Remarkable aquatic predators in the genus *Ocyptamus* (Diptera, Syrphidae)

[Bemerkenswerte aquatische Prädatoren in der Gattung *Ocyptamus* (Diptera, Syrphidae)]

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Abstract Third-stage larvae, puparia and adults are described for two species of *Ocyptamus* MACQUART and new synonyms are proposed. The larvae were found in water pockets within epiphytic Bromeliaceae in Costa Rica. They attacked a wide taxonomic range of insect larvae that characteristically co-occur in these phytotelmata, apparently subduing prey with venom and sucking out the internal contents. They possess a number of morphological and behavioural features not known in other predatory syrphids. These features include an enlarged and flattened anal end bearing a sucker, elongate posterior breathing tubes with vertically inclined spiracular plates, and patches of needle-like spicules on the underside of the thorax. Although only two species were reared, larvae of 6 other species were discovered, which suggest that many more species occur in bromeliads.

Key words Predator, phytotelmata, bromeliads, anal sucker, venom

Zusammenfassung Von zwei Arten der Gattung *Ocyptamus* MACQUART werden die dritten Larvenstadien, die Puparien und die Imagines beschrieben und charakterisiert sowie neue Synonyme festgelegt. Die Larven wurden in Phytothelmata von epiphytischen Bromelien in Kostarika gefunden. Sie attackieren ein weites Spektrum von Insektenlarven, die hier gemeinsam mit den Syrphidenlarven leben. Offensichtlich lähmen sie die Beute mittels eines Giftes und saugen dann den deren Körperinhalt aus. Die Larven besitzen eine ganze Anzahl von besonderen morphologischen und verhaltensbiologischen Besonderheiten, die von anderen prädatorischen Syrphiden bislang nicht bekannt waren. So umfassen sie ein verlängertes und abgeflachtes Analende, das einen Saugmechanismus zum Festheften trägt, verlängerte Hinterstigmata mit vertikal geneigten Stigmenplatten und an der Unterseite des Thorax befinden sich mit nadelartigen Microtrichen besetzte Flecken. Obwohl nur zwei Arten gezüchtet wurden, sind die Phytothelmata der Bromelien viel artenreicher an *Ocyptamus*-Larven, denn präimaginalstadien weiterer 6 Spezies dieser Gattung wurden in Bromelien gefunden.

Stichwörter Prädator, Phytotelmata, Bromeliaceen, analer Saughaftapparat, Gift

Introduction

Among the Diptera, Syrphidae have outstandingly diverse larvae (VOCKEROTH & THOMPSON 1987, ROTHERAY & GILBERT 1999). A prominent feeding mode is predation, which occurs in about a third of the known species. Syrphid predators include the Syrphinae (sensu ROTHERAY & GILBERT 1999), the Microdontinae (sensu VOCKEROTH & THOMPSON 1987), the Pipizini (variously classified as Syrphinae or Eristalinae) and some *Volucella* GEOFFROY, 1762. The prey used by these groups are colonial or aggregative insects: most syrphines and pipizines attack soft-bodied Homoptera (ROTHERAY 1993); microdontines feed on early stages of ants (Formicidae) (DUFFIELD 1981, GARNETT et al. 1985); most *Volucella* are facultative or obligatory predators of the early stages of social aculeates (RUPP 1989, ROTHERAY 1999). This last-mentioned taxon includes at least one non-predatory species, *Volucella inflata* (FABRICIUS), which is a saprophage in exuded tree-sap (ROTHERAY 1999). In an investigation of syrphid phylogeny based on larval stages including mouthparts, the predatory taxa formed a single lineage with the sequence: *Volucella* - *Microdon* - Pipizini - Syrphinae (ROTHERAY & GILBERT 1999).

In 1994 GER received from N. WAITZBAUER, via F. S. GILBERT, four preserved syrphid larvae and one puparium found in *Vriesea* bromeliads (Bromeliaceae) from Richterberg, Bogota, Colombia. These larvae were similar to those of other Syrphinae, except for several unique features such as a long posterior respiratory process, with a peculiar arrangement of spiracular openings, and suckers on the ventral surface. In Costa Rica in 1999, we found many larvae with similar features occurring in bromeliads. Observations revealed that they were predators of aquatic insect larvae. From these larvae, we reared two species of *Ocyptamus*. *Ocyptamus* is an endemic new world taxon that has over 300 species in the neotropics and 22 in the Nearctic Region (THOMPSON 1999, 2000). In this paper, we describe the larvae, puparia, and adults of these two *Ocyptamus* species, and provide nomenclatural data and new synonymies. We also describe the predatory behaviour and functional morphology of the larval stages.

Nomenclature and descriptions

Genus *Ocyptamus* MACQUART

Ocyptamus MACQUART, 1834 – MACQUART 1834: 554. Type-species, *fascipennis* MACQUART (COQUILLETT 1910: 577) = *fuscipennis* SAY.
Hermesomyia VOCKEROTH, 1969 – VOCKEROTH 1969: 121. Type-species, *bacchiformis* VOCKEROTH (original designation) = *wulpianus* LYNCH ARRIBÁLZAGA.

Ocyptamus luctuosus (BIGOT, 1883)

