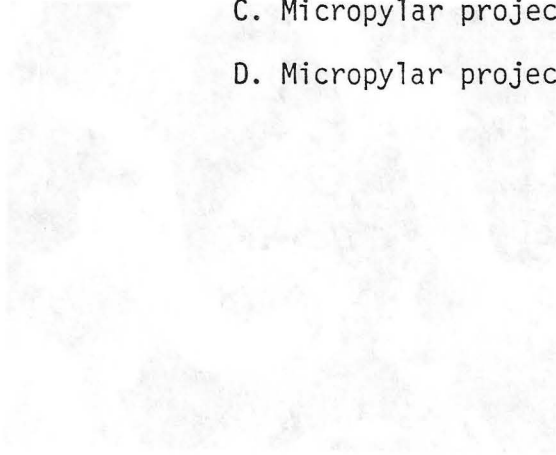




←→
.05mm

PLATE V. Micropylar Projections

- A. Micropylar projection of *Sialis glabella* (arrow represents 0.25 mm)
- B. Micropylar projection of *Sialis mohri*.
- C. Micropylar projection of *Sialis velata*.
- D. Micropylar projection of *Sialis itasca*.



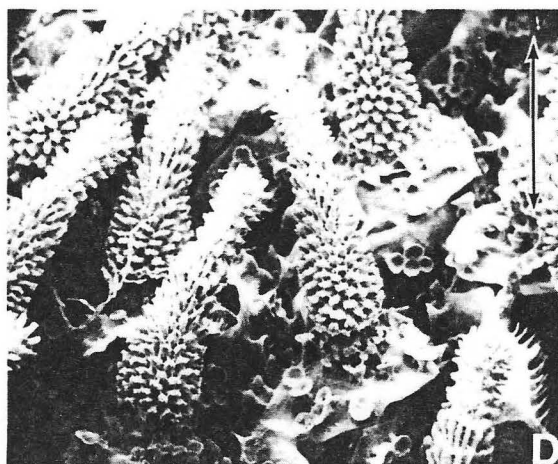
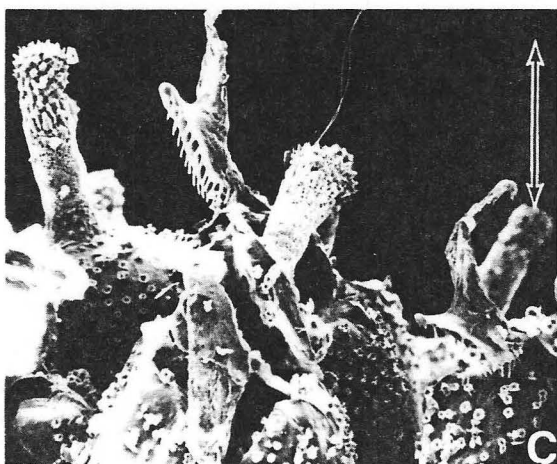
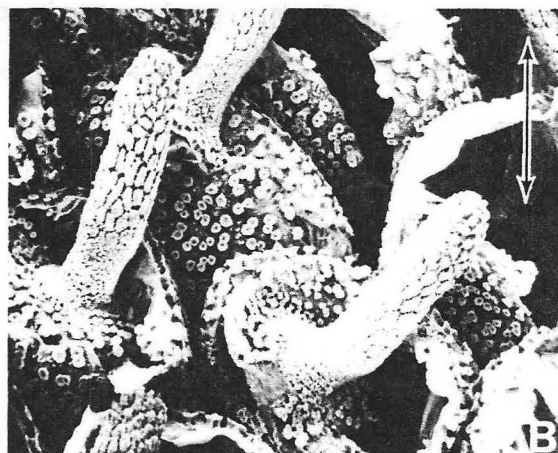
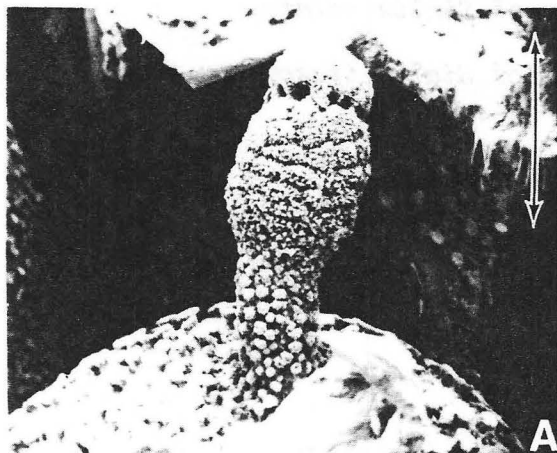
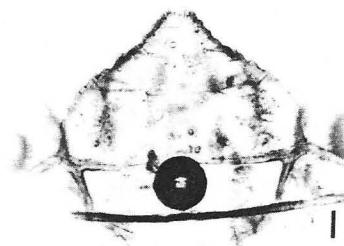
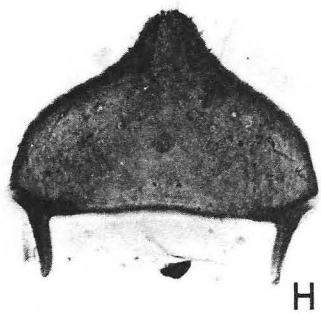
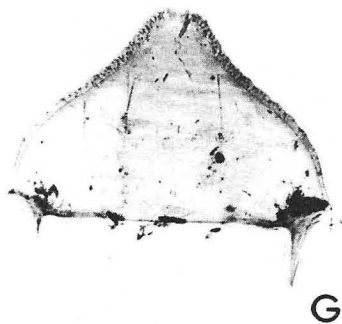
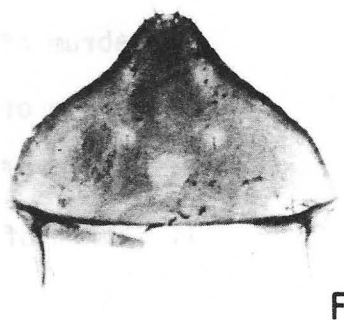
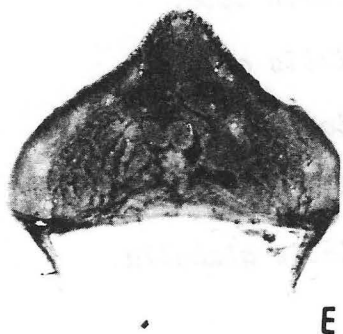
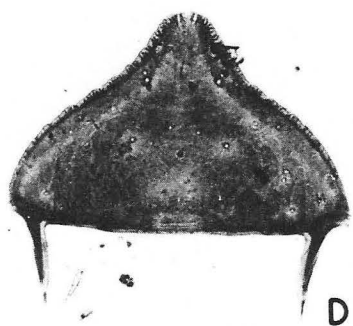
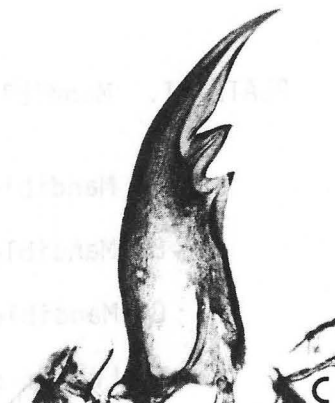
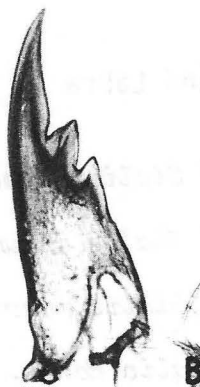


