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Authors: Gbedjissi, Ghélus Louis, and Vala, Jean-Claude

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Life-cycle of the Afrotropical snail-killing fly *Sepedon (Parasepedon) ruficeps* Becker, 1923

Ghélus Louis Gbedjissi[1] and **Jean-Claude Vala**[2]

[1]Université Abomey-Calavi, Box 526, Cotonou, Republic of Benin;
ghelus_louis@yahoo.fr

[2]Université d'Orléans, Laboratoire de biologie des Ligneux et des Grandes Cultures, UPRES EA 2107, BP 6759, 45067 Orléans Cedex 2, France;
jean-claude.vala@univ-orleans.fr, jean-claude.vala@wanadoo.fr

ABSTRACT

Sepedon ruficeps is a widespread species among Sciomyzidae in the Afrotropical Region. Its general distribution, and more specifically that in Benin, is mapped. The complete life-cycle, from egg to adult, and descriptions of all immature stages are presented. Larval predation of freshwater molluscs is analyzed, with the main objective of discovering biological control agents for snail intermediate hosts of trematodes, principally *Schistosoma* and *Fasciola* species which affect man and domestic animals. The results reported here relate to *Radix natalensis*, snail host of *Fasciola gigantea*. In the absence of sufficient mollusc-prey, however, the fly larvae show alternative predation at the expense of the freshwater snail *Aulophorus furcatus*. This particularity could allow intensive laboratory rearing, before release of all stages of the fly in the field for biocontrol of distomiasis. *S. ruficeps* is undoubtedly polyphagous and multivoltine.

KEY WORDS: Immature stages, larval feeding behaviour, larval predation, biological control agent, oligochaete, fascioliasis, *Radix natalensis*.

INTRODUCTION

This publication is especially dedicated to the memory of the late Brian Roy Stuckenberg. One of the authors (J-CV) met him at the 5th International Congress of Dipterology in Australia in 2002. There, we appreciated his papers on "an overview of Afrotropical Diptera, "the phylogenetic implications of labial morphology," and his dynamic and enjoyable presentation, which was a real success, on the "Gondwana breakup". The personal and cordial discussions that we had then were certainly fruitful and reflective of a very cooperative colleague with a particular ability to listen to others. Indeed, he subsequently sent us documents for our research on Afrotropical Diptera and the Sciomyzidae. His generous nature was also underlined by Verbeke in his descriptions of *Sepedon (Parasepedon) stuckenbergi* in 1961 and *Salticella stuckenberg*i in 1962, from specimens of Diptera sent to him by Brian Stuckenberg for study.

Of the 536 Sciomyzidae (snail-killing or marsh flies) species and 61 genera described world-wide, only 64 species and 12 genera are found in the Afrotropical Region (Knutson & Vala 2011). However, there are always new species awaiting description. Full or incomplete life-cycles are available for 203 species in the world and only ten in the Afrotropics, including unpublished data for two of them (Gbedjissi & Vala in prep.).

The purpose of the present study is to supplement knowledge on the biology of Sciomyzidae in the Afrotropical Region. Currently available publications concern the following: the life-cycle of *Sepedon hispanica hispanica* Loew, 1862, larvae of which are parasitoids/predators of freshwater snails; a description and some drawings of the third instar larva and pupa of *Sepedon ruficeps* Becker, 1923 and *S. (P.) scapularis* Adams, 1905 (Knutson *et al.* 1967); the life-cycle of *S. (P.) neavei* Steyskal, 1956 and *S. testacea* Loew, 1862, larvae of which are polyphagous predators of the freshwater

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molluscs *Physa*, *Biomphalaria*, *Lymnaea* and *Planorbis* (Barraclough 1983); life-cycle and biology of *S. (P.) trichrooscelis* Speisser, 1910, larvae of which are strictly parasitoids/saprophages of the semi-terrestrial aquatic snails Succineidae (Vala *et al.* 1995); and life-cycle of *Sepedonella nana* Verbeke, 1950, larvae of which attack and eat strictly the freshwater oligochaete *Aulophorus furcatus* (Müller) (Naididae) (Vala & Gbedjissi 2011). We must include the life-cycle of *Hydromya dorsalis* (Fabricius, 1775), which is a Palaearctic species, also collected in the south of Egypt. Its larvae are polyphages of freshwater pulmonate snails and egg masses of *Lymnaea* species (Knutson & Berg 1963). In addition, larval feeding descriptions have been given for *S. scapularis* by Maharaj (1991) and Maharaj *et al.* (1992), particularly concerning relationships between the sizes of the larvae and the molluscs/prey during progression of larval feeding in South Africa. Likewise, Gbedjissi *et al.* (2003) provided information for *S. ruficeps* in Benin. Knutson (2008) added some larval feeding behaviour aspects for *S. trichrooscelis* and *S. h. hispanica*.

Our present contribution brings up to date the current knowledge of *S. ruficeps* (Fig. 1), a species typical of freshwater habitats. For the first time, we describe all immature stages, of which details for some morphological parts of the third instar larva and the puparium were previously published by Knutson *et al.* (1967) from Dr W.C. Frohne's rearings in Ethiopia. We report experimental results of predation on the snail *Radix natalensis* (Krauss), implicated in the life-cycle of bovine liver flukes. This work supplements the previous publication by Gbedjissi *et al.* (2003) on population dynamics of the adult flies and predation on snails involved in transmission of *Schistosoma* species in Benin.

MATERIAL AND METHODS

Adults of *S. ruficeps* were captured in some localities in Benin using a traditional sweeping net in two types of aquatic biotopes: (1) permanent water biotopes in Calavi, Cotonou, Porto-Novo and Parakou, mainly composed of shallow areas of cultivated vegetables along the shoreline, and wet areas near rivers or lakes; and (2) temporary water biotopes in Agnavo, Cocotomey and Djeffa, presenting a set of isolated, stagnant or residual pools or ponds formed during the rainfall period but which are dried up during the dry period. We collected the species in 22 supplementary localities in Benin, and also in the neighbouring countries of Togo and Nigeria (Fig. 3).

In the laboratory, we kept all flies in large jars (35 cm diameter) at external ambient temperatures (25–30°C) and photoperiods (12:12), or as pairs in small jars (diameter 9 cm, height 11 cm). We provided pieces of fruit, mainly banana and pineapple, as well as sugar and water as food, and added plants for resting places and as oviposition sites for adults. Jars were observed two times every day in order to collect newly hatched eggs, which were placed individually in a plastic Petri dish (5 cm diameter) on wet filter paper. Then, each neonate larva was moved into a separate dish containing water (depth up to 4 mm) and small freshwater molluscs. Every day, the molluscs were completely consumed by the larvae – which progressively increase in size – and were replaced by an identical number of living snails of exactly the same size. All pupae obtained were also kept individually in Petri dishes until adult emergence. To collect freshwater molluscs, we used a metal sieve (30 cm diameter) and carried the snails to the laboratory in water taken from each site. From these samples kept in breeding, we could obtain all sizes of prey required for experiments based on the size of *S. ruficeps* larval stages. We have

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Fig. 1. *Sepedon (Parasepedon) ruficeps*, male: (A) Habitus, right hind leg is broken; (B) head, dorsal view. (Photos: A. Mantilleri)

distinguished three classes of *Radix natalensis* according to their length, *Pc* (small size, <4 mm), *Mc* (medium size, 4–7 mm), and *Gc* (large size, >7–10 mm). For predation experiments, each with a minimum of 10 repetitions, we put one larva (first, second or third instar) and three snails together in the same Petri dish.

RESULTS

Sepedon (Parasepedon) ruficeps Becker, 1923

Sepedon ruficeps: Becker 1923: 71
Sepedon (Parasepedon) adamsi Steyskal in Steyskal & Verbeke 1956 (South Yemen): 3; Verbeke 1963: 59 (synonymy).
Sepedon (Parasepedon) spectabilis Frey, 1958: 59 (Cape Verde Is); Verbeke 1963: 59 (synonymy).

