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BIOLOGY AND IMMATURE STAGES
of
MALACOPHAGOUS DIPTERA
of the
GENUS *SEPEDON* (SCIOMYZIDAE)

S. E. Neff, Virginia Polytechnic Institute and C. O' Berg, Cornell University

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Agricultural Experiment Station
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SUMMARY

Biological and morphological data are presented on 10 Nearctic, 4 Neotropical, and 2 Palearctic species of *Sepedon* (Diptera : Sciomyzidae), the larvae of which kill and consume fresh-water, pulmonate snails. These data include : seasonal aspects, geographic distribution, habitats, and natural enemies ; activities of adults such as feeding, mating, and oviposition; incubation and hatching of eggs ; food snails and feeding behavior, growth and development, and aquatic adaptations of the larvae; and puparium formation and emergence. This information is based on laboratory rearings of all species through complete life cycles, augmented with observations in the field.

The functional morphology of sciomyzid larvae in general is summarized as a background for more detailed descriptions of larvae of *Sepedon*. Eggs, the 3 larval instars, and puparia are described, figured, and compared, with particular emphasis on diagnostic features. Keys are presented for eggs, mature larvae, and puparia. Illustrations include photographs of egg masses, drawings of puparia and of diagnostic larval features, and maps showing the known distribution of all species included.

Sepedon is one of the most widespread and best-known genera of Sciomyzidae in the world. Adult flies tend to stay in or near marshes, swamps, and pond margins used as larval breeding sites. They remain active in all except near-freezing weather. Female flies are known to lay only a few eggs at a time, but to oviposit at frequent intervals for several weeks. Larvae kill snails quickly, remain in the shells only long enough to feed to repletion, and attack other snails when hungry again. They consume aquatic snails of all common pulmonate families with little selectivity, and each larva commonly destroys more than a dozen individuals. Preliminary experiments in the use of aquatic, predatory sciomyzid larvae for the biological control of undesirable snails are cited and summarized.

The relevance of this research is discussed in the hope of stimulating other studies similarly focused on a group of closely related organisms, and designed to illuminate the comparative ecology and morphology of all stages in the life cycle.

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Biology and Immature Stages of Malacophagous Diptera of the Genus *Sepedon* (Sciomyzidae).

INTRODUCTION

The early literature on relationships of Diptera to gastropod mollusks contains little evidence to support stated conclusions. Writers who had never seen certain larvae speculated that they must be parasitic on snails because puparia of those species were found in snail shells. Another author contended that one alleged snail parasite "is certainly no snail-feeder" because he had found one or more puparia that were not in snail shells. No one reared malacophagous larvae in laboratory dishes so their feeding habits could be clearly observed and their food positively determined. In the absence of such empirical evidence, decisions seemed to be based on an intuitively accepted rule — species which pupate in snail shells must be snail killers, but those which do not cannot be. Both propositions are patently untrue. Larvae may pupate in snail shells after entering them either to consume the decaying remains of dead snails or simply to pupate in shelter. On the other hand, pupation in snail shells is not routine in any reared species in the subfamily Tetanocerinae (which includes *Sepedon*) although all are killers of gastropod mollusks.

Confusion concerning food relationships resulted from failure to rear and failure to observe what reared larvae were eating. When the first complete rearing of a malacophagous dipteran was made, feeding of the larvae was not observed, their obligate relationship to snails was not discovered, and a completely erroneous conclusion concerning their food was published. Thus, Gercke (1876 :147) indicated that larvae of *Sepedon sphaegee* feed either on aquatic plants or on the mucus they secrete. His evidence seemed so convincing that subsequent writers can be excused for repeating this error. He had reared the larvae from hatching to pupation, and the only food ever given them (to his knowledge) was vegetation (mostly *Lemna trisulca* L.) he had gathered in wet ditches. If he had thought to look for pulmonate snails amidst this aquatic vegetation, or if he had observed a feeding larva with a hand lens, the snail-killing habits of the Sciomyzidae would have been discovered long ago. And, the much repeated error that many sciomyzid larvae are phytophagous might never have entered the literature.

Little was learned about the food of sciomyzid larvae during the next 75 years. No one saw a larva kill a snail, and no one suggested that tetanocerine larvae may be malacophagous. Although it was proposed that a few species of Sciomyzinae reared from

puparia found in snail shells may feed on living snails, those larvae were regarded as an "exception . . . as regards . . . their feeding habits" (Lundbeck, 1923:104). Other alleged "foods" were already well established in the literature, and the only evidence of snail eating was the circumstance of finding puparia in snail shells. Many seemed to dismiss this as coincidence. Sack (1939:7) wrote, "Die Larven leben an der Oberfläche stehender Gewässer zwischen Wasserpflanzen, von denen sie sich höchstwahrscheinlich ernähren" (The larvae live on the surface of standing water between aquatic plants, on which they most likely feed themselves). Lacking any real information on the subject, some writers discussed larval feeding in such broad terms they were almost certain to include the correct food. Bertrand (1954:479) summarized, "Leur régime est varié; beaucoup sont surtout saprophages, parfois phytophages, à l'occasion carnivores, s'attaquant à de petits Invertébrés: insectes et mollusques . . ." (Their diet is varied; many are principally saprophagous, occasionally [some are] phytophagous, and at times carnivorous, attacking small invertebrates: insects and mollusks. . .). Other contemporary entomologists have characterized the sciomyzid larvae as "probably saprophagous" (Hinton, 1955), "mostly phytophagous" (Imms, 1957), and "catholic in their feeding habits" (Colyer and Hammond, 1951).

The first conclusive evidence that several sciomyzid larvae kill and consume gastropod mollusks (Berg, 1953) suggested that these Diptera may be useful in the biological control of undesirable snails. Subsequent observations have lent support to this idea. All reared sciomyzid larvae have fed on snails and slugs, introduced alive into their rearing jars. They have never attacked each other or other invertebrates found associated with them, nor fed on any plant or insect material even under starvation conditions. Although fundamental studies have dominated our attention, some practical applications also have been considered and partially investigated. Larvae that were particularly effective against dangerous or destructive snails or slugs have been observed carefully to determine fecundity, host range, average numbers of gastropods killed per larva, adaptability to physical conditions prevalent in problem areas, environmental factors that limit their rates of population increase, etc. Species of *Sepedon* show more promise for use in biological control than most other Sciomyzidae, and they have been involved in both laboratory trials and experimental introductions.

Preliminary laboratory exposures of several snail hosts of schistosomiasis indicate that planorbid hosts of *Schistosoma mansoni* Sambon are vulnerable, the *Bulinus* species that harbor *S. haematobium* (Bilharz) are intermediate, and the operculate hosts of *S. japonicum* Katsurada are invulnerable, under the conditions of those experiments. Larvae of the 4 species of *Sepedon* used (*S. armipes*, *S. caerulea*, *S. fuscipennis*, and *S. tenuicornis*) attacked all snails exposed to them. Larger larvae were somewhat more aggressive and efficient; otherwise, no remarkable differences were noticed in performances of different species of *Sepedon*, or even between *Sepedon* larvae and larvae of *Tetanocera* and *Dictya*. They

killed almost as many snails per exposure day in quiet water, deeper than the lengths of their bodies, as they did on a substrate of moist sand.

Experimental introductions of *Sepedon* larvae have been concerned only with the control of fascioliasis. *S. macropus* was sent to Hawaii and Guam for the control of *Lymnaea ollula* Gould, host of the giant liver fluke of cattle, *Fasciola gigantica* Cobbold. *S. praemiosa* was sent to Australia for control of *L. tomentosa* Pfeiffer, the host of sheep liver fluke, *F. hepatica* L. The larvae of *S. macropus* attacked *L. ollula*, killed them easily, and thrived so well that a large laboratory colony was obtained. Releases in breeding sites of *L. ollula* were successful; this tropical American species is now established in nature on the 4 major islands of Hawaii and on Guam. Larvae are known to kill snails of the target species in nature as well as in the laboratory, and there is some subjective evidence of reduced snail populations. The work with *S. praemiosa* in Australia was done without benefit of an adequate laboratory staff for mass rearing, releases, and checks on successful colonization. Although larvae of *S. praemiosa* attacked the target snail in Australia just as readily and successfully as larvae of *S. macropus* performed in the laboratory in Hawaii, there is no proof that it is established in nature in Australia. The experiments summarized in this and the preceding paragraph have been reported in detail elsewhere (Berg, 1964a; Neff, 1964). Techniques used in the mass rearings in Hawaii are summarized on page 12, and new data obtained there on the characteristics and host range of *S. macropus* are included in the discussion of that species.

Like the study of larval food and other matters of basic biology, descriptions of immature stages of *Sciomyzidae* also were ~~delayed~~. Early research on the natural history and immature stages of the Diptera was mostly confined to species of known economic and medical importance. *Sciomyzidae* were studied only by taxonomists (e.g. Hendel, 1902, 1923, 1932; Cresson, 1920; Melander, 1920; Malloch, 1928, 1933; Sack, 1939), who showed little interest in biology, ecology, and immature stages. Although aquatic biologists often see the immature stages of *Sepedon* and could collect them easily, the literature contains descriptions of puparia of only 4 species, mature larvae of 3, and the egg of 1. These descriptions are not presented in adequate detail and with appropriate focus on diagnostic characters; the 2 shortest include only 1 sentence each. No descriptions or figures have been published of first-instar or second-instar larvae of any species.

Detailed accounts of natural history and immature stages of *Sciomyzidae* written by us and our associates have not concerned species in any large genus. We are not anxious to publish until all accessible species of a genus have been reared, studied, and compared. As a result, our detailed papers have concerned only monotypic genera (Foote *et al.*, 1960; Knutson and Berg, 1963), small

When this manuscript was in press, Nagatomi and Kushigemachi (1965) published on the biology and immature stages of *Sepedon sauteri* Hendel. Specimens from Japan labelled "*S. sauteri*" which we have examined appear conspecific with *S. sphaecea*.

genera of which more than one species were reared (Foote, 1959; Neff and Berg, 1962; Knutson and Berg, 1964), and a genus in which the unreared species are so remote geographically that they seemed unobtainable (Neff and Berg, 1961). Fisher and Orth (1964) presented detailed information on one of the Nearctic species in a larger genus.

As the first paper to present detailed biological data on several species in a large sciomyzid genus, this work has a twofold purpose: (1) to report comparative ecology and ethology of adults and larvae of all species of *Sepedon* that we could observe in the field and laboratory; and (2) to present diagnostic descriptions and illustrations of the eggs, larvae, and puparia of these species to elucidate their comparative morphology. It includes 10 of the 12 Nearctic species, 4 Neotropical species, and both species that are widespread and common in Europe. Keys describing eggs, mature larvae, and puparia are presented to facilitate recognition and stimulate further study of this interesting genus.

MATERIAL AND METHODS

Adult flies were captured by sweeping or beating vegetation in marshes and wet meadows with an aerial insect net. Since adult sciomyzids leave a net slowly, a catch could be sorted in the field by simply opening the net and allowing swift-flying insects to escape. The sciomyzids usually rested on the sides of the net and were transferred to 2- or 3-dram homeopathic vials. The vials were stoppered and taken to the laboratory for sorting to species and sex. Pairs or groups of males and females were placed in breeding jars in order to obtain eggs for rearings.

Larvae and puparia were obtained by searching the floating refuse in areas where adult flies had been observed. They were also collected by pushing emergent vegetation beneath the surface of the water to dislodge individuals on or between the leaves. Larvae and puparia freed in this manner usually floated to the surface and were seen easily. Puparia were most frequently found in refuse that collected along the down-wind sides of marshes and ponds. They were often difficult to separate from floating seeds of various aquatic and semi-aquatic plants.

Flies returned to the laboratory for breeding were placed in 8-ounce, wide-mouth jars. They were provisioned and cared for as described by Neff and Berg (1961, 1962). A layer of moss, 2 to 3 cm thick, was placed in the bottom of the jar to provide water for the flies and aid in maintaining the high humidities associated with their natural habitats. A short section of *Typha* leaf or strip of cardboard was slanted from the moss to the side of the jar. This provided the flies with a resting surface and site for oviposition. Usually several living snails of various species were placed on the moss, because odor stimuli released by snails may be necessary to cause oviposition (Foote, 1959).

Eggs were removed from the breeding jars every third or fourth day, and the jar was flooded with distilled water to recover any small larvae in the moss. The eggs and larvae were placed in one-ounce, wide-mouth display jars, 4 cm high and 4 cm in diameter. Screw tops of these rearing jars were replaced with large corks.

The larvae were provided fresh, living snails daily, and dead, partially consumed snails were removed. The rearing jars were rinsed with tap water to remove waste products before fresh snails were added. Smaller (2 to 5 mm diameter) snails were generally offered the first- and second-instar larvae. Larval mortality was usually higher if large snails were used with small larvae. The quantity of mucus secreted by larger snails seemed to account for this, because dead larvae were frequently covered with mucus. Their deaths were attributed to asphyxiation by occlusion of their spiracles by the mucus.

Snails used in the rearings of larvae were either held in laboratory aquaria or collected in the field. The following species of snails were used: *Helisoma trivolvis* (Say), *Helisoma* sp., *Lymnaea* (*Stagnicola*) *palustris* (Muller), *L. humilis* (Say), *Physa* sp., *Australorbis glabratus* (Say), *Gyraulus parvus* (Say), *Oxyloma retusa* (Lea), *O. decampi* gouldi Pilsbury, *Succinea avara* (Say), *Zonitoides arboreus* (Say), *Cionella lubrica* (Muller), *Deroceras laeve* Muller, and *Planorbis planorbis* L.

At various times, plant and animal tissue (other than snails) were offered to developing larvae. Duckweed (*Lemna minor* L.), naiad (*Najas flexilis* [Wind.] Rastk & Schmidt), and bits of moss were often placed in the rearing jars. Larvae were never observed feeding upon any of these plants, the plant tissues showed no feeding injury, and the larval digestive tract was generally devoid of green material. Larvae were seen that did have what appeared to be plant material in their digestive tracts, which occurred when larvae were fed small snails that had previously been fed fresh lettuce. The larvae consumed these small snails completely.

Small ostracods, rotifers, and oligochaete annelids were placed in the rearing jars, but these were not killed and devoured. Only one observation of a larval attack on an oligochaete worm was made, and this seemed to be an accidental encounter. After striking the worm with its mouthhooks, the larva withdrew and did not return to the injured worm.

Artificial media of homogenized liver, homogenized liver and snail, and an agar-liver-oyster mixture were unsuccessful. Larvae placed on them were observed to touch them with their mouthhooks, but soon deserted the artificial food. Dead snails elicited the same response as the artificial media. Unlike some sciomyzine larvae, *Sepedon* larvae will feed only on living or freshly killed snails.

As larvae completed their development and formed puparia, they were removed and placed in emergence vials. These vials were 8.5 cm high and 2 cm in diameter. The mouth of the vial was covered by a small square of cheesecloth held in place by a rubber band or plugged with a piece of cotton. These vials were examined

each morning. Adult flies that emerged were provided with food and held for about 48 hours to permit hardening of the exoskeleton.

Additional techniques for the collection and rearing of *Sepedon* are suggested by the experiences of Hawaiian entomologists in rearing *Sepedon macropus* prior to its release in Hawaii. C. J. Davis, Q. C. Chock, M. Chong, J. Kim, and others have contributed especially to knowledge of nutrition and mass-rearing methods.

The rearing of larvae in small jars and providing fresh food daily demanded too much time when large quantities of flies were needed for release in nature. Large redwood tanks (47 x 17 x 15 inches) were adopted as aquaria, and stocked in advance with *Lymnaea* and *Physa* of all stages, including eggs (Chock *et al.*, 1961). Adult flies were held in gallon jars containing honey and crushed snails for food, a saturated sponge to provide water, and a bouquet of grass to furnish resting places and sites for oviposition. After 2 days, all adults were transferred to a freshly made-up jar. Pieces of grass on which egg masses were cemented were then floated in the redwood tanks. Larvae which hatched in these tanks required no care; there was no handling from the time eggs were dropped onto the water until floating puparia were lifted out. The puparia were placed in the gallon jars for emergence, mating, and oviposition. With the change from petri dishes to large tanks, average production increased from about 400 to around 4,500 adult flies per month.

This mass rearing technique resulted in other innovations of considerable academic interest, as well as practical value in future experimental introductions. Hawaiian entomologists pointed out the benefits of adding crushed snails to the diet of the adult Sciomyzidae (Chock *et al.*, 1961), and reported that further supplementing the diet with granular protein hydrolysate results in additional increase in egg production (Kim, 1962). They first reported that sciomyzid larvae feed well on embryonated snail eggs (Chock *et al.*, 1961), a fact that adds significantly to their potential value as predators. Finally, Kim (1962) reported that aureomycin added to crushed snails fed to the immature larvae has decreased larval mortality appreciably. He added that terrestrial larvae can be held 36 to 48 hours longer before transfer to fresh rearing dishes, and that a teaspoon of aureomycin added to each large rearing tank clears the water and effects a considerable reduction in the activity of microorganisms.

The *S. macropus* introduced in Hawaii multiplied so well in nature that material for release in other snail breeding sites soon was available in adequate quantities. If a means could be found to collect adult flies easily, quickly, and without injuring them, the work of laboratory propagation could be discontinued. McPhail invaginated-glass traps, made for trapping fruit flies, were baited with crushed snails and set about 2 feet above the ground or water in swamps or taro paddies where *S. macropus* had been introduced. Adult flies were thus trapped at rates of 100 to 400 per hour, and released in snail-breeding sites not yet occupied by the fly (Chock *et al.*, 1961).

This suggested a new technique for collecting Sciomyzidae in places where it is difficult to wade and swing a sweep net. However, the system has given disappointing results in North and South America, and Europe. A few Sciomyzidae have been trapped, but not enough to warrant carrying traps along on extensive collecting trips. It is difficult to understand why this technique works so much better in Hawaii than elsewhere. It seems probable that air temperatures in the Northeastern States are not high enough to volatilize the aromatic substances in snail tissues that function as the attractant. But, this hypothesis does not explain failures of the technique in the heat of Italy and Brazil. A few Sciomyzidae were collected by sweeping near the traps in both countries. It is possible that baited traps attract Sciomyzidae only for short distances. If so, catches as large as those obtained in Hawaii are possible only in remarkably dense populations.

ANATOMICAL FEATURES OF IMMATURE STAGES OF THE **SCIOMYZIDAE**

Present knowledge concerning immature stages of the acalyptrate Diptera is so limited that distinguishing features can be proposed only provisionally. Diagnostic characters for sciomyzid larvae, for instance, cannot be stipulated with any confidence because others among the many unknown larvae in the Acalyptrata may possess the same characters. Like the Sciomyzidae, most other Acalyptrata have been neglected because they had no known medical or economic importance. Until a few years ago, natural history and immature stages of only 7% of the acalyptrate Diptera were known (Hennig, 1948). Much of the information on this large group of families is sketchy — generalizations rest on mere conjecture, on hasty observations, and on observations of only 1 or 2 species. Discussions of some immature stages are based on incorrectly determined material. In his key to the known larvae of the "Musci-formia," Hennig (1952) did not attempt to separate the larvae of the Acalyptrata from those of the Calyptrata. Although incomplete, his key is probably the best available, and serves to emphasize the paucity of information on acalyptrate larvae. Perhaps despairing of ever finding enough reliable morphological characteristics, Hennig suggested the possibility of a key supplemented by data on situations in which the larvae are found.

The fusiform or elongate-oval eggs of Sciomyzidae are not distinguishable in shape from those of other dipterous families. Colors and patterns of chorion sculpturing also fail to present distinguishing characters, both being quite variable in this and other families. Almost all known eggs in the subfamily Sciomyzinae have the exposed surface uniformly sculptured in a reticulate pattern. The eggs of *Sepedon* and nearly all other genera of Tetanocerinae are sculptured primarily with longitudinal ridges and furrows (Fig. 1), but some include a dorsal reticulate area (Fig. 7).

In all reared species of Sciomyzidae, the first-instar larva is metapneustic (with posterior spiracles only), and the second- and

third-instar larvae are amphipneustic (with anterior and posterior spiracles). Tetanocerine larvae which live in aquatic or shore-line habitats (including *Sepeidon*) are quite distinctive, resembling the aquatic larvae of many Tipulidae. There is no head capsule, but the long, tapered anterior end can be retracted into the succeeding body segments like the head of a tipulid larva. The integument, which is often dusky and sometimes deeply pigmented, has a leathery appearance with numerous grooves, folds, and warty tubercles. The posterior spiracular disc (Figs. 13, 14) is surrounded by up to 5 pairs of fleshy lobes, and the more ventrally situated ones are often long and conspicuous as on tipulid larvae. Each spiracular plate usually bears 4 palmately-branched interspiracular processes or "float hairs" on its border. Creeping welts of the type so commonly seen on other cyclorrhaphous larvae are lacking on most segments, their function perhaps having been taken over by the wartlike tubercles.

Descriptions such as the one given above have been applied generally but erroneously to all larvae in this family. Peterson (1953) was repeating the statements of previous authors when he wrote, "All larvae of known species are aquatic . . ." and described the gross, external features mentioned above as distinguishing characteristics for the family. No other type of sciomyzid larva was known until recently, because the aquatic, predatory Tetanocerinae are the only larvae commonly found in nature. Being based entirely on larvae of this group but applied to "larvae of the Sciomyzidae" as a whole, these descriptions are misleading because of their omissions.

Larvae of 2 other groups, those Tetanocerinae which feed on *terrestrial* gastropods and the Sciomyzinae, were discovered more recently through life cycle studies of the Sciomyzidae. These larvae resemble each other far more closely than either group resembles the aquatic Tetanocerinae in general appearance, gross external characters, ways of life, and microhabitats. Larvae of both groups are so different from the aquatic Tetanocerinae they could not be recognized from the description given above. All are conical-cylindrical with abruptly truncated posterior ends, like muscoid larvae. Conspicuous features of the aquatic Tetanocerinae—warty body tubercles, fleshy lobes surrounding the posterior spiracular disc, and branching float hairs—are all absent or greatly reduced. The smooth, shining integument is white, cream-colored, or light gray. External characteristics of sciomyzid larvae thus vary too much among themselves to present any distinguishing feature for the group as a whole.

As explained in greater detail by Foote *et al.* (1960), the most reliable characteristics to distinguish sciomyzid larvae from those of other dipterous families are found internally in the cephalopharyngeal skeleton (Fig. 12, cps). In all or nearly all species of Sciomyzidae, this structure bears an unpaired ventral arch having a serrate anterior margin (Fig. 23, VA; Figs. 30-33). Presence of the serrate ventral arch and lack of food canals on the pseudocephalic segment (Fig. 12, #1) apparently will distinguish

sciomyzid larvae from those of all other cyclorrhaphous Diptera. Hennig 1952, pp. 131, 241 has pointed out that the ventral arch (*Chitinbrücke*), associated with the mouthhooks to form a "geschlossenen Skelettring," may be a distinctive feature of sciomyzid larvae. In most species, attachment between the mouthhooks and the ventral arch is a ligamentous one which allows considerable movement between these sclerites.

If grouped according to similarities in form and general appearance, sciomyzid puparia also make up 3 major groups. These are correlated with the places where pupation occurs, and do not correspond exactly with the 3 larval groups. 1 The puparia formed by specialized, parasitoid Sciomyzinae which pupate in snail shells have shapes that are dictated by the form of the shells. All are not shaped alike (see Foote *et. al.*, 1960). Small puparia in relatively large shells are only slightly modified, but puparia which nearly fill one whorl of the shell have strangely asymmetrical, arcuate, and spiral shapes. 2 The less specialized Sciomyzinae and the terrestrial Tetanocerinae, both of which pupate in litter and soil, form compact, cylindrical puparia that are not distinctive when compared with puparia of other families of Diptera. The posterior ends are abruptly tapered and not curved dorsally. 3 The puparia of most of the aquatic, tetanocerine larvae are formed in water and clearly adapted for floating. Because they are curved dorsally at the posterior end and the float hairs on the posterior spiracular plates retain their hydrofuge properties, they float with the posterior larval spiracles projecting into the air (Figs. 50-65). Like the larvae, puparia of the Sciomyzidae differ greatly from each other and have no conspicuous unifying feature that distinguishes them from puparia of other families. Puparia of species whose larvae are known often can be identified by the larval structures that persist, especially the spiracles, cephalopharyngeal skeleton, and integumentary spinules and pigment patterns. The cephalopharyngeal character given above for distinguishing sciomyzid larvae, a ventral arch with a serrate anterior margin, is also the best character known to us for distinguishing puparia of this family.

SEPEDON LATREILLE

Tableau methodique des insectes

In Deterville's Nouveau dictionnaire d'histoire naturelle

24:196 . 1804

Type : *Syrphus sphaegeus* Fabr.
(Monobasic)

With about 90 nominal species, *Sepedon* is the largest genus in the Tetanocerinae and the best known genus of Sciomyzidae in the world. The adults are easily seen and readily recognized. They are more abundant in many habitats than individuals of any other sciomyzid genus. Occurring in all zoogeographic regions, *Sepedon* has a much wider distribution than any other genus in the Tetanocerinae.

Imagines of many species in this genus are large and conspicuous, and all are distinctive in form and habits. The unusual appearance of the long, porrect antennae and the large, grasshopper-like hind legs (see cover) probably fascinates collectors, and helps to make *Sepedon* better known than other genera of Sciomyzidae.

Several species of *Sepedon* are so common that they dominate the sciomyzid faunas in their regions. As examples in the Western Hemisphere, *S. fuscipennis* and *S. armipes* are collected more often than other Sciomyzidae in many marshes, swamps, and pond borders of eastern and central North America. Farther west, they are joined or replaced by another successful and abundant species, *S. praemiosa*. Collections from Caribbean America often contain more specimens of *S. macropus* than other species. And in tropical South America, many sciomyzid habitats are dominated by *S. bipuncticeps* and the species of the *S. lindneri* group.

Sepedon is also widely distributed in the Eastern Hemisphere. The genus is represented only by *S. sphaegea* and *S. spinipes* throughout most of Europe, and both species are well known by European entomologists. *Sepedon sphaegea* spreads eastward through Asia. *S. plumbella* is either the dominant or the only species in part of India, China, northern Australia, and islands of the Southwest Pacific. In Africa, where most sciomyzid genera apparently have not established themselves and *Sepedon* is relieved from competition with them, this evolutionary line has proliferated and speciated extensively. Adaptive radiation in the stock has progressed so far in the Congo that Verbeke (1950) erected the genera *Sepedonella*, *Sepedoninus*, and *Sepedonomyia* to receive some of the most divergent species, placing them with *Sepedon* in his proposed subfamily Sepedoninae. This group so dominates the sciomyzid fauna of central Africa that Verbeke recognized 36 species, compared with a combined total of 6 species in all other genera.

Although species of *Sepedon* have successfully invaded tropical and sub-tropical regions, and thus greatly extended the generic range, other genera of Tetanocerinae are more abundant in both species

and individuals in colder regions. Only 3 species of *Sepedon* are known from Alaska, compared with 11 species of *Tetanocera* (Steyskal, 1954), and specimens of *Tetanocera* are collected more commonly than *Sepedon* at many collecting sites in northern North America. The same is true in central and northern Europe, where there are only 2 species of *Sepedon* but 24 species of *Tetanocera*. In temperate South America, the *Sepedon* fauna becomes sparse, is unknown in Chile and Argentina, and is replaced there by species of *Tetanoceroides* and *Protodictya*. In Australia, *S. plumbella* extends throughout the warm northern regions but is replaced in South Australia, Victoria, and most of New South Wales by *Dichetophora* and *Neolimnia*.

Steyskal (1950, 1956, 1960) provided reliable taxonomic treatment of the genus *Sepedon* in North and South America, following contributions by Hendel (1932) and Malloch (1933) on the Neotropical species. Sack (1939) and Verbeke (1948, 1964) have done the same for the Palearctic species. Verbeke (1950, 1956, 1961, 1962, 1962a, 1962b) and Steyskal and Verbeke (1956) have made important contributions toward a taxonomic understanding of the African fauna. Brunetti (1907) reviewed the species in China and the East Indies.

Sepedon can be distinguished from other genera of *Tetanocerinae* in possessing the following combination of characters: arista white, pubescent; ocellar bristles greatly reduced or lacking; 2 scutellar bristles; wing membrane generally immaculate; preapical bristles on hind tibiae lacking.

Primarily on the basis of the 2 scutellar bristles, the elongate antennae, and the white arista, Cresson (1920) proposed the tribe *Sepedonini* to include *Sepedon*, *Thecomyia*, and *Dichetophora*. Verbeke (1950) held the opinion that characters used by Cresson are inadequate and do not justify the inclusion of these 3 genera in a single tribe. Using characters largely concerned with the male terminalia, he removed *Thecomyia* and *Dichetophora* from the group and elevated it to subfamily rank as indicated above. Unfortunately, the immature stages of *Sepedonomyia* Verb., *Sepedoninus* Verb., and *Sepedonella* Verb. are unknown, and no larval or pupal characteristics are available that might help to clarify this classification. The characteristics of the known *Sepedon* larvae are quite similar to those of other larvae in the *Tetanocerinae*; they do not seem to provide support for separation of the genus and its African allies as a distinct subfamily.

Adult

The English vernacular names "marsh flies" and "swale flies" are far more appropriately applied to *Sepedon* than to some other sciomyzid genera. All sciomyzid adults tend to remain in the immediate vicinity of larval breeding sites. Whereas this restricts the *Sepedon* species discussed here to habitats of aquatic, pulmonate snails, it confines species in other genera to habitats of terrestrial snails and slugs. In distinct zonation of adult *Sciomyzidae* along the shore of a pond, *Sepedon* species are the farthest out over the

water. Rozkošný (1959) commented similarly concerning *S. spegea* and *S. spinipes* and indicated that the Czech vernacular name for the Sciomyzidae, which translates as "damp lovers," is quite fitting.

Adults of *Sepedon* are easily recognized in the field, being distinctive in body form, posture, and habits. Because of the long, porrect antennae and large hind legs, they appear more slender and elongate than other Tetanocerinae. This apt account of the characteristic posture of adults in nature (Needham and Betten, 1901:578) is based on observations of *S. fuscipennis* at Saranac Inn, New York. It applies to all species of *Sepedon* known to us :

The flies sit on the erect burred leaves with wings laid flat on their backs, their long hind legs folded together, the tip of the abdomen sloping down and nearly touching the leaf and the head lifted high above it, in quite a frog-like attitude. They fly but little — that little rather poorly — sweeping betimes, from one resting place to another near by. They rest on the leaves head downward more often than otherwise; I have frequently seen them sitting thus, close to the surface of the water, and apparently feeding on the stuff which collects about the bases of the leaves just above the water line.

Adults of *Sepedon* utilize several different foods. Specimens of *S. tenuicornis* in the United States National Museum were collected on apple blossoms. Near Havana, Illinois, *S. fuscipennis* has been collected on "willow in bloom" and on *Cardamine* flowers (C. A. Hart, Ill. Nat. Hist. Surv.), and both *S. fuscipennis* and *S. armipes* have been taken on the flowers of marsh marigold, *Caltha palustris* L. (Judd, 1964). However, the Sciomyzidae are not commonly collected on flowers. The implication of Needham and Betten that *Sepedon* adults may be scavengers had already been stated more positively. Glover (1874) wrote that *Sepedon* adults "frequent putrifying substances." They feed on fresh as well as putrescent animal matters ; flies of this and other sciomyzid genera often feed on the hemolymph that exudes from other flies injured during transfer from the net into collecting vials. Adults in breeding jars feed readily on a mixture of honey and brewers' yeast, and many survive for several weeks without other food. However, their egg production is greatly increased if crushed snail is added to this diet (Chock *et al.*, 1961). This evidence seems to indicate that sciomyzid flies may live as nectar feeders, but the females never attain full potential of egg production unless they have access to some protein supplement. Several sources of supplementary protein are available in the marshes and swamps inhabited by *Sepedon*, especially snails which their larvae have killed but not completely consumed. Thus, adults may be somewhat dependent on the larvae for an adequate diet.

The mating of all reared species was observed in the laboratory ; that of *S. fuscipennis* and *S. armipes* was watched in the field also. However, no detailed ethological study of the courtship behavior has been made. Courtship behavior was observed in males as early as 6 to 12 hours after their emergence from the puparium. Newly emerged females differ from those of some other sciomyzid genera

in usually resisting the advances of males for several days after emergence. Copulation in the laboratory was most frequently seen in the morning between 8:00 and 10:30 and continued for 5 minutes to 3 hours. We have attempted to follow the terminology of Spieth (1952) in the brief, generalized description that follows.

Prior to mating, the male moves back and forth in front and to either side of the female in a path that describes an arc of about 180°. As he moves in this path, the forelegs are raised and lowered nervously and a bobbing motion of the abdomen occurs. His wings are extended laterally from their resting position over the abdomen, vibrated rapidly for several seconds, and then returned to the resting position. The frequency of these wing vibrations increases as long as the female remains still and presumably receptive; however, if she backs away and flicks her wings several times in quick scissors-like movements, the male ceases his display. If the female remains still and gives no wing motion, the male circles behind her slowly and mounts her from behind.

As the male moves into the copulating position, his forelegs and middle legs aid in spreading the female's wings. He grips the basal section of the female's wings between the femur and tibia of his middle legs and holds them motionless in a partially spread position. His fore tarsi extend over the female's front, and his tarsal claws grasp her antennae. His hind legs are used to manipulate the genitalia until intromission is accomplished; then they are flexed slightly and rest on the female's abdomen.

The preoviposition period (Hutchinson, 1916), or length of time from emergence of the adult female to deposition of her first egg mass, varies with individuals. For example, 12 first-generation females of *S. caerulea* had preoviposition periods varying from 4 to 24 days — the average was 9.6 days.

Oviposition by *S. fuscipennis*, *S. guatemalana*, and *S. macropus* was observed on several occasions. The sequence, essentially the same in these 3 species, was as follows: The female rested on the side of the breeding jar in a head-downward position. The hind leg were spread slightly and the apical part of the abdomen was lowered so that it almost touched the substratum. About 2/3 of the total length of the egg was extruded rapidly from the female's vulva, and the egg was held in this position for 1 or 2 seconds. At this time, the female presumably coated the micropylar end of the egg (the end retained in her abdomen) with a small quantity of sperm from her spermathecae. The tip of the abdomen then was lowered, and the egg was placed gently on the substratum. The female touched the exposed side of the egg she had just laid, and the substratum to the right of it, with the end of her abdomen. Thus oriented with the surfaces the next egg would contact, she elevated the tip of her abdomen and partially extruded the egg, as before. She repeated this process until a group of 10 to 30 eggs was laid.

