First non-predaceous syrphine flower fly (Diptera: Syrphidae): A new leaf-mining *Allograpta* from Costa Rica

[Die erste, nicht räuberisch lebende Schwebfliege aus der Unterfamilie der Syrphinae (Diptera: Syrphidae): Eine neue blattminierende *Allograpta* aus Costa Rica]

by
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Abstract The first syrphine flower fly with non-predaceous larva (***Allograpta centropogonis* NISHIDA spec. nov.**) is described from Costa Rica. The larva is a leaf-miner in *Centropogon* species (Campanulaceae). The biology as well as all life-stages are described in detail.

Key words Syrphidae, Syrphinae, *Allograpta*, new species, *Centropogon* spp., leaf-miner, life history, taxonomy, Neotropical

Zusammenfassung Mit ***Allograpta centropogonis* NISHIDA spec. nov.** aus Costa Rica wird die erste Schwebfliege aus der Unterfamilie der Syrphinae mit nicht-räuberisch lebender Larve beschrieben. Ihre Larven minieren in *Centropogon*-Arten (Campanulaceae). Ihre Biologie und alle Entwicklungsstadien werden detailliert beschrieben.

Stichwörter Syrphidae, Syrphinae, *Allograpta*, neu Art, *Centropogon* spp., Blattminierer, Entwicklungszyklus, Taxonomie, Neotropis

Introduction

Flower flies are major components of most ecosystems. The adults are crucial pollinators of flowers and the immatures recycle nutrients. Of the three major groups (clades) of flower flies, the subfamily Syrphinae (a group of some 1,770 species), has previously been assumed to contain only species whose larvae are predators on various insects and mites. In the past phytophagous larvae were only known for the subfamily Eristalinae (mainly the genus *Cheilosia*).

We here report the first instance in which a syrphine species has switched to feeding on plant tissue. This species belongs to the genus *Allograpta*, a New World genus consisting of species that are predators of aphids, where the biology is known (METCALF 1912, 1916). Thus, to find a species which mines leaves was a great surprise, and may have important implications. For example, agricultural quarantine specialists have ignored the presence of syrphine maggots on plant products as they have always assumed that they were harmless predators. So, now that we know of one species of phytophagous Syrphinae, there is a question as to how many of the other Neotropical syrphines of current unknown biology may also be plant feeders.

Methods

Host plant: The genus *Centropogon* (Campanulaceae) is one of the most diverse genera in western South America, containing 230 species, and is best represented in the cloud forests. The genus contains mostly succulent herbs, but a few species are semi-shrub-like and characterized by often numerous, brightly-colored red or yellow flowers and fleshy fruit (GENTRY

1996). Sixteen species have been recorded in Costa Rica (INBio 2000). The flowers of *C. talamancensis* and *C. valerii* (Fig. 11) are usually pollinated by hummingbirds (COLWELL et al. 1974, KOPTUR et al. 1990).

General description of the region of investigation: The study was carried out in a high-elevation (2,800 to 3,100 m), oak forest in Villa Mills, Cerro de la Muerte (Fig. 10), Cartago and San José Provinces, Costa Rica. The forest in this region is described as a Tropical Montane Rain Forest or as a Tropical Montane Cloud Forest. The region is heavily populated by black oaks (*Quercus costaricencis* Liebmann), with scattered white oaks (*Q. copeyensis* C. H. MULLER). Other abundant plant species include *Miconia biplifera* COGNIAUX, *M. schnellii* WURDACK (Melastomataceae), *Vaccinium consanguineum* KLOTZSCH (Ericaceae), *Weinmannia pinnata* LINNAEUS (Cunoniaceae), and *Schefflera rodriguesiana* D. G. FRODIN (Araliaceae), and various species of *Chusquea* (Poaceae). The climate is characterized by a wet and a dry season. The dry season lasts from December or January through April. During this time of the year, rain is infrequent, although humidity remains high and dense fog is common in the afternoons. The wet season lasts from April through November or December. Heavy rains are common during these months, and the area receives a yearly annual rainfall of 2812 mm. The average temperature is 10.9 ºC and sometimes can reach 3 ºC below zero during the dry season (HARTSHORN, 1983, KAPPELLE 1996).

Collection sites for eggs and larvae are as follows (locality; host plants; months collected):

- Estación Biológica Cerro de la Muerte (3,050–3,100 m); *C. valerii*; Mar., Apr., May, June, July, Aug., Sept. 2000–2001
- La Georgina, Villa Mills (3,000 m); *C. valerii, C. talamancensis*; Mar., Apr., May, June, July, Aug. 2000–2001
- Mirador de Quetzales (2,650 m); *C. ferrugineus*; Feb. 2000
- CATIE, Cuericí (2,800 m); *C. ferrugineus*; June 2000
- Tapantí, Orosi, Alto Roble (2,200 m); *C. ferrugineus*; July 2001
- Reserva Biológica, San Gerardo de Dota (2,000 m); *C. costaricae*; Jan., 2001

Taxonomy: The adult terminology follows THOMPSON (1999); terminology for the immature stages follows ROTHERAY (1993).

Biology: Between January, 2000 and August, 2001, especially in the months of April through October, 2000, the search for, and the collection and observation of, adults, eggs, larvae and pupae of *Allograpta centropogonis* were carried out in various sites in the Cerro de la Muerte. The investigation was carried out mostly along the dirt paths near La Georgina, Villa Mills (elevation: 3,000–3,100 m) (Fig. 12) and Estación Biológica Cerro de la Muerte (3,050–3,100 m). The eggs and larvae were collected with the host plants, put in transparent plastic bags, and placed in an air-conditioned room at a temperature of approximately 16–18 °C for rearing. Rearing was done in the Museo de Insectos, Universidad de Costa Rica, in San Pedro (1,150 m). Some of the eggs, larvae and puparia were preserved in 70–75 % alcohol (ROTHERAY 1993). Reared adults were pin-mounted. Most of the collected and reared specimens are deposited in the Universidad de Costa Rica (UCR), and Instituto Nacional de Biodiversidad (INBio). The holotype is deposited in INBio, paratypes will be disseminated to various museums, such as the Canadian National Collection (CNC); the Natural History Museum, London (NHM); and United States National Museum, Washington (USNM). To determine the site of pupation under somewhat natural conditions, mature larvae were placed in fine-mesh bags along with the host plants, soil and leaf litter, epiphylls (moss, lichens, and liverworts), and fresh *Chusquea* leaves (these elements were abundantly found in the habitat).