Baccha luctuosa BIGOT, 1883. – BIGOT 1883: 334. Type-locality: Mexico. Holotype (not) BMNH. WILLISTON 1891: 39 (description, Costa Rica); ALDRICH 1905: 356 (catalog citation); HULL 1949: 126 (key reference, abdomen pattern); FLUKE 1956: 252 (catalog citation).
Allograpta? luctuosa. HULL 1943a: 10, 1943d: 47 (probable placement based on type).
Ocyptamus luctuosus. THOMPSON et al. 1976: 21 (catalog citation).
Mesogramma trilineatum ENDERLEIN, 1938. – ENDERLEIN 1938: 232. Type-locality: "St. Jean.". Holotype ZMHU. **Syn. nov.**
Mesograpta trilineatum. FLUKE 1956: 231 (catalog citation).
Toxomerus trilineatus. THOMPSON et al. 1976: 55 (catalog citation).
Baccha rica CURRAN, 1939. – CURRAN 1939: 6. Type-locality: Puerto Rico, Mayaguez. Holotype AMNH. HULL 1949: 127 (key reference, abdomen pattern); FLUKE 1956: 261 (catalog citation). **Syn. nov.**
Ocyptamus ricus. THOMPSON et al. 1976: 26 (catalog citation); THOMPSON 1981: 53 (taxonomy).
Baccha pinkusi CURRAN, 1939. – CURRAN 1939: 5. Type-locality: Trinidad, Tabaquite. Holotype ANMH. HULL 1949: 126 (key reference, abdomen pattern); FLUKE 1956: 259 (catalog citation). **Syn. nov.**
Ocyptamus pinkusi. THOMPSON et al. 1976: 25 (catalog citation).
Baccha brunnipennis HULL, 1942. – HULL 1942a: 73. Type-locality: Brazil, São Paulo. Holotype CNC. HULL 1949: 128 (key reference, abdomen pattern); FLUKE 1956: 239 (catalog citation). **Syn. nov.**
Ocyptamus brunnipennis. THOMPSON et al. 1976: 14 (catalog citation).
Baccha papilio HULL, 1942. – HULL 1942b: 45. Type-locality: Brazil, São Jose. Holotype CNC. HULL 1949: 127 (key reference, abdomen pattern); FLUKE 1956: 257 (catalog citation). **Syn. nov.**
Ocyptamus papilio. THOMPSON et al. 1976: 24 (catalog citation).
Baccha vespuccia HULL, 1943. – HULL 1943c: 73. Type-locality: Brazil, Santa Catarina, Nova Teutonia. Holotype AMNH. HULL 1949: 129 (key reference, abdomen pattern); FLUKE 1956: 266 (catalog citation). **Syn. nov.**
Ocyptamus vespuccia. THOMPSON et al. 1976: 29 (catalog citation).
Baccha ochreolinea HULL 1943: 98, fig. 89. **Nomen nudum.**
Baccha ochreolinea HULL 1944. – HULL 1944: 31. Type-locality: Panama, Canal Zone, Barro Colorado Island. Holotype MCZ. HULL 1949: 210 (key reference, abdomen pattern); FLUKE 1956: 256 (catalog citation). **Syn. nov.**
Ocyptamus ochreolinea. THOMPSON et al. 1976: 23 (catalog citation).

Baccha fragmentaria HULL 1947. – HULL 1947: 405. Type-locality: Mexico, Tapachula Mountains. Holotype AMNH. HULL 1949: 127 (key reference, abdomen pattern); FLUKE 1956: 247 (catalog citation). **Syn. nov.**
Ocyptamus fragmentaria. THOMPSON et al. 1976: 18 (catalog citation).
Baccha lepida of CURRAN 1941: 262, HULL 1949: 127 (misidentifications)
Ocyptamus sp. j of FLEMING 1985: 695 (pollination of *Piper* spp.)

Description of adult

Head: face yellow, shiny, black pilose; tubercle low, convex, on ventral 1/2 of face; gena narrow, yellow, bare; lunula brown on medial 1/2 or more, yellow laterally; frontal triangle yellow except narrowly brown medially along margin with lunula, black pilose; frons black medially and on dorsal 1/3, yellow laterally on ventral 2/3, broadly yellow ventrally but narrowed dorsally, medial black area broad basally and dorsally, constricted medially, black pilose; vertical triangle anterior, about twice its height from posterior margin of eye, black, brown pollinose, black pilose; occiput black, yellow pollinose except more brownish yellow on dorsal 1/4, yellow pilose ventrally becoming black on dorsal 1/3, with 2-3 rows of pile medially, reduced to single row on dorsal 1/3; antenna yellow except basoflagellomere brown except basoventral 1/4 yellow, black pilose; arista black.
Thorax: prothorax black except yellow postpronotum and epimeron (area dorsad to procoxa); scutum black except broadly yellow laterally, with postalar callus yellow, sparsely brown pollinose, with indistinct submedial and medial darker pollinose vittae, with purple iridescence from some angles, sparsely black pilose; scutellum yellow, sparsely black pilose, without ventral fringe; pleuron black except yellow posterior anepisternum, dorsal 1/3 of katepisternum and anterior anepimeron, yellow pilose; metasternum yellow, bare; metathoracic episternum yellow, bare; postmetacoxal bridge absent, with metathoracic epimera widely separated; plumula absent; calypter brown, with no fringe on dorsal lobe, with very short fringe on ventral lobe; halter orange, with capitulum sometimes darker; wing brown, microtrichose; alula narrow, about as wide as cell C. **Legs**: Proleg yellow, yellow pilose; mesocoxa brown, black pilose; mesotrochanter yellow, yellow pilose; mesofemur yellow, yellow pilose except black pilose posteriorly; mesotibia and tarsus yellow, yellow pilose; metacoxa yellow, yellow pilose except with a few black pili apically; metatrochanter yellow, yellow pilose; metafemur brownish yellow except black on apical 1/3 except apex, black pilose; metatibia black, black pilose; metatarsus yellow to brownish yellow, yellow pilose to extensively black pilose.
Abdomen: elongate, about 1.3 times as long as thorax, parallel-sided, expanded slightly beyond 1st segment, widest at apex of 3rd segement; sterna yellow to orange, black pilose except yellow on 1st; terga black except yellow maculae, dull black pollinose except subshiny apical and lateral margins and base of 2nd tergum, black pilose; 2nd tergum slightly wider than long, about as long as 3rd, with single angulate yellow fascia medially, with fascia narrowly isolated from lateral margin, with fascia continuous or very narrowly separated medially; 3rd tergum with submedial triangular yellow maculae, with very small macula on base and larger macula medially, rarely medial macula broken into two, sometimes basal and medial maculae connected; 3rd and 4th terga quadrate, only slightly wider than long; 4th tergum with submedial yellow vitta on basal 3/4 and sublateral oblique vitta on basal 1/2, with sublateral vitta usually connected to submedial vitta, frequently with base of submedial vitta expanded triangularly, rarely with sublateral vitta absent and submedial vitta greatly reduced; 5th tergum trapezoidal, about twice as wide as long, with lateral margin convex, with yellow slightly arcuate long submedial vitta on basal 4/5 and short sublateral vitta, with sublateral and submedial vittae connected along base, rarely with sublateral vitta isolated or absent.

