

## Pollen feeding in the larva of *Toxomerus pulchellus* (Diptera, Syrphidae)

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**Abstract.** – The biology and morphology of the larva of *Toxomerus pulchellus* (Macquart, 1846) are described. The larvae were observed feeding on pollen of seven grasses species in the Lesser Antilles (Martinique, Guadeloupe) and French Guiana. In Martinique, feeding behaviour of adults and larvae on Para grass [*Brachiaria purpurascens* (Raddi) Henr.] took place from 5:00 to 9:00 am. These hours coincide with the period of maximum pollen availability. During the rest of the day and night, larvae stay in the superior leaf sheaths. The larva of *T. pulchellus* is compared with those larvae of known pollen-feeding species, *Toxomerus politus* (Say, 1823) and *Toxomerus apeiensis* (Harbach, 1974). The cephalopharyngeal skeleton of *T. pulchellus* has features similar to that in *T. politus* and *T. apeiensis*.

**Résumé.** – **Palynophagie chez la larve de *Toxomerus pulchellus* (Diptera, Syrphidae).** La biologie et la morphologie des larves de *Toxomerus pulchellus* (Macquart, 1846) sont décrites. Des larves visitant les fleurs de sept espèces de graminées et se nourrissant de leur pollen ont été observées dans les Petites Antilles (Martinique, Guadeloupe) et en Guyane française. En Martinique, l'activité alimentaire des adultes et des larves sur l'herbe de Para [*Brachiaria purpurascens* (Raddi) Henr.] a lieu entre 5 h 00 et 9 h 00, coïncidant avec la période durant laquelle un maximum de pollen est disponible. Durant le reste de la journée, les larves restent cachées dans les gaines foliaires supérieures. La larve de *T. pulchellus* est comparée avec celles des espèces dont l'activité palynophage est connue, *Toxomerus politus* (Say, 1823) et *Toxomerus apeiensis* (Harbach, 1974). Le squelette céphalopharyngien de *T. pulchellus* présente des caractéristiques morphologiques similaires à ceux de *T. politus* et *T. apeiensis*.

**Keywords.** – Hoverflies, larval stage, host plant, *Brachiaria purpurascens*, Lesser Antilles, French Guiana.

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*Toxomerus* Macquart, 1855, is the only genus included in the tribe Toxomerini (Syrphinae). Native to the New World, it consists of 141 species including 132 species known from the Neotropical region (THOMPSON *et al.*, 2010). In 2013, *Toxomerus floralis* (Fabricius, 1798) was reported for the first time in afrotropics, becoming the second non-African hoverfly species in this region (JORDAENS *et al.*, 2015). In the New World, some species such as *T. dispar* (Fabricius, 1794), *T. floralis* and *T. politus* (Say, 1823) are widely distributed (THOMPSON, 1981; METZ & THOMPSON, 2001; MONTOYA *et al.*, 2012).

Immature stages of some species in the genus are known to be predatory on Sternorrhyncha whereas other species are pollen-feeding (ROJO *et al.*, 2003; THOMPSON *et al.*, 2010). *Toxomerus politus* is the first species whose pollinivory (on corn, *Zea mays* L.) in the immature stages was discovered in 1888 by Riley and Howard in New Jersey (MARIN, 1969). It would seem that this species was known to the Aztecs as an indicator of good corn harvest (THOMPSON *et al.*, 2010). In Brazil, this species was observed while visiting the inflorescences of *Sorghum bicolor* (L.) Moench and feeding on pollen from the anthers (NUNES-SILVA *et al.*, 2010).

On the basis of field observations and a description of the larval cephalopharyngeal skeleton of *Toxomerus apeiensis* (Harbach, 1974), REEMER & ROTHERAY (2009) showed that this species feeds on pollen of *Olyra obliquifolia* Steud., a bambusoid grass growing in the Suriname tropical rainforest.

In 2012, six syrphid larvae were collected from panicles of a large colony of Para grass [*Brachiaria purpurascens* (Raddi) Henr., Poaceae] growing in the edge of a sugarcane

field located in the agricultural plain of Lamentin (Martinique, Bois-Rouge: 14°35.820'N - 60°58.694'W). All larvae were placed in containers for rearing. The adult flies emerged from the pupae and were identified as *T. pulchellus* using THOMPSON (1981). *T. pulchellus* is a widespread syrphid species known from Mexico to southern America, including the Large Antilles (Cuba, Jamaica and Hispaniola) and the Lesser Antilles (St. Croix, Montserrat, Guadeloupe, Martinique, St. Vincent).