Type specimens: ♂ ♀ in good condition (Naturhistorisches Museum, Vienna, Austria); reviewed by Verbeke (1963).

Systematic aspects, distribution and biology of Sepedon ruficeps

Verbeke (1963) rectified two of his previous identifications: a species cited in 1950 as *S. scapularis* Adams, 1903, and a species cited in 1961 as *S. neavei* Steyskal, 1956, were in reality *S. ruficeps*. However, *S. scapularis* and *S. neavei* are indeed two valid species among Afrotropical sciomyzids. During a recent review of the Afrotropical fauna on the basis of material located in Belgian museums, we examined these specimens studied by Verbeke – adults and microscopic preparations of genitalia – and share his conclusions.

The Afrotropical *Sepedon* species are 52.5% of the species described globally. Since many are distinct in respect of some cryptic characters, Verbeke (1950, 1961) proposed classification of species into nine groups, mainly based on the male postabdomen. *S. ruficeps* is at present included in his *senegalensis* group. Steyskal (1973) proposed

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the inclusion together in a single "*Sepedon* Group" of all allied genera known in the world: *Sepedonea* Steyskal, 1973, *Sepedomerus* Steyskal, 1973, *Thecomyia* Perty, 1833, *Sepedonella* Verbeke, *Sepedoninus* Verbeke, and *Sepedon s. str.* Latreille, 1804 (including Verbeke's three 1950 subgenera *Parasepedon*, *Mesosepedon* and *Sepedomyia* [originally of generic rank]). Knutson and Orth (2001) proposed nine groups, with the Afrotropical species being scattered in their *trichrooscelis*, *dispersa* and *nasuta* groups; *S. ruficeps* would fit into the first. However, as noted by Barraclough (1985: 489), "the Afrotropical *Sepedon* fauna is rather poorly known … a comprehensive revision of the genus *Sepedon* [is needed] in the region." As some species are close to *S. ruficeps*, its diagnosis is provided below.

Adults (Fig. 1). Body length 6.1–8.0 mm (Fig. 1A). Head, face and frons yellow-orange with some blackish pruinosity (Fig. 2B); antenna: scape yellow-orange, pedicel mostly blackish, flagellomere lanceolate and with black pruinosity. Thorax dorsally bluish (metallic) to brownish; humeral callus light yellow-reddish; pleura subshining greyish; ⅓–½ of basal part of femora yellowish, whereas the apical portion is reddish. Wings 7 mm, hyaline, brownish infuscated. Abdominal segments yellow-orange to red dish. Male genitalia with a praeputium (distal part of aedeagus) having a few hairs and two opposite expansions; surstyli with strong bristles; tubular appendix of aedeagus elongated, apex curved, with a dorsal pre-apical spine. Verbeke's figures (1950 [noted as *S. scapularis*], 1961, 1963) are reproduced here (Fig. 2A, B).

Verbeke (1963) commented that *S. ruficeps* has been often confused with *S. (P.) senegalensis* Macquart, 1844. He stated that this species is distinguished by the rather reddish frons; humeral callus dark brown, only slightly distinct from thorax coloration, and tubular appendix of aedeagus not elongated, apex not curved (Figs 2C, D).

Judging from the specialized literature, *S. ruficeps* appears to be the most widely distributed species of Afrotropical Sciomyzidae (Fig. 3). In West Africa, the species is known from along the Atlantic Ocean coast of the Republic of Cabo Verde, Senegal, Ivory Coast (new data), Togo, Benin, Nigeria and Gabon (new data); from Egypt[1] to Namibia, near Lake Chad (new data), Central African Republic (Nola; new data), Botswana, Zimbabwe (Harare), through the Sudan (Kordofan), Rwanda, Burundi and the Democratic Republic of the Congo. In East Africa, it has been identified in Ethiopia, but also from the Arabian Peninsula (South Yemen). The altitudinal range is very large, from a few metres above sea level in Benin (Cotonou and Djeffa; present data) to 4,000 m above sea level, as cited by Verbeke (1963), in the National Park at Virunga (ex Parc Albert), Democratic Republic of the Congo. In addition, this species has been collected in Saudi Arabia (J. Deeming pers. comm., 22 Jan. 2013).

Adults do not fly very far from the wetlands. In Benin, the profile of the populations was significantly related to the succession of heavy rains and dry months. Thus, in temporary water biotopes, the population profile is mainly characterized by flies not being captured from January to July, and followed by an annual peak, the level and temporal position of which varies according to the geographic zone, for example in Agnavo (Fig. 4A). In permanent water biotopes, the maximum population size was usually observed from June to November, after the period of heavy rain, and decreases in other months without reaching zero, for example in Cotonou (Fig. 4B).

The unusual site "Bati Hot Springs" among Dr Frohne's collecting sites (Gambela, Kola, Bati, Ethiopia) and reported by Knutson *et al*. (1967), is noteworthy: "There is

[1] Verbeke (1963) cited the species from specimens collected in Bahania Oasis and preserved in the Cairo Museum under the name *Sepedon hispanica* Loew, 1862.

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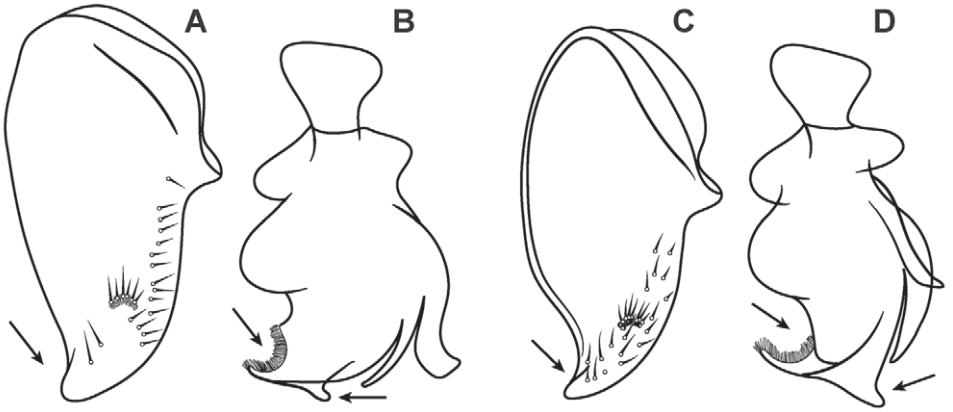


Fig. 2. Surstylus and aedeagus: (A, B) *Sepedon (Parasepedon) ruficeps*; (C, D) *S. (P.) senegalensis*. Arrows show main differences. (Modified from Verbeke (1950), © Institut Royal des Sciences Naturelles de Belgique)

a huge flow of very hot and sulphurous water which is azoic at first but soon becomes ... with many kinds of blue-green algae." Despite this hostile habitat, eight adults were collected on 8 February 1962. This observation allows consideration of *S. ruficeps* as a resistant species, the larvae of which have become adapted to hydrological conditions that are often unfavourable to the survival of many freshwater taxa.

In the laboratory, mating of neonate adults started very early, from 24 to 48 hours after emergence, and could last for several hours. The first eggs were laid 6–8 days after emergence, individually or in groups of 2 to 10 without special arrangement, varying between 50 and 250 eggs per female. The percentage of eggs that hatched often exceeded 95 %, regardless of season or location where the female was collected. The duration of each immature stage in the laboratory and complete life-cycle are indicated in Fig. 5. Our results show that the length of the whole life-cycle is about 16–19 days. This short duration explains the polyvoltine situation observed in nature for this *Sepedon* species, and corroborates the data given by previous authors. During the larval period, the percentage mortality was higher for first instar larvae and gradually decreased to become insignificant by the end of larval development. From 100 eggs, we obtained successively 96 L1, 67 L2, 48 L3, 46 pupae and 45 adults, and the average lifespan of an adult in captivity was 3–4 months.