Length: body 8 mm (range 7.5-8.8 mm, n =4); wing 7 mm (range 6.3-7.9 mm n=4)

Description of third stage larva

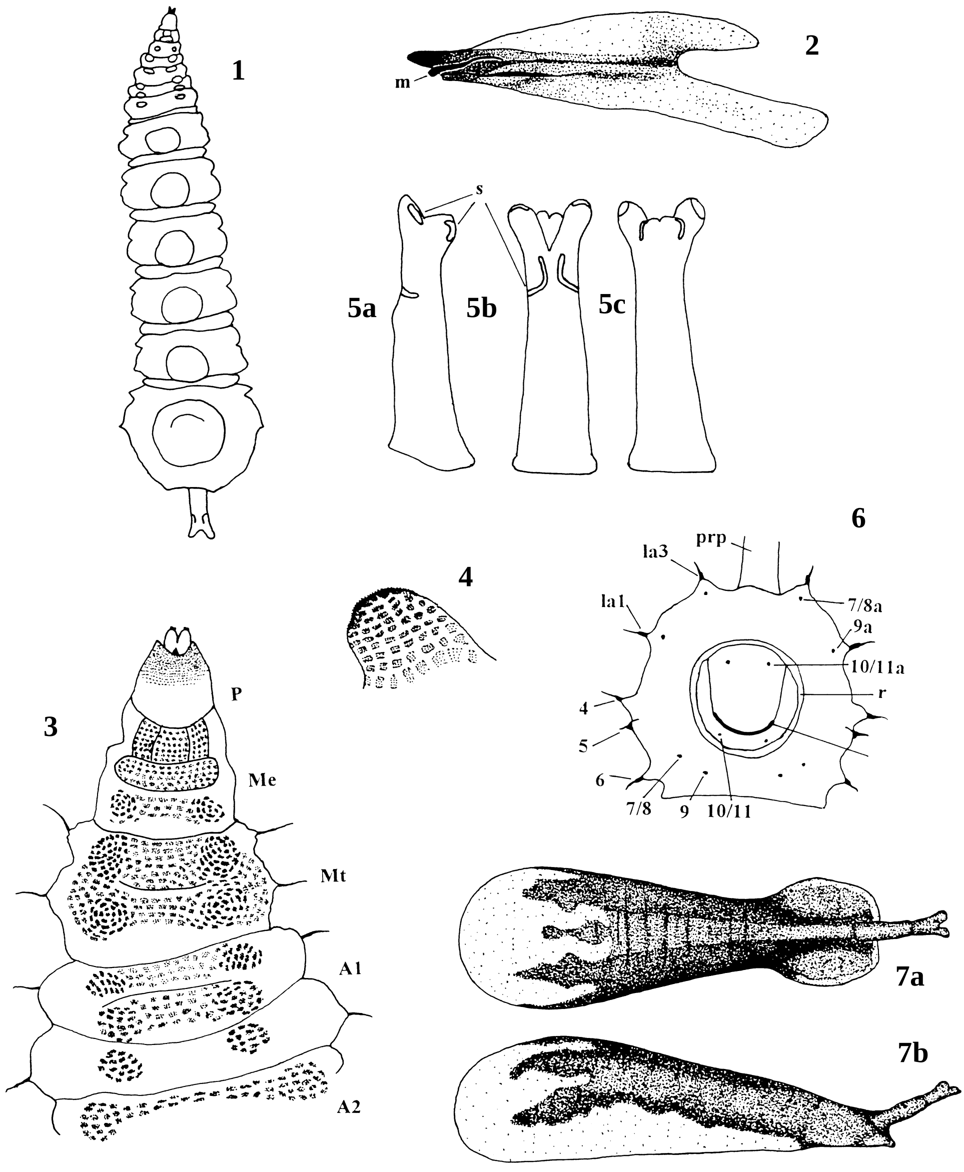
Overall size and shape: length 11-13 mm, n=3; larva tapering from anal segment to prothorax (width, anal segment 3.2 mm; width, prothorax 0.3 mm) (Fig. 1); 7th and 8th abdominal segments forming a single enlarged unit without an indented margin separating the segments as occurs between rest of abdominal segments (Figs 1, 6); larva somewhat dorsoventrally flattened as shown by cross-section and lateral sensilla group 4 being almost on same horizontal line as sensilla 5 and 6 (Fig. 6) rather

than above these sensilla as occurs in more subcylindrical larvae; truncate posteriorly with a pair of indistinct rounded projections bearing apical sensillum; larva translucent, lacking an obvious colour pattern and thereby tending to taking up colour of the background substrate, except for black hind gut and surrounding white fat body; vestiture on the dorsal surface of entire body papillose and becoming dark-pigmented posteriorly; sensilla pattern same as other Syrphidae (Rotheray & Gilbert 1999).
Head: antennomaxillary organs mounted on a fleshy projection apparently formed from dorsal lip and base of the antennomaxillary organs. Cephalopharyngeal skeleton typical for syrphine larvae (Roberts 1970) with anterior ends of labrum and labium drawn out to a sharp point and the mandibles reduced to a pair of thin stylets which lie lateral to sharpened tips of labrum and labium (Fig. 2).
Thorax: prothoracic lateral lips without a black sclerotised apex, but fleshy and covered with spicules; needle-like spicules aggregated into patches over ventral thoracic surface, first abdominal segment and anterior part of second abdominal segment (Figs 3, 4); ventro-lateral margins of mesothorax, metathorax and first abdominal segment formed into lobes (Figs 3, 4).
Abdomen: ventral sensillum 11 not anterior to sensilla 9 and 10 on abdominal segments 1-6; dorsal and lateral abdominal sensilla 1-6 with a single seta much longer than basal papilla (0.18 mm v 0.015 mm), many setae missing from basal papillae, presumably rubbed off; ventral sensilla lacking setae; ventral surface of 7th and 8th abdominal segments with a disc-like sucker with a raised rim (Fig. 6); crescent-shaped anus within the sucker (Fig. 6); sensilla 10/11 anterior to anus within sucker; sensilla 7/8 and 9 of 7th abdominal segment outside sucker (Fig. 6); sensilla 10/11 of anal segment posterior to anus within sucker (Fig. 6); flattened ventral surface outside sucker coated with patches of needle-like spicules; ventral surface of abdominal segments 2-6 with similar oval-shaped suckers bearing sensilla 9-11 on anterior margin; rest of abdominal ventral surface with shagreened areas lacking grooves and needle-like spicules.
Posterior respiratory process: length 2 mm, basal half tapering towards a mid-point constriction and matt with a rugose surface sculpture; upper half above constriction with 3 spiracular openings, one pair low down on ventral surface with remaining two pairs on bifurcating processes, middle pair longer than anterior pair; circular scar on anterior pair of processes (Fig. 5).

Description of puparium
Length: 7-9 mm; inflated anteriorly, dorsoventrally flattened posteriorly. Distal part with a dark brown marking extending to inflated portion (Fig. 7). Pupal spiracles absent.

Distribution: Mexico, Guatemala, Costa Rica, Panamá, Puerto Rico, Brazil.

