# BIOLOGY OF A NEOTROPICAL SNAIL-KILLING FLY, SEPEDONEA ISTHMI (DIPTERA: SCIOMYZIDAE)

## Lloyd Knutson and Karl Valley

Abstract.—Sepedonea isthmi (Steyskal) is known from the Canal Zone, Panama, Trinidad, Venezuela, Colombia, Bolivia and Brazil. The species is found in various fresh-water situations, where the larvae are obligate predators of pulmonate snails. Females collected in Venezuela in April, Trinidad in May and Colombia in June laid up to 406 eggs each in the laboratory. The incubation period was 2–6 days; the first larval stadium lasted 2–4 days; the second, 3–6; the third, 5–8; and the pupal period was 8–14 days, at room temperatures. Larvae killed and ate as many as 23 aquatic snails ranging in size from 1–6 mm. Prey species included Biomphalaria glabrata (Say), Drepanotrema (Fossulorbis) depressissimum Moricand, D. (F.) lucidum Pfeiffer, Helisoma trivolve (Say), Physa venustula Gould and Lymnaea sp. in the laboratory. The morphology of the immature stages of the Sepedon Group is discussed; and the egg, all three larval stages and the puparium of Sepedonea isthmi are described and figured.

The introduction of Sepedomerus macropus (Walker) from Nicaragua into Hawaii in 1958 and 1959 for control of Lymnaea ollula Gould1, the snail host of the cattle liver fluke, Fasciola gigantica Cobbold (Chock et al., 1961; Berg, 1973), has shown that it is possible to rear Sciomyzidae in large quantities and that an exotic species can disperse from release sites and build up large and persistent populations. Future use of Sciomyzidae as biological control agents must be based not only on quantitative and experimental field and laboratory studies of critical aspects such as predation and competition, e.g. Eckblad and Berg (1972) and Berg (1973), but also on knowledge of the behavior of many different candidate predator species. Most snails that are important as intermediate hosts of parasitic worms of humans and domestic animals are pulmonate, aquatic and amphibious species in tropical and subtropical regions. Sepedon Latreille and related genera are the dominant Sciomyzidae in tropical regions, and the larvae of most reared species are highly specialized predators of aquatic snails. Thus it is of special interest to broaden our knowledge of the basic life cycles of species belonging to these genera.

The fundamental work on the life histories and morphology of immature stages of Sepedon and some related genera is the treatment of ten Nearctic, four Neotropical and two Palearctic species by Neff and Berg (1966). The larvae of all species discussed in that paper are predators of fresh-water pulmonate snails. Knutson et al. (1967) described the biology of the first Sepedon known to be a parasitoid of terrestrial snails in the genus Succinea

Draparnaud, and they added two African species to the list of aquatic predators. Abercrombie (1970) presented extensive biological information on six species of *Sepedonea* Steyskal. Abercrombie and Berg (1975) reported on the biology of *Thecomyia limbata* (Wiedemann), a Neotropical member of the *Sepedon* Group. The present paper treats the biology and immature stages of a Neotropical, aquatic, predaceous species, *Sepedonea isthmi* (Steyskal).

## Taxonomy

The genera of Sciomyzidae related to Sepedon have been treated as a subtribe, tribe or subfamily by various authors. Steyskal (1973) regarded these genera as forming only a "Group" that is not particularly distinctive from typical Tetanocerini (subfamily Sciomyzinae). Steyskal included the following genera in the "Sepedon Group": Sepedon Latreille, Sepedonella Verbeke, Sepedoninus Verbeke, Thecomyia Perty, and his new genera Sepedomerus and Sepedonea (= Sepedon lindneri Group of authors). The Neotropical genus Sepedonea includes the species discussed herein (Sepedonea isthmi), seven other described species (S. barbosai Knutson and Bredt, S. canabravana Knutson and Bredt, S. guatemalana (Steyskal), S. guianica (Steyskal), S. lagoa (Steyskal), S. lindneri (Hendel), and S. telson (Steyskal)), and five undescribed species known to us.