Feeding behaviour in respect of number of snails consumed

Except for the two operculate Ampullariidae (Pulmonata) *Lanistes varicus* (Müller) and *Lanistes ovum* Peter, the larvae attacked all other freshwater snails species collected at the respective sites for maintenance of our laboratory cultures. These were Bulinidae: *Bulinus forskali* (Ehrenberg), *B. globosus* (Morelet), *B. truncatus* (Audouin); Lymnaeidae: *Radix natalensis*; Physidae: *Aplexa waterloti* Germain, *Physa* sp.; Planorbidae: *Afrogyrus coretus* (de Blainville), *Biomphalaria pfeifferi* (Krauss).

Gbedjissi *et al*. (2003) limited their study on larval predation to *Bulinus forskali* (intermediate host of *Schistosoma intercalatum* Fischer) and *Biomphalaria pfeifferi* (intermediate host of *S. mansoni* Sambon), implicated in transmission of human schi-

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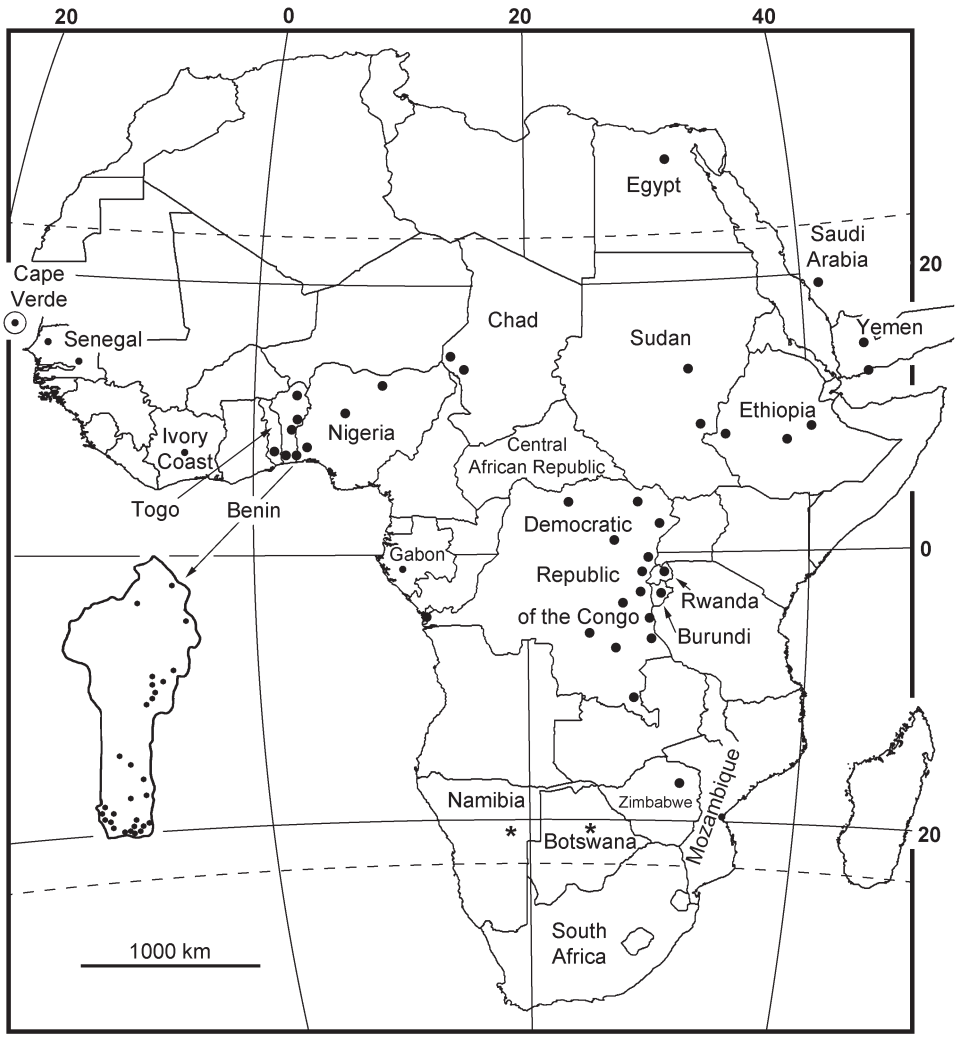


Fig. 3. General distribution of *Sepedon (Parasepedon) ruficeps*. Dots – known locations, stars – occurrence of the fly in a country is ubiquitous. Data from Verbeke (1950, 1961, 1962, 1963), Knutson *et al*. (1967), and our own collections as well as those of colleagues in some African countries.

stosomiasis in Benin. Both snail species live in shallow water areas which are frequented by man or used as drinking-trough sites for domestic animals.

Here, we provide results of veterinary interest as regards the possibility of reducing transmission of the liver fluke *Fasciola gigantica* (Cobbold), a cause of bovine fascioliasis, the widely distributed snail *Radix natalensis* being one of the intermediate hosts in Africa as well as in tropical regions of southern and south-eastern Asia. Humans can be inadvertently infected with *F. gigantica* as a result of the ingestion of metacercariae – formed by mature cercariae that emerge from the snail – and which are glued to aquatic vegetables. Utzinger and Tanner (2000) indicated that *R. natalensis* showed a microhabitat preference for shallow water with a peak water depth of up to 4 mm, as

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TABLE 1

Number of *Radix natalensis* consumed by each larval stage of *Sepedon ruficeps* in proportion to three size classes of the mollusc. Abbreviations: A – healthy snails, B – parasitized snails, *Gc* – large size, *Mc* – medium size, *Pc* – small size.

	Larval stage	Non-parasitized mollusc size classes		
		Pc	*Mc*	*Gc*
A	L1	4.36 ± 1.60	2.25 ± 0.34	0
	L2	7.53 ± 1.22	3.64 ± 0.51	2.13 ± 0.12
	L3	25.50 ± 2.10	9.68 ± 1.37	5.13 ± 1.63
	Total	37.39 ± 1.64	15.57 ± 0.74	7.26 ± 0.87
		Parasitized mollusc size classes		
		Pc	*Mc*	*Gc*
B	L1	4.30 ± 1.31	2.27 ± 0.36	0
	L2	7.60 ± 1.52	3.70 ± 0.62	2.16 ± 0.15
	L3	26.12 ± 2.30	10.74 ± 1.44	6.20 ± 1.12
	Total	38.02 ± 1.71	16.71 ± 0.80	8.36 ± 0.63

used in our experiments. This habitat type is greatly frequented by man and cattle, and favours transmission of distomiasis. Moreover, from serial malacological experiments with this snail in Senegal, Vassiliades (1978) showed that under dry conditions, the older individuals survived for 15–30 days and the younger ones for 60–90 days. We consider that, in nature, large *R. natalensis* die quickly because of their greater demand for water, whereas smaller snails could use the humidity of the air (95 % in experiments) to satisfy their minimal need for water. Thus, the resilience of the snail in respect of water requirements decreases as it grows in size. Furthermore, the snails can survive for months buried in mud, and produce a large number of eggs.

In our first experimental series, conducted with healthy *R. natalensis* as prey (Table 1A), the first instar larva (L1) of *S. ruficeps* attacked and ate mainly the small size class of mollusc *Pc* (x = 4.36 ± 1.60); and *Mc* (x = 2.25 ± 0.34), and never the largest individuals (*Gc* class). We found that the second (L2) and third (L3) instar larvae predated on all size classes. By comparison in terms of numbers (based on class *Pc* only), the second instar larvae ate about two times more snails than the first; and the third 5–6 times more than the L1 and 3–4 times more than the L2 flies.