The longevity of adults in the laboratory was usually about 3 to 5 months. The *S. neili* adults that emerged in the laboratory in August 1958, produced viable eggs in April 1959, and finally died in July. This was the maximum longevity period (351 days) recorded during this study.

Eggs

Most of the eggs obtained in laboratory breeding jars were laid on upright grasses, sedges, and other longitudinally ribbed vegetation. They were grouped in orderly masses, each composed of a single vertical row of horizontally placed eggs (Fig. 1). *Sepedon* eggs that we found in nature, those of *S. fuscipennis* and *S. armipes*, were similarly placed near the leaf margins on emergent vegetation, especially on *Typha* spp. Rows of up to 25 eggs were observed in nature; some egg masses laid in the laboratory were larger. Field-collected eggs were commonly 5 to 25 cm above the water or wet soil, but they also were found up to 1.5 meters above the substrate.

Although species of the *pusilla* group (*S. borealis*, *S. neili*, and *S. pusilla*) also rest on the upright *Typha* leaves placed in their breeding jars, they do not oviposit on them. Instead, they lay their eggs, singly or in groups of 2 or 3, on the leaves and sporophytes projecting from the moss which covers the bottoms of breeding jars (Figs. 8, 10).

Oviposition sites of *Sepedon* evidently are not completely fixed. In the only published record on this matter known to us, Gercke (1876) reported finding the eggs of *S. sphaecea* on *Lemna trisulca* L., in groups of 5 to 7 per leaf. In laboratory breeding jars, however, this species oviposited on upright *Typha* leaves (Fig. 6). Many of their egg masses contained more than 7 eggs, and were so long that they could not have been attached to the small leaves of *Lemna*.

The known eggs of *Sepedon* differ from other sciomyzid eggs in having rather coarse longitudinal striations on the dorsal and dorsolateral surface of the chorion. The striations may cover the whole dorsal surface (Fig. 1), or they may be confined to the dorsolateral margins (Fig. 7) with the area between exhibiting a reticulate pattern. The end of the egg opposite the micropyle bears a more or less prominent hemispherical or conical protuberance which is covered with minute punctations. The micropyle is a simple pore and may be shielded dorsally by 4 or 5 small, irregular tubercles or by a single, low, rounded tubercle.

Sizes of eggs vary with species and even with individual females of each species. Members of the *pusilla* group produce the smallest eggs seen (0.8 to 0.9 mm long); females of *S. caerulea* lay some of the largest (1.35 to 1.45 mm long). The eggs of each mass are quite uniform and may vary only a few hundredths of a millimeter in their dimensions.

Freshly laid eggs of most species considered here are white or only lightly pigmented, but those of some species become quite deeply colored during development of the embryo. Eggs of *S. macropus* turn from cream-colored to orange in 24 to 36 hours after being laid, and other eggs become yellow to plumbeous gray. There also are color differences in the eggs produced by different females of a species. Some individuals of *S. fuscipennis* lay silvery white eggs, but others produce dark, lead-gray ones. Although most species have unicolorous egg chorions, 2 species are exceptions. In *S. praemiosa*, prominent, irregular, plumbeous spots appear on the

dorsal egg surface 24 to 36 hours after oviposition (Fig. 1). In *S. armipes*, a dark, transverse band that covers the middle $1/3$ of the egg is characteristic of certain females.

Eggs do not necessarily hatch in the sequence in which they were laid. A group of 17 eggs of *S. macropus* was noticed as the first 3 larvae were hatching from the second, fourth, and thirteenth eggs. An hour later, all except the first, sixth, and eleventh eggs had hatched. Similar irregularity in the hatching sequence was observed in egg masses of *S. guatemalana* and *S. fuscipennis*. Thus, position in the row does not confer any predictable advantage on a young larva.

Observations of the hatching process indicated the 3 presumptive axes of the embryo in the egg are coincident with the 3 axes of the female parent. This is in accordance with a rule formulated by Hallez (1886), which has been called "Hallez's Law."

Larvae

Like the adults, larvae of *Sepedon* probably are known to more entomologists than those of any other sciomyzid genus. They are often found in nature, floating freely just beneath the water surface in quiet ponds and marshes, with their posterior spiracular plates thrust through the surface film. Whether floating or resting on floating and emergent objects and wet soils near shore, they are much more exposed to view than corresponding stages of sciomyzine species which remain in snail shells throughout both larval and pupal stages. Larvae can be collected so easily on most continents that their discovery by early entomologists is not at all surprising. *Sepedon* larvae have been known for so many years that persistent ignorance of their food habits is baffling.

Larvae of the genus *Sepedon* (Figs. 11, 12) have tapered and remarkably retractile anterior segments, tuberculate and somewhat annulate abdominal segments, and a posterior spiracular disc surrounded by fleshy lobes reminiscent of the posterior disc of tipulid larvae. These external features are conspicuous, and some or all of them have been mentioned by everyone who has attempted to describe *Sepedon* larvae (e.g. Gercke, 1876; Needham and Betten, 1901; Dyar, 1902; Brocher, 1913; Vimmer, 1925; Johannsen, 1935; Wesenberg-Lund, 1943; Peterson, 1953). These morphological characteristics are not diagnostic for *Sepedon* larvae, since other aquatic, tetanocerine larvae have the same general appearance. Unfortunately these easily observed features are shared too broadly to diagnose the genus, yet not broadly enough to characterize the family or even the whole subfamily.

As long as many larvae remain unknown, diagnostic characters cannot be stipulated with finality. The character most likely to prove diagnostic for *Sepedon*, like the one suggested above for the family, is found in the cephalopharyngeal skeleton. All larvae of *Sepedon* known to us have a broad, median notch in the posterior border of the ventral arch (Figs. 30 through 33). Another characteristic helpful in recognition of most *Sepedon* larvae is that their integuments are generally transparent, whereas those of most

tetanocerine genera are opaque. This character does not apply universally. Although most aquatic, tetanocerine larvae have pigmented integuments that are opaque or barely translucent, larvae of *Elgiva* have just as lightly colored and transparent integuments as the larvae of *Sepedon* (see Knutson and Berg, 1964, for other distinguishing characteristics of *Elgiva* larvae). On the other hand, 2 species, *S. spinipes* and *S. tenuicornis*, have translucent to opaque, brown integuments with an iridescent sheen. The integument is covered with minute, triangular scales, the distribution of which seems to account for the various patterns observed in some larvae. *Sepedon* larvae differ from larvae in most of the closely related genera in having the posterior spiracular disc surrounded by 5 pairs of fleshy lobes or tubercles. Although the larva of *Protodictya hondurana* Steyskal also has 5 pairs (Neff and Berg, 1961), most sciomyzid larvae have 4 or less.

The small, inconspicuous anterior spiracles of the second- and third-instar larvae are situated posterolaterally on the second, or prothoracic, segment (Fig. 12, as). In the species of *Sepedon* discussed here, the spiracle may bear 4 to 12 round papillae on the distal portion. Numbers of papillae differ considerably between individuals of a species and even between the right and left spiracles of an individual. The portion between the spiracular scar (Fig. 49, ss) and the terminal disc bearing the papillae may either expand slightly toward the apex (Figs. 48, 49), remain uniform in diameter (Figs. 45, 46), or taper apically (Fig. 40).

The prominent, warty tubercles on the abdominal segments of *Sepedon* larvae have been mentioned by various authors, but their arrangement has not always been described and figured correctly. Each abdominal segment is subdivided into 3 rings by transverse folds that are particularly evident on the ventral surface. The central ring bears many tubercles arranged in definite groups around the segment (Figs. 11, 12). Some larvae have a pair of piliferous tubercles on each side of the mid-dorsal line, the dorsal and dorso-lateral hair patches, respectively (Fig. 11, dhp and dlhp). In other larvae, these hair patches are greatly reduced or lacking. Laterally, on each side of the segment, there is a group of 3 close-set tubercles (Fig. 12, ltg). The middle tubercle is slightly anterior to the upper and lower ones of the group. Ventrally, there is a transverse row of 4 tubercles (Fig. 12, vtg). Anterior to this transverse row and separated from it by a fold is a pair of wide-set tubercles. Integumentary folds and furrows are well developed ventrally and ventrolaterally and may obscure the lateral and ventral tubercles in living specimens.

The caudal end (segment 12) of the body terminates in a flattened, circular area, the posterior spiracular disc (Figs. 13, 14), bearing the paired spiracular plates near its center. In *Sepedon*, the margin of the disc bears 2 pairs of prominent lobes ventrally and ventrolaterally, and 3 pairs of low, rounded lobes laterally and dorsally. The pair of ventral lobes may be long, lanceolate (Fig. 13, VL) or they may be short and blunt (Fig. 14). The ventrolateral lobes may appear 2-segmented, the distal portion being attenuated

and longer than the basal part (Fig. 13, VLL), or these lobes may be blunt with a small, pointed, thumb-like projection on the dorsoapical margin (Fig. 14). The lobes provide a reliable character for the separation of larvae into 2 groups. One group which includes *S. caerulea*, *S. fuscipennis*, and others (see key) possesses the lanceolate ventral lobes and 2-segmented ventrolateral lobes. The other group includes the *armipes* group (*S. armipes*, *S. anchista*, *S. bifida*, and *S. haplobasis*) and the *pusilla* group (*S. pusilla*, *S. borealis*, and *S. neili*) as defined by Steyskal (1950). This character can be used for all 3 larval instars (see Figs. 13, 15, 17 and 14, 16, 18).

The 2 posterior spiracular plates situated in the central area of the disc are slightly elevated above the disc surface on short, sclerotized, tube-like structures, here called spiracular tubes. The outer surface of these tubes is tuberculate or papillose (Figs. 37, 39). Because sclerotized parts darken with age, this surface and the upper surface of the plate are lightly to heavily pigmented depending upon the time elapsed since the last molt. Each plate has on its outer margin 4 palmately-branched hairs or interspiracular processes which are constantly covered by a film of oil secreted by the perispiracular glands. Being hydrofuge, these hairs also are resistant to being pulled down through the surface film. They function importantly when a larva which has nothing that it can grasp to support its own position must hold a snail heavier than itself at the surface while feeding on it (Berg, 1964, Fig. 1). These so-called "float hairs" radiate from positions between the spiracular slits. They are present in all 3 larval instars, but they appear more prominently branched in second- and third-instar larvae. Each spiracular slit appears elongate, oval in shape following a molt, but the opening is partially occluded by numerous transparent trabeculae. These become apparent by darkening as the stadium proceeds, and the spiracular opening then appears as a sinuous line (Fig. 37). The first-instar larva has a B-shaped spiracular opening surrounded by a poorly developed peritreme (Figs. 17, 18).

The anus is situated ventrally on the median line of segment 12 (eighth abdominal segment). The anal slit is longitudinal and is bordered on either side by a clear area called the anal plate. The plate is almost twice as wide as long, and has on its anterior margin a wide, retractile proturbance called the anal proleg. This proleg has poorly developed, hyaline hooks on its surface and is used for prehension and locomotion.

As stated above, larvae are often found in nature floating just beneath the water surface with their posterior spiracular plates thrust through the surface film. A large bubble of air is present in the anterior end of the midgut. Brocher (1913:385) was right when he stated concerning *Sepeidon* larvae, "... leur tube digestif contient une grosse bulle d'air. Cet air a, probablement, été dégluti intentionnellement; il contribue a faire flotter le corps" (. . . their digestive tract contains a large bubble of air. This air has probably been swallowed intentionally; it contributes to buoyance of the body). Larvae intentionally ingest quantities of air, often during

interruptions of their feeding activities. The anterior end is stretched forward and upward, the mouthhooks are spread slightly, and a single, long line of small, silvery bubbles passes down the esophagus, each breaking into the large bubble in the midgut. The buoyancy caused by this bubble reduces the excess weight of a larva and its food snail enough to enable the hydrofuge float hairs to hold them at the surface. If the surface film is broken and both larva and snail sink, the larva needs only to release the snail and this bubble returns it quickly to the surface (Berg, 1964). Wesenberg-Lund (1943) suggested the large air bubble may fill enough space to create turgidity needed by the larva to crawl effectively. This function seems to explain the presence of such air bubbles in the intestines of terrestrial as well as aquatic sciomyzid larvae. Williams (1938) observed that aquatic larvae of certain Ephydriidae (*Brachydeutera* and *Scatella*) similarly ingest air; he explained simply that this serves to increase their buoyancy.

Sepedon larvae swim with 2 effective but remarkably different Methods. If placed in the center of a large dish or aquarium so they have no contact with floating or emergent objects, most larvae soon use one of these techniques. Oriented in the normal floating position with dorsal surface up, a larva extends its anterior body segments forward, then sweeps them downward and backward in a quick stroke which propels the larva forward. This motion is accompanied by an extension, then contraction of the intermediate abdominal segments. The posterior spiracular disc dips into the water during the swimming stroke, but is raised so the spiracular plates are again exposed to the air as the larva returns its extended anterior end to a position parallel to the surface film, prior to the next downward stroke.

Sometimes an equally effective and more remarkable swimming motion is seen. When the larva has lowered its extended anterior end several times and thrust it to both right and left without touching any substrate, it stretches out just below the surface, rolls from side to side to develop momentum, then rolls over completely so that its ventral side is up. Then it bends the posterior 1/3 of the body down and snaps it sharply backward and upward. This swimming motion has been observed in *S. sphaecea*, *S. fuscipennis* (Needham and Betten, 1901), and *S. s. spinipes* (L. V. Knutson, in *litt.*). Brocher (1913) probably saw the same swimming motion in *Sepedon* larvae (species not named); however, he did not state that the swimming larvae were in inverted positions. Both swimming motions described above are smoothly coordinated series of rhythmic movements which result in rapid propulsion.

Larvae are seldom encountered in nature attacking or feeding on snails. Like other predators, they kill their victims quickly, leave them as soon as their immediate hunger is satisfied, and attack another individual when they again get hungry. A *Lymnaea emarginata* was collected in Alaska just when it was being killed and consumed by a larva of *S. fuscipennis* (Berg, 1953). In the marshes where *S. macropus* has become established in Hawaii, anyone who collects a quantity of *Lymnaea ollula* is apt to find at least one snail

being killed by a *S. macropus* larva. Yet the collector who is concentrating on larvae rather than snails can collect hundreds of them without ever finding one that is feeding, as the long-standing ignorance of larval food habits clearly indicates.

The swift, though sure attack of a larva in a laboratory rearing jar is easily observed (Figs. 66-68). The hungry larva thrusts its sharp mouthhooks into the exposed foot, and the snail suddenly retracts into its shell. If attached, the larva is pulled in ; if not, it follows quickly. In snails having red hemolymph (e.g. *Helisoma* sp.), the escape of this fluid is apparent almost immediately. Death (cessation of the snail heartbeat) comes quickly. A *Physa* sp. 4 mm long usually succumbs in less than 20 minutes. A *Helisoma trivolvis* 4 to 6 mm in diameter may live for almost an hour, but its heartbeat usually slows and weakens appreciably in about 10 minutes. Periods of survival after a larva attacks suggest that the snail's death may be caused by bleeding, which would be slower or faster depending on the extent of the opening torn into the hemocoel. The larva evidently feeds rapidly after the initial attack. Protracting and retracting the cephalopharyngeal skeleton in quick movements, it seems to ingest hemolymph and bits of snail flesh indiscriminately. No differences in the mode of attack and feeding were observed among larvae of the 15 species discussed here.

To ascertain the total number of snails that a single larva can kill between hatching and pupation, newly hatched larvae were isolated in individual rearing jars. Each larva was offered 4 fresh *Helisoma trivolvis* daily. Since a larva seldom destroys 4 snails in a 24-hour period even when mature, each larva was thus supplied with an abundance of food. Each larva of *S. caerulea* killed and consumed 12 to 18 snails during its 3 larval stadia, depending upon the sizes of snails used.

In a test to determine the effect of relative sizes of larvae and snails on vulnerability, mature larvae subdued snails up to 19 times their own weight.

Puparia

The puparia of all except 3 of the species discussed here float in the marshes, swamps, ponds, canals, ditches, and slow-flowing streams frequented by adults and larvae. They occur amidst bits of floating debris or in contact with floating or emergent vegetation, where they are not easily seen. The most effective way of finding them is to push the vegetation and flotsam beneath the surface, thus forcing them to float free. Their concealment is enhanced by their great similarity to seeds (especially *Impatiens* spp.) which are commonly found floating with puparia in both North America and Europe (Needham and Betten, 1901; Brocher, 1913). The larvae of 2 species, *S. tenuicornis* and *S. spinipes*, before pupating usually crawl on emergent vegetation to well above the water surface and glue themselves in place there with secreted mucus. Puparia of both species have been detached accidentally and collected in the net while we were sweeping for adults, and attached puparia of *S. tenuicornis* have been found almost a meter above the water. Puparia

of *S. borealis* have not been found in nature, but larvae in rearing jars have burrowed into the substrate to form partly buried puparia.

Tetanocerine puparia formed in water and adapted for floating are curved dorsally at the posterior end, and to a lesser degree at the anterior end. This curvature brings both anterior and posterior spiracles up near, or even through, the surface film and results in characteristically shaped puparia which are flattened dorsally but markedly convex ventrally (see lateral views, Figs. 51 through 65). Each puparium is abruptly contracted anteriorly to form a dorso-ventrally flattened rostral prominence, truncate in dorsal view, which bears the larval anterior spiracles at its anterolateral corners. The blunt anterior ends give these puparia a stubby appearance which is more evident in the broad, somewhat globose puparia of *Sepedon* than in the narrower, more cylindrical puparia of other aquatic Tetanocerinae. The dorsally curved posterior end forms a short pedicel which bears the shrunken posterior spiracular disc. This pedicel usually forms an obtuse angle of 100 to 120° with the longitudinal axis of the puparium body.

Most external features of *Sepedon* puparia seem more useful for recognizing certain species than for distinguishing the genus as a whole from related genera. The broad, globose, or ovoid shape mentioned above is far more characteristic of *S. fuscipennis* and *S. praemiosa* puparia than of the small species in the *armipes* and *pusilla* groups. Transverse constrictions at the middle are peculiar to *S. tenuicornis* and *S. spinipes* puparia, the only ones situated above the water and soil, and well exposed to the air. Another species that seems to pupate in an exceptional situation, *S. borealis*, forms puparia which differ from those of other aquatic Tetanocerinae (including species in related genera as well as *Sepedon*) in having little if any dorsal curvature of the posterior end (Fig. 61). Although *Sepedon* puparia have some obvious color patterns, these patterns characterize species rather than genus. Indeed, some puparium colors do not even characterize a species completely, for some species produce puparia of 2 different color phases. Puparia of *fuscipennis*, *macropus*, and *caerulea*, for instance, may be light brown with evident bicolorous shadings dorsally and laterally, or they may be wholly dark brown, almost black, with the sites of the larval body tubercles somewhat lighter than the ground color. The dark oblique lines on puparia of *armipes*, *anchista*, and *haplobasis* distinguish these puparia of the *armipes* group from known puparia of the *pusilla* group (*pusilla*, *borealis*, and *neili*). These oblique lines are more evident on puparia than on larvae; they are so conspicuous on the puparium of *S. anchista* (Figs. 58, 59) that they distinguish it from all other *Sepedon* puparia.

Although the puparium is the contracted and hardened integument of the mature larva, some of the most prominent external features of the larvae are useless in identifying puparia because they are difficult or impossible to see. The characteristic distribution of the hair patches and tubercles is almost obliterated on the surface of the puparium. These areas appear as small, lightly shagreen

areas, and the bristles of the dorsal hair patches are closely appressed to the puparium surface. Although the posterior spiracular plates are evident above the shrunken disc at the end of the pedicel, the lobes surrounding the posterior spiracular disc are too shrunken to be positively identified and counted. The anal plate forms a slight notch in the ventral surface of the upturned pedicel, but it is somewhat obscured by creases and folds in the puparium wall and its shape is not readily ascertained.

The most reliable diagnostic features for *Sepedon* puparia as a group seem to be the cephalopharyngeal skeleton characters mentioned under *Sepedon* larvae. These larval structures are easily removed from the inner surface of the ventral cephalic cap, cleaned, cleared, and mounted for study. As mentioned above, their light pigmentation and the deep, median notch in the posterior edge of the ventral arch are quite distinctive. Cephalopharyngeal skeletons of *Elgiva* also are lightly pigmented, and their ventral arches have shallow median notches or concavities posteriorly. However, all known *Elgiva* puparia are distinctive, with the terminal segment narrowly attenuated and at least twice as long as wide (Knutson and Berg, 1964). The anterior spiracles provide positive differentiation of *Sepedon* puparia from those of some genera (e.g. *Tetanocera*) in which the number of papillae is always greater.

The circular seam which enables the emerging adult to push off the anterior end of the puparium is formed around the first abdominal segment. (The pseudocephalic segment is completely invaginated when the larva contracts to form the puparium, so the first visible segment of the puparium is segment 2.) A line of weakness which develops laterally, anterior to the circular seam, progresses forward to the rostral prominence at the anterior end and frontally across it. The anterior end that is pushed off during emergence breaks along this line to form the dorsal and ventral cephalic caps, bearing the anterior spiracles and the cephalopharyngeal skeleton of the larva, respectively.

The larval anterior spiracles are borne on the anterolateral corners of the dorsal cephalic cap. They are somewhat shorter than in the larva. As Meijere (1902) stated for *S. spegea*, no pupal respiratory processes penetrate the puparium wall in this genus. Although such processes of the pupa are found in many cyclorrhaphous Diptera, they do not occur in any known sciomyzid puparium.

Seasonal Aspects

Adults of *Sepedon* are active in all except the coldest of weather. The most common species in the area around Ithaca, New York, *S. fuscipennis* and *S. armipes*, have been encountered from early spring to mid-autumn. Our earliest record for *armipes* is in late winter, March 10, when ponds and marshes in the area were still covered with ice. *Sepedon spegea* has been collected in Denmark from March 30 to December 20. At Almeria, Spain, L. V. Knutson collected adults of both *S. spegea* and *S. spinipes spinipes* on January 28, 1964. In the tropics and warmer temperate regions,

Sepedon species fly throughout the year. This is true of *S. praemiosa* at Riverside, California, of *S. caerulea* in Puerto Rico, and of *S. macropus* both in its native countries of Central America and in Hawaii.

Seasonal interruptions of adult activity in colder regions are direct responses to the cold, and do not occur at favorable temperatures. *Sepedon* adults held in the heated laboratory in winter (*fuscipennis* and *neili* from the Ithaca region and *sphegea* from Kandahar, Afghanistan, as well as the Neotropical species) have remained active throughout the winter. Species from regions of cold winters usually differ from tropical species in foregoing reproductive activity until spring. However, the *S. sphegea* adults collected in Afghanistan on October 1 and 3 began to mate and lay viable eggs in late December and January, after 2½ months without reproductive activity in the laboratory. Eggs held at room temperatures in January developed directly, hatching in 3 days. Most of the eggs that were set outside and exposed to winter temperatures down to -18°C did not develop, even when returned to the heated laboratory. The few that did, began to hatch 3 days after they were brought into temperatures of 21 to 25°C .

The observations given above indicate that species of *Sepedon* which must survive winter conditions do so as hibernating adults (or, perhaps rarely, as eggs). This suggestion is supported by the following observations at Ithaca, which has a mean January temperature of -3.9°C with mean monthly minimum and maximum of -8.3°C and 0.5°C . Adults taken in March and April usually have frayed wing margins and broken or missing setae; they appear to have been around for a long time. Furthermore, larvae cannot be found in winter, even in breeding sites in which they are abundant during warmer seasons. Although a very few puparia have been found in winter and early spring, all have failed to produce adults. They evidently were formed the previous summer and fall, and they remained intact because the pupae within had died.

Most species seem to breed continuously during the flying season, one generation following directly after the other with no diapause or other delay anywhere in the life cycle. Because each female usually continues to lay a few eggs each day for a period that greatly exceeds the time required for the entire life cycle, she lays eggs for some time after her first daughters begin to oviposit. As a result, generations spread in time, overlap each other, and become unrecognizable. Thus oviposition, hatching, pupation, and emergence go on continuously throughout the favorable season, and all stages of the life cycle occur in the same pond on the same day. One can compute the number of generations theoretically possible per year by dividing the total flying season by the time required for a complete life cycle, but the figure obtained may have little relevance to field conditions in species that breed in this way.

Species in the *S. pusilla* group may differ from other species of *Sepedon* in always having 2 generations per year. Adults of *S. borealis* collected near Ithaca in May and June laid viable eggs soon after being collected, but flies taken in August did not oviposit.

Similarly, *S. neili* females collected on July 3 produced eggs, and a generation was reared in the laboratory. Adults emerged between August 20 and 25, but they neither mated nor laid eggs until the following spring (mid-April to early July), after remaining active all winter in the laboratory. Adults which developed from those eggs began to emerge in May. They produced viable eggs in July, which gave rise to a late summer generation of adults in August and early September. This suggests that 2 generations per year, with the late summer generation hibernating as adults, may be a fixed rule in *S. neili* and *S. borealis*.

However, the seasonal aspects of these species of the *S. pusilla* group may not be essentially different from those of other *Sepedon* species. Oviposition of overwintered *S. neili* females on many dates from April 18 to early July strongly indicates that generations of *S. neili* in nature are just as spread, overlapped, and unrecognizable as those of other species of *Sepedon*. We can be certain after the continuous observation of wild-caught *S. neili* and their progeny for 15 months, that there were 2 generations per year in that instance, but this may not always be true of *S. neili* and *S. borealis*. Other boreal species probably are also confined to 2 generations per year, or even to 1, near the northern limits of their ranges. Although overwintering prior to mating and oviposition may be genetically fixed and obligatory in the second generation, it could also be a response to some ecological factor such as decreasing day length (Lees, 1955). If so, this late summer or autumn cessation of reproductive activity could occur in delayed first-generation flies in the northern part of the range or in advanced third-generation individuals in the southern part. This phenomenon should be expected in individuals destined to hibernate, whether there is a fixed number of generations per year or not. The long delay mentioned above before autumn-caught adults of *S. sphaecea* began reproductive activity indicates that it occurs also in that species.

Natural Enemies

Future progress of ecological studies on *Sepedon* and other Sciomyzidae depends in part on the recognition and evaluation of environmental factors which limit their capacities for population increase. Only fragmentary information on this subject is available. We can neither list such factors completely nor estimate quantitatively their impact on *Sepedon* populations.

Pathogenic microorganisms that attack *Sepedon* larvae evidently include both bacteria and viruses. Contagious and deadly, but fortunately uncommon, the virus that induces characteristic symptoms in sciomyzid larvae has occurred in the Cornell laboratory only twice in the past 12 years. Histolysis of the affected larvae progresses quickly; when listlessness and lack of appetite are first noticed, larval bodies are already reduced to mere sacs of transparent fluid. By the time of death they are completely amorphous, the body wall being so thin and fragile that it usually ruptures on touch, if not spontaneously.

Especially during hot, humid weather, rearing jars in which snails are killed but not completely eaten may develop visible bacterial films between one day's cleaning and the next. Under such conditions, larvae leave the moist gravel which is contaminated with decomposing snail tissue soon after each feeding, crawl up the sides of the jar, and come to rest on the cork. Death of larvae in contaminated jars is not uncommon, especially if they are crowded. Larval death rates decreased significantly in the insectary at Honolulu when aureomycin was added to the rearing jars.

The most commonly encountered enemies of *Sepedon* are parasitoid Hymenoptera of 5 families which attack egg, larva, and pupa stages. Trichogrammatidae which attack the eggs are relatively poorly known because Sciomyzidae are not often collected in the egg stage. Many were reared from eggs of *S. fuscipennis* collected near Ithaca, and the only egg mass of *S. s. spinipes* that we found in nature (in Denmark) had emergence holes indicating that every egg had been destroyed by these minute wasps (Fig. 9). They may exert important controls on *Sepedon* populations, but this will be difficult to determine.

The parasitoid Hymenoptera most frequently reared from sciomyzid larvae and puparia are Ichneumonidae: Gelinae, 23 species belonging to the genera *Eriplanus* (12), *Mesoleptus* (7), and *Phygadeuon* (4) (Townes, *in litt.*). We have obtained some of these from *Sepedon* collected as larvae and held in closed containers. The parasitized larvae attacked snails in the usual way and formed apparently normal puparia from which the parasitoid wasps emerged. Study of the biology of these wasps would be interesting and certainly rewarding, but most species remain undescribed.

Less frequently, parasitoid Hymenoptera of the families Diapriidae, Braconidae, and Pteromalidae emerge from sciomyzid puparia collected in nature. The former are known to oviposit directly into puparia (Knutson and Berg, 1963). Foote *et al.* (1960) obtained an average of 3 *Aphaereta pallipes* (Say) (Braconidae) from each of 50 parasitized puparia of *Atrichomelina pubera* (Loew).

Only fragmentary observations are available on predators of Sciomyzidae. Birds known to prey on adult flies include blackbirds (G. H. Orians, *in litt.*) and the common nighthawk (J. C. Moser, *in litt.*) Chock *et al.* (1961) mentioned dragonfly and damselfly naiads and the aquatic bug *Mesovelia mulsanti* (White) as predators of the larvae and pupae of *Sepedon macropus* in Hawaii. Although vulnerability of these aquatic stages to a strictly terrestrial species may seem surprising, they also listed an imported tropical ant, *Pheidole megacephala* Fabr. as an important predator. Krombein (1964) reported that the hibiscus wasp, *Ectemnius paucimaculatus* (Packard), uses *Sepedon* sp. and *S. armipes* adults as prey in provisioning nests. Knutson (1965) observed that a single tabanid larva (*Hybomitra schineri* Lyneborg) killed and devoured 37 sciomyzid larvae (*Tetanocera ferruginea* Fall.) between the time of its collection and its pupation.