Sepedonea can be distinguished from related genera by using the characters given by Steyskal (1973). Sepedonea isthmi is distinguished from other Sepedonea by the following features: (1) hind femur with apical dark marking but without pre-apical marks, (2) middle femur posteroventrally with 10–12 spinules extending ¾ distance to base, (3) wing with anterior and posterior crossveins distinctly infumated. The male genitalia also show important specific differences and indicate that S. isthmi is most closely related to S. guianica. The species of Sepedonea were catalogued by Knutson et al. (1976).

### Distribution

Sepedonea isthmi has been recorded from the Canal Zone, Panama, Trinidad, Venezuela, Colombia, Bolivia and Brazil. Steyskal (1951) described this species from three specimens from Panamá, Canal Zone, Corazal, 1 March 1912, 1 & (holotype), No. 60905, USNM, 1 & (allotype), and Juan Mina, 2 September 1923, 1 & (paratype), USNM. Also, we have collected or seen the following specimens: BOLIVIA: Beni: Rurrenabaque, 175 m., 10–23 October 1956, 1 &, L. E. Peña, CNC. BRAZIL: Amazonas: Paraná da Cigana, Parintins, November 1969, 1 &, 1 &, Exp. Perm. Amaz., USNM. Pará: Breves, Ilha do Marajó, September 1969, 1 &, Exp. Perm. Amaz., MZUSP. Goiás: Rio Preto, 70 km NE Brasilia, 20 km S Formosa, 7 Novem-

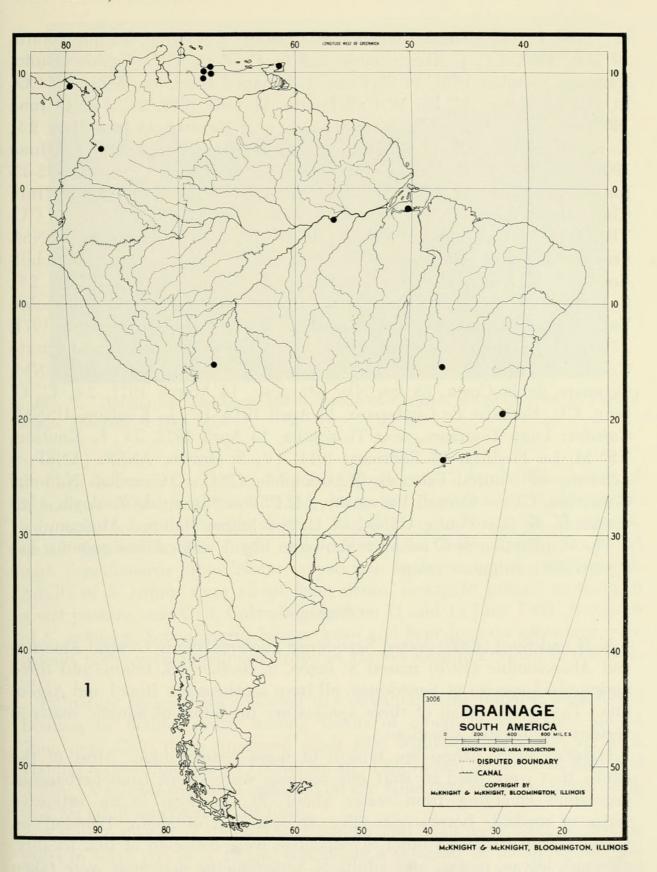


Fig. 1. Collecting sites for Sepedonea isthmi.