Fig. 1: *Allograpta centropogonis* Nishida spec. nov., imago, dorsal view (drawing by Leonardo Donzo).

Results

Allograpta centropogonis Nishida spec. nov.

[Figs. 1–3a–c (imago), 4–9 (larval morphology), 10–35 (biology)]

Imagines (male and female) (Fig. 1).

Head (Fig. 2): Face projecting anteriorly, with distinct but low tubercle, whitish yellow except black medial vitta, shiny, black pilose; gena broad, bare, shiny and yellow on anterior half, brownish, white pollinose and black and white pilose posteriorly; lunule black; frontal triangle yellow except narrowly black along eye margin and dorsad to lunule, dull, black pilose; frons black except yellow arcuate fascia on anterior half, dull, black pilose; male eye contiguity angle about 100 degrees; vertical triangle and vertex black, dull, black pilose; occiput white to yellow on ventral 2/3, black dorsally, white pollinose and pilose on ventral 2/3, silvery pollinose and black pilose dorsally; antenna black, black pilose; basoflagellomere elongate oval, about as long as scape and pedicel together; arista as long as antenna.

Thorax: Bluish black except yellow on notopleuron, postalar callus and scutellum; postpronotum dark brownish black, slightly paler laterally; scutum dull gray to silvery pollinose with darker black medial pollinose vitta, black pilose; scutellum whitish yellow except black laterally and narrowly along margins, sometimes disc darker brownish yellow, dull, black pilose; pleuron silvery pollinose, black pilose except white pilose on katepimeron; spiracular fringes white; plumula large, white; calypter white with black margin and fringe; halter black. **Wing**: Hyaline except stigma brownish, microtrichose except bare basal 2/3 of 2nd costal cell; vein M_1 joining R_{4+5} perpendicularly; alula normal, microtrichose. **Legs**: Black pilose; coxae black, silvery pollinose, black pilose; trochanters black, black pilose; pro- and mesofemora brownish orange except black basal third, dull; metafemur black except brownish orange apical third; pro- and mesotibiae brownish orange; metatibia brownish orange except black apex and with subapical black annulus; tarsi black.

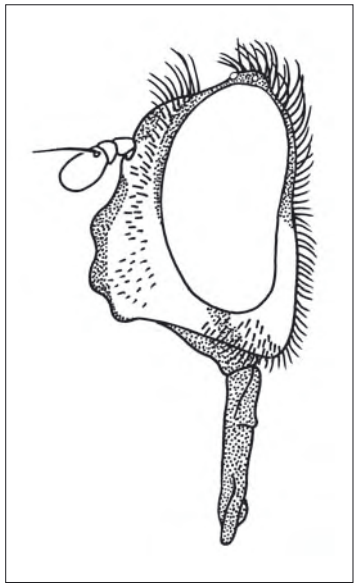


Fig. 2: *Allograpta centropogonis* Nishida spec. nov., head, lateral view.

Abdomen: Black with 5 pairs of circular oblique yellow maculae; 1st tergum black except broadly yellow laterally, dull, black pilose; 2nd through 5th terga black except for yellow maculae, dull, black pilose; sterna yellow to orange, mainly black pilose, with some white pile intermixed on 1st to 3rd sterna; male genitalia (Fig. 3a–c) black, enlarged, with surstyle reddish brown, with surstylar apodeme produced into a medial projecting tubercle between dorsomesial bases of surstyles.