This paper reports for the first time ecological traits of *Toxomerus pulchellus*, describing the feeding behaviour of larvae observed on several grass species in the Lesser Antilles (Martinique, Guadeloupe) and French Guiana.

#### MATERIAL AND METHODS

**Collection of larvae.** – From 2013 to 2015, several surveys were conducted in Lesser Antilles and French Guiana to find larvae of Syrphidae visiting inflorescences of grass species that form large monospecific colonies, like *Brachiaria purpurascens*, in disturbed, man-made areas (fields, road edges, gardens) and open natural areas of forests (glades, tracks...). During a dipterological survey in Saül (French Guiana) in 2014 and in Guadeloupe in 2015, similar larvae were collected and reared from grass panicles (*Paspalum virgatum* L. and *Brachiaria* sp.).

During the surveys, only third instar larvae found on inflorescences of grasses were collected for rearing in Petri dishes ( $\varnothing = 14$  cm). Each dish contained a moist piece of paper to prevent desiccation and they were kept in ambient conditions of temperature and relative humidity ( $T_{\min}$ : 28°C -  $T_{\max}$ : 30°C;  $RH_{\min}$ : 70 % -  $RH_{\max}$ : 85 %). Every two days, 3-10 racemes were added to each dish to provide an excess of pollen for larval development.

**Monitoring adult and larval activity on Para grass.** – Adults and larvae of *Toxomerus pulchellus* were only observed during the anthesis of the host grasses. This flowering stage occurred when the mature anthers hang in the breeze and the two plumose stigmas are exposed (WILLMER, 2011).

In Martinique, two 4 m × 4 m quadrats were placed and demarcated with PVC-tubes (length: 1.20 m) in three of eight prospected monospecific grass sites formed by Para grass (table I; see details of device on fig. 1). In each quadrat all panicles with anthesing flowers were counted. In order to determine the activity of adults and larvae, the method used by NUNES-SIVA *et al.* (2010) for studying behavioural aspects of *T. politus* was applied in each quadrat.

Table I. – List of areas selected to evaluate the activity of *Toxomerus pulchellus* (Macquart)  
[Q, quadrats; T° (°C), temperature in degrees Celsius; RH, Relative Humidity].

Site	Locality	alt.	Type of environment	Date	Nb. panicles with anthesing flowers Q <sub>1</sub> - Q <sub>2</sub>	T° (°C)		RH (%)	
						min	max	min	max
1	Bois rouge, Le Lamentin 14°35'820"N - 60°58'694"W	15 m	Edge of a sugarcane field	27.XI.2013	8-10	24	28	75	85
2	Rivière Mathurin, Trois-Îlets 14°32'00.9"N - 61°00'42.8"W	4 m	Bank of a river of xerophitic area	8.XII.2013	8-12	25	29	75	90
3	Petit Morne, Le Lamentin 14°37'28.6"N - 60°58'26.5"W	10 m	Edge of a sugarcane field	12.I.2014	9-10	23	28	72	85

– The number of adults and larvae of *T. pulchellus* visiting flowers per hour from 5:00 am to 6:00 pm (5 minutes per quadrat). The adults of the other common syrphid species (*T. floralis* and *T. dispar*) visiting the grass flowers during the same time period were not counted because their immature stages are already known to be predators on various homopterous insects (ROJO *et al.*, 2003).

– The behaviour of each fly visiting the quadrat (feeding, mating and oviposition) was recorded per hour. Pollen feeding in *T. pulchellus* was determined when the mouth-parts of adults were seen to apply on anthers and when the larvae had the head in the spikelets.

About ten larvae were collected to examine their gut contents. The extracted pollen was identified at the laboratory of the *Institut des Sciences de l'Évolution–Montpellier* (ISEM).

#### Identification of grasses and Syrphidae. –

All grass species (Poaceae) were identified following HITCHCOCK (1936) and FOURNET (2002). *Toxomerus spp.* were identified using THOMPSON (1981) and BORGES & COURI (2009), and are conserved in the personal collection of the author.

*Toxomerus pulchellus* is easily recognized by the characteristic abdominal pattern in the female and the shape of the genitalic appendages in the male: the abdomen of the female is yellow with black bean-shaped spots on 3<sup>rd</sup>, 4<sup>th</sup> and 5<sup>th</sup> tergite (fig. 2) and the male genitalia have a surstylus that is strongly enlarged in the apical half (THOMPSON, 1981: fig. 127a).