KEYS TO THE IMMATURE STAGES OF **SEPEDON**

Eggs

1. Chorion with a wide longitudinal groove on each side dorsolaterally (Figs. 4, 7; lg) bordered laterally and mesally by ridges, the latter demarking regularly reticulate central area (Figs. 4, 7; Ca); single rounded transverse or broadly triangular tubercle shielding micropyle dorsally 2.
Chorion without wide longitudinal grooves dorsolaterally; no reticulate central area; dorsal surface with narrow, anastomosing, longitudinal ridges (Figs. 1, 2); single transverse tubercle or 2 to 5 small tubercles shielding micropyle dorsally. 5.
2. Tubercle shielding micropyle broadly triangular (Fig. 6); central area between mesal longitudinal ridges dark lead-gray, almost black. Eurasia ----- *S. spegea*
Tubercle shielding micropyle rounded, transverse (Figs. 4, 7); central area between mesal longitudinal ridges white or orange-white --- 3.
3. Tubercle at end opposite micropyle round, distinctly hemispherical (Fig 7, ht); chorion milk-white. Eurasia, northern United States, Canada, and Alaska *S. spinipes*
Tubercle at end opposite micropyle more or less conical (Fig. 4, ht); chorion usually orange-white 4.
4. Dorsal depression often present at micropylar end (as Fig. 3, dd); tubercle at end opposite micropyle with minute punctations. Mexico, Central America, northern South America, and West Indies *S. macropus*
No dorsal depression at micropylar end; tubercle at end opposite micropyle with prominent punctations. Southern Mexico to Costa Rica *S. guatemalana*
5. Dorsal depression at micropylar end (Fig. 3, dd); low, anastomosing, longitudinal ridges on chorion dorsally. Puerto Rico and Hispaniola *S. caerulea*
No dorsal depression present at micropylar end; anastomosing longitudinal ridges sharp, prominent (Fig. 1, 2), or longitudinal ridges interrupted, forming tubercles and elongate ridges (Fig. 5). 6.
6. Two to 5 small tubercles shielding micropyle dorsally; longitudinal grooves between ridges without minute transverse septa (Figs. 1, 2); chorion white with gray spots or uniform light gray to lead gray; 1.1 to 1.5 mm long 7.
Single, rounded, transverse tubercle shielding micropyle dorsally; longitudinal grooves between ridges with minute transverse septa giving chorion punctate appearance (Figs. 8, 10); chorion white to orange-white; 0.8 to 1.2 mm long. 9.
7. Tubercle at end opposite micropyle produced, hemispherical or somewhat conical; longitudinal ridges with sharp crests, running almost full length of egg 8.
Tubercle at end opposite micropyle not produced; longitudinal ridges interrupted, forming tubercles and short, elongate ridges; 2 or 3 tubercles shielding micropyle dorsally (Fig. 5). Central and eastern United States and southern Ontario. *S. tenuicornis*
8. Chorion bicolourous, with lead gray spots dorsally, longitudinal ridges with somewhat uneven or emarginate crests; 3 to 5 truncate

- tubercles shielding micropyle dorsally (Fig. 1); 1.4 to 1.5 mm long. Western North America, including the southwestern states and Mexico. *S. praemiosa*
- Chorion unicolorous, uniformly gray to lead gray; longitudinal ridges with even, sharp crests; 4 to 5 tubercles shielding micropyle dorsally (Fig. 2); 1.1 to 1.3 mm long. Common throughout the United States (except the southwestern states), Canada, and parts of Alaska. *S. fuscipennis*
9. Often bearing wide, conspicuous, transverse band of lead gray covering middle third of egg (but may lack this band completely). Widespread in the United States and Canada, southwest to Arizona and California *S. armipes*
- Unicolorous and not banded (as Figs. 8, 10)
- Western Canada and northwestern to midwestern United States *S. anchista*
- California *S. bifida*
- Mexico *S. haplobasis*
- Northern United States, Canada, and Alaska (Fig. 8) *S. borealis*
- United States and southern Canada (Fig. 10) *S. neilli*
- Eastern United States, north to central Ohio *S. pusilla*

Mature Larvae

1. Posterior spiracular disc with ventral lobes (Fig. 13, VL) elongate, lanceolate; ventrolateral lobes apparently 2-segmented, apical portion as long as basal portion; segments 5 through 10 with hair patches dorsally and dorsolaterally (Fig. 11; dhp, dlhp). 2.
- Posterior spiracular disc with ventral lobes more or less ovate, rounded apically (Fig. 14); ventrolateral lobes with apical portion a small, thumblike dorsoapical projection on truncate basal portion; segments 5 through 10 with hair patches greatly reduced, bearing 1 to 3 bristles in each patch, or hair patches wholly lacking. 8.
2. Integument appearing bicolorous, yellowish with dark oblique stripes (Fig. 11, os) laterally; segment 5 with dark, truncate marking dorsally extending posteriorly as interrupted and middorsal stripe (Fig. 11, mds); uppermost accessory tooth of mouthhook darkly pigmented and larger than lower teeth, (Fig. 35). Mexico and Central America. *S. guatemalana*
- Integument appearing more or less unicolorous, light yellowish white to dark yellow-brown; oblique stripes, when present, faint, diffuse lines dorsolaterally on segments 6 through 9; segment 5 without dark, truncate marking dorsally; middorsal stripe, when present, extending full length of body; accessory teeth on mouthhooks all similar in size and color. 3.
3. Integument dark yellow-brown, often with greenish iridescent reflections (living material); body of anterior spiracle below papillae cylindrical (Fig. 45); basal portion of spiracle body slightly inflated proximal to stigmatic scar. 4.
- Integument light, yellowish white, without iridescent reflections; body of anterior spiracle slightly expanded below papillae (Fig. 49), not cylindrical; or basal portion not greatly inflated below stigmatic scar (Fig. 46). 5.
4. Middorsal stripe lacking on segments 5 through 8, only faintly evident on segment 9; cephalopharyngeal skeleton with pharyngeal sclerite lacking pigmented area on dorsal cornua (c.f. Fig. 28, PA). Central

- and eastern United States and southern Ontario. *S. tenuicornis*
 Middorsal stripe present on segments 5 through 9; pharyngeal sclerite usually with pigmented area on dorsal cornua (as Fig. 28, PA). Eurasia, northern United States, Canada, and Alaska *S. spinipes*
5. Accessory teeth of mouthhooks darkly pigmented, only slightly decurved (Fig. 34); anterior spiracles not inflated distal to stigmatic scar (Fig. 46); pharyngeal sclerite with pigmented area (Fig. 28, PA) present on dorsal cornua:
 Puerto Rico and Hispaniola *S. caerulea*
 Mexico, Central America, northern South America, and West Indies *S. macropus*
 Accessory teeth of mouthhooks lightly pigmented, decurved (Figs. 36, 38); anterior spiracle somewhat inflated distal to stigmatic scar (Fig. 49); pharyngeal sclerite with pigmented area on dorsal cornua present or absent. 6.
6. Pharyngeal sclerite lightly pigmented (Fig. 23) ; usually 4 decurved accessory teeth on each mouthhook (as Fig. 38). Common throughout the United States (except the southwestern states), Canada, and parts of Alaska. *S. fuscipennis*
 Pharyngeal sclerite dark (as Fig. 28); mouthhooks with 3 or 4 decurved accessory teeth. 7.
7. Anal proleg with distinct median lobe; mouthhook with distinct bend near apex, usually with 4 decurved accessory teeth beneath hook portion (Fig. 38). Eurasia *S. spegea*
 Anal proleg a low, transverse protuberance, without a distinct median lobe; mouthhooks lacking bend in apical portion, usually with 3 decurved accessory teeth (as Fig. 36). Western North America. *S. praemiosa*
8. Posterior spiracular plates with interspiracular processes as long as spiracular tube (Fig. 37). 9.
 Posterior spiracular plates with interspiracular processes only half as long as spiracular tube (Fig. 39); 3 accessory teeth on each mouthhook.
 Northern United States, Canada, and Alaska *S. borealis*
 United States and southern Canada *S. neili*
9. Dorsum of segment 10 with integumentary scales almost twice as long as wide, imbricate (Fig. 20). Eastern United States, north to central Ohio *S. pusilla*
 Dorsum of segment 10 with integumentary scales about as long as wide, broadly triangular, not imbricate (Fig. 21).
 Widespread in the United States and Canada, southwest to Arizona and California *S. armipes*
 Western Canada and northwestern to north-central United States *S. anchista*
 California *S. bifida*
 Mexico *S. haplobasis*

Puparia

1. Body of puparium uniformly dark brown; integument thick, coriaceous; dorsum slightly concave in lateral view (Figs. 52, 53) 2.
 Body of puparium unicolorous or bicolorous; integument thin, not coriaceous; dorsum flat or convex in lateral view. 3.
2. Middorsal stripe present; 1.7 to 2.3 mm wide. Eurasia, northern United States, Canada, and Alaska *S. spinipes*

- Middorsal stripe absent; 2.3 to 2.7 mm wide. Central and eastern United States and southern Ontario *S. tenuicornis*
3. Puparium in dorsal view with round protuberance at posterolateral borders of dorsal and ventral cephalic caps (Fig. 64). Eurasia *S. sphaegee*
 Puparium in dorsal view without round protuberance at posterolateral borders of cephalic caps (Fig. 50). Western Hemisphere. 4.
4. Broad, stramineous, V-shaped mark on dorsal cephalic cap, arms of "V" extending posterolaterally (Fig. 54); puparium appearing rectangular in lateral view (Fig. 55). Central America. *S. guatemalana*
 No V-shaped mark on dorsal cephalic cap; puparium more or less elliptical in lateral view (Figs. 51, 57, 59, 63). 5.
5. Puparium appearing ovate in dorsal view (Fig. 50) 6.
 Puparium elongate-elliptical to cylindrical in dorsal view (Figs. 56, 58, 60, 62). 7.
6. Five reddish-brown to brown spots often present laterally on segments 6 through 10 (Fig. 51). Throughout America north of Mexico, except the southwestern states. *S. fuscipennis*
 No reddish-brown or brown spots present laterally on segments 6 through 10. Western North America, including the southwestern states and Mexico. *S. praemiosa*
7. Stramineous oblique stripes present dorsolaterally on segments 6 through 9 (Figs. 56, 57, 58, 59). 8.
 No stramineous stripes present dorsolaterally on segments 6 through 9 (Figs. 60, 61, 62, 63). 10.
8. Three accessory teeth on mouthhooks of cephalopharyngeal skeleton darkly pigmented, slightly decurved (Fig. 34); puparia large, 5.5 to 8.0 mm long:
 Puerto Rico and Hispaniola *S. caerulea*
 Mexico, Central America, northern South America and West Indies *S. macropus*
 Three or 4 accessory teeth on mouthhooks lightly pigmented, somewhat decurved (Fig. 36); puparia usually small, 3.8 to 6.1 mm long. 9.
9. Puparium dark brown with light oblique stripes dorsolaterally (Figs. 58, 59). Western Canada and northwestern to north central United States. *S. anchista*
 Puparium yellowish-brown to brown:
 United States and Canada *S. armipes*
 Mexico *S. haplobasis*
10. Body color brown, usually unicolorous; dorsal cephalic cap usually bearing transverse crescentic stripe (as Fig. 62); float hairs of spiracular plates as long as supporting spiracular tube (Fig. 37):
 Eastern United States, north to central Ohio *S. pusilla*
 California *S. bifida*
 Body color light, stramineous; transverse crescentic stripe on dorsal cephalic cap not evident; float hairs of spiracular plates only half as long as spiracular tube (Fig. 39). 11.
11. Posterior end of puparium upturned, forming angle of 100 to 140° with longitudinal axis of body (similar to Figs. 62, 63). United States and southern Canada. *S. neili*
 Posterior end of puparium not strongly upturned, forming angle of 150 to 180° with longitudinal axis of body (Figs. 60, 61). Northern United States, Canada, and Alaska. *S. borealis*

SEPEDON CAERULEA Melander

Annals Ent. Soc. Amer., 13:322. 1920.

Like other species of the *S. macro pus* group, *S. caerulea* is a large (6 to 8 mm long) black-bodied fly with tawny brown head and legs and disproportionately long hind femora. It differs from other species in that group in having the entire apical 1/3 of the hind femora darkened.

Known only from Puerto Rico, the Dominican Republic, and Haiti (Map A), the adults occur in open, unshaded wet areas along the margins of lakes and ponds. Their habitat closely resembles those of *S. fuscipennis* and *S. armipes* in North America.

This species was reared through 3 complete generations at Ithaca, New York between January 5 and May 15, 1958. Puparia and adults collected in Puerto Rico January 2 at the southeast end of Cartagena Lagoon, and in the ponds of the Agricultural Experiment Station at Mayaguez, provided the living material from which these rearings originated.

Adults confined in breeding jars laid eggs on the sides of the jar near the surface of the moss and on cardboard strips set vertically to simulate the positions of *Typha* leaves on which other species had oviposited. The eggs occurred singly or in groups of up to 22. Each egg mass was composed of a single vertical row with the long axis of each egg being horizontal (Fig. 3).

Eggs hatched in 3 to 4 days in the laboratory (15 observations). On 2 occasions, hatching of groups of eggs removed from the breeding jars was observed. This did not occur in the order in which the eggs were laid. In a group of 11 eggs, eggs 1, 2, 5 and 7 hatched within 15 minutes. Eggs 3 and 4 in this series hatched last, about an hour and twenty minutes after the first 2 had hatched.

Larvae were fed *Australorbis glabratus*, *Helisoma trivolvis*, and *Physa* sp. and individuals of these 3 species were destroyed with equal facility. First-instar larvae attacking *H. trivolvis* were far more successful with snails 2 to 6 mm in diameter than with individuals 6 to 12 mm in diameter. Even these large snails remained relatively passive to a larval attack. Withdrawing into the body whorl as far as possible, they made no movements with the foot that would repulse the larva's attack. However, the large snails often produced enough mucus as they withdrew to fill the aperture with it. This mucus entangled the small larvae and effectively terminated their activity. Although first-instar larvae seemed most susceptible to this danger, second- and third-instar larvae occasionally succumbed after being entrapped in copious secretions of mucus.

The 3 larval stadia had durations as follows: first, 2 1/4 to 4 days; second, 2 1/4 to 4 days; third, 4 to 7 days (based on 25 observations).

Puparia formed in the laboratory yielded adult flies in 7 to 9 days (25 observations).

The preoviposition period (time from emergence to laying of the first eggs), total number of eggs laid, average egg production per day, and longevity of 12 laboratory-reared females are given

in Table 1. Preoviposition periods varied from 4 to 24 days, averaging 9.6 days. Egg production in this group of females seemed to decline several weeks after their emergence, and this decline was subsequently attributed to an inadequate diet. These females were provided with the brewers' yeast and honey mixture. Subsequent rearings with *S. macropus*, in which this food mixture was supplemented with crushed snails, indicate these *S. caerulea* females did not receive a complete diet. Egg production in these *S. macropus* females was almost double that of *S. caerulea* females during a comparable interval.

- The longevity of laboratory-reared flies ranged from 24 to 148 days for females and 44 to 125 days for males.

Table 1.—Egg production of 12 *S. caerulea* females fed on brewers' yeast and honey diet. January through June, 1958.

	<i>Preoviposition period</i>	<i>No. of eggs laid</i>	<i>No. of eggs per day</i>	<i>Longevity</i>
1	7	301	2.4	131
2	4	183	1.5	121
3	4	137	3.8	40
4	5	251	2.4	107
5	7	179	1.2	148
6	11	172	1.5	122
7	18	97	1.0	112
8	8	150	1.5	107
9	24	103	0.9	130
10	7	303	2.4	132
11	8	97	1.0	105
12	13	12	1.0	24

Description of Immature Stages

Egg: (Fig. 3). Cream white, often with orange shading. Length 1.35 to 1.45 mm (\bar{X} = 1.40 mm); width 0.32 to 0.36 mm (\bar{X} = 0.34 mm). Single, broad tubercle with dorsal depression above (Fig. 3, dd) shielding micropyle dorsally. Low, anastomosing longitudinal ridges on chorion surface dorsally producing irregular pattern. End opposite micropyle with rounded protuberance. Ventral and lateral surfaces regularly reticulate. (Based on 10 specimens, Mayaguez.)

First-instar larva: White; integument transparent. Length 1.9 to 4.5 mm (\bar{X} = 2.9 mm); width 0.2 to 0.6 mm (\bar{X} = 0.4 mm). Segment 1 (pseudoccephalic segment) bilobed anteriorly with minute 2-segmented sensory papilla on each lobe, posterior border with well-developed band of spines almost encircling segment. Cephalopharyngeal skeleton (Fig. 24), length 0.33 to 0.38 mm (\bar{X} = 0.37 mm); with paired mouthhooks, each with bifid hook anteriorly, posterior parts articulating with fused hypostomal-pharyngeal sclerite; ventral arch beneath mouthhooks prominent. Segments 5 to 10 each with 2 pairs of dorsal hair patches: mesal pair transverse, wider than long; lateral pair circular. Three lateral tubercles in close-set group on each side; transverse row of 4 tubercles with prominent integumentary folds ventrally. Posterior spiracular disc (as Fig. 17) with 2 pairs of well-developed elongate lobes ventrally and ventrolaterally, each of the latter pair appearing 2-segmented. Two spiracular plates, each plate with

4 palmately-branched interspiracular processes serving as float hairs and surrounding B-shaped spiracular opening. Anal plate only half as long as wide, anal proleg inconspicuous. (Based on 14 specimens; Mayaguez.)

Second-instar larva: White to light tan, dark middorsal stripe and faint oblique stripes (as Fig. 11, os); integument transparent. Length 4.5 to 8.5 mm (\bar{X} = 6.1 mm); width 0.7 to 1.7 mm (\bar{X} = 1.2 mm). Segment 1 (pseudocephalic segment) bilobed; each lobe with 2-segmented sensory papilla, a circular sensory plate below this, and a labral sensilla ventrolaterally; no pseudotracheae or labral rami ventrally. Postoral spine band prominent posteroventrally. Cephalopharyngeal skeleton (Fig. 26), length 0.56 to 0.61 mm (\bar{X} = 0.58 mm) with paired mouthhooks; each with 2 or 3 slightly decurved accessory teeth below hook; ventral margins articulating with unpaired sclerite, ventral arch, beneath; posterior margins articulating with fused hypostomal-pharyngeal sclerite, epistomal sclerite evident above hypostomal portion. Segment 2 with pair of anterior spiracles, one on each side near posterior border, each with 4 to 6 rudimentary papillae. Segments 3 and 4 with 9 or 10 anteroventral, transverse rows of minute spinules. Segments 5 through 10 each with 2 pairs of dorsal hair patches: mesal pair transverse, wider than long; lateral pair circular. Three lateral tubercles on each side: middle tubercle slightly anterior to upper and lower tubercles. Transverse row of 4 tubercles ventrally, with a pair of wide-set tubercles anterior to transverse row; secondary integumentary folds prominent ventrally and ventrolaterally. Segment 11 lacking dorsal and dorsolateral hair patches. Posterior spiracular disc (as Fig. 15) with 2 pairs of prominent lobes; ventral pair elongate, ventrolateral pair apparently 2-segmented. Lateral, dorsolateral, and dorsal lobes inconspicuous, low protuberances. Two spiracular plates; each with 4 groups of palmately-branched interspiracular processes alternating with 3 elongate spiracular slits surmounting a short, tubular structure rising above surface of disc. Anal plate on ventral surface of segment 12, half as long as wide; anal slit longitudinal. Anal proleg a transverse protuberance at anterior margin of anal plate. (Based on 16 specimens, Mayaguez.)

Third-instar larva: Light tan often with faint oblique markings on segments 5 to 8 (as Fig. 11, os); integument transparent. Length 8.0 to 13.0 mm (\bar{X} = 11.0 mm) width 1.4 to 2.8 mm (\bar{X} = 2.3 mm). Segment 1 bilobed anteriorly (as Fig. 19); each lobe with a 2-segmented sensory papilla (TSP), circular sensory plate (CSP) below this, and labral sensilla (LSP) ventrolaterally on each side of atrium; no pseudotracheae or labral rami ventrally; prominent postoral spine band (POSB) on posterior margin ventrally. Cephalopharyngeal skeleton (Fig. 28), length 0.87 to 0.97 mm (\bar{X} = 0.93 mm), with paired mouthhooks; each with 3 slightly decurved, darkly pigmented accessory teeth below hook (Fig. 34); ventral arch (Fig. 30) articulating with ventral margin of mouthhooks; anterior margin with 22 to 28 minute teeth; posterior margin with broad, median, V-shaped notch. Posterior margins of mouthhooks articulating with hypostomal sclerite; lingual sclerite (Fig. 19, LS) anterior to hypostomal sclerite, enclosing lightly pigmented sensory plate; epistomal sclerite (Fig. 23, ES) dorsal to hypostomal sclerite (Figs. 19, 23; HS), with parastomal rods fused with pharyngeal sclerite (Figs. 19, 23, PS); pharyngeal sclerite wing-like, lacking distinct hyaline areas in dorsal cornuae (Fig. 23, DC), pigmented area (Fig. 28, PA) developing on posterodorsal border late in stadium. Segment 2 with pair of anterior spiracles, 1 on each side near posterolateral margin; each spiracle (Fig. 46) with 5 to 8 papillae around slightly expanded distal portion, body of spiracle not greatly constricted just above stigmatic scar. Segments 3 and 4 lacking tubercles or hair patches, but

with 8 subequally spaced bristles around middle of segments. Segments 5 to 10 each with 2 pairs of hair patches: mesal pair (as Fig. 11, dhp) transverse, wider than long; lateral pair (as Fig. 11, dlhp) circular. Lateral tubercle group (as Fig. 12, ltg) with 3 contiguous tubercles, the middle one slightly anterior to the upper and lower; transverse group (as Fig. 12, vtg) of 4 tubercles ventrally with 2 widest tubercles anterior to transverse group and separated from it by secondary integumentary fold. Segment 11 lacking hair patches dorsally and dorsolaterally. Posterior spiracular disc (as Fig. 13) with a pair of lanceolate ventral lobes (VL) and a pair of apparently 2-segmented ventrolateral lobes (VLL); a pair of low, conical lateral lobes (LL); dorsolateral (DLL) and dorsal lobes (DL) low, inconspicuous protuberances forming dorsal border of disc. Two spiracular plates (Fig. 13, SP); each elevated above surface of disc on short, lightly pigmented tube; each plate with 4 palmately-branched interspiracular bristles (ISB) serving as float hairs and alternating with 3 elongate, sinuous slits. Ventral side of segment 12 with anal plate slightly bilobed, half as long as wide, with transverse anal proleg at anterior margin. Anal slit longitudinal. (Based on 14 specimens, Mayaguez.)

Puparium: (As Figs. 56, 57). Brown to black dorsally, often with oblique markings dorsolaterally; light tan to dark brown ventrally. Length 5.5 to 7.7 mm ($\bar{X} = 6.2$ mm); width 2.5 to 3.3 mm = 2.7 mm) Dorsal cephalic cap bearing inconspicuous anterior spiracles at anterolateral corners, with light yellow, irregular spots at posterolateral angles. Dorsal hair patches visible on segments 5 to 10, hairs appressed to surface. Lateral tubercles often with brown shading between them, tubercles appearing as round, shagreen areas. Ventral surface with transverse tubercle rows as shagreen areas, with brown specks over surface. Posterior spiracular disc on upturned posterior end; upturned portion forming obtuse angle of 100 to 130° with longitudinal axis of puparium body. Ventral and ventrolateral lobes withered below shrunken disc, spiracular plates elevated above disc surface on their short tubes with float hairs appressed to rugose surface of tube. Anal plate black, forming notch on posterior side of upturned caudal portion. (Based on 14 specimens, Mayaguez.)

SEPEDON MACROPUS Walker

List of Dipterous Insects in Brit. Mus., Pt. IV :1078. 1849.

This large (6.5 to 8 mm long) distinctively marked species (see cover) was originally described from material collected in Jamaica. It is as large as *S. caerulea* and has similarly long hind legs, but *S. macropus* has a conspicuous preapical annulus on the hind femora, in addition to the darkened apex.

It is widespread, conspicuous, and easily recognized throughout Central America, the eastern lowlands of Mexico, and the West Indies (Map A). However, in a part of its range in South America, where *S. bipuncticeps* occurs in the same breeding sites, *macropus* is not so easily recognized. That species also has the disproportionately long hind femora typical of the *S. macropus* group, and its color (tawny brown and black) and markings are almost identical with those of *macropus*. What was believed to be *macropus* was collected over a pasture pond near Cali, Colombia recently, but when examined with a stereoscopic microscope it was found that 27 of the 35 were *S. bipuncticeps*.

The eggs, larvae, and puparia used in this study were obtained from adults collected in Guatemala and Nicaragua. A single female was taken in an open *Typha angustifolia* ? stand, elevation 1,475 meters, 35 kilometers southwest of Guatemala City on July 21, 1958. A series of 5 females and 7 males was captured in a roadside *Typha* marsh (probably *Typha domingensis* Pers. — see Standley and Steyermark, 1958), elevation 65.5 meters, 13 kilometers north of Managua on July 27, 1958; and another collection of 1 male and 3 females was made by sweeping cattail along the margin of a lake, elevation 492 meters, 74 kilometers north of Managua on July 28, 1958. Subsequent rearings could easily have been made from other areas which provided habitats of relatively open stands of cattail, unshaded grass-sedge meadows, and vegetation bordering ponds and small lakes. For example, flies of this species were collected at all 4 localities visited near San José, Costa Rica in June 1964, and they began to lay eggs the first day after capture.

In the laboratory, eggs were laid on the sides of the breeding jars, on short sections of cattail leaves, and on grass leaves in groups of 9 to 22, with the eggs side by side in the group (as in Figs. 4 and 9). They are almost milk-white when first laid but rapidly develop a characteristic light orange color. An egg mass observed before it was complete (while the female continued to oviposit) exhibited this range in color.

The larvae attacked and devoured the following snails: *Australorbis glabratus*, *Helisoma trivolvis*, *Physa* sp., *Lymnaea palustris*, *L. humilis*, and *Oxyloma retusa*. In the quarantine laboratory in Hawaii, they also destroyed *Lymnaea ollula*, L. (*Pseudosuccinea*) *columella*, and *Physa compacta* (Chock, et al, 1961). Third-instar larvae were offered several slugs, *Deroceras* laeve, which they almost entirely consumed, leaving only the sclerotized upper jaw and the small calcareous portion (vestigial shell) of the mantle. Larvae that were reared in isolation each killed and ate as many as 20 *H. trivolvis*. As with *S. caerulea*, some of the larvae died before completion of their development, and it was apparent that numbers of snails killed varied inversely with their size.

In order to obtain some idea of the size difference between a host snail and a larva, 2 third-instar *S. macropus* larvae that weighed 20.2 mg and 27.1 mg were each offered a *Helisoma trivolvis* snail. The 2 snails weighed (including the shell) 385.2 mg and 429.9 mg or almost 20 times more than the larvae (16 and 19 times respectively). Despite this difference in weight, the larvae attacked, easily killed, and fed upon the snails. Twenty-four hours later, both larvae and snails were weighed again. The larvae had gained 13.0 mg and 5.7 mg, while the 2 dead snails showed weight losses of 77.0 mg and 126.8 mg respectively. The discrepancy between loss of weight by the snails and weight gain by the larvae was attributed to loss of hemolymph by the snails, drying of the snail tissues, and defecation of ingested material by the larvae.

The duration of each larval instar was: first, 3 to 5 days; second, 2 to 5 days; third, 5 to 8 days (20 observations). Pupation time, the time from formation of the puparium to emergence of the

adult, ranged from 6 to 9 days (28 observations). Chock *et al.* (1961) reported similar but less variable development time in Hawaii: egg incubation time, 3 days; total larval period, 11 to 12 days; pupation time, 7 to 8 days; and preoviposition period, 4 days. Thus, the life cycle is completed every 22 to 24 days in Hawaii.

Four females obtained from rearings had preoviposition periods of 3 to 10 days, averaging 8.5 days. On 2 occasions, virgin females still in emergence vials 4 and 5 days after emergence laid groups of infertile eggs.

An interesting comparison of the effect of food quality on egg production can be made. Three females that had been fed the brewers' yeast and honey produced 196, 178, and 140 eggs, averaging only 2.1, 1.8 and 0.9 eggs per day, respectively. Two females whose diet was augmented with crushed snails (*H. trivolvis*) produced 395 and 323 eggs, averaging 4.3 and 5.2 eggs per day. This comparison indicates that protein material is needed for continued egg production, since all the females laid roughly the same number of eggs the first 2 weeks after their emergence. Although the females that received the yeast and honey diet lived longer, their egg production dropped off markedly.

The longevity of 5 laboratory-reared females ranged from 28 to 155 days; that of 7 reared males ranged from 41 to 163 days.

Description of Immature Stages

Egg: (Fig. 4). Cream white usually with orange tinge. Length 1.17 to 1.28 mm ($\bar{X} = 1.24$ mm); width 0.34 to 0.37 mm = 0.35 mm). Single broad, transverse tubercle shielding micropyle dorsally, usually tubercle bearing longitudinal dorsal depression, as in *S. caerulea* (Fig. 3, dd). Wide longitudinal grooves (Fig. 4, lg) on each side dorsolaterally bordered by prominent longitudinal ridges. Central area (Fig. 4, ca) between mesal ridges and surface in grooves irregularly reticulate. End opposite micropyle with low, conical, minutely punctate tubercle (Fig. 4, ht). Ventral surface of chorion regularly reticulate. (Based on 25 specimens, Guatemala City.)

First-instar larva: White; integument transparent. Length 1.6 to 4.0 mm ($\bar{X} = 2.5$ mm); width 0.2 to 0.6 mm = 0.4 mm). Closely resembling first-instar *S. caerulea* larva. Cephalopharyngeal skeleton (as Fig. 24), length 0.32 to 0.41 mm ($\bar{X} = 0.37$ mm); with paired mouthhooks, bifid anteriorly, articulating with ventral arch below and with fused hypostomal-pharyngeal sclerite posteriorly. Distribution of tubercles and hair patches on abdominal segments as *S. caerulea*. Posterior spiracular disc (as Fig. 17) with 2 pairs of prominent lobes; ventral pair elongate; ventrolateral pair elongate, appearing 2-segmented. Two spiracular plates, each with B-shaped spiracular opening and 4 radiate interspiracular bristles. (Based on 26 specimens, Guatemala City.)

Second-instar larva: Yellowish-white, often with middorsal stripe prominent and indistinct oblique stripes dorsolaterally on segments 5 to 9 (similar to Fig. 11, as); integument transparent. Length 2.8 to 8.7 mm ($\bar{X} = 4.7$ mm); width 0.5 to 1.5 mm ($\bar{X} = 0.8$ mm). Resembling second-instar *S. caerulea* larva. Cephalopharyngeal skeleton (as Fig. 26), length 0.58 to 0.63 mm = 0.61 mm); with paired mouthhooks, each with 2 or 3 pigmented, slightly decurved accessory teeth below hook portion. Segment 2 with anterior spiracles on each side posterolaterally, each spiracle bearing 4 to 6 rudimentary papillae. Distribution of hair patches and tubercles on

abdominal segments as *S. caerulea*. Posterior spiracular disc (as Fig. 15) with 2 pairs of prominent lobes: ventral pair elongate; ventro-lateral pair appearing 2-segmented. Two spiracular plates, each with 4 palmately-branched interspiracular bristles alternating with 3 elongate spiracular openings. (Based on 31 specimens, Guatemala City.)

Third-instar larvae: Yellow or orange-white with obscure middorsal and faint oblique stripes; integument transparent. Length 7.8 to 13.5 mm ($\bar{X} = 11.3$ mm); width 1.4 to 3.1 mm ($\bar{X} = 2.4$ mm). Closely resembling third-instar *S. caerulea* larva. Cephalopharyngeal skeleton (as Fig. 28), length 0.85 to 0.90 mm ($\bar{X} = 0.87$ mm); with paired mouthhooks, each bearing 3 darkly pigmented, slightly decurved accessory teeth (as Fig. 34). Segment 2 with pair of anterior spiracles, 1 on each side posterolaterally; each spiracle (similar to Fig. 46) with 4 to 7 papillae distally. Distribution of hair patches and tubercles on abdominal segments as in *S. caerulea*. Posterior spiracular disc (as Fig. 13) with 2 pairs of prominent lobes; ventral pair elongate, lanceolate; ventrolateral pair appearing 2-segmented; lateral, dorsolateral, dorsal lobes usually low, conical protuberances. Two spiracular plates; each plate with 4 palmately-branched interspiracular bristles alternating with 3 elongate sinuous spiracular slits. (Based on 23 specimens, Guatemala City.)

Puparium: (Figs. 56, 57). Brown dorsally with faint oblique markings, stramineous ventrally or wholly brown-black with irregular light markings ventrally and laterally, posterolateral margins of cephalic caps with light dorsoventral stripe. Length 5.6 to 8.00 mm ($\bar{X} = 6.5$ mm); width 2.5 to 3.2 mm ($\bar{X} = 2.7$ mm). Most closely resembling puparium of *S. caerulea* in size and shape. Upturned posterior end forming obtuse angle of 100 to 130° with longitudinal axis of puparium. (Based on 30 specimens, Guatemala City.)

SEPEDON GUATEMALANA Steyskal

Wasman Jour. Bio. 8 (3) : 293-95. 1950.

Sepedon guatemalana (4.5 to 6.5 mm long) is the only species of the predominantly South American *lindneri* group (Steyskal, 1950) that ranges so far northwestward into Central America. Species of this group differ from most species of *Sepedon* in possessing an oval dark spot, elongated vertically, in each ventrolateral corner of the face. This characteristic facial spotting makes *S. guatemalana* quite distinctive throughout its known range. However, if it occurs also in Panama, or if *S. isthmi* ranges into Costa Rica, neither will seem at all distinctive in the region of overlap. One must expect the same difficulty in identifying living flies there as in regions where 2 or 3 species of this group occur sympatrically in Brazil.

This species has been known only from the 2 localities mentioned in the original description — Los Amaté, Guatemala and Chinandega, Nicaragua (Steyskal, 1950). As a result of the present study, 3 additional localities can be included, extending the known range appreciably (Map A). The first record of its occurrence in Mexico is based upon a collection made 3.5 kilometers southeast of Las Cruces, Chiapas (elevation 732 meters), on July 16, 1958. A second Guatemalan locality is 2.1 kilometers east of Barberena,

Santa Rosa (elevation 1,341 meters), where 2 males and 1 female were collected July 23, 1958. Four males and 1 female were collected at San Antonio-Desamparados, just south of San José, Costa Rica (elevation 1,160 meters), June 16, 1964.

Sepedon guatemalana was encountered in moist, upland meadows (Barberena) and open wet areas. The adults captured at Las Cruces were taken by sweeping dense mats of water hyacinth (*Eichornia crassipes* Mart.) Solms. which clogged a slow-flowing stream. Shaded areas of the stream failed to yield flies, even though considerable effort was made surveying these areas. The collecting site in Costa Rica was an open, sunlit marsh characterized by the accumulation of much soft, spongy organic matter which gave treacherous footing.

Inmature stages upon which the descriptions were based were obtained through laboratory rearings. The progeny of 2 females from the Las Cruces locality provided all the material. No eggs, larvae, or puparia were observed in the field.

- Females confined in laboratory breeding jars deposited eggs on the sides of the jar near the moss. Eggs were seldom placed on sections of grass and *Typha* leaves that were placed vertically. On 2 occasions the act of oviposition was observed, and the process appeared identical to that of *S. macropus*. The female, poised with her extended abdomen, rapidly extruded an egg about 2/3 its length, held it in this position for a few seconds, then placed it gently on the surface. Before the next egg appeared, the female touched the lateral surface of the egg she had just laid and the substratum. The abdomen was then elevated and another egg was extruded.

Even though eggs were laid in a regular sequence, hatching of a group of eggs was observed to proceed in an irregular manner, as in other *Sepedon* species.

Eggs hatched in 4 to 4 1/2 days (8 observations) and the newly-emerged larvae were active and readily attacked small individuals of *Australorbis glabratus*, *Helisoma trivolvis*, and *Physa* sp. Based on 15 observations, the first and second stadia occupied 3 to 4 days, with a larva daily consuming 1 or 2 *H. trivolvis*, 4 to 6 mm in diameter. The third stadium was completed in 5 to 7 days, and again 1 or 2 snails were attacked and destroyed each day. As with other known species of the genus, the larva attacked and killed the host snail quickly and then fed upon the fresh tissue.

- Although first- and second-instar larvae do not differ in general appearance from other known *Sepedon* larvae of these stages, the third-instar larva (Figs. 11, 12) is strikingly different. The color pattern on the dorsum of the larva, especially the broad, inverted V-shaped mark on the fifth body segment, is distinctive. Perhaps this pattern is a general characteristic of the *lindneri* group.

Pupation time was from 7 to 11 days in the laboratory (15 observations).

The preoviposition period, obtained in 2 instances, was 10 and 30 days. In another instance, a female which lived 28 days was seen mating on several occasions but died without laying any eggs.

Longevity of adults in the laboratory ranged from 28 days (a female and 2 males) to 169 days (2 males).

Description of Immature Stages

Eggs: Orange-white, closely resembling eggs of *S. macropus* (Fig. 4). Length 1.26 to 1.40 mm ($\bar{X} = 1.32$ mm); width 0.25 to 0.35 mm ($\bar{X} = 0.30$ mm). Broad transverse protuberance shielding micropyle dorsally. Shallow longitudinal grooves (Fig. 4, lg) on each side dorsolaterally demarcating a reticulate central area (as Fig. 4, Ca). **Tube**rcle at end opposite micropyle more conical than in *S. macropus*, with coarse punctations on its surface. Lateral and ventral surfaces regularly reticulate. (Based on 15 specimens.)

First-instar larva: White; integument transparent. Length 1.4 to 3.5 mm ($\bar{X} = 2.2$ mm); width 0.2 to 0.5 mm ($\bar{X} = 0.3$ mm). Resembling first-instar larva of *S. caerulea* and allies. Cephalopharyngeal skeleton (as Fig. 24), length 0.24 to 0.28 mm ($\bar{X} = 0.25$ mm). Segments 5 to 10 each with a single transverse dorsal hair patch. Posterior spiracular disc with 2 pairs of prominent lobes: ventral pair elongate; ventrolateral pair apparently 2-segmented (as Fig. 17). Two spiracular plates, each plate with B-shaped spiracular opening and 4 palmately-branched interspiracular bristles. (Based on 14 specimens.)