PLATE VI. Mandibles and Labra

- A. Mandible of *Sialis glabella*.
- B. Mandible of *Sialis infumata*.
- C. Mandible of *Sialis mohri*.
- D. Labrum of *Sialis hasta*.
- E. Labrum of *Sialis iola*.
- F. Labrum of *Sialis aequalis*.
- G. Labrum of *Sialis itasca*.
- H. Labrum of *Sialis joppa*.
- I. Labrum of *Sialis glabella*.

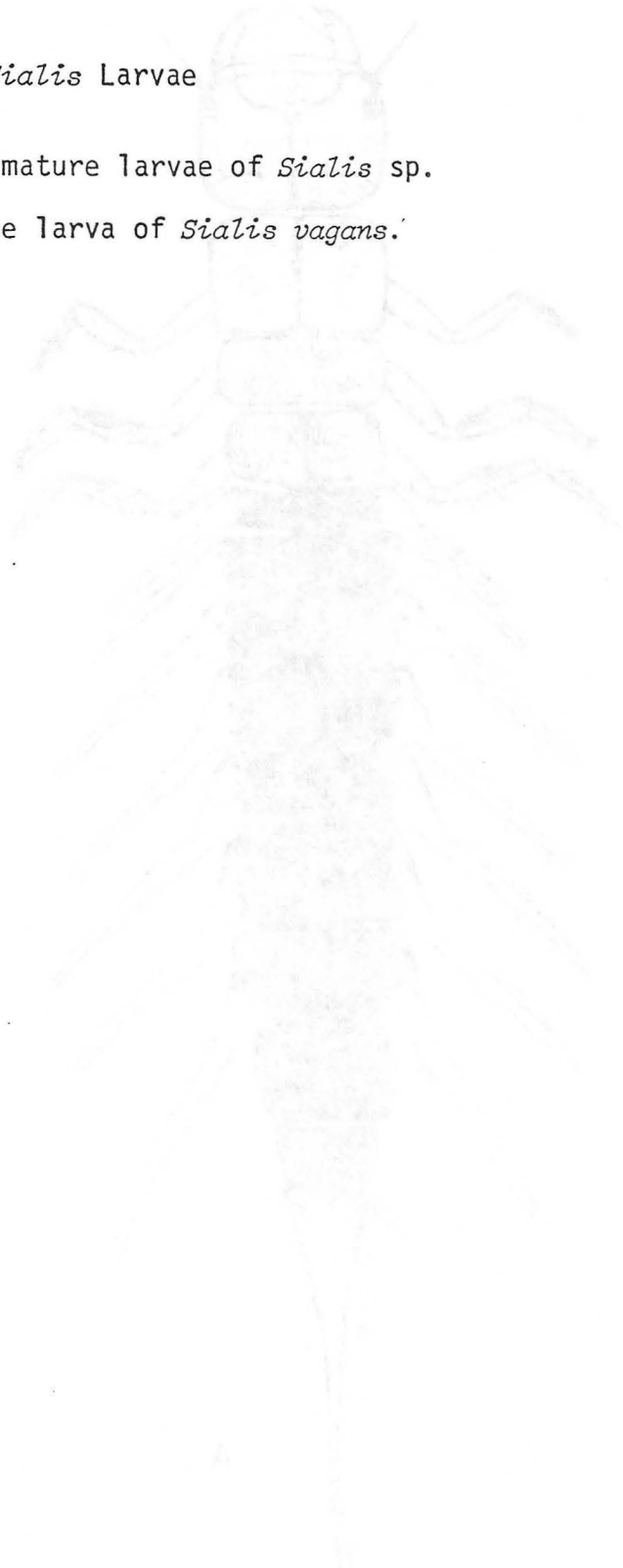


1 M M

PLATE VII. Dorsal view of *Sialis* Larvae

A. Dorsal view of a mature larvae of *Sialis* sp.

B. Dorsal view of the larva of *Sialis vagans*.



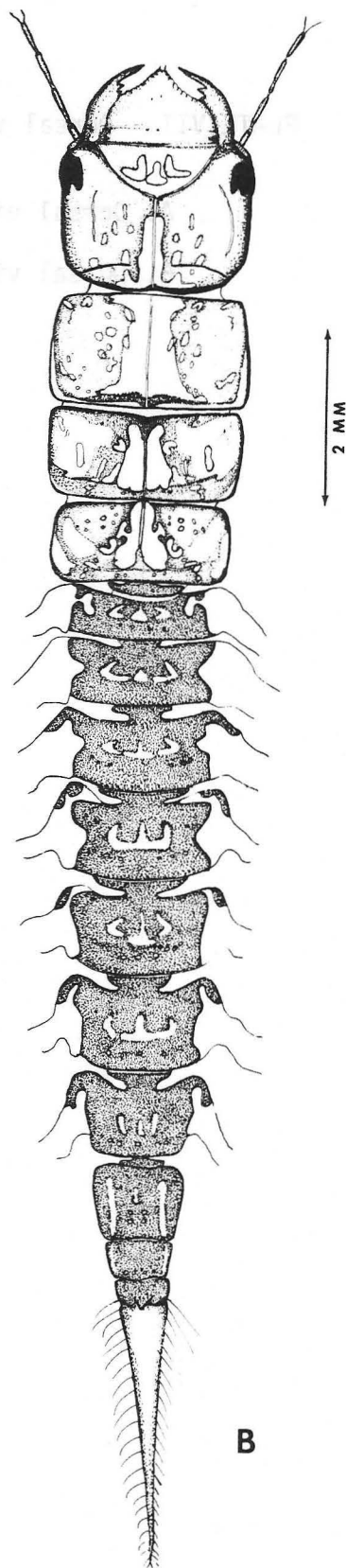
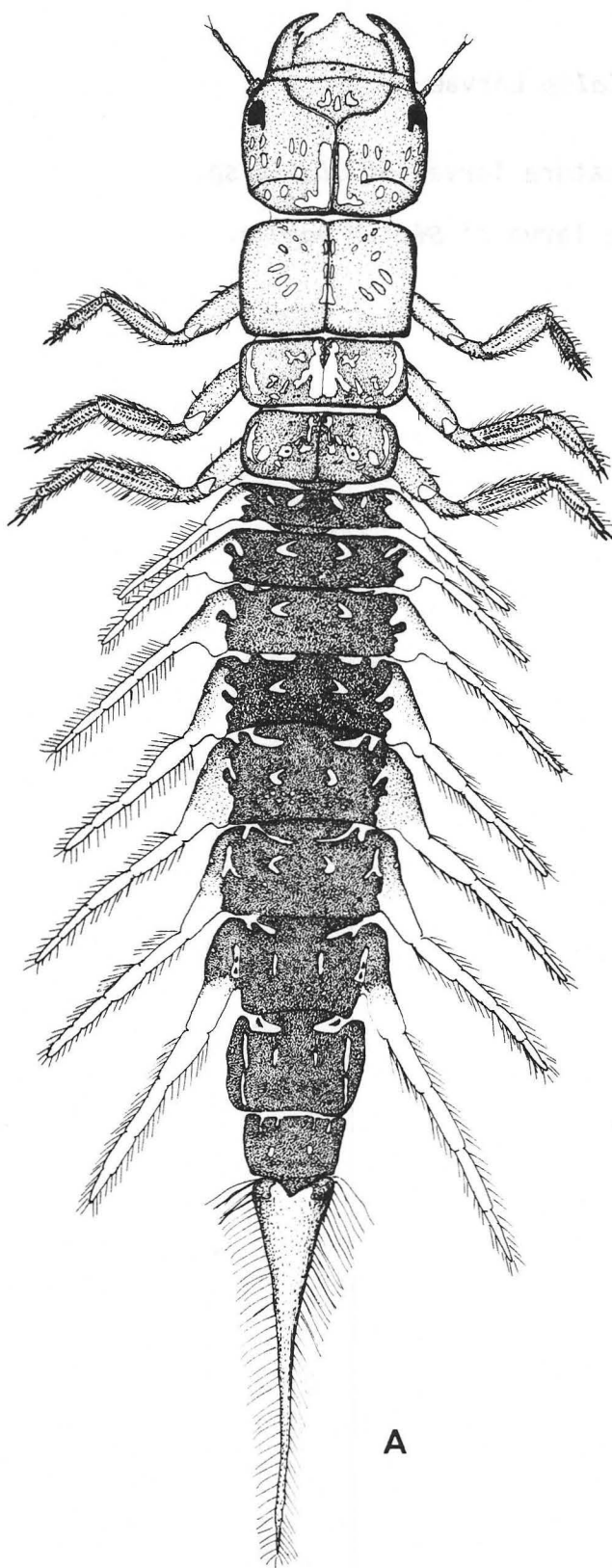


PLATE VIII. Anatomy of *Sialis* LarvaA. Dorsal view of the head and thorax of *Sialis* spp.

- | | |
|---|--|
| A. Clypeus | K. Pronotal median spots |
| B. Anterior arm of ecdysial cleavage line (epicranial suture) | L. Lateral wing crescents |
| C. Coronal angular markings | M. Posterior lateral spots |
| D. Occipital spot | N. Posterior circles |
| E. Frontal angular marking | O. Anterolateral irregular spots |
| F. Ecdysial cleavage line (epicranial suture) | P. Mesonotal angular markings |
| G. Elongate genal spots | Q. Posterolateral membranous marks |
| H. Occipital suture | R. Metanotal angular markings |
| I. Postoccipital suture | S. Anterior portion of metanotal angular marking |
| J. Elliptical pronotal spots | T. Posterolateral semicircular spots |

B. Ventral view of head of *Sialis*

- A. Labial palpus
- B. Cardo
- C. Mentum
- D. Submentum
- E. Lacina
- F. Maxillary palpus
- G. Ligula
- H. Stipes