## RESULTS

**Host range.** – A total of 39 grass species in Martinique, Saül (French Guiana) and Guadeloupe have been monitored for *T. pulchellus*. Fourteen of the grass species were visited by adults and seven species were hosted by larvae (table II).

Fifty-two larvae collected in Martinique successfully developed into adults in the rearing dishes. All of these were identified as *T. pulchellus*. Larvae collected in French Guiana (n = 14) were parasitized by a Chalcidoidea species while those collected in Guadeloupe (n = 10) did not reach the adult state.

Table II. – List of the 39 grass species which have been monitored for *Toxomerus pulchellus* (Macquart) (×: species of grasses visited by adults or hosted by larvae).

Species of grasses	Larvae	Adults
<i>Andropogon bicornis</i> L.		
<i>Axonopus compressus</i> (Sw.) Beauv.		
<i>Bothriochloa pertusa</i> (L.) A. Camus		
<i>Brachiaria purpurascens</i> (Raddi) Henr.	×	×
<i>Brachiaria sp.</i>	×	×
<i>Cenchrus echinatus</i> L.		
<i>Chloris inflata</i> Link		×
<i>Chloris radiata</i> (L.) Sw.		
<i>Cynodon dactylon</i> (L.) Pers.		
<i>Dactyloctenium aegyptium</i> (L.) Beauv.		
<i>Dichantium annulatum</i> (Forssk.) Stapf		×
<i>Digitaria spp.</i>		
<i>Echinochloa colona</i> (L.) Link		×
<i>Echinochloa polystachya</i> (Kunth) Hitchc.	×	×
<i>Eleusine indica</i> (L.)		×
<i>Eragrostis sp.</i>		
<i>Homolepis aturensis</i> (Kunth) Chase		
<i>Hymenachne amplexicaulis</i> (Rudge) Nees		
<i>Ichnanthus pallens</i> (Sw.) Munro		
<i>Ischaemum latifolium</i> (Prengr.) Kunth	×	×
<i>Ischaemum timorense</i> Kunth	×	×
<i>Lasiacis spp.</i>		
<i>Leptochloa filiformis</i> (Lam.) Beauv.		
<i>Leptochloa virgata</i> (Lam.) Beauv.		
<i>Oplismenus hirtellus</i> (Lam.) Beauv.		
<i>Panicum maximum</i> Jacq.		
<i>Paspalum conjugatum</i> B. Bergius		
<i>Paspalum fimbriatum</i> Kunth		
<i>Paspalum paniculatum</i> L.		×
<i>Paspalum pleostachyum</i> Doell		×
<i>Paspalum saccharoides</i> Nees		
<i>Paspalum virgatum</i> L.	×	×
<i>Pennisetum purpureum</i> Schumach.		
<i>Pharus latifolius</i> L.		
<i>Saccharum officinarum</i> L.		
<i>Setaria barbata</i> (Lam.) Kunth		
<i>Sorghum arundinaceum</i> (Willd.) R. & S.		×
<i>Sorghum bicolor</i> (L.) Moench	×	×
<i>Sporobolus spp.</i>		