In a second series of experiments, *R. natalensis* was exposed to miracidia from eggs of *Fasciola gigantica* that were obtained from the slaughterhouse in Cotonou. We started the predation experiments at least three weeks after infestation of the snails. This is the estimated period required for development of the immature parasite stages at laboratory temperature. The success of infestation was determined by observation under light microscope or dissection of some snails to detect the presence of sporocysts or rediae in the snail's hepatopancreas. The results (Table 1B) showed that first instar larvae ate molluscs of classes *Pc* (x = 4.30 ± 1.31) and *Mc* (x = 2.27 ± 0.36), whereas L2 and L3 larvae indifferently consumed molluscs of all classes. The experiments conducted only with class *Pc* showed that the third instar consumed 6 times more than the L1 and 3–4 times more than the L2.

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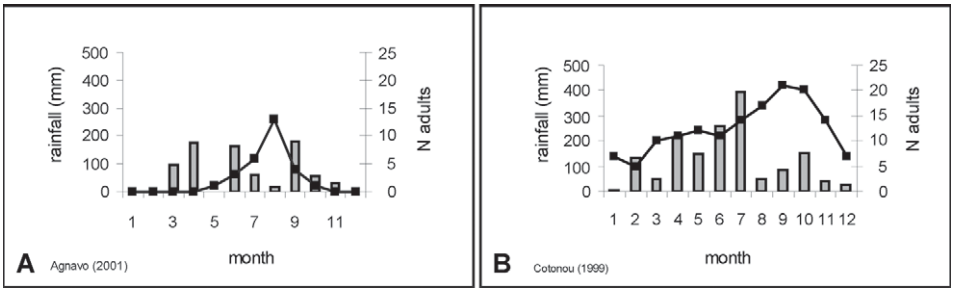


Fig. 4. Examples of annual population evolution of *Sepedon (Parasepedon) ruficeps*, based on adults collected in freshwater habitats: (A) Agnavo, typical temporary freshwater habitat; (B) Cotonou, typical permanent freshwater habitat. Histogram, rainfall; curve, number of flies.

Correlated with the health status of *R. natalensis* (Table 1), a significant difference was observed between the three classes *Pc*, *Mc* and *Gc* for each predator stage. However, there were significant predation differences between healthy and infested snails only for the *Mc* and *Gc* classes. The L3 larva consumed 9.68 ± 1.37 (*Mc*), 5.13 ± 1.63 (*Gc*) of healthy individuals (Table 1A) as compared to 10.74 ± 1.44 (*Mc*), 6.20 ± 1.12 (*Gc*) of parasitized individuals (Table 1B). These data show more feeding on the infested snails (Wilcoxon test). We did not observe emission of cercariae during consumption of parasitized snails of the *Mc* and *Gc* classes. At this time, parasite development had not yet reached the cercarial shedding stage. That aside, *S. ruficeps* appears to be very effective as a predator of parasitized *R. natalensis*. Globally, the three larval stages eat a lot of juvenile as well as sexually mature snails, and thus contribute to reducing reduce the population level of snails of the subsequent generation.

Predation on oligochaetes

Whereas the fly larvae attack and eat freshwater snails, they also predate extensively on the small and abundant oligochaete *Aulophorus furcatus*, which lives in the same biotopes. We observed this predation both in the laboratory and in the field, behaviour recently mentioned by Gbedjissi *et al*. (2003). This small worm lives inside a tiny floating tube, open at both ends, which is constructed with conglomerated vegetal debris. *S. ruficeps* was seen to attack the oligochaete at the front end where the head emerges. A total of 60–70 prey individuals was eaten up to when a fly larva reached the pupal stage. The number of oligochaetes fed upon increased between the first and third instar larval phases, but we did not calculate the corresponding food ratio between molluscs and oligochaetes, needed to complete larval development. Sometimes, a few worms were attacked and only partially eaten. This scenario is similar to the "wasteful feeding" reported in many circumstances for the larvae of some sciomyzids reared in the presence of a surfeit of molluscs (Eckblad 1976; Valley & Berg 1977; Vala 1989). If this significant oligophagous feeding behaviour is alternative for *S. ruficeps*, it is obligatory for the sciomyzids *Sepedonella nana* Verbeke, 1950 (Vala & Gbedjissi 2011) and *Sepedon (Parasepedon) knutsoni* Vala, Gbedjissi and Dossou, 1994, described from Benin (Vala *et al.* 2002). Both of these species are known only from the Afrotopical Region.

Description:

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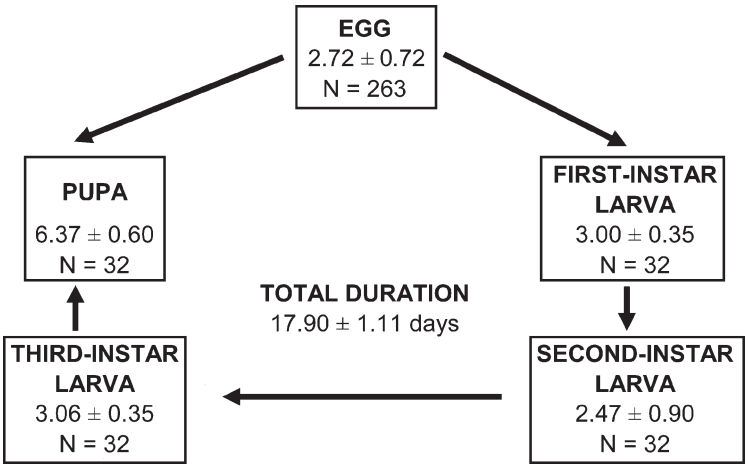


Fig. 5. *Sepedon (Parasepedon) ruficeps*, span of life cycle and development of immature stages, in days.

Immature stages

Egg (Fig. 6A–D). Reticulate chorion showing hexagonal contiguous structures. Four longitudinal ridges (Fig. 6A) present: two subdorsal (Sdr), delimiting a dorsal face (DF), more or less flat; two sublateral (Slr), delimiting a very convex ventral face (VF), largely covered with a glue (Fig. 6B, Gl) for pasting on to emerging stems of aquatic vegetation. The longitudinal subdorsal and sublateral ridges on each side of egg delimit a narrow side face (LF). Anterior end of egg (Fig. 6C) with one arched dorsal expansion, perforated by a large number of aeropyles (Ae) overlying the subterminal micropyle (My). Posterior end rounded (Fig. 6D), many aeropyles present.

Larvae (Figs 6E–H, 7, 8). Like all Sciomyzidae species, three successive larval stages precede a characteristic pupal stage. The larval stages have the same morphology, being composed of 12 segments (I to XII). These stages are distinguished by their size, colour, presence or absence of certain attributes such as absence of the pair of spiracles in the first larval stage (L1). We present below a general description of larvae, followed by the description of each stage with their distinctive characters. Each character is paired and symmetrically distributed according to the sagittal plane. Therefore, we detail them only for one side of the body.

General larval segments

Segment I (cephalic segment). Anteriorly bilobed. Each lobe (CL) with one elongated and leaf-shaped antennal organ (AO); one rounded maxillary organ (MO) bearing sensilla (Fig. 6E); mouth midventral, each lateral edge with two sensilla. One strong postoral spinule band (Fig. 6F, Post B) arranged into 8–10 rows of spines (simple apex) positioned at posterior margin of the segment.