Material examined: Types. Holotype male: COSTA RICA, San José, Cerro de la Muerte, Mirador de Quetzales, 2,700 m, 18–20 March 2000, reared by K. Nishida, from larva collected by P. E. Hanson, from *Centropogon ferrugineus*, with puparium, deposited in the Entomological Collection of the Instituto Nacional de Biodiversidad (INBio), Santo Domingo, Heredia, Costa Rica. **Paratypes** (39 males, 35 females). **COSTA RICA**. **Cartago**: Finca El Sitia, 3 km NE of Villa Mills, 2,600 m, LS 391700_497900, 20 August 1996, A. Picado, lot # 8361 (1 female INBIOCRI002472363 INBIO); Estación Ojo de Agua, 2,980 m, LS 396800_482400, 9 December 1997, E. Alfaro, lot # 48825 (1 male INBIOCRI002408388 INBIO); ..., Río Macho, Alrededor de la Estación, 3,000-3,017 m, LS 396600_482600, 17 September 1997, B. Gamboa, lot # 47752 (1 male INBIOCRI002572008 INBIO); ..., Sendero a Torre 47, 2,960 m, LS 396700_482800, 28 April 1997, A. Picado, lot # 468300 (1 male INBIOCRI002541971 INBIO); ..., 18 September 1997, B. Gamboa, lot # 47753 (1 male, 1 female INBIOCRI002572057-8 INBIO); Reserva Forestal Río Macho, Río Macho, Alto Roble, 8 km S of Orosi, 2,200 m, LN 190000_552300, 10 October 1999, K. Caballero, Lot # 53884 (1 male INB0003044373 INBIO); Río Macho, 3 km E of Villa Mills, Camino Principal del CATIE, 2,750 m, LS 390400_498100, 6 July 1996, A. Picado, lot # 7719, (2 males, 3 females INBIOCRI002444111-3, ...115-6 INBIO). **San José**: Cerro de la Muerte, 6 km west Villa Mills, InterAmerican Highway, 3,340 m, on flowers of *Senecio oerestedianus* Benth (voucher # 234), 22 October 1971, 0645-1000 AM, E. R. Heithaus #10538 (1 male USNM), 23 October 1971, 0715-1030 AM, E. R. Heithaus (1 female USNM); 26 October 1971, 0700-1030 AM, E. R. Heithaus #11460 (1 female USNM), 26 November 1971, 0730-1115 AM, E. R. Heithaus #8518 (1 male USNM); ... on flowers of *Ranunculus peruviana* Pers. (Voucher #258), 23 October 1971, 0915-0945 AM, E. R. Heithaus #10696 (1 female USNM); …, a Orillas de los Torres de T.V., 1.5 km W of Villa Mills, 3150 m, LS 389700_493500, 30 November 1996, A. Picado, lot # 4477 (1 female INBIOCRI002494041 INBIO); Villa Mills, 1.5 km al E del Rest La Georgina, 3,055m, LS 389800_495400, 14 January 1997, M. Segura, lot # 45293 (1 male INBIOCRI002535214 INBIO); Carretera Interamericana Km 94, Cerro Estaquero, 3,200 m, 20 May 1997, M. A. Zumbado, lot # 48049 (1 male INBIOCRI002578295 INBIO); Los Santos a la Izquierda de Camino a Providencia, 3100 m, LS 394400_483100, 25 July 1997, B. Gamboa, lot # 47472 (1 male, 1 female INBIOCRI002546439-0 INBIO); …, 12 September 1997, B. Gamboa, lot # 47751, some on flowers of *Senecio costaricensis* (8 males, 4 females INBIOCRI002571939-43, …946-9, …951, …953-4 INBIO); Reserva Forestal Los Santos, Camino a Providencia de Dota, Camino Viejo, 2,900 m, LS 395500_482500, 8–10 November 1997, E. Alfaro, lot # 48824 (3 females, INBIOCRI002408273-5 INBIO); Monte Sin Fe, Sendero Principal del Cerro Chirripó, 3.4 km SW of Cerro Ventisqueno, 3,200 m, LS 377700_515700, 29 July 1966, A. Picado, lot # 7912 (1 female INBIOCRI002469992 INBIO); Reserva Forestal Río Macho, Estación Ojo de Agua, 3,000 m, LS 396500_482050, 12-19 May 1997, M. Segura, lot # 46240 (1 male, 1 female INBIO CRI002538891, …895 INBIO); ..., January 1997, M. Segura, Lot # 45292 (2 males, l female INBIOCRI002535168, ...170-1 INBIO); …, Calle a Providencia, 3,000 m, LS 395800_483100, 11 September 1997, B. Gamboa, lot # 47750 (1 female INBIOCRI002571914 INBIO); Cerro Cuericí, 8 km NE of Villa Mills, 3,345 m, LS 392300_503200, 19 September 1995, A. Picado, lot # 6305 (1 male INBIOCRI00256839 INBIO); …7 January 1996, B. Gamboa, lot # 6775 (1 male INBIOCRI002392351 INBIO); Estación Cuericí, 4.6 km E of Villa Mills, 2,600–2,640 m, LS 389400_499600, 14 July 1996, A. Picado, lot # 7722 (1 female INBIOCRI002467211 INBIO); …, Sendero al Mirador, 4.6 km E of Villa Mills, 2,640 m, LS 389700_499600, 21–24 October 1995, A. Picado, at lights, lot # 6314 (2 females INBIOCRI002389156-7 INBIO); …, 2,700 m, LS 389700_499600, 25 October, A. Picado, lot # 6316 (1 male, 1 female INBIOCRI002363045, …047 INBIO); …, 26 November 1995, A. Picado, lot # 6424 (1 male, l female INBIOCRI002365182, …200 INBIO); …, Camino a la Auxiliadora, 3.5 km E Villa Mills, 2,700 m, LS 389500_499000, 22 August 1996, A. Picado, lot # 8363 (1 female INBIOCRI002472556 INBIO); …, Sendero el Carbón, 5 km E Villa Mills, 2,600 m, LS 390100_500100, 26 October 1995, B. Gamboa, lot # 6328 (1 female INBIOCRI002468198

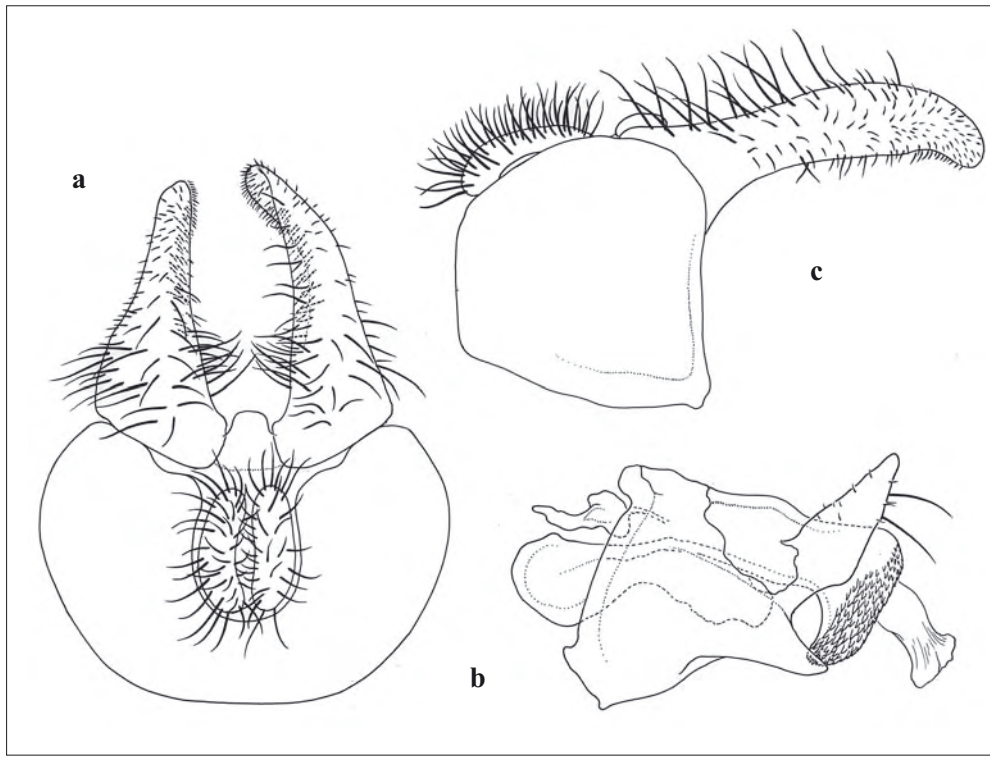


Fig. 3a–c: *Allograpta centropogonis* Nishida spec. nov., male genitalia. – **a**: 9th tergum and associated structures, dorsal view; – **b**: 9th tergum and associated structures, lateral view; – **c**: 9th sternum and associated structures, lateral view.