Second-instar larva: White with dusky shading around dorsal hair patches and lateral tubercle groups; integument transparent. Length 3.3 to 5.8 mm ($\bar{X} = 4.3$ mm); width 0.5 to 1.3 mm ($\bar{X} = 0.8$ mm). Resembling *S. caerulea* and allies in appearance. Cephalopharyngeal skeleton (as Fig. 26), length 0.43 to 0.47 mm ($\bar{X} = 0.45$ mm); each mouthhook with 3 accessory teeth; hypostomal and pharyngeal sclerites fused. Anterior spiracles with 4 to 5 poorly developed papillae. Dorsal hair patches, lateral tubercles, and ventral tubercles on segments 5 through 10 as in *S. caerulea*. Posterior spiracular disc (as Fig. 15), with prominent ventral and ventrolateral lobes. Two spiracular plates, each plate with 3 elongate-oval spiracular slits and 4 palmately-branched interspiracular bristles. (Based on 18 specimens.)

Third-instar larva: (Figs. 11, 12). Yellowish-white with incomplete middorsal stripe (Fig. 11, mds); broad, truncate, dark marking dorsally on segment 5; oblique stripes (Fig. 11, os) running from posterodorsal to anterolateral areas of segments 6 to 9; lateral tubercle groups with dark shading between tubercles; integument translucent. Length 6.4 to 10.8 mm ($\bar{X} = 8.9$ mm); width 1.2 to 2.3 mm ($\bar{X} = 1.8$ mm). Slightly smaller than *S. caerulea*, but resembling the third-instar larva of that species in general features. Cephalopharyngeal skeleton (similar to Fig. 28), length 0.71 to 0.77 mm ($\bar{X} = 0.75$ mm), each mouthhook bearing 4 accessory teeth beneath hook (Fig. 35), the uppermost accessory tooth deeply pigmented, decurved, more developed than other teeth; ventral arch as Fig. 32. Anterior spiracles (Fig. 48), bearing 5 to 6 small papillae on slightly inflated apical end of spiracle. Posterior spiracular disc (as Fig. 13) with 2 pairs of prominent lobes: ventral pair elongate, lanceolate; ventrolateral pair elongate, appearing 2-segmented. Lateral, dorsolateral, and dorsal lobes inconspicuous protuberances. Two spiracular plates, each with 3 sinuous slits and 4 palmately-branched interspiracular bristles serving as float hairs. (Based on 17 specimens.)

Puparium: (Figs. 54, 55). Brown with light V-shaped marking anterodorsally. Length 4.7 to 5.3 mm ($\bar{X} = 4.9$ mm); width 2.0 to 2.4 mm ($\bar{X} = 2.2$ mm). Dorsal hair patches with bristles appressed to puparium surface, tubercles appearing as shagreen areas. Posterior disc on upturned posterior end forming angle of 110 to 120° with longitudinal axis of puparium. Puparium not constricted in middle as *S. tenuicornis* (Fig. 53), posteroventral portion but slightly inflated, in lateral view (Fig. 55) appearing more angular than others of genus. (Based on 14 specimens.)

SEPEDON FUSCIPENNIS Loew

Wien. ent. Monatsch. 3:209. 1859

This large, brown fly (6 to 8 mm body length) is widely distributed in North America except in the Southwestern States, Mexico, and Central America, and perhaps in poorly collected regions of northern Canada (Map **B**). Being common and conspicuous, it is probably better known to more entomologists than any other Nearctic species of Sciomyzidae. Its extensive range overlaps that of the superficially similar *S. praemiosa* in northwestern parts of the United States and southwestern Canada, and *S. fuscipennis* is replaced by that species in the Southwest. A subspecies, *S. f. floridensis*, has been described from Florida (Steyskal, 1950).

The larvae and puparia of *S. fuscipennis* also seem better known than those of any other Nearctic sciomyzid. They were first described by Needham and Betten (1901) and later by Dyar (1902), Johannsen (1935), and Peterson (1953). Five or 6 years before the first of these reports, puparia were collected in nature and identified by the adults that emerged from them by C. A. Hart (unpublished). The Illinois Natural History Survey collection has adults pinned with their empty puparia collected in the Survey of Illinois River System, 1895-96.

These were the first *Sepedon* larvae to be recognized as snail killers. They were collected in marshes in the Matanuska Valley, Alaska and in Oakland County, Michigan. They were fed by adding living individuals of *Lymnaea palustris*, *L. emarginata*, *L. stagnalis*, *Helisoma* sp., and *Oxyloma decampi* to their rearing dishes. The larvae pupated during June, July, and August, and adult flies emerged from these puparia 7 to 9½ days after pupation (Berg, 1953).

The larvae, pupae, and adults used to initiate rearings of this species were obtained from widely separated areas. Localities near Ithaca included Bull Pasture Pond (elevation 975 feet), Cornell University Golf Course, 1.4 miles northeast of Ithaca; Inlet Valley Marsh (Larch Meadows) (elevation 410 feet), about 1.6 miles south of Ithaca; and White Church Marsh (elevation 974 feet), 3.2 miles south of Brooktondale, New York. To investigate possible geographic variations in natural history and morphology, rearings were also made from adults collected at the Town Reservoir, 0.6 miles north of Hardinsburg, Breckinridge Co., Kentucky; and at Ellerslie Slough, about 6 miles south of Edmonton, Alberta, Canada; and from all stages of the life cycle (including eggs) collected at Douglas Lake, Cheboygan County, Michigan. No geographic variations were noted in this material.

Adults of this species are common in open, unshaded cattail marshes where they rest in their characteristic posture on emergent vegetation. They also have been encountered in low vegetation along the margins of lakes and ponds.

Egg masses were observed on cattail and other emergent vegetation in the field. They occur most commonly 10 to 30 cm above the water or soil surface, but some were discovered as high as 1.5

meters above the water. Although masses of 35 to 45 eggs were obtained in the laboratory, those collected in nature usually contained 10 to 25 eggs. Eggs laid in the laboratory hatched 4 to 5 days later.

First-instar larvae were fed small *Helisoma trivolvis*, *Australorbis glabratus*, and *Physa* sp. Groups of 4 to 7 small, first-instar larvae often were seen feeding in a single snail. On one occasion, cessation of the snail's heart beat occurred 13 minutes after a larva attacked.

Based on 21 observations, the duration of the larval stadia was: first, 2 to 3 $\frac{1}{2}$ days; second, 3 to 4 days; third, 6 to 8 days.

As the third stadium was reached, the large larvae attacked and destroyed individuals of *H. trivolvis* and *A. glabratus*, 10 to 14 mm in diameter. Usually the soft parts of 4 or 5 of these snails were wholly or partially consumed during this stadium. Each larva became distinctly yellow because of the increased size and color of fat bodies beneath the transparent integument from 24 to 36 hours before formation of the puparium. Puparia were formed on the moist sand in the rearing jars and just beneath the water's surface. Pupation time occupied 7 to 8 days (15 observations). Two normal adults emerged from partially submerged puparia.

This species probably overwinters in the adult stage. Capture records in the Ithaca area range from March 27 to November 6. Adult flies taken in early spring (March 30, April 6) have frayed wing margins and broken or missing setae. Few puparia have been found in winter, and those collected at that time have invariably failed to produce adults although several have produced ichneumonid wasps. On the other hand, puparia found in late May and early June (in company with mature larvae) contain viable pupae. Also, 2 females captured October 15, 1955 survived in the laboratory until the middle of March (March 16 and 19, 1956).

The number of generations per year produced by this species cannot be stipulated. Throughout the summer, all stages of the life cycle may be collected with some effort. This fact, coupled with the observed variation in preoviposition period of the female and the long period during which each female may continue to oviposit, indicates that a number of overlapping generations develop. In the laboratory, females have continued to lay viable eggs after their daughters matured and began to lay theirs. Thus, it is impossible to specify the number of generations per year.

Parasitoid ichneumonid wasps of several species have been obtained from puparia either collected in nature or formed by larvae collected in nature. Since all immature stages were held in closed containers after collection, these wasps evidently oviposit in the larvae. The parasitized larvae appeared normal, attacked snails in the usual manner, and formed apparently normal puparia from which the parasitoid wasps emerged. The species of ichneumonid wasps associated with *S. fuscipennis* have been identified and tentatively designated by H. K. Townes, Jr. as *Eriplanus* sp. A, *Eriplanus* sp. B, *Mesoleptus declivus* (Provanch.), and *Mesoleptus* sp. A.

Many eggs of *S. fuscipennis* found on emergent vegetation produced another parasitoid wasp, a member of the Trichogrammatidae. These wasps were tentatively identified as *Trichogramma* sp. by H. E. Evans.

The distinctive diapiiid *Phaenopria popei* Muesebeck was described from material reared by Berg from puparia of *S. fuscipennis* collected at Sodon Lake, Oakland County, Michigan (Muesebeck, 1949). We have not obtained this wasp again from any of the hundreds of *Sepedon* puparia held for emergence since the type material was reared. However, it has been reared from puparia of both *Dictya* and *Elgiva*, and a laboratory-reared generation showed that adults may emerge only 18 days after oviposition directly into a *Dictya* puparium (Knutson and Berg, 1963).

Description of Immature Stages

Egg: (Fig. 2). Silver to plumbeous gray. Length 1.08 to 1.28 mm (= 1.19 mm); width 0.24 to 0.31 mm (X = 0.27 mm). Two to 4 irregular tubercles shielding micropyle dorsally; dorsal surface with 5 to 8 prominent interrupted, sharp longitudinal ridges, these often anastomosing; grooves between ridges punctate. End opposite micropyle with finely punctate hemispherical tubercle. Ventral surface regularly reticulate. (Based on 20 specimens; Bull Pasture Pond.)

First-instar larva: White; integument transparent. Length 1.4 to 3.7 mm (= 2.9 mm); width 0.3 to 0.7 mm (X = 0.5 mm). Not visibly different from first-instar larva of *S. caerulea* in general appearance. Cephalopharyngeal skeleton (as Fig. 24), length 0.29 to 0.37 mm (X = 0.33 mm) with paired bifid mouthhooks articulating with combined hypostomal-pharyngeal sclerite. Segments 5 through 10 with paired dorsal hair patches. Posterior spiracular disc (as Fig. 17) with paired elongate ventral lobes and paired, 2-segmented ventrolateral lobes. Two spiracular plates, each plate with B-shaped spiracular slit and 4 groups of palmately-branched interspiracular processes. (Based on 11 specimens; Inlet Valley.)

Second-instar larva: White to light tan; integument transparent. Length 5.0 to 8.0 mm (= 6.4 mm); width 1.0 to 1.5 mm (= 1.2 mm). Resembling the second-instar larva of *S. caerulea* and others possessing the lanceolate ventral lobes of posterior spiracular disc. Cephalopharyngeal skeleton (as Fig. 26) length 0.55 to 0.66 mm (= 0.57 mm), with paired mouthhooks, each bearing 3 decurved accessory teeth below hook; pharyngeal part of fused hypostomal-pharyngeal sclerite usually light with pigmented longitudinal stripe. Anterior spiracles with 4 to 6 rudimentary papillae. Dorsal hair patches, lateral tubercles, ventral tubercle groups as *S. caerulea* second-instar larva. Posterior spiracular disc (as Fig. 15) with paired elongate ventral lobes and paired, 2-segmented ventrolateral lobes. Two posterior spiracular plates, each bearing 3 elongate-oval slits with 4 palmately-branched interspiracular bristles alternating with spiracular openings. (Based on 15 specimens; Inlet Valley.)

Third-instar larva: Yellowish white to light tan; integument transparent. Length 8.0 to 12.0 mm (X = 9.7 mm); width 1.2 to 2.4 mm (X = 1.8 mm). Resembling in general appearance third-instar larvae of *S. caerulea*. Cephalopharyngeal skeleton (Fig. 23), length 0.80 to 0.92 mm (X = 0.87 mm); with paired mouthhooks, each bearing 3 or 4 lightly pigmented, strongly decurved accessory teeth (as Fig. 36); pharyngeal sclerite lightly pigmented with longitudinal pigmented line broadening at anterior end. Anterior

spiracles (as Fig. 49) at posterolateral border of segment 2, each spiracle bearing 4 to 7 papillae on expanded apical portion, body of spiracle only slightly constricted basally. Dorsal hair patches, lateral tubercles groups, ventral transverse **tubercle** groups as in *S. caerulea*. Posterior spiracular disc (as Fig. 13) with paired lanceolate ventral lobes and 2-segmented ventrolateral lobes; lateral, dorsolateral, dorsal lobes low protuberances or obsolescent. Two spiracular discs; each with 3 elongate, sinuous slits, 4 palmately-branched interspiracular bristles serving as float hairs and alternating with spiracular openings. (Based on 35 specimens; Inlet Valley, 8; White Church, 11; Hardinsburg, 16.)

Puparium: (Figs. 50, 51). Light brown dorsally, stramineous ventrally with scattered brown speckling, bearing on each side 5 reddish brown spots, often with longitudinal brown stripe connecting these spots; or wholly blackish brown. Length 4.8 to 5.8 mm ($X = 5.5$ mm); width 2.5 to 3.2 mm = 2.8 mm). Anterior end blunt, body globose, inflated posteroventrally. Posterior end upturned, forming an obtuse angle of 110 to 120° with longitudinal axis of body. (Based on 19 specimens; Bull Pasture Pond.)

SEPEDON PRAEMIOSA Giglio-Tos

Boll. Mus. Zool. Anat. Comp. Reale Univ. Torino.
8 (no. 158). 1893.

This large tawny brown species (6 to 8.5 mm long) is widely distributed in western North America. Its known range extends from southern Saskatchewan and Alberta, through North and South Dakota and western Kansas, south to Oaxaca, Mexico, and west to the Pacific Coast (Map **B**). To the east, north, and northwest of its range, *S. praemiosa* seems to be replaced by *S. fuscipennis*, which occurs in Alaska and is common in the open marshes and sloughs of central Saskatchewan and Alberta.

The adults that supplied immature stages for rearings were obtained from localities at the extreme ends and an intermediate point in the known range. One collection was made at Cypress Lake, 16 miles south of Cypress Provincial Park, Maple Creek, Saskatchewan on July 2, 1957. Another was made 9.7 kilometers north of Oaxaca, Mexico, along Federal Route 190 (elevation 1,525 meters), on August 10, 1958. Finally, living flies collected in Riverside and Los Angeles Counties, California were provided by E. C. Bay. They were collected in January and February 1961, in marshes bordering the Santa Ana River at Riverside and in the Rio Hondo water spreading grounds of the Los Angeles County Flood Control District in Montebello, California. All collections were made in open, unshaded, wet areas. The Cypress Lake material was taken in a heavy stand of *Typha latifolia* L., and *S. praemiosa* was collected in about equal numbers with *S. fuscipennis*. The Oaxaca locality was a wet area along the road which had a mixed stand of sedges on its margins. *S. praemiosa* was uncommon (only 2 males and 1 female were taken), but *Dictya abnormis* Stey., *Hoplodictya spinicornis* (Lw.), and *Pherbellia* sp. were collected in greater numbers.

No eggs were encountered during field collections, but they were readily obtained from females in laboratory breeding jars. They

were laid on the sides of the jar or on sections of grass or *Typha* leaves in a manner similar to that of *S. fuscipennis*. Eggs produced by wild-caught and laboratory-reared females from all 3 localities exhibited a characteristic spotting of the egg chorion (Fig. 1). These irregular, plumbeous spots became evident on the chorion surface 24 to 36 hours after the eggs had been laid.

In the laboratory, eggs hatched in $3\frac{1}{2}$ to 5 days (9 observations). First-instar larvae fed readily on small (2 to 4 mm diameter) *Helisoma trivolvis*, *Physa* sp., and *Australorbis glabratus*. Based on 11 observations, first and second larval stadia were each 3 to 6 days in duration, the third stadium was 6 to 8 days. Larvae were observed to destroy 14 to 17 snails during the 3 stadia, the number evidently depending upon the sizes of snails.

Progeny of the adults collected in California in winter were reared throughout late winter and spring at Cornell University. Besides attacking the snail species used in previous rearings, the larvae destroyed *Lymnaea palustris*, *L. humilis*, and *Aplexa hypnorum*. Larvae of *S. praemiosa* were taken to Hawaii and Australia the following August to see whether they would attack the snail hosts of liver fluke. They killed and consumed *Lymnaea ollula* Gould in Hawaii and *L. tomentosa* Pfeiffer in Australia.

Pupation time ranged from 5 to 9 days (14 observations). But the minimum number of days was obtained at Louisville, Kentucky, in August when temperatures were appreciably higher (33 to 36° C) than those encountered in the laboratory at Ithaca.

Preoviposition periods of 5, 7, and 34 days were observed. Two females obtained from the Oaxaca material and fed the brewers' yeast, honey mixture and crushed snail produced totals of 432 and 556 eggs, averaging 4.7 and 5.6 eggs per day.

This species breeds throughout the year in southern California, and there has been no indication of diapause (no delay in the sequence of events in the life cycle) in the successive generations reared in laboratories at Ithaca; Louisville, Kentucky; Honolulu, Hawaii; or Adelaide, Australia. In northern parts of its range, the species probably survives the winter as hibernating adult flies. These may retain their eggs, as observed in *S. sphaecea* and other species, as a response to cooler temperatures or decreasing day length at higher latitudes in autumn.

The longevity of laboratory-reared flies ranged from 69 to 140 days (69 to 134 for 4 females; 86 to 140 for 5 males).

Description of Immature Stages

Egg: (Fig. 1). Cream white to gray white with irregular lead-colored spots on dorsal surface. Length 1.40 to 1.48 (\bar{X} = 1.44 mm); width 0.35 to 0.38 (\bar{X} = 0.36 mm). Three to 5 small truncate tubercles shielding micropyle dorsally. Dorsal surface with 8 to 15 anastomosing longitudinal ridges, ridges near micropylar end becoming discrete tubercles. Grooves between ridges irregularly punctate. End opposite micropyle with low hemispherical tubercle bearing fine punctations. Ventral surface regularly reticulate. (Based on 20 specimens: Cypress Lake, 10; Oaxaca, 10.)

First-instar larva: White with dusky shading dorsally; integument transparent. Length 1.9 to 4.7 mm (\bar{X} = 2.8 mm); width 0.3 to 0.7 mm (\bar{X} = 0.4 mm).

mm). Resembling first-instar larva of *S. caerulea*. Cephalopharyngeal skeleton (as Fig. 24), length 0.31 to 0.40 ($\bar{X} = 0.35$ mm), with bifid mouthhooks articulating ventrally with ventral arch and posteriorly with fused hypostomal-pharyngeal sclerite. Segments 5 to 10 each with 2 pairs of dorsal hair patches, lateral tubercle groups, ventral transverse tubercles, as in *S. caerulea*. Posterior spiracular disc (as Fig. 17) with paired elongate ventral lobes, 2-segmented ventrolateral lobes; lateral lobes inconspicuous, dorsolateral and dorsal lobes forming rounded dorsal border of disc. Two spiracular plates, each with B-shaped opening and 4 palmately-branched interspiracular bristles. (Based on 23 specimens: Cypress Lake, 11; Oaxaca, 12.)

Second-instar larva: White with irregular shading dorsally; integument transparent. Length 2.7 to 8.2 ($\bar{X} = 5.3$ mm); width 0.6 to 1.7 mm ($\bar{X} = 1.08$ mm). Closely resembling *S. caerulea* second-instar larva in appearance. Cephalopharyngeal skeleton (as Fig. 26), length 0.131 to 0.66 mm ($\bar{X} = 0.62$ mm), with paired mouthhooks; each bearing 2 or 3 decurved, accessory teeth beneath hook; posterior margins of mouthhooks articulating with fused hypostomal-pharyngeal sclerite; ventral margins of mouthhooks articulating with ventral arch beneath. Segment 2 with anterior spiracles on each side posterolaterally, each with 5 to 8 inconspicuous papillae apically. Segments 5 to 10 with 2 pairs of dorsal hair patches, 3 lateral tubercles on each side, 4 tubercles in transverse group ventrally. Posterior spiracular disc (as Fig. 15) with paired elongate ventral lobes and paired elongate, 2-segmented ventrolateral lobes; lateral, dorsolateral, dorsal lobes inconspicuous, forming rounded crescentic dorsal border of disc. Two spiracular plates each with 3 elongate-oval openings and 4 palmately-branched interspiracular processes. Anal proleg on anterior margin of anal plate inconspicuous. (Based on 20 specimens: Cypress Lake, 6; Oaxaca, 14.)

Third-instar larva: Yellowish white; integument transparent. Length 6.0 to 13.2 mm ($\bar{X} = 10.2$ mm); width 1.6 to 2.8 mm ($\bar{X} = 2.2$ mm). Closely resembling the third-instar larva of *S. caerulea* and *S. fuscipennis*, in general appearance. Cephalopharyngeal skeleton length 0.86 to 0.91 mm ($\bar{X} = 0.87$ mm), as Fig. 28; paired mouthhooks, each usually with 3 or 4 decurved accessory teeth (similar to Fig. 36) beneath hook; pharyngeal sclerite dark brown often with pigmented area (Fig. 28, PA) at posterodorsal margin. Segment 2 with anterior spiracles (Fig. 49) laterally near posterior border, each with 5 to 8 round papillae on margin of slightly expanded apical portion. Segments 5 to 10 with 2 pairs of dorsal hair patches, lateral tubercle group on each side, ventral transverse group as in *S. caerulea*. Posterior spiracular disc (as Fig. 13) with paired lanceolate ventral lobes and 2-segmented ventrolateral lobes; lateral, dorsolateral, dorsal lobes low conical protuberances. Two spiracular plates, each with 3 spiracular openings and 4 palmately-branched float hairs. Anal proleg inconspicuous, with fine spinules on posterodorsal surface. (Based on 22 specimens: Cypress Lake, 11; Oaxaca, 11.)

Puparium: Light brown dorsally, middorsal stripe evident; light yellow ventrally; opaque. Length 5.5 to 6.5 mm ($\bar{X} = 5.8$ mm); width 2.5 to 3.1 mm ($\bar{X} = 2.7$ mm). Similar to *S. fuscipennis* in general appearance, but often not so inflated and globose posteroventrally (c.f. Figs. 50, 51). Dorsal cephalic cap light yellow posteriorly; dark, irregular shading on posterolateral edges. Dorsal hair patches visible on segments 5 to 10, hairs appressed. Lateral and ventral tubercle groups appearing as shagreen areas, lateral groups lacking reddish brown or brown shading, as in *S. fuscipennis*. Ventral surface usually without scattered brown speckling. Upturned

posterior end forming 100 to 140° angle with longitudinal axis, bearing contracted disc with conspicuous spiracular plates above disc surface, float hairs appressed to tube bearing plates. Anal plate dark brown, slightly bilobed. (Based on 20 specimens; Cypress Lake, 13; Oaxaca, 7.)

SEPEDON TENUICORNIS Cresson

Trans. Amer. Ent. Soc. 46:84-85. 1920.

Sepedon tenuicornis is another large (6 to 8 mm body length) brown fly, similar in size and color to *S. fuscipennis* and *S. praemiosa*. It differs from those species in its long, narrow antennae, the second segment of which is nearly 5 times as long as wide in lateral view.

The species is sympatric with *S. fuscipennis* throughout its range in the central and eastern half of the United States and southern Ontario (Map C). However, *S. tenuicornis* is not nearly as common as *fuscipennis*, and its range is much less extensive northward and westward. It breeds in some extensive wetlands also occupied by *S. fuscipennis*, but evidently avoids much competition with that species by choosing a different habitat. Whereas *tenuicornis* occurs in shaded, swampy sections, *fuscipennis* is found in open, sunlit marshes.

The immature stages described were reared from adults collected in a swamp 6.2 miles east of Barrie Corners, Orleans Co., New York, on August 4, 1957, and a swamp on Benson Avenue, Minetto, Oswego Co., New York, on August 18, 1957. Larvae were obtained in a wooded section of the Inlet Valley marsh locality (see *S. fuscipennis*) on June 13, 1958. Puparia were also collected at the Benson Avenue locality. All 3 of the areas where adults were taken are protected by large trees (*Acer rubrum* L.). Shrubs (*Cephalanthus occidentalis* L. and *Cornus stolonifera* Michx.) were also present at the Barrie Corners locality. At Minetto, *S. fuscipennis* adults were common in an exposed, unprotected part of the area. The *S. tenuicornis* adults and puparia were collected in shaded parts by sweeping thick stands of bur-reed (*Sparganium americanum* Nutt.).

Captured females placed in breeding jars oviposited 5 to 7 days later. The eggs were deposited on the sides of the jar and on short sections of *Typha* leaves. They were not laid in the uniformly parallel pattern (as Fig. 1) observed in *S. fuscipennis*, *S. praemiosa*, and other species; groups containing 3 to 7 eggs were most often seen. Eggs obtained from breeding jars hatched 4 to 4½ days later (3 observations).

First-instar larvae were offered small (2 to 4 mm) *Helisoma trivolvis* which they attacked and consumed quickly. The first and second stadia were each 3 to 5 days in duration (9 observations). During the second stadium, larvae killed and fed on *H. trivolvis*, *Australorbis glabratus*, and *Physa* sp. The third-instar larvae also fed on snails of these species, killing them quickly and devouring the fresh, soft tissues. The third stadium occupied 4 to 6 days (9 observations). The period from formation of the puparium to emergence of the adult was 10 to 11 days (6 observations).

To ascertain the total number of snails a single larva could kill, 8 larvae were segregated and each was offered 4 snails (*H. trivolvis*) daily. First-instar larvae were given snails 2 to 4 mm in diameter and second- and third-instar larvae were offered larger snails (usually 5 to 10 mm in diameter). Only 3 larvae completed their development. One larva destroyed 11 snails while each of the others killed 12. Each larva consumed a snail per day during its development.

As larval feeding terminates and pupation approaches, the mature larva leaves the water or moist substrate and crawls up the leaves and stems of emergent vegetation. The puparium is formed above the water and is firmly attached to the leaf or stem with a mucilaginous fluid secreted by the larva.

Fourteen puparia were found on the leaves of bur-reed at the Minetto locality. These puparia were firmly attached to the leaves and were 2 to 93 cm above the water surface (average height was 51 cm). This tendency to form the puparium above the water or substratum was observed in the laboratory rearings. Puparia were invariably found attached to the bottom of the rearing jar cork.

Capture dates of adults vary from May 2 (Cresson, 1920) to September 12, 1956 (Neff). Mature larvae taken at Inlet Valley on June 13, and puparia taken at Minetto on August 18, which produced adults August 30, suggest this species overwinters as an adult.

A single puparium collected February 10, 1955 produced a parasitoid wasp, *Eriplanus* sp. (determined H. K. Townes, Jr.).

Adult longevity records in the laboratory ranged from 129 to 256 days (from September 12 to April 27).

Adults collected at Barrie Corners on September 12, 1956 failed to mate and produce eggs in rearing jars. In order to subject these flies to seasonal change, they were placed outdoors on October 6. On November 7, as food was being added to the jar, the remaining males persistently attempted to mate with the females. The females were just as persistent in their resistance.

First generation females failed to produce eggs in the laboratory, and information on preoviposition period and egg production was not obtained.

Description of Immature Stages

Egg: (Fig. 5). Grayish white with plumbeous shading dorsally. Length 1.25 to 1.40 (\bar{X} = 1.33 mm); width 0.28 to 0.42 mm (\bar{X} = 0.35 mm). Two or 3 small, truncate tubercles shielding micropyle dorsally. Longitudinal grooves anastomosing, with transverse grooves dividing ridges into elongate tubercles and irregular projections. End opposite micropyle bearing low, rounded tubercle with roughened surface. Ventral surface regularly reticulate. (Based on 11 specimens: Minetto.)

First-instar larva: White with dusky shading dorsally; integument transparent. Length 1.6 to 3.0 mm (\bar{X} = 2.1 mm); width 0.3 to 0.5 mm (\bar{X} = 0.3 mm). Resembling the first stage larva of *S. caerulea* in general aspects. Cephalopharyngeal skeleton (as Fig. 24) length 0.36 to 0.41 mm (\bar{X} = 0.39 mm), with paired mouthhooks, each bearing bifid hook anteriorly, articulating with ventral arch below and posteriorly with fused hypostomal-pharyngeal sclerite. Segments 5 to 10 each with 2 pairs of dorsal hair

patches, lateral **tubercle** groups, ventral transverse **tubercle** group. Posterior spiracular disc (Fig. 17) with paired elongate ventral lobes, 2-segmented ventrolateral lobes, lateral lobes not developed, merging with dorsolateral and dorsal lobes forming rounded dorsal border of disc. Two spiracular plates, each with B-shaped opening and 4 palmately-branched interspiracular bristles. (Based on 12 specimens: Minetto.)

Second-instar larva: Yellowish brown; integument transparent. Length 3.2 to 5.3 mm ($\bar{X} = 4.0$ mm); width 0.7 to 1.7 mm ($\bar{X} = 1.0$ mm). Resembling second-instar larva of *S. caerulea*. Cephalopharyngeal skeleton (as Fig. 26) length 0.59 to 0.64 mm ($\bar{X} = 0.61$ mm); with paired mouthhooks, each bearing 3 decurved teeth below hook, ventral margin articulating with ventral arch below, posterior edge with fused hypostomal-pharyngeal sclerite. Segment 2 with anterior spiracles on posterolateral margins, each with 4 to 6 rudimentary papillae. Segments 5 to 10 each with 2 pairs of dorsal hair patches, lateral **tubercle** groups, ventral transverse **tubercle** group. Posterior spiracular disc (Fig. 15) with paired elongate ventral and ventrolateral lobes, lateral lobes inconspicuous. Two spiracular plates, each with 3 oval spiracular openings and 4 palmately-branched interspiracular bristles. (Based on 9 specimens: Minetto.)

Third-instar larva: Light brown to dark brown with greenish iridescence, middorsal stripe not evident; **translucent**. Length 8.0 to 11.5 mm ($\bar{X} = 9.6$ mm); width 2.0 to 2.6 mm ($\bar{X} = 2.3$ mm). Resembling third-stage larvae of *S. caerulea*, but differing in the darker integument color. Cephalopharyngeal skeleton (similar to Fig. 28), length 0.91 to 0.96 mm ($\bar{X} = 0.93$ mm), with paired mouthhooks; each bearing 3 or 4 pale, decurved accessory teeth (Fig. 36) beneath hook; ventral borders of mouthhooks articulating with ventral arch (Fig. 31) below, posterior margins with hypostomal sclerite behind. Pharyngeal sclerite dark, heavily pigmented. Segment 2 with anterior spiracles (Fig. 45) on posterolateral margins, each with 4 to 6 papillae on slightly inflated apical portion, spiracle body twice as long as wide. Segments 5 to 10 each with 2 pairs of dorsal hair patches, lateral **tubercle** group on each side, ventral **tubercle** group below. Posterior spiracular disc (Fig. 13) with paired elongate-lanceolate ventral lobes (VL); elongate, 2-segmented ventrolateral lobes (VLL); low conical lateral lobes (LL), low dorsolateral lobes (DLL), dorsal lobes (DL). Two spiracular plates (SP) in center of disc, each bearing 3 sinuous spiracular slits, prominent spiracular scar (SS) and 4 palmately-branched interspiracular bristles (ISB) acting as floating hairs. (Based on 9 specimens: Minetto.)

Puparium: (Figs. 52, 53). Uniformly dark brown to black with iridescent reflections, middorsal stripe not evident; **opaque**. Length 5.0 to 5.8 mm ($\bar{X} = 5.4$ mm); width 2.3 to 2.7 mm ($\bar{X} = 2.5$ mm). Puparium body slightly concave in middle dorsally. Dorsal hair patches evident on segments 5 to 10, hairs appressed. Lateral **tubercle** groups and ventral **tubercles** appearing as shagreen areas. Upturned posterior end forming obtuse angle of 110 to 130° with longitudinal axis of puparium body, bearing shrunken, posterior spiracular disc apically. Spiracular plates on short tubular structure, prominent above surface of disc; float hairs appressed to surface of tube. (Based on 14 specimens: Minetto.)

SEPEDON SPINIPES AMERICANA Steyskal

Wasman Jour. Bio. 8(3) :277. 1950.

The only recognized morphological differences between adults of the European and the North American subspecies of *S. spinipes* are in the male genitalia. Both subspecies are concolorous, light reddish brown, and 5.5 to 7.0 mm long. A few Nearctic species sympatric with *S. s. americana* resemble it superficially (e.g. females of *S. armipes* and *anchista* and both sexes of *S. neili* and perhaps *borealis*), and this subspecies can be identified positively only by microscopic examination.

Sepedon spinipes americana is as truly boreal as any *Sepedon* in the Western Hemisphere. Its known distribution (Map C) is quite similar to that of *S. borealis* (Map F), but capture records of *spinipes americana* extend even farther north in Canada and Alaska and they do not go quite so far south in the Rocky Mountains. Adults of this subspecies are not often seen near Ithaca, which is near the southern edge of its range. By contrast, *S. s. americana* was encountered more commonly than any other sciomyzid in late June and early July, 1957, in the sloughs of central Alberta and Saskatchewan. Capture records for adult flies, March 29, 1962 in the vicinity of Ithaca, attest to cold-hardiness suggested by its boreal distribution. Most ponds in the Ithaca area remained frozen until the last week of March in 1962.

The wild-caught flies from which laboratory rearings originated were collected by sweeping low vegetation in open marshes and wet meadows. One pair was captured at White Church Marsh, a boreal upland marsh (elevation 974 feet) 3.2 miles south of Brooktondale, Tompkins County, New York on June 18, 1956. Other adults used in laboratory rearing were collected at Paignon Beach, Waskesiu Lake, Prince Albert National Park, Saskatchewan, on July 7, 1957.

Females confined in breeding jars produced relatively few eggs compared to females of other species of *Sepedon*. The female from White Church Marsh produced a total of 47 eggs during a 6-week period. Material from Waskesiu Lake was in a mixed collection with *S. armipes*, and individual egg counts were not obtained. None of the laboratory-reared females ever produced eggs, although mating was observed on several occasions.

Eggs laid in the laboratory were attached to the sides of the breeding jars in groups of 8 to 15, arranged like those of *S. fuscipennis*, *S. caerulea*, and others (Fig. 7). The incubation period was 4 to 4½ days.