Segments II–IV (thoracic segments). Mainly characterized by presence of a pair of Keilin organs (Fig. 6G, no. 2) on ventral surface, each with three long setae arising from a unique pit camouflaging their basal attachment. All segments without dorsal swimming tuft of setae. Except on segment II, one transverse spinulate ventral band of 13–16 rows on anterior margin, first 5–6 rows more or less expanded laterally and dorsally than others (Fig. 6G, H, Tsv B). This formation has been noted for the Palaearctic species

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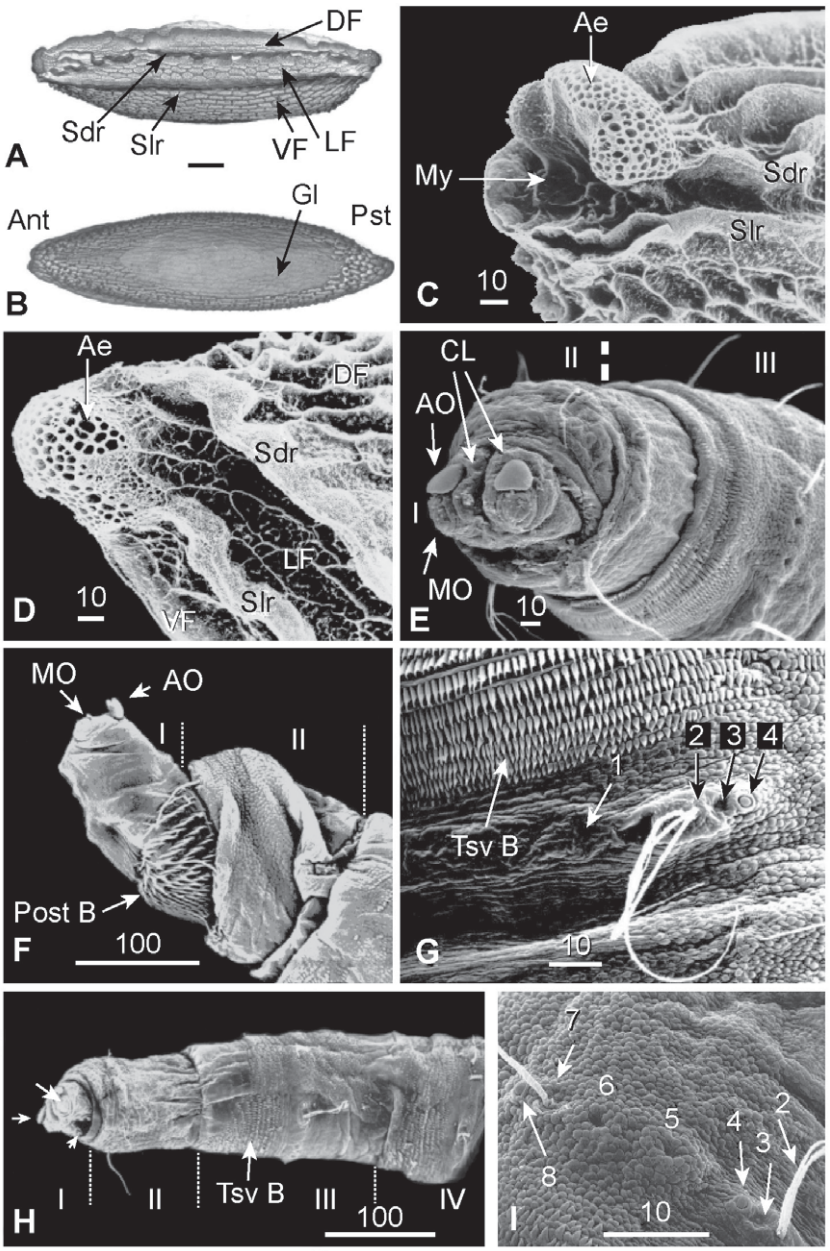


Fig. 6. *Sepedon (Parasepedon) ruficeps*, details of larval immature stages: (A–D) egg, lateral (A) and ventral (B) views, anterior (C) and posterior (D) ends; (E–H) first instar larva: (E) anterior end showing cephalic (I) and thoracic (II–III) segments, frontal view; (F) first instar larva, anterior end in lateral view; (G) characteristic details of thoracic segment; (H) first instar larva more or less in ventrolateral view, segments I–IV showing position of the spinulate ventral band; (I) thoracic sensilla 2–8. Abbreviations: Ae – aeropyle, Ant – anterior end, AO – antennal organ, arabic numbers – sensilla, CL – cephalic lobe, DF – dorsal face, Gl – glue, I–IV – segment numbers, LF – lateral face, MO – maxillary organ, My – micropyle, Pst – posterior end, Post B – post oral spinulated band, Sdr – subdorsal ridge, Slr – sublateral ridge, Tsv B – transverse spinulate ventral band, VF – ventral face. Scale bars in µm.

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Euthycera cribrata (Rondani, 1868) by Vala *et al*. (1983). Other thoracic sensilla (Fig. 6I) are referred to below in the section on sensory receptors.
Segments V–XI (abdominal segments) (Fig. 7) with three ventral pairs of ventral tubercles (Vt1–Vt3), each with long sensilla (Fig. 7A); on each lateral side, three lateral tubercles (Lt1–Lt3), also with sensilla (Fig. 7B, C); then dorsolaterally, one small tuft of long setae and one sensillum (Fig. 7D, E); dorsally, a swimming tuft (Wt) (except on XI) composed by long setae surrounding 2 sensilla (Fig. 7B, D).
Segment XII (last abdominal) (Fig. 7F–H) with pre-anal lobe and anal lobe; lateral lobe present; posterior disc with five pairs of peripheral lobes fringed with bristle devices (Fig. 7H): one well-developed ventrally (VL), triangular, elongated; one lateroventral (VLL), triangular, bi-segmented, and well expanded; one lateral (LL); one laterodorsal (DLL), both triangular and less developed; one dorsal (DL), somewhat indistinct. Each spiracular plate (Sp) with four palmate interspiracular processes (IP), alternating with three spiracular openings.

General larval sensory receptors

The types of sensory receptor and their disposition show a symmetrical distribution along the sagittal plane of the larvae. On the side of each thoracic and abdominal segment, eleven sensilla are present. Results are based on three specimens examined by stereoscan microscopy as established by Vala (1989) and numbered successively from ventral no. 1 to dorsal no. 11.
Cephalic segment (Fig. 6E, F). On each cephalic lobe: one antennal organ (AO) on the apex; one circular maxillary organ (MO) on dorsal surface supporting two or three low styloconicum sensilla, three of the coeloconicum type; two labial sensilla (coeloconicum type) on each lateral part of the mouth.
Thoracic segments (Fig. 6G, I). One coeloconicum sensillum (no. 1) (or ampulaceum type) within a deep cavity (note: not visible on the figure (Fig. 6G), similar to nos 3, 5 and 6); one Keilin organ (no. 2) with its three long chaeticum sensilla (Fig. 6G). Three basiconicum sensilla (Fig. 6I, nos 4, 8 and 9, unfortunately no. 9 is absent in this figure), club-like. Four long trichodeum sensilla (nos 7, 10 and 11) arising from a thin cuticular membranous base (Fig. 6I, no. 11 missing in this figure).
Abdominal segments (Fig. 7A–E). Eleven sensilla are also present on each segment from ventral to dorsal surface. They are positioned mainly on ventral (Vt1–Vt3) and lateral (Lt1–Lt3) tubercles and on the swimming tufts (Wt). The coeloconicum type is dominant and generally the basal edge shows two long, denticulate seta-like structures (Fig. 7E). Other sensilla are of the trichoid type. On ventral surface: successively one, two and one coeloconicum sensillum on Vt1 (no. 1), Vt2 (nos 2, 3) and Vt3 (no. 4). Laterally: Lt1, one coeloconicum (no. 5) (seta-like) plus one long trichodeum (no. 6); Lt2 with sensillum (no. 7) similar to no. 5; Lt3, one long trichodeum sensillum (no. 8) like no. 6. In laterodorsal position, one coeloconicum type with two long setae (45–65 µm long) (no. 9); dorsally, three sensilla within each tuft: one low flower-like coeloconicum (no. 10a), edge with a few short expansions, one long trichodeum sensillum (no. 10) similar to no. 9 – not visible in this picture – and close to longitudinal dorsal axis, one coeloconicum (no. 11) with two long, seta-like expansions on basal edge. Abdominal segment 8 with posterior disc also with eleven pairs of sensilla. Ventrally, coelonicum sensilla (nos 2, 3) on the pre-anal lobe; lateral tubercle with sensillum no. 1; ventral

