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Pollen feeding larvae in the presumed predatory syrphine genus *Toxomerus* Macquart (Diptera, Syrphidae)

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The morphology and biology of the larva of *Toxomerus apegiensis* (Harbach, 1974) are described from Suriname. This larva feeds on pollen of *Olyra obliquifolia* Steudel, a bambusoid grass (Poaceae) that grows in the understorey of tropical rainforests. The morphology of the larva of *Toxomerus politus* (Say, 1823), which feeds on pollen of corn, *Zea mays*, is redescribed. These species are the only known phytophages within the otherwise predatory genus *Toxomerus*. The cephalopharyngeal skeleton of *T. apegiensis* shows features that are hypothesized to be modifications towards pollen feeding. These features are absent in the larva of *T. politus*. Possible evolutionary scenarios of the development of phytophagy within *Toxomerus* are briefly discussed based on published information on phylogeny of the genus.

Keywords: *Toxomerus apegiensis*; *Toxomerus politus*; shift in feeding mode; *Olyra obliquifolia*; Neotropical rainforest; Suriname

Introduction

Within the Syrphidae, the large subfamily Syrphinae has until recently been considered to consist almost exclusively of species with terrestrial predatory larvae, mostly developing on Aphidoidea (Rotheray 1993; Thompson and Rotheray 1998). However, subaquatic larvae of a species group within the Neotropical syrphine genus, *Ocyrtamus* Macquart, have been found developing on a wide range of Diptera and Coleoptera larvae in the water tanks of bromeliads (Bromeliaceae) (Rotheray et al. 2000). An even more radical shift has also been discovered. Two Neotropical species of *Allograpta* Osten Sacken, 1875 were found with phytophagous larvae: one is a leaf miner (Nishida et al. 2002), while the other one feeds on pollen (Weng and Rotheray, forthcoming). Prior to these findings, the old reports of the larva of the widespread New World species *Toxomerus politus* (Say, 1823) feeding on pollen of corn *Zea mays* (Riley and Howard 1888; Richardson 1915) have lacked confirmation. However, field reports of pollen feeding in the larva of this species (Marin 1969) and larvae and associated data of this species from the collection of syrphid early stages in the Smithsonian Collection studied by G.E.R., have together provided confirmation of the pollen feeding habits of this species. Adult *T. politus* has been redescribed by Metz and Thompson (2001) and a generalized larval description with figures is provided by Riley and Howard (1888).

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In this paper we introduce a fourth phytophagous syrphine species, *Toxomerus apeiensis* (Harbach, 1974). We describe the morphology, biology and ecology of this species and compare the larva with that of *T. politus*.

Material and methods

Study areas

In 2006, larvae and adults of *T. apeiensis* were collected in the Brownsberg nature reserve (04°56'N, 55°10'W) and the Nassau Mountains (04°48'N, 54°36'W), located in northeastern Suriname. Both areas are more or less isolated mountain plateaus at an altitude of approximately 500 m, surrounded by forested lowland areas. The plateaus are mainly covered with primary forest. Annual rainfall is 2250–2500 mm (Haverschmidt and Mees 1994). Additionally studied adult specimens of *T. apeiensis* are from Sipaliwini in the south of Suriname. Apart from the altitude (400–500 m), nothing is known about the collection site of these specimens.

Specimens of *Toxomerus* examined

Table 1 lists all the studied specimens of *T. apeiensis* and *T. politus*. The two females of *T. apeiensis* from Sipaliwini have previously been recorded from Suriname as *T. nymphalius* (Hull, 1942) by Van Doesburg (1966). Adult specimens of *T. apeiensis* were identified by comparing them with the description by Harbach (1974). Genitalia of related species are depicted in Harbach (1984).

Host plant

Olyra obliquifolia Steudel (Poaceae) is a large, somewhat bamboo-like grass of 50–100 cm high (Figure 1). This grass occurs from Suriname and French Guyana to Brazil (Pará and Maranhão districts) and is locally dominant in moist forest groundstorey at elevations up to 780 m. It flowers throughout the year, with a peak in July–October. The inflorescences are arranged on bisexual panicles, with the male spikelets on the basal parts and the female spikelets on the apical parts of the panicle (Figure 2). The inflorescences contain oils, which probably attract dispersing ants, and they are frequently visited by *Trigona* bees (Meliponini) (Görts-van Rijn 1990).

