

BIOLOGY OF SNAIL-KILLING FLIES (*SEPEDON*) FROM
SOUTHEAST ASIA (DIPTERA: SCIOMYZIDAE)

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Abstract.—Life cycle information is presented for five species of *Sepedon* (Diptera: Sciomyzidae) from southeast Asia. The aquatic larvae of all species (*Sepedon ferruginosa* Wiedemann, *S. plumbella* Wiedemann, *S. senex* Wiedemann, *S. spangleri* O. Beaver, and *S. aenescens* Wiedemann) are found in various types of marsh and pond habitats. All are predatory on aquatic, pulmonate snails, especially *Gyraulus bakeri* Brandt, *G. convexiusculus* Hutton, *Indoplanorbis exustus* Deshayes, and *Lymnaea (Radix) auricularia swinhoei* H. Adam. In the laboratory, they also fed on crushed operculate snails of three species (*Hydrobiodes nassa* Theobald, *Idiopoma ingallsiana* Lea, and *I. pilosa* (Reeve)). Duration of incubation periods and of all three larval stadia, periods within the puparium, and preoviposition periods observed during laboratory rearings of all five species in Thailand are presented. New morphological characters to distinguish adults of *Sepedon plumbella* and *S. senex* are described.

Although sciomyzid larvae of many species are known to be snail killers (Berg, 1961), relatively little is known about the habits and ecological relationships of tropical species of Sciomyzidae. This is particularly unfortunate because increasing problems with snails, especially schistosomiasis and other snail-borne diseases of man and domestic animals, are concentrated in the tropics and subtropics. Thus Sciomyzidae (or marsh flies) adapted for life in the tropics may prove particularly useful biological control agents (Berg, 1973). However, they cannot be so utilized until the habitat requirements, preferred prey species, and other important ecological factors affecting both adults and larvae are understood well enough so that we know which species can be used against each vector snail in the various areas where snail-borne diseases are problems.

The paucity of knowledge about the marsh flies of warm regions is illustrated by the situation in southeast Asia. Although these flies have been mentioned several times in biological literature, most references to them are fragmentary, and the Sciomyzidae of this region remain relatively poorly known. Notes on Sciomyzidae collected in rice fields have been written by Yasumatsu (1967) and Yano (1968), and a key to species occurring in rice fields was presented by Nishida and Torii (1970). Papers on the biology and immature stages of *Sepedon* of that region include a life history of *S. aenescens* Wiedemann (Nagatomi and Kushigemachi, 1965), a description of its eggs (Nagatomi and Tanaka, 1967), and some observa-

tions on its overwintering (ChannaBasavanna and Yano, 1969) (as *S. sauteri* Hendel in all 3 papers). Bhuangprakone and Areekul (1973) discussed the biology of *S. plumbella* Wiedemann, particularly survival on different species of snails, snail-killing ability, and prey preference of larvae. Nagatomi and Kushigemachi (1965), Yasumatsu (1967), and Yano (1975) have stated that *S. aenescens* plays an important role in the biological control of rice stem borers (lepidopterans) because its eggs "serve as an alternate host of *Trichogramma* spp., egg parasites of rice stem borers, when the egg masses of the borers are not available in the fields" (Yano, 1975). Chandavimol et al. (1975) have published on the biology of *Sepedon spangleri* O. Beaver.

The Oriental Sciomyzidae are in great need of taxonomic revision; there are at least two endemic genera and seven species that have not been described (Knutson, in preparation). With 26 described species in six genera, the Oriental sciomyzid fauna is apparently smaller than that of any other region. *Sepedon*, with 11 species, and *Pherbellia*, with six species, are the dominant genera. Several Oriental species of *Sepedon* belong to the subgenus *Parasepedon*, a large and distinctive group known elsewhere only from the Ethiopian Region. The relationships of the Oriental and Ethiopian *Sepedon* faunas have been indicated by Steyskal and Knutson (1975), based on studies of derived characters of adults.