Material examined
Adults: (18 ♂♂, 54 ♀♀): Unknown Country**.** St. Jean, Mortiz S [=sammlung**]**, (Holotype *trilineata* ♀, ZMHU)**. Mexico**. [no precise locality](Holotype *luctuosa* ♀, BMNH); [Chiapas?], Tapachula Mountains, F. M. Synder, 17-19 Aug 1943 (Holotype *fragmentaria* ♂, AMNH). **Guatemala**. Puerto Barrios, D. G. Hall, 1943 (USNM ENT 00030184 USNM); Peten, Tikal, N. L. H. Krauss, Sep 1959 (♀ USNM ENT 00030187). **Costa Rica**. Alajuela: P. N. Guanacaste, Sector San Ramón, 800 m, LN 318100 381900, M. Zumbado, 11-15 Apr 1994, Lot# 2857 (♀ INBIOCRI001820346 INBIO); Upala, Dos Ríos, 620 m, F. A. Quesada, Mar-13 Apr 1995, Lot# 5274 (♂ INBIOCRI002462260 INBIO), Cartago: Caché, about 2000 ft., H. Roger (♀ USNM ENT 0030190 BMNH); Cartago, Orosi, Río Grande, P. N. Tapantí, Sector el Humo, 1400-1700 m, LN 189500 560200, R. Guzmán, Feb 1997, Lot#45463 (♂ INBIOCRI002552222 INBIO); ... desde Adminstración hasta Sendero La Pava, 1150-1600 m, LN 192500 560400, R. Guzmán, May 1997, Lot#46359 (♂ INBIOCRI002569220 INBIO). Guanacaste: Estación Pitilla, 9 km S Santa Cecilia, 700 m, LN 330200 380200, C. Moraga, Feb 1993 (♂ INBIOCRI001203328 USNM), C. Moraga, R. Blanco & P. Rios, Feb 1990 (♀ INBIOCRI000125294 USNM), Feb 1994 (♀ INBIOCRI001828837 USNM); Estación Cacao, 2 km SW del Cerro Cacao, 1000-1400 m, LN 323100 375800, M. A. Zumbado, 24 July-3 Aug 1995, Lot#6266 (♂ INBIOCRI002341872 UNSM); Santa Rosa National Park, A. Penry, 8 Aug 1979, on *Piper marginatum* (#79-11358)(♂ USNM ENT 00030189 USNM); ... T. H. Fleming, 12 Jun-8 Aug 1980, on *Piper* spec. (8♀♀ 80-SRNP-17, 53, 63, 65-67. 112-113 USNM); La Pacifica, 4 miles NW Cañas, P. A. Opler, 17 Oct 1971, on *Piper marginatum*, (1♂, 4♀♀ OTS Ecosyst Analysis Specimen # 26255-59 USNM); ... 5 Sep 1971 (♀ OTS Ecosyst Analysis Specimen # 213339 USNM); Cometec, 8 km NW Bagaces, P. A. Opler, 16 Sep 1971, on *Piper pseudofuligineum* (3♀♀ OTS Ecosyst Analysis Specimen # 13393-95 USNM); Hacienda COMELCO, 24 km NW Cañas on Inter-American Highway, 50 m., E. R. Heithaus, 18 May 1971, 0830 hours, on *Piper* sp. (#88)(♀ 2394 USNM); ... 1 Sep 1971, 1000 hours, on *Piper* spec. (#342)(5♀♀ 7452-6 USNM); ... 21 Sep 1971, 1100-1130 hours, on *Piper* spec. (#342)(2♀♀ 8346-7); ... 5 Oct 1971, 1045 hours, on *Piper* sp. (#117)(2♀♀ 9482-3 USNM); ... 7 Oct 1971, 1130 hours, on *Piper* spec. (#342)(7♀♀ 9559-65 USNM). Heredia:



Figs 1-6: *Ocyptamus luctosus* (Bigot, 1883). – **1**: whole third stage larva, ventral view; – **2**: Cephalopharyngeal skeleton, lateral view, m = mandible; – **3**: thorax and first two abdominal segments, ventral view, P = prothorax, Me = mesothorax, Mt = metathorax, A1 = abdominal segment one, A2 = abdominal segment two; – **4**: anterior lobe on ventral surface of metathorax, lateral view; – **5a-c**: posterior respiratory process; – **a**: lateral view; – **b**: ventral view; – **c**: dorsal view; – **6**: 7th abdominal and anal segment, ventral view, a = anus, la1 = lappet one, la3 = lappet three, prp = posterior respiratory process, r = raised rim of sucker, 7/8a, 9a, 10/11a = sensilla numbers on anal segment, 4,5,6, 7/8, 9, 10/11 = sensilla numbers on 7th abdominal segment; 7a-b whole puparium; a, dorsal view; b, lateral view.

La Selva, 3 km S Puerto Viejo, 75 m, P. A. OPLER, 5-6 Sep 1973, on *Piper auritum* (♀ USNM ENT 00030188 USNM). Puntarenas: Monteverde, San Luis, Finca Buen Amigo, 4 km S de la Reserva, 1000-1350 m, LN 250850 449250, Z. Fuentes, Mar 1996 (♀ INBIOCRI002399252 INBIO); ... 20-30 Jan 1997 (♂ INBIOCRI002534620 INBIO). San José: P. N. CHIRRIPÓ, Llano Bonito, 4.4 km SW of C. Ventisqueros, 2450 m, LS 378500 513200, E. NAVARRO, 4 May 1997, Lot#46275 (♀ INBIOCRI002551478 INBIO); Pérez Zeledón, P. I. La Amistad, Estación Santa Elena, 1210 m, LS 371750 507800, M. SEGURA, 5-21 July 1996, Lot#7888 (♂ INBIOCRI002469657 INBIO); ... Sendero La Fila, 1690 m, LS 373600 507500, E. ALFARO, 18 Mar 1997, Lot#45550 (♀ INBIOCRI0025034451 INBIO). **Panama**. Canal Zone: Barro Colorado Island, N. BANKS, 24 July 1924 (Holotype ♀ *ochreolinea*, MCZ). **Puerto Rico**. Mayaguez, J. BLANCH, 7 Sep 1932, (Holotype ♀ *rica*, AMNH); ... R. H. VAN ZWALENBERG, 1 Aug 1914 (♀ USNM ENT 00030070 USNM). **Virgin Islands**. St. Thomas, Magens Bay, M. A. IVIE, 14 July 1979 (♀ USNM ENT 00030185 USNM). **Trinidad**. Tabaquite, A. S. PINKUS, 22 Aug 1933 (Holotype ♀ *pinkusi*, AMNH). **Brazil**. [state?]: São Jose, May 1905 (Holotype ♀ *papilio*, CNC). São Paulo: São Paulo, J. LANE, 6 Apr 1939 (Holotype ♂ *brunnipennis*, CNC). Santa Catarina: Nova Teutonia, F. PLAUMANN (Holotype ♂ *vespuccia*, AMNH); ... Jan 1965 (♂ USNM ENT 00030075 USNM), Feb 1965 (3♂♂ 1♀ USNM ENT 00030072-5 USNM), Mar 1965 (♂♀ USNM ENT 00030071, ...77 USNM), Oct 1964 (♀ USNM ENT 00030079 USNM), Oct 1971 (♂ USNM ENT 00030078 USNM); Iguazu, R. C. Shannon, 6 Oct 1927 (♀ USNM ENT 000330186 USNM).