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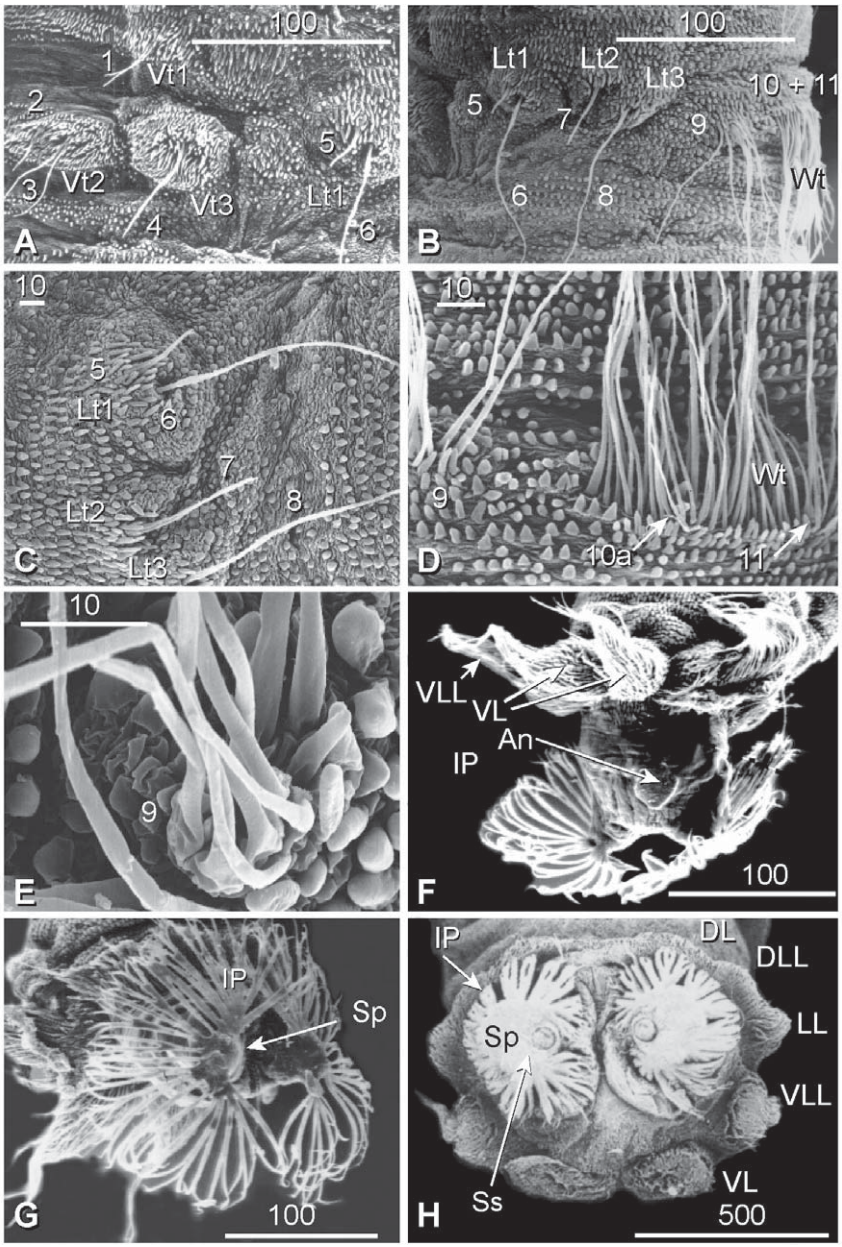


Fig. 7. *Sepedon (Parasepedon) ruficeps*, details of larval abdominal segments: (A) disposition of ventral tubercles; (B) disposition of lateral tubercles and sensilla nos 5 to 11; (C) enlargement of lateral tubercles showing their sensillum types; (D), dorsolateral no. 9 and dorsal 10a sensilla, and dorsal swimming tuft; (E) coeloconicum sensillum type showing basal seta-like expansions; (F–H) last abdominal segment: (F) first instar larva, ventral view; (G) first instar larva, posterior spiracular disc; (H) third instar larva, posterior spiracular disc. Abbreviations: An – anal plate, arabic numbers (including 10a) – sensilla, DL – dorsal lobe, DLL – dorsolateral lobe, IP – interspiracular processes, LL – lateral lobe, Lt1–Lt3 – lateral tubercles, Sp – spiracular plate, Ss – spiracular scar, VL – ventral lobe, VLL – ventrolateral lobe, Vt1–Vt3 – ventral tubercles, Wt – swimming tuft. Scale bar in µm.

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lobe (VL) with sensilla nos 4, 5, 6; ventrolateral lobe (VLL) bears sensilla nos 7–9 and 10a; lateral lobe (LL) and dorsal lobe (DL) with sensilla no. 10 and no. 11 respectively on their apex, styloconicum type.

Instars

First instar larva (L1) (Figs 6E–I; 7A–G; 8A, B). Subcylindric. Length 1.50–3.00 mm; greatest width 0.46–0.78 mm. Integument translucent. No anterior spiracles. Cephalopharyngeal skeleton sclerotized (Fig. 8A, B). Length 0.35–0.39 mm; mouth hook (MH) with bifid hook anteriorly, without accessory tooth, posterior margin fused with complex hypostomal-pharyngeal sclerite; ventral arch (VA) beneath and articulated with mouth hook, anterior margin finely denticulate, lateral edges slightly emerged; pharyngeal sclerite (PS), apex of dorsal cornu very tapered (Dc), ventral cornu (Vc) clear, without window. Spiracular openings B-shaped. Description based on 10 specimens.

Second instar larva (L2) (Fig. 8C–I). Length 3–7 mm. Integument greyish, transparent. Anterior spiracle with 6–7 rudimentary papillae more or less carved on segment II (Fig. 8I). Cephalopharyngeal skeleton length 0.62–0.66 mm (Fig. 8C–H). Mouth hook (MH) sclerified, hook strong, sharp, irregularly decurved line, apex portion abruptly turned in ventral direction; three slightly dark, shared and decurved teeth (At) below the hook; mouth hook body with one small foramen; one small and strong mid-dorsal projection; two posterior projections, thicker dorsal one more elongated than the ventral projection. Ventral arch (VA) articulating with ventral margin of mouth hook, sclerotized, two foramens, anterior margin with 20–24 denticles, posterior margin V-shaped; epistomal sclerite (ES) bilobed, welded to both parastomal bars (PB), all C-shaped; parastomal bars posteriorly fused with pharyngeal sclerites. Hypostomal sclerite (HS) U-shaped, strongly black, one foramen, anteriorly enclosing arched lingual sclerite (LS). Pharyngeal sclerite (PS) wing-like, cornua without window. On each spiracular plate (Sp), three elongated spiracular openings, four interspiracular processes (IP), one round and slightly yellow spiracular scar (Ss). Description based on 10 specimens.

Third instar larva (L3) (Fig 7H; 8J–P). Length 8.5–12.2 mm; greatest width 2.1–2.8mm. Integument brown, translucent, one distinct mid-dorsal stripe. Anterior spiracle with six to seven distinct papillae (Fig. 8P, pa). Cephalopharyngeal skeleton length 0.8–1.2 mm (Fig. 8J–P). Mouth hook (MH) as in second instar, but larger, two foramens, four accessory teeth, mid-dorsal projection very strong and stout; behind, articulated with hypostomal sclerite. Ventral arch with 26–28 regular teeth on anterior margin, posterior part with a long median notch. Epistomal sclerite (ES) dark black except for lightly pigmented anterior margin; two foramina, posteriorly fused with parastomal bars (PB), connected to anteromesal margin of pharyngeal sclerite. Hypostomal sclerite (HS) as in second instar, very stout, with large central hole; lingual sclerite (LS) arched, slightly separated from the arms of hypostomal sclerite; pharyngeal sclerite (PS) with irregular black pigmentation, lacking distinct hyaline area in cornua. Indentation index 32–35. On each spiracular plate (Fig. 7H, Sp), one blackish and round stigmatic scar (Ss), very conspicuous; interspiracular processes robust, large; stigmatic openings elliptic, elongated and wide. Description based on 10 specimens.