ber 1974, 18, L. Knutson, USNM. São Paulo: S. Vicente, Parque Bitaru, 29 May 1967, 18, J. Abercrombie and C. O. Berg, CU. Espirito Santo, Itaguaçu, October 1970, P. C. Elias, 1 damaged specimen, MZUSP. CO-LOMBIA: Valle: 1.7 km W Cali Puerto, 11 June 1969, 38, 19; 14 June 1969, 29, K. R. Valley, CU. 5 km SE Cali, near Navarro, 11 June 1969, 28, K. R. Valley, CU. 6.5 km SE Cali, Navarro, 11 June 1969, 5 8, 4 ♀, 14 June 1969, 8¢, 10♀, K. R. Valley, CU. Morga, 20 km SE of University, 22-25 June 1964, 19, C. O. Berg, USNM. PANAMÁ: Panamá, La Jagua Hunt Club, about 32 km ENE Balboa, 1 July 1969, 19, K. R. Valley, CU. TRINIDAD: Caroni River, 12 October 1918, 19, H. Morrison, USNM. Princess Margaret Highway, 0.15 km south of junction with Churchill-Roosevelt Highway, 9 km west of Port of Spain, 4, 5 May 1972, 88, 29, F. D. Bennett, M. Yaseen, L. Knutson, USNM. VENEZUELA: Carabobo: Valle Seco, January 1940, 1 &, P. Anduze, USNM. Valencia, 16 March 1971, 19, C. O. Berg, CU. Aragua: Pto. de Cata, between Caracas and Puerto Cabello, 17 April 1972, 98, 19, C. J. Rosales and L. Knutson, USNM. Ocumare de la Costa, 28 km NW Maracay, 14 March 1971, 28, C. O. Berg, CU. Embalse de Guataparo, 13 April 1972, 18, L. Knutson, USNM. Cojedes: Lago Taguanes, near Tinaquilla, 13 April 1972, 39, L. Knutson, USNM. La Piedrita, 16 February 1911, 19, S. Brown, ANSP. (ANSP = Academy of Natural Sciences, Philadelphia, CNC = Canadian National Collection, CU = Cornell University, MZUSP = Museu de Zoologia, Universidade de São Paulo, USNM = United States National Museum.)

The distribution of *S. isthmi* is shown in Fig. 1. Sepedonea guianica has a partially contiguous range.

## Biology

Neff and Berg (1966) reared Sepedonea guatemalana in Central America, and Abercrombie (1970) reared S. lagoa, S. lindneri, S. telson, and three undescribed species of Sepedonea, all from southeastern Brazil and Argentina. The larvae of all of these species are predators of aquatic snails in various fresh-water situations.

Habitats of S. isthmi are typical of many Sciomyzidae. Most of the adults that were used to start our rearings were swept from herbaceous vegetation emerging from water about 30 cm deep in an extensive series of roadside borrow pits (Fig. 2) near Port of Spain, Trinidad, on 4 and 5 May 1972. No other Sciomyzidae were collected at that locality, although larvae, pupae, and adults of Sepedomerus macropus were taken on 5 May at the edge of nearby Caroni Swamp, San Juan, Trinidad. The only other Sciomyzidae known from Trinidad are Sepedomerus bipuncticeps trinidadensis (Steyskal) and an undescribed species of Thecomyia.

In Venezuela, adults of Sepedonea isthmi and Sepedomerus bipuncticeps (Malloch) were swept from weed-choked, roadside ditches at Puerto



Fig. 2. Habitat of Sepedonea isthmi, fresh-water marsh, six miles west of Port of Spain, Trinidad, 4 May 1972.

de Cata, between Caracas and Puerto Cabello, on 17 April 1972. Adults of Sepedonea isthmi, with those of S. guianica and Sepedomerus bipuncticeps, were collected at the margin of Lago Taguanes, near Tinaquilla, Venezuela, on 13 April 1972. The single male collected in Goiás, Brazil, was found with Sepedomerus bipuncticeps, Sepedonea barbosai, and S. canabravana. Adults of S. isthmi were swept from dense, emergent grasses growing in a wet pasture near Cali, Colombia between 11 and 14 June 1969. Imagines of S. guianica, Sepedomerus bipuncticeps and Sepedomerus macropus were usually taken with Sepedonea isthmi in various localities visited in the Caliarea.