C. Legs of *Sialis* spp.

- A. Trochanter
- B. Coxa
- C. Femur
- D. Tarsus
- E. Tibia
- F. Tarsal claws

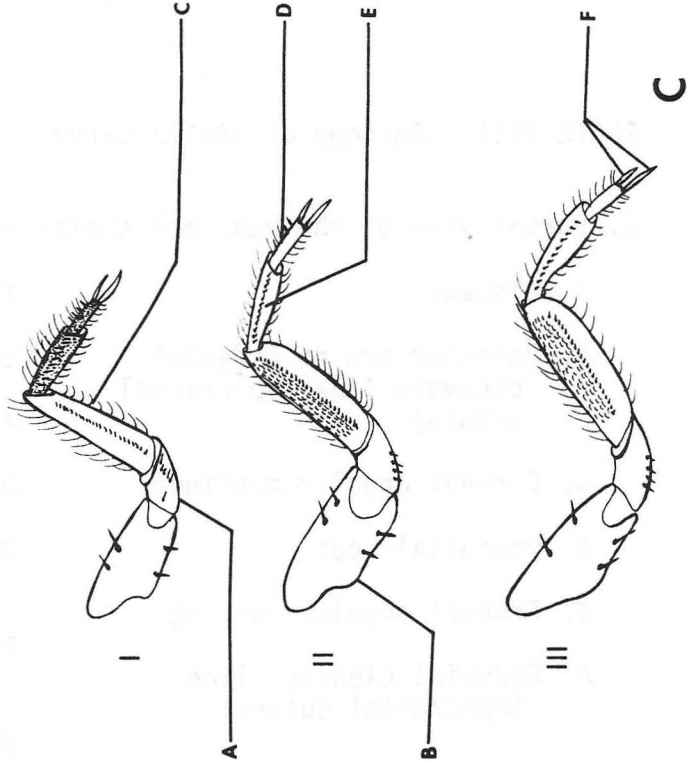
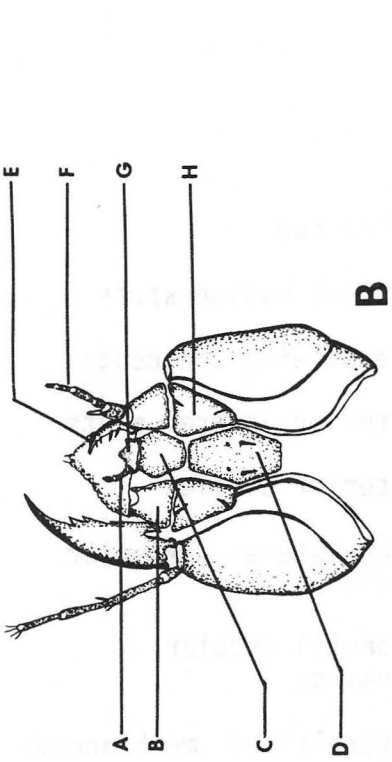
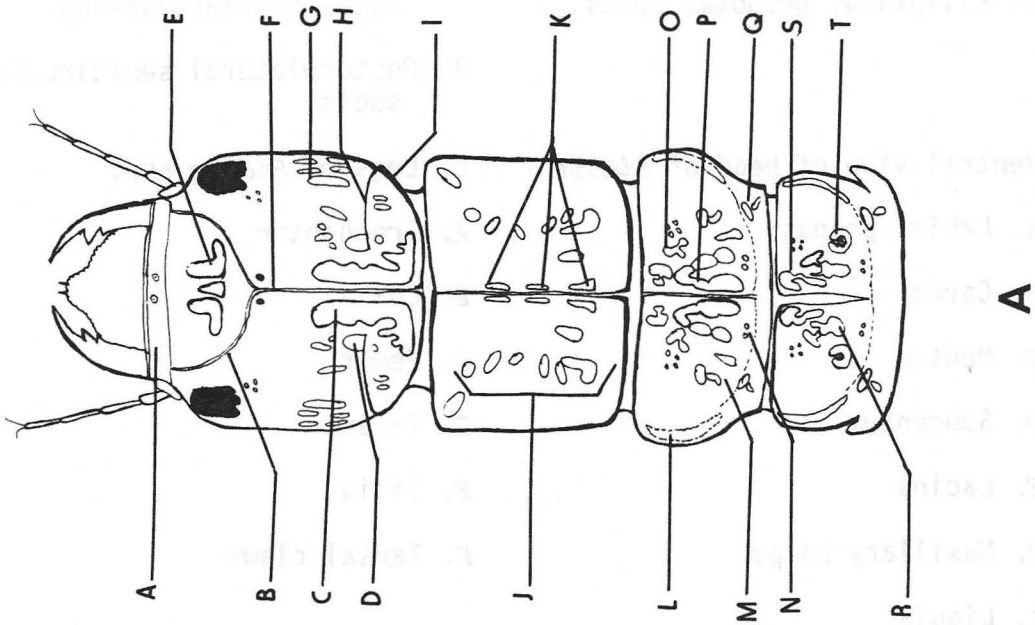


PLATE IX. Ventral View of Abdomens

- A. Ventral view of the abdomen of *Sialis iola*