**Material reared from Martinique.** – *E. Dumbardon-Martial* leg. and coll., all adults reared from larvae. 10 ♀ and 5 ♂, 30.XII.2012, Lamentin, Bois-Rouge, 14°36'04.1"N - 60°57'57.8"W, alt. 13 m, larvae ex. panicles of *Brachiaria purpurascens*; 6 ♀ and 6 ♂, *idem*, 23.XI.2013; 3 ♀ and 2 ♂, *idem*, 31.XII.2013; 1 ♀, 21.I.2013, Croix-Rivail, Ducos, 14°36'18.0"N - 60°57'42.9"W, alt. 25 m, larvae ex. panicles of *Sorghum bicolor* (L.) Moench; 1 ♀, *idem*, 21.I.2013, larvae ex. panicles of *Brachiaria purpurascens*; 1 ♂, *idem*, 23.VI.2013, larvae ex. panicles of *Paspalum virgatum* L.; 2 ♀ and 2 ♂, 1.XII.2013, Fort-de-France, Dillon, 14°36'06.3"N - 61°02'59.0"W, alt. 3 m, larvae ex. panicles of *Brachiaria purpurascens*; 1 ♀ and 2 ♂, 27.XII.2013, Fort-de-France, plateau Boucher, 14°43'13.4"N - 61°05'53.8"W, alt. 654 m, larvae ex. panicles of *Brachiaria purpurascens*; 1 ♂, 15.XII.2013, Trois-Îlets, domaine Château-Gaillard, 14°31'35.1"N - 61°00'15.6"W, larvae ex. panicles of *Brachiaria purpurascens*; 1 ♀, *idem*, 22.XII.2013; 2 ♀ et 2 ♂, 29.III.2014, forêt d'Atila, Caplet, Morne-Vert, 14°42'50.8"N - 61°07'26.5"W, alt. 553 m, larvae ex. panicles of *Ischaemum timorense* Kunth; 1 ♀, 7.XII.2014, Rivière-Salée, 14°31'56.4"N - 60°58'56.3"W, alt. 4 m, larvae ex. panicles of *Echinochloa polystachya* (Kunth) Hitchc.; 3 ♀, *idem*, larvae ex. panicles of *Brachiaria purpurascens*; 1 ♀, 27.XII.2013, Trace des Jésuites, 14°44'42.6"N - 61°05'94.6"W, alt. 554 m, larvae ex. panicles of *Ischaemum latifolium* (Spreng.) Kunth.

**Material from French Guiana.** – 14 parasitized pupae (by Chalcidoidea), 9.X.2014, Saül, 3°37'27.5"N - 53°12'38.0"W, alt. 200 m, larvae ex. panicles of *Paspalum virgatum* L., *C. Pierre* & *E. Dumbardon-Martial* leg., coll. *E. Dumbardon-Martial*.

**Material from Guadeloupe.** – 10 larvae, 4.XI.2015, Sofaïa (parking), 16°17'30.7"N - 61°43'37.2"W, alt. 325 m, ex. panicles *Brachiaria* sp., *E. Dumbardon-Martial* leg.

**Biology of *Toxomerus pulchellus* on Para grass.** – Fig. 3 shows the abundance of larvae and adults visiting panicles during a day. Larvae start to visit Para grass flowers at 5:00 am and the number of visits increase rapidly during the next two hours. During this time the larvae crawl along the racemes and insert their head in spikelets (fig. 4). Between 7:00 am and 9:00 am the number of larvae decreased. Larvae were seen crawling down along the primary axis and peduncle of panicles to reach the superior leaf sheaths where they remained for the rest of day (fig. 5). The examination of the gut content of larvae revealed a large amount of ingested pollen grains (fig. 6) which have the exact features of typical Poales pollen morphology, nearly spherical shape and with single pore (LINDER & FERGUSON, 1985).

The feeding time of adults coincided with that of the larvae. However, adults flower visit and feeding started 30 to 60 minutes later than visits by larvae (fig. 7).

From 9:00 am, the number of adults visiting flowers decreased rapidly and only a few adults were on flowers after 12:00 am, however, without feeding on pollen. Mating was observed between 8:00 am and 12:00 am in the surrounding low vegetation or on panicles of Para grass (fig. 8). Although many gravid females (fig. 7) were seen to fly in low vegetation, none of them was seen laying eggs.

**Description of third stage larva of *Toxomerus pulchellus*.** – Length 6.5-7 mm; width 2 mm (n = 5); thorax narrower than abdomen; body smooth, translucent allowing the yellow gut contents to be observed (fig. 9). Integument with four sinuate rows of red pigmented dots: two lateral rows and two dorsal rows regularly spaced and converging in posterior part of body (fig. 9).

Cephalopharyngeal skeleton sclerotized, black (fig. 10); pharyngeal sclerite with dorsal and ventral cornua about equal in width and length; labrum and labium pointed and strongly sclerotized apically; mandibles slender, curved up at apex.