This paper deals with five species of *Sepedon* (*S. ferruginosa* Wiedemann, *S. plumbella*, *S. senex* Wiedemann, *S. spangleri*, and *S. aenescens* (= *S. sphegea* (Fabricius) in part, and *S. sauteri* and *S. violacea*). A visit by Berg to Thailand and Indonesia in 1970 to study problems of interest to the Office of Environmental Sciences, Smithsonian Institution, provided the opportunity to collect Sciomyzidae native to those countries. Living adults of *S. plumbella* and *S. senex*, both collected in Thailand and Indonesia, were transported successfully to Washington, D.C. and were reared through complete life cycles. Subsequently, Beaver studied all five species at Chiang Mai University, Thailand during 1971–1974.

Adults of all five species were found in marshy areas and around ponds near rice fields. The marshes are flooded, with maximum water depths of about $\frac{1}{3}$ to 1 m, during the rainy season. During the rest of the year, usually November through June, their soil is exposed. Water-tolerant grasses and sedges and other, more aquatic, plants grow throughout these marshy areas. The ponds differ in being covered with water throughout the year, with average maximum depths of 1 to 2 m during the rainy season and $\frac{1}{3}$ to 1 m during the dry season. Whether located in marshy areas or not, most ponds are surrounded by hygrophilous vegetation, including many of the plant species also found in marshes. In the permanently inundated areas, there is a zonation and progression from this typical marsh flora to such truly aquatic spermatophytes as *Jussiaea repens* L., *Pistia stratiotes*

Table 1. The range and mean $\pm$ S.D. of incubation period, the larval instar periods, the puparial period, and the preoviposition period of the species studied.

Sciomyzids	Incubation period (days)		First larval stadium (days)		Second larval stadium (days)	
	R	M $\pm$ S.D.	R	M $\pm$ S.D.	R	M $\pm$ S.D.
<i>S. ferruginosa</i>	1-6	3.16 $\pm$ 0.73	2-8	3.74 $\pm$ 1.45	2-8	3.78 $\pm$ 1.38
<i>S. plumbella</i>	1-5	2.86 $\pm$ 0.66	2-7	3.38 $\pm$ 0.79	2-6	3.48 $\pm$ 0.70
<i>S. senex</i>	1-7	3.09 $\pm$ 0.79	4-5	4.38 $\pm$ 0.48	3-5	3.83 $\pm$ 0.69
<i>S. spangleri</i>	1-10	3.38 $\pm$ 1.20	2-11	4.89 $\pm$ 1.46	2-9	3.84 $\pm$ 1.35
<i>S. spangleri</i> ¹	3-4	3.55 $\pm$ 0.51	4-5	4.35 $\pm$ 0.49	2-4	2.95 $\pm$ 0.76
<i>S. aenescens</i>	1-6	2.65 $\pm$ 0.93	2-5	3.03 $\pm$ 0.78	2-5	3.48 $\pm$ 0.78
	Third larval stadium (days)		Puparial period ² (days)		Preoviposition period (days)	
	R	M $\pm$ S.D.	R	M $\pm$ S.D.	R	M $\pm$ S.D.
<i>S. ferruginosa</i>	2-10	4.90 $\pm$ 1.58	5-22	7.21 $\pm$ 1.61	2-22	13.84 $\pm$ 6.10
<i>S. plumbella</i>	3-9	4.66 $\pm$ 1.14	5-14	7.27 $\pm$ 1.94	5-20	8.54 $\pm$ 3.97
<i>S. senex</i>	3-4	3.40 $\pm$ 0.49	3-6	5.00 $\pm$ 1.00	3-18	10.75 $\pm$ 5.34
<i>S. spangleri</i>	3-12	6.08 $\pm$ 2.38	5-17	8.06 $\pm$ 3.38	2-10	4.70 $\pm$ 1.78
<i>S. spangleri</i> ¹	3-5	4.45 $\pm$ 0.61	8	8.00 $\pm$ 0.00	3-5	4.60 $\pm$ 0.86
<i>S. aenescens</i>	2-5	3.46 $\pm$ 0.72	3-8	5.31 $\pm$ 1.04	7-23	14.50 $\pm$ 5.68

¹ Data of Chandavimol et al., 1975.
² Period from puparium formation to emergence of adult.