- B. Ventral view of the abdomen of *Sialis vagans*
- C. Ventral view of the abdomen of *Sialis* spp.



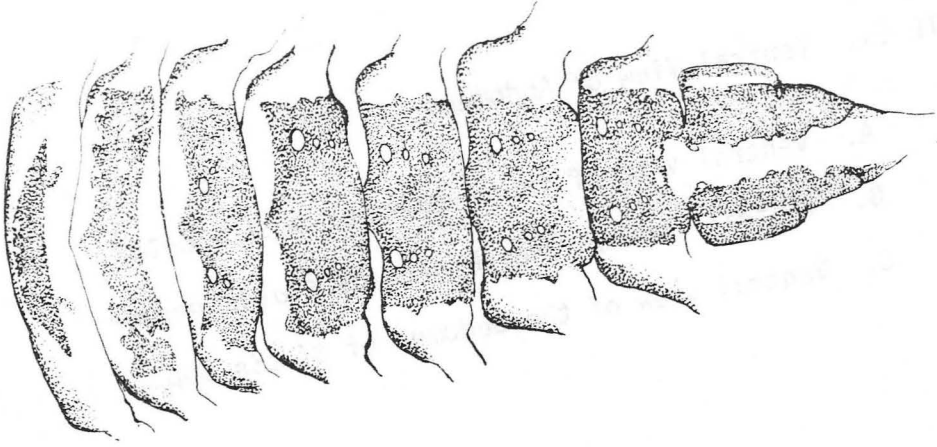
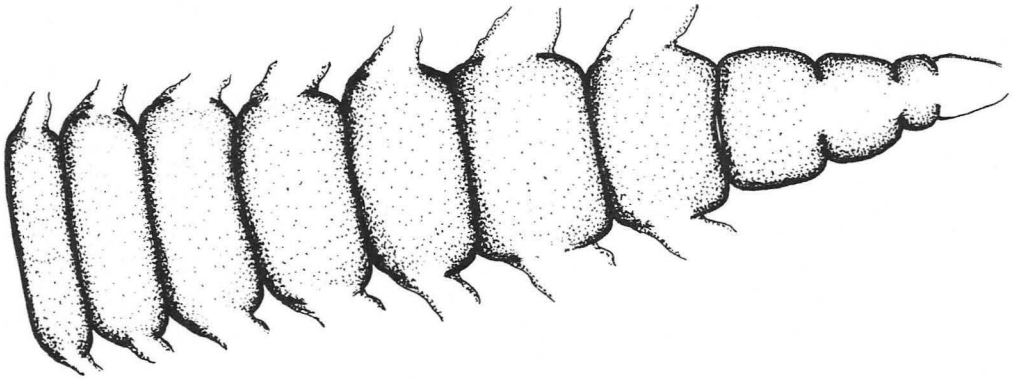
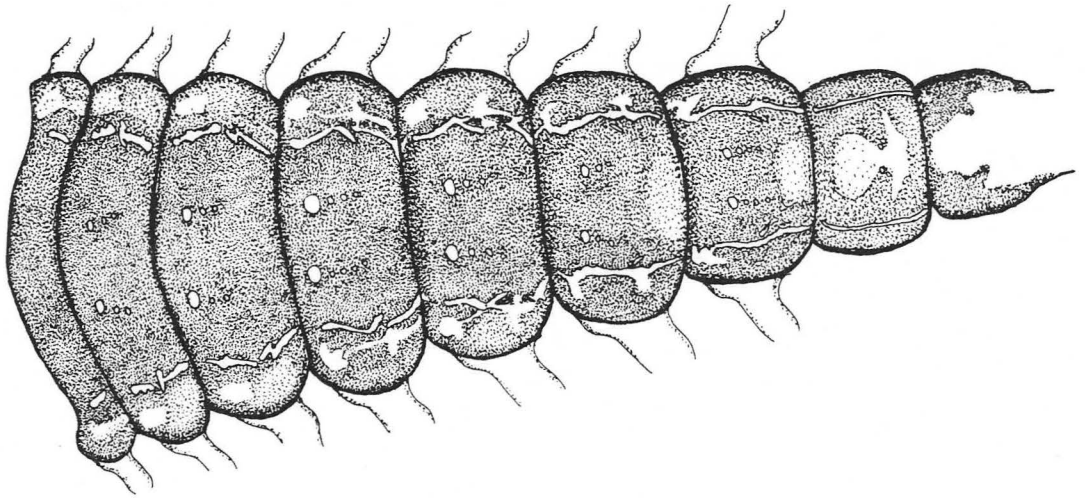
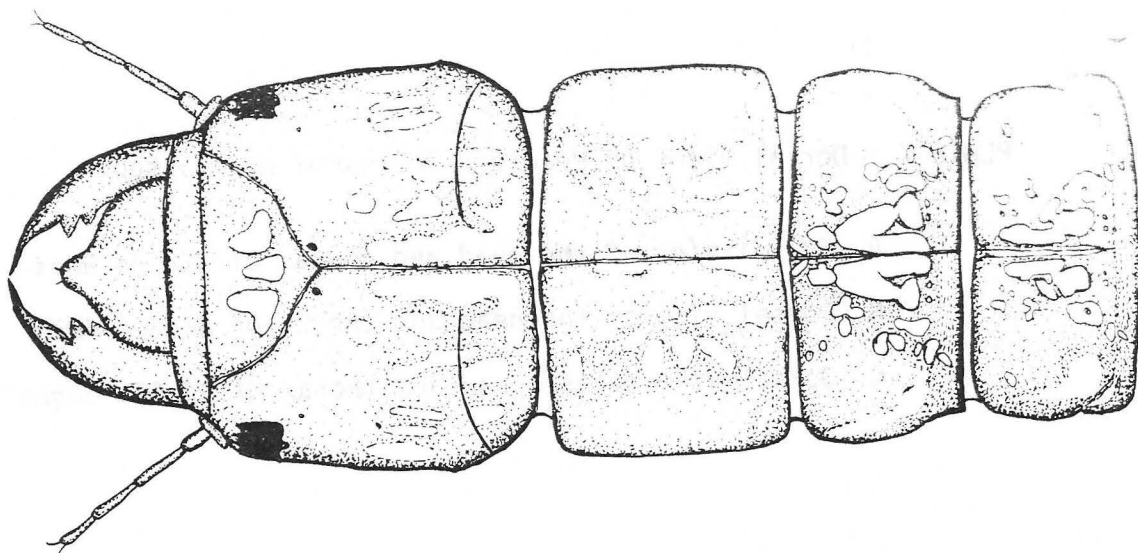