Puparium (Fig. 8Q, R). Length 6.0–8.0 mm, width 2.3–3.2 mm. Subcylindrical, ridged. Black-brown, rarely brown, iridescent. With mid-dorsal brownish stripe. Lateral and dorsolateral tubercle vestiges of third instar present, hardened, very conspicuous;

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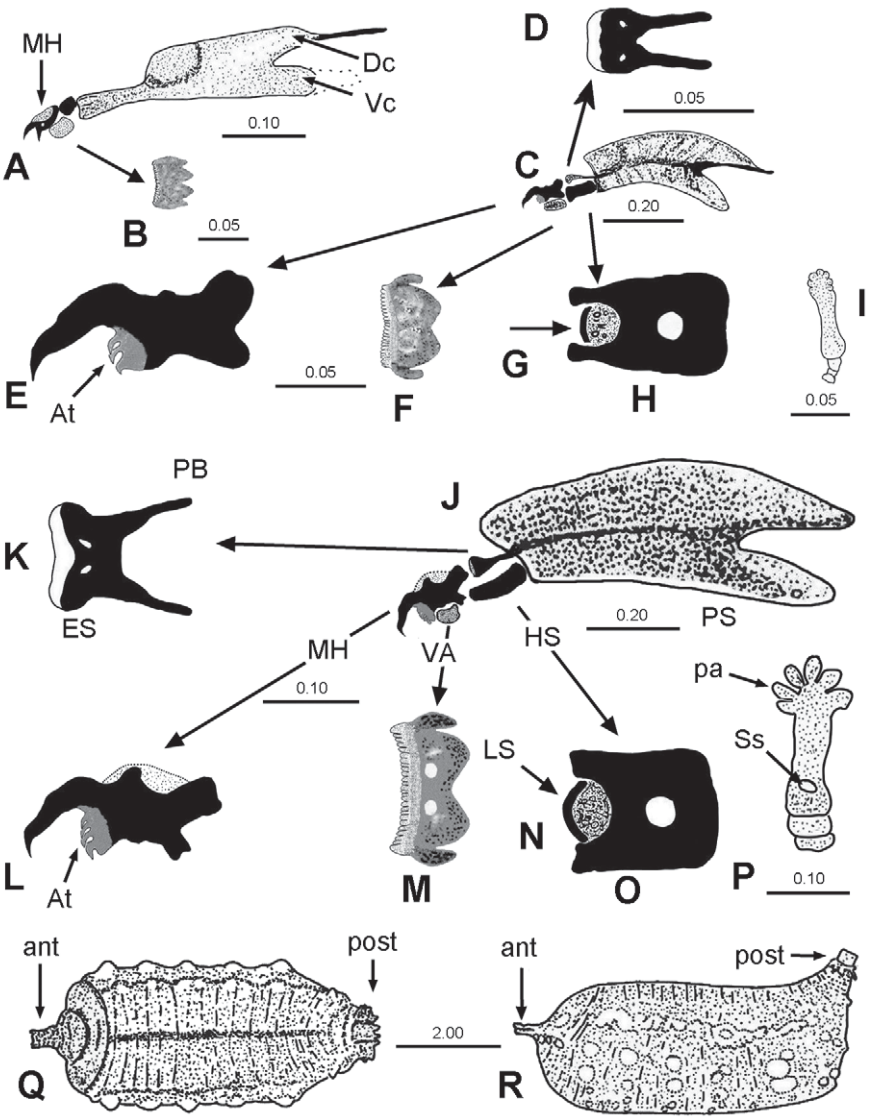


Fig. 8. *Sepedon (Parasepedon) ruficeps*, details of immature stages: (A–H, J–O) cephalopharyngeal skeleton: (A, B) first instar larva; (C–H) second instar larva; (J–O) third instar larva. (I, P) anterior spiracle of second and third instar larva, respectively. (Q, R) puparium: dorsal (Q) and lateral (R) views. Abbreviations: ant – anterior end, At – accessory teeth, (Dc) dorsal cornua, ES – epistomal sclerite, HS – hypostomal sclerite, LS – lingual sclerite, MH – mouth hook, pa – papilla, PB – parastomal bar, post – posterior end, PS – pharyngeal sclerite, Ss – spiracular scar, VA – ventral arch, Vc – ventral cornua. Scale bars in mm.

ventral tubercle vestiges distinct, darkened. Anterior end (ant) abruptly narrower, slightly upturned; tiny anterior spiracles present. Posterior end (post) strongly upturned and higher than the puparial dorsal surface; spiracular disc shrunken; lobes vestigial, hardened and visible; interspiracular processes stunted, bonded, free, folded or raised. Description based on 10 specimens.

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DISCUSSION AND CONCLUSION

On the basis of laboratory rearing performance, quantitative observations and fly collecting periods, we consider *S. ruficeps* to be a multivoltine species without a diapause period. In relation to the last feature, the phenology is entirely compatible with the Group 6 defined by Barker *et al*. (2004). Morphologically, the larvae are typical of a species adapted to freshwater habitats. The dominant characters are the presence of swimming tufts on dorsal abdominal segments, the peripheral lobes and interspiracular processes which are well developed on the posterior disc, and the very long setae of the sensilla, including long setae of the Keilin organs.

As reported elsewhere in many studies (Mullens & Meyer 1987; Lysyk 1993), rainfall and temperature were the main climatic factors influencing the seasonal abundance of flies. Our observations in temporary freshwater habitats showed that the dry period reduced the number of *S. ruficeps* larvae and adults. Thus, from January to May, adults were absent and their number increased slowly until reaching a peak in September–October, just after the main rains. The rainy season was contemporaneous with the breeding period of prey molluscs, when a broad range of snail sizes are available to the fly larvae. In contrast, adults were collected throughout the year in the permanent aquatic habitats, with minor fluctuations and a high peak after heavy rains, the period of precipitation being dependent on the geographical zone. In permanent aquatic habitats, larvae of *S. ruficeps* can always find an adequate number of snails of various sizes and mollusc species to feed upon throughout the year. The information obtained during this study enhances our knowledge concerning *S. ruficeps* and enables us to assess its population dynamics as well as the appropriate periods for application of biological control of molluscs that are intermediate hosts of Trematoda.

This species of fly seems to be an efficient potential agent for biological control of snails implicated in transmission of distomiasis. Indeed, all sizes of *Radix natalensis* were attacked by the three larval fly stages. The second and third instars consumed mainly large, reproductively mature molluscs. Consequently, this feeding behaviour has a direct effect on a given molluscan population by reducing the level of the next generation in terms of numbers of snails. Moreover, we found that if the larvae attacked and consumed both healthy and infested snails, they ate significantly more of the latter.

In the laboratory, *S. ruficeps* larvae ate the oligochaete *Aulophorus furcatus* in the absence of molluscs, and some of our field surveys in Cotonou and Agnavo confirmed that this alternative feeding behaviour occurs in nature. In part, this propensity may explain the widespread distribution of *S. ruficeps* in the Afrotropical region. In practice and at lower cost, this worm could perhaps be used for extensive rearing of the fly in order to get enough adults, larvae, and/or pupae to release in nature as a biological agent against intermediate snail hosts of trematodes.