L., *Lemna polyrhiza* L., *L. paucicostata* Hegelm., *Scirpus grossus* L., *Monochoria hastata* Solms., *Typha angustifolia* L., *T. elephantina* Roxb., and *Ipomoea aquatica* Forsk.

Except for minor differences noted below, the methods described by Neff and Berg (1966) for collecting and rearing species of *Sepedon* were employed in this study. Wooden applicator sticks about 2 mm in diameter were used as resting and oviposition sites in the breeding jars. These are readily available in pharmacies and medical dispensaries, and they remain rigid even when wet. Absorbent cotton or "cotton wool" was used in place of sphagnum moss to provide a moisture-retaining substrate in the breeding jars. The eggs laid each day were transferred to closed, plastic petri dishes containing 5 mm of water. The technique used for shipping live flies great distances was described by Kaczynski et al. (1969).

The ranges, means, and standard deviations of the incubation period, three larval stadia, puparial period (period from puparium formation to emergence of adult), and preoviposition period for all five species included are given in Table 1. Information is given on the biology and life cycles of all species.

Sepedon ferruginosa Wiedemann

Sepedon ferruginosa has been collected from widely dispersed localities ranging from western Pakistan, through continental southeast Asia, to Taiwan and the Philippines (Luzon) (Fig. 1). Nothing has been published on the biology of this species. Yano (1968) noted that it, "... seems to be more abundant than *plumbella* or *senex* in the paddy fields."

Adult flies have been collected during all months except April. In seasonally wet marshes in Thailand, adults are most abundant shortly after the beginning of the rainy season.

Our rearings were started from eggs laid by flies caught at Chiang Mai and Bangkok, Thailand during July, August, and September, 1971 and during 1972.

Adult longevity in the laboratory was 30 to 177 days. Flies mated readily, and eggs were laid in rows, disordered clumps, or singly on leaves or stems of aquatic plants, on the side of the rearing jars, or on the gauze stretched across the openings of the jars. Newly laid eggs are white, but the chorion becomes straw colored after a few hours. Wild-caught females that were placed in breeding jars in the laboratory usually started to lay eggs on the day they were caught. Each female oviposited daily, with interruptions of only a day or two at irregular intervals. In one exceptional case, a female did not oviposit for 12 days, then resumed egg production. Most females oviposited until the day before they were found dead.

The oviposition period in the laboratory ranged from 1 to 40 days but was usually between 10 and 30 days. Individual females produced from 6 to 790 eggs after being captured and confined. The maximum number (790) of eggs laid by any individual female was produced over a period of 23 days. Only 339 eggs were laid by the female with the longest observed oviposition period (40 days).

The larvae are aquatic predators. Newly hatched larvae are white and about 1 mm long. They swim actively and attack snail prey readily. They survived for 24 hours without food and still attacked effectively when they encountered suitable food snails.

The larvae were usually fed on snails found in the habitats of sciomyzid flies. Included were four pulmonate species, *Indoplanorbis exustus* Deshayes, *Lymnaea (Radix) auricularia swinhoei* H. Adam, *Gyraulus bakeri* Brandt, and *G. convexiusculus* Hutton and three operculate species, *Idiopoma filosa* (Reeve), *Hydrobiodes nassa* (Theobald), and *Idiopoma ingallsiana* (Lea). Larvae of all instars attacked and killed pulmonate snails of suitable sizes. First-instar larvae only 1 mm long frequently were able to kill snails (*Indoplanorbis exustus*) 3 mm in diameter. Larger snails often were killed when they were attacked by more than one larva simultaneously.