INBIO); …, 8 July 1996, A. Picado, lot # 7721 (1 female INBIOCRI002467119 INBIO); …, Sendero el Carbon, 4.6 km E of Villa Mills, 2,700 m, LS 390100_500100, 26 October 1995, A. Picado, lot # 6318 (2 females INBIOCRI002363194-5 INBIO); ..., Límite de la Finca Cuericí, 3 km E Villa Mills, 2,800 m, LS 389500_498600, 4 January 1996, A. Picado, lot # 6797 (1 male INBIOCRI002367480 INBIO); … 23 June 1996, A. Picado, lot # 7699 (1 female INBIOCRI002452410 INBIO). **Heredia**: P. N. Braulio Carrillo, Volcán Barva, 2,600–2,880 m, LN 235200_524600,15 January 1997, M. A. Zumbado & F. C. Thompson, lot # 45317 (8 males, 2 females INBIO CRI002489060, ...63, ...69-72, ...86-89, ...91, ...96, ...101 INBIO, USNM); ..., Estación Barva, 2,500 m, LN 233400_523200, 24 January 1993, M. A. Zumbado (1 male, 2 females INBIOCRI001304979, ...981-982 INBIO); ..., Sendero Laguna Barva, 2,600–2,800 m, LN 234100_523200, 11 June 1997, M. A. Zumbado, lot # 46834 (2 males, 1 female (INBIOCRI00255084-6 INBIO).

Etymology. The epithet, *centropogonis*, a noun in the genitive case, is derived from the Greek name of the host plants and reflects the most significant feature of the species: its conspicuous leaf-mining feeding behaviour.

Distribution. *Allograpta centropogonis* was found in the high elevations (2,000 m and above) in the mountains of the Talamanca region and Volcán Barva in Costa Rica. Adults were found in most months (no records for February and March), with the peak being from September to January.

Egg. (Figs 13, 33) ca. 1 mm long, white, elongate, oval-cylindrical.

Description of the third stage larva and puparium

Overall appearance: A subcyclindrical green larva with a white fat body covering the hind gut; tapering anteriorly, truncate posteriorly; locomotory organs with shallow grooves, lack-

ing prolegs and crochets; papillae bearing antenno-maxillary organs flattened laterally and surrounding the mouth; apex of head skeleton with serrated dorsal and ventral margins; posterior respiratory process short, broader than long with a non-sclerotised, fleshy base and three pairs of radially arranged spiracular openings extending down the sides of the dark brown apex.

Third stage larva: Length 9–11 mm; width 1.5–2 mm; subcyclindrical in cross section, tapering anteriorly, truncate posteriorly (Fig. 4). Dorsal and ventral sensilla accompanied by single setae, sensilla on prothorax, ventral surface and anal segment lacking setae. Pattern of segmental sensilla as for other syrphid larvae (ROTHERAY & GILBERT 1999).

Head: Antennomaxillary organs mounted on large, laterally flattened papillae (basal width 0.17 mm) that cover the sides of the mouth (Fig. 6). **Head skeleton**: Arrangement similar to other syrphines (HARTLEY 1963, ROBERTS 1970), i.e. labrum and labium elongate and equally produced at the tip of the head skeleton. The tips of the labrum and labium not sharply pointed as in other syrphines. Instead the dorsal surface of the labrum bears two rows of 4–5 hooks. These rows taper and the hooks become larger toward the apex of the labrum (Fig. 7). The ventral surface of the labium bears similar rows of hooks so that, in the lateral view, the tip of the head skeleton appears serrated (Fig. 7). Mandibles apparently reduced or lost. Dorsal cornu narrow and spike-shaped.

Thorax: Dorsal and ventral margins of prothorax above and below the mouth with a fleshy lobe (width 0.08 mm). Lateral margins of the thorax and the first abdominal segment coated with sclerotised vestiture, this vestiture extending onto dorsal surface on anterior margins of transverse folds. Elsewhere surface of integument matt. Anterior spiracles present on posterior fold of prothorax. Ventral surface of mesothorax with a pair of raised pads.