In the study areas, the plant was only found on the plateaus, not on the surrounding slopes. It grew along forest trails in half-shady conditions. Specimens of *O. obliquifolia* have been identified using Görts-van Rijn (1990) and conserved specimens from the collection of the National Herbarium of Suriname. A local Surinamese name for the plant is “dagu-alesi” (dog rice), a name which has been recorded for three other, similar looking grass species (Klooster et al. 2003).

Larval morphology

The head and thorax were dissected from larvae and treated in a cold 10% potassium hydroxide solution for 1 hour, subsequently preserved in glycerol. Drawings were made using a drawing tube attached to a microscope. Terminology is based on Rotheray and Gilbert (1999).

Table 1. Examined specimens of *Toxomerus*.

Species	Number/stage/sex	Country	Locality	Date	Leg/Col	Remarks
<i>Toxomerus apugiensis</i>	3 larvae and 1 puparium	Suriname	Brownsberg	4 March 2006	M. Reemer	
	1 puparium (found as larva)	Suriname	Nassau Mountains	24 April 2006	M. Reemer	Parasitized by Hymenoptera Chalcidoidea
	2 females (adult)	Suriname	Sipaliwini	9 and 13 June 1963	P.H. van Doesburg Jr./RMNH	
	6 males and 4 females (adult)	Suriname	Brownsberg	4 March 2006	M. Reemer/RMNH	
	3 males and 2 females (adult)	Suriname	Brownsberg	5 March 2006	M. Reemer/RMNH	
	2 males and 4 females (adult)	Suriname	Brownsberg	2 April 2006	M. Reemer/RMNH	
	2 females (adult)	Suriname	Brownsberg	14 to 20 February 2008	A. Gangadin and K.-D.B. Dijkstra/RMNH	malaise trap
<i>Toxomerus politus</i>	10+ larvae	USA	Florida, Homestead	3 February 1944	det. C.T. greene, col. USNM	Lot 44-788, S.S. #9321
	20+ larvae, 3 puparia	USA	Virginia, Holland	1 August 1949	leg. G.M. Boush, col. USNM	“in corn tassal”
	20+ larvae	Venezuela	El Limon, Marsua	VIII	leg. J.C. Marin, col. USNM	“larvae feeding on corn pollen”

RMNH, Nationaal Natuurhistorisch Museum, Leiden; USNM, Smithsonian Institution, Natural History Museum, Washington D.C., USA.



Figure 1. Branch of *Olyra obliquifolia* (Suriname, Brownsberg, 1 April 2006).

Results

***Toxomerus apeiensis* (Harbach)**

Description of third stage larva (Figures 3–5)

Length 6.5 mm; width approximately 2 mm ($n=1$). Subcylindrical in cross-section, widest in the middle part. In lateral view with highest point in the middle (1.5 mm).

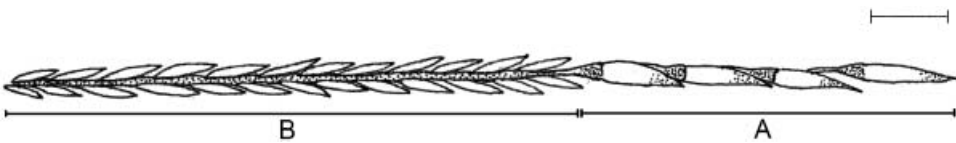


Figure 2. Panicle of *Olyra obliquifolia*, with four female spikelets on top (A) and many male spikelets on the lower part (B). Both larvae and adults of *Toxomerus apeiensis* could be found on the male spikelets. Scale bar: 1 cm.



Figure 3. Young larva of *Toxomerus apegensis* moving along the male spikelets of *Olyra obliquifolia*. Its pale yellow gut contents can be seen shining through its somewhat translucent body.



Figure 4. Full-grown larva of *Toxomerus apegensis* after emptying its gut contents. Its body colour has changed from pale yellow to greenish.

Body colour yellowish white, somewhat translucent. After emptying gut contents the colour changed to pale green (see *Observations*).

Antennomaxillary organs on fleshy projections and separated by more than their length with a groove between them (presumably acting as a guide for the retractile apex of the head skeleton); lateral lips fleshy, not sclerotized. Mandibles long and slender, projecting clearly beyond labrum in lateral view, extended anteriorly into the fleshy lobes and apparently used to operate these. Head skeleton with labrum and labium strongly sclerotized and with sharp apices, which are curved respectively dorsad and ventrad. Dorsal and ventral bridges translucent, not sclerotized.