Although the larvae probably cannot kill operculate snails, they fed on them when these snails were crushed. When the snail supply was limited, larvae were reared from hatching to pupation on snails of the three operculate species listed above. The death rate of newly hatched larvae appeared to be less if they were fed crushed snails, even when the alternative was living, pulmonate snails of suitable sizes. Large, third-instar larvae can attack larger snails, and they also have a higher overall ratio of successful attacks than the younger, smaller larvae.

Third-instar larvae and pupae were found in marshes during October. Some pupae were parasitized by *Eupteromalus* sp. (Chalcididae). Six to 15 parasites were reared from each parasitized pupa.

Sepedon plumbella Wiedemann

Sepedon javanensis Robineau-Desvoidy, 1830

Sepedon javana Macquart, 1843

Sepedon fuscinervis Brunetti, 1907

Sepedon sanguinipes Brunetti, 1907

Sepedon plumbella and another species treated herein, *S. senex*, are common species which are frequently found together and are very similar morphologically. Any study of the biology or ecology of Sciomyzidae involving the two species will require a reliable and preferably simple method of separating them. Yano (1968) described several useful diagnostic characters: Males of both species have distinctive surstyli; in males of *S. senex* the basal segment of the fore tarsus is simple, whereas this segment in males of *S. plumbella* is broadened and has a characteristic diagonal groove dorsally; females of *S. plumbella* have the second segment of the fore tarsus shorter than half the length of the first segment, whereas this segment is equal to or longer than half the length of this segment in *S. senex*; the hind tibia of *S. plumbella* has no distinct dark patch, whereas that of *S. senex* has a basal and an apical dark patch. We have found additional characters of both males and females that are very reliable. Abdominal segments 1 plus 2 are strongly constricted laterally at the basal third in *S. senex* and these terga are transversely rugulose dorsally, whereas in *S. plumbella* these segments are not constricted and they are smooth.

As might be expected of a broadly distributed species such as *S. plumbella*, adults show considerable morphological variation. The infuscation of the wing is particularly variable, ranging from entirely dark brown (central and southern parts of the range) to hyaline with the infuscation at the apex of the wing blending with the infuscation around the posterior crossvein and usually extending along the third vein to the anterior crossvein (northern parts of the range). In *S. senex*, the infuscation at the wing