## DISCUSSION

Even if no larvae from French Guiana and Guadeloupe developed into adults, there is no doubt that they were of *Toxomerus pulchellus* because they were morphologically very similar to the larvae reared from Martinique. Furthermore, *T. dispar*, *T. floralis* and *T. pulchellus* were the only species of syrphid observed on the different species of grasses in each area. The immature



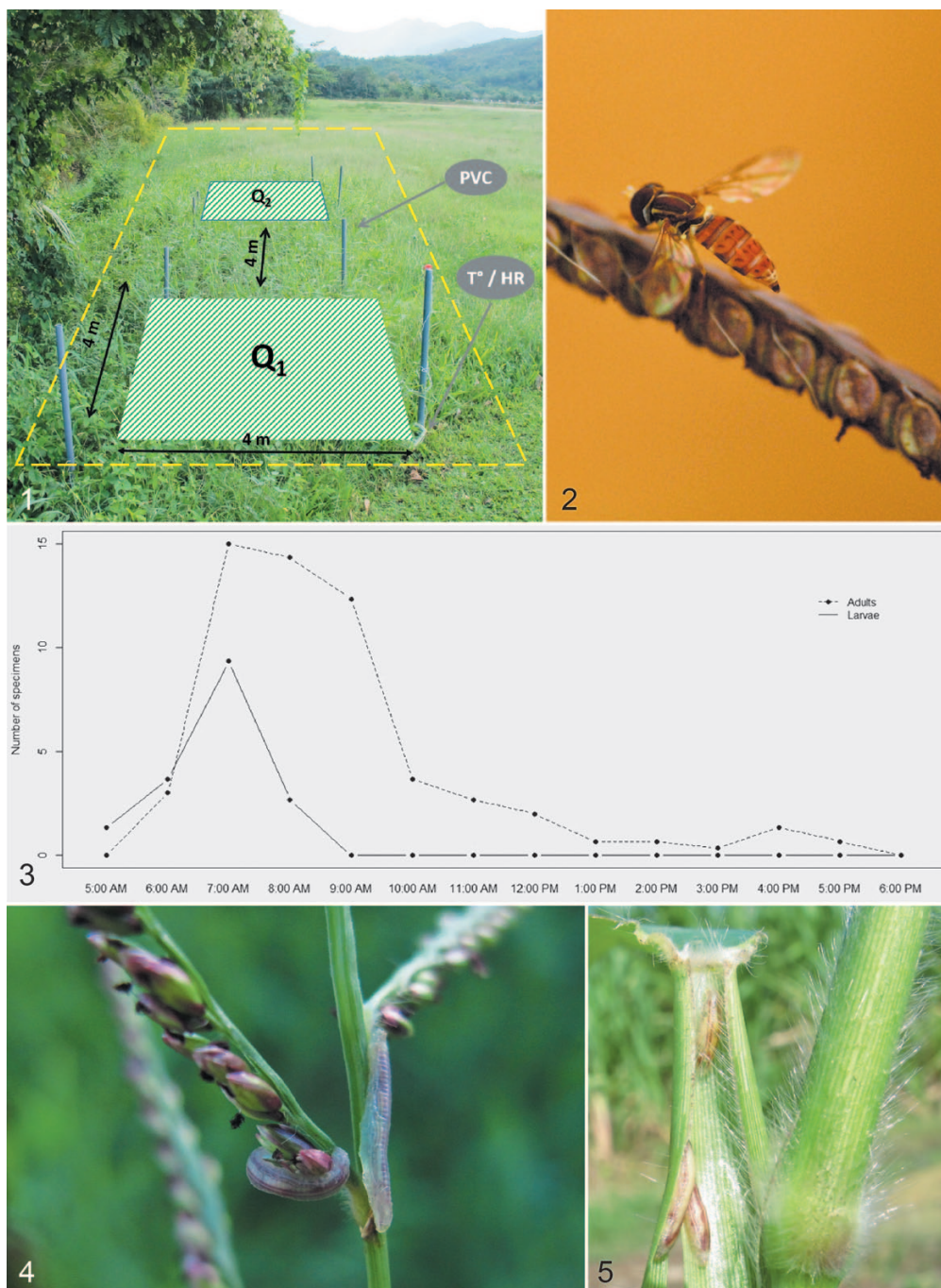


Fig. 1-5. – *Toxomerus pulchellus* (Macquart). – 1, Quadrats for studying activity of larvae and adults (8.XII.2013, Trois-Îlets, Martinique). – 2, Female with characteristic black, bean-shaped marks on the abdomen (9.X.2014, Saül, Guyane, on raceme of *Paspalum virgatum*). – 3, Mean number of larvae and adults visiting panicles during a day. – 4, Two larvae searching for pollen in a panicle of Para grass (12.I.2014, Petit-Morne, Le Lamentin). – 5, Larvae in superior leaf sheaths of Para grass (30.XII.2012, Bois-Rouge, Le Lamentin). (Photos: 1, 4, 5, E. Dumbardon-Martal; 2, C. Pierre; 3, Th. Dumbardon-Martal).