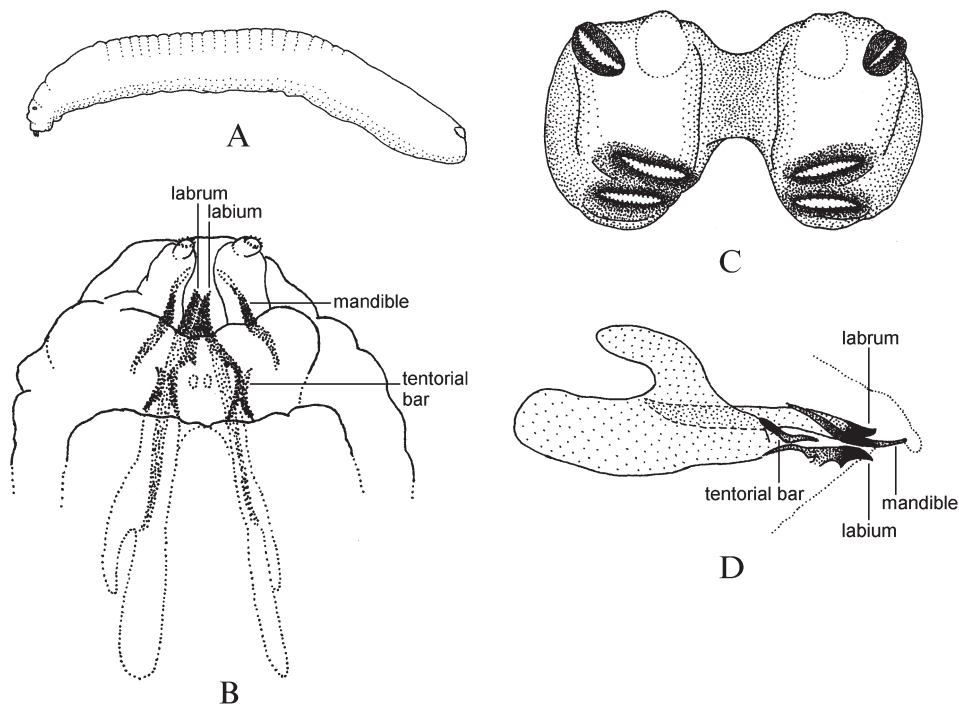


Figure 5. Larva of *Toxomerus apeiensis*. (A) Habitus, lateral view, head to the left; (B) head and prothorax, ventral (and slightly lateral) view, with parts of the underlying head skeleton drawn in dotted lines; (C) posterior breathing organs, apical view; (D) head skeleton, lateral view.

Posterior breathing tubes on a slightly projecting fleshy bar and not joined by sclerotization; spiracular plates oval, opening 1 less tall than basally wide, openings 2 and 3 separated from opening 1 and diverging slightly from inner ends; cuticular scar next to opening 1.

Description of puparium (Figure 6)

Length 5.5 mm ($n=2$). Convexly inflated anteriorly, dorsoventrally flattened posteriorly. Colour brownish, with irregular pattern of darker and paler maculae.

Observations

Adults of *T. apeiensis* (Figure 7) were observed on 4 March, 5 March and 2 April 2006 on the plateau of the Brownsberg nature reserve, and on 24 April 2006 in the Nassau Mountains. Males and females were seen flying around stands of *O. obliquifolia* (Poaceae). Both males and females were feeding on the male inflorescences. Some males were hovering nearby at a height of 50–100 cm. Some females were observed ovipositing on the underside of the inflorescences. The adult flies were only found at sites where the host plant occurred in numbers, not in places with only solitary plants. No other species of Syrphidae were seen near these plants.

Larvae of *T. apeiensis* were found on 4 March 2006 in the Brownsberg nature reserve and on 24 April 2006 in the Nassau Mountains. Most of the larvae had first



Figure 6. Pupa of *Toxomerus apeiensis*.



Figure 7. Adult male of *Toxomerus apeiensis*.

been noticed after taking the inflorescences of *O. obliquifolia* and placing them in plastic containers. Apparently the larvae had been hiding among the male spikelets, relying on their cryptic colouration (Figure 3). Later, presumably when food became scarce, they started crawling around in the boxes. Despite searching, no Homoptera or other invertebrates could be found on the inflorescences. Nevertheless, the larvae were growing. Although active feeding of the larvae was not observed with certainty, microscopic examination of their yellow gut contents revealed that the larvae fed on pollen. Unfortunately, the grass panicles started moulding within a few days, which was probably the reason why most of the larvae did not reach maturity.