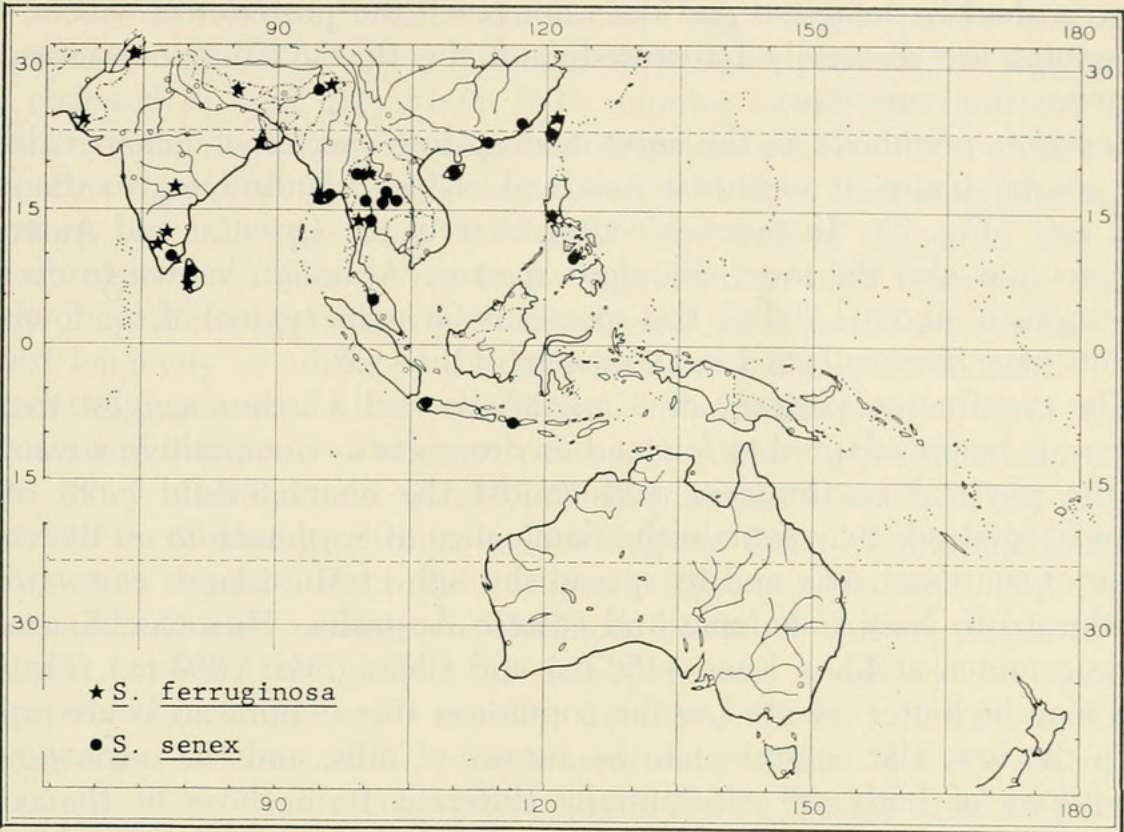


Fig. 1. Distribution of *Sepedon ferruginosa* and *S. senex*.

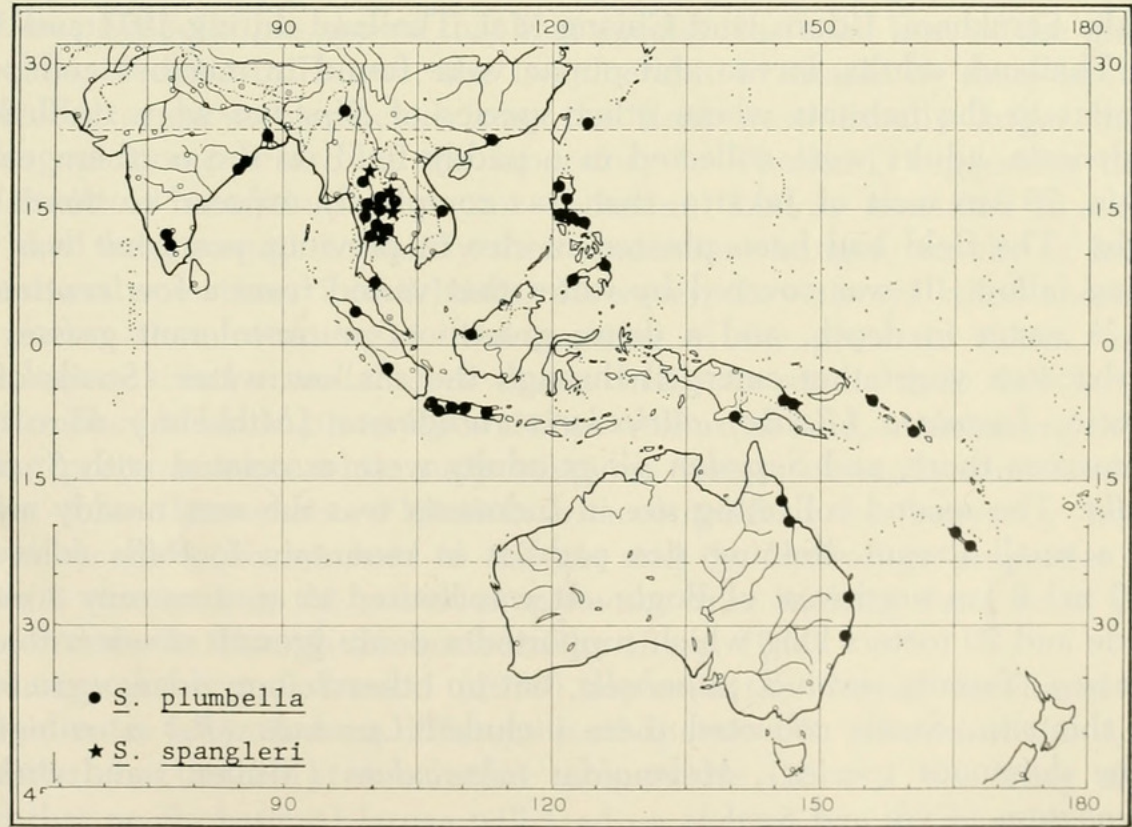


Fig. 2. Distribution of *Sepedon plumbella* and *S. spangleri*.