Larvae killed and fed upon *Physa* sp., *Helisoma trivolvis*, and *Australorbis glabratus*. As with other species of *Sepedon* reared in the laboratory, a single larva killed and ate 1 or 2 snails daily, the number depending upon the sizes of snails.

The swift attacks of larvae were usually successful, but exceptions were noticed. A larva was observed attacking a large *Physa* sp. (9 mm diameter), which secreted copious amounts of

mucus. The larva was soon covered with this mucus, which apparently occluded the spiracular openings and caused the larva to end its attack ; the larva was dead the following morning.

Based on 15 observations, the durations of larval stadia were: first, 2 to 4 days ; second, 2 to 4 days ; third, 5 to 9 days.

Each larva crawled up the side of the rearing jar to the cork or inner lip of the jar and formed its puparium. As in *S. tenuicornis*, a viscous fluid was first secreted and served to affix the puparium to the surface. Although no puparium of this subspecies was discovered in nature, it seems reasonable to assume that puparia are formed out of the water in a manner similar to that of *S. tenuicornis*.

Pupation time in the laboratory ranged from 7 to 10 days (12 observations). Eight adults that emerged were held in breeding jars, but no eggs were obtained. The longevity of these reared flies ranged from 160 to 165 days.

No anatomical differences between immature stages of the 2 subspecies of *S. spinipes* have been discovered. The following descriptions are based primarily on Nearctic subspecies, but they are applicable to immature stages of the Palearctic subspecies also.

Description of Immature Stages

Egg: (Fig. 7). Milk white. Length 1.16 to 1.22 mm (= 1.19 mm) ; width 0.22 to 0.28 mm (= 0.24 mm). Single rounded tubercle (tt) shielding micropyle dorsally. Shallow longitudinal groove (lg) on each side dorsolaterally with low longitudinal ridges on margins. Mesal ridges demarking regularly reticulate central area (ca). End opposite micropyle with blunt hemispherical tubercle (ht). Ventral surface regularly reticulate. (Based on 16 specimens: Paignon Beach.)

First-instar larva: White; integument transparent. Length 2.3 to 3.5 mm (\bar{X} = 2.8 mm) ; width 0.3 to 0.5 mm (X = 0.4 mm). Resembling the first-instar larva of *S. caerulea*. Cephalopharyngeal skeleton, as Fig. 24, length 0.28 to 0.31 mm (= 0.29 mm) ; with paired mouthhooks, each with bifid hook anteriorly, articulating with ventral arch below and with fused hypostomal-pharyngeal sclerite posteriorly. Segments 5 to 10 each with paired dorsal hair patches, lateral tubercle group on each side, ventral transverse tubercle group. Posterior spiracular disc (as Fig. 17) with paired elongate ventral lobes; paired, 2-segmented ventrolateral lobes; lateral, dorsolateral, and dorsal lobes not developed, contiguous, forming crescentic dorsal border of disc. Two spiracular plates in center of disc, each with B-shaped opening and 4 palmately-branched interspiracular bristles. (Based on 5 specimens: Paignon Beach.)

Second-instar larva: Yellowish white or light brown dorsally, white ventrally; integument transparent. Length 4.5 to 6.6 mm (= 5.3 mm) ; width 0.6 to 1.4 mm (= 0.9 mm). Resembling second-instar larva of *S. caerulea* in form, but differing in bearing prominent yellowish brown integumentary scales dorsally. Cephalopharyngeal skeleton, as Fig. 26, length 0.46 to 0.55 mm (X = 0.51 mm) ; with paired mouthhooks, each with 3 accessory teeth below hook; ventral margins of mouthhooks articulating with ventral arch below; posterior margins of mouthhooks with fused hypostomal-pharyngeal sclerite behind. Segment 2 with anterior spiracles on each side near posterolateral border, each with 3 to 4 rudimentary papillae. Segments 5 to 10, each with 2 pairs of dorsal hair patches, lateral tubercle group on each side, and ventral transverse tubercle group.

Posterior spiracular disc (as Fig. 15) with paired elongate ventral lobes; paired, 2-segmented ventrolateral lobes; lateral lobes low conical protuberances; dorsolateral and dorsal lobes inconspicuous, forming dorsal border of disc. Two spiracular plates in center of disc, each with 3 elongate oval openings and 4 palmately-branched interspiracular bristles. (Based on 11 specimens; Paignon Beach.)

Third-instar larva: Orange brown to dark brown with greenish iridescence, middorsal stripe prominent; integument translucent. Length 5.5 to 12.0 mm ($X = 8.3$ mm); width 1.3 to 2.4 mm ($= 1.7$ mm). Resembling third-instar larva of *S. caerulea* in general form, but differing in possessing dark integument and complete middorsal stripe. Cephalopharyngeal skeleton, as Fig. 28, length 0.77 to 0.81 mm ($X = 0.78$ mm); with paired mouthhooks, each with 3 or 4 pale decurved accessory teeth (as Fig. 36); ventral borders of mouthhooks articulating with ventral arch below, posterior margins of mouthhooks articulating with hypostomal sclerite behind; pharyngeal sclerite with dark pigmentation with or without pigmented area (Fig. 28, PA) on posterodorsal border. Segment 2 with anterior spiracles (as Fig. 45) on each side near posterolateral border, each with 3 to 5 round papillae. Segments 5 to 10 each with 2 pairs of dorsal hair patches, lateral tubercle group on each side, and ventral transverse tubercle group of 4 tubercles. Posterior spiracular disc (as Fig. 13) with paired elongate lanceolate ventral lobes; paired, 2-segmented ventrolateral lobes; lateral lobes low conical protuberances; dorsolateral lobes inconspicuous; dorsal lobes conical, forming rounded dorsal border of disc. Two spiracular plates (SP) in center of disc, each with 3 elongate, sinuous slits, prominent stigmatic scar (SS) and 4 palmately-branched interspiracular bristles (ISB) acting as float hairs. (Based on 16 specimens: Paignon Beach.)

Puparium: (As Figs. 52, 53). Uniformly dark brown with visible middorsal stripe. Length 4.3 to 5.5 mm ($X = 4.7$ mm); width 1.7 to 2.3 mm ($= 2.0$ mm). Middle $\frac{1}{3}$ of body slightly concave dorsally. Posterior end upturned, forming obtuse angle of 100 to 120° with longitudinal axis of body. Spiracular plates evident above shrunken disc. (Based on 17 specimens: Paignon Beach, 14; White Church, 3.)

SEPEDON SPINIPES SPINIPES Scopoli

Entomologia Carniolica, p. 342. Vindobonae, I. T. Trattner. 1763.

Adults of this subspecies (including living flies moving about in the insect net) are easily identified; no European species is even superficially similar to *S. spinipes*. The stilt-like appearance given to *Sepedon* by the long legs and narrow body is shared by only one other European genus of Sciomyzidae, *Dichetophora*, and flies of that genus have pictured wings. The only other species of *Sepedon* that is widespread and common in Europe is distinctly darker and somewhat larger. Whereas *S. s. spinipes* is concolorous, light reddish-brown and only 5.5 to 7.0 mm long, *S. sphaecea* is shiny jet black on head, thorax, and abdomen and the European specimens are 7.0 to 8.5 mm long. The only other *Sepedon* reported from Europe, *S. hispanica*, is known only from Andalusia, southern Spain. In the region where all 3 species occur together, L. V. Knutson reports that all are quite distinctive as living flies. Adults of *hispanica* are as small as, or even smaller than, *spinipes* (5.0 to 6.5 mm long)

but closer to the color of *sphegea*. However, the blackish-brown head, thorax, and abdomen of *hispanica* are quite different from the shiny jet black of *sphegea* in dorsal view, and a heavy pruinosity gives the pleura a decidedly niveous appearance.

It is fortunate that *S. s. spinipes* and *S. sphaea* are readily distinguished from each other, as well as from other European Sciomyzidae. The 2 species occur together in many breeding sites from the Scandinavian countries south to Spain, Italy, Greece, and the Near East (Map D).

A laboratory rearing of *S. s. spinipes* was made at Ithaca. The adults (1 male, 4 females) used in this rearing were collected (by Berg), July 5-7, 1959, at Rouge Cloître, Auderghem, Brabant, Belgium.

Eggs were laid on the sides of laboratory breeding jars and on short sections of *Typha* leaves in the jars. Their size, color, chorion sculpturing, and arrangement (Fig. 9) seem identical to those of the American subspecies (Fig. 7). They hatched $3\frac{1}{2}$ to 4 days after being laid (2 observations). The egg mass discovered in nature at Hilleroed, Denmark (Fig. 9) was laid on a dried, brown leaf that had fallen from a deciduous tree. Emergence holes on the empty egg membranes indicated that all embryos in these eggs had been destroyed by a hymenopterous egg parasite.

Larvae were fed *H. trivolvis*, *A. glabratus*, and *Physa* sp. They attacked and destroyed these snails rapidly in the manner characteristic of other *Sepedon* larvae. Based on 6 observations, the durations of the 3 larval stadia were : first, 3 to $4\frac{1}{2}$ days; second, 3 to 5 days ; third, 5 to 6 days.

As pupation approached, larvae crawled up the sides of the rearing jar and formed their puparia on the bottom of the cork. These puparia were firmly attached to the cork with a mucus-like secretion, as was observed in *S. spinipes americana* and *S. tenuicornis*. A puparium of the Palearctic subspecies was collected by Berg at Hilleroed, Denmark on July 21, 1959. It was firmly affixed to a dry grass spikelet that had been broken from the plant by vigorous sweeping motions with the insect net. This confirms the supposition that *S. spinipes* behaves as *S. tenuicornis* does in forming the puparium above the substratum. Pupation time in the (warm) laboratory was 8 to $8\frac{1}{2}$ days (5 observations).

Larvae of *S. s. spinipes* were collected in nature by L. V. Knutson on Crete (13. IV. 1963) and Corfu (26. IV. 1963). The first collecting site is an open, sunlit, fresh-water marsh near the seacoast at Gerani, 15 kilometers west of Canea. The second is an irrigation ditch choked with emergent vegetation at Hricida, 7 kilometers south of Corfu. The larvae killed and ate the *Planorbis planorbis* that occurred in these habitats. Most, but not all, larvae that pupated left the water and crawled up the side of the rearing dish before doing so. Knutson (*in litt.*) mentioned "a clear, colorless, mucilaginous substance (evidently produced by the pupating larva) that held the puparium in place." The pupation time observed by Knutson was 10 to 14 days, with most individuals emerging 12 days after

their puparia were formed (9 observations). These rearings were conducted in an unheated laboratory, where the daily temperature maxima ranged from 16° to 25° C.

Description of Immature Stages

(See descriptions and figures given for *S. s. americana*.)

SEPEDON SPHEGEA (Fabricius)

Systema Entomologiae :768. 1775.

(as *Syrphus sphegeus*)

This species was originally based on specimens taken in England, but it is widely distributed throughout the Palearctic region (see Map D). Specimens from the Far East possess a more metallic coloration than their European counterparts, and these have been designated as distinct species (*S. aenescens* and *S. violacea*) by Wiedemann (1830) and Hendel (1909). On the basis of the male genitalia and available immature stages (one puparium), these species seem to be only color forms or, at most, subspecies of *S. sphegea*.

Adult flies that initiated our first laboratory rearings of this species were captured on June 25, 1959 at Etang de Saint Hubert, Seine et Oise, France. The following descriptions of the immature stages are based primarily on material obtained in that rearing. The laboratory-reared larvae and puparia have been compared with larvae and puparia collected in nature in Sweden, Finland, Belgium, Germany, and Afghanistan. All stages of the material from France were compared with those obtained in a laboratory rearing of *S. sphegea* from Afghanistan. Individual variation within population samples was noted without consistent differences between populations. In all parts of its range familiar to us (including Denmark, Spain, Austria, and Italy as well as the countries named above), adults, larvae, and puparia were taken only in more-or-less open ponds, canals, lake margins, and marshlands.

In the laboratory, females laid their eggs in long rows with the longitudinal axis of each egg perpendicular to the long axis of the row (as Fig. 1). All eggs obtained in these rearings were light, silvery gray when first laid but darkened to lead gray as the embryo developed. Gercke's term "milchweiss" (1876) hardly seems appropriate for freshly laid eggs and certainly not for older ones. On the basis of many observations at laboratory temperatures, eggs hatched 3 to 4 days after being laid.

Newly hatched larvae attacked and quickly killed small individuals of *Physa* sp., *H. trivolvris*, *A. glabratus*, and *Gyraulus parvus*. Their mode of attack did not differ visibly from that of other *Sepedon* reared during this study.

An experiment was made to check Gercke's statement that the larvae of *S. sphegea* probably feed on plant tissue. First- and second-instar larvae were confined in a rearing jar with quantities of *Lemna minor* L. (*Lemna trisulca* was not readily available). The

duckweed was thoroughly washed to remove small snails that could have served as food for the larvae. Larvae survived for not more than 5 days in these jars. At no time did they have visible plant material in the gut. Their vigor decreased markedly on the third and fourth day of their confinement, and all were dead by the end of the fifth day. A similar rearing jar with small snails included with the duckweed yielded well-developed second- and third-instar larvae at the end of the 5-day period.

The duration of larval stadia in the Ithaca laboratory for the material collected in France was: first, $2\frac{1}{2}$ to 4 days; second, $3\frac{1}{2}$ to $4\frac{1}{4}$ days; third, $4\frac{1}{4}$ to 7 days (10 observations).

All puparia found in nature, and those formed in rearing jars containing much water, were floating. Puparia formed in drier jars were found on or partly in the moist sand at the bottom. A round protuberance on each side just posterior to the circular seam of the cephalic caps gives them a distinctive outline in dorsal view (Fig. 64). Pupation time for the rearing from France in the laboratory varied from $5\frac{1}{2}$ to 12 days (21 observations), with most flies emerging 6 to 9 days after their puparia were formed. Pupal development for the Afghanistan material required 5 to 8 days in the heated laboratory.

Female flies that emerged while day lengths were shortening in summer and fall waited for surprisingly long periods before laying any eggs. Two first-generation females reared from the adults collected in France had preoviposition periods of 70 to 76 days. None of the 8 females that emerged October 9-12, 1964 from puparia collected in Afghanistan laid any eggs until December 22, at least 71 days after emergence. All 8 started to oviposit (in the heated laboratory) before the middle of January, and they continued with no interruption of more than 3 or 4 days until shortly before they began to die on March 22. In contrast to this long preoviposition period, females of the next 2 generations reared from the Afghanistan material began to lay eggs within a week to 10 days after emergence. Some mechanism that tends to suppress oviposition in the fall apparently affected the first laboratory reared generation from Afghanistan, but not the next 2.

Individual egg counts on the Afghanistan flies were interrupted after 1 fly had laid 156 eggs in her first 6 days of oviposition. A fly reared from the adults collected in France laid 45 eggs in 3 days but died on the fourth day. Another lived for 28 days after she began to oviposit and laid a total of 274 eggs, averaging 9.7 eggs per day. None of these totals is high enough to indicate the capacity of these flies. Those that oviposited from about January 1 to about March 15 were often confined together so that egg counts on individuals were impossible.

Records on *sphgea* support the generalization that breeding seasons of *Sepedon* are interrupted only briefly in cool climates, and not at all in regions of mild winters. Adults have been collected in Denmark from March 30 to December 20. They have been taken as early as March 17 in Italy, and January 28 in southern Spain.

As observed in other species, hatching, emergence, oviposition, and other events in the life cycle evidently go on continuously during the warm season, so generations merge into each other and become unrecognizable. This observation is supported and explained by the long period of oviposition for the first generation flies from Afghanistan (long enough for the 2 following generations to complete their life cycles while these flies continued to oviposit). The females collected in France on June 25 oviposited at somewhat irregular intervals, but never with interruptions of more than 2 or 3 days, from July 2 to July 12. Puparia collected at Hoeilaart, Belgium on July 11 began to yield adults the next morning and continued for 5 days. Puparia collected August 11 at Maisinger See, 30 kilometers southwest of Munich, Germany yielded adults for a week after collection. The laboratory-reared generation from France was in egg and larval stages during emergence of the adults collected as pupae in Belgium, and in larval and pupal stages during emergence of individuals collected in Sweden and Germany. The interruptions in capture records observed by Soós (1958) during the flight season of *spegea* do not indicate real interruptions in the occurrence of adults in nature; they must result from sporadic collecting efforts.

The longevity of adults in the laboratory is remarkable, especially during the season when flies in nature would be hibernating. Progeny of the individuals collected as larvae and pupae in Afghanistan survived up to 226 days after emergence in the laboratory October 9-12, 1964. Of the 18 adults that emerged in October, only 4 lived less than 5 months.

Several mature larvae of *S. spegea* collected at Lake Erken, Sweden, August 7, 1959 fed in a typical manner and formed normal puparia. However, these puparia yielded parasitoid wasps of the family Ichneumonidae which have been tentatively identified by H. K. Townes, Jr. as *Mesoleptus ripicola* Thomson. Like Ichneumonidae reared from *S. fuscipennis*, these wasps evidently oviposit into the larva, but their eggs or young larvae do not hinder normal activities of the host until its puparium has been formed. The incidence of infestation by this or a closely related species must be quite high near Hamburg, Germany.. Gercke (1876) wrote, "würde ihre Vermehrung eine noch viel grössere sein, wenn nicht eine, zu den Cryptiden gehorige Wespe: *Phygadeuon cinctorius* Gravenh., gar arge Verwüstung unter der Brut anrichtete!" . . . their increase would be a much greater one if a cryptid wasp, *Phygadeuon cinctorius*, did not cause severe destruction among the brood).

Description of Immature Stages

Egg: (Fig. 6). Silver to plumbeous gray. Length 1.34 to 1.51 mm = 1.42 mm); width 0.33 to 0.37 mm (X = 0.35 mm). Single, broadly triangular tubercle shielding micropyle dorsally. Shallow longitudinal grooves on each side dorsolaterally, grooves bordered by raised longitudinal ridges. Mesal ridges enclosing a regularly reticulate central area (as Fig. 4, ca), reticulations often with black shading. End opposite micropyle with smooth, blunt tubercle Ventral and lateral surfaces reticulate. (Based on 16 specimens.)

First-instar larva: White; integument transparent. Length 2.4 to 4.6 mm (\bar{X} = 3.5 mm); width 0.4 to 0.8 mm (\bar{X} = 0.6 mm). Resembling first-instar larva of *S. caerulea*. Cephalopharyngeal skeleton (as Fig. 24), length 0.34 to 0.41 mm (\bar{X} = 0.37 mm); with paired mouthhooks, each bifid anteriorly, ventral margins articulating with ventral arch below, posterior margins articulating with fused hypostomal-pharyngeal sclerite behind. Distribution of hair patches and tubercle groups as in *S. caerulea*. Posterior spiracular disc (as Fig. 17) with 2 pairs of prominent lobes: ventral pair elongate; ventrolateral pair elongate, appearing 2-segmented. Lateral, dorsolateral, and dorsal lobes inconspicuous protuberances. Two spiracular plates, each with B-shaped spiracular opening and 4 palmately-branched interspiracular processes. (Based on 16 specimens.)

Second-instar larva: White to light brown; integument transparent. Length 5.5 to 8.5 mm (\bar{X} = 6.8 mm); width 1.0 to 1.8 mm (\bar{X} = 1.3 mm). Resembling second-instar larva of *S. caerulea*. Cephalopharyngeal skeleton (as Fig. 26), length 0.56 to 0.65 mm (\bar{X} = 0.60 mm); with paired mouthhooks, each bearing 3 slightly decurved accessory teeth below hook, ventral margins of mouthhooks articulating with ventral arch below, posterior margins with fused hypostomal-pharyngeal sclerite behind. Segment 2 with pair of anterior spiracles, one on each side posterolaterally; each spiracle bearing 5 to 8 rudimentary papillae on apical end. Segments 5 to 10 each with 2 pairs of dorsal and dorsolateral hair patches, lateral tubercle groups, ventral transverse tubercle groups as in *S. caerulea*. Posterior spiracular disc (as Fig. 15) with 2 pairs of prominent lobes; ventral pair elongate, lanceolate; ventrolateral lobes elongate, appearing 2-segmented. Lateral lobes low, conical protuberance; dorsolateral and dorsal lobes inconspicuous protuberances, forming crescentic dorsal border of disc. Two spiracular plates in center of disc; each plate with 3 oval spiracular openings and 4 palmately-branched interspiracular bristles alternating with spiracular openings. Anal plate with anal proleg on anterior margin; proleg with round median protuberance. (Based on 14 specimens.)

Third-instar larva: Yellowish brown; integument transparent. Length 7.6 to 12.3 mm (\bar{X} = 9.6 mm); width 1.5 to 2.4 mm (\bar{X} = 1.9 mm). Closely resembling third-instar larva of *S. caerulea* in general appearance. Cephalopharyngeal skeleton (similar to Fig. 28), length 0.88 to 0.97 mm (\bar{X} = 0.92 mm); with paired mouthhooks, each mouthhook (Fig. 38) slightly angulate apically, with 3 or 4 decurved accessory teeth beneath hook, ventral margins of mouthhooks articulating with ventral arch below; ventral arch (Fig. 33) with broad, median notch in posterior border, anterior margin with 22 to 26 minute teeth; posterior margin of mouthhooks articulating with hypostomal sclerite (Fig. 23, HS) behind; pharyngeal sclerite lightly pigmented (as Fig. 23, PS), with dark, thin, longitudinal stripe. Segment 2 bearing pair of anterior spiracles, one on each side posterolaterally; each spiracle (Fig. 47) with 5 to 8 round papillae on slightly inflated apical portion, base of spiracle somewhat expanded below stigmatic scar. Segments 5 to 10 each with 2 pairs of dorsal and dorsolateral hair patches, a dark transverse mark often present between dorsal and dorsolateral patch on each side; lateral tubercle group on each side with middle tubercle slightly anterior to upper and lower ones; ventral transverse group of 4 tubercles with 2 widely spaced tubercles anterior to transverse group; secondary integumentary folds prominent ventrally and laterally. Posterior spiracular disc (as Fig. 13) with 2 pairs of prominent lobes; ventral pair elongate, lanceolate; ventrolateral pair elongate, appearing 2-segmented. Lateral lobes on each side low, conical protuberances; dorsolateral and dorsal lobes inconspicuous, rounded protuberances. Two spiracular plates in center of disc,

each with 3 elongate, sinuous spiracular slits alternating with 4 palmately-branched interspiracular processes. Anal plate bilobed, half as long as wide, with anal proleg on anterior margin; proleg with round, median protuberance. (Based on 11 specimens.)

Puparium: (Figs. 64, 65). Uniformly dark brown. Length 6.3 to 7.2 mm ($X = 6.7$ mm) ; width 2.3 to 3.0 mm ($X = 2.8$ mm). Dorsal cephalic cap without stramineous markings posterolaterally. Prominent round protuberance laterally just posterior to circular emergence suture (circular seam). Middorsal stripe faint; no oblique stripes. Dorsal and dorsolateral hair patches visible, hairs appressed. Lateral and ventral tubercles appearing as round shagreen areas. Uprturned posterior end forming obtuse angle of 100 to 130° with longitudinal axis of puparium body. Spiracular plates prominent above shrunken posterior disc on upturned end; float hairs appressed to spiracular tube supporting plate. Anal plate black, forming notch on posterior side of upturned caudal portion. (Based on 12 specimens.)

SEPEDON HAPLOBASIS Steyskal

Proc. Entomol. Soc. Wash. 62:42. 1960.

This and the following 3 species are members of the *armipes* group. Until Steyskal's 1950 revision appeared, *S. armipes* was applied to any small (4 to 6 mm body length) *Sepedon* whose male possessed notched hind femora. Steyskal demonstrated that "*S. armipes*" comprised at least 3 species (*armipes*, *bifida*, and *melanderi*), and he questioned the numerous references to the species in the northwest and southern California. *S. haplobasis* and *S. anchista* were discovered in the course of this study. The former is known only from material taken at the type locality and material obtained from subsequent rearings at Ithaca. The collection of 8 males and 6 females was made near the boundary between the states of Mexico and Distrito Federal, Mexico on August 10, 1958. The flies (5 to 6 mm long) were collected by sweeping in an open, roadside ditch along Federal Ruta 190, km 13-15, which was choked with water hyacinth and intermittent stands of cattail, and had no cover shading the area.

Females confined in the laboratory laid small groups of 3 to 8 eggs, on the sides of the breeding jar and on sections of grass and *Typha* leaves in the jar. The eggs hatched in $3\frac{1}{2}$ to $4\frac{1}{2}$ days (8 observations).

Larvae attacked and fed upon *Helisoma trivolvis* and *Australorbis glabratus*. A hungry larva moved into the aperture of the snail and could be seen nipping the snail's flesh with its mouth-hooks. Often the larva was dragged farther into the aperture as it held onto the flesh as the snail retracted. Once a larval attack had commenced, the larva persisted and the host was usually subdued within 30 minutes. However, small (first-instar) larvae were often repulsed by snails as large as 4 to 8 mm in diameter. As the snail thrashed its foot around the aperture, these movements usually dislodged the larva and occasionally encased it in a coat of mucus. Small larvae trapped in mucus were usually found dead 24 hours later.

Based on 13 observations, duration of the larval stadia was : first, 4 to 4½ days; second, 3½ to 4½ days; third, 6 to 9 days.

The puparium was formed in the sand at the bottom of the rearing jar. It has a middorsal stripe and 4 or 5 oblique stripes dorsolaterally that are not evident in the mature larva. These oblique stripes (see Figs. 58, 59) on the puparium are characteristic of most species in the *S. armipes* group, being evident on puparia of *S. haplobasis*, *S. anchista*, and *S. armipes*.

Adult flies emerged from the puparia 7 to 9 days after their formation (15 observations). First-generation males and females were confined in breeding jars so that preoviposition periods and longevity records could be obtained. Unfortunately, none of the 6 females produced eggs, even though they lived from 22 to 85 days. Laboratory reared males had a shorter life span which ranged from 8 to 33 days.

Description of Immature Stages

Egg: (Similar to Fig. 10). Yellowish white. Length 1.08 to 1.18 mm (R = 1.13 mm); width 0.31 to 0.34 mm (= 0.32 mm). Broad, transverse tubercle shielding micropyle dorsally; 7 to 9 anastomosing, longitudinal ridges with grooves between bearing incomplete transverse ridges. End opposite micropyle with hemispherical tubercle bearing minute punctations on its surface. (Based on 8 specimens.)

First-instar larva: White; integument transparent. Length 1.6 to 3.3 mm (= 2.0 mm); width 0.3 to 0.6 mm (\bar{X} = 0.4 mm).) Segment 1 (pseudocephalic) bilobed anteriorly, bearing sensory papillae apically; prominent postoral spine band on posteroventral border, almost encircling segment. Cephalopharyngeal skeleton (Fig. 29), length 0.30 to 0.34 mm (= 0.31 mm); with paired mouthhooks, each bifid anteriorly, with wing-like posterior part articulating with fused hypostomal-pharyngeal sclerite; ventral arch beneath mouthhooks. Segments 5 to 10, each lacking dorsal and dorsolateral hair patches; lateral tubercle groups present, but tubercles ill-defined; ventral transverse group of 4 tubercles present; secondary integumentary folds evident on each segment. Posterior spiracular disc (Fig. 18) with 2 pairs of prominent lobes; ventral pair blunt, ovate, almost as long as wide; ventrolateral pair blunt, with thumb-like projection dorsally; dorsal and lateral border of disc rounded, distinct lobes lacking. Two spiracular plates in center of disc, each with 4 palmately-branched interspiracular processes surrounding B-shaped spiracular opening. Anal plate half as long as wide; anal proleg inconspicuous. (Based on 5 specimens.)

Second-instar larva: White or light tan; integument transparent. Length 4.1 to 7.3 mm (= 5.5 mm); width 0.8 to 1.5 mm (= 1.1 mm). Segment 1 (pseudocephalic) bilobed anteriorly; each lobe bearing minute, 2-segmented sensory papilla, circular sensory plate, and labral sensory papilla lateral to atrium; prominent postoral spine band at posteroventral border (similar to Fig. 19 POSB). Cephalopharyngeal skeleton (Fig. 27), length 0.54 to 0.58 mm (\bar{X} = 0.57 mm); with paired mouthhooks, each with 2 or 3 accessory teeth beneath hook; ventral arch beneath mouthhooks, with broad median notch on posterior border; posterior margins of mouthhooks articulating with fused hypostomal-pharyngeal sclerite behind, epistomal sclerite evident above hypostomal portion of combined sclerite. Segment 2 with pair of anterior spiracles, one on each side posterolaterally, each bearing 8 to 10 rudimentary papillae apically. Segments 5 to 10 with minute, triangular scales covering integument; each with dorsal and dorsolateral hair patches appearing as small, circular areas bearing 1 to 4 bristles,

or hair patches lacking; lateral tubercle group with 3 tubercles, middle tubercle slightly anterior to upper and lower tubercles; ventral transverse tubercle group with 4 tubercles, 2 widely spaced tubercles anterior to transverse group; secondary integumentary folds evident. Posterior spiracular disc (Fig. 16) with 2 pairs of prominent lobes; ventral pair rounded apically, slightly longer than broad; ventrolateral pair blunt, with thumb-like projection dorsoapically. Lateral lobes appearing as low, conical protuberances; dorsolateral and dorsal lobes inconspicuously protuberances. Two spiracular plates in center of disc, each with 4 palmately-branched interspiracular processes alternating with 3 elongate, oval spiracular openings. Anal plate half as long as wide, with anal proleg on anterior margin appearing as low, rounded protuberance. Anal slit longitudinal. (Based on 15 specimens.)

Third-instar larva: Light yellowish brown; integument transparent. Length 5.7 to 10.6 mm (\bar{X} = 8.9 mm); width 1.2 to 2.8 mm (X = 2.1 mm). Segment 1 (pseudocephalic) bilobed (appearing as Fig. 19); each lobe with 2-segmented sensory papilla (TSP), circular sensory plate (CSP), and labral sensory papilla (LSP) laterad to atrium. Postoral spine band prominent on posteroventral border, almost encircling segment (as Fig. 19, POSB). Cephalopharyngeal skeleton (Fig. 25), length 0.84 to 0.96 mm (X = 0.91 mm); with paired mouthhooks, each bearing 3 or 4 pointed, slightly decurved, accessory teeth (as Fig. 36); ventral arch beneath mouthhooks, with broad, median notch in posterior border (as Fig. 30), anterior margin with 22 to 28 minute teeth; posterior edge of mouthhooks articulating with hypostomal sclerite (as Fig. 23, HS) and epistomal sclerite (ES); crescentic lingual sclerite (as Fig. 19, LS) anterior to hypostomal sclerite ventrally; pharyngeal sclerite bearing dark, longitudinal pigmentation stripe with radiating areas dorsally, ventral cornua with light oval area. Segment 2 with pair of anterior spiracles, one on each side near posterolateral borders; each (as Fig. 41) bearing 9 to 12 papillae on slightly expanded, apical portion. Segments 5 to 10 with minute triangular scales (as Fig. 21) covering integument; each with dorsal and dorsolateral hair patches appearing as 2 pairs of small, circular areas bearing 1 to 4 bristles, or hair patches lacking; lateral tubercle group with 3 contiguous tubercles, middle one slightly anterior to upper and lower tubercle, lower tubercle the largest; ventral transverse tubercle group with 4 tubercles, 2 widely spaced tubercles anterior to transverse group; secondary integumentary folds evident dorsally and ventrally. Posterior spiracular disc (Fig. 14) with 2 pairs of prominent lobes; ventral pair slightly longer than broad, rounded apically; ventrolateral pair blunt, with thumb-like projection dorsoapically. Lateral lobes appearing as low, conical protuberances; dorsolateral and dorsal lobes low, inconspicuous protuberances on margin of disc. Two spiracular plates (as Fig. 37) in center of disc; each with 4 palmately-branched interspiracular processes (.112 to .160 mm in length) alternating with 3 elongate, oval spiracular openings, these processes as long as tuberculate spiracular tube (Fig. 37, ST). Anal plate with anal proleg along anterior margin appearing as low, transverse protuberance; anal slit longitudinal. (Based on 15 specimens.)

Puparium: (Similar to Figs. 58, 59). Light brown to brown dorsally; yellowish brown ventrally; translucent. Length 4.7 to 6.1 mm (X = 5.4 mm); width 2.2 to 2.7 mm (\bar{X} = 2.4 mm). Middorsal stripe evident; light oblique stripes running posterodorsal-anterolaterally on segments 6 to 9. Tubercle groups appearing as shagreen areas laterally and ventrally. Uprturned posterior end forming angle of 110 to 130° with longitudinal axis of body, bearing spiracular plates above shrunken disc apically. (Based on 11 specimens.)

SEPEDON ARMIPES Loew

Wien. ent. Monatsch, 3:298. 1859.

The range of this common, small, brown fly (Map E) is almost as extensive as that of *S. fuscipennis*. Although it apparently does not extend as far south in the Gulf States, northeast into Newfoundland, or northwest into Alaska, it exceeds the range of *fuscipennis* in the Southwest by including parts of California and Arizona.

The material examined and reared in the laboratory was obtained at several localities near Ithaca. These were Bull Pasture Pond, Cornell Golf Course on July 14, 1956; White Church Marsh, 3.2 miles south of Brooktondale, on June 18, 1956; and McLean Reservation, 1 mile east of McLean, on June 24, 1958 and June 14, 1959. Other adults were collected at the Town Reservoir, Hardinsburg, Kentucky on July 18, 1956 and August 28, 1957; and 4 miles north of Red Deer, Alberta, Canada on July 4, 1957. Adults taken at these localities were confined in breeding jars and eggs were obtained for subsequent rearings at Ithaca.

The eggs laid by certain females of this species differed from eggs of other members of the *armipes* group and from those laid by other *S. armipes* females. These eggs developed a dark, lead-gray band dorsally and laterally on the middle third of the chorion. This transverse band developed 24 to 36 hours after oviposition. At the Hardinsburg locality, where field conditions did not permit careful separation of *S. armipes* and *S. pusilla* adults, this feature of the *S. armipes* eggs enabled separation of these eggs from eggs of *S. pusilla*. Subsequent rearings substantiated the reliability of this characteristic in separating these 2 species from Hardinsburg. However, this characteristic marking was found to be lacking in eggs of some females taken in the Ithaca area. This feature of the egg has not been investigated fully. Because egg differences have been found to show species differences in other Diptera (Hackett, 1937; Bates and Hackett, 1939), *S. armipes* must be studied further to determine whether females laying banded and unbanded eggs represent different species.