Larvae and puparia: **Costa Rica**. Cartago, P. N. Tapantí, Estación Quebrada Segundo, 1200 m LN-193800, 560000, two larvae MAV-03.2, MAV-22; two larvae JDG-002, JDG-019; one puparium MAZ-05.1, male emerged 27.ii.1999; all larvae and puparia from unidentified epiphytic bromeliads (NMS, INBio).

Taxonomic notes: This species has been described many times, always from short series, usually singletons. The principal characters used to distinguish these new species were small differences in the yellow maculae on the abdominal terga. Now, with fairly long series of adults from Costa Rica and Brazil (Nova Teutonia), these differences can be seen as trivial individual variation. Hence, we have synonymized eight names. HULL (1949) was the last worker to deal with all these names. In his key, he separated two groups based on whether the sublateral oblique vittae were connected or not with the submedial ones. Then he separated out the numerous variants: for specimens that have maculae of 3rd tergum broken into smaller ones he used *pinkusi* CURRAN; for specimens with fascia on 2nd tergum narrowed divided medially, *brunnipennis*; for specimens with maculae on 3rd tergum reduced, *vespuccia*; *et cetera*. Years ago DUSEK and LASKA (1974) demonstrated that color variation such as this is caused by temperature variation during pupal development. THOMPSON (1981: 53), under the name *ricus*, provided a key to differentiate this species from related ones.

Ocyptamus wulpianus (LYNCH ARRIBÁLZAGA, 1891)

Baccha tricincta VAN DER WULP, 1888. – VAN DER WULP 1888: 376, pl. 10: 8 (preocc. BIGOT 1883). Type-locality: Argentina, Prov. Tucumán. Neotype BMNH here designated.
Baccha wulpiana LYNCH ARRIBÁLZAGA 1891: 250 (new name for *tricincta* VAN DER Wulp). KERTÉSZ 1910: 165 (catalog citation); FLUKE 1956: 267 (catalog citation).
Ocyptamus wulpianus. THOMPSON et al. 1976: 30 (catalog citation).
Baccha pirata CURRAN 1939. – CURRAN 1939: 7. Type-locality: Brazil, São Paulo. Holotype AMNH. HULL 1949: 126 (key reference, abdomen pattern); FLUKE 1956: 259 (catalog citation). **Syn. nov.**
Ocyptamus pirata. THOMPSON et al. 1976: 25 (catalog citation).
Baccha phobifer HULL 1943. – HULL 1943b: 50. Type-locality: Ecuador, Oriente, Puyo, 1250 m. Holotype AMNH. HULL 1949: 126 (key reference, abdomen pattern); FLUKE 1956: 259 (catalog citation). **Syn. nov.**
Ocyptamus phobifer. THOMPSON et al. 1976: 25 (catalog citation).
Hermesomyia bacchiformis VOCKEROTH, 1969. – VOCKEROTH 1969: 122, figs. 13, 17. Type-locality: Ecuador, Pichincha, Tandapi, 40 km SW Quito. HT CNC. Synonymy THOMPSON et al. 1976: 25.

Description of adult

Head: face yellow, pollinose except shiny tubercle, white pollinose ventrally becoming more golden on dorsal 1/2, black pilose dorsally, yellow pilose ventrally, black and yellow pilose medially; tubercle distinct, convex, occupying medial 1/2 of face; gena yellow, shiny and bare anteriorly, white pollinose and pilose posteriorly; lunule brownish black; frontal triangle yellowish orange on ventral 1/2 except for brownish black medial macula continuous with dark lunule, blackish on dorsal 1/2, densely golden pollinose, black pilose; eye contiguity long, about as long as frontal triangle; frons yellow to orange on ventral 1/4, black dorsally, yellow pollinose ventrally, greenish-brown pollinose dorsally, black pilose; vertical triangle black, greenish-brown pollinose, black pilose, short, about 2/3 as long as eye contiguity; occiput yellow ventrally, black on dorsal 2/3, white pollinose on ventral 2/3, greenish-brown pollinose dorsally, thick yellow pilose on ventral 2/3, with about 3-4 rows of pile at mid-point, black pilose on dorsal 1/3; antenna orange except apicodorsal 2/3 of basoflagellomere brownish black, black pilose; arista brownish black.

Thorax: postpronotum orange, yellow pollinose; scutum black except yellow notopleuron and postalar callus, densely greenish-brown pollinose except yellow pollinose on notopleuron, yellow and black pilose, some specimens with very indistinct submedial vittae anteriorly; scutellum yellow, rarely dark basomedially, densely yellow pollinose altho more brownish-yellow pollinose basally, black pilose; subscutellar fringe of long black pile in males, greatly reduced in females; anepisternum and dorsad to procoxa yellow, golden pollinose, yellow pilose except for a few black pili posteriorly; katepisternum black on ventral 2/3, yellow dorsally, densely yellow pollinose, yellow pilose; anepimeron yellow on anterior 1/2, darker posteriorly, yellow pollinose, yellow pilose except with black pile intermixed posteriorly; katepimeron yellow, yellow pollinose and pilose; meron dark, yellow pollinose; metasternum yellow, bare; metathoracic episternum yellow, yellow and black pilose; postmetacoxal bridge absent, with metathoracic epimera widely separated; metanotum black; plumula short, unbranched, yellow; calypter orange, with yellow to yellow and black fringe; halter orange; wing brown, microtrichose; alula elongate, about as wide as cell BM, about twice as wide as cell C. **Legs**: Coxae and trochanters yellow, yellow and black pilose; pro- and mesofemur brownish black except pale on base and apical 1/5 or more, black pilose except for a few pale pile basally; pro and mesotibiae and tarsi brownish, black pilose; metafemur and tarsus black, black pilose.