Only two larvae made it to the pupal stage. A third instar larva found on 4 March pupated on 8 March but for unclear reasons never hatched. Another third instar larva was found on 24 April. This was kept in a plastic box with some panicles

of *O. obliquifolia*. After 1 day it emptied its gut contents and its colour changed from whitish yellow to pale green (Figure 4). Perhaps this is a form of camouflage, because when its colour changed, the larva moved from the whitish yellow inflorescences to the underside of the green stem of the panicle, where it became inactive. After another day it had pupated (Figure 6). Approximately 12 days later the pupa appeared to be parasitized: a number of tiny Chalcidoidea (Hymenoptera) emerged from the pupa.

***Toxomerus politus* (Say)**

Description of third stage larva (Figure 8A–D)

Length 7–9 mm; width 1.5–2.5 mm. Subcylindrical in cross-section; tapered anteriorly, truncate posteriorly. Body colour pale yellowish green.

Antennomaxillary organs on fleshy projections and separated by more than their length with a groove between them acting as a guide for the retractile apex of the head skeleton; lateral lips fleshy, not sclerotized. Mandibles slender, not projecting beyond labrum in lateral view. Head skeleton with apex of labrum projecting anteriorly more than labium and more heavily sclerotized; dorsal and ventral bridges translucent, not sclerotized.

Ventral surface of prothorax with stippled rows dorsally and laterally, vestiture, i.e. microsculpturing of the integument, consisting of 0.015-mm tall domes, as tall as they were basally broad and separated by about twice the basal width; ventral surface mostly matt with some shiny areas; anterior spiracles tapering, about 0.04 mm tall and as tall as broad, flat tipped with two spiracular openings.

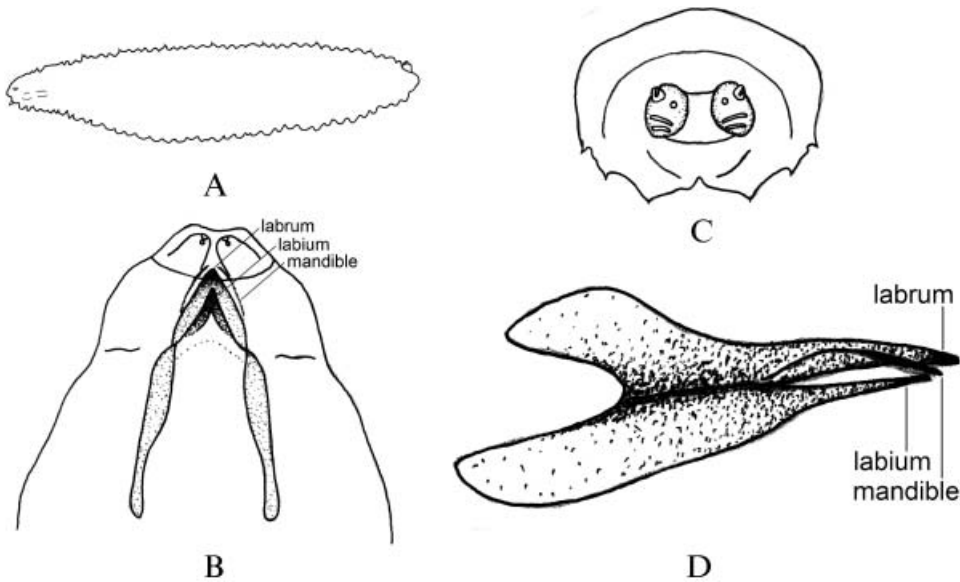


Figure 8. Larva of *Toxomerus politus*. (A) Habitus, lateral view, head to the left; (B) head and prothorax, ventral view; (C) posterior breathing organs, apical view; (D) head skeleton, lateral view.

Sensilla 9–11 aligned on abdominal locomotory prominences; segmental sensilla on slight fleshy projections with a single accompanying seta, basal projection about 0.03 mm tall and same length as seta; apex of anal segment with a pair of slight fleshy projections with sensilla.

Posterior breathing tubes on a slightly projecting fleshy bar and not joined by sclerotization; spiracular plates rounded, opening 1 about as tall as basally wide, openings 2 and 3 separated from opening 1 and diverging slightly from inner ends; cuticular scar next to opening 1.

Discussion

Although no larvae of *T. apugiensis* have been reared to the adult stage, we have no doubts that the larvae belong to this species. *Toxomerus apugiensis* was the only species of this genus that was observed on and around *O. obliquifolia*, and female *T. apugiensis* were observed ovipositing on the inflorescences of this grass.