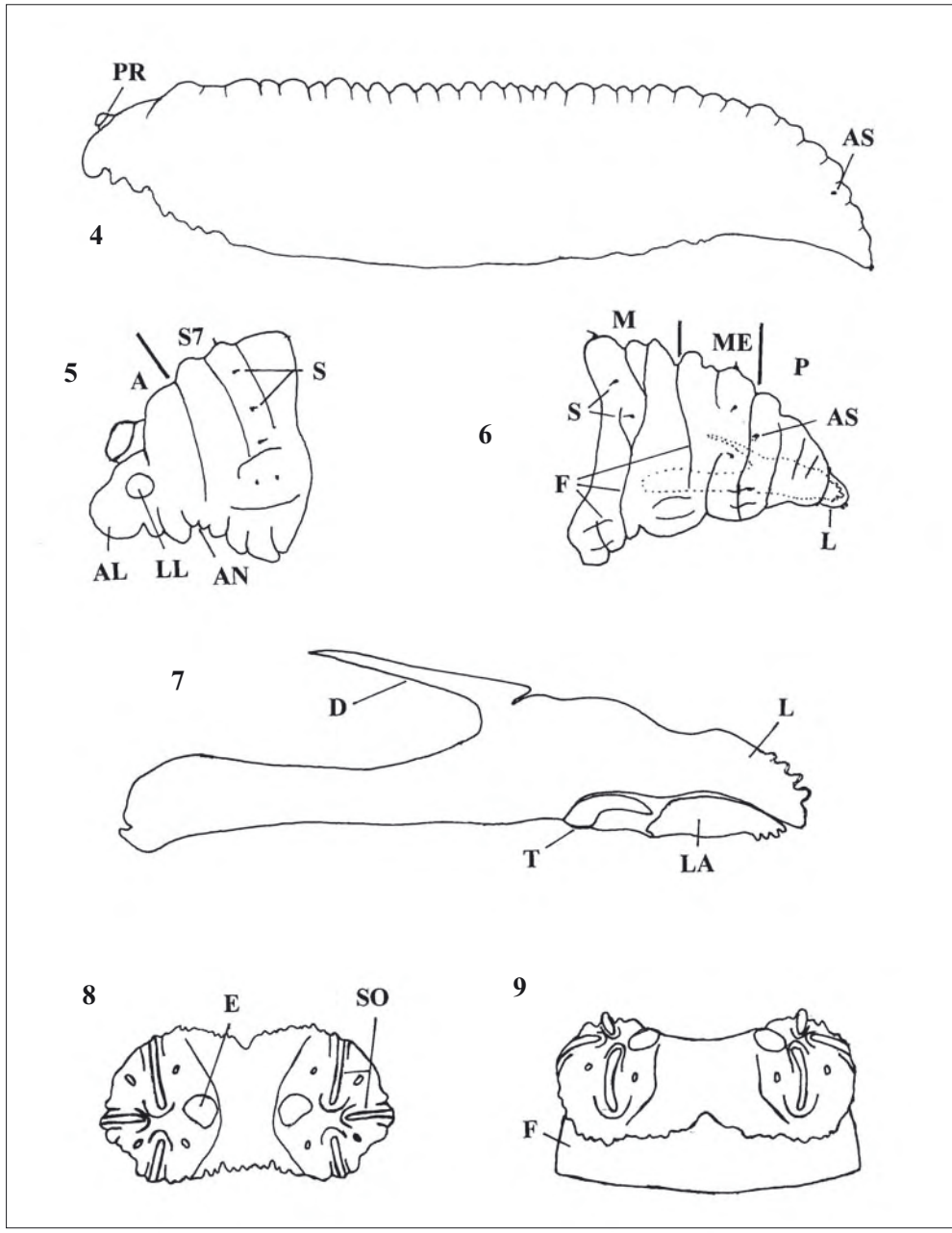
Abdomen: Abdominal segments 1–7 with four transverse dorsal folds. Surface of integument matt, lacking sclerotised spicules. Paired locomotory prominences on abdominal segments 1–7 bearing sensilla 9 and 10 with apex matt bearing shallow grooves. **Anal segment**: about equally developed dorsally and ventrally with two dorsal and three ventral folds. Not as high as abdominal segment seven (height at mid-point: anal segment 1.28 mm versus abdominal segment seven 2 mm) and truncate at apex. Apex bearing a pair of lobes (0.34 mm wide by 0.28 mm long) and a pair of smaller more lateral lobes (0.2 mm wide by 0.17 mm long) (Fig. 5). Anal opening transverse. **Posterior respiratory process**: (Figs 8–9); length 0.25 mm; basal width 0.57 mm; base fleshy, not sclerotised, upper half bearing spiracular plates sclerotised and nodulate. Spiracular plates with three pairs of spiracular openings extending over the sides of the sclerotised apex. Four pairs of interspiracular nodules bearing setae present, often individual setae lacking.

Puparium (Figs 31–32): Length 5–6 mm; dark brown dorsally; anterior segments with green transverse bands; creamy white color "zigzag" stripe laterally; pale brown to brown ventrally; dorsal surface inflated and arched dorsally. Anal segment small and narrow compared with rest of puparium. Pupal respiratory process absent.

Material examined. Immature Stages: About 20 third stage larvae and puparia preserved in 70 % alcohol. Costa Rica, San José, Cerro de la Muerte, Estación Biológica Cerro de la Muerte, 3,050 m, April and May 2000. Larvae ex leaf mines on *Centropogon valerii*.

Biology

The larvae were found mining the leaves of four species of *Centropogon*: *C. costaricae* (VATKE) MCVAUGH and *C. ferrugineus* (L. f.) GLEASON at lower elevations (around 2,800 m or below), and *C. talamancensis* WILBUR (Fig. 11 pink flower on the right) and *C. valerii* STANDL.



Figs 4–9: *Allograpta centropogonis* Nishida spec. nov., third stage larva. – **4**: Whole larva, lateral view, head to the right, dorsal side uppermost, length = 11 mm, PR = posterior respiratory process; AS = Anterior spiracle; – **5**: Lateral view, anal end, S = sensilla; S7 = segment 7; A = anal segment; AL = apical lobe; LL = lateral lobe; AN = anus; – **6**: Lateral view, thorax, length about 1.8 mm, L = lobe bearing antennomaxillary process; AS = anterior spiracle; P = prothorax; ME = mesothorax; M = metathorax; S = sensilla; F = integumental fold; dotted line = outline position of head skeleton; – **7**: Head skeleton, lateral view, length = 1.1 mm, L = labrum; LA = labium; T = tentorial bar; D = dorsal cornu; – **8**: Posterior respiratory process, apical view, width = 0.57 mm, So = spiracular openings; E = ecdysial scar; – **9**: Posterior respiratory process, anterior view, length = 0.25 mm, F = fleshy base.

(Fig. 11 red flower on the left) at higher elevations (3,000–3,100 m). Their feeding left conspicuous blotch mines on the leaves (Figs 14–15). The infested plants were encountered mostly in light gaps and shaded areas. The eggs (Fig. 13) were laid in clusters on the abaxial side of the relatively mature leaves of the host plants and were usually located near the outer margin between the leaf veins. The number of eggs in clusters ranged from 9 to 72 (mean = 44, S.D. = 17.4, n = 31). About one-third of these clusters had some eggs damaged or detached (Fig. 13). Mostly one or two clusters of eggs were observed on a single plant; in a few cases, up to four clusters, but not frequently on the same leaf. No female ovipositional behavior was observed during the investigation.

The first instar larvae, after hatching from the eggs, fed gregariously on the leaf tissue adjacent to where they hatched, toward the central vein of the leaf. In the field, recently-hatched first instar larvae were encountered between the hours of 12:00 p.m. and 1:00 p.m (n = 2). At this position, the larvae did not mine the leaf; instead, they fed on the tissue from the outside by puncturing the leaf epidermis and mesophyll. This feeding behavior left relatively small (approximately 6 mm × 4 mm) white blotches on mature leaves (Figs 16–17); these white blotches were easily seen in the field. After feeding on this part of the plant, it appears that the larvae crawled up to the plant apex and fed on folded young leaves, then young unfolded leaves, again without mining (Figs 20–21); some larvae were between the leaf folds. Feeding by larvae at the apex caused secretion of plant latex which coagulated and adhered to the surface (Figs 18–22), and was also observed on some flower buds and fruits located at the tip of the plants. Later, the larvae were observed gregariously mining, lined up side by side ("shoulder to shoulder"), in a young unfolded leaf near the apex (Figs. 22–23), and later in a mature leaf located lower down (Fig. 26). This feeding pattern, and the switching of feeding positions, was observed on all infested plants (n = ca. 50); however, it was not possible to document the migration of the larvae from one feeding position to the next in the field. Under laboratory conditions, the first instar larvae migrated gregariously in a single line, one behind the other, crawling along on the central vein near lamina of the plant (n = 1).