Abdomen: elongate, parallel-sided, slightly narrowed at apex of 3rd segment and expanded at apex of 4th, as long as wing, about 3 time as as long as thorax; 1st tergum black except yellow lateral margin, sparsely grayish-white pollinose, black pilose with yellow pile intermixed laterally; 2nd tergum black except yellow lateral margin on basal 1/2 and yellow interrupted medial fascia in males, with medial fascia absent in females, dull black pollinose on basal 3/4 except pale areas, subshiny (very sparsely pollinose) on apical 1/4, black pilose; 3rd thru 5th terga black except single yellow fasciae on basal 1/3 but separated from base by their widths or more, with fasciae broad in males and narrow in females; dull black pollinose on basal 3/4 except pale areas, subshiny (very sparsely pollinose) on apical 1/4, black pilose; 1st sternum yellow, yellow pilose; 2rd thru 5th sterna orange, black pilose; male genitalia brownish black, black pilose.

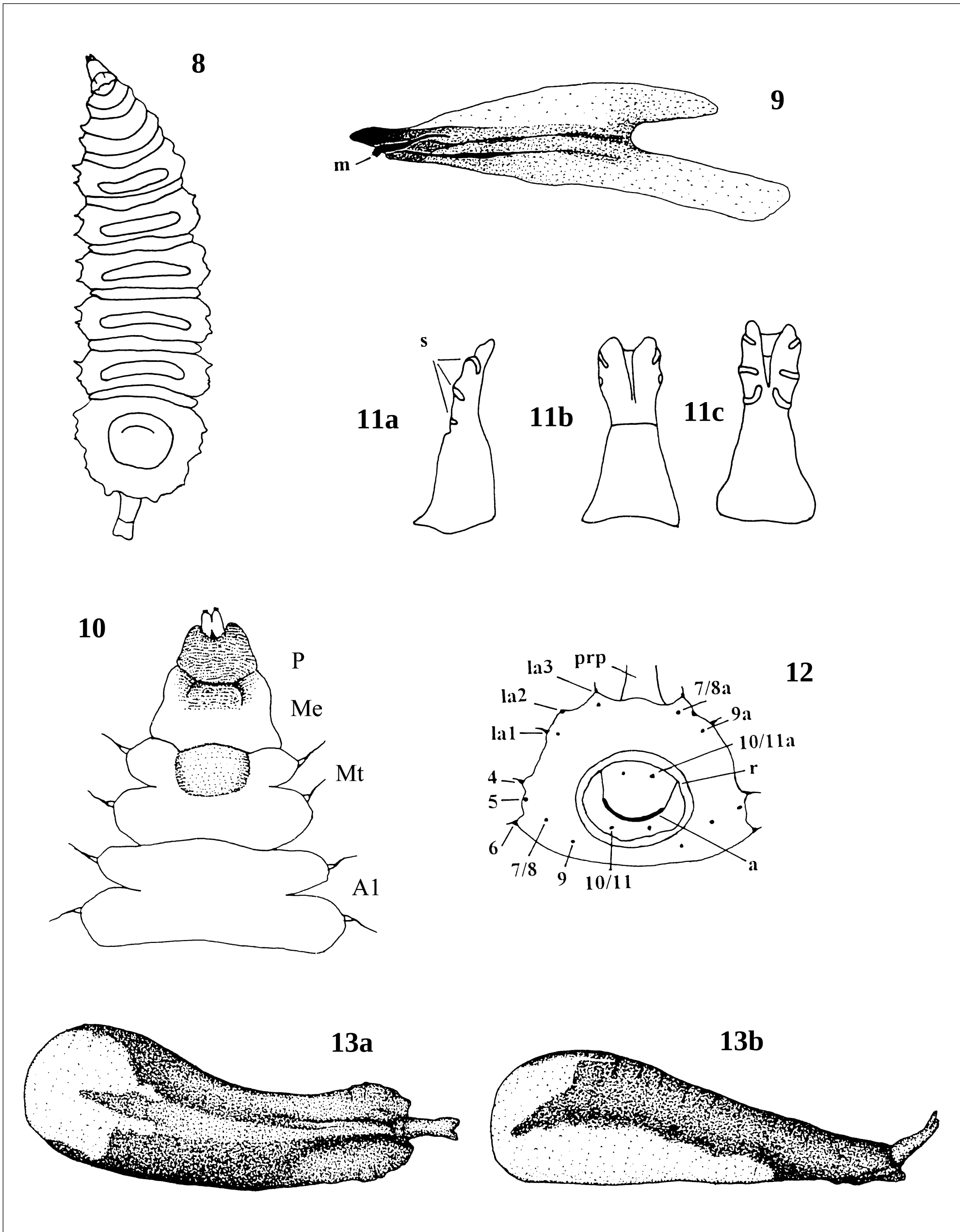
Length: body 11.5-12.8 mm; wing, 9.8-10.4 mm, n=2.

Description of third stage larva

Overall size and shape: length 10 mm, n=3; larva tapering from anal segment to prothorax (width anal segment 3.2 mm to width prothorax 0.3 mm) (Fig. 8); 7th and 8th abdominal segments forming a single enlarged unit without an indented margin separating segments as occurs between rest of abdominal segments (Fig. 12); larva somewhat dorsoventrally flattened as shown by cross-section and lateral sensilla group 4 being almost on same horizontal line as sensilla 5 and 6 rather than above these sensilla as occurs in more subcyclindrical larvae; truncate posteriorly with a pair of rounded projections about 2.5 mm long bearing sensilla; larva translucent, lacking an obvious colour pattern and thereby taking up colour of the background substrate, except for black hind gut and surrounding white fat body; vestiture on the dorsal surface of entire body papillose and uniformally pale; sensilla pattern same as other Syrphidae (Rotheray & Gilbert 1999).

Head: antennomaxillary organs mounted on a fleshy projection apparently formed from dorsal lip and base of antennomaxillary organs. Cephalopharyngeal skeleton typical for syrphine larvae (Roberts 1970) with anterior ends of labrum and labium drawn out to a sharp point and mandibles reduced to a pair of thin stylets which lie lateral to sharpened tips of labrum and labium (Fig. 9).

Thorax: lateral lips without a black sclerotised apex, but fleshy and covered with needle-like spicules; these needle-like spicules extending over ventral margins of prothorax and anterior part of mesothorax and also present medially on the ventral surface of metathorax (Fig. 10).



Figs 7-12: *Ocyptamus wulpianus* (LYNCH ARRIBÁLZAGA, 1891). – **8**: whole third stage larva, ventral view; – **9**: cephalopharyngeal skeleton, lateral view, m = mandible; – **10**: thorax and first abdominal segment, ventral view, P = prothorax, Me = mesothorax, Mt = metathorax, A1 = abdominal segment one; – **11a-c**: posterior respiratory process; – **a**: dorsal view; – **b**: ventral view; – **c**: lateral view; – **12**: 7th abdominal and anal segment, ventral view, a = anus, la1 = lappet one, la2 = lappet two, la3 = lappet three, prp = posterior respiratory process, r = raised rim of sucker, 7/8a, 9a, 10/11a = sensilla numbers on anal segment, 4,5,6, 7/8, 9, 10/11 = sensilla numbers on 7th abdominal segment; 13a-b whole puparium; a, dorsal view; b, lateral view.