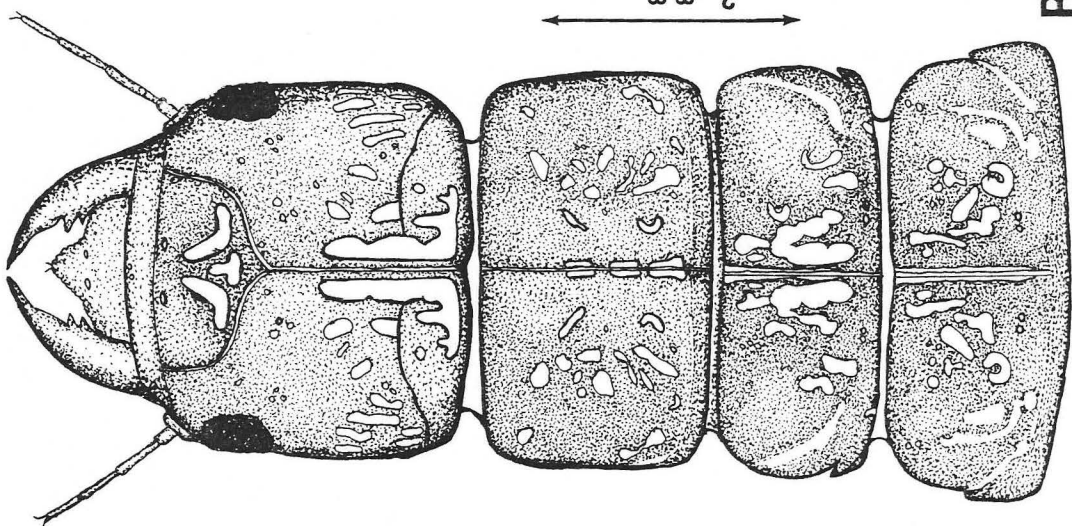
PLATE X. Dorsal Views of Head and Thorax of *Sialis* spp.

- A. Dorsal view of the head and thorax of *Sialis hasta*
- B. Dorsal view of the head and thorax of *Sialis iola*
- C. Dorsal view of the head and thorax of *Sialis aequalis*



2 mm

B



A

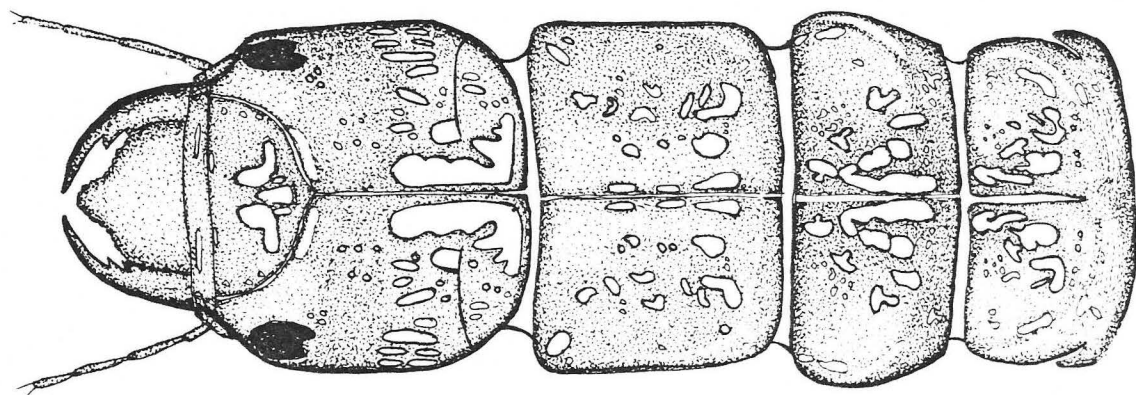


PLATE XI. Dorsal Views of Head and Thorax of *Sialis* spp.