To begin mining, the larvae scrape through the epidermis with their mouth hooks, making one to a few holes on the abaxial surface of the leaves (Figs 24–25). Evidently this entrance hole can also serve as the exit hole; some of the empty mines presented only one hole. The larvae twisted the head and placed the mouthparts side-ways, using the labium and labrum like scissors (opening and closing) for food intake (Figs. 27, 35a–b). When the head is twisted to the right, the larva feeds toward the left (Fig. 35a), and when the head is twisted to the left, the larva feeds toward the right (Fig. 35b). A first instar larva opened and closed the labium 100 times in 48 seconds (2.08 times/second), giving three head turns of 0.5 mm right to left. The feeding distance advanced about 1.5 mm toward the apex in 20 minutes. A third instar

10	11
12	13
14	15
16	17

Explanation to figures on next page:
Figs. 10–17: On the biology of *Allograpta centropogonis* NISHIDA spec. nov. – **10**: Habitat in a high-elevation, 2,800 m to 3,100 m, oak forest in Villa Mills, Cerro de la Muerte, province of Cartago and San José, Costa Rica; – **11**: Host plants: *C. valerii* (orangish red flower on the left), *C. talamancensis* (pink flower on the right); – **12**: Habitat in dirt trail paths near La Georgina, Villa Mills, elevation: 3,000–3,100 m, arrow pointing at patch of *C. talamancensis*; – **13**: Eggs: batch of eggs two days before hatching (note some damaged eggs and detached eggs); – **14**: Leaf mines on *C. ferrugineus* (scale in mm along bottom of the photo); –**15**: Leaf mines on *C. valerii*; – **16**: White blotch caused by feeding of first instar larva right after hatching (scale in mm along left side of photo); – **17**: Batch of empty eggshells remain attached to leaf and the leaf damage made by recently hatched larvae.

larva opened and closed the labium 100 times in 46 seconds (2.17 times/second), giving three head turns of 3 to 4 mm right to left (or left to right). Both cases were observed under laboratory conditions (temperature: 23–24 °C).

First instar larvae molted in the mines; molts and head skeletons were found inside the mines. The second instar larvae molted in and outside of the mine. Presumably the larvae were gregarious until the last part of the second instar. The molting took from the posterior to the anterior of the body. The third (last) instar larva (Fig. 28) was usually mining alone or in small groups of two or three individuals per mine (Fig. 29), scattered on several mature leaves. Several recently molted third instars were resting outside of the mine and later started to mine the leaf (Fig. 30). The larvae commenced the mine near the tip of a mature leaf and mined in the direction of the base of the leaf. In most cases, the leaf-mining larvae switched leaves before consuming an entire leaf. In several cases, the second and third instar larvae were found resting on the surface of leaves or in mines without mining. A mature larva outside of the leaf moved about 60 mm in 30 seconds in a straight line on the flat surface of a leaf (n = 1, air temp. = 15 °C). Larval fecal matter was observed inside and outside of mines (Fig. 29). Larvae defecated at least twice during their development: while feeding in the last instar and before prepupation.

In the field, puparia were not found on the host plants and it was not possible to locate the place of pupation. Under laboratory conditions, the larvae pupated in the plastic bags away from, on or between the leaves (Fig. 31). The mature larvae (n = ca. 20) which were placed in fine-mesh bags and left in the field pupated between the bases of leafy liverworts (Fig. 32), moss, and lichens. No puparia were found in the soil or leaf litter.

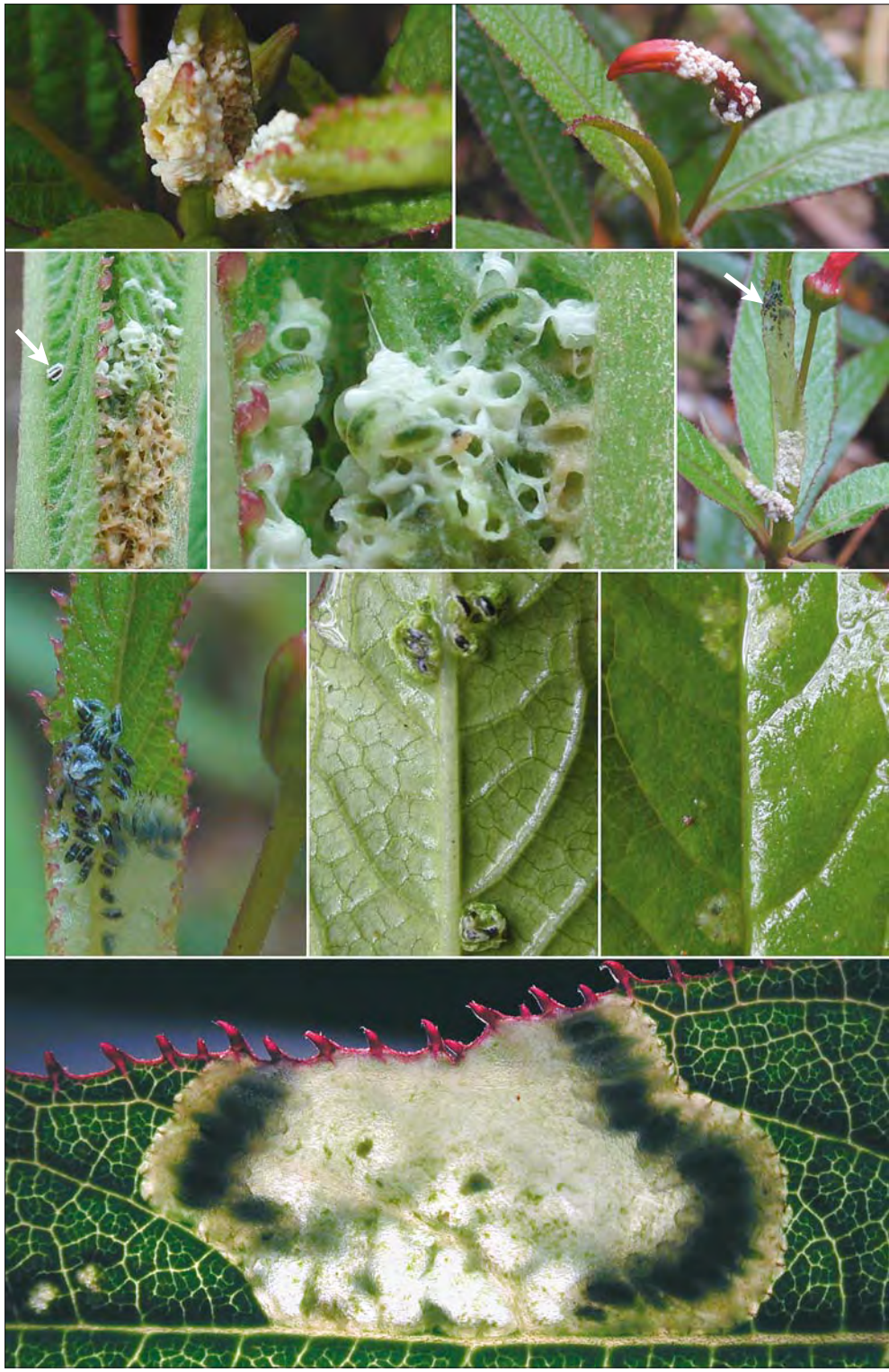
The majority of the mines, eggs, and larvae were found on *Centropogon valerii*. Plants of *C. talamancensis* were abundant at the same sites, but only two groups of larvae were mining leaves. In contrast, more than 50 groups were counted on the *C. valerii*. Under laboratory conditions, *C. talamancensis* was presented to a group of larvae which were mining the leaves *C. valerii* under natural conditions and adults were successfully reared.