Abdomen: ventral sensilla 11 not anterior to sensilla 9 and 10 on abdominal segments 1-6; dorsal and lateral abdominal sensilla 1-6 with a single seta just longer than basal papilla; ventral sensilla lacking setae; ventral surface of 7th and 8th abdominal segments with a disc-like sucker with a raised rim (Fig. 12); crescent-shaped anus within sucker (Fig. 12); sensilla 10/11 anterior to anus within sucker; sensilla 7/8 and 9 of the 7th abdominal segment outside sucker(Fig. 12); sensilla 10/11 of anal segment posterior to anus within sucker(Fig. 12); flattened ventral surface outside sucker shagreened, not covered with needle-like spicules; rest of abdominal ventral surface with shagreened areas otherwise smooth, without suckers or grooves; locomotory prominence on each segment 1-6 forming a transverse bar, not developed into a pair of separate structures.
Posterior respiratory process: length 1 mm, basal half tapering towards a mid-point constriction and matt with a rugose surface sculpture; upper half above constriction with 3 spiracular openings mostly on ventral surface with circular scar at tip; lower pair of openings longer than upper two pairs (Fig. 11).

Description of puparium
Length: 7-9 mm; inflated anteriorly, dorso-ventrally flattened posteriorly. Distal part with a dark brown marking extending to inflated portion (Fig. 13). Pupal spiracles absent.

Distribution: Costa Rica, Ecuador, Brazil, Argentina.

Material examined
Adult (6♂♂, 4♀♀): **Costa Rica**. Cartago: Río Grande de Orosi, desde Administracion hasta sendero La Pava, 1150-1600 m, LN 192500 560400, Feb 1997, R. Guzman, Lot# 45463 (2♂♂ INBIOCRI002537006-7 INBIO, USNM); ... Quebrada Segundo, 1150 m, LN 194000 5560000, G. Mora, Sept 1994, Lot#3247 (♀ INBIOCRI002311211 INBIO). **Ecuador**. Oriente: Puyo, 1,250 m, 20 March 1939, F. M. & H. H. Brown (Holotype ♂ *phobifer*, AMNH); Pichincha: Tandapi, 10 km SW Quito, 1300-1500 m, 15-21 June 1965, L. E. Peña (Holotype ♂ *bacchiformis*, CNC). **Brazil**. São Paulo: São Paulo. F. Lane (Holotype ♀ *pirata*, AMNH). Paraná: Colombo, EMBRAPA Br 476 Km 20, 10 Nov 1986, Lev. Ent. PROFAUPAR, Malaise Trap (1♀ USNM); São Jose Pinhais, Ser. Mar Br 277 Km 54, 24 Nov 1986, Lev. Ent. PROFAUPAR, Malaise Trap (♂ USNM). **Argentina**. Tucumán: Horco Molle, circa 12 km W Tucumán, 700 m, 17 March 1974, C. R. Vardy, Malaise Trap (Neotype ♂ *tricincta*, BMNH; ♂ USNM).
Larvae and puparia: **Costa Rica**. Cartago, P. N. Tapantí, Est. Quebrada Segundo, 1200 m LN-193800, 560000, one larva APC 0010; one larva MAV-07; one larva JDG-001; one puparium APC-0003, female emerged 20.ii.1999; one puparium 16.ii.1999, male emerged 18.ii.1999; all reared adults, larvae and puparia from unidentified epiphytic bromeliads (INBIO, NMS).

Taxonomic notes: *Ocyptamus wulpianus* is a very distinctive species; everyone who has seen it has described it as a new species or a new genus. Adults are quite rare in collections, perhaps because they are restricted to the canopy.

The type of *Baccha tricincta* and those of the other species described by van der Wulp (1888) have not been found neither in Leiden, Amsterdam, nor Buenos Aires, where FCT has searched for them. Fairchild (personal communications), likewise, was unable to find the tabanid types described in this paper. Hence, we consider the type of *tricincta* to be lost. To ensure that the name *wulpianus* Lynch Arribálzaga is properly and consistently applied, we here designate as neotype a male from Argentina, Tucumán, Horco Molle, circa 12 km west of Tucumán, 700 m (17 March 1974, collected in Malaise trap by C. R. Vardy), deposited in The Natural History Museum, London. This specimen agrees perfectly with the original description and color-habitus figure and is from the type locality.

Ocyptamus behavior

In culture tubes, *Ocyptamus* larvae were found frequently with the anterior half of the body under and the posterior half above the water. However, larvae also spent extended periods (several hours) underwater. Larvae were able to move forward, backward and sideways using mouthparts and suckers to hold on. Movements were initiated by the mouthparts gripping the substrate. The anal segment was then lifted slightly, moved to a new position, and reapplied to the substrate and the cycle repeated.

The inner surface of the large sucker posterior to the anus slopes obliquely between the posterior rim of the sucker and the anus (Figs. 6,12). When the sucker was applied to a substrate, this inner surface retracted, presumably creating pressure by adhering it to the substrate. Pressure is apparently maintained by the raised rim of the sucker flattening against the substrate. Pressure appeared to be released and the sucker loosened by the retractile inner surface expanding downward toward the substrate and the whole anal end of the larva contracting slightly.

If dislodged into the water, these *Ocyptamus* larvae twisted their bodies repeatedly until the side of the tube was touched and a hold was regained. It is unlikely that these larvae are able to pursue prey through the open water and that most time is probably spent holding on to the smooth sides of the bromeliad. Empty puparia were often found higher up on the plant in dry places between the leaves, suggesting that larvae out of the water to pupate. The characteristic black mark on the dorsum of the puparia (Figs 7, 13) is probably part of crypsis and disruptive in function.

These aquatic predators used a sit-and-wait strategy to catch prey. However, they are probably capable of more active searching if, for example, they are starved. Potential prey appear to be detected via tactile cues from prey movement. In response, the front end of the larva lashed out and prey was captured by the thorax that was wrapped around the prey. The mouthparts seemed to pierce the prey but feeding did not always occur. If feeding did not occur, the larva held on to the struggling prey for several minutes until they became inactive. The prey was then released. The immobilised prey appeared to be paralysed or dead. Immobilised prey examined with a binocular microscope at the point where *Ocyptamus* larvae held on to them, showed little external sign of the attack. In culture tubes immobilised prey were often fed on by *Ocyptamus* larvae several hours or days later. When feeding the larva pierced the integument of the prey, inserted the mouthparts, and removed the haemolymph and soft tissues in a way similar to other syrphine predators of soft-bodied Homoptera.