During a study on the pollination of rainforest grasses in Brazil, Soderstrom and Calderón (1971) observed a *Toxomerus* species feeding on the male flowers of *O. obliquifolia*. They suggested that "...the female may be ovipositing and the larvae may also be feeding on pollen." They identified the *Toxomerus* species as *T. croesus* (Hull, 1940). At the time, *T. apugiensis* had not yet been described. Harbach (1974) points out that *T. apugiensis* specimens will key to *T. croesus* using the key of Hull (1943), so it is possible that the hoverflies observed by Soderstrom and Calderón (1971) belonged to *T. apugiensis*. This becomes even more likely considering the fact that the observations by Soderstrom and Calderón (1971) took place in the same area from which *T. apugiensis* was described.

Weng and Rotheray (forthcoming) describe some unique morphological features of the cephalopharyngeal skeleton and prothorax of *Allograpta micrura* (Osten Sacken, 1877), which appear to be adaptations to its pollen feeding mode of development. For example, the lateral lips are enlarged and help to guide pollen into the mouth and the apices of the labrum and labium are outcurved to help break into the flowers of the host plant. The larva of *T. apugiensis* also appears to have mouthparts modified for gathering pollen. The mandibles are unusually long and slender and can be extended beyond the labrum/labium into the groove between the pair of fleshy lobes on which the antennomaxillary organs are situated, but the lateral lips are not developed as in *A. micrura*. Possibly, these lobes work with the mandibles to help gather pollen into the mouth. Furthermore, the dorsally curved apex of the labrum and ventrally curved apex of the labium are atypical among larvae of Syrphinae. This feature is shared with *A. micrura*, where the curved labrum and labium assist in breaking into the flowers of the host plant to access pollen. They may play a similar role in *T. apugiensis*.

In contrast, the larva of *T. politus* shows no such modifications to pollen feeding. The mandibles and lateral lips are not developed more than in predatory syrphines, and the apices of the labrum and labium are not outcurved. However, the larva of *T. politus* has not only been reported feeding on pollen, but also on leaves and stalks of corn plants (Richardson 1915; Riley and Howard 1888). In certain parts of the USA larvae could not be observed feeding on pollen, but seemed to feed exclusively on leaves and stalks. Larvae were observed puncturing the saccharine cells of the corn tissues and sucking up the exuding juice. As entomophagy is considered to be the

plesiomorphic feeding mode in Syrphinae and other *Toxomerus* species are known as predators (Rotheray and Gilbert 1999; Rojo et al. 2003; Ståhls et al. 2003), the larva of *T. politus* may represent a species that is relatively basal in a group that has shifted to phytophagy within *Toxomerus*. This could explain the absence of modified mouthparts.

At present, species of Syrphinae with phytophagous larvae are only known from the genera *Allograpta* and *Toxomerus*. Both genera also contain species with predatory larvae (Rojo et al. 2003). As these genera are not considered to be sister-groups within the Syrphinae (Mengual et al. 2008), phytophagy appears to have developed independently on at least two occasions.

The phylogenetic relationship between *T. apeiensis* and *T. politus* is indicated by a phylogenetic analysis of Toxomerini based on sequence data of three gene regions by Mengual (2008), which showed that both species belong to the same clade together with six other species for which no larval information is known [*T. aeolus* (Hull, 1924), *T. lacrymosus* (Bigot, 1884), *T. musicus* (Fabricius, 1805), *T. ochraceus* (Hull, 1942), *T. pictus* (Macquart, 1842), *T. pulchellus* (Macquart, 1846)]. This may represent a phytophagous clade with pollen feeding or possibly some other form of phytophagy characterizing the mode of larval development in the unknown six species, but this is merely speculation.

Toxomerus is a large genus, confined to the New World, with about 140 presently valid species names (Thompson and Thompson 2006). Information on larval biology is published for six species, which are all predators (Rojo et al. 2003). With so little information available on the larval biology of these species, it seems possible that other pollen feeding or phytophagous species may occur. One way to find some of these larvae may be by searching on plant species related to *O. obliquifolia*. This grass belongs to a “bambusoid” (bamboo-like) species group, which contains the majority of grasses adapted to conditions of the rainforest. Within this group, the genus *Olyra* is the richest genus, containing about 25 species, predominantly occurring in South America (Soderstrom and Calderón 1971; Oliveira and Longhi-Wagner 2005). Considering this, it seems conceivable that several other species of *Toxomerus* have developed a similar larval feeding mode on related grass species in Neotropical forests.

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