apex is sharply delimited and does not reach the posterior crossvein; both crossveins are discretely infuscated; and the third vein is not infuscated between the crossveins.

Sepedon plumbella is the most widespread species of Sciomyzidae on the coastal plains of southeast Asia and on the islands lying to the south and east (Fig. 2). In many breeding sites in the Oriental and Australian regions it is also the most abundant species. Although known to occur at elevations of about 1,700 m, this species is far more typical of the lowlands. Adults have been collected in all months of the year.

The distribution patterns of *S. plumbella* and *S. senex* suggest that the former is better adapted to lowland environments. Competitive advantages in the physical environment and amidst the characteristic biota of the tropical lowlands may explain the dominance of *S. plumbella* on the coastal plain of southeast Asia and its spread through Pacific islands eastward and southward to New Caledonia and eastern Australia. However, *S. senex* is more common at Khon Kaen (150 m) and Chiang Mai (300 m), Thailand, and may be better adapted to the conditions there. Both areas are isolated from the low, flat coastal plain by ranges of hills, and the environmental conditions of both are substantially different from those of the coastal plain.

We reared *S. plumbella* from adults collected near Jakarta and Bogor, Indonesia, during late November 1970, and from adults collected in Kalasin, Maha Sarakham, Udorn, and Chiang Mai, Thailand during 1971 and 1972. In Thailand, adults, larvae and pupae were found in marshes and ponds similar to the habitats where other species of *Sepedon* were studied. In Indonesia, adults were collected in a paddy field on the northern coastal plain, 29 km west of Jakarta, that was completely exposed to direct sunlight. The field had been planted in rice in previous years but was then lying fallow. It was covered by water that varied from a few centimeters to $\frac{1}{3}$ meter in depth, and a dense growth of water-tolerant grasses and herbaceous vegetation emerged through the shallow water. Snails of the species *Lymnaea* (*Radix*) *auricularia rubiginosa* (Michelin) were quite numerous there, and *Sepedon senex* adults were associated with *S. plumbella*. The second collecting site in Indonesia was the wet, muddy margin of a small stream draining rice paddies in mountain foothills (elevation 250 m) 6 km northwest of Bogor. It was limited to an area only 3 meters wide and 20 meters long which supported a dense growth of water-tolerant grasses. Twenty-seven *S. plumbella*, but no other Sciomyzidae, were found at this site. Snails collected there included *Lymnaea* (*R.*) *a. rubiginosa* (the dominant species), *Melanoides tuberculata* (Müller), and *Bithynia truncatum* (Eyd. and Soul.).

Both reared and wild-caught adults mated readily in laboratory breeding

jars. In the laboratory, females usually laid eggs singly, in clumps, or in rows of a few eggs. The newly laid eggs were straw colored, but they gradually changed to light grey about 5–10 minutes later. The flies laid eggs nearly every day, with an occasional interruption of a few days, until 1 to 7 days before they died. A female that lived for 31 days after emerging in the laboratory laid 126 eggs and was found dead only a day after she had stopped ovipositing. She started to lay eggs 20 days after emerging, which was the longest preoviposition period observed for *Sepedon plumbella*. The greatest longevity of adults in the laboratory was about 2½ months.