- A. Dorsal view of head and thorax of *Sialis glabella*
- B. Dorsal view of head and thorax of *Sialis infumata*
- C. Dorsal view of head and thorax of *Sialis joppa*

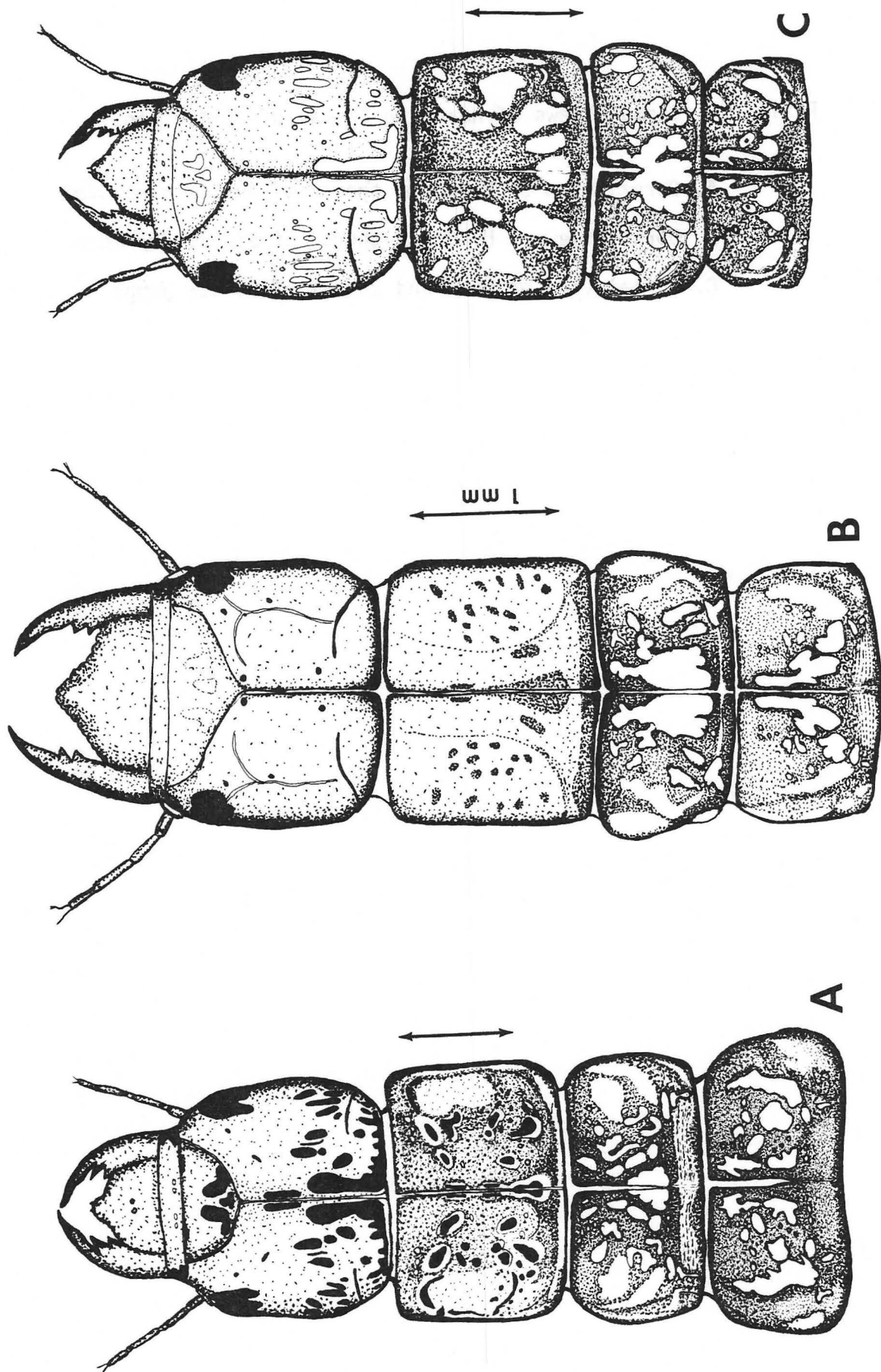


PLATE XII. Dorsal Views of Head and Thorax of *Sialis* spp.

- A. Dorsal view of head and thorax of *Sialis itasca*
- B. Dorsal view of head and thorax of *Sialis mohri*
- C. Dorsal view of head and thorax of *Sialis velata*