Immature stages were collected in Colombia. Nine puparia were found floating in shallow water among shoots of emergent vegetation on 14 June near Cali; three produced adult flies within six days and six each yielded a parasitoid wasp (*Trichopria* sp., Diapriidae) between 20 June and 3 July. A third-instar larva collected on the same date near Cali pupariated, and an adult emerged on 29 June.

Adults collected in Trinidad, Colombia and Venezuela were placed by pairs in small jars  $(6 \times 12 \text{ cm})$  containing a substrate of damp cotton, provisioned with crushed snails and a mixture of powdered milk, honey and brewer's yeast and covered with mesh cloth. A pair of imagines collected on 14 June in Colombia were first observed copulating 10 days later; they mated approximately 30 minutes. Adults collected on 5 May in Trinidad were first seen mating on 16 May, and they continued to mate infrequently

until 8 September. Flies collected on 17 April in Venezuela were seen mating on 7 May. Adults that emerged in the laboratory during August did not mate during the following 3 months in the laboratory. The copulatory posture is similar to that of most other Sciomyzidae (male's front tarsi on parafrontal area of female's head, male's middle tarsi on sides of female's thorax, and male's hind tarsi grasping end of female's abdomen).

One female collected in Colombia on 11 June deposited 104 eggs during the following four days; daily egg counts ranged from 26 to 31. A laboratory reared male and female that emerged on 21 July were placed in a breeding container the next day, but the three eggs that the female deposited on 6 August were inviable. Four females were collected in Trinidad on 5 May, and they respectively laid 406 eggs between 16 May and 5 October, 214 between 16 May and 23 August, 30 between 10 May and 6 June and 4 on 12 May. A female collected in Venezuela on 17 April laid 38 eggs between 6 and 25 May. Laboratory reared females from Trinidad did not oviposit.

Eggs were laid side by side in rows of 2–14 on pieces of vegetation or on the dry walls of the breeding jars, but not on shells of crushed or living aquatic snails. The eggs gradually darkened, and the incubation period was 2–6 days at room temperatures (20–22°C).

Larvae killed and ate the aquatic snails Biomphalaria glabrata (Say), Drepanotrema (Fossulorbis) depressissimum Moricand, D. (F.) lucidum Pfeiffer, Helisoma trivolve (Say), Physa venustula Gould and Lymnaea sp. during laboratory rearings. Biomphalaria glabrata and Physa sp. were the dominant aquatic snails at the collecting sites in Trinidad, and Drepanotrema depressissimum, D. lucidum, and Physa venustula were the dominant aquatic snails at the collecting sites in Colombia. None of the larvae fed in egg masses of Helisoma trivolve, but a few second-instar larvae penetrated egg masses of Physa sp. and ate the embryonic snails.

First-instar larvae preyed upon newly hatched and small snails (1–2 mm in greatest dimension). As the larvae grew in size they attacked larger snails; mature *Helisoma trivolve* were frequently killed by large, third-instar larvae. One larva killed and fed on 22 snails (1–6 mm) during its three stadia; another consumed parts of 23 prey individuals (1–4.2 mm). During their 5-day third stadia, two larvae killed and consumed, respectively, seven and eight snails, measuring 4–6.5 mm. The larvae remained in the shells, consuming relatively fresh tissue, for less than 1 day. They rested under the wet sand or gravel in the rearing containers, with their posterior spiracles exposed above the water surface. Larvae lived a relatively long time without food; three first-instar larvae survived 1–4 days and nine second-instar larvae lived 6–11 days in starvation chambers. The first stadium lasted about 2–4 days; the second, 3–6 days; and the third, about 5–8 days. The larval period ranged from 13–17 days.