Larvae of *S. plumbella* live equally well on a moist substrate or in standing water and qualify in all other respects as predatory, aquatic, tetanocerine larvae. They attacked and quickly killed pulmonate snails of all genera exposed to them during rearings in Washington, D.C.: *Biomphalaria* Preston, *Gyraulus* Agassiz, *Helisoma* Swainson, *Lymnaea* Lamarck, and *Physa* Draparnaud. During rearings in Thailand, larvae at various stages of development attacked and killed all non-operculate snails of the suitable sizes provided (*Indoplanorbis exustus*, *Lymnaea* (*Radix*) *auricularia swinhoei*, *Gyraulus bakeri*, and *G. convexiusculus*), but they did not kill operculate snails. First- and second-instar larvae fed on freshly crushed pulmonate and operculate snails when there was a shortage of pulmonate snails small enough for the larvae to kill. Experimental exposure of *Lymnaea* (*Radix*) *viridis* (Quoy and Gaimard) (= *L. ollula* Gould) to larvae of *Sepedon plumbella* has shown that that species, the snail host of the giant liver fluke of cattle in Hawaii, also is vulnerable to attacks by these larvae.

Third-instar larvae collected from the field were usually larger than the largest larvae reared in the laboratory in Thailand, suggesting that the laboratory conditions were not optimum. Larvae remained in each snail shell long enough to satisfy their immediate hunger, usually at least an hour and sometimes 2 or 3 hours. However, they always killed another snail rather than returning to the remains of the previous victim, and some larvae killed more than a dozen snails to attain their full larval growth. They killed snails in the water as well as on land, maintaining their floating positions even while supporting the weight of snails considerably heavier than themselves. Flotation is accomplished by buoyancy from the bubble of air always held in the gut and the hydrofuge properties of the hairs surrounding the posterior spiracular slits, making them resist being pulled down through the surface film (Berg, 1964).

Bhuangprakone and Areekul (1973) reported that larvae developed at different rates when fed on different snail species (*G. convexiusculus* and *I. exustus*) but reared at a constant temperature ($25 \pm 1^\circ\text{C}$). They also found that newly hatched larvae will feed on eggs of *L. (R.) a. rubiginosa* and *I. exustus*.

Sepedon senex Wiedemann

Characters for recognition of *Sepedon senex* are presented under *S. plumbella*, above. Literature references to *S. senex* deal solely with capture data, external morphology, and distinguishing characters; nothing has been published on the biology of this species.

On the mainland of southeast Asia, *S. senex* has been collected in all countries in which *S. plumbella* has been reported except Laos. However, its range in the islands southeast of Asia is far less extensive and confined to the west of Weber's line (Fig. 1).

As other species of *Sepedon*, *S. senex* has been collected in all months of the year, but adults became rare during January in Chiang Mai.

Our rearings of *S. senex* were started with adults collected from the grassy margin of a shallow pond, fully exposed to sunlight, near Ban Keng, about 24 km east of Khon Kaen, Thailand on November 14, 1970, and with adults collected at Khon Kaen and Chiang Mai during 1971 and 1972.

Field-collected adults mated readily. The preoviposition period of most of the females bred in the laboratory ranged from 5 to 12 days. Females placed eggs in the same manner as *S. plumbella*, but their eggs became dark grey 5 to 10 minutes after being laid. By laying eggs daily for most of the oviposition period, most females laid 100 to 200 eggs in the laboratory. The maximum number (452) of eggs laid was produced by a wild-caught female that lived 36 days and had the longest oviposition period (34 days) observed for this species. The greatest longevity observed for *S. senex* was 45 days, but this female stopped laying eggs 22 days before she died.

The larvae of all instars attacked and killed pulmonate snails of all species provided during rearings in Thailand. Larvae reared in Washington, D.C. killed and consumed *Helisoma trivolvis* (Say) and *Physa* sp. Newly hatched larvae survived about 24 hours without food.