During the investigation, more than 15 cohorts of the *Allograpta centropogonis* were reared. However, no parasitoids were obtained, and no parasitoids attacking the eggs or larvae were observed. The only natural enemy found was a larva of an unknown syrphid species which was preying on the eggs of the *Allograpta centropogonis* (Fig. 33). Rearing of this predatory syrphid was thwarted by vandalism in the field. Along with the larvae of *A. centropogonis*, individuals of a species of Ortheziidae (Homoptera) (Fig. 20) were frequently found on the abaxial surface of leaves of *Centropogon* spp.; however, no predatory behavior toward the homopteran was observed.

The eggs and larvae were observed more frequently in May through September than in April or October. In the laboratory, eggs collected on the 8th of April hatched on the 10th of the same month. Pupation took place on the 26th to 28th of the same month (the larval stage

18	19
20	21 22
23	24 25
26	

Explanation to figures on next page:
Figs. 18–26: On the biology of *Allograpta centropogonis* NISHIDA spec. nov. – **18–19**: Coagulated latex on the *C. valerii* adhered to the surface: **18**: At tip on leaf buds; **19**: On flower bud; – **20–21**: First instar larvae feeding on folded leaf. **20**: (arrow pointing at an Ortheziidae). **21**: Close up image; – **22–23**: First instar larvae mining young unfolded leaf. **22**: Arrow pointing to the larvae (note the coagulated latex and the migration feeding pattern). **23**: Close up image; – **24**: First instar larvae commencing a new mine entering from abaxial of a *C. valerii* leaf (note: the leaf is wet from the rain); – **25**: Top view of the fig. 24; – **26**: Second instar larvae mining a mature leaf of *C. valerii.*



27	28
29	30
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33	34

Figs. 27–34: On the biology of *Allograpta centropogonis* NISHIDA spec. nov. – **27**: Third instar larva feeding on leaf mesophyll using labium and labrum like scissors (picture shows the labium opened); – **28**: Mature third instar larva; – **29**: Mature larva resting (bottom-center), and its miconium (black spot in top-right) in the mine; – **30**: Third instar larva just molted entering the leaf of *C. valerii*; – **31**: Pupated on the leaf of *C. valerii* (under captivity conditions, note the color pattern of the pupae); – **32**: Pupated between the bases of leafy liverworts, arrow pointing at the pupa (experimental condition in the field); – **33**: Natural enemy (larva of a syrphid species) preying on the eggs; – **34**: Male *A. centropogonis* visiting flower of *Senecio oerstedianus* (Asteraceae) at Estación Biológica Cerro de la Muerte.

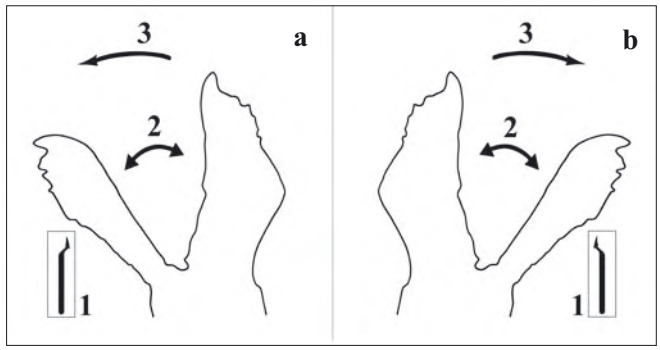

Fig. 35a–b: *Allograpta centropogonis* NISHIDA spec. nov., mouth part of larvae, diagrams showing feeding behaviour. – **a**: Larval head twisted to the right; – **b**: Larval head twisted to the left. Arrows: #1 = direction of the head twisted; #2 = movement of labium; #3 = movement of labrum and head.

lasted 17 to 19 days including the prepupal stage). Adults emerged on the 15th to 16th of May (the pupal stage lasted approximately 21 days). In the field (Estación Biológica Cerro de la Muerte, March to July, 2001), the egg stage took more than two weeks, the larval stage about a month, and the pupal stage lasted close to two months.

Some adult males visiting flowers of *Senecio oerstedianus* BENTH. and *Ageratina ixiocladon* (BENTH.) R. M. KING & H. ROB. (Asteraceae) were seen around 10:30-11: 30 A.M. when the sun was shining strongly (Fig. 34, photographed: March 3, 2001). Other flower associations are noted in the materials examined section.