Puparia were formed in wet sand, among pebbles of gravel and on the

dry undersides of lids of rearing containers; they are obviously adapted for flotation (Fig. 17). Eighteen puparia formed between 29 July and 4 August produced adults 10–13 days later; of 17 puparia formed between 8 and 28 July, 16 produced adults in 8–9 days and one yielded an adult after 14 days. Field collected adults lived up to 78 days in the laboratory.

## Morphology of Immature Stages Sepedon Group

Immature stages of species of the Sepedon Group are among the most distinctive in the family, but because less than 10% of the immature stages of acalyptrate Diptera have been described, diagnostic features can be stated only provisionally. The major source of information on the morphology of the immature stages of Sepedon and related genera is Neff and Berg's treatment (1966) of 16 species. Knutson et al. (1967) described the immature stages of three African species of Sepedon, Nagatomi and Tanaka (1967) provided a thorough description of the egg of Sepedon sauteri Hendel, and Abercrombie (1970) characterized the immature stages of six species of Sepedonea. Abercrombie and Berg (1975) described the developmental stages of Thecomyia limbata.

Although eggs of some species of the Sepedon Group are distinctive, there is no single character that distinguishes them reliably from other genera of Sciomyzidae. All described eggs of this group bear a subterminal micropyle, characteristic of all known eggs of the Tetanocerini. Neff and Berg (1966) stated that the coarse longitudinal striations on eggs of reared Sepedon are rather distinctive for this genus. The patterns of chorionic sculpturing, color and dimensions have been useful characters for separating eggs of various members of the Sepedon Group.

Mature larvae of the aquatic Sepedon Group have a tapered, strongly retractile anterior end; truncate posterior end with three or five pairs of fleshy lobes around the spiracular disc; paired posterior spiracles each with three slits and four profusely branched, interspiracular float hairs; frequently a dark, patterned integument with many folds and wrinkles, and hair patches dorsally; wartlike body tubercles with those on the ventral surface functioning as pseudopods; and inconspicuous anterior spiracles.

Larvae of the Sepedon Group are further characterized by the following features diagnostic of the cephalopharyngeal skeleton of all reared Sciomyzidae: An unpaired, anteriorly serrate, transverse ventral arch present between the anteroventral margins of the mandibular sclerites, posterior arms of hypostomal sclerite not overlapping the anteroventral process of the pharyngeal sclerites in third instar, ventral cornu without dorsobasal lobe and no oral grooves around the mouth opening or longitudinal ridges in the floor of the pharynx (except subfamily Salticellinae). Also, larvae

of the *Sepedon* Group have three to seven accessory teeth on the basal part of the mandibular sclerite, a ventral arch with a relatively deep emargination posteriorly, no dorsal bridge between the pharyngeal sclerites, no window in the dorsal cornu of the pharyngeal sclerites and an indentation index of less than 50.

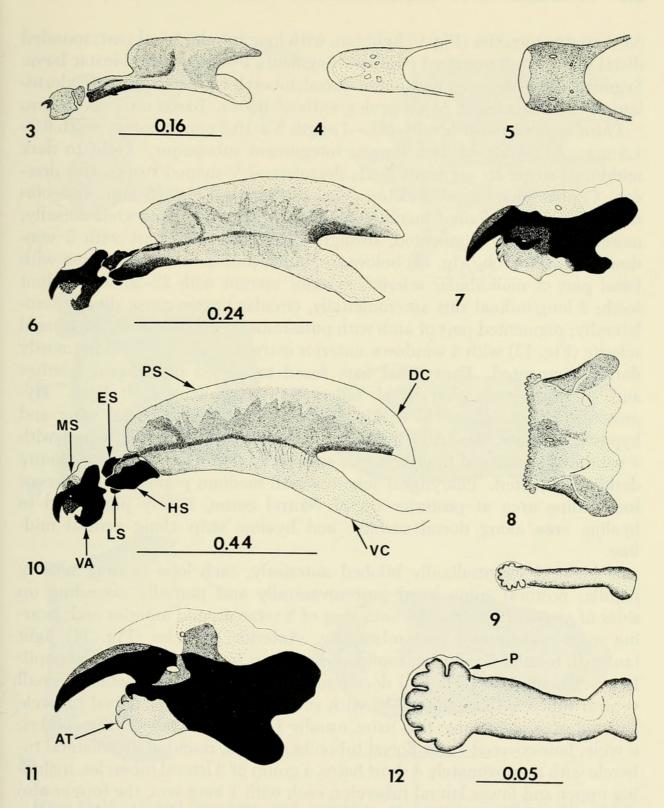
Puparia of the Sepedon Group have the posterior end curved dorsally so that the posterior spiracles with their hydrofuge float hairs project above the water surface. The anterior spiracles project only slightly from the anterolateral angle of the puparium. The body surface retains to some extent the color pattern of the mature larva, and it frequently has a distinctive texture, with lateral bumps and grooves.