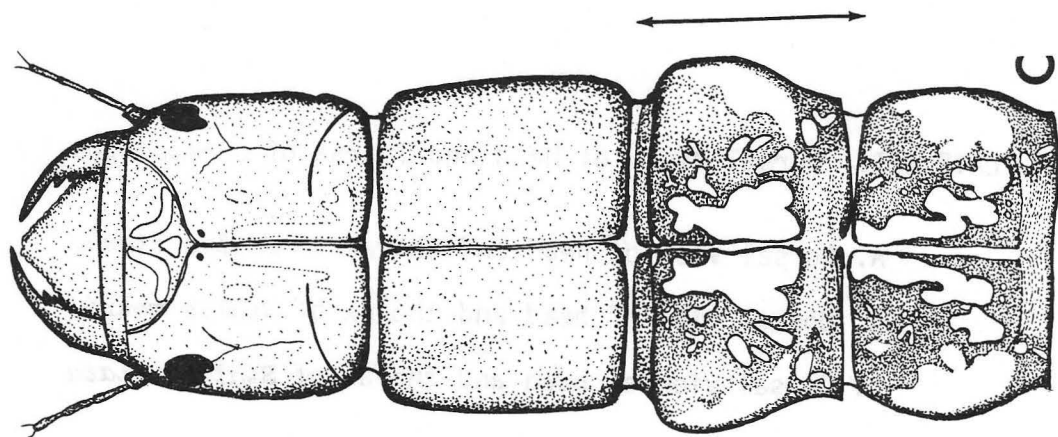
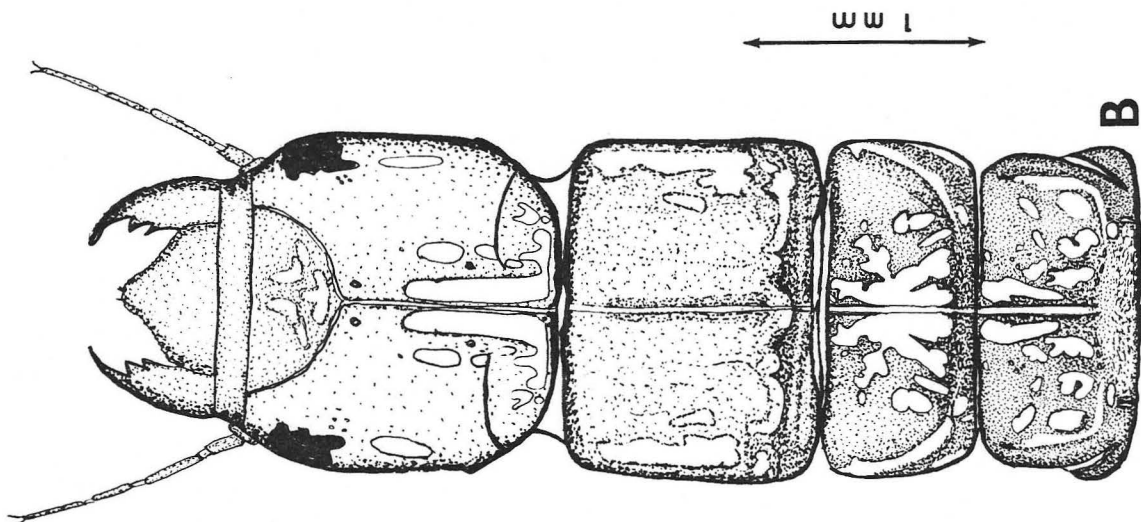
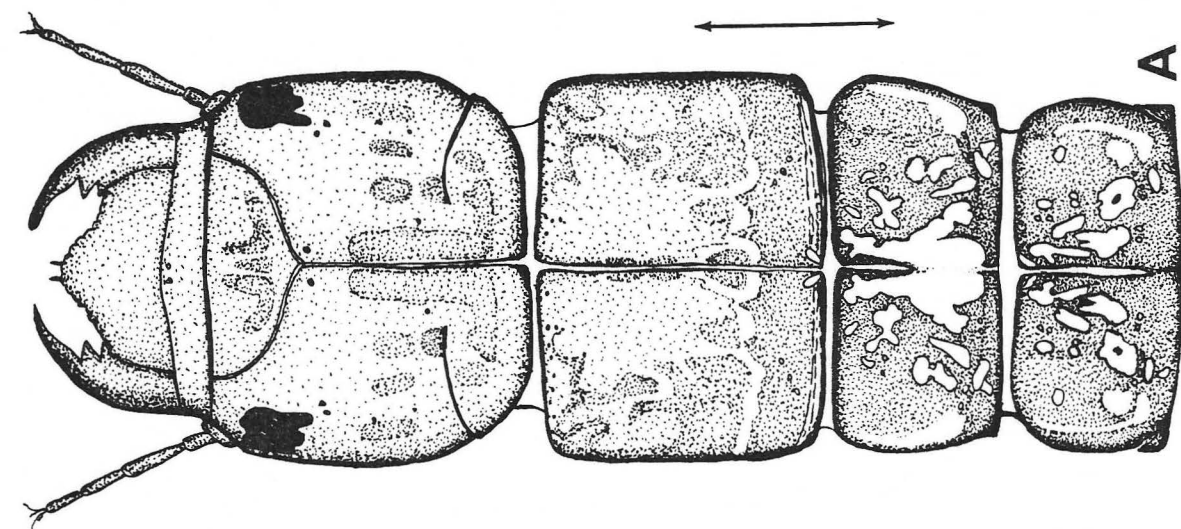