Fig. 6-10. – *Toxomerus pulchellus* (Macquart). – 6, Pollen grains of Para grass ingested by larvae. – 7, Female feeding on pollen from a spikelet of Para grass (11.I.2013, Croix-Rivail, Ducos). – 8, Copulating pair on a panicle of Para grass. – 9, Third stage larva. – 10, Cephalopharyngeal skeleton (*Lbm*, labium; *Lbr*, labrum; *Md*, mandible; *Ph scl*, pharyngeal sclerite). (Photos: 6, S. Muller; 7, M.-C. Lefrançois; 8-9, E. Dumbardon-Martial; 10, V. Balmes).

stages of *T. dispar* are known to have predatory activities (ROJO *et al.*, 2003) but no colonies of potential preys (homopterous insects) were observed on the grasses. Those of *T. floralis*, which are probably both predaceous and pollenivorous, have translucent body without colored sinuate rows (JORDEANS *et al.*, 2015).

At present, four species of the genus *Toxomerus* are known to have pollen-feeding larvae. The cephalopharyngeal skeleton of *T. pulchellus* larvae is similar to that of the other *Toxomerus* species with phytophagous larvae, viz. *T. politus* and *T. apeiensis* (REEMER & ROTHERAY, 2009). Like these species, larvae of *T. pulchellus* have a head skeleton that is modified for gathering pollen: long and slender mandibles that extend beyond the labrum and a labium that is used to gather pollen into the mouth (REEMER & ROTHERAY, 2009). *Toxomerus pulchellus* larvae are distinguished from both other species by the rows of red pigmented dots along the body. The larvae of *T. politus* and *T. apeiensis* have a yellowish white body lacking any pigment (REEMER & ROTHERAY, 2009).

Larvae of *Toxomerus pulchellus* have also a diurnal activity pattern similar to that of *T. politus* on *Sorghum bicolor*, i. e. feeding confined to the hours 5:00 am to 7:00 am. During this period, the climate is cool (21-26°C) and humid (RH > 85 %), dew is on the foliage and in both plants, pollen has not begun to be dispersed by the wind. The early morning feeding by the larvae of these two species is probably an adaptation to the availability of pollen.

Despite their field observations, REEMER & ROTHERAY (2009) and NUNES-SILVA *et al.* (2010) did not report where larvae were located post feeding. Observations of *T. pulchellus* larvae on Para grass inflorescences revealed that they move into the superior leaf sheaths and stay there until they are ready to feed again the next day. It is probable that *T. politus* and *T. apeiensis* have similar behaviour on their host grasses.

*Allograpta micrura* Osten Sacken, 1877, is another Syrphinae known to have a pollen-feeding larva. WENG & ROTHERAY (2008) described the biology of this species which feeds inside flowers of *Castilleja talamensis* Holmgren (Scrophulariaceae) in the highlands of Costa Rica. While their direct observation and analysis of frass show that larvae feed on pollen of *C. talamensis*, on the other hand they also consume plant tissue, especially after emerging from the egg. *Toxomerus politus* has also been observed puncturing the saccharine cells of the corn tissues (REEMER & ROTHERAY, 2009). In Africa, JORDEANS *et al.* (2015) reported the pollinivory in larvae of *Toxomerus floralis* known to be predatory of Sternorrhyncha in America. Although investigations are necessary to observe larvae of *Toxomerus floralis* feeding on aphids in the Afrotropics, it could be that the larvae are both predaceous and pollenivorous (JORDEANS *et al.*, 2015). Consequently, an unresolved question concerns the feeding behaviour of *T. pulchellus* larvae when they are in the leaf sheaths of their host plant during most of the day: do they only use these sheaths as a shelter or do they also consume plant tissue or homopterous insects in addition to the pollen feeding on the panicles?

The phylogenetic analysis of Toxomerini by MENGUAL (2008) shows that *T. politus* and *T. apeiensis* (with pollen-feeding larvae) belong to the same clade as *T. pulchellus* and five other species. The larval feeding ecology in the latter species remains unknown. Nevertheless, this new record on pollen-feeding in larvae of *T. pulchellus* described here adds to the assumption by REEMER & ROTHERAY (2009) that all species of the above mentioned clade in Toxomerini share pollinivory.

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