Another species of syrphid larva was observed feeding on *Centropogon* plants. Second and third instar larvae (n = 3) were found boring in the stem of *C. talamancensis* and *C. valerii*. Unfortunately, we were unable to rear them though to the adult stage.

Discussion

Adult taxonomy. *Allograpta centropogonis* belongs to the subgenus *Fazia*, which includes those *Allograpta* species with the face greatly projected anteriorly, and to the *bullaephora* (SHANNON, 1927) species group, those *Fazia* species with black antennae and four pairs of round yellow maculae on the abdomen. In the previously published key (FLUKE 1942), this species would run to either *eupeltata* BIGOT or *imitator* CURRAN. Both these species have small male genitalia and *eupeltata* has a partially pale antenna. *Allograpta centropogonis* is most closely related to three other undescribed species, all of which are apparently restricted to the higher elevations of Costa Rica and probably adjacent Panama. All these species appear identical, differing only in the details of the male genitalia. These new species are very closely related to a Chilean species, *Allograpta* (*Fazia*) *bullaephora* (SHANNON 1927), of which there are two old specimens in the USNM which were reared (have attached puparia) and have a label with the plant name, *Lobelia constitucim* M. J. RIVERA (Campanulaceae). Unfortunately, beyond the name of the plant there is no more information. However, this is enough to suggest that there is a "clade" of leaf-miners who breed in other Campanulaceae and range from Neotropical Mexico (Chiapas) to Chile.

Biology and immature taxonomy. In comparison with other known syrphine larvae, the larva of *A. centropogonis* is unusual. All other syrphines of known biology are predators (ROTHERAY & GILBERT 1999), but this species is a leaf-miner. It also has several unique morphological features. These are not unexpected, considering that a shift from a predaceous ancestor has probably occurred.

The head skeleton is of the usual syrphine type except that in *A. centropogonis*, there are rows of dorsal and ventral hooks at the apex and the mandibles are apparently reduced or lost. Observations of actively feeding larvae revealed that the labrum and labium are extended through the mouth and rapidly and repeatedly opened and closed. These movements appear to puncture the cells of the leaf whose contents are then imbibed. The papillae bearing the antennomaxillary organs, which in predaceous syrphines are above the mouth, are in this species large and flattened and lie on each side of the mouth. They possibly help channel the contents of the punctured leaf cells into the mouth. The small lobes above and below the mouth probably also assist in this function.

Locomotion within the leaf-mine and maintenance of position when feeding is probably assisted by the spicules which coat the lateral and, to a lesser extent, the dorsal surface of the thorax and first abdominal segments. This is probably a convergent feature with stem-boring and leaf-mining larvae within the genus *Cheilosia* MEIGEN, 1822 (Subfamily Eristalinae), in which spicules occur in similar positions (ROTHERAY 1990). Another convergent feature appears to be the presence of hooks in the head skeleton. The number of these vary in *Cheilosia* larvae, depending, in part, on the hardness of plant tissue attacked. Leaf-mining species have the greatest numbers of hooks (ROTHERAY 1990).

An additional unique feature is the fleshy base of the posterior respiratory process. In other syrphine larvae the base is sclerotised. In *A. centropogonis* the posterior respiratory process is very short. A reduction in length may prevent its being an impediment to movement within the leaf mine. This is additionally facilitated by the flexible base and small anal segment.

Concerning the migration of the larvae from one feeding position to the next, an additional experiment showed that when exposed to cold temperature (ca. 6 °C), they barely fed or migrated as they did at higher temperatures (16–18 °C). This suggests that in nature, migration probably takes place during the daytime when the temperature is higher, usually around mid-day; and it is probably done in a short period of time. It also appears that the larvae can also migrate to another individual plant situated close by and continue feeding. Empty egg shells and evidence of early instar feeding on the plant were not observed, but there were third instar larvae mining the leaves (n = 1).

The larvae show a predictable feeding pattern, which makes them easy to spot in the field. The recently hatched first instar larvae probably need to gain energy by feeding at the hatching spot and then migrating up to the plant apex where they can consume soft "nutritious" plant tissue. Mining behavior probably provides the maximum consumption of leaf mesophyll and may also provide protection from some type of predators. It is possible that mining also provides some protection from the cold, wet conditions that are prevalent in the region.

The gregarious behavior of this species in its early instars may benefit the rate of survival of individuals, e.g. mining gregariously might reduce the energy used in entering the leaf and mining. During the dry season, a number of cases of first and second instar deaths in the mine were noted. Several dead larvae were scattered in collapsed mines. However, the cause of these deaths was not determined.

Poking settled third instar larvae (n = 5) with a pair of fine-pointed forceps resulted in the larvae's secreting clear fluids from the anal region and wetting their entire body. The larvae usually crawled away after being poked a second time. Anal secretions are mostly used for locomotion and further research is needed to determine whether these secretions might also be used in defense.

No parasitoids have been reared from the eggs, larvae or pupae of *A. centropogonis*, although there is a possibility that there are parasitoids attacking the pupae since pupae were difficult to locate in the field and were, therefore, not reared. Most parasitoids of syrphids are associated with predators of homopterans that excrete honeydew, and the latter is usually used as a cue for finding hosts (ROTHERAY 1981). Thus it is possible that the usual parasitoids of syrphid larvae are unable to locate A. centropogonis because of the absence of honeydew. Another posibility is that the *Centropogon* plants are highly toxic like some other lobeliad plants (WARREN et al. 1980), and the larvae of *A. centropogonis* are utilizing the toxicity of the plant as defense.

Further investigations on this new species and the other phytophagous syrphids on *Centropogon* and related plants, would provide valuable contributions to the little-known biology of the Neotropical syrphid fauna.

Resumen Se reporta el primer Syrphinae no depredador, basado en una nueva especie (*Allograpta centropogonis* NISHIDA) de Costa Rica. La especie es minador de hojas de unas especies de *Centropogon*. Se describe en detalle la biología y los estadios inmaduros.

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This work began with NISHIDA's discovering and rearing the new species. K. NISHIDA is responsible for the description of the biology, the rearing data, and discussion of the larval biology. G. ROTHERAY is responsible for the description of the immature stages and discussion of the larval morphology and behaviour. C. THOMPSON is responsible for working out the adult taxonomy and placing the species in the existing classification.

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