PLATE XIII. Distribution of Sialidae

Star indicates type locality

Dark circle indicates previous record

Open circle indicates new record

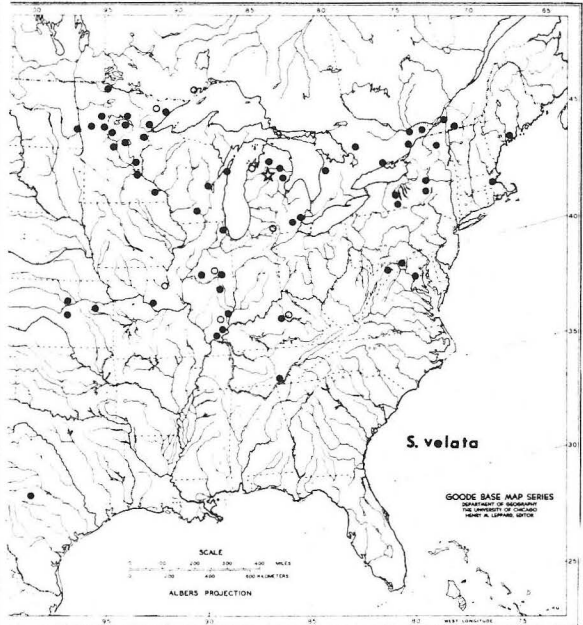
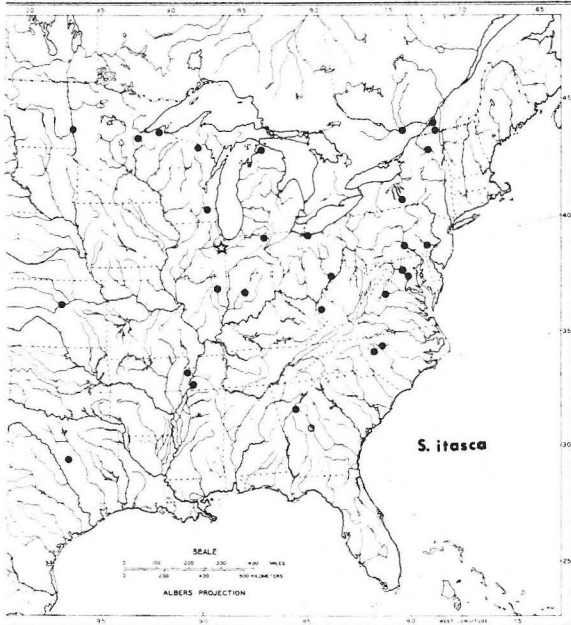
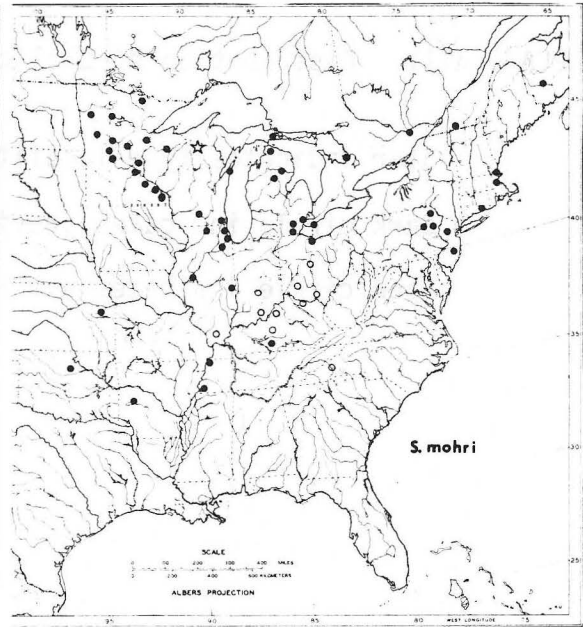
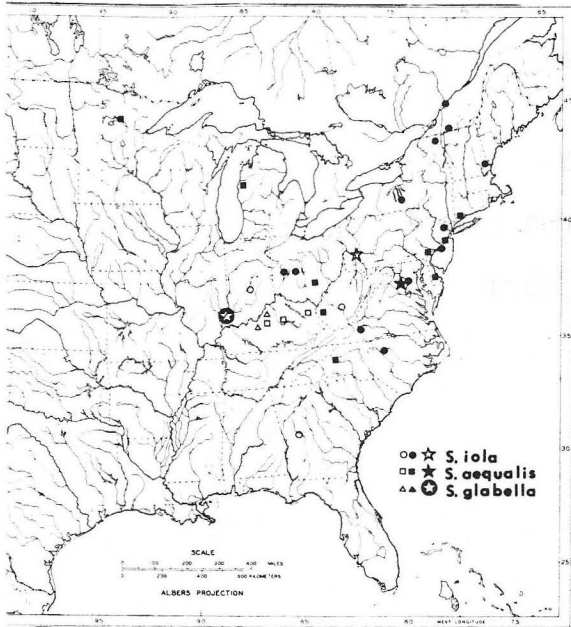
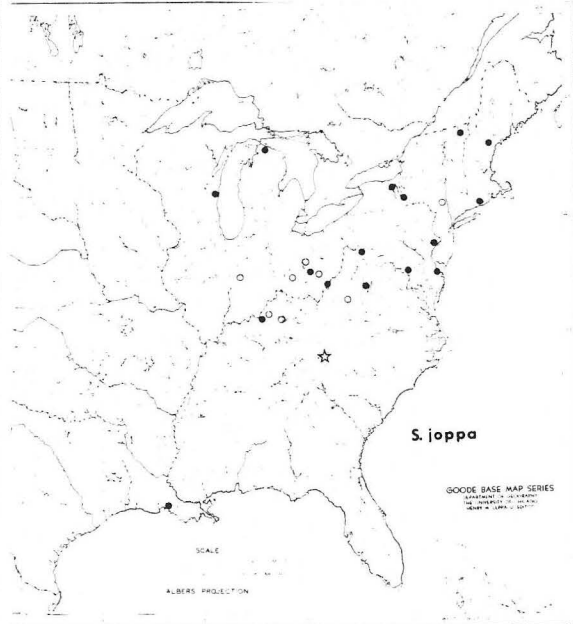
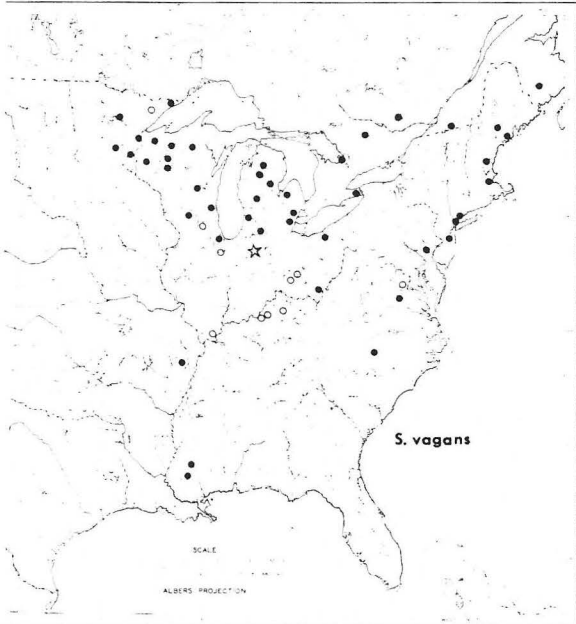
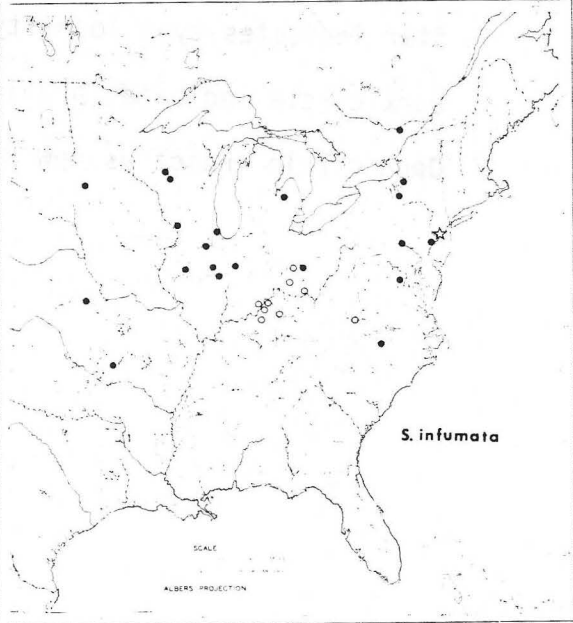
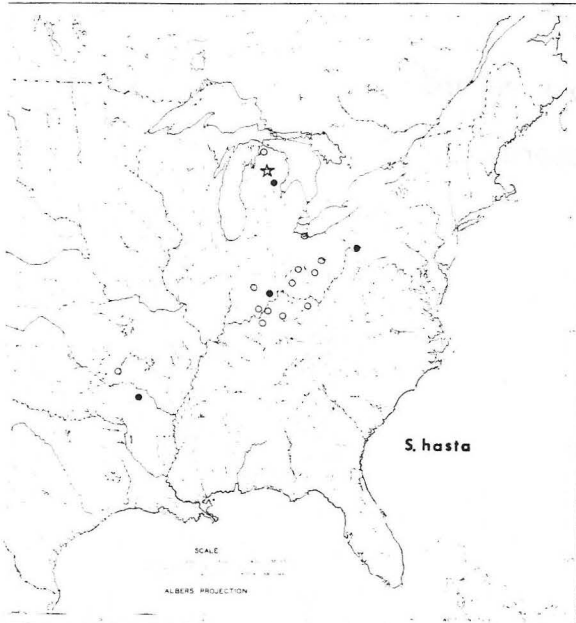


PLATE XIV. Distribution of Sialidae

Star indicates type locality

Dark circle indicates previous record

Open circle indicates new record



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