## Sepedonea isthmi (Steyskal)

Egg.—Length 1.28–1.38 mm; greatest width 0.30–0.36 mm. White. Elongate-ovoid. Dorsum with 2 prominent longitudinal ridges. Small dorso-lateral ridge visible dorsally. Anterior and posterior poles with distinct punctures. Reticulations on chorion strongest between dorsal ridges, becoming faint laterally and ventrally. Based on 10 specimens.

First-instar larva (Figs. 3, 4).—Length 1.8-3.4 mm; greatest width 0.3-0.4 mm. White. Integument transparent, sparsely covered with spinules as compared to later larval instars. Cephalopharyngeal skeleton (Fig. 3) length 0.29-0.32 mm; mandibular sclerite composed of darkly pigmented, small, decurved portion anteriorly, a larger intermediate portion, and a darkly pigmented, triangular portion posteriorly, the latter connected to intermediate portion by a thin strap; ventral arch below intermediate portion; epistomal sclerite (Fig. 4) with 5 windows; hypostomal sclerite fused to pharyngeal sclerite, hypostomal plate with 4-6 windows; pharyngeal sclerite light brown, darker along pharyngeal indentation and at anterior 1/3 of sclerite; indentation index 30-37. Metapneustic. Segments 5-10 with inner and outer dorsal tubercles contiguous, hair covered. Segment 11 with number of hairs on dorsal tubercles greatly reduced. Spiracular plates light tan, with B-shaped spiracular openings. Anal proleg with short decurved spinules. Spiracular disc, except bare central area, with many long, fine hairs. Based on 25 specimens.

Second-instar larva (Figs. 5–9).—Length 3.8–4.5 mm; greatest width 0.6–0.8 mm. Light tan to brown. Integument translucent, densely covered with spinules. No middorsal stripe or dorsolateral V-shaped stripes. Cephalopharyngeal skeleton (Fig. 6) length 0.48–0.58 mm; mandibular sclerite (Fig. 7) 0.11–0.12 mm long, with 3–4 accessory teeth; ventral arch (Fig. 8) with 21–26 teeth anteriorly; epistomal sclerite (Fig. 5) with 4 windows; hypostomal sclerite fused to pharyngeal sclerite, hypostomal plate with 4 windows; pharyngeal sclerite without dorsal wing; indentation index 31–