Indoplanorbis exustus very probably is the natural food snail of *Sepedon senex* larvae, at least in the pond near Ban Keng where breeding stock of *senex* was obtained. All other snails collected there, *Bithynia siamensis* (Lea) and *Idiopoma ingallsiana* (both abundant) and *I. bengalensis* (Lamarck), *Pila polita* (Deshayes) and *P. gracilis* (Lea) (less common), are operculates. Although larvae of *senex* fed as readily as other larvae on freshly crushed operculates, it is unlikely that they can kill and feed on operculate snails in nature.

Sepedon spangleri O. Beaver

This recently described species is known only from Bangkok, Maha Sarakham, Khon Kaen, and Chiang Mai, Thailand (Fig. 2). Adults have been collected throughout the year at seven sites just north of the Lam-

pang-Chiang Mai Highway between km 85 and km 93. The species has been reared recently by Chandavimol et al. (1975).

Wild-caught adults lived up to 30 days after being captured and confined. Females laid eggs singly or in clumps on leaves, on the sides of the jars, and on the gauze coverings. Most of the females began laying eggs on the day they were caught or the day after, but two of them delayed oviposition until 11 days after they were caught. The longest oviposition period was 18 days, and that female produced 106 eggs. The greatest number of eggs laid by any individual in the laboratory, 116, was produced in 5 days by a female that survived only 6 days after she was caught and confined.

The developmental periods given in Table 1 agree closely with those obtained by Chandavimol et al. (1975). The latter authors kept adults alive in the laboratory from 84 to 267 days (mean, 193.3), and the 10 females that they reared produced from 213 to 613 eggs (mean, 414.7).

The larvae are aquatic predators, and they were able to kill pulmonate snails of suitable sizes during all larval stadia. However, young first-instar larvae were not as active swimmers as young larvae of the other species of *Sepedon* studied. Also, the mortality of newly hatched larvae was high in comparison with that of the 4 other species.

Sepedon aenescens Wiedemann

S. imbuta Wiedemann, 1830

S. violacea Hendel, 1909

S. sauteri Hendel, 1911

S. sinensis Mayer, 1953

Various authors have considered the common *Sepedon sphegea* (Fabricius) as ranging from western Europe throughout Eurasia and much of the Oriental region. Other authors have applied the above names to Oriental specimens that differ from typical *S. sphegea* primarily in color characters. Rozkošný (1969) recognized *S. sphegea* and *S. aenescens* from eastern Afghanistan on the basis of male genitalic characters. Recent study of specimens from throughout the distribution of this complex has revealed new characters of the male postabdomen that show that only two species are involved (Orth, et al., in preparation). *Sepedon sphegea* extends from Europe eastward to Afghanistan and northwestern India and northeastward to Mongolia and northeastern Siberia. *Sepedon aenescens* occurs southeast of this area, extending to southern India, Thailand, and the northern Philippine Islands.

The biology of *S. sphegea* has been discussed by Neff and Berg (1966). Nagatomi and Kushigemachi (1965) and ChannaBasavanna and Yano (1969) have written on the biology of *S. aenescens* (as *S. sauteri*).

In this study, *S. aenescens* was reared from adults collected around swamps and ponds in Udorn, Karasin, Khonkan, and Chiang Mai, Thailand, during 1971 and 1972. The flight period at Chiang Mai was from June to November in 1971 and from the middle of July to December in 1972. A few adults were collected at Chiang Mai in April 1974, and from other localities in May 1971. Adults have been collected during all months of the year in various parts of the geographical range of the species.

Adults mated readily and frequently in the laboratory, within 1 to 7 days after they were captured. Eggs were laid in rows on leaves included in the rearing jars, on the walls of the jars and on the cloth covers.

The larvae are active aquatic predators; they tolerated water fouled by dead snails better than larvae of the other species of *Sepedon* included in this study. Larvae of all three stadia attacked and killed all non-operculate snails exposed to them. More than one larva often attacked the same snail. Third-instar larvae were able to kill snails quicker than were first- and second-instar larvae. Further life cycle details are shown in Table 1.

Six to 15 parasitic wasps (*Eupteromalus* sp., Pteromalidae) were reared from each of several puparia of *S. aenescens*.

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