Ocyptamus larvae attacked anything that came within reach, but are probably effective only at capturing soft-bodied prey, such as larvae of other insects. In culture tubes they fed on larvae of craneflies (Tipulidae), mosquitoes (Culicidae), and aquatic beetles (Coleoptera, Helodidae), all of which were common in bromeliads. They also attacked and fed on syrphid larvae from other habitats, such as *Ornidia obesa* (FABRICIUS) from decaying coffee seeds and *Quichuana angustiventris* (MACQUART) from heliconias when introduced experimentally into the culture tubes. Cannibalism, however, was not observed. Prey varied in size from 5x1 mm mosquito larvae to 18 × 4 mm tipulid larvae, suggesting that these predators have a wide prey range, both in terms of size and taxonomic affinity.

Ocyptamus adults are typical of flower flies. Males hover in light spots in dark forests or take station at flowers or breeding sites. Females take pollen and nectar from flowers and search for breeding sites. No specific information is available for *wulpianus*, but *luctuosus* is attracted to and pollinates the flowers of *Piper* (Piperaceae)(FLEMING 1985).

Discussion

Ocyptamus is a New World syrphine taxon that is species-rich in the tropics, with declining diversity toward the cooler latitudes and is absent from the highest latitudes. Rearing data are scarce but show that Nearctic and some Central American *Ocyptamus* larvae are predators of aggregated plant-feeding insects such as aphids, soft scales, mealybugs, plant hoppers, thrips, whiteflies, and also mites (CLAUSEN 1915, HEISS 1938, HARRIS & HAMRUN 1968, Burns & Donley 1970, Gonçalves & Gonçalves 1976, Eisner & Silberglied 1988, Zumbado & Thompson 2000). The larvae of these *Ocyptamus* species are similar morphologically to other Syrphinae and lack the enlarged anal segments and suckers characteristic of the species we found in bromeliads. However, few Neotropical species of aphid exist (Vockeroth 1969, Dixon 1985). Possibly too few aggregated plant-feeding insects occur in the neotropics to provide prey for all known *Ocyptamus.*

The discovery of *Ocyptamus* larvae developing in bromeliads and feeding on various inhabitants of them extends the range of known prey of Syrphidae. The exploitation of prey other than aggregated plant-feeding insects helps explain the high diversity of Neotropical *Ocyptamus*. Bromeliads are common and widespread in the neotropics and diversification of *Ocyptamus* into them may involve many species. For example, from just one site, Tapantí in Costa Rica, we encountered six species in the larval stage, including the two reared and identified. Furthermore the specimens from *Vriesea* bromeliads in Columbia collected by N. Waitzbauer appear to represent another species and we have seen one other distinctive larva collected but not reared from bromeliads in Peru, making a total of eight species. Whether *Ocyptamus* species are specific to particular bromeliads is unknown. However, following examination of many bromeliads of numerous species in Costa Rica, Trinidad, and Mexico, it seems that the state of decay and amount of water present are more important factors.

Predatory syrphid larvae are blind and, lacking legs, have limited mobility (Rotheray 1993). A characteristic feature of their prey, from ant larvae to aphids, is that they comprise many individuals aggregated together. Such prey help them overcome the problems of finding food (Rotheray & Gilbert 1999). Shifts to alternative prey are likely to be made only if these prey are also aggregated, colonial, or confined to a limited space. Bromeliads offer just such an opportunity. They have an open centre with overlapping leaves growing round the base. Water and debris tend to accumulate in the centre of the plant, held by the leaves. Discrete amounts of water held within plants like bromeliads are termed phytotelmata. In the tropics phytotelmata harbour a rich source of animal life and many insects breed in them (Picado 1913, Maguire 1971).

The two reared *Ocyptamus*, plus the six others, share the following characters: an enlarged anal segment with a large ventral sucker; groups of needle-like spines on the ventral surface of the thorax; and an elongate posterior breathing tube with one or more spiracular openings in a vertical not horizontal plane. The main differences among them are in the vestiture of the dorsal surface, distribution of needle-like spines on the thorax, and in the detailed arrangement of the posterior spiracular openings.

The development of suckers provides an enhanced means of holding on to the smooth sides of the bromeliad. This is probably advantageous for catching and holding on to prey that can be large and active in relation to these predators. The patches of needle-like spines on the underside of the thorax facilitate gripping prey while feeding and, possibly also assist in gripping the sides of the bromeliad during locomotion. The elongate posterior breathing tube and vertically arranged pairs of spiracular openings presumably enable the larvae to continue respiring and, at the same time, to have the head underwater waiting for prey.

The development of suckers as a means of holding onto the substrate has also occurred in some species of another syrphid genus, *Copestylum* Macquart, which we also found in bromeliads. G E R and E G H reared *Copestylum circumdatum* (Walker) and *Copestylum cordiae* (Townsend) from bromeliads in Trinidad. These species have suckers on abdominal segments 1-6, and we found *Copestylum* larvae with a similar arrangement of suckers in bromeliads in Costa Rica. However *Copestylum* larvae are saprophages not predators and appear to filter-feed on microbes from the bottom detritus.

The larva of *O. wulpianus* differs from that of *O. luctuosus* in a number of ways suggesing that it has more plesiomorphic character states. It has suckers only on the anal segment, not on abdominal segments 2-6 as in *O. luctuosus*. The arrangement of needle-like spines on the thorax is simple in relation to that of *O. luctuosus,* in which they are more extensive and occur on raised lobes. The posterior breathing tube is also shorter in *O. wulpianus*. These similarities and differences suggest that aquatic predation arose once in *Ocyptamus* and involved gradual change in relation to mechanisms of locomotion, respiration and prey capture.

Another unique feature may be the use of venom in the saliva as a means to subdue prey. Although it is unclear that venom is used by these predators, it is consistent with the frequent observations of struggling prey slowly becoming immobile when held by *Ocyptamus* larvae and the lack of apparent damage to the prey at the point they were held. In contrast to other predatory syrphids, these *Ocyptamus* larvae often attack prey much larger than themselves and, therefore, having a means of subduing such large prey would be advantageous. Other syrphid predators use sticky saliva to hold prey or lift them off the substrate (ROTHERAY 1993). The venom appears to affect a wide range of insect larvae. An acceptance of diverse prey, both in terms of taxonomic affinity and size, would be an advantage for predators living in bromeliads where the occurrence of particular prey species is patchy.

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