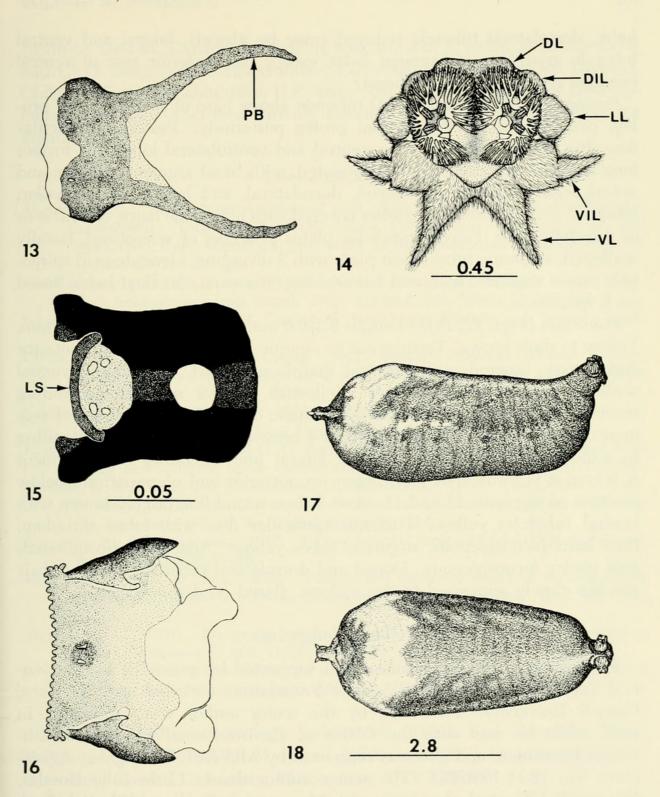


Figs. 3–12. Larval structures of Sepedonea isthmi. 3. First-instar larva, cephalopharyngeal skeleton; 4. Same, epistomal sclerite and parastomal bars; 5. Secondinstar larva, epistomal sclerite and parastomal bars; 6. Same, cephalopharyngeal skeleton; 7. Same, mandibular sclerite; 8. Same, ventral arch; 9. Same, anterior spiracle; 10. Third-instar larva, cephalopharyngeal skeleton; 11. Same, mandibular sclerite; 12. Same, anterior spiracle. The scale for figures 4, 5, 7–9, 11, and 12 is below figure 12. (AT = accessory tooth, DC = dorsal cornu, ES = epistomal sclerite, HS = hypostomal sclerite, LS = ligulate sclerite, MS = mandibular sclerite, P = papilla, PS = pharyngeal sclerite, VA = ventral arch, VC = ventral cornu).

35. Anterior spiracles (Fig. 9) light tan, with long tubular basal part; rounded distal part with 8 marginal papillae. Segments 1–10 as in third-instar larva. Segment 11 with inner and outer dorsal tubercles greatly reduced; dorso-lateral tubercle absent. Anal proleg without hooks. Based on 7 specimens. Third-instar larva (Figs. 10–16).—Length 5.3–10.8 mm; greatest width 0.9–

Third-instar larva (Figs. 10–16).—Length 5.3–10.8 mm; greatest width 0.9–1.8 mm. Light tan to dark brown; integument subopaque. Light to dark middorsal stripe on segments 3–11; dorsolateral V-shaped stripes also present. Cephalopharyngeal skeleton (Fig. 10) length 0.79–0.88 mm. Indentation index 36–38. Paired mandibular sclerites (Fig. 11) connected dorsally; mouthhook darkly pigmented, strongly decurved; basal part with 2 windows. Ventral arch (Fig. 16) below and either joined to or articulating with basal part of mandibular sclerite; anterior margin with 22–26 short, blunt teeth; 2 longitudinal slits anteromesially, circular to transverse slits posterolaterally; pigmented part of arch with posteromedian indentation. Epistomal sclerite (Fig. 13) with 4 windows, anterior margin hyaline, remainder mostly darkly pigmented. Parastomal bars fused to paired pharyngeal sclerites and continuing to pharyngeal indentation as salient dark lines. Hypostomal sclerite (Fig. 15) darkly pigmented except for dorsal wing and hypostomal plate, the latter between anterior rami of the sclerite and with 4 windows; connected to pharyngeal sclerites by thin strap. Ligulate sclerite darkly pigmented. Pharyngeal sclerites with medium pigmentation, except for hyaline area at posterior tip of ventral cornu, lightly pigmented to hyaline area along dorsal surface, and hyaline strip along ventral midline.