Eggs hatched in $3\frac{1}{2}$ to $4\frac{1}{2}$ days after being laid (10 observations). The first-instar larvae that emerged were active and readily attacked *Helisoma trivolvis* and *Physa* sp. First-instar larvae usually completed the first stadium in $3\frac{1}{2}$ to 4 days and each larva killed at least 2 small (2 to 4 mm) *H. trivolvis* daily. The second stadium occupied $3\frac{1}{2}$ to 5 days, and the third stadium was 5 to $7\frac{1}{2}$ days in duration. These stadia periods are based on 11 observations.

Second- and third-instar larvae generally attacked and daily devoured a single medium (4 to 6 mm) or large (6 to 8 mm) *H. trivolvis*.

Puparia were formed in the sand on the bottom of rearing jars. They possessed the characteristic stramineous oblique stripes on the abdominal segments. Pupation time was 5 to 7 days in the laboratory (9 observations). Preoviposition periods obtained on 3 females were 6, 8, and 11 days.

Collecting dates for adults in the Ithaca area ranged from March 10 to September 12. Mature larvae have been taken May 30, Bull Pasture Pond and June 6, Inlet Valley in company with *S. fuscipennis* larvae. As with *S. fuscipennis*, the few puparia encountered in the early spring either produced parasitoid wasps or proved inviable. Puparia taken in June and July produced normal adults. From these facts come the conclusion that *S. armipes* passes the winter in the Ithaca area as an adult.

"Parasitic" wasps obtained from *S. armipes* puparia and identified by H. K. Townes, Jr. are :

Ichneumonidae — *Mesoleptus declivus* Provancher, *Mesoleptus* sp. A., *Eriplanus* sp. B., *Eriplanus* sp. F.;

Pteromalidae - *Urolepis rufipes* (Ashm.)

Description of Immature Stages

Egg: (Similar to Figs. 8, 10). Yellowish white, often dark transverse band encircling middle $\frac{1}{3}$ of egg. Length 0.89 to 0.96 mm (\bar{X} = 0.92 mm); width 0.22 to 0.24 mm = 0.23 mm). Single, rounded protuberance shielding micropyle dorsally, 5 to 8 anastomosing longitudinal ridges with transverse septations in grooves between ridges not evident. Dome-like hemispherical tubercle at end opposite micropyle bearing minute punctations. Interrupted longitudinal ridges laterally and ventrally. (Based on 11 specimens: Bull Pasture Pond.)

First-instar larva: White; transparent. Length 1.2 to 2.1 mm (X = 1.4 mm); width 0.2 to 0.6 mm = 0.4 mm). Closely resembling first-instar larva of *S. haplobasis*. Cephalopharyngeal skeleton (as Fig. 29), length 0.24 to 0.29 mm (X = 0.26 mm), with paired mouthhooks, each with bifid hook anteriorly; ventral arch beneath mouthhooks; fused hypostomal-pharyngeal sclerite articulating with posterior margins of mouthhooks. Posterior spiracular disc (as Fig. 18) with 2 spiracular plates, each with 4 palmately-branched interspiracular bristles surrounding B-shaped spiracular opening. (Based on 8 specimens: Bull Pasture Pond, 4; Hardinsburg, 4.)

Second-instar larva: White, transparent. Length 2.7 to 4.0 mm (\bar{X} = 3.2 mm); width 0.6 to 1.7 mm (X = 0.9 mm). Closely resembling *S. haplobasis* larva of this stage. Cephalopharyngeal skeleton (as Fig. 27), length 0.44 to 0.51 mm (X = 0.47 mm); with paired mouthhooks, each bearing 3 slightly decurved accessory teeth beneath hook; ventral arch articulating with ventral margin of mouthhooks, with serrate anterior margin and bilobed posterior margin; fused hypostomal-pharyngeal sclerite articulating with posterior edges of mouthhooks. Anterior spiracles posterolaterally on segment 2, each with 9 to 10 rudimentary papillae on distal border. Segments 5 to 10 each with dorsal and dorsolateral hair patches inconspicuous, or wholly lacking; lateral tubercle groups and ventral transverse tubercle groups as in second-instar *S. haplobasis* larva. Posterior spiracular disc (as Fig. 16) with 2 pairs of rounded lobes: ventral pair rounded apically; ventrolateral pair bearing thumb-like projection dorsoapically. Two spiracular plates in central area of disc, each with 4 palmately-branched interspiracular processes alternating with 3 elongate oval spiracular openings. Anal proleg rounded transverse protuberance on anterior margin of anal plate. (Based on 6 specimens: Bull Pasture Pond.)

Third-instar larva: White to yellowish white, transparent. Length 4.5 to 7.4 mm (X = 6.2 mm); width 1.0 to 2.0 mm (X = 1.6 mm). Closely resembling third-instar larva of *S. haplobasis*. Cephalopharyngeal skeleton

(similar Fig. 25), length 0.72 to 0.81 (\bar{X} = 0.77 mm); with paired mouthhooks, each with 3 or 4 pointed, slightly decurved accessory teeth (as Fig. 36) below hook; ventral arch beneath mouthhook bearing 22 to 28 teeth on anterior margin, posterior border bilobed (as Fig. 30); pharyngeal sclerite darkly pigmented, light oval area in ventral cornua. Segment 2 with anterior spiracles on each side posterolaterally, each spiracle (Fig. 41) bearing 9 to 11 papillae on slightly expanded distal portion. Segments 5 to 10, each with small, triangular integumentary scales (Fig. 21); dorsal and dorsolateral hair patches, lateral tubercle groups, ventral transverse tubercles, as in *S. haplobasis*. Posterior spiracular disc (similar to Fig. 14) with 2 pairs of prominent lobes: ventral pair rounded apically, about as wide as long; ventrolateral pair blunt apically with thumb-like projection on dorsoapical border. Two spiracular plates (Fig. 37, SP), each with 4 palmately-branched interspiracular processes serving as float hairs (.098 to .112 mm in length) (Fig. 37, FH) alternating with 3 oval spiracular openings, float hairs as long as tuberculate spiracular tube. Circular stigmatic scar evident. Anal proleg rounded transverse protuberance at anterior margin of anal plate. (Based on 14 specimens: Bull Pasture Pond.)

Puparium: (Similar to Figs. 58, 59). Yellowish brown to brown; opaque. Length 3.8 to 4.8 mm (\bar{X} = 4.5 mm); width 1.7 to 2.2 mm (\bar{X} = 1.9 mm). Middorsal stripe faint, occasionally lacking. Oblique stripes evident as 4 to 5 light lines running anterolaterally on segments 5 to 9. Shagreen areas laterally and ventrally marking positions of lateral and transverse tubercle groups. Uprturned posterior end forming angle of 90 to 120° with the longitudinal axis of puparium body, bearing spiracular disc apically. Lobes of disc shrunken; spiracular plates prominent above surface of disc, interspiracular processes appressed to tuberculate spiracular tube. Anal plate inconspicuous, forming a notch on posterior side of upturned portion. (Based on 14 specimens: Bull Pasture Pond, 6; Hardinsburg, 5; Red Deer, 3.)

SEPEDON ANCHISTA Steyskal

Papers Mich. Acad. Sci. Arts, and Letters 41:87. 1956.

This species resembles *S. armipes* closely, differing primarily in characters of the male genitalia and in position of the basal and basimedial prongs of the hind femora of the male, but *S. anchista* (4 to 5 mm long) seems to be somewhat smaller than *S. armipes*. *Sepedon anchista* was based upon a single specimen discovered in the Cornell University collection and subsequently described by Steyskal. The specimen with the locality given simply as "Montana" was included in a collection of insects purchased in 1883 by Prof. Comstock from H. K. Morrison.

During this study, collections made in Alberta yielded members of this species, and further study has produced more information on its distribution (Map E). *S. anchista* was taken at Patricia Lake, Jasper National Park, Alberta on June 25, 1957; Saint Alberts, 6 miles north of Edmonton, Alberta on June 28; 4 miles north of Red Deer, Alberta on July 4. Laboratory rearings conducted at Ithaca were carried out with adults from the Red Deer locality.

Eggs laid in the breeding jars were placed on short sections of *Typha* leaves in groups of 5 to 8. These groups resembled eggs of

other *Sepedon* spp. (Fig. 1). They hatched 4 to 4½ days after oviposition (4 observations).

First-instar larvae were offered individuals of *Helisoma trivolvis* and *Physa* sp. The larvae attacked these snails readily and fed on the soft parts. The first stadium was 3½ to 4 days in duration (12 observations).

Second- and third-instar larvae were offered *Australorbis glabratus*, in addition to *H. trivolvis* and *Physa* sp., and these were killed and consumed with the same facility as the others. The second stadium occupied 3 to 4 days, and the third was 5 to 7 days in duration (12 observations on each stadium). Although size of the snails seemed to influence the total number of individual snails destroyed, a larva usually accounted for at least one snail daily during these stadia.

The third stadium terminated with the formation of the dark brown puparium. Although eggs and larvae of this species were indistinguishable from the eggs and larvae of *S. armipes*, differences in the color and markings of their puparia permitted easy separation of the 2 species. Mixed cultures of larvae set up in the field were sorted using these puparia characters. However, these differences must be used cautiously, for several species of this genus, notably *S. caerulea*, *S. macro pus*, and *S. fuscipennis*, have been observed to produce puparia of distinctly different (light and dark) color phases.

Time from formation of the puparium to emergence of the adult was 6 to 7 days (9 observations). The newly emerged adults were placed in breeding jars. The preoviposition period was determined for one female; 3 other females laid no eggs. The single female which emerged on August 4, 1957 eventually laid a total of 82 viable eggs from December 29 to January 22, 1958. Her preoviposition period was 147 days, one of the longest observed during this study. All females were given the mixture of brewers' yeast and honey, and were handled in the same manner.

The failure of other females to produce eggs suggests this female's performance was exceptional. It may be that long periods of illumination in the laboratory, coupled with relatively constant temperatures, stimulated egg production. Further study of the effects of the cycle of illumination (Lees, 1955) on vitellogenesis and egg production is necessary before conclusions can be reached.

The longevity of laboratory-reared flies was 158 to 178 days for 4 females and 160 to 178 days for 5 males.

Description of Immature Stages

Egg: (Similar to Fig. 10). Yellowish white. Length 0.86 to 0.95 mm (= 0.90 mm); width 0.23 to 0.26 mm (X = 0.24 mm). Single rounded, transverse protuberance shielding micropyle dorsally. Five to 8 anastomosing longitudinal ridges with incomplete transverse ridges in grooves between longitudinal ridges. End opposite micropyle with hemispherical tubercle bearing minute punctations on surface. Ventral and lateral surface with longitudinal ridges. (Based on 7 specimens.)

First-instar larva: White; integument transparent. Length 1.3 to 1.7 mm (X = 1.4 mm); width 0.3 to 0.4 mm (X = 0.32 mm). Closely resembling the first-instar larva of *S. haplobasis*. Cephalopharyngeal skeleton

(as Fig. 29), length 0.26 to 0.28 ($X = 0.27$ mm) with paired mouthhooks, each with bifid hook anteriorly; ventral arch beneath mouthhooks; fused hypostomal-pharyngeal sclerite articulating with posterior borders of mouthhooks. Segments 5 to 10 each with disposition of tubercles as in *S. haplobasis*. Posterior spiracular disc (as Fig. 18) with 2 pairs of prominent lobes, ventral pair rounded apically, ventrolateral pair with thumb-like projection dorsoapically. Two spiracular plates, each with 4 palmately-branched interspiracular bristles, surrounding B-shaped spiracular opening. (Based on 4 specimens.)

Second-instar larva: White; integument transparent. Length 2.0 to 3.1 mm ($X = 2.5$ mm); width 0.7 to 1.1 mm ($\bar{x} = 0.9$ mm). Closely resembling the second-instar larvae of *S. haplobasis* and *S. armipes*. Cephalopharyngeal skeleton (as Fig. 27), length 0.48 to 0.50 mm ($\bar{X} = 0.49$ mm) with paired mouthhooks, each bearing 3 decurved accessory teeth beneath hook portion; ventral arch below mouthhooks with 22 to 26 teeth on anterior margin, posterior border bilobed (as Fig. 30); fused hypostomal-pharyngeal sclerite articulating with posterior edges of mouthhooks. Segment 2 with anterior spiracles on each side posterolaterally, each with 6 to 8 rudimentary papillae. Segments 5 to 10 each bearing close-set, triangular integumentary scales (as Fig. 21) dorsally and laterally; dorsal, dorsolateral hair patches small, circular areas bearing 1 to 5 bristles each; lateral tubercle groups and ventral transverse groups with arrangement as *S. haplobasis*. Posterior spiracular disc (as Fig. 16), with 2 pairs of prominent lobes, ventral pair triangular rounded apically, ventrolateral pair blunt apically with thumb-like projection dorsoapically. Two spiracular plates, each with 4 palmately-branched processes serving as float hairs alternating with 3 elongate, oval spiracular openings. (Based on 3 specimens.)

Third-instar larva: Yellowish white to light brown; integument transparent. Length 6.3 to 8.2 mm ($X = 7.4$ mm); width 1.6 to 2.1 mm ($\bar{x} = 1.8$ mm). Resembling in most respects the third-star larva of *S. haplobasis*. Cephalopharyngeal skeleton (as Fig. 25), length 0.70 to 0.77 mm ($X = 0.73$ mm), with paired mouthhooks, each bearing 3 or 4 decurved accessory teeth beneath hook portion; ventral arch articulating with ventral margins of mouthhooks, bearing 22 to 28 teeth on anterior edge, posterior border bilobed (as Fig. 30); pharyngeal sclerite with dark longitudinal stripe extending from parastomal rods, dark pigmentation lines extending from longitudinal stripe. Segment 2 with anterior spiracles, one on each side posterolaterally, each spiracle (Fig. 40) bearing 7 to 10 papillae on slightly expanded distal portion, body of spiracle tapering apically. Segments 5 to 10 bearing tan, triangular integumentary scales dorsally and laterally, hyaline scales forming light oblique stripes running posterodorsally (similar to Fig. 11, os); dorsal and dorsolateral hair patches small circular areas bearing 1 to 5 bristles; lateral and ventral transverse tubercle groups as *S. haplobasis*. Posterior spiracular disc (as Fig. 14) with 2 pairs of prominent lobes, ventral pair about as wide as long, rounded apically, ventrolateral pair with a thumb-like projection dorsoapically; paired lateral lobes low, conical projections; dorsal and dorsolateral pair usually inconspicuous protuberances of dorsal, crescentic border of disc. Two spiracular plates, each with 4 palmately-branched processes (.096 to .120 mm in length) alternating with 3 spiracular openings, processes as long as tuberculate spiracle tube (Fig. 37, ST). Anal plate twice as wide as long with anal proleg on anterior margin. (Based on 18 specimens.)

Puparium: (Figs. 58, 59). Dark brown with stramineous markings. Length 4.3 to 4.8 mm ($\bar{x} = 4.6$ mm); width 1.6 to 2.0 mm ($\bar{x} = 1.7$ mm).

Middorsal stripe evident, bordered on each side by lighter iridescent lines. Lateral edges of dorsal cephalic cap light tan. Oblique stripes on segments 6 to 9 light tan. Light, shagreen areas markings positions of lateral and ventral tubercle groups. Upturned posterior end forming 105 to 115° angle with longitudinal axis of body, bearing spiracular plates on shrunken disc, float hairs appressed to surface of spiracle tube. (Based on 14 specimens.)

SEPEDON BIFIDA Steyskal

Wasman Jour. Bio. 8(3) :280-82. 1950.

This California species differs from other members in the *armipes* group in possessing only traces of parafrontal spots. Males have the basimedial prong on the hind femur distinctly bifid. *Sepedon bifida* is similar to the more widespread *S. armipes* in size (4.5 to 6.0 mm long). Prior to Steyskal's 1950 revision, it probably had been misdetermined frequently as *S. armipes*. From collection records, *S. bifida* seems much more restricted in distribution than *S. armipes* (Map E). Although the distribution indicated here is broader than previously reported, *S. bifida* seems confined to the central and southern regions of California.

The material for this rearing was provided by Dr. T. W. Fisher, Department of Biological Control, University of California, Riverside. Adults were collected at Vail Lake, Riverside Co., California, on October 22, 1964. Rearings were carried out in a constant temperature room in the Department of Biology, Virginia Polytechnic Institute, Blacksburg, Virginia. A temperature of 20° C and a relative humidity of 50% were maintained during the rearing period.

Females oviposited on the sides of the breeding jars or on moss sprigs at the bottom of the jar. Eggs were usually laid in groups of 4 to 6, although single eggs were observed. Eggs hatched in 4 to 5½ days (12 observations).

Newly-hatched larvae were provided with small individuals of *Helisoma trivolvis*, *Physa* sp., and *Gyraulus parvus*. These snails were attacked, killed, and devoured in several hours. Each larva killed and devoured from 8 to 15 snails. Based on 18 observations, durations of 3 larval stadia were : first, 3 to 5 days ; second, 4 to 6 days ; third, 5 to 8 days. The period from puparium formation to emergence of the adult was 10 to 12 days (16 observations).

In 8 instances, the preoviposition period ranged from 19 to 28 days ; average was 21 days. In its native habitat, *S. bifida* behaves as *S. praemiosa* and *S. macropus* — breeding throughout the year with no recognizable generations. During the winter (January through March) or dry periods, population numbers are reduced.

Longevity records for laboratory-reared material ranged from 80 to 140 days for 7 females, and 52 to 131 days for 5 males.

Description of Immature Stages

Egg: (Resembling Fig. 10). Dirty cream-white. Length 0.90 to 1.06 mm = 1.00 mm ; width 0.29 to 0.48 mm = 0.33 mm). Single transverse tubercle shielding micropyle dorsally. Five to 9 anastomosing longitudinal ridges dorsally, with small transverse ridges in grooves between longitudinal ridges. End opposite micropyle with prominent hemispherical punctate tubercle. Ventral and lateral chorion surface with longitudinal ridges. (Based on 15 specimens.)

First-instar larva: White; integument transparent. Length 1.0 to 2.8 mm (X = 1.8 mm); width 0.3 to 0.8 mm (X = 0.5 mm). Resembling first-instar larvae of *S. haplobasis* and *S. armipes*. Cephalopharyngeal skeleton (as Fig. 29), length 0.20 to 0.22 mm (X = 0.21 mm) with paired mouthhooks, each hook bifid anteriorly; ventral arch beneath mouthhooks; combined hypostomal-pharyngeal sclerite articulating with posterior margins of mouthhooks. Tubercle arrangement on segments 5 to 10 as in *S. haplobasis*. Posterior spiracular disc (similar to Fig. 18) with 2 pairs of prominent lobes, a ventral pair rounded apically, a ventrolateral pair with a dorsoapical projection. Each spiracular plate with 4 palmately-branched interspiracular processes surrounding B-shaped spiracle opening. (Based on 10 specimens.)

Second-instar larva: Dirty white; integument transparent. Length 2.6 to 5.2 mm (X = 4.1 mm); width 0.6 to 1.4 mm (X = 1.0 mm). Resembling second-instar larva of *S. haplobasis*. Cephalopharyngeal skeleton (as Fig. 27), length 0.44 to 0.47 mm (X = 0.45 mm), with paired mouthhooks, each hook with 3 accessory teeth beneath apical portion; ventral arch below mouthhooks, posterior margin bilobed (as Fig. 30); fused hypostomal-pharyngeal sclerite articulating with posterior edges of mouthhooks. Segment 2 with anterior spiracles, one on each side posterolaterally, each with 6 to 8 rudimentary papillae. Segments 5 to 10 each with lateral and ventral tubercle groups and integumentary scales as in *S. haplobasis*. Posterior spiracular disc (as Fig. 16) with 2 or 3 pairs of prominent lobes, ventral pair triangular or conical, ventrolateral pair with pronounced thumb-like projection dorsoapically, lateral pair conical when produced. Two spiracular plates, each with 4 interspiracular processes alternating with 3 elongate, oval, almost-parallel spiracular slits. (Based on 10 specimens.)

Third-instar larva: Yellowish brown to brown; integument transparent. Length 7.0 to 9.5 mm (X = 8.3 mm); width 2.0 to 2.8 mm (X = 2.4 mm). Resembling closely the third-instar larva of *S. haplobasis*. Cephalopharyngeal skeleton (as Fig. 25), length 0.69 to 0.75 mm (X = 0.71 mm) with paired mouthhooks, each bearing 3 or 4 decurved accessory teeth beneath hook portion, ventral arch articulating with ventral margins of mouthhooks, bearing 22 to 26 small teeth on anterior edge, posterior border bilobed (as Fig. 30); hypostomal and pharyngeal sclerites as in *S. haplobasis*. Segment 2 with anterior spiracles, one on each side posterolaterally, each spiracle (as Fig. 41) bearing 8 to 10 papillae on expanded distal portion. Segments 5 to 10 with dorsal and dorsolateral hair patches, lateral, and ventral transverse tubercle groups as in *S. haplobasis*. Posterior spiracular disc (as Fig. 14) with 2 or 3 pairs of prominent lobes; ventral pair about as wide as long, rounded apically; ventrolateral pair with a pronounced thumb-like projection dorsoapically; lateral lobes often produced as conical projections; dorsal and dorsolateral tubercles inconspicuous. Two spiracular plates, each plate with 4 palmately-branched interspiracular processes alternating with 3 elongate-oval spiracular openings, the processes as long as tuberculate spiracular tube. (Based on 12 specimens.)

Puparium: (Figs. 62, 63). Dark yellowish-brown without lighter markings. Length 5.3 to 5.7 mm (X = 5.5 mm); width 2.2 to 2.5 mm (X = 2.4 mm). Middorsal stripe lacking and no oblique stripes evident on segments 5 to 9. Light shagreen areas marking lateral and ventral tubercle groups. Posterior end upturned, forming 100 to 130° angle with longitudinal axis of body. Spiracular plates on shrunken disc, interspiracular processes appressed to spiracular tubes. (Based on 10 specimens.)

SEPEDON NEILI Steyskal

Wasman Jour. Bio. 8(3) :286-87. 1950.

This is one of the four species (*borealis*, *lignator*, *neili*, and *pusilla*) that were included in "*Sepedon pusilla*" of authors until Steyskal (1950) found distinguishing characters in the male genitalia. Adults of all are small, dark brown flies, 4.0 to 6.0 mm long. These species are so similar that wild-caught females cannot be distinguished. Consequently, the notes and preserved material resulting from a rearing in this group cannot be assigned to any species until an adult male has been reared, killed, and properly prepared.

Sepedon neili occurs from New Hampshire and Massachusetts south to North Carolina and west to Idaho and Utah (Map F). Although widely distributed, it is "most abundant in the Northeast" (Steyskal, 1950). The type locality is Rushton, Livingston Co., Michigan.

Adults used in the laboratory rearings at Ithaca, N. Y. were obtained at Cedar Swamp Preserve, 7.3 miles south of Urbana, Champaign Co., Ohio on July 3, 1958. They were collected with *S. armipes* from low grasses and sedges along the unshaded and relatively open margins of a slow-moving stream.

Eggs were laid singly or in groups of 2 to 4 on moss sprigs at the bottoms of breeding jars (Fig. 10). They hatched in $3\frac{1}{2}$ to 4 days (3 observations).

First-instar larvae were offered *Helisoma trivolvis*, 2 to 4 mm in diameter. These were attacked and consumed in several hours. As the larvae developed, they also were offered *Australorbis glabratus*, *Lymnaea palustris*, and *Physa* sp. All snails were killed with equal facility. Based on 8 observations, durations of the 3 larval stadia were: first, 3 to 4 days; second, 3 to 4 days; third, 5 to 6 days. Time from puparium formation to emergence was 7 to 9 days (7 observations).

Reproductive activities of a wild-caught female and of laboratory-reared adults that emerged August 23-28, 1958 provided some evidence concerning the seasonal aspects of this species. The parent female died October 2, after laying her last viable eggs on September 27. The adults that developed from her eggs (4 males, 3 females) neither mated nor oviposited until the following spring. One pair was first observed mating April 15, 1959, and eggs were first seen on April 18. Another female laid her first eggs on April 23, but a third did not oviposit until June 2. The overwintered females continued to produce eggs until they died in late June and early July. Although the third pair survived until August 13, the female produced her last eggs on July 11. Rearings initiated with eggs laid by the overwintered flies produced the first adults of a spring-summer generation on May 23. These adults began to oviposit in the middle of July and survived until October 5.

This species evidently overwinters in the adult stage and probably has 2 generations per year. The second generation of the season, produced in mid- to late summer, overwinters and lays no eggs until the following spring. The spring-summer generation produced from

these eggs then oviposits from the middle of July to early September to produce another overwintering generation. Although the data are not as complete for *S. borealis* and *S. pusilla*, available evidence indicates that their reproductive activity is similarly synchronized with the seasons.

The preoviposition periods for the overwintering females were 240, 244, and 279 days, and they produced 107, 84, and 67 eggs, respectively. A female of the spring-summer generation had a preoviposition period of 53 days and laid 79 eggs. The wild-caught female from Cedar Swamp (presumably an individual of the spring-summer generation) produced 228 eggs after she was captured on July 3.

Longevity records for laboratory-reared adults of the overwintering generation ranged from 178 to 351 days. Those of the spring-summer generation were 111 and 136 days (male and female, respectively).

Description of Immature Stages

Egg: (Fig. 10). White or yellowish white. Length 0.88 to 0.91 mm (\bar{X} = 0.89 mm); width 0.26 to 0.27 mm (\bar{X} = 0.264 mm). Rounded, transverse protuberance bearing minute punctations shielding micropyle dorsally. Seven to 10 anastomosing longitudinal ridges dorsally; grooves between ridges with incomplete transverse ridges, giving reticulate appearance to chorion surface. Slightly flattened hemispherical tubercle at end opposite micropyle with punctations. Ventral and lateral surfaces with low, longitudinal ridges. (Based on 9 specimens.)

First-instar larva: White; integument transparent. Length 1.1 to 2.7 mm (\bar{X} = 1.9 mm); width 0.2 to 0.5 mm (\bar{X} = 0.4 mm). Closely resembling first-instar larva of *S. haplobasis*. Cephalopharyngeal skeleton (as Fig. 29) length 0.18 to 0.29 mm (\bar{X} = 0.24 mm) with paired mouthhooks, each with bifid hook anteriorly; ventral margins of mouthhooks articulating with ventral arch below, posterior margins articulating with fused hypostomal-pharyngeal sclerite behind. Segments 5 to 10 without evident dorsal and dorsolateral hair patches; lateral tubercle groups and ventral transverse tubercle groups arranged as in *S. haplobasis*. Posterior spiracular disc (as Fig. 18) with 2 pairs of prominent lobes ventral and ventrolaterally. Two spiracular plates in central area of disc, each with 4 palmately branched processes surrounding B-shaped spiracular openings. Anal proleg small, inconspicuous protuberance on anterior margin of anal plate. (Based on 6 specimens.)

Second-instar larva: White; integument transparent. Length 2.7 to 5.3 mm (\bar{X} = 3.4 mm); width 0.4 to 1.1 mm (\bar{X} = 0.6 mm). Closely resembling second-instar larva of *S. haplobasis*. Cephalopharyngeal skeleton (as Fig. 27), length 0.34 to 0.40 mm (\bar{X} = 0.37 mm); with paired mouthhooks, each bearing 3 slightly decurved accessory teeth beneath hook, ventral margins articulating with ventral arch below, posterior margins with fused hypostomal-pharyngeal sclerite behind. Segment 2 with anterior spiracles on each side posterolaterally, each spiracle bearing 6 to 8 rudimentary papillae on distal margin. Segments 5 to 10 lacking dorsal and dorsolateral hair patches; lateral tubercle group and ventral transverse groups as in second-instar *S. haplobasis*. Posterior spiracular disc (as Fig. 16) with 2 pairs of prominent lobes; ventral pair rounded apically; ventrolateral pair with thumb-like projection dorsoapically. Lateral lobes low, conical protuberances; dorsolateral and dorsal lobes inconspicuous. Two spiracular plates

in central area of disc, each with 4 palmately-branched interspiracular processes alternating with 3 elongate spiracular slits; processes only half as long as tuberculate spiracular tube (Fig. 39). Anal plate slightly bilobed, with anal proleg on anterior border. (Based on 14 specimens.)

Third-instar larva: White or yellowish white; integument transparent. Length 6.3 to 8.2 mm (\bar{X} = 7.3 mm); width 1.5 to 1.8 mm (\bar{X} = 1.7 mm). Closely resembling third-instar larva of *S. haplobasis*. Cephalopharyngeal skeleton (as Fig. 22), length 0.60 to 0.72 mm (\bar{X} = 0.64 mm); with paired mouthhooks, each with 3 slightly decurved accessory teeth beneath hook (as Fig. 36), ventral margins of mouthhooks articulating with ventral arch beneath, posterior margins with hypostomal sclerite behind; pharyngeal sclerite dark with pigmentation lines radiating from dark central area of sclerite. Segment 2 bearing anterior spiracles on each side posterolaterally, each spiracle (Fig. 43) with 9 to 11 round papillae on slightly expanded distal portion. Segments 5 to 10 lacking dorsal and dorsolateral hair patches; lateral tubercle groups and central transverse tubercle groups as in *S. haplobasis*. Posterior spiracular disc (as Fig. 14) with 2 pairs of prominent lobes, as in *S. haplobasis*: ventral pair rounded apically; ventrolateral pair blunt, with thumb-like dorsoapical projection. Two spiracular plates, each with 4 palmately-branched interspiracular processes (.052 to .062 mm long) alternating with 3 elongate spiracular openings; processes only half as long as tuberculate spiracular tube bearing spiracular plate. Anal plate bearing anal proleg on anterior margin. (Based on 16 specimens.)

Puparium: (Similar to Figs. 62, 63). Light yellowish brown; opaque. Length 3.8 to 4.5 mm (\bar{X} = 4.2 mm); width 1.6 to 2.0 mm (\bar{X} = 1.7 mm). Middorsal stripe not evident. Posterolateral margins of dorsal cephalic cap lighter than median area. Segments 6 to 9 lacking oblique stripes dorsolaterally; lateral and ventral transverse tubercle groups appearing as shagreen areas, lateral group with brown shadings. Upturned posterior end forming angle of 100° to 140° with longitudinal axis of body, bearing apically shrunken spiracular disc with spiracular tubes above surface of disc. Anal plate dark brown. (Based on 10 specimens.)

SEPEDON PUSILLA Loew

Wien. ent. Monatsch. 3:299. 1859.

Until Steyskal's revision (1950), this species was considered to be widely distributed in North America. It had been recognized as distinct from *S. armipes*, since the males of *S. pusilla* lack the prominent emargination of the hind femora. As in the *S. armipes* group, "*S. pusilla*" of authors was found to be a complex of species, known since 1950 as the "*pusilla* group." In diagnosing the *S. pusilla* group, Steyskal applied the name *pusilla* to the species distributed in the southeastern United States on the basis of material included in Loew's type series.

Sepedon pusilla has been recorded from the District of Columbia south to Georgia, and west to Indiana and Kentucky (Map F). Adults used in the laboratory rearings were collected, together with adults of *S. armipes* and *S. fuscipennis*, at the Town Reservoir, 0.6 of a mile north of Hardinsburg, Breckinridge Co., Kentucky on July 18, 1956. The flies were found resting on grasses growing under a canopy of sycamores (*Platanus occidentalis* L.). Willows

(*Salix* sp. ?) and alders (*Alnus* sp. ?) were also common along the margins of the reservoir.

Females confined in laboratory breeding jars laid their eggs singly or in groups of 2 or 3 on upright sprigs of moss at the bottom of the jar. Their positions were similar to those of *S. neili* eggs, illustrated in Fig. 10. This method of laying eggs singly or in small groups was observed in other members of the *pusilla* group, *S. neili* and *S. borealis*, that were studied in the laboratory.

Eggs hatched in 3 to 4 days (2 observations), and the first-instar larvae were given small individuals of *H. trivolvris*, *Physa* sp., and *Australorbis glabratus*. The larvae attacked and destroyed these snails with facility. As the larvae developed, larger snails (5 to 10 mm diameter) were placed in the rearing jars and were also consumed. The larval stadia were : first, $2\frac{1}{2}$ to $3\frac{1}{2}$ days; second, 3 to 4 days; third, 5 to 7 days (duration of each stadium based on 7 observations).

Puparia, quite similar in appearance to puparia of *S. armipes* but lacking oblique stripes laterally, were formed on sand in the rearing jar. In 6 to 9 days after the puparia were formed, adult flies emerged (7 observations). These flies were held in order to determine longevity, egg production, and preoviposition period. Six females were obtained in the rearings, but the 3 males that emerged died within 10 days after emergence. As a result, the females were not mated and no eggs were obtained. These females lived from August 14, 1956 until March 26, 1957 (224 days).

There are indications that seasonal aspects of *S. pusilla* are similar to those of *S. neili* and *S. borealis*. Apparently all species overwinter as adults. The overwintered adults produced eggs from late spring to early summer. These eggs give rise to a generation of adults early in July. The adults of the spring-summer generation produce a generation that appears by the middle of August. This late-summer generation produces no eggs until the following spring.

A comparison of 2 collections of *S. pusilla* from the Hardinsburg, Kentucky locality may be instructive. The July 18, 1956 collection was the basis of this rearing, and the adults reproduced as readily as any species of the *pusilla* group reared in the laboratory. Another collection made at the Town Reservoir on August 28, 1957 netted 5 females and 4 males. Although these adults survived in the laboratory until March 24, 1958, the females produced no eggs. This suggests the overwintering generation was encountered in the August collection, while the July collection represented a part of the spring-summer generation.

Description of Immature Stages

Egg: (Similar to Fig. 10). Yellowish white, length 0.97 to 0.98 mm (= 0.974 mm); width 0.33 to 0.34 mm (X = 0.334 mm). Single truncate protuberance shielding micropyle dorsally. Five to 9 anastomosing longitudinal ridges dorsally, with prominent transverse ridges in grooves producing irregular polygonal areas over dorsal surface. End opposite micropyle with small hemispherical tubercle bearing minute punctations on its surface. Ventral and lateral surfaces with low longitudinal ridges. (Based on 7 specimens.)