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REFERENCES

Barker, G.M., Knutson, L., Vala, J.-C., Coupland, J.B. & Barnes, J.K. 2004. Overview of the biology of marsh flies (Diptera: Sciomyzidae), with special reference to predators and parasitoids of terrestrial gastropods. *In*: Barker, G.M., ed., *Natural enemies of terrestrial molluscs*. Wallingford: CABI Publishing, pp. 159–225.

Barraclough, D.A. 1983. The biology and immature stages of some *Sepedon* snail-killing flies in Natal (Diptera: Sciomyzidae). *Annals of the Natal Museum* **25** (2): 293–317.

———1985. Two new species of *Sepedon* (*Mesosepedon*) from southern Africa (Diptera: Sciomyzidae). *Annals of the Natal Museum* **26** (2): 489–495.

Eckblad, J. 1976. Biomass and energy transfer by a specialized predator of aquatic snails. *Freshwater Biology* **6** (1): 19–21.

Frey, R. 1958. Kanarische Diptera brachycera p.p., von Håkan Lindberg gesammelt. (Entomologische Ergebnisse der finnländischen Kanaren-Expedition, 1947–51, No: 15). *Commentationes Biologicae* **17** (4): 1-63.

Gbedjissi, L.G., Vala, J.-C., Knutson, L. & Dossou, C. 2003. Predation by larvae of *Sepedon ruficeps* (Diptera: Sciomyzidae) and population dynamics of the adult flies and their freshwater prey. *Revue Suisse de Zoologie* **110** (4): 817–832.

Knutson, L. 2008 (2000). Biology of two parasitoid snail-killing flies (*Sepedon trichrooscelis* and *S. hispanica ruhengeriensis*) attacking succineid snails in Africa, and proposal of a new category of larval food selection/behavior in the Sciomyzidae (Diptera). *Colemania* **7**: 1–11.

Knutson, L.V. & Berg, C.O. 1963. Biology and immature stages of a snail-killing fly, *Hydromya dorsalis* (Fabricius) (Diptera: Sciomyzidae). *Proceedings of the Royal Entomological Society of London, Series A, General Entomol*ogy **38** (4–6): 45–58.

Knutson, L.V., Neff, S.E. & Berg. C.O. 1967. Biology of snail-killing flies from Africa and southern Spain (Sciomyzidae: *Sepedon*). *Parasitology* **57** (3): 487–505.

Knutson, L. & Orth, R.E. 2001. *Sepedon mcphersoni* n. sp., key to North American *Sepedon*, groups in *Sepedon s. s*., and intra- and intergeneric comparison (Diptera: Sciomyzidae). *Proceedings of the Entomological Society of Washington* **103** (3): 620–635.

Knutson, L.V. & Vala, J.-C. 2011. *Biology of snail-killing Sciomyzidae flies*. Cambridge, UK: Cambridge University Press.

Lysyk, T.J. 1993. Seasonal abundance of stable flies and house flies (Diptera: Muscidae) in dairies in Alberta, Canada. *Journal of Medical Entomology* **30**: 888–895.

Maharaj, R. 1991. *Predator-prey interactions between sciomyzid fly larvae (*Sepedon *spp.) and aquatic snails*. M.Sc. thesis, University of Natal, Pietermaritzburg, South Africa.

Maharaj, R., Appleton, C.C. & Miller, R.M. 1992. Snail predation by larvae of *Sepedon scapularis* Adams (Diptera: Sciomyzidae), a potential biocontrol agent of snail intermediate hosts of schistosomiasis in South Africa. *Medical and Veterinary Entomology* **6**: 183–187.

Mullens, B.A. & Meyer, J.A. 1987. Seasonal abundance of stable flies (Diptera: Muscidae) in California dairies. *Journal of Economic Entomology* **80**: 1039–1043.

Steyskal, G.C. 1973. A new classification of the *Sepedon* group of the family Sciomyzidae (Diptera) with two new genera. *Entomological News* **84** (5): 143–146.

Steyskal, G.C. & Verbeke, J. 1956. Sepedoninae (Sciomyzidae, Diptera) from Africa and southern Arabia. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique* **32** (7): 1–14.

Utzinger, J. & Tanner, M. 2000. Microhabitat preferences of *Biomphalaria pfeifferi* and *Lymnaea natalensis* in a natural and a man-made habitat in southeastern Tanzania. *Memórias do Instituto Oswaldo Cruz* **95** (3): 287–294.

Vala, J.-C. 1989. *Diptères Sciomyzidae Euro-méditerranéens*. Faune de France. France et Régions limitrophes. N° 72. Paris: Fédération Française des Sociétés de Sciences Naturelles.

Vala, J.-C., Gasc, C., Gbedjissi, G. & Dossou, C. 1995. Life history, immature stages and sensory receptors of *Sepedon (Parasepedon) trichrooscelis* an Afrotropical snail-killing fly (Diptera: Sciomyzidae). *Journal of Natural History* **29**: 1005–1014.

Vala, J.-C. & Gbedjissi, L.G. 2011. Biology of the Afrotropical *Sepedonella nana* (Diptera: Sciomyzidae), whose larvae feed only on freshwater *Aulophorus furcatus* (Oligochaeta: Naididae). *Zootaxa* **3102**: 50–68.

Vala, J.-C., Gbedjissi, G. & Dossou, C. 1994. Les Sciomyzidae du Bénin, description de *Sepedon* (*Mesosepedon*) *knutsoni* n. sp. (Diptera, Sciomyzidae). *Bulletin de la Société Entomologique de France* **99** (5): 497–504.

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VALA, J.-C., GBEDJISSI, G., KNUTSON, L. & DOSSOU, C. 2002. *Sepedon knutsoni*, a second oligochaete feeding sciomyzid from Africa. *In*: *Fifth International Congress of Dipterology*, 29th September to 4th October 2002, University of Queensland, Brisbane, Australia, Abstracts Volume, p. 250.

VALA, J.-C., REIDENBACH, J.-M. & GASC, C. 1983. Biologie des stades larvaires d'*Euthycera cribrata* (Rondani 1868), parasitoïde de Gastéropodes terrestres. *Bulletin de la Société Entomologique de France* **88**: 250–258.

VALLEY, K.R. & BERG, C.O. 1977. Biology, immature stages, and new species of snail-killing Diptera of the genus *Dictya* (Sciomyzidae). *Search: Agriculture – Entomology* 18 *(Ithaca)* **7** (2): 1–45.

VASSILIADES, G. 1978. Capacité de résistance à la sécheresse de la limnée (*Limnaea natalensis*), mollusque hôte intermédiaire de *Fasciola gigantica*, au Sénégal. *Revue d'Élevage et de Médecine Vétérinaire des Pays Tropicaux* **31**: 57–62.

VERBEKE, J. 1950. Sciomyzidae (Diptera Cyclorrhapha). *In*: *Exploration du Parc National Albert. Mission G. F. de Witte (1933–1935)*. Fascicule 66. Bruxelles: Institut des Parcs Nationaux du Congo Belge, pp. 1–97.

———1961. Sciomyzidae (Diptera Brachycera Malacophaga). *In*: *Exploration du Parc National de l'Upemba*. *Mission G.F. de Witte (1946–1949)*. Fascicule 61. Bruxelles: Institut des Parcs Nationaux du Congo et du Ruanda-Urundi, pp. 1–37.

———1962. Contribution à l'étude des diptères malacophages. I. Sciomyzidae nouveaux ou peu connus d'Afrique du Sud et de Madagascar. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique* **38** (54): 1–16.

———1963. Sciomyzidae Sepedoninae (Diptera Brachycera). *In*: *Exploration du Parc National de la Garamba. Mission H. de Saeger (1949–1952)*. Fascicule 39. Bruxelles: Institut des Parcs Nationaux du Congo et du Ruanda, pp. 51–86.

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