Segment 1 longitudinally bilobed anteriorly, each lobe bearing sensory papilla; postoral spine band posteroventrally and partially extending up sides of segment. Segment 2 with ring of 8 setae around anterior end; bearing anterior spiracles posterolaterally. Anterior spiracles (Fig. 12) light tan, with tubular basal part; rounded distal part bearing 7–8 marginal papillae. Segments 3 and 4 with 1 dorsal and 1 lateral seta, and 3 setae on small ventral tubercle. Segments 5-10 with small, rounded inner dorsal tubercle covered with many long, fine hairs, usually 1 longer and heavier than others; a wide, hair-covered outer dorsal tubercle; a small, rounded dorsolateral tubercle with approximately 4 short hairs; a group of 3 lateral tubercles, including upper and lower lateral tubercles, each with 1 long seta, the former also with a group of about 4 shorter hairs, and a middle lateral tubercle, smaller and slightly anterior to the others and with group of about 4 short hairs; a ventral tubercle group consisting of a conspicuous middle row of 4 tubercles, each with tuft of about 4 short hairs, an anterior row of 2 widely separated tubercles, each with tuft of about 4 hairs, and a posterior row apparently devoid of distinct tubercles and appearing as creeping welt. Segment 11 with inner and outer dorsal tubercles reduced, the latter with only 2 long



Figs. 13–18. Larval structures and puparium of Sepedonea isthmi. 13. Third-instar larva, epistomal sclerite and parastomal bars; 14. Same, posterior spiracular disc; 15. Same, ligulate sclerite and venter of hypostomal sclerite; 16. Same, ventral arch; 17. Puparium, lateral view; 18. Same, dorsal view. The scale for figures 13, 15, and 16 is below figure 15. (DL = dorsal lobe, DlL = dorsolateral lobe, LL = lateral lobe, PB = parastomal bar, VL = ventral lobe, VlL = ventrolateral lobe.)

hairs; dorsolateral tubercle reduced (may be absent); lateral and ventral tubercle groups as in segment 5–10, except the posterior row of ventral tubercle group reduced or absent.

Segment 12 with small lateral tubercle above base of hookless anal proleg; perianal pad bordering anal proleg posteriorly. Posterior spiracular disc (Fig. 14) with conspicuous ventral and ventrolateral lobes, the former long and tapered, the latter, 2-segmented, with basal segment truncate and apical segment digitiform; dorsal, dorsolateral, and lateral lobes smaller, rounded, and inconspicuous; lobes covered with many fine hairs; central area of disc base bare. Paired spiracular plates at apices of sclerotized, basally scalloped, stigmatic tubes; each plate with 3 diverging, elongate-oval spiracular slits, a stigmatic scar, and 4 branching interspiracular float hairs. Based on 5 specimens.

Puparium (Figs. 17, 18).—Length 5.3–6.0 mm; greatest width 1.9–2.3 mm. Yellow to dark brown. Translucent to opaque. Barrel-shaped with anterior end narrow, tapered; posterior end sharply upturned. Cephalopharyngeal skeleton as in third-instar larva. Yellowish anterior spiracles protruding from anterolateral corners of dorsal cephalic caps. Most of dorsum of segments 5 and 6 yellow. Dorsum with 3–4 brown, V-shaped stripes extending to middle tubercle groups. Yellow lateral line extending from segment 5, where it is infuscated with brown to posterior end of puparium, below junction of segments 11 and 12. Area below lateral line largely brown with ventral tubercles yellow. Posterior spiracular disc with lobes shrunken; float hairs inconspicuous; stigmatic tubes yellow. Anal plate invaginated; anal proleg inconspicuous. Dorsal and dorsolateral tubercles reduced, hair patches closely appressed to the surface. Based on 4 specimens.

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#### Footnote

<sup>1</sup> This species is considered as a possible synonym of *Galba viridis* (Quay and Giaimard) by B. Hubendick, 1951, Recent Lymnaeidae, Kungl. Svensk. Vittenskapakad, Fjärdel 1, Bd. 3, no. 1, pp. 1–223, 5 pls.



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