First-instar larva: White; integument transparent. Length 1.5 to 1.6 mm (= 1.53 mm); width 0.3 mm ($X = 0.3$ mm). Closely resembling first-instar larva of *S. haplobasis*. Cephalopharyngeal skeleton (similar to Fig. 29), length 0.22 to 0.24 mm (= 0.23 mm); with paired mouthhooks, each bearing bifid hook anteriorly; ventral arch articulating with ventral margins of mouthhooks below; fused hypostomal-pharyngeal sclerite articulating with wing-like posterior borders of mouthhooks. Dorsal hair patches, lateral tubercles, and ventral transverse groups as in *S. haplobasis*. Posterior spiracular disc (as Fig. 18) with 2 pairs of lobes: ventral pair rounded apically; ventrolateral pair bearing short, thumb-like projection dorsoapically. Dorsal border of disc evenly arcuate. Two spiracular plates in center of disc, each with 4 palmately-branched processes surrounding B-shaped spiracular opening. Anal proleg small, inconspicuous. (Based on 3 specimens.)

Second-instar larva: White with tan shading dorsally; integument transparent. Length 2.6 to 4.0 mm ($\bar{X} = 3.4$ mm); width 0.6 to 1.1 mm (= 0.8 mm). Closely resembling second-instar larva of *S. haplobasis*. Cephalopharyngeal skeleton (similar to Fig. 27) length 0.42 to 0.45 mm ($X = 0.44$ mm); paired mouthhooks, each bearing 2 to 3 decurved accessory teeth beneath hook; ventral arch below mouthhooks, with 22 to 26 teeth on anterior margin, posterior margin bilobed, fused hypostomal-pharyngeal sclerite articulating with posterior margins of mouthhooks. Segment 2 with anterior spiracles, one on each side posterolaterally, each bearing 6 to 8 rudimentary papillae apically. Segments 5 to 10 each bearing groups of tan integumentary scales dorsally and laterally; dorsal and dorsolateral hair patches small circular areas bearing 1 to 4 bristles, or patches lacking; lateral and ventral transverse tubercle groups arranged as in *S. haplobasis*. Posterior spiracular disc (similar to Fig. 16) with 2 pairs of prominent lobes: ventral pair tapering, rounded apically; ventrolateral pair bearing pointed, thumb-like projection dorsoapically. Lateral, dorsolateral, dorsal lobes inconspicuous, low tubercles. Two spiracular plates in central area of disc, each with 4 palmately-branched interspiracular processes alternating with 3 spiracular openings; processes as long as spiracular tube supporting spiracular plate. Anal plate twice as wide as long, with anal proleg a rounded protuberance on anterior border. (Based on 6 specimens.)

Third-instar larva: Yellowish white with brown shading; integument transparent. Length 5.4 to 7.2 mm ($X = 6.3$ mm); width 1.3 to 2.2 mm ($\bar{X} = 1.7$ mm). Resembling *S. haplobasis* third-instar larva. Cephalopharyngeal skeleton (as Fig. 25), length 0.66 to 0.72 mm ($X = 0.68$ mm); paired mouthhooks, each bearing 3 to 4 decurved accessory teeth below hook portion; ventral arch beneath mouthhooks, with 22 to 26 teeth on anterior margin, posterior border conspicuously bilobed (as Figs. 30 through 33); posterior margin of mouthhooks articulating with hypostomal sclerite; pharyngeal sclerite with lines of pigmentation radiating from pigmented longitudinal stripe. Segment 2 bearing anterior spiracles, one on each side posterolaterally, each spiracle (Fig. 44) bearing 9 to 11 round papillae on slightly expanded distal portion. Segment 4 usually with a transverse brown stripe dorsally. Segments 5 to 10 each with close-set, brown, integumentary scales dorsally and laterally, those of segment 10 imbricate, elongate (Fig. 20); dorsal and dorsolateral hair patches small, circular areas bearing 1 to 4 bristles, or lacking; lateral and ventral transverse tubercle groups as in *S. haplobasis*. Posterior spiracular disc (as Fig. 14) with 2 pairs of conspicuous lobes: ventral pair about as long as wide, rounded apically; ventrolateral pair with pointed, thumb-like projection dorsoapically. Lateral lobes low, conical; dorsolateral and dorsal lobes low, rounded, forming

dorsal border of disc. Two spiracular plates in central area of disc, each with 4 palmately-branched interspiracular processes or "float hairs" (.080 to .118 mm in length) alternating with 3 spiracular openings; processes as long as tuberculate spiracular tube supporting spiracular plate (Fig. 37, ST). Anal plate twice as wide as long, with anal proleg a round protuberance on anterior margin. (Based on 9 specimens.)

Puparium: (Similar to Figs. 62, 63). Brown, with dorsal and ventral cephalic caps yellowish. Length 4.1 to 4.7 mm = 4.5 mm; width 1.7 to 2.0 mm (X = 1.8 mm). Middorsal stripe absent. Brown crescentic transverse stripe in middle of dorsal cephalic cap. No oblique stripes on segments 6 to 9; secondary segmental furrows light brown; lateral and ventral transverse tubercle groups appearing as shagreen areas. Uprturned posterior end forming angle of 110 to 140° with longitudinal axis of puparium with spiracular plates evident above shrunken disc. Interspiracular processes appressed to sides of spiracular tube bearing spiracular plate. (Based on 7 specimens.)

SEPEDON BOREALIS Steyskal

Wasman Jour. Bio. 8(3) : 283-85. 1950.

This species is closely related to *S. pusilla* but can be reliably distinguished from it by characteristics of the male genitalia. It is practically impossible to identify living flies moving around in a collecting vial in any area where more than one of the sibling species in the *pusilla* group occurs.

Sepedon borealis has a wide distribution in North America north of the 37th parallel, north latitude (Map F). The type locality is Yale, Idaho. Many of the northern and western records of *S. pusilla* prove to be errors based on specimens of *S. borealis* and *S. neili*. The adults that produced the immature stages described below were collected in the grass-sedge meadow surrounding Mud Pond at the McLean Reservation, 41½ miles northeast of Dryden, Tompkins Co., New York, on May 22, 1956, June 29, 1958, and June 14, 1959. The flies seemed especially common in the wetter areas of the meadow and near the alder thickets at the borders of Mud Pond. Although other sciomyzids were commonly collected in the more shaded areas of the site, *S. borealis* was not encountered there.

Eggs laid in the breeding jars were attached (singly or in groups of 2 to 4) to sprigs of moss at the bottom of the jars. The females often laid several groups of eggs on the same oviposition site at different periods (Fig. 8). They seemed to select the moss for oviposition rather than sections of *Typha leaf*.

Eggs hatched in 3½ to 4 days (6 observations), and the small, first-instar larvae were fed individuals of *Helisoma trivolvis*, 2 to 6 mm in diameter. These larvae quickly attacked and destroyed the snails in typical fashion. In the course of the rearings, *Physa sp.*, *Lymnaea humilis*, and *Australorbis glabratus* were also killed and consumed by the developing larvae. Based on 15 observations, durations of the larval stadia were : first, 3 to 4 days ; second, 4 to 5 days; third, 8 to 10 days.

The puparium of this species has not been found in nature. In rearing jars, puparia were often buried in small clumps of moss or under the sand with only the anterior end visible. This observation coupled with the fact that the posterior end of the puparium is not upturned as it is in the majority of the known *Sepedon* spp. (presumably an adaptation of floating puparia to obtain air through the surface film) suggests that the habit of burrowing into the substrate may be common in nature.

Adult flies emerged 8 to 10 days after formation of the puparia (8 observations). Although laboratory females lived up to 72 days after emergence, they neither mated nor laid eggs. Attempts to keep adults in the laboratory during the winter were unsuccessful; the majority of adults died by the middle of November.

The available evidence suggests that *S. borealis* overwinters in the Ithaca area as an adult. The seasonal activities of this species seem to be quite similar to those proposed for *S. neili* and *S. pusilla*. Adults taken in May and June (May 22, 1956; June 29, 1958; June 14, 1959) had ragged wing margins, missing tarsal segments, and broken or missing setae, suggesting that they had lived through the winter. These wild-caught flies survived in the laboratory until about August 1st. The females produced viable eggs early in their confinement but usually became sluggish and ceased ovipositing around the middle of July. The adult females reared from these eggs failed to oviposit and did not survive well in the laboratory (see above).

Although *S. borealis* probably is similar to other species of the *pusilla* group in producing 2 generations per year, these generations may be overlapped and poorly defined in nature. Laboratory observations of adult survival and duration of the life cycle indicate that overwintering females may continue to lay eggs as their daughters enter the adult population and begin to oviposit, if an adequate diet is available. It is also possible that some of the daughters produce eggs soon after emergence, while others remain barren until the following spring. Wild-caught females taken in August laid no eggs; they probably represented that part of the population destined to go through the winter.

Description of Immature Stages

Egg: (Fig. 8). White or yellowish white. Length 0.81 to 0.93 mm (= 0.89 mm); width 0.25 to 0.28 mm (= 0.27 mm). Rounded transverse, minutely punctate protuberance shielding micropyle dorsally. Seven to 10 anastomosing longitudinal ridges, grooves between with incomplete transverse ridges. End opposite micropyle with inconspicuous, punctate hemispherical tubercle. Ventral and lateral surfaces with low, longitudinal ridges. (Based on 16 specimens.)

First-instar larva: White; integument transparent. Length 1.5 to 2.4 mm (\bar{X} = 2.0 mm); width 0.3 to 0.5 mm (\bar{X} = 0.4 mm). Closely resembling the first-instar larva of *S. haplobasis*. Cephalopharyngeal skeleton (as Fig. 29), length 0.25 to 0.28 mm (= 0.26 mm); with paired mouthhooks, each with bifid hook anteriorly; ventral arch beneath mouthhooks, articulating with their ventral margins; fused hypostomal-pharyngeal sclerite articulating with wing-like posterior borders of mouthhooks. Segments 5 to 10, each with hair patches, lateral tubercles, ventral transverse tubercles as in *S.*

haplobasis. Posterior spiracular disc (similar to Fig. 18) with 2 pairs of prominent lobes, as in *S. haplobasis*. Two spiracular plates in central area of disc, each with 4 palmately-branched processes around the B-shaped spiracular opening. Anal plate twice as wide as long, with inconspicuous anal proleg on anterior margin. (Based on 7 specimens.)

Second-instar larva: White; integument transparent. Length 2.2 to 4.5 mm ($\bar{X} = 3.5$ mm); width 0.4 to 0.9 mm ($\bar{X} = 0.7$ mm). Resembling second-instar larva of *S. haplobasis*. Cephalopharyngeal skeleton (similar to Fig. 27) length 0.33 to 0.38 mm ($\bar{X} = 0.35$ mm); with paired mouthhooks, each bearing 2 or 3 decurved accessory teeth beneath hook; ventral arch with 22 to 26 teeth on anterior border, posterior margin *bilobed*; fused hypostomal-pharyngeal sclerite articulating with posterior margin of mouthhooks. Segment 2 bearing anterior spiracles, 1 on each side posterolaterally; each spiracle with 5 to 7 rudimentary papillae on distal border. Segments 5 to 10 without evident dorsal and dorsolateral hair patches; lateral tubercle groups and ventral transverse groups as in *S. haplobasis*. Posterior spiracular disc (similar to Fig. 16) with 2 pairs of prominent lobes, ventrally and ventrolaterally. Lateral lobes low, conical protuberances; dorsolateral and dorsal lobes inconspicuous, forming dorsal border of disc. Two spiracular plates, each bearing 4 palmately-branched processes alternating with 3 spiracular openings. Anal plate and proleg as in *S. haplobasis*. (Based on 19 specimens.)

Third-instar larva: White or yellowish white; integument transparent. Length 4.5 to 7.2 mm ($\bar{X} = 5.8$ mm); width 0.8 to 1.7 mm ($\bar{X} = 1.2$ mm). Resembling third-stage larva of *S. haplobasis*. Cephalopharyngeal skeleton (Fig. 22), length 0.54 to 0.62 mm ($\bar{X} = 0.58$ mm); with paired mouthhooks, each bearing 3 decurved accessory teeth below hook (similar to Fig. 36); ventral arch beneath articulating with ventral margins of mouthhooks, bearing 22 to 28 teeth on anterior margin, posterior border *bilobed* (as Figs. 31, 33); hypostomal sclerite articulating with posterior margins of mouthhooks; pharyngeal sclerite with lines of pigmentation as in Fig. 22. Segment 2 bearing anterior spiracles, 1 on each side posterolaterally; each spiracle (Fig. 42) bearing 5 to 8 papillae on slightly expanded distal portion. Segments 5 to 10 lacking dorsal and dorsolateral hair patches; lateral tubercle groups prominent, lower tubercle largest of group; ventral transverse tubercle groups and secondary segmental furrows evident ventrally. Posterior spiracular disc (similar to Fig. 14) with 2 pairs of prominent lobes: ventral pair tapering, rounded apically; ventrolateral pair with pointed, thumb-like projection dorsoapically. Lateral lobes low conical protuberances; dorsolateral and dorsal lobes inconspicuous, forming slightly scalloped dorsal border of disc. Two spiracular plates, each with 4 small, palmately-branched interspiracular processes (.046 to .052 mm in length) alternating with 3 spiracular openings (Fig. 39); processes only half as long as spiracular tube (Fig. 37, ST). Anal plate twice as wide as long, with anal proleg an inconspicuous protuberance on anterior border. (Based on 16 specimens.)

Puparium: (Figs. 60, 61). Light tan, without conspicuous markings. Length 3.8 to 4.8 mm ($\bar{X} = 4.4$ mm); width 1.6 to 2.0 mm ($\bar{X} = 1.8$ mm). Middorsal stripe lacking, segments 6 to 9 unicolorous, oblique stripes lacking. Secondary segmental furrows usually somewhat darker than ground color; lateral and ventral transverse tubercle groups flattened, appearing as shagreen areas. Posterior end slightly upturned, if at all, forming an angle of 150 to 180° with longitudinal axis of puparium body. Spiracular tubes bearing spiracular plates elevated above shrunken posterior spiracular disc. Float hairs inconspicuous. Anal plate dark brown forming a shallow notch in ventral surface of posterior end. (Based on 8 specimens.)

DISCUSSION

I: Relevance to Systematics

Studies of the biology and immature stages of groups of insects lead eventually to consideration of these factors in classification. Although the adaptive nature of many larval characters somewhat restricts their usefulness in taxonomy, larval attributes often provide important information that confirms or disputes conclusions suggested by characteristics of the adults. Hennig (1950) and van Emden (1957) discussed the taxonomic use of larval characters in the Diptera, and pointed out that classification schemes should make use of as many attributes as possible. Evidence provided by knowledge of the immature stages seems to bear importantly on 3 questions concerning systematic relationships in the Sciomyzidae.

Hennig (1958) was unable to decide whether the Sciomyzidae represent a monophyletic group. He remarked that at least 8 characters of the adults are primitive or plesiomorphic and concluded that in their morphological characters this family is rather close to the primitive, basic stock of the Schizophora. Since derived or apomorphic characteristics that might aid in resolving the question were difficult to detect and interpret, Hennig suggested that larvae of the family might provide them.

Support for Hennig's suggestion can be derived from genera whose larvae are known. This includes genera in the subfamilies Sciomyzinae (including both Ditaeniinae and Tetanurinae), Tetanocerinae (including Sepedoninae), and Salticellinae. The following discussion excludes genera of Helosciomyzinae and Huttonininae, because their inclusion in the Sciomyzidae seems questionable, and the fact that larvae in these groups have been neither described in the literature nor investigated by us.

Berg (1953) first suggested that snail eating is widespread among the Sciomyzidae and that the family may be integrated biologically by common food of the larvae. Subsequent research strongly supports this suggestion. All 143 species investigated (representing 26 genera) kill and feed upon gastropod mollusks. Relationships of larvae to snails range from highly specialized parasitoids that may feed upon their hosts 7 or 8 days before killing them (Foote, 1959) to the quick-killing aquatic predators discussed here. The efficiency of predatory larvae and the intimate association of parasitoid types testifies to a long evolutionary history of the sciomyzid-snail relationship. Thus, both choice of food and feeding methods of sciomyzid larvae (almost certainly apomorphic characteristics) indicate a monophyletic origin of this family.

Secondly, it is instructive to consider whether larval characters support the grouping of several genera into the subfamily Tetanocerinae, implying that they differ less among each other than they all do from the other major subfamily, Sciomyzinae. The habits and morphology of *Sepedon* larvae exemplify many genera of the Tetanocerinae, most known larvae of which are aquatic and predatory. Female flies oviposit on emergent vegetation in or near

water. Most larvae kill their prey quickly and each individual destroys a dozen or more snails. They attack and feed upon aquatic pulmonates of various families and exhibit little, if any, host specificity. Because larvae leave their last food snails just as quickly as their previous victims, puparia are not formed inside snail shells. Those of most species float freely in waters inhabited by the aquatic larvae; they are conspicuously modified to float with posterior spiracular plates thrust through the surface film and exposed to the air. Adults are found in wet areas, especially open *Typha* marshes, grass-sedge meadows, and partly shaded swamps.

Most of the known larvae of the Sciomyzinae are intimately associated with the snails they eat. Females of some species oviposit directly onto living host snails. A developing larva often feeds on the snail several days before killing it, and each larva usually destroys only 1 or 2 snails. Each larva of *Sciomyza aristalis* destroys only one snail (Foote, 1959), and there are indications of host specificity in this species. Some larvae routinely form their puparia within the host's shell, although others may leave the snail and pupate in the ground. Parasitoid habits in this family are best developed in terrestrial species, and many members of the Sciomyzinae are found in mesophytic woodlands rather than open marshes and wet meadows.

As indicated by the foregoing discussion, characters of the immature stages provide strong support for the grouping of many sciomyzid genera into the 2 major subfamilies recognized by virtually all taxonomists who have worked on this family. The major dichotomy in the known immature stages indicates essentially the same division into these 2 large subfamilies as that delineated long ago solely on morphological characters of the adults.

The third question concerns a "purely tentative" classification of the Acalyptratae (Crampton, 1944) based primarily on characteristics of the male terminalia. Without elaborating on the evidence, Crampton suggested the genus *Sepedon* is sufficiently different to be recognized as a distinct family or "possibly merely a subfamily of the Tetanoceratidae." As mentioned on page 22, Cresson (1920) and Verbeke (1950) also expressed opinions that *Sepedon*, together with certain other genera, should be segregated as a distinct subfamily. However, these taxonomists did not agree on the genera, other than *Sepedon*, to be included.

All morphological and behavioral attributes of the known *Sepedon* larvae seem to negate the separation of this genus as a subfamily. As stated above, the habits and morphology of *Sepedon* larvae are so typical of aquatic larvae in the Tetanocerinae that they exemplify the entire group rather well. *Sepedon* larvae differ no more from the known aquatic larvae of *Dichetophora*, *Dictya*, *Dictyodes*, *Elegiva*, *Guatemalaia*, *Hoplodictya*, *Hydromya*, *Knutsonia*, *Neolimnia*, *Tetanocera*, and *Tetanoceroidea* than larvae of these other tetanocerine genera differ among each other. Aquatic adaptations that characterize the entire group include tuberculate and somewhat flaccid bodies, integuments bearing minute scales and bristles, broad spiracular discs with prominent marginal lobes, and palmate float

hairs around the spiracular openings. Adaptations for effective attacks of these predators on their food snails are strong mouthhooks bearing accessory teeth, well developed ventral arches, and postoral spine bands which prevent them from slipping back when they thrust the mouthhooks forward. Larvae in all these genera have retained relatively primitive feeding behavior while elaborating body structures that maintain them more effectively in the aquatic environment.

While supplying some evidence for a monophyletic origin of the Sciomyzidae and supporting the separation of the Tetanocerinae from the Sciomyzinae, larval characters thus tend to dispute erection of the proposed subfamily Sepedoninae.

II. Relevance to Ecology

Distinctly different techniques have been used to investigate the relationships of organisms to their environments. Two of the most commonly employed approaches are almost direct opposites of each other. In one, the biologist selects a biotope or specific study area, investigates the biota and factors that may control or influence it, and often tries to analyze the ecological roles played by organisms in the community. In the other, he selects a group of organisms, studies them in as many different habitats and geographic regions as possible, and seeks to determine the conditions of life of each species in whatever community it may be found.

Both approaches are potentially rewarding, but the contributions most apt to result from each differ considerably. The first approach may enable the investigator to analyze both community structure and food web and to make quantitative estimates of both biomass and trophic dynamics. However, he needs considerable knowledge of the basic biology of species in the study area to avoid difficult problems. Certain organisms require peculiar sampling methods, and few investigators are expert in all specialized techniques. Widely divergent groups are encountered, and the help of many taxonomists is needed to compile a reliable species list. In some groups, reliable keys have never been written and contemporary specialists do not exist. Other species could be identified if the larvae collected were reared and adult males obtained. But rearing takes considerable time, even when the correct food and rearing methods are known. The investigator confronted with animals from several unfamiliar groups usually has some frustrating failures and then abandons the effort.

His list of the biota remains incomplete for all of these reasons, and his knowledge of ecological relationships often proves to be virtually nonexistent. Having been conscientious about reading and recording daily ranges in temperature, wind velocity, saturation deficit, etc., and in making a general collection, he has found little time in which to observe what the animals are doing. As a result, the really important conditions of life — those relatively few factors of the total environment that impinge critically on a species' existence and rate of population growth — are seldom recognized and elucidated by this approach.

Focusing on a single group gives the advantage of intensive comparative study of closely related organisms which share many similar characteristics. Every successful rearing suggests a likely solution to a rearing problem ; every behavioral and morphological attribute observed suggests a worthwhile point for observation on some other species. In this approach, the investigator studies until he can recognize species as members of his group without help from a taxonomic specialist. This must be true even of species he has never seen before, and it must extend to all stages of the life cycle. He learns to recognize the different breeding places occupied by various species and develops techniques of collecting living individuals of all stages to initiate laboratory rearings. In groups whose food is as uniform and predictable as in the Sciomyzidae, he can acquire such proficiency in rearing methods that a single pair of living adults gives him a better than even chance of observing the entire life cycle in the laboratory. He watches such activities as mating, oviposition, hatching, feeding, pupation, and emergence in the laboratory, and thus learns where and when to look for the same processes in nature. He observes which of the many associated species seem incidental and which are of crucial importance as prey, predators, hosts, parasites, or competitors. Also, his studies extend beyond basic biology and ecological relationships into other biological disciplines. As he draws up descriptions and figures of previously unknown immature stages, he can explain the adaptive morphology from a comparative point of view. Such intensive studies lead naturally to conclusions about evolution of and within the group and suggest investigations in physiology, genetics, and other areas of biology.

One could object that Sciomyzidae, being unusually favorable subjects for investigations, make the group-of-organisms approach look better than it turns out to be in many other groups. All larvae reared to date kill gastropod mollusks, hence it is usually no problem to find acceptable foods even for unknown larvae. Adults remain relatively calm in rearing jars and do not kill themselves by flying against the container. Perhaps most important, the Sciomyzidae are potentially valuable in the biological control of noxious snails. This provides medical and economic incentives for studying them, especially at a time when schistosomiasis, liver fluke, and other snail-borne diseases are spreading with the expansion of irrigation throughout the world. The great stimulus given to this study by the possibility that knowledge of sciomyzid biology may prove useful to mankind is evident when this research is contrasted with the study of another group of acalyptrate flies (*Drosophila* spp.) which suffered "two handicaps : the lack of economic interest and its geographic limitation" (Bates, 1949 :5). Bates continued, "Natural-history studies of *Drosophila* in the field are apt to be carried out in the vicinity of the great research centers, while many of the biological processes that demand intensive study involve the tropics and areas remote from research centers. Support for such work is almost unobtainable without a direct economic incentive." Because man's problems with snail-borne diseases are primarily tropical, we can hope for an unusually complete geographic distribution of effort

on the Sciomyzidae similar to the world-wide study of the Culicidae, another group of great economic importance in the tropics.

As has been true of other organisms studied for economic reasons, the purely theoretical and academic phases of sciomyzid research may advance well beyond comparable studies of non-economic groups and may prove ultimately to be the most important aspects of this study. Whether aspirations to use the Sciomyzidae in the biological control of noxious snails and slugs ever work out or not, that hope has stimulated and supported the fundamental research program. In the short time since the first direct observation of snail killing by a sciomyzid larva, more has been learned about the basic biology of these flies, in comparison with what was already known, than in any other family of Diptera. This does not mean that biology of the Sciomyzidae is as well known as genetics of *Drosophila* or biology of the Culicidae. The 143 species reared by a small research group centered at Cornell University constitutes only about one-third of the known species. Only 2 Asian, 2 African, and 3 Australian species have been reared. But there has been gratifying progress in North America and Europe, and a good start has been made in South America. Furthermore, outstanding accomplishments attained on other groups through similarly oriented studies raise the hope that this research may progress much further. Among several notable examples, studies of the solitary wasps (Evans, 1957), research on water mites (Mitchell, 1964, and earlier papers cited there), studies of termites (Emerson, 1938), and the imaginative recent work on ants (see especially Brown and Wilson, 1959) are particularly noteworthy. To quote Bates again, this study is now beginning to demonstrate "what might be called the 'law of the multiplication of the potential value of a subject of study': the more that is known about a given animal or group of animals, the more valuable it becomes for further work. *Drosophila* was used at first because of the ease with which it could be manipulated in the laboratory; as studies accumulated, it became increasingly valuable for new studies merely because of the background provided by this earlier work . . ." (Bates, 1949: 3-4). Similarly, the Sciomyzidae were first reared only because their food habits seemed interesting and potentially useful. But as comparative data accumulate with each completed life cycle there are added objectives, and the value of future research is enhanced.

Opportunities for the group-of-organisms approach now are better than ever before, because the specialist can make a much wider geographic coverage of his group than was possible a few years ago. In this age of jet travel, field studies can be conducted in remote areas and many living animals can be shipped rapidly and safely from distant points to sites of more refined laboratory facilities. Indeed, the outlook for world-wide studies of non-economic groups especially has changed completely in the 16 years since Bates wrote about the problems in *Drosophila* research.³ Simultaneous with the development of rapid means of travel, biologists and sup-

³Convincing evidence of this is found in a recent study of Neotropical *Drosophila*. See P. J. J. (Amer. Mid. Nat. 74. 1965).

porting foundations seem to have acquired genuine appreciation of Bates' principle of multiplication of the potential value of a subject with each additional study made of it. The man who pursues an effective and exhaustive research program on any group now has a better chance than ever before of getting the opportunity to study most of the world fauna in that group.

This combination of circumstances may result in some fortunate developments and new emphases. Ecology has gone through, or is still going through, a period in which considerably more effort seems to be expended in formulating hypotheses and principles than in digging out the facts needed to support them. This trend may be building ecological science into an elaborate house of cards with chinks in the mortar of supporting evidence. If this paper convinces anyone of the value of down-to-earth studies of what animals are doing, and thus helps to develop a biologist who will mortar up some of the chinks, we will feel repaid for the many hours spent in its preparation.

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PLATE I

- Figure 1. *Sepedon praemiosa*, eggs.
Figure 2. *Sepedon fuscipennis*, eggs.
Figure 3. *Sepedon caerulea*, eggs. dd — dorsal depression.
Figure 4. *Sepedon macropus*, [eggs. ht](#) — hemispherical tubercle;
lg — longitudinal groove; ca — central area.
Figure 5. *Sepedon tenuicornis*, eggs.
Figure 6. *Sepedon sphegea*, eggs.

NOTE: Line at the left of each figure equals one millimeter. Micropylar end of egg is on the right in each figure.

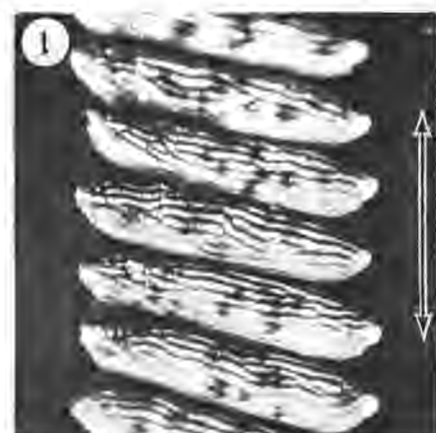
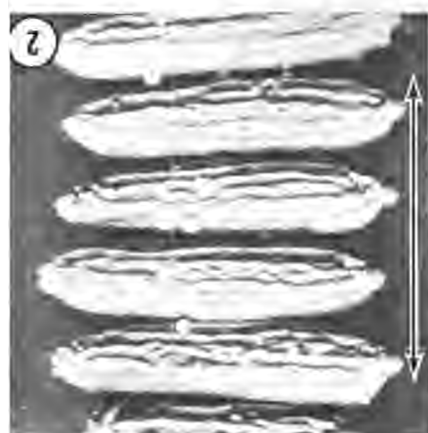
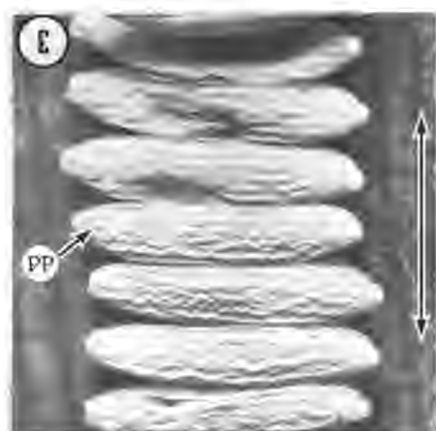
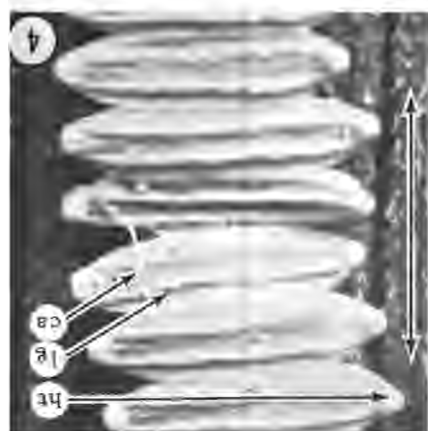
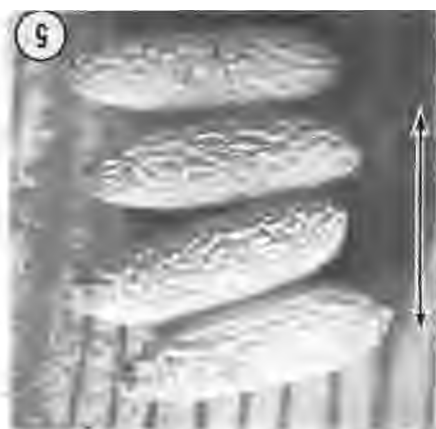
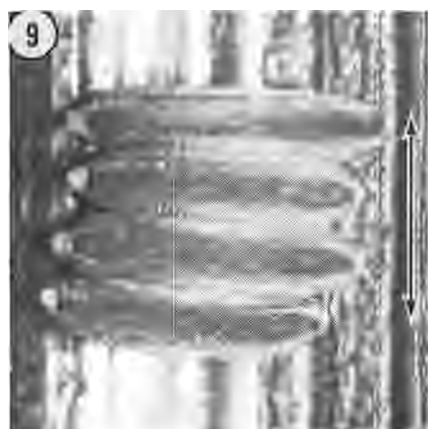


PLATE II

- Figure 7. *Sepedon spinipes americana*, [eggs. ht](#) — hemispherical tubercle; *ca* — central area; *tt* — transverse tubercle; *lg* — longitudinal groove.
- Figure 8. *Sepedon borealis*, eggs.
- Figure 9. *Sepedon spinipes spinipes*, group of parasitized eggs showing emergence holes of trichogrammid wasp.
- Figure 10. *Sepedon neili*, eggs.

NOTE: Line at left of each figure equals one millimeter.

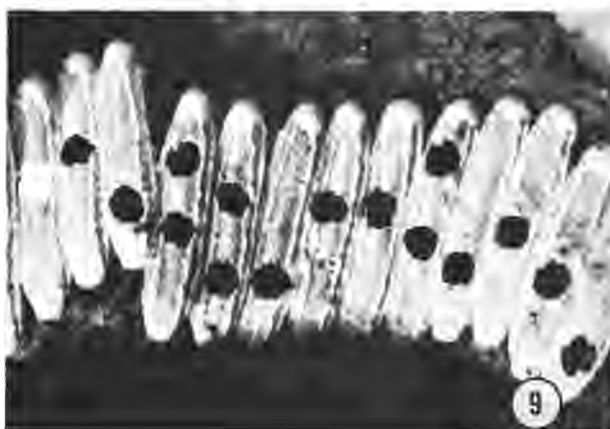
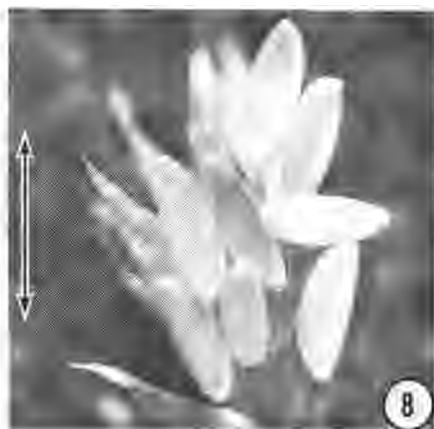
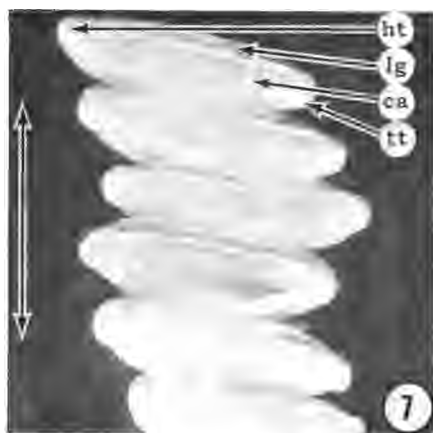


PLATE III

Figure 11. *Sepedon guatemalana*, dorsal view of third-instar larva.

Figure 12. *Sepedon guatemalana*, lateral view of third-instar larva.

as — anterior spiracle; *cps* — cephalopharyngeal skeleton; *dhp* — dorsal hair patch; *dllhp* — dorsolateral hair patch; *ltg* — lateral tubercle group; *ltt* — longitudinal tracheal trunk; *mds* — middorsal stripe; *os* — oblique stripes; *posb* — postoral spine band; *psd* — posterior spiracular disc; *psp* — posterior spiracular plate; *vl* — ventral lobe; *vll* — ventrolateral lobe; *vtg* — ventral transverse tubercle group.

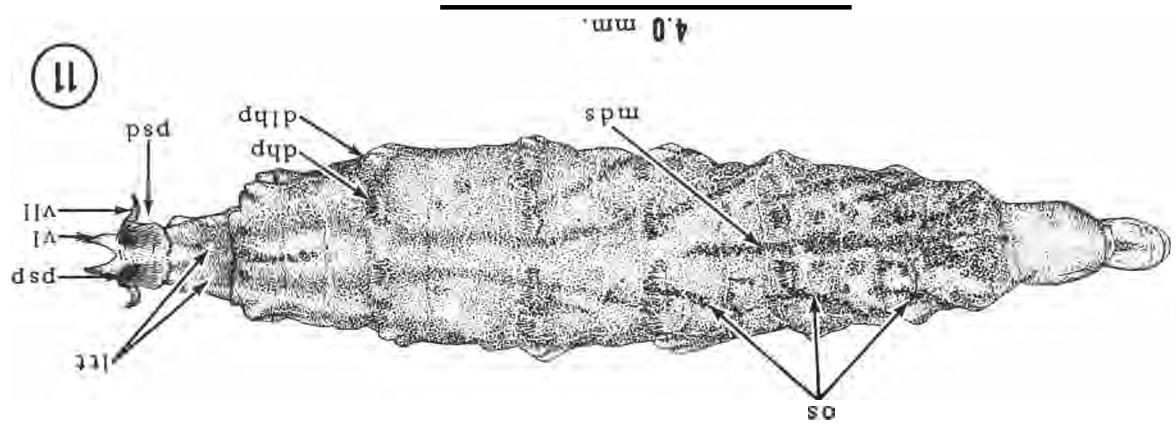
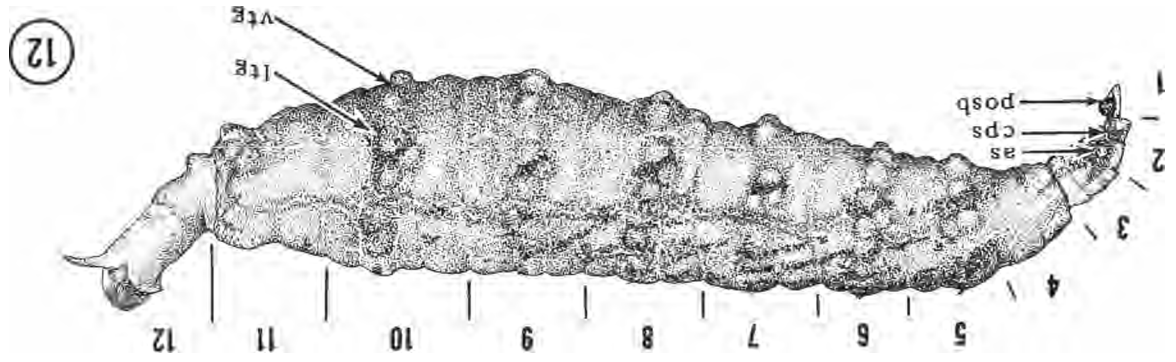


PLATE IV

- Figure 13. *Sepedon tenuicornis*, posterior spiracular disc of third-instar larva. DL — dorsal lobe; DLL — dorsolateral lobe; ISB — palmately-branched interspiracular bristle; LL — lateral lobe; SP — spiracular plate; SS — stigmatic scar; VL — ventral lobe; VLL — ventrolateral lobe.
- Figure 14. *Sepedon haplobasis*, posterior spiracular disc of third-instar larva.
- Figure 15. *Sepedon tenuicornis*, posterior disc of second-instar larva.
- Figure 16. *Sepedon haplobasis*, posterior disc of second-instar larva.
- Figure 17. *Sepedon tenuicornis*, posterior disc of first-instar larva.
- Figure 18. *Sepedon haplobasis*, posterior disc of first-instar larva.

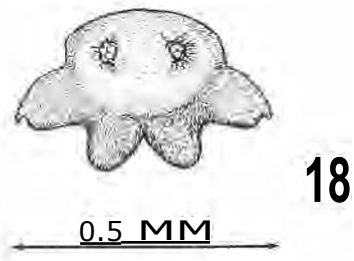
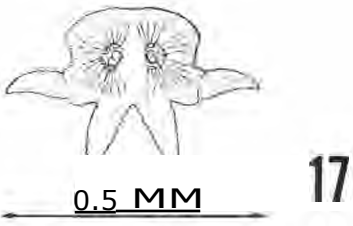
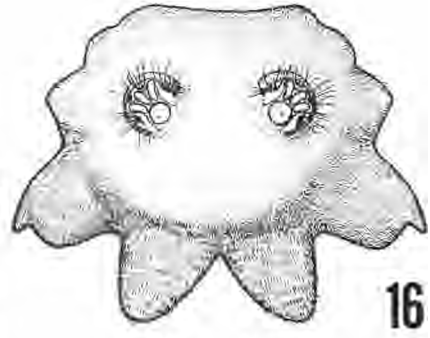
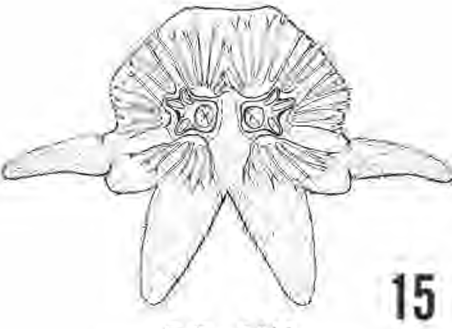
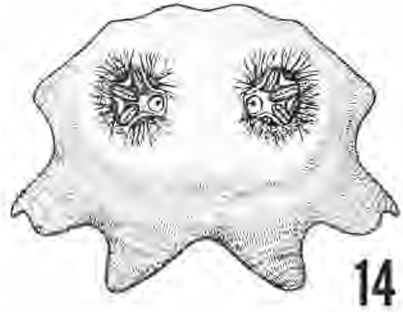
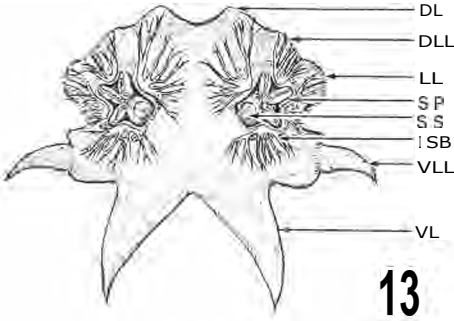


PLATE V

- Figure 19. *Sepedon fuscipennis*, ventral view of anterior end of third-instar larva. **CSP** — circular sensory plate; **HS** — hypostomal sclerite; **LS** — lingual sclerite; **LSP** — labral sensory papilla; **MH** — mouthhook; **PC** — pseudocephalic segment; **POSE** — post-oral spine band; **PR** — parastomal rod; **PS** — pharyngeal sclerite; **SDO** — salivary duct opening; **TSP** — 2-segmented sensory papilla; **VA** — ventral arch.
- Figure 20. *Sepedon pusilla*, integumentary scales of tenth segment of third-instar larva.
- Figure 21. *Sepedon armipes*, integumentary scales of tenth segment of third-instar larva.
- Figure 22. *Sepedon borealis*, cephalopharyngeal skeleton of third-instar larva.
- Figure 23. *Sepedon fuscipennis*, cephalopharyngeal skeleton of third-instar larva. **ACT** — accessory teeth; **DC** — dorsal cornua; **ES** — epistomal sclerite; **HS** — hypostomal sclerite; **LS** — lingual sclerite; **MH** — mouthhook; **PS** — pharyngeal sclerite; **VA** — ventral arch; **VC** — ventral cornua.
- Figure 24. *Sepedon caerulea*, cephalopharyngeal skeleton of first-instar larva.
- Figure 25. *Sepedon haplobasis*, cephalopharyngeal skeleton of third-instar larva.
- Figure 26. *Sepedon caerulea*, cephalopharyngeal skeleton of second-instar larva.
- Figure 27. *Sepedon haplobasis*, cephalopharyngeal skeleton of second-instar larva.
- Figure 28. *Sepedon caerulea*, cephalopharyngeal skeleton of third-instar larva. **PA** — pigmented area.
- Figure 29. *Sepedon haplobasis*, cephalopharyngeal skeleton of first-instar larva.

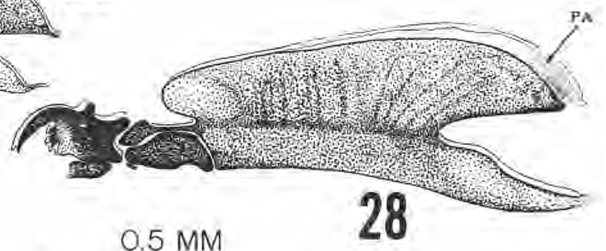
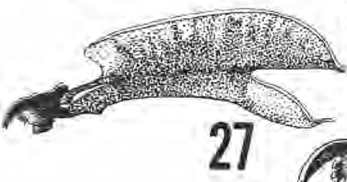
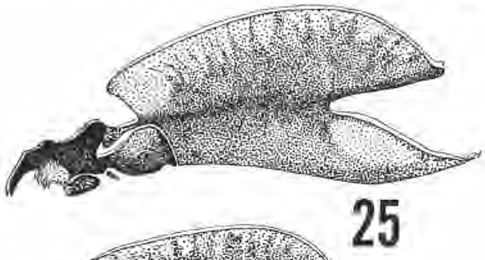
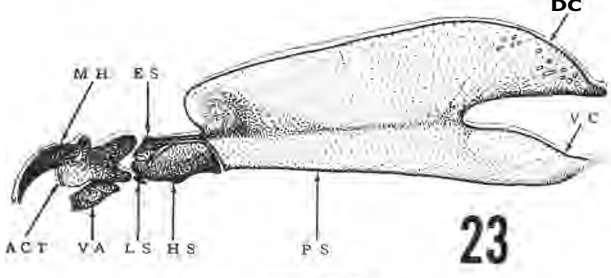
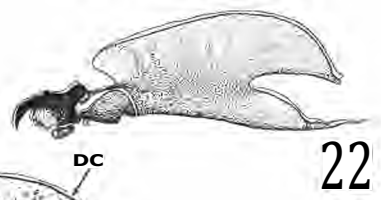
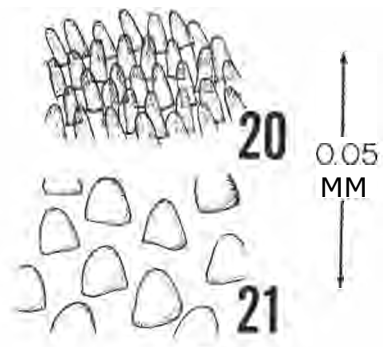
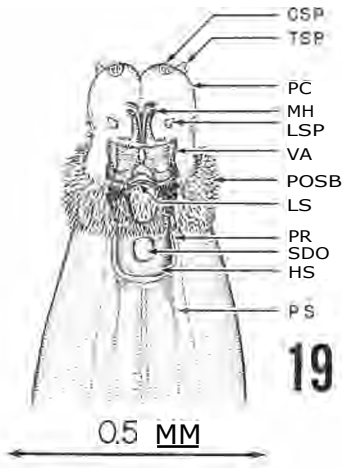


PLATE VI

- Figure 30. *Sepedon caerulea*, dorsal view of ventral arch.
Figure 31. *Sepedon tenuicornis*, dorsal view of ventral arch.
Figure 32. *Sepedon guatemalana*, dorsal view of ventral arch.
Figure 33. *Sepedon spehegea*, dorsal view of ventral arch.
Figure 34. *Sepedon caerulea*, mesial view of right mouthhook.
Figure 35. *Sepedon guatemalana*, mesial view of right mouthhook.
Figure 36. *Sepedon tenuicornis*, mesial view of right mouthhook.
Figure 37. *Sepedon armipes*, posterior spiracle of third-instar larva. FH — palmately-branched float hairs; SP — spiracular plate; SS — stigmatic scar; ST — spiracular tube.
Figure 38. *Sepedon spehegea*, mesial view of right mouthhook.
Figure 39. *Sepedon borealis*, posterior spiracle of third-instar larva.
Figure 40. *Sepedon anchista*, anterior spiracle of third-instar larva.
Figure 41. *Sepedon armipes*, anterior spiracle of third-instar larva.
Figure 42. *Sepedon borealis*, anterior spiracle of third-instar larva.
Figure 43. *Sepedon neili*, anterior spiracle of third-instar larva.
Figure 44. *Sepedon pusilla*, anterior spiracle of third-instar larva.
Figure 45. *Sepedon tenuicornis*, anterior spiracle of third-instar larva.
Figure 46. *Sepedon caerulea*, anterior spiracle of third-instar larva.
Figure 47. *Sepedon spehegea*, anterior spiracle of third-instar larva.
Figure 48. *Sepedon guatemalana*, anterior spiracle of third-instar larva.
Figure 49. *Sepedon praemiosa*, anterior spiracle of third-instar larva.



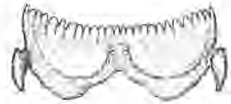
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0.1 MM



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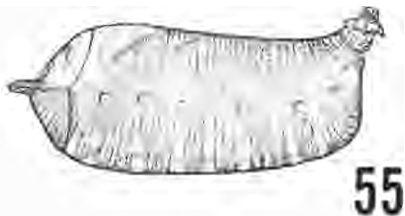
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PLATE VII

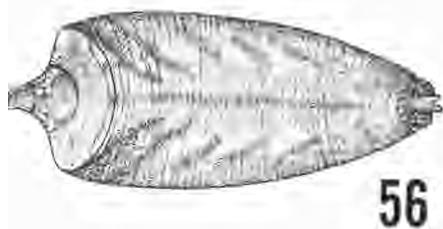
- Figure 50. *Sepedon fuscipennis*, dorsal view of puparium.
Figure 51. *Sepedon fuscipennis*, lateral view of puparium.
Figure 52. *Sepedon tenuicornis*, dorsal view of puparium.
Figure 53. *Sepedon tenuicornis*, lateral view of puparium.
Figure 54. *Sepedon guatemalana*, dorsal view of puparium.
Figure 55. *Sepedon guatemalana*, lateral view of puparium.
Figure 56. *Sepedon macropus*, dorsal view of puparium.
Figure 57. *Sepedon macropus*, lateral view of puparium.



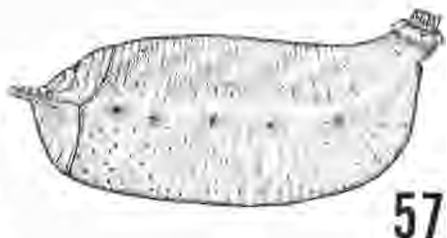
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57

5.0 MM

PLATE VIII

- Figure 58. *Sepedon anchista*, dorsal view of puparium.
Figure 59. *Sepedon anchista*, lateral view of puparium.
Figure 60. *Sepedon borealis*, dorsal view of puparium.
Figure 61. *Sepedon borealis*, lateral view of puparium.
Figure 62. *Sepedon bifida*, dorsal view of puparium.
Figure 63. *Sepedon bifida*, lateral view of puparium.
Figure 64. *Sepedon sphegea*, dorsal view of puparium.
Figure 65. *Sepedon sphegea*, lateral view of puparium.

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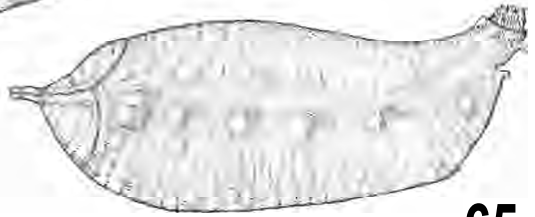
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64

4.0 MM



65

PLATE IX

Sequence illustration of an attack by a mature *Sepedon macropus* larva on *Australorbis glabratus*.

Figure 66. Approach of larva.

Figure 67. Moment of contact between larva and snail. Note localized contraction of snail's foot.

Figure 68. Injured snail has retracted into body whorl of shell as larva follows.

Photos: E. C. Bay



68



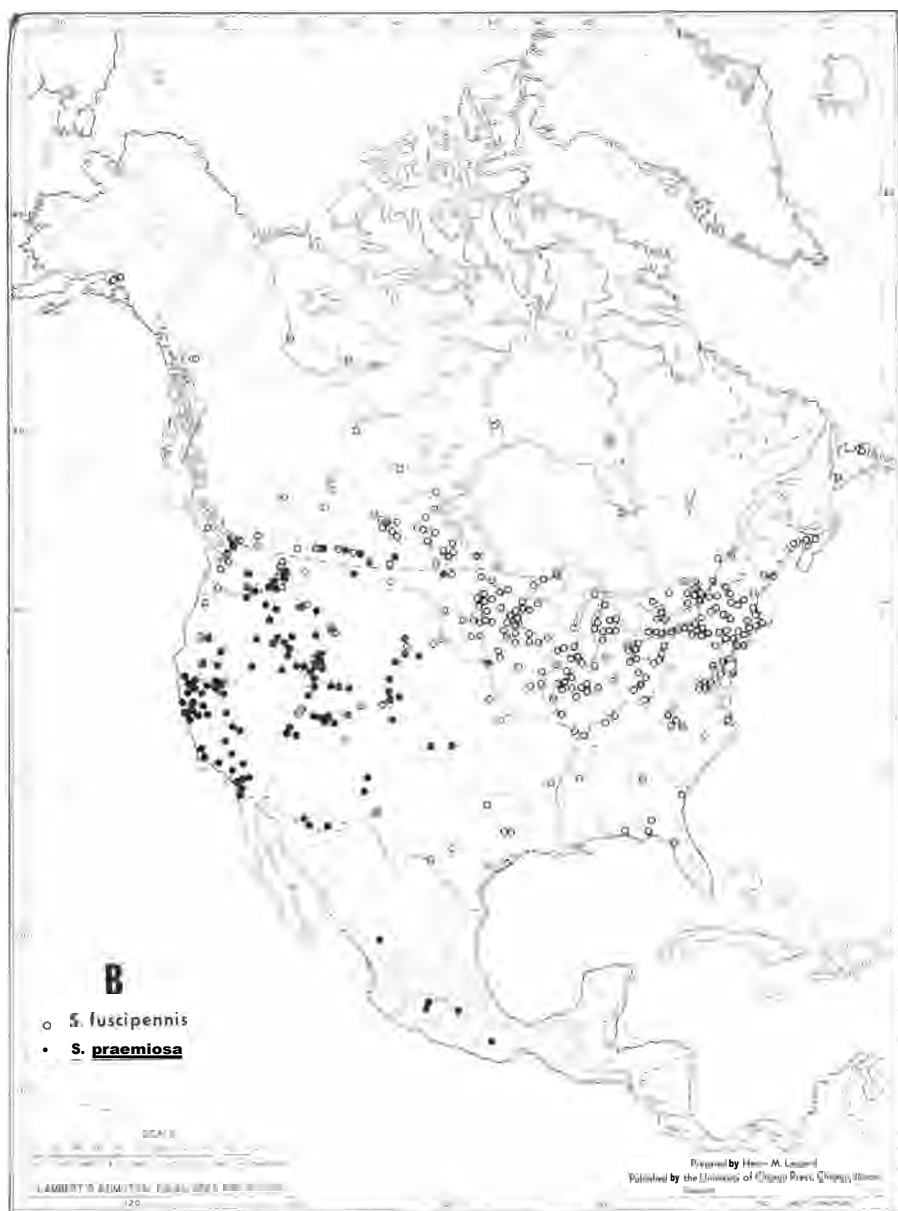
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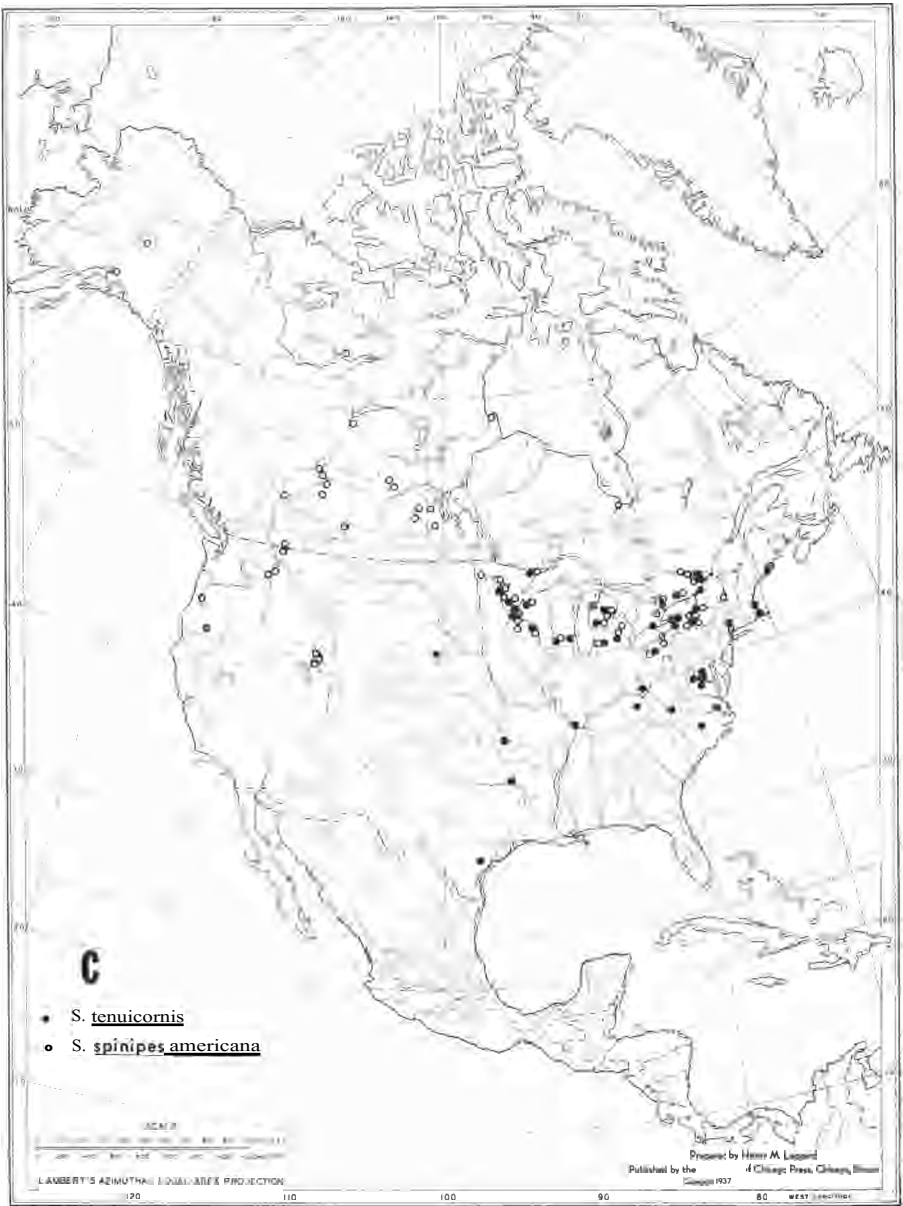
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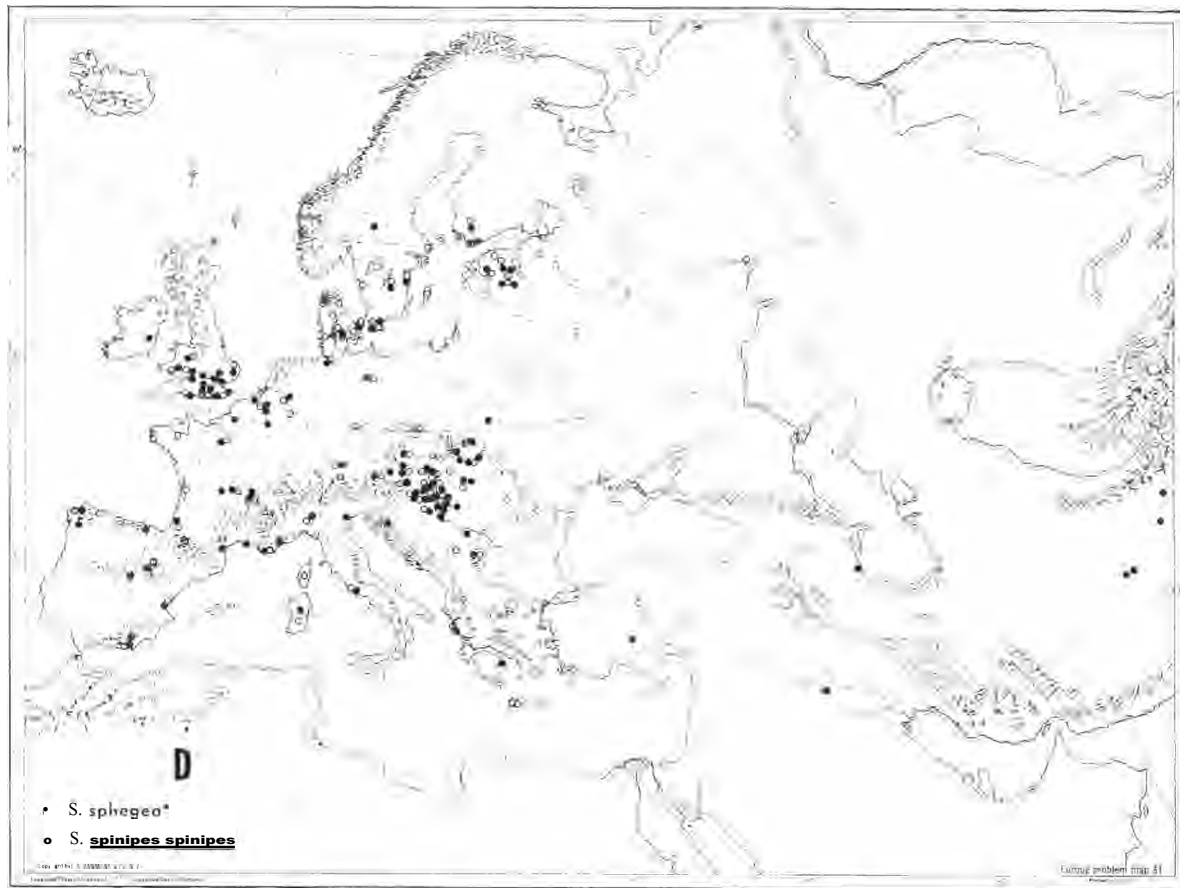
Map. A: Collecting sites for *S. caerulea*, *S. macropus*, and *S. guatemalana*. **S. guatemalana* also has been collected south of the area shown on this map, at Canete and Lima, Peru.



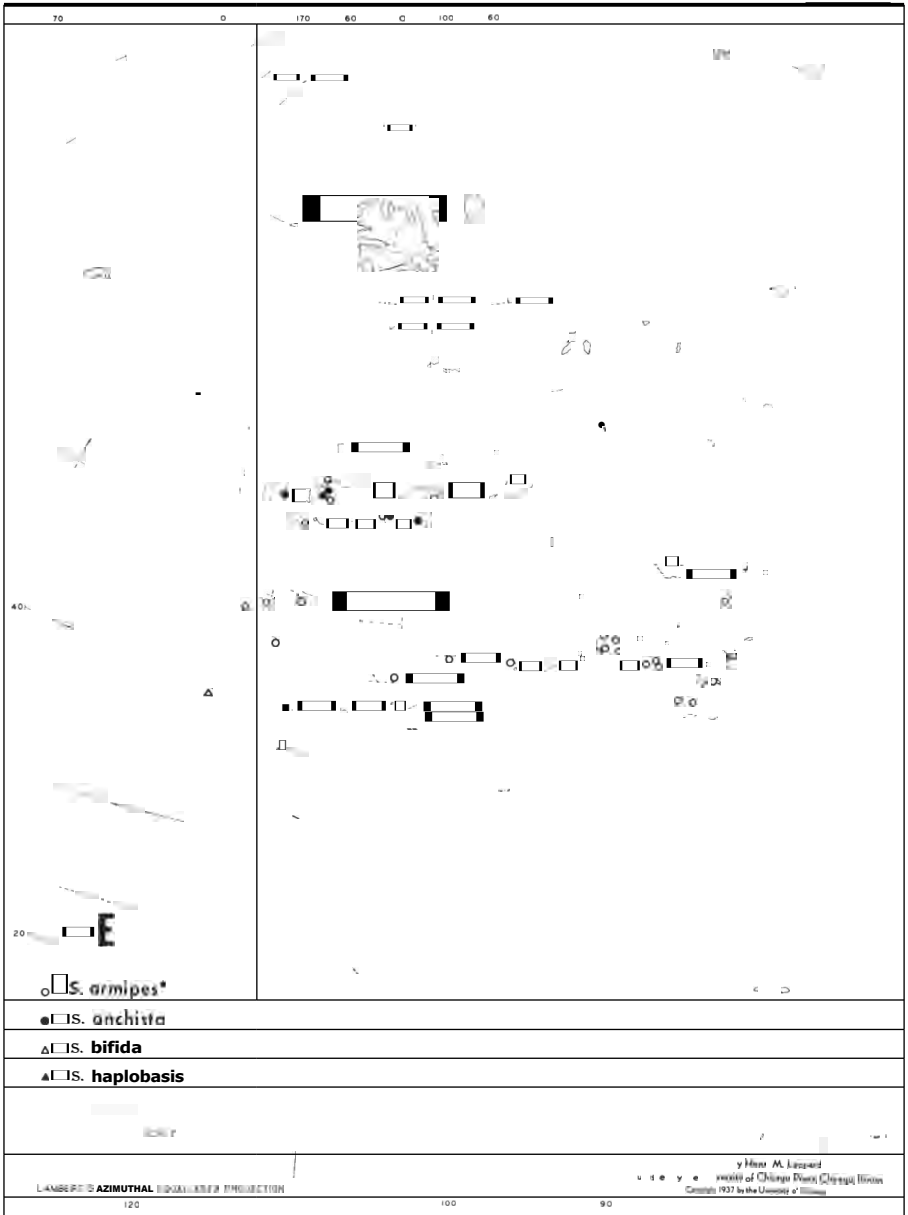
Map B. Collecting sites for *Sepedon fuscipennis* and *S. praemiosa*.



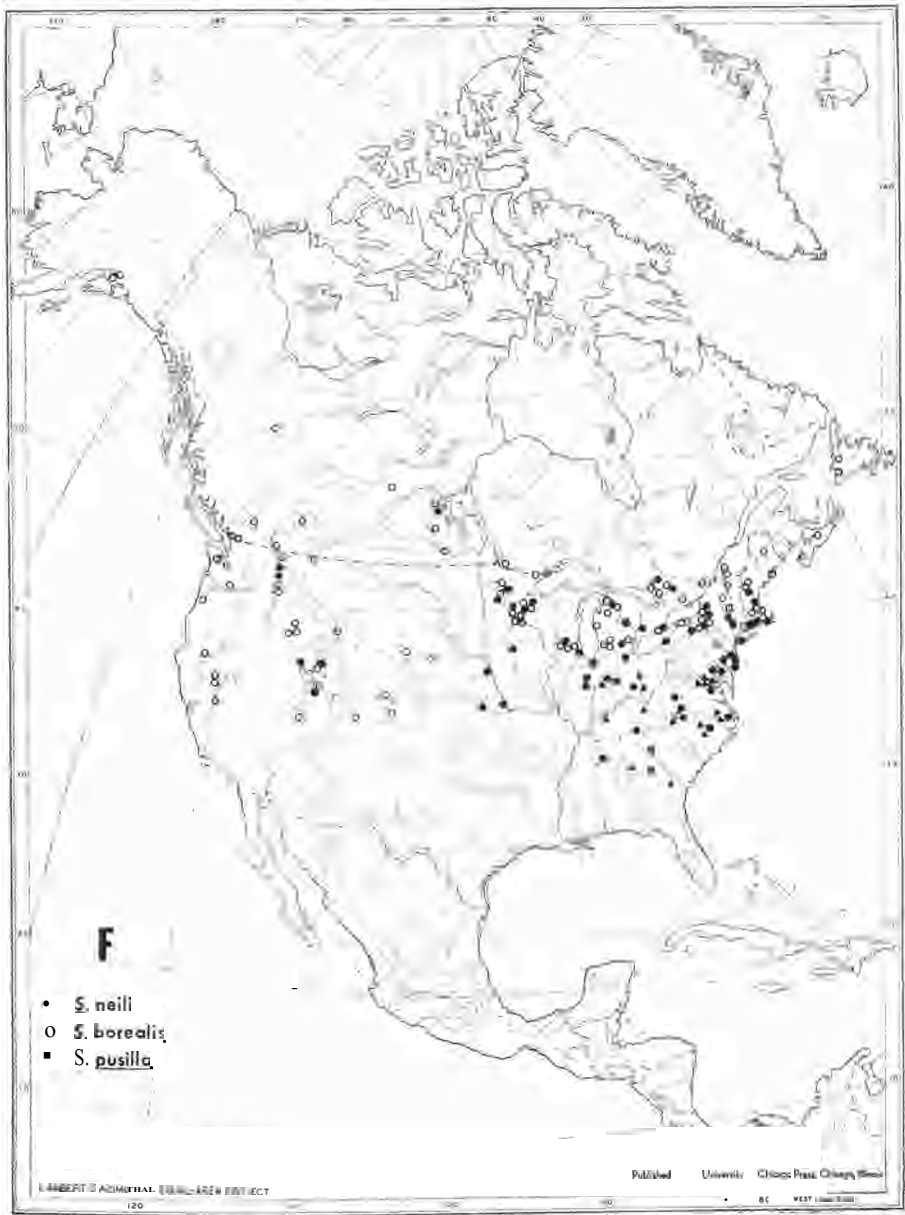
Map C: Collecting sites for *Sepedon tenuicornis* and *S. spinipes americana*.



Map D: Collecting sites for *Sepedon sphegeo* and *S. spinipes spinipes*. **Sepedon sphegeo* extends eastward through Asia.



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Map F: Collecting sites for *Sepedon neili*, *S. borealis*, and *